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SYSTEMATICS, PHYLOGENY AND BIOGEOGRAPHY OF NEW WORLD WEEVILS TRADITIONALLY OF THE TRIBE CLEONINI (COLEOPTERA: CURCULIONIDAE; CLEONINAE)

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ABSTRACT

A survey of representatives of generic-group names in Cleoninae and consideration of their phylogenetic relationships indicates four genera are represented in the New World. These are: Cleonis *Dejean (introduced; 1 species);* Stephanocleonus *Motschulsky (Holarctic, northern; 6 species including* S. confusus *n. sp. [type locality, Black Hills, South Dakota],* S. immaculatus *n. sp. [type locality, Fort McMurray, Alberta],* S. parshus *n. sp. [type locality, Chalk River, Ontario], and* S. stenothorax *n. sp. [type locality, Bluefish Caves, Yukon Territory]);* Apleurus *Chevrolat (southwestern North America, arid lands; 8 species); and,* Cleonidius *Casey (eastern and western North America, semi-arid and arid lands; 19 species including* C. eustictorrhinus *n.sp. [type locality, Sacramento, California],* C. infrequens *n. sp. [type locality, Scott City, Kansas], and,* C. notolomus *n. sp. [type locality, Grant County, New Mexico]).* Cleonidius *is hypothesized to be phylogenetically more closely related to traditional Lixini rather than Cleonini and present tribal classification of Cleoninae is regarded as unsatisfactory. The following new generic-group synonymies are presented:* Lixus *Fabricius (=*Epimeces *Billberg [type species* Curculio filiformis *Fabricius, here designated]);* Stephanocleonus *Motschulsky (=*Coniocleonus *Motschulsky);* Apleurus *Chevrolat (=*Centrocleonus *LeConte,* Cleonopsis *LeConte,* Cleonaspis *LeConte, and* Dinocleus *Casey); and,* Cleonidius *Casey (=*Lixestus *Reitter).*

The following information is given in detail for each of Cleonis, Stephanocleonus, Apleurus (Gibbostethus) *n. subg. (type species,* Dinocleus hystrix *Fall by monotypy),* Apleurus (Apleurus), *and* Cleonidius*: synonymic list, notes about synonymy, diagnosis, description, list of included species, and a discussion of phylogenetic relationships. Keys to species of North American* Stephanocleonus *and* Apleurus, *and world* Cleonidius, *are presented. The following information is given in detail for each species considered: synonymic list, notes about synonymy, problems in recognition, description, distribution, natural history information, and chorological relationships.*

Lixus mixtus *LeConte is a junior homonym and is replaced with* Cleonidius longinasus, *new name. The following new species-group synonymies are presented:* Apleurus lutulentus *(LeConte) (=*Cleonus pulvereus *LeConte,* Apleurus fossus *Chevrolat, and* Dinocleus bryanti *Van Dyke);* Apleurus porosus *(LeConte)(=*Dinocleus farctus *Casey); Apleurus angularis* (LeConte) (*=Dinocleus denticollis* Casey and *Dinocleus porcatus* Casey); Apleurus jacobinus *(Casey) (=*Centrocleonus pilosus *LeConte and* Cleonus (Dinocleus) capillosus *Csiki);* Apleurus

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albovestitus *(Casey) (=*Cleonus molitor *LeConte,* Dinocleus densus *Casey,* Dinocleus wickhami *Casey,* Dinocleus interruptus *Casey,* Dinocleus mexicanus *Casey, and* Cleonus (Dinocleus) structor *Csiki);* Apleurus saginatus *(Casey) (=*Dinocleus dentatus *Champion);* Cleonidius subcylindricus *Casey (=*Cleonus (Cleonidius) graniferus *Casey);* Cleonidius texanus *(LeConte) (=*Cleonus (Cleonidius) circumductus *Casey);* Cleonidius frontalis *(LeConte) (=*Cleonus sparsus *LeConte and* Cleonus (Cleonidius) stratus *Csiki);* Cleonidius poricollis *(Mannerheim) (=*Cleonus (Cleonidius) lobigerinus *Casey and* Cleonus (Cleonidius) kirbyi *Casey);* Cleonidius boucardi *(Chevrolat) (=*Cleonus carinicollis *LeConte and* Cleonus (Cleonidius) lecontellus *Csiki); and,* Cleonidius trivittatus *(Say) (=*Cleonus inornatus *LeConte and* Cleonus (Cleonidius) bicarinatus *Casey).* Lixus californicus *Motschulsky is considered a nomen dubium.*

Only for species of Apleurus *and* Cleonidius *are reconstructed phylogenies presented based on analyses of 31 characters in* Apleurus and 22 characters in Cleonidius. Apleurus *is hypothesized to be the monophyletic sister genus of the Palearctic* Chromoderus. *In* Apleurus, *two monophyletic subgenera are recognized. These are* Gibbostethus *(1 species,* A. hystrix*) and* Apleurus s. s. *(7 species). Within* Apleurus s. s. *included species and hypothesized phylogenetic relationships are as follows: ((((*A. albovestitus + A. saginatus*) + ((*A. jacobinus + A. angularis*) +* A. porosus*)) +* A. lutulentus*) +* A. aztecus*).* Cleonidius *is monophyletic and hypothesized to comprise an unresolved trichotomy with the Palearctic* Lixus (Lixoglyptus) *and* Cylindropterus. *Four monophyletic species groups are recognized in* Cleonidius. *Along with constituent species and hypothesized phylogenetic relationships, these are:* C. erysimi *group, (((*C. texanus + C. longinasus*) +* C. subcylindricus*) +* C. pleuralis + *(*C. erysimi + C. eustictorrhinus)); C. americanus *group, ((((*C. puberulus + C. infrequens) + (C. collaris + C. notolomus*)) +* C. canescens*) +(*C. americanus + C. frontalis*));* C. poricollis *group, (*C. poricollis + C. calandroides*); and* C. boucardi *group, (((*C. placidus + C. quadrilineatus*) +* C. trivittatus*) +* C. boucardi*). Phylogenetic relationships of groups are (((*C. boucardi *group +* C. poricollis *group) +* C. americanus *group) +* C. erysimi *group). Phylogenetic relationships of the Nearctic species component of* Cleonidius *are unresolved but the latter is likely sister to the Palearctic species component.*

Both Apleurus *and* Cleonidius *are hypothesized to have entered North America in savanna or grassland habitats (or their precursors) across Beringia during late Eocene time. In North America, primary diversification has taken place in the arid lands of the southwestern United States although two species of* Cleonidius *are found in coastal regions of eastern North America. In both genera there appears to be an initial vicariance of lineages, on Compositae, in grassland or mesquite-grassland habitats between California, central México, and the southern Rocky Mountains. Further speciation events in* Apleurus *appear due primarily to shifts to new, apotypic habitat types at differing altitudes brought about by increased aridity during the later Tertiary; host plant shifts are not a factor because* Apleurus *species are all associated with Compositae. Host plant shifts, however, primarily between Leguminosae-Rosaceae and likely also Compositae-Cruciferae, and within-habitat-type allopatric speciation appear to predominate as the causes of further speciation in* Cleonidius, *most species of which remain associated with plesiotypic less-arid habitat types. Habitat shifts promoting speciation in* Cleonidius *are evident, but are not as associated with formation of increasingly arid habitats as in* Apleurus.

Evolutionary trends in Apleurus *and* Cleonidius *are discussed and patterns and predictions of biogeographic or evolutionary interest summarized and presented for examination for* *general applicability.*

RÉSUMÉ

Une diagnose des charactres de la sous-famille est aussi brièvement discutée. L'examen de représentants des groupes-genres de Cleoninae et leurs relations phylétiques indiquent que quatre genres sont représentés dans le Nouveau-Monde. Ils sont: Cleonis *Dejean (introduit; 1 espèce);* Stephanocleonus *Motschulsky (Holoartique, nordique; 6 espèces incluant* S. confusus *n. esp. [localité-type, Black Hills, Dakota du Sud],* S. immaculatus *n. esp. [localité-type, Fort McMurray, Alberta],* S. parshus *n. esp. [localité-type, Chalk River, Ontario], et* S. stenothorax *n. esp. [localité-type, Bluefish Caves, Territoire du Yukon];* Apleurus *Chevrolat (sud-ouest de l'Amérique du Nord, terres arides; 8 espèces); et* Cleonidius *Casey (est et ouest de l'Amérique du Nord, terres arides et semi-arides; 19 espèces incluant* C. eustictorrhinus *n. esp [localité-type, Sacramento, Califournie],* C. infrequens *n. esp. [localité-type, Scott City, Kansas], et* C. notolomus *n. esp. [localité-type, Grant County, Nouveau Mexique].* Cleonidius *est suggéré comme étant phylétiquement plus apparenté aux traditionels Lixini plutôt qu'aux Cleonini, et la classification actuelle de Cleoninae est considérée comme étant insatisfaisante. De nouvelles synonymies de groupe-genres sont présentée:* Lixus *Fabricius* (=Epimeces *Billberg [espèce-type* Curculio filiformis *Fabricius, ici désignée]);* Stephanocleonus *Motschulsky* (=Coniocleonus *Motschulsky);* Apleurus *Chevrolat* (=Centrocleonus *LeConte,* Cleonopsis *LeConte,* Cleonaspis *LeConte, et* Dinocleus *Casey); et* Cleonidius *Casey* (=Lixestus *Reitter).*

L'information suivante est présentée en détail pour chacun des Cleonis, Stephanocleonus, Apleurus (Gibbostethus) *nouveau sous-genre (espèce-type,* Dinocleus hystrix *Fall par monotypie),* Apleurus (Apleurus), *et* Cleonidius: *liste synonymique et notes les concernant, diagnose, description, liste des espèces incluses, et une discussion concernant les relations phylétiques. Des clefs d'identification à l'espèce pour les* Stephanocleonus *et* Apleurus *de l'Amérique du Nord, et les* Cleonidius *Mondiaux sont produites. L'information suivante est aussi présentée en détail pour chacune des espèces considérées: liste synonymique et notes les concernant, problèmes associés à l'identification, description, distribution, histoire naturelle, et relations chorologiques.*

Lixus mixtus *LeConte est considéré comme homonyme plus récent et est remplacé par* Cleonidius longinasus, *nouveau nom. Les nouvelles synonymies suivantes des groupes-espèces sont présentées:* Apleurus lutulentus *(LeConte),* (=Cleonis pulvereus *LeConte,* Apleurus fossus *Chevrolat, et* Dinocleus bryanti *Van Dyke);* Apleurus porosus *(LeConte)* (=Dinocleus farctus *Casey);* Apleurus angularis *(LeConte)* (=Dinocleus denticollis *Casey et* Dinocleus porcatus *Casey);* Apleurus jacobinus *(Casey)* (=Centrocleonus pilosus *LeConte et* Cleonus (Dinocleus) capillosus *Csiki);* Apleurus albovestitus *(Casey)* (=Cleonus molitor *LeConte,* Dinocleus densus *Casey,* Dinocleus wickhami *Casey,* Dinocleus interruptus *Casey,* Dinocleus mexicanus *Casey, et* Cleonus (Dinocleus) structor *Csiki);* Apleurus saginatus *(Casey)* (=Dinocleus dentatus *Champion);* Cleonidius subcylindricus *Casey* (=Cleonus (Cleonidius) graniferus *Casey);* Cleonidius texanus *(LeConte)* (=Cleonus (Cleonidius) circumductus *Casey);* Cleonidius frontalis *(LeConte)* (=Cleonus sparsus *LeConte et* Cleonus (Cleonidius) stratus *Csiki);* Cleonidius poricollis *(Mannerheim)* (=Cleonus (Cleonidius) lobigerinus *Casey et* Cleonus (Cleonidius) kirbyi *Casey);* Cleonidius boucardi *(Chevrolat)* (=Cleonus carinicollis *LeConte et* Cleonus (Cleonidius) lecontellus *Csiki); et* Cleonidius trivittatus *(Say)* (=Cleonus inornatus *LeConte et* Cleonus (Cleonidius) bicarinatus *Casey).* Lixus californicus *Motschulsky est considérée* nomen dubium.

*Des reconstitutions phylétiques sont présentées pour les espèces d'*Apleurus *et* Cleonidius *uniquement, et sont basées sur l'analyse de 31 charactères pour* Apleurus *et 22 charactères pour* Cleonidius. Apleurus *est suggéré comme étant le genre-soeur monophylétique du* Chromoderus *paléartique. A l'intérieur d'*Alleurus, *deux sous-genres monophylétiques sont reconnus. Ils sont* Gibbostethus *(1 espèce,* A. hystrix) *et* Apleurus s. s. *(7 espèces). A l'interieur d'*Apleurus s. s. *les espèces incluses ainsi que les relations phylétiques suggérées sont les suivantes: ((((*A. albovestitus + A. saginatus + *((*A. jacobinus + A. angularis*)* + A. porosus*))* + A. lutulentus*)* + A. aztecus*).* Cleonidius *est monophylétique et est proposé comme englobant une trichotomie non-résolue avec le* Lixus (Lixoglypus) *paléartique et* Cylindropterus. *Quatre groupe-espèces monophylétiques sont reconnus pour* Cleonidius. *De conserve avec les espèces constituantes et les relations phylétiques suggérées, ils sont: le groupe* C. erysimi, *(((*C. texanus + C. longinasus*)* + C. subcylindricus*)* + C. pleuralis + *(*C. erysimi + C. eustictorrhinus*))*; *le groupe* C. americanus, ((((C. puberulus + C. infrequens*)* + *(*C. collaris + C. notolomus*))* + C. canescens*)* + *(*C. americanus + C. frontalis*))*; *le groupe* C. poricollis, *(*C. poricollis + C. calandroides*)*; *et le groupe* C. boucardi, *(((*C. placidus + C. quadrilineatus*)* + C. trivattatus*)* + C. boucardi*). Les relations phylétiques des groupes sont: (((*C. boucardi *groupe* + C. poricollis *groupe* + C. americanus *groupe* + C. erysimi *groupe. Les relations phylétiques entre les espèces de* Cleonidius *de la composante néartique sont non-résolues, cependent cette dernière est vraisemblablement soeur de la composante paléartique.*

*L'hypothèse qu'*Apleurus *et* Cleonidius *atteignirent l'Amérique du Nord via Béringia, aux travers des savanes ou des prairies (ou de leurs précurseurs) durant l'Éocène supérieur, est avançée. En Amérique du Nord, une diversification initiale aurait pris place dans les terres arides du sud-ouest des États-Unis, bien que deux espèces de* Cleonidius *soient retrouvées dans les régions côtières de l'est de l'Amérique du Nord. Il semble, qu'à l'intérieur de ces deux genres, les lignées démontrent une vicariance initiale, sur Compositae, en prairies avec ou sans mesquites entre la Califournie, le Mexique Central, et le sud des Montagnes Rocheuses. Plus ample évènements de spéciation chez* Apleurus *sont apparus dûes principalement aux déplacements vers de nouveaux habitats apotypiques-types aux différantes altitudes, induits par l'aridité accrue raignant au Tertiaire supérieur; le déplacement vers de nouvelles plantes-hôtes n'est pas un facteur* *puisque toutes les espèces d'*Apleurus *sont associées aux Compositae. Cependent, le déplacement vers de nouvelles plantes-hôtes, principalement entre Leguminosae-Rosacae et vraisemblablement Compositae-Cruciferae, de-même qu'une spéciation intra-habitats de type allopatrique semblent dominer en tant qu'instigateurs de plus ample spéciations chez* Cleonidius, *la majorité de ces dernier demeurant associés à la formation d'habitats plésiotypiques moins arides. Les déplacement vers de nouveaux habitats encourageant la spéciation chez* Cleonidius *sont évidents, mais ne sont pas aussi fortement associés à l'apparition d'habitats de plus en plus arides comme chez* Apleurus.

Les tendances évolutionaires chez Apleurus *et* Cleonidius *sont discutées et les patrons de distribution ainsi que des prédictions d'intérêts biogéographiques ou évolutionaires sont résumés et présentés pour examen de leur applicabilité globale.*

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INTRODUCTION

J.B.S. Haldane, in an oft repeated quote, once stated that the creator must have held a special fondness for beetles for he made so many of them. To this I would hasten to add that he must also have had a special predilection towards weevils, for the Curculionidae are the largest single family of organisms known. More than 44883 species had been described as of 1971 (O'Brien and Wibmer, 1978) and countless others no doubt await discovery and formal scientific description. In so far as numerous species await description, some clearer understanding has yet to be achieved of those taxa already formally recognized. Crowson (1955), commenting on this very problem, noted that "A satisfactory resolution of the Curculionidae into subfamilies and tribes is probably the largest and most important outstanding problem in the higher classification of Coleoptera particularly as a great number of the species are more or less seriously injurious to economically valuable crops."

But to begin to make progress towards achieving this goal, we must start at some lower level, come to some understanding of a subfamily, tribe or genus, and then proceed to the larger and more complex problem. This I have chosen to do by conducting a study of the North American species that have traditionally been placed in the tribe Cleonini of the Cleoninae. The group had not been revised since LeConte and Horn (1876) and subsequently Casey (1891), and has been recently widely recognized by curculionid systematists as problematical and in need of work. Not only were species very difficult to reliably identify, but classification of the North American fauna in a world perspective had not been attempted. Use of the group in applied problems (*e.g.*, as biological control agents of pest weeds), or to address theoretical problems of general evolutionary or biogeographic importance, was not yet possible.

This study will alleviate those problems of identification and provide more detailed and reliable definitions of species and species-group taxa than those previously presented. It will also address the classification of the North American fauna in a world perspective and represent a start at a consistent scheme for use by scientists in all faunal regions. Phylogenetic and biogeographic patterns can then be recognized and resultant process-hypotheses formulated so as to be available for general consideration and applicability by students from a wide array of disciplines, not just those interested in Curculionoidea.

MATERIALS AND METHODS

Materials

This study was based on examination of 9498 adult specimens of *Cleonidius* (3586); *Apleurus* (5627); North American *Stephanocleonus* (224), and *Cleonis pigra* (61), borrowed from various collections, both institutional and private, and including material I personally collected in the western United States and Canada. The following codens represent these collections, both individual and institutional, and their respective curators.

AMNH	American Museum of Natural History, Central Park West at 79th Street, New York, New York, 10024, U.S.A.; L.H. Herman.
ASUT	Arizona State University, Tempe, Arizona, 85281, U.S.A.; F.F. Hasbrouck.
BMNH	British Museum (Natural History), Cromwell Road, London, SW7 5BD, England; R.T. Thompson and C.H.C. Lyal.
CASC	California Academy of Sciences, Department of Entomology, Golden Gate Park, San Francisco, California, 94118, U.S.A.; D.H. Kavanaugh.
CDFA	California Department of Food and Agriculture, 1220 N Street, Sacramento, California, 95814, U.S.A.; T.N. Seeno.
CNCI	Canadian National Collection of Insects, Arachnids and Nematodes, Biosystematics Research Centre, Research Branch, Ottawa, Ontario, K1A 0C6, Canada; D.E. Bright.
CUIC	Cornell University Insect Collections, Department of Entomology, Cornell University, Ithaca, New York, 14853, U.S.A.; J.K. Liebherr.
CWOB	Charles W. O'Brien Collection, Department of Entomology, Florida Agricultural and Mechanical University, Tallahassee, Florida, 32307, U.S.A.; C.W. O'Brien.

DLCC	Douglas L. Caldwell Collection, Chemical Lawn R & D Center, P.O. Box 395, Milford Center, Ohio, 43045, U.S.A.; D.L. Caldwell.
ELSC	Elbert L. Sleeper Collection, Department of Biology, California State University at Long Beach, Long Beach, California, 90801, U.S.A.; E.L. Sleeper.
FMNH	Field Museum of Natural History, Roosevelt Road and Lake Shore Drive, Chicago, Illinois, 60605, U.S.A.; L.E. Watrous.
HAHC	Henry F. and Anne T. Howden Collection, Department of Biology, Carleton University, Ottawa, Ontario, K1S 5B6, Canada; A.T. Howden.
JLCC	John L. and Alberta F. Carr Collection, 23 Dalrymple Green NW, Calgary, Alberta, T3A 1Y2, Canada; J.L. Carr.
JVMC	John V. Matthews Collection, Energy, Mines, and Resources Canada, 601 Booth Street, Ottawa, Ontario, K1A 0E8, Canada; J.V. Matthews.
LACM	Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California, 90007, U.S.A.; R.R. Snelling.
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MAssachusetts, 02138, U.S.A.; A.F. Newton, Jr.
MNHP	Muséum National d'Histoire Naturelle, Entomologie, 45 Rue Buffon, Paris, France; N. Berti.
MSUC	Montana State University, Department of Biology , Bozeman, Montana, 59717, U.S.A.; S. Rose.
NMSU	New Mexico State University, Department of Biology, Las Cruces, New Mexico, 88003, U.S.A.; J.R. Zimmerman.
NRS	Naturhistoriska Riksmuseet, Sektionen för entomologi, S-104 05, Stockholm, Sweden; P.I. Persson.
NSDA	Nevada State Department of Agriculture, 350 Capitol Hill Avenue, P.O. Box 11100, Reno, Nevada, 89510, U.S.A.; R.C. Bechtel.
OSDA	Oregon State Department of Agriculture, 635 Capitol Street N.E., Salem, Oregon, 97310, U.S.A.; R.L. Westcott.
OSUC	Oregon State University, Department of Entomology, Corvallis, Oregon, 97331, U.S.A.; G.L. Peters.
PUL	Purdue University, Department of Entomology, West Lafayette, Indiana, 47907, U.S.A.; A. Provonsha.
RSAN	denotes specimens in my own personal collection.
SBMN	Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, California, 93105, U.S.A.; S. Miller and L. Marx.
SMC	Scott McCleve Collection, 2210 13th Street, Douglas, Arizona, 85607, U.S.A.; S. McCleve.
TAMU	Texas Agricultural and Mechanical University, Department of Entomology, College Station, Texas, 77843, U.S.A.; H.R. Burke.
UASM	University of Alberta, Strickland Museum, Department of Entomology, Edmonton, Alberta, T6G 2E3, Canada; G.E. Ball and D. Shpeley.
UAT	University of Arizona, Department of Entomology, Tucson, Arizona, 85721, U.S.A.; F.G. Werner.
UCBC	University of California, Division of Entomology and Parasitology, Berkeley, California, 94720, U.S.A.; J.A. Chemsak.

UCMC	University of Colorado Museum, Campus Box 218, Boulder, Colorado; U.N. Lanham.
UIM	University of Idaho, Department of Entomology, Moscow, Idaho, 83843, U.S.A.; W.F. Barr.
UNSM	University of Nebraska State Museum, Research and Systematics Collections, W-436 Nebraska Hall, Lincoln, Nebraska, 68588, U.S.A.; B.C. Ratcliffe.
USNM	United States National Museum (Natural History), Washington D.C., 20560, U.S.A.; D.R. Whitehead.
WECC	Wayne E. Clark Collection, Department of Entomology, Auburn University, Auburn, Alabama, 36849, U.S.A.; W.E. Clark.
WSU	Washington State University, Department of Entomology, Pullman, Washington, 99164, U.S.A.; R.S. Zack.
ZMMU	Zoological Museum of the Moscow Lomonosov State University, Herzen Street 6, Moscow K-9, U.S.S.R.; N. Nikitsky.

Classification of the North American fauna in a world perspective required knowledge of structural diversity of taxa from other regions of the world. In view of this, representatives of type-species (where designated) of 50 of a total of 77 described genus-group names of the tribe Cleonini (not including New World taxa or junior homonyms where replacement names are available) from the British Museum (Natural History) were studied. In instances where a type-species has not been designated for a given genus-group name, representatives of a species initially placed in that taxon (and thus available for subsequent designation as type-species) were selected for study. These taxa are listed in Appendix II.

Methods

Collection of specimens.— Most specimens of Cleoninae collected by me were acquired simply by placing a standard entomological beating sheet underneath foliage of a particular plant and then striking the plant sharply with a sturdy stick in a downward motion over the sheet. Weevils then on the plant feign death and drop downward onto the white sheet where they are easily seen and captured. Specimens were killed in vials containing fine ethyl acetate-soaked wood chips. A few specimens were also collected by sweeping low vegetation or were handpicked from bare soil. Deciduous shrubs in oak-pinyon-juniper woodlands and annual or perennial woody shrubs along dry stream beds, desert washes, or various lotic waterways were the most productive places to concentrate collecting efforts.

Specimen preparation and examination.— A Wild M5® stereo dissecting microscope was used for routine examination of external structural features of dried adult specimens. Dissections were made of mouthparts and internal genitalia and these were examined with both a Wild M5® dissecting microscope and a Leitz SM-Lux® compound brightfield microscope. Special preparation procedures for specific characters examined in detail are given following. For such characters, note is made in the text of the number of specimens that were examined in detail.

For each species, a variable number of male and female individuals were selected from various localities for study of internal genitalic structure. Individuals of both sexes were first softened by immersion in hot distilled water, to which a few drops of liquid soap had been added. Dissection consisted of insertion of the apices of a pair of fine forceps into the sternal suture separating the base of the abdomen from the metasternum. Careful application of pressure resulted in separation of the abdomen which was then placed into hot 5–10% KOH (aqueous) for a variable amount of time to remove soft tissues. Repeated examinations were made of the abdomen during this process to determine the suitable degree of treatment. The abdomen was then transferred to a 5–10% acetic acid-alcohol solution to neutralize KOH activity, and then to distilled water. Genitalia were then removed from the abdomen and placed in 95% ethanol and then into glycerine for subsequent examination. The abdomen was dried and mounted on a card placed on the specimen pin.

No special techniques were used in the examination of female genitalia; however, for the internal sac of the aedeagus of males to be adequately examined, it was necessary that it be everted and inflated. This was best accomplished using an unpublished technique devised by Mr. Richard T. Thompson of the British Museum (Natural History).

Most practical for large specimens, this technique consists of eversion of the internal sac following softening and treatment with KOH by careful insertion of a hooked minuten pin mounted on the end of a wooden probe into the apex of the aedeagus. Slow and numerous repeated tugs on the sac, which is visible through the wall of the aedeagus, worked best and could be continued until the sac was completely everted, the apical sclerite complex exposed and apical. Attempts to extract the sac rapidly and using only one or a few insertions of the minuten pin frequently damaged the sac such that inflation was not possible. Following eversion, the aedeagus was placed in a liquid (water was used most frequently but a liquid of higher viscosity, such as glycerine, is recommended). The base of the aedeagus was placed at the end of a narrow piece of flexible rubber tubing and the rubber adjacent to the base of the aedeagus pinched with a pair of flat-tipped forceps placed firmly in a hole in a rubber stopper attached to a sturdy metal stand. A continuous force was maintained on the forceps by placing a small elastic band around the forceps near their apices such that they needed to be forced open using another pair of forceps. It was important that the aedeagus was held firmly in place in the apex of the tubing, but that the base of the aedeagus was not sealed by the forceps. The other end of the piece of tubing was attached to a syringe filled with the liquid in which the aedeagus was immersed. The syringe was also placed in a hole in a rubber stopper attached to a separate sturdy metal stand. Gentle pressure on the syringe forced the liquid out the apex of the tubing but ideally only through the aedeagus and thus the internal sac. As liquid passed into the sac it became inflated and remained so for short periods of time while the pressure exerted by the syringe continued to exceed the force limiting inflation of the sac. Drawings were thus made of the sac by repeated application of slight pressure on the syringe. Various views of the sac were obtained by manipulation of the aedeagus in the apex of the tubing and repetition of entire procedure. Proper placement of the base of the aedeagus in the tubing was often difficult because more often than not, pressure on the syringe did not inflate the sac because either the forceps were sealing the base of the aedeagus or, too much liquid was passing out the tubing adjacent to the base of the aedeagus and not through it. In this latter instance the aedeagus was expelled from the apex of the tubing because it was not held firmly in place by the pressure exerted onto the tubing by the forceps. Repeated attempts and manipulation of the location of pressure of the forceps were required for good results.

Following examination, internal genitalia were placed in glycerine in a microvial attached to the specimen pin. To examine mouthparts, heads were removed from individuals softened as noted above, and placed in 5–10% KOH (aqueous) for a variable amount of time as required for removal of soft tissues. The head was then transferred to a 10% hydrogen peroxide-95%

ethanol solution to bleach cuticle to facilitate examination of surface features with a brightfield microscope. Following removal to a 95% ethanol-distilled water solution, maxillary palpi and the prementum were carefully removed from the head by severing connections to the apex of the rostrum with a hooked minuten pin mounted on a wooden probe. These structures were then transferred to glycerine on a depression slide for detailed examination using a brightfield microscope. The head was air dried and mounted on a card placed on the specimen pin. Following examination, mouthparts were placed in glycerine in a microvial attached to the specimen pin. Detailed mouthpart examination was only carried out for species of *Apleurus*. Initial surveys of diversity of mouthpart structure in *Cleonidius* and *Stephanocleonus* species did not prove promising and were discontinued.

Structural terms.— Structural terms follow those of Kissinger (1970) except as noted in Anderson (1984b). Structure of the internal sac of the aedeagus of males in Cleoninae has not been previously studied and an informal nomenclature has been developed (Fig. 115). Future detailed studies on other Cleoninae should result in a more formal nomenclature based on apparent homology between structures in a more comprehensive survey of structural diversity.

Ambiguity in descriptors used in association with various structural terms is a problem worthy of comment. Objectively delimited character states (*e.g.*, presence/absence, red/black, three setae/one seta, *etc.*) are ideal for taxonomic and phylogenetic purposes because there is no ambiguity in assigning a state to a particular taxon. Most character states however, are subjectively expressed (*e.g.*, elongate-narrow/robust, large/small, deep/shallow, *etc.*). For these latter characters to be maximally useful in a taxonomic sense as criteria for identification or otherwise, ambiguity must be reduced in assigning a state to a particular taxon without requiring reference to other taxa. I have attempted to do this for those character states that are taxonomically important in this study but which are not augmented in the text in a quantitative manner or accompanied with figures. Characters and their states in which there is little ambiguity involved are not considered.

Vestiture. I term all body vestiture of apparent non-sensory primary function as scales. Body vestiture is important both phylogenetically and taxonomically. Pronotal scale patterns serve to distinguish genera, elytral scale patterns species of *Stephanocleonus*, and species groups and species of *Cleonidius*. Abdominal scale patterns are important in separating some species of *Apleurus*.

Scales vary from flat or appressed, to recumbent, sub-erect and erect. I use the terms flat or appressed for scales at an angle of 0°–5° relative to body surface; recumbent, 6°–45°; sub-erect, 46°–85°; and erect, 86°–90°.

Shape and size of the scale is important in determining macroscopic patterns of surface vestiture. Small, fine scales obscure less of the underlying dark cuticle and thus the ground color of the cuticle predominates in the pattern; larger, robust scales obscure more cuticle and impart a predominantly whitish color to the pattern. Density of the scales is not as important as size and shape in determining the macroscopic pattern.

More elongate, sub-erect or erect scales are termed "hair-like scales", a name that would correspond to most concepts of "hair". Length of "hair-like scales" is important both taxonomically and phylogenetically. Members of some species clearly lack sub-erect or erect surface vestiture; members of most species have short sub-erect or erect vestiture that is not more than approximately twice the length of the largest appressed scales on that particular body part. Members of few species have moderately long sub-erect or erect vestiture between twice and three times the length of the largest appressed scale. Finally, members of few species have long vestiture, greater than three times the length of the largest appressed scale. Sub-erect or erect vestiture is abraded to various degrees on some specimens causing problems in identification.

Density of all vestiture and size of scales are indicated qualitatively with reference to other taxa.

Punctation. Punctation is important both phylogenetically and taxonomically. Three aspects of punctation are described: size, density and depth. States of all three aspects are part of a continuum from small, sparse or shallow, to large, dense and deep.

Density of punctation is defined on the basis of the relationship between diameter of a puncture and the distance between it and adjacent punctures. Sparse punctures are those with diameters less than the distance between punctures; moderately dense are those with diameters more or less equal to the distance between punctures; and dense are those with diameters exceeding the distance between punctures.

Size and depth of punctation are more difficult to assess in an objective manner. Shallow punctures are those with the walls of the puncture at about a 45° angle or less; deep are those with walls between 45° and 90°. Moderately deep are those with the state difficult to assign as either deep or shallow. Small punctures are those where a very rough estimate of the number of punctures, if lined side by side spanning that body part, would number more than 50; large are those where the number is less than 25. Estimates between 25 and 50 are considered moderately large.

Punctation of the head, rostrum and pronotum are most important and most frequently referred to in keys and descriptions.

Illustrations.— With the specimen placed in glycerine, all drawings of genitalia and mouthparts were made on paper with the aid of a camera lucida attached to Wild M5® or Leitz SM-Lux® microscopes at various magnifications and later traced, then inked, onto mylar drafting film for reproduction. Drawings of other structural features were similarly made of dried pinned specimens with the aid of a camera lucida attached to a Wild M5® microscope. Details of surface vestiture and sculpture, unless taxonomically or phylogenetically valuable, are not shown on illustrations. Homologous structures are drawn to the same scale (in most instances) and orientation to facilitate comparisons. Only taxonomically or phylogenetically valuable structures are illustrated; thus, comparisons of certain attributes of the structures for the purposes of identification may be misleading. Such attributes although illustrated for aesthetic completeness are not discussed in the text.

Distribution maps are presented for all species with the exception of *C. vibex*. Special maps and illustrations were prepared to illustrate general ecological and historical biogeographic patterns, evolutionary trends or adaptations, *etc.*, or as accompanying visual simplifications of various discussions in the text.

Hubbs-Hubbs diagrams representing intraspecific and interspecific variation in certain mensural attributes were prepared separately for each sex. Range, mean, 1.5 standard deviations (SD) on either side of the mean, and two standard errors (SE) on either side of the mean are plotted. Choice of 1.5 SD and 2 SE follows Whitehead (1971) as noted in the section on descriptive statistics.

Features illustrated are as follows: LEl, WRA/LR, WRA/WF, WElM/LEl, LP/LEl for *Stephanocleonus* (Figs. 49–53) and *Cleonidius* (Figs. 197–201); and, LEl, WRA/LR, WRA/WF, WElM/LEl, LP/LEl, WPT/WPB for *Apleurus* (Figs. 105–110). Features illustrated were selected on the basis of their taxonomic and/or phylogenetic value. Hubbs-Hubbs diagrams were also prepared to illustrate the altitudinal distributions of

Apleurus (Fig. 232) and *Cleonidius* (Fig. 233) species. Samples used for preparation of Hubbs-Hubbs diagrams minimally include those samples used in preparation of descriptive statistics tables. In those instances where measurements were taken of individuals from more than the sample used in the descriptive statistics tables, these other samples constituted part of an examination for possible intraspecific variation in mensural features.

Measurements and descriptive statistics.— Measurements were made on pinned specimens at various magnifications with the aid of an ocular micrometer in a Wild M5® microscope. Measurements selected for detailed study and for presentation were those that upon initial survey revealed differences between species of potential taxonomic or phylogenetic value. For this reason not all measurements or ratios presented were taken on species of all genera.

These measurements and their abbreviations are:
LR, length of rostrum measured in lateral aspect from anterior margin of eye to point of articulation of mandible; **WF,** minimum width of frons between eyes in dorsal aspect; **WRA,** maximum width of rostrum measured across apex in dorsal aspect; **LP,** length of pronotum measured along midline from anterior to posterior margins in dorsal aspect; **WPB,** width of pronotum measured across base in dorsal aspect; **WPT,** width of pronotum measured across apical one-third or one-quarter at tubercles (if present) or immediately posterior to sub-apical constriction in dorsal aspect; **WElH,** width of elytra measured across base at humeri with elytra contiguous throughout length at suture in dorsal aspect; **WElM,** width of elytra measured across midlength with elytra contiguous throughout length at suture in dorsal aspect; **LEl,** length of elytra measured along suture from apex of scutellum to apex of elytra in dorsal aspect; **LEy,** maximum length of eye measured in lateral aspect; **WEy,** maximum width of eye measured in lateral aspect.

Some of these measurements were used to obtain ratios which serve to express the form of a particular part of the body. These ratios are; WEy/LEy, shape of eye; WPB/LP, form of pronotum; WRA/LR, relative length of rostrum; WF/WRA, relative separation of eyes; WElM/LEl, form of elytra; WP/LEl, relative length of elytra; and, WPT/WPB, position of maximum width of pronotum.

A comprehensive set of descriptive statistics is given for one sample of each species treated. (See Appendix 1, Tables 1–33). Statistical analysis is less comprehensive for those species where there was not adequate material. Sexes are treated separately and ideally each sample includes eight members of each sex collected at the same locality and time. This ideal is not met for all species and some samples have fewer than eitht specimens of one of the sexes or, for the purposes of more comprehensive statistical analysis, if markedly less than eight specimens are represented, are composed of a number of specimens collected from a more extensive geographic area. Least preferred samples are composed of all specimens of the species available for study. Mensural data treated in the descriptive statistics section include only those measurements and ratios given previously. Number of specimens, geographic locality of the specimens, range, mean, 1.5 standard deviations (SD), and 2 standard errors (SE) are given where number of specimens permits. In instances where too few specimens were available for meaningful statistical treatment, values for SD and SE are not given. Number of standard deviations and standard errors on either side of the mean were chosen following Whitehead (1971). Non-overlap of two standard errors from the mean is equivalent to a t-test at 0.05 probability, and indicates samples to be statistically significantly different; non-overlap of 1.5 standard deviations from the mean indicates that 90% or more of the specimens from one sample can be distinguished from 90% or more from the other sample, and indicates samples to be taxonomically significantly different (Whitehead, 1971).

For most species these mensural features serve primarily as aids in identification and as characters valuable for phylogenetic analysis. For some species, mensural features are the primary, although not sole, criteria for species recognition. In these latter instances, the mensural features have been verified as reliable by further measurements taken on a larger number of specimens than that indicated in the descriptive statistics tables or on the Hubbs-Hubbs diagrams (*e.g.*, rostrum length in *C. texanus-C. longinasus*, form of elytra in *C. trivittatus-C. quadrilineatus*).

Analysis of geographic variation.— Where problems in species recognition were apparent in terms of geographic variation in structural features, population samples from sites throughout the species range were selected and examined to determine the taxonomic significance of this variation. If more or less extensive differences were found between samples, geographically intermediate samples (if available) were examined to infer the degree of reproductive isolation of the geographically more distant samples. Should geographically intermediate populations prove structurally intermediate between the two more distant samples, gene flow is inferred and all samples are considered conspecific. Divergence from both of the more distant samples or close similarity to any one of the two distant samples by the intermediate sample may indicate barriers to gene flow and may result in separate species status for the two most distant samples, particularly if geographically correlated with other variable structural features or aspects of natural history.

Descriptive format.— For each nomenclaturally valid taxon considered, a complete list of synonymy is given. Type material examined and depository are noted following each of the names of the nominal taxa. Lectotypes and neotypes are designated where appropriate; paralectotypes have not been designated. Complete label data for primary type material examined, type locality, gender, and type species are given where appropriate for species, subgenera and genera. All literature citations of names of North American species, *Cleonidius vibex* (Pallas), and all citations pertaining to *Cleonis pigra* (Scopoli) in North America are given. A concerted attempt has been made to make these listings as complete as possible. Page numbers have not been given for all citations, but only for those wherein new species are described. Published misidentifications ("misident." in synonymy list) are indicated under both the incorrect and correct names. Notes in parentheses following most literature references indicate the nature of that reference as follows: biol., biology; catal., catalog; check., checklist; desc., description; distn., distribution; and redesc., redescription. Lack of any notation indicates use of that name with little or no added information about the taxon.

For each species, subgenus or genus, a "Problems in recognition" section is presented which I feel to be more desirable than a diagnosis because the latter, in most instances, simply gives characters and their states already presented in the keys. In this section I discuss particular species that I had problems separating from, and perhaps at one time misidentified or confused with, the species in question. In this manner I point out the species with which others are likely to make errors. This section is meant to be consulted after a tentative identification has been made using the keys.

A section with notes about synonymy and type material follows and deals in various detail with specific criteria for newly proposed synonymy and with other details about type material as required. For all newly described species, label data for holotype and allotype are given in full with data from each label enclosed in separate quotation marks starting from the top label down. Separate lines on each label are indicated by a "/". A specific type locality is designated.

Paratypes are treated less rigorously and label information is given in a simple standard format of: locality, date, collector, sex, location of deposition. Specimens are ordered alphabetically according to locality. Derivation of the specific epithet is also given.

Following this section is a detailed description of the taxon including structural variation. Complementing this verbal description are various illustrations of important structural features and for all species, a set of variously comprehensive descriptive statistics from one population for each of males and females. Only attributes that vary between species are described. Character states are described in consistent order to facilitate comparisons. Subjective terms such as "large" and "small" have been avoided as much as possible but if by necessity used, are augmented with illustrations. All structural variation is incorporated in the appropriate places in the species description.

Geographic distribution of each species is presented in the form of dot maps illustrating positions of localities of collections. State records and questionable localities of collection are noted in the text but not placed on maps. Literature records are not placed on maps nor noted in text unless they fall outside the known range of the species based on other specimens examined. Complete lists of specimens examined for each species are not presented but have been placed in the Archives of the Department of Entomology, University of Alberta.

Natural history information from publications, specimen label data, and personal collecting experiences are summarized for each species. For the purposes of biogeographic and evolutionary interpretations, habitat associations were recognized using, as appropriate, schemes by Rzedowski (1978), Brown (1982), or Livingston and Shreve (1921). Elevations of collection localities are either taken directly from specimen labels (if noted), or, if site of collection is a major geographic feature, are taken from a gazetteer or one of a number of maps. Hubbs-Hubbs diagrams illustrate variation in elevational distribution within and among species of *Cleonidius* and *Apleurus* but no statistical tests are performed on these data. A Hubbs-Hubbs diagram is used only for the purpose of visual presentation of the altitudinal ranges. Seasonal data are taken from labels. Supra-generic classification of plants follows Cronquist (1968). Generic names of plants follow Kearney and Peebles (1960); species names follow Kearny and Peebles (1960), Munz and Keck (1968) and Correll and Johnston (1970).

Patterns of allopatry and sympatry for each species are summarized in the chorological relationships section. They are summarized for *Apleurus* and *Stephanocleonus* species, but presented in a table format for *Cleonidius* species. Consultation of this section not only reduces possible misidentifications in instances where specimen locality is known, but also indicates retention of species identity under variable conditions of species packing and species occurrence. For this reason special attention is given to chorological relationships with close phylogenetic relatives.

A section about phylogenetic relationships concludes the descriptive format and verbally states the immediate phylogenetic relationships of the taxon. For species of *Apleurus* and *Cleonidius*, further details are given in the "Phylogeny" section. Phylogenetic relationships have not been examined for species of *Stephanocleonus*.

For species groups of *Cleonidius*, only a short diagnosis and a statement of evidence for monophyly and phylogenetic relationships are presented. Structural features not variable within a species group but variable within *Cleonidius* are repeated in the species group diagnosis and all species descriptions.

Criteria for recognition of species-group taxa.— As with most systematists, my primary criterion for species recognition is the biological species concept (Mayr, 1963). I find the evolutionary species concept of Wiley (1981), although theoretically desirable, so vague as to be of little practical applicability. Since experimental evidence of reproductive isolation is lacking for most insect species, Cleoninae being no exception, such isolation is inferred from differences primarily in structural features, but also in features of natural history, especially host plant associations.

In instances of sympatry, individuals are regarded as belonging to separate biological species if variable numbers of structural features are substantially and consistently different. Differing host plant associations alone are not evidence of separate species status, but in combination with differences in structural features are used herein to indicate separate species status. This consideration is especially important should the degree of structural difference be less than is found in sympatric species where host plant associations are broader or not consistently different yet structural differences are relatively extensive.

For allopatric individuals the situation is more complex and difficult to resolve. Allopatric individuals are regarded as conspecific if they exhibit structural features that do not differ, or if differing, do so to a lesser degree than differences noted between separate sympatric species and in a geographically based clinal manner. If the allopatric forms differ in various features of structure and/or natural history, and these features cannot be shown to have a consistent geographically determined pattern of continuous variation, the forms are considered separate species. Obviously, the more characters that differ in this manner, the more marked the evidence for separate species status. It is very important to note that marked phenetic differences are not the primary consideration, rather it is the pattern of geographic variation (assumed indicative of degree of gene flow) that determines the taxonomic status of the various populations. Phenetic differences may simply be the result of locally different selection pressures and not reproductive isolation.

These are my general criteria. Especially complicated and/or problematical patterns of structural variation must be considered individually and as such are discussed in detail in the text where appropriate.

The subspecific category has not been used. As expressed elsewhere (Anderson and Peck, 1986), I feel that this category should only be used for allopatric populations where lack of intermediate populations precludes analysis of geographic variation and inference of degree of reproductive isolation. In no instances in this study was such a consideration warranted; geographically intermediate populations and natural history information were consistently available to permit assessment of extent of gene flow and recognition of status at the species level.

Criteria for recognition of genus-group taxa with notes about classification.— Some consideration must be here given to criteria for recognition and ranking of genus-group taxa for this study is concerned with a regional fauna and classification of its constituents in terms of the world fauna. All genus-group taxa should preferably be monophyletic (holophyletic) although paraphyletic taxa are acceptable in certain special situations; polyphyletic taxa are not acceptable. Genus-group taxa should contain an assemblage of related species sharing structural features and/or features of natural history, and separated from other assemblages by a gap in such features. Aside from this requirement, naming and ranking of taxa are always debatable because there are no objective criteria for formal recognition of taxa, and if recognized, at what hierarchical level they should be placed. Although this has been attempted (Hennig, 1966), it has not met with widespread acceptance or success.

All decisions about naming and ranking must be made with reference to related taxa with genealogical and phenetic relationships of the taxa as the prime considerations. Genealogical relationships (including some consideration of confidence in them), should take priority over phenetic relationships because only classifications based on evolutionary parameters can logically contain more information, due to inheritance, than was initially used in their creation (Whitehead, 1972). Classifications of this nature may be maximally predictive and highest in information content, but may prove difficult to employ as information retrieval systems depending upon their complexity and intricacy. Many recent books (*e.g.*, Eldredge and Cracraft, 1980; Wiley, 1981; and references cited therein) have dealt with this problem at length and simple compromise between information content and facility for use is perhaps the most important general consideration in constructing classifications.

Four genera are recognized in this study as occurring in North America. *Cleonis* is monobasic; *Stephanocleonus* is represented in North America by only 6 species but in the Palearctic region by numerous species, so no intrageneric classification has been attempted (species in North America are herein arranged alphabetically); *Cleonidius* is represented by 20 species; 19 Nearctic, 1 Palearctic (at least); *Apleurus* is represented by 8 Nearctic species.

In *Cleonidius* only informal species groups, including the *incertae sedis* category, are recognized primarily because of low confidence in genealogical relationships and thus possible instability of the resultant classification, and little variation in structural features. By using only species groups, the possible predictive value of the classification is enhanced and can be tested without the problems associated with increased nomenclatural complexity, not desirable for such a small number of species of a relatively restricted geographic distribution.

In *Apleurus*, two subgenera have been recognized rather than species groups. Although *Apleurus* contains only eight species, the genealogically most primitive member of *Apleurus* differs from other species of *Apleurus* in a number of structural features, some not yet found elsewhere in Cleoninae. Confidence in this primitive phylogenetic position is high and structural differences are marked, with remaining *Apleurus* species forming a structurally cohesive grouping. For these reasons, recognition of subgenera was deemed desirable. Furthermore, desire for recognition of *Gibbostethus* as a subgenus is enhanced by the largely unknown natural history, restricted distribution, and possible endangered status of this phylogenetically most primitive species of *Apleurus*.

Classification above the generic level is not attempted, although some statements concerning relatives of genera occurring in North America and their shared character states are made, forming part of the basis for a future reclassification of the subfamily.

NATURAL HISTORY OF CLEONINAE

Members of the subfamily Cleoninae are found from mesic to very arid habitats. Taxa traditionally placed in the tribe Lixini are those usually associated with more mesic habitats whereas most traditional Cleonini are found in arid habitats. Exceptions, especially of some *Lixus* species associated with arid habitats, are known.

Most species breed in herbs or shrubs of a wide variety of plant taxa but most notably Chenopodiaceae, Compositae, Leguminosae, Rosaceae, Cruciferae and Polygonaceae. Larvae of most species mine stems or roots of these plants but those of some feed in flower heads or on seeds (*e.g.*, *Rhinocyllus conicus*, *Larinus planus*, *Microlarinus* spp.). Natural history of *Microlarinus* spp. (Kirkland and Goeden, 1977; 1978a, b) and of *Rhinocyllus conicus* (Zwölfer and Harris, 1984) have been particularly well studied; however, most other information about natural history of Cleoninae, especially in North America, is brief and fragmentary (*e.g.*, Bargagli, 1884; Pierce, 1907).

Adults of most species of traditional Cleonini are brachypterous and even those that are macropterous have not been observed to fly. Most traditional Lixini are macropterous.

Adults of various species have been collected as prey of *Bufo* sp. (Amphibia), *Geococcyx californicus* (Aves), and various predatory Hymenoptera. Tachinidae (Diptera) (Arnaud, 1978) and various parasitic Hymenoptera (Krombein *et al.*, 1979) have been recorded as parasites of members of the genus *Lixus* in North America.

Various species of Cleoninae have been employed as, or are being considered as, biological control agents of weeds including thistle (*Cirsium*, Compositae), knapweed (*Centaurea*, Compositae), and puncturevine (*Tribulus*, Zygophyllaceae) (Anderson, 1984a; Kirkland and Goeden, 1978a, b; Maddox, 1976; Wheeler and Whitehead, 1985; Zwölfer and Harris, 1984). None of the species are considered to be economic pests although some are occasionally found on cultivated Chenopodiaceae or Cruciferae.

SUPRASPECIFIC TAXA AND INCLUDED SPECIES

SUBFAMILY CLEONINAE

Historical review

As of 1978, 1445 species of Cleoninae had been described (O'Brien and Wibmer 1978). However, the number of genera stated is perhaps on the low side for many taxa given subgeneric rank under *Cleonus* likely require separate generic status. The subfamily name Cleoninae (first used as the vernacular "Cleonides") and generic name *Cleonus* were first proposed by Schoenherr (1826) but three years earlier, Schoenherr (1823) had also used the vernacular name "Geomorides" and the generic name *Geomorus* for the same taxa. Earlier still, Dejean (1821) had also proposed the name *Cleonis* to include species, some of which were subsequently placed by Schoenherr in *Geomorus* and *Cleonus*. Since Schoenherr (1823) used the vernacular name "Geomorides" and this was never latinized as Geomorinae, under Article 11f of the International Code of Zoological Nomenclature it is not a valid family-group name. Under Article 40, Cleoninae, even though the name of the type genus *Cleonus*, is a junior synonym, should not be replaced and is maintained as the valid family-group name. The name Cleoninae has been in widespread and constant use since its introduction (*e.g.*, Schoenherr, 1834; Chevrolat, 1873; Faust, 1904; Csiki, 1934; O'Brien and Wibmer, 1982).

North American species have traditionally been included in the tribe Cleonini (Casey, 1891; LeConte 1876a; LeConte and Horn, 1883) which is comparable to Cleoninae of other authors (*e.g.*, Csiki, 1934). There has been little confusion regarding included world taxa with the exception of the Holarctic genus *Lepyrus* now generally regarded not to be a cleonine.

Recognition of Cleoninae

Adults of the subfamily Cleoninae are recognized by two features not known in other Curculionidae. These are: 1), short, telescoping, ventrally situated, three-articled labial palpi; and 2), presence of paired symbiont sacs attached to the vagina near the base of gonocoxite II in females. A more detailed diagnosis describing other features of the subfamily is not presented, pending examination of further taxa.

Sex differentiation

Sexes are differentiated in Cleoninae as in most other weevils. Males are easily distinguished by flat to concave abdominal sterna III and IV and by possession of two clearly recognizable sclerotized terga at the abdominal apex, usually only visible upon displacement of the elytral apices. Females possess more evenly convex abdominal sterna III and IV and possess only a single sclerotized tergum at the abdominal apex. In addition, females tend to have a longer rostrum than do males (especially in *Cleonidius*) and are generally larger in body size.

Key to genera of New World Cleoninae

1 Rostrum, in dorsal view, from apex of epistoma to anterior margin of eye, more or less as long as greatest width (Figs. 1–2) 2

1′ Rostrum, in dorsal view, from apex of epistoma to anterior margin of eye, much longer than greatest width (Figs. 3–4, 10, 25–30, 81–88, 137–156) 4

2 (1) Prosternum with a pair of prominent ridges which form a deep ventral channel . . . . *Bangasternus* Gozis
(two species, one deliberately introduced, one under consideration for deliberate introduction)

2′ Prosternum lacking ridges, no channel evident 3

3 (2′) Elytron with intervals each with row of conspicuous erect setae. Anterolateral margin of pronotum straight, with long postocular vibrissae immediately behind eye (Fig. 1). Eye more or less round (Fig. 1) . . . . *Microlarinus* Hochhuth
(two species, deliberately introduced)

3′ Elytron with intervals without row of erect setae. Anterolateral margin of pronotum with rounded postocular lobe and short postocular vibrissae behind eye (Fig. 2). Eye distinctly elongate-oval (Fig. 2) . . . . *Rhinocyllus* Germar
(one species, deliberately introduced)

4 (1′) Pronotum dorsally and laterally with numerous shiny glabrous tubercles, lacking distinct punctures 5

4′ Pronotum dorsally and laterally distinctly punctate, with at most the outer margins of punctures of lateral margins swollen, glabrous and shiny 6

5 (4) Rostrum dorsomedially sulcate throughout length (Fig. 10). Pronotum with anterolateral margins with rounded postocular lobe (Fig. 9) . . . . *Cleonis* Dejean, p. 449
(one species, adventive)

5′ Rostrum dorsomedially carinate throughout length; lateral margins raised basally, appearing as lateral carinae. Pronotum with anterolateral margins straight, lacking rounded postocular lobe . . . . *Cyphocleonus* Motschulsky
(one species, under consideration for deliberate introduction)

6 (4′) Mesosternum with mesosternal process markedly tumescent (Fig. 58). Male with aedeagus markedly expanded laterally from midlength to apical one-third (Fig. 97e) . . . *Apleurus* subgenus *Gibbostethus* Anderson, p. 468
(one species, native)

6′ Mesosternum with mesosternal process flat or at most only slightly convex, not tumescent (Fig. 59). Male with aedeagus more or less uniform in width throughout median portion of length 7

7 (6′) Tibia with corbel ridge rounded (Fig. 5). Elytron with all intervals equally flat or with at most only humerus and very base of interval 3 swollen and convex. Pronotum with disk with scale pattern various. Prosternum with or without swellings; swellings, if present, situated immediately anterior to each procoxal cavity (Fig. 8) 8

7′ Tibia with corbel ridge sharp (Fig. 6). Elytron with all intervals equally flat or with humerus and variously, sutural interval and intervals 3, 5, 7, and 9 elevated and convex throughout the greater part of their lengths. Pronotum with disk with large white scales in lateral stripe of various width, small and fine in moderately broad to very broad apically narrowed median stripe; median area largely black in color, underlying dark cuticle not obscured by overlying scales. Prosternum with or without swellings; swellings, if present, situated immediately anterior to each prosternal impression (Fig. 7) 10

8 (7) Antenna with article 2 of funiculus distinctly longer than wide, distinctly longer than each of articles 3 to 6, slightly shorter than to distinctly longer than article 1 (Fig. 4). Pronotum with anterolateral margins straight, slightly sinuate, or with at most variously developed (usually small) acute postocular projection; postocular vibrissae unequal in length, greatest length (more or less equal to or greater than one-half width of eye) behind base of eye (Fig. 4). Ventral surface of femur dentate or not. (Some South American species of *Lixus* have slightly developed rounded postocular lobes and moderately long postocular vibrissae of more or less equal length, but have dentate femora) . . . . *Lixus* Fabricius
(numerous species, native; worldwide)

8′ Antenna with article 2 of funiculus more or less as long as wide, more or less subequal in length to each of articles 3 to 6, shorter than article 1 (Figs. 3, 137–156). Pronotum with anterolateral margins straight or with slightly to well-developed, rounded postocular lobe; postocular vibrissae uniformly short (less than one-half width of eye in length) to unequal in length, greatest length (more or less equal to or greater than one-half width of eye) behind base of eye (Figs. 3, 137–156). Femur not dentate 9

9 (8′) Elytra elongate-narrow (width at midlength less than 0.65 times length) (Figs. 118–136). Pronotal disk with distinct white scales of various sizes (Figs. 118–136). Elytra with white scales, various in size, but more or less obscuring view of underlying cuticle over large part of elytral surface (Figs. 118–136) . . . . *Cleonidius* Casey, p.492
(19 species, native; also in Palearctic Region)

9′ Elytra more robust (width at midlength greater than 0.65 times length). Pronotal disk with at most only very short indistinct setae, distinct scales absent. Elytra with scattered patches of elongate fine scales in addition to very short setae; underlying cuticle not obscured by scale cover . . . . *Larinus* Schoenherr
(one species, introduced)

10 (7′) Epistoma with anterior margin emarginate (Figs 25–30). Pronotum with well-developed, rounded postocular lobes; postocular vibrissae indistinct, uniformly short (Figs. 25–30). Eye elongate "kidney shaped" (Figs. 25–30); flat, or only slightly convex in dorsal view .... *Stephanocleonus* Motschulsky, p. 453 (six species, native; also in Palearctic Region)

10′ Epistoma with anterior margin rounded (Fig. 82–88). Pronotum with anterior margin straight behind eyes or with small acute postocular projection immediately behind base of eye; postocular vibrissae distinct and long, longest immediately behind base of eye (Figs. 82–88). Eye "teardrop shaped" (Figs. 82–88); protruding and moderately to markedly convex in dorsal view .... *Apleurus* subgenus *Apleurus* Chevrolat, p. 470 (seven species, native)

Ileomus Schoenherr is not given separate generic status in this key. Champion (1902–1906), although regarding it as a separate genus, states that "it is scarcely distinct from *Lixus*". Accordingly, individuals of species that are assigned to *Ileomus* by O'Brien and Wibmer (1982) key out in the above key to *Lixus*. Detailed study of phylogenetic relationships of the various groupings of *Lixus* species is needed to assess their validity as nominal subgeneric or generic taxa.

Genus *Cleonis* Dejean

Curculio; Scopoli 1763 (in part; sp. desc.). Linnaeus 1767 (in part; sp. desc.). Goeze 1777 (in part; sp. desc.). Knoch 1781 (in part; sp. desc.). Villers 1789 (in part; sp. desc.). Gmelin 1790 (in part; sp. desc.).

Cleonis Dejean 1821:96. Gender, feminine. Type species *Curculio sulcirostris* Linnaeus by subsequent designation (O'Brien and Wibmer 1982:73). Silfverberg 1979 (in part; check.). O'Brien and Wibmer 1982 (in part; catal., distn., misident. *Apleurus*, *Cleonidius*, *Stephanocleonus*). O'Brien and Wibmer 1984 (in part; misident. *Apleurus*, *Cleonidius*, *Stephanocleonus*).

Geomorus Schoenherr 1823: column 1141. Gender, masculine. Type species *Curculio sulcirostris* Linnaeus by original designation.

Cleonus Schoenherr 1826:145. Unjustified replacement name for *Geomorus* Schoenherr. Type species *Curculio sulcirostris* Linnaeus according to Article 67(h) of International Code of Zoological Nomenclature. Say 1831 (misident. *Cleonidius*). Kirby 1837 (misident. *Cleonidius*). LeConte 1850 (misident. *Stephanocleonus*). Melsheimer 1853 (misident. *Cleonidius*). LeConte 1858 (misident. *Apleurus*). LeConte 1859 (misident. *Apleurus*). Gemminger and von Harold 1871 (in part; misident. *Apleurus*, *Cleonidius*). LeConte 1876a (misident. *Cleonidius*). Henshaw 1881–1882 (misident. *Cleonidius*). LeConte and Horn 1883 (misident. *Cleonidius*). Henshaw 1885 (misident. *Cleonidius*). Wickham 1889 (misident. *Cleonidius*). Wickham 1896 (misident. *Cleonidius*). Fall 1897 (misident. *Cleonidius*). Fall 1901 (misident. *Cleonidius*). Wickham 1902 (misident. *Cleonidius*). Fletcher 1906 (misident. *Cleonidius*). Fall and Cockerell 1907 (misident. *Cleonidius*). Pierce 1907 (misident. *Cleonidius*). Ely 1913 (misident. *Cleonidius*). Gibson 1914 (misident. *Cleonidius*). Anderson 1914 (misident. *Cleonidius*). Blatchley and Leng 1916 (misident. *Cleonidius*). Yothers 1916 (misident. *Cleonidius*). Leng 1920 (misident. *Stephanocleonus*, *Apleurus*, *Cleonidius*). Leonard 1926 (misident. *Stephanocleonus*, *Cleonidius*). Böving 1927 (in part; larval key). Bradley 1930 (misident. *Apleurus*, *Cleonidius*). Crosby and Blauvelt 1930 (biol.). Leng and Mutchler 1933 (catal.). Wilcox *et al.* 1934 (misident. *Cleonidius*). Bleasdell 1937 (misident. *Stephanocleonus*, *Cleonidius*). Brimley 1938 (misident. *Cleonidius*). Brown 1940 (distn.). Blackwelder 1947 (misident. *Apleurus*, *Cleonidius*). Bruhn 1947 (misident. *Cleonidius*). Hicks 1947 (distn.). Hicks 1949 (distn.). Anderson 1956 (biol., distn.). Essig 1958 (misident. *Cleonidius*). Sanders 1960 (misident. *Cleonidius*). Kissinger 1964 (in part; biol.). Tanner 1966 (misident. *Apleurus*, *Cleonidius*). Kingsolver 1972 (misident. *Cleonidius*). Burke and Anderson 1976 (biblio.). Kumar *et al.* 1976 (misident. *Cleonidius*). Krombein 1979 (misident. *Stephanocleonus*, *Apleurus*). Arnett *et al.* 1980 (misident. *Cleonidius*). Batra *et al.* 1981 (distn.). Peschken 1984 (biol.).

Cleonus s.s.; Csiki 1934 (catal.).

Cleonus (*Cleonidius*); Arnett 1960–1962 (in part; misident. *Apleurus*).

Notes about synonymy.— *Epimeces* Billberg, 1820, p. 45, predates *Cleonis* Dejean, 1821 and originally included various Cleoninae (among others, *Curculio sulcirostris* Linnaeus, the type species of *Cleonis* Dejean, and, *Curculio filiformis* Fabricius, presently assigned to *Lixus* Fabricius [Csiki 1934]). The name *Epimeces*, to my knowledge, has not subsequently been used but because no type species has been designated for the genus, the name represents a threat to the priority of *Cleonis* Dejean. I therefore here designate *Curculio filiformis* Fabricius, 1781, p. 172, as the type species of *Epimeces* Billberg, 1820, p. 45. *Epimeces* therefore becomes a new junior subjective synonym of *Lixus* Fabricius, 1801, p. 498, type species *Curculio paraplecticus* Linnaeus, 1758, p. 380, by subsequent designation (Latreille, 1810, p. 430).

Schoenherr (1823), seeking consistency in gender of generic names, changed all feminine generic names in Curculionidae to a masculine name (not always the masculine form of the former feminine name). As a result of this, and according to Schoenherr (1823), inadequate characterization to recognize a type species, use of the name *Cleonis* Dejean, 1821 was discontinued, and the species initially placed in *Cleonis* were assigned to one of four genera by Schoenherr (1826). One of these was *Geomorus* Schoenherr, 1823. As such, *Geomorus* cannot be regarded as an express replacement name for *Cleonis*. Subsequently, Schoenherr (1826) proposed the genus *Cleonus* expressly as a replacement name (although unjustified) for *Geomorus* as indicated by his designation of *Curculio sulcirostris* Linnaeus, 1767 as the type species. This same species had already been designated by him as the type species of *Geomorus*. Schoenherr (1826) also placed all species initially included in *Geomorus* in *Cleonus*. The generic name *Cleonus* has since been in widespread use. However the name *Cleonis* was recently resurrected by Silfverberg (1979) and used by O'Brien and Wibmer (1982), Lohse (1983), and Wheeler and Whitehead (1985).

Cleonis Dejean is here used in a very restricted sense (subgenus *Cleonis* of Csiki [1934]) including only *C. pigra* (Scopoli), *C. japonicus* (Faust), and *C. sardous* (Chevrolat), the latter two species not examined by me. *Cleonis* appears closely related to *Cyphocleonus* Motschulsky and *Adosomus* Faust, and subsequent phylogenetic analysis may reveal the three to be congeneric.

Diagnosis.— Adult Cleoninae with moderately robust body form (Fig. 19). Rostrum with broad low median carina longitudinally sulcate throughout length (Fig. 10). Pronotum with small glabrous shiny tubercles, not distinctly punctate; pronotal postocular lobes slightly to moderately well-developed, rounded. Tibia with corbel ridge sharp (as in Fig. 6). Elytra with strial punctures individually indistinct, dorsal surface of elytra with scattered, small, irregularly shaped (usually transverse), glabrous, shiny swellings.

Description.— *Size.* Moderately large, moderately robust in form. *Mouthparts.* Prementum flat, with single large seta on each side. Maxillary palpus with palpifer and stipes each with large seta. Basal articles of labial palpi separated by distance subequal to width of a palpus. *Rostrum.* Moderately robust; with broad low median carina longitudinally moderately deeply sulcate throughout length from base of epistoma to base of frons; not medially tumescent (Figs. 9–10). Epistoma slightly swollen, with apical margin emarginate medially. Antenna with funiculus with article 1 very slightly longer than article 2 (Fig. 9); apical three articles of club with placoidal sensillae. *Head.* Eye elongate-quadrate, slightly wider at top than bottom; flat (Fig. 9). *Vestiture.* Dorsum lacking erect or suberect vestiture, with only simple elongate-narrow appressed white scales. Procoxae, mesocoxae, metasternum and base of abdominal sternum III of both sexes with moderately long suberect hair-like scales. *Prothorax.* Dorsal surface of pronotum with small glabrous shiny tubercles, not distinctly punctate. Median basal area shallowly impressed. Disk with elongate, moderately large, moderately dense, white scales present in broad lateral stripe and narrow median line, with scales small and fine in pair of paramedian apically narrowed stripes; median area largely black in color, underlying dark cuticle not obscured by overlying scales (Fig. 19). Pronotum widest at base, lateral margins slightly rounded and convergent from base to apex; apical constriction very slight (Fig. 19). Pronotal postocular lobes rounded, slightly to moderately well-developed (Fig. 9). Prosternum with slight impression anterolaterad of each procoxal cavity and with slight swelling immediately anterior to each prosternal impression. *Legs.* Tarsi broad, articles 2 and 3 more or less as broad as long, subequal in length; article 1 only slightly longer than articles 2 or 3; article 3 deeply bilobed (Fig. 18). Ventral tarsal pilosity extensive, covering entire ventral surface of articles 1 to 3 (Fig. 18). Claws connate in basal one-third, not to slightly divergent. Foretibia with small to moderately well-developed second spur; inner margin with moderately large denticles throughout greater portion of length. Tibia with corbel ridge sharp. Metatibia of male with uncus with ventral margin slightly sinuate. *Wings.* Present. *Elytra.* Base of interval 3 and humerus very slightly swollen and convex, otherwise intervals uniformly flat. Humeri distinct. Strial punctures individually indistinct, dorsal surface of elytra with scattered small irregularly shaped (usually transverse) glabrous shiny swellings. *Abdomen.* Ventral surface with small shiny glabrous patches, each with single small appressed scale. *Genitalia.* Female. Abdominal sternum VIII lacking basal arm (Fig. 17). Gonocoxite II elongate-triangular, apex not prolonged into marked lobe; stylus moderately large, apical in position (Fig. 15). Spermathecal gland slightly elongate-oval (Fig. 16). Male. Aedeagus elongate, moderately robust; in lateral view, moderately arcuate near base then only slightly arcuate throughout rest of length (Fig. 13). Apex slightly spatulate. Internal sac with median dorsal pocket high; various lobes present; apical and dorsal median pockets individually distinct; apical sclerite complex present, individual sclerites distinctly scythe-like (Figs. 11, 12, 14).

Comparisons.— As noted, *Cleonis* species are very similar to those of *Adosomus* and *Cyphocleonus* in that all possess a pronotum and elytra that are distinctly tuberculate and not punctate. *Adosomus* and *Cleonis* species possess moderately well-developed, rounded, postocular lobes, whereas postocular lobe are lacking from *Cyphocleonus* species. The only feature which distinguishes *Cleonis* from both of these two genera is the medially longitudinally sulcate rostrum of the former. In *Adosomus* the rostrum is medially tumescent and not carinate or sulcate, whereas in *Cyphocleonus* species, the rostrum is variously medially tumescent and carinate. *Cyphocleonus trisulcatus* (Herbst) has a low broad median carina but which is only apicomedially sulcate.

Checklist of included species.— Following Csiki (1934), three species are recognized. They are *C. japonicus* (Faust), *C. sardous* (Chevrolat), and *C. pigra* (Scopoli). *Cleonis pigra* is the only one of the three species that I have examined and is the only one that occurs in the Nearctic Region.

Faust (1904) distinguishes *C. pigra* and *C. japonicus* from *C. sardous* by the latter having metatarsal article 2 slightly longer than article 3 and by differences in the pronotal scale patterns. *Cleonis pigra* and *C. japonicus* are separated on the basis of extent of distribution and development of the pronotal and elytral tubercles, the distribution of the ventral abdominal glabrous patches, and body shape. Based upon examination of only Nearctic representatives of *C. pigra*, I find all of these characters vary somewhat, and suspect that the three included species may prove conspecific.

Phylogenetic relationships.— *Cleonis, Cyphocleonus* and *Adosomus* appear to represent a monophyletic group based on the presence of a tuberculate rather than punctate pronotum and elytra. Beyond this, affinities of the group are uncertain.

Cleonis pigra (Scopoli)
(Figs. 9–19, 213)

Curculio piger Scopoli 1763:23.
Curculio sulcirostris Linnaeus 1767:617.
Curculio transversofasciatus Goeze 1777:409.
Curculio nebulosus Knoch 1781:87 [not Linnaeus 1758:385].
Curculio fasciatus Villers 1789:216 [not Müller 1776:86].
Curculio fasciatus Gmelin 1790:1804.
Cleonis sulcirostris; Dejean 1821.
Cleonus sulcirostris; Gyllenhal 1834.
Cleonus indicus Fåhraeus 1842:55.
Cleonus piger; Everts 1903.

Cleonis piger; Silfverberg 1979 (check.). O'Brien and Wibmer 1982 (catal., distn.).
Cleonis pigra; O'Brien and Wibmer 1984.

Notes about synonymy.— The synonymical list follows Csiki (1934); I have not examined type material of this species or of any of its conspecific forms. This is the species frequently referred to in previous publications as *C. sulcirostris.*

Description.— *Specimens examined.* 61 unsexed. *Size.* Length, male, 7.5–13.4 mm; female, 11.4–14.8 mm. Width, male, 3.7–6.6 mm; female, 5.8–7.0 mm. *Rostrum.* Lateral margins sharp, indicated by low rounded carina from above point of antennal insertion to frons (Fig. 10). Side portion of rostrum immediately ventrad of lateral carina moderately deeply sulcate from immediately anterior to eye to point of antennal insertion; with moderately deep elongate-narrow punctures, most linearly confluent or nearly so. *Prothorax.* Surface dorsally and laterally with numerous small shiny glabrous tubercles; medially with small to large elongate-oval shiny glabrous swelling. Prosternum in lateral view with apical portion flat, slightly shorter than adjacent posterior steeply declivous portion. *Elytra.* Sutural interval in basal one-half, intervals 2 to 5 basally, and two obliquely posteromedially directed patches (at basal one-third from intervals 2 to 5 and at apical one-third from intervals 2 to 4) with small irregular slightly elevated shiny glabrous patches (Fig. 19). *Wings.* Long (greater than elytra in length). Bases of 2A joined but very lightly sclerotized. *Abdomen.* Ventral surface with small shiny glabrous patches distinct and dense on abdominal sterna III and IV, less distinct on sterna V to VII. *Genitalia.* Female (2 specimens). Abdominal sternum VIII with lateral arms narrow, evenly and slightly inwardly arcuate throughout length, expanded apically (Fig. 17). Male (2 specimens). Aedeagus robust; in lateral view narrowed from approximately apical one-third to apex (Fig. 13). Internal sac with single, large, broad, dorsally directed, lobe; with moderately large, paired, laterally directed, lobes and small dorsally directed median lobe on dorsal surface at midlength; with small dorsolaterally directed paired lobes at midlength and midheight (Figs. 11–12). Eversible apical sclerite complex with paired scythe-like sclerites, each with median elongate-narrow projection long, visible in lateral view (Figs. 11, 14); adjacent ventral surface and basal portion of sides of apex of sac with pair of large transverse dark sclerites (Fig. 11).

Geographic distribution.— This species was accidentally introduced into North America from Europe prior to 1919, the year of the earliest known North American record (Anderson, 1956). It occurs throughout New York and southern Ontario, west to Michigan and east to eastern Quebec and New Brunswick (Fig. 213). It is widespread in the Palearctic Region (Csiki, 1934).

Variation.— As part of a program investigating the potential for use of *C. pigra* as a biological control agent for the introduced *Centaurea diffusa* Lam. (diffuse knapweed) in the prairie provinces of Canada, a study of variation based on 15 mensural features was carried out on adult individuals of *C. pigra* reared from species of *Cirsium*, *Carduus* and *Centaurea* (all Compositae) to determine if structurally distinct host races exist (Anderson, 1984a). Measurements were made of 15 characters and a linear discriminant analysis was performed. Separation using the generated discriminant function proved unreliable and because absolute size was the principal component upon which the function was based, it was concluded that only a single polyphagous morphotype was present. Differences in absolute size are likely a result of structural attributes of the different larval feeding and pupation sites in the different host plants and are doubtfully heritable.

Natural history.— Anderson (1956) summarizes information about the natural history of this species in North America as follows. Adults are the overwintering stage and are first found on Canada thistle, *Cirsium arvense* (L.) Scop., or bull thistle, *Cirsium vulgare* (Savi) Tenore, in early June. Copulation and oviposition take place through mid-July. Eggs are laid singly in the lower portions of the stems in cavities chewed by the females and subsequently plugged with frass following deposition of the egg. Larvae bore downward into the primary root where they feed for approximately 30 days. Pupation takes place in the root. Adults emerge in August or September and overwinter under ground debris. Although a wide range of Compositae serve as host plants in Europe (Anderson, 1956; Peschken, 1984, and references cited therein), only two plants, *Cirsium arvense* and *Cirsium vulgare*, both adventive, are known to serve as hosts in North America (Anderson 1956). Native North American *Cirsium* species or other Compositae are not attacked by the weevils.

A similar range of host plant associations to those of *C. pigra* in Europe is also found in another species of Cleoninae, *Rhinocyllus conicus* Froelich, which was recently shown to consist of various host specific races (Zwölfer and Preiss, 1983). As such, host plant races are also suspected in *C. pigra* although, as noted, an examination of the structural features of adults reared from various Compositae did not reveal differences between individuals reared from different plant taxa.

Immature stages were described by La Ferla (1939).

Genus *Stephanocleonus* Motschulsky

Cleonus; LeConte 1850 (in part). Leng 1920 (in part; catal.). Leonard 1926 (in part; check.). Bleasdell 1937 (in part). Krombein 1979 (in part; as prey).

Stephanocleonus Motschulsky 1860:540 (in key). Gender, masculine. Type species *Curculio flaviceps* Palliser by original designation. LeConte 1876a (key, sp. descs.). Henshaw 1881–1882 (in part; check.). LeConte and Horn 1883 (key). Henshaw 1885 (check.). Blatchley and Leng 1916 (key, sp. redesc.).

Coniocleonus Motschulsky 1860:540 (in key). NEW SYNONYMY. Gender, masculine. Type species *Cleonus carinirostris* Gyllenhal by original designation.

Plagiographus Chevrolat 1873:21. Gender, masculine. Type species not designated.

Cleonus (*Stephanocleonus*); Casey 1891 (in part; key). Fall and Cockerell 1907 (in part; check.). Csiki 1934 (in part; catal.). Arnett 1960–1962 (in part; catal., key). Kissinger 1964 (in part; key).

Cleonis; O'Brien and Wibmer 1982 (in part; catal., distn.). O'Brien and Wibmer 1984 (in part).

Notes about synonymy.— The genera *Stephanocleonus* and *Coniocleonus* were both originally proposed by Motschulsky (1860). They were distinguished by the rostrum having only a single median carina in the latter, whereas in *Stephanocleonus*, the rostrum, in addition to the median carina, also had a smaller oblique carina on each side. *Stephanocleonus* is also noted as being apterous but nothing is said of the state of the wings in *Coniocleonus*. I have examined specimens of *Stephanocleonus flaviceps* Palliser, the type species of *Stephanocleonus*, and, in the single male available, did not see small oblique lateral carinae, but only a single uniformly steeply declivous median carina. The two females examined have the median carina similarly steeply declivous basally but decreasingly declivous apically. A very slight oblique carina is present where this more gradual apical declivity meets the flat surface of the rostrum on each side of the median carina. All three individuals are wingless.

I have not seen specimens of *Coniocleonus carinirostris* Gyllenhal, the type species of that genus, but I have examined a male and a female of each of *C. excoriatus* Gyllenhal and *C. glaucus* Fabricius, a female of *C. cineritius* Gyllenhal, and a male of each of *C. cinerascens* Hochhuth and *C. ferrugineus* Fåhraeus. Individuals of *C. excoriatus* and *C. glaucus* are macropterous and the rostrum has a single median carina which is gradually declivous throughout its length. There are no small lateral carinae evident. However, the specimens of *C. cineritius*, *C. cinerascens* and *C. ferrugineus* each have a rostrum with slightly to moderately well-developed oblique lateral carinae in the same position as in the females of *S. flaviceps*, and have wings of variable length.

In view of this variation and the lack of other distinguishing characters, I cannot accept other than that *Stephanocleonus* is simply an apterous *Coniocleonus*. I do not think the rostral differences between the type species warrant separate generic status. I therefore consider *Stephanocleonus* and *Coniocleonus* to be new subjective synonyms, a decision anticipated by Casey (1891:188) who stated, regarding the Nearctic species, that "It is a question whether our species should be placed in *Stephanocleonus* or *Plagiographus* [a junior synonym of *Coniocleonus* according to Faust, 1904 and Csiki, 1934], but this is a matter of but slight importance as the differences between the subgenera appear to be very inconsiderable".

I choose to give the name *Stephanocleonus* priority over *Coniocleonus* because the former has been the only name used in reference to the Nearctic species here placed in the genus. Furthermore, no major works have recently appeared dealing with *Coniocleonus*, however, a recent review by Ter-Minasyan (1979) of the *Stephanocleonus* of the Palearctic Region includes species that in my opinion are congeneric with species in North America.

Diagnosis.— Adult Cleoninae with moderately robust to robust body form (Figs. 20–23). Eye kidney-shaped, flat (Figs. 25–30). Rostrum with well-developed sharp median carina (Figs. 25–30). Pronotum punctate; pronotal postocular lobes well-developed, rounded; postocular vibrissae uniformly short (Figs. 25–30). Meso- and especially metatarsus elongate-narrow, with all articles markedly longer than broad; article 2 distinctly longer than article 3; article 1 markedly longer than articles 2 or 3. Tibia with corbel ridge sharp (as in Fig. 6). Procoxae, mesocoxae, metasternum, metacoxae and base of abdominal sternum III of male with moderately long to very long erect hair-like scales; hair-like scales sparse to lacking in female. Pronotal disk with elongate, white, moderately large, moderately dense scales present in lateral stripe of various width, small and fine in moderately broad to very broad, apically narrowed, median stripe, and variously small and fine to moderately large and elongate along lateral margins; median area largely black in color, underlying dark cuticle not obscured by overlying scales (Figs. 20–23). Prosternum with or without swellings, swellings, if present, immediately anterior to each prosternal impression (as in Fig. 7). Metauncus of male with ventral margin slightly to markedly sinuate. Female with abdominal sternum VIII with basal arm very long (Figs. 37–42); gonocoxite II rounded basally, with apex prolonged into a marked lobe (Fig. 54). Male with apex of aedeagus spatulate or not (Figs. 31–36); internal sac with or without large paired sclerite at midlength (Figs. 31–36).

Description.— *Size.* Moderately large, moderately robust to robust in body form (Figs. 20–23). *Mouthparts.* Prementum ventrally longitudinally carinate, slightly swollen to flat, with one or more large setae on each side. Maxillary palpus with palpifer and stipes each with at least one large seta. Bases of labial palpi separated by distance subequal to width of basal article of labial palpus. *Rostrum.* Moderately to markedly robust, not medially tumescent; with low to high, sharp median carina (Figs. 25–30). Epistoma markedly swollen or not, with apical margin emarginate medially (Figs. 25–30). Antenna with funiculus with article 1 slightly to markedly longer than article 2 (Figs. 25–30); apical three articles of club with placoidal sensilla. *Head.* Eye kidney-shaped, flat (Figs. 25–30). Upper margin of eye rounded to sharp, frons convex to markedly concave. *Vestiture.* Dorsum lacking or with at most only very short indistinct suberect or erect vestiture, with simple elongate-narrow appressed white scales of various size and density. Procoxae, mesocoxae, metasternum, metacoxae and base of abdominal sternum III of male with moderately long to very long erect hair-like scales; hair-like scales sparse to lacking from female. *Prothorax.* Dorsal surface of pronotum punctate. Pronotum with median basal area shallowly to deeply impressed, disk with or without various other impressions. Disk with elongate white moderately large moderately dense scales present in lateral stripe of various width, small and fine in moderately broad to very broad apically narrowed median stripe, and variously small and fine to moderately large and elongate along lateral margins; median area largely black in color, underlying dark cuticle not obscured by overlying scales (Figs. 20–23). Pronotum widest at base to subequal in width from base to apical one-quarter, then constricted to various extent and convergent to apex (Figs. 20–23). Pronotal postocular lobes moderately to well-developed, postocular vibrissae uniformly short (length less than one-half maximum width of eye) (Figs.; 25–30). Prosternum with slight impression anterolaterad of each procoxal cavity; with or without slight swelling immediately anterior to each prosternal impression (as in Fig. 7). *Legs.* Foretarsus moderately broad, articles 2 and 3 more or less subequal in length, at most slightly longer than broad; article 1 only slightly longer than articles 2 or 3; article 3 moderately deeply bilobed. Meso- and especially metatarsus elongate-narrow; all articles markedly longer than broad, article 2 distinctly longer than article 3; article 1 markedly longer than articles 2 or 3, article three slightly bilobed. Ventral tarsal pilosity various in extent, lacking entirely on at least more basal articles in most species. Claws connate in basal one-third, not to slightly divergent. Foretibia with inner margin near apex with moderately-developed subapical tooth, inner margin with at most only small denticles in apical one-half. Metatibia of male with uncus with ventral margin slightly to markedly sinuate. Tibia with corbel ridge sharp. *Wings.* Absent or present (various in length). *Elytra.* Intervals flat to variously slightly swollen and convex; striae distinctly punctate. Humeri acute to rounded. Dorsal surface of most species with variously developed, posteromedially directed oblique patches of small and fine scales at each of basal one-third and apical one-third to midlength (Figs. 20, 22–23). *Abdomen.* Ventral surface with small shiny glabrous patches, each with single small appressed scale. Sternum VII of male with apex variously medially emarginate in most species. *Genitalia.* Female. Abdominal sternum VIII with long basal arm

(Figs. 37–42). Gonocoxite II rounded basally, with apex prolonged into marked lobe; stylus moderately large, apical in position (Fig. 54). Spermathecal gland round (Fig. 48). Male. Aedeagus robust and short to elongate-narrow, various in shape in lateral view; apex not to markedly spatulate (Figs. 31–36). Internal sac various; median pocket low, apical and dorsal median pockets individually distinct or not, various lobes present; apical sclerite complex with individual sclerites distinctly scythe-like, large paired sclerite at midlength present or absent (Figs. 43–48).

Comparisons.— *Stephanocleonus* is very similar to *Pleurocleonus* however, the latter lacks pronotal postocular lobes, has an elongate-teardrop-shaped eye, tarsal claws that are widely divergent, and a low broad longitudinally sulcate median rostral carina. Species of *Stephanocleonus* may also be confused with *Nomimonyx* and *Epirhynchus* because of similarities in head and rostral form, and eye shape. *Epirhynchus* however, has a single tarsal claw, and both have short broad tarsal articles, not the markedly elongate-narrow articles of *Stephanocleonus* species.

Although unlikely, some *Conorhynchus, Bothynoderes* and *Chromonotus* may also be confused with *Stephanocleonus* species. These taxa however have article 2 of the antennal funiculus longer than article 1; in *Stephanocleonus* species, article 1 is longer than article 2.

Checklist of included species.— In the Nearctic Region, six species are placed in *Stephanocleonus*. Numerous species occur in the Palearctic Region (Csiki 1934; Ter-Minasyan 1979) but are not listed here. The six Nearctic species are as follows:

1. *S. confusus* Anderson, n. sp.
2. *S. cristaticollis* Csiki
3. *S. immaculatus* Anderson, n. sp.
4. *S. parshus* Anderson, n. sp.
5. *S. plumbeus* (LeConte)
6. *S. stenothorax* Anderson, n. sp.

Phylogenetic relationships.— Distribution of the apotypic character state of female gonocoxite II (rounded basally and with a marked apical lobe [Fig. 54]) suggests that *Stephanocleonus*, *Pleurocleonus* Motschulsky, *Menecleonus* Faust, *Xanthochelus* Chevrolat, and *Conorhynchus* Motschulsky (=*Temnorhinus* Chevrolat) form a monophyletic group. *Menecleonus, Xanthochelus* and *Pleurocleonus* appear to further comprise another monophyletic group (based upon presence of an unpaired sclerite near the confluence of the apical pocket and the dorsal median pocket in the internal sac of the aedeagus of males) that is the sister-group of *Stephanocleonus*. This proposed sister-group relationship is based of article 1 of the antennal funiculus being longer than article 2. *Conorhynchus* has article 2 of the funiculus longer than article 1 and is likely the sister-group to the *Stephanocleonus-Pleurocleonus, Menecleonus, Xanthochelus* lineage. *Bothynoderes* Schoenherr, *Chromonotus* Motschulsky and also *Chromosomus* Motschulsky, have the apotypic state of elongate-narrow meso- and metatarsi and together with the above taxa likely comprise another monophyletic group based upon shared possession of this character state. They also have a very similar "elongate-teardrop" eye-shape to *Conorhynchus* and similarly all have article 2 of the antennal funiculus longer than article 1.

Key to species of adult *Stephanocleonus*

1 Dorsal surface of elytra uniformly covered with small white scales, without distinct maculations; with or without small shiny glabrous area at confluence of intervals 4 to 6 (Fig. 21). Elytra with humeri distinct; lateral margins more or less straight in basal one-half (Fig. 21) .... *S. immaculatus* Anderson, p. 460

1′ Dorsal surface of elytra faintly to distinctly maculate, with small white scales less dense in two posteriorly directed oblique patches (one at basal one-third from intervals 2 to 6; the other at apical one-third from intervals 2 to 4), and with small triangular shiny glabrous area at confluence of intervals 4 to 6 (Figs. 20, 22–23). Elytra with humeri less distinct or rounded; lateral margins more or less arcuate in basal one-half (Figs. 20, 22–23) 2

2 (1′) Elytra fused together; thoracic wings short, approximately equal to one-half length of elytra 3

2′ Elytra not fused together; thoracic wings long, approximately equal to or greater than length of elytra 4

3 (2) Elytra with scattered small recurved hair-like scales, most evident on declivity from sutural interval to interval 3; with greater part of length of sutural interval and intervals 3 and 5 elevated and convex. Female with sternum VII flat, lacking paired tumescence. Male with median lobe elongate; apex slightly spatulate; in lateral view narrowed from apical one-third to apex; with at most small basal ventral tubercle (Fig. 31) . . . . *S. confusus* Anderson, p. 457

3′ Elytra lacking erect hair-like scales, with only the extreme base of interval 3 convex, otherwise with all intervals flat throughout their length. Female with ventral surface of sternum VII with paired tumescence. Male with median lobe less elongate; apex markedly spatulate; in lateral view, narrowed from approximately midlength to apex; with large basal ventral tubercle (Fig. 32) . . . . *S. cristaticollis* Csiki, p. 459

4 (2′) Pronotum with subapical constriction well-defined dorsally and laterally, with distinct moderately deep impressions laterad of median carina at apical one-quarter laterally continuous with subapical constriction; with apical margin broadly and moderately deeply emarginate at middle. Elytra with tubercle at confluence of intervals 4 to 6 markedly elevated. Rostrum robust (width at apex greater than 0.90 times length); approximately uniform in width throughout length (Fig. 30) . . . . *S. stenothorax* Anderson, p. 465

4′ Pronotum with subapical constriction only laterally well-defined, lacking or with at most only very shallow indistinct impressions laterad of median carina; with apical margin not or only very slightly emarginate at middle. Elytra with tubercle at confluence of intervals 4 to 6 only slightly elevated. Rostrum more elongate-narrow (width at apex less than 0.90 times length); slightly narrowed at midlength (Figs. 28–29) 5

5 (4′) Pronotum with punctures large, deep and dense, distance between punctures distinctly less than diameter of a puncture (Fig. 28). Female metatarsal article 3 with large ventral pilose pads. Male with median lobe in ventral view with apex symmetrical (Fig. 34b); internal sac lacking median dorsal pocket and large dorsally directed paired lobes on dorsal surface immediately anterior to midlength (Fig. 46) . . . .

. . . . *S. parshus* Anderson, p. 461

5′ Pronotum with punctures small, shallow and sparse, distance between punctures greater than diameter of a puncture (Fig. 29). Female metatarsal article 3 entirely spinose, lacking ventral pilose pads. Male with median lobe in ventral view with apex asymmetrical (Fig. 35b); internal sac with median dorsal pocket and without dorsally directed lobes from dorsal surface (Fig. 47) . . . . *S. plumbeus* (LeConte), p. 464

Stephanocleonus confusus Anderson, new species
(Figs. 20, 25, 31, 37, 43, 204)

Stephanocleonus plumbeus; LeConte 1876a (in part; desc., misident., mixed type series). Henshaw 1881–1882 (in part; check., misident.). Henshaw 1885 (in part; check., misident.). Wickham 1902 (check., misident.). Wickham 1909 (check., misident.). Leng 1919 (in part; check., poss. misident.). Leng 1920 (in part; catal., misident.). Danks 1981 (in part; check., poss. misident.).
Cleonus cristatus; Casey 1891 (key, misident.).
Cleonus (*Stephanocleonus*) *plumbeus*; Fall and Cockerell 1907 (in part; check., misident.).
Stephanocleonus cristatus; LeConte 1878 (distn., misident.). Leng 1920 (in part; catal., misident.).
Cleonus plumbeus: Krombein 1979 (in part; prey, poss. misident.).
Cleonis cristaticollis; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).
Cleonis plumbeus; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Type Material.— Holotype, male, labelled with a red label "HOLOTYPE", "Spearfish Canyon/ Black Hills, S.D./ 15–18:VI:1910.", inverted "*Cleonus/ cristatus/* Lec.", "HOLOTYPE/ *Stephanocleonus/ confusus/* Anderson" and with abdomen on card and genitaliain microvial attached to pin (USNM). Allotype, female, labelled with red label "ALLOTYPE", "Tp.21 Rge.6/ W.4 Mer. Alberta/ 12.V.1980/ Lot 3 BF&JL Carr", "ALLOTYPE/ *Stephanocleonus/ confusus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Type locality, Spearfish Canyon, Black Hills, South Dakota.

Paratypes. 37 males, 29 females. CANADA: Alberta: Township 1, Range 4, West 4 Meridian, 23.V.82, B.F. and J.L. Carr, 1M (RSAN); Township 13, Range 14, West 4 Meridian, 16.IV.82, B.F. and J.L. Carr, 1M (JLCC); Township 14, Range 25, West 4 Meridian, 15.V.82, B.F. and J.L. Carr, 1F (JLCC); Township 10, Range 2, West 5 Meridian, 11.V.82, B.F. and J.L. Carr, 1F (RSAN); Township 30, Range 21, West 4 Meridian, 17.IV.82, B.F. and J.L. Carr, 1M (RSAN); Medicine Hat, 22.IV.29, F.S. Carr, 1F (UASM), 13.VI.32, F.S. Carr, 2M, 1F (UASM), 24.VI.30, F.S. Carr, 1F (UASM), 27.III.27, F.S. Carr, 1F (UASM), 14.IV.26, F.S. Carr, 1F (UASM), 13.VI.33, F.S. Carr, 1F (UASM), 2.VII.23, F.S. Carr, 1M (UASM), 11.V.32, F.S. Carr, 1M (UASM), 13.V.27, F.S. Carr, 1M (RSAN), 13.V.23, F.S. Carr, 1M (UASM), 6.IX.27, F.S. Carr, 1F (UASM), 12.VII.24, F.S. Carr, 1F (RSAN), 18.II.24, F.S. Carr, 1F (UASM), 8.V.65, J.L. Carr, 1F (JLCC); Township 14, Range 13, West 4 Meridian, 22.VII.79, J.L. Carr, 1M (JLCC); Ghost Dam, 2.VII.80, B.F. and J.L. Carr, 1F (JLCC); Seebe, 7.VI.73, B.F. and J.L. Carr, 1M (JLCC); Suffield, 20.IV.23, 1F (UASM); Township 6, Range 1, West 4 Meridian, 20.V.80, B.F. and J.L. Carr, 1F (JLCC); Township 10, Range 2, West 5 Meridian, 28.IV.81, B.F. and J.L. Carr, 1M (JLCC); Township 15, Range 14, West 4 Meridian, 9.V.80, B.F. and J.L. Carr, 1F (JLCC); 27mi. sw. Nordegg, 13.VI.66, R. Frietag/T.L. Erwin, 1F (CWOB); Calgary, IV.11, Criddle, 1F (CNCI); Lethbridge, 6.V.30, J.H. Pepper, 1M (CNCI). Northwest Territories: 1M (CNCI). Saskatchewan: Township 6, Range 2, West 3 Meridian, 13.VIII.73, B.F. and J.L. Carr, 1M (RSAN); Cypress Hills Provincial Park, 29.V.63, Cook *et al.*, 1F (CNCI).

UNITED STATES OF AMERICA: Arizona: Coconino County, 2.4mi. n. Kaibab Lodge, 28.VII.71, Lawton/Willis, 2M (CWOB). Colorado: Grant/Jackson County, Rabbit Ears Pass, 2872 me., 19.VI.81, M. Kaulbars, 1M (RSAN); Top of Range below Sapello and Pecos Rivers, 11,000 ft., 1.VIII.00, H.F. Wickham, 1M (USNM); Cumbres Pass, 10,000 ft., 22.VI.35, E.C. Van Dyke, 1M (CASC); 1mi. n. Nederland, 11.VIII.73, C.W. O'Brien, 1M (CWOB); Longs Peak, 10–11,000 ft., 8.VII.26, E.C. Van Dyke, 1M (CASC); Argentine Road, H.F. Wickham, 1M (USNM); Kenosha Pass, 16.VII.38, J.W. Green, 1F (CASC); Gore Pass, 15.IX.48, O. Bryant, 1F (CASC); Leadville, 7–14.VII.96, H.F. Wickham, 1M (USNM). Montana: Helena, Hubbard and Schwarz, 2M (USNM); Flathead Lake, 12.VII.11, 1F (USNM); Gallatin County, 9.IV.32, 1M (MSU), 8.V.32, 1F (MSU), 1VI.31, 1F (MSU); Bozeman, 17.V.28, 1M (MSU), 11.V.25, 1M (MSU); 15mi. ne. Bozeman, 30.VI.72, Burleson, 1M (MSU); 6mi. e. Dell, 30.VI.54, Anderson, 1M (MSU). Nevada: White Pine County, 17.7mi. n., 3.5mi. nw. McGill, Monte Neva Hot Springs, 25.VII.71, Lawton and Willis, 1M, 1F (CWOB). New Mexico: 1F (MCZ); Cloudcroft, V.18, 1M (CASC). Utah: Alta, 29.VI.47, O. Bryant, 1F (CASC). Wyoming: 1F (USNM); Beulah, 21.VII., T.D.A. Cockerell, 1M (UASM); Park County, Beartooth Plateau, 6.VII.61, S.M. Sutton, 1M (UCM), 31.VIII.59, J.G. Edwards, 1F (CWOB); Beartooth Plateau, Hairgrass Canyon, 7.VII.59, 1F (CWOB); Bighorn Mountains, Medicine Mountain, 18.VIII.62, J.G. Edwards, 1F (CWOB); Tie Siding, VIII.25, 1F (USNM).

Notes about synonymy.— An individual of this species from New Mexico was included in the original type series of *S. plumbeus* LeConte. *Stephanocleonus plumbeus* as herein recognized does not occur in New Mexico.

Derivation of specific epithet.— From the Latin "*confusio*" meaning mixed or confused. This name is used in reference to the previous confusion of this species with *S. plumbeus.*

Problems in recognition.— This is the only species of North American *Stephanocleonus* in which the elytra have small recurved hair-like scales on the dorsal surface and in which elytral intervals 3 and 5 are markedly elevated and convex throughout the greater part of their lengths. The internal sac of the male aedeagus is also distinctive (Fig. 43).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 1. *Size.* Length, male, 9.2–15.0 mm; female, 10.5–14.8 mm. Width, male, 4.7–6.5 mm; female,4.9–7.2 mm. *Head.* Frons with punctures large, sparse, shallow, not confluent; also with small broad appressed white scales, dense laterally, sparse medially. Some specimens with slightly raised carina on vertex. *Rostrum.* Moderately robust, slightly more so in males (width at apex 0.85-0.95 times length in male; 0.810-0.909 in female) (Fig. 25). With well-developed, sharp, steeply declivous, low, median carina from above point of antennal insertion to base of rostrum; both basally and apically terminated at small, moderately deep fovea (Fig. 25). Rostrum flat from immediately laterad of median carina to lateral margins, lateral margins sharp from above point of antennal insertion to anterior margin of eye, indicated in few specimens by slightly raised rounded carina. Dorsal punctures large, sparse, shallow, not confluent. With scales small broad appressed white, dense laterally, sparse medially. *Pronotum.* Dorsal apical margin not or shallowly emarginate at middle. With low broad indistinct median carina in anterior one-half. Subapical constriction well defined laterally, not so dorsally; some specimens with shallow impressions laterad of median carina, but discontinuous with lateral portion of subapical constriction. Median basal area narrowly, moderately deeply impressed. Dorsal punctures moderately large to large, dense and moderately deep; medially, distance between punctures markedly less than diameter of single puncture, some punctures confluent and irregularly impressed; laterally, the distance between punctures subequal to or greater than diameter of an individual puncture. *Prosternum.* With shallow impression anterior to each procoxal cavity, and with slightly to moderately developed transverse swelling anterior to each impression. *Elytra.* Robust in general form (width at midlength 0.64-0.72 times length in male; 0.62–0.71 in female) (Fig. 20). In dorsal view with lateral margins evenly arcuate from midlength to base, humerus rounded, not distinct (Fig. 20). Sutural interval and intervals 3 and 5 (in some specimens also basal one-half of interval 7) elevated and convex throughout the greater part of their lengths. Scales white small moderately dense; smaller and less dense in two posteromedially directed oblique patches, one at basal one-third from intervals 2 to 6, the other at apical one-third from intervals 2 to 4. With slightly elevated triangular glabrous shiny area at apical one-quarter at confluence of intervals 4 to 6 (Fig. 20). With scattered very short recurved hair-like scales, most evident on declivity from sutural interval to interval 3. *Wings.* Short (more or less equal to one-half length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small to moderately large, indistinct to distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as small elongate-narrow pads on apical one-quarter of article 1, as large elongate-oval pads on apical three-quarters of article 2, and as large elongate-oval pads on more or less entire ventral surface of article 3; of female, pilose vestiture lacking from article 1, lacking to present as elongate-narrow pads on apical one-quarter to one-half of article 2, as elongate-oval pads on apical one-half of article 3; of mesotarsus of male, lacking to as apical tufts on outer lobe of article 1, as elongate-narrow pads on apical three-quarters on outer lobe and as apical tufts on inner lobe of article 2, as large elongate-oval pads on apical three-quarters of article 3; of mesotarsus of female, lacking from article 1, lacking from to as elongate-narrow pads on apical one-half on outer lobe of article 2, as small to large elongate-oval pads on apical one-third to two-thirds of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-oval pads on apical one-quarter to three-quarters of article 3; of metatarsus of female, lacking from articles 1 to 3 to as elongate-oval pads covering apical one-third of article 3. *Abdomen.* Abdominal sternum VII in female evenly rounded, not tumescent; in male with apical margin slightly emarginate medially. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm expanded at apex; lateral arms narrow, slightly inwardly and evenly arcuate throughout length (Fig. 37). Male (12 examined). Abdominal sternum VIII with paired sclerite with inner apices truncate (Fig. 31c). Aedeagus elongate-narrow; in lateral view slightly and evenly arcuate throughout length, narrowed from approximately apical one-third to apex, apex slightly spatulate; in ventral view with apex symmetrical, medially produced into acuminate apical projection (Figs. 31a,b). Base of aedeagus with at most small ventral tubercle. Internal sac elongate with large dorsally directed paired lobe on dorsal surface at apical one-third; median dorsal pocket high, with large laterally directed paramedial lobes at basal one-third near ventral margin (Fig. 43). In lateral view with basal paired sclerite and apical sclerite complex widely separated (Fig. 43a).

Geographic distribution.— This species is known from southern Alberta and southern Saskatchewan, south to Arizona and New Mexico (Fig. 204). Most published records of *S. cristaticollis* refer to this species.

Natural history.— Adults of this species have been collected in prairie habitats in southern Alberta to alpine habitats at elevations of 3400 m in Colorado and New Mexico.

Chorological relationships.— This species is broadly sympatric with *S. cristaticollis* and *S. parshus*, and narrowly sympatric with *S. immaculatus* along the western limits of the range of the latter.

Stephanocleonus cristaticollis Csiki
(Figs. 26, 32, 38, 44, 205)

Stephanocleonus cristatus LeConte 1876a:147 [not Chevrolat 1873:98]. Holotype (examined), female, labelled "Utah", "*S./ cristatus/* Lec", "Horn Coll/ H8514" and with my label indicating it as the holotype "*Stephanocleonus/ cristatus* LeConte/ HOLOTYPE labelled/ by Anderson" (MCZC). Type locality, Utah. LeConte 1878 (distn., misident. of *S. confusus*). Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Leng 1920 (in part; catal., misident. *Stephanocleonus confusus*).

Cleonus (*Stephanocleonus*) *cristatus*; Casey 1891 (key, misident. *Stephanocleonus confusus*). Csiki 1934 (catal.).

Cleonus (*Stephanocleonus*) *cristaticollis* Csiki 1934:26. New name for *Stephanocleonus cristatus* LeConte.

Cleonis cristatus; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).

Cleonis cristaticollis; O'Brien and Wibmer 1982 (in part; catal., distn., misident. *Stephanocleonus confusus*).

Problems in recognition.— This is one of two brachypterous species of North American *Stephanocleonus*. Unlike *S. confusus* individuals, in which elytral intervals 3 and 5 are elevated and convex throughout the greater part of their lengths, individuals of *S. cristaticollis* have only the extreme base of interval 3 slightly elevated and convex. They also do not possess the short recurved hair-like scales on the dorsal surface of the elytra that are found in *S. confusus*. Abdominal sternum VII of females has a pair of low rounded swellings, and the shape of the male aedeagus and form of the internal sac are distinctive (Figs. 32, 44).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEI, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 2. *Size.* Length, male, 13.8 mm; female, 13.6–14.1 mm. Width, male, 6.4 mm; female, 6.4–6.6 mm. *Head.* Frons with punctures large, sparse, shallow, indistinct; also with small elongate appressed white scales, dense laterally, sparse medially. *Rostrum.* Moderately robust (width at apex 0.86 times length in male; 0.91 in female) (Fig. 26). With well-developed, sharp, steeply declivous, low, median carina from above point of antennal insertion to base of rostrum; both basally and apically terminated at small, moderately deep fovea (Fig. 26). Rostrum with shallow trough immediately laterad of median carina, lateral margins sharp from above point of antennal insertion to anterior margin of eye, indicated by slightly raised rounded carina. Dorsal punctures large, sparse, shallow, indistinct. With scales small, elongate, appressed, white, dense laterally, sparse medially. *Pronotum.* Dorsal apical margin shallowly emarginate at middle. With low broad indistinct median carina in anterior one-half. Subapical constriction well defined laterally, not so dorsally; with shallow impressions laterad of median carina, but discontinuous with lateral portion of subapical constriction. Median basal area broadly, moderately deeply impressed. Dorsal punctures small, sparse and shallow; medially and laterally with distance between punctures subequal to or greater than diameter of single puncture; punctures irregularly impressed and dense in median basal area. *Prosternum.* With only shallow impression anterior to each procoxal cavity. *Elytra.* Moderately robust in general form (width at midlength 0.63 times length in male; 0.65 in female). In dorsal view with lateral margins evenly arcuate from midlength to base, humerus rounded, not distinct. Base of interval 3 swollen and convex, otherwise elytral intervals uniformly flat. Scales white small moderately dense; smaller and less dense in two posteromedially directed oblique patches, one at basal one-third from intervals 2 to 6, the other at apical one-third from intervals 2 to 4. With slightly elevated triangular glabrous shiny area at apical one-quarter at confluence of intervals 4 to 6. Suberect or erect vestiture lacking. *Wings.* Short (more or less equal to one-half length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small, distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as small elongate-oval pads on apical one-third of article 1, as large elongate-oval pads on apical three-quarters of article 2, and as large elongate-oval pads on more or less entire ventral surface of article 3; of female, pilose vestiture lacking from article 1, present as apical tufts of article 2, as large elongate-oval pads on apical three-quarters of article 3; of mesotarsus of male, as elongate-narrow pads on apical one-quarter of outer lobe, lacking from inner lobe of article 1, as elongate-narrow pads on apical three-quarters of article 2, as large elongate-oval pads on more or less entire ventral surface of article 3; of mesotarsus of female, lacking from articles 1 and 2, as elongate-narrow pads covering apical three-quarters of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-oval pads on apical three-quarters of article 3; of metatarsus of female, lacking from articles 1 to 3. *Abdomen.* Abdominal sternum VII in female with pair of rounded swellings at midlength; in male with apical margin slightly emarginate medially. *Genitalia.* Female (one examined). Abdominal sternum VIII with basal arm slightly expanded at apex; lateral arms broad, slightly inwardly and evenly arcuate throughout length (Fig. 38). Male (two examined). Abdominal sternum VIII with paired sclerite with inner apices acuminate (Fig. 32c). Aedeagus moderately robust; in lateral view markedly arcuate, more so in basal one-half, narrowed gradually from midlength to apex, apex markedly spatulate; in ventral view with apex symmetrical, medially produced into elongate rounded apical projection (Figs. 32a,b). Base of aedeagus with large ventral tubercle (Fig. 32a). Internal sac globose with dorsally directed median lobe on dorsal surface; with moderately large dorsolaterally directed paired lobe at midlength near dorsal margin (Fig. 44). In lateral view with basal paired sclerite and apical sclerite complex approximate (Fig. 44a).

Geographic distribution.— This species is known from only four specimens: two males and a female from southern Alberta (Medicine Hat, Monarch, Gorge Creek), and the female holotype from Utah (no further locality data given) (Fig. 205). Most published records of this species refer to *S. confusus.*

Chorological relationships.— The distribution of the few known specimens indicates that this species is probably broadly sympatric with *S. confusus* and narrowly sympatric with western *S. parshus.*

Stephanocleonus immaculatus Anderson, new species
(Figs. 21, 27, 33, 39, 45, 202)

Cleonus (*Stephanocleonus*) *plumbeus*; Fall and Cockerell 1907 (in part; check., misident.). Csiki 1934 (in part; catal., misident.).

Stephanocleonus plumbeus; Blatchley and Leng 1916 (in part; key, redesc., misident.). Leng 1919 (in part; check., poss. misident.). Leng 1920 (in part; catal., misident.). Danks 1981 (in part; check., poss. misident.).

Cleonus plumbeus; Leonard 1926 (in part; check., poss. misident.). Krombein 1979 (in part; prey, poss. misident.).

Cleonis plumbeus; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Type Material.— Holotype, male, with a red label "HOLOTYPE", "McMurray,/ Alta. V.10.53/ W.J. Brown", "HOLOTYPE/ *Stephanocleonus/ immaculatus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Allotype, female, with a red label "ALLOTYPE", "Gillam Man./ 10.VI.1949/ J.B. Wallis", "ALLOTYPE/ *Stephanocleonus/ immaculatus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Type locality, Fort McMurray, Alberta.

Paratypes. 10 males, 16 females. CANADA: Alberta: Township 93, Range 10, West 4 Meridian, 1.VI.85, B.F. and J.L. Carr, 1F (JLCC); McMurray, 21.VI.53, W.J. Brown, 1F (CNCI), 29.VII.53, G.E. Ball, 1M (RSAN), 22.VI.53, G.E. Ball, 1F (CNCI); Lac La Biche, NE shore, 30.VI.63, L.M. Kenakin, 1F (CWOB); Township 37, Range 18, West 5 Meridian, 18.VII.73, B.F. and J.L. Carr, 1F (RSAN); Township 35, Range 18, West 5 Meridian, 18.VIII.67, B.F. and J.L. Carr, 1F (JLCC); Exshaw, 27.VI.54, B.F. and J.L. Carr, 1M, 1F (JLCC); High Prairie, 26.VII.61, A.R. Brooks, 1F (CNCI). British Columbia: Canal Flats, 13.V.82, B.F. and J.L. Carr, 1M (RSAN). Manitoba: Gillam, 16.VI.50, F. McAlpine, 1F (CNCI); Aweme, 31.V.10, N. Criddle, 1F (USNM); Beaujou [sic], 24.VI.61, H.E. Milliron, 1M (CNCI). Northwest Territories: Fort Smith, 17.V.50, J.B. Wallis, 1F (CNCI), 16.VI.50, W.G. Helps, 1F (CNCI). Ontario: Lake Superior, Whitefish Point, 46°38'N 84°33'W, Hubbard and Schwarz, 1M, 1F (USNM). Saskatchewan: Junction Highways 2 and 165 east, 22.VI.85, B.F. and J.L. Carr, 1M, 1F (JLCC); Hudson Bay, 9.VII.54, Brooks-Wallis, 1M, 1F (CNCI).

UNITED STATES OF AMERICA: Colorado: Douglas County, 19.IV.15, 1M (CASC). Minnesota: 1F (USNM). Nebraska: Lincoln, 29.VI., Wolcott, 1F (UNSM). South Dakota: Englewood, Haggard, 1M (UNSM).

Derivation of specific epithet.— From the Latin "*im*" meaning not, and "*macula*" meaning spot or mark. This name is used in reference to the lack of distinct elytral markings in most individuals of this species.

Problems in recognition.— This is the only species of North American *Stephanocleonus* in which the elytra are more or less uniformly covered with small white scales and in which most specimens lack a distinct pattern of elytral maculations (Fig. 21). Most specimens also lack the small triangular shiny glabrous area at the confluence of intervals 4 to 6 which is found in all other North American *Stephanocleonus* (Fig. 21). The shape of the male aedeagus and form of the internal sac are also distinctive (Figs. 33, 45).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 3. *Size*. Length, male, 13.3–15.6 mm; female, 14.8–16.8 mm. Width, male, 5.9–6.8 mm; female, 6.8–7.5 mm. *Head*. Frons with punctures large, moderately dense, moderately deep, many punctures longitudinally confluent, appearance longitudinally rugose; also with small broad appressed white scales, sparse laterally, absent to very sparse medially. Most specimens with slightly raised carina on vertex. *Rostrum*. Moderately robust, slightly more so in females (width at apex 0.80-0.95 times length in male; 0.79-0.96 in female) (Fig. 27). With well-developed, sharp, steeply declivous, high, median carina from above point of antennal insertion to base of rostrum; both basally and apically terminated at small, moderately deep fovea (Fig. 27). Rostrum flat from immediately laterad of median carina to lateral margins, lateral margins rounded to sharp from above point of antennal insertion to anterior margin of eye. Dorsal punctures large, moderately dense, moderately deep, many punctures confluent. With scales small uniformly dense, elongate-narrow appressed, white. *Pronotum*. Dorsal apical margin not or shallowly emarginate at middle. With low broad distinct median carina in anterior one-half. Subapical constriction slightly to well defined laterally, not so dorsally; with shallow impressions laterad of median carina, but discontinuous with lateral portion of subapical constriction. Median basal area narrowly, shallowly impressed. Dorsal punctures moderately large, dense and moderately deep; medially, the distance between punctures less than diameter of individual puncture, some punctures confluent or nearly so and irregularly impressed; laterally, distance between punctures subequal to diameter of individual puncture. *Prosternum*. With only very shallow impression anterior to each procoxal cavity. *Elytra*. Moderately robust in general form (width at midlength 0.58-0.68 times length in male; 0.56-0.67 in female) (Fig. 21). In dorsal view with lateral margins straight, slightly convergent from slightly past midlength to base, humerus acute, very distinct (Fig. 21). All elytral intervals more or less flat. Scales white, small, dense, no distinct maculations present (Fig. 21). Some specimens with a slightly elevated, small, triangular, glabrous, shiny area at apical one-quarter at confluence of intervals 4 to 6. Suberect or erect vestiture lacking. *Wings*. Long (greater than length of elytra). *Legs*. Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth moderately large, distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male elongate-narrow pads on apical one-quarter to one-half of article 1, as large elongate-oval pads on apical three-quarters to more or less entire ventral surface of articles 2 and 3; of female, pilose vestiture lacking from article 1, as apical tufts to elongate-narrow pads on apical one-half of article 2, as elongate-oval pads on apical three-quarters of article 3; of mesotarsus of male, lacking from, to as an elongate-narrow pad on apical one-third of outer lobe of article 1, as elongate-narrow pads on apical three-quarters of article 2, as large elongate-oval pads on apical three-quarters to more or less entire ventral surface of article 3; of mesotarsus of female, lacking from article 1, lacking from, to as elongate-narrow pad on apical one-half of outer lobe of article 2, as large elongate-oval pads on apical two-thirds of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-narrow pads on apical two-thirds of article 3; of metatarsus of female, lacking from articles 1 and 2, as apical tufts to small elongate-oval pads on apical one-half of article 3. *Abdomen*. Abdominal sternum VII in female evenly rounded, not tumescent; in male with apical margin slightly emarginate medially. *Genitalia*. Female (five examined). Abdominal sternum VIII with basal arm expanded at apex; lateral arms broad, inwardly arcuate at midlength (Fig. 39). Male (six examined). Abdominal sternum VIII with paired sclerite with inner apices rounded (Fig. 33c). Aedeagus elongate-narrow; in lateral view slightly and evenly arcuate throughout length, narrowed from approximately apical one-third to apex, apex slightly spatulate; in ventral view with apex symmetrical, medially produced into truncate apical projection (Figs. 33a,b). Base of aedeagus with at most small ventral tubercle (Fig. 33a). Internal sac elongate with small laterally directed paired lobe near ventral margin at or slightly beyond midlength; median dorsal pocket high, with large dorsolaterally directed paired lobe at basal one-third near ventral margin, separated from base of median pocket by distinct trough (Fig. 45). In lateral view with basal paired sclerite and apical sclerite complex widely separated (Fig. 45a).

Geographic distribution.— This species is known from widely scattered localities in the southwestern Northwest Territories, northern Manitoba, and central Ontario, south in the west to Colorado and Nebraska (Fig. 202).

Natural history.— A single adult has been collected on *Rosa* sp. (Rosaceae).

Chorological relationships.— his species is broadly sympatric throughout the northern part ofits range with *S. plumbeus* and *S. parshus*, and is narrowly sympatric in the western part of its range with *S. confusus*.

Stephanocleonus parshus Anderson, new species
(Figs. 28, 34, 40, 46, 203)

Cleonus (*Stephanocleonus*) *plumbeus*; Casey 1891 (key). Csiki 1934 (in part; catal., misident.). Kissinger 1964 (biol., misident.).

Stephanocleonus plumbeus; Blatchley and Leng 1916 (in part; key, redesc., misident.). Leng 1919 (in part; check., poss.

misident.). Leng 1920 (in part; catal., misident.). Marcovitch 1923 (biol., redesc., larvae, misident.). Danks 1981 (in part; check., poss. misident.).

Cleonus plumbeus; Leonard 1926 (in part; check., poss. misident.). Bleasdell 1937 (check., prob. misident.). Krombein 1979 (in part; prey, poss. misident.).

Cleonis plumbeus; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Type Material.— Holotype, male, with a red label "HOLOTYPE", "Chalk River, Ont./ May 16, 1938/ N.R. Brown", "HOLOTYPE/ *Stephanocleonus/ parshus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Allotype, female, with a red label "ALLOTYPE", "Tp. 36 Rge. 15/ W.5 Mer Alberta/ 16.VII.1973/ B&J Carr Lot 3", "ALLOTYPE/ *Stephanocleonus/ parshus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Type locality, Chalk River, Ontario.

Paratypes. 39 males, 43 females. CANADA: Alberta: Township 24, Range 8, West 5 Meridian, 8.VII.82, B.F. and J.L. Carr, 1M (RSAN); Bragg Creek, 31.V.75, F.A.H. Sperling, 1M, 1F (RSAN); Pincher Creek, 20.VI.61, H.E. Milliron, 1M (CNCI); McMurray, 4.VI.53, W.J. Brown, 1M (CNCI), 6.VI.53, W.J. Brown, 1F (CNCI); Township 25, Range 3, West 5 Meridian, 7.VI.73, B.F. and J.L. Carr, 2M (JLCC, RSAN); Township 29, Range 5, West 5 Meridian, 28.VI.64, B.F. and J.L. Carr, 1M (JLCC); Calgary, 28.VI.64, B.F. and J.L. Carr, 1M (RSAN); Exshaw, 27.VI.54, B.F. and J.L. Carr, 1M (JLCC), 19.V.60, J.L. Carr, 1M (JLCC); Willow Creek, 9.VIII.28, H. Richmond, 1M (CASC); Ghost Dam, B.F. and J.L. Carr, 1F (JLCC); Edmonton, 26.V.19, F.S. Carr, 1M, 1F (UASM), 14.V.20, F.S. Carr, 1F (UASM), 13.V.18, F.S. Carr, 1M (UASM); Medicine Hat, 13.VI.32, F.S. Carr, 2M, 1F (UASM); Crow's Nest Pass, 9.VI.30, J.H. Pepper, 1M (CNCI); Beaverlodge, 1F (UASM); near Josephburg, 53°41'N 113°55'W, 23.V.79, K. Shaw and J. Sutcliffe, 1F (UASM). British Columbia: Rolla, 21.VII.27, Vroom, 1F (CASC); Pouce Coupe, 1.VII.27, Vroom, 1F (CASC); Baynes Lake, 9.V.76, B.F. and J.L. Carr, 1F (JLCC); Canal Flats, 13.V.82, B.F. and J.L. Carr, 1M, 1F (JLCC); Skookumchuck, 30.V.84, B.F. and J.L. Carr, 1M (JLCC). Manitoba: Aweme, 12.VIII.29, R.H. Handford, 1F (RSAN), 2.VII.29, N. Criddle, 1M (CNCI), 20.IV.06, N. Criddle, 1F (CNCI), 31.V.10, N. Criddle, 1F (USNM), 9.VI.14, N. Criddle, 1M, 1F (CNCI), 24.IX.28, N. Criddle, 1M (CNCI), VI, N. Criddle, 1M (USNM), 1.VII.05, N. Criddle, 1F (USNM), V.12, N. Criddle, 1M (USNM), 3.VIII., N. Criddle, 1F (USNM); Township 14, Range 105, 12.V.24, J.B. Wallis, 1F (CNCI); Riding Mountain National Park, 12.VI.38, W.J. Brown, 1F (CNCI); Melita, 8.VI.20, N. Criddle, 1F (CNCI); Shell River, VII.27, E. Criddle, 1F (CNCI); Winnipeg, 1F (USNM); Treesbank, 24.VI.48, Criddle, 1F (CNCI); Sandilands, 22.VI.30, W.J. Brodie, 1F (CNCI); 24km. w. Haddashville, 27.VI.84, I. Askevold, 1M (CWOB). Northwest Territories: Fort Wrigley, 27.IX.29, O. Bryant, 1M (CASC); Fort Simpson, Manners Creek, 11.VI.72, Smetana, 1F (CNCI). Ontario: Blackburn, 6.VI.32, W.J. Brown, 1F (CNCI); Ridgeville, VI.35, S.D. Hicks, 1F (CNCI); Toronto, 1M (USNM); Dunrobin, 18.V.77, J.E. O'Hara, 1M (RSAN). Quebec: Kazubazua, 25.V.33, W.J. Brown, 1M (CNCI); Fort Coulonge, 25.VI.19, J. Beaulne, 1M (CNCI). Saskatchewan: 8mi. e. Saskatoon, 17.VI.73, C.K. Starr, 1F (CWOB); Township 35, Range 6, West 3 Meridian, 20.VII.85, B.F. and J.L. Carr, 1M (JLCC); Pike Lake, 5.I.42, King & Glen, 1F (CNCI); Prince Albert, 4.VII.54, Brooks-Wallis, 1F (CNCI).

UNITED STATES OF AMERICA: Connecticut: New Hartford, 26.IV.20, Zappe, 1F (CWOB). Iowa: Ames, 1F (USNM). Maine: 1M (USNM). Massachusetts: Woodshole, 1F (CASC). Michigan: Emmet County, Mackinaw City, 28.VI.20, M.H. Hatch, 1M (USNM). Minnesota: 1F (CASC); Crow Wing County, Pelican Lake, 25.VIII.10, Wolcott, 1F (UNSM), 28.VIII.08, Wolcott, 1F (UNSM). Montana: Missoula, 16.V.04, 1F, 11.VII.04, 1M (USNM); Helena, Hubbard and Schwarz, 1F (USNM); Flathead County, Echo Lake, 31.V.35, Eichmann, 1F (MSU); Hamilton, 16.VIII.26, 1M (MSU); Lake County, 6.VII.36, 1M (MSU). Nebraska: Lincoln, VI., 1F (UNSM); Bellevue, 20.V.02, Bruner, 1M (UNSM). New Mexico: 1F (MCZC). South Dakota: Englewood, Haggard, 1F (UNSM). Tennessee: Knoxville, 12.IV.55, H. and A. Howden, 1F (HAHC), 17.V.57, H. and A. Howden, 1M (HAHC). Vermont: Bennington County, G.H. Horn, 1M (USNM); Lyndon, 22.VIII.00, Melander, 1M, 1F (OCUC).

Country unknown: Bridge, 31.V.14, 1F (CNCI).

Derivation of specific epithet.— An arbitrary combination of letters.

Problems in recognition.— Among macropterous North American *Stephanocleonus* species with elytral maculations, individuals of *S. parshus* can be recognized by the large deep and dense pronotal punctures, the distance between punctures distinctly less than the diameter of a puncture (Fig. 28a). As in individuals of *S. plumbeus*, the pronotum has the lateral subapical constriction not defined dorsally and has the apical margin entire and not emarginate. In addition to other features, females of *S. parshus* can further be distinguished from those of other North American macropterous species by the metatarsus with article 3 with elongate pilose pads; males can be distinguished from males of other species by the distinctive shape of the aedeagus and form of the internal sac (Figs. 34, 46).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 4. *Size.* Length, male, 10.4–12.0 mm; female, 10.9–13.6 mm. Width, male, 4.8–5.6 mm; female, 5.0–5.9 mm. *Head.* Frons with punctures large, dense, moderately deep, many punctures confluent, appearance longitudinally rugose; also with small elongate-narrow appressed white, dense scales. Most specimens with slightly raised carina on vertex. *Rostrum.* Moderately elongate-narrow, slightly more so in males (width at apex 0.76-0.84 times length in male; 0.77-0.84 in female) (Fig. 28). With well-developed, sharp, gradually declivous, high, median carina from above point of antennal insertion to base of rostrum; both basally and apically terminated at small, shallow fovea (Fig. 28). Rostrum rounded to flat from immediately laterad of median carina to lateral margins, lateral margins rounded to sharp from above point of antennal insertion to anterior margin of eye, indicated in very few specimens by slightly raised rounded carina. Dorsal punctures large, moderately dense, moderately deep, many confluent. With scales small, elongate-narrow, appressed, white, dense. *Pronotum.* Dorsal apical margin not or shallowly emarginate at middle. With low, broad, distinct median carina in anterior one-half. Subapical constriction slightly to well defined laterally, not so dorsally; with shallow impressions laterad of median carina, but discontinuous with lateral portion of subapical constriction. Median basal area narrowly, shallowly impressed. Dorsal punctures large, dense and deep; medially, most confluent and irregularly impressed; laterally, distance between punctures much less than diameter of individual puncture (Fig. 28a). *Prosternum.* With shallow impression anterior to each procoxal cavity, and with or without slightly developed transverse swelling anterior to each impression. *Elytra.* Moderately robust in general form (width at midlength 0.61–0.68 times length in male; 0.59-0.65 in female) (Fig. 22). In dorsal view with lateral margins straight and convergent from midlength to base, humerus obtuse, distinct. All elytral intervals more or less uniformly flat. Scales white small moderately dense; smaller and less dense in two posteromedially directed oblique patches, one at basal one-third from intervals 2 to 6, other at apical one-third from intervals 2 to 4. With slightly elevated triangular glabrous shiny area at apical one-quarter at confluence of intervals 4 to 6. Suberect or erect vestiture lacking. *Wings.* Long (equal to or greater than length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small to moderately large, indistinct to distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-oval pads on apical one-half of article 1, as large elongate-oval pads on apical three-quarters of article 2, and as large elongate-oval pads on more or less entire ventral surface of article 3; of female, pilose vestiture lacking from article 1, present as elongate-oval pads on apical one-half of article 2, as elongate-oval pads on more or less entire ventral surface of article 3; of mesotarsus of male, lacking from to present as an apical tuft of outer lobe of article 1, as elongate-narrow pads on apical three-quarters of article 2, as large elongate-oval pads on more or less entire ventral surface of article 3; of mesotarsus of female, lacking from article 1, lacking from to present as an elongate-narrow pad on apical one-half of outer lobe of article 2, as large elongate-oval pads on more or less entire ventral surface of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-oval pads on apical one-third to one-half of article 3; of metatarsus of female, lacking from articles 1 and 2, as an elongate-oval pad on apical one-third to one-half of outer lobe and apical one-half to two-thirds of inner lobe of article 3. *Abdomen.* Abdominal sternum VII in female evenly rounded, not tumescent; in male with apical margin slightly emarginate medially. *Genitalia.* Female (three examined). Abdominal sternum VIII with basal arm expanded at apex; lateral arms narrow, inwardly arcuate at midlength (Fig. 40). Male (12 examined). Abdominal sternum VIII with paired sclerite with inner apices rounded (Fig. 34c). Aedeagus elongate-narrow; in lateral view slightly and evenly arcuate throughout length, narrowed from approximately apical one-third to apex, apex slightly spatulate; in ventral view with apex symmetrical, medially produced into rounded apical projection (Figs. 34a,b). Base of aedeagus with at most small ventral tubercle. Internal sac elongate with large dorsally-directed paired lobe on dorsal surface immediately beyond midlength; median dorsal pocket lacking, with large dorsolaterally directed paired lobe at basal one-third near dorsal margin (Fig. 46). In lateral view with basal paired sclerite and apical sclerite complex widely separated (Fig. 46a).

Geographic distribution.— This species is widely distributed in North America from Maine and Massachusetts south to Tennessee, west to Nebraska and Iowa in the south, British Columbia and Alberta in the north (Fig. 203). A single state record for New Mexico is in the Horn collection at the Museum of Comparative Zoology, Harvard University.

Natural history.— At Knoxville, Tennessee, Marcovitch (1923) records larvae of this species feeding on roots of strawberry in June, July, December and March. Pupae were found on July 13 and a single adult emerged on July 25. Although identified as *S. plumbeus*, the description provided notes that the thorax is coarsely punctured. This, and the verified occurence of only *S. parshus* at Knoxville, indicates that this is the species to which he referred.

Chorological relationships.— This, the most widespread species of North American *Stephanocleonus*, is sympatric in the northern part of its range with *S. plumbeus*; in the northeastern part of its range with *S. immaculatus*; and, in the western part of its range with *S. cristaticollis* and *S. confusus*.

Stephanocleonus plumbeus LeConte
(Figs. 22, 29, 35, 41, 47, 205)

Cleonus obliquus; LeConte 1850 (check., misident.).

Stephanocleonus plumbeus LeConte 1876a:146. Lectotype (here designated), male, one of an undetermined number of syntypes, labelled with a pale blue circle (=Lake Superior), "Type/ 5259", and with card with abdomen attached, microvial containing genitalia, and my designation label "*Stephanocleonus/ plumbeus* LeC./ LECTOTYPE/ desig. Anderson" (MCZC). Type locality, north shore of Lake Superior. LeConte 1876a (in part; desc., misident. *Stephanocleonus confusus*, mixed type series). Henshaw 1881–1882 (in part; check., misident. *Stephanocleonus confusus*). Henshaw 1885 (in part; check., misident. *Stephanocleonus confusus*). Wickham 1902 (check., misident. *Stephanocleonus confusus*). Wickham 1909 (check., misident. *Stephanocleonus confusus*). Blatchley and Leng 1916 (in part; key, redesc., misident. *Stephanocleonus immaculatus*, *Stephanocleonus parshus*). Leng 1919 (in part; check., poss. misident. *Stephanocleonus immaculatus*, *Stephanocleonus parshus*, *Stephanocleonus confusus*, *Stephanocleonus stenothorax*). Leng 1920 (in part; catal., misident. *Stephanocleonus immaculatus*, *Stephanocleonus parshus*, *Stephanocleonus confusus*). Marcovitch 1923 (biol., redesc., larvae, misident. *Stephanocleonus parshus*). Danks 1981 (in part; check., poss. misident. *Stephanocleonus immaculatus*, *Stephanocleonus parshus*, *Stephanocleonus confusus*, *Stephanocleonus stenothorax*).

Cleonus (*Stephanocleonus*) *plumbeus*; Casey 1891 (key). Fall and Cockerell 1907 (check., misident. *Stephanocleonus immaculatus*, *Stephanocleonus confusus*). Csiki 1934 (in part; catal., misident. *Stephanocleonus immaculatus*, *Stephanocleonus parshus*, *Stephanocleonus confusus*).

Cleonus plumbeus; Leonard 1926 (in part; check., poss. misident. *Stephanocleonus immaculatus*, *Stephanocleonus parshus*). Bleasdell 1937 (check., poss. misident. *Stephanocleonus parshus*). Kissinger 1964 (biol., misident. *Stephanocleonus parshus*). Krombein 1979 (in part; as prey, poss. misident. *Stephanocleonus immaculatus*, *Stephanocleonus parshus*, *Stephanocleonus confusus*).

Cleonis plumbeus; O'Brien and Wibmer 1982 (in part; catal., distn., misident. *Stephanocleonus immaculatus*, *Stephanocleonus parshus*, *Stephanocleonus confusus*).

Problems in recognition.— Among North American *Stephanocleonus* species that are macropterous and possess maculated elytra, this species can be recognized by the following combination of characters: pronotum with lateral subapical constriction not defined dorsally; apical margin of pronotum entire, not emarginate at middle; and pronotal punctures small, shallow and sparse, distance between punctures greater than diameter of individual puncture (Fig. 29a). Females of this species have the metatarsus with article 3 lacking ventral pilose pads.

Individuals of this species are most likely to be confused with those of *S. parshus*, but the two can be readily separated by characters noted in the key and above.

Notes about synonymy.— I have been unable to ascertain the exact constitution of the type series of *S. plumbeus* LeConte. The species was described from an unspecified number of specimens from the north shore of Lake Superior and from New Mexico. In the LeConte collection at the Museum of Comparative Zoology, there are three specimens labelled as types; two specimens with pale blue circles attached (= Lake Superior), and a single specimen labelled "N.M." (= New Mexico). I have selected one of the two Lake Superior specimens as lectotype and believe that these three specimens likely initially constituted the type series of *S. plumbeus*. The other specimen from Lake Superior is conspecific with the lectotype, but the specimen labelled "N.M." is *S. confusus*.

Other specimens in the LeConte and Horn collections, but not labelled as types and therefore questionably part of the type series, include one of *S. immaculatus* with no locality data; two of *S. plumbeus* with no locality data; and one of *S. parshus* from New Mexico.

Description.— *Specimens examined.* 13 males, 11 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 5. *Size.* Length, male, 10.9–13.0 mm; female, 11.2–15.6 mm. Width, male, 4.9–6.0 mm; female, 5.2–7.2 mm. *Head.* Frons lacking distinct large punctures; uniformly covered with small elongate-narrow appressed white scales. Some specimens with slightly raised carina on vertex. *Rostrum.* Moderately elongate-narrow to moderately robust, (width at apex 0.82–0.90 times length in male; 0.82–0.94 in female) (Fig. 29). With well-developed, sharp, gradually declivous, high, median carina from above point of antennal insertion to base of rostrum; basally terminated at small, shallow fovea

(Fig. 29a). Rostrum rounded from immediately laterad of median carina to lateral margins, lateral margins rounded from above point of antennal insertion to anterior margin of eye. Dorsally lacking distinct large punctures. With small elongate-narrow appressed white, dense scales. *Pronotum.* Dorsal apical margin not or shallowly emarginate at middle. With sharp distinct median carina in anterior one-half. Subapical constriction slightly defined laterally, not so dorsally; with shallow impressions laterad of median carina, but discontinuous with lateral portion of subapical constriction. Median basal area broadly, shallowly to moderately deeply impressed. Dorsal punctures uniformly small, sparse and shallow, distance between punctures greater than diameter of one puncture (Fig. 29a). *Prosternum.* With shallow impression anterior to each procoxal cavity, and slightly developed transverse swelling anterior to each impression. *Elytra.* Moderately robust in general form (width at midlength 0.60-0.64 times length in male; 0.57-0.62 in female) (Fig. 22). In dorsal view with lateral margins straight and convergent from midlength to base, humerus obtuse, distinct (Fig. 22). All elytral intervals more or less uniformly flat. Scales white small moderately dense; smaller and less dense in two posteromedially directed oblique patches, one at basal one-third from intervals 2 to 6, the other at apical one-third from intervals 2 to 4 (Fig. 22). With slightly elevated triangular glabrous shiny area at apical one-quarter at confluence of intervals 4 to 6. Suberect or erect vestiture lacking. *Wings.* Long (equal to or greater than length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small to moderately large, indistinct to distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-oval pads on apical one-third of article 1, as large elongate-oval pads on apical three-quarters of article 2, and as large elongate-oval pads on more or less entire ventral surface of article 3; of female, pilose vestiture lacking from articles 1 and 2, present as elongate-oval pads on apical three-quarters of article 3; of mesotarsus of male, lacking from to as apical tuft of outer lobe of article 1, as elongate-narrow pads on apical three-quarters of article 2, as large elongate-oval pads on apical three-quarters of article 3; of mesotarsus of female, lacking from articles 1 and 2, as small elongate-narrow pads on apical one-third of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-oval pads on apical three-quarters of article 3; of metatarsus of female, lacking from articles 1 to 3. *Abdomen.* Abdominal sternum VII in female evenly rounded, not tumescent; in male with apical margin slightly emarginate medially. *Genitalia.* Female (three examined). Abdominal sternum VIII with basal arm expanded at apex; lateral arms narrow, inwardly arcuate at midlength (Fig. 41). Male (seven examined). Abdominal sternum VIII with paired sclerite with inner apices truncate (Fig. 35c). Aedeagus elongate-narrow; in lateral view markedly arcuate, more so in basal one-half, narrowed from approximately apical one-third to apex, apex slightly spatulate; in ventral view with apex asymmetrical, produced into rounded apical projection (Figs. 35a,b). Base of aedeagus with at most small ventral tubercle. Internal sac elongate with small dorsolaterally directed paired lobe on dorsal surface immediately beyond midlength; median dorsal pocket high, with large dorsolaterally directed paired lobe at basal one-third near ventral margin, separated from base of median pocket by trough (Fig. 47). In lateral view with basal paired sclerite and apical sclerite complex widely separated (Fig. 47a).

Geographic distribution.— This species is known from widely scattered localities from Newfoundland west to Alberta (Fig. 205).

Chorological relationships.— This species is sympatric throughout the central and western part of its range with *S. parshus* and *S. immaculatus*. Individuals of these three species have been collected within a few days of each other at Fort McMurray, Alberta.

Stephanocleonus stenothorax Anderson, new species

(Figs. 23, 30, 36, 42, 48, 204)

Stephanocleonus plumbeus; Leng 1919 (in part; check., poss. misident.). Danks 1981 (in part; check., poss. misident.).

Type Material.— Holotype, male, with a red label "HOLOTYPE", "YT. Bluefish caves/ 67°08'N 140°48'W/ 2000' 4.vii.1983/R.J. Cannings", "HOLOTYPE/ *Stephanocleonus*/ *stenothorax*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Allotype, female, with a red label "ALLOTYPE", "YUKON: Dog. Ck./ 30.VII.77/ R.E. Roughley", "ALLOTYPE/ *Stephanocleonus*/ *stenothorax*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CNCI). Type locality, Bluefish Caves archaeological site, Yukon Territory.

Paratypes. 12 males, 11 females. Canada: Yukon Territory, Keele Range, Bluefish Caves archaeological site, 67°08'N 140°47'W, 1983, J. Cinq-Mars, 12M, 11F. (CNC, CWOB, JVM, RSAN, USNM, ZIL)

Derivation of specific epithet.— From the Greek "*stenos*" meaning narrowed, and "*thorax*" meaning breastplate. This name is used in reference to the apically narrowed form of the pronotum.

Problems in recognition.— Among North American species of *Stephanocleonus* with maculate elytra, individuals of this species are recognized by the pronotum with the lateral subapical constriction continued and well-defined dorsally, and with the apical margin shallowly emarginate at the middle. The glabrous shiny tubercle at the confluence of elytral intervals 4 to 6 is markedly elevated and lateral arms of abdominal sternum VIII of the female are very broad and medially approximate to continguous near their apices (Fig. 42). The shape of the aedeagus of the male is also distinctive (Figs. 36a,b).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEI, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 6. *Size.* Length, male, 12.5–13.1 mm; female, 12.8–14.9 mm. Width, male, 5.3–6.2 mm; female, 5.6–6.2 mm. *Head.* Frons with punctures large, moderately dense and deep, many punctures confluent in some specimens, surface thus longitudinally rugose; uniformly covered with small broad appressed white scales, dense laterally, sparse medially. Most specimens with slightly raised carina on vertex. *Rostrum.* Robust, (width at apex 0.90-0.95 times length in male; 0.90–1.00 in female) (Fig. 30). With well-developed, sharp, steeply declivous, low, median carina from above point of antennal insertion to base of rostrum; basally and apically terminated at small, shallow fovea (Fig. 30a). Rostrum flat from immediately laterad of median carina to lateral margins, lateral margins rounded to sharp from above point of antennal insertion to anterior margin of eye. Dorsally with punctures large moderately dense and deep, many confluent in some specimens, surface thus longitudinally rugose. With small elongate-narrow appressed white, scales; dense laterally, sparse medially. *Pronotum.* Dorsal apical margin broadly and moderately deeply emarginate at middle. With sharp distinct median carina in anterior one-half. Subapical constriction well defined laterally and dorsally; with distinct moderately deep impressions laterad of median carina continuous with lateral portion of subapical constriction. Median basal area broadly and moderately deeply impressed. Dorsal punctures small, sparse and shallow laterally and medially (except basally at middle where punctures are dense, deep, approximate and irregularly impressed), distance between punctures subequal to or greater than diameter of one puncture. *Prosternum.* With shallow impression anterior to each procoxal cavity, and with or without slightly to moderately developed transverse swelling anterior to each impression. *Elytra.* Moderately elongate-narrow in general form (width at midlength 0.57-0.60 times length in male; 0.55-0.61 in female) (Fig. 23). In dorsal view with lateral margins straight and convergent from midlength to base, humerus obtuse, distinct (Fig. 23). All elytral intervals more or less uniformly flat. Scales white small moderately dense; smaller and less dense in two posteromedially directed oblique patches, one at basal one-third from intervals 2 to 6, other at apical one-third from intervals 2 to 4 (Fig. 23). With markedly elevated triangular glabrous shiny area at apical one-quarter at confluence of intervals 4 to 6. Suberect or erect vestiture lacking. *Wings.* Long (equal to or greater than length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth moderately large, distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-oval pads on apical one-half of article 1, as large elongate-oval pads on apical two-thirds of article 2, and as large elongate-oval pads on more or less entire ventral surface of article 3; of female, pilose vestiture lacking from articles 1 and 2, present as elongate-oval pads on apical one-half of article 3; of mesotarsus of male, lacking from to as apical tuft of outer lobe of article 1, as elongate-narrow pads on apical two-thirds of outer lobe and apical one-half on inner lobe of article 2, as large elongate-oval pads on apical three-quarters of article 3; of mesotarsus of female, lacking from articles 1 and 2, as elongate-oval pad on apical one-half of outer lobe and as apical tuft of inner lobe of article 3; of metatarsus of male, lacking from articles 1 and 2, as elongate-oval pads on apical two-thirds of article 3; of metatarsus of female, lacking from articles 1 to 3. *Abdomen.* Abdominal sternum VII in female evenly rounded, not tumescent; in male with apical margin slightly emarginate medially. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm expanded at apex; lateral arms very broad, medially approximate or contiguous near apices, inwardly arcuate at midlength (Fig. 42). Male (four examined). Abdominal sternum VIII with paired sclerite with inner apices truncate (Fig. 36c). Aedeagus elongate-narrow; in lateral view slightly and evenly arcuate throughout length, narrowed from approximately apical one-third to apex, apex not spatulate; in ventral view with apex symmetrical, medially rounded but not produced into distinct apical projection (Figs. 36a,b). Base of aedeagus with at most small ventral tubercle. Internal sac elongate with small dorsolaterally directed paired lobe on dorsal surface at midlength; median dorsal pocket moderately high, with moderately large dorsolaterally directed paired lobe at basal one-third near dorsal margin (Fig. 48). In lateral view with basal paired sclerite and apical sclerite complex widely separated (Fig. 48a).

Geographic distribution.— This species is known only from two localities in the northern Yukon Territory (Fig. 204).

Natural history.— Most specimens of the type series were collected in unbaited pitfall traps set in a partly forested limestone upland and fell-field. They were collected in association with *Lepidophorus lineaticollis* Kirby and *Vitavitus thulius* Kissinger and several species of dry-tundra Carabidae.

Chorological relationships.— This species is allopatric to all other *Stephanocleonus* species.

Genus *Apleurus* Chevrolat

Apleurus Chevrolat 1873:78. Gender, masculine. Type species *Apleurus fossus* Chevrolat (= *Cleonus lutulentus* LeConte) by subsequent designation (Casey 1891:186). Chevrolat 1873 (in part; catal., sp. desc.). Faust 1904 (key).

Notes about synonymy.— See "Notes about synonymy" section under subgenus *Apleurus*.

Diagnosis.— Adult Cleoninae with moderately elongate-narrow to very robust body form (Figs. 24, 68–80). Eye elongate teardrop shaped, slightly to moderately prominent and convex in dorsal view (Figs. 81–88). Rostrum with median carina lacking to variously developed (Figs. 84–86). Pronotum punctate, anterolateral margin of pronotum straight to with variously developed acute postocular projection; postocular vibrissae long, of unequal length and longest behind base of eye (Figs. 81–88). Disk with elongate white moderately large moderately dense scales present in lateral stripe of variable width, small and fine in moderately broad to very broad apically narrowed median stripe, and variously small and fine to moderately large and elongate along lateral margins; median area largely black in color, underlying dark cuticle not obscured by overlying scales (Figs. 24, 68–80). Antenna with funiculus with article 1 longer than, to more or less equal in length to, article 2; article 2 more or less as long as wide, to slightly longer than wide (Figs. 81–88). Ventral tarsal pilosity various but reduced to some extent (not extended over entire ventral surface of tarsal article) to lacking entirely from at least more basal tarsal articles (especially of metatarsus). Tibia with corbel ridge sharp (Fig. 6). Prosternum with swellings absent or present, if present, located immediately anterior to each prosternal impression (Fig. 7). Female with abdominal sternum VIII lacking basal arm (Figs. 89–96).

Description.— *Size*. Small to large, moderately elongate-narrow to very robust in body form. *Mouthparts*. Prementum flat to slightly swollen, lacking or with as many as five large setae on each side (Figs. 61–63). Maxillary palpus with palpifer with large seta, stipes with or without large seta (Figs. 64–65). Labial palpi separated by a distance varied from subequal to, to twice width of basal article of a labial palpus (Figs. 61–63). *Rostrum*. Moderately to markedly robust, not medially tumescent (Figs. 81–88). Median carina lacking to low, moderately rounded to sharp (Figs. 81–88). Epistoma not swollen, produced anteriorly, with apical margin emarginate (Fig. 81b) or rounded medially (Figs. 82b–88b). Antenna with funiculus with article 1 subequal in length to, to slightly longer than article 2 (Figs. 81a–88a); apical three articles of club with placoid sensillae. *Head*. Eye elongate teardrop shaped, slightly to moderately prominent and convex in dorsal view (Figs. 81–88). Area behind eye with moderately deep irregular punctures. Upper margin of eye rounded to sharp, frons convex to more or less flat. *Vestiture*. Dorsum with suberect or erect vestiture lacking to very long and dense; with simple elongate-narrow appressed white scales of variable size and density. *Prothorax*. Dorsal surface of pronotum punctate. Pronotum with median basal area shallowly to deeply impressed; anterolateral margin, behind eyes, straight to with variously developed acute postocular projection; postocular vibrissae long, of unequal length and longest behind base of eye (maximum length greater than or equal to one-half width of eye) (Figs. 81a–88a); disk with elongate white moderately large moderately dense scales present in lateral stripe of various width, small and fine in moderately broad to very broad apically narrowed median stripe, and variously small and fine to moderately large and elongate along lateral margins; median area largely black in color, underlying dark cuticle not obscured by overlying scales (Figs. 24, 68–80). Prosternum with slight to moderately deep impression anterolaterad of each procoxal cavity; with or without slight to markedly developed swelling immediately anterior to each prosternal impression (Fig. 7). *Legs*. Foretarsus moderately broad, articles 2 and 3 more or less subequal in length, at most only slightly longer than broad; article 1 only slightly longer than articles 2 or 3; article 3 moderately deeply bilobed. Meso- and especially metatarsus slightly more elongate-narrow, article 2 slightly to distinctly longer than article 3; article 1 distinctly longer than articles 2 or 3; article 3 moderately deeply bilobed. Ventral tarsal pilosity various but reduced to some extent (not covering entire ventral surface of a tarsal article) to lacking entirely from at least more basal tarsal articles (especially of metatarsus). Claws variously connate from near base to through basal one-third, slightly to markedly divergent. Foretibia with inner margin with at most only small denticles in apical one-half; near apex with second spur very slightly to moderately well-developed. Metatibia of male with ventral margin of uncus evenly rounded. Tibia with corbel ridge sharp (Fig. 6). *Wings*. Absent or present (various in length). *Elytra*. Intervals, except humerus and bases of intervals 3 and 5 flat, to with sutural interval and intervals 3, 5, 7, and 9 variously slightly to markedly swollen and convex. Striae distinctly punctate. Humeri acute to rounded. Scale pattern various (Figs. 24, 68–80). *Abdomen*. Ventral surface with small shiny glabrous patches, each with single small appressed scale to uniformly covered with fine dense hair-like scales. Abdominal sternum VII in males with apical margin at middle with or without small dorsally directed median tooth. Abdominal terga VII and VIII of female not, or slightly to markedly longitudinally carinate. *Genitalia*. Female. Abdominal sternum VIII lacking basal arm (Figs. 89a–96a).

Gonocoxite II elongate triangular in form, apex not prolonged into marked lobe; stylus absent or present, small to moderately large in size; apical to slightly anteapical in position (Figs. 89b–96b). Spermathecal gland round (Fig. 60). Male. Abdominal sternum VIII with interior angle of each sclerite lacking basal projection to with basal projection slightly to markedly developed (Figs. 97f, 101e, 103e). Aedeagus moderately robust, in lateral view more or less evenly arcuate throughout length; apex not spatulate (Figs. 97d, 98c–104c). Internal sac various; with dorsal median pocket low to high; apical and dorsal median pockets individually distinct; various lobes present, lobe A absent (Figs. 97a,b–104a,b). Apical sclerite complex with individual sclerites scythe-like (Figs. 97c, 98d–104d).

Comparisons.— Species of *Apleurus* are most likely to be confused with the Palearctic *Chromoderus* and the South African *Cnemodontus*. Members of these three genera either lack pronotal postocular lobes entirely or possess variously developed acute postocular projections. *Apleurus* species are separated from species of these other two genera by the ventral tarsal pilosity reduced in extent and also by characters in the male genitalia (see "Phylogenetic Analysis" section). Species of *Pleurocleonus* also lack a pronotal postocular lobe but are readily separated from *Apleurus* by the possession of a low broad longitudinally sulcate median rostral carina, flat eyes, and characters of male and female genitalia.

In the New World, some *Apleurus* species may be confused with large *Cleonidius* species which lack a pronotal postocular lobe. Consultation of diagnoses and key characters will readly separate the two.

Checklist of included species.— Eight species, assigned to two subgenera, are included in this endemic New World genus. These species are:

Subgenus *Gibbostethus* Anderson, new subgenus
    1. A.(G.) hystrix (Fall)
Subgenus *Apleurus* Chevrolat
    2. *A.(A.) aztecus* (Champion)
    3. *A.(A.) lutulentus* (LeConte)
    4. *A.(A.) porosus* (LeConte)
    5. *A.(A.) angularis* (LeConte)
    6. *A.(A.) jacobinus* (Casey)
    7. *A.(A.) albovestitus* (Casey)
    8. *A.(A.) saginatus* (Casey)

Phylogenetic relationships.— See "Phylogenetic analysis" section.

Subgenus *Gibbostethus* Anderson, new subgenus

Dinocleus; Fall 1913 (in part; sp. desc.). Leng 1920 (in part; catal.).
Cleonus (*Dinocleus*); Csiki 1934 (in part; catal.).
Cleonis; O'Brien and Wibmer 1982 (in part; catal., distn.).

Derivation of name.— Derived from the Greek "*gibbos*" meaning protuberant or swollen, and "*stethos*" meaning chest or breast. This name is used in reference to the tumescent mesosternal process of members of the single species placed in this subgenus.

Type species.— *Dinocleus hystrix* Fall by monotypy.

Diagnosis.— *Apleurus* with moderately elongate-narrow body form (Fig. 24). Dorsal erect vestiture dense and long. Prementum with bases of labial palpi separated by distance more or less equal to twice width of basal article of labial palpus (Fig. 61). Maxillary palpus with palpifer with large seta (Fig. 65). Rostrum with epistoma with apical margin emarginate medially (Fig. 81b). Mesosternum with mesosternal process markedly tumescent and convex (Fig. 58). Female with abdominal sternum VIII with lateral arms arcuate (Fig. 89a);

gonocoxite II with stylus moderately large, apical in position (Fig. 89b). Male with abdominal sternum VIII with each sclerite with rounded interior angles, basal projections lacking (Fig. 97f); aedeagus in dorsal view markedly laterally expanded from midlength to apical one-third (Fig. 97e).

Included species.— *Apleurus (Gibbostethus) hystrix* Fall from southern California is the only species in the subgenus.

Phylogenetic relationships.— This subgenus is sister to the remainder of *Apleurus*. Recognition as a distinct subgenus is warranted by the primitive phylogenetic position of the species and the sister-group relationship with the remainder of *Apleurus*, by a restricted and likely relictual distribution (Fig. 212), and by various autapotypic character states and character states exhibited by *Gibbostethus* which although interpreted as evolved independently, are homoplasious in derived *Apleurus* species (see "Phylogeny" section).

Apleurus (Gibbostethus) hystrix (Fall), new combination
(Figs. 24, 58, 61, 65, 81, 89, 97, 212)

Dinocleus hystrix Fall 1913:41. Holotype (examined), male, labelled "Pasadena/ Cal.", "Feb.", "Not in/ Lec.Coll.", "TYPE", "M.C.Z./ Type/ 25191", "H.C.FALL/ COLLECTION", "*Dinocleus/ hystrix/* Fall" (MCZC). Type locality, Pasadena, California. Leng 1920 (catal.).
Cleonus (*Dinocleus*) *hystrix*; Csiki 1934 (catal.).
Cleonis hystrix; O'Brien and Wibmer 1982 (catal., distn.).

Problems in recognition.— A distinctive and easily recognized species, *A. hystrix* is characterized by the markedly tumescent mesosternal process (Fig. 58) and the rostrum with the apical margin of the epistoma emarginate medially (Fig. 81b). The markedly laterally expanded aedeagus of males is also characteristic of this species (Fig. 97e).

Although it is unlikely that *A. hystrix* may be confused with other species of *Apleurus*, individuals may be confused with species of *Cleonidius* because of their small size and more elongate general body form (Fig. 24). Among other characters, *A. hystrix* individuals can be separated from *Cleonidius* individuals by the presence in the former of low rounded swellings on the prosternum immediately anterior to the prosternal impressions (Fig. 7). Swellings may or may not be present in *Cleonidius* species, but if present are situated immediately anterior to the procoxal cavities, adjacent to the prosternal impression (Fig. 8).

Description.— *Specimens examined.* 18 males, 11 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEI, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 7. *Size.* Length, male, 7.0–9.5 mm; female, 8.0–10.6 mm. Width, male, 2.8–3.5 mm; female, 3.0–4.2 mm. *Head.* Eye very prominent and convex in dorsal view. Frons and vertex with dense, large, irregularly impressed, deep punctures. Frons also with dense, very long erect white hair-like scales. Area immediately behind posterior margin of eye with very large, deep, irregularly impressed punctures. Area above eyes slightly to moderately elevated above rest of frons (eyes apparently browed in anterior view). Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.69-0.85 times length in male; 0.70-0.82 in female) (Fig. 81). Median carina absent. Dorsal and lateral punctation dense, large, deep and irregularly impressed, some punctures longitudinally confluent medially. Dorsally, excluding epistoma, with dense, very long, erect white hair-like scales and dense very elongate-narrow recumbent white scales. In lateral view only slightly declivous from point of antennal insertion to apex (Fig. 81a). Epistoma with apical margin shallowly emarginate at middle (Fig. 81b). *Mouthparts.* Maxillary palpus with stipes lacking large seta on outer margin (Fig. 65). Labial palpi separated by more or less twice width of base of a labial palpus (Fig. 61). Prementum with one pair of large setae (Fig. 61). *Pronotum.* In dorsal view with lateral margins subparallel to slightly divergent from base to apical one-quarter; constricted at oblique angle anterior to apical one-quarter; apical one-quarter and base subequal in width to slightly wider at apical one-quarter; distinct lateral tubercles not evident (Fig. 24). Dorsal punctation large to very large, dense and deep; punctures sparser smaller and shallower laterally and on flanks. Scales white, elongate-narrow, recumbent, sparse and small or lacking medially from disk (except for midline and along apical margin), uniformly dense laterally, sparser at lateral margins and on flanks (Fig. 24). Median carina lacking. Dorsally covered throughout with dense very long erect white hair-like scales each situated within large puncture. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 81a). *Prosternum.* With very shallow impression anterior to each procoxal cavity and with moderately developed rounded swelling anterior to each prosternal impression (Fig. 81a). *Elytra.* Moderately elongate-narrow in general form (width at midlength 0.53–0.66 times length in males; 0.54–0.64 in females) (Fig. 24). In dorsal view with lateral margins straight to very slightly arcuate from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex (Fig. 24). Humerus rounded, indistinct. Dorsally with dense, very long erect hair-like scales. Sutural interval, and intervals 3 and 5 very slightly elevated and convex, especially basally. Scales elongate-narrow, recumbent, white, uniformly moderately dense except absent to sparse small and fine on interval 4 at basal one-third and apical one-third (Fig. 24) *Wings.* Absent. *Legs.* Foretibia of female with inner margin with small denticles in apical one-third; subapical tooth small, indistinct from tibial denticles. Foretibial, mesotibial and metatibial unci of both sexes large. Tarsal claws not to very slightly divergent, basal internal flange distinct. Ventral tarsal pilose vestiture of foretarsus of male and female present as small rounded apical pads of article 1, as small rounded pads on apical one-third of article 2 and apical one-half of article 3; of mesotarsus of male present as apical tufts to small rounded apical pads of article 1, as small rounded apical pads to small rounded pads on apical one-third of article 2 and apical one-third to one-half of article 3; of mesotarsus of female present as apical tufts of article 1, as small rounded apical pads of article 2, and as rounded pads on apical one-third of article 3; of metatarsus of male and female present as apical tufts of article 1, as small rounded apical pads of article 2, and as rounded pads covering apical one-third of article 3. *Mesosternum.* Mesosternal process markedly swollen and tumescent (Fig. 58). *Abdomen.* Ventral surface with moderately dense, elongate-fine recumbent white scales and short suberect white hair-like scales. Abdominal sterna lacking distinct glabrous patches. Apex of abdominal sternum VII of male lacking dorsally directed tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (two examined). Abdominal sternum VIII with lateral arms narrow, straight and divergent in basal one-half, moderately and evenly inwardly arcuate from midlength to apex (Fig. 89a). Gonocoxite II with stylusmoderately large, slightly anteapical in position (Fig. 89b). Male (two examined). Abdominal sternum VIII with paired sclerite with inner apices lacking ventral projections (Fig. 97f). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view markedly laterally expanded at approximately midlength (Figs. 97d,e). Internal sac short and high, markedly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe at midheight and midlength and small laterally directed lobes near basal margin at basal one-third (Figs. 97a,b). Eversible apical sclerite complex with paired scythe-like sclerites only slightly sclerotized, each with small median projection (Fig. 97c); adjacent ventral surface and basal portion of sides of apex of internal sac unsclerotized (Fig. 97a).

Geographic distribution.— This species has the most restricted distribution of any species of *Apleurus.* It has been found only in southern California, primarily in Los Angeles County at the El Segundo sand dunes but also at Pasadena; a single specimen is from Palm Springs, Riverside County (Fig. 212).

Natural history.— This species appears to be restricted to sand dune habitats in the Pacific semi-desert region of southern California. Adults have been collected on *Chaenactis glabriuscula* DC., *Aplopappus ericoides* (Less.) H. & A. (Compositae); *Croton californicus* Muell.-Arg. (Euphorbiaceae); and, *Lupinus albifrons* Benth. (Leguminosae). Definite host plants have yet to be determined. Adults have been collected from February to July at elevations of from 33–313 m (N=3) (Fig. 232).

Chorological relationships.— This species is sympatric with extreme western *A. angularis* and *A. albovestitus*, and southern *A. jacobinus.*

Phylogenetic relationships.— This species is the sister-group to the rest of *Apleurus* (Figs. 234 and 235).

Subgenus *Apleurus* Chevrolat

Cleonus; LeConte 1858 (sp. descs.). LeConte 1859 (sp. desc.). Gemminger and von Harold 1871 (in part; catal.). Leng 1920 (in part; catal.). Bradley 1930 (in part; key). Blackwelder 1947 (in part; check.). Arnett 1960–1962 (in part; key, catal.). Tanner 1966 (in part; sp. redesc., biol.). Krombein 1979 (in part).

Apleurus Chevrolat 1873:78. Gender, masculine. Type species *Apleurus fossus* Chevrolat (= *Cleonus lutulentus* LeConte) by subsequent designation (Casey 1891:186). Chevrolat 1873 (in part; catal., sp. desc.). Faust 1904 (key).

Centrocleonus LeConte 1876a:145 [not Chevrolat 1873:62]. NEW SYNONYMY Type species *Cleonus angularis* LeConte, according to article 67 (h) of the International Code of Zoological Nomenclature. Gender, masculine. Henshaw 1881–1882 (check.). LeConte and Horn 1883 (key). Henshaw 1885 (check.). Wickham 1889. Horn 1894 (check.).

Cleonopsis LeConte 1876a:147. NEW SYNONYMY Gender, feminine. Type species *Cleonus pulvereus* LeConte (= *Cleonus lutulentus* LeConte) by monotypy. LeConte and Horn 1883 (key). Henshaw 1885 (check.). Wickham 1889.

Wickham 1896 (check.).

Cleonaspis LeConte 1876a:153. NEW SYNONYMY Gender, feminine. Type species *Cleonus lutulentus* LeConte by monotypy. Henshaw 1881–1882 (check.). LeConte and Horn 1883 (key). Henshaw 1885 (check.). Wickham 1902 (check.).

Stephanocleonus; Henshaw 1881–1882 (in part; check.).

Dinocleus Casey 1891:176. NEW SYNONYMY. Gender, masculine. New name for *Centrocleonus* LeConte. Type species *Cleonus angularis* LeConte by subsequent designation (Faust 1904:190, error as "Typus *angulatus* Lac", subsequently listed, p. 274, as "*angularis* Lec"). Wickham 1896 (check.). Fall 1901 (check.). Wickham 1902 (check.). Champion 1902–1906 (sp. desc., notes). Casey 1904 (sp. desc.). Faust 1904 (key). Fall and Cockerell 1907 (check.). Leng 1920 (catal.). Bradley 1930 (key). Tanner 1934 (check.). Ting 1936 (morphol.). Bruhn 1947 (morphol.). Van Dyke 1953 (sp. desc.). Essig 1958 (biol.). Sanders 1960 (morphol.). Arnett 1960–1962 (key, catal.). Hatch 1971 (key).

Cleonus (*Apleurus*); Casey 1891 (key). Champion 1902–1906 (sp. desc., redescs.). Fall and Cockerell 1907 (check.). Csiki 1934 (catal.).

Cleonurus Faust 1904:274. *Nomem nudum*, incorrectly attributed to LeConte 1876a:152.

Cleonus (*Dinocleus*); Csiki 1934 (catal.). Blackwelder 1939 (check.). Kissinger 1964 (check.).

Cleonus (*Cleonopsis*); Kissinger 1964 (check.).

Cleonis; O'Brien and Wibmer 1982 (in part; catal., distn.). O'Brien and Wibmer 1984 (in part).

Notes about synonymy.— The genus *Apleurus* was initially established by Chevrolat (1873) to include three new Mexican and southwestern United States species, and one previously described southwestern United States species. Three of these species, *A. boucardi, A. trivittatus* and *A. quadrilineatus*, were regarded as "espèces lyxiformes" by Chevrolat (1873:109) thereby indicating their similarity to members of the genus *Lixus* and focusing attention on their lack of similarity to *A. fossus*, the fourth member of the genus.

No type species was designated by Chevrolat although he (1873:80) stated in his treatment of *A. boucardi* that "le corps de cet insecte est plus ovalaire que chez le type". This suggests that he considered as type one of the other two species (*Cleonidius trivittatus* was not treated in detail but merely placed in *Apleurus* by Chevrolat). *Apleurus fossus* was subsequently clearly designated as the type species by Casey (1891:76).

LeConte (1876a) undertook the first comprehensive revision of North American Cleoninae, wherein he proposed three new genera; *Centrocleonus* (a junior homonym of *Centrocleonus* Chevrolat), *Cleonopsis* and *Cleonaspis.* Species of *Centrocleonus* LeConte were characterized by the supposed unique presence of prosternal spines in front of the procoxae. Both *Cleonopsis* and *Cleonaspis* were monobasic genera distinguished from other Cleoninae, most notably *Cleonus*, primarily on the basis of features of the tarsi and antennae. I find LeConte's proposal of *Cleonopsis* and *Cleonaspis* puzzling for they are based on forms which I consider to be conspecific, differing only slightly in the extent of ventral tarsal pilosity, but otherwise not to the extent discussed by LeConte (1876a:144–145, in key) as characteristic (see also "Notes on synonymy" of *A. lutulentus*). Apparently LeConte (1876a) was not concerned that these two genera might be confused, for in his descriptions of each, only characters permitting separation from *Cleonus* are discussed.

LeConte (1876a) assigned the "espèces lyxiformes" of Chevrolat (1873) to *Cleonus* along with a number of newly described North American species which Casey (1891) subsequently placed in his new subgenus *Cleonidius*. No mention is made of *A. fossus* by LeConte (1876a) and it is likely that he did not see this species for it did not occur within the geographic area of immediate concern to him.

In the next major work on North American species, Casey (1891) recognized that the distribution of the character states considered diagnostic of *Apleurus* also necessitated inclusion of the species of *Cleonopsis* and *Cleonaspis*, and that these latter two taxa did not warrant separate generic group status. He did not, however, consider *Apleurus* as warranting any more than subgeneric status under *Cleonus*. *Dinocleus*, proposed as a new name for

Centrocleonus LeConte, and considered as of generic rank, included all of LeConte's *Centrocleonus* as well as many new species.

My use of *Apleurus* is decidedly broader than that of any of these authors, including not only those species regarded as *Apleurus* by Casey (1891) but also all those placed in *Dinocleus* Casey (1891), all subsequently described *Dinocleus* species and lastly, *Cleonus aztecus* Champion. Support for this broader definition is seen in the reconstructed phylogeny of these species wherein species of *Dinocleus* are placed as no more than derived species of *Apleurus*. Recognition of *Dinocleus* as a distinct genus would make *Apleurus* paraphyletic, an undesirable result because *Apleurus* are insufficiently structurally or biologically distinct from *Dinocleus* to warrant recognition as a formal paraphyletic taxon. The broader definition of *Apleurus* employed herein was also indirectly suggested by Van Dyke (1953) in his description of *Dinocleus bryanti*. Because *D. bryanti* is clearly conspecific with forms then regarded by Casey (1891), and I suspect also by Van Dyke, as *Apleurus*, Van Dyke's placement of his new species suggests a broader definition of *Dinocleus* and implies recognition of the similarities of members of that genus to those previously assigned to *Apleurus* even though it is doubtful he examined representatives of the latter.

Diagnosis.— Adult *Apleurus* with moderately robust to very robust body form (Figs. 68–80). Dorsal suberect or erect vestiture absent to very long and dense. Prementum with labial palpi separated by distance subequal to width of basal article of labial palpus (Figs. 62–63). Maxillary palpus with palpifer and stipes each with large seta, or with only palpifer with large seta (Fig. 64). Rostrum with epistoma with apical margin rounded medially (Figs. 82b–88b). Mesosternum with mesosternal process flat to only slightly convex (Fig. 59). Female with abdominal sternum VIII with lateral arms straight or arcuate (Figs. 90a–96); gonocoxite II with stylus absent or present, small to moderately large, apical to anteapical in position (Figs. 90b–96b). Male with abdominal sternum VIII with each sclerite with basal projection at interior angle slightly to markedly developed (Figs. 101e, 103e). Aedeagus in dorsal view more or less uniform in width throughout median portion of length.

Included species.— Seven species are placed in the subgenus *Apleurus*. They are found in the southwestern United States of America south to southern Mexico.

Phylogenetic relationships.— This subgenus is the monophyletic sister-group of the subgenus *Gibbostethus* (see "Phylogeny" section).

Key to species of adult *Apleurus (Apleurus)*

1 Elytra with sutural interval, intervals 3, 5, 7, and 9 markedly elevated and convex throughout greater part of their lengths. Metathoracic wings absent 2

1′ Elytra with all intervals flat or with sutural interval, intervals 3, 5, and 7 only very slightly elevated and convex. Metathoracic wings present, variable in length from short (approximately one-half length of elytra) to long (equal to or greater than elytra in length) 6

2 (1) Prosternum lacking swelling or with at most low rounded swelling anterior to each prosternal impression (Fig. 82a). Rostrum lacking median carina. Elytra very robust (width at midlength greater than 0.70 times length) (Fig. 68) . . . . . . *A. aztecus* (Champion), p. 474

2′ Prosternum with prominent swelling anterior to each prosternal impression (Figs. 84a–88a). Rostrum with median carina (obscured in some specimens by large deep punctures) (Figs. 84–86). Elytra less robust (width at midlength less than 0.75 times length) (Figs. 70–73) 3

3 (2′) Tarsal claws slender, widely divergent, each lacking basal internal flange, tapered evenly from base to apex (Fig. 66). Dorsal erect vestiture of pronotum and elytra short 4

3′ Tarsal claws robust, not widely divergent, each with basal internal flange, tapered abruptly from midlength to apex (Fig. 67). Dorsal erect vestiture of pronotum and elytra short or long 5

4 (3) Abdomen ventrally with scales broad, moderately dense; at least sterna III and IV with distinct glabrous shiny patches, each with single long and erect hair .... *A. angularis* (LeConte) (in part), p. 481

4′ Abdomen ventrally with scales fine and elongate, extremely dense; no glabrous patches present .... *A. porosus* (LeConte) (in part), p. 478

5 (3′) Elytra with sutural interval, intervals 3, 5, 7, and 9 (especially 3 and 5 near base) markedly elevated and convex. Most specimens with dorsal vestiture of head, pronotum and elytra very long and erect and with rostrum with carina moderately well-developed (Fig. 86). Abdomen ventrally with scales fine and elongate, moderately dense; sterna III and IV with distinct glabrous shiny patches, each with single long and erect hair .... *A. jacobinus* (Casey), p. 484

5′ Elytra with sutural interval, intervals 3, 5, 7, and 9 less markedly elevated and convex. Dorsal vestiture of head, pronotum and elytra short and suberect. Rostrum with carina only slightly developed, almost entirely obscured in some specimens by large deep punctures (Fig. 84). Abdomen ventrally with scales very fine and elongate, extremely dense; no glabrous patches present .... *A. porosus* (LeConte) (in part), p. 478

6 (1′) Pronotum laterally expanded immediately posterior to subapical constriction (giving distinctly tuberculate appearance); with base and apical one-quarter approximately equal in width to distinctly widest at apical one-quarter (Figs. 72–73). Tarsal claws slender, widely divergent, each lacking basal internal flange and tapered evenly from base to apex (Fig. 66) .... *A. angularis* (LeConte) (in part), p. 481

6′ Pronotum not laterally expanded immediately posterior to subapical constriction (not appearing distinctly tuberculate); with base and apical one-quarter approximately equal in width to distinctly widest at base (Figs. 69, 74–80). Tarsal claws robust, not widely divergent; each with basal internal flange and tapered abruptly from midlength to apex (as in Fig. 67) 7

7 (6′) Tarsus of hind leg with venter of article 3 with large pubescent pad. Prosternum lacking swelling or with swelling anterior to each prosternal impression only slightly developed (Fig. 83a). Female with tergum VII not longitudinally carinate; gonocoxite II with stylus large (Fig. 91b) .... *A. lutulentus* (LeConte), p. 475

7′ Tarsus of hind leg with venter of article 3 lacking large pubescent pad, with at most small apical tuft of pubescence. Prosternum with prominent swelling anterior to each prosternal impression (Figs. 87–88). Female with tergum VII longitudinally carinate; gonocoxite II lacking stylus (Figs. 95–96) 8

8 (7′) Tarsus of fore- and middle leg with venter of article 3 with large pubescent pad . . . . *A. saginatus* (Casey) (in part; males), p. 491

8′ Tarsus of fore- and middle leg with venter of article 3 lacking large pubescent pad, with at most small apical tuft of pubescence 9

9 (8′) Pronotum with lateral margins with outer margins of large punctures swollen, shiny and glabrous (appearing as small distinct tubercles). Abdomen ventrally (especially sterna III and IV) with distinct large glabrous patches, each with single short and suberect scale situated in the center . . . . *A. saginatus* (Casey) (in part; females), p. 491

9′ Pronotum with lateral margins with outer margins of large punctures not swollen, glabrous or shiny. Abdomen ventrally either lacking glabrous patches and with scales extremely dense; with small glabrous patches; or, with most scales abraded . . . . *A. albovestitus* (Casey), p. 486

Apleurus (Apleurus) aztecus (Champion), new combination
(Figs. 68, 82, 90, 98, 210)

Cleonus aztecus Champion 1902–1906:99. Lectotype (here designated), male, one of two syntypes, labelled "Type", inverted "Sp. figured", "Refugio/ Durango/ Hoge.", "B.C.A. Col. IV.4./ *Cleonus/ aztecus,/* Champ." and with my designation label "LECTOTYPE/ *Cleonus aztecus/* Champ. desig./ Anderson" (BMNH). Type locality, Refugio, Durango, Mexico.

Cleonis aztecus; O'Brien and Wibmer 1982 (catal., distn.).

Problems in recognition.— Members of this species are most likely to be confused with brachypterous specimens of *A. lutulentus*. In these latter specimens, the alternate elytral intervals are slightly elevated and convex and the elytra are moderately robust (more so than in macropterous *A. lutulentus*). These individuals are sympatric with *A. aztecus* and although superficially similar, *A. aztecus* individuals are distinguished by the tarsal claws each lacking a basal internal flange (as in Fig. 66), lack of metathoracic wings, and lack of a dorsally directed tooth on the apical margin of abdominal sternum VII in males.

A. aztecus individuals may also be confused with those other species of *Apleurus* in which alternate elytral intervals are elevated and convex. Key characters should readily serve to separate these species.

Description.— *Specimens examined.* 16 males, 7 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WElM, LEl, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 8. *Size.* Length, male, 5.6–9.4 mm; female, 5.2–9.4 mm. Width, male, 2.9–4.6 mm; female, 2.5–4.8 mm. *Head.* Eye prominent and convex in dorsal view. Frons and vertex with moderately dense, small to moderately large, deep punctures. Frons also with sparse, short suberect white hair-like scales immediately above eyes. Area immediately behind posterior margin of eye with large, deep, irregularly impressed punctures. Area above eyes slightly elevated above rest of frons (eyes apparently browed in anterior view). Width of frons greater than width at apex of rostrum. *Rostrum.* Robust (width at apex 0.79–1.00 times length in male; 0.78–0.91 in female) (Fig. 82). Median carina absent. Dorsal and lateral punctation moderately dense, small to large, deep. Dorsally, excluding epistoma, with moderately dense, short, suberect white hair-like scales and moderately dense elongate-narrow appressed white scales. In lateral view with apical portion flat to only very slightly declivous from point of antennal insertion to apex (Fig. 82a). Epistoma with apical margin rounded at middle (Fig. 82b). *Mouthparts.* Maxillary palpus with stipes lacking large seta on outer margin (as in Fig. 65). Labial palpi separated by more or less width of basal article of labial palpus (as in Fig. 62–63). Prementum with one pair of large setae (as in Fig. 62). *Pronotum.* In dorsal view with lateral margins subparallel to slightly divergent from base to apical one-quarter; constricted at oblique angle anterior to apical one-quarter; apical one-quarter and base subequal in width to slightly wider at apical one-quarter; without distinct lateral tubercles (Fig. 68). Dorsal and lateral punctation small, sparse to moderately dense and shallow; punctures sparser and smaller on flanks. Scales white, elongate-narrow, appressed, sparse and small or lacking medially from disk and dorsally from flanks (except for midline and area anterior to low transverse carina if present), dense laterally to lateral margins in anterior two-thirds and ventrally on flanks. Median carina lacking; some specimens with low median transverse carina or impunctate area at midlength. Dorsally with dense very short fine suberect white hair-like scales each situated within large puncture. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 82a). *Prosternum.* With very shallow impression anterior to each procoxal cavity and with at most a low slightly developed rounded swelling anterior to each prosternal impression (Fig. 82a). *Elytra.* Very robust in general form (width at midlength 0.70–0.90 times length in males; 0.72–0.80 in females) (Fig. 68). In dorsal view with lateral margins moderately arcuate throughout length (Fig. 68). Humerus rounded, indistinct. Dorsally with sutural interval and intervals 3, 5, 7, and 9 with multiple rows of short fine suberect hair-like scales; intervals 2, 4, 6, and 8 with only single row of similar hair-like scales. Sutural interval, and intervals 3, 5, 7, and 9 markedly elevated and convex throughout their lengths. Scales various in density and size; elongate-narrow, pattern various but with at least small glabrous (or nearly so) area immediately apicad of midlength on interval 4 (Fig. 68). *Wings.* Absent. *Legs.* Foretibia of female with inner margin with small denticles in apical one-third; subapical tooth large, distinct from tibial denticles. Foretibial and mesotibial unci of both sexes large, metatibial uncus of both sexes small. Tarsal claws widely divergent, no basal internal flange present (as in Fig. 66). Ventral tarsal pilose vestiture of foretarsus of male present as small rounded apical pads of article 1, as elongate-oval pads on apical one-half of article 2, and as large elongate-oval pads covering apical two-thirds of article 3; of foretarsus of female present as small rounded apical pads on articles 1 and 2, as rounded pads on apical one-third to one-half of article 3; of mesotarsus of male present as minute apical tufts on articles 1 and 2, and as small rounded apical pads to small rounded pads on apical one-half of article 3; of mesotarsus of female absent to present as minute apical tufts on articles 1 and 2, and as small rounded apical pads of article 3; of metatarsus of male present as minute apical tufts on articles 1 and 2, and as minute to small apical tufts of article 3; of metatarsus of female absent on articles 1 and 2, and present as minute apical tuft of article 3. *Mesosternum.* Mesosternal process moderately convex but not tumescent (as in Fig. 59). *Abdomen.* Ventral surface with moderately dense, elongate-fine appressed white scales. Abdominal sterna III to VI (especially III and IV) with moderately dense, small, individually indistinct to distinct rounded glabrous shiny patches, each with large puncture and single long erect hair-like scale situated in or near center. Apex of abdominal sternum VII of male lacking dorsally directed tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (two examined). Abdominal sternum VIII with lateral arms narrow, very slightly sinuate and markedly inwardly arcuate near apex (Fig. 90a). Gonocoxite II with stylus moderately large, slightly anteapical in position (Fig. 90b). Male (three examined). Abdominal sternum VIII with paired sclerite with inner apices lacking or with only slightly developed ventral projections. Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel sided throughout length. Internal sac elongate and low, only slightly apically deflexed; median dorsal pocket low, with moderately large dorsolaterally directed paramedial lobe at midheight at basal one-third, small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket, and moderately large dorsolaterally directed paramedial lobes at midheight at apical one-third (Figs. 98a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites well sclerotized, each lacking median projection (Fig. 98d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of well-developed transverse sclerites (Fig. 98a).

Geographic distribution.— This species is found throughout the highlands of central México (Fig. 210).

Natural history.— This species appears to be restricted to the xeric high-elevation mesquite-grasslands of central México (pastizal and perhaps pastizal-matorral xerofilo transition of Rzedowski [1978]). Adults have been collected on *Solidago* sp. (Compositae). Other adults have been collected from under prickly-pear pads, stones and dry cow dung. Definite host plants are unknown. Adults have been collected from June to August at elevations from 2250–3385 m (N=8) (Fig. 232).

Chorological relationships.— This species is sympatric throughout its range with *A. lutulentus*. Adult specimens of the two species have been collected together at 1.5 mi. S. Fresnillo (Zacatecas) and 20 mi. NE. Dolores Hidalgo (Guanajuato).

Phylogenetic relationships.— This species is the sister-species of the rest of the species in the subgenus *Apleurus* (Figs. 234–235).

Apleurus (Apleurus) lutulentus (LeConte), new combination
(Figs. 6, 59, 62, 69, 83, 91, 99, 207)

Cleonus lutulentus LeConte 1859a:18. Lectotype (here designated), female, one of two syntypes (only one examined), labelled with a dark green circle (=New Mexico), "Type/ 5186", "*Cleonaspis/ lutulentus/* (Lec)" and with my designation label "*Cleonus/ lutulentus/* LeC. LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Santa Fe, New Mexico. Gemminger and von Harold 1871 (catal.). Leng 1920 (catal.).

Cleonus pulvereus LeConte 1859a:18. NEW SYNONYMY Holotype (examined), female, labelled "Dallas/ Tex/ Boll", "Type/ 5185", "*Cleonopsis/ pulvereus/* (Lec)" (MCZC). Type locality, Dallas, Texas. Gemminger and von Harold 1871 (catal.). Leng 1920 (catal., error as *Cleonus pluvereus*). Blackwelder 1947 (check.). Krombein 1979 (as prey).

Apleurus fossus Chevrolat 1873:78. NEW SYNONYMY Lectotype (here designated), female, one of two syntypes, labelled "12....", "Mexico/ Au. Salle", "TYPUS", "40", "473/ 85", "Riksmuseum/ Stockholm" and with my designation label "*Apleurus fossus*/ Chevrolat/ LECTOTYPE/ desig. Anderson" (Riksmuseum, Stockholm; other syntype in BMNH). Type locality, Mexico. Faust 1904.

Cleonaspis lutulentus; LeConte 1876a (redesc.). Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1902 (check.).

Cleonopsis pulvereus; LeConte 1876a (redesc.). Henshaw 1885 (check.). Wickham 1889. Wickham 1896 (check.).

Stephanocleonus pulvereus; Henshaw 1881–1882 (check.).

Cleonus (*Apleurus*) *fossus*; Casey 1891 (designation as type species of *Apleurus* Chevrolat). Champion 1902–1906 (syn., distn.). Csiki 1934 (catal.).

Cleonus (*Apleurus*) *lutulentus*; Casey 1891 (key). Fall and Cockerell 1907 (check.). Csiki 1934 (catal.).

Cleonus (*Apleurus*) *pulvereus*; Casey 1891 (key). Champion 1902–1906 (syn., distn.). Fall and Cockerell 1907 (check.). Csiki 1934 (catal.).

Cleonus fossus; Blackwelder 1947 (check.).

Dinocleus bryanti Van Dyke 1953:101. NEW SYNONYMY Holotype (examined), male, labelled "Seligman,/ Ariz. VIII 3 36/ Bryant.112.", "From the/ O. Bryant/ Collection", "Holotype" (CASC). Type locality, Seligman, Arizona.

Cleonis bryanti; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis fossus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis lutulentus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis pulvereus; O'Brien and Wibmer 1982 (catal., distn.).

lutatentus, incertae sedis; Chevrolat 1873 (error, misspelling).

pulverosus, incertae sedis; Chevrolat 1873 (error, misspelling).

Notes about synonymy.— I can find no consistent differences that warrant separation of *Cleonus pulvereus* LeConte, *Cleonus lutulentus* LeConte and *Dinocleus bryanti* Van Dyke as distinct species. LeConte (1859a) emphasized characters (extent of ventral tarsal vestiture and degree of development of rostral carina) which are intraspecifically variable in describing *C. pulvereus* and *C. lutulentus* and subsequently placing them in separate genera (LeConte, 1876a) (see "Notes about synonymy" section for *Apleurus*). I have not seen any specimens of *A. lutulentus* from which the ventral tarsal pilose vestiture is entirely lacking and in which the tarsal articles are not bilobed, as was given by LeConte (1876a) as in part characteristic of *C. lutulentus*, and I do not find that the characters subsequently given by Casey (1891) to separate the two species represent anything more than intraspecific variation.

Dinocleus bryanti Van Dyke is clearly *A. lutulentus*. Van Dyke (1953) considered *D. bryanti* a member of the genus *Dinocleus*, however, since he did not mention either *Cleonus pulvereus* or *Cleonus lutulentus*, and since neither was then considered to be *Dinocleus*, I suspect that Van Dyke did not look at representatives of these forms in describing *D. bryanti*, but only at those forms already placed in *Dinocleus*. As a result, he found his new species to be very distinct from those then included in *Dinocleus*. As discussed elsewhere ("Notes about synonymy" section for *Apleurus*) this placement of *D. bryanti* in *Dinocleus* concurs with my classification of species of *Dinocleus* and *Apleurus* (including *Cleonaspis* and *Cleonopsis*) herein as congeneric.

I also consider the Mexican brachypterous *A. fossus* as conspecific with the other forms discussed previously in this section. No specific type locality was given for this species but because brachypterous individuals are otherwise only known from central and southern México I suspect this is the area of collection of the type series. These brachypterous forms are otherwise distinguished from typical *C. lutulentus* by a more robust and globose elytral form, possession of elytral intervals 3, 5 and 7 slightly elevated and convex, and possession of deep and large punctures on the head, pronotum and elytra. Although only this brachypterous form occurs in the southern Mexican highlands of Oaxaca and Puebla, some of these similarly brachypterous individuals are also known to be sympatric with typically macropterous individuals in central México. Because wing length polymorphism and associated variation in elytral form is found in sympatric individuals of other species of *Apleurus* (*A. angularis* and *A. albovestitus*), I concur with Champion (1902–1906:98) that *A. fossus* is "probably nothing more than a southern form of *C. pulvereus* LeC.".

Problems in recognition.— Brachypterous specimens of this species may be confused with individuals of *A. aztecus* as noted in the "Problems in recognition" section for that species. They may also be confused with small *A. saginatus* or *A. albovestitus*, or macropterous *A. angularis*, but the presence of distinct prosternal swellings anterior to the prosternal impressions in members of the latter three species (Figs. 85, 87–88), among other key characters, will readily separate them from *A. lutulentus*.

Description.— *Specimens examined.* 334 males, 369 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEI, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 9. *Size.* Length, male, 5.3–10.3 mm; female, 6.4–11.4 mm. Width, male, 2.4–4.8 mm; female, 2.9–5.5 mm. *Head.* Eye prominent and convex in dorsal view. Frons and vertex with moderately dense, small to large, deep punctures. Frons lacking suberect or erect vestiture; with only sparse elongate-narrow appressed white scales. Area immediately behind posterior margin of eye with large, deep, irregularly impressed punctures. Area above eyes flat, not distinct from rest of frons (eyes not appearing distinctly browed in anterior view). Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.65-0.91 times length in male; 0.67-0.84 in female) (Fig. 83). Median carina absent or at most only slightly developed and indistinct. Dorsal and lateral punctation moderately dense, small to large, deep; sparser apically and irregularly impressed medially in some specimens). Dorsally, excluding epistoma, with scattered very short, fine, suberect hair-like scales towards apex, and sparse elongate-narrow appressed white scales. In lateral view with apical portion flat to only very slightly declivous from point of antennal insertion to apex (Fig. 83a). Epistoma with apical margin rounded at middle (Fig. 83b). *Mouthparts.* Maxillary palpus with stipes with large seta on outer margin (as in Fig. 64). Labial palpi separated by more or less width of basal article of a labial palpus (Fig. 62). Prementum with one pair of large setae (Fig. 62). *Pronotum.* In dorsal view with lateral margins slightly arcuate from base to apical one-quarter; constricted at oblique angle anterior to apical one-quarter; pronotum widest at base to subequal in width at base and at apical one-quarter; distinct lateral tubercles not evident (Fig. 69). Dorsal and lateral punctation small to large, moderately dense to dense, and deep; punctures sparser and smaller on flanks. Scales white, elongate-narrow, appressed, sparse and small or lacking medially from disk in a broad, apically narrowed patch (except for midline in some specimens), and at lateral margins near base; uniformly dense laterally to lateral margins in anterior one-half and ventrally on flanks. Median carina lacking. Dorsally lacking suberect or erect vestiture. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 83a). *Prosternum.* With very shallow impression anterior to each procoxal cavity and with at most low slightly developed rounded swelling anterior to each prosternal impression (Fig. 83a). *Elytra.* Moderately robust in general form (width at midlength 0.57-0.72 times length in males; 0.52–0.76 in females) (Fig. 69). In dorsal view with lateral margins slightly arcuate and convergent to subparallel from apical one-third to humerus; markedly arcuate from apical one-third to apex; humerus obtuse to acute, moderately distinct to distinct (Fig. 69). Dorsal suberect or erect vestiture absent or at most with sutural interval and intervals 2 and 3 with very short suberect hair-like scales. Dorsally with all elytral intervals flat to slightly convex, to with sutural interval and intervals 3, 5, and 7 slightly swollen and convex in brachypterous individuals. Scales various in density and size; elongate-narrow, pattern various with numerous irregularly distributed small glabrous or nearly so areas (Fig. 69). *Wings.* Short (very slightly shorter than elytra in length [2.1%, N=15]) to long (greater than elytra in length [97.9%, N=688]). Branches of 2A not joined at base. *Legs.* Foretibia of female with inner margin with small to moderately large denticles throughout most of length; subapical tooth moderately large, distinct from tibial denticles. Foretibial and mesotibial unci of both sexes large, metatibial uncus of both sexes moderately large. Tarsal claws not divergent, with well-developed basal internal flange present. Ventral tarsal pilose vestiture of foretarsus of male present as small elongate apical pads of article 1, as elongate-oval pads on apical one-half of article 2, and as large elongate-oval pads on apical two-thirds of article 3; of foretarsus of female present as small elongate apical pads of article 1, as moderately large elongate-oval pads on apical one-half of article 2, and as large elongate-oval pads on apical one-half to two-thirds of article 3; of mesotarsus of male present as elongate-narrow pads on apical one-third of article 1 and apical one-half of article 2, and as large elongate-oval pads on apical one-half to two-thirds of article 3; of mesotarsus of female present as elongate-narrow pads on apical one-third of article 1, as elongate-oval pads on apical one-half of article 2, and as large rounded pads on apical one-half of article 3; of metatarsus of male absent of article 1, present as elongate very narrow pads of article 2, and as elongate-oval pads on apical one-half of article 3; of metatarsus of female absent to as small elongate-narrow pads on apical one-quarter of article 1, as elongate very narrow pads on apical one-third of article 2, and as large rounded pads on apical one-half to two-thirds of article 3. *Mesosternum.* Mesosternal process flat to very slightly convex but not tumescent (Fig 59). *Abdomen.* Ventral surface with dense, elongate-fine appressed white scales. Abdominal sterna III to VI (especially III and IV) with sparse to moderately dense, small, individually indistinct to distinct rounded glabrous shiny patches, each with large puncture and single short erect hair-like scale situated in or near center. Apex of abdominal sternum VII of male with large dorsally directed median truncate tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (three examined). Abdominal sternum VIII with lateral arms narrow, very slightly inwardly arcuate in basal three-quarters, then markedly inwardly arcuate to apex (Fig. 91a). Gonocoxite II with stylus moderately large, anteapical in position by more or less length of stylus (Fig. 91b). Male (12 examined). Abdominal sternum VIII with paired sclerite with inner apices with slightly to moderately developed ventral projections. Aedeagus elongate-narrow, in lateral view subequal in thickness from base to midlength (Fig. 99c); in ventral view more or less parallel sided throughout length. Internal sac elongate and low, only slightly apically deflexed; median dorsal pocket low, with moderately large dorsolaterally directed paramedial lobe at midheight at basal one-third and small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket (Figs. 99a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites well sclerotized, each with short median projection (Fig. 99d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of well-developed transverse sclerites (Fig. 99a).

Geographic variation.— Some specimens from central México have larger and deeper punctures of the head, pronotum and elytra; more robust and globose elytra; elytral intervals 3, 5, and 7 slightly elevated and convex; and short wings. Only specimens with extreme states in all of these characters are found in the area of the southern border of the species range in the Mexican states of Oaxaca and Puebla.

Geographic distribution.— This species is found from Kansas, Oklahoma and eastern Texas, west to Arizona, disjunct to central and southern México (Fig. 207). The species does not appear to be found in the Chihuahuan desert region in México. There is a single questionable record from northeastern California.

Natural history.— This is the most widely distributed species of *Apleurus*. It is found in mesquite-grassland, grassland, and desert-grassland transitional habitats in México and the United States, and in the grassland-deciduous forest transitional zone. Adults have been collected in dry upland desert washes and grasslands on a wide variety of plants, but mostly Compositae, as follows: *Gossypium hirsutum* L. (cotton, Malvaceae); *Chenopodium* sp. (Chenopodiaceae); *Asclepias* sp., *A. subverticillata* (Gray) Vail (Asclepiadaceae); *Koeberlinia spinosa* Zucc. (Capparaceae); *Acacia* sp. (Leguminosae); *Baccharis* sp., *B. glutinosa* Pers., *Baileya pleniradiata* Harv. and Gray, *Chrysothamnus nauseosus* (Pall.) Britton,, *Flourensia cernua* DC., *Gutierrezia* sp., *Solidago* sp., *Verbesina enceloides* (Cav.) Benth. and Hook., *V. oreophila* Woot. and Standl., *Xanthium* sp. (all Compositae). Definite host plants are not known. Adults have been collected from March to October at elevations from 9–3058 m (N=77) (Fig. 232).

Chorological relationships.— This species is sympatric with *A. saginatus* in southern Arizona and New Mexico; with *A. aztecus* in central México; with *A. angularis* in New Mexico, western Texas, Colorado, western Oklahoma, and Arizona; and with *A. albovestitus* in Arizona, New Mexico, and western Texas.

Adults of *A. lutulentus* and *A. albovestitus* have been caught together near Portal, Arizona, on *Chrysothamnus nauseosus*. Adult specimens of *A. lutulentus* and *A. aztecus* have been collected together 1.5 mi. S. Fresnillo (Zacatecas), on *Solidago* sp., and 20 mi. NE. Dolores Hidalgo (Guanajuato).

Phylogenetic relationships.— This species is the sister-species of the *A. porosus-A. angularis-A. jacobinus-A. saginatus-A. albovestitus* lineage of *Apleurus* (Figs. 234–235).

Apleurus (Apleurus) porosus (LeConte), new combination

(Figs. 70, 84, 92, 102, 210)

Centrocleonus porosus LeConte 1876a:146. Holotype (examined), female, labelled with a silver circle with portion cut away (=Baja California) "Type/ 5239", "*C. porosus*/ Lec" (MCZC). Type locality, Cape San Lucas, Baja California Sur, Mexico. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Horn 1894 (check.).

Dinocleus farctus Casey 1891:181. NEW SYNONYMY Holotype (examined), male, labelled "Cal", "CASEY/ bequest/

1925", "TYPE USNM/ 37271", "*D./ farctus/* Cas." (USNM). Type locality, California, near the southern border. Fall 1901 (check.). Leng 1920 (catal.).

Dinocleus porosus; Casey 1891 (key, redesc.). Leng 1920 (catal.).

Cleonus (*Dinocleus*) *farctus*; Csiki 1934 (catal.).

Cleonus (*Dinocleus*) *porosus*; Csiki 1934 (catal.).

Cleonus porosus; Blackwelder 1947 (check.).

Cleonus farctus; Hardy and Andrews 1976 (distn., prob. misident. *A. angularis*).

Cleonis farctus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis porosus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— Both LeConte (1876a) and Casey (1891) based their species descriptions of *Centrocleonus porosus* and *Dinocleus farctus* on unique specimens. Having examined larger numbers of individuals from various localities, I conclude that the two are conspecific and the differences noted by Casey (1891) as species-specific are due to intraspecific variation or secondary sexual characteristics (the holotype of *C. porosus* is a female; that of *D. farctus*, a male).

The type locality of *D. farctus* is given by Casey (1891) as California, near the southern border. I have not seen any other *A. porosus* from the state of California.

Problems in recognition.— Members of this species are likely to be confused with *A. angularis* but can be distinguished from individuals of that species by the robust form of the tarsal claws, each possessing a basal internal flange in most specimens (as in Fig. 67); by the lack of distinct glabrous patches on the abdominal sterna; and by presence of only very short suberect dorsal vestiture in the former. Some specimens of *A. porosus* from various localities however, possess tarsal claws, which although moderately robust, lack a distinct internal flange.

Apleurus porosus specimens are also likely to be confused with *A. jacobinus* individuals particularly in Baja California Norte (and possibly also in southern California) where the species appear to be narrowly sympatric. *Apleurus jacobinus* specimens are distinguished from those of *A. porosus* by the long dorsal erect vestiture; alternate elytral intervals markedly elevated and convex; and abdominal sterna with distinct glabrous patches in the former. However, in the southern part of the range of *A. jacobinus* in Baja California Norte, individuals I examined have shorter dorsal erect vestiture and less markedly elevated elytral intervals than elsewhere throughout the species range, thus, approaching the states in *A. porosus* in these characters. Although the differences in degree of elevation of the elytral intervals and length of dorsal vestiture in these individuals should still allow for separation of *A. jacobinus* and *A. porosus*, the presence of distinct glabrous patches on the abdominal sterna of the former will allow for unequivocal separation of the two species. *Apleurus porosus* specimens also have the pronotum with scales uniformly very dense laterally and on the flanks, more or less obscuring the individual large punctures.

Many *A. porosus* can also be separated from *A. jacobinus* and *A. angularis* by their larger size, more elongate-narrow rostrum, and by the pronotum being widest at the base (see Figs. 105–106, 109).

Description.— *Specimens examined.* 23 males, 32 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEI, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 10. *Size.* Length, male, 5.8–13.6 mm; female, 6.9–15.2 mm. Width, male, 2.6–6.1 mm; female, 3.0–7.2 mm. *Head.* Eye very prominent and convex in dorsal view. Frons and vertex with dense, large to very large, deep punctures. Frons and area immediately above eyes with sparse to moderately dense short suberect hair-like scales. Area immediately behind posterior margin of eye with large, deep, irregularly impressed punctures. Area above eyes slightly elevated above rest of frons (eyes appearing distinctly browed in anterior view). Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately elongate-narrow (width at apex 0.61–0.68 times length in male; 0.62–0.69 in female) (Fig. 84). Median carina absent to slightly developed but distinct, almost entirely obscured in some specimens by large deep punctures. Dorsal and lateral punctation moderately dense, large, deep. Dorsally, excluding epistoma, with scattered short, fine, suberect hair-like scales towards apex, and dense elongate-narrow appressed white scales. In lateral view with apical portion steeply declivous from point of antennal insertion to apex (Fig. 84a). Epistoma with apical margin rounded at middle (Fig. 84b). *Mouthparts.* Maxillary palpus with stipes lacking large seta on outer margin (as in Fig. 65). Labial palpi separated by more or less width of basal article of a labial palpus (as in Figs. 62–63). Prementum with two or three pairs of large setae (as in Fig. 63). *Pronotum.* In dorsal view with lateral margins subparallel to slightly convergent from base to apical one-quarter; constricted at acute angle anterior to apical one-quarter; widest at base to subequal in width at base and apical one-quarter; distinct lateral tubercles evident (Fig. 70). Dorsal and lateral punctation large, moderately deep to deep, dense; punctures sparser and smaller on flanks. Scales white, elongate-narrow, appressed, sparse and small or lacking medially from disk in broad, apically narrowed patch (except for midline in some specimens); uniformly dense laterally, at lateral margins and ventrally on flanks, more or less obscuring large punctures. Median carina lacking. Dorsally covered throughout with sparse, fine, short, erect hair-like scales. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 84a). *Prosternum.* With shallow impression anterior to each procoxal cavity and with well-developed rounded swelling anterior to each prosternal impression (Fig. 84a). *Elytra.* Moderately robust in general form (width at midlength 0.65-0.70 times length in males; 0.65-0.73 in females) (Fig. 70). In dorsal view with lateral margins moderately arcuate throughout length; humerus rounded, not distinct (Fig. 70). Sutural interval and intervals 3, 5, 7, and 9 with sparse, very short, suberect hair-like scales. Dorsally with sutural interval and intervals 3, 5, 7, and 9 slightly swollen and convex (more so basally in some specimens). Scales elongate-narrow, various in density and size; pattern various but in most specimens with two extensive glabrous (or nearly so) areas, one from area behind humerus, posteromedially directed to sutural interval at midlength, other continous with the former at midlength and directed laterally from sutural interval to interval 9; some specimens also with glabrous (or nearly so) area of variable extent at confluence of intervals 4 to 7 (Fig. 70). *Wings.* Absent. *Legs.* Foretibia of female with inner margin with small denticles in apical one-third; subapical tooth small, not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes large, metatibial uncus of both sexes moderately large. Tarsal claws not divergent, basal internal flange absent to present, well-developed. Ventral tarsal pilose vestiture of foretarsus of male absent of article 1, present as minute apical tufts of article 2, as moderately large rounded pads on apical one-third to one-half of article 3; of foretarsus of female, mesotarsus of male and female, and metatarsus of male, lacking from articles 1 and 2, present as small rounded pads at apex of article 3; of metatarsus of female lacking from articles 1 and 2, present as minute pads at apex of article 3. *Mesosternum.* Mesosternal process flat to very slightly convex but not tumescent (as in Fig. 59). *Abdomen.* Ventral surface with very dense, elongate-fine appressed white scales and scattered suberect hair-like scales. Abdominal sterna lacking distinct glabrous patches, with at most only lateral margins of abdominal sterna III and IV with very small indistinct glabrous patches. Apex of abdominal sternum VII of male with small dorsally directed median truncate tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (four examined). Abdominal sternum VIII with lateral arms narrow, slightly outwardly arcuate in basal one-half, then parallel to near apex, markedly inwardly arcuate immediately before apex (Fig. 92a). Gonocoxite II with stylus very small, anteapical in position by more or less one-half length of stylus (Fig. 92b). Male (five examined). Abdominal sternum VIII with paired sclerite with inner apices with slightly to moderately developed ventral projections (as in Fig. 101e). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel sided throughout length. Internal sac short and high, markedly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe at midheight and midlength; small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket (Figs. 102a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites lightly sclerotized, each lacking median projection (as in Figs. 100d-101d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of indistinct lightly sclerotized transverse sclerites (Fig. 102a).

Geographic variation.— None noted, but this may be due to the small number of specimens examined, especially from Baja California Norte where this species is at most narrowly sympatric with *A. angularis* and *A. jacobinus.*

Geographic distribution.— This species is found throughout Baja California Sud and Baja California Norte, México (Fig. 210). It may occur in the extreme south of California.

Natural history.— Label data indicate that most adults have been caught in sand dune areas in the "matorral xerofilo" of Baja California (Sonoran desert) and Pacific semi-desert region at elevations of from 6–144 m (N=5) (Fig. 232). Sleeper (pers. comm.) has collected numerous specimens from a woody *Encelia* species and a single specimen from *Encelia laciniata* Vasey and Rose (Compositae). Definite host plants are not known.

Chorological relationships.— This species has one of the more restricted distributions of *Apleurus* species. It is sympatric with extreme southern *A. albovestitus*, and at most narrowly sympatric to parapatric with its close relatives *A. angularis* and *A. jacobinus.*

Phylogenetic relationships.— *Apleurus porosus* is the sister-species of the *A. angularis-A. jacobinus* sister-species pair (Fig. 235). Presence of the apotypic state of tarsal claws each lacking a basal internal flange in some *A. porosus* and in *A. angularis* (Fig. 66) is either a result of hybridization or of homoplasy, more likely the former.

Apleurus (Apleurus) angularis (LeConte), new combination
(Figs. 66, 72–74, 85, 93, 100, 211)

Cleonus angularis LeConte 1859a:18. Lectotype (here designated), male, one of two syntypes (only one examined), labelled with a pale green circle (=Wyoming Territory) "*C. angularis*/ Beckwith Lec.", "Type/ 5182" and with my designation label "*Cleonus*/ *angularis*/ LeC. LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Kansas. LeConte 1858 (*nomen nudum*). Gemminger and von Harold 1871 (catal.). Hatch 1971.

Centrocleonus angularis; LeConte 1876a (key, diag.). Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1889.

Dinocleus denticollis Casey 1891:180. NEW SYNONYMY. Lectotype (here designated), female, one of five syntypes, labelled "Ari", "CASEY/ bequest/ 1925", "TYPE USNM/ 37269", "*D.*/ *denticollis*/ Cas." and with my designation label "*Dinocleus*/ *denticollis*/ Csy. LECTOTYPE/ desig. Anderson" (USNM). Type locality, Peach Springs, Arizona. Wickham 1896 (check.). Casey 1904. Van Dyke 1953. Hatch 1971 (redesc.).

Dinocleus angularis; Casey 1891 (key, redescr.). Wickham 1902 (check.). Faust 1904 (desig. as type species of *Apleurus* Chevrolat; error as "*angulatus* Lac").

Dinocleus porcatus Casey 1904:321. NEW SYNONYMY Lectotype (here designated), female, one of two syntypes, labelled "Ogden/ Ut. Solt", "CASEY/ BEQUEST/ 1925", "TYPE USNM/ 37270", "*porcatus*" and with my designation label "*Dinocleus*/ *porcatus*/ Csy. LECTOTYPE/ desig. Anderson" (USNM). Type locality, Ogden, Utah. Fall and Cockerell 1907 (check.). Leng 1920 (catal.).

Cleonus denticollis; Leng 1920 (catal.). Tanner 1966 (biol.).

Cleonus (*Dinocleus*) *angularis*; Csiki 1934 (catal.).

Cleonus (*Dinocleus*) *denticollis*; Csiki 1934 (catal.).

Cleonus (*Dinocleus*) *porcatus*; Csiki 1934 (catal.).

Cleonus farctus; Hardy and Andrews 1976 (distn., prob. misident.).

Cleonis angularis; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis denticollis; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis porcatus; O'Brien and Wibmer 1982 (catal., distn.).

angularis, incertae sedis; Chevrolat 1873.

Notes about synonymy.— Geographic patterns of variation in states of structural features considered characteristic of *Cleonus angularis* LeConte, *Dinocleus denticollis* Casey, and *Dinocleus porcatus* Casey, suggest that only a single species warrants recognition and that these three names be placed in synonymy (see "Geographic variation" section).

I have only been able to locate and examine one of the two syntypes of *Cleonus angularis* LeConte.

Problems in recognition.— *Apleurus angularis* and *A. aztecus* are the only two species of *Apleurus* in which all individuals have the tarsal claws widely divergent and each lacking a basal internal flange (Fig. 66). This character state should serve to separate nearly all *A. angularis* from *A. jacobinus* and *A. porosus*. Most *A. angularis* can further be separated from most *A. jacobinus* by the presence of long dorsal erect vestiture and markedly elevated alternate elytral intervals in the latter. A very few specimens of *A. jacobinus* from Baja California Norte have less markedly elevated alternate elytral intervals and have shorter dorsal erect vestiture than throughout the rest of the species range and are thus difficult to separate from *A. angularis*. Although these character states are such that they still allow for recognition of these individuals as *A. jacobinus*, they can also be more easily recognized by the robust and less markedly divergent tarsal claws. (See also "Problems in recognition" section for *A. porosus*).

Description.— *Specimens examined.* 218 males, 246 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEI, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 11. *Size.* Length, male, 5.7–10.6 mm; female, 6.9–12.2 mm. Width, male, 2.6–5.2 mm; female, 3.0–5.6 mm. *Head.* Eye very prominent and convex in dorsal view. Frons and vertex with moderately dense, small to moderately large, deep punctures. Frons and area immediately above eyes with sparse short erect hair-like scales. Area immediately behind posterior margin of eye with large, shallow to deep, irregularly impressed punctures. Area above eyes markedly elevated above rest of frons (eyes appearing distinctly browed in anterior view). Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.66-0.91 times length in male; 0.62–0.92 in female) (Fig. 85). Median carina slightly to well-developed, low and rounded but distinct, to high and sharp (Fig. 85). Dorsal and lateral punctation small, moderately deep, sparse to moderately dense. Dorsally, excluding epistoma, with dense short, suberect hair-like scales, and dense elongate-narrow to broad appressed white scales. In lateral view with apical portion steeply declivous from point of antennal insertion to apex (Fig. 85a). Epistoma with apical margin rounded at middle (Fig. 85b). *Mouthparts.* Maxillary palpus with stipes lacking large seta on outer margin (as in Fig. 65). Labial palpi separated by more or less width of basal article of labial palpus (as in Figs. 62–63). Prementum with two or three pairs of large setae (as in Fig. 63). *Pronotum.* In dorsal view with lateral margins subparallel from base to almost apical one-quarter, then divergent to apical one-quarter (giving a distinctly laterally tuberculate appearance); markedly constricted at acute angle anterior to apical one-quarter, then straight or slightly convergent to apex; widest at tubercles to subequal in width at base and apical one-quarter (Figs. 72–74). Dorsal and lateral punctation moderately large to large, deep, sparse to moderately dense, in some specimens areas between punctures irregularly elevated thus apparently sculptured; punctures sparser and smaller on flanks. Scales white, elongate-narrow to broad, appressed, sparse and small or lacking medially from disk in broad, apically narrowed patch (except for midline in some specimens); dense laterally in pair of posterolaterally directed arcuate stripes; scales sparser at lateral margins and ventrally on flanks, to uniformly dense laterally, at lateral margins and on flanks, individual large punctures not obscured. Median carina lacking. Dorsally covered throughout with moderately dense, fine, short, erect hair-like scales. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 85a). *Prosternum.* With shallow impression anterior to each procoxal cavity and with moderately to well-developed rounded swelling anterior to each prosternal impression (Fig. 85a). *Elytra.* Moderately robust in general form (width at midlength 0.57-0.76 times length in males; 0.59-0.75 in females) (Figs. 72–74). In dorsal view with lateral margins slightly arcuate throughout length or with margins slightly convergent to subparallel from apical one-third to humerus; humerus rounded to obtuse, not distinct to distinct (Figs. 72–74). Sutural interval and intervals 3, 5, 7, and 9 with moderately dense, short, erect hair-like scales; sparser on other intervals. Dorsally with sutural interval and intervals 3, 5, 7, and 9 slightly to moderately swollen and convex (more so basally in some specimens). Scales elongate-narrow, various in density and size. Pattern extremely various; many specimens with two variously sized posteromedially directed glabrous or nearly so areas, one at basal one-third from intervals 4 to 6, other at apical one-third from intervals 2 to 7, and with various number of scattered small glabrous (or nearly so) patches (Fig. 72); other specimens with glabrous areas of various extent on interval 2 at basal one-quarter and from midlength to apical one-quarter, interval 4 at basal one-third, interval 6 at basal one-quarter and apical one-quarter, and interval 8 at midlength; scales confined to median portion of intervals, striae and immediately adjacent portion of intervals lacking scales (Fig. 73). *Wings.* Absent (95.5%, N=443) or present, long (greater than elytra in length [4.5%, N=21]). Branches of 2A not complete, not joined at base. *Legs.* Foretibia of female with inner margin with small denticles in apical one-third; subapical tooth small, not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes large, metatibial uncus of both sexes small. Tarsal claws widely divergent, basal internal flange absent (Fig. 66). Ventral tarsal pilose vestiture of foretarsus of male absent from article 1, present as minute apical tufts of article 2, as small apical pads of article 3; of foretarsus of female, mesotarsus of male and female, and metatarsus of female, lacking from articles 1 and 2, present as minute to small pads at apex of article 3; of metatarsus of male lacking from articles 1 and 2, lacking from to present as minute pads at apex of article 3. *Mesosternum.* Mesosternal process flat to very slightly convex but not tumescent (as in Fig. 59). *Abdomen.* Ventral surface with moderately dense, elongate-fine appressed white scales. Abdominal sterna III to VI (especially III and IV) with moderately dense, individually distinct circular glabrous patches, each with large puncture and single long erect hair-like scale situated in or near center. Apex of abdominal sternum VII of male with small dorsally directed median truncate tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (nine examined). Abdominal sternum VIII with lateral arms narrow, slightly outwardly arcuate in basal one-half, then parallel to near apex, markedly inwardly arcuate immediately before apex (Fig. 93a). Gonocoxite II with stylus very small, anteapical in position by more or less one-half length of stylus (Fig. 93b). Male (10 examined). Abdominal sternum VIII with paired sclerite with inner apices with slightly to moderately developed ventral projections (as in Fig. 101e). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel-sided throughout length. Internal sac short and high, markedly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe at midheight and midlength; small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket (Figs. 100a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites lightly sclerotized, each lacking median projection (Fig. 100d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of indistinct lightly sclerotized transverse sclerites (Fig. 100a).

Geographic variation.— Geographic variation is extensive in a number of characters in members of this species. As a result there has been a lot of confusion regarding the specific limits of the previously recognized species (the names of which are here placed in synonymy) and identity of various specimens. Specimens I examined bear label notes either indicating a questionable identification or indicating that the specimen represents a probable new species. One manuscript name is also represented on these labels.

Both macropterous and apterous individuals are known. Macropterous individuals have only slightly elevat d and convex alternate elytral intervals and have more or less parallel-sided elytra withdistinct humeri. Apterous individuals on the other hand have alternate elytral intervals that are more markedly elevated and convex, and have elytra with the lateral margins more arcuate with indistinct humeri. There appears to be no geographic component to this variation because macropterous individuals, although few in number, are found throughout most of the species range, with the notable exception of Colorado. This has no doubt contributed to confusion, but the main cause of the confusion is due to the patterns of geographic variation in other structural features. Specimens from eastern and central Colorado, western Oklahoma, and western Texas (called hereafter the "eastern morph" and including typical *Cleonus angularis* LeConte), are different from those to the west in California, Nevada, Utah, and northern Arizona (called hereafter the "western morph" and including typical *Dinocleus denticollis* Casey and *Dinocleus porcatus* Casey).

Eastern morphs (Fig. 73) differ from western morphs (Fig. 72) in states of the following characters: shorter and more robust rostrum; rostral carina higher and sharper; eyes slightly less prominent and convex in dorsal view; pronotal punctures denser, larger, deeper and more irregularly impressed; slightly more markedly elevated alternate elytral intervals; generally a more globose and robust elytral form; elytra with glabrous patches primarily transversely oriented (Fig. 72) not longitudinally oriented (Fig. 73). Specimens from southern Arizona and southern New Mexico however, are not reliably assignable to either form. They are intermediate in many structural features which characterize the eastern and western morphs and it is in this area that apparent intergradation takes place. Elytral scale patterns are not clearly of one or the other form (Fig. 74); rostra are variable in form, and carinae both in form and in degree of elevation; pronotal punctation is variable in depth, density and regularity of impression; and elytral characters (other than scale pattern) are also variable. Based upon this intergradation, I conclude that the eastern and western morphs and the individuals from southern New Mexico and southern Arizona are all conspecific.

It appears that members of certain species of *Apleurus* (and also *Cleonidius*) are largely restricted to sandy habitats such as dune fields, sand hills, dry washes, stream beds, and riparian habitats. These are either localized and discontinuous dune fields, or although widespread, washes and riparian communities restricted in their degree of continuity. Dispersal possibilities are therefore, I believe, markedly influenced by the continuity of drainage patterns or other suitable habitats, and also as is true for all insects, by the presence or absence of wings. Population distinctiveness and apparent lack of intergradation in the north in Colorado and adjacent Utah and northern Arizona, is perhaps due to a combination of a higher continental divide in this area with a more marked discontinuity between eastern and western drainage patterns, consequently more localized and disjunct habitats, and general overall low number of macropterous individuals including presence of only apterous individuals in Colorado. These features may all combine to reduce the probability of dispersal between eastern and western drainages resulting in local selection for differences between the two morphs. On the other hand, this is not so in southern Arizona and New Mexico where the continental divide is much lower, drainage patterns are not as markedly discontinuous and localized and where macropterous individuals although still few in number, are present in both drainages. Dispersal and interbreeding of individuals is therefore possible in this area with the result that there is no local selection for differences between the two drainages.

This pattern is similar to that found in *C. canescens* which also differs between Colorado and adjacent Utah in the north but not so in the south in New Mexico and Arizona, and all individuals of which are brachypterous and incapable of flight. Species which are found in these same areas but which are macropterous do not show distinctive populations on the eastern and western sides of the continental divide.

Geographic distribution.— This species is widespread in the southwestern United States of America from Colorado, western Oklahoma and western Texas, west to Nevada in the north, extreme southern coastal California and Baja California Norte, Mexico in the south (Fig. 211).

Natural history.— This species is associated with grassland, desert-grassland transitional habitats, Pacific semi-desert, and Great Basin, desert. Specimens have been collected in sand dune habitats in California, Arizona, Utah, and New Mexico, and otherwise in dry washes and streambeds throughout the species range. Adults have been collected largely on Compositae as follows: *Chaenactis stevioides* Hook. and Arn., *Chrysothamnus nauseosus* (Pall.) Britton, *C. viscidiflorus* (Hook.) Nutt. var. *pumilis, Gutierrezia lucida* Greene, *G. microcephala* (DC.) Gray, *Aplopappus arcadenius* (Greene) Blake, *A. linearifolius* DC (all Compositae); *Atriplex lentiformis* (Torr.) Wats. (Chenopodiaceae). Adults have also been collected from roots of *Aplopappus tenuisectus* (Greene) Blake and *Psilostrope cooperi* (Gray) Greene (Compositae). It is likely that many shrubby Compositae, especially those on which adults are commonly found, act as hosts for this species. Adults have been collected throughout the year at elevations of from 15–2876 m (N=63) (Fig. 232).

Adults have been collected in the stomach contents of the roadrunner, *Geococcyx californicus* (Aves) at Carlsbad, New Mexico.

Chorological relationships.— This species is sympatric throughout nearly its entire range with *A. albovestitus*; throughout Arizona, New Mexico, and western Texas with *A. lutulentus*; and throughout southeastern Arizona with *A. saginatus*. It is at most narrowly sympatric with its close relatives *A. jacobinus* in southeastern California, and *A. porosus* in Baja California Norte, México.

Phylogenetic relationships.— *Apleurus angularis* is the sister-species of *A. jacobinus* (Fig. 235). Presence of the apotypic state of tarsal claws each lacking a basal internal flange in some *A. porosus* and in *A. angularis* is a result of either hybridization or of homoplasy, more likely the former.

Apleurus (Apleurus) jacobinus (Casey), new combination
(Figs. 67, 71, 86, 94, 101, 208)

Centrocleonus pilosus LeConte 1876a:145 [not Chevrolat 1873:42]. NEW SYNONYMY Holotype (examined), male, labelled "Calif.", "type/ 5240", "*Centrocleonus/ pilosus* Lec." (MCZC). Type locality, California. Henshaw 1881–1882 (check.). Henshaw 1885 (check.).

Dinocleus jacobinus Casey 1891:179. Lectotype (here designated), female, one of eight syntypes, labelled "Cal.", "Casey/ bequest/ 1925", "TYPE USNM/ 37268", "*D./ jacobinus/* Cas." and with my designation label "*Dinocleus/ jacobinus/* Casey LECTOTYPE/ desig. Anderson" (USNM). Type locality, San Diego, California. Fall 1901 (check.). Fall 1913. Leng 1920 (catal.).

Dinocleus pilosus; Casey 1891 (key, redesc.). Fall 1901 (check.). Fall 1913. Leng 1920 (catal.). Essig 1958 (biol., misident. of *Apleurus albovestitus*).

Cleonus (*Dinocleus*) *capillosus* Csiki 1934:66. NEW SYNONYMY New name for *Centrocleonus pilosus* LeConte. Blackwelder 1939 (check.).

Cleonus (Dinocleus) jacobinus; Csiki 1934 (catal.).

Cleonus (*Dinocleus*) *pilosus*; Csiki 1934 (catal., as jr. homonym).

Cleonis capillosus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis jacobinus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis pilosus; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).

Notes about synonymy.— Based upon examination of very few specimens, Casey (1891) distinguished *Dinocleus jacobinus* Casey from *Dinocleus pilosus* (LeConte) on the basis of the smaller size, coarser darker and sparser elytral erect vestiture, more parallel-sided elytra with exposed humeri, and less markedly elevated alternate elytral intervals of the former. Having now examined large numbers of individuals I find that unequivocal assignment to either of the forms is not possible because of variation in all but one of the above characters, and conclude that the two forms are conspecific. I can see no differences in degree of coarseness or color of the erect elytral vestiture as noted by Casey (1891).

Problems in recognition.— Many specimens of *A. jacobinus* are confused with individuals of *A. angularis* and *A. porosus*. Characters and their states allowing for the separation of these species from *A. jacobinus* are discussed in the respective "Problems in recognition" sections for those species.

Description.— *Specimens examined.* 123 males, 255 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEI, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 12. *Size.* Length, male, 7.8–11.8 mm; female, 5.8–14.3 mm. Width, male, 3.7–5.5 mm; female, 2.8–6.5 mm. *Head.* Eye very prominent and convex in dorsal view. Frons and vertex with sparse to dense, large to very large, deep punctures. Frons and area immediately above eyes with dense very long erect hair-like scales (short or lacking in few specimens). Area immediately behind posterior margin of eye with large, deep, irregularly impressed punctures. Area above eyes markedly elevated above rest of frons (eyes apparently distinctly browed in anterior view). Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.67-0.79 times length in male; 0.65-0.80 in female) (Fig. 86). Median carina slightly to well-developed, low to high, rounded, in part obscured in many specimens by large deep punctures (Fig. 86). Dorsal and lateral punctation large to very large, deep, moderately dense to dense. Dorsally, excluding epistoma, with dense very long, erect hair-like scales (short or lacking from few specimens), and dense elongate-narrow appressed white scales. In lateral view with apical portion steeply declivous from point of antennal insertion to apex (Fig. 86a). Epistoma with apical margin rounded at middle (Fig. 86b). *Mouthparts.* Maxillary palpus with stipes lacking large seta on outer margin (as in Fig. 65). Labial palpi separated by more or less width of basal article of labial palpus (as in Figs. 62–63). Prementum with two or three pairs of large setae (as in Fig. 63). *Pronotum.* In dorsal view with lateral margins subparallel from base to almost apical one-quarter, then divergent to apical one-quarter (thus distinctly laterally tuberculate in appearance); markedly constricted at acute angle anterior to apical one-quarter, then straight or slightly convergent to apex; widest at tubercles to subequal in width at base and apical one-quarter (Fig. 71). Dorsal and lateral punctation moderately large to large, deep, sparse to moderately dense, in some specimens areas between punctures irregularly elevated thus appearing sculptured; punctures sparser and smaller on flanks. Scales white, elongate-fine to elongate-narrow, appressed, sparse and small or lacking medially from disk in broad, apically narrowed patch (except for midline in most specimens); dense laterally in pair of posterolaterally directed arcuate stripes; scales sparser at lateral margins and ventrally on flanks, to uniformly dense laterally, at lateral margins and on flanks, not obscuring individual large punctures. Median carina absent to present and distinct in some specimens. Dorsally covered throughout with sparse to moderately dense, fine, very long, erect hair-like scales, each situated in large puncture. Anterolateral margin with postocular projection absent or at most very slightly developed (Fig. 86a). *Prosternum.* With shallow impression anterior to each procoxal cavity and with well-developed rounded swelling anterior to each prosternal impression (Fig. 86a). *Elytra.* Moderately robust in general form (width at midlength 0.65-0.75 times length in males; 0.61–0.76 in females) (Fig. 71). In dorsal view with lateral margins slightly arcuate throughout length; humerus rounded, not distinct (Fig. 71). Sutural interval and intervals 3, 5, 7, and 9 with dense, very long, erect hair-like scales; sparser and slightly shorter on other intervals (short or lacking in some specimens). Dorsally with sutural interval and intervals 3, 5, 7, and 9 moderately to markedly swollen and convex (interval 5 at basal one-third and intervals 7 and 9 near base only slightly swollen in some specimens). Scales elongate-narrow, various in density and size; pattern slightly various, but generally with two variously sized posteromedially directed glabrous or nearly so areas, one at basal one-third from intervals 4 to 6, other at apical one-third from intervals 2 to 7, and with various number of scattered small glabrous or nearly so patches (Fig. 71). *Wings.* Absent. *Legs.* Foretibia of female with inner margin with small denticles in apical one-third; subapical tooth small, not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large to large, metatibial uncus of both sexes small. Tarsal claws slightly divergent, basal internal flange present, slightly to well-developed (Fig. 67). Ventral tarsal pilose vestiture of foretarsus of male absent of article 1, present as minute apical tufts of article 2, as small apical pads to moderately large pads on apical one-third of article 3; of foretarsus of female, lacking from article 1, present as minute to small pads at apex of articles 2 and 3; of mesotarsus and metatarsus of male, lacking from all three articles to as minute apical pads of article 2, and as small apical pads to moderately large pads on apical one-third of article 3; of mesotarsus and metatarsus of female, lacking from articles 1 and 2, present as minute apical tufts of article 3. *Mesosternum.* Mesosternal process flat to very slightly convex but not at all tumescent (as in Fig. 59). *Abdomen.* Ventral surface with moderately dense, elongate-fine appressed white scales. Abdominal sterna III to VI (especially III and IV) with moderately dense, individually distinct circular glabrous patches, each with large puncture and single long erect hair-like scale situated in or near center. Apex of abdominal sternum VII of male with small dorsally directed median truncate tooth. Abdominal tergum VIII uniformly convex, apical margin slightly elevated and reflexed. *Genitalia.* Female (six examined). Abdominal sternum VIII with lateral arms narrow, slightly outwardly arcuate in basal one-half, then parallel to near apex, markedly inwardly arcuate immediately before apex (Fig. 94a). Gonocoxite II with stylus very small, anteapical in position by more or less one-half length of stylus (Fig. 94b). Male (seven examined). Abdominal sternum VIII with paired sclerite with inner apices with slightly to moderately developed ventral projections (Fig. 101e). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel-sided throughout length. Internal sac short and high, markedly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe at midheight and midlength; small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket (Figs. 101a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites lightly sclerotized, each lacking median projection (Fig. 101d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of indistinct lightly sclerotized transverse sclerites (Fig. 101a).

Geographic variation.— Specimens from the southern part of the species range in extreme southern California and Baja California Norte, México have shorter and sparser dorsal erect vestiture than do individuals from the northern inland portions of the range. These same specimens tend to have the elytral intervals less markedly elevated throughout (Baja California Norte) or have only intervals 5 and 7 variously swollen basally (extreme southern California). Tarsal claws of the Baja California Norte individuals, although robust and not widely divergent, each have only a slightly developed basal internal flange. All of these southern individuals possess distinct glabrous patches on the abdominal sterna.

Two specimens from Point Reyes National Seashore and two specimens from Redwoods Regional Park near Oakland lack or else have extremely short dorsal erect vestiture (apparently not due to abrasion), but otherwise are typical *A. jacobinus.*

Geographic distribution.— This species is found in California from the San Francisco Bay area south through coastal and central California to northern coastal Baja California Norte, Mexico (Fig. 208).

Natural history.— This species is associated exclusively with Pacific semi-desert habitat. Adults of have been collected on *Aster* sp., *Hemizonia* sp., *H. pungens* (H. and A.) T. and G. (Compositae); beans (Leguminosae); *Gossypium hirsutum* L. (cotton; Malvaceae); and carrots (Umbelliferae). They have also been found in various shipments of beans and raisins. Definite hosts are not known. Adults have been collected throughout the year at elevations of from 5–424 m (N=15) (Fig. 232).

Chorological relationships.— This species is sympatric throughout its range with western *A. albovestitus*, and is at most narrowly sympatric with southern Californian *A. angularis* and *A. porosus* from southern California or northern Baja California Norte, México.

Phylogenetic relationships.— *Apleurus jacobinus* is the sister-species of *A. angularis* (Fig. 235).

Apleurus (Apleurus) albovestitus (Casey), new combination
(Figs. 75–79, 88, 95, 103, 209)

Cleonus molitor LeConte 1858:78 [not Gyllenhal 1834:174]. NEW SYNONYMY Holotype (examined), female, labelled with a gold circle (=California), "*Cleonus/ molitor/* Lec.", "Type/ 5183", "Anobium!/ parasitic!" (MCZC). Type locality, California. Gemminger and von Harold 1871 (catal.).

Centrocleonus molitor; LeConte 1876a (key, diag.). Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1889.

Dinocleus albovestitus Casey 1891:183. Lectotype (here designated), male, one of an undetermined number of syntypes, labelled "Los Angeles/ Co. CAL", "TYPE USNM/ 37273", "CASEY/ bequest/ 1925", "*D./ albovestitus/* Cas." and with my designation label "*Dinocleus albovestitus/* Csy. LECTOTYPE/ desig. Anderson" and genitalia in microvial under labels (USNM). Type locality, Los Angeles, California. Fall 1901 (check.). Casey 1904. Leng 1920 (catal.). Ting 1936 (morphol.). Bruhn 1947 (morphol.). Sanders 1960 (morphol.).

Dinocleus densus Casey 1891:185. NEW SYNONYMY Lectotype (here designated), male, one of four syntypes, labelled "Winslow", "CASEY/ bequest/ 1925", "TYPE USNM/ 37277", "*D./ densus*/ Cas." and with my designation label "*Dinocleus/ densus* Csy./ LECTOTYPE/ desig. Anderson" (USNM). Type locality, Winslow, Arizona. Wickham 1896 (check.). Leng 1920 (catal.).

Dinocleus molitor; Casey 1891 (key, redesc.). Fall 1901 (check.). Champion 1902–1906 (syn., distn.). Casey 1904. Leng 1920 (catal.).

Dinocleus wickhami Casey 1891:184. NEW SYNONYMY Holotype (examined), male, labelled "Indio/ California/ Wickham", "CASEY/ bequest/ 1925", "TYPE USNM/ 37276", "*D./ wickhami*/ Cas." (USNM). Type locality, Indio, California. Fall 1901 (check.). Leng 1920 (catal.). Tanner 1934 (check.).

Dinocleus interruptus Casey 1904:322 [not Zoubkoff 1829:162]. NEW SYNONYMY Lectotype (here designated), male, one of three syntypes, labelled "Ut", "CASEY/ bequest/ 1925", "TYPE USNM/ 37274", "*interruptus*" and with my designation label "*Dinocleus/ interruptus* Csy./ LECTOTYPE/ desig. Anderson" (USNM). Type locality, Utah. Leng 1920 (catal.).

Dinocleus mexicanus Casey 1904:322. NEW SYNONYMY Lectotype (here designated), male, one of two syntypes, labelled "Guer.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37275", "*mexicanus*" and with my designation label "*Dinocleus/ mexicanus* Csy./ LECTOTYPE/ desig. Anderson" (USNM). Type locality, Guerrero, México. Champion 1902–1906 (distn.).

Cleonus (*Dinocleus*) *albovestitus*; Csiki 1934 (catal.).

Cleonus (*Dinocleus*) *densus*; Csiki 1934 (catal.).

Cleonus (*Dinocleus*) *interruptus*; Csiki 1934 (catal.).

Cleonus (*Dinocleus*) *mexicanus*; Csiki 1934 (catal.).

Cleonus (*Dinocleus*) *structor* Csiki 1934:67. NEW SYNONYMY New name for *Cleonus molitor* LeConte. Blackwelder 1939 (check.).

Cleonus (*Dinocleus*) *wickhami*; Csiki 1934 (catal.).

Cleonus mexicanus; Blackwelder 1947 (check.).

Dinocleus pilosus; Essig 1958 (biol., misident.).

Cleonus albovestitus; Hardy and Andrews 1976 (distn., biol.). Andrews *et al.* 1979 (distn., biol.).

Cleonis albovestitus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis densus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis interruptus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis mexicanus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis molitor; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).

Cleonis structor; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis wickhami; O'Brien and Wibmer 1982 (catal., distn.).

molitor, incertae sedis; Chevrolat 1873.

Notes about synonymy.— I consider *A. albovestitus* to be composed of a number of largely allopatric morphotypes most of which are distinguished solely on the basis of patterns of surface vestiture (Figs. 75–79), but which exhibit continuous intergradation in zones of parapatry or narrow sympatry (see "Geographic variation" section).

One of these morphotypes is largely black and glabrous, most of the surface vestiture having been abraded (Figs. 78–79). This is *Centrocleonus molitor* LeConte. *Dinocleus mexicanus* Casey is a form of this same morphotype, but in which the scales have not been extensively abraded. *Dinocleus densus* Casey, is a form in which there has been no abrasion of scales. This morphotype is confined to the Colorado and Gila River drainages.

The second morphotype, that with dense elytral and ventral abdominal scales and lacking abdominal glabrous patches but with small elytral glabrous patches, includes *Dinocleus interruptus* Casey, *D. wickhami* Casey, and *D. albovestitus* Casey (Figs. 76–77).

The third morphotype is recognized, among other characters, by the larger and more numerous elytral and abdominal glabrous patches (Fig. 75).

Since I have been unable to find other structural features which correlate with the variation in patterns of surface vestiture to allow for reliable separation of the various morphotypes, I conclude that a single species is present, but with allopatric forms having different locally adaptive patterns of surface vestiture.

Champion (1902–1906) incorrectly stated that *D. mexicanus* Casey is a new name for *Centrocleonus molitor* LeConte.

Problems in recognition.— Individuals of *A. albovestitus* might only be confused with those of *A. saginatus* although key characters should serve to reliably separate all members of the two species. Special note should be made of the marked secondary sexual dimorphism in extent of ventral tarsal vestiture in *A. saginatus* that is not as marked in *A. albovestitus*. This allows for easy recognition of males of *A. saginatus*.

All *A. albovestitus* that possess glabrous ventral abdominal patches are found only in western California; those *A. albovestitus* found sympatrically with *A. saginatus* have extremely dense scales on the abdominal sterna and lack the glabrous patches present in all *A. saginatus*.

Description.— *Specimens examined.* 1251 males, 1470 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEI, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 13. *Size.* Length, male, 11.8–16.8 mm; female, 12.8–21.4 mm. Width, male, 5.1–7.2 mm; female, 5.4–8.8 mm. *Head.* Eye slightly prominent and convex in dorsal view. Frons and vertex with sparse to moderately dense, small, shallow punctures. Frons largely lacking suberect or erect vestiture, with at most only sparse, small suberect scales immediately above eyes. Area immediately behind posterior margin of eye with small, shallow to moderately deep, irregularly impressed punctures. Area above eyes continuous with and not elevated above rest of frons (eyes not browed in anterior view). Width of frons greater than to subequal in width to apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.62–0.78 times length in male; 0.63–0.79 in female) (Fig. 88). Median carina lacking. Dorsal and lateral punctation small to moderately large, moderately deep, sparse to moderately dense. Dorsally, excluding epistoma, either lacking suberect or erect vestiture or with at most scattered short suberect scales; and lacking (abraded) or with dense elongate-narrow appressed white scales. In lateral view with apical portion steeply declivous from point of antennal insertion to apex (Fig 88a). Epistoma with apical margin rounded at middle (Fig. 88b). *Mouthparts.* Maxillary palpus with stipes with large seta on outer margin (as in Fig. 64). Labial palpi separated by more or less width of basal article of labial palpus (as in Fig. 62–63). Prementum with two or three pairs of large setae (as in Fig. 63). *Pronotum.* In dorsal view with lateral margins straight and subparallel to slightly convergent from base to almost apical one-quarter, not to slightly expanded laterally at apical one-quarter (thus indistinctly laterally tuberculate in appearance); moderately constricted at obtuse to subacute angle anterior to apical one-quarter, then straight and slightly convergent to apex; widest at base to subequal in width at base and apical one-quarter (Figs. 75–79). Dorsal and lateral punctation small, shallow, sparse to moderately dense; punctures sparser on flanks; outer margins of larger punctures not swollen or glabrous. Scales white, elongate-narrow to broad, appressed, entirely lacking (abraded) to sparse and small or lacking medially from disk in broad, apically narrowed patch (except for midline in most specimens); very dense laterally and ventrally on flanks onto prosternum; scales sparser at lateral margins. Median carina lacking to present but irregularly developed but with at least a broad low rounded median swelling in most specimens. Dorsally lacking suberect or erect vestiture or with sparse, short, erect hair-like scales, each situated in large puncture. Anterolateral margin with postocular projection slightly to moderately developed (Fig. 88a). *Prosternum.* With shallow impression anterior to each procoxal cavity and with well-developed rounded swelling anterior to each prosternal impression (Fig. 88a). *Elytra.* Moderately robust to moderately elongate-narrow in general form (width at midlength 0.59-0.72 times length in males; 0.56-0.69 in females) (Figs. 75–79). In dorsal view with lateral margins straight, slightly convergent to divergent from apical one-third to humerus; humerus rounded to obtuse, indistinct to distinct, with at most only very few small glabrous shiny tubercles. Dorsal suberect or erect vestiture lacking to sparse, short and fine. Dorsally with all intervals flat. Scales, if present, elongate-narrow to elongate-fine, white to golden. Scale pattern extremely various; with scales entirely or largely lacking (abraded) except near apex on declivity (Figs. 78–79), to present to various extent (not abraded), uniformly dense and large on sutural interval and intervals 3, 5, 7, and 9, uniformly sparse and small on intervals 2, 4, 6, and 8, distinct glabrous patches absent (Fig. 77); or, to scales not abraded, uniformly dense and large on sutural interval and intervals 3, 5, 7, and 9, and sparse and small to various degree on intervals 2, 4, 6, and 8, with at most scattered but few glabrous patches present (Fig. 76); or, to sutural interval with scales sparse and small or large and dense, otherwise with scales of elytral intervals extremely various in size and density, with numerous irregularly distributed small and moderately large glabrous or nearly so patches present (Fig. 75). *Wings.* Short (slightly shorter than elytra in length [0.2%, N=4]), to long (slightly greater than elytra in length [99.8%, N=1717]). Branches of 2A complete and joined at base. *Legs.* Foretibia of female with inner margin with small to minute denticles in apical one-third; subapical tooth minute, not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large to large, metatibial uncus of both sexes small. Tarsal claws slightly divergent, basal internal flange present, well-developed (as in Fig. 67). Ventral tarsal pilose vestiture of foretarsus of male absent to present as minute apical tufts on articles 1 to 3; of mesotarsus of male, lacking from articles 1 and 2, present as minute apical tufts of article 3; lacking from articles 1 to 3 of all tarsi of female and from articles 1 to 3 of metatarsus of male. *Mesosternum.* Mesosternal process flat to very slightly convex but not at all tumescent (as in Fig. 59). *Abdomen.* Ventral surface either with scales present, white, appressed, along posterior margins of abdominal sterna, also with scattered, suberect short hair-like scales, each situated in large puncture; or, with white appressed scales uniformly very dense, abdominal sterna III to VI without glabrous patches to with scales moderately dense, individually distinct circular glabrous patches present (especially on abdominal sterna III and IV), each with large puncture and single short suberect hair-like scale situated in or near center. Apex of abdominal sternum VII of male with large dorsally directed median truncate tooth. Abdominal tergum VII of female slightly medially longitudinally carinate, apical margin moderately elevated and reflexed; abdominal tergum VIII of female markedly medially longitudinally carinate, apical margin moderately elevated and reflexed. *Genitalia.* Female (12 examined). Abdominal sternum VIII with lateral arms broad, straight and slightly divergent from base to apical one-third, slightly inwardly arcuate from apical one-third to apex (Fig. 95a). Gonocoxite II with stylus absent, with darkly sclerotized slightly elevated dorsal subapical ridge (Fig. 95b). Male (eight examined). Abdominal sternum VIII with paired sclerite with inner apices with well-developed ventral projections (Fig. 103e). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel-sided throughout length. Internal sac short and high, slightly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe near dorsal margin at midlength; small median lobe on dorsal surface immediately anterior to crest of median dorsal pocket (Figs. 103a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites darkly sclerotized, each with long dorsoapically directed median projection (Fig. 103d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of indistinct lightly sclerotized transverse sclerites (Fig. 103a).

Geographic variation.— Variation in the pattern of surface vestiture in members of this species is very extensive (Figs. 75–79). There is also slight variation in other structural features but these could not be reliably correlated with the variation in vestiture to allow recognition of more than one species (see also "Notes about synonymy" section). However, I recognize three largely allopatric or parapatric morphotypes. In the first of these, vestiture is abraded or at least subject to abrasion. Such specimens are primarily black and glabrous (except for the tibiae and tarsi) and possess moderately dense to dense scales only along the lateral margins of the elytra and the posterior margins of the abdominal sterna (especially V and VI), and to a various extent in some specimens, also in the apical one-third of the elytra, onto the elytral declivity (Figs. 78–79). Scattered single scales are also found variably on the thoracic and abdominal sterna, elytra and femora. In individuals in which scales are variably present on the elytra, the scales are uniformly dense and large on all intervals to slightly less dense and smaller on intervals 2, 4, and 6. Scales are very easily abraded on these specimens. Individuals of this morphotype have been collected at elevations of from -67–870 m (N=23).

This form is found throughout the southern portion of the Colorado River drainage, the western portion of the Gila River drainage, and throughout Imperial County, California. Individuals from the latter area tend to have the elytral scales denser and not abraded and although lacking distinct glabrous elytral patches, the general scale pattern clearly grades into that pattern to be discussed next in which small elytral glabrous patches are present (Fig. 76). Individuals of this morphotype seem restricted to *Pluchea sericea* (Nutt.) Coville (Compositae) in sand dune habitats along the margins of waterways in these areas.

A second form of *A. albovestitus* is also found in these and other areas, and although the ranges of the two morphotypes narrowly overlap, they have not been collected together at the same time and place. Individuals of this form possess large and dense elytral surface vestiture that is not prone to abrasion. All abdominal sterna have uniformly very dense scales; no glabrous patches are present. Elytral scales are uniformly large and dense to very dense, but are lacking or very sparse in scattered small to moderately large patches on elytral intervals 2 to 8 (Fig. 76). Scales of the sutural interval of many of these specimens are uniformly small and sparse. Punctures of elytral striae are small and indistinct. This form is widespread from Nevada and Utah south to extreme western Texas, New Mexico, Arizona and southeastern California, south into Baja California Sur, Mexico. Individuals of this form in Utah and northern Arizona, along the northern Colorado and Virgin River drainages, differ from those elsewhere by largely lacking glabrous or nearly so patches on the elytra (Fig. 77). Scales of some individuals in these areas are less dense and smaller on intervals 2, 4, and 6, much the same pattern as in specimens of the largely glabrous morphotype in which elytral scales have not been extensively abraded. This similarity in scale pattern suggests the notion that the largely glabrous individuals of morphotype 1 in the southern portion of the Colorado River drainage may have reached this area as a result of downriver dispersal from parent populations along the Virgin and northern Colorado Rivers. Individuals of this morphotype have been collected at elevations of from 2–1446 m (N=49).

A third pattern of vestiture is found in individuals from southern coastal to northern coastal and central California. In this form, scales of the elytra are less dense and smaller than in the previous forms, and the elytral glabrous or nearly so patches are generally larger and more numerous (Fig. 75). Punctures of the elytral striae are generally slightly larger and more distinct than in the other morphotypes. Abdominal sterna (especially III and IV) of many individuals with this elytral scale pattern possess small to moderately large indistinct to distinct glabrous areas, each with a single short suberect hair-like scale situated in the center. Suberect vestiture, lacking from the elytra on the other morphotypes, is short, sparse and fine on the elytra of many of these specimens. Elytral scale patterns of this and of the second morphotype completely intergrade in southern California. Individuals of this third morphotype have been collected at elevations of from -41–3185 m (N=61).

The potential adaptive significance of variation in surface vestiture is not known but is suspected to be influenced by thermoregulatory effects, or, more likely, by cryptic effects resulting from similarity in color and pattern to the ground substrate (see "Evolutionary Trends" section).

Brachypterous specimens of *A. albovestitus* are only known from two localities in Baja California Norte, México.

Geographic distribution.— This species is distributed from New Mexico and western Texas west through Utah and Nevada to northern California in the north, through Arizona and extreme northwestern México to southern California and Baja California Sur, México in the south (Fig. 209).

Natural history.— This species is associated with a variety of habitats as follows; desert-grassland transitional, Pacific semi-desert, and Great Basin, Chihuahuan, Mojave, and Sonoran deserts. Adults of this species have been collected in sand dune habitats in California, Arizona, Utah, Nevada (label data; Andrews *et al.* 1979; Hardy and Andrews 1976) and otherwise primarily in dry washes and stream beds throughout the species range. Andrews *et al.* 1979 tentatively suggest that the species is an obligate sand associate.

Adults have been collected on a wide variety of plants as follows: *Ephedra* sp., *E. californica* Wats. (Ephedraceae); *Ambrosia* sp., *A. psilostachya* DC., *Artemesia tridentata* Nutt., *Baileya multiradiata* Harv. and Gray, *B. pleniradiata* Harv. and Gray, *Baccharis glutinosa* Pers., *Chrysothamnus nauseosus* (Pall.) Britton, *Dicoria* sp., *Franseria* sp., *F. confertiflora* (DC.) Rydb., *F. dumosa* Gray, *Flourensia cernua* DC., *Gutierrezia microcephala* (DC.) Gray, *Aplopappus acradenius* (Greene) Blake, *Hymenoclea* sp., *H. salsola* T. and G., *Hymenothrix wislizeni* Gray, "*Palafoxia arida*", *P. linearis* (Cav.) Lag., *Pluchea sericea* (Nutt.) Coville, *Verbesina enceloides* (Cav.) Benth. and Hook., *Xanthium* sp., (all Compositae); *Larrea tridentata* (DC.) Coville (Zygophyllaceae); *Hordeum* sp., *Sitanion* sp., (Graminae); *Datura* sp., (Solanaceae); *Gossypium* sp., (Malvaceae); *Eriogonum fasciculatum* Benth. var. *polifolium* (Polygonaceae); *Astragalus* sp., *Cercidium floridum* Benth., *Medicago sativa* L., *Olneya tesota* Gray, *Prosopis juliflora* (Swartz) DC. (all Leguminosae); *Atriplex* sp., *A. lentiformis* (Torr.) Wats., *Salsola kali* L., *Sarcobatus vermiculatus* (Hook.) Torr. (all Chenopodiaceae); *Vitus* sp. (Vitaceae); *Prunus persica* Batsch. (peach; Rosaceae); *Raphanus sativus* L. (radish; Cruciferae). No definite hosts are known, but the vast majority of plant association are with Compositae; records of occurrence on members of other families are generally single instances of but one or two individuals and very likely represent chance occurrences. I suspect that a wide variety of Compositae serve as host plants for this species.

Adults have been collected throughout the year at elevations from -67–3185 m (N=133) (Fig. 232).

As noted in the "Geographic variation" section, individuals of each of the three morphotypes occur over slightly different elevational ranges.

Chorological relationships.— This species is sympatric with *A. lutulentus* in Arizona, New Mexico and western Texas; with *A. angularis* throughout most of its range, with the exception of northern California; with *A. jacobinus* throughout entire range of that species in California; narrowly sympatric with *A. porosus* in Baja California Norte, México and southern California; and sympatric with its sister-species *A. saginatus* throughout Arizona, southern New Mexico, and extreme nothwestern México.

I have caught large numbers of specimens of *A. albovestitus* together with *A. lutulentus* on *Chrysothamnus nauseosus* (Compositae) in the vicinity of Portal, Arizona and Animas, New Mexico.

Phylogenetic relationships.— *Apleurus albovestitus* and *A. saginatus* are sister-species (Fig. 235).

Apleurus (Apleurus) saginatus (Casey), new combination
(Figs. 63–64, 80, 87, 96, 104, 206)

Dinocleus saginatus Casey 1891:182. Holotype (examined), male, labelled "Ariz.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37272", "*D./ saginatus/* Cas." (USNM). Type locality, Arizona. Leng 1920 (catal.).

Dinocleus dentatus Champion 1902–1906:100. NEW SYNONYMY Holotype (examined), female, labelled "Type", inverted "Sp. figured", "Pinos Altos/ Chihuahua,/ Mexico/ Buchan-Hepburn", "B.C.A. Col. IV.4./ *Dinocleus/ dentatus,/* Champ.", inverted "*dentatus*, Ch." (BMNH).Type locality, Pinos Altos, Chihuahua, Mexico.

Cleonus (*Dinocleus*) *dentatus*; Csiki 1934 (catal.).

Cleonus dentatus; Blackwelder 1947 (check.).

Cleonus (*Dinocleus*) *saginatus*; Csiki 1934 (catal.).

Cleonis dentatus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis saginatus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— Following examination of types and numerous specimens I regard *Dinocleus saginatus* Casey and *D. dentatus* Casey as conspecific.

Problems in recognition.— Individuals of this species might only be confused with those of *A. albovestitus* (see "Problems in recognition" section for *A. albovestitus*).

Description.— *Specimens examined.* 597 males, 657 females. Data about variation in LR, WF, WRA, LP, WPB, WPT, WEIM, LEI, WPB/LP, WPT/WPB, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 14. *Size.* Length, male, 14.9–19.5 mm; female, 15.9–21.8 mm. Width, male, 5.8–8.0 mm; female, 6.2–9.0 mm. *Head.* Eye slightly prominent and convex in dorsal view. Frons and vertex with sparse, small, shallow punctures. Frons largely lacking suberect or erect vestiture, with at most only sparse, small suberect scales immediately above eyes; white elongate-narrow appressed scales dense above eyes, sparser medially. Area immediately behind posterior margin of eye with small, shallow to moderately deep, irregularly impressed punctures. Area above eyes continuous with and not elevated above rest of frons (eyes not browed in anterior view). Width of frons greater than to subequal in width to apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.63–0.73 times length in male; 0.63–0.74 in female) (Fig. 87). Median carina lacking to variously developed as low rounded to sharp fine glabrous line. Dorsal and lateral punctation small, shallow, sparse. Dorsally, excluding epistoma, with short scattered suberect scales; and with dense elongate-narrow appressed white scales. In lateral view with apical portion steeply declivous from point of antennal insertion to apex (Fig. 87a). Epistoma with apical margin rounded at middle (Fig. 87b). *Mouthparts.* Maxillary palpus with stipes with large seta on outer margin (Fig. 64). Labial palpi separated by more or less width of basal article of labial palpus (Fig. 63). Prementum with two or three pairs of large setae (Fig. 63). *Pronotum.* In dorsal view with lateral margins slightly arcuate to straight and subparallel to slightly convergent from base to almost apical one-quarter, not to slightly expanded laterally at apical one-quarter (thus indistinctly laterally tuberculate in appearance); moderately constricted at obtuse to subacute angle anterior to apical one-quarter, then straight and slightly convergent to apex; widest at base to subequal in width at base and apical one-quarter (Fig. 80). Dorsal and lateral punctation small, shallow, sparse to moderately dense; punctures sparser and shallower on flanks; outer margins of larger punctures swollen, glabrous and shiny (appearing as small tubercles). Scales white, elongate-narrow to broad, appressed sparse and small or lacking medially on disk in broad, apically narrowed patch (except for midline in most specimens); very dense laterally and ventrally on flanks onto prosternum; scales sparser at lateral margins. Median carina lacking to present and irregularly developed in basal one-half as low, broad glabrous line. Dorsally with sparse, short, erect hair-like scales, each situated in large puncture. Anterolateral margin with postocular projection slightly developed (Fig. 87a). *Prosternum.* With shallow impression anterior to each procoxal cavity and with well-developed rounded swelling anterior to each prosternal impression (Fig. 87a). *Elytra.* Moderately robust to moderately elongate-narrow in general form (width at midlength 0.59-0.62 times length in males; 0.56-0.64 in females) (Fig. 80). In dorsal view with lateral margins straight or nearly so, slightly convergent from apical one-third to humerus; humerus obtuse, distinct, with numerous distinct small glabrous shiny tubercles (also present at bases of adjacent elytral intervals) (Fig. 80). Dorsal suberect or erect vestiture lacking. Dorsally with all intervals flat. Scales appressed, white to golden in color, various in size and density. Scale pattern various, with numerous small irregularly distributed glabrous or nearly so patches (Fig. 80). *Wings.* Long (slightly greater than elytra in length). Branches of 2A complete and joined at base. *Legs.* Foretibia of female with inner margin with small to minute denticles in apical one-third; subapical tooth minute to small, not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large to large, metatibial uncus of both sexes small. Tarsal claws slightly divergent, basal internal flange present, well-developed (as in Fig. 67). Ventral tarsal pilose vestiture of foretarsus of male present as small rounded apical pads of article 1, as moderately large rounded pads on apical one-half of article 2, and as large rounded pads on apical one-half of article 3; of foretarsus of female, lacking from articles 1 and 2, present as minute apical tufts of article 3; of mesotarsus of male, absent to present as minute apical tufts of article 1, present as small apical pads of article 2, and present as moderately large round pads on apical one-third of article 3; of metatarsus of male, absent from article 1, present as minute apical tufts of article 2, and present as small apical pads of article 3; lacking from articles 1 to 3 of mesotarsus and metatarsus of female. *Mesosternum.* Mesosternal process flat to very slightly convex but not tumescent (as in Fig. 59). *Abdomen.* Ventral surface with very dense elongate-narrow to broad, white, appressed scales; abdominal sterna III to VI (especially III and IV) with moderately dense individually distinct large circular glabrous shiny patches, each with large puncture and single short suberect hair-like scale situated in or near center. Apex of abdominal sternum VII of male with large dorsally directed median truncate tooth. Abdominal tergum VII of female slightly medially longitudinally carinate, apical margin moderately elevated and reflexed; abdominal tergum VIII of female markedly medially longitudinally carinate, apical margin moderately elevated and reflexed. *Genitalia.* Female (six examined). Abdominal sternum VIII with lateral arms broad, straight and slightly divergent from base to near apex, slightly inwardly arcuate near apex (Fig. 96a). Gonocoxite II with stylus absent, with darkly sclerotized slightly elevated dorsal subapical ridge (Fig. 96b). Male (six examined). Abdominal sternum VIII with paired sclerite with inner apices with well-developed ventral projections (as in Fig. 103e). Aedeagus elongate-narrow, in lateral view thickest at midlength; in ventral view more or less parallel sided throughout length. Internal sac short and high, slightly apically deflexed; median dorsal pocket high, with moderately large dorsolaterally directed paramedial lobe near dorsal margin at midlength (Figs. 104a,b). Eversible apical sclerite complex with paired narrow scythe-like sclerites darkly sclerotized, each with long dorsoapically directed median projection (Fig. 104d); adjacent ventral surface and basal portion of sides of apex of internal sac with pair of indistinct lightly sclerotized transverse sclerites (Fig. 104a).

Geographic distribution.— This species is found in southeastern Arizona and extreme southwestern New Mexico, south into northwestern Mexico (Fig. 206).

Natural history.— This species appears restricted to dry washes and riparian habitats in the desert-grassland transitional habitat bordering the eastern Sonoran desert region. Adults have been collected on *Baccharis glutinosa* Pers., *Chrysothamnus nauseosus* (Pall.) Britton, *Hymenoclea monogyra* Torr. and Gray (all Compositae). Definite hosts are not known. Adults have been collected throughout the year at elevations of from 283–1820 m (N=36) (Fig. 232).

Chorological relationships.— This species is sympatric throughout its range with *A. angularis*, *A. lutulentus*, and its sister-species *A. albovestitus*. I know of no records of *A. saginatus* being caught with any of these three species.

Phylogenetic relationships.— *Apleurus saginatus* and *A. albovestitus* are sister-species (Fig. 235).

Genus *Cleonidius* Casey

Curculio; Pallas 1781 (sp. desc.). Herbst 1795.

Cleonus; Say 1831 (sp. desc.). Melsheimer 1853 (in part; check.). Gemminger and von Harold 1871 (in part; catal.). LeConte 1876a (key, sp. descs.). Henshaw 1881–1882 (check.). LeConte and Horn 1883 (key). Henshaw 1885 (check.). Wickham 1899. Wickham 1896 (check.). Fall 1897 (sp. desc.). Fall 1901 (check.). Wickham 1902 (check.). Fletcher 1906. Fall and Cockerell 1907 (in part; check.). Pierce 1907 (biol.). Chittenden 1911 (biol.). Ely 1913 (biol.). Gibson 1914. Anderson 1914. Blatchley and Leng 1916 (key, sp. redescs.). Yothers 1916. Leng 1920 (in part; catal.). Leonard 1926 (in part; check.). Böving 1927 (in part; larval key). Bradley 1930 (in part; key). Wilcox *et al.* 1934. Brimley 1938 (check.). Blackwelder 1947 (in part; check.). Bruhn 1947 (morphol.). Essig 1958 (biol.). Sanders 1960 (morphol.). Tanner 1966 (in part; sp. redesc., biol.). Kingsolver 1972. Kumar *et al.* 1976 (biol.). Arnett *et al.* 1980 (key, biol.).

Rhynchophorus; Say 1831 (in part; sp. desc.).

Cleonis; Kirby 1837 (sp. desc.). O'Brien and Wibmer 1982 (catal., distn.). O'Brien and Wibmer 1984 (in part).

Lixus; Zoubkoff 1833 (sp. desc.). Boheman 1836 (sp. desc.). Randall 1838 (in part; sp. desc.). Mannerheim 1843 (sp. desc.). Motschulsky 1845 (sp. desc.). Gemminger and von Harold 1871 (in part; catal.). Capiomont and Leprieur 1874 (sp. redesc.). Sprague and Austin 1875. LeConte 1876a (in part; key, sp. descs.). Henshaw 1881–1882 (in part; check.). LeConte and Horn 1883 (in part; key). Henshaw 1885 (in part; check.). Wickham 1889. Faust 1890. Casey 1891 (in part; key). Horn 1894 (in part; check.). Petri 1905 (key). Petri 1912. Blatchley 1914 (sp. desc.). Blatchley and Leng 1916 (in part; key, sp. redesc.). Leng 1920 (in part; catal.). Lukjanovitsh 1926. Blatchley 1930. Bradley 1930 (in part; key). Arnett 1960–1962 (in part; key). Kissinger 1964 (in part; key).

Apleurus; Chevrolat 1873 (in part, espèces lyxiformes; check., key, sp. descs.).

Cleonidius Casey 1891:186. As subgenus of *Cleonus*. Gender, masculine. Type species *Cleonis vittatus* Kirby (=*Lixus poricollis* Mannerheim) by subsequent designation (Faust 1904:190). Champion 1902–1906 (sp. redesc.). Csiki 1934 (catal.). Blackwelder 1939 (check.). Arnett 1960–1962 (key, catal.). Kissinger 1964 (key). Hatch 1971 (key, sp. redescs.)

Cleonidius; Faust 1904 (key, check., type species desig.).

Lixestus Reitter 1916:89. As subgenus of *Lixus*. NEW SYNONYMY. Gender, masculine. Type species *Curculio vibex* Pallas by monotypy. Csiki 1934 (catal.).

Lixus (Lixesthus); Ter-Minasyan 1978 (error, misspelling).

Notes about synonymy.— The subgenus *Cleonidius* was first proposed by Casey (1891) to accomodate those *Cleonus* with a cylindrical rostrum, more or less vittate elytral scale pattern, and an elongate-narrow body form approaching that of *Lixus*. Indeed species of *Cleonidius* very closely resemble *Lixus* and species of the two genera are often difficult to separate. This is evidenced by the placement of some species, now regarded as *Cleonidius*, originally in *Lixus*, and by the herein proposed new synonymy of *Lixestus* Reitter, a subgenus of *Lixus*, with *Cleonidius*.

Among *Lixus* species examined, only *Lixus (Lixestus) vibex* Pallas (type species of *Lixestus*), was found to possess a small dorsal median tubercle at the basal margin of variously abdominal sterna V to VII, that is characteristic of *Cleonidius*. However, other *Lixus* species, as yet not examined for this character, may also prove to require inclusion in *Cleonidius* should they possess the apotypic state as noted above. This is not surprising given the similarity of the two genera, their apparent close phylogenetic relationship, and previous lack of consideration of *Cleonidius* species in past studies and resulting classifications of Palearctic *Lixus* species. Thus there is the need for a reevaluation of the validity of at least the subgeneric groupings of *Lixus* in this light. Whether *Cleonidius* will remain as a valid genus when this is done remains to be seen; undoubtedly *Lixus* species will require reclassification.

Prior to the present study, *Cleonidius* had been given generic status by Faust (1904), only.

Diagnosis.— Adult Cleoninae with elongate-narrow to moderately robust body form (Figs. 118–136). Eye more or less oval to elongate-oval, flat (Figs. 137–156). Rostrum elongate-narrow to moderately robust, with at most only low median carina (indicated in the majority of species by low glabrous shiny line) (Figs. 137–156). Antennal funiculus with article 1 longer than article 2; article 2 more or less as wide as long (Figs. 137–156). Pronotal postocular lobes lacking to present and well-developed; postocular vibrissae uniformly short to long but of unequal length, longest immediately behind base of eye (Figs. 137–156). Pronotal disk slightly to distinctly vittate, with white scales largest and/or densest immediately laterad of midline, smaller and/or sparser laterally; largely whitish in color, underlying dark cuticle largely obscured by white scales (Figs. 118–136). Prosternal swellings absent or present, if present, situated immediately anterior to each procoxal cavity (Fig. 8). Ventral tarsal pilosity extensive (covering greater part of ventral surface of each tarsal article) to reduced in extent or lacking from at least the basal tarsal articles of some species. Tibia with corbel ridge rounded (Fig. 5). Abdominal sternum VII (at least) of females dorsally (internally) with variously developed basal median glabrous shiny tubercle, evident externally as shallow impression. Abdominal sternum VIII of female with basal arm short to long (Figs. 157–176).

Description.— *Size.* Small to moderately large; elongate-narrow to moderately robust in general body form (Figs. 118–136). *Mouthparts.* Prementum flat to slightly swollen ventrally; with as many as three large setae on each side. Maxillary palpus with palpifer and stipes each with at least one large seta. Labial palpi separated by distance subequal to width of basal article of labial palpus. *Rostrum.* Elongate-narrow to robust, not to markedly medially tumescent, with at most only low median carina indicated in majority of species by fine glabrous shiny line (Figs. 137–156). Epistoma not to moderately swollen, with apical margin emarginate medially (Figs. 137b-156b). Antenna with funiculus with article 1 longer than article 2; article 2 more or less as long as wide; apical three articles of club lacking placoidal sensillae. *Head.* Eye oval to elongate-oval; flat (Figs. 137–156). Upper margin of eye rounded, frons flat to variously convex. *Vestiture.* Dorsum with suberect to erect vestiture absent to present and dense, short to very long in length; with simple appressed white scales of various size and density. *Pronotum.* Dorsal surface punctate, median basal area shallowly to deeply impressed; disk with or without various other impressions. Pronotal disk slightly to distinctly vittate, with white scales largest and/or densest immediately laterad of midline, smaller and/or sparser laterally; largely whitish in color, underlying dark cuticle medially largely obscured by white scales (Figs. 118–136). Lateral margins with white scales large and/or dense. Pronotum widest at base to subequal in width from base to near apex, lateral margins arcuate, more or less parallel or slightly convergent from base to near apex, then variously constricted and more convergent to apex (Figs. 118–136). Pronotal postocular lobes lacking to present and well-developed; postocular vibrissae uniformly short (length less than one-half width of an eye) to long but of unequal length, longest behind base of eye (greatest length greater than one-half width of an eye) (Figs. 137a-156a). *Prosternum.* With shallow, rounded impression anterolaterad of each procoxal cavity; with or without variously developed rounded swelling immediately anterior to each procoxal cavity (Fig. 8). *Legs.* Tarsus moderately broad to broad; articles 2 and 3 more or less subequal in length, width and length of each article subequal to slightly wider than long; article 1 only slightly longer than articles 2 or 3; article 3 moderately deeply bilobed. Ventral tarsal pilosity various in extent from dense and covering almost entire ventral surface of each tarsal article, to lacking entirely from at least more basal articles in few species. Claws connate only at very base to from very base through basal one-third to midlength, not to markedly divergent. Tibia with corbel ridge rounded (Fig. 5). Foretibia with inner margin with small to large denticles in apical one-half to two-thirds; near apex with small, indistinct to moderately large subapical tooth. Metatibia of male with uncus with ventral margin evenly rounded. *Wings.* Absent or present (various in length). *Elytra.* All intervals equally flat except humerus and very base of interval 3 variously swollen and convex. Scale pattern various, more or less vittate (Figs. 131, 133–134, 136) or as marginal band of large white scales (Figs. 118–123). Humeri acute to rounded. *Abdomen.* Ventral surface with small shiny glabrous patches, each with single small appressed to suberect scale-like seta. Female with base of abdominal sternum VII (in some individuals also sterna V and VI) internally (dorsally) with variously developed rounded glabrous shiny median tubercle, evident externally (ventrally) as rounded shallow impression. *Genitalia.* Female. Abdominal sternum VIII with basal arm short to long; lateral arms various in shape (Figs. 157–176). Gonocoxite II elongate triangular in shape; apex not prolonged into marked lobe; stylus moderately large, apical in position (Fig. 117). Spermathecal gland round (Fig. 116). Male. Paired sternite of abdominal sternum VIII lacking distinct basal projections (as in Fig. 97f). Aedeagus moderately robust; in lateral view more or less evenly arcuate throughout length; apex not spatulate (Figs. 177c-196c). Internal sac various, with median dorsal pocket low to high; apical and dorsal median pocket individually distinct or not; various lobes present (Figs. 177a,b-196a,b). Apical sclerite complex present, individual sclerites distinctly scythe-like, simple, lacking median projection.

Comparisons.— *Cleonidius* species will prove most difficult to distinguish from various *Lixus* species. Some Old World species presently regarded as *Lixus*, but not examined by me, may prove to be *Cleonidius*. In North America, north of Mexico, the area where most species of *Cleonidius* are found, no *Lixus* species has a rounded pronotal postocular lobe; at most they possess a variously developed, but usually small, acute postocular projection or else have the anterolateral margin of the pronotum straight to slightly sinuate (Fig. 4). Postocular vibrissae in most New World *Lixus* are of unequal length, long, and have their greatest length behind the base of the eye (Fig. 4). All New World *Lixus* I have examined which possess a variously developed postocular lobe and that have postocular vibrissae of more or less uniform length have the inner margin of the femora variously dentate. Femora are not dentate in any *Cleonidius* species.

Unfortunately there are species of *Cleonidius* which lack or have only slightly developed postocular lobes and have postocular vibrissae as in most *Lixus* species (Figs. 145a, 152a-155a). These can be distinguished from *Lixus* by the relative lengths of the antennal articles, by having a more robust rostrum, and by having the ventral tarsal pilosity variously reduced in extent.

Although there are exceptions (Fig. 141a), world *Lixus* species in general have a very elongate-narrow rostrum (Fig. 4) whereas *Cleonidius* species have a more robust rostrum (Figs. 137a-140a, 142a-156a). Eyes are rounded and slightly convex in many *Lixus*, otherwise are oval to elongate-oval as in all *Cleonidius*. Whereas characters used herein to separate *Lixus* from *Cleonidius* work for the New World fauna, the structural diversity of *Lixus* species in other geographic areas does not permit separation on the basis of these same characters. In the Old World, some *Lixus* species examined are separable from *Cleonidius* species only by lack of the internal tubercle at base of abdominal sternum VII in females, the presence of which is, by definition, universally diagnostic for *Cleonidius*. Such is the situation with *Cylindropterus luxeri* Chevrolat, *Lixus (Lixoglyptus) spartii* Olivier, and *Lixus (Lixoglyptus) circumcinctus* Boheman, the taxa chosen as the out-groups for the phylogenetic analysis of relationships of species of *Cleonidius*.

Apleurus (Gibbostethus) hystrix Fall, because of its more elongate-narrow body form (Fig. 24), may be confused with some *Cleonidius* species, but the tumescent mesosternal process (Fig. 58), robust and deeply punctate rostrum, and prosternal swellings immediately in front of the prosternal impressions (Fig. 7) in the former will readily separate the two.

Checklist of included species.— Nineteen species are recognized in the New World from Nicaragua north to southern Canada. The genus also occurs in the Palearctic Region where it is represented by at least, species formerly placed in the subgenus *Lixestus* Reitter of *Lixus* Fabricius. Of species placed in *Lixestus*, I have examined, and therefore herein include only *Lixus (Lixestus) vibex* (Pallas), the type species of that subgenus by monotypy. Subsequently, aside from species regarded as synonyms of *L. vibex*, Csiki (1934) included *L. pallasi* Faust, originally described as a variation of *L. vibex* and therefore likely a *Cleonidius*, and Ter-Minasyan (1978) further included *L. meles* Boheman. Inclusion of *L. meles* in *Lixestus* by Ter-Minasyan (1978) is supported by Petri (1905) wherein *L. vibex* and *L. meles* key out adjacent to one another. A key to separate the three species included in *Lixestus* is given by Ter-Minasyan (1978).

The twenty species herein placed in *Cleonidius* are as follows:

Cleonidius erysimi species group
  1. *C. erysimi* (Fall)
  2. *C. eustictorrhinus* Anderson
  3. *C. pleuralis* (LeConte)
  4. *C. subcylindricus* Casey
  5. *C. longinasus* Anderson
  6. *C. texanus* (LeConte)

Cleonidius americanus species group
  7. *C. americanus* Csiki
  8. *C. frontalis* (LeConte)
  9. *C. canescens* (LeConte)
  10. *C. infrequens* Anderson

11. *C. puberulus* (LeConte)
12. *C. collaris* (LeConte)
13. *C. notolomus* Anderson

Cleonidius poricollis species group

14. *C. poricollis* (Mannerheim)
15. *C. calandroides* (Randall)

Cleonidius boucardi species group

16. *C. boucardi* (Chevrolat)
17. *C. trivittatus* (Say)
18. *C. placidus* Csiki
19. *C. quadrilineatus* (Chevrolat)

Incertae sedis

20. *C. vibex* (Pallas)

Phylogenetic relationships.— See "Phylogenetic analysis" section.

Key to species of adult *Cleonidius*

1 Tarsal claws widely divergent, lacking basal internal flange (as in Fig. 66) . . . . *C. vibex* (Pallas), p. 544

1′ Tarsal claws at most only slightly divergent, basal internal flange well-developed (as in Fig. 67) 2

2 (1′) Head above eye with deep straight sulcus extended posteroventrally from above dorsal margin of eye to area under postocular lobe (Fig. 139). Elytra with apices produced and acuminate (Fig. 120) . . . . *C. pleuralis* (LeConte), p. 504

2′ Head above eye lacking deep straight sulcus. Elytra with apices rounded to at most only slightly acuminate and slightly produced 3

3 (2′) Pronotum extremely irregularly elevated; markedly constricted dorsolaterally near apical margin, deeply and broadly impressed medially at base and longitudinally along lateral margins; with larger punctures on disk very sparse, shallow and indistinct. Metathoracic wings short (approximately equal to one-half length of elytra) . . . . *C. collaris* (LeConte), p. 523

3′ Pronotum more regular in elevation and sculpture; only shallowly to moderately deeply impressed medially at base (also shallowly longitudinally along lateral margins in very few specimens); with larger punctures on disk denser, deeper and more distinct. Metathoracic wings short (approximately equal to or less than one-half length of elytra) to long (approximately equal to or greater than length of elytra) 4

4 (3′) [2] Pronotum with postocular lobes moderately to well-developed and with postocular vibrissae short to moderately long (maximum length equal to or less than one-half width of eye in lateral view) (Figs. 137a-144a,

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[2] An intermediate specimen will key out through both halves of this couplet.

146a-151a). Prosternum in lateral view with anterior flat portion one-third as long as, to approximately equal in length to, more posterior angulate portion (Figs. 137a-144a, 146a-151a) 5

4′ Pronotum with postocular lobes lacking to at most moderately developed and with postocular vibrissae long (maximum length equal to or greater than one-half width of eye in lateral view) (Figs. 145a, 152a-155a). Prosternum in lateral view with anterior flat portion no more than one-half as long as more posterior angulate portion (Fig. 145a, 152a-155a) 19

5 (4) Elytra with sutural intervals lacking scales throughout the greater part of their length, with at most scattered very fine erect hair-like scales (Fig. 118); interval 2 with scales contrastingly dense. .. *C. erysimi* (Fall), p. 500

5′ Elytra with sutural interval with scales uniformly distributed throughout their length (although sparsely so or abraded in some specimens); interval 2 with scales similar in density to those of sutural interval 6

6 (5′) Head behind eye with moderately deep curved sulcus extended posteroventrally from upper one-half of posterior margin of eye to area under postocular lobe (largely covered in many specimens by postocular lobe) (Fig. 150) 7

6′ Head behind eye lacking distinct curved sulcus, with at most one or more wrinkles of cuticle 8

7 (6) Distributed in the northern Atlantic coastal states of the United States and Atlantic coastal provinces of Canada (Fig. 229). Dorsal surface of pronotum and elytra with suberect vestiture short, indistinct. Elytral scale pattern of most specimens not distinctly vittate; scales on interval 2 and intervals 6 to 8 not markedly smaller than scales on adjacent intervals; underlying dark cuticle on interval 2 and intervals 6 to 8 largely obscured by overlying white scales (Fig. 132) .... *C. calandroides* (Randall) (in part), p. 531

7′ Distributed in Mexico, and/or Canada and the United States west of 85° W longitude (Fig. 228). Dorsal surface of pronotum and elytra with erect vestiture short to moderately long, distinct. Elytral scale pattern distinctly vittate; scales on interval 2 and intervals 6 to 8 markedly smaller than scales on adjacent intervals; underlying dark cuticle on interval 2 and intervals 6 to 8 not largely obscured by overlying white scales (Fig. 131) .... *C. poricollis* (Mannerheim) (in part), p. 527

8 (6′) Elytra distinctly laterally margined with white scales (especially in basal one-half); intervals 9 to 11 with dense moderately elongate broad white scales; otherwise moderately densely uniformly covered with fine white scales smaller than those on intervals 9 to 11 (Figs. 119, 121–123) 9

8′ Elytra not laterally margined, either vittate (Figs. 130–131), more or less uniformly densely scaled (Fig. 129), or mottled with irregularly distributed patches of larger and denser scales (Figs. 124–125); intervals other than 9 to 11 with scales equally large to those on intervals 9 to 11 12

9 (8) Head, pronotum and elytra lacking dorsal erect or suberect vestiture (Fig. 140a). Postocular lobes only moderately developed (Fig. 140a) .... *C. subcylindricus* Casey, p. 506

9′ Head, pronotum and elytra with dorsal erect or suberect vestiture short to long (Figs. 138a, 141a-142a). Postocular lobes well-developed (Figs. 138a, 141a-142a) 10

10 (9′) Rostrum with large deep dense punctures; medially longitudinally tumescent and with median carina as fine shiny line at crest of median tumescence; robust (width at apex greater than 0.58 times length) (Fig. 138). . . . . *C. eustictorrhinus* Anderson, p. 502

10′ Rostrum with small shallow moderately dense punctures; not medially longitudinally tumescent, carina lacking to as variously developed fine shiny line; robust to elongate-narrow (width at apex less than 0.62 times length) (Figs. 141–142). 11

11 (10′) Rostrum (especially in females) very long and narrow (width at apex less than 0.50 times length) (Fig. 141a). Head, pronotum and elytral declivity (and to a lesser extent elytral disk) with dorsal erect vestiture moderately long to very long (lacking from a very few specimens) (Fig. 141a). Associated with Leguminosae . . . . *C. longinasus* Anderson, p. 508

11′ Rostrum (of both sexes) shorter and more robust (width at apex greater than 0.50 times length) (Fig. 142). Head, pronotum and elytra with dorsal suberect to erect vestiture short to moderately long (Fig. 142a). Associated primarily with Rosaceae and Rhamnaceae, rarely Leguminosae at lower altitudes . . . . *C. texanus* (LeConte), p. 510

12 (8′) Dorsum (especially of head, pronotum and elytral declivity) with erect vestiture long to very long (Fig. 143a). Rostrum in lateral view with prementum swollen ventrally (Fig. 143a); in dorsal view slightly expanded laterally at midlength (Fig. 143b) . . . . *C. americanus* Csiki, p. 513

12′ Dorsum with suberect to erect vestiture either lacking or short variously on head, pronotum, and elytra (Figs. 144a, 146a-147a, 149a-152a). Rostrum in lateral view with prementum flat to slightly swollen ventrally (Fig. 144b); in dorsal view not to slightly expanded laterally at midlength (Fig. 144a). 13

13 (12′) Distributed in the northern Atlantic coastal states of the United States and Atlantic coastal provinces of Canada (Fig. 229) . . . . *C. calandroides* (Randall), p. 531

13′ Distributed in Mexico, and/or Canada and the United States west of 85° W longitude 14

14 (13′) All tarsi with similar and extensive ventral pilose vestiture, articles 1 to 3 with large elongate-oval ventral pilose pads on virtually entire ventral surface of each article (except basal one-third to one-half of article 1) 15

14′ Tarsi with ventral pilose pads small, decreased in extent on more posterior tarsi, either with articles 1 and 2 with small elongate-narrow ventral pilose pads, apical tufts of pilosity, or, with pads lacking; article 3 with moderately large pads not on more than apical two-thirds of ventral surface 16

15 (14) Rostrum not dorsally medially tumescent; base in lateral view appearing continuous with frons (Fig. 152a). Elytra with interval 3 (in some specimens also intervals 4 and 5), and intervals 9 to 11 with dense white

scales, otherwise with scales very sparse or lacking (Fig. 133) .... *C. boucardi* (Chevrolat) (in part), p. 534

15′ Rostrum dorsally medially longitudinally tumescent; base in lateral view separated from frons by distinct transverse impression (Fig. 150a). Elytra with scales white, fine and sparse, densest on sutural interval, intervals 3 to 7, and 9 to 11 .... *C. poricollis* (Mannerheim) (in part), p. 527

16 (14′) Rostrum very short and robust (width at apex greater than 0.70 times length) (Figs. 146–147) 17

16′ Rostrum more elongate-narrow (width at apex less than 0.70 times length) (Figs. 144, 149) 18

17 (16) Rostrum with median carina very distinct, sharp and elevated, also with faint lateral carinae at lateral margins (Fig. 146b); rostrum flat from immediately laterad of median carina to lateral margins; rostrum more or less quadrate in cross-section, lateral margins sharp. Articles of tarsus of hind leg with ventral pilose pads moderately large. Metathoracic wings long (greater than length of elytra) to short (approximately one-half or less than length of elytra) .... *C. infrequens* Anderson, p. 520

17 Rostrum with median carina indistinct, low and only slightly elevated, without trace of lateral carinae (Fig. 147b); rostrum declivous from immediately laterad of median carina to lateral margins; rostrum less quadrate in cross-section, the lateral margins rounded. Articles of tarsus of hind leg with ventral pilose pads small. Metathoracic wings short (less than one-half length of elytra) .... *C. puberulus* (LeConte), p. 522

18(16′) Elytra elongate compared to pronotal length (LP/LEl less than 0.40) (Fig. 125). Metathoracic wings long (greater than elytra in length). Rostrum more or less circular in cross-section, lateral margins rounded; in dorsal view, slightly swollen laterally at midlength; in lateral view with prementum slightly swollen ventrally. Fore-tibia of most females with inner margin with very large prominent denticles (Fig. 144c) .... *C. frontalis* (LeConte), p. 515

18′ Elytra more robust compared to pronotal length (LP/LEl more than 0.40) (Fig. 130). Metathoracic wings present, varied in length from short (approximately equal to one-half length of elytra) to long (greater than elytra in length). Rostrum more or less quadrate in cross-section, lateral margins sharp; in dorsal view, not swollen laterally at midlength; in lateral view with prementum flat. Fore-tibia of female with inner margin with slightly developed, small denticles .... *C. notolomus* Anderson, p. 525

19 (4′) Metathoracic wings short, approximately equal to one-half length of elytra. Eye oval (width greater than 0.60 times length) (Fig. 145a) .... *C. canescens* (LeConte), p. 518

19′ Metathoracic wings long (approximately equal to or greater than length of elytra). Eye elongate-oval (width less than 0.65 times length) (Figs. 152a-155a) 20

20 (19′) Elytra, except sutural interval and portions of interval 2, uniformly covered with dense white scales (Fig. 135) .... *C. placidus* Csiki, p. 539

20′ Elytra distinctly vittate, intervals 6 to 8 with scales lacking or very sparse compared to intervals 3 to 5 and 9 to 11 (Figs. 133–134, 136) 21

21 (20′) Rostrum not or only slightly dorsally medially tumescent, not distinctly carinate (very slightly so in few specimens) (Fig. 152a). Metatarsus with articles 2 and 3 with ventral pilose pads large, onvirtually entire ventral surface; article 1 with pads elongate-broad, on apical two-thirds of the ventral surface . . . . *C. boucardi* (Chevrolat) (in part), p. 534

21′ Rostrum dorsally medially tumescent, with low rounded carina (Figs. 153a, 155a). Metatarsus with article 3 with ventral pilose pads moderately large, covering the apical one-half to two-thirds of ventral surface; article 2 with pads elongate-narrow, covering the apical two-thirds of the ventral surface; article 1 with pads either present as apical tufts, or elongate and very narrow, covering not more than the apical one-half of the ventral surface 22

22 (21′) Elytra elongate-narrow (width less than 0.55 times length) (Fig. 136). Pronotal disk with moderately long erect hair-like scales (Fig. 155a). Associated primarily with Rosaceae and Rhamnaceae, rarely Leguminosae. . . . . *C. quadrilineatus* (Chevrolat), p. 541

22′ Elytra more robust (width greater than 0.55 times length) (Fig. 134). Pronotal disk with at most short, suberect, indistinct hair-like scales (Fig. 153a). Associated with Leguminosae. . . . . *C. trivittatus* (Say), p. 536

Cleonidius erysimi species group

Diagnosis.— Size small to moderate for *Cleonidius* (Fig. 197). Dorsal erect or suberect vestiture absent (Fig. 140a) to present, dense and very long (Fig. 141a). Rostrum very elongate-narrow (Fig. 141a) to moderately robust (Fig. 138a), not to markedly medially tumescent, not to variously carinate; lateral margins rounded. Pronotum with postocular lobes moderately (Fig. 140a) to well-developed (Fig. 141a); postocular vibrissae uniformly short to more or less uniformly moderately long. Elytra with marginal band of scales, only intervals 9 to 11 with white scales large and broad, otherwise with intervals with scales small and fine to absent (Figs. 118–123). Tarsus with ventral pilose vestiture extensive (on almost entire ventral surface of each article) to slightly reduced in extent (on not less than apical one-half of articles 2 and 3). Wings present, length various. Female with abdominal sternum VIII with basal arm short; lateral arms more or less straight and divergent throughout length (Figs. 157–162). Male aedeagus with internal sac with apex of dorsal median pocket rounded (Figs. 177b-182b); lobes B, D, and E absent in some species (Figs. 180a,b-182a,b); dorsal median pocket low to high in lateral view.

Phylogenetic relationships.— The *C. erysimi* group is hypothesized to be sister group to the remainder of North American *Cleonidius* (Figs. 236–237).

Cleonidius erysimi (Fall)
(Figs. 118, 137, 157, 177, 219)

Lixus poricollis; LeConte 1876a,b (misident.). Henshaw 1885 (check., misident.).

Cleonus erysimi Fall 1901:261. Lectotype (here designated), male, one of an undetermined number of syntypes, labelled "‘male symbol‘", "Redondo/ Cal. 4.7.94.", "Type/ *erysimi*", "M.C.Z./ Type/ 25193", "H.C. FALL/ COLLECTION" and with my designation label "*Cleonus/ erysimi/* Fall LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Redondo, California. Leng 1920 (catal.).

Cleonus (*Cleonidius*) *erysimi*; Csiki 1934 (catal.).

Cleonis erysimi; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— This species has infrequently been erroneously referred to as *Lixus poricollis* Mannerheim.

Problems in recognition.— Individuals of this species are easily recognized by the sutural interval of the elytra lacking scales, with at most only scattered very fine erect hair-like scales; interval 2 has scales that are contrastingly dense (Fig. 118). Although some individuals of *C. pleuralis* are superficially similarly patterned, close examination of sutural interval reveals small scales. Regardless, *C. pleuralis* individuals are easily recognized by the deep straight sulcus above each eye (Fig. 139).

Individuals of *C. eustictorrhinus* and *C. texanus*, especially the former, may also prove difficult to separate from those of *C. erysimi* should the elytra be largely abraded of vestiture. *Cleonidius texanus* specimens have a slightly more elongate-narrow rostrum (Fig. 142) and the length of the elytra as compared to the length of the pronotum is greater (see Figs. 197, 200). *Cleonidius eustictorrhinus* and *C. erysimi* individuals will prove most difficult to separate, if abraded, although most *C. erysimi* are brachypterous, whereas all *C. eustictorrhinus* are macropterous.

Description.— *Specimens examined.* 129 males, 179 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEI, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 15. *Size.* Length, male, 7.2–11.3 mm; female, 6.1–12.0 mm. Width, male, 2.2–4.1 mm; female, 2.1–4.5 mm. *Head.* Eye elongate-oval. Area behind eye with numerous wrinkles of cuticle. Frons with sparse to moderately dense, small, shallow to moderately deep punctures, some longitudinally confluent and irregularly impressed immediately above eyes, punctures sparser medially; interspersed with minute punctures. Frons also with moderately dense to dense, elongate-narrow erect hair-like scales immediately above eyes; otherwise with scattered erect hair-like scales and moderately dense to dense, elongate-narrow appressed white scales, sparse to absent medially. Frons separated from base of rostrum by moderately deep to deep transverse impression (Fig. 137a). Base of median tumescence or carina of rostrum with small moderately deep fovea. Width of frons greater than or subequal to width at apex of rostrum. *Rostrum.* Moderately robust, slightly more so in males (width at apex 0.57-0.80 times length) (Fig. 137). In lateral view straight to very slightly curved downward. In dorsal view with postgenae not to very slightly expanded laterally, antennal scrobes very slightly visible. Slightly to markedly medially tumescent from point of antennal insertion to middle of frons (more markedly so basally), with median carina variously developed as rounded to sharp, moderately elevated, fine to broad, glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense to dense, small to moderately large, shallow to deep (longitudinally confluent in many specimens), smaller and not longitudinally confluent apically, dorsally interspersed with minute punctures. Dorsally (especially laterally) with sparse to moderately dense, moderately long erect hair-like scales, and laterally with sparse to moderately dense, elongate-narrow white appressed to recumbent scales, medially with vestiture absent to very sparse, appressed, elongate-fine. Epistoma not swollen. *Pronotum.* Median carina variously developed in anterior one-half to three-quarters as slightly to moderately elevated glabrous shiny broad line. Dorsal punctation moderately large to large, moderately dense to dense, deep; smaller and shallower apically; shallower on flanks; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally with moderately dense, moderately long erect hair-like scales each situated in large puncture (Fig. 137a). Scales dorsally absent along midline, moderately dense, elongate-fine, appressed in pair of paramedian apically slightly narrowed stripes; laterally, absent to very small and sparse. Lateral margins with appressed white scales elongate-fine to elongate-narrow, moderately dense in moderately broad stripe. Flanks with scales smaller and slightly less dense than along lateral margins. Median basal area of disk very shallowly to moderately deeply impressed. Anterolateral margin with pronotal postocular lobes moderately to well-developed; postocular vibrissae short, of uniform length to very slightly longer immediately behind base of eye (approximately one-half width of eye or less) (Fig. 137a). In dorsal view with lateral margins very slightly arcuate and convergent from base to apex; subapical constriction very slight and indistinct. *Prosternum.* With moderately large, moderately deep to deep impression, and moderately to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion, anterior and posterior portions not to slightly differentiated by shallow transverse impression (Fig. 137a). *Elytra.* Elongate-narrow in general form (width at midlength 0.45-0.55 times length in males; 0.48-0.53 in females) (Fig. 118). In dorsal view with lateral margins straight to very slightly arcuate or very slightly sinuate, slightly convergent from apical one-third to humerus; slightly to moderately and evenly arcuate from apical one-third to apex. Elytral apices slightly produced, rounded to sub-acuminate, not to slightly divergent. Humerus indistinct, rounded. Dorsally with sparse to moderately dense, suberect to erect, short hair-like scales (abraded in many specimens). Sutural interval with scales lacking throughout greater part of length, with sparse fine scales only at very base; intervals 2 to 7 with scales uniformly moderately dense, various in size from elongate-fine to elongate-narrow on alternate intervals in many specimens; interval 8 with scales absent to very small, fine and sparse; intervals 9 to 11 with scales uniformly moderately dense to dense, moderately large and elongate-narrow, sparser and smaller apically and at base of interval 11 (Fig. 118). Punctures of elytral striae small, individually distinct, larger and less individually distinct basally, arranged in regular rows. *Wings*. Long (greater than length of elytra [9%, N=29]) to short (less than one-half length of elytra [91%, N=279]). *Legs*. Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth small, indistinct to distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third to one-half, not to slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsi of male and female present as elongate-narrow pads on apical one-half to three-quarters of article 1, as rounded pads on apical one-half of article 2, and as large rounded pads on apical two-thirds to more or less entire ventral surface of article 3. *Abdomen*. Ventral surface with sparse to dense appressed elongate-narrow to very elongate-narrow white scales (abraded in part in many specimens). Abdominal sterna III and IV laterally with individually indistinct glabrous patches, each with large puncture and single elongate recumbent to suberect hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with moderately developed median shiny tubercle. *Genitalia*. Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms straight and divergent from base to apical one-third; markedly inwardly arcuate at apical one-third and convergent to apex, moderately expanded at apex (Fig. 157). Stylus moderately large in length compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 177a,b) elongate and low; median dorsal pocket low, with single elongate moderately broad dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with small paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe at midlength near dorsal margin (lobe D), with moderately large paired dorsolaterally directed lobe at apical one-third at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apex of median dorsal pocket rounded in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired small ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is found from southern British Columbia and Alberta, east to Manitoba, south to southern California, Arizona and extreme western Texas (Fig. 219).

Natural history.— This species is associated with grassland, desert-grassland transitional habitats, Pacific semi-desert, and Great Basin desert. Adults of this species have been collected on a variety of plants (but especially Cruciferae) as follows; *Cleome* sp. (Capparaceae); *Aplopappus ericoides* (Less.) H. and A., *Senecio* sp. (both Compositae); *Brassica* sp., *Brassica oleracea* L. (cabbage), *Dithyrea californica* Harv., *Erysimum* sp., *E. suffrutescens* (Abrams) G. Rossb., *Raphanus sativus* L. (radish), *Stanleya pinnata* (Pursh.) Britton var.*inyoensis* (all Cruciferae); *Adenostoma fasciculatum* H. and A., *Prunus persica* (L.) Batsch. (peach) (Rosaceae). The type series of *Cleonus erysimi* Fall was collected from flowers of *Erysimum capitatum* (Dougl.) Greene on sandhills at Redondo Beach, California (Fall 1901). Adults have been reared from larvae found in crowns of *Lobularia maritima* (L.) Desv. (Cruciferae) at Harris Ranch, Los Alamos, Santa Barbara Co., California.

Adults of the species have been frequently collected in sand dune habitats in coastal California and in other sandy habitats throughout the species range. Adults have been collected throughout the year at altitudes of 15–2359 m (N=40) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister species of *C. eustictorrhinus*, the two species forming a lineage that is a member of an unresolved trichotomy including *C. pleuralis* and the *C. subcylindricus-C. longinasus-C. texanus* lineage (Fig. 237).

Cleonidius eustictorrhinus Anderson, new species

(Figs. 119, 138, 158, 178, 216)

Type Material.— Holotype, male, with a red label "HOLOTYPE", "SACRAMENTO/ CALIF/ XII-13-1949", "D.GIULIANI/ COLLECTOR", "Derham Giuliani/ Collection/ Calif. Acad. Sci./ Accession 1967", "Collection of the/ CALIFORNIA ACADEMY/ OF SCIENCES, San/ Francisco Calif.", "HOLOTYPE/ *Cleonidius/ eustictorrhinus*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CASC). Allotype, female, with a red label "ALLOTYPE", "Orange Vale/ Sacto.Co./ July 31, 1938/ Quentin Tornich", "ALLOTYPE/ *Cleonidius/ eustictorrhinus/* Anderson" and with abdomen on card and genitalia in microvial attached to pin (UCBC, on indefinite loan to CASC). Type locality, Sacramento, California.

Paratypes. 11 males, 12 females. UNITED STATES OF AMERICA: California: Orange Vale, 31.VII.38, Q. Tornish, 1F (UCBC); Lancaster, 19.V.37, E.P. Van Duzee, 1M (CASC); 4mi. w. Meadow Valley, 13.V.49, Middlekauff, 1F (UCBC); Madera County, Bates, 25.III.17, 1F (AMNH); Antioch, 1.IX.37, M. Cazier, 1M (AMNH), 26.IV.68, Monroe, 1F (CWOB); Irvine, Davis, 1M (CNCI); San Diego County, 26.IV.91, Blaisdell, 1M (CASC); Stanford, III.04, 1M (LACM), 11.III.06, 1F (LACM); Fresno County, Waltham Canyon, 26.III.37, Blum, 1F (RSAN); Baldwin Hills, 11.VII.53, Menke, 1F (LACM); Vine Hill, 23.V.65, Johnson, 1F (CWOB); Atascadero, 18.VI.46, Mansfield, 1M (CASC); Laguna Beach, 30.XII.49, 1M (CWOB); Idyllwild, 12.V.34, Stone, 1F (OSUC); Laguna, 20.VI.30, 1F (OSUC), 30.VI.30, 1M (CNCI); Irvine, 1M (RSAN); Yosemite, 17.VI.31, Essig, 1F (UCBC); Stanislaus, XII.35, 1M (CFDA); Carmichael, 17.V.58, Wilkey, 1M (CDFA); Napa County, Pope Valley, 9.V.55, Raven, 1F (CASC).

Derivation of specific epithet.— From the Greek "*eu*" meaning very or exceedingly; "*stiktos*" meaning punctured; and, "*rhinos*" meaning nose. This name is used in reference to the markedly punctured rostrum of members of this species.

Problems in recognition.— Individuals of this species are likely to be confused only with *C. texanus*, *C. subcylindricus*, and *C. erysimi*. Individuals of *C. eustictorrhinus* are easily separated from sympatric individuals of *C. erysimi* by the sutural interval lacking scales in the latter (Fig. 118) and by most *C. erysimi* being brachypterous whereas all *C. eustictorrhinus* are macropterous. Individuals of *C. eustictorrhinus* are easily separated from *C. subcylindricus* by geographic distribution, the former being restricted to California (Fig. 216), the latter to the Atlantic Coastal Plain from Florida north to New York (Fig. 215). *C. subcylindricus* individuals also lack suberect or erect dorsal vestiture (Fig. 140a) whereas *C. eustictorrhinus* have short but distinct erect dorsal vestiture (Fig. 138a). Specimens of *C. eustictorrhinus* will prove most difficult to separate from sympatric individuals of *C. texanus*. In *C. eustictorrhinus* individuals (Fig. 138), the rostrum is medially tumescent, distinctly carinate and has large deep punctures; in *C. texanus* specimens (Fig. 142), the rostrum is not medially tumescent or carinate and has only small shallow punctures. The rostrum is slightly more robust in *C. eustictorrhinus* (Fig. 138) than in *C. texanus* (Fig. 142), *C. eustictorrhinus* tend to be larger than *C. texanus*, and the length of the elytra as compared to the length of the pronotum tends to be greater in *C. texanus* than in *C. eustictorrhinus* (see Figs. 197, 200).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEI, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 16. *Size.* Length, male, 8.8–10.4 mm; female, 8.8–11.0 mm. Width, male, 3.2–3.9 mm; female, 3.2–4.0 mm. *Head.* Eye elongate-oval. Area behind eye with numerous wrinkles of cuticle. Frons with moderately dense, small to moderately large, shallow punctures; longitudinally confluent and very irregularly impressed immediately above eyes; larger punctures interspersed with sparse minute punctures. Frons also with scales sparse to moderately dense elongate-narrow, erect immediately above eyes; medially and laterally with sparse to moderately dense elongate-narrow appressed to suberect white scales; laterally with moderately dense, short to moderately long fine erect hair-like scales. Frons either continuous with base of rostrum, or slightly separated by shallow transverse impression (Fig. 138a). Base of median tumescence or carina of rostrum with small shallow to moderately deep fovea. Width of frons greater than or subequal to width at apex of rostrum. *Rostrum.* Moderately robust, slightly more so in males (width at apex 0.56-0.69 times length) (Fig. 138). In lateral view slightly curved downward. In dorsal view with postgenae not to slightly laterally expanded, antennal scrobes slightly visible. Moderately to markedly medially tumescent from point of antennal insertion to middle of frons, with median carina variously developed as a rounded, slightly to moderately elevated, broad, glabrous, shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense to dense, moderately large to large, shallow to deep (longitudinally confluent in many specimens), smaller and shallower apically, dorsally interspersed with few minute punctures. Dorsally (especially laterally) with sparse to moderately dense, moderately long, suberect to erect hair-like scales, and laterally and medially with sparse to moderately dense, elongate-fine to elongate-narrow, appressed to recumbent, white scales. Epistoma not to very slightly transversely swollen at base. *Pronotum.* Median carina variously developed in anterior one-half as slightly elevated glabrous narrow to broad line. Dorsal punctation small, dense, shallow; smaller and sparser apically; sparser on flanks; areas between dorsal punctures with dense minute regularly impressed punctures. Dorsally with moderately dense, short erect hair-like scales each situated in larger puncture (Fig. 138a). Scales dorsally absent to sparse, small and fine along midline; moderately dense to dense, elongate-fine, appressed laterad of median line, but not as distinct stripes; laterally, absent to sparse, small and fine. Lateral margins with scales moderately dense to dense, elongate-narrow to moderately robust, appressed to recumbent in moderately broad stripe. Flanks with scales moderately dense to dense, elongate-fine. Median basal area of disk very shallowly, broadly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae uniformly short (Fig. 138a). In dorsal view with lateral margins uniformly moderately arcuate and convergent from base to apex; subapical constriction at apical one-fifth indistinct or slight, then straight and convergent to apex (Fig. 119). *Prosternum.* With shallow to moderately deep impression and moderately to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion moderately long, approximately one-half length of posterior more angulate portion; anterior and posterior portions not or slightly differentiated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.49-0.58 times length in males; 0.49-0.55 in females) (Fig. 119). In dorsal view with lateral margins very slightly sinuate, slightly convergent from apical one-third to humerus; slightly to moderately and evenly arcuate from apical one-third to apex. Elytral apices slightly produced, rounded to sub-acuminate. Humerus distinct. Dorsally with sparse to moderately dense, suberect to erect, very short to short, hair-like scales. Sutural interval to interval 7 with uniformly moderately dense, fine to elongate-fine, white scales and with scattered patches of larger white scates; interval 8 with scales absent to moderately dense, small and fine basally to elongate-fine apically; intervals 9 to 11 with scales moderately dense to dense, moderately large and elongate-narrow to robust, smaller and finer apically in most specimens (Fig. 119). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-half, not to slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsi of male and female present as elongate-narrow pads on apical one-half to three-quarters of article 1, as rounded pads on apical one-half of article 2, and as large rounded pads on apical two-thirds to more or less entire ventral surface of article 3. *Abdomen.* Ventral surface with moderately dense to dense elongate-narrow appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct glabrous patches, each with large puncture and single suberect to erect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally with slightly developed median shiny tubercle. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm short; lateral arms straight and divergent from base to apical one-third; markedly abruptly inwardly arcuate at apical one-third; apical one-half to one-third markedly expanded (Fig. 158). Stylus moderately large in length compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 178a,b) elongate and low; median dorsal pocket low, with single elongate moderately broad dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe near midlength on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired anterodorsolaterally directed lobe at apical one-third at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apex of median dorsal pocket rounded in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is known only from California (Fig. 216).

Natural history.— This species is found only in the Pacific semi-desert region. Adults of *C. eustictorrhinus* have been collected only on *Arctostaphylos* sp. (Ericaceae); *Eriogonum* sp. (Polygonaceae); and beans (Leguminosae). Definite host records are not known. Adults have been collected from March to July, and December at altitudes of 9–2002 m (N = 8) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister species of *C. erysimi* (Figs. 236 and 237).

Cleonidius pleuralis (LeConte)
(Figs. 120, 139, 159, 179, 217)

Lixus pleuralis LeConte 1858:78. Holotype (examined), female, labelled with a gold circle (=California), "1062", "Type/ 5177", "*L./ pleuralis/* Lec." (MCZC). Type locality, on Colorado River below the Gila River, California. Gemminger and von Harold 1871 (catal.). LeConte 1876a,b (key, redesc.). Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1889. Horn 1894 (check.).

Lixus californicus; Gemminger and von Harold 1871 (catal.). LeConte 1876a.

Lixus modestus; Gemminger and von Harold 1871 (catal.). LeConte 1876a,b. Henshaw 1885 (check.).

Cleonus (*Cleonidius*) *californicus*; Casey 1891 (as synonym).

Cleonus (*Cleonidius*) *modestus*; Casey 1891 (key). Wickham 1896 (check.). Fall 1901 (check.). Leng 1920 (catal.). Csiki 1934 (catal.). Blackwelder 1947 (check.). Hatch 1971 (key, misident. of *Cleonidius longinasus*).

Cleonus (*Cleonidius*) *pleuralis*; Casey 1891 (as synonym). Fall 1901 (check.).
Cleonus modestus; Wickham 1896 (check.). Fall 1901 (check.). Leng 1920 (catal.). Blackwelder 1947 (check.).
Cleonis californicus; O'Brien and Wibmer 1982 (catal., distn., as synonym).
Cleonis modestus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis pleuralis; O'Brien and Wibmer 1982 (catal., distn., as synonym).

Notes about synonymy.— This species has been referred to as *Lixus modestus* Mannerheim (1843:291) and *L. californicus* Motschulsky (1845:378). The holotype of *Lixus modestus* has been examined (ZMMU) and as noted elsewhere ("*Nomen dubium*" section) is not a *Cleonidius* and is doubtfully a New World *Lixus*. The name *Lixus californicus* Motschulsky is herein considered a *nomen dubium* and not considered in the nomenclature (see "*Nomen dubium*" section) of any species of *Cleonidius*.

Problems in recognition.— Adults of this species are very easily recognized by the deep straight sulcus above each eye (Fig. 139) and the produced and acuminate elytral apices (Fig. 120). Most individuals of *C. poricollis* and some *C. calandroides* possess a shallow curved sulcus behind the eye (covered by the pronotal postocular lobe in some specimens and difficult to see) (Fig. 150a), but this should not be confused with the deep straight sulcus in members of *C. pleuralis*.

Description.— *Specimens examined.* 89 males, 90 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 17. *Size.* Length, male, 7.2–10.0 mm; female, 7.3–10.8 mm. Width, male, 2.1–3.1 mm; female, 2.2–3.5 mm. *Head.* Eye elongate-oval. Vertex, above eye with deep straight sulcus extended posteriorly from dorsal margin of eye to area under pronotal postocular lobe. Frons with scattered small shallow punctures and moderately dense minute punctures; also with moderately dense erect hair-like scales above eyes and moderately dense elongate fine appressed white scales, slightly sparser medially in most specimens. Frons continuous with base of rostrum, not separated by transverse impression (Fig. 139a). Most specimens with a shallow median fovea at base of median tumescence or carina of rostrum. Width of frons greater than or subequal to width at apex of rostrum. *Rostrum.* Elongate-narrow, slightly more so in females (width at apex 0.44-0.57 times length) (Fig. 139). In lateral view straight to very slightly curved downward. In dorsal view slightly narrowed apically, postgenae not laterally expanded, antennal scrobes not distinctly visible. Slightly medially tumescent with median carina in most specimens very low, glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation sparse, small and shallow, interspersed with moderately dense minute punctures. Dorsally (especially laterally) with moderately dense erect fine hair-like scales and with moderately dense fine elongate white appressed scales smaller, finer and sparser apicad of point of antennal insertion. Epistoma not swollen. *Pronotum.* Median carina lacking in most specimens, indicated in very few specimens by low, glabrous shiny line in anterior one-half. Dorsal and lateral punctation moderately large, moderately dense, deep; smaller, sparser and shallower apically and medially, the areas between large dorsal punctures with minute, very shallow punctures. Dorsally with moderately dense, short to moderately long, fine erect hair-like scales each situated in large puncture (Fig. 139a). Scales dorsally very sparse to absent along median line, moderately dense, moderately large and elongate in pair of broad paramedian apically slightly narrowed stripes; laterally, small and fine. Lateral margins with appressed white scales large and elongate-narrow in moderately broad stripe. Flanks with scales moderately dense, small and fine. Median basal area of disk deeply and broadly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae very short, of uniform length (Fig. 139a). In dorsal view with lateral margins slightly arcuate and slightly convergent apically from base to more or less apical one-fifth; gradually to abruptly constricted at apical one-fifth, convergent to apex (Fig. 120). *Prosternum.* With moderately deep impression, and moderately to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion short, not distinctly differentiated from longer posterior more angulate portion. *Elytra.* Very elongate-narrow in general form (width at midlength 0.40-0.46 times length in males; 0.39-0.47 in females) (Fig. 120). In dorsal view with lateral margins straight, subparallel to slightly divergent from apical one-third to humerus; slightly and evenly arcuate from apical one-third to apex. Elytral apices produced, acuminate and divergent. Humerus distinct. Dorsally with moderately dense, erect, short to moderately long, fine hair-like scales. Scale pattern various; sutural interval to interval 8 with uniformly moderately dense, elongate fine appressed white scales to moderately dense, elongate fine on intervals 2 to 5 and moderately dense but smaller and finer on sutural interval and intervals 6 to 8 (interval 8 with scales very sparse to lacking in some specimens); intervals 9 to 11 with scales more or less uniformly moderately dense, moderately large and elongate-narrow (Fig. 120). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth small, indistinct from tibial denticles. Foretibial uncus of both sexes moderately large, mesotibial and metatibial unci small. Tarsal claws connate in basal one-third to one-half, not divergent, basal internal flange lacking. Ventral tarsal pilose vestiture of all tarsi of male and female present as elongate-narrow pads on apical one-half of article 1, as rounded pads on apical one-half of article 2, and as large rounded pads on apical three-quarters of article 3. *Abdomen.* Ventral surface with moderately dense to dense appressed very elongate-narrow white scales, sparser along midline. Abdominal sterna III to VI (especially III and IV) with moderately large individually distinct to indistinct glabrous patches, each with large puncture and single elongate appressed to suberect hair-like scale in or near center. Base of abdominal sternum VII of female internally (dorsally) with slightly developed, median, shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm very short, indistinct; lateral arms straight and divergent from base to apical one-quarter, markedly inwardly arcuate at apical one-quarter and convergent to apex, slightly expanded at apex (Fig. 159). Stylus moderately large in length compared to length of gonocoxite II. Male (three examined). Internal sac (Figs. 179a,b) elongate and low; median dorsal pocket low, with single short broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsally directed lobe at midlength near dorsal margin (lobe D), with moderately large paired dorsolaterally directed lobe at apical one-third at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apex of median dorsal pocket truncate in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— Members of this species are found in the southwestern United States of America and adjacent northern Mexico from California, southern Nevada, southern Utah, central New Mexico and extreme western Texas, south to the Mexican border, except in the west where they are found south into Baja California Norte, Mexico (Fig. 217).

Natural history.— This species is associated with desert-grassland transitional habitat, and Chihuahuan, Mojave and Sonoran deserts. Adults of this species have been collected in various sandy habitats such as dunes and dry stream beds or desert washes on *Ephedra californica* Wats. (Ephedraceae); *Chrysothamnus nauseosus* (Pall.) Britton, *C. paniculatus* (Gray) H.M. Hall, *Hymenoclea* sp., *H. salsola* Torr. and Gray, (all Compositae); *Asclepias* sp. (Asclepiadaceae); *Atriplex polycarpa* (Torr.) Wats. (Chenopodiaceae); *Medicago sativa* L. (Leguminosae); and *Brassica*? sp., *Lepidium* sp. (Cruciferae). Definite hosts are not known.

Adults have been collected from February to October at altitudes ranging from -96–1747 m (N=26) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is a member of an unresolved trichotomy that also includes the *C. erysimi-C. eustictorrhinus* lineage and the *C. subcylindricus-C. longinasus-C. texanus* lineage (Fig. 237).

Cleonidius subcylindricus Casey
(Figs. 121, 140, 160, 180, 215)

Cleonus (*Cleonidius*) *subcylindricus* Casey 1891:193. Holotype (examined), female, labelled "Fla", "CASEY/ bequest/ 1925", "TYPE USNM/ 37283", "*C.Cl./ subcylindricus/* Cas" (USNM). Type locality, Florida. Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *graniferus* Casey 1891:194. NEW SYNONYMY Holotype (examined), female, labelled "Ga.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37284", "*C.Cl./ graniferus/* Cas." (USNM). Type locality, Georgia. Csiki 1934 (catal.).

Lixus lupinus Blatchley 1914:248. Lectotype (designated by Blatchley [1930:38, error as female] examined), male, labelled "TYPE", "Dunedin, Fla./ W.S.B. Coll./ 1.24.1913", "Purdue/ Blatchley/ collection" and with lectotype designation label of Blatchley (Purdue). Type locality, Dunedin, Florida. Blatchley and Leng 1916 (key, redesc.). Leng 1920 (catal). Blatchley 1930.

Cleonus subcylindricus; Blatchley and Leng 1916 (key, redesc.). Leng 1920 (catal.).

Cleonus graniferus; Blatchley and Leng 1916 (key, redesc.). Leng 1920 (catal.).

Cleonus lupinus; Kingsolver 1972 (synonymy with *Cleonus subcylindricus*).

Cleonis graniferus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis lupinus; O'Brien and Wibmer 1982 (catal., distn., as synonym).

Cleonis subcylindricus; O'Brien and Wibmer 1982 (catal., distn.).

lupinus, incertae sedis; Csiki 1934 (catal.).

Notes about synonymy.— *Cleonus graniferus* Casey is a developmentally abnormal female of *C. subcylindricus* with a short robust rostrum, legs and antennae. Similar developmental abnormalities are also known in other species of *Cleonidius. Lixus lupinus* Blatchley was placed in synonymy with *Cleonus subcylindricus* Casey by Kingsolver (1972).

Problems in recognition.— This species is one of only two species of *Cleonidius* found in and restricted to eastern North America (Figs. 215, 229). These two species differ markedly in many structural features and there should be no problem in separating individuals of the two. *C. subcylindricus* individuals are easily distinguished from other members of the *C. texanus* group, with which they may be confused, by the only slightly developed pronotal postocular lobes and by lack of dorsal suberect or erect vestiture (Fig. 140a).

Problems in separation of *C. subcylindricus* from eastern species of *Lixus* are resolved by *Lixus* species, among other characters, lacking broadly rounded pronotal postocular lobes and instead possessing at most a small acute postocular projection and postocular vibrissae that are not more or less uniform in length, but rather variable in length and distinctly longest at some point behind the eye (Fig. 4).

Description.— *Specimens examined.* 11 males, 18 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 18. *Size.* Length, male, 8.9–10.5 mm; female, 8.5–11.3 mm. Width, male, 2.9–3.5 mm; female, 2.8–3.9 mm. *Head.* Eye elongate-oval. Area behind eye with numerous wrinkles of cuticle. Frons with very dense, small, shallow punctures, some confluent in some specimens. Frons lacking suberect or erect vestiture, with moderately dense, small to moderately large, very fine and elongate appressed white scales (scales abraded medially in most specimens). Frons separated from base of rostrum by shallow transverse impression (Fig. 140a). Base of rostral carina with small shallow fovea. Width of frons less than width at apex of rostrum. *Rostrum.* Moderately robust, very slightly more so in males (width at apex 0.56-0.69 times length) (Fig. 140). In lateral view slightly curved downward. In dorsal view with postgenae slightly expanded laterally, antennal scrobes partially visible. Slightly medially tumescent from point of antennal insertion to base of frons, with distinct, low, glabrous median carina from point of antennal insertion to middle of frons. Dorsal and lateral punctation very dense, small, shallow (many punctures longitudinally confluent in some specimens). Dorsally lacking suberect or erect vestiture; with moderately dense elongate-fine appressed white scales, scales smaller medially. Epistoma slightly elevated and swollen. *Pronotum.* Median carina lacking to variously developed as low, glabrous, shiny line. Dorsal punctation small, dense and shallow; larger and sparser on flanks; areas between larger dorsal punctures with very dense shallow minute punctures, areas between shiny and irregularly elevated. Dorsally lacking suberect or erect vestiture (Fig. 140a). Scales dorsally absent to moderately dense and very small along midline; moderately dense, small and fine, appressed in pair of broad paramedian apically narrowed stripes; laterally absent to moderately dense and very small. Lateral margins with appressed white scales large and robust, moderately dense in a moderately broad stripe. Flanks with scales small and fine. Median basal area of disk very shallowly and very broadly impressed. Anterolateral margin with rounded pronotal postocular lobes moderately developed; postocular vibrissae of approximately uniform length (slightly longer behind basal portion of eye in some specimens with less well-developed postocular lobes). In dorsal view with lateral margins straight, slightly convergent from base to apical one-quarter, then straight and more markedly convergent to apex; subapical constriction indistinct (Fig. 121). *Prosternum.* With shallow to moderately deep transverse impression and with prosternal swelling lacking to slightly developed anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion short, not distinctly differentiated from posterior longer more angulate portion. *Elytra.* Elongate-narrow in general form (width at midlength 0.45-0.50 times length in males; 0.43–0.53 in females) (Fig. 121). In dorsal view with lateral margins subparallel from apical one-third to humerus; moderately evenly arcuate from apical one-third to apex. Elytral apices not produced, sub-acuminate, not divergent. Humerus distinct. Dorsally lacking suberect or erect vestiture. Sutural interval to interval 8 with scales uniformly moderately dense, fine and elongate, white, with scattered patches of slightly larger white scales; intervals 9 to 11 with scales uniformly moderately dense, large, robust and white (Fig. 121). Punctures of elytral striae small, individually distinct, larger and less individually distinct towards base, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth small, indistinct from tibial denticles. Foretibial, mesotibial, and metatibial unci of both sexes moderately large. Tarsal claws connate in basal one-half, not divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsi of male and female extensive, present as rounded pads which cover more or less entire ventral surface of all articles, with exception of basal portion of article 1. *Abdomen.* Ventral surface with moderately dense appressed very elongate white scales. Abdominal sterna III and IV (especially laterally), with distinct moderately large glabrous patches, each with large puncture and single elongate appressed scale situated in or near center; lacking suberect or erect vestiture except for small, scattered, sparse hair-like scales on sternum VII of male. Base of abdominal sternum VII of female internally (dorsally) with slightly developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm very short; lateral arms straight to very slightly sinuate and divergent from base to apex, apices not expanded (Fig. 160). Stylus large in length compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 180a,b) elongate, moderately high; median dorsal pocket moderately high, with single narrow moderately elongate dorsally directed basal lobe (lobe A), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), and with small ventrally directed paired lobe near base near ventral margin (lobe F); lobes B, D, and E lacking. Apex of median dorsal pocket rounded in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is distributed, perhaps discontinuously, along the Atlantic Coastal Plain from New York south to Florida (Fig. 215).

Natural history.— This species is found at various localities on the Atlantic Coastal Plain in the southeastern mesophytic evergreen forest region. This species was described from several specimens collected on flowers of the hoary lupine, *Lupinus diffusus* Nutt. (Leguminosae) near Dunedin, Florida between January 24 and March 18 (Blatchley 1914; Blatchley and Leng 1916). Other adults have been collected in roots of *Lupinus* sp. (Wilmington, North Carolina) and have been reared from *Lupinus cumulicola* Small (Spring Valley, Florida). Adult specimens have been collected from January to May at elevations of sea level to 182 m (N=7) (Fig. 233).

Chorological relationships.— Table V. This species is sympatric with *C. calandroides* in the northern part of its range in New York.

Phylogenetic relationships.— This species is the sister species of the *C. longinasus*-*C. texanus* lineage (Fig. 237).

Cleonidius longinasus Anderson, new name
(Figs. 122, 141, 161, 181, 214)

Lixus mixtus LeConte 1876a:416 [not Fabricius 1792:417]. Holotype (examined), female, labelled "Col", "B.D.Smith", "Type/ 5178", "*L. mixtus*/ Lec." (MCZC). Type locality, Colorado. Henshaw 1881–1882 (check.). Henshaw 1885 (check.) Leng 1920 (catal.).
Cleonus (*Cleonidius*) *modestus*; Hatch 1971 (key, redesc., misident.).
Cleonus mixtus; Kingsolver 1972.
Cleonis mixtus; O'Brien and Wibmer 1982 (catal., distn.).
mixtus, incertae sedis; Csiki 1934 (catal.).

Notes about synonymy.— The name *Lixus mixtus* LeConte is a junior homonym and is here replaced with the name *C. longinasus* Anderson.

Derivation of specific epithet.— From the Latin "*longus*" meaning long and "*nasus*" meaning nose. This name is used in reference to the very long rostrum of females of this species (Fig. 141a).

Problems in recognition.— Most individuals, especially females, of this species are easily recognized by the long and narrow rostrum (Fig. 141a). Otherwise, individuals, especially males, are likely only to be confused with *C. eustictorrhinus*, *C. subcylindricus* and *C. texanus*. Individuals of *C. longinasus* are separated from *C. subcylindricus* by the latter entirely lacking suberect or erect dorsal vestiture and being distributed only along the Atlantic Coastal Plain from New York south to Florida. *C. longinasus* and *C. eustictorrhinus* are sympatric in California but individuals are easily distinguished by the more robust, medially tumescent rostrum of the latter (Fig. 138). On the other hand, although most *C. texanus* and *C. longinasus*, where they are sympatric in California and Oregon, can be separated on the basis of the length and width of the rostrum, length of erect dorsal vestiture, and association with different plant taxa, some specimens, especially males, are very difficult to reliably separate as discussed under the "Problems in recognition" section for *C. texanus*.

A very few individuals of *C. longinasus* have scales on elytral intervals 3 to 5 larger than those on adjacent intervals giving the elytra an indistinctly vittate scale pattern and perhaps resulting in confusion with species with distinctly vittate scale patterns. Specimens from San Francisco, California entirely lack suberect or erect vestiture but have the long narrow rostrum typical of members of this species.

Description.— *Specimens examined.* 44 males, 80 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 19. *Size.* Length, male, 7.2–9.8 mm; female, 6.1–11.2 mm. Width, male, 2.2–3.4 mm; female, 2.1–3–8 mm. *Head.* Eye elongate-oval. Area behind eye with numerous wrinkles of cuticle. Frons with sparse to moderately dense, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed with minute punctures. Frons also with sparse to moderately dense, elongate-fine to elongate-narrow, white, appressed to suberect scales medially, elongate-narrow and erect immediately above eyes. Some specimens also with moderately dense very elongate-fine erect hair-like scales medially and immediately above eyes. Frons continuous with base of rostrum or only very slightly separated by very shallow indistinct transverse impression (Fig. 141a). Base of median carina of rostrum (if present) with small, shallow fovea. Width of frons greater than width at apex of rostrum. *Rostrum.* Very elongate-narrow, especially so in females (width at apex in male 0.40-0.56 times length; 0.34-0.44 in female) (Fig. 141). In lateral view straight to moderately curved downward (markedly so near apex in some specimens). In dorsal view with postgenae not laterally expanded, antennal scrobes not or only very slightly visible. Rostrum not medially tumescent, with median carina lacking to variously developed as rounded slightly elevated fine glabrous shiny line. Dorsal and lateral punctation dense, small, shallow (longitudinally confluent in many specimens), smaller and not longitudinally confluent apically, dorsally interspersed with minute punctures. Dorsally with suberect or erect vestiture lacking (few specimens) to with sparse to moderately dense, moderately long to very long, erect hair-like scales in basal one-half, erect vestiture lacking from apical one-half; with sparse to moderately dense appressed to suberect elongate-fine scales in basal one-half, lacking from (perhaps abraded) or very sparse in apical one-half in most specimens. Epistoma not swollen. *Pronotum.* Median carina lacking to variously developed in anterior one-half as slightly elevated narrow shiny glabrous line. Dorsal punctation moderately large, moderately dense to dense, moderately deep; smaller and shallower apically; sparser on flanks; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally (especially laterally) with sparse to moderately dense, moderately long to very long, erect hair-like scales, each situated in large puncture (Fig. 141a). Scales dorsally absent to moderately dense, small and fine along median line; sparse to dense, elongate-fine to elongate-narrow laterad of median line (forming distinct apically narrowed stripes in many specimens); laterally, absent or sparse to moderately dense, small and fine. Lateral margins with scales moderately dense to dense, elongate-narrow to moderately robust, appressed to recumbent in moderately broad stripe. Flanks with scales moderately dense to dense, elongate-narrow. Median basal area of disk broadly and shallowly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae uniformly short. In dorsal view with lateral margins uniformly very slightly arcuate and convergent from base to apex; subapical constriction indistinct. *Prosternum.* With very shallow, indistinct impression and very slightly to moderately developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion; anterior and posterior portions not to slightly differentiated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.48-0.54 times length in males; 0.48-0.58 in females) (Fig. 122). In dorsal view with lateral margins straight to very slightly arcuate or slightly sinuate, slightly convergent from apical one-third to humerus; slightly to moderately and evenly arcuate from apical one-third to apex. Elytral apices slightly produced, rounded to sub-acuminate. Humerus distinct. Dorsally with sparse to moderately dense, short to very long erect hair-like scales (longest and densest on declivity of most specimens; absent on specimens from San Francisco, California). Sutural interval to interval 7 with uniformly moderately dense, fine to elongate-fine scales, scales on intervals 3 to 5 larger than those on sutural interval and interval 2, and intervals 6 and 7 in some specimens; interval 8 with scales small, very fine to fine, sparse to moderately dense; intervals 9 to 11 with scales moderately dense to dense, elongate-narrow to moderately robust, sparser and smaller apically in some specimens (Fig. 122). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small, indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes large to moderately large, metatibial uncus small. Tarsal claws connate in basal one-third to one-half, not divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsi of male and female present as elongate-narrow pads on apical one-half to two-thirds of article 1, as large oval pads on apical three-quarters to more or less entire ventral surface of article 2, and as large rounded pads on apical three-quarters to more or less entire ventral surface of article 3. *Abdomen.* Ventral surface with moderately dense, elongate-narrow appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct glabrous patches, each with large puncture and single suberect to erect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with well-developed median shiny tubercle. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm short; lateral arms straight and divergent from base to apical one-quarter, inwardly arcuate at apical one-quarter and convergent to apex, apices slightly expanded (Fig. 161). Stylus moderately large compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 181a,b) elongate, moderately high; median dorsal pocket moderately high, with single moderately broad elongate dorsally directed basal lobe (lobe A), with large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), and with small ventrally directed paired lobe near base near ventral margin (lobe F); lobes B, D, and E lacking. Apex of median dorsal pocket rounded in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation.— Specimens from San Francisco, California lack dorsal suberect or erect vestiture but are otherwise typical *C. longinasus*. Some specimens from California and Oregon have less elongate-narrow rostra than typical for this species, perhaps due to hydridization with *C. texanus* which in these areas also occurs on Leguminosae. It does not appear to be host plant induced for all *C. longinasus* are found on Leguminosae.

Geographic distribution.— This species is distributed from southern British Columbia and Washington, south to Idaho, western Montana and Wyoming in the east, south to southern California in the west (Fig. 214).

Natural history.— This species is associated with grassland, Pacific semi-desert and Great Basin desert habitats. Adults of this species have only been found associated with Leguminosae. They have been collected on *Lupinus* spp. and *Astragalus* spp. (both Leguminosae) throughout California. No definite host records are known but it is likely that various annual legumes serve as potential host plants throughout the species range. Adults have been collected from February to December at elevations of from 31–2293 m (N=14) (Fig. 233). Unlike adults of *C. texanus* which are known to occur, albeit rarely, on low altitude Leguminosae, *C. longinasus* are not known from Rosaceae, the presumed primary host of the former species.

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister species of *C. texanus* (Fig. 237).

Cleonidius texanus (LeConte)
(Figs. 123, 142, 162, 182, 218)

Lixus texanus LeConte 1876a:155. Lectotype (here designated), one of two syntypes, male, labelled with a dark red circle (=Texas), "67", "TYPE/ 5250", "*L.texanus*/ Lec" and with my designation label "*Lixus*/ *texanus* LeC./ LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Texas. LeConte 1876a (in part; misident. of *Cleonidius quadrilineatus*, [mixed type series]). Henshaw 1881–1882 (check.). Henshaw 1885 (check.).

Cleonus (*Cleonidius*) *circumductus* Casey 1891:192. NEW SYNONYMY Holotype (examined), male, labelled "Ari.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37282", "*C.Cl.*/ *circumductus*/ Cas." (USNM). Type locality, Arizona. Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *texanus*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus circumductus; Wickham 1902 (check.). Leng 1920 (catal.).

Cleonus texanus; Wickham 1902 (check.). Leng 1920 (catal.).

Cleonus canescens; Yothers 1916 (misident.). Essig 1958 (biol., misident.).

Cleonis circumductus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis modestus; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Cleonis texanus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— Casey (1891) distinguished *C. circumductus* Casey from *C. texanus* (LeConte) by the longer, denser and more erect dorsal vestiture. These features of the dorsal vestiture vary throughout the species range and do not warrant separate species status. (See also sections on "Problems in recognition" and "Variation".)

Problems in recognition.— Individuals of this species are likely to be confused only with individuals of *C. longinasus*, *C. eustictorrhinus*, and *C. subcylindricus*. *C. subcylindricus* individuals are easily separated as they lack suberect or erect dorsal vestiture and are found only along the Atlantic Coastal Plain of the eastern United States of America. Separation of *C.*

eustictorrhinus and *C. texanus* individuals is more difficult. Both species occur in California but can be separated by the more robust and medially tumescent rostrum of *C. eustictorrhinus* (Fig. 138) as outlined in the key.

Individuals, especially males, of *C. texanus* and *C. longinasus* are perhaps the most difficult species of *Cleonidius* to reliably separate. Both species are sympatric over a wide geographic range but are especially problematical to distinguish in California and Oregon. Most *C. longinasus* are slightly larger in size, have long to very long dorsal erect vestiture (Fig. 141a), a very elongate-narrow rostrum (especially so in females) (Fig. 141a), and are associated with both low and high altitude Leguminosae. Most *C. texanus* on the other hand have generally shorter dorsal erect vestiture (Fig. 142a), a shorter, slightly more robust rostrum (Fig. 142a), and are associated with Rosaceae or Rhamnaceae. All individuals from Rosaceae or Rhamnaceae are structurally typical *C. texanus*, although not all specimens associated with Leguminosae are *C. longinasus*. I have seen both male and female specimens with short rostra and short dorsal erect vestiture, both character states of *C. texanus*, from low altitude Leguminosae. I consider these as *C. texanus*. Various individuals from the area of sympatry, including some females, but especially males and those individuals lacking data on plant associations, are less easy to separate based on these structural differences. The rostrum in these specimens is generally of a length precluding reliable assignment to either species, however, length of dorsal erect vestiture of many specimens allows for a tentative identification. As a consequence of this variation, some may consider these twoforms as questionably warranting separate species status, but the moderately extensive distribution of *C. longinasus*, yet the lack of *C. longinasus* or *C. texanus* on Leguminosae from areas (particularly Arizona and Texas) where *C. texanus* is found on Rosaceae and Rhamnaceae, and the lack of individuals with structural character states of *C. longinasus* from Rosaceae or Rhamnaceae yet presence of individuals with structural features of *C. texanus* from Leguminosae, argues against conspecificity (the structural differences perhaps induced by association with different host plants). I suspect hybridization to be the likely cause of the complexities in variation but because of the noted assymmetry in plant associations, do not regard it as warranting conspecificity of the two forms.

Description.— *Specimens examined*. 156 males, 174 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEI, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 20. *Size*. Length, male, 6.2–8.6 mm; female, 5.3–8.8 mm. Width, male, 1.9–3.2 mm; female, 1.8–3.0 mm. *Head*. Eye elongate-oval. Area behind eye with numerous wrinkles of cuticle. Frons with sparse to moderately dense, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed with minute punctures. Frons also with moderately dense, elongate-fine, white appressed to suberect scales medially, elongate-narrow and erect immediately above eyes. Frons continuous with base of rostrum or only very slightly separated by very shallow indistinct transverse impression (Fig. 142a). Base of median carina of rostrum (if present) with small, shallow fovea. Width of frons greater than or subequal to width at apex of rostrum. *Rostrum*. Elongate-narrow, slightly more so in females (width at apex 0.51–0.68 times length in male; 0.46-0.66 in female) (Fig. 142). In lateral view slightly curved downward (markedly so near apex in some specimens). In dorsal view with postgenae not to very slightly laterally expanded, antennal scrobes only very slightly visible. Rostrum not to very slightly medially tumescent, with median carina lacking. Dorsal and lateral punctation moderately dense to dense, small, shallow (longitudinally confluent in some specimens), smaller and not longitudinally confluent apically, dorsally interspersed with minute punctures. Dorsally with suberect or erect vestiture lacking (few specimens) to with sparse, short, sub-erect to erect hair-like scales laterally and basally, erect vestiture lacking from apical one-half; with sparse to moderately dense recumbent elongate-very-fine to elongate-fine scales laterally in basal one-half, lacking from (perhaps abraded) or very sparse in apical one-half and medially in most specimens. Epistoma not swollen. *Pronotum*. Median carina lacking to variously developed in anterior one-half as indistinct slightly elevated narrow shiny glabrous line. Dorsal punctation moderately large, moderately dense to dense, moderately deep; smaller andshallower apically; sparser on flanks; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally (especially laterally) with sparse to moderately dense, short to moderately long, erect hair-like scales, each situated in large puncture (Fig. 142a). Scales dorsally sparse to moderately dense, small and fine along median line; moderately dense, elongate-fine to elongate-narrow laterad of median line; laterally, sparse to moderately dense, small and fine. Lateral margins with scales moderately dense to dense, elongate-narrow to moderately robust, appressed to recumbent in moderately broad stripe. Flanks with scales moderately dense, elongate-narrow. Median basal area of disk broadly and shallowly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae uniformly short. In dorsal view with lateral margins uniformly very slightly arcuate and convergent from base to apex; subapical constriction indistinct, or straight and convergent from base to apical one-quarter, slightly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With shallow to moderately deep impression and very slightly to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion; anterior and posterior portions not to slightly differentiated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.45-0.51 times length in males; 0.44-0.51 in females) (Fig. 123). In dorsal view with lateral margins straight to very slightly arcuate or slightly sinuate, slightly convergent from apical one-third to humerus; slightly to moderately and evenly arcuate from apical one-third to apex. Elytral apices slightly produced, rounded to sub-acuminate. Humerus distinct. Dorsally with sparse to moderately dense, short suberect to erect hair-like scales (longest and densest on declivity of most specimens). Sutural interval to interval 7 with uniformly moderately dense, fine to elongate-fine scales, interval 8 with scales small, very fine to fine, sparse to moderately dense; intervals 9 to 11 with scales moderately dense to dense, elongate-narrow to moderately robust, sparser and smaller apically in some specimens (Fig. 123). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth small, indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes large to moderately large, metatibial uncus small. Tarsal claws connate in basal one-half, not divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsi of male and female present as elongate-narrow pads on apical one-half to two-thirds of article 1, as large oval pads on apical three-quarters to more or less entire ventral surface of article 2, and as large rounded pads on apical three-quarters to more or less entire ventral surface of article 3. *Abdomen.* Ventral surface with moderately dense, elongate-narrow appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct glabrous patches, each with large puncture and single suberect to erect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with well-developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms straight and divergent from base to apical one-third, inwardly arcuate at apical one-third and convergent to apex, apices slightly expanded (Fig. 162). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 182a,b) elongate, moderately high; median dorsal pocket moderately high, with single moderately broad elongate dorsally directed basal lobe (lobe A), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), and with small ventrally directed paired lobe near base near ventral margin (lobe F); lobes B, D, and E lacking. Apex of median dorsal pocket rounded in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation..— None noted, but see "Geographic variation" section for *C. longinasus* and "Problems in recognition" section for *C. texanus.*

Geographic distribution.— This species is distributed from Washington and Idaho, east to Colorado, south to southeastern Texas in the east, and southern California in the west (Fig. 218).

Natural history.— This species is associated with the western xerophytic evergreen forest habitat. Adults have been collected primarily on Rosaceae and Rhamnaceae throughout the species range, but also on Leguminosae, although only in coastal California and Oregon. Records from Rosaceae and Rhamnaceae are primarily at higher altitudes, regardless of geographic location (although especially in oak-piñon-juniper woodlands). Records from Leguminosae are known only from lower altitudes. Adults have been collected on the following plants; *Lupinus* sp. (Leguminosae); *Ceanothus* sp., *C. cuneatus* (Hook.) Nutt., *C. leucodermis* Greene, *C. integerrimus* Hook. and Arn. (Rhamnaceae); *Cercocarpus* sp., *C. ledifolius* Nutt., *C. montanus* Raf., *Cowania mexicana* D. Don., *Prunus amygdalus* Batsch. (almond), *P. persica* Batsch. (peach), *Pyrus communis* L. (pear), *Purshia tridentata* (Pursh.) DC. (all Rosaceae). Adults have been reared only from *Lupinus affinis* J.G. Agardh. (Leguminosae) at Berkeley, California, but I suspect that a variety of Rosaceae and Rhamnaceae serve as hosts at higher altitudes throughout most of the species range. Adults have been collected from January to October at altitudes ranging from 15–2998 m (N=56) (Fig. 233). Other individuals and I have collected specimens of *C. texanus* and *C. quadrilineatus* together on various Rosaceae and Rhamnaceae in Arizona and Texas.

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister species of *C. longinasus* (Fig. 237).

Cleonidius americanus species group

Diagnosis.— Size small to moderate for *Cleonidius* (Fig. 197). Dorsal erect or suberect vestiture absent to present, dense, short to very long. Rostrum moderately elongate-narrow (Fig. 143) to very robust (Figs. 146–147), slightly to markedly medially tumescent, not to variously carinate; lateral margins rounded to sharp. Pronotum with postocular lobes absent (Fig. 145) to present and well-developed (Fig. 143); postocular vibrissae uniformly short to long, of unequal length, and longest behind base of eye. Elytra with scale pattern vittate, intervals other than 9 to 11 with white scales equal in size to those on intervals 9 to 11 (Figs. 146,149), or, with scattered patches of large white scales in mottled appearance (Figs. 143–144). Tarsus with ventral pilose vestiture slightly to markedly reduced in extent (on apical one-half to two-thirds of articles 2 and 3) to absent or nearly so on all articles. Wings present, length various. Female with abdominal sternum VIII with basal arm short to long; lateral arms arcuate to more or less straight throughout length. Male with aedeagus with internal sac with apex of dorsal median pocket rounded; lobes A to F present; dorsal median pocket low in lateral view.

Phylogenetic relationships.— Monophyly of this species group is based only on distribution of the apotypic states of extent of ventral tarsal pilosity (homoplasious within *Cleonidius* in species of the *C. boucardi* group). This monophyly is further weakly supported by the tendency for individuals of some species placed in the *C. americanus* group to be brachypterous more so than individuals of species in other groups and to be the only species group whose members may exhibit a mottled elytral scale pattern. These states however cannot be considered synapotypic for they are not shared by all members of the species group and independent evolution of the apotypic state within species of the group is equally parsimonious with consideration of the apotypic state as a groundplan state for the group with subsequent reversions to the plesiotypic state having taken place. The *C. americanus* group is hypothesized to be the sister group to the *C. poricollis* group-*C. boucardi* group lineage, this lineage then sister to the *C. erysimi* group (Figs. 236–237).

Cleonidius americanus Csiki
(Figs. 124, 143, 163, 183, 223)

Cleonus (*Cleonidius*) *sparsus*; Casey 1891 (key, misident.).

Cleonus basalis Fall 1897:242 [not Chevrolat 1860:80]. Holotype (examined), male, labelled "S.Clemente/ Id. CAL./ 5.29.97", "TYPE", "*basalis*/ Fall", "M.C.Z./ Type/ 25192", "H.C. FALL/ COLLECTION" (MCZC). Type locality, San Clemente Island, California.

Cleonus (*Cleonidius*) *americanus* Csiki 1934:64. New name for *Cleonus basalis* Fall. Blackwelder 1939 (check.).

Cleonis americanus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis basalis; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).

Problems in recognition.— Unabraded specimens of this species should be easily recognized because of the long dorsal erect vestiture (Fig. 143a). Only specimens of *C. longinasus* have equally long erect dorsal vestiture, but they have a different elytral scale pattern and a more elongate-narrow rostrum that is neither laterally expanded at midlength nor with the prementum swollen ventrally, as in members of *C. americanus* (Fig. 143). Indeed, *C. americanus* and *C. frontalis* are the only species of *Cleonidius* in which the rostrum, in lateral view, has the prementum slightly to markedly swollen ventrally, and in dorsal view is variously expanded laterally at midlength (Figs. 143–144). Abraded specimens throughout the species range in California might therefore only be otherwise confused with *C. frontalis*. From *C. frontalis*, individuals of *C. americanus* can be distinguished by their larger, deeper, and denser dorsal pronotal punctation, absence of large denticles on the inner margin of the fore-tibia of females (Fig. 143c), and the rostrum straight, not slightly curved downward.

Description.— *Specimens examined.* 65 males, 69 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEI, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 21. *Size.* Length, male, 4.9–10.9 mm; female, 5.4–11.3 mm. Width, male, 1.9–4.1 mm; female, 2.1–4.1 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse to moderately dense, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed with minute punctures. Frons also with sparse, elongate-fine, white appressed to recumbent scales medially, moderately dense, elongate-narrow and erect immediately above eyes; with dense, very long erect hair-like scales laterally, lacking medially. Frons continuous with base of rostrum or only very slightly separated by shallow transverse impression (Fig. 143a). Base of median carina of rostrum (if present) with small, shallow fovea. Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately elongate-narrow (width at apex 0.51–0.63 times length in males; 0.43–0.59 in females) (Figs. 143a,b). In lateral view straight. In dorsal view with postgenae not to very slightly laterally expanded, antennal scrobes not distinctly visible. Rostrum not to very slightly medially tumescent; slightly laterally expanded at midlength (Fig. 143b); lateral margins more or less rounded, not sharp; with median carina variously developed as moderately elevated broad shiny glabrous line. Dorsal and lateral punctation sparse to moderately dense, small, shallow to deep (longitudinally confluent in many specimens), dorsally interspersed with minute punctures. Dorsally with moderately dense to dense, very long, erect hair-like scales (especially laterally); with moderately dense recumbent elongate-fine scales laterally in basal one-half, lacking from (perhaps abraded) or very sparse in apical one-half and medially in most specimens. Epistoma not swollen. Rostrum in lateral view with submentum slightly to markedly swollen ventrally (Fig. 143a). *Pronotum.* Median carina lacking to variously developed in anterior one-half as low, narrow shiny glabrous line. Dorsal punctation and that of flanks large, dense, deep; smaller, sparser and shallower apically; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally with moderately dense, very long, erect hair-like scales, each situated in large puncture (Fig. 143a). Scales dorsally absent to sparse, small and fine along median line; moderately dense, elongate-fine, appressed to recumbent in pair of paramedian slightly apically narrowed stripes; laterally, absent to very sparse, small and fine. Lateral margins with scales moderately dense, elongate-narrow, appressed in narrow stripe. Flanks with scales uniformly moderately dense, elongate-fine. Median basal area of disk broadly and shallowly to moderately deeply impressed. Anterolateral margin with pronotal postocular lobes moderately-developed; postocular vibrissae uniformly short to of unequal length, moderately long and with greatest width approximately one-half width of eye, immediately behind base of eye (Fig. 143a). In dorsal view with lateral margins slightly arcuate and convergent from base to apical one-third, slightly constricted at apical one-third then straight and convergent to apex. *Prosternum.* With small shallow impression and very slightly to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately two-thirds length of posterior more angulate portion; anterior and posterior portions slightly differentiated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.50-0.60 times length in males; 0.50-0.56 in females) (Fig. 124). In dorsal view with lateral margins straight, slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, not divergent. Humerus distinct. Dorsally with moderately dense, moderately long erect hair-like scales. Scales various in color from golden to white; scale pattern various from mottled, with uniformly moderately dense small, fine scales and irregularly distributed patches of denser and larger white scales (Fig. 124); to vittate, with scales uniformly moderately dense, sutural interval and interval 2 (except at base) with golden scales elongate-very-fine, stria 1 with irregularly distributed patches of larger elongate-narrow white scales, base of interval 2 and intervals 3 to 5 with scales elongate-narrow, white, intervals 6 to 11 various from with irregularly distributed patches of denser and larger, elongate-narrow white scales interspersed among elongate-very-fine white or golden scales; to uniformly covered (except intervals 6 and 7 at basal one-third) with large elongate-narrow white scales. Punctures of elytral striae small, individually distinct, larger and less individually distinct basally; arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth small, indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes large to moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, not divergent, each with basal internal flange slightly developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-narrow pads on apical one-third to one-half of article 1, as elongate-oval pads on apical one-half to two-thirds of article 2, and as large rounded pads on apical two-thirds to more or less entire ventral surface of article 3; of foretarsus of female, as apical tufts to small elongate pads on apical one-quarter of article 1, as small rounded pads on apical one-third of article 2, as moderately large rounded pads on apical two-thirds of article 3; of mesotarsus of male, as elongate-narrow pads on apical one-half of article

1, as elongate-oval pads on apical one-half to two-thirds of article 2, as large rounded pads on apical two-thirds to three-quarters of article 3; of mesotarsus of female, as apical tufts to small elongate pads on apical one-quarter of article 1, as small rounded pads on apical one-third of article 2, as moderately large rounded pads on apical one-half to two-thirds of article 3; of metatarsus of male, as elongate-narrow pads on apical one-third to one-half of article 1, as elongate-oval pads on apical one-half to two-thirds of article 2, as large rounded pads on apical two-thirds to three-quarters of article 3; of metatarsus of female, as apical tufts to small elongate pads on apical one-quarter of article 1, as small rounded pads on apical one-third of article 2, as moderately large rounded pads on apical one-half of article 3. *Abdomen.* Ventral surface with moderately dense, elongate-narrow appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large glabrous patches, each with large puncture and single erect very long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with only very slightly developed median shiny tubercle. *Genitalia.* Female (three examined). Abdominal sternum VIII with basal arm short; lateral arms moderately and evenly inwardly arcuate at point slightly beyond midlength, apices slightly expanded (Fig. 163). Stylus moderately large compared to length of gonocoxite II. Male (three examined). Internal sac (Figs. 183a,b) elongate and low; median dorsal pocket low, with single elongate narrow dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apex of median dorsal pocket truncate in dorsal view. Apical pocket individually distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is found only in California, from the San Francisco Bay region south along the coast and central valleys to the Mexican border (Fig. 223).

Natural history.— This species is found only in the Pacific semi-desert habitat. Adults of this species have been collected on *Artemesia tridentata* Nutt., *Chrysothamnus nauseosus* (Pall.) Britton, *Franseria* sp., *Gutierrezia* sp., and *Aplopappus* sp. (all Compositae). No definite hosts are known but it is probable that a variety of Compositae serve as potential hosts. Adults have been collected from March to November at elevations of from 15–1446 m (N=7) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. frontalis* (Figs. 236 and 237).

Cleonidius frontalis (LeConte)
(Figs. 125, 144, 164, 184, 226)

Cleonus frontalis LeConte 1876a:150. Lectotype (here designated), female, one of three syntypes, labelled with a pale green circle (=Wyoming Territory), "Black Hills/ Hammond", "TYPE/ 5245", "*C. frontalis*/ Lec." and with my designation label "*Cleonus*/ *frontalis* LeC./ LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Black Hills, South Dakota. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1889. Wickham 1902 (check.). Fall and Cockerell 1907 (check.). Blatchley and Leng 1916 (key, redesc.). Leng 1920 (catal.). Bleasdell 1937 (check.).

Cleonus sparsus LeConte 1876a:152 [not Zoubkoff 1833:334]. NEW SYNONYMY. Holotype (examined), female, labelled "Col", "*C.*/ *sparsus*/ TYPE Lec.", "Horn Coll/ H8528" and with a red square label (MCZC). Type locality, Colorado. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1902 (check.). Leng 1920 (catal.). Essig 1958 (biol., in part misident. of *Cleonidius poricollis*). Arnett *et al.* 1980 (probable misident. of *Cleonidius poricollis*).

Cleonus (*Cleonidius*) *frontalis*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *sparsus*; Casey 1891 (key, misident. of *Cleonidius americanus*). Hatch 1971 (key, redesc., in part misident. of *Cleonidius poricollis*).

Cleonus (*Cleonidius*) *stratus* Csiki 1934:65. NEW SYNONYMY New name for *Cleonus sparsus* LeConte. Blackwelder 1939 (check.).

Cleonis frontalis; O'Brien and Wibmer 1982 (catal., distn., in part misident. of *Cleonidius poricollis* and *Cleonidius puberulus*).

Cleonis sparsus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis stratus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— To initially distinguish *C. sparsus* and *C. frontalis* as separate species, LeConte (1876a) emphasized differences in the extent of ventral pilosity and form of hind tarsal article 3. Variation in these characters is continuous and known to occur in a number of other widespread species, thus I consider these two forms as conspecific. *Cleonidius frontalis* was artibrarily chosen over *C. sparsus* as the valid name for this species.

Casey (1891) incorrectly placed *C. puberulus* as a junior synonym of *C. frontalis* and misidentified individuals of *C. americanus* as *C. sparsus* in his key. Likewise, other authors have frequently confused *C. frontalis*, *C. puberulus*, *C. sparsus*, and less frequently also *C. poricollis*.

Problems in recognition.— Individuals of this species are very likely to be confused with those of *C. americanus*, *C. notolomus* and perhaps, *C. poricollis* and *C. trivittatus*. They are easily separated from *C. americanus* by the long to very long erect dorsal vestiture and dense, large and deep pronotal punctures of the latter. Furthermore, only a few *C. frontalis* are known from California (Fig. 226), whereas *C. americanus* is restricted to that state (Fig. 223). Separation from *C. poricollis* is quite simple as members of that species, where the two are sympatric, possess a curved sulcus behind each eye (Fig. 150a). Similarly, separation from *C. trivittatus* is simple, as individuals of that species lack or at mosthave only very slightly developed postocular lobes (Fig. 153a).

Separation from *C. notolomus* is most difficult and discussed under "Problems in recognition" section for that species.

Most individuals of *Cleonidius* with an elytral scale pattern that is mottled with irregularly distributed patches of larger white scales, and not distinctly vittate (Fig. 125), are this species.

Description.— *Specimens examined.* 121 males, 115 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 22. *Size.* Length, male, 5.7–10.5 mm; female, 5.7–10.8 mm. Width, male, 2.2–3.9 mm; female, 2.2–4.1 mm. *Head.* Eye elongate-oval (Fig. 145a). Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse to moderately dense, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed throughout with minute punctures. Frons also with moderately dense, elongate-narrow, white appressed to recumbent scales medially, moderately dense, elongate-narrow and suberect to erect immediately above eyes; otherwise lacking suberect or erect vestiture. Frons slightly separated from base of rostrum by shallow to moderately deep transverse impression (Fig. 144a). Base of median carina of rostrum (if present) with small, shallow fovea. Width of frons greater than, to subequal to, width at apex of rostrum. *Rostrum.* Moderately robust, slightly less so in females (width at apex 0.56-0.71 times length in male; 0.54-0.65 in female) (Figs. 144a,b). In lateral view straight to very slightly curved downward. In dorsal view with postgenae not to very slightly laterally expanded, antenna scrobes very slightly visible. Rostrum slightly to moderately medially tumescent from point of antennal insertion to middle of frons (more markedly so basally); not distinctly to slightly laterally expanded at midlength; lateral margins more or less rounded, not sharp; with median carina absent to variously developed as low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation sparse to dense, small, shallow (longitudinally confluent in some specimens); smaller and less dense apically; dorsally interspersed with minute punctures. Dorsally with sparse to moderately dense, short, suberect hair-like scales (especially laterally); with moderately dense appressed elongate-narrow scales laterally in basal one-half, sparse in apical one-half and medially in most specimens. Epistoma not swollen. Rostrum in lateral view with submentum slightly swollen ventrally (Fig. 144a). *Pronotum.* Median carina lacking to variously developed in anterior one-half as low, rounded, moderately broad shiny glabrous line. Dorsal punctation moderately large, moderately dense, moderately deep to deep; smaller, sparser and shallower apically and on flanks; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally with moderately dense, short to moderately long, suberect to erect hair-like scales, each situated in large puncture (Fig. 144a). Scales dorsally absent to very sparse, small and fine along median line; moderately dense, elongate-fine, appressed in pair of narrow paramedian stripes; laterally, absent to very sparse, small and fine. Lateral margins with scales moderately dense to dense, elongate-fine to elongate-narrow, appressed to recumbent in moderately broad stripe. Flanks with scales moderately dense, elongate-fine to elongate-narrow. Median basal area of disk broadly and shallowly to moderately deeply impressed. Anterolateral margin with pronotal postocular lobes moderately to well-developed; postocular vibrissae uniformly short (Fig. 144a). In dorsal view with lateral margins slightly to moderately arcuate and slightly convergent from base to apex, or slightly constricted at apical one-third to one-quarter then straight and convergent to apex. *Prosternum.* With small shallow to moderately deep impression and slightly to well-developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately two-thirds length of, to slightly shorter than, length of posterior more angulate portion; anterior and posterior portions not to very slightly differentiated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.50-0.56 times length in males; 0.49-0.58 in females) (Fig. 125). In dorsal view with lateral margins straight to very slightly sinuate, slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, not to very slightly divergent. Humerus distinct. Dorsally with sparse, indistinct, very short suberect hair-like scales. Scales various in color from golden to white; scale pattern various with sutural interval and interval 2 with golden to white scales sparse to moderately dense, very small and fine to elongate-fine, intervals 3 to 5 with scales moderately dense, elongate-fine to elongate-narrow, white, intervals 6 to 8 with scales sparse to moderately dense, small and fine to elongate-narrow, white, intervals 9 to 11 with scales moderately dense, elongate-fine to elongate narrow, white; striae of many specimens variously with irregularly distributed patches of larger white scales giving mottled appearance (Fig. 125). Punctures of elytral striae small, individually distinct; arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with very large denticles in apical three-quarters; subapical tooth large, indistinct to distinct from tibial denticles (Fig. 144c). Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, not divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-oval pads on apical one-quarter to one-third of article 1, as rounded pads on apical one-third to one-half of article 2, and as large rounded pads on apical one-half to two-thirds of article 3; of foretarsus of female, as apical tufts of article 1, as small rounded pads on apical one-quarter of article 2, as moderately large rounded pads on apical one-half of article 3; of mesotarsus of male, as elongate-narrow pads on apical one-third of article 1, as elongate-oval pads on apical one-third to one-half of article 2, as large rounded pads on apical one-half to two-thirds of article 3; of mesotarsus of female, as apical tufts of article 1, as small elongate-oval pads on apical one-third of article 2, as moderately large rounded pads on apical one-half of article 3; of metatarsus of male, as elongate-narrow pads on apical one-quarter to one-half of article 1, as elongate-narrow pads on apical one-third to one-half of article 2, as elongate-oval to rounded pads on apical one-half to two-thirds of article 3; of metatarsus of female, as elongate-narrow pads on apical one-quarter to one-half of article 1, as elongate-oval pads on apical one-third of article 2, as moderately large rounded pads on apical one-half of article 3. *Abdomen.* Ventral surface with dense, elongate-narrow to broad appressed white scales, sparser and smaller medially on abdominal sterna V to VII. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct large rounded glabrous patches, each with large puncture and single suberect to erect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with moderately to well-developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms very slightly and evenly inwardly arcuate from base to apical one-quarter, more markedly inwardly arcuate at apical one-quarter and convergent to apex, apices slightly expanded (Fig. 164). Stylus moderately large compared to length of gonocoxite II. Male (three examined). Internal sac (Figs. 184a,b) elongate and low; median dorsal pocket low, with single broad short dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apex of median dorsal pocket truncate in dorsal view. Apical pocket individually distinct from mediandorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is distributed from southern Alberta east to southern Manitoba, south to California in the west, east to Nebraska, Kansas and western Texas (Fig. 226).

Natural history.— This species is found in grassland, desert-grassland transitional habitats, and Great Basin desert. Very little is known of the natural history of this species despite the large number of specimens collected and examined. Plant associations are very few, the only records known are of adults on *Atriplex* sp., *A. canescens* (Pursh) Nutt., (Chenopodiaceae); and *Melilotus* sp. (Leguminosae). No definite hosts are known. Adults have been collected from January to November, primarily in grassland habitats, at elevations of from 339–3130 m (N=38) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. americanus* (Figs. 236 and 237).

Cleonidius canescens (LeConte)

(Figs. 126, 145, 165, 185, 227)

Cleonus canescens LeConte 1876a:151. Lectotype (here designated), male, one of three syntypes, labelled "Col.", "Type/ 5243", "*C. canescens*/ Lec." and with my designation label "*Cleonus*/ *canescens*/ Lec. LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Colorado. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1902 (check.). Fall and Cockerell 1907 (check.). Yothers 1916 (misident. of *Cleonidius texanus*). Leng 1920 (catal.). Essig 1958 (biol., misident. of *Cleonidius texanus*).

Cleonus (*Cleonidius*) *canescens*; Casey 1891 (key).

Cleonus (*Cleonidius*) *grandirostris* Casey 1891:189. Lectotype (here designated), male, one of five syntypes, labelled "N.M.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37278", "*C.Cl.*/ *grandirostris*/ Cas." and with my designation label "*Cleonidius*/ *grandirostris*/ Cas./ LECTOTYPE/ desig. Anderson" (USNM). Type locality, New Mexico. Csiki 1934 (catal.).

Cleonus grandirostris; Wickham 1896 (check.). Fall and Cockerell 1907 (check.). Leng 1920 (catal.).

Cleonus (*Cleonidius*) *coloradensis* Csiki 1934:64. Unjustified replacement name for *Cleonus canescens* LeConte. Blackwelder 1939 (check.).

Cleonis canescens; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis coloradensis; O'Brien and Wibmer 1982 (catal., distn., as synonym).

Cleonis grandirostris; O'Brien and Wibmer 1982 (catal., distn., as synonym).

Notes about synonymy.— O'Brien and Wibmer (1982) synonymized *C. canescens* and *C. grandirostris*. *Cleonus coloradensis* is an unjustified replacement name for *C. canescens*.

Problems in recognition.— This species is easily recognized by the less elongate-oval form of the eye (width greater than 0.60 times length) (Fig. 145a), markedly medially tumescent and robust rostrum (Fig. 145a), anterolateral margin of pronotum lacking postocular lobe (Fig. 145a), and short metathoracic wings.

Description.— *Specimens examined.* 182 males, 216 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEI, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 23. *Size.* Length, male, 6.8–8.8 mm; female, 6.9–10.5 mm. Width, male, 2.5–3.7 mm; female, 2.3–4.5 mm. *Head.* Eye more or less oval (width greater than 0.60 times length). Area behind eye with at most only two or three slight wrinkles of cuticle. Frons with moderately dense, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed throughout with minute punctures. Frons also with dense, elongate-narrow, white suberect scales, slightly smaller medially in some specimens, moderately dense, elongate-narrow and erect immediately above eyes; with moderately dense short suberect hair-like scales. Frons continuous with base of rostrum (Fig. 145a). Base of median tumescence or carina of rostrum (if present) with small, shallow fovea. Width of frons greater than, to subequal to, width at apex of rostrum. *Rostrum.* Robust, (width at apex 0.64-0.84 times length in males; 0.64-0.87 in females) (Fig. 145). In lateral view markedly curved downward. In dorsal view with postgenae moderately laterally expanded, antennal scrobes distinctly visible. Rostrum markedly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins more or less rounded, not sharp; with median carina absent to variously developed as low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense, small, shallow to deep; dorsally interspersed with minute punctures. Dorsally with moderately dense, short, erect hair-like scales (especially laterally); with dense suberect moderately robust scales, smaller and finer apicad of point of antennal insertion. Epistoma moderately transversely swollen at base. *Pronotum.* Median carina lacking to slightly developed in anterior one-half as low, rounded, shiny narrow glabrous line. Dorsal and lateral punctation small to moderately large, moderately dense, shallow to deep; smaller apically; areas between large dorsal punctures with minute regularly impressed punctures. Dorsally with moderately dense, very short, fine erect hair-like scales, each situated in large puncture (Fig. 145a). Scales dorsally either uniformly moderately dense medially on disk, or absent along median line; moderately dense, moderately robust, appressed in pair of broad apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and fine. Lateral margins with scales moderately dense, moderately robust, appressed. Flanks with scales moderately dense in dorsal one-half, slightly larger in ventral one-half, elongate-fine to elongate-narrow. Median basal area of disk narrowly and moderately deeply impressed. Anterolateral margin with pronotal postocular lobes lacking; postocular vibrissae of unequal length, long, greatest length (approximately two-thirds width of eye) immediately behind base of eye (Fig. 145a). In dorsal view with lateral margins straight to slightly arcuate and slightly convergent from base to apical one-quarter; slightly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With small shallow impression and at most very slight rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion lacking or at most very short and indistinct from posterior more angulate portion. *Elytra.* Moderately robust in general form (width at midlength 0.56-0.62 times length in males; 0.54-0.62 in females) (Fig. 126). In dorsal view with lateral margins very slightly arcuate from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, subacuminate, not divergent. Humerus rounded, indistinct. Dorsally with moderately dense, short suberect hair-like scales.

Scale pattern various; either more or less mottled, with scales moderately dense, small, elongate-narrow to moderately robust on sutural interval and interval 2, moderately dense, large, moderately robust on intervals 3 to 6, moderately dense, large, but with scattered patches of very much smaller scales on intervals 7 to 11 (Fig. 126); or vittate, with scales moderately dense, small and fine on sutural interval and interval 2, moderately dense, uniformly large, moderately robust on intervals 3 to 5, moderately dense, moderately robust, small on intervals 6 and 7, absent to sparse, small, fine on interval 8, uniformly moderately dense, large, moderately robust on intervals 9 to 11. Punctures of elytral striae small, individually distinct; arranged in regular rows. *Wings*. Short (approximately equal to one-half length of elytra). *Legs*. Foretibia of female with inner margin with small denticles in apical two-thirds; subapical tooth small, indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes large to moderately large, metatibial uncus small. Tarsal claws connate in basal one-half, not divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate-narrow pads on apical one-quarter of article 1, as elongate-oval pads on apical one-quarter to one-half of article 2, and as large rounded pads on apical two-thirds of article 3; of foretarsus of female, as apical tufts of article 1, as small rounded pads at ventral apex of article 2, as moderately large rounded pads on apical one-half to two-thirds of article 3; of mesotarsus of male, as elongate-narrow pads on apical one-quarter of article 1, as elongate-oval pads on apical one-third of article 2, as large rounded pads on apical one-half to two-thirds of article 3; of mesotarsus of female, as apical tufts of article 1, as small rounded pads at ventral apex of article 2, as moderately large rounded pads on apical one-half to two-thirds of article 3; of metatarsus of male, as apical tufts of article 1, as small elongate pads at ventral apex of article 2, as large rounded pads on apical one-half to two-thirds of article 3; of metatarsus of female, as apical tufts of article 1, as small elongate pads at ventral apex of article 2, as moderately large elongate pads on apical one-half to two-thirds of article 3. *Abdomen*. Ventral surface with moderately dense to dense, elongate-narrow appressed white scales, sparser and smaller medially on abdominal sterna V to VII. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct small to large rounded glabrous patches, each with large puncture and single suberect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with at most very slightly-developed median shiny tubercle. *Genitalia*. Female (four examined). Abdominal sternum VIII with basal arm long; lateral arms markedly inwardly arcuate at midlength, apical one-half of each arm laterally expanded (Fig. 165). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 185a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with moderately large median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F); lobe C absent. Apical pocket not distinct from median dorsal pocket. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation.— Elytral and abdominal scale patterns and depth and size of head, rostral and pronotal punctation vary geographically. Specimens from the western part of the species range in Arizona, Utah and Idaho have the vittate form of elytral scale pattern. The ventral surface of the abdomen of these individuals has only small indistinct glabrous patches, and head, rostral and pronotal punctures are small and shallow. Specimens from the rest of the species range to the east have a mottled form of elytral scale pattern (Fig. 126), with ventral abdominal glabrous patches large and distinct, and punctation of the head, rostrum and pronotum slightly larger and deeper.

The rostrum is also more elongate-narrow in the western form than in the eastern form based on measurements of rostral width at apex compared to length of rostrum in both male and female individuals from populations at 6 miles SE. Turkey, Texas; 19 miles SW. Kayenta, Arizona; and Denver, Colorado. Individuals from the population at Denver have the most robust rostra (males, $X=0.805$ $N=8$; females, $X=0.824$ $N=8$), those from 6 mi. SE. Turkey have an intermediate sized rostrum (males, $X=0.780$ $N=8$; females, $X=0.751$ $N=7$), and those from 19 mi. SW Kayenta have the least robust rostrum (males, $X=0.673$ $N=12$; females, $X=0.669$ $N=6$).

Patterns of variation in all characters in this species parallel those in *A. angularis* wherein gene flow appears to be occuring across the continental divide in southern New Mexico and Arizona, but not to the north, in Colorado and Utah.

Geographic distribution.— This species is distributed in the southcentral United States of America from extreme southeastern Idaho east to Nebraska, south in the west to southern

Arizona, east to extreme southern Texas (Fig. 227). There is a questionable record from Lassen National Park in northern California.

Natural history.— This appears to be a species of low to high elevation grassland, desert-grassland transitional, Texas semi-desert, and Great Basin desert habitats. Plant associations are few. Adults have been collected only on *Symphoricarpos* sp. (Caprifoliaceae); *Atriplex canescens* (Pursh) Nutt. (Chenopodiaceae); *Medicago sativa* L. (alfalfa) (Leguminosae); and *Mentzelia* sp. (Loasaceae). Definite hosts are not known. Specimens have been collected in all months of the year at elevations of 200–2868 m (N=56) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister group of the *C. notolomus*-*C. collaris*-*C. infrequens*-*C. puberulus* lineage (Fig. 237).

Cleonidius infrequens Anderson, new species
(Figs. 5, 127, 146, 166, 186, 222)

Type Material.— Holotype, male, with a red label "HOLOTYPE", "Scott City, Kan./5-29-59/H. Willis", "HOLOTYPE/ *Cleonidius*/ *infrequens*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CWOB). Allotype, female, with a red label "ALLOTYPE", "TEX. Muleshoe/Bailey Co./16.IV.1971/G.B. Marshall, "ALLOTYPE/ *Cleonidius*/ *infrequens*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (CWOB). Type locality, Scott City, Kansas.

Paratypes. 1 male, 5 females. MEXICO: San Luis Potosi: San Luis Potosi, 17.VI.68, Arsego, 1F (USNM).

UNITED STATES OF AMERICA: New Mexico: Fort Sumner, 19.VIII.51, Robinson, 1M (CWOB); 15mi. n. Las Cruces, 24.VII.79, Richmond, 1F (RSAN). Texas: 4mi. s. Big Springs, 3.VI.72, C.W. O'Brien, 1F (CWOB); D'Hanis, 23.II.63, Fohn, 1F (TAMU); Van Horn, 24.VI.42, Scullen, 1F (OSUC).

Derivation of specific epithet.— From the Latin "*in*" meaning not and "*frequens*" meaning frequent. This name is used in reference to the rarity of individuals of this species.

Problems in recognition.— Individuals of this species are likely to be confused only with those of *C. puberulus* and perhaps also *C. notolomus*. From *C. notolomus*, specimens are easily distinguished by their possession of a more robust, sharply and distinctly medially carinate rostrum, and differently impressed pronotum. Characters allowing for separation of *C. infrequens* from *C. puberulus* are discussed under "Problems in recognition" section for that species.

Description.— Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEI, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 24. *Size.* Length, male, 8.3–8.8 mm; female, 8.2–10.0 mm. Width, male, 3.1–3.3 mm; female, 3.0–3.8 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed throughout with minute punctures. Frons also with moderately dense to dense, elongate-fine to elongate-narrow, white appressed scales medially, suberect to erect immediately above eyes; otherwise lacking suberect or erect vestiture. Frons distinctly separated from base of rostrum by deep transverse impression (Fig. 146a). Base of median carina of rostrum with small, shallow fovea. Width of frons less than to subequal to width at apex of rostrum. *Rostrum.* Robust, (width at apex 0.78-0.79 times length in males; 0.75-0.92 in females) (Fig. 146). In lateral view straight to very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes partially visible. Rostrum slightly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins sharp, rostrum flat from immediately laterad of median carina to lateral margins; with median carina present, very distinct, as sharp, elevated, glabrous shiny line at crest of median tumescence; also with indistinct low lateral carina at lateral margin in most specimens (Fig. 146b). Dorsal and lateral punctation moderately dense, moderately large to large, moderately deep and longitudinally confluent (especially so immediately laterad of median carina); dorsally interspersed with sparse minute punctures. Dorsally lacking suberect or erect vestiture; with sparse to moderately dense elongate-narrow to robust appressed white scales. Epistoma transversely swollen at base. *Pronotum.* Median carina lacking to variously developed in anterior one-half as very low, indistinct, broad glabrous line. Dorsal and lateral punctation small to moderately large, moderately dense to dense, moderately deep, not confluent; smaller sparser and shallower apically; areas between large dorsal punctures with minute regularly impressed punctures; punctation sparser and shallower on flanks. Dorsally with moderately dense, short, suberect hair-like scales, each situated in large puncture (Fig. 146a). Scales dorsally absent to sparse, small and fine along median line: dense, elongate-fine to elongate-narrow, appressed in pair of apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and fine. Lateral margins with scales dense, elongate-narrow, appressed in moderately broad stripe. Flanks with scales moderately dense to dense, elongate-fine to elongate-narrow. Median basal area of disk broadly and moderately deeply impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae of unequal length, short, greatest length immediately behind base of eye (Fig. 146a). In dorsal view with lateral margins straight and subparallel to slightly and evenly arcuate from base to apical one-third to one-quarter; constricted at apical one-third to one-quarter then straight and convergent to apex. *Prosternum.* With small shallow impression and very slightly to moderately developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion; posterior and anterior portions not or only slightly separated by shallow transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.55-0.61 times length in males; 0.52–0.60 in females) (Fig. 127). In dorsal view with lateral margins very slightly sinuate and convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, subacuminate, not divergent. Humerus rounded, indistinct. Dorsally with very sparse, irregularly distributed very short suberect hair-like scales; with sutural interval and interval 2 with very sparse to moderately dense, very small and fine to elongate-fine white scales; stria 1 with irregularly distributed patches of larger and denser white scales; intervals 3 to 5 with uniformly dense, elongate-narrow to moderately robust white scales; intervals 6 to 8 with scales absent to very sparse, very small and fine; stria 6 and 7 with irregularly distributed patches of larger and denser white scales; intervals 9 to 11 with scales uniformly dense, white, elongate-narrow to robust (Fig. 127). Punctures of elytral striae small, individually distinct, regular rows. *Wings.* Long (greater than length of elytra [62%, N=5]) to short (approximately equal to one-half length of elytra or less [38%, N=3]). *Legs.* Foretibia of female with inner margin with small to large denticles in apical three-quarters; distinct subapical tooth present. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-half, slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of both sexes present as elongate pad on apical one-third of article 1, as large rounded pad on apical one-half of article 2 and apical three quarters of article 3; of mesotarsus of both sexes as elongate pad on apical one-quarter to one-third of article 1, as large rounded pad on apical one-half of article 2 and apical three quarters of article 3; and of metatarsus of both sexes as elongate pad on apical one-quarter to one-third of article 1, as small rounded to elongate pad on apical one-half of article 2 and as elongate-oval pad on apical one-half to two-thirds of article 3. *Abdomen.* Ventral surface with moderately dense to dense, elongate-narrow to moderately robust appressed white scales, sparser and smaller medially on abdominal sternum VII of female. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large rounded glabrous patches, each with large puncture and single suberect to erect, short to moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with a slightly-developed median shiny tubercle. *Genitalia.* Female (five examined). Abdominal sternum VIII with basal arm long; lateral arms very slightly inwardly arcuate throughout length, expanded abruptly at apex (Fig. 166). Stylus moderately large compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 186a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket rounded in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— Very few individuals of this species are known from western Kansas, southern New Mexico, and western and central Texas, south to San Luis Potosi, Mexico (Fig. 222).

Natural history.— No definite hosts or host plant associations are known for this species. Adults have been collected in grassland and desert-grassland transitional habitats from February to August at elevations of 873–2242 m (N= 7) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. puberulus* (Figs. 236 and 237).

Cleonidius puberulus (LeConte)
(Figs. 115, 128, 147, 167, 187, 225)

Cleonus puberulus LeConte 1876a:151. Lectotype (here designated), female, one of seven syntypes, labelled "N", "Type/ 5242", "*C. puberulus*/ Lec." and with my designation label "*Cleonus*/ *puberulus*/ LeC. LECTOTYPE/ desig. Anderson" (MCZC). Type locality, Nevada. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Leng 1920 (catal., misinterp. as synonym *Cleonidius frontalis*.

Cleonus (*Cleonidius*) *puberulus*; Casey 1891 (misinterp. as synonym *Cleonidius frontalis*). Csiki 1934 (catal., misinterp. as synonym *Cleonidius frontalis*).

Cleonus (*Cleonidius*) *lobigerinus*; Champion 1902–1906 (in part, distn., misident.).

Cleonis puberulus; O'Brien and Wibmer 1982 (catal., distn., misinterp. as synonym *Cleonidius frontalis*).

Notes about synonymy.— The type locality for this species, given as Nevada (LeConte 1876a), lies outside the geographic range as indicated by specimens I have examined. Perhaps LeConte (1876a) was in error in that the type locality may have been Nebraska, not Nevada (presumably an interpretation made by LeConte based on the "N" on the specimen labels).

Problems in recognition.— Individuals of this species are likely to be confused only with those of *C. infrequens*. Members of both species possess a very broad rostrum not found in other *Cleonidius* species (Figs. 146–147). In *C. infrequens* however, the median rostral carina is sharply elevated and distinct, the lateral margins of the rostrum are sharp, the dorsal surface of the rostrum flat from immediately laterad of the median carina to the lateral margins, the rostral punctures are deep and large, there are very slight low lateral rostral carinae, ventral pilose tarsal vestiture is moderately extensive, and both macropterous and brachypterous forms are known. All of these character states differ from those of *C. puberulus* individuals. Known geographic distributions of the two species (Figs. 222, 225) are allopatric, but there may be sympatry in Colorado or Kansas.

Specimens of *C. puberulus* may also be confused with small *C. poricollis*, *C. notolomus*, and *C. frontalis* but can be distinguished by their more robust rostrum (Fig. 147) and lack of the various diagnostic character states of these other species.

Description.— *Specimens examined.* 10 males, 26 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEI, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 25. *Size.* Length, male, 5.1–8.3 mm; female, 6.4–8.4 mm. Width, male, 2.1–3.1 mm; female, 2.6–3.3 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse, small, shallow punctures, some longitudinally confluent and irregularly impressed immediately above eyes, interspersed throughout with minute punctures. Frons also with moderately dense to dense, elongate-fine to elongate-narrow, white appressed scales medially, suberect to erect immediately above eyes; otherwise lacking suberect or erect vestiture. Frons separated from base of rostrum by shallow to moderately-deep transverse impression (Fig. 147a). Base of median carina of rostrum with small, shallow fovea. Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Robust, (width at apex 0.71–0.87 times length in males; 0.74-0.82 in females) (Fig. 147). In lateral view very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes partially visible. Rostrum slightly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins rounded, rostrum declivous from immediately laterad of median carina to lateral margins; with median carina present as variously developed slightly elevated, narrow line, more or less obscured in most specimens by overlying scales. Dorsal and lateral punctation moderately dense, small to moderately large, shallow, not longitudinally confluent; dorsally interspersed with dense minute punctures. Dorsally lacking suberect or erect vestiture to with sparse short suberect hair-like scales; moderately dense to dense, elongate-fine to robust appressed white scales. Epistoma transversely swollen at base. *Pronotum.* Median carina lacking to indistinctly developed as very low, broad glabrous line. Dorsal and lateral punctation small, moderately dense to dense, shallow, not confluent; smaller sparser and shallower apically; areas between large dorsal punctures with minute regularly impressed punctures; punctation sparser and shallower on flanks. Dorsally with sparse to moderately dense, very short, suberect hair-like scales, each situated in large puncture (Fig. 147a). Scales dorsally absent to sparse, small and fine along median line; dense, elongate-fine to elongate-narrow, appressed in pair of apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and fine. Lateral margins with scales dense, elongate-narrow, appressed in moderately broad stripe. Flanks with scales moderately dense to dense, elongate-fine to elongate-narrow. Median basal area of disk broadly and moderately deeply impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae of unequal length, short, greatest length immediately behind base of eye (Fig. 147a). In dorsal view with lateral margins straight and subparallel to slightly and evenly arcuate from base to apical one-third to one-quarter;

constricted at apical one-third to one-quarter then straight and convergent to apex. *Prosternum.* With small shallow impression and a very slightly developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion; posterior and anterior portions separated by shallow to moderately deep transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.53–0.61 times length in males; 0.54-0.60 in females) (Fig. 128). In dorsal view with lateral margins very slightly sinuate and convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded to subacuminate, not to very slightly divergent. Humerus rounded, indistinct. Dorsally with sparse to moderately dense, very short suberect hair-like scales; with sutural interval and interval 2 with very sparse to moderately dense, very small and fine to elongate-fine white scales; stria 1 with irregularly distributed patches of larger and denser white scales; intervals 3 to 5 with uniformly dense, elongate-narrow to moderately robust white scales; intervals 6 to 8 with scales absent to dense, very small and fine to moderately robust; stria 6 and 7 with irregularly distributed patches of larger and denser white scales in those specimens with scales of intervals 6 to 8 small and fine; intervals 9 to 11 with scales uniformly dense, white, elongate-narrow to robust (Fig. 148). Punctures of elytral striae small, individually distinct; arranged in regular rows. *Wings.* Very short (approximately one-quarter to one-third length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; no distinct subapical tooth present. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-quarter to one-third, slightly divergent, each with basal internal flange moderately to well-developed. Ventral tarsal pilose vestiture of foretarsus of male present as small elongate pad on apical one-quarter to one-third of article 1, as small rounded pad on apical one-half of article 2, and as large round pad on apical two-thirds of article 3; of female as apical tuft of article 1, as small rounded pad on apical one-quarter of article 2, and as large rounded pad on apical one-half of article 3; of mesotarsus of male as apical tuft to small elongate pad on apical one-quarter of article 1, as apical tuft to small elongate pad on apical one-third of article 2, and as small rounded pad on apical one-third of article 3; of female as apical tuft on articles 1 and 2, and as small rounded pad on apical one-third of article 3; of metatarsus of male lacking from, to as small elongate pad on apical one-quarter of article 1, as apical tuft to small elongate pad on apical one-third of article 2, and as small elongate pad on apical one-third of article 3; of female lacking from, to as apical tuft of article 1, as apical tuft of article 2, and a small elongate pad on apical one-quarter of article 3. *Abdomen.* Ventral surface with moderately dense to dense, elongate-narrow to moderately robust appressed white scales, sparser and smaller medially on abdominal sternum VII of female. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large rounded glabrous patches, each with large puncture and single suberect, short hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with slightly to moderately developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm moderately long; lateral arms slightly inwardly arcuate at mid-length, very slightly expanded at apex (Fig. 167). Stylus moderately large compared to length of gonocoxite II. Male (three examined). Internal sac (Figs. 187a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket rounded in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is known only from extreme southern Alberta and Manitoba, south to southern Wyoming and Colorado (Fig. 225).

Natural history.— A single adult has been collected on *Lesquerella ludoviciana* (Nutt.) Wats. (Cruciferae) in Kansas. Definite hosts are not known. Adults have been collected from April to October in grassland habitats at elevations of 1369–2607 m (N=4) (Fig. 233).

Chorological relationships.— Table V. This species is allopatric with its sister-species *C. infrequens.*

Phylogenetic relationships.— This species is the sister-species of *C. infrequens* (Figs. 236 and 237).

Cleonidius collaris (LeConte)
(Figs. 129, 148, 168, 188, 223)

Cleonus collaris LeConte 1876a:149. Holotype (examined), male, labelled "Col", "*Cleonus/ collaris/* TYPE LeC.", "Horn Coll/ H 8517" and with red square label (MCZC). Type locality, Colorado. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1902 (check.). Leng 1920 (catal.).

Cleonus (*Cleonidius*) *collaris*; Casey 1891 (key). Csiki 1934 (catal.).
Cleonis collaris; O'Brien and Wibmer 1982 (catal., distn.).

Problems in recognition.— The markedly irregularly elevated and sculptured pronotum with only sparse shallow and indistinct large punctures is characteristic of members this species and should serve for reliable identification. The pronotum of some specimens of *C. notolomus* is similarly broadly and deeply medially impressed at the base and has shallow longitudinal impressions but is otherwise not as irregularly sculptured as that of *C. collaris*; it also has distinct moderately large, moderately deep dorsal punctation.

Description.— *Specimens examined.* 7 males, 6 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 26. *Size.* Length, male, 8.4–10.4 mm; female, 9.3–10.9 mm. Width, male, 3.3–4.4 mm; female, 4.0–4.6 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with only dense minute punctures. Frons also with dense, moderately robust, pale brownish appressed scales medially, suberect to erect immediately above eyes; otherwise lacking suberect or erect vestiture. Frons very slightly separated from base of rostrum by very shallow transverse impression (Fig. 148a). Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately robust (width at apex 0.61–0.73 times length in male; 0.61–0.69 in female) (Fig. 148). In lateral view very slightly curved downward. In dorsal view with postgenae slightly to moderately laterally expanded, antennal scrobes partially visible. Rostrum slightly medially tumescent from point of antennal insertion to middle of frons (more markedly so basally); not laterally expanded at midlength; lateral margins sharp; with median carina present as variously developed slightly elevated, glabrous, shiny narrow line at crest of median tumescence. Dorsal and lateral punctation sparse, small, shallow, not longitudinally confluent; dorsally interspersed with dense minute punctures. Dorsally lacking suberect or erect vestiture; with dense moderately robust to robust appressed white to pale brown scales. Epistoma moderately transversely swollen at base. *Pronotum.* Extremely irregulary elevated, markedly constricted dorsolaterally at apical one-quarter, deeply and broadly impressed medially at base and longitudinally along lateral margins. Median carina variously developed in anterior one-half from absent to as low, rounded moderately broad glabrous line. Dorsal and lateral punctation and that of flanks small, very sparse, shallow and indistinct; areas between larger dorsal punctures with dense minute regularly impressed punctures. Dorsolaterally with sparse, short, suberect hair-like scales, each situated in large puncture; medially lacking suberect or erect vestiture (Fig. 148a). Scales dorsally absent to sparse, moderately robust along median line; very dense, moderately robust, appressed in pair of broad apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and elongate-fine. Lateral margins with scales very dense, moderately robust, appressed to recumbent. Flanks with scales dense to very dense, moderately robust, appressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae of unequal length, moderately long, greatest length (approximately one-half width of eye) immediately behind base of eye (Fig. 148a). In dorsal view with lateral margins straight, sinuate or slightly arcuate from base to apical one-quarter; markedly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With small shallow impression and slightly developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to two-thirds length of posterior more angulate portion; posterior and anterior portions slightly to markedly separated by shallow to moderately deep transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.59-0.64 times length in males; 0.60-0.65 in females) (Fig. 129). In dorsal view with lateral margins very slightly and evenly arcuate, sinuate at basal one-quarter and convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, not to very slightly divergent. Humerus distinct. Dorsally lacking suberect or erect vestiture; with uniformly dense to very dense, moderately robust appressed white to pale brown scales, absent to sparse and small in scattered patches on striae 1 and 2, and intervals 9 to 11 (Fig. 129). Punctures of elytral striae individually indistinct, obscured by overlying scales. *Wings.* Short (approximately one-half length of elytra). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; no distinct subapical tooth present. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, not divergent, each with basal internal flange slightly developed. Ventral tarsal pilose vestiture of foretarsus of male present as elongate pad on apical one-third of article 1, as large rounded pad on apical one-half of article 2, and as large round pad on apical three-quarters of article 3; of female as small elongate pad at apex of article 1, as small rounded pad at apex of article 2, and as large round pad on apical one-half of article 3; of mesotarsus of male as small elongate pad on apical one-quarter to one-third of article 1, as moderately large elongate pad on apical one-third to one-half of article 2, and as large elongate-oval pad on apical two-thirds of article 3; of female as small elongate pad at apex on articles 1 and 2, and as large rounded pad on apical one-half of article 3; of metatarsus of male as small elongate tuft at apex to on apical one-quarter of article 1, as small elongate pad on apical one-third to one-half of article 2, and as large elongate-oval pad on apical one-half of article 3; of female lacking from, to as apical tuft of article 1, as apical tuft on article 2, and as elongate-oval pad on apical one-half of article 3. *Abdomen.* Ventral surface with moderately dense to dense, moderately robust appressed white to pale-brown scales, sparser and smaller medially on abdominal sterna V to VII. Abdominal sterna III to VI (especially III and IV laterally) with individually distinct large rounded glabrous patches, each with large puncture and single recumbent to suberect, moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internal y (dorsally) with markedly developed median shiny tubercle. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm moderately long; lateral arms slightly inwardly arcuate throughout length, very slightly expanded at apex (Fig. 168). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 188a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with small paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket truncate in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is known only from Colorado and adjacent southern Wyoming, western Kansas and northern New Mexico (Fig. 223).

Natural history.— A single adult specimen from Greeley, Colorado was collected on *Lepidium* sp. (pepper-grass; Cruciferae). The very few adults known have been collected in grassland habitats from March to May at elevations of 1697–2608 m (N=3) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. notolomus* (Fig. 237).

Cleonidius notolomus Anderson, new species
(Figs. 130, 149, 169, 189, 225)

Cleonis frontalis; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Type Material.— Holotype, male, with a red label "HOLOTYPE", "Grant Co NM/ X 1932", "RT Kellogg", "HOLOTYPE/ *Cleonidius*/ *notolomus*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (USNM). Allotype, female, with a red label "ALLOTYPE", "New Mex: Hidalgo/Co.,1Mi.W.Rodeo/VII-31-1971, J. Doyen & Tschinkel", "J.Doyen Lot/71G20", "ALLOTYPE/ *Cleonidius*/ *notolomus*/ Anderson" and with abdomen on card and genitalia in microvial attached to pin (UCBC, on indefinite loan to CASC). Type locality, Grant Co., New Mexico.

Paratypes. 15 males, 16 females. MEXICO: Durango: 26mi. w. Durango, 13.VII.75, L.E. Watrous, 1M (CWOB). Mexico: Chapingo, 5.VII.55, Gonzalez, 1F (USNM).

UNITED STATES OF AMERICA: Arizona: Cochise County, Guadalupe Canyon, 31.VII.75, S. McCleve, 1F (SMC); 25mi. n. Douglas, 10.VII.74, S. McCleve, 1M (RSAN); Tucson, XII.27, Downe, 1F (UAT); Cochise, 5.VIII.54, F. Werner, 1F (UAT); Douglas, 23.VIII.27, Jones, 1M (LACM); Chiricahua Mountains, Shake Gulch, 8.VI.68, Menke, 1F (USNM); Sabino Canyon, 2.VII.52, Kelsey, 1F (UAT); Aguirre Lake (10mi. ne. Sasabe), 2.VIII.78, Hetz, 1M (UAT); Hereford, 3.III.41, Jones, 1M (USNM); Green Valley, VII.78, R. Lenczy, iM (USNM); Santa Cruz County, Carmen, 3.VIII.64, Eiland, 1M (USNM); 5mi. s. Cochise, 29.V.61, Statham, 1F (AMNH); Sierra Vista, 4.VIII.79, A.E. Lewis, 1M (CWOB). New Mexico: Grant County, 27.IX.35, Kellogg, 1F (CASC); Silver City, VI.33, Kellogg, 2F (OSUC); White Sands National Monument, Lake Lucero, 2.VIII.74, D. Chandler, 1M (CWOB); White Sands National Monument, R. Lenczy, 1F (USNM), VIII.78, R. Lenczy, 1M (USNM); 5mi. n. Carlsbad, 21.IX.56, MacSwain, 1F (UCBC); Catron County, Quemado, 24.III.64, Hogg, 1F (NMSU). Texas: El Paso, VII, H.F. Wickham, 2M, 4F (USNM); Van Horn, 24.VI.42, Scullen, 1M (OSUC). Utah: Callao, 8.VI.22, Spalding, 1M (USNM).

Derivation of specific epithet.— From the Greek "*notos*" meaning south and "*lomus*" meaning border. This name is used in reference to the distribution of individuals of this species near the southern border of the United States of America.

Problems in recognition.— Adult individuals of this species are most difficult to separate from those of *C. frontalis* . Individuals of both sexes of *C. frontalis* generally have a proportionately longer pronotum compared to elytra (see Fig. 200), more elongate-narrow elytra (see Fig. 197), and more rounded lateral margins of the rostrum. Nearly all *C. frontalis* females are easily distinguished from *C. notolomus* females because the former possess very large denticles along the inner margin of the fore-tibia (Fig. 144c); these denticles are small in all *C. notolomus*. Most *C. frontalis* individuals have the rostrum very slightly laterally swollen at midlength and have the submentum slightly ventrally swollen (Figs. 144a,b); this is not so for *C. notolomus*. All *C. frontalis* are also macropterous, whereas *C. notolomus* are either macropterous or brachypterous. The two species also are largely allopatric although there is a zone of sympatry in eastern New Mexico and western Texas.

Individuals of *C. notolomus* may also be confused with those of *C. collaris*, *C. infrequens*, *C. puberulus*, *C. poricollis*, and *C. trivittatus*. *Cleonidius infrequens* and *C. puberulus* individuals are distinguished by their more robust rostra (Figs. 146–147); *C. collaris* by the much more irregularly sculptured and shallowly and indistinctly punctate pronotum, and not distinctly vittate scale pattern; *C. trivittatus* by the at most only slightly developed postocular lobes (Fig. 153a); *C. poricollis* by the curved sulcus behind the eye and the more elongate erect dorsal vestiture (Fig. 150a).

Description.— Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 27. *Size*. Length, male, 7.2–10.8 mm; female, 8.4–11.4 mm. Width, male, 3.0–4.7 mm; female, 3.6–4.7 mm. *Head*. Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse to moderately dense, small shallow punctures, interspersed with minute punctures. Frons also with moderately dense, elongate-narrow appressed white scales medially, suberect to erect immediately above eyes; otherwise lacking suberect or erect vestiture. Frons slightly separated from base of rostrum by shallow transverse impression (Fig. 149a). Base of median carina of rostrum with small, shallow fovea. Width of frons greater than width at apex of rostrum. *Rostrum*. Moderately robust, (width at apex 0.60-0.77 times length in male; 0.59-0.68 in female) (Fig. 149). In lateral view slightly curved downward. In dorsal view with postgenae at most slightly laterally expanded, antennal scrobes partially visible. Rostrum slightly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins sharp; with median carina as narrow, low, sharp, and distinct shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense to dense, small to moderately large, shallow to moderately deep; smaller and less dense apicad of point of antennal insertion; dorsally interspersed with dense minute punctures. Dorsally (especially laterally) with sparse to moderately dense, very short, suberect hair-like scales; also with moderately dense, elongate-narrow, appressed white scales. Epistoma slightly swollen. *Pronotum*. Median carina variously developed in anterior one-half from absent to as low, rounded moderately broad glabrous line. Dorsal and lateral punctation small to moderately large, moderately dense, moderately deep, not confluent; smaller, sparser and shallower apically and on flanks; areas between larger dorsal punctures with minute regularly impressed punctures. Dorsally with moderately dense, short, suberect hair-like scales, each situated in large puncture (Fig. 149a). Scales dorsally absent along median line; dense, elongate-narrow, appressed in pair of broad apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and elongate-fine. Lateral margins with scales dense, elongate-narrow, appressed to recumbent in moderately broad stripe. Flanks with scales elongate-narrow, slightly less dense than on lateral margins. Median basal portion of disk deeply and broadly impressed; also longitudinally shallowly impressed along lateral margins in most specimens. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae of unequal length, moderately long, greatest length (approximately one-half width of eye) immediately behind base of eye (Fig. 149a). In dorsal view with lateral margins slightly to moderately arcuate and convergent to apex; in some specimens, slightly constricted at apical one-quarter then straight and convergent to apex. *Prosternum*. With small shallow impression and slightly to moderately developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately one-half to subequal in length to posterior more angulate portion; posterior and anterior portions not or slightly separated by shallow to moderately deep transverse impression. *Elytra*. Moderately robust in general form (width at midlength 0.56-0.64 times length in males; 0.58-0.64 in females) (Fig. 130). In dorsal view with lateral margins straight to very slightly sinuate to slightly and evenly arcuate and convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, very slightly divergent. Humerus distinct to indistinct. Dorsally with moderately dense, short, suberect to erect hair-like scales; with sutural interval and interval 2 with very sparse to moderately dense, very small and fine to elongate-fine, golden to white scales; intervals 3 to 5 with uniformly dense, elongate-narrow to moderately robust white scales; intervals 6 to 8 with scales lacking to very sparse, very small and very fine, golden to white; intervals 9 to 11 with uniformly dense, elongate-narrow to moderately robust white scales; striae 1, 6 and 7 with irregularly distributed patches of larger and denser white scales than on adjacent intervals (Fig. 130). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings*. Long (greater than elytra in length [21%, N=7]), to short (approximately one-half length of elytra or less [79%, N=26]). *Legs*. Foretibia of female with inner margin with small denticles in apical three-quarters; small subapical tooth present, slightly distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus of male and female present as elongate-narrow pad on apical one-third to one-half of article 1, as moderately large elongate pad on apical one-third to one-half of article 2, and as large rounded pad on apical two-thirds of article 3; of mesotarsus of male and female as small elongate pad at apex of article 1, as small rounded pad on apical one-quarter to one-third of article 2, and as moderately large rounded pad on apical one-third to one-half of article 3; of metatarsus of male and female as elongate-narrow inner pad on apical one-half and as outer apical tuft of article 1, as elongate-narrow pad on apical one-half of article 2, and as moderately large elongate-oval pad on apical one-half to two-thirds of article 3.

Abdomen. Ventral surface with dense, moderately robust appressed white scales, sparser and smaller medially on abdominal sternum VII of female. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large rounded glabrous patches, each with large puncture and single suberect to erect, short to moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with slightly to markedly developed median shiny tubercle. *Genitalia.* Female (five examined). Abdominal sternum VIII with basal arm moderately long; lateral arms slightly to moderately inwardly arcuate at midlength; slightly expanded at apex (Fig. 169). Stylus moderately large compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 189a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with small paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket truncate in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is known only from southeastern Arizona, southern New Mexico, and extreme western Texas, south to central México (Fig. 225).

Natural history.— This species appears to be associated with desert-grassland transitional habitats. There is only a single record of one adult on *Atriplex canescens* (Pursh) Nutt. (Chenopodiaceae). No definite hosts are known. Two individuals have been collected at ultraviolet lights. Adults have been collected from March to December at elevations of 870–2161 m (N=14) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. collaris* (Fig 237).

Cleonidius poricollis species group

Diagnosis.— Size small for *Cleonidius* (Fig. 197). Dorsal erect or suberect vestiture absent (Fig. 151a) to present, dense and moderately long (Fig. 150a). Head behind eye with or without variously developed curved sulcus extended from above eye to area under postocular lobe (Fig. 150a). Rostrum moderately robust, moderately to markedly medially tumescent, not to very slightly carinate; lateral margins rounded. Pronotum with postocular lobes well-developed; postocular vibrissae uniformly short (Figs. 150a-151a). Elytra with scale pattern more or less vittate, intervals other than 9 to 11 with white scales equal in size to those on intervals 9 to 11 (Figs. 131–132). Tarsus with ventral pilose vestiture extensive (on greater part of ventral surface of each article) to slightly reduced in extent (on not less than apical one-half of articles 2 and 3). Wings present, of variable length (short in only few specimens). Female with abdominal sternum VIII with basal arm short; lateral arms arcuate (Figs. 170–171). Male with aedeagus with internal sac with apex of dorsal median pocket rounded; lobes A to F present; dorsal median pocket low in lateral view (Figs. 190–191).

Phylogenetic relationships.— Monophyly of this species group is based only on the presence of a curved sulcus behind the eye. The *C. poricollis* group is the sister-group to the *C. boucardi* species group, this lineage sister to the *C. americanus* species group (Fig. 237).

Cleonidius poricollis (Mannerheim)
(Figs. 131, 150, 170, 190, 228)

Cleonis vittatus Kirby 1837:199 [not Zoubkoff 1829:163]. Lectotype (here designated), male, one of two syntypes, labelled "Co-type", "namer", "*Cleonus/ vittatus/* Kirby/ Co-type" and with my designation label "LECTOTYPE/ *Cleonis vittatus/* Kirby desig./ Anderson" (BMNH). Type locality, North America. O'Brien and Wibmer 1982 (catal., distn.).

Lixus poricollis Mannerheim 1843:291. Holotype (examined) female, labelled only with a handwritten label "*poricollis*"/ Escholtz/ Escholtz (ZMMU). Type locality, California. Gemminger and von Harold 1871 (catal.)[3].

Cleonus vittatus; Melsheimer 1853 (check.). Gemminger and von Harold 1871 (catal.). LeConte 1876a (key). Henshaw 1885 (check.). Fall 1901 (check.). Fletcher 1906. Fall and Cockerell 1907 (check.). Gibson 1914. Leng 1920 (catal.).

Cleonus virgatus LeConte 1876a:150 [not Gyllenhal 1834:242]. Holotype (examined), male, labelled "Cal", "*C./ virgatus*/ TYPE Lec.", "Horn Coll/ H8521" and a red square label (MCZC). Type locality, Owen's Valley, California. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1889. Leng 1920 (catal., as synonym).

Cleonus (*Cleonidius*) *lobigerinus* Casey 1891:191. Lectotype (here designated), female, one of eight syntypes, labelled "Ari", "CASEY/ bequest/ 1925", "TYPE USNM/ 37281", "*C.Cl./ lobigerinus*/ Cas" and with my designation label "*Cleonus/ lobigerinus* Csy./ LECTOTYPE/ desig. Anderson" (USNM). Type locality, Peach Springs, Arizona. Champion 1902–1906 (in part; distn., misident. of *Cleonidius puberulus*). Csiki 1934 (catal.). Hatch 1971 (key, redesc.).

Cleonus (*Cleonidius*) *kirbyi* Casey 1891:188 (in key). NEW SYNONYMY Holotype (examined), female, labelled "Vic./ Vanc.I.", "CASEY/ bequest/ 1925", "TYPE USNM/ 37299", "*C.Cl./ kirbyi*/ Cas." (USNM). Type locality, Victoria, British Columbia. Csiki 1934 (catal.). Hatch 1971 (key, redesc.).

Cleonus (*Cleonidius*) *poricollis*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *virgatus*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *vittatus*; Casey 1891 (key). Hatch 1971 (key, redesc.).

Cleonus lobigerinus; Wickham 1896 (check.). Fall 1901 (check.). Yothers 1916. Leng 1920 (catal.). Tanner 1966 (redesc., biol.).

Cleonus (*Cleonidius*) *boucardi*; Champion 1902–1906 (in part; distn., misident.).

Cleonus kirbyi; Wilcox *et al.*. 1934. Wickham 1902 (check.). Leng 1920 (catal.).

Cleonidius vittatus; Faust 1904 (desig. as type species of *Cleonidius*).

Cleonus quadrilineatus; Anderson 1914 (misident.).

Cleonus poricollis; Leng 1920 (catal.).

Cleonus sparsus; Essig 1958 (in part; biol., misident.). Arnett *et al.* 1980 (probable misident.).

Cleonus (*Cleonidius*) *quadrilineatus*; Hatch 1971 (key, redesc., misident.).

Cleonus (*Cleonidius*) *sparsus*; Hatch 1971 (in part; key, redesc., misident.).

Cleonis frontalis; O'Brien and Wibmer 1982 (in part; catal., distn., misident.).

Cleonis kirbyi; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis lobigerinus; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis poricollis; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis virgatus; O'Brien and Wibmer 1982 (catal., distn.).

vittatus, incertae sedis; Chevrolat 1873.

Notes about synonymy.— There has been much confusion regarding this species and consequently, numerous published misidentifications. *Cleonidius poricollis*, as considered here, includes all those western North American individuals that possess a variously developed, curved sulcus behind each eye (Fig. 150a). Mixed series are however known that include specimens with the sulcus well to only slightly developed, to absent. These sympatric specimens are otherwise indistinguishable and are considered herein to be conspecific. Primary types of *Lixus poricollis* Mannerheim, *Cleonis vittatus* Kirby, *Cleonus virgatus* LeConte, *Cleonus (Cleonidius) lobigerinus* Casey, and *Cleonus (Cleonidius) kirbyi* Casey each possess a curved sulcus behind the eye.

Cleonus (Cleonidius) kirbyi Casey was initially proposed by Casey (1891) as a replacement name for *Cleonus vittatus* LeConte, however LeConte (1876a) did not describe a new species, *Cleonus vittatus*, but rather was referring to *Cleonus vittatus* Kirby contrary to assertions of Casey (1891). Thus *Cleonus (Cleonidius) kirbyi* Casey should be considered a new species description and not a replacement name. Casey (1891), based only on the brief and inadequate published descriptions of *Cleonis vittatus* Kirby and *Lixus poricollis* Mannerheim, incorrectly considered *Cleonis vittatus* Kirby as a distinct species from *Cleonus vittatus* Kirby, *sensu* LeConte (1876a), but correctly as conspecific with *Cleonus poricollis* (Mannerheim).

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[3] Leconte 1876a,b (misident. *Cleonidius erysimi*). Henshaw 1885 (check., misident. *Cleonidius erysimi*).

Both *Cleonis vittatus* Kirby and *Cleonus virgatus* LeConte are junior homonyms.

Faust (1904) designated *Cleonis vittatus* Kirby as the type species of *Cleonidius*. I have seen a specimen in the British Museum (Natural History), correctly determined by Faust and labelled in his distinctive handwriting.

Problems in recognition.— Most members of this widespread species are easily recognized by the presence of a variously developed (usually deep) curved sulcus behind each eye (Fig. 150a). In many specimens the sulcus is present but largely to completely covered by the postocular lobe. In specimens in which the postocular lobe covers the sulcus, reorientation of the head exposes the sulcus to view. If this is not done, such individuals prove difficult to separate from other species, especially *C. notolomus* and *C. frontalis*. Specimens lacking a sulcus or with only a slightly developed sulcus appear confined to Oregon and British Columbia (perhaps also Washington, although no such specimens have been seen from that area) and are separated from other species of *Cleonidius* by the sparse scales of the elytra (forming a faintly vittate pattern), possession of large pilose ventral tarsal pads, and rostrum with distinct median tumescence, the base of the rostrum distinctly separated from the frons by a transverse impression (Fig. 150a).

The eastern *C. calandroides* is distinguished from the western *C. poricollis* by the short suberect dorsal vestiture (Fig. 151a) and less distinctly vittate elytral scale pattern (intervals 6 to 8 with scales as large as those on intervals 9 to 11) (Fig. 132) in the former. The sulcus is variously developed in individuals of both species but is moderately deep and more distinct in most *C. poricollis* and in only few *C. calandroides*.

Description.— *Specimens examined.* 387 males, 459 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 28. *Size.* Length, male, 4.3–9.3 mm; female, 5.6–10.3 mm. Width, male, 1.8–3.6 mm; female, 2.0–4.0 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle or with variously developed (moderately deeply in most specimens) curved sulcus extended posteroventrally from upper one-half of posterior margin of eye to area under postocular lobe (sulci continued ventrally and joined at gular suture but covered by prothorax and not visible) (Fig. 150a). Frons with sparse to moderately dense, small shallow punctures, interspersed with minute punctures. Frons also with very sparse to moderately dense, short to moderately long, suberect to erect hair-like scales, moderately dense elongate-fine appressed white scales medially, suberect to erect immediately above eyes. Frons distinctly separated from base of rostrum by moderately deep to deep transverse impression (Fig. 150a). Base of median tumescence of rostrum with small, shallow to moderately deep fovea. Width of frons less than, to subequal to, width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.57-0.71 times length in male; 0.57-0.76 in female) (Fig. 150). In lateral view straight to very slightly curved downward. In dorsal view with postgenae moderately to markedly laterally expanded, antennal scrobes distinctly visible. Rostrum moderately to markedly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as narrow low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense to dense, small, shallow (many longitudinally confluent); dorsally interspersed with dense minute punctures. Dorsally with very sparse to moderately dense, short to moderately long, suberect to erect hair-like scales; also with moderately dense, elongate-fine, appressed to recumbent white scales, sparser medially. Epistoma slightly swollen. *Pronotum.* Median carina variously developed in anterior one-half from absent to as low, rounded moderately broad glabrous line. Dorsal and lateral punctation moderately large, moderately dense to dense, moderately deep to deep, not confluent; smaller, sparser and shallower apically and on flanks; areas between larger dorsal punctures with or without minute regularly impressed punctures. Dorsally with moderately dense, short to long, erect hair-like scales, each in large puncture (Fig. 150a). Scales dorsally absent to small fine and sparse along median line; moderately dense to dense, elongate-fine to elongate-narrow, appressed in pair of broad apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and elongate-fine. Lateral margins with scales moderately dense to dense, elongate-fine to elongate-narrow, appressed to recumbent in moderately broad stripe. Flanks with scales elongate-fine to elongate-narrow, sparse to moderately dense. Median basal portion of disk shallowly to deeply and narrowly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae uniformly short (Fig. 150a). In dorsal view with lateral margins slightly arcuate and convergent from base to apical one-quarter, slightly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With small shallow to moderately deep impression and moderately to markedly developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, approximately two-thirds to subequal in length to, posterior more angulate portion; posterior and anterior portions not or slightly separated by shallow transverse impression. *Elytra.* Elongate-narrow in general form (width at midlength 0.50-0.63 times length in males; 0.50-0.64 in females) (Fig. 131). In dorsal view with lateral margins straight to very slightly sinuate and slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, slightly divergent. Humerus distinct. Dorsally with suberect or erect vestiture lacking to dense, moderately long, erect hair-like scales; with sutural interval with dense, very small and fine to elongate-fine, golden to white scales, interspersed with scattered patches of larger white scales, to with scales uniformly white, dense, small and elongate-fine; intervals 2 with scales golden to white, dense, very small and fine, with scattered patches of larger white scales; intervals 3 to 5 with dense, small and fine to elongate-narrow white scales; intervals 6 to 8 with scales dense, very small and very fine, golden to white, with scattered patches of larger white scales; intervals 9 to 11 with uniformly dense, small to large, elongate-fine to elongate-narrow white scales (Fig. 131). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings*. Long (greater than elytra in length [99%, N=838]), to short (approximately one-half length of elytra or less [1%, N=8]). *Legs*. Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth indistinct from tibial denticles. Foretibial uncus of both sexes moderately large, mesotibial and metatibial unci small. Tarsal claws connate in basal one-third, not divergent, each with basal internal flange slightly developed. Ventral tarsal pilose vestiture of foretarsus, mesotarsus, and metatarsus of male and female present as elongate-oval pad on apical one-half to three-quarters of article 1, as moderately large rounded pad on apical one-half of article 2, and as large round pad on apical three-quarters of article 3 in male, apical one-half to three-quarters in female. *Abdomen*. Ventral surface with moderately dense, elongate-narrow to moderately robust appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large rounded glabrous patches, each with large puncture and single suberect to erect, moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with slightly to well-developed median shiny tubercle. *Genitalia*. Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms slightly inwardly arcuate throughout length; very slightly expanded at apex (Fig. 170). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 190a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket rounded in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation.— Specimens from coastal localities in Oregon and British Columbia (likely also Washington) differ in a number of respects from individuals from throughout the rest of the species range, exhibiting: generally slightly larger prosternal swellings; generally deeper and denser punctation of head, rostrum and pronotum; smaller elytral scales, the pattern only faintly vittate; lack of sulcus behind the eye; lack of or else very short indistinct dorsal suberect or erect vestiture; and broad foretarsal articles with more extensive ventral pilosity. Not all individuals however possess all of these character states; mixed series are known in which some individuals possess various combinations of the above character states but otherwise possess the typical *C. poricollis* states. As such, no consistent set of character states can be used to justify separation of these Pacific Northwest individuals as a distinct taxonomic entity. A large number of these specimens have been reared from *Erysimum* sp. (wallflower; Cruciferae at Victoria, British Columbia, but other typical *C. poricollis* have also been reared from various Cruciferae throughout the species range. *C. calandroides*, sister-species of *C. poricollis* also occurs on Cruciferae.

Individuals from a series of specimens from San Francisco, California, have the elytra uniformly covered with moderately dense, elongate-fine white scales; the elytra do not appear distinctly vittate. Otherwise these specimens are typical *C. poricollis* and in my view do not warrant separate status.

Geographic distribution.— This is the most widely distributed species of *Cleonidius*, ranging throughout western North America across southern British Columbia, Alberta and Saskatchewan in Canada into the adjacent United States of America east to Michigan in the north, south along the west coast to California in the west and south to western Texas and central México in the east (Fig. 228).

Smith (1957) discusses taxa with populations in prairie habitats in Michigan that are disjunct from populations in the western prairie. The distribution of *C. poricollis* in the northern United States appears to fit this pattern.

Natural history.— This species is associated with a wide variety of habitats: grassland, desert-grassland transitional, Pacific semi-desert, Great Basin desert, Sonoran desert, Mojave desert, and western xerophytic evergreen forest. Adults of this species have been collected on a wide taxonomic range of plants as follows: *Asclepias* sp. (Asclepiadaceae); *Atriplex* sp., *A. nutalli* Wats., *A. rosea* L., *Beta vulgaris* L. (beet), *Eurotia lanata* (Pursh) Moq., *Salsola kali* L. (all Chenopodiaceae); *Ambrosia* sp., *Franseria confertiflora* (DC.) Rydb., *Chrysothamnus* sp., *C. nauseosus* (Pall.) Britton, *C. viscidiflorus* (Hook.) Nutt. var. *typicus*, *Gutierrezia californica* (DC.) Torr. and Gray, *Aplopappus acradenius* (Greene) Blake, *A. venetus* Blake ssp. *vernonioides* (Nutt.) Hall, *Hymenoclea monogyra* T. and G., *Zinnia* sp. (all Compositae); *Sisymbrium altissimum* L., "*S. pestifer*", *Erysimum* sp. (wallflower), *Descurainia sophia,*(L.) Webb., *Brassica campestris* L. (mustard), *B. oleracea* L. (broccoli) (all Cruciferae); *Salvia* sp. (Labiatae); *Lupinus* sp., *Trifolium* sp., *Melilotus albus* Desr., *Medicago sativa* L. (all Leguminosae); *Fragaria* sp., *Rubus* sp., *Purshia tridentata* (Pursh) DC. (all Rosaceae). Adults have been reared or collected from the roots of *Chrysothamnus* sp., *Gutierrezia* sp., *G. microcephala* (DC.) Gray, *Aplopappus* sp., *A. venetus* (Hbk.) Blake (all Compositae); *Brassica* sp., *Raphanus sativus* L. (radish), *Erysimum* sp., *Descurainia pinnata* (Walt.) Britton (all Cruciferae). Tanner (1966) reports collection of adults from a *Grayia-Lycium* community, a *Salsola* community, and on *Atriplex canescens* (Pursh) Nutt.. Hatch (1971) notes larvae of this species injuring radishes at Corvallis, Oregon (as *Cleonus sparsus*) and as attacking wallflower roots on a seed farm on Vancouver Island, British Columbia (as *Cleonus kirbyi*).

This species has been collected on various types of vegetation primarily in dry washes and stream beds throughout the species range. Individuals have also been collected on sand dunes or other sandy habitats.

I have seen a single specimen collected from the stomach of *Bufo* sp. (Amphibia).

Adults have been collected from June to November at elevations from sea level to 4004 m (N=132) (Fig. 233).

Chorological relationships.— Table V. *C. poricollis* is allopatric to its sister-species *C. calandroides*.

Phylogenetic relationships.— This species is the sister-species of *C. calandroides*, the only other species in the *C. poricollis* species group (Fig. 236).

Cleonidius calandroides (Randall)
(Figs. 132, 151, 171, 191, 229)

Lixus calandroides Randall 1838:42. Type(s) lost. Gemminger and von Harold 1871 (catal.). Sprague and Austin 1875. LeConte 1876a (misinterpret., as synonym of *Lixus musculus*).

Cleonus calandroides; LeConte 1876b (diagnosis). Henshaw 1885 (check.). Casey 1891 (key). Ely 1913 (biol.). Blatchley and Leng 1916 (key, redesc., biol.). Leng 1920 (catal.). Leonard 1926 (check., biol.). Csiki 1934 (catal.). Bruhn 1947 (morphol.). Sanders 1960 (morphol.). Kissinger 1964 (biol.).

Cleonus (*Cleonidius*) *calandroides*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonis calandroides; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— *Lixus calandroides* was described from an unspecified number of specimens from Chelsea Beach, Massachusetts (Randall 1838). Unfortunately type material of Randall has been lost (Sprague and Austin 1875). Following reccomendations of the

International Code of Zoological Nomenclature, no neotype designation is required, because there has been no recent confusion regarding identity of this species. After identification of specimens as this species by Sprague and Austin (1875), LeConte (1876b), based on examination of specimens sent to him by Austin, transferred the species to *Cleonus* and removed the name from his previously proposed synonymy with *Lixus musculus* Say (LeConte 1876a).

Problems in recognition.— This is one of only two species of *Cleonidius* restricted to eastern North America (Figs. 215, 229). These two differ markedly in structural features and should not be confused. The eastern *C. calandroides* is distinguished from the western *C. poricollis* by the short suberect dorsal vestiture (Fig. 151a) and less distinctly vittate elytral scale pattern (intervals 6 to 8 with scales as large as those on intervals 9 to 11) (Fig. 132) in the former. The sulcus behind the eye is variously developed in individuals of both species but is moderately deep and distinct in most *C. poricollis* and in only few *C. calandroides* (see descriptions).

Description.— *Specimens examined.* 65 males, 63 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 29. *Size.* Length, male, 8.0–9.3 mm; female, 5.5–9.6 mm. Width, male, 3.0–3.6 mm; female, 2.1–3.9 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle or with variously developed (moderately deeply in only few specimens) curved sulcus extended posteroventrally from upper one-half of posterior margin of eye to area under postocular lobe (sulci continued ventrally to juncture at gular suture but covered by prothoracic structures and not visible) (as in Fig. 150a). Frons with only scattered small shallow punctures, interspersed with minute punctures. Frons also with moderately dense, short, suberect hair-like scales, sparse to moderately dense elongate-fine appressed white scales medially, suberect to erect immediately above eyes. Frons distinctly separated from base of rostrum by moderately deep to deep transverse impression (Fig. 151a). Base of median tumescence of rostrum with small, shallow to moderately deep fovea. Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Moderately robust, slightly less so in females (width at apex 0.60-0.68 times length in male; 0.56-0.65 in female) (Fig. 151). In lateral view straight to very slightly curved downward. In dorsal view with postgenae moderately laterally expanded, antennal scrobes partially visible. Rostrum medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as narrow low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation moderately dense, small, shallow (many longitudinally confluent); dorsally interspersed with dense minute punctures. Dorsally with very sparse to moderately dense, short, suberect hair-like scales (especiallly laterally); also with moderately dense, elongate-fine appressed to recumbent white scales, sparser medially. Epistoma slightly swollen. *Pronotum.* Median carina variously developed in anterior one-half from absent to as low, rounded narrow glabrous line. Dorsal and lateral punctation moderately large, moderately dense to dense, shallow, not confluent; smaller apically and on flanks; areas between larger dorsal punctures with or without minute regularly impressed punctures. Dorsally with moderately dense, very short, suberect hair-like scales, each situated in large puncture (Fig. 151a). Scales dorsally absent to small fine and sparse along median line; moderately dense, elongate-narrow, appressed in pair of broad apically slightly narrowed paramedian stripes; laterally, absent to sparse, small and elongate-fine. Lateral margins with scales dense, elongate-narrow, appressed in moderately broad stripe. Flanks with scales dense, elongate-fine to elongate-narrow. Median basal portion of disk shallowly to deeply and narrowly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae uniformly short (Fig. 151a). In dorsal view with lateral margins slightly arcuate and slightly convergent from base to apical one-quarter, slightly constricted at apical one-quarter then straight and convergent to apex. *Prosternum.* With small shallow impression and slight to moderately developed rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion long, subequal in length to posterior more angulate portion; posterior and anterior portions slightly separated by shallow transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.57-0.60 times length in males; 0.55-0.63 in females) (Fig. 132). In dorsal view with lateral margins straight, subparallel to slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not produced, rounded, slightly divergent. Humerus distinct. Dorsally with moderately dense, very short, suberect, indistinct hair-like scales; scales more or less uniformly dense, white; with sutural interval and interval 2 with scales small and fine; intervals 3 to 5 and 9 to 11 with scales large and elongate-narrow; scales small and fine to large and elongate-narrow on intervals 6 to 8 (Fig. 132). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical one-half; subapical tooth indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-half, slightly divergent, each with basal internal flange slightly developed. Ventral tarsal pilose vestiture of foretarsus of male present as large pads on more or less entire ventral surface of articles 2 and 3 and apical one-half of article 1; of female, as elongate pad on apical one-half of article 1, as large oval pad on apical three-quarters of article 2, and as large round pad on more or less entire ventral surface of article

3; of mesotarsus of male and female as small elongate-narrow pad on apical one-half of article 1, as large elongate pad on more or less entire ventral surface on articles 2 and 3; of metatarsus of male and female as elongate pad on apical three-quarters of article 1, as large elongate-oval pad on apical one-half of article 2, and as large oval pad on apical three-quarters of article 3. *Abdomen.* Ventral surface with moderately dense to dense, elongate-narrow appressed white scales. Abdominal sterna III to VI (especially III and IV) with individually indistinct to distinct moderately large rounded glabrous patches, each with large puncture and single appressed hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with moderately developed median shiny tubercle. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm short; lateral arms slightly inwardly arcuate throughout length; very slightly expanded at apex (Fig. 171). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 191a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket rounded in dorsal view. Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is distributed along the northern Atlantic Coast from Long Island, New York, north to New Hampshire and New Brunswick (Fig. 229).

Natural history.— This species breeds in the sea-rocket, *Cakile edentula* (Bigel.) Hook. (Cruciferae). Ely (1913) collected various life stages from larvae to adults in the roots of this plant in mid-August. He reports that larvae live entirely within the root and that the portion of the root living within two or three inches of the surface of the ground is most commonly attacked. Pupation takes place in a coccoon constructed of small shreds of plant material built up in a longitudinal excavation in one side of the root. He further states that the beetles must be very common as virtually all plants examined showed evidence of feeding by larvae. Blatchley and Leng (1916) also state that larvae breed in *Cakile edentula* and other specimens I have examined bear label data indicating they were reared from this plant species. No other plant associations are known. Adults have been collected only on sea beaches from April to October.

Chorological relationships.— Table V. *Cleonidius calandroides* is sympatric only with northern populations of *C. subcylindricus.*

Phylogenetic relationships.— This species is the sister-species of *C. poricollis*, the only other species in the *C. poricollis* species group (Fig. 236).

Cleonidius boucardi species group

Diagnosis.— Size moderately large to large for *Cleonidius* (Fig. 197). Dorsal erect or suberect vestiture absent (Fig. 152a) to present, moderately dense and moderately long (Fig. 155a). Rostrum moderately robust, not (Fig. 152a) to moderately (Fig. 155a) medially tumescent, not to variously carinate; lateral margins rounded. Pronotum with postocular lobes absent (Fig. 155a) to very slightly developed (Fig. 152a); postocular vibrissae moderately long to long, of unequal length and longest behind base of eye. Elytra with scale pattern more or less vittate, intervals other than 9 to 11 with white scales equal in size to those on intervals 9 to 11 (Figs. 133–136). Tarsus with ventral pilose vestiture extensive (on greater part of ventral surface of each article) to slightly reduced in extent (on not less than apical one-half of articles 2 and 3). Wings present, long. Female with abdominal sternum VIII with basal arm short to moderate in length; lateral arms arcuate (Figs. 172–175). Male with aedeagus with internal sac with apex of dorsal median pocket variously emarginate or sinuate (Figs. 192a,b-195a,b); lobes A to F present; dorsal median pocket low in lateral view.

Phylogenetic relationships.— Primary characters show this species group to be monophyletic and a member of the unresolved heptachotomy also including the *C. frontalis-C. americanus* lineage, the *C. infrequens-C. puberulus* lineage, *C. canescens*, *C. collaris*, *C. notolomus* (all of the *C. americanus* group), and the *C. poricollis* species group (Fig. 236). Secondary characters further support the monophyly of the group and indicate that the *C. boucardi* group is the sister-group to the *C. poricollis* species group, this lineage sister to the *C. americanus* species group (Fig. 237).

Cleonidius boucardi (Chevrolat)
(Figs. 133, 152, 172, 192, 221)

Apleurus boucardi Chevrolat 1873:79. Holotype (examined), male, labelled "Puebla", "[letter illegible] Boucard", pale blue square label, "Typus", "41", "471/ 85", "Riksmuseum/ Stockholm" and with my label "*Apleurus boucardi*/ Chevrolat/ HOLOTYPE/ lab. Anderson" (NRS). Type locality, Puebla, Mexico.

Cleonus carinicollis LeConte 1876a:152 [not Gyllenhal 1834:241]. NEW SYNONYMY. Holotype (examined), female, labelled with a pale green circle (=Wyoming Territory), "Type/ 5241", "*C. carinicollis*/ Lec." (MCZC). Type locality, Colorado. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Wickham 1902 (check.). Blatchley and Leng 1916 (key, redesc.). Leng 1920 (catal.). Brimley 1938 (check.). Arnett *et al.* 1980.

Cleonus (*Cleonidius*) *boucardi*; Casey 1891 (key). Champion 1902–1906 (in part; distn., misident of *Cleonidius poricollis*). Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *carinicollis*; Casey 1891 (key, misident. of *Cleonidius trivittatus* Say).

Cleonus (*Cleonidius*) *lecontei* Casey 1891:190. NEW SYNONYMY Holotype (examined), female, labelled "Ari", "CASEY/ bequest/ 1925", "TYPE USNM/ 37280", "*C.Cl./ lecontei*/ Cas."(USNM). Type locality, Arizona. Csiki 1934 (catal.).

Cleonus lecontei; Leng 1920 (catal.).

Cleonus (*Cleonidius*) *lecontellus* Csiki 1934:64. NEW SYNONYMY New name for *Cleonus carinicollis* LeConte. Blackwelder 1939 (check.).

Cleonus boucardi; Blackwelder 1947 (check.).

Cleonis boucardi; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis carinicollis; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).

Cleonis lecontei; O'Brien and Wibmer 1982 (catal., distn.).

Cleonis lecontellus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— Chevrolat (1873), in describing *C. boucardi* noted the similarity to *C. trivittatus* (Say). Although most individuals of the two species are quite distinct, some individuals are difficult to reliably assign as belonging to either species. One such specimen is the holotype of *Cleonus carinicollis* LeConte, which has dense, extensive ventral tarsal pilose pads, moderately developed postocular lobes (both character states of *C. boucardi*), but also has a rostrum that is medially tumescent and has a low median carina, and an elytral scale pattern which is not that of most *C. boucardi* (the latter, all states of *C. trivittatus*). The type locality is "Colorado Territory" and therefore within the ranges of both species. I have chosen to regard this individual as conspecific with *C. boucardi* and accordingly emphasize the taxonomic significance of the characters of extent of ventral tarsal vestiture and development of postocular lobes as diagnostic for these two species.

Cleonidius lecontellus Csiki is a typical *C. boucardi*, differing from the latter, as noted by Casey (1891), only in details of the elytral scale pattern.

Problems in recognition.— Most individuals of this species are likely to be confused only with *C. trivittatus* and *C. quadrilineatus*. They are however, easily separated by the rostrum not or only slightly dorsally medially tumescent (Fig. 152a), postocular lobes slightly to moderately developed (Fig. 152a), and with all tarsal articles with extensive ventral pilose pads (on more or less entire ventral surface of each article) in *C. boucardi* specimens. In both *C. trivittatus* and *C. quadrilineatus* the rostrum is medially dorsally tumescent and carinate (Figs. 153a, 155a), the postocular lobes are not to moderately developed (but only in few specimens of

C. trivittatus, especially in northern part of the species range in southern Canada) (Figs. 153a, 155a), and the ventral tarsal vestiture is less extensive. A few *C. boucardi* specimens from Kansas and Texas are very similar to *C. trivittatus* in elytral scale pattern and in rostral characters but can be separated by their extensive ventral tarsal pilosity and moderately developed postocular lobes.

Cleonidius boucardi may also be confused with some *C. poricollis* that have a similar faintly vittate elytral scale pattern and lack the curved sulcus behind the eye. Although *C. boucardi* and *C. poricollis* are sympatric over part of their ranges, those individuals of *C. poricollis* that are most likely to be confused with *C. boucardi* are found only in the Pacific Northwest; *C. boucardi* does not occur in this or adjacent areas.

This is the only species of *Cleonidius* that has been extensively collected in Mexico (Fig. 221).

Description.— *Specimens examined.* 73 males, 82 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 30. *Size.* Length, male, 7.5–14.7 mm; female, 8.4–18.6 mm. Width, male, 3.2–5.9 mm; female, 3.4–7.0 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with sparse to moderately dense, small to large, shallow to deep punctures, largest, deepest and longitudinally confluent in many specimens immediately above eyes; interspersed with sparse minute punctures. Frons also with sparse, short, suberect hair-like scales, sparse to moderately dense elongate-fine, appressed to recumbent white scales medially, suberect to erect immediately above eyes. Frons continuous with base of rostrum or only very slightly separated from base of rostrum by very shallow transverse impression (Fig. 152a). Base of median tumescence of rostrum with small, shallow to moderately deep fovea. Width of frons subequal to width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.57-0.67 times length in male; 0.59-0.66 in female) (Fig. 152). In lateral view straight to very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes distinctly visible. Rostrum not to very slightly medially tumescent from point of antennal insertion to middle of frons; not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as narrow to broad low glabrous shiny line. Dorsal and lateral punctation sparse to dense, small to large, moderately deep to deep (dense and large in most specimens with many punctures longitudinally confluent); punctures smaller and shallower apically; dorsally interspersed with dense minute punctures. Dorsally with scattered, short, suberect hair-like scales in some specimens; also with sparse to moderately dense, elongate-fine to elongate-narrow, appressed to recumbent white scales. Epistoma very slightly swollen. *Pronotum.* Median carina variously developed in anterior one-half from as minutely punctate slightly elevated broad line to elevated sharp narrow glabrous shiny line, well-developed and distinct in most specimens. Dorsal and lateral punctation small, moderately dense, shallow, not confluent; smaller apically and on flanks; areas between larger dorsal punctures with dense minute regularly impressed punctures. Lacking dorsal suberect or erect vestiture (Fig. 152a). Scales dorsally absent in moderately broad median longitudinal line; moderately dense, elongate-fine to elongate-narrow, appressed in pair of narrow to broad apically slightly narrowed paramedian stripes; laterally, scales absent to very sparse, small and fine. Lateral margins with scales moderately dense, elongate-narrow, appressed in moderately broad stripe. Flanks with scales sparse to moderately dense, elongate-fine. Median basal portion of disk shallowly to moderately deeply and broadly impressed. Anterolateral margin with pronotal postocular lobes very slightly to moderately developed; postocular vibrissae of unequal length, moderately long to long, greatest length (from one-half to two-thirds width of eye) behind base of eye (Fig. 152a). In dorsal view with lateral margins uniformly slightly arcuate and convergent from base to apex, or slightly constricted at apical one-quarter, then straight and convergent to apex. *Prosternum.* With small very shallow indistinct impression and lacking or with at most only very slight rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion short, approximately equal to one-half length of posterior more angulate portion; posterior and anterior portions not to slightly differentiated by shallow transverse impression. *Elytra.* Moderately robust in general form (width at midlength 0.57-0.62 times length in males; 0.54-0.61 in females) (Fig. 133). In dorsal view with lateral margins straight, to very slightly sinuate and slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not to slightly produced, rounded to subacuminate, not to slightly divergent. Humerus distinct. Dorsally lacking suberect or erect dorsal vestiture; sutural interval with moderately dense, small fine white scales; interval 2 with scales absent to sparse small and fine; interval 3 with scales moderately dense large elongate-narrow; intervals 4 and 5 with scales absent to moderately dense, moderately large and elongate-fine; intervals 6 to 8 with scales absent to sparse small and fine; intervals 9 to 11 with scales moderately dense, large elongate-narrow; striae 1, 6 and 7 with irregularly distributed patches of larger and denser white scales (Fig. 133). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small to large denticles in apical three-quarters; subapical tooth large, distinct from apical denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third to one-half, not to slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of all tarsal articles present as large pads on more or less entire ventral surface of articles 2 and 3 and apical one-half to three-quarters of article 1. *Abdomen.* Ventral surface with sparse to moderately dense, elongate-fine to elongate-narrow appressed white scales. Abdominal sterna III to VI lacking glabrous patches or with sterna III and IV with individually indistinct small rounded glabrous patches, each with large puncture and single appressed hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with very slightly developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms moderately inwardly arcuate throughout length; slightly expanded at apex (Fig. 172). Stylus moderately large compared to length of gonocoxite II. Male (three examined). Internal sac (Figs. 192a,b) elongate and low; median dorsal pocket low, with single narrow elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired markedly dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with small paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket slightly emarginate medially in dorsal view (Fig. 192b). Ventral median pocket large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation.— Specimens from Kansas and Texas in the northern part of the species range have a rostrum that is slightly medially tumescent with smaller dorsal punctation, and an elytral scale pattern that is more distinctly vittate.

Geographic distribution.— This species is found from extreme southern California and Arizona in the west, and Kansas and northern Texas in the east, south through central México to Honduras (Fig. 221).

Natural history.— This species lives in mesquite-grassland and grassland habitat throughout Mexico and the southern United States. Plant associations are not known for adults of this species, which have been collected from March to September at elevations of 255–3385 m (N=29) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of the *C. trivittatus-C. quadrilineatus-C. placidus* lineage in the *C. boucardi* group (Fig. 237).

Cleonidius trivittatus (Say)
(Figs. 134, 153, 173, 193, 220)

Cleonus trivittatus Say 1831:10. Neotype (here designated, from the LeConte Collection), female, labelled with a pale green circle (=Wyoming Territory), "1847", "J. LECONTE/ COLLECTION", "*Cl./ trivittatus*/ Say" and with my designation label "*Cleonus trivittatus*/ Say NEOTYPE/ desig. Anderson" (MCZC). Type locality, Colorado. Melsheimer 1853 (check.). LeConte 1859b (error as *C. vittatus* Say). Gemminger and von Harold 1871 (catal.). LeConte 1876a (key). Henshaw 1885 (check.). Wickham 1902 (check.). Fall and Cockerell 1907 (check.). Leng 1920 (catal.). Blackwelder 1947 (check.). Essig 1958 (biol.). Kumar *et al.* 1976 (in part; biol.).

Rhynchophorus praepotens Say 1831:21. Type destroyed.

Lixus praepotens; Boheman 1836 (redescr.).

Apleurus trivittatus; Chevrolat 1873.

Cleonus inornatus LeConte 1876a:149. NEW SYNONYMY Holotype (examined), female, labelled "Cal", "*C./ inornatus*/ TYPE LeC", "Horn Coll/ H 8519" (MCZC). Type locality, Owen's Valley, California. Henshaw 1881–1882 (check.). Henshaw 1885 (check.). Fall 1901 (check.). Leng 1920 (catal.).

Cleonus (*Cleonidius*) *bicarinatus* Casey 1891:190 [not Gebler 1830:158]. NEW SYNONYMY Holotype (examined), male, labelled "Tex", "CASEY/ bequest/ 1925", "TYPE USNM/ 37279", "*C.Cl./ bicarinatus*/ Cas" (USNM). Type locality, near Austin, Texas. Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *carinicollis*; Casey 1891 (key, misident.).

Cleonus (*Cleonidius*) *inornatus*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus (*Cleonidius*) *praepotens*; Casey 1891 (as synonym).

Cleonus (*Cleonidius*) *trivittatus*; Casey 1891 (key). Csiki 1934 (catal.).

Cleonus bicarinatus; Leng 1920 (catal.).

Cleonus quadrilineatus; Pierce 1907 (biol., misident.). Chittenden 1911 (biol., misident.). Blatchley and Leng 1916 (figure, misident.). Yothers 1916 (misident., in part). Essig 1958 (biol., misident.). Arnett *et al.* 1980 (key, redesc., biol., misident.).

Cleonis bicarinatus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis inornatus; O'Brien and Wibmer 1982 (catal., distn.).
Cleonis praepotens; O'Brien and Wibmer 1982 (catal., distn. as synonym).
Cleonis trivittatus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— The type series of this species has been lost. I have selected and designated as neotype, a specimen from the LeConte collection, because it is generally considered that LeConte compared his material with that of Say before the loss of the latter. This collection thus represents one of the best sources of reliably identified specimens of Say species. The type locality of the original type series is given as "Arkansaw" (Say 1831) but it is later stated that he (Say) "obtained two or three specimens near the Rocky Mountains". The neotype selected is from "Colorado Territory" which probably refers to the same general area as that intended by the use of "Arkansaw" by Say (1831), which, as indicated by the reference to the Rocky Mountains, undoubtedly refers to more than what is presently the state of Arkansas.

Rhynchophorus praepotens Say (type lost) was regarded by LeConte (1859b) as conspecific with *Cleonus trivittatus* Say. This synonymy has since been generally followed and thus no neotype designation is required. LeConte (1859b) also states that *Lixus praepotens* (Say) of Boheman (1836) is evidently this same species. *Lixus praepotens* (Say) of Boheman (1836) therefore represents only a reassignment from *Rhynchophorus* to *Lixus* and a species redescription, not description of a new species as indicated by Csiki (1934) and O'Brien and Wibmer (1982).

The holotype of *Cleonus inornatus* LeConte from Owen's Valley, California, as noted under "Notes about synonymy" section for *C. placidus*, although possessing a similar elytral scale pattern to *C. placidus* individuals, is here considered conspecific with *C. trivittatus*. This decision is based on the character states of the reduced extent of tarsal vestiture, presence of slight postocular lobes, and short dorsal erect vestiture on the pronotum shared with *C. trivittatus* and not *C. placidus*. *Cleonus (Cleonidius) bicarinatus* Casey is a typical, but abraded *C. trivittatus*.

Problems in recognition.— Specimens of *C. trivittatus* are most likely to be confused with those of *C. quadrilineatus*, *C. placidus* and *C. boucardi*. Discussions of characters allowing for separation of the former are given under the "Problems in recognition" section for each of the latter three species.

Description.— *Specimens examined.* 128 males, 159 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 31. *Size.* Length, male, 9.4–17.3 mm; female, 8.2–18.4 mm. Width, male, 3.8–9.4 mm; female, 3.0–8.2 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with punctures sparse to moderately dense, small, shallow, some large and longitudinally confluent immediately above eyes; interspersed with dense minute punctures. Frons also with sparse to moderately dense, elongate-narrow appressed to recumbent white scales medially, erect immediately above eyes. Frons separated from base of rostrum by shallow to moderately deep transverse impression (Fig. 153a). Base of median tumescence of rostrum with small, shallow fovea. Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.58-0.73 times length in male; 0.57-0.80 in female) (Fig. 153). In lateral view very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes partially visible. Rostrum slightly to markedly medially tumescent from point of antennal insertion to middle of frons (especially basally) (Fig. 153a); not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as narrow low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation sparse to dense, small, shallow; dorsally interspersed with dense minute punctures. Dorsally either lacking suberect or erect vestiture or with at most sparse to moderately dense, short, suberect hair-like scales; also with moderately dense to dense, elongate-narrow, appressed to recumbent white scales laterally, scales sparser medially and apically. Epistoma not to very slightly transversely swollen at base. *Pronotum.* Median carina variously developed in anterior one-half from as minutely punctate, slightly elevated broad glabrous line to slightly elevated narrow glabrous shiny line. Dorsal and lateral punctation small to moderately large, sparse to moderately dense, shallow to moderately deep; smaller and shallower apically; sparser and shallower on flanks; areas between larger dorsal punctures with dense minute regularly impressed punctures. Lacking dorsal suberect or erect vestiture or with sparse to moderately dense, short, suberect hair-like scales each situated in large puncture (Fig. 153a). Scales dorsally absent to sparse small and fine along median line; moderately dense to dense, elongate-narrow, appressed in pair of narrow to broad apically slightly narrowed paramedian stripes; laterally, scales absent to sparse, small and fine. Lateral margins with scales moderately dense to dense, elongate-narrow, appressed in moderately broad stripe. Flanks with scales moderately dense to dense, elongate-narrow. Median basal portion of disk shallowly to moderately deeply and broadly impressed. Anterolateral margin with pronotal postocular lobes lacking (most specimens) to moderately developed (few specimens); postocular vibrissae of unequal length, moderately long to very long, greatest length (from one-half to slightly greater than two-thirds width of eye) behind base of eye (Fig. 153a). In dorsal view with lateral margins uniformly slightly arcuate to straight and convergent from base to apical one-quarter to one-third, slightly constricted at apical one-quarter to one-third, then straight and convergent to apex. *Prosternum*. With small shallow to moderately deep impression and lacking or with at most only very slight rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion very short to short, approximately one-half length of posterior more angulate portion or less; posterior and anterior portions not to slightly differentiated by a shallow transverse impression. *Elytra*. Moderately robust in general form (width at midlength 0.55-0.62 times length in males; 0.52–0.61 in females) (Fig. 134). In dorsal view with lateral margins very slightly sinuate to moderately and evenly arcuate and slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not to slightly produced, rounded to subacuminate, not to slightly divergent. Humerus distinct. Dorsally lacking suberect or erect dorsal vestiture or with at most sparse, short suberect hair-like scales on declivity; sutural interval with dense, small, fine to elongate-fine white (rarely golden) scales; interval 2 with scales very sparse to dense small and fine; intervals 3 to 5 with scales dense large elongate-narrow; intervals 6 to 8 with scales absent to moderately dense small and fine to elongate-fine; intervals 9 to 11 with scales dense, large elongate-narrow; striae 1, 6 and 7 with irregularly distributed patches of larger and denser white scales (Fig. 134). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings*. Long (greater than elytra in length). *Legs*. Foretibia of female with inner margin with small to large denticles in apical three-quarters; subapical tooth small to large, not to distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus and mesotarsus of male present as small elongate pads on apical one-third of article 1, as rounded pads on apical one-half of article 2, and as large rounded pads on apical three-quarters of article 3; of foretarsus and mesotarsus of female as apical tufts to small elongate-narrow pads on apical one-third of article 1, as rounded pads on apical one-quarter to one-half of article 2, and as large rounded pads on apical one-half to two-thirds of article 3; of metatarsus of male as elongate-narrow pad on apical one-quarter on inner lobe and as apical tuft on outer lobe of article 1, as elongate pads on apical one-half of article 2, as moderately large elongate-oval pads on apical one-half to three-quarters of article 3; of metatarsus of female as apical tuft to elongate-narrow pad on apical one-quarter on inner lobe and as elongate-narrow pad on apical one-half on outer lobe of article 1, as elongate pads on apical one-quarter to three-quarters of article 2, as elongate-oval pads on apical one-third to one-half of article 3. *Abdomen*. Ventral surface with moderately dense, elongate-narrow to moderately robust appressed white scales. Abdominal sterna III to VI (especially sterna III and IV) with distinct rounded glabrous patches, each with large puncture and single appressed to suberect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with very slightly developed median shiny tubercle. *Genitalia*. Female (six examined). Abdominal sternum VIII with basal arm short; lateral arms moderately inwardly arcuate throughout length; not to slightly expanded at apex (Fig. 173). Stylus moderately large compared to length of gonocoxite II. Male (six examined). Internal sac (Figs. 193a,b) elongate and low; median dorsal pocket low, with single moderately broad dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired markedly dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with small paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket slightly emarginate medially in dorsal view (Fig. 193b). Ventral median pocket large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic variation.— Individuals from the northern part of the species range (especially Alberta, Canada) possess moderately developed postocular lobes and correspondingly shorter postocular vibrissae. Throughout the rest of the species range, lobes are lacking or only slightly developed and postocular vibrissae are longer.

In the western part of the species range in California and Nevada (especially the former), individuals possess short suberect dorsal vestiture on the head and pronotum. Throughout the rest of the species range, dorsal suberect or erect dorsal vestiture is lacking or at most very short and indistinct.

Geographic distribution.— This species is widespread in the western United States of America and Canada from extreme southern British Columbia south to southern California in the west, and from southern Manitoba, south through eastern South Dakota, Kansas to western Texas (Fig. 220).

Natural history.— This species appears to be associated primarily with grassland and desert-grassland transitional habitats throughout the species range. Adults have been collected exclusively on Leguminosae as follows; *Astragalus* spp. (as "loco" or "locoweed"), *A. bisulcatus* (Hook.) Gray var. *haydenianus*, *A. earlei* Greene *ex.* Rydb., *A. flavus* Nutt., *A. utahensis* Torr. and Gray, *A. wootoni* Sheldon, *Oxytropis lambertii* Pursh, and *O. sericea* Nutt. Adults have been reared from *Astragalus* sp. (as "locoweed"). Adults have been collected throughout the year at elevations of from 131–3640 m (N=42) (Fig. 233).

A single specimen was found in the stomach contents of *Bufo* sp. (Amphibia).

Chorological relationships.— Table V.

Phylogenetic relationships.— Primary characters indicate only that this species is a member of an unresolved quadrichotomy composed of the four species in the *C. boucardi* group (Fig. 236). Distribution of the apotypic state of the secondary character of length of dorsal vestiture place this species as the sister-species to the *C. quadrilineatus-C. placidus* lineage in the *C. boucardi* group (Fig. 237).

Cleonidius placidus Csiki
(Figs. 135, 154, 174, 194, 222)

Cleonus pacificus Fall 1901:260 [not Olivier 1807:268]. Holotype (examined), male, labelled "Redondo/ Cal.4.7.98", "TYPE/ *pacificus*", "M.C.Z./ Type/ 25194", "H.C.FALL/ COLLECTION", "*Cleonus/ pacificus/* Fall" (MCZC). Type locality, Redondo, California. Leng 1920 (catal.).

Cleonus (*Cleonidius*) *placidus* Csiki 1934:65. New name for *Cleonus pacificus* Fall. Blackwelder 1939 (check.).

Cleonis pacificus; O'Brien and Wibmer 1982 (catal., distn., as jr. homonym).

Cleonis placidus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— This species is commonly known as *C. pacificus* (Fall). This name is a junior homonym and *C. placidus* Csiki is the valid name. The holotype of *Cleonus inornatus* LeConte from Owen's Valley, California has an elytral scale pattern similar to that of *C. placidus* (Fig. 135) but differs in other structural features (possession of short dorsal suberect vestiture of the head and pronotum, slightly developed postocular lobes, and less extensive ventral tarsal pilosity) that are found in Californian *C. trivittatus*. *Cleonus inornatus* herein regarded as conspecific with *C. trivittatus* (see also "Notes about synonymy" section under *C. trivittatus*).

Problems in recognition.— Most individuals of this species are easily recognized by the lack of, or at most only very slightly developed postocular lobes (Fig. 154a), moderately long dorsal erect vestiture of the head and pronotum (Fig. 154a), and distinctive elytral scale pattern (Fig. 135). From *C. trivittatus*, most individuals are separated by the elytral scale pattern and also by the presence of moderately long dorsal erect vestiture on the head and pronotum in *C. placidus*; in *C. trivittatus*, dorsal erect or suberect vestiture is lacking or at most only suberect and short (Fig. 153a). The two species are also largely allopatric in their distributions; *C. placidus* is known only from California (Fig. 222), whereas *C. trivittatus* is widely distributed in western North America, but known from only a few localities in California (Fig. 220). These few *C. trivittatus* from California are difficult to separate from *C. placidus*, however, most of them possess short erect dorsal vestiture, whereas this vestiture is slightly longer on the head and pronotum of most *C. placidus*; they also possess less extensive ventral tarsal pilosity, slightly developed postocular lobes, and lack the distinctive elytral scale pattern of *C. placidus*. Both species are known only from Leguminosae.

Cleonidius placidus individuals may also be confused with individuals of *C. quadrilineatus*, but as for *C. trivittatus* specimens, the distinctive scale pattern of *C. placidus* should serve to separate the two (Fig. 135). Otherwise, *C. placidus* is known only from Leguminosae and is found in California, whereas *C. quadrilineatus* is known from Rosaceae and Rhamnaceae (rarely from Leguminosae) and is widespread in southwestern North America (including California). Most individuals of *C. placidus* are also slightly larger than are most *C. quadrilineatus* (see Fig. 197).

Description.— *Specimens examined.* 57 males, 49 females. Data about variation in LR, WF, WRA, LP, WPB, WEIH, WEIM, LEI, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WEIM/LEI, and LP/LEI are presented in Table 32. *Size.* Length, male, 9.9–17.1 mm; female, 12.6–17.6 mm. Width, male, 3.7–6.2 mm; female, 4.3–6.7 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with punctures sparse to moderately dense, small to moderately large, shallow, some longitudinally confluent immediately above eyes; interspersed with dense minute punctures. Frons also with moderately dense, moderately long, erect hair-like scales and sparse to dense, elongate-narrow appressed white scales medially, erect immediately above eyes. Frons continuous with base of rostrum or only slightly separated by shallow transverse impression (Fig. 154a). Base of median tumescence of rostrum with small, shallow fovea. Width of frons greater than width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.59-0.65 times length in male; 0.57-0.62 in female) (Fig. 154). In lateral view very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes visible. Rostrum slightly to moderately medially tumescent from point of antennal insertion to middle of frons (Fig. 154a); not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as rounded to sharp, narrow low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation sparse to moderately dense, small to moderately large, shallow to moderately deep; punctures smaller and irregularly impressed apically, in some specimens dorsally interspersed with dense minute punctures. Dorsally with moderately dense, moderately long to long, erect hair-like scales; also with sparse, elongate-narrow, recumbent white scales laterally, scales sparser medially and apically. Epistoma not to very slightly transversely swollen at base. *Pronotum.* Median carina variously developed in anterior one-half from as minutely punctate, slightly elevated broad glabrous line to slightly elevated narrow glabrous shiny line, well-developed and distinct in most specimens. Dorsal and lateral punctation moderately large, moderately dense to dense, moderately deep; smaller and shallower apically; sparser, smaller and shallower on flanks; areas between larger dorsal punctures with dense minute regularly impressed punctures. Dorsally, laterally and medially with moderately dense, moderately long to long, erect hair-like scales each situated in large puncture (Fig. 154a). Scales dorsally absent along broad median line; moderately dense to dense, elongate-narrow, appressed in pair of narrow apically convergent and slightly narrowed paramedian stripes; laterally, scales absent. Lateral margins and flanks with scales moderately dense to dense, elongate-narrow. Median basal portion of disk moderately deeply to deeply and broadly impressed. Anterolateral margin with pronotal postocular lobes lacking (most specimens) to only very slightly developed (few specimens); postocular vibrissae of unequal length, very long, greatest length (slightly greater than two-thirds width of eye) behind base of eye (Fig. 154a). In dorsal view with lateral margins uniformly very slightly arcuate and convergent from base to apical one-quarter, slightly constricted at apical one-quarter, then straight and convergent to apex. *Prosternum.* With small shallow to moderately deep impression and lacking or with at most only very slight rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion very short, indistinct. *Elytra.* Moderately elongate-narrow in general form (width at midlength 0.51–0.56 times length in males; 0.50-0.57 in females) (Fig. 135). In dorsal view with lateral margins straight to very slightly sinuate and slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not to slightly produced, rounded to subacuminate, not to slightly divergent. Humerus distinct. Dorsally with sparse, short suberect hair-like scales (most evident on declivity); sutural interval with sparse to moderately dense, small fine white scales; interval 2 with irregularly distributed patches of dense, elongate-fine white scales, otherwise with scales absent to sparse, small and fine; intervals 3 to 11 with scales uniformly moderately dense to dense, elongate-fine to elongate-narrow (some specimens with irregularly distributed patches of even larger denser, white scales, especially on intervals 9 to 11) (Fig. 135). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small denticles in apical three-quarters; subapical tooth not distinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus and mesotarsus of male present as elongate pads on apical two-thirds of article 1, as large rounded pads on apical two-thirds of article 2, and as large rounded pads on more or less entire ventral surface of article 3; of foretarsus of female as small elongate pads on apical one-third of article 1, as rounded pads on apical one-half of article 2, as large rounded pads on apical three-quarters of article 3; of mesotarsus of female as small elongate pads on apical one-quarter to one-third of article 1, as rounded pads on apical one-half of article 2, as large rounded pads on apical two-thirds of article 3; of metatarsus of male as elongate pads on apical one-half to two-thirds of article 1, as large rounded pads on apical two-thirds of article 2, as large rounded pads on more or less entire ventral surface of article 3; of metatarsus of female as elongate-narrow pads on apical one-quarter to two-thirds of article 1, as elongate pads on apical one-half to two-thirds of article 2, as large rounded pads on apical two-thirds of article 3. *Abdomen.* Ventral surface with moderately dense to dense, elongate-narrow to moderately robust appressed white scales; scales sparser along midline on sternum VII of female. Abdominal sterna III to VI (especially sterna III and IV) with distinct large rounded glabrous patches, each with large puncture and single recumbent to suberect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with very slightly developed median shiny tubercle. *Genitalia.* Female (two examined). Abdominal sternum VIII with basal arm moderate in length; lateral arms moderately inwardly arcuate at midlength; slightly expanded at apex (Fig. 174). Stylus moderately large compared to length of gonocoxite II. Male (two examined). Internal sac (Figs. 194a,b) elongate and low; median dorsal pocket low, with single moderately broad dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with moderately large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket bisinuate medially in dorsal view (Fig. 194b). Ventral median pocket moderately large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is known only from California in the coastal and central valleys from San Francisco south to San Diego (Fig. 222).

Natural history.— This species is found only in the Pacific semi-desert region. Adults have been collected almost exclusively from *Astragalus* spp. (Leguminosae). A single specimen was collected on parsnip, *Pastinaca sativa* L. (Umbelliferae). Adults have also been reared from roots of *Astragalus* sp. Adults have been collected throughout the year at elevations of from 9–1747 m (N=10) (Fig. 233).

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. quadrilineatus*, the two species forming a lineage that is the sister group of *C. trivittatus* (Fig. 237).

Cleonidius quadrilineatus (Chevrolat)
(Figs. 136, 155, 175, 195, 224)

Apleurus quadrilineatus Chevrolat 1873:80. Holotype (examined), male, labelled "66", "ex coll./ Sallè", "MUSÉUM PARIS/ 1952/ COLL R OBERTHUR", "*apleurus/ quadrilineatus/* Chev. type texas", and with an inverted label "*Lixus/ praepotens/* Boh. Texas", and with a label indicating it as the holotype "*Apleurus/ quadrilineatus/* Chev. HOLOTYPE/ labelled Anderson" (MNHP). Type locality, Texas.

Cleonus quadrilineatus; LeConte 1876a (key, diag.). Henshaw 1885 (check.). Wickham 1889. Wickham 1896 (check.). Fall 1897. Fall 1901. Wickham 1902 (check.). Fall and Cockerell 1907 (check.). Pierce 1907 (biol., misident. of *Cleonidius trivittatus*). Chittenden 1911 (biol., misident. of *Cleonidius trivittatus*). Anderson 1914 (misident. of *Cleonidius poricollis*). Blatchley and Leng 1916 (figure, misident. of *Cleonidius trivittatus*). Yothers 1916 (prob. misident. of *Cleonidius trivittatus*, in part). Leng 1920 (catal.). Essig 1958 (biol., misident. of *Cleonidius trivittatus*). Arnett *et al.* 1980 (key, redesc., biol., misident. of *Cleonidius trivittatus*).

Lixus texanus; LeConte 1876a (in part, mixed type series).

Cleonus (*Cleonidius*) *quadrilineatus*; Casey 1891 (key). Csiki 1934 (catal.). Hatch 1971 (key, redesc., misident. of *Cleonidius poricollis*).

Cleonis quadrilineatus; O'Brien and Wibmer 1982 (catal., distn.).

Notes about synonymy.— The holotype of *C. quadrilineatus* is the typical elongate-narrow Rosaceae form. Many published references to *C. trivittatus* are to this species.

Problems in recognition.— Specimens of *C. quadrilineatus* are very likely to be commonly confused with those of the broadly sympatric *C. trivittatus*. *Cleonidius quadrilineatus* specimens are separated from the latter by their more elongate-narrow elytral form (Fig. 136) and by presence of moderately long erect hair-like scales on the pronotal disk (Fig. 155a), which in *C. trivittatus* are at most only short, suberect and indistinct (Fig. 153a). Most *C. quadrilineatus* are also associated with Rosaceae or Rhamnaceae, although rarely also with

Leguminosae, whereas all *C. trivittatus* are associated with Leguminosae. Some *C. trivittatus* have slightly to moderately developed postocular lobes (especially from the northern part of the range) whereas all *C. quadrilineatus* lack postocular lobes entirely (Fig. 155a).

In California, specimens of *C. quadrilineatus* may be confused with *C. placidus*, especially specimens of the latter in which the distinctive elytral scale pattern (Fig. 135) is abraded. Individuals of *C. placidus* have moderately long, erect hair-like scales on the pronotum (Fig. 154a), as do *C. quadrilineatus*, but are associated exclusively with Leguminosae. *C. placidus* individuals are also slightly larger than are those of *C. quadrilineatus* (Fig. 197) and have slightly more extensive ventral tarsal pilosity.

Description.— *Specimens examined.* 108 males, 107 females. Data about variation in LR, WF, WRA, LP, WPB, WElH, WElM, LEl, LEy, WEy, WEy/LEy, WPB/LP, WRA/LR, WRA/WF, WElM/LEl, and LP/LEl are presented in Table 33. *Size.* Length, male, 8.3–14.3 mm; female, 9.3–13.1 mm. Width, male, 2.9–5.3 mm; female, 3.2–4.8 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with punctures sparse to moderately dense, small to moderately large, shallow, some large and longitudinally confluent immediately above eyes; interspersed with minute punctures. Frons also with sparse to moderately dense, elongate-narrow appressed white scales medially, erect immediately above eyes. Frons continuous with base of rostrum or separated from base of rostrum by shallow transverse impression (Fig. 155a). Base of median tumescence of rostrum with small, shallow fovea. Width of frons greater than to subequal to width at apex of rostrum. *Rostrum.* Moderately robust, (width at apex 0.60-0.70 times length in male; 0.58-0.69 in female) (Fig. 155). In lateral view very slightly curved downward. In dorsal view with postgenae slightly laterally expanded, antennal scrobes partially visible. Rostrum moderately medially tumescent from point of antennal insertion to middle of frons (especially basally) (Fig. 155a); not laterally expanded at midlength; lateral margins rounded; with median carina variously developed as narrow low glabrous shiny line at crest of median tumescence. Dorsal and lateral punctation sparse to dense, small to moderately large, shallow; punctures smaller apically; dorsally interspersed with dense minute punctures. Dorsally with moderately dense, moderately long, suberect to erect, hair-like scales (especially laterally); also with moderately dense, elongate-narrow, recumbent white scales laterally, scales absent to sparse medially and apically. Epistoma not to very slightly transversely swollen at base. *Pronotum.* Median carina variously developed in anterior one-half from as minutely punctate, slightly elevated broad glabrous line to slightly elevated narrow glabrous shiny distinct line. Dorsal and lateral punctation moderately large, moderately dense, moderately deep; smaller and shallower apically; sparser and shallower on flanks; areas between larger dorsal punctures with dense minute regularly impressed punctures. Dorsally, laterally and medially, with moderately dense, moderately long, erect hair-like scales each situated in large puncture (Fig. 155a). Scales dorsally absent to sparse small and fine along median line; moderately dense, elongate-fine to elongate-narrow, appressed in pair of narrow apically slightly narrowed paramedian stripes; laterally, scales absent to sparse, small and fine. Lateral margins with scales moderately dense to dense, elongate-narrow to moderately robust, appressed in moderately broad stripe. Flanks with scales moderately dense, elongate-fine to elongate-narrow. Median basal portion of disk shallowly to moderately deeply and broadly impressed. Anterolateral margin with pronotal postocular lobes lacking; postocular vibrissae of unequal length, very long, greatest length (greater than two-thirds width of eye) behind base of eye (Fig. 155a). In dorsal view with lateral margins uniformly slightly arcuate and convergent from base to apex, to straight and convergent from base to apical one-quarter to one-third, slightly constricted at apical one-quarter to one-third, then straight and convergent to apex. *Prosternum.* With small shallow to moderately deep impression and slight rounded swelling anterior to each procoxal cavity. In lateral view with anterior flat to slightly angulate portion very short, indistinct. *Elytra.* Elongate-narrow in general form (width at midlength 0.48-0.55 times length in males; 0.48-0.52 in females) (Fig. 136). In dorsal view with lateral margins straight to very slightly sinuate slightly convergent from apical one-third to humerus; moderately and evenly arcuate from apical one-third to apex. Elytral apices not to slightly produced, rounded to subacuminate, not to slightly divergent. Humerus distinct. Dorsally with sparse, short suberect hair-like scales (most evident on declivity); sutural interval with dense, small fine golden to white scales; interval 2 with scales very sparse to dense small and fine, white; intervals 3 to 5 with scales dense large elongate-narrow, white; intervals 6 to 8 with scales sparse to moderately dense, small and fine to elongate-fine, white; intervals 9 to 11 with scales dense, large elongate-narrow, white; striae 1, 6 and 7 with irregularly distributed patches of larger and denser white scales (Fig. 136). Punctures of elytral striae small, individually distinct, arranged in regular rows. *Wings.* Long (greater than elytra in length). *Legs.* Foretibia of female with inner margin with small to moderately large denticles in apical three-quarters; subapical tooth indistinct from tibial denticles. Foretibial and mesotibial unci of both sexes moderately large, metatibial uncus small. Tarsal claws connate in basal one-third, slightly divergent, each with basal internal flange well-developed. Ventral tarsal pilose vestiture of foretarsus and mesotarsus of male present as small elongate pads on apical one-half of article 1, as large, elongate-oval pads on apical two-thirds of article 2, and as large rounded pads on apical three-quarters of article 3; of foretarsus and mesotarsus of female as as small elongate-narrow pads on apical one-quarter of article 1, as small rounded pads on apical one-third of article 2, and as moderately large rounded pads on apical one-half to two-thirds of article 3; of metatarsus of male as elongate-narrow pad on apical one-half on inner lobe and apical one-third on outer lobe of article 1, as elongate pads on apical one-half to two-thirds of article 2, as large rounded pads on apical three-quarters of article 3; of metatarsus of female as elongate-very-narrow pad on apical one-half on inner lobe and apical one-third on outer lobe of article 1, as elongate pads on apical one-third to one-half of article 2, as moderately large elongate-oval pads on apical one-half to two-thirds of article 3. *Abdomen.* Ventral surface with moderately dense, elongate-narrow to moderately robust appressed white scales. Abdominal sterna III to VI (especially sterna III and IV) with distinct rounded glabrous patches, each with large puncture and single appressed to erect moderately long hair-like scale situated in or near center. Base of abdominal sternum VII of female internally (dorsally) with slightly to moderately developed median shiny tubercle. *Genitalia.* Female (four examined). Abdominal sternum VIII with basal arm short; lateral arms moderately inwardly arcuate throughout length; not to slightly expanded at apex (Fig. 175). Stylus moderately large compared to length of gonocoxite II. Male (four examined). Internal sac (Figs. 195a,b) elongate and low; median dorsal pocket low, with single moderately broad dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third on dorsal surface (lobe C), with moderately large paired markedly dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with small paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket and median dorsal pocket individually distinct; apex of dorsal median pocket slightly emarginate medially in dorsal view (Fig. 195b). Ventral median pocket large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface and basal portion of sides of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— This species is found from California east to eastern Nebraska, Oklahoma, and central Texas (Fig. 224). There is a single Mexican record from near Zacatecas.

Natural history.— This species is found primarily in the western xerophytic evergreen forest region but also in desert-grassland transitional habitats. Many adults have been collected primarily on Rosaceae or Rhamnaceae, especially in oak-pinyon-juniper woodlands throughout the species range; a few have been found on Leguminosae in Arizona. Adults have been collected on *Astragalus wootoni* Sheldon, *Lupinus* sp. (Leguminosae); *Ceanothus* sp. (Rhamnaceae); *Cercocarpus montanus* Raf., *Rosa* sp. (Rosaceae). Adults have been reared only from *Astragalus* sp. roots at Sulphur Springs Valley, Arizona. I suspect that a variety of Rosaceae or Rhamnaceae serve as hosts at higher altitudes throughout the species range. Adults have been collected from January to October at elevations from 15–4186 m (N=63) (Fig. 233).

Adults have been found in the stomach contents of *Geococcyx californicus'* (roadrunner; Aves) at Carlsbad, New Mexico.

Other individuals and I have collected this species and *C. texanus* together on various Rosaceae and Rhamnaceae in Texas and Arizona.

Chorological relationships.— Table V.

Phylogenetic relationships.— This species is the sister-species of *C. placidus*, the two species forming a lineage that is the sister group of *C. trivittatus* (Fig. 237).

Incertae sedis

This category is used herein for a single species of uncertain placement, *Cleonidius vibex* (Pallas). Although adults of *C. vibex* have a vittate elytral scale pattern, lack extensive ventral tarsal pilose pads, possess a moderately broad rostrum, and are brachypterous, all of which suggest inclusion in the *C. americanus* group, the nature of formation of the vittate scale pattern is fundamentally different from that in other *Cleonidius* and thus not homologous. In other *Cleonidius* the vittate pattern is produced as a result of differing sizes and densities of scales on the various elytral intervals; in *C. vibex*, the pattern is apparently produced as a result of presence or absence of white pigment in the individual scales. This suggests independent derivation of a vittate elytal pattern and perhaps of states of other characters as well.

Placement of *C. vibex* as sister to the remainder of *Cleonidius* can only be substantiated by an adaptive argument concerning the low likelihood of evolution of the fundamentally different vittate elytral scale pattern of that species from the scale pattern of other *Cleonidius*, which is formed in a very different non-homologous manner.

Cleonidius vibex (Pallas), new combination
(Figs. 156, 176, 196)

Curculio vibex Pallas 1781:32. Types not examined. Herbst 1795.
Lixus denudatus Zoubkoff 1833:319. Types not examined. Faust 1890. Petri 1912.
Lixus karelini Boheman 1836:22. Types not examined. Faust 1890. Petri 1912.
Lixus vibex; Boheman 1836. Capiomont and Leprieur 1874. Faust 1890. Petri 1912. Lukjanovitsh 1926.
Lixus vibex scutellaris Petri 1905:103. Types not examined.
Lixus (Lixestus) vibex; Reitter 1916. Csiki 1934.
Lixus (Lixesthus) vibex; Ter-Minasyan 1978.

Notes about synonymy.— No types associated with the names recorded above have been examined by me. Synonymy presented here follows Petri (1912) and Csiki (1934).

Two additional species have been placed in *Lixus (Lixestus)* by Ter-Minasyan (1978). These are *L. pallasi* Faust and *L. meles* Boheman. These species will likely also prove to be *Cleonidius* but representatives have not been examined by me.

Problems in recognition.— Individuals of this species are easily distinguished from Nearctic *Cleonidius* by the widely divergent tarsal claws each lacking a basal internal flange, and the large unci especially on the fore- and mesotibiae. The rostrum of this species has uniformly very dense and small punctures, but no or else very few larger punctures typical of Nearctic species of *Cleonidius*. Individuals also differ from those of Nearctic species in that the contrasting dark and light areas of the pronotum and elytra are a result of apparently having white scales, such that the underlying dark cuticle is obscured, or unpigmented, such that the dark cuticle is not obscured. Individuals of Nearctic species on the other hand, have a vittate elytral scale pattern and a pronotal scale pattern that is a result of differing sizes of scales; small scales do not obscure the dark cuticle, whereas larger scales do.

The robust, downwardly curved rostrum and elytral scale pattern of individuals of this species result in superficial resemblance to *C. canescens*.

Description.— *Specimens examined.* 1 male, 1 female. *Size.* Length, male, 7.3 mm; female, 7.1 mm. Width, male, 2.7 mm; female, 2.6 mm. *Head.* Eye elongate-oval. Area behind eye with numerous slight wrinkles of cuticle. Frons with only uniformly very dense minute punctures. Frons also with very dense, truncate grey-brown appressed scales. Frons continuous with base of rostrum (Fig. 156a). Base of median tumescence or carina of rostrum (if present) with small, shallow fovea. Width of frons greater than width at apex of rostrum. *Rostrum.* Robust, (width at apex 0.73 times length in male; 0.75 in female) (Fig. 156). In lateral view moderately curved downward. In dorsal view with postgenae very slightly laterally expanded, antennal scrobes distinctly visible. Rostrum markedly medially tumescent from point of antennal insertion to middle of frons (Fig. 156a); not laterally expanded at midlength; lateral margins more or less rounded, not sharp; with median carina absent. Dorsal and lateral punctation very sparse, small, shallow; sparser apically and medially; dorsally interspersed with minute punctures. Dorsally lacking suberect or erect vestiture, with only uniformly very dense, appressed truncate grey-brown scales (punctation almost completely obscured), sparser apically and medially. Epistoma not swollen. *Pronotum.* Median carina lacking. Dorsal and lateral punctation sparse, small, shallow, interspersed with very dense minute regularly impressed punctures. Suberect or erect vestiture lacking. Scales dorsally uniformly dense small truncate appressed medially; laterally transparent in pair of narrow stripes (apparently black). Lateral margins and flanks with scales uniformly dense, small, truncate and appressed, punctation almost completely obscured. Median basal area of disk broadly and very shallowly impressed. Anterolateral margin with pronotal postocular lobes well-developed; postocular vibrissae short, of uniform length (Fig. 156a). In dorsal view with lateral margins straight and convergent from apical one-third to base; slightly arcuate from apical one-third to apex; subapical constriction indistinct. *Prosternum.* With moderately large, moderately deep impression anterior to each procoxal cavity; swelling lacking. In lateral view with anterior flat to slightly angulate portion moderately long, approximately one-half length of posterior more angulate portion; anterior and posterior portions slightly differentiated by shallow transverse impression. *Elytra.* Moderately elongate-narrow in general form (width at midlength 0.52 times length in male; 0.53 in female). In dorsal view with lateral margins very slightly sinuate and slightly convergent from apical one-third to humerus; moderately arcuate at apical one-third then straight and convergent to apex. Elytral apices not produced, rounded, slightly divergent. Humerus rounded, indistinct. Dorsally lacking suberect or erect vestiture. Scales uniformly very dense, small, robust, appressed grey-brown on sutural interval and intervals 2 to 5 and 8 to 11; intervals 6 and 7 with scales truncate, transparent, underlying dark cuticle visible through scales. Punctures of elytral striae small, individually distinct; arranged in regular rows. *Wings*. Moderate (slightly shorter than length of elytra). *Legs*. Foretibia of female with inner margin with small denticles in apical one-half; no distinct subapical tooth present. Foretibial and mesotibial unci of both sexes very large, metatibial uncus moderately large. Tarsal claws widely divergent, each lacking distinct basal internal flange. Ventral tarsal pilose vestiture of foretarsus and mesotarsus of both sexes lacking from articles 1 and 2, present as small rounded apical tuft of article 3; of metatarsus of both sexes, lacking from articles 1 and 2, present as minute apical tuft of article 3. *Abdomen*. Ventral surface with dense, truncate, small appressed grey-brown scales. Abdominal sterna III to VI sparse moderately large shallow punctures, no distinct glabrous patches or suberect or erect vestiture present. Base of abdominal sternum VII of female internally (dorsally) with at most moderately-developed median shiny tubercle. *Genitalia*. Female (one examined). Abdominal sternum VIII with basal arm long; lateral arms straight and divergent from base to approximately apical one-third; moderately inwardly arcuate at apical one-third and slightly convergent to apex; apices moderately expanded (Fig. 176). Stylus moderately large compared to length of gonocoxite II. Male (one examined). Internal sac (Figs. 196a,b) elongate and low; median dorsal pocket low, with single moderately broad elongate dorsally directed basal lobe (lobe A), with small median dorsally directed lobe at midlength on dorsal surface (lobe B), with moderately large paired dorsally directed lobe at basal one-third at dorsal margin (lobe C), with moderately large paired dorsolaterally directed lobe near midlength near dorsal margin (lobe D), with large paired dorsolaterally directed lobe just beyond midlength at dorsal margin (lobe E), and with small ventrally directed paired lobe near base near ventral margin (lobe F). Apical pocket individually distinct from median dorsal pocket; apex of median dorsal pocket rounded in dorsal view. Ventral median pocket large. Apical pocket with paired moderately large ventrally directed lobe near apical one-third at ventral margin. Eversible apical sclerite complex with paired simple scythe-like sclerite; adjacent ventral surface of apical pocket with pair of large, dark, longitudinal sclerites.

Geographic distribution.— Southern Russia, Persia, Siberia and Mongolia (Csiki 1934).

Natural history.— No information is available about the natural history of this species. Based on its general geographic distribution I suspect that it is a grassland or semi-desert inhabiting species.

Chorological relationships.— This is the only Palearctic species of *Cleonidius* I have seen.

Phylogenetic relationships.— See "*Incertae sedis*" section preceding.

Nomen dubium

Lixus californicus Motschulsky is herein treated as a *nomen dubium*. Motschulsky (1845:378) in his original description of this species noted only that its type was smaller, more elongate, and whiter than specimens of either *Lixus poricollis* Mannerheim and *L. modestus* Mannerheim. He further stated that he thought it likely that it was a male of *L. modestus*. Based upon examination of the holotype (on loan from Zoological Museum of the Moscow Lomonosov State University) *Lixus modestus* Mannerheim is, however, not a *Cleonidius* nor is it conspecific with any North American *Lixus* species known to me. Furthermore, *L. modestus* does not possess character states of the New World *Lixus* species component and thus I suspect has been erroneously labelled as having been collected in California. This notion of a misidentified type locality is supported by Mannerheim (1843: 291), who stated that Eschscholtz (*in litteris*) had referred to *L. modestus* or *Lixus adspersus* (a species described by Boheman (1836) from the Republic of South Africa).

In view of this confusion regarding the type locality of *Lixus modestus* Mannerheim, the statement by Motschulsky (1845) that he suspects *L. californicus* Motschulsky is a male of *L. modestus* (the type of *L. modestus* incidentally is a male), and the inadequate characterization (and the apparent loss of type material) of *L. californicus*, I consider recognition of *Lixus californicus* Motschulsky as a *nomen dubium* to be in the best interests of a stable nomenclature.

ADVENTITIOUS TAXA

During the course of study, individuals of two adventitious species were encountered from North American localities. These are *Stephanocleonus glaucus* labelled "S.C." (1), and "Ames, Iowa" (1); and, an unidentified species of *Tetragonothorax* from "Mobile, Alabama" (1). These species are considered not to be established in North America.

EXTANT TAXA ERRONEOUSLY PLACED IN CLEONINAE

Cleonis chilensis Blanchard 1851:326 is listed in both *Cleonus (Incertae Sedis)* and *Adioristus* in the Coleopterorum Catalogus (Csiki 1934; Schenkling and Marshall 1931) and also in Blackwelder (1947). Kuschel (1949:31) subsequently placed it in *Scotoeborus* (Leptopiinae [now Entiminae], Cylydrorhinini). I have examined the type of this species (deposited in MHNP) and agree that it is not cleonine.

Argentinorhynchus breyeri Brèthes 1910:211 was described from Argentina and originally noted as "Cleonidarum". It has since been regarded as cleonine by (Csiki 1934) who placed the genus as a subgenus of *Cleonus*. Likewise, and probably following Csiki, Blackwelder (1947) lists the species in *Cleonus*. Kuschel (1950:112) subsequently returned *Argentinorhynchus* to generic status and placed it in Erirhininae. The holotype of this species is located in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" but has not been examined by me (Bachman *in litt.*, 1985).

The genus *Lepyrus* is also not Cleoninae and has been removed to Molytinae (Hylobiinae of authors) (Solari 1941; Ter-Minasyan 1963).

FOSSIL MATERIAL

Various Tertiary coleopterous fossils have been identified as Cleoninae but, preservation is such that most of these are actually not reliably identifiable to subfamily, according to Kingsolver (1961) who has examined much of the material of Scudder (1893) and Wickham (1911, 1912) deposited at the Museum of Comparative Zoology, Harvard University. Matthews (1977) also notes a *Cleonus* sp. from the Tertiary of Banks Island in the Canadian Arctic but this identification is based only on elytral fragments. I have not examined any of these specimens.

Sleeper (1969) described two species of *Cleonidius* (as *Cleonus*) from Pleistocene Rita Blanca Lake deposits in Texas. Unfortunately I have not seen the specimens, and descriptions and figures do not provide information permitting meaningful comparison with extant species. Sleeper (1969) states that *Cleonidius ritablancensis* is near *Cleonidius sparsus* and that *Cleonidius channingensis* is near *Cleonidius circumductus*, but, the history of misidentification in *Cleonidius* and subtle differences between many of the species necessitates re-examination. Unfortunately location of the specimen depository was not stated by Sleeper (1969).

Fossils of species identified as the genus *Cleonus* are frequently encountered in late Pleistocene deposits in northern North America (Matthews, 1974, 1975; Hughes *et al.*, 1981; Mott *et al.*, 1981; Morlan and Matthews, 1983). Some of these have been tentatively identified as *Cleonus plumbeus*, but as noted by Morgan *et al.* (1985), they may actually represent one or more Palearctic species or even one of the herein-newly-described Nearctic species. All of this northern Pleistocene material actually belongs in the genus *Stephanocleonus*, and the present revision of North American members of that genus reveals that taxa traditionally regarded as *S. plumbeus* are a complex of six species, four of which are newly described herein. All of this fossil material is deposited with John V. Matthews, Jr., Geological Survey of Canada, Ottawa; none of it has been examined by me.

EVOLUTIONARY ANALYSIS: RECONSTRUCTED PHYLOGENY

> *My profession embodies one theme even more inclusive than evolution--the nature and meaning of history. History employs evolution to structure biological events in time. History subverts the stereotype of science as a precise, heartless enterprise that strips the uniqueness from any complexity and reduces everything to timeless, repeatable, controlled experiments in a laboratory. Historical sciences are different, not lesser. Their methods are comparative, not always experimental; they explain, but usually do not try to predict; they recognize the irreducible quirkiness that history entails, and acknowledge the limited power of present circumstances to impose or elicit optimal solutions.*
>
> Steven Jay Gould, Prologue to "The Flamingo's Smile", 1985.

Inquiry in historical science proceeds primarily by investigation of relationships between pattern and process. Factual data are assembled and patterns are searched for and recognized in these data. Recognition of a pattern, especially if repeated within the study group or in other groups, begs explanation by proposal of a common causal mechanism in the form of a testable hypothesis. Proposal and subsequent testing of this hypothesis, the former inductive, the latter hypothetico-deductive, are the cornerstones of science in general and systematic research in particular. Comparison of these approaches in systematics is adequately treated by Wiley (1981) and application of the hypothetico-deductive method to systematics by Gaffney (1979).

In this study, aspects of both inductive and hypothetico-deductive science are employed and applied. Although some recent authors advocate only the hypothetico-deductive approach, I believe that much useful information and advances in biological knowledge have been and should continue to be, achieved through use of both approaches, but that they operate best at different stages in the process of scientific inquiry; induction for hypothesis formulation, deduction for hypothesis testing.

Herein, an inductive approach is used primarily to attempt to formulate explanations of details of the evolutionary and biogeographic history of the weevil subfamily Cleoninae, especially species of the genera *Cleonidius* and *Apleurus* in North America. From these analyses, evident patterns are identified and more general hypotheses concerning biogeographic patterns and evolutionary trends in arid-land-adapted organisms are proposed, to be available for subsequent testing in future studies for their applicability and predictive value. In addition, some competing and previously proposed hypotheses concerning general evolutionary or biogeographic patterns are tested by application of the appropriate results of this study of North American Cleoninae.

Methods of phylogeny reconstruction

Since the publication of Hennig (1966), there has been an expanding emphasis on both theoretical and practical aspects of phylogenetic and biogeographic studies. While the pages of *Systematic Zoology* clearly document an intense interest in theoretical aspects, increased attention to practical aspects and applications is evidenced simply by the numbers of revisionary works that deal extensively with reconstruction of phylogeny and its applicability to character evolution, classification and biogeography. The appeal of the phylogenetic approach (Hennig, 1966) to phylogeny reconstruction over various other approaches (Wiley, 1981) is primarily in the potential for critical assessment of resultant hypotheses of relationship, their logical predictive nature and their general applicability. The approach I have taken herein is phylogenetic (Hennig, 1966). Character states are determined as apotypic (derived) or plesiotypic (primitive) and only distributions of apotypic states are used in the analysis.

Of paramount importance in reconstructing phylogeny are: one, determination of polarity of character states; and two, recognition of homoplasy or simply, determination of which characters actually reflect descent from a common ancestor, not other processes.

Out-group criteria were used to polarize character states of all primary characters (Watrous and Wheeler, 1981). For secondary characters, out-group criteria were employed where possible although in-group or local parsimony (Maddison *et al.*, 1984), or the functional out-group of Watrous and Wheeler (1981), were also used, especially in instances where more than one character state occurs in the out-groups or where, although both out-groups have the same state, there is incompatibility with the reconstructed phylogeny as determined by primary characters.

Character weighting was employed. Characters used in the phylogenetic analysis of species in *Cleonidius* and *Apleurus* are considered at two levels as indicated above. Primary characters are those which are deemed of high weight because there is no ambiguity in determining polarity of the various character states based on an out-group analysis (Watrous and Wheeler, 1981; Maddison *et al.*, 1984), and the apotypic state, so determined, is not widely distributed elsewhere in Cleoninae. Characters meeting these criteria are given further support as primary characters should they, as a group, result in a reconstructed phylogeny of the genus in question in which the distributions of apotypic states of the various characters are compatible, with the result that there is minimal homoplasy. Characters that exhibit more than a little homoplasy elsewhere in Cleoninae may be regarded as primary should the distribution of their apotypic states be entirely compatible with the distribution of apotypic states of numerous other primary characters.

Secondary characters are those considered to be of lesser weight because of widespread presence of the apotypic state elsewhere in Cleoninae. Lack of complete compatibility with primary characters, and/or problems in determining polarity of the character states based strictly on an out-group analysis necessitating reference to in-group relationships previously resolved on the basis of the distribution of states of primary characters also results in such characters being considered at a secondary level. Distribution of apotypic states of secondary characters may or may not be compatible with distributions of apotypic states of primary or other secondary characters with the result that there is generally more homoplasy in characters included in this more resolved reconstructed phylogeny of the genus is question.

Characters examined but not included in the phylogenetic analysis are those that exhibit extensive homoplasy elsewhere in Cleoninae and are not compatible with, or, when compared with other potential secondary characters, exhibit minimal compatibility with, distributions of apotypic states of primary characters.

Primary characters are the characters used to establish a basic set of relationships that may or may not be totally dichotomously resolved, but in which confidence can generally be regarded as high. This set of relationships is then accepted *a priori* and the distribution of states of secondary characters considered with reference to this reconstructed phylogeny. Thus secondary characters can only be used to reinforce previously established relationships or to further resolve the reconstructed phylogeny by providing additional characters in which confidence is low.

I do not use a complex system of weighting characters such as that of Hecht and Edwards (1976, 1977). Instead, I use this simple two level weighting system which depends solely upon the distributions of character states, and makes no inferences or assumptions about complexity, function or adaptive value which may not have a logically sound basis. As such, I think this system better reflects the confidence level for a given set of relationships especially when these are depicted on successively more resolved cladograms.

Phylogenetic position of Cleoninae

The detailed phylogenetic position of Cleoninae is unclear although relationships at some level appear to be with Molytinae, specifically the Hylobiinae, of authors. Taxonomy of these two subfamilies has a history of repeated misclassification and a repeated concern for adequate distinction (Aslam, 1963; Marshall, 1932; Solari, 1941; Ter-Minasyan, 1963). In addition, Aslam (1961) has noted that among Curculionidae, the Molytinae and Cleoninae are unique in their possession of free-lobed testes, and, along with a few other subfamilies, both have the vasa efferentia free from the testicular lobes and each of the latter with numerous follicles. These states however, all appear to be symplesiotypic for they are all found in primitive Curculionoidea (Morimoto, 1962) and cannot be considered evidence for a sister-group relationship but rather, as will be noted forthwith, for a primitive position for Cleoninae with respect to other Curculionidae. Although unjustified by synapotypy as sister-taxon to Cleoninae, certain Molytinae are employed herein as the out-group for the purpose of tentative polarization of character states in genera of Cleoninae.

Evidence that Cleoninae are a very primitive lineage within Curculionidae is extensive. Indeed they may prove sister to the rest of the Curculionidae based on the large number of plesiotypic character states that they possess.

Buchner (1933, 1953) and Scheinert (1933) discuss at length the mechanism by which adult female Cleoninae pass on symbiotic bacteria to the egg and site of localization of these symbionts in the larvae. In Cleoninae, symbiont pouches are paired and attach to the vagina near the base of gonocoxite II. Bacteria develop in these pouches embedded in a secretion originating from the epithelial cells of the pouch. As eggs pass through the vagina they are coated with bacteria which are then ingested by young larvae. In the larvae, there are four variously shaped evaginations in the anterior part of the midgut where the bacteria are localized. Both of these states are unique within Curculionidae to Cleoninae and are very similar to those of Anobiidae, Lagriidae and Cerambycidae (Buchner, 1953). Recently, Mann and Crowson (1984) noted that similar pouches to those in adult female Cleoninae also occur in various Chrysomelidae, a constituent taxon of the presumed sister-lineage of Curculionoidea; site of localization in larvae was not examined. Although Curculionoidea generally regarded to be primitive have not been examined for these characters, the widespread distribution of the states in related groups suggests that these states are plesiotypic in Curculionidae and that Cleoninae is a very primitive lineage within that family.

Wing structure is also primitive (Kingsolver, 1961), because in at least some Cleoninae, the branches of the second anal vein are joined at the base and the basal one-half of the first anal vein is present. These features appear to be unique to Cleoninae within Curculionidae and are undoubtedly plesiotypic because they are found in primitive Curculionoidea.

Ting (1936) has also noted that in Curculionidae, Cleoninae are the only subfamily in which adults have the labial palpi ventral in their site of attachment to the labium. Although Ting (1936) suggests this to be the autapotypic state, the fact that the same state is found in primitive Curculionoidea suggests that it is plesiotypic.

Further evidence for a primitive phylogenetic position for the subfamily comes from the structure of the testes (as noted previously), and generalized stem or root mining habits of larvae of the subfamily.

Monophyly of Cleoninae is indicated by structure of the labial palpi, which, although described as of one article (Aslam, 1963; Ter-Minasyan, 1963), are of three very small and telescoped articles (Figs. 61–63). This character state appears to be unique to Cleoninae within Curculionoidea. Most other Curculionoidea possess larger three-segmented labial palpi; some lack palpi entirely or have the palpi variously modified, but these latter states are clearly autapotypic. At present, this is the only autapotypic character state supporting monophyly of Cleoninae.

Phylogenetic relationships among tribes of Cleoninae

Within Cleoninae, Csiki (1934) recognized four tribes: Lepyrini, Cleonini, Rhinocyllini, and Lixini. Lepyrini, has since been removed from Cleoninae and placed in Molytinae (Solari, 1941; Ter-Minasyan, 1963). Since then, Aslam (1963) and Ter-Minasyan (1978) have recognized only two tribes, Cleonini and Lixini; O'Brien and Wibmer (1982) continue to recognize three tribes, as above, excluding Lepyrini.

In general, the tribe Lixini are all those Cleoninae whose adults have a more elongate-narrow cylindrical rostrum and elongate-narrow body form. The tribe Cleonini on the other hand, includes taxa whose adults have a more robust rostrum and body form. Cleonini are generally associated with arid habitats; Lixini, with mesic habitats. Rhinocyllini, when used, is reserved for the genera *Rhinocyllus* and *Bangasternus* which are otherwise placed as Lixini.

No satisfactory suprageneric classification has been proposed for Cleoninae, because the phylogenetic relationships of the world genera must be assessed before such can be realized. No tribal placement is therefore herein attempted although generic relationships of North American taxa, traditionally placed as Cleonini, are discussed and represent a start at a reconstructed phylogeny of genera and revised tribal classification.

Phylogenetic relationships of genera of New World Cleonini

In an attempt to determine the relative position of *Apleurus* and *Cleonidius*, a survey of representatives of 50 genera of world Cleoninae was undertaken (Appendix 2). In instances where type species have not been designated for a given genus, the species considered representative of that genus is one originally included and which could subsequently be designated as the type species. Where possible, relationships were inferred on the basis of shared, presumably derived character states, preferably unique to those taxa or found in few other Cleoninae (preferably those taxa, which for reasons of distribution of other more widespread and presumably apotypic character states, are not considered closely related to the genus under study). Inferred monophyly of this grouping was then corroborated by examination of distribution of either apotypic or plesiotypic states of other characters (with more widespread distributions) for concordance.

Confidence in phylogenetic relationships of *Apleurus* is high because a large number of representatives of genus-group names in Cleonini were examined and considered in the search for out-groups. Unfortunately, confidence in out-group relationships of *Cleonidius* is low, largely because few representatives of genus-group names of Lixini were examined. Although *Cleonidius* has traditionally been considered a member of Cleonini (the initial seach for an out-group accepted that premise), indications are that *Cleonidius* (and *Cylindropterus*) is more closely related to Lixini than to any traditional Cleonini. In fact, as noted elsewhere, some *Lixus* species proved to belong in *Cleonidius*. A revision of this large and structurally divergent genus is required on a world basis to better formulate the phylogenetic relationships of *Cleonidius*.

For *Apleurus*, out-groups *Cnemodontus* and *Chromoderus*, together with *Apleurus* itself, are inferred to compose a monophyletic group based primarily upon presence of a variously developed acute pronotal postocular projection fringed with anteriorly directed, long, postocular vibrissae of unequal length (Figs. 81–88). This state is otherwise found only in species of *Lixus* (Fig. 4), *Lixocleonus* and *Microlarinus* (Fig. 1), taxa that on the basis of distributions of states of other characters are not considered closely related to *Apleurus*.

Recognition of this group as monophyletic is supported by the distributions of the following character states, which are shared, except as noted, by members of the three genera and in most instances, by a variable number of other genera as well. Polarity of the states of these characters may or may not have been determined.

1. Body form more or less robust. The three taxa under consideration possess this state as do numerous other Cleoninae. Molytinae of phylogenetic interest are also more or less robust in body form; therefore, this state is likely plesiotypic.

2. Pronotum with scale pattern with large white scales present in a lateral stripe of variable width, small and fine in a moderately broad to very broad apically narrowed median stripe; median area largely black in color, the underlying dark cuticle not obscured by the overlying scales (Figs. 24, 68–80). This state is present in *Apleurus* and *Chromoderus*, as well as numerous other genera of Cleoninae. A distinct pronotal scale pattern is not evident in *Cnemodontus*. Polarity of the states of this character has not been determined.

3. Eye like an inverted, elongate teardrop in shape. This state is found in the three genera in question as well as in numerous other genera of Cleoninae. Polarity of the states of this character has not been determined.

4. Eye prominent and convex in dorsal view. This state is found in *Apleurus* and *Cnemodontus* (but not *Chromoderus*), as well as in various *Lixus* species and *Lixocleonus*. Polarity of the states of this character has not been determined.

5. Female with abdominal sternum VIII with basal arm absent (Figs. 56e-57e, 89a-96a). This state is found in all three genera as well as in numerous other genera of Cleoninae. Molytinae possess a long basal arm and thus lack of the arm is likely apotypic but also homoplasious.

6. Tarsi with articles moderately wide, not markedly elongate-narrow. This state is found in *Chromoderus*, *Cnemodontus* and some *Apleurus* species as well as numerous other Cleoninae. Molytinae of phylogenetic interest also possess this state and thus it is likely plesiotypic.

7. Tarsi with ventral pilose pads present, large and distinctly delimited. This state is found in *Chromoderus*, *Cnemodontus* and some *Apleurus* species as well as numerous other Cleoninae. Molytinae of phylogenetic interest also possess this state and thus it is likely plesiotypic.

8. Pronotum with dorsal surface punctate, not tuberculate. This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

9. Female with spermathecal gland spherical, not variously elongate and cylindrical. This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

10. Rostrum moderately elongate-narrow to robust. This state is found in the three taxa in question as well as various other Cleoninae. Polarity of the states of this character has not been determined.

11. Tibiae with corbel ridge sharp (as in Fig. 6). This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

12. Ventral surface of male lacking extensive long erect vestiture. This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as numerous other Cleoninae. Molytinae of phylogenetic interest also possess this state and thus it is likely plesiotypic.

13. Female with gonocoxite II triangular in shape (Figs. 89b-96b), apex not prolonged into a marked lobe (Fig. 54). This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as numerous other Cleoninae. Molytinae of phylogenetic interest also possess this state and thus it is likely plesiotypic.

14. Antenna with apical three articles with placoidal sensilla. This state is found in *Chromoderus*, *Cnemodontus* and *Apleurus* species as well as various other Cleoninae. Polarity of the states of this character has not been determined and not all Cleoninae have been examined in detail for this character.

For *Cleonidius*, out-groups *Lixus (Lixoglyptus)* and *Cylindropterus* were selected largely because of their close resemblance to *Cleonidius* species, yet lack of the internal swelling at the base of abdominal sternum VII in the female which characterizes the latter. No synapotypies were identified to unite the three taxa as a monophyletic group and indeed, the group may prove to be paraphyletic. Distributions of the states of the following characters support a close but unresolved relationship among these three taxa.

1. Body form more or less elongate-narrow, cylindrical. The three taxa under consideration possess this state as do *Mecaspis*, *Lixocleonus*, and most *Lixus*. Molytinae of phylogenetic interest are more robust in body form therefore elongate-narrow form is likely apotypic.

2. Pronotum with scale pattern slightly to distinctly vittate, with white scales largest and/or densest immediately laterad of midline, smaller and/or sparser laterally; largely whitish in color, the underlying dark cuticle largely obscured by the white scales (Figs. 118–136). This state is present in *Lixoglyptus* and *Cleonidius* species as well as *Pseudocleonus*, *Mecaspis*, and various other species of *Lixus*. A distinct pronotal scale pattern is lacking from many genera including *Cylindropterus*.

3. Eye elongate-oval in shape. This state is found in the three genera in question as well as numerous other genera of Cleoninae. Polarity of the states of this character has not been determined.

4. Eye more or less flat in dorsal view. This state is found in the three taxa in question as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

5. Tibiae with corbel ridge rounded (as in Fig. 5). This state is present in the three taxa in question, *Lixocleonus*, *Menocleonus*, *Epirhynchus*, and all *Lixus* species. Polarity of the states of this character has not been determined.

6. Tarsi with articles moderately wide, not markedly elongate-narrow. This state is found in the three taxa in question as well as numerous other Cleoninae. Molytinae of interest also possess this state and thus it is likely plesiotypic.

7. Tarsi with ventral pilose pads present, large and distinctly delimited. This state is found in the three taxa in question as well as numerous other Cleoninae. Molytinae of interest also

possess this state and thus it is likely plesiotypic.

8. Pronotum with dorsal surface punctate, not tuberculate. This state is found in the taxa in question as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

9. Female with spermathecal gland spherical, not elongate and cylindrical. This state is found in the three taxa in question as well as numerous other Cleoninae. Polarity of the states of this character has not been determined.

10. Rostrum moderately to very elongate-narrow. This state is found in the three taxa in question (although not all species of *Cleonidius*) as well as various other Cleoninae. Polarity of the states of this character has not been determined.

11. Pronotum with postocular lobes present. This state is found in the three taxa in question (although not in all species of *Cleonidius*) as well as numerous other Cleoninae. Molytinae of interest also possess this state and thus it is likely plesiotypic.

12. Female with abdominal sternum VIII with basal arm present, short to long (Figs. 113–114, 157–176). This state is found in the three taxa in question as well as in numerous other genera of Cleoninae. Molytinae of interest possess a long basal arm and thus this state is likely plesiotypic with a successively shorter arm increasingly apotypic.

13. Antenna with apical three articles with placoidal sensillae lacking or else very few in number. This state is found in the three genera in question as well as *Lixocleonus* and *Lixus* species. Polarity of states of this character has not been determined and not all Cleoninae have been examined in detail for this character.

14. Prosternum with swelling in front of fore-coxal cavity. This state is found in the three taxa in question and *Cosmogaster, Mecaspis, Lixocleonus, Microcleonus* and *Lixus*. Polarity of states of this character has not been determined.

Genus *Apleurus* Chevrolat

Character evolution

Character state 1 for each character is considered plesiotypic; other states are considered apotypic at various levels (see Table I).

Primary characters

Character 1. Epistoma, apical margin.— Two states of this character are recognized:

1. emarginate (Fig. 81b);
2. rounded and produced (Figs. 82b-88b).

Out-groups, most Cleoninae, and Molytinae possess an emarginate epistoma. An apically rounded epistoma is otherwise known only in *Gonocleonus*, *Leucochromus*, *Eurycleonus*, and *Koenigius*.

Character 2. Prementum, setae.— Two arbitrarily defined states of this character are recognized:

1. lacking or with only one large seta per side (Figs. 61–62);
2. with two or more large setae per side (Fig. 63).

Out-groups *Cnemodontus* and *Chromoderus* lack and possess one large seta per side respectively. Other Cleoninae were not examined in detail for this character, however, at least some species of *Lixus* and *Cleonidius* possess two or more long setae on each side of the prementum.

Character 3. Pronotum, tubercles, development and shape of anterior angles.— Three states are recognized:

1. absent (Figs. 24, 68–69);
2. present, anterior angles obtuse (Figs. 75–80);
3. present, anterior angles acute (Figs. 70–74).

Out-groups lack distinct tubercles but the pronota are slightly constricted at the apical one-third to one-quarter, the position of the tubercles if developed. This and lack of acutely-angled tubercles in other Cleoninae which possess variously developed pronotal tubercles, justify recognition of obtusely angled tubercles as plesiotypic.

Character 4. Tarsus, ventral pilose vestiture.— Three arbitrarily defined states are recognized:

1. extensive;
2. moderately reduced in extent;
3. markedly reduced in extent, or absent.

Out-groups each possess extensive ventral tarsal pilose vestiture. This state is considered plesiotypic and successive stages in reduced extent of pilose vestiture increasingly apotypic. Molytinae possess extensive ventral pilose vestiture. Extent of ventral tarsal pilose vestiture varies extensively in Cleoninae and on that basis alone this character should perhaps best be regarded as of a secondary nature. However, compatibility of successively apotypic states of this character with numerous other primary characters results in increased confidence that it also be considered primary.

Character 5. Female, stylus, size.— Three states are recognized:

1. large (Figs. 89b-91b);
2. small (Figs. 92b-94b);
3. absent (Figs. 95b-96b).

Out-groups and all Cleoninae examined (except for *Brachycleonus* in which a stylus is absent) possess a moderately large stylus. Decreased size is considered increasingly apotypic.

Character 6. Female, stylus, position.— Three states are recognized:

1. apical (Figs. 89b-91b);
2. anteapical (Figs. 92b-94b);
3. absent, anteapical sclerotized ridge present (Figs. 95b-96b).

Out-groups and all Cleoninae examined in which a stylus is present, possess an apically situated stylus. The anteapical sclerotized ridge is regarded as positionally homologous with the stylus in other *Apleurus* species and thus state 3 is not considered as increasingly apotypic.

Character 7. Male, abdominal sternum VII, dorsally directed tooth at apical margin.— Two states are recognized:

1. absent;
2. present.

Out-groups and all Cleoninae except *Brachycleonus* and *Centrocleonus* lack a dorsally directed tooth on the apical margin of abdominal sternum VII.

Character 8. Male, abdominal sternum VIII, interior angles of each sternite.— Three states are recognized:

1. basal projection absent (Fig. 97f);
2. basal projection slightly to moderately developed (Fig. 101e);
3. basal projection present, markedly developed (Fig. 103e).

Both out-groups lack a basal projection. Extent of development from slight to marked represents successively apotypic states. Other Cleoninae have not been examined in detail for this character although a distinct basal projection is lacking from both *Cleonidius* and *Stephanocleonus*.

Secondary characters

Character 9. Size, length of elytra.— Three arbitrarily defined states are recognized (Fig. 105).

1. $X<7.0$ mm;
2. $7.0 \text{ mm}<X<9.0$ mm;
3. $X>9.0$ mm.

Large size (state 3) is widespread in Cleoninae but the out-groups *Chromoderus* and *Cnemodontus* possess state 1 and state 2 respectively. Small size of *Chromoderus* and primitive *Apleurus* species, however, suggests that the common ancestor of *Chromoderus* and *Apleurus* was also of small size, and that medium to large sizes (states 2 and 3) in *Apleurus* are successively apotypic. Whether the medium size of *Chromoderus* is then primitive or represents an independent increase in size is not known.

Character 10. Eye, prominence and convexity.— Three arbitrarily defined states are recognized:

1. markedly convex and prominent;
2. slightly to moderately prominent and convex;
3. flat.

Flat, non-prominent eyes are known in virtually all Cleoninae with the exception of *Lixocleonus*, *Microlarinus*, and various *Lixus* species. Out-groups *Cnemodontus* and *Chromoderus* have markedly convex and flat eyes respectively. As for character 9, occurrence of markedly convex eyes in one of the out-groups and in primitive species of *Apleurus*, suggests that this state is plesiotypic. Decreased prominence and convexity of eyes is thus considered apotypic.

Character 11. Suberect or erect vestiture, length.— Three states are recognized:

1. absent or indistinct;
2. short;
3. long.

Out-groups lack distinct erect vestiture. Presence and subsequently increased length of vestiture are considered successively apotypic. Long suberect or erect vestiture is known in numerous genera of Cleoninae and other Curculionidae (*e.g.*, Trigonoscuta, Miloderes, *etc.*) and appears correlated with life in sand substrates.

Character 12. Rostrum, carina.— Two states are recognized:

1. present (Figs. 84–86);
2. absent (Figs. 81–83, 87–88).

Both out-groups possess a rostral carina. However, primitive *Apleurus* species lack a carina. This suggests that lack of a carina is apotypic for *Apleurus* but that presence of a carina in certain species of *Apleurus* is also apotypic.

Character 13. Rostrum, declivity at apex.— Two states are recognized:

1. flat to at most slightly declivous (Figs. 81a-83a);
2. moderately to steeply declivous (Figs. 84a-88a).

Out-groups possess a flat to slightly declivous rostral apex. A rostrum with a steeply declivous apex also occurs in many other Cleoninae.

Character 14. Maxillary palpus, setae.— Two states are recognized:

1. one large seta on palpifer, one on stipes (Fig. 64);
2. one large seta on palpifer (Fig. 65).

Out-groups possess large setae on both palpifer and stipes. Whether this seta is lacking or simply reduced in size was not determined. Other Cleoninae were not examined in detail for this character.

Character 15. Pronotum, width.— Two states are recognized (see Fig. 109):

1. width greatest at base to width at base more or less subequal to width at tubercles;
2. width distinctly greatest at tubercles.

Out-groups have pronota that are widest at the base. Pronota that are distinctly widest at the tubercles are also known in *Tetragonothorax* and *Gonocleonus*.

Character 16. Pronotum, punctation.— Two states are recognized:

1. small and shallow;
2. large and deep.

Out-groups have pronota that have small shallow punctures. No other Cleoninae examined have similarly large and deep pronotal punctures.

Character 17. Pronotum, median carina.— Two states are recognized:

1. absent;
2. present, of variable extent.

Out-groups lack a pronotal carina. Presence of a carina is widespread and common in most genera of Cleoninae.

Character 18. Prosternum, impressions and swellings.— Four arbitrarily defined states are recognized in this lineage:

1. impression anterolaterad of fore-coxal cavity present; no swelling present;
2. impression anterolaterad of fore-coxal cavity present; swelling immediately anterior to impression present, low and rounded (Figs. 82a-83a);
3. impression anterolaterad of fore-coxal cavity present; swelling immediately anterior to impression present, high (Figs. 81a, 84a-88a);
4. impression anterolaterad of fore-coxal cavity present; swelling immediately anterior to impression present, low and rounded; low rounded swelling also present immediately in front of fore-coxal cavity.

All Cleoninae possess an impression, although various in depth and extent, immediately anterolaterad of each fore-coxal cavity. Swellings, if present, are found in two locations, one, immediately in front of the fore-coxal cavity, adjacent to the impression, or two, immediately in front of the impression. Out-group *Cnemodontus* lacks swellings and *Chromoderus* is unique in Cleoninae examined in that it has swellings in front of both the fore-coxal cavity and the impression. Primitive *Apleurus* have low rounded swellings anterior to the impression, thus this state is judged plesiotypic for *Apleurus*; high swellings in front of the prosternal impressions are considered apotypic. Swellings in front of the impression are widespread in Cleoninae but are generally low and rounded except in *Stephanocleonus* and *Conorhynchus*. They are however absent from most genera. *Cosmogaster, Mecaspis, Lixocleonus, Microcleonus, Lixus* and *Cleonidius* all have a swelling of variable extent in front of the fore-coxal cavity.

Character 19. Elytra, elevation of intervals.— Two states are recognized;

1. all intervals equally flat or only slightly elevated and convex;

2. sutural interval and intervals 3, 5, 7, and 9 slightly to markedly elevated and convex.

Out-groups possess state 1. The apotypic state occurs in many genera of Cleoninae and other Curculionidae. Development of elevated and convex elytral intervals appears to be correlated with reduction in size or absence of the metathoracic wings.

Character 20. Fore-tibia of female, apex.— Two states are recognized:

1. uncus and large subapical tooth present;
2. uncus and at most only small subapical tooth present.

Out-groups each possess a large tooth in addition to the uncus. Both states are widespread in Cleoninae.

Character 21. Fore-tibia, inner margins.— Two states are recognized:

1. large denticles present;
2. with at most only small denticles present.

Cnemodontus individuals possess large fore-tibial denticles; *Chromoderus* individuals, only small denticles. Both states are widespread in other Cleoninae.

Character 22. Female abdominal sternum VIII, lateral arms.— Two states are recognized:

1. more or less straight throughout length (Figs. 49e-50e, 90b-91b, 95b-96b);
2. arcuate (Figs. 89b, 92b-94b).

Abdominal sternum VIII in females of both out-groups has lateral arms that are more or less straight. Both states are widespread in Cleoninae.

Character 23. Female abdominal tergum VII, median longitudinal carina.— Three states are recognized:

1. absent;
2. slightly developed;
3. markedly developed.

Cnemodontus lacks a longitudinal carina whereas a markedly developed carina is present in *Chromoderus*. Other Cleoninae examined lack a carina.

Character 24. Female abdominal tergum VIII, median longitudinal carina.— Three states are recognized:

1. absent;
2. slightly developed;
3. markedly developed.

Cnemodontus lacks a longitudinal carina whereas a slightly developed carina is present in *Chromoderus*. Other Cleoninae examined lack a carina.

Character 25. Male, aedeagus, curvature.— Two states are recognized:

1. markedly arcuate at base (Figs. 56a-57a);
2. more or less evenly arcuate throughout length (Figs. 97d, 98c-104c).

Both out-groups possess an aedeagus that is markedly arcuate at the base. Both states occur in *Stephanocleonus* (Ter-Minasyan 1979). The aedeagus of all *Cleonidius* species, *Lixoglyptus* and *Cylindropterus* is evenly arcuate throughout its length. Other Cleoninae have not been examined in detail for this character.

Character 26. Male, aedeagus, apex.— Two states are recognized:

1. spatulate (Figs. 56a-57a);
2. not spatulate (Figs. 97d, 98c-104c).

Both out-groups possess an aedeagus with a spatulate apex. Both states are widely distributed in Cleoninae.

Character 27. Male, aedeagus, internal sac, paired lateral sclerite at midlength.— Two states are recognized:

1. present (Fig. 57b);
2. absent (Figs. 56b, 97a-104a).

Cnemodontus males possess a distinct paired lateral sclerite at the midlength of the internal sac; *Chromoderus* males lack such sclerites. *Stephanocleonus*, *Prionorhinus*, and *Lixomorphus* males also possess such sclerites, and another unpaired sclerite, situated in a ventral position closer to the apex of the internal sac, is present in *Menocleonus, Pleurocleonus*, and *Xanthochelus*. This latter sclerite, however, is questionably homologous with the paired sclerite at midlength.

Character 28. Male, aedeagus, internal sac, shape.— Two states are recognized:

1. dorsal median pocket low and with two pairs of lobes (Figs. 56b-57b, 97a-99a);
2. dorsal median pocket high and with one pair of lobes (Figs. 100a-104a).

Cnemodontus males possess an internal sac with state 1; *Chromoderus* males possess an internal sac with state 2. The shape of the internal sac varies in other Cleoninae examined, but only in some species of *Cleonidius* is it similarly high and possessing of only a single pair of lobes.

Character 29. Male, aedeagus, internal sac, lobe A.— Two states are recognized:

1. present (Figs. 56b,c-57b,c);
2. absent (Figs. 97a,b-104a,b).

Males of each out-group possess lobe A. This character has not been examined in detail in other Cleoninae. However, lobe A is present in at least *Cleonidius*, *Lixoglyptus, Cylindropterus, Adosomus, Cleonis* and *Cyphocleonus*. It is absent from those *Stephanocleonus* examined.

Character 30. Male, aedeagus, internal sac, apical sclerite complex, median projection.— Two states are recognized:

1. long (Figs. 56d-57d, 103d-104d);
2. absent or present, but short and indistinct (Figs. 97c, 98d-101d).

Both *Cnemodontus* and *Chromoderus* males possess apical sclerite complexes with a well-developed median projection. Presence of state 2 in primitive *Apleurus* species suggests presence of state 1 within *Apleurus* is secondarily apotypic. This character has not been examined in detail in other Cleoninae.

Character 31. Male, aedeagus, internal sac, apical sclerite complex, sclerotization of base and sides of the apical pocket.— Two states are recognized:

1. well-sclerotized, dark brown in color;
2. lightly-sclerotized, pale brown in color.

Males of each out-group have the base and sides of the apical pocket markedly sclerotized. This character has not been examined in detail in other Cleoninae.

Table I. Plesiotypic and apotypic states of characters used in phylogenetic analysis of *Apleurus* species and related taxa

Character	Plesiotypic	Apotypic
1. Epistoma, apical margin	—emarginate	—rounded and produced
2. Prementum, setae	—setae lacking or only one large seta per side	—2 or more large setae per side
3. Pronotum, tubercles, development and shape of anterior angles	—tubercles absent	—tubercles present, anterior angles obtuse (2) —tubercles present, anterior angles acute (3)
4. Tarsus, ventral pilose vestiture	—present, extensive	—present, moderately reduced in extent (2) —present, markedly reduced in extent or absent (3)
5. Female, stylus, size	—present, large	—present small (2) —absent (3)
6. Female, stylus, position	—present, apical	—present, anteapical (2) —absent, anteapical sclerotized ridge present (3)
7. Male, abdominal sternum VII, dorsally directed tooth at apical margin	—absent	—present
8. Male, abdominal sternum VIII, interior angles of each sternite	—basal projection absent	—basal projection present, slightly to moderately developed (2) —basal projection present, markedly developed (3)
9. Size, length of elytra	—$X < 7.0$ mm	—$7.0 \text{ mm} < X < 9.0$ mm (2) —$X > 9.0$ mm (3)
10. Eye, prominence and convexity	—markedly convex and prominent	—slightly to moderately prominent and convex (2) —flat (3)
11. Suberect or erect vestiture, length	—absent or indistinct	—present, short (2) —present, long (3)
12. Rostrum, carina	—present	—absent
13. Rostrum, declivity at apex	—flat to slightly declivous	—moderately to steeply declivous
14. Maxillary palpus, setae	—one large seta on palpifer, one on stipes	—one large seta on palpifer
15. Pronotum, width	—greatest at base to subequal at base and tubercles	—greatest at tubercles

(continued on next page)

Table I (continued)

Character	Plesiotypic	Apotypic
16. Pronotum, punctation	—small and shallow	—large and deep
17. Pronotum, median carina	—absent	—present, various in extent
18. Prosternum, impressions and swellings	—impression anterolaterad of fore-coxal cavity; no swelling present	—impression anterolaterad of fore-coxal cavity; low rounded swelling present immediately anterior to impression (2) —impression anterolaterad of fore-coxal cavity; high sharp swelling present immediately anterior to impression (3) —impression anterolaterad of fore-coxal cavity; low rounded swelling present immediately anterior to impression and low rounded swelling present immediately in front of fore-coxal cavity (4)
19. Elytra, elevation of intervals	—all intervals equally flat or slightly elevated and convex	—sutural and intervals 3, 5, 7, and 9 slightly to markedly elevated and convex
20. Fore-tibia of female, apex	—uncus and large subapical tooth present	—uncus and at most small subapical tooth present
21. Fore-tibia, inner margins	—large denticles present	—small denticles present
22. Female abdominal sternum VIII, lateral arms	—more or less straight throughout length	—arcuate
23. Female abdominal tergum VII, median longitudinal carina	—absent	—present, slightly developed (2) —present, markedly developed (3)
24. Female abdominal tergum VIII, median longitudinal carina	—absent	—present, slightly developed (2) —present, markedly developed (3)
25. Male, aedeagus, curvature	—markedly arcuate at base	—more or less evenly arcuate throughout length
26. Male, aedeagus, apex	—spatulate	—not spatulate

(continued on next page)

Table I (continued)

Character	Plesiotypic	Apotypic
27. Male, aedeagus, internal sac, paired lateral sclerite at midlength	—present	—absent
28. Male, aedeagus, internal sac, shape	—dorsal median pocket low, two pairs of lobes	—dorsal median pocket high, one pair of lobes
29. Male, aedeagus, internal sac, lobe A	—present	—absent
30. Male, aedeagus, internal sac, apical sclerite complex, median projection	—present, long	—present, short and indistinct or absent
31. Male, aedeagus, internal sac, apical sclerite complex, sclerotization of base and sides or apical pocket	—well-sclerotized, dark brown in color	—lightly-sclerotized, pale brown in color

Table II. Character states in *Apleurus* species and related taxa

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
A. hystrix	1	1	1	2	1	1	1	1	1	1	3	2	1	2	1	2	1	2	1	2	2	2	1	1	2	1	2	2	2	2	2
A. aztecus	2	1	1	2	1	1	1	1	1	1	1	2	1	2	1	1	1	2	2	1	2	1	1	1	2	2	2	1	2	2	1
A. lutulentus	2	1	1	2	1	1	2	2	1	1	1	2	1	1	1	1	1	2	1	2	2	1	1	1	2	2	2	1	2	2	1
A. porosus	2	2	3	3	2	2	2	2	3	1	1	1	2	2	1	2	1	3	2	2	2	2	1	1	2	2	2	2	2	2	2
A. angularis	2	2	3	3	2	2	2	2	2	1	3	1	2	2	2	2	1	3	2	2	2	2	1	1	2	2	2	2	2	2	2
A. jacobinus	2	2	3	3	2	2	2	2	2	1	3	1	2	2	2	2	2	3	2	2	2	2	1	1	2	2	2	2	2	2	2
A. albovestitus	2	2	2	3	3	3	2	3	3	2	1	2	2	1	1	1	2	3	1	2	2	1	2	3	2	3	2	2	2	1	1
A. saginatus	2	2	2	3	3	3	2	3	3	2	1	2	2	1	1	1	2	3	1	2	2	1	2	3	2	2	2	2	2	1	1
Chromoderus	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	2	1	3	2	1	1	2	2	1	1	1
Cnemodontus	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Phylogenetic relationships of included species

Distribution of character states is shown in Table II.

Confidence in phylogenetic relationships of species of *Apleurus* (Figs. 234–235) is high; most primary characters exhibit very little homoplasy elsewhere in Cleoninae and the distribution of apotypic states is concordant with distributions of apotypic states in most secondary characters. Furthermore, primary characters are employed to define most major lineages and are more general in their applicability (Fig. 234) (*i.e.*, not all primary characters are used to define the same or few lineages). Because of this, confidence in recognizing homoplasy in secondary characters is enhanced and their applicability amplified.

Relationships among *Chromoderus, Cnemodontus* and *Apleurus* based on primary characters are unclear (Fig. 234). Apotypic states of secondary characters of size of female fore-tibial denticles, and presence or absence of a paired lateral sclerite at midlength in the internal sac of the aedeagus of males, suggests *Chromoderus* is the sister group to *Apleurus*, with *Cnemodontus* as sister to the *Chromoderus-Apleurus* lineage (Fig. 235). Flat eyes in *Chromoderus* and most other Cleoninae, and shared presence of swollen and convex eyes in *Cnemodontus* and most *Apleurus* is the only evidence that *Cnemodontus* is sister to *Apleurus*. However, I favour consideration of flat eyes as independently derived in *Chromoderus* and swollen and convex eyes as plesiotypic for the lineage.

Monophyly of *Apleurus* is based upon distribution of apotypic states of a number of characters, both primary and secondary. All *Apleurus* have ventral tarsal pilose vestiture moderately to markedly reduced in extent, the aedeagus of males is evenly arcuate throughout its length, the apex of the aedeagus is not spatulate, and the internal sac of the aedeagus lacks lobe A. These apotypic states all occur elsewhere in Cleoninae but not in those taxa believed closely related to *Apleurus*. Although there is homoplasy within *Apleurus*, distributions of apotypic states of other characters also support monophyly of the genus. These states are lack of a rostral carina (secondarily derived in *A. angularis-A. jacobinus-A. porosus* lineage), fore-tibia of female with small subapical second spur (secondarily derived in *A. aztecus*), and internal sac of aedeagus of male with the median projection of the apical sclerite complex absent or short and indistinct (secondarily derived in *A. albovestitus-A. saginatus* lineage).

Apleurus (Gibbostethus) hystrix is hypothesized to be the most primitive species of *Apleurus* (Figs. 234–235). It is the only species of *Apleurus* which has an emarginate epistoma; all other *Apleurus* species have the epistoma rounded. *Apleurus hystrix* is autapotypic in a number of characters (see species treatment of *A. hystrix*), and also shares, with various other species of *Apleurus*, a number of apotypic states which are best regarded as homoplasious. All of these apotypic states are of secondary characters and are otherwise found only in the *A. angularis-A. jacobinus-A. porosus* lineage or the common ancestor of this lineage and the *A. albovestitus-A. saginatus* lineage. This suggests that *A. hystrix* might be better placed with these species, but distribution of apotypic states of all primary characters in the analysis argues against this proposal (Fig. 234).

Apleurus aztecus is the next most primitive species and is sister to the remainder of the subgenus *Apleurus* (Figs. 234–235). Phylogenetic position of this species is based upon possession of a rounded epistoma, lack of a dorsally directed tooth at the apical margin of abdominal sternum VII in males, and lack of basal projections on the interior angles of each sternite of abdominal sternum VIII also in males.

Apleurus lutulentus is sister to the ancestor of the *A. angularis-A. jacobinus-A. porosus* and *A. albovestitus-A. saginatus* lineages (Figs. 234–235). This position is due to distributions of apotypic states of numerous primary as well as secondary characters. These latter five species comprise a monophyletic group divisible into two lineages as noted above. Monophyly of the *A. angularis-A. jacobinus-A. porosus* lineage is based upon possession of acute-angled pronotal tubercles, presence of rostral carina, maxillary palpus with only one large seta on palpifer, large and deep pronotal punctation, alternate elytral intervals elevated and convex, female abdominal sternum VIII with arcuate lateral arms, female abdominal tergum VIII with slight median longitudinal carina, and internal sac of aedeagus of male with sides and base of apical pocket only lightly sclerotized. Within this group of species, long erect dorsal vestiture and relative width of the basal and apical portions of the pronotum suggests an *A. angularis-A. jacobinus* sister species relationship. Widely divergent tarsal claws in all *A. angularis* and some *A. porosus* are likely a result of independent evolution or of hybridization.

The sister species status of *A. albovestitus* and *A. saginatus* (Figs. 234–235) is strongly supported by the lack of a stylus on gonocoxite II of the female and by markedly developed basal projections on the interior angles of each sternite of abdominal sternum VIII in males. Distribution of apotypic states of numerous secondary characters supports this relationship.

Alternative hypotheses

The only apparent possible alternative hypothesis of phylogenetic relationship to that presented in Figure 235 concerns the placement of *Apleurus hystrix*. Although primary characters indicate a primitive phylogenetic position for this species, there are a number of secondary character states homoplasious with the *A. porosus-A. jacobinus-A. angularis* lineage which could be interpreted as suggesting inclusion in that lineage.

Genus *Cleonidius* Casey

Character evolution

Character state 1 for each character is considered plesiotypic; other states are considered apotypic at various levels (see Table III).

Primary characters

Character 1. Submentum, degree of ventral swelling.— Two states of this character are recognized:

1. flat, not ventrally swollen (Figs. 137a-142a, 145a-156a);
2. swollen ventrally (Figs. 143a-144a).

Out-groups and all Cleoninae examined possess a submentum that is not swollen ventrally.

Character 2. Rostrum, ratio of length to width in females.— Four arbitrarily defined states are recognized (see Fig. 198):

-1. very elongate, $X<0.45$ (Fig. 141);
1. moderately elongate, $0.45<X<0.65$ (Figs. 137–140, 142–144, 148–155);
2. short, robust, $0.65<X<0.77$ (Figs. 145, 156);
3. very short, very robust, $X>0.77$ (Figs. 146–147).

Out-groups possess a rostrum that is moderately elongate. Successively shorter and more robust rostra are considered increasingly apotypic. A very elongate rostrum is also considered apotypic. States of this character are widely distributed in Cleoninae although in general members of the tribe Lixini possess a more elongate, narrow rostrum than do members of the Cleonini. Rostral length in Molytinae of phylogenetic interest varies from moderately to very elongate.

Character 3. Rostrum, degree of lateral swelling.— Two states are recognized:
1. not swollen at midlength in dorsal view (Figs. 137b-142b, 145b-156b);
2. swollen at midlength in dorsal view (Figs. 143b-144b).

Out-groups possess state 1. No other Cleoninae or Molytinae of phylogenetic concern examined possess a similarly laterally expanded rostrum.

Character 4. Frons/vertex, surface sculpture.— Three states of this character are recognized:
1. area behind eye with wrinkles of cuticle;
2. area behind eye with a curved sulcus (Fig. 150a);
3. area behind eye with a deep, straight sulcus (Fig. 139).

Other than various punctures, out-groups and most Cleoninae possess at most only a few wrinkles of the cuticle behind the eye. Some African *Lixus* possess a very deep elongate impression above the eye. State 3 is unlikely homologous with states 1 and 2.

Character 5. Elytra, scale pattern.— Three states of this character are recognized:
1. marginal; intervals 9 to 11 with dense, moderately large, white scales, otherwise moderately densely and uniformly covered with fine white scales which are smaller than those on intervals 9 to 11 (Figs. 118–123);
2. vittate; intervals other than 9 to 11 with scales as large as those on intervals 9 to 11 (Figs. 127–128, 130–136);
3. mottled; with irregularly scattered and sized patches of large white scales (Figs. 124–126, 129).

Of the out-groups, *Cylindropterus* lacks a distinct scale pattern whereas *Lixoglyptus* species both have elytral scale patterns that are of the marginal type. Most *Lixus* species possess uniformly dense small fine scales on the elytra although elytra of individuals of a few species are distinctly vittate. Members of the Cleonini have various elytral scale patterns, but these are not recognizable as any of the states discussed herein for *Cleonidius*. State 1 is considered plesiotypic based largely on its occurrence in *Lixoglyptus* species. This state is assumed to represent an intermediate stage between the uniformly distributed small fine scales of most *Lixus* and the vittate state of certain *Cleonidius* species. The mottled state is then assumed to be a result of decreased scale size at various positions of the vittate pattern and is homoplasious within *Cleonidius* although restricted to a single species group.

Character 6. Abdomen of female, ornamentation of abdominal sternum VII.— Two states of this character are recognized:
1. basal margin uniformly flat;
2. basal margin at middle internally (dorsally) with variously developed glabrous shiny tubercle.

Out-groups and all other Cleoninae examined possess state 1. Within *Cleonidius* there is variation within and between species in the degree of development of the tubercle. Very slightly developed tubercles or glabrous patches are also present at the basal margin of abdominal sterna V and VI in some specimens, but in these individuals, the most markedly developed tubercle is that on sternum VII.

Character 7. Male, aedeagus, internal sac, height of dorsal median pocket.— Two states of this character are recognized:
1. low (Figs. 111a-112a, 177a-179a, 183a-196a);
2. high (Figs. 180a-182a).

Out-groups possess a low dorsal median pocket. Both states occur elsewhere in Cleoninae but the character has not been examined in detail.

Character 8. Male, aedeagus, internal sac, apex of dorsal median pocket.— Two states of this character are recognized:
1. rounded or truncate in dorsal view (Figs. 111b-112b, 177b-191b, 196b);
2. emarginate or sinuate in dorsal view (Figs. 192b-195b).

Out-groups possess a dorsal median pocket with a rounded to truncate apical margin. Other Cleoninae have not been examined in detail for this character.

Character 9. Male, aedeagus, internal sac, lobe B.— Two states of this character are recognized:
1. present (Figs. 111a-112a, 177a-179a, 183a-196a);
2. absent (Figs. 180a-182a).

Out-groups possess a lobe B on the internal sac. Other Cleoninae have not been examined in detail for this character although both states are found in *Apleurus* species, *Cleonis* and *Cnemodontus* possess a lobe B, and the lobe is lacking from *Stephanocleonus* species examined and *Chromoderus*.

Character 10. Male, aedeagus, internal sac, lobe D.— Two states of this character are recognized:
1. present (Figs. 111a-112a, 177a-179a, 183a-196a);
2. absent (Figs. 180a-182a).

The internal sac of each out-group possesses a lobe D, however, the lobe is small in *L. spartii*. Lobe D is present in all species of *Apleurus*, *Cleonis*, *Stephanocleonus*, *Chromoderus*, and *Cnemodontus* examined.

Secondary characters

Character 11. Size, length of elytra.— Two arbitrarily defined states of this character are recognized (see Fig. 197):
1. large, X>9mm;
2. small, X<9mm.

Individuals of both out-groups are large in size but distribution of states of primary characters within *Cleonidius* suggests large size of some *Cleonidius* species is secondarily apotypic. Within and between species variation in size is extensive in most Cleoninae.

Character 12. Rostrum, punctation.— Two states are recognized:
1. apical portion with punctures moderately dense and moderately deep;
2. apical portion with punctures sparse, small and shallow.

Out-groups each possess state 1. State 2 occurs in most species of *Lixus* and appears associated with an elongate-narrow rostrum. The apotypic state of this character is homoplasious within *Cleonidius*.

Character 13. Rostrum, median tumescence.— Three states are recognized:
1. absent (Figs. 139b, 141b-142b, 152b);
2. present, slightly developed (Figs. 140b, 143b-144b, 146b-149b);
3. present, markedly developed (Figs. 137b-138b, 145b, 150b-151b, 153b-156b).

Out-groups each possess state 1. Increased degree of development of the median tumescence is considered increasingly apotypic. There is extensive homoplasy in this character.

Character 14. Rostrum, lateral margins.— Two states are recognized:
1. rounded;

2. sharp.

Out-groups each possess state 1. Species of *Lixus* and *Larinus* examined possess rounded lateral margins; species of Cleonini have either state.

Character 15. Pronotum, anterolateral margins.— Three states are recognized:

1. postocular lobe rounded, well-developed (Figs. 137a-139a, 141a-144a, 146a-151a);
2. postocular lobe rounded, slightly developed (Figs. 140a, 152a);
3. postocular lobe absent, margin straight (Figs. 145a, 153a-155a).

Out-groups and most other Cleoninae possess well-developed postocular lobes. Successively less markedly developed postocular lobes are increasingly apotypic. Acute pronotal postocular projections, although present in some Cleoninae which lack rounded postocular lobes (*e.g.*, *Lixus*, *Apleurus*), are not present in those *Cleonidius* species that lack a postocular lobe. This character is homoplasious in *Cleonidius*.

Character 16. Pronotum, impressions.— Two states are recognized:

1. basal median area shallowly to moderately deeply impressed;
2. basal median area deeply impressed, lateral margins variously longitudinally impressed.

State 1 occurs in both out-groups. Similar sculpture is not present in other Cleoninae examined.

Character 17. Suberect or erect vestiture, length.— Three states are recognized:

1. absent (Figs. 140a, 152a, 156a);
2. present, short to moderate in length (Figs. 138a-139a, 145a-149a, 151a, 153a);
3. present, long (Figs. 137a, 141a-144a, 150a, 154a-155a).

Both out-groups and many *Lixus* lack suberect or erect vestiture. Increased length of vestiture is considered as increasingly apotypic. There is extensive homoplasy in this character in *Cleonidius* and in Cleoninae in general.

Character 18. Tarsus, ventral pilose vestiture.— Three states are recognized:

1. extensive;
2. moderately reduced in extent;
3. markedly reduced in extent, to absent.

Both out-groups, all *Lixus* species examined, many Cleonini, and Molytinae possess extensive ventral pilose vestiture. Successive stages in reduction of vestiture are considered as increasingly apotypic. Reduced ventral pilose vestiture is otherwise confined to members of Cleonini. This character is homoplasious in *Cleonidius*.

Character 19. Foretibia of female, inner margin.— Two states are recognized:

1. large denticles present (as in Fig. 144c);
2. only small denticles present (as in Fig. 143c).

Both out-groups possess large denticles on the inner margin of the foretibia. Distribution of states of primary characters within *Cleonidius* suggests presence of large denticles in some species of *Cleonidius* is secondarily apotypic and homoplasious. Both states of this character occur in other Cleoninae.

Character 20. Female abdominal sternum VIII, length of basal arm.— Two states are recognized:

1. long (Figs. 165, 167–169, 174);
2. short (Figs. 157–164, 166, 170–174, 175–176).

Out-groups each possess a long basal arm. Both states of this character are widely distributed in Cleoninae, but as Molytinae examined possess a long basal arm, this state is likely plesiotypic for Cleoninae. This character is homoplasious in *Cleonidius*.

Character 21. Female abdominal sternum VIII, shape of lateral arms.— Two states are recognized:

1. arcuate (Figs. 163, 165–175);
2. more or less straight, divergent (Figs. 157–162, 164, 176).

Out-groups each possess state 1. This character is homoplasious in *Cleonidius*. Both states occur in other Cleoninae.

Character 22. Male, aedeagus, internal sac, lobe E.— Two states are recognized:

1. present (Figs. 111a, 177a-179a, 183a-196a);
2. absent (Figs. 112a, 180a-182a).

The internal sac of *Cylindropterus* possesses a lobe E; that of *Lixoglyptus* lacks lobe E. Lobe E is present in species of *Cleonis*, *Cnemodontus*, some *Apleurus* and at least some *Stephanocleonus*. Distribution of states of primary characters within *Cleonidius* suggests presence of lobe E be considered plesiotypic.

Table III. Plesiotypic and apotypic states of characters used in phylogenetic analysis of *Cleonidius* species and related taxa

Character	Plesiotypic	Apotypic
1. Submentum, degree of ventral swelling	—flat	—swollen
2. Rostrum, ratio of length to width	—moderately elongate, $0.45 < X < 0.65$	—very elongate, $X < 0.45$ (-1) —short, robust, $0.65 < X < 0.77$ (2) —very short, robust, $X > 0.77$ (3)
3. Rostrum, degree of lateral swelling	—not swollen at midlength	—swollen at midlength
4. Frons/vertex, surface sculpture	—area behind eye with wrinkles of cuticle	—area behind eye with curved sulcus (2) —area behind eye with deep, straight sulcus (3)
5. Elytra, scale pattern	—marginal (see text)	—vittate (see text) (2) —mottled (see text) (3)
6. Abdomen of female, ornamentation of abdominal sternum VII	—basal margin uniformly flat	—basal margin at middle internally with variously developed glabrous shiny tubercles
7. Male, aedeagus, internal sac, height of dorsal median pocket	—low	—high
8. Male, aedeagus, internal sac, apex of dorsal median pocket	—rounded or truncate in dorsal view	—emarginate or sinuate in dorsal view
9. Male, aedeagus, internal sac, lobe B	—present	—absent
10. Male, aedeagus, internal sac, lobe D	—present	—absent
11. Size, length of elytra	—$X > 9$ mm	—$X < 9$ mm
12. Rostrum, punctation	—apical portion with punctures moderately large, dense and moderately deep	—apical portion with punctures sparse, small and shallow
13. Rostrum, median tumescence	—absent	—present, slightly developed (2) —present, markedly developed (3)
14. Rostrum, lateral margins	—rounded	—sharp

(continued on next page)

Table III (continued)

Character	Plesiotypic	Apotypic
15. Pronotum, anterolateral margins	—postocular lobe rounded, well-developed	—postocular lobe rounded, slightly developed (2) —postocular lobe absent, margin straight (3)
16. Pronotum, impressions	—basal median area shallowly to moderately deeply impressed	—basal median area deeply impressed, lateral margins variously longitudinally impressed
17. Suberect or erect vestiture, length	—absent	—present, short to moderate (2) —present, long (3)
18. Tarsus, ventral pilose vestiture	—present, extensive	—present, moderately reduced (2) —present, markedly reduced, or absent (3)
19. Fore-tibia of female, inner margin	—large denticles present	—small denticles present
20. Female abdominal sternum VIII, length of basal arm	—long	—short
21. Female abdominal sternum VIII, shape of lateral arms	—arcuate	—more or less straight, divergent
22. Male, aedeagus, internal sac, lobe E	—present	—absent

Table IV. Character states in *Cleonidius* species and related taxa

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
C. erysimi	1	1	1	1	1	2	1	1	1	1	2	1	3	1	1	1	3	2	2	2	2	1
C. eustictorrhinus	1	1	1	1	2	2	1	1	1	1	2	1	3	1	1	1	2	2	2	2	2	1
C. pleuralis	1	1	1	3	1	2	1	1	1	1	2	2	1	1	1	1	2	1	2	2	2	1
C. subcylindricus	1	1	1	1	1	2	2	1	2	2	2	1	2	1	2	1	1	1	2	2	2	2
C. longinasus	1	-1	1	1	1	2	2	1	2	2	2	2	1	1	1	1	3	1	2	2	2	2
C. texanus	1	1	1	1	1	2	2	1	2	2	2	2	1	1	1	1	3	1	2	2	2	2
C. americanus	2	1	2	1	2/3	2	1	1	1	1	2	2	2	1	1	1	3	2	2	2	1	1
C. frontalis	2	1	2	1	2/3	2	1	1	1	1	2	1	2	1	1	1	3	2	1	2	2	1
C. canescens	1	2	1	1	2/3	2	1	/	1	1	2	1	3	1	3	1	2	2	2	1	1	1
C. infrequens	1	3	1	1	2	2	1	1	1	1	2	1	2	2	1	1	2	2	1	2	1	1
C. puberulus	1	3	1	1	2	2	1	1	1	1	2	1	2	1	1	1	2	3	2	1	1	1
C. collaris	1	1	1	1	3	2	1	1	1	1	2	1	2	2	1	2	2	2	2	1	1	1
C. notolomus	1	1	1	1	2	2	1	1	1	1	2	1	2	2	1	2	2	2	2	1	1	1
C. poricollis	1	1	1	1/2	2	2	1	1	1	1	2	1	3	1	1	1	3	1	2	2	1	1
C. calandroides	1	1	1	1/2	2	2	1	1	1	1	2	1	3	1	1	1	2	1	2	2	1	1
C. boucardi	1	1	1	1	2	2	1	2	1	1	1	1	1	1	2	1	1	1	1/2	2	1	1
C. trivittatus	1	1	1	1	2	2	1	2	1	1	1	1	3	1	2/3	1	2	2	1/2	2	1	1
C. placidus	1	1	1	1	1	2	1	2	1	1	1	1	3	1	2/3	1	3	2	2	1	1	1
C. quadrilineatus	1	1	1	1	2	2	1	2	1	1	2	1	3	1	3	1	3	2	2	2	1	1
C. vibex	1	2	1	1	2	2	1	1	1	1	2	1	3	2	1	1	1	3	2	1	2	1
Lixoglyptus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
Cylindropterus	1	1	1	1	/	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Phylogenetic relationships of included species

Distribution of character states is shown in Table IV.

In contrast to *Apleurus*, confidence in phylogenetic relationships in *Cleonidius* is low, due to the low numbers of primary characters as compared to the number of species in the genus, but especially the level at which the primary characters are applicable. Seven of the ten primary characters apply to lineages of only 2 or 3 species; only 3 apply at more general levels, one of which is used to define the monophyly of *Cleonidius* (Fig. 236). This leaves a large number of relationships subject to resolution only on the basis of secondary characters (Fig. 237). Unfortunately, secondary characters containing any phylogenetic information are also not numerous, few are applicable at a general level, and many, especially the latter, are subject to marked homoplasy within *Cleonidius* (Fig. 237).

Basal relationships among *Cleonidius*, *Cylindropterus* and *Lixoglyptus* are very unclear and, as discussed elsewhere (see "Phylogenetic relationships of genera of New World Cleonini") are left as unresolved (Fig. 237). Monophyly of *Cleonidius* however, is strongly supported by the presence of a variously internally (dorsally) developed glabrous shiny median tubercle at the base of abdominal sternum VII of the female. All secondary characters used in support of monophyly of *Cleonidius* involve homoplasy within *Cleonidius* (Fig. 237).

Relationships of the Palearctic species component of *Cleonidius* are herein left as unresolved because of unavailability of series of specimens of *C. vibex* and lack of specimens of other Palearctic species that are potentially *Cleonidius*. Further examination of Palearctic taxa should resolve the placement of the Palearctic species component of *Cleonidius*.

Among species groups, monophyly of each of the *C. boucardi* and *C. poricollis* groups is substantiated by a single primary character (Fig. 236) and also in the *C. boucardi* group by an additional two secondary characters (Fig. 237). Other species groups are defined as monophyletic strictly on the basis of secondary characters, some of which involve extensive homoplasy. Monophyly of the *C. poricollis* group, which contains only two species, is based upon the primary character of presence or absence of a curved sulcus behind the eye. The apotypic state is found in both *C. poricollis* and *C. calandroides*, but, not in all individuals of either species. Monophyly of the *C. boucardi* group is based upon the emarginate or sinuate apex of the dorsal median pocket of the internal sac of males, larger size (secondarily reduced in *C. quadrilineatus*), and reduced pronotal postocular lobes (homoplasious in *C. canescens*). In the *C. americanus* group, monophyly is based upon the ventral tarsal pilose pads being reduced in extent (homoplasious in other *Cleonidius* and other Cleoninae). High incidence of brachyptery and of a mottled elytral scale pattern may further support monophyly of this group. Monophyly of the *C. erysimi* group is based upon apotypic states of two secondary characters of abdominal sternum VIII of female; lateral arms straight; and basal arm short. Both of these characters exhibit homoplasy elsewhere in *Cleonidius*.

Within the *C. erysimi* group, three primary characters indicate that *C. subcylindricus*-*C. texanus*-*C. longinasus* comprise a monophyletic group. Relationships of this lineage to the rest of the species group, however, are unclear (Fig. 237). *Cleonidius erysimi* and *C. eustictorrhinus* are considered sister-species, and this lineage along with *C. pleuralis* and the *C. subcylindricus*-*C. texanus*-*C. longinasus* lineage, are left as elements of an unresolved trichotomy. *Cleonidius texanus* and *C. longinasus* are regarded as sister-species because they lack large punctures apically on the rostrum and have long dorsal erect vestiture. *Cleonidius subcylindricus* is therefore sister to the *C. texanus*-*C. longinasus* lineage.

In the *C. americanus* group, primary characters support only the sister-species status of each of *C. americanus* and *C. frontalis*, and *C. infrequens* and *C. puberulus* (Fig. 236); all other relationships are based on secondary characters (Fig. 237). *Cleonidius notolomus* and *C. collaris* are regarded as sister-species based upon pronotal sculpture although the state in *C. collaris* is much more extreme in its irregularity than that in *C. notolomus*. A moderately broad rostrum is used to propose monophyly of the *C. canescens-C. infrequens-C. puberulus-C. notolomus-C. collaris* lineage, and sharp lateral margins of the rostrum, the sister group status of the *C. infrequens-C. puberulus* and *C. notolomus-C. collaris* lineages. Acceptance of the *C. notolomus-C. collaris* lineage as having a secondarily plesiotypic, more elongate-narrow rostrum and of *C. puberulus* having secondarily rounded lateral rostral margins is necessitated by the sister-species status of *C. puberulus* and *C. infrequens*. Other interpretations require that these two not be sister-species and are in my view less parsimonious than that presented above. *Cleonidius canescens* is thus the sister-species of the *C. infrequens-C. puberulus-C. notolomus-C. collaris* lineage and the *C. americanus-C. frontalis* lineage sister to the remainder of species in the *C. americanus* group.

In the *C. boucardi* group, *C. boucardi* is considered sister to the remaining three species in the group based upon the ventral tarsal pilose pads being reduced in extent and the pronotal postocular lobes also reduced (both homoplasious in *Cleonidius*) in the latter three species. *C. quadrilineatus* and *C. placidus* are considered sister-species, with *C. trivittatus* as sister to that lineage, because of long dorsal erect vestiture in the former two species.

In the reconstructed phylogeny of *Cleonidius*, great emphasis is placed on scale pattern because this is the only primary character applicable in a broad or general sense within this genus (Fig. 236). As a result, misinterpretation of distributions of states of other characters are influenced by the topology established on the basis of this one character. If this character is misinterpreted, radical changes in the reconstructed phylogeny would result.

Alternative hypotheses

Alternative hypotheses of phylogeny in *Cleonidius* mainly concern phylogenetic relationships of the species in the *C. boucardi* group. In all other species groups, hypothesized phylogenetic relationships are largely consistent with specific instances of character state intergradation between geographically approximate species (*i.e.*, instances of intergradation are between geographically approximate sister-species) and with geographical distribution of lineages in general (*i.e.*, sister lineages are largely geographically approximate). In the *C. boucardi* group however, this is not so because character state intergradation is marked between each of *C. boucardi, C. trivittatus*, and *C. placidus*, none of which are hypothesized as sister-species of any one of the others (see Fig. 237). To be consistent with patterns of intergradation, *C. quadrilineatus* would have to be the sister-species of a lineage composed of *C. boucardi, C. trivittatus*, and*C. placidus*, an unfavourable revision in the hypothesized phylogeny that would require additional and unsatisfying homoplasy in the characters of form of the anterolateral margins of the pronotum, and extent of ventral pilose tarsal vestiture, and, reconsideration of long suberect or erect body vestiture as plesiotypic for the species group. Ability to interbreed, presumably the likely cause of the intergradation, is a plesiotypic feature and thus cannot be used as evidence of common ancestry although it may be tempting to do so.

Alternatively, the observed intergradation in character states among *C. boucardi, C. trivittatus*, and *C. placidus*, geographically approximate distributions of the three, and association with Leguminosae for at least *C. trivittatus* and *C. placidus* (plant relationships are unknown in *C. boucardi*), could warrant recognition of only a single species composed of three geographically distinct forms.

I do not favour either of these approaches, the former because it necessitates additional homoplasy, and the latter because it necessitates extensive polymorphism in a number of otherwise phylogenetically informative characters. I prefer recognition of three species, and attribute the geographical inconsistency to the host shift from Leguminosae to Roseaceae/Rhamnaceae in *C. quadrilineatus*, which has likely promoted structural differentiation in that species and which has permitted redispersal such that *C. quadrilineatus* is now largely sympatric with other members of the *C. boucardi* group.

EVOLUTIONARY ANALYSIS: BIOGEOGRAPHY

Methods of Biogeographic Analysis

Historical and ecological factors combine to produce the observed distributions of plants and animals, the explanation of which is the goal of the science of biogeography. Unfortunately many past studies of biogeography attempt to explain the distributions observed in terms of only one of ecology or history (Endler, 1982). Distinguishing the relative roles of these factors must at least be considered although most agree it is very difficult to separate the effects of the two and to estimate their relative roles (Endler, 1982; Vuilleumier and Simberloff, 1980). The present study is no exception and my approach, although attempting to encompass aspects of both historical and ecological biogeography, will be largely historical in its focus.

Knowledge of distribution and aspects of natural history combine with knowledge of phylogenetic relationships and of earth history to allow for discussion of the historical biogeography and ultimately, the evolutionary history of the taxon in question. Ecological biogeography on the other hand does not require knowledge of phylogeny and earth history, but rather ecological theory and principles. Systematists and ecologists are the proponents of the historical and ecological approaches respectively. Rarely are the two approaches combined in a single study and relative roles assessed. This is brought about simply by the nature of the data bases because systematists frequently have not carried out the detailed sampling necessary for the application of ecological theory. Similarly, more often than not, ecologists do not have the knowledge of phylogeny that predicates all historical biogeographic analyses.

In ecological biogeography, the units selected for study are usually communities or various guilds of taxa that share association with a particular resource, be it habitat, food, geographic area, *etc.* (Cody and Diamond, 1975). Ecological biogeographers are primarily concerned with temporally proximate factors that determine the composition of the species assemblage but not the origins of these same factors. Little concern or attention is expressed or given to the phylogenetic relationships of the constituent taxa and thus there is a large or even total disregard for historical components because notions about the latter can only be developed in terms of detailed knowledge of phylogeny. Less frequently, ecological determinants of distributions of constituents of monophyletic groups, say a genus or family, have been studied, although rarely if at all with specific reference to detailed phylogenetic relationships.

Much of ecological biogeography addresses questions of dynamics and proximal origins of diversity, best applicable to islands or insular situations. Diversity patterns on continents are much more complex and are not so easily studied. Unfortunately, knowledge of population dynamics and detailed data about natural history attributes, permitting determination of niche breadths, are required for much meaningful ecological biogeography to be conducted (Cody, 1975; Pianka, 1975). Because of this, the approach I will take herein is only one of examination of natural history attributes and distributions, with specific reference to present environmental parameters.

Historical biogeographers, on the other hand, recognize and stress the need for knowledge of phylogeny, but generally at the expense of ignoring the role ecology might play in determining distributions. Indeed, to many, knowledge of phylogeny is essential prior to attempts at any meaningful historical biogeography. Wiley (1981) has noted three schools of historical biogeographers: 1, evolutionary; 2, phylogenetic; 3, vicariance (or panbiogeographic, although Croizat [1982] has disputed this). Detailed knowledge of phylogeny and strictly monophyletic groups are the units of study for adherents of phylogenetic and vicariance biogeography and stress vicariance and allopatric speciation. Evolutionary biogeography however, emphasizes the role of dispersal with little or no regard for speciation mechanism or for details of phylogeny. This latter is not employed by many contemporary biogeographers for it is the approach resulting in the narratives and "scenarios" frowned upon for their *ad hoc* nature, and lack of applicability and rigour. Heuristic advantages of the phylogenetic and vicariance schools of biogeography are consistent with the advantages of a phylogenetic approach to phylogeny reconstruction and are discussed in more detail by Wiley (1981), Patterson (1981), and Platnick and Nelson (1978).

Ball (1975) recognizes three phases through which biogeographic studies pass: 1, descriptive or empirical phase; 2, narrative phase; and 3, analytical phase. These phases, as noted elsewhere herein and by Patterson (1981), apply equally well to systematic studies, especially methods of phylogeny reconstruction. Descriptive or empirical biogeography is simply the data base. What are the extant distributions and natural history attributes of the taxa in question? What habitats do they occupy? What do they eat? When are they active?

In large part, narrative and analytical phases contrast inductive and hypothetico-deductive approaches to biogeographic studies. Narrative explanations, or general evolutionary "scenarios" as they have been called by Eldredge (1979), have frequently been criticized as pseudo-science or bad science because of their unfalsifiable and *ad hoc* nature, and for their explanatory value, which is, more often than not, concerned only with particulars as they apply to the taxon in question (Goudge, 1961; Hull, 1974; Ball, 1975; Eldredge, 1979; Eldredge and Cracraft, 1980; Brown and Gibson, 1983). General applicability is not usually a concern of narrative explanations, although there is no reason why it should not be.

Consequently, Eldredge (1979) notes two ways of improving these "scenarios". Firstly, base them more explicitly on knowledge of phylogenetic relationships, and secondly, eliminate some if not all of the more purely speculative elements. To these suggestions, I add a third; formulate explanations as hypotheses in terms that are testable, predictive, and have potential for more general applicability than just the taxon in question. With these improvements in mind, "scenarios" are capable of producing ideas that can be subsequently rigorously tested in a hypothetico-deductive manner for acceptance as general scientific facts, ideally of widespread applicability and significance. In essence, this is the analytical phase of Ball (1975).

In my analysis of historical biogeography I employ a phylogenetic approach to place aspects of the phylogeny of North American Cleoninae in a geographic perspective and thus come to some degree of understanding of the geographic history of that specific taxon. Resultant potential generalizations and predictions based on these results are enumerated, discussed and formulated as hypotheses of general potential utility.

A vicariance approach, examining distribution patterns of other North American arid land taxa and the plotting of generalized tracks will not be attempted herein but should be carried out as more studies of such taxa, that include a phylogenetic basis, become available.

Genus *Apleurus* Chevrolat

Diversity patterns

The genus *Apleurus* is represented in arid land habitats of southwestern North America and Mexico by eight species placed in two subgenera. Maximum species diversity is in southern California, northwestern Mexico (including Baja California Norte), southern Arizona and southern New Mexico (Fig. 230). Diversity decreases beyond this area especially to the east and the north. Species of *Apleurus* do not occur north of 45°N latitude, east of 95°W longitude, or south of 15°N latitude (Fig. 230).

Five of the eight species are stenotopic, variously restricted in their distributions and of these five, only two, *A. jacobinus* and *A. hystrix* are macrosympatric. The remaining three species, *A. lutulentus*, *A. angularis*, and *A. albovestitus*, are eurytopic, widespread and broadly sympatric with each other and various of the five geographically restricted species. Gross geographic range overlap is relatively low with 12 of 28 possible species pairs (42.8%) having at least partial sympatry. Nine of the 12 sympatric species pairs exhibit overlapping distributions; three are nested (the area of distribution of one species occurring entirely within the area of distribution of the other).

Habitat associations

Habitat associations of the species are varied, ranging from grasslands to desert-grassland transitional habitats or deserts in eurytopic species (three of the eight); others are more stenotopic, found only in grasslands, desert-grassland transitional habitats, or in deserts (five of the eight) (Fig. 238).

Apleurus aztecus is a mesquite-grassland inhabitant in central México. *Apleurus lutulentus*, although also found in desert-grassland transitional habitats, is primarily a mesquite-grassland and grassland inhabitant as evidenced by its more easterly distribution into eastern Texas, Oklahoma and Kansas and disjunct southerly distribution into central México, but not in the Mexican portion of the Chihuahuan desert (Fig. 207). *Apleurus angularis* is also found in grasslands, however, in contrast to *A. lutulentus*, does not extend as far east or south as does that species. Rather, *A. angularis* extends further west and north into Great Basin desert. *Apleurus jacobinus* and *A. porosus* are semi-desert and semi-desert to desert inhabiting species respectively. *Apleurus albovestitus* is distributed even more to the west than is *A. angularis*. It occurs in most western semi-desert and desert, and desert-grassland transitional habitats. *Apleurus saginatus* is a desert-grassland inhabitant bordering the eastern Sonoran Desert region (Fig. 206). *Apleurus hystrix* is a sand dune inhabiting species in the California semi-desert habitat.

Relative measures of association of species with particular types of habitats reveals a slightly higher level of association with desert-grassland transitional habitats than with others. These measures were obtained by summing the total number of species of *Apleurus* occupying a particular habitat type scoring one for a marked association (solid box in Fig. 238) and one-half for a less marked association (half box in Fig. 238). This number is then divided by the number of possible associations with that habitat type to give a relative measure of the degree to which species of the genus occur in the various habitat types. Measures of association with the four desert habitats is 0.156; with semi-deserts, 0.250; with desert-grassland transition habitat, 0.375; and, with mesquite-grasslands and grasslands, 0.313.

Plant associations

Details of host plant associations are largely unknown for all species and so all plant associations, many likely accidental, have been used as indicative of the probable taxonomic range of host plants (Fig. 239). Adults of all species are found primarily or exclusively on Compositae although in some species, especially *A. albovestitus*, adults are found sporadically on a variety of other types of plants as well. Other than Compositae, Chenopodiaceae and Leguminosae constitute the bulk of the remainder of the associations. Clear associations with taxa lower than the hierarchical level of family are not evident.

Altitudinal zonation

Altitudinal ranges are shown as a Hubbs-Hubbs diagram (Fig. 232). Although species may be represented over an extensive range of altitudes, most members of each species are found over a narrower part of this range.

Apleurus hystrix, *A. jacobinus* and *A. porosus*, species restricted to the Pacific coastal areas, are found over a much narrower range of altitudes than are more widespread species. Altitudinal ranges of these three coastal species overlap extensively. On the other hand, among the remaining species, only *A. lutulentus* and *A. aztecus* have altitudinal ranges which overlap extensively. The three remaining species, *A. angularis*, *A. albovestitus*, and *A. saginatus*, have altitudinal ranges which differ from each other, and from any other species in the genus. There is, in general, little overlap in the altitudinal ranges of species of *Apleurus* (Fig. 232). There is also a trend towards occupation of lower altitudes by increasingly derived species in the genus.

Seasonal occurrence

Patterns of adult seasonal occurrence are broad with *A. angularis*, *A. jacobinus*, *A. albovestitus* and *A. saginatus* found throughout the year. *Apleurus porosus* adults are found from January to November and are likely active throughout entire year. On the other hand, *A. lutulentus* adults are known from March to October; *A. aztecus* from June to August; and *A. hystrix* from February to July. Few records are available, however, for these last two species. Detailed life histories are unknown for all species.

Co-existence

Consideration of these various niche dimensions as a group reveals that no two species of *Apleurus* share the same or largely overlapping ranges in all niche dimensions. Statistical measures aside, inspection shows species differences along the dimensions of altitude, geographic distribution, and habitat association. All species share a plant association with Compositae. Macrosympatric species differ in various aspects of altitudinal range and habitat association. Species with overlapping altitude ranges are allopatric or differ in habitat association. In general, niche overlap between species of *Apleurus* is low.

Wing length polymorphism

At least some adult members of most *Apleurus* species lack wings; 97.9% of *A. lutulentus*, 4.5% of *A. angularis*, 99.8% of *A. albovestitus*, and all *A. saginatus* are the only macropterous individuals known. Adults examined of species of restricted distribution such as *A. hystrix*, *A. aztecus*, *A. jacobinus* and *A. porosus* are all apterous. The most widespread species, *A.*

albovestitus, *A. lutulentus* and *A. angularis* have various percentages of macropterous individuals. These individuals are scattered throughout the species ranges and are not restricted in their distributions.

Genus *Cleonidius* Chevrolat

Diversity patterns

The genus *Cleonidius* is represented in North and Central America by 19 species; a single species has so far been recognized from the Palearctic Region but is not considered further in the biogeographic discussions following. Maximum species diversity is in the southwestern United States, especially southern and central California, southern Nevada, Arizona, southern Utah, New Mexico, Colorado and western Texas (Fig. 231). Diversity decreases slightly to the north in northern Utah and Wyoming into eastern Washington and western Montana, but more markedly into Oregon and western Washington to the west, into eastern Texas, Oklahoma and Kansas to the east, and especially to the south into México (Fig. 231) (although this may prove an artifact of insufficient collecting). Species of the genus extend north into southern Canada and south as far as Honduras; two species occur along the east coast of North America.

Species of *Cleonidius* tend to be more or less widespread in their geographic distributions. I consider only five of the nineteen species restricted in their geographic distributions. Three of these five, *C. americanus*, *C. placidus*, and *C. eustictorrhinus* are macrosympatric and found only in California; *C. collaris* is found only in eastern Colorado and nearby localities in adjacent states; and *C. calandroides* is found only along the northern Atlantic coast. Three other species (*C. puberulus*, *C. notolomus*, and *C. infrequens*) are slightly less restricted in their distributions. Of the remaining 11 species, 10 are moderately to very widespread in the western or southwestern United States and Mexico and are largely macrosympatric with each other and with various of the species with restricted distributions. One species, *C. subcylindricus*, is found along the Atlantic Coastal Plain. One of the six species in the *C. erysimi* group, one of two in the *C. poricollis* group, one of four in the *C. boucardi* group, and five of seven in the *C. americanus* group have more or less restricted distributions.

Gross geographic range overlap is slightly more extensive than in *Apleurus*. In the *C. erysimi* group, eight of 15 possible species pairs have at least partial sympatry (three overlapping, five nested); two of six comparisons in the *C. boucardi* group (two overlapping) and 11 of 21 in the *C. americanus* group (seven overlapping, four nested) result in at least partial sympatry. Species in the *C. poricollis* group are allopatric. For the genus *Cleonidius* as a whole, 87 of 171 possible combinations result in at least some sympatry (62 overlapping, 25 nested). In other words, a single species is on average macrosympatric with 50.9% of the genus, or 9.67 other species of *Cleonidius*.

Habitat associations

Habitat associations are varied in species of the genus, ranging, as in *Apleurus* species, from grasslands to deserts in some, to principally deserts, to principally grasslands in others (Fig. 240). Measures of primary habitat associations (calculated as for *Apleurus* species), differ slightly from those in *Apleurus* however, because in *Cleonidius*, association with desert habitats is low (0.099), increasing in semi-desert habitats to 0.171, and desert-grassland transitional habitats to 0.316. The highest assocation is with mesquite-grasslands and grasslands (0.474). Association with western xerophytic evergreen forest is 0.132 whereas no

Apleurus were associated with this habitat type. Among the species groups, the *C. erysimi* group is relatively well represented in deserts (0.125), also in semi-desert (0.250), but less so in desert-grassland (0.167) and markedly less so in mesquite-grasslands and grasslands (0.083). In contrast, the *C. americanus* group has values of 0.054 for deserts, 0.107 for semi-desert, 0.429 for desert-grassland, and 0.714 for mesquite-grasslands and grasslands. The *C. boucardi* group has values of 0.000, 0.125, 0.250, and 0.500 respectively for these same habitats. The only southwestern species in the *C. poricollis* group is found in a variety of habitats. With the exception of this species, *C. poricollis*, other *Cleonidius* species are restricted to one or only a few habitat types.

Plant associations

Unlike in *Apleurus* species, which are all associated primarily with Compositae, plant associations in *Cleonidius* species are much more varied and span a much broader taxonomic range of plant families (Fig. 241). A number of species are associated with Compositae, Rosaceae, Cruciferae, and Leguminosae. There is slight association with Chenopodiaceae and scattered records of associations with members of various other plant families. In the *C. erysimi* group, associations are varied, with one species on each of Compositae, Rosaceae and Rhamnaceae, and Cruciferae, and two on Leguminosae. Plant associations are not well known for *C. eustictorrhinus*. In the *C. boucardi* group, two species are associated with Leguminosae, one species with Rosaceae and Rhamnaceae, but also Leguminosae; plant associations are not known for *C. boucardi*. Associations are primarily with Compositae and Cruciferae in *C. poricollis*; exclusively with Cruciferae in *C. calandroides*. Finally, plant associations are few for most species in the *C. americanus* group with the exception of *C. americanus* which appears to be associated with Compositae.

Altitudinal zonation

Altitudinal ranges are shown as a Hubbs-Hubbs diagram (Fig. 233). In general, each species is found over a wide range of altitudes which overlap extensively with ranges of many other species such that *Cleonidius* species are not as markedly altitudinally segregated as are *Apleurus* species. This marked overlap also exists within each of the species groups as well. *Cleonidius poricollis*, and three members of the *C. boucardi* group, *C. boucardi*, *C. trivittatus* and *C. quadrilineatus*, have the largest altitudinal ranges of species in *Cleonidius*. Individuals of these species have been recorded at maximum altitudes ranging from 3276 to 4004 m.

Seasonal occurrence

Patterns of adult seasonal occurrence are broad with most species found throughout the greater part of the year from early spring to late winter months.

Co-existence

In contrast to species of *Apleurus*, examination by inspection of niche dimensions as a group shows the majority of *Cleonidius* species differ most in terms of host plant (Fig. 241) and habitat associations (Fig. 240). Species geographic range overlap is generally high (see Table V), as is the degree of altitudinal range overlap and as is overlap in seasonal occurrence. Within the *C. erysimi* group, extent of sympatry and altitudinal range overlap are high, but different species in the group are associated with different habitat types and with different plant families. In the *C. americanus* group, extent of sympatry and altitudinal range overlap are low

Table V. Chorological relationships of *Cleonidius* species

	C. erysimi	*C. eustictorrhinus*	*C. pleuralis*	*C. subcylindricus*	*C. longinasus*	*C. texanus*	*C. americanus*	*C. frontalis*	*C. canescens*	*C. infrequens*	*C. puberulus*	*C. collaris*	*C. notolomus*	*C. poricollis*	*C. calandroides*	*C. boucardi*	*C. trivittatus*	*C. placidus*
C. eustictorrhinus	S																	
C. pleuralis	BS	P																
C. subcylindricus	A	A	A															
C. longinasus	BS	S	A	A														
C. texanus	BS	S	BS	A	BS													
C. americanus	S	S	P	A	S	S												
C. frontalis	BS	P	BS	A	BS	BS	P											
C. canescens	BS	A	BS	A	A	NS	A	BS										
C. infrequens	P	A	A	A	A	S	A	S	S									
C. puberulus	S	A	A	A	A	A	A	S	S	P								
C. collaris	S	A	A	A	A	A	A	S	S	S	S							
C. notolomus	P	A	S	A	A	S	A	S	S	NS	A	A						
C. poricollis	BS	S	BS	A	BS	BS	S	BS	BS	S	S	S	S					
C. calandroides	A	A	A	NS	A	A	A	A	A	A	A	A	A	A				
C. boucardi	P	A	P	A	NS	NS	A	A	A	NS	A	A	P	BS	A			
C. trivittatus	BS	P	BS	A	BS	BS	P	BS	BS	S	BS	S	S	BS	A	P		
C. placidus	S	S	P	A	S	S	S	P	A	A	A	A	A	S	A	P	P	
C. quadrilineatus	BS	S	BS	A	BS	BS	S	BS	BS	S	NS	S	S	BS	A	A	BS	NS

S, sympatric ; BS, broadly sympatric ; NS, narrowly sympatric ;
P, parapatric ; A, allopatric.

and habitat associations overlap extensively; plant associations are mostly unknown. In the *C. boucardi* group, sympatry is low, habitat associations differ, host plant associations differ slightly, but altitudinal range overlap is high.

The genus *Cleonidius* is more diverse than *Apleurus* and is more extensive in its distribution. Whereas *Apleurus* species appear to be more associated with deserts and less so with grasslands, *Cleonidius* is very well-diversified in grasslands and desert-grassland transitional habitats and is not associated with deserts to any significant degree (except for species in the *C. erysimi* group). Only in *Cleonidius* are some species associated with the western xerophytic evergreen forest. Patterns in host plant association differ markedly, for species of *Apleurus* are almost exclusively associated with Compositae, whereas species of *Cleonidius* are associated to various degrees with one of Compositae, Cruciferae, Leguminosae, Rhamnaceae, Rosaceae and to a lesser extent Chenopodiaceae.

Wing length polymorphism.— All individuals examined of the *C. boucardi* group are macropterous; in the *C. poricollis* group 99% of *C. poricollis* and all *C. calandroides* are macropterous; and, in the *C. erysimi* group, only in *C. erysimi* are brachypterous individuals known (91%). In contrast, in the *C. americanus* group, all *C. canescens*, *C. puberulus* and *C. collaris*, and 79% of *C. notolomus* and 38% of *C. infrequens*, are brachypterous.

Apleurus and *Cleonidius*: Historical biogeography of New World species

Introductory Comments – A Warning

The evolutionary history of plant and animal taxa that presently inhabit the southwestern United States and adjacent areas has been very complex. Not surprisingly, determination of what this history has been is also a very difficult task and based on various assumptions. Changing, locally variable climates, mainly a trend during the Tertiary of increasing aridity (but here and there punctuated by pluvial periods of various duration) resulting in various and ephemeral habitat types, continual but localized orogenic activity, and locally variable topography, all result in a complex framework for speciation events to be understood and even approximately dated. Adding to this is perhaps the most significant problem, that of the Quaternary, for it is known that distributions of many organisms changed radically during this time period (Coope, 1979). Owing to these presumptive changes, many of the distribution patterns may reflect only Quaternary distributional shifts and not original speciation events, these perhaps having occurred elsewhere and under very different ecological conditions. In other words, the present distributions may be the result of secondary, not primary contact zones (Endler, 1977). In the absence of fossils, the heuristic value of historical biogeography may therefore be questioned because in order to overcome this problem, assumptions about habitat associations, other ecological attributes, and especially distributions of the species at different times, or of their ancestors, are required, based on these features in extant species. These can only be made with reference to a reconstructed phylogeny and as such the claim of phylogeny before biogeography is in large part valid for analyses to be maximally scientific. Whether or not these assumptions should be accepted is a moot point.

Because biogeographic statements are so dependent on a reconstructed phylogeny, another problem is that of confidence in the reconstructed phylogeny. A weak reconstructed phylogeny results in weak biogeographic statements that may prove misleading should they be uncritically accepted as facts.

In *Apleurus*, only the possibility of changed distributions is a problem, for confidence in the reconstructed phylogeny is high. On the other hand, both are problems in *Cleonidius*. Confidence in the fully resolved reconstructed phylogeny is low due to the large number of secondary characters used in the analysis and concomitant homoplasy in these characters. Some biogeographic statements about details of species origins in *Cleonidius* must therefore be cautiously accepted, and alternatives, some of which are discussed, must also be considered.

A further complication in *Cleonidius* is recognition of a Palearctic species component which is not herein considered in the reconstructed phylogeny. The single species examined from the Palearctic region can, however, be placed either as sister to the Nearctic *Cleonidius*, or as a member of the *C. americanus* group. Biogeographic significance of both placements will be discussed.

Historical Explanations

In *Apleurus*, diversity gradients do not appear to be easily explainable in terms of latitude, elevation, or any other climatic factor with the possible exception of regional degree of variation in aridity. As noted elsewhere, evolution of *Apleurus* appears to parallel evolution of increasingly arid habitats. This is supported by comparison not only of habitat associations with the reconstructed phylogeny (Fig. 238), but also of altitudinal ranges with the reconstructed phylogeny which trend toward occupation of lower, and thus likely more arid altitudes. Thus, if any ecological factor might prove important in explaining why southern California, Arizona, New Mexico and extreme northwestern Méhave the highest species diversity (Fig. 230), it is likely the degree of habitat and associated floral complexity largely due to the occurrence of desert and desert-grassland transitional habitats in these areas. Species diversity drops markedly beyond the area where these habitats occur.

Similarly, in *Cleonidius*, maximum species diversity is again noted in these same areas, but is also high throughout the rest of Arizona and New Mexico, western Texas, central California, and southern Nevada, Utah, Colorado and Wyoming (Fig. 231). Species diversity thus appears again to be influenced by degree of arid habitat complexity. However, high species diversity is more widespread in *Cleonidius* because of the higher level of association of the species in the genus with more widespread grassland and woodland habitats (Fig. 240). Although evolution in this genus has likely also been influenced by increasing aridity in southwestern North America, these influences are not as clearly indicated as in *Apleurus*. In *Cleonidius*, adaptation to the most arid habitats is low, and to the least arid, relatively high. Furthermore, there is no clearly evident evolutionary trend for species of the genus to be found in increasingly arid habitats (Fig. 240), or at successively lower altitudes as are noted in *Apleurus*. High diversity in *Cleonidius* thus extends outside the area of the highest habitat complexity and especially into areas of grassland, woodland, and desert-grassland transitional habitats. High degree of association with less arid habitats also explains the broader geographic and altitudinal range of the species in the genus and perhaps also the occurrence of the genus in the Palearctic region as well. In addition to the effects of habitat on the evolution of the group, unlike *Apleurus*, which are all apparently associated with Compositae, species of *Cleonidius* are associated with a much broader taxonomic array of plants (Fig. 241). Clearly, host plant shifts are an additional factor to consider in the evolution of this latter genus.

In the present study I address the hypothesis that evolution and speciation within *Apleurus* and *Cleonidius* closely parallel increasing aridity and associated changes in distribution and composition of habitat types in the southwestern United States and Mexico. History of distribution and composition of habitats in these areas has been dealt with extensively in paleobotanical studies by Axelrod (1950, 1975, 1979, 1985), Axelrod and Raven (1985) and Raven and Axelrod (1978) and thus interpretation of the geographical history of *Apleurus* and *Cleonidius* draws largely upon the results of these publications.

Of three possible origins of arid land faunas in North America, only two are likely for Cleonini. First, as discussed by Axelrod (1975), a continuous North American-western Eurasian belt of Madrean-Tethyan sclerophyll woodland vegetation may have lived in the early Paleogene, with subsequent vicariance of this habitat, as a result of Atlantic Ocean floor spreading, proposed to account for any present disjunctions in distributions. Secondly, and perhaps the generally more favourable hypothesis, Webb (1977) notes the marked similarity between savanna-adapted mammal faunas in Asia and North America in the late Eocene (postdating similarities between the faunas of Europe and North America), and invokes subsequent vicariance of these habitats across Beringia as responsible for present distributions. A third possibility, South American origins, as noted by Raven (1963) and Wells and Hunziker (1976) for various plants, does not appear likely, because no Cleonini are known from that continent (Wibmer and O'Brien, 1986) and the *Lixus* known from there do not appear related to *Cleonidius*.

Apleurus seems to be North American in origin and likely evolved *in situ*, on Compositae, in isolation from its sister genus, the Palearctic *Chromoderus*, as a result of vicariance of sclerophyll woodland or savanna habitats in Holarctica, either between western Europe and North America no later than early Eocene or between eastern Asia and North America no earlier than the late Eocene (Fig. 242) respectively. Accepting that *Apleurus* evolved in North America and on Compositae, investigation of the role of history proceeds by examination of distributions and aspects of natural history with respect to the reconstructed phylogeny.

First, aside from *A. hystrix*, the next two most plesiotypic species, *A. aztecus* and *A. lutulentus*, are exclusively and primarily mesquite-grassland and grassland inhabiting species, respectively (Fig. 238). This, and the increased association of more derived species with semi-desert and desert habitats, demonstrates a clear trend from mesquite-grassland and grassland to desert habitation within species of the genus (Fig. 238), and indicates that mesquite-grasslands, grassland, or a precursory habitat type not present today, or present but lacking association with any *Apleurus* species, was likely the ancestral habitat for the genus. This habitat was likely a grassland or savanna habitat, because no *Apleurus* are known from woodland habitats, plesiotypic *Apleurus* are currently associated with this or a similar type of habitat (Fig. 238), no eastern North American *Apleurus* are known, and *Chromoderus* species judging from their distributions, are likely steppe or grassland inhabitants. In view of this, a trans-Beringian savanna or grassland vicariance origin of *Apleurus* (Fig. 242) is to be preferred over the Madrean-Tethyan vicariance of Axelrod (1975), which would predict southwestern North America-Mediterreanean area relationships, presence of plesiotypic species in woodland habitats, presence of plesiotypic species in southeastern North America, and presence of closely related taxa in similar extralimital woodland habitats.

Grasses were present in North America in the early Tertiary as evidenced by first appearance of grass pollen in the Paleocene, and first grass macrofossils and first appearance of structural adaptations in mammals to open habitats (including especially, the initial albeit slight development of high crowned teeth resistant to the abrasive properties of grasses) in the Oligocene (Clayton, 1981; Webb, 1977).

Savanna or woodland precursors of mesquite-grassland and grassland and desert habitats likely first emerged as distinct habitats in the mid- to late-Eocene as a result of a slowly expanding dry climate and a marked increase in seasonal aridity fostering *in situ* adaptation by already existing subhumid plants to these new and increasingly semi-arid conditions (Axelrod, 1950, 1975, 1979; Axelrod and Raven, 1985; Cronquist, 1978; Webb, 1977). Arboreal vertebrates are less frequent in fossil deposits of this age, a number of North American groups developed special adaptations to savanna habitation, and new, savanna-adapted groups emigrated from Asia where they had already developed their adaptations for this type of life (Webb, 1977). Adaptation and radiation in animals and plants (especially dicotyledonous herbs) continued into the Oligocene as arid habitats proceeded to expand and diversify (Axelrod, 1979; Cronquist, 1978; Webb, 1977). At this time semi-arid woodland or savanna habitats were apparently relatively extensive in North America (Axelrod, 1975) and were likely interspersed with localized grasslands. Both faunas of late Eocene (Webb, 1977), and floras of the Oligocene (Axelrod, 1979), document relationships between taxa in southern California and those in the Rocky Mountain region (Axelrod, 1975; Raven and Axelrod, 1978). Axelrod (1979, Figure 6) and Raven and Axelrod (1978) further note that a number of congeneric "closely related" woodland taxa are presently disjunct in insular and maritime southern California and the highlands of central México. A continuum may therefore have commented these two areas and perhaps also the southern Rocky Mountain region from perhaps the late Eocene, at the earliest, into the Miocene (Axelrod, 1950; Raven and Axelrod, 1978). The present woodland in the uplands of central México is the habitat thought to be most like the ancestral Oligocene-Miocene woodland, hence the name Madrean for this vegetation type (Axelrod, 1975, 1979). Development of increasingly arid habitats intermediate between these areas throughout the later Tertiary, likely resulted in at least some of these present disjunctions (Axelrod, 1975).

This geographic pattern applies well to *Apleurus* because the most plesiotypic species of *Apleurus*, *A. hystrix*, is found in sand dunes in southern California, whereas the next two most plesiotypic species, *A. aztecus* and *A. lutulentus*, live respectively, inland in central México, and in central México, Arizona, New Mexico, Texas and adjacent states, (Fig. 242). This pattern, although between a California sand dune species and Mexican or southern Rocky Mountain mesquite-grassland and grassland taxa, is geographically similar to the relict disjunctions noted above for semi-arid woodland plants and is suggestive that the same may also apply to taxa initially adapted to savanna or grasslands. If isolation and the relict nature of *A. hystrix* is a result of an early vicariance of California and inland semi-arid grassland or savanna habitats, we might expect similar phylogenetic and geographic relationships to those in *Apleurus* in other taxa in which a structurally markedly distinct species is restricted to one of the southern California coastal dune habitats. Unfortunately, although endemics are known to occur in many California dune fields (Andrews *et al.*, 1979), phylogenetic and geographic relationships of the endemics have not been studied in detail. Most extensive survey efforts have also concentrated principally on inland dune fields (Andrews *et al.*, 1979; Hardy and Andrews, 1976). Some of these endemics are also not of a relict nature and are likely a product of the later Tertiary climatic changes that fostered the rapid and numerous speciation events thought to have contributed so extensively to the marked levels of endemism in the California flora (Stebbins and Major, 1965; Raven and Axelrod, 1978). Perhaps relicts such as *A. hystrix* in California, are managing to survive in restricted or marginal habitats having changed habitat associations from the grassland or savanna habitat perhaps due to exclusion by newly evolved competitively superior species, or due to the changing nature and ephemeral status of habitats to which they were initially adapted. Raven and Axelrod (1978) note that among plants, a number of Tertiary relicts have survived in California owing to its sheltered and equable climate.

Grassland habitat only reached its present form and more extensive distribution during the Miocene and early Pliocene (but especially at the Miocene-Pliocene transition) (Axelrod, 1950, 1985; Webb, 1977). Because of this, it is unlikely that divergence between *A. aztecus* and the ancestor of the remainder of *Apleurus* took place before this time. Restriction of *A. aztecus* to mesquite-grasslands, and primary association of *A. lutulentus* with mesquite-grasslands and grasslands, suggests that the ancestor of the subgenus *Apleurus*, like the ancestor of the genus *Apleurus* as noted, was also associated with grassland-like habitats. Present restriction of *A. aztecus* to central México is unlikely to have been a result of competitive exclusion by *A. lutulentus* in the grasslands of the United States, for *A. lutulentus* coexists with *A. aztecus* in central México (Figs. 207, 210). Rather, a late Miocene or early Pliocene north-south vicariance of Plains and Mexican Plateau grasslands as a result of increasing aridity and development of more extensive semi-desert habitats (Webb, 1977) can account for the distribution, with a subsequent dispersal of *A. lutulentus* south through desert-grassland transitional habitat into central Mexican mesquite-grasslands and the Hidalgan Desert region (term of Shreve, 1940; Axelrod, 1979) of a later Pleistocene origin. This later dispersal route may have been through a desert-grassland transitional habitat, not grassland or mesquite-grassland, because of the absence of concomitant dispersal north by *A. aztecus*. Alternatively, lack of dispersal by the latter species may be due to individuals being flightless whereas those of *A. lutulentus* are macropterous and presumably capable of flight. Webb (1977) has drawn attention to the role of central México, noting that Miocene faunules from this area play a focal role in the history of the semi-arid biota of North America. Similarly, Cronquist (1978) notes that the tribe Heliantheae of the Asteraceae (Compositae herein) has its present center of diversity in the arid highlands of central México, suggesting that this area has been important in the evolutionary history of the group.

Increased aridity during the middle Pliocene resulted in increased extent of semi-desert habitats and likely the origin of the ancestor of the remainder of *Apleurus* in western desert-grassland transitional habitats, and *A. lutulentus* in more easterly, primarily grassland, habitats (Fig. 243).

Divergence of the *A. porosus-A. jacobinus-A. angularis* and *A. saginatus-A. albovestitus* lineages is more problematical, for extant species of the two groups, especially *A. angularis* and *A. albovestitus*, do not differ much in their habitat associations or distributions.

In the *A. saginatus-A. albovestitus* lineage, an east-west vicariance of desert-grassland and semi-desert habitats respectively (Axelrod 1979, figure 4) as a result of late Quaternary aridity following the increased precipitation of the late Pliocene and early Pleistocene (Axelrod, 1979) likely resulted in the origin of *A. saginatus* and *A. albovestitus* respectively (Fig. 245). Although *A. albovestitus* is presently a widespread species, examination of intraspecific variation shows the most plesiotypic form to be that from coastal Californian semi-desert (possession of large glabrous abdominal patches, deeper and larger punctation; see "Geographic variation" of *A. albovestitus*). Presence of other forms of *A. albovestitus* to the east in other semi-desert and desert habitats is therefore suggestive of recent dispersal followed by post-glacial local or regional selection pressures in various regional habitats which are hypothesized to be largely of a recent origin in the late Quaternary (Spaulding *et al.*, 1985).

Unlike *A. albovestitus*, *A. saginatus* has not expanded its range and is still found only in the desert-grassland transition bordering the eastern portion of the Sonoran desert (Fig. 206).

In the *A. porosus-A. angularis-A. jacobinus* lineage, patterns of vicariance (Fig. 244) among the three species are clearly evident for they are allopatric (Figs. 208, 210–211). Because it has only been during the last four million years that Baja California reached its present position and acquired a notably drier climate and coastal foggy desert (Axelrod, 1979), origin of *A. porosus* does not likely predate that time. Increased aridity in the area likely allowed entry of a desert-grassland-adapted ancestor from the north, as Baja California was reaching its present position. This form is presumed to have evolved *in situ* into *A. porosus*. An east-west vicariance of desert-grassland and semi-desert-adapted populations of the ancestor of *A. jacobinus-A. angularis*, as in the *A. albovestitus-A. saginatus* lineage, likely accounts for the origin and present distribution of *A. jacobinus* and *A. angularis* . Present distributions of *A. porosus* , *A. jacobinus*, and *A. angularis* may be maintained as allopatric by competitive exclusion or by selection pressures promoting reproductive isolation.

For *Apleurus* then, increasing aridity and concomitant changes in habitat structure and availability appears to be the scenario most consistent with ideas and evidence about paleoenvironments and their distribution in space and time in southwestern North America.

In *Cleonidius*, the pattern is somewhat different. *Cleonidius* species, in general, appear to parallel some of the aspects of evolution of *Apleurus* species or lineages, but differ markedly in various others.

As mentioned, at least one species of *Cleonidius* is known from the Palearctic Region. However, its relationships are at present unclear (see Phylogeny section).

Unlike *Apleurus* , *Cleonidius* does not appear to be North American in origin because the Palearctic species component of *Cleonidius* appears to be sister to the Nearctic species component (Fig. 246). Thus, a Palearctic origin for the genus is to be preferred with subsequent entry into North America of this ancestral stock. It is most likely that a trans-Beringian grassland or savanna vicariance of this stock (Fig. 246), such as that proposed for the origin of *Apleurus*, resulted in the evolution of Nearctic *Cleonidius*. The evidence for this is as follows: 1, Palearctic *Cleonidius* are eastern in their distribution and are apparently associated with grassland or steppe habitat; 2, association with grasslands is widespread in *Cleonidius* (although not restricted to primitive lineages or species) (Fig. 240); 3, association with woodland, although widespread, is only in more derived species (Fig. 240) (suggestive of secondary entry into that habitat type, a hypothesis supported by patterns of host plant association); and 4, the two eastern North American species are unrelated and also of a generally more derived nature. This trans-Beringian savanna or grassland event is likely to have occurred only post-late Eocene.

Within *Cleonidius* there are five of what I consider to be main, perhaps interrelated, differences from *Apleurus*: 1, species of *Cleonidius* are known from western xerophytic conifer woodland (Fig. 240); 2, species of *Cleonidius* are known from eastern North America (Figs. 215, 229); 3, species exhibit primary host plant associations with one of a various number of plant families (Fig. 241); 4, habitat association overlap (Fig. 240), altitudinal range overlap (Fig. 233), and association with less arid habitats are high; and 5, comparison of habitat associations or altitudinal ranges with the reconstructed phylogeny does not demonstrate a clear correlation with increasingly arid habitats (Fig. 240) or with lower altitudes, respectively. These differences are certainly suggestive of a different evolutionary history, one influenced less so by shifts to increasingly arid habitats, but rather by host plant shifts, allopatric speciation within a habitat type, and habitat shifts to both more and less arid types at both lower and higher elevations over a more extensive geographic range.

There are, however, some similarities. Distributions of three of the four species groups can be geographically centered in certain areas. The *C. erysimi* group has five of six species distributed in whole or in part in California (Fig. 257); the *C. americanus* group has six of seven species distributed in whole or in part in the southern Rocky Mountain region (Fig. 258); and, the *C. boucardi* group has three of four species in the central to southern Rocky Mountain region or central México (the most primitive being in central México) (Fig. 259). With certain restrictions, namely the question of the origin of the *C. poricollis* group, this pattern brings to mind the California-central México-southern Rocky Mountain pattern in primitive *Apleurus* (Fig. 242) because the common ancestor of the *C. boucardi* group (México) and the *C. poricollis* group (questionable origin) is sister to the *C. americanus* group (southern Rocky Mountains), the common ancestor of which is sister to the *C. erysimi* group (California).

This pattern is suggestive of similar historical processes accounting for diversification in the basal lineages of the two genera, although it is possible that in *Cleonidius* the ancestral habitat association is with sclerophyll woodland rather than grasslands or savanna for the two were undoubtedly intermixed (Axelrod 1979). As such, an Eocene to Miocene vicariance of California, southern Rocky Mountain region, and central México was likely responsible for the initial diversification within the genus (Fig. 246).

Parsimony, however, dictates preference for an association with grasslands or savanna habitat because most *C. americanus* group members have a primary association with that habitat type; *C. poricollis* and *C. erysimi* group members, although not primarily associated with grasslands, are not primarily associated with woodlands; and primitive *C. boucardi* members are associated with grasslands (Fig. 240). Furthermore, the two species associated with western xerophytic conifer woodland and the single species associated with eastern North American mesophytic evergreen forest, are more or less structurally derived and not relictual in distribution. Similarly, the other eastern North American species is also structurally derived, and although restricted in distribution, is the sister-species of a structurally similar western North American species (Fig. 236).

The best evidence, however, for association with xerophytic woodland being secondarily derived concerns host plant associations. *Cleonidius texanus* and *C. quadrilineatus* are both associated primarily with Rosaceae and Rhamnaceae and each have their two closest relatives associated exclusively with Leguminosae (Fig. 241). This, and presence of infrequent association of *C. texanus* and *C. quadrilineatus* with Leguminosae (but not of relatives on Rosaceae or Rhamnaceae), suggests Leguminosae was the plesiotypic host plant for these lineages and that Rosaceae and concomitantly association with xerophytic woodland, derived.

Indeed, the widespread distribution and abundance of species associations with Leguminosae suggests that association with this family, or an ancestral form of this family, Rosaceae and Rhamnaceae (the families are phylogenetically closely related and placed in the order Rosales [Cronquist, 1968]), may be ancestral for *Cleonidius* as a whole. Even more parsimonious, however, is the hypothesis that association with Compositae is ancestral for the genus. Association with this family is equally widespread and abundant in the genus, but unlike Leguminosae, is found particularly in plesiotypic species in the *C. erysimi*, *C. americanus*, and *C. poricollis* species groups, not in the more derived species, as is the association with Leguminosae. Association with Compositae is also known in numerous other Cleoninae (*e.g.*, *Apleurus*, *Cleonis*, *Cyphocleonus*, some *Lixus*). Accordingly, preference must herein be given to a plesiotypic association with Compositae, but final resolution of these competing hypotheses rests largely on determination of host plant relationships in those *Cleonidius* species in which they are as yet unknown, particularly, those of a primitive phylogenetic position and especially those of the Palearctic species component.

Further supportive of the more recent trans-Beringian vicariance of savanna or grassland are: 1, non-relictual geographic or structural status of any *Cleonidius*; 2, lack of extensive structural divergence between species perhaps indicative of less available time for evolutionary change to have occurred; and 3, likelihood that *C. vibex* and relatives are the sister group to Nearctic *Cleonidius* (see Phylogeny section).

Axelrod's (1975) Madrean-Tethyan hypothesis has not been given much support from other studies. Floras of the eastern Gulf Coast and southeastern North America do not show evidence of arid-adapted taxa (Graham, 1965). The hypothesis also does not receive any clear support from the biogeographic analyses presented herein. Clearly, I believe we must accept an ancestral association with grassland or savanna, as in *Apleurus*. Diversification in *Cleonidius*, however, has apparently been much more complex than in *Apleurus* as evidenced by: lack of a clear correlation between phylogeny and habitat association (Fig. 240); numerous different and variable habitat associations of the species (Fig. 240); different host plant associations (Fig. 241); and present relatively extensive species sympatry and altitudinal range overlap (Fig. 233).

Within species groups, caution must be exercized because degree of confidence in various of the hypothesized relationships is low (Fig. 237). Within the *C. erysimi* group, monophyly of *C. subcylindricus*-*C. texanus*-*C. longinasus* is strongly supported by three primary characters. Relationships of this lineage and the remaining three species in the species group are however much less clear and are left as an unresolved trichotomy (Fig. 237). Assuming, as noted, that the *C. erysimi* species group evolved in California (Fig. 246), it is likely that, as conditions became more arid, there was an entry into semi-desert habitat in the *C. eustictorrhinus*-*C. erysimi* lineage (Fig. 247). The hypothesized ancestral association with Compositae was retained in this lineage and *C. pleuralis*, and the ancestor of the *C. subcylindricus*-*C. texanus*-*C. longinasus* lineage likely shifted onto Leguminosae. *C. eustictorrhinus* and *C. erysimi* may then have diverged in part as a result of an east-west vicariance between California and the Great Basin Region with subsequent dispersal of *C. erysimi* back into California (Fig. 248). This event likely also involved, or may have even been exclusively due to, a host plant shift involving Compositae and the phylogenetically unrelated (Cronquist, 1968) Cruciferae. Evidence for this is as follows. The sister-species *C. americanus* and *C. frontalis* (of the *C. americanus* group) have similar geographic distributions to *C. eustictorrhinus* and *C. erysimi*; *C. americanus* is associated with Compositae in California; host plant associations of *C. frontalis* are not known. In *C. eustictorrhinus* and *C. erysimi* the opposite is true; the widespread *C. erysimi* is found on Cruciferae whereas plant associations of the California *C. eustictorrhinus* are not known. Furthermore, in the *C. poricollis* group, both *C. poricollis* and *C. calandroides* are associated with Cruciferae, but *C. poricollis* is also markedly associated with Compositae. Patterns of Cruciferae-Compositae association between closely related taxa therefore (and, as noted, Leguminosae-Rosaceae/Rhamnaceae associations of a similar nature), appear to repeat within *Cleonidius* (Fig. 241) and may thus represent more general patterns of host plant relationships. In view of this, association with Compositae can be hypothesized for *C. eustictorrhinus*, and association with Cruciferae for *C. frontalis*. If *C. pleuralis* ultimately proves sister-species of the *C. eustictorrhinus*-*C. erysimi* lineage then evidence for *C. eustictorrhinus* being associated with Compositae is more marked, because then only one shift from Compositae in the evolution of the three species is required. Within *C. pleuralis* there has been a continued adaptation to more markedly arid lands (Fig. 240), perhaps interrelated with association with Compositae (note relatively high level of association with arid habitats in *Apleurus*, all of which are on Compositae; association of *C. poricollis*, the only other *Cleonidius* that is associated with desert habitats, is also with Compositae).

In the *C. subcylindricus*-*C. texanus*-*C. longinasus* lineage there appears to be independent entry into xerophytic and mesophytic evergreen woodlands in the central-southern Rocky Mountain region and eastern North America by *C. texanus* and *C. subcylindricus* respectively as evidenced by the pattern of host plant associations. An initial vicariance in this lineage between *C. subcylindricus* in eastern North America and the *C. texanus*-*C. longinasus* lineage in western North America, lineages both ancestrally on Leguminosae, was likely followed by a host plant shift from Leguminosae to Rosaceae and Rhamnaceae and concurrent shifts to xerophytic woodland habitat by *C. texanus* and to mesophytic woodland habitat by *C. subcylindricus* (Fig. 249).

Within the *C. americanus* group, most of the species are primarily associated with grasslands; *C. americanus* and *C. notolomus* are associated exclusively with Pacific semi-desert and desert-grassland transition respectively (Fig. 240). Vicariance patterns are clearly evident in the present distributions of species in this group. A California-Great Basin or southern Great Plains vicariance can be proposed to account for the origin of the *C. americanus*-*C. frontalis* lineage and the ancestor of the remainder of the *C. americanus* group (Fig. 250). Within the former lineage, a California-inland vicariance again very likely explains the evolution of *C. americanus* and *C. frontalis* (Fig. 251). This was likely concomitant with a shift to more arid habitats, especially by *C. americanus*.

Origins of *C. canescens* and of the *C. notolomus*-*C. collaris* and *C. puberulus*-*C. infrequens* lineages are not clear. However, a north-south vicariance of both *C. collaris* and *C. notolomus* (Fig. 253), and of *C. puberulus* and *C. infrequens* (Fig. 252), accounts for the present distribution of these species. Of the four, only *C. notolomus* has changed from a grassland association to desert-grassland transitional habitat (Fig. 240). Few structural differences between these sister-species, and the allopatric distributions favour a relatively recent occurrence of these speciation events. Association with Compositae is hypothesized as plesiotypic for the species group.

Origin of the *C. poricollis* group is unclear principally because of the widespread distribution and eurytopic nature of *C. poricollis* (Fig. 228). It was undoubtedly concurrent with the hypothesized initial radiation of species group lineages and while an east coast isolation of *C. calandroides* likely accounts for the origin of that species, it is not clear where the ancestor of *C. poricollis* and *C. calandroides* evolved. Association with Compositae is proposed as ancestral for this species group as well.

In the *C. boucardi* group, there was likely a Mexican highlands isolation of *C. boucardi* in mesquite-grassland and a southern Rocky Mountain isolation of the *C. trivittatus*-*C. quadrilineatus*-*C. placidus* lineage in grassland habitat, an event brought about by increasing aridity and the formation of intermediate desert-grassland transitional or semi-desert habitats (Fig. 254). In the *C. trivittatus*-*C. quadrilineatus*-*C. placidus* lineage, in which association was likely with Leguminosae, an east-west vicariance of *C. trivittatus* and *C. quadrilineatus*-*C. placidus* in grassland and semi-desert habitats respectively, appears to account for the origin of *C. trivittatus* (Fig. 255). Subsequent entry into xerophytic evergreen woodland habitat by the semi-desert adapted ancestor, which, as in the *C. erysimi* group, continued to be associated with Leguminosae, resulted in *C. quadrilineatus* in the eastern xerophytic woodlands and *C. placidus* in the semi-desert habitat of California (Fig. 256). Concurrent with this habitat shift by *C. quadrilineatus* was a host plant shift to Rosaceae and Rhamnaceae; *C. placidus* continued to be associated with Leguminosae. Present occurrence of *C. quadrilineatus* in California is likely a recent dispersal event. Ancestral host plant relationships of this group are also likely with Compositae.

Summarizing, both *Apleurus* and *Cleonidius* are hypothesized to have entered North America in savanna or grassland habitats (or their precursors) across Beringia during late Eocene time. In both genera there appears to be an initial association with Compositae and vicariance of lineages in grassland or mesquite-grassland between California, central México, and the southern Rocky Mountains. Further speciation event in *Apleurus* appear due primarily to shifts to apotypic habitat types brought about by increased aridity during the later Tertiary; there is little within habitat-type allopatric speciation. Host plant shifts are not a factor, for all *Apleurus* species remain associated with Compositae. Host plant shifts, however, primarily between Leguminosae-Rosaceae and Compositae-Cruciferae, and, to a lesser degree, within-habitat-type allopatric speciation, appear to predominate as the causes of further speciation in *Cleonidius*, most species of which remain associated with plesiotypic less-arid habitat types such as grasslands and desert-grasslands.

Evolutionary trends and adaptations

Adaptive trends to arid conditions

Numerous apparent adaptations to arid habitats are known in Coleoptera, including Curculionidae (Crowson, 1981). Some of these are exhibited in Cleoninae.

Wing length and flightlessness.— Adults of various species of North American Cleoninae are apterous or brachypterous to varying degrees and in varying frequency. Some, such as *Stephanocleonus confusus* or *Apleurus aztecus*, have the elytra more or less solidly fused together along the median suture. The cuticle is also thick and hard in many of these same individuals. Flightlessness appears more frequenty in traditional Cleonini than in traditional Lixini.

In *Apleurus* no clear phylogenetic trend is evident in this character although adults of the closely related *A. angularis*, *A. jacobinus* and *A. porosus* are all more or less apterous. Lack of a trend in *Apleurus* is perhaps surprising in view of the correlation of phylogenetic position with occupation of increasingly arid habitats (Fig. 238). Similarly, in *Cleonidius*, there is no clear phylogenetic trend in this character. Adults of species of the *C. americanus* group are predominantly brachypterous but they are mostly associated with grassland habitats and not more arid habitats. Undoubtedly, degree of aridity is not the sole Undoubtedly, degree of aridity is not the sole factor influencing the frequency of brachyptery and although the aforementioned adaptations may serve to prevent desiccation in arid environments, the spatial distribution of the habitat-type or of host plants, likely also influences the tendency towards or away from brachyptery. Compromise between these differing selective forces likely results in the wing-length polymorphisms noted in some species and the lack of a clear trend.

In species in the southwestern United States, populations on both sides of the Continental Divide, in which individuals are flightless, are structurally more distinct in the north, where the divide is high in elevation, as compared to the south, where the divide is low in elevation and where gene flow seems likely. Species exhibiting similar distributions but which are composed of macropterous individuals do not show such patterns of variation.

Diel activity.— There is no evidence to indicate distinct peaks of diel activity in North American Cleoninae which might indicate avoidance of diurnal stressful conditions in an arid habitat. Such diel activity is known in other arid land Curculionidae (C.W. O'Brien, E.L. Sleeper, pers. comms.).

Burrowing adaptations.— Modifications of legs for burrowing are not known in North American Cleoninae. This is not surprising in view of 2, above. There are, however, adults of some species that possess long erect surface vestiture which may prove correlated with life on sand dunes and which may facilitate movement through sandy substrates. Such long vestiture is known in various obligate sand dune Scarabaeidae and other Curculionidae.

Ventral tarsal pilose vestiture.— Within *Apleurus* (Figs. 234–235), and to a lesser extent also in *Cleonidius* (Figs. 236–237), a clear trend is evident towards reduction in ventral tarsal pilose vestiture. This reduction has been reasonably suggested to be due to living predominantly on the ground rather than on plants (Kissinger, 1964; Crowson, 1981) and is widespread in many arid-adapted Curculionidae. In *Apleurus* the trend is as expected, because those more derived species in more arid environments, where plants are more widely spaced, and where it is less desirable to spend time exposed on the plant, lack ventral tarsal pilose vestiture or have pilose pads that are markedly reduced. In *Cleonidius* however, this is not clearly so, for although more arid habitat species (*e.g., C. erysimi*) possess reduced pilose pads, it is the members of the *C. americanus* group which exhibit the greatest frequency of lack of ventral tarsal pilose vestiture. This is perhaps surprising, for the species in this group are associated principally with plesiotypic grassland habitats; predicted adaptive correlates are thus not always evident in *Cleonidius.*

Other evolutionary trends

Host plant associations.— No trends in host plant relationships are evident in *Apleurus*, because all species appear associated with Compositae (Fig. 239). In *Cleonidius* however, two repeated patterns warrant mention (Fig. 241). Leguminosae-Rosaceae/Rhamnaceae associations are found in the sister-species *C. longinasus-C. texanus* and *C. placidus-C. quadrilineatus*, and Compositae-Cruciferae associations are found in *C. poricollis-C. calandroides* and are hypothesized in *C. americanus-C. frontalis* and *C. eustictorrhinus-C. erysimi*. It is unlikely that the Compositae-Cruciferae association is phylogenetically based, but rather reflects the co-occurence (perhaps recent) of these two plant taxa in the same, more arid habitats. The Leguminosae-Rosaceae/Rhamnaceae association, however, is likely phylogenetically based for the taxa involved are closely related and the host plant shift is concomitant with a shift in habitat association.

Groups in which sympatry is low, altitude range overlap low, and habitat association overlap low, tend to have species which differ little in host plant relationships. Increasing levels of these factors appear to be correlated with more varied host associations. Host plant associations, largely unknown in the *C. americanus* group, can thus be predicted to vary little in terms of their taxonomic range and thus largely be with Compositae or Cruciferae.

There is no trend from generalist to specialist feeding in either *Apleurus* or *Cleonidius*.

Habitat associations.— As noted in detail in the biogeography section, there is a clear trend in *Apleurus* for phylogenetically more derived species to be associated with increasingly arid habitats (Fig. 238) and lower elevations. This is not so in *Cleonidius* wherein most species are associated with grassland or grassland-desert habitats (Fig. 240).

Size.— Within *Apleurus* there is a tendency towards increased size (Figs. 234–235); such is not clearly evident in *Cleonidius*. Increased size in an arid environment may serve to aid in prevention of water loss for surface area to volume ratios would be lower in larger individuals which are, notably, found in more arid environments. In *Cleonidius* however, the largest species are those in the *C. boucardi* group. These are not found in notably arid habitats but rather grasslands, semi-desert and xerophytic evergreen woodlands.

Genitalia.— Form of male genitalia including the internal sac is very conservative in species of both *Apleurus* (Figs. 99–104) and *Cleonidius* (Figs. 177–196) and form of female genitalia is very conservative in *Cleonidius* (Figs. 157–176). Such is not so in females of *Apleurus* wherein there is a clear trend towards reduction in size of the stylus on gonocoxite II and an increasingly subapical position of attachment of the same (Figs. 89–96). This trend is likely related to the oviposition habits of the species but such are not known in detail for any North American species of Cleoninae.

Form of the aedeagus (Figs. 31–36) and of the internal sac (Figs. 43–48) differs markedly between species of *Stephanocleonus*, in contrast to the lack of differences in *Cleonidius* and *Apleurus*. Reasons for this are unknown.

Elytral scale patterns.— Elytral scale patterns are generally uniform within and between *Apleurus* species except for *A. angularis* (Figs. 72–74) and *A. albovestitus* (Figs. 75–79) wherein various forms are recognizable. Correlation of particular scale patterns with geographic distribution suggests a local adaptive significance, one I believe associated with crypsis on the ground substrate or in debris under host plants. A thermoregulatory role however, may apply to those *A. albovestitus* in the lower Colorado River drainage. In *Apleurus* there are no species which possess a distinctly vittate scale pattern; most are more or less mottled in general appearance.

In *Cleonidius* elytral patterns vary between species but not to a significant extent within a species (with the exception of *C. canescens*). Adaptive significance of the vittate pattern (*e.g.*, Fig. 131) found in most *Cleonidius* is likely one of concealment on host plants or in debris under the host plant. Crypsis on the ground substrate is not likely, except perhaps in the *C. americanus* group, for otherwise, most species have moderately developed ventral tarsal pilose vestiture indicating life predominantly on plants. Only in the *C. americanus* group is there predominance of species in which individuals have reduced ventral tarsal pilose vestiture. Also in this group are found the only species with mottled elytral scale patterns (*e.g.*, Figs. 124–125). These patterns are similar to those of *Apleurus* species, and likely serve as an adaptation to life on the ground substrate.

Vittate (and margined [Figs. 118–123]) patterns predominate in species of *Cleonidius* with extensive ventral tarsal pilosity; non-vittate patterns predominate in species with reduced tarsal vestiture. Wide ranging species with reduced ventral pilose tarsal vestiture in *Apleurus* exhibit geographic variation in scale pattern, whereas restricted species or those wide-ranging species with extensive ventral pilose vestiture do not show variation in elytral scale pattern. In *Cleonidius* nearly all species exhibit little or no variation in elytral scale pattern (except for *C. canescens* of the *C. americanus* group, which like *A. angularis*, has more or less vittate and non-vittate forms occurring on the west and east sides of the Continental Divide). Within the *C. americanus* group, which contains mostly allopatric species with reduced ventral vestiture, there is the most extensive within-species-group variation in scale pattern. Other species groups do not show within group variation in scale pattern. It thus appears that there is an inverse correlation in both *Apleurus* and *Cleonidius* between degree of variation in elytral pattern and extent of ventral tarsal pilose vestiture, but only seen in species or species groups distributed over large geographic areas.

Patterns and predictions

From results of this study of Cleoninae, some tentative generalizations can be made as regards arid adapted faunas in North America.

1. Preference must go to a post-late Eocene vicariance of savanna or grassland habitat, or precursory habitat, across Beringia as the original mode of isolation of Nearctic arid land taxa which possess Palearctic relatives also inhabiting arid lands (Figs. 242, 246). There is no evidence for direct Madrean-Tethyan connections as proposed by Axelrod (1975).
2. The most plesiotypic species or lineages in the Nearctic region will be found on Compositae in various combinations of the mesquite-grasslands of the highlands of central México, the southern Rocky Mountain grasslands, and in one of various habitats in California which may be relictual or predominantly grassland in nature (Figs. 242, 246).
3. Arid-adapted species in eastern North America are more recent in origin, not relictual, and are related to a species or a lineage of few species in western North America.
4. California is the geographical area recognizable as possessing the most arid land endemics. All have their closest relatives outside of California.
5. Evolution in arid-adapted taxa may involve a trend toward occupation of increasingly arid habit by successively more derived species (Fig. 238). This is accompanied by few or no host plant shifts (Fig. 239), and may be limited to non-speciose groups. Sympatry, altitudinal range overlap, and habitat association overlap is low in these taxa.
6. Alternatively to 5 above, host plant shifts (Fig. 241) permit sympatry, altitudinal range overlap and habitat association overlap and are perhaps associated only with more speciose groups. No clear correlation between phylogenetic position of the species and degree of aridity of habitat occupied is evident (Fig. 240).
7. Species inhabiting North American desert habitats are of recent origin (but not necessarily of derived phylogenetic position), and are related to taxa associated with precursory North American non-desert habitats although not in a generally predictable manner. That regional deserts are composed of taxa from non-desert arid habitats and are of recent origin is supported. No regional desert endemics are known in *Apleurus* or *Cleonidius* .
8. Contrary to statements of other authors (Axelrod, 1985), grassland endemics are known, are primitive or derived in their phylogenetic position, and should thus be expected in other arid land adapted taxa.
9. Compositae-Cruciferae and Leguminosae-Rosaceae/Rhamnaceae host plant shifts may represent general patterns to be found in other phytophagous taxa that feed on vegetative plant structures. Shifts from Leguminosae to Rosaceae and Rhamnaceae may prove generally associated with entry into western upland xerophytic evergreen woodland habitat by some phytophagous taxa. These shifts appear to have a phylogenetic basis as indicated by the fact that the families are placed in the order Rosales (Cronquist, 1968).

In contrast, Compositae-Cruciferae host plant shifts are likely due to occurrence of both the two plant and two weevil taxa in the same habitat types. No phylogenetic basis can be inferred because the two families are not apparently phylogenetically closely related as indicated by their placement in separate, unrelated subclasses (Cronquist, 1968).

CONCLUSIONS AND FUTURE RESEARCH

Scientific studies should not only attempt to answer specific questions but should also strive to pose questions which might prove the basis for further inquiry. More than anything else, I believe this study draws attention to the need for examination of world faunas or at the least, regional faunas placed in a world perspective. Traditionally, North American Cleonini have all been treated as *Cleonis*, but as now should be clearly evident, the relationships of many taxa in North America are actually quite phylogenetically distant.

Relationships of *Apleurus* are largely resolved. Unfortunately, this cannot be said with the same confidence for *Cleonidius*. World study of the speciose and structurally diverse genus *Lixus* should help resolve the still problematical relationships and even species constituency of *Cleonidius*. What other Old World *Lixus* may require placement in *Cleonidius* and subsequent study of large numbers of individuals of these species and determination of what their relationships are to North American *Cleonidius*, should help to resolve the phylogenetic placement of the Old World *Cleonidius* , further resolve the interrelationships of North American species, and answer some still remaining questions of biogeographic importance. This will be a large task, for within *Lixus* are placed a great number of species. More complete knowledge of structural diversity of *Lixus* species and the phylogenetic relationships of component species-groups or subgenera should ultimately lead to a clearer understanding of suprageneric relationships in Cleoninae and a well substantiated tribal classification.

Not to be forgotten are the interrelationships among genera of traditional Cleonini. A start at a study of these relationships leading, I hope, to a generic reclassification, has been made as part of this present study. Results are not presented in detail here; only characters of relevance to our understanding of the North American fauna have been included. Study of representatives of generic-group names not yet examined is required, as is study of more species in more speciose genera to assure proper placement and uniformity of features that appear to prove phylogenetically valuable at the generic level.

Even within the North American fauna itself, work remains to be done. For *Apleurus* and *Cleonidius* , I feel confident that no new species will be discovered; for *Stephanocleonus* , largely because the genus is northern and Holarctic, I suspect that one or more new species remain to be discovered, perhaps in the Yukon Territory and Alaska. Whether any of the North American species are Holarctic in distribution (and perhaps conspecific with nominal Old World species) also needs to be determined for it has not been possible to examine types or representatives of even a small number of the many Palearctic species. Only when this has been done can phylogenetic relationships of the species in this genus be reconstructed.

For all Cleoninae, more host plant information needs to be compiled. Hosts, even plant associations, are not known for *Stephanocleonus* species; the relationship with Compositae needs to be further substantiated in *Apleurus* species; and, various of the species of *Cleonidius* do not have hosts or even plant associations established, and those that are established need variable degrees of further supportive data. With host plant shifts appearing to play an integral role in *Cleonidius*, more such information can only increase understanding of the evolution of species in that genus and determine whether predictions about specific host plant relationships made herein, and whether predictions that these patterns are repeated and general are borne out.

Immature stages of Cleoninae are largely unknown and unstudied. Collection and study of eggs, larva and pupae, particularly in North America, may provide characters of phylogenetic use in substantiating relationships as based on adult characters, or, in resolving problematical relationships or those in which confidence is low.

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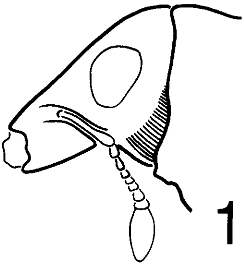
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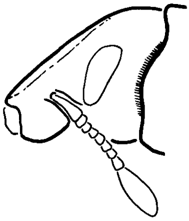
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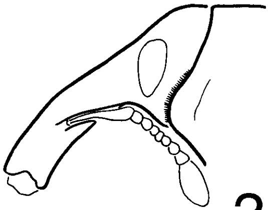
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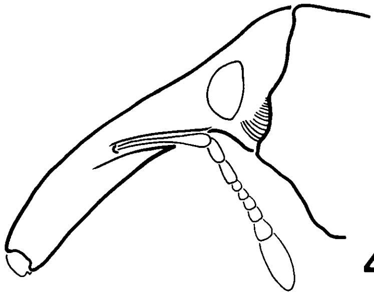
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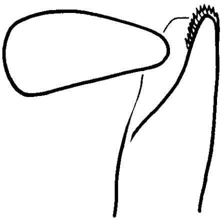
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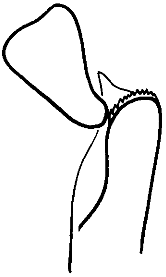
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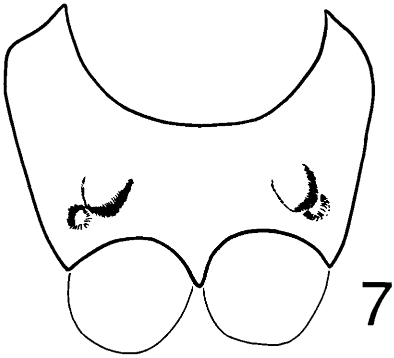
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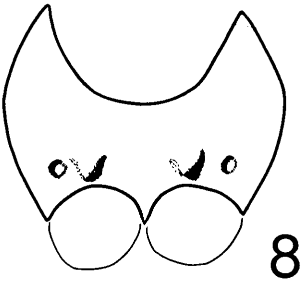
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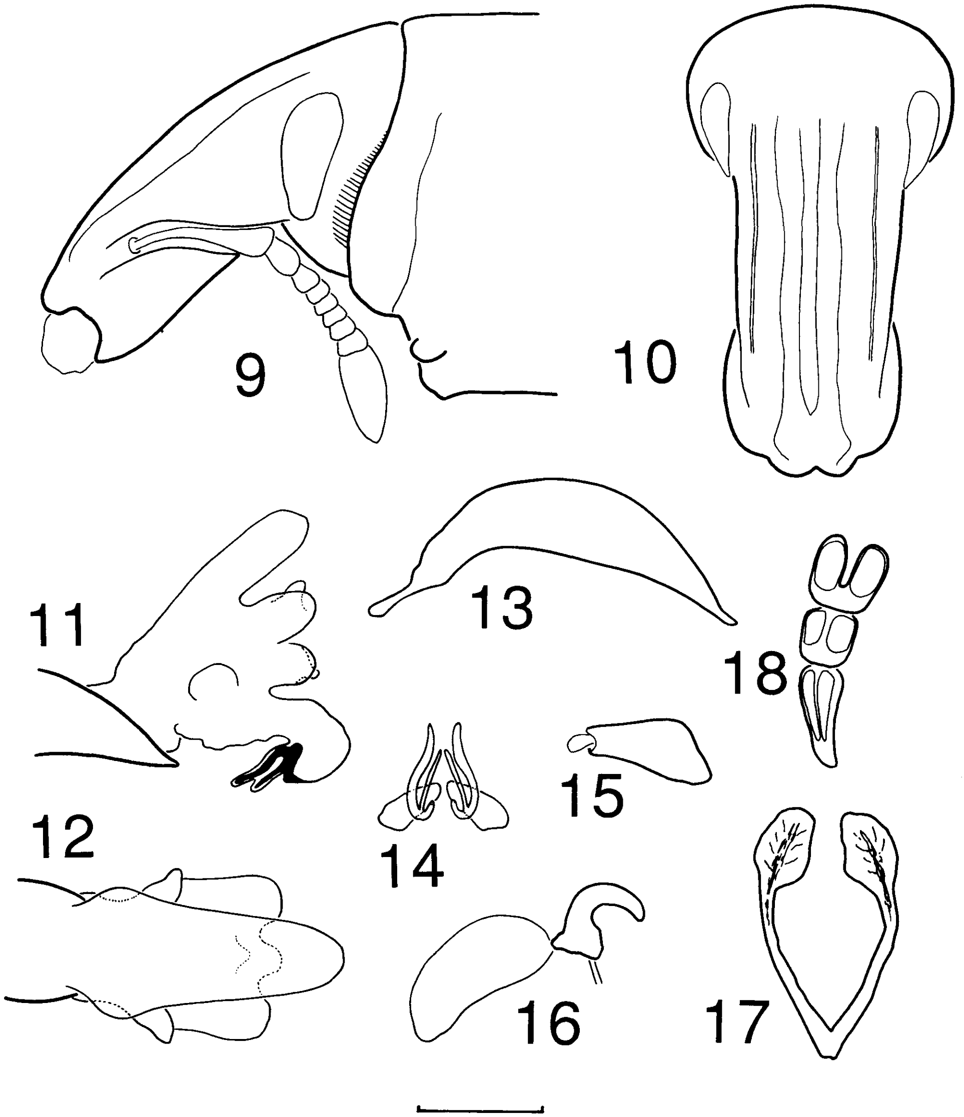
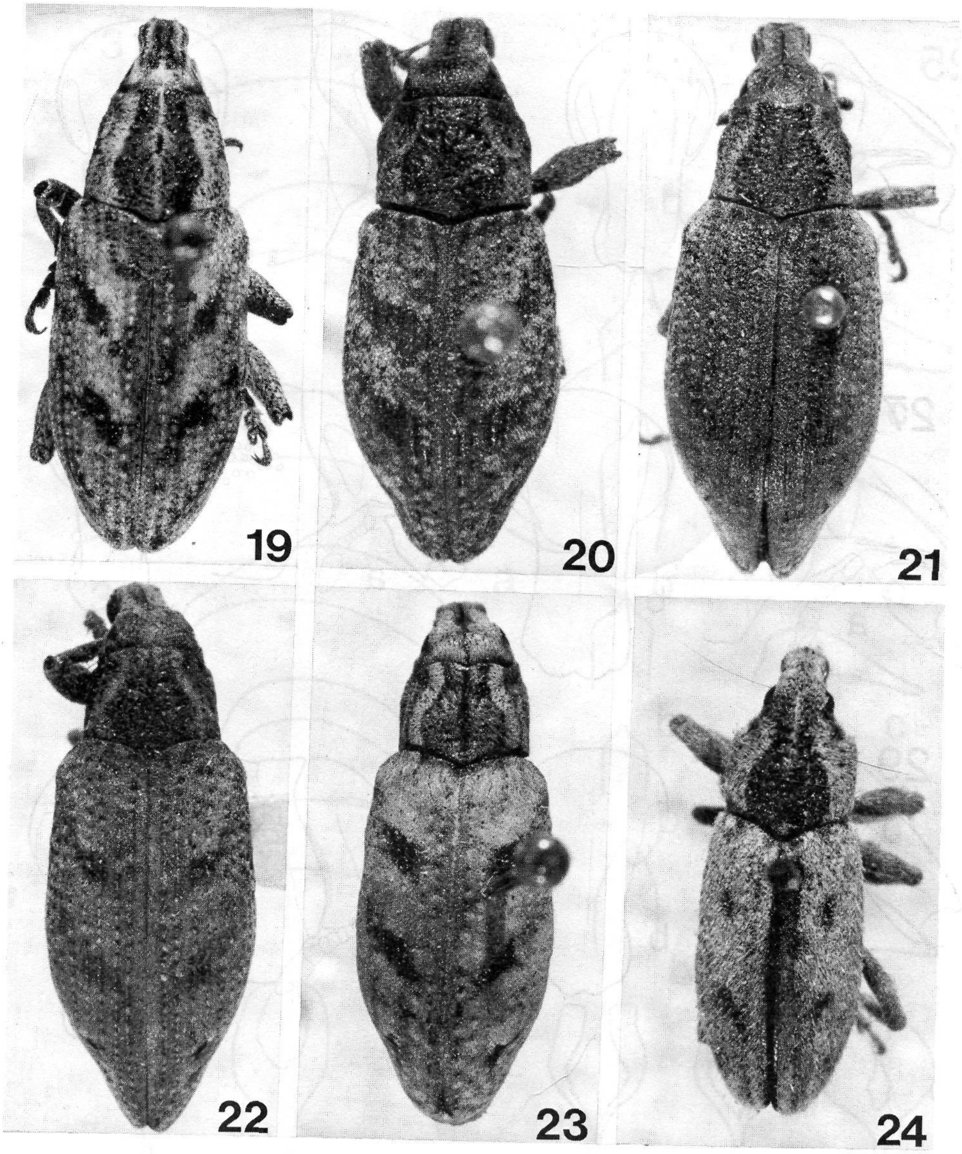
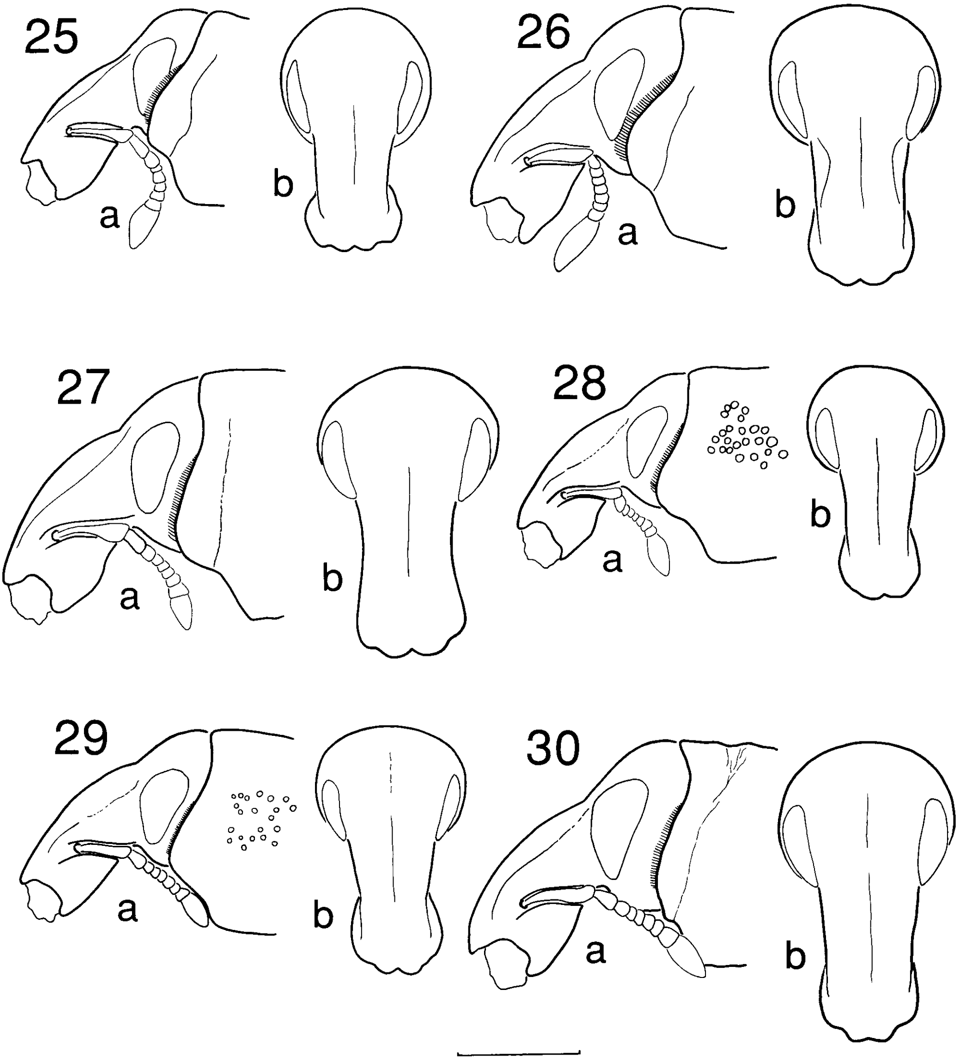
Figures 1–4. Lateral view of head of various Cleoninae. 1, *Microlarinus* species (Scale bar = 0.8 mm); 2, *Rhinocyllus conicus* (Scale bar = 1.6 mm); 3, *Larinus planus* (Scale bar = 1.6 mm); 4, *Lixus scrobicollis* (Scale bar = 1.6 mm). Figures 5–6. Apex of tibia of various Cleoninae (Scale bar = 0.5 mm). 5, *Cleonidius infrequens*; 6, *Apleurus lutulentus*. Figures 7–8. Ventral view of prosternum of various Cleoninae (Scale bar = 1.6 mm). 7, *Apleurus* species; 8, *Cleonidius* species.



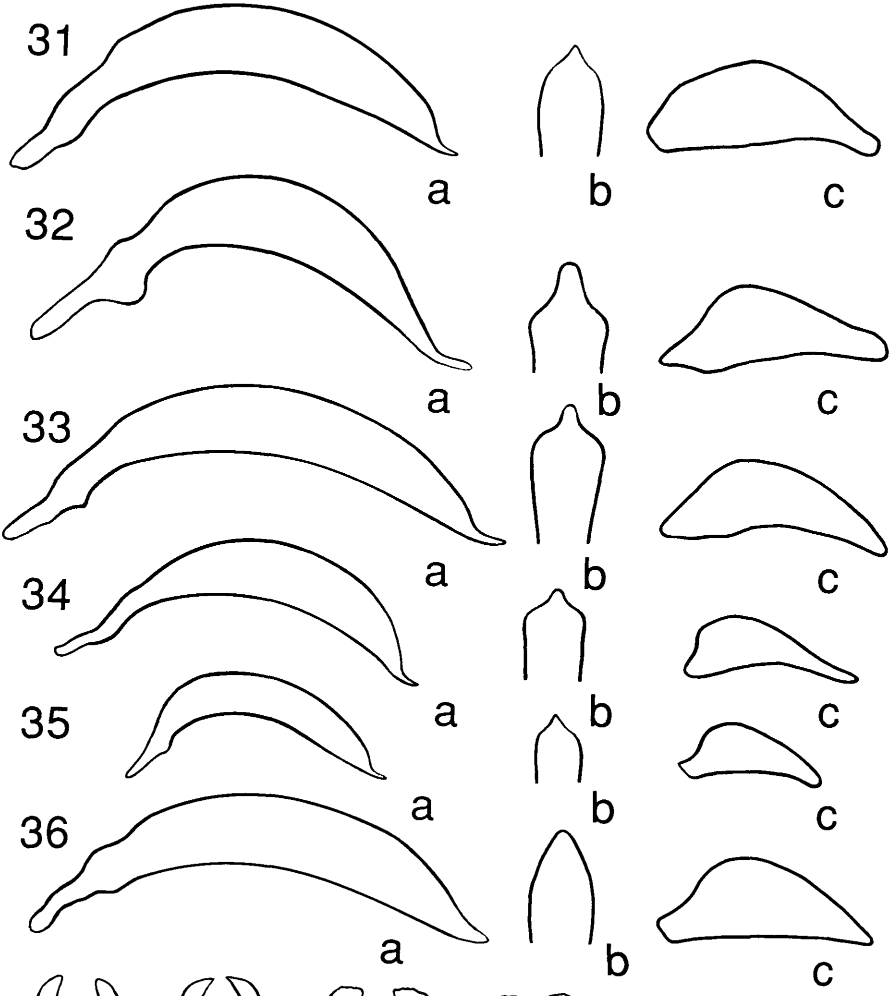
Figures 9– 18. *Cleonis pigra*. 9, lateral view of head (Scale bar = 1.1 mm); 10, dorsal view of head (Scale bar = 1.1 mm); 11, lateral view of internal sac of male (Scale bar = 0.7 mm); 12, dorsal view of internal sac of male (Scale bar = 0.7 mm); 13, lateral view of aedeagus of male (Scale bar = 1.3 mm); 14, ventral view of apical sclerite complex of internal sac of male (Scale bar = 0,6 mm); 15, lateral view of gonocoxite II and stylus of female (Scale bar = 1.3 mm); 16, spermatheca of female (Scale bar = 0.7 mm); 17, ventral view of sternum VIII of female (Scale bar = 1.3 mm); 18, ventral view of metatarsus (Scale bar = 1.3 mm).

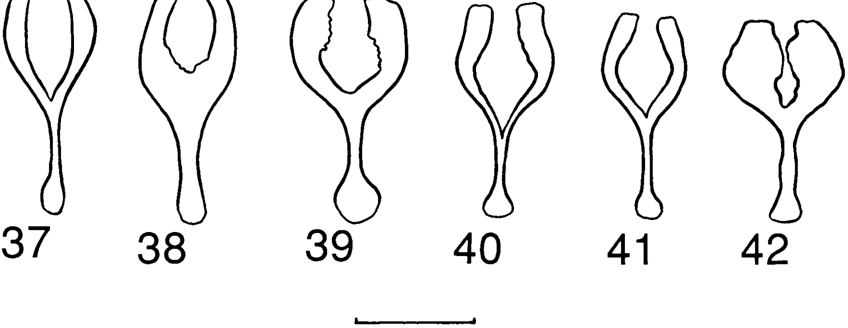


Figures 19–24. Dorsal habitus of: 19, *Cleonis pigra* (Scale bar = 5.0 mm); 20, *Stephanocleonus confusus* (Scale bar = 5.0 mm); 21, *S. immaculatus* (Scale bar = 5.0 mm); 22, *S. plumbeus* (Scale bar = 5.0 mm); 23, *S. stenothorax* (Scale bar = 5.0 mm); 24, *Apleurus (Gibbostethus) hystrix* (Scale bar = 2.5 mm).

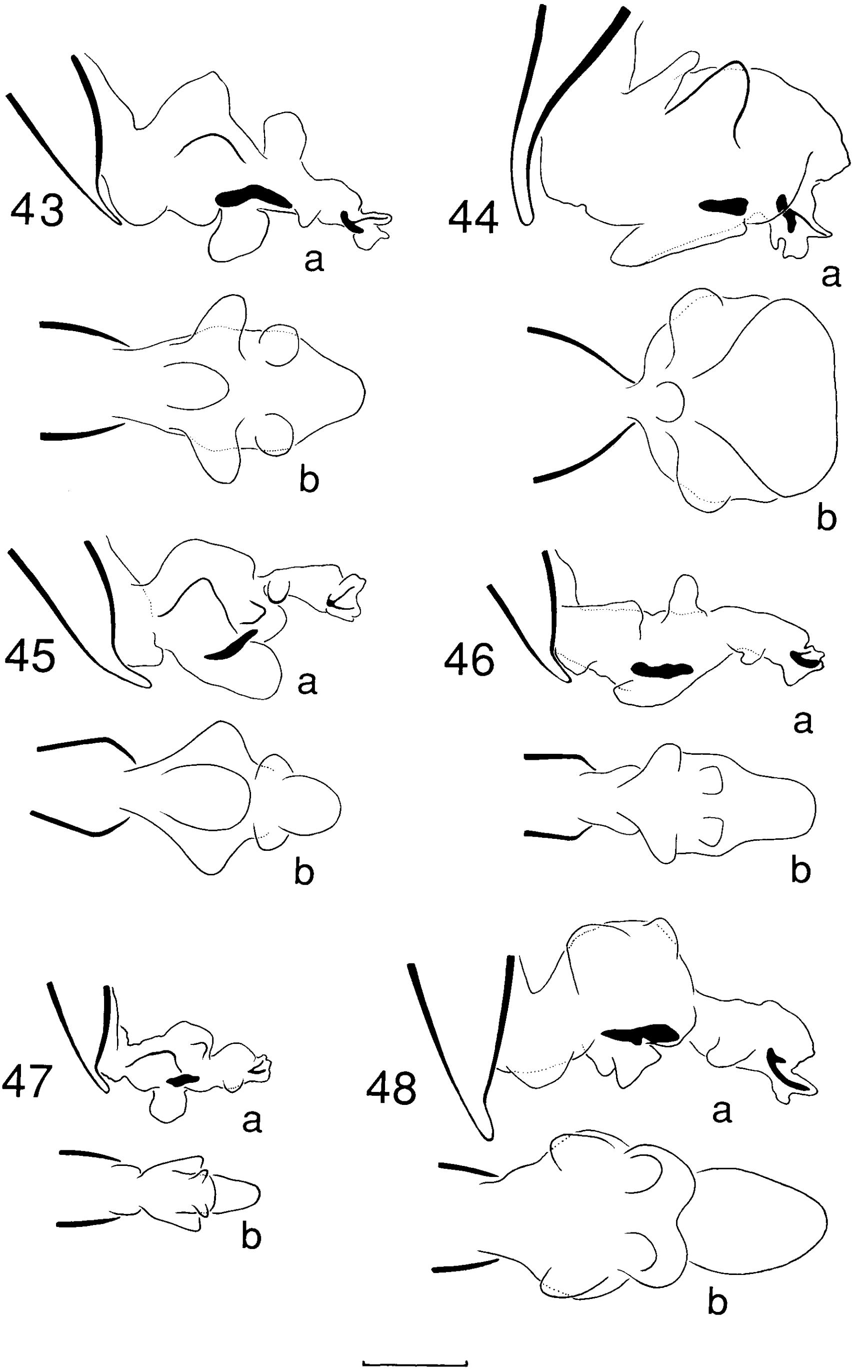


Figures 25–30. Head of *Stephanocleonus* species (Scale bar = 2.4 mm) – a, lateral view; b, dorsal view. 25, *S. confusus*; 26, *S. cristaticollis*; 27, *S. immaculatus*; 28, *S. parshus*; 29, *S. plumbeus*; 30, *S. stenothorax*.





Figures 31–36. Male genitalia of *Stephanocleonus* species (Scale bar = 1.3 mm) – a and b, lateral and ventral views of aedeagus, respectively; c, ventral view of sternum VII. 31, *S. confusus*; 32, *S. cristaticollis*; 33, *S. immaculatus*; 34, *S. parshus*; 35, *S. plumbeus*; 36, *S. stenothorax*. Figures 37–42. Ventral view of sternum VIII of female *Stephanocleonus* species (Scale bar = 1.3 mm). 37, *S. confusus*; 38, *S. cristaticollis*; 39, *S. immaculatus*; 40, *S. parshus*; 41, *S. plumbeus*; 42, *S. stenothorax*.



Figures 43–48. Internal sac of male *Stephanocleonus* species (Scale bar = 0.7 mm) – a and b, lateral and dorsal view, respectively. 43, *S. confusus*; 44, *S. cristaticollis*; 45. *S. immaculatus*; 46, *S. parshus*; 47, *S. plumbeus*. 48, *S. stenothorax*.

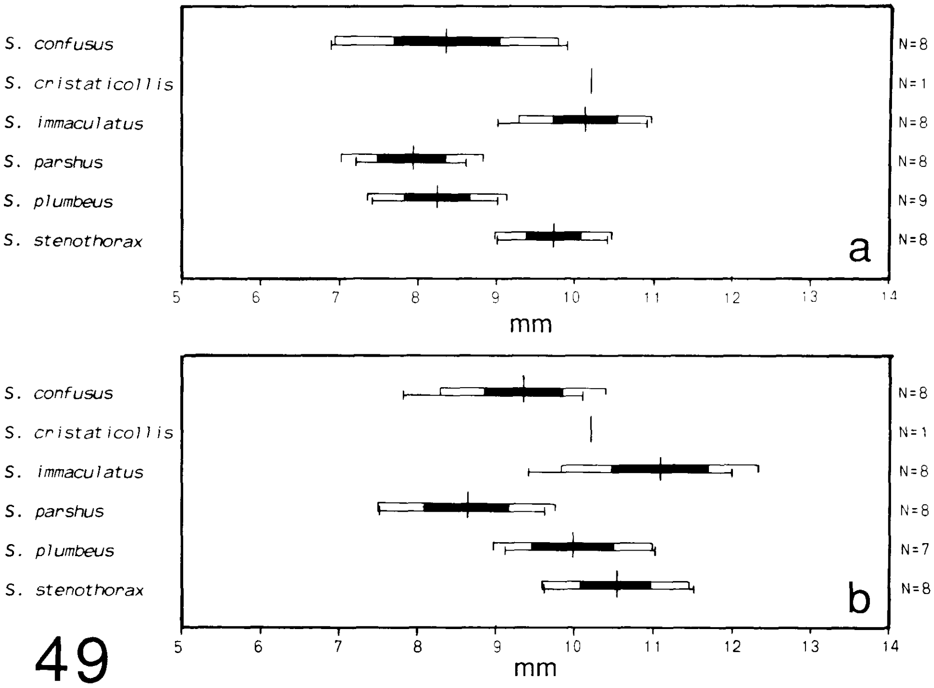
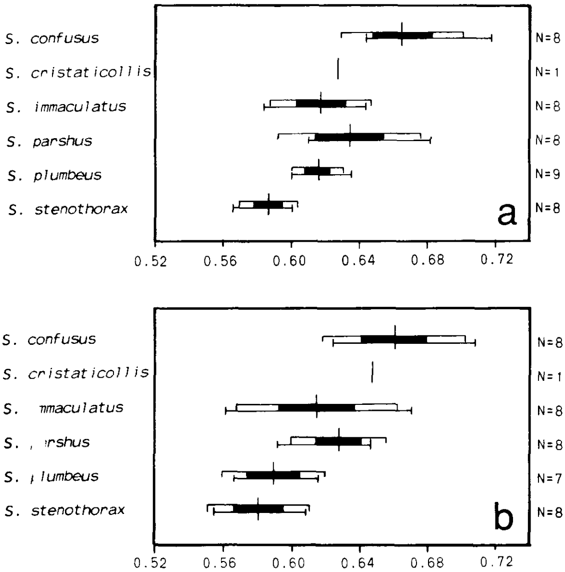


Figure 49. Hubbs-Hubbs diagram illustrating variation among specimens of *Stephanocleonus* species: length of elytra (LEI) – a, males; b, females. The range of each species is indicated by a horizontal line and the mean by a long vertical line. A solid rectangle represents two standard errors on either side of the mean and a hollow rectangle represents 1.5 standard deviations on either side of the mean. Only mean and range are shown for samples with less than five specimens.



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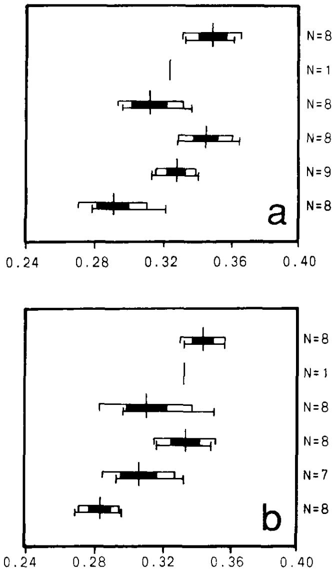

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Figures 50–51. Hubbs-Hubbs diagrams illustrating variation among specimens of *Stephanocleonus* species – a, males; b, females. See caption for Fig. 49 for explanation. 50, form of elytra (WElM/LEl); 51, relative length of pronotum compared to elytra (LP/LEl).

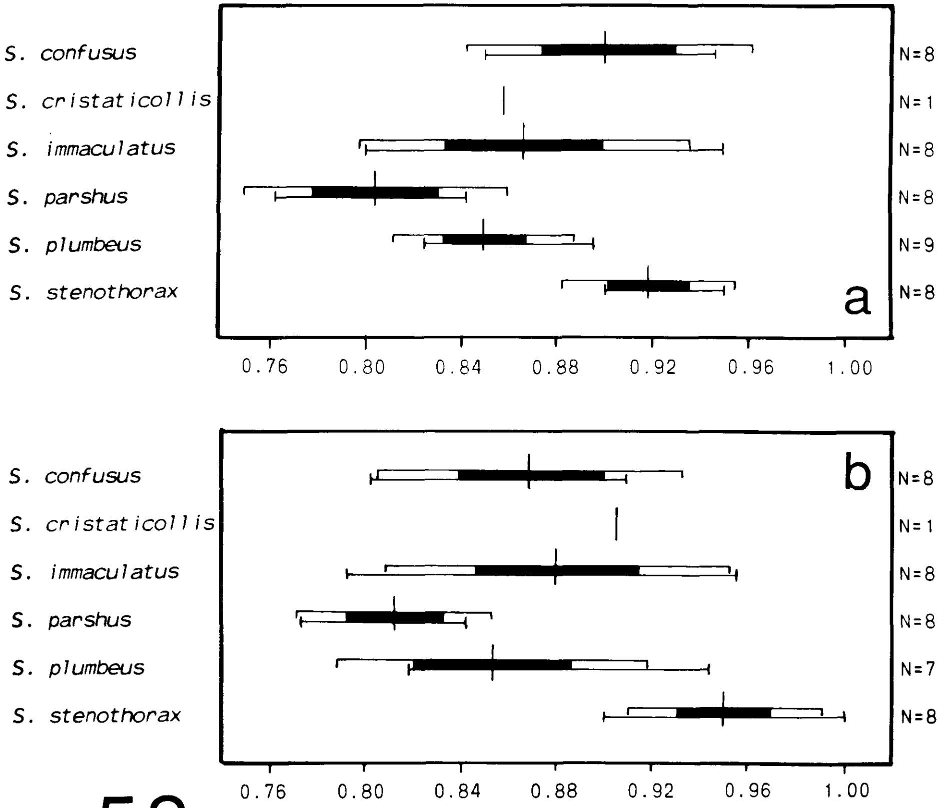

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Figure 52. Hubbs-Hubbs diagram illustrating variation among specimens of *Stephanocleonus* species: form of rostrum (WRA/WF) – a, males; b, females. See caption for Fig. 49 for explanation.

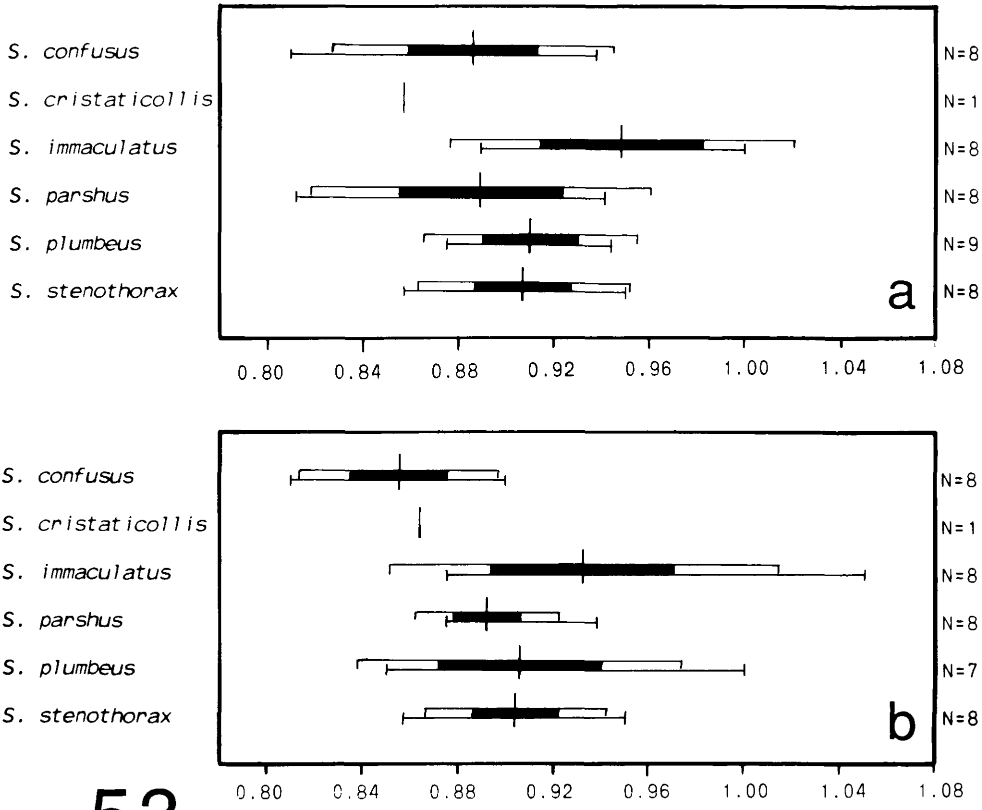

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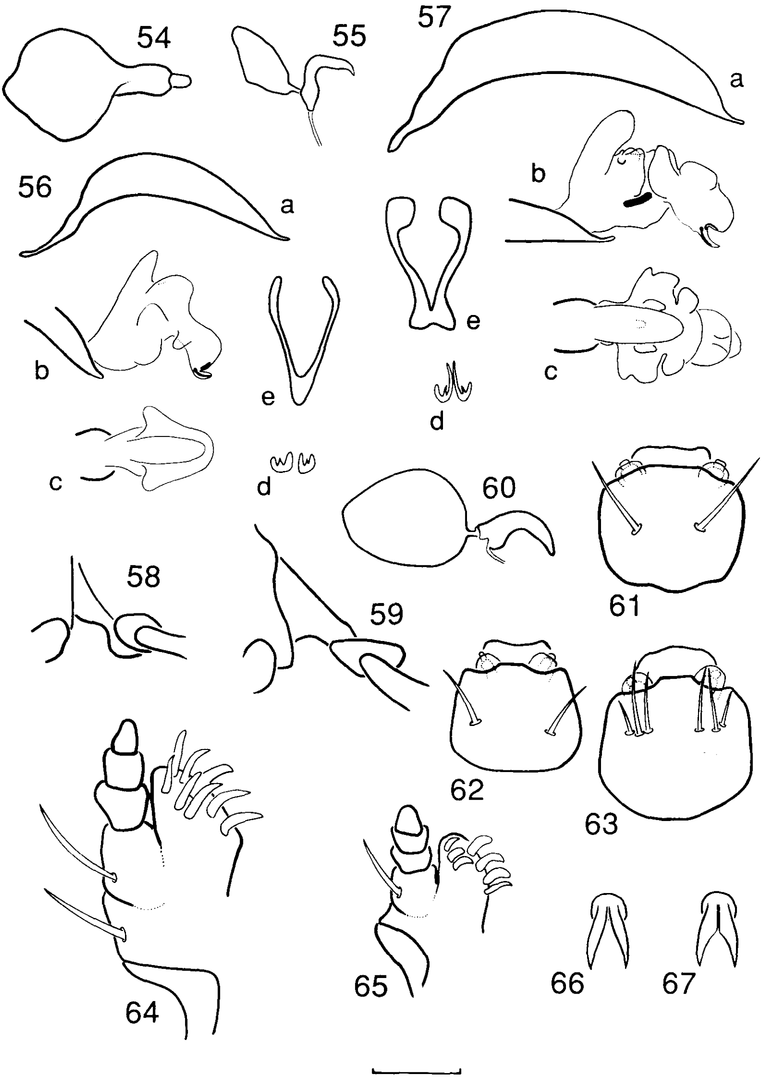
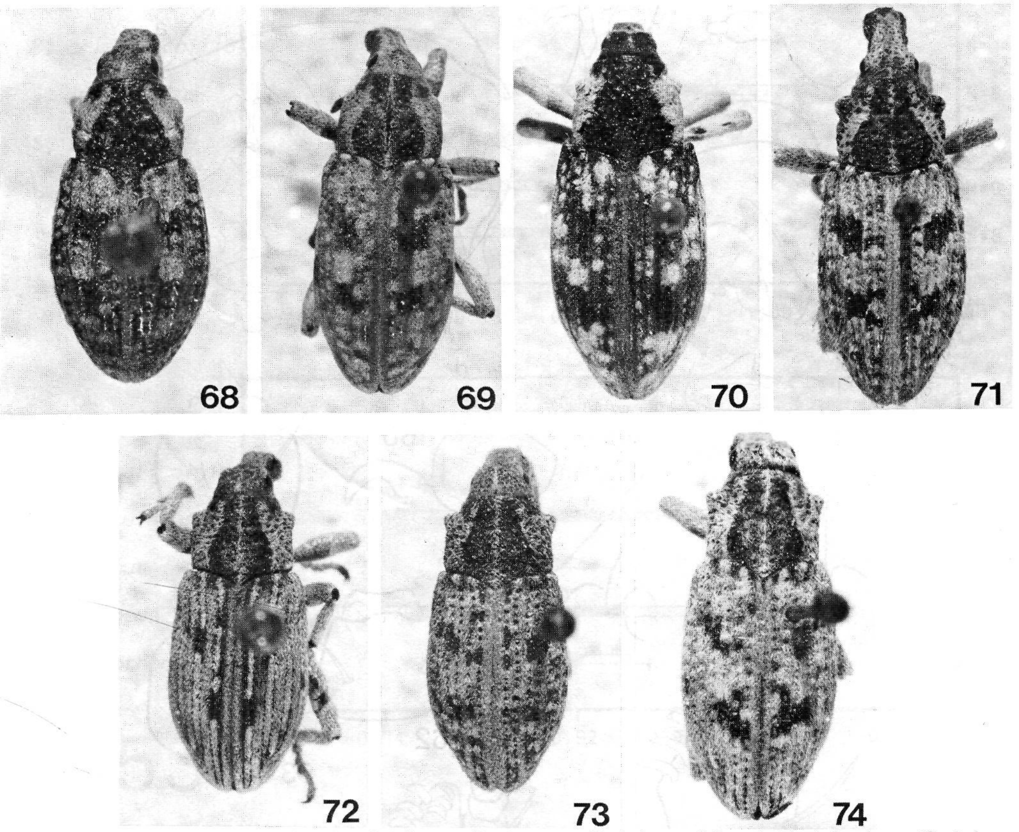
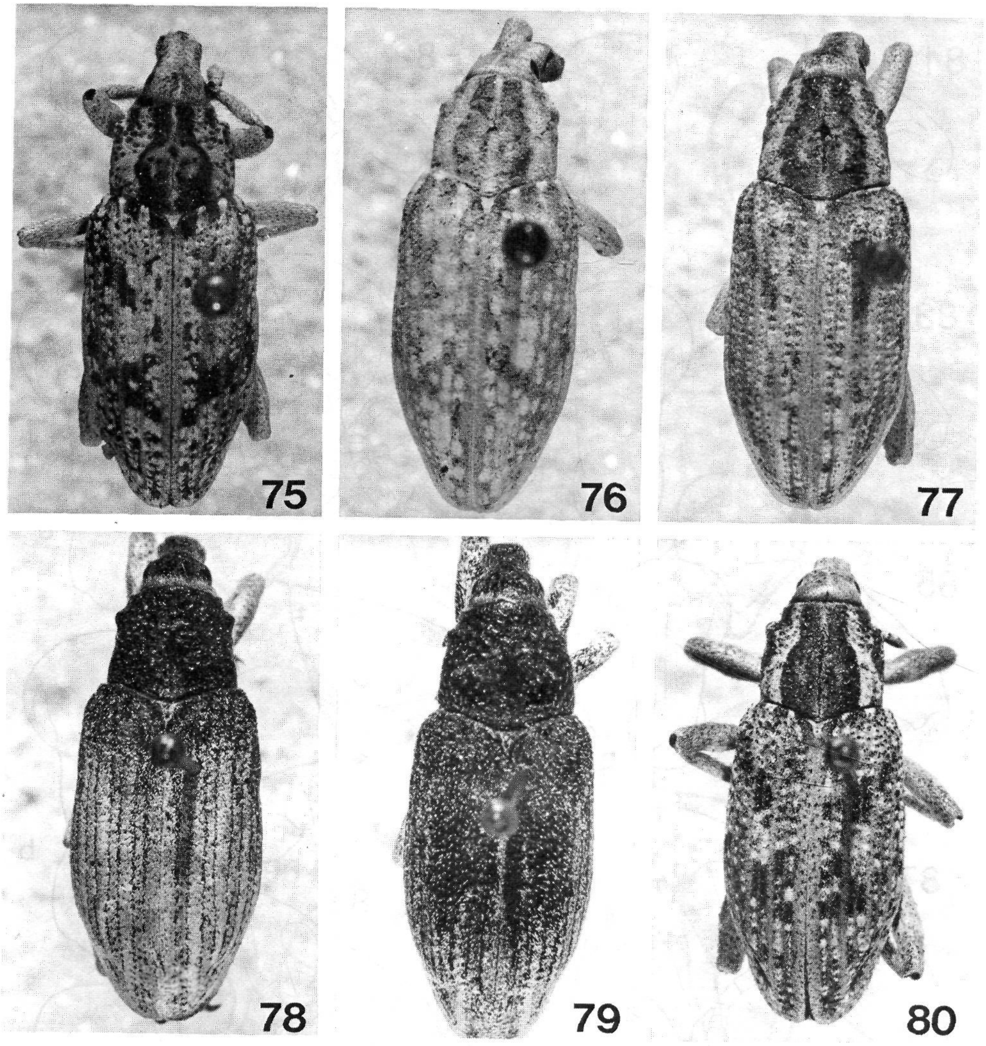
Figure 53. Hubbs-Hubbs diagram illustrating variation among specimens of *Stephanocleonus* species: relative width of frons compared to rostrum (WRA/WF) – a, males; b, females. See caption for Fig. 49 for explanation.



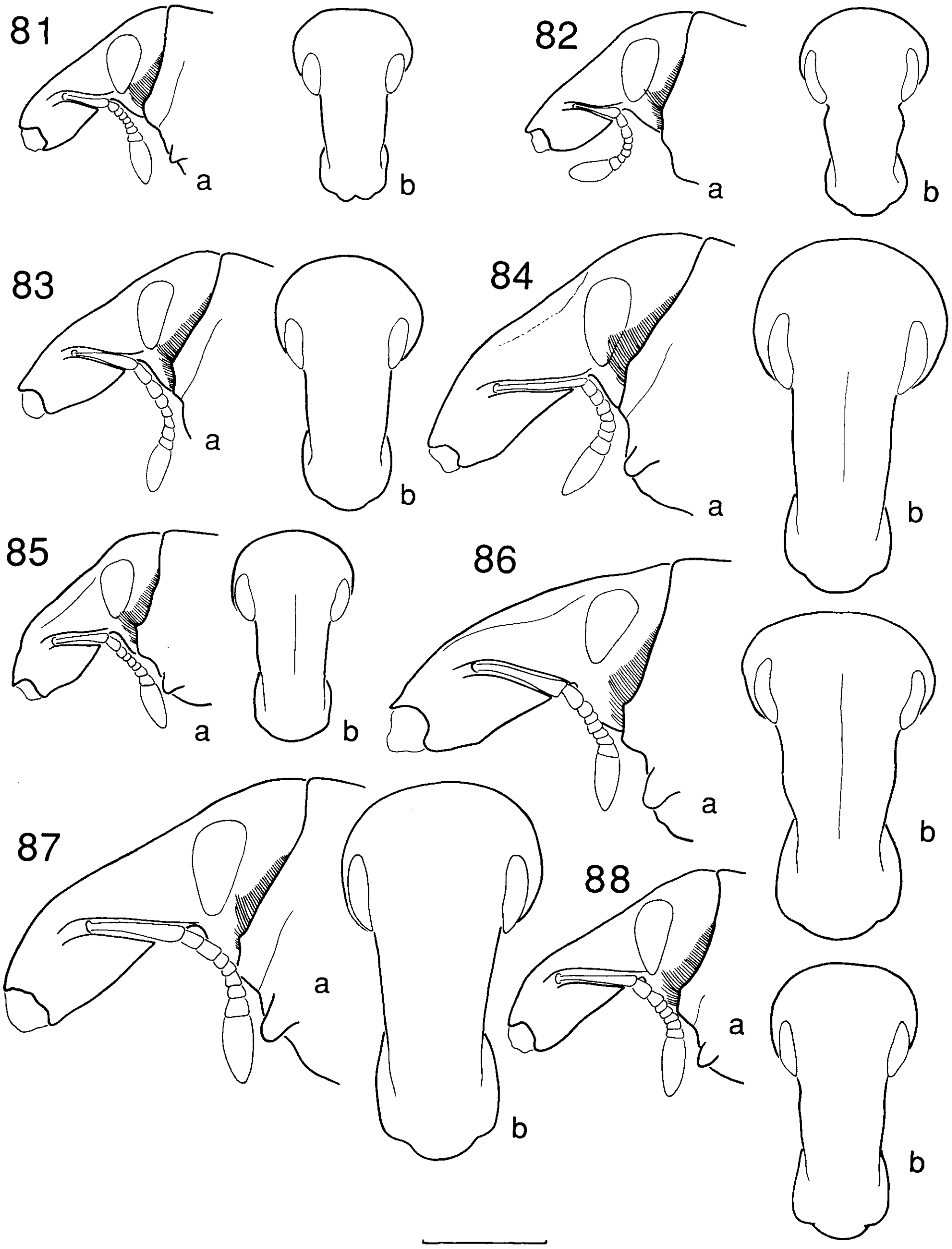
Figures 54–67. 54, lateral view of gonocoxite II and stylus of female *Stephanocleonus* (Scale bar = 0.7 mm). 55, spermatheca of female *Stephanocleonus* (Scale bar = 0.7 mm). 56, genitalia of *Chromoderus fasciatus*; a, lateral view of aedeagus of male (Scale bar = 1.3 mm); b, lateral view of internal sac of male (Scale bar = 0.7 mm); c, dorsal view of internal sac of male (Scale bar = 0.7 mm); d, ventral view of apical sclerite complex of internal sac of male (Scale bar = 0.6 mm); e, ventral view of sternum VIII of female (Scale bar = 1.3 mm). 57, genitalia of *Cnemodontus limpidus*; a, lateral view of aedeagus of male (Scale bar = 1.3 mm); b, lateral view of internal sac of male (Scale bar = 0.7 mm); c, dorsal view of internal sac of male (Scale bar = 0.7 mm); d, ventral view of apical sclerite complex of internal sac of male (Scale bar = 0.6 mm); e, ventral view of sternum VIII of female (Scale bar = 1.3 mm). 58, lateral view of mesosternum of *Apleurus (Gibbostethus) hystrix* (Scale bar = 1.3 mm). 59, lateral view of mesosternum of *Apleurus (Apleurus) lutulentus* (Scale bar = 1.3 mm). 60, spermatheca of female *Apleurus* (Scale bar = 0.7 mm). 61, ventral view of ligula of *Apleurus (Gibbostethus) hystrix* (Scale bar = 0.2 mm). 62, ventral view of ligula of *Apleurus (Apleurus) lutulentus* (Scale bar = 0.4 mm). 63, ventral view of ligula of *Apleurus (Apleurus) saginatus* (Scale bar = 0.4 mm). 64, ventral view of maxilla of *Apleurus (Apleurus) saginatus* (Scale bar = 0.4 mm). 65, ventral view of maxilla of *Apleurus (Gibbostethus) hystrix* (Scale bar = 0.4 mm). 66, tarsal claws of *Apleurus angularis* (Scale bar = 0.7 mm). 67, tarsal claws of *Apleurus jacobinus* (Scale bar = 0.7 mm).



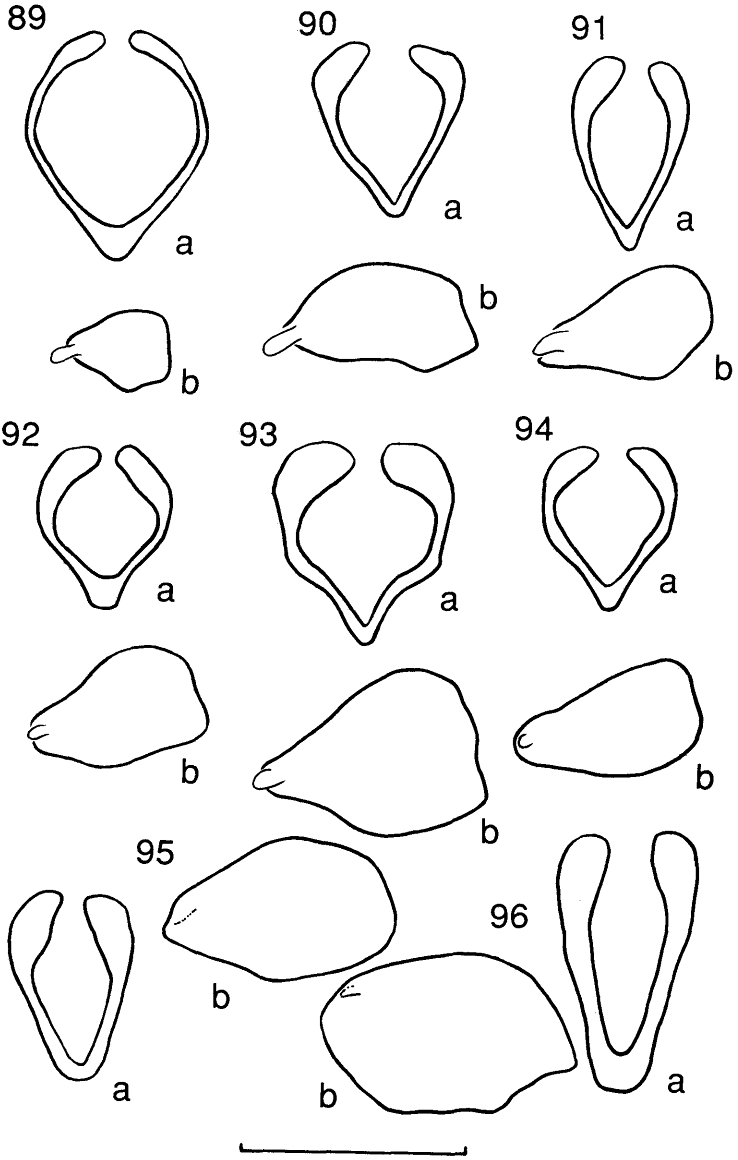
Figures 68–74. Dorsal habitus of species of *Apleurus*. 68, *A. aztecus* (Scale bar = 2.0 mm); 69, *A. lutulentus* (Scale bar = 4.0 mm); 70, *A. porosus* (Scale bar = 4.0 mm); 71, *A. jacobinus* (Scale bar = 4.0 mm); 72, *A. angularis* (3 mi. N Baker, Nevada) (Scale bar = 4.0 mm); 73, *A. angularis* (Colorado Springs, Colorado) (Scale bar = 4.0 mm); 74, *A. angularis* (Baboquivari Mountains, Arizona) (Scale bar = 3.0 mm).



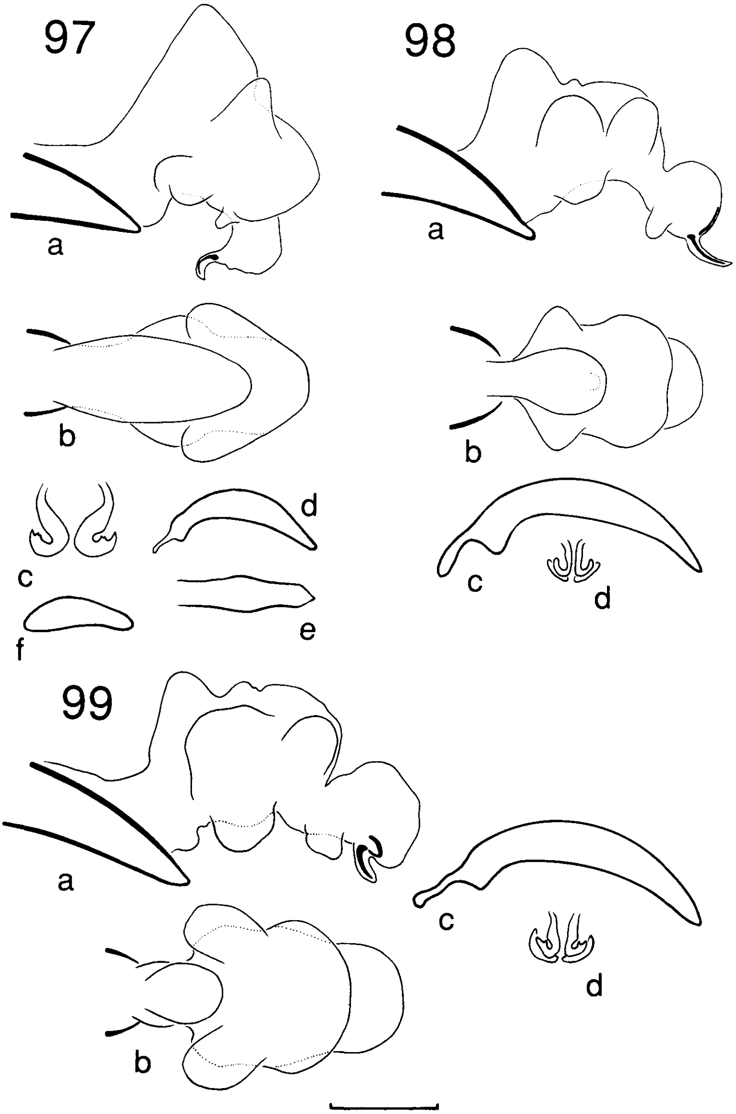
Figures 75–80. Dorsal habitus of species of *Apleurus* (Scale bar = 5.0 mm). 75, *A. albovestitus* (18 mi. SW Mendota, California); 76, *A. albovestitus* (16 mi. S. Vidal, California); 77, *A. albovestitus* (Virgin, Utah); 78, *A. albovestitus* (Phoenix, Arizona); 79, *A. albovestitus* (Yuma, Arizona); 80, *A. saginatus*.



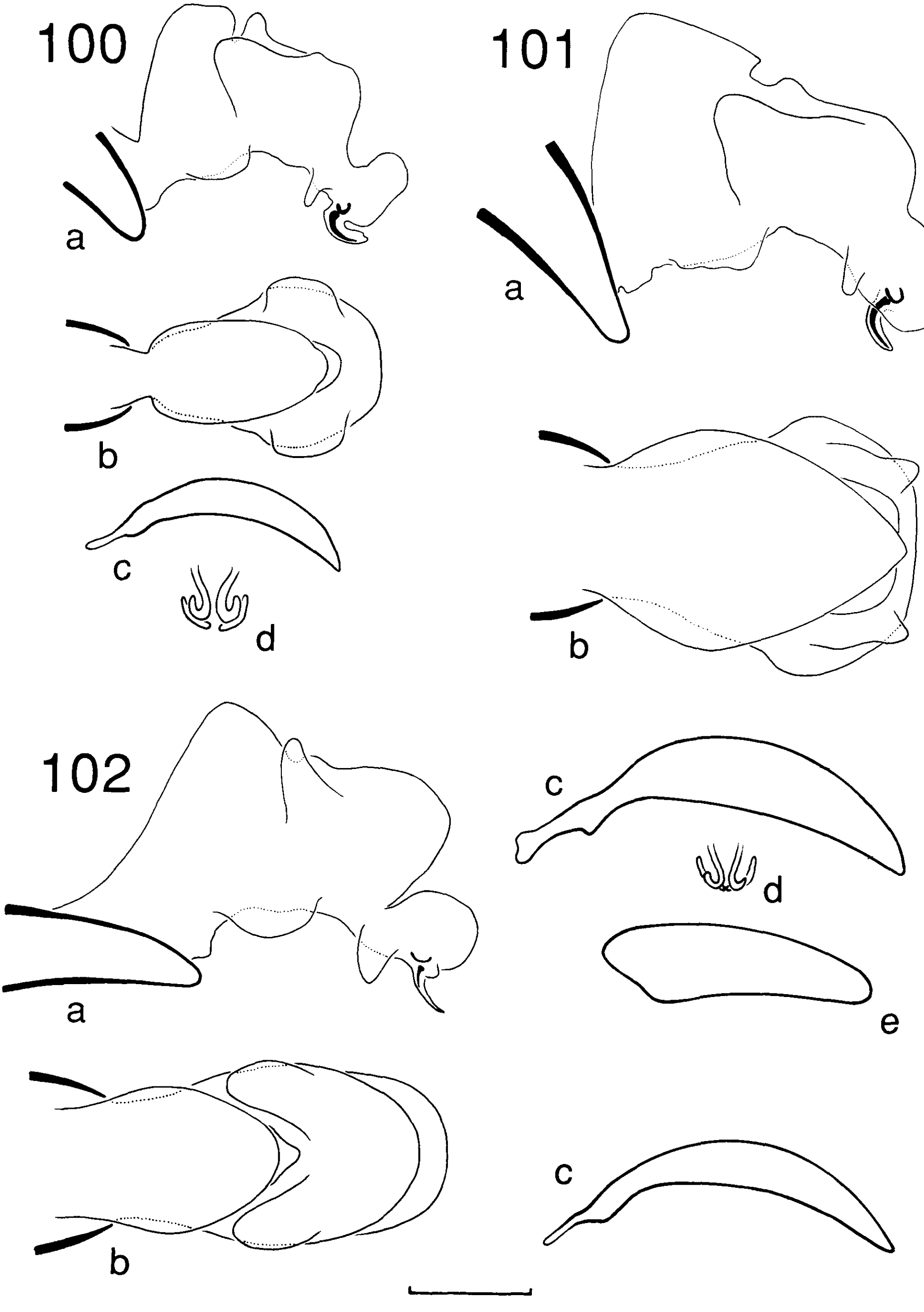
Figures 81–88. Head of *Apleurus* species (Scale bar = 2.4 mm) – a and b, lateral and dorsal views, respectively. 81, *A. hystrix*; 82, *A. aztecus*; 83, *A. lutulentus*; 84, *A. porosus*; 85, *A. angularis*; 86, *A. jacobinus*; 87, *A. saginatus*; 88, *A. albovestitus*.



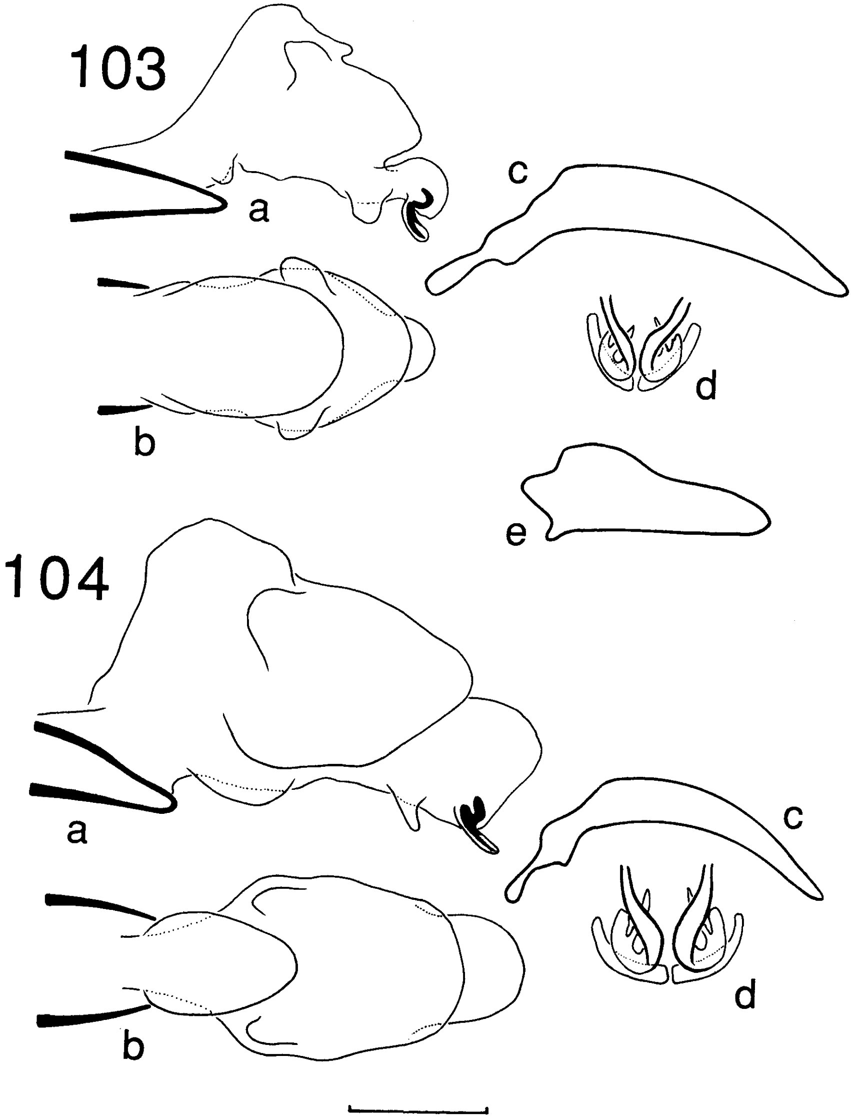
Figures 89–96. Female genitalia of *Apleurus* species. 89, *A. hystrix* (Scale bar = 1.0 mm); a, ventral view of sternum VIII; b, lateral view of gonocoxite II and stylus. 90, *A. aztecus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 91, *A. lutulentus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 92, *A. porosus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 93, *A. angularis*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 94, *A. jacobinus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 95, *A. albovestitus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm). 96, *A. saginatus*; a, ventral view of sternum VIII (Scale bar = 2.0 mm); b, lateral view of gonocoxite II and stylus (Scale bar = 1.0 mm).



Figures 97–99. Male genitalia of *Apleurus* species. 97, *A. hystrix*; a, lateral view of internal sac (Scale bar = 0.4 mm); b, dorsal view of internal sac (Scale bar = 0.4 mm); c, ventral view of apical sclerite complex of internal sac (Scale bar = 0.3 mm); d, lateral view of aedeagus (Scale bar = 1.3 mm); e, ventral view of aedeagus (Scale bar = 1.3 mm); f, ventral view of sternite of sternum VII (Scale bar = 1.3 mm). 98, *A. aztecus*; a, lateral view of internal sac (Scale bar = 0.7 mm); b, dorsal view of internal sac (Scale bar = 0.7 mm); c, lateral view of aedeagus (Scale bar = 1.3 mm); d, ventral view of apical sclerite complex of internal sac (Scale bar = 0.6 mm). 99, *A. lutulentus* (Scale bars as in Fig. 98); a, lateral view of internal sac; b, dorsal view of internal sac; c, lateral view of aedeagus; d, ventral view of apical sclerite complex of internal sac.



Figures 100–102. Male genitalia of *Apleurus* species – a, lateral view of internal sac (Scale bar = 0.7 mm); b, dorsal view of internal sac (Scale bar = 0.7 mm); c, lateral view of aedeagus (Scale bar = 1.3 mm); d, ventral view of apical sclerite complex of internal sac (Scale bar = 0.6 mm); e, ventral view of sternite of sternum VII. 100, *A. angularis*; 101, *A. jacobinus*; 102, *A. porosus*.



Figures 103–104. Male genitalia of *Apleurus* species – a, lateral view of internal sac (Scale bar = 0.7 mm); b, dorsal view of internal sac (Scale bar = 0.7 mm); c, lateral view of aedeagus (Scale bar = 1.3 mm); d, ventral view of apical sclerite complex of internal sac (Scale bar = 0.6 mm); e, ventral view of sternite of sternum VII (Scale bar = 1.3 mm). 103, *A. albovestitus*; 104, *A. saginatus*.

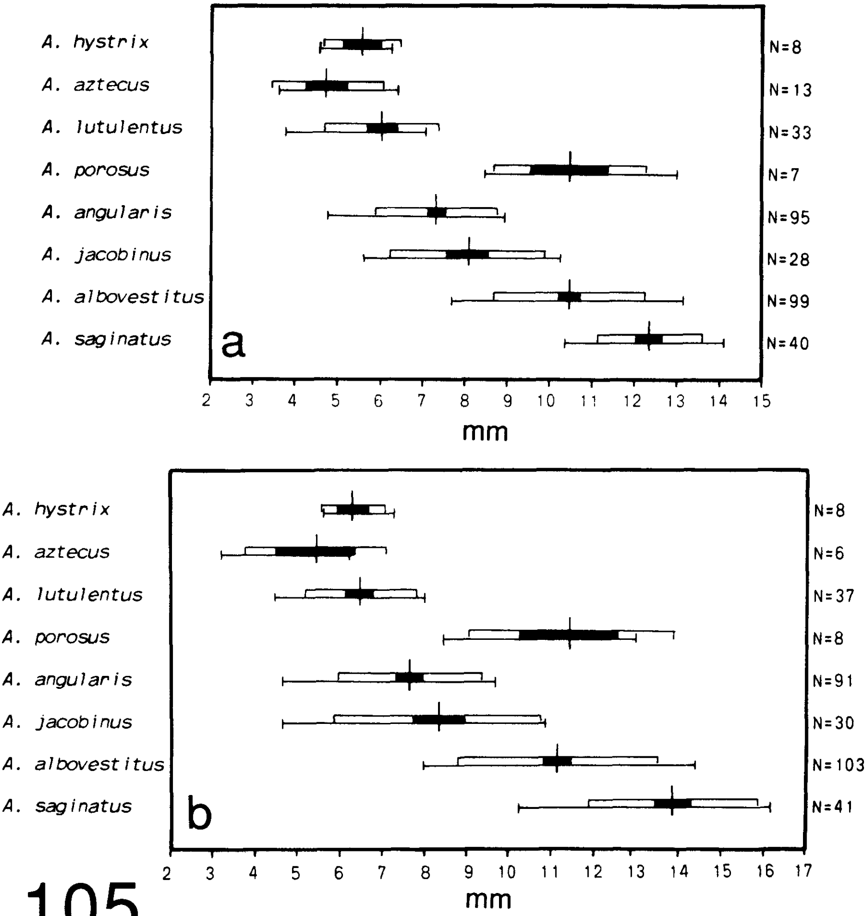


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Figure 105. Hubbs-Hubbs diagram illustrating variation among specimens of *Apleurus* species: length of elytra (LEl) – a, males; b, females. See caption for Fig. 49 for explanation.

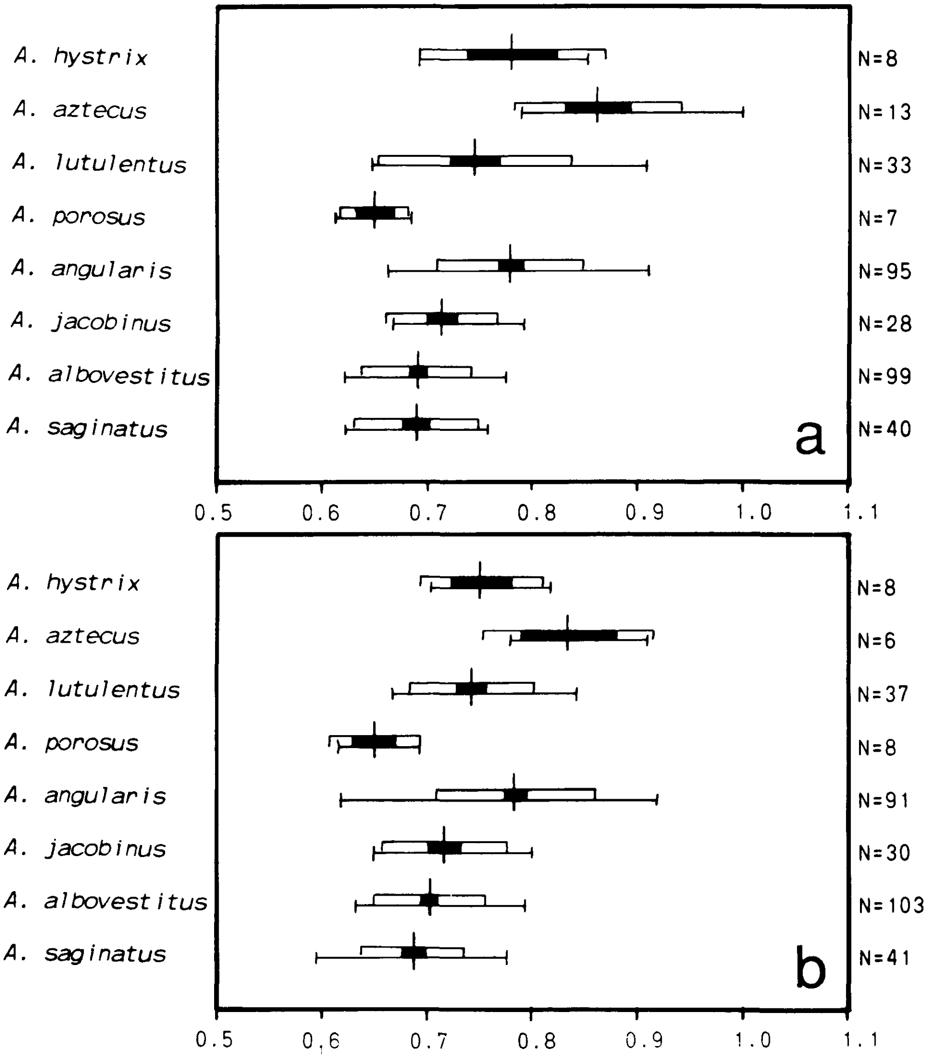

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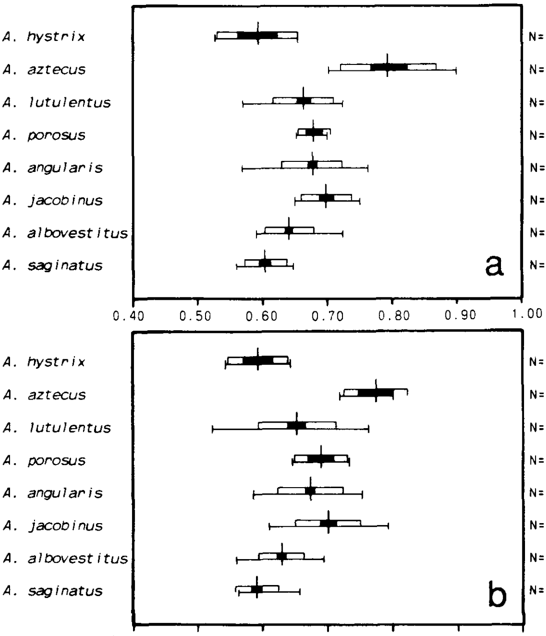
Figure 106. Hubbs-Hubbs diagram illustrating variation among specimens of *Apleurus* species: form of rostrum (WRA/LR) – a, males; b, females. See caption for Fig. 49 for explanation.



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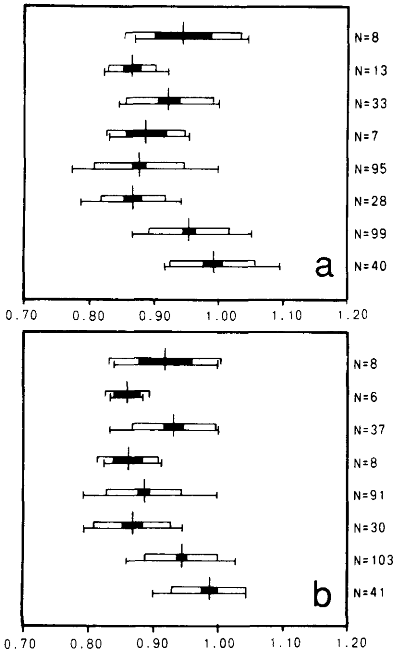
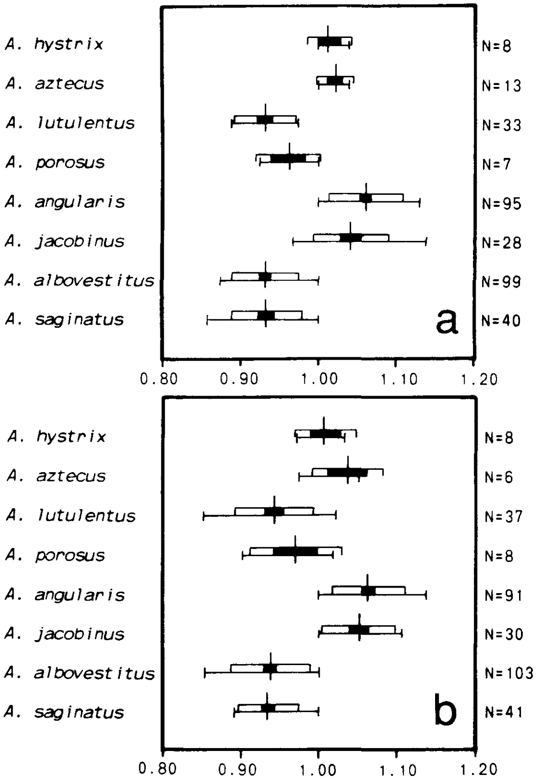


108

Figures 107–108. Hubbs-Hubbs diagrams illustrating variation among specimens of *Apleurus* species – a, males; b, females. See caption for Fig. 49 for explanation. 107, form of elytra (WElM/LEl); 108, width of frons compared to width at apex of rostrum (WRA/WF).



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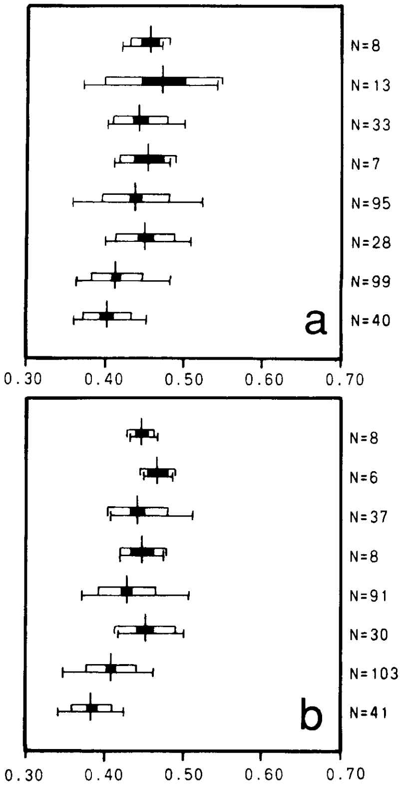
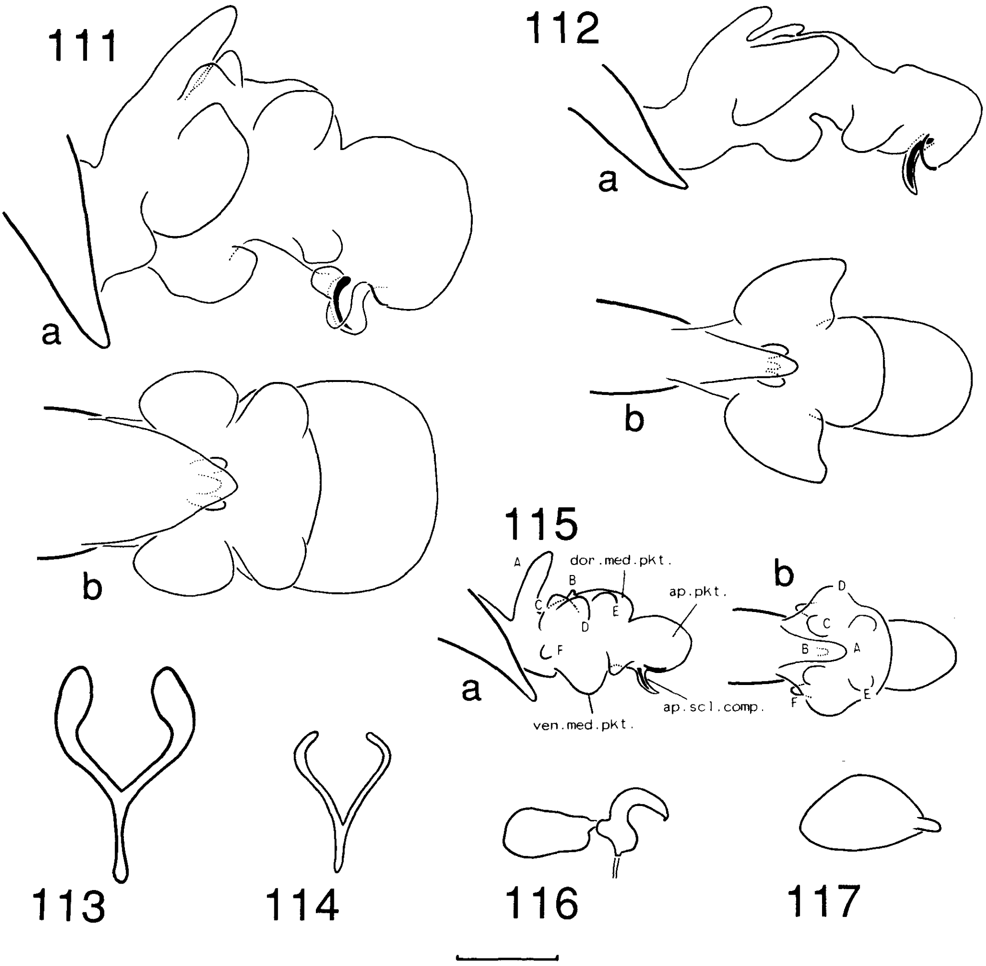
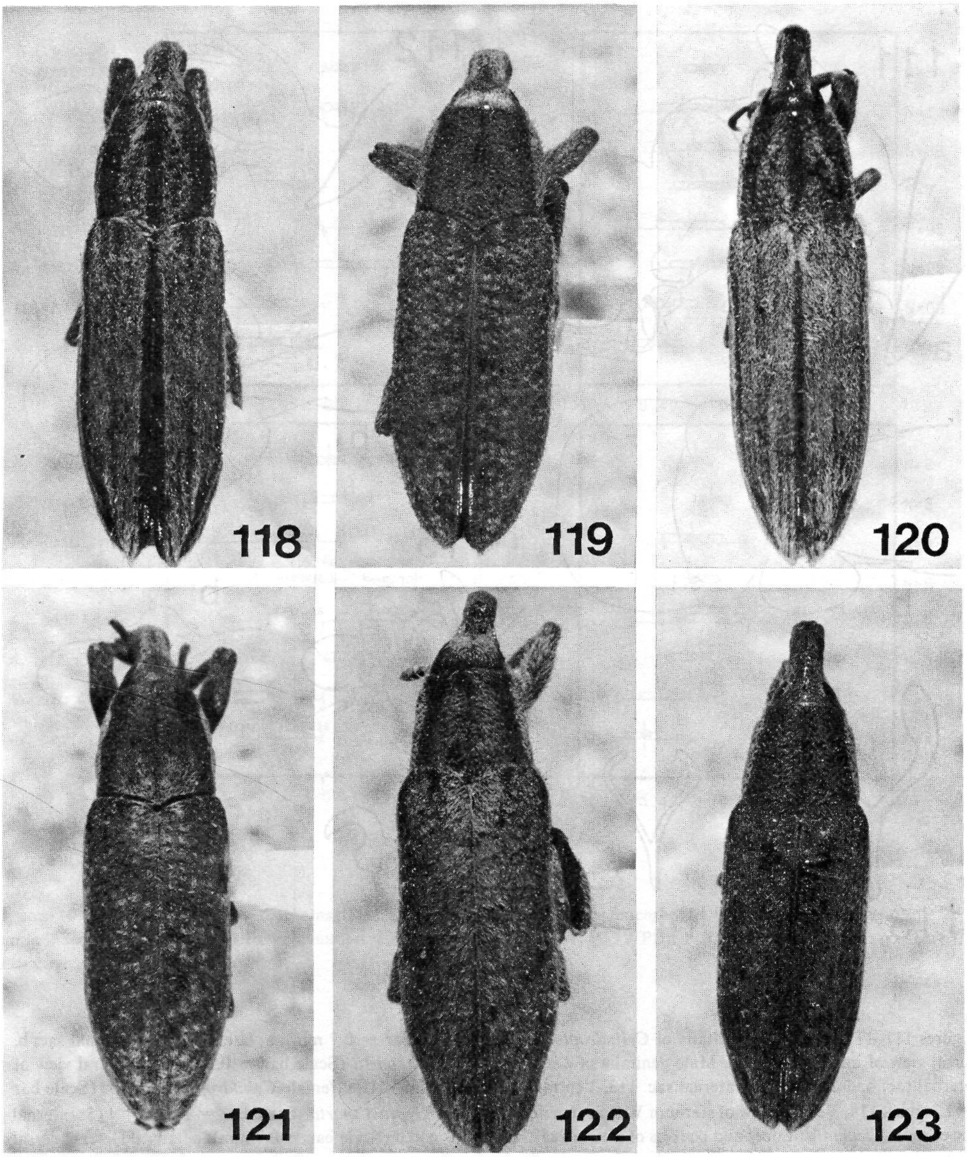


110

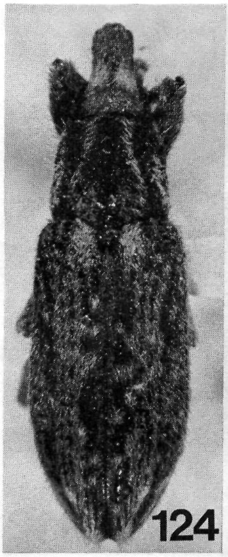
Figures 109–110: Hubbs-Hubbs diagrams illustrating variation among specimens of *Apleurus* species – a, males; b, females. See caption for Fig. 49 for explanation. 109, form of pronotum (WPT/WPB); 110, length of pronotum compared to length elytra (LP/LEl).



Figures 111–117. 111, Male genitalia of *Cylindropterus luxeri* (Scale bar = 0.7 mm); a, lateral view of internal sac; b, dorsal view of internal sac. 112, Male genitalia of *Lixus (Lixoglyptus) spartii* (Scale bar = 0.7 mm); a, lateral view of internal sac; b, dorsal view of internal sac. 113, Ventral view of sternum VIII of female *Cylindropterus luxeri* (Scale bar = 1.3 mm). 114, Ventral view of sternum VIII of female *Lixus (Lixoglyptus) spartii* (Scale bar = 1.3 mm). 115, Internal sac of male *Cleonidius* Lobes and pockets of internal sac labelled as noted (Scale bar = 0.7 mm); a, lateral view; b, dorsal view. 116, Spermatheca of female *Cleonidius* (Scale bar = 0.3 mm). 117, Lateral view of gonocoxite II and stylus of *Cleonidius* (Scale bar = 0.7 mm).



Figures 118–123. Dorsal habitus of: 118, *Cleonidius erysimi* (Scale bar = 4.0 mm); 119, *C. eustictorrhinus* (Scale bar = 4.0 mm); 120, *C. pleuralis* (Scale bar = 4.0 mm); 121, *C. subcylindricus* (Scale bar = 4.0 mm); 122, *C. longinasus* (Scale bar = 4.0 mm); 123, *C. texanus* (Scale bar = 4.0 mm).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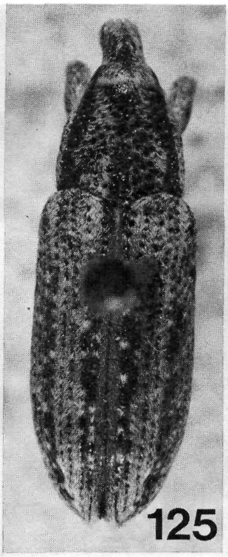
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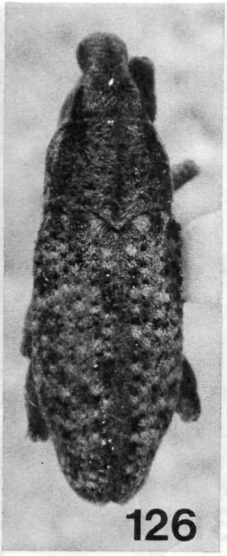
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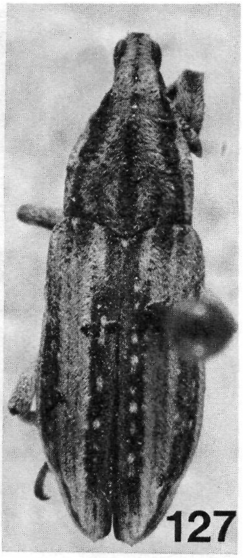
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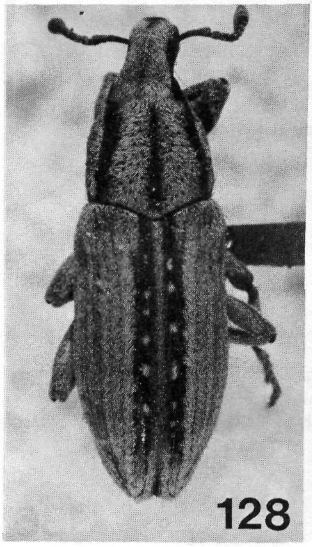
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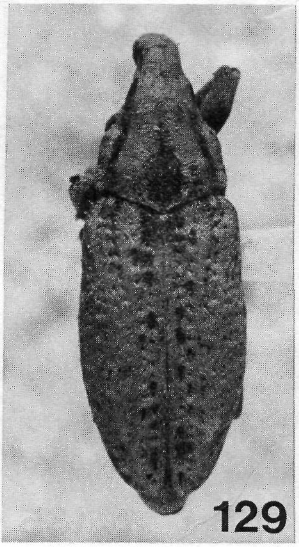
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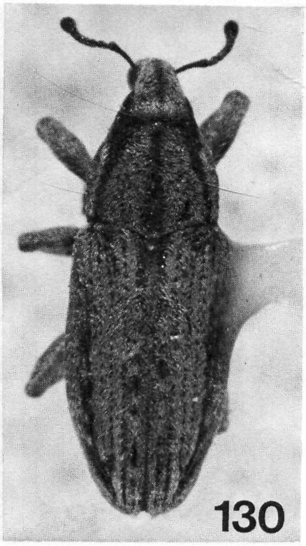
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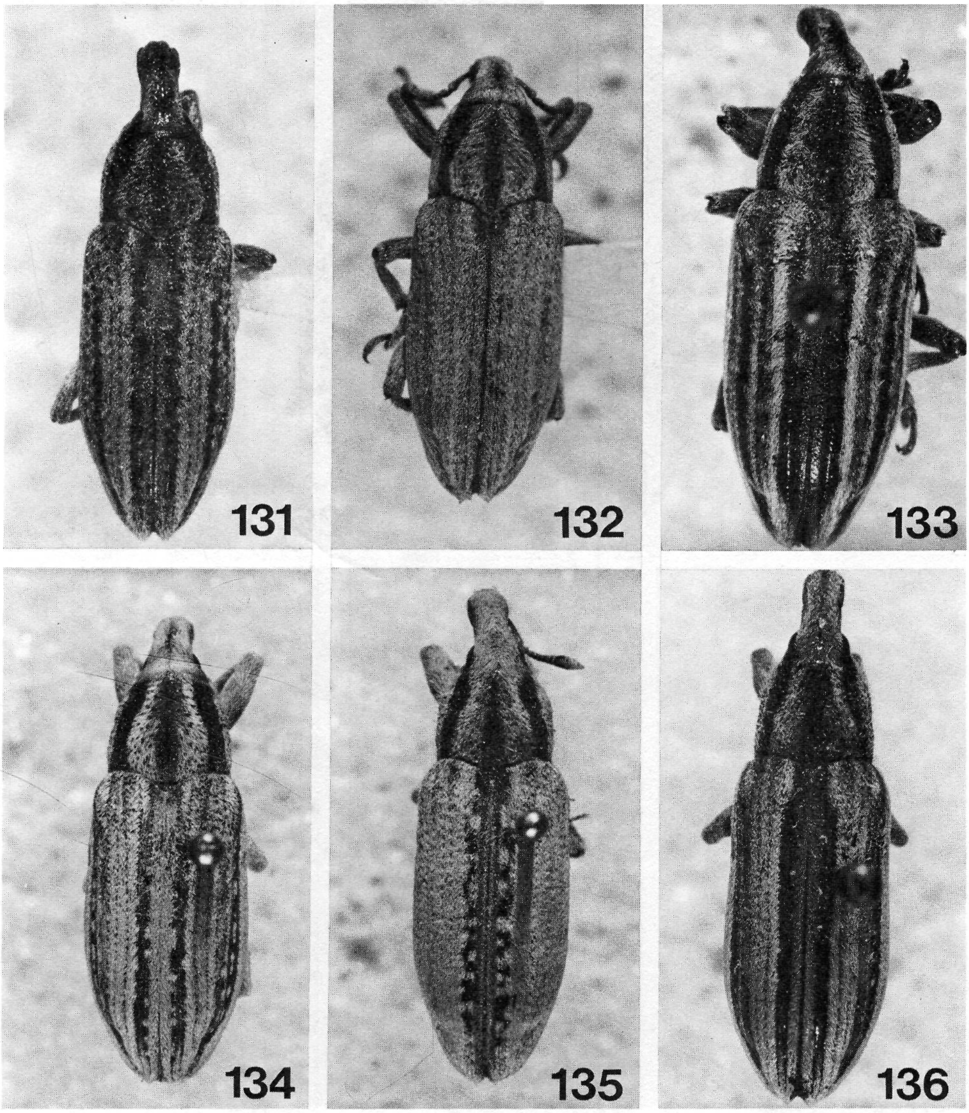
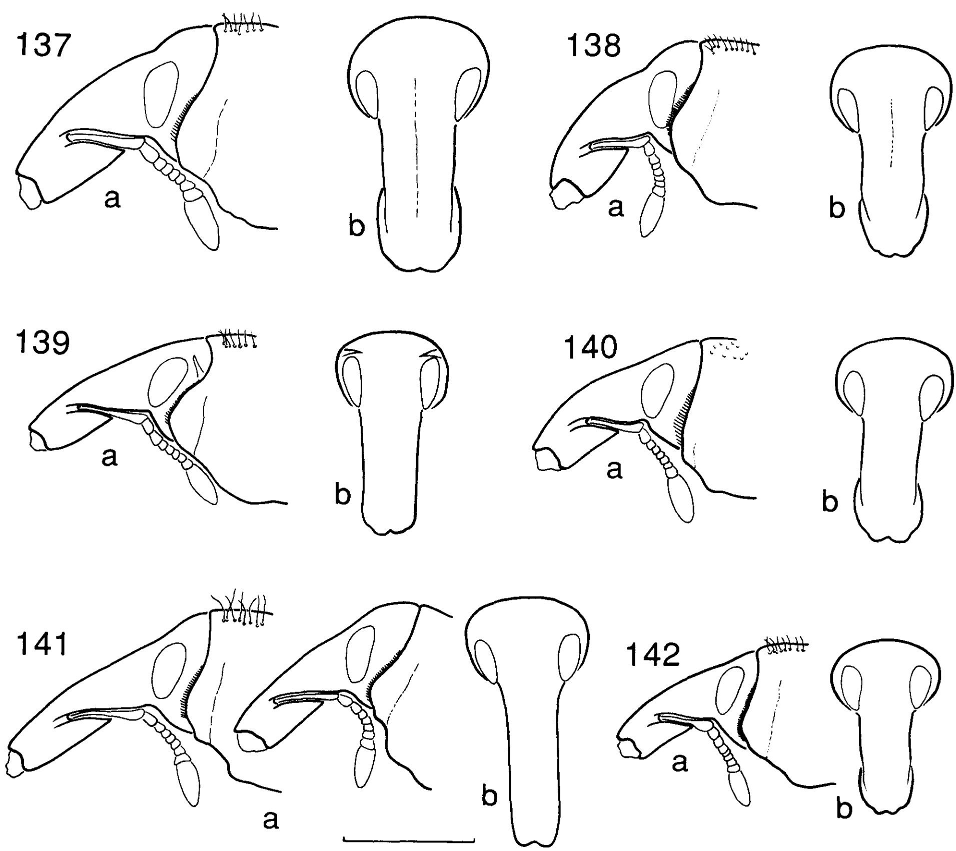
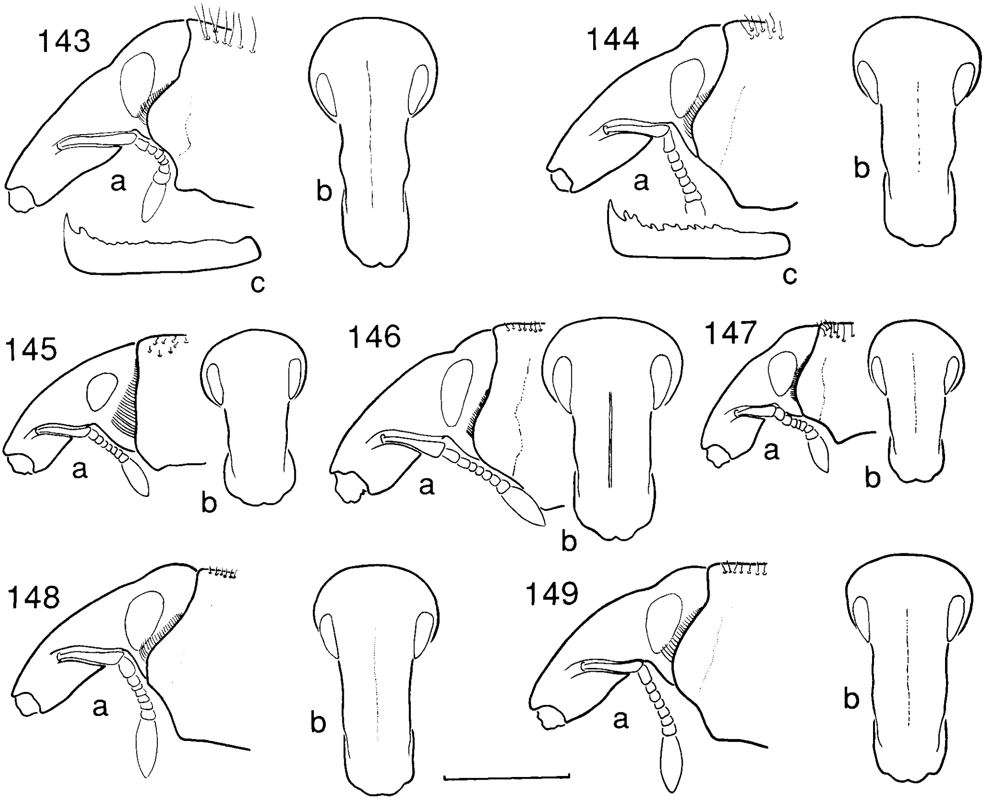
Figures 124–130. Dorsal habitus of: 124, *Cleonidius americanus* 125, *C. frontalis* (Scale bar = 4.0 mm); 126, *C. canescens* (Scale bar = 4.0 mm); 127, *C. infrequens* (Scale bar = 4.0 mm); 128, *C. puberulus* (Scale bar = 4.0 mm); 129, *C. collaris* (Scale bar = 4.0 mm); 130, *C. notolomus*. (Scale bar = 4.0 mm).



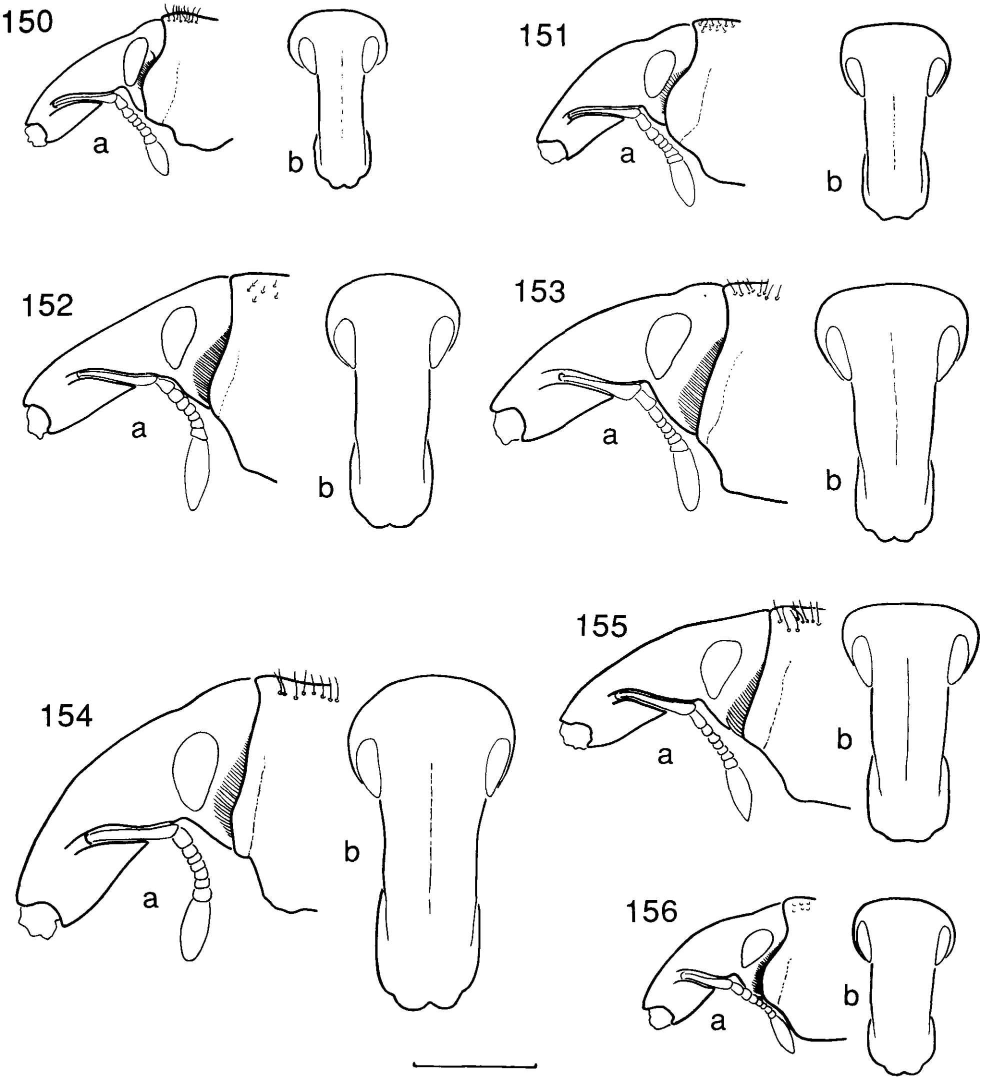
Figures 131–136. Dorsal habitus of: 131, *Cleonidius poricollis* (Scale bar = 4.0 mm); 132, *C. calandroides* (Scale bar = 4.0 mm); 133, *C. boucardi* (Scale bar = 5.0 mm); 134, *C. trivittatus* (Scale bar = 5.0 mm); 135, *C. placidus* (Scale bar = 5.0 mm); 136, *C. quadrilineatus* (Scale bar = 4.0 mm).



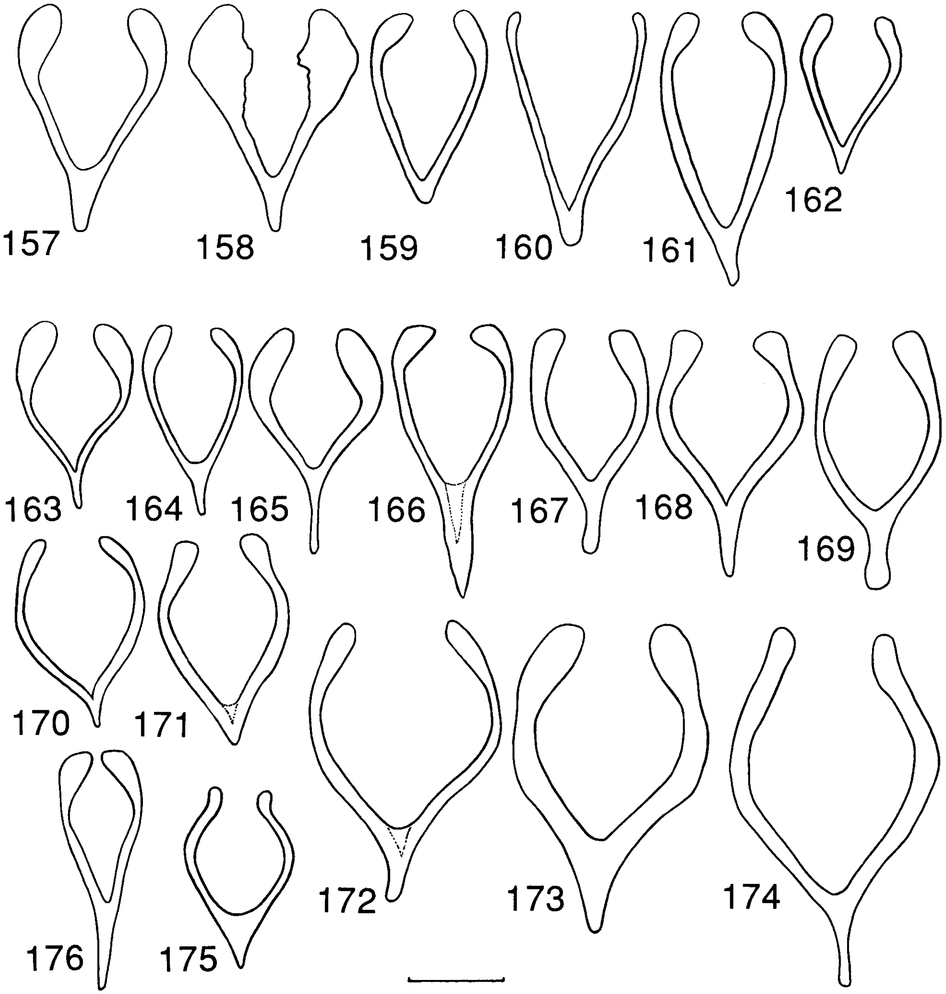
Figures 137–142. Head of *Cleonidius* species (Scale bar = 2.3 mm) – a and b, lateral and dorsal view, respectively. 137, *Cleonidius erysimi*; 138, *C. eustictorrhinus*; 139, *C. pleuralis*; 140, *C. subcylindricus*; 141, *C. longinasus*; a, Lateral view of heads of male and female; b, Dorsal view of head of female; 142, *Cleonidius texanus*.



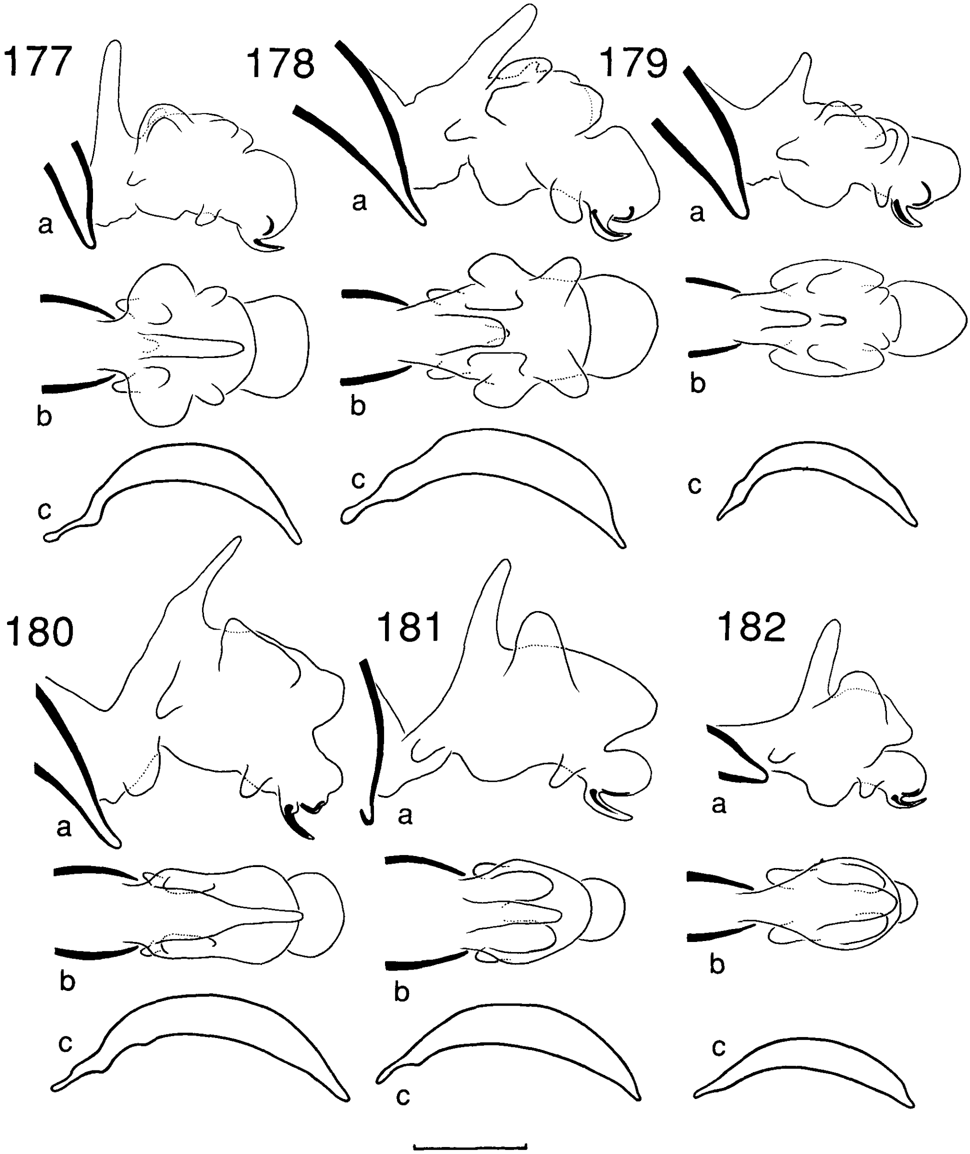
Figures 143–149. Head and femur of *Cleonidius* species – (Scale bar = 2.3 mm) a and b, lateral and dorsal view of head, respectively; c, lateral view of pro-tibia of female. 143, *C. americanus*; 144, *C. frontalis*; 145, *C. canescens*; 146, *C. infrequens*; 147, *C. puberulus*; 148, *C. collaris*; 149, *C. notolomus*.



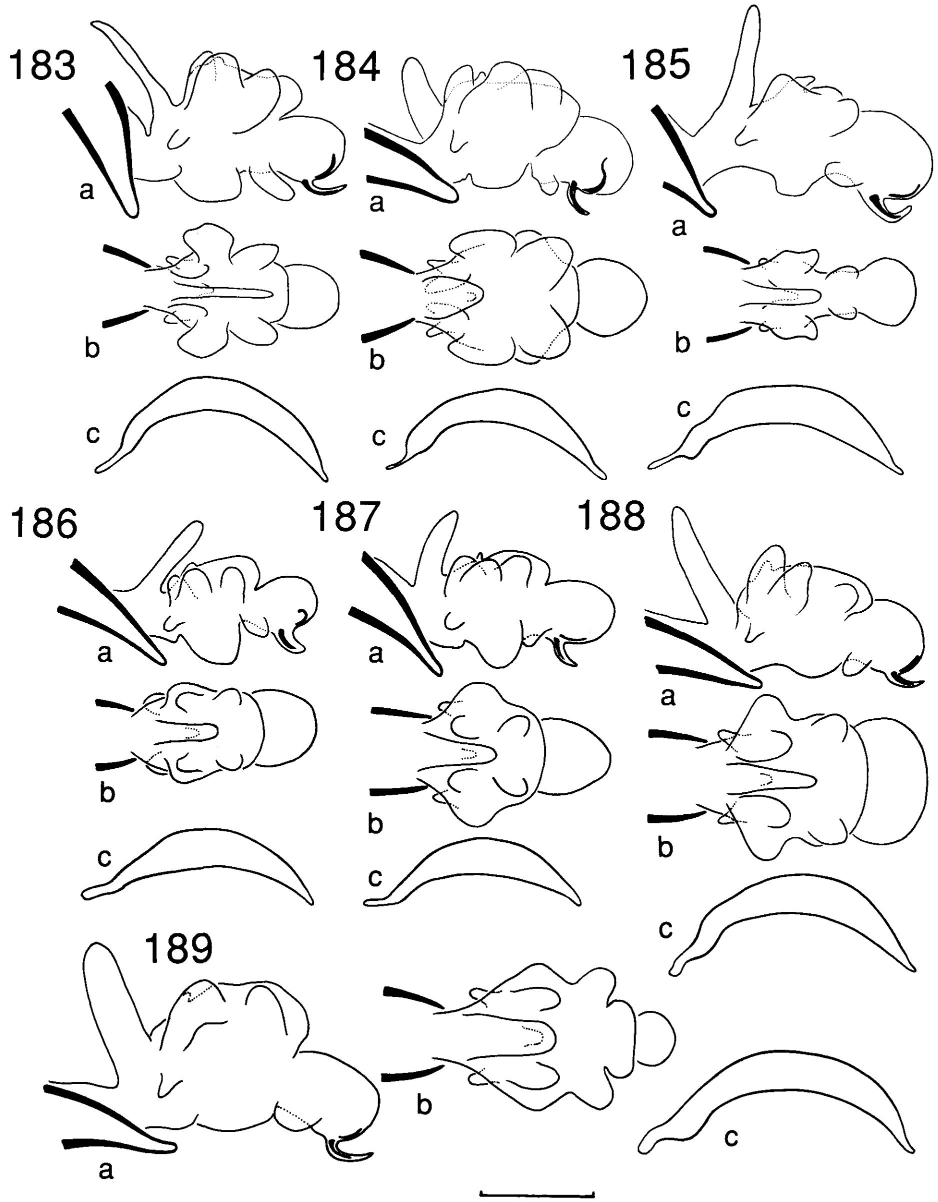
Figures 150–156. Head of *Cleonidius* species (Scale bar = 2.3 mm) – a and b, lateral and dorsal vies, respectively. 150, *C. poricollis*; 151, *C. calandroides*; 152, *C. boucardi*; 153, *C. trivittatus*; 154, *C. placidus*; 155, *C. quadrilineatus*; 156, *C. vibex*. (Scale bar = 2.3 mm).



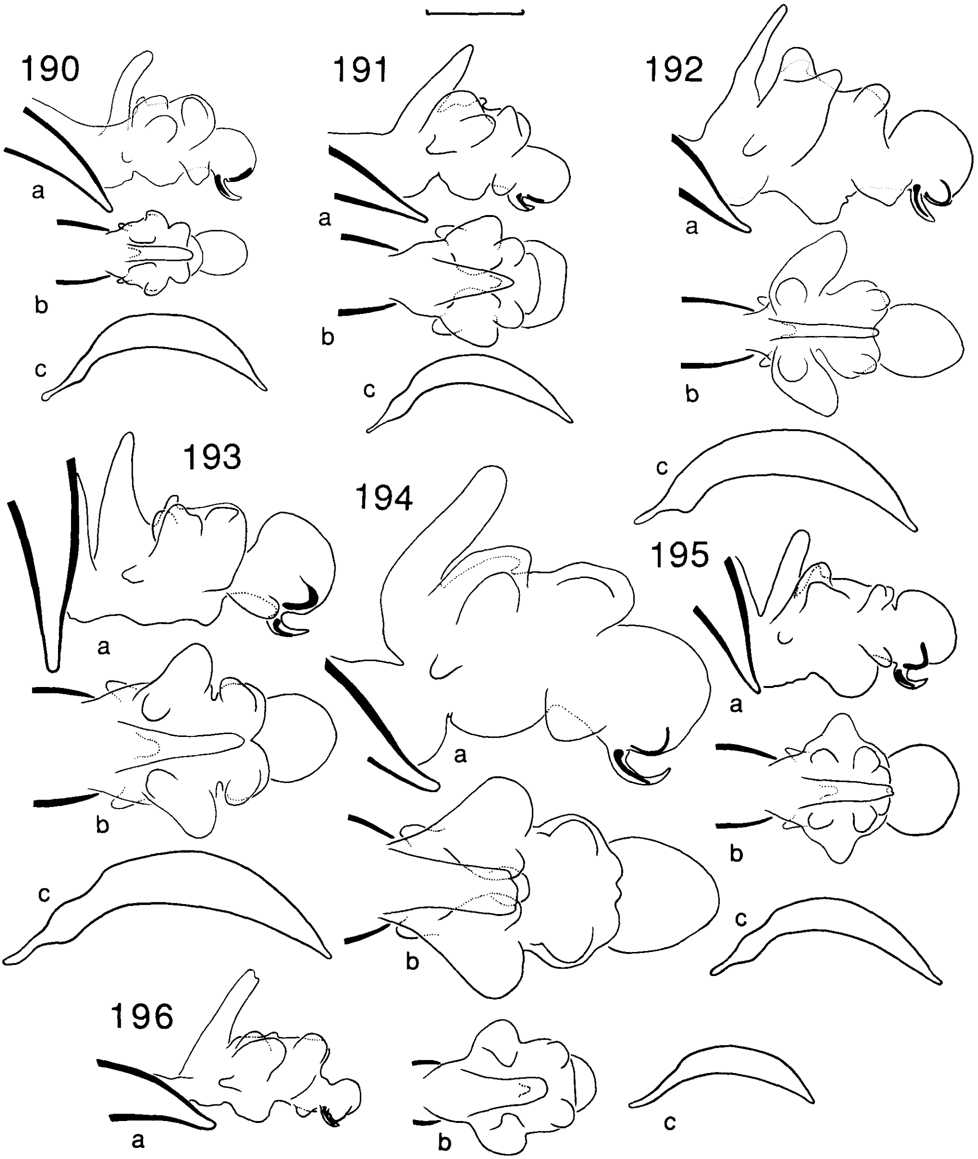
Figures 157–176. Ventral view of sternum VIII of female *Cleonidius* species (Scale bar = 0.8 mm). 157, *C. erysimi*; 158, *C. eustictorrhinus*; 159, *C. pleuralis*; 160, *C. subcylindricus*; 161, *C. longinasus*; 162, *C. texanus*; 163, *C. americanus*; 164, *C. frontalis*; 165, *C. canescens*; 166, *C. infrequens*; 167, *C. puberulus*; 168, *C. notolomus*; 169, *C. collaris*; 170, *C. poricollis*; 171, *C. calandroides*; 172, *C. boucardi*; 173, *C. trivittatus*; 174, *C. placidus*; 175, *C. quadrilineatus*; 176, *C. vibex*. (Scale bar = 0.8 mm).



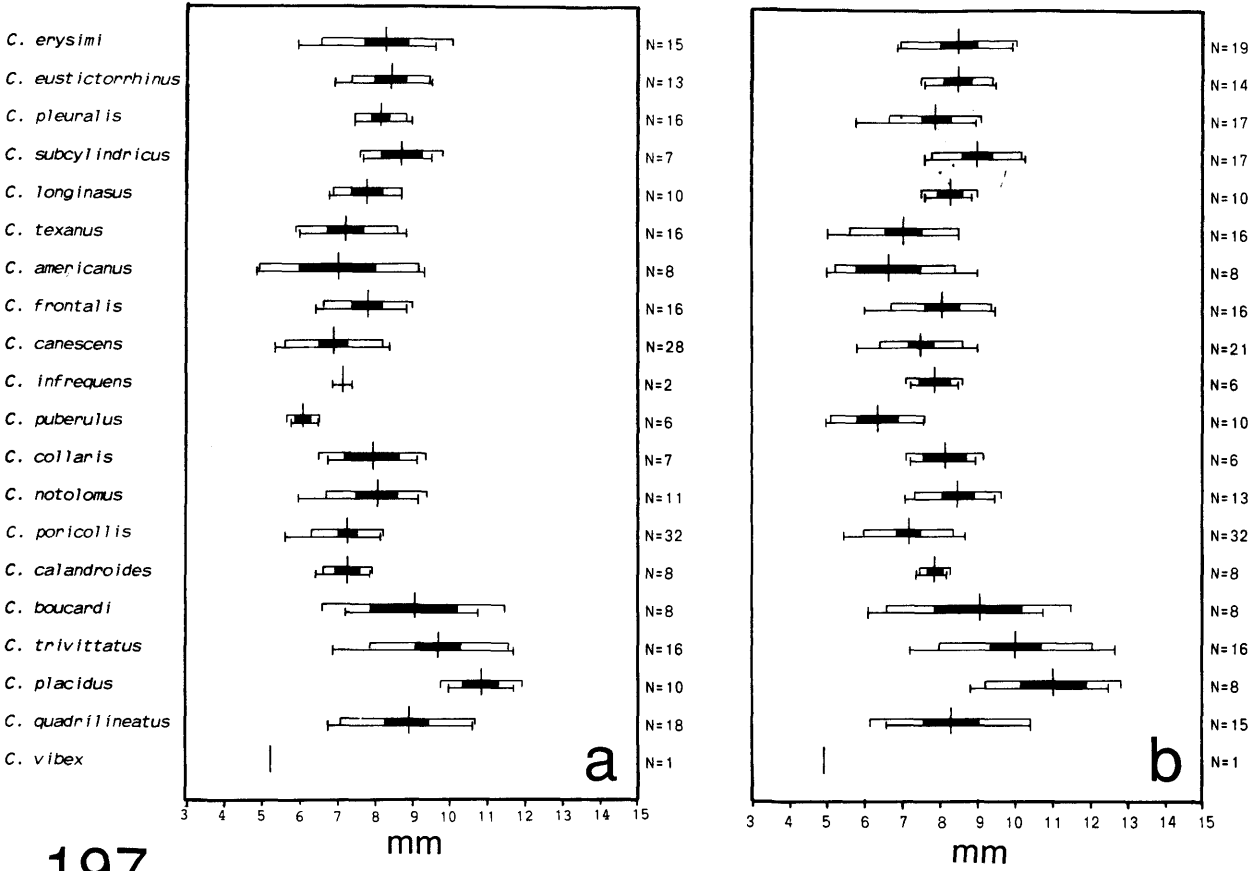
Figures 177–182. Male genitalia of *Cleonidius* species – a and b, internal sac, lateral and dorsal view, respectively; c, lateral view of aedeagus (Scale bars, 0.7 mm, 0.7 mm and 1.3 mm respectively). 177, *C. erysimi*; 178, *C. eustictorrhinus*; 179, *C. pleuralis*; 180, *C. subcylindricus*; 181, *C. longinasus*; 182, *C. texanus*.



Figures 183–189. Male genitalia of *Cleonidius* species – a and b, internal sac, lateral and dorsal view, respectively; c, lateral view of aedeagus (Scale bars, 0.7 mm, 0.7 mm and 1.3 mm respectively). 183, *C. americanus*; 184. *C. frontalis*; 185, *C. canescens*; 186, *C. infrequens*; 187, *C. puberulus*; 188, *C. notolomus*; 189, *C. collaris*.



Figures 190–196. Male genitalia of *Cleonidius* species – a and b, internal sac, lateral and dorsal views, respectively; c, lateral view of adeagus (Scale bars, 0.7 mm, 0.7 mm and 1.3 mm, respectively): 190, *C. poricollis*; 191, *C. calandroides*; 192, *C. boucardi*; 193, *C. trivittatus*; 194, *C. placidus*; 195, *C. quadrilineatus*; 196, *C. vibex*.



197

Figure 197. Hubbs-Hubbs diagram illustrating variation among specimens of *Cleonidius* species; length of elytra (LEl) – a, males; b, females. See caption for Fig. 49 for explanation.

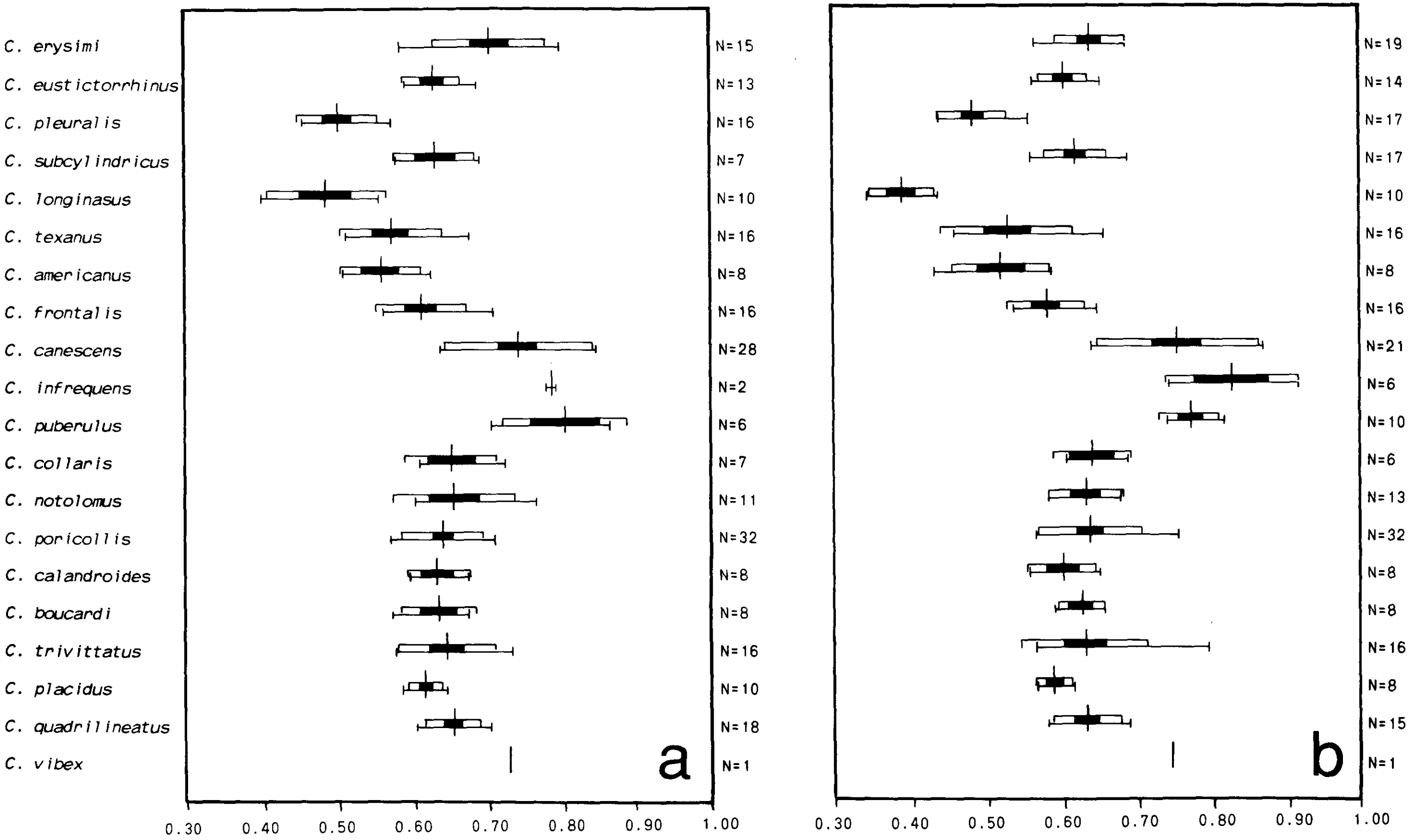


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Figure 198. Hubbs-Hubbs diagram illustrating variation among specimens of *Cleonidius* species; form of rostrum (WRA/LR) – a, males; b, females. See caption for Fig. 49 for explanation.

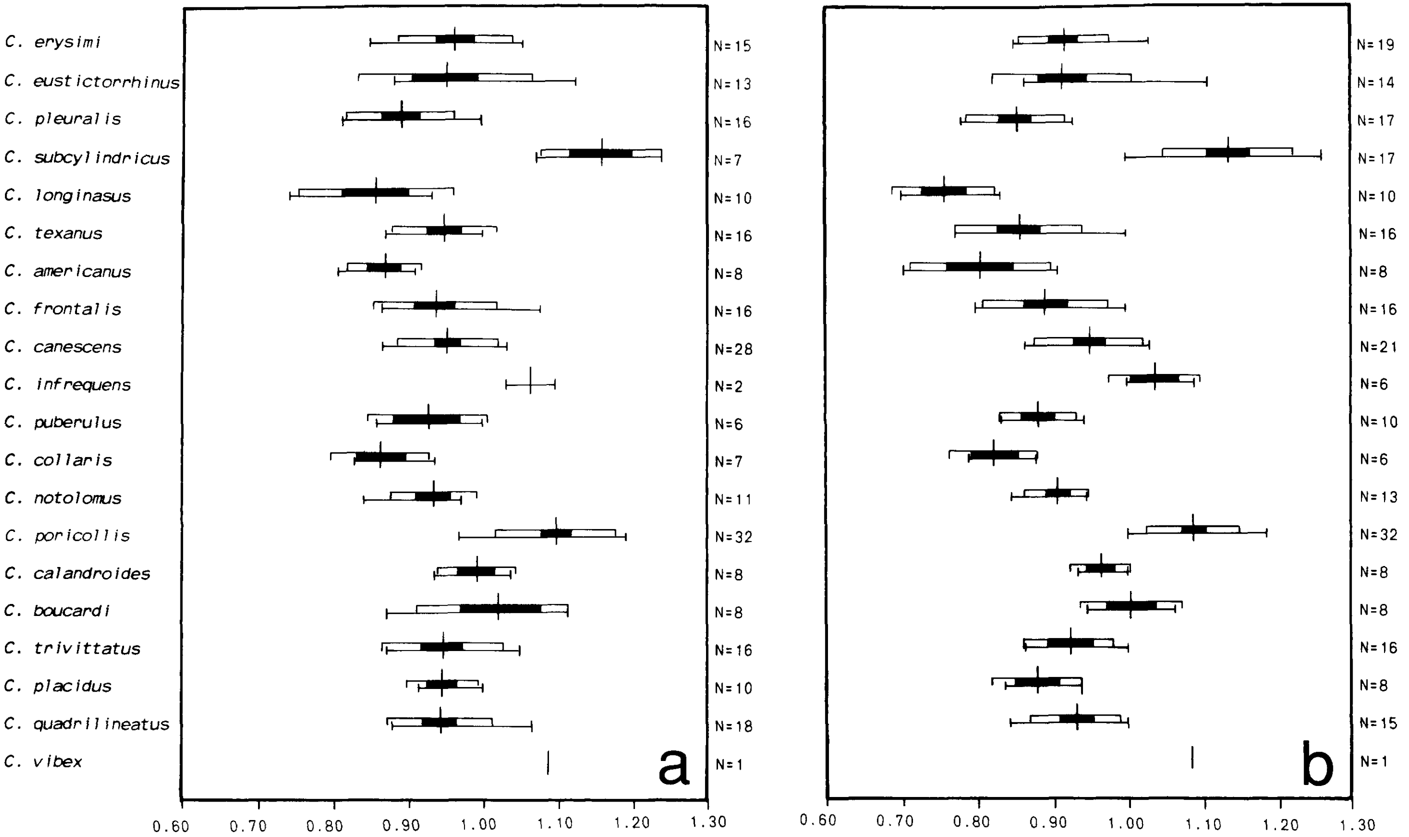

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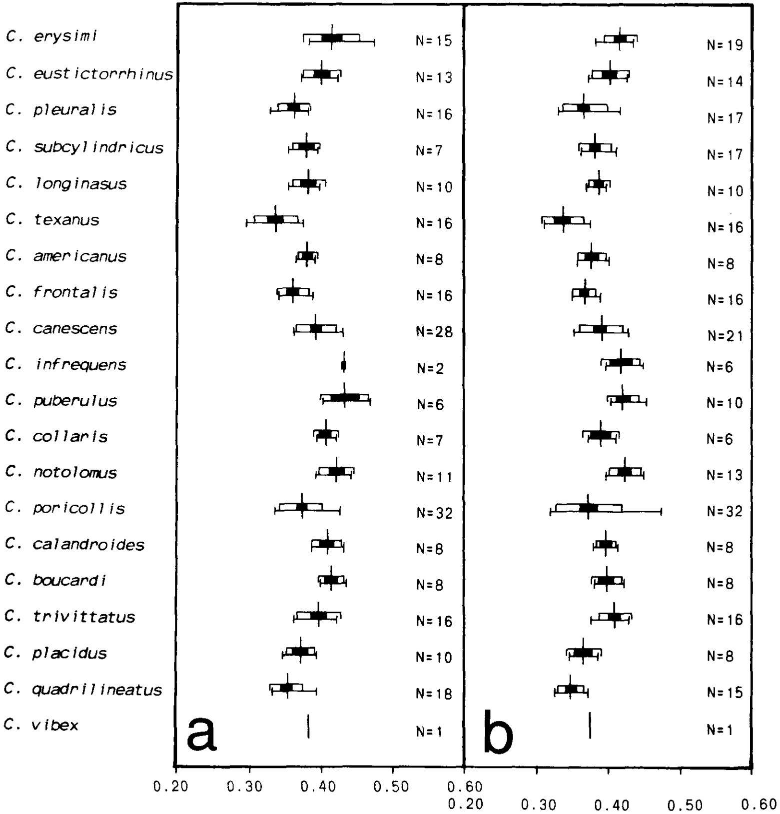
Figure 199. Hubbs-Hubbs diagram illustrating variation among specimens of *Cleonidius* species; width frons compared to width at apex of rostrum (WRA/WF) – a, males; b, females. See caption for Fig. 49 for explanation.



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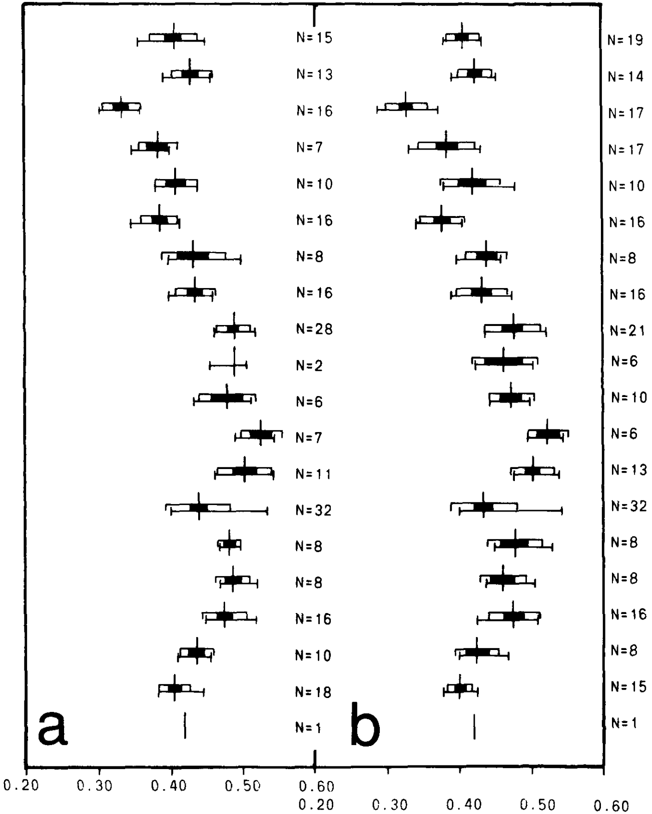

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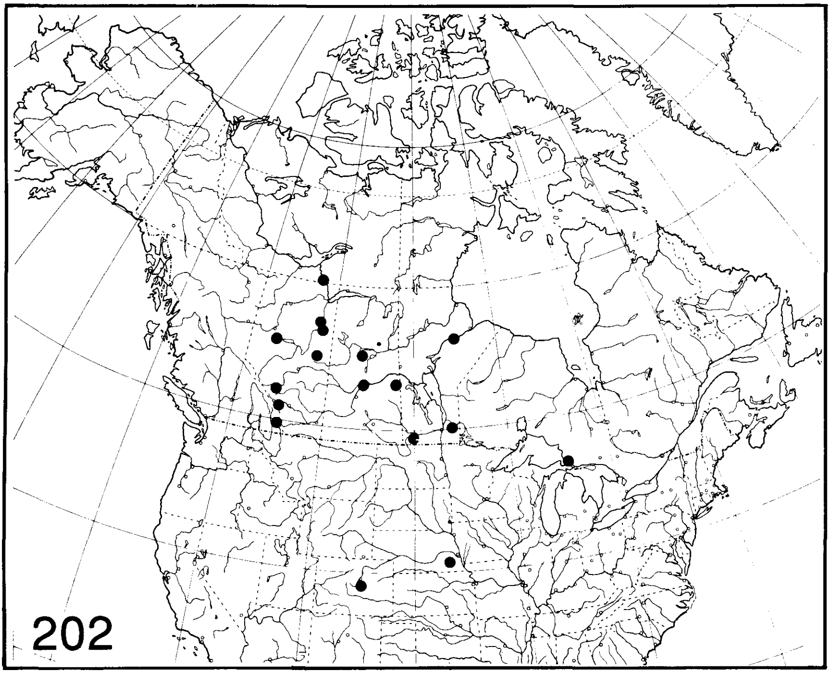
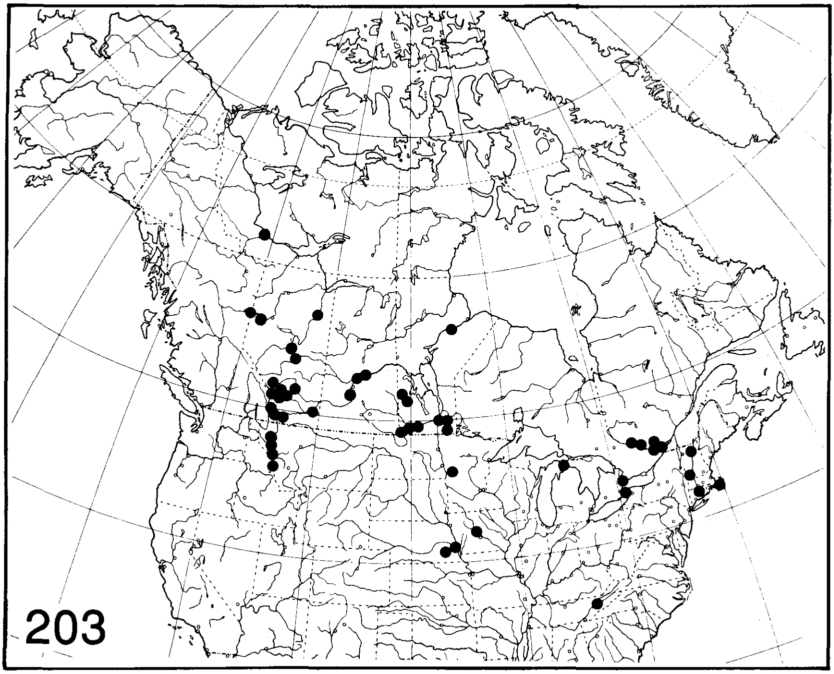
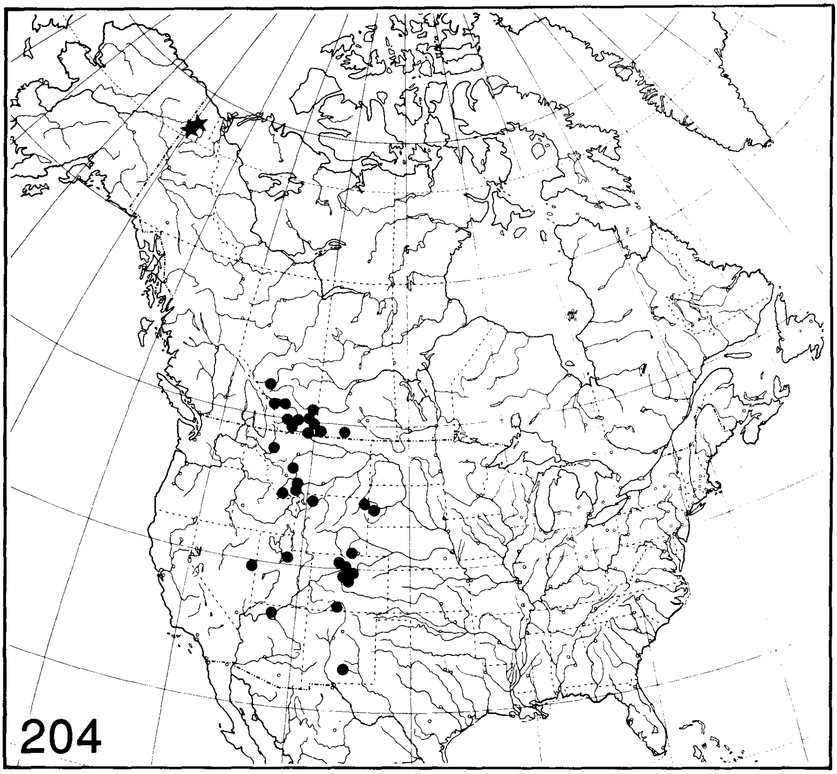
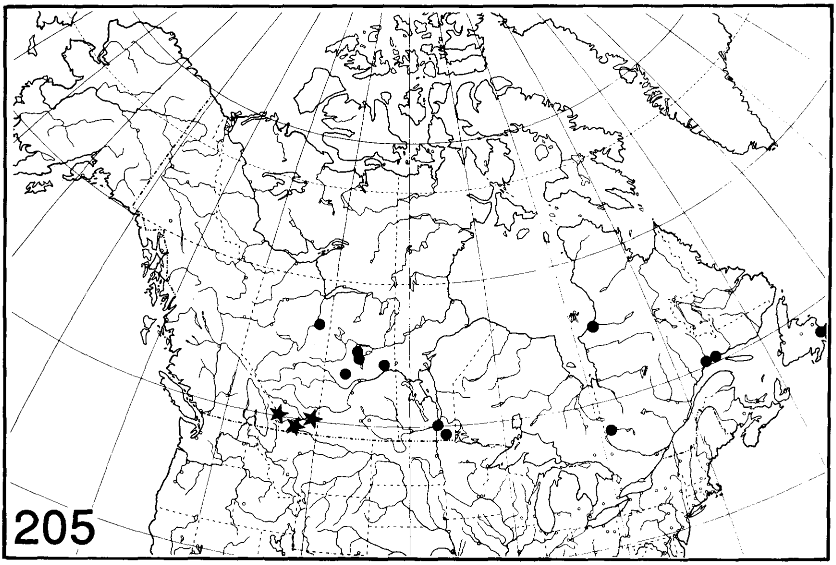
Figures 200–201. Hubbs-Hubbs diagrams illustrating variation among specimens of *Cleonidius* species – a, males; b, females. See caption for Fig. 49 for explanation. 200, length pronotum compared to length of elytra (LP/LEl); 201, form of elytra (WElM/LEl).



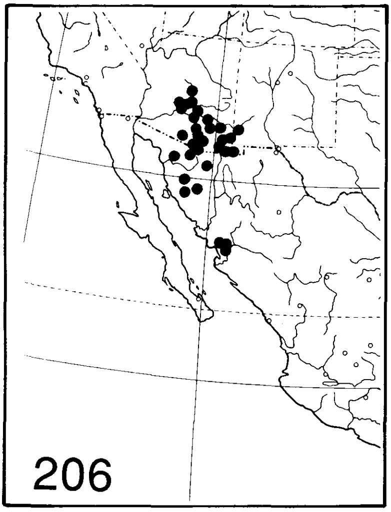


Figures 202–203. Maps illustrating position of collecting localities for: 202, *Stephanocleonus immaculatus*; 203, *S. parshus*.





Figures 204–205. Maps illustrating position of collecting localities for: 204, *Stephanocleonus confusus* (dots) and *S. stenothorax* (stars); 205, *S. plumbeus* (dots) and *S. cristaticollis* (stars).



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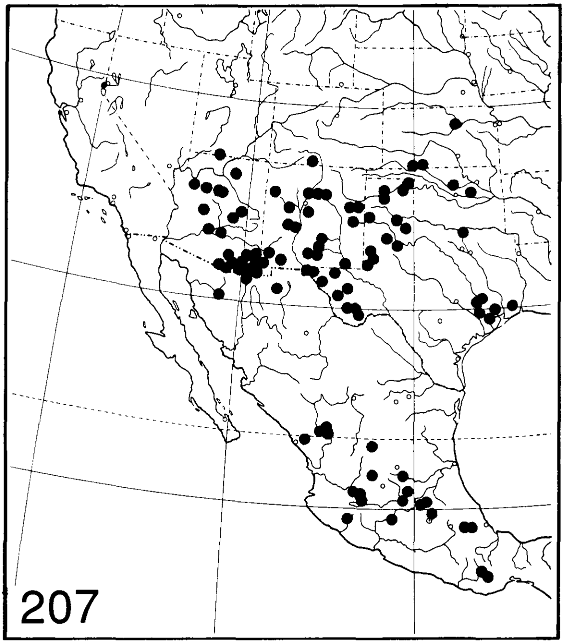

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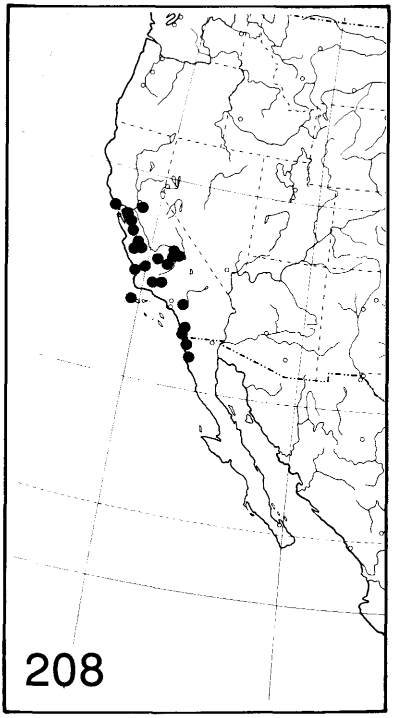

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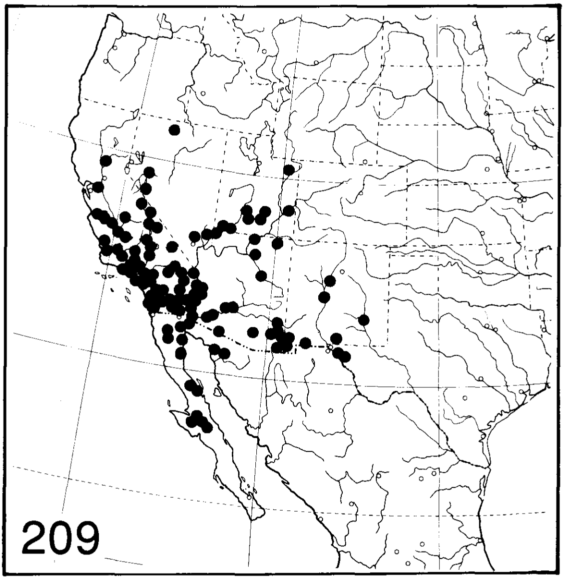

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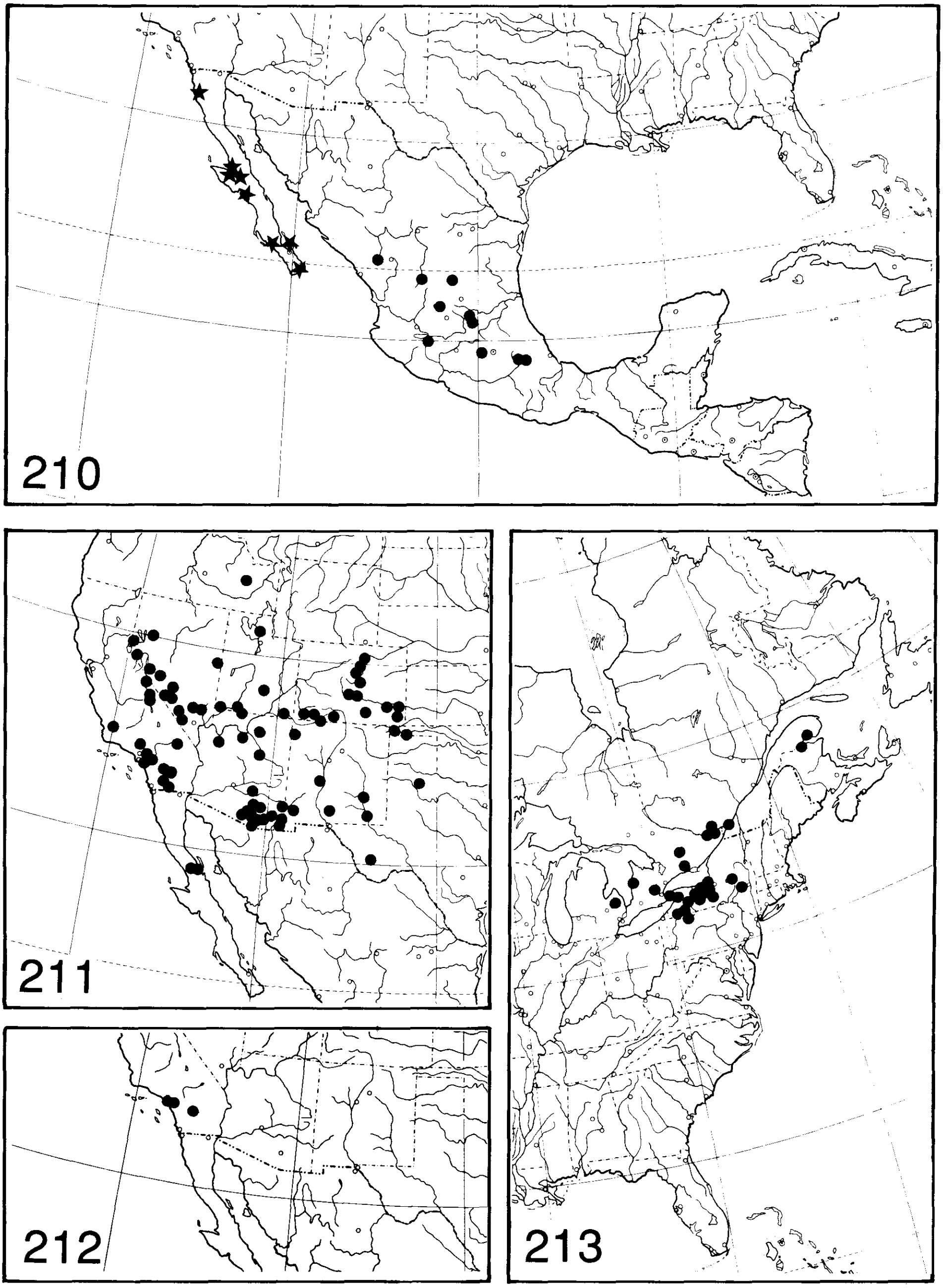
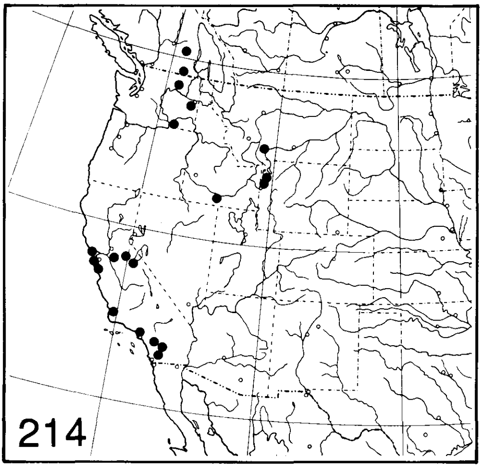
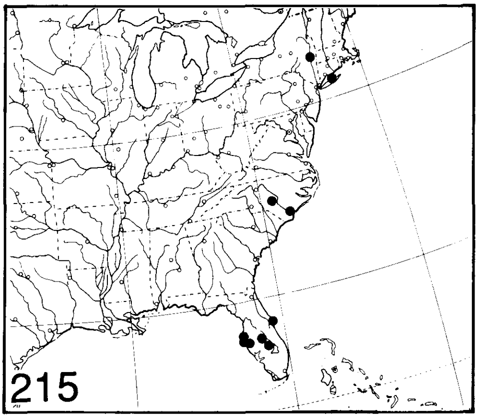
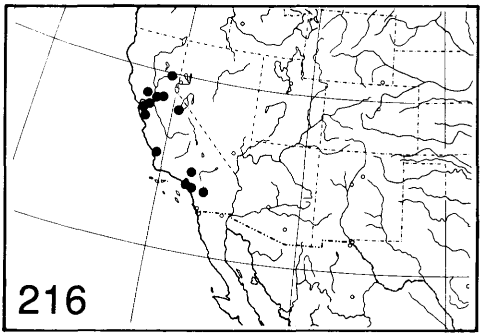
Figures 206–209. Maps illustrating position of collecting localities for: 206, *Apleurus saginatus*; 207, *A. lutulentus*; 208, *A. jacobinus*; 209, *A. albovestitus*.

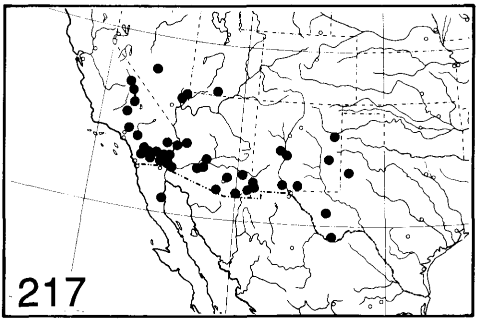


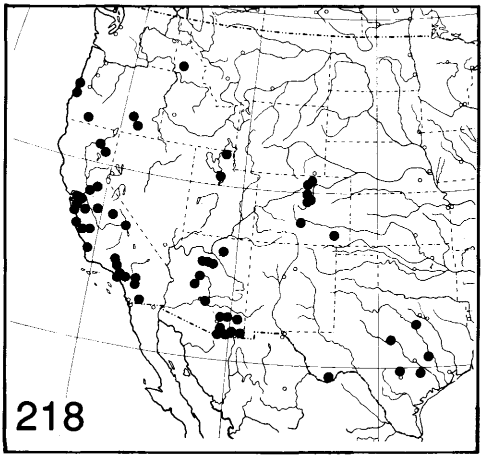
Figures 210–213, Maps illustrating position of collecting localities for: 210, *Apleurus aztecus* (dots) and *A. porosus* (stars); 211, *A. angularis*; 212, *A. hystrix*; 213, *Cleonis pigra*.

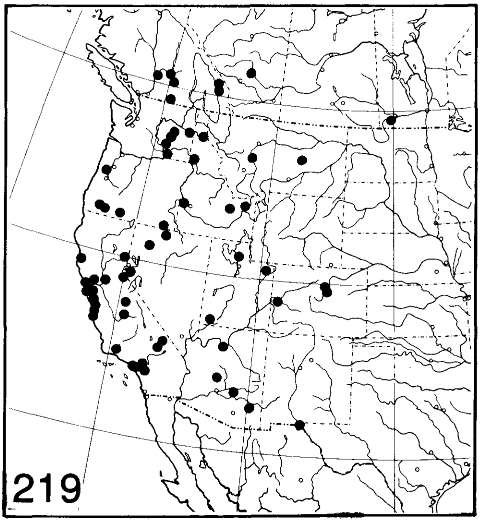




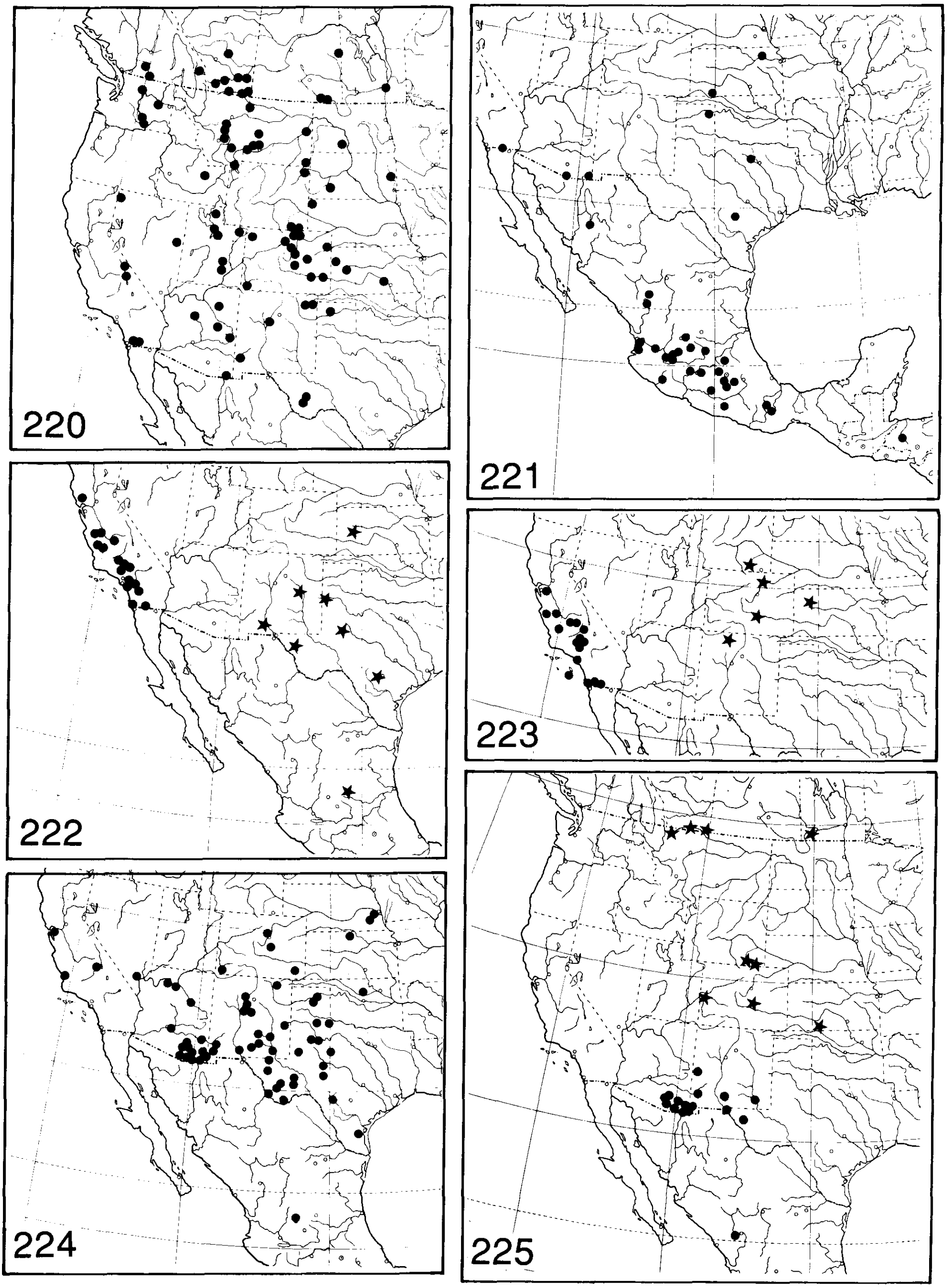




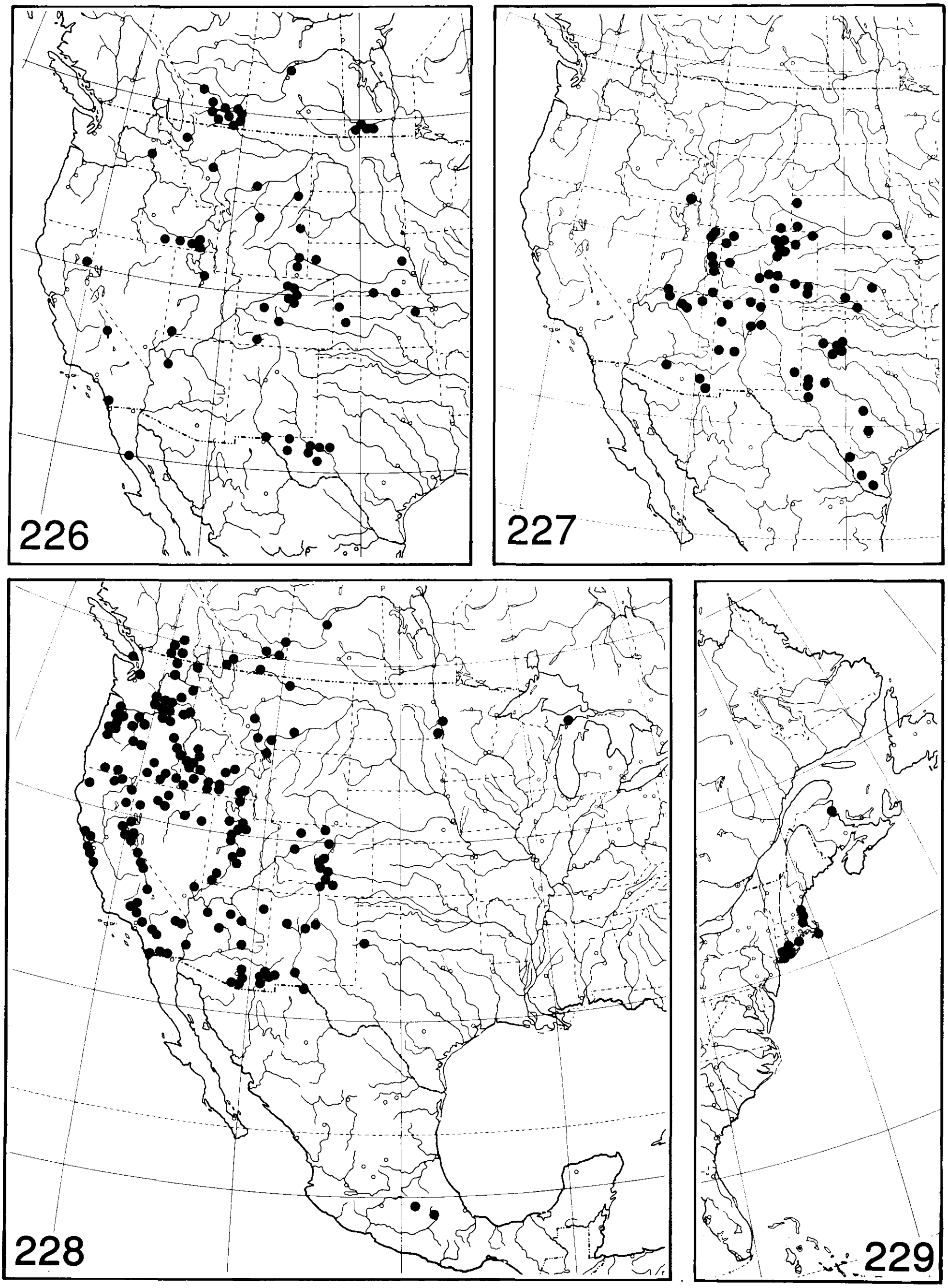




Figures 214–219. Maps illustrating position of collecting localities for: 214, *Cleonidius longinasus*; 215, *C. subcylindricus*; 216, *C. eustictorrhinus*; 217, *C. pleuralis*; 218, *C. texanus*; 219, *C. erysimi*.



Figures 220–225. Maps illustrating position of collecting localities for: 220, *Cleonidius trivittatus*; 221, *C. boucardi*; 222, *C. placidus* (dots) and *C. infrequens* (stars); 223, *C. americanus* (dots) and *C. collaris* (stars); 224, *C. quadrilineatus*; 225, *C. notolomus* (dots) and *C. puberulus* (stars).



Figures 226–229. Maps illustrating position of collecting localities for: 226, *Cleonidius frontalis*; 227, *C. canescens*; 228, *C. poricollis*; 229, *C. calandroides*.

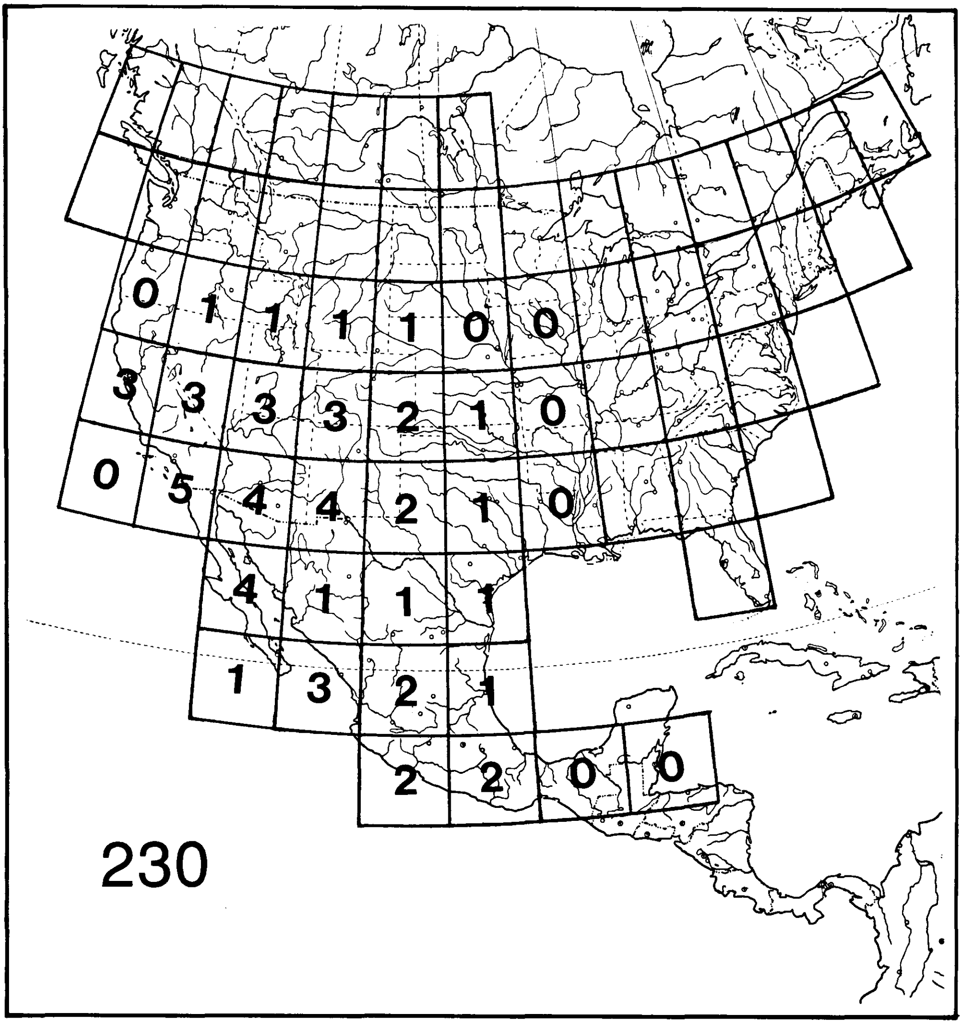


Figure 230. Numbers of species of *Apleurus* in 5° intervals.

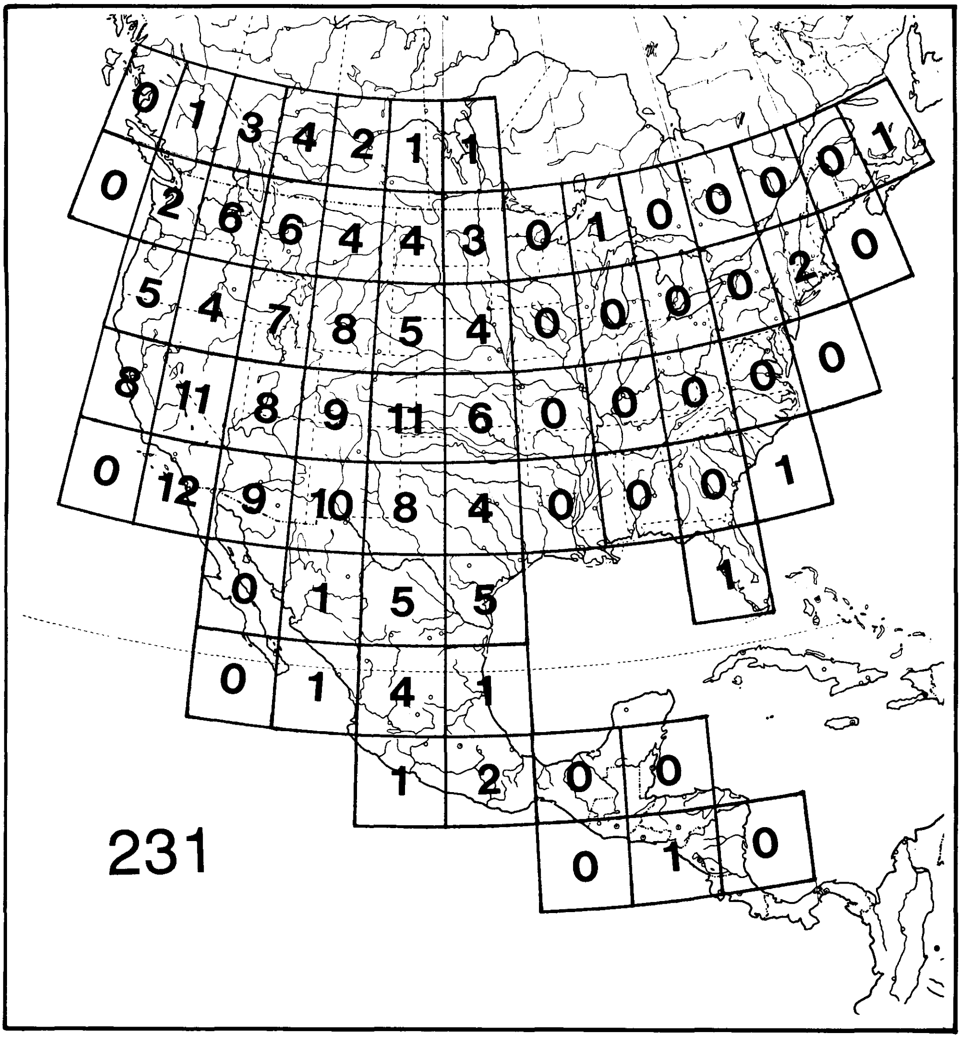
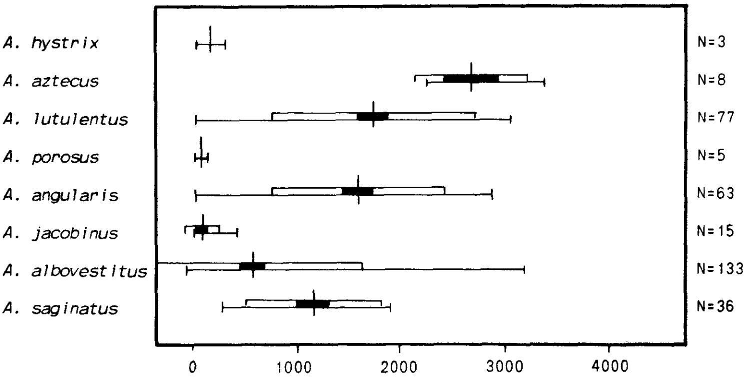
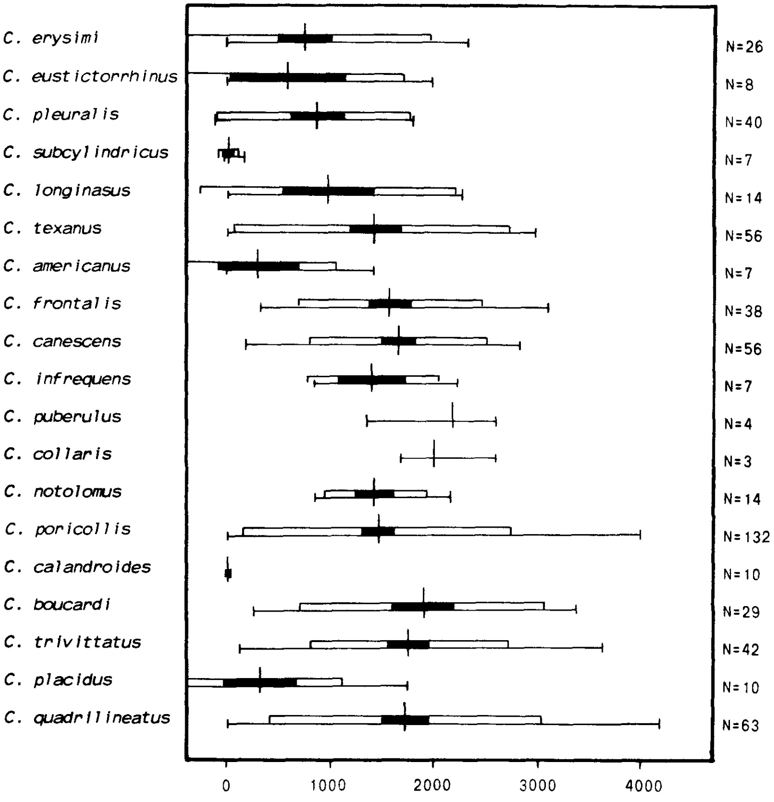


Figure 231. Numbers of species of *Cleonidius* in 5° intervals.

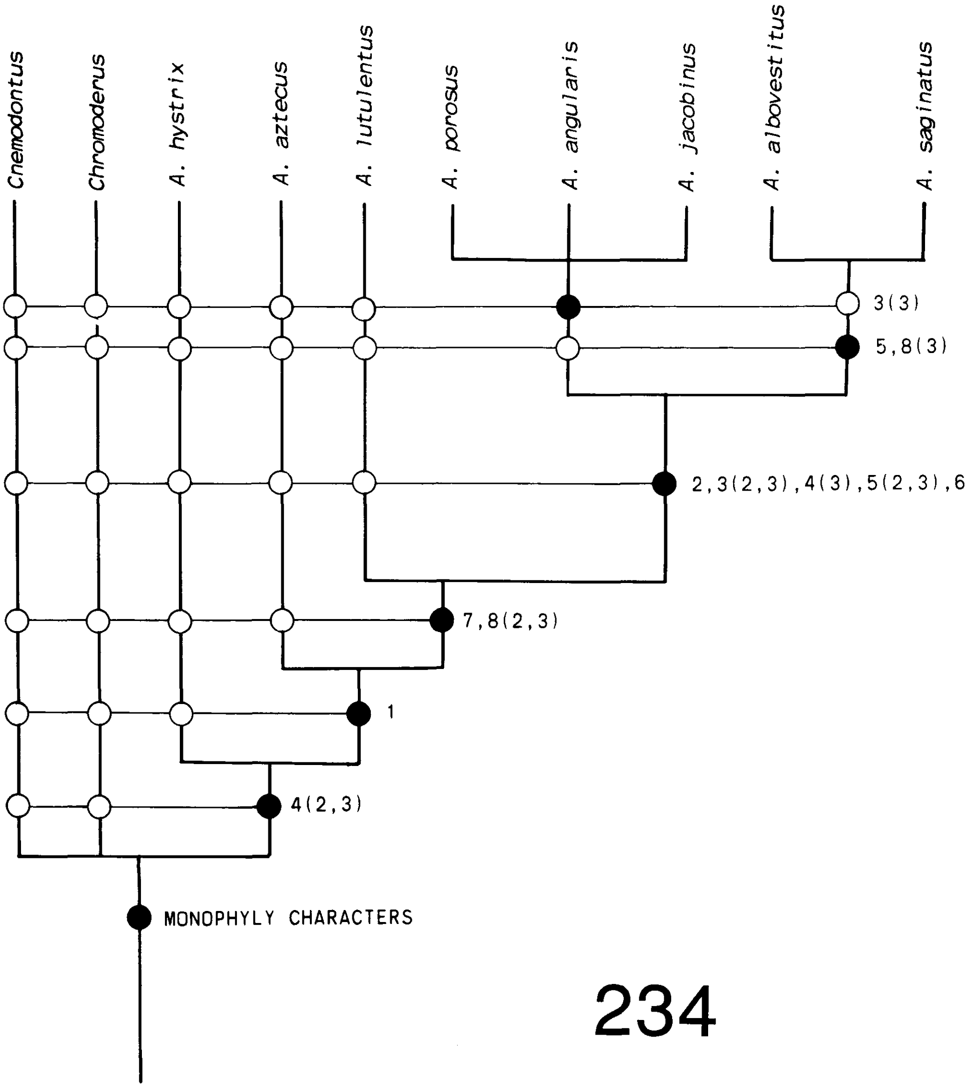


232



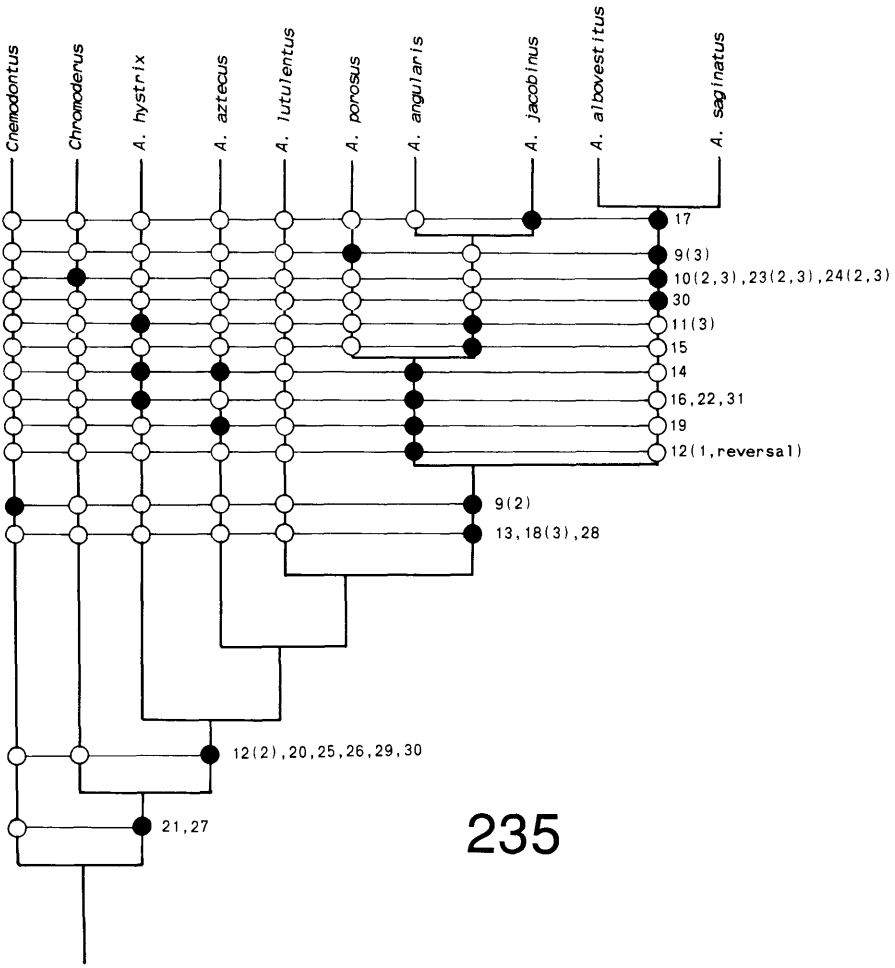
233

Figures 232–233. Hubbs-Hubbs diagrams illustrating variation among specimens of: 232, *Apleurus* species; elevation; 233, *Cleonidius* species; elevation. See caption for Fig. 49 for explanation.



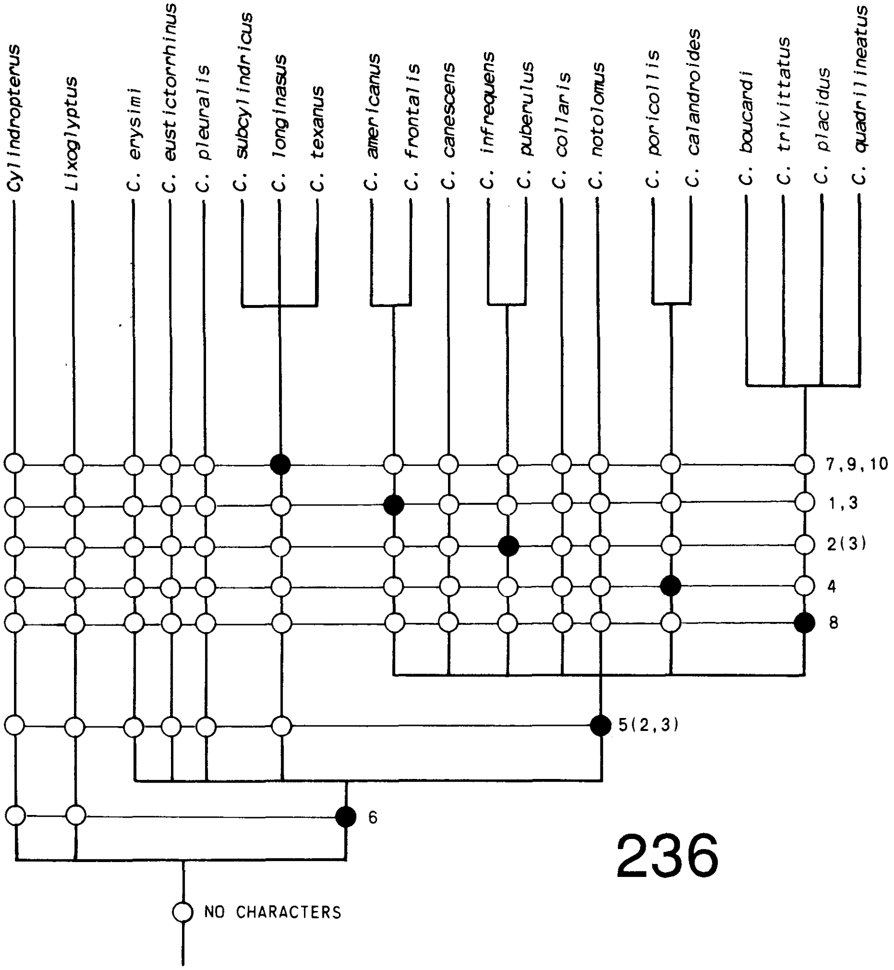
234

Figure 234. Reconstructed phylogeny based on primary characters illustrating hypothesized phylogenetic relationships among *Apleurus* species and related out-groups. Dots denote apotypic character states, open circles plesiotypic states. See "Phylogeny" section and Tables I and II for discussion of characters and states (numbers in parentheses).



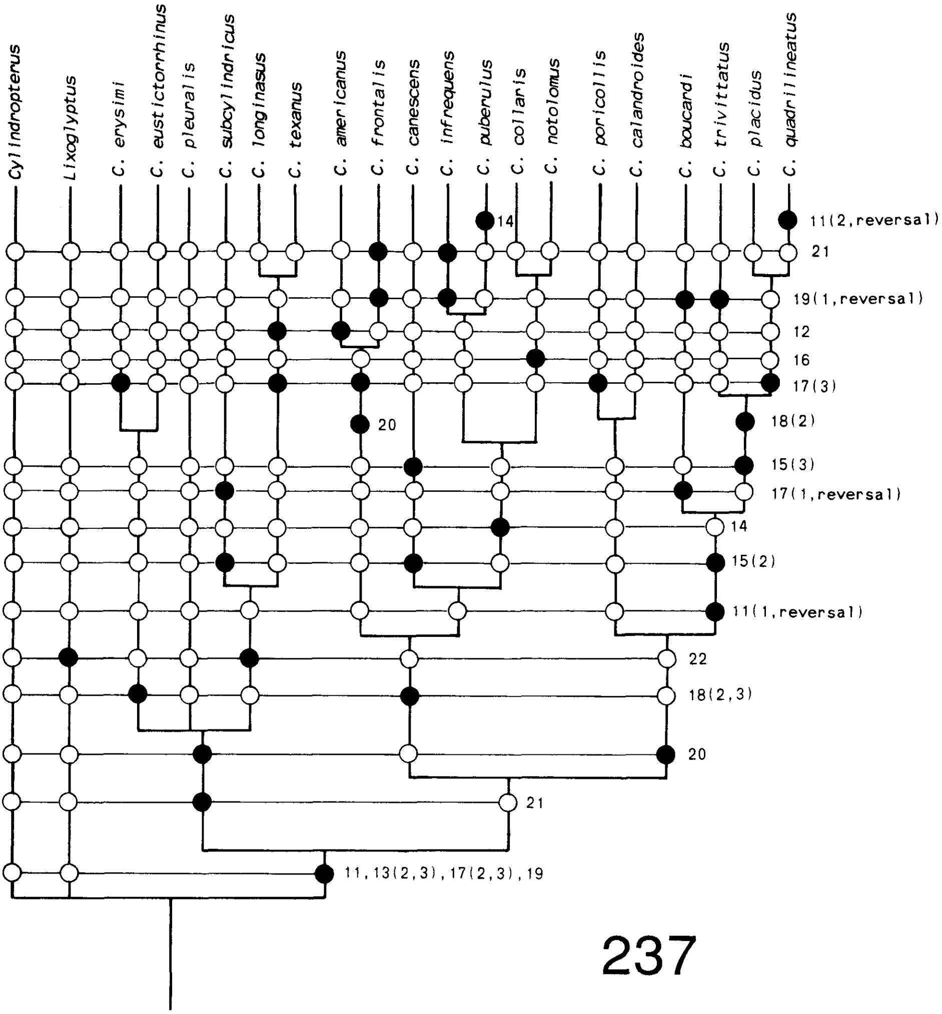
235

Figure 235. Reconstructed phylogeny based on primary and secondary characters illustrating hypothesized phylogenetic relationships among *Apleurus* species and related out-groups. Dots denote apotypic character states, open circles plesiotypic states. See "Phylogeny" section and Tables I and II for discussion of characters and states (numbers in parentheses).



236

Figure 236. Reconstructed phylogeny based on primary characters illustrating hypothesized phylogenetic relationships among *Cleonidius* species and related out-groups. Dots denote apotypic character states, open circles plesiotypic states. See "Phylogeny" section and Tables III and IV for discussion of characters and states (numbers in parentheses).



237

Figure 237. Reconstructed phylogeny based on primary and secondary characters illustrating hypothesized phylogenetic relationships among *Cleonidius* species and related out-groups. Dots denote apotypic character states, open circles plesiotypic states. See "Phylogeny" section and Tables III and IV for discussion of characters and states (numbers in parentheses).

	A. hystrix	*A. aztecus*	*A. lutulentus*	*A. porosus*	*A. angularis*	*A. jacobinus*	*A. albovestitus*	*A. saginatus*
Mojave Desert							■	
Sonoran Desert				■			■	
Chihuahuan Desert							◩	
Great Basin Desert					■		◩	
Texas Semi-desert								
Pacific Semi-desert	■			◩	◩	■	■	
Desert-Grassland			■		◩		◩	■
Grassland			■		◩			
Grassland-Dec.For.			◩					
Mesquite Grassland		■	■					

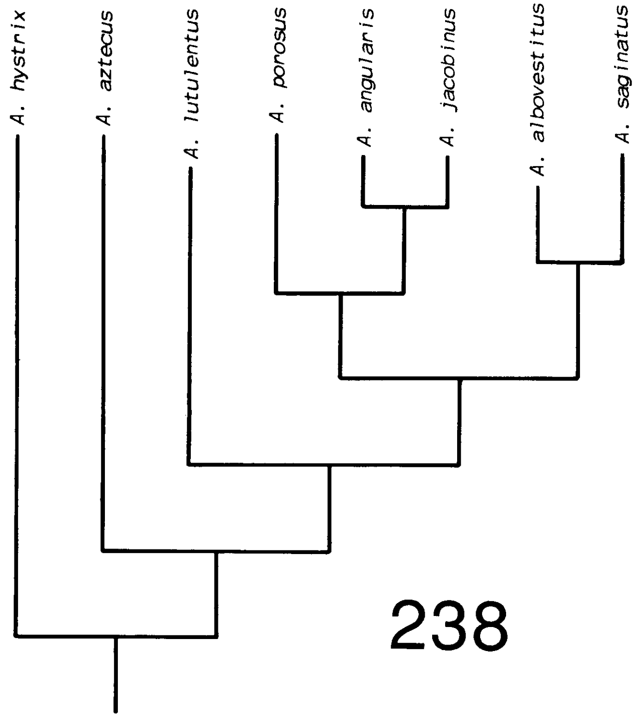


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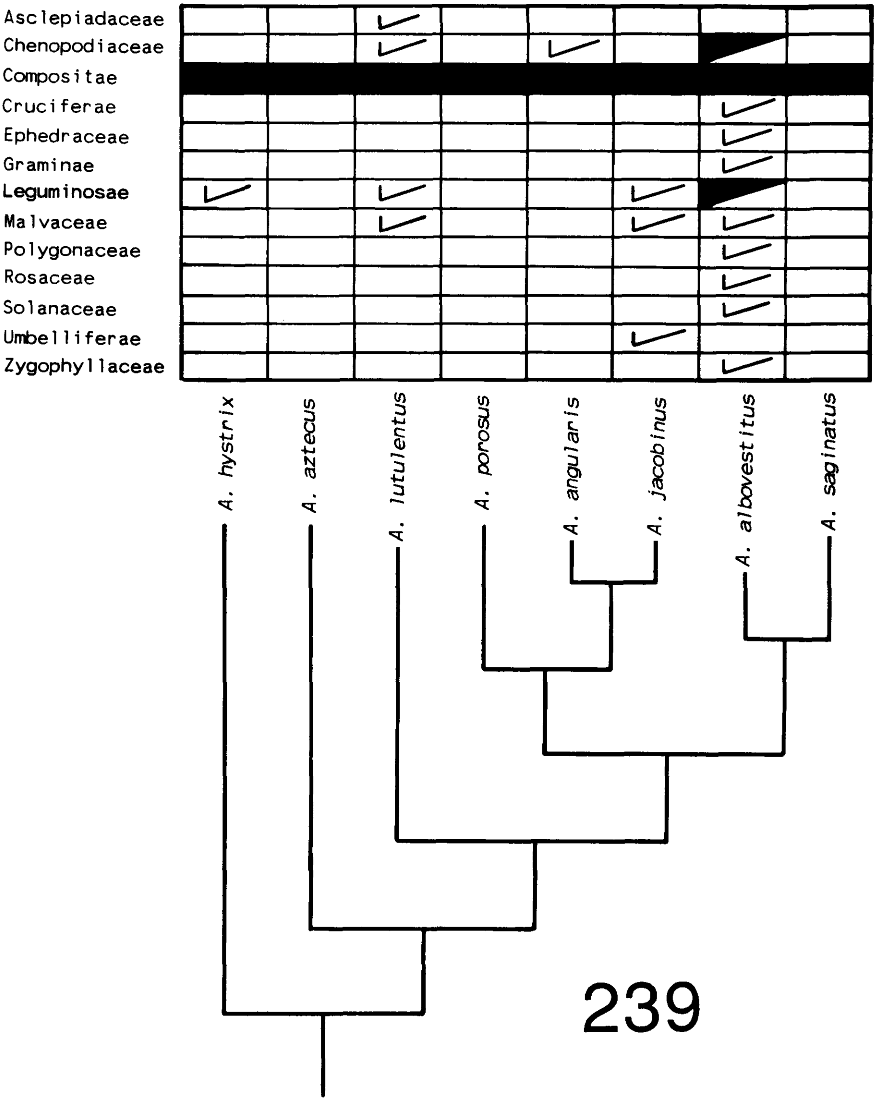
Figure 238. Habitat associations of *Apleurus* species Solid box denotes marked association, half-box slight association. Phylogeny following 235.



	A. hystrix	A. aztecus	A. lutulentus	A. porosus	A. angularis	A. jacobinus	A. albovestitus	A. saginatus
Asclepiadaceae			✓					
Chenopodiaceae			✓		✓		◢	
Compositae	■	■	■	■	■	■	■	■
Cruciferae							✓	
Ephedraceae							✓	
Graminae							✓	
Leguminosae	✓		✓			✓	◢	
Malvaceae			✓			✓	✓	
Polygonaceae							✓	
Rosaceae							✓	
Solanaceae							✓	
Umbelliferae						✓		
Zygophyllaceae							✓	

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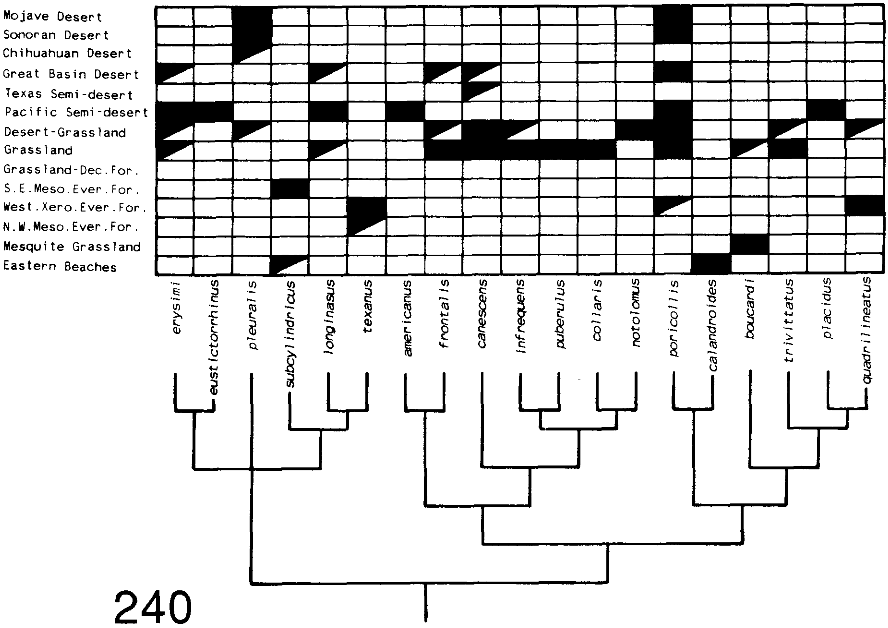
Figure 239. Plant associations of *Apleurus* species Solid box denotes marked association, half-box slight association, check mark few collection records. Plant taxa are listed alphabetically. Phylogeny following 235.



	erysimi	*eustictorrhinus*	*pleuralis*	*subcylindricus*	*longinasus*	*texanus*	*americanus*	*frontalis*	*canescens*	*infrequens*	*puberulus*	*collaris*	*notolomus*	*poricollis*	*calandroides*	*boucardi*	*trivittatus*	*placidus*	*quadrilineatus*
Mojave Desert			■											■					
Sonoran Desert			■											■					
Chihuahuan Desert			◩																
Great Basin Desert	◩				◩			◩	◩					■					
Texas Semi-desert									◩										
Pacific Semi-desert	■	■			■		■							■				■	
Desert-Grassland	◩		◩					◩	■	◩			■	■			◩		◩
Grassland	◩				◩			■	■	■	■	■		■		◩	■		
Grassland-Dec.For.																			
S.E.Meso.Ever.For.				■															
West.Xero.Ever.For.						■								◩					■
N.W.Meso.Ever.For.						◩													
Mesquite Grassland																■			
Eastern Beaches				◩											■				

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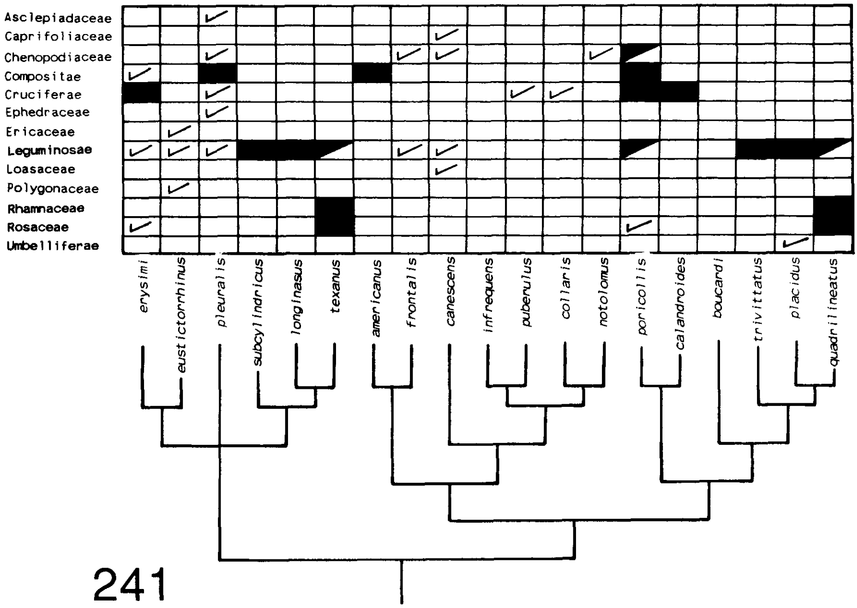
Figure 240. Habitat associations of *Cleonidius* species Solid box denotes marked association, half-box slight association. Phylogeny following 237.



241

Figure 241. Plant associations of *Cleonidius* species. Solid box denotes marked association, half-box slight association, check mark few collection records. Plant associations are unknown for some species. Plant taxa are listed alphabetically. Phylogeny following 237.

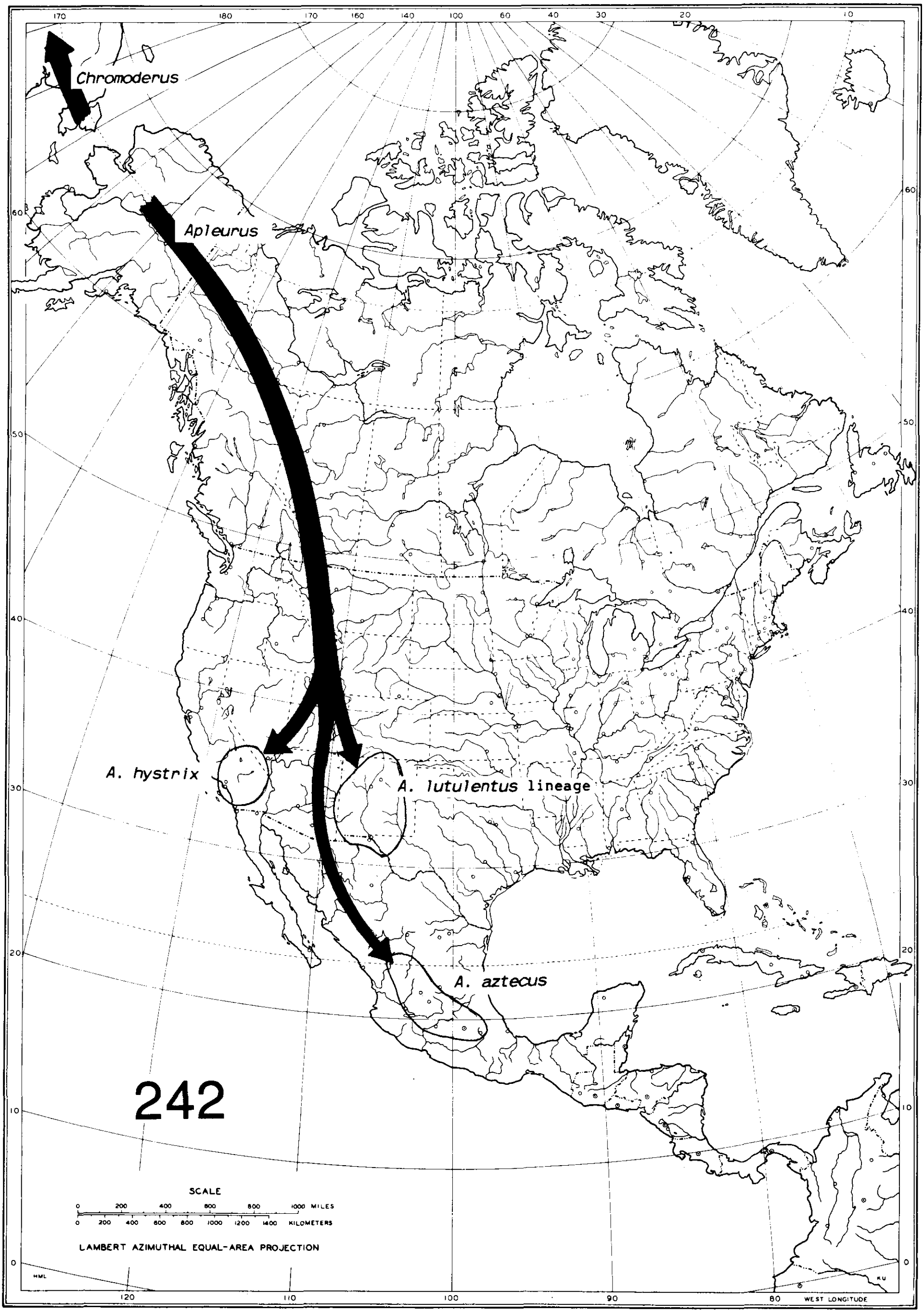
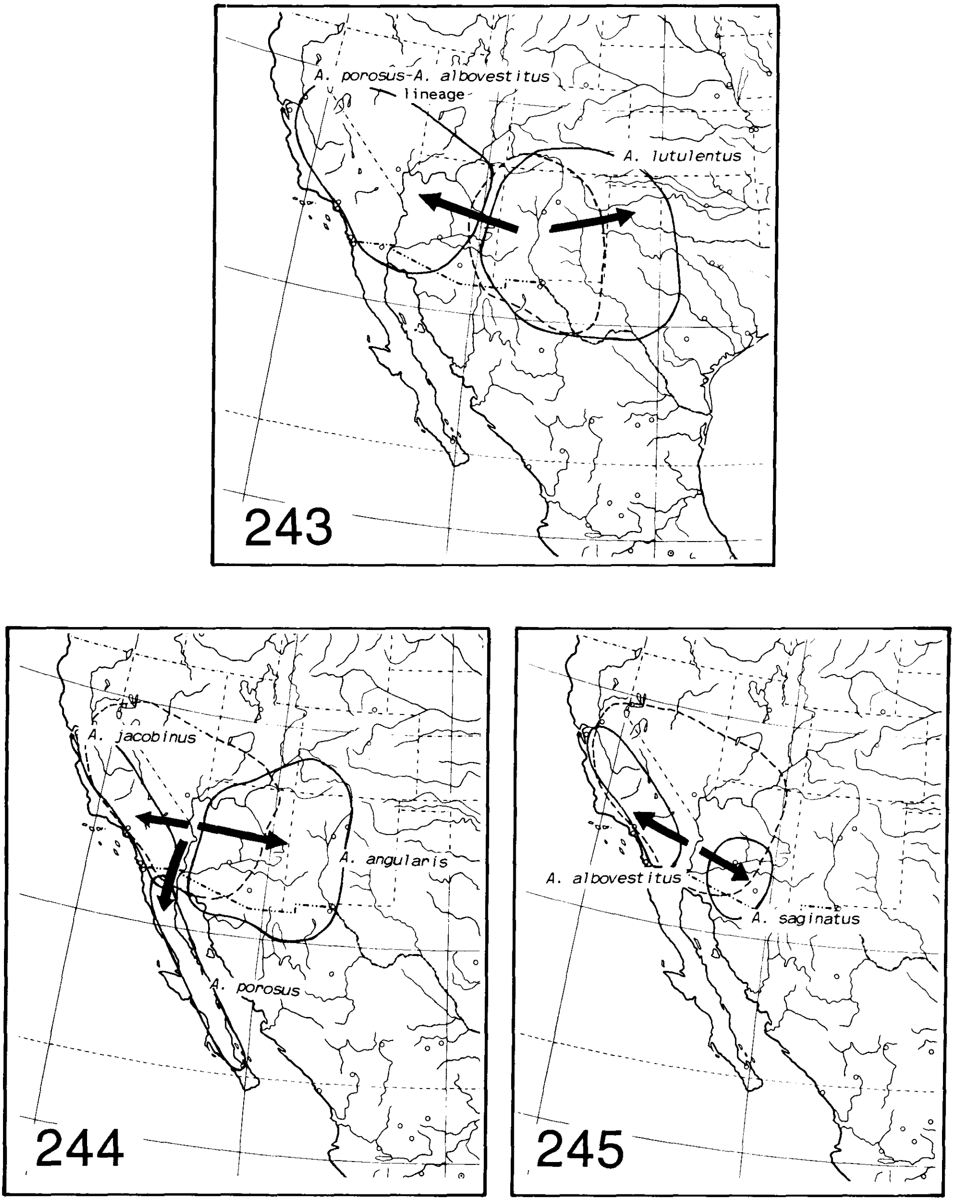


Figure 242. Origin and initial diversification of *Apleurus* in North America: *A. hystrix*, *A. aztecus*, and *A. lutulentus-A. porosus-A. angularis-A. jacobinus-A. albovestitus-A. saginatus* lineage. See text for detailed explanation.



Figures 243–245. Diversification of *Apleurus* in North America (see text for detailed explanation; dashed lines indicate hypothesized ancestral distribution, solid lines indicate present distributions. 243, *A. lutulentus* and *A. porosus-A. angularis-A. jacobinus-A. albovestitus-A. saginatus* lineage; 244, *A. angularis*, *A. jacobinus* and *A. porosus*; 245, *A. albovestitus* and *A. saginatus*.

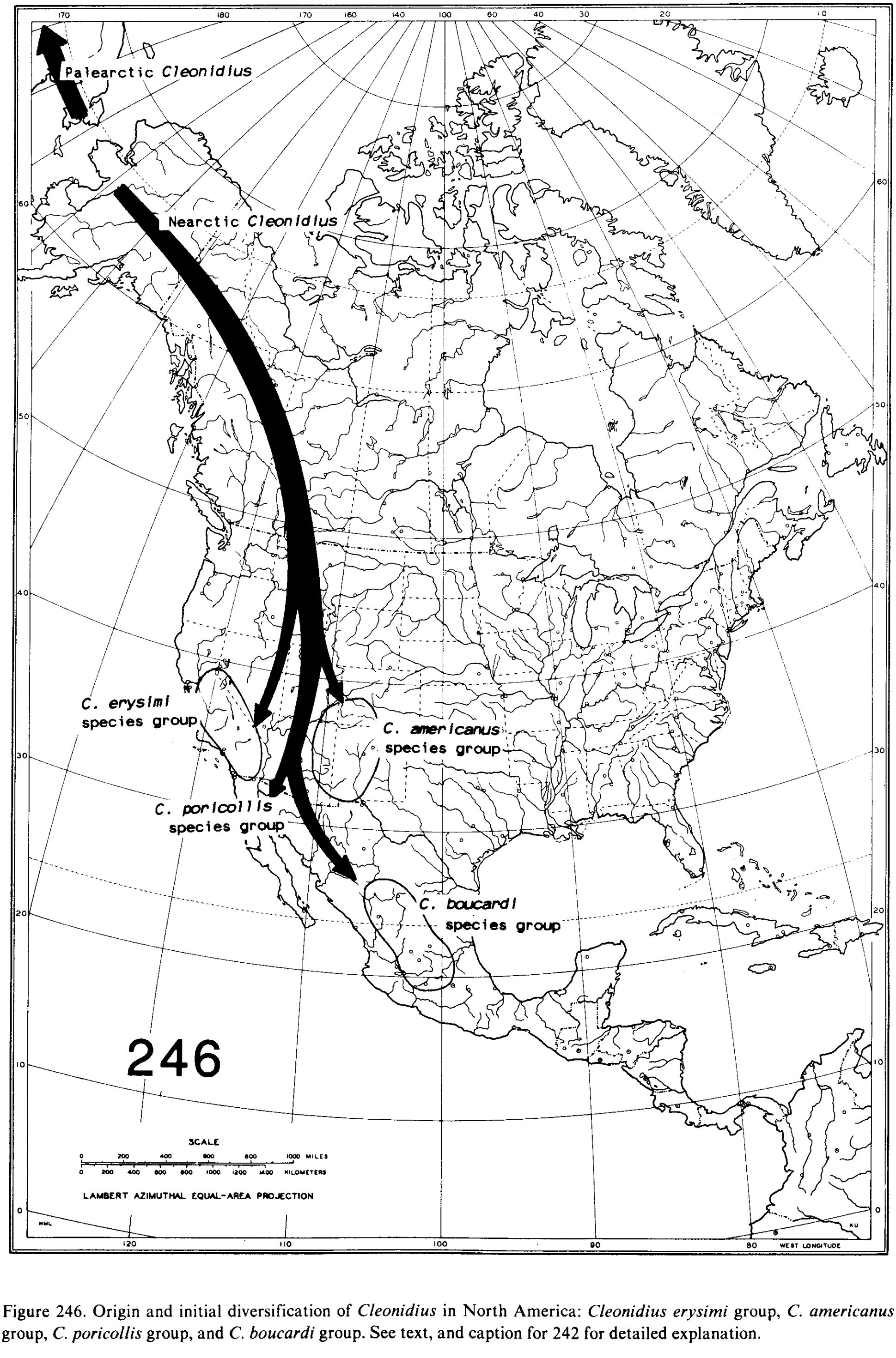
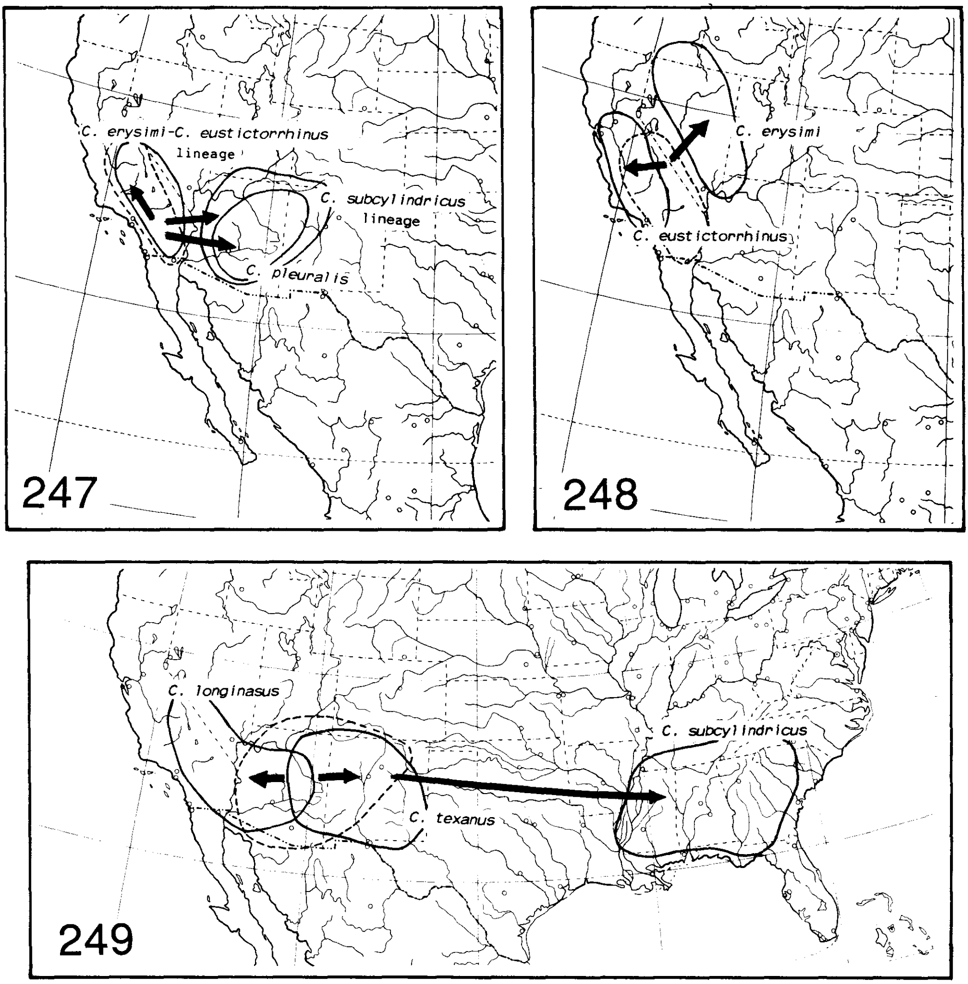
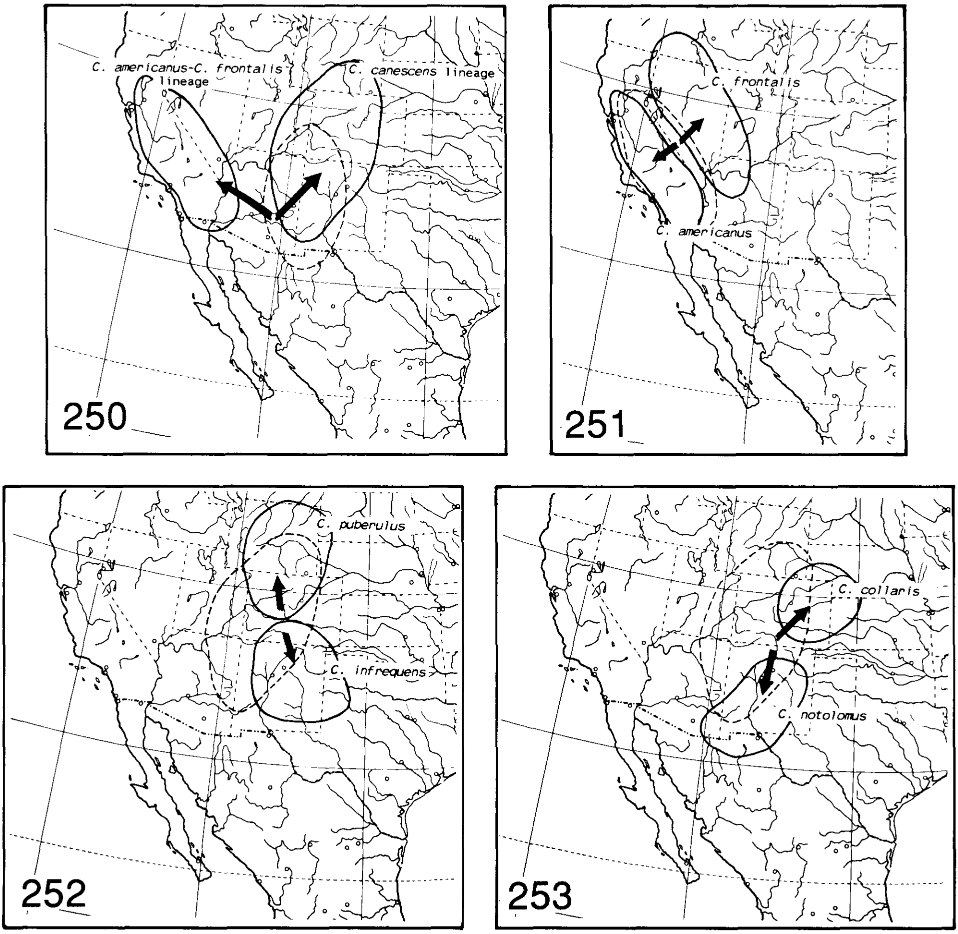


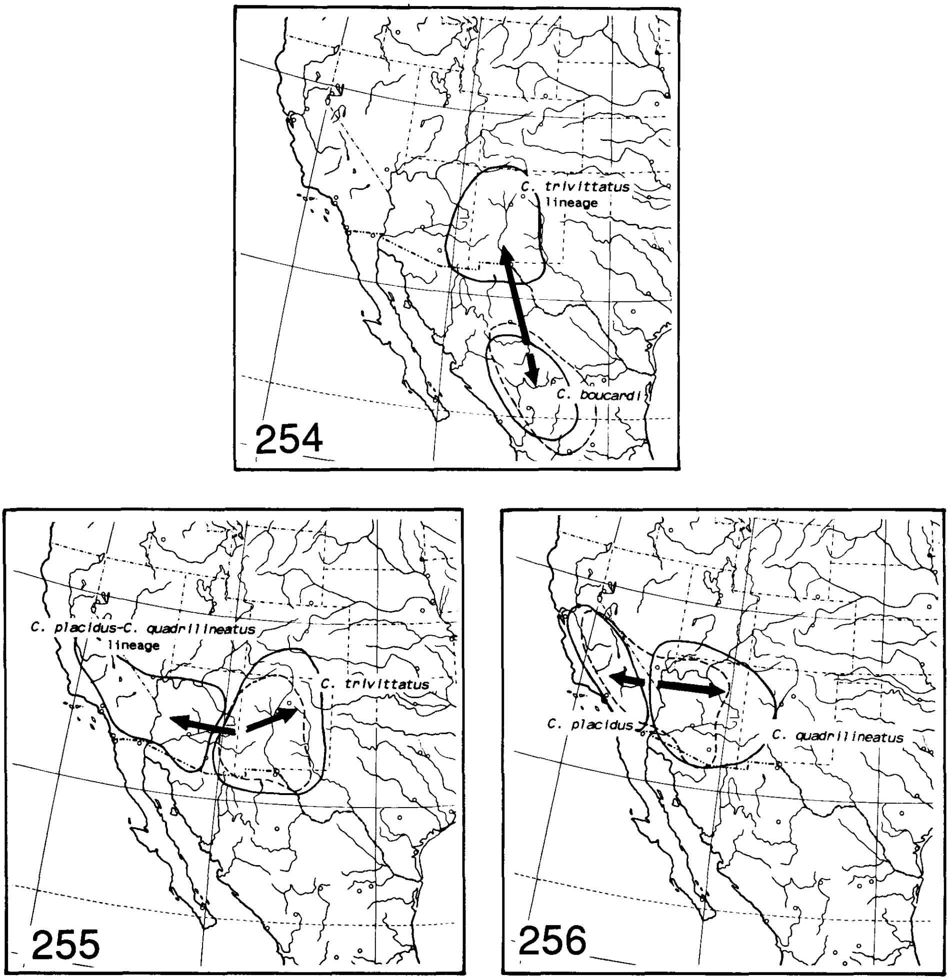
Figure 246. Origin and initial diversification of *Cleonidius* in North America: *Cleonidius erysimi* group, *C. americanus* group, *C. poricollis* group, and *C. boucardi* group. See text, and caption for 242 for detailed explanation.



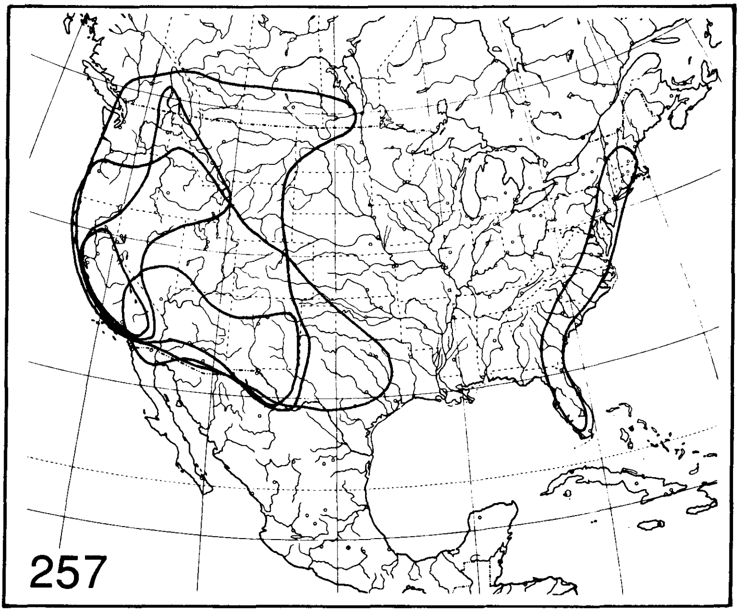
Figures 247–249. Diversification of *Cleonidius* in North America. See text, and captions for 243–245 for detailed explanation. 247, *C. erysimi-C. eustictorrhinus*, *C. pleuralis*, and *C. subcylindricus-C. longinasus-C. texanus* lineages; 248, *C. erysimi* and *C. eustictorrhinus*; 249, *C. subcylindricus*, *C. longinasus* and *C. texanus*.

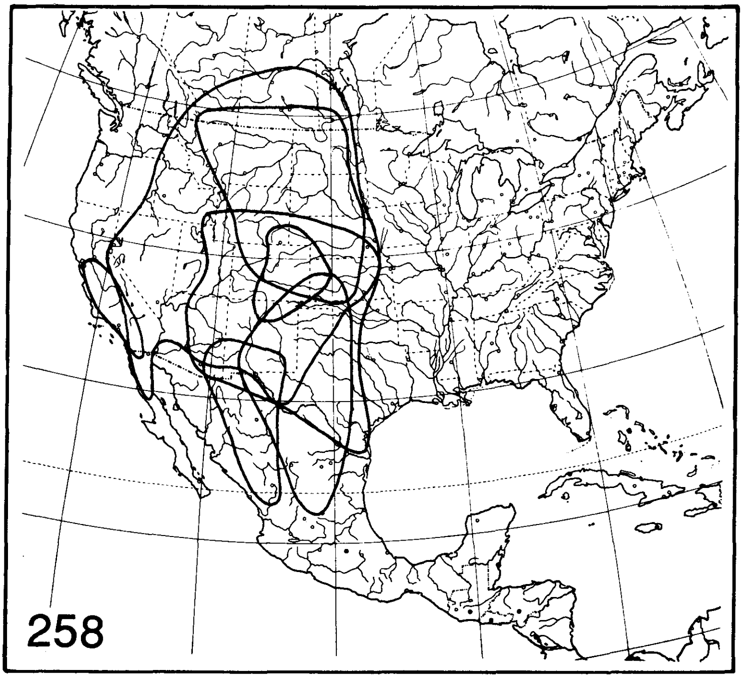


Figures 250–253. Diversification of *Cleonidius* in North America. See text, and captions for 243–245 for detailed explanation. 250, *Cleonidius americanus-C. frontalis*, *C. canescens-C. infrequens-C. puberulus-C. collaris-C. notolomus* lineages; 251, *C. americanus* and *C. frontalis*; 252, *C. puberulus* and *C. infrequens*; 253, *C. collaris* and *C. notolomus*.

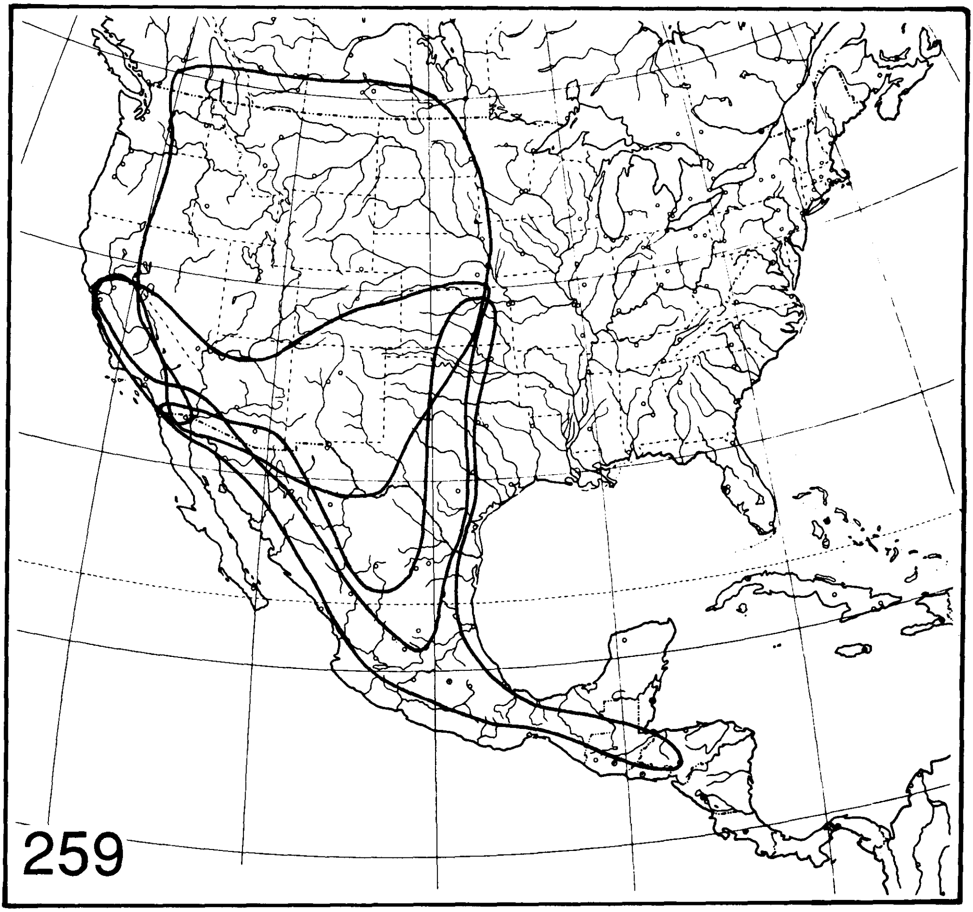


Figures 254–256. Diversification of *Cleonidius* in North America. See text, and captions for 243–245 for detailed explanation. 254, *Cleonidius boucardi* and *C. trivittatus-C. placidus-C. quadrilineatus* lineage; 255, *C. trivittatus* and *C. placidus-C. quadrilineatus* lineage; 256, *C. placidus* and *C. quadrilineatus*.





Figures 257–258. Geographic ranges of species in: 257, *Cleonidius erysimi* species group; 258, *C. americanus* species group.



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259. Geographic ranges of species in the *Cleonidius boucardi* species group

Table 1. Descriptive statistics for *S. confusus* based on eight males and eight females from Medicine Hat, Alberta

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.60 – 2.20	1.900	0.278	0.131
WF	1.60 – 2.20	1.938	0.299	0.141
WRA	1.50 – 2.00	1.713	0.246	0.116
LP	2.40 – 3.40	2.913	0.477	0.225
WPB	3.00 – 4.30	3.725	0.698	0.329
WElH	3.80 – 5.30	4.638	0.810	0.382
WElM	4.60 – 6.40	5.550	0.935	0.441
LEl	6.90 – 9.90	8.350	1.425	0.672
LEy	1.30 – 1.70	1.513	0.246	0.116
WEy	0.60 – 0.80	0.763	0.112	0.053
B. Proportions.				
WEy/LEy	0.46 – 0.57	0.506	0.058	0.027
WPB/LP	1.23 – 1.40	1.278	0.080	0.038
WRA/LR	0.85 – 0.95	0.902	0.060	0.028
WRA/WF	0.81 – 0.94	0.886	0.059	0.027
WElM/LEl	0.64 – 0.72	0.665	0.036	0.017
LP/LEl	0.33 – 0.36	0.349	0.017	0.008
Females				
A. Measurements, in mm.				
LR	1.80 – 2.30	2.113	0.233	0.110
WF	1.80 – 2.40	2.150	0.289	0.136
WRA	1.50 – 2.00	1.838	0.265	0.125
LP	2.70 – 3.50	3.213	0.396	0.186
WPB	3.30 – 4.60	4.113	0.682	0.321
WElH	4.20 – 5.80	5.175	0.768	0.362
WElM	5.00 – 7.00	6.163	0.948	0.447
LEl	7.80 –10.10	9.325	1.048	0.493
LEy	1.40 – 1.80	1.613	0.187	0.088
WEy	0.70 – 0.90	0.800	0.113	0.053
B. Proportions				
WEy/LEy	0.47 – 0.53	0.496	0.029	0.013
WPB/LP	1.22 – 1.35	1.278	0.070	0.033
WRA/LR	0.81 – 0.91	0.869	0.064	0.030
WRA/WF	0.81 – 0.90	0.855	0.042	0.020
WElM/LEl	0.62 – 0.71	0.660	0.042	0.019
LP/LEl	0.33 – 0.36	0.344	0.013	0.006

Table 2. Descriptive statistics for *S. cristaticollis* based on one male and one female from Medicine Hat, Alberta

Character	Range	Mean	1.5SD	2SE
Male				
A. Measurements, in mm.				
LR	2.10	2.10	–	–
WF	2.10	2.10	–	–
WRA	1.80	1.80	–	–
LP	3.30	3.30	–	–
WPB	4.10	4.10	–	–
WElH	5.40	5.40	–	–
WElM	6.40	6.40	–	–
LEl	10.20	10.20	–	–
LEy	1.70	1.70	–	–
WEy	0.80	0.80	–	–
B. Proportions.				
WEy/LEy	0.47	0.47	–	–
WPB/LP	1.24	1.24	–	–
WRA/LR	0.86	0.86	–	–
WRA/WF	0.86	0.86	–	–
WElM/LEl	0.64	0.64	–	–
LP/LEl	0.32	0.32	–	–
Female				
A. Measurements, in mm.				
LR	2.10	2.10	–	–
WF	2.20	2.20	–	–
WRA	1.90	1.90	–	–
LP	3.40	3.40	–	–
WPB	4.30	4.30	–	–
WElH	5.60	5.60	–	–
WElM	6.60	6.60	–	–
LEl	10.20	10.2	–	–
LEy	1.80	1.80	–	–
WEy	0.80	0.80	–	–
B. Proportions.				
WEy/LEy	0.44	0.44	–	–
WPB/LP	1.27	1.27	–	–
WRA/LR	0.91	0.91	–	–
WRA/WF	0.86	0.86	–	–
WElM/LEl	0.65	0.65	–	–
LP/LEl	0.33	0.33	–	–

Table 3. Descriptive statistics for *S. immaculatus* based on eight males and eight females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.00 – 2.30	2.138	0.195	0.092
WF	1.80 – 2.00	1.950	0.113	0.053
WRA	1.60 – 2.00	1.850	0.196	0.092
LP	2.90 – 3.40	3.163	0.310	0.146
WPB	3.80 – 4.40	4.138	0.288	0.136
WElH	4.80 – 5.80	5.400	0.488	0.230
WElM	5.50 – 6.60	6.238	0.555	0.262
LEl	9.00 –10.90	10.112	0.850	0.400
LEy	1.40 – 1.80	1.588	0.169	0.080
WEy	0.70 – 0.90	0.800	0.080	0.038
B. Proportions.				
WEy/LEy	0.50 – 0.53	0.504	0.018	0.008
WPB/LP	1.24 – 1.40	1.310	0.078	0.037
WRA/LR	0.80 – 0.95	0.866	0.069	0.033
WRA/WF	0.89 – 1.00	0.948	0.072	0.034
WElM/LEl	0.58 – 0.64	0.617	0.030	0.014
LP/LEl	0.30 – 0.34	0.313	0.019	0.009
Females				
A. Measurements, in mm.				
LR	2.20 – 2.40	2.275	0.133	0.063
WF	2.00 – 2.40	2.150	0.196	0.092
WRA	1.90 – 2.10	2.000	0.139	0.065
LP	3.20 – 3.60	3.438	0.226	0.106
WPB	4.20 – 4.70	4.425	0.328	0.155
WElH	5.50 – 6.40	6.000	0.488	0.230
WElM	6.30 – 7.30	6.788	0.522	0.246
LEl	9.40 –12.00	11.075	1.254	0.591
LEy	1.50 – 1.80	1.675	0.155	0.073
WEy	0.80 – 1.00	0.900	0.113	0.053
B. Proportions.				
WEy/LEy	0.47 – 0.60	0.538	0.069	0.032
WPB/LP	1.19 – 1.44	1.289	0.121	0.057
WRA/LR	0.79 – 0.96	0.880	0.072	0.034
WRA/WF	0.88 – 1.05	0.932	0.081	0.038
WElM/LEl	0.56 – 0.67	0.614	0.047	0.022
LP/LEl	0.30 – 0.35	0.311	0.027	0.012

Table 4. Descriptive statistics for *S. parshus* based on eight males and eight females from southern Manitoba and Ontario

Character	Range	Mean	1.5SD	2SE
Male				
A. Measurements, in mm.				
LR	1.70 – 2.10	1.850	0.196	0.013
WF	1.50 – 1.90	1.675	0.192	0.091
WRA	1.30 – 1.60	1.488	0.187	0.088
LP	2.50 – 3.00	2.725	0.275	0.130
WPB	3.00 – 3.80	3.363	0.453	0.214
WElH	3.80 – 5.30	4.450	0.717	0.338
WElM	4.50 – 5.80	5.025	0.825	0.388
LEl	7.20 – 8.60	7.913	0.909	0.428
LEy	1.20 – 1.50	1.350	0.179	0.084
WEy	0.60 – 0.80	0.688	0.125	0.059
B. Proportions.				
WEy/LEy	0.46 – 0.58	0.509	0.060	0.028
WPB/LP	1.15 – 1.31	1.233	0.079	0.037
WRA/LR	0.76 – 0.84	0.804	0.055	0.026
WRA/WF	0.81 – 0.94	0.889	0.071	0.034
WElM/LEl	0.61 – 0.68	0.634	0.042	0.020
LP/LEl	0.33 – 0.37	0.345	0.016	0.007
Females				
A. Measurements, in mm.				
LR	1.70 – 2.20	1.913	0.233	0.110
WF	1.60 – 1.90	1.738	0.178	0.084
WRA	1.40 – 1.70	1.550	0.160	0.076
LP	2.60 – 3.30	2.875	0.399	0.188
WPB	3.20 – 4.00	3.625	0.466	0.220
WElH	4.20 – 5.40	4.838	0.708	0.334
WElM	4.70 – 6.20	5.400	0.765	0.360
LEl	7.50 – 9.60	8.613	1.132	0.534
LEy	1.30 – 1.60	1.425	0.175	0.082
WEy	0.60 – 0.80	0.738	0.112	0.053
B. Proportions.				
WEy/LEy	0.46 – 0.54	0.517	0.041	0.019
WPB/LP	1.18 – 1.36	1.262	0.076	0.036
WRA/LR	0.77 – 0.84	0.812	0.041	0.020
WRA/WF	0.88 – 0.94	0.892	0.030	0.014
WElM/LEl	0.59 – 0.65	0.627	0.028	0.013
LP/LEl	0.32 – 0.35	0.334	0.018	0.008

Table 5. Descriptive statistics for *S. plumbeus* based on eight males and eight females from Rivière – au – Tonnerre, Québec

Character	Range	Mean	1.5SD	2SE
Male				
A. Measurements, in mm.				
LR	1.70 – 1.90	1.844	0.109	0.048
WF	1.60 – 1.80	1.722	0.125	0.055
WRA	1.40 – 1.70	1.567	0.130	0.058
LP	2.50 – 3.00	2.700	0.281	0.125
WPB	3.00 – 3.60	3.356	0.368	0.164
WElH	4.10 – 5.20	4.600	0.618	0.275
WElM	4.60 – 5.60	5.067	0.586	0.260
LEl	7.40 – 9.00	8.233	0.891	0.396
LEy	1.20 – 1.50	1.356	0.170	0.075
WEy	0.70 – 0.90	0.767	0.106	0.047
B. Proportions.				
WEy/LEy	0.50 – 0.64	0.567	0.068	0.030
WPB/LP	1.20 – 1.32	1.243	0.062	0.028
WRA/LR	0.82 – 0.90	0.849	0.038	0.017
WRA/WF	0.88 – 0.94	0.910	0.045	0.020
WElM/LEl	0.60 – 0.64	0.615	0.015	0.007
LP/LEl	0.31 – 0.34	0.328	0.012	0.005
Females				
A. Measurements, in mm.				
LR	1.80 – 2.40	2.100	0.287	0.145
WF	1.90 – 2.00	1.971	0.073	0.037
WRA	1.70 – 2.00	1.786	0.160	0.081
LP	2.80 – 3.30	3.057	0.272	0.137
WPB	3.60 – 4.20	3.886	0.351	0.177
WElH	4.90 – 6.00	5.386	0.551	0.277
WElM	5.40 – 6.60	5.857	0.567	0.286
LEl	9.10 –11.00	9.957	1.017	0.512
LEy	1.30 – 1.60	1.486	0.182	0.092
WEy	0.70 – 0.80	0.757	0.080	0.040
B. Proportions.				
WEy/LEy	0.44 – 0.57	0.511	0.063	0.032
WPB/LP	1.22 – 1.32	1.272	0.054	0.027
WRA/LR	0.82 – 0.94	0.853	0.065	0.033
WRA/WF	0.85 – 1.00	0.906	0.068	0.034
WElM/LEl	0.57 – 0.62	0.589	0.030	0.015
LP/LEl	0.29 – 0.33	0.307	0.021	0.010

Table 6. Descriptive statistics for *S. stenothorax* based on eight males and eight females from Bluefish Caves Archaeological Site, Yukon Territory

Character	Range	Mean	1.5SD	2SE
Male				
A. Measurements, in mm.				
LR	1.80 – 2.10	1.975	0.133	0.063
WF	1.80 – 2.10	2.000	0.139	0.065
WRA	1.70 – 1.90	1.813	0.096	0.045
LP	2.60 – 2.90	2.825	0.155	0.073
WPB	3.50 – 3.90	3.700	0.196	0.093
WElH	4.60 – 5.40	5.025	0.365	0.172
WElM	5.30 – 6.10	5.688	0.388	0.183
LEl	9.00 –10.40	9.713	0.745	0.351
LEy	1.60 – 1.80	1.713	0.125	0.059
WEy	0.80 – 0.90	0.875	0.069	0.033
B. Proportions.				
WEy/LEy	0.47 – 0.56	0.512	0.042	0.020
WPB/LP	1.24 – 1.35	1.310	0.051	0.024
WRA/LR	0.90 – 0.95	0.918	0.036	0.017
WRA/WF	0.86 – 0.95	0.907	0.044	0.020
WElM/LEl	0.57 – 0.60	0.586	0.017	0.008
LP/LEl	0.28 – 0.32	0.291	0.020	0.009
Females				
A. Measurements, in mm.				
LR	1.80 – 2.10	1.988	0.169	0.080
WF	1.90 – 2.20	2.088	0.169	0.080
WRA	1.70 – 2.00	1.888	0.169	0.080
LP	2.70 – 3.20	2.988	0.233	0.110
WPB	3.50 – 4.20	3.925	0.356	0.168
WElH	4.70 – 5.80	5.388	0.575	0.271
WElM	5.40 – 6.40	6.088	0.450	0.212
LEl	9.60 –11.50	10.512	0.930	0.438
LEy	1.50 – 1.90	1.750	0.212	0.100
WEy	0.80 – 0.90	0.863	0.078	0.037
B. Proportions.				
WEy/LEy	0.47 – 0.53	0.494	0.031	0.015
WPB/LP	1.27 – 1.36	1.314	0.042	0.020
WRA/LR	0.90 – 1.00	0.950	0.040	0.019
WRA/WF	0.86 – 0.95	0.904	0.038	0.018
WElM/LEl	0.55 – 0.61	0.580	0.030	0.014
LP/LEl	0.27 – 0.30	0.284	0.012	0.006

Table 7. Descriptive statistics for *A. hystrix* based on eight males and eight females from the El Segundo Sand Dunes, Los Angeles County, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.08 – 1.56	1.345	0.283	0.133
WF	0.88 – 1.24	1.105	0.181	0.085
WRA	0.88 – 1.12	1.040	0.132	0.062
LP	2.08 – 2.72	2.530	0.384	0.181
WPB	2.00 – 2.80	2.530	0.444	0.209
WPT	2.08 – 2.88	2.560	0.411	0.194
WElM	2.40 – 3.68	3.280	0.615	0.290
LEl	4.56 – 6.24	5.540	0.918	0.433
B. Proportions.				
WPB/LP	0.96 – 1.06	0.999	0.050	0.024
WPT/WPB	1.00 – 1.04	1.013	0.028	0.013
WRA/LR	0.69 – 0.85	0.780	0.088	0.041
WRA/WF	0.87 – 1.05	0.945	0.090	0.043
WElM/LEl	0.53 – 0.66	0.592	0.062	0.029
LP/LEl	0.42 – 0.47	0.457	0.024	0.011
Females				
A. Measurements, in mm.				
LR	1.36 – 1.64	1.500	0.124	0.059
WF	1.04 – 1.40	1.230	0.162	0.077
WRA	1.04 – 1.24	1.125	0.113	0.053
LP	2.48 – 3.28	2.800	0.345	0.163
WPB	2.48 – 3.20	2.840	0.333	0.157
WPT	2.56 – 3.28	2.860	0.325	0.153
WElM	3.12 – 4.24	3.720	0.525	0.247
LEl	5.60 – 7.28	6.280	0.775	0.365
B. Proportions.				
WPB/LP	0.97 – 1.06	1.015	0.060	0.028
WPT/WPB	0.97 – 1.03	1.008	0.038	0.018
WRA/LR	0.70 – 0.82	0.751	0.058	0.028
WRA/WF	0.84 – 1.00	0.918	0.086	0.040
WElM/LEl	0.54 – 0.64	0.592	0.047	0.022
LP/LEl	0.43 – 0.47	0.446	0.017	0.008

Table 8. Descriptive statistics for *A. aztecus* based on 13 males and six females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	0.96 – 1.52	1.182	0.251	0.093
WF	0.92 – 1.36	1.172	0.224	0.083
WRA	0.80 – 1.20	1.015	0.198	0.073
LP	1.76 – 2.88	2.209	0.607	0.225
WPB	1.84 – 3.20	2.566	0.658	0.244
WPT	1.84 – 3.28	2.622	0.674	0.249
WElM	2.88 – 4.56	3.699	0.856	0.317
LEl	3.60 – 6.40	4.701	1.300	0.481
B. Proportions.				
WPB/LP	1.05 – 1.27	1.165	0.094	0.035
WPT/WPB	1.00 – 1.04	1.021	0.023	0.008
WRA/LR	0.79 – 1.00	0.862	0.081	0.030
WRA/WF	0.82 – 0.92	0.866	0.036	0.013
WElM/LEl	0.70 – 0.90	0.792	0.074	0.028
LP/LEl	0.37 – 0.54	0.473	0.073	0.027
Females				
A. Measurements, in mm.				
LR	0.88 – 1.60	1.387	0.384	0.209
WF	0.96 – 1.52	1.333	0.310	0.169
WRA	0.80 – 1.28	1.147	0.270	0.147
LP	1.52 – 2.88	2.520	0.754	0.411
WPB	1.76 – 3.44	2.947	0.899	0.490
WPT	1.84 – 3.60	3.053	0.928	0.505
WElM	2.56 – 4.80	4.173	1.211	0.659
LEl	3.20 – 6.24	5.413	1.678	0.914
B. Proportions.				
WPB/LP	1.12 – 1.21	1.169	0.053	0.029
WPT/WPB	0.98 – 1.05	1.037	0.046	0.025
WRA/LR	0.78 – 0.91	0.833	0.082	0.045
WRA/WF	0.83 – 0.88	0.859	0.034	0.019
WElM/LEl	0.72 – 0.80	0.774	0.049	0.026
LP/LEl	0.45 – 0.49	0.467	0.022	0.012

Table 9. Descriptive statistics for *A. lutulentus* based on eight males and eight females from 2 mi. NE. Portal, Arizona

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.44 – 1.76	1.660	0.167	0.079
WF	1.20 – 1.44	1.300	0.140	0.066
WRA	1.04 – 1.28	1.180	0.140	0.066
LP	2.56 – 3.36	3.050	0.478	0.202
WPB	2.72 – 3.52	3.160	0.406	0.191
WPT	2.56 – 3.20	2.930	0.327	0.154
WElM	3.36 – 4.80	4.340	0.693	0.327
LEl	5.92 – 7.04	6.560	0.588	0.277
B. Proportions.				
WPB/LP	1.00 – 1.08	1.037	0.038	0.018
WPT/WPB	0.90 – 0.95	0.928	0.024	0.011
WRA/LR	0.67 – 0.76	0.711	0.045	0.021
WRA/WF	0.87 – 0.94	0.908	0.048	0.023
WElM/LEl	0.57 – 0.72	0.661	0.072	0.034
LP/LEl	0.43 – 0.50	0.464	0.039	0.018
Females				
A. Measurements, in mm.				
LR	1.60 – 1.84	1.750	0.119	0.056
WF	1.20 – 1.44	1.350	0.150	0.070
WRA	1.12 – 1.36	1.250	0.127	0.060
LP	2.80 – 3.44	3.160	0.368	0.174
WPB	2.88 – 3.92	3.350	0.478	0.225
WPT	2.72 – 3.52	3.180	0.419	0.198
WElM	3.92 – 5.20	4.540	0.562	0.265
LEl	6.48 – 7.92	7.110	0.763	0.360
B. Proportions.				
WPB/LP	1.03 – 1.14	1.060	0.056	0.026
WPT/WPB	0.90 – 1.00	0.950	0.052	0.024
WRA/LR	0.67 – 0.74	0.714	0.036	0.017
WRA/WF	0.89 – 0.94	0.926	0.035	0.017
WElM/LEl	0.61 – 0.66	0.639	0.028	0.013
LP/LEl	0.42 – 0.47	0.445	0.028	0.013

Table 10. Descriptive statistics for *A. porosus* based on seven males and eight females from 68.0 km. W. Ejido Viscaino, Baja California Sur, México

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.37 – 3.20	2.904	0.473	0.238
WF	1.86 – 2.32	2.124	0.261	0.132
WRA	1.55 – 2.12	1.887	0.293	0.148
LP	3.82 – 5.57	4.747	0.890	0.448
WPB	4.13 – 5.88	5.189	0.934	0.471
WPT	4.02 – 5.68	4.984	0.864	0.435
WElM	5.57 – 8.05	7.106	1.266	0.638
LEl	8.46 –11.76	10.467	1.820	0.917
B. Proportions.				
WPB/LP	1.02 – 1.17	1.095	0.088	0.044
WPT/WPB	0.93 – 1.00	0.961	0.041	0.021
WRA/LR	0.61 – 0.68	0.650	0.033	0.017
WRA/WF	0.83 – 0.96	0.887	0.061	0.031
WElM/LEl	0.65 – 0.70	0.679	0.026	0.013
LP/LEl	0.41 – 0.48	0.454	0.035	0.018
Females				
A. Measurements, in mm.				
LR	2.32 – 3.51	3.095	0.580	0.274
WF	1.86 – 2.63	2.329	0.389	0.183
WRA	1.60 – 2.32	2.006	0.356	0.168
LP	4.02 – 5.68	5.096	0.866	0.408
WPB	4.23 – 6.40	5.549	1.155	0.544
WPT	4.23 – 6.09	5.366	0.960	0.452
WElM	5.99 – 8.88	7.858	1.508	0.711
LEl	8.46 –13.00	11.430	2.411	1.136
B. Proportions.				
WPB/LP	1.05 – 1.13	1.086	0.054	0.025
WPT/WPB	0.90 – 1.02	0.970	0.058	0.027
WRA/LR	0.62 – 0.69	0.650	0.043	0.020
WRA/WF	0.83 – 0.91	0.861	0.047	0.022
WElM/LEl	0.65 – 0.73	0.689	0.041	0.019
LP/LEl	0.42 – 0.48	0.448	0.028	0.013

Table 11. Descriptive statistics for *A. angularis* based on 15 males and 10 females from Mercury, Nevada

Character	Range	Mean	1.5SD	
Males				
A. Measurements, in mm.				
LR	1.55 – 2.23	1.861	0.283	0.097
WF	1.44 – 1.75	1.615	0.190	0.065
WRA	1.14 – 1.65	1.430	0.239	0.082
LP	2.48 – 3.82	3.111	0.573	0.197
WPB	2.99 – 4.33	3.563	0.606	0.209
WPT	3.20 – 4.54	3.818	0.586	0.201
WElM	3.72 – 5.78	4.918	0.884	0.304
LEl	5.68 – 8.57	7.376	1.183	0.407
B. Proprotions.				
WPB/LP	1.07 – 1.29	1.148	0.081	0.028
WPT/WPB	1.03 – 1.13	1.073	0.045	0.016
WRA/LR	0.66 – 0.84	0.769	0.075	0.026
WRA/WF	0.79 – 0.94	0.884	0.068	0.023
WElM/LEl	0.57 – 0.72	0.670	0.062	0.021
LP/LEl	0.36 – 0.46	0.422	0.034	0.012
Females				
A. Measurements, in mm.				
LR	1.55 – 2.33	1.892	0.356	0.150
WF	1.44 – 1.86	1.651	0.208	0.088
WRA	1.24 – 1.65	1.464	0.204	0.086
LP	2.79 – 3.61	3.168	0.399	0.168
WPB	3.10 – 4.13	3.562	0.511	0.216
WPT	3.10 – 4.33	3.818	0.583	0.246
WElM	3.92 – 5.78	4.984	0.894	0.377
LEl	6.09 – 9.49	7.565	1.503	0.634
B. Proportions.				
WPB/LP	1.03 – 1.17	1.123	0.055	0.023
WPT/WPB	1.00 – 1.13	1.066	0.062	0.026
WRA/LR	0.71 – 0.84	0.777	0.060	0.025
WRA/WF	0.82 – 0.94	0.887	0.057	0.024
WElM/LEl	0.61 – 0.71	0.660	0.047	0.020
LP/LEl	0.38 – 0.46	0.421	0.036	0.015

Table 12. Descriptive statistics for *A. jacobinus* based on eight males and eight females from Turlock, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.16 – 2.88	2.530	0.314	0.148
WF	1.76 – 2.24	2.070	0.226	0.107
WRA	1.52 – 1.92	1.770	0.175	0.082
LP	3.36 – 4.32	3.920	0.425	0.201
WPB	3.68 – 4.64	4.320	0.497	0.234
WPT	3.84 – 4.96	4.440	0.525	0.247
WElM	5.12 – 6.88	6.140	0.769	0.362
LEl	7.20 –10.24	9.000	1.325	0.625
B. Proportions.				
WPB/LP	1.07 – 1.16	1.102	0.044	0.021
WPT/WPB	0.97 – 1.07	1.028	0.047	0.022
WRA/LR	0.67 – 0.73	0.701	0.035	0.017
WRA/WF	0.79 – 0.89	0.856	0.056	0.026
WElM/LEl	0.65 – 0.71	0.684	0.032	0.015
LP/LEl	0.40 – 0.47	0.437	0.033	0.016
Females				
A. Measurements, in mm.				
LR	2.08 – 3.04	2.670	0.471	0.222
WF	1.84 – 2.48	2.150	0.336	0.158
WRA	1.60 – 2.08	1.840	0.213	0.100
LP	3.36 – 4.80	4.120	0.723	0.341
WPB	3.68 – 4.96	4.420	0.666	0.314
WPT	3.84 – 5.28	4.580	0.736	0.347
WElM	5.12 – 7.52	6.480	1.183	0.557
LEl	7.52 –10.88	9.600	1.702	0.802
B. Proportions.				
WPB/LP	1.03 – 1.13	1.075	0.055	0.026
WPT/WPB	1.00 – 1.07	1.036	0.039	0.018
WRA/LR	0.65 – 0.77	0.693	0.056	0.026
WRA/WF	0.79 – 0.92	0.859	0.058	0.027
WElM/LEl	0.66 – 0.69	0.675	0.014	0.006
LP/LEl	0.42 – 0.45	0.429	0.018	0.008

Table 13. Descriptive statistics for *A. albovestitus* based on eight males and eight females from Portal, Arizona

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.24 – 3.04	2.600	0.449	0.212
WF	1.60 – 2.00	1.820	0.200	0.094
WRA	1.60 – 2.00	1.800	0.231	0.109
LP	3.52 – 4.80	4.280	0.688	0.324
WPB	3.68 – 5.28	4.520	0.756	0.356
WPT	3.60 – 4.80	4.290	0.608	0.287
WElM	5.28 – 7.36	6.440	1.087	0.512
LEl	8.48 –11.68	10.000	1.653	0.779
B. Proportions.				
WPB/LP	1.03 – 1.10	1.056	0.039	0.018
WPT/WPB	0.91 – 1.00	0.951	0.045	0.021
WRA/LR	0.63 – 0.75	0.695	0.061	0.029
WRA/WF	0.91 – 1.00	0.989	0.048	0.023
WElM/LEl	0.60 – 0.72	0.645	0.055	0.026
LP/LEl	0.40 – 0.45	0.428	0.024	0.011
Females				
A. Measurements, in mm.				
LR	2.24 – 3.36	2.770	0.559	0.263
WF	1.60 – 2.32	2.030	0.400	0.189
WRA	1.52 – 2.24	1.940	0.414	0.195
LP	3.68 – 5.12	4.550	0.820	0.387
WPB	3.84 – 5.60	4.780	1.012	0.477
WPT	3.84 – 5.44	4.640	0.907	0.428
WElM	5.60 – 8.16	6.840	1.450	0.683
LEl	8.48 –13.76	10.780	2.623	1.236
B. Proportions.				
WPB/LP	0.98 – 1.09	1.049	0.061	0.029
WPT/WPB	0.94 – 1.00	0.972	0.031	0.015
WRA/LR	0.67 – 0.74	0.700	0.047	0.022
WRA/WF	0.92 – 1.00	0.955	0.038	0.018
WElM/LEl	0.95 – 0.69	0.637	0.054	0.025
LP/LEl	0.37 – 0.46	0.425	0.039	0.018

Table 14. Descriptive statistics for *A. saginatus* based on eight males and eight females from 5 mi. SW. Patagonia, Arizona

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.72 – 3.28	2.940	0.285	0.134
WF	1.84 – 2.16	1.980	0.154	0.072
WRA	1.76 – 2.16	1.950	0.212	0.100
LP	4.32 – 5.60	4.840	0.676	0.319
WPB	4.48 – 5.60	5.080	0.555	0.262
WPT	4.32 – 5.12	4.720	0.406	0.191
WElM	6.56 – 7.84	7.280	0.691	0.326
LEl	11.04 –13.12	12.060	1.133	0.534
B. Proportions.				
WPB/LP	1.00 – 1.11	1.052	0.062	0.029
WPT/WPB	0.88 – 0.97	0.930	0.044	0.021
WRA/LR	0.63 – 0.73	0.664	0.056	0.026
WRA/WF	0.92 – 1.08	0.985	0.079	0.037
WElM/LEl	0.59 – 0.62	0.604	0.016	0.007
LP/LEl	0.38 – 0.43	0.401	0.024	0.011
Females				
A. Measurements, in mm.				
LR	2.96 – 3.60	3.156	0.288	0.128
WF	2.00 – 2.32	2.151	0.152	0.068
WRA	1.92 – 2.40	2.169	0.228	0.101
LP	4.96 – 5.92	5.351	0.418	0.186
WPB	4.96 – 6.08	5.511	0.525	0.233
WPT	4.64 – 5.76	5.156	0.573	0.255
WElM	7.36 – 8.96	8.018	0.782	0.348
LEl	12.48 –14.72	13.387	1.170	0.520
B. Proportions.				
WPB/LP	1.00 – 1.06	1.029	0.031	0.014
WPT/WPB	0.91 – 0.97	0.935	0.030	0.013
WRA/LR	0.63 – 0.74	0.688	0.056	0.025
WRA/WF	0.96 – 1.04	1.007	0.046	0.021
WElM/LEl	0.56 – 0.64	0.599	0.030	0.013
LP/LEl	0.39 – 0.43	0.400	0.017	0.008

Table 15. Descriptive statistics for *C. erysimi* based on eight males and eight females from Redondo, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.68 – 2.16	1.925	0.279	0.131
WF	1.24 – 1.56	1.410	0.160	0.075
WRA	1.24 – 1.56	1.390	0.184	0.087
LP	3.04 – 3.68	3.400	0.454	0.214
WPB	2.96 – 4.16	3.510	0.603	0.284
WElH	3.28 – 4.64	3.930	0.721	0.340
WElM	3.60 – 4.96	4.300	0.780	0.367
LEl	7.04 – 9.60	8.480	1.405	0.662
LEy	0.92 – 1.20	1.060	0.143	0.068
WEy	0.56 – 0.68	0.625	0.078	0.037
B. Proportions.				
WEy/LEy	0.57 – 0.61	0.590	0.026	0.012
WPB/LP	0.97 – 1.13	1.031	0.077	0.036
WRA/LR	0.69 – 0.76	0.723	0.039	0.019
WRA/WF	0.94 – 1.05	0.986	0.054	0.026
WElM/LEl	0.49 – 0.53	0.507	0.021	0.010
LP/LEl	0.38 – 0.43	0.402	0.022	0.010
Females				
A. Measurements, in mm.				
LR	1.84 – 2.32	2.050	0.252	0.119
WF	1.28 – 1.60	1.420	0.154	0.072
WRA	1.20 – 1.36	1.310	0.095	0.045
LP	3.12 – 3.92	3.510	0.365	0.172
WPB	3.04 – 3.76	3.530	0.398	0.187
WElH	3.36 – 4.40	3.960	0.476	0.224
WElM	3.92 – 4.80	4.420	0.409	0.193
LEl	7.52 – 9.76	8.720	1.073	0.506
LEy	0.88 – 1.12	1.035	0.113	0.053
WEy	0.52 – 0.72	0.640	0.101	0.048
B. Proportions.				
WEy/LEy	0.58 – 0.67	0.618	0.047	0.022
WPB/LP	0.96 – 1.07	1.006	0.057	0.027
WRA/LR	0.57 – 0.68	0.641	0.054	0.026
WRA/WF	0.85 – 1.03	0.925	0.074	0.035
WElM/LEl	0.49 – 0.53	0.508	0.020	0.009
LP/LEl	0.38 – 0.42	0.403	0.023	0.011

Table 16. Descriptive statistics for *C. eustictorrhinus* based on 13 males and 14 females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.80 – 2.20	2.000	0.171	0.063
WF	0.96 – 1.48	1.329	0.238	0.088
WRA	1.08 – 1.40	1.255	0.142	0.052
LP	2.64 – 3.60	3.360	0.421	0.156
WPB	2.80 – 3.92	3.502	0.439	0.162
WElH	3.44 – 4.64	4.148	0.547	0.203
WElM	3.68 – 4.96	4.437	0.558	0.206
LEl	6.88 – 9.44	8.369	1.057	0.391
LEy	0.96 – 1.16	1.068	0.096	0.036
WEy	0.52 – 0.72	0.637	0.075	0.028
B. Proportions.				
WEy/LEy	0.54 – 0.67	0.597	0.062	0.023
WPB/LP	1.02 – 1.09	1.043	0.029	0.011
WRA/LR	0.59 – 0.69	0.627	0.038	0.014
WRA/WF	0.88 – 1.13	0.952	0.116	0.043
WElM/LEl	0.49 – 0.56	0.530	0.028	0.010
LP/LEl	0.38 – 0.43	0.402	0.026	0.010
Females				
A. Measurements, in mm.				
LR	1.80 – 2.20	2.011	0.200	0.071
WF	1.08 – 1.52	1.331	0.170	0.061
WRA	1.12 – 1.36	1.214	0.109	0.039
LP	2.88 – 3.76	3.406	0.329	0.117
WPB	3.12 – 4.00	3.543	0.422	0.151
WElH	3.60 – 4.64	4.126	0.509	0.181
WElM	3.92 – 5.04	4.423	0.497	0.177
LEl	0.75 – 9.44	8.434	0.962	0.343
LEy	1.00 – 1.20	1.089	0.113	0.040
WEy	0.56 – 0.68	0.620	0.056	0.020
B. Proportions.				
WEy/LEy	0.52 – 0.64	0.571	0.056	0.020
WPB/LP	0.98 – 1.14	1.040	0.059	0.021
WRA/LR	0.56 – 0.65	0.604	0.033	0.012
WRA/WF	0.87 – 1.11	0.916	0.092	0.033
WElM/LEl	0.49 – 0.55	0.525	0.024	0.009
LP/LEl	0.38 – 0.43	0.404	0.026	0.009

Table 17. Descriptive statistics for *C. pleuralis* based on eight males and eight females from Palm Springs, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.72 – 1.96	1.840	0.140	0.066
WF	0.96 – 1.12	1.040	0.096	0.045
WRA	0.80 – 1.00	0.935	0.090	0.043
LP	2.72 – 3.04	2.900	0.154	0.072
WPB	2.40 – 3.04	2.800	0.308	0.145
WElH	3.04 – 3.68	3.460	0.378	0.178
WElM	3.20 – 3.60	3.430	0.235	0.111
LEl	7.44 – 8.72	8.040	0.700	0.330
LEy	0.84 – 1.00	0.955	0.081	0.038
WEy	0.44 – 0.56	0.495	0.064	0.030
B. Proportions.				
WEy/LEy	0.46 – 0.58	0.519	0.068	0.032
WPB/LP	0.88 – 1.03	0.965	0.065	0.031
WRA/LR	0.47 – 0.56	0.509	0.049	0.023
WRA/WF	0.83 – 1.00	0.900	0.086	0.041
WElM/LEl	0.40 – 0.46	0.427	0.031	0.014
LP/LEl	0.35 – 0.38	0.361	0.023	0.011
Females				
A. Measurements, in mm.				
LR	1.48 – 1.92	1.710	0.258	0.122
WF	0.88 – 1.08	0.990	0.110	0.052
WRA	0.72 – 1.00	0.865	0.140	0.066
LP	2.40 – 3.04	2.720	0.385	0.181
WPB	2.24 – 3.04	2.650	0.442	0.208
WElH	2.80 – 3.68	3.230	0.540	0.255
WElM	2.72 – 3.68	3.110	0.546	0.257
LEl	5.76 – 8.96	7.410	1.556	0.733
LEy	0.76 – 1.00	0.915	0.122	0.057
WEy	0.40 – 0.56	0.485	0.081	0.038
B. Proportions.				
WEy/LEy	0.46 – 0.57	0.530	0.053	0.025
WPB/LP	0.93 – 1.03	0.973	0.060	0.029
WRA/LR	0.46 – 0.53	0.506	0.040	0.019
WRA/WF	0.78 – 0.93	0.873	0.078	0.037
WElM/LEl	0.39 – 0.47	0.422	0.038	0.018
LP/LEl	0.33 – 0.42	0.370	0.043	0.020

Table 18. Descriptive statistics for *C. subcylindricus* based on seven males and 17 females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.68 – 2.08	1.937	0.227	0.114
WF	1.00 – 1.16	1.051	0.102	0.052
WRA	1.12 – 1.36	1.217	0.124	0.062
LP	2.96 – 3.52	3.291	0.313	0.158
WPB	2.88 – 3.68	3.303	0.431	0.217
WElH	3.52 – 4.32	3.943	0.425	0.214
WElM	3.68 – 4.64	4.206	0.571	0.288
LEl	7.68 – 9.44	8.663	1.077	0.543
LEy	0.92 – 1.12	1.034	0.117	0.059
WEy	0.56 – 0.68	0.617	0.068	0.034
B. Proportions.				
WEy/LEy	0.57 – 0.64	0.597	0.036	0.018
WPB/LP	0.95 – 1.05	1.002	0.053	0.027
WRA/LR	0.58 – 0.69	0.630	0.054	0.027
WRA/WF	1.07 – 1.24	1.158	0.081	0.041
WElM/LEl	0.45 – 0.50	0.485	0.028	0.014
LP/LEl	0.36 – 0.40	0.381	0.019	0.010
Females				
A. Measurements, in mm.				
LR	1.68 – 2.28	2.049	0.281	0.091
WF	0.92 – 1.40	1.118	0.168	0.054
WRA	1.12 – 1.40	1.266	0.134	0.043
LP	2.80 – 3.92	3.426	0.515	0.166
WPB	2.80 – 4.00	3.449	0.502	0.162
WElH	3.28 – 4.72	4.061	0.643	0.208
WElM	3.52 – 5.12	4.348	0.766	0.248
LEl	7.52 –10.24	8.951	1.210	0.391
LEy	0.88 – 1.16	1.052	0.123	0.040
WEy	0.52 – 0.76	0.609	0.084	0.027
B. Proportions.				
WEy/LEy	0.52 – 0.68	0.580	0.065	0.021
WPB/LP	0.96 – 1.07	1.008	0.052	0.017
WRA/LR	0.56 – 0.69	0.619	0.042	0.013
WRA/WF	1.00 – 1.26	1.137	0.087	0.028
WElM/LEl	0.43 – 0.53	0.485	0.039	0.013
LP/LEl	0.36 – 0.41	0.383	0.022	0.007

Table 19. Descriptive statistics for *C. longinasus* based on 10 males and 10 females from Hemet Reservoir, Herkey Creek, and Idyllwild, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.80 – 2.28	1.980	0.283	0.119
WF	1.04 – 1.24	1.112	0.089	0.037
WRA	0.84 – 1.08	0.952	0.101	0.043
LP	2.56 – 3.44	2.976	0.434	0.183
WPB	2.72 – 3.44	3.056	0.298	0.126
WElH	3.20 – 4.00	3.560	0.345	0.145
WElM	3.52 – 4.40	3.936	0.466	0.196
LEl	6.72 – 8.64	7.744	0.934	0.394
LEy	0.92 – 1.04	0.960	0.063	0.027
WEy	0.52 – 0.64	0.556	0.066	0.028
B. Proportions.				
WEy/LEy	0.52 – 0.65	0.579	0.060	0.025
WPB/LP	0.97 – 1.13	1.030	0.071	0.030
WRA/LR	0.40 – 0.56	0.485	0.080	0.034
WRA/WF	0.74 – 0.93	0.858	0.130	0.043
WElM/LEl	0.48 – 0.54	0.509	0.031	0.013
LP/LEl	0.36 – 0.40	0.384	0.023	0.010
Females				
A. Measurements, in mm.				
LR	1.92 – 2.52	2.296	0.261	0.110
WF	1.08 – 1.20	1.172	0.064	0.027
WRA	0.80 – 1.00	0.888	0.093	0.039
LP	2.96 – 3.44	3.184	0.232	0.098
WPB	2.96 – 3.36	3.264	0.202	0.085
WElH	3.36 – 4.08	3.824	0.329	0.139
WElM	3.84 – 4.64	4.272	0.432	0.182
LEl	7.52 – 8.80	8.224	0.744	0.313
LEy	0.92 – 1.08	0.984	0.064	0.027
WEy	0.52 – 0.60	0.564	0.034	0.014
B. Proportions.				
WEy/LEy	0.52 – 0.63	0.574	0.048	0.020
WPB/LP	0.95 – 1.11	1.027	0.081	0.034
WRA/LR	0.34 – 0.44	0.388	0.043	0.018
WRA/WF	0.70 – 0.83	0.758	0.069	0.029
WElM/LEl	0.48 – 0.58	0.520	0.043	0.018
LP/LEl	0.37 – 0.40	0.388	0.015	0.006

Table 20. Descriptive statistics for *C. texanus* based on eight males and eight females from Mile 19, Hitchcock Highway, Santa Catalina Mountains, Arizona

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.44 – 1.64	1.535	0.101	0.048
WF	0.84 – 0.96	0.900	0.064	0.030
WRA	0.80 – 0.88	0.830	0.042	0.020
LP	2.16 – 2.56	2.320	0.192	0.090
WPB	2.48 – 2.56	2.510	0.062	0.029
WElH	2.88 – 3.20	3.030	0.175	0.082
WElM	3.12 – 3.36	3.230	0.156	0.052
LEl	6.32 – 6.96	6.580	0.325	0.153
LEy	0.80 – 0.88	0.825	0.045	0.021
WEy	0.44 – 0.52	0.475	0.038	0.018
B. Proportions.				
WEy/LEy	0.52 – 0.62	0.576	0.051	0.024
WPB/LP	1.00 – 1.15	1.084	0.072	0.034
WRA/LR	0.51 – 0.56	0.541	0.025	0.012
WRA/WF	0.87 – 1.00	0.924	0.073	0.034
WElM/LEl	0.47 – 0.51	0.491	0.021	0.010
LP/LEl	0.34 – 0.38	0.353	0.023	0.011
Females				
A. Measurements, in mm.				
LR	1.32 – 1.72	1.515	0.199	0.094
WF	0.84 – 1.00	0.905	0.078	0.026
WRA	0.68 – 0.80	0.740	0.064	0.030
LP	2.00 – 2.56	2.360	0.301	0.142
WPB	2.24 – 2.72	2.530	0.231	0.109
WElH	2.56 – 3.20	2.990	0.307	0.145
WElM	2.72 – 3.44	3.210	0.336	0.158
LEl	5.52 – 7.04	6.530	0.748	0.352
LEy	0.76 – 0.92	0.830	0.077	0.036
WEy	0.44 – 0.52	0.480	0.056	0.026
B. Proportions.				
WEy/LEy	0.55 – 0.62	0.578	0.036	0.017
WPB/LP	1.00 – 1.12	1.075	0.063	0.030
WRA/LR	0.46 – 0.55	0.490	0.045	0.021
WRA/WF	0.77 – 0.87	0.818	0.048	0.023
WElM/LEl	0.48 – 0.51	0.492	0.017	0.008
LP/LEl	0.34 – 0.38	0.361	0.016	0.008

Table 21. Descriptive statistics for *C. americanus* based on eight males and eight females from Mercy Hot Springs, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.28 – 2.44	1.815	0.555	0.262
WF	0.88 – 1.44	1.155	0.261	0.123
WRA	0.80 – 1.24	1.005	0.234	0.111
LP	1.84 – 3.60	2.670	0.836	0.394
WPB	1.92 – 3.60	2.760	0.831	0.392
WElH	2.40 – 4.56	3.390	1.058	0.499
WElM	2.88 – 4.88	3.700	0.985	0.464
LEl	4.80 – 9.28	6.980	2.135	1.007
LEy	0.72 – 1.16	0.950	0.239	0.113
WEy	0.40 – 0.72	0.570	0.156	0.073
B. Proportions.				
WEy/LEy	0.54 – 0.65	0.600	0.053	0.025
WPB/LP	1.00 – 1.09	1.035	0.044	0.021
WRA/LR	0.51 – 0.63	0.559	0.052	0.025
WRA/WF	0.81 – 0.91	0.870	0.049	0.023
WElM/LEl	0.50 – 0.60	0.534	0.044	0.021
LP/LEl	0.37 – 0.40	0.383	0.013	0.006
Females				
A. Measurements, in mm.				
LR	1.36 – 2.44	1.755	0.504	0.238
WF	0.88 – 1.52	1.130	0.294	0.138
WRA	0.72 – 1.28	0.910	0.260	0.123
LP	2.00 – 3.44	2.480	0.669	0.316
WPB	1.92 – 3.68	2.610	0.806	0.380
WElH	2.40 – 4.48	3.180	0.931	0.439
WElM	2.72 – 4.88	3.540	0.981	0.462
LEl	4.96 – 8.96	6.560	1.796	0.846
LEy	0.72 – 1.28	0.925	0.251	0.118
WEy	0.40 – 0.72	0.540	0.136	0.064
B. Proportions.				
WEy/LEy	0.53 – 0.67	0.586	0.064	0.030
WPB/LP	0.96 – 1.10	1.048	0.073	0.034
WRA/LR	0.43 – 0.59	0.521	0.065	0.031
WRA/WF	0.70 – 0.91	0.806	0.094	0.044
WElM/LEl	0.50 – 0.56	0.540	0.029	0.013
LP/LEl	0.36 – 0.40	0.379	0.020	0.009

Table 22. Descriptive statistics for *C. frontalis* based on eight males and eight females from Medicine Hat, Alberta

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.52 – 2.00	1.745	0.231	0.109
WF	1.00 – 1.28	1.145	0.150	0.071
WRA	0.92 – 1.20	1.070	0.163	0.077
LP	2.32 – 3.04	2.710	0.376	0.177
WPB	2.64 – 3.44	3.030	0.437	0.206
WElH	3.20 – 4.16	3.650	0.544	0.256
WElM	3.52 – 4.56	4.020	0.634	0.299
LEl	6.40 – 8.80	7.540	1.279	0.603
LEy	0.80 – 1.00	0.925	0.130	0.061
WEy	0.52 – 0.64	0.565	0.075	0.035
B. Proportions				
WEy/LEy	0.54 – 0.65	0.612	0.055	0.026
WPB/LP	1.09 – 1.14	1.118	0.028	0.013
WRA/LR	0.56 – 0.71	0.614	0.064	0.030
WRA/WF	0.89 – 0.97	0.934	0.037	0.017
WElM/LEl	0.50 – 0.55	0.534	0.029	0.014
LP/LEl	0.35 – 0.38	0.360	0.017	0.008
Females				
A. Measurements, in mm.				
LR	1.52 – 2.04	1.785	0.264	0.125
WF	1.00 – 1.36	1.170	0.183	0.087
WRA	0.96 – 1.12	1.055	0.078	0.037
LP	2.40 – 3.12	2.880	0.406	0.191
WPB	2.64 – 3.60	3.140	0.424	0.200
WElH	3.20 – 4.40	3.830	0.542	0.256
WElM	3.52 – 4.88	4.220	0.601	0.283
LEl	6.56 – 8.48	7.740	1.034	0.487
LEy	0.80 – 1.12	1.000	0.150	0.071
WEy	0.48 – 0.60	0.570	0.070	0.033
B. Proportions.				
WEy/LEy	0.52 – 0.60	0.572	0.052	0.025
WPB/LP	1.03 – 1.16	1.092	0.074	0.035
WRA/LR	0.55 – 0.65	0.594	0.055	0.026
WRA/WF	0.82 – 1.00	0.907	0.090	0.042
WElM/LEl	0.52 – 0.58	0.545	0.030	0.014
LP/LEl	0.36 – 0.39	0.372	0.016	0.007

Table 23. Descriptive statistics for *C. canescens* based on eight males and eight females from Denver, Colorado

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.48 – 2.00	1.860	0.246	0.116
WF	1.28 – 1.64	1.510	0.156	0.074
WRA	1.24 – 1.60	1.495	0.163	0.077
LP	2.24 – 3.20	2.820	0.419	0.198
WPB	2.64 – 3.76	3.370	0.507	0.239
WElH	3.12 – 4.24	3.870	0.497	0.234
WElM	3.28 – 4.64	4.190	0.608	0.287
LEl	5.60 – 7.76	7.100	1.086	0.512
LEy	0.80 – 1.00	0.965	0.104	0.049
WEy	0.56 – 0.72	0.645	0.075	0.035
B. Proportions				
WEy/LEy	0.63 – 0.72	0.669	0.049	0.023
WPB/LP	1.16 – 1.25	1.195	0.046	0.022
WRA/LR	0.77 – 0.84	0.805	0.037	0.017
WRA/WF	0.97 – 1.03	0.990	0.037	0.017
WElM/LEl	0.57 – 0.61	0.591	0.022	0.010
LP/LEl	0.38 – 0.42	0.398	0.023	0.011
Females				
A. Measurements, in mm.				
LR	1.52 – 2.04	1.880	0.276	0.130
WF	1.28 – 1.72	1.565	0.199	0.094
WRA	1.32 – 1.72	1.545	0.195	0.092
LP	2.40 – 3.12	2.880	0.357	0.168
WPB	2.72 – 3.84	3.390	0.517	0.244
WElH	3.20 – 4.40	3.940	0.614	0.290
WElM	3.36 – 4.88	4.300	0.740	0.348
LEl	5.76 – 8.00	7.220	1.220	0.575
LEy	0.88 – 1.08	0.985	0.124	0.058
WEy	0.56 – 0.72	0.660	0.085	0.040
B. Proportions				
WEy/LEy	0.62 – 0.73	0.671	0.061	0.029
WPB/LP	1.13 – 1.23	1.176	0.052	0.025
WRA/LR	0.76 – 0.87	0.824	0.054	0.025
WRA/WF	0.95 – 1.03	0.988	0.048	0.022
WElM/LEl	0.57 – 0.62	0.596	0.028	0.013
LP/LEl	0.38 – 0.43	0.400	0.026	0.012

Table 24. Descriptive statistics for *C. infrequens* based on two males and six females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.64 – 1.72	1.68	–	–
WF	1.24 – 1.24	1.24	–	–
WRA	1.28 – 1.36	1.32	–	–
LP	2.96 – 3.20	3.08	–	–
WPB	2.96 – 3.44	3.20	–	–
WElH	3.52 – 3.92	3.72	–	–
WElM	4.08 – 4.16	4.12	–	–
LEl	6.88 – 7.36	7.12	–	–
LEy	0.88 – 1.00	0.94	–	–
WEy	0.52 – 0.60	0.56	–	–
B. Proportions				
WEy/LEy	0.59 – 0.60	0.60	–	–
WPB/LP	1.00 – 1.08	1.04	–	–
WRA/LR	0.78 – 0.79	0.79	–	–
WRA/WF	1.03 – 1.10	1.07	–	–
WElM/LEl	0.55 – 0.61	0.58	–	–
LP/LEl	0.43 – 0.44	0.43	–	–
Females				
A. Measurements, in mm.				
LR	1.44 – 1.88	1.667	0.239	0.130
WF	1.24 – 1.40	1.327	0.080	0.043
WRA	1.32 – 1.44	1.373	0.090	0.049
LP	3.04 – 3.52	3.267	0.308	0.167
WPB	3.12 – 3.60	3.373	0.278	0.151
WElH	3.60 – 4.32	4.040	0.460	0.251
WElM	3.76 – 4.72	4.400	0.563	0.307
LEl	7.20 – 8.48	7.840	0.759	0.413
LEy	0.96 – 1.16	1.067	0.105	0.057
WEy	0.52 – 0.60	0.573	0.049	0.027
B. Proportions.				
WEy/LEy	0.52 – 0.58	0.538	0.032	0.018
WPB/LP	1.00 – 1.05	1.033	0.031	0.017
WRA/LR	0.75 – 0.92	0.828	0.088	0.048
WRA/WF	1.00 – 1.09	1.036	0.061	0.033
WElM/LEl	0.52 – 0.60	0.561	0.046	0.025
LP/LEl	0.40 – 0.45	0.417	0.027	0.015

Table 25. Descriptive statistics for *C. puberulus* based on six males and 10 females from Colorado Springs, Colorado

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm				
LR	1.44 – 1.64	1.513	0.128	0.070
WF	1.24 – 1.40	1.313	0.110	0.060
WRA	1.16 – 1.28	1.213	0.082	0.045
LP	2.48 – 3.04	2.627	0.317	0.173
WPB	2.64 – 2.96	2.760	0.197	0.107
WElH	3.04 – 3.44	3.200	0.201	0.109
WElM	3.36 – 3.60	3.493	0.145	0.079
LEl	5.76 – 6.48	6.067	0.425	0.232
LEy	0.84 – 1.04	0.900	0.106	0.058
WEy	0.52 – 0.56	0.533	0.031	0.017
B. Proportions.				
WEy/LEy	0.50 – 0.67	0.600	0.085	0.046
WPB/LP	0.97 – 1.13	1.054	0.086	0.047
WRA/LR	0.71 – 0.87	0.804	0.083	0.045
WRA/WF	0.86 – 1.00	0.926	0.080	0.044
WElM/LEl	0.53 – 0.61	0.577	0.039	0.021
LP/LEl	0.40 – 0.47	0.433	0.033	0.018
Females				
A. Measurements, in mm.				
LR	1.28 – 1.76	1.548	0.255	0.107
WF	1.20 – 1.48	1.356	0.161	0.068
WRA	1.00 – 1.36	1.196	0.178	0.075
LP	2.24 – 3.04	2.648	0.454	0.192
WPB	2.24 – 3.36	2.792	0.520	0.219
WElH	2.64 – 3.84	3.280	0.640	0.270
WElM	2.96 – 4.08	3.608	0.597	0.252
LEl	4.96 – 7.52	6.328	1.253	0.529
LEy	0.76 – 1.04	0.916	0.159	0.067
WEy	0.48 – 0.60	0.552	0.079	0.033
B. Proportions.				
WEy/LEy	0.58 – 0.63	0.604	0.035	0.015
WPB/LP	0.97 – 1.11	1.054	0.067	0.028
WRA/LR	0.74 – 0.82	0.774	0.037	0.015
WRA/WF	0.83 – 0.94	0.881	0.050	0.021
WElM/LEl	0.54 – 0.60	0.572	0.031	0.013
LP/LEl	0.40 – 0.45	0.420	0.021	0.009

Table 26. Descriptive statistics for *C. collaris* based on seven males and six females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.60 – 2.20	1.971	0.333	0.168
WF	1.24 – 1.72	1.486	0.248	0.125
WRA	1.16 – 1.44	1.280	0.162	0.082
LP	2.72 – 3.84	3.211	0.633	0.319
WPB	3.04 – 4.24	3.611	0.673	0.339
WElH	3.68 – 5.20	4.446	0.840	0.423
WElM	4.24 – 5.60	4.937	0.758	0.382
LEl	6.72 – 9.12	7.909	1.412	0.712
LEy	0.88 – 1.24	1.011	0.176	0.089
WEy	0.56 – 0.72	0.629	0.090	0.045
B. Proportions.				
WEy/LEy				
WPB/LP	1.07 – 1.21	1.126	0.075	0.038
WRA/LR	0.61 – 0.73	0.652	0.062	0.031
WRA/WF	0.83 – 0.94	0.864	0.065	0.033
WElM/LEl	0.59 – 0.64	0.625	0.028	0.014
LP/LEl	0.40 – 0.42	0.406	0.017	0.008
Females				
A. Measurements, in mm.				
LR	1.68 – 2.24	1.940	0.321	0.175
WF	1.32 – 1.72	1.513	0.219	0.119
WRA	1.16 – 1.36	1.240	0.126	0.069
LP	2.80 – 3.68	3.173	0.561	0.306
WPB	3.28 – 4.16	3.747	0.534	0.291
WElH	3.84 – 5.12	4.507	0.798	0.435
WElM	4.40 – 5.76	5.080	0.861	0.469
LEl	7.20 – 8.96	8.133	1.034	0.563
LEy	1.00 – 1.08	1.053	0.049	0.027
WEy	0.56 – 0.72	0.633	0.110	0.060
B. Proportions.				
WEy/LEy	0.52 – 0.67	0.601	0.094	0.051
WPB/LP	1.13 – 1.24	1.183	0.060	0.033
WRA/LR	0.61 – 0.69	0.642	0.051	0.028
WRA/WF	0.79 – 0.88	0.822	0.058	0.031
WElM/LEl	0.60 – 0.65	0.623	0.028	0.015
LP/LEl	0.37 – 0.41	0.390	0.025	0.014

Table 27. Descriptive statistics for *C. notolomus* based on 11 males and 13 females from throughout the species range

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.56 – 2.24	2.015	0.298	0.120
WF	1.20 – 1.52	1.407	0.144	0.058
WRA	1.16 – 1.40	1.313	0.096	0.039
LP	2.48 – 3.68	3.389	0.518	0.208
WPB	2.88 – 4.00	3.615	0.425	0.171
WElH	3.36 – 4.64	4.327	0.541	0.217
WElM	3.68 – 5.20	4.822	0.666	0.268
LEl	5.92 – 9.12	8.044	1.337	0.537
LEy	0.96 – 1.16	1.058	0.102	0.041
WEy	0.56 – 0.72	0.636	0.068	0.027
B. Proportions				
WEy/LEy	0.55 – 0.65	0.602	0.057	0.023
WPB/LP	1.02 – 1.16	1.070	0.061	0.025
WRA/LR	0.60 – 0.77	0.656	0.081	0.033
WRA/WF	0.84 – 0.97	0.935	0.057	0.023
WElM/LEl	0.56 – 0.64	0.601	0.038	0.015
LP/LEl	0.40 – 0.44	0.422	0.024	0.010
Females				
A. Measurements, in mm.				
LR	1.80 – 2.32	2.059	0.242	0.090
WF	1.24 – 1.60	1.437	0.177	0.066
WRA	1.16 – 1.48	1.302	0.162	0.060
LP	3.12 – 4.16	3.575	0.466	0.172
WPB	3.20 – 4.40	3.809	0.555	0.206
WElH	3.76 – 5.12	4.517	0.675	0.250
WElM	4.24 – 5.92	5.083	0.760	0.281
LEl	7.04 – 9.44	8.455	1.159	0.429
LEy	0.96 – 1.20	1.083	0.119	0.044
WEy	0.56 – 0.72	0.646	0.073	0.027
B. Proportions				
WEy/LEy	0.54 – 0.65	0.597	0.051	0.019
WPB/LP	1.00 – 1.12	1.065	0.051	0.019
WRA/LR	0.59 – 0.68	0.633	0.049	0.018
WRA/WF	0.85 – 0.95	0.906	0.042	0.015
WElM/LEl	0.58 – 0.64	0.601	0.030	0.011
LP/LEl	0.40 – 0.45	0.423	0.022	0.008

Table 28. Descriptive statistics for *C. poricollis* based on eight males and eight females from 1 mi. N. Little Lake, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.52 – 1.88	1.700	0.195	0.092
WF	0.88 – 1.08	0.950	0.131	0.062
WRA	0.96 – 1.12	1.045	0.087	0.041
LP	2.24 – 2.72	2.500	0.238	0.112
WPB	2.48 – 3.04	2.730	0.268	0.126
WElH	2.96 – 3.68	3.320	0.345	0.163
WElM	3.20 – 3.76	3.530	0.311	0.146
LEl	6.40 – 7.36	6.880	0.602	0.284
LEy	0.84 – 1.00	0.920	0.072	0.034
WEy	0.44 – 0.52	0.475	0.038	0.018
B. Proportions				
WEy/LEy	0.48 – 0.55	0.517	0.038	0.018
WPB/LP	1.03 – 1.15	1.093	0.061	0.029
WRA/LR	0.59 – 0.68	0.616	0.049	0.023
WRA/WF	1.00 – 1.18	1.104	0.083	0.039
WElM/LEl	0.50 – 0.53	0.513	0.015	0.007
LP/LEl	0.34 – 0.39	0.364	0.027	0.013
Females				
A. Measurements, in mm.				
LR	1.52 – 1.92	1.735	0.208	0.098
WF	0.88 – 1.12	0.980	0.120	0.057
WRA	1.00 – 1.24	1.075	0.122	0.057
LP	2.24 – 2.96	2.530	0.345	0.163
WPB	2.56 – 3.28	2.860	0.394	0.186
WElH	2.96 – 4.16	3.430	0.582	0.274
WElM	3.36 – 4.56	3.750	0.600	0.283
LEl	6.40 – 8.64	7.260	1.096	0.516
LEy	0.84 – 1.04	0.940	0.091	0.043
WEy	0.44 – 0.56	0.500	0.072	0.034
B. Proportions.				
WEy/LEy	0.50 – 0.58	0.532	0.047	0.022
WPB/LP	1.09 – 1.25	1.132	0.079	0.037
WRA/LR	0.57 – 0.71	0.621	0.070	0.033
WRA/WF	1.04 – 1.14	1.098	0.059	0.028
WElM/LEl	0.50 – 0.53	0.516	0.015	0.007
LP/LEl	0.32 – 0.36	0.349	0.024	0.011

Table 29. Descriptive statistics for *C. calandroides* based on eight males and eight females from Hampton, New Hampshire

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.60 – 1.96	1.850	0.166	0.078
WF	1.08 – 1.24	1.180	0.085	0.040
WRA	1.08 – 1.24	1.170	0.089	0.042
LP	2.56 – 3.12	2.960	0.280	0.132
WPB	2.80 – 3.44	3.180	0.338	0.159
WElH	3.20 – 4.08	3.740	0.399	0.188
WElM	3.68 – 4.56	4.210	0.430	0.203
LEl	6.40 – 7.84	7.240	0.638	0.301
LEy	0.84 – 0.96	0.910	0.053	0.025
WEy	0.44 – 0.52	0.485	0.038	0.018
B. Proportions				
WEy/LEy	0.52 – 0.57	0.533	0.024	0.011
WPB/LP	1.00 – 1.13	1.075	0.064	0.030
WRA/LR	0.60 – 0.68	0.633	0.044	0.021
WRA/WF	0.94 – 1.04	0.992	0.053	0.025
WElM/LEl	0.57 – 0.60	0.581	0.016	0.007
LP/LEl	0.39 – 0.43	0.409	0.021	0.010
Females				
A. Measurements, in mm.				
LR	1.92 – 2.08	1.975	0.078	0.037
WF	1.20 – 1.28	1.235	0.050	0.024
WRA	1.12 – 1.28	1.190	0.077	0.036
LP	3.04 – 3.20	3.100	0.085	0.040
WPB	3.20 – 3.60	3.370	0.197	0.093
WElH	3.84 – 4.24	4.030	0.202	0.095
WElM	4.24 – 4.72	4.510	0.256	0.121
LEl	7.36 – 8.16	7.820	0.394	0.186
LEy	0.88 – 1.08	0.955	0.093	0.044
WEy	0.48 – 0.56	0.530	0.042	0.020
B. Proportions				
WEy/LEy	0.52 – 0.64	0.556	0.055	0.026
WPB/LP	1.03 – 1.18	1.087	0.070	0.033
WRA/LR	0.56 – 0.65	0.603	0.046	0.021
WRA/WF	0.93 – 1.00	0.964	0.040	0.019
WElM/LEl	0.55 – 0.63	0.577	0.038	0.018
LP/LEl	0.38 – 0.41	0.397	0.015	0.007

Table 30. Descriptive statistics for *C. boucardi* based on eight males and eight females from north of Tepatitlan, Jalisco, México

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.80 – 2.52	2.065	0.386	0.182
WF	1.08 – 1.48	1.280	0.190	0.089
WRA	1.08 – 1.68	1.315	0.307	0.145
LP	2.96 – 4.40	3.570	0.714	0.337
WPB	3.12 – 4.80	3.810	0.791	0.373
WElH	3.76 – 5.68	4.550	0.972	0.458
WElM	4.24 – 6.16	5.040	0.981	0.462
LEl	7.20 –10.72	8.62	1.900	0.896
LEy	0.96 – 1.32	1.095	0.192	0.091
WEy	0.60 – 0.76	0.665	0.106	0.050
B. Proportions				
WEy/LEy	0.58 – 0.64	0.608	0.036	0.017
WPB/LP	1.04 – 1.09	1.067	0.022	0.010
WRA/LR	0.57 – 0.67	0.635	0.051	0.024
WRA/WF	0.87 – 1.14	1.024	0.113	0.053
WElM/LEl	0.57 – 0.62	0.586	0.024	0.011
LP/LEl	0.40 – 0.44	0.415	0.018	0.009
Females				
A. Measurements, in mm.				
LR	1.52 – 2.40	2.115	0.501	0.236
WF	0.96 – 1.52	1.320	0.308	0.145
WRA	1.00 – 1.48	1.320	0.264	0.125
LP	2.56 – 4.16	3.560	0.846	0.399
WPB	2.48 – 4.56	3.760	1.073	0.506
WElH	3.04 – 5.44	4.550	1.284	0.605
WElM	3.68 – 5.76	5.03	1.177	0.555
LEl	6.08 –10.72	9.020	2.461	1.160
LEy	0.84 – 1.32	1.105	0.217	0.102
WEy	0.56 – 0.80	0.650	0.110	0.052
B. Proportions				
WEy/LEy	0.54 – 0.67	0.591	0.061	0.029
WPB/LP	0.97 – 1.13	1.051	0.075	0.036
WRA/LR	0.59 – 0.66	0.627	0.031	0.014
WRA/WF	0.95 – 1.06	1.004	0.068	0.032
WElM/LEl	0.54 – 0.61	0.560	0.032	0.015
LP/LEl	0.38 – 0.42	0.397	0.021	0.010

Table 31. Descriptive statistics for *C. trivittatus* based on eight males eight females from Albuquerque, New México

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.32 – 2.72	2.565	0.253	0.119
WF	1.60 – 1.88	1.740	0.190	0.089
WRA	1.44 – 1.76	1.585	0.178	0.084
LP	3.92 – 4.72	4.270	0.374	0.176
WPB	4.32 – 5.52	4.670	0.577	0.272
WElH	4.80 – 6.08	5.330	0.608	0.287
WElM	5.44 – 6.64	5.900	0.604	0.285
LEl	9.28 –11.68	10.400	1.126	0.531
LEy	1.08 – 1.52	1.270	0.212	0.100
WEy	0.60 – 0.84	0.735	0.120	0.056
B. Proportions				
WEy/LEy	0.55 – 0.63	0.579	0.035	0.017
WPB/LP	1.06 – 1.17	1.093	0.055	0.026
WRA/LR	0.58 – 0.65	0.618	0.031	0.015
WRA/WF	0.87 – 0.98	0.911	0.051	0.024
WElM/LEl	0.55 – 0.59	0.568	0.018	0.009
LP/LEl	0.39 – 0.42	0.411	0.017	0.008
Females				
A. Measurements, in mm.				
LR	1.92 – 2.96	2.450	0.495	0.350
WF	1.32 – 1.84	1.670	0.279	0.132
WRA	1.16 – 1.68	1.500	0.246	0.116
LP	3.28 – 4.56	4.120	0.714	0.337
WPB	3.36 – 5.04	4.440	0.889	0.419
WElH	3.76 – 6.16	5.170	1.202	0.566
WElM	4.32 – 6.64	5.700	1.191	0.561
LEl	7.68 –11.20	9.940	1.789	0.843
LEy	0.96 – 1.44	1.225	0.231	0.109
WEy	0.56 – 0.80	0.710	0.119	0.056
B. Proportions				
WEy/LEy	0.56 – 0.61	0.581	0.030	0.014
WPB/LP	1.02 – 1.12	1.076	0.047	0.022
WRA/LR	0.57 – 0.68	0.615	0.061	0.029
WRA/WF	0.86 – 0.95	0.899	0.040	0.019
WElM/LEl	0.55 – 0.59	0.572	0.024	0.011
LP/LEl	0.41 – 0.43	0.415	0.016	0.007

Table 32. Descriptive statistics for *C. placidus* based on 10 males and eight females from Panoche, California

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	2.40 – 2.80	2.592	0.240	0.101
WF	1.56 – 1.84	1.692	0.174	0.074
WRA	1.48 – 1.72	1.596	0.134	0.057
LP	3.60 – 4.32	4.008	0.364	0.154
WPB	4.00 – 4.88	4.408	0.465	0.196
WElH	4.80 – 5.76	5.304	0.463	0.195
WElM	5.20 – 6.48	5.776	0.699	0.295
LEl	9.92 –11.68	10.800	1.104	0.466
LEy	1.28 – 1.48	1.364	0.125	0.053
WEy	0.72 – 0.84	0.764	0.052	0.022
B. Proportions				
WEy/LEy	0.53 – 0.59	0.561	0.032	0.013
WPB/LP	1.04 – 1.18	1.100	0.072	0.030
WRA/LR	0.59 – 0.65	0.616	0.022	0.009
WRA/WF	0.91 – 1.00	0.945	0.048	0.020
WElM/LEl	0.51 – 0.56	0.535	0.024	0.010
LP/LEl	0.35 – 0.40	0.372	0.021	0.009
Females				
A. Measurements, in mm.				
LR	2.12 – 2.96	2.565	0.439	0.207
WF	1.32 – 2.00	1.725	0.307	0.145
WRA	1.24 – 1.68	1.510	0.228	0.108
LP	3.12 – 4.56	4.020	0.669	0.315
WPB	3.36 – 4.96	4.290	0.793	0.374
WElH	4.16 – 6.08	5.250	0.916	0.432
WElM	4.64 – 6.80	5.760	0.996	0.469
LEl	8.80 –12.48	11.000	1.799	0.848
LEy	1.08 – 1.48	1.325	0.191	0.090
WEy	0.68 – 0.80	0.740	0.079	0.037
B. Proportions				
WEy/LEy	0.52 – 0.63	0.561	0.060	0.028
WPB/LP	1.00 – 1.11	1.066	0.056	0.026
WRA/LR	0.57 – 0.62	0.590	0.024	0.011
WRA/WF	0.84 – 0.94	0.878	0.060	0.028
WElM/LEl	0.50 – 0.57	0.524	0.030	0.014
LP/LEl	0.35 – 0.39	0.366	0.024	0.011

Table 33. Descriptive statistics for *C. quadrilineatus* based on eight males and eight females from southern Arizona localities

Character	Range	Mean	1.5SD	2SE
Males				
A. Measurements, in mm.				
LR	1.84 – 2.36	2.055	0.270	0.127
WF	1.24 – 1.52	1.365	0.185	0.087
WRA	1.16 – 1.48	1.320	0.181	0.086
LP	3.04 – 3.76	3.380	0.434	0.204
WPB	3.28 – 4.08	3.620	0.496	0.234
WElH	3.84 – 5.04	4.360	0.609	0.287
WElM	4.32 – 5.76	4.850	0.714	0.337
LEl	8.48 –10.56	9.500	1.065	0.502
LEy	1.00 – 1.28	1.140	0.128	0.060
WEy	0.60 – 0.76	0.670	0.077	0.036
B. Proportions				
WEy/LEy	0.53 – 0.61	0.588	0.038	0.018
WPB/LP	1.05 – 1.09	1.071	0.022	0.010
WRA/LR	0.60 – 0.67	0.643	0.035	0.017
WRA/WF	0.91 – 1.07	0.968	0.084	0.040
WElM/LEl	0.48 – 0.55	0.510	0.027	0.013
LP/LEl	0.34 – 0.37	0.356	0.014	0.007
Females				
A. Measurements, in mm.				
LR	1.68 – 2.20	1.985	0.353	0.166
WF	1.04 – 1.52	1.325	0.269	0.127
WRA	1.00 – 1.40	1.230	0.207	0.098
LP	2.48 – 3.68	3.250	0.672	0.317
WPB	2.72 – 3.92	3.440	0.670	0.316
WElH	3.20 – 4.88	4.190	0.918	0.433
WElM	3.60 – 5.36	4.670	0.985	0.464
LEl	7.20 –10.40	9.220	1.809	0.853
LEy	0.92 – 1.20	1.110	0.153	0.072
WEy	0.56 – 0.72	0.655	0.084	0.040
B. Proportions				
WEy/LEy	0.55 – 0.64	0.591	0.046	0.022
WPB/LP	1.02 – 1.10	1.060	0.043	0.020
WRA/LR	0.58 – 0.69	0.621	0.050	0.023
WRA/WF	0.84 – 1.00	0.932	0.076	0.036
WElM/LEl	0.49 – 0.52	0.506	0.019	0.009
LP/LEl	0.34 – 0.37	0.352	0.015	0.007

Appendix II: Species of genera of Cleoninae examined for purposes of determining relationships of New World taxa. Genus-group name is listed first, followed by species examined on loan from BMNH. An asterisk indicates that the species examined is the type-species of that generic-group name. No asterisk indicates that the type species was not examined because, no type-species has yet been designated for that genus-group name; or, type species was not available for study in the BMNH.

Adosomus Faust	*A. granulosus* (Mannerheim)
Amblysomus Faust	*A. brevis* (Fåhraeus) *
Ammocleonus Bedel	*A. hieroglyphicus* (Olivier) *
Atactogaster Faust	*A. orientalis* (Chevrolat) *
Bothynoderes Schoenherr	*B. punctiventris* (Germar) *
Brachycleonus Faust	*B. fronto* (Fischer von Waldheim) *
Calodemas Faust	*C. vetustus* Faust
Centrocleonus Chevrolat	*C. fallax* (Fåhraeus) *
Chromoderus Motschulsky	*C. albidus* (Fabricius) * [= *C. fasciatus* (Vill.)]
Chromonotus Motschulsky	*C. vittatus* (Hochhuth) *
Chromosomus Motschulsky	*C. fischeri* (Fåhraeus) *
Cnemodontus Chevrolat	*C. limpidus* (Gyllenhal)
Coniocleonus Motschulsky	*C. excoriatus* (Gyllenhal) [type species, *C. carinirostris* (Gyllenhal)]
Conorhynchus Motschulsky	*C. conirostris* (Gebler) *
Cosmogaster Faust	*C. lateralis* (Gyllenhal) *
Cylindropterus Chevrolat	*C. luxeri* Chevrolat *
Cyphocleonus Motschulsky	*C. cenchrus* (Pallas) *
Epirhynchus Schoenherr	*E. humerosus* Faust [type species, *E. argus* (Sparrm.)]
Eumecops Hochhuth	*Eumecops* sp. [type species, *E. kittaryi* Hochhuth]
Eurycleonus Bedel	*E. baluchicus* Marshall [type species, *E. gigas* Mars.]
Gonocleonus Chevrolat	*G. helferi* Chevrolat *
Isomerus Motschulsky	*I. granosus* (Zoubkoff) *
Koenigius Heyd.	*K. palaestinus* Heyd. *
Leucochromus Motschulsky	*L. imperialis* (Zoubkoff) *
Leucomigus Motschulsky	*L. candidatus* (Pallas) *
Leucosomus Motschulsky	*L. opthalmicus* (Rossi) *
Liocleonus Motschulsky	*L. clathratus* (Olivier) *
Lixocleonus Marshall	*L. incanus* Marshall *
Lixomorphus Faust	*L. ocularis* (Fabricius) *
Mecaspis Schoenherr	*M. palmatus* (Olivier)
Menocleonus Faust	*M. implicatus* Faust
Microcleonus Faust	*M. panderi* (Fischer von Waldheim) *
Nemoxenus Faust	*N. zebra* (Chevrolat)
Neocleonus Chevrolat	*N. sannio* (Herbst) *

Nomimonyx Faust	*N. perturbans* Faust *
Pachycerus Schoenherr	*P. cordiger* (Germar) [type species, *P. scabrosus* Brullé]
Pentatropis Faust	*P. sparsus* (Fåhraeus) [type species, *P. formosus* (Fåhraeus)]
Phaulosomus Faust	*P. kilimanus* Faust
Pleurocleonus Motchulsky	*P. quadrivittatus* (Zoubkoff) *
Porocleonus Motschulsky	*P. candidus* (Olivier) *
Prionorhinus Chevrolat	*P. stillatus* (Gyllenhal)
Pseudocleonus Chevrolat	*P. cinereus* (Schrank)
Rhabdorhynchus Motschulsky	*R. anchusae* Chevrolat [type species, *R. menetriesi* (Gyllenhal)]
Stephanocleonus Motschulsky	*S. flaviceps* (Pallas) *
Temnorhinus Chevrolat	*T. brevirostris* (Gyllenhal) *
Tetragonothorax Chevrolat	*T. retusus* (Fabricius) *
Trichocleonus Motschulsky	*T. leucophyllus* (Fischer von Waldheim) *
Xanthochelus Chevrolat	*X. longus* Chevrolat *
Xenomacrus Faust	*X. glacialis* (Herbst)

INDEX TO NAMES OF TAXA

(Synonyms in italics)