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THE TRIBE CICINDINI BÄNNINGER (COLEOPTERA: CARABIDAE): COMPARATIVE MORPHOLOGY, CLASSIFICATION, NATURAL HISTORY, AND EVOLUTION

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Abstract.—The two species of the Gondwanian carabid beetle tribe, Cicindini, are redescribed in detail and their relationships within the Carabidae and among themselves are reassessed. On the basis of several autapotypic features, a new genus, ***Archaeocindis,*** is erected for the Persian Gulf species, *Cicindis johnbeckeri* Bänninger. The type locality for *Cicindis horni* Bruch is restricted to Guanaco Muerto, Cordoba Province, Argentina. For each taxon, a synthesis of available literature on both taxonomy and natural history is presented. The name of the tribe is determined to be Cicindini, not Cicindisini, according to the rules of zoological nomenclature. Based on a detailed analysis of characters of external structure and genitalia and consideration of past and present classifications of carabidae, cicindines are placed in a separate supertribe, the Cicinditae, near the Nebriitae and Elaphritae (*sensu* Kryzhanovskiy 1976). Present geographical distributions of the tribe and genera suggest that cicindines are a western Gondwanian lineage, the distribution of which was divided by development of the South Atlantic Basin in the Late Mesozoic. Resulting South American and African isolates gave rise to *Cicindis* and *Archaeocindis,* respectively. Members of the former taxon occupy interior saline lake shore habitats, those of the latter occur in tidal flats of bays in the Persian Gulf. Based on interpretation of a suite of unusual structural features, cicindines probably behave like diurnal tiger beetles that also can survive submersion in and swim on the surface of salt water.

Key Words: Cicindini, *Cicindis, Archaeocindis,* Gondwanian lineages, carabid classification

In 1979, one of us (TLE) wrote that species of the tribe Cicindini "surely represent the most obscure group of carabid beetles remaining today. Their bizarre features in combination with lack of available material make them nearly impossible to deal with effectively." Eleven years later, we reject the latter, rather defeatist notion, and take up the challenge to better understand this obscure group, even though only one more specimen is now available to aid in the study. Luckily, this specimen came with important new biological information that should enable us to gather additional specimens and data in the future. It is with this prospect in mind that we provide a synthesis of current knowledge and add new information on the structure, distribution, and phylogenetic relationships of these beetles, based on our study of available specimens.

Bruch (1908) recognized his new species as something peculiar and placed it near the tiger beetles. He did so without formally classifying them, probably because he was not a carabid specialist. Bänninger (1925, 1927a, b) studied the Argentine specimen described by Bruch and another specimen collected at Būshehr, Iran, which he described as new, concluding that the genus was related to the basal lineages of carabids, as understood in the early part of this century. He classified the lineage near the Ozaenini, with which he was very familiar (Bänninger 1927b), as an independent group within the Isochaeta. He mentioned in his 1925 paper that the lineage should be given tribal status, but did not provide a name; subsequently, he did so in his 1927a paper. For several decades, Bänninger's classification was either accepted or not dealt with (for example, see Csiki 1927, Crowson 1955, Blackwelder 1944, Kryzhanovskiy 1976). Reichardt (1977) elevated the group's status to the rank of subfamily, but left it in a position near the Paussinae (which contains the Ozaenini). Ball (1979) and Erwin (1979), without recourse to the specimens, also tacitly accepted this classification, but later Ball and McCleve (1990) removed the lineage from the paussines assemblage, leaving its status, in their opinion, as *incertae sedis.* However, after studying one of the specimens, Erwin (1985: 467) concluded that the group, at the rank of tribe, belonged to the Nebriitae lineage of the Carabinae, near the tribe Notiophilini.

Reichardt (1977) reported that specimens of *Cicindis horni* Bruch had been collected by A. Martinez near salt lakes in desertic areas. We were informed that the specimen collected in 1979 by R. A. Ronderos (pers. comm.) listed below was found at a light, at night, near the enormous salt lake bed of Salinas Grandes in the northern part of Cordoba Province, Argentina. Stork (1982) reported on a specimen of *Cicindis johnbeckeri* Bänninger received for identification. It had been collected as part of a study of "mud skippers" in the Persian Gulf, taken from a tidal flat, probably esturine, in a bay some 20 km north of Kuwait City. The type specimen of this species, collected almost directly across the Persian Gulf from Kuwait, at Būshehr, Iran, also may have been collected from a similar tidal flat, perhaps in the Bay of Soltani (Khowr-e Soltani).

Limits of the present study were determined by the paucity and condition of available specimens. One species is known only from females and both species are known to us from only two specimens each (additional specimens of *C. horni* are reportedly in the UNLP or MACN but have not been made available to us). One of the specimens studied is in poor condition with most appendages missing, a second specimen has been damaged by previous dissections, and a third is teneral. Thus, complete disarticulation of one or more specimens, to properly study all structural features, was necessarily ruled out. Nonetheless, we feel that our review of the form and structure of cicindines, through conservative dissection, the results of which are presented here, provides new information that better represents structural diversity within the group and relationships of its members to other lineages of Carabidae.

MATERIALS AND METHODS

General procedural methods are those which we have used before (Erwin and Kavanaugh 1981). Measures for body length, and pronotal and elytral dimensions are coded as follows and are presented in the species descriptions as ranges based on the smaller and larger of specimens studied. All specimens were measured with an ocular micrometer in a Wild microscope and measures are presented in millimeters. SBL, standardized body length = the sum of head length (midline distance from apical margin of clypeus to a point opposite posterior margin of eyes) + pronotal length (midline distance from anterior [apical] to posterior [basal] margin) + elytral length (midline distance from apex of scutellum to a point opposite apex of longer elytron) (see Kavanaugh 1979, Erwin and Kavanaugh, 1981). TW, total width across the widest portion of the elytra = width of left elytron, measured at widest point, and doubled to obtain value. We use the term *forebody* to indicate the head and pronotum together. Accept where noted, scale lines in all figures are equal to 1.0 mm length.

For conciseness, we have grouped the characters and their states in three categories, depending on their perceived utility in outgroup comparisons with equivalent rank taxa. For example, if the state of some character is of general importance at the tribal level we place it in the tribal diagnosis, whereas minor characteristics such as color are placed within the species descriptions, because these have value only among species level groups. We do not repeat descriptors at successive higher or lower taxon levels.

Specimens were borrowed from the following institutions for this study:

BMNH	Department of Entomology, British Museum (Natural History), Cromwell Road, London, England
DEIE	Institut für Pflanzenschutzforschung (BZA) der Akademie der Landwirtschaftswissenschaften der Deutschen Demokratischen Republik, DDR 13, Eberswalde - Finow 1
MACN	Museo Argentina de Ciencias Naturales, Av. Angel Gallerdo 470, Buenos Aires, Argentina
UNLP	Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque 1900, La Plata, Argentina

Tribe Cicindini Bänninger

Cicindisini Bänninger 1927a: 119.
Cicindisini Bänninger 1927b: 177.
Cicindini Csiki 1927: 425.
Cicindini Blackwelder 1944: 22.
Cicindini Crowson 1955: 6.
Cicindisini Kryzhanovskiy 1976: 56.
Cicindisinae Reichardt 1977: 375.
Cicindisini Reichardt 1977: 357, 1979: 319, 321.
Cicindisini Ball 1979: 91, 95, 100.
Cicindisini Erwin 1979: 589, 1985:467.

Tribal nomenclature.—Bänninger (1925) first proposed that the genus *Cicindis* be classified in its own tribe, but did not mention a name for such until later, where he used Cicindisini (Bänninger 1927a). In the same year, Csiki (1927), citing Bänninger's 1925 paper, listed *Cicindis* under the tribal name Cicindini. Both spellings have been used since, and repeatedly, in the literature. Because Bänninger's paper was published on November 10 and Csiki's on December 22, 1927, Bänninger's use of a tribal name, Cicindisini, has priority. However, Bänninger applied the tribal ending, *-ini,* to the complete generic name rather than its stem, whereas Csiki's name, Cicindini, is formed correctly. Based on Article 11f (ii) of the International Code of Zoological Nomenclature, the valid tribal name is Cicindini, and Bänninger is its author.

Tribal diagnosis.—*Adults:* Slightly hypognathous. Ventral surface of body (except for gular region of head) and coxae, trochanters, and femora covered with fine pubescence of slightly to moderately decumbent and curved setae. Head without or with one pair of supraorbital setiferous punctures; frons without longitudinal ridges; vertex slightly concave; gena with a sharp-edged longitudinal flange ventral to eye, postgenal groove present, distinctly biarcuate; compound eye very large, longitudinal diameter equal to or more than 1.5 times width of labrum, dorsomedial margin markedly concave; clypeus narrower than distance between antennal sockets; mandible (Figs. 6, 7) with terebral blade long and markedly down-curved, scrobe asetose and delimited dorsomedially by a prominent elevated ridge extended apically onto blade, terebral tooth triangular, retinaculum with both anterior and posterior retinacular teeth (the former larger and more acuminate on right mandible than left), small accessory tooth (homology unknown) on each mandible between terebral and posterior retinacular teeth, molar region undeveloped, setiferous ventral groove present, longer on left than on right mandible; maxilla, mentum, and submentum without setiferous spiniform processes or ridges; lacinia of maxilla (Fig. 8) with apical tooth articulated; ligula of labium (Fig. 10) with paraglossae short but distinct. Prothorax with front coxal cavities bridged (biperforate) (Fig. 14A) and separate internally (Fig. 14B), closed posteriorly by narrow medial extension of propleuron with prosternal projection overlapped posteriorly; front tibia (Fig. 19) with apex only slightly oblique (posterior angle slightly displaced proximally) and both spurs apical, anteroventral margin with row of short fine densely arranged setae along apical two-thirds, setae progressively longer apically, antenna cleaner simple, sulcate, with two long, curled setae proximal to posterior apical spur. Pterothorax with elytron (Fig. 15) with nine complete, shallowly impressed interneurs, scutellar interneur short, present only on basal one-seventh; interval 2 much narrower than intervals 3 and 4 together; discal setae absent or present only on interval 3, umbilicate series present on interval 9, with 12 to 14 setae positioned as in Fig. 15); internal plica simple, keel-like, faintly defined (especially near apex), not extended to epipleuron apically; metathoracic wing (Fig. 16) with Oblongum Cell narrowed posteriorly, stalked, M4 vein positioned slightly anterior to middle of Oblongum Cell, Third Radial Cell larger than Anterior Sector Cell; metepimeron (Fig. 17) present, triangular; middle coxal cavities disjunct, confluent (through very small hole); hind coxal cavities conjunct, confluent, delimited laterally by metepimera and second (first visible) abdominal sternum; hind tarsomeres (Fig. 25) 1 to 4 with ventroapical margin lobate anteriorly, lobes and associated setae longer on successive tarsomeres; tarsal claws (Fig. 23) asymmetric in length, the anterior claw longer. Female genitalia with eighth sternum (Fig. 28) and ninth/tenth tergum (Fig. 29) undivided; gonangulum (Fig. 30) with scattered setae dorsomedially; coxostylus (Fig. 31) short, stout, with three or four spines lateroventrally and two or three spines dorsomedially. *Larvae:* Unknown.

Tribal distribution.—The widely disjunct distribution (Fig. 33) includes two rather circumscribed areas along the bays of the northern Persian Gulf and among the lakes of the great salt flats of northwestern Argentina.

KEY TO SPECIES

1\. Anterior pair of supraorbital setigerous punctures present; elytral margin serrate, more so apically . . *Archaeocindis johnbeckeri* (Bänninger)

1′. Supraorbital setigerous punctures absent; elytral margin smooth . . . . *Cicindis horni* Bruch

Archaeocindis Kavanaugh and Erwin, NEW GENUS

Type species.—*Cicindis johnbeckeri* Bänninger 1927a: 119.

Derivation of genus name.—From the Greek, *archaeon,* meaning ancient, and a part of the genus name, *Cicindis,* referring to the occurrence of this genus in the Palaearctic Region, particularly near the mouth of the historically important Tigris and Euphrates Rivers.

Diagnosis.—Body deep, subcylindrical. Head (Fig. 3A) with one pair of supraorbital setiferous punctures near medial margin of eye (anterior one-sixth); area between posterior margin of eye and postgenal groove slightly depressed; antennomeres 1 to 3 and basal four-fifths of 4 glabrous (except for apical whorl of fixed setae), apical one-fifth of antennomere 4 with a few, small setae, antennomeres 5 to 11 densely and evenly pubescent (Fig. 4A); dorsal surface of mandible smooth, without macrosculpture; last (fourth) maxillary palpomere (Fig. 8) with a sensory pit ventromedially in apical one-half; ligula (Fig. 10A) deeply emarginate apically, paraglossae, short, much shorter than fused glossae; mentum (Fig. 11A) with anteromedial emargination deep, dentate, tooth broadly entire and with one pair of paramedial setiferous punctures at base, epilobes narrowly rounded, broadly toothed anteromedially and without setae; submentum broad anteriorly, only slightly narrower than mentum, with one pair of lateral setiferous punctures, gular portion with sides subparallel. Pterothoracic elytron-locking mechanism (Fig. 18A) with deeply emarginate internal and short external metapleural flanges, external flange with posterior bulge inserted in elytral epipleural cavity (when elytra are closed), elytral epipleuron markedly notched. Femora longitudinally concave, front femoral and hind femoral concavities shallow anteriorly and deep posteriorly, middle femoral concavities deep both anteriorly and posteriorly. Middle and hind tibiae (Figs. 20A, 21A) without accessory setae; hind tibia straight; tibial spurs of anterior tibia longer than tarsomere 1, posterior spur of middle tibia and anterior spur of hind tibia subequal to length of respective first tarsomeres. Tarsi (Figs. 22A, 24A, 25A) without fringes of accessory setae; posterior claw (Fig. 23A) of all tarsi at least two-thirds the length of anterior claw. First visible (second) abdominal sternum without lateral concavity.

Geographic distribution.—Known only from both sides of the north end of the Persian Gulf.

Archaeocindis johnbeckeri (Bänninger), New Combination

Cicindis johnbeckeri Bänninger 1927: 119. Holotype female, in DEIE, labelled: "Holotypus" [red label]/ "Bushere Becker 22.IV.27"/ "Type [written vertical] Cicindis John-Beckeri m." ["8.1927" on underside]. Type locality: IRAN, Būshehr [28°59′N 50°50′E].

Diagnosis.—Clypeus narrower than distance between antennal sockets, anterior supraorbital setiferous punctures present, and pronotal and elytral margins finely serrate.

Description of form and structure of adults.—Size medium, standard body length of females 9.6 and 10.2 mm. Form (Fig. 1) with elytra proportionately short in relation to forebody (ratio: elytral length/forebody length = 1.63 [mean]).

Color: Head, body, and appendages pale yellowish tan, except eyes piceous and apices and medial margins of mandibles infuscated; elytra with very pale marginal pattern (Fig. 15A).

Luster: Entire body surface moderately shiny, except elytra slightly duller.

Microsculpture: Entire body with isodiametric meshes, well impressed on labrum, legs, and elytra, more faintly impressed on forebody and venter.

Head: Smooth dorsally; frons slightly convex, frontal furrows absent; antenna (Fig. 4A) with scape long, length about equal to width of labrum, markedly narrowed basally, and form slightly sinuate; clypeus (Fig. 5A) with anterior margin straight; penultimate labial palpomere (Fig. 10A) with three setae anteriorly.

Prothorax: Pronotum (Fig. 12A) broad, greatest width wider than width of head across eyes, slightly cordate, slightly narrowed basally, smooth medially, without obliquely transverse and shallow rugulae laterally; disc markedly convex; apical margin markedly bisinuate; lateral margin crenulate or faintly serrate and arcuate, with basal sinuation shallow and long; lateral explanation narrowed medially, broadened apically and basally; basal margin markedly bisinuate; apical angles long, narrow, markedly projected anteriorly; basal angles obtuse and sinuate, slightly projected posteriorly; apical margination deeply impressed laterally, absent from middle one-sixth; lateral bead narrow, poorly defined anteriorly, effaced near apical angle, elevated and well defined at basolateral setiferous puncture, absent from sinuation of basal angle; basal margination effaced medially and laterally, faintly defined paralaterally; anterior transverse impression broadly and shallowly defined; median longitudinal impression nar-

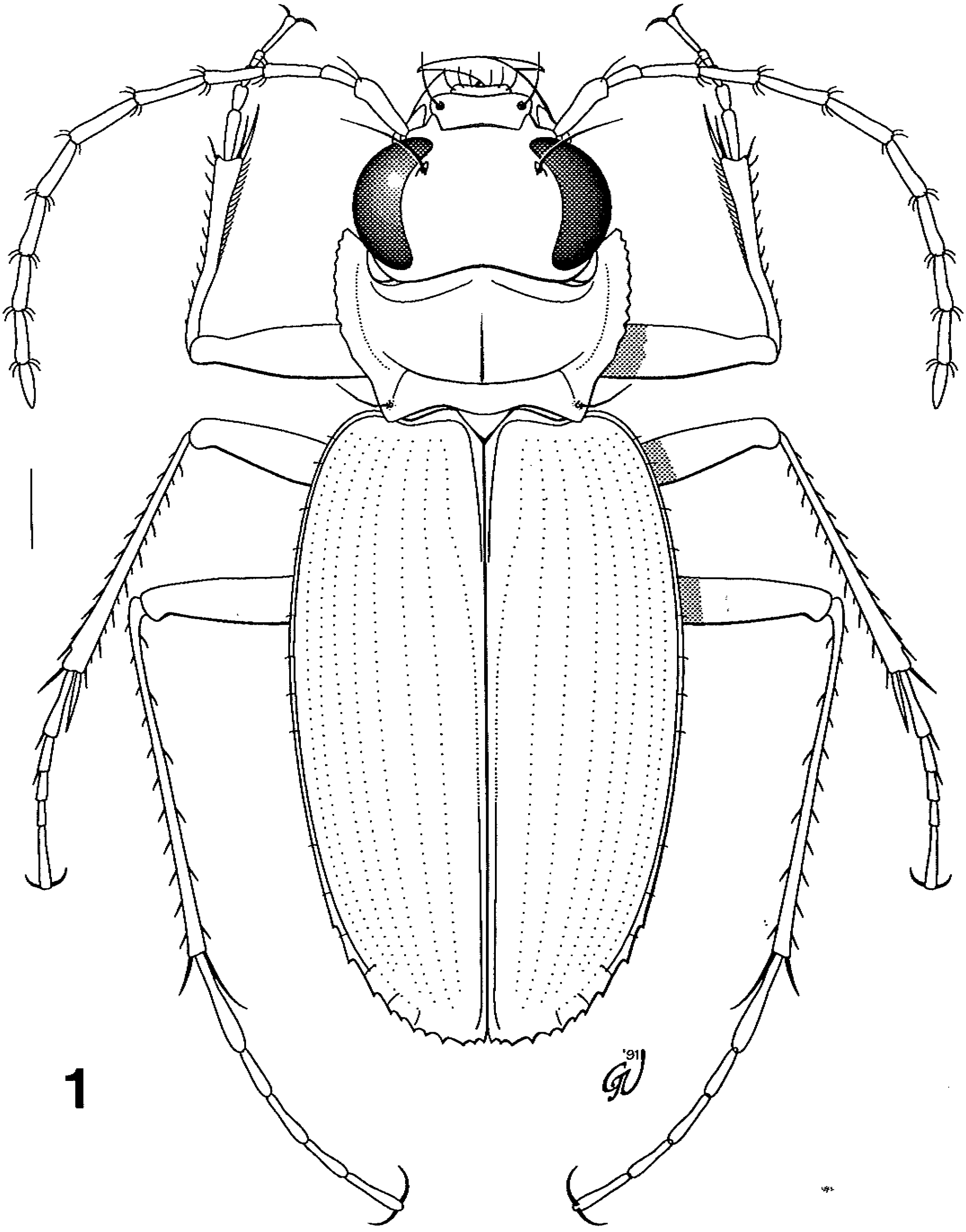

Fig. 1. Habitus, dorsal aspect, *Archaeocindis johnbeckeri* (Bänninger).

rowly and finely defined; posterior transverse impression smooth to slightly rugulose, narrowly and deeply defined, extended laterally to basal foveae, distinctly arcuate; basal foveae deep anteriorly, posteriorly moderately deep, slightly divergent, and confluent with lateral explanation; mid-lateral setiferous puncture absent, basolateral setiferous puncture inserted on posterior end of elevated lateral margination distinctly anterior to basal angle. Prosternal intercoxal process (Fig. 13) broadly spatulate in ventral aspect.

Pterothorax: Elytra (Fig. 15A) with silhouette subfusiform, widest anterior to middle, lateral margins faintly and apical margins distinctly serrate; elytron convex, with basal margination complete, deeply impressed and markedly sinuate, lateral margination complete and very narrow, slightly broadened near middle, effaced from apex, humerus rounded, lateral and basal margination joined at markedly obtuse angle, with humeral angle produced anteriorly, interneurs 1 to 7 finely striate, 8 and 9 very faintly punctulate, intervals smooth, impunctate, slightly convex or flat; metathoracic wing (Fig. 16A) full-sized, with stalk of Oblongum Cell short.

Legs: All legs long and slender; front tarsomeres 1 to 4 slender and without pads of adhesive setae ventrally in female (male unknown).

Abdomen: Last visible (seventh) sternum moderately emarginate apicomedially and with two pairs of long paramedial marginal setae in female (male unknown).

Male genitalia: Male unknown.

Female genitalia: Coxostylus (Fig. 31A) slightly rounded apically, with four ventrolateral and two dorsomedial spines. Form and structure of bursa copulatrix and spermathecal apparatus unknown (one specimen damaged, the other too teneral for dissection).

Dispersal potential.—The wings are fully developed, and as with the following species, we believe that adults have strong powers of flight.

Natural history.—Stork (1982) presented all the available information on the habitat distribution of this species, and we use these data in the discussion below. A specimen collected in April, 1982, was teneral, which suggests that adult emergence occurs at that time. Nothing else is known about the life history or behavior of members of this species.

Locality records.—(Fig. 34). Known only from the type locality (in IRAN) and KUWAIT, Al Jahrah (29°20′E 47°40′N) (BMNH; 1 female).

Cicindis Bruch

Cicindis Bruch 1908: 497.

Type species.—*Cicindis horni* Bruch 1908: 499.

Diagnosis.—Body moderately depressed. Head (Fig. 3B) without supraorbital setiferous punctures; area between posterior margin of eye and postgenal groove markedly depressed; antennomeres 1 to 4 glabrous (except for apical whorl of fixed setae), 5 to 11 densely and evenly pubescent (Fig. 4B); dorsal surface of mandible (Figs. 6, 7) with obliquely transverse grooves and ridges; last (fourth) maxillary palpomere (Fig. 9) without sensory pit ventromedially in apical one-half; ligula of labium (Fig. 10B) with apical margin deeply emarginate, paraglossae short but equal in length to fused glossae; mentum (Fig. 11B) with anteromedial emargination shallow, dentate, tooth bifid, with two pairs of paramedial setiferous punctures at base, epilobes broadly rounded, narrowly toothed anterormedially and with six or seven pairs of marginal and several pairs of basal setiferous punctures; submentum narrow anteriorly, much narrower than mentum, with three or four pairs of anterolateral setiferous punctures, gular portion with sides divergent posteriorly. Pterothoracic elytron-locking mechanism (Fig. 18B) with long internal and external metapleural flanges, external flange without posterior bulge (elytron with poorly defined receptive cavity), epipleuron entire. Femora with both anterior and posterior surfaces convex. Middle tibia (Fig. 20B) with posterodorsal fringe of long, fine accessory setae; hind tibia (Fig. 21B) markedly arcuate; tibial spurs of anterior tibia shorter than tarsomere 1, posterior spur of middle tibia and anterior spur of hind tibia less than or equal to one-half length of respective first tarsomeres. Front tarsomere 1 (Fig. 22B) with posterodorsal fringe of accessory setae, middle tarsomeres 1 to 5 (Fig. 24B) with anteroventral and posterodorsal fringes of accessory setae, hind tarsomere 1 (Fig. 25B) with anteroventral and posterodorsal fringes of accessory setae, tarsomeres 2 to 5 with anteroventral fringe only; posterior claw (Fig. 23B) of all tarsi equal to or less than one-half the length of anterior claw. First visible (second) abdominal sternum (Fig. 17) with deep lateral concavity.

Geographic distribution.—Known only from the great salt lake region of northwestern Cordoba Province, Argentina.

Cicindis horni Bruch

Cicindis horni Bruch 1908: 499. Holotype female, in MACN, labelled: "Rep Argentina Prov. Cordoba [illegible number] C. Bruch"/ "Col. C. BRUCH" [white label with black border]/ "Cicindis Horni Bruch C. BRUCH DETERM." [white label with black border] "Typus" [light green label]/ "HOLOTYPUS" [red label with black border]. Type locality: ARGENTINA, Cordoba Province, Guanaco Muerto [30°29′S 65°03′W], herewith restricted.

Diagnosis.—Clypeus narrower than distance between antennal sockets, supraorbital setiferous punctures absent, and pronotal and elytral margins smooth.

Description of form and structure of adults.—Size medium, standard body length of male 10.2 mm, female 10.5 mm. Form (Fig. 2) with elytra proportionately long in relation to forebody (ratio: standardized elytral length/forebody length = 1.95 [mean]).

Color: Head, body, and appendages pale yellowish tan, except eyes piceous and apices and medial margins of mandibles infuscated; elytra with very pale marginal pattern (Fig. 15B).

Luster: Entire body surface moderately shiny, slightly duller on elytra of female.

Microsculpture: Entire body with small, isodiametric meshes, well impressed on labrum, legs, and venter of both sexes and elytra of female, effaced or nearly so from forebody of both sexes, less impressed on elytra of male especially on crowns of intervals.

Head: Smooth dorsally; frons slightly convex, frontal furrows broadly impressed, parallel, and limited to area medial to anterior half of eye; antenna (Fig. 4B) with scape short, length about 0.7 times width of labrum, cylindrical, and form straight; clypeus (Fig. 5B) with anterior margin slightly emarginate; penultimate labial palpomere (Fig. 10B) with four setae anteriorly.

Prothorax: Pronotum (Fig. 12B) narrow, greatest width less than or equal to width of head across eyes, markedly cordate, narrowed basally, smooth medially, with obliquely transverse and shallow rugulae laterally; disc markedly convex; apical margin markedly bisinuate; lateral margin smoothly arcuate, with basal sinuation moderately deep and abrupt; lateral explanation narrow, slightly broadened apically and basally; basal margin slightly bisinuate; apical angles long, narrow, markedly projected anteriorly; basal angles subrectangular, not at all projected posteriorly; apical margination deeply impressed laterally, absent from middle one-third; lateral bead narrow, poorly defined, effaced near apical and basal angles; basal margination absent; anterior transverse impression broadly and deeply defined; median longitudinal impression narrowly and finely defined; posterior transverse impression smooth to slightly rugulose, narrowly and deeply defined, extended laterally to basal foveae, straight; basal foveae deep anteriorly, posteriorly very shallow, slightly divergent, and confluent with lateral explanation; midlateral setiferous puncture absent, basolateral setiferous puncture inserted slightly anterior to basal angle. Prosternal intercoxal process (Fig. 14A) narrowly sublanceolate in ventral aspect.

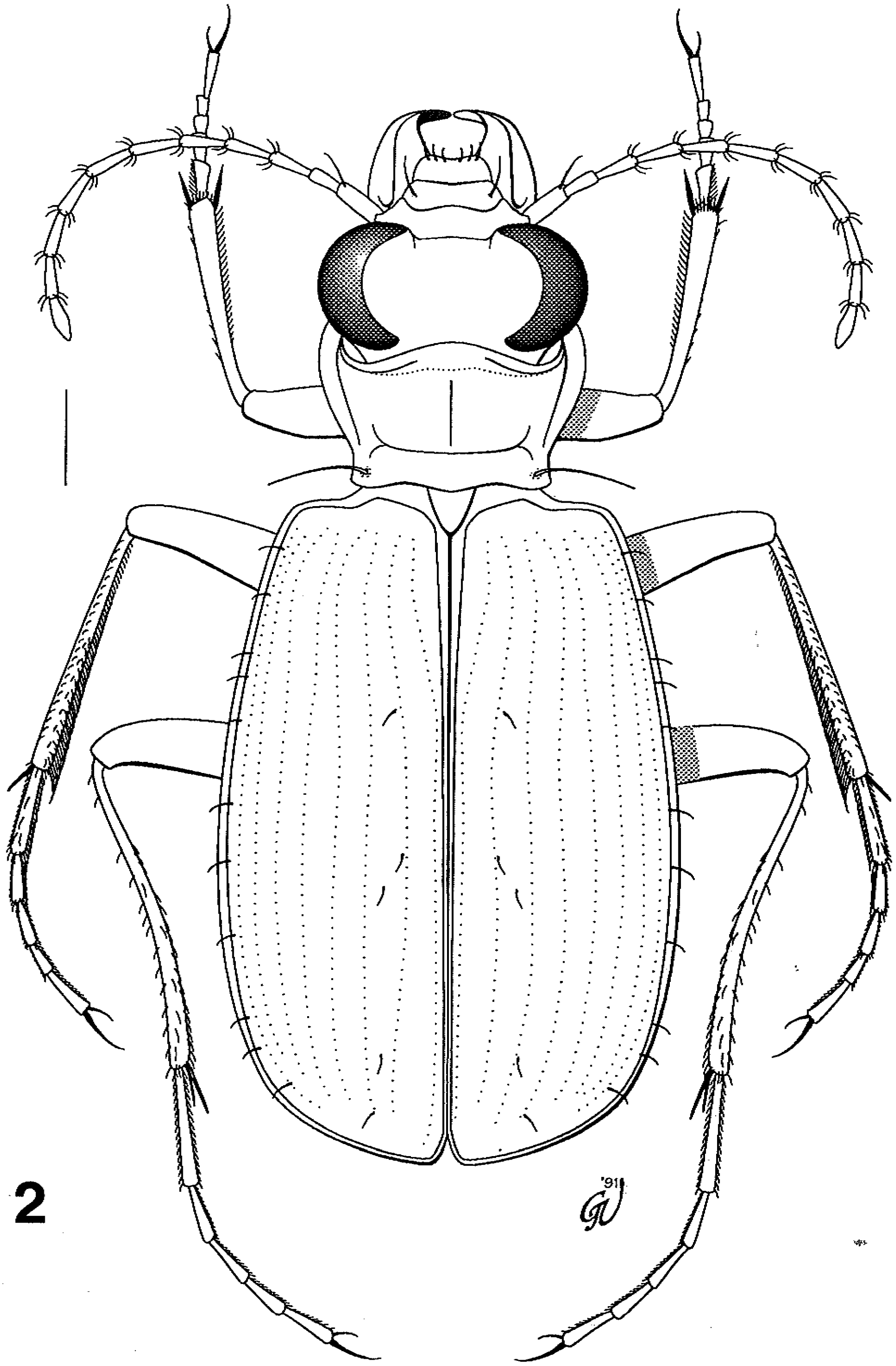

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Fig. 2. Habitus, dorsal aspect, *Cicindis horni* Bruch.

Pterothorax: Elytra (Fig. 15B) with silhouette subrectangulate, widest posterior to middle, lateral and apical margins smooth; elytron slightly depressed, with basal margination complete, deeply impressed and slightly sinuate, lateral margination complete and very narrow throughout, humerus squared, lateral and basal margination joined at slightly obtuse angle, interneurs 1 to 7 finely striatiopunctulate, less distinctly so apically, 8 and 9 finely punctulate, intervals smooth, impunctate, 1 and 3 to 8 moderately convex to apex, 2 and 9 slightly convex or flat; metathoracic wing (Fig. 16B) full-sized and functional, with stalk of Oblongum Cell long.

Legs: All legs long and slender; front tarsomeres 1 to 4 slightly expanded laterally and with pads of adhesive setae ventrally in male (front tarsi of female specimen missing).

Abdomen: Last visible (seventh) sternum slightly emarginate apicomedially in female but entire in male, with two pairs of long paramedial marginal setae in female, and apparently one pair in male (only male available for study has one such seta on one side).

Male genitalia: Ring sclerite (Fig. 26) ovoid, slightly asymmetrical, slightly narrowed anteroventrally; median lobe (Fig. 27) short, with broad apical orifice. Parameres slightly asymmetrical, with left paramere slightly longer and narrower than the right, both bisetose apically.

Female genitalia: Coxostylus (Fig. 31B) pointed apically, slightly serrate apicolaterally, with three ventrolateral and three dorsomedial spines. Bursa copulatrix (Fig. 32) with anterodorsal lobe broad, apex deflected right of midline anteriorly, short and wide posteroventral lobe present; spermatheca subequal in diameter to spermathecal duct, slightly twisted; spermathecal duct slender, inserted anteriorly on anteroventral lobe of bursa copulatrix.

Sexual dimorphism: In addition to leg and abdominal characters described above, female slightly larger overall than male.

Dispersal potential.—The wings are fully developed and one specimen was recorded as having flown into a light (R. A. Ronderos, pers. comm.). Although fringe setae on the legs suggest that these beetles are swimmers, we believe they have strong powers of flight as well.

Natural history.—These beetles are recorded only from salt lakes and we suspect that they are confined to such areas. Their swimming hairs, elevated eyes, and mouthparts lead us to suggest that they are superspecialist, amphibious predators at the edges of shallow alkaline lakes, the carabid equivalent of a crocodile. The adult specimen, taken at light in December, 1979, is unusually soft for a mature adult carabid, which suggests that it may have been slightly teneral when collected. With the possible exception of this indication of adult emergence period, nothing is known about the life history or behavior of members of this species.

Locality record.—(Fig. 35). ARGENTINA, Cordoba Province (MACN; 1 female) Guanaco Muerto (UNLP; 1 male).

DISCUSSION

A review of the descriptions provided above for the tribe, genera, and species of cicindines reveals an array of features of form and structure that, even for the trained specialist on carabid beetles, represent a unique and surprising combination of traits. What justification is there for assigning the two known species to distinct genera and these genera to a distinct tribe? What evidence is available in support of the monophyly of the tribe Cicindini as here defined and how is this taxon related to other tribes and more inclusive groups of carabids? What, if anything, can we infer about the biogeographic history of the group from present knowledge of the geographical and habitat distributions of extant cicindine taxa? To what extent can we relate apparent specializations in form and structure to habitat or behavior? What future research efforts are required to generate the kinds of additional data needed to better answer all of these and other questions? In the following discussion, we address each of these topics.

PHYLOGENETIC RELATIONSHIPS AND CLASSIFICATION

In his review of the present system of classification of carabid beetles and its historical development, Ball (1979) suggested that "higher-ranking taxa are in part clade-based, and in part grade-based." He identified five evolutionary trends in carabid evolution, with reference to which the basic framework of that classification has been constructed. Trends included were (1) development of a more complex antenna-cleaning organ on the front tibia; (2) modifications of the pterothorax; (3) loss of a setiferous puncture from the scrobe of the mandible; (4) reduction of the apex and other modifications to the parameres in males; and (5) reduction of elytral apices and enhancement of the ability to take flight. Together, the presumed starting points (i.e. plesiotypic states) of each of these trends (characters or suits of characters) define the basic ground plan of the hypothetical ancestral carabid. Attempts to establish phylogenetic relationships among suprageneric carabid taxa using the characters involved in these trends (Sloane 1923, Jeannel 1941, Crowson 1955, Bell 1965, 1967, Kryzhanovskiy 1976) have all failed, at least partially, due to homoplasy (convergence) in these traits, as shown by the discordant distributions of character states among the taxa considered. As demonstrated below, cladograms generated with reference to different characters suggest very different patterns of relationships. The present classification is therefore a compromise arrangement, the analog of a consensus tree, the different nodes of which are a mixture of grades and clades, just as Ball (1979) suggested.

Kavanaugh and Nègre (1982) tried to determine phylogenetic relationships of the tribe Notiokasiini with other member tribes of supertribe Nebriitae but noted that the "main difficulty with [phylogenetic] studies of nebriite genera is in establishing a suitable outgroup for character analysis," against which character transformations can be polarized. Failure to agree on a suitable outgroup for the Carabidae results in the same problem at a higher level. For example, Kavanaugh (1986) followed Ponomarenko (1977) in suggesting that trachypachines (as presumed living representatives of the Jurassic-Cretaceous eodromine radiation) are the sister group of the remaining Carabidae and, with them, form a monophyletic group. Acceptance of this view results in a cladogram for the Carabidae that approximates, in broad outline but not in detail, a tree reflecting the present classification (Kavanaugh, study in progress). However, Bell (1966, 1982), Hammond (1979), and Roughley (1981) interpreted available data as supporting a sister group relationship between trachypachines and at least some Hydradephaga (the dytiscoid families in particular). Further, Bell (1966) suggested a sister group relationship between trachypachines + some hydradephagans and Metriini + Ozaenini + Paussini. If this interpretation is correct, then Carabidae, including metriines, ozaenines, and paussines, but excluding either trachypachines + some hydradephagans or these hydradephagans alone, is a paraphyletic group. A suitable outgroup for this entire assemblage must be sought at or outside the basal radiation of suborder Adephaga. Acceptance of this view requires a radical reclassification of Adephaga in general and of Carabidae in particular.

Preliminary cladistic analyses with characters and/or character systems traditionally used in carabid classification above the genus level have failed to provide an unambiguous resolution of phylogenetic relationships among even the better known higher taxa of carabids (Ball 1979, Kavanaugh 1986 and study in progress). Such a basic framework of caraboid relationships, which is prerequisite to understanding the relationships of cicindines and their proper place in a classification, must await more uniform, detailed, and broad-based study of form and structure across the Adephaga, particularly with internal organ systems of adults and internal and external structures of immatures. Molecular studies may also aid in this effort.

For the present, we limit ourselves to placement of cicindines within the present hybrid cladistic/gradistic carabid classification, based on our study of their form and structure and our reinterpretation of traditionally used characters and their transformations. To do this, we examine the characters individually and then place the tribe, on the basis of synapotypic features shared with other tribes, in the existing classification. For these purposes, we accept trachypachines as the sister group of all other carabids (Kavanaugh 1978, 1986) and character transformations are polarized accordingly.

Coxal cavities and thoracic structure.—Bell (1965, 1967) provided the most thorough analysis of the arrangement of thoracic sclerites that form the cavities surrounding the three pairs of coxae in Adephaga, although several other workers (Sloane 1923, Jeannel 1941, Ball 1960, 1979, Lindroth 1969, Hlavac 1972, 1975, Ponomarenko 1977) have also discussed these features and their use in classification. In our discussions here, Bell's (1967) analysis and nomenclature are used, except as noted, and each thoracic segment is considered separately.

Prothorax: In cicindines, the front coxal cavities are enclosed behind by a medial extension of the propleuron (not proepimeron; see Hlavac 1975) that makes contact, with a slight posterior overlap, with the prosternal intercoxal process (Fig. 14); right and left coxal cavities are completely separated medially by a sclerotized internal septum (Fig. 14B); and the dorsum of each cavity is spanned by a narrow sclerotized bridge that divides the dorsal unsclerotized opening into two parts (Fig. 14A), the so-called biperforate (Sloane 1923) or bridged (Bell 1967) condition. The states of each of these three characters found in cicindines, namely closed, separate, and biperforate coxal cavities, traditionally have been considered the apotypic state (Sloane 1923, Bell 1967) in relation to their respective alternate state (i.e. open, confluent, and unbridged). However, Hlavac (1975) reported the bridged condition in several groups (e.g. in *Leistus, Carabus, Hiletus* and cicindelines) whose members were thought to have uniperforate coxae only (Bell 1967, Erwin and Stork 1985). The distribution of bridged front coxal cavities as reported by Hlavac (1975) suggests that this condition represents the plesiotypic state of this character among Adephaga. Also, detailed examination of the area of contact between propleuron and prosternum that forms the posterior closure of the cavity suggests that the method of closure differs in different groups (Bell 1967, Hlavac 1975) and hence, that closure may have evolved several times independently.

Cicindines share the apotypic pair of features, closed and separate coxal cavities, with a majority of the tribes of Carabidae, but not with hydradephagans, trachypachines, or a few other carabid-tribes—namely those thought to represent the basal grade of carabid evolution. Among the groups he examined, Bell (1967) found five of the eight possible combinations of states for the three two-state characters, and Hlavac (1975) reported on a sixth combination (e.g. open, separate, bridged) in *Hiletus*. Clearly, homoplasy is involved in the present distribution of these character states.

Mesothorax: The lateral wall of the middle coxal cavities in cicindines includes the medial margin of the mesepimeron (Fig. 17), the so-called *disjunct* condition (Sloane 1923, Jeannel 1941). Medially, mesosternal and metasternal processes meet but do not completely separate the right and left coxal cavities, which therefore remain at least partly confluent internally (Fig. 17).

Sloane (1923) grouped those tribes whose members had disjunct middle coxal cavities under the name Carabidae Disjunctae and called the remaining carabids, in which the mesepimeron is separated from the coxal cavity by a posterolateral extension of the mesosternum, the Carabidae Conjunctae. However, the disjunct and confluent middle coxae probably represent the plesiotypic states of each of these characters (Bell 1967, Kavanaugh 1986), so the monophyly of the Carabidae Disjunctae is unsupported. Bell (1967) suggested that conjunct middle coxal cavities evolved independently in Notiophilini and that Gehringiini may have evolved the disjunct condition secondarily. Aside from those possible exceptions, the distribution of states of this character among carabid tribes suggests that little or no homoplasy is involved, and the Carabidae Conjunctae may well be a monophyletic group. If so, then most of the tribes with which the Cicindini share closed and separate front coxal cavities form a monophyletic group that does not include them, and independent closure of front coxal cavities in the cicindines is again suggested.

Metathorax: In cicindines, a distinct metepimeron forms the lateral wall of the hind coxal cavities (Fig. 17). Bell (1967) called this condition *disjunct,* and recognized three other states of this character: *conjunct,* in which the metepimeron is apparently absent; *lobate,* in which the posterior edge of the metepimeron is free and partially overlaps the first visible sternum; and *incomplete,* in which the coxa extends to the margin of the body and the metepimeron is apparently absent. The hind coxal cavities are confluent medially in cicindines, as in all other Adephaga except gehringiines and rhysodines.

Bell (1967) suggested that the disjunct condition is the ancestral (plesiotypic) state and that the other states are apotypic, not necessarily in any graded sequence. He proposed that the incomplete condition, found only in trachypachines, gehringiines, rhysodines, and hydradephagans among extant Adephaga, is a synapomorphy for the trachypachines and at least some hydradephagans (Gehringiini and Rhysodini were excluded on other grounds; Bell 1964, 1967). However, this arrangement of hind coxae is found also in fossil protocoleopterans, fossil and extant archostematans, and fossil eodromines, as well as all extant hydradephagans and trachypachines (Ponomarenko 1977). Kavanaugh (1986) suggested that this trait was plesiotypic for Adephaga, with other states evolved from it. Bell's hypothesis for the transformation of this character rests on the assumption that the ancestral metathoracic arrangement of pleural sclerites was similar to, if not serially homologous with, the mesothoracic arrangement found in extant forms with disjunct middle coxal cavities (see Bell 1967: Fig. 1). If, however, the incomplete condition is plesiotypic, then the ancestral adephagan may have lacked a distinct metepimeron, and the sclerite found in extant cicindines and many other carabids (and called the *metepimeron*) may not be serially homologous with the mesepimeron.

Metepimera of the type that define the disjunct condition of hind coxal cavities are found in varied form among cicindines, cicindelines, elaphrines, loricerines, and scaritines, but they are best developed in the first and last of these groups. If this character state is apotypic, as we suggest, then it may be either synapotypic for these tribes or independently evolved in some or all of them. Because few other synapotypic features appear to support close relationships between cicindines and any of these particular tribes, we suspect that homoplasy is involved in the character state distribution of this character.

Front tibial spurs and antenna cleaner.—Jeannel (1941) divided Carabidae into two groups, based on the location of the front tibial spurs, form of the tibial apex, and form and location of the antenna cleaner. Those beetles with both spurs positioned apically and the tibial apex truncate or nearly so, but with the antenna cleaner (setal band; Hlavac 1971) extended and developed proximal to both spurs were included in his Isochaeta. Among these were trachypachines, gehringiines, metriines, ozaenines, and paussines. Ball (1979) added nototylines and cicindines (but see below) to this group. The remaining carabids form a second group, which Jeannel did not name, but which has come to be called the Anisochaeta (see Ball 1979). As Hlavac (1971) noted, Anisochaeta includes a few groups like the cicindelines and opisthiines in which both tibial spurs are apical, the tibial apex is only slightly oblique, and the antenna cleaner is of the sulcate type (simply a transverse setal band across the concave tibial apex between the spurs). However, it also includes groups in which the posterior tibial spur is displaced proximally with the posterior end of the setal band to form an antenna cleaner more or less removed from the tibial apex.

Jeannel (1941) was the first to recognize that, among carabids, a proximal shift of the antenna cleaner occurred both with and without proximal displacement of the posterior tibial spur. However, it was Hlavac (1971) who suggested that the arrangement of tibial spurs, tibial apex, and setal band found in cicindelines, opisthiines (i.e. the sulcate type of antenna cleaner) could serve as a starting point from which development of a proximally displaced antennal cleaner could evolve along two different lines: one involving proximal displacement of the posterior tibial spur (the anisochaetous mode) and one independent of spur displacement (the isochaetous mode). The anisochaetous antenna cleaner has probably evolved several times independently among Carabidae, perhaps the most striking single example of which is its occurrence in Pamborini, a group that is certainly closely related to cychrines and carabines (Moore 1966), all of which have sulcate antenna cleaners. Cicindines have the antenna cleaner sulcate (Fig. 19B), the plesiotypic state for this character.

Mandibular setae.—Cicindines lack a setiferous puncture in the scrobe of the mandible. Presence of this seta is considered plesiotypic, its loss apotypic. However, loss of the seta has probably evolved in several lineages independently. Carabid with specialized mandibles (*Loricera,* hiletines, and *Promecognathus,* for example) lack a scrobal seta. Cicindine mandibles have a well-developed scrobe but modified terebral blade, which may account for absence of the seta. Although Jeannel (1941) and others have relied heavily on this character in their classifications (Ball 1979), it contributes little to an understanding of cicindine relationships.

Labral setae.—Bell (1964) identified the number of setiferous punctures on the anterior margin of the labrum dorsally as an important character for corroborating Jeannel's Isochaeta. He suggested that six was the plesiotypic number of setae in carabids and that a higher number characterized the Isochaeta. Trachypachines, metriines, paussines, and many ozaenines have approximately 12 such setae. Mainly on this basis, Bell was able to exclude gehringiines, which have only six labral setae, from the Isochaeta (with which they share incomplete hind coxal cavities).

Labrum with six setae, the number found in cicindines, is certainly the most widespread condition among carabids, and it also may be the plesiotypic state for this character at the family level, as Bell suggested. However, some cicindelines and carabines also have a higher number of labral setae, up to 10 or 12. Phylogenetic relationships among genera and species groups within these tribes are still unclear, so the plesiotypic number of labral setae for each of them cannot be determined at present. Among ozaenines, Ball and McCleve (1990) found a range of from 0 to 17 setae and suggested that the highest numbers were plesiotypic, the lower numbers apotypic. These data and the fact that trachypachines, our choice as the sister group for all other carabids, have a high number of seta, suggest that this may be the plesiotypic state for Carabidae. Six or fewer (as in loricerines, for example) labral setae may be apotypic within carabids, but certainly not synapotypic for all taxa with this trait (e.g. the independent reduction in number of setae within ozaenines already cited).

Other assorted setae.—Presence or absence of several other fixed setiferous punctures has been used widely in carabid classification (see Ball 1979 for summary). The supraorbital setae, pronotal (midlateral and basolateral) setae, and the discal and umbilicate series of elytral setae have been most often considered. In cicindines, the posterior supraorbital and midlateral pronotal setae are absent. The anterior supraorbital setae are also absent from *Cicindis horni* specimens examined. A few very short and fine discal setae occur on elytral interval 3 in *C. horni,* but the elytral disc is asetose in *Archaeocindis johnbeckeri.* Both species have a well-developed umbilicate series of 12 to 14 very short, fine setae on interval 9.

With each of the setal characters just mentioned, absence (or a reduction in number of setae in a series) is probably apotypic in relation to the number and arrangement in the hypothetical ancestral carabid. The usefulness of these characters as indicators of phylogenetic relationship, however, is varied and probably less important than their use as aides for identification, at least for the present. The pattern of presence and absence of these setae in cicindines suggests no particular phylogenetic affinity with one or more other tribes of carabids.

Metathoracic wing.—Ward (1979) examined metathoracic wing venation patterns in Adephaga and found several characters that he suggested are useful indicators of phylogenetic relationship. Among these are (1) shape of the Oblongum Cell (OC) and relationship of 4m-cu and 5m-cu crossveins to the M4 and Cubitus veins; (2) point of insertion of M4 on the distal side of the OC; (3) relative sizes of the Third Radial (3RC) and Anterior Sector (SAC) cells. He proposed that the plesiotypic states of these characters are as follows: (1) OC transversely rectangular, with 4m-cu and 5m-cu crossveins clearly separated posteriorly; (2) M4 inserted in the anterior one-third of the distal wall of the OC; and (3) 3RC subequal in size to SAC.

In cicindines (Fig. 16), the OC is narrowed posteriorly, with the 4m-cu and 5m-cu crossveins fused anterior to the Cubitus to form a stalk for the OC; M4 is inserted at or slightly anterior to the middle of the distal wall of the OC; and 3RC appears to be larger than SAC. This combination of traits is not represented among examples that Ward provided; and whether or not it is shared with any of the many other carabid groups that he did not discussed we cannot judge.

The degree of usefulness of venational characters in phylogenetic reconstruction that Ward suggested remains untested in our view. For example, among the nebriines alone, shape of the OC varies from nearly rectangular to distinctly triangular, with the 4m-cu and 5m-cu crossveins separate at the Cubitus in some species, or fused for greater or lesser distances anterior to the Cubitus, resulting in shorter or longer stalks for the OC in other species (Kavanaugh 1978). In most, but not all, nebriines, M4 is inserted on the distal wall of the OC distinctly posterior to its midpoint (Kavanaugh 1979, Figs. 33–35), whereas insertion closer to the midpoint is at least suggested by Ward's cladogram (Ward 1979, Fig. 22). Clearly, additional detailed and comparative study of venation patterns is needed before the value of these characters can be determined.

Parameres of male genitalia.—Jeannel (1941) made a detailed study of the parameres of male carabids and relied heavily on differences found among them in constructing his classification. Important features included the degree of symmetry of right and left parameres in shape and size and the presence and distribution of setae on them. Symmetrical and setose parameres have been considered plesiotypic by most workers following Jeannel.

In the *Cicindis horni* male examined, the parameres are moderately long and slender, only slightly asymmetrical (Fig. 27), with the left slightly longer and narrower than the right, and both apparently with two setae apically. This arrangement is very similar to that seen among bembidiines, trechines, pogonines, and patrobines among Jeannel's (1941) Stylifera, a group with which cicindines share few other apotypic features.

Coxostyli of female genitalia.—Bell (1982) and others have suggested that the apparent absence of a gonostylus (or stylomere two) from the ovipositors of female hydradephagans, trachypachines, metriines, ozaenines, and paussines (i.e. the Isochaeta of Bell 1967) may be a synapotypic feature for this group. However, Kavanaugh (1986) noted that opisthiines, nebriines, notiokasiines, and, in fact, many basal-grade carabid groups also have females with a gonostylus either absent or fused with the gonocoxite (or stylomere one) to form an unjointed ovipositor. He suggested that this condition was apotypic for the suborder Adephaga, not just for the Isochaeta (*sensu* Bell), and that structures called gonostyli (second stylomeres) in female cicindelines, carabines, cychrines, and most intermediate- and advanced-grade carabids may not, in fact, be homologous with the gonostyli of female Archostemata and Polyphaga. In cicindines, the ovipositor blades, which we refer to as the coxostyli, are unjointed, the condition that we view as plesiotypic within Carabidae.

Placement of Cicindini in relation to past and present classifications.—We provided a brief history of the placement of Cicindini in carabid classification in our introduction. But where would cicindines have been placed in some of the more important classification schemes in which they were not considered, and where should they be placed now?

In the classification proposed by Sloane (1923), Cicindini would be grouped with the Carabidae Disjunctae-Clausae, but they cannot be identified using Sloane's key. The only tribes listed whose members have disjunct middle coxal cavities, closed front coxal cavities, and terminal front tibial spurs are the ozaenines and metriines; but ozaenines have the lateral elytral margin "with a process [= the flange of Coanda; Ball and McCleve 1990] on each side," and metriines have a mandibular scrobal seta. In addition, the antennal cleaner is of the isochaetous type in members of both of these groups.

Cicindines cannot be placed within any of the supratribal groups proposed by Jeannel (1941). The sulcate antenna cleaner excludes them from Isochaeta, the large, distinct metepimeron from the Simplicia, shape and vestiture of the parameres of males from the Scrobifera, and the disjunct middle coxal cavities from the Stylifera, Conchifera, and Balteifera. They would have to be placed in a separate group within the Limbata, near the Scrobifera.

In his informal classification scheme, Bell (1967) recognized a group that he called Anisochaeta-Isopleuri, members of which have front coxal cavities closed, separate, and unbridged, middle coxal cavities disjunct and confluent, metacoxal cavities disjunct and confluent, and antenna cleaner sulcate or proximally displaced in the anisochaetous mode (i.e. posterior tibial spur also displaced proximally). Among these traits, the only one not found in cicindines is unbridged front coxal cavities. As noted above, distribution of the bridged condition, found in cicindines, is still too poorly known among adephagans to justify exclusion or inclusion of cicindines on this basis alone.

Cicindelines, loricerines, elaphrines, and scaritines were included in the Isopleuri as defined by Bell. Ball (1979) suggested that Bell's groupings of tribes may represent grades attained independently by different clades, and we suspect that, in this view, he is at least partially correct. Our reinterpretation of some of the character polarities reinforces this opinion.

The classification of carabids that most closely reflects both our present understanding and our ignorance of phylogenetic relationships (Ball 1979) among extant suprageneric carabid taxa is that proposed by Kryzhanovskiy (1976). In that classification, the four tribes in Bell's Isopleuri are distributed among two subfamilies (Cicindelinae [= Cicindelini *sensu* Bell, and as we have used the name in this report] and Carabinae) and three supertribes in the latter subfamily (i.e. the Elaphritae, Loriceritae, and Scarititae). We suggest that the best placement of Cicindini in Kryzhanovskiy's scheme is in a supertribe of its own, the Cicinditae, between the Nebriitae and Elaphritae.

Monophyly of cicindine taxa and justification for their ranking.—Our placement of the Cicindini in the present carabid classification is both tentative and unsubstantiated by an unambiguous set of nested synapomorphies with other suprageneric taxa. Nonetheless, the evidence for the monophyly of the group and justification for its recognition as a distinct tribe are provided by a suite of autapotypic features that includes the following: (1) orientation of mouthparts slightly hypognathous; (2) except for gular region of head, entire ventral surface of body and all surfaces of coxae, trochanters, and femora covered with fine pubescence; (3) gena with a sharp flange ventral to eye; (4) compound eye very large; (5) mandible with terebral blade long and markedly down-curved; (6) mandibular scrobe without a setiferous puncture; (7) front coxal cavities closed and separate; (8) tarsal claws asymmetric in length, with anterior claw longer than posterior; and (9) eighth sternum and ninth/tenth tergum undivided. A tenth feature, hind coxal cavities disjunct (metepimeron present and large), may also be synapotypic for the group. Two of these characters, (6) and (7), have been used repeatedly as distinguishing features at the tribal level. The remaining seven or eight characters represent significant evolutionary novelties among carabid beetles that, in concert, suggest a group with a long and unique evolutionary history.

Justification for recognition of a distinct genus for each of the two cicindine species is based on autapotypic traits for each of these taxa that suggest a degree of differentiation between them at least as great as between most pairs of closely related carabid genera in other tribes. The following autapotypic features are recognized for *Archaeocindis*: (1) body deep, subcylindrical; (2) apical maxillary palpomere with large sensory pit ventromedially in apical one-half; (3) pterothoracic elytron-locking mechanism and elytral epipleuron as in Fig. 18A; and (4) femora longitudinally concave. Autapotypic features for *Cicindis* include (1) head without supraorbital setiferous punctures; (2) dorsal surface of mandible with obliquely transverse grooves and ridges; (3) epilobes of mentum broadly rounded, narrowly toothed anteromedially, and with six or seven pairs of marginal and several pairs of basal setiferous punctures; (4) submentum narrow anteriorly, much narrower then mentum, with three or four pairs of anterolateral setiferous punctures; (5) middle tibia with a posterodorsal fringe of long, fine accessory setae; (6) hind tibia markedly arcuate; (7) one or more tarsomeres on each leg with fringes of accessory setae (see Figs. 22B–25B for distribution of fringes); and (8) first visible (second) abdominal sternum with deep lateral concavity.

HISTORICAL BIOGEOGRAPHY

Jeannel (1942) recognized several carabid groups whose present distributions include at least parts of the Guyana and Brazilian Shields of South America, tropical and southern Africa, Madagascar, and India. He noted that, during the Mesozoic, these areas were part of the western portion of the supercontinent, Gondwanaland, prior to the development of the South Atlantic oceanic basin by the end of that era. He called groups with such extant distributions *lignées inabrésiennes* (Jeannel 1941, 1942) and suggested that these disjunctions reflect the fragmentation of what were more widespread ranges in western Gondwanaland through development of the southern Atlantic Basin [vicariant event] in late Mesozoic time. Reichardt (1977, 1979) and Noonan (1985) discussed the distribution of cicindines and listed several other carabid tribes with South American/African disjunctions (e.g. hiletines, siagonines, and apotomines). They agreed with Jeannel in dating the initiation of these disjunctions [vicariance] to the opening of the South Atlantic, at least 65 million years ago. If this timing of vicariance is correct, as we also suggest, then *Archaeocindis* and *Cicindis* have had at least that long to evolve independently. Development of hypotheses concerning the origins of the Cicindini and their pre- or early-Gondwanian history must await discovery (or at least recognition) of their sister group.

Available data suggest that the two known cicindine species differ in their habitat distributions: *A. johnbeckeri* adults apparently occur on saline, intertidal mudflats of bays in the Persian Gulf, and *C. horni* adults have been found only in the vicinity (microhabitat still unknown) of salt lakes in the interior of Argentina. Were ancestral cicindines coastal, sea beach inhabitants that subsequently invaded interior saline lake beds, or were they originally interior forms that radiated into coastal areas?

Analogous to this apparent difference between cicindines are the different habitat distributions of three pogonine species in North America. *Diplochaetus lecontei* Horn ranges from the Gulf Coast of Texas east to Florida and north to New Jersey. Its members are confined to sandy sea beach areas, where they occur at the margins of standing freshwater pools in dune areas (TLE, personal observations). *Diplochaetus desertus* Van Dyke is known only from the shores of the Salton Sea in southern California. This saline water body was connected with the Gulf of California until the late Tertiary (early Pliocene) (Hunt 1974). Throughout Quaternary time, its water levels have fluctuated greatly, due to subsidence of its basin, sedimentation, continued development of the Colorado River delta across its southern end, and changes in the channel of that river itself (Shelton 1966). *Pogonistes planatus* Horn is found throughout the interior of the western United States, from Oklahoma and Kansas northwest through Utah to eastern Oregon, where it occurs at the margins of saline lakes. These three habitat types form a series, from coastal sea beach to interior saline lake shore, with shores of the relatively recently isolated Salton Sea perhaps representing an intermediate stage between these extremes. Has *D. desertus* evolved from an ancestral, coastal form that became isolated from the sea coast with the separation of the Salton Sea from the Gulf of California? Could similar (yet unknown) events account for the evolution of other forms, living at the margins of saline lake beds, that have relatives in coastal areas?

Although the three pogonine species are probably closely related (Van Dyke 1953), phylogenetic relationships among them have not been analyzed, nor has a suitable sister group for them been proposed. Without reference to the habitat distributions of respective sister groups, the polarity of apparent transformations in habitat cannot be determined for either the pogonines or the cicindines considered. It is also possible that present habitat distributions of one or both groups are relictual, and that extinct or yet unknown sister groups occupied (or presently occupy) completely different (e.g. nonsaline) habitats. The recognition of the sister group of cicindines is the necessary next step to understanding this and other aspects of the evolutionary history of this group.

STRUCTURAL EVOLUTION, HABITAT, AND BEHAVIOR

Several features of adult form or structure in one or both cicindine species are conspicuous or otherwise of special interest and warrant at least brief comment here concerning their possible function or significance.

With a cicindine specimen in hand, one is at first struck by its great similarity in overall form to that of some tiger beetles (Cicindelini). With many species in several genera of cicindelines, it shares a similar general body form, large compound eyes, long legs, and an elytral pattern of marginal pale markings. Additional similarities are apparent under microscopic examination. Cicindines and cicindelines both have closed front coxal cavities and at least most species of the latter group also have an apparent metepimeron. Many tiger beetles (e.g. *Platychila pallida* Fabricius and *Megacephala limata* Perty) have genal flanges, serrate elytral margins (especially apically) and long tibial spurs, just as in cicindines. In all tiger beetles we examined, we found a metapleural elytron-locking mechanism very similar to that occurring in cicindines. Based on many other important features in which cicindines and cicindelines differ (see previous discussion), it is clear that most, if not all, of these similarities represent independent (convergent) developments in the two groups, probably in response to similar behavioral and/or habitat distribution patterns. In fact most of these features are shared with other carabid taxa as well.

Enlarged eyes, similar in form to those in cicindines, are found also in *Notiophilus, Elaphrus,* and *Graphipterus* adults and in at least some genera of many other tribes (e.g. Bembidiini and Lebiini) in addition to cicindelines. Members of most, if not all, of these other groups are mainly day-active, visually-oriented predators, although individuals are sometimes attracted to lights at night.

Genal flanges seen in at least some cicindelines (e.g. *Megacephala limata*) appear to be posterior extensions of the carinate rim of the maxillary fossa across the gena. Those in cicindines (Fig. 3) are separate from and dorsal to a line drawn posterior to the rim of the fossa. The cicindine flange appears to serve as a forward extension of the thin, finlike plane established by the anteriorly extended apical angle of the pronotum under the eye (see additional comments below). Further expansion of this flange on the gena, beyond the condition seen in extant cicindines, might result in a functional arrangement similar to that seen in most gyrinids, where a broad, sharp flange on the sclerite that divides each compound eye into dorsal and ventral fields continues the trimline of the pronotum anteriorly on the head. This is no doubt a streamlining (perhaps also hydrofoil) adaptation in gyrinids for swimming rapidly at the surface. Its function in cicindines, where it is only partially developed, may be similar if less efficient.

Closure of the front coxal cavities provides better protection ventrally for the membranous intersegmental connection between pro- and mesothoraces and permits increased ventral motion of the prothorax (Hlavac 1975). Because tiger beetles often assume a stance in which the venter is well above the substrate (see below) and exposed, coxal closure may be an important protective adaptation in this group, and perhaps in cicindines as well. The functional significance of the metepimeron is unknown.

Very little comparative study has been made of elytron-locking mechanisms in carabid beetles to date. The metapleural mechanisms in cicindines and cicindelines are at least similar in general form. Tiger beetles depend on their ability to take flight instantly, mainly for predator avoidance in exposed areas. Their elytron-locking mechanism must facilitate rapid release; and the arrangement of metapleural and elytral epipleural parts that form this observed mechanism would seem to provide such an opportunity. It appears that release would involve simply lifting the elytra slightly, or depressing the abdomen and posterior portion of the metathorax slightly, or both. The presence of such a mechanism in cicindines suggests that they too can take flight quickly.

Serrate elytral margins occur among many species and genera of cicindelines and also in several bembidiine taxa (e.g. especially among subtribes Anillina and Tachyina), some carabines (e.g. a few *Calosoma* spp.), and in single species in several other tribes. Carabids with serrate elytra occupy a wide range of habitats, from sandy sea beaches and the open shores of lakes and streams to the margins of forested swamps in tropical regions. No pattern of co-occurrence with a particular habitat or behavior pattern is apparent to us at present, but this feature must have some important function to have developed independently in several different lineages.

Long, slender legs occur in many carabid groups, but particularly in cicindelines, nebriines, cychrines, and platynines. Members of each of these groups are fast runners, but among these, cicindelines are probably the fastest. Tiger beetles, the only one of these groups with diurnally active members, also have legs most similar in form to those in cicindines. Long legs not only facilitate longer strides, hence speed, but also may permit the beetle to lift itself (behavior known as *stilting*) well above the substrate, an important advantage for life in open, exposed areas where daytime temperatures at the substrate surface may be extremely high (Pearson 1988).

Exceptionally long tibial spurs (especially on the hind leg) are found in several different carabid groups, including many cicindelines, all masoreines, and in the genus *Nemotarsus* among lebiines. These cicindelines and some masoreines (e.g. *Tetragonoderus* spp.) run on open, sandy substrates, whereas *Nemotarsus* adults and other masoreines (e.g. *Sarothrocrepis* spp.) are foliage or tree-trunk runners. The habitat distributions of cicindines species suggest that, like certain tiger beetles (e.g. *Megacephala* and *Platychila* spp.), they run on loose, particulate substrate. Long tibial spurs may assist in gripping such substrates and thereby facilitate running.

The only feature shared uniquely by cicindines and cicindelines (especially *Cicindela* and *Megacephala* spp.) is the elytral pattern of marginal pale spots. In fact, the patterns are different in detail in the two groups; but, overall, they are more similar to each other than either is to any other carabid with which we are familiar. The pattern is probably cryptic, an example of disruptive coloration, in the respective habitats of these beetles.

Cicindines share other features with a diverse array of other adephagans, again, clearly through independent development of these traits. A pale body and appendages is shared with many carabids, especially with species that live in sea beach, desert playa, or other exposed habitats. Such species include *Nebria diversa* LeConte and *Eurynebria complanata* (Linnaeus) (Nebriini), *Platychila pallida* (Cicindelini), *Pogonistes planatus* (Pogonini), and *Tetragonoderus pallidus* Horn (Masoreini). Among carabids, only cicindines are known to have asymmetrical tarsal claws; however, several group of dytiscids (e.g. Colymbetini, Hydriphini, and a few genera in other tribes) have adults with asymmetry in claw length. Setal fringes on tibiae and tarsi, which aid in swimming, are widespread among hydradephagans, but among carabids, they are known to us only in *C. horni* adults. Anterior projection of the apical pronotal angles, lateral or ventral to the compound eyes, as thin, fin-like planes that are closely fit against the head, occurs in cicindines, some cicindelines (e.g. *Platychila pallida*), omophronines, amphizoids, many dytiscoids, and gyrinids.

One feature of adults of both *C. horni* and *A. johnbeckeri* that occurs elsewhere among adephaga chiefly in a few genera or species of the higher-grade carabid tribes (e.g. harpalines or chlaeniines), is the presence of dense setae on the venter. These setae may be hydrofuge in function and serve to trap air in a functional gill (Hinton 1976) for respiration during submersion underwater. Alternately, they may contribute to thermoregulation by providing insulation from heat rising from the substrate. In fact, they may serve both functions under appropriate conditions.

Although almost nothing has been observed directly about the microhabitat requirements or behavior of cicindines, consideration of their unusual suite of structural features suggests to us several hypotheses about their biology that can be tested by subsequent observations of these beetles in the the field. We suggest that they behave, in many ways, like many diurnal tiger beetles, as fast-running, visually oriented predators that inhabit hot, open, saline habitats and take to flight rapidly, at least when disturbed. Both species have features that suggest an ability to withstand submersion (hydrofuge hairs) and to swim (tibial and tarsal setal fringes in *C. horni,* concave femora in *A. johnbeckeri,* asymmetrical tarsal claws in both), perhaps chiefly at the water surface (genal flanges and anteriorly projected apical pronotal angles below the compound eyes). In general, structural features interpreted as adaptations for swimming (i.e. setal fringes, asymmetry of tarsal claws) are more highly developed (relatively apotypic) in *C. horni* adults, those for running on hot, loose substrates (longer legs, exceptionally long tibial spurs) are better developed in *A. johnbeckeri* adults.

Prospectus for Future Study

Further advance in our understanding of cicindine carabids must await additional specimens, both dead and alive, and field observations of behavior and habitat distributions. Additional museum specimens will permit greater freedom for dissection, thereby allowing a review of structures not yet properly examined, especially the male and female genitalia of both species. Live adults are needed for rearing cicindine larvae, which remain unknown. Larval features may provide additional clues to relationships of this tribe with others. Field observations of habits and habitats are needed to confirm our suggestion, for example, that *C. horni* adults are excellent surface swimmers, using their specialized legs for this purpose. Comprehensive morphological studies of both adults and larvae are urgently needed throughout the Adephaga to broaden and refine the base of comparative data available about carabid form and structure. Characters used traditionally in carabid systematics have helped to establish a classification that functions moderately well but has failed to provide us with a clear understanding of relationships. New characters must be identified and surveyed and new techniques employed to resolve present conflicting observations.

Acknowledgments

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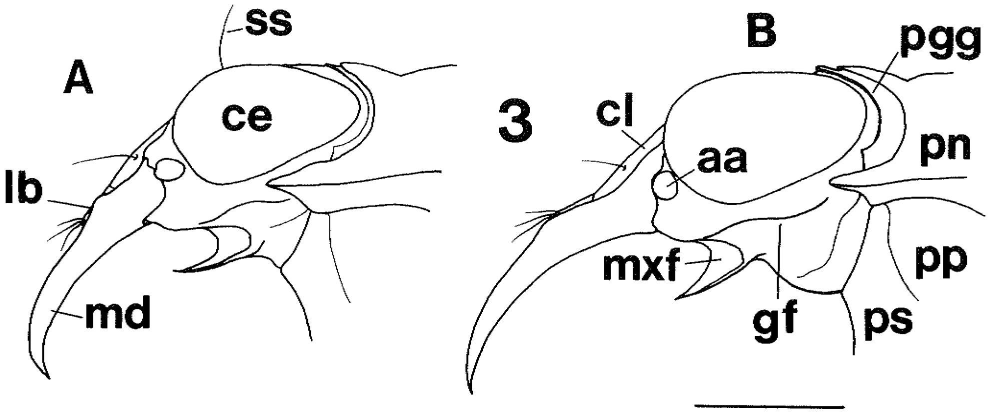
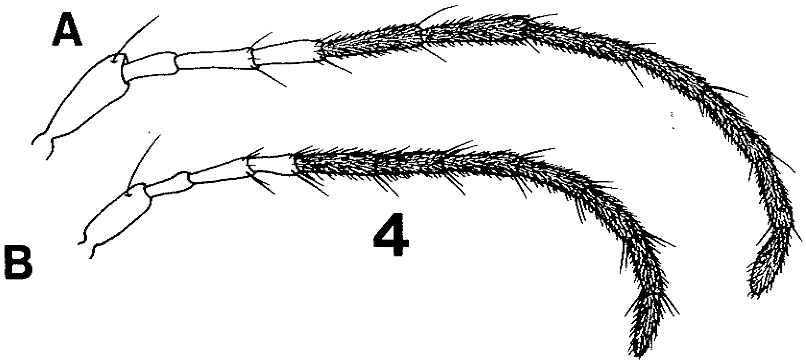
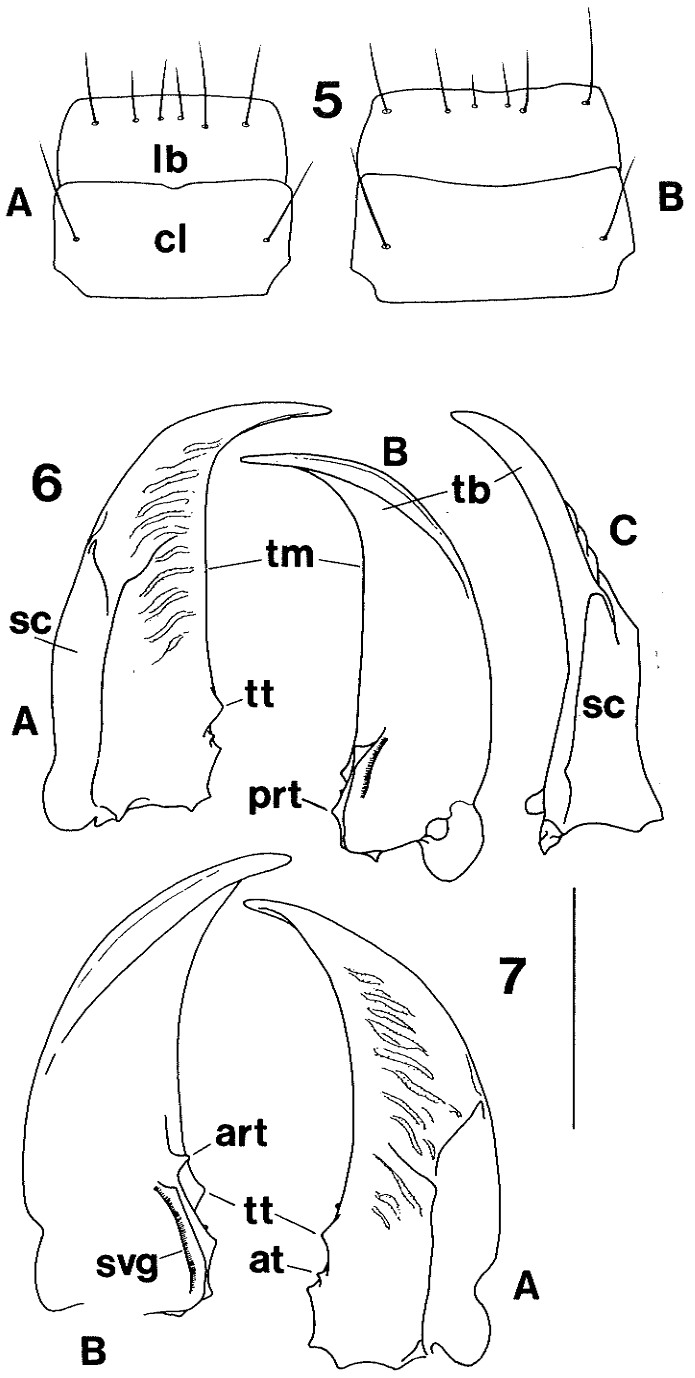
Finally, to the memory of our departed friend and colleague, Donald R. Whitehead, we dedicate this paper.





Figs. 3, 4. Fig. 3. Head, left lateral aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch; aa = antennal articulation; ce = compound eye; cl = clypeus; gf = genal flange; lb = labrum; md = mandible; mxf = maxillary fossa; pgg = postgenal groove; pn = pronotum; pp = propleuron; ps = prosternum; ss = supraorbital seta. Fig. 4. Right antenna, dorsal aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch.



Figs. 5–7. Fig. 5. Labrum and clypeus, dorsal aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch; cl = clypeus; lb = labrum. Figs. 6, 7. Mandibles, *Cicindis horni* Bruch; A, dorsal aspect; B, ventral; C, lateral aspects. Fig. 6. Left mandible. Fig. 7. Right mandible. At = accessory tooth (homology unknown); art = anterior retinacular tooth; prt = posterior retinacular tooth; sc = scrobe; svg = setiferous ventral groove; tb = terebral blade; tm = terebral margin; tt = terebral tooth.

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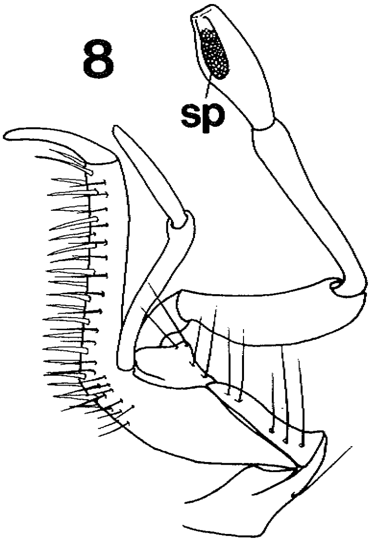

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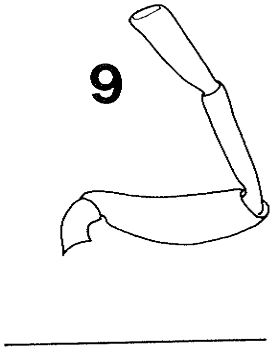

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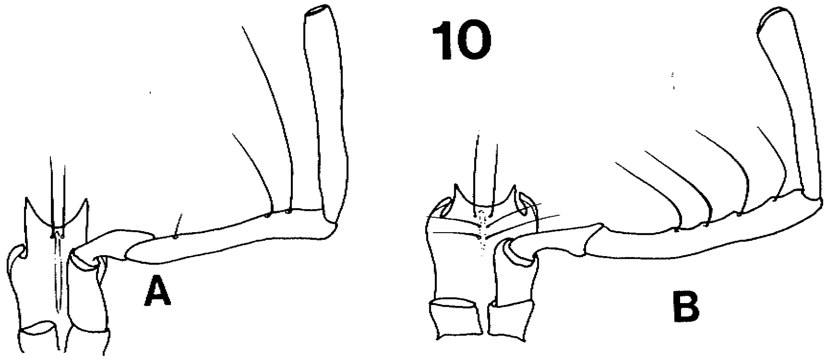

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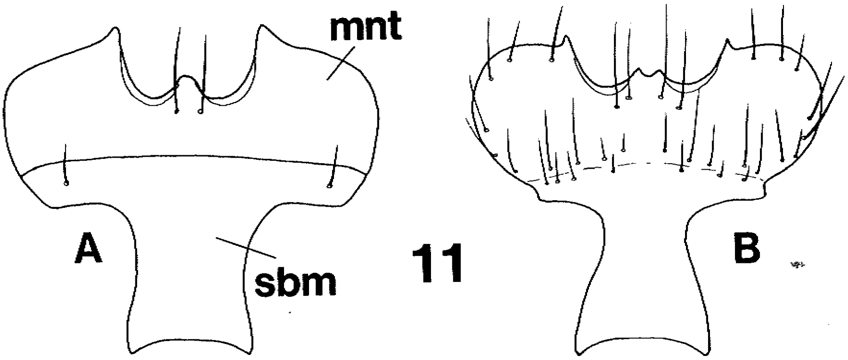

Figs. 8–11. Fig. 8. Left maxilla, ventral aspect, *Archaeocindis johnbeckeri* (Bänninger); sp = sensory pit. Fig. 9. Left maxillary palpus, ventral aspect, *Cicindis horni* Bruch. Fig. 10. Labium, ventral aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch. Fig. 11. Mentum and submentum, ventral aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch; mnt = mentum; sbm = submentum.

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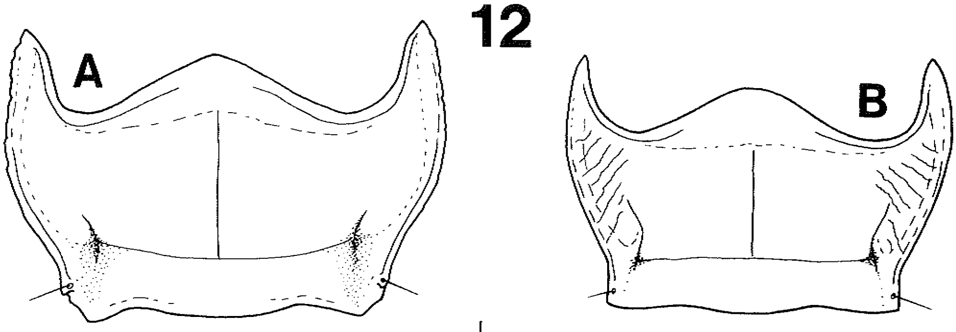

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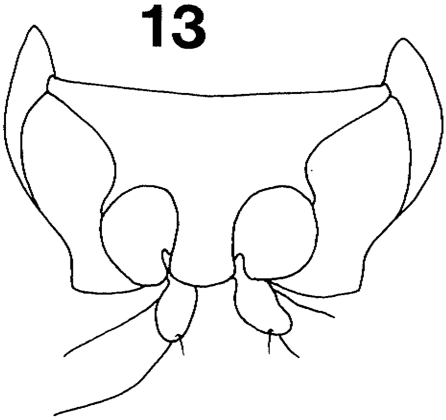

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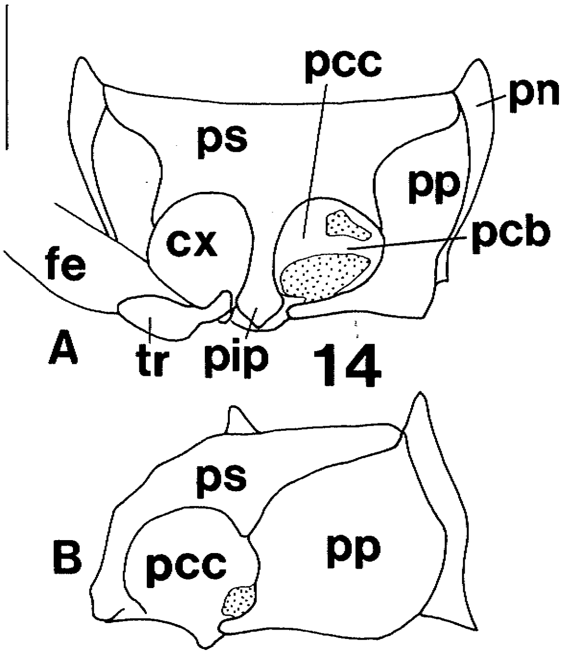

Figs. 12–14. Prothorax. Fig. 12. Pronotum, dorsal aspect; A. *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch. Fig. 13. *Archaeocindis johnbeckeri* (Bänninger), ventral aspect. Fig. 14. *Cicindis horni* Bruch; A, ventral aspect; B, left ventrolateral oblique aspect. Cx = front coxa; fe = front femur; pcb = dorsal bridge of front coxal cavity; pcc = front coxal cavity; pip = prosternal intercoxal process; pn = pronotum; pp = propleuron; ps = prosternum; tr = front trochanter; stippled areas = non-sclerotized areas.

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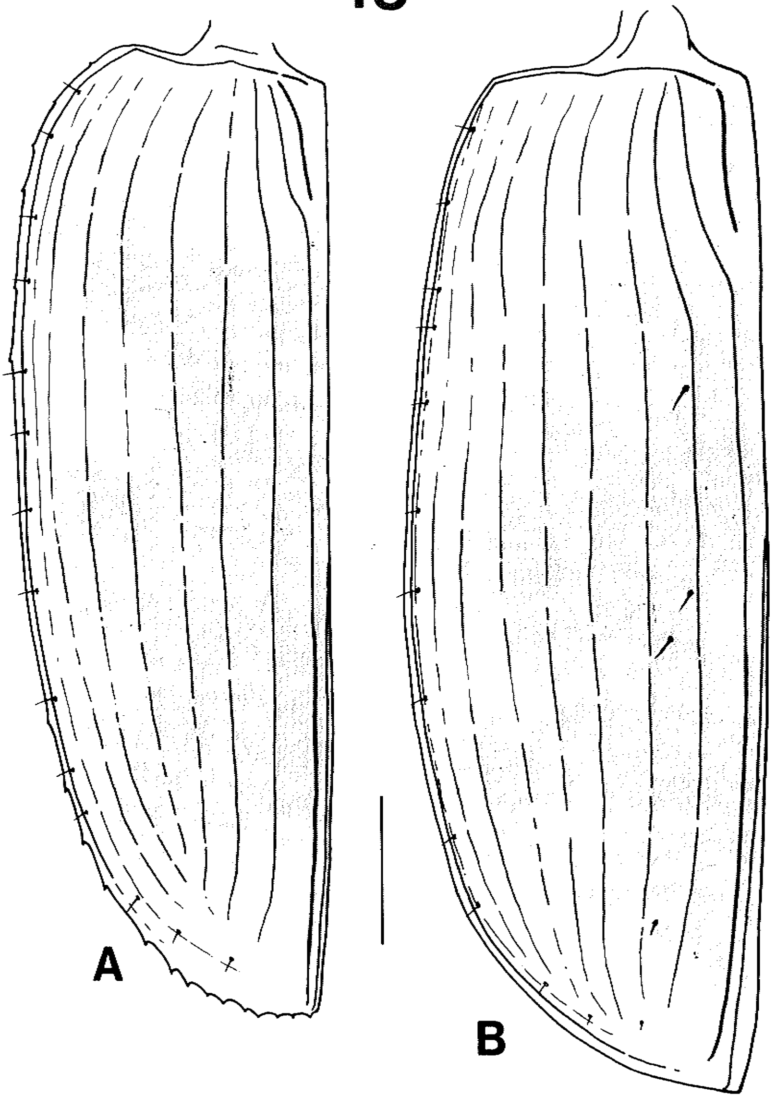
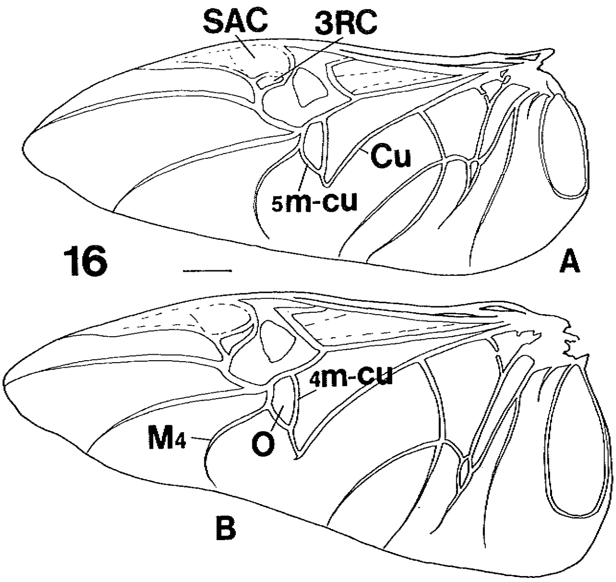
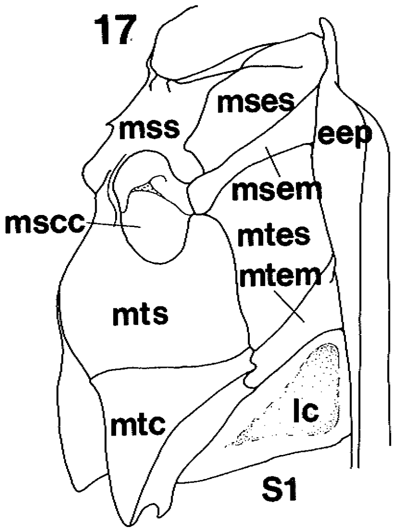
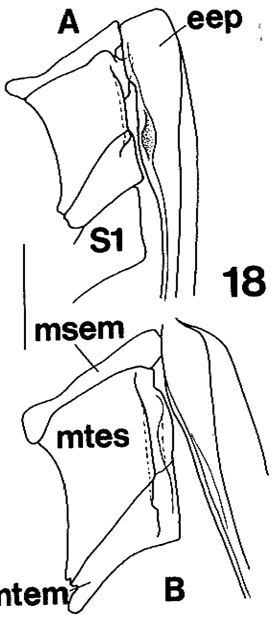


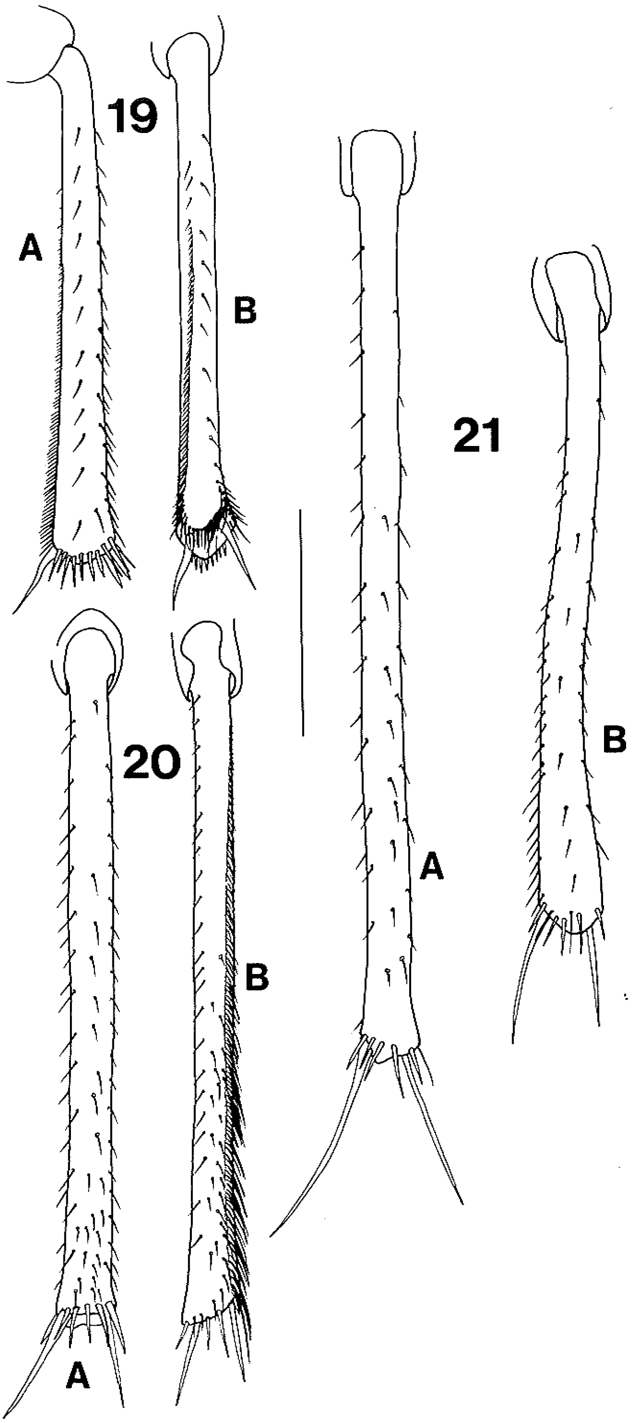
Fig. 15. Left elytron, dorsal aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch.



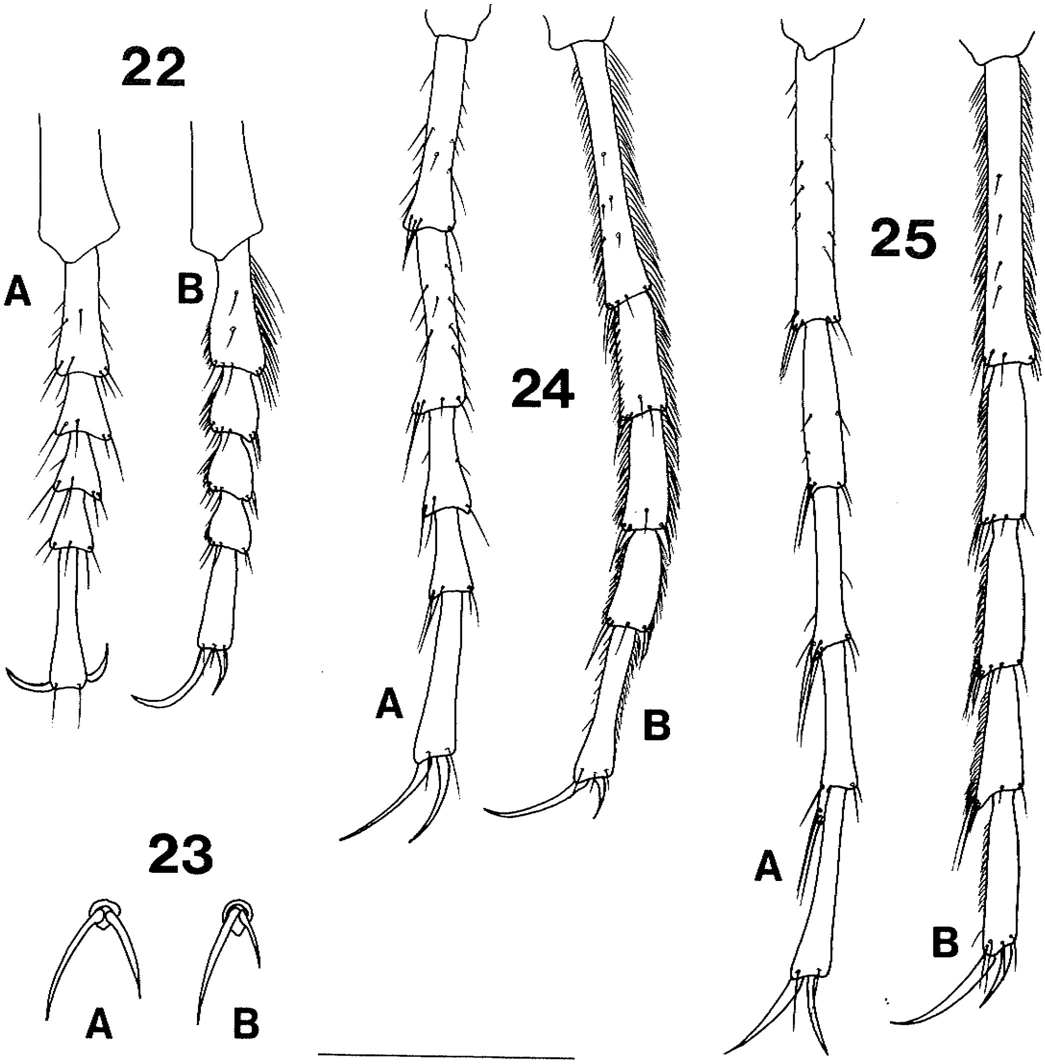




Figs. 16–18. Fig. 16. Left metathoracic wing, dorsal aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch; Cu = Cubitus; M4 = fourth branch of the Media; O = Oblongum Cell; SAC = Anterior Sector Cell; 3RC = Third Radial Cell; 4m-cu = fourth medio-cubital crossvein; 5m-cu = fifth medio-cubital crossvein. Fig. 17. Pterothorax, left ventrolateral oblique aspect, *Cicindis horni* Bruch; eep = elytral epipleuron; lc = lateral concavity of first visible sternum; mscc = middle coxal cavity; msem = mesepimeron; mses = mesepisternum; mss = mesosternum; mtc = metacoxa; mtem = metepimeron; mtes = metepisternum; mts = metasternum; S1 = first visible sternum; stippled areas = nonsclerotized. Fig. 18. Metathoracic elytron-locking mechanism, left ventrolateral oblique aspect; elytron lifted slightly dorsad of resting position; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch; eep = elytral epipleuron; msem = mesepimeron; mtem = metepimeron; mtes = metepisternum; S1 = first visible sternum.



Figs. 19–21. Left tibiae. Fig. 19. Front tibia, *Cicindis horni* Bruch; A, anterodorsal oblique aspect; B, ventral aspect. Fig. 20. Middle tibia, dorsal aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch. Fig. 21. Hind tibia, dorsal aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch.



Figs. 22–25. Left tarsi; A, *Archaeocindis johnbeckeri* (Bänninger), female; B, *Cicindis horni* Bruch, male. Fig. 22. Front tarsus, dorsal aspect. Fig. 23. Front tarsal claws, apical aspect. Fig. 24. Middle tarsus, dorsal aspect. Fig. 25. Hind tarsus, dorsal aspect.

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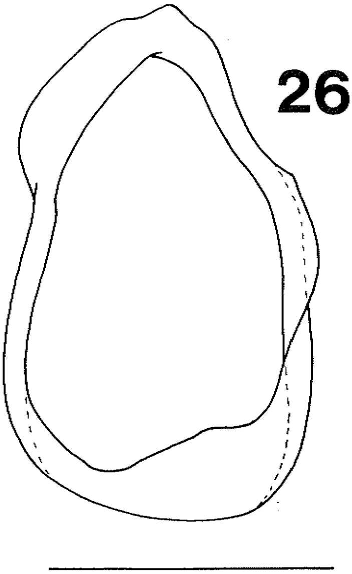

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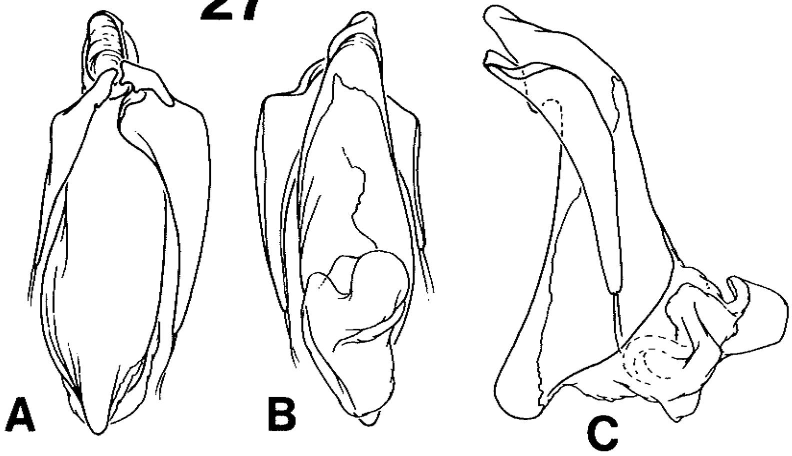

Figs. 26, 27. Male genitalia, *Cicindis horni* Bruch. Fig. 26. Ring sclerite, dorsal aspect. Fig. 27. Median lobe and parameres; A, ventral aspect; B, dorsal aspect; C, left lateral aspect.

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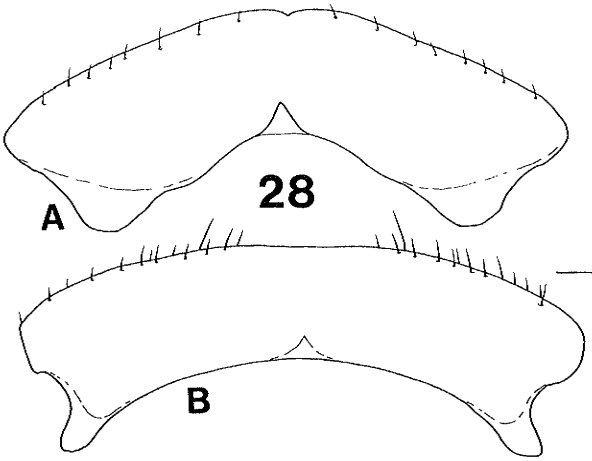

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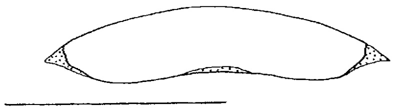

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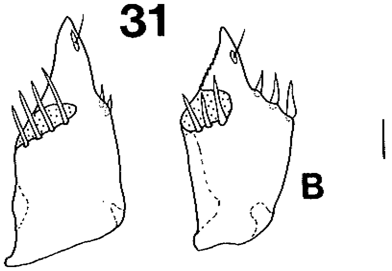

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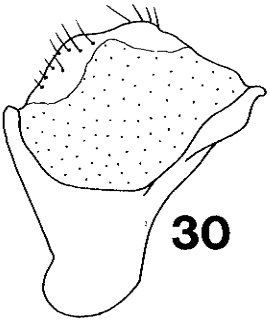

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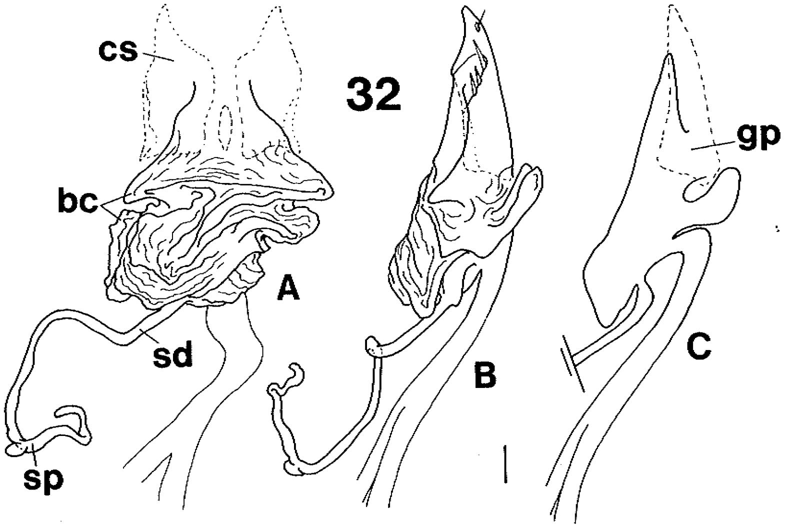
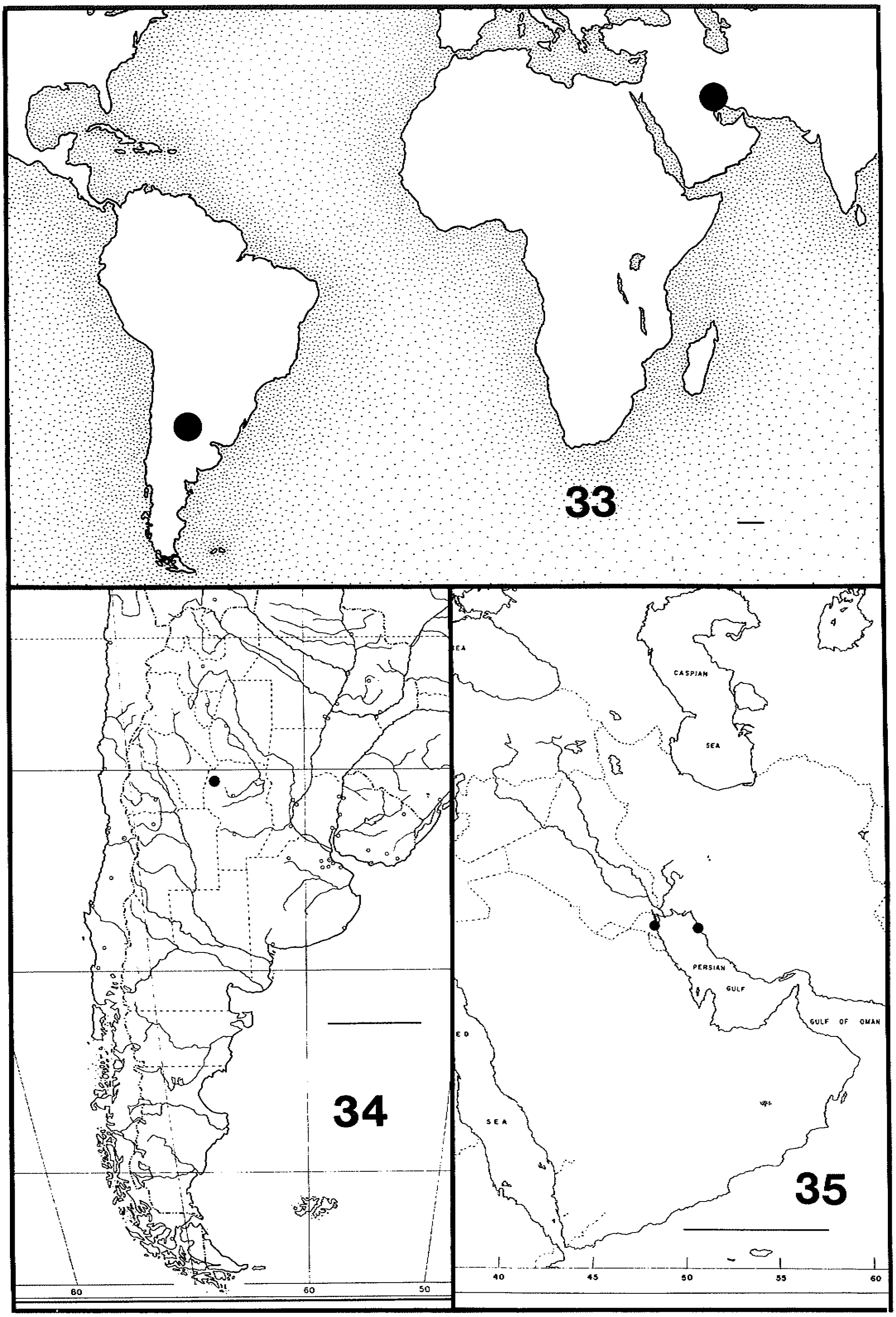


Figs. 28–32. Female genitalia; stippled areas = unsclerotized areas. Fig. 28. Eighth sternum, ventral aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch. Fig. 29. Ninth/tenth tergum, dorsal aspect, *Cicindis horni* Bruch. Fig. 30. Left gonangulum, ventrolateral aspect, *Cicindis horni* Bruch; scale line = 0.1 mm. Fig. 31. Left coxostylus, ventral aspect; A, *Archaeocindis johnbeckeri* (Bänninger); B, *Cicindis horni* Bruch; scale line = 0.1 mm. Fig. 32. Bursa copulatrix and spermathecal apparatus, *Cicindis horni* Bruch; A, dorsal aspect; B, left lateral aspect; C, schematic, left lateral aspect; bc = bursa copulatrix; cs = coxostylus; gp = gonopore; sd = spermathecal duct; sp = spermatheca; scale line = 0.1 mm.



Figs. 33–35. Geographical distribution maps. Fig. 33. Tribe Cicindini. Fig. 34. *Cicindis horni* Bruch. Fig. 35. *Archaeocindis johnbeckeri* (Bänninger). Scale line = 500 km.

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