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New Morphological Aspects and Phylogenetic Considerations of *Cicindis* Bruch (Coleoptera: Carabidae: Cicindini)

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Abstract

Cicindis Bruch is a monospecific genus of carabid beetles endemic to Argentina. In this contribution, *Cicindis horni* Bruch is re-described, with addition of new morphological features of male internal sac, female genital tract and elytral closure. New information on the species' habitat and distribution is also provided. The phylogenetic placement and relationships of *Cicindis* within the family Carabidae are discussed on the basis of a cladistic analysis. Terminal taxa included representatives of all subfamilies of Carabidae and supertribes of Carabinae, with a major sampling of those taxa considered to be closely related to Cicindini by previous authors. The phylogenetic analysis shows the basal position of *Cicindis* in a clade that includes Ozaeninae, Omophronini, Scaritinae and Conjuncta. A close relationship of *Cicindis* with Ozaenini + Metriini is supported by the particular closure of the procoxa and the ventral position of the oviduct with respect to the spermatheca.

Introduction

The monotypic genus *Cicindis* Bruch constitutes one of the several enigmatic carabid beetles endemic to the southern regions of South America. It is classified within the tribe Cicindini together with the genus *Archaeocindis* Chaudoir. Southern southamerican carabid beetles (as other austral American insects groups) are phylogentically related with the carabid fauna from other regions of the world. Southern southamerican carabids such as zolines, migadopines, and broscines are related to groups occurring in other austral continents (Jeannel 1938, 1967, Darlington Jr 1965, Roig-Juñent & Cicchino 2001). Other members of the southern South America fauna such as trachypachids (*Systolosoma* Solier) and omines (the genus *Pycnochila* Motschulsky of the tribe Megacephalini) are relictual lineages related to groups also occurring in North America (Roig-Juñent *et al* 2008). In southern South America there are also Pangean taxa such as Cnemalobini (Roig-Juñent 1993), Notiokasini (Kavanaugh & Nègre 1983), and Cicindini (Kavanaugh & Erwin 1991) which are related to holarctic or tropical carabids.

Beyond the particular pattern of distribution of the tribe Cicindini, with one species in South America and other in Iran, the unusual combination of morphological characters exhibited by *Cicindis* and *Archaeocicindis* had led taxonomists to propose appreciably different hypotheses about its relationship with other carabid groups. When Bruch (1908) described the genus *Cicindis*, he considered it to be related to Nebriini and Omphronini. Other classification schemes considered this genus to be a unique taxon within the tribe Cicindini, related to Ozaenini and Metriini (Bänninger 1925, Bruch 1927, Kryzhanovsky 1976, Reichardt 1977). Erwin & Sims (1984) classified Cicindini within the supertribe Nebriitae, subfamily Carabinae, along with the tribes Nebriini, Notiokasini, Opisthiini, and Notiophilini. Later, Erwin (1985) hypothesized that Cicindini were closely related to the tribe Notiophilini. Finally, Kavanaugh & Erwin (1991) modified Kryzhanovsky's classification scheme by elevating Cicinditae to the supertribe level and placing it taxonomically between Nebriitae and Elaphritae.

Kavanaugh (1998) presented a phylogenetic analysis including both genera of the tribe Cicindini, and proposed that the tribe is the sister group of a clade comprising *Omophron* Latreille (Omophronini), *Cicindela* L. (Cicindelini), *Omus* Eschscholtz (Megacephalini), *Scaphinotus* Latreille (Cychrini), and *Carabus* L. (Carabini). Because representatives of Ozaeninae and other carabid subfamilies such as Psydrinae were not included in Kavanaugh's analysis, the relationships of Cicindini with these taxa were not tested.

Liebherr & Will (1998) in a phylogenetic analysis using characters from female genitalia found *Cicindis* as part of a polytomy with Migadopini, Amblytelina, Carabidae Limbata, and a monophyletic group conformed by Siagonini, Cychrini, Pamborini, Carabini, and Cicindelini. Liebherr & Will (1998) considered Cicindini in a middle level grade because it posses gonocoxal rami, but lacks harpalidian type of abdomen. These authors also pointed out the absence of accessory spermathecal gland.

Representatives of the tribe Cicindini have not been included in other phylogenetic analyses using morphological (e.g. Beutel 1998, Kavanaugh 1998), or molecular data (Maddison *et al* 1998, 1999, 2009, Balke *et al* 2005).

The main objectives of this paper are to describe new morphological features of *Cicindis horni* Bruch*,* such as male and female internal structures and the particular closure of the elytra, and to perform a preliminary cladistic analysis based on adult morphology in order to explore the phylogenetic placement of *Cicindis* within the family Carabidae.

Material and Methods

The description of the morphological variability of *C. horni* is based on examination of 25 males and 14 females. Several specimens of 25 other carabid and trachypachid species were studied for the cladistic analysis (See *Online Supplementary Material 1*). Material for this study was borrowed from entomological collections of the following institutions: Instituto Argentino de Investigaciones de Zonas Áridas Mendoza, Argentina (Sergio Roig-Juñent) (IADIZA), Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia," Buenos Aires, Argentina (Arturo Roig- Alsina) (MACN), Museo de Ciencias Naturales de La Plata, La Plata, Argentina (Alberto Abramovich) (MLPA), University of Nebraska State Museum, USA (Brett Ratcliffe) (UNSM), National Museum of Natural History, Smithsonian, Washington D.C, USA (Terry Erwin) (USNM).

Dissections were made following the techniques used in previous contributions of Carabidae (Roig-Juñent 2000). Drawings were made with camera lucida adapted to a stereomicroscope. Elytral structures were examined and photographed under a compound microscope. A tranverse section of the elytron was made using a microtome after inclusion of the elytron in paraplast solution. Scanning electron microscope pictures were taken using a LEO 1450 VP microscope. Terminology used follows previous revisions (Deuve 1988, 1993, Liebherr & Will 1998, Roig-Juñent 1998, 2000, Roig-Juñent & Cicchino 2001).

Cladistic analyses

In our analyses we included representatives of all the supertribes of Carabinae and of the other carabid subfamilies, especially those for which previous authors proposed closer phylogenetic relationships with *Cicindis*.

For the cladistic analysis, a total of 50 adult morphological characters (*Online Supplementary Material* 2) were scored for 27 species belonging to six subfamilies and 20 tribes. These species represent all the subfamilies proposed by Erwin & Sims (1984) and 20 of the 86 tribes. Characters in the text are referred to by number and their states appear in superscript (*i.e.* 10^1).

A representative species of the family Trachypachidae, regarded as the sister taxon of Carabidae in previous works (Erwin 1985, Beutel 1998, Kavanaugh 1998, Roig-Juñent 1998), was used to root the tree.

Morphological characters used in this analysis correspond to those proposed for the higher classification of Carabidae in previous studies (Sloane 1923, Jeannel 1941, 1955, Bell 1967, Erwin 1985, Nichols 1985, Deuve 1993, Baehr 1998, Liebherr & Will 1998, Roig-Juñent & Cicchino 2001). All characters were considered to be non-additive (unordered). The data matrix is presented as the *Online Supplementary Material 3*.

Data analysis

Phylogenetic analyses were performed using parsimony software TNT (Goloboff *et al* 2003). The data set was analyzed using two procedures: (a) equally weighted character analysis, and (b) implied weighting method (Goloboff 1993), exploring the topologies obtained with different K (constant concavity) values from K = 1 to K = 6. All analyses were conducted using a traditional heuristic search on the base of Wagner trees, 100 random addition sequences, followed by the tree-bisection reconnection (TBR) swapping algorithm, saving 100 trees per replicate. Branch robustness was assessed by standard Bootstrapping and Jackknifing (removal probability = 36), with 500 replicates, searching among trees with traditional search for the equally weighted analysis. Bremer support and symmetric resampling (change probability = 33) were used as support values for implied weighting analyses since neither of these two measures is distorted by weight. All support numbers are given as relative values.

Redescription

Characters not described in Kavanaugh & Erwin (1991) are provided.

Systematic remarks

The new material of *C. horni* shows some interesting morphological differences from that described by Kavanaugh & Erwin (1991) and from the material preserved in MACN and MLPA. The most remarkable difference is in the color pattern (the frontal and central part of the pronotum, and the tarsi have a darker coloration with red tones). Other characters showing variation are the number of glossal sclerites and the number of parameral setae. New features previously not noticed are antennomeres 5-11 with a lateral relief colored and asetose, the special closure of the elytra, a post-orbital furrow and the ventral position of oviduct with respect to the spermatheca.

Male

Color. Base of head, body, and appendages pale yellowish-white. Apex of mandibles reddish-black to black (Fig 1). Elytra with distinct dark pattern, reddish-brown, with median maculae covering almost the whole surface of the elytra (Figs 1, 16). Elytral lateral margin and first interneur pale yellowish (nearly white).

Head: *Mouthparts*. Glossal sclerite with apical margin concave with four setae, two apical and two medial on the midline (Fig 2); paraglossa not fused to the glossal sclerite, equal in length to the glossal sclerite. Mentum with epilobes rounded, narrowly toothed antemedially (Fig 3), with two paramedian setae, nine pairs of marginal setae, and three pairs of central and basal setae. Maxillary palpi long and slender (Figs 4-5). Frons with sulcus obsolete. *Antennae*. Antennomeres 5-11 with a lateral relief extending from base to preapex (Figs 6-7). *Eyes*. Ocular furrow behind the eyes (Figs 8-11) covered with pronotum setae, these setae with a particular brush-like shape. Another particularity are the setae on the basal pronotum margin.

Legs. Fore tarsomeres 1-4 not expanded laterally, pads of articulo-setae with straight cylindrical shafts bearing regular round plates (Figs 14-15). Posterior procoxal

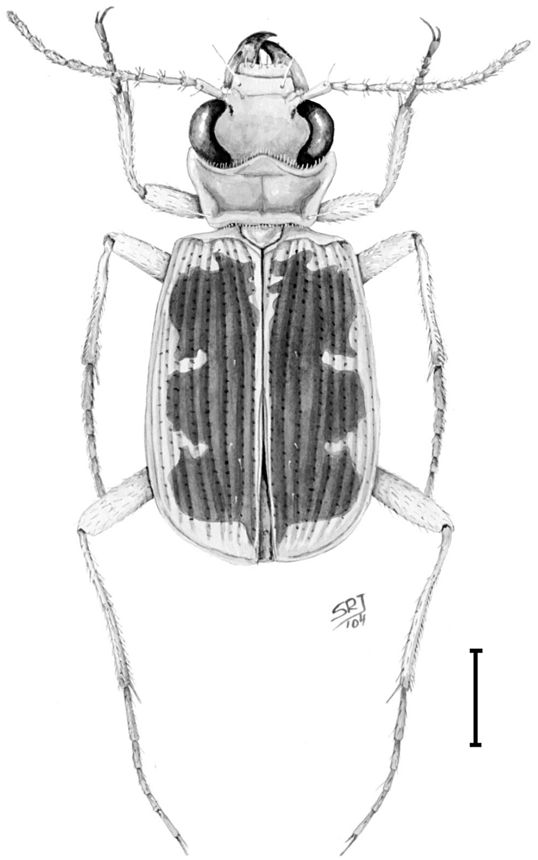
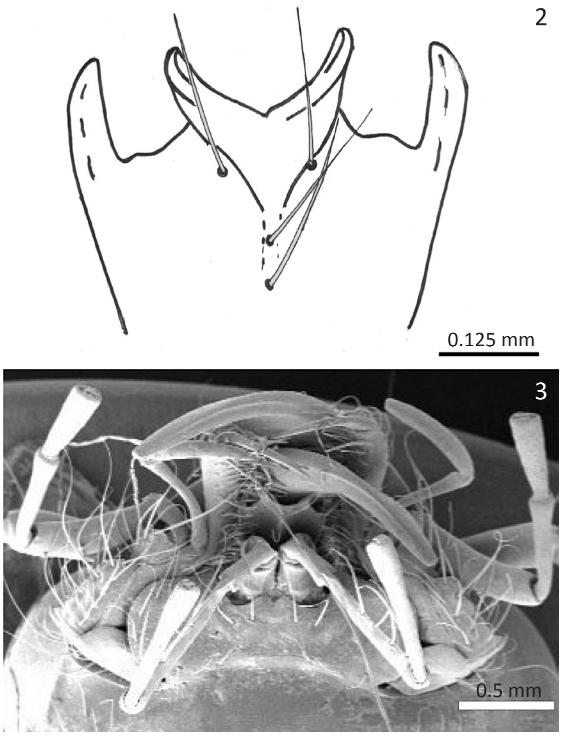
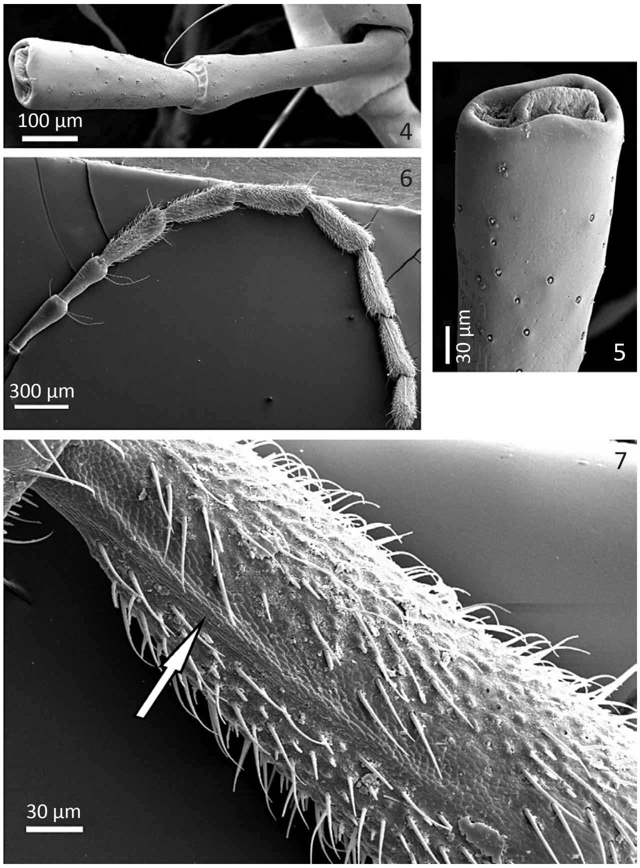


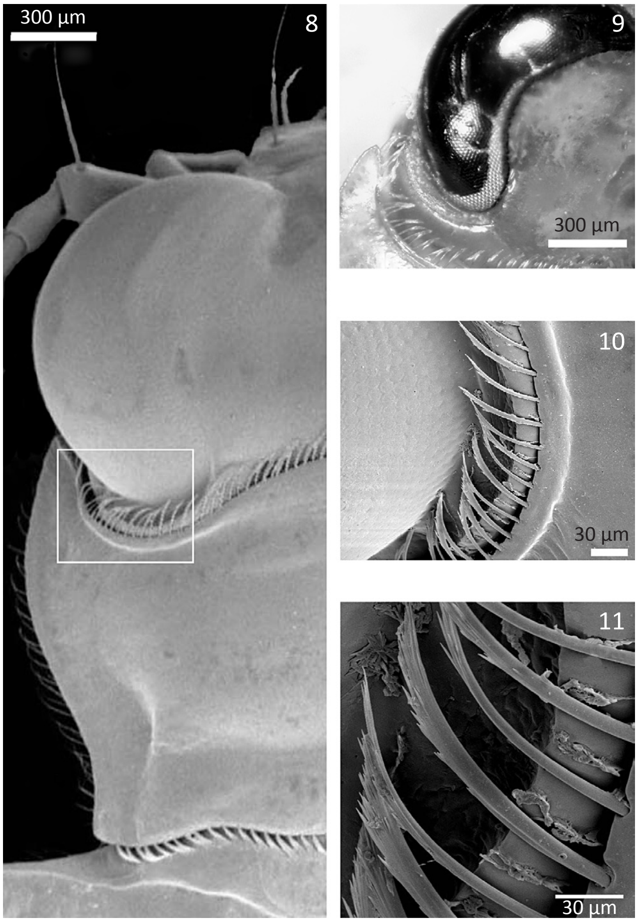
Fig 1 Dorsal habitus of *Cicindis horni* Bruch, male. Scale 1 mm.



Figs 2-3 *Cicindis horni*. 2) Glossa and paraglossa; 3) Mouthparts, ventral view.



Figs 4-7 *Cicindis horni* 4) Right maxillary palpi; 5) Right maxillary palpomere; 6) Antenna; 7) Antenna relief.



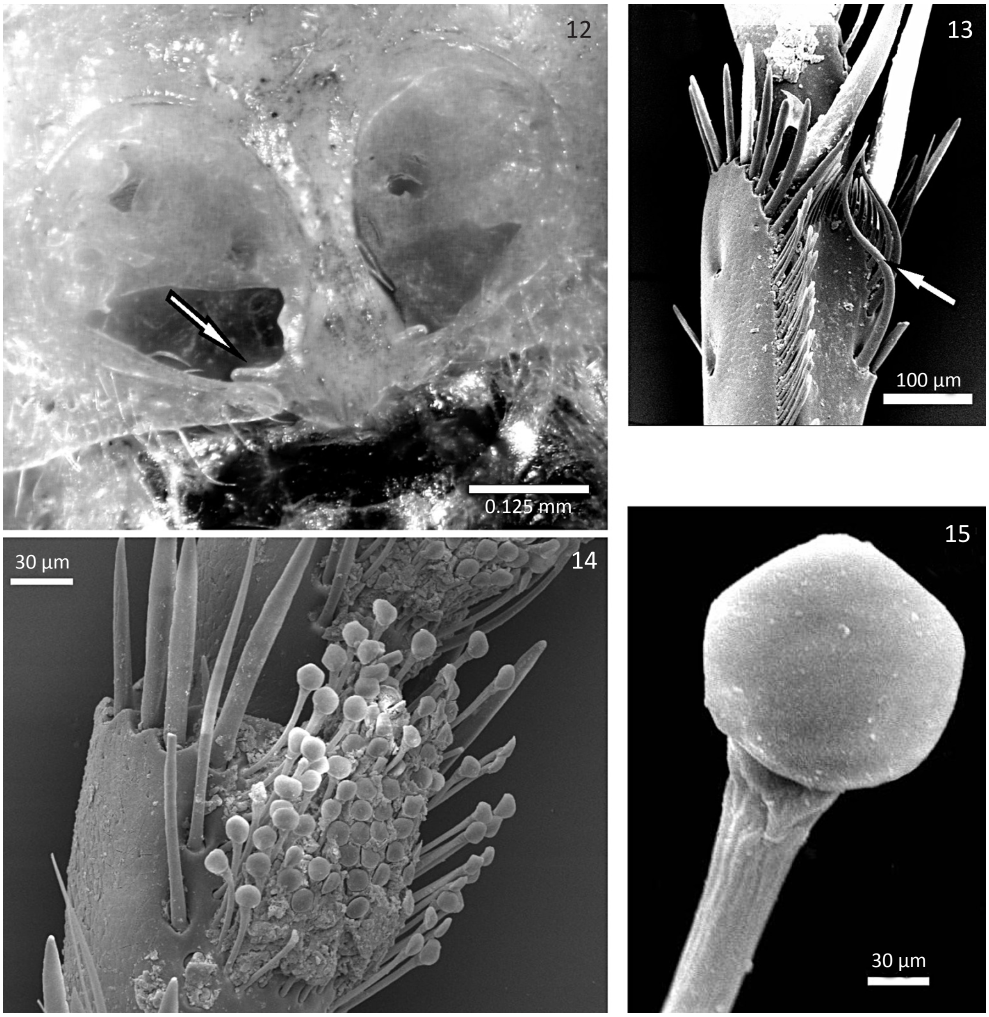
Figs 8-11 *Cicindis horni* 8) Sagital cut of left region of eye and pronotum; 9) Ocular furrow; 10) Detail of ocular furrow; 11) Pronotum setae over ocular furrow.

closure with proepimeron fitted into the lateral arm of the prosternal process (Fig 12). Posterior claws of anterior and posterior tarsi equal to 0.66 the length of anterior claw, posterior claw of middle tarsi 0.5 the length of anterior claw. Cleaning organ with curved clamp setae (Fig 13).

Elytra. Humeral region well developed, rounded; elytra apex rounded (Fig 16). Interneurs 1 to 7 striatopunctate, intervals slightly convex. *Cicindis* adults have two different elytral closure systems; the first one goes from the elytral base to about 0.5 mm after the scutellum (Fig 17) and consists of a thickened fusiform structure, a transverse cut of this region (Fig 18) shows that this structure is hollow, and presents several rows of spicules on the inner side which, together with the metanotal furrow (Fig 19) seem to be responsible for the strong elytral locking. This helps confirm the observation presented in Erwin & Aschero (2004) that these beetles carry air bubbles under the elytra for diving. The second closure system extends between the end of the first one and the elytral apex. This system is formed by the two sutural borders of each elytron, the right elytron (Figs 20-21) has a furrow into which fits a membranous region of the left elytron (Fig 22). Both elytral margins have several rows of tapered spines (Fig 23) that could help to a better joining between both elytra. The relevance of this elytral closure-system is both functional and physiological, we suggest that this system might aid the maintenance of an air bubble during submergence for short period of time as observed by Erwin & Aschero (2004). Although the dense vestiture of the abdomen (Fig 24) seems appropriate to act as a plastron, we could not observed air trapped into it, neither did Erwin & Aschero (2004), therefore the bubble trapped by the elytral closure might aid underwater respiratory function.

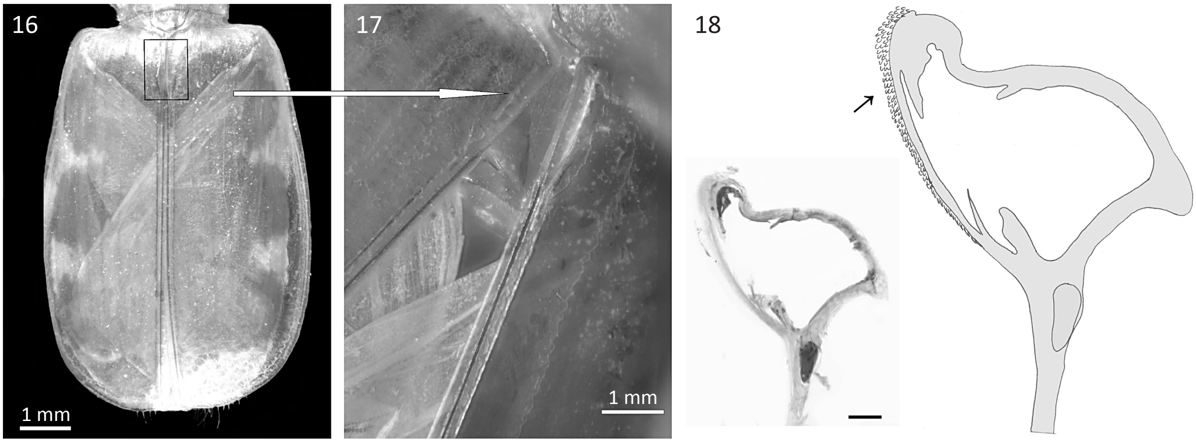
Abdomen. First visible sternite of abdominal sternum with lateral concavity weakly impressed.

Male genitalia. Median lobe (Figs 25-28) short, with broad apical orifice. Parameres similar in shape, with two-four apical setae on the left paramere (Fig 26), and two or three on the right paramere (Fig 27). Internal sac (Figs 29-30). Apical orifice opened dorsally in the central region, a series of grouped spicules is visible in cleared material of internal



Figs 12-15 *Cicindis horni* 12) Procoxal closure; 13) Curved clamp setae; 14) First and second male protarsomeres with pads; 15) Ventose pads.

sac. Figs 29-30 show progressive eversion of internal sac. The internal sac is composed of two groups of non-fused spicules. There is a group of apical spicules (Figs 29-30 *ap*) surrounding the gonopore, and another cluster of spicules forming an incomplete ring (Figs 29-30 *r*) which is basal to the other group. In cleared non-everted internal sac a group of spicules (Fig 30a, *sp*) is visible. These spicules are in a position similar to the X sclerite present in other



Figs 16-18 *Cicindis horni* 16) Elytra, dorsal view; 17) Basal thickness of the elytra. First elytral closure system; 18) Transverse cut of the first elytral closure system. Scale 25x.

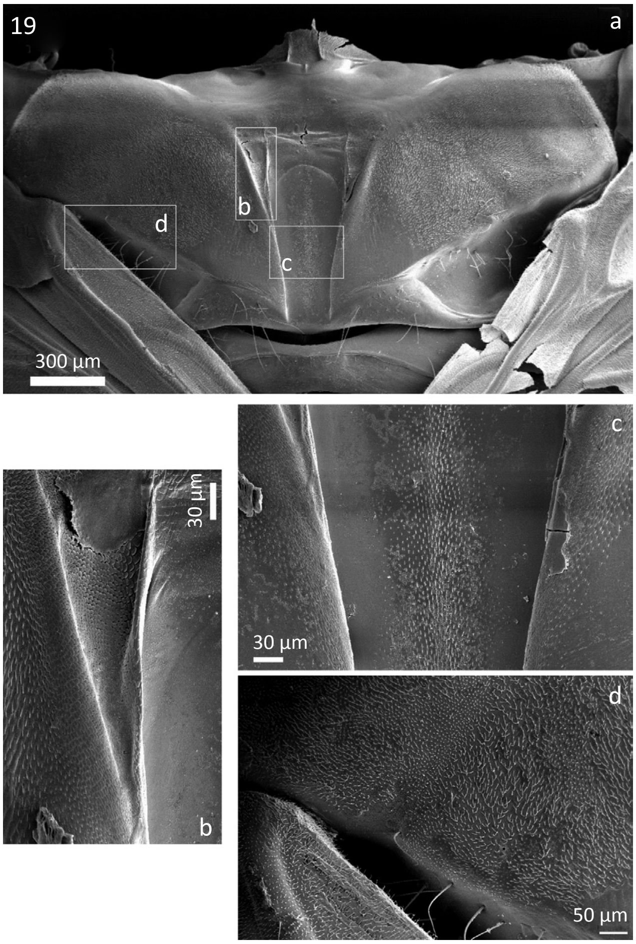
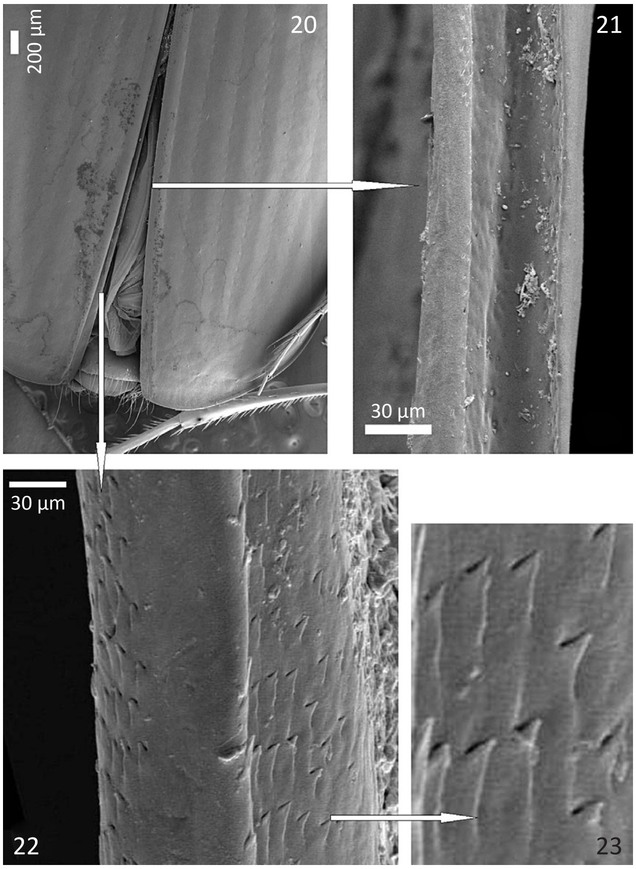


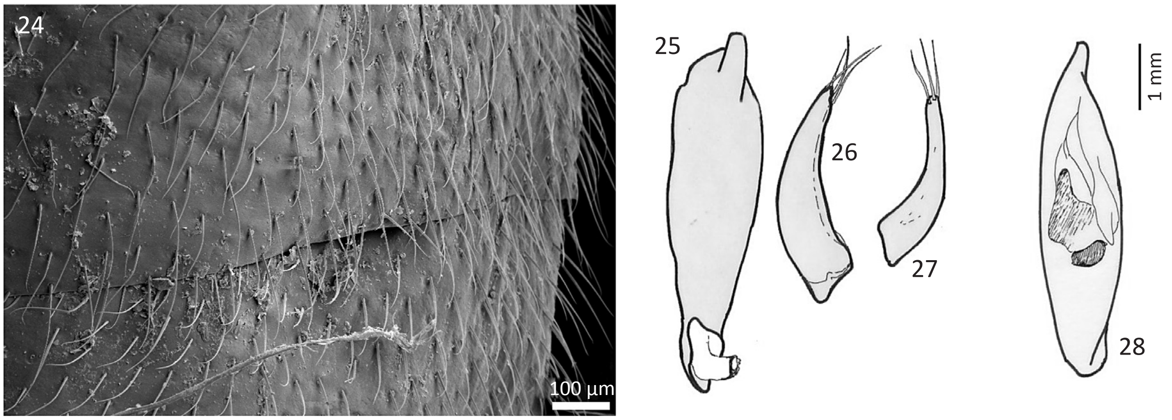
Fig 19 *Cicindis horni* Metanotum: a) Complete metanotum; b) Detail of superior left furrow; c) Detail of middle furrow; d) Surface detail of metanotum and membranous wing.



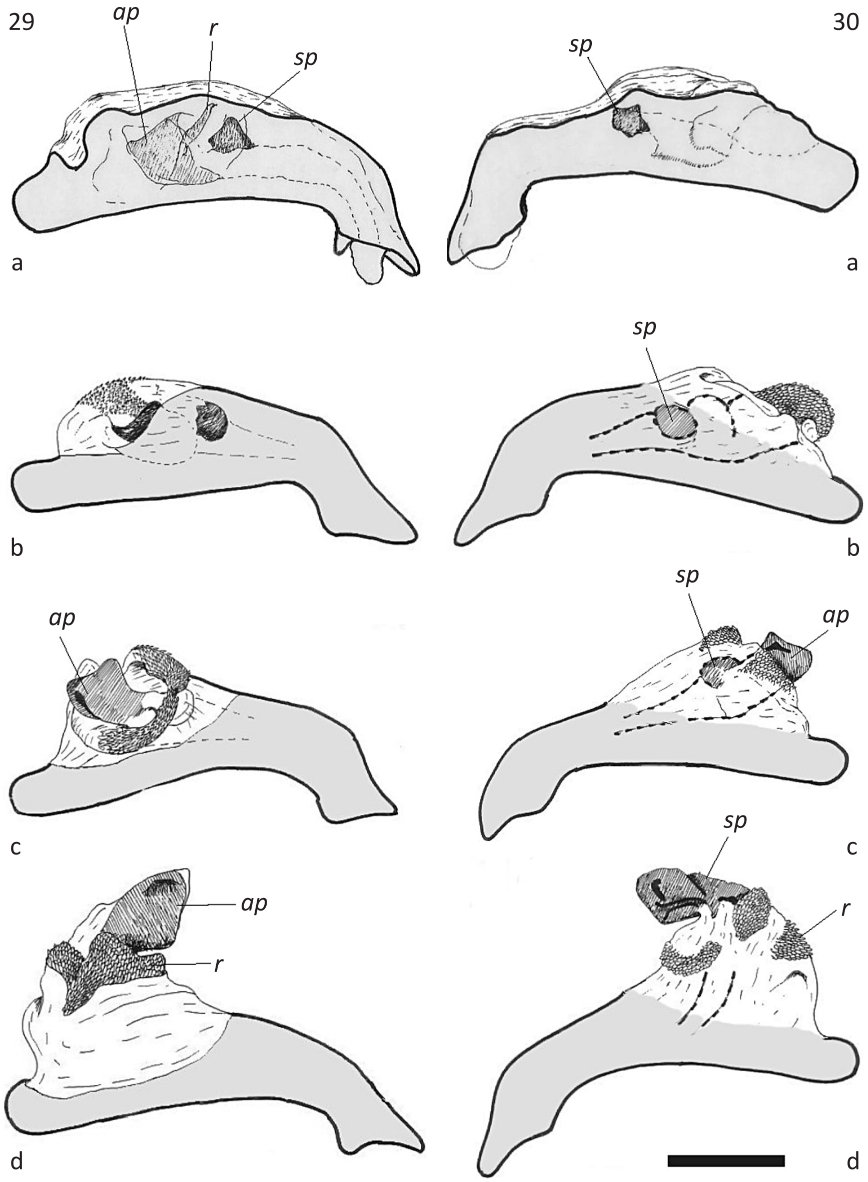
Figs 20-23 *Cicindis horni* 20) Apical region of the elytra, dorsal view; 21) Second elytral closure system: groove on the right elytron 22) Second elytral closure system: membrane on the left elytron; 23) Elytral closure system (spicules).

carabid groups, such as Broscini and Paussinae (Roig-Juñent 1998). However, in the fully everted internal sac, it is easy to see that it is not a sclerotized plate, but a group of free non-fused spicules immersed in a folded region of the membrane, and this is part of the group of apical spicules (*ap*).

Female genitalia. Kavanaugh & Erwin (1991) described the female genitalia with monomerous gonopods, with a sub-apical setiferous organ with one nematiform



Figs 24-28 *Cicindis horni* 24) Abdomen vestiture; 25) Male genitalia, ventral view; 26) Left paramere; 27) Right paramere; 28) Male genitalia, dorsal view.



Figs 29-30 *Cicindis horni*, internal sac eversion at different steps from a. (rest position) to d. (completely everted): 29) right lateral view; 30) left lateral view. *ap* (group of apical spicules), *r* (ring of spicules), *sp* (spicules). Scale 1 mm.

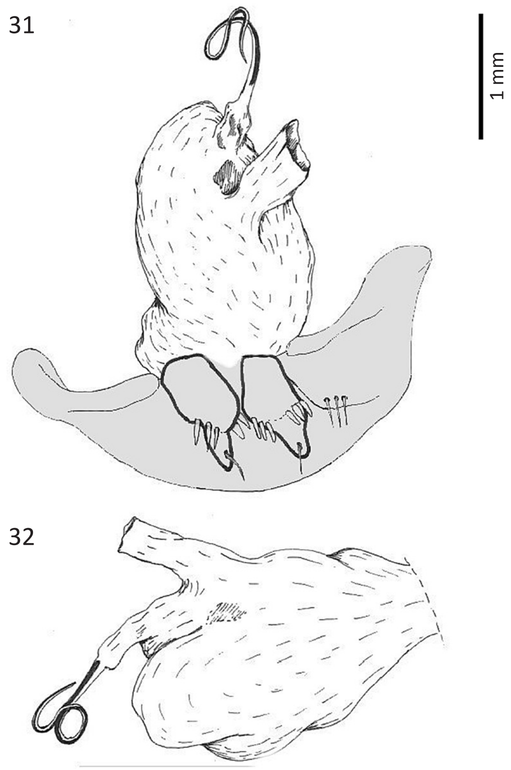
seta. In the present study we report the presence of the helminthoid sclerite, which is present in the spermatheca of several groups of basal carabids (Deuve 1988). The gonopod VIII (ramus coxae in Liebherr & Will 1998) is absent. The latter authors considered this structure as present for *Cicindis* in their data matrix. Another important character is the relative position of the spermatheca, which is ventral with respect to the oviduct (Figs 31-32). Deuve (1988) mentioned that this character is present in Paussinae, constituting an apomorphy of the group.

Material Examined

Holotype. *Cicindis horni* Bruch, female at MACN, Córdoba, Argentina.

Type locality. Bruch (1927) mentioned that the specimen was captured by Ernesto Piotti in light trap. Bruch did not know the type locality; he supposed that this species inhabits the mountain regions near Cordoba city, although Kavanaugh & Erwin (1991) designated Guanaco Muerto as the type locality. We argue that the type locality remains unknown, since specimens from Guanaco Muerto are not the type material.

Other material examined. **Catamarca**: two males and one female, 30 km S of Recreo, intersection of Routes 167 and 60, 3-12-2003, Gómez, Ocampo & Roig-Juñent coll. 29° 30' 29" S 64° 55' 38" W (IADIZA) (one male preserved in 100% ethanol at -20C° at IADIZA) **(New record)**; 20 males and ten females from the same locality, 25/2-5/3-2006, Roig-Juñent, Erwin, Sallenave & Agrain colls. (IADIZA, MLPA) (13 males and eight females in ethanol).



Figs 31-32 *Cicindis horni* 31) Female genitalia; 32) Bursa and spermatheca.

Córdoba: two females from Route 60 km 895.5, 30º 00 S, 64º 30 W, 13-I-2004, Erwin & Aschero colls.; one male from Guanaco Muerto 30° 28' 60 S, 65° 2' 60 W 12/1979, Ronderos coll. (MLPA). One female, San Luis between Agro Candelaria and Mina Los Dos Buhos (31° 59´09" S, 65° 58´00" W), 378 m. 7-IV-2010, Ocampo & Roig-Juñent Coll. (IADIZA) (in ethanol).

Geographical distribution. New specimens were collected from two different provinces. The first is from Catamarca (30 km S of Recreo). This locality is about 100 km away from Guanaco Muerto (previously known locality of *C. horni*), and about 40 km N of the locality cited by Erwin & Aschero (2004). This is the first record for Catamarca province in Argentina. The second new material was collected in San Luis province at night with normal + UV lights, in a locality characterized by dry forest vegetation, in the Espinal Biogeographical Province. This locality is about 59.6 km W from the nearest salt area: Pampa de Las Salinas, more than 200 km S from the southern known locality (Guanaco Muerto) and 138 km from the southern tip of Salinas Grandes. The latter new record could support the idea that this species is distributed in other Salines in Argentina, and future explorations are needed to known if is present in other northern or southern salines areas. Furthermore, the presence of *Cincindis* in dry areas, far from Salines may indicate that this species have a higher dispersion power than previously thought.

Habitat

The information that follows is supplemental to that provided by Erwin & Aschero (2004). The new collected material of *C. horni* was found in the saline habitat of "Jumedales" (*sensu* Ragonesse 1951). Water analyses for the two collection areas are presented in Table 1 and shows a great concentration of salt. This is important because this enigmatic carabid beetle swing and prey in these high concentrate salt water (Erwin & Aschero). This habitat is a halophytic community that covers large areas of salty soils. The two dominant plant species are *Allenrolfea patagonica* (jume), and *Atriplex argentina* (zampa), both succulent Chenopodiaceae, between 0.3 and 0.8 m high, adapted to high salinity soils of Argentinean deserts. These plants grow in clumps forming an open low shrub community. In the place where *C. horni* was found, vegetation cover is about 60%. There were also other shrub-like plants in the area such as *Heterostachys hritteriana* (jumecillo) (Chenopodiaceae), *Grahamia bracteata* (Portulacaceae), and *Prosopis reptans* (retortuño) (Fabaceae), the latter being a species endemic to the Argentinean "Salinas" (Ragonesse 1951). Among herbaceous plants there are *Monantochloe littoralis* (Gramineae) and *Helitdropum johnstonii* (Boraginaceae). The area where the specimens of *C. horni* were collected forms part of "Salinas Grandes", one of the areas studied by Ragonesse (1951, p. 46).

The climate in the area is characterized as continental, semiarid, and mesothermal, with dry winters and extreme temperatures. Average annual humidity is 58% and annual precipitation in localities close to the area is between 305 mm and 491 mm, usually occurring between November and March. The pool where *Cicindis* was collected has about 6% salt concentration. Some specimens were collected swimming on the water. It is interesting to note that when some collected specimens were placed in fresh water, they sank, losing their ability to float.

Cladistic Analyses

For the equally weighted analysis the program analyzed a total of 7,614,223 rearrangements, and the best score hit 87 times out of 100. Four optimal trees of 176 steps were obtained. The strict consensus tree is shown in Fig 33. The cladogram shows *C. horni* as related to Scaritinae, Paussinae, and Carabidae Conjuncta. Paussinae and Carabidae Conjuncta are monophyletic groups, but not Scaritinae, where Migadopini (*Migadops* Waterhouse and *Antarctonomus* Chaudoir) and Loricerini (*Loricera* Latreille) constitute a polytomy, and Elaphrini (*Elaphrus* Fabricius) is more closely related to Carabidae Conjuncta

Table 1 Water chemical analyses results for each studied site.

Variables / ions	Córdoba		Catamarca	
	Meq/l	Ppm	Meq/l	Ppm
Ca^{++}	80.00	1600.00	64.00	1280.00
Mg^{++}	20.00	243.00	16.00	194.40
Na^{+}	4000.00	92000.00	750.00	17250.00
K^{+}	10.53	411.72	2.46	96.19
$CO_3^{=}$	0.00	0.00	0.00	0.00
HCO_3^{++}	1.60	97.60	2.00	122.00
Cl^{-}	4260.00	151017.00	760.00	269.42
$SO_4^{=}$	120.00	5760.00	160.00	7680.00
NO_3^{-}	Negative	Negative	Negative	Negative
B	Negative	Negative	Negative	Negative
Conductivity: microsiemens/cm at 25ºC)	208000		66400	
pH	7.49		7.14	
Dry residuum (ppm)	277340		56648	
Sodium adsorption ratio (SAR)	565.00		118.67	
Total ions (Mg/l)	252720.32		26649.52	

Percentage between electric conductivity and salt residuum equal to 22% of total saline material for Cordoba site, and 6.15% for Catamarca site (expressed as NaCl).

than the other Scaritinae. Paussinae is the first group splitting from this clade, the second is *Cicindis*, and finally Scaritinae + Carabidae Conjuncta. This consensus tree is highly congruent with the general classification of Carabidae proposed by Erwin & Sims (1984), except for the position of *Cicindis*. Erwin & Sims (1984) placed *Cicindis* within the Carabinae, a group that after this analysis turned out to be polyphyletic. Carabidae Conjuncta constitutes a monophyletic group (Fig 33), which is congruent with the divisions Melaeniforms plus Psydriforms presented by Erwin & Sims (1984). The conjuncta condition (character 22^1) was parallelly acquired by *Notiophilus* Dumeril. The analysis shows that the group defined by Jeannel (1941) as Stylifera is currently separated into two subfamilies, Broscinae and Psydrinae (Roig-Juñent & Cicchino 2001), and is paraphyletic in this analysis. Support values to the different clades are relatively low. For this reason a second analysis using implied weighting to reduce homoplasy was performed.

Analyses using implied weighting method resulted in all cases (tested K values = 1 to 6) in only one tree. There were no differences in the proposed phylogenetic relationships of *Cicindis* between the cladograms obtained with K = 2 to K = 6, but the topology is different for the phylogenetic relationships of the remaining Carabinae when K = 1 is applied (Fig 34). With K = 1, Carabinae constitute a paraphyletic group, where Nebriini (*Nebria* Latreille and *Leistus* Frölich) is the basal group of Carabidae, and of the following sequence: Notiophilini, Opisthiini, Carabini + Ceroglossini + Cychrini, and Cicindelini + Megacephalini. Omophronini is more closely related to Scaritinae + Carabidae Conjuncta. With K = 3 (Fig 35) or higher, Opisthiini is the basal clade of Carabidae, followed by Nebriini, and the remaining Carabinae (except *Cicindis* and *Omophron*) constitute a monophyletic group.

In the analysis under equal weigth, *Cicindis* + Scaritinae + Paussinae + Carabidae Conjuncta constitute a monophyletic group. In the analyses using implied weighting method this clade is also recovered, but including the tribe Omophronini. This clade is separated from the rest of the Carabinae, and is supported by synapomorphies 0^1, 10^1, and 30^{12}. Support values are still very low (Fig 35). Anyhow the relationships inside the generated clades are the same and the support values for this alternative topology are also very low (5). In all cases *Cicindis* constitutes a monophyletic group with the Paussinae, supported by two exclusive characters, the particular condition of the procoxal closure (19^2) and the position of the oviduct with respect to the spermatheca (49^1).

Discussion

The study of a longer series of *Cicindis* specimens yields

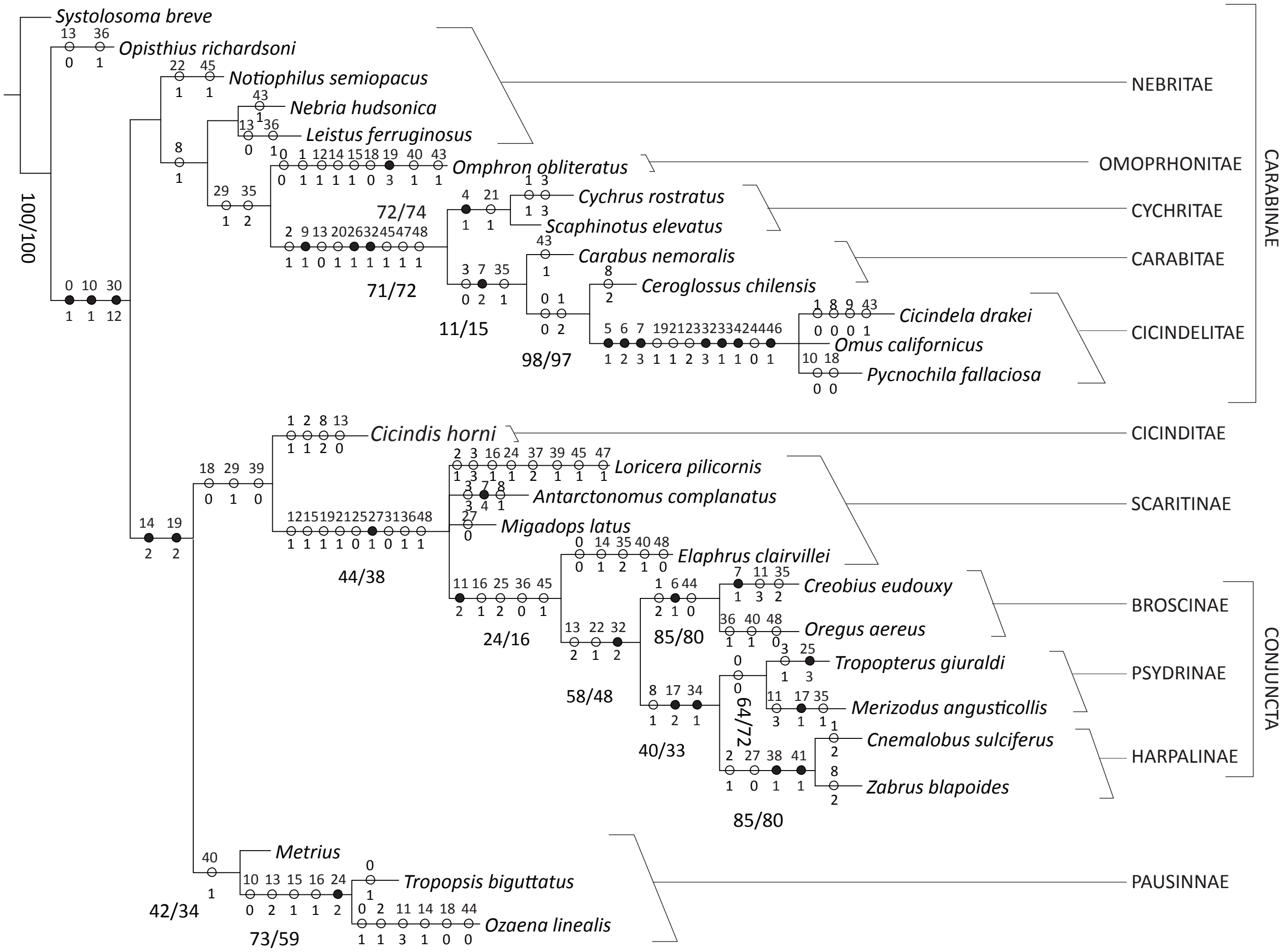


Fig 33 Strict consensus tree of four trees. Analysis under equal weights. With Jackknife (left) and Bootstrap (right) of tree resulting from equally weighted analysis (relative values).

new characters such as those of male and female genitalia and the closure of the elytra, and also the recognition of color variation previously unknown.

Results of the cladistic analyses, based on adult morphological characters, show differences from the current classification and from recent proposals on the relationships of *Cicindis*. Based on the phylogeny obtained, *Cicindis* should be regarded as a member of, or as related to, the subfamily Paussinae instead of Carabinae as suggested by Kavanaugh & Erwin (1991). Kavanaugh (1998) pointed out that the inclusion of *Cicindis* and *Archaeocindis* in the clade that contains Carabinae is supported by 11 synapomorphies. But he did not list the 153 characters used in his analysis, so it is not possible for us to compare his characters with the characters used herein.

As mentioned previously Liebherr & Will (1998) considered Cicindini in a middle grade group of Carabidae together with Migadopini, Amblytelina and a monophyletic group of tribes (Siagonini, Cychrini, Pamborini, Carabini and Cicindelini). These latter authors only used characters from female genitalia, highlighting the importance of the gonocoxal rami in Cicindini as to include it in this group of Carabidae. Nevertheless, after the dissection of several females we did not found the gonocoxal rami in the female track.

Relationships between *Cicindis* and Paussinae (*Metrius*, *Ozaena* and *Tropopsis* in our analysis) were also previously proposed by Bänninger (1925) and followed by several other authors (Bruch 1927, Kryzhanovsky 1976, Reichardt 1977). Bänninger (1925) considered *Cicindis* to be related to Metriini because of its particular protibial structure (mainly the antenna cleaning organ) and procoxal closure. The presence of curved clamp setae in the cleaning organ (14^2) supports the group that includes *Cicindis* + Paussinae + Scaritinae + Carabidae (Conjuncta). Additional characters shared with other members of the clade are: spurs equal in size, both apical (11^0), the disjunct condition of the mesocoxae (22^0), the left paramere with few setae (37^1), and the right paramere setose (39^0) and plesiomorphic, and thus not useful for grouping *Cicindis* with other carabids. The

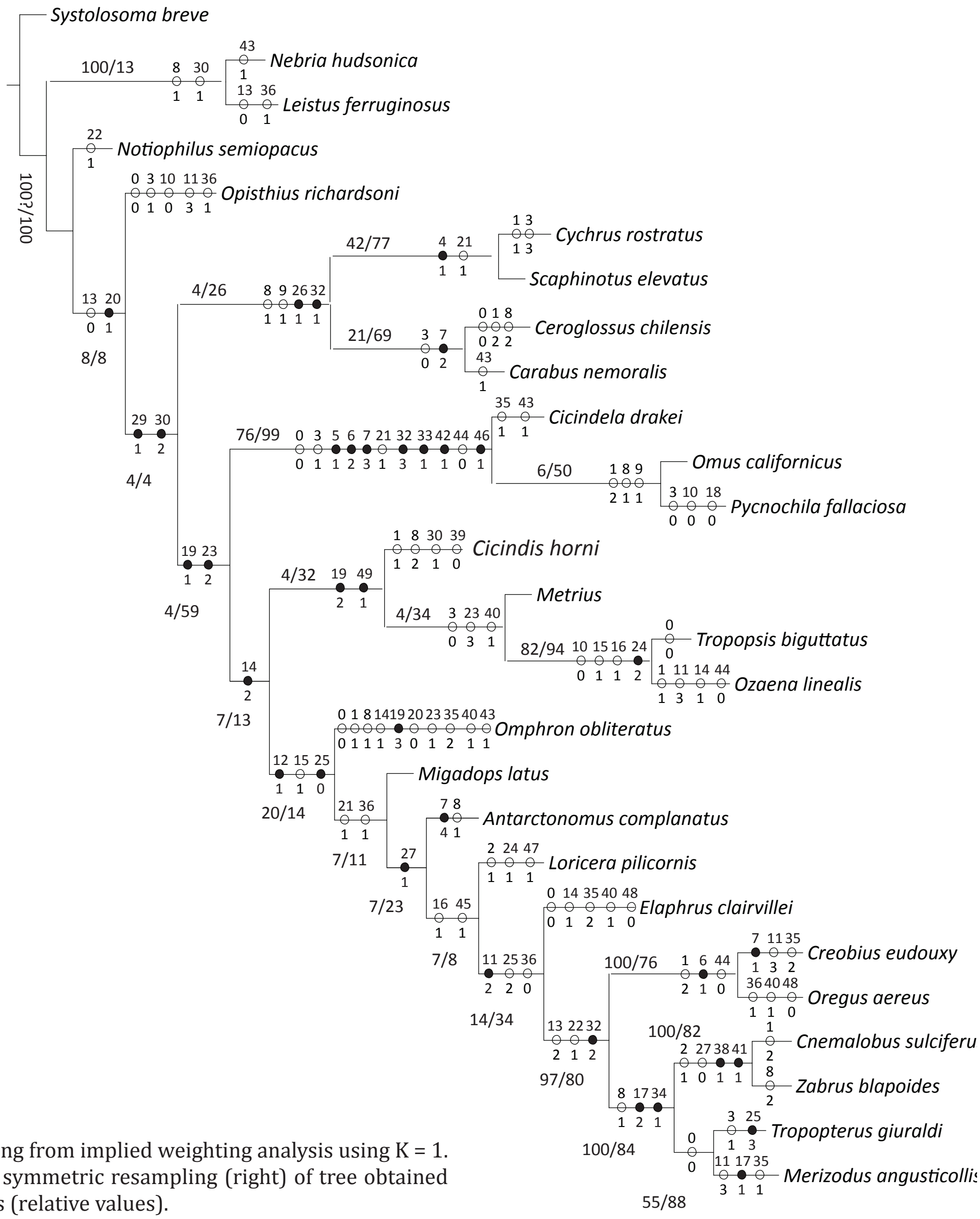


Fig 34 Tree resulting from implied weighting analysis using K = 1. Bremer (left) and symmetric resampling (right) of tree obtained with K = 1 analysis (relative values).

only two apomorphies which are exclusive characters of Paussinae and *Cicindis*, and support this relationship under K = 1, are the particular condition of the procoxal closure (19^2) and the position of the oviduct with respect to the spermatheca (49^1). Confidence in the phylogenetic value of these two characters is provided by Nichols (1985), who made an analysis of the different kinds of coxal closure, and pointed out that the proepimeron overlapping the prosternum is exclusive to Paussinae, and by Deuve (1988), who described the female genital tract of almost all Carabidae and noticed that only in Paussinae is the oviduct dorsal with respect to the spermatheca (49^1). Our finding that *Cicindis* has the same character condition as described for the Paussinae is worth knowing.

A further difference from the classification by Erwin & Sims (1984) is that the subfamily Carabinae does not constitute a monophyletic group in our cladograms where Omophronini (*Omophron* Latreille) is more closely related to Carabidae Conjuncta, and Opisthiini (*Opisthius* Kirby) and Nebriini could be considered to be the adelphotaxon of all Carabidae. The only group of Carabinae recovered as natural by our analysis consists of the supertribes Cychritae and Cicindelitae.

Scaritinae do not constitute a natural group in our analysis. Kavanaugh (1998), in his analysis of basal groups of Carabidae, also found Scaritinae as non-monophyletic, with *Blethisia* (Elaphrini, Scaritinae) being the sister group of *Loricera* (Loricerini, Scaritinae) + *Calathus* Bonelli (Platynini, Harpalinae). Nevertheless,

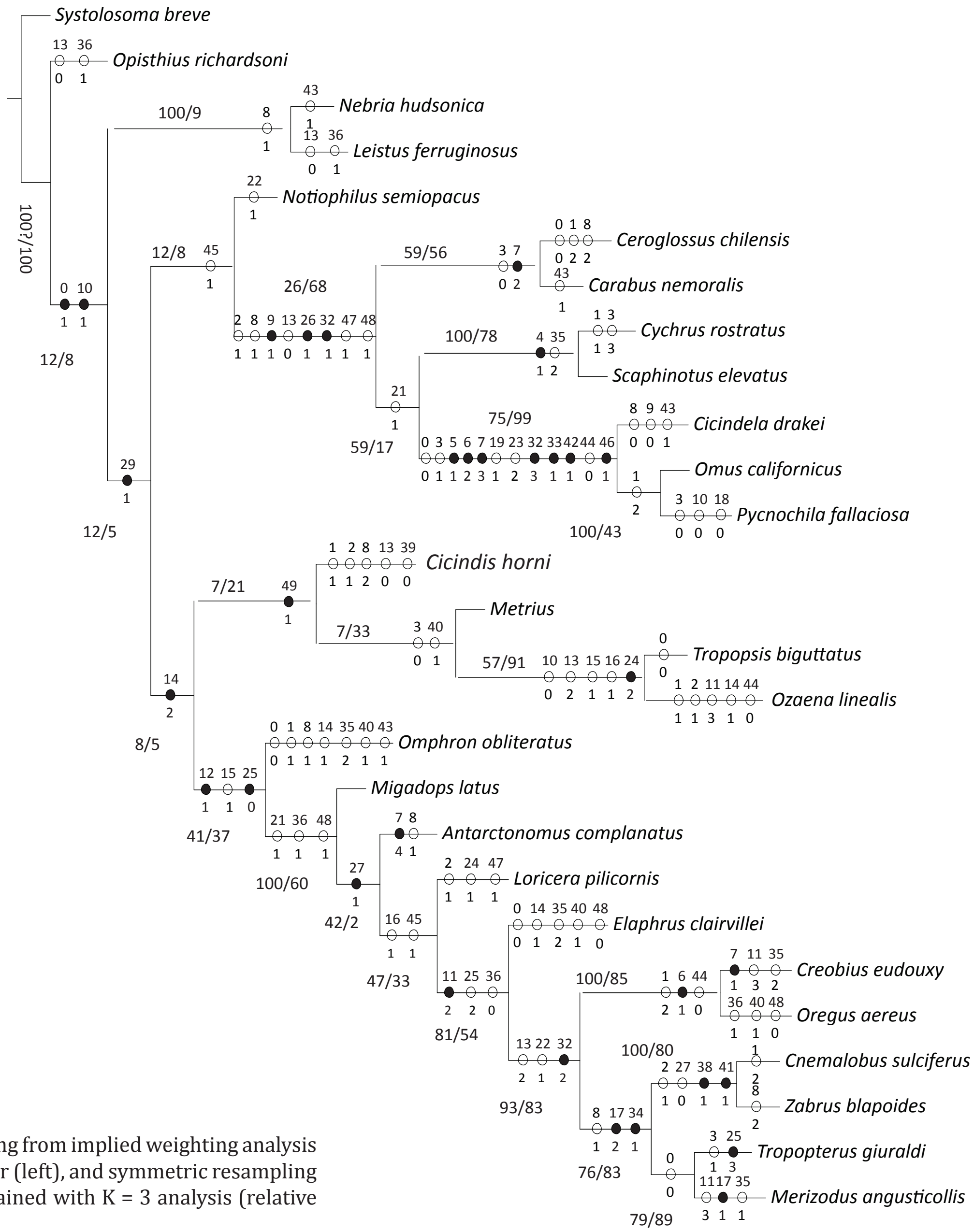


Fig 35 Tree resulting from implied weighting analysis using K = 3. Bremer (left), and symmetric resampling (right) of tree obtained with K = 3 analysis (relative values).

there is a significant difference between Kavanaugh's 1998 analysis and ours. In the former, Scaritinae + Carabidae (Conjuncta) is the sister group of Carabinae (including *Cicindis*) and in the present analysis this group is more closely related to Omophronini + Paussinae + *Cicindis*.

In summary, although weakly supported, the obtained topologies show important differences from previous classifications, since in our study *Cicindis* always forms a monophyletic group with the Paussinae. Additional, independent sets of data, such as molecular or larval characters, will help us to get a better knowledge of the evolutionary history of *Cicindis*.

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