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Cladistic Analysis of *Barypus* Dejean 1828 (Coleoptera: Carabidae: Broscini)

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ABSTRACT

Barypus comprises 22 species that occur in southern South America. This genus is a monophyletic group defined by synapomorphies of external features and male and female genitalia. A cladistic analysis based on 41 characters of external morphology and male and female genitalia, with the genus *Diglymma* Sharp as outgroup, yielded three most parsimonious cladograms, each with length of 80 steps. The strict consensus tree calculated from these cladograms has the same length and was chosen to represent the reconstructed phylogeny of the species. The consensus shows three monophyletic groups: the subgenera

Barypus, *Cardiophthalmus* Curtis, and *Arathymus* Guérin-Ménéville. Information on body size and geographical distribution was used along with the consensus tree to analyze evolutionary patterns and vicariant events. The species of *Barypus* show a positive correlation between body size and cladogram position, in relation to xeric habitat conditions. *Barypus* might have originated in western Gondwanaland during Cretaceous times and the differentiation of the three subgenera could be related to the formation of epicontinental seas in the Lower Tertiary.

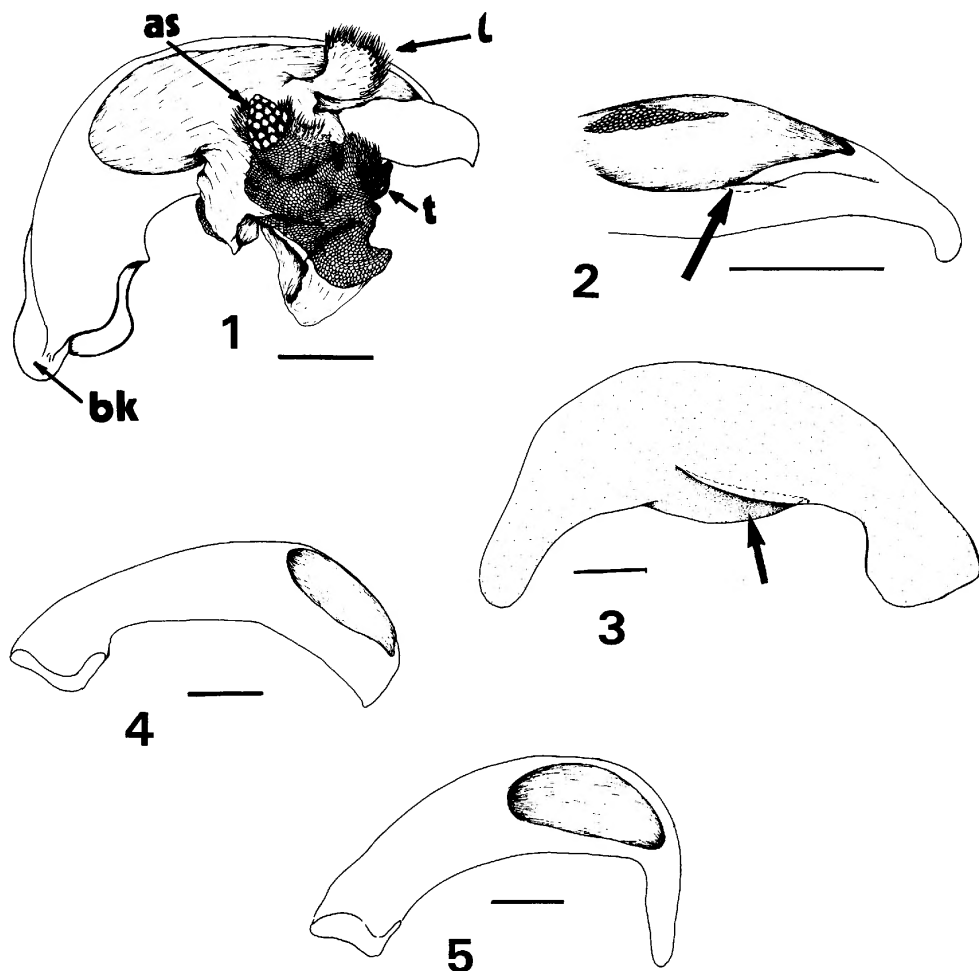
INTRODUCTION

Barypus Dejean, 1828, belongs to the tribe Broscini, subtribe Barypina, and comprises 22 species arranged in three subgenera (Putzeys, 1868): *Barypus* (s.s.) with 6 species; *Cardiophthalmus* Curtis, 1839, with 14 species; and *Arathymus* Guérin-Ménéville, 1841, with

2. The taxonomy of the species has been elucidated recently by Roig-Juñent and Cicchino (1989) and Roig-Juñent (1992a, b).

The tribe Broscini includes 31 genera, arrayed in three subtribes: the amphipolar Broscina, the wide-ranging austral Creobiina,

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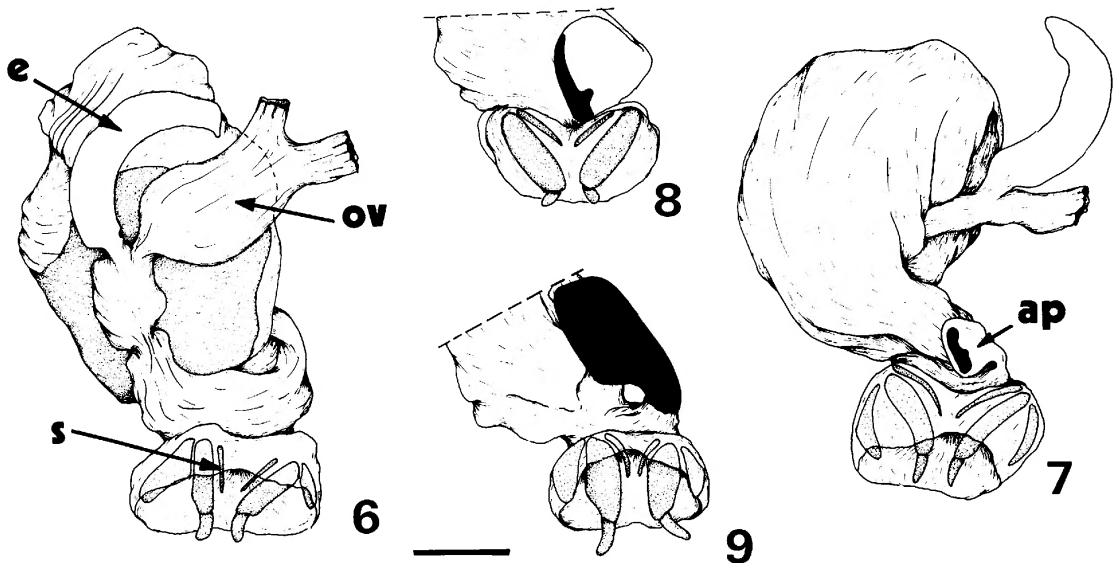


Figs. 1–5. Median lobe of male genitalia: as = alpha sclerite, bk = basal keel, l = ligula; t = tooth of internal sac. 1, Left lateral aspect of *B. speciosus* showing the internal sac. 2, Left lateral aspect of *B. deplanatus* showing the ventral doubling of ostium. 3, Right lateral aspect of *B. gentilii* showing the ventral doubling. 4, 5, Left lateral aspect of *B. neuquensis* and *B. gaii* showing the ostium.

and the southern South American Barypina (Ball, 1956). Jeannel (1941) established Barypina as the subfamily Barypitae, which included *Barypus* and various austral genera of the family Broscidae; he placed northern genera in the subfamily Broscitae. (Jeannel ranked most carabid tribes as families and elevated less inclusive groups accordingly.) Ball (1956), using principally genitalic features, reclassified the broscine genera into the subtribes noted above. The Barypina, as redefined, contains only the single genus *Barypus*; the other genera considered by Jeannel are moved to a natural group of the subtribe Broscina. Although Ball postulated that each

of these subtribes was monophyletic, he did not analyze their relationships. Roig-Juñent (1992b) concluded that the Barypina might be the closest relative of the austral Broscina, because both groups share most of the features used by Ball to justify monophyly of the latter group.

The geographical relationships of austral Broscini have been discussed by Jeannel (1942, 1967), Britton (1949), and Ball (1956), who postulated that this tribe arose in the Paleantarctic continent, during Cretaceous time. Darlington (1965), to the contrary, proposed that this tribe arose in the Holarctic region and reached the southern regions in-



Figs. 6–9. Genitalic female tract, ventral aspect: ap = pocket of apex; e = spermatheca; ov = median oviduct; s = gonopod VIII. 6, *B. gentilii* showing the basal joining of median oviduct. 7–9, Variations of size and sclerotization of pocket of apex: 7, *B. minus*; 8, *B. chubutensis*; 9, *B. gii*.

TABLE 1
Checklist of *Barypus*

Taxa	Distribution
<i>Barypus</i> (<i>Arathymus</i>)	
<i>B. bonvouloiri</i> (Chaudoir, 1861)	Central and southern Chile
<i>B. parallelus</i> (Guérin-Ménéville, 1838)	Central and southern Chile
<i>Barypus</i> (<i>Barypus</i>)	
<i>B. aequicostis</i> (Chaudoir, 1876)	Uruguay
<i>B. calchaquensis</i> Roig-J., 1992b	Northwestern Argentina
<i>B. comechingonensis</i> Roig-J., 1992b	Central Argentina
<i>B. pulchellus</i> Burmeister, 1868	East central Argentina
<i>B. rivalis</i> (Germar, 1824)	East central Argentina and Uruguay
<i>B. speciosus</i> Dejean, 1831	Uruguay
<i>Barypus</i> (<i>Cardiophthalmus</i>)	
<i>B. chubutensis</i> Roig-J., 1992a	Western Patagonia
<i>B. clivinooides</i> (Curtis, 1839)	Patagonia
<i>B. dentipenis</i> Roig-J., 1992a	Western Patagonia
<i>B. deplanatus</i> Roig-J. and Cicchino, 1989	Southern Patagonia
<i>B. flaccus</i> Roig-J. and Cicchino, 1989	Central Patagonia
<i>B. gentilii</i> Roig-J., 1992a	Northwestern Patagonia
<i>B. gii</i> Roig-J., 1992a	Northwestern Patagonia
<i>B. longitarsis</i> (Waterhouse, 1841)	Southern Patagonia
<i>B. mendozensis</i> Roig-J. and Cicchino, 1989	West central Argentina
<i>B. minus</i> Roig-J., 1992a	Western Patagonia
<i>B. neuquensis</i> Roig-J., 1992a	Northwestern Patagonia
<i>B. painensis</i> Roig-J. and Cicchino, 1989	Southern Patagonia
<i>B. schajovskoi</i> Roig-J., 1992a	Northwestern Patagonia
<i>B. sulcatipenis</i> Roig-J., 1992a	Northwestern Patagonia

TABLE 2
Characters and Character States Used in the Cladistic Analysis of *Barypus*
 (plesiomorphic state = 0; apomorphic states = 1-5)

Character	Character states
1 Coloration	Nonmetallic (0); metallic (1)
2 Setae of submentum	Four (0); two (1)
3 Tooth of mentum	Apex shallowly emarginate (0); emargination deep, lateral projections curved (1)
4 Maxillary palpomeres	Slender (0); broad (1)
5 Antennomeres 4-10	1 × longer than broad (0); 2 × longer than broad (1); 3 × longer than broad (2)
6 Row of setae of antennomeres 2-11	Absent (0); present (1)
7 Frontal grooves	Absent (0); shallow (1); deep, thin (2); deep, broad (3)
8 Eyes	Rounded (0); with emargination in front of antennal insertion (1)
9 Prosternal setae	Absent (0); present (1)
10 Elytral epipleura	Slender (0); broad (1)
11 Setae of elytral intervals 3, 5, 7	Absent (0); present (1)
12 Setae of 9th elytral interval	Five to 15 (0); 20-51 (1)
13 Metepimeron	Transverse and slender (0); transverse and broad (1); subquadrangular (2)
14 Setae of protrochanter	One (0); two (1)
15 Protibiae	Not prolonged externally to a point at apex (0); prolonged externally (1)
16 First protarsomere of male	Expanded on inner side (0); not expanded (1); quadrangular (2)
17 Patch of hairs of protarsomeres	Apical (0); absent (1); over entire ventral surface (2)
18 Protarsomeres of female	Not expanded on inner side (0); expanded on inner side (1)
19 Meso- and metatarsomeres	Broad (0); slender (1)
20 Row of setae in mesocoxa	Absent (0); present (1)
21 Lateral row of setae of mesotibia	Absent (0); present (1)
22 Anal setae	Separated centrally (0); not separated (1)
23 Anal setae	Only on median half of

TABLE 2—(Continued)

Character	Character states
24 Apical groove of abdominal sterna	apical margin (0); in all entire margin (1) Absent (0); present (1)
25 Basal keel of median lobe	Absent (0); present (1)
26 Dorsal surface of median lobe	Partly sclerotized (0); completely sclerotized (1)
27 Lateral apical groove of median lobe	Absent (0); short (1); long and straight (2); long and curved (3)
28 Lateral grooves of median lobe	Absent (0); present, curved (1)
29 Ventral groove of median lobe	Absent (0); slender (1); broad (2)
30 Ventral doubling of median lobe (fig. 3)	Absent (0); present (1)
31 Ventral doubling of ostium (fig. 2)	Absent (0); present (1)
32 Ostium	Long and broad, dorsolateral (0); broad, left lateral (1) (fig. 1); small, dorsoapical (2) (fig. 4); small, left lateral (3) (fig. 5)
33 Tooth of internal sac	Absent (0); conical, broad (1); spatulate (2); conical, slender (3); short (4); conical, very long (5)
34 Sclerite alpha	Absent (0); with spicules separated (fig. 1) (1); with spicules fused (1)
35 Sclerites X and Y	Present (0); absent (1)
36 Internal sac eversion	From right side (0); from dorsum (1); from left (2)
37 Median oviduct union on bursa copulatrix	Apical (fig. 7) (0); basal (1) (fig. 6)
38 Spermathecal union on bursa copulatrix	Sessile (0); with median oviduct (figs. 6, 7) (1)
39 Accessory gland of bursa copulatrix	Present (0); absent (1)
40 Pocket of apex of bursa copulatrix	Absent (0) (fig. 6); small, with a little portion sclerotized (fig. 7) (1); small with a long sector sclerotized (fig. 8) (2); long, completely sclerotized (fig. 9) (3)
41 Gonopod VIII	Long and slender (0); short (1); long and broad (2)

TABLE 3
Taxon Character Matrix of Species in the Genus *Barypus*
(plesiomorphic states = 0; apomorphic states = 1–5; missing data = ?)

Species	Characters															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Diglymma</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>B. parallelus</i>	0	1	1	0	1	1	0	1	0	1	0	1	0	0	0	0
<i>B. bonvouloiri</i>	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	0
<i>B. rivalis</i>	1	0	1	0	1	1	0	1	0	0	0	1	1	1	0	1
<i>B. pulchellus</i>	1	0	1	0	1	1	1	1	1	0	0	1	1	1	0	0
<i>B. speciosus</i>	1	0	1	0	1	1	1	1	0	0	0	1	1	1	0	0
<i>B. aequicostis</i>	1	0	1	0	1	1	1	1	0	0	0	1	1	1	0	0
<i>B. comechingonensis</i>	1	0	1	0	1	1	1	1	0	0	0	1	1	1	0	0
<i>B. calchaquensis</i>	1	0	1	0	1	1	1	1	0	0	0	1	1	1	0	0
<i>B. longitarsis</i>	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0
<i>B. schajovskoi</i>	0	1	1	0	1	1	0	1	1	1	1	1	1	1	0	0
<i>B. gentilii</i>	0	1	1	0	1	1	0	1	1	1	1	1	1	1	0	0
<i>B. mendozensis</i>	0	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0
<i>B. flaccus</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0
<i>B. painensis</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0
<i>B. deplanatus</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0
<i>B. sulcatipenis</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0
<i>B. neuquensis</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0
<i>B. giaini</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0
<i>B. dentipenis</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0
<i>B. chubutensis</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0
<i>B. minus</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0
<i>B. clivinoides</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0

dependently via the Northern Hemisphere. Ball (1956) proposed that *Barypus* spread in Mesozoic time from an ancestral stock on an Antarctic continent, reaching southern South America following a southern route.

The geographical range of *Barypus* extends south of latitude 25°S in Chile, Argentina, and Uruguay. The species inhabit the Patagonian steppes, the Pampas of Uruguay and Argentina, the grasslands of the Sierras de Córdoba, San Luis, and Salta in Argentina, and the chaparral regions of central Chile.

The purpose of this paper is to develop a hypothesis of relationships of the species of *Barypus* by cladistic analysis, using external morphological characters and female and male genitalia. Cladograms obtained independently from theories about processes offer a basis to check the theories of body size presented by Liebherr (1988, 1989). Data about geographical distribution are used in conjunction with the results of the cladistic

analysis to investigate vicariant events in *Barypus*.

MATERIALS AND METHODS

Barypus is a monophyletic group of species separated from other genera of Broscini by the following synapomorphies (Roig-Juñent, 1992b):

1. Male with basal keel of median lobe present (fig. 1).
2. Median oviduct and spermatheca join together in a common duct before entering the bursa copulatrix (figs. 6, 7).
3. Bursa copulatrix lacks an accessory gland.

The chosen outgroup, within the New Zealand and Australian Broscina, is the genus *Diglymma* Sharp, 1886, considered by Ball (1956) as the most primitive genus within the austral Broscina.

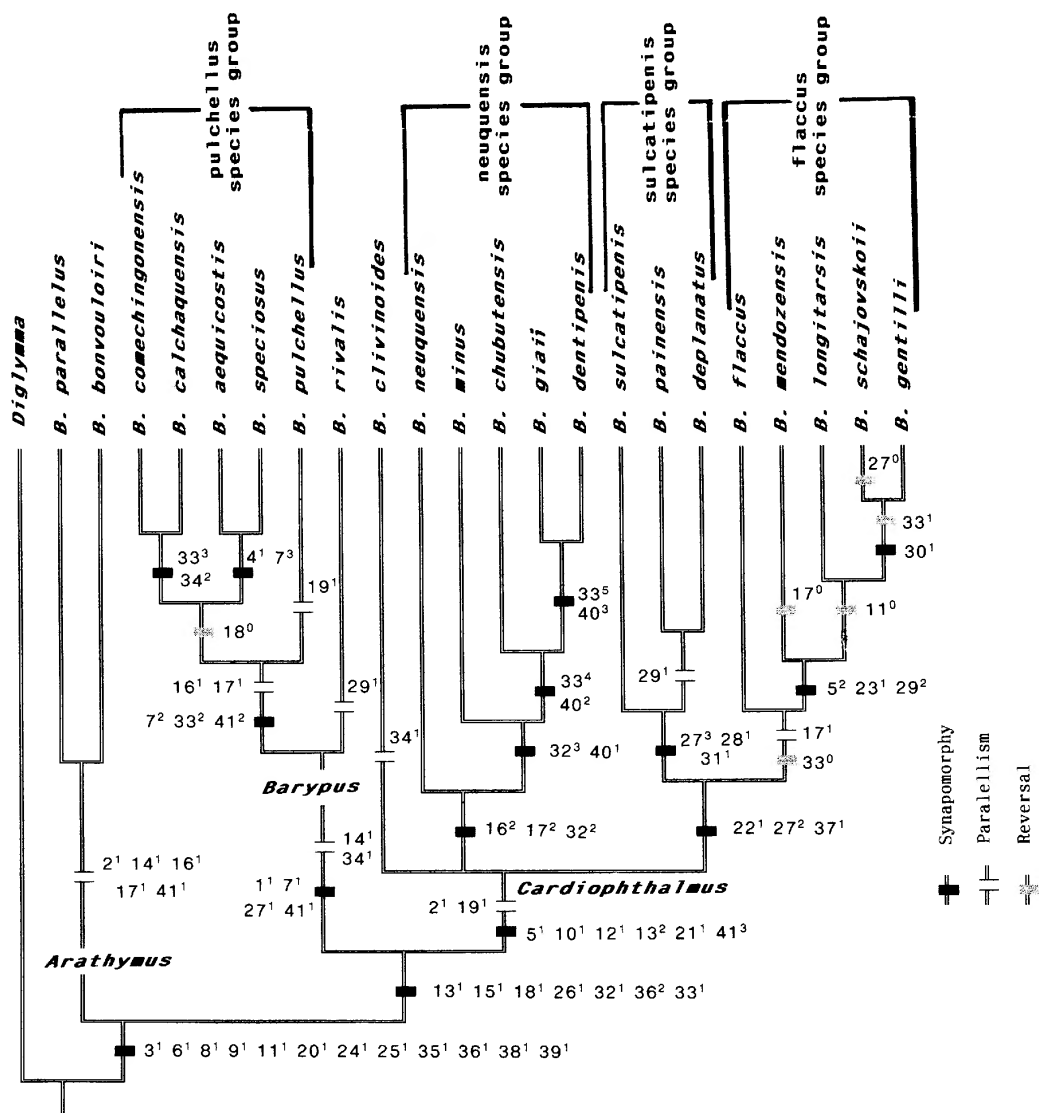


Fig. 10. Cladogram showing relationships of the species of *Barypus* with *Diglymma* as outgroup.

The species of *Barypus* (table 1) and the genus *Diglymma* are considered terminal taxa.

The 41 characters used are derived from the external morphology (24), the aedeagus (12), and the female genitalia (5). These characters, with their postulated plesiomorphic and apomorphic states, are listed in table 2. The distribution of states among the terminal taxa is indicated in the data matrix (table 3).

Character polarity was determined by the outgroup comparison method (Watrous and Wheeler, 1981; Maddison et al., 1984). Char-

acter 40 (size of pocket of apex) is ordered in a logical sequence (figs. 7–9). The pocket of the apex increases in size and in the degree of sclerotization in the following sequence: *B. minus*, *B. chubutensis*, *B. gii*, and finally *B. dentipenis*. For characters 16, 32, 33, and 41 where it was not possible to make a correlation between apomorphic states, each state was considered independently from the others, i.e., they were nonadditive.

The data set was analyzed using the Farris phylogenetic package Hennig86 version 1.5 (Farris, 1988), applying the implicit enumer-

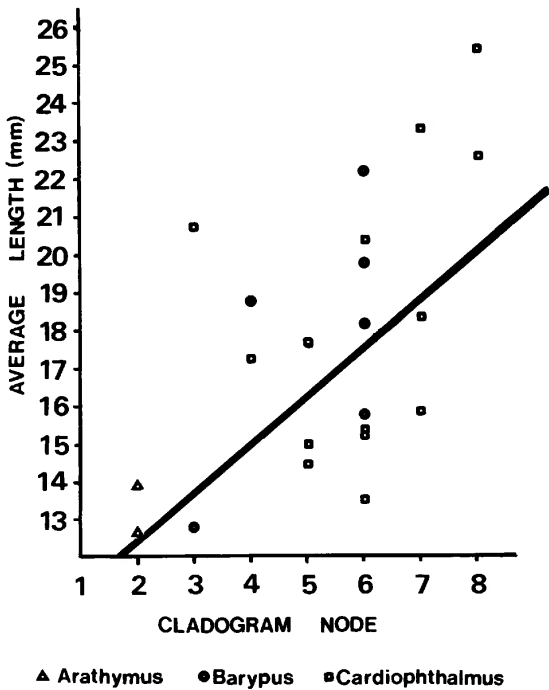


Fig. 11. Regression analysis of average body length (in mm) observed in species on cladogram node for 22 species of *Barypus*. Length = 11.20 + 1.22 (node), $r = 0.588$.

ation option and the successive weighting procedure.

Length was the parameter used for study of the evolution of body size. The measurements were taken from the clypeus to the apex of the elytra, and means were taken for the series of specimens of each species (table 4). The number node of each species on the cladogram was determined by counting the number of nodes that separated the species from the root (Liebherr, 1988, 1989). The node where the outgroup joins the ingroup is considered node zero.

CLADISTIC ANALYSIS

Three most parsimonious cladograms of 80 steps and consistency index of 0.76 were obtained. The consistency index was 0.73 and the retention index 0.90, ignoring synapomorphies of the whole genus (characters 3, 6, 8, 9, 20, 24, 25, 35, 38, and 39). The successive weighting procedure did not discriminate among the three trees. The strict consensus tree (fig. 10), which had the same length

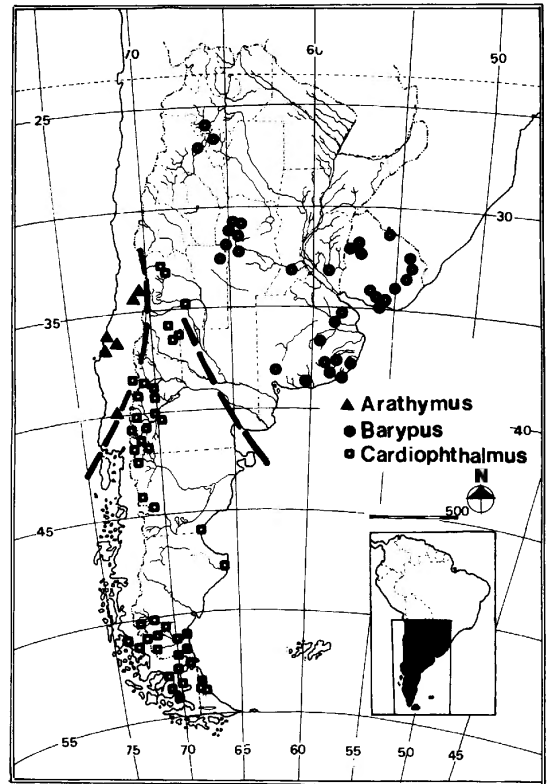


Fig. 12. Distribution of the three subgenera of *Barypus*.

as the original three trees, was chosen. The reason for this choice is that the implicit enumeration option of Hennig86 regards trees as distinct if there is any possible character interpretation that will distinguish them (Bruce et al., 1990). If the strict tree is not longer than the several trees from this option, then the extra branches, although possibly supported, are not necessary to account for the characters (Bruce et al., 1990).

PHYLOGENY OF *BARYPUS*

Barypus is a monophyletic group of species supported by ten synapomorphies. Six are from external morphology: tooth of mentum with lateral expansions (character 3); row of setae on the antennomeres (6); eyes emarginate (8); prosternum with apical setae (9); row of metacoxal setae (20); apical groove of the abdominal sterna (24). Two are of male genitalia: basal keel present (25), and loss of sclerites x and y (35). Two are from female

TABLE 4

Species	Node	Body size (length in mm)	
		Range	Mean
<i>B. parallelus</i>	2	12.0–13.30	12.65
<i>B. bonvouloiri</i>	3	13.60–14.20	13.90
<i>B. rivalis</i>	3	11.90–13.57	12.75
<i>B. pulchellus</i>	4	17.49–20.05	18.77
<i>B. speciosus</i>	6	21.71–22.91	22.31
<i>B. aequicostis</i>	6		19.89
<i>B. comechingonensis</i>	6	16.74–19.45	18.10
<i>B. calchaquensis</i>	6	14.62–16.87	15.72
<i>B. longitarsis</i>	7	22.19–24.70	23.44
<i>B. schajovskoi</i>	8	25.05–25.88	25.46
<i>B. gentilii</i>	8	20.20–25.88	23.04
<i>B. mendozensis</i>	6	18.62–22.21	20.41
<i>B. flaccus</i>	5	17.31–17.97	17.64
<i>B. painensis</i>	6	12.59–14.47	13.53
<i>B. deplanatus</i>	6		15.27
<i>B. sulcatipenis</i>	5	14.52–16.52	15.52
<i>B. neuquensis</i>	4	15.36–19.37	17.36
<i>B. giaini</i>	7	14.90–17.70	16.30
<i>B. dentipenis</i>	7	16.30–20.50	18.40
<i>B. chubutensis</i>	6	14.20–16.40	15.30
<i>B. minus</i>	5	13.40–15.50	14.45
<i>B. clivinoides</i>	3	14.70–26.89	20.79

genitalia: spermatheca and median oviduct joined together before entering the bursa copulatrix (38) and the absence of an accessory gland (39).

The three subgenera proposed by Putzeys (1868) are monophyletic groups, with *Ara-thymus* the sister group of the subgenera *Barypus* and *Cardiophthalmus* (fig. 10).

Most species relationships are resolved, as indicated in figure 10. However, for *Cardiophthalmus*, *B. clivinoides* is placed in the basal node of the subgenus, and constitutes an unresolved trichotomy with two main clades, the *sulcatipenis-flaccus* species groups and the *neuquensis* species group.

Character analysis. Four characters were treated as nonadditive:

Character 16 (shape of the male protarsomere) has two apomorphic states independently derived from the plesiomorphic state. State 1 (not expanded) has evolved twice.

For character 41 (gonopod VIII of the female), the apomorphic state 1 (that evolved twice) and state 2 were derived independently from state 0.

Character 32 (shape of the ostium of median lobe) has evolved from the ancestral condition (dorsal) to a left lateral condition (state 1, fig. 1), whereas in other Broscini the ostium displaced to the right side. From state 1 the ostium is reduced and displaced to the apex (state 2, fig. 4 and then 3, fig. 5) in the *neuquensis* group.

Character 33 (tooth of the internal sac) has six states, and the plesiomorphic condition could not be determined until the cladogram was obtained. Based on the results, the most parsimonious option for character 33 is to consider the state 0 (absent) as the plesiomorphic condition. From this condition evolved state 1 (conical and broad) in the basal node, which joins the subgenera *Barypus* and *Cardiophthalmus*. From this node there are three different trends:

1. The tooth is lost and regained (states 0 and 1) in the *flaccus* group.
2. The tooth evolved in state 2 (spatulate) and then in state 3 (conical and slender) in the *pulchellus* group.
3. The length of the tooth increases (state 4) and reaches its greatest length (state 5) in the *neuquensis* group. *B. minus* has an internal sac tooth like that in *B. clivinoides* and other species (state 0). The length of the tooth increases in the following order: *B. chubutensis*, *B. giaini*, and finally *B. dentipenis*, which has the longest tooth of the genus.

The evolution of character 34 (alpha sclerite) has two possible interpretations. The alpha sclerite may evolve twice to state 1 (present), in the subgenus *Barypus* and in *B. clivinoides*, or, it may change from state 0 to state 1 in the basal node of *Barypus-Cardiophthalmus* and become lost in the *flaccus-sulcatipenis* and the *neuquensis* groups. Thus the basal trichotomy in *Cardiophthalmus* depends on the different interpretations of the alpha sclerite of the internal sac. If a loss occurred, the absence of the alpha sclerite is a synapomorphy uniting the *flaccus-sulcatipenis* and the *neuquensis* groups. I conclude that *B. clivinoides* can be placed as the sister taxon of the remaining species of *Cardiophthalmus* only if we accept the hypothesis that the loss of the alpha sclerite is more probable

than its independent acquisition. The remaining characters of the analysis do not support this hypothesis, so additional characters are needed in order to give it credibility.

EVOLUTION OF BODY SIZE

Liebherr (1988, 1989) showed that a positive correlation between maximum body size and cladogram position is commonly observed in Carabidae taxa inhabiting stable, favorable habitats. Larger bodies can be interpreted as an adaptation occurring especially in brachypterous taxa, and Liebherr hypothesized that removal of the functional metathoracic flight apparatus may favor increased size (Liebherr, 1988). Thus size increase occurs predominantly in lineages composed of a sequence of locally adapted species (Liebherr, 1988).

In *Barypus*, which is flightless, a positive increase of body size was found (fig. 11). Within the genus the clade *flaccus-sulcatis* showed the most important increase of body size (length = $0.30 + 2.97 \times \text{node}$; $r = 0.800$). The area that this clade inhabits is the desert grassland of Patagonia. It appears that phyletic size increase is more likely to occur in *Barypus* species that live in more xeric conditions. Noonan (1982) noted that greater desiccation stress, characteristic of arid areas, led to development of large adults of carabid beetles. The same is true for intra-specific variation of body size in *Barypus clinoides*, where larger specimens are found in dry areas, and the smallest specimens are found in the most austral parts of its range (the wet area) (Roig-Juñent and Cicchino, 1989).

BIOGEOGRAPHY

Without a hypothesis about the cladistic relationships of the diverse fauna of Broscini of the austral region and the Palearctic region it is possible to offer only general conclusions about the geographical origin of the genus *Barypus*.

The study of disjunct distributional patterns of extant organisms occurring in southern South America, New Zealand, Australia, New Guinea, New Caledonia, and other southern land masses may be best explained

by southern continental connections from Triassic to upper Cretaceous times (Keast, 1973). *Barypus* must have evolved from an austral broscine stock that inhabited west Gondwana before the breakup of that supercontinent. Thus *Barypus* and the allied Broscini shared an austral relationship (Jeannel, 1941, 1942, 1967; Britton, 1949; Ball, 1956) approximately in the mid or late Cretaceous period, as observed in other austral taxa (Britton, 1949; Jeannel, 1967; Keast, 1973).

Barypus occurs in southern South America between latitudes 25° and 54°S. Within this area of distribution we can recognize three major areas of endemism (fig. 12). The first is congruent with the Santiago biogeographic province of O'Brien (1971) and corresponds to the range of *Arathymus*. The second area comprises extra-Andean Patagonia, reaching the Mendoza province, and corresponds to the distribution of *Cardiophthalmus*. The third area corresponds to the distribution of the subgenus *Barypus* and comprises the Pampas of Argentina and Uruguay, the northwestern Córdoba, the northern region of San Luis, and the Calchaquíes Valleys. Whereas the subgenera of *Barypus* are allopatric, within each subgenera some species are sympatric.

The cladogram (fig. 10) indicates that the ancestral stock diverged first into *Arathymus* and the ancestor of the subgenera *Barypus* and *Cardiophthalmus*. The second divergence separated the last two subgenera. The sequence of divergence might be related to the formation of two main epicontinental seas. The first could be the result of the isolation of the Central Chile area by a Maestrichtian sea in the late Cretaceous period (Ceccioni, 1970). The second event (divergence of *Cardiophthalmus-Barypus*) might be related to the formation of an epicontinental sea between the Deseado-Patagonian massifs and the Pampean ridge of mountains, in the Lower Tertiary (Harrington, 1968; Ceccioni, 1970).

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REFERENCES

- Ball, G.
1956. Notes on the genus *Zacotus* Le Conte, 1869 and on the classification of the tribe Broscini (Broscidae *sensu* Jeannel, 1941, Coleoptera Carabidae). *Coleopt. Bull.* 10(3): 33–52.
- Britton, F. B.
1949. The Carabidae (Col.) of New Zealand. Part III. A revision of the tribe Broscini. *Trans. R. Soc. New Zealand* 77(4): 533–881.
- Bruce, L. C., J. V. Crisci, and P. C. Hoch
1990. A cladistic analysis of the genus *Gaura* (Onagraceae). *Syst. Bot.* 15(3): 454–461.
- Burmeister, H.
1868. Bemerkungen über Gattungen *Barypus*, *Cardiophthalmus* und *Odontoscelis*. *Stett. Entomol. Z.* 29: 225–229.
- Ceccioni, G.
1970. Esquema de Paleogeografía chilena. Ed. Universitaria, Santiago de Chile, 144 pp.
- Chaudoir, M. de
1861. Matériaux pour servir à l'étude des cindélites et des Carabiques. *Bull. Soc. Imp. Nat. Moscou* 34(2): 491–576.
1876. Notes et additions au mémoire de M. Reed sur les carabiques du Chili inséré dans les *Proceedings of the Zoological Society of London* (January 1874: 48). Première partie. *Ann. Soc. Entomol. Belgique* 19: 105–124.
- Curtis, J.
1839. Descriptions, &c. of the Insects collected by Captain P. P. King, R. N. F. R. S. & L. S. in the survey of the Straits of Magellan. *Trans. Linn. Soc. London* 18: 181–205, pl. 15.
- Darlington, P. J., Jr.
1965. Biogeography of the southern end of the world. Distribution and History of far southern life and land with assessment of continental drift. Cambridge, MA: Harvard Univ. Press, 236 pp.
- Dejean, P.
1828. *Spécies général des Coléoptères de la collection de M. Le Compte Dejean*. Vol. 3. Paris: Mequignon, 556 pp.
1831. *Spécies général des Coléoptères de la collection de M. Le Compte Dejean*. Vol. 5. Paris: Mequignon, 883 pp.
- Farris, J. S.
1988. Hennig86. version 1.5. Port Jefferson, NY, available from the author.
- Germar, E.
1824. *Coleopterorum (Insectorum) species nova et minus cognitae, descriptionibus illustrate, Halae.*
- Guérin-Ménéville, F.
1838. *Insectes du voyage de La Favorite*. *Mag. Zool.* 8 (Classe IX): 1–80.
1841. Descriptions de quelques coléoptères provenant de la Tasmanie, de îles Vavao et Tenate, de Triton Bay, à la Nouvelle-Guinée, et du Port Famine, dans le *Detroit de Magellan*. *Rev. Zool.* 1841: 186–188.
- Harrington, H.
1968. Desarrollo paleogeográfico de Sudamérica. *Univ. Nac. Tucumán. Miscelanea* 26.
- Jeannel, R.
1941. Coléoptères carabiques: Première partie. *Faune France* 39: 571 pp.
1942. *La Genèse des Faunes terrestres: éléments de biogéographie*. Press Univ. France, 513 pp.
1967. *Biogéographie de l'Amérique Australe*. In C. D. Delamare Deboutteville et E. Rapoport (eds.), *Biologie de l'Amérique Austral* 3: 401–460. Paris: CHRS et CNIT.
- Keast, A.
1973. Contemporary biotas and the separation sequence of southern Continents. In D. H. Tarling and S. K. Runcorn (eds.), *Implications of Continental Drift to the Earth Sciences* 1: 307–343. London and New York: Academic Press.
- Liebherr, J. K.
1988. Brachyptery and phyletic size increase in Carabidae (Coleoptera). *Ann. Entomol. Soc. Am.* 81(2): 157–163.
1989. Redefinition of the *Platynus jaegeri* group, with a taxonomic revision of the Mexican and Central American species (Coleoptera: Carabidae: Platynini). *Trans. Am. Entomol. Soc.* 114: 167–214.
- Maddison, W. P., M. J. Donoghue, and D. R. Maddison

1984. Outgroup analysis and parsimony. *Syst. Zool.* 33(1): 83–103.
- Noonan, G. R.
1982. The subgenus *Anisotarsus* Chaudoir (Genus *Notiobia* Perty; Coleoptera; Carabidae) in South America. *Coleopt. Bull.* 36(4): 531–548.
- O'Brien, C. W.
1971. The biogeography of Chile through entomofaunal regions. *Entomol. News* 82: 197–207.
- Putzeys, J.
1868. Les Broscides. *Stett. Entomol. Z.* 10–12: 305–379.
- Roig-Juñent, S.
1992a. Revisión del género *Barypus* Dejean, 1828 (Coleoptera, Carabidae, Broscini). Parte II. *Rev. Soc. Entomol. Argent.* 50(1–4): 89–117.
1992b. Revisión del género *Barypus* Dejean, 1828 (Coleoptera, Carabidae, Broscini). Parte III. *Rev. Soc. Entomol. Argentina* 51: 1–27.
- Roig-Juñent, S. and A. Cicchino
1989. Revisión del género *Barypus* Dejean, 1828 (Coleoptera: Carabidae: Broscini). Parte I. *Bol. Soc. Biol. Concepción* 60: 201–225.
- Sharp, M. B.
1886. On New Zealand Coleoptera, with descriptions of new genera and species. *Trans. R. Dublin Soc.* 3(2): 351–453.
- Townsend, J.
1971. Entomology of the Aucklands and other islands south of New Zealand: Coleoptera: Carabidae: Broscini. *Pacific. Insect Monogr.* 27: 173–184.
- Waterhouse, G. R.
1841. Descriptions of some new species of carabideous Insects from the collection made by C. Darwin, Esq., in the southern parts of South America. *Ann. Mag. Nat. Hist.* 4(2): 354–362.
- Watrous, L. E., and Q. D. Wheeler
1981. The out-group method of character analysis. *Syst. Zool.* 30: 1–11.

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