

CLADISTIC ANALYSIS OF *PRIOCYPHIS* HUSTACHE AND
RELATED GENERA (COLEOPTERA: CURCULIONIDAE)

ANALIA A. LANTERI AND JUAN J. MORRONE

División Entomología and Laboratorio de Sistemática y Biología Evolutiva, Museo de La Plata, Paseo del Bosque, 1900 La Plata, Argentina.

Abstract.—This paper presents the cladistic analysis and relationships of *Priocyphus* Hustache and related genera to test their monophyly and determines the taxonomic placement of some critical species. The cladistic analysis was carried out using 45 transformation series from the external morphology (including mouthparts) and male and female genitalia. Polarity decisions were based on the outgroup comparison with the genera *Thoracocyphus* Emden and *Lamprocyphus* Marshall. The most parsimonious cladogram obtained shows the following phylogenetic sequence: *Lamprocyphopsis* Lanteri [*L. viridinitens* (Kuschel) and *L. paraguayensis* Lanteri], *Priocyphopsis* Lanteri [*P. humeridens* (Hustache)], *Mendozella* Hustache [*M. curvispinis* (Hustache)], *Cyrtomon* Schoenherr [*C. hirsutus* (Hustache) *nov. comb.*, *C. ovalipennis* (Hustache), *C. glaucus* (Bovie), and *C. gibber* species group Lanteri], and *Priocyphus* Hustache (*P. bosqi* species group Lanteri and *P. inops* species group Lanteri). Characters from the female and male genitalia are the most important to elucidate the relationships of the taxa under study.

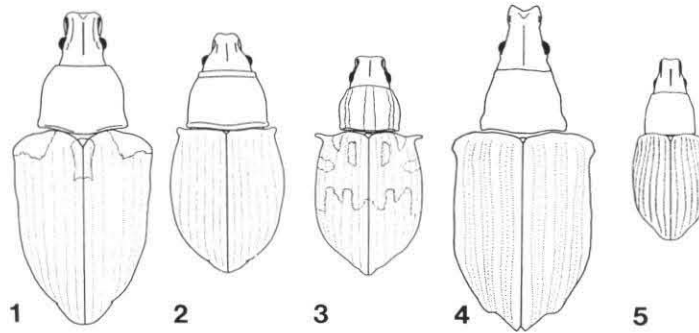
Key Words: Cladistic analysis, *Priocyphus*, *Cyrtomon*, *Priocyphopsis*, *Lamprocyphopsis*, *Mendozella*, Curculionidae, Naupactini

The genus *Priocyphus* Hustache belongs to the tribe Naupactini and is restricted to the grasslands and savannahs of the Chacoan domain (*sensu* Cabrera and Willink 1973) from Paraguay to central Argentina. This genus was established by Hustache (1939) and included three species, *P. bosqi* Hustache 1939, *P. hirsutus* Hustache 1939 and *P. humeridens* (Hustache 1926) (transferred from *Trichocyphus* Heller). Kuschel (1950) described *Priocyphus inops*, *C. hustachei*, and *P. viridinitens*. He also added two species originally assigned to *Neocyphus* Bovie (= *Cyrtomon* Schoenherr and *Cyphus* Germar), *P. glaucus* (Bovie 1907) and *P. ovalipennis* (Hustache 1938).

Lanteri (1990a) hypothesized that *Priocyphus sensu* Kuschel (1950) was not nat-

ural and split the group into three genera: *Priocyphus* (*Priocyphus bosqi*, *P. hustachei*, *P. inops*, and *P. kuscheli* Lanteri, 1990), *Priocyphopsis* (*Priocyphopsis humeridens* and *P. hirsutus*), and *Lamprocyphopsis* (*Lamprocyphopsis viridinitens* and *L. paraguayensis* Lanteri, 1990a). Moreover, she placed *P. glaucus* and *P. ovalipennis* again in *Cyrtomon* (Lanteri 1990b) and suggested that the genus *Mendozella* Hustache is related to both *Priocyphus* and *Cyrtomon* (Lanteri 1989).

We consider the genera *Lamprocyphopsis*, *Priocyphopsis*, *Mendozella*, *Cyrtomon* (*sensu* Lanteri 1990b), and *Priocyphus* (*sensu* Lanteri 1990a) to be a monophyletic group (Figs. 1-5). Synapomorphies that justify this group are as follows:



Figs. 1–5. Female, dorsal view. 1, *Lamprocyphopsis viridinitens* (Kuschel); 2, *Priocyphopsis humeridens* (Hustache); 3, *Mendozella curvispinis* (Hustache); 4, *Cyrtomon gibber* (Pallas); 5, *Priocyphus bosqi* Hustache.

–maxillae with subrectangular mala, having long lacinial teeth, and with truncate-conical palpal article 3;

–dorsal comb of hind tibiae as long as to longer than apical comb; and

–sclerites in the internal sac present.

The relationships and monophyly of these genera are uncertain, as well as the placement of some critical species (*Priocyphopsis hirsutus*, *Cyrtomon glaucus*, and *C. ovalipennis*). A cladistic analysis seems to be the most appropriate resolution to these problems and to developing a phylogenetic classification of the group.

MATERIALS AND METHODS

The study was based on the revisionary works of Lanteri (1989, 1990a, b), and the examination of specimens borrowed from the following collections:

- CWOB Charles W. O'Brien Collection, Tallahassee, Florida, USA
 DZUP Departamento de Zoologia da Universidade Federal do Parana, Curitiba, Brazil
 FIML Fundación e Instituto Miguel Lillo, San Miguel de Tucumán, Argentina
 MACN Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina
 MLPC Museo de La Plata, La Plata, Argentina

MZSP Museu de Zoologia da Universidade de S. Paulo, S. Paulo, Brazil

MNHN Museum National d'Histoire Naturelle, Paris, France

NZAC New Zealand Arthropod Collection, Auckland, New Zealand

The cladistic methodology here applied is summarized in Nelson and Platnick (1981), and Wiley (1981).

Terminal taxa.—We selected nine terminal units (Table 1): the genus *Lamprocyphopsis*, *Cyrtomon gibber* species group, *Priocyphus bosqi* and *P. inops* species groups, and the single species *Mendozella curvispinis*, *Priocyphopsis humeridens*, *P. hirsutus*, *Cyrtomon glaucus*, and *C. ovalipennis*.

Lamprocyphopsis is a very homogeneous genus, including two species. *Cyrtomon gibber* species group comprises four taxa (Lanteri 1990b), that according to Kuschel (1958) should be considered as a single species. The two species groups of *Priocyphus* are homogeneous and clearly monophyletic (Lanteri 1990a). *Mendozella* is a monotypic genus. The two species of the genus *Priocyphopsis* were considered as separate units because *P. hirsutus* has a doubtful taxonomic placement; this species was originally described in *Priocyphus* (Hustache 1939) and tentatively assigned to *Priocyphopsis* (Lanteri 1990a). *Cyrtomon glaucus* and *C. ovalipennis* are critical species that

Table 1. Terminal units, including species and geographical distribution.

Species Groups	Species	Geographical Distribution
1 <i>Cyrtomon gibber</i> species group Lanteri 1990b	<i>C. gibber</i> (Pallas 1781) <i>C. luridus</i> (Boheman 1840) <i>C. pistos</i> (Boheman 1833) <i>C. inhalatus</i> (Germar 1824)	From central-eastern Brazil to Bolivia, Paraguay, and central Argentina.
2 <i>Cyrtomon glaucus</i> (Bovie 1907)		Central-eastern Argentina.
3 <i>Cyrtomon ovalipennis</i> (Hustache 1938)		Central-northern Argentina.
4 <i>Lamprocyphopsis</i> Lanteri 1990a	<i>L. viridinitens</i> (Kuschel 1950) <i>L. paraguayensis</i> Lanteri 1990a	Northeastern Argentina and Paraguay.
5 <i>Mendozella curvispinis</i> (Hustache 1926)		Central-western Argentina.
6 <i>Priocyphopsis hirsutus</i> (Hustache 1939)		Central-western Argentina.
7 <i>Priocyphopsis humeridens</i> (Hustache 1926)		Northwestern Argentina.
8 <i>Priocyphus bosqi</i> species group Lanteri 1990a	<i>P. bosqi</i> Hustache 1939 <i>P. hustachei</i> Kuschel 1950	Central Argentina.
9 <i>Priocyphus inops</i> species group Lanteri 1990a	<i>P. inops</i> Kuschel 1950 <i>P. kuscheli</i> Lanteri 1990a	Northeastern Argentina and Paraguay.

were described in *Cyphus* and *Neocyphus*, transferred to *Priocyphus* (Kuschel 1950), and included in *Cyrtomon* (Lanteri 1990b).

Transformation series.—A detailed morphological study indicated 45 transformation series, 29 from the external morphology (head, mouthparts, pronotum, elytra, and tibiae) and 16 from the genitalia (sternum 8 of female, ovipositor, spermatheca, and aedeagus). Morphometric features with overlapping ranges and characters variable within a taxon were excluded.

Male and female genitalia were not evaluated in much detail or were ignored by earlier specialists (e.g. Germar 1824, Schoenherr 1833, Marshall 1922, Emden 1936, Hustache 1939, Kuschel 1950). The last revisionary works (Lanteri 1989, 1990a, b) considered them for diagnosing the genera of the group under study. Recent contributions (Diaz et al. 1990a, b) showed the importance of mouthparts to separate some taxa of the group, and several characters from this source were incorporated in this analysis.

Identification of apomorphic characters

was based on the outgroup comparison (Watrous and Wheeler 1981) with *Thora-chocyphus* Emden as the first outgroup and *Lamprocyphus* Marshall as the second outgroup.

Binary coding was applied, except for twelve transformation series with more than one apomorphic character. Seven of these series (1, 7, 9, 15, 16, 22, 39, and 44) were treated as additive, and five (3, 22, 31, 40, and 43) as non-additive.

The transformation series and characters are listed in Table 2.

In the data matrix (Table 3), plesiomorphic characters were coded with 0, apomorphic ones with numbers 1 and 2 (additive) or letters a, b, and c (non-additive), and unknown characters with question marks.

Data analysis.—The data set was analyzed using the phylogenetic program HENNIG86 version 1.5 (Farris 1988), applying the implicit enumeration option. The consistency (Kluge and Farris 1969) and retention (Farris 1989) indices were calculated excluding autapomorphies.

Table 2. Series of transformation and characters.

Plesiomorphic Characters (0)	Apomorphic Characters (1, 2, or a, b, c)
1 Rostrum not truncate-conical.	slightly truncate-conical (WF/WR = 1.15–1.45) (1). moderately truncate-conical (WF/WR = 1.50–1.65) (2).
2 Rostral groove narrow to moderately wide.	very wide (1).
3 Rostral lateral carinae indistinct.	distinct, reaching fore margin of eyes (a). distinct, reaching hind margin of eyes (b).
4 Scrobes extending below eyes.	evanescent (1).
5 Preocular depression distinct.	indistinct (1).
6 Supraocular lobes absent.	present (1).
7 Eyes strongly convex.	slightly to moderately convex (1). flat (2).
8 Antennae robust.	slender (1).
9 Scape not reaching hind margin of eyes.	reaching or slightly exceeding hind margin of eyes (1). largely exceeding hind margin of eyes (2).
10 Funicular article 2 longer than 1.	about as long as 1 (1).
11 Mandibular pharyngeal process short and wide.	long and narrow (1).
12 Maxillary mala suboval, with short lacinial teeth.	subrectangular, with long lacinial teeth (1).
13 Article 3 of maxillary palpus subcylindrical.	truncate-conical (1).
14 Prementum hexagonal.	subcircular (1).
15 Prementum with 15–25 short fine setae.	with less than 11 long coarse setae (1). lacking setae (2).
16 Disc of pronotum flat to depressed, lacking groove.	convex, with distinct groove (1).
17 Disc of pronotum rugose.	smooth (1).
18 Pronotum lacking lateral tubercles.	with lateral tubercles (1).
19 Base of pronotum not to slightly thickened.	conspicuously thickened (1).
20 Base of pronotum and elytra bisinuate.	straight (1).
21 Humeri strongly prominent.	moderately to slightly prominent (1).
22 Humeri not tuberculate.	moderately tuberculate postero-laterally (a). moderately tuberculate antero-laterally (b). strongly tuberculate antero-laterally (c).
23 Elytral declivity not abrupt.	abrupt (1).
24 Supernumerary striae of even intervals absent.	present (1).
25 Elytral setae recumbent.	erect (1).
26 Elytral scales round to round-oval.	lanceolate (1).
27 Tibial denticles present.	absent (1).
28 Number of tibial denticles 6–13.	4–5 (1).
29 Dorsal comb of hind tibiae shorter than apical comb.	as long as, to longer than apical comb (1).
30 Female sternum 8 elongate.	transversal (1).
31 Apodeme of sternum 8 1.25–2.5× as long as plate.	about as long as plate (a). about 3.5× as long as plate (b).
32 Ovipositor lacking sclerotized dorsal plates.	with a pair of sclerotized dorsal plates (1).
33 Coxites of ovipositor slightly sclerotized.	strongly sclerotized (1).
34 Membrane between coxites with three folds.	with several folds (1).
35 Styli not concealed by coxites.	concealed by coxites (1).
36 Spermatheca subglobose.	subcylindrical (1).
37 Nodulus of spermatheca truncate-conical.	tubular (1).
38 Nodulus of spermatheca short.	medium-length (1). long (2).

Table 2. Continued.

Plesiomorphic Characters (0)	Apomorphic Characters (1, 2, or a, b, c)
39 Nodus of spermatheca not curved.	slightly curved (1). strongly curved (2).
40 Spermathecal duct shorter than abdomen.	twice as long as abdomen (a). as long as spermatheca (b).
41 Spermathecal duct fine (narrower than nodulus at apex).	moderately to very wide (wider than nodulus at apex) (1).
42 Spermathecal duct membranous.	sclerotized (1).
43 Apex of aedeagus acute.	truncate (a). arrow-pointed (b).
44 Aedeagal apodemes shorter than aedeagus.	as long as aedeagus (1). longer than aedeagus (2).
45 Sclerites of internal sac inconspicuous.	conspicuous (1).

RESULTS AND DISCUSSION

A single most parsimonious cladogram was obtained (Fig. 6), with 65 steps, a consistency index of 0.72, and a retention index of 0.74.

The relationship between the outgroup *Thoracocyphus* and the group under study is based on the synapomorphies "disc of pronotum convex, with distinct groove" (16), "coxites of ovipositor strongly sclerotized" (33), and "style concealed by coxites" (35).

The monophyly of *Priocyphus* and related genera is justified by the synapomorphies "antennae slender" (8), "scape reaching or slightly exceeding hind margin of eyes" (9.1), "maxillary mala subrectangular, with long

lacinal teeth" (12), "article 3 of maxillary palpus truncate-conical" (13), "prementum lacking setae" (15.2), "dorsal comb of hind tibiae as long as to longer than apical comb" (29), and "sclerites of internal sac conspicuous" (45). *Lamprocyphopsis* is the sister genus to the remaining taxa, which form a clade based on the synapomorphies "rostrum slightly truncate-conical" (1.1), "scrobes evanescent" (4), "preocular depression indistinct" (5), "humeri moderately to slightly prominent" (21), "spermatheca subcylindrical" (36), "spermathecal duct moderately to very wide" (41), "spermathecal duct sclerotized" (42), and "aedeagal apodemes as long as aedeagus" (44.1). *Priocyphopsis* is the sister genus to *Mendozella*,

Table 3. Data matrix.

<i>Lamprocyphus</i>	00
<i>Thoracocyphus</i>	000000000010000101000a00010000a11010000000000
<i>Cyrtomon gibber</i> species group	00011011201110100000000110000100000001121a11b11
<i>Cyrtomon glaucus</i>	110110112011101110001010000010b00001121a11b11
<i>Cyrtomon ovalipennis</i>	100110112011101100001000000010000001111a11b11
<i>Lamprocyphopsis</i>	000000012011102100000010000011a01110000000a01
<i>Mendozella</i>	100111112001111100001c00100010001011010a11b11
<i>Priocyphopsis hirsutus</i>	10a1101110????1000010001000100000001121a11???
<i>Priocyphopsis humeridens</i>	20b110011001102100101b00000110001011000011021
<i>Priocyphus bosgi</i> species group	10a110211101101100011000000010001011121011b11
<i>Priocyphus inops</i> species group	20011021111????0100110100001?10001011122b01???

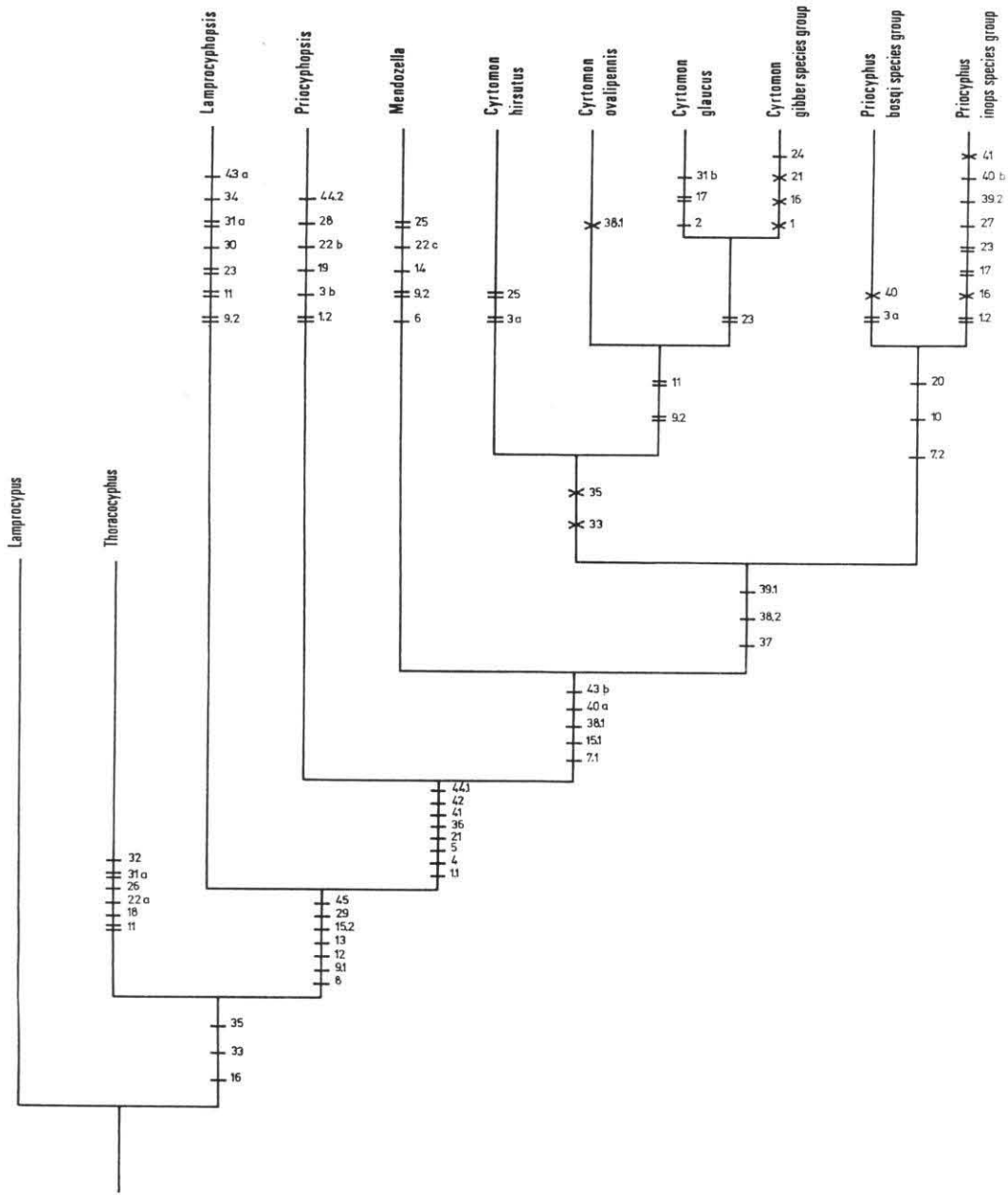


Fig. 6. Most parsimonious cladogram. —: apomorphies; =: parallelisms; *: reversals.

Cyrtomon, and *Priocyphus*; these three genera share the apomorphies “eyes slightly to moderately convex” (7.1), “prementum with less than 11 coarse setae” (15.1), “nodulcs of spermatheca medium-length” (38.1),

“spermathecal duct twice as long as abdomen” (40.a), and “apex of aedeagus arrow-pointed” (43.b). The taxa included in *Cyrtomon* and *Priocyphus* form a monophyletic group having three synapomorphies of the

spermatheca, "nodulus tubular" (37), "long" (38.2), and "slightly curved" (39.1).

Cyrtomon is a monophyletic group that is justified by the reversals "coxites of ovipositor slightly sclerotized" (33) and "styli not concealed by coxites" (35), and comprises *C. hirsutus*, *C. ovalipennis*, *C. glaucus*, and the *C. gibber* species group. *Cyrtomon ovalipennis* is related to the clade *C. glaucus*-*C. gibber* species group by the synapomorphies "scape largely exceeding hind margin of eyes" (9.2) and "mandibular pharyngeal process long and narrow" (11), with parallel evolution in *Lamprocyphopsis*. The sister taxa *C. glaucus* and *C. gibber* species group share the synapomorphy "elytral declivity abrupt" (23), with parallel evolution in *Lamprocyphopsis* and the *P. inops* species group.

Priocyphus includes the *inops* and *bosqi* species groups. The monophyly of the genus is supported by the synapomorphies "eyes flat" (7.2), "funicular article 2 about as long as 1" (10), and "base of pronotum and elytra straight" (20).

All the terminal units are characterized by autapomorphies.

Character analysis.—*External morphology*: Characters of the rostrum do not contribute substantially to the elucidation of relationships among the taxa under study. The shape of the rostrum evolves from truncate-conical to moderately truncate-conical, a change that occurs in other genera of the tribe Naupactini, e.g. the genus *Atrichonotus* Buchanan (Lanteri and O'Brien 1990).

The eyes are slightly to moderately convex in *Mendozella* and *Cyrtomon*. The transformation has a further change in *Priocyphus* where the eyes become flat. The most apomorphic condition has evolved coincidentally in single species of several genera of Naupactini, e.g. *Eurymetopus* Schoenherr (Lanteri 1984), and *Phacepholis* Horn (Lanteri 1990c).

The evanescent scrobes and indistinct preocular depression are correlated char-

acters that justify the monophyly of the ingroup except *Lamprocyphopsis*. These characters are rather uniform in the tribe Naupactini and vary among genera or groups of genera.

The antennae do not vary significantly within the group under study, but help distinguish it from the outgroups. Within the ingroup, the most conspicuous change is the shortening of funicular article 2 in *Priocyphus*. Most Naupactini have funicular article 2 longer than 1, but in some genera, such as *Atrichonotus* (Lanteri and O'Brien 1990) and *Eurymetopus* (Lanteri 1984) both articles have the same length or article 1 is slightly shorter than article 2.

The shape of the mala and palpal article 3 of the maxillae and the reduction of setae on the labial prementum are correlated characters that establish the monophyly of the ingroup. The remaining characters of mouthparts are autapomorphies of different taxa.

Characters of the pronotum and elytra are not very helpful to recognize clades within the group under study, but are important to characterize taxa. The humeri evolve from strongly prominent to slightly prominent and sometimes (*Priocyphopsis* and *Mendozella*) there are also tubercles. The reduction of humeri and the occurrence of tubercles are apomorphic characters that occur independently in other Naupactini, e.g. *Enoplopactus* Heller (Lanteri 1990d).

The presence of denticles on the tibiae is the most primitive condition in the tribe Naupactini. Within the ingroup these denticles are lost in the *Priocyphus inops* species group. In other genera, such as *Eurymetopus* (Lanteri 1984), all species lack the tibial denticles.

Genitalia: Sternum 8 of most Naupactini is elongate and subrhomboidal, with the apodeme about 2× as long as the plate. Within the group under study, the shape of sternum 8 of each taxon is slightly different, but in *Lamprocyphopsis* the shape is transversal and completely different. The length

of the apodeme evolves in two opposite directions, it becomes much shorter in *Lamprocyphopsis* and longer in *C. glaucus*.

In the ovipositor, the presence of strongly sclerotized coxites concealing styli is an apomorphic condition that is reversed in *Cyrtomon*. This condition appears independently in other non-related genera of Naupactini, e.g. *Atrichonotus* (Lanteri and O'Brien 1990), *Eurymetopus* (Lanteri 1984), and *Teratopactus* (Lanteri 1981).

The spermathecal body evolves from subglobose to subcylindrical, and the nodules from subconical and short to tubular, long, and curved. The second condition is a clear synapomorphy at *Priocyphus* and *Cyrtomon*. Other non-related genera of Naupactini such as *Asynonychus* Crotch or *Aramigus* Horn (Lanteri et al. in press) also have tubular and long nodulus, but the spermathecal shape is different. The length and width of the spermathecal duct evolve in two different directions, very long and wide, and very short and narrow. In some genera of Naupactini, e.g. *Enoplopactus* (Lanteri 1990d), the spermathecal duct is very uniform, whereas in others, e.g. *Aramigus* (Lanteri et al. in press) it has a great variation.

The apex of the aedeagus arrow-pointed is a clear synapomorphy of *Mendozella*, *Priocyphus*, and *Cyrtomon*, and seems to be correlated to apomorphic conditions of the spermatheca. In most Naupactini, the apex of the aedeagus is acute.

CONCLUSIONS

According to the most parsimonious cladogram *Priocyphus sensu* Kuschel (1950) is not a natural group because it does not include either the genus *Mendozella* or the *Cyrtomon gibber* species group. This result corroborates the hypothesis of non-monophyly that led Lanteri (1990a) to split *Priocyphus* into three different genera.

Lamprocyphopsis was named in reference to its similarity to *Lamprocyphus* (Lanteri 1990a). The cladogram obtained shows that

this similarity is due to plesiomorphic characters.

Priocyphopsis sensu Lanteri (1990a) is not a natural group because *P. humeridens* and *P. hirsutus* do not share any synapomorphy. Therefore, this generic name is herein restricted to the type species, *P. humeridens*. The similarity of *Priocyphopsis* and *Priocyphus* is due to plesiomorphies.

The critical species *hirsutus* was previously assigned to *Priocyphus* (Hustache 1939) and *Priocyphopsis* (Lanteri 1990a), and according to the cladogram, it belongs to *Cyrtomon*. The external morphology of this species is a mosaic of characters of the three genera, but the female genitalia determine its inclusion in *Cyrtomon*. On the same basis, *C. ovalipennis* and *C. glaucus* are placed in *Cyrtomon*.

The results of the cladistic analysis support the hypothesis of Lanteri (1989) that *Mendozella* is closely related to *Cyrtomon* and *Priocyphus*, and that the latter two are sister genera. Moreover, they confirm that the male and female genitalia are essential to elucidate the relationships among these genera.

Since cladistics does not provide any rule to rank the natural groups in a cladogram, we may treat the group under study (*Priocyphus sensu* Kuschel + *Mendozella* + *Cyrtomon gibber* species group) as a single genus, or keep the five generic names proposed until present (*Lamprocyphopsis*, *Priocyphopsis*, *Mendozella*, *Cyrtomon*, and *Priocyphus*), with the condition that *C. hirsutus*, *C. ovalipennis*, and *C. glaucus* belong to *Cyrtomon*. The first alternative would imply the recognition of a very heterogeneous genus, difficult to diagnose. On the contrary, the second allows definition of small, homogeneous, and easily identifiable genera, with greater chance of representing natural units.

We chose the second option because it agrees better with the criteria applied to recognize other genera of the tribe Naupactini (Lanteri 1989, 1990c, d; Lanteri and O'Brien

1990). This option disrupts the present classification as little as possible and is particularly convenient for the tribe Naupactini, where the construction of a phylogenetic system is still developing.

The cladistic classification proposed, applying the method of phylogenetic sequencing (Nelson, 1974), is as follows:

- Genus *Lamprocyphopsis* Lanteri 1990a
L. viridinitens (Kuschel 1950)
L. paraguayensis Lanteri 1990a
 Genus *Priocyphopsis* Lanteri 1990a
P. humeridens (Hustache 1926)
 Genus *Mendozella* Hustache 1939
M. curvispinis (Hustache 1926)
 Genus *Cyrtomon* Schoenherr 1823
C. hirsutus (Hustache 1939) *nov. comb.*
C. ovalipennis (Hustache 1938)
C. glaucus (Bovie 1907)
C. gibber species group
C. inhalatus (Germar 1824)
C. luridus (Boheman 1840)
C. pistos (Boheman 1833)
C. gibber (Pallas 1781)
 Genus *Priocyphus* Hustache
P. bosqi species group
P. bosqi Hustache 1939
P. hustachei Kuschel 1950
P. inops species group
P. inops Kuschel 1950
P. kuscheli Lanteri 1990a

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