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Systematic position and cladistic analysis of *Gyrasida* Koch, a remarkable genus of Praocini (Coleoptera: Tenebrionidae) from Chile

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Abstract

Gyrasida Koch (Pimeliinae: Praocini), distributed in central Chile is elevated to generic status and transferred from Asidini to Praocini on the basis of constant tribal level characters. Prior to this study *Gyrasida* was considered a subgenus of the South African *Afrasida* Wilke. Character states of *Gyrasida* shared with the other genera of Praocini and not shared with genera of Asidini are discussed. A cladistic analysis of the six species of the genus is presented including: *G. propensa* (Wilke) (type species), *G. lucianoi* Flores & Vidal, *G. fernandoi* Flores & Vidal, *G. tomasi* Vidal, *G. franciscae* Vidal, and *G. camilae* Vidal. This article includes a redescription of the genus, habitus photographs, illustrations of external morphology and genitalic features, a cladogram, and a distribution map.

Key words: Tenebrionidae, *Afrasida*, *Gyrasida*, Chile, Asidini, Praocini

Introduction

The South African genus *Afrasida* was described by Wilke (1921) and assigned to the tribe Asidini. Within *Afrasida*, Wilke included eight known species (transferred from other genera) plus six new species, which he arranged in three subgenera: *Afrasida (Afrasida)*, *A. (Archasida)* and *A. (Asidomachla)*. One of the new species, *Afrasida propensa* Wilke, was described with only one specimen labeled as from Natal, South Africa, obtained from Kraatz´s collection, and placed in the subgenus *A.* (*Archasida*) (Wilke 1921). Later, Wilke (1924) reviewed *Afrasida* describing some new species, transferring others and providing a key for the species.

Koch (1962) studied the genera of Asidini from Africa South of Sahara and Madagascar. He transferred the species of the subgenus *Afrasida* (*Asidomachla*) to the genus *Machlomorpha* Péringuey. At the same time he created a new monotypic subgenus of *Afrasida* which he named *A.* (*Gyrasida*) based on *A. propensa* (Koch 1962).

Specimens of *Afrasida propensa* were found in central Chile and identified as such by Wilke, Kulzer, and Kaszab in the 20th century. During our extensive explorations in South America through the years we found different species of *Afrasida* (*Gyrasida*) in central Chile. According to a note written by Kulzer, the type of *Afrasida propensa* was thought to be lost and we could not establish which of these species was the originally described as *A. propensa* and which no yet described species were. During last years we were able to find the Wilke´s type of *Afrasida propensa* in Museum für Naturkunde der Humboldt Universität, Berlin (Germany), establishing five new species for Chile which have been recently described (Vidal & Flores 2007). Later, we requested some other known species of *Afrasida* and a systematic research was carried out to establish if *Afrasida (Gyrasida)* belongs to *Asidini* as described originally, as there were no other members of this tribe

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described for South America west of the Andes mountains (Flores & Pizarro-Araya 2006). Through a detailed discussion of the characters, we demonstrate that *Afrasida (Gyrasida) propensa* is not congeneric with the remaining species of *Afrasida*, that it is not Asidini, that it shares most of these characters with all or some genera of the South American tribe Praocini, and that they deserve recognition as a separate genus, *Gyrasida* Koch together with other five species recently described. The objectives of this study are to redescribe the genus *Gyrasida*, to establish a natural tribal placement of *Gyrasida* and to conduct a cladistic analysis of their species.

Materials and methods

Specimens were obtained from the following institutions: Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina (IADIZA) (Sergio Roig-Juñent), Museo Nacional de Historia Natural, Santiago, Chile (MNNC) (Mario Elgueta), Pedro Vidal G.H., private collection, Santiago, Chile (PVGH), Transvaal Museum, Pretoria, South Africa (TMSA) (James Harrison), and Museum fur Naturkunde der Humboldt Universität, Berlin, Germany (MNHUB) (Manfred Uhlig, Bernd Jaeger).

All measurements were taken with a micrometer eyepiece. Body length was measured dorsally, along the midline, from anterior margin of labrum to elytral apex. For paraproct length/ coxite length we considered the ratio proposed by Doyen (1994); for basal lamina of tegmen length/ lateral styles length and median lobe length/ tegmen length, we considered the ratios proposed by Flores (1996). Dissection methods for genital structures are those used by Tschinkel & Doyen (1980) and by Flores (1997) for internal skeletal anatomy. Drawings were made with a camera lucida adapted to a stereoscopic microscope. The entomofaunal regions considered in the distribution of the species are adopted from Peña (1966). The methodology of cladistic analysis herein applied is explained under the heading "Cladistic analysis".

Taxonomic Placement of *Gyrasida*

Gyrasida propensa (Fig. 1) was originally placed in the genus *Afrasida* (Wilke 1921), which belongs to the Asidini, a large tribe of Pimeliinae with more than 1,000 species distributed in North and South America, Africa south of Sahara, Madagascar, and the Mediterranean area (Koch 1955).

Koch (1962) created the monotypic subgenus *Afrasida* (*Gyrasida)* based on the species *Afrasida propensa*, previously placed in the subgenus *A. (Archasida)* by Wilke (1921). Koch stated: “it differs very sharply and probably generically from all other *Afrasida* by the rounded sides of pronotum and the middle of base of pronotum produced into an elongate, narrow, apically obtuse lobe projecting backwards on to the scutellum” (Koch 1962: 127).

We have studied the following characters within the species of *Afrasida*, some of which have been used to study the relationships between the tribes of Pimeliinae (Doyen 1994), to group together the South African Asidini (Koch 1955), and to define the tribe Praocini (Kulzer 1958; Flores 2001). We found that *Afrasida* (*Gyrasida*) *propensa* and the five recently described species (Vidal & Flores 2007) share all of these characters with all or some genera of Praocini and not with the species of *Afrasida*. The species of *Afrasida* examined from TMSA are *A. (Afrasida) caryophyllea* (Wiedemann) (type species) and *A.* (*Afrasida*) *turbida* (Péringuey) (Fig. 2).

1 Length of antennomere 3: equal to length of antennomere 4 in *Afrasida* (Figs. 3–4); in *Gyrasida* and Praocini longer than antennomere 4 (Figs. 5–8).
2 Size of antennomere 11: very small, even rudimentary in *Afrasida* (Figs. 3–4); in *Gyrasida* and Praocini well developed, sometimes equal to or longer than antennomere 10 (Figs. 5–8).

3 Subgenal process (defined by Doyen 1994: 454): subadjacent with mentum in *Afrasida* (Fig. 9; Doyen 1994: Figs. 22–25); in *Gyrasida* and Praocini it is remote from mentum (Fig. 10; Doyen 1994: Fig. 21).

4 Maxilla, articulation of cardo: concealed in socket in submentum in *Afrasida* (Fig. 9); in *Gyrasida* and Praocini exposed laterad of submentum (Fig. 10).

5 Position of ligula: nearly or entirely concealed beneath mentum in *Afrasida* (Fig. 9); in *Gyrasida* and Praocini it is entirely exposed anterad mentum (Fig. 10), with the articulating membrane visible.

6 Ligula, relative size: very small, less than a quarter the size of mentum in *Afrasida* (Fig. 9)*;* in *Gyrasida* and Praocini it is larger than half of mentum, sometimes equal to the size of mentum (Fig. 10).

7 Mesotrochantin: lacking a disctinct trochantin of mesocoxae in *Afrasida* species, as well as all the South African Asidini (Koch 1955); in *Gyrasida* and all Praocini it is well developed.

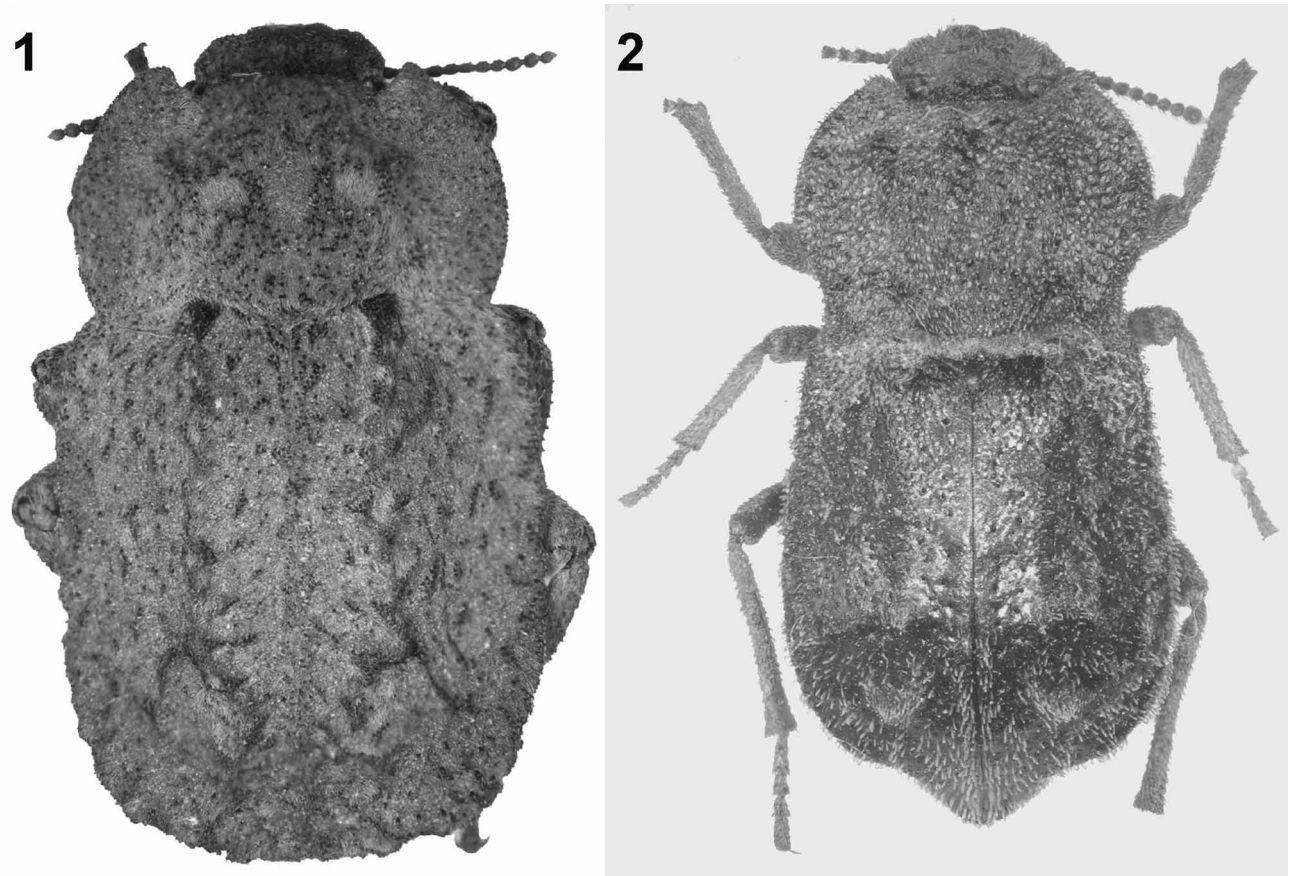
8 Mesepimeron: long, reaching the base of elytral epipleuron in *Afrasida* (Fig. 11), in *Gyrasida* and Praocini it is short, not reaching the base of elytral epipleuron (Fig. 12).

9 Metepisternum: broadened in *Afrasida* (Fig. 11); in *Gyrasida* and Praocini it is narrow (Fig. 12).

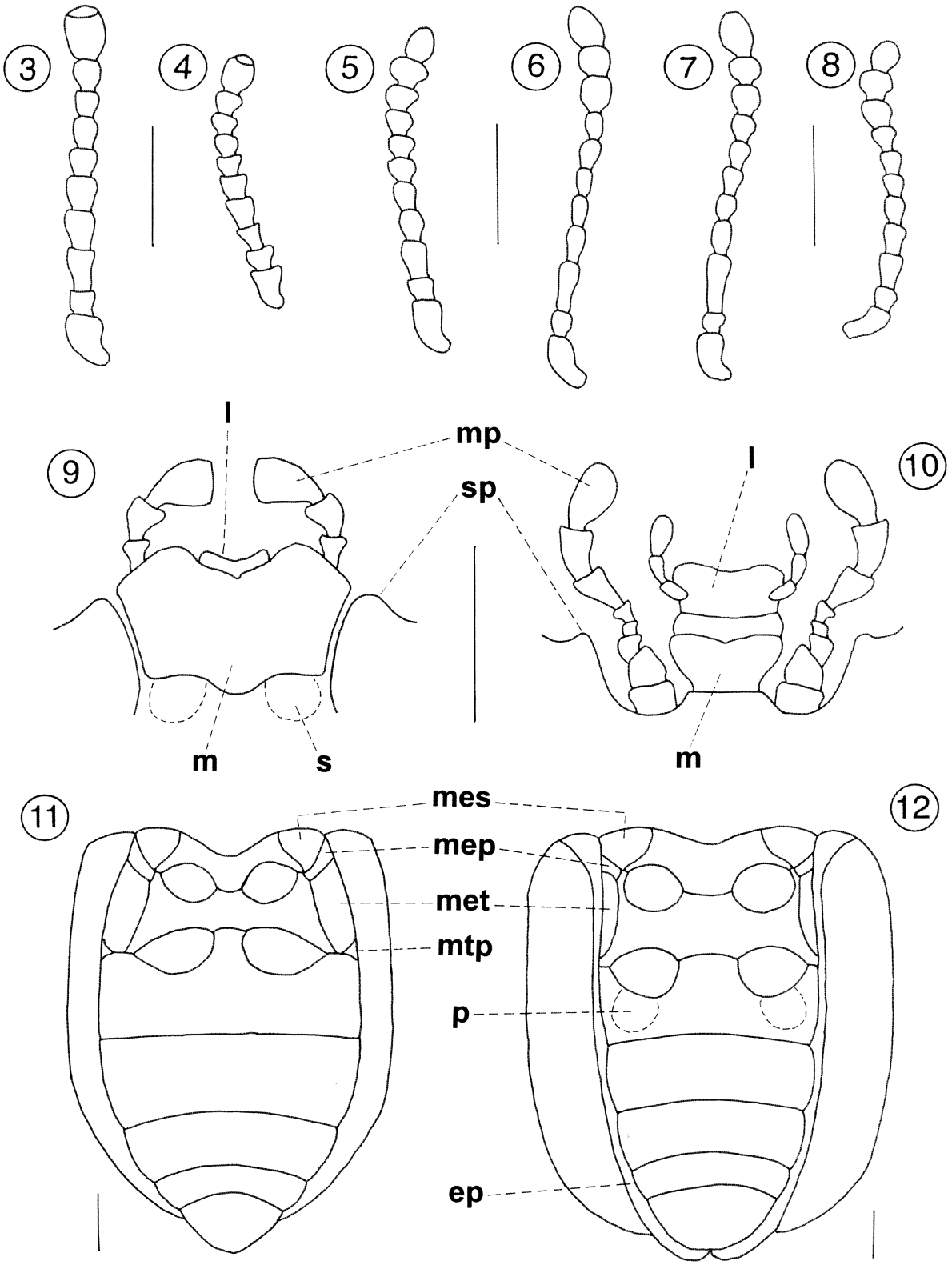
10 Metepimeron: transverse in *Afrasida*, separating the metacoxal cavities from the elytral epipleuron (Fig. 11); in *Gyrasida* and Praocini it is not evident, since the metacoxal cavities are very close to the elytral epipleuron (Fig. 12).

11 Distance between meso- and metacoxae: does not exceed half of metacoxal length in *Afrasida* (Fig. 11); in *Gyrasida* and Praocini it exceeds half or is equal to metacoxal length (Fig. 12).

We also studied these 11 characters in the two South American genera of Asidini: *Cardigenius* Solier and *Scotinus* Kirby. The genus *Cardigenius* is found in Uruguay and East Central Argentina, whereas *Scotinus* is endemic to Brazil (Gebien 1937).



FIGURES 1–2. Habitus in dorsal view. 1, *Gyrasida propensa*; 2, *Afrasida turbida*.



FIGURES 3–12. External structure. 3–8, Antennae, dorsal view. 3, *Afrasida turbida*; 4, *A. caryophyllea*; 5, *Gyrasida fernandoi*; 6, *G. lucianoi*; 7, *G. franciscae*; 8, *Praocis rufipes*. 9–10, Mouth parts, ventral view. 9, *Afrasida turbida*; 10, *Gyrasida camilae*. Abbreviations: l, ligula, m, mentum, mp, maxillary palpus, s, socket in submentum, sp, subgenal process. 11–12, Mesothorax, metathorax and abdomen, ventral view. 11, *Afrasida caryophyllea*; 12, *Gyrasida lucianoi*. Abbreviations: ep, epipleuron, mes, mesepisternum, mep, mesepimeron, met, metepisternum, mtp, metepimeron, p, patches of brown setae behind metacoxae. Scale bars: 1 mm.

These two South American genera of Asidini differ from the South African ones in five of these 11 characters, namely: antennomere 3 is longer than antennomere 4 (Fig. 6), the subgenal process is remote from mentum (Fig. 10), the articulation of cardo of maxila is exposed laterad of submentum (Fig. 10), the ligula is entirely exposed anterad of mentum (Fig. 10) and the mesotrochantin is well developed.

The six characters shared by both South African and South American genera of Asidini (but not with *Gyrasida*) are: antennomere 11 rudimentary (Figs. 3–4), ligula very small, smaller than one quarter of size of mentum (Fig. 9), mesepimeron long, reaching the base of elytral epipleuron (Fig.11), metepisternum broadened (Fig. 11), metepimeron transverse, separating the metacoxal cavities from elytral margin (Fig.11) and distance between meso- and metacoxae not exceeding a half of metacoxal length (Fig. 11).

Gyrasida belongs to the Tenebrionidae subfamily Pimeliinae by lacking defensive glands, having the aedeagus rotated 180°, having the medial lobe dorsal to the tegmen and lacking external membranes between the abdominal sternites V and VI and VI and VII (Watt 1974, Doyen 1994).

In his cladistic analysis of Pimeliinae, Doyen (1994) found that all genera of Asidini (from South African, Madagascar, Mediterranean, North and South American regions) constitute a monophyletic group defined by six synapomorphies, five of which are not present in *Gyrasida*: bridge of tentorium absent or incomplete, antennae with ten segments plus the reduced eleventh antennomere, abdominal laterotergites extremely small, apicodorsal lobe of proctiger ending at coxite base, and baculus of proctiger extending proximad, equal to baculus of paraproct. Furthermore Doyen (1994) pointed out that the first two are synapomorphies unique to Asidini within the Pimeliinae.

Within Pimeliinae, *Gyrasida* must be placed within Asidine clade (Doyen 1994) by having multiple, long, slender spermathecal tubes which open as a fascicle into the base of the accesory gland duct or into the vagina near the duct (Fig. 17). Within this Asidine clade, *Gyrasida* belongs to the subclade of South American tribes Nycteliini, Physogasterini and Praocini by having metendosternites arms fused with mesocoxal inflexions (Vidal & Flores 2007: Fig. 3). *Gyrasida* is placed in the tribe Praocini according to the definition of that tribe by Kulzer (1958) and Flores (2001), but the following three changes in that tribal concept should be mentioned: 1) some genera exhibit sexual dimorphism, such as *Antofagapraocis* Flores (Flores 2000a), *Platesthes* Waterhouse (Flores 2004), and *Gyrasida* (Vidal & Flores 2007); 2) antennomere 11 can be longer than 10 and 3) the aedeagus exhibits diagnostic characters at generic level.

The most recent key provided for the genera of Praocini is that by Kulzer (1958), modified by Flores (2000a) at couplet 2 to key out *Falsopraocis* Kulzer together with *Antofagapraocis* and by Flores (2001) at couplet 2b to key out *Praocidia* Fairmaire and *Pilobaloderes* Kulzer, which follows in couplet 2c. Within the first modification, *Gyrasida* keys out at couplet 2a, which should be modified as follows:

2. Pronotum widest at or anterior of mid-point; anterior quarter of epipleuron twice as wide as posterior half 2a
- Pronotum widest posterior of middle; anterior quarter of epipleuron three or four times as wide as posterior half ..... 2b (follows in Flores 2001)

2a Profemora with a conspicuous, smooth, glabrous, and shiny longitudinal ridge on proximal half of anterior surface; anterior area of clypeus inclined downwards forming an angle; frons with two tranverse carinae forming an inverted "V", covering dorsally the clypeal suture ..... *Gyrasida* Koch
- Profemora lacking smooth, glabrous, and shiny longitudinal ridge on proximal half of anterior surface; anterior area of clypeus inclined straight; frons lacking transverse carinae forming an inverted "V" 2d

2d Clypeal suture as horizontal groove, clypeus lower than frons; pronotum widest at the mid point, anterior margin lacking edge, width of anterior margin exceeding width of posterior margin..... *Falsopraocis* Kulzer
- Clypeal suture as vertical depression, clypeus and frons at same level; pronotum widest before mid point, anterior margin with slender edge, width of anterior margin not exceeding width of posterior margin... *Antofagapraocis* Flores

***Gyrasida* Koch**

Gyrasida Koch 1962: 127 (as a subgenus of *Afrasida*); Vidal & Flores 2007: 409.

Type species: *Afrasida propensa* Wilke 1921, by monotypy. Holotype of *G. propensa* in MNHUB.

Species included. *Gyrasida* includes six species: *G. propensa* (Wilke) (type species), plus five species described by Vidal & Flores (2007): *G. lucianoi* Flores & Vidal, *G. fernandoi* Flores & Vidal, *G. tomasi* Vidal, *G. franciscae* Vidal, and *G. camilae* Vidal. Key to species in Vidal & Flores 2007: 415.

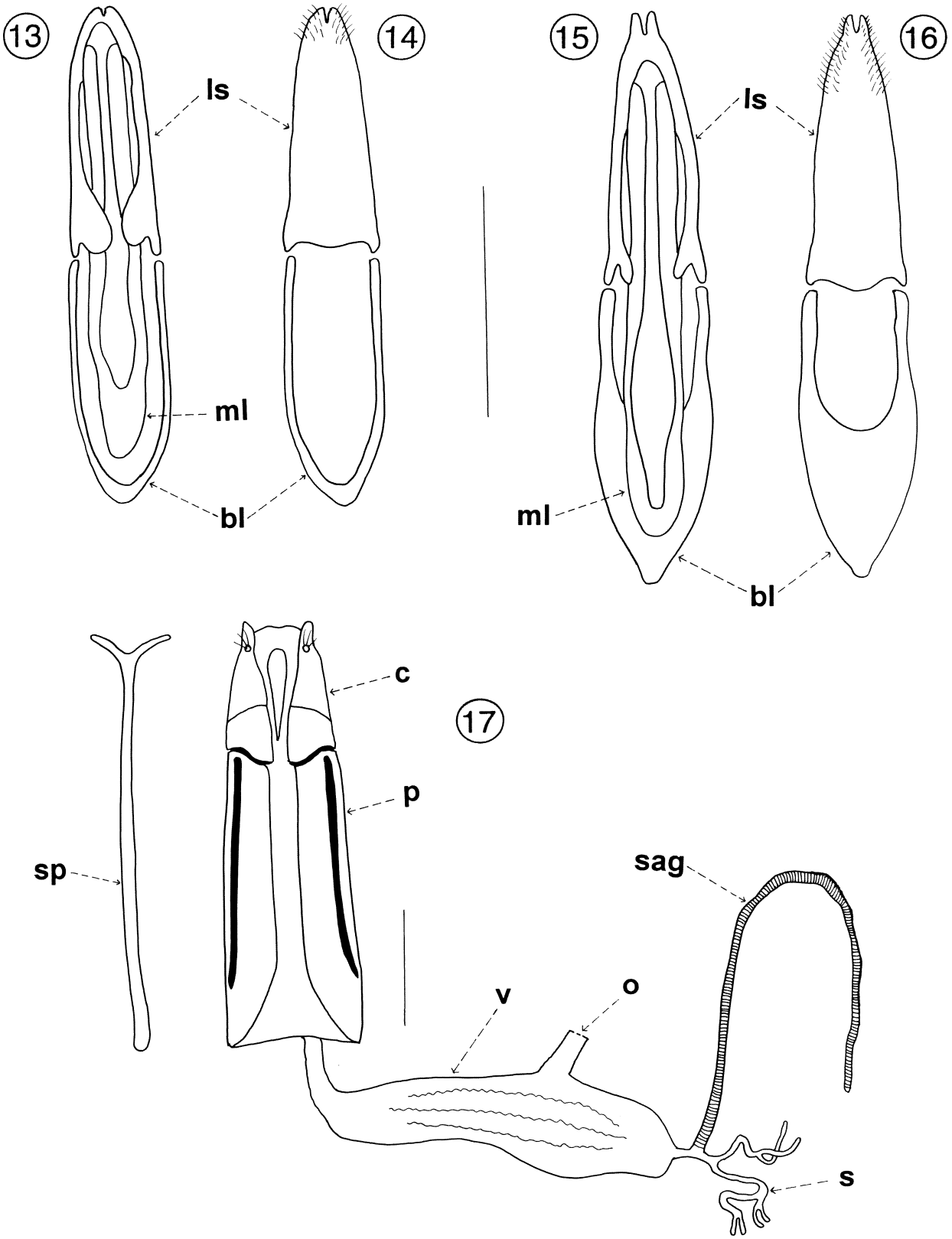
Diagnosis. Recognized among other Praocini by the following combination of characters: profemora with a conspicuous, smooth, glabrous, and shiny longitudinal ridge on proximal half of anterior surface; anterior area of clypeus inclined downwards forming an angle; clypeal suture as horizontal groove, clypeus lower than frons; frons with two transverse carinae forming an inverted "V", covering dorsally the clypeal suture; maxillary palpi with last segment subcylindrical; antennomere 11 longer than 10; pronotum widest at the midpoint; central area of anterior margin of pronotum notched and broadened; elytron with a main paramedian carina; anterior quarter of epipleuron twice as wide as posterior half; sexual dimorphism: female with a central nipple-shaped process on central area of metasternum, male lacking central process on central area of metasternum.

Redescription. Length 7.5–15.0 mm; habitus oval, flattened or convex; body dark brown to black with antennae and legs dark brown to black.

Head. Hypognathous. Epipharynx with anterior margin dorsally exposed. Labrum with large punctures and setae, widest at the midpoint. Clypeus notched anteriorly, with deep and irregular punctures, with setae, and two lateral depressions; anterior area of clypeal surface inclined downwards forming an angle; clypeal suture wide, as horizontal groove divided centrally by a longitudinal depression going up towards frons; clypeus lower than frons. Frons pubescent, with two transverse carinae forming an inverted "V", covering dorsally the clypeal suture, with a longitudinal groove, and with two protuberances medial to eyes. Ligula sclerotized and ventrally exposed, exceeding half mentum area, subequal in width and size to mentum (Fig. 10); labial palps inserted at middle of ventral surface of ligula; base of mandible two times higher in respect to apex; maxillary palpi with last segment subcylindrical (Fig. 10). Eyes oval, not depressed by frontal proyection. Antennae short, reaching 1/3 to 1/2 of lateral margin of pronotal length; length of antennomere 11 longer than 10; antennomeres 9 and 10 with a unique semicircular terminal tomentose sensory patch.

Thorax. Pronotum with two kinds of setae, one stout, arising in spinae, dark brown, and other finer arising from slightly raised protuberances, golden or light brown; with large, irregular punctures and protuberances; anterior angles rounded; anterior margin with central area notched, broadened, lacking edge, without groove between anterior margin and disc, width of anterior margin not exceeding the width of posterior margin; lateral margin concave (Fig. 1), remote from disc, widest at the midpoint, with frequent stout setae and very few finer ones; posterior margin bisinuate, with a slightly marked median notch, of similar width to base of elytra, joined in central half to elytra; disc convex, with a longitudinal central groove wider in central area, with two smaller lateral depressions, with two or four large protuberances, and many small, irregular protuberances, sometimes confluent. Prosternum horizontal to discretely convex, with distinctive anterior margin projected anteriorly covering mouthparts ventrally. Proepisternum with setae and protuberances, without grooves. Prosternal apophysis subrectangular or rounded, expanded or not distally. Mesosternum inclined forward, separated from prosternum. Meso- and metepisternum with punctures, with rugose striae.

Elytron with dorsal surface arched, pubescent, without punctures, with many irregular protuberances, sometimes sharp or spine like; with a main carina paramedian, raised, with or without secondary lateral carina; suture slightly raised or not; posterior third with two protuberances continuous with main carina; dorsal surface with symmetrical rows of wrinkles and protuberances irregularly arranged pointing downwards between suture and main carina; lateral margin simple and sinuate; pseudopleuron with protuberances and setae, some of which arising from protuberances, without punctures; epipleuron conspicuous or not, with setae and protuberances, similar to pseudopleuron in texture, wider anteriorly, anterior quarter twice as wide as posterior half, anterior margin not reaching elytral humeri nor posterior pronotal angle, texture similar to that of elytron, and with a slight posterior longitudinal groove over its medial side related to ventrites 6 and 7.



FIGURES 13–17. Male and female genitalia of *Gyrasida* spp. 13–16, Male genitalia in dorsal and ventral views. 13–14, *G. franciscae;* 15–16, *G. camilae*. Abbreviations: bl, basal lamina of tegmen, ls, lateral styles of tegmen, ml, median lobe. 17, Ovipositor (ventral view), spiculum and internal female reproductive tract of *G. propensa*. Abbreviations: c, coxite, o, oviduct, p, paraproct, s, spermatheca, sag, spermathecal accessory gland, sp, spiculum, v, vagina. Scale bars: 1 mm.

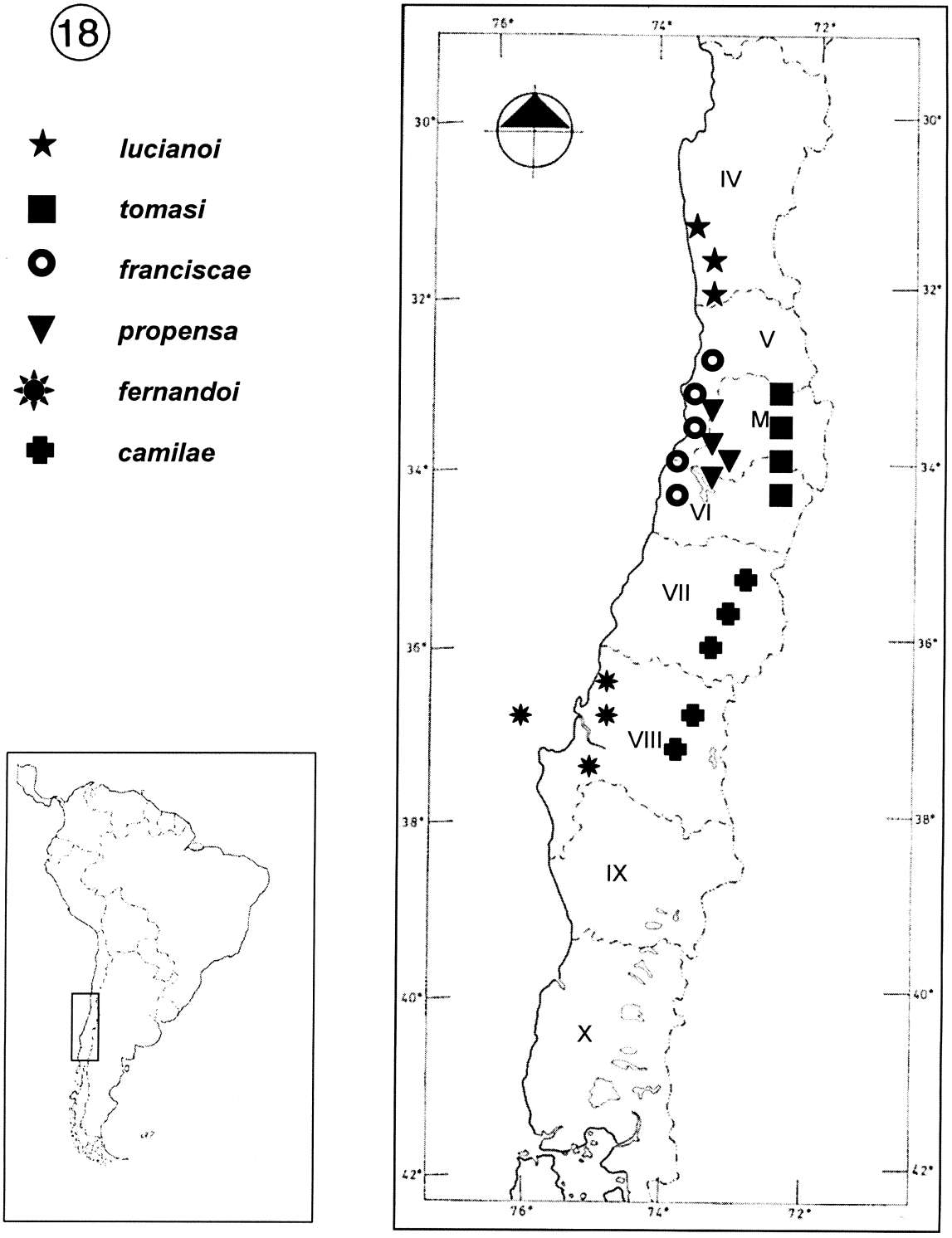


FIGURE 18. Geographical distribution of the six species of *Gyrasida*.

Venter. Distance between meso- and metacoxae exceeding half of metacoxal length (Fig. 12). Abdominal sterna with many setae and some spines and protuberances irregularly distributed.

Legs. Densely covered by setae, many of them arising from sharp spines. Profemora with a conspicuous, smooth, glabrous, and shiny longitudinal ridge on proximal half of anterior surface. Tibiae with multiple spines, external process of distal margin of protibiae of equal length of protarsomere 1 + 2 combined.

Sexual dimorphism. Female with a nipple-shaped process on central area of metasternum, glabrous, shiny, pink to dark brown (Vidal & Flores 2007: Fig. 2), male lacking central process on central area of metasternum.

Internal skeletal anatomy. Tentorium with medial straight bridge. Proendosternite joined to posterior part of procoxal cavities, with posterior arms short, directed posterad and broadened in posterior margin. Mesendosternite with horizontal arms short, with long, slender dorsal arms three times as long as horizontal arms, extended about half distance to tergum. Metendosternite (Vidal & Flores 2007: Fig. 3) with arms long, fused with mesocoxal inflexions, extending beyond mesocoxal inflections about one third distance to tergum; width of stem equal to metacoxal width, length of stem exceeding width, and stem wider in upper than basal part. Elytral-abdominal fusion accomplished by a ridge in the elytral epipleuron, which joins by a simple coaptation without interlocking with the abdominal sterna (Doyen 1994: Fig. 205).

Male genitalia (Figs. 13–16). Dorsal membrane of proctiger concave, with two sclerotized areas. Basal lamina of tegmen long (B/E > 1.0). Lateral styles of tegmen distally separated, widest at base, with setae on lateral margin and ventral surface. Median lobe moderate (0.75 < L/T ≤ 1.00), sheath-shaped, with apex rounded, not sclerotized ventrally, half the width in respect to tegmen, of equal width throughout.

Female genitalia (Fig. 17). Spiculum with arms "V"-shaped. Coxites with short setae, basal lobe not extended over paraproct, baculi inclined 45°, midventral sclerite distally broadened. Paraprocts long (2.0 < P/C ≤ 3.0), glabrous. Proctiger with apicodorsal lobe extending length of coxite and with dorsal baculus extending proximad much beyond paraproct baculus. Vagina saccate. Spermathecal accesory gland two times length of vagina, with duct annulate and thick. Spermatheca with three tubes or less, shorter than vagina, all similar in width and branching pattern. Substantial variation in female genitalia was not found between the species of *Gyrasida*.

Geographic distribution. The species of *Gyrasida* occur in central Chile, in regions IV, V, VI, VII, VIII, and Metropolitan, from parallel 32º South to parallel 38º South (Fig. 18).

Habitat. The distribution range of the genus is from sea level to an altitude of 2000 meters. Its species occur in plain and mountain arid and semiarid environments of entomofaunal regions Coquimban Desert, Central Valley, Central Coastal Cordillera, and Northern Valdivian Forest (Peña 1966).

Biology. Members of this genus live in leaf litter, under small logs and branches, always covered by the shadow of trees, usually well away from the sunlight. They are not found where the forest has been destroyed. Adults are nocturnal, and feed on plant debris. Copulating specimens have been observed to spend several hours coupled. Females lay their eggs by burying them in moist soil.

Cladistic analysis of *Gyrasida*

Methods. Outgroups. Character polarity was determined by the outgroup comparison method (Nixon & Carpenter 1993). Outgroups were used to provide a root for the cladogram and to test the monophyly of *Gyrasida*, not to explore the sister group relationships of *Gyrasida*. Since no phylogeny for the genera of Praocini was available, the chosen outgroups within Praocini were the genera *Praocis* Eschscholtz, *Platesthes* Waterhouse, *Falsopraocis* Kulzer, *Antofagapraocis* Flores, and *Platyholmus* Solier. The present analysis is based on 11 terminal units: six species of *Gyrasida* plus the following outgroup species: *Praocis rufipes* Eschscholtz (type species), *Platesthes similis* Kulzer, *Falsopraocis ricardae* (Solier) (type species), *Antofagapraocis subnudus* Flores, and *Platyholmus uspallatensis* Fairmaire.

Characters. We used 90 characters (Appendix 1) of which 78 are derived from the external morphology, 10 from male genitalia, and 2 from female genitalia. The distribution of states among the terminal taxa is indicated in the data matrix (Appendix 2). For basal lamina/lateral styles of tegmen length (character 81), we considered the ratio proposed by Flores (1996), and for paraproct length/ coxite length (character 90), we considered the ratio proposed by Doyen (1994). Multistate characters 12, 13, 15, 18, 24, 25, 27, 30, 31, 33, 36, 37, 38, 48, 59, 60, 62, 71, 79, 83, 84, 86, 87, and 88 were treated as non-additive because it was not possible to

make a correlation between apomorphic states. Multistate characters 66 and 75 were ordered as a logical sequence. For the different states exhibited by the main carinae (characters 48-51), the absence of carinae was coded only once in the character 48 to avoid repeat this state four times and the consequently heavily weighting of this character state. In characters 49-51 the absence of carinae was coded as non comparable (–) for the species *Praocis rufipes*, *Antofagapraocis subnudus*, and *Platyholmus uspallatensis*.

Procedure. The data matrix (Appendix 2) was analyzed with Nona version 2.0 (Goloboff 1993), applying the command sequence hold 10,000; hold/100; mult* 100, and max*. The consistency and retention indices (Farris 1989) were calculated excluding autapomorphies (characters 19, 20, 26, 39, 44, 46, 52, 54, 70, and 76) because they inflate consistency index and do not support groups of taxa (Forey et al. 1992). Clados version 1.8.1 (Nixon 1993) was employed for examination of character distribution and to print the cladogram.

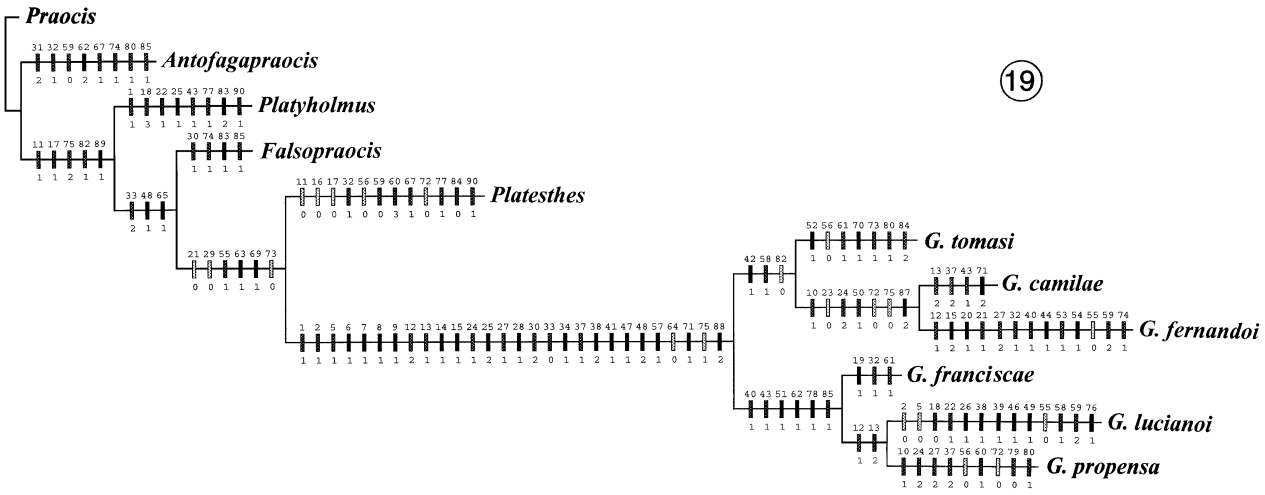


FIGURE 19. Cladogram showing relationships of species of *Gyrasida*. Black squares: non-homoplasious apomorphies; dotted squares: homoplasies.

Results and discussion. The analysis of the data matrix (Appendix 2) produced one most parsimonious cladogram 187 steps long, with a consistency index (CI) of 0.60 and a retention index (RI) of 0.68 (Fig. 19). The monophyly of *Gyrasida* is established by the following 20 synapomorphies (Fig. 19), of which 19 are from external morphology: character states 6.1, 7.1, 8.1, 9.1, 12.2, 14.1, 15.1, 24.1, 25.2, 27.1, 28.1, 30.2, 34.1, 38.2, 41.1, 47.1, 48.2, 57.1, 71.1, and one from male genitalia: apex of median lobe rounded, not sclerotized ventrally (87.2). Examination of the external morphology of species from all the remaining genera of Praocini (*sensu* Kulzer 1958; Flores 2000b, 2001, 2004; Flores & Chani-Posse 2005) not used as outgroups in this analysis, revealed that the character states clypeus with medial area raised (7.1), clypeus with two medial depressions (9.1), frons with two transverse carinae (with two states within *Gyrasida*, 12.2 and 12.1), frons with two protuberances medial to eyes (with two states within *Gyrasida*, 15.1 and 15.2), pronotum with stout setae arising from spinae (with two states within *Gyrasida*, 24.1 and 24.2), lateral margin of pronotum with frequent stout setae (30.2), pronotum with two lateral depressions to groove (with two states within *Gyrasida*, 38.2 and 38.1), metasternum of female with a central nipple-shaped process (47.1), lateral margin of elytra sinuate (57.1), and profemora with a longitudinal ridge on proximal half of anterior surface (with two states within *Gyrasida*, 71.1 and 71.2) are unique to *Gyrasida* within Praocini. The character states clypeus with anterior area inclined downwards (6.1) and pronotum with raising anterior of disc (34.1) are shared with the species of *Calymmophorus* Solier; lateral depressions present in anterior area of clypeus (8.1) is shared with the monotypic genus *Asidelia* Fairmaire and some species of *Praocis* (*Filotarsus*) Solier; frons with longitudinal groove (14.1) is shared with the monotypic genus *Neopraocis* Kulzer; pronotum with frequent finer setae arising from protuberances (25.2) is shared with the monotypic genus *Eutelocera* Solier and the species of *Thylacoderes* Solier; pro-

notum with depression formed by anterior angle and anterior margin (with two states within *Gyrasida*, 27.1 and 27.2), is shared with the species of *Calymmophorus* and *Neopraocis*; anterior margin of pronotum notched (28.1) is shared with the species of *Eutelocera* and *Neopraocis*; prosternum covering mouth parts ventrally (41.1) is shared with the species of *Calymmophorus* and *Thylacoderes*, and elytron with one main carina (48.1) is shared with the monotypic genera *Neopraocis* and *Pilobaloderes* Kulzer, both species of *Praocidia* Fairmaire, and some species of *Praocis* (*Hemipraocis*) Kulzer.

The species of *Gyrasida* are grouped in two clades, one includes three species in the sequence (*G. tomasi*, (*G. camilae*, *G. fernandoi*)) and the other clade is formed by three species in the sequence (*G. franciscae* (*G. lucianoi*, *G. propensa*)) (Fig. 19).

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Appendix 1. Characters and character states used in the cladistic analysis of *Gyrasida* (0= plesiomorphic; 1, 2, 3 = apomorphic)

Characters	Character states
Head	
1. Head, position	Prognathus (0); hypognathus (1).
2. Labrum, anterior margin	Notched in central area (0); slightly notched in central area (1).
3. Labrum, setae	On all entire surface (0); only on distal margin (1).
4. Clypeus, setae	Uniform (0); more frequent in posterior 2/3 (1).
5. Clypeus, punctures	Small and shallow (0); large and deep (1).
6. Clypeus, anterior area	Straight (0); inclined downwards (1).
7. Clypeus, medial area	Not raised (0); raised (1).
8. Clypeus, lateral depressions in anterior area	Absent (0); present (1).
9. Clypeus, medial depressions	Absent (0); present (1).
10. Clypeus, anterolateral margin	Not pronounced (0); pronounced (1).
11. Clypeal suture	Vertical (0); horizontal (1).
12. Frontal transverse carinae	Absent (0); present, not prominent (1); present, prominent (2).
13. Frontal transverse carinae	Absent (0); present, of similar height along its entire surface (1); present, higher medially (2).
14. Frontal longitudinal groove	Absent (0); present (1).
15. Frontal protuberances medial to eyes	Absent (0); present, of equal height or lower than eyes (1); present, higher than eyes (2).
16. Maxillary palpus, last segment	Axe-shaped (0); subcylindrical (1).
17. Groove between eyes and frons	Absent (0); present (1).
18. Antennal length	Reaching the half of lateral margin of pronotum (0); reaching 1/3 of lateral margin of pronotum (1); reaching 3/4 of lateral margin of pronotum (2); reaching posterior margin of pronotum (3).
19. Antennomere 3, length	Not exceeding length of 4+5 (0); exceeding length of 4+5 (1).
20. Long setae on antennomeres 9, 10, and 11	Abundant (0); sparse (1).
21. Short setae on antennomeres 9, 10, and 11	Sparse (0); abundant (1).
22. Antennomere 10, width	Width equal to length or exceeding length (0); length exceeding width (1).

23. Antennomere 11, width	Not exceeding width of 10 (0); equal to width of 10 (1).
Pronotum	
24. Stout setae arising from spinae	Absent (0); present, frequent (1); present, sparse (2).
25. Finer setae arising from protuberances	Absent (0); present, sparse (1); present, frequent (2).
26. Squamous setae	Absent (0); present (1).
27. Depression formed by anterior angle and anterior margin	Absent (0); present, shallow (1); present, deep (2).
28. Anterior margin	Continuous (0); notched (1).
29. Lateral margin	Remote from disc (0); contiguous with disc (1).
30. Lateral margin	Lacking setae (0); with frequent finer setae (1); with frequent stout setae (2).
31. Widest	Behind midpoint (0); at the midpoint (1); before midpoint (2).
32. Posterior angles	Not overlapping elytral humeri (0); projecting backward over elytral humeri (1).
33. Posterior margin	Bisinuate (0); concave (1); straight (2).
34. Raising anterior of disc	Absent (0); present (1).
35. Raising posterior of disc	Absent (0); present (1).
36. Longitudinal medial groove	Absent (0); present, incomplete (1); present, complete (2).
37. Lateral protuberances to groove	Absent (0); present, merging together (1); present, not merging together (2).
38. Lateral depressions to groove	Absent (0); present, shallow (1); present, deep (2).
Proepisternum	
39. Surface	Lacking squamous setae (0); with squamous setae (1).
Prosternum	
40. Anterior margin	Rounded, not raised (0); sharp, raised (1).
41. Arrangement	Not overlapping mouth parts ventrally (0); covering mouth parts ventrally (1).
42. Distance between anterior margin and procoxae	Shorter than procoxal length (0); longer than procoxal length (1).
43. Apophysis	Lacking central groove (0); with central groove (1).
Meso- and metathorax	
44. Mesosternum	Higher than metasternum (0); of equal height to metasternum (1).
45. Mesosternum, finer setae	On all entire surface (0); on anterior half (1).
46. Mesosternum	Lacking squamous setae (0); with squamous setae on posterior half (1).
47. Metasternum of female	Smooth (0); with a central nipple-shaped process (Vidal & Flores 2007: Fig. 2) (1).
Elytra	
48. Main carinae	Absent (0); two (1); one (2).
49. Main carinae	Complete (0); incomplete (1).
50. Main carinae	Thin (0); thick (1).
51. Main carinae	Straight (0); sinuate (1).
52. Secondary lateral carina	Absent (0); present (1).
53. Suture	Not raised (0); raised (1).
54. Suture	Thin (0); thick (1).
55. Lateral margin	Rounded (0); prominent (1).
56. Lateral margin	Thin (0); thick (1).
57. Lateral margin	Straight (0); sinuate (1).
58. Lateral margin, posterior part	V-shaped (0); parallel to suture (1).
59. Pseudopleuron, protuberances	Absent (0); present, not grouped (1); present, grouped (2).
60. Epipleuron	Conspicuous throughout (0); conspicuous only in anterior half (1); not conspicuous (2); conspicuous in posterior 4/5 (3).

61. Epipleuron	Not broadened posteriorly in relation to ventrite 7 (0); broadened posteriorly in relation to ventrite 7 (1).
62. Epipleuron	With setae on all entire surface (0); glabrous on anterior part (1); glabrous (2).
63. Epipleuron, texture	Different than that of elytra (0); similar to that of elytra (1).
64. Epipleuron, anterior margin	Not reaching elytral humeri (0); reaching elytral humeri (1).
65. Epipleuron, anterior margin	Reaching posterior angle of pronotum (0); not reaching posterior angle of pronotum (1).
66. Epipleuron, anterior quarter	Four times as wide as posterior half (0); three times as wide as posterior half (1); twice as wide as posterior half (2).
67. Epipleuron surface	With protuberances (0); punctate (1).
Abdominal sternum 3	
68. Two patches of brown setae behind metacoxae	Absent (0); present (Fig. 12) (1).
Legs	
69. Ventral surface of trochanters	With brush-like pubescence (0); with uniform pubescence (1).
70. Femora	Lacking wooly setae (0); with wooly setae (Vidal & Flores 2007: Fig. 9) (1).
71. Ridge on profemora	Absent (0); present, on upper half of proximal anterior surface (1); present, on entire proximal anterior surface (2).
72. Mesofemora, posterior surface	Glabrous (0); with setae (1).
73. Metafemora, posterior surface	Glabrous (0); with setae (1).
74. Protibiae, distal margin	U-shaped (0); straight (1).
75. Protibiae, width of distal margin	Exceeding 1/3 protibial length, but not exceeding half protibial length (0); equal to 1/3 protibial length (1); equal to 1/4 protibial length (2).
76. Apical process of distal margin of protibiae	Rounded (0); acute (1).
77. Apical process of distal margin of protibiae	Exceeding length of protarsomere 1 (0); equal or not exceeding length of protarsomere 1 (1).
78. Setae on ventral surface of tarsi	Sparse (0); with a tuft of golden setae (1).
Male genitalia	
79. Rods of sternum IX	"V"-shaped (0); close at basal third (Flores 1996: Fig. 33) (1); close at basal half (2).
80. Distance between rods of sternum IX	Not exceeding width of aedeagus (0); exceeding width of aedeagus (1).
81. Length basal lamina/ lateral styles of tegmen	Long (B/E > 1.00) (Fig. 16) (0); short (B/E ≤ 1.00) (1).
82. Lateral styles of tegmen, apex	Narrow (0); wider (1).
83. Lateral styles of tegmen	Widest at base (Fig. 16) (0); widest at base and mid point (1); widest at distal third (2).
84. Lateral styles of tegmen	Ventrally concave (0); ventrally bisinuate (1); ventrally triangular (2).
85. Lateral styles of tegmen	Not overlapping dorsally median lobe (0); projecting dorsally over median lobe (1).
86. Setae of lateral styles of tegmen	On ventral surface and lateral margins (Fig. 16) (0); only on lateral margins (1); on ventral surface, lateral margins, and dorsal surface (2).
87. Setae of lateral styles of tegmen	On distal 1/5 (Fig. 14) (0); on distal half (1); on distal third (Fig. 16) (2).
88. Apex of median lobe	Acute, sclerotized ventrally (0); rounded, sclerotized ventrally (1); rounded, not sclerotized ventrally (Figs. 14, 16) (2).
Female genitalia	
89. Paraprocts	With setae (0); glabrous (1).
90. Length paraproct/ coxite	Long (2,0 < P/C ≤ 3,0) (Fig. 17) (0); very long (P/C > 3,0) (Flores 1996: Fig. 1) (1).

APPENDIX 2. Data matrix of species of *Gyrasida* plus the outgroups *Praocis*, *Antofagapraocis, Platyhomus, Falsopraocis,* and *Platesthes*. 0-3= character states; a, polymorphy, a= 0/1; – = non comparable.

Taxa	Characters 1 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
Praocis	0000000000 0000000000 1000000001 0000000000 00000000–– –000000010 0000000000 0110000000 0000000000
Platesthes	0000000000 0000000000 0010000000 0120000000 0000000100 0000100003 0011111010 0000201010 0100020111
Platyholmus	1000000000 1000011300 1110100010 0010000000 00100000–– –000010010 0001010000 0110201010 1121010111
Falsopraocis	0000000000 1000011200 1010000011 1020000000 0000000101 0000010010 0001120000 0111200010 0111110110
Antofagapra.	0000000000 0000010200 1010000010 2110000000 00000000–– –000010000 0201021000 0111100011 1002110100
G. tomasi	1111111110 1211111100 0011201102 1001111200 1100101200 0100101112 1010120111 1110100001 0002000210
G. camilae	1111111111 1221111100 0002201102 1001122200 1110101201 0000111110 0010120110 2000000020 0001002210
G. fernandoi	1100111111 1111211101 1002202102 1101111201 1101101201 0011011122 0010120110 1001000020 0001002210
G. franciscae	1100111110 1211111110 0011201102 1101121201 1010001200 1010111010 1110120010 11a0100110 0101100210
G. lucianoi	1000011110 1121111000 0111211102 1001021111 1010111210 1000011120 0110120110 1100110110 0101100210
G. propensa	1100111111 1121111100 0012202102 1001022201 1010101200 1010101011 0110120110 1000100101 0101100210