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Revision of the Neotropical ant subfamily Leptanilloidinae

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Abstract. The rare Neotropical ant subfamily Leptanilloidinae is revised and its internal phylogeny and biogeography discussed. A new genus, *Asphinctanilloides* gen.n., including three new species, *A. amazona*, *A. anae* and *A. manauara*, and three new species of *Leptanilloides*, *L. improvisa*, *L. legionaria* and *L. sculpturata* are described. The only previously known species of the subfamily, *L. biconstricta* Mann (1923), is redescribed, and the larva of *L. legionaria* sp.n. is described. Keys to the genera and the species, and a phylogeny of the group are provided. Emphasis has been placed on the study of abdominal and sting characters.

Introduction

Mann (1923) described the monotypic genus *Leptanilloides*, considering it an aberrant Dorylinae (in the concept that currently corresponds to Ecitoninae), with a 'head structure that associates it more closely to *Eciton*, although closely similar in overall appearance to *Leptanilla*'.

Borgmeier (1955) redescribed and illustrated a worker of the type series, saying that it 'shows a mixture of characters of the Ecitoninae and Leptanillinae, but cannot be placed in either of these groups. Perhaps the concept of the subfamily Leptanillinae should be expanded and a tribe established just for *Leptanilloides*.' However, Bolton (1990b) did not recognize *Leptanilloides* as a Leptanillinae.

Brown (1975) included *Leptanilloides* in the Cerapachyini within the Cerapachyinae, close to *Sphinctomyrmex*. This arrangement was followed by Bolton (1990c) in his definition of the doryline section of the ant subfamilies.

Bolton (1990a) was the first to study the rather special construction of the abdominal segments in ants, defining the abdominal character terminology of ants in general, and of Cerapachyinae in particular. He included *Leptanilloides* in the Cerapachyini, along with *Cerapachys*, *Simopone* and *Sphinctomyrmex*.

In their phylogenetic analysis of the subfamilies of ants, Baroni Urbani *et al*. (1992) raised *Leptanilloides* to subfamily status because *Leptanilloides* turned out to be the sister group of (Cerapachyinae + (Ecitoninae + (Dorylinae + Aenictinae + Aenictogitoninae))). The only apomorphy they accepted for the subfamily was the extremely reduced pygidium (tergite of the abdominal segment 7 = gastral segment 4), represented by a small, U-shaped sclerite, which is overhung by the tergite of the sixth abdominal segment (= gastral segment 3). This result was later confirmed by Grimaldi *et al*. (1997). Bolton (1994) provided a full diagnosis of the Leptanilloidinae, but did not distinguish between plesiomorphic and apomorphic states.

Until this study, the Leptanilloidinae was a monotypic subfamily, including one species of subterranean living ants, collected under stones in the Andean slopes. A search in various collections and faunistic and ecological fieldwork turned out to be rather successful in adding several new species, which are described below. Bolton (1990a: Fig. 23) mentioned and illustrated one undescribed species of *Leptanilloides* which he studied from the Museum of Comparative Zoology in Harvard.

However, it is questionable whether leptanilloidine ants are to be considered truly rare, or whether the low numbers in collections represents an artifact. It seems to be a common feature in ant systematics at the moment that rare ants turn out to be more common than previously assumed, based on published records and specimens available in collections. The most important reason for such a change is the recent use of specialized mass collection techniques, such as the Winkler extraction apparatus, soil samples or Berlese funnels. Thus, rare ants seem to be suddenly much more widespread and common. To give an example, the South American species of *Probolomyrmex*, which were earlier recorded only from two localities (Taylor, 1965), are known now from almost the entire

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range of the tropical wet forests (Agosti, 1995). However, this is not an exclusively tropical phenomenon. It has also been documented in the temperate regions, where in the vicinity of a small swimming pool in suburban Barcelona many of the ants considered to be extremely rare in Spain were found recently (Espadaler & López-Soria, 1991).

In the case of Leptanilloidinae, specimens of two new species described here were recovered from soil samples in just one spot in Central Amazonia, the only place until now where this method has been employed systematically.

We are aware of the fact that each of the new, recently discovered samples represents a new species. However, each of these new species is characterized by at least one discrete apomorphy and further characters, which even allow us to make a phylogenetic inference at species level (see below). We here formally revise the whole subfamily, based on workers and larvae, reassess the characters, especially those of the sting apparatus, comment on the paucity of biological information available and provide a phylogenetic analysis.

Materials, abbreviations, methods and measurements

All available specimens from the following collections were included in this study: American Museum of Natural History, New York, U.S.A. (AMNH); Centro de Pesquisas do Cacau, Itabuna, BA, Brazil (CEPLAC); Instituto de Pesquisas da Amazonia, Manaus, AM, Brazil (INPA); J. L. M. Diniz collection (JLMD); Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A. (MCZ); Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP); and National Museum of Natural History, Washington, DC, U.S.A. (NMNH).

In addition to the species mentioned below, the following species were also studied for phylogenetic purposes: *Eciton hamatum* Panama, Barro Colorado Island (Canal Zone) W. M. Wheeler # 190 (AMNH), Borgmeier det.; *Leptanilla* sp. Indonesia, Sumatra, G. Kerinci, Agosti, Burckhardt and Löbl col. (AMNH), and *Protanilla* sp. Pakistan, Malan Jaba, 18.v.1983, M. Brancucci col. # 17B, Agosti det. 1989 (AMNH). The characters of their venom apparatus have been extracted from Kugler (1992), and for *Eciton hamatum* from Hermann & Blum (1967).

The terminology for the ant characters follows those of Baroni Urbani *et al*. (1992). For study of the sting apparatus the specimens were dissected using the procedure described by Kugler (1978), with the following modifications: treatment for a few minutes in 40°C warm 10% potassium hydroxide or sodium hydroxide (until the muscular tissues are almost all removed) instead of hot lactophenol. The dissected parts were mounted in Hoyer's solution (30–40 ml water, 30 g of arabic gum, 200 g of chloral hydrate and 20 ml of glycerin) instead of glycerin jelly or Canada balsam.

The following measurements and indices were used: HL, head length from the anterior median clypeal border (not including the lamellate apron) to the median occipital border; HW, maximum head width in full-face view; SL, scape length excluding the condylar bulb; WL, alitrunk length from the base of anterior slope of pronotum to the lower posterior angle of propodeum (these measurements are given in mm). CI, cephalic index (HW × 100/HL), SI, scape index (SL × 100/HW). The sting reduction index, as employed by Kugler (1992) is defined as SRI (sting shaft length/pronotal width).

A Hitachi S600 was used for scanning electron microscopy (SEM) illustration, which allowed uncoated specimens to be studied. The larvae were critical point dried, coated and then treated for the SEM.

An abbreviated description of the character states and the data matrix are presented in Table 1. The matrix can be downloaded from http://research.amnh.org/entomology/social_insects.

HENNIG86 was used for the phylogenetic analyses. All characters were treated as unordered, and an exhaustive search was performed, using *ie**. Successive weighting was applied. The trees were generated by CLADOS (Nixon, 1992).

Leptanilloidinae Bolton

Leptanilloidinae Bolton, in Baroni Urbani *et al*., 1992: 317; Bolton, 1994: 71, Figs 170, 171.

Diagnosis. Leptanilloidinae is a monophyletic taxon diagnosed by the following apomorphies (workers only): (1) lateral blunt teeth on genae, overhanging the mandibles (Figs 15–18, 20); very small and not produced in *Asphinctanilloides anae* sp.n. (Fig. 19); (2) metatibial gland absent; (3) pygidium (tergite of abdominal segment 7 = gastral segment 4) extremely reduced to a small U-shaped sclerite, which is overhung by the tergite of abdominal segment 6 (= gastral segment 3) (Fig. 60); (4) gonostylus fused to the posterior arm of the oblong plate along its width, wide, without long setae; (5) several microtrichia and 2 longer sensillae at the presumed junction of gonostylus with posterior arm of oblong plate; (6) base of sting shaft with a pair of long setae that almost reach the sting apex. The inference of characters 3 to 6 as apomorphies for Leptanilloidinae is based on comparisons with the other subfamilies of the doryline-section *sensu* Bolton (1990c).

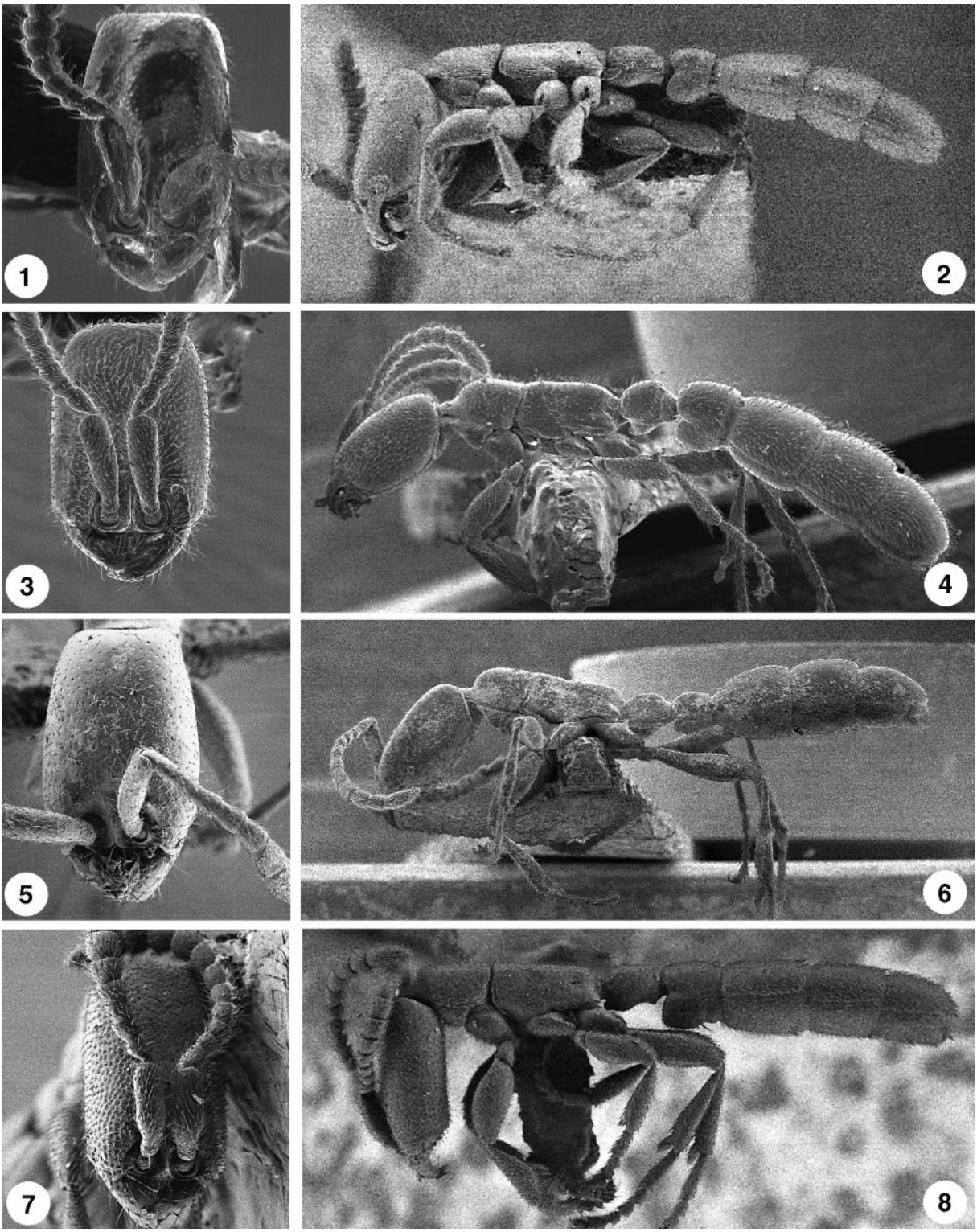
Description. Workers. Head subrectangular. Mandibles triangular elongate, with apex bent downwards in lateral view of dissected mandibles, with basal and masticatory margins distinct, the margins meet in a gentle angle (not marked by a tooth); with apical tooth and 7–10 preapical denticles. Palp formula 2:2. Clypeus in full-face view reduced to a small triangle, narrow front to back, especially in front of antennal sockets, anterior margin with a median seta and below with a fine, often transparent lamellate, triangular anterior apron. Vertical and very low frontal carinae border the horizontal antennal sockets medially, the latter in the plane of transverse axis of head; frontal carinae sometimes distinct from one another anteriorely between the sockets, although even then they are very closely approximated and in some species form a single vertical wall; antennal sockets always exposed in full-face view. Antennae 12-jointed, with enlarged scape reaching midlength of head; narrow neck joining condylar bulb of antennal scape to shaft of scape proper straight, not sharply

Table 1. Character matrix of the seven species of Leptanilloidinae and, as outgroups, *Leptanilla* sp. and *Protanilla* sp. *Eciton hamatum* was treated as an ingroup. All characters are treated as non-additive.

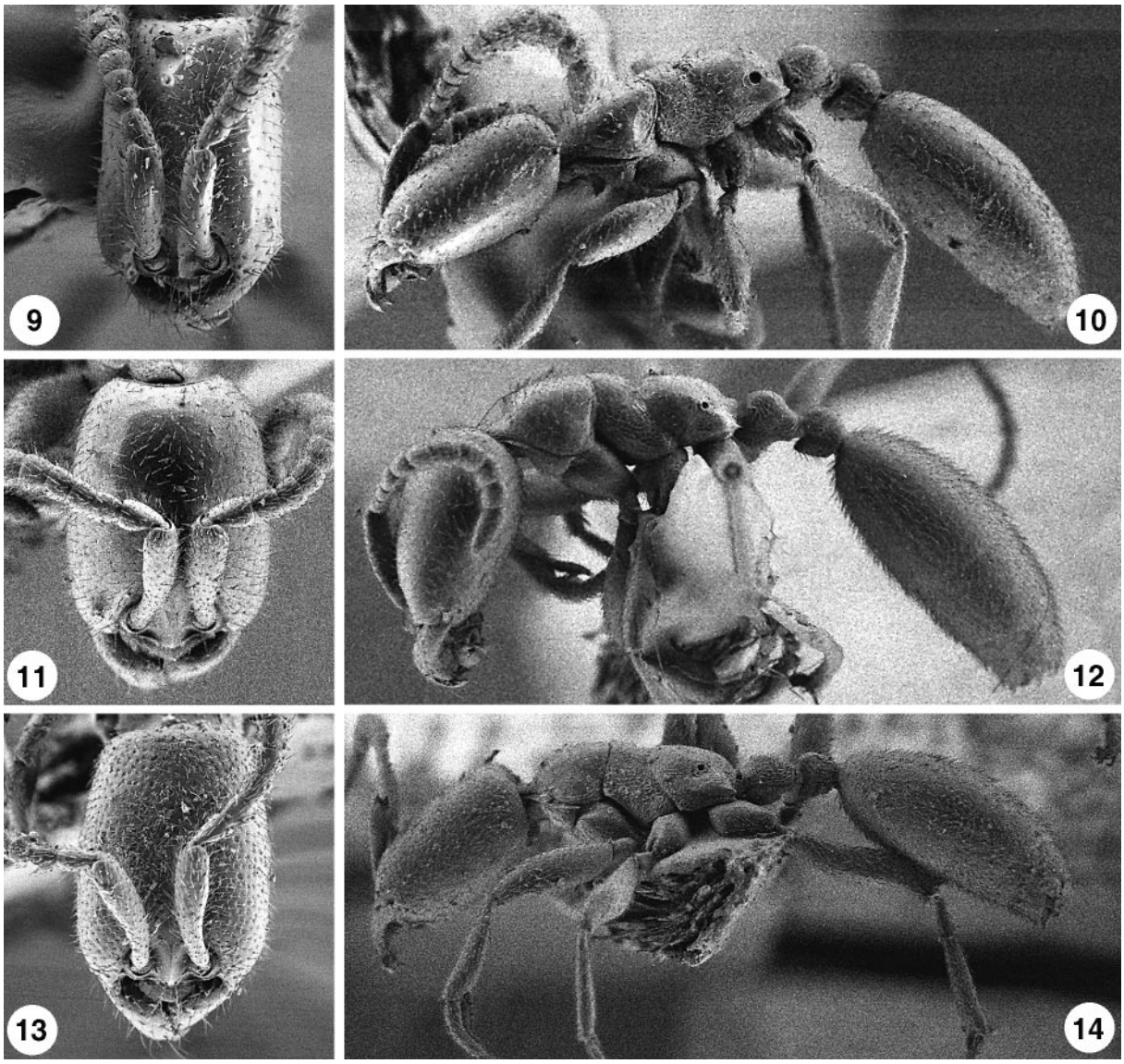
	1	1111111112	2222222223	3
	1234567890	1234567890	1234567890	1
Eciton hamatum	0110201011	00012–1000	1–––323000	1
Leptanilla sp.	0010000111	10–0220000	010021201–	2
Protanilla sp.	0110001111	10–1000–1–	––––0110–0	2
L. biconstricta	1001000000	0100000001	2000002100	0
L. improvisa	1011001000	01––––––––	1–––––––––	–
L. legionaria	1011101000	011––011–1	1011012101	1
L. sculpturata	1001001000	01–––––––1	––––––––––	–
A. amazona	1101010011	0120111011	2110110111	1
A. anae	1101010011	0121100111	2000110101	1
A. manauara	1101010011	0121110011	2110110110	1

1. *Lateral blunt teeth on genae*: (0) absent; (1) overhanging the mandibles.
2. *Propodeal dorsum*: (0) at least two times longer than declivity; (1) equal size.
3. *Flange over the metapleural gland opening*: (0) sharply pointed posteriorly (Figs 21, 24); (1) rounded (Figs 22, 23).
4. *Metatibial gland*: (0) present; (1) absent.
5. *Ventral process of the petiole*: (0) without a posterior angle; (1) with posterior angle; (2) projecting backward as a long spine.
6. *Postpetiolar spiracles*: (0) situated anteriorly; (1) at the midlength.
7. *Petiole*: (0) longer than the postpetiole; (1) shorter or same size.
8. *Helcium with sternite*: (0) well developed, bulging ventrally; (1) reduced, non bulging.
9. *Gaster with constrictions*: (0) between abdominal segments 4 and 5; (1) without.
10. *Gaster with constrictions*: (0) between abdominal segments 5 and 6; (1) without.
11. *Abdominal spiracles 5–7*: (0) backwards on post tergite and visible; (1) near the pretergite and always concealed.
12. *Pygidium (tergite of abdominal segment 7)*: (0) normally developed; (1) extremely reduced to an U-shaped sclerite, which is overhung by the tergite of abdominal segment 6.
13. *Anterior margin of the median connection between the two spiracular plates*: (0) straight; (1) convex; (2) bilobed.
14. *Quadrate plate*: (0) with antero-dorsal corner with long projection; (1) without.
15. *Quadrate plate apodeme*: (0) smaller or as wide as body of the plate; (1) wider; (2) not differentiated.
16. *Oblong plate*: (0) with postincision towards the dorsal margin, although it may not touch it; (1) with no postincision; (2) with postincision parallel to the dorsal margin.
17. *Oblong plate*: (0) sclerotized; (1) weakly sclerotized.
18. *Ventral arm of apodeme*: (0) reduced; (1) developed.
19. *Fulcral arm*: (0) present; (1) absent.
20. *Gonostylus*: (0) unfused and separated from the posterior arm of oblong plate; (1) fused along its width.
21. *Sensillae on gonostylus*: (0) clumped on the distal end and with a pair of setae; (1) several microthrichiae and two longer sensillae at the presumed junction of gonostylus with posterior arm of oblong plate; (2) scattered all over the plate.
22. *Gonostylus*: (0) with more than 30 sensillae; (1) with less than 30.
23. *Sensillae on anal plate*: (0) with socket; (1) without.
24. *Microtrichiae (no sockets visible) on anal plate*: (0) present; (1) absent.
25. *Furcula*: (0) convex; (1) concave; (2) Y-shaped; (3) absent.
26. *Furcula*: (0) with long lateral arms, so that inner margin of furcula is separated from sting base (Fig. 59); (1) without; (2) furcula not present.
27. *Wing projections of furcula*: (0) long; (1) present as tubercles; (2) absent; (3) furcula not present.
28. *Base of sting shaft*: (0) without a pair of setae; (1) with a pair of long setae that almost reach sting apex.
29. *Sting with bulb base*: (0) rounded; (1) emarginate.
30. *Basal ridge of sting*: (0) visible; (1) not visible.
31. *Anterolateral process of sting base*: (0) long (Fig. 59); (1) short; (2) absent.

angled or bent downwards in frontal or full-face view; anterior region of scape shaft bent outwards; funicular segments wider at antennal apex, although not forming a club. Blunt lateral teeth on gena, overhanging mandibles (Figs 15–18, 20), very small and not produced in *Asphinctanilloides anae* sp.n. (Fig. 19). Eyes absent. Margin of vertex present, but not too marked. Promesonotal suture present and flexible, distinct laterally and dorsally, although dorsal profile of alitrunk may be flat; pronotum capable of movement relative to mesonotum. Propodeum unarmed, with spiracles at midlength of sclerite side. Propodeal lobes absent. Metapleural gland opening laterally in lower posterior corner of metapleuron, concealed behind by a ventrally directed translucent cuticular flange, posteriorly produced. Metacoxal cavity closed; cuticular annulus around cavity broad and complete, not broken medioventrally nor with a flexible suture traversing annulus from coxal cavity to cavity in which the petiole articulates. Metatibial gland absent; basitarsal sulcus absent. Simple and small spur on mesotibia; spur on hind tibia triangular, broadly pectinate. Claws simple. Abdominal segment 2 (petiole) with



Figs 1–8. Head in full-face view and lateral view of the whole body of *Leptanilloides spp.* 1,2, *L. biconstricta*; 3,4, *L. improvisa*; 5,6, *L. legionaria*; 7,8, *L. sculpturata*.



Figs 9–14. Head in full-face view and lateral view of the whole body of *Asphinctanilloides spp.* 9,10, *A. amazona*; 11,12, *A. anae*; 13,14, *A. manauara*.

tergosternal fusion. Petiole sternite with a simple posterior margin and simple articulation to postpetiole. Presclerites of abdominal segment 3 (helcium) fused, at least posteriorly; presternite of helcium large and convex, protruding ventrally and thus not covered by pretergites, visible in mounted specimens; tergite of helcium lacking a notch or impression in dorsal margin anteriorly. Abdominal segment 3 (postpetiole) with tergosternal fusion, but with a visible suture. Spiracles on side of postpetiole situated either forward or at midlength of segment. Abdominal stridulatory system absent. Abdominal segment 4 (gastral segment 1) with presclerites sharply defined and differentiated from postsclerites, the former fitting tightly within posterior end of third abdominal segment. Abdominal segments 4–7 not fused, with spiracles not concealed by posterior margins of preceding segments and visible without distention or dissection of gaster. Pygidium (tergite of abdominal segment 7 = gastral segment 4) extremely reduced to a small U-shaped sclerite, overhung by tergite of abdominal segment 6 (= gastral segment 3), convex, unarmed; hypopygium (sternite of 7th abdominal segment) straight and flattened. Sting present, not reduced. Spiracular plate diamond-shaped; median connection sclerotized, posterior margin continuous with anal plate and quadrate plate connections; without dorsal notch; anterior apodema reduced, posteroventral corner produced ventrad as a clearly defined tubercle; spiracle very large, covering almost half plate; no posterodorsal lobe. Quadrate plate rectangular, long, narrow; reduced body, at most with size of apodema; anterior margin of apodema without

sclerotized swelling; anterodorsal corner prominent, sharp, somewhat produced in *L. biconstricta;* posterior margin continuous. Anal plate very large, triangular, usually wide at base, not divided in small plates as in *Leptanilla*, with attenuate apex, not very much sclerotized and always without long setae, but with several microtrichiae. Elongate triangular plate length at least twice width; always with dorsoapical and ventral processes, never with median and dorsal tubercles. Oblong plate anterior apodema well developed, long and weakly sclerotized, with blunt end; 3 or 4 intervalvifer sensillae; postincision distinct in some species, but never reaches dorsal margin of posterior arm; some species lack postincision; ventral arm short and not so well sclerotized as rest of plate; fulcral arm small, tuberculate, visible only in some species. Gonostylus fused to posterior arm of oblong plate along width, wide, without long setae; several microtrichiae and 2 longer sensillae at presumed junction of gonostylus with posterior arm of oblong plate; without terminal membranous flange. Lancet with acute apex without barbs, with 2 valves. Furcula fused to sting base; without dorsal arm. Sting with short and acute shaft; base of sting shaft with a pair of long setae that almost reach sting apex, sting apex without barbs; valvules at median region of sting, within valve chamber; basal ridge confluent with furcula (see *L. biconstricta*); articular process short, at basal portion of sting bulb; anterolateral process short, a little anterior to articular process, in special in *L. biconstricta.*

Queens and males. Unknown.

Larvae (description based on characters defined by Wheeler & Wheeler, 1976; see description for *Leptanilloides* larvae below). Shape leptanilloid (elongate, slender, club-shaped), with a small neck (encompassing pronotum and mesonotum). Body hairs smooth and unbranched, mostly short, a few long and slightly curved. Head pyriform. Antennae one-segmented, subcylindrical with 2 terminal sensillae. Labrum modified and bulging, circular when viewed in frontal aspect. Mandibles with slender, sharp-pointed teeth directed outwards.

Comments. Leptanilloidinae have relatively small body size, slender body shape, brownish-yellowish colour, rectangular head, fully exposed and horizontal antennal sockets, short antennal scape that fails to reach the head vertex, eyes absent, extremely reduced clypeus in frontal view, promesonotal suture movable, the metapleural gland opening covered by a translucent flange and the helcium sternite convex. The lateral teeth on the genae are similar to those in some amblyoponines and the fossil ponerine *Brownimecia* (Agosti *et al*. 1998; Grimaldi *et al*., 1997). They can be recognized from all other ants by their unarmed pygidium reduced to an U-shaped sclerite almost concealed by the 6th abdominal tergite.

Distribution and biology. Leptanilloidinae are exclusively Neotropical. Information on the biology of the subfamily is almost nonexistent; the only observation, by Jorge L. M. Diniz, refers to *Asphinctanilloides anae* sp.n., preying on an unidentified arthropod and walking in columns similar to those of army ants. The only known sample of *L. legionaria* includes workers and larvae, one of the workers carrying a larva under its alitrunk. The position of Leptanilloidinae as the supposed sister group of (Cerapachyinae + (Ecitoninae + (Dorylinae + Aenictinae + Aenictogitoninae))) (Baroni Urbani *et al*., 1992) as part of the doryline section, their morphological similarity with the hypogaeic foraging army ants, and the cited observation on one species, suggest an army ant life style. The similar size of all the larvae suggests furthermore a synchronized production of offspring, another character of army ants (see Gotwald, 1995 for further references).

Phylogenetic position. The Leptanilloidinae share with the other doryline-section subfamilies (*sensu* Bolton, 1990c; modified by Baroni Urbani *et al*., 1992) the clypeal and antennal sockets structures, the narrow neck joining the antennal condylus to the scape shaft, the cuticular flange covering the metapleural gland orifice, the convex helcium sternite (although not as bulging as in other subfamilies of the doryline-section) and the gastral spiracles shifted backwards in the tergites, fully visible without dissection or distention of the segments. As pointed out by Bolton (1990c), *Leptanilloides* lacks even the orifice of the metatibial gland. Our preparations of *Asphinctanilloides* confirm the lack of any trace of this gland in the subfamily. The only clear autapomorphy accepted by Baroni Urbani *et al*. (1992) for Leptanilloidinae is the reduced pygidium (tergite of the 7th abdominal segment) covered dorsally by the abdominal tergum 6. Further autapomorphies are given above. The following characters of Baroni Urbani's *et al*. (1992) matrix were recorded (originally coded as unknown): the labium has no pair of cylindrical pegs (their character 3), the petiole presents a tergosternal fusion (16), and the larval haemolymph feeding organ is absent (63). However, these changes do not affect the topology of the parsimony tree.

Although Bolton (1990c) states that the furcula appear, apomorphically, to be universally lost in the subfamilies of the doryline section, other authors (e.g. Hermann & Chao, 1983) consider the furcula present, but fused with the anterior end of the sting. In Leptanilloidinae, the furcula is not always fused to the base of the sting bulb, and appears to be freely movable in the non-fused condition.

Key to the genera (workers only)

1. Alitrunk flat without metanotal groove on dorsum; abdominal segments 5 and 6 (gaster segments 2 and 3) with a distinct, much narrower presclerite and wider postsclerite, resulting in constrictions between abdominal segments 4 and 5 (gaster segments 1 and 2), and 5 and 6 (gaster segments 2 and 3) (Figs 2, 4, 6, 8).....*Leptanilloides* Mann
– Alitrunk flat with a metanotal groove on the dorsum; abdominal segments 5 and 6 without separation into pre- and postsclerites and thus without constrictions between abdominal segments 4 and 5, and 5 and 6 (Figs 10, 12, 14) .....*Asphinctanilloides* gen.n.

Leptanilloides Mann (Figs 1–8, 15–17, 21–24, 28–35, 48–67)

Leptanilloides Mann, 1923: 13–15, Fig. 1. Type species: *Leptanilloides biconstricta* (by monotypy).
Leptanilloides: Borgmeier, 1955: 652 (redescription of worker).
Leptanilloides: Brown, 1975: 34 (transferred from Leptanillinae to Cerapachyini, Cerapachyinae).
Leptanilloides: Bolton, 1990c: 1357 (included in Cerapachyinae).
Leptanilloides: Bolton, 1990a: 61–63 (Figs 22, 23) (included in Cerapachyinae).
Leptanilloides: Bolton, 1994: 71 (Figs 170, 171).
Leptanilloides: Bolton, 1995a: 1040 (distribution).
Leptanilloides: Bolton, 1995b: 33 (catalogue).

Diagnosis. Leptanilloidine ants with the following synapomorphies (only worker caste and larvae known): (1) propodeal dorsum at least 2 times longer than declivity; (2) gaster with segments 1 and 2, and 2 and 3 separated by deep incisions.

Description. Workers. Alitrunk flat, with a metathoracic-propodeal suture visible on sides of sclerite that may be represented by a faint depression, but never a groove; propodeal dorsum at least 2 times longer than declivity, the faces separated by an attenuate angle; petiole (2nd abdominal segment) longer than high; postpetiole spiracles situated forward of midlength of the segment; abdominal segments 5 and 6 with a distinct, much narrower presclerites and wider postsclerites, resulting in constrictions between abdominal segments 4 and 5, and 5 and 6 (Figs 2, 4, 6, 8); spiracular plate median connection of sting apparatus with anterior margin convex or straight; furcula in the shape of an U (Figs 59, 67) and weakly sclerotized; lateral wing-shaped projections absent; sting with bulb base rounded.

Larva (description based on larva of *L. legionaria* sp.*n*., see below). First 5 abdominal segments clearly differentiated from another; posterior somites indistinct (Fig. 48). Long (50 μm) unbranched, smooth, slightly curved hairs, and a continuous covering of very small (less than 10 μm) unbranched, smooth, slightly curved to flexuous hairs. Head longer than wide (Fig. 49); genae bulging and frons depressed (Fig. 50); antennae relatively long, almost as long as mandibles, with 2 apical sensillae; labrum circular or heart-shaped in face view, elongate. Mandibles without striae or spinules, their outer border furnished with 6 slender sharp-pointed teeth; apical and subapical teeth longer than remaining (Figs 49, 51). Maxillae without paxiliform or digitiform palp, with apical sensillae.

Comments. *Leptanilloides* is exclusively Neotropical, recorded from the Andean foothills at 440 m in Bolivia and in higher altitudes (> 3200 m and up) in Colombia and Ecuador. The biology is completely unknown, except some indication of army ant life style by the study of *L. legionaria* larvae. The strong girdling constrictions separating the three visible gastral segments is unique among leptanilloidine ants and a similar situation is only found in the cerapachyine *Sphinctomyrmex*, which has the armed pygidium not reduced. Although the larvae we have in hand are not well preserved, we found nothing similar to the larval haemolymph structure described by Masuko (1989) in *Leptanilla japonica*.

Key to the species of *Leptanilloides* (workers only)

1. Postpetiole in profile very much narrower dorsoventrally than fourth abdominal segment (Fig. 6); head sculpture fine, at most 10–12 shallow foveolae covering a straight transverse line at head midlength (Fig. 5)..... ..... *legionaria* sp.n. (Colombia)
– Postpetiole in profile nearly as deep dorsoventrally as fourth abdominal segment (Figs 2, 4, 8); head sculpture fine or course, with at least 15 foveolae covering a transverse straight line at head midlength (Figs 1, 3, 7). 2
2(1). Flange over the metapleural gland opening rounded posteriorly (Fig. 22); head sculpture coarse, about 20 deeper foveolae covering a straight transverse line at head midlength (Fig. 3)..... *improvisa* sp.n. (Ecuador)
– Flange over the metapleural gland opening sharply pointed posteriorly (Figs 21, 24); head sculpture with 15 or 25 foveolae covering a transverse straight line at head midlength (Figs 1, 7).....3
3(2). Petiole, in lateral view, longer than postpetiole (Fig. 2); head sculpture finer, with 15 shallow foveolae covering a transverse straight line at head midlength (Fig. 1)..... .....*biconstricta* Mann (Bolivia)
– Petiole, in lateral view, as long as postpetiole (Fig. 8); head sculpture coarser 25 deep foveolae covering a transverse straight line at head midlength (Fig. 7)..... .....*sculpturata* sp.n. (Colombia)

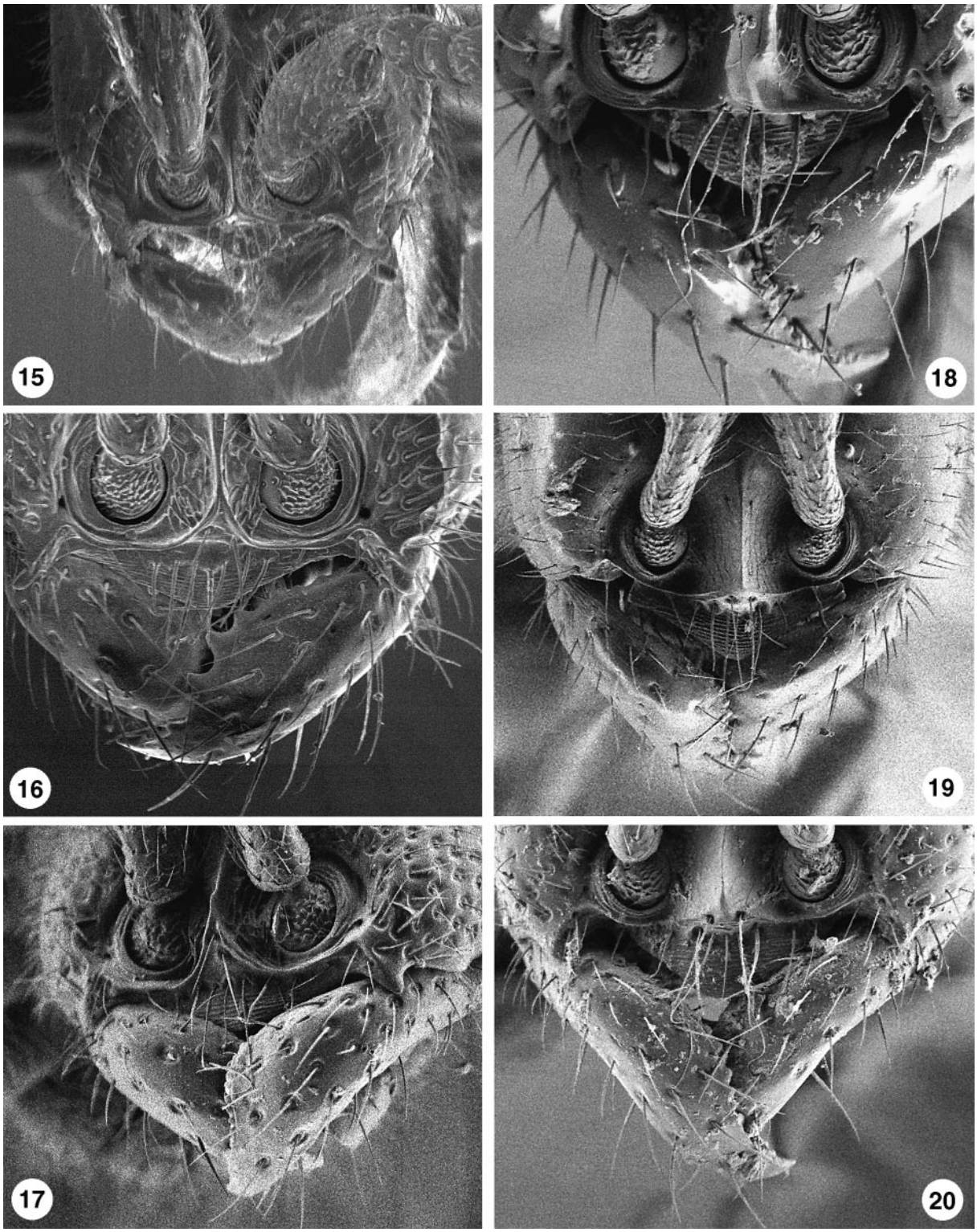
Leptanilloides biconstricta Mann (Figs 1–2, 15, 21, 28–31, 53–59)

Leptanilloides biconstricta Mann, 1923: 13–15. Lectotype worker, BOLIVIA, Beni, Tumupasa, W. M. Mann, NMNH type 25705 (examined, designated here). Worker paralectotypes, NMNH, four worker paralectotypes (MCZ type 20289); two paralectotypes (MZUSP, one dissected, preserved on glass slide), all same series as lectotype (examined).
Leptanilloides biconstricta: Borgmeier, 1955: 652 (redescription of worker).
Leptanilloides biconstricta: Bolton, 1990a: 61–63 (Fig. 22).

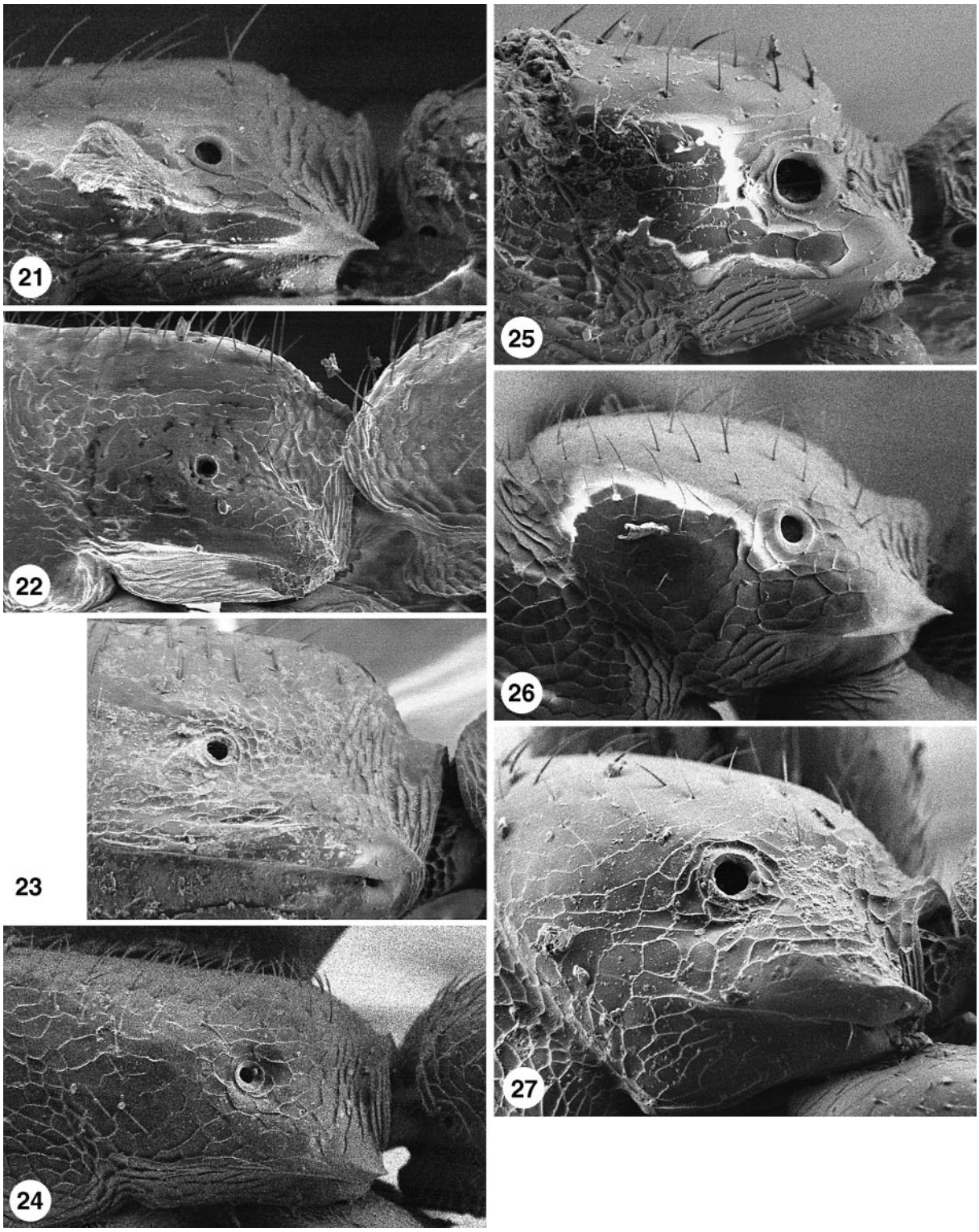
Material examined. Only type series available.

Worker paralectotype (MZUSP) (in mm): HL 0.49, HW 0.28, SL 0.15, WL 0.54, CI 57, SI 55, SRI 76.

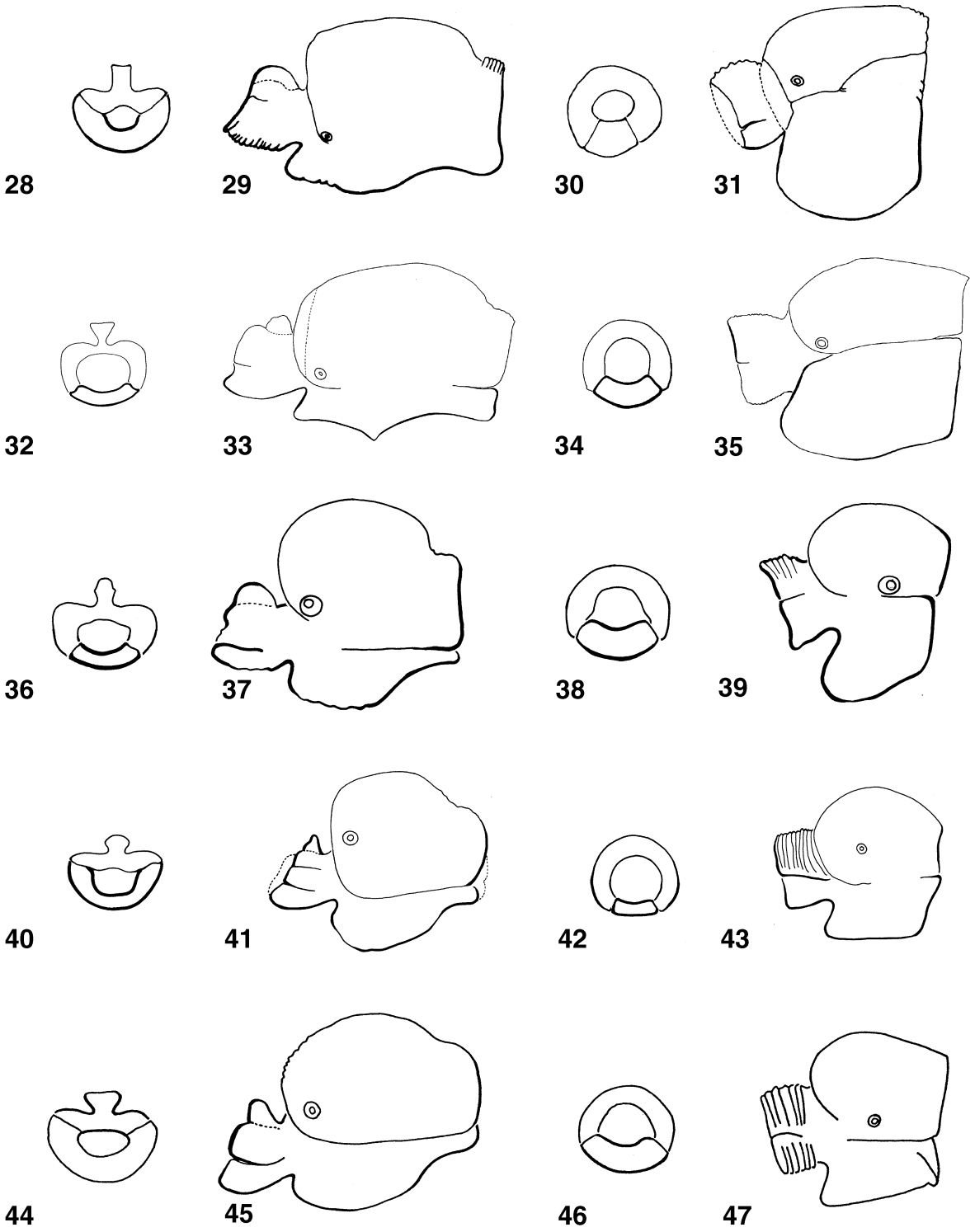
Diagnosis. The combination of the following characters distinguishes *L. biconstricta* from all other species in the genus: postpetiole in profile nearly as deep dorsoventrally as first gastral segment (Fig. 2), head sculpture fine with *c*. 15 shallow



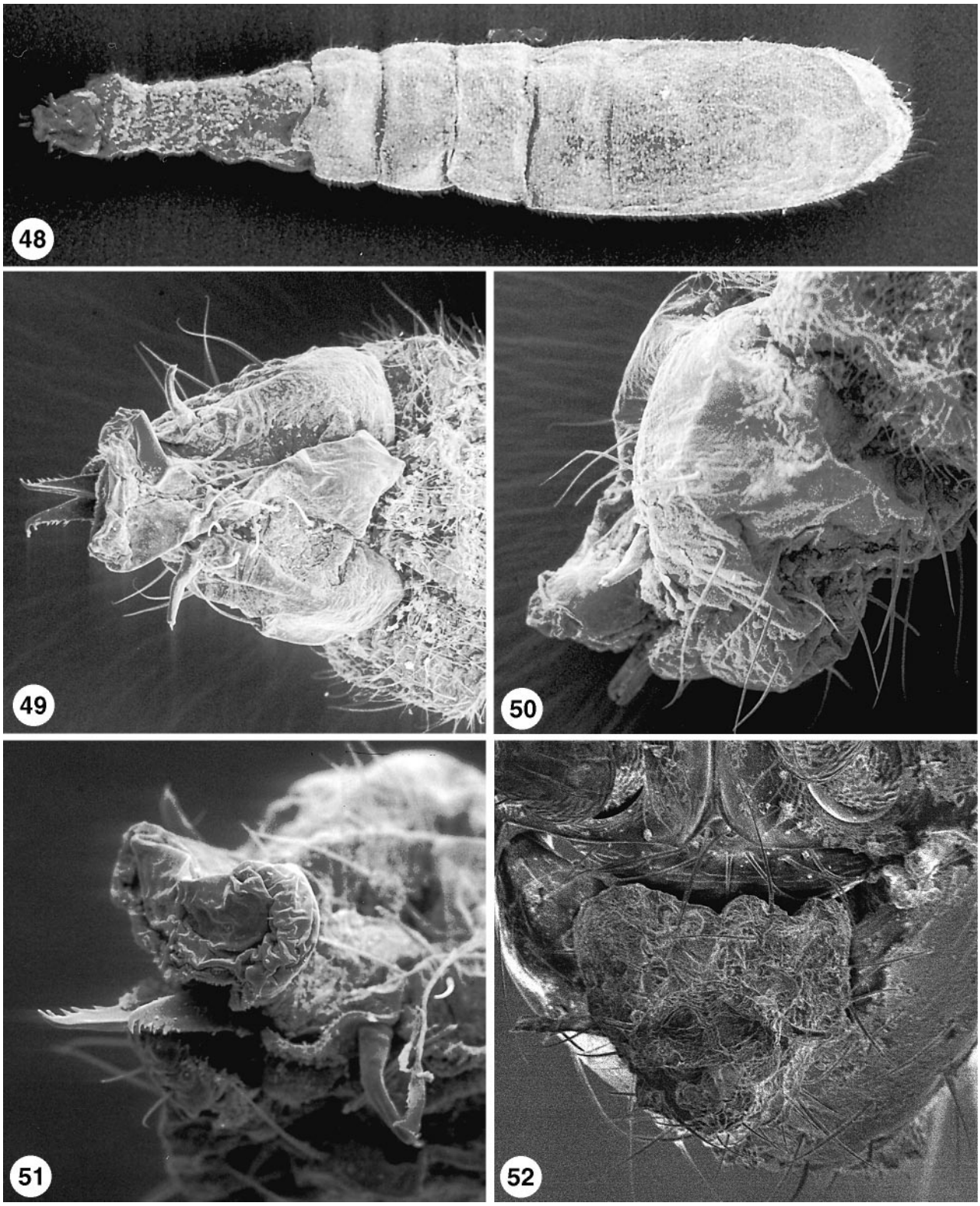
Figs 15–20. Anterior part of head in full-face view. 15, *Leptanilloides biconstricta*; 16, *L. improvisa*; 17, *L. sculpturata*; 18, *Asphinctanilloides amazona*; 19, *A. anae*; 20, *A. manauara*.



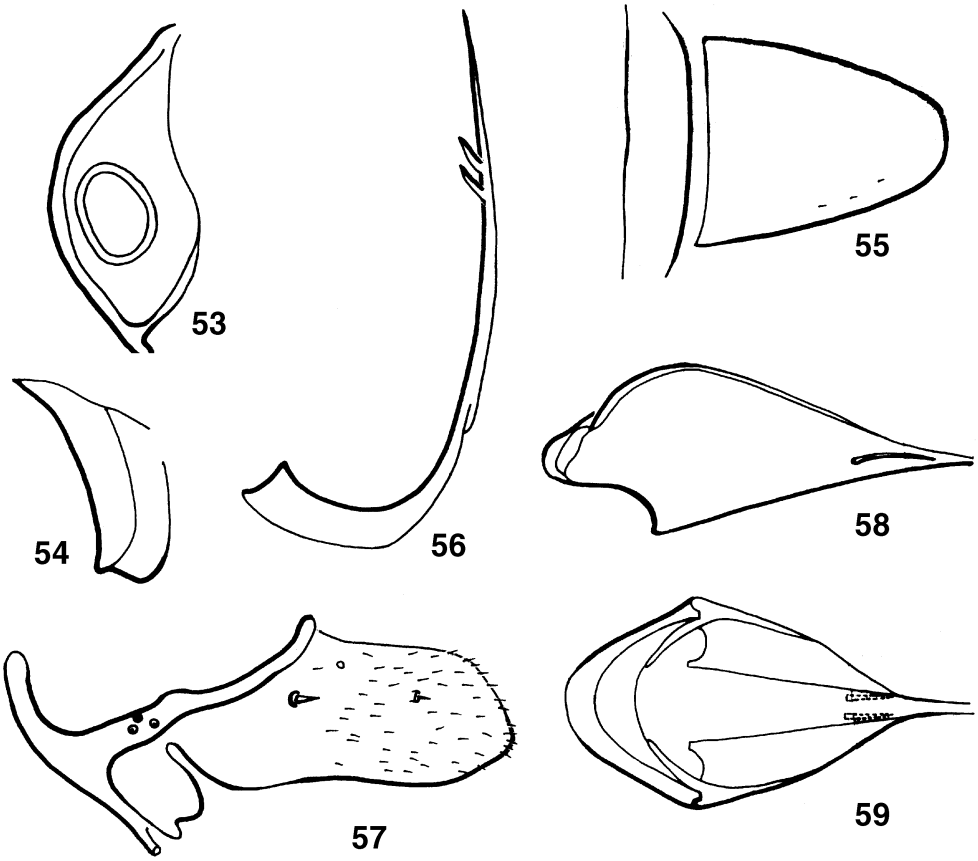
Figs 21–27. Propodeum in lateral view. 21, *Leptanilloides biconstricta*; 22, *L. improvisa*; 23, *L. legionaria*; 24, *L. sculpturata*; 25, *Asphinctanilloides amazona*; 26, *A. anae*; 27, *A. manauara*.



Figs 28–47. Frontal and lateral view of petiole and postpetiole. 28–31, *Leptanilloides biconstricta*; 32–35, *L. legionaria*; 36–39, *Asphinctanilloides amazona*; 40–43, *A. anae*; 44–47, *A. manauara*.



Figs 48–52. The larva of *Leptanilloides legionaria*. 48, Dorsal view of the whole larva; 49, head in dorsal view; 50, head in side view; 51, frontal oblique view of head; 52, full frontal view of the larva, being carried by a worker (see also Fig. 6).



Figs 53–59. Sting apparatus of *Leptanilloides biconstricta*. 53, Spiracular plate; 54, quadrate plate; 55, anal plate (right) and medial connection; 56, triangular plate and lancet with valves; 57, oblong plate and gonostylus; 58, sting and furcula in lateral view; 59, sting and furcula in ventral view.

foveolae covering a transverse straight line at head midlength (Fig. 1), and the flange over the metapleural gland opening sharply pointed posteriorly (Fig. 21). Other relevant characters include: petiole is longer than the postpetiole and the ventral process of the petiole does not have a posterior angle (Fig. 29). In relation to the venom apparatus, the spiracular plate median connection anterior margin is straight (Fig. 55); the quadrate plate antero-dorsal corner bears a long projection and has the apex acute; the anal plate (Fig. 55) is longer than wide and weakly sclerotized with 6 sensillae; the oblong plate (Fig. 57) has the postincision directed towards the dorsal margin, although it does not touch it and the ventral arm of the apodema is reduced; the fulcral arm is relatively small and in the shape of a rounded tubercle; the gonostylus presents approximately 80 small sensillae; the furcula is convex, with long lateral arms; the sting bulb base is rounded (Fig. 59), with the basal ridge slightly larger than the width of the furcula, the anterolateral process long and anterior to the articular process and the short articular process in the basal region of the sting bulb.

Comments. W. M. Mann travelled along the Beni River in Bolivia as a member of the Mulford Biological Expedition, between 1921 and 1922. Other ant species collected at the type locality of *Leptanilloides biconstricta* (Tumupasa), deposited at the MZUSP (*Megalomyrmex balzani*, see Brandão, 1990) bear a label saying 'Dec.', so the date of the collection may be December of 1921.

Leptanilloides improvisa sp.n. (Figs 3–4, 16, 22)

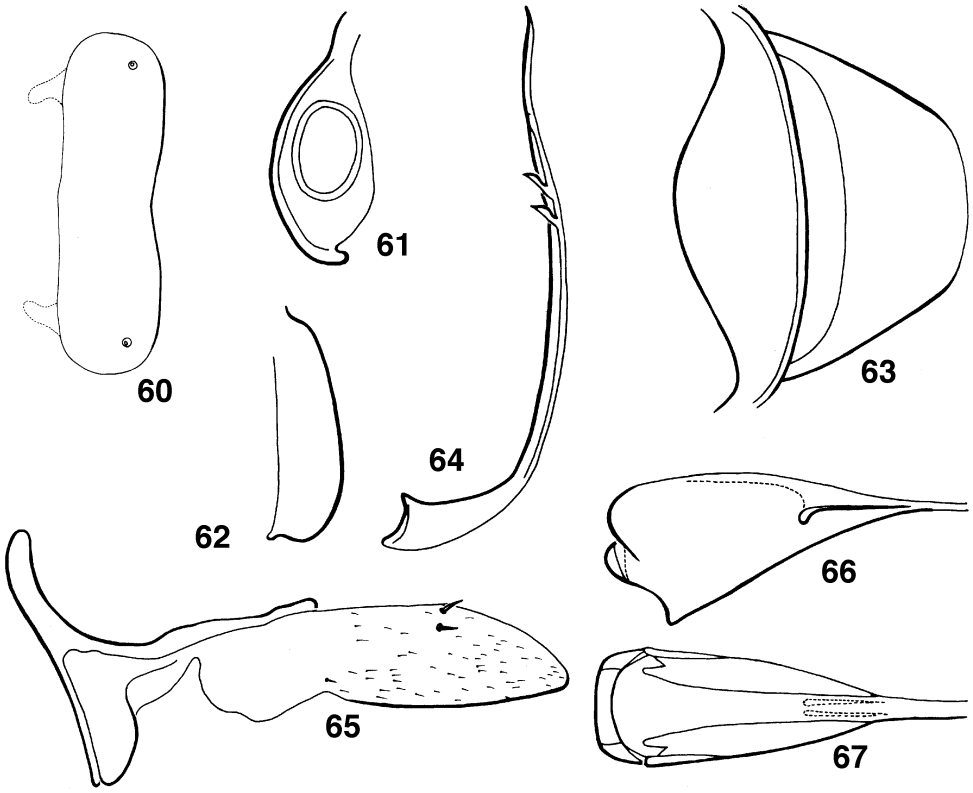
Leptanilloides improvisa. Brandão, Diniz, Agosti & Delabie, sp.n. Holotype worker deposited at MCZ. Type-locality: Ecuador, Volcán Cotopaxi, NNE Latacunga, Paramo Moss, shrub litter, 3350 m, 23.vi.1975, B-305, leg. S. & J. Peck.

Material examined. Only holotype available.

Worker holotype (MCZ) (in mm): HL 0.50, HW 0.38, SL 0.26, WL 0.68, CI 76, SI 68, SRI.

Etymology. Improvisa, a noun in apposition, meaning unexpected in Latin, referring to the fact that this manuscript was almost ready when we found this unique specimen among other samples of *Leptanilloides*.

Diagnosis. The postpetiole nearly as high dorsoventrally than the first fourth abdominal segment (Fig. 4). The coarser head sculpture and mandibular teeth, better developed in



Figs 60–67. Reduced seventh tergite and sting apparatus of *Leptanilloides legionaria*. 60, Seventh tergite; 61, spiracular plate; 62, quadrate plate; 63, anal plate (right) and medial connection; 64, triangular plate and lancet with valves; 65, oblong plate and gonostylus; 66, sting and furcula in lateral view; 67, sting and furcula in ventral view.

relation to the other species in the genus (Fig. 16), distinguishes *L. improvisa* sp.n. from all other *Leptanilloides*.

Other relevant characters include: head with convex sides in full-face view, head sculpture with up to 20 deep foveolae covering a straight transverse line at head midlength (Fig. 3); inner margins of the frontal carinae are separated from each other (Fig. 16); flange over the metapleural gland opening rounded, and it does not surpass the lateral propodeum profile (Fig. 22).

Comments. The sting apparatus of the unique specimen has not been dissected.

Leptanilloides legionaria sp.n. (Figs 5, 6, 23, 32–35, 48–52, 60–67)

Leptanilloides legionaria Brandão, Diniz, Agosti & Delabie, sp.n. Holotype worker deposited at MCZ (labelled Leptanilloides sp.n., S. Cover det. 1988, and *Leptanilloides legionaria* Brandão *et al*., 1966). Worker paratypes: AMNH, BMNH, MCZ (one each), MZUSP (one dissected, preserved on glass slide, one mounted on triangle, sting apparatus removed). Figures, see Bolton, 1994: 72 (Figs 170, 171). Type-locality: Colombia, Santa Marta Mts, Walker Expedition, #55, 7.vii.1913, F. M. Gaige leg.

Leptanilloides sp. Bolton, 1990a: 61–63 (Fig. 23).
Leptanilloides sp. Bolton, 1994: 71–72 (Figs 170, 171).

Material examined. Only type series available.

Worker (two paratypes, MZUSP) (in mm): HL 0.70–0.68, HW 0.54–0.50, SL 0.35–0.30, WL 0.80–0.098, CI 77–80, SI 61–65, SRI 78.

Etymology. Legionaria, a noun in apposition, meaning belonging to a legion in Latin, referring to the fact that one of the worker paratypes was preserved while holding a larva in the fashion usually adopted by army ants.

Diagnosis. *Leptanilloides legionaria* sp.n. has the largest body size of all *Leptanilloides*, and the postpetiole much reduced in size, very much lower dorsoventrally than the fourth abdominal segment (Fig. 6). Other relevant characters include: the sides of head rounded in full-face view; head sculpture relatively not so coarse, at most 10–12 shallow foveolae covering a straight transverse line at head midlength (Fig. 5); flange over the metapleural gland opening rounded posteriorly (Fig. 23); petiolar ventral process subrectangular, with marked anterior and posterior angles (Fig. 33). In relation to the venom apparatus, the anterior margin of the spiracular plate is convex

(Fig. 63); the quadrate plate body is apparently absent (the anterodorsal corner was lost during preparation); the anal plate (Fig. 63) base is wider than long, weakly sclerotized at apex and bears 6–8 superficial sensillae at the lateral sides of the margin; the oblong plate is weakly sclerotized, with plate limits not well marked (Fig. 65), ventral arm developed; fulcral arm is relatively small; the gonostylus has 70–80 sensillae of similar size; the furcula is bar-shaped (Fig. 67), with a continuous width and is weakly sclerotized throughout, except its lateral apex, lateral arms are absent; the sting shaft is pointed and weakly sclerotized, the basal ridge is not visible, probably fused with the furcula, the anterolateral process is short, anterior to the articular process and the articular process at the basal region of the sting bulb is also short.

Comments. One of the preserved workers is carrying a larva in between the mandibles (Figs 6, 52), holding it in a fashion similar to that employed by army ants. The MCZ collection has a series of up to forty larvae, all with similar size, and possibly similar age, suggesting a synchronized production of immatures (another character possibly related to a legionary life style). This is the species mentioned by Bolton (1990a) as undescribed.

Leptanilloides sculpturata sp.n. (Figs 7, 8, 17, 24)

Leptanilloides sculpturata Brandão, Diniz, Agosti & Delabie, sp.n. Holotype worker deposited at NMNH. Type-locality: Colombia: Venecia (near Medellin) # 56–6029, v.1956, Stanley E. Flanders leg. 'associated with *R. fuhrmanni* on healthy coffee trees'. Three paratype workers (same series as holotype), deposited one each at AMNH, MCZ and MZUSP.

Material examined. Only type series available.

Worker (MZUSP paratype) (in mm): HL 0.29, HW 0.17, SL 0.09, WL 0.48, CI 58, SI 48.

Etymology. Sculpturata, a noun in apposition, meaning carved in Latin, referring to the conspicuous deep foveolae that almost cover the head of this species.

Diagnosis. The combination of the postpetiole as long as the petiole (Fig. 8), the coarse foveolate sculpture (Fig. 7) and the minute mandibular teeth (Fig. 17) distinguishes this species from all other *Leptanilloides*. Other relevant characters include: head with parallel sides in full-face view, head sculpture coarse with up to 25 deep foveolae covering a straight transverse line at head midlength (Fig. 7); inner margins of the frontal carinae do not touch (Fig. 17); flange over the metapleural gland opening pointed posteriorly (Fig. 24); petiole, in lateral view, as long as postpetiole; postpetiole nearly as high than the fourth abdominal segment (Fig. 8).

Comments. The petiole, postpetiole and sting apparatus of the only four specimens known have not been dissected.

Asphinctanilloides gen.n. (Figs 9–14, 18–20, 25–27, 36–47, 68–88)

Asphinctanilloides Brandão, Diniz, Agosti & Delabie, gen.n. Type of the genus *Asphinctanilloides anae* sp.n. (present designation).

Etymology. Asphinctus means without constrictions in Greek, referring to the continuous profile of the gaster.

Diagnosis. Leptanilloidine ants with the following synapomorphies. Only worker caste known: (1) postpetiole extremely reduced in size, smaller than petiole in profile (Figs 10, 12, 14), with spiracles at the midlength; (2) spiracular plate median connection of the sting apparatus with bilobed anterior region (Figs 68, 75, 82); (3) quadrate plate apodeme wider than body of the plate; (4) fulcral arms absent; (5) basal ridge of sting not visible, furcula of the sting in the shape of an inverted U (Figs 74, 80, 88) and weakly sclerotized, lateral wing shaped projections developed.

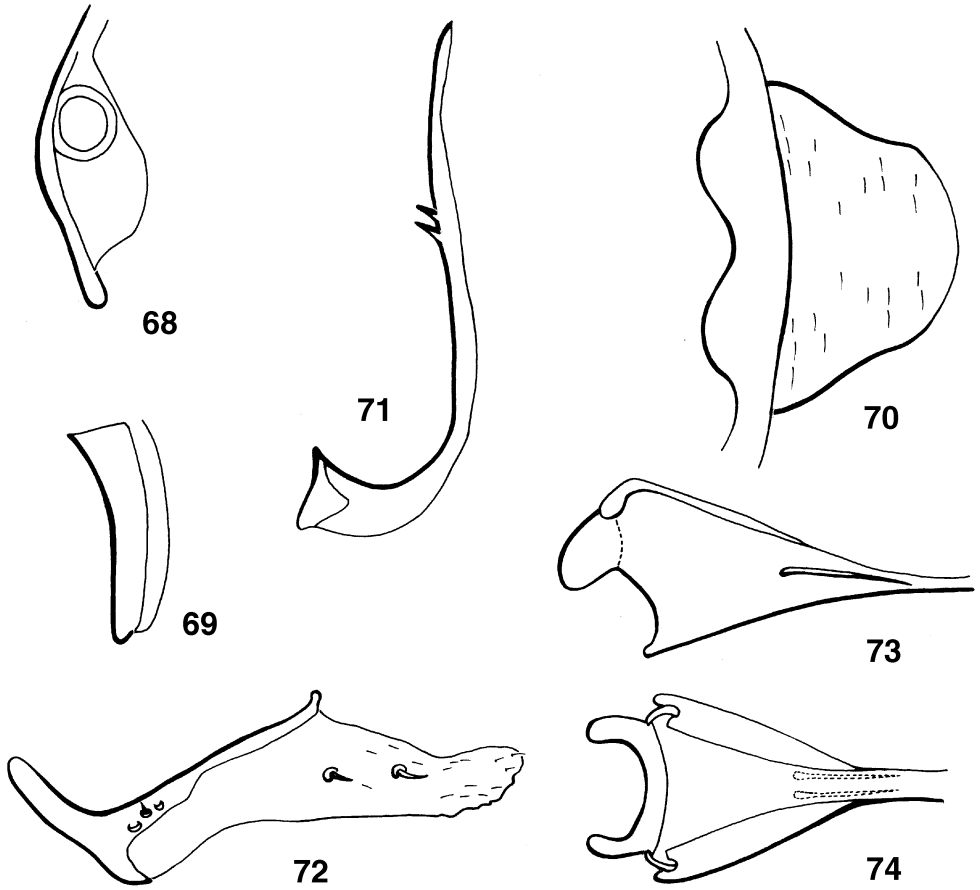
Description: Alitrunk not as flat as *Leptanilloides*, but with a metasternal-propodeal suture visible at sides and a metanotal groove on dorsum of sclerite; propodeal dorsum subequal to declivity, the faces separated by an attenuate angle or continuous; petiole (2nd abdominal segment) as long as high; flange over the metapleural gland sharply pointed posteriorly (Figs 25–27); postpetiole reduced in size in relation to that of *Leptanilloides*, always shorter than petiole in lateral view; postpetiole spiracles situated at midlength of segment; gaster profile continuous, without constrictions between segments; spiracular plate median connection of sting apparatus with anterior region with 2 lobes; quadrate plate anterior apodema wider than plate itself; anal plate always triangular with about 25 microtrichia; furcula in shape of an inverted U and weakly sclerotized; lateral wing shaped projections developed.

Comment. The continuous profile of the gaster segments, without constrictions differentiates this genus from *Leptanilloides*.

Distribution and biology. Asphinctanilloides is exclusively Neotropical, recorded in central Amazon and in a *Eucalyptus* plantation, replacing a broad-leaved forest in the São Paulo State, south-eastern Brazil. Nothing is known about its biology, except that it was caught in soil samples and in one case on the soil surface, with workers feeding on a dead arthropod.

Key to the species of *Asphinctanilloides* (workers)

1. Very small and not produced blunt teeth on genae (seen only in high magnifications, 80×) (Fig. 19); propodeum in profile clearly separated from mesonotum by a deep metanotal groove (Fig. 12) ..... *anae* sp.n.
– Blunt teeth on genae produced (clearly seen in low magnifications, 20×) (Figs 18, 20); alitrunk profile continuous; it may have an impression between mesonotum



Figs 68–74. Sting apparatus of *Asphinctanilloides amazona*. 68, Spiracular plate; 69, quadrate plate; 70, anal plate (right) and medial connection; 71, triangular plate and lancet with valves; 72, oblong plate and gonostylus; 73, sting and furcula in lateral view; 74, sting and furcula in ventral view.

and propodeum, but this does not interrupt the dorsal profile (Figs 10, 14).....2

2. Propodeal dorsum separated from the declivity by an angle in lateral view (Fig. 10); postpetiole ventral process bulging, large and rounded anteriorly (Fig. 39) ..... *amazona* sp.n.
– Propodeal dorsum continuous with the declivity through a rounded curve (Fig. 14); postpetiole ventral process not so large, straight below, and angulate anteriorly (Fig. 47)..... ..... *manauara* sp.n.

Asphinctanilloides amazona sp.n. (Figs 9, 10, 18, 25, 36–39, 68–74)

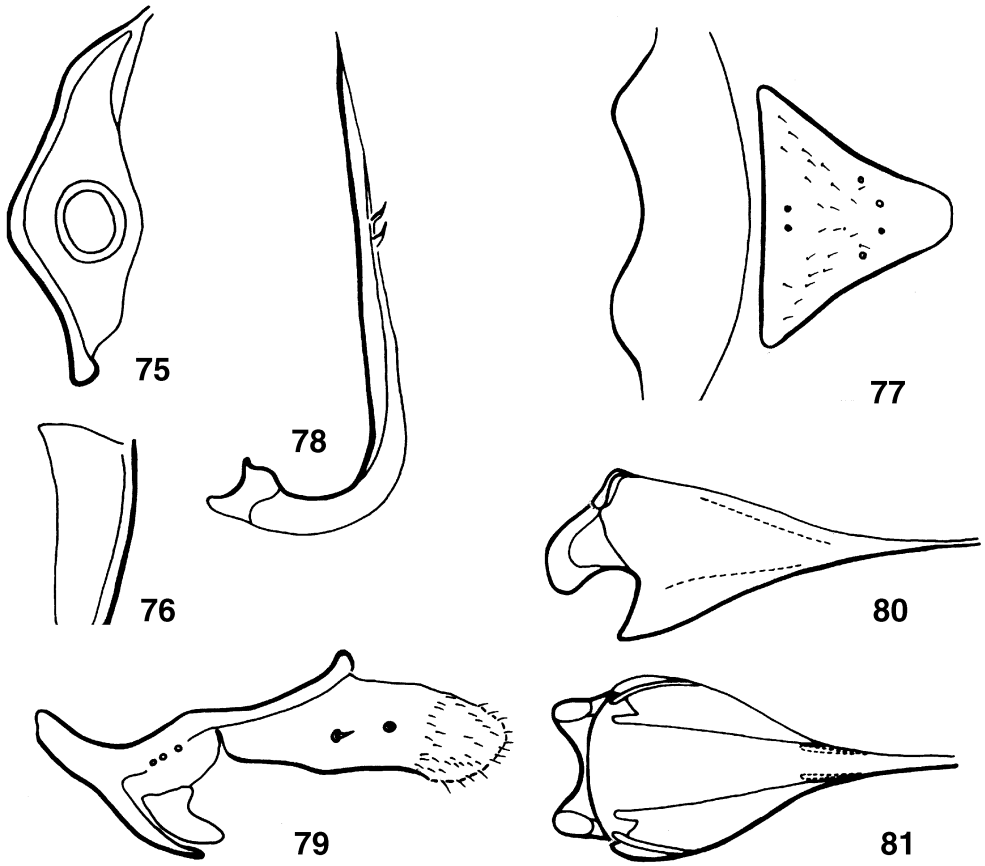
Asphinctanilloides amazona Brandão, Diniz, Agosti & Delabie, sp.n. Holotype worker deposited at INPA. Type-locality: BRAZIL, Amazonas, 4832, *c*. 70 km N of Manaus, Fazenda Esteio, Reserva 1202 (02°24′50″S, 59°52′11″W), ZF 23 Road, km 28. Projeto Dinâmica Biológica de Fragmentos Florestais, INPA/Smithsonian, 12.xi.1993, soil sample M14. A. B. Casimiro col # 1003. Seven paratype workers (same series as holotype) deposited at AMNH, BMNH, CEPLAC, MCZ and MZUSP (two dissected preserved on slide).

Material examined. Only the type series is available.

Worker. Two MZUSP paratypes (in mm): HL 0.35–0.35, HW 0.27–0.28, SL 0.16–0.17, WL 0.41–0.46, CI 76–79, SI 57–59, SRI 104.

Etymology. Amazona, a noun in apposition, related to the legendary female warriors, so named by the Spaniards, who believed they inhabited the shores of the River Amazonas.

Diagnosis. The combination of head shape in full-face view (Fig. 9), the flat dorsum of the trunk (Fig. 10) and the presence of a clearly defined declivity of the propodeum (Fig. 10) is unique for *A. amazona* sp.n. Other relevant characters include: head in full-face view with parallel sides and emarginate occiput (Fig. 9); blunt teeth on genae produced (Fig. 18); dorsal outline of alitrunk, in lateral view, straight, continuous, not interrupted by the promesonotal suture and metanotal groove which are present (Fig. 10); relatively small body size (WL $<$ 0.41 mm); dorsum of propodeum distinct from declivity; postpetiole ventral process bulging, large and rounded anteriorly (Fig. 39). Venom apparatus: spiracular plate posterodorsal corner strongly tuberculate (Fig. 68), prominent;



Figs 75–81. Sting apparatus of *Asphinctanilloides anae*. 75, Spiracular plate; 76, quadrate plate; 77, anal plate (right) and medial connection; 78, triangular plate and lancet with valves; 79, oblong plate and gonostylus; 80, sting and furcula in lateral view; 81, sting and furcula in ventral view.

quadrate plate anterodorsal corner with acute apex (Fig. 69); anal plate (Fig. 70) as a very much attenuate triangle at apex; oblong plate (Fig. 72) weakly sclerotized, its limits weakly visible, postincision absent, ventral arm of the apodema indistinct of the remains of the plate; fulcral arm absent; gonostylus with about twenty sensillae and two long cheatae; furcula, with wing shaped projections long, parallel, sclerotized and linked to the median region of the furcula only at their basal region, lateral arms absent; sting with triangular bulb (Fig. 74), basal ridge not visible, probably fused to the furcula; anterolateral process anterior and similar in size to the articular process, and articular process short at the basal region of the sting bulb.

Comment. This species was collected in a soil sample in a forest reserve of tropical lowland primary forest near Manaus, Brazil.

Asphinctanilloides anae sp.n. (Figs 11, 12, 19, 26, 40–43, 75–81)

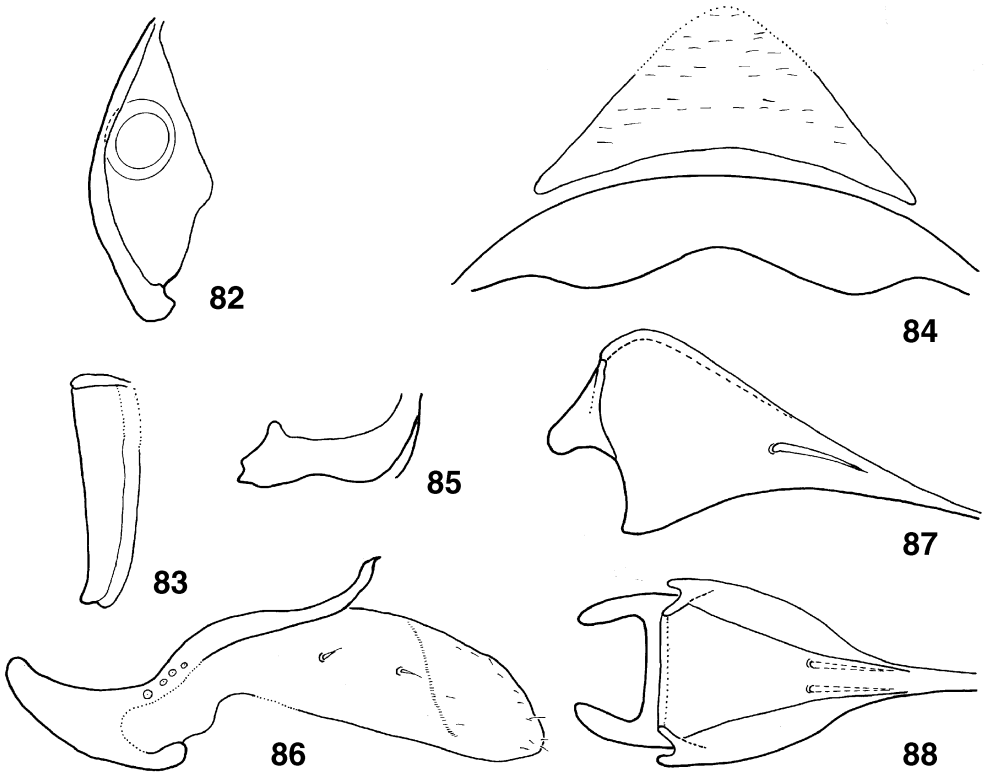
Asphinctanilloides anae Brandão, Diniz, Agosti & Delabie, sp.n. Holotype worker deposited at MZUSP. Type-locality: Brazil, São Paulo, Mirassol, Fazenda da Lima, 30.iv.1979, J. L. M. Diniz coll. # 1850. Eighteen paratype workers (same series as holotype), deposited at AMNH, BMNH, MCZ, MZUSP (six, one dissected and mounted on slide), JLMD (seven, one dissected and mounted on slide), INPA and CEPLAC.

Material examined. Only the type series is available.

Workers (all non-dissected specimens, $n = 16$) (average, minimum and maximum; in mm): HL 0.46, 0.44–0.47; HW 0.37, 0.35–0.38; SL 0.23, 0.21–0.24; WL 0.52, 0.50–0.60; CI 80, 77–82; SI 62, 57–66, SRI 117.

Etymology. Anae, a noun in apposition, as an homage to Ana Diniz, daughter of Jorge L. M. Diniz.

Diagnosis. The rounded head sides in full-face view (Fig. 11) and the deep emargination of the alitrunk (Fig. 12) is an unique combination for *Asphinctanilloides anae* sp.n. Other relevant characters include: lateral blunt teeth on genae very much reduced and not produced, although present and visible in high magnifications (80×) (Fig. 19); propodeum in profile clearly separated from mesonotum by a deep metanotal groove; propodeum evenly convex (Fig. 12). Venom apparatus: anal



Figs 82–88. Sting apparatus of *Asphinctanilloides manauara*. 82, Spiracular plate; 83, quadrate plate; 84, anal plate and medial connection; 85, triangular plate and lancet with valves; 86, oblong plate and gonostylus; 87, sting and furcula in lateral view; 88, sting and furcula in ventral view.

plate (Fig. 77) as an equilateral triangle with rounded apex, projected, weakly sclerotized, with 6 bigger sensillae; oblong plate (Fig. 79) postincision almost reaches the margin dorsal, ventral arm developed; fulcral arm absent; gonostylus with about 60 small and 2 large sensillae; furcula with lateral wing-shaped projections elongate (Fig. 80), sclerotized and linked to the median region of the furcula in all his width, lateral arms absent (Fig. 81); sting with bulb base rounded, basal ridge not visible, probably fused to furcula, and anterolateral process as long as articular process, anterior to the articular process.

Comments. Jorge Diniz collected the type series over the ground on a cloudy morning in an *Eucalyptus* plantation near a stream (Córrego da Lima). Originally this area was covered by broad-leaved tropical forest (Marinis & Camargo, 1964). Several workers were found below a piece of cow dung, preying on an unidentified and partially eaten arthropod; from these remains departed a column of workers, in a fashion that called his attention as being similar to the usual *Neivamyrmex* army ants column. He came back to the same spot on the next day, and dug the hole where they were seen entering, but found no ants there.

Asphinctanilloides manauara sp.n. (Figs 13–14, 20, 27, 44–47, 82–88)

Asphinctanilloides manauara Brandão, Diniz, Agosti & Delabie, sp.n. Holotype worker deposited at INPA. Type-locality: BRAZIL, Amazonas, 4832, *c*. 70 km N of Manaus, Fazenda Esteio, Reserva 1301(02°26′13″S, 59°48′35″W), ZF 23 Road, km 28. 'Projeto Dinâmica Biológica de Fragmentos Florestais, INPA/Smithsonian', 14.xii.1993, soil sample H46. A. B. Casimiro col # 1001. Paratype workers (same series as holotype) deposited (one each) at AMNH, BMNH, CEPLAC, MCZ and MZUSP.

Material examined. Only type series available.

Worker paratype (MZUSP, in mm, $n = 1$): HL 0.41, HW 0.35, SL 0.27, WL 0.44, CI 87, SI 76, SRI 78.

Etymology. Manauara, a noun in apposition, related to the way local people living in the Manaus and surroundings call themselves.

Diagnosis. The coarse sculpture on the head (Fig. 13), the shape of the propodeum, the concave dorsal outline of the alitrunk (Fig. 14) and the relatively small petiolar ventral process (Fig. 45) is an unique combination for *Asphinctanilloides manauara* sp.n. Other relevant characters include: head wide (CI > 85), coarsely sculptured; sides rounded in full-face view; blunt teeth on genae produced (Fig. 20); in lateral view, dorsal outline of alitrunk slightly concave at the metanotal groove; propodeum dorsum continuous with declivity (Fig. 14). Venom apparatus: quadrate plate anterodorsal corner short without apex (Fig. 83); anal

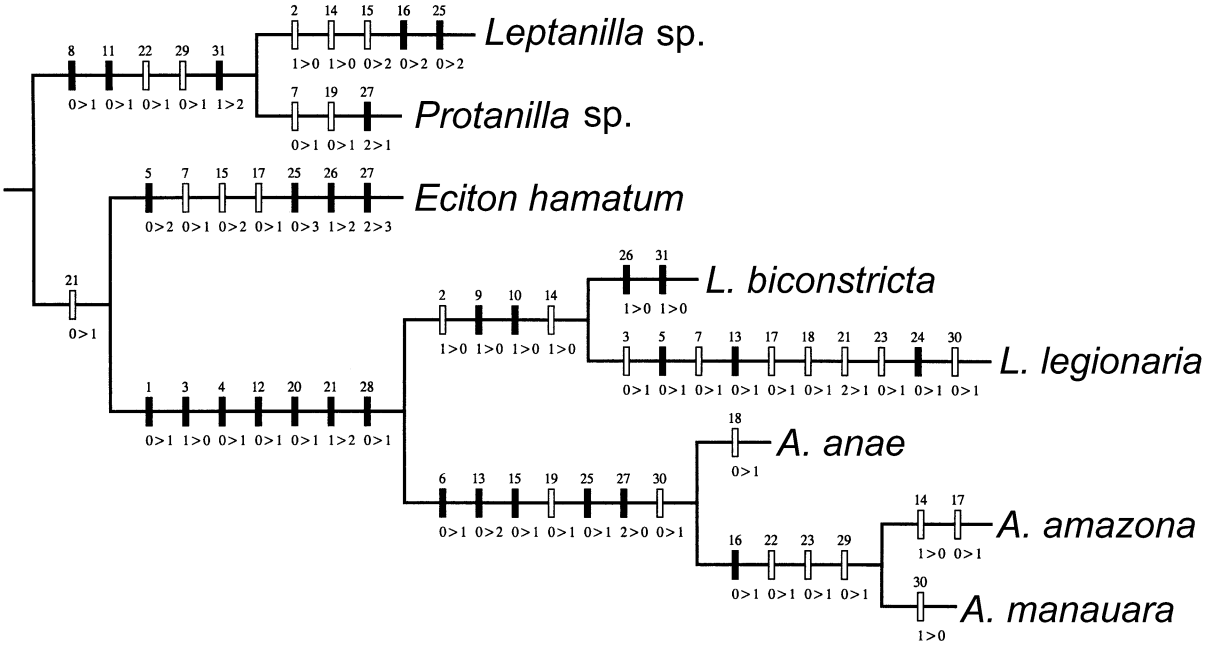


Fig. 89. The phylogeny of Leptanilloidinae. An initial exhaustive search, using HENNIG86 (Farris, 1988) found four shortest trees (length 59, CI 71, RI 69), which were stable to successive weighting (4 trees:, i.e. length 360, CI 88, RI 88). *Leptanilla* sp. and *Protanilla* sp. were included as outgroup, and *Eciton hamatum* was treated as ingroup. Three out of four trees share the same basic topology with *Leptanilloides* and *Asphinctanilloides* as monophyletic groups. Omitting *L. improvisa* and *L. sculpturata* with only 40% of the characters known because of missing information on the venom apparatus, resulted in two trees (using exhaustive search; length 59, CI 71, RI 63), with the same topology as those of the extended matrix. The tree shown here represents in our view the most plausible phylogenetic and biogeographic hypothesis. Character states are given in Table 1. Black = apomorphies; hashed = reversals or polymorphisms.

plate triangular, with width at base twice its height, with about thirty sensillae (Fig. 84); oblong plate anterior apodema wide (Fig. 86); postincision absent, ventral arm of the apodema indistinct; fulcral arm absent; gonostylus with about twelve very small sensillae; furcula with elongate wing like convergent sclerotized projections, linked to the median region of the furcula only at basal region, lateral arms absent; sting with triangular bulb base (Fig. 88); basal ridge narrow, anterolateral process short and anterior to the articular process, and short articular process at the basal region of the sting bulb.

Comment. This species was only collected in one soil sample in a reserve of 100 ha of primary Amazonian forest, surrounded by continuous primary lowland forest.

Phylogeny and biogeography of the Leptanilloidinae

An initial exhaustive search, using HENNIG86 (Farris, 1988) found four shortest trees (length 59, CI 71, RI 69), which were stable to successive weighting (four trees:, i.e. length 360, CI 88, RI 88). *Leptanilla* sp. and *Protanilla* sp. were included as outgroups, and *Eciton hamatum* was treated as ingroup. Three out of four trees share the same basic topology with *Leptanilloides* and A*sphinctanilloides* as monophyletic groups. Omitting *L. improvisa* and *L. sculpturatai,* for which we had no information on the venom apparatus, resulted in two trees which had the same topology as those of the extended matrix. The tree presented herein was chosen from the smaller group with two trees (length 59, CI 71, RI 63), and represents, in our view, the most plausible biogeographic hypothesis. Character states are given in Table 1.

Leptanilloidinae is supported by six synapomorphies, *Asphinctanilloides* by nine and *Leptanilloides* by four (Fig. 89; apomorphies given in the diagnosis of the two taxa). Within the subfamily, two major clades can be recognized, the *Leptanilloides* and *Asphinctanilloides* (Figs 89, 90), including, respectively, four and three species, although we did not include two *Leptanilloides* species in this analysis, as mentioned before. However, in Fig. 90 we depict our hypothesis of relationship for all taxa. The two clades indicate a divide between the species in one Andean group and another group further divided between the species of the Amazon plain and those of the drier forests of the coastal Mata Atlântica. The completely disjunct distribution pattern, with three *Leptanilloides* species (*L. improvisa* sp.n., *L. legionaria* sp.n. and *L. sculpturata* sp.n.) inhabiting places above 3000 m in the Andes, and *L. biconstricta* collected on the Andean slopes at an altitude of *c.* 440 m, and *Asphinctanilloides* inhabiting lowland sites in Central Amazon and in the Atlantic forest in south-eastern Brazil, suggests a pattern which is not a mere artifact due to the low number of samples of this extremely rare ant subfamily, but rather an actually existing pattern.

Fig. 90. The biogeography of Leptanilloidinae. The Leptanilloidinae are endemic to South America. The two major clades, the *Leptanilloides* and the *Asphinctanilloides*, are (1) distributed along the Andes and (2) in the plains of the Amazon and the Atlantic forest, respectively.

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