The ant genus Leptanilla: discovery of the worker-associated male of L.japonica, and a description of a new species from Taiwan (Hymenoptera: Formicidae: Leptanillinae)

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Abstract. The male and female of Leptanilla japonica Baroni Urbani are described. This is the first worker-associated male to be discovered in subfamily Leptanillinae. Leptanilla taiwanensis is described as new based on the worker and female from Taiwan, the first record of Leptanillinae from the island. An ecological note on the food of the ants is given. Implications of the male morphology and taxonomic positions of the other leptanilline genera based on males are discussed.

Introduction

The uncommon genus Leptanilla is distributed from the warmer temperate zone to the tropics of the Old World. Bolton (1990) recently revised the subfamily Leptanillinae and provided a definition of the tribe Leptanillini for the worker caste. This tribal definition can be interpreted as generic for Leptanilla, because the worker of the tribe is known only in this genus.

Ant taxonomy has been based chiefly on worker morphology because this caste is frequently and easily collected, but this is not the case for *Leptanilla*. Supposed males of Leptanillinae have been captured more frequently than workers and females by sweeping, water pan traps and malaise traps. Among thirty-five described species of *Leptanilla*, thirteen were based solely on unassociated males; as yet there have been no worker-associated males. Therefore the discovery of worker-associated males has been long awaited (Bolton, 1990).

As the leptanillines are minute and completely cryptobiotic ants, knowledge of their biology has been very limited until recently. Masuko (1989, 1990), however, collected eleven colonies of *Leptanilla japonica* and succeeded in rearing some of them and making important observations on their behaviour (see also Hölldobler *et al.*, 1989; Wheeler & Wheeler, 1989). More importantly for ant taxonomy, the colonies he collected included a few

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males. This material provides important information for the generic definition of *Leptanilla*. In addition, one of the authors (M.T.) recently collected a colony of *Leptanilla* in Taiwan and obtained information on the ants' food in the field.

The present paper gives descriptions of the reproductives of *L.japonica* and a new Taiwanese species with a field observation of the new species. Taxonomic positions of male-based genera of Leptanillinae are also discussed.

Leptanilla japonica Baroni Urbani (Figs 1-11)

Leptanilla japonica Baroni Urbani, 1977: 460. Holotype worker, Japan: Manazuru, Kanagawa Pref.

Female. HW (head width) $0.25 \,\mathrm{mm}$, HL (head length) $0.33 \,\mathrm{mm}$, CI (cephalic index: $\mathrm{HW} \times 100/\mathrm{HL}$) 75.8, SL (scape length) $0.13 \,\mathrm{mm}$, PW (pronotal width) $0.21 \,\mathrm{mm}$, WL (Weber's length of trunk) $0.54 \,\mathrm{mm}$, PNL (petiolar node length) $0.13 \,\mathrm{mm}$, PNW (petiolar node width) $0.16 \,\mathrm{mm}$, TL (total length) $1.8 \,\mathrm{mm}$ (1 individual measured).

Head subrectangular with concave posterior margin and subparallel sides; posterior corners rounded. Mandibles stout, edentate. Clypeus with transverse anterior margin. Antennal insertion situated close to anterior margin of head. Antennae 12-segmented; scape short and robust; pedicel longer than broad, separated from the rest of funiculus by constriction; antennal segments 3–11 each broader than long; apical segment longer than two pre-

ceding segments together. Eyes present, each consisting of two facets, situated on the midlength of sides of head. Ocelli absent.

Trunk flattened; sides subparallel in dorsal view, nearly $3 \times$ as long as broad. Pronotum without anterior corners in dorsal view; posterior margin straight. Propleuron large. Metanotal groove absent. Metapleural gland distinct. Propodeum with distinct spiracle situated above hind coxal base. Middle leg with single small tibial spur; hind leg with one larger pectinate spur and small simple spur.

Petiolar node broader than long, about 1.5× as broad as long, narrower than trunk; oval in dorsal view. Ventral portion of petiole produced, with distinct anterior process.

Gaster large; first gastral segment about 1.3× as broad as long. Body colour light reddish yellow. Hairs short, abundant on gaster.

Male. HW 0.19, HL 0.25, CI 75, PW 0.19, WL 0.43, forewing L 1.06, hindwing L 0.60, PNL 0.11, PNW 0.08, TL 1.30 (1 individual measured).

Head longer than broad, with rounded posterior corners and subparallel sides; posterior margin slightly emarginate without occipical carina. Mandibles reduced, non-opposable, forming small rounded and flattened lobes with concave dorsal surface. Palp formula 1,1. Clypeus narrow, shallowly depressed and fused to cranium posteriorly; anterior margin almost straight. Antennae 13-segmented; scape short and stout, reaching posteriormost portion of eye; funiculus filiform, each segment subglobose and slightly longer than broad except for apical one; apical segment longest, nearly as long as two preceding segments together. Eyes hairy, large and convex, situated anteriorly. Ocelli developed.

Trunk elongate. Pronotum long, nearly twice as long as propleuron; anterior projection thin, not forming cercival collar; posterolateral portion concave; both sides close to each other at posteroventral portion. Propleuron short, very convex ventrally. Mesoscutum elongate, about half as long as trunk; dorsal surface arched, without notauli and parapsidal furrows. Mesoscutellum slightly raised, not overhanging metanotum. Metanotum small, forming short transverse sclerite. Oblique furrow on mesepisternum weakly developed. Propodeum cylindrical and marginate posteriorly, with arched node. Metapleural gland absent. Middle leg with a single small spur; hind leg with two small spurs.

Forewing with weakly developed vein Sc + R + Rs; other veins and pterostigma absent. Hindwing narrow without any veins.

Petiole subglobous, constricted posteriorly, without anterior peduncle. Cerci absent.

Hypopygium small, short and broad, with rounded apical projection which is low and never bifurcate. Genitalia not retractile; basal ring small and thin, weakly sclerotized and fused to hypopygium ventrally; basal portion of parameres widely separated dorsally, but contiguous to each other ventrally; apical portion of parameres extended dorsally, forming flattened apices each with one outer and two inner teeth; digitus small, cuspis absent;

aedeagal plate flattened, dorsally projecting without serrate ventral margin.

Specimens examined. JAPAN: 19, Manazuru, Kanagawa Pref., Honshu, 14.viii.1982 (K. Masuko); 13, same locality, 11.vii.1981 (K. Masuko).

Distribution. Japan.

Remarks. The female of this species is unique in having eyes. The male is also characteristic in having hairy eyes, small projections on the parameres and a simple hypopygium which is not bifurcate apically.

Masuko (1989, 1990) reported the biology of this species. Hölldobler *et al.* (1989) described exocrine glands. Wheeler & Wheeler (1989) described the larval morphology.

Leptanilla taiwanensis sp.n. (Figs 12-18)

Worker. HW 0.24-0.25, HL 0.31-0.33, CI 73.1-76.9, SL 0.14-0.15, SI 55.0-63.2, PW 0.14-0.15, WL 0.38-0.40, PNL 0.09-0.10, PNW 0.09, PPNL (postpetiolar node length) 0.08-0.09, PPNW (postpetiolar node width) 0.09-0.10, TL 1.06-1.34 (5 individuals measured).

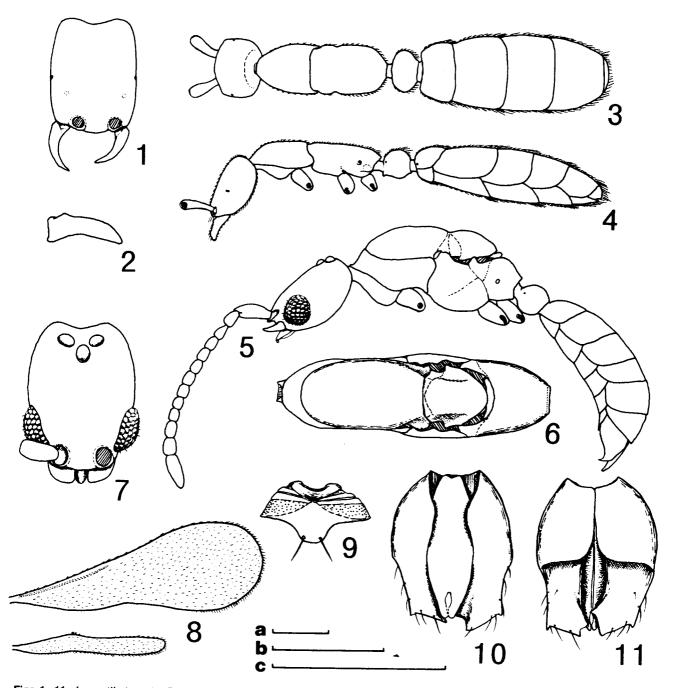
Head longer than broad, with subparallel sides, slightly concave posterior border and rounded posterior corners. Occipital carina absent. Mandibles narrow, armed with 3 teeth; apical tooth larger and acute; preapical tooth small and low; basal tooth small but distinct, pointed inward and some distance from the preapical tooth. Palp formula 1,1. Clypeus depressed; anterior margin almost straight with low median notch. Antennal insertions exposed, widely separated by low convexity and situated at anterior margin of clypeus with well-marked antennal sclerites. Antennae 12-segmented; scape clavate, extending beyond middle of head, but not reaching posterior margin of head; pedicel separated from the rest of funiculus by constriction; rest of funiculus incrassate, more or less stout, each segment except for apical one broader than long; apical segment longer than broad, about as long as two preceding segments together. Eyes absent.

Trunk slender, with depressed node and subparallel sides. Pronotum with rounded anterior margin and straight posterior margin in dorsal view. Metanotal groove absent. Metapleural gland distinct. Posterior portion of propodeum rounded without distinct posterior declivity; propodeal spiracle small. Legs short and stout; middle tibia with a small simple spur; hind tibia with a small pectinate spur.

Petiole subglobous, longer than broad; petiolar node slightly convex in dorsal view; ventral portion produced with small anterior projection. Postpetiole globous, nearly as long as broad; posterior margin rounded; dorsal surface very convex; ventral portion notably produced.

Gaster rather flattened dorsally; first gastral segment tapering basally, without distinct anterior corners in dorsal view; sting small but distinct.

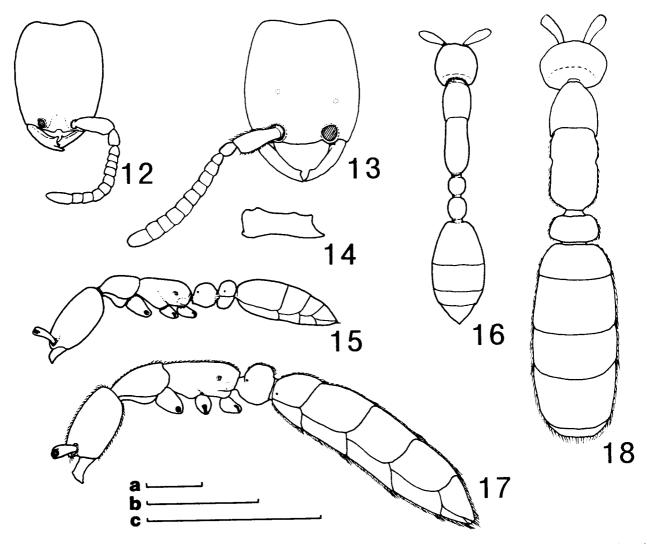
Female. HW 0.31, HL 0.34, CI 91.2, SL 0.14, SI 45.2,



Figs 1-11. Leptanilla japonica Baroni Urbani. 1, female, head; 2, female, right mandible, outer lateral; 3, female, dorsal; 4, female, lateral; 5, male, lateral; 6 male, trunk, dorsal; 7, male, head; 8, male, right wings; 9, male, hypopygium, ventral; 10, male, genitalia, dorsal; 11, male, genitalia, ventral. Scale bars: a; 0.1 mm for 2, 6, 7, b; 0.1 mm for 3, 4, 8, c; 0.5 mm for 1, 5, 9-11.

PW 0.23, WL 0.56, PNL 0.13, PNW 0.21, TL 2.0 (1 individual measured).

Head subrectangular with sides less convex than those of worker; posterior margin concave in the middle; posterior corners rounded; anterior portion not so narrowed as in worker. Mandibles robust, with narrow masticatory margin armed with blunt basal tooth and acute apical tooth. Anterior margin of clypeus broadly rounded without incision. Antennal insertions like those of worker. Antennae 12-segmented; scape stout, pedicel distinguished from the rest of funicular segments by constriction; antennal segments 3-11 each broader than long; apical segment almost as long as two preceding segments together. Eyes



Figs 12-18. Leptanilla taiwanensis n.sp. 12, worker, head; 13, female, head; 14, female, right mandible, outer lateral; 15, worker, lateral; 16, worker, dorsal; 17, female, lateral; 18, female, dorsal. Scale bars: a; 0.1 mm for 14, b; 0.5 mm for 15-18, c; 0.5 mm for 12 and 13.

and ocelli absent. Two small red spots present on dorsal surface of head through integument, which may be mandibular glands.

Trunk flattened, about 2.5× as broad as long. Pronotum occupying about two-fifths of whole length of trunk; rounded anteriorly without distinct anterior corners in dorsal view; posterior margin straight. Propleuron large. Metanotal groove absent. Metapleural gland distinct. Ventral processes absent on meso- and metasterna. Propodeal spiracle situated above area between bases of mid and hind coxae. Middle leg with one small and simple tibial spur; hind leg with one small and simple spur and one pectinate spur.

Petiolar node about 1.7× as broad as long, almost same width as trunk with flattened dorsal surface; in dorsal view, anterior margin slightly concave, sides convex, posterior margin almost straight; ventral portion broadly rounded, not forming any projections.

Gaster large; first gastral segment 1.6× as broad as petiole. Terminal portion without specialized projections.

Body colour pale yellow; hairs short, abundant on gaster. Holotype, worker, TAIWAN: Wushe, Nantou Hsien. 14.vii.1982 (M. Terayama) (Type depository: Entomological Laboratory, Faculty of Agriculture, Kyushu University, Type No. 2903).

Paratypes. 19, 145 workers (same colony as holotype), same nest as holotype (Type depository: Entomological Laboratory, Faculty of Agriculture, Kyushu University; National Institute of Agro-Environmental Sciences, Tsukuba; National Science Museum, Tokyo).

Distribution. Taiwan.

Ecological note. The colony was found in clay soil about 15 cm in depth by a roadside cutting. In the nest many larvae were found feeding on a geophilomorph centipede, which was identified as *Mecistocephalus* sp. through the courtesy of K. Shinohara. The larvae put their heads into

the body of the centipede via its pleura. Although the posterior half of the centipede's body had been consumed by the larvae, the total length was estimated about 4 cm based on its head size (Shinohara, pers. comm.). In the laboratory colonies of *Leptanilla japonica*, Masuko (1990) also observed that the ant preferably hunted and consumed geophilomorph centipedes. These field and laboratory observations suggest that *Leptanilla* is specialized on this group of centipedes.

Remarks. The simple clypeus with shallow median incision in the anterior margin also occurs in L.oceanica from the Ogasawara Islands and L.vaucheri from Morocco. But this new species is separable by the combination of the characters of 3 teeth on the mandibles, the less-produced median portion of the clypeus, the subglobular petiole, the globular postpetiole and the anteriorly narrowed first gastral segment. This is the first record of the subfamily from Taiwan.

Taxonomic notes

Males of Leptanilla

Bolton (1990) listed seven characters of leptanilline males as a 'tentative' diagnosis of Leptanillini. As he complained, however, all the males described until that time were 'presumed' ones. Apart from the males of L.japonica, we have examined several undetermined leptanilline males collected from various localities including Australia, Southeast Asia and Japan. The specimens examined are listed in the Appendix. We do not intend to describe these as new, but can confirm the generic characters of leptanilline males. Figs 19-23 show a male collected from Mt Hikosan, Japan, the type locality of L. morimotoi. Figs 24-29 show the genitalia of a male collected from Iriomote Is., Ryukyus, Japan. The males are minute and have reduced wing veins. However, wing reduction is seen in small species of many ant genera (Ogata, 1991). Thus little weight can be placed on the poor venation as a unique character of the genus. The genus is characterized by the subrectangular head with rounded posterior corners, the reduced clypeus, and anteriorly located antennal insertions. These characters are more or less shared with the worker caste. The hairy eyes and the concave occipital border in L. japonica are species-specific characters.

The unique structure of the male genitalia has been noticed by previous authors. The terminology of male genitalia used here is that of Ogata (1991), who followed Snodgrass (1941), though Petersen (1968) and Kugler (1987) used that of Michener (1956) in their descriptions. The correspondence between our terminology and that of Petersen and Kugler is given in Table 1.

Petersen (1968) interpreted the ring-shaped structure as a rudiment of the ninth abdominal tergum and stated that the basal ring was completely lost. However, the ninth tergum is lost in many aculeate Hymenoptera and, if present, it is in the form of weakly sclerotized hemitergites. The ring is thus more probably not a rudiment of the ninth tergum but the basal ring. The shape of the parameres, in

Table 1. Terminology of male genitalia, with a comparison of that of previous authors.

Present paper (cf. Ogata, 1991)	Petersen (1968) and Kugler (1987) (cf. Michener, 1956)
Basal ring	Gonobase
Paramere	Gonocoxite
(Volsella) digitus	(Volsella) digitus
Cuspis	Cuspis
Aedeagal plate	Penis valves
- •	(Gonapophyses)
Hypopygium	Subgenital plate
	(ninth sternum)
Cerci	Pygostyli

particular their apical portions, differs between species. Some are variously armed with denticles and others are folded inward. In any case, males of *Leptanilla* commonly have the apical portion flattened dorsoventrally. The flattened aedeagal plates are unique within the Formicidae (cf. Ogata, 1991).

In summary, the following are diagnostic of *Leptanilla* males:

- (1) Head longer than broad, with subparallel sides and rounded posterior corners.
 - (2) Eyes medium in size, situated anteriorly.
 - (3) Mandibles reduced, forming non-opposable lobes.
 - (4) Palp formula 1,1.
- (5) Antennal insertions close to anterior margin of cranium.
- (6) Antennal insertions exposed; antennae with 13 segments.
- (7) Pronotum elongate with concave posterolateral portion.
- (8) Mesoscutum long and narrow, not overhanging pronotum, with arched dorsal surface.
 - (9) Notauli absent on mesoscutum.
- (10) Mesoscutellum less raised, not overhanging metanotum.
- (11) Forewing lacking pterostigma and with poor venation (Sc + R + Rs).
 - (12) Hindwing narrow, lacking any veins.
- (13) Middle tibia with one small apical spur; hind tibia with two small apical spurs.
 - (14) Metapleural gland absent.
 - (15) Propodeum cylindrical, with arched dorsal surface.
- (16) Petiole isolated, subglobous without anterior peduncle.
 - (17) Third abdominal segment not forming postpetiole.
 - (18) Cerci absent.
- (19) Hypopygium small and broad, sometimes bifurcate posteriorly.
 - (20) Basal ring small, thin, weakly sclerotized.
 - (21) Digitus simple and elongate.
- (22) Apical portion of parameres thin, flattened, dorsally protruding, sometimes armed with small teeth.

(23) Aedeagal plates flattened, often broad, without serrate ventral margin.

Taxonomic positions of other genera based on males

Presently the subfamily Leptanillinae comprises seven genera (Baroni Urbani et al., 1992): Leptanilla, Noonilla, Phaulomyrma, Scyphodon, Yavnella, Anomalomyrma and Protanilla. Among them, Noonilla, Phaulomyrma, Scyphodon and Yavnella are known only from males, but there have been until now no worker-associated males known in the subfamily. The genus Apomyrma, originally described as a member of Amblyoponini of Ponerinae, was transferred to Leptanillinae by Bolton (1990), and the pharate male was known. However, the genus has since been treated as a separate subfamily (Baroni Urbani et al., 1992).

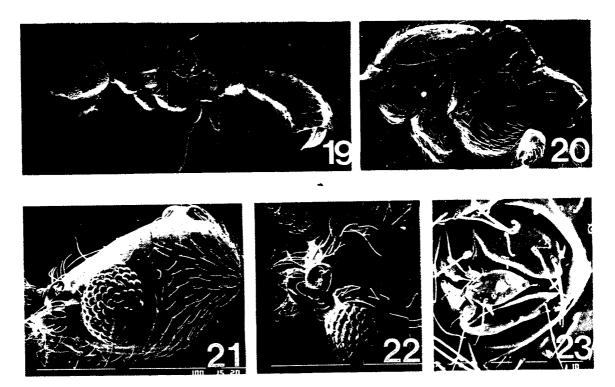
Phaulomyrma and Yavnella males have similar male genitalia to the leptanillines described in this paper, particularly in the shape of the aedeagal plates and parameres. They are distinguishable from Leptanilla by the shape of the antennal segments or the head. It is certain that Phaulomyrma and Yavnella are members of Leptanillinae.

Noonilla was established based on a single species, copiosa Petersen from the Philippines. To justify its taxonomic position as a member of Leptanillinae, Petersen (1968) mentioned several characters: (1) one-segmented maxillary and labial palpi; (2) the shape of the pronotum; (3) the strong and crooked fore femora; (4) the reduction

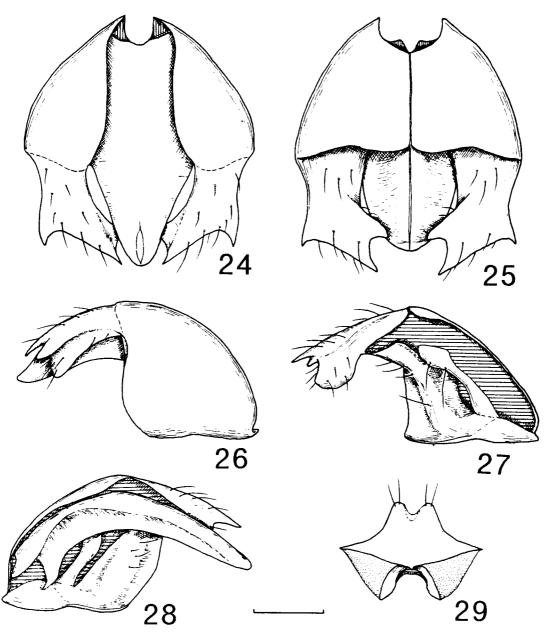
of veins; (5) the absence of the metapleural gland; (6) the reduction of the terminal abdominal segment; (7) the absence of a true basal ring; (8) the absence of volsellar cuspital lobes. However, his characters (1), (4), (5) and (8) do not provide strong evidence, bacause the palp formula, wing veins, metapleural gland and cuspis are reduced in males of many ant genera. His character (3) is not present in several species of *Leptanilla*. Characters (6) and (7) are of doubtful interpretation. Therefore the present position of *Noonilla* is questionable.

Although we did not examine the type of N.copiosa, we checked a congeneric species from Philippines (courtesy of R. W. Taylor). The species differs from copiosa in having a longer petiole, but shares the flap-like projection on the fore coxa. Since we were not able to dissect the genitalia, we could not determine the shape of the hypopygium and the basal ring. However, it is certain that the genus has completely different genitalia from those of Leptanilla. The paramere is lobe-shaped and curved dorsally [misinterpreted as digitus by Petersen (1968); however, the true digitus is visible between the paramere and aedeagus and has an elongate acuminate apex]; aedeagal plates are fused to each other and compressed, forming a tubular structure, curving ventrally with an acute ventral corner. Furthermore Noonilla has a clear occipital carina which is lost in Leptanilla. All these characters also occur in Aenictus (Aenictinae). It is reasonable to remove Noonilla from Leptanillinae.

The Sumatran genus Scyphodon was originally considered as incertae sedis by Brues (1925) and later assigned



Figs 19-23. Leptanilla sp. 1, male (Mt Hikosan, Kyushu, Japan). 19, lateral; 20, trunk, lateral; 21, head, lateral; 22, anterior portion of head, dorsolateral; 23, mouth parts, ventral.



Figs 24–29. Leptanilla sp. 2, male genitalia (Ushikumori, Iriomote Is., Ryukyus, Japan). 24, dorsal: 25, ventral: 26, lateral: 27, left paramere, inner lateral: 28, right paramere and aedeagal plate, inner lateral: 29, basal ring and hypopygium, ventral. Scale bar = 0.1 mm.

to its present position by Petersen (1968). Although we could not examine the types, we consider the present taxonomic position doubtful because the following characters never occur in Formicidae: (1) the segmentation of abdomen (according to the interpretation of Petersen (1968), the fourth and fifth abdominal segments are fused); (2) the structure of the pronotum; (3) the genitalic structure (quite different from any other genera of ants in having a tubular aedeagus). All these suggest that the genus is not a formicid.

Thus we tentatively conclude as follows:

Family Formicidae

Subfamily Leptanillinae Emery 1910

Anomalomyrma Taylor in Bolton, 1990

Protanilla Taylor in Bolton, 1990

Leptanilla Emery, 1870

Phaulomyrma Wheeler & Wheeler, 1930

Yavnella Kugler, 1987

Subfamily incertae sedis

Noonilla Petersen, 1968

Family incertae sedis

Scyphodon Brues, 1925

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Appendix. List of species examined

Abbreviations: ANIC = Australian National Insect Collection, CSIRO, Canberra, Australia; EKU = Entomological Laboratory, Faculty of Agriculture, Kyushu University, Japan; OPMN = Osaka Prefectural Museum of Natural History, Japan.

Leptanilla escheri Kutter, 10 workers, INDIA: Travancore, nr Vandaravu, 10.iv.1927 (K. Escher) (ANIC).

Leptanilla havilandi Forel, 4 workers, SINGAPORE: Bukit Timah Res., 18.vi.1969 (D. H. Murphy) (ANIC).

Leptanilla japonica Baroni Urbani, 2 workers (paratypes), JAPAN: Manazuru, Kanagawa Pref., 24.vii.1968 (M. Kubota) (OPMN).

Leptanilla kubotai Baroni Urbani, 2 workers (paratypes), JAPAN: Hiro-okakami, Kochi Pref., 29.iii.1967 (M. Kubota) (OPMN).

Leptanilla morimotoi Yasumatsu, 6 workers (paratypes), JAPAN: Mt Hiko, Kyushu, JAPAN (K. Morimoto) (EKU).

Leptanilla oceanica Baroni Urbani, 1 worker (paratype), JAPAN: Mukojima, Ogasawara ls., 1.x.1975 (M. Shindo) (ANIC).

Leptanilla swani Wheeler, 3 workers (paratypes), AUSTRALIA: Gayamin Pool, Chitterina, W. Australia (D. C. Swan) (ANIC).

Leptanilla tanakai Baroni Urbani, 6 workers (paratypes), JAPAN: Amboh, Yaku Is., 22.xi.1974 (M. Tanaka) (OPMN).

Leptanilla thai Baroni Urbani, 1 worker (paratype), THAILAND: Khao Chong, South Thailand, 28.xii.1964 (H. Watanabe) (OPMN).

Leptanilla sp. 1, 3 males, JAPAN: Mt Hikosan, Kyushu (K. Takeno) (EKU).

Leptanilla sp. 2, 5 males, JAPAN: Ushikumori, Ryukyus (G. A. Samuelson) (EKU).

Leptanilla spp. (males), JAPAN: 1 male, Minaminoma, Awa, Shikoku (S. Miyamoto) (EKU); 1 male, Kosugidani-Hananoego, Yakushima Is. (T. Hidaka) (EKU); 1 male, Mt Omotodake, Ishigaki Is., Ryukyus (G. A. Samuelson) (EKU); 1 male, Shirahama, Iriomote Is., Ryukyus (G. A. Samuelson) (EKU). PHILIPPINES: 2 males, Mt Apo, Mindanao Is. (T. Hirowatari & Y. Funatsu) (EKU). AUSTRALIA: 1 male, Arramall Cave, W. Australia (ANIC); 1 male, Katherine George, Northern Territory (ANIC).

Noonilla sp., 1 male, PHILIPPINES: Misamis Or., Minalwang, 1050 m, 24.iii-4.iv.1961 (at light) (H. Torrevillas) (ANIC).