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Some Novelties in Presumed Males of Leptanillinae (Hym., Formicidae).

By

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The very interesting, systematically isolated ant subfamily Leptanillinae comprises only very few known species, and knowledge of the subfamily is very scanty (see G. C. Wheeler & E. W. Wheeler, 1930; Kutter, 1948, and the important study on the peculiar larvae by G. C. Wheeler & J. Wheeler, 1965). One of the merits of the Noona Dan Expedition (Petersen, 1966) was therefore, the capture of two new ant species which probably belong to this subfamily. Unfortunately, the captured specimens are males which were taken without associate workers or queens, but they are so remarkable that they require formal naming and description.

During the study of these new species it was necessary to take other male-based leptanillines into consideration, and in the present paper notes are presented on all species.

First, I have been able to study the material of the four male-based species assigned to *Leptanilla* by Santchi (1907, 1908). Like Santchi, I feel that these males may reasonably be regarded as true leptanillines, but it must be taken into consideration that none of the male-based species assigned to the Leptanillinae, or any like them, have been taken in association with workers or queens, and although it is a rather good evidence, the fact that both sexes have been recorded once from the very same area in Tunisia by Santchi (1915) is no proof of mutual connexion. If these male-based species should ultimately prove not to be leptanillines, it would presumably be necessary to create a new family for them, as they cannot be placed in any other ant group now recognized. In fact, the male-based leptanillines are so peculiar that, as mentioned

below, ant specialists have doubted whether they were true ants.

My notes below on other species than those described by Santschi are based on the literature alone or, in case of *Leptanilla palauensis* (M. R. Smith, 1953), based on literature and on information kindly supplied by a colleague, Dr. D. R. Smith, who studied the type.

The notes also cover *Scyphodon anomalum* Brues, 1925. This forgotten genus and species is recognized as a male ant and transferred to the Leptanillinae from an uncertain systematic position among Bethyloidea or Proctotrupoidea.

The first of the new species described below fits rather well into the main assembly of leptanilline males and is assigned to the genus *Leptanilla*, although it has aberrant genitalia.

The second species is quite unique, and a new genus, *Noonilla* n. gen., is erected for it. It probably deserves a higher rank in the hierarchy, as it is not only isolated as a leptanilline but is an astonishing ant, and further, a very peculiar hymenopteron.

The new information which is given on the terminalia of *palauensis* (Smith), included in the Leptanillinae by Taylor (1965), and the inclusion of *Noonilla copiosa* n. gen., n. sp. and *Scyphodon anomalum* Brues (which is also an extraordinary hymenopteron) in the Leptanillinae, makes the assembly of male-based species of this subfamily extremely diverse, but in my opinion there is no other place to assign these odd species. Fortunately enough there are good reasons for their placement as leptanillines, and further, it is not surprising that male leptanillines are diverse and peculiar ants as also the workers and queens, and especially the larvae, are unique.

***Leptanilla astylina* n. sp. (Figs. 1—5)**

H o l o t y p e, ♂. Philippines, PALAWAN: Mantalingajan Range, Pinigisan, 600 m., 24 Sept., 1961; caught in a Malaise trap placed inside primary forest. In the Zoological Museum, Copenhagen.

D e s c r i p t i o n. Length without antennae about 1.15 mm., without protruding part of the genitalia about 1 mm.; antennae 0.6 mm.

Colour of the alcohol-preserved specimen light brownish to testaceous. Any kind of conspicuous sculpture lacking. Pilosity also inconspicuous, short semi-erect setae present all over, well spaced, longest on dorsal surfaces and on femora.

Head twice as long as high and almost 1.5 times longer than broad at greatest width just behind the eyes, moderately tapered posteriorly; the concavity of occiput, seen from above, as deep as half the diameter of an ocellus. Eyes hairy, with large facets, semi-globular but hind margin straightened; ratio of longest and shortest diameter about 4:3. Ocelli large, prominent, distance from front ocellus to lateral ocelli as long as ocellar diameter, distance between lateral ocelli twice as long. Antennal sockets close to oral aperture leaving only a small space for the frontoclypeal area which is apparently undifferentiated; distance between antennal sockets as long as distance to eyes; a weak parafrontal ridge present laterad of sockets. Mandibles vestigial, about as long as broad, setaceous. Antennae almost as long as head and thorax combined; scape rather swollen, about 2.5 times as long as wide; pedicel pear-shaped, twice as long as wide, one third shorter than scape and clearly wider than proximal joints of flagellum; 1st flagellar joint slightly longer than 2nd, following joints gradually increasing in size distally, about one third longer than wide; terminal joint, however, a little more than 3 times as long as wide and as long as the two preceding joints combined.

Thorax narrower than head, a little more than 1.5 times higher than broad and about twice as long as high. Pronotum long, its

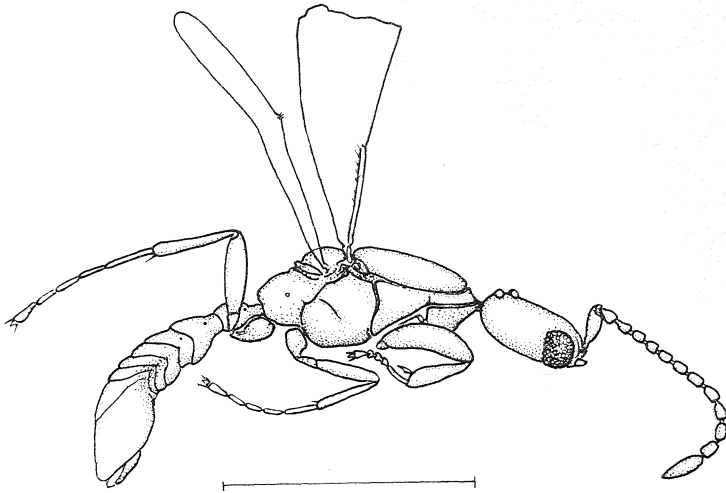


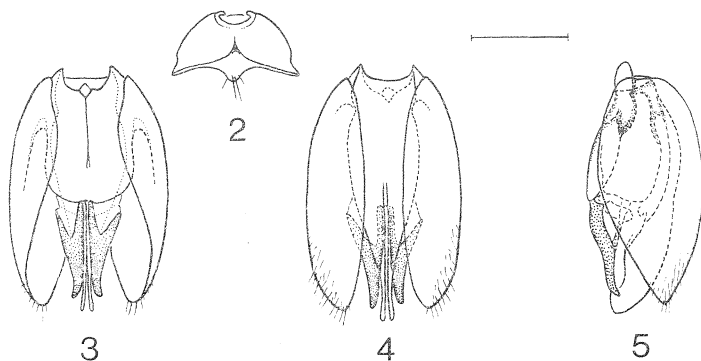
Fig. 1. *Leptanilla astylina* n. sp., holotype ♂, lateral view; forewing broken, setae omitted. Scale 0.5 mm.

lateral parts narrow anteriorly, its posterolateral corners almost meeting ventrally; propleuron bulging posteriorly; prosternum triangular, comparatively large, almost vertical. Mesoscutum almost twice as long as wide, greatest width situated far posteriorly; scutellum moderately convex. Central area of metanotum a narrow, transverse, somewhat protruding tubercle. Metapleural glands lacking.

Fore wings broken, at least distal one third missing. Venation lacking apart from a weak subcosta, indicated almost solely by a fold bearing a few long setae; subcosta ends rather abruptly; costal cell as long as mesoscutum or the head. Hind wing long and narrow, a little shorter than head and thorax combined.

Legs rather short, their proportions appear from fig. 1. Fore legs somewhat modified with strong, slightly crooked femora and thick tibiae; segments 2—4 of fore tarsus dilated, as long as broad. Tibial spur formula 1:1:2.

Abdomen including genitalia a little longer than thorax; genitalia alone almost half as long as abdomen. 2nd (petiole) and 3rd abdominal segment subequal in length, much longer than any of segments 4—7 which are decreasing in length posteriorly. Petiole with rather long anterior stalk, petiolar node simple, subglobular. Sternum 8 very small; tergum 8 very long dorsally, posteriorly extremely thin. Sternal and tergal plates of segments 2—8 separate, but in segment 9 fused (fig. 2). Tergum 9 very thin, obliquely



Figs. 2—5. *Leptanilla astylina* n. sp., holotype ♂, (2) abdominal segment 9, ventral view showing the reduced sternum fused with the ring-shaped tergum; (3—5) genitalia, ventral, dorsal and lateral view, respectively. — Scale 0.1 mm.

ring-shaped as its lateral parts fuse ventrally; sternum 9 very reduced, rhomb-like; segment 9 as a whole is thus a cup-shaped holder which fits the anterior end of the genitalia and is hidden inside the abdomen.

Genitalia as shown in figs. 3—5. Gonobase not recognizable; gonocoxites large valve-like structures with free margins, well separated both dorsally and ventrally; gonostyli not present. A tongue-shaped, ventral sclerite is interpreted as the medially fused volsellar plates, and two strongly sclerotized, proximally bifurcated rods are regarded as the volsellar digiti; these are closer associated with aedeagus than with volsellae; volsellar cuspi lacking. Distal part of aedeagus strongly laterally compressed, apex reaches just behind gonocoxites.

Queens and workers unknown.

Remarks. This new species is readily differentiated from all known male-based species of Leptanillinae by the shape of the genitalia and less obviously, by the wing venation. In other features it is principally very similar to other species placed in *Leptanilla* and *Phaulomyrma*. I have been able to compare it directly with the *Leptanilla* males described by Santchi (1907, 1908).

The genitalia of *L. astylina* n. sp. deviate from those of the *Leptanilla* species described by Santchi (see below, figs. 11—13) in the following ways, 1) the gonocoxites do not meet ventrally, 2) the gonostyli are lacking, 3) the volsellar plates are not inflected, but horizontal, medially fused to form a single tongue-shaped structure, 4) the volsellar digiti are not rod-like and largely free, but proximally bifurcated and associated with the aedeagus, and 5) the aedeagus is laterally compressed distally, not forming a flattened shield. On almost the same grounds the new species can readily be separated from *Phaulomyrma javana* G. C. & E. W. Wheeler (see below, figs. 16A, C). It is also clearly different from *Leptanilla santchi* G. C. & E. W. Wheeler (fig. 16D) in the shape of the genitalia, but the absence of gonostyli is common to both species and may indicate some relationship, but even in this case *L. astylina* n. sp. deviates to such an extent that it might deserve the erection of a new genus. However, at this state of our knowledge of the leptanillines I have found it premature to create a new genus formally and the species is enclosed in *Leptanilla*.

The wing venation in *L. astylina* n. sp. represents the most re-

duced state so far found in the Leptanillinae as only one vein is present, the subcosta. Some of the *Leptanilla* species described by Santschi were said to be veinless, but as shown below this is not true. Compared to the conditions in other *Leptanilla* species (fig. 14) or *Phaulomyrma* (fig. 16) the subcosta of *astylina* n. sp. is relatively long and it ends rather abruptly without any tendency to continue in a marginalis.

Noonilla n. gen.

Diagnosis based on male; queens and workers unknown. General features as shown in figs. 6—10.

Type species: *Noonilla copiosa* n. sp. described below.

♂. Head vertical; frontoclypeal region not differentiated by sutures or carinae (fig. 7). Antennae fifiform, 13-jointed. Mandibles vestigial, cylindrical, bluntly rounded apically, setaceous. Maxillary and labial palpi one-segmented.

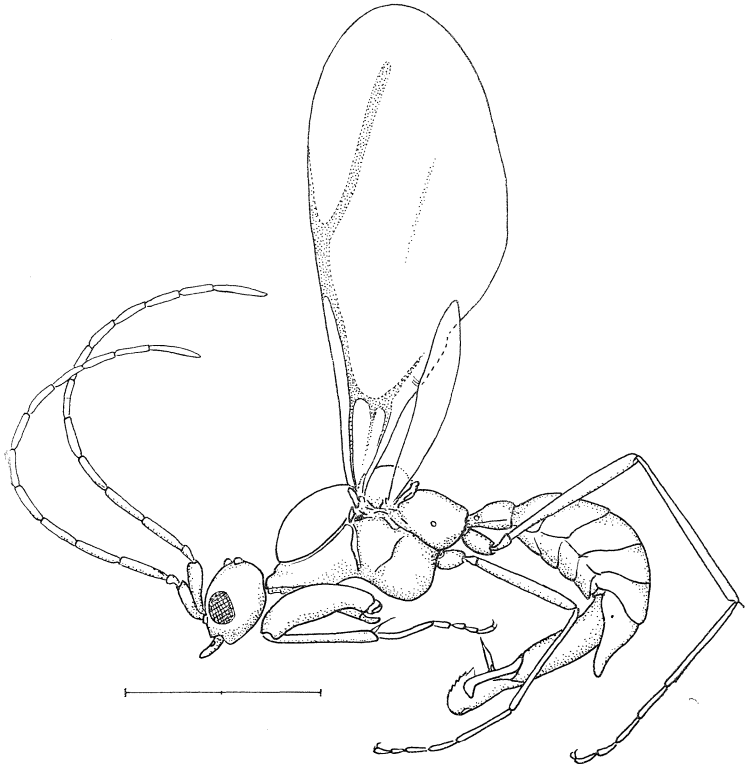
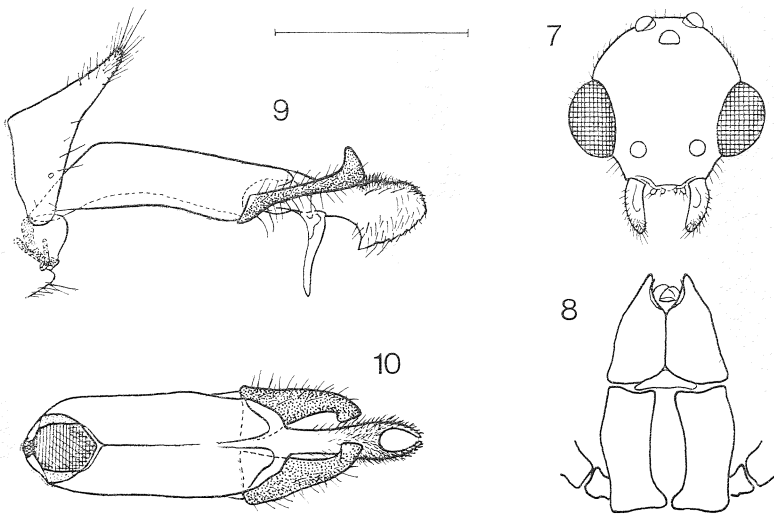


Fig. 6. *Noonilla copiosa* n. sp., holotype ♂, lateral view; setae omitted. — Scale 1 mm.

Thorax not compressed and not elongated (as in other leptanillines). Dorsal part of pronotum neck-like, lateral parts long, posterolateral borders extend onto the ventral surface; propleuron undivided; prosternum small, triangular (fig. 8). Mesoscutum lacking notauli and parapsidal lines; scutellum simple, strongly convex; mesopleuron large, strongly bulging ventrally, oblique pleural line weak. Metanotum narrow, central area prominent; metapleuron undivided, invisibly fused to propodeum; metapleural glands lacking.

Legs long and slender; fore femora, however, strong and curved; fore coxae flattened, with apical prolongations beyond insertion of trochanters (fig. 8). Tibial spur formula 1:2:2. Claws simple.

Wings as shown in fig. 6. Venation of fore wing strongly reduced with only three cells, the costal cell and two basal cells hardly separated by the weak median vein; main stem of venation consists of subcosta, marginal vein replacing pterostigma which is not truly developed, a short submarginalis and a very long radialis; perpendicularly to subcosta upper and lower basal



Figs. 7—10. *Noonilla copiosa* n. sp., paratype ♂, (7) head from in. front; (8) propleura, prosternum, fore coxae and trochanters, ventral view; (9) abdominal segment 8 and genitalia, lateral view; (10) genitalia, dorsal view. — Scale 0.5 mm.

veins extend to meet an almost complete analis. Costa indicated proximally. Hind wing short, veinless; anal lobe lacking.

Abdomen curved as shown in fig. 6. Terga and sterna separate in all segments. Abdominal segment 2 (petiole) simple, anteriorly flattened with the spiracles on lateral prominences, posteriorly cylindrical without a node. Tergum 8 elongated dorsally, attenuated, apex rounded. Tergum 9 (+10) membraneous, short, covered by tergum 8; pygostyli lacking. Sternum 8 strongly reduced, its lateral portions still plate-like but ventrally it is a narrow, strongly sclerotized bar. This bar supports the two arms of a reversed v-shaped, strongly sclerotized structure in firm connection with the genitalia, probably a true gonocondyle; the structure bears a short anteromedian process. Sternum 9 not recognizable as a normal sclerite; it might have been strongly modified into the structure mentioned above, or it might have fused with the ventral bar of sternum 8.

Genitalia*) very large, non-retractile (figs. 9, 10). Gonobase lacking; basal shaft of genital organ consists presumably of fused strongly reduced gonocoxites, dorsally, and medially fused volsellar plates, ventrally; gonostyli lacking; volsellar digiti strongly sclerotized, bluntly hooked at apices; penis valves proximally united constituting a cylindrical tube, distally and ventrally separated from tip of dorsal, oval phallotreme to well anterior to the unusual trigger-like ventral structure which is also divided into two symmetrical parts.

R e m a r k s. This new genus is readily differentiated from all other ant genera, in fact from all other Hymeoptera, by the highly unusual shape of the genitalia including the supporting structure in connection with sternum 8. The absence of a distinct gonobase and the strongly reduced gonocoxites recall the condition in some Chalcidoidea (Snodgrass, 1941). Other unique and distinctive characters of *Noonilla* are the shape of the coxae with prolongations beyond the trochanters and probably the shape of the petiole with the spiracles placed on prominences.

The wing venation of *Noonilla* n. gen. is also extraordinary, but not unique as almost exactly the same pattern exists in the genus *Scyphodon* (fig. 15A). The wing venation of *Scyphodon* is just a little more reduced and the marginalis longer and narrower, and this type of venation is no doubt transitional between *Noonilla*

*) Terminology of Michener (1956) used throughout the paper.

n. gen. and the condition found in *Phaulomyrma* (fig. 16A) and *Leptanilla* (fig. 14). On account of the type of venation and the peculiar shortened shape of the proximal part of the forewing it is apparent that *Noonilla* n. gen. is closely related to these Leptanillinae with which *Noonilla* shares several other features which are mainly apomorphic, e. g. the one-segmented maxillary and labial palpi, the shape of the pronotum, the strong and crooked fore femora, the absence of metapleural glands, the reduction of the terminal abdominal segments, the absence of a true gonobase, and the absence of volsellar cuspidal lobes.

On the other hand it is apparent that *Noonilla* n. gen. occupies a rather isolated position within the Leptanillinae, not because of the unique and specialised features of the fore coxae, the petiole, and the genitalia, but because the genus has retained some plesiomorphic features which are apomorphic in all other known leptanilline males, viz., the vertical head and the normal, rather short, uncompressed thorax which give *Noonilla* a quite different general appearance to other leptanillines which have a horizontal head and an elongated, laterally compressed thorax. This clear gap between two groups of leptanilline males may give rise to phylogenetic speculations, but in the present state of knowledge of the subfamily and without knowing workers and queens, these seem premature.

***Noonilla copiosa* n. sp. (Figs. 6—10)**

H o l o t y p e, ♂. Philippines, PALAWAN: Mantalingajan Range, Pinigisan, 600 m., 13. Sept., 1961. Caught in a Malaise trap outside primary forest. Paratype, ♂, same locality, but 6. Sept. and caught in a trap inside primary forest. Types in the Zoological Museum, Copenhagen.

D e s c r i p t i o n. Length of holotype without antennae 3.6 mm, without protruding portion of genitalia 2.9 mm; antennae 2.6 mm; fore wing 2.3 mm.

Colour of the alcohol preserved specimens mainly various shades from light to medium brown; yellowish are antennae especially pedicellus, mandibles, fore tarsi in strong contrast to other parts of fore legs, mid and hind legs apart from coxae, and genitalia apart from volsellar digiti.

Sculpture of any conspicuous kind lacking.

Pilosity also inconspicuous. Semi-erect setae of moderate length

and density present all over, longest at apices of terga, increasing in length caudally. Antennal setae almost as long as diameter of joints; setae at outline of head and on mandibles are shown in fig. 7 and pilosity scheme of genitalia is sketched in figs. 9 and 10.

Head seen from in front almost circular (fig. 7), measured over the eyes somewhat broader than high (ratio 8:7), behind the eyes only slightly narrower than high. Eyes almost hemispheric, strongly bulging, hind margin straightened; ratio of longest and shortest diameter 6:5; distance between eyes about half as long as width of head. Ocelli large and prominent, distance from front ocellus to lateral ocelli hardly as long as ocellar diameter, distance between lateral ocelli 2.5 times as long as ocellar diameter or about as long as their distance to occiput. Rim of antennal sockets prominent. Antennae almost as long as head, thorax and abdomen (without genitalia) combined; relative lengths of scape, pedicel, 1st., 2nd., 10th and 11th flagellar joints 32:12:37:31:25:36, relative widths 9:7:6:6:5:5; scape thus slightly longer than 2nd flagellar joint, flagellar joints decrease in size distally, apical joint, however, considerably longer than preceding ones and about as long as joint 1. Frontoclypeal area not differentiated either by sutures or carinae; shape of clypeal margin shown in fig. 7. Mandibles finger-shaped, twice as long as malar space or half as long as 1st flagellar joint, densely setaceous at apices. Labial and maxillary palpi almost equal in size, ovoid.

Thorax twice as long as broad and 1.5 times as long as high; relative lengths of pronotum, mesonotum, scutellum and propodeum measured at mid-line 8:38:18:18. Lateral view of thorax shown in fig. 6; ventral view of propleura and prosternum sketched in fig. 8.

Legs very long and slender, e. g. hind legs as long as combined length of head, thorax and abdomen without genitalia. Approximate lengths of various parts of legs are measurable from fig. 6. Fore coxae in ventral view a little more than twice as long as wide at apex (fig. 8); fore femora curved and strong, length slightly more than four times greatest width.

Fore wing 2.5 times longer than wide; proportions of venation may be measured from fig. 6. Hind wing about 7 times longer than wide, less than half as long as fore wing; 3 long hamuli present distally to mid-length of wing.

Abdomen strongly curved as shown in fig. 6, probably also in

life. Segment 2 (petiole) almost twice as long as greatest diameter of posterior cylindrical portion; spiracles placed in anterior one third of petiole, interdistance as long as petiolar diameter. Lengths of terga 3—7 at mid-line almost equal, slightly more than half length of attenuated, apically rounded tergum 8. Sternum 7 half as long as preceding sterna; sternum 8 and segment 9 described in the diagnosis of the genus. Genitalia as long as thorax, measurements may be taken from figs. 9 and 10.

Workers and queens unknown.

The male-based *Leptanilla* species of Santchi

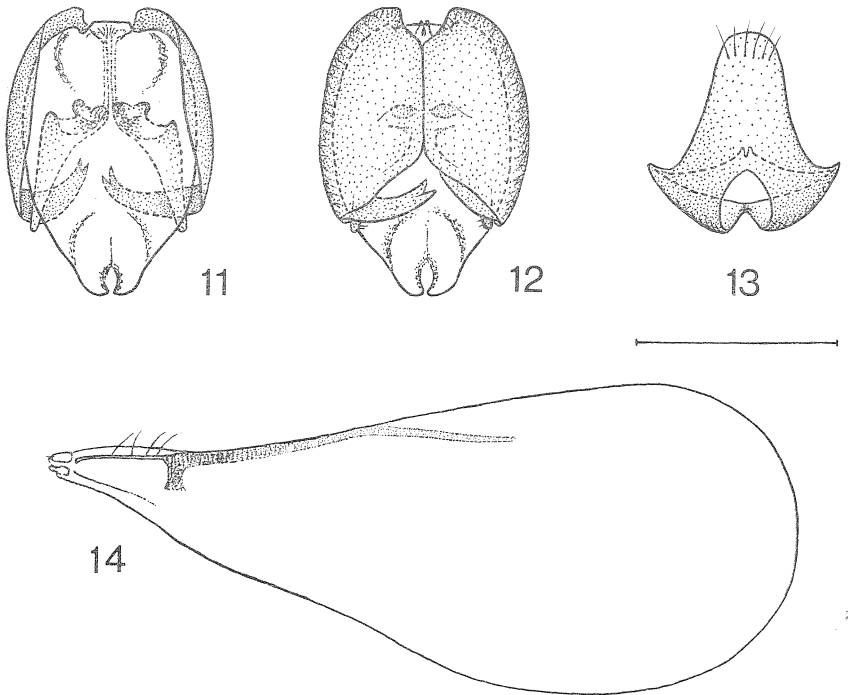
Through the kindness of Dr. Fred Keiser I have been able to study the surviving specimens of the male-based *Leptanilla* species described by Santchi (1907, 1908). These belong to Naturhistorisches Museum, Basel and consist of a single type-labelled specimen and two additional specimens of each of the four species, e. g. *Leptanilla tenuis*, *L. minuscula*, and *L. tanit* described in 1907, and *L. exigua* described in 1908. All of these specimens were labelled by Santchi but not all of them belong to the true type material. Thus the two additional specimens, labelled as *L. tenuis*, are not from the type locality, Kairouan, and they do not seem to be that species but rather they represent respectively *L. tanit* (locality: Hammaref, Tunisie) and an apparently new species (locality: Le Kef, Tunisie, Dr. Normand). Also one of the Santchi labelled specimens of *tanit* is probably wrongly identified and seems close to the apparently new species just mentioned from Le Kef.

Unfortunately, except for the two additional specimens of *tenuis* mentioned above, all specimens are mounted in balsam between cover-glasses and thus difficult to examine due to awkward positions and sometimes severe shrinking. A revision and redescription of the Santchi species, therefore, must await the capture of fresh material. However, since Santchi's papers contain several errors and his figures are especially unreliable, it is in order to make some remarks, first of all on two features of generic interest, the wing venation and the terminalia.

Wing venation. In the fore wing Santchi recognized the presence of a vein only in one of his species, namely *L. tanit*, but his figure of it is far from correct (fig. 2a in his 1907 paper, not fig. 3a which shows *minuscula*, the figure texts are transpos-

ed). It shows a straight vein which in all its length runs obliquely to the costal margin of the wing. In fact the venation, although very much reduced, is more complicated as can be seen from fig. 14. The main vein complex consists of 1) a narrow but very distinct subcosta, 2) a very long marginalis, 3) a straight radialis, and 4) a short, upper basal vein; in addition a weakly indicated analis is present. A true pterostigma is lacking; it is obvious transformed into the long marginal vein. The proximal part of the marginalis and the basal vein have a brownish pigmentation of a conspicuous, cracked appearance. Subcosta bears a few long setae.

This type of venation is also found in the other Santchi species, although in a still more reduced form. Only in *L. minuscula* a complete wing could be studied. It lacks the radialis and the basal



Figs. 11—13. *Leptanilla* sp., ♂ from Le Kef, Tunisia, (11—12) genitalia, dorsal and ventral view; 13) abdominal segment 9, dorsal view, the small sternum with bifurcate apex is seen through the larger tergum. — Fig. 14. *Leptanilla tanit* Santchi, fore wing, type specimen, ♂. — Figs. 11—13, scale 0.2 mm.; fig. 14, scale 0.4 mm.

vein, but the subcosta and the long marginalis, with the characteristic pigmentation, are both present. Apparently *L. tenuis* and *L. exigua* have the same venation but I have only been able to study the proximal part of the fore wing in these species. Apart from a clearly shorter radialis, the above-mentioned *Leptanilla* specimen from Le Kef has a venation similar to that of *L. tanit*.

The reduced venation in species like *L. minuscula* represents one of the extremities of a morphological cline within the Leptanillinae. The other extremity of the cline is the relatively rich venation of *Noonilla copiosa* n. sp. (fig. 6), whereas the conditions in species like *Scyphodon anomalum* (fig. 15), *Phaulomyrma javana* (fig. 16), and *L. tanit* (fig. 14) are connecting links in the chain.

Terminalia. Santchi was especially unlucky when he figured the abdomen of his species. It is not very serious that his figures show, erroneously, that *L. tenuis* (1907, fig. 1) and *L. minuscula* (1907, fig. 3) have a long and slender abdomen, but it is a bad error and very confusing to have turned the genitalia upside down obviously in all four species. In reality the distal, flattened part of the aedeagus is dorsal in all species, and not ventral as shown by Santchi in all figures of his paper from 1907. In other features of the genitalia his drawings are by no means perfect, but on the other hand, not too bad, as they show roughly what can be seen in the preparations of the specimens. However, the bad standard of preservation allowed only the larger parts of the genitalia to be drawn with some confidence, whereas the more delicate structures, such as the volsellae, could not be reliably reproduced. Fortunately an unmounted specimen from Santchi's collection could be dissected and studied in some detail and a better understanding of the general build of the terminalia could be obtained. The specimen studied is the above-mentioned one from Le Kef.

The abdominal segment 9 is shown in fig. 13. The sternum is a small rhomboidal or triangular plate with a bifurcated posterior tip. It is in firm connection with the much larger, posteriorly very weakly sclerotized tergum, the lateral portions of which bend over on to the venter and fuse for a short distance. As in *L. astylina* n. sp. described above, segment 9 is thus a socket into which the genital capsule is fitted. Pygostyli are lacking. A row of setae on

tergum 9 may indicate the line where tergum 10 could be fused to tergum 9.

The genital capsule is shown in figs. 11 and 12. A gonobase is totally lacking. The gonocoxites are large valve-like structures with free margins all the way round; they are widely separated dorsally, but ventrally they meet each other. The gonostyli are apically bifurcated and turned inward under the aedeagus. The inner side of the gonocoxites below the gonostyli is moderately convex and setaceous. The volsellar plates are not fully recognizable as they are very delicate; they are probably inflected dorsally into the lumen of the proximal part of the aedeagus from the ventral margins of the gonocoxites. A pair of large, rod-like lobes are the volsellar digiti; they are provided with rather long setae on the free distal portion. Volsellar cuspidal lobes are not recognizable. The aedeagus is broad and its proximal part is thick and sub-cylindrical whereas the distal part is flattened and covers the volsellar digiti and the inflected gonostyli like a shield. The tip of the aedeagus is divided as shown in the figures.

As far as they could be studied the terminalia of the four Santchi species are build in the same way as described above in the *Leptanilla* specimen from Le Kef, but the elements of the terminalia vary in shape from species to species and are of taxonomic value. This appears already from Santchi's papers and I can mainly confirm what he says about the form of the aedeagus and the tips of the gonostyli in the different species, for example, but his descriptions of the volsellae and his figures of these structures are not reliable, as already mentioned above. Unfortunately the study of Santchi's material does not give much new information on these structures. The volsellar digiti of *L. exigua* are build almost as in the specimen from Le Kef; the lobes are somewhat longer, richly setaceous and relatively well sclerotized. In the remaining species the digiti are apparently much smaller. This is definitely so in *L. minuscula* as already can be seen from the figure by Santchi (1907, fig. 3c).

The *Leptanilla* species from Tunisia, Africa, obviously make up a rather uniform group which can be differentiated from other leptanilline taxa on the basis of the structure of the genitalia. Surprisingly enough the investigations on the material from the collection of Santchi have shown me that all four Santchi species are good species, and a fifth species (from Le Kef) may be added.

These five species are distinguishable by features of the genitalia, but also characters of the head capsule, the antennae and the petiole provide good landmarks for the recognition of the species.

L. tenuis and *L. tanit* both have a short head (about one third longer than wide) in combination with long flagellar joints (about twice as long as wide), whereas *L. minuscula*, *L. exigua* and the *Leptanilla* species from Le Kef have a long head (at least more than 1.75 times longer than wide) and short, quadrate flagellar joints. *L. tanit* is readily distinguished from the other species by the shape of the node of the petiole; in profile the node in this species is very strongly convex anterodorsally rather than evenly slanting as in the other species, in dorsal view the anterior margin of the node looks slightly bilobate due to the advanced lateral parts, faintly recalling the condition in the queen of *L. theryi* Forel as described by Santchi (1915, p. 57, fig. 3).

***Scyphodon anomalum* Brues, 1925 (Fig. 15)**

This peculiar hymenopteron was described by Charles T. Brues in 1925 on the basis of two specimens from Sumatra.

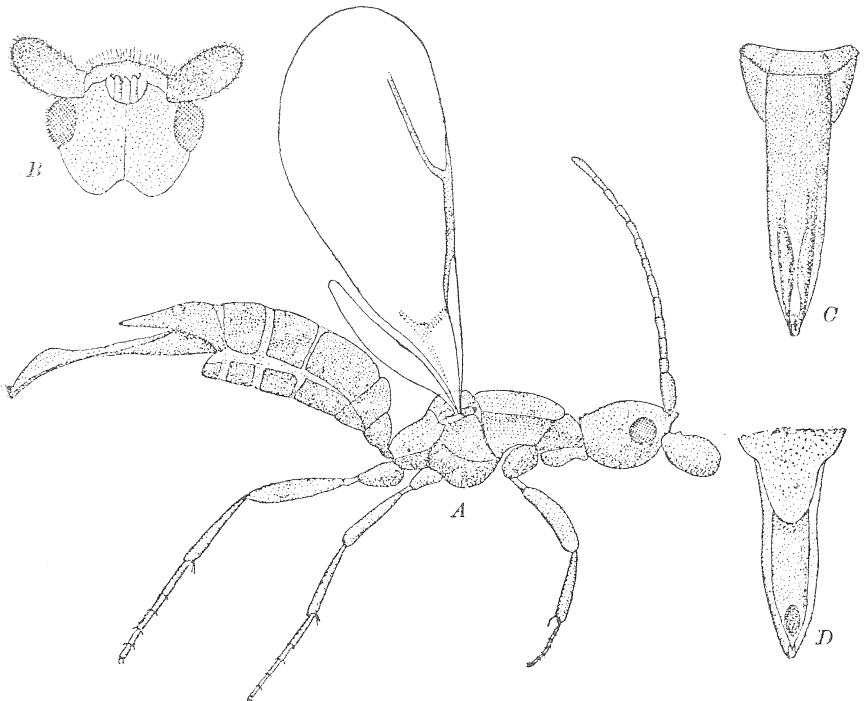
As Brues himself said, he was unable to determine the systematic position of the species with any degree of satisfaction, and the well-known hymenopterologists Rohwer and Fagan, whom he consulted, were also unable to solve the question; all three could not even definitely determine the sex of the specimen. As far as can be judged from the short and somewhat unconvincing discussion in his paper, Brues thought that his striking species would find its place in the Bethyloidea or Proctotrupoidea or perhaps in a family of its own. (Surprisingly enough, Brues at first found a position near Braconidae reasonable).

The systematic position of *Scyphodon* has apparently not been discussed since the original description, though Brues himself probably indulged in some reflections on the question when, as editor of "Psyche", he processed the paper by G. C. & E. W. Wheeler (1930) on the leptanilline ant species *Phaulomyrma javana*. Although there are some striking differences between the mandibles and terminalia of *Scyphodon* and *Phaulomyrma* it is clear that they are related (compare figs. 15 and 16) in such a way that Brues could have transferred his species to the Formicidae, with the male-based species then placed in the subfamily Leptanillinae. This transfer is hereby formally made, on the basis

of the description and figures by Brues, and a redescription may be presented later if the types are found; (they are not in the Museum of Comparative Zoology, Cambridge, according to Dr. Howard E. Evans, and Dr. David R. Smith has been unable to find them in the U.S. National Museum, Washington; Dr. M. A. Lieftinck, Leiden, informs me that the collectors very likely gave the specimens to Brues).

Scyphodon should no doubt be retained as a separate genus within the Leptanillinae, characterized mainly by three apomorphic features: 1) the large paddle-shaped mandibles, 2) the long apparently fourth segment of the abdomen, which I consider to represent the fused segments 4 and 5 of the abdomen, and 3) the unique genital structure. The mandibles and the genitalia are quite unique among the Hymenoptera.

It is impossible to interpret the genital structure with confidence



Figs. 15. *Scyphodon anomalum* Brues, (A) lateral view, (B) head, ventral view, (C) terminalia, dorsal view, (D) terminalia, ventral view. (Copied from Brues, 1925).

from the description and figures of Brues (reproduced in figs. 15A, C, D). According to him the genitalia proper constitute the tubular piece with the large oval aperture anterior to the acutely pointed tip. This tube is supported by, and fused to, the long sternum 9. Such a fusion of the genitalia and the hypopygium would be most unusual and it seems unlikely that it has actually taken place. I hazard the guess that the terminal structure of *Scyphodon* is somewhat like that of *Noonilla* n. gen. as described above, and therefore the dorsal tube is interpreted as the aedeagus, with a dorsal, oval, phallosome as in *Noonilla*. The ventral supporting sclerite is interpreted as a modification of the proximal shaft of the genital organ, which in *Noonilla* is composed of the strongly reduced gonocoxites and the volsellar plates, and the pair of longitudinal thickenings near the apex (fig. 15C) may be homologous with volsellar digiti. Sternum 9 is apparently strongly reduced, as is tergite 9 (+10). However, as long as the actual specimens cannot be studied this interpretation of these peculiar genitalia is mere guess-work.

The wing structure and venation of *Scyphodon* are closest to *Noonilla* (fig. 6), but in other general characters the species is more similar to the *Leptanilla-Phaulomyrma* complex, due especially to the horizontal head and laterally compressed thorax.

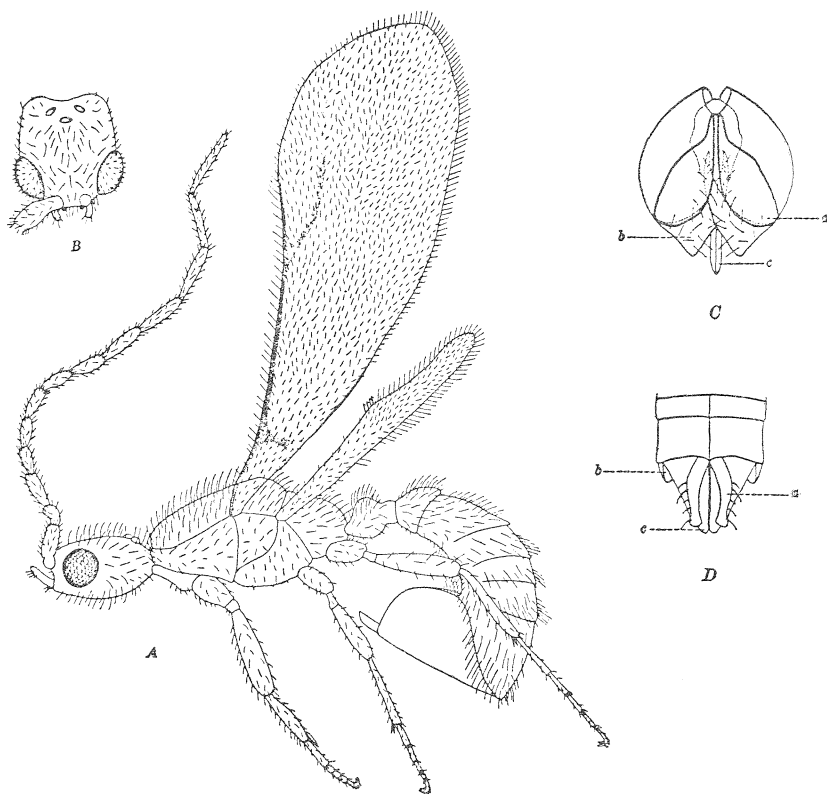
It is quite understandable that Brues did not consider *Scyphodon anomalum* to be an ant. This species is less ant-like than e.g. *Leptanilla palauensis* (Smith, 1925), and Dr. Robert W. Taylor (*i. l.*) informs me from his experience working with *palauensis* in 1964, that "though Drs. Evans, Burks and Krombein all felt that Smith's *palauensis* was definitely an ant; Brown, Wilson and myself, as ant specialists were, at least initially, somewhat dubious". Dr. Taylor now considers that placement of these species, and the others discussed here, in the subfamily Leptanillinae is acceptable, but emphasises the need for collection of such males in association with workers or queens before the assignment are conclusively proved.

***Phaulomyrma javana* G. C. & E. W. Wheeler, 1930 (Figs. 16 A—C)**

This species was described on the basis of two males from Buitenzorg, Java. The authors found it necessary to create a new genus for it, in which they also included *Leptanilla tanit* Santchi, 1907, from Tunisia.

The reasons for the erection of the new genus are vague. In the paper it is briefly stated that *Phaulomyrma* is to be distinguished from *Leptanilla* by the presence of wing veins and the unusually large genitalia. Further it is seen from the description that the tibial spur formula of *Phaulomyrma* is 1:2:2 rather than 1:1:2 in *Leptanilla* (also in *L. tanit* which was included in the new genus), but in all other features of some generic value the two genera are similar.

This also applies to the wing venation which was regarded as distinctive. New investigations on the wings of *Leptanilla* show that both *Leptanilla* and *Phaulomyrma* have the same type of



Figs. 16A—C. *Phaulomyrma javana* Wheeler & Wheeler, (A) lateral view, (B) head, dorsal view, (C) genitalia, ventral view. — Fig. 16D. *Leptanilla santschi* Wheeler & Wheeler, apex of abdomen, ventral view. (a) volsella in C, volsellar cuspis in D, (b) gonostylus in C, gonocoxite (without gonostylus) in D, (c) aedeagus. (Copied from G. C. Wheeler & E. W. Wheeler, 1930).

venation in the fore wing (see p. 587, and fig. 14 and 16A); in my opinion the original drawing of the wings of *Phaulomyrma javana* is not quite correct and a correction would probably give an almost the same venation as found in *L. tanit*, perhaps not quite as reduced.

However, *Phaulomyrma* may be retained as a separate genus on the basis of the genital structures if the description and figuring of these are fully correct. The genital capsule of *Phaulomyrma javana* (figs. 16A, C) is not unlike that of *Leptanilla* in the general appearance of the gonocoxites and the inflected gonostyli, but the volsellae are large, plate-like with broadly rounded free margins and without digiti in *Phaulomyrma* rather than small and probably inflected in *Leptanilla* and provided with rod-like digiti. There are probably other differences, however, which are not fully recognizable and understandable on the basis of the descriptions and figures alone.

Leptanilla tanit Santchi must be included in the genus *Leptanilla* again. This species has quite normal *Leptanilla* genitalia, as appears already from the original description, and the results of my examination of type material are confirmative.

***Leptanilla santchi* G. C. & E. W. Wheeler, 1930 (Fig. 16 D)**

This species was based on a single male from Buitenzorg, Java. In general features it fits well into the group of species assigned to *Leptanilla* and *Phaulomyrma*. However, according to the description and figure in the original paper (see fig. 16D), the genitalia have a rather aberrant shape. In fact it is surprising that the authors did not create a new genus for this species as they did for *Phaulomyrma javana* described in the same paper; the genitalia of *L. santchi* obviously deviate much more from *Leptanilla* genitalia than those of *javana*. The greatest difference lies in the reduction of the gonocoxites (fig. 16Db) and the absence of gonostyli. Also the volsellar digiti are differently shaped, being very large, with knob-like apices (fig. 16Aa).

Although *L. santchi* is thus clearly different from *Leptanilla* and *Phaulomyrma*, I refrain from erecting a new genus for this species based only on the conditions of the genitalia, as I did in the case of *Leptanilla astylina* n. sp. Unfortunately the type of *L. santchi* cannot be studied as it is probably lost, according to a personal communication from Dr. R. W. Taylor.

Within the male-based species assigned to the Leptanillinae, *L. santchi* is closest to *L. astylina* n. sp. as gonostyli are lacking in both species. Otherwise their genitalia are not very similar. The shape of the digiti and their association with the aedeagus in *L. santchi* may have some resemblance to the conditions in *Noonilla copiosa* n. sp.

Leptanilla palauensis (M. R. Smith, 1953)

This male-based species from the Palau Islands was originally described in the ponerine genus *Probolomyrmex* by Marion R. Smith (1953, p. 127, figs. 1—2), but was later excluded from that genus and transferred to the Leptanillinae, with a queried assignment to the genus *Leptanilla*, by Taylor (1965, p. 363). Taylor gives very good reasons for the transfer to Leptanillinae, but I consider that *palauensis* is not as close to *Leptanilla* (or to the almost identical genus *Phaulomyrma*) as he thought. The conditions of the genitalia of *palauensis* are so different from *Leptanilla* that *palauensis* probably deserves a genus of its own.

Taylor considered the genitalia of *L. palauensis*, of *Phaulomyrma javana* G. C. & E. W. Wheeler and of Santschi's *Leptanilla* species to be similar, mainly in the shape of the gonoforceps, but unfortunately he was misled by Smith's inaccurate description of the genitalia in *palauensis*. Smith surprisingly confused tergum 8 with the gonoforceps, apparently because tergum 8 has a peculiar form, with long posterolateral projections. These were accepted as apices of gonoforceps (gonostyli) by Taylor, following Smith. However, the peculiar terminal sclerite is in fact the tergum of the eighth abdominal segment, and it should be noted that Smith's figure 2 shows a spiracle on this sclerite. At my request Dr. David R. Smith has kindly examined the type of *palauensis* located in the collections of the U.S. National Museum, Washington, and he confirms my view on the identity of the sclerite in question.

After this correction it is clear that the genitalia of *palauensis* bear no obvious resemblance to those of *Leptanilla* and *Phaulomyrma*, apparently being at least partly retractile and presumably without large gonocoxites. Information and sketches provided by Dr. Smith show that the genitalia are apparently very large and unusually retracted, in fact, in such a way that the 6th and following sterna are withdrawn by the genitalia into the abdomen

and probably strongly reduced, a most unusual condition. According to Dr. Smith, fig. 2 in the original paper on *palauensis* is quite wrong in its interpretation of the terminal sterna. On the other hand, however, he has confirmed the figuring of the aedeagus, which is a compressed, blade-like structure with the dorsal edge thicker than the ventral one. It is very long and can be seen from below to extend right into the fifth sternum at about the middle of the abdomen. Dr. Smith has also confirmed the presence of the structures called volsellae in the original description, but these are unfortunately almost hidden under tergum 8. What can be seen are presumably the tips of the volsellar digiti. In Dr. Smith's sketches they are slightly hooked and their bases may be associated with the aedeagus in much the same way as those of *Noonilla copiosa* n. sp. (figs. 6, 9, 10).

Unfortunately the U.S. National Museum does not loan holotypes, and until the single specimen of *palauensis* can be exhaustively studied and its genitalia dissected, I refrain from formally erecting a new genus for this remarkable hymenopteron.

Acknowledgements

During this study I have received help of various kinds from several colleagues, to whom I wish to express my sincere thanks. This applies especially to Dr. Robert W. Taylor, Canberra, who gave me valuable advice and read parts of the manuscript during a stay in Copenhagen; also Dr. Howard E. Evans, Cambridge, Mass., and through him Drs. W. L. Brown, Jr., New York, and E. O. Wilson, Cambridge, commented on *Noonilla copiosa*. Dr. David R. Smith, Washington, readily answered my questions about the type of *Leptanilla palauensis*, Dr. Fred Keiser, Basel, lent me the typematerial of all four Santchi species, and Dr. M. A. Leiftnick, Leiden, commented on the location of the types of *Scyphodon anomalum*.

Summary

Leptanilla astylina n. sp. and *Noonilla copiosa* n. gen., n. sp. are described from Palawan, Philippine Islands. The type material of Santchi's *Leptanilla* species from Tunisia, Africa, is examined and new information is given, especially with regard to the terminalia and fore wing venation. *Scyphodon anomalum* Brues is recognized as a male ant and transferred to the Leptanillinae from an uncertain systematic position. Notes are provided on the remaining male-based leptanillines,

including a new interpretation of the terminalia of *Leptanilla palauensis* (M. R. Smith). The inclusion of *Noonilla copiosa* n. sp. and *Scyphodon anomalum*, both very extraordinary Hymenoptera, in the Leptanillinae, makes the subfamily extremely diverse, and the existence of such species sustains the view that the Leptanillinae are isolated among ants.

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