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Secostruma, a new subterranean tetramoriine ant genus (Hymenoptera: Formicidae)

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ABSTRACT. *Secostruma*, a very specialized new subterranean ant recovered from a soil-core sample taken in Sabah, East Malaysia, is described for the first time. Its most striking adaptations and their possible functions are discussed, and its affinities investigated. Analysis of its main features and comparison with two possible parent-groups leads to the conclusion that *Secostruma* is a member of the *Tetramorium*-group of genera.

Introduction

The genus *Secostruma*, which is described and discussed below, represents yet another rare myrmicine ant taxon recovered by a specialized collecting technique. In recent years collecting by means of Berlese funnels, Winkler bags and soil-core samples has produced a wealth of extremely interesting and taxonomically important myrmicine ants from all parts of the tropics and subtropics. Some of these samples have provided our first glimpses of extant forms whose closest relatives are only known from the fossil record, for example *Tatuidris*, the only living member of the otherwise extinct tribe Agroecomyrmecini (Brown & Kempf, 1967). Others have shown remarkably wide distributions of related rare genera which appear to represent relicts of an earlier ant fauna, now mostly displaced by more recently evolved forms. In this category fall *Phalacromyrmex* from Brazil (Kempf, 1960), *Pilotrochus* from Madagascar (Brown, 1978) and *Ishakidris* from Sarawak (Bolton, 1984), all of which are now placed in a single genus-group. These specialized collecting techniques have also been responsible for the production of evidence supporting new genus-level synonymy, the establishment of new and more accurate associations between previously known taxa, and an increase in our understanding of higher classification and phylogeny in the Myrmicinae as a whole.

Some of the recently described myrmicine genus-level taxa show vague relationships with one or two others but mostly remain mysterious (e.g. *Baracidris* (Bolton, 1981), *Indomyrma* (Brown, 1986)), whilst others can be placed confidently within well-established tribes or genus-groups (e.g. *Asketogenys* (Brown, 1972), *Cladarogenys* (Brown, 1976) *Protalaridris* (Brown, 1980a)). *Secostruma*, recovered from a soil-core sample taken in Sabah, East Malaysia, nearly falls into this last category. Although easily defined in morphological terms by means of its several striking autapomorphic developments, it nevertheless remains difficult to place with absolute certainty in a genus-group. In part this is because its autopomorphic developments have masked some characters and in part because one critical character is located on the sting, which in the holotype is completely withdrawn. As pointed out below, it is apparent that *Secostruma* falls either into the *Myrmica*-group or the very closely related *Tetramorium*-group.

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A critical examination of the holotype and point by point comparison with members of each group lead to the conclusion that *Secostruma* should be included with the tetramoriines. The recovery of more material, whose gasters can be dissected to examine the sting, will quickly confirm or refute this statement.

Secostruma is well adapted for a subterranean and apparently carnivorous lifeway. It has vestigial eyes, large powerful mandibles, and a striking modification of the gaster which, it is postulated, is specialized to bring the sting into play in confined spaces or tunnels in the earth. The genus and its only known species *S. lethifera*, are described below. This is followed by a discussion of the genus, its specializations and possible lifeway, and an investigation of the affinities of the genus which led to its inclusion in the *Tetramorium*-group.

Secostruma **gen.n.**

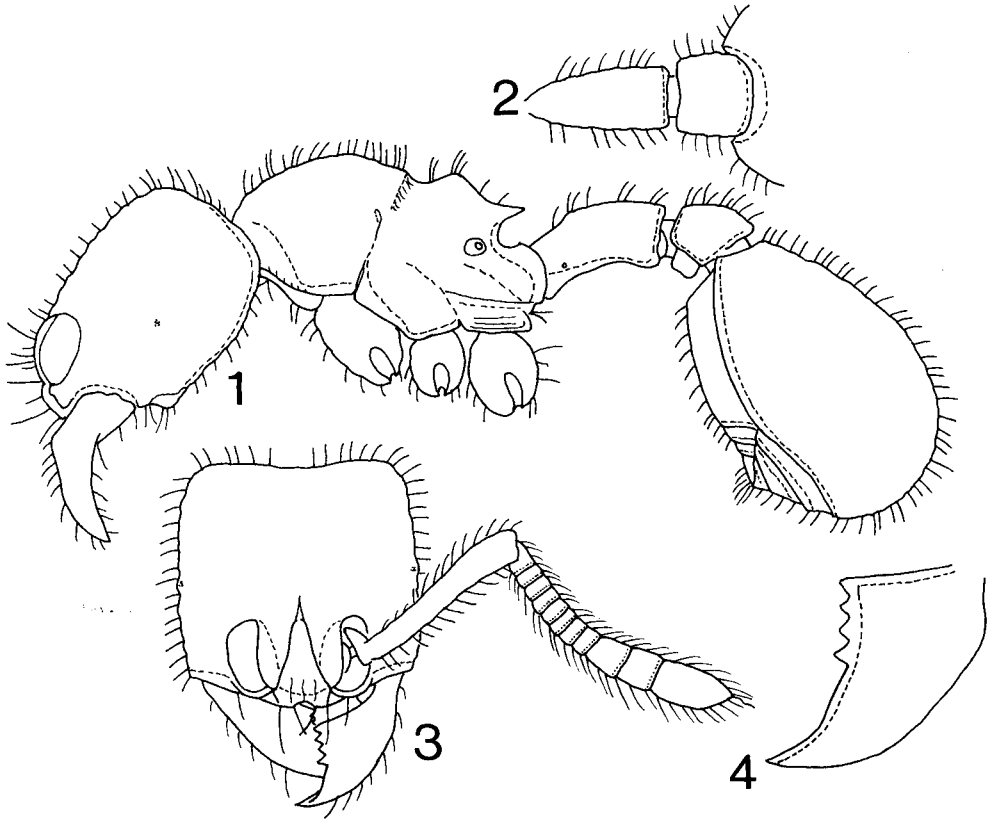
DIAGNOSIS OF WORKER. Subterranean ants belonging to the subfamily Myrmicinae, with the following combination of characters.

1. Palp formula 4,3 (*in situ* count); right maxillary palp broken.

2. Masticatory margin of mandible with a stout curved acute apical tooth, subtended by a long edentate section of the margin. Basad of the edentate section the margin with a row of 4 small teeth. Edentate section of margin longer than tooth-bearing section (Fig. 4).

3. Median clypeal seta absent. Median indentation of anterior clypeal margin with a seta on each side, these setae directed anteromedially and their apices crossing over.

4. Lateral portions of clypeus raised into sharp



FIGS. 1–4. *Secostruma lethifera*, holotype worker: 1, body in profile, antennae and legs omitted; 2, petiole and postpetiole in dorsal view; 3, head in full-face view; 4, left mandible to show dentition, fringing pilosity omitted.

narrow ridges or shield-walls in front of the antennal insertions (Fig. 3).

5. Median portion of clypeus posteriorly broadly inserted between wide strongly developed frontal lobes. Anterior quarter of median portion of clypeus suddenly angled downwards to the margin; the latter indented medially.

6. Frontal triangle depressed and sharply demarcated.

7. Areas of antennal articulations deep, bounded externally by a carina on each side which curves anteriorly from the hind end of the frontal lobe and is confluent with the narrow raised portion of the clypeal margin.

8. Antennae with 12 segments, the three apical segments forming a strong club.

9. Antennal scape with a right-angled bend near the base, the portion proximal to the bend expanded and concealing the scape articulation. Articulatory stem and condylar bulb projecting into antennal socket at roughly a right-angle from the downbent basal section of the scape.

10. Frontal carinae and antennal scrobes absent (Fig. 3).

11. Eyes vestigial, marked only by an irregular spot at the approximate midlength of the side of the head.

12. Alitrunk compact, promesonotum convex in profile, propodeum humped in profile and with a pair of short spines (Fig. 1).

13. Metapleural lobes very large and broadly rounded, connected to the propodeal spines by short lamellae.

14. Propodeal spiracle very low on side of sclerite, at junction with metapleuron and close to the margin of the declivity.

15. Ventral alitrunk with a long narrow V-shaped open cleft running from the posterior margin forwards between the hind coxal cavities. (Presence of metasternal process cannot be confirmed because of position of coxae.)

16. Simple tibial spurs present on middle and hind legs.

17. Petiole in profile or in dorsal view elongate and subcylindrical, with a short broad anterior peduncle and lacking a developed node (Figs. 1, 2).

18. Entirety of gastral dorsum formed by the much-expanded first tergite; this curves strongly downwards posteriorly so that tergites 2–4 are on what is functionally the ventral surface of the gaster. Anal and sting orifices mid-ventral in profile view of gaster (Fig. 1).

19. Cuticle thick and strong, armoured and strongly sculptured.

Type-species: *Secostruma lethifera* sp.n.

***Secostruma lethifera* sp.n.** (Figs. 1–4)

HOLOTYPE WORKER. TL 4.5, HL 1.00, HW 0.94, CI 94, SL 0.82, SI 87, PW 0.70, AL 1.20 (measurements in millimetres, as defined in Bolton, 1980).

With characters of generic diagnosis and habitus shown in Figs. 1–4. First and fourth teeth of the mandibular dental row very slightly larger than second and third teeth. Mandibles longitudinally rugose basally, the sculpture fading out apically so that the vicinity of the large apical tooth is smooth. Median indentation of anterior clypeal margin continued on short near-vertical anteriormost section of clypeus as a narrow transverse concavity. Median portion of clypeus, behind the downcurved anteriormost section, with 2–3 longitudinal rugae but the sharply defined frontal triangle unsculptured. Remainder of head capsule, dorsally, laterally and ventrally, strongly reticulate-rugose everywhere. Funicular segments 2–8 of antenna much broader than long, the antennal club sharply differentiated and the segments conspicuously larger than those preceding. Vestigial eye-spots almost invisible on sides of head, at about the midlength, measuring only about 0.02; extremely difficult to see in full-face view. Dorsal, posterior and leading edge of antennal scapes with erect to suberect hairs, and also with finer, more reclinate pilosity present. All surfaces of head with short erect to suberect hairs, the dorsum also with sparse fine pubescence which is roughly directed towards the midline. Alitrunk dorsally and laterally reticulate-rugose, the forecoxae similarly sculptured. Femora and tibiae rugulose to reticulate-rugulose, the basitarsi with fine longtidinal rugular sculpture. Dorsal alitrunk and all surfaces of legs with numerous erect to suberect short hairs. Side of pronotum with a flattened to slightly concave anterolateral area, behind the lower occipital corners of the head. Mesopleuron with a broad cuticular flange anteriorly which overlaps the posterior margin of the front coxa. Promesonotum convex, metanotal groove not impressed. Anterior portion of propodeal dor-

sum shallowly concave; behind this the propodeal dorsum in profile humped, rising to a blunt peak then sloping posteriorly to the triangular and more or less horizontal short spines. Metapleural lobes broad and deep, rounded, projecting farther posteriorly than the apices of the propodeal spines and linked to the spines by short narrow lamellae down the margins of the declivity. Petiole and postpetiole reticulate-rugose dorsally and laterally, both with numerous short standing hairs. Petiole in profile lacking a strongly differentiated node; with a short stout anterior peduncle which is almost as deep as the remainder of the subcylindrical and weakly curved segment. Petiolar spiracle situated in anterior one-third of length of segment, approximately at the end of the peduncular section. Subpetiolar process very low and rounded, giving rise ventrally to a pair of roughly parallel longitudinal ridges. Petiole subcylindrical in dorsal view, narrowing at the anterior peduncle and broadening posteriorly. Petiole in dorsal view 0.58 long and 0.26 wide at maximum. Postpetiole fractionally broader (width 0.34) than long (0.30), with more or less straight sides and a convex posterior margin. Sternite of postpetiole reduced, very small in profile in comparison with the tergite. Gaster immediately behind postpetiole with a short flattened surface both dorsally and ventrally. First tergite comprising most of the gaster, as stated in generic diagnosis. Gaster reticulate-rugose to foveate-rugose everywhere, the sculpture on the first sternite coarser and more sharply defined than on most of the first tergite. Erect to suberect short hairs numerous on all surfaces of gaster. Colour a dull red throughout, the legs slightly lighter in shade than the body.

Holotype worker, EAST MALAYSIA: Sabah, Gn. Silam, 810 m, soil sample, A18/9.2, 1983 (*R. Leakey*) (BMNH).

Discussion

The single known worker of *Secostruma lethifera* was extracted from a soil-core sample taken on the forested slopes of Gunong Silam, Sabah. Autapomorphies isolating this genus include the unique structure of the mandibles (character 2, above; Fig. 4) and the construction of the gaster (character 18; Fig. 1) which are not duplicated elsewhere in the Myrmicinae. The combination of characters given in the diagnosis of the genus immediately isolates *Secostruma* from all other known myrmicine ants.

Like many deeply subterranean ants *S. lethifera* has very reduced eyes, but it is not depigmented and its sculpture everywhere is strong. The whole ant has a very armoured appearance and the aspect of a thoroughly predaceous species. The striking modification of the gaster gives added protection to the dorsum, but primarily it brings the sting into a ventral position when the gaster is horizontal (Fig. 1). This is most probably an aid to employing the sting in a relatively confined space, where free movement of the entire gaster to bring an apically-placed sting into play would be very difficult. If the long narrow petiole is elevated against the propodeal declivity and the postpetiole and gaster are flexed downwards at the petiole–postpetiole and postpetiole–gaster joints, then the sting would be directed approximately anteriorly, between the legs.

This useful adaptation to life in subterranean confined spaces, coupled with the strong sculpture and armour of this ant, and its powerful specialized mandibles, renders speculation about its prey very interesting. Some ponerine genera which feed on arthropod eggs, such as *Proceratium* and *Discothyrea* (Brown, 1980b), also have the gaster downcurved. However, the mandibles in these genera are feeble by comparison and hardly resemble the powerful blades of *Secostruma*. The most striking feature of the mandibles of *S. lethifera* is their division into a sharp, blake-like edentate 'incisor' region apically, and a dentate projecting 'molar' region basally (Fig. 4). Such a mandible would provide a good combination of penetrating and gripping power, sufficient to hold prey firmly until the sting could be brought into action. I doubt if such specializations would be necessary to deal with eggs or soft-bodied prey such as earthworms or even termites, but, taken in combination with the armoured body and deeply recessed, strongly protected, antennal insertions, they would be very efficient in coping with hard-bodied arthropods struggling in an earth tunnel or confined space in the soil. I am tempted to speculate that the prey may be geophilomorph centipedes, or even millipedes.

A few other genera of Myrmicinae show hypertrophy of the first gastral tergite. In the arboreal genus *Cataulacus* the first tergite forms

the gastral dorsum, but here the gaster is elongate and usually flattened, segments behind the first being apicoventral and reduced. The function here is one of protection (Bolton, 1974). When threatened *Cataulacus* species either grip firmly onto the bark and present an almost unbroken armoured surface to an aggressor, or roll into a protective ball. The modification of the gaster in this genus has not been for the same reasons as in *Secostruma*. *Ankylomyrma* shows a development of the first gastral tergite far beyond that seen in *Secostruma*. In this genus (Bolton, 1981) the first tergite forms almost the whole of the gaster; it is ball-like with an anteroventral orifice within which the remaining gastral segments are telescoped. The relatively powerful sting projects anteriorly. The modification here appears to have taken place for the same reasons as in *Secostruma* but in a very different habitat. As far as is known *Ankylomyrma* occurs only in the topmost branches of high rainforest trees in West and Central Africa; its prey and biology remains unknown.

Affinities of Secostruma

Secostruma exhibits a combination of features characteristic of the *Myrmica*-group and the *Tetramorium*-group, and has a petiolar structure acquired by convergence or parallel evolution with a member of the *Podomyrma*-group, as discussed below.

Although it is certain that *Secostruma* should be included in either the *Myrmica*-group or the *Tetramorium*-group, it is difficult to decide which. The main synapomorphies of the *Tetramorium*-group include specialized mandibular dentition and the presence of a lamellate appendage apicodorsally on the sting in workers and females, and the presence of an elongate fusion-segment in the antennal funiculus of males (Bolton, 1980). Members of the *Myrmica*-group lack these features but have a characteristic pattern of forewing vein-reduction (Kusnezov, 1951; Bolton, 1988). None of these can be confirmed for *Secostruma* as the only available specimen is the holotype worker, which unfortunately has its sting completely withdrawn, and has evolved an autopomorphic mandibular structure.

The *Tetramorium*- and *Myrmica*-groups are very closely related, appearing to be linked at a higher level by a characteristic ventral alitrunk structure, form and position of propodeal spiracles, and construction of promesonotum, mandibles and clypeus, though work on these characters remains incomplete as yet. A review of the main characters of *Secostruma*, in an attempt to place the genus accurately, follows. The numbers duplicate the position in the generic diagnosis of *Secostruma* given above.

1. The palp formula count of 4, 3 is vastly predominant in *Tetramorium* (Bolton, 1980), but also occurs in *Hylomyrma* (Kempf, 1973), and in most *Ephebomyrmex*, and universally in *Pogonomyrmex* (Cole, 1968) of the *Myrmica*-group.

2. The form of the mandibles is autapomorphic in *Secostruma*, but their structure may be derived from a tetramoriine ancestral pattern or from a myrmicine one. In *Tetramorium* the dentition consists of an apical series of 3 larger teeth followed by a basal series of (usually) 4 smaller teeth (Bolton, 1980). In *Myrmica* and its allies the dentition consists of a series of 6 or more teeth which more or less regularly decrease in size from the apical tooth. The loss of a few preapical teeth from either of these would give a condition approximating that exhibited by *Secostruma* (Fig. 4). However, it seems that the most parsimonious alternative is to assume that the mandible in *Secostruma* has evolved from a tetramoriine form by the loss of two preapical teeth, leaving the apical and 4 small basals. This implies fewer and less dramatic modifications than would be necessary to obtain this mandibular form directly from a *Myrmica*-like ancestor.

3. Absence of an isolated strongly developed median clypeal seta (at the midpoint of the anterior clypeal margin) is common to both the tetramoriines and myrmicines, and is a plesiomorphic state. An indentation at the midpoint of the clypeal margin is a feature commonly encountered in *Tetramorium* (Bolton, 1977, 1980), but is apparently never developed in the *Myrmica*-group.

4. Modification of the lateral portions of the clypeus into a shield-wall in front of the antennal insertions in universal in the tetramoriines. It is also widely and variably developed in the *Myrmica*-group in some species of *Hylomyrma*, *Pogonomyrmex* and *Myrmica*. However, in those members of the *Myrmica*-group showing this feature, the shield-wall is generally not as

Groups:
Myrmica
Tetramorium
Podomyrma

strongly developed as in the tetramoriines, and *Secostruma* appears more *Tetramorium*-like in this aspect (Fig. 3).

5 and 6. A broad median portion of the clypeus which is broadly inserted between widely separated and strongly developed frontal lobes, and the presence of a sharply demarcated frontal triangle, is plesiomorphic in the Myrmicinae as a whole. These character states are shared by both the *Tetramorium*- and *Myrmica*-groups. The shape of the median portion of the clypeus, with its anterior quarter suddenly angled downwards, is common in *Tetramorium* but is much less frequently encountered in the *Myrmica*-group. It reaches its best expression in some species of *Hylomyrma*.

7–9. The form of antennal articulation and shape of the base of the scape seen in *Secostruma* occur widely but by no means consistently in both the tetramoriines and myrmicines. In the latter, however, the antennal club is usually 4-segmented (sometimes the basal club segment, funiculus segment 8, is only weakly differentiated). *Secostruma*, like the tetramoriines, has a strongly defined 3-segmented antennal club (Fig. 3).

10. Lack of frontal carinae and antennal scrobes, a plesiomorphic state in Myrmicinae, is universal in the *Myrmica*-group. These features are usually present in the tetramoriines but may be lacking, perhaps secondarily, in some *Tetramorium* and all *Rhoptromyrmex*.

11. The extreme reduction of the eyes is autapomorphic in *Secostruma*. It is paralleled in two *Tetramorium* species-groups, the *T. inglebyi*-group of the Oriental region and the *T.shilohense*-group of the Afrotropical region. Eyes are always large and conspicuous in members of the *Myrmica*-group.

12 and 13. A compact alitrunk with convex promesonotum and large metapleural lobes occurs in both the tetramoriines and myrmicines. Interestingly at least one African species of the *T.shilohense*-group mentioned above (*T.diomandei*) shows a humped propodeum reminiscent of that seen in *Secostruma* (Fig. 1).

14. The propodeal spiracle is characteristically situated low on the side in both the tetramoriine and myrmicine genus-groups. There is also a marked tendency in both groups for the position of the spiracle to be shifted back, beyond the midlength of the propodeum or even to the margin of the propodeal declivity. The position of the propodeal spiracle seen in *Secostruma* is duplicated extensively in both the *Tetramorium*- and the *Myrmica*-group.

15. The *Secostruma* configuration of the alitrunk–petiole articulation ventrally, with a long narrow V-shaped open cleft running forward from the posteroventral margin of the alitrunk and between the hind coxae, is predominant in both tetramoriine and myrmicine groups. This articulatory structure is extremely rare and isolated elsewhere in the Myrmicinae, and is certainly a convergent acquisition outside the *Myrmica*- and *Tetramorium*-groups. Within these groups this configuration is found in twelve species-groups of *Tetramorium* and in other tetramoriine genera such as *Rhoptromyrmex*, and in *Pogonomyrmex*, *Ephebomyrmex* and *Hylomyrma* of the *Myrmica*-group. In *Myrmica*, *Manica*, *Decamorium* and two species-groups of *Tetramorium* the cleft remains unopen, but its area is bounded by strong post-processional carinae which diverge posteriorly from the metasternal process, implying that this area may have gained a secondary floor from an originally open condition. In both genus-groups a strongly developed metasternal process is present. Unfortunately the presence of such a process cannot be confirmed in *Secostruma* because of the position of the hind coxae of the holotype.

16. The old character of presence of pectinate tibial spurs on the hind legs, previously much used to diagnose the *Myrmica*-group, is not only very variably developed but is plesiomorphic. The apomorphic condition, exhibited by most members of the *Tetramorium*-group, is the presence of simple spurs or their reduction or loss. *Secostruma* has strongly developed simple spurs on the hind tibiae, but this feature is rendered useless in a phylogenetic sense as some *Myrmica*-group members have finely barbulate to simple spurs, as do some members of the *Tetramorium*-group.

17. The shape of the petiole in *Secostruma* (Figs. 1, 2) is most reminiscent of that seen in *Hylomyrma*, particularly *H.immanis* and *H.praepotens* (Kempf, 1973), in which the node and peduncle lose their separate identities through a shortening of the node's anterior face. Obviously these are parallel developments in *H.immanis* and *Secostruma* as other members of *Hylomyrma* show stages back to a more strongly differentiated node (e.g. through forms such as

H.reginae, *dolichops*, *blandiens* and *balzani*). This form of petiole is not known in any tetramoriine species, and so must be considered autapomorphic in *Secostruma*.

The *Secostruma* shape of petiole also occurs convergently in some *Dilobocondyla*, a member of the *Podomyrma*-group. The possibility of *Secostruma* being related to *Dilobocondyla* is ruled out by the latter's failure to exhibit any of the *Tetramorium*-group or *Myrmica*-group characteristics exhibited by *Secostruma*, and by its possession of apomorphies not shown in either of these groups (for example, the presence of an isolated median clypeal seta, strongly swollen hind femora, sharply angulate or dentate occipital corners, loss of metasternal process).

18. The strange configuration of the gaster in *Secostruma* (Fig. 1) is autapomorphic. It is not duplicated anywhere else in the Myrmicinae, though massive expansion of the first tergite at the expense of the remaining gastral segments is known in a few unrelated genera (e.g. *Ankylomyrma*, *Cataulacus*, as mentioned in the discussion of *Secostruma*, above.)

On balance then, the characters and states exhibited by the holotype of *Secostruma lethifera* favour a tentative placement in the *Tetramorium*-group rather than in the *Myrmica*-group. Within the *Tetramorium*-group *Secostruma* is immediately isolated and identified by its autapomorphic characters in combination (characters 2, 11, 17, 18). Solid confirmation of this placement must await the discovery of further specimens so that the sting may be dissected and examined for the presence of the lamellar structure synapomorphic in tetramoriines. When discovered, the male of *S.lethifera* should possess an elongate fusion segment in the antennal funiculi, if this current placement of *Secostruma* among the tetramoriines is correct.

Assuming that the placement is correct, is there any species-group of *Tetramorium* which shares apparently apomorphic characters or states with *Secostruma*, and if so are the characters or states truly apomorphies or the results of convergence? Tentatively the answer must be that *T.elisabethae* of the *inglebyi*-group shares a number of characters with *S.lethifera*, but that these cannot be considered synapomorphies; they must be regarded as convergence phenomena.

In *T.elisabethae* workers (Bolton, 1977) the anterior clypeal margin has a median indentation, frontal carinae are very short and antennal scrobes are absent, the eyes are very small, propodeal spines are short, and metapleural lobes are broad and rounded. *T.elisabethae* belongs to a group of small (TL 2.8–3.1) depigmented species with reduced sculpture, all known species of which are restricted to the Indian subcontinent. Members of the group show all the characters just mentioned and also share a specialized and distinctively shaped base to the gaster, which is not seen in *Secostruma*. Only *elisabethae* of this group has rounded metapleural lobes, which must therefore be regarded as an autapomorphy of *elisabethae* within the *inglebyi*-group, and not as synapomorphic with *Secostruma*.

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