

A REVIEW OF *PARATOPULA* WHEELER,  
A FORGOTTEN GENUS OF MYRMICINE ANTS  
(HYM., FORMICIDAE)

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ABSTRACT

The small myrmicine genus *Paratopula* Wheeler is defined and reviewed for the first time. Four new species are described (*ankistra*, *catocha*, *demeta*, *macta*) and tentative associations of workers with sexual forms are made where possible. Nine named species are recognized in the genus. The species *oculatus* (Smith), originally described in *Cera-pachys* (Ponerinae) is transferred into *Paratopula*, as is *andamanensis* (Forel), originally described in *Tetraopona* (= *Sima*) (Pseudomyrmecinae). Keys are presented for the workers and known males and the history and affinities of the genus are discussed.

INTRODUCTION

*Paratopula* is a very poorly known and little understood genus of myrmicine ants, some of whose component species have been widely scattered in the Formicidae. The purpose of this paper is to define the genus, which has never been formally undertaken, and to present a synopsis of what little is known, or can be inferred, about the genus and its components.

The relatively few valid species of *Paratopula* (9) all appear to be arboreal and are restricted in distribution to the Oriental and Indo-Australian zoogeographical regions, the centre of speciation being in Borneo. Their representation in the world's leading collections of ants is very sparse and their biology remains utterly unknown. Added to this lack of general knowledge is the confusion caused in the past by attempts to place members of the genus in or near other supposedly related groups. For example, one of the earliest described species currently retained in the genus, *ceylonica*, was originally described (Emery, 1901) in *Atopomyrmex*, now a solely Afrotropical genus (Bolton, 1981). It was later shifted (Emery, 1912) into the spurious genus *Atopula*, which is now a junior synonym of *Tetramorium* as its type-species was found to belong in this latter genus (Bolton, 1976; 1980). Other species formerly placed in *Atopula* are now dispersed as shown in the table below.

The year after Emery's description Forel (1902) described a second species, *taylori*, but placed it in *Leptothorax*. He later realized (Forel, 1913b) that *taylori* was close to *ceylonica*, and accordingly shifted the former into *Atopula*, which at that time was also the generic combination of *ceylonica*. In a later publication Forel (1917) changed his mind again and regarded both as components of *Leptothorax*. Wheeler (1919) created the genus *Paratopula* for *ceylonica* and its few described relatives and varieties as he disagreed with Forel's (1917) interpretation. He also stated that they could not be retained in *Atopula*, though he did not give any reasons why this should be so. Finally Emery (1922), in his

catalogue of world Myrmicinae, retained *ceylonica* and its varieties, and a few other species which were then thought to be related, in *Atopula*. By this time *Atopula* had become very much a catch-all genus for oddities peripheral to several different genus-groups.

To complicate this already confused situation still further, it is now apparent that two male-based species described in different subfamilies, one in *Cerapachys* (Ponerinae) and the other in *Tetraponera* (Pseudomyrmecinae), are really members of *Paratopula* (Myrmicinae).

The table below lists all the previously described species-level names that have been associated with the genus-level name *Atopula* (now a junior synonym of *Tetramorium*), or are now associated with *Paratopula*. Columns one and two show the original authors and generic combinations of each taxon. The third column shows any subsequent changes in generic combination prior to the presently accepted placement, and the authorities for the changes. The fourth column indicates the presently accepted generic combination of the species-level name.

Thus *Paratopula* contains six nominal forms derived from earlier descriptive efforts, two of which (*oculata* and *andamanensis*) are newly recognized as belonging to the genus in this paper. Of these six names *taylori* is now considered to be a synonym of *ceylonica*, and *sumatrensis* is a nomen dubium, the holotype female (and only known specimen) having been lost and the original description being too vague for accurate identification. The remaining four, *andamanensis*, *ceylonica*, *longispina* and *oculata*, are considered to be valid species though only *ceylonica* is certainly known from more than one caste. *P. longispina* was described from a single female and remains known only from this caste. The single known specimen of *andamanensis* is a male. It has never been collected again and possibly conspecific females or workers remain undetected. *P. oculata* was described from a male; a possibly conspecific female is discussed below.

Apart from these, four new *Paratopula* species are described here, based on workers. Tentative associations of these with females are proposed where possible, relying on characters apparently consistent between the two castes, and a number of as yet unassociated females and males are discussed.

Until now the concept of a genus *Paratopula* has been based on workers and females. To the present no males have been described as belonging here, those earlier described males which are now included in the genus having originally been misplaced in genera as widely separated as *Cerapachys* and *Tetraponera*. A single male specimen which has somehow come to be included in the type-series of *taylori* (MHN), and is not mentioned in the original description, is a *Pheidole* and has no type-status. It was apparently wrongly added to the type-series some time later but never discussed in print. The males and workers referred to by Wheeler (1919) as *sumatrensis* cannot now be found in the MCZ collection and must be presumed lost.

Therefore, as no directly associated males are known, reasons must be given for linking the isolated males discussed in this paper with females and workers in the genus *Paratopula*. The argument for including these males in the genus is twofold. First, other myrmicine genera of the region whose males are already known can be excluded from consideration. Similarly, genera belonging to myrmicine groups in which males are known for some but not all constituents can be excluded, as those which are known show common diagnostic characters not exhibited by, or different from, those males which are now applied to *Paratopula*. Second, as is usual among myrmicines, there is sexual dimorphism between males and the female castes, but a number of characters common to all suggest most strongly that the males here included in *Paratopula* for the first time are correctly associated with the better known female castes. The matching characters in males and the female castes which are considered as being of primary importance are as follows.

- 1 High palp formula (5, 3) and strongly developed multidentate mandibles.
- 2 Broad median portion to the clypeus, which is very broadly inserted between the antennal sockets.
- 3 Similarity of construction of head capsule in full-face view (figs 6-8).
- 4 Alitrunk in males and alate females elongate and low in profile, narrow in dorsal view.
- 5 Common venation (figs 11, 13-15).
- 6 Swollen femora on the middle and hind legs.
- 7 Lack of tibial spurs on the middle and hind legs.
- 8 Elongate low postpetiole.
- 9 Position of petiolar spiracle, close to the articulation with the alitrunk (figs 1-5, 12, 16, 17).
- 10 Presence of large metapleural lobes.
- 11 Presence of basigastral costulae.

Standard measurements (in millimetres) and ratios encountered in this paper are as defined in Bolton (1981, 1982). The institutions are as follows: MHN = Muséum d'Histoire Naturelle, Geneva, Switzerland; MCZ = Museum of Comparative Zoology, Cambridge, Mass., USA; MCSN = Museo Civico di Storia Naturale "Giacoma Doria", Genoa, Italy; MNHU = Museum für Naturkunde an der Humboldt-Universität zu Berlin, Germany (DDR); UM = Hope Entomological Collections, University Museum, Oxford, U.K.

DISPOSITION OF PREVIOUSLY DESCRIBED NAMES ASSOCIATED WITH  
*ATOPULA* AND *PARATOPULA*.

SPECIES-GROUP NAME	ORIGINAL GENERIC COMBINATION	LATER GENERIC COMBINATION(S)	PRESENT GENERIC COMBINATION
<i>belti</i> Forel, 1895	<i>Aphaenogaster</i>	<i>Brunella</i> (Forel, 1917) <i>Atopula</i> (Emery, 1922)	<i>Aphaenogaster</i> (Bolton, 1982)

<i>andamanensis</i> Forel, 1903	<i>Sima</i>	<i>Tetraopnera</i> (Donisthorpe, 1916)	<i>Paratopula</i> (this paper)
<i>ceylonicus</i> Emery, 1901	<i>Atopomyrmex</i>	<i>Atopula</i> (Emery, 1912) <i>Leptothorax</i> (Forel, 1917)	<i>Paratopula</i> (Wheeler, 1919)
<i>hortensis</i> Bernard, 1948	<i>Atopula</i>	—	<i>Tetramorium</i> (Bolton, 1976; 1980)
<i>jacobsoni</i> Forel, 1915	<i>Atopula</i>	—	<i>Leptothorax</i> (Emery, 1922)
<i>longispina</i> Stitz, 1938	<i>Atopula</i>	—	<i>Paratopula</i> (Bolton, 1976)
<i>nodifer</i> Emery, 1901	<i>Atopomyrmex</i>	<i>Atopula</i> (Emery, 1912)	<i>Tetramorium</i> (Bolton, 1976; 1980)
<i>oculatus</i> Smith, 1857	<i>Cerapachys</i>	<i>Sima</i> (Dalla Torre, 1893) <i>Rhopalothrix</i> ? (Donisthorpe, 1932) <i>Acanthomyrmex</i> ? (Brown, 1975)	<i>Paratopula</i> (this paper)
<i>sumatrensis</i> Forel, 1913a	<i>Atopula</i>	—	<i>Paratopula</i> (Wheeler, 1919)
<i>taylori</i> Forel, 1902	<i>Leptothorax</i>	<i>Atopula</i> (Forel, 1913b) <i>Leptothorax</i> (Forel, 1917)	<i>Paratopula</i> (implied by Wheeler, 1919, as <i>taylori</i> treated as a variety of <i>ceylonica</i> by Forel, 1917)

SYNOPSIS OF *PARATOPULA* SPECIES

SPECIES	KNOWN CASTES		DISTRIBUTION
	worker	female male	
<i>andamanensis</i> (Forel), 1903. comb. n.		+	Andaman Is.
<i>ankistra</i> sp. n.	+	+(?)	Borneo
<i>catocha</i> sp. n.	+		Sulawesi
<i>ceylonica</i> (Emery), 1901 (= <i>taylori</i> Forel, 1902. syn. n.)	+	+	India, Sri Lanka
<i>demeta</i> sp. n.	+		Borneo
<i>longispina</i> (Stitz), 1938.		+	Borneo
<i>macta</i> sp. n.	+	+(?)	Borneo, Philippines
<i>oculata</i> (Smith), 1857. comb. n.		+(?)	Borneo, W. Malaysia, Singapore
<i>sumatrensis</i> (Forel), 1913a. stat. n.		+	Sumatra

## DIAGNOSIS OF THE GENUS

*PARATOPULA* Wheeler

*Paratopula* Wheeler, 1919: 144. Type-species: *Atopomyrmex ceylonicus* Emery, 1901: 114, by monotypy.

## WORKER (figs 1-6).

Palp formula 5.3. Mandibles large and triangular, armed with 8-11 teeth, the teeth decreasing in size from apex to base. Anterior clypeal margin indented medially, lacking a median seta. Median portion of clypeus broad and biconvex, broadly inserted between the frontal lobes. Frontal lobes present, narrow, each lobe distinctly narrower than the portion of the clypeus which is inserted between them. Frontal carinae absent to feebly present, when the latter the carinae represented by rugae running backward from the lobes; antennal scrobes absent. Antennae 12-segmented with a well defined apical club of 3 segments. Eyes slightly in front of midlength of sides of head in full-face view. Alitrunk elongate and low in profile, the promesonotum not domed-convex. Metanotal groove conspicuously impressed. Mesonotum and propodeum of approximately equal width in dorsal view, much narrower than the maximum pronotal width. Propodeum bispinose. Propodeal spiracle low on side (abutting metapleuron), at about the midlength of the sclerite. Metapleural lobes conspicuous, rounded and prominent to hooked. Metasternal process vestigial, represented by a minute peak on each side of the midline; ventral midline and metasternal pit not concealed. Petiolar articulatory cavity on posteroventral alitrunk truncated and transverse at about the midlength of the hind coxal cavities. Femora strongly thickened medially, narrowing basally and apically. Tibial spurs absent from middle and hind legs. Petiolar spiracle situated in front of the midlength of the peduncle, close to the articulation with the alitrunk; petiole nodiform, with an elongate anterior peduncle and small anteroventral process. Postpetiole large, long and low, broad dorsally and narrowly articulated to the first gastral tergite. Sting simple, strong and functional. Cuticle thick and armoured, strongly sculptured with extensive rugation or a rugoreticulum except on gaster; basigastral costulae present. Pilosity present, moderately dense, the individual hairs usually short, either acute or blunt apically.

## FEMALE (fig. 11)

As worker except that 3 small ocelli are present and the alitrunk has a full complement of flight sclerites; winged when virgin. The metanotal groove is not as in the worker, and the relative sizes of alitrunk sclerites given above do not apply. Additional characters of females include the following.

Pronotum extensive on dorsal alitrunk, forming a thick collar in front of and to the sides of the mesoscutum. Mesoscutum elongate and narrow, narrowly rounded anteriorly. Parapsidal grooves vestigial to absent. Axillae in dorsal view appearing as a pair of lobes which are more or less fused to the mesoscutellum and which are separated centrally by an anterior triangular projection of the mesoscutellum. Propodeal spines shorter and more obtuse than in the worker. Venation as indicated in fig. 11. Radial (= marginal) cell closed behind the forewing margin. Cross-vein *r-m* absent; veins *Rs* and *M* widely divergent beyond the point of splitting of *Rs+M*, this divergence occurring considerably proximal of the intersection of cross-vein *2r* with vein *Rs*.

## MALE (figs 7-10, 12-17)

Palp formula 5, 3 (*in situ* count). Mandibles broad and strongly developed, meeting at midline, with 5-8 teeth which decrease in size from apex to base. Median clypeal seta absent. Median portion of clypeus biconvex. Frontal triangle present and shallowly depressed. Antennae with 13 segments, not clavate apically. Scape elongate, first funicular segment short, second funicular segment elongate, third segment short and with a characteristic kink or indentation in its leading edge; fourth funicular segment slightly longer than third and sometimes also with an indentation. Relative lengths of scape and first four funicular segments are as follows in the four known males.

## MALE OF:

## LENGTHS OF ANTENNAL SEGMENTS

	<i>Scape</i>	<i>Funic. 1</i>	<i>Funic. 2</i>	<i>Funic. 3</i>	<i>Funic. 4</i>
<i>oculata</i>	0.50	0.10	0.26	0.14	0.16
<i>ceylonica</i>	0.56	0.16	0.28	0.16	0.18
unassociated	0.48	0.12	0.24	0.12	0.16
<i>andamanensis</i>	0.54	0.11	0.30	0.16	0.16

Thus the first funicular is about half the length of the second, the second funicular is about half the length of the scape, the third funicular is about the same as the first, and the fourth funicular is the same as or slightly longer than the third.

Eyes large, in full-face view in front of the midlength of the sides. Ocelli large and set well in front of the occipital margin. Pronotum visible as a U-shaped collar in dorsal view, running from tegula to tegula. Notauli present, parapsidal grooves faint. Propodeum massive and rounded, unarmed. Posterior femora clavate, middle femora less strongly so; tibial spurs absent from middle and hind legs. Pterostigma distinct on forewing. Radial (= marginal) cell closed or narrowly open on forewing due to the fading out of the distalmost portion of *Rs* (figs 13–15). Petiolar spiracle close to articulation with alitrunk. Postpetiole a large elongate segment (figs 12, 16, 17). Gaster distinctly narrowed basally (both in dorsal and lateral view) at its junction with the postpetiole. Sides of gastral tergites 1–3 with long projecting hair tufts. Parameres of genitalia elongate and prominent.

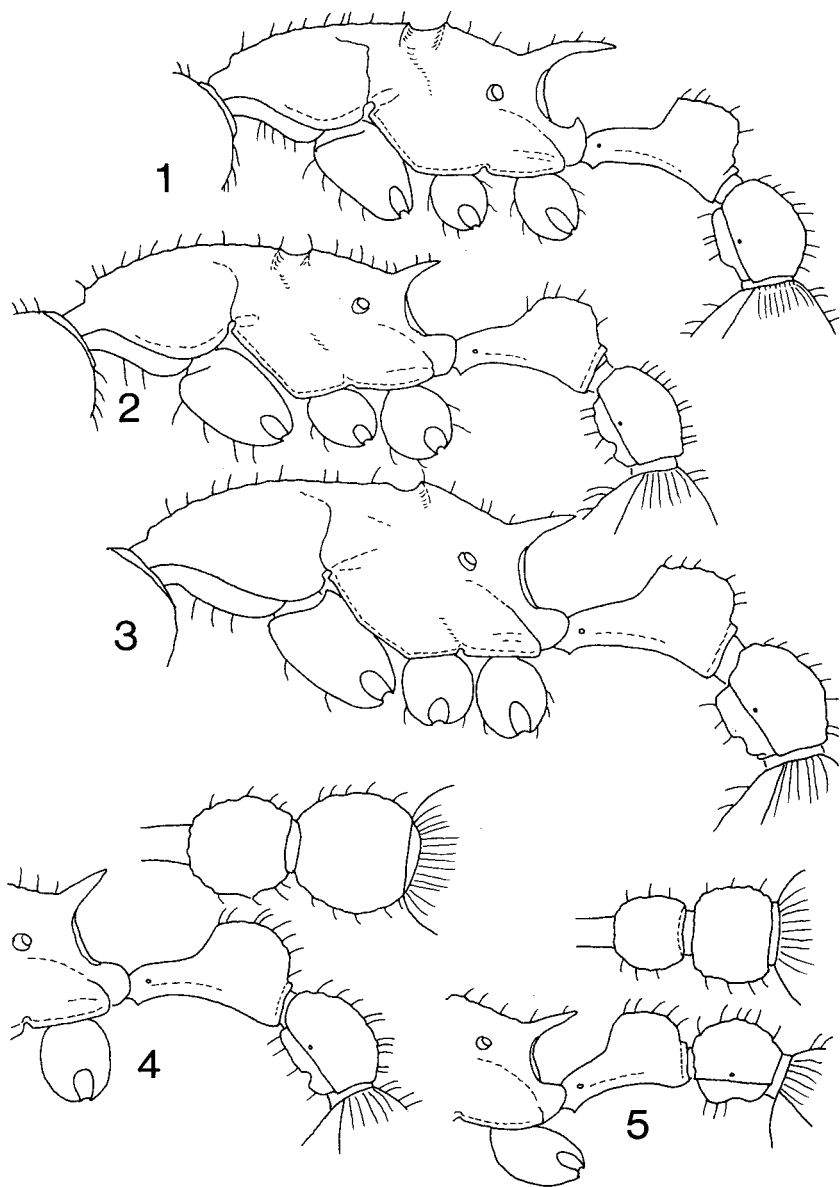
AFFINITIES OF *PARATOPULA*

The classical but now outdated arrangements of myrmicine ant taxonomy arrived at by Emery (1921, 1922) and Wheeler (1922) both placed *Paratopula* in the tribe Myrmecini. However, as Emery (1922) pointed out, the tribe could not be defined by positive characters and was thus a convenience taxon, to which genera that did not easily fit elsewhere in their system were consigned.

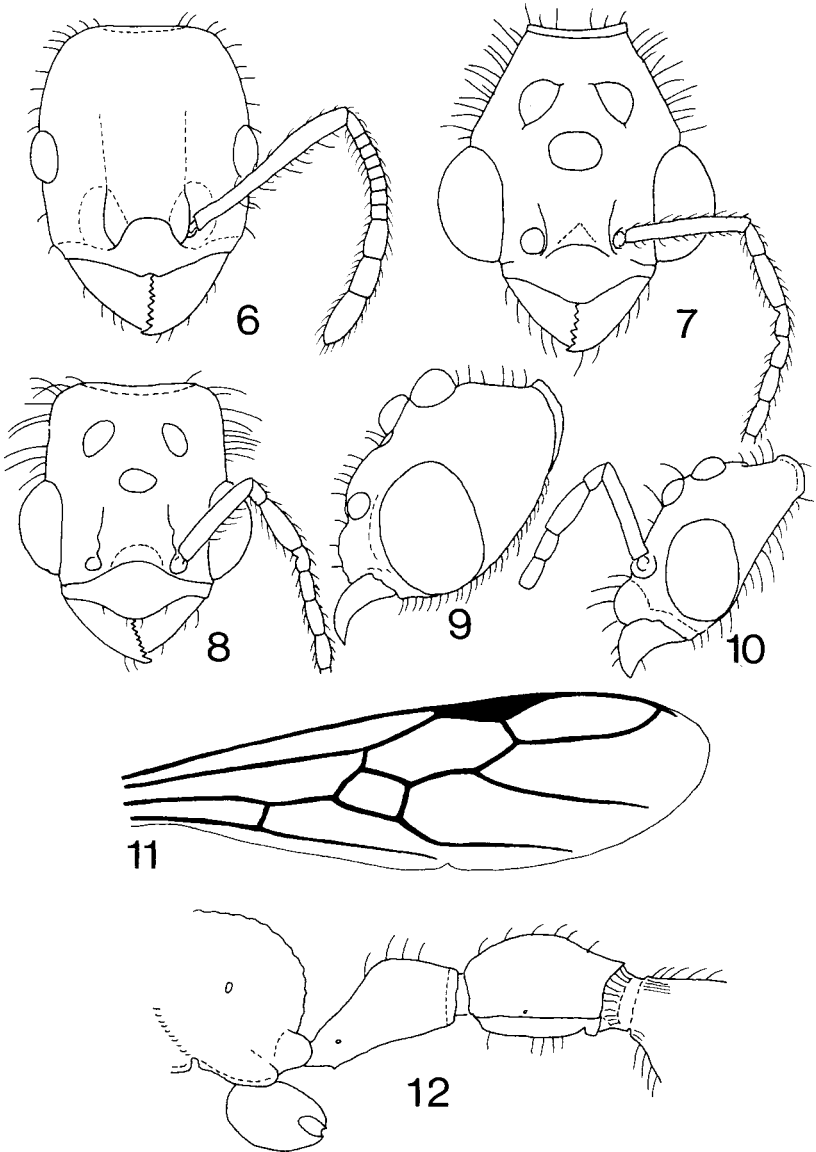
More recently a consensus of opinion has arisen which indicates that some genera of the old tribe Myrmecini may indeed be closely related and may in time constitute a definable genus-group (Taylor, 1970; Bolton, 1981). Unfortunately *Myrmecina*, type-genus of the old tribe, does not belong in this group. Of the genera given in the Emery-Wheeler classification as constituting their tribe Myrmecini, and which are still considered valid (*i.e.* *Atopula* is a junior synonym of *Tetramorium*, and *Brunella* a junior synonym of *Aphaenogaster*), the genera *Podomyrma*, *Atopomyrmex*, *Terataner*, *Dilobocondyla*, and part of *Dacryon*, which appears to contain elements of two genus-level taxa, form a group. To these may be added the genera *Peronomyrmex*, *Pseudopodomyrma*, and the isolated small genus *Ireneopone*.

*Lordomyrma*, *Myrmecina*, *Pristomyrmex*, and *Acanthomyrmex* are excluded from this group. *Lordomyrma* is definitely not closely related to any of these, or to the *Podomyrma*-group, but Moffett (1986) suspects that the last three names may form a discrete genus-group, although some doubt remains.

The species which here constitute the genus *Paratopula* show some affinities with the *Podomyrma*-group but also exhibit a number of leptothoracine features. In the Indo-Australian zoogeographical region there are numerous taxa which are currently difficult or impossible to assign to either group, and form an extensive grey area between the pod-



Figs 1-5 — *Paratopula* workers. 1-3, alitrunk profiles of: 1, *ankistra*; 2, *macta*; 3, *demeta*. 4-5, petiole and postpetiole of: 4, *catocha*; 5, *ceylonica*.



Figs 6–12 — *Paratopula* species. 6–8, full-face view of head in: 6, *ankistra* worker; 7, *ceylonica* male; 8, *oculata* male. 9–10, head profiles of: 9, *ceylonica* male; 10, *oculata* male. 11, forewing venation of *ceylonica* female. 12, petiole and postpetiole of *ceylonica* male.



myrmecines and the leptothoracines as the latter is presently constituted. An understanding of these uninvestigated forms and a detailed analysis of all members of these groups will be essential before any sort of sense can be made of the present confusion.

#### KEY TO KNOWN WORKERS OF *PARATOPULA*

- 1 Dorsal (outer) and other surfaces of middle and hind tibiae with short stout erect to suberect hairs, and also with short decumbent to appressed pubescence. (Brunei; E. Malaysia: Sabah) ..... *macta* sp. n.
- Dorsal (outer) and other surfaces of middle and hind tibiae lacking standing hairs, at most with short decumbent to appressed pubescence ..... 2
- 2 Propodeal spines long and stout, downcurved along their length. Metapleural lobes sharply hooked upwards apically, their apices directed vertically (fig. 1). (Brunei) ..... *ankistra* sp. n.
- Propodeal spines either straight or weakly downcurved along their length; if the latter the spines relatively short and slender. Metapleural lobes always rounded, never hooked upwards apically so that their apices are directed vertically (figs 3–5) ..... 3
- 3 Hairs on first gastral tergite short and parallel sided, not tapering apically; instead abruptly truncated apically so that they appear very blunt. Pronotum in dorsal view as long as or slightly longer than broad. Pronotal humeri angulate in dorsal view. (E. Malaysia: Sarawak) ..... *demeta* sp. n.
- Hairs on first gastral tergite short but tapering apically to a narrow or distinctly acute point. Pronotum in dorsal view broader than long. Pronotal humeri rounded in dorsal view ..... 4
- 4 Postpetiole in profile with tergite relatively long low and shallowly convex. Sternite of postpetiole elongate and narrow in profile. Postpetiole in dorsal view more nearly globular (fig. 4). (Indonesia: Sulawesi) ..... *catocha* sp. n.
- Postpetiole in profile with tergite relatively short and more strongly convex. Sternite of postpetiole short and deep in profile. Postpetiole in dorsal view more obviously transverse (fig. 5). (India, Sri Lanka) ..... *ceylonica*

#### KEY TO KNOWN MALES

- 1 Head in full-face view with the sides behind the eyes strongly convergent posteriorly (fig. 7). Propodeal spiracle close to midlength of side (fig. 12). Head in profile not dorsoventrally flattened (fig. 9). Mandibles with 5–6 teeth. Leading edges of funicular segments 3 and 4 indented (fig. 7). (India, Sri Lanka) ..... *ceylonica*
- Head in full-face view with the sides behind the eyes approximately parallel (fig. 8). Propodeal spiracle well behind midlength of side (figs 16, 17). Head in profile strongly dorsoventrally flattened (fig. 10). Mandibles with 7–8 teeth. Leading edge of only funicular segment 3 indented (fig. 8) ..... 2
- 2 Petiole node in profile with a low rounded node which does not have a sharply defined vertical posterior face. In dorsal view the petiole with a low broadly rounded transverse welt-like node, which is not strongly prominent laterally. Projecting genital parameres strongly curved towards the midline. (W. Malaysia) ..... unassociated male
- Petiole node in profile with a high crest-like node which has a sharply defined near-vertical posterior face (figs 16, 17). In dorsal view the petiole with a raised narrow transversely crest-like dorsum to the node, which is strongly prominent laterally (figs 16, 17). Projecting genital parameres not curved towards the midline ..... 3
- 3 In dorsal view the postpetiole broadest at about its midlength, narrowing anteriorly and posteriorly (fig. 16). Fifth gastral tergite elongate and triangular, mostly concealing the parameres. Dorsal (outer) surfaces of middle and hind tibiae lacking long projecting hairs. (Andaman Is.) ..... *andamanensis*
- In dorsal view the postpetiole broadest close to the posterior margin (fig. 17). Fifth gastral tergite short and transverse, not concealing the elongate parameres. Dorsal (outer) surfaces of middle and hind tibiae with conspicuously projecting long fine hairs. (E. Malaysia: Sarawak) ..... *oculata*

## TREATMENT OF SPECIES

*Paratopula andamanensis* (Forel) **comb. n.**  
(figs 15, 16)

*Sima andamanensis* Forel, 1903: 403. Holotype male, ANDAMAN IS.: Petite Andaman Bumla Creek (MHN) [examined].

Known only from a single male, *andamanensis* was brought to my attention by Philip S. Ward of the University of California. Whilst checking type-material of Pseudomyrmecinae he noticed that this specimen definitely did not fit in that subfamily. At BMNH we showed its close relationship with *oculata* and *ceylonica* males (diagnosis above), and hereby transfer *andamanensis* into the genus *Paratopula*.

## MALE.

*P. andamanensis* is closely related to *oculata*, the two sharing the same form of depressed rectangular head capsule (fig. 8), characteristic overall shape of petiole and postpetiole (figs 16, 17), and alitrunk structure. The two differ in the following respects. In *andamanensis* the middle and hind tibiae lack projecting hairs, whereas in *oculata* long fine tapering projecting hairs are conspicuous. In *andamanensis* the fifth gastral tergite is broadly triangular, enlarged and shield-like, and conceals the elongate genital parameres from dorsal view. Conversely, in *oculata* the fifth gastral tergite is a narrow transverse sclerite and the elongate parameres project freely from the gastral apex. The propodeal declivity is more nearly vertical in *andamanensis* and the dorsum and declivity round together through a narrower curve than in *oculata*, where the declivity is not so steeply sloped (figs 16, 17). With the alitrunk in profile the propodeal spiracle is closer to the margin of the declivity in *oculata* than in *andamanensis*, and comparison of figs 16 and 17 will show the differences in shape and relative dimensions of the petiole and postpetiole.

## WORKER &amp; FEMALE.

Unknown. Just possibly *andamanensis* may represent the male of one of the species known from Borneo. The possibility is faint but must be borne in mind by any future student of this genus.

***Paratopula ankistra* sp. n.**  
(figs 1, 6)

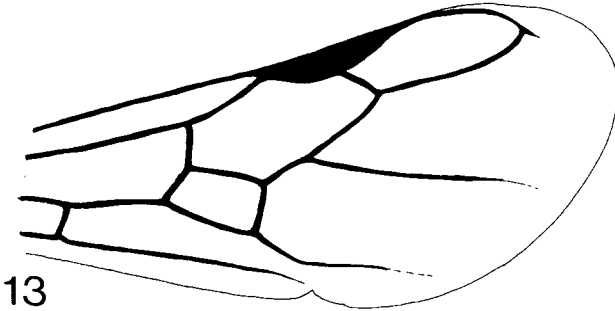
## HOLOTYPE WORKER.

TL 5.9, HL 1.20, HW 1.00, CI 83, SL 0.90, SI 90, PW 0.72, AL 1.68. Propodeal spines elongate, downcurved along their length (fig. 1). Metapleural lobes relatively large and hooked upwards at their tips. Dorsal (outer) surfaces of middle and hind tibiae with appressed fine pubescence but lacking stouter suberect to erect hairs.

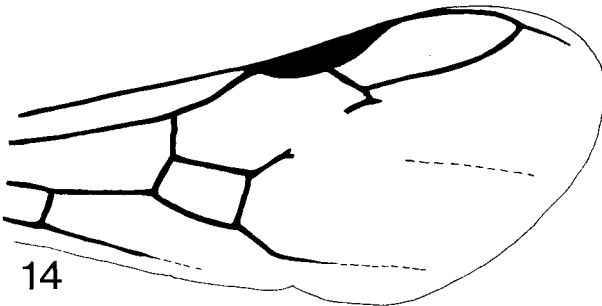
Mandibles finely and densely shagreenate, with a few scattered shallow pits which are almost effaced; equipped with 9 visible teeth (perhaps a tenth tooth concealed by the clypeal margin). Median impression of clypeus shallow. Head slightly more elongate and narrower than is usual in the genus (CI 83), and the scapes relatively long (SI 90). Maximum diameter of eye 0.26 x HW. Leading edge of scape with a distinctive row of short erect hairs. Weakly developed frontal carinae present. Dorsum of head between frontal carinae predominantly longitudinally rugose, but occipitally and in the space between the carinae and the eyes a loose open rugoreticulum is present. Ground-sculpture everywhere finely granulate to reticulate-punctate. Pronotal dorsum very shallowly transversely concave. Lateral margin of pronotum separated from mesonotum by a distinct impression. Maximum width of mesonotal dorsum about equal to that of propodeum (c.0.40) distinctly less than the width of the pronotal dorsum. Metanotal groove broad and shallow. Alitrunk everywhere with a loose open rugoreticulum, many of the reticular meshes broken or incomplete. Ground-sculpture as head, opaque. Petiole node in dorsal

view broader than long, broadest posteriorly. Postpetiole slightly broader than long, broadest at its midlength and with evenly convex sides. Both waist segments reticulate-rugose, the petiole more strongly so than the postpetiole. Basigastral costulae present but weakly developed. All dorsal surfaces of head and body with numerous short blunt hairs; ventral surfaces of femora with a row of similar hairs. Colour dull yellowish brown.

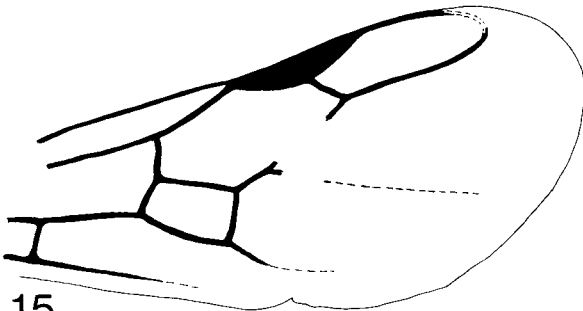
Holotype worker, BRUNEI: Bukit Sulang, nr. Lamunin, BM 1982-388, fogging, 20.viii-10.ix.1982, sample T2/1 (*N.E. Stork*) (BMNH).



13



14



15

Figs 13-15 — *Paratopula* males to show forewing venation in: 13, unassociated West Malaysian species; 14, *oculata*; 15, *andamanensis*.

## PUTATIVE FEMALE.

A single female from East Malaysia: Sabah, Sandakan (*Baker*) (MCZ) is proposed here as the possible female of *ankistra*. Like the worker it has hooked metapleural lobes, but in the female the propodeal spines are short and blunt.

MALE: unknown.

The holotype, and only known, worker was brought down by fogging a forest tree with insecticide. In the worker the shape of the propodeal spines and metapleural lobes, coupled with the relatively narrow head, long scapes, and hairless tibiae, immediately isolate *ankistra*. This species has relatively the longest antennal scapes and narrowest head of any yet known in the genus, as indicated below where workers are arranged by increasing relative length of scape.

WORKER OF:	SI	HW	CI
<i>macta</i>	76-78	1.10-1.18	89-94
<i>ceylonica</i>	77-81	1.04-1.32	87-89
<i>catocha</i>	80-83	1.16-1.28	85-87
<i>demeta</i>	83	1.20	86
<i>ankistra</i>	90	1.00	83

**Paratopula catocha** sp. n.  
(fig. 4)

## HOLOTYPE WORKER.

TL 6.4, HL 1.34, HW 1.16, CI 87, SL 0.96, SI 83, PW 0.86, AL 1.90. Propodeal spines relatively short and straight. Metapleural lobes not hooked upward apically. Dorsal (outer) surfaces of middle and hind tibiae without projecting hairs. Pilosity of first gastral tergite not abruptly truncated. Pronotum broader than long. Petiole and postpetiole as in fig. 4.

Mandibles finely shagreenate with a few scattered shallow pits. Masticatory margin with 8-9 teeth present. Median indentation of anterior clypeal margin shallow. Frontal carinae absent, the apices of the frontal lobes diverging posteriorly and merging with the rugoreticulum of the sides of the head. Rugoreticulum present everywhere on head except on clypeus and the area between and just behind the frontal lobes, where longitudinal rugae occur. Granular to reticulate-punctate ground-sculpture present everywhere between the rugae. Maximum diameter of eye 0.24 x HW. Pronotal dorsum more or less flat transversely. Metanotal groove broad and distinctly impressed. Propodeal spines short and straight and the metapleural lobes broadly rounded. Entirety of alitrunk reticulate-rugose with punctulate to shagreenate ground-sculpture. Petiole and postpetiole also reticulate-rugose, the latter less strongly so than the former. Postpetiole in profile with the tergum relatively long and low, shallowly convex. All dorsal surfaces of head and body with short erect hairs which are pointed apically. Legs with short appressed pubescence but lacking projecting hairs except on the ventral surface of the middle and hind femora, where 1 or 2 hairs are present basally. Colour a dull yellowish brown.

## PARATYPE WORKERS

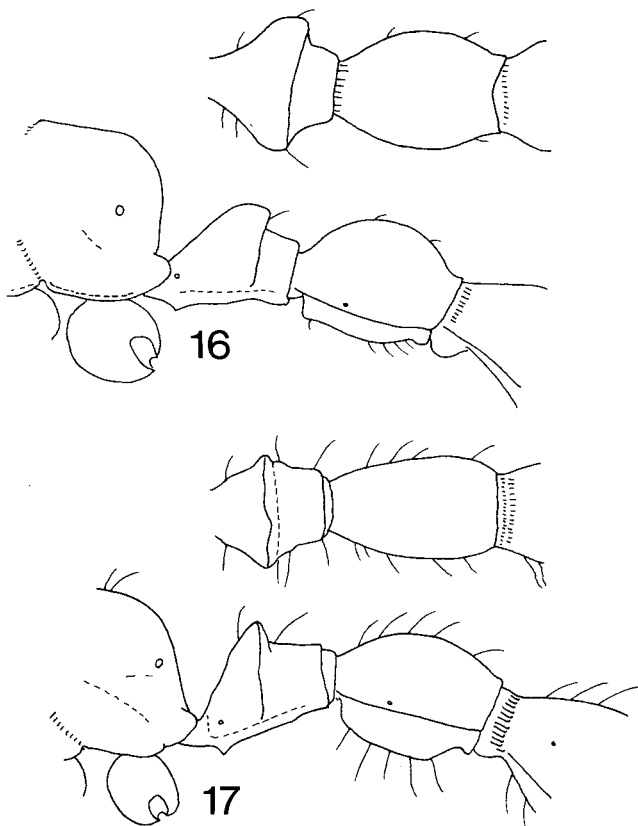
TL 6.6-7.0, HL 1.40-1.50, HW 1.20-1.28, CI 85-86, SL 0.98-1.02, SI 80-82, PW 0.90-0.94, AL 1.98-2.06. As holotype but both paratypes slightly larger than the holotype. The smaller paratype a little paler in colour than the holotype, the larger paratype slightly darker than the holotype.

Holotype worker, INDONESIA: Sulawesi Utara, Dumoga Bone Nat. Pk, 400 m, 11.ii.1985, plot C fog 5 (*N. Stork*) (BMNH).

Paratype workers; one with same data as holotype and one with same locality but 200–400 m, lowland forest, fog plot B, 8.ii.1985 (*P.M. Hammond*) (BMNH; MCZ).

FEMALE & MALE: unknown.

This species is known only from Sulawesi and only in the worker caste. No sexual forms attributable, even tentatively, to this species have been found. The closest relative of *catocha* appears to be *ceylonica* but this averages slightly shorter scapes and broader head (see table under *ankistra*). The postpetiole of *catocha* is longer and lower in profile than in *ceylonica*, its dorsum is more shallowly convex in profile and its sternite narrower. In dorsal view the postpetiole of *catocha* has more evenly rounded sides (compare figs 4 and 5).



Figs 16–17 — *Paratopula* males. Petiole and postpetiole in dorsal and lateral view of: 16, *andamanensis*; 17, *oculata*.

*Paratopula ceylonica* (Emery)  
(figs 5, 7, 9, 11, 12)

*Atopomyrmex ceylonicus* Emery, 1901: 114, fig. Holotype female, SRI LANKA. (MCSN) [not seen].

*Leptothorax taylori* Forel, 1902: 228. Syntype worker and female, INDIA: Orissa (Taylor), and Barrakpur (Rothney) (MHN) [examined]. **Syn. n.**

*Paratopula ceylonica* (Emery) Wheeler, 1919: 144.

**WORKER.**

TL 5.6–7.0, HL 1.20–1.48, HW 1.04–1.32, CI 87–89, SL 0.84–1.02, SI 77–81, PW 0.72–0.92, AL 1.64–2.00. Propodeal spines relatively short, straight to very feebly downcurved. Metapleural lobes rounded, not hooked upwards apically. Dorsal (outer) surfaces of middle and hind tibiae without projecting stout hairs but with short appressed pubescence. Hairs on first gastral tergite not abruptly truncated apically. Pronotum broader than long in dorsal view. Petiole node in profile relatively short and deep, in dorsal view short and transverse, broader than long (fig. 5). Mandible with 9–11 teeth.

**FEMALE.**

As worker but larger, alate when virgin. Propodeal spines much shorter than in worker and pronotum a broad collar in front of the mesoscutum. On the forewing (fig. 11) vein  $R_s+M$  splits into its components ( $R_s$  and  $M$ ) some considerable distance distal of the intersection of cross-vein  $m-cu$  with  $R_s+M$ . In the putative females of *macta* and *oculata* the splitting of  $R_s+M$  into  $R_s$  and  $M$  occurs noticeably closer to the intersection of  $m-cu$  with  $R_s+M$ .

**PUTATIVE MALE.**

Leading edges of funicular segments 3 and 4 each with a distinct indentation (fig. 7). Head in full-face view with sides convergent behind the eyes. Propodeal spiracle close to midlength of sides. Mandible with 5–6 teeth. Petiole node in profile evenly rounded, not raised to a peak with a vertical posterior face (fig. 12). In dorsal view the petiole node not traversed by a sharp ridge. Postpetiole in dorsal view with sides evenly convex, broadest at about the midlength and longer than broad. Gaster strongly constricted basally in dorsal view, the lateral hair tufts very conspicuous. Last visible gastral tergite enlarged and roughly triangular, mostly concealing the parameres from dorsal view. As in the female, middle and hind tibiae lack projecting hairs of any description.

The worker of *ceylonica* most closely resembles that of *catocha*. Details of their separation are given under the latter name. Other worker-based species are separated by the characters noted in the key and the table of dimensions given under *ankistra*.

*P. ceylonica* females separate from those of *oculata*, *macta* and an unassociated alate female from Sarawak (BMNH) as the last three have projecting tibial hairs which are either long and fine (*oculata*) or short and stout (*macta* and Sarawak female). Also the females of *oculata* and *macta* have the venational difference noted above. The female of *longispina* is very large compared with that of *ceylonica* (HW > 2.00 in *longispina*) and has long conspicuous but appressed pubescence on the middle and hind tibiae. The ventral surfaces of the femora also possess a continuous row of long projecting hairs in *longispina*. This does not occur in *ceylonica* where at most a few hairs are present close to the femoral base ventrally. A short series of unassociated females from several localities in the Philippines (MCZ) appear closely related to the female of *ceylonica* but the postpetiole is differently constructed and the

first gastral tergite lacks a dark band, which is apparently universal in *ceylonica*.

As can be seen from the key and the notes given above, the putative males of *ceylonica* are easily distinguished from all other known males of the genus.

**Paratopula demeta** sp. n.

(fig. 3)

HOLOTYPE WORKER.

TL 6.8, HL 1.40, HW 1.20, CI 86, SL 1.00, SI 83, PW 0.87, AL 1.90. Propodeal spines relatively short, straight. Metapleural lobes rounded, not hooked apically. Dorsal (outer) surfaces of middle and hind tibiae without standing hairs. Pronotum at least as long as broad in dorsal view. Hairs on first gastral tergite abruptly truncated apically, especially near the base of the sclerite.

Mandibles shagreenate with scattered shallow pits. Masticatory margin of mandible with 9 teeth. Median indentation of anterior clypeal margin shallow. Frontal carinae weakly developed, the sculpture between them of longitudinal rugae with a few weak or incomplete cross-meshes. Occipitally and on sides of head a strong rugoreticulum is present. Ground-sculpture everywhere granular to reticulate-punctate. Maximum diameter of eye 0.25 x HW. Central portion of pronotal dorsum shallowly transversely concave. Pronotal humeri angular in dorsal view. Metanotal groove broad and conspicuously impressed. Entirety of alitrunk with a loose open rugoreticulum, many of the cross-meshes incomplete. Ground-sculpture everywhere on alitrunk granulate to reticulate-punctate, as on head. Petiole and postpetiole closely and coarsely reticulate-rugose. Basigastral costulae of first tergite dense and strongly developed. All dorsal surfaces of head and body with numerous short erect blunt hairs. Standing hairs absent from dorsal surfaces of middle and hind tibiae but femora ventrally may have one or two hairs near the base. Colour uniform dull yellowish brown.

Holotype worker, EAST MALAYSIA: Sarawak, 4th division, Gunong Mulu Nat. Pk, limestone area, forest, 27.v.1978 (*H. Vallack*) (BMNH).

FEMALE & MALE: unknown.

Known only from the holotype worker, this species possesses pilosity on the alitrunk and gaster which is shorter than usual in the genus, and which is blunted or truncated apically. In workers of other species the pilosity tends to be short, but the individual hairs generally taper along their length or come to a point apically, or both. This character, coupled with the relatively narrow pronotum, hairless outer tibial surfaces, and form of the propodeal spines and metapleural lobes, renders *demeta* easily recognisable.

*Paratopula longispina* (Stitz)

*Atopula longispina* Stitz, 1938: 103, fig. 4. Holotype female, "NORTH BORNEO" (probably E. Malaysia: Sabah) (*V. Kühlwein*) (MNHU) [not seen].

*Paratopula longispina* (Stitz) Bolton, 1976: 363.

FEMALE.

Stitz (1938) gives the total length of his holotype female as 11.0. A single female in BMNH which fits his original description and comes from the same general area (E. Malaysia: Sabah, Mt Kinabalu) is even larger, TL 12.5. HL in this specimen is 2.50,

HW 2.10. Taken on size alone *longispina* is distinct from all other known *Paratopula* females except for a single unassociated female from E. Malaysia: Sarawak, 4th division, Gunong Mulu Nat. Pk (BMNH) which falls into the same size range: TL 11.2, HL 2.10, HW 1.90. This specimen however has short erect hairs projecting from the dorsal (outer) surfaces of the middle and hind tibiae, a feature not recorded in *longispina*.

Other features characterizing *longispina* include a row of hairs projecting from the ventral surface of each middle and hind femur, along the entire length of each femur; relatively long propodeal spines which are conspicuously longer than the metapleural lobes, and long low petiole and postpetiole when viewed in profile.

On the forewing *Rs+M* splits into its components just over half way between the intersection of *Rs+M* with cross-vein *m-cu* and the intersection of *Rs* with cross-vein *2r*, an arrangement very similar to that seen in *ceylonica* (fig. 11).

WORKER & MALE: unknown.

If the female bears the same size relationship to the workers as is seen in other *Paratopula* species, then the worker of *longispina* is probably a large ant, with TL 8–9 or so.

### ***Paratopula macta* sp. n.** (fig. 2)

#### HOLOTYPE WORKER.

TL 6.0, HL 1.24, HW 1.10, CI 89, SL 0.84, SI 76, PW 0.76, AL 1.74. Propodeal spines relatively short, elevated and weakly downcurved along their length. Dorsal (outer) surfaces of middle and hind tibiae with numerous short projecting stout hairs. Metapleural lobes not hooked upwards apically.

Mandible with 9 teeth, the blades finely shagreenate and with scattered small shallow pits. Median indentation of anterior clypeal margin shallow but distinct. Weak frontal carinae present, the sculpture between them predominantly of longitudinal rugae but with a few irregular and scattered cross-meshes. Elsewhere the head loosely reticulate-rugose and everywhere a fine granulate to reticulate-punctate ground-sculpture is present. Maximum diameter of eye 0.24 x HW. Pronotum in dorsal view about as long as the dorsum is broad, the median portion of the dorsum shallowly transversely concave. Metanotal groove conspicuously impressed. Metapleural lobes rounded apically but the dorsal edge of each lobe more or less flat. Dorsal alitrunk rugose, the pronotum predominantly longitudinally so; elsewhere with a loose open rugoreticulum. Sides of alitrunk more finely reticulate-rugose, the reticulum uneven. Ground-sculpture of alitrunk granulate to reticulate-punctate. Petiole and postpetiole reticulate-rugose and with strong ground-sculpture. Basigastral costulae short but conspicuous. All dorsal surfaces of head and body with numerous short erect to suberect hairs present. Femora and tibiae of middle and hind legs with numerous projecting hairs; the femora with a row of projecting hairs ventrally which runs the length of each femur. Colour medium yellowish brown.

#### PARATYPE WORKER.

TL 6.3, HL 1.26, HW 1.18, CI 94, SL 0.92, SI 78, PW 0.84, AL 1.80.

As holotype but slightly darker brown in colour.

Holotype worker, BRUNEI: Ulu Temburong, 16–22.ii.1982, LP283MT (*M.C. Day*) (BMNH). Paratype worker, EAST MALAYSIA: Sabah, Danum Valley, 10.xi.1986 (*P. Eggleton*) (MCZ).

#### PUTATIVE FEMALE:

A female from E. Malaysia: Sarawak, Gunong Mulu Nat. Pk (BMNH), another from L. Navang in Borneo (MCZ), and several from Dumaguette and Los Banos, Philippines (MCZ) are suspected of being the female caste of *macta*. All these females show the characteristic leg pilosity exhibited by the worker. Only one other female, also from



Gunong Mulu Nat. Pk (BMNH) shares this pilosity, but this specimen is currently excluded from consideration as the female of *macta* for the following reasons.

- 1 Size. The isolated female is relatively very large, HW 1.90, as opposed to HW 1.60 for the largest female currently identified as *macta*.
- 2 Pilosity. The females here associated with *macta* have, like the worker, numerous standing hairs on the first gastral tergite, the hairs with a maximum length of about 0.14. In the excluded female gastral pilosity on the first tergite is much denser and is shorter, about 0.11 maximum despite the overall much larger size of the individual.
- 3 Venation. In females here associated with *macta* vein  $Rs+M$  splits into its components closer to the junction of cross-vein *m-cu* with  $Rs+M$ , at a point proximal of the midlength between the intersections of cross-veins *m-cu* and  $2r$  with the longitudinal veins. In the isolated female  $Rs+M$  splits into its components close to the midlength between the intersections of *m-cu* and  $2r$  with the longitudinal veins.

MALE: unknown.

The worker caste of *macta* is easily identified by the numerous short stout erect hairs which project from the dorsal (outer) surfaces of the middle and hind tibiae. Workers applicable to the female excluded from *macta*, above, should be much larger than those of *macta* and may also have gastral pilosity differences reflecting those described for the females.

*Paratopula oculata* (Smith) **comb. n.**  
(figs 8, 10, 14, 17)

*Cerapachys oculatus* Smith, 1857: 74, pl. 1, figs 20–24. Holotype male, EAST MALAYSIA: Sarawak (*A.R. Wallace*) (UM) [examined].

MALE.

Known from the holotype (UM) and a second, headless, male in BMNH. Characters given in the key, in figs 8, 10, 14, and 17, and the notes under the discussion of *andamanensis*, will isolate *oculata* from all other known *Paratopula* males. The unique character shown by this species, which immediately separates it from all other known members of the genus, is the presence of relatively long curved fine hairs arising from the middle and hind tibiae on the dorsal (outer) surfaces as well as elsewhere on the legs.

PUTATIVE FEMALE.

Two female specimens in BMNH, one from Singapore and the other from West Malaysia, are here tentatively associated with the holotype of *oculata*. Like the male these females have long acute curved hairs projecting from the tibiae. Also, as in the male, standing pilosity on the dorsal surfaces of the head and body is elongate fine curved and acutely pointed; much longer and finer than is usual in this genus.

WORKER: unknown.

Given the diagnostic presence of long fine pilosity in both male and female, the worker may well also exhibit this character. If so, it should be immediately recognisable within the genus. In other species which possess hairs projecting from the dorsal (outer) tibial surfaces in workers and females the hairs are short, stout and straight, conspicuously different from the condition seen in *oculata*.

*Paratopula sumatrensis* (Forel) **stat. n., nomen dubium**

*Atopula ceylonica* var. *sumatrensis* Forel, 1913a: 64. Holotype female, INDONESIA: Sumatra, Tandjong Slamet, 1911–12, at light (*v. Buttel-Reepen*) (holotype presumed lost, not in MHN).

*Paratopula ceylonica* var. *sumatrensis* (Forel) Wheeler, 1919: 144.

## FEMALE.

Known only from the holotype female, which can no longer be found, this form remains a mystery. It is the only representative of the genus recorded from Sumatra and, from the very sketchy original description, should not be associated with *ceylonica*. For this reason *sumatrensis* is given new status here as a separate species, although it must remain as a *nomen dubium* due to lack of information. Wheeler (1919) recorded that he had received "all three phases of this ant from the Philippines (*F.X. Williams*)." Only two females collected by Williams have been detected in the MCZ collection and they do not match the meagre description of *sumatrensis* sufficiently. The males and workers from Williams's series have apparently since been misplaced or lost.

## UNASSOCIATED MALES AND FEMALES

After the tentative associations of castes indicated in this paper have been made, there remain a few females and a male which cannot at present be linked to any known named form.

(1) A male, from West Malaysia: Sg. Patani (BMNH), is run out as "unassociated male" in the key. The head of this specimen is shaped as in *oculata* (fig. 8), and the mandibles have 7–8 teeth. Unlike *oculata* and *andamanensis* (fig. 14, 15) the venation in the centre of the forewing does not fade out in this male (fig. 13) and the petiole is not transversely crest-like. Its genital parameres in dorsal view project beyond the apex of the last sternite and are curved towards the midline.

Only *oculata* is known to occur in West Malaysia though some or all species currently recorded from Borneo may well be present in the peninsula. These include *ankistra*, *demeta*, *longispina*, and *macta*; this unassociated male may prove to belong to one of these species. It is certainly not conspecific with the *oculata* male for the reasons noted above and in the key.

(2) A large alate female from East Malaysia: Sarawak, 4th division, Gunong Mulu Nat. Pk (BMNH) shows tibial pilosity reminiscent of *macta* but is excluded from that species for the reasons detailed under *macta*. This large female is also mentioned in the notes on *ceylonica* and *longispina*.

(3) A short series of 6 alate females from three localities in the Philippines: Los Banos, Mt Makiling, and Davao (MCZ) which may represent more than one species as differences in size and venation are discernable. As so little is known of the Philippines' fauna very little can be said of these females at present, except that they do not give a satisfactory match with any other form currently placed in *Paratopula*, although they appear to be close to *ceylonica*.

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#### REVIEW

'DARWIN'S INSECTS, CHARLES DARWIN'S ENTOMOLOGICAL NOTES WITH AN INTRODUCTION AND COMMENTS' By KENNETH G.V. SMITH (*Bull. Br. Mus. nat. Hist.* (Hist. Ser.)) Vol. **14**, No. 1 143 pp., 19 figs. 25.5 x 18.5 cm, wrappers. British Museum (Nat. Hist.), London. 1987. Price £25.

To many of us, Darwin's interest in entomology might be equated with beetle collecting. In the present work Kenneth Smith clearly shows that while beetles were important, they were only a portion of the insects Darwin collected. This work is primarily a compendium of Darwin's insects collected during the *Beagle* voyage and in England which the author was able to track down in the British Museum (Natural History), the University Museums of Oxford and Cambridge, the National Museum of Ireland (Dublin), Down House, and in other institutions. Darwin's hitherto unpublished *Insect notes* (in BMNH, London) and *Insects in Spirits of Wine* (Cambridge) provide the framework for records of Insects taken during the voyage. Given the patience needed for such a task (not to mention the subject matter), this carefully researched work could only have been done by a taxonomist.

I was pleased that the author provided relevant notes about the particular insects mentioned by Darwin. Thus, a person not completely familiar with the nomenclature could still benefit from reading this work. Toward the end of the monograph Smith provides a comprehensive list of all generic and specific names of insects derived from Darwin's name (close to 150), with appropriate comments.

From the historian's standpoint, the notebook entries might be the most interesting aspect of this work. By examining these entries, Darwin's inquisitive observational skills are evident. Here, Darwin is not churning ideas over and over in his head. He is asking relevant questions about the behaviour and form of actual organisms. This work should be interesting, not only to entomologists, but to anyone interested in Darwin's biological research. — MARY M. BARTLEY