Best regards,

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Taxonomy, phylogeny and biogeography of the ant genus *Tetraponera* (Hymenoptera: Formicidae) in the Oriental and Australian regions

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Abstract. A revision of the ant genus *Tetraponera* in the Oriental and Australian regions reveals 33 species (18 new), belonging to four informal species-groups: *allaborans*-group (*T. allaborans* (Walker), *T. apiculata*, sp. nov., *T. avia*, sp. nov., *T. bita*, sp. nov., *T. brevis*, sp. nov., *T. conica*, sp. nov., *T. connectens*, sp. nov., *T. crassiuscula* (Emery) stat. nov., *T. extenuata*, sp. nov., *T. microcarpa* Wu & Wang, and *T. modesta* (F. Smith)); *nigra*-group (*T. aitkenii* (Forel), *T. atra* Donisthorpe, *T. attenuata* F. Smith, *T. binghami* (Forel), *T. buops*, sp. nov., *T. difficilis* (Emery), *T. inversinodis*, sp. nov., *T. laeviceps* (F. Smith), *T. mimula*, sp. nov., *T. nigra* (Jerdon), *T. nitida* (F. Smith), *T. nixa*, sp. nov., *T. nodosa*, sp. nov., *T. notabilis*, sp. nov., *T. polita*, sp. nov., *T. punctulata* F. Smith, *T. rotula*, sp. nov., *T. tucurua*, sp. nov., *T. vivax*, sp. nov., and *T. volucris*, sp. nov.); *pilosa*-group (*T. pilosa* (F. Smith)), and *rufonigra*-group (*T. rufonigra* (Jerdon)). Keys are provided for identification of workers, queens and males, although the sexual forms remain unknown in some species. Phylogenetic analysis indicates that the four species-groups represent independent lineages, each with its nearest extant relatives in the Afrotropical region. There have been multiple invasions of Asia from Africa, and at least four west-to-east transgressions of Wallace's line into the Australian region. Plate tectonic events postulated to have been important in facilitating such dispersal include the collision of India with Asia in the Eocene and the approach of the Australian plate to Laurasia in the mid-Miocene.

Introduction

The subfamily Pseudomyrmecinae is a group of slender-bodied, large-eyed, arboreal ants found throughout the Old and New World tropics. The Old World species belong to the genus *Tetraponera* F. Smith, containing approximately 110 nominal species or subspecies (Ward 1990; Bolton 1995). Species of *Tetraponera* have piqued the interests of biologists studying ant-plant interactions (Hocking 1970; Janzen 1972; Ward 1991; Klein *et al.* 1992; Klein *et al.* 1993; Buschinger *et al.* 1994; Young *et al.* 1997; Djieto-Lordon and Dejean 1999; Palmer *et al.* 2000), ant defensive chemistry (Braekman *et al.* 1987; Merlin *et al.* 1988; Renson *et al.* 1994; Devijver *et al.* 1995) and gut anatomy (Billen and Buschinger 2001). Yet there has been no modern taxonomic treatment of the genus at the species level. This paper attempts to redress this problem for the Oriental and Australian regions by revising the *Tetraponera* species found in this part of the world. Some of the results must be considered provisional because of uncertainties about species boundaries. Nevertheless, it has been possible to circumscribe most taxa with reasonable clarity and to offer worker-, queen- and male-based keys to the species. Four species-groups are defined, and aspects of their phylogeny and biogeography are explored.

Early taxonomic work on the Indo-Australian *Tetraponera* consists of isolated species descriptions by Donisthorpe (1948, 1949), Emery (1889, 1900, 1901), Forel (1902, 1903*b*, 1909*b*, 1912*a*, 1912*b*, 1915*b*), Jerdon (1851), Karavaiev (1933), Motschoulsky (1863), Roger (1863*a*), Smith (1852, 1858, 1859, 1860, 1863, 1877), Stitz (1925), Viehmeyer (1916), and Walker (1859). Keys to species were given in Bingham (1903), Emery (1900) and Forel (1903*a*), but these now have little utility. Several recent papers have dealt with species of *Tetraponera* from China and adjacent regions (Wu and Wang 1990; Dlussky and Radchenko 1990; Radchenko 1997; Zhou and Jiang 1997). The characteristics of the genus as a whole were summarised in Ward (1990).

One conclusion to emerge from the present study is that many of the names proposed for *Tetraponera* species represent junior synonyms, a circumstance that arises in part because relevant type material was not always examined by previous investigators. In addition, however, it is now apparent that some species of *Tetraponera* can show remarkable variation in size and shape, both within populations and over larger geographical scales. Thus,

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progress on the species-level taxonomy of these ants requires the analysis of *geographically extensive* population samples, and an appreciation of the potential for species to show substantial phenotypic variation.

Most collections of Indo-Australian *Tetraponera* consist of isolated workers, unassociated with sexual alates, and often lacking biological data. Our knowledge of the ecology and behavior of these ants would be enhanced if more emphasis were placed on the procurement of nest series. This would also allow the accumulation of worker-associated queens and males, whose characteristics may prove to be more reliable for delimiting species. Males are known for only about half the species (and in small sample sizes for some of these) but the available data indicate that the genitalia provide good diagnostic traits for some species and clades.

Materials and methods

Sources of material

Specimens were examined and/or deposited in the collections listed below. Codes for public institutions follow those in Arnett *et al.* (1993), where available.

AMNH	American Museum of Natural History, New York, NY, USA
AMSA	Australian Museum, Sydney, Australia
ANIC	Australian National Insect Collection, CSIRO, Canberra, Australia
ASIC	Andreas Schulz Collection, Leichlingen, Germany
BMNH	Natural History Museum, London, UK
CASC	California Academy of Sciences, San Francisco, CA, USA
CESB	Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India
CMNH	Carnegie Museum of Natural History, Pittsburg, PA, USA
CPDC	Jacques Delabie Collection, CEPEC/CEPLAC, Itabuna, Bahia, Brazil
CUIC	Cornell University Insect Collection, Ithaca, NY, USA
DZUC	Department of Zoology, University of Calicut, Kerala, India
FRCK	Forest Research Centre, Kuching, Sarawak, Malaysia
HNHM	Hungarian Natural History Museum, Budapest, Hungary
HZIC	Herbert Zettel Collection, Vienna, Austria
JDMC	J. D. Majer Collection, Curtin University of Technology, Perth, Australia
KFBG	Kadoorie Farm and Botanic Garden, Hong Kong, China
KUBC	Faculty of Forestry, Kasetsart University, Bangkok, Thailand
KUEC	Institute of Tropical Agriculture, Kyushu University, Fukuoka, Japan
KUES	Seiki Yamane Collection, Kagoshima University, Kagoshima, Japan
LACM	Natural History Museum of Los Angeles County, Los Angeles, CA, USA
MCSN	Museo Civico de Historia Natural 'Giacomo Doria', Genoa, Italy
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MZLU	Museum of Zoology, Lund University, Lund, Sweden
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHMV	Naturhistorisches Museum, Vienna, Austria
NTUC	Department of Entomology, National Taiwan University, Taipei, Taiwan
OXUM	Hope Entomological Collections, University Museum, Oxford, UK
PSWC	P. S. Ward Collection, University of California at Davis, CA, USA
RMBR	Raffles Museum of Biodiversity Research, National University of Singapore, Singapore
RMNH	Nationaal Natuurhistorische Museum, Leiden, Netherlands
ROME	Royal Ontario Museum, Toronto, Canada
SAMC	South African Museum, Cape Town, South Africa
SMNK	Staatliches Museum für Naturkunde, Karlsruhe, Germany
TERC	Tropical Ecosystems Research Centre, CSIRO, Winnellie, Australia
UASK	Institute of Zoology, Ukrainian Academy of Science, Kiev, Ukraine
UCDC	Bohart Museum of Entomology, University of California at Davis, CA, USA
UCRC	Entomology Research Museum, University of California at Riverside, CA, USA
UMSC	Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia
USNM	National Museum of Natural History, Washington, DC, USA
ZMAS	Zoological Institute, Russian Academy of Science, St Petersburg, Russia
ZMHB	Museum für Naturkunde der Humboldt Universität, Berlin, Germany
ZMPA	Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland
ZMUM	Zoological Museum, University of Moscow, Moscow, Russia

Additional abbreviations used (specimens not examined):

CFRB	Chinese Academy of Forestry, Beijing, China
GNUC	Department of Biology, Guangxi Normal University, Guilin, Guangxi, China

Analysis of morphology

To quantify interspecific differences in size and shape a series of measurements was taken on a representative sample of *Tetraponera* workers ($n = 380$), queens ($n = 92$) and males ($n = 41$). For each apparent species or species-complex specimens were chosen from throughout the range of the taxon and, in general, no more than one individual was measured from each nest series or local collection. This restriction was lifted for rare species in which samples were limited to one or a few collections. Measurements were made at 50× using a Wild M5A microscope and a dual-axis Nikon micrometer wired to a digital readout. Measurements were recorded to the nearest 0.001 mm, but are presented here to the second decimal place. For three frequently used metrics, HW (head width), HL (head length) and EL (eye length), an estimate of precision was obtained by taking five repeated measurements at different time intervals on 10 worker specimens of *Tetraponera punctulata*. This yielded estimates of mean values of the average deviation from the mean of 0.003 mm, 0.005 mm, and 0.003 mm, respectively.

The linear measurements and indices employed in this study are described below. The first four measurements are taken with the head in full-face, dorsal view (head considered prognathous). This involves positioning the head so that its posterior margin and anterolateral corners (above the mandibular insertions) are in the same plane of view.

HW	Head width: maximum width of head, including the eyes.
HL	Head length: midline length of head proper, from the posterior margin of the head to the anterior extremity of the clypeus. When the anterolateral margins of the clypeus have a greater anterior reach than the clypeal midpoint, head length is measured to the midpoint of a line drawn across the anterolateral margins.
EL	Eye length: length of compound eye, measured in the same view as HL. In taking this measurement it is important to have adequate lighting to discern the margins of the eye, since the outer circlet of ommatidia is usually darkened and inconspicuous.
MFC	Minimum frontal carinal distance: minimum distance between the frontal carinae.
SL	Scape length: length of the first antennal segment, excluding the radicle (Fig. 1).
LF2, LF3, LF4	Length of funicular segments 2, 3 and 4: maximum measurable lengths of the second, third and fourth funicular segments (third, fourth and fifth antennal segments), respectively.
FL	Profemur length: length of the profemur, measured along its long axis in posterior view (Fig. 2).
FW	Profemur width: maximum measurable width of the profemur, measured from the same view as FL, at right angles to the line of measurement of FL (Fig. 2).
PrWM	Pronotum width: maximum width of the pronotum at the dorsolateral margins. In species in which the lateral margins of the pronotum are not well defined, PrWM is measured at the point where the pronotal surface becomes vertical.
PDH	Propodeum height: height of the propodeum, measured in lateral view, from the base of the metapleuron to the maximum height of the propodeum, along a line orthogonal to the lower metapleural margin (Fig. 3).
MTW	Metapleural width: maximum distance between the metapleura, measured in dorsal view (Fig. 4).
PL	Petiole length: length of the petiole, measured in lateral view from the lateral flanges of the anterior peduncle to the posterior margin of the petiole (Fig. 3).
PH	Petiole height: maximum height of the petiole, measured in lateral view at right angles to PL (Fig. 3), but excluding any protruding teeth or lobes at the anteroventral or posteroventral extremities of the petiole (e.g. Figs 56, 82).
DPW	Dorsal petiole width: maximum width of the petiole, measured in dorsal view.
LHT	Metatibia length: length of the hind tibia, excluding the proximomedial part of the articulation that is received into the distal end of the metafemur (Fig. 5). This measurement is taken with the extensor surface of the tibia in full view, so that the line of view corresponds with the plane of tibial flexion.
CI	Cephalic index: HW/HL
REL	Relative eye length: EL/HL
REL2	Relative eye length, using HW: EL/HW
FCI	Frontal carinal index: MFC/HW
SI	Scape index: SL/HW
SI2	Scape index, using HL: SL/HL
SI3	Scape index, using EL: SL/EL
FI	Profemur index: FW/FL
PDI	Propodeal index: PDH/MTW
PLI	Petiole length index: PH/PL
PWI	Petiole width index: DPW/PL

The following quantitative assessments of pilosity were used:

CSC	Cephalic setal count: number of standing hairs, i.e. those forming an angle of 45° or more with the surface (Wilson 1955), visible on the posterior half of the dorsum of the head, as seen in lateral and posterior views.
MSC	Mesosomal setal count: number of standing hairs visible in profile on the mesosoma dorsum.

The cephalic setal count essentially covers the area between, and posterior to, the middle of the compound eyes. Often there is only a single pair of erect setae here, one on each side of the head at the posteromesial margin of the eye. This is referred to as the supraocular pair of setae. In most species of *Tetraponera* the standing hairs on the dorsum of the head and mesosoma are clearly distinguishable from the appressed pubescence, by their greater length and more erect appearance. In some species, however, the standing hairs tend to grade into suberect and decumbent pubescence (e.g. Figs 65–68), and in such instances the cephalic and mesosomal setal counts are necessarily approximate.

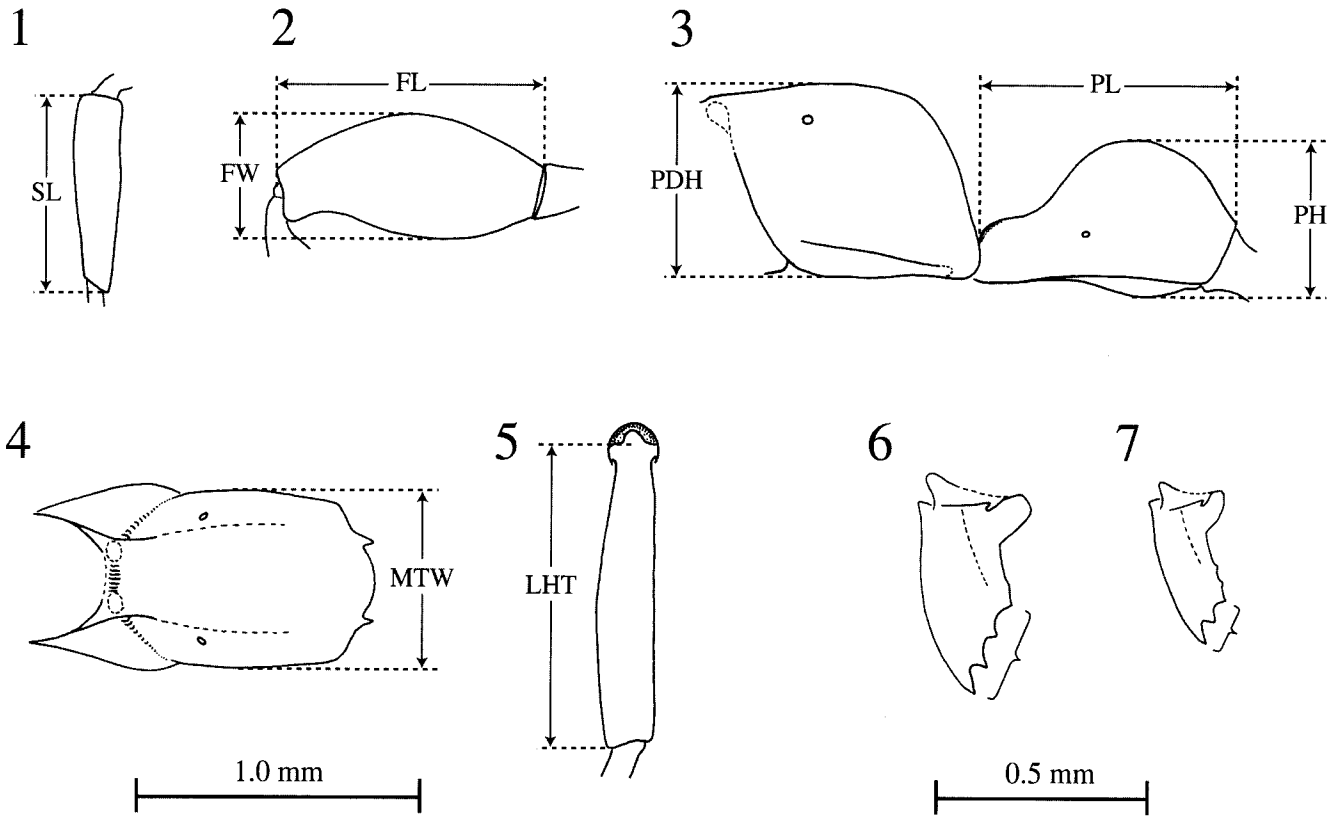
Mandibular dentition is an important character but it can be difficult to assess when the mandibles are tightly closed against one another or when the teeth are abraded. Moreover, in some *Tetraponera* species the masticatory (chewing) and basal margins of the mandible meet at a rather oblique angle, and there may be difficulty in determining their limits, and hence the number of teeth on each. The interpretation adopted here is as follows: the masticatory margin is considered to be composed of those teeth, beginning with the apical tooth, whose apices lie more or less in a straight line and whose basal-most tooth, the *apicobasal tooth*, lies along a straight-line extension of the proximal portion of the basal margin (Fig. 6). Thus, a line drawn between the apicobasal tooth and the origin of the basal margin more or less parallels that margin. The apicobasal tooth is counted as part of the dentition of the masticatory margin but not that of the basal margin. Most Asian *Tetraponera* have four teeth on the masticatory margin (five in *T. rufonigra*). In those species that are considered to have three teeth (*allaborans*-group) (Fig. 7) there is an adjacent tooth, lying on the basal margin of the mandible (as here defined), that might well represent an offset fourth tooth of the masticatory margin.

The term *mesopropodeal impression* is used for the transversely depressed region on the mesosoma dorsum between the mesonotum and the propodeum. This is commonly referred to as the 'metanotal groove'. In *Tetraponera* workers, however, there can be a small, raised welt-like structure in the middle of this impression (Fig. 44), which is here interpreted as the metanotum since it is flanked by the metathoracic spiracles. It is particularly well developed in some Malagasy and African species of *Tetraponera*, but also occurs in a few Asian taxa.

The terms for integument sculpture follow Harris (1977). Sculpture is best observed with soft lighting, which can be achieved by placing an opaque filter (e.g. Mylar plastic) between the specimen and the source of illumination.

Inferring species boundaries

The view adopted in this paper is that in sexually reproducing organisms, such as *Tetraponera*, species are most usefully conceived as groups of populations linked together by recent or ongoing gene flow and having inherited characteristics that cause them to be reproductively isolated from other populations (Mayr 1942). This *biological species concept* motivates the search for discrete morphological gaps that indicate the occurrence of reproductive boundaries. The resulting inferences about species limits are working hypotheses, subject to further testing with additional morphological characters, genetic markers, or direct behavioural observations. In



Figs 1–7. Worker morphology, *Tetraponera punctulata* (*1–6*) and *T. allaborans* (*7*), illustrating various measurements (SL, FL, FW, PDH, PL, PH, MTW and LHT: see text) and mandibular dentition. *1*, scape, dorsal view; *2*, profemur, posterior view; *3*, metapleuron, propodeum and petiole, lateral view; *4*, mesopleuron, metapleuron and propodeum, dorsal view; *5*, metatibia, lateral (external) view; *6*, *7*, mandible, dorsal view, with masticatory margin bracketed. Scale bar = 1.0 mm for Figs 1–5 and 0.5 mm for Figs 6–7.

many animal taxa the male genitalia exhibit species-specific characteristics (Eberhard 1986). This appears to be true of *Tetraponera*, and where male specimens were available I used features of the male genitalia to refine decisions about species limits based on worker and queen morphology.

Not all observed morphological discontinuities indicate species boundaries. They may be artifacts of insufficient sampling—especially where the only available specimens are from geographically distant locations—or they may reflect the existence of discrete intraspecific polymorphism. Bearing in mind that *Tetraponera* has not been intensively sampled in most areas, I have taken a conservative approach towards species delimitation. Some of the polytypic species recognised in this study, such as *T. allaborans* and *T. punctulata*, encompass a considerable range of phenotypes, here interpreted as geographical variants or—where they are sympatric—as intrapopulation variation, perhaps ecotypic in nature. Careful genetic and ecological studies will be needed to demonstrate whether the variation in such polytypic taxa represents different species, intraspecific polymorphism, or an intermediate situation involving assortative mating and partial (but incomplete) reproductive isolation. Of course, for closely related populations that are strictly allopatric and partly differentiated there may be no non-arbitrary resolution of species status.

Phylogenetic analysis

For the purposes of assessing whether the Indo-Australian *Tetraponera* fauna comprises a monophyletic group or a polyphyletic assemblage, a morphological data set developed for the entire subfamily Pseudomyrmecinae (Ward 1991) was reanalysed, restricting it to species in the genus *Tetraponera* and one outgroup taxon, *Pseudomyrmex gracilis*. The result was a dataset of 88 characters, drawn from the set of 125 characters listed in Ward (1991), but excluding 37 characters that became invariant for this more restricted set of taxa. This exemplar data set contained 16 representative species of *Tetraponera*, seven from the Indo-Australian region and the remainder from the Afrotropical region. The Indo-Australian species included examples from all four species-groups recognised in the present study.

To examine in more detail the history of one species-group in Southeast Asia and Australia, a new set of morphological characters was developed for the *nigra*-group. This data set covered 16 of the 20 known species (four taxa being too poorly sampled). Also included in the data set were three other Asian *Tetraponera* (one from each of the other three species-groups), and two Afrotropical species of *Tetraponera* (*T. clypeata*, *T. natalensis*). Two species of *Pseudomyrmex* (*P. gracilis*, *P. termitarius*) were used as outgroups. To test the status of the *nigra*-group, it was not constrained to be monophyletic. The morphological characters and their alternate states are as follows.

(1) Worker, basal margin of mandible (0) subequal to, or shorter than, masticatory margin (Fig. 6); (1) longer than masticatory margin (Fig. 7)

(2) Worker, number of teeth on masticatory margin of mandible (0) 3; (1) 4; (2) 5; (3) >5

(3) Worker, proximal tooth on basal margin of mandible (0) present; (1) absent

(4) Worker, with head in full-face view and mandibles closed, dorsal abductor swelling of mandible (0) visible; (1) not visible, covered by the anterolateral margin of clypeus
(5) Worker, labrum, proximal half (0) lacking teeth or protuberances; (1) with a single median tubercle; (2) with median tubercle, flanked by a lateral pair; (3) with lateral pair of tubercles only
(6) Worker, median portion of clypeus, ventral surface adjacent to junction with labrum (0) lacking transverse carina; (1) with transverse carina
(7) Worker head (0) relatively broad, CI ≥0.78; (1) more elongate, CI <0.78
(8) Worker, compound eye (0) small to medium-sized, REL2 0.32–0.53; (1) relatively large, REL2 ≥0.54, and falling in upper cloud of points in bivariate plot of EL *v.* HW (Fig. 110)
(9) Worker, eye length relative to LHT (0) small, EL/LHT <0.42; (1) medium-large, EL/LHT 0.42–0.88; see also Fig. 111
(10) Worker, eye (0) elongate, >1.5× longer than wide; (1) oval, ≤1.5× longer than wide
(11) Worker, scape length in relation to HW (0) short, SI usually <0.60; (1) longer, SI ≥0.60, and falling in upper cloud of points in bivariate plot of SL *v.* HW (Fig. 112)
(12) Worker, scape length, in relation to EL (0) short, SI3 0.83–0.98; (1) medium, SI3 1.02–1.54; (2) long, SI3 ≥1.55; see also Fig. 113
(13) Worker, head (0) with three distinct ocelli; (1) with two distinct ocelli, the third (median) ocellus weak or absent; (2) lacking distinct ocelli
(14) Worker, queen, head (0) densely punctate, lacking extensive shiny interspaces between the punctures; (1) less densely punctate, with conspicuous shiny interspaces between the punctures
(15) Worker, queen, punctures on dorsum of head between compound eyes (0) coarser, mostly 0.010–0.020 mm in diameter and separated by about their diameters or less; (1) finer, mostly 0.005–0.015 mm in diameter and usually separated by several diameters
(16) Worker and queen, standing pilosity on posterior half of head dorsum (0) sparse: 0–8 hairs, usually arranged in pairs; (1) common: 10 or more hairs scattered across upper head surface
(17) Worker, queen, pronotal humeri as seen in dorsal view (0) subangulate (Figs 59–60); (1) rounded (Figs 30–36)
(18) Worker, profemur (0) slender, FI usually ≤0.40; (1) broader, FI ≥ 0.42, and/or falling in left upper regions in bivariate plots of FW *v.* FL and FI *v.* HW (Figs 114–115)
(19) Worker, profemur length, relative to HL (0) short, FL/HL usually <0.65; (1) longer, FL/HL usually ≥0.65, and falling in upper region in bivariate plot of FL *v.* HL (Fig. 116)
(20) Worker, mesopropodeal impression (0) short and transverse, width of impression (measured as distance between the metanotal spiracles) four or more times its length; (1) longer and subquadrate, width of impression (distance between metanotal spiracles) not more than about three times its length
(21) Worker, mesopropodeal impression (0) lacking pit-like depression; (1) with a pit-like depression posteriorly, preceded by an open, transverse strip of integument; (2) with a pit-like depression, occupying more or less the entire impression
(22) Worker, dorsal face of propodeum (0) flattened or weakly convex in profile (Figs 94–99); (1) moderately to strongly convex in profile, declining posteriorly (Figs 91–93)
(23) Worker, metatibia (0) relatively long, LHT/HL 0.80–0.97; (1) short, LHT/HL 0.58–0.79; see also Figs 117–118
(24) Worker, queen, metabasitarsal sulcus (0) absent; (1) present, simple; (2) present, subtended by a raised carina
(25) Worker, queen, anterior quarter of pronotum (0) lacking a dense patch of punctation, that contrasts with sparser punctures elsewhere on the pronotum and on dorsum of head; (1) with such sculpture
(26) Worker, queen, mesosternum (0) mostly smooth and shiny; (1) densely pubescent
(27) Worker, standing pilosity on mesosoma (0) sparse, MSC 0–8; (1) common, MSC >8
(28) Worker, queen, posteroventral margin of petiole (0) unmodified: forming ventral part of structure against which helcium articulates; (1) modified as a ventral, protruding hood, which is separated from the surface against which the helcium articulates
(29) Worker, queen, mid-posterior portion of petiolar sternite, as viewed in profile (0) flat to weakly convex; (1) strongly convex (Figs 94–96)
(30) Worker, queen, petiole (0) lacking posteroventral teeth; (1) with posteroventral teeth (Figs 79–84)
(31) Worker, petiole, in lateral view (0) relatively robust, PLI usually >0.52 (but varying with body size: see Figs 119–120); (1) slender and attenuate, PLI usually <0.52, and falling in lower cloud of points in bivariate plots of PH *v.* PL and PLI *v.* HW (Figs 119–120)
(32) Worker, petiole length in relation to head length (0) more than half HL (PL/HL 0.54–0.92); (1) shorter, about one-half HL or less (PL/HL usually _0.52, and falling in lower region of points in bivariate plot of PL *v.* HL; see Fig. 121)
(33) Worker, queen, pubescence on abdominal tergite IV (0) consisting of a relatively dense mat of fine, overlapping hairs; (1) relatively sparse, hairs scattered, separated by their lengths or more
(34) Worker size (0) small-medium (HW <0.95); (1) large (HW >0.95)
(35) Male, head (0) notably broader than long (CI ≥1.06); (1) approximately as long as broad, or longer (CI <1.06)
(36) Male, antenna (0) moderately long, its length subequal to, or greater than, mesosoma length; (LF2 + LF3 + LF4)/HL 0.80–1.40; (1) very short, length of antenna less than mesosoma length; (LF2 + LF3 +LF4)/HL approximately 0.50
(37) Male, scape length relative to head width (0) smaller, SI <0.35; (1) larger, SI ~ 0.36
(38) Male, scape length relative to head length (0) larger, SI2 ~ 0.30; (1) smaller, SI ~ 0.20–0.27
(39) Male, length of second funicular segment (0) notably less than combined length of scape and fourth funicular segment (LF2/(SL + LF4) 0.40–0.72); (1) as long as, or almost as long as, combined length of scape and fourth funicular segment (LF2/(SL + LF4) 0.82–1.00)
(40) Male, mesoscutum, as seen in dorsal view (0) narrowing gradually towards anterior end; (1) broadened posteriorly, anterior part suddenly and strongly constricted
(41) Male, mesoscutum (0) densely punctate-reticulate, the punctures subcontiguous and the integument subopaque; (1) less heavily sculptured, with scattered punctures separated by one to several diameters, and interspaces sublucid
(42) Male, hypopygium (sternite IX) (0) semicircular to subtriangular in shape (Figs 126, 128–133); (1) subrectangular (Fig. 127)
(43) Male, hypopygium (sternite IX), anterolateral extremity, position in relation to median apodeme (0) posterior; (1) anterior
(44) Male, hypopygium (sternite IX), anterolateral arms (0) simple (Figs 126–128); (1) subtended by a thin, weakly sclerotised, lamellate extension (Figs 129–133)
(45) Male, hypopygium (sternite IX), posteromedial section that bears most setae (0) more or less flat; (1) depressed dorsad
(46) Male, hypopygium (sternite IX), posterior margin, as seen in ventral view (0) convex (Figs 128–129, 133); (1) straight or weakly (broadly) concave (Figs 126, 127); (2) strongly and narrowly concave (Figs 130–132)
(47) Male, hypopygium (sternite IX), posteromedial extremity, as seen in ventral view (0) lacking small, thin, ligulate protrusion; (1) with such a protrusion, extended posteriorly (Fig. 129)

(48) Male, hypopygium (sternite IX), posteromedial margin, as seen in posterior view (0) relatively thin (Fig. 129); (1) notably thickened (Figs 130–133)
(49) Male, hypopygium (sternite IX), posteromedial margin, as seen in posterior view, thin lamellate extension (0) absent; (1) present, depressed dorsad; (2) present, depressed posterodorsad
(50) Male, hypopygium (sternite IX), posteromedial margin, as seen in posterior view, thin lamellate extension (0) absent; (1) present, broadly transverse, not protruding strongly (Fig. 131); (2) present, narrower, obviously protruding (Fig. 130, 132)
(51) Male, paramere, inner proximal dorsal margin (0) diverging gradually from midline (Fig. 167); (1) diverging suddenly from midline, at a sharply rounded angle (Figs 168–178)
(52) Male, paramere, inner proximal dorsal margin (0) not suddenly directed lateroventrally and passing below inner distal dorsal margin; (1) of such a form
(53) Male, paramere, distal end (0) lacking digitiform processes; (1) with a pair of digitiform lobes (Fig. 154)
(54) Male, paramere, distal end, as seen in lateral view (0) pointed; (1) truncate and rounded (Figs 153, 155) (2) truncate and subquadrate (Figs 156–166)
(55) Male, paramere, distal end, as seen in lateral view (0) not elongate subrectangular and extended posteroventrally (Figs 156–161); (1) so shaped (Figs 162–166)
(56) Male, paramere, distal end in posterolateral view (0) lacking a deep, obliquely transverse, dorsal impression; (1) with such an impression
(57) Male, paramere, distal end in dorsal view (0) not notably narrowed (Figs 167–170); (1) narrowing towards tip (Figs 171–178)
(58) Male, paramere, inner distal margin, as seen in dorsal view (0) lacking beak-like mesial protrusion (Figs 171–176); (1) with such a protrusion (Figs 168–170, 177–178)
(59) Male, paramere, distal end, inner (mesial) surface, saucer-shaped concavity (0) not visible in dorsal view; (1) partially visible in dorsal view (Figs 168–173); (2) fully visible in dorsal view (Figs 174–178)
(60) Male, paramere, mesiodistal concavity (0) not extending to dorsal margin of distal extremity of paramere; (1) extending to dorsal margin of distal extremity of paramere
(61) Male, paramere, mesiodistal concavity (0) not visible or only slightly visible in posterior view (e.g. Figs 145, 152); (1) largely exposed in posterior view (Figs 142–144, 147)
(62) Male, paramere, mesiodistal concavity, posterior margin (0) mostly thick, non-translucent; (1) thin, semi-translucent
(63) Male, paramere, mesiodistal concavity, posterior margin (0) straight or broadly concave, as seen in posterior view (e.g. Figs 145, 152); (1) narrowly concave, as seen in posterior view (Figs 142–144, 148–149)
(64) Male, volsella, distal end (0) free from paramere; (1) fused to inner face of paramere
(65) Male, aedeagus, lateral apodeme (0) shorter than anterior apodeme (Figs 135–136); (1) as long as, or longer than, anterior apodeme (Figs 134, 137–141)
(66) Male, aedeagus, single posteroventral tooth or spine (0) absent (Figs 134–136); (1) present (Figs 137–141)
(67) Male, aedeagus, posteroventral extremity, small lamellate protrusion anterior to posteroventral tooth (0) absent (Figs 138–140); (1) present (Figs 137, 141)
(68) Male, aedeagus, external face, arched carina originating anteroventrally and ending at or near posteroventral tooth (0) absent; (1) present (Figs 137–141) (hereafter termed 'lower oblique carina')
(69) Male, aedeagus, lower oblique carina, if present (0) broadly arched, well developed throughout (Figs 137–139, 141); (1) forming an angular junction at midpoint (Fig. 140), and slightly weakened here
(70) Male, aedeagus, oblique carina on posterodorsal extremity of external face (0) absent (Fig. 139); (1) present (Figs 137–138, 140–141) (hereafter termed 'upper oblique carina')
(71) Male, aedeagus, upper oblique carina, if present (0) situated much closer to posterodorsal margin than to lower oblique carina (Figs 140–141); (1) situated about midway between lower oblique carina and posterodorsal margin (Fig. 137)
(72) Male, queen, typical number of forewing cubital cells (0) 2; (1) 1

In the above data set characters 5, 49, 50 and 54 were treated as unordered. The remaining characters were treated as ordered, in the sequence listed above. A separate analysis in which all characters were unordered gave similar results, but with slightly reduced resolution. For both the 88-character (17-taxon) and 72-character (23-taxon) data sets searches for the most parsimonious trees were carried out using PAUP* (version 4.0b4a) (Swofford 2000), with 100 random addition replicates and TBR branch swapping. Bootstrap analyses employed the same heuristic search strategies, with 1000 bootstrap replicates. MacClade (version 3) (Maddison and Maddison 1992) was used to trace traits of interest on the trees.

Geography

The expression 'Indo-Australian region' is used to refer to the area formed by the combination of the Oriental and Australian biogeographic regions. The boundary between these two regions involves a transition zone in the area between Wallace's line and Lydekker's line, i.e. between the eastern margin of the Sunda shelf and the western limit of the Sahul shelf (Whitmore 1981; Hall and Holloway 1998). As used here the term 'Wallace's line' refers to the original version of the line (Wallace 1863), running east of Bali, Borneo and the Philippines.

In the lists of 'Material examined' the records for each species are arranged alphabetically by country and by primary administrative division within each country. Administrative divisions are omitted for Brunei, Bhutan, the Seychelles and Singapore. Most collection data have been abbreviated to locality and collector, with the source collections indicated at the end of each list. A more complete enumeration of the collection data is available as 'Accessory Material' on the *Invertebrate Taxonomy* web page (http://www.publish.csiro.au/journals/it/). In some instances the locality names on the specimen label have been emended for clarity, with the original orthography given in quotes (e.g. Bengkulu [as 'Benculen']). The abbreviation 'c.u.' signifies that the collector could not be determined.

Coordinates (latitude and longitude) were determined for almost all collection sites, except those with imprecise locality data (such as 'Borneo', 'Sumatra' and 'N. Guinea'). The shareware program Versamap (Version 2.05) was used to plot species distributions. The following references provided useful information about old locality names not found in modern gazetteers or atlases: Andersson (1913), Beccari (1921), Broersma (1916), Chapman and Chapman (1947), Dohrn (1898), Fea (1896), Fruhstorfer (1903), Gressitt (1936*a*, 1936*b*), Karny (1922), Mantero (1903), McClure (1929, 1934), Mjöberg (1930), Modigliani (1892), Soderberg (1919) and Wallace (1890).

Synopsis of the genus *Tetraponera* F. Smith 1852

Tetraponera is one of three genera in the ant subfamily Pseudomyrmecinae. For a full listing of generic synonymy see Ward (1990) or Bolton (1995). The workers of this genus have the following characteristics:

1. Mandible short, usually with 3–4 (rarely 5–6) teeth on the masticatory margin and 0–2 small teeth on the basal margin; basal margin lacking proximal tooth (Figs 6–7).
2. Palp formula 6,4 (reduced to 4,3 in one African species).
3. Posteromedial margin of clypeus not prolonged backwards between the frontal carinae.
4. Anterodorsal surface of median portion of clypeus continuous, non-truncate (in contrast to *Pseudomyrmex*), its anterior margin with a line of clypeal setae, and varying from straight and entire to protruding and dentate (e.g. Figs 8–18, 61–64).
5. Median lobe of antennal sclerite expanded laterally and covering most of the basal condyle of the antenna when head is observed in full-face view.
6. Antenna 12-segmented.
7. Scape short, less than three-quarters of head length (SI2 0.38–0.68 in Oriental/Australian species).
8. Frontal carinae relatively well separated, the minimum distance between them greater than basal scape width (FCI 0.08–0.20 in Oriental/Australian species).
9. Compound eye relatively large (REL 0.25–0.53 in Oriental/Australian species), width of eye two-thirds or more of length.
10. Ocelli present (usually 3) or absent.
11. Pronotum and mesonotum not fused, freely articulating with one another.
12. Mesopropodeal impression usually well marked, sometimes containing a plate-like sclerite, apparently of metanotal origin.
13. Propodeal spiracle circular to elongate, located well forward on upper third of propodeum.
14. Metapleural gland well developed, the opening directed ventrolaterally or posterolaterally, and preceded by an impression along the lower margin of the metapleuron, whose dorsal margin is marked by an oblique longitudinal carina.
15. Metabasitarsal sulcus nearly always present, reduced in some species (absent in three African species).
16. Meso- and metatibiae each with a pair of the apical spurs, the posterior spur well developed and pectinate, the anterior spur smaller, sometimes very reduced.
17. Terga and sterna of abdominal segments II (petiole), III (postpetiole) and IV not laterally fused.
18. Postpetiole distinctly developed.
19. Pupa naked.
20. Larva with trophothylax (food pocket) on ventral surface of thorax.

For practical purposes workers of *Tetraponera* can be distinguished from those of all other ants by the combination of well-developed postpetiole, short mandibles, large oval eyes, and a flexible promesonotal suture.

Synonymic list of *Tetraponera* species from the Oriental and Australian regions

In this study, 33 species of Indo-Australian *Tetraponera* are recognised (18 new), belonging to four species-groups. Most of the diversity is apportioned between two groups (*allaborans*-group, *nigra*-group), with the two remaining groups each containing a single, taxonomically isolated species.

allaborans-group

allaborans (Walker, 1859: 375)
= *minuta* (Jerdon, 1851: 112) **syn. nov.** (nomen oblitum)
= *rufipes* (Jerdon, 1851: 112) **syn. nov.** (nomen oblitum)
= *compressa* (Roger, 1863*a*: 179) (synonymy by F. Smith, 1877: 69)
= *femoralis* (Motschoulsky, 1863: 21) (synonymy by Dalla Torre, 1893: 53)
= *ceylonica* (Motschoulsky, 1863: 22) (synonymy by Dalla Torre, 1893: 53)
= *subtilis* (Emery, 1889: 500) (synonymy by Dalla Torre, 1893: 53)
= *longinoda* (Forel, 1909*b*: 394) **syn. nov.**
= *allaborans sumatrensis* (Emery, 1900: 676) **syn. nov.**
apiculata, sp. nov.
avia, sp. nov.
bita, sp. nov.
brevis, sp. nov.
conica, sp. nov.
connectens, sp. nov.
crassiuscula (Emery, 1900: 677) **stat. nov.**
extenuata, sp. nov.
microcarpa Wu & Wang, 1990: 515
modesta (F. Smith, 1860: 106)
= *fulva* (Viehmeyer, 1916: 117) **syn. nov.**
= *pisarskii* Radchenko, 1997: 480 **syn. nov.**

nigra-group

aitkenii (Forel, 1902: 245)
atra Donisthorpe, 1949: 493
attenuata F. Smith, 1877: 71
= *attenuata tenuissima* (Emery, 1900: 675) (synonymy by Forel, 1912*b*: 54)
= *birmana* (Forel, 1902: 245) **syn. nov.**
= *thagatensis* (Forel, 1902: 249) **syn. nov.**
binghami (Forel, 1902: 243)
= *binghami lindgreeni* (Forel, 1902: 245) **syn. nov.**
buops, sp. nov.
difficilis (Emery, 1900: 677)
= *nitens* (Stitz, 1925: 117) **syn. nov.**
= *dilatata* (Karavaiev, 1933: 267) **syn. nov.**
= *stipitum* (Forel, 1912*b*: 54) **syn. nov.**
inversinodis, sp. nov.
laeviceps (F. Smith, 1859: 145)
= *humerosa* (Emery, 1900: 674) **syn. nov.**
= *dentifera* (Karavaiev, 1933: 266) **syn. nov.**
= *platynota* (Karavaiev, 1933: 269) **syn. nov.**
mimula, sp. nov.
nigra (Jerdon, 1851: 112)
= *atrata* F. Smith, 1852: 44 (synonymy by Dalla Torre, 1893: 54)
= *petiolata* F. Smith, 1877: 70 **syn. nov.**
= *nigra krama* (Forel, 1912*a*: 105) **syn. nov.**
= *nigra insularis* (Emery, 1901: 113) **syn. nov.**
= *nigra fergusoni* (Forel, 1902: 248) **syn. nov.**
nitida (F. Smith, 1860: 106)
= *carbonaria* (F. Smith, 1863: 20) **syn. nov.**
= *brevicornis* (Emery, 1900: 675) **syn. nov.**
= *difficilis longiceps* (Forel, 1902: 247) **syn. nov.**
= *siggi* (Forel, 1902: 246) **syn. nov.**
= *siggi nebulosa* (Forel, 1903*b*: 404) **syn. nov.**

= *siggi setifera* (Viehmeyer, 1916: 119) **syn. nov.**
= *bidentata* (Karavaiev, 1933: 264) **syn. nov.**
= *bidentata angusticeps* (Karavaiev, 1933: 266) **syn. nov.**
= *maffini* Donisthorpe, 1948: 591 **syn. nov.**
= *shankouensis* Zhou & Jiang, 1997: 72 **syn. nov.**
nixa, sp. nov.
nodosa, sp. nov.
notabilis, sp. nov.
polita, sp. nov.
punctulata F. Smith, 1877: 72
= *punctulata kimberleyensis* (Forel, 1915*b*: 37) **syn. nov.**
rotula, sp. nov.
tucurua, sp. nov.
vivax, sp. nov.
volucris, sp. nov.

***pilosa*-group**

pilosa (F. Smith, 1858: 160)
= *nicobarensis* (Forel, 1903*b*: 402) **syn. nov.**

***rufonigra*-group**

rufonigra (Jerdon, 1851: 111)
= *rufonigra yeensis* (Forel, 1902: 248) **syn. nov.**
= *rufonigra testaceonigra* (Forel, 1903*b*: 402) **syn. nov.**
= *rufonigra ceylonensis* (Forel, 1909*b*: 394) **syn. nov.**

Tetraponera of the Oriental and Australian regions: key to species, based on the worker caste

This key excludes *T. vivax* and *T. volucris*, two species known only from the queen caste.

1. Head with three distinct ocelli; in dorsal view pronotal humeri appearing subangulate (Figs 59–60); head densely punctate, and lacking extensive shiny interspaces between the punctures; large species, HW 1.14–2.07 2
– Head almost always lacking ocelli, very rarely with two or three faint ocelli (in a few large workers of *T. nigra* and *T. punctulata*); pronotal humeri varying from narrowly to broadly rounded (e.g. Figs 30–36), but not subangulate; head usually less densely punctate and with conspicuous shiny interspaces between the punctures (always the case in species with HW >1.10); size variable (HW 0.49–1.48) 3
2. Larger species (HW 1.62–2.07), with smaller eyes (REL2 0.35–0.37) (Fig. 55); usually bicolored, the dark head and gaster contrasting with the orange-brown mesosoma (the latter infuscated in some populations); standing pilosity common on the mesosoma dorsum, including the propodeum, MSC 20–66 (Fig. 56) (Pakistan to southern China, south to Sumatra and Java; introduced into the Seychelles) ..... *T. rufonigra* (Jerdon)
– Smaller species (HW 1.14–1.51), with larger eyes (REL2 0.49–0.56) (Fig. 57); body unicolorous dark brown; standing pilosity sparse on the mesosoma dorsum, absent from the propodeum, MSC 3–6 (Fig. 58) (Myanmar to Vietnam, south to Palawan, Borneo, Sumatra and Java) ..... *T. pilosa* (F. Smith)
3. Mandible slender, with three teeth on the masticatory margin, and 1–2 denticles on the basal margin (Fig. 7); basal margin of mandible much longer than masticatory margin; posteroventral margin of petiole in the form of a thin, ventrally protruding hood, which is distinctly separated from the helcium venter (Fig. 40) when the postpetiole is in its normal horizontal position; mesosternum densely pubescent; abdominal tergite IV sparsely pubescent, the appressed hairs separated by their lengths or more; relatively small species, HW 0.49–0.93 (*allaborans*-group) 4
– Mandible more robust, with four teeth on the masticatory margin, and 0–1 denticles on the basal margin (Fig. 6); basal margin of mandible subequal to, or shorter than, masticatory margin; posteroventral margin of the petiole closely associated with the helcium venter (e.g. Figs 68, 94), although it may be flanked by ventrolateral flanges (Figs 79–84); most of the mesosternum devoid of pubescence; abdominal tergite IV usually densely pubescent; size variable, HW 0.63–1.48 (*nigra*-group) 4
4. Small, black species (HW 0.58–0.61, LHT 0.50–0.52), with disproportionately small eyes (REL 0.32–0.34) (Fig. 13), short scapes (SI2 0.42–0.45) and broad profemur (FI 0.47–0.48); pronotal dorsum rounding into sides, lateral margins poorly developed (Fig. 24); mesopropodeal impression lacking a distinct metanotal plate but may be bisected by a weak transverse ridge that interrupts the longitudinally rugulate sculpture (Thailand) ..... *T. connectens*, sp. nov.
– Size, color, scapes and profemur variable but if small (HW <0.65 and LHT <0.55) and black, then eyes larger (REL 0.35–0.41); either lateral pronotal margins better developed or mesopropodeal impression with a distinct, flattened metanotal plate 5
5. Mesopropodeal impression with irregular longitudinal rugulae, interrupted by a small, raised transverse welt (metanotal plate), which is bounded laterally by the metanotal spiracles and which lacks rugulate sculpture (Fig. 44); pronotum lacking distinct lateral margins, the dorsum rounding gently into the sides, as seen in posterior view (Figs 20–23); profemur short and broad, FI 0.44–0.53; dark brown to black species 6
– Mesopropodeal impression with irregular longitudinal rugulae, sometimes crossed at the midpoint by a broken transverse rugule, but lacking a raised metanotal plate; pronotum with more or less distinct lateral margins, which vary from sharp to blunt-edged; in posterior view pronotal dorsum meeting the sides at a sharply rounded angle (Figs 19, 25–29); profemur usually more slender (FI 0.36–0.48); color variable 9
6. Median clypeal lobe subtriangular, protruding, and pointed (Fig. 9); petiole narrow in dorsal view (DPW/MTW 0.61–0.64) (Borneo) ..... *T. apiculata*, sp. nov.
– Median portion of clypeus broadly convex, not prominently protruding and pointed (Figs 10–12); petiole broader in dorsal view (DPW/MTW 0.65–0.73) 7
7. Larger species, with broad head (HW 0.82, CI 0.92) and large eyes (REL 0.42); anterior clypeal margin edentate and non-protruding (Fig. 10); petiole slender (PLI 0.51) (Fig. 45); mesopleuron extensively longitudinally carinulate (West Malaysia) ..... *T. avia*, sp. nov.
– Smaller, with more elongate head (HW 0.63–0.75, CI 0.73–0.84) and smaller eyes (REL 0.35–0.39); anterior margin of clypeus with a modestly protruding and crenulate median lobe (Figs 11–12); petiole more robust (PLI 0.58–0.67) (Figs 47–48); mesopleuron predominantly smooth and shining 8
8. Smaller species with more elongate head (HW 0.63–0.65, CI 0.73–0.75) (Fig. 11); eye larger in relation to scape length (SI3 1.19–1.21); petiole relatively slender (PLI 0.58–0.62) (Borneo, ?West Malaysia) ..... *T. bita*, sp. nov.
– Larger species with broader head (HW 0.73–0.75, CI 0.82–0.84) (Fig. 12); eye smaller in relation to scape length (SI3 1.25–1.30); petiole shorter and more robust (PLI 0.63–0.67) (West Malaysia) ..... *T. brevis*, sp. nov.
9. Small species (HW 0.60–0.64), with short scapes (SI 0.52–0.57, SI2 0.41–0.44); median clypeal lobe bidentate (Fig. 18); pronotum relatively narrow (PrWM/MTW 1.14–1.21), with

sharp, subparallel margins, as seen in dorsal view (Fig. 36), and appearing rather flattened in posterior view(Fig. 29); profemur broad (FI 0.42–0.48) (China, Vietnam) ..... *T. microcarpa* Wu & Wang

– Scapes longer (SI 0.57–0.68, SI2 0.45–0.57); median clypeal lobe usually with three or four teeth (Figs 8, 14–16), or lacking teeth altogether, rarely with a pair of well developed teeth; size variable but if falling within the above range then usually the pronotal margins are soft-edged and convex in dorsal view (Figs 30–35) and the profemur is more slender; dorsal surface of pronotum more convex in posterior view (Figs 19, 25–28) ... 10

10. Larger species (HW 0.62–0.93, usually >0.70); body predominantly black, although petiole, postpetiole and limb appendages may be lighter in color; propodeum typically low and broad, such that PDI 0.91–1.09 (Figs 38, 40); in one rare aberrant morph with HW >0.79 the propodeum is inflated and prominently raised (Figs 37, 43); pronotal margin varying from sharp- to soft-edged, and maximum width of the pronotum generally occurring below the margin (Fig. 19) (widespread and highly variable species, distributed from India to southern China, south to New Guinea and northern Australia) ..... *T. allaborans* (Walker)

– Smaller species (HW 0.49–0.79), color variable but often with at least the postpetiole—and sometimes most of the body—yellow or orange-brown; if HW >0.65 then body mostly dark brown to black but propodeum notably tall (lateral view) and slender (posterior view), such that PDI 1.12–1.24 (Figs 39, 50); pronotal margin usually relatively soft-edged and occurring at the point of maximum width of the pronotum (Figs 25–28) 11

11. Small species (HW 0.64) with large eyes (REL 0.42) (Fig. 14); propodeum conical in profile, the prominent apex located far forward, so that the short inclined dorsal face of the propodeum rounds into a much longer, sloping declivitous face (Fig. 52); petiole short and broad (PWI 0.54, PL/LHT 0.72), subtriangular in profile and without a well differentiated anterior peduncle (Fig. 52); castaneous brown (Borneo) ..... *T. conica*, sp. nov.

– Eyes smaller (REL 0.34–0.41); propodeum not conical in profile, the dorsal face convex and rounding gradually into a steep declivitous face of approximately the same length (Figs 50, 53–54); petiole longer and narrower (PWI 0.38–0.54, PL/LHT 0.83–0.98), a differentiated anterior peduncle and posterior node evident in profile (Figs 50, 53–54); size and color variable (*modesta*-complex) 12

12. Small species (HW 0.53–0.61), with a relatively short, high petiole (PLI 0.60–0.68, PWI 0.46–0.54, PL/SL 1.09–1.19) (Fig. 53); body and legs dark to medium brown (pronotum, petiole and postpetiole may be lighter in color); standing pilosity tending to be rather common, with 8–10 long setae often visible in profile on the promesonotum (but sparse or abraded in some specimens) (Thailand, West Malaysia, Borneo, Sumatra) ..... *T. crassiuscula* (Emery)

– Petiole more slender (PLI 0.45–0.59, PWI 0.38–0.48, PL/SL 1.20–1.41) (Figs 50, 54); standing pilosity relatively sparse, 1–2 pairs of long erect setae visible in profile on the pronotum, none on the mesonotum; size (HW 0.51–0.79) and color variable 13

13. Head, mesosoma, and most of gaster black or dark brownish black, the other body parts variable in color, postpetiole and tibiae often a contrasting lighter yellow or orange-brown; larger species, on average (HW 0.54–0.79, usually greater than 0.60) (Malay Peninsula south and east to Lombok, Sulawesi and the Philippines) ..... *T. extenuata*, sp. nov.

– Body color predominantly yellow- or orange-brown, the gaster sometimes partially or wholly dark brown; problematic specimens with more darkened head and mesosoma also occur, see discussion in text; smaller species (HW 0.51–0.64) (north-east India to China, south to New Guinea)... *T. modesta* (F. Smith)

14. Larger species (HW 0.95–1.48), with long legs (LHT/HL 0.80–0.97); standing pilosity common, MSC 6–71 (usually >10) and CSC 10–40, the cephalic hairs scattered over the dorsal surface of the head and often grading into shorter, suberect pubescence; mesopropodeal impression flanked laterally by raised prominences (containing the metanotal spiracles) but otherwise more or less open, not bounded by lateral ridges that enclose a pit-like depression (a shallow pit present in *T. binghami*) 15

– Smaller species, on average (HW 0.63–1.44); if HW >0.92, then standing pilosity less common (MSC 0–22, CSC 0–4) and the sparse cephalic hairs arranged in pairs on the dorsum of the head, distinct from the much shorter, appressed pubescence; legs generally shorter (LHT/HL 0.58–0.86, rarely >0.80); mesopropodeal impression partly or entirely flanked laterally by raised ridges that enclose a pit-like depression 18

15. Head elongate (CI 0.70–0.77) (Figs 61–62) and petiole very slender (PLI 0.34–0.43) (Figs 65–66) 16

– Head broader (CI 0.76–0.94, usually >0.80) (Figs 63–64); petiole shape variable but if CI <0.80 (a few individuals of *T. nigra*) then petiole more robust (PLI >0.50) 17

16. Smaller species (HW 0.96–0.97), with relatively large and conspicuous eyes (REL 0.40–0.42) (Fig. 62); profemur short and broad (FI 0.45–0.47) (Borneo) ..... *T. buops*, sp. nov.

– Larger species (HW 1.06–1.27), with relatively smaller eyes (REL 0.25–0.30) (Fig. 61); profemur slender (FI 0.37–0.40) (India and Nepal, east to southern China, south to West Malaysia) ..... *T. binghami* (Forel)

17. Petiole long and slender, PLI 0.38–0.47, PL/HL 0.74–0.92 (Fig. 67); mesosoma, petiole and postpetiole, when viewed in profile, with scattered standing pilosity accompanied by, and often grading into, a dense mat of shorter suberect hairs, present on all dorsal surfaces (Fig. 67); (north-east India to China, south to Sumatra, Java, Borneo and Palawan) .... *T. attenuata* F. Smith

– Petiole shorter and higher, PLI 0.52–0.64, PL/HL 0.57–0.72 (Fig. 68); mesosoma, petiole and postpetiole, when viewed in profile, with standing pilosity and underlying suberect pubescence variably developed (and variably distinguishable), but at least the promesonotum and the anterior peduncle of petiole lacking a dense mat of short suberect hairs (Fig. 68); (Pakistan to Thailand, south to Borneo and Java) ..... *T. nigra* (Jerdon)

18. Petiole with a pair of acute, posteroventral teeth, formed from ventrolateral extensions of the petiolar sternite (Figs 79–84); pronotum with dense punctate sculpture on its anterior quarter which contrasts with the shiny (and less densely sculptured) posterior half of head and with the more sparsely punctate posterior regions of the pronotum; scapes shorter than eye length (SI3 0.83–0.98) 19

– Petiole lacking a pair of posteroventral teeth (Figs 77–78, 91–99, 102–103); pronotal sculpture variable but punctures more evenly distributed, not concentrated solely on the anterior quarter (although they may be sparse medially) and usually not occurring in a density that contrasts strongly with that of the posterior half of the head; scapes longer than eye length (SI3 1.02–1.55) 22

19. Head elongate (CI 0.73–0.77) (Fig. 76); petiole very slender (PLI 0.43–0.49) (Fig. 84) (Thailand, West Malaysia) ..... *T. notabilis*, sp. nov.

– Head broader (CI 0.78–0.90) (Figs 71–75); petiole much shorter (PLI 0.60–0.79) (Figs 79–83) 20

20. Larger species (HW 0.83–0.95), with dense pubescence on postpetiole and abdominal tergite IV, which obscures the sheen of the integument; frontal carinae more widely separated (MFC

0.12–0.15, FCI 0.15–0.16) (Fig. 75) (Borneo, Thailand) ..... *T. nodosa*, sp. nov.

– Smaller species (HW 0.63–0.83), pubescence generally sparser on postpetiole (hairs separated by about their lengths) and varying from sparse to moderately dense on abdominal tergite IV, not obscuring the sheen of the integument; frontal carinae less widely separated (MFC 0.07–0.10, FCI 0.10–0.14) (Figs 71–74) 21

21. Short standing pilosity (0.03–0.05 mm in length) common on most body surfaces, including sides of head (Fig. 74), dorsum of head (CSC 15–25), and mesosoma (MSC 30–56) (Fig. 81) (northern Australia) ..... *T. nixa*, sp. nov.

– Standing pilosity much less common on head (CSC 0–6), absent or sparse on the sides when head is observed in full-face view (Figs 71–73); standing hairs generally sparse on mesosoma (MSC usually <10), but occasionally quite common; if MSC >20 then some hairs relatively long (0.10–0.20 mm in length) (India to southern China, south to northern Australia) ..... *T. nitida* (F. Smith)

22. Mesopropodeal impression flanked more or less entirely by lateral ridges, so that the pit-shaped depression extends to the posterior margin of the mesonotum; species found east of Wallace's line (Australia, New Guinea, and adjacent islands) 23

– Mesopropodeal impression with flanking ridges much reduced or lacking anteriorly, so that the pit-shaped depression is separated from the posterior margin of the mesonotum by an open, transverse strip of integument, with longitudinally rugulate sculpture; species found west of Wallace's line (India to the Philippines, Borneo, Sumatra and Java) 28

23. Petiole short and very broad (PL/HW 0.57–0.59; PWI 0.79–0.88) (Fig. 96); postpetiole about 1.4× broader than long; frontal carinae widely separated (FCI 0.19–0.20) (Fig. 90) (Australia) ..... *T. tucurua*, sp. nov.

– Petiole longer and less broad (PL/HW 0.62–0.96; PWI 0.33–0.70) (Figs 91–95); postpetiole approximately as long as, or longer than, broad; frontal carinae less widely separated (FCI 0.12–0.19) (Figs 85–89) 24

24. Posterior half of petiolar sternite flat or weakly convex in profile (Figs 91–93); petiole relatively slender (PLI 0.37–0.61, PWI 0.33–0.57); eyes larger (REL 0.36–0.45); punctures on head between compound eyes relatively coarse, mostly 0.010–0.020 mm in diameter; propodeum somewhat elevated (PDI 1.10–1.34), its dorsal face usually convex in profile, inclined downward posteriorly, and grading insensibly into declivitous face (Figs 91–92) 25

– Posterior half of petiolar sternite with prominent ventral protrusion (Figs 94–95); petiole usually more robust (PLI 0.57–0.80, PWI 0.50–0.70) and eyes tending to be smaller (REL 0.30–0.41); punctures on head between compound eyes finer, mostly 0.005–0.015 mm in diameter; propodeum lower in profile (PDI 1.00–1.19), its dorsal usually flatter and more strongly differentiated from the declivitous face (Figs 94–95, 97–99) 27

25. Head densely punctate, opaque; larger species (HW 0.94–1.04, LHT 0.84–1.00), with long legs and scapes (LHT/HL 0.79–0.86; SI2 0.53–0.55) (New Guinea) ..... *T. atra* Donisthorpe

– Head less densely sculptured, the punctures separated by about their diameters and the interspaces shiny; smaller species (HW 0.75–0.94; LHT 0.63–0.78), with shorter legs and scapes (LHT/HL 0.65–0.74; SI2 0.43–0.50) 26

26. Frontal carinae widely separated (FCI 0.17–0.19) and eyes relatively small (REL 0.36–0.39, REL2 0.41–0.45) (Fig. 87), such that MFC/EL 0.38–0.45; pronotum slender, as seen in dorsal view (PrWM/MTW 1.04–1.16); petiole relatively short and broad (PLI 0.58–0.61, PWI 0.55–0.57) (Fig. 93) (New Guinea) ..... *T. mimula*, sp. nov.

– Frontal carinae less widely separated (FCI 0.12–0.16) and eyes larger (REL 0.40–0.45, REL2 0.47–0.53) (Fig. 86), such that MFC/EL 0.25–0.30; pronotum slightly to strongly expanded laterally (PrWM/MTW 1.15–1.37); petiole shape variable but generally longer and more slender (PLI 0.45–0.59, PWI 0.40–0.49) (Fig. 92) (New Guinea and adjacent islands; northern Australia) ..... *T. laeviceps* (F. Smith)

27. Small species (HW 0.73–0.81); petiole with short anterior peduncle and large globose node, with steep anterior and posterior faces (Fig. 95) (FW/PH 0.51–0.62); punctures on head and pronotum mostly very fine, about 0.005 mm in diameter (New Guinea, northern Australia) ..... *T. rotula*, sp. nov.

– Larger species (HW 0.80–1.44), with less globose petiolar node, the anterior and posterior faces more gently sloping (Figs 94, 97–99) (FW/PH 0.60–0.88); punctures on head and mesosoma mostly larger, approximately 0.010–0.015 mm in diameter (New Guinea, Australia) ..... *T. punctulata* F. Smith

28. Standing pilosity common on head and mesosoma (CSC 18–28, MSC 26–54), including mesonotum and propodeum (Figs 77–78) 29

– Standing pilosity sparse on head and mesosoma (CSC 2–4, MSC 1–5), absent from mesonotum and propodeum (Figs 102–103) 30

29. Eyes large (REL 0.41–0.44) (Fig. 69); lateral pronotal margin sharp-edged; appressed hairs present in moderate density on abdominal tergite IV, in addition to scattered standing hairs (India, West Malaysia) ..... *T. aitkenii* (Forel)

– Eyes smaller (REL 0.33–0.36) (Fig. 70); lateral pronotal margin not well developed; abdominal tergite IV with abundant, short standing pilosity but appressed hairs very sparse and inconspicuous (Borneo) ..... *T. polita*, sp. nov.

30. Eyes larger (REL2 0.51–0.56) (Fig. 101); profemur shorter (FL/HL 0.53–0.62, EL/FL 0.74–0.82); petiolar node usually with a short, steep anterior face and much longer, more shallowly inclined posterior face (Fig. 103) (Borneo, Palawan) ..... *T. inversinodis*, sp. nov.

– Eyes smaller (REL2 0.44–0.48) (Fig. 100); profemur longer (FL/HL 0.60–0.67, EL/FL 0.60–0.66); anterior face of petiolar node usually not much steeper than posterior face (Fig. 102) (Malay Peninsula south and east to Sumatra, Java, Borneo and the Philippines) ..... *T. difficilis* (Emery)

Tetraponera of the Oriental and Australian regions: provisional key to species, based on the queen caste

This key should be used with caution. The queen caste is not known for all species, and the limits of variation remain uncertain in species for which only a few specimens are known. When a range of metric measurements is cited in the key, this is followed by the sample size (e.g. HW 1.88–2.29; n = 5). The sample size is the same for all subsequent measurements given within the same lug of a couplet. There are four species in the *nigra*-group (out of 20) for which the queen caste is unknown (*T. buops*, *T. mimula*, *T. nodosa* and *T. polita*). I have inserted them in the key where I would expect the queens to come out, extrapolating from distinctive features of worker morphology. Such inferences are always accompanied by an explicit statement that the queen caste is

actually unknown (e.g. couplet 6). The *allaborans*-group is keyed no farther than species-group because the queens are known for too few taxa in this group.

1. Pronotal humeri subangulate (as in Figs 59–60); most of upper (dorsal) surface of head densely punctate, and lacking extensive shiny interspaces between the punctures; large species, HW 1.26–2.29 (n = 10) 2
– Pronotal humeri varying from narrowly to broadly rounded (as in Figs 30–36), but not subangulate; head usually lucid or sublucid, with conspicuous shiny interspaces between the scattered punctures; size variable 3
2. Larger species (HW 1.88–2.29; n = 5), with disproportionately small eyes (REL2 0.33–0.36); body usually bicolored, the dark head and gaster contrasting with orange-brown mesosoma (the latter infuscated in some populations) (Pakistan to southern China, south to Sumatra and Java; introduced to the Seychelles) ..... *T. rufonigra* (Jerdon)
– Smaller species (HW 1.26–1.51; n = 5), with larger eyes (REL2 0.50–0.55); body unicolorous dark brown (Myanmar to Vietnam, south to Palawan, Borneo, Sumatra and Java) ..... *T. pilosa* (F. Smith)
3. Forewing with one cubital cell; insertion of postpetiole into petiole shifted dorsad, and posteroventral margin of petiole developed as a semi-translucent, ventrally protruding hood, which is distinctly separated from the helcium (as in Fig. 40) when the postpetiole is in its normal horizontal position; mesosternum densely pubescent; relatively small species, range of HW approximately 0.55–1.08 (usually <0.90) .... *allaborans*-group
– Forewing usually with two cubital cells; insertion of postpetiole into petiole not shifted dorsad, the posteroventral margin of the petiole closely associated with the helcium, although it may be flanked by ventrolateral flanges; most of the mesosternum devoid of pubescence; medium to large species, HW 0.72–1.59 (n = 81) (*nigra*-group) 4
4. Larger species, with long legs (HW 1.20–1.59, LHT 1.15–1.73; n = 18); standing pilosity common on dorsum of head, CSC 10–40 5
– Smaller species, on average, with shorter legs (HW 0.72–1.49, LHT 0.56–1.25; n = 63); standing pilosity usually sparse on dorsum of head, CSC 0–24; if CSC >9, then HW <1.05 and LHT <0.90 8
5. Head very elongate (CI 0.59–0.62; n = 5) and petiole slender (PLI 0.37–0.42) 6
– Head broader (CI 0.68–0.83; n = 13); petiole shape variable (PLI 0.38–0.54) 7
6. Large species (HW 1.35–1.50; n = 5), with small eyes (REL 0.22–0.24) and relatively slender profemur (FI 0.42–0.46) (India and Nepal, east to southern China, south to West Malaysia) ..... *T. binghami* (Forel)
– Queen caste unknown, but expected to be smaller (HW <1.30), with larger eyes (REL >0.30) and more robust profemur (FI >0.48) (Borneo) ..... *T. buops*, sp. nov.
7. Dense suberect pubescence conspicuous on dorsum of mesosoma, petiole and postpetiole; petiole slender, PLI 0.38–0.46 and PL/HL 0.77–0.83 (n = 6) (north-east India to China, south to Sumatra, Java, Borneo and Palawan) ..... *T. attenuata* F. Smith
– Suberect pubescence variably developed, usually relatively sparse and inconspicuous on at least the pronotum and anterior peduncle of petiole; petiole shorter and higher, PLI 0.47–0.54 and PL/HL 0.64–0.74 (n = 7) (Pakistan to Thailand, south to Borneo and Java) ..... *T. nigra* (Jerdon)
8. Petiole with a pair of acute, posteroventral teeth, formed from ventrolateral extensions of the petiolar sternite (as in Figs 79–84); pronotum with dense punctate sculpture on its anterior quarter which contrasts with the shiny (and less densely sculptured) posterior half of head and with the more sparsely punctate posterior regions of the pronotum; scape length less than, or equal to, eye length (SI3 0.85–0.99; n = 12) 9
– Petiole lacking a pair of posteroventral teeth; pronotal sculpture variable but punctures more evenly distributed, not concentrated solely on the anterior quarter (although they may be sparse medially) and usually not occurring in a density that contrasts strongly with that of the posterior half of the head; scape length usually greater than eye length (SI3 1.01–1.40; n = 61) 12
9. Head and petiole very elongate (CI 0.66, PLI 0.38 and PWI 0.32, in the only known queen specimen) (Thailand, West Malaysia) ..... *T. notabilis*, sp. nov.
– Head slightly less elongate (CI 0.67–0.73; n = 11); petiole much shorter (PLI 0.54–0.61, PWI 0.42–0.46) 10
10. Small species (HW 0.74–0.91; n = 11); frontal carinae moderately well separated (MFC 0.10–0.14, FCI 0.13–0.16); pubescence generally sparse on postpetiole, the hairs separated by their lengths or more 11
– Queen caste not known but expected to be larger (HW >0.92) with frontal carinae more widely separated and with dense pubescence on the postpetiole (Borneo) ..... *T. nodosa*, sp. nov.
11. Short standing pilosity (0.03–0.08 mm in length) common on dorsum of head (CSC ~ 24; n = 1) and on sides of head, when head is observed in full-face view (northern Australia) ..... *T. nixa*, sp. nov.
– Standing pilosity much less common on head (CSC 0–4; n = 10), absent or sparse on the sides when head is observed in full-face view (India to southern China, south to northern Australia) ..... *T. nitida* (F. Smith)
12. Legs short (LHT/HL 0.51–0.62; n = 13) and petiole relatively slender in dorsal view (PWI 0.39–0.47); species found west of Wallace's line (India to the Philippines, Borneo, Sumatra and Java) 18
– Either legs longer (LHT/HL ≥0.62) and/or petiole broader (PWI >0.50); species found east of Wallace's line (Australia, New Guinea, and adjacent islands) 13
13. Frontal carinae widely separated (FCI 0.24–0.25; n = 5); profemur very short and broad (FI 0.54–0.56, FW/PL 0.47–0.53); postpetiole 1.2–1.3× broader than long (Australia) ..... *T. tucurua*, sp. nov.
– Frontal carinae less widely separated (FCI 0.15–0.21; n = 33); profemur generally more slender (FI 0.44–0.54, FW/PL 0.33–0.48); postpetiole varying from slightly (1.1×) broader than long to longer than broad 14
14. Posterior half of petiolar sternite flat or weakly convex in profile (as in Figs 91–93); head broader (CI 0.74–0.85; n = 13) and petiole relatively long and slender (PLI 0.41–0.54; but probably greater than this in *T. mimula*, for which the queen is unknown); punctures on dorsum of head between compound eyes larger, about 0.015–0.020 mm in diameter 15
Posterior half of petiolar sternite with prominent ventral protrusion (as in Figs 94–95); head more elongate (CI 0.62–0.75; n = 20) and petiole usually more robust (PLI 0.54–0.75); punctures on dorsum of head between compound eyes finer, mostly 0.005–0.015 mm in diameter 17
15. Head densely punctate, opaque; larger species (HW 1.12–1.32, LHT 0.97–1.19; n = 3), with disproportionately long legs (LHT/HL 0.68–0.73) (New Guinea) ..... *T. atra* Donisthorpe
– Head less densely sculptured, the punctures separated by about their diameters and the interspaces shiny; smaller species (HW 0.91–1.02, LHT 0.77–0.85; n = 10), with shorter legs (LHT/HL 0.62–0.66) 16

16. Frontal carinae moderately well separated (FCI 0.15–0.18; $n = 10$) and eyes relatively large (REL2 0.46–0.51); petiole generally long and slender (PLI 0.41–0.54) (New Guinea and adjacent islands; northern Australia) ..... *T. laeviceps* (F. Smith)
– Queen unknown but expected to have frontal carinae more widely separated (FCI >0.18), eyes smaller (REL2 <0.46), and petiole shorter and higher (PLI >0.54) (New Guinea) ..... *T. mimula*, sp. nov.
17. Smaller species (HW 0.72–0.79; $n = 4$) with large eyes (REL 0.35–0.37); profemur slender (FI 0.44–0.49); punctures on dorsum of head and pronotum very fine, about 0.005 mm in diameter (New Guinea, northern Australia) ..... *T. rotula*, sp. nov.
Larger species (HW 0.90–1.49; $n = 16$) with smaller eyes (REL 0.26–0.30); profemur usually more robust (FI 0.48–0.54); punctures on dorsum of head and pronotum mostly larger, approximately 0.010–0.015 mm in diameter (New Guinea, Australia) ..... *T. punctulata* F. Smith
18. Standing pilosity relatively sparse on dorsum and sides of head (CSC <6) 19
– Standing pilosity common on dorsum and sides of head (CSC >10) 22
19. Larger species (HL 1.92–2.18, LHT 1.06–1.12; $n = 3$); head elongate (CI 0.62–0.64) and clypeal margin adorned with prominent teeth or a medial protrusion (Figs 104, 106) 20
– Smaller species (HL 1.32–1.73, LHT 0.76–1.00; $n = 10$); head less elongate (CI 0.68–0.75) and clypeal margin lacking prominent teeth or protrusions (Figs 108–109) 21
20. Anterior clypeal margin edentate, with a prominent spatulate protrusion underlying the margin (Fig. 104); frontal carinae moderately well separated (FCI 0.18–0.19; $n = 2$); eyes smaller, REL2 0.38–0.40 (Singapore, Borneo, Java) .... *T. vivax*, sp. nov.
– Anterior clypeal margin with three strong, blunt teeth, but no underlying spatulate protrusion (Fig. 106); frontal carinae very widely separated (FCI 0.27; $n = 1$); eyes larger, REL2 0.45 (Singapore) ..... *T. volucris*, sp. nov.
21. Smaller species (HW 0.94–0.98, LHT 0.76; $n = 4$) with disproportionately larger eyes (REL2 0.50–0.52) (Fig. 109) and shorter profemur (FL/HL 0.50–0.51) (Borneo, Palawan) ..... *T. inversinodis*, sp. nov.
– Larger species (HW 1.05–1.26, LHT 0.88–1.00; $n = 6$) with smaller eyes (REL2 0.42–0.47) (Fig. 108) and longer profemur (FL/HL 0.51–0.56) (Malay Peninsula south and east to Sumatra, Java, Borneo and the Philippines) ..... *T. difficilis* (Emery)
22. Pronotum with sharp lateral margins; petiole relatively thin (PWI 0.42; $n = 1$); pubescence moderately dense on abdominal tergite IV, appressed hairs separated by about their lengths (India, West Malaysia) ..... *T. aitkenii* (Forel)
– Queen unknown, but expected to have weakly marginate pronotum, broader petiole (PWI >0.50), and sparse and inconspicuous pubescence on abdominal tergite IV (Borneo) ..... *T. polita*, sp. nov.

Tetraponera of the Oriental and Australian regions: provisional key to known males

This key will permit males to be identified at least to species-group. The *allaborans*-group is taken no farther than this, but all the species in the *nigra*-group for which males are known (11 of 20 species) have been included in the key, accompanied by cautionary notes regarding some of the related species whose males are as yet undiscovered. Some of the most distinctive features of the males reside in characteristics of the terminalia, and assessing these usually requires dissection.

1. Mesoscutum densely punctate or punctate-reticulate and (sub)opaque; larger species, HW >1.20 2
– Mesoscutum with scattered punctures mostly separated by their diameters or more, and interspaces weakly to strongly shining; smaller species, on average, range of HW approximately 0.50–1.45 3
2. Head sublucid, with relatively small eyes (REL2 ~ 0.42); hypopygium semicircular (Fig. 126); distal end of paramere lacking digitiform lobes (Fig. 153); aedeagal plate elongate-rectangular in profile (Fig. 134) (Pakistan to southern China, south to Sumatra and Java; introduced to the Seychelles) ..... *T. rufonigra* (Jerdon)
– Head opaque, with larger eyes (REL2 ~ 0.52); hypopygium subrectangular (Fig. 127); distal end of paramere with a pair of digitiform lobes (Fig. 154); aedeagal plate triangular in profile (Fig. 135) (Myanmar to Vietnam, south to Palawan, Borneo, Sumatra and Java) ..... *T. pilosa* (F. Smith)
3. Forewing with one cubital cell; anterolateral arms of hypopygium not protruding forward nor subtended by a lamellate, sclerotised extension (Fig. 128); distal end of paramere with a very deep, obliquely transverse, dorsal impression; external face of aedeagus with a longitudinal carina that ends on the posterior margin, not terminating in a tooth or spine (Fig. 136) ..... *allaborans*-group
– Forewing usually with two cubital cells; anterolateral arms of hypopygium protruding forward and subtended by a lamellate, sclerotised extension (Figs 129–133); distal end of paramere lacking a deep transverse impression; external face of aedeagus with an arched carina terminating at or near a sharp posteroventral tooth or spine (Figs 137–141) (*nigra*-group) ... 4
4. Large species (HW 1.03–1.44, LHT 1.17–1.72; $n = 9$), with disproportionately long scapes (SI2 0.27–0.33) and legs (LHT/HL 1.06–1.45); distal end of paramere, as seen in dorsal view, not notably narrowed (Figs 168–170) 5
– Smaller species, on average (HW 0.67–1.24, LHT 0.60–1.15; $n = 28$), with shorter scapes (SI2 0.20–0.28) and legs (LHT/HL 0.74–1.08); distal end of paramere, as seen in dorsal view, conspicuously narrowing towards tip (Figs 171–178) 7
5. Head broader than long (CI 1.07–1.17; $n = 6$); posteromedial margin of hypopygium thickened but not deflected dorsally ... 6
– Head longer than broad (CI 0.86–0.92; $n = 3$); posteromedial margin of hypopygium not thickened but with a thin ligulate extension that is deflected dorsally (India and Nepal, east to southern China, south to West Malaysia) ... *T. binghami* (Forel) (Note: *T. buops* may also key out here.)
6. Anterior portion of mesoscutum strongly narrowed and constricted; posterior margin of hypopygium convex (Fig. 133); distal end of paramere, as seen in posterior view, with a deep mesial excavation (Fig. 144); posterior half of aedeagus with a single oblique carina on its external face (Fig. 139) (north-east India to China, south to Sumatra, Java, Borneo and Palawan) ..... *T. attenuata* F. Smith
– Anterior portion of mesoscutum not strongly constricted; posterior margin of hypopygium concave; distal end of paramere, as seen in posterior view, lacking a deep mesial excavation (Fig. 143); posterior half of aedeagus with a pair of oblique carinae on its external face (Fig. 138) (Pakistan to Thailand, south to Borneo and Java) ..... *T. nigra* (Jerdon)
7. Second funicular segment notably elongate, its length approaching the combined lengths of scape and fourth funicular segment

(LF2/(SL + LF4) 0.82–1.00; *n* = 11); distal end of paramere, as seen in dorsal view, with saucer-shaped mesial concavity only partly visible (Figs 171–173) 8

– Second funicular segment not notably elongate, its length considerably less than the combined lengths of scape and fourth funicular segment (LF2/(SL + LF4) 0.47–0.72; *n* = 17); distal end of paramere, as seen in dorsal view, with saucer-shaped mesial concavity fully visible (Figs 174–178) 10

8. Petiole lacking posteroventral teeth; eyes slightly smaller (REL2 0.53–0.58; *n* = 6); posteromedial margin of hypopygium convex in ventral view (Fig. 129); distal end of paramere, when seen in posterior view, with well-developed, lamellate margin, which conceals the preceding saucer-shaped concavity (Figs 145–146) 9

– Petiole with a pair of posteroventral teeth formed by angular extensions of the petiolar sternite; eyes larger (REL2 0.59–0.61; *n* = 5); posteromedial margin of hypopygium narrowly concave in ventral view (Fig. 130); distal end of paramere, when seen in posterior view, lacking well-developed, lamellate margin, the preceding saucer-shaped concavity easily visible (Fig. 147) (India to southern China, south to northern Australia) ..... *T. nitida* (F. Smith)
(Note: *T. nixa*, *T. nodosa* and *T. notabilis* also expected to key out here.)

9. Smaller species (HW 0.76–0.81; *n* = 3), with shorter legs (LHT/HL 0.77–0.96); distal end of paramere lacking ventral protrusion (Fig. 160) (Borneo, Palawan) ..... *T. inversinodis*, sp. nov.

– Larger species (HW 0.87–0.92; *n* = 3), with disproportionately longer legs (LHT/HL 1.03–1.05); distal end of paramere with blunt posteroventral protrusion (Fig. 159) (Malay Peninsula south and east to Sumatra, Java, Borneo and the Philippines) ..... *T. difficilis* (Emery)
(Note: with more material these differences may narrow.)

10. Anterior portion of mesoscutum strongly narrowed and constricted; antenna very short, owing to unusually short funicular segments, such that second funicular segment shorter than scape (LF2/SL 0.72–0.85; *n* = 6) and combined lengths of funicular segments 2–4 about twice scape length ((LF2 + LF3 +LF4)/SL 1.83–2.15); distal end of paramere, as seen in posterior view, narrowly excavate mesially (Figs 148–149)... 11

– Anterior portion of mesoscutum not strongly constricted; antenna longer, second funicular segment as long as or longer than scape (LF2/SL 1.00–1.69; *n* = 11) and combined lengths of funicular segments 2–4 much more than twice scape length ((LF2 + LF3 +LF4)/SL 3.03–4.52); distal end of paramere, as seen in posterior view, not narrowly excavate mesially (Figs 150–152) 12

11. Larger species (HW 0.85, LHT 1.03; *n* = 1) with disproportionately long legs (LHT/HL 1.08) (New Guinea) ..... *T. atra* Donisthorpe

– Smaller species (HW 0.68–0.79, LHT 0.71–0.85; *n* = 5) with shorter legs (LHT/HL 0.98–1.05) (New Guinea and adjacent islands; northern Australia) ..... *T. laeviceps* (F. Smith)
(Note: *T. mimula* expected to key out here.)

12. Eye small (REL2 0.43–0.45; *n* = 3); distal end of paramere, as seen in dorsal view, lacking beak-like mesial protrusion (Fig. 176) (Australia) ..... *T. tucurua*, sp. nov.

– Eye larger (REL2 0.48–0.57; *n* = 8); distal end of paramere, as seen in dorsal view, with beak-like mesial protrusion (Figs 177–178) 13

13. Smaller species (HW 0.80–0.87; *n* = 3) with large eyes (REL2 0.57) (New Guinea, northern Australia) ..... *T. rotula*, sp. nov.

– Larger species (HW 0.91–1.24; *n* = 5) with smaller eyes (REL2 0.48–0.52) (New Guinea, Australia) ..... *T. punctulata* F. Smith

Species accounts

Tetraponera allaborans-group

Workers of the *allaborans*-group can be recognised by the following features: (*1*) The mandible is slender, with the masticatory margin notably shorter than the basal margin and adorned with only three teeth (Fig. 7). The basal margin has 1–2 small teeth or denticles. (*2*) With the head in full-face view, the dorsal abductor swelling at the base of the mandible is not visible, being hidden by the anterolateral extremity of the clypeus. (*3*) The mesopropodeal impression is well developed and open at the sides, the surface typically with irregular longitudinal rugulae that also extend down the side of the mesosoma. In one subset of species there is also a small, raised, transverse plate, an apparent metanotum. (*4*) The structure of the posterior end of the petiole has been substantially altered from the condition seen in other Asian species of *Tetraponera*: the semicircular margin of the petiolar sternite, against which the helcial sternite articulates, has retreated internally (dorsomesially) and a new, hood-like extension of the sternum has developed which forms the effective posterior margin. The result is that the lower part of the postpetiolar insertion is shifted dorsad, and there is a conspicuous space between the venter of the helcium and the posteroventral part of the petiole, when the postpetiole is in normal resting position (i.e. directed caudad) (Figs 40–43, 45–54). (*5*) Conspicuous standing pilosity is relatively sparse. There are usually only 1–2 pairs of long setae on the pronotum and none on the remainder of the mesosoma dorsum (exception: *T. crassiuscula*). (*6*) The mesosternum is densely pubescent almost throughout. (*7*) Abdominal tergite IV is sparsely pubescent.

Features (*2*) (*4*) (*6*) and (*7*) are also characteristic of the queen caste (known definitively for *T. allaborans*, *T. bita*, *T. crassiuscula*, *T. extenuata* and *T. modesta*). In addition, both males and queens of the *allaborans*-group have one cubital cell in the forewing. There are generally two cubital cells in other Asian/Australian *Tetraponera* species for which the winged forms are known.

The males of the *allaborans*-group (known for *T. allaborans*, *T. crassiuscula*, *T. extenuata* and *T. modesta*) also share the following distinctive suite of characters, here contrasted with the corresponding condition in the *nigra*-group: (*1*) lateral arms of the hypopygium (sternite IX) extending outwards at right angles to the long axis of the sternite (Fig. 128) (*nigra*-group: arms protruding anteriorly and subtended by a thin lamellate plate (Figs 129–133)); (*2*) paramere, inner proximal dorsal margin diverging gradually from midline (Fig. 167) (*nigra*-group: diverging at a sharply rounded angle from midline (Figs 168–178)); (*3*) paramere, distal end, in posterolateral (or dorsal) view, with a very deep, obliquely transverse, dorsal impression (*nigra*-group: lacking such an impression); (*4*) aedeagus, lateral

apodeme shorter than anterior apodeme (Fig. 136) (*nigra*-group: lateral apodeme as long as, or longer than, the anterior apodeme (Figs 137–141)); (*5*) aedeagus, external face with a straight or slightly curved carina, originating anteromedially, directed distad, and meeting the posterior margin without forming a tooth or sharp angle (Fig. 136) (*nigra*-group: with an arched carina, directed posteroventrally, and terminating near a tooth or spine at the posteroventral extremity (Figs 137–141)); (*6*) aedeagus, posterior margin bent laterad at a right angle to the sagittal plane (*nigra*-group: posterior margin directed posteriorly or posterolaterally).

The most commonly encountered members of the *allaborans*-group are *T. allaborans* and the species in the *T. modesta*-complex. In these taxa (and in *T. microcarpa*) the median clypeal lobe of the worker is usually developed as a narrow, conspicuously protruding, denticulate structure, well set off from the rest of the clypeus (Figs 8, 14–18), although it may be somewhat reduced and devoid of teeth. The lateral pronotal margins are well defined, and the mesopropodeal impression lacks a raised, metanotal plate or welt. In a second set of species, much less frequently collected, the median clypeal lobe of the worker is differently formed: it is a blunt triangular point in one species (*T. apiculata*) (Fig. 9) but in the others it is broadly convex and less protruding (Figs 10–12). In the second group of species the pronotal margins are weakly defined or absent, and the mesosoma has a small, transverse metanotal welt. The anomalous *T. connectens* possesses a mix of the features of these two subgroups of species.

There remains considerable uncertainty about species limits in some members of the *allaborans*-group. The three taxa that constitute the *modesta*-complex (*T. crassiuscula*, *T. extenuata*, *T. modesta*) are particularly troublesome. The diagnostic features attributed to them are rather tenuous and, as more material accumulates, the complex may prove to be over-split. At the other extreme, I have used the name '*T. allaborans*' to encompass a highly variable assemblage of populations that may well comprise more than one species, but among which I have been unable to find clear diagnostic differences. At this stage it is possible to do no more than offer working hypotheses about species boundaries. To avoid future synonymy (and bearing in mind the evidence for extensive intraspecific variation in some species of *Tetraponera*) I have taken a cautious approach towards recognition of new taxa.

In addition I have examined a few isolated queens and males, unassociated with workers, which belong to the *allaborans*-group but cannot be assigned to species. Several taxa are involved and they might be conspecific with some of the newly described, worker-based species (*T. apiculata*, *T. avia*, *T. bita*, *T. brevis*, *T. connectens*), or they may represent additional undescribed taxa. The question is not likely to be resolved until we have more collections of nest series containing all three castes.

The *allaborans*-group is widely distributed on the Indian subcontinent and in Southeast Asia, reaching New Guinea and the Cape York region of northern Australia. As far as known, the species are all generalist inhabitants of dead twigs and are not exclusively associated with particular plant species. The biology of the less common species is almost completely unknown, however, and surprises undoubtedly await.

Tetraponera allaborans (Walker)

(Figs 8, 19, 30–32, 37–38, 40–43, 155, 167, 128, 136)

Pseudomyrma? *allaborans* Walker, 1859: 375.
Eciton rufipes Jerdon, 1851: 112. **Syn. nov.** Nomen oblitum, under ICZN Article 23.9.2 (see discussion below).
Eciton minuta Jerdon, 1851: 112. **Syn. nov.** Nomen oblitum, under ICZN Article 23.9.2 (see discussion below).
Sima compressa Roger, 1863*a*: 179. Synonymy by F. Smith, 1877: 69; here confirmed.
Cerapachys femoralis Motschoulsky, 1863: 21. Synonymy by Dalla Torre, 1893: 53; here confirmed.
Cerapachys ceylonica Motschoulsky, 1863: 22. Synonymy by Dalla Torre, 1893: 53; here confirmed.
Sima subtilis Emery, 1889: 500. Synonymy by Dalla Torre, 1893: 53; here confirmed.
Sima allaborans var. *sumatrensis* Emery, 1900: 676. **Syn. nov.**
Sima allaborans var. *longinoda* Forel, 1909*b*: 395. **Syn. nov.**
Tetraponera allaborans (Walker); F. Smith, 1877: 69. First combination in *Tetraponera*.
Tetraponera allaborans (Walker); Wheeler and Wheeler, 1956: 390. Description of larva.
Tetraponera aitkeni; Wheeler and Wheeler (nec Forel), 1956: 388. Description of larva, misidentified as *T. aitkenii*.
Tetraponera allaborans (Walker); Hung *et al.*, 1972: 1024. Description of karyotype.

For a detailed nomenclatural history of *T. allaborans* and its junior synonyms see Bolton (1995: 417–419). Note also the following nomenclatural event not recorded therein: *T. longinoda* (Forel); raised to species by Dlussky and Radchenko (1990: 122).

Types (not examined)

Eciton rufipes Jerdon. Syntype worker(s), Salem district, India [type(s) lost].

Eciton minuta Jerdon. Syntype worker(s), southern India [type(s) lost].

Type material examined

Pseudomyrma? *allaborans* Walker. Syntypes, 2 workers, 1 dealate queen, 'Ceylon' (BMNH). Note: original description also included male.

Sima compressa Roger. Syntype, 1 worker, 'Ceilon' (BMNH).

Cerapachys femoralis Motschoulsky. Syntype, 1 alate queen, Montagnes de Nura-Ellia, Sri Lanka [as 'Mt. N. E.'] (ZMUM).

Cerapachys ceylonica Motschoulsky. Syntypes, 2 workers, Montagnes de Nura-Ellia, Sri Lanka [as 'Mt. N. E.'] (ZMUM).

Sima subtilis Emery. Syntype, 1 worker, Bhamó, Myanmar (Fea) (MCSN).

Sima allaborans var. *sumatrensis* Emery. Syntypes, 7 workers, 1 alate queen, 2 dealate queens, D. Tolong, Sumatra, Indonesia (E. Modigliani) (MCSN, MHNG).

Sima allaborans var. *longinoda* Forel. Syntypes, 2 workers, Ambalangoda, Sri Lanka (Bugnion) (MHNG).

Other material examined

(1) *allaborans*, excluding variants 2–5 (see explanation of variants below, under *Discussion*)

Australia: *Queensland*: Archer R. (C. N. Smithers); Bamaga, Cape York Penn. (J. Sedlacek); East Claudie R., Iron Range (G. Monteith; D. Cook); Lockerbie Scrub, Cape York (G. B. Monteith); Lockerbie, Cape York (G. B. Monteith); Lockerbie, Cape York Penn. (J. Sedlacek); Rocky R. (C. N. Smithers). **Bangladesh:** *Dhaka*: Dhaka [as 'Decca'] (L. Chilson). **Bhutan:** Changra, 18 km S Tongsa, 1900 m (NHMB – Bhutan Expedition 1972); Khala, 200 m (NHMB – Bhutan Expedition 1972); Phuntsholing, 200–400 m (NHMB – Bhutan Expedition 1972); Samchi, 350–450 m (NHMB – Bhutan Expedition 1972); Sampa-Kotoka, 1400–2600 m (NHMB – Bhutan Expedition 1972); Tan Chu, 23 km E Wangdiphodrang [as 'Tan Chu, 23 km O Wangdi P.'] (NHMB – Bhutan Expedition 1972). **China:** *Guangdong*: Ding-Hu Mts., 60 km W Guangzhou (Boucek); *Guangxi*: Shiwandashan (J. R. Fellowes); Yongfu County, 800 m (S. Zhou); *Hainan*: Lumuwan, 260 m (J. R. Fellowes); Ta Hian (J. L. Gressitt); *Hong Kong*: Lantau I.: Shui Hau, 20–50 m (R. R. Snelling); Lantau I.: Shui Hau, 20–50 m (R. R. Snelling); N.T.: Kadoorie Agric. Res. Centre, Shek Kong (J. R. Fellowes); N.T.: Tai Lung Farm, Sheung Shui (S. Yamane); N.T.: Tai Mong Tsai (J. R. Fellowes); *Yunnan*: 20 km E Jinghong, 900 m (C. Carpenter; N. Nordensten). **India:** *Assam*: Chabua (D. E. Hardy); Kaziranga, 75 m (W. Wittmer; C. Baroni Urbani); *Goa*: Canacona, Cortigao [sic] Sanctuary, 100 m (A. Schulz; K. Vock); Mormugao, vic. Velsao, 5 km E Dabolim Airport, 50 m (A. Schulz; K. Vock); *Gujarat*: Gujarat [as 'Gujerath'] (Wroughton); *Karnataka*: 10 km SW Heggadadevankote, 760 m (P. S. Ward); 25 km W Mudigere (J. Noyes); Belgaum (Wroughton); Dharwad ('G. R.'); I.I.Sc. Campus, Bangalore (T. Varghese); Indian Institute of Science, Bangalore, 900 m (P. S. Ward); Jubilee Garden, Bangalore (T. Varghese); Ranganathittu Bird Sanct., 710 m (P. S. Ward); *Kerala*: Calicut (A. B. Soans); Calicut (F. Rickson); Calicut University campus (S. Sheela); Irinjalakuda, Trichur Dist. (A. B. Soans); Kannoth, Cannanore Dist., 100 m (A. B. Soans; W. L. Brown); Kunnamthanam (S. Sheela); Muthappanpuzhe, 460 m (P. S. Ward); Pandalam, Pavvathu Malai, 70 m (A. B. Soans); Periyar (J. Noyes); Silent Valley Res., 16 km W Mukkali (A. B. Soans; W. L. Brown); Talasseri [as 'Thalassery'] (S. Sheela); Thirunelly, Wynaad Taluk, 900 m (A. B. Soans; W. L. Brown); *Maharashtra*: Poona (Wroughton); Poona (c.u.); *Meghalaya*: Barapani Old Road, 1000 m (W. Wittmer; C. Baroni Urbani); Darugiri, Garo Hills, 450 m (W. Wittmer; C. Baroni Urbani); Garo Hills, vic. Tura, 700–900 m (C. Besuchet; I. Löbl); Shillong (W. Wittmer; C. Baroni Urbani); Songsak, Garo (W. Wittmer; C. Baroni Urbani); Umtyngar-Cherrapunjee (W. Wittmer; C. Baroni Urbani); *Orissa*: 'Orissa' (Taylor); Barkuda Isld., Chilka Lake, Ganjam Dist. (N. Annandale); Puri [as 'Pooree'] (Walsh); *Sikkim*: Pam, S Gangtok, 980 m (Bhatka B.); Rangeli R., 900 m (Bhatka B.); *Tamil Nadu*: Cherangoole, Nilgiri Hills, 3500 ft (P. S. Nathan); Gudalur, Nilgiri Hills, 3500 ft (P. S. Nathan); Madras Snake Park (G. Ekis); Mudumalai Anim. Sanct. (J. Noyes); Valparai (J. Noyes); *West Bengal*: Barakpur [as 'Barrackpore'] (Rothney); Calcutta (Rothney); Calcutta (c.u.). **Indonesia:** *Aceh*: Bireuen (W. M. Mann); *Irian Jaya*: 50 km S Manokwari, Arfak Mtns Nature Res, 25 m (G. D. Alpert); Korim, Biak Isl. (R. R. Snelling); *Jakarta Raya*: Jakarta [as 'Batavia'] (Bryant & Palmer); *Jawa Barat*: Jasinga, nr Bogor (S. Yamane); Salak, nr Bogor (S. Yamane); Tjibodas (B. Bolton); Ujong Kulon Natl Pk, W. Java (G. D. Alpert); West Java (Carny); *Jawa Tengah*: Semarang (L. G. E. Kalshoven); Semarang [as 'Samarang'] (E. Jacobson); Sigaluh (Hamann); Wonosobo (E. Jacobson); *Kalimantan Timur*: Teluk Kabah, Kutai Natl Pk (S. Yamane); *Maluku*: Pulau Bacan [as 'Batchian'] (c.u.); *Nusa Tenggara Barat*: Sapit, Lombok I. (Imai *et al.*); *Nusa Tenggara Timur*: Sumba: Baing (Exp. Bühler-Sutter); Sumba: Waimangura (Exp. Bühler-Sutter); *Sulawesi Tengah*: E of Lore Lindu, near Palu (S. Yamane); *Sumatera Barat*: Indropura (Fritsehler); Mentawei, Sipora, Sereinu (E. Modigliani); *Sumatera Utara*: Bandarbaru [as 'Banda Baru'] (von Buttel-Reepen); D. Tolong (E. Modigliani); Pangherang-Pisang (E. Modigliani); Sibolga [as 'Siboga'] (E. Modigliani); Si-Rambe (E. Modigliani). **Laos:** *Vientiane*: Phou Khao Khouay NP, env. Tad Leuk Waterfall, 200 m (Schillhammer). **Malaysia:** *Johor*: 13 km NE Kota Tinggi, 50 m (P. S. Ward); *Sabah*: Bundu Tuhan, 6 km S Mt Kinabalu Natl Pk, 1070 m (B. B. Lowery); Danum Valley (E. Widodo); Keningau, 1100 m (S. Yamane); Umas Umas, nr Tawau (R. W. Taylor); *Sarawak*: Bako Natl Pk (D. H. Janzen); Gunung Kanyi [as 'Mt. Poi'] (E. Mjöberg); Gunung Penrissen [as 'Mt. Penrissen'] (E. Mjöberg); Tower, Lambir Natl Pk, Miri (S. Yamane); *Selangor*: Ulu Gombak (A. Schellerich); Ulu Gombak, 250 m (S. Yamane); Ulu Gombak, 30 km NE Kuala Lumpur, 240–500 m (A. Schellerich); Ulu Gombak, nr Kuala Lumpur, 800 ft (R. W. Taylor). **Myanmar:** *Kachin*: Bhamò (Fea); *Pegu*: Palon, Pegù (L. Fea); *Shan*: Taunggyi, 5000 ft (Bingham). **Nepal:** *Bagmati*: Bajra Barai, Kathmandu V. (W. Wittmer; C. Baroni Urbani); Godavari, 1450 m (W. Wittmer; C. Baroni Urbani); Gokarnaban, Kathmandu (W. Wittmer; C. Baroni Urbani); *Dhaulagiri*: 18 km N Baglung, 1020 m (P. S. Ward); *Gandaki*: Pokhara, 820 m (W. Wittmer; C. Baroni Urbani); *Mechi*(?): zw. Iwa Khola u. Sablako Pass, [near] Taplejung, 940–1200 m (J. Martens; W. Schawaller). **Papua New Guinea:** *Central*: Aroa Ptn. (J. H. Barrett); Bisianumu, nr Sogeri, 500 m (E. O. Wilson); Brown R. (B. B. Lowery); Karema, Brown R. (E. O. Wilson); *East Sepik*: 2 km E Maprik, 200 m (P. S. Ward); *Madang*: Madang [as 'Friedrich- Wilh. –hafen'] (Biró); *Morobe*: Bulolo R. valley, 6 km NE [sic] Wau, 1100 m (R. W. Taylor). **Philippines:** *Basilan*: I. of Basilan (Baker); *Bataan*: Mariveles (B. B. Lowery); *Bukidnon*: 7 km S Malaybalay, 670 m (B. B. Lowery); Malaybalay, Kaamulan Site, 650 m (H. Zettel); *Cebu*: S Badian Matutinao, Kawasan Falls, 2–50 m (H. Zettel); *Dumaguete*: Dumaguete (J. W. Chapman); *Ilocos Norte*: 'Pila Laoag' [= Pila to Laoag?] (C. K. Starr); *Laguna*: Los Banos, Mt Makiling, 600 m (B. B. Lowery); Mt Makiling (H. Zettel); Mt Makiling, above Mad Springs, 400–700 m (J. Kodada); Mt Maquiling (R. C. McGregor); *Manila*: Manila (in quarantine, San Francisco, USA) (M. E. Johnson); Manila [as 'Manilla'] (Simon); *Masbate*: 3.5 km SE Masbate, Tugbo, Tugbo R. (H. Zettel); *Mindanao*: Talacogon (B. B. Lowery); *Mindoro Occidental*: San Jose (E. S. Ross); *Mindoro Oriental*: W Puerto Galera, Tamaraw Beach, Talipanan R. (H. Zettel); *Mountain*: 5 km S Bontoc, Balitian R., 900 m (H. Zettel); Bontoc (J. W. Chapman); *Negros Oriental*: Dumaguete, Camp Lookout, 1500 ft (J. W. Chapman); Dumaguete, Camp, 1600 ft (J. W. Chapman); W Dumaguete, Valencia Banica Valley Resort (H. Zettel); *Palawan*: 10 km W Puerto Princesa, Iwahig Penal Colony (H. Zettel); Bacungan, 60 m (B. B. Lowery); Iwahig Penal Col., *c.* Puerto Princesa, 60 m (B. B. Lowery); San Juan, Aborlan (C. K. Starr); *Quezon*: Atimonan, Quezon NP, Old Zigzag Rd. (H. Zettel); *Rizal*: Antipolo (Simon); Ateneo de Manila (B. B. Lowery); San Pedro (B. B. Lowery); *Zamboango del Sur*: 8 km NE Pagadian, Manga Falls (H. Zettel). **Singapore:** Bukit Timah, 50 m (P. S. Ward); Kent Ridge (D. H. Murphy); Kent Ridge, 30 m (P. S. Ward); Lim Chu Kang, <5 m (P. S. Ward); Mandai (D. H. Murphy); Mandai, <5 m (P. S. Ward). **Sri Lanka:** *Central*: Kandy (Simon); Kandy (Bingham); Kandy (G. E. Bryant); Kandy, 1800 ft (Davis; Rowe); Kandy, Udawattakele [as 'Udawattakele'], 2100 ft (K. V. Krombein *et al.*); Peradeniya (A. Rutherford); Peradenyia (T. Schoener); *North Western*: Lunuwila (B. Bolton); *Southern*: Ambalantota (B. Bolton); Galle [as 'Galli'] (E. Bugnion); *Uva*: Bibile (R. Winney); Uva Egodapitiya Nilgala

(T. F. Halstead); *Western*: Colombo (Simon); Colombo (U. Maschwitz); Colombo (T. F. Halstead); Labugama, Colombo distr. (A. E. Stubbs; P. J. Chandler); Laxapathiya, nr Colombo (K. L. A. Perera); Yakkala (K. L. A. Perera); *district unknown*: 'Ceilon' (c.u.); 'Ceylon' (Bugnion); 'Ceylon' (Escherich); 'Ceylon' (Horn); 'Ceylon' (Rothney); 'Ceylon' (Thwaites); 'Ceylon' (c.u.). **Taiwan:** *Hualien*: Mizuho (L. Gressitt); *Kaohsiung*: Rokki [= Liu-kuei] (J. L. Gressitt); Shanping, 640 m (R. Davidson *et al.*); *Nantou*: Bukai (L. Gressitt); Huei-sun Forest (C. C. Lin); Kung-yin Falls (C. C. Lin); Lan Wa Chu (D. G. Furth); Meiyuan (S. Yamane); Sun Moon Lake (E. I. Schlinger); Sun-Moon L. (A. C. F. Hung); Ts'ui-feng [as 'Tsuey Feng'] (I. D. Gauld); *Pingtung*: Kuraru (L. Gressitt); Manchou (K. Tsuneki); *Taichung*: Kukuan [misspelled as 'Fukuan'] (D. G. Furth); *Taipei*: Ankeng [misspelled as 'Aukung'] (D. G. Furth); Hua Yuan Hsing Chang (C. C. Lin); Taipei, 30 m (J. Klapperich; S. Klapperich); *Taitung*: Chih-pen Hot Springs (C. C. Lin); Li-chia Forest (C. C. Lin). **Thailand:** *Chaiyaphum*: Phu Khieo WS (D. Wiwatwitaya); *Chiang Mai*: Doi Pui, 1420 m (W. L. Brown; I. Burikam); Doi Suthep (S. Yamane); Doi Suthep region (D. Kovac); Maerim (R. Beaver); Maerim (R. R. Snelling); Pau Pau Falls (D. G. Furth); *Kanchanaburi*: Lam Ta Pen R., 5 km NW Lat Ya (W. J. Pulawski); *Krabi*: Ao Nang (Madl); Thanboke Khoranee Natl Pk, 10 km S Ao Luk, 50 m (A. Schulz; K. Vock); *Krung Thep Mahanakhon*: Bangkok (P. S. Messenger); Bangkok University (c.u.); *Nakhon Nayok*: Khao Yai Natl Pk, 700 m (I. Burikam; W. L. Brown); Khao Yai Natl Pk, 720 m (I. Burikam; W. L. Brown); Khao Yai Natl Pk, 1180 m (I. Burikam; W. L. Brown); *Nakhon Ratchasima*: Khao Yai Natl Pk (D. Wiwatwitaya); *Phangnga*: Khao Lak (A. Schulz); *Ranong*: Ranong (D. H. Murphy); *Satun*: Thale Ban Natl Pk, 20–30 km E Satun, 200–400 m (A. Schulz; K. Vock); *Surat Thani*: Tai Rom Yen Natl Pk (D. Kovac); *Tak*: Tung Yai W.S., near Myanmar border (W. Jaitrong); Tung Yai (D. Wiwatwitaya); *Trang*: Khao Chong Nature Education Centre (R. R. Snelling; S. Sonthichai); *province unknown*: near Nangecung (T. D. A. Cockerell). **Vietnam:** *Ha Nam Ninh*: Cúc-phu'óng (R. Bielawski; B. Pisarski); *Ha Noi*: Co-loa, 20 km NE Hà-nôi (R. Bielawski; B. Pisarski); *Ha Sonh Binh*: Da Bac, Tuly (Belokobylskij); *Khanh Hoa*: Hon Tré [as 'Isl. Che'] (A. Radchenko); *Kien Giang*: Hòn Thom [as 'Isl. Thom'] (A. Radchenko); *Nghe An*: Na Xan, Que Phong Distr, 500 m (B. T. Viet); *Quang Ninh*: D. Dông Khoa [as 'Isl. Dongkho'] (A. Radchenko); *Soc Trang*: Côn Dao [as 'Isl. Kondao'] (A. Radchenko)

(2) *allaborans* – variant 2

China: *Hainan*: Tien Fong Mts. (Boucek). **Thailand:** *Chiang Mai*: Doi Suthep, 500–700 m (S. Yamane); *Nakhon Nayok*: Khao Yai Natl Pk, 1180 m (I. Burikam; W. L. Brown). **Vietnam:** *Vinh Phuc*: Tam Dao, 1000 m (Belokobylskij); Tam Dao, 900–1240 m (H. Ôkido); Tamdao, 900m (Medvedev)

(3) *allaborans* – variant 3

Malaysia: *Pahang*: Cameron Highlands, Ringlet (T. S. Bellows); *Selangor*: Gombak Field Stn., 30 km NE Kuala Lumpur, 250 m (W. Dorow); Ulu Gombak (A. Schellerich); Ulu Gombak, 30 km NE Kuala Lumpur, 240–500 m (A. Schellerich). **Thailand** *Mae Hong Son*: 10 km S Khun Yuam [as 'Khum Yuam'], 300 m (Schulz; Vock).

(4) *allaborans* – variant 4

Malaysia: *Sabah*: Bundu Tuhan, 4 km S Mt Kinabalu Natl Pk, 1220 m (B. B. Lowery); *Sarawak*: Sadong, Kampong Tapuh, 300–450 m (T. C. Maa); *Selangor*: Gombak Field Stn., 30 km NE Kuala Lumpur, 250 m (W. Dorow); Ulu Gombak (U. Maschwitz); Ulu Gombak (A. Schellerich); Ulu Gombak, 30 km NE Kuala Lumpur, 240–500 m (A. Schellerich).

(5) *allaborans* – variant 5

Indonesia: *Sulawesi Utara*: Dumoga-Bone Natl Pk, 200–400 m (P. M. Hammond); Dumoga-Bone Natl Pk, 400 m (N. Stork); Dumoga-Bone Natl Pk, 1100 m (N. Stork).

(Collections: AMSA, ANIC, ASIC, BMNH, CASC, CESB, CMNH, DZUC, HNHM, HZIC, KFBG, KUBC, KUEC, KUES, LACM, MCSN, MCZC, MHNG, NHMB, NHMV, NTUC, PSWC, RMBR, SAMC, UASK, UCRC, UMSC, USNM, ZMAS, ZMPA, ZMUM).

Worker measurements ($n = 64$)

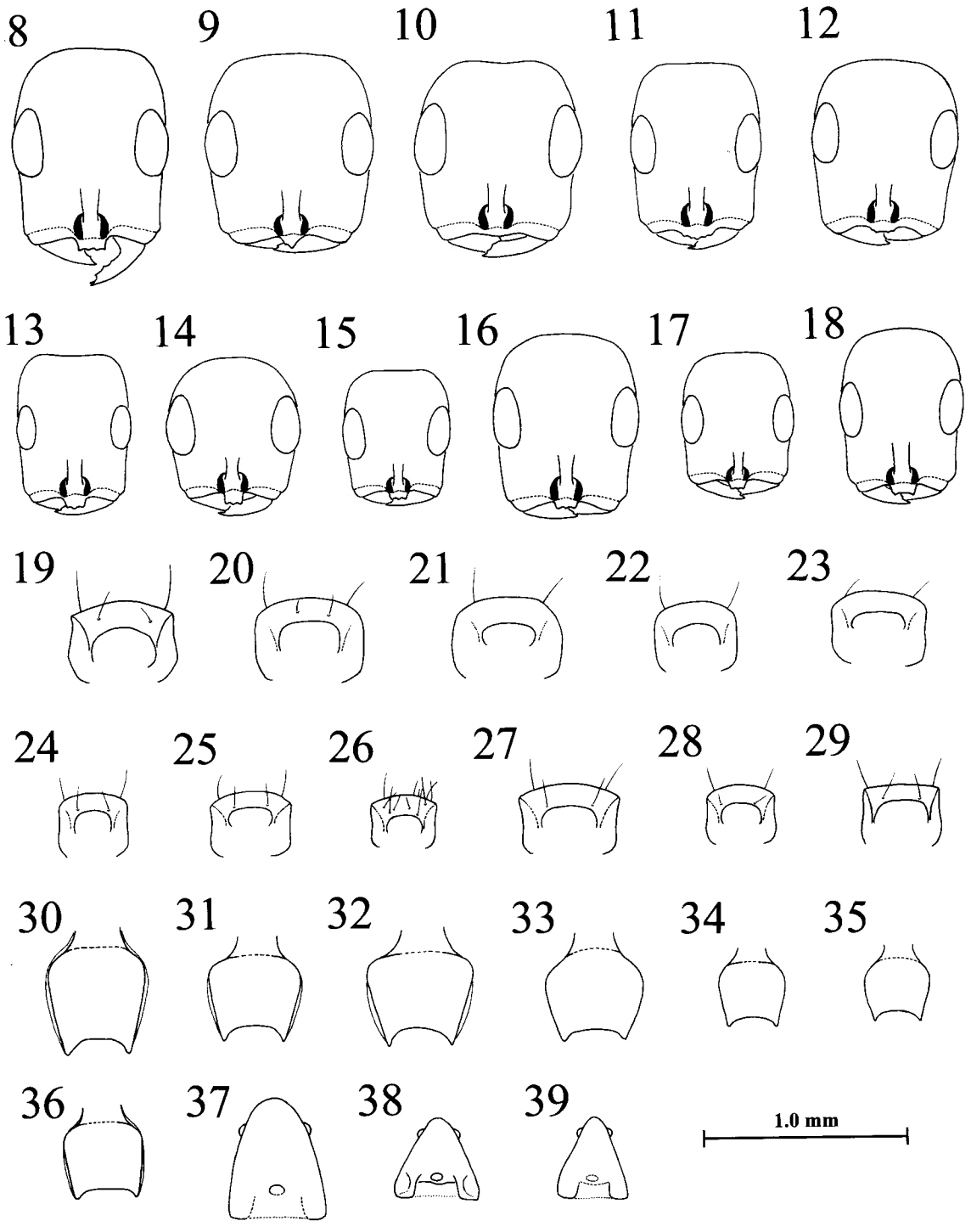
HW 0.62–0.93, HL 0.76–1.10, LHT 0.54–0.80, CI 0.75–0.92, FCI 0.08–0.13, REL 0.33–0.41, REL2 0.41–0.49, SI 0.57–0.65, SI3 1.21–1.53, FI 0.36–0.45, PLI 0.41–0.64, PWI 0.34–0.52, PDI 0.91–1.28, LHT/HW 0.78–0.95, CSC 0–3, MSC 0–6.

Worker description

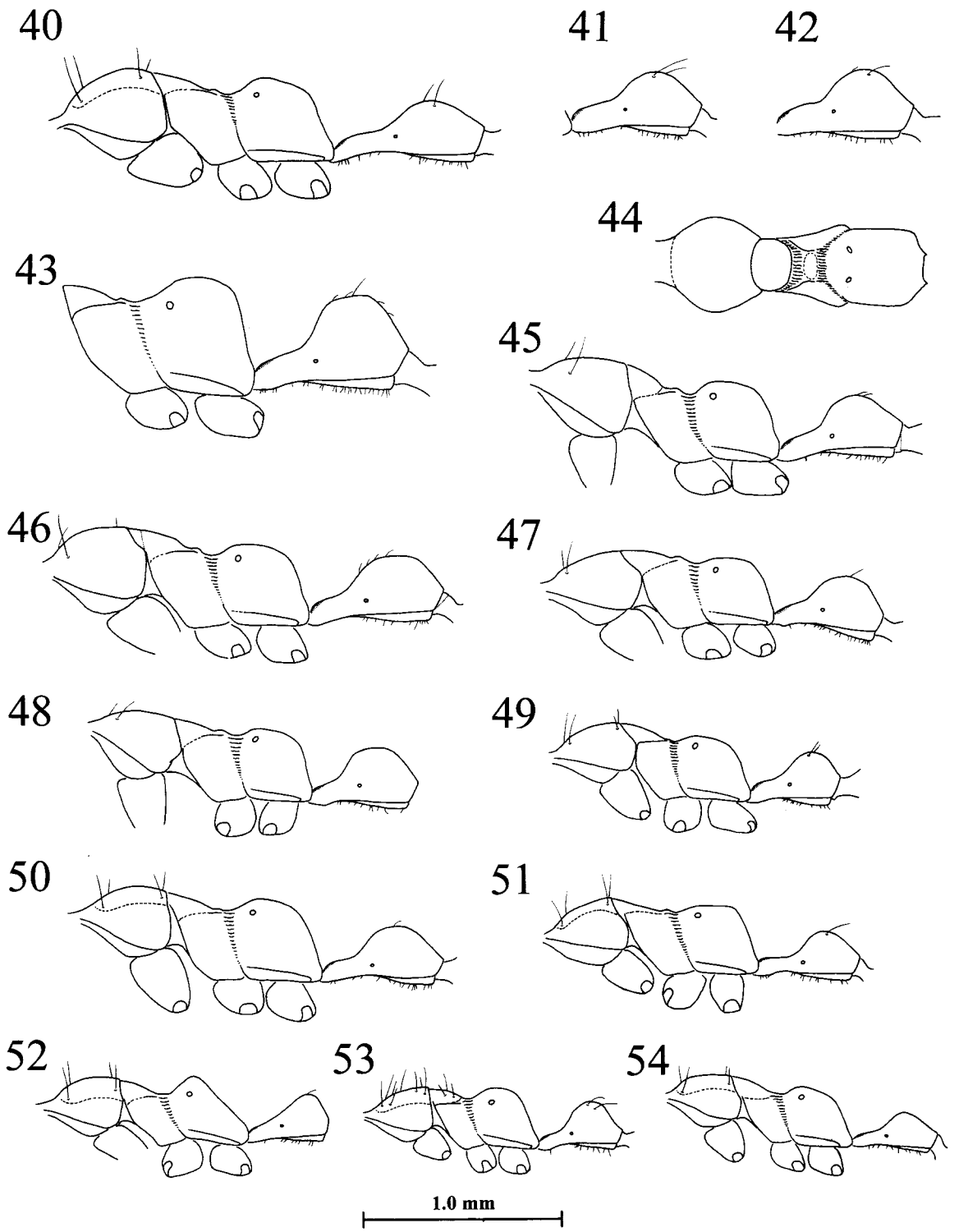
Small to medium-sized species (see ranges of HW, HL and LHT); median clypeal lobe narrow, usually well set off from the rest of the clypeal margin, conspicuously protruding and adorned with 2–4 teeth (Fig. 8), but sometimes reduced in size; eyes of moderate size (see REL and REL2 values); profemur relatively slender (FI usually <0.44); pronotum laterally marginate, varying from sharp-edged to blunt; in dorsal view pronotum typically as in Fig. 30, the sides weakly convex and converging posteriorly; maximum width of pronotum generally occurring below the pronotal margins (Fig. 19); mesopropodeal impression with irregular longitudinal rugulae, and sometimes additionally with a transverse rugule, but lacking a raised metanotal plate; propodeum rather low and broad (Figs 38, 40) such that PDI 0.91–1.09; in an exceptional population from Sulawesi the propodeum large and inflated (PDI 1.09–1.28) (Figs 37, 43); petiole typically long and slender (Fig. 40), but individuals with shorter, more robust petiolar nodes also occur (Figs 41–43; see discussion below). Integument moderately to strongly shiny, with scattered punctures on a background of fine reticulations and irregular lineations; most punctures on head about 0.008–0.015 mm in diameter, and separated by much more than their diameters; lower malar area longitudinally carinate; fine longitudinal carinulae may be present on mesopleuron, metapleuron and side of propodeum. Pilosity not common, long standing setae (>0.06 mm in length) present on gaster, apex of head, and as follows: one supraocular pair, 1–2 pairs (usually two) on pronotum, 1–2 pairs on petiole, and 1–2 pairs on postpetiole; much shorter appressed pubescence scattered sparsely over body, tending to become suberect on venter of head, petiole and postpetiole. Body black or dark brownish-black, the appendages frequently lighter in color (brown to yellowish-brown); petiole and postpetiole varying from concolorous with rest of body to contrastingly lighter.

Discussion

Tetraponera allaborans workers can be recognised by the combination of (*i*) black or dark brownish-black body (appendages, petiole and postpetiole may be contrastingly lighter), (*ii*) small to medium size (see HW and LHT values), (*iii*) laterally marginate pronotum whose maximum width generally occurs below the margin (Fig. 19), and (*iv*) relatively low, wide propodeum (Figs 38, 40). In addition, the



Figs 8–39. *Tetraponera allaborans*-group, workers, full-face (dorsal) view of head (*8–18*), posterior view of pronotum (*19–29*), dorsal view of pronotum (*30–36*) and posterior view of propodeum (*37–39*). *8*, *T. allaborans* (India); *9*, *T. apiculata*, holotype (Malaysia); *10*, *T. avia*, holotype (Malaysia); *11*, *T. bita*, holotype (Malaysia); *12*, *T. brevis*, holotype (Malaysia); *13*, *T. connectens*, holotype (Thailand); *14*, *T. conica*, holotype (Malaysia); *15*, *T. crassiuscula* (Malaysia); *16*, *T. extenuata*, holotype (Singapore); *17*, *T. modesta* (Papua New Guinea); *18*, *T. microcarpa* (Hong Kong); *19–29*: same individuals and sequence as Figs *8–18*; *30–32*, *T. allaborans*, showing variation in pronotum shape (*30*, India; *31*, Malaysia; *32*, Malaysia); *33*, *T. extenuata*, holotype (Singapore); *34*, *T. modesta* (Papua New Guinea); *35*, *T. crassiuscula* (Malaysia); *36*, *T. microcarpa* (Hong Kong); *37*, *T. allaborans*, variant 5 (Indonesia); *38*, *T. allaborans* (Singapore); *39*, *T. extenuata*, holotype (Singapore).



Figs 40–54. *Tetraponera allaborans*-group, workers, lateral view of mesosoma and petiole (*40*, *45–54*), lateral view of posterior mesosoma and petiole (*43*), lateral view of petiole (*41–42*) and dorsal view of mesosoma (*44*). *40*, *T. allaborans* (India); *41*, *T. allaborans* (Singapore); *42*, *T. allaborans* (Papua New Guinea); *43*, *T. allaborans*, variant 5 (Indonesia); *44–45*, *T. avia*, holotype (Malaysia); *46*, *T. apiculata*, holotype (Malaysia); *47*, *T. bita*, holotype (Malaysia); *48*, *T. brevis*, holotype (Malaysia); *49*, *T. connectens*, holotype (Thailand); *50*, *T. extenuata*, holotype (Singapore); *51*, *T. microcarpa* (Hong Kong); *52*, *T. conica*, holotype (Malaysia); *53*, *T. crassiuscula* (Malaysia); *54*, *T. modesta* (Papua New Guinea).

mesopropodeal impression lacks a metanotal plate. Other dark-bodied species in the *allaborans*-group differ in the shape of the propodeum, the margination of the pronotum and/or the structure of the mesopropodeal impression.

Tetraponera allaborans is a highly variable taxon and quite possibly (as treated here) composed of more than one species. Provisional sorting of worker material from the Indian subcontinent, including Sri Lanka, suggests the existence of two forms. One of these, *T. allaborans* (s.s.), has a slender petiole (PLI 0.42–0.51; n = 8), broad pronotum (PrWM/HW 0.64–0.66) and a tendency towards light-colored, yellowish-brown legs. The other form (here referred to as 'variant 1') has a shorter, more robust petiole (PLI 0.53–0.64; n = 8), narrower and more sharp-edged pronotum (PrWM/HW 0.57–0.64) and darker appendages. Whether these forms are reliably diagnosable and represent different species remains to be determined. Males associated with both forms have been examined and their genitalia are very similar, indicating that they are either conspecific or very closely related. The syntypes of *T. allaborans* and all of its junior synonyms match the form with the slender petiole. (Approximate PLI values of the worker syntypes are as follows: *allaborans*, 0.43; *compressa*, 0.46; *ceylonica*, 0.47; *subtilis*, 0.47; *sumatrensis*, 0.44; and *longinoda*, 0.42.) Outside the Indian subcontinent the phenotypic distinctions cannot be sustained, since one finds all degrees of intermediacy in petiole shape, pronotal width, and color (PLI 0.41–0.63, PrWM/HW 0.55–0.71, in a sample of 48 workers from other parts of Asia and northern Australia).

The following variants from Southeast Asia are also treated as conspecific with *T. allaborans* until more information is available on their status.

Variant 2. This is a small form (HW 0.62–0.71), known only from a few workers from Thailand, Vietnam and China. The body is dark brown to black, with brown or yellowish-brown appendages, and a tendency for the petiole and postpetiole to be similarly light-colored. Although light-colored nodes and appendages are common in *T. allaborans* workers from the Indian subcontinent, in the rest of Asia *T. allaborans* workers tend to be more uniformly dark and to be larger in size (HW usually >0.70). The size and coloration of variant 2 are suggestive of *T. extenuata* (q.v.), but the propodeal shape (PDI 1.00–1.08; n = 5) and pronotal margination match that of *T. allaborans*.

Variant 3. In some small- to medium-sized workers (HW 0.67–0.78) from central Malaysia and Thailand the pronotum is expanded laterally and, when seen in dorsal view, appears unusually broad and subtrapezoidal in shape, with rather sharply rounded humeri (Fig. 32). However, workers with intermediate degrees of pronotal expansion also occur (Fig. 31), and the ratio of pronotal width to head width (PrWM/HW) varies continuously from about 0.71 in the most broad-shouldered workers to values more typical of *T. allaborans* workers (~0.65).

Variant 4. Some large specimens (worker HW 0.84–0.91) from peninsular Malaysia and Borneo have the median clypeal lobe reduced so that the anterolateral corners of the clypeus are in a more anterior position than the median lobe. The sculpture on these large individuals also tends to be more strongly defined. The differences are not striking, however, and might be partly due to allometric relationships between these traits and body size.

Variant 5. From one locality in Indonesia (Sulawesi: Dumoga-Bone Natl Pk) comes a small series of relatively large workers in which the propodeum is strikingly enlarged and the petiolar node is short and robust (Fig. 43). At first glance it would seem that these must be a different species: the PDI and PLI values of most workers are well outside the normal range for *T. allaborans*. For example, sample measurements of seven workers (with HW ranging from 0.80 to 0.93) yielded the following results: PDI 1.20–1.28, PLI 0.59–0.63. (By contrast, in *T. allaborans*, other than variant 5, PDI 0.91–1.09, and in *T. allaborans*, other than variant 1 and variant 5, PLI 0.41–0.59). But among the series of 11 workers, there are two obviously conspecific individuals (HW 0.80 and 0.85) with propodeal and petiolar shapes that are less exaggerated (PDI 1.10, 1.09; PLI 0.55, 0.54), which effectively links them to more 'typical' *T. allaborans*. Without more knowledge of the significance of these rather bizarre workers, it seems prudent to treat them as a part of *T. allaborans* (s.l.). Interestingly, a tendency towards a conspicuously elevated propodeum also occurs in some Australian populations of *T. punctulata* (Figs 97–99).

To summarise, the preceding variants of *T. allaborans* represent modal forms, usually connected by intermediates to more typical specimens, at least when the variation present throughout the range of *T. allaborans* is considered. A more in-depth analysis, using genetic markers, is needed to determine the extent to which the sexual forms associated with these worker morphs are reproductively isolated from one another.

A few remarks are needed concerning the two taxa described by Jerdon (1851), here newly synonymised under *T. allaborans*. These *nomina oblita* (*T. rufipes* and *T. minuta*) have not been used as the names of recognisable, valid species since their original description (Jerdon 1851). They have appeared in a few catalogues and other works (Dalla Torre 1893; Bingham 1903; Emery 1921; Chapman and Capco 1952; Bolton 1995) but, with the exception of Forel's (1903*a*: 709) consignment of *T. rufipes* to synonymy under *T. allaborans* (without comment or explanation), their identities have not been clarified or discussed. No type specimens of *T. rufipes* or *T. minuta* are known to exist but their placement in *Tetraponera* is reasonable given that Jerdon (1851) treated them, along with two subsequently recognisable species (*T. nigra* Jerdon and *T. rufonigra* Jerdon), as belonging to a single genus characterised by having 'a long slender body, oblong head, large eyes, short antennae, inserted

very near the mouth, linear or oblong jaws' and a severe sting. Among *Tetraponera* species known to occur in southern India the description of *T. rufipes* matches only that of *T. allaborans*, especially with respect to size ('11–48th of an inch'), color ('black with rufous legs') and shape of the petiole ('long, low'). The description of *T. minuta* is more meager, but the small size ('1–6th of an inch'), black color, and 'very slender' body would seem to preclude any other species. *Tetraponera allaborans* (Walker) has been used as the valid name of this common species for more than a century and has appeared in numerous publications, so there is ample justification for maintaining prevailing usage (ICZN 1999, Article 23.9).

Distribution and biology

This is a wide-ranging species found from India and Sri Lanka east to mainland China and Taiwan, and south through Southeast Asia to northern Australia (Fig. 183). It occupies a broad range of habitats including primary rainforest, secondary rainforest, montane rainforest, broad-leaved evergreen forest (in the Himalayan foothills), oak-pine forest, bamboo forest, tropical dry forest, riparian forest, mangrove, rubber plantation, roadside, and urban parkland. I have collected colonies in dead twigs of *Citharexylum spinosum*, *Clerodendrum disparifolium*, *Delonix regia*, *Gliricidia sepium*, *Hibiscus tiliaceus*, *Mallotus* sp., *Passiflora* sp., and *Vitex pubescens*. There are also records from dead twigs of *Sonneratia* and from leaf sheathes and twig internodes of *Gigantochloa* species. Some colonies in *Gigantochloa* leaf sheathes contain Coccoidea (A. Schellerich-Kaaden personal communication). *Tetraponera allaborans* undoubtedly utilises preformed cavities of a wide variety of other plant species.

Tetraponera apiculata, sp. nov.

(Figs 9, 20, 46)

Type material examined

Holotype. Worker, Danum Valley, Sabah, Malaysia, xi.1986 (P. Eggleton) (BMNH).

Paratypes. 2 workers, same data as holotype (PSWC, UMSC).

Worker measurements ($n = 3$)

HW 0.80–0.82, HL 0.95–1.01, LHT 0.68–0.71, CI 0.82–0.84, FCI 0.10–0.11, REL 0.36–0.37, REL2 0.44–0.45, SI 0.60–0.61, SI3 1.34–1.37, FI 0.46–0.47, PLI 0.51–0.53, PWI 0.40–0.43, PDI 0.97–1.02, LHT/HW 0.84–0.88, CSC 2, MSC 3–4.

Worker description

Median clypeal lobe narrow and triangular, the slightly crenulate sides converging to a blunt point, the apex of which exceeds the reach of the anterolateral margins of the clypeus, when head is in full-face, dorsal view (Fig. 9); eyes of modest size (see indices); profemur short and broad (FI >0.45); pronotal dorsum rounding broadly into the sides; mesopropodeal impression with irregular longitudinal rugulation, interrupted in the middle by a small, raised, transverse welt (apparent metanotum); propodeum relatively low and broad (see PDI values), in profile its dorsal face rounding gradually into the declivitous face (Fig. 46); in posterior view outline of propodeum approximating an equilateral triangle, with rounded apex; petiole relatively long and narrow (PWI 0.40–0.43; DPW/MTW 0.61–0.64). Integument smooth and shining, with scattered punctulae and fine, irregular lineations; lower malar area longitudinally carinate; metapleuron with a few weak, longitudinal carinulae. Standing pilosity (>0.07 mm in length) sparse, scattered on gaster and apex of head, also one supraocular pair, two pairs on the pronotum, and one pair on the postpetiole; a much shorter (<0.05 mm), less conspicuous, subdecumbent pilosity scattered over the body, becoming suberect to erect in places, especially on the petiole and postpetiole; these shorter hairs usually separated by their lengths or more, and not obscuring the sheen of the integument. Black, with the scapes, frontoclypeal complex, mandibles and legs dark brown to medium brown.

Discussion

Tetraponera apiculata is at once recognised by the distinctive shape of the median clypeal lobe (Fig. 9). It belongs to a group of species in which the pronotum is broadly rounded (not marginate) laterally, the mesosoma dorsum has a metanotal welt, and the profemur is short and broad. It differs from the other species with these characteristics (*T. avia*, *T. bita*, *T. brevis*) by the protruding pointed clypeus, narrower petiole, and perhaps by the slightly smaller eyes (EL/LHT 0.51–0.53, compared with 0.56–0.58 in the other three species; $n = 3$ and 7 workers, respectively).

Distribution and biology

The type specimens were collected at a forested site in the Danum Valley, Sabah.

Tetraponera avia, sp. nov.

(Figs 10, 21, 44–45)

Type material examined

Holotype. Worker, Pasoh Forest Reserve, Negeri Sembilan, Malaysia, 16.ii.1992 (Rosciszewski FN 1442) (SMNK).

Other material examined

Provisionally identified as *T. avia*: **Malaysia:** *Selangor*: Ulu Gombak, 30 km NE Kuala Lumpur, 240–500 m (A. Schellerich) (1 alate queen) (PSWC).

Worker measurements ($n = 1$)

HW 0.82, HL 0.89, LHT 0.66, CI 0.92, FCI 0.10, REL 0.42, REL2 0.45, SI 0.60, SI3 1.32, FI 0.44, PLI 0.51, PWI 0.43, PDI 1.04, LHT/HW 0.81, CSC 3, MSC 2.

Worker description

Anterior clypeal margin weakly convex medially, edentate, and non-protruding, the anterior-most point of the clypeus occurring at the lateral corners, not medially (Fig. 10); head broad (CI 0.92), with large eyes; profemur moderately robust; pronotum not laterally margined, and in posterior view the dorsal surface of the pronotum rounding very broadly into the sides (Fig. 21); a small but distinct, raised metanotal welt present, followed by a longitudinally rugulate metanotal groove and also preceded by a similar transverse groove or impression (Fig. 44); propodeum relatively low and broad, in profile the dorsal face rounding insensibly into the declivitous face; petiole slender (see petiolar indices). Integument mostly smooth and shining, with fine, irregular lineations; lower malar area longitudinally carinate; mesopleuron and metapleuron covered with fine, longitudinal carinulae. Excepting hairs on the clypeal margin, mandibles, and gastric apex, long (>0.10 mm) erect setae sparse, distributed as follows: one pair on the frontal carinae, one supraocular pair plus one extra seta on left side, one pair on the pronotal humeri, and about 6–8 setae on abdominal segments 4 and 5; a less conspicuous subdecumbent to suberect pilosity (with most hairs <0.05 mm long) scattered over the body. Black, mandibles and other appendages dark to medium brown.

Discussion

This appears to be a taxonomically isolated species in the *allaborans*-group, easily distinguished from *T. allaborans* and relatives by the weakly convex and non-protruding median portion of the clypeus, by the laterally rounded pronotum, and by the presence of a metanotal welt. Among species possessing the last two characteristics, *T. avia* can be recognised by its broad head, large eyes, edentate clypeus, slender petiole, and carinulate sculpture on the mesopleuron and metapleuron.

An isolated alate queen from Ulu Gombak, Selangor, Malaysia (A. Schellerich #17.3.3) (PSWC) might belong to this species. It is a member of the *allaborans*-group, with a large and relatively broad head (HW 1.07, CI 0.83), edentate and medially retracted clypeus, laterally rounded pronotum, and carinulate pleura.

Distribution and biology

Known definitely only from Pasoh Forest Reserve, Malaysia, a lowland rainforest site. The holotype was collected on twigs at 12–15 m height. The putative queen from Ulu Gombak was collected in a twig internode of *Gigantochloa scortechinii*.

Tetraponera bita, sp. nov.

(Figs 11, 22, 47)

Type material examined

Holotype. Worker, Kota Kinabalu, Sabah, Malaysia, 20m, 5°59′S 116°04′E, 9.x.1978 (B. B. Lowery) (ANIC).

Paratypes. 1 worker, 1 alate queen, same data as holotype (ANIC, UMSC).

Other material examined

Brunei: Labi (I. Gauld) (1 worker) (BMNH).

Provisionally identified as *T. bita*: **Malaysia:** *Negeri Sembilan*: Pasoh Forest Reserve (K. Rosciszewski) (1 dealate queen) (SMNK).

Worker measurements ($n = 3$)

HW 0.63–0.65, HL 0.86–0.87, LHT 0.55–0.56, CI 0.73–0.75, FCI 0.12–0.13, REL 0.35–0.37, REL2 0.48–0.49, SI 0.58–0.59, SI3 1.19–1.21, FI 0.47–0.53, PLI 0.58–0.62, PWI 0.47–0.53, PDI 0.99–1.00, LHT/HW 0.85–0.86, CSC 2, MSC 2. Note: $n = 2$ for LHT and LHT/HW.

Worker description

Median clypeal lobe crenulate, with about five blunt denticles, protruding slightly beyond the reach of the anterolateral clypeal margins; clypeal lobe somewhat broad and less sharply set off from the rest of the clypeus than in *T. allaborans* (Fig. 11); eyes moderately large, especially in relation to head width (see REL2 values); profemur short and broad (FI >0.46); pronotal dorsum rounding broadly into the sides; mesopropodeal impression relatively shallow, interrupted in the middle by a small, raised, transverse platform (apparent metanotum), which is joined to lateral ridges that arch forward; metanotum preceded and followed by longitudinally rugulate grooves, the posterior groove more deeply impressed than the anterior groove; propodeum low and broad, as wide as high (see PDI values), in profile its dorsal face rounding gradually into the declivitous face; petiole relatively short and broad (see indices). Integument smooth and shining, with scattered minute punctures (<0.010 mm in diameter) and very faint irregular lineations; lower malar area longitudinally carinate anteriorly. Standing pilosity (>0.07 mm in length) sparse, scattered on gaster and apex of head, also one supraocular pair, and one pair on the pronotum; 1–2 shorter standing hairs (0.05–0.07 mm in length) on the petiole and postpetiole; in addition, short (0.02–0.05 mm), sparse, inconspicuous appressed hairs scattered over the body, becoming suberect to erect on venter of the petiole and postpetiole. Medium to dark brown, antennae, mandibles and tarsi somewhat lighter.

Discussion

Workers of *T. bita* can be distinguished from those of other species, except *T. brevis*, by their broadly convex, crenulate and slightly protruding clypeal lobe (Fig. 11); short, robust

profemur; laterally rounded pronotum; and presence of a metanotal welt. The most striking difference between *T. bita* and *T. brevis* is the broader head of the latter (worker CI 0.82–0.84). For discussion of additional differences, see *T. brevis*.

There is one collection of a dealate queen from Pasoh Forest Reserve, Malaysia (leg. Rosciszewski) that matches reasonably well the paratype queen of *T. bita*, especially with respect to the clypeal margin (furnished with a pair of long, blunt mediolateral teeth and a much shorter, pointed median tooth, as in the *bita* paratype queen), elongate head (CI 0.62 compared with 0.60 in the paratype), broad profemur (FI 0.54, as in paratype), and slender petiole (PLI 0.54 compared with 0.55 in the paratype), although the Pasoh queen is larger (HW 0.68 *v.* 0.61 in the paratype). The elongate head and slender petiole suggest that this queen is *T. bita*, not the related species, *T. brevis*, described below.

Distribution and biology

Known from two localities on the island of Borneo and one probable site on peninsular Malaysia. Lowery's Kota Kinabalu material was collected in 'gardens and relict rain forest'. The queen from Pasoh Forest Reserve was collected 'in a dead twig in *c.* 32 m height'.

Tetraponera brevis, sp. nov.

(Figs 12, 23, 48)

Type material examined

Holotype. Worker, Pasoh For. Res., Negeri Sembilan, Malaysia, xi.1994 (M. Brendell, K. Jackson & S. Lewis) (BMNH).
Paratype. 1 worker, same data as holotype (ANIC).

Other material examined

Malaysia: *Negeri Sembilan*: Pasoh Forest Reserve (K. Rosciskewski) (2 workers) (PSWC).

Worker measurements (*n* = *4*)

HW 0.73–0.75, HL 0.86–0.91, LHT 0.59–0.62, CI 0.82–0.84, FCI 0.11–0.12, REL 0.37–0.39, REL2 0.45–0.47, SI 0.58–0.59, SI3 1.25–1.30, FI 0.49–0.52, PLI 0.63–0.67, PWI 0.48–0.51, PDI 0.98–1.04, LHT/HW 0.81–0.83, CSC 2, MSC 2.

Worker description

Similar to *T. bita* except as follows: larger species (compare HW and LHT values), with broader head (CI >0.80); median clypeal lobe less protruding, so that the anterolateral margins of the clypeus equal or exceed the reach of the median lobe, when head is seen in full-face view; eye shorter in relation to scape length (SI3 >1.23); pronotal dorsum rounding less gradually into the sides; mesopropodeal impression more deeply excavated, due to more elevated propodeum; metanotal welt a little less clearly defined; petiole slightly shorter and higher (compare PLI values); integument sculpture a little more strongly defined, although body still predominantly smooth and shining; short suberect to erect pilosity better developed, notably on head venter; darker in color, the body essentially black, with dark brown appendages.

Discussion

Tetraponera brevis appears to be closely related to *T. bita* and given that existing collection records for the workers come from different regions—peninsular Malaysia and Borneo, respectively—they might be interpreted as allopatric variants of a single species. However, the differences in size, head shape, configuration of the clypeus, form of the pronotum and mesopropodeal impression, petiole shape, pilosity and color are together quite suggestive. Moreover, if the putative queen of *T. bita* from Pasoh (discussed above, under *T. bita*) has been correctly identified it establishes a sympatric occurrence of that species and *T. brevis* on the mainland.

Distribution and biology

Known only from lowland forest (Pasoh Forest Reserve) in peninsular Malaysia.

Tetraponera conica, sp. nov.

(Figs 14, 25, 52)

Type material examined

Holotype. Worker, Semengoh For. Reserve, 11 mi. SW Kuching, Sarawak, Malaysia, 28–31.v.1968 (R. W. Taylor #68.166) (ANIC).

Worker measurements (*n* = *1*)

HW 0.64, HL 0.76, LHT 0.53, CI 0.85, FCI 0.09, REL 0.42, REL2 0.49, SI 0.61, SI3 1.24, FI 0.39, PLI 0.63, PWI 0.54, PDI 1.09, LHT/HW 0.83, CSC 2, MSC 4.

Worker description

Small with relatively broad head and large eyes; median clypeal lobe prominent but narrow, its straight anterior margin with three denticles; clypeal lobe exceeding the reach of the anterolateral clypeal margins; sides of head convex, rounding insensibly into the posterior margin (Fig. 14); profemur slender; pronotal margins broadly convex in dorsal view, soft-edged, and occurring at the maximum width of pronotum; mesopropodeal impression well marked, lacking a metanotal plate; propodeum conical in profile, the prominent apex situated far forward and raised above the level of the mesonotum, so that the short posteriorly inclined dorsal face of the propodeum rounds into a much longer, sloping declivitous face (Fig. 52); petiole short and broad (PWI 0.54, PL/HW 0.60, PL/LHT 0.72), in profile

subtriangular and lacking a well differentiated anterior peduncle. Integument smooth and shiny, with scattered small punctures and irregular lineations; lower malar area longitudinally carinate. Standing pilosity scarce, one pair of long setae (>0.07 mm in length) on the frontal carinae, one supraocular pair, two pairs on the pronotum, and one pair on the postpetiole; short, inconspicuous pubescence scattered over the body. Castaneous brown, the pronotum, postpetiole and appendages a lighter yellow-brown to orange-brown.

Discussion

This is a small, brown species in the *allaborans*-group, which can be distinguished from all other known *Tetraponera* by the peculiar conical shape of the propodeum (Fig. 52). In view of the uniqueness of the only known specimen, one might speculate that it is an anomalous mutant. But comparison of *T. conica* with its close relatives in the *T. modesta*-complex reveals additional, more typical species-level differences, such as larger eyes, a broadly rounded head, and a shorter petiole.

Distribution and biology

Known only from Sarawak, Malaysia. The collection was made in a remnant patch of lowland rain forest (R. W. Taylor personal communication).

Tetraponera connectens, sp. nov.

(Figs 13, 24, 49)

Type material examined

Holotype. Worker, Khao Lak Natl Pk, Thone Chong Fa Fall, Thailand, 300 m, 8°40′N 98°18′E, 15–16.i.1998 (A. Schulz & K. Vock) (BMNH).

Paratypes. 5 workers, same data as holotype (KUBC, NHMV, PSWC).

Worker measurements ($n = 5$)

HW 0.58–0.63, HL 0.77–0.84, LHT 0.50–0.52, CI 0.73–0.78, FCI 0.12–0.13, REL 0.32–0.34, REL2 0.44–0.45, SI 0.57–0.58, SI3 1.29–1.33, FI 0.47–0.48, PLI 0.56–0.61, PWI 0.43–0.46, PDI 0.97–1.04, LHT/HW 0.83–0.87, CSC 2, MSC 4.

Worker description

Median clypeal lobe narrow, protruding beyond the reach of the anterolateral clypeal margins, and furnished with three blunt teeth (Fig. 13); eyes rather small (REL <0.35); profemur short and broad (FI >0.46); pronotal dorsum rounding into the sides, sharp lateral margins lacking; mesopropodeal impression with a very weak transverse ridge (obsolete in three of the workers) which interrupts the longitudinally rugulate sculpture but does not form a distinct metanotal plate; propodeum low and broad, as wide as high (see PDI values), in profile its dorsal face convex and rounding rather gradually into the declivitous face; petiole relatively short and broad (see indices). Integument smooth and shining, with scattered fine punctures (<0.01 mm diameter) and faint irregular lineations; lower malar area longitudinally carinate, only immediately above the mandibular insertions. Standing pilosity (>0.06 mm in length) sparse, scattered on gaster and apex of head, and as follows: one supraocular pair, two pairs on the pronotum, and one pair each on the petiole and postpetiole; sparse, inconspicuous appressed hairs scattered over the body, becoming suberect to erect on venter of the petiole and postpetiole. Black to dark brownish-black; antennae, mandibles, tarsi and (to a lesser extent) tibiae lighter brown.

Discussion

This species bears some similarity to *T. bita*, especially with respect to the short scapes, elongate head, laterally rounded pronotum, broad profemur, and small size, but it lacks the distinct metanotal plate and broadly convex median clypeal lobe of that species. *T. connectens* workers differ from those of both *T. bita* and other small black species (*T. extenuata*, *T. microcarpa*) by their smaller eyes (REL 0.32–0.34, *v.* 0.35–0.41 in the other three species). In addition, workers of *T. microcarpa* have much sharper lateral pronotal margins and those of *T. extenuata* have longer scapes (SI2 0.47–0.54), a more slender profemur (FI 0.38–0.43), and more elevated propodeum (PDI 1.12–1.24) compared with those of *T. connectens*. The smallest workers of *T. allaborans* approach the known size range of *T. connectens* (for *T. allaborans* HW 0.62–0.93 and LHT 0.54–0.80) but have larger eyes (EL 0.30–0.42 compared with 0.26–0.27 in *T. connectens*), longer scapes (SI2 0.46–0.57 *v.* 0.42–0.45) and a more slender profemur (FI 0.36–0.45 *v.* 0.47–0.48; FL/HL 0.58–0.67 *v.* 0.52–0.56 in *T. connectens*), in addition to better developed pronotal margins.

Distribution and biology

Known from only from the type locality. The types were collected from canopy fogging of semi-primary dipterocarp hilltop forest.

Tetraponera crassiuscula (Emery), stat. nov.

(Figs 15, 26, 35, 53)

Sima allaborans subsp. *crassiuscula* Emery, 1900: 677.

Sima (*Tetraponera*) *allaborans* subsp. *crassiuscula* Emery; Viehmeyer, 1916: 117.

Tetraponera (*Tetraponera*) *allaborans* var. *crassioscula* [sic] (Emery); Chapman and Capco, 1951: 78. First combination in *Tetraponera*.

Type material examined

Sima allaborans subsp. *crassiuscula* Emery. Syntypes, 2 workers, D. Tolong, Sumatra, Indonesia (E. Modigliani) (MCSN).

Other material examined

Indonesia: *Sumatera Barat*: Bukittinggi [as 'Fort de Kock'] (E. Jacobson); Limau Manis, nr Padang (S. Yamane). **Malaysia:** *Negeri Sembilan*: Pasoh For. Res. (M. Brendell *et al.*); Pasoh Forest Reserve (K. Rosciszewski); *Sarawak*: 2 km N Santubong (S. L. Heydon; S. Fung); *Selangor*: Kepong (U. Maschwitz). **Thailand:** *Surat Thani*: Khao Sok Natl Pk (A. N. Andersen).

(Collections: BMNH, KUES, MCZC, PSWC, SMNK).

Additional material, provisionally identified as *T. crassiuscula*: **Malaysia:** *Sabah*: Quoin Hill, Tawau (Y. Hirashima) (ANIC); Umas Umas, nr Tawau (R. W. Taylor) (ANIC).

Worker measurements ($n = 6$)

HW 0.53–0.61, HL 0.66–0.73, LHT 0.45–0.52, CI 0.73–0.84, FCI 0.08–0.11, REL 0.36–0.40, REL2 0.46–0.50, SI 0.60–0.66, SI3 1.24–1.36, FI 0.40–0.43, PLI 0.60–0.68, PWI 0.46–0.54, PDI 1.14–1.26, LHT/HW 0.81–0.91, CSC 1–10, MSC 1–19.

Worker description

Small species; median clypeal lobe narrow but moderately prominent, furnished with three blunt denticles; anterior margin of clypeal lobe slightly exceeding the reach of the anterolateral margins of the clypeus; profemur slender; lateral margins of pronotum soft-edged, convex in dorsal view, and corresponding to the maximum width of pronotum; mesopropodeal impression deep but somewhat short (from anterior to posterior ends), lacking metanotal plate; propodeum high and narrow, such that PDI >1.12; petiole relatively short, with a prominent node (PL 0.38–0.46, PL/SL 1.09–1.19; see also PLI and PWI values). Integument smooth and shiny, with scattered fine punctures (*c.* 0.01 mm diameter) and fine irregular lineations; lower malar area longitudinally carinate; weak carinulae variably developed (may be absent) on side of posterior mesosoma. Pilosity variable (MSC 1–19), but tending to be more common than in related taxa; some workers with four or more standing hairs (>0.05 mm in length) visible in profile on each of the following: dorsum of head, pronotum, mesonotum, petiole and postpetiole; such setae grading into shorter decumbent and appressed hairs; in other specimens standing pilosity much sparser (or abraded). Dark brown, with lighter brown petiole, postpetiole, pronotum and appendages; legs concolorous medium brown.

Discussion

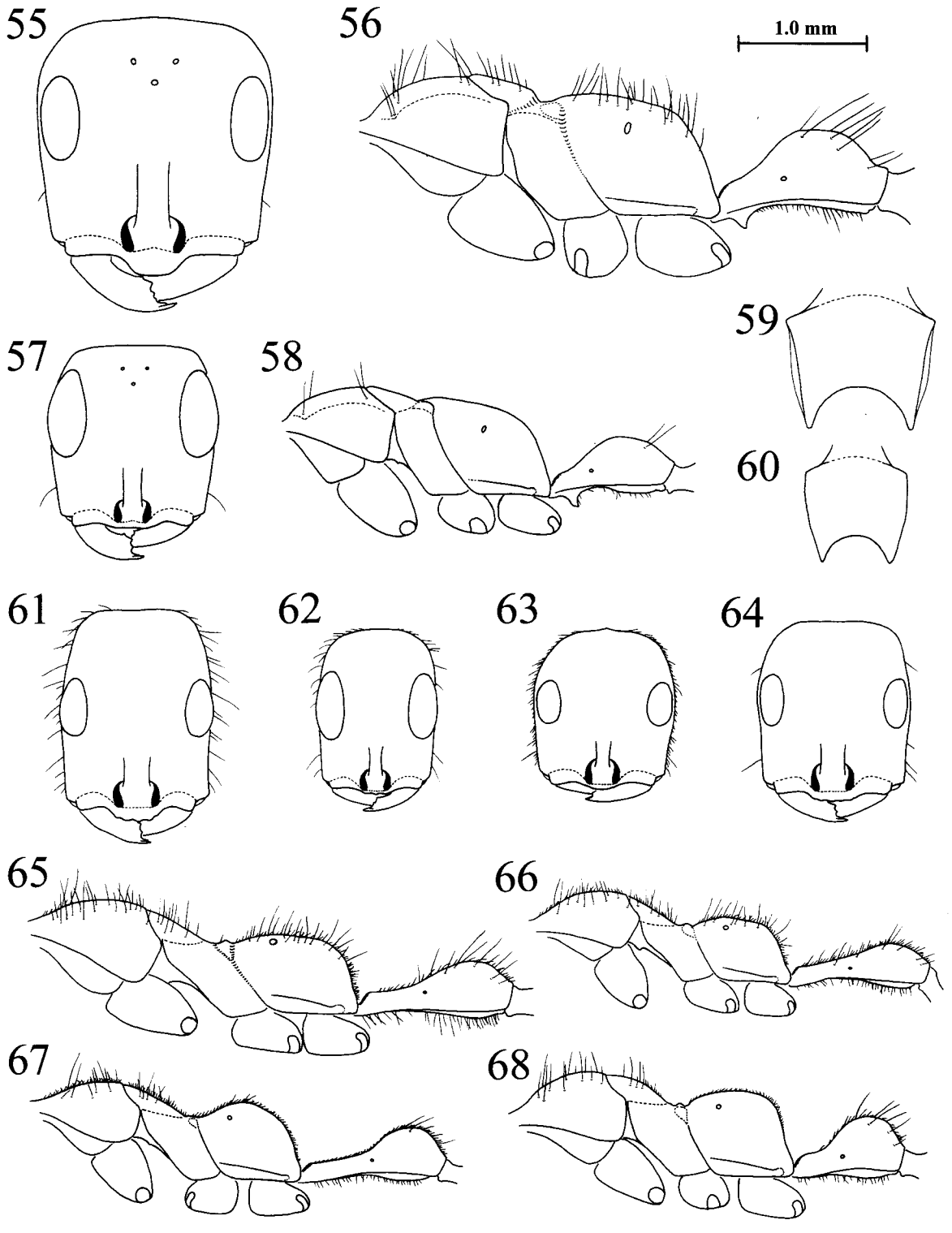
Tetraponera crassiuscula belongs to a group of closely related taxa, here termed the *T. modesta*-complex. Three morphotypes can be tentatively recognised: *T. crassiuscula*, a dark brown form with a short, broad petiole (worker PLI 0.60–0.68); *T. modesta*, a smaller, yellow or orange-brown species, with more slender petiole (PLI 0.45–0.59); and *T. extenuata*, similar to *T. modesta* but with relatively large, mostly black workers. Sympatric associations of at least two of the three forms are known from some localities (Bukit Timah, Singapore: *T. extenuata* and *T. modesta*; Pasoh Forest, Malaysia: *T. crassiuscula*, *T. extenuata* and *T. modesta*; Poring Spring, Malaysia: *T. extenuata* and *T. modesta*), suggesting that they represent good species. Not all collections can be easily assigned to one of these three taxa, however.

The two syntype workers of *T. crassiuscula* from Sumatra agree reasonably well with material from the Malay Peninsula that I am considering conspecific. One of the syntypes has the following approximate measurements and indices: HW 0.59, HL 0.74, PrWM 0.38, PL 0.44, PDI 1.26, PLI 0.61, PWI 0.48. This syntype lacks the conspicuous mesosomal setae seen in the peninsular populations, but the pilosity may have been abraded because there is very little evident on any part of the body except the mandibles, clypeal lobe and scapes. The second syntype has more standing pilosity, including minute suberect (curved) hairs on the upper body surface, as well as a few conspicuous longer hairs on the pronotum, petiole and gaster. The coloration of the *T. crassiuscula* syntypes is dark castaneous brown, with lighter brown petiole and postpetiole, and luteous mandibles and antennae.

Accepting that both the Sumatran and peninsular populations do indeed represent *T. crassiuscula*, we are faced with two problematic workers from Borneo (Sabah), which have short petioles (PLI 0.62) but little standing pilosity (MSC 1–3). One of these workers, from Umas Umas near Tawau (leg. Taylor) (ANIC), is medium to dark brown with contrastingly light yellow-brown postpetiole and tibiae; the other specimen, from Quoin Hill, Tawau (leg. Hirashima) (ANIC) is reddish brown with a dark brown gaster. In coloration these Bornean workers begin to approach workers of *T. extenuata* and *T. modesta*, respectively. Additional samples, especially worker-associated queens and males, might help to resolve the relationship between these closely related forms. Ultimately it may be necessary to conduct a genetic analysis of the populations to determine the extent of gene flow.

Distribution and biology

As interpreted here, *T. crassiuscula* is known from Thailand, peninsular Malaysia, Sumatra, and Borneo. Very little is known about its biology. A collection from Kepong, Malaysia (leg. Maschwitz) was made from twigs of Rhizophoraceae. The worker from Umas Umas, Borneo was taken 'ex trunks, tops, recently felled trees, rainforest'.



Figs 55–68. *Tetraponera* workers, full-face view of head (*55*, *57*, *61–64*), lateral view of mesosoma and petiole (*56*, *58*, *65–68*), and dorsal view of pronotum (*59–60*). *55–56*, *59*, *T. rufonigra* (Singapore); *57–58*, *60*, *T. pilosa* (Malaysia); *61*, *65*, *T. binghami* (Malaysia); *62*, *66*, *T. buops*, holotype (Brunei); *63*, *67*, *T. attenuata* (Malaysia); *64*, *68*, *T. nigra* (India).

Tetraponera extenuata, sp. nov.

(Figs 16, 27, 33, 39, 50)

Type material examined

Holotype. Worker, Bukit Timah, Singapore, 100 m, 1°21′N 103°47′E, 20.xi.1988 (P. S. Ward #9570) (BMNH).

Paratypes. Series of workers, 1 dealate queen, same data as holotype (ANIC, KUBC, KUEC, KUES, MCZC, PSWC, RMBR, UASK, UCDC, UMSC).

Other material examined

Brunei: Bukit Sulang, nr Lamunin (N. E. Stork). **Indonesia:** *Lampung*: Liwa (1984 Zool. Expd.); *Nusa Tenggara Barat*: Sesaot, Lombok I. (Imai *et al.*); *province unknown*: 'Java' (Jakobson). **Malaysia:** *Negeri Sembilan*: Pasoh For. Res. (M. Brendell *et al.*); Pasoh Forest Reserve (K. Rosciszewski); *Pahang*: Tanah Rata, Cameron Highlands (Windschnurer); *Perak*: 'Perak' (Staudinger); *Sabah*: Bundu Tuhan, 6 km S Mt Kinabalu Natl Pk, 1070 m (B. B. Lowery); Danum Valley (H. Ôkido); Danum Valley (E. Widodo); Forest Camp, 19 km N Kalabakan, 180 m (Y. Hirashima); Poring Spring, >650 m (A. Floren); Poring, Kinabalu, HQ, 550 m (S. Yamane); Sg. Kalang, Tenom, 800–1000 m (S. Yamane); Sipitang, Mendolong (S. Adebratt); Umas Umas, nr Tawau (R. W. Taylor); *Sarawak*: Bt. Lambir, Lambir Natl Pk, Miri (J. Otsubo); Buda Camp, sw. Gn. Buda, 64 km S Limbang (S. L. Heydon; S. Fung); G. Mulu Natl Pk (V. F. Eastop); G. Mulu Natl Pk (B. Bolton); Merirai Valley, nr Kapit, 30–300 m (T. C. Maa); Sadong, Kampong Tapuh, 300–450 m (T. C. Maa); Semengoh For. Reserve, 11 mi SW Kuching (R. W. Taylor); SW of Tapuh (T. C. Maa); *Selangor*: Bunga Bua, Genting Highlands, W Kuala Lumpur (W. Dorow); Bunga Buah, nr Genting H.L., 1000 m (S. Yamane); Ulu Gombak Field Stn. (A. Buschinger); *Terengganu*: P. Perhentian Besar (Windschnurer). **Philippines:** *Bukidnon*: Malaybalay, Kaamulan Site, 650 m (H. Zettel); *Laguna*: Los Banos, Mt Makiling, 600 m (B. B. Lowery); Los Banos, Mt Makiling, 800 m (B. B. Lowery); Mt Makiling, nr Mud Spring, 400 m (W. L. Brown); *Mindanao*:11 km W Alanib, 1160 m (B. B. Lowery); Talacogon (B. B. Lowery); *Quezon*: Atimonan, Quezon NP, Old Zigzag Rd. (H. Zettel); Quezon Natl Pk, 5 km NW Malicboy, 400 m (D. M. Olson). **Singapore**: Bukit Timah, 100 m (P. S. Ward); Kent Ridge (D. H. Murphy); Pierce Reservoir, 40 m (P. S. Ward). **Thailand:** *Nakhon Ratchasima*: Sakaerat Exp. Sta. (I. Franz).

(Collections: AMNH, ANIC, ASIC, BMNH, HZIC, KUES, LACM, MCZC, MHNG, MZLU, NHMB, NHMV, PSWC, RMBR, SMNK, UMSC).

Additional material, provisionally identified as *T. extenuata*: **Indonesia:** *Bali*: Kintamani (W. Dorow) (PSWC); *Sulawesi*: Tengah Kebung Kopi, near Palu (S. Yamane) (KUES). **Malaysia:** *Sabah*: Forest Camp, 19 km N Kalabakan, 180 m (Y. Hirashima) (ANIC).

Worker measurements ($n = 16$)

HW 0.54–0.79, HL 0.70–0.95, LHT 0.45–0.74, CI 0.76–0.87, FCI 0.08–0.13, REL 0.36–0.41, REL2 0.44–0.51, SI 0.60–0.65, SI3 1.18–1.43, FI 0.38–0.43, PLI 0.47–0.59, PWI 0.38–0.48, PDI 1.12–1.24, LHT/HW 0.84–0.94, CSC 1–2, MSC 3–4.

Worker description

Small to medium-sized species; median clypeal lobe narrow, distinctly set off from the rest of the clypeal margin, and furnished with three weak denticles (sometimes effaced); anterior margin of clypeal lobe variably extended, often rather short and not exceeding the reach of the anterolateral clypeal margins, but more protruding in some workers; profemur slender; lateral margins of pronotum soft-edged, convex in dorsal view, and corresponding to the maximum width of pronotum; mesopropodeal impression well developed, longitudinally rugulate, and lacking metanotal plate; propodeum high and narrow (Fig. 39), such that PDI >1.10; petiole relatively slender (see PLI and PWI values). Integument smooth and shiny, with scattered fine punctures (*c.* 0.01 mm diameter) and fine irregular lineations; malar area longitudinally carinate, such sculpture usually covering less than half the distance between the mandibular insertions and the lower margin of the compound eye; a few weak longitudinal carinulae may be present on the mesopleuron, metapleuron and side of propodeum. Standing pilosity sparse; long standing hairs (>0.06 mm) present on gaster and apex of head and as follows: one supraocular pair, two pairs on pronotum, 0–1 pair on petiole and 0–1 pair on postpetiole; shorter appressed and subdecumbent hairs scattered over body, tending to becoming suberect ventrally, especially on petiole and postpetiole. Typically black or dark brownish-black, with contrasting lighter (yellow or orange-brown) postpetiole, tibiae, tarsi, and scapes; lighter coloration may also extend to the petiole, base of abdominal tergite IV, profemur, frontoclypeal complex and mandibles.

Discussion

This species is superficially similar to small specimens of *T. allaborans*, especially those in which the appendages and postpetiolar node are lighter in color than the rest of the body (see discussion of 'variant 2' under *T. allaborans*). However, workers of *T. extenuata* can be consistently separated from those of *T. allaborans* by the taller and more slender propodeum (compare Figs 38 and 39, and PDI values). In addition the pronotal margins are more convex (dorsal view) and soft-edged than in most *T. allaborans*, and the maximum width of the pronotum occurs at the pronotal margins (Fig. 27), not below the margins as in many *T. allaborans* (Fig. 19).

More problematic is the relationship of *T. extenuata* to *T. modesta*. These two are rather similar with respect to the shapes of the pronotum, propodeum and petiole. *T. extenuata* averages larger in size and is much darker in coloration than 'typical' orange-yellow *T. modesta*. Moreover, in *T. extenuata* workers there is usually a strong contrast between the dark body and orange-brown postpetiole, and between the dark brown femora and pale yellow (or cream) tibiae. But color is variable, and in some workers of *T. extenuata* from Borneo (Sabah) and the Philippines the postpetiole is dark brown and does not contrast with the rest of the body. In these individuals the legs are nevertheless conspicuously bicolored. Conversely, in a series of workers from Kintamani, Bali (leg. Dorow), tentatively identified as *T. extenuata*, the postpetiole exhibits a contrasting orange-

brown color, but the legs are uniformly dark brown! Many samples of *T. extenuata* consist of relatively large workers (HW >0.65) and these can be separated from *T. modesta* by size alone. But workers at the lower size limit of *T. extenuata* (HW 0.54–0.65) can be difficult to distinguish from some samples of *T. modesta*, in which there is a darkening of the integument. See further discussion under *T. modesta*.

Distribution and biology

Tetraponea extenuata is found from Thailand and peninsular Malaysia east to the Philippines and south to the lesser Sundas (Bali and Lombok) (Fig. 187). Habitats from which it has been recorded include primary and secondary growth lowland rainforest (Singapore, Borneo, Luzon), lower montane mixed dipterocarp forest (Borneo), and 'relict rainforest' (Mindanao). Two nest series from Singapore are from dead twigs of *Timonius* sp. and *Rhodamnia trinervia*, respectively. Most other collections consist of foraging workers on low vegetation or specimens taken in fogging samples.

Tetraponera microcarpa Wu & Wang

(Figs 18, 29, 36, 51)

Tetraponera microcarpa Wu and Wang, 1990: 515.

Types (not examined)

Tetraponera microcarpa Wu and Wang. Holotype, worker, Taishan County, Guangdong, China (Wu Jian); paratypes: 24 workers, same data as holotype; 2 workers, Fenyi County, Jiangxi, China (Wang Changlu) (CFRB) [not examined].

Material examined

China: *Guangxi*: Nong Gang Natural Reserve, 600 m (S. Zhou); *Hong Kong*: N.T.: campus C.U.H.K., Shatin, 20 m (R. R. Snelling); N.T.: Shing Mun (J. R. Fellowes); N.T.: Tai Lung Farm, Sheung Shui (S. Yamane). **Vietnam:** *Ha Sonh Binh*: Da Bac, Tuly (Belokobylskij); Ky Son, Cao Phong (Belokobylskij).

(Collections: KUES, LACM, PSWC, ZMAS).

Worker measurements (n = 10)

HW 0.60–0.64, HL 0.73–0.83, LHT 0.46–0.51, CI 0.76–0.83, FCI 0.09–0.12, REL 0.36–0.40, REL2 0.46–0.50, SI 0.52–0.57, SI3 1.10–1.20, FI 0.42–0.48, PLI 0.53–0.59, PWI 0.44–0.48, PDI 1.01–1.15, LHT/HW 0.76–0.83, CSC 0–2, MSC 3–4.

Worker description

Small species (HW <0.66), with somewhat elongate head (CI <0.85) and large eyes (REL2 >0.45); median clypeal lobe narrow, protruding moderately, its anterior margin concave and furnished with a pair of blunt lateral teeth, whose anterior reach exceeds that of the anterolateral clypeal margins; scape relatively short (see indices); profemur somewhat short and broad; lateral pronotal margins sharp-edged; pronotum narrow in dorsal view (PrWM/HW 0.56–0.62; PrWM/MTW 1.14–1.21), with margins that are straight and diverge only slightly anteriorly (Fig. 36); in posterior view, pronotum appearing relatively flat (Fig. 29); mesopropodeal impression longitudinally rugulate, lacking a metanotal plate; propodeum generally low and broad, PDI ~ 1.04 (somewhat more elevated in workers from Vietnam, where PDI ~ 1.10); in profile, propodeum appearing almost quadrate, the dorsal face somewhat flattened, and rounding rather suddenly into the straight declivitous face; petiole relatively short and high (see PLI and PWI values). Integument smooth and shiny, with scattered punctures and fine irregular lineations; malar area rather extensively longitudinally carinate, such sculpture extending about two-thirds of the distance from the mandibular insertions to the lower margin of the compound eye. Pilosity sparse, long standing hairs (>0.05 mm in length) scattered on gaster and apex of head, and elsewhere as follows: one supraocular pair; two pairs on pronotum, and one pair each on petiole and postpetiole; much shorter, inconspicuous appressed hairs scattered over body, becoming suberect on venter of head and petiole. Black or brownish-black, with petiole, postpetiole and appendages generally lighter medium-brown.

Discussion

It has not been possible to examine the types of *T. microcarpa*, but among specimens that I have studied from China and Vietnam is a distinctive species that agrees closely with the original description of *T. microcarpa*. As I interpret it, this is a small, dark species superficially similar to *T. allaborans* but possessing shorter scapes in the worker (SI 0.52–0.57, SI2 0.41–0.44, SI3 1.10–1.20 *v.* 0.57–0.65, 0.46–0.57, and 1.21–1.53 in *T. allaborans*) and a more flattened (Fig. 29) and straight-sided pronotum (Fig. 36). Additionally, among the few small (HW <0.70) workers of *T. allaborans* that potentially overlap in size with those of *T. microcarpa*, the latter can be distinguished by their wider petiole relative to pronotal width and petiole length (DPW/PrWM 0.54–0.58 *v.* 0.47–0.51; PWI 0.44–0.48 *v.* 0.34–0.43), and shorter petiole relative to head length (PL/HL 0.56–0.59 *v.* 0.60–0.70).

Workers of *T. microcarpa* differ from those of the *T. modesta*-complex by their pronotal margins being more sharp-edged, subparallel, and closer to one another (PrWM/MTW 1.14–1.21 compared with 1.21–1.44 in the *T. modesta*-complex) (compare Fig. 36 with Figs 33–35), by the flatter pronotal dorsum (compare Fig. 29 with Figs 26–28), and by their shorter scapes (SI 0.52–0.57, SI2 0.41–0.44 *v.* 0.58–0.68 and 0.45–0.54). *Tetraponear microcarpa* workers are also darker in color than those of *T. modesta* and *T. crassiuscula*, and differ from *T. extenuata* workers by the shorter legs (LHT/HW 0.76–0.83 *v.* 0.84–0.94).

Also characteristic (but not absolutely diagnostic) of *T. microcarpa* workers are the bidentate median clypeal lobe (Fig. 18), which occurs occasionally in *T. allaborans* workers, and the broad profemur (FI 0.42–0.48, *v.* 0.36–0.45 in *T. allaborans* and 0.36–0.43 in the *T. modesta*-complex).

Distribution and biology

Records come from southern China and northern Vietnam (Fig. 187). Little information is available on the biology of *T. microcarpa*. In Hong Kong foraging workers were collected on a bamboo stalk on a wooded hillside (Roy Snelling personal communication).

Tetraponera modesta (F. Smith)

(Figs 17, 28, 34, 54)

Pseudomyrma modesta F. Smith, 1860: 106.
Sima (Tetraponera) fulva Viehmeyer, 1916: 117. **Syn. nov.**
Tetraponera pisarskii Radchenko, 1997: 480. **Syn. nov.**
Sima modesta (F. Smith); Dalla Torre, 1893: 54.
Tetraponera modesta (F. Smith); Donisthorpe, 1932: 462. First combination in *Tetraponera*.
Tetraponera (Tetraponera) fulva (Viehmeyer); Chapman and Capco, 1951: 80.

Type material examined

Pseudomyrma modesta F. Smith. Holotype (by monotypy), worker, Bachian [as 'Bac.'], Indonesia (OXUM).

Sima (Tetraponera) fulva Viehmeyer. Syntypes, 2 workers, Singapore (H. Overbeck) (MHNG, NHMB).

Tetraponera pisarskii Radchenko. Holotype, worker, Pyongyang, North Korea (B. Pisarski; J. Prószynski) (ZMPA).

Other material examined

Brunei: Andalau, 50 m (N. Mawdsley). **China:** *Fujian*: Foochow (L. Gressitt); *Guangdong*: Ding-Hu Mts., 60 km W Guangzhou (Boucek); Gutian (M. Wang); *Guangxi*: Da Yao Shan Natural Reserve, 600 m (S. Zhou); Fenzhan, Dayaoshan, 850 m (J. R. Fellowes); Huaping (J. R. Fellowes); *Hainan*: Ta Hian (J. L. Gressitt). **India:** *Manipur*: Imphal (T. Clay). **Indonesia:** *Bali*: Besakih (U. Maschwitz); no specific locality ['Bali'] (A. N. Andersen); *Kalimantan Selatan*: 17–46 km W Batulitjin (W. L. Brown); *Nusa Tenggara Barat*: Sapit, Lombok I. (Imai *et al.*); *Sulawesi Utara*: Dumoga-Bone Natl Pk, 400 m (N. Stork). **Malaysia:** *Negeri Sembilan*: Pasoh For. Res. (M. Brendell *et al.*); *Sabah*: Danum Valley (E. Widodo); Poring Spring, >650 m (A. Floren); Quoin Hill, Tawau (Y. Hirashima); *Sarawak*: G. Mulu Natl Pk (B. Bolton); Mulu (lowland) (S. Yamane); Semengoh For. Reserve, 11 mi SW Kuching (R. W. Taylor); sw Gunung Buda, 64 km S Limbang (S. L. Heydon; S. Fung). **Papua New Guinea:** *Central*: Karema, Brown R. (E. O. Wilson); *Gulf*: Ivimka camp, Lakekamu Basin, 200 m (R. R. Snelling); *Morobe*: lower Busu R., Huon Penn. (E. O. Wilson). **Philippines:** *Palawan*: Iwahig, Puerto Princesa (C. K. Starr). **Singapore:** Bukit Timah Forest (D. H. Murphy); Bukit Timah NaT. Res. (D. H. Murphy); Bukit Timah, 100 m (P. S. Ward). **Taiwan:** *Pingtung*: Kuraru (L. Gressitt). **Thailand:** *Satun*: Thale Ban Natl Pk, 20–30 km E Satun, 200–400 m (A. Schulz; K. Vock). **Vietnam:** *Ha Sonh Binh*: Da Bac, Tuly (Belokobylskij); *Vinh Phuc*: Tam Dao, 1000 m (Belokobylskij).

(Collections: ANIC, ASIC, BMNH, KFBG, KUES, LACM, MCZC, PSWC, RMBR, UMSC, ZMAS).

Additional material, provisionally identified as *T. modesta*: **Malaysia:** *Sabah*: Danum Valley (P. Eggleton) (BMNH); Poring Spring, >650 m (A. Floren) (PSWC); *Sarawak*: Tower Region, Lambir Natl Pk, Miri (S. Yamane) (KUES). **Philippines:** *Dumaguete*: Dumaguete (J. W. Chapman) (MCZC, PSWC); *Negros Oriental*: Dumaguete, Camp Lookout, 1500 ft (J. W. Chapman) (MCZC, PSWC); *Romblon*: Sibuyan, E Magdiwang W Silum, Lambigan Falls (H. Zettel) (HZIC); Tablas, S. Agustin, Dubduban Busai Falls (H. Zettel) (HZIC).

Worker measurements (n = 14)

HW 0.49–0.64, HL 0.63–0.77, LHT 0.43–0.58, CI 0.71–0.84, FCI 0.08–0.12, REL 0.34–0.41, REL2 0.43–0.52, SI 0.58–0.68, SI3 1.17–1.48, FI 0.36–0.43, PLI 0.45–0.59, PWI 0.38–0.44, PDI 1.03–1.29, LHT/HW 0.82–0.92, CSC 1–2, MSC 2–4.

Worker description

Small species (HW <0.65); median clypeal lobe narrow, furnished with 2–3 small denticles (often effaced), and usually extending anteriorly beyond the reach of the anterolateral clypeal margins (but shorter than the anterolateral margins in some specimens); profemur relatively slender; lateral margins of pronotum soft-edged, convex in dorsal view, and corresponding to the maximum width of pronotum (Figs 28, 34); mesopropodeal impression well developed, longitudinally rugulate, and lacking metanotal plate; propodeum relatively high and narrow, PDI usually >1.10, less than this in some northern samples; petiole relatively slender (see PLI and PWI values). Integument smooth and shiny, with scattered fine punctures (*c.* 0.01 mm diameter) and fine irregular lineations; lower malar area longitudinally carinate; a few weak longitudinal carinulae may be present on the mesopleuron, metapleuron and side of propodeum. Standing pilosity sparse; long standing hairs (>0.05 mm) present on gaster and apex of head and as follows: one supraocular pair, 1–2 pairs (usually two) on pronotum, 0–1 pair on petiole and 0–1 pair on postpetiole; shorter, mostly appressed hairs scattered over body, inconspicuous. Body color varying from light yellow to medium orange-brown, the gaster either concolorous, partially infuscated, or wholly dark brown; appendages usually somewhat lighter than body.

Discussion

Tetraponera modesta can be recognised by the combination of small size (HW <0.65, LHT <0.58), yellow to orange-brown coloration of the head and mesosoma, and relatively slender petiole (PLI <0.60). Throughout its rather wide range this species shows a substantial amount of variation in color and body form, but I cannot find any discontinuities that would support the recognition of more than one species. The holotype worker of *T. pisarskii* is like other northern specimens of *T. modesta*, which have more uniform light

yellow coloration, relatively low propodeum (PDI 1.04), and dorsal face of the propodeum shorter than the declivitous face (although the dorsal and declivitous surfaces of the propodeum grade insensibly into one another so that no precise boundary between the two can be drawn). Although the type locality of *T. pisarksii* is given as Pyongyang, North Korea it is doubtful that *T. modesta* is established that far north. Assuming that the specimen was not mislabeled, it seems likely that it represents a transient introduction from southern China or Indochina.

As one proceeds south there is a gradual trend towards darkening of the gaster, this being most pronounced in samples from Bali, Lombok and New Guinea where the gaster is uniformly dark brown. In intervening regions one finds workers with intermediate (and variable) maculation on the gaster. More puzzling are a few samples of *modesta*-like specimens from Borneo (Sabah: Poring Spring) and the Philippines (Dumaguete) that show a tendency towards darkening of the head, posterior mesosoma and femora. These specimens thus show contrasts in body color similar to those of *T. extenuata*, and the distinction between the two becomes difficult to sustain. It is possible that there is some genetic introgression between the two forms in these localities, but additional studies are needed to address this question.

Distribution and biology

Tetraponera modesta is distributed widely, from eastern India to southern China south through Malaysia and Indonesia to Papua New Guinea (Fig. 184). Collections with habitat information include foraging workers from lowland rainforest vegetation (New Guinea, Sarawak, Singapore), fogging samples from *Dryobalanops beccarri* in mixed dipterocarp forest (Brunei), and fogging samples from *Aporusa* sp. in lower montane dipterocarp forest (Sabah). The localities from which this species has been collected cover a much wider range of habitats, however.

Tetraponera nigra-group

In this group the worker caste is characterised by the following traits. (*1*) The mandible is short and robust, with the masticatory margin being as long as, or longer than, the basal margin, and bearing four teeth; the basal margin has 0–1 small teeth or denticles (Fig. 6). (*2*) The clypeus is short and lacks a strongly protruding median lobe, its anterior margin being flat or broadly convex (e.g. Figs 61–64). (*3*) The mesopropodeal impression varies from elongate and open at the sides to short, transverse and pit-shaped; a metanotal plate is always absent. (*4*) The metabasitarsal sulcus is well developed and usually lies in a conspicuously darkened strip of cuticle, subtended by a low ridge. (*5*) Except at the edges, the mesosternum is largely smooth and shining and lacks the dense pubescence seen in *allaborans*-group workers. (*6*) Abdominal tergite IV usually has a moderate to high density of appressed pubescence, the hairs being separated by their lengths or less (exceptions occur).

The known queens of the *nigra*-group exhibit features (*4*), (*5*) and (*6*), but are more variable with respect to mandible and clypeus shape. In both males and queens, the forewing has two cubital cells, with rare (and apparently aberrant) exceptions. The male genitalia and associated structures (i.e. sternite IX) are distinctive: see description and comparison in the discussion of the *allaborans*-group (above, page 601). Recent anatomical investigations by Billen and Buschinger (2001) have revealed the existence of a novel gut structure—termed the bacterial pouch—in workers of several *Tetraponera* species, all members of the *nigra*-group. This structure is apparently absent in other *Tetraponera* species and in *Pseudomyrmex*.

At present the *nigra*-group contains 20 recognised species and is distributed throughout most of the Indo-Australian region. Several clusters of related species can be identified, based on similarities in the worker and queen castes and features of the male genitalia:

1. difficilis-complex (*T. difficilis*, *T. inversinodis*)

2. laeviceps-complex (*T. atra*, *T. laeviceps*, *T. mimula*, *T. punctulata*, *T. rotula*, *T. tucurua*)

3. nigra-complex (*T. attenuata*, *T. binghami*, *T. buops*, *T. nigra*)

4. nitida-complex (*T. nitida*, *T. nixa*, *T. nodosa*, *T. notabilis*)

Left unassigned to these complexes are four taxonomically peculiar and apparently uncommon species, two known primarily from the worker caste (*T. aitkenii*, *T. polita*) and two based on queens only (*T. vivax* and *T. volucris*).

The nesting habits of most *nigra*-group species appear to be generalised, with colonies occupying dead twigs or branches of unspecialised plants. But *T. tucurua* and *T. binghami* are obligate inhabitants of live plant cavities (domatia) of *Cupaniopsis* and bamboos, respectively, in which they keep scale insects (Coccoidea) (Ward 1991; Klein *et al.* 1992). In addition, some individual colonies of *T. nigra* and *T. punctulata* have been found occupying live plant cavities (Ward 1991; D. McKey personal communication), so there appears to be a propensity to develop habits along these lines.

Tetraponera aitkenii (Forel)

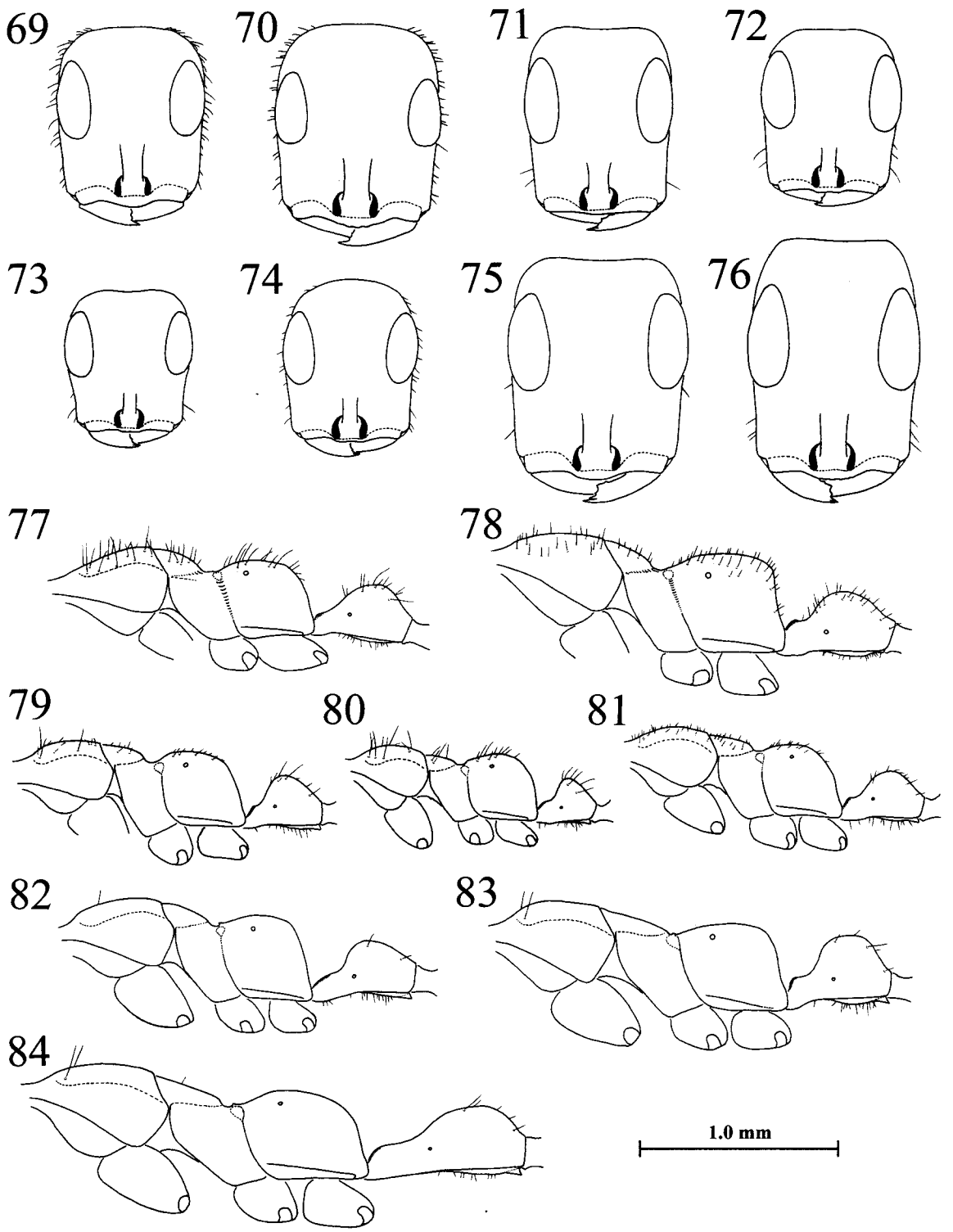
(Figs 69, 77)

Sima aitkenii Forel, 1902: 245.

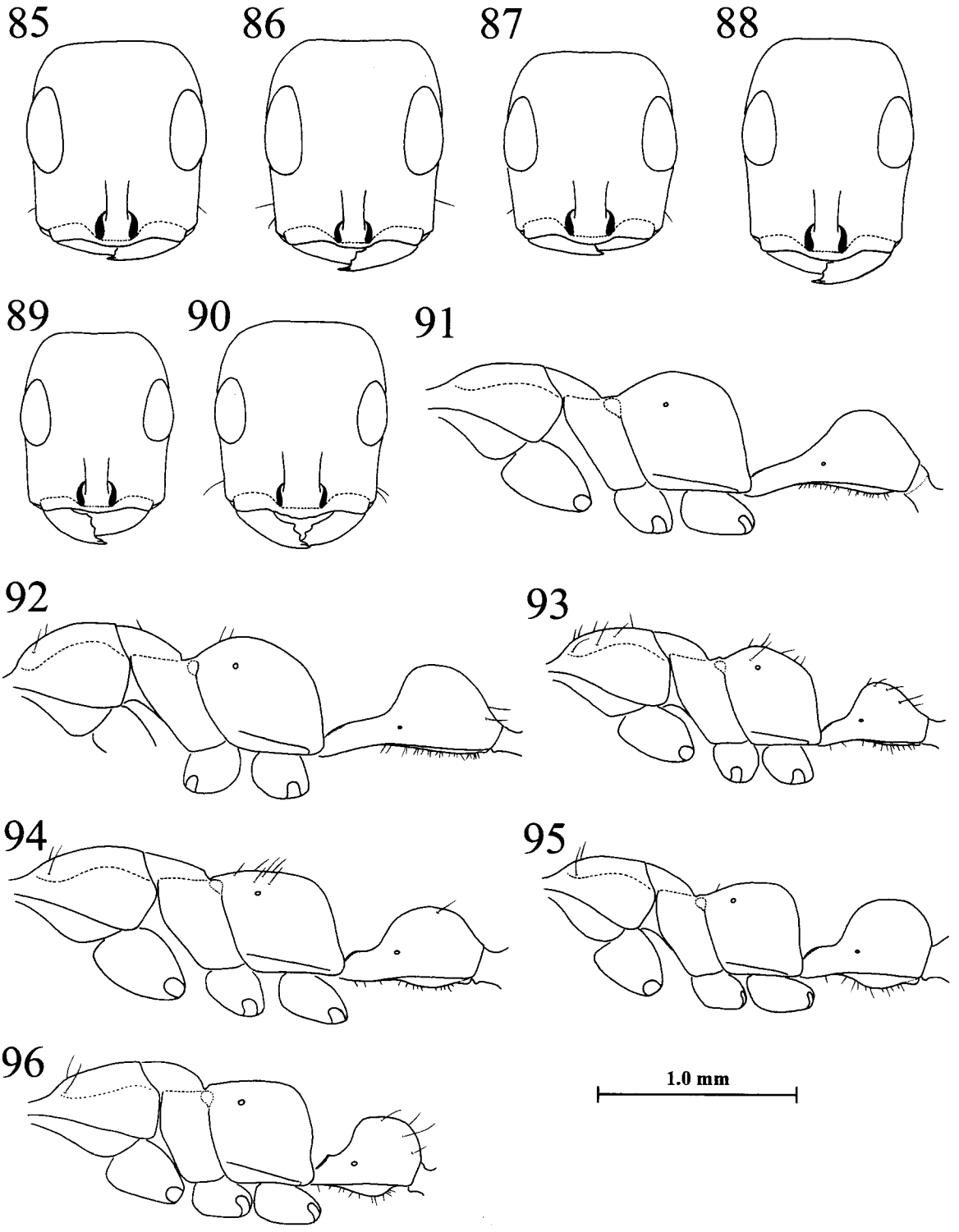
Sima aitkenii Forel; Forel, 1903*b*: 401. Information given on type locality (omitted in original description).

Sima (*Tetraponera*) *aitkeni* Forel; Emery, 1921: 25.

Tetraponera (*Tetraponera*) *aitkeni* (Forel); Chapman and Capco, 1951: 78. First combination in *Tetraponera*.



Figs 69–84. *Tetraponera nigra*-group, workers, full-face view of head (*69–76*) and lateral view of mesosoma and petiole (*77–84*). *69*, *77*, *T. aitkenii* (India); *70*, *78*, *T. polita*, holotype (Malaysia); *71*, *82*, *T. nitida* (Papua New Guinea); *72*, *79*, *T. nitida* (Brunei); *73*, *80*, *T. nitida* (Malaysia); *74*, *81*, *T. nixa*, holotype (Australia); *75*, *83*, *T. nodosa*, holotype (Malaysia); *76*, *84*, *T. notabilis*, holotype (Thailand).



Figs 85–96. *Tetraponera nigra*-group, workers, full-face view of head (*85–90*) and lateral view of mesosoma and petiole (*91–96*). *85*, *91*, *T. atra* (Papua New Guinea); *86*, *92*, *T. laeviceps* (Papua New Guinea); *87*, *93*, *T. mimula*, holotype (Papua New Guinea); *88*, *94*, *T. punctulata* (Australia); *89*, *95*, *T. rotula*, holotype (Australia); *90*, *96*, *T. tucurua*, holotype (Australia).

Type material examined

Sima aitkenii Forel. Syntype (unique?), worker, Kanara, India (Aitken) (MHNG).

Other material examined

India: *Goa*: Mormugao, vic. Velsao, 5 km E Dabolim Airport, 50 m (A. Schulz; K. Vock); *Karnataka*: Bangalore (S. Kumar; S. Hari); I.I.Sc. Campus, Bangalore (P. Nair); Mangalore (J. C.Bridwell); *Kerala*: Calicut (F. Rickson); Calicut University campus (S. Sheela); *Tamil Nadu*: Walajanagar, N. Arcot (A. P. Nathan). **Malaysia:** *Terengganu*: P. Perhentian Besar (Windschnurer).

(Collections: ASIC, CESB, DZUC, PSWC, USNM).

Worker measurements (n = 7)

HW 0.75–0.85, HL 0.87–1.05, LHT 0.62–0.68, CI 0.81–0.87, FCI 0.11–0.14, REL 0.41–0.44, REL2 0.48–0.55, SI 0.57–0.64, SI3 1.04–1.28, FI 0.42–0.48, PLI 0.58–0.64, PWI 0.49–0.55, PDI 0.99–1.05, LHT/HW 0.80–0.85, CSC 18–27, MSC 26–48.

Worker description

Relatively small species (HW <0.90, LHT <0.70); anterior clypeal margin broadly convex, edentate (Fig. 69); distance between frontal carinae approximately equal to, or slightly greater than, maximum scape width; eyes of modest size (see REL and REL2 values), eye length shorter than scape length; profemur moderately robust (FI 0.42–0.48); pronotum with sharply defined lateral margins; anterior half of mesopropodeal impression open and with irregular longitudinal rugulae, posterior half flanked by a pair of raised ridges (immediately mesad of the metanotal spiracles) that create a small, pit-like depression; propodeum about as high as wide (PDI ~ 1.00), the summit broadly rounded when seen in posterior view; in lateral profile, dorsal face rounding gradually into the declivitous face; petiole as sketched (Fig. 77), about twice as long as wide, lacking posteroventral teeth; metabasitarsal sulcus well developed, adjacent to a prominent darkened ridge, occupying about half the length of the metabasitarsus. Integument largely smooth and shiny, with scattered punctures and fine, irregular lineations; largest punctures on head about 0.010–0.015 mm in diameter, usually separated by several to many diameters, but accompanied by, and grading into, more numerous, very fine punctures; lower malar area with coarser punctures and weak, irregular longitudinal rugulae. Standing pilosity (slender, fine-tipped hairs) common on most body surfaces (Figs 69, 77), including scapes, legs, venter of head, sides and upper surface of head, mesosoma dorsum, petiole, postpetiole and gaster; setae on head and mesosoma variable in length, mostly 0.08–0.20 mm long; shorter appressed pubescence occurring in moderate density on body; appressed hairs on abdominal tergite IV separated by about their lengths or less. Body black to brownish-black, appendages lighter (dark to medium brown).

Discussion

Tetraponera aitkenii can be identified by the combination of small size (worker HW <0.90, queen HW ~ 0.95), abundant pilosity on the mesosoma (MSC >20) and sides of head, and moderately dense pubescence on the gaster. Workers differ from those of the superficially similar *T. polita* by the larger eyes (REL >0.40), thinner petiole (PWI <0.58), and longer standing hairs (compare Figs 69, 77 with 70, 78). Workers of *T. aitkenii* might also be confused with those of *T. nixa* and the more setose forms of *T. nitida*, but these latter have shorter scapes (SI <0.56, SI3 <1.00), posteroventral teeth on the petiole, and dense punctate sculpture on the anterior quarter of the pronotum.

Distribution and biology

Tetraponera aitkenii is known only from southern India and (one collection) peninsular Malaysia (Fig. 189). We have almost no information about its biology. Workers collected by Fred Rickson at Calicut, India were visiting extrafloral nectary glands of cashew trees (*Anacardium occidentale*). Wheeler and Wheeler's (1956) description of the larva of '*Tetraponera aitkeni*' is actually that of *T. allaborans*.

Tetraponera atra Donisthorpe

(Figs 85, 91, 148, 162, 174)

Tetraponera atra Donisthorpe, 1949: 493.

Type (not examined)

Tetraponera atra Donisthorpe. Holotype queen (by monotypy), Maffin Bay, Indonesia (E. S. Ross) [type not in CASC, apparently lost].

Material examined

Papua New Guinea: *Madang*: Awar Plantation, Hansa Bay (J. M. Pasteels); 40 km W Madang, 140 m (P. S. Ward); *Morobe*: lower Busu R., Huon Penin. (E. O. Wilson); Nadzab (E. O. Wilson).

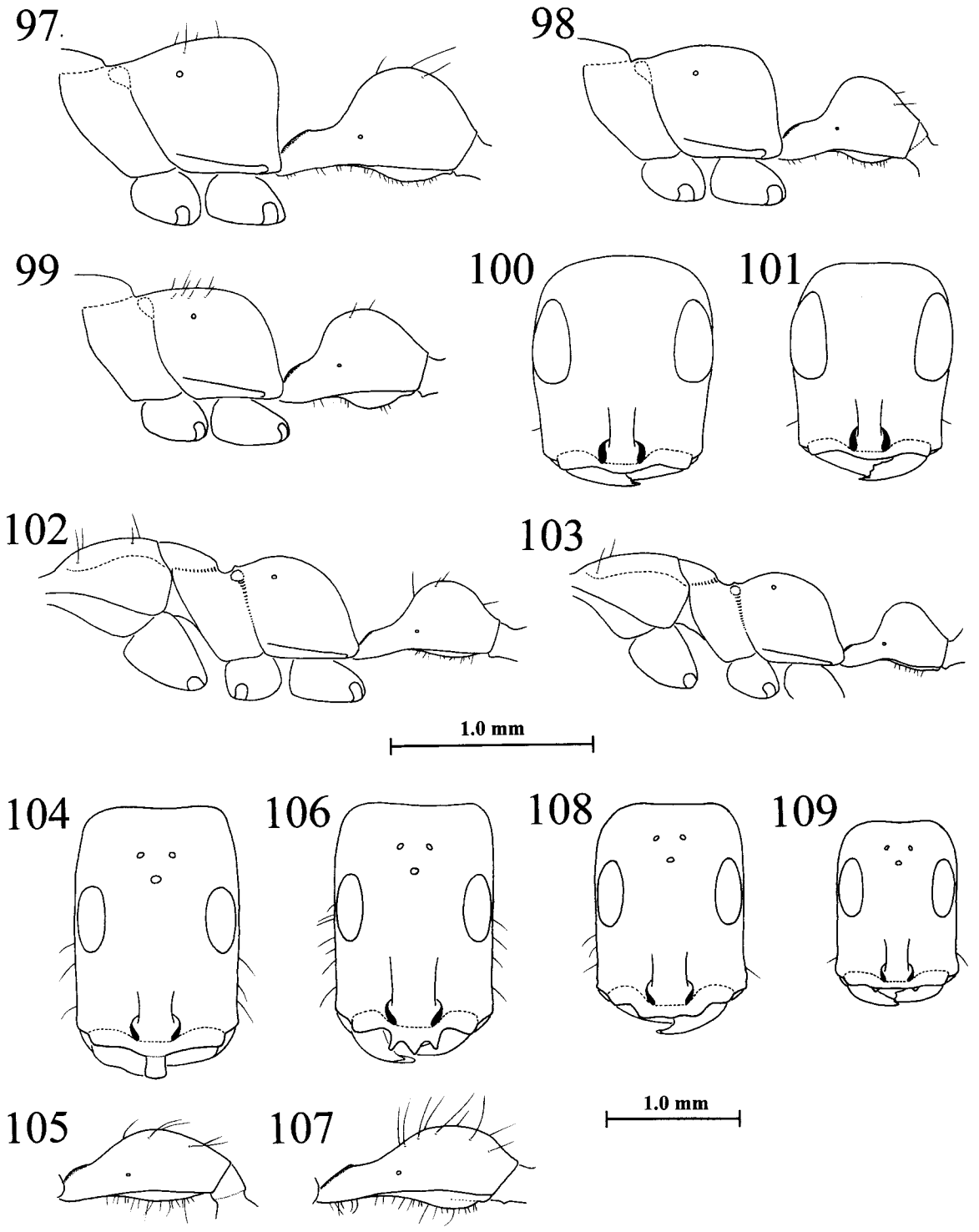
(Collections: MCZC, PSWC).

Worker measurements (n = 6)

HW 0.94–1.04, HL 1.04–1.18, LHT 0.84–1.00, CI 0.86–0.90, FCI 0.12–0.14, REL 0.38–0.42, REL2 0.44–0.47, SI 0.61–0.62, SI3 1.29–1.39, FI 0.41–0.44, PLI 0.38–0.51, PWI 0.33–0.45, PDI 1.24–1.31, LHT/HW 0.90–0.96, CSC 0–2, MSC 0–2.

Worker description

Medium-large species, with broad head; clypeus short, its anteromedial portion protruding only slightly beyond level of the anterolateral clypeal margin (Fig. 85); frontal carinae moderately well separated, the distance between them subequal to maximum scape width; eye relatively large (see REL and REL2 values); scape rather long (SI2 0.53–0.55; SI3 >1.26); profemur slender; pronotum slightly to



Figs 97–109. *Tetraponera nigra*-group, workers (*97–103*) and queens (*104–109*), full-face view of head (*100*, *101*, *104*, *106*, *108*, *109*), lateral view of posterior mesosoma and petiole (*97–99*), lateral view of mesosoma and petiole (*102*, *103*), and lateral view of petiole (*105*, *107*). *97–99*, *T. punctulata* (Australia), showing variation in propodeum and petiole shape; *100*, *102*, *T. difficilis* (Singapore); *101*, *103*, *T. inversinodis*, holotype (Malaysia); *104*, *105*, *T. vivax*, holotype (Singapore); *106*, *107*, *T. volucris*, holotype (Singapore); *108*, *T. difficilis* (Malaysia); *109*, *T. inversinodis* (Malaysia). Large scale bar applies to Figs *97–103*, smaller scale bar to Figs *104–109*.

moderately expanded laterally (PrWM/MTW 1.15–1.30), its anteromedial portion flat or weakly concave; lateral pronotal margins blunt-edged; mesopropodeal impression well marked but short, consisting of a pit-shaped depression, flanked by lateral ridges; propodeum conspicuously elevated, markedly higher than wide, dorsal face moderately to strongly convex in profile, and rounding insensibly into declivitous face; legs rather long, LHT/HL 0.79–0.86; petiole long and slender, with well differentiated anterior peduncle (Fig. 91); petiolar node somewhat variable in height and width (see range of PLI and PWI values); postpetiole as long as, or longer than, wide; metabasitarsal sulcus well developed, lying in a darkened patch of cuticle and adjacent to a low carina that occupies 0.5–0.7× the length of the basitarsus. Dorsum of head, mesosoma and petiole covered with dense, subcontiguous punctures which render much of the surface opaque; cephalic punctures mostly 0.015–0.020 mm in diameter; mesosomal and petiolar punctures smaller, and tending to become effaced on the sides (especially pronotum) where the integument is correspondingly shinier; postpetiole and gaster finely puncticulate, sublucid; lower malar area rugulopunctate. Standing pilosity very scarce, present on gaster and apex of head, and on the following dorsal surfaces: posterior half of head (0–2), pronotum (0–2), petiole (0–3), and postpetiole (0–3); short appressed pubescence forming a rather dense cover on most of body including abdominal tergite IV. Black to dark brownish-black, appendages lighter (medium brown to yellowish-brown), especially scape, first several funicular segments, protibia and tarsi.

Discussion

This species is closely related to *T. laeviceps* and *T. mimula*, but it can be distinguished by the much denser punctate sculpture on the head and mesosoma dorsum, which renders these parts of the body more or less opaque. *T. atra* is also larger on average, with disproportionately longer legs and scapes (see keys). Even among the small series of specimens examined there is considerable variation in the shapes of the pronotum, propodeum and petiole. The petiolar node is notably lower and thinner in two specimens from eastern Papua New Guinea. Sculpture also varies somewhat, especially on the side of the pronotum, which can range from smooth and shiny to punctulate and subopaque.

Although the holotype queen of *T. atra* is apparently lost, there are enough details in the original description to associate the name with the opaque, densely sculptured species recognised here. In particular, Donisthorpe's (1949) description of the color, sculpture, pilosity, head shape, mandibular dentition, petiole shape (long with a thin peduncle) and size (8.5 mm long) of the type specimen allows one to eliminate all other New Guinea species for which the queen is known (*T. allaborans*, *T. laeviceps*, *T. modesta*, *T. nitida*, *T. punctulata* and *T. rotula*). The original description approaches that of the *T. laeviceps* queen except that *T. atra* is described as being 'rather dull, clothed with fine pubescence' and having 'mesonotum more distinctly punctured than pronotum, which is very finely punctured'. These are characteristic features of the species that is here assigned the name *T. atra*. Moreover, although there is one other New Guinea species (*T. mimula*), for which the queen is unknown, the worker of this species has a shiny integument and relatively short petiole, so its queen almost certainly does not correspond to that of *T. atra*.

Distribution and biology

Apart from the type locality in Irian Jaya, there are records of *T. atra* from several sites in Papua New Guinea (Fig. 193). Collections with habitat data are from 'rainforest', 'lowland rainforest' and 'dry evergreen forest'.

Tetraponera attenuata F. Smith

(Figs 63, 67, 133, 139, 144, 158, 170)

Tetraponera attenuata F. Smith, 1877: 71.
Sima attenuata var. *tenuissima* Emery, 1900: 675. Synonymy by Forel, 1912*b*: 54; here confirmed.
Sima birmana Forel, 1902: 245. **Syn. nov.**
Sima attenuata var. *thagatensis* Forel, 1902: 249. **Syn. nov.**

For details on the nomenclatural history of *T. attenuata* and its junior synonyms, see Bolton (1995: 417–419).

Type material examined

Tetraponera attenuata F. Smith. Syntype (unique?), worker, Sarawak (labeled 'Sar.'), Malaysia (BMNH).

Sima attenuata var. *tenuissima* Emery. Syntypes, 4 workers, 1 dealate queen, Pangherang-Pisang, Sumatra (E. Modigliani) (MCSN).

Sima birmana Forel. Holotype (by monotypy), dealate queen, 'Burma' (Bingham) (MHNG).

Sima attenuata var. *thagatensis* Forel. Syntype, worker, Thagata, Tenasserim, Myanmar (Fea) (MHNG).

Other material examined

Brunei: Bukit Sulang, nr Lamunin (N. E. Stork); K. Belalong, 300 m (N. Mawdsley). **China:** *Guangdong*: Conghua [as 'Cun-hua, 96 km NO ad Canton'] (R. Bielawski); Gutian (J. R. Fellowes); Heishiding (J. R. Fellowes); Xinjiadong (Z. Li); *Guangxi*: Bobai County, 550 m (S. Zhou); Long Hu Shan Natural Reserve, 600 m (S. Zhou); Luoxiang, Dayaoshan (J. R. Fellowes); Nong Gang Natural Reserve, 600 m (S. Zhou); Qinglongshan (J. R. Fellowes); Shiwandashan (J. R. Fellowes); *Hainan*: Diaoluoshan, 130 m (J. R. Fellowes); Diaoluoshan, 350 m (J. R. Fellowes); Fan Ta (J. L. Gressitt); Fan Ta Chuen (Hung Mo Tung valley) to Poh Shaang (Lingnan U. 5th Hainan I. Exped.); Jianfengling (J. R. Fellowes); Jiaxi, 680 m (J. R. Fellowes); Lumuwan, 260 m (J. R. Fellowes); Nada [as 'Nodoa'] (J. L. Gressitt); Ta Han (J. L. Gressitt); Ta Hian (J. L. Gressitt); Tien Fong Mts. (Boucek); Tun Chang (J. R. Fellowes); Wuzhishan, 690 m (J. R. Fellowes); Xing Long (J. R. Fellowes); *Hong Kong*: N.T.: Tai Po Kau (J. R. Fellowes). **India:** *Assam*: 'Assam' (Smythies); Chabua (A. C. Cole); *West Bengal*: Kalimpang [as 'Kalimpong'] (POE: El Paso, Tex.) (c.u.). **Indonesia:** *Aceh*: Langsa (W. M. Mann); *Jawa Barat*: Tjibodas, 1400 m [= Cibodas] (H. H. F. Hamann); *Jawa Tengah*: Pemalang (L. G. E. Kalshoven); Semarang (L.

G. E. Kalshoven); *Kalimantan Barat*: Gunung Palung Natl Pk, Cabanti Panti Res. Stn., 100–400 m (D. C. Darling *et al.*); Gunung Palung Natl Pk, Cabanti Panti Res. Stn., 100 m (D. C. Darling *et al.*); *Kalimantan Selatan*: Tanjung [as 'Tandjong'] (F. Suck); *Kalimantan Timur*: Bulongan, Long Tua, 440 m (D. C. Darling); *Lampung*: Lang Eiland, Krakatau (Jacobson); *Sumatera Barat*: Bukittinggi (E. S. Ross); Indropura (Fritsehler); *Sumatera Utara*: Banda Baru, 47 km S Medan, 600 m (E. S. Ross); Bandarbaru [as 'Bandar Baru'] (von Buttel-Reepen); Liangagas (Dohrn); Pematang Siantar (J. Matthews); Pematang Siantar (W. M. Mann); Sibolga [as 'Siboga'] (E. Modigliani); Soekaranda (Dohrn); *province unknown*: 'Sumatra' (Klüg). **Japan:** *Okinawa*: Mt Yonaha-Dake (H. Makihara). **Laos:** *Sekong*: Bolavens-Pl., N-slope, *c.*10 km N Mg. Tha Theng, 500–700 m (Schillhammer); *Vientiane*: Phou Khao Khouay NP, env. Tad Leuk Waterfall, 200 m (Schillhammer). **Malaysia:** *Johor*: Kluang F. R. (C. G. Roche); *Negeri Sembilan*: Berenthian Tingi (Martin); Hutan Lipur Ulu Bendol, 230m (T. Livschultz; D. Schott); Pasoh (P. J. Greenslade); Pasoh For. Res. (M. Brendell *et al.*); Pasoh Forest Reserve (K. Rosciszewski); Sungai [as 'Sungei'] Menyala For. Res., nr Port Dickson (W. L. Brown; T. Y. Pong); *Pahang*: Genting Highlands, 800 m (U. Maschwitz); Kuala Lompat Natl Pk (D. G. Furth); *Sabah*: Borneo Rainforest Lodge, Danum Valley Conserv. Area, 760 m (D. M. Olson); Bundu Tuhan, 6 km S Mt Kinabalu Natl Pk, 1070 m (B. B. Lowery); Crocker Range NP, Mawar Waterfall (c.u.); Danum Valley (E. Widodo); Forest Camp, 19 km N Kalabakan, 180 m (Y. Hirashima); Gunong Rara, Tawau (K. Eguchi); mi. 45, Labuk Rd., ex Sandakan (Lungmanis) (R. W. Taylor); Poring (U. Maschwitz); Poring Spring, >650 m (A. Floren); Sandakan (Baker); Sandakan Bay (NW), Sepilok For. Res., 1–10 m (J. L. Gressitt); Sepilok Forest (H. Ôkido); Sepilok Forest Res., nr Sandakan (R. W. Taylor); Tawau Residency, Kalabakan R., 30 mi. W Tawau (L. W. Quate); Tawau, Quoin Hill (R. W. Taylor); Tunku Abdul Raman Natl Pk, 0–250 m (B. B. Lowery); Umas Umas, nr Tawau (R. W. Taylor); *Sarawak*: Bt Pantu, Lambir Natl Pk, Miri (S. Yamane); G. Mulu Natl Pk (D. Hollis; B. Bolton); Gn. Mulu Natl Pk (M. Collins); Gn. Mulu Natl Pk, Melinau Gorge (F. Wanless); Kelabit Highland, 1000–1200 m, Bereo Arur-Dalam (c.u.); Kuching (J. Hewitt); Lambir (U. Maschwitz); Lambir Natl Pk, Miri (S. Yamane); Merirai Valley, nr Kapit, 30–300 m (T. C. Maa); Mt Matang (G. E. Bryant); Mulu NP (H. Zettel); s Gunung Buda, 64 km S Limbang (S. L. Heydon; S. Fung); Serambu, Mt Kuching (Harrison Smith); Tower Region, Lambir Natl Pk, Miri (S. Yamane); *Selangor*: 16 mi NE Kuala Lumpur (E. S. Ross; D. Q. Cavagnaro); Gombak (B. Bolton); Gombak Field Stn., 30 km NE Kuala Lumpur, 250 m (W. Dorow); Kepong (U. Maschwitz); Serdang [misspelled as 'Serdano'] (c.u.); Ulu Gombak (H. Zettel); Ulu Gombak (U. Maschwitz); Ulu Gombak (M. Kubota); Ulu Gombak Field Stn. (A. Buschinger); Ulu Gombak, 250 m (S. Yamane); Ulu Gombak, 350 m (R. Klein); *Terengganu*: Bukit Renggit Field Stn. (W. Dorow); *Wilayah Persekutuan*: Kuala Lumpur (E. S. Ross; D. Q.Cavagnaro). **Myanmar:** *Kachin*: Bhamo (Bingham); *Kayin*: Carin Ascuui Chebà, 1200–1300 m (L. Fea); Carin Chebà, 900–1100 m (L. Fea); *Mandalay*: Maymyo, 3000 ft (Bingham); *Pegu*: Minhla (Comotto); *Sagaing*: Chattin Wildlife Sanctuary, 200 m (Schillhammer); Tanbya [as 'Tanbaiyah'] (c.u.); *Shan*: Carin Ghecù, 1300–1400 m (L. Fea); *Tanintharyi*: Mergui (Bingham); Tenasserim, Thagatà (Fea); *Yangon*: Rangoon (G. E. Gates). **Philippines:** *Palawan*: Busuanga Is., 5 km NW Coron, Mabintangen R. (H. Zettel); Irawan (J. H. Martin); Iwahig Penal Col., *c.*Puerto Princesa, 60m (B. B. Lowery). **Singapore:** Seletar Res., 25 ft (E. S. Ross; D. Q.Cavagnaro). **Taiwan:** *Kaohsiung*: Rokki [= Liu-kuei] (L. Gressitt); Shanping, 640 m (R. Davidson *et al.*); Shanping, 640 m (J. Rawlins *et al.*); *Nantou*: Hori [misspelled as 'Honi'] (L. Gressitt); Musha (L. Gressitt); *Pingtung*: Kangkou [as 'Kankan', misspelling of 'Kankau'] (Sauter); Kuraru (L. Gressitt); **Thailand:** *Chanthaburi*: Khao Soi Dao W.S. (S. Yamane); Khao Soi Dao W.S. (H. Ôkido); *Chiang Mai*: Chiang Mai (D. Jackson); Doi Bo, 1126 m (E. S. Ross); Doi Sutep NP Headquarters, 1020 m (R. R. Snelling; S. Sonthichai); Doi Suthep (W. J. Pulawski); Doi Suthep NP, Doi Suthep nr Ruesse Cave, 900–1000 m (H. Zettel); Maehatai (W. Jaitrong); Maerim (R. R. Snelling); Maerim (R. Beaver); Monthatarn Falls, Doi Suthep Natl Pk, 635 m (S. Sonthichai); Phadang (W. Jaitrong); *Kalasin*: Pusithan (D. Wiwatwitaya); *Mae Hong Son*: 20 km NW Pai, 1000 m (Schulz; Vock); 30 km S Mae Sariang, 500 m (Schulz; Vock); *Nakhon Nayok*: Khao Yai Natl Pk, 780 m (I. Burikam; W. L. Brown); *Nakhon Ratchasima*: Khao Yai Natl Pk, Wung Jumpee (D. H. & A. C. Kistner); Kao Yai (D. Wiwatwitaya); Sakaerat ERS (D. Wiwatwitaya); Sakaerat lowland forest (DEF) (S. Yamane); *Phangnga*: Khao Lak Natl Pk, Thone Chong Fa Fall, 300 m (A. Schulz; K. Vock); *Prachin Buri*: *c.* 53 km N Krabinburi (G. R. Ballmer); *Ranong*: Ranong (D. H. Murphy); *Rayong*: Ban Phe, 14 km E Rayong (W. J. Pulawski); *Satun*: Thale Ban NP (Madl); Thale Ban NP, 20–30 km E Satun, 200–400 m (A. Schulz; K.Vock); *Songkhla*: Longkong orch., Sadao Distr. (S. Yamane); Ton Nga Chang Natl Pk (S. Yamane); Ton Nga Chang Natl Pk (H. Ôkido); *Surat Thani*: Koh Tao (H. Smith); *Tak*: Tung Yai W.S., near Myanmar border (W. Jaitrong); Tung Yai (D. Wiwatwitaya); *Trang*: Khao Chong Nature Education Centre (R. R. Snelling; S. Sonthichai); *Yala*: Betong (J. Horák); *province unknown*: Tenasserim Border (K. G. Gairdner). **Vietnam:** *Da Nang*: 14 km N Da Nang (H. P. Shurtleff); *Ha Nam Ninh*: Cúc-phu'óng (R. Bielawski; B. Pisarski); *Ha Sonh Binh*: Da Bac, Tuly (Belokobylskij); Ky Son, Cao Phong (Belokobylskij); *Khanh Hoa*: Cam Ranh Bay (T. R. Taylor); Hon Tré [as 'Isl. Che'] (A. Radchenko); *Nghe An*: Ban Khom, Que Phong Distr. (B. T. Viet); Que Phong Distr. (B. T. Viet); *Soc Trang*: Côn Dao [as 'Isl. Kondao'] (A. Radchenko); Hòn Bai Canh [as 'Isl. Baikan'] (A. Radchenko); *Thanh Hoa*(?): Cuc Phuong NP, 100 km S Hanoi (E. Jendek); *Vinh Long*: Binh Minh (M. Barzman); *Vinh Phuc*: Tam Dao, <900 m (K. Eguchi).

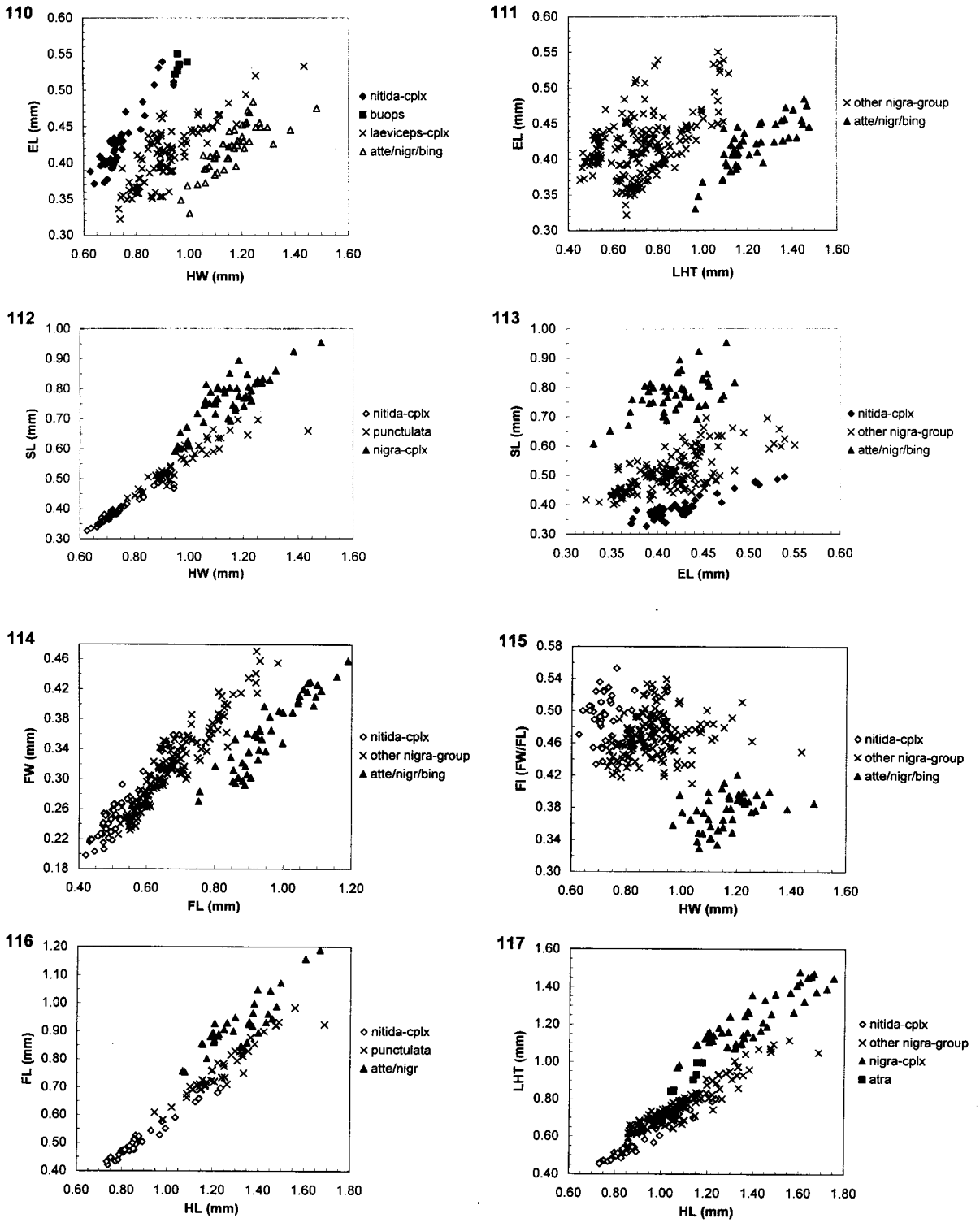
(Collections: AMNH, ANIC, ASIC, BMNH, CASC, CMNH, CUIC, HZIC, KFBG, KUBC, KUEC, KUES, LACM, MCSN, MCZC, MHNG, NHMV, PSWC, RMBR, ROME, SMNK, UASK, UMSC, USNM, ZMAS, ZMPA).

Worker measurements (*n* = 20)

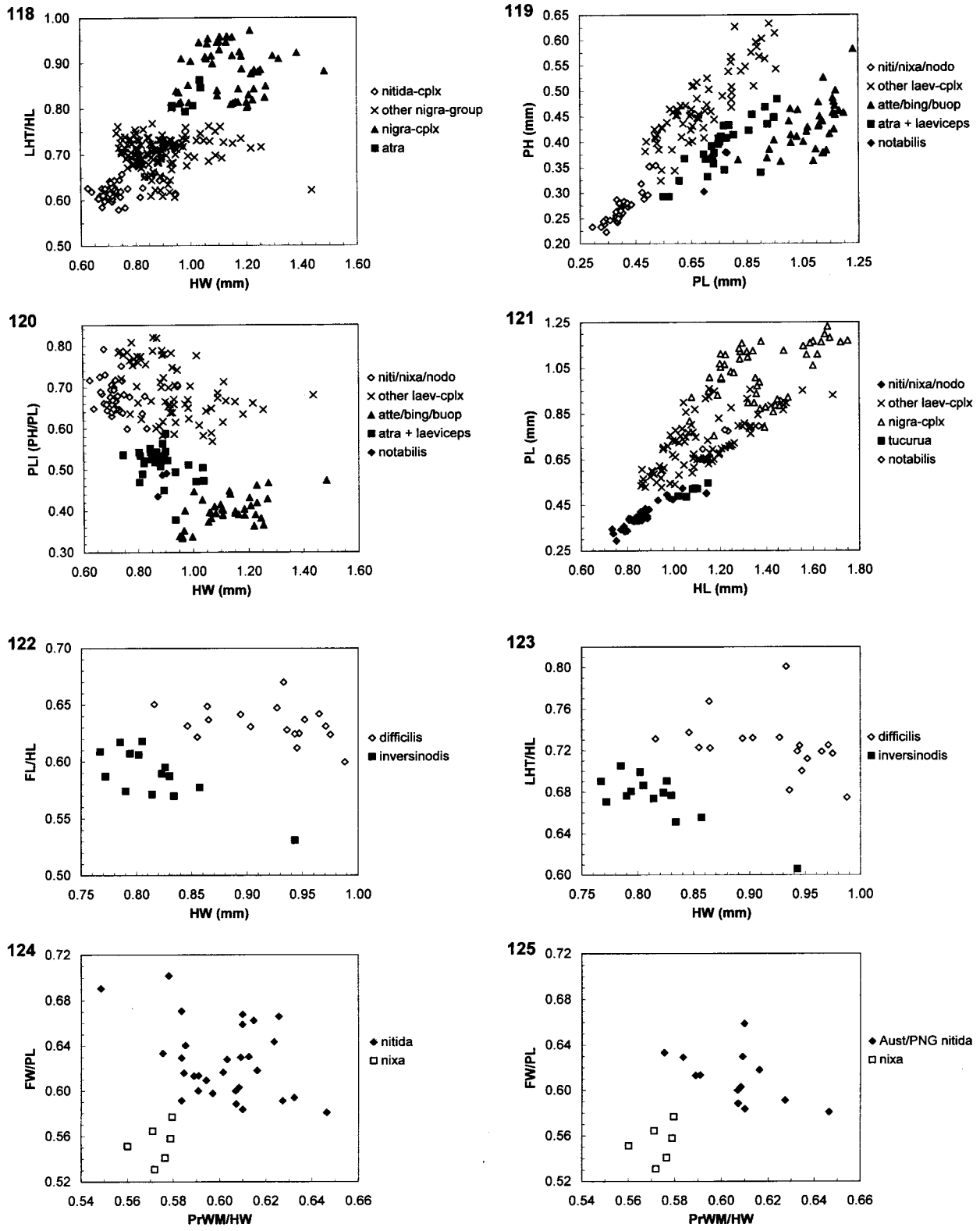
HW 0.97–1.48, HL 1.07–1.67, LHT 0.97–1.47, CI 0.84–0.94, FCI 0.11–0.15, REL 0.29–0.34, REL2 0.32–0.38, SI 0.61–0.76, SI3 1.84–2.11, FI 0.33–0.40, PLI 0.38–0.47, PWI 0.29–0.44, PDI 0.97–1.06, LHT/HW 0.93–1.08, CSC 10–26, MSC 6–44.

Worker description

Relatively large and slender species, with broad head (CI >0.82); clypeus short (Fig. 63), its anteromedial margin varying from broadly convex to straight; anteromedial margin of clypeus joining anterolateral margin in a smooth curve or (less commonly) at a slight angle; frontal carinae moderately well separated, the distance between them exceeding basal scape width; eyes relatively small (see REL and REL2 values), scape length about twice eye length; lateral margins of head rounding broadly into posterior margin; profemur slender; pronotum usually lacking prominent lateral margins; mesopropodeal impression well-marked, long and open, flanked by low metanotal tubercles that are usually not prominent in profile; propodeum about as high as wide, dorsal face rounding gradually and continously into the declivitous face; legs long relative to head size, LHT/HL 0.84–0.96; petiole somewhat variable in shape but always rather long and slender (PLI <0.48), often



Figs 110–117. Bivariate plots of various metric measurements and indices in *Tetraponera* workers. Taxon abbreviations: atte, *T. attenuata*; bing, *T. binghami*; nigr, *T. nigra*.



Figs 118–125. Bivariate plots of various metric measurements and indices in *Tetraponera* workers. Taxon abbreviations: atte, *T. attenuata*; bing, *T. binghami*; buop, *P. buops*; laev-cplx, *laeviceps*-complex; niti, *nitida*; nodo, *nodosa*.

markedly so, and with a well differentiated anterior peduncle and node (Fig. 67); petiole more than twice as long as broad; postpetiole 1.1–1.4× longer than broad; metabasitarsal sulcus lying in a darkened patch of cuticle subtended by a raised ridge, occupying about 0.15–0.30 the length of the basitarsus. Integument with numerous fine punctures, the interspaces (sub)lucid and smooth or weakly reticulate; punctures on dorsum of head and mesosoma mostly 0.005–0.015 mm in diameter (pronotal punctures sometimes larger) and separated by one to several diameters; punctures on side of mesosoma finer, less conspicuous; lower malar area with coarse punctures intermixed with irregular longitudinal rugulae. Standing pilosity common (see CSC and MSC values), the hairs up to 0.30–0.35 mm long, and tending to grade into shorter suberect and decumbent pubescence which forms a dense cover on most of the body, including the mesosoma dorsum and petiole (Fig. 67). Black to dark brownish-black, scape and first several funicular segments often lighter (medium- to yellowish-brown).

Discussion

This species can be recognised by the broad head, elongate petiole, and dense covering of suberect pubescence and standing pilosity on most of the body. Workers from northern populations of *T. attenuata* tend to have more widely separated frontal carinae, smaller eyes, a shorter petiole and a longer metabasitarsal sulcus. But the relevant indices (FCI, REL, REL2, PLI and PWI) overlap substantially, and the variation appears to be clinal in nature. Queens of *T. attenuata* show comparable geographical variation in the same features. In addition, the queens vary in the shape of the clypeus (anterolateral teeth variably developed, occasionally absent) and the size of the malar pit (varying from well developed to absent), but variation in these latter traits does not show a clear-cut geographical pattern.

Distribution and biology

Tetraponera attenuata ranges from northeast India to southern China, south to Sumatra, Java, and Borneo (Fig. 189). The only Philippines records come from Palawan. A single dealate queen has also been taken on Okinawa in Japan. Specimens of *T. attenuata* whose labels include habitat information indicate occurrences in 'lowland rainforest', 'primary rainforest', 'primary dipterocarp forest', 'lower montane mixed dipterocarp forest', 'hilltop dipterocarp forest', 'second-growth forest' and (male only) 'mangrove'. There are a few colony series from dead twigs or dead branches, indicating that this species has generalist nesting habits.

Tetraponera binghami (Forel)

(Figs 61, 65, 137, 142, 156, 168)

Sima Binghami Forel, 1902: 243.
Sima Binghami var. *Lindgreeni* Forel, 1902: 245. **Syn. nov.**
Sima (*Tetraponera*) *binghami* Forel; Emery, 1921: 25.
Tetraponera binghami (Forel); Wheeler, 1921: 529. First combination in *Tetraponera*.

Type material examined

Sima Binghami Forel. Syntypes, 6 workers, 1 alate queen, 3 males, Moulmain, Myanmar (Hodgson) (MCSN, MHNG); syntypes, 3 workers, Ye Valley, Myanmar (Bingham) (MHNG); syntypes, 3 workers, N. Konkan, Myanmar (Wroughton) (NHMB); syntypes, 8 workers, 1 male, Assam, India (Smythies) (MHNG).

Sima Binghami var. *Lindgreeni* Forel. Syntypes, 7 workers, Delbrugarh, India (Lindgreen) (MCSN, MHNG, NHMB).

Other material examined

Bhutan: Phuntsholing, 200–400 m (NHMB – Bhutan Expedition 1972). **China:** *Guangxi*: Shi Wan Da Shan Natural Reserve, 650 m (S. Zhou); Xidamingshan (J. R. Fellowes); *Hong Kong*: 'Hong Kong' (Terry); 'Hong Kong' (J. J. Walker); Lantau I.: Butterfly Hill (J. R. Fellowes); Lantau I.: Shui Hau, 20–50 m (R. R. Snelling); N.T.: campus C.U.H.K., Shatin, 20 m (R. R. Snelling); N.T.: Pak Ngau Shek (J. R. Fellowes); N.T.: Tai Po Kau (J. R. Fellowes); N.T.: Tai Po Kau Nature Reserve (R. R. Snelling); N.T.: Taipo Kau (S. Yamane); N.T.: Wong Chuk Yeung (J. R. Fellowes). **India:** *Tamil Nadu*: Nilgiri Hills (P. S. Nathan); *West Bengal*: Tukvar, 4000 ft (Mallet; Bingham). **Malaysia:** *Pahang*: Genting Highlands, 800 m (U. Maschwitz); Sungai Kinchin, Endau-Rompin region (D. Kovac); *Selangor*: Ulu Gombak (R. Klein); Ulu Gombak (U. Maschwitz); Ulu Gombak (D. Kovac); Ulu Gombak, 350 m (R. Klein). **Myanmar:** *Kayin*: Carin Chebà, 900–1100 m (L. Fea); *Mon*: Moulmein (Bingham); *Tanintharyi*: Mergui (Bingham); *Yangon*: Rangoon (G. E. Gates); *state/division unknown*: 'Birmanien' (c.u.); 'Burma' (c.u.). **Nepal:** *Narayani*: Amlekganj, 520 m (E. I. Coher). **Thailand:** *Chiang Mai*: Doi Inthanon NP: Nam Tok Mae Ya, 600 m (R. R. Snelling; S.Sonthichai); Doi Suthep region (D. Kovac); *Mae Hong Son*: 10 km S Khun Yuam [as 'Khum Yuam'], 300 m (Schulz; Vock); 15 km NW Pai, 700 m (A. Schulz; K. Vock); Sappong, near Lisu Lodge (D. Kovac). **Vietnam:** *Quang Ninh*: D. Dông Khoa [as 'Isl. Dongkho'] (A. Radchenko).

(Collections: AMNH, ASIC, BMNH, KFBG, KUES, LACM, MCSN, MCZC, NHMB, NHMV, PSWC, UASK).

Worker measurements (*n = 11*)

HW 1.06–1.27, HL 1.36–1.75, LHT 1.24–1.46, CI 0.70–0.78, FCI 0.16–0.20, REL 0.25–0.30, REL2 0.36–0.39, SI 0.62–0.66, SI3 1.62–1.84, FI 0.37–0.40, PLI 0.36–0.43, PWI 0.36–0.42, PDI 0.90–0.99, LHT/HW 1.05–1.20, CSC 24–40, MSC 34–71.

Worker description

Large, slender species, with elongate head (CI <0.80); clypeus with moderately prominent median lobe, the anterior margin convex and weakly crenulate (Fig. 61); frontal carinae well separated, the distance between them exceeding maximum scape width; eyes relatively small (see REL, REL2 and SI3 values); head capsule usually widest on

anterior half and converging slightly posteriorly; posterior margin of head straight; profemur slender; lateral margins of pronotum not well defined; mesopropodeal impression well developed and elongate, the anterior half open and furnished with irregular rugulae, usually longitudinal in orientation; posterior half consisting of a shallow depression flanked by low metanotal tubercles that are discernable in profile; propodeum long and low (PDI <1.00), it dorsal face rounding gradually into the declivitous face (Fig. 65); legs long relative to head size, LHT/HL 0.80–0.91; petiole long and slender (PLI <0.45), the node rather weakly differentiated from the anterior peduncle (Fig. 65); petiole about 2.5× longer than broad; postpetiole about 1.4× longer than broad; metabasitarsal sulcus well developed, lying in a darkened patch of cuticle and subtended by a low ridge, occupying about 0.60–0.70× the length of the basitarsus; mesobasitarsus with a small remnant of a comparable sulcus. Integument with numerous fine punctures, the interspaces smooth and shiny; punctures on dorsum of head and mesosoma mostly 0.005–0.015 mm in diameter and separated by one to several diameters, less dense along mesosomal midline (especially on pronotal midline which is smooth and shiny); punctures on side of mesosoma finer, less conspicuous, except for dense patch on metapleuron and adjacent mesepisternum; lower malar area with coarse punctures intermixed with irregular longitudinal rugulae. Standing pilosity common and conspicuous on most of body (CSC >20, MSC >30), and grading into shorter suberect and decumbent pubescence (Fig. 65). Black to dark brownish-black, tarsi and antennae often lighter (medium- to yellowish-brown).

Discussion

Characteristic features of *T. binghami* workers include the elongate head, prominent clypeal lobe, small eyes, well separated frontal carinae, slender mesosoma and petiole, and abundant pilosity. Compared with other Asian congeners *T. binghami* does not exhibit marked variation in morphology. Workers from more southern populations (Nilgiri Hills, India; West Malaysia) tend to have less elongate heads and those from southern India also have shorter petioles, but the differences are not striking.

Distribution and biology

Tetraponera binghami ranges from Nepal to southern China and south to the Malay Peninsula. There is also an isolated population in the Nilgiri Hills of south India (Fig. 188). This species appears to be confined to wet forest habitats. As far as known it always nests in the live culms of bamboos, in which the ants keep scale insects as well as brood. The nesting biology has been well studied in populations from West Malaysia, in which *Gigantochloa* is the host bamboo (Buschinger *et al.* 1994). Here *T. binghami* forms large monogynous colonies, occupying multiple stem internodes, and always in association with the mealybug *Kermicus wroughtoni* Newstead. The workers do not aggressively defend their hostplant, however. Among other intriguing behavioral observations, colony-founding queens have been demonstrated to carry coccoids between their mandibles (Klein *et al.* 1992), and workers have been described bailing unwanted water out of their nests by ingestion and regurgitation (Klein *et al.* 1993). In these and other recent publications (e.g. Ward 1991), the species is referred to by the code name '*Tetraponera* sp. PSW–80'.

Tetraponera buops, sp. nov.

(Figs 62, 66)

Type material examined

Holotype. Worker, Bukit Sulang, nr Lamunin, Brunei, 20.viii.–10.ix.1982, fogging (N. E. Stork) (BMNH).

Paratypes. 5 workers, same data as holotype (BMNH, PSWC, UMSC).

Worker measurements ($n = 5$)

HW 0.95–1.00, HL 1.28–1.34, LHT 1.07–1.09, CI 0.73–0.75, FCI 0.10–0.12, REL 0.40–0.42, REL2 0.54–0.57, SI 0.62–0.63, SI3 1.10–1.16, FI 0.45–0.47, PLI 0.33–0.35, PWI 0.25–0.28, PDI 0.91–1.01, LHT/HW 1.10–1.13, CSC 12–18, MSC 44–51.

Worker description

Medium-sized, slender species, with elongate head (CI <0.78); clypeus very short and anterior clypeal margin almost straight, its anteromedial portion protruding only very slightly beyond the level of the anterolateral margins (Fig. 62); frontal carinae relatively close, MFC less than maximum scape width; eyes large (see REL and REL2 values) and scape length only slightly greater than eye length (SI3 <1.20); sides of head subparallel and rounding broadly into posterior margin of head; profemur robust (FI >0.44); lateral margins of pronotum not well defined; mesopropodeal impression well marked but rather short, flanked laterally by low metanotal tubercles that are visible in profile; propodeum relatively low, with a somewhat flattened dorsal face that meets the declivitous face at a rounded juncture (Fig. 66); legs long relative to head size, LHT/HL 0.81–0.84; petiole very long and slender (PLI <0.38, PWI <0.30), with an extended anterior peduncle that is only weakly differentiated from the node (Fig. 66); petiole about 4× longer than broad; postpetiole about 1.6× longer than broad; metabasitarsal sulcus not prominent, lying adjacent to a low ridge and occupying about 0.60× the length of the basitarsus. Integument with numerous fine punctures, the interspaces smooth and shiny; punctures on dorsum of head and mesosoma mostly 0.005–0.015 mm in diameter

(some larger) and separated by one to several diameters; punctures on side of mesosoma tending to be finer, less conspicuous; lower malar area with coarse punctures intermixed with irregular longitudinal rugulae. Standing pilosity common on most of body (CSC >10, MSC >40), and grading into shorter suberect and decumbent pubescence (Fig. 66). Black to dark brownish-black, scape and protibia mottled yellowish-brown and dark brown.

Discussion

With its elongate head, slender petiole and abundant pilosity the worker caste of *T. buops* is most similar to that of *T. binghami*, but it is easily distinguished from that species by the smaller body size (compare HW and LHT), larger eyes (compare REL and REL2), shorter clypeus, more closely adjacent frontal carinae (FCI <0.13, compared with 0.16–0.20 in *T. binghami*), broader profemur (FI >0.44 compared with 0.37–0.40 in *T. binghami*), and narrower petiole (PWI <0.30 compared with 0.36–0.42 in *T. binghami*). Worker differences between *T. buops* and *T. attenuata* include the broader head, smaller eyes, more slender profemur, and more nodiform petiole of the latter species.

Distribution and biology

Tetraponera buops is known only from several workers collected in fogging samples in lowland rainforest at the type locality in Brunei. Nothing is known about its biology but from the robust profemur of the worker I would surmise that it nests in rather hard, dead wood, or has some other feature of its life history that requires powerful proleg movement.

Tetraponera difficilis (Emery)

(Figs 100, 102, 108, 129, 140, 145, 159, 171)

Sima difficilis Emery, 1900: 677.
Sima stipitum Forel, 1912*b*: 54. **Syn. nov.**
Sima nitens Stitz, 1925: 117. **Syn. nov.**
Sima (*Tetraponera*) *dilatata* Karavaiev, 1933: 267. **Syn. nov.**
Sima (*Tetraponera*) *difficilis* Emery; Emery, 1921: 26.
Sima (*Tetraponera*) *stipitum* Forel; Emery, 1921: 27.
Tetraponera difficilis (Emery); Wheeler, 1919: 65. First combination in *Tetraponera*.
Tetraponera (*Tetraponera*) *dilatata* (Karavaiev); Chapman and Capco, 1951: 80.
Tetraponera (*Tetraponera*) *nitens* (Stitz); Chapman and Capco, 1951: 81.
Tetraponera (*Tetraponera*) *stipitum* (Forel); Chapman and Capco, 1951: 82.

Type material examined

Sima difficilis Emery. Syntypes, 2 workers, Benculen, Sumatra, Indonesia (E. Modigliani) (MCSN).

Sima stipitum Forel. Syntype, worker, Singapore (A. Müller) (MHNG).

Sima nitens Stitz. Syntypes, 2 workers, 1 queen, Manila, Philippines (Boettcher) (MCZC, ZMHB).

Sima (*Tetraponera*) *dilatata* Karavaiev. Holotype (by monotypy), worker, Prinsen-Eiland, Indonesia (Karavaiev) (UASK).

Other material examined

Brunei: Andalau, 50 m (N. Mawdsley); Bukit Sulang, nr Lamunin (N. E. Stork); Labi (I. Gauld). **Indonesia:** *Jawa Barat*: 3 km S Kalipucang (Imai *et al.*); Bogor (O. D. Deputy); Bogor (S. Yamane); *Kalimantan Barat*: Gunung Palung Natl Pk, Cabanti Panti Res. Stn., 100 m (D. C. Darling *et al.*); *Kalimantan Timur*: 31 km N Balikpapan, E. Borneo (W. L. Brown); *Lampung*: Wai Lima (Karny); *Sumatera Barat*: Limau Manis, nr Padang (S. Yamane); Padang (K. Nakamura). **Malaysia:** *Negeri Sembilan*: Pasoh For. Res. (M. Brendell *et al.*); *Pahang*: 'Pahang/Malacca' (R. Martin); *Sabah*: Danum Valley (H. Ôkido); Danum Valley (S. Yamane); Danum Valley (C. Brühl); Danum Valley (E. Widodo); Forest Camp, 19 km N Kalabakan, 180 m (Y. Hirashima); Kalabakan (T. C. Maa); Kota Kinabalu, 20 m (B. B. Lowery); mi. 45, Labuk Rd., ex Sandakan (Lungmanis) (R. W. Taylor); near Keningau, 210 m (S. Yamane); Poring Spring, >650 m (A. Floren); Quoin Hill, Tawau (Y. Hirashima); Ranau (Y. Hashimoto); Sepilok Forest (S. Yamane); *Sarawak*: 'Sarawak' (S. Doria; Beccari); Gn. Mulu Natl Pk (I. Hanski); Head Quarter R., Lambir Natl Pk, Miri (S. Yamane); *Selangor*: UKM campus (D. G. Furth). **Philippines:** *Bulacan*: Abulalas, Hagonoy (C. K. Starr); *Catanduanes*: E San Andres (H. Zettel); *Davao City*: Matina Heights, Davao (H. Kurokawa); *Dumaguete*: Dumaguete (L. M. Morato); Dumaguete (J. W. Chapman); *Eastern Samar*: Borongan (C. K. Starr); *Laguna*: Los Banos, Mt Makiling, 300 m (B. B. Lowery); Los Banos, Mt Makiling, 600 m (B. B. Lowery); Mt Makiling (H. Zettel); *Leyte*: Baybay (R. Vane-Wright); *Manila*: Manila (R. Brown); Manila (c.u.); *Negros Occidental*: Mambucal (T. Tano); Manapla (W. D. Pierce); *Negros Oriental*: Cuernos de Negros [as 'Horns of Negros'] (c.u.); Cuernos Mts. (Baker); Dumaguete, C. Lookout (J. W. Chapman); *Palawan*: 10 km W Puerto Princesa, Iwahig Penal Colony (H. Zettel); Iwahig Penal Col., *c.* Puerto Princesa, 60 m (B. B. Lowery); *Quezon*: Atimonan, Quezon NP, Old Zigzag Rd. (H. Zettel); *Rizal*: Ateneo de Manila (B. B. Lowery); Wawa Dam (B. B. Lowery); *Tacloban*: Tacloban, Leyte (E. S. Ross). **Singapore:** Bot. Gardens (R. W. Taylor); Changi Beach (M. Kubota); Pierce Reservoir, 40 m (P. S. Ward); Seletar Reservoir, 20 m (P. S. Ward); Singapore (J. Billen); University Area (W. Dorow). **Thailand:** *Kanchanaburi*: Linthin (D. Wiwatwitaya); *Nakhon Si Thammarat*: Khao Luang Natl Pk, Karom Falls, 200–500 m (Schulz; Vock); Phrom Lok [as 'Phromm Lok'] Waterfall, 25 km NW Nakhon, 100–300 m (A. Schulz; K. Vock); *Phangnga*: Khao Lak (Schulz; Vock); Tone Chang-Fah Waterfall, 20 km S Takuapa, 100–200 m (A. Schulz; K. Vock); *Ranong*: Ranong (D. H. Murphy); *Satun*: Thale Ban Natl Pk, 50 m (A. Schulz; K. Vock); *Yala*: Betong (J. Horák).

(Collections: ANIC, ASIC, BMNH, CASC, HZIC, KUBC, KUES, LACM, MCSN, MCZC, MHNG, NHMV, PSWC, UMSC, USNM).

Worker measurements (*n = 18*)

HW 0.82–0.99, HL 0.90–1.22, LHT 0.66–0.84, CI 0.81–0.90, FCI 0.11–0.15, REL 0.38–0.44, REL2 0.44–0.48, SI 0.55–0.62, SI3 1.15–1.32, FI 0.43–0.51, PLI 0.57–0.63, PWI 0.44–0.51, PDI 0.97–1.12, LHT/HW 0.77–0.90, CSC 2–4, MSC 2–5.

Worker description

Medium-sized species; clypeus short, its anteromedial margin weakly convex and even with, or protruding only slightly beyond the level of, the anterolateral clypeal margin (Fig. 100); frontal carinae moderately well separated, the

distance between them exceeding basal scape width; eye relatively modest in size, scape notably longer than eye (SI3 >1.14); profemur relatively slender, FI usually <0.48 in all but largest workers; lateral pronotal margins present, blunt-edged; mesopropodeal impression consisting of two sections: anteriorly, an open transverse, strip of integument with varying density of longitudinal rugulae or carinulae; posteriorly, a pit-shaped depression defined by flanking lateral ridges that decline anteriorly, usually rather suddenly and at a point marked by a weak denticle, visible on the profile of the mesosoma (Fig. 102); propodeum usually about as high as wide, and somewhat depressed below the level of the promesonotum; dorsal face of propodeum rounding gradually and continously into the declivitous face; petiole with short but well differentiated anterior peduncle and with relatively slender node (PL/HL 0.54–0.61); posteroventral petiolar teeth lacking; in profile petiole typically as illustrated (Fig. 102), with the node rather broadly and evenly rounded, its anterior face only slightly steeper than its gently declining posterior face; petiole about twice as long as wide (see PWI values); postpetiole about as long as, or slightly longer than, wide; metabasitarsal sulcus prominent, occurring in a darkened patch of raised cuticle and occupying more than half the length of the basitarsus. Integument smooth and shiny, with scattered fine punctures, mostly ≤0.010 mm in diameter, and separated by several to many diameters, leaving conspicuous shiny interspaces, especially on the side of the mesosoma; lower malar area with coarser punctures and weak longitudinal rugulae. Standing pilosity scarce, present on gaster and apex of head, and on the following dorsal surfaces: posterior half of head (2–4, usually 2), pronotum (2–5), petiole (0–5), and postpetiole (0–5); with head in full-face view, standing hairs absent from sides of head, except for one or two near the mandibular insertions; short appressed pubescence scattered over body, generally somewhat inconspicuous; appressed hairs on abdominal tergite IV (first gastric tergite) varying considerably in density, from very dense (hairs overlapping extensively) to sparse (hairs separated by more than their lengths). Body black to dark brownish-black; appendages varying from dark brown to light yellowish-brown (antennae, protibia and tarsi usually the lightest in color).

Discussion

As indicated by the new synonyms, *T. difficilis* has eluded recognition in the literature. Workers of this species can be distinguished from those of others in the *nigra*-group by the combination of intermediate eye size (REL2 0.44–0.48), sparse pilosity (CSC 2–4, MSC 0–5), and the structure of the mesopropodeal impression: open anteriorly, with a pit-shaped depression posteriorly. The shiny, puncticulate integument and relatively slender petiole (Fig. 102) are also characteristic. Workers show modest variation in size, shape of the petiole, amounts of standing pilosity, and color of the appendages. More striking is the variability of the appressed pubescence on the gaster. In most workers the appressed hairs occur in moderate to high density on the gaster, sufficient to dull the lustre of the underlying integument. But in some individuals from Borneo and the Philippines the hairs are short, sparse, and separated by more than their lengths, and the gaster is correspondingly shinier. Finally, while the legs are only moderately long in most workers (LHT/HL 0.67–0.77; LHT/HW 0.77–0.88), they are unusually long in one worker examined from Danum Valley, Sabah (leg. H. Ôkido) (LHT/HL 0.80, LHT/HW 0.90).

Distribution and biology

Tetraponera difficilis occurs on the Malay Peninsula, Borneo, Java, Sumatra, and in the Philippines (Fig. 191). Habitats from which it has been recorded include primary and secondary rainforest, rainforest edge, 'gardens and relict rain forest', 'lower montane mixed dipterocarp forest', '*Acacia mangium* plantation', and mangrove. Colonies have been collected from dead twigs of *Xylocarpa granatum* (in mangrove) and *Mallotus* sp. (rainforest edge), and from a dead twig of an unidentified woody plant, lying loose in a patch of *Gleichinia* fern (second-growth rainforest). Thus, it appears to be have generalised nesting habits. Colonies of *T. difficilis* that I encountered in Singapore were polydomous and had rather aggressive, actively stinging workers. This was in contrast to the more passive behavior of workers from sympatric colonies of *T. allaborans*, *T. extenuata*, and *T. nitida*.

Tetraponera inversinodis, sp. nov.

(Figs 101, 103, 109, 146, 160, 172)

Type material examined

Holotype. Worker, Kota Kinabalu, Sabah, Malaysia, 5°59′N 116°04′E, 14.x.1978 (B. B. Lowery) (ANIC).

Paratypes. Series of workers, alate queens, males, same data as holotype (ANIC, BMNH, FRCK, KUBC, KUEC, KUES, MCZC, PSWC, RMBR, UASK, UCDC, UMSC).

Other material examined

Indonesia: *Kalimantan Barat*: Gunung Palung Natl Pk, Cabanti Panti Res. Stn., 100–400 m (D. C. Darling *et al.*); Gunung Palung Natl Pk, Cabanti Panti Res. Stn., 100 m (D. C. Darling *et al.*); *Kalimantan Timur*: nr Bontang (S. Yamane). **Malaysia:** *Sabah*: Danum Valley (P. Eggleton); Danum Valley (E. Widodo); Forest Camp, 19 km N Kalabakan, 180 m (Y. Hirashima); Kota Kinabalu, 20 m (B. B. Lowery); Kota Kinabalu (S. Yamane); Quoin Hill, Tawau (Y. Hirashima); Umas Umas, nr Tawau (R. W. Taylor); *Sarawak*: Baco Natl Pk, nr Kuching (R. W. Taylor); G. Mulu Natl Pk (B. Bolton); G. Mulu Natl Pk (D. Hollis: B. Bolton); Gn. Mulu Natl Pk (H. Vallack); Gn. Mulu Natl Pk (M. Collins); sw Gunung Buda, 64 km S Limbang (S. L.Heydon; S Fung). **Philippines:** *Palawan*: Aborlan (C. K. Starr; M. J. P. Cañete).

(Collections: ANIC, BMNH, KUES, LACM, MCZC, PSWC, UMSC).

Worker measurements (*n* = *14*)

HW 0.77–0.94, HL 0.86–1.23, LHT 0.59–0.74, CI 0.77–0.89, FCI 0.13–0.15, REL 0.39–0.47, REL2 0.51–0.56, SI 0.55–0.59, SI3 1.01–1.13, FI 0.46–0.54, PLI 0.58–0.68, PWI 0.44–0.56, PDI 1.03–1.17, LHT/HW 0.77–0.82, CSC 2–3, MSC 1–3.

Worker description

Similar to *T. difficilis* except as follows: averaging smaller in size, FL 0.52–0.65 (0.60–0.73 in *T. difficilis*; compare also HW and LHT values); eyes more elongate, REL2 >0.50 and EL/LHT 0.64–0.70 (*T. difficilis*: REL2 0.44–0.48; EL/LHT 0.52–0.60); scape length exceeding eye length, but not markedly so (SI3 <1.15); profemur broader and shorter, FL/HL 0.53–0.62, EL/FL 0.74–0.82 (*T. difficilis*: FL/HL 0.60–0.67; EL/FL 0.60–0.66); profemur index (FI) values overlapping those of *T. difficilis*, but generally not within a given size class; hind leg shorter, LHT/HL 0.61–0.71 (*T. difficilis*: LHT/HL 0.67–0.80), and these values also not overlapping those of *T. difficilis* with the same head width (Fig. 123); petiole shorter, PL/HL 0.50–0.55 (*v.* 0.54–0.61 in *T. difficilis*), the anterior face of the node usually much shorter and more steeply inclined than the posterior face (Fig. 103). Standing pilosity even less common than in *T. difficilis*: CSC 2–3, MSC 1–3, dorsum of petiole and postpetiole usually lacking standing pilosity, rarely with several very short (0.03–0.06 mm long) erect or suberect setae. Appressed pubescence on abdominal tergite IV moderately dense, the hairs separated by their lengths or less.

Discussion

This species is closely related to, and sympatric with, *T. difficilis*, from which it can be consistently separated by the larger eye size. The differences in the shape of the profemur (shorter and broader in *T. inversinodis*) and length of the metatibia (shorter in *T. inversinodis*) are also diagnostic, when body size is taken into account (see Figs 122–123). Another generally useful feature for recognising *T. inversinodis* workers is the 'reversed-node' shape of the petiole, in which the anterior face of the node is short and steep and contrasts with the longer and more gently sloping posterior face (Fig. 103). In *T. difficilis* the node is usually more symmetrical in profile (Fig. 102). Some caution should be exercised in using this character, however, because it covaries with size, and the largest *T. inversinodis* workers (HW >0.85) have a petiole shape approaching that of *T. difficilis*.

Distribution and biology

Tetraponera inversinodis is known only from Borneo and the adjacent island of Palawan in the Philippines (Fig. 192). Most collections are from lowland rainforest but the type series was collected from mangrove twigs. Another Lowery collection has the habitat given as 'gardens and relict rain forest'.

Tetraponera laeviceps (F. Smith)

(Figs 86, 92, 131, 149, 163, 175)

Pseudomyrma laeviceps F. Smith, 1859: 145.
Sima humerosa Emery, 1900: 674. **Syn. nov.**
Sima (*Tetraponera*) *dentifera* Karavaiev, 1933: 266. **Syn. nov.**
Sima (*Tetraponera*) *platynota* Karavaiev, 1933: 269. **Syn. nov.**
Tetraponera laeviceps (F. Smith); F. Smith, 1877: 69. First combination in *Tetraponera*.

For a detailed nomenclatural history of *T. laeviceps* and its junior synonyms, see Bolton (1995: 417–419).

Type material examined

Pseudomyrma laeviceps F. Smith. Syntypes, 3 workers, Aru, Indonesia (Wallace) (BMNH, OXUM).

Sima humerosa Emery. Holotype (by monotypy), worker, 'N. Guinea' (H. Fruhstorfer) (MCSN).

Sima (*Tetraponera*) *dentifera* Karavaiev. Holotype (by monotypy), dealate queen, Wammar, Aru, Indonesia (Karavaiev) (UASK).

Sima (*Tetraponera*) *platynota* Karavaiev. Syntype, worker, Wammar, Aru, Indonesia [labeled '5365'] (Karavaiev) (UASK).

Other material examined

Australia: *Queensland*: 10 mi. N Cairns (R. W. Taylor); 11 km ENE Mt Tozer (T. Weir; A. Calder); 6 km SSW Cape Tribulation, <5 m (P. S.Ward); 9 km ENE Mt Tozer (T. Weir; A. Calder); Bamaga, Cape York Penn. (J. Sedlacek); Bellenden Ker Range, Cableway Base Stn., 100 m (Earthwatch/Qld Museum); Cairns (R. W. Taylor); Cairns dist. (A. M. Lea); Cape Tribulation, <5 m (P. S. Ward); Cooper Ck, near Daintree (R. W. Taylor; J. Feehan); East Claudie R., Iron Range (G. Monteith; D. Cook); Iron Range, Cape York Penn. (J. Sedlacek); Leo Ck (B. Gray); Lockerbie Scrub, Cape York (G. B. Monteith); Lockerbie, Cape York Penn. (J. Sedlacek); Mt Webb Natl Pk (J. C. Cardale). **Indonesia:** *Irian Jaya*: 50 km S Manokwari, Arfak Mtns Nature Res, 25 m (G. D. Alpert); Maffin Bay (E. S. Ross); *Maluku*: Piroe, Ceram (W. M. Mann); Pulau Morotai [as 'Morty I.'] (A. R. Wallace). **Papua New Guinea:** *Central*: Bisianumu, nr Sogeri, 500 m (E. O. Wilson); Bisianumu, Port Moresby (W. N. Lock); Brown R. (B. B. Lowery); *c.*15 mi. N Port Moresby, Rubulogo Ck (R. Pullen); *East Sepik*: Cape Moem, 7 km E Wewak, <5 m (P. S. Ward); *Gulf*: Ivimka camp, Lakekamu Basin, 110–120 m (R. R. Snelling); Ivimka camp, Lakekamu Basin, 120 m (R. R. Snelling); *Madang*: 40 km W Madang, 140 m (P. S. Ward); 8 km N Madang, <5 m (P. S. Ward); Laing Is., Hansa Bay (J. M. Pasteels); Nobonob Hill, 7 km NW Madang (M. Wasbauer); Tab I., 7 km NE Madang, <5 m (P. S. Ward); *Manus*: Manus I., Sabon 2, 10 km W Lorengau (W. L. Brown); *Morobe*: Bulolo R. valley, 6 km NE [sic] Wau, 1100 m (R. W. Taylor); Bulolo, 2300 ft (B. B. Lowery); Bupu R. area, Lae (B. B. Lowery); Buso For. (J. H. Martin); Didiman Ck., Lae (E. O. Wilson); lower Busu R., Huon Penin. (E. O. Wilson); Nadzab (E. O. Wilson); Surprise Ck (Stevens); *North Solomons*: Bougainville: Torokina R., Empress Augusta Bay (B. D. Valentine); *Northern*: 12 mi. N Popondetta (B. B. Lowery); near Popondetta, <50 m (R. W. Taylor); *Western*: Fly R. (L. M. D'Albertis). **Solomon Is:** *Central*: Nggela: Rara (P. Greenslade); *Guadalcanal*: Honiara, 0–200 m (N. L. H. Krauss); Kukum (P. Greenslade); Mt Austen (P. Greenslade); *Isabel*: Buala [as 'Buab'] (P. Greenslade); Buala [as 'Ruala'] (P. Greenslade); Fulakora (W. M. Mann).

(Collections: AMNH, ANIC, BMNH, CASC, KUEC, KUES, LACM, MCSN, MCZC, PSWC, UASK, UMSC, USNM).

Worker measurements (n = 21)

HW 0.75–0.91, HL 0.86–1.10, LHT 0.63–0.78, CI 0.81–0.87, FCI 0.12–0.16, REL 0.40–0.45, REL2 0.46–0.53, SI 0.52–0.60, SI3 1.02–1.20, FI 0.43–0.51, PLI 0.45–0.59, PWI 0.40–0.49, PDI 1.11–1.34, LHT/HW 0.77–0.87, CSC 1–25, MSC 4–42.

Worker description

Medium-sized species, with relatively broad head; clypeus short, its anteromedial portion protruding only slightly beyond level of the anterolateral clypeal margin (Fig. 86); distance between frontal carinae approximately equal to maximum scape width; eye relatively large (see REL and REL2 values); scape length exceeding eye length; profemur moderately robust (see FI values); pronotum slightly to strongly expanded laterally (PrWM/MTW 1.15–1.37), its anteromedial surface varying from convex to slightly concave; lateral pronotal margins present, blunt-edged; mesopropodeal impression well marked but short, consisting of a pit-shaped depression, flanked by lateral ridges; propodeum usually conspicuously elevated, always notably higher than wide (PDI >1.10), its dorsal face varying in profile from strongly convex and peaking far forward, above the propodeal spiracle, to broadly convex and somewhat flattened; dorsal face of propodeum rounding gradually into declivitous face; petiole relatively slender (PLI <0.60, PWI <0.50), with well differentiated anterior peduncle and node (Fig. 92); petiole somewhat variable in size and shape (PL/HW 0.68–0.96, PL/HL 0.59–0.80, DPW/MTW 0.61–0.86; see also range of PLI and PWI values); postpetiole approximately as long as wide; metabasitarsal sulcus well developed, lying in a darkened patch of cuticle and adjacent to a low carina that occupies about 0.3–0.6× the length of the basitarsus. Integument with numerous small-medium punctures, interspaces smooth and shiny; larger punctures on dorsum of head and mesosoma 0.010–0.015 mm in diameter and separated by one to several diameters (occasionally denser on the pronotum); sculpture weaker elsewhere on mesosoma and petiole; integument largely smooth and shiny on side of pronotum, anterior part of mesepisternum, and side of petiole; postpetiole and gaster finely puncticulate, sublucid; lower malar area rugulopunctate. Standing pilosity varying from sparse to moderately common (see range of CSC and MSC values), when common then often grading into shorter, subdecumbent pubescence; appressed pubescence common on most of body, especially dense on postpetiole and abdominal tergites. Black to dark brownish-black, appendages variably lighter (scape, protibia and tarsi often contrastingly yellow-brown).

Discussion

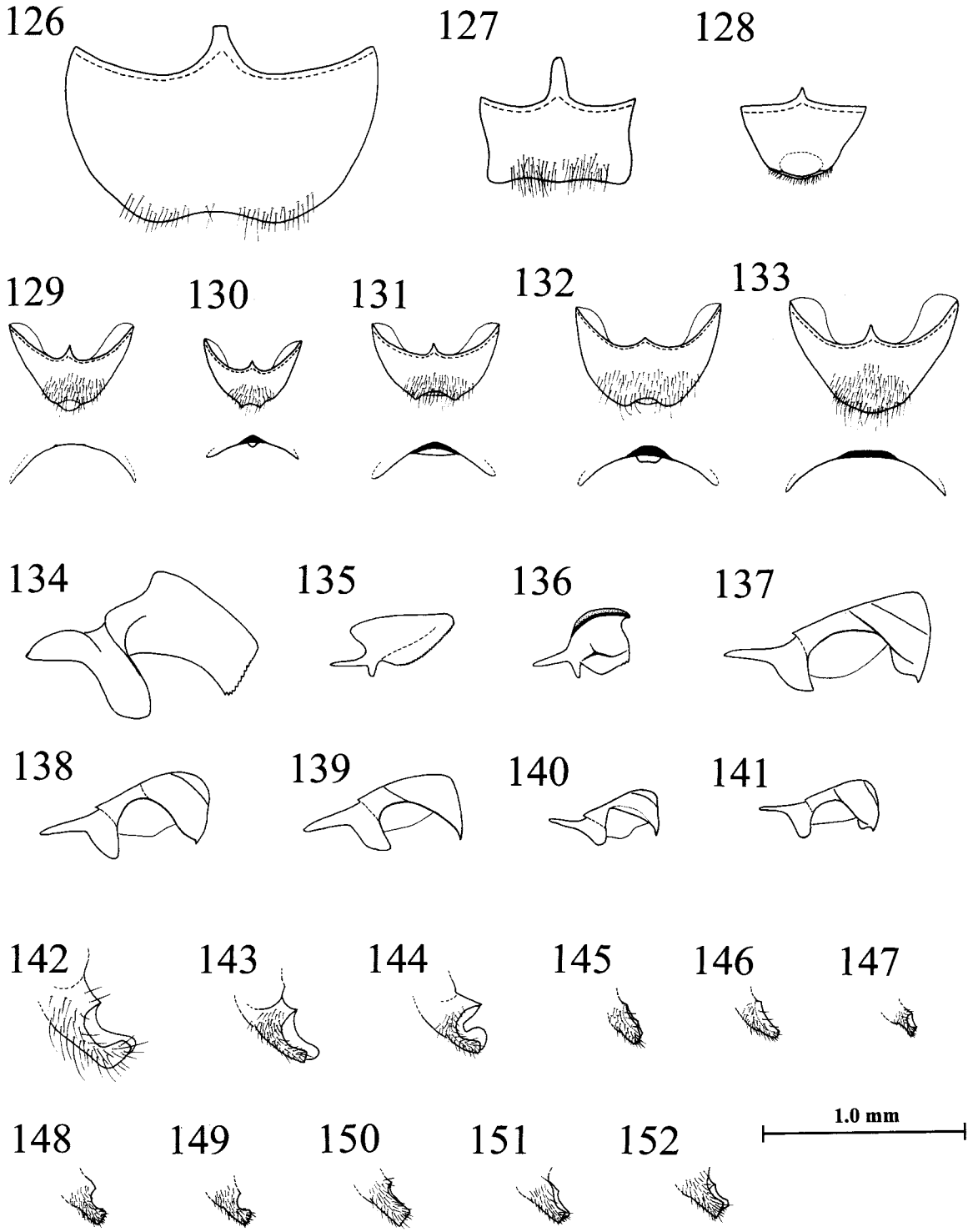
Workers of *T. laeviceps* can be distinguished from those of related species by: (*1*) the relatively large punctures on the head (0.010–0.015 mm in diameter), separated by one or more diameters, with the interspaces smooth and shiny; (*2*) the moderate distance between the frontal carinae (MFC approximately equal to maximum scape width); (*3*) the relatively large eyes (see ocular indices); (*4*) the elevated propodeum; and (*5*) the relatively slender petiole.

As here interpreted, *T. laeviceps* is a polytypic species, showing considerable variation in head shape, sculpture, width of the pronotum, configuration of the propodeum, and shape of the petiole. The syntype workers of *T. laeviceps* conform to the following facies (with measurements given for the syntype in OXUM): rather broad shiny head (CI 0.86), narrow pronotum without well-developed humeral angles (PrWM/HW 0.60, PrWM/MTW *c.* 1.15), relatively low propodeum (PDI *c.* 1.13), and short petiole (PLI 0.59; PL/HW 0.69). In contrast the worker types of *T. humerosa* and *T. platynota* have the pronotum more expanded laterally, the propodeum more conspicuously elevated, and the petiole more elongate (PLI *c.* 0.45 in *T. platynota*); the head is broad in *T. humerosa* (CI *c.* 0.90), more elongate in *platynota* (CI 0.84). Available non-type specimens include a panoply of intermediate phenotypes, suggesting the existence of a single variable species, although most specimens tend to have rather broad pronota and long petioles. More material is needed from the poorly sampled western part of the distribution (Irian Jaya and Maluku). If future investigation does indicate that there are two species here, then the name *T. humerosa* (with junior synonyms *platynota* and *dentifera*) is available for the form with the prominent humeri and elongate petiole. Possible morphometric differences between the two forms are indicated below. It is worth stressing that sample sizes for these measurements are small, *n* = 3 for *T. laeviceps* (s.s.) and *n* = 18 for *T. humerosa*-like workers, with most of the latter coming from Papua New Guinea and all of the *T. laeviceps* (s.s.) from farther west. As more material accumulates, especially from geographically intermediate locations, these differences may disappear.

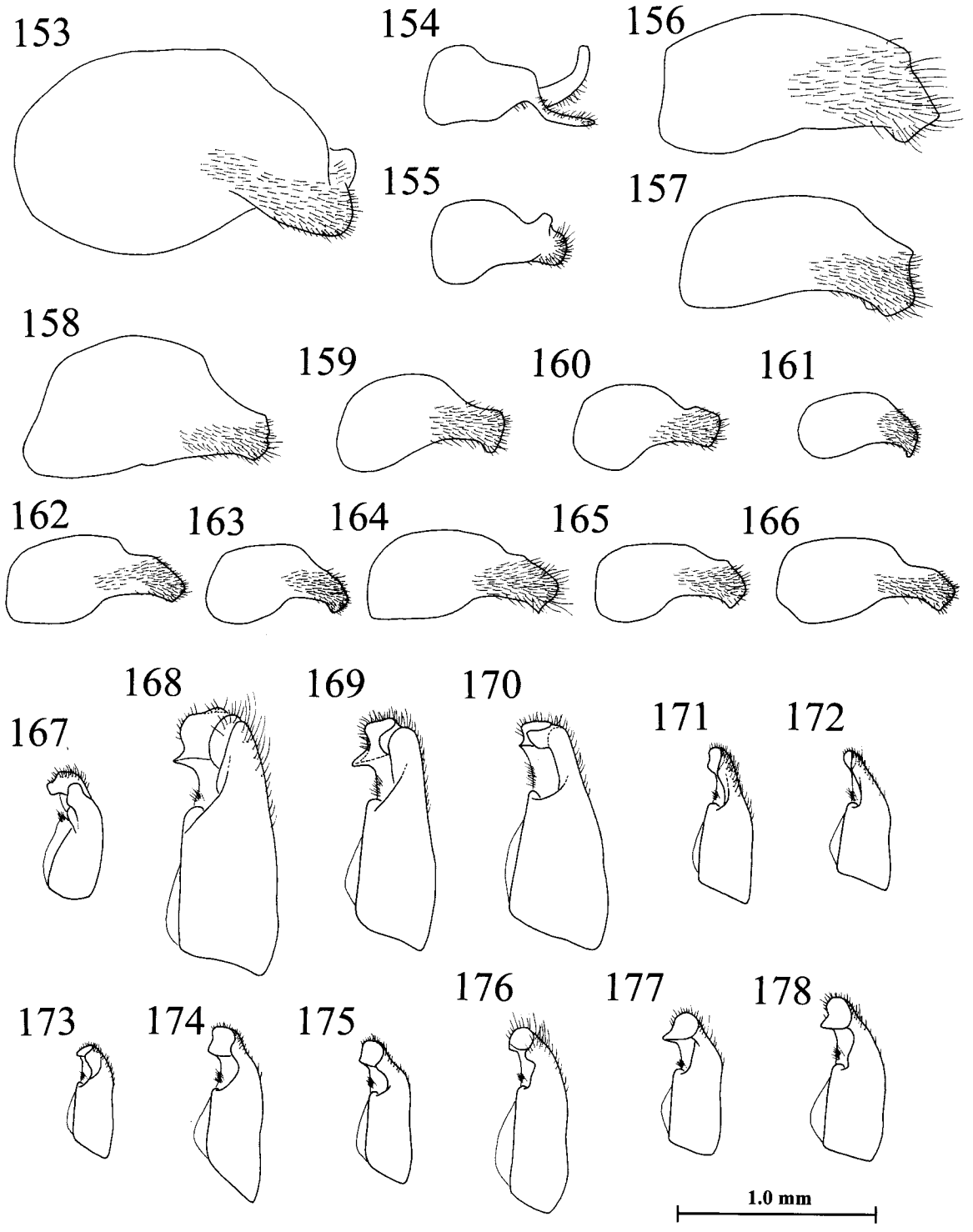
	T. laeviceps (s.s.)	*T. humerosa*-like
PrWM/HW	0.59–0.60	0.62–0.69
PL/HW	0.68–0.69	0.81–0.96
PL/LHT	0.84–0.90	0.96–1.11
DPW/HW	0.30–0.34	0.35–0.44

Distribution and biology

As the species is treated here *T. laeviceps* ranges from Maluku to the Solomon Is, south through the main island of New Guinea to northern Australia (Fig. 194). Habitat records include secondary forest, littoral vegetation, and rainforest. The species appears to be an opportunistic colonist of dead plant cavities. I have found colonies in dead twigs of



Figs 126–152. *Tetraponera* males, ventral view of sternite IX, anterior margin uppermost (*126–133*), paired posterior view of sternite IX, ventral surface uppermost (*129–133*), lateral view of aedeagus, left side (*134–141*), and posterior view of left paramere (*142–152*). *126*, *134*, *T. rufonigra* (Singapore); *127*, *135*, *T. pilosa* (Malaysia); *128*, *136*, *T. allaborans* (India); *129*, *140*, *145*, *T. difficilis* (Singapore); *130*, *147*, *T. nitida* (Papua New Guinea); *131*, *149*, *T. laeviceps* (Papua New Guinea); *132*, *141*, *152*, *T punctulata* (Australia); *133*, *139*, *144*, *T. attenuata* (Malaysia); *137*, *142*, *T. binghami* (Malaysia); *138*, *143*, *T. nigra* (India); *146*, *T. inversinodis* (Malaysia); *148*, *T. atra* (Papua New Guinea); *150*, *T. tucurua* (Australia); *151*, *T. rotula* (Australia).



Figs 153–178. *Tetraponera* males, lateral view (*153–166*) and dorsal view (*167–178*) of left paramere. *153*, *T. rufonigra* (Singapore); *154*, *T. pilosa* (Malaysia); *155*, *167*, *T. allaborans* (India); *156*, *168*, *T. binghami* (Malaysia); *157*, *169*, *T. nigra* (India); *158*, *170*, *T. attenuata* (Malaysia); *159*, *171*, *T. difficilis* (Singapore); *160*, *172*, *T. inversinodis* (Malaysia); *161*, *173*, *T. nitida* (Papua New Guinea); *162*, *174*, *T. atra* (Papua New Guinea); *163*, *175*, *T. laeviceps* (Papua New Guinea); *164*, *176*, *T. tucurua* (Australia); *165*, *177*, *T. rotula* (Australia); *166*, *178*, *T. punctulata* (Australia).

Hibiscus tiliaceus, *Gnetum* sp., *Premna serratifolia*, *Ximenia americana*, and unidentified vines, shrubs and small trees. There are also records of workers from the foliage and trunks of recently felled rainforest trees, in both New Guinea and northern Australia (Cape York).

Tetraponera mimula, sp. nov.

(Figs 87, 93)

Type material examined

Holotype. Worker, Bulolo R. valley, 6 km NE [sic] Wau, Papua New Guinea, 1100 m, vi.1962 (R. W. Taylor #2048) (ANIC). Locality is actually north-west of Wau.

Paratype. Worker, same data as holotype (PSWC).

Other material examined

Papua New Guinea: *Gulf*: Ivimka camp, Lakekamu Basin, 200 m (R. R. Snelling) (1 worker) (LACM).

Worker measurements ($n = 3$)

HW 0.87–0.94, HL 1.01–1.08, LHT 0.66–0.78, CI 0.82–0.87, FCI 0.17–0.19, REL 0.36–0.39, REL2 0.41–0.45, SI 0.50–0.54, SI3 1.11–1.28, FI 0.49–0.50, PLI 0.58–0.61, PWI 0.55–0.57, PDI 1.10–1.15, LHT/HW 0.77–0.83, CSC 3–5, MSC 11–18.

Worker description

Medium-sized species, with relatively broad head; similar to *T. laeviceps* in many respects, but frontal carinae more widely separated, the distance between them clearly exceeding maximum scape width; eyes smaller (Fig. 87), REL <0.40, REL2 <0.46; profemur more robust than that of most *T. laeviceps* workers (see FI values); pronotum relatively narrow (PrWM/HW 0.57–0.60, PrWM/MTW 1.04–1.16), its maximum width occurring below the lateral margins; anteromedial surface of pronotum essentially flat; propodeum moderately elevated (see PDI values), its dorsal face somewhat flattened in profile, declining posteriorly, and more or less differentiated from the declivitous face (Fig. 93); petiole relatively short and broad (see PLI and PWI values); postpetiole broader than long; metabasitarsal sulcus well developed, lying in a patch of darkened, raised cuticle occupying a little more than half the length of the basitarsus. Integument sculpture as in *T. laeviceps*, punctures rather dense (subcontiguous) on anteriormost portions of head and pronotum. Standing pilosity moderately well developed (see CSC and MSC values); appressed pubescence common on most of body, dense on postpetiole and abdominal tergites. Black to dark brownish-black, mandibles, antennae, protibia and tarsi medium brown.

Discussion

This species is closely similar to *T. laeviceps*, but it can be diagnosed by a suite of worker traits: the eyes are smaller (see REL and REL2 values), the frontal carinae are farther apart (FCI ~ 0.18), and the petiole is shorter and broader (compare PWI values). The index, MFC/EL, provides the sharpest distinction: 0.38–0.45 in *T. mimula* and 0.25–0.30 in *T. laeviceps*. Most *T. laeviceps* workers also have a more slender profemur, broader pronotum, and more elevated propodeum than those of *T. mimula* but *T. laeviceps* is sufficiently variable that these differences are not diagnostic (FI, PrWM/MTW and PDI values overlap). *T. mimula* is known from only two localities and at both of these it is sympatric with *T. laeviceps*, strengthening the inference that these are two different species.

Distribution and biology

Tetraponera mimula is known from two locations in Papua New Guinea. The types were collected 'ex trunks and tops of felled trees' in rainforest at 1100 m. A more recent collection by Roy Snelling was made in lowland rainforest.

Tetraponera nigra (Jerdon)

(Figs 64, 68, 138, 143, 157, 169)

Eciton nigrum Jerdon, 1851: 112.
Tetraponera atrata F. Smith, 1852: 44. Synonymy by Dalla Torre, 1893: 54; here confirmed.
Tetraponera petiolata F. Smith, 1877: 70. **Syn. nov.**
Sima nigra var. *insularis* Emery, 1901: 113. **Syn. nov.**
Sima nigra r. *Fergusoni* Forel, 1902: 248. **Syn. nov.**
Sima nigra var. *Krama* Forel, 1912*a*: 105. **Syn. nov.**
Tetraponera nigra (Jerdon); F. Smith, 1877: 68. First combination in *Tetraponera*.

For a detailed nomenclatural history of *T. nigra* and its junior synonyms see Bolton (1995: 417–419).

Types (*not examined*)

Eciton nigrum Jerdon. Syntypes, workers, queens, southern India [types lost]. From original description: 'rare in Malabar, but tolerably common in parts of the Carnatic'.

Type material examined

Tetraponera atrata F. Smith. Syntype, dealate queen, Bombay, India (Downes) (BMNH).

Tetraponera petiolata F. Smith. Syntype, dealate queen, 'Ceylon' (BMNH). Note: original description also includes worker and male.

Sima nigra var. *insularis* Emery. Syntypes, 2 workers, 'Ceylon' (Horn) (MCSN). Note: original description includes queen.

Sima nigra r. *Fergusoni* Forel. Holotype (by monotypy), worker, Travancore, India (Ferguson) (MHNG).

Sima nigra var. *Krama* Forel. Syntype, queen, Batavia, Java, Indonesia (E. Jacobson) (MHNG).

Other material examined

India: *Andhra Pradesh*: 15 mi SW Rajahmundry, 15 m (E. S. Ross; D. Q. Cavagnaro); *Karnataka*: 5 mi W Hunsur, 850 m (E. S. Ross; D. Q. Cavagnaro); Bangalore (S. Kumar; S. Hari); Bangalore (Rothney); Bangalore (T. C. Lawrence); I.I.Sc. Campus, Bangalore (P. Nair); Kabini (D. McKey); Ranganathittu Bird Sanct., 710 m (P. S. Ward); *Kerala*: Aralam [as 'Aaralum'] (c.u.); Calicut (A. P. Rosy); Calicut University campus (S. Sheela); Calicut University, 20 m (P. S. Ward); Changanacherry (A. B. Soans); Irinjalakuda, Trichur Dist. (A. B. Soans); Muthanga (P. S. Ward); Nilambur (A. B. Soans); S. Malabar (P. S. Nathan); Talasseri [as 'Thalassery'] (c.u.); Travancore (Ferguson); *Madhya Pradesh*: 9 mi N Pharasgaon, 580 m (E. S. Ross; D. Q. Cavagnaro); *Maharashtra*: Bombay (J. C.Bridwell); Bombay (Mathéran); Poona (Wroughton); Poona (c.u.); Savantvad (J. C.Bridwell); *Orissa*: Puri [as 'Pooree'] (Walsh); Puri [as 'Pooree'] (Walker); *Pondicherry*: Karikal (P. B. Nathan); *Tamil Nadu*: 19 km E Oothu (D. McKey); 5 mi SW Nanguneri, 125 m (E. S. Ross; D. Q. Cavagnaro); Dohnavur, Tinnevelly Dist., 350 ft (B.M. –C.M. Expdn. to S. India); Madras (Rothney); Madras (c.u.); Mudumalai Anim. Sanct. (J. Noyes); *Uttar Pradesh*: Ranipur, 6 km S Hardwar, 300 m (A. K. Mehrotra); vic. Rajaji Natl Pk, 10 km NW Rickikesh, 300–500 m (A. Schulz; K. Vock); vic. Rajaji Natl Pk, 10 km SE Dehra Dun, 600–700 m (A. Schulz; K. Vock); *West Bengal*: Baragachi [as 'Baigachi'] (L. H. Weatherill); Barakpur [as 'Barrackpore'] (L. H. Weatherill); Calcutta (Rothney); Calcutta (E. S. Ross; D. Q. Cavagnaro); Calcutta (c.u.). **Indonesia:** *Kalimantan Selatan*: 22 km E Bandjarmasin (W. L. Brown). **Malaysia:** *Negeri Sembilan*: Pasoh For. Res. (M. Brendell *et al.*); *Sabah*: Sepilok Forest Res., nr Sandakan (R. W. Taylor). **Myanmar:** *Chin*: Chin Hills (Watson); *Pegu*: Palon, Pegù (L. Fea); *Yangon*: Rangoon (G. E. Gates). **Nepal:** *Narayani*: Amlekganj, 520 m (E. I. Coher). **Pakistan:** *Sind*: Karachi [as 'Kurrachee'] (Maindron). **Sri Lanka:** *Central*: Dambulla (Horn); Kandy (Simon); Peradeniya (R. Winney); Peradenyia (Bugnion); *North Central*: Anuradhapura (A. E. Stubbs; P. J. Chandler); Pollonaruwa (K. L. A. Perera); *North Eastern*: Maha-Oya Dist. (R. Winney); *Southern*: Ruhunu Natl Pk (Univ. London Ceylon Expdn.); Yala (U. Maschwitz); *Uva*: Bibile (R. Winney); Egodapitiya Nilgala (P. B. Karunaratne; T. F. Halstead); *Western*: Padukka Group Estate, 3 mi S Padukka Rubber Estate (T. F. Halstead); Yakkala (K. L. A. Perera); *district unknown*: 'Ceylon' (Bugnion); 'Ceylon' (Escherich); 'Ceylon' (Yerbury); 'up-country/ Ceylan' (E. Bugnion). **Thailand:** *Chiang Mai*: E slope, Doi Sutep, 875–950 m (E. S. Ross; D. Q. Cavagnaro); Obluang (D. Wiwatwitaya); *Krung Thep Mahanakhon*: Bangkok (E. G. Alexander); *Lumpang*: Huai Tak (c.u.); *Phangnga*: Khao Lak (A. Schulz; K. Vock); *Ranong*: Ranong (D. H. Murphy); *Satun*: Thale Ban NP, 20–30 km E Satun, 200–400 m (A. Schulz; K. Vock); *province unknown*: Pahtoop Mts. (T. D. A. Cockerell).

(Collections: AMNH, ANIC, BMNH, CASC, CESB, DZUC, KUBC, KUEC, KUES, LACM, MCSN, MCZC, MHNG, MNHN, NHMV, PSWC, UMSC, USNM).

Worker measurements (n = 14)

HW 0.99–1.38, HL 1.18–1.60, LHT 1.00–1.48, CI 0.76–0.89, FCI 0.13–0.17, REL 0.28–0.33, REL2 0.32–0.38, SI 0.60–0.70, SI3 1.55–2.07, FI 0.38–0.42, PLI 0.52–0.64, PWI 0.41–0.51, PDI 1.02–1.10, LHT/HW 0.93–1.11, CSC 10–24, MSC 6–50.

Worker description

Relatively large, black species; head moderately broad (CI usually >0.80); clypeus short, its anteromedial margin convex and often weakly crenulate (Fig. 64); distance between frontal carinae equal to or exceeding maximum scape width; eyes relatively small (see REL, REL2 and SI3 values); with head in full-face view lateral margins rounding into straight or slightly convex posterior margin; profemur slender; pronotum with lateral margins weakly to moderately developed; mesopropodeal impression well developed and relatively open, flanked by low metanotal tubercles that are usually clearly visible in profile (Fig. 68); propodeum slightly higher than wide, dorsal face rounding gradually into the declivitous face and varying from somewhat flattened to strongly convex in profile; legs long relative to head size, LHT/HL 0.81–0.97; petiole with distinctly differentiated peduncle and node (Fig. 68); petiole less than twice as long as high (PLI >0.50) and 2.0–2.4× longer than broad; postpetiole varying from slightly longer than broad to broader than long; metabasitarsal sulcus well developed, often darker than the surrounding cuticle, and lying adjacent to a raised ridge of variable length (from 0.2× to 0.6× the length of the basitarsus). Integument with numerous small punctures, the interspaces sublucid and finely reticulate; sculpture becoming more effaced, and integument correspondingly shinier, on side of mesosoma and on petiole, postpetiole and gaster; punctures on dorsum of head and mesosoma mostly 0.005–0.015 mm in diameter and separated by one to several diameters; lower malar area with coarser punctures, sometimes intermixed with irregular longitudinal rugulae. Standing pilosity common on much of body (CSC >9, MSC usually >10) (Fig. 68), often grading into shorter suberect and decumbent pubescence; the latter may be especially conspicuous on the propodeum, petiolar and postpetiolar nodes, gaster and legs, but is generally absent from the pronotum where the pubescence consists mostly of short, appressed hairs. Black to brownish-black, appendages usually more or less concolorous, but scape and first several funicular segments may be lighter.

Discussion

Workers of *T. nigra* can be distinguished from those of related species (*T. attenuata*, *T. binghami* and *T. buops*) by the short robust petiole (PLI >0.50) (Fig. 68). In addition, *T. nigra* workers can be separated from those of *T. attenuata* by the sparser pubescence on the pronotum and from those of *T. binghami* and *T. buops* by the better-developed background sculpture on the head (interspaces between cephalic punctures finely reticulate as opposed to predominantly smooth and shiny). The head is also generally broader in *T. nigra* (CI rarely <0.80) than in *T. binghami* and *T. buops* (CI 0.70–0.78).

Tetraponera nigra workers exhibit variation in pilosity (especially the number of standing hairs on the mesosoma dorsum: see range of MSC values), integument sculpture, propodeum shape, and head shape, at both local and broad geographical scales. Variation in head shape is even more pronounced in the queens, with CI ranging from 0.68 to 0.82 in a sample of five queens from southern India. The queen

with the most elongate head (CI 0.68) is part of a nest series from Kabini, Karnataka (D. McKey #46), taken from live branches of *Stereospermum personatum*. The workers in this series also have unusually long heads (CI ~ 0.76–0.77), but a second *Stereospermum* nest series from the same locality (D. McKey #47) has otherwise similar workers whose heads are more typically broad: CI 0.82–0.85 (no queen available from this second series). This would appear to be yet another example of the substantial within-population variation that can occur in *Tetraponera* species.

Distribution and biology

The range of *T. nigra* encompasses much of the Indian subcontinent (Pakistan, India, Sri Lanka) and Southeast Asia south to Java and Borneo (Fig. 190). Habitats from which the species has been recorded include tropical dry forest, riparian forest, semideciduous forest, rainforest, 'kerangas woodland' and mangrove. Most nest series come from dead twigs or branches but Doyle McKey collected colonies from live stems of *Stereospermum personatum* (Kabini, Karnataka) and from live thorns of *Acacia horrida* (19 km E Oothu, Tamil Nadu), indicating that the species is a facultative inhabitant of live plant cavities.

Tetraponera nitida (F. Smith)

(Figs 71–73, 79–80, 82, 130, 147, 161, 173)

Pseudomyrma nitida F. Smith, 1860: 106.
Pseudomyrma carbonaria F. Smith, 1863: 20. **Syn. nov.**
Sima brevicornis Emery, 1900: 675. **Syn. nov.**
Sima siggi Forel, 1902: 246. **Syn. nov.**
Sima difficilis r. *longiceps* Forel, 1902: 247. **Syn. nov.**
Sima Siggii var. *nebulosa* Forel, 1903*b*: 404. **Syn. nov.**
Sima (*Tetraponera*) *siggi* var. *setifera* Viehmeyer, 1916: 119. **Syn. nov.**
Sima (*Tetraponera*) *bidentata* Karavaiev, 1933: 264. **Syn. nov.**
Sima (*Tetraponera*) *bidentata* var. *angusticeps* Karavaiev, 1933: 266. **Syn. nov.**
Tetraponera (*Tetraponera*) *maffini* Donisthorpe, 1948: 591. **Syn. nov.**
Tetraponera shankouensis Zhou & Jiang, 1997: 72. **Syn. nov.**
Sima nitida (F. Smith); Dalla Torre, 1893: 54.
Sima siggii Forel; Forel, 1909*a*: 226. Description of queen.
Sima (*Tetraponera*) *nitida* (F. Smith); Emery, 1921: 26.
Tetraponera nitida (F. Smith); Donisthorpe, 1932: 462. First combination in *Tetraponera*.

For additional details on the nomenclatural history of *T. nitida* and its junior synonyms, consult Bolton (1995: 417–419).

Type material examined

Pseudomyrma nitida F. Smith. Holotype (by monotypy), worker, Bachian [labeled 'Bac.'], Indonesia (Wallace) (OXUM).

Pseudomyrma carbonaria F. Smith. Syntype, worker, Bouru [labeled 'B'], Indonesia (Wallace) (OXUM). Note: original description also includes queen.

Sima brevicornis Emery. Holotype (by monotypy), worker, Quruña [labeled 'Qurugna'], Luzon, Philippines (Simon) (MCSN).

Sima siggi Forel. Syntypes, 6 workers, Bangkok, Thailand (Sigg) (MCSN, MHNG).

Sima difficilis r. *longiceps* Forel. Syntypes, 10 workers, Travancore, India (Ferguson) (MCSN, MHNG, NHMB).

Sima siggii var. *nebulosa* Forel. Syntype (unique?), worker, Alexandra Kajar, Great Nicobare, India (MHNG).

Sima (*Tetraponera*) *siggi* var. *setifera* Viehmeyer. Syntypes, 2 workers, 1 dealate queen, Singapore (H. Overbeck) (ZMHB).

Sima (*Tetraponera*) *bidentata* Karavaiev. Syntypes, 2 workers, Buitenzorg, Java, Indonesia (Karavaiev) (UASK).

Sima (*Tetraponera*) *bidentata* var. *angusticeps* Karavaiev. Holotype (by monotypy), worker, Buitenzorg, Java, Indonesia (Karavaiev) (UASK).

Tetraponera (*Tetraponera*) *maffini* Donisthorpe. Holotype (by monotypy), dealate queen, Maffin Bay, Indonesia (E. S. Ross) (CASC).

Tetraponera shankouensis Zhou & Jiang. Holotype, worker, Shankou Mangrove Natural Reserve, 10 m, Guangxi, China (R. Wu) (GNUC) [not examined]; 3 paratype workers, same data [examined] [sent by Zhou to Ward].

Other material examined

Australia: *Northern Territory*: 3 mi NE Darwin (W. L. Brown); 7 km NW by N of Cahills Crossing (R. W. Taylor); Baroalba Spring (R. W. Taylor); Berry Springs, nr Darwin (B. B. Lowery); Black Point, Cobourg Penn. (E. D. Edwards); Darwin (R. Mercer); Darwin (W. L. Brown); Darwin (Weatherill); Howards Springs, near Darwin (B. B. Lowery); Litchfield Natl Pk, near Wangi Falls (B. B. Lowery); Port Darwin (N. E. Gee); Rimbija Is., Wessel Is (E. D. Edwards); Robins Falls, 5 km SSE Adelaide R., 80 m (D. Hlavaty); slopes above Baroalba Spring (R. W. Taylor); *Queensland*: 11 km ENE Mt Tozer (T. Weir; A. Calder); 30 mi. N Cairns (R. W. Taylor); 3 km NNW Shute Hbr., 40 m (P. S. Ward); 4 km ENE Cairns, <5 m (P. S. Ward); Alexandra Range, 10 km N Daintree (B. B. Lowery); Barron Falls Gorge (B. B. Lowery); Cairncross West I., Great Barrier Reef (H. Heatwole); Cairns (L. Weatherill); Cairns North, <5 m (P. S. Ward); Cape Tribulation, <5 m (P. S. Ward); Edge Hill, Cairns (B. B. Lowery); Finch Hatton Gorge, 200 m (R. W. Taylor; T. A. Weier); Giru (B. B. Lowery); Giru Cromarty Landing (B. B. Lowery); Green I., <5 m (P. S. Ward); Ingram I. (R. C. Buckley); Jourama Natl Pk, 20 km S Ingham (B. B. Lowery); Lakefield Natl Pk, 75 km N Laura (G. Monteith); Lockerbie, Cape York Penn. (J. Sedlacek); Mt Garnet (B. B. Lowery); Mt Jim Crow, 80 m (P. S. Ward); Nymph I., Gt. Barrier Reef (H. Heatwole); Port Douglas (B. Hölldobler); Russell R., at Bellenden Kerr Landing, 5 m (Earthwatch/Qld Museum); Sarina (B. B. Lowery); Scraggy Pt, Hinchinbrook I., 5 m (P. S. Ward); Torres Strait, Moa (=Banks) I., nr St Paul's Mission (H. Heatwole; E. Cameron); Tozer's Gap (R. W. Taylor; J. Feehan); *Western Australia*: SW Osborne I., Kimberley region (J. D. Majer). **Brunei:** Labi (I. Gauld). **China:** *Hong Kong*: Lantau I.: Shui Hau, 20–50 m (R. R. Snelling); N.T.: Three Fathom Cove (J. R. Fellowes). **India:** *Andaman and Nicobar Is.*: Alexandra Is., Andaman Is. (G. Rogers); Andaman Is. (G. Rogers); S. Andaman Is. (G. Rogers). **Indonesia:** *Aceh*: Labuan Bajau [as 'Labuan Badjau'] (E. Jacobson); *Irian Jaya*: 50 km S Manokwari, Arfak Mtns Nature Res, 25 m (G. D. Alpert); Fakfak (H. Smith); Maffin Bay (E. S. Ross); Manokwari (island in bay) (G. D. Alpert); *Kalimantan Barat*: Gunung Palung Natl Pk, Cabanti Panti Res. Stn., 100–400 m (D. C. Darling *et al.*); *Kalimantan Selatan*: 22 km E Bandjarmasin (W. L. Brown); Pulau Laut, *c.* 6 km E Stagen dock, SE Borneo (W. L. Brown); *Kalimantan Timur*: Kutai (T. Yajima); *Lampung*: Krakatau (E. Jacobson); *Nusa Tenggara Timur*: Sumba: Melolo (Exp. Bühler-Sutter); *province unknown*: 'Java' (Jacobson); 'Java/Shandigar[?]' (c.u.). **Malaysia:** *Johor*: 11 km NE

Kota Tinggi, 40 m (P. S. Ward); *Melaka*: Melaka [as 'Malacca'] (Saida); *Negeri Sembilan*: Pasoh Forest Reserve (K. Rosciszewski); Port Dickson (N. L. H. Krauss); Sungai [as 'Sungei'] Menyala For. Res., nr Port Dickson (W. L. Brown; T. Y. Pong); *Sabah*: Danum Valley (P. Eggleton); Kota Kinabalu (B. B. Lowery); Poring Spring, >650 m (A. Floren); Sandakan (Baker); Sepilok Forest (S. Yamane); Tunku Abdul Raman Natl Pk, 0–250 m (B. B. Lowery); *Sarawak*: Bako Natl Pk (D. H. Janzen); Bako NP, N Kuching (H. Zettel); s Gunung Buda, 64 km S Limbang (S. L. Heydon; S. Fung); sw Gunung Buda, 64 km S Limbang (S. L. Heydon; S. Fung); Tower Region, Lambir Natl Pk, Miri (S. Yamane); *Selangor*: Ulu Gombak Field Stn. (A. Buschinger); *Terengganu*: P. Perhentian Besar (Madl). **Papua New Guinea:** *Central*: Brown R. (B. B. Lowery); Karema (E. O. Wilson); Musgrave R., nr Port Moresby (D. H. Colless); *East Sepik*: Cape Moem, 7 km E Wewak, <5 m (P. S. Ward); Cape Wom, <5 m (P. S. Ward); *Gulf*: Ivimka camp, Lakekamu Basin, 180 m (R. R. Snelling); *Madang*: 40 km W Madang, 140 m (P. S. Ward); 8 km N Madang, <5 m (P. S. Ward); Ameria, Madang Dist. (B. Gray); Hansa Bay, Bogia Dist. (J. M. Pasteels); Nobonob Hill, 7 km NW Madang (M. Wasbauer); *Manus*: Lorengau (P. M. Room); Ndrilo (P. M. Room); *Milne Bay*: KB Mission, Milne Bay (K. V. Krombein); *Morobe*: Bulolo R. flats (B. B. Lowery); Bulolo R. valley, 6 km NE [sic] Wau, 1100 m (R. W. Taylor); Bulolo R., 2200 ft (B. B. Lowery); Bupu R. area, Lae (B. B. Lowery); Lae (B. B. Lowery); lower Busu R., Huon Penin. (E. O. Wilson); *National Capital*: 8 km NW Port Moresby, <5 m (P. S. Ward); Port Moresby, Paga Hill (A. Mann; J. Szent-Ivany). **Philippines:** *Davao City*: Davao (A. Reyes); *Dumaguete*: Dumaguete (J. W. Chapman); *Laguna*: Los Banos (F. X. Williams); *Leyte*: Baybay (R. Vane-Wright); *Misamis Oriental*: Anakan Lumber Co., Gingoog (A. Reyes); *Negros Oriental*: Cuernos de Negros [as 'Horns of Negros'] (J. W. Chapman); *Palawan*: Sicud, 5 km N Culasian (M. Doll); *Quezon City*: Novaliches (B. B. Lowery); *Rizal*: Wawa Dam (B. B. Lowery); *province unknown*: Bulbulan, Luzon (c.u.). **Singapore:** Bukit Timah, 50 m (P. S. Ward); Kent Ridge (D. H. Murphy); Lim Chu Kang, <5 m (P. S. Ward); Mandai, <5 m (P. S. Ward); Seletar Reservoir, 20 m (P. S. Ward); Singapore (Baker); Singapore (c.u.). **Sri Lanka:** *Central*: Kandy (Bingham); *Western*: Dehiwala, Colombo (W. L. Brown); Yakkala (K. L. A. Perera). **Thailand:** *Kanchanaburi*: Tham Than Lot (W. L. Brown); *Krabi*: Ko Phi Phi [as 'Koh Pee Pee '] (W. Dorow); Noppharat Thara (Madl); *Nakhon Ratchasima*: Khao Yai Garden Lodge, Pak Chong (A. Buschinger); Sakaerat lowland (S. Yamane); *Nakhon Si Thammarat*: Khao Luang Natl Pk, Karom Falls, 200–500 m (A. Schulz; K. Vock); *Sisaket*: Kanthararom [as 'Kantararom, Vil. 1, Ban Pak Paew'] (G. R. Ballmer); *Songkhla*: Hat Yai (H. Ôkido). **Vietnam:** *Kien Giang*: Hòn Thom [as 'Isl. Thom'] (A. Radchenko). **Country unknown:** 'N. Guinea' (Biró)

(Collections: ANIC, ASIC, BMNH, CASC, HZIC, JDMC, KUEC, KUES, LACM, MCSN, MCZC, MHNG, NHMB, NHMV, PSWC, RMBR, SMNK, TERC, UASK, UMSC, USNM).

Worker measurements (n = 31)

HW 0.63–0.83, HL 0.73–1.04, LHT 0.45–0.65, CI 0.78–0.90, FCI 0.10–0.13, REL 0.45–0.53, REL2 0.55–0.62, SI 0.51–0.55, SI3 0.83–0.98, FI 0.45–0.55, PLI 0.60–0.79, PWI 0.44–0.56, PDI 0.95–1.23, LHT/HW 0.69–0.79, CSC 0–4, MSC 0–22.

Worker description

Small species (HW <0.85); clypeus very short, its anterior margin appearing more or less straight when head is held in full-face view (Fig. 71), or with a very slightly protruding median lobe, whose anterior reach is about equal to (i.e. does not strongly exceed) that of the anterolateral margins (Figs 72–73); distance between frontal carinae subequal to maximum scape width; eye large, its length exceeding that of the scape; profemur short and robust (FI usually >0.48); lateral pronotal margins well developed, sharp-edged; mesopropodeal impression with a transverse, pit-shaped depression posteriorly (at junction with propodeum), whose flanking ridges decline anteriorly (sometimes precipitously, as in Fig. 82), leaving an open strip of integument which is usually longitudinally rugulate/carinulate; propodeum usually higher than wide, with a flattened dorsal face that rounds into the declivitous face; petiole with prominent posteroventral teeth and with a 'reversed-node' shape, i.e. with steep anterior face and more shallowly declining posterior face (Figs 79–80, 82); petiole variable in length and height (see PLI values), but nearly always less than half the length of the head (PL/HL 0.39–0.51); petiole about twice as long as wide (see PWI values); postpetiole varying from slightly longer than wide to wider than long; metabasitarsal sulcus prominent, subtended by a low ridge and occupying a darkened patch of cuticle which is half or more the length of the basitarsus. Integument smooth and shiny, with scattered fine punctures; those on posterior half of head mostly ≤0.010 mm in diameter, and separated by several to many diameters, leaving conspicuous shiny interspaces; punctures contrastingly coarser (about 0.015 mm in diameter) and denser (separated by about their diameters) on anterior third of pronotum; generally of same size but lower density on remainder of pronotum, on mesonotum and on dorsal face of propodeum; lower malar area also with coarser punctures, intermixed with weak longitudinal rugulae; side of mesosoma and of petiole with extensive smooth shiny patches that are mostly devoid of sculpture. Pilosity generally inconspicuous, sparse on posterior half of head dorsum (CSC 0–6); when head is seen in full-face view, standing hairs absent from sides of head, except for one to several setae below the level of the eyes (Figs 71–73); standing pilosity usually sparse on mesosoma (MSC 0–9), petiole and postpetiole, but more abundant in some workers (MSC ≥10; see discussion below); short appressed pubescence scattered over body, of light to moderate density on most surfaces, including the postpetiole (where the hairs are separated by their lengths or more). Black to dark brownish-black, mandibles, antennae, and apical portions of legs lighter brown; scape and first funicular segment often (not always) contrastingly lighter than remainder of funiculus.

Discussion

Tetraponera nitida is a small, black shiny species (worker HW <0.85, worker LHT <0.66), with a characteristic pair of posteroventral petiolar teeth (Fig. 82), formed by lateral angular extensions of sternite II. Sometimes the petiolar

teeth cannot be easily discerned if the postpetiole is bent downward, but two other useful distinguishing features of *T. nitida* are: (*i*) the combination of short scapes and large eyes, such that SI3 (SL/EL) is less than 1.00, and (*ii*) the densely punctate sculpture near the pronotal margin which contrasts with the more dispersed punctures on the upper head and elsewhere on the pronotum. *Tetraponera nitida* shares these traits with only three other species: *T. nixa*, *T. nodosa* and *T. notabilis*. The last two are larger, with more protruding clypeal margins (compare Figs 71–73 with 75–76) and denser appressed pubescence on the postpetiole and gaster, while *T. nixa* has numerous, short standing hairs on the head (Fig. 74).

The extensive synonymy under *T. nitida* is partly a reflection of the fact that this is a widespread and variable species. In workers from Southeast Asia the petiole tends to be rather short (PLI often >0.70) (Figs 79–80) while in more austral locations it is usually more elongate (PLI ~ 0.65); the worker illustrated from New Guinea (Fig. 82) demonstrates the limit of variation in this direction (PLI 0.60). It should be emphasised, however, that there is substantial variation in petiole shape within, as well as between, regions. Head shape also varies from elongate to rather broad (see range of CI values), but with a less clear geographic pattern. Karavaiev's (1933) '*bidentata* var. *angusticeps*' represents one extreme of head shape, with CI in the holotype worker being about 0.76. Broad-headed workers (CI >0.86) occur widely and such individuals tend to be smaller than average.

More puzzling is the variation in the density and length of standing pilosity. In most workers the standing hairs are relatively short and sparse (Fig. 82) (MSC <8) but in some individuals the hairs are longer (up to 0.20 mm or more) and notably more common on the mesosoma, petiole, postpetiole and gaster (Fig. 80) (MSC >20). This is the basis for Viehmeyer's (1916) 'variety' *setifera*. Such 'hairy morphs' are found in scattered locations in the northern part of the range of *T. nitida*, being known from the Andaman I.s, Malay Peninsula, and Borneo. Apart from exhibiting differences in pilosity, they are structurally similar to 'typical' *T. nitida* from the same regions. Among material examined from Brunei and Sabah I have also seen a few workers with intermediate quantities of standing pilosity (MSC 8–20); in these the hairs are mostly shorter and grade into suberect and decumbent pubescence (Fig. 79). Given the apparently continuous (albeit bimodal) distribution of this pilosity character, I am treating these forms as conspecific, although the question of their status deserves more detailed investigation.

Tetraponera nixa, from northern Australia, appears at first glance to be an equivalent 'hairy morph' of *T. nitida* from the southern portion of its range. However, *T. nixa* has shorter hairs and these are abundant on the sides and upper surface of the head, a condition not seen in any *T. nitida* workers. The rationale for recognising *T. nixa*, but not *T. setifera*, as a different species is discussed in more detail below.

Distribution and biology

Tetraponera nitida has a very wide distribution, being found from India to southern China, and south to Indonesia, Papua New Guinea and northern Australia (Fig. 182). Collection records indicate that it is a generalist inhabitant of dead twigs or stems of plants. I have found colonies in dead twigs of the following plants, with the habitat(s) given in parentheses: *Allophylus cobbe* (mangrove); *Avicennia alba* (mangrove); *Chionanthus ramiflorus* (rainforest); *Clerodendrum inerme* (mangrove); *Colubrina asiatica* (littoral vegetation); *Excoecaria agallocha* (mangrove); *Gnetum* sp. (rainforest); *Hibiscus tiliaceus* (littoral vegetation); *Mallotus* sp. (rainforest edge; roadside); *Premna serratifolia* (littoral vegetation); *Rhizophora* sp. (mangrove); *Terminalia catappa* (littoral vegetation); and *Vitex trifolia* (littoral vegetation). Other habitat records include dry, rocky *Eucalyptus* woodland; *Eucalyptus* savanna; monsoon forest; gallery rainforest; and dry sclerophyll forest. This tolerance of a broad range of habitats probably contributes to the wide distribution of *T. nitida*.

Tetraponera nixa, sp. nov.

(Figs 74, 81)

Type material examined

Holotype. Worker, Weipa, Queensland, Australia, vii.1982 (J. D. Majer) (ANIC).

Paratypes. 4 workers, same data as holotype (ANIC, JDMC, PSWC).

Other material examined

Australia: *Queensland*:; Cairncross West I., Great Barrier Reef (H. Heatwole); Gabba I., Torres Strait (H. Heatwole; E. Cameron); Saibai I., nr Saibai village, Torres Strait (H. Heatwole; E. Cameron).

(Collection: ANIC).

Worker measurements ($n = 6$)

HW 0.69–0.75, HL 0.81–0.88, LHT 0.50–0.54, CI 0.84–0.88, FCI 0.12–0.14, REL 0.46–0.49, REL2 0.55–0.56, SI 0.53–0.55, SI3 0.95–1.01, FI 0.43–0.47, PLI 0.64–0.67, PWI 0.50–0.52, PDI 1.02–1.11, LHT/HW 0.70–0.75, CSC 15–25, MSC 30–56.

Worker description

Similar to *T. nitida* (see above), except as follows: profemur slightly less robust: FI 0.43–0.47 and FW/PL 0.53–0.58 (*v.* 0.45–0.55 and 0.58–0.70, respectively, in *T. nitida*); mesosoma more slender, on average: PrWM/HW 0.56–0.58 and MTW/HW 0.46–0.47 (*v.* 0.58–0.65 and 0.47–0.52, respectively, in Australian and New Guinea samples of *T.*

nitida); patch of dense punctures on anterior portion of pronotum less extensive, more confined to the anterior margin. Short standing hairs (0.03–0.05mm long) common and conspicuous on most of body, including the upper surface of head, sides of head, scapes and tibiae, as well as the mesosoma, petiole, postpetiole and gaster (Figs 74, 81); CSC approximately 15–25, MSC ≥30; standing hairs tending to grade into pubescence (so that setal counts are approximate only). Black to dark brownish-black, appendages dark to medium brown, becoming lighter yellowish-brown on scape, first funicular segment, protibia and tarsi.

Discussion

Tetraponera nixa is evidently closely related to *T. nitida* and differs primarily by the much denser (and very short) pilosity on the head, mesosoma and appendages. Given that the amount of pilosity varies considerably in northern populations of *T. nitida* (see above) I was initially inclined to treat the hairy forms from Australia as conspecific as well. Several lines of evidence suggest, however, that *T. nixa* is a distinct species. (*1*) Among a reasonably extensive series of *nitida*-like specimens examined from northern Australia and New Guinea (about 240 workers and 35 queens, from 70 localities) the amount of standing pilosity falls into two discrete classes (CSC 0–4 and MSC 0–10, *v.* CSC 15–25 and MSC 30–56), without the intermediates that are seen in northern populations of *T. nitida*. Nevertheless, among this large number of specimens, only seven workers and one queen (from four localities) are referable to *T. nixa*, so additional samples are desirable. (*2*) From one locality, Cairncross West I. on the Great Barrier Reef, there are collections of both forms (one worker each) (ANIC), establishing their sympatric occurrence. (*3*) In *T. nixa*, standing pilosity is common on the dorsum of the head and on the sides (Fig. 74), a feature not seen in any *T. nitida* workers, including hairy individuals ('*setifera*') from northern localities (Figs 72–73). (*4*) There are additional slight morphological differences between *T. nixa* and *T. nitida*, in the shapes of the profemur and mesosoma (see description above), and bivariate plots of some measurement ratios separate the two taxa (e.g. Fig. 124). The differences are accentuated when *T. nixa* workers are compared with just those *T. nitida* workers coming from the same region (Australia, New Guinea) (Fig. 125).

Distribution and biology

Tetraponera nixa appears to be restricted to Cape York Peninsula and adjacent Torres Strait islands. At the type locality it was collected in open *Eucalyptus tetradonta* forest (Majer personal communication) and on revegetated bauxite mine-sites (Majer 1984; as '*Tetraponera* sp. WE108').

Tetraponera nodosa, sp. nov.

(Figs 75, 83)

Type material examined

Holotype. Worker, Bako Natl Pk, Sarawak, Malaysia, 21–22.iv.1993 (S. Yamane) (FRCK).

Paratype. 1 worker, same data as holotype (KUES).

Other material examined

Indonesia: *Sumatera Utara*: Pangherang-Pisang (E. Modigliani) (1 worker) (MCSN); **Thailand** *Songkhla*: Hat Yai (H. Ôkido) (1 worker) (KUEC).

Worker measurements (*n* = *3*)

HW 0.83–0.94, HL 0.98–1.14, LHT 0.64–0.70, CI 0.83–0.85, FCI 0.15–0.16, REL 0.44–0.47, REL2 0.54–0.56, SI 0.49–0.53, SI3 0.91–0.94, FI 0.49–0.53, PLI 0.60–0.71, PWI 0.48–0.54, PDI 1.01–1.05, LHT/HW 0.74–0.77, CSC 4, MSC 2.

Worker description

Medium-sized species, with relatively broad head (CI >0.80); anterior clypeal margin broadly convex, its medial portion in a more anterior position than the anterolateral margins (Fig. 75); frontal carinae well separated, the distance between them notably greater than maximum scape width; eye large, its length greater than that of the scape; profemur relatively short and robust; lateral pronotal margins well developed; mesopropodeal impression very short, consisting of a transverse, pit-shaped depression, with longitudinal carinulae or rugulae; propodeum about as high as wide, with a somewhat flattened dorsal face that rounds rather suddenly into the declivitous face; petiole as illustrated (Fig. 83), with a short anterior peduncle and prominent posteroventral teeth; petiolar node rounded and approximately symmetrical in profile (anterior and posterior faces meeting the summit at about the same angle); metabasitarsal sulcus associated with a darkened ridge and occupying about three-fifths the length of the segment. Integument essentially smooth and shiny, overlain by numerous fine punctures; punctures on upper half of head mostly ≤0.010 mm in diameter, and separated by several diameters; punctures larger and denser on anterior quarter of pronotum, on mesonotum and on dorsal face of propodeum; lower malar area also with coarser punctures, intermixed with weak longitudinal rugulae. Standing pilosity sparse, scattered on gaster, venter and apex of head, and on following dorsal surfaces: two pairs on posterior third of head (near inner margin of eye), one pair on the pronotum, 4–6 short hairs on petiole, and 8–10 short hairs on postpetiole; 2–3 standing hairs also present on scape and on posterior face of profemur; shorter appressed pubescence present but inconspicuous on head and most of mesosoma, moderately common on petiole, and forming a dense mat on postpetiole and gaster, which obscures the sheen of the

integument. Black, with mandibles, antennae, tarsi and tibiae dark brown to medium brown (protibia and protarsus lightest).

Discussion

This species is similar to *T. nitida* but differs from that species by the larger size, better developed median clypeal lobe, more widely separated frontal carinae (Fig. 75), more globose petiolar node (Fig. 83), denser body sculpture, and presence of a thick mat of appressed pubescence on the postpetiole and gaster.

Distribution and biology

Tetraponera nodosa is known from three disparate locations, in Thailand, Sarawak (Malaysia) and Sumatra (Indonesia). The type material from Bako Natl Pk, Sarawak was collected in mangrove.

Tetraponera notabilis, sp. nov.

(Figs 76, 84)

Type material examined

Holotype. Worker, Sakaerat lowland, Nakhon Ratchasima, Thailand, 10.vii.1999 (S. Yamane) (BMNH).

Paratypes. 2 workers, 1 alate queen, same data as holotype (KUBC, KUES, PSWC).

Other material examined

Malaysia: *Negeri Sembilan*: Pasoh For. Res. (M. Brendell *et al.*) (1 worker) (BMNH).

Worker measurements ($n = 3$)

HW 0.87–0.90, HL 1.13–1.24, LHT 0.74–0.80, CI 0.73–0.77, FCI 0.14, REL 0.43–0.45, REL2 0.58–0.60, SI 0.55, SI3 0.92–0.94, FI 0.52–0.53, PLI 0.43–0.49, PWI 0.36–0.38, PDI 1.03–1.07, LHT/HW 0.85–0.89, CSC 2–4, MSC 2–3.

Worker description

Slender, medium-sized species, with elongate head (CI <0.80); anterior clypeal margin broadly convex, slightly crenulate medially (Fig. 76); distance between frontal carinae slightly exceeding maximum scape width; eye large, its length greater than that of the scape; profemur short and broad (FI >0.50); mesosoma elongate, with well defined lateral pronotal margins; mesopropodeal impression with a short transverse band of longitudinal carinulae followed by a smooth, pit-shaped depression; propodeum slightly higher than wide, in posterior view the summit broadly rounded; in lateral profile, dorsal face of propodeum rounding gradually into the declivitous face; petiole elongate (Fig. 84) and thin, much longer than high or wide (see PLI and PWI indices), and with a pair of posteroventral teeth formed by lateral projections of the petiolar sternite; metabasitarsal sulcus associated with a slightly darkened ridge and occupying about two-thirds the length of the segment. Integument with numerous fine punctures on a smooth, shiny background; punctures on upper half of head mostly ≤0.015 mm in diameter, and separated by several to many diameters; punctures denser (separated by about their diameters or less) on anteromedial third of pronotum, on mesonotum and on dorsal face of propodeum; lower malar area with coarser punctures and with weak, irregular longitudinal rugulae. Standing pilosity relatively scarce, present on gaster, venter and apex of head and on the following dorsal surfaces: 2–4 setae on posterior third of head, 2–3 on pronotum, 4–6 on petiole and 7–9 on postpetiole; several standing hairs also present on scape and on posterior face of profemur; shorter appressed pubescence common on most of body, forming a dense mat on postpetiole and gaster where the appressed hairs overlap extensively. Black, with mandibles, tarsi and funicular segments 2–11 dark brown; protibia, protarsus, scape and first funicular segment lighter medium-brown.

Discussion

The presence of posteroventral petiolar teeth, short scapes, large eyes and dense punctate sculpture on the anteromedial third of the pronotum places *T. notabilis* in the *T. nitida*-complex. Within this complex it is easily identified by its elongate head, slender petiole, and longer legs (LHT/HW 0.85–0.89, *v.* 0.69–0.79 in other members of the complex). An alate queen from the type locality exhibits the same features as the workers, in more exaggerated form (CI 0.66, PLI 0.38, PWI 0.32, LHT/HW 0.90).

Distribution and biology

This species is known from the type locality in northern Thailand and from a lowland rainforest site in peninsular Malaysia.

Tetraponera polita, sp. nov.

(Figs 70, 78)

Type material examined

Holotype. Worker, Danum Valley, Sabah, Malaysia, 30.viii.1995 (S. Yamane) (UMSC).

Paratypes. 7 workers, same data as holotype (ANIC, BMNH, KUES, PSWC, UMSC).

Other material examined

Malaysia: *Sabah*: Danum Valley (H. Ôkido) (2 workers) (PSWC).

Worker measurements ($n = 6$)

HW 0.82–0.89, HL 1.01–1.11, LHT 0.70–0.76, CI 0.79–0.81, FCI 0.15–0.16, REL 0.33–0.36, REL2 0.42–0.45, SI 0.61–0.65, SI3 1.35–1.48, FI 0.46–0.49, PLI 0.62–0.68, PWI

0.61–0.66, PDI 0.98–1.04, LHT/HW 0.85–0.87, CSC 20–28, MSC 38–54.

Worker description

Medium-sized, black shiny species; anterior clypeal margin broadly convex, very slightly crenulate medially (Fig. 70); distance between frontal carinae slightly exceeding maximum scape width; eyes relatively small, much shorter than scape length; profemur moderately robust (see FI values); lateral margins of pronotum not well defined; mesopropodeal impression with an open, transverse strip of integument anteriorly, with fine longitudinal carinae or rugulae (most pronounced on sides), posterior to this is a pit-like depression, whose interior surface is mostly smooth and shining; propodeum about as high as wide (PDI ~ 1.00), the summit broadly rounded when seen in posterior view; in lateral profile, dorsal face rounding gradually into the declivitous face; petiole about 1.5× longer than high or wide, and with a short robust anterior peduncle (Fig. 78); postpetiole broader than long, in dorsal view; metabasitarsal sulcus somewhat inconspicuous but occupying more than two-thirds the length of the metabasitarsus. Integument smooth and shiny, with scattered fine punctures of variable size; punctures coarsest on malar area (up to 0.02 mm in diameter) and accompanied here by irregular longitudinal rugulae immediately above the mandibular insertions. Short, standing pilosity common on body and appendages; setae on dorsum of head and mesosoma mostly 0.04–0.08 mm long; appressed pubescence sparse and generally inconspicuous (except on the mesopleuron); appressed hairs on abdominal tergite IV separated by much more than their lengths. Body black; legs dark brownish-black, becoming slightly paler apically; mandible, scape and first funicular segment medium-brown to reddish-brown, and contrasting with dark brown funicular segments 2–11.

Discussion

This attractive species can be recognised by the conspicuous short standing pilosity covering most body surfaces and the scarcity of appressed pubescence, especially on the gaster. Other hairy species are either larger (*nigra*-complex) and/or have denser pubescence on the gaster. Other characteristic features of *T. polita* include the relatively small eyes and long scapes, broad petiole and postpetiole, and the black shiny appearance.

Distribution and biology

Tetraponrea polita is known only from the type locality (Danum Valley, Sabah), where a colony was collected in secondary forest.

Tetraponera punctulata F. Smith

(Figs 1–6, 88, 94, 97–99, 132, 141, 152, 166, 178)

Tetraponera punctulata F. Smith, 1877: 72.
Sima punctulata var. *Kimberleyensis* Forel, 1915*b*: 37. **Syn. nov.**
Sima punctulata (F. Smith); Dalla Torre, 1893: 55.
Sima (*Tetraponera*) *punctulata* (F. Smith); Emery, 1921: 26.
Tetraponera (*Tetraponera*) *punctulata* F. Smith; Chapman and Capco, 1951: 81.

Types (not examined)

Tetraponera punctulata F. Smith. Syntype(s), queen(s), Champion Bay, Western Australia [type(s) apparently lost].

Type material examined

Sima punctulata var. *Kimberleyensis* Forel. Syntypes, 6 workers, Kimberley Distr., Australia (Mjöberg) (ANIC, MCZC, MHNG); syntypes, 8 workers, Colosseum, Queensland, Australia (Mjöberg) (MNHG, NHMB).

Other material examined

Australia: *New South Wales*: Bom Bom S. F., 5 mi. S Grafton, 100 ft (B. B. Lowery); Bugaldie (B. B. Lowery); Gwandalan near Swansea (B. B. Lowery); Killarney S. F., Narrabri (P. M. Room); Millthorpe (W. W. Froggatt); Mungindi, bank of Barwon R. (B. B. Lowery); Narrabri (K. C. McKeown); Narrabri (M. I. Nikitin); Whiporie (B. B. Lowery); *Northern Territory*: 13–17 km NE Darwin (W. L. Brown); 1 km NE Cahills Crossing (R. W. Taylor); 20 km S Katherine (B. B. Lowery); 20 km W Katherine (B. B. Lowery); 30 km NW Katherine (P. J. M. Greenslade); 34 km NW Katherine (P. J. M. Greenslade); 47 km SW Katherine (P. J. M. Greenslade); 48 km SW Katherine (P. J. M. Greenslade); 48 mi SW Daly R. (M. Mendum); 55 km SW Katherine (P. J. M. Greenslade); 5 km S Jabiru, Alligator R.s area (P. J. M. Greenslade); 5 km S Tor Rock (R. W. Taylor); 6 km SW by S of Oenpelli (R. W. Taylor); 7 km NW by N of Cahills Crossing (R. W. Taylor); 8 km SE Katherine (P. J. M. Greenslade); 9 km NW Adelaide R., 80 m (P. S. Ward); Adelaide R. (c.u.); Alice Springs (A. N. Andersen); Baroalba Gorge (R. W. Taylor; J. E. Feehan); Baroalba Spring (R. W. Taylor); Batten Point, 30 km NE by E of Borroloola (J. E. Feehan); Berry Springs, near Darwin (B. B. Lowery); bk. of Finniss R. (R. Parkinson); Black Point, Cobourg Penn. (E. D. Edwards); Black Point, Cobourg Penn. (T. A. Weir); Daly R. Mission (J. Hutchinson); Darwin (A. Douglas); Darwin (A. M. Lea); Darwin (L. Weatherill); Douglas Hot Springs (B. B. Lowery); Edith Falls, Katherine Gorge Natl Pk (S. O. Shattuck); Emerald Springs Roadhouse (B. B. Lowery); Fannie Bay (G. Campbell); Fanny Bay Beach, Darwin (G. Campbell); Fort Darwin (c.u.); Gove (J. D. Majer); Groote Eylandt (J. D. Majer); Headquarters, Katherine Gorge Natl Pk (S. O. Shattuck); Humpty Doo (P. Duelli); Jabiru, Alligator R. area (P. J. M. Greenslade); Kapalga, 30 m (D. Hlavaty); Kapalga, Alligator R. area (P. J. M. Greenslade); Kapalga, Kakadu Natl Pk (A. N. Andersen); Kapalga, Kakadu Natl Pk (S. Shattuck); Katherine (D. Rackemann); Koolpinyah (G. F. Hill); Litchfield Natl Pk (B. B. Lowery); Litchfield Natl Pk, above Florence Falls (B. B. Lowery); Manbulloo, SW Katherine (P. J. M. Greenslade); Marrakai (T. G. Campbell); Newry (R. Munyard); Nourlangie Rock, 25 km SSW Jabiru, 20 m (D. Hlavaty); Nourlangie Rock, Kakadu Natl Pk (A. N. Andersen); Nourlangie Rock, Kakadu Natl Pk (R. Savolainen); Powell Ck (E. AllChurch); Ross R., 75 km E Alice Springs (A. Andersen); Sawcut Gorge (R. W. Taylor); Stapleton Ck, Stuart Hwy, N of Adelaide R. (B. B. Lowery); Surprise Ck, 45 km SSW Borrroloola (M. S. Upton); Threeways, Stuart Hwy (B. B. Lowery); Timber Ck (P. Duelli); UDP Falls (P. Duelli); Victoria R. (B. B. Lowery); Yirrkala (J.

A. L. Watson); *Queensland*: 'Queensland' (D. Emery); 'Queensland' (c.u.); 100 km N Charters Towers (B. B. Lowery); 10 km N Koumala (B. B. Lowery); 10 km N Mareeba (B. B. Lowery); 10 km S Mossman (B. B. Lowery); 10 km SW Giru (B. B. Lowery); 11 km N St Lawrence (P. S. Ward); 11 km SSE Miriam Vale, 120 m (P. S. Ward); 14 km E Mingela (B. B. Lowery); 16 km S Mareeba, 600 m (P. S. Ward); 17 km SW Yeppoon, 30 m (P. S. Ward); 17 mi. WNW Townsville (J. E. Dowse); 18 km N Charters Towers (B. B. Lowery); 18 km SW Walkerston (B. B. Lowery); 20 km N Miles (B. B. Lowery); 25 km N Coen, 180 m (P. S. Ward); 25 km S Ayr (B. B. Lowery); 25 km W Giru (B. B. Lowery); 30 km E Lockhart R., 60 m (P. S. Ward); 30 km N Charters Towers (B. B. Lowery); 30 km N Giru, nr A.I.M. beach (B. B. Lowery); 30 km NE Cairns, 40 m (P. S. Ward); 30 km S Sarina (B. B. Lowery); 30 km W Mt Carbine (B. B. Lowery); 30 mi. ESE Camooweal (J. E. Dowse); 30 mi. N Cairns (R. W. Taylor); 3 km NE Mt Webb (J. C. Cardale); 3 km NE Mt Webb (J. E. Feehan); 3 km W Rainbow Beach, <5 m (P. S. Ward); 46 km NW Townsville (P. J. M. Greenslade); 50 km NW Charters Towers, 15 km from Red Falls (B. B. Lowery); 5 mi. WNW Mary Kathleen (J. E. Dowse); 60 km NW Charters Towers, Red Falls, Burdekin R. (B. B. Lowery); 6 km E Charters Towers (B. B. Lowery); 6 km N Cunnamulla (J. A. Watson; R. Barrett); 6 km SSW Cape Tribulation, <5 m (P. S. Ward); 6 mi SE Biloela (B. B. Lowery); 70 km S Ayr (B. B. Lowery); 7 km E Charters Towers (B. B. Lowery); 8 km E Charters Towers (B. B. Lowery); 8 km W Bowen (B. B. Lowery); 9 mi. ESE Capella (J. E. Dowse); Abergowrie, Ingham (R. Makim); Alligator Ck Natl Pk, nr Giru (B. B. Lowery); Aplin Islet, Great Barrier Reef (R. C. Buckley); Baird I., Great Barrier Reef (R. C. Buckley); Bamaga, Cape York Penn. (J. Sedlacek); Bamaga, N. Cape York ('Darlingtons'); Binstead I., Great Barrier Reef (R. C. Buckley); Bloomsbury (R. R. Snelling; J. Grey); Brisbane (R. Kumar); Brisbane (W. M. Wheeler); Bundaberg (c.u.); Bundaberg (R. C. L. Perkins); Bushy I., Great Barrier Reef (R. C. Buckley); Cairncross East I., Great Barrier Reef (H. Heatwole); Cairncross West I., Great Barrier Reef (H. Heatwole); Cairns (S. Conleth); Cairns (P. Duelli); Cairns (N. L. H. Krauss); Cairns (R. W. Taylor); Cairns (W. M. Wheeler); Cairns, 5 m (P. S. Ward); Cape Hillsborough Natl Pk (E. A. Sugden); Cape Hillsborough Natl Pk, 55 km N MacKay (A. Colvin; P. Colvin); Cape Pallarenda, Townsville (E. O. Wilson); Cape Upstart (B. B. Lowery); Cardwell (R. R. Snelling; J. Grey); Carnarvon Gorge, 400 m (P. S. Ward); Cedar Ck Falls, 15 km SE Proserpine (B. B. Lowery); Charters Towers (B. B. Lowery); Coen (C. Oke); Coen Aerodrome (C. N. Smithers); Coen, Cape York (Darlington); Como S Camp (P. J. M. Greenslade); Conroy Beach, 27 km SE Proserpine (B. B. Lowery); Cooktown (Beauglehale); Cooloola [as 'Coloola'] Natl Pk (B. B. Lowery); Cooloola, Kabali [?] E (P. J. M. Greenslade); Cooloola, Teewah Ck (P. J. M. Greenslade); Coppabella, 100 mi. SW MacKay (B. B. Lowery); Cunnamulla (B. B. Lowery); Curtis I. (E. M. Exley); Dawes, 20 mi. SE Biloela (B. B. Lowery); Don R., SW of Bowen (J. Pontifex); Douglas I., Great Barrier Reef (R. C. Buckley); Eimeo (T. F. Houston); Eliot Ck (A. Wells); Eurimbula NP, near Miriam Vale (D. J. Bickel); Farmer I., Great Barrier Reef (H. Heatwole); Farmer I., Great Barrier Reef (R. C. Buckley); Gayndah (A. M. Lea); Gayndah (c.u.); Gin Gin (c.u.); Giru Cromarty Landing (B. B. Lowery); Gladstone (Lea); Gladstone (R. H. Taylor); Granite Rock Park (D. G. Furth); Halfway I., Great Barrier Reef (R. C. Buckley); Hannibal East I., Great Barrier Reef (H. Heatwole); Hannibal I., Great Barrier Reef (H. Heatwole); Hayman I. (C. T. Mercovich); Indooroopilly (Z. Boucek); Ingram I., Great Barrier Reef (R. C. Buckley); Iron Range, Cape York Penn. (G. B. Monteith); Iron Range, Cape York Penn. (J. Sedlacek); Karumba (L. Weatherill); Kuranda (W. M. Wheeler); Kuranda to Mareeba, *c.* 1000 ft ('Darlingtons'); Lakefield Natl Pk, 75 km N Laura (G. Monteith); Leggatt I., Great Barrier Reef (R. C. Buckley); Lizard I., Great Barrier Reef (H. Heatwole); Lockerbie, Cape York Penn. (J. Sedlacek); Lornaville, nr Marlborough (D. Rakemann); Lotus Ck, 96 km NW Marlborough, 200 m (P. S. Ward); Lotus Ck, Hwy 1 south of Sarina (P. S. Ward); Lowrie I., Great Barrier Reef (R. C. Buckley); Macarthur Rampart, Great Barrier Reef (R. C. Buckley); Mackay (F. H. Taylor); Mackay (R. E. Turner); Mareeba (J. G. Brooks); Mareeba (H. E. Hill); Mareeba (B. B. Lowery); Monduran Dam, 20 km N Gin Gin (H. Frauca); Mt Carbine (B. B. Lowery); Mt Coot-tha, Brisbane (B. B. Lowery); Mt Coot-tha, Brisbane, 100–900 ft (B. B. Lowery); Mt Coot-tha, Brisbane, 600 ft (B. B. Lowery); Mt Cottell, 640 m (R. W. Taylor; J. Feehan); Mt Elliot Rge, SW Lingum Townsville (P. F. Darlington); Mt Elliott Natl Pk, 22 km SW Giru (B. B. Lowery); Mt Elliott Natl Pk, McKenzie Ck, Giru (B. B. Lowery); Mt Elliott Natl Pk, Giru (B. B. Lowery); Mt Larcom (B. B. Lowery); Mt Webb Natl Pk (J. E. Feehan); Mt Webb Natl Pk (J. C. Cardale); nr Reid R., *c.* 60 km S Townsville (B. B. Lowery); Pallareada (B. B. Lowery); Petherbridge Is., Great Barrier Reef (H. Heatwole); Pipon I., Great Barrier Reef (H. Heatwole); Port Douglas (B. Hölldobler); Port Mackay (Turner); Rockhampton ('Darlingtons'); Rockhampton (A. M. Lea); Rockhampton (c.u.); Roeburne (W. D. Dodd); Scraggy Pt, Hinchinbrook I., 5 m (P. S. Ward); Silver Plains, Cape York ('Darlingtons'); St George (B. B. Lowery); Tambo (B. B. Lowery); Tern I., Great Barrier Reef (R. C. Buckley); Torres Strait, Boigu I., nr Boigu village (H. Heatwole; E. Cameron); Torres Strait, Dowar I., Murray I. (H. Heatwole; E. Cameron); Torres Strait, Gabba I. (H. Heatwole; E. Cameron); Torres Strait, Hammond I. (H. Heatwole; E. Cameron); Torres Strait, Mabulag (=Jervis) I. (H. Heatwole; E. Cameron); Torres Strait, Moa (=Banks) I., nr St Paul's Mission (H. Heatwole; E. Cameron); Torres Strait, Murray Is., Maeri (H. Heatwole; E. Cameron); Torres Strait, Prince of Wales I. (H. Heatwole; E. Cameron); Torres Strait, Saibai I., nr Saibai village (H. Heatwole; E. Cameron); Townsville (F. P. Dodd); Townsville (F. H. Taylor); Townsville (W. M. Wheeler); Townsville, Heatley Park (D. B. Grund); Tozers Gap, 110 m (P. S. Ward); Turtle I., Great Barrier Reef (R. C. Buckley); W of Ravenshoe, Atherton Tableland, *c.* 3000 ft ('Darlingtons'); Weipa (A. N. Andersen); Yaamba, Bruce Hwy (B. B. Lowery); Yarrabah Miss., nr Cairns (R. W. Taylor); *South Australia*: Brachina Gorge, Flinders Ranges, 270 m (P. S. Ward); Parachilna Ck, 15 km WSW Blinman (P. J. M. Greenslade); *Victoria*: Geelong (Davey); *Western Australia*: 'N. W. Australie' (Mjöberg); 10 km S Hall Ck (R. R. Snelling; J. Grey); 15 mi. SE Wittenoom (McInnes; Dowse); 25 km E Broome (B. B. Lowery); 26 mi. ENE Norseman (K. Key); 27 km ENE Norseman, 310 m (P. S. Ward); 27 mi. SE by S of Xanthus (R. W. Taylor); 2 km N Halls Ck (B. B. Lowery); 3 km S Wundowie (P. S. Ward); 40 km S Dongara (B. B. Lowery); 47 km S Derby, 20 m (P. S. Ward); 48 km W Fitzroy Crossing [as '48 km W Fitzroy'] (B. B. Lowery); 4 mi. NNE Norseman (K. Key); 4 mi. NNE Norseman (R. W. Taylor); 58 km E Nanutarra, 150 m (P. S. Ward); 8 km E Inglis, King Leopold Range, 270 m (P. S. Ward); Barrow I. (H. Heatwole); Bell's Pass, W. Kimberley (S. A. Harrington); Camp Ck, 1 km S Mining Camp, Mitchell Plateau, Kimberley Dist. (D. C. F. Rentz; J. Balderson); Carson Escarpment (I. F. B. Common; M. S. Upton); Chapman R., Geraldton (W. M. Wheeler); Derby (J. G. Campbell); Derby (Mjöberg); Dongara [as 'Dongarra'] (R. E. Turner); Drysdale R. valley, Kimberley area (W. Leutert); Drysdale R. (I. F. B. Common; M. S. Upton); Fletcher Ck, 100 km N Halls Ck (B. B. Lowery); Geraldton (Darlington); Geraldton (W. M. Wheeler); Green Head (G. A. Holloway); Grotto Ck (J. A. L. Watson); Hovea (J. Clark); Kalbarri Natl Pk (B. B. Lowery); Kimberley (J. G. Campbell); King Edward R. crossing camp (S. O. Shattuck); Koolan I. (P. R. Davis); La Grange (N. B. Tindale); Lake Argyle Motel (B. B. Lowery); Marandoo (N. Dunlop); Marandoo, Pilbara (P. A. Varris); Millstream Natl Pk, 300 m (P. S. Ward); Mt Anderson Stn., Kimberly (D. James); Mundaring (J. Clark); Nanutarra Roadhouse (A. N. Andersen); Narrogin (S. Curry); nr Airfield Swamp, Mitchell Plateau, Kimberley Dist. (D. C. F. Rentz; J. Balderson); Parry Harbour (C. Bougaiville); Parry Harbour (J. J. Walker); Port George (J. R. B. Love); Streeters Station [as 'Streeters'] (Mjöberg); Surveyor's

Pool Camp, Mitchell Plateau (S. O. Shattuck); Tammin (J. Clark); Tardun, 400 ft (C. T. Mercovich); Tunnel Ck Natl Pk (S. Shattuck); Tunnel Ck Natl Pk, 150 m (P. S. Ward); Windjana Gorge Natl Pk, 100 m (P. S. Ward); Wyndham, Goose Hill Lagoon (R. Lukins). **Papua New Guinea:** *Central*: Brown R. (B. B. Lowery); Karema, Brown R. (E. O. Wilson); Port Moresby, near Brown R. (B. B. Lowery); *National Capital*: Port Moresby (C. Levy); Port Moresby (B. B. Lowery); Port Moresby (N. L. H. Krauss); Port Moresby (Y. Roisin); Port Moresby (P. S. Ward); Waigani (A. Wieland); Waigani, Port Moresby, 40 m (P. S. Ward); *Northern*: Musa Valley, Dari, 200 m (R. W. Taylor); Safia (P. M. Room); *Western*: Middle Morehead R. (R. Pullen).

(Collections: AMNH, AMSA ANIC, BMNH, CPDC, CUIC, JDMC, KUEC, KUES, LACM, MCSN, MCZC, MHNG, MNHN, MZLU, NHMB, NHMV, PSWC, TERC, UASK, UCDC, USNM).

Worker measurements ($n = 45$)

HW 0.77–1.44, HL 0.95–1.69, LHT 0.69–1.12, CI 0.69–0.88, FCI 0.13–0.18, REL 0.30–0.39, REL2 0.37–0.48, SI 0.46–0.62, SI3 1.12–1.54, FI 0.43–0.53, PLI 0.57–0.78, PWI 0.50–0.70, PDI 1.00–1.19, LHT/HW 0.80–0.85, CSC 0–5, MSC 0–22.

Worker description

Medium- to large-sized species; head ranging from moderately broad to somewhat elongate (see CI values); clypeus relatively short, its anteromedial margin broadly convex and protruding beyond level of anterolateral margins (Fig. 88), often weakly crenulate; distance between frontal carinae approximately equal to, or slightly exceeding, maximum scape width; eye relatively small (REL <0.40; REL2 usually <0.46); scape length exceeding eye length, often strongly so (SI3 usually >1.20); profemur moderately robust (see range of FI values); pronotum relatively slender, lacking strong lateral expansion (PrWM/MTW 1.04–1.25); lateral pronotal margins well developed, blunt-edged; mesopropodeal impression with a transverse, pit-shaped depression, flanked by lateral ridges; propodeum as high as, or higher than, wide (see PDI values); dorsal face of propodeum usually somewhat flattened in profile and rounding into the steep declivitous face (Fig. 94), occasionally the propodeum more strikingly elevated (Fig. 97); petiole with distinctly differentiated anterior peduncle and node, the posterior face of node gently inclined towards the rounded summit, the anterior face a little steeper; posterior half of petiolar sternite with prominent ventral protrusion (Fig. 94); petiole variable in height and width (see range of PLI and PWI values), although never more than twice as long as wide; postpetiole varying from about 1.2× wider than long to slightly longer than wide; metabasitarsal sulcus well developed, lying in a darkened patch of cuticle adjacent to a slight carina and occupying about one half to two thirds the length of the basitarsus. Integument with numerous small punctures, the interspaces varying from smooth and shiny to finely reticulate and sublucid; punctures on dorsum of head mostly about 0.010 mm in diameter and separated by more than their diameters; punctures on dorsum of mesosoma and petiole tending to be coarser and denser, those on pronotum about 0.015 mm in diameter and often separated by no more than their diameters; side of mesosoma partly smooth and shiny anteriorly (especially on side of pronotum), becoming increasingly punctate or reticulopunctate posteriorly; postpetiole and gaster puncticulate, sublucid; malar area rugulopunctate. Standing pilosity varying from sparse to moderately common (see CSC and MSC values), present on gaster and apex of head, and on the dorsal surfaces of the following: upper half of head (0–5), pronotum (0–9), mesonotum (0–3), propodeum (0–17), petiole (0–7) and postpetiole (0–8); appressed pubescence common on most of body, especially dense on postpetiole and gastric tergites. Black to dark brownish-black; mandibles, antennae, tarsi and sometimes one or more tibiae lighter, varying from medium-brown to yellowish-brown.

Discussion

In common with other members of the *T. laeviceps*-complex, the worker caste of *T. punctulata* has an enclosed, pit-shaped mesopropodeal impression. *T. punctulata* workers can be distinguished from those of related species by the following features: (*1*) most punctures on head relatively small (typically about 0.010 mm in diameter), separated by several diameters, and contrasting with the coarser, denser punctures on the pronotum; (*2*) in profile dorsal face of propodeum more or less flattened (Fig. 94) or occasionally elevated posteriorly (Fig. 97), but not depressed posteriorly; (*3*) posterior half of petiolar sternite strongly protruding ventrally; and (*4*) petiole relatively broad (PWI 0.50–0.70). In addition, the eyes are of moderate size (REL 0.30–0.39); appressed pubescence is rather dense on the body, especially on the postpetiole and gaster; and the petiolar node, while variable in shape, always has the posterior face descending gently (Figs 94, 97–99) rather than steeply (Fig. 95) from the rounded summit. Queens and males can be recognised by the features listed in the keys. Although there are apparently no surviving types of *T. punctulata*, the original description and the type locality leave little doubt about the application of this name.

Workers of *T. punctulata* show rather extensive and complex patterns of morphological variation. Body size varies considerably, even within populations. At some localities in north Queensland and Northern Territory it is possible to distinguish nest series containing either large (HW ~ 1.10 mm) or small (HW ~ 0.90 mm) workers, each occupying different *Eucalyptus* trees. The larger workers tend to have disproportionately smaller eyes, more elongate heads, and more robust petiolar nodes, but these differences appear to be due to allometric effects. From the series of worker measurements taken over the entire range of *T. punctulata* ($n = 45$) there is no evidence of bimodality of body size (nor of eye size, head shape or petiolar shape), but further studies are needed of individual populations. It is possible that size-based ecotypes occur in some regions, among which

there is assortative mating but not complete reproductive isolation. Males associated with nest series of different-sized workers are correlated in size with workers but they do not show any obvious differences in their genitalia.

Head shape also varies geographically, with individuals from southwestern and central Australia tending to have the most elongate heads (CI values as low as 0.69 and 0.62, in workers and queens, respectively), but again there is also considerable within-regional variation. The broadest heads occur in a nest series from central Queensland (17 km SW Yeppoon), in which some (but not all) workers and males have unusually inflated heads. In northern Queensland some *T. punctulata* workers have the propodeum conspicuously elevated (Fig. 97), yielding atypically high PDI values (PDI >1.10). The shape of the petiolar node varies continuously from rather long and slender to short and robust (Figs 94, 97–99), with the most robust petioles (those with the highest PLI values) occurring in workers from northwestern Australia. Body pilosity ranges from sparse to common, as reflected in the range of CSC and MSC values, without showing any marked geographical tendencies. Standing hairs are always uncommon on the upper half of the head and on the mesonotum. Finally, there is variation in the density and size of the punctures on the head and mesosoma, and in the texture of the interspaces. As a result of weaker background sculpture (i.e. interspaces tending to be smooth and shiny), the sheen of the integument is generally stronger in eastern coastal populations, when compared with samples from drier inland localities.

Among all the samples of *T. punctulata* that I have examined, a population from southern Queensland (3 km W Rainbow Beach) is perhaps the most phenotypically distinct and merits further investigation. The workers and queens are unusually small (worker HW ~ 0.78, queen HW ~ 0.90), with a rather shiny integument. This is a mangrove population, utilising dead twigs of *Rhizophora* as nest sites.

Distribution and biology

Tetraponera punctulata is the most wide-ranging species of *Tetraponera* in Australia, occurring across much of the continent except the far south and parts of the arid interior (Fig. 195). Isolated populations occur in the Flinders Ranges of South Australia and in the MacDonnell Ranges of central Australia. In MHNG there is an old worker from 'Geelong, Viktoria' (leg. Davey), but I suspect that this has been mislabeled. There are no contemporary locality records anywhere near the state of Victoria. Outside Australia *T. punctulata* is known from a number of sites in southern Papua New Guinea.

Most localities from which *T. punctulata* has been recorded are in *Eucalyptus* woodland or open forest. In the more northern parts of Australia and in savannas near Port Moresby, Papua New Guinea, workers are often seen foraging on the trunks of *Eucalyptus* trees, and nests occur in dead branches in the canopy of the same trees. Specific nest site records include dead branches of *E. alba*, *E. camaldulensis*, *E. dichromophloia*, *E. maculata*, and *E. papuana*. Other habitat records include riparian woodland (Western Australia), monsoon gully forest (Northern Territory), mangrove (Northern Territory, Queensland), rainforest (Queensland, Papua New Guinea), gallery rainforest (Queensland), urban parkland (Queensland, Papua New Guinea), and littoral vegetation (Queensland). Nest site records from these other habitats include dead twigs or branches of *Avicennia eucalyptifolia, Calophyllum inophyllum*, and *Rhizophora* sp.

Tetraponera punctulata is able to occupy large dead branches, often composed of rather hard wood, by taking advantage of cavities previously excavated by coleopteran and lepidopteran larvae. I have twice encountered colonies whose galleries extended into live wood and in both instances the workers were tending coccids in the nest. One such nest was in branches of *Eucalyptus camaldulensis* (47 km S Derby, Western Australia) with scales of the genus *Myzolecanium*. The second record was from a live, beetle-bored branch of *Avicennia eucalyptifolia* (Scraggy Point, Hitchinbrook I., Queensland), with scales identified as ?*Coccus* sp. These observations point to the kind of biology that might characterise transitions from generalist nesting habits to specialised ant-plant inhabitation (Ward 1991).

Tetraponera rotula, sp. nov.

(Figs 89, 95, 151, 165, 177)

Type material examined

Holotype. Worker, 4 km ENE Cairns, Queensland, Australia, <5 m, 16°55′S 145°48′E, 17.i.1989 (P. S. Ward #10002) (ANIC).

Paratypes. Series of workers and males, same data as holotype (AMSA ANIC, BMNH, KUBC, KUEC, KUES, LACM, MCZC, PSWC, RMBR, TERC, UASK, UCDC, UMSC).

Other material examined

Australia: *Northern Territory*: Cahills Crossing, Kakadu Natl Pk (A. N. Andersen); Howard Springs, Darwin dist. (W. L. Brown); Litchfield Natl Pk, near Wangi Falls (B. B. Lowery); Podocarpus Canyon, Arnhem Land (H. Reichel); Robins Falls, 5 km SSE Adelaide R., 80 m (D. Hlavaty); *Queensland*: Cairns (B. B. Lowery); Scraggy Pt, Hinchinbrook I., 5 m (P. S. Ward). **Papua New Guinea** *East Sepik*: Cape Wom, 5 km NW Wewak, 5 m (P. S. Ward); *Madang*: 40 km W Madang, 140 m (P. S. Ward); Hansa Bay, Bogia Dist. (J. M. Pasteels); Laing Is., Bogia (J. M. Pasteels); *National Capital*: Port Moresby (R. Pullen). **Country unknown:** 'N. Guinea' (Biró).

(Collections: ANIC, BMNH, MCSN, MHNG, NHMV, PSWC, TERC).

Worker measurements ($n = 14$)

HW 0.73–0.81, HL 0.86–1.01, LHT 0.62–0.73, CI 0.81–0.88, FCI 0.13–0.17, REL 0.36–0.41, REL2 0.44–0.48, SI

0.54–0.57, SI3 1.14–1.29, FI 0.42–0.47, PLI 0.70–0.81, PWI 0.56–0.67, PDI 1.06–1.14, LHT/HW 0.83–0.90, CSC 1–2, MSC 0–8.

Worker description

Relatively small species, with moderately broad head (CI >0.80); clypeus short, its anteromedial portion even with, or protruding only slightly beyond, the anterolateral clypeal margin (Fig. 89); distance between frontal carinae subequal to, or slightly exceeding, maximum scape width; eye of moderate size (see REL and REL2 values), scape length always markedly greater than eye length (SI3 >1.12); profemur not notably robust (FI <0.48); pronotum relatively slender (PrWM/MTW 1.04–1.17), with well defined lateral margins; mesopropodeal impression with a pit-shaped depression, flanked by lateral ridges; propodeum slightly higher than wide, its dorsal face somewhat flattened in profile (weakly convex) and rounding into the steep declivitous face (Fig. 95); petiole with a short anterior peduncle and a large globular node, with steep anterior and posterior faces and a broadly rounded summit (Fig. 95); posterior half of petiolar sternite with prominent ventral protrusion; postpetiole appearing spherical in dorsal view and about as wide as long; metabasitarsal sulcus well developed, lying in a darkened patch of cuticle adjacent to a slight carina and occupying about 0.5–0.6× the length of the basitarsus. Integument smooth and shiny, with numerous very fine punctures, about 0.005 mm in diameter, and separated by several diameters; malar area with coarser and more elongate punctures. Standing pilosity generally uncommon (see CSC and MSC values), absent from mesonotum; petiole and postpetiole with 0–2 and 0–4 short standing hairs, respectively; appressed pubescence present but rather sparse on most of body (hairs separated by about their lengths), becoming moderately dense on abdominal tergite IV. Black to dark brownish-black, mandibles, antennae and tarsi medium-brown.

Discussion

Workers of *T. rotula* can be distinguished from those of the related species, *T. punctulata*, by the shiny, puncticulate integument (punctures about 0.005 mm in diameter); sparse pubescence, especially on the pronotum; and large globose petiolar node, with steep anterior and posterior faces (Fig. 95). *Tetraponera rotula* workers are also smaller on average, with proportionally larger eyes, differences that are diagnostic in the queen caste (see key to queens).

Distribution and biology

Tetraponera rotula is known from northern Australia (Queensland, Northern Territory) and New Guinea (Fig. 196). The type series was taken from a dead twig of *Clerodendrum inerme*, at edge of mangrove, in north Queensland. A second nest series was collected from a dead twig of *Pometia pinnata* in rainforest near Madang, Papua New Guinea. Other habitat records include 'rainforest edge', 'semi-dry littoral forest', 'riparian monsoon forest' and 'dry, rocky *Eucalyptus* woodland'. The species has also been reported nesting in hollow stems of lianas and visiting extrafloral nectaries of malvaceous bushes (Braekman *et al.* 1987). These data suggest that the species is somewhat generalised with respect to habitat and nest-site usage, although with a tendency to occur in wetter sites than *T. punctulata*. When foraging workers of *T. rotula* are disturbed they exhibit a distinctive behavior: they run rapidly with the gaster turned at right angles to the long axis of the body.

Braekman *et al.* (1987) isolated venom gland compounds from workers of a New Guinea population of *T. rotula*—the ant was identified only as a species of *Tetraponera* related to *T. punctulata*—and discovered a series of novel alkaloidal contact poisons, which they termed tetraponerines (see also Merlin *et al.* 1988; Renson *et al.* 1994; Devijver *et al.* 1995). These are released from the tip of the sting apparatus and applied to adversaries by smearing rather than stinging. This defense mechanism was observed to be effective in deterring attack by workers of the aggressive ant, *Anoplolepis gracilipes*. Braekman *et al.* (1987) noted that the lancets of the sting apparatus of *T. rotula* are enlarged and splayed at the tip, make the sting more suited to depositing the venom than injecting it.

Comparative studies of other members of the *nigra*-group are needed to determine the extent to which tetraponerines and modified sting morphology are uniquely characteristic of *T. rotula*. Certainly the gaster-turning behavior does not appear to occur in workers of related species, based on field observations of *T. punctulata*, *T. tucurua*, *T. laeviceps*, and *T. atra* (Ward personal observation).

Tetraponera tucurua, sp. nov.

(Figs 90, 96, 150, 164, 176)

Type material examined

Holotype. Worker, 11 km SSE Miriam Vale, Queensland, Australia, 120 m, 24°26′S 151°36′E, 5.i.1989 (P. S. Ward #9884) (ANIC).

Paratypes. Series of workers, alate queens and males, same data as holotype (AMSA, ANIC, BMNH, KUBC, KUEC, KUES, LACM, MCZC, PSWC, RMBR, TERC, UASK, UCDC, UMSC).

Other material examined

Australia: *Queensland*: 11 km SSE Miriam Vale, 120 m (P. S. Ward) (dealate queens) (PSWC); Arthur Point, Thirsty Sound (A. Musgrave) (2 workers, 1 male) (MCZC); E of Arthur Point, Thirsty Sound (A. Musgrave; G. P. Whitley) (1 worker, 1 male) (AMSA).

Worker measurements ($n = 6$)

HW 0.86–0.92, HL 1.02–1.15, LHT 0.64–0.71, CI 0.81–0.84, FCI 0.19–0.20, REL 0.31–0.34, REL2 0.39–0.41, SI 0.49–0.51, SI3 1.23–1.27, FI 0.50–0.53, PLI 0.78–0.82, PWI 0.79–0.88, PDI 0.99–1.07, LHT/HW 0.74–0.77, CSC 2–3, MSC 2–3.

Worker description

Medium-sized species, with relatively broad head; clypeus rather short, its anteromedial portion convex, weakly crenulate, and protruding beyond level of the anterolateral clypeal margin (Fig. 90); frontal carinae widely separated, the distance between them about 1.4× maximum scape width; eye small (REL <0.36); scape length notably longer than eye length (SI3 >1.20); profemur short and broad (see FI values); pronotum not strongly expanded laterally (PrWM/MTW 1.13–1.22); lateral pronotal margins weakly developed; mesopropodeal impression consisting of a short, transverse pit-shaped depression, flanked by lateral ridges; propodeum about as high as wide, with a flattened and broad dorsal face that lies distinctly below the level of the promesonotum; dorsal face rounding gradually into the declivitous face (Fig. 96); petiole with a short anterior peduncle and a broad, globular node (PLI >0.76, PWI >0.78); posterior half of petiolar sternite with prominent ventral protrusion (Fig. 96); postpetiole about 1.4× wider than long; metabasitarsal sulcus well developed, lying in a darkened patch of cuticle occupying about half the length of the basitarsus. Integument smooth and shiny, with numerous fine punctures; punctures on dorsum of head and mesosoma mostly 0.005–0.015 mm in diameter, and separated by several diameters or more; side of mesosoma with smooth, shiny and impunctate areas, grading into regions of denser punctation on the lower mesepisternum and on the metapleuron; petiole, postpetiole and gaster finely puncticulate, sublucid; lower malar area rugulopunctate but this sculpture less extensive than in most *nigra*-group species. Standing pilosity relatively sparse (see CSC and MSC values), absent from mesonotum and propodeum; petiole and postpetiole each with several (about 4–6) standing hairs of variable length; rather dense pilosity (grading from erect setae to shorter suberect pubescence) on underside of head; appressed pubescence present on most of body, moderately dense on abdominal tergite IV (hairs separated by less than their lengths). Black to dark brownish-black, antennae, protibia, tarsi and (to some degree) mandibles lighter, medium-brown.

Discussion

Workers of *T. tucurua* are readily identified by their small eyes, widely separated frontal carinae (Fig. 90), and very broad petiole and postpetiole (PWI 0.79–0.88). The combination of small eyes and well-separated frontal carinae yields a ratio, MFC/EL, which is greater than that of all other *Tetraponera* species in Australia (0.47–0.52, *v.* 0.17–0.41 in six other species). The shiny integument, robust profemur, broad dorsal face of the propodeum (lying below the level of the promesonotum), and absence of standing pilosity on the mesonotum and propodeum are also characteristic features of this species.

Distribution and biology

Tetraponera tucurua is known from only two localities in southeast Queensland (Fig. 196). At the type locality it occurred in a small patch of closed evergreen forest ('vine forest') in a gully, with *Eucalyptus* overstorey. Here the species was found living inside live terminal branches of a sapindaceous tree, *Cupaniopsis anacardioides*, whose pith had been removed. The cavities so occupied contained adult workers, alates, brood and scale insects (*Myzolecanium* sp.). The workers would sting when molested. On a *Cupaniopsis* sapling I observed several dealate queens (one with a hindwing still attached) walking over new shoots. There were also dealate queens *inside* some of the new branches of this same sapling, each in a separate excavated cavity with an exit hole. Thus, it appears that colony-founding queens of *T. tucurua* chew their way into new shoots of *Cupaniopsis*, and mature colonies later occupy multiple branches. The species was briefly discussed in Ward (1991), using the appellation '*Tetraponera* sp. PSW–77'.

The second locality is Arthur Point, Thirsty Sound, Qld, from which there is a series of three workers and two males, collected from the hollow twig of a tree (27.v.1957; leg. A. Musgrave & G. P. Whitley) (AMSA, MCZC). No additional biological information is available on the specimen labels, but Whitley (1970: 40) discusses a collection of three ant species—identified as belonging to the genera *Tetraponera* and *Colobopsis* (=*Camponotus*)—from the same location and date, taken from live, hollow twigs of *Cupaniopsis anacardioides*. There is also a herbarium specimen of *Cupaniopsis anacardioides* in the Royal Botanic Gardens, Sydney from Thirsty Sound, Qld (28 May 1957; leg. A. Musgrave & G. P. Whitley) with the annotation 'stems hollowed out by small black ants which inhabit the galleries so formed'.

Musgrave and Whitley were on a 'pilgrimage' to Thirsty Sound to commemorate Joseph Banks' visit to the same region in May 1770 (Whitley 1970). They were specifically looking for an ant-tree that Banks had encountered there and had described in his journal of 29 May 1770 as follows: 'In another species of tree *Xanthoxiloides mite*, a small sort of black ants had bord all the twigs and livd in quantities in the hollow part where the pith should be, the tree nevertheless flourishing, bearing leaves and flowers upon those very branches as freely and well as upon others that were sound' (Beaglehole 1963: 71). Banks also records that 'we of course gatherd the branches and were surprizd to find our hands

instantly coverd with legions of these small animals who stung most intolerably' (Beaglehole 1963: 119). The identity of the plant is unclear—a later annotation in the Banks journal by the botanist Robert Brown gives the name as *Acronychia laevis*—but there is at least strong circumstantial evidence to suggest that Banks had an encounter with a *Cupaniopsis* tree inhabited by *Tetraponera tucurua*.

Cupaniopsis anacardioides is widespread in coastal wet forest in eastern and northern Australia, with a few records from New Guinea (Reynolds 1985; Adema 1991). It appears that most populations are not associated with *T. tucurua*. Examining herbarium specimens in the Royal Botanic Gardens (Sydney) and the Australian National Herbarium (Canberra), I found that most plant specimens did not show evidence of ant occupancy, but one collection from Dorrigo, New South Wales (Nov. 1913; R. Baker) had a suggestive exit hole in a terminal twig. It would be interesting to survey populations of *C. anacardioides* for their ant associates and to investigate the degree to which the ant/plant interactions are mutualistic.

Species known only from queen caste

The two new species described below are represented by the queen caste only. Given that some species in the *nigra*-group are known only from workers, it might seem prudent to refrain from giving names to these queens. They are very distinct, however, and are clearly not conspecific with any other named taxa. That they belong to the *nigra*-group is indicated by their possession of the following traits (which are not repeated in the descriptions below): articulatory margin of mandible visible when head is held in full-face view; mesosternum predominantly smooth and shiny, lacking dense pubescence; metabasitarsal sulcus well developed; and posteromesial margin of petiolar sternite closely appressed to helcium.

Tetraponera vivax, sp. nov.

(Fig. 104, 105)

Type material examined

Holotype. Alate queen: Singapore, no date, Baker (MCZC). Labeled as follows: 'Singapore/Coll. Baker' and 'Gift of W./M. Wheeler'.

Other material examined

Indonesia: *Jawa Barat*: Bogor (Hamann) (1 queen) (NHMV). **Malaysia:** *Sabah*: Poring, Kinabalu, HQ, 550 m (S. Yamane) (1 alate queen) (KUES).

Queen measurements ($n = 2$)

HW 1.30–1.39, HL 2.09–2.18, LHT 1.06–1.12, CI 0.62–0.64, FCI 0.18–0.19, REL 0.24–0.25, REL2 0.38–0.40, SI 0.53, SI3 1.32–1.38, FI 0.56–0.58, PLI 0.49–0.53, PWI 0.44–0.46, LHT/HW 0.80–0.81, CSC 4.

Queen description

Head elongate, with parallel sides; masticatory margin of mandible with four teeth, with a gap between the 2nd and 3rd teeth; anterior clypeal margin broadly convex and edentate, and with a stout, tongue-like ventromedial protrusion (Fig. 104), extending beyond the clypeus proper by about 0.16 mm; frontal carinae moderately well separated, the distance between them about 1.25× maximum scape width; median lobes of the antennal sclerites expanded laterally and covering most of the antennal insertions, when head is observed in full-face view; malar pit present, transverse; eyes relatively small; lateral pronotal margins present but rather weakly defined; profemur very short and robust; petiole as illustrated (Fig. 105), rather long, low and narrow; postpetiole slightly broader than long, not attenuate anteriorly when observed in dorsal view; metabasitarsal sulcus prominent, occupying a darkened patch of cuticle about 3/4 the length of the basitarsus. Integument smooth and shiny, with scattered fine punctures mostly about 0.010 mm in diameter or less; punctures on most of head and mesosoma separated by several diameters, with interspaces smooth and shining; punctures denser and coarser on malar area and posterior portion of katepisternum. Long, standing pilosity moderately common on apex and venter of head, mesosoma dorsum, petiole (Fig. 105), postpetiole and gaster, but sparse on upper half of dorsum of head (four setae, in pairs posteromesial to the compound eye). Appressed pubescence scattered over body, mostly not very conspicuous, dense on posterior portion of katepisternum; most appressed hairs on abdominal tergite IV separated by about their lengths, becoming denser towards the anterior margin. Brownish-black, the antennae, protibia and tarsi medium-brown.

Discussion

The ligulate protrusion on the anterior margin of the clypeus makes the queen of *T. vivax* instantly recognisable. Other notable features are the elongate head, small eyes, shiny puncticulate integument, and broad profemur.

Distribution and biology

This species is known only from three queens, collected in Singapore, Sabah and Java. The biology of *T. vivax* remains a mystery but the configuration of the clypeus suggests specialised (perhaps parasitic) colony-founding habits.

Tetraponera volucris, sp. nov.

(Fig. 106, 107)

Type material examined

Holotype. Alate queen, Singapore, no date, Baker (MCZC). Labeled as follows: 'Singapore/Coll. Baker' '9209' and 'Gift of W./M. Wheeler'.

Queen measurements (n = 1)

HW 1.21, HL 1.92, LHT 1.08, CI 0.63, FCI 0.27, REL 0.29, REL2 0.45, SI 0.53, SI3 1.16, FI 0.54, PLI 0.49, PWI 0.44, LHT/HW 0.89, CSC 3.

Queen description

Head elongate, subrectangular; masticatory margin of mandible with four blunt, equally spaced teeth; anterior clypeal margin furnished with three stout teeth protruding well beyond the anterolateral margins (Fig. 106); frontal carinae widely separated, the distance between them almost twice the maximum scape width; median lobes of the antennal sclerites expanded laterally and covering most of the antennal insertions, when head is observed in full-face view; malar pit absent; eyes of modest size (see indices); lateral pronotal margins weakly defined; profemur relatively robust; petiole moderately long and slender, with a differentiated anterior peduncle and node (Fig. 107); postpetiole slightly longer than broad, narrowing anteriorly; metabasitarsal sulcus present as a thin impressed line, occupying about half the length of the basitarsus, not associated with a darkened patch of cuticle. Integument smooth and shiny, with scattered fine punctures mostly about 0.010 mm in diameter or less; punctures on most of head and mesosoma separated by several diameters, with interspaces smooth and shining; punctures denser and coarser on malar area, the lower portion of which is rugulopunctate. Long, standing pilosity common on anterior half of head (including the sides, see Fig. 106), venter of head, mesosoma dorsum, petiole (Fig. 107), postpetiole and gaster, but sparse on upper half of dorsum of head (two pairs, posteromesial to the compound eye). Appressed pubescence scattered over body, most dense on posterior portion of katepisternum and on gastric tergites (abdominal tergites IV-VII) where most hairs separated by about their lengths or less. Dark brownish-black, antennae, protibia and tarsi medium-brown.

Discussion

The queen of this species can be recognised by the elongate head, shiny puncticulate integument, tridentate clypeal margin, and widely separated frontal carinae. It is perhaps most closely similar to *T. vivax*, but differs from that species by the afore-mentioned clypeal and frontal carinal characters, as well as various other traits such as larger eyes, equally spaced mandibular dentition, absence of a malar pit, more slender profemur, elongate postpetiole, and more abundant pilosity on the side of the head.

Distribution and biology

Known only from the holotype, an old specimen collected in Singapore by C. F. Baker. This would probably have been during 1917–1918 when Baker, then professor of agronomy at the University of the Philippines, took a year's leave of absence to be the assistant director of the Singapore Botanic Gardens (Essig 1927).

Tetraponera pilosa-group

This group contains a single, taxonomically isolated species whose workers are characterised by the presence of ocelli, large eyes (REL >0.40), subangulate humeri, shallow mesopropodeal impression, and dense punctate sculpture. The anteromedial lobe of the clypeus is poorly developed (Fig. 57) and standing pilosity is relatively sparse. Queens show the same traits (although the presence of ocelli is not discriminating since these are present in all *Tetraponera* queens). Males have very distinctive terminalia: the hypopygium is subrectangular in shape (Fig. 127); the paramere bears a pair of digitiform lobes at its posterior end (Fig. 154); and the aedeagus is subtriangular, with a row of fine teeth on the posteroventral margin (Fig. 135).

Tetraponera pilosa (F. Smith)

(Figs 57–58, 60, 127, 135, 154)

Pseudomyrma pilosa F. Smith, 1858: 160.
Sima nicobarensis Forel, 1903*b*: 402. **Syn. nov.**
Sima pilosa (F. Smith); Emery, 1887: 449.
Sima pilosa (F. Smith); Forel, 1915*a*: 23. Description of queen.
Sima pilosa (F. Smith); Viehmeyer, 1916: 117. Description of male.
Tetraponera pilosa (F. Smith); Wheeler, 1919: 65. First combination in *Tetraponera*.
Tetraponera (*Tetraponera*) *nicobarensis* (Forel); Chapman and Capco, 1951: 80.

Type material examined

Pseudomyrma pilosa F. Smith. Syntype (unique?), worker, 'Borneo' (BMNH).

Sima nicobarensis Forel. Syntype (unique?), worker, Alexandra Kajar, Ile Nicobare, India (MHNG).

Other material examined

Brunei: Bukit Sulang, nr Lamunin (N. E. Stork). **Indonesia:** *Aceh*: Sinabang (E. Jacobson); *Bengkulu*: Bengkulu [as 'Benculen'] (E. Modigliani); Kepahiang, 1960ft (H. C. Kellers); *Jawa Barat*: Bogor [as 'Buitenzorg'] (Solms); *Jawa Tengah*: Semarang (L. G. E. Kalshoven); *Kalimantan Selatan*: Pulo Laut (c.u.); *Kalimantan Timur*: 31 km N Balikpapan, E. Borneo (W. L. Brown); Kutai (T. Yajima); Long Bagun Ulu (Seyfert; Graindl); *Lampung*: Wai Lima (Karny); *Sumatera Barat*: Indropura (Fritsehler); Mentawei, Si Oban (E. Modigliani); Mentawei, Sipora, Sereinu (Modigliani); *Sumatera Utara*: Banda Baru, 47 km S Medan, 600 m (E. S. Ross); Pangherang-Pisang (E. Modigliani); Pematang Siantar (J. Matthews); Pematang Siantar (W. M. Mann); *province unknown*: 'Sumatra' (Jacobson). **Malaysia:** *Johor*: 13 km NE Kota Tinggi, 50 m (P. S. Ward); Kluang F. R. (C. G. Roche); *Pahang*: Genting Highlands, 800 m (U. Maschwitz); *Perak*: 'Perak' (c.u.); *Pulau Pinang*: Batu Ferringi, Penang I., 60 m (R. Crozier); 'Penang' (N. L. H. Krauss); *Sabah*: Crocker Range NP, Mawar Waterfall (c.u.); Danum Valley (S. Yamane); Danum Valley (E. Widodo); Forest Camp, 19 km N Kalabakan, 180 m (Y. Hirashima); Liawan (T. C. Maa); Poring

Spring, >650 m (A. Floren); Quoin Hill, Tawau (Y. Hirashima); Sandakan (Baker); Umas Umas, nr Tawau (R. W. Taylor); *Sarawak*: Bako Natl Pk (D. H. Janzen); G. Mulu Natl Pk (B. Bolton); G. Mulu Natl Pk (M. Collins); G. Mulu Natl Pk, Melinau Gorge (F. Wanless); Kuching (J. Hewitt); Mt Dulit, R. Koyan, 2500 ft (B. M. Hobby; A. W. Moore); Niah Natl Pk (H. Ôkido); Serambu Mt (H. Smith); s Gunung Buda, 64 km S Limbang (S. L. Heydon; S. Fung); SW Gunung Buda, 64 km S Limbang (S. L. Heydon; S. Fung); *Selangor*: UKM campus (D. G. Furth); Ulu Gombak (A. Buschinger); Ulu Gombak (U. Maschwitz); Ulu Gombak, 350 m (R. Klein); *Terengganu*: P. Perhentian Besar (Madl); P. Perhentian Besar (Windschnurer); *Wilayah Persekutuan*: Kuala Lumpur (N. L. H. Krauss). **Myanmar** *Tanintharyi*: Tenasserim, Thagatà (Fea). **Philippines** *Palawan*: Iwahig Penal Col., *c.* Puerto Princesa, 60 m (B. B. Lowery); Iwahig, Puerto Princesa (C. K. Starr); Puerto Princesa (R. C. McGregor). **Singapore** Bukit Timah Nat. Res. (D. H. Murphy); Kent Ridge, 30 m (P. S. Ward); Pierce Reservoir, 40 m (P. S. Ward); Seletar Reservoir, 20 m (P. S. Ward); Singapore (Baker); Singapore (H. Overbeck); Singapore (S. Yamane); Toh Tuck [as 'Toe Tuck'] wasteland (D. H. Murphy). **Thailand** *Chanthaburi*: 20 mi SE Chantaburi, 75 m (E. S. Ross; D. Q. Cavagnaro); *Phangnga*: Tone Chang-Fah Waterfall, 20 km S Takuapa, 100–200 m (A. Schulz; K. Vock); *Songkhla*: Ton Nga Chang Natl Pk (H. Ôkido); *Trang*: Khao Chong (river side) (S. Yamane). **Vietnam:** *Soc Trang*: Côn Dao [as 'Isl. Kondao'] (A. Radchenko). **Country unknown:** S. Saranibo, N. Borneo (E. Mjöberg); 'Siamese Malay States' (Annandale; Robinson)

(Collections: AMNH, ANIC, ASIC, BMNH, CASC, HZIC, KUEC, KUES, LACM, MCSN, MCZC, MHNG, NHMB, NHMV, PSWC, RMBR, UASK, UMSC, USNM).

Worker measurements (*n* = *10*)

HW 1.14–1.51, HL 1.28–1.70, LHT 0.93–1.31, CI 0.86–0.93, FCI 0.09–0.13, REL 0.43–0.49, REL2 0.49–0.56, SI 0.56–0.59, SI3 1.02–1.18, FI 0.43–0.49, PLI 0.48–0.53, PWI 0.45–0.52, PDI 1.01–1.08, LHT/HW 0.81–0.87, CSC 5–9, MSC 3–6.

Worker description

Relatively large species, with broad head (CI >0.85); clypeus short, the anteromedial lobe broad, flat, and weakly developed (Fig. 57); distance between frontal carinae less than or equal to maximum scape width; eyes large and prominent; ocelli present; profemur relatively robust (see FI values); pronotum with lateral margins well developed, and with humeri subangulate, when seen in dorsal view (Fig. 60); mesopropodeal impression consisting of a short, transverse furrow, only moderately incised; propodeum slightly higher than wide, the dorsal face broad and flattened, and rounding gradually into the declivitous face; petiole as illustrated (Fig. 58), long and low, with gently sloping anterodorsal and posterodorsal faces, and with prominent recurved anteroventral tooth; petiole about twice as long as broad; postpetiole as long as or slightly longer than broad; metabasitarsal sulcus present, lying in a thin strip of slightly darkened cuticle, occupying about 0.5–0.6× the length of the basitarsus. Head, mesosoma and petiole densely punctate to reticulopunctate, and subopaque; punctures becoming finer on postpetiole and gaster. Standing pilosity relatively sparse (see CSC and MSC values), absent from propodeum; short, appressed pubescence common on body, becoming denser posteriorly, and forming a thick mat on abdominal tergite IV. Body dark brown, mandibles, antennae and apices of legs tending to be lighter medium-brown.

Discussion

Tetraponera pilosa can be easily recognised by the features listed in the species-group diagnosis and in the keys. In comparison with other Asian *Tetraponera* species, it shows relatively little variation in morphology.

Distribution and biology

This species is found from southern Indochina to Sumatra, Java, Borneo, and Palawan (Fig. 186). Habitats from which it has been recorded include second-growth rainforest, rainforest edge, 'lower montane mixed dipterocarp forest', and 'rainforest along creek beds'. Colonies have been collected in dead twigs of *Hevea brasiliensis*, *Vitex pubescens*, *Piper* sp., and unidentifed vines and trees.

Tetraponera rufonigra-group

This is another monotypic species-group. Both workers and queens have well developed ocelli, five teeth on the masticatory margin of the mandible, a prominent median clypeal lobe, angulate humeri, and abundant standing pilosity. The eyes are relatively small (REL <0.35) and the integument of the head and mesosoma is densely punctate to rugulopunctate. Male sternite IX is semicircular in shape, with a broadly concave posterior margin (Fig. 126); the paramere is large and tapers posteriorly to a rounded boss, subtended by a mesial plate-like lobe (Fig. 153); the aedeagal plate is subrectangular in shape, with a row of denticles along the posteroventral margin (Fig. 134).

Tetraponera rufonigra (Jerdon)

(Fig. 55–56, 59, 126, 134, 153)

Eciton? *Rufonigrum* Jerdon, 1851: 111
Sima rufonigra var. *yeensis* Forel, 1902: 248. **Syn. nov.**
Sima rufonigra var. *testaceo-nigra* Forel, 1903*b*: 402. **Syn. nov.**
Sima rufonigra var. *ceylonensis* Forel, 1909*b*: 394. **Syn. nov.**
Pseudomyrma rufo-nigra (Jerdon); F. Smith, 1858: 159.
Sima rufo-nigra (Jerdon); Roger, 1863*b*: 25.
Tetraponera rufonigra (Jerdon); F. Smith, 1877: 68. First combination in *Tetraponera*.

Types (*not examined*)

Eciton? *Rufonigrum* Jerdon. Syntypes, workers, southern India [apparently lost]. Original description: 'very common in the Carnatic, less so in Malabar'.

Type material examined

Sima rufonigra var. *yeensis* Forel. Syntype, 1 alate queen, Ye Valley, Myanmar (Bingham) (MHNG).

Sima rufonigra var. *testaceo-nigra* Forel. Syntypes, 3 workers, Nankowry, I. Nicobar, India (MCSN, MHNG).

Sima rufonigra var. *ceylonensis* Forel. Syntypes, 3 workers, 1 alate queen, Ceylon (Yerbury) (MHNG); 21 workers, Ceylon (Bugnion) (MHNG).

Other material examined

Bangladesh: *Chittagong*: Chittagong (E. S. Ross; D. Q.Cavagnaro); *Dhaka*: 'Dacca' (D. Leston). **Bhutan** Phuntsholing (NHMB – Bhutan Expedition 1972); Samchi (NHMB – Bhutan Expedition 1972). **China** *Hainan*: Dwa Bi (J. L. Gressitt); Lumuwan, 180 m (J. R. Fellowes); Ta Hau (J. L. Gressitt); Ta Hian (J. L. Gressitt). **India** *Andaman & Nicobar Is.*: Car Nicobar I. [as 'Kar Nikob.'] (c.u.); 'Ga Nicobar' (c.u.); Nicobar Is. (G. Rogers); *Assam*: 'Assam' (W. F. Badgley); Chabua (W. L. Jellison); Dibrugarh (W. L. Jellison); Gauhauti (W. Wittmer; C. Baroni Urbani); Jorhat (A. C. Cole); Kobo, 400 ft (Abor Exped.); Sibsagar [as 'Sibsorgar'] (c.u.); *Delhi*: Delhi University (H. S. Vishnoi); *Goa*: Chapora (C. Peeters); Mormugao (J. C.Bridwell); *Gujarat*: Disa (=Deesa) (W. J. Pulawski); *Karnataka*: 10 mi N Belgaum, 800 m (E. S. Ross; D. Q. Cavagnaro); 15 mi S Chikmagalur, 900 m (E. S. Ross; D. Q. Cavagnaro); 5 mi W Hunsur, 850 m (E. S. Ross; D. Q. Cavagnaro); Bangalore (T. C. Lawrence); I.I.Sc. Campus, Bangalore (T. Varghese); Indian Institute of Science, Bangalore, 900 m (P. S. Ward); Kanara (Wroughton); Mangalore (J. C.Bridwell); Sagar, 600 m (E. S. Ross; D. Q. Cavagnaro); *Kerala*: Calicut University campus (S. Sheela); Muthanga (S. Sheela); Nilambur (A. B. Soans); Parambikulam Dam (F. Rickson); Periyar Sanctuary, vic. Thekkady, 500–1000 m (A. Schulz; K. Vock); Tenmalai, Travancore, 500–800 ft (B.M. –C.M. Expdn. to S. India); Thekkadi, Periyar Dam, Travancore (B.M. –C.M. Expdn. to S. India); Thirunelly, Wynaad Taluk, W. Ghats (A. B. Soans; W. L. Brown); *Maharashtra*: 5 mi SE Indapur, 450 m (E. S. Ross; D. Q. Cavagnaro); Bandra, Bombay (E. S. Ross; D. Q. Cavagnaro); Bombay (Mathéran); Deesa, Bombay (C. G. Nurse); Poona (Wroughton); Savantvad (J. C.Bridwell); *Meghalaya*: Garo Hills (P. J. Schmitt); Garo Hills, 400 m, Songsak (C. Besuchet; I. Löbl); Songsak, Garo Hills (W. Wittmer; C. Baroni Urbani); *Orissa*: Barkuda I., Chilka Lake, Ganjam Dist. (N. Annandale); Puri [as 'Pooree'] (Walsh); *Pondicherry*: Karikal (P. B. Nathan); *Rajasthan*: E slope, Mt Abu, 750 m (E. S. Ross; D. Q. Cavagnaro); *Tamil Nadu*: 10 mi NW Satyamangalam (E. S. Ross; D. Q. Cavagnaro); Coimbatore (c.u.); Dohnavur, Tinnevelly Dist., 350 ft (B.M. –C.M. Expdn. to S. India); Mudumalai Anim. Sanct. (J. Noyes); Muthikolam, Coimbatore Dist., 3000 ft (B.M. –C.M. Expdn. to S. India); Nedungadu, Tanjore (P. S. Nathan); Tuticorin (c.u.); Vedanthangal (E. S. Ross; D. Q. Cavagnaro); Walajanagar, N. Arcot (A. P. Nathan); *Uttar Pradesh*: 5 mi SW Dehra Dun, 600 m (E. S. Ross; D. Q. Cavagnaro); Bamrauli (L. H. Weatherill); Dimli Pass, Sivalik Hills (W. Wittmer); Kheri Forest ('H. G. C.'); Ranipur, 6 km S Hardwar, 300 m (A. K. Mehrotra); vic. Rajaji Natl Pk, 10 km SE Dehra Dun, 600–700 m (A. Schulz; K. Vock); *West Bengal*: 'Bengal' (c.u.); Baragachi [as 'Baigachi'] (L. H. Weatherill); Barakpur [as 'Barrakpur'] (Minchin); Barakpur [as 'Barrackpore'] (Rothney); Calcutta (E. Brunetti); Calcutta (E. S. Ross; D. Q. Cavagnaro); Calcutta (Rothney); Calcutta (Schulthess/Rechenberg); Calcutta (Stolizka); Calcutta (c.u.); Darjeeling (Bates). **Indonesia:** *Jakarta Raya*: Meester Cornelis, 25 m (J. Olthof); *Jawa Barat*: Pelabuhanratu [as 'Pelabuamatu'] (Hamann); Salatri (K. M. Walsh); Tjisolok [as 'Tjisotok'] (Hamann); *Jawa Tengah*: Rembang (L. G. E. Kalshoven); Semarang (L. G. E. Kalshoven); *Lampung*: Krakatau (Dammerman); Krakatau (E. Jacobson); Krakatau (c.u.); Liwa (Gribodo); Pulau Anak Krakatau (S. Yamane); Wai Lima (Karny); *Sumatera Barat*: Indropura (Fritsehler); *Sumatera Utara*: Labuhanbilik [as 'Labouan Bilik'] (K. Surbek); Medan (L. Fulmek); Pematang Siantar (J. Matthews); Pematang Siantar (NGS SI Exped.); *province unknown*: 'Sumatra' (Fritcher). **Laos:** *Champasak*: Bolavens Plateau, M. Paksong – B. Nam Thang, 800–1100 m (Schillhammer). **Malaysia:** *Kedah*: P. Langkawi, Tarjung Rhu (Madl); *Negeri Sembilan*: 11 mi SE Seremban, 90 m (E. S. Ross; D. Q. Cavagnaro); *Perak*: Gedong, Batang Padang (Annandale; Robinson); Lenggong (Lea *et al.*); Parit Buntar (c.u.); Teluk Intan [as 'T. Intan'] (K. C. Khoo); *Pulau Pinang*: 'Penang' (U. Maschwitz); Kent Estate (c.u.); *Selangor*: Ampang Res. (L. F. Bang-Rouhet); Gombak Valley (H. M. Pendlebury); Kepong (Army Scrub Typhus Unit); near Sekinchan (K. Rosciszewski); Petaling Jaya (A. J. Beck); Serdang (N. L. H. Krauss); *Wilayah Persekutuan*: Kuala Lumpur (R. Crozier); Kuala Lumpur (N. L. H. Krauss); Kuala Lumpur (Lea *et al.*); Kuala Lumpur (U. Maschwitz); Kuala Lumpur (H. M. Pendlebury); Kuala Lumpur (E. S. Ross; D. Q. Cavagnaro); Kuala Lumpur (C. Y. Siew); Kuala Lumpur (c.u.). **Myanmar:** *Ayeyarwady*: Res. Forest Area, near Kadonkini [sic], S of Bogale (J. B. Jackson); *Kachin*: Bhamò (Fea); Metanja (Fea); Teinzo (Fea); *Kayin*: Carin Chebà, 900–1100 m (L. Fea); Thaungyin [River] (Bingham); *Mandalay*: Mandalay (Swinhoe); Mandalay Maymyo Rd., 2000 ft (Bingham); *Mon*: Moulmain (Hodgson); *Sagaing*: Chattin Wildlife Sanctuary, 200 m (Schillhammer); Ruby Mines, 2800 ft (C. Bingham); *Tanintharyi*: Tenasserim, Ataran (Bingham); Tenasserim, Meetan (Fea); *Yangon*: Rangoon (Fea); Rangoon (G. E. Gates). **Nepal:** *Gandaki*: 4 mi W Pokhara, 3000 ft (J. Quinlan); Pokhara, 820 m (W. Wittmer; C. Baroni Urbani); *Janakpur*: Jiri-Thodung (W. Wittmer; C. Baroni Urbani); *Kosi*: 12 km ENE Tumlingtar, 1150 m (C. Carpenter); Arun Valley, 2000 ft (L. Swan); *Narayani*: 9 mi W Hitaura, 400 m (E. S. Ross; D. Q. Cavagnaro); Royal Chitwan Natl Pk, 60 km SW Kathmandu, 600 m (A. Hackländer). **Pakistan:** *Punjab*: Lahore, 250 m (E. S. Ross; D. Q. Cavagnaro). **Seychelles:** Mahe (Scott); Silhouette (Percy Sladen Trust Exped.). **Singapore:** Bukit Panjang (H. C. Abraham); Bukit Timah Nat. Res. (D. H. Murphy); Mandai, <5 m (P. S. Ward); Seletar (D. H. Murphy); Singapore (N. L. H. Krauss); Singapore, intercepted at quarantine Brisbane (c.u.); University Campus (D. H. Murphy). **Sri Lanka:** *Central*: Kandalama (A. M. Boulton); Nalanda (Pagel); *North Central*: Anuradhapura (U. Maschwitz); Medirigiriya, nr Pollonaruwa (K. L. A. Perera); Mihintale (A. E. Stubbs; P. J. Chandler); Pollonaruwa (K. L. A. Perera); Polonnaruwa (K. V. Krombein; P. B. Karunaratne); *North Eastern*: Jaffna (G. Fairchild); Kantalai [as 'Kanthalay'] (Horn); Nunaragala, Maha-Oya Dist. (R. Winney); Paraiyanalankulam [as 'Parayanalankulam'] Irrigation Canal, 25mi NW Medawachchiya, 100 ft (Davis; Rowe); *North Western*: Kadaimparu, 15 mi N Negombo (Brinck *et al.*); Lunuwila (B. Bolton); *Sabaragamuwa*: Uggalkaltota, 350 ft (Davis; Rowe); Walawe Ganga, 34 mi SE Ratnapura (Brinck *et al.*); *Southern*: Hambantota ('T. B. F.'); Hikkaduwa Yala (Ruhuna Natl Pk) (U. Maschwitz); Palatupana (K. V. Krombein *et al.*); *Uva*: Dunhinda Falls, 1300ft (G. Ekis); Uda Walawe, 300 ft (G. Ekis); *Western*: Beruwala, Bentota R. [as 'Benuwela am Fluss Bentata'] (Gerten); *district unknown*: 'Ceilon' (Sichel); 'Ceylon' (Horn); 'Ceylon' (c.u.). **Thailand:** *Chiang Mai*: agric. exp. stn. NW of Chieng Mai, 800 m (E. S. Ross); Chomtong (H. Smith); Doi Inthanon NP: Wachiratharn Falls, 750 m (R. R. Snelling; S. Sonthichai); Doi Sutep (W. P. Cockerell); Doi Sutep (D. & E. Thurman); Doi Suthep, 500–700 m (S. Yamane); Doi Suthep-Pui, 600–1400 m (H. Ôkido); E slope, Doi Sutep, 1100–1275 m (E. S. Ross; D. Q. Cavagnaro); E slope, Doi Sutep, 260 m (E. S. Ross; D. Q. Cavagnaro); Mae Chaem [as 'Maecham'] (W. Jaitrong); Mai Wang Dist.: Huay Ko Haeng, 450 m (R. R. Snelling; S. Sonthichai); Vachiratharn Falls, Doi Inthanon Natl Pk, 70 km SW Chiang Mai, 800 m (B. V. Brown); W Mae Rim, Mae Sa NP, Mae Sa Falls (H. Zettel); *Krabi*: Krabi (Risch); Noppharat Thara (Madl); *Krung Thep Mahanakhon*: Bangkok [as 'Bankok'] (H. Hillman); Bangkok (H. Smith); Kasetsart Univ., Bangkok (S. Yamane); Kasetsart Univ., Bangkok (H. Ôkido); Wat Salak (W. R. S. Ladell); *Mae Hong Son*: Pangmapa (D. Kovac); *Nakhon Ratchasima*: Nong Hoi (D. Jackson);

Nakhon Si Thammarat: Thung Yai [as 'Tung Yai'] (G. R. Ballmer); *Phrae*: Phrae [as 'Prae'] (E. G. Alexander); *Phuket*: Puket Salang (H. Smith); *Surat Thani*: Koh Tao (H. Smith); *Tak*: Lan Sang NP [as 'Larnsang NP'] (Madl). **Vietnam:** *Ha Noi*: Co-loa, 20 km NE Hà-nôi (R. Bielawski; B. Pisarski); *Ha Sonh Binh*: Ky Son, Cao Phong (Belokobylskij); *Khanh Hoa*: Cam Ranh Bay (R. H. Taylor); *Quang Nam*: Phuc-Son (H. Fruhstorfer); *Yen Bai*: Yen Bai [as 'Yen Bei'] (Fouquet); Yenbai (c.u.); *province unknown*: Phjöng-san, Annam (c.u.).

(Collections: AMNH, ANIC, BMNH, CASC, CESB, CUIC, DZUC, KFBG, KUBC, KUES, LACM, MCSN, MCZC, MHNG, MNHN, MZLU, NHMB, NHMV, PSWC, RMBR, RMNH, SAMC, UCDC, USNM, ZMAS, ZMPA).

Worker measurements (n = 10)

HW 1.62–2.07, HL 1.76–2.37, LHT 1.52–2.04, CI 0.87–0.95, FCI 0.13–0.16, REL 0.31–0.34, REL2 0.35–0.37, SI 0.58–0.63, SI3 1.61–1.74, FI 0.30–0.36, PLI 0.46–0.53, PWI 0.43–0.52, PDI 0.99–1.03, LHT/HW 0.86–0.98, CSC 12–24, MSC 20–66.

Worker description

Large species, with broad head (CI >0.85); masticatory margin of mandible with five teeth; anteromedial lobe of clypeus narrow but prominently protruding (Fig. 55); distance between frontal carinae exceeding maximum scape width; eyes relatively small; ocelli well developed; profemur slender (FI <0.38); pronotum with lateral margins well developed, and with humeri angulate, when seen in dorsal view (Fig. 59); mesonotum descending suddenly to mesopropodeal impression, latter moderately long (Fig. 56), consisting of a rugulose transverse furrow, flanked by low tubercles (containing metanotal spiracles); propodeum about as high as wide, dorsal face broad and flattened, and rounding gradually into the shorter declivitous face; petiole with short anterior peduncle and somewhat elongate and flattened node (Fig. 56); anteroventral petiolar tooth usually prominent, directed ventrad; petiole varying from about 1.9–2.3× longer than broad; postpetiole longer than broad; metabasitarsal sulcus well developed, occupying about 0.7–0.8× length of the metabasitarsus; mesobasitarsal sulcus also present, occupying 0.5–0.6× length of mesobasitarsus. Head densely punctate; punctures separated by their diameters or less, interspaces sublucid to subopaque; mesosoma and petiole densely punctate to rugulopunctate, subopaque; punctures finer on postpetiole and gaster, and integument correspondingly shinier. Standing pilosity abundant on most of body (see CSC and MSC values), including mesonotum and propodeum; appressed pubescence common, moderately dense on abdominal tergite IV. Head and gaster dark brown to brownish-black, mesosoma and petiole usually a constrastingly lighter orange-brown, postpetiole variable (less commonly mesosoma and petiole darker, approaching color of head and gaster); mandibles, antennae, protibia and tarsi medium-brown to yellowish-brown.

Discussion

This species can be recognised by the traits listed in the species-group diagnosis and in the key. Although no type specimens of *T. rufonigra* are currently known to exist, the species is so distinctive that its identity has never been in doubt. It shows modest variation in integument sculpture (especially the sheen of the head), petiole shape (see range of PLI and PWI values), and pilosity (see CSC and MSC values). More striking is the variation in the color of the mesosoma and petiole—these parts of the body are usually a light orange-brown that contrasts strongly with the dark head and gaster, thereby imparting a bicolored appearance. But in some populations, especially those from Sri Lanka, the middle part of the body can be heavily infuscated. The darkest Sri Lankan workers are essentially unicolored (the basis of Forel's 'variety' *ceylonensis*).

Distribution and biology

Tetraponmera rufonigra is widely distributed on the Indian subcontinent, and ranges through Southeast Asia as far south as Sumatra and Java (Fig. 185). There is also an introduced population in the Seychelles. Habitats occupied by *T. rufonigra* include semideciduous woodland, mangrove, urban parkland, gardens, and 'degraded coastal hill forest'. The species nests in cavities in dead and living wood, and the workers can be rather aggressive (Bingham 1903). A colony that I encountered at Mandai, Singapore was occupying live beetle-bored branches of *Sonneratia ovata* and also extended into cavities in the bole of the tree. In Bangalore, India I found a nest in the primary stem of a *Santalum album* sapling. The nest inside the live stem conformed to the presumed burrows of a beetle larva (most likely a cerambycid), but also contained incomplete septa, apparently made of dirt that appeared to have been added by the *Tetraponera* workers. The nest in the *Santalum* sapling contained workers, eggs, larvae and a large, mature coccid.

Phylogeny and biogeography

Origin of the Indo-Australian Tetraponera *fauna*

Species of *Tetraponera* are found throughout the Old World tropics (Ward 1990). The four species-groups here recognised from the Indo-Australian region show considerable disparity in morphology, suggesting that they do not collectively constitute a monophyletic group. This was confirmed by phylogenetic analysis of a morphological data set (Table 1) containing a representative selection of *Tetraponera* species from Africa, Madagascar, Asia and Australia. Parsimony analysis yielded a single minimum-length tree (length 266, consistency index 0.48, retention index 0.51), in which the Oriental/Australian species emerge at multiple locations in the tree (Fig. 179). The most parsimonious reconstruction of ancestral distribution on the cladogram (Fig. 180) indicates an African origin for the

Table 1. Morphological data set used for assessing the origin of the *Tetraponera* fauna of Asia

Data taken from Ward (1991). Characters 1–55 are worker- and queen-based; characters 56-88 are taken from the male caste. Characters 10, 16, 18, 53, 54, 63 and 64 were treated as unordered. The first taxon is the outgroup. '?' indicates inapplicable or ambiguous.

	10	20	30	40	50	60	70	80
Pseudomyrmex gracilis	0101000141	0200000001	0010011002	0021120310	0000121001	0102011111	0000010000	1000100210 00110010
T. aethiops	20102?1112	1000110200	0100000010	0030121102	2202110002	1203001111	0000100000	0001000111 00100000
T. mocquerysi	1021??1103	1000140000	0001010001	1020111211	2211120001	0101001111	0021100000	0000000211 00010000
T. pilosa	20102?1112	1000100200	0100000010	0020111211	1211120001	0101000110	0000000100	0010000211 00100000
T. rufonigra	010?111023	1000100210	0100000002	0030111101	2212110001	1032001111	0002100000	0111000121 10100000
T. grandidieri	001?2?1012	1000130000	0000010010	0020211101	2222110101	0031101100	0000100000	0000000211 01011000
T. ambigua	111?1?1013	1200100000	0001011000	0110111212	2210020001	0131001110	0000100000	0001010221 00100?0
T. ophthalmica	010?1?1013	1200100000	0001011010	0100211211	2210020000	0031001010	0000100000	0001010221 00100100
T. tessmanni	1000111122	1031000010	0002111010	1000011002	2202020112	1134001110	0000000000	0011000221 01001001
T. penzigi	100?2?1012	1100100010	0002110010	1010111102	3201020012	1101001010	0000101000	0001000221 11101001
T. clypeata	1021??1203	1100100000	1002110010	1000111101	2212020100	0123101010	0000100010	0001001221 01101?1
T. morondaviensis	110?1?1013	1000101000	0002010000	1010211101	2212020001	0123001110	0001100001	0011000121 11100?0
T. allaborans	2021??1202	1100120000	1002011010	0010111201	2211020100	0004101010	1000100000	0001001221 01101001
T. attenuata	10102?1112	1100110310	0002010101	0010211101	2212110200	0005001110	0002100010	0111000221 12010000
T. nigra	10102?1112	1100110410	0001010101	0010211101	2212120201	0103001111	0002100010	0111000121 13010?0
T. nitida	20001?1113	1000110000	0002000110	0010011211	2200020101	0104001111	0102100010	0111000221 13010000
T. punctulata	100?2?1013	1100110510	0002010100	0010111201	2211030001	0105001111	0102100010	0111000221 13010000

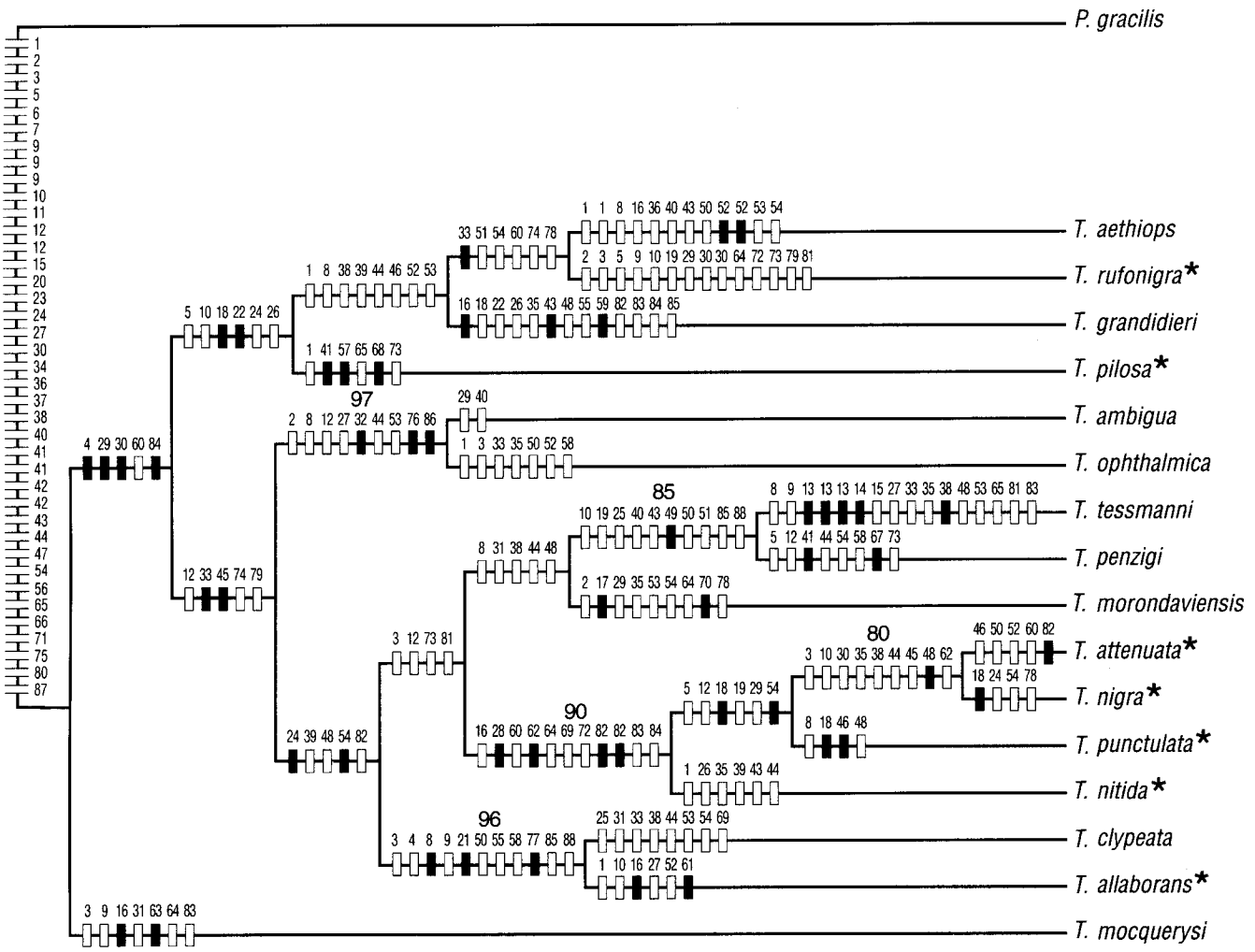


Fig. 179. Single most parsimonious tree (length 266, consistency index 0.48, retention index 0.51) obtained from analysis of the *Tetraponera* data set in Table 1. Smaller numbers refer to characters; larger numbers indicate bootstrap values greater than 50%, based on a separate bootstrap analysis with 1000 replicates. Open bars: homoplasious changes (convergences and reversals); closed bars: non-homoplasious changes. For some characters there are multiple equally parsimonious reconstructions of character state change; the reconstruction shown here favours change near the root of the tree (ACCTRAN). Species marked with an asterisk are from the Indo-Australian region; other *Tetraponera* taxa are from the Afrotropical region (Madagascar: *T. grandidieri*, *T. morondaviensis*; Africa: *T. aethiops*, *T. ambigua*, *T. ophthalmica*, *T. tessmanni*, *T. penzigi*, *T. clypeata*, *T. mocquerysi*).

genus, and reveals four different Indo-Australian clades—corresponding to the *allaborans*-group, *nigra*-group, *pilosa*-group and *rufonigra*-group, respectively—whose nearest extant relatives are in the Afrotropical region. Although support for some parts of the tree is weak (as indicated by branches with few synapomorphies and low bootstrap values, see Fig. 179), constraining the Indo-Australian species to form a monophyletic group increases tree length to 287 steps, a highly significant difference (Wilcoxon signed-ranks test, $P < 0.004$). So it seems reasonable to conclude that the Indo-Australian *Tetraponera* fauna is a polyphyletic assemblage comprising at least two (probably four) different lineages, each derived from African ancestors. Note also that the sister group of *Tetraponera* is the Neotropical genus *Pseudomyrmex* (Ward 1990), which points to a Gondwanan origin for the subfamily Pseudomyrmecinae as a whole.

How is the presence of four *Tetraponera* clades in Asia and Australia to be explained? Several possibilities can be considered. One is that *Tetraponera* is another example among many (Briggs 1987, 1995; Macey *et al.* 2000) of a taxon whose ancestors were dispersed via the breakup of Gondwana in the Mesozoic and early Cenozoic. Since the Australian representatives of *Tetraponera* appear to be derived relatively recently from Asian taxa (see below), and these in turn have their closest relatives in Africa, it seems unlikely that rifting of terranes from Gondwanan Australia to Laurasia in the Mesozoic (Metcalfe 1998) has played any

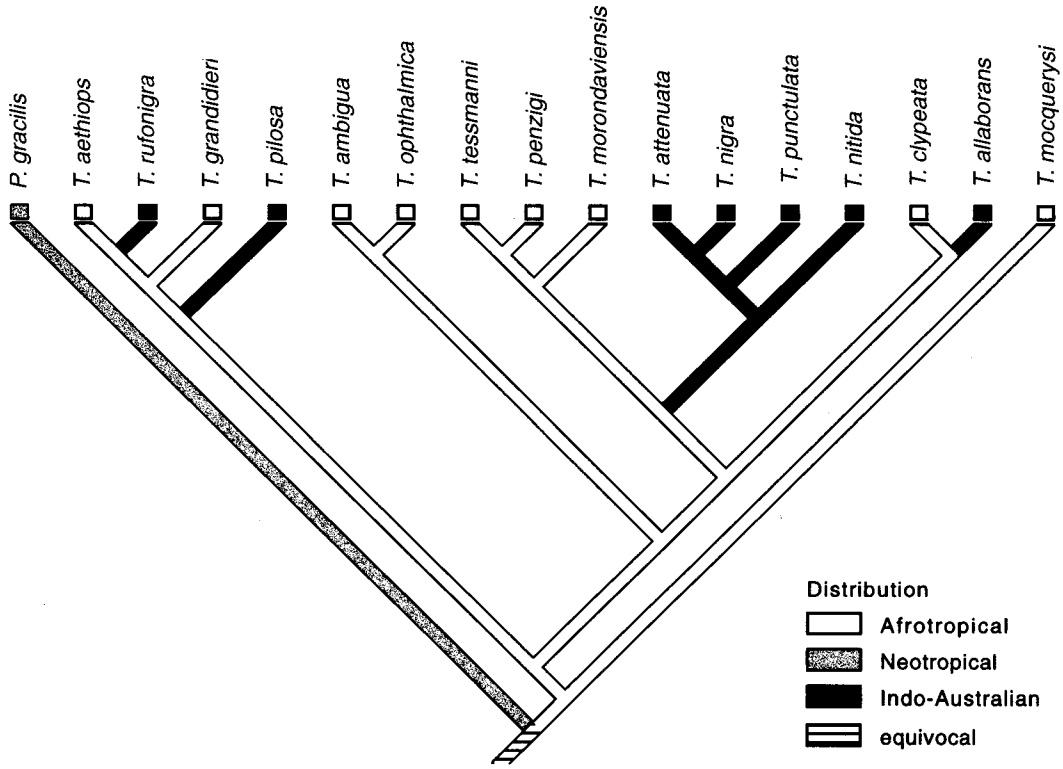


Fig. 180. Taxon distribution mapped on the tree from Fig. 179.

role in the current distribution of *Tetraponera*. But the Cretaceous separation of India from Gondawana, and its subsequent collision with the Asian plate in the Eocene (Hall 1998; Mattauer *et al.* 1999), provides a possible mechanism whereby one or more African clades could have been transported to Asia. This would imply that either the genus *Tetraponera* had diversified into multiple lineages when India/Madagascar separated from the African plate, or that the drifting Indian fragment remained sufficiently close to the African continent (Briggs 1989) to be colonised by *Tetraponera* originating from Madagascar or east Africa. In either event, an arrival in Asia via India seems plausible for both the *allaborans*-group and the *nigra*-group, which have affinities with taxa in southern and eastern Africa (e.g. *T. clypeata* (Emery), *T. penzigi* (Mayr)) and Madagascar (e.g. *T. morondaviensis* (Forel)) (Fig. 179). Moreover, these two species-groups have undergone substantial diversification in Asia (11 and 20 known species, respectively), an outcome consistent with a presence in the region since the Eocene. In contrast, the *pilosa*- and *rufonigra*-groups each contain a single species, suggesting more recent origins, perhaps via mid-Tertiary dispersal from Africa/Arabia or Europe.

Although the genus *Tetraponera* is absent from Europe today, there are four fossil species known from Baltic amber (Mayr 1868; Wheeler 1915; Dlussky 1997), probably of late Eocene or early Oligocene age (Larrson 1978; Rasnitsyn and Kulicka 1990; Poinar 1992). There is also a fifth fossil species, assigned to the genus *Tetraponera*, from Oligocene deposits in France (Théobald 1937). Thus, *Tetraponera* was represented in Europe during periods of warmer climate in the Tertiary, and this suggests the possibility of trans-Tethys migration (and subsequent dispersal to Asia) independent of transport on the Indian plate.

The relationship of the Baltic amber *Tetraponera* to extant taxa needs further study. In discussing two Baltic amber species, *T. simplex* (Mayr) and *T. angustata* (Mayr), Wheeler (1915) stated that they were 'closely related' to a series of Asian species that are now known to be divided between the *nigra*- and *allaborans*-groups. He also cited two Malagasy species as close relatives of the Baltic amber taxa. Obviously these casual assertions need validation. From perusal of the original descriptions I would judge that *T. simplex* and *T. angustata* are not particularly closely related to the *allaborans*-group since *T. simplex* has the masticatory margin of the mandible longer than the basal margin, and Wheeler's (1915) illustration of *T. angustata* (as *T. lacrimarum* (Wheeler)) shows a posteroventral petiolar configuration more like that of the *nigra*-group than the *allaborans*-group. The other two Baltic amber species of *Tetraponera*, *T. klebsi* (Wheeler) and *T. ocellata* (Mayr) are large and possess ocelli in the worker; *T. klebsi* has five teeth on the masticatory margin of the mandible (Wheeler 1915:

41). From the descriptions I cannot discern any obvious derived features that would indicate a close relationship to the *Tetraponera* species found in Asia today.

Regardless of which routes were taken by the African progenitors of the Asian *Tetraponera*, a consideration of the paleogeographic evidence suggests the likelihood that at least some *Tetraponera* species—especially the ancestors of the species-rich *allaborans*- and *nigra*-groups—have been present in this region since the Eocene.

Distribution and history of Tetraponera *in Asia and Australia*

If we examine the distributions of individual species of *Tetraponera* in Southeast Asia and Australia (Figs 181–196 and Table 2) several patterns become apparent. First, most of the 33 species do not cross Wallace's line. Twenty-three species are restricted to the Oriental region, while seven species (the *laeviceps*-complex and *T. nixa*) are confined to Australia, New Guinea and adjacent islands. Only three wide-ranging species (*T. allaborans*, *T. modesta* and *T. nitida*) occur in both the Oriental and Australian biogeographic realms (Figs 182–184). Second, species richness is greatest in Borneo and the Malay Peninsula, which have 17 and 18 species, respectively. There is a secondary peak of diversity in New Guinea (eight species). These centers of diversity correspond to the largest blocks of perhumid rainforest in Malesia (Whitmore 1984). Third, closely related species are often sympatric. As revealed by a cladistic analysis (below), there are four pairs of sister species in the *nigra*-group and all of them exhibit overlapping ranges—compare *T. attenuata* and *T. nigra* (Figs 189, 190), *T. difficilis* and *T. inversinodis* (Figs 191, 192), *T. atra* and *T. laeviceps* (Figs 193, 194), and *T. punctulata* and *T. rotula* (Figs 195, 196).

These observations indicate that the *Tetraponera* species of the Indo-Australian region are relatively old taxa, with sufficient time having elapsed for substantial sympatry to develop among related species. Range overlap among sister taxa is not unexpected. As far as known the queens of Asian and Australian *Tetraponera* species are always fully winged and capable of dispersing over moderate distances. *Tetraponera* species occur on many of the islands in the Malay archipelago, and Krakatau had acquired three species (*T. attenuata*, *T. nitida* and *T. rufonigra*) within 25 years of its explosion (Forel 1909*a*). Yet no *Tetraponera* species are shared between Africa and Asia and, as mentioned previously, only three (of 33) species occur in both the Oriental and Australian regions.

Quite apart from intrinsic constraints on long-distance dispersal, habitat specialisation may have limited range expansion in some species. It is not surprising that the most widespread species of *Tetraponera* use a broad range of habitats, including seasonally dry environments. Species restricted to wet forests tend to have smaller ranges or—in the case of *T. binghami*—a disjunct distribution within Asia (Fig. 188). The role of habitat and climatic tolerances in determining the distribution of plant and animal taxa on either side of Wallace's line has been emphasised by other commentators (van Steenis 1979; Whitmore 1981; Morley 1998).

To explore more thoroughly the biogeographic history of *Tetraponera* in Asia and Australia, a detailed phylogenetic analysis was carried out on the *nigra*-group, using the morphological data set given in Table 3. Parsimony analysis yielded six minimum-length trees (length 156, consistency index 0.54, retention index 0.77), of which the strict consensus is shown in Fig. 197. The consensus tree is well resolved except for two trichotomies near the tips of the tree. There is modest bootstrap support for monophyly of the *nigra*-group (80%) and for the four species complexes recognised within the group: *nigra*-complex (73% bootstrap support), *difficilis*-complex (96%), *nitida*-complex (74%), and *laeviceps*-complex (83%). Fig. 198 illustrates character-state changes for one of the six trees.

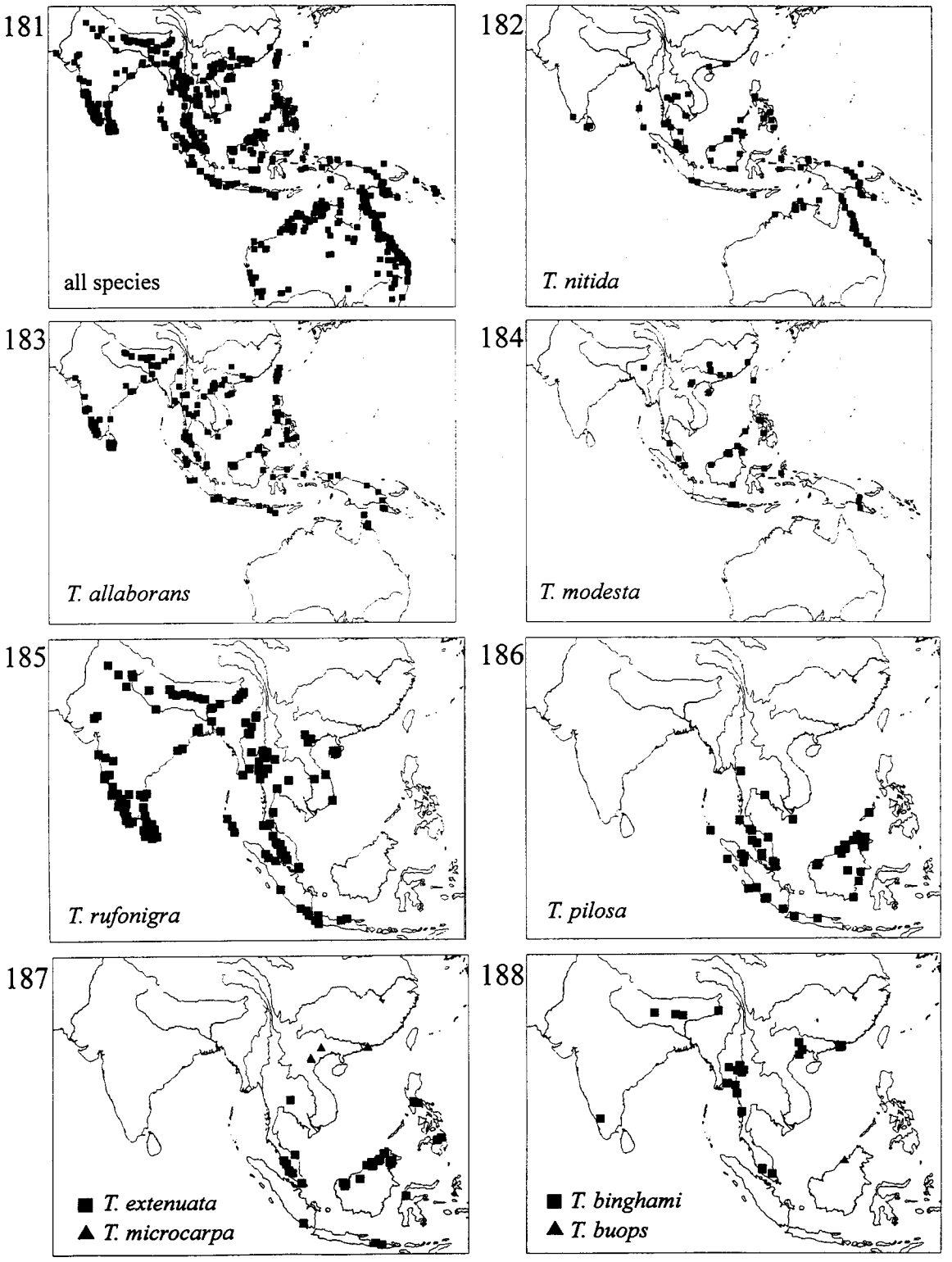
Among species in the *nigra*-group, only *T. nitida* traverses Wallace's line (Fig. 182), the others being more restricted in distribution (Figs 188–196). Plotting biogeographic regions on the phylogeny (Fig. 199) strongly implicates an Asian origin of the group, with at least two dispersal events to the Australian region. One of these, involving the antecedent of the *laeviceps*-complex, led to a proliferation of six species. This is consistent with arrival on the Australian plate about 20 million years ago when the two landmasses first approached one another (Hall 1998). The *nitida*-complex is less well represented in the Australian region, having only one endemic species (*T. nixa*) and a close relative, the widespread *T. nitida*, which may well be paraphyletic relative to *T. nixa*. These may represent two, more recent, double invasions of the Australian region. The other two members of the *T. nitida*-complex are Oriental taxa, as are the remaining members of the *nigra*-group. This is also true of the four rare *nigra*-group species (*T. aitkenii*, *T. polita*, *T. vivax*, *T. volucris*) that were excluded from the phylogenetic analysis because of scarcity of material. (A preliminary assessment of *T. aitkenii* and *T. polita* places them as a pair of sister species at the base of the *nigra*-complex.)

Optimisation of habitat preferences on the phylogeny of the *nigra*-group (Fig. 200) illustrates that the ancestral condition is likely to have involved association with rain forest, with drier habitats having been secondarily colonised, on both the Indian subcontinent (*T. nigra*) and in the Australian region (*T. nitida*, *T. nixa* and *T. punctulata*).

Although the relationships among members of the *allaborans*-group have not been analysed in detail, this group is similarly centred in Asian rainforests, with only two of the 11 known species also occurring in (but not confined to) Australia/New Guinea. These two species, *T. allaborans* and

Table 2. Distribution of *Tetraponera* species in the Indo-Australian region

Species-group	Species	Indian sub-continent, including Sri Lanka	China, Taiwan, Japan	Indochina, excluding peninsular Malaysia	Peninsular Malaysia, Singapore	Sumatra	Java	Borneo	Philippines	Lesser Sundas, Sulawesi	New Guinea and adjacent islands	Australia
allaborans	*allaborans*	X	X	X	X	X	X	X	X	X	X	X
	apiculata							X				
	avia				X							
	bita				X			X				
	brevis				X							
	conica							X				
	connectens			X								
	crassiuscula			X	X	X		X				
	extenuata			X	X	X	X	X	X	X		
	microcarpa		X	X								
	modesta	X	X	X	X			X	X	X	X	
nigra	*aitkenii*	X			X							
	atra										X	
	attenuata	X	X	X	X	X	X	X	X			
	binghami	X	X	X	X							
	buops							X				
	difficilis			X	X	X	X	X	X			
	inversinodis							X	X			
	laeviceps										X	X
	mimula										X	
	nigra	X		X	X		X	X				
	nitida	X	X	X	X	X	X	X	X	X	X	X
	nixa											X
	nodosa			X		X		X				
	notabilis			X	X							
	polita							X				
	punctulata										X	X
	rotula										X	X
	tucurua											X
	vivax				X		X	X				
	volucris				X							
pilosa	*pilosa*			X	X	X	X	X	X			
rufonigra	*rufonigra*	X	X	X	X	X	X					
Total number of species		8	7	15	18	9	9	17	8	4	8	7



Figs 181–196. Distribution of *Tetraponera* species in the Indo-Australian region. Excluded are two dubious records (*T. modesta* from North Korea and *T. punctulata* from Victoria, Australia) and an introduced population of *T. rufonigra* in the Seychelles.

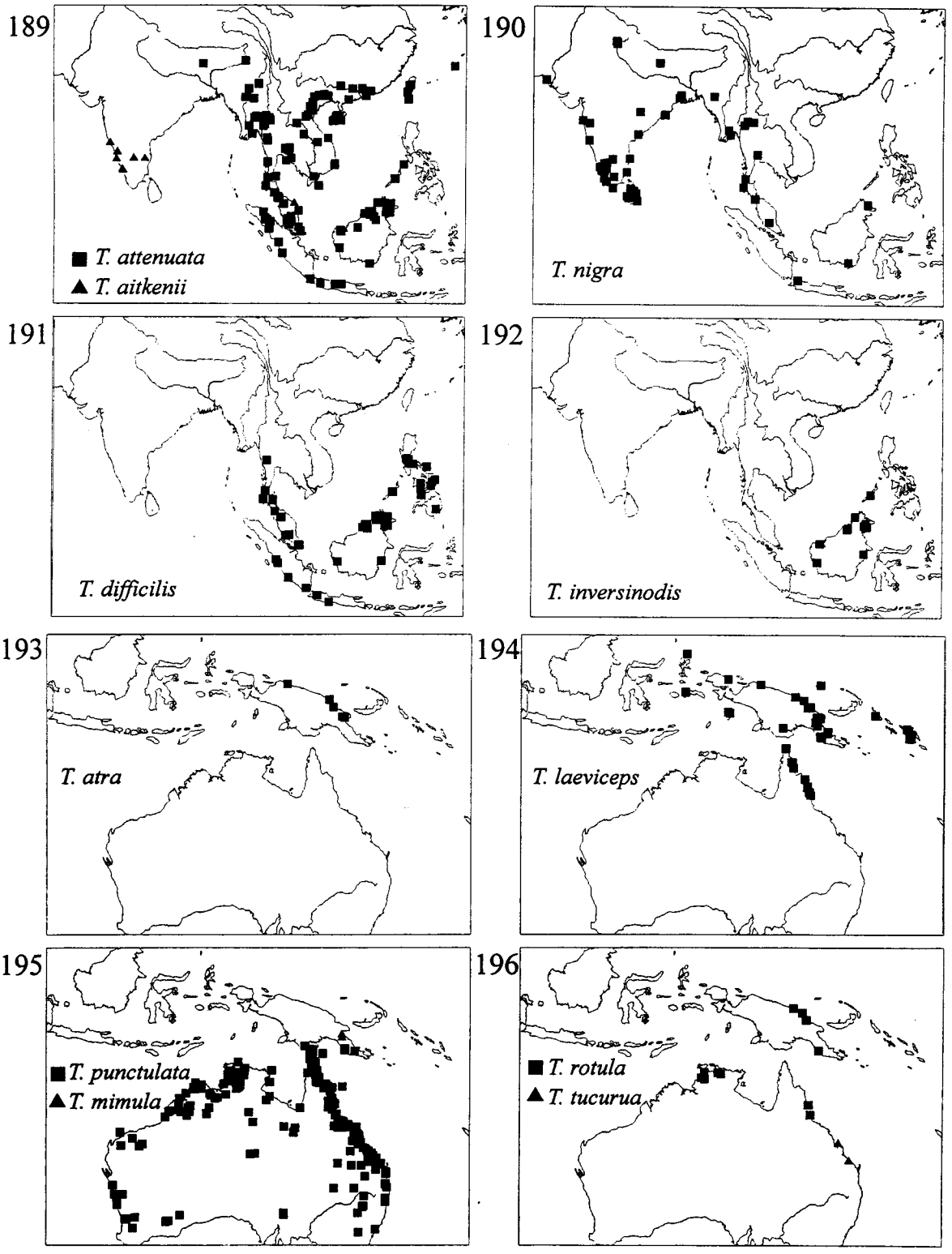

189
■ T. attenuata
▲ T. aitkenii
190
T. nigra
191
T. difficilis
192
T. inversinodis
193
T. atra
194
T. laeviceps
195
■ T. punctulata
▲ T. mimula
196
■ T. rotula
▲ T. tucurua

Table 3. Morphological data set used for phylogenetic analysis of the *Tetraponera nigra*-group

Character numbers correspond to those listed in the text (under 'Materials and methods'). The first two taxa were used as outgroups. The *nigra*-group begins with *T. attenuata*. '?' signifies ambiguous or inapplicable; '–' indicates unknown.

	10	20	30	40	50	60	70	
Pseudomyrmex gracilis	0300000110	0000?11010	0000001000	0001000100	0000020000	0000001002	???00000?0	?0
Pseudomyrmex termitarius	0300000110	0000?00010	0000000000	0101100000	0000011000	0002000002	???00000?0	?0
Tetraponera natalensis	1010300?11	01100??100	0011002100	0001100000	1100120000	1001000002	???00000?0	?0
Tetraponera pilosa	0110010?11	0100000110	0011000000	0001000000	0100110000	0010000002	???00000?0	?0
Tetraponera rufonigra	0210010001	?200010010	0001001000	0001000000	0000010000	1001000000	0101100?0	?0
Tetraponera clypeata	1011001011	1121101101	0011010100	1010101000	1000000000	0001010000	0101000?0	?1
Tetraponera allaborans	101120?011	1121101101	0?11010100	?010101000	1000000100	0001010000	0101000?0	?1
Tetraponera attenuata	0110100001	1221111011	0?02001000	1001000001	1011000100	1102000110	1011110100	?0
Tetraponera nigra	011010?001	1221111011	0?02001000	0001000000	1011010100	1102000110	1011110101	?0
Tetraponera binghami	0110101001	1221111001	0002001000	1001100000	1011010012	1102000110	1011111101	10
Tetraponera buops	0110001111	1121111101	0002001000	1001------	----------	----------	----------	--
Tetraponera nitida	0110100111	0021101101	1012102001	0100100110	1011020112	1102001011	1001111101	10
Tetraponera nixa	0110100111	0021111101	1012101001	0100------	----------	----------	----------	--
Tetraponera nodosa	0110000111	0021101100	1012100001	0100------	----------	----------	----------	--
Tetraponera notabilis	0110101111	0021101101	1012100001	1000------	----------	----------	----------	-0
Tetraponera atra	0110100011	1120001111	2102000000	100?110101	1011020121	1102101021	0011111101	00
Tetraponera laeviceps	0110100011	01210?1101	2112002000	1000110101	1011020121	1102101021	0011111101	00
Tetraponera mimula	0110100011	0121001101	2112001000	0000------	----------	----------	----------	--
Tetraponera rotula	0110100011	0121101101	2012000010	0000100100	1011020122	1102101121	0001111101	00
Tetraponera punctulata	011010?011	0121101101	2012002010	000?100100	1011020122	1102101121	0001111101	00
Tetraponera tucurua	0110100011	0121101100	2012000010	0100100100	1011020121	1102101021	0001111101	00
Tetraponera difficilis	0110100011	0121101101	1012000000	000?100110	1011001000	1102001011	0101110111	00
Tetraponera inversinodis	0110100?11	0121101101	1012000000	0?00100110	1011001000	1102001011	0101110111	00

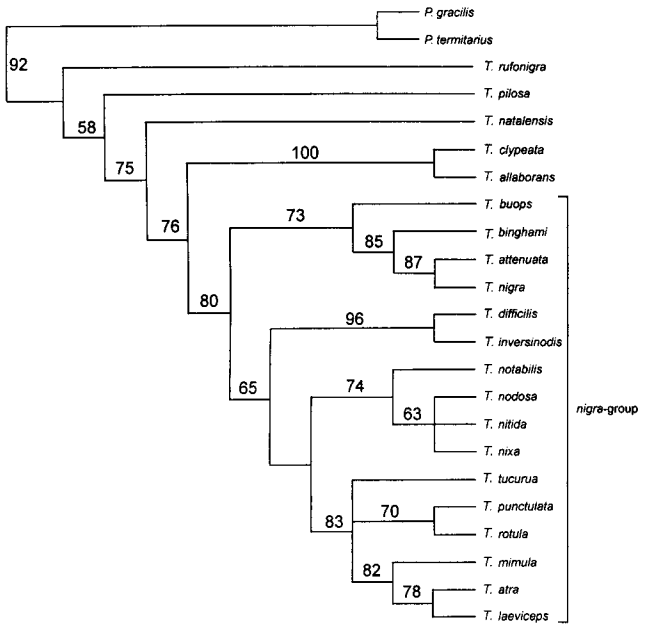


Fig. 197. Phylogeny of the *Tetraponera nigra*-group, based on the data set in Table 3. This is the strict consensus of six most parsimonious trees (each of length 156, consistency index 0.54, retention index 0.77). Bootstrap values greater than 50% are also placed on the tree; these are derived from a separate bootstrap analysis with 1000 replicates.

T. modesta, are not sister taxa, *T. modesta* being more closely related to *T. crassiuscula* and *T. extenuata* (see taxonomic revision). Hence, they evidently represent two independent invasions of the Australian region.

In summary, the biogeographic history of the genus *Tetraponera* appears to involve several movements out of Africa into Asia, and at least four dispersal events from Asia to Australia. A timeframe for these events remains uncertain, but the mid-Eocene collision of India with Asia and a later (mid-Miocene) approach between the Australian and Asian plates provides a reasonable chronology for at least some of the taxa involved. From this perspective, the most recent common ancestor of the *nigra*-group is estimated to have existed about 50 million years ago, and 20 million years is a likely maximum age of the Australian-based *laeviceps*-complex.

Concluding remarks

The ant genus *Tetraponera* occurs throughout most of the Indo-Australian region (Fig. 181). Eighteen of the 33 currently recognised species are newly described in this paper and many of these taxa, especially those associated with rainforest, are recorded from only one or two localities. It is highly likely that additional species remain undiscovered or unrecognised, especially in the *T. allaborans*-group. Exploration of the rainforest canopy and an emphasis on collection of nest series (containing workers, queens and males) are promising avenues for expanding our knowledge of the systematics and biology of these ants. Although most species of Asian and Australian *Tetraponera* for which nesting habits are known appear to be generalist inhabitants of dead hollow twigs and stems, at least two species live in live plant cavities (myrmecodomatia). Specialised habits may characterise some of the rare species for which we have little or no biological data.

The more wide-ranging species of *Tetraponera* tend to be quite variable in morphology. Some of this apparent intraspecific variation may be due to the presence of cryptic species, but in those taxa where large sample sizes have been available for study (e.g. *T. allaborans*, *T. punctulata*) there is enough phenotypic intermediacy to indicate that these are single, polytypic species. Substantial morphological variation can be observed on a small spatial scale, however, which raises interesting questions about the nature of selective forces maintaining such variation and suggests the possibility that some *Tetraponera* species consist of multiple 'ecotypes', somewhat analogous to the trophic polymorphisms reported in other animal taxa (Smith and Skulason 1996). Certainly it is clear that species-level taxonomic problems in *Tetraponera* are not likely to be resolved without the examination of *large population samples*, taken throughout the entire geographic range of the taxon. Ultimately, understanding such difficult groups as the *T. modesta*-complex may require detailed studies with molecular markers, although the analysis of male genital morphology also holds considerable promise.

Each of the four species-groups of *Tetraponera* recognised in the Indo-Australian region consititutes an independent lineage, whose nearest living relatives are in the Afrotropical region. Dispersal in these ants has been sufficiently constrained that broad-scale biogeographic patterns can still be discerned. Evidence points to several dispersal events from Africa to Asia and from Asia to Australia, over a timespan of 50+ million years and in a manner that suggests an important role for plate tectonics.

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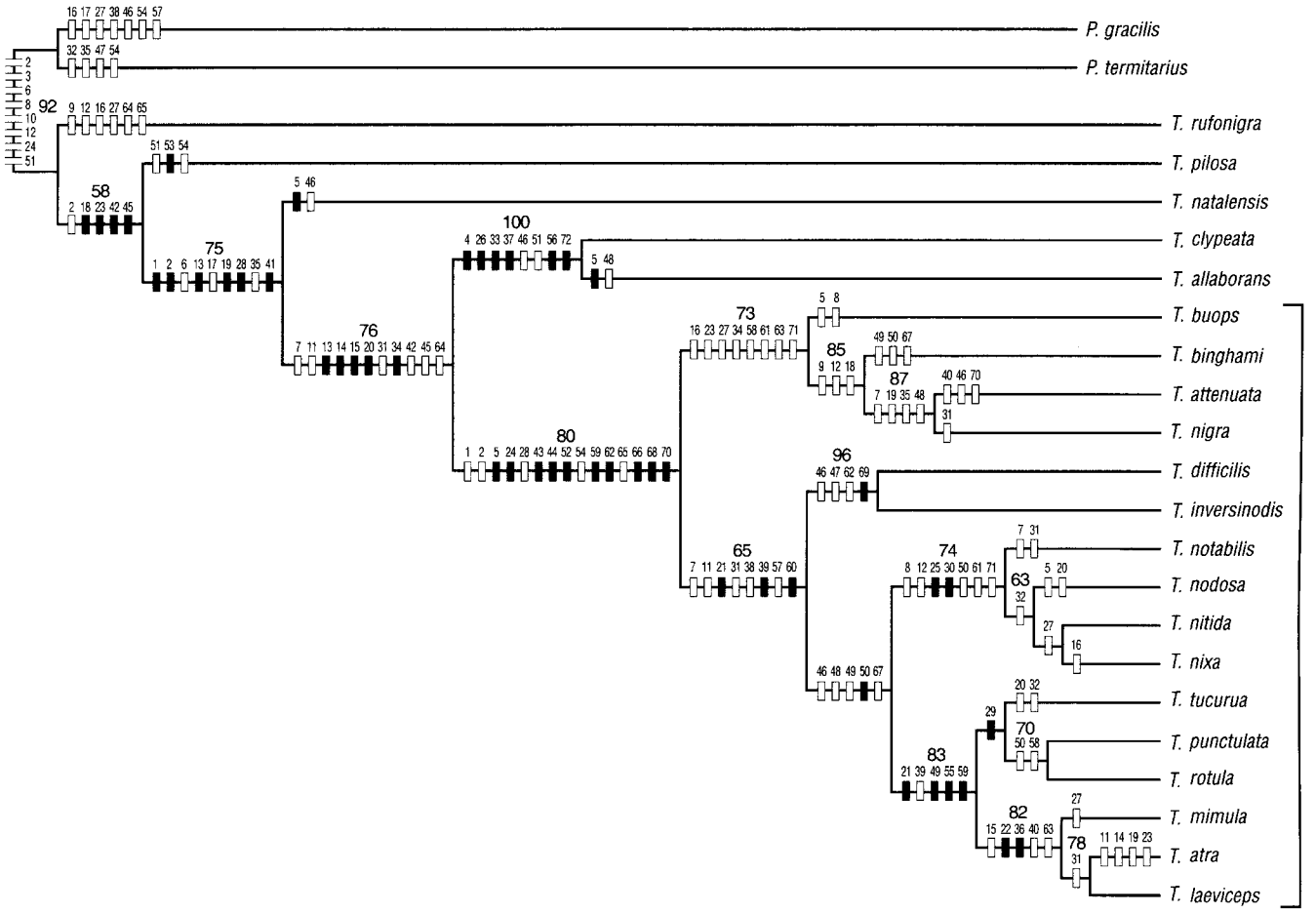

Fig. 198. One of the six most parsimonious trees obtained from analysis of the *Tetraponera* data set in Table 3, showing ACCTRAN reconstruction of character state changes. Smaller numbers refer to characters; larger numbers indicate bootstrap values greater than 50%. Open bars: homoplasious changes (convergences and reversals); closed bars: non-homoplasious changes. Vertical line brackets the *nigra*-group.

Merz (MHNG), Janine Casevitz-Weulersse (MNHN), Roy Danielsson (MZLU), Michel Brancucci (NHMB), Max Fischer and Stefan Schödl (NHMV), Chung-Chi Lin (NTUC), George McGavin (OXUM), D. H. Murphy (RMBR), Chris Darling (ROME), Hamish Robertson (SAMC), Krzysztof Rościszewski (SMNK), Alan Andersen (TERC), Alexander Radchenko (UASK), Maryati Mohamed (UMSC), Ted Schultz (USNM), Frank Koch (ZMHB), Wojciech Czechowski (ZMPA) and Alexander Antropov (ZMUM). Alex Radchenko also kindly shared with me specimens that he had on loan from ZMAS (St Petersburg) and ZMUM (Moscow). Useful samples of *Tetraponera* were also received from April Boulton, Carsten Brühl, Alfred Buschinger, Chris Carpenter, Michael Doll, Wolfgang Dorow, Andreas Floren, Deb Hlavaty, David Kistner, Rudi Klein, Damir Kovac, Doyle McKey, Nick Mills, Dave Olson, Jacques Pasteels, Christian Peeters, Fred Rickson, Riita Savolainen, Angela Schellerich, and Shanyi Zhou. For providing plant and scale insect identifications I am grateful to Tony Irvine and Penny Gullan, respectively. I thank Alan Andersen, Alex Wild, and two anonymous reviewers for helpful comments on the manuscript. This research was supported by the United States National Science Foundation, most recently through grant DEB–9903650.

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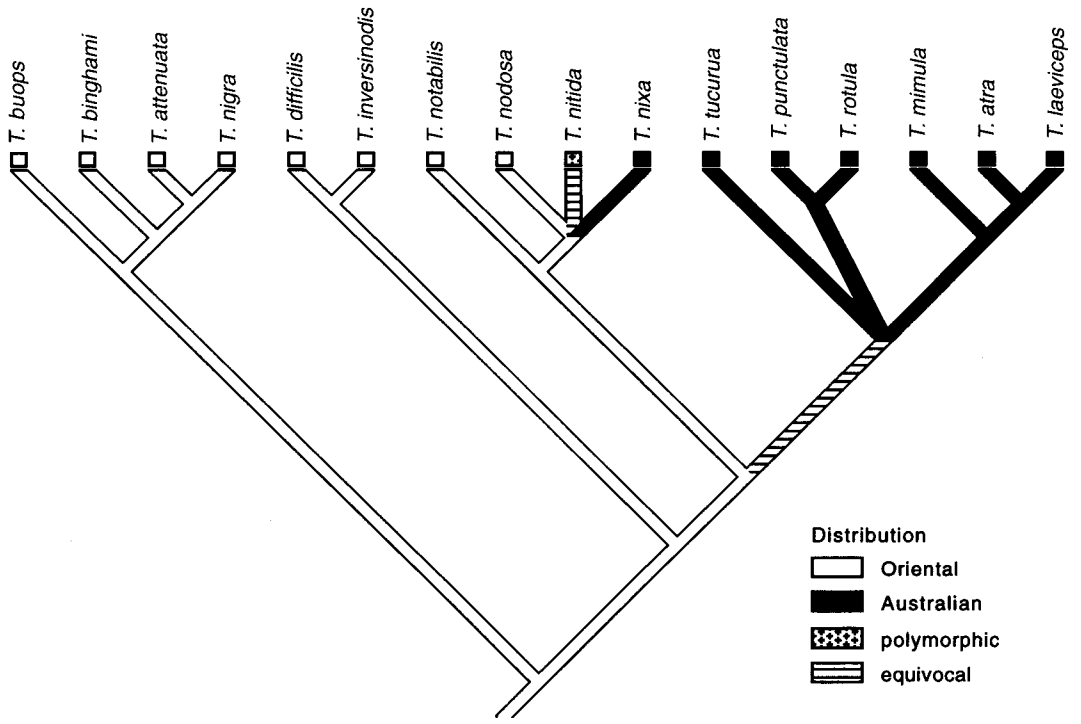

Fig. 199. Distribution of species in the *nigra*-group, mapped on the phylogeny from Fig. 197.

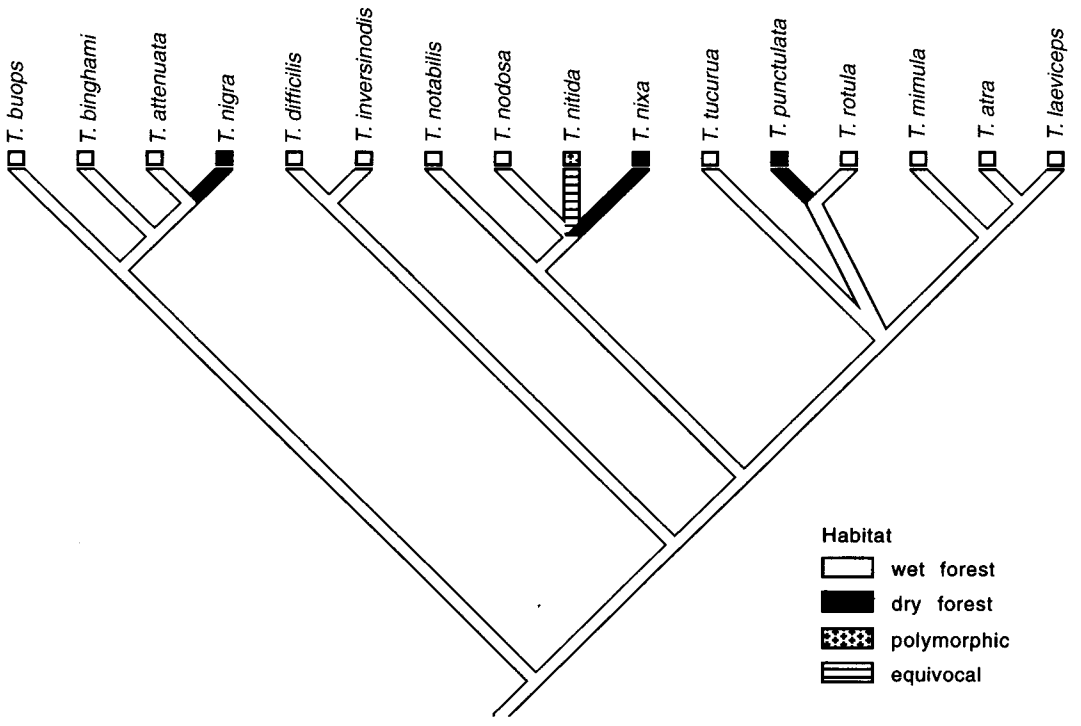

Fig. 200. Habitat preferences of species in the *nigra*-group, mapped on the phylogeny from Fig. 197. 'Wet forest' species are those recorded primarily from localities with rainforest or closed evergreen forest; 'dry forest' species are those occurring predominantly in drier habitats, such as semideciduous forest, *Eucalyptus* woodland, and savanna.

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