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Universidad Central de Venezuela, Maracay

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Abstract.

A taxonomic revision of the genus *Gnamptogenys* Roger in Southeast Asia and Australasia, based on the workers, recognizes forty nine species, twenty five of which are new, as follows: *G. albiclava* (Mann), *G. aterrima* (Mann), *G. atrata* sp. n., *G. bicolor* (Emery), *G. biloba* sp. n., *G. binghamii* (Forel), *G. biroi* (Emery), *G. bulbopila* sp. n., *G. chapmani* Brown, *G. costata* (Emery), *G. coxalis* (Roger), *G. crassicornis* (Forel), *G. crenaticeps* (Mann), *G. cribrata* (Emery), *G. delta* sp. n., *G. epinotalis* (Emery), *G. fistulosa* sp. n., *G. gabata* sp. n., *G. gastrodeia* sp. n., *G. grammodes* Brown, *G. helisa* sp. n., *G. hyalina* sp. n., *G. lacunosa* sp. n., *G. laevior* (Forel), *G. leiolabia* sp. n., *G. lucida* (Mann), *G. luzonensis* (Wheeler), *G. macretes* Brown, *G. major* (Emery), *G. malaensis* (Mann), *G. meghalaya* sp. n., *G. menadensis* (Mayr), *G. niuguinense* sp. n., *G. ortostoma* sp. n., *G. palamala* sp. n., *G. panda* (Brown), *G. paso* sp. n., *G. pertusa* sp. n., *G. polytreta* sp. n., *G. posteropsis* (Gregg), *G. preciosa* sp. n., *G. rugodens* sp. n., *G. scalpta* sp. n., *G. sichuanensis* sp. n., *G. sila* sp. n., *G. sinensis* Wu and Xiao, *G. solomonensis* sp. n., *G. taivanensis* (Wheeler), and *G. treta* sp. n. Five new synonymies are proposed: *G. bicolor* = *G. bannana* Xu and Zhang; *G. crassicornis* = *G. spiralis* (Karavaiev); *G. cribrata* = *G. diehlii* (Forel) = *G. dammermani* (Wheeler); *G. laevior* = *G. kalabit* Brown. Keys, illustrations, and species accounts are provided. Five species groups are recognized. A phylogenetic analysis for nineteen terminal taxa and sixty morphological characters using parsimony was carried out with PAUP, using the following taxa as outgroups: *Heteroponera* Mayr, *Platythyrea* Roger, and *Myrmica incompleta* Provancher. Four

Old World *Gnamptogenys* species groups, as well as five individual species of a weakly supported clade were part of the ingroup. Additional ingroup taxa included five New World species of *Gnamptogenys*, *Ectatomma* F. Smith, and the *Rhytidoponera impressa* group. Monophyly of a clade formed by the genera *Ectatomma*, *Rhytidoponera* Mayr, and *Gnamptogenys* Roger is strongly supported. Monophyly of *Gnamptogenys* is supported by loss of a fore tibial seta. Neotropical taxa form sister relationships with Old World lineages at several points in the tree.

INTRODUCTION

Gnamptogenys Roger is a group of predatory ponerine ants found in tropical and subtropical, mesic forested areas in Southeast Asia and Australasia and from the southern United States to northern Argentina. Most species nest at ground level in rotten wood or leaf litter, but some are arboreal. Their colonies are relatively small, with at most a few hundred workers (Lattke, 1994; Gobin, Peeters, and Billen, 1998a). Reproduction is generally through queens, though worker reproduction is known in some species from Southeast Asia (Gobin, 1994). While many species are generalist predators, specialized diets such as millipede predation have arisen in several New World lineages (Brown, 1993; Lattke, 1995). The biology of Old World species is poorly known. The last generic revision recognized 81 species, with 26 Old World species (Brown, 1958). After this study, knowledge of the Palaeotropical fauna has been mostly restricted to scattered taxonomic descriptions (Wu and Xiao, 1987; Xu and Zhang, 1996), though recently the group is figuring with increasing frequency in ecological studies and surveys (Brühl Gunsalam, and Linsenmair, 1998; Gobin, 1994; Gobin, Peeters, and Billen, 1998a, 1998b; Gobin, et. al., 1998; Yamane and Nona, 1994). Bolton (1995b), in his conspectus of the world ant fauna, recorded 99 species of *Gnamptogenys* worldwide, making it one of the most speciose groups within the subfamily Ponerinae. Recent collecting in the Old World has enriched museum holdings to the point that species determination is impossible using the key in Brown (1958).

Gnamptogenys was included within the Tribe Ectatommini along with the genera *Acanthoponera* Mayr, *Aulacopone* Arnoldi, *Discothyrea* Roger, *Ectatomma* F. Smith, *Heteroponera* Mayr, *Paraponera* F. Smith, *Proceratium* Roger, and *Rhytidoponera* Mayr by Brown (1958). Kugler (1991), in a phylogenetic analysis of some of these taxa, showed close ties between *Ectatomma*, *Gnamptogenys*, and *Rhytidoponera*. This finding was subsequently supported by a study of worker morphology involving most of the aforementioned genera (Lattke, 1994). In the latter study ectatommines were reduced to *Acanthoponera*, *Ectatomma*, *Gnamptogenys*, *Heteroponera*, and *Rhytidoponera*. While reliable diagnostic characters have permitted definitions for *Rhytidoponera* and *Ectatomma*, the same cannot be said for *Gnamptogenys*. Most diagnoses have relied on the presence of a denticle on the metacoxal dorsum, but it is absent in a number of species. Apomorphies for *Gnamptogenys* were not explicitly stated in Lattke (1994, 1995), though Kugler (1991) found three potential apomorphies in the sting apparatus. In this work I present a taxonomic revision of the species of *Gnamptogenys* from the Old World, show evidence for their monophyly, and assess their phylogenetic relationships. The New World species were revised in Lattke (1995).

MATERIALS AND METHODS

Collections

Specimens were examined or deposited in the following collections:

- AMNH American Museum of Natural History, New York, New York, U.S.A.
- ANIC Australian National Insect Collection, Commonwealth Scientific and Industrial Research Organisation, Canberra, Australia
- BMNH The Natural History Museum, London, England, U.K.
- CASC California Academy of Sciences Collection, San Francisco, U.S.A.
- CFRB Forestry Research Institute, Chinese Academy of Forestry, Beijing, China
- ISNB Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
- LACM Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A.
- MBBJ Bogor Zoological Museum, Bogor, Indonesia
- MCSN Museo Civico di Storia Naturale, Genova, Italy
- MCZC Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
- MHNG Musee d'Histoire Naturelle, Geneva, Switzerland
- MIZA Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela
- NHMW Naturhistorisches Museum, Vienna, Austria
- NMKL National Museum, Kuala Lumpur, Malaysia

- OXUM Hope Entomological Collections, University Museum, Oxford, England,
Great Britain
- PSWC Philip S. Ward Collection, University of California, Davis, U.S.A.
- SNUC Shaanxi Normal University Collection, Xi'an, China
- SMSM Sarawak Museum, Natural History Division, Kuching, Sarawak,
Malaysia
- UASK Institute of Zoology, Ukrainian Academy of Science, Kiev, Ukraine
- UCDC Bohart Museum of Entomology, University of California, Davis, U.S.A.
- USNM United States National Museum, Washington, D.C., U.S.A.
- ZMHB Museum für Naturkunde der Humboldt Universität, Berlin, Germany

Dissected outgroup and ingroup specimens are deposited in MIZA.

Measurements and Indices.

Most morphological measurements were made using a Wild stereoscope with a Nikon double-axis positioning stage wired to an Autometronics dual-axis digital readout. All measurements are expressed in millimeters. The following measurements were taken:

- HL Head length: midline length of the cephalic capsule, measured in full-face (dorsal) view, from the anterior margin of the clypeus to the midpoint of a line drawn across the occipital margin (including occipital lobes if present).
- HW Head width: maximum width of head, measured in the same plane as HL, excluding the eyes.

- ML Mandible length: straight-line length of a mandible, measured from the base at the insertion into the head capsule, to the apex. Measured in the same plane as HL.
- SL Scape length: length of the first antennal segment, excluding the neck and basal condyle.
- ED Eye diameter: diameter of the compound eye, measured along its long axis in lateral view.
- WL Weber's length of the mesosoma (alitrunk): diagonal length, measured in lateral view from the anterior margin of the pronotum (excluding the collar) to the posterior extremity of the metapleural lobe.

The following indices were calculated from the preceding measurements:

- CI Cephalic index: HW/HL
- MI Mandibular index: ML/HW
- SI Scape index: SL/HW
- OI Ocular index: ED/HW

Morphology

Descriptive terms for cuticular sculpturing features follow Harris (1979) as close as possible. Most morphological terms used here are standard for ant taxonomic descriptions, as defined in Hölldobler and Wilson (1990), Bolton (1994), and Shattuck (1999), except for the following terminology:

Clypeal lamella—A narrow and thin, transverse strip of cuticle found along the anterior clypeal border; also referred to as the clypeal apron (Brown, 1958).

Occipital carina—A low ridge on the posterior cephalic surface that separates the occiput from the vertex and gena.

Occipital lamella—An extension of the occipital carina that continues on the posterolateral cephalic corners, usually becoming higher and more prominent than the occipital carina and easily visible in lateral cephalic view.

Occipital lobe—A posterior to posteroventral lobelike extension of the posterolateral cephalic corners (Figs. 16a, 19a, 29a).

Postpetiolar process—A forward-projecting, shelf like prominence located on the anterior face of the postpetiolar sternite, just below the petiolar insertion.

Strigil—The curved comblike movable spur on the apex of the fore tibia (Torre-Bueno, 1989).

A set of characters rarely used in ant taxonomy was found on the prosternum. This segment is dissected out of the mesosoma by removing the fore coxae and then prying out the propleura. Sometimes the prosternum came out along with the pleura and they were separated after clearing. Separation was done by immersion in alcohol and ginger use of insect pins of diverse sizes. Immersion avoids sudden popping out and catapulting of parts. Clearing of soft tissue was accomplished by soaking in 10% KOH at room temperature overnight or sometimes for two days. The prosternum was then point mounted using very diluted glue, adhering it by the dorsum (phragmal end) to the point. The prosternum was manipulated by moistening the end of a fine forceps and bringing it to the ventral end of the prosternum. The sclerite would stick to the forceps and the phragmal apex was then gently pushed into the glue. Terms used to describe the various parts are adapted from Snodgrass (1956).

Three major regions of the prosternum were recognized: the basisternum, furcasternum, and endosternum, each with its own components (Figs. 1-3). The basisternum is a triangular sternal plate located between the fore coxae and the

posteromedian ends of the propleura. It has a basisternal lobe, an anteriorly projecting, generally narrow lobe of varying length that projects beneath the propleura (Fig. 4). The furcasternum is the part immediately next to the basisternum, internally bent. Its posterior surface is generally visible without dissection. The furcasternum has the following regions:

Furcasternal ridges—A pair of brief longitudinal ridges on the ventromedian apex of the furcasternum that join with the posterior basisternum (Fig. 2).

Median lobe—A transverse lobe projecting between the ridges, absent in some groups (Fig. 4).

Prosternal process—The combination of the furcasternal ridges and median lobe.

Posterodorsal convexity—Swelling on furcasternum, generally forming a ventral shelf to the neural chord.

Posterodorsal ridge—Rounded crest that goes around the posterodorsal margin of the furcasternum.

The last major prosternal region is the endosternum, a structure supported on the furcasternum by two lateral arms and a broad horizontal bridge between the arms. It is made up of the following parts:

Neural foramen—Cavity situated between the furcasternum and lateral endosternal arms (Figs. 1, 5).

Lateroventral lobes—Lobes projecting from the ventrolateral ends of the endosternal bridge.

Posterior keel—A longitudinal lamellate keel of varying development present on the posteromedian surface of the endosternal phragma (Fig. 2).

Phragma—Broad transverse, laminate structure that makes up the dorsal end of the endosternum (Figs. 1, 2, 5).

Sheath—Brief posterior extension of lamellate cuticle surrounding the neural foramen (Fig. 5).

Many of the descriptions and diagnoses describe outlines of particular body part margins; these are best seen by using reflected background lighting. The shiny cuticle typical of these ants makes observing sculpture details difficult because of reflected light. This is attenuated by using a small rectangle of mylar plastic to diffuse light and create an opaque image similar to a scanning electron micrograph. The plastic is held erect and as close as possible to the specimen, and a concentrated light source is pointed at the specimen from the other side of the mylar. A bit of experimentation should determine the best setup. Compound eyes in some specimens (particularly the *laevior* group) may appear to be smaller and more elongate if illuminated from only one angle. The search for taxonomic references was greatly facilitated by consulting Bolton (1995a) and Ward et. al. (1996).

Phylogenetics

Phylogenetic relations within the Old World species of *Gnamptogenys* were determined at the level of species groups and not individual species. Determination of clades used as terminal taxa was done after alpha taxonomic work was carried out. Diagnostic characters for each group were noted and checked by comparison with representatives from each species. Some apomorphies supporting monophyly of Old World groups were recognized a priori by comparison with the outgroups, and others

were elucidated from the results of analysis by phylogenetic inference software (PAUP* 4.0b1 by Swofford, 1998).

The following groups were recognized: *coxalis* group (22 species), *taivanensis* group (4 species), *laevior* group (11 species), and *epinotalis* group (7 species). Only five Old World species could not be placed in a particular group (*G. albiclava*, *G. aterrima*, *G. crenaticeps*, *G. preciosa*, and *G. solomonensis*); consequently each was considered a terminal taxon in the analysis. *G. lucida*, a putative sister species to *G. albiclava* based on sculptural features and the shared apomorphy of white-tipped antenna, was not included in the analysis. Five additional species were chosen as representative of several major lineages from the neotropics to determine if the Old World species were more closely related to each other than to the New World taxa. The five species were *G. minuta* (Emery), *G. concinna* (F. Smith), *G. bispinosa* (Emery), *G. relictata* (Mann), and *G. striatula* Mayr. Because of some concern over monophyly of *Gnamptogenys*, the ingroups included not only *Gnamptogenys* terminal taxa but in addition the Neotropical genus *Ectatomma* and the *impressa* group of the genus *Rhytidoponera* Mayr. The *Rhytidoponera impressa* group was chosen to represent this diverse genus because of its basal or primitive nature based on morphology and biology (Ward, 1980), and molecular data (H. Reichel, pers. com.).

Choosing an outgroup for a study of *Ectatomma*, *Gnamptogenys*, and *Rhytidoponera* is problematic because of the "basal" or morphologically unspecialized nature of these ponerine ants. Two plesiomorphous ponerine genera were used. One choice was *Heteroponera* Mayr, an ectatommine genus that occurs in New World tropics and Australia–New Zealand (Brown, 1958; Kugler, 1991; Lattke,

1994). The pantropical genus *Platythyrea* Roger was chosen because of its generalized morphology and its position as a sister group to other ponerines in the analysis by Grimaldi, Agosti, and Carpenter (1997). In addition, *Myrmica incompleta* Provancher was included as a plesiomorphic representative of the Myrmicinae. This myrmicine was included because of the potentially close relationship between ectatommines and Myrmicinae (Brown, 1958; Ward, 1994). Thus three outgroup taxa were used. Since a considerable number of characters were found during the course of the study, all generic-level taxa were redescribed.

The data set was analyzed using PAUP* 4.0b3a (Swofford, 1998). The most parsimonious trees produced by a heuristic search using random stepwise addition holding one tree at each step and three hundred replicates. To choose among equally parsimonious trees and test stability of the analyses, we reanalyzed the data using successive approximations weighting (SAW) of characters (Farris, 1969; Carpenter, 1988). Characters were reweighted based on the maximum value of the rescaled consistency index and a base weight of 1,000 until tree length was stable. When SAW characters were reassigned weights of one, the final tree length was identical to that of the original unweighted tree. This implies that SAW selected one of the most parsimonious trees, and the analysis was considered stable. Decay Indices were calculated manually by a simple addition heuristic search, successively increasing one step from the shortest tree, each time calculating a strict consensus tree. The nodes on the first consensus tree (length: 204) were given a value of one, and this was incremented by one for each time the node survived the next highest step increase. Bootstrap values were obtained from five hundred replicates.

Characters.

A suite of sixty morphological characters (see Character State Data Matrix) was used for the phylogenetic analysis. Characters were scored as ? when more than one state was present within a single taxon, when the character could not be evaluated, when the character state did not correspond to any of the definitions, or homologies were uncertain. The following characters are considered ordered: 1, 12, 25, 28, 29, 56; 17 and 18 are considered irreversible, while the rest are defined as unordered. Except for character 60, all characters are based on the workers.

Head

- 1 *Cephalic vertex*: (0) continuously curves on to frons; (1) sharply curved; (2) forms a distinct area separated from frons by a blunt angle. Evaluated by drawing an imaginary plane perpendicular to the cephalic dorsal surface and tracing the margin of contact with the head.
- 2 *Cephalic vertex*: (0) sculptured over half or more of its surface, generally a continuation of sculpturing on frons; (1) mostly smooth over half or more of its surface, usually in contrast to sculpturing on frons. Even if cephalic sculpturing is also mostly smooth it is scored as one.
- 3 *Occipital lobes*: (0) absent (Figs. 13b, 35a, 39); (1) present (Figs. 19a, 29a, 36a). In lateral view the lobe is considered present if there is a distinct convexity that forms part of the cephalic capsule rising above and interrupting an otherwise continuous margin. A mere difference in curvature is not considered an occipital lobe, nor is a lobe formed only by the occipital lamella.

- 4 *Occipital carina*: (0) absent; (1) laterally present but medially missing or indistinguishable from the surrounding sculpture; (2) continuously present.
- 5 *Eye*: (0) normal sized, not small and reduced ($OI > 0.15$); (1) small and reduced ($OI < 0.15$). *Heteroponera* is polymorphic for this character.
- 6 *Eye*: (0) with a globulose, hemispherical cross section; (1) with a convex to flattened cross section, not noticeably protuberant. Protuberant eyes are not only found in *Ectatomma*, but also in other plesiomorphous ant taxa: *Myrmecia*, *Nothomyrmecia*, *Paraponera*, and *Brownimecia* (Grimaldi, Agosti, and Carpenter, 1997).
- 7 *Dorsal lobe of torulus*: (0) separate from frontal lobe and close to base of torulus; (1) partially fused to ventral surface of frontal lobe but still distinct as a separate sclerite. In *G. minuta* the torulus lacks a recognizable dorsal lobe immediately above the insertions of the condyle. This species has a blunt denticle on the lateral margin of each frontal lobe, and it is possible that the denticle represents the lobe of the torulus, fused to the frontal lobe. It is not clear if the lack of a lobe in *Platythyrea* represents a plesiomorphic or derived condition.
- 8 *Scape*: (0) when laid back and with head in frontal view surpasses posterior cephalic border by more than one apical width; (1) surpasses posterior cephalic border by one width at most, usually not reaching the border. *Platythyrea* is polymorphic for this character.
- 9 *Scape in dorsal view*: (0) with dense longitudinal strigulae/striae covering most of the surface, longer than the maximum apical width; (1) strigulae, if present, are few and never longer than the maximum scape width. The *coxalis* group is polymorphic for this character.

- 10 *Scape in dorsal view*: (0) sparsely punctate; (1) densely punctate. Punctae and punctulae were considered independently of all other sculpturing.
- 11 *Scape in dorsal view*: (0) without a layer of abundant, erect to suberect, short hairs of uniform length along the dorsal margin; (1) with a layer of abundant, erect to suberect, short hairs of uniform length along the dorsal margin.
- 12 *Third antennal segment*: (0) longer than wide; (1) as wide as long; (2) wider than long.
- 13 *Frontal lobe*: (0) projects dorsolaterally, in an oblique posterior view the dorsal margin of each lobe forming an angle of 150° or less with the intermediate posteroclypeal margin; (1) projects laterally, the dorsal margin of each lobe forming an angle of more than 150°, almost planar, with the intermediate posteroclypeal margin.
- 14 *Clypeal lamella*: (0) absent, the anterior clypeal margin lacking a transverse crest or thin strip; (1) present, a distinct narrow laminate structure is present. *G. albiclava* lacks a typical lamella but has a subquadrate projection on the anteromedian clypeus that could be derived from the lamella so it was coded as (1).
- 15 *Mandibular dorsum*: (0) with a relatively continuously thick internal and masticatory margin; (1) with a thin, lamellate internal and masticatory margin, bordered by an arching thicker section; (2) with a distinct ridge defining a narrow, parallel-sided sector along the internal margin, sometimes extending slightly onto the masticatory margin. In the New World species *G. relictata* and a few Old World *epinotalis* group members the ridge extends the entire length of the masticatory border.

- 16 *Mandibular dorsum*: (0) mostly longitudinally striate-rugulose; (1) basally rugose and apically smooth with punctae; (2) mostly smooth with scattered punctae. The mandibles in the *coxalis* group are mostly rugulose, with a few isolated exceptions (e.g., *G. bulbopila*, *G. meghalaya*). *Platythyrea* has a sculpture pattern that is not applicable to the above character states.
- 17 *Number of maxillary palp segments*: (0) 6; (1) 5; (2) 4; (3) 3; (4) 2; (5) 1. The palpal formula in *G. minuta* is 1,2 (Borgmeier, 1957). In the case of variability the highest count was chosen as representative of the ground plan for each group. The number of maxillary and labial palp segments varies in *Platythyrea* (Brown, 1975), but the most numerous count (6,4) was used in this case. The palpal formula also varies in *Heteroponera* (Brown, 1958), so the highest number (4,3) was used as it presumably represents the group's ground plan.
- 18 *Number of labial palp segments*: (0) 4; (1) 3; (2) 2. See comments for preceding character.

Mesosoma

- 19 *Humeral angle*: (0) absent, the lateral and anterior pronotal areas joined through a continuous curving surface; (1) present, the lateral and anterior pronotal areas delimited by a sharp change in curvature or a raised ridge.
- 20 *Pronotal posteroventral process*: (0) with a flattened cross section overlapping the mesothoracic presternite (Fig. 6); (1) with an L-shaped cross section, partially formed by an internal lamella that abuts against the sides of a reduced mesothoracic presternite (Fig. 7). The fore coxae are preferably removed for

evaluation of this and the following four characters. In *Myrmica incompleta* the process has a shape that does not fit any of the alternatives.

- 21 *Prosternal process*: (0) without a median lobe; (1) with a median lobe narrowly separating the prosternal ridges; (2) with a median lobe widely separating prosternal ridges.
- 22 *Median lobe of prosternal process*: (0) lacking; (1) apex entire; (2) apex bidentate.
- 23 *Median lobe of prosternal process in ventral view*: (0) not extending beyond prosternal ridges; (1) extending beyond ridges.
- 24 *Basisternal process in ventral view*: (0) longer than basal width; (1) shorter than or equal to basal width. The prosternum must be extracted, separated from the propleura, and cleared to evaluate this and the next two characters.
- 25 *Endosternal nerve foramen*: (0) without a sheath extending from the endosternum and furcasternum (Fig. 1); (1) with a sheath extending from the endosternum and furcasternum and forming a distinct lamellate wall on the endosternum (Fig. 5); (2) with a sheath extending from the endosternum and furcasternum and forming a low ridge on the endosternum. *Myrmica* has a laminate structure forming a sheath shaped differently from ectatommines, which suggests independent development.
- 26 *Mesothoracic presternite in ventral view*: (0) not reduced, of a relatively uniform length throughout its width; (1) reduced to a median triangular process. The state in this structure was inferred for *G. preciosa*, *G. albiclava*, and *G. crenaticeps* because of the state in all other observed ectatommines.

- 27 *Pronotum in lateral view*: (0) without a longitudinal sulcus parallel to the ventral margin; (1) with a longitudinal sulcus parallel to the ventral margin.
- 28 *Promesonotal suture*: (0) flexible, distinct in dorsal view and interrupting sculpture; (1) inflexible but distinct in dorsal view, interrupting dorsal sculpture; (2) inflexible, feebly impressed or absent, not interrupting sculpture. Baroni Urbani, Bolton, and Ward (1992) code this character in two states: mobile and fused.
- 29 *Metanotal sulcus*: (0) broad and deeply impressed; (1) narrow and shallow, distinctly impressed; (2) feebly impressed or totally effaced.
- 30 *Anepisternum*: (0) clearly separated from metapleuron by a distinct suture (Figs. 22a, 24, 56a); (1) not separated by suture, even though gauge and texture of sculpturing may change (Figs. 41, 42).
- 31 *Metathoracic spiracle*: (0) accompanied by a protruding tubercle; (1) tubercle absent. This tubercle is distinctly present in the plesiomorphous genera *Nothomyrmecia*, *Myrmecia*, *Paraponera*, and *Brownimecia* (Grimaldi, Agosti, and Carpenter 1997).
- 32 *Mesopleural suture*: (0) well impressed and deep, continuous from one end to the other; (1) poorly impressed and incomplete; (2) absent or indistinguishable from surrounding sculpture.
- 33 *Mesopleural suture*: (0) distinct from the mesometapleural suture, meeting it at an angle (Figs. 36a, 53a); (1) forming a continuous groove with the mesometapleural suture around the katapisternum (Figs. 41, 42).
- 34 *Groove between metapleuron and propodeum*: (0) well impressed and continuous, easily distinct from surrounding sculpture (Figs. 19a, 21); (1) weakly

- impressed: broken or very shallow; (2) not impressed or indistinguishable from surrounding sculpture (Figs. 13b, 41).
- 35 *Propodeal spiracle in lateral view*: (0) separated from the declivity by more than two diameters; (1) by 1 to 2 diameters; (2) by less than 1 diameter.
- 36 *Propodeum*: (0) without denticles, (1) with denticles. Propodeal armature is a feature found across many different ant lineages, implying that it is a character fraught with homoplasy. The denticles in *Ectatomma* are thought to be an independent development from those of *Gnamptogenys* (Lattke, 1994). The denticulate lobes found in *Platythyrea* were not considered proper denticles.
- 37 *Propodeal declivity*: (0) separated from the lateral propodeal surface by a rounded curve; (1) separated by sharp or abrupt angle. This character can be regarded as the outline formed by the intersection of the propodeum with an imaginary horizontal plane parallel to the ant's longitudinal axis, just above the spiracles.
- 38 *Propodeal declivity posterad of spiracles*: (0) without lateral ridges or crests; (1) with lateral ridges or laminate crests that extend down to and frequently join the metapleural lobes. This character was scored as ? for *Myrmica incompleta* because of the huge propodeal denticles that made homologies doubtful.
- 39 *Metapleuron*: (0) not bordered by a posterior lobe; (1) bordered by a posterior lobe.
- 40 *Metacoxal cavities*: (0) in ventral view and with the metacoxae removed, connected through a gap or slit with the propodeal insertion; (1) solidly surrounded by cuticle, not connected with the petiolar insertion. *Heteroponera* is

polymorphic for this character. The sutured condition proved dominant in the ponerines sampled by Baroni Urbani, Bolton, and Ward (1992).

- 41 *Propodeal declivity*: (0) sculptured on more than half of its area; (1) unsculptured, or tending to smooth on more than half of its area. The *coxalis* and *epinotalis* groups are polymorphic for this character.

Petiole

- 42 *Petiole node in dorsal view*: (0) wider than long; (1) as long as wide; (2) longer than wide. *Platythyrea* is polymorphic for this character.
- 43 *Petiole in dorsal view*: (0) without an anterior ridge; (1) with an anterior transverse ridge joining the anterolateral petiolar corners.
- 44 *Petiole node in lateral view*: (0) erect, with semiparallel anterior and posterior margins and a well-defined dorsal margin (Figs. 13b, 42, 44); (1) low and rounded, the anterior margin curving continuously onto the dorsal margin (Figs. 19a, 21, 52a, 54a).
- 45 *Petiole spiracle*: (0) situated above or at the same level as a crest extending from the anterolateral petiolar corner; (1) situated beneath such a crest. *Ectatomma* is polymorphic for this character but was scored as (0), reflecting the presumed ground plan of the genus.
- 46 *Petiole tergum and sternite*: (0) not fused; (1) fused totally or partially. Coded as in Baroni Urbani, Bolton, and Ward (1992).
- 47 *Subpetiolar process in ventral view*: (0) rounded posterobasally, the broad lateral face and narrow posterior face meeting at a convexity; (1) with two lateral posterobasal margins, the lateral face meeting the posterior face at a sharp angle.

- 48 *Subpetiolar process in ventral view*: (0) relatively straight and parallel sided, never posteriorly notched; (1) with a cuneiform ventral margin, posteriorly notched.

Gaster

- 49 *Postpetiolar process*: (0) in an oblique anterior view absent or poorly developed; (1) forming a relatively straight to concave transverse ridge; (2) forming a V-shaped ridge.
- 50 *Stridulitrum of fourth abdominal presternite*: (0) absent; (1) present. Interpreted as present when a distinct longitudinal band of refracted light is visible.
- 51 *Stridulitrum of fourth abdominal pretergite*: (0) absent; (1) present. Coded as in Baroni Urbani, Bolton, and Ward (1992), Ward (1994).

Legs

- 52 *Apex of fore tibia*: (0) with at least a single stout apical seta; (1) devoid of any setae. The number of setae on the fore tibial apex varies in different ant genera, but in general plesiomorphous groups tend to have them. Two stout setae are present in *Myrmecia*, *Nothomyrmecia*, and *Typhlomyrmex*. Two setae are apparently present in the extinct Cretaceous ant *Brownimecia* (per Fig. 11 in Grimaldi, Agosti, and Carpenter, 1997). A single seta is present in *Amblyopone* Erichson, *Myopopone* Roger, and *Centromyrmex* Mayr. *Paraponera* is one plesiomorphous ant genus that does lack these setae, as in *Gnamptogenys*. The genus *Platythyrea* is polymorphic for this character. Since the presence is inferred to be plesiomorphic and this is the state for *P. cribrinodis*, the genus is

scored as 0 assuming that the spine in this plesiomorphic species represents the ground plan for the genus.

- 53 *Exterior fore tarsal base opposite strigil*: (0) with row of stout setae; (1) with one stout seta, either alone or followed by a row of several more slender setae. *Platythyrea*, *Heteroponera*, and the *G. coxalis* group are polymorphic for this character. In all three cases the presence of setae was considered representative of the ground plan and it was scored as 0.
- 54 *Dorsum of basal fore tarsal segment*: (0) longitudinally striate/rugulose or punctate with some longitudinal undulations; (1) mostly smooth with scattered punctulae.
- 55 *Apex of second fore tarsal segment*: (0) with 8 or more stout spines along the ventral edge; (1) with 6 spines; (2) with 4 spines. In some intermediate cases the outermost spines are more slender than the median spines but thicker than the surrounding pilosity and were considered stout. The *coxalis* group is polymorphic for this character, with some species presenting 6 and others 4 spines. The highest count was taken to represent the group ground plan.
- 56 *Metacoxal tooth*: (0) absent; (1) indistinct, a low tubercle may be present; (2) present, a distinctly raised lobe or denticle is easily discernible.
- 57 *Mesotibial apical spurs*: (0) two; (1) one.
- 58 *Metatibial apical spurs*: (0) two; (1) one.
- 59 *Apical tarsomere*: (0) with an arolium; (1) without an arolium.
- 60 *Hind wings of male and female*: (0) with an anal lobe; (1) without an anal lobe.

Species Accounts

The descriptions for each species, as well as species group, are accompanied by a diagnosis intended to help the user of the keys in identifying specimens. The most reliable morphological characters are listed in each diagnosis and should generally be enough to avoid having to go through the whole description. Useful characters for separating a species from closely resembling species are listed in the Comments section for each species.

The Metrics section presents measurements and indices for either a set of the studied specimens or sometimes for all specimens studied. When the number of measured specimens exceeds two, the range for each metric refers to the minimum and maximum values encountered, regardless of whether they belong to different specimens. When the number of measured specimens is two, then the numbers for each metric express the first and second specimen respectively. When a holotype has been measured along with other specimens, its measurements are in square brackets. If a holotype is the only specimen measured for a new species described in the present revision, then no square brackets are used. Omitted from the description for each species are characters common to the species group that encompasses it; these characters are considered in the description for each species group. The Comments section for each species provides additional data regarding the species identity, biological information, and other facts relevant to the species being considered.

Label data have been transcribed from the original source as faithfully as possible, though changes have been made in the collection date format for the sake of

consistency. All English measurements taken from the literature and locality labels have been converted to the metric system. Data either added or commented on by the author are enclosed in square brackets. Common abbreviations include “ca.” or “nr.,” both meaning “near” or “close to”; and “confl.,” or confluence. For each locality the number of specimens studied for each caste in each collection is stated. The castes are abbreviated as follows: w = worker, q = queen, m = male. In Specimens Examined the geographic localities for each studied specimen has been arranged in alphabetical order starting with country and followed by the next main internal political subdivision, such as state or province. The spelling of the names of such internal divisions is as close as possible to the native spelling. Various maps and atlases proved useful. The GEOnet Names Server (URL: <http://164.214.2.59/gns/html>) of the National Imagery and Mapping Agency (U.S. Government) was extensively used for pinpointing localities on specimen data labels.

PHYLOGENETICS

Results.

The phylogenetic analysis produced two most parsimonious (MP) trees (length 204, c.i. 0.40, r.i. 0.64). Successive weighting selected one of the two trees of same length and topology (Fig. 8). The alternate topology placed *G. solomonensis* as more apical and as sister group to *G. preciosa*. A consensus of the two MP trees resulted in a collapse of this apical node. Bootstrap support and decay indices (di) are shown on the same tree. Successive single step increments produced 28 trees with 205 steps, 178 trees with 206 steps, 721 trees with 207 steps, 2,969 trees with 208 steps, and 11,427 trees with 209 steps. No additional increments were made above 209 steps. An unordered analysis gave 11 trees (length 195, c.i. 0.42, r.i. 0.56) that were 9 steps shorter than the ordered analysis but of similar topology. Successive weighting of these trees gave one tree identical to the SAW tree of the ordered data (Fig. 8).

Unambiguous character step changes are depicted in Fig. 9. Good support was obtained for the monophyly of *Gnamptogenys* + *Ectatomma* + *Rhytidoponera* (bootstrap 86; di 5). A sister group relationship between *Ectatomma* and the *R. impressa* group had poor support (bootstrap 54; di 1). *Gnamptogenys* resolved into a weakly supported clade, sister to *Ectatomma* and *Rhytidoponera*. Two branches are formed at the base of *Gnamptogenys*. One branch ends with the *coxalis* and *laevior* groups, as well as the New World species *G. minuta*, *G. concinna*, and *G. bispinosa*. *Gnamptogenys concinna* and *G. bispinosa* are sister to each other, and they in turn are sister to (*coxalis* + (*laevior* gp. + *G. minuta*)). The *laevior* group resolved as sister taxon to *G. minuta*, with good di support but poor bootstrap support. All nodes

in this branch, except for *laevior* group + *G. minuta*, collapsed on the first step increment calculating the di. The second of the two basal stems making up *Gnamptogenys* is the *epinotalis* + *striatula* + *taivanensis* group branch. The sister relationship between the Neotropical *G. relictata* with Old World species of the *epinotalis* group is the most strongly supported in this study (bootstrap 98; di 5). They are related (bootstrap 59; di 3) to a tenuously supported clade formed by species endemic to the Solomon Islands and Fiji (*G. albiclava*, *G. aterrima*, *G. crenaticeps*, *G. preciosa*, and *G. solomonensis*). The only differences between the two most parsimonious trees lay in relationships among these island endemics. *G. epinotalis*, *G. relictata*, and the Melanesian clade are supported as a clade (bootstrap 64; di 4) with a well-supported sister relationship (bootstrap 73; di 4) to the ubiquitous New World species *G. striatula*. The *taivanensis* group has weak support as sister to the other two lineages.

Discussion

Several apomorphies provide strong support for the monophyly of the clade *Gnamptogenys* + *Ectatomma* + *Rhytidoponera*; the presence of a continuous occipital carina [character 4: state 2]; reduction of the labial palps to two segments [18:2]; configuration of the pronotal posteroventral process [20:1] and prosternal process [21:2]; and presence of a sheath surrounding the prosternal nerve foramen [25:1]. The weak sister relationship between *Rhytidoponera* and *Ectatomma* may find some additional support in characters not included in the matrix, such as the vertexal lobes present in *Ectatomma* (compared with those of species such as *R. nexa* Stitz and *R.*

araneoides Le Guillou). These species also have rough convexities on the pronotum that could be homologous with pronotal processes present in *Ectatomma*.

At the onset of this study a paraphyletic *Gnamptogenys* seemed possible given the absence of any apomorphy, or any other diagnostic character for that matter, that could be reliably assigned to the genus. Previous studies allude to the metacoxal tooth, but it is not present in all members of the genus. Tracing the unambiguous state changes for this character using MacClade (Maddison and Maddison, 1997), one finds the metacoxal tooth is lost [56:0] in relatively few instances: two Neotropical species (*G. concinna* and *G. minuta*) and in three species of the *albiclava* group. This makes for a total of five changes, with three of these changes in species of the *albiclava* group. It may be possible to postulate fewer state changes depending on how the *albiclava* group polytomy is resolved. Despite the homoplasy, it seems reasonable to consider the presence of metacoxal teeth as part of the *Gnamptogenys* ground plan. An invariable autapomorphy for *Gnamptogenys* is the loss of the apical seta on the fore tibia [52:1], in contrast to *Ectatomma* and *Rhytidoponera*, which always have one [52:0]. The use of this single autapomorphic character and a slightly homoplasious metacoxal tooth provides support for the monophyly of *Gnamptogenys*. This monophyly is corroborated by Kugler's (1991) study of sting apparatus morphology in ectatommines that found three autapomorphic features for *Gnamptogenys* from a sample of 15 Neotropical species. He found the spiracle of the spiracular plate situated very near the posterior edge of the plate, the distal segment of the gonostylus much longer than the proximal segment, and the presence of lateral flanges on the sting of many species. His results were not used in the present study.

The genus *Gnamptogenys* branches into two main lineages (Fig. 8). The branch formed by the *coxalis* group, *laevior* group, *G. minuta*, and the Neotropical species *G. concinna* and *G. bispinosa* is supported by the obsolescence of the promesonotal suture [28:2] and the low, convex shape of the petiolar node [44:1]. There is additional support for a close relationship between the first three taxa based on the presence of foveolate sculpturing, a sculpturing character state not considered in the matrix, which is not found in other lineages. In the *laevior* and *coxalis* groups the foveolae are less dense along a longitudinal median strip on the cephalic and mesosomal dorsum, and consequently this area tends to have a greater proportion of smooth cuticle than surrounding areas. A similar foveolate pattern is found in some species belonging to the Neotropical *minuta* group, such as *G. bufonis*, *G. striolata*, and *G. falcifera* (Lattke, 1992). The *laevior* group and *G. minuta* share a thickened sheath around the prosternal nerve foramen and an obsolescent transverse ridge on the endosternum joining the sheaths. Even though the occipital lobes frequently found in the *coxalis* group are absent in *minuta*, the plesiomorphous species of the *minuta* group, *G. petiscapa* from northern Venezuela, has distinct occipital lobes (Lattke, 1990).

The other main branch of *Gnamptogenys* terminal taxa (*taivanensis* group, *G. epinotalis*, *G. relictata*, the five island endemic species, and *G. striatula*) is supported by the presence of short pilosity on the antennal scapes [11:1] and smooth sculpture on the first fore tarsal dorsum [54:1]. The *laevior* group also exhibits this last character state. The *taivanensis* group conserves an interesting suite of plesiomorphic character states, such as the number of maxillary palp segments [17:3] and the position of the propodeal [35:1] and petiolar spiracles [45:0]. The next clade from

this branch (*G. epinotalis*, *G. relictata*, the five island endemic species, and *G. striatula*) is supported by having two-segmented maxillary palps [17:4], a relatively short basisternal process [24:1], and the propodeal spiracle next to the propodeal declivity [35:2]. The position of the propodeal spiracle is not without homoplasy, as *G. minuta* appears to have independently acquired the same character state and *G. albiclava* exhibits the plesiomorphous state. *Ectatomma* has two-segmented maxillary palps [17:4]. The close relationship among the taxa on this branch may find additional support in the shared presence of even and parallel ridges on the cuticle, such as striae or costulae, a character not considered in the matrix. Such sculpture is frequent in New World species but quite limited in the Old World. Regular costulae or carinulae are found on the mesonotum of *G. albiclava* and on the frons of *epinotalis* group members. It should be noted that very fine striate patterns are found in *G. concinna*, some *minuta* group members and in a few *coxalis* group members (e.g., *G. niuginensis*). The pattern of regular parallel sculpturing can be found in the outgroup, *Ectatomma*, where fine striae are present in species such as *E. brunneum*. In this context, rugulose sculpturing is considered to be plesiomorphous with smooth, foveolate or evenly costulate sculpturing determined as derived.

The species of the *epinotalis* group and the *albiclava* group have the following synapomorphies: presence of a ridge along the basal mandibular margin [15:2] and a continuous groove around the katepisternum [33:1]. They also have a sulcus along the ventral pronotal margin [27:1], but so do the outgroup taxa *Heteroponera* and *Platythyrea*. In addition, with the exception of *albiclava*, they have the number of spines on the second fore tarsal segment apex reduced to four [55:2]. Unfortunately, while the sister relationship of the *albiclava* assemblage of species to the *epinotalis*

group has support, its status as a clade is dubious, with no clear apomorphy. Some characters not considered in the matrix lend support to sister relations among two of these species, such as the bicolored antennal tips in *G. albiclava* and *G. lucida*. The globular eyes, elongate antenna, slender habitus, distinct anepisternum, and shape of the clypeal lamella suggest *G. solomonensis* and *G. preciosa* are more related to each other than to *G. aterrima*. Even though the eyes in the first two species are subglobulose, the ommatidia are relatively large in comparison to the eye diameter, especially in *G. solomonensis*. This suggests the subglobular shape is actually derived from reduced eyes, compensating the diminished number of ommatidia by enlargement of the remaining facets, making the character state for these two species synapomorphic and not primitive [6]. Of the two species, *G. solomonensis* retains the greatest number of plesiomorphies, such as the presence of a metanotal groove, a convex mesonotum, and the mesopleural suture meeting the mesometapleural suture at a rough right angle, the sutures not as deeply impressed as in other species of the *albiclava* group. Other species of the *albiclava* group have moderately reduced eyes and a more compact mesosoma that closely resembles the *epinotalis* group aspect. Totally smooth body sculpturing is unknown for any *Gnamptogenys*, but the Solomon Island endemics *G. crenata*, *G. lucida*, and *G. albiclava* come close.

A sister relationship between the *epinotalis* group and the New World species *G. relictata* is strongly supported by the angle formed between the cephalic dorsum and vertex [1:2], reduced eyes [5:1], angular margin between the lateral and declivious propodeal faces [37:1], and subpetiolar process shape [48:1]. They also share densely punctulate scapes [10:1], although the same character state is found in *G. striatula*. Although species of the *taivanensis* group tend to have reduced eyes, the eyes are

even more reduced in species of the *epinotalis* group. The angular posterior cephalic dorsum is shared with the *laevior* group, and the angular propodeal margin can be found in the outgroup taxa.

DESCRIPTIONS OF GENERIC-LEVEL OUTGROUP TAXA

Heteroponera Mayr

(Figs. 1-3, 6)

Heteroponera Mayr, 1887:532. Type species: *Heteroponera carinifrons* Mayr, 1887:533 by monotypy. Considered junior synonym of *Acanthoponera* Mayr by Emery, 1911:35. Considered a subgenus of *Acanthoponera* by Forel, 1917:236. Raised to genus by Brown, 1952b:70.

Paranomopone Wheeler, W.M., 1915:117. Type species: *Paranomopone relictata* Wheeler, 1915:118 by monotypy. Synonymized by Brown, 1958:194.

Anacanthoponera Wheeler, 1923:176. Type species: *Ponera dolo* Roger, 1860:293 by original designation. Synonymized by Brown, 1952b:70.

Worker description. Head in frontal view with broadly convex lateral margins, posterior margin concave; anterior clypeal margin broadly convex, lamella present. Scape not reaching posterior cephalic margin, gradually widening apicad, slightly sinuate, irregularly rugulose; first funicular segment wider than long. Vertex sculptured and rounded, not flattened; occipital carina present or absent, occipital lobe generally absent (present in *H. relictata*). Eye convex to almost flat, with variable diameter. Mandible triangular, masticatory border dentate-denticulate; dorsum rugulose or smooth with punctae; cross section wedge shaped; dorsal margin convex

in lateral view, lateral sulcus present from base. Antennal scrobe present or absent; frontal lobe projects mostly laterally. Clypeus and frons with median longitudinal ridge. Head in lateral view with or without occipital lobes; occipital crests present or absent. Palpal formula 4,3 or less.

Mesosomal dorsal margin mostly convex in lateral view. Ventral pronotal margin straight, with parallel sulcus; anteroventrally bluntly angular; anterior pronotal face separated from lateral pronotal face by sharp angle. Promesonotal suture flexible, well impressed, interrupting dorsal sculpturing; metanotal sulcus indistinct to vaguely impressed; mesometapleural suture well impressed; mesopleural suture obsolescent. Katepisternum with anterior lamella, parallel sulcus present or absent; suture between metapleuron and propodeum indistinct to vaguely impressed. Propodeal spiracle opening directed posterolaterally (lateral in *H. microps*), more than two spiracular diameters away from declivity. Propodeal declivity mostly smooth, sharply edged laterally, flat to slightly concave with dorsolateral lobes. Metapleuron with or without posterior lobe, gland opening dorsal to posterolateral.

Propleura not fused, propleural posterior margin slightly thickened and shiny. Posterolateral pronotal lobes free, extending ventral over mesothoracic presternite in ventral view, tapering to an acute apex, cross section flat. Prosternal process with an arching, posteriorly projecting transverse lobe between longitudinal crests, apically either bifurcate or lobed. Basisternal lobe long, apex ending in rounded point, ventral margin slightly bent apicad in lateral view, forming obtuse angle. Prosternal process with apically convex median lobe, convex in transverse cross section; furcasternal ridges separated by lobe, ridges project slightly beyond lobe. Furcasternum with posterodorsal convexity and ridge. Lateral lobe of endosternum with narrow base;

neural foramen with rounded dorsal outline, without posterior sheath; keel narrow, extending whole length of endosternal phragma.

Mesothoracic presternite well developed, slightly longer medially than laterally, anterior mesosternal ridge projecting ventrally, anteroventrally fitting into prosternal process. Mesosternum not sharply delimited from presternite by transverse ridge, laterally bound by anterior crests of katepisternum, surface forming two elongate shallow convexities, anterior mesosternum not sharply bound from posterior by transverse ridge. Meso- and metasternal processes forming low ridges. Metacoxal openings completely surrounded by cuticle forming relatively narrow band along the posterior and internal margins. Excision for petiolar insertion shaped as triangular lobe, preceded anteriorly by a longitudinal sulcus.

Petiole in lateral view relatively erect, dorsal margin shorter than anterior margin, convex or with a denticle or tooth; spiracle below anterolateral process; subpetiolar process subquadrate; node in dorsal view wider than long, without anterior ridge. Petiolar tergum and sternite unfused. Postpetiolar process forming projecting solid lobe, not lip shaped; forming relatively slender triangular lobe in ventral view. Curvature of gaster variable, from relatively straight to strongly undercurved. Fore tibial apex with single spur besides strigil; basal fore tarsal segment with either row of stout setae or single seta opposite strigil, fore tarsal dorsum rugulose. Apex of second fore tarsal segment with 6 stout setae. Fore tarsal segments 2-4 relatively short at most not much longer than wide; metacoxal dorsum unarmed. Metatibia with a conspicuous yellowish, slightly sunken spot above insertion of strigil; metatarsal claws edentate, arolia absent.

Species studied: *H. dentinodis* (Mayr), *H. imbellis* (Emery), *H. leae* (Wheeler), *H. relictata* (Wheeler), and three undetermined species, each one respectively close to *H. imbellis*, *H. leae*, *H. microps* Borgmeier. **Species dissected:** *H. dentinodis*.

Distribution. The genus *Heteroponera* is found in the Neotropical and Australasian regions (Bolton, 1995b).

Comments. A novel diagnostic character and apomorphy for this group is the yellowish sunken spot on the metatibial apex. In other taxa studied the metatibia presented nothing that could be interpreted as a glandular area, in contrast to the prominent yellowish and depressed area in *Heteroponera*. Bolton (1990) discussed the metatibial gland in an assessment of army ant phylogeny and classification of the doryline section of Formicidae. The ventral location of the gland, immediately behind the metatibial median spur, is typical of the doryline section (subfamilies Dorylinae, Aenictinae, Cerapachyinae, and Ectoninae) and was lacking in other ants he surveyed. Only some Ponerini have a metatibial gland but in a different location, leading Bolton (1990) to conclude it is not homologous with the gland of doryline section members. The location of the gland in *Heteroponera* corresponds to that of the doryline section, and it is not clear if it is convergent or homologous.

Platythyrea Roger

Platythyrea Roger, 1863:172. Type species: *Pachycondyla punctata* (F. Smith), by subsequent designation of Bingham, 1903:73.

Eubothroponera Clark, 1930:8. Type species: *Eubothroponera dentinodis* (Clark), by original designation. Synonymized by Brown, 1975:6.

Worker description. Head in frontal view elongate, posterior margin slightly concave, lateral margins subparallel to slightly convergent anterad; anterior clypeal margin variable in shape: convex to relatively straight to slightly concave; clypeal lamella present or absent. Eye normal, not reduced, convex to broadly convex in cross section, situated near or anterad of cephalic mid length. Vertex sculpted, rounded, and not sharply delimited from frons, occipital carina and lobes absent. Frontal triangle, either absent or very shallowly impressed. Frontal lobe separated, broad and flat, covering antennal insertions in frontal view; no lobes of torulus apparent. Scape relatively straight, gradually widening apically, densely punctate; usually surpassing posterior cephalic margin by at least one apical width, occasionally not quite reaching margin; condyle of scape with a convex plate covering most of it; torulus apparently without dorsal lobe; funiculus without constrictions between segments, first segment longer than wide. Mandible triangular, masticatory border serially dentate or denticulate, or edentate and cultrate; mandibular dorsum convex, densely punctate. Maxillary palps with 6-4 segments; labial palps with 3 or 2 segments.

Mesosomal dorsal margin in lateral view with one convexity formed by pronotum and another very broad, almost straight convexity formed by mesometanotum and dorsum of propodeum; declivitous margin separated from dorsum by angle or lobes. Promesonotal suture well impressed, flexible, pronotum not rigidly fused to mesonotum, humerus rounded; pronotal ventral margin rounded to bluntly angular, fine ventral sulcus present. Mesometapleural suture well impressed, delimiting mesopleuron; mesopleural suture absent; katapisternum

without anterior sulcus; anterior lamella reduced or absent; suture between metapleuron and propodeum indistinct. Metapleuron without posterior plate; gland opening relatively large, elongate, oriented dorsolaterally, a brief swelling or lobe may be present beneath opening; bulla not conspicuous. Metanotal groove absent to vestigial. Propodeal spiracle round to oval, at same level as surrounding cuticle, separated from propodeal declivity by at least 4 diameters; declivitous face relatively flat, generally carinate laterally, frequently with dorsolateral posteriorly projecting lobes.

Posterolateral pronotal lobe free, situated ventrad to mesothoracic presternite, their cross section flat, apex subquadrate. Propleura unfused, propleural posterior margin relatively flat. Prosternal process without a posteriorly projecting transverse lobe between median longitudinal ridges. Basisternal lobe long, apex bluntly rounded, in lateral view ventral margin slightly convex. Prosternal process without median lobe, ridges merge posterad into single triangular point in dorsal view, not projecting beyond basisternal surface in lateral view. Furcasternum with posterodorsal convexity and ridge. Lateral lobes of endosternum with narrow base; foramen with rounded dorsal outline, without posterior sheath; keel reduced, present only toward dorsal apex.

Mesothoracic presternite well developed in ventral view, slightly longer medially than laterally, with longitudinal median crest. Anterior mesosternum relatively flat, forming inclined plane to tip of mesosternal process, abruptly separated anteriorly from presternite by ridge, laterally rounded or anterolaterally bound by low ridges, posteriorly sharply bound by ridge arching anterad of mesocoxal cavities. Meso- and metasternal processes both shaped as pair of denticles. Medial length of posterior

mesosternum approximately equal to diameter of mesocoxal cavity. Most or all of metacoxal cavity surrounded by cuticle, which may have thin fissure to petiolar insertion; excision of petiolar insertion forming elongate lobe extending to metacoxal midpoint.

Petiolar node in lateral view subquadrate; subpetiolar process small, forming anteroventrally projecting lobe in lateral view; spiracle posteroventrad of anterolateral swelling; posterior petiolar face with sharp lateral carinae, lobes or both (except in *P. cribrinodis*); anterior transverse petiolar crest absent. Postpetiolar process reduced, either absent, projecting anterad as low swelling, or with low V-shaped or concave ridge. Fourth abdominal segment relatively straight, not noticeably undercurved; postpetiole longer than petiole; stridulitrum present on pretergite of fourth abdominal segment. Fore tibial apex without stout setae (except *P. cribrinodis*). Basal fore tarsal segment dorsally corarious, area opposite strigil either with one, one contiguous pair, or several separate stout setae; apex of second fore tarsal segment generally with 8-10 stout setae; apex of meso- and metatibiae with two spurs; arolium present. Metacoxal dorsum with or without stout dorsal denticle. Sculpture opaque to subopaque pruinosity.

Species examined: *P. angusta* Forel, *P. arthuri* Forel, *P. cribrinodis* Gerstäcker, *P. frontalis* Emery, *P. mocquerysi* Emery, *P. modesta* Emery, *P. parallela* F. Smith, *P. pilosula* F. Smith, *P. punctata* F. Smith, *P. quadridentata* Donisthorpe, *P. sinuata* Roger, *P. turneri* Forel. **Species dissected:** *P. angusta*, *P. parallela*, *P. mocquerysi*.

Distribution. *Platythyrea* is found throughout the tropics (Bolton, 1995b).

Comments. Information for the preceding description was taken from specimens and gleaned from Brown (1952a, 1975). The degree of closure of the metacoxal cavities

is quite variable, totally closed, as in *P. parallela*, or with a distinct gap, as in *P. angusta*. One novel character, the shield like process on the condyle of the scape, is apparently missing in *Probolomyrmex* Mayr. This genus is the closest known relative of *Platythyrea* (Brown, 1975), and the shield could represent an apomorphy of *Platythyrea*.

The large African species, *P. cribrinodis*, has several stout setae on the fore tibial apex, a feature absent in the other species examined. The fore tibial apex in *P. cribrinodis* may have a series of setae and also two or one preapical seta near the base of the strigil. The mesonotum forms a slight convexity in lateral view, making it more conspicuous than the mesonotum in other congeners. Neither its propodeal declivity nor is posterior petiolar face are laterally sharply carinate as typical in the genus but are separated by a rounded margin. These traits are typically plesiomorphic for ants and contrast with the more derived aspect in species of the *turneri* group, which up to now have been considered the most "primitive" members of the genus (Brown, 1975). Given this combination of traits, *P. cribrinodis* is assumed to represent a more plesiomorphic condition than in the other inspected congeners.

Ectatomma F. Smith

Ectatomma Smith, F., 1858:102. Type species: *Formica tuberculata*, by subsequent designation of Bingham, 1903:82.

Worker description. Head in frontal view longer than wide, lateral margin broadly convex, posterior margin broadly convex to mostly straight. Anterior clypeal margin

convex to medially bluntly angular. Eye set in posterior third of head, large and hemispherical, ommatidia small. Dorsal lobe of torulus separate from frontal lobe and close to base of torulus. Scape mostly slender, slightly widening apically, apex with low lobe at each side of pedicel, longitudinally rugulose, length surpassing posterior cephalic margin by several apical widths; with sparse erect hairs, no pubescence. Second funicular segment more than twice as long as wide. Vertex sculptured and curving onto frons or occasionally flattened, with reduced sculpturing; sometimes with lateral lobe. Frontal lobe project mostly dorsally. Clypeus with or without median longitudinal crest, lamella absent. Mandible triangular, chewing border denticulate, dorsally roughly striate, wedge-shaped in cross section; laterally with evenly convex dorsal margin, brief lateral sulcus present apicad. Palpal formula: 2,2.

Mesosoma with dorsal margin laterally divided into three convexities: pronotum, mesonotum, and propodeum; metanotal sulcus deep. Humeri rounded; pronotum with anterodorsal process and lateral humeral processes, ventral pronotal margin evenly convex in lateral view, without parallel sulcus. Promesonotal suture fused but well impressed and may or may not interrupt sculpture, surface convex. Propleura not fused, posterior margin with thin upturned flange, best developed laterally. Posterolateral pronotal lobe ending in acute point, L-shaped in cross section with lamellate flange abutting side of anterior mesosternal process. Basisternal lobe long, apex bluntly rounded, ventral margin slightly convex in lateral view. Prosternal process with apically bidentate, posteriorly projecting median lobe, lobe projecting slightly beyond ridges in ventral view, relatively straight in transverse cross section. Furcasternum with posterodorsal convexity and ridges, ridges separated by lobe, not projecting beyond basisternal surface in lateral view. Lateral lobes of endosternum

with broad base; neural foramen with posterior sheath, its apical dorsal outline tapering, joined with broad keel, extending whole length of endosternal phragma.

Anepisternum trapezoid, metanotal spiracle with prominent lobe; mesopleural sulcus broad, not deep; katepisternum with anterior lamella, parallel sulcus absent, anteroventral corner ventral. Mesothoracic presternite reduced to triangular process, with base as long as mesosternum, and variably developed median longitudinal crest. Mesosternum with two longitudinal shallow convexities, laterally bound by anepisternal lamella. Median length of posterior mesosternum less than one mesocoxal diameter; mesosternal process reduced, forming crest or lobes, not dentiform. Mesometapleural sulcus well developed to obsolescent; anepisternum not divided posteriorly by suture. Metapleuron not posteriorly bound by crest; bulla prominent and convex; gland opening dorsal, wider posteriorly than anteriorly. Metasternal process shaped as paired denticles. Metacoxal cavities open on internal side, posteriorly surrounded by narrow strip of cuticle; bullae forming conspicuous hemispherical posterior projections. Suture between metapleuron and propodeum generally indistinct. Propodeal spiracle several spiracular diameters from declivitous edge, planar with surrounding cuticle or slightly elevated, opening elliptical or slit shaped. Propodeum denticulate; denticles low, triangular, mostly transverse; declivity sculptured, relatively flat, not delimited by crests or ridges.

Petiole erect in lateral view; dorsal margin shorter than anterior margin; ventral process anteriorly projecting; spiracle either on or beneath anterolateral process; anterior crest absent. Postpetiolar process concave in anterior view, ventrally with a convex anterior margin, no posterior crest. Apex of protibia with a single stout spur besides strigil; basal segment of fore tarsus with row of stout setae opposite strigil,

dorsum longitudinally rugulose; strigil stout, with a basal brush of long hairs; apex of second fore tarsal segment with 6 stout setae and 2 slender lateral setae; apex of meso- and metatibia with one spur each. Metacoxal dorsum unarmed.

Species studied: *E. brunneum* (F. Smith), *E. edentatum* Roger, *E. lugens* Emery, *E. permagnum* Forel, *E. ruidum* Roger, *E. tuberculatum* (Olivier). **Species dissected:** *E. brunneum*, *E. lugens*, *E. ruidum*, *E. tuberculatum*.

Distribution. The genus *Ectatomma* is exclusively Neotropical in distribution (Bolton, 1995b).

Comments. The posterior cephalic lobes present in some members of this group differ from the lobes in *Gnamptogenys*, which are of occipital origin, while in *Ectatomma* they originate in the vertex. During dissection of specimens, there was more difficulty in separating the prosterna from the propleura than in comparison with the other studied groups, a sign of greater fusion of the prosterna to the propleura.

Rhytidoponera impressa group

Worker description. Head in frontal view with broadly convex lateral margins, slightly wider posterad than anterad, posterior margin straight to broadly convex; anterior clypeal margin convex to bluntly angular medially, clypeal lamella present. Cephalic vertex sculptured and not sharply separated from frons by angles. Head generally without occipital lobes, lobe if present relatively small (as in *R. enigmatica*), occipital lamella may also form distinct lobe. Eye convex and not reduced. Frontal lobe projecting dorsolaterally and slightly concave along outer

margin, partially exposing dorsal lobe of torulus and condyle. Scape longitudinally rugulose, mostly slender, except for basal widening, and slight bulge approximately one-third from apex; apex surpasses posterior cephalic margin by several apical widths; little pilosity, only a few erect hairs at most. First funicular segment more than twice as long as wide. Mandible triangular, chewing border denticulate, and dorsum with longitudinal rugulae; cross section cuneiform; with evenly convex dorsal margin in lateral view.

Mesosoma with dorsal margin divided into three regions in lateral view by convexities: pronotum, mesonotum, and propodeum. Humeri rounded, without crests or angles. Pronotum anteroventrally with acute denticle, posteroventrally with brief lobe, no ventral sulcus. Promesonotal suture well impressed; mesonotum broadly convex in all directions; metanotal sulcus absent. Mesothoracic spiracle without dorsal process. Anepisternum relatively broad, trapezoidal and not cuneiform, not distinctly separated from metapleura by suture, though sculpturing may differ. Katepisternum distinctly delimited by broad, deeply impressed mesopleural and mesometapleural sutures. Metapleuron posteriorly bordered by flange; gland opening directed posterodorsally; metapleuron and propodeum separated by broad and shallow sulcus. Propodeal spiracle round to oval, directed posterolaterally, separated more than one spiracular diameter from declivity; propodeal declivity sculptured, unarmed, relatively flat, curving onto lateral propodeal face, separated from metapleuron by brief longitudinal crest.

Propleura not fused, posterior margin with a ventrally projecting flange; posterolateral pronotal lobe ending in acute point, lobe L-shaped in cross section with lamellate flange abutting against side of anterior mesosternal process. Basisternal

lobe long, apex bluntly rounded, ventral margin convex in lateral view. Prosternal process with single prominent, posteroventrally projecting lobe, furcasternal ridges widely separated by lobe and projecting beyond ventral basisternal surface, lobe projecting beyond ridges in both ventral and lateral views. Furcasternum with posterodorsal convexity and ridge. Lateral lobes of endosternum with narrow base, foramen with posterior sheath, its apical dorsal outline tapering, joined with broad keel extending whole length of endosternal phragma. Mesothoracic presternite reduced to triangular process, with base narrower than mesosternum, and with well developed median longitudinal crest. Mesosternum with two longitudinal shallow convexities, laterally bound by anepisternal lamella. Median length of posterior mesosternum roughly equal to one mesocoxal diameter; mesosternal process reduced, forming crest or lobes, not dentiform; metasternal process forming paired denticles. Metacoxal cavities open on inner side, posteriorly surrounded by narrow strip of cuticle.

Petiole in lateral view slightly pedunculate, relatively erect; dorsal margin longer than height of anterior margin and broadly convex; anterior margin broadly concave, posterior shelf present. Node wider than long in dorsal view; anterior ridge present. Petiolar spiracle situated laterally, directly on anterolateral process. Subpetiolar process projecting anterad. Anterior postpetiolar process lip shaped, convex in ventral view, relatively straight to slightly concave in anterior view. Dorsal postpetiolar margin sinuous in lateral view. Fore tibiae with longitudinal rugulae, gradually widening apically, not incrassate; apex with a single stout seta. Meso- and metatibia each with single apical spur. Base of protarsus longitudinally rugulose

dorsally, with row of spines opposite strigil; apex of second protarsal segment with 6 stout spines. Metacoxal dorsum unarmed.

Studied species: *R. impressa* (Mayr), *R. chalybea* Emery, *R. confusa* Ward, *R. enigmatica* Ward, *R. purpurea* (Emery). **Dissected species:** *R. impressa*, *R. purpurea*, *R. chalybea*.

Distribution. The species of the *impressa* group are found in mesic forested areas of eastern Australia and in New Guinea (Ward, 1980).

Comments. The *impressa* group of *Rhytidoponera* was recognized by Brown (1953, 1954a) based on biological and morphological grounds, with particular emphasis on the shallow but distinct constriction between the posterior mesonotum and anterior propodeum. This group of species is considered to be one of the more plesiomorphic groups within the genus because of its reproductive biology and habitat preference. They prefer mesic forested areas, compared to the arid habitats favored by most species. They can also reproduce through queens, unlike most other species, which have replaced queens with gamergates (Brown, 1958; Ward, 1980, 1981).

TAXONOMY

Genus *Gnamptogenys* Roger, 1863

Gnamptogenys Roger, 1863:174. Type species: *Ponera tornata* Roger, 1861:15 by subsequent designation of Emery, 1911:44. Placed as subgenus of *Ectatomma* F. Smith by Mayr, 1887:540. Revived status as genus by Brown, 1958:211.

Stictoponera Mayr, 1887:539. Considered subgenus of *Ectatomma* F. Smith. Type species: *Ponera coxalis* Roger, 1860:308 by subsequent designation of Bingham, 1903:82. Raised to genus by Emery, 1911:47. Synonymized by Brown, 1958:212.

Holcoponera Mayr, 1887:540. Considered subgenus of *Ectatomma* F. Smith. Type species: *Gnamptogenys striatula* Mayr, 1884:32 by subsequent designation of Emery, 1911:40. Raised to genus by Emery, 1902:181. Synonymized by Brown, 1958:211.

Alfaria Emery, 1896:177. Type species: *Alfaria simulans* Emery, 1896:177 by original designation. Synonymized by Brown, 1958:211.

Poneracantha Emery, 1897:547. Considered subgenus of *Ectatomma* F. Smith. Type species: *Ectatomma (Holcoponera) bispinosum* Emery, 1890:40 by original designation. Synonymized by Brown, 1958:211.

Rhopalopone Emery, 1897:549. Type species: *Rhopalopone epinotalis* Emery, 1897:550 by monotypy. Synonymized by Brown, 1958:211.

Emeryella Forel, 1901b:334. Type species: *Emeryella schmitti* Forel, 1901b:334 by monotypy. Synonymized by Brown, 1958:211.

Parectatomma Emery, 1911:44. Considered subgenus of *Ectatomma* F. Smith. Type species: *Ectatomma triangulare* Mayr, 1887:544 by original designation. Placed as subgenus of *Gnamptogenys* Roger by Forel, 1917: 236. Synonymized by Brown, 1958:212.

Spaniopone Wheeler, W. and Mann, 1914:11. Type species: *Spaniopone haytiana* Wheeler, W. and Mann, 1914:11 by monotypy. Synonymized by Brown, 1958:212.

Wheeleripone Mann, 1919:282. Type species: *Wheeleripone albiclava* Mann, 1919:283 by original designation. Synonymized by Brown, 1958:212.

Commateta Santschi, 1929:476. Type species: *Ectatomma (Parectatomma) bruchi* Santschi, 1922:241 by original designation. Synonymized by Brown, 1958:212.

Tammoteca Santschi, 1929:476. Type species: *Ectatomma concinnum* F. Smith, 1858:103 by original designation. Synonymized by Brown, 1958:212.

Barbourella Wheeler, W.M. 1930:10. Type species: *Emeryella (Barbourella) banksi* Wheeler, 1930:10 by original designation. Synonymized by Brown, 1958:212.

Old World worker description. Head elongate with broadly convex lateral margins, subparallel to each other or diverging posterad in frontal view; posterior cephalic margin usually concave to straight; compound eye on cephalic mid length or posterad, ranging in size from reduced, with only three ommatidia, to large and subglobular; frontal lobe subparallel, covering all or most of antennal condyle; funiculus filiform or incrassate, never forming distinct club; anterior clypeal margin

with narrow, transverse strip of lamellate cuticle; mandibles triangular with denticulate chewing border; palpal formula 3,2 or 2,2.

Pronotum unarmed (except *G. sinensis*), humeral angle usually well developed; propleura not fused to each other, posterior margin with a ventrally projecting flange; promesonotal suture present or absent, pronotum fused to mesonotum. Posterolateral pronotal lobe ending in acute point, L-shaped in cross section with lamellate flange abutting side of anterior mesosternal process (Fig. 7); basisternal lobe with apex bluntly rounded or slightly bidentate; prosternal process with single prominent, posteroventrally projecting lobe, ridges variably separated by lobe and projecting beyond ventral basisternal surface; furcasternum with posterodorsal convexity and ridge; endosternal foramen with posterior sheath, apical dorsal outline of sheath tapered or rounded, joined with keel extending whole length of endosternal phragma. Anteroventral margin of katepisternum with narrow lamellate process and parallel narrow sulcus; katepisternum distinctly surrounded by sutures; anepisternum may or may not be distinct; metanotal sulcus usually effaced; mesothoracic presternite reduced to triangular process, with narrower base than mesosternum; propodeal spiracle round to oval, never slitlike, separated not more than two spiracular diameters from propodeal declivity in lateral view.

Petiolar node either with semiparallel anterior and posterior margins or mostly convex in lateral view; subpetiolar process present, variable in shape, usually ranging from subquadrate to triangular in lateral view. Pretergites and sternites of third abdominal segment situated at midheight on anterior postpetiolar margin when seen laterally; third abdominal sternite with anterior shelflike process; constriction between third and fourth abdominal segments well developed; fourth abdominal

segment usually with long, convex tergite and reduced sternite, causing gaster to be pointed ventrally in lateral view. Fore tibial apex lacking stout setae; metacoxal dorsum usually with a lobe or denticle; apex of meso- and metatibia with two spurs; claws generally bidentate, arolium lacking. Coloration ranging from yellowish, brown to black; ferruginous brown is most common color, with antennae, mandibles, and legs usually lighter shade than rest of body. Pilosity on head, thorax, and abdomen usually consisting of scattered suberect to subdecumbent standing hairs with little if any pubescence. Most pilosity concentrated on antennae, gastral apex, and parts of ventral side. Cuticle hard and polished. Sculpture variable, mesosoma frequently foveolate or punctate over smooth ground sculpturing, also strigulose, rugulose, striate, carinulate, or mostly smooth.

Synonymic Checklist of *Gnamptogenys* in Southeast Asia and Australasia

albiclava (Mann, 1919). Solomon Islands

aterrima (Mann, 1921). Fiji

atrata **sp. n.** Sulawesi

bicolor (Emery, 1889). Myanmar to Java, southern China

= *bannana* Xu and Zhang 1996 **syn. n.**

biloba **sp. n.** Borneo

binghamii (Forel, 1900). India to New Guinea, Philippines

= *borneensis* (Emery, 1900b)

biroi (Emery, 1901). New Guinea to northern Queensland

bulbopila **sp. n.** Philippines

chapmani Brown, 1958. Malaysia to Borneo, Philippines

costata (Emery, 1889). Myanmar to Sulawesi, Philippines

= *parva* (Forel, 1913)

= *pinealis* (Wheeler, 1929)

= *simalurensis* (Forel, 1915)

= *unicolor* (Forel, 1901b)

= *wallacei* (Donisthorpe, 1932)

coxalis (Roger, 1860). Sri Lanka

crassicornis (Forel, 1912b). Sumatra to Java

= *spiralis* (Karavaiev, 1925) **syn. n.**

crenaticeps (Mann, 1919). Solomon Islands

cribrata (Emery, 1900a). Malaysia to New Guinea, Philippines

= *diehlii* (Forel, 1901a) **syn. n.**

= *dammermani* (Wheeler, 1924) **syn. n.**

delta **sp. n.** western Malaysia

epinotalis (Emery, 1897). New Guinea

fistulosa **sp. n.** Philippines

gastrodeia **sp. n.** Sumatra to Java

gabata **sp. n.** western Malaysia to Borneo

grammodes Brown, 1958. New Guinea

helisa **sp. n.** Borneo

hyalina **sp. n.** Singapore

lacunosa **sp. n.** Borneo

laevior (Forel, 1905). western Malaysia to Sulawesi, Philippines

= *avia* (Forel, 1912a)

= *kalabit* Brown, 1958 **syn. n.**

leiolabia **sp. n.** Philippines

lucida (Mann, 1919). Solomon Islands

luzonensis (Wheeler, 1929). Philippines

macretes Brown, 1958. New Guinea

major (Emery, 1901). New Guinea

malaensis (Mann, 1919). Solomon Islands

meghalaya **sp. n.** western India

menadensis (Mayr, 1887). western Malaysia to New Guinea, Philippines

= *obscura* (Santschi, 1932)

= *stylata* (Menozzi, 1925)

niuguinense **sp. n.** New Guinea

ortostoma **sp. n.** Thailand to Borneo

palamala **sp. n.** Borneo

panda (Brown, 1948). southwestern China

paso **sp. n.** western Malaysia

pertusa **sp. n.** Borneo

polytreta **sp. n.** Thailand to western Malaysia

posteropsis (Gregg, 1951). western Malaysia to Borneo, Philippines

preciosa **sp. n.** Solomon Islands

rugodens **sp. n.** western Malaysia

scalpta **sp. n.** Borneo

sichuanensis **sp. n.** southwestern China

сила **sp. n.** Borneo

sinensis Wu and Xiao, 1987. southwestern China

solomonensis **sp. n.** Solomon Islands

taivanensis (Wheeler, 1929). Taiwan

treta **sp. n.** Borneo

Key to Old World species groups of *Gnamptogenys*

and to species of the *albiclava* and *taivanensis* groups (workers)

1. Metacoxal dorsum smooth, without a denticle or lobe, a slight ridge present at most 2

- Metacoxal dorsum with a denticle or raised lobe 5
- 2. Antennae bicolored: ferruginous except for the white four apical segments; HL more than 1.20; WL more than 1.69 mm (Solomon Islands) *albiclava* (Mann)
- Antennal funiculus totally ferruginous; HL less than 1.20; WL less than 1.69 mm 3
- 3. Subpetiolar process in lateral view shaped as an anteriorly projecting acute lobe with a concave posterior margin; head very elongate, CI less than 0.71 (Fig. 14a; Solomon Islands) *preciosa* sp. n.
- Subpetiolar process in lateral view subquadrate or shaped as a rounded lobe, posterior margin not concave; head not particularly elongate, CI more than 0.71 (Fig. 12a) 4
- 4. Mesosomal dorsum smooth; cephalic dorsum posterolaterally punctate (Fiji Islands) *aterrima* (Mann)
- Mesosomal dorsum posterad of pronotum transversely strigose; cephalic dorsum with longitudinal costulae (Solomon Islands) *solomonensis* sp. n.
- 5. Antennae bicolored, four apical antennal segments white, the rest ferruginous (Solomon Islands) *lucida* (Mann)
- Antennal funiculus totally ferruginous 6
- 6. The petiole relatively low and paniform with the anterior and posterior margins forming a relatively even convexity (Figs. 19a, 24, 30, 35a, 51a) 7
- In lateral view the petiole higher than long, with relatively steep anterior and posterior margins, forming almost parallel sides (Figs. 12b, 13b, 39, 61a) 8

7. Propodeal denticles usually present (Figs. 16a, 21, 24); metapleuron separated from propodeum by broad and convex, arching sulcus; eyes rounded and convex in cross section (Figs. 17a, 18b, 29b) ***coxalis*** group
- Propodeal denticles absent (Figs. 50a, 52a, 57a); metapleuron and propodeum separated by arching row of irregularly shaped depressions, not forming a continuous sulcus; eyes broadly convex, almost flattened in cross section (Figs. 50b, 51b, 57b) ***laevior*** group
8. In lateral view propodeal spiracle separated from propodeal declivitous margin by less than one diameter (Figs. 13b, 42) 9
- Propodeal spiracle separated from declivitous margin by more than one diameter (Figs. 61a, 63a) ***taivanensis*** group 10
9. Apex of antennal scapes surpass occipital margin by more than two apical widths; mesosomal dorsum mostly smooth (Solomon Islands) ***crenaticeps*** (Mann)
- The apex of each scape may surpass the median occipital margin by a fraction of its apical width at most, usually shorter; mesosomal dorsum variable, usually sculptured ***epinotalis*** group
10. Pronotum with a stout denticle on each humeral area (Hunan, China)
..... ***sinensis*** Wu and Xiao
- Pronotum without denticles 11
11. Occipital lamella shaped as a blunt triangular denticle, not convex; anterior clypeal margin with a blunt median point and sinuate sides (Sichuan, China).....
..... ***panda*** (Brown)

- Occipital lamella in lateral view with a convex posterior margin; anterior margin of clypeal lamella in frontal view evenly convex 12
- 12. Occipital lamella narrow and inconspicuous (Fig. 63a); dorsum of fourth abdominal tergite mostly smooth with abundant punctae, without carinulae (Taiwan) *taivanensis* (Wheeler)
- Occipital lamella well developed, conspicuous (Fig. 62a); dorsum of fourth abdominal tergite with abundant patches of brief carinulae and effaced rugulae (Sichuan, China) *sichuanensis* sp. n.

albiclava group

Diagnosis. Over half of cephalic vertex smooth; scape mostly smooth with moderate to dense punctulation, scape surpassing posterior cephalic margin by more than one apical width; third antennal segment longer than wide. Pronotum lacking humeral angle; mesopleural suture well impressed and deep, continuous from one end to other, forming single groove with mesometapleural suture around katepisternum. Subpetiolar process with two lateral posterobasal margins in ventral view, sides diverging posterad.

Description. Cephalic vertex smooth over half of surface; occipital lobes lacking, occipital ridge present; anterior clypeal margin convex or bluntly angular (modified in *G. albiclava*); eye not reduced in diameter (OI 0.16-0.31), cross section convex to globulose, not flattened. Dorsal lobe of torulus partially fused to ventral surface of

frontal lobe (totally separate in *G. preciosa*); scape mostly smooth, with moderate to dense punctulation, scape surpassing posterior cephalic margin by more than one apical width (SI 1.00-1.60); third antennal segment longer than wide, scape with abundant short suberect pilosity of uniform length, besides other standing hairs. Mandibular dorsum with distinct ridge defining narrow, parallel-sided sector along basal margin, sculpture mostly smooth with scattered punctae (basally rugose and apically smooth with punctae in *G. solomonensis*); palpal formula 2,2 (not ascertained in *G. solomonensis* and *G. crenaticeps*). Pronotum lacking humeral angle, with longitudinal sulcus parallel to ventral margin in lateral view; prosternal process with ridges widely separated by median lobe in ventral view, median lobe not extending beyond prosternal ridges in ventral view (not ascertained in *G. albiclava* and *G. crenaticeps*), with undivided apex (bidentate in *G. solomonensis*); promesonotal suture distinctly impressed (feebly impressed in *G. crenaticeps*); metanotal groove usually present (not apparent in *G. albiclava*); anepisternum not clearly separated from metapleuron by suture (except *G. solomonensis*); mesopleural suture well impressed and deep, continuous from one end to other, forming single groove with mesometapleural suture around katepisternum; metapleuron and propodeum not separated by distinct suture or groove; propodeal spiracle separated from declivitous margin in lateral view by less than one spiracular diameter (approximately one diameter in *G. albiclava*), not elevated above surrounding cuticular surface, propodeum unarmed. Petiole with or without anterior ridge in dorsal view, erect in lateral view (slightly suberect in *G. albiclava*), petiolar spiracle situated beneath anterolateral crest (at same level as crest in *G. preciosa*); subpetiolar process with two lateral posterobasal margins in ventral view, sides relatively parallel

to each other. Fore tarsal base opposite strigil with one stout seta (*G. aterrima* with row of setae); dorsum mostly smooth with scattered punctulae; apex of fore tarsal segment with 4 stout spines (6 in *G. albiclava*). Metacoxal tooth present in *G. crenaticeps* and *G. lucida*, absent in other species.

Included species: *G. aterrima*, *G. albiclava*, *G. crenaticeps*, *G. lucida*, *G. preciosa*, *G. solomonensis*.

Comments. The geographic range of these species is restricted to the Solomon Islands, with the exception of *G. aterrima*, endemic to Fiji. They constitute the most isolated species of *Gnamptogenys* and are the easternmost in the geographic range for the Old World fauna. The *albiclava* group forms a weakly supported clade (see discussion in Phylogeny section) that is close to the *epinotalis* group. There is no clear apomorphy for this assemblage of species, and the species group description contains more exceptions than are found in the other species groups. It seems possible that they may constitute a series of lineages departing from the lineage leading to the *epinotalis* group. Some of these species (*G. albiclava*, *G. crenaticeps*, and *G. lucida*) were previously considered part of the genus *Wheeleripone*, designated by Mann (1919), and allied to *Stictoponera*. Both names were eventually sunk by Brown (1958).

***Gnamptogenys albiclava* (Mann)**

(Fig. 10)

Wheeleripone albiclava Mann, 1919:283, Fig. 3. Syntype workers: Solomon Islands, Isabel Island, Fulakora (Mann) (MCZC) [Examined].

Gnamptogenys albiclava (Mann); Brown, 1958:227. Placed in *Gnamptogenys*.

Diagnosis. Apical four funicular segments white, the rest of antenna brown; occipital lobes absent; anterior clypeal margin with two lateral blunt angles and median quadrate projection. Humeri rounded, without crests; body mostly smooth except for longitudinal costulae on lower part of mesonotum and metapleura; metacoxal dorsum without a denticle. Large, HL 1.34-1.40, WL 1.89-2.11mm.

Worker. Metrics ($n = 3$): HL 1.34-1.40, HW 1.12-1.25, ML 0.77-0.85, SL 1.29-1.40, ED 0.19-0.21, WL 1.89-2.11 mm. CI 0.84-0.89, SI 1.12-1.16, MI 0.68-0.69, OI 0.16-0.17. Head subrectangular in frontal view, wider posterad than anterad, sides slightly concave, posterior margin medially excised; frons with longitudinal costae fading laterally to smooth surface with piligerous punctae, costae extend medially to vertex; vertex otherwise mostly smooth and rounded, not sharply separated from frons; occipital lobes absent. Frontal lobe brief, exposing dorsal lobe of torulus in frontal view; scape surpasses posterior cephalic margin by more than one apical width, shaft gradually widening apically, cross section oval, dorsum smooth with sparse punctulae, scape with abundant appressed pilosity present; first funicular segment at least twice as long as wide. Clypeus longitudinally costulate, median shallow sulcus present; anterior margin with two lateral blunt angles and median quadrate projection, lamella apparently absent; eye with convex cross section; mandibular dorsum smooth with punctulae, masticatory border denticulate.

Pronotum with anteroventral angle in lateral view, ventral sulcus present; promesonotal suture distinct from side to side, metanotal sulcus indistinct; mesosoma mostly smooth, mesonotum longitudinally costulate; anepisternum indistinct, except

for occasional brief impressed line; posterior metapleuron with longitudinal carinulae; propodeal spiracle separated by approximately one diameter from declivity, propodeal declivity relatively flat to slightly convex. Dorsal mesosomal margin evenly convex in lateral view, curving into straight propodeal margin. Petiole anterodorsally convex in lateral view, more sharply curved posterad than anterad, posterior margin brief, vertical; petiolar spiracles situated ventrad of anterolateral lobes, anterior crest absent; subpetiolar process triangular, anteriorly projecting; petiole and gaster mostly smooth; procoxa laterally smooth; fore tarsal base with single stout seta opposite strigil, dorsum punctulate; second fore tarsal segment with 6 apical stout setae; fore tarsal segments 2-4 slightly longer than wide; metacoxal dorsum unarmed, slight elevation or corner may be present. Body without standing pilosity; appressed hairs present on funiculus, coxae, tarsi, and gastral apex. Body brown; legs and mandibles ferruginous; antennae ferruginous except for white terminal four segments of funiculus.

Queen. Metrics ($n = 1$): HL 1.56, HW 1.37, ML 0.91, SL 1.47, ED 0.26, WL 2.44 mm. CI 0.88, SI 1.07, MI 0.66, OI 0.19. Very much as worker except for caste differences. Metapleuron with larger patch of longitudinal costulae that extends dorsally to bottom edge of propodeal spiracle. Mesoscutum and scutellum longitudinally costulate.

Male. Unknown.

Comments. Mann's (1919) description is comprehensive, but I disagree with his assertion that the antennal scapes surpass the posterior occipital margin by less than their apical width. This length was consistently found to be longer than the apical width, even taking into account the apical flange of the scape. The anterior clypeal

border is strigulose and not densely punctulate as he describes. The mandibles are just as shiny as the rest of the body, and the pilosity is yellowish, not black as in Mann (1919). The only other *Gnamptogenys* with a similarly colored antenna, *G. lucida*, is also from the Solomon Islands but has only been found on Malaita, not Guadalcanal. It is much smaller (HL < 1.0; WL < 1.3 mm) than *G. albiclava* and has a metacoxal tooth and a smooth mesonotum. They both share the pointed anteroventral pronotal corner, but *lucida* lacks the median antero-clypeal projection.

This species shares with *G. solomonensis*, another Solomon Islands endemic, the single stout seta on the basal fore tarsal concavity, lack of a metacoxal spine, and exposure of the dorsal lobe of the torulus. The postpetiolar process in *G. albiclava*, having two lateral lobes and a median denticle, seems similar to that of *G. solomonensis*, which also appears trilobed. The apparent lack of a clypeal lamella in *G. albiclava* is unique in *Gnamptogenys*, though the anterior clypeal projection could be derived from the lamella. The petiolar node of *G. albiclava* is not as high and compressed as in other members of this group, but its shape is also unlike the regular convexity of the *coxalis* or *laevior* group, with a higher posterodorsal margin on the node than its anterodorsal margin. The type specimens were taken on the ground in forest.

Specimens examined. SOLOMON ISLANDS. Guadalcanal, Mt. Austen, 13-x-1965, P. Greenslade 20678, 20676, 2w ANIC; Guadalcanal, Mt. Austen, ii-1966, P. Greenslade 21135, 1q ANIC; Guadalcanal, Mt. Tonapan, 1143m, 5-v-1965, P. Greenslade 18151, 1w ANIC; Isabel Island, Fulakora, W. Mann, 1916, 1w MCZC.

Gnamptogenys aterrima (Mann)

(Fig. 12)

Wheeleripone aterrima Mann, 1921:411, Fig. 2. Syntype workers, queen, male: Fiji,

Viti Levu, Waiyanitu (Mann) (LACM) [Examined].

Gnamptogenys aterrima (Mann); Brown, 1958:227. Placed in *Gnamptogenys*.

Diagnosis. Frons mostly smooth medially with piligerous punctae laterally; mesosoma, petiole, and gaster mostly smooth; promesonotal suture reduced or indistinct; metanotal sulcus distinct; metacoxal dorsum unarmed. Endemic to Fiji.

Worker. Metrics ($n = 9$): HL 0.86-0.92, HW 0.69-0.74, ML 0.38-0.44, SL 0.72-0.79, ED 0.13-0.18, WL 1.03-1.10 mm. CI 0.79-0.84, SI 1.00-1.08, MI 0.54-0.60, OI 0.18-0.22. Head oval in frontal view, wider posterad than anterad, posterior margin with brief median concavity; anterior clypeal margin convex; frons mostly smooth medially, laterally with rows of piligerous punctae, occipital lobe absent; dorsal lobe of torulus not covered by frontal lobe; scape gradually widened apically, slightly arched basally, dorsum punctate with decumbent pilosity, scape surpassing posterior cephalic margin by at least two apical widths; first funicular segment slightly longer than wide. Clypeus with shallow posteromedian longitudinal sulcus, mostly smooth medially, laterally longitudinally strigulose, brief strigulae present along anterior margin, spilling onto lamella, lamella with small median lobe. Mandibular dorsum smooth with shallow piligerous punctae, masticatory border bluntly denticulate. Dorsal cephalic margin posteriorly evenly convex until anterior margin of frontal lobes in lateral view. Clypeus divided into convex posterior region and anterior

sharply inclined margin in lateral view; ommatidia large. Ventral cephalic sculpturing foveolate-rugulose.

Mesosomal dorsal margin evenly convex in lateral view; pronotum anteroventrally angulose, ventral sulcus present; promesonotal suture obsolescent; mesosoma mostly smooth laterally, with sparse punctae and low rugulae; mesosomal dorsum mostly smooth with lateral punctae; metanotal sulcus distinctly impressed as series of contiguous depressions, wider than promesonotal suture. Anepisternum mostly indistinct, sometimes delimited posteriorly by series of brief longitudinal impressions; strigulae present on posteroventral metapleuron; propodeal declivity broadly concave in lateral view, propodeal spiracle separated from declivity by less than one spiracular diameter, propodeal declivity glabrous. Petiole compressed in lateral view, dorsal margin shorter than anterior margin, spiracle situated below anterolateral process, anterior ridge present; postpetiolar process V-shaped in anterior view, with two lateral lobes; gaster mostly smooth with sparse punctae on postpetiole and punctulae on fourth abdominal segment. Fore coxa mostly smooth, some transverse strigulae present along posteroapical region; basal fore tarsal segment with a series of stout setae opposite strigil, dorsally smooth with punctulae; apex of second fore tarsal segment with 4 stout setae; fore tarsal segments 2-4 slightly longer than wide; metacoxal dorsum unarmed. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, gaster brown; mandibles, antennae, legs ferruginous brown.

Queen. Metrics ($n = 1$): HL 0.90, HW 0.76, ML 0.39, SL 0.79, ED 0.18, WL 1.18 mm. CI 0.85, SI 1.04, MI 0.51, OI 0.24. As worker, except for clearly defined anepisternum, with small elongate region of longitudinal parallel carinulae just below

tegula; katapisternum with some transverse-oblique strigulae along posterior margin. Nota and dorsal propodeal surface smooth, with sparse punctulae laterally; declivity glabrous.

Male. Metrics ($n = 1$): HL 0.67, HW 0.59, ML 0.33, SL 0.36, ED 0.29, WL 1.14 mm. CI 0.88, SI 0.61, MI 0.567, OI 0.49. See Mann, 1921.

Comments. This is the only known species of *Gnamptogenys* from the Fiji Islands. It has been reported from the islands of Viti Levu, Vanua Levu, Kadavu, and Taveuni (Mann, 1921). The Nausori series was found in a rotten stick in leaf litter; the Kadavu specimens were taken from sifted rainforest leaf litter.

Specimens examined. FIJI. Kadavu, Mt. Korogatule, nr. Matasawalevu, 300m, 18/59'S 178/28'E, 4-vii-1987, G. Monteith, 2w ANIC; Kadavu, Vanua Ava, 1w MCZC; Vanua Levu, Lasema, 1q 2w MCZC, 1w ANIC; Viti Levu, Nausori Highlands, SW Viti Levu, Nasaucoko to Bukuya, 30/v-3/vi-1972, W.L. Brown, 8w 1q 1m MCZC, 2w BMNH; Viti Levu, Waiyanitu, W.M. Mann, 1w LACM.

***Gnamptogenys crenaticeps* (Mann)**

(Fig. 13)

Wheeleripone crenaticeps Mann, 1919:285, Fig. 4. Syntype workers: Solomon Islands, Isabel Island, Fulakora (Mann) (MCZC) [Examined].

Gnamptogenys crenaticeps (Mann); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Scape surpasses posterior cephalic margin by at least twice apical width; third antennal segment longer than wide; frons longitudinally strigulose, densely rugulo-punctate laterally; promesonotal suture fine, partially impressed; metanotal sulcus fully developed but fine; metacoxal dorsum with low triangular tooth. Subpetiolar process roughly triangular in lateral view, projecting anterad, ventrally parallel sided, not cuneiform. Endemic to Solomon Islands.

Worker. Metrics ($n = 1$): HL 0.88, HW 0.70, ML 0.44, SL 0.80, ED 0.12, WL 1.10 mm. CI 0.80, SI 1.14, MI 0.63, OI 0.17. Head elongate in frontal view, lateral margins broadly convex, posterior margin medially concave; anterior clypeal margin convex, lamella convex with median convex lobe; vertex mostly smooth, gradually curving onto frons; frontal lobe leaves dorsal lobe of torulus partially exposed; scape gradually widens apically, slightly arched basally, punctulate, surpassing posterior cephalic margin by at least twice apical width; first funicular segment longer than wide; frons longitudinally strigulose, densely rugulose-punctate laterally; clypeus longitudinally strigulose; mandibular dorsum shining and shallowly punctate, masticatory border denticulate. Eye hemispherical with reduced diameter (OI 0.17), but ommatidia large.

Pronotum anteroventrally pointed, ventral sulcus present; promesonotal suture fine, well impressed along half of pronotal width, absent along other half; metanotal sulcus slightly broader, well impressed; anepisternum indistinct; katepisternum with anterior sulcus. Dorsal mesosomal margin broadly convex in lateral view, metanotal sulcus slightly impressed; mesosoma mostly smooth, with sparse shallow punctae; brief longitudinal to oblique carinulae present around propodeal spiracle and metapleural ventral margin; metapleural propodeal sulcus impressed, forming broken

series of fine lines; propodeal declivity flat, higher than wide, glabrous, without denticles or ridges, propodeal spiracle on rounded elevation, projecting slightly beyond declivity in lateral view, declivitous propodeal margin relatively straight, forming obtuse angle with dorsal margin in lateral view. Petiole in lateral view erect, dorsal margin convex, shorter than broadly convex anterior margin; subpetiolar process roughly triangular, projecting anterad; petiolar spiracle situated below anterolateral process, anterior ridge forms low transverse crest; postpetiolar process forming V-shaped overturned lip in anterior view, slightly swollen laterally; gaster mostly smooth. Basal fore tarsal segment with single stout seta opposite strigil, dorsum smooth with some punctae; second segment with four stout apical setae; segments 2-4 as long as wide; metacoxal dorsum with low triangular tooth. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster dark brown; mandibles, scape, legs ferruginous brown.

Queen and male. Unknown.

Comments. *G. crenaticeps* could be mistaken for a member of the *epinotalis* group on first examination because of the petiolar node shape, reduced eyes, indistinct anepisternum, well-defined katepisternum, and the close distance of the propodeal spiracle from the declivity. The antennal scapes in the *epinotalis* group do not surpass the posterior cephalic border, the subpetiolar process is subquadrate in shape, and there is more sculpturing on the body such as strigulae and punctate. Nevertheless, some of the shared characteristics hint at a close relation with the *epinotalis* species. This species is still only known from the type series, found by Mann beneath a stone.

Specimens examined. SOLOMON ISLANDS. Isabel, Fulakora, W. Mann, 1w MCZC.

***Gnamptogenys lucida* (Mann)**

(Fig. 11)

Wheeleripone lucida Mann, 1919:285. Holotype worker by monotypy: Solomon Islands, Malaita Island, Auki (USNM) [Examined].

Gnamptogenys lucida (Mann); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Antenna bicolored with four apical segments white and the rest ferruginous. Promesonotal suture and metanotal sulcus both impressed as fine transverse lines, rest of mesosomal dorsum smooth. Postpetiolar process forming two contiguous convexities with brief posteromedian carina in ventral view. Metacoxal dorsum armed.

Worker. Metrics. Holotype: HL 0.87, HW 0.68, ML 0.40, SL 0.79, ED 0.07, WL 1.05 mm. CI 0.78, SI 1.16, MI 0.59, OI 0.10. Head with longitudinal strigulae medially and punctate laterally in frontal view; anterior clypeal margin with projecting median convexity. Pronotum with blunt anteroventral denticle in lateral view; promesonotal suture and metanotal sulcus impressed as fine transverse lines; subpetiolar process triangular; postpetiolar process forms two contiguous convexities

in ventral view, with brief posteromedian carinae. Mesosoma, petiole, and abdomen smooth. Fore tarsal base with one seta; metacoxal dorsum armed.

Queen and male. Unknown.

Comments. There are only two species of *Gnamptogenys* with white-tipped antennae: *G. albiclava* and *G. lucida*. *G. albiclava*, another Solomon Island endemic, is larger (HL > 1.00; WL > 1.50 mm) and has a lower petiolar node and a longitudinally costulate mesonotum and lacks a denticle or lobe on the metacoxa. *G. lucida* has more globulose eyes than *G. albiclava*, with relatively larger ommatidia. The mandibles of *G. lucida* are not as slender as in *G. albiclava* and the petiolar node of *G. lucida* is more compressed.

Specimens examined. SOLOMON ISLANDS. Malaita, Auki, 1w USNM.

***Gnamptogenys preciosa* sp. n.**

(Fig. 14)

Diagnosis. Eyes subglobulose; head elongate (CI 0.69); scapes slender, surpassing posterior cephalic margin by more than two apical widths, smooth with sparse punctae; clypeal lamella convex with median lobe. Petiole reclined in lateral view, anterior margin straight, dorsal margin convex and slightly overhanging concave posterior margin, spiracle on anterolateral process, not below it; subpetiolar process forming narrow anteriorly projecting lobe; metacoxal dorsum unarmed. Endemic to Solomon Islands.

Type material. Holotype worker. Solomon Islands: Guadalcanal, Mt. Austen, ix-xi-1964, P. Greenslade 21478. Deposited in ANIC. Paratype. One dealate queen with same data as holotype deposited in ANIC.

Worker. Metrics. Holotype: HL 1.07, HW 0.74, ML 0.48, SL 1.13, ED 0.14, WL 1.48 mm. CI 0.69, SI 1.53, MI 0.65, OI 0.19. Head markedly elongate in frontal view, lateral margins subparallel; posterior margin with shallow median concavity; anterior clypeal margin convex; vertex mostly smooth; occipital lamella present; occipital lobe absent; frontal lobe projecting dorsolaterally, with convex anterior margin and straight posterior margin; scape slender, surpassing posterior cephalic margin by more than two apical widths, smooth with sparse punctae, shaft slightly enlarged preapically; first funicular segment longer than wide. Frons rugose-punctate, area posterad of frontal triangle bulging, noticeably higher than surrounding surface; clypeal lamella convex, with median lobe; mandibles dorsally smooth, sparsely punctae, masticatory border denticulate. Eye subglobulose, reduced in diameter, ommatidia large.

Pronotum mostly smooth, laterally with shallow foveolae, anteroventral corner rounded; promesonotal suture impressed as fine line; mesonotum mostly smooth with sparse punctae and strigulae; metanotal groove indistinct; anepisternum semirectangular, not distinctly separated from metapleuron by suture; metapleuron relatively broad, longitudinally strigulose; propodeum laterally mostly smooth, spiracle separated from declivity by less than one spiracular diameter, propodeal declivity smooth; propodeal dorsum and declivitous margin respectively broadly convex, almost straight in lateral view. Petiole reclined in lateral view, anterior margin straight, dorsal margin convex and slightly overhanging concave posterior

margin; subpetiolar process forming narrow anteriorly projecting lobe, anterior ridge present, spiracle situated on anterolateral process, not below it. Postpetiolar process straight in anterior view, ventrally convex; petiole and gaster mostly smooth, some strigulae present along anterior petiolar surface. Fore coxa smooth laterally; basal fore tarsal segment smooth with sparse punctulae, single stout seta situated opposite strigil; second fore tarsal segment with four stout apical setae; fore tarsal segments 2-4 longer than wide; denticle of tarsal claws reduced; meso- and metacoxae dorsally transversely strigulose; metacoxal dorsum unarmed. Dorsum of thorax, and abdominal segments 1-4 usually with scattered erect to subdecumbent hairs. Head, mesosoma light brown; petiole, gaster ferruginous; legs, antenna, mandibles ferruginous yellow.

Queen. Metrics ($n = 1$): HL 1.08, HW 0.76, ML 0.51, SL 1.12, ED 0.19, WL 1.59 mm. CI 0.70, SI 1.47, MI 0.67, OI 0.25. Sculpturing more defined than worker. Pronotum laterally foveolate; mesopleuron obliquely strigulose; mesonotum longitudinally strigulose; axilla with large punctae on smooth background; scutellum convex, relatively prominent, with median longitudinal sulcus and some punctae, posteriorly with transverse parallel carinulae; metapleuron longitudinally strigulose, metanotum with oblique to longitudinal strigulae.

Male. Unknown.

Comments. This is one of the most striking and distinct of all Old World *Gnamptogenys* due to its very elongate body, posteriorly inclined petiolar node and bulging eyes. The summit of Mt. Austen, the type locality, is only 410m high. Most of the area surrounding Mt. Austen has suffered extensive deforestation in recent years.

Etymology. The species name is derived from the Latin *pretiosus*, meaning “dear” or “precious” and alludes to the aesthetic appeal of this ant.

***Gnamptogenys solomonensis* sp. n.**

(Fig.15)

Diagnosis. Frons with longitudinal costulae; eyes subglobulose, ommatidia relatively large. Dorsal margin of mesosoma with anterior convexity in lateral view formed by promesonotum, abruptly ending at broad and concave metanotal sulcus. Postpetiolar process V-shaped in anterior view, with two lateral denticle-like lobes connected in varying degrees to lower intermediate lobe by ridges; metacoxal dorsum unarmed.

Endemic to the Solomon Islands.

Type material. Holotype worker. Solomon Islands, Kolombangara Island, E Kuzi, 305m, 3-9-1965, P.M. Greenslade. Deposited in ANIC. Paratypes. One worker and one dealate queen with same data as holotype deposited in ANIC.

Worker. Metrics. [Holotype] Paratypes ($n = 5$): HL [0.81] 0.83-0.88, HW [0.61] 0.61-0.66, ML [0.39] 0.41-0.44, SL [0.89] 0.91-1.05, ED [0.16] 0.17-0.18, WL [1.05] 1.05-1.18 mm. CI [0.75] 0.73-0.76, SI [1.44] 1.49-1.60, MI [0.64] 0.64-0.67, OI [0.26] 0.26-0.31. Head elongate in frontal view, oval and wider posteriorly than anteriorly, posterior margin with median concavity; clypeal lamella angular medially; occipital ridge present, no lobe or lamella; vertex relatively flattened, mostly smooth with few small strigulae; frons longitudinally costulate with sparse piligerous punctae, medially with longitudinal sulci that anastomize laterally; frontal lobe with

flattened dorsal surface, exposing dorsal lobe of torulus; scape surpasses posterior cephalic margin by more than two apical widths, shaft relatively straight with slight preapical thickening, dorsum smooth; first funicular segment approximately twice as long as wide; scape with subdecumbent hairs, pubescence absent; frons with longitudinal strigulae and some punctae; clypeus mostly smooth, with brief longitudinal strigulae posteriorly and anteriorly. Eye not reduced, cross section subglobulose, ommatidia large. Mandibular dorsum mostly smooth with sparse punctures, masticatory border finely denticulate.

Pronotum smooth, with sparse piligerous punctulae, anterolaterally with few strigulae; pronotum with bluntly angular anteroventral corner in lateral view, ventral sulcus present; mesonotum, sides and dorsum of propodeum with shallow transverse strigulae; anepisternum trapezoidal, relatively narrow, distinctly delimited; katepisternum mostly smooth with low rugulae. Dorsal margin of mesosoma with anterior convexity in lateral view formed by promesonotum, abruptly ending at broad and concave metanotal sulcus; promesonotal suture distinctly impressed as fine line; propodeal dorsal margin broadly convex in lateral view, declivity relatively straight; propodeal spiracle separated by less than one spiracular diameter from declivity in lateral view. Petiole erect in lateral view, dorsal margin shorter than height of anterior margin, spiracle slightly below anterolateral process, anterior crest present; subpetiolar process triangular, projecting anteriorly in lateral view, ventral edge narrow; petiole and gaster mostly smooth, some undulations and strigulae may be present on anterior dorsum of petiole; postpetiolar process V-shaped in anterior view, with two lateral denticle-like lobes connected in varying degrees to lower intermediate lobe by ridges, projecting anterad. Fore coxae smooth laterally; basal

fore tarsal segment dorsally smooth, ventrally with single stout seta opposite of strigil; second fore tarsal segment with four stout apical setae; metacoxal dorsum unarmed. Dorsum of thorax, and abdominal segments 1-4 usually with scattered erect to subdecumbent hairs. Body ferruginous brown; mandibles and legs beige to pale yellow; antennae and coxae orange.

Queen. Metrics (n=2): HL 0.80, 0.89; HW 0.59, 0.66; ML 0.35, 0.40; SL 0.84, 1.01; ED 0.17, 0.21; WL 1.00, 1.21 mm. CI 0.74, 0.61; SI 1.43, 1.54; MI 0.59, 0.61; OI 0.29, 0.31. Pronotum with low transverse strigulae along anterior margin, rest mostly smooth with sparse shallow punctae; meso- and metanotum longitudinally strigulose, axillae punctate; propodeal dorsum transversely strigulose, declivitous face smooth.

Male. Unknown.

Comments. The only other *Gnamptogenys* with a trilobed sternal postpetiolar process is *G. albiclava*, which has a process with an anterior concave margin, with two lateral lobes and a small median denticle. The broad metanotal sulcus and bulging compound eyes with relatively large ommatidia of *G. solomonensis* make it easy to recognize.

Etymology. The species name is derived from the name of the collection locality.

Additional specimens examined. SOLOMON ISLANDS. Guadalcanal, Mt.

Jonapau, 762m, 4-v-1965, P. Greenslade, 2w BMNH; Guadalcanal, Mt. Jonapau,

793m, 4-v-1965, P. Greenslade, 1w 1q MCZC, 1w MIZA; Guadalcanal, Mt. Gallego,

914m, 12-vii-1965, "Mass Forest," P.N. Lawrence, Roy. Soc. Exped. Brit. Mus.

1966-1 131-160, 1q LACM.

***coxalis* group**

Worker diagnosis. Eye generally convex; scape surpassing median posterior cephalic margin by at least one apical width. Mesosoma with relatively evenly convex dorsal margin in lateral view; promesonotal suture and metanotal sulcus absent to weakly impressed; anepisternum broad or narrow, distinct on all sides; metapleuron separated from propodeum by broad and arching sulcus; propodeal denticles usually present. Petiolar node with convex dorsal margin in lateral view, anterior crest present.

Worker description. Head longer than wide in frontal view, posterior margin ranging from concave to straight, occipital lobes present or absent; anterior clypeal margin generally convex to medially bluntly angular (occasionally straight); frontal lobe always covering dorsal lobe of torulus; scape surpassing median posterior cephalic margin by at least one apical width; scape longitudinally rugulose to smooth; third and fourth antennal segments usually longer than wide. Clypeus frequently longitudinally strigulose; mandible triangular, cuneiform in cross section, posterior masticatory border and internal margin noticeably thinned and laminate, dorsum usually longitudinally rugulose, masticatory border denticulate. Eye convex, not reduced (except in *G. meghalaya*), never flattened, ommatidia normal to slightly reduced; occipital lamella present; occipital lobe present or absent; dorsal cephalic margin continuously convex in lateral view. Pronotum laterally with bluntly angular anterolateral corner, posterior lobe present, ventral sulcus absent, humeral angle present (except in *G. grammodes*); basisternal lobe of prosternum short, apex bluntly rounded, ventral margin convex in lateral view; prosternal process with posteriorly

projecting lobe, apically bluntly bidentate, tapering ventrally in posterior view; furcasternal ridges widely separated by lobe and slightly projecting beyond ventral basisternal surface; furcasternum with posterodorsal convexity and ridge; lateral lobes of endosternum with narrow base. Anepisternum broad or narrow, distinct on all sides; mesopleural (indistinct in *G. coxalis*) and mesometapleural sutures well developed; katepisternum with thick anteroventral lamella and well developed sulcus; promesonotal suture and metanotal sulcus absent to weakly impressed; metapleuron separated from propodeum by broad and arching sulcus; propodeal spiracle at same level as surrounding cuticle, separated at least 1.5 spiracular diameters from declivity in lateral view, propodeal denticle just above or more than one diameter above longitudinal line drawn through upper margin of spiracle; propodeal declivity mostly smooth, posterolaterally partially or entirely delimited by low crests (greatly expanded in some species, reduced or absent in *G. macretes*, *G. biroi*, *G. grammodes*); propodeal denticles low, usually triangular, occasionally absent; mesosoma with evenly convex dorsal margin in lateral view.

Petiole with convex dorsal margin in lateral view; subpetiolar process variable in shape, spiracle situated below anterolateral process, petiolar anterior crest present; postpetiolar process concave in anterior view, convex in ventral view; fourth abdominal segment lacking ventral stridulitrum. Basal fore tarsal segment with varying degrees of longitudinal strigulae dorsally; ventrally with at least one stout seta, alone or followed by row of setae, either stout or slender, opposite strigil; fore tarsal segments 2-4 reduced in length, almost as long as wide; metacoxal tooth well developed, always present. Scape, dorsum of thorax, and abdominal segments 1-4 usually with scattered erect to subdecumbent hairs.

Included species: *G. bicolor*, *G. binghamii*, *G. biroi*, *G. bulbopila*, *G. costata*, *G. coxalis*, *G. crassicornis*, *G. fontana*, *G. gabata*, *G. gastrodeia*, *G. grammodes*, *G. helisa*, *G. macretes*, *G. meghalaya*, *G. menadensis*, *G. niuguinense*, *G. ortostoma*, *G. palamala*, *G. paso*, *G. posteropsis*, *G. scalpta*, *G. toronates*, *G. treta*. **Dissected species:** *G. costata*, *G. menadensis*.

Comments. This group, with over twenty species, is the most species rich in Southeast Asia. It is also the most morphologically plastic of all species groups, with notable variation in size, development of the occipital lobes, position of the eyes, sculpturing, configuration of the fore tarsal setae, and gastral specializations. Their defining apomorphy is the presence of well-defined propodeal denticles. They share with the *taivanensis* group the posterolateral ridges on the propodeum [37:1], which may be diminished in some species. The lamellate lobe frequently found along the basal mandibular margin in species of the *coxalis* group can also be found in some New World species groups, such as in the *triangularis* group. The rest of the mandible remains thick, with the thickening describing a convexity along its posterior internal margin, suggestive of subtriangular development. No species of the *coxalis* group, or any other Old World *Gnamptogenys* for that matter, have mandibles that stray far from the triangular shape, in contrast to some of the Neotropical species, such as *G. schmitti* Forel, with falcate mandibles. The mesosomal sculpture of the *coxalis* group is generally foveolate to punctate over a smooth to strigulose ground sculpture. The mesosomal and petiolar node dorsum is usually smoother medially than laterally, with less foveolae and punctae.

Key to workers of the *coxalis* group

1. Fourth abdominal tergite with abundant costae, strigulae, or striae, this sculpture usually extending at least over the anterior third or more of the segment, sometimes mostly limited to sides (next to sternite) 2
 - Fourth abdominal tergite mostly either smooth or punctate, sculptured otherwise than in the preceding couplet; traces of strigulae or rugulae, if present, are restricted to small area immediately around spiracle 13
2. Fourth abdominal tergite with distinct, sharply defined costae or strigulae covering all of surface 3
 - Fourth abdominal tergite with striae and strigulae mostly limited to sides (next to sternite), dorsum tending to smooth, with longitudinal sculpture, such as costae, reduced to shallow undulations 10
3. Postpetiolar tergite in dorsal view finely striate, at least along posterior half 4
 - Postpetiolar tergite not striate; costate, foveolate or otherwise 5
4. Scape longitudinally strigulose; propodeum transversely striate (New Guinea) *niuguinense* sp. n.
 - Scape mostly smooth; propodeum foveolate (New Guinea) *macretes* Brown
5. Dorsum of fourth abdominal tergite with anterior half transversely costate and swollen, posterior half longitudinally costate and not swollen (Borneo) *palamala* sp. n.
 - Dorsum of fourth abdominal tergite without transverse costae and not swollen .. 6
6. Compound eyes placed within one-half or less their diameter from the vertex, as seen in lateral view (Fig. 34a); postpetiolar sternum with a posteromedian

- longitudinal keel that projects slightly beyond posterior sternal margin (western Malaysia to Borneo, Philippines) *posteropsis* (Gregg)
- Compound eyes separated from vertex by more than one diameter (Figs. 19a, 20a); postpetiolar sternum without a posteromedian keel 7
7. Subpetiolar process lobe like or subquadrate in lateral view (Figs. 19a, 20a) 8
- Subpetiolar process tapering anterad to narrow acute point (Fig. 17b, 36a) 9
8. Pronotal dorsum with transverse rugulae that arch anterad and become longitudinal along posterior half and on mesonotum; propodeal dorsum transversely strigulose (Sri Lanka) *coxalis* (Roger)
- Pronotal dorsum foveolate to areolate, without rugulae as described previously; propodeal dorsum foveolate or areolate, without strigulae (Myanmar to Sulawesi, Philippines) *costata* (Emery) (in part)
9. Cephalic dorsum mostly smooth with scattered punctae/foveolae; clypeal lamella in frontal view with an anterior median convexity surrounded by two lateral points (Borneo) *toronates* sp. n.
- Cephalic dorsum densely foveolate; clypeal lamella with a single median blunt angle (New Guinea to northern Queensland) *biroi* (Emery) (in part)
10. Discal area of pronotum with low longitudinal striae; anterior two-thirds to one-half of postpetiolar dorsum transversely striate, the rest longitudinally striate (Borneo) *scalpta* sp. n.
- Discal area of pronotum mostly smooth, surrounded by foveolae or punctae; posteromedian area of postpetiolar tergite mostly smooth, with scattered punctae 11

11. Fourth abdominal tergite in dorsal view (view of greatest length) with straight to broadly convex lateral margins (Fig. 46a; Myanmar to Sulawesi, Philippines) *costata* (Emery) (in part)
- Fourth abdominal tergite funnel shaped, with anterolateral concave margins (Fig. 46b) 12
12. Antennal scapes deeply strigulose; petiolar node in dorsal view with smooth cuticle between foveolae; punctae of fourth abdominal tergite smooth (Sumatra to Java) *crassicornis* (Forel)
- Antennal scapes mostly smooth; petiolar node with transverse rugulae between foveolae; punctae of fourth abdominal tergite hatched with fine parallel striae (Borneo) *helisa* sp. n.
13. Fourth abdominal sternite mostly smooth, scattered punctae or punctulae may be present but do not form ridges or strigulae (Fig. 47c) 14
- Fourth abdominal sternite with transverse rugae or rugulae on most of surface (Fig. 47b) 17
14. Head in dorsal view elongate and relatively parallel sided; anterior margin of the clypeal lamella mostly straight. (Note: do not confuse lamella with labrum.) (Fig. 31b; Thailand to Borneo) *ortostoma* sp. n.
- Head in dorsal view not noticeably elongate, sides usually broadly convex, clypeal lamella with an anteromedian blunt point or angle 15
15. Occipital lobe in lateral view evenly convex, without acute angles (Fig. 37); metacoxal tooth short and triangular; subpetiolar process ending in an acutely pointed anteroventral point (Borneo) *treta* sp. n.

- S Occipital lobe not evenly convex, usually presenting upper as well as lower angles (Figs. 16a, 33a); metacoxal tooth elongate and tapering to an acute point; subpetiolar process ending anterad in a rounded angle or lobe 16
16. Cephalic dorsum and sides with fine longitudinal striae on cuticle between foveolae; striae frequently present on katepisternum; HL more than 1.50; WL more than 2.00 mm (western Malaysia) *paso* sp. n.
- Cuticle between foveolae on cephalic dorsum and sides, as well as katepisternum, smooth; HL less than 1.50; WL less than 2.00 mm (India to New Guinea, Philippines) *binghamii* (Forel) (in part)
17. Occipital lobes posteroventrally protuberant; eyes separated from posterior cephalic margin, excluding lobes, by one ED or less (Figs. 24, 29a) 18
- Occipital lobes modest, usually more ventrally protuberant; eyes separated from posterior cephalic margin by more than one ED (Figs. 16a, 25a) 20
18. Fourth abdominal tergite areolate and with a basal median tumosity (Fig. 24; Sumatra to Java) *gastrodeia* sp. n.
- Fourth abdominal tergite mostly smooth, no tumosity present 19
19. Full adult color generally piceous to black over body; mesosomal dorsal margin in lateral view devoid of standing hairs, one or two at most; metacoxal spine robust and hooked; mesonotum with a narrow, mostly smooth median strip (western Malaysia to New Guinea, Philippines) *menadensis* (Mayr)
- Full adult color usually with gaster (and often the head) piceous, mesosoma much lighter, orange-ferruginous; mesosomal dorsal margin with abundant, scattered standing hairs; metacoxal spine usually straight and slender;

- mesonotum with median strip of longitudinal rugulae (Myanmar to Java, southern China) *bicolor* (Emery)
20. Occipital lamella auriculate to bluntly angular in lateral view; occipital lobe lacking (Fig. 25a) 21
- Occipital lamella generally parallel sided and convex; occipital lobe present or absent (Fig. 16a) 22
21. Postpetiolar tergite transversely strigate or mostly smooth with scattered punctae on anterior half and longitudinal carinulae on posterior half to one-third (New Guinea) *grammodes* Brown
- Postpetiolar tergite foveolate on basal two-thirds and foveolate-rugulose on posterior one-third (New Guinea to northern Queensland) *biroi* (Emery) (in part)
22. Antennal scapes mostly smooth, usually with scattered punctae, sometimes with faint and brief strigae 23
- Antennal scapes mostly strigate to strigulose, smooth areas restricted to less than one-fourth of area (India to Sulawesi, Philippines) *binghamii* (Forel) (in part)
23. Humeral area mostly evenly convex, humeral angle developed as a brief low ridge; petiolar node in lateral view elongate (Fig. 18c); scapes with basally bulbous, semi erect hairs (Philippines) *bulbopila* sp. n.
- Humeral area with a distinct concavity opposite of the occipital lobes, humeral angle well developed; petiolar node approximately dome shaped in lateral view; standing hairs on scape slender, without a swollen base 24
24. Occipital lobe in lateral view relatively broad (Figs. 22a, 23a) 25

- Occipital lobe relatively narrow (Figs. 16a, 28a) 26
- 25. Subpetiolar process in lateral view subquadrate with an anteroventral lobe; posterior metapleural lobes greatly expanded, partially surrounding the propodeal declivity; anterior margin of clypeal lamella with a median angle (western Malaysia to Borneo) *gabata* sp. n.
- Subpetiolar process in lateral view subquadrate with an acute posterior angle; posterior metapleural lobes lacking or very low, never partially surrounding the propodeal declivity; anterior margin of clypeal lamella with a median convex lobe (Borneo) *fontana* sp. n.
- 26. Antennal scapes without any trace of longitudinal strigae; occipital lobes lacking; cephalic dorsum rugulose-punctate with smooth ridges between foveolae and rugulae (western India) *meghalaya* sp. n.
- Antennal scapes usually present traces of strigae; occipital lobes modest but distinct; cephalic dorsum rugulose-punctate with striae on ridges between foveolae and rugulae (India to New Guinea, Philippines) *binghamii* (Forel) (in part)

***Gnamptogenys bicolor* (Emery)**

(Fig. 45a)

Ectatomma (Stictoponera) bicolor Emery, 1889:493. Syntype workers: Birmania [Myanmar], Tienzo (Fea) (MCSN) [Examined].

Ectatomma (*Stictoponera*) *coxale* var. *bicolor* Emery; Emery, 1895:458. Considered a variety of *coxalis* (Roger, 1860).

Ectatomma (*Stictoponera*) *bicolor* var. *minor* Forel, 1900:317. Syntype workers: Birmania [Myanmar] (MHNG) [Not examined]. Synonymized by Brown, 1950:245.

Stictoponera menadensis subsp. *bicolor* (Emery); Emery, 1911:48. Placed in *Stictoponera* and considered a subspecies of *menadensis* (Mayr, 1887).

Stictoponera bicolor (Emery); Brown, 1950:245. Raised to species.

Gnamptogenys bicolor (Emery); Brown, 1958: 227. Placed in *Gnamptogenys*.

Gnamptogenys bannana Xu and Zhang, 1996:55. Holotype worker: China, Yunnan, Menglun Town (Niu Yao) (SNUC) [Not examined]. **New synonymy.**

Diagnosis. Occipital lobes prominent, projecting posteroventrally in lateral view; eyes situated on posterior half of head, usually less than one eye diameter from vertex. Mesosomal dorsum densely foveolate to areolate, with median longitudinal strip of strigae-rugulae extending from posterior pronotum to mesonotum. Mesosomal dorsal margin with more than ten standing hairs in lateral view. Propodeal declivitous face medially with raised posteriorly diverging surface that usually ends before anterior margin in small oval depression. Metacoxal tooth slender and straight.

Worker. Metrics ($n = 10$): HL 1.03-1.46, HW 0.86-1.17, ML 0.53-0.69, SL 0.79-1.17, ED 0.21-0.28, WL 1.37-1.96 mm. CI 0.78-0.88, SI 0.92-1.03, MI 0.57-0.66, OI 0.22-0.27. Head with broadly convex lateral margins that converge anteriorly in frontal view, posterior margin relatively straight with lateral protruding

occipital lobes, anterior margin of clypeal lamella forming blunt angle, sometimes projecting anterad as narrow lobe with straight to weakly sinuate sides; frons rugulose-foveolate with sharp, roughly longitudinal ridges, foveolae with smooth, convex bottoms; frontal triangle divided through middle by longitudinal ridge; frontal lobe with subparallel lateral margin; scape with variable degree of longitudinal strigulae, from very strigulose to mostly smooth; clypeus longitudinally strigose. Occipital lobe prominent, projecting posteroventrally in lateral view; occipital lamella convex, low, with extremities either angular or convex; eye situated on posterior half of head, usually less than one ocular diameter distant from vertex.

Pronotum with lamellate humeral angle, ventral pronotal margin relatively narrow, frequently with sharply angular anteroventral corner, densely foveolate with occasional fine strigulae posterad; promesonotal suture marked as series of transverse depressions; mesosomal dorsum densely foveolate to areolate with median longitudinal strip of strigae-rugulae extending from posterior pronotum to mesonotum; anepisternum narrow, rectangular to cuneiform, usually smooth with some foveolae; katepisternum foveolate, with or without strigulae; metapleuron posteroventrally strigose, anterodorsally with narrow strip of mostly smooth or undulate cuticle; propodeum foveolate, unarmed, declivitous face medially with raised surface that diverges posteriorly, elevated area usually ends in small oval depression before anterior propodeal margin, cuticle surrounding raised area usually smooth. Petiolar node dorsally foveolate, with subquadrate to lobe like ventral process in lateral view; postpetiolar dorsum foveolate, foveolae well impressed, denser anterad than posterad, tergite densely foveolate anterolaterally; postpetiolar sternum transversely strigulose, laterally punctate-foveolate; dorsum of abdominal

segment 4 mostly smooth with scattered punctulae, laterally with scattered punctae. Fore coxa transversely strigulose in lateral view; fore tarsus opposite strigil with single prominent basal seta, occasionally followed apically by row of slender setae; metacoxal tooth straight and slender. Most of body with scattered suberect to subdecumbent hairs. Mesosoma ferruginous to ferruginous brown; head slightly darker; gaster darkest, usually brown to nearly black.

Queen. Unknown.

Male. Metrics ($n = 1$): HL 0.88, HW 0.83, ML 0.47, SL 0.24, ED 0.38, WL 1.70 mm. CI 0.94, SI 0.29, MI 0.57, OI 0.46. Frons mostly areolate in frontal view with oval depression just anterad of median ocellus; with single, sharp ridge extending from depression to posterior end of clypeus. Clypeal shield with median longitudinal sulcus, mostly smooth with lateral ridges; frontal triangle large, smooth bottomed. Occipital lobes modest, subquadrate, not as developed as workers. Pronotum densely foveolate; mesopleuron foveolate, mesopleural suture well impressed; anepisternum with some strigulae, especially posterad. Metapleuron and propodeum densely foveolate. Mesonotum foveolate with some rugosity, scutellum densely foveolate.

Comments. This species shares with *G. menadensis* the protuberant occipital lobes and posteriorly displaced eyes and other features; consequently the two species are easily confused. Brown (1950, 1954b) described the variability in color and other morphological aspects that have caused confusion separating these species, as well as the reasons for the synonymy of *G. minor*. Even though Brown (1954b) cited the smooth promesonotal area in *G. menadensis* versus the strigulose surface in *G. bicolor* as a fairly reliable distinction, he still expressed the possibility of their synonymy. *G. menadensis* can be distinguished from *G. bicolor* in having (1) the

lateral margins of the frontal lobes tending to be straight and parallel to each other; (2) the promesonotum with a smooth longitudinal median area; (3) the propodeal declivity with a parallel-sided raised area; and (4) the metacoxal tooth usually bent close to its base. *G. menadensis* generally has fewer foveolae on the postpetiole, and they are shallower and smaller in diameter than in *G. bicolor*. The sides of the fourth abdominal tergite in *G. menadensis* tend to be smoother with less-developed punctae. The hairs on the mesosomal dorsum of *G. menadensis* are very short, rarely protruding above the foveolae from which they originate. Queens have never been described for *G. bicolor*, notwithstanding its abundance in some areas and the copious amount of material in museums. In the closely related species *G. menadensis*, most reproduction is through gamergates (Gobin, Peeters, and Billen 1998a), so it seems reasonable to expect a similar situation for *G. bicolor*.

Xu and Zhang (1996) described *G. bannana* from a series of workers taken in southern China. They describe it as very close to *G. bicolor* but differing in the development of the occipital lobe, gauge of the foveolate sculpture, and coloration. The color scheme of *G. bannana* can be found in *G. bicolor*, and the development of the occipital lobe also fits *G. bicolor*. The metrics for their type series mostly overlap those of *G. bicolor* specimens found in southern China. The ants were examined in 1997 by the myrmecologist Zhou Shanyi, and he could not find any difference between *G. bannana* and *G. bicolor*. So although the types were not personally seen in the course of this revision, it seems relatively safe to recognize *G. bannana* as a junior synonym of *G. bicolor*.

Most habitat labels indicate mesic, forested habitats, especially rotten wood, as the favorite haunt of this species. One worker was recovered from the stomach of the

frog *Kaloula mediolineata* (Smith). Wu and Wang (1995:36) included *G. bicolor* in a key to the species of *Gnamptogenys* present in China. See Comments under *G. menadensis* for an additional discussion of differences between these two species. For a habitus drawing of *G. bicolor* the reader can consult Figure 29, which is really *G. menadensis* but is suitable on account of the similarities between the two species.

Specimens examined. CHINA. **Hainan:** Tai Pitu[?], 28-vi-1935, H. Gressitt, 1w USNM; Nodua, 15/17-vii-1935; J. Gressitt, 2w USNM. **Hong Kong:** Tai Po Kau Nature Reserve, 22/39'N 114/17'E, 6-vii-1996, R. Snelling 96-11, 21w LACM; Tai Po Kau Nature Reserve, 22/39'N 114/17'E, 12-vii-1996, R. Snelling 96-32, 12w LACM; loc. cit., R. Snelling 96-33, 8w LACM; loc. cit., 4-x-1979, R. Taylor, 3w ANIC; Terry, 1w ANIC. **Kwantung:** Vim Na San, 12-vi-1936, H. Gressitt, 1w USNM. INDIA. **Assam:** Misamari, ii-iv-1944, A.C. Cole, 1w LACM; Garo Hills, iii-1899, Bingham, 1w OXUM. **West Bengal:** Darjeeling, Tiger Hills, 17-iv-1938, T.C. Maa, 2w LACM; Darjeeling, 30-v-1937, T.C. Maal, 1w LACM. INDONESIA. **Bali:** Gitgit Waterfall, 18-iii-1987, H. Imai, Kubota & Iskandar, HI 87-57, 3w ANIC. **Jawa Timur:** Kebun Raya Purwodadi, 20km N Malang 7/48'S 112/44'E, x-1998, F. Ito FI98-270, 2w 1q MIZA; loc. cit., x-1998, F. Ito FI98-269, 2w MIZA; loc. cit., x-1998, F. Ito FI98-268, 2w MIZA; loc. cit., i-1994, F. Ito FI94-36, 4w MIZA. MALAYSIA. **Pahang:** Kuala Lompat Natl. Pk. (MV Lite), 25-viii-1992, D. Furth, 2w MCZC. MYANMAR. Tienzo, v-1886, L. Fea. 4w USNM, 1w MCSN; Upper Myanmar, Ruby Mines, 1220m, 11-1900, Bingham, 1w LACM. THAILAND. **Chiang Mai:** Chiang Dao Cave area, 14-viii-1992, D. Furth, 3w MCZC; Chiang Rai, Fang, Hort. Res. Sta., 15-viii-1992, D. Furth, 2w MCZC; Doi Inthanon Natl. Pk., Vachiratharn Waterfall, 18/58'N 98/48'E, 750m, 9-vii-1996, S. Sonthichai, R.

Snelling 96-65, 8w LACM; Doi Suthep Natl. Pk., Pha Ngoep, 18/81'N 98/94'E, 490m, 15-vii-1996, S. Sonthichai, R. Snelling 96-98, 18w LACM; Mae Wang Dist., Huay Kno Haeng, 450m, 16-vii-1996, S. Sonthichai, R. Snelling 96-105, 21w LACM; Mae Wang Dist., Ban Huai Kho, 360m, 17-vii-1996, S. Sonthichai, R. Snelling 96-121, 14w LACM; Muthatan Falls, 13-viii-1992, D. Furth, 10w MCZC; Doi Sutep, 23-iii-1952, D. & E. Thurman, 1w USNM; Chiang Mai, 300m, 14-vii-1972, E. Ross, 1w CASC. **Kanchanaburi**: River Kwai Resort Hotel, 10/17'N 99/00'E, 100m, P.S. Ward 3124, 1w 1q 1m PSWC; loc. cit., P.S. Ward 3122-7, 2w PSWC. **Trang**: Khao Chong Nature Education Centre, 7/35'N 99/46'E, 21/24-vii-1996, S. Sonthichai, R. Snelling 96-141, 6w LACM; Nam Tok, 10/14'N 99/04'E, 100m, 29-vii-1978, P.S. Ward 3116-4, 2w PSWC.

Undetermined localities: NE Thailand, Chong Mad [?], 1w LACM. VIETNAM. Katum, 20-xii-1967, A. Lewis, 1w LACM; Indo-China, Dong Mo, [50km from Hanoi], 10-ii-1925, F. Silvestri, 9w LACM.

***Gnamptogenys binghamii* (Forel)**

(Fig. 16)

Ectatomma (Stictoponera) binghamii Forel, 1900:317. Syntype workers: Burma [Myanmar] (Bingham) (MHNG) [Examined].

Stictoponera borneensis Emery, 1900b:662. Holotype worker by monotypy: Sarawak (MCSN) [Not examined]. Synonymy by Brown, 1954b:5.

Stictoponera binghami (Forel); Emery, 1911:47. Invalid emendation.

Gnamptogenys binghamii (Forel); Brown, 1958:227. Placed in *Gnamptogenys*.

Diagnosis. Head subquadrate in frontal view, lateral margins broadly convex and subparallel, anterior margin of clypeal lamella with anteromedian lobe convex to bluntly pointed; occipital lobes small or obsolescent. Mesosoma with broadly convex dorsal margins in lateral view, declivitous margin concave; petiolar node with evenly convex dorsal margin in lateral view; ventral petiolar process subquadrate to triangular with posterior angle.

Worker. Metrics ($n = 22$): HL 1.05-1.35, HW 0.86-1.07, ML 0.54-0.65, SL 0.78-1.11, ED 0.16-0.26, WL 1.39-1.78 mm. CI 0.76-0.88, SI 0.88-1.05, MI 0.55-0.65, OI 0.17-0.28. Head subquadrate in frontal view, lateral margins broadly convex and subparallel, anterior margin of clypeal lamella with anteromedian convex to bluntly pointed lobe; frons rugulose-punctate with fine striae on transverse arcs between punctae; clypeus longitudinally strigulose, with strigulae partially extending onto lamella; scape varies from mostly smooth to mostly strigulose; occipital lobes small, occipital lamella well developed, convex to slightly angular at ends.

Mesosoma with broadly convex dorsal margin in lateral view; pronotum with lamellate humeral angle; mesosomal dorsum foveolate with longitudinal median smooth area extending from posterior pronotum to mesonotum; propodeal dorsum densely foveolate, side mostly foveolate, propodeal declivity concave to convex in lateral view, propodeal declivity mostly smooth; propodeal denticles low, triangular or subcylindrical. Dorsal margin of petiolar node usually evenly convex in lateral view, dorsal margin varies from dome shaped to slightly flattened dorsally; dorsum usually densely foveolate; ventral process subquadrate to triangular, usually with

posterior angle; postpetiolar dorsum punctate or foveolate, with posterior band of narrow strigulae; sternum with transverse strigulae; dorsum of abdominal segment 4 mostly smooth with scattered punctulae or punctae, depressions denser and deeper on sides, small strigulose area occasionally present on anterolateral corner, sternum strigulose. Fore coxa mostly smooth anterad in lateral view and transversely strigulose posterad; fore tarsus opposite strigil with single seta followed apically by row of slenderer setae; metacoxal tooth relatively straight. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body color ranging from dark brown to ferruginous; mandibles, antennae, legs lighter colored.

Queen. Metrics ($n = 1$): HL 1.46, HW 1.13, ML 0.75, SL 1.20, ED 0.28, WL 2.07 mm. CI 0.77, SI 1.06, MI 0.66, OI 0.25. Pronotum foveolate; mesopleuron foveolate with low longitudinal striae; mesonotum with scattered punctae and low longitudinal undulations, propodeal dorsum densely foveolate.

Male. Metrics ($n = 1$): HL 0.93, HW 0.82, ML 0.52, SL 0.30, ED 0.33, WL 1.73 mm. CI 0.88, SI 0.37, MI 0.63, OI 0.40. Frons strigulose, becoming irregularly areolate laterally; with longitudinal crest extending from posterior margin of clypeus to anterior margin of median ocellus, clypeus mostly smooth with few longitudinal strigulae, anterior margin of clypeal lamella forming blunt obtuse angle. Pronotum foveolate; mesonotum mostly smooth with few scattered foveolae; mesopleuron mostly smooth with scattered foveolae; metapleuron mostly rugulose; propodeal dorsum areolate-rugulose. Postpetiole mostly smooth with scattered foveolae and low longitudinal strigulae; fourth abdominal tergite smooth.

Comments. *G. binghamii* is the most widely distributed species, found from India to Papua New Guinea, as well as in the Philippines. Most specimens studied fall into

two allopatric morphotypes. Larger specimens have abundant strigulae on the scapes, a convex anteromedian clypeal margin, propodeal denticles with parallel sides, slightly arched and basally bent metacoxal teeth, and smooth cuticle on the dorsoposterior margin of the fourth abdominal tergite. They are found from western Malaysia to Borneo and into the Philippines. Smaller forms bear more resemblance to the syntypes of *G. binghamii* (especially those from Kottiyor, India, MCZC) and tend to have less strigulate scapes, a narrow posterior band of striae on the fourth abdominal tergite, triangular propodeal denticles, straight metacoxal teeth, and the clypeal lamella produced anteromedially as a blunt denticle or angle. This smaller form is found from India to Thailand, with a single specimen recorded from Borneo. The large eastern forms have smaller eyes than the smaller-bodied western populations. Besides these two morphotypes, there are a few specimens from Thailand representing intermediate forms and a nest series of small forms from Borneo with a smooth posterior margin on the fourth abdominal dorsum, strigulose scapes, and a clypeal lamella with an anteromedian point. Specimens from the Philippines and New Guinea have a larger degree of smooth cuticle on the petiolar node and propodeal dorsum, including the fourth abdominal sternite. They may also have a triangular subpetiolar process without a posterior angle.

The illustration of *G. binghamii* in Tang et al. (1995:28) is not *G. binghamii* but could be a member of the *taivanensis* group based on the compressed petiolar node. *G. crassicornis* (of the *coxalis* group) could be confused with *G. binghamii*, but *G. crassicornis* has smaller eyes, a more flattened petiolar dorsum when seen laterally, strigulae on most of the fourth abdominal tergite in lateral view, and antennal segments 3-4 longer than wide. In *G. binghamii* the fourth abdominal tergite when

seen dorsally in full-length view has evenly convex lateral margins that gradually converge with each other posterad; in *G. crassicornis* the tergite is roughly funnel shaped with the anterolateral margins abruptly converging for a short distance before gradually converging posterad. Wheeler and Wheeler (1976:43) described larvae of *G. binghamii* from Sulawesi and Imai et al. (1984) described the karyotype. Viehmeyer (1916:112) described the queen and male of *G. binghamii*, though the male probably represents a different species. A single male from Singapore (H. Overbeck leg) in the MHNG is labeled as a cotype of *Stictoponera binghamii*, yet Forel (1900) described the species from workers only. This male has abundant rugosities on the postpetiolar tergite, fine strigulae on the fourth abdominal tergite, and a triangular subpetiolar process, all characters that are not found on worker-associated *G. binghamii* males. Habitat labels indicate that *G. binghamii* mostly inhabits mesic forested areas, from lowlands to about 1500m, including dipterocarp-mixed forests and pine-oak forest in northern Thailand.

Specimens examined. INDIA. **Assam:** Manas, 200m, C. Besuchet & I. Löbl #25c, 23-x-1978, 1q 1w ANIC. **Kerala:** Kottiyor, Wynaad Taluk, 650m, 7-iv-1969, A.B. Soans & W.L. Brown, 4w 1m MCZC, 1w MIZA; Periyar Lake, 900m, 23-iii-1962, E. Ross & D. Cavagnaro, 1w CASC. **Madras:** Varushanad, Suruli Falls, 550m, 8-xi-1972, C. Besuchet, I. Löbl, Mussard, 1w BMNH. **Meghalaya:** Garo Hills, Rongrengiri, 400m, C. Besuchet & I. Löbl #39b, 3-ix-1978, 4w ANIC, 1w MIZA; Garo Hills, Songsak, 400m, C. Besuchet & I. Löbl #38c, 3-ix-1978, 2w ANIC. INDONESIA. **Kalimantan Barat:** Gunung Palung Natl. Park, Cabang Panti Res. Sta., 100m, 1/15'S 110/5'E, 15-vi/viii-1991, Darling, Rosichon, Sutrisno, 1w MCZC. **Sulawesi Utara:** Dumoga-Bone Natl. Pk., 200-400m, P.M. Hammond BB4, ix-1985,

2w BMNH. Sulawesi Tengah: nr. Morowali, Ranu River area, 27-i/20/iv-1980, P.M. Hammond, 1w BMNH. MALAYSIA. **Negeri Sembilan**: Pasoh Forest Reserve, iii/xi-1994, M. Brendell, K. Jackson, S. Lewis, 4w BMNH; Sungei Menyala Forest Reserve, near Port Dickson, 25-v-1973, W.L. Brown, 5w 1m MCZC, 1w MIZA. **Pahang**: Taman Negara, Tembeling trail, 90-120m, 10/13-iii-1993, I. Löbl & Calame 1a, 1w BMNH; Cameron Highlands, Gunung Jasar, trail 11, 1550m, 24-iii-1993, I. Löbl & Calame 18b, 1w BMNH. **Perak**: Perak Bruak, valley, 5-viii-1964, D.H. Murphy, 1q 1w ANIC. **Sabah**: Danum Valley, ca. 100m, west trail, 18/22-viii-1997, C. Brühl, 5w MIZA; Poring Mtn, Kinabalu Natl. Pk., 550m, 23-x-1978, B.B. Lowery, 2m 1q ANIC; Poring Hot Springs, 500m, 7-v-1987, 7-v-1987. 1w BMNH; Tawau, Quoin Hill, 750ft, 16/18-vi-1978, R.W. Taylor 68.584, 5w ANIC, 1w MIZA; mi 45, Labuk Rd. ex Sandakan, 12/13-vi-1968, R.W. Taylor, 1w ANIC. **Sarawak**: Fourth Division, Gunung Mulu Natl. Pk., P.M. Hammond, J.E. Marshall, v/viii-1978, 1w BMNH; Fourth Division, Gunung Mulu Natl. Pk., I. Hanski, iii-1978, 2w BMNH; Semengoh Forest Reserve, 11km SW Kuching, 1/4-vi-1968, RWT 68.259, 1w 1q BMNH, 1w ANIC; confl. Sun Oyan and Mujong Riv., E. Kapit, 150m, 19-v-1994, I. Löbl & D. Burckhardt 6a, 2w BMNH; confl. Sun Oyan and Mujong Riv., E. Kapit, 50m, 18-v-1994, I. Löbl & D. Burckhardt 5a, 4w BMNH; 1/39'N 113/35'E, 14-ii-1963, E. & A. Emerson, 3w 1q ANIC. **Selangor**: Ulu Gombak, near Kuala Lumpur, 800ft, 11/14-vii-1968; R.W. Taylor, 3w ANIC. PAPUA NEW GUINEA. **Central**: N. District, Kokoda, 305m, 17-i-1971, B.B. Lowery, 7w 1q 1m ANIC, 2w BMNH, 2w MCZC, 2w MIZA. PHILIPPINES. **Negros Oriental**: Dumaguete, Camp 9-v-1927, J.W. Chapman, 3w MCZC; Dumaguete, 5-v-1927, J.W. Chapman, 2w MZCZ, 1w ANIC, 5w USNM; Dumaguete, Camp 20-iv-1931, J.W. Chapman, 4w

USNM, 2w MIZA. THAILAND. **Chiang Mai**: Doi Sutep, 260m, 15-vii-1962, E. Ross, 2w MCZC; Doi Pui, 1420m, 18-iv-1981, W.L. Brown & I. Burikam, 1w MCZC; Chiang Mai, 2-ix-1985, I. Löbl & D. Burckhardt, 1w BMNH. **Petchburi**: Kaen Krachang Natl. Pk., 17/19-xi-1985, I. Löbl & D. Burckhardt, 2w BMNH. **Prachin Buri**: ca. 53km N Krabinbur, 17-ix-1970, G. Ballmer, 1w LACM.

Gnamptogenys biroi (Emery)

(Fig. 17)

Stictoponera biroi Emery, 1901:154. Holotype worker by monotypy: New Guinea, Sattelberg (Biró) (MCSN) [Examined].

Gnamptogenys biroi (Emery); Brown, 1958:227. Placed in *Gnamptogenys*.

Diagnosis. Head subquadrate in frontal view, without occipital lobes; occipital lamella well developed, convex. Petiolar node with small, narrow anteriorly projecting ventral process in lateral view. Dorsum of abdominal segment 4 varying from longitudinally costulate to mostly smooth with scattered punctae, some punctae elongate with brief longitudinal crests, posterolateral margins with brief longitudinal strigulae.

Worker. Metrics ($n = 5$): HL 1.25-1.38, HW 1.05-1.19, ML 0.62-0.73, SL 1.10-1.20, ED 0.28-0.39, WL 1.78-1.98 mm. CI 0.82-0.88, SI 0.99-1.08, MI 0.57-0.66, OI 0.27-0.34. Head subquadrate in frontal view, lateral margins relatively straight, posterior margin straight to slightly concave, posterolaterally rounded, anterior margin of

clypeal lamella projecting anterad into blunt point with slightly sinuate sides; frons densely foveolate with fine strigae frequently present on cuticle between foveolae; clypeus longitudinally costulate; vertex foveolate along anterior margin, mostly smooth posterad and bound by sulcus. Scape varies from mostly smooth to longitudinally strigulose; eye relatively large; no occipital lobes; occipital lamella well developed, convex.

Lateral mesosoma mostly densely foveolate; mesosomal dorsum densely foveolate; anepisterum cuneiform; metapleuron with some longitudinal costulae posteroventrally; propodeal declivity depressed, mostly smooth, sometimes with longitudinal low costulae or rugosity. Petiolar node with small, narrow anteriorly projecting ventral process in lateral view, dorsum foveolate; postpetiolar dorsum longitudinally foveolate to rugulose-foveolate, foveolae round anterad, becoming progressively more elongate posterad; sternum undulate with transverse strigulae, especially anterad, sternum laterally foveolate; dorsum of abdominal segment 4 varies from longitudinally costulate to mostly smooth with scattered punctae, some punctae elongate and with brief longitudinal crests, posterolateral margins with brief longitudinal strigulae. Fore coxa varies from mostly smooth to moderately transversely strigulose in lateral view, most strigulae concentrated apically; fore tarsus opposite strigil with single stout setae, followed apically by row of smaller setae. Dorsum of thorax and abdominal segments 1-4 with abundant erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster brown; mandibles, antennae, legs ferruginous.

Queen. Metrics ($n = 2$): HL 1.28, 1.42; HW 1.14, 1.23; ML 0.66, 0.75; SL 1.14, 1.38; ED 0.39, 0.40; WL 2.02, 2.22 mm. CI 0.89, 0.87; SI 1.00, 1.12; MI 0.58, 0.61;

OI 0.35, 0.33. Pronotum densely foveolate, occasionally with median smooth area; mesoscutum longitudinally rugose-punctate; anepisternum with variable degree of longitudinal strigulae and smooth areas; katepisternum foveolate, posterad frequently with finely strigulose cuticle or mostly foveolate; scutellum densely foveolate to strigulose-punctate; propodeum densely foveolate.

Male. Metrics ($n = 1$): HL 0.90, HW 0.83, ML 0.49, SL 0.47, ED 0.35, WL 1.66 mm. CI 0.92, SI 0.57, MI 0.59, OI 0.42. Frons with low irregular rugulae and large patches of undulate sculpturing, foveolae tend to be areolate posterolaterally in frontal view; frons with fine longitudinal carina extending posterad from posteromedian clypeal margin to eye level in frontal view; clypeus separated from frons by broad sulcus, three ridges cross sulcus joining frons with clypeus; clypeus mostly undulate with scattered strigulae, lamella converging to blunt angle along anterior margin. Pronotum with shallow, flat-bottomed and undulate foveolae, with smooth cuticle between foveolae; mesopleuron mostly smooth with scattered punctae; mesoscutum foveolate, scutellum rugulose-foveolate; propodeum areolate; petiolar node strigulose. Postpetiole mostly smooth with undulations, especially anterolaterally; fourth abdominal tergite smooth.

Comments. This is the only species of *Gnamptogenys* found in Australia, where the genus *Rhytidoponera* Mayr is the dominant ectatommine. *G. biroi* keys out close to *G. grammodes* and may be closely related to it based on similarities in the occipital lamella and the shape of the subpetiolar process. The postpetiolar dorsum of *G. grammodes* differs from that of *G. biroi* in having a posterior strip of longitudinal carinulae and smoother cuticle anterad with punctae and no foveolae as in *G. biroi*. *G. grammodes* has a mostly smooth fourth abdominal tergite and is a smaller ant (HL

> 1.2 mm; WL > 1.60 mm) than *G. biroi*. Nests and individuals of *G. biroi* have been recorded from rotten wood in rainforest and secondary lowland forest.

Specimens examined. AUSTRALIA. **Queensland:** 27km NNE Coen, 13/44'S 143/20'E, 7-viii-1983, 530m, P.S. Ward 6042, 3w 4q 1m PSWC, 2w LACM; W. Claudie R., 12km WNW Lockhart R, 12/44'S 143/14'S, 10-viii-1983, 30m, P.S. Ward 6086, 3w 2q 2m PSWC; 11km ENE Mt. Tozer, 12/43'S 143/18'E, 11/16-vii-1986, T. Weir, 3w 1q ANIC; Iron Range, 12/42'S 143/18'S, 9/15-vi-1971, R.W. Taylor, 2w 1m ANIC. INDONESIA. **Irian Jaya:** PT, Freeport Concession, Wapoga Camp, 3/14'S 136/57'E, 1128m, 25-iv-1998, R.R. Snelling 98-191a, 1q LACM; PT, Freeport Concession, Wapoga Camp, 3/14'S 136/57'E, 1052m, 1-v-1998, R.R. Snelling 98-230b, 1w LACM. PAPUA NEW GUINEA. **Central:** Bisianumu nr. Sogeri, 500m, 15/20-iii-1955, E.O. Wilson, 6w 1q MCZC; Brown River, R.W. Taylor, vi-1962, 4w ANIC. **East New Britain:** "Timber Track," 16km NW Lau, 220m, 12-vi-1962, R.W. Taylor, 1w ANIC, 7w 2q MIZA. Gulf: Tapini, 1000-1200m, R.W. Taylor, viii-1962, 3w 1q ANIC. **Morobe:** Bulolo River Valley, 16km NE Wau, 1100m, R.W. Taylor 2008, vi-1962, 1w ANIC; Bulolo Gorge, 2500ft (762m), 26-xii-1967, B.B. Lowery, 10w ANIC; Bulolo Gorge, 1066m, 20-xii-1967, B.B. Lowery N633, 6w MIZA; Bulolo Gorge, 900m, 5-i-1971, B.B. Lowery, 5w 2q 1m ANIC; Bulolo Gorge, 980m, 19-xii-1970, B.B. Lowery, 9w ANIC; Wau Gorge, 26-xii-1967, B.B. Lowery, 2w ANIC. **Oro:** N. District, Togao Road, 15-v-1973, P.M. Room, 2w ANIC.

***Gnamptogenys bulbopila* sp. n.**

(Fig. 18)

Diagnosis. Head elongate with evenly convex lateral margins in frontal view, posterior margin concave, frons punctate over smooth cuticle; scape punctate with scattered brief longitudinal strigulae, abundant semi erect hairs present, each hair basally bulbous, then gradually tapers apically.

Type material. Holotype worker. Philippine Islands, Misamis Oriental, Minubanan, 1050-1200m, 5/9-iv-1961, H. Torrevillas. Deposited in LACM.

Worker. Metrics. Holotype: HL 1.60, HW 1.18, ML 0.79, SL 1.45, ED 0.29, WL 2.20 mm. CI 0.74, SI 1.23, MI 0.67, OI 0.20. Head elongate with evenly convex lateral margins in frontal view, posterior margin concave, anterior margin of clypeal lamella with median convex lobe, laterally curved; frons punctate over smooth cuticle; clypeus with longitudinal ridges that extend partially onto lamella, shallow median sulcus present; mandibles with low strigulae; occipital lobes lacking; occipital lamella well developed; scape punctate with scattered brief longitudinal strigulae, abundant suberect hairs present, each hair basally bulbous, then gradually tapering apically.

Mesosoma mostly punctate over smooth cuticle; humeral angle poorly developed; mesosomal dorsal margin broadly convex in lateral view; propodeal declivity concave in lateral view, propodeal declivitous face mostly smooth with fine rugosities anterad; propodeal denticle small, triangular. Petiolar node with convex dorsal margin in lateral view, anteriorly broadly convex, higher posterad than anterad; ventral process forming sharply pointed anteriorly projecting triangular lobe;

postpetiolar dorsum punctate over smooth cuticle, sternum punctate with scattered low strigulae; dorsum of abdominal segment 4 mostly smooth with scattered punctulae, sternum strigulose. Fore coxa transversely strigulose in lateral view; fore tarsus opposite strigil with single stout seta followed apically by row of smaller setae; metacoxal tooth low, triangular. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. General body color ferruginous.

Queen and male. Unknown.

Comments. This species is unique among *Gnamptogenys* in having hairs on the scape that have a bulbous base and gradually taper toward the apex. These specialized hairs are only found on the scapes and not elsewhere on the ant.

Etymology. The species epithet is a compound name derived from the Latin words for a fleshy underground stem or bulb, *bulbus*, and for hair, *pilus* (m). It alludes to the uniquely shaped hairs on the scapes.

Gnamptogenys costata (Emery)

(Figs. 19, 46a)

Ectatomma (*Stictoponera*) *costatum* Emery, 1889:494. Holotype worker by monotypy: Burma [Myanmar], Tenasserim (Fea) (MCSN) [Examined].

Ponera rugosa Smith, F., 1857:66. Holotype queen by monotypy: [Malaysia], Borneo, Sarawak (OXUM) [Examined]. Junior primary homonym of *Ponera rugosa* Le Guillou, 1842:318.

Stictoponera costata (Emery); Emery, 1900b:662. Placed in *Stictoponera*.

Stictoponera costata var. *unicolor* Forel, 1901b:335. Syntype workers, queen:

Borneo (MHNG) [Not examined]. Synonymy by Brown, 1954b:7.

Stictoponera rugosa var. *parva* Forel, 1913:6. Holotype worker by monotypy:

Sumatra (MHNG) [Not examined]. Synonymy by Brown, 1954b:7.

Stictoponera costata var. *simalurensis* Forel, 1915:23. Holotype worker by

monotypy: Sumatra (MHNG) [Not examined]. Synonymy by Brown, 1954b:7.

Stictoponera costata var. *pinealis* Wheeler, W.M. 1929:31. Holotype queen by

monotypy: Malaysia, Penang (Silvestri) (MCZC) [Examined]. Synonymy by Brown, 1954b:7.

Stictoponera wallacei Donisthorpe, 1932:447. Replacement name for *Ponera rugosa*

Smith, F. 1857:66. Synonymy by Brown, 1954b:7.

Gnamptogenys costata (Emery); Brown, 1958:227. Placed in *Gnamptogenys*.

Gnamptogenys costata (Emery); Wheeler, G.C. and Wheeler, J. 1976:44. Larva described.

Diagnosis. Frons densely foveolate; clypeus with median area laterally defined by two carinae that extend from anterior margin of frontal lobes to lateral margins of clypeal lamella; occipital lamella usually with sharply angular ends in lateral view. Mesosomal dorsum usually densely foveolate; petiolar node with ventral process usually subquadrate in lateral view, sometimes projecting more anterad than posterad but generally with posterior angle. Dorsum of abdominal segment 4 longitudinally costate, occasionally with elongate foveolae and brief costae, not covering whole tergite.

Worker. Metrics ($n = 12$): HL 1.24-2.11, HW 1.03-1.64, ML 0.61-1.05, SL 1.05-1.88, ED 0.23-0.40, WL 1.67-3.00 mm. CI 0.78-0.90, SI 0.96-1.21, MI 0.56-0.64, OI 0.20-0.27. Head with mostly straight lateral margins in frontal view, posterior margin straight, occipital lobes posterolaterally projecting; clypeal lamella narrow, its anterior margin with slightly projecting median blunt angle, sides bluntly angular; frons densely foveolate, foveolae forming posteriorly diverging rows with costae between them; gena longitudinally strigate; clypeus with median area laterally defined by two carinae that extend from anterior margin of frontal lobes to lateral margins of clypeal lamella; scape mostly smooth to mostly strigulose; occipital lamella usually with sharply angular ends in lateral view. Lateral pronotal face foveolate, foveolae denser anterad than posterad, humeral angles with convex lamella; mesopleuron foveolate; anepisterum subrectangular; metapleuron smooth to longitudinally costate posterodorsally and foveolate anterodorsally; mesosomal dorsum usually densely foveolate, transverse impressions usually obsolescent; propodeal declivity mostly smooth, depressed with posteromedian raised area, denticles small, occasionally absent.

Petiolar node with ventral process usually subquadrate in lateral view, sometimes projecting more anterad than posterad but generally with posterior angle; petiolar dorsum with transversely ovaloid foveolae, sometimes with transverse strigulae; postpetiolar dorsum varies from foveolate on smooth cuticle to longitudinally strigulose-foveolate, anterior foveolae usually round, becoming progressively more elongate posterad and forming irregular sulci along posterior margin, posterior margin usually with median costulate depression; postpetiolar sternum medially smooth with series of fine transverse strigae anterad, laterally foveolate to foveolate

rugulose, with narrow posterior face; dorsum of abdominal segment 4 longitudinally costate, occasionally with elongate foveolae and brief costae, not covering whole tergite. Fore coxa transversely strigulose in lateral view; fore tarsus opposite strigil with row of stout setae, sometimes with single very stout basal seta followed apically by row of less stout setae. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster brown to very dark brown, occasionally almost black; mandibles, antennae, legs slightly lighter colored than rest of body.

Queen. Metrics ($n = 1$): HL 1.76, HW 1.40, ML 0.90, SL 1.36, ED 0.35, WL 2.68 mm. CI 0.80, SI 0.97, MI 0.64, OI 0.25. Pronotum densely foveolate with smooth strip along posterior margin in lateral view; anepisternum rugulose-punctate; katepisternum foveolate with smooth cuticle between depressions, some strigulae present along posterior margin; mesonotum longitudinally rugulose-punctate; metapleuron foveolate; propodeum laterally densely foveolate.

Male. Metrics ($n = 1$): HL 1.17, HW 1.00, ML 0.57, SL 0.32, ED 0.40, WL 2.07 mm. CI 0.86, SI 0.32, MI 0.57, OI 0.40. Frons with dense, shallow areolae; with carina extending from posteromedian margin of clypeus to mid point of compound eye; clypeus prominent, longitudinally strigulose, surrounded by sulcus; anterior clypeal margin evenly convex. Pronotum laterally with dense foveolae; mesopleuron mostly smooth with scattered punctae; mesoscutum foveolate, metanotum rugulose-foveolate; propodeum laterally areolate, propodeal denticles form small blunt lobes. Petiolar node with irregular foveolae and punctae; postpetiole with shallow foveolae laterally, dorsomedially undulate; fourth abdominal tergite mostly smooth, with scattered shallow punctae.

Comments. This widespread species has been found mostly in lowland rainforest, within rotten logs and leaf litter, and foraging. Brown (1954b:9) provided an excellent account of the variability of this species and his justification for the synonymies of the above names. He treats the differences in color, size, and sculpturing on postpetiole. While the mesosomal dorsum is usually densely foveolate, specimens with mostly smooth sculpturing and scattered foveolae/punctae will show up, occasionally from Sulawesi. These specimens also tend to have some oblique strigulae on the sides of the fourth abdominal tergite. Even though Brown (1954b) alluded to the variability of the shape of the occipital lamella (which he calls ears or lobes) there does seem to be a large degree of constancy in the angular shape of the two ends of the lamella. Only rarely is one end convex, and no cases were observed in which both ends are convex.

G. toronates may be confused with *G. costata*, but *G. toronates* has the propodeal spiracle farther away from the propodeal dorsum when seen laterally, the declivitous and dorsal propodeal margins are separated anterad of the denticle, and the subpetiolar process forms an anteriorly projecting sharp lobe. In *G. costata* the denticles are between the two propodeal margins.

Specimens examined. BRUNEI. Brooketon, E. Mjöberg, 1w MCZC. MALAYSIA. **Sabah:** Tawau, Quoin Hill, 229m, 16/18-vi-1968, R.W. Taylor, 68.537, 3w ANIC; mi 43 Labuk Road ex Sandakan, (Lungmanis) 12/13-vi-1968, R.W. Taylor, 3w 1q ANIC; Sepilok Forest Reserve, near Sandakan, 8/10-vi-1968, R.W. Taylor, 3w 1q ANIC; Poring Hot Springs, 500m, 7-v-1987, D. Burckhardt, 1w BMNH; Poring Hot Springs, 600m, 9-vi-1987, D. Burckhardt & I. Löbl (18), 2w BMNH; Poring Hot

Springs, 600m, 7-v-1987, D. Burckhardt & I. Löbl (14a), 1w BMNH. **Sarawak:** Third Division, Belaga, Uma Aging Longhouse, 20-iii-1970, J. Tobler, 4w CASC; 4th Division, Gunung Mulu Natl. Pk., Long Pala, 20-x-1977, B. Bolton, 1w BMNH; Santubong, 32km N Kuching, 0-100m, 11/16-v-1994 1a, I. Löbl, D. Burckhardt, 1w BMNH; Mt. Tibang, Mjöberg, 1w MCZC; 4th Division, Gunung Mulu Natl. Pk., Roy. Geogr. Soc. Exped. Long Pala, 17-x-1977, B. Bolton, 2w BMNH. **Sabah/Sarawak?:** Pajan, E. Mjöberg, 1w MCZC; Baian River, E. Mjöberg, 8w 1m MCZC; N. Borneo, Mjöberg, 6w MCZC. **Selangor:** Ulu Gombak, vii/x-1992, F. Ito, 3w MIZA; 16km NEE Kuala Lumpur, 304m, 12-viii-1962, E. Ross, D. Cavagnaro, 2w CASC. INDONESIA. **Java Barat:** Gunung Gede, 914-2134m, ix-1937, Lebak Sioe, 1w BMNH; Dungus Iwul, 9km W Djasinga, 9-vi-1972, W.L. Brown, 1w MCZC; Ujung Kulon Natl. Pk., 190km SW Jakarta, 14-iii-1997, F. Ito, 2w MIZA; **Kalimantan Selatan:** 46km W Batulicin, 28-vi/2-vii-1972, W.L. Brown, 10w MCZC. **Lampung:** Liwa, 5,04'S 104,03'E, 5-ix-1984, M.S. Harvey, 1q ANIC; Langkat, E Coast, Namoe Dengas Est, 2-ii, Jourin, 2w MCZC, 1w USNM. **Sulawesi Selatan:** Balampesoang Forest, 5-8km NE Tanete, 400m, 8-10-vii-1977, W.L. Brown, 1w MCZC. **Sulawesi Utara:** Dumoga Bone Natl. Pk., 12-i-1985, 1w BMNH. **Sulawesi Tenggara:** 1-2km E Wolasi, 42km S Kendari, 350m, 12/14-vii-1972, W.L. Brown, 9w 1q MCZC, 1w MIZA. **Sumatera Barat:** Sitiung, 1,00'S 101,38'S, 105m, 7-i-1992, F. Ito, 2w MIZA; Sipisang, near Padang, 3,00'S 100,14'E, 18-viii-1996, 2w MIZA. PHILIPPINES. **Laguna:** Los Baños, Mt. Makiling, 14/10N 121/11'E, 21-ix-1978, B.B. Lowery, 1w ANIC; **Mindanao:** Momungan, Lanao, D. Empesa, 7w USNM. SINGAPORE. Bukit Timah Nat. Res., 29-v-1968, D.H. Murphy, 1w BMNH.

THAILAND. **Chiang Mai**: nr. Chiang Dao Cave, 25-vi-1970, G.R. Ballmer, 1w LACM; Nakhon Ratchasima: Khao Yai Natl. Pk., 780m, 13-iv-1981, I. Burikam & W.L. Brown, 3w MCZC; Khao Yai National Pk, 750m, 26-vii-1962, E. Ross, D. Cavagnaro, 2w CASC. **Trang**: Khao Chong Nature Education Centre, 7/35'N 99/46'E, 21/24-vii-1996, Snelling & Sonthichai, RRS 96-141, 2w LACM.

***Gnamptogenys coxalis* (Roger)**

(Fig. 20)

Ponera coxalis Roger, 1860:308. Lectotype worker: Ceylon [Sri Lanka] (Nietner) (ZMHB) [Not examined]. Designated by Brown, 1954b:9.

Ectatomma (Rhytidoponera) coxalis (Roger); Mayr, 1862:732. Placed in subgenus *Rhytidoponera* of *Ectatomma*.

Ectatomma (Stictoponera) coxalis (Roger); Mayr, 1887:539. Placed in subgenus *Stictoponera* of *Ectatomma*.

Stictoponera coxalis (Roger); Emery, 1900b:622. Placed in genus *Stictoponera*.

Gnamptogenys coxalis (Roger); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Clypeal lamella projecting anterad as broad triangular lobe; occipital lobes poorly developed. Pronotal dorsum punctate, with rough transverse strigae that arch anterad, becoming longitudinal on posterior pronotum and mesonotum; propodeum unarmed and transversely strigose.

Worker. Metrics ($n = 2$): HL 1.52, 1.58; HW 1.36, 1.29; ML 0.83, 0.74; SL 1.37, 1.33; ED 0.27, 0.25; WL 2.25, 2.08 mm. CI 0.90, 0.82; SI 1.01, 1.03; MI 0.67, 0.57. Head with concave posterior margin in frontal view, relatively straight posterolateral margins, and convex oculomalar margin; clypeal lamella projecting anterad as broadly triangular median lobe; frons longitudinally strigulose, strigulae diverging posterad and arching over eyes; mandibular dorsum strigose. Scape mostly smooth and shining with sparse punctae; occipital lobe poorly developed, occipital lamella dorsally convex, ventrally angular.

Pronotal dorsum with punctae over rough transverse strigae that arch anterad, becoming longitudinal on posterior pronotum and mesonotum, humeral angle well developed; promesonotal suture and metanotal groove lacking; mesopleuron foveolate, mesopleural suture not distinctly impressed, katepisternum with rugosity; metapleuron with foveolae, mostly smooth and shining anterodorsally, becoming longitudinally strigose posteroventrally; propodeum unarmed, transversely strigose. Petiole dorsally irregularly foveolate; foveolae becoming more regular laterally; subpetiolar process projects anterad as a triangular lobe in lateral view; postpetiolar tergite with longitudinal strigulae enclosing elongate depressions, sternum strigulose, with longitudinal costulae extending posterad from anterior process; tergite of fourth abdominal segment longitudinally strigulose. Fore coxae laterally with transverse strigulae; fore tarsal base opposite strigil with uniform comb of spines; metacoxal teeth usually straight, sometimes slightly curved. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body mostly ferruginous

brown, gaster usually darker; head, mesosoma, and gaster with abundant fine inclined hairs.

Queen and male. Unknown.

Comments. Roger (1860) described *Ponera coxalis* as a replacement name for *P. rugosa*, a homonym coined by F. Smith (1857) for what is now *G. costata*. Roger apparently based his description on a series of specimens from Sri Lanka, thinking they were the same species. Emery (1901) studied type material from Berlin and discerned characters useful for separating the two species, though he hinted at the possibility of its synonymy with Smith's *P. rugosa*. Brown (1954b) confirmed Emery's characters and cited more differences between *G. coxalis* and *G. costata*, though he still shared Emery's second thoughts about its distinctness from *G. costata*. He studied specimens in the NHMW that Roger sent to G. Mayr from Berlin and designated one of these specimens as a lectotype (Brown, 1954b). The material examined for this revision came from the NHMW bearing a determination label as "*coxalis*" in what apparently is Roger's handwriting and the same collection data as the lectotype studied by Brown. The NHMW specimens also conform to Brown's (1954b) description of *G. coxalis*. The discreteness of *G. coxalis* from *G. costata* is based on the following characters: *G. costata* has a distinct mesopleural suture; in *G. costata* the postpetiolar tergite is more foveolate, while in *G. coxalis* it is mostly strigulose; *G. coxalis* has a strigulose fourth abdominal tergite, not costate as in *G. costata*. In *G. costata* the propodeal declivity is concave and mostly smooth and shining, dorsally bordered by a transverse ridge between the propodeal teeth. In *G. coxalis* the propodeal declivity is transversely strigose and the dorsal and declivitous

faces are not sharply divided by a ridge. The specimens from the ZMHB are minuten mounted, with one lacking a considerable part of the promesonotum. This species is known only from Sri Lanka.

***Gnamptogenys crassicornis* (Forel)**

(Figs. 21, 46b)

Ectatomma (*Stictoponera*) *binghami* subsp. *crassicorne* Forel, 1912b:51. Holotype worker by monotypy: [Indonesia], Sumatra, Indrapura (Tritschler) (MHNG)[Examined].

Stictoponera spiralis Karavaiev, 1925:79. Holotype worker by monotypy: [Indonesia] Java, Buitenzorg (UASK) [Examined] **syn. n.**

Stictoponera crassicornis (Forel); Brown, 1954b:6. Raised to species.

Gnamptogenys crassicornis (Forel); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Anterior margin of clypeal lamella ending in median convex lobe; scape mostly longitudinally strigulose; occipital lamella well developed, convex at both ends. Dorsum of abdominal segment 4 smooth with scattered punctae, laterally with longitudinally oblique costae and costulae.

Worker. Metrics ($n = 7$): HL 1.38-1.52, HW 1.07-1.18, ML 0.68-0.75, SL 1.10-1.21, ED 0.19-0.23, WL 1.85-1.97 mm. CI 0.76-0.80, SI 0.99-1.06, MI 0.61-0.66, OI 0.18-0.20. Head slightly wider posterad than anterad in frontal view, lateral margins

relatively straight, posterior margin broadly concave, anterior margin of clypeal lamella with median convex lobe; frons rugulose-punctate with traces of striae; clypeus longitudinally carinate. Scape mostly longitudinally strigulose; occipital lamella well developed, convex at both ends.

Lateral mesosoma mostly foveolate over smooth background; katapisternum densely foveolate; mesosomal dorsum with round foveolae on smooth background; promesonotal suture faint; longitudinal smooth area present on median promesonotum; propodeal dorsum areolate. Petiolar node with convex dorsal margin in lateral view, dorsum foveolate, subpetiolar process subquadrate in lateral view; postpetiolar dorsum punctate, punctae become more shallow and sparse posterad, posterior margin scrobiculate to strigulose; postpetiolar sternum mostly smooth with low transverse strigulae; dorsum of abdominal segment 4 smooth with scattered punctae, laterally with longitudinally oblique costae and costulae; sternum transversely rugulose. Fore coxa transversely striate in lateral view; fore tarsus opposite strigil with row of stout setae; metacoxal tooth relatively straight, not hooked. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Coloration uniformly light brown.

Queen. Metrics ($n = 2$): HL 1.43, 1.47; HW 1.11, 1.11; ML 0.70, 0.73; SL 1.11, 1.16; ED 0.26, 0.29; WL 0.18, 0.19 mm. CI 0.78, 0.75; SI 0.99, 1.04; MI 0.63, 0.66; OI 0.23, 0.26. Striae on frons more noticeable; pronotum foveolate, mesonotum longitudinally strigulose-foveolate; katapisternum foveolate or striate; propodeum densely foveolate, declivity mostly smooth.

Male. Unknown.

Comments. The type of *G. spiralis* is a typical *G. crassicornis* and shows nothing to distinguish it as a separate species. Brown (1954b) already suspected that it was a synonym of *G. crassicornis*, based on the description. *G. crassicornis* is similar to *binghamii* in many aspects and was originally described by Forel (1912b) as a subspecies of *G. binghamii*. Brown (1954) elevated *crassicornis* to species based on the anterior position of its compound eyes in comparison with *G. binghamii*. Even though the eyes are a bit more forward on the head when compared with *G. binghamii*, the difference is not striking. The following characters of *G. binghamii* will separate it from *G. crassicornis*: more evenly convex dorsal margin of the petiolar node when seen laterally, third and fourth antennal segments about as long as wide, no extensive striae or costulae on the sides of the fourth abdominal tergite, such sculpturing, if present, limited to small patch on the anteroventral corner of the segment in lateral view. In *G. binghamii* the fourth abdominal tergite has evenly convex lateral margins that gradually converge with each other posteriorly when seen dorsally in full-length view. In *G. crassicornis* the tergite is roughly funnel shaped with the anterolateral margins abruptly converging for a short distance before gradually converging posteriorly. *G. costata* could be confused with *G. crassicornis*, especially some of the forms with a smooth fourth abdominal tergite, but it has more protuberant occipital lobes and no anteromedian lobe on the clypeal lamella.

Specimens examined. INDONESIA. **Java Barat:** Dungus Iwul, 9km W Djasinga, 9-vi-1972, W.L. Brown, 9w 3q MCZC, 1w ANIC, 1w MIZA; Buitenzorg, 1912, UASK. **Kalimantan Selatan:** Pulau Laut, ca. 6km E Stagen dock, 3-vii-1972, W.L. Brown, 1w MCZC. **Sumatera Utara:** Langkat, Namoe Dengas Est., ii-1925, Jourin,

1w ANIC. MALAYSIA. **Negeri Sembilan**: Sungei Menlaya Forest Reserve, nr. Port Dickson, 25-v-1981, W.L. Brown, T. Yow Pong, 1w MCZC.

***Gnamptogenys fontana* sp. n.**

(Fig. 22)

Diagnosis. Head subquadrate in frontal view, lateral margins broadly convex gradually curving onto broadly concave posterior margin, anterior margin of clypeal lamella forming very obtuse blunt angle. Occipital lamella relatively broad, convex, anterior extremely curved, posterior extremely angular.

Type material. Holotype worker. Malaysia, Sabah, Poring Hot Springs, 900m, 12-v-1987, D. Burckhardt & I. Löbl 22a. Deposited in MHNG. Paratype. One worker on same pin as holotype in MHNG.

Worker. Metrics. [Holotype] Paratype: HL [1.11] 1.11, HW [0.95] 0.92, ML [0.62] 0.58, SL [1.01] 0.98, ED [0.25] 0.22, WL [1.54] 1.54 mm. CI [0.86] 0.83, SI [1.06] 1.07, MI [0.65] 0.63, OI [0.26] 0.24. Head subquadrate in frontal view, lateral margins broadly convex gradually curving onto broadly concave posterior margin, anterior margin of clypeal lamella forming obtuse blunt angles laterally, medially with modest convex lobe; frons mostly foveolate over smooth cuticle, frons rugulose-foveolate; frontal lobe evenly convex, barely covering radicle; clypeus longitudinally strigulose with broad smooth areas; foveolae on cephalic sides denser than on dorsum; occipital lamella broad and convex, anterior end curved, posterior end angular. Scape mostly smooth with scattered punctae and occasional strigulae.

Mesosoma mostly foveolate over smooth cuticle in lateral view; mesosomal dorsum foveolate, with smooth area on posteromedian pronotum and part of mesonotum; promesonotal suture poorly impressed, sometimes present as transverse series of punctulae, laterally indistinct; metanotal sulcus well impressed; metapleuron posteroventrally with transverse ridges; propodeal declivity concave with raised posteromedian area. Petiolar node with anterior margin longer than posterior margin in lateral view; dorsum foveolate over smooth cuticle; ventral process subquadrate with acutely angular posterior corner; postpetiolar dorsum mostly smooth with scattered piligerous punctae, punctae deeper and more elongate posterad, posterior margin with narrow band of longitudinal strigulae; foveolae on postpetiolar sides deeper than on dorsum; postpetiolar sternum with low transverse strigulae; dorsum of abdominal segment 4 mostly smooth with piligerous punctulae, posterolaterally with narrow band of longitudinal striae and brief carinae anterad of spiracle. Fore coxa transversely strigulose in lateral view; fore tarsus opposite strigil with row of stout setae; metacoxal tooth straight, without lateral ridge. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster black; mandibles, antennae, legs brown.

Queen and male. Unknown.

Comments. This species may be confused with *G. binghamii*, but in lateral view the occipital lamella in *G. binghamii* is much narrower, its eyes are not as protuberant, and the ridges between the foveolae are sharply crested, not rounded as in *G. fontana*. The acute posterior angle of the subpetiolar process in *G. fontana* is not found in *G. binghamii* and the setae opposite the fore tarsal strigil in *G. binghamii* tend to be

more slender than in *G. fontana*. *G. gabata* is different in the sharp angles separating the concave posterior cephalic margin from the sides when seen in frontal view, while in *G. fontana* the posterior cephalic margin is relatively straight and the occipital lamella is inconspicuously visible in the background as a pair of small horns. *G. gabata* has smaller eyes, and the anterior margin of the clypeal lamella forms an obtuse and blunt median angle. The subpetiolar process of *G. gabata* is more triangular, without an acute posterior angle, and the propodeum has prominent posterolateral crests. The holotype of *G. fontana* is the top specimen on the pin and has the point marked in red.

Etymology. The species name is derived from the Latin term for "of a spring," *fontanus*, which itself is derived from *fons* (m.) and alludes to the type locality, Poring Hot Springs.

***Gnamptogenys gabata* sp. n.**

(Fig. 23)

Diagnosis. Head densely foveolate in lateral view; occipital lamella convex, relatively broad. Humeral angle well developed, lamellate; pronotum anteroventrally with blunt point. Mesosomal dorsal margin, just posterad of denticles, with declivitous margin extending posterad in lateral view, forming shelf like outline. Propodeal declivity mostly smooth with posteromedian, parallel-sided raised area and prominent posterolateral crests.

Type material. Holotype worker. Malaysia, Sarawak, Gunung Matang, 20km W Kuching, 800m, 13-v-1994, I. Löbl & D. Burckhardt 2a. Deposited in BMNH.

Paratypes. One worker on same pin as holotype deposited in BMNH. Two workers in BMNH, 1w in MIZA from Malaysia, Sarawak, Gunung Penrissen, 1000m, 23-v-1994, I. Löbl & D. Burckhardt 9a.

Worker. Metrics. [Holotype] Paratypes ($n = 3$): HL [1.21] 1.03-1.20, HW [1.02] 0.89-1.00, ML [0.67] 0.54-0.64, SL [1.07] 0.90-1.02, ED [0.20] 0.19-0.22, WL [1.70] 1.45-1.69 mm. CI [0.84] 0.83-0.86, SI [1.05] 1.00-1.05, MI [0.66] 0.61-0.64, OI [0.20] 0.20-0.22. Head with broadly convex lateral margins in frontal view, posterior margin relatively flat, anterior margin of clypeal lamella converging medially to brief convex lobe; frons rugulose-foveolate; clypeus longitudinally strigulose, posterolaterally foveolate; scape mostly smooth with scattered longitudinal strigulae; head densely foveolate in lateral view; occipital lamella convex, relatively broad, curved or angular at either end. Mesosoma mostly densely foveolate in lateral view; humeral angle lamellate, pronotum anteroventrally with blunt point; mesopleuron with scattered longitudinal strigulae; anterodorsal metapleural extension slender; foveolae on lateral propodeal face not as dense as on pronotum; mesosomal and petiolar node dorsum mostly densely foveolate; propodeal declivity mostly smooth with posteromedian, parallel-sided raised area and prominent posterolateral crests, propodeal denticle slender, short. Petiolar node higher posterad than anterad in lateral view; ventral process projecting anterad, posteriorly angular; postpetiolar dorsum mostly smooth with scattered foveolae, each more abruptly depressed anterad than posterad, posterior margin with narrow

strigulose strip; postpetiole laterally foveolate, foveolae not as oval as on dorsum; dorsum of abdominal segment 4 varying from mostly smooth to undulate with scattered punctae; posterior margin with narrow band of longitudinal strigulae; tergite anteroventrally with brief oblique strigulae; sternum strigulose. Fore coxa transversely strigulose in lateral view; fore tarsus opposite strigil with stout seta followed apically by row of slender setae; metacoxal tooth slender, slightly arched. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster dark brown; mandibles, antennae, legs ferruginous brown.

Queen and male. Unknown.

Comments. This species keys close to *G. binghamii* and to *G. fontana*. *G. binghamii* has much narrower occipital lobes when seen laterally and a lower posteromedian propodeal elevation and lacks the prominent posterolateral crests, as seen in *G. gabata*. Differences from *G. fontana* are discussed under that species.

Etymology. The species name of *G. gabata* is derived from the Latin noun for “dish” or “platter”, *gabata* (f.), and alludes to the broad posterolateral propodeal lobes.

Additional specimens examined. INDONESIA. **Kalimantan Selantan:** SE Borneo, 17-46km W Batulitjin [Batulicin?], 28/vi-2/vii-1972, W.L. Brown, 1w MCZC. MALAYSIA. **Pahang:** Fraser's Hill, 1050m, 19-iii-1993, I. Löbl & Calama 12b, 1w BMNH. **Sarawak:** confl. Suan Oyan and Mujong Rivers, E of Kapit, 150m, 19-v-1994, I. Löbl & D. Burckhardt 6a, 3w BMNH; Semengoh Forest Reserve, 11 miles SW Kuching, 28/31-v-1968, R.W. Taylor, 2w ANIC.

Gnamptogenys gastrodeia sp. n.

(Fig. 24)

Diagnosis. Cephalic vertex posteriorly bound by prominent thick lamella, visible in full-face view and merging with occipital lamella. Propodeal spiracle lighter in color than surrounding cuticle; dorsum of abdominal segment 4 bulging into prominent convexity that extends to halfway point, mostly foveolate with foveolae on bulge becoming very elongate.

Type material. Holotype worker. Indonesia, Sumatera Barat, Sukarami, 1/5-i-1992, F. Ito FI. Deposited in MBBJ. Paratype. One queen in BMNH from Indonesia, C. Java, res. Kedoe, Mt. Tamojo, 1200ft, 29-x-1939, M.A. Lieftinck.

Worker. Metrics. Holotype: HL 2.06, HW 1.58, ML 1.05, SL 1.92, ED 0.32, WL 2.98 mm. CI 0.77, SI 1.22, MI 0.66, OI 0.20. Head with broadly convex lateral margins in frontal view, posterior margin concave, anterior margin of clypeal lamella evenly convex; frons densely foveolate; clypeus longitudinally strigulose-punctate, with fine longitudinal sulcus extending posterad from frontal triangle almost to anterior level of eye in frontal view; vertex posteriorly bound by prominent thick lamella, visible in full-face view, merges with occipital lamella; mandibular dorsum longitudinally costulate, with large gap separating internal mandibular margin from clypeus. Scape mostly smooth, with scattered longitudinal strigulae-carinae, especially apically; occipital lamella prominent, with transverse ridges.

Mesosoma densely foveolate in lateral view, foveolae ranging from rounded to irregularly oval; anepisternum narrow; mesosomal dorsum densely foveolate,

mesonotum with longitudinal strigulae; promesonotal suture and metanotal sulcus present as fine transverse impressed lines; propodeal spiracle lighter in color than surrounding cuticle, propodeal declivity foveolate anteriorly, smooth posteriorly. Petiolar dorsum foveolate, ventral process forming small anteriorly placed denticle in lateral view; postpetiolar dorsum with mostly oval foveolae, posterior margin drops sharply forming distinct, but narrow scrobiculate-strigose posterior face; postpetiolar sternum with V-shaped anterior process, discal area mostly smooth with lateral foveolae; postpetiole with round foveolae anteriorly and elongate foveolae posteriorly in lateral view; dorsum of abdominal segment 4 with narrow transverse anterior smooth patch, afterward bulging into prominent convexity that extends posteriorly halfway, foveolate with foveolae on bulge very elongate. Fore coxae strigulose in lateral view, fore tarsus opposite strigil with row of stout setae. Dorsum of thorax and abdominal segments 1-4 with relatively long, erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster dark brown to black; mandibles, antennae, legs brown.

Queen. Metrics (MBBJ specimen): HL 1.82, HW 1.45, ML 0.92, SL 1.57, ED 0.32, WL 2.78 mm. CI 0.80, SI 1.08, MI 0.63, OI 0.24. Pronotum and mesonotum mostly areolate; mesonotum with longitudinal strigulae; anepisternum partly areolate, partly striate; katepisternum with foveolae; metanotum smooth; propodeum areolate dorsally and laterally. Postpetiolar dorsum with elongate oval to pyriform depressions, with smooth intervening cuticle, posterior margin strigose; postpetiolar sternum mostly smooth with some lateral areolae, anterior process V-shaped, two

longitudinal carinae form low median keel. Dorsum of abdominal segment 4 areolate and with prominent anteromedian tumosity.

Male. Unknown.

Comments. This striking species could be confused with *G. palamala* because of the bulge on the fourth abdominal tergite, but *G. palamala* can be recognized by its mostly smooth mandibular dorsum with its diverging basal and masticatory margins. *G. palamala* also has longitudinal costae on the posterior half of the fourth abdominal dorsum, in contrast with the areolae of *G. gastrodeia*. The standing hairs on the mesosoma of *G. gastrodeia* are longer than in most other species of *Gnamptogenys* examined.

Etymology. The species name is derived from the Greek term for “potbellied”, *gastrodes*.

Additional specimen examined. INDONESIA. **Sumatera Barat:** Sukarami, 1/5-i-1992, F. Ito FI92-109, 1q MBBJ.

Gnamptogenys grammodes Brown

(Fig. 25)

Gnamptogenys grammodes Brown, 1958:310, Fig. 41. Holotype worker: Papua New Guinea, Bisianumu, near Sogeri (Wilson) (MCZC) [Examined].

Diagnosis. Head with convex lateral margins that curve gradually onto straight to slightly convex posterior margin in frontal view; occipital lobe lacking, occipital lamella forming blunt, triangular lobe. Postpetiolar dorsum with scattered foveolae over mostly smooth background sculpturing, posterior one-third up to one-half with longitudinal parallel carinulae.

Worker. Metrics ($n = 5$): HL 1.04-1.14, HW 0.90-0.96, ML 0.53-0.58, SL 0.91-1.02, ED 0.23-0.29, WL 1.41-1.53 mm. CI 0.83-0.87, SI 1.01-1.06, MI 0.55-0.62, OI 0.24-0.31. Head with convex lateral margins curving gradually onto straight to slightly convex posterior margin in frontal view, anterior margin of clypeal lamella with median convex lobe; frons longitudinally strigulose-foveolate; vertex mostly smooth; clypeus longitudinally strigulose. Scape mostly smooth with longitudinal strigulae; occipital lobe lacking, occipital lamella forming blunt, triangular lobe. Pronotum foveolate with smooth posteromedian area; mesometanotum longitudinally rugose-foveolate; katapisternum mostly rugulose-foveolate; metapleuron anterodorsally mostly smooth, posteroventrally longitudinally strigulose; propodeum foveolate with scattered longitudinal to oblique undulations and rugulae, propodeal dorsum foveolate with low transverse undulations and strigulae, propodeal dorsum curves gradually onto mostly smooth declivity.

Petiolar node with anterior margin forming gradual convexity in lateral view, higher posterad than anterad; dorsum mostly smooth with scattered lateral foveolae; ventral process projecting anterad as small, acute triangular lobe; postpetiole mostly smooth laterally with scattered foveolae, each foveola abruptly impressed anterad and gradually sloping posterad, posterior margin with longitudinal strigulae; postpetiolar

dorsum with scattered foveolae over background sculpturing ranging from mostly smooth to transversely strigulose, posterior one-third up to one-half with longitudinal parallel carinulae; dorsum of abdominal segment 4 mostly smooth with scattered punctulae, posterolaterally with narrow band of longitudinal striae, sternum rugulose. Fore coxa transversely strigulose in lateral view; fore tarsus opposite strigil with single stout seta followed apically by row of slender setae; metacoxal tooth triangular and slender. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster dark brown; mandibles, antennae, legs ferruginous brown.

Queen. Metrics ($n = 1$): HL 1.25, HW 1.06, ML 0.65, SL 1.03, ED 0.36, WL 1.79 mm. CI 0.85, SI 0.97, MI 0.61, OI 0.34. Pronotum foveolate in lateral view, foveolae irregularly distributed among smooth areas; mesonotum with scattered foveolae and low longitudinal strigulae; mesoscutum longitudinally strigulose-punctulate; lateral propodeal face transversely rugulose-punctate; petiolar node with smooth median area and transverse strigulae on anterior and posterior margins in dorsal view. Postpetiole with transverse strigulae along anterior one-third, longitudinally strigulose along posterior two-thirds.

Male. Metrics ($n = 1$): HL 0.84, HW 0.77, ML 0.43, SL 0.28, ED 0.31, WL 1.48 mm. CI 0.92, SI 0.36, MI 0.56, OI 0.40. Frons irregularly areolate on low rugulae; median longitudinal ridge extends from posterior clypeal margin to between antennal insertions on elevated area; frontal triangle relatively wide and flat bottomed; clypeus strigulose; mandible longitudinally strigulose. Pronotum, mesopleuron mostly smooth with scattered shallow foveolae in lateral view; metapleuron, lateral

propodeal face rugulose; mesonotum with large smooth areas and irregularly scattered shallow foveolae; scutellum strigulose. Fourth abdominal tergite with low, fine longitudinal undulations, slightly colliculate; fourth abdominal sternite strigulose.

Comments. The habitat labels on the studied specimens indicate rainforests as collection sites for this New Guinea endemic. Some specimens were found in rotten logs. This species keys out close to *G. biroi*. For additional information on separating these two species, see *G. biroi*.

Specimens examined. INDONESIA. **Irian Jaya:** PT, Freeport Concession, Siewa Camp, 3/04'S 136/38'E, 61m, 6/15-iv-1998, R.R. Snelling, 3w LACM. PAPUA NEW GUINEA. **Central:** Ofi Creek, 8km SW Naoro, 9/18'S 147/34'E, 650m, 15/16-viii-1976, P.S. Ward 1956, 1w PSWC; Kawai River, Manari, 9/11'S 147/37'E, 700m, 13/14-viii-1976, P.S. Ward 1917, 1w PSWC; Bisianumu, nr. Sogeri, 500m, 15/20-iii-1955, E.O. Wilson, 1w USNM, 3w MCZC. **Gulf:** Ivimka Camp, Lakekamu Basin, 7/7'S 146/8'E, 110-120m, 15/16-xi-1996, R.R. Snelling 96-328/338, 4w LACM; Tapini, 100-1200m, vii-1962, R.W. Taylor, 1w 1q ANIC. **Oro:** Divi Range, Kokoda Road, 396m, 18-i-1971, B.B. Lowery, 1w 1m ANIC; N. District, Kokoda, 6-iv-1972, P.M. Room, 1w ANIC.

***Gnamptogenys helisa* sp. n.**

(Fig. 26)

Diagnosis. Occipital lamella convex, wider medially than at ends, ends bluntly angular. Pronotum punctate with mixed smooth-striate areas in lateral view; striae form semicircle from ventral margin to posterior margin, around broad and shallow posteroventral depression. Petiolar node with broadly convex anterodorsal margin in lateral view, posterior margin brief, sharply dropping; ventral process projecting anterad as pointed denticle. Postpetiolar dorsum mostly smooth with abundant punctae; each puncture abruptly impressed anterad and sloping posterad, each puncture also marked by patch of striae.

Type material. Holotype worker. Malaysia, Sarawak, 4th Division, Gunung Mulu Natl. Pk., 1700-1800m, v-1978, I. Hanski. Deposited in BMNH. Paratypes. Seven workers, all from same series as holotype: 4w in BMNH, 1w in ANIC, 1w in MCZC, 1w in MIZA.

Worker. Metrics. [Holotype] Paratypes ($n = 6$): HL [1.77] 1.66-1.89, HW [1.44] 1.35-1.45, ML [0.94] 0.89-0.95, SL [1.64] 1.63-1.81, ED [0.27] 0.25-0.27, WL [2.57] 2.42-2.57 mm. CI [0.82] 0.76-0.83, SI [1.14] 1.18-1.26, MI [0.65] 0.63-0.68, OI [0.18] 0.17-0.20. Head with subparallel lateral margins in frontal view, posterior margin concave, anterior margin of clypeal lamella converging into median blunt point; frons strigulose-punctate including vertex; clypeus longitudinally strigulose, strigulae extending onto lamella; scape mostly smooth with scattered longitudinal strigulae; small occipital lobe present; occipital lamella convex, wider medially than at ends. Pronotum with anteroventral angle in lateral view, humeral angle well developed, not lamellate; pronotum laterally punctate with mixed smooth-striate areas, striae forming semicircle from ventral margin to posterior margin, around

broad and shallow posteroventral depression; pronotum punctate in dorsal view, punctae united by strigulae, forming posteriorly diverging rows, posteromedian smooth area present; anepisternum mostly smooth with variable amount of strigulae; katepisternum strigulose-punctate; metapleuron anterodorsally smooth, posteroventrally strigulose; mesometanotum and propodeal dorsum punctate with low, partially effaced, transverse strigulae, strigulae may swirl on mesonotum; propodeal declivity anteromedially strigulose, rest mostly smooth; propodeal side mostly smooth with scattered punctae.

Petiolar node with broadly convex anterodorsal margin in lateral view, posterior margin brief, sharply dropping; dorsum punctate with transverse strigulae; ventral process projecting anterad as pointed denticle; postpetiolar dorsum mostly smooth with abundant punctae, each puncture abruptly impressed anterad and sloping posterad, each puncture also marked by patch of striae; postpetiolar sternum with low oblique to transverse strigulae, especially posterolaterally, anteromedially mostly smooth with low longitudinal extending from anterior process to posterior margin; dorsum of abdominal segment 4 mostly smooth with abundant shallow punctae, each one accompanied by striate area, tergite mostly obliquely strigulose in lateral view, sternum carinulate. Fore coxa transversely strigulose in lateral view; fore tarsus opposite strigil with row of stout setae; metacoxal tooth placed on posterior margin. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster dark brown; mandibles, antennae, legs ferruginous.

Queen and male. Unknown.

Comments. This species is similar to *G. crassicornis*, but *G. crassicornis* is on average much lighter colored, usually ferruginous, with totally strigulose scapes and smooth ground sculpture, and is lacking the striae of *G. helisa*. *G. crassicornis* is smaller (HL < 1.6; WL < 2.2 mm). This species shares with *G. scalpta* the fine striations on the body, but *G. scalpta* is a smaller species (HL < 1.0; WL < 2.2 mm), with mostly strigulose scapes, the anterior margin of its clypeal lamella is more sinuate, not rapidly converging to a median lobe as in *G. scalpta*. The petiolar node in *G. scalpta* when seen laterally is evenly convex, with its subpetiolar process subquadrate in shape, and it lacks propodeal denticles. The standing hairs on the body of *G. helisa* are relatively shorter than in other examined species of *Gnamptogenys*. The type series of *G. helisa* was taken from a pitfall trap.

Etymology. The species name is a modification of the Greek term for “turning around,” *helisso*, which is derived from *helix* (f.), meaning to spiral or whirl. The epithet alludes to the circling striae on the pronotal sides.

***Gnamptogenys macretes* Brown**

(Fig. 27)

Gnamptogenys macretes Brown, 1958:313. Holotype worker: New Guinea, Bisianumu, near Sogeri (Wilson) (MCZC) [Examined].

Diagnosis. Occipital lobe lacking, occipital lamella prominent and convex. Postpetiolar dorsum striate with scattered piligerous punctae, striae transverse on

anterior face curving around medially becoming longitudinal posterad. Dorsum of abdominal segment 4 with narrow anteromedian strip of transverse striae posteriorly bordered by arching low sulcus, with a patch of longitudinal striae extending on anterior one-third to one-half, striae longest medially becoming progressively shorter laterally, rest of tergite mostly smooth with scattered punctures.

Worker. Metrics ($n = 4$): HL 1.20-1.28, HW 1.01-1.10, ML 0.61-0.67, SL 1.09-1.18, ED 0.27-0.31, WL 1.72-1.84 mm. CI 0.82-0.88, SI 1.07-1.10, MI 0.57-0.61, OI 0.27-0.29. Head subquadrate with longitudinal lateral margins in frontal view, posterior margin relatively straight, anterior margin of clypeal lamella ending in median blunt angle; frons with strigae forming posteriorly diverging rows surrounding round to oval smooth-bottomed foveolae, with strigulae between foveolae; clypeus longitudinally strigulose, strigulae partially extending onto lamella. Scape mostly smooth with scattered piligerous punctae; mandibular dorsum mostly longitudinally costulae; occipital lobe lacking, occipital lamella prominent and convex. Lateral pronotal face mostly foveolate, strigulae present posterad, posteromedian corner mostly smooth with some punctae; anepisternum mostly smooth with some foveolae-punctae; katepisternum with abundant round to oval foveolae and scattered low strigulae; metapleuron anterodorsally undulate to vaguely strigulose, posteroventrally longitudinally strigulose; promesonotum densely foveolate in dorsal view, foveolae forming approximate concentric circles around median patch of longitudinal strigulae; promesonotal suture vaguely impressed; propodeum densely foveolate to areolate, declivity mostly smooth.

Petiolar node with shorter posterior margin than anterior margin in lateral view, dorsum with low transverse strigulae and scattered foveolae; ventral process forming anteriorly projecting narrow lobe; postpetiolar dorsum striate with scattered piligerous punctae, striae on anterior face transverse, curving around medially and becoming longitudinal posterad; postpetiole laterally with anterior one-third transversely strigulose, dorsal half longitudinally strigulose, posteroventral corner mostly smooth; postpetiolar sternum mostly smooth with very low transverse rugulae and undulations; dorsum of abdominal segment 4 with narrow anteromedian strip of transverse striae posteriorly bordered by arching low sulcus; longitudinal striae extend along anterior one-half to one-third of tergite, striae longest medially, becoming progressively shorter laterally, rest of tergite mostly smooth with scattered punctae. Fore coxa mostly smooth with variable degree of transverse strigulae apically in lateral view; fore tarsus opposite strigil with one stout seta. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster brown; mandibles, antennae, legs ferruginous.

Queen. Metrics ($n = 2$): HL 1.28, 1.29; HW 1.10, 1.09; ML 0.66, 0.68; SL 1.20, 1.22; ED 0.34, 0.35; WL 2.06, 1.98 mm. CI 0.85, 0.85; SI 1.09, 1.12; MI 0.60, 0.62; OI 0.31, 0.32. Pronotum mostly foveolate with dorsomedian smooth area, ventral margin pitted with irregular punctae and strigulae in lateral view; mesonotum longitudinally strigulose-punctate; anepisternum longitudinally strigulose, with scattered foveolae; katepisternum with variable degree of longitudinal strigulae, foveolae and punctae present especially posteriorly.

Male. Metrics ($n = 1$): HL 0.89, HW 0.74, ML 0.49, SL 0.30, ED 0.34, WL 1.69 mm. CI 0.83, SI 0.41, MI 0.66, OI 0.46. Clypeus with fine longitudinal strigulae, with longitudinal carina extending posterad from clypeus to posterior antennal socket level, reappearing just before median ocellus; gena rugulose; scape mostly smooth with abundant piligerous punctulae, especially basally; frons with irregular rugulae and broad smooth to undulate space in between; mesoscutum mostly smooth with scattered foveolae, axillae longitudinally carinate, scutellum mostly smooth with scattered foveolae; propodeum rugulose with undulate cuticle in between; dorsum of node and gaster mostly smooth.

Comments. This species seems to be a sister species of *G. niuginense* based on several synapomorphies such as lack of an occipital lobe and shared trends of surface sculpture. For additional information on differences between these two species, see discussion under *G. niuginense*. Specimens of *G. macretes* have been found in rotten logs in rainforest.

Specimens examined. PAPUA NEW GUINEA. **Central:** Ofi Creek, 8km SW Naoro, 9/18'S 147/34'E, 15/16-viii-1976, 650m, P.S. Ward 1961, 2w 1q PSWC, 2w ANIC; Bisianumu, nr. Sogeri, 500m, 15/20-iv-1955, E.O. Wilson, 3w 1m 1q MCZC, 1w 1m 1q USNM.

***Gnamptogenys meghalaya* sp. n.**

(Fig. 28)

Diagnosis. Head elongate in frontal view; lateral margins broadly convex, diverging posterad; posterior margin concave, forming blunt obtuse angle; anterior margin of clypeal lamella forming obtuse angle, medially projecting; eye small; occipital lobe lacking; occipital lamella small; scape mostly smooth with scattered punctulae. Petiolar node evenly convex in lateral view; ventral process subquadrate.

Type material. Holotype worker. India, Meghalaya, Khasi Hill, 1000m, Mawsynram to Balat, 27-x-1978, C. Besuchet & I. Löbl 30b. Deposited in ANIC. Paratypes. One dealate queen on same pin as holotype, in ANIC. Two workers in ANIC, 2w in MCZC with same data as holotype. Two workers in ANIC from India, Meghalaya, Khasi Hills, 700m, Nongpoh, 5-xi-1978, C. Besuchet & I. Löbl 42.

Worker. Metrics. [Holotype] Paratypes ($n = 5$): HL [0.95] 0.90-1.00, HW [0.87] 0.77-0.89, ML [0.52] 0.44-0.52, SL [0.74] 0.68-0.77, ED [0.14] 0.14-0.17, WL [1.32] 1.23-1.37 mm. CI [0.92] 0.84-0.89, SI [0.85] 0.87-0.96, MI [0.60] 0.56-0.64, OI [0.16] 0.17-0.22. Head with broadly convex lateral margins in frontal view, posterior margin concave, forming blunt obtuse angle; anterior margin of clypeal lamella forming medially projecting obtuse angle; frons densely rugulose-punctate, ridges between punctae rounded or flat, not sharp; clypeus longitudinally strigulose; eye small; occipital lobe lacking; occipital lamella relatively small; scape mostly smooth with scattered punctulae; mesosoma foveolate in lateral view; katepisterum with some strigulae; posteroventral metapleuron longitudinally strigulose; mesosomal dorsal margin anteriorly convex, dorsally broadly convex, with broadly concave declivitous margin in lateral view. Mesosomal dorsum densely foveolate with median shallow longitudinal sulcus on mesonotum, sometimes extending onto posteromedian

pronotum; propodeal declivitous face mostly smooth, denticles triangular. Petiolar node evenly convex in lateral view, ventral process subquadrate; postpetiolar dorsum foveolate-punctate with shallow undulations and slight scalloping, foveolae denser, more ovaloid on sides; sternum posterolaterally foveolate, medially mostly smooth with median strigulose strip; dorsum of abdominal segment 4 mostly smooth with abundant punctae, punctae deeper laterally, posterior margin with narrow band of longitudinal strigulae. Fore coxa transversely strigulose in lateral view; fore tarsus opposite strigil with single stout seta; metacoxal tooth elongate and triangular. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster dark brown; mandibles, antennae, legs ferruginous.

Queen. Metrics ($n = 1$): HL 1.02, HW 0.93, ML 0.54, SL 0.81, ED 0.15, WL 1.54 mm. CI 0.91, SI 0.87, MI 0.58, OI 0.16. Mesosoma foveolate in lateral view; mesoscutum strigulose-punctate; scutellum smooth with scattered punctae; propodeal dorsum densely foveolate. Dorsum of petiolar node foveolate with median smooth area; punctures on postpetiolar dorsum smaller in diameter than on workers.

Male. Unknown.

Comments. This species is similar to *G. binghamii* from the western part of its geographic range and is sympatric with it in the Garo Hills of the Indian state of Meghalaya. *G. binghamii* has distinct occipital lobes, and the lateral cephalic margins are relatively parallel in frontal view and are not diverging posterad as in *G. meghalaya*. The frons of *G. binghamii* has striae on the transverse ridges between the foveolae, while the ridges in *G. meghalaya* are mostly glazed or rounded. *G.*

meghalaya is also slightly smaller than *G. binghamii* on average. All specimens were taken in forest litter.

Etymology. The species name is derived from the name of the type collection site in the Indian state of Meghalaya.

Additional specimens examined. INDIA. **Meghalaya:** Garo Hills, 400m, Rongrengiri, 3-xi-1978, C. Besuchet & I. Löbl 39b, 1w MIZA; Garo Hills, 15km N Darugiri, 400m, 4-xi-1978, C. Besuchet & I. Löbl 40b, 2w BMNH; Garo Hills, Tura Peak, 700-900m, 1-xi-1978, C. Besuchet & I. Löbl 37b, 2w 1q ANIC.

***Gnamptogenys menadensis* (Mayr)**

(Figs. 29, 45b)

Ectatomma (Stictoponera) menadensis Mayr, 1887:539. Holotype worker by monotypy: [Indonesia], Celebes [Sulawesi], Menado [Manado] (Radoszkowski) (NHMW) [Examined].

Stictoponera menadensis (Mayr); Emery, 1911:48. Placed in genus *Stictoponera*.

Stictoponera stylata Menozzi, 1925:440, Fig. 2. Holotype worker by monotypy: [Philippines], Luzon, Mt. Makiling (Baker) (USNM) [Probable holotype examined]. Synonymy by Brown, 1954b:2.

Stictoponera menadensis var. *obscura*: Santschi, 1932:11. Holotype worker by monotypy: [Indonesia], Celebes [Sulawesi] (ISNB) [Not examined] Junior

secondary homonym of *Ectatomma (Holcaponera) obscurum* Emery, 1896:48.

Synonymy by Brown, 1954b:2.

Gnamptogenys menadensis (Mayr); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Occipital lobes prominent, projecting posteroventrally in lateral view; eyes situated on posterior half of head, usually less than one ocular diameter distant from vertex. Mesosomal dorsum mostly densely foveolate to areolate with median longitudinal strip of smooth cuticle, devoid of foveolae on mesonotum; mesosomal dorsal margin mostly devoid of standing hairs in lateral view; propodeal declivity medially with raised posteriorly surface with parallel lateral margins. Metacoxal teeth robust and curved.

Worker. Metrics ($n = 16$): HL 1.30-1.55, HW 1.07-1.23, ML 0.61-0.75, SL 1.13-1.37, ED 0.25-0.31, WL 1.76-2.11 mm. CI 0.77-0.83, SI 1.03-1.15, MI 0.55-0.61, OI 0.24-0.26. Head with broadly convex lateral margins in frontal view, posterior margin straight with laterally protruding occipital lobes, anterior margin of clypeal lamella forms blunt angle, sometimes projecting anterad as narrow lobe; frons rugulose-foveolate with sharp, roughly longitudinal ridges, foveolae with smooth, convex bottoms; frontal lobe with straight lateral margin; clypeus longitudinally strigose; scape varies from very strigulose to mostly smooth; occipital lobe prominent, projecting posteroventrally in lateral view, lamella convex, low, with ends either angular or convex, usually convex; eye situated posteriorly on head, usually less than one ocular diameter from vertex.

Humeral angle lamellate, pronotal ventral margin narrow, anteroventral corner frequently angular, side densely foveolate with fine strigulae on posterior margin; pronotal dorsum densely foveolate with sharp ridges between depressions, median broad groove present on posterior half; promesonotal suture marked as fine line; mesonotum usually with median longitudinal strip of mostly smooth cuticle; anepisternum narrow, rectangular to cuneiform, usually smooth with some foveolae; katepisternum foveolate, with or without strigulae; metapleuron posteroventrally strigose, anterodorsally with narrow strip of mostly smooth or undulate cuticle; propodeum foveolate, propodeal declivity surrounded posterolaterally by ridges forming denticle or low triangular projection, medially with raised, parallel-sided surface that ends before anterior margin, cuticle surrounding raised area usually smooth. Petiolar node dorsally foveolate; with subquadrate to lobe like ventral process in lateral view; postpetiolar dorsum foveolate anterad, foveolae becoming shallower and sparser posterad, laterally densely foveolate anteriorly; postpetiolar sternum transversely strigulose, laterally foveolate to punctate; dorsum of abdominal segment 4 mostly smooth with scattered punctulae; fourth abdominal sternite strigulose-punctate. Fore coxa transversely strigulose in lateral view; fore tarsus opposite strigil with single prominent basal seta, occasionally followed apically by row of slender setae; metacoxal spine usually curved from the base. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster ferruginous brown to brown, gaster frequently darker colored than rest of body.

Queen. Metrics ($n = 1$): HL 1.27, HW 1.03, ML 0.60, SL 1.14, ED 0.21, WL 1.83 mm. CI 0.81, SI 1.11, MI 0.58, OI 0.20. Pronotum densely foveolate, laterally with narrow mostly smooth band along posterior margin, rest of lateral mesosoma densely foveolate; mesoscutum with shallow foveolae, median longitudinal and shallow sulcus present; propodeal dorsum densely foveolate.

Male. Metrics ($n = 1$): HL 1.09, HW 1.00, ML 0.53, SL 0.25, ED 0.43, WL 2.00 mm. CI 1.09, SI 0.25, MI 0.53, OI 0.43. Frons mostly foveolate, mandibular dorsum mostly smooth with scattered punctae, clypeus mostly smooth with longitudinal undulations and scattered foveolae laterally. Mesonotum mostly rugulose-punctate in lateral view; anepisternum approximately equal in size to katepisternum; mesoscutum foveolate with large intervening smooth areas, propodeum densely foveolate. Petiolar node densely foveolate. Fore coxa mostly smooth in lateral view, slightly colliculate dorsad, with low transverse strigulae apically.

Comments. *G. menadensis* is a relatively common ant found in the Philippines, southwest into Indonesia, and reaching its western range limit in northeastern peninsular Malaysia. There is a single record from New Guinea. Its range is mostly east of and separated from that of the similar *G. bicolor*, though they are sympatric in western Malaysia and Sumatra. *G. bicolor* is a Southeast Asian ant found from Myanmar eastward, including southern China. Most reproduction in *G. menadensis* is through gamergates.

This species is easily confused with *G. bicolor*, having similar sculpturing patterns, well developed occipital lobes, and posteriorly placed eyes. *G. bicolor* differs from *G. menadensis* by the longitudinally strigulose median area on the promesonotum,

the propodeal declivity with a posteromedian raised area and anteriorly diverging sides, and a usually straight metacoxal tooth. *G. bicolor* generally has more foveolae on the postpetiole, which are deeper and larger in diameter than in *G. menadensis*; the sides of the fourth abdominal tergite in *G. bicolor* likewise have larger punctae. *G. bicolor* has abundant long standing hairs on the mesosomal dorsum when seen in lateral view with background lighting, in contrast to their virtual absence in *G. menadensis*.

There are field data and behavioral information from Fuminori Ito and Bruno Gobin (pers. com.) that suggest the presence of more than one species identifiable as *G. menadensis*. In Ulu Gombak, Malaysia, they were able to distinguish two forms in the field by the more reddish coloration of one but found the color difference vague in specimens kept in the lab or stored in alcohol. A study of males from this site shows differences in the development of the occipital lobes between the red and nonred forms, but when males from the whole range of *G. menadensis* are included, these differences collapse. In addition, the number of males available for study is too small to assess the variability of their morphological features. *G. menadensis* from Ulu Gombak nest in the ground and have an average of 500 workers, in contrast to the arboreal habits and smaller nests of *G. menadensis* from Sulawesi (F. Ito, pers. com.). Thus specimens recognized here as *G. menadensis* may belong to more than one species, but no consistent morphological differences were detected during the course of this study.

Most habitat labels indicate collection from mesic forested areas. In the Philippines *G. menadensis* commonly forages on foilage, with nests being found in

rotting wood, in tree fern stems, and under moss on rocks (Brown 1954b). In Sulawesi, Indonesia, the ants are arboreal, with foraging and nesting on trees and shrubs. Nests are constructed in preexisting cavities and sealed with a lining of organic material. Colonies are generally small, with an average of 100 workers (Gobin, Peeters, and Billen 1998a). Occasional nesting sites included cavities in limestone rocks and rattan palm leaf shafts. Nests eventually split by budding. Besides hunting for prey, workers also bite flowering buds and lick the exuding sap (Gobin, Peeters, and Billen 1998a). Foragers use chemical trails to home to their nests as well as to recruit to foraging areas (Gobin et al., 1998) by sting-tapping on the substrate. Virgin workers in this species produce trophic eggs (Gobin, Peeters, and Billen 1998b).

The type of *Stictoponera stylata* was present in the collection of J. Chapman but apparently became separated from its label during World War II. Specimens from Chapman's collection made their way to the MCZC where Brown (1954b) and Chapman determined that the *S. stylata* type was among the material they were studying. During the course of the present revision, these specimens were not found in the MCZC, but a series of point-mounted workers of *G. menadensis* from Mt. Makiling, collected by Baker, were found in the USNM. Among this series is a worker with an additional label bearing only the number 20408. This number is similar to those found on "MCZ Cotype" labels for type specimens deposited there during that time (e.g., 20419 for the holotype of *G. taivanensis*). On this evidence the aforementioned specimen is considered the probable holotype of *S. stylata* and has been labeled as such: "Probable holotype."

Specimens examined. INDONESIA. **Kalimantan Barat:** Gunung Palong Natl. Pk., Labang Pantil Res. Sta., 1/15'S 110/5'E, 100-400m, 15-vi/15-viii-1991, Darling, Sutriyono, 25w MCZC. **Lampung:** Liwa, 700m, 1/6-ix-1984, 1984 Zool. Exped., 6w ANIC. **Sulawesi Selatan:** Karaenta Natl. Pk., 25km NE Maros, via Watampone (Bone), 12/15-ii-1995, B. Gobin 8, 2w MIZA; loc. cit.; loc. cit., B. Gobin 9, 2w MIZA; loc. cit., B. Gobin 10, 2w 1m MIZA; loc. cit., B. Gobin 13, 4w MIZA; loc. cit., B. Gobin 18, 2w 2w 1m MIZA; loc. cit., B. Gobin 13, 1q MIZA; nr. Maros, SW Sulawesi, i-1994, B. Gobin, C. Peeters, 1w 1m MIZA. **Sulawesi Tenggara:** 1-2km E Wolasi, 42km S Kendari, 350m, 12/14-vii-1972, W.L. Brown, 3w LACM, 9w MCZC. **Sumatera Barat:** Kotabaru, 1937, Mann, NGS-SI Exped., 4w USNM; Moeara Mahat [Muaramahat, 0/16'N 100/49'E], 1937, Mann, NGS-SI Exped., 1w USNM; Sikaping, Loebeck [Lubuk], 1937, Mann, NGS-SI Exped., 4w USNM. **Sumatera Selatan:** Pagaralum, 1937, Mann, NGS-SI Exped., 1w USNM. **Sumatera Utara:** Pematangsiantar, J. Matthews, 2w USNM; Pematangsiantar, 1937, Mann, NGS-SI Exp, 32w USNM, 1w LACM. **Undetermined Sumatra:** Betanquahat, 1937, Mann, NGS-SI Exp, 1w USNM. MALAYSIA. **Negeri Sembilan:** Pasoh, 30-ix-1966, P. Greenslade, 4w ANIC. **Pahang:** Kuala Lompat, Natl. Pk. (MV light), 25-viii-1992, D. Furth, 2w MCZC; loc. cit., 26-viii-1992, D. Furth, 6w MCZC. **Sabah:** Sepilok Forest Reserve, nr. Sandakan, 10-vi-1968, R.W. Taylor 68.407, 2w ANIC; Deramakot Forest Reserve, 23-iii-1998, C. Brühl, 4w MIZA. **Sarawak:** Kapit District, Merirai Valley, 28-31-vii-1958, T.C. Maa, 1w LACM; Bau District, Bidi, 90-240m, 2-ix-1958, T.C. Maa, 1w LACM; Buda Camp, SW Gn Buda, 64km S Limbang, 4/22'N 114/09'E, 9-xi-1996, S.L. Heydon, S. Fung, 8w LACM; Fourth

Division, Gunung Mulu Natl. Pk., v/viii-1978, P.M. Hammond, J.E. Marshall, BM1978-49, 3w BMNH; Semengoh Forest Reserve, 11 miles SW Kuching, 2/3-vii-1968, R.W. Taylor 68.769, 3w ANIC, loc. cit., 1/4-vi-1968, R.W. Taylor 68.218, 3w ANIC. **Undetermined Borneo:** Pajan, E. Mjöberg, 1w USNM. **Selangor:** Upper Gombak Valley, nr. Kuala Lumpur, 13-vii-1968, ca. 1500ft, R.W. Taylor 68.819, 3w ANIC; Ulu Gombak, nr. Kuala Lumpur, 11/14-vii-1968, ca. 800ft, R.W. Taylor 68.818, 5w ANIC; Gombak, 5-x-1973, B. Bolton, 3w LACM, 6w MCZC; loc. cit., 30-ix-1973, B. Bolton, 3w MCZC; Ulu Gombak, 3/20'N 101/45'E, 15km NNE Kuala Lumpur, 220m, vii-ix-1992, F. Ito, FI92MG-29, 4w MIZA; loc. cit., vii-ix-1992, F. Ito, FI92MG-331, 6w MIZA; loc. cit., 19-ix-1996, F. Ito, FI96-541, 6w MIZA; loc. cit., 24-ix-1996, F. Ito, FI96-677, 1w MIZA; loc. cit., vii-1998, F. Ito FI98-159, 3w MIZA; loc. cit., vii-1998, F. Ito FI98-186, 2w MIZA; Ulu Gombak, 3/20'N 101/45'E, 15km NNE Kuala Lumpur, 220m, vii-1998, B. Gobin BG98-11, 2w MIZA; loc. cit., vii-1998, B. Gobin BG98-19, 2w MIZA; loc. cit., vii-1998, B. Gobin BG98-28, 2w 1m MIZA; loc. cit., xi-1998, B. Gobin BG98-44, 2w 1m MIZA; loc. cit., xi-1998, B. Gobin BG98-45, 1w 1m MIZA; loc. cit., xi-1998, B. Gobin BG98-49, 1w 1m MIZA; loc. cit., xi-1998, B. Gobin BG98-50, 2w MIZA; loc. cit., xi-1998, B. Gobin BG98-52, 4w MIZA. **Terengganu:** Besut, Mt. Gunong, Tebu, 400ft, iii-1958, 1w USNM; Besut, Mt. (Gunong) Tebu, iii-1958, 400ft, 1w USNM. PAPUA NEW GUINEA. **Madang:** Karker I., ca. 800m, H. Gay 220, 12w LACM. PHILIPPINES. **Lanao del Norte:** Kolambugan, 1914, Banks, 1w USNM. **Laguna:** Mt. Makiling, Baker, 4w USNM; Mt. Makiling, 3-ii-1931, F.C. Hadden, 2w CASC; Mud Spring, Mt. Makiling, 5-v-1985, P.J. & J.O. Schmidt, 1w LACM; Laguna, Mt. Makiling, above

Los Baños, 24-x-1986, K. Starr 1252, 8w LACM; loc. cit., 13-vii-1985, K. Starr 1183, 5w LACM; Los Baños, Mt. Makiling, 14/10'N 121/11'E, 21-ix-1978, B.B. Lowery, 5w ANIC; Mt. Makiling, Baker, 9w USNM. **Leyte:** V.I.S.C.A., Baybay, 28-xii-1982, K. Starr 442, 6w LACM; loc. cit., K. Starr 443, 9w LACM. **Misamis Oriental:** Hindangon, 20km S Gingoog, 600-700m, 20/24-iv-1960, H. Torrevillas. **Negros Oriental:** Dumaguete, various dates 1931-25, Chapman, 55w, 2q, 1m USNM; Horns of Negros, 1100m, 1942-43, 1w USNM; Mt. Manapla, 14-xi-1930, S. del Rosario, 2w USNM; Dumaguete, 20-iii-1922, Chapman 1w LACM; loc. cit., Chapman, 3w LACM; loc. cit., 7-vii-1943, Chapman, 5w LACM. **Quezon:** National Botanical Gardens, 28km S Real, 300m, 14/40'N 121/36'E, 4-ix-1978, B.B. Lowery, 2w ANIC; 16km S Real, 300m, 14/40'N 121/36'E, 2-ix-1978, B.B. Lowery, 4w ANIC.

***Gnamptogenys niuguinense* sp. n.**

(Fig. 30)

Diagnosis. Scape longitudinally strigulose; no occipital lobe; occipital lamella subquadrate. Fore coxa transversely strigose to strigulose in lateral view, femur mostly smooth with scattered low transverse strigulae that become longitudinal apically, meso- and metafemur with angular apical paired lobes. Postpetiolar dorsum transversely strigate anterad, curving posteriorly becoming longitudinal, laterally

with transverse strigae anterad, obliquely strigate posterodorsad and strigulose posteroventrally.

Type material. Holotype worker. Papua New Guinea, [Oro], N. District, Popondetta [8/45'S 148/15'E], 27-vi-1973, P.M. Room, deposited in ANIC. Paratypes. One worker in ANIC from Papua New Guinea, Oro, N. District, Saiho, 28-vi-1973, P.M. Room. One worker in ANIC from Papua New Guinea, Oro, N. District, Kokoda, 9-iii-1972, P.M. Room.

Worker. Metrics. [Holotype] Paratypes ($n = 2$): HL [1.18] 1.17, 1.25; HW [0.99] 0.99, 1.02; ML [0.67] 0.62, 0.64; SL [1.13] 1.06, 1.14; ED [0.35] 0.30, 0.39; WL [1.81] 1.69, 1.90 mm. CI [0.84] 0.82, 1.18; SI [1.14] 1.07, 1.14; MI [0.68] 0.63, 0.63; OI [0.35] 0.30, 0.38. Head with broadly convex lateral margins in frontal view, posterior margin relatively straight, anterior margin of clypeal lamella projecting anterad as blunt angle; frons longitudinally rugulose with abundant smooth-bottomed foveolae; clypeus longitudinally strigulose, strigulae more irregular than on frons and partially extending onto lamella; scape longitudinally strigulose; no occipital lobe; occipital lamella subquadrate. Lateral pronotal face longitudinally strigate with scattered foveolae, pronotum in dorsal view longitudinally strigate with foveolae laterally and anteriorly; mesonotum longitudinally strigate with scattered punctae; anepisternum rectangular with anteroventral triangular lobe, mostly strigulose with some foveolae; katepisternum longitudinally strigulose with foveolae; metapleuron anterodorsally strigulose and posteroventrally longitudinally costate; metanotum and propodeal dorsum transversely strigate with lateral foveolae; propodeal armature

usually wanting, sometimes minute denticles present, declivity anteriorly rugulose-punctate and posteriorly mostly smooth.

Petiolar node dorsum foveolate with transverse strigae, ventral process forms two sharp denticles separated by broad concavity in lateral view; postpetiolar dorsum transversely strigate anterad, posteriorly becoming longitudinal, laterally with transverse strigae anterad, obliquely strigate posterodorsad and strigulose posteroventrally; postpetiolar sternum transversely strigulose with smooth median area; dorsum of abdominal segment 4 finely strigate except for fine anteromedian strip of transverse strigae, laterally with arching strigae. Fore coxa transversely strigose to strigulose in lateral view; femora mostly smooth with scattered low transverse strigulae that become longitudinal apically, meso- and metafemora with angular apical paired lobes; tibia longitudinally strigulose-punctate; fore tarsus opposite strigil with row of stout setae. Dorsum of thorax and abdominal segments 1-4 with few standing hairs, most restricted to promesonotum. Head, mesosoma, petiole, and gaster brown; mandibles, antennae, legs ferruginous brown.

Queen. Metrics ($n = 1$): HL 1.29, HW 1.14, ML 0.72, SL 1.15, ED 0.39, WL 0.88 mm. CI 0.63, SI 1.00, MI 0.63, OI 0.34. Pronotum transversely strigate on anterior face, arching around laterally becoming longitudinal; mesopleuron and mesonotum longitudinally striate with scattered foveolae; propodeum transversely strigate with scattered foveolae.

Male. Unknown.

Comments. This New Guinea endemic is apparently a sister species of *G. macretes*, sharing many of the general patterns of sculpturing and the lack of an occipital lobe.

G. macretes differs from *G. niuguinense* in the following characters: clypeal lamella protruding less, scape mostly smooth, occipital lamella convex, tibiae longitudinally strigulose punctate, femora and tibiae smooth, meso- and metafemora with convex apical paired lobes, fore tarsus opposite strigil with a single stout seta.

Etymology. The species name is derived from the Papuan Pidgin English name for New Guinea: Niu Guini.

Additional specimens examined. PAPUA NEW GUINEA. **Central:** Brown River Station, 21-i-1971, B.B. Lowery, 1q ANIC. **Madang:** 35 km SW Madang, 160m, 5/26'S 145/34'E, 31-i-1989, P.S. Ward 10097-4, 1w MCZC.

***Gnamptogenys ortostoma* sp. n.**

(Fig. 31)

Diagnosis. Head subrectangular in frontal view, with anterior margin of clypeal lamella relatively straight to slightly concave, laterally angular; mandibular dorsum mostly smooth with piligerous punctae. Lateral pronotal face densely foveolate, anteroventral corner forming acute angle; humeral angle lamellate.

Type material. Holotype worker. Singapore, Bukit Timah, 17-iii-1967, D.H. Murphy. Deposited in ANIC. Paratype. One queen on same pin as holotype in ANIC.

Worker. Metrics. [Holotype] Paratype ($n = 1$): HL [0.94] 0.98, HW [0.70] 0.74, ML [0.42] 0.38, SL [0.76] 0.83, ED [0.18] 0.20, WL [1.24] 1.23 mm. CI [0.78] 0.76, SI [1.09] 0.97, MI [0.60] 0.51, OI [0.26] 0.24. Head subrectangular in frontal view,

lateral margins straight to broadly convex, posterior margin broadly concave, anterior margin of clypeal lamella straight to slightly concave, laterally angular; frons densely punctate, almost areolate, ridges between depressions rounded, not sharp; fine median longitudinal sulcus extends from posterior clypeal margin to eye height; clypeus smooth with round punctures, lamella rugulose-scrobiculate; scape mostly smooth with scattered punctulae; mandibular dorsum mostly smooth with piligerous punctae, punctae deeper and more elongate basally; occipital lobe well developed, lamella narrow, angular at ends.

Lateral pronotal face densely foveolate, anteroventral corner forming acute angle; humeral angle well developed, lamellate; anepisternum mostly smooth with scattered punctae; metapleuron mostly smooth; mesosomal dorsum densely foveolate, promesonotal suture impressed as brief transverse line, laterally obliterated; propodeal declivity mostly smooth, bordered by carina contiguous with propodeal denticles. Petiolar node evenly convex in lateral view, ventral process forming anteriorly projecting lobe, dorsum smooth with foveolae; postpetiolar dorsum mostly smooth with scattered punctae, punctae deeper and more abundant anterad than posterad, laterally with deeper and more punctae than dorsally; sternum mostly smooth with scattered punctae; dorsum of abdominal segment 4 mostly smooth with scattered punctulae. Fore coxa smooth in lateral view; fore tarsus opposite strigil with single stout seta; metacoxal tooth slender, triangular, relatively straight. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster dark brown to black; mandibles, antennae, legs ferruginous.

Queen. Metrics ($n = 1$): HL 0.94, HW 0.73, ML 0.44, SL 0.74, ED 0.23, WL 1.34 mm. CI 0.78, SI 1.01, MI 0.60, OI 0.21. Pronotum areolate, with almost denticle-like anteroventral corner in lateral view; mesonotum mostly longitudinally rugulose-punctate; mesopleuron mostly smooth with scattered foveolae; dorsal propodeal face areolate. Metacoxal tooth stout, arched.

Male. Unknown.

Comments. The elongate habitus of this species, especially the rectangular head shape, is reminiscent of similar morphologies seen in the *laevior* group. The presence of propodeal teeth in *G. ortostoma* precludes its inclusion in the *laevior* group, which lacks propodeal armature.

Etymology. The species name is derived from a conjugation of the Greek words for “straight,” *orthos*, and “mouth,” *stoma* (n.).

Additional specimens examined. MALAYSIA. **Sarawak:** Fourth Division, Gunung Mulu Natl. Pk., 28-iii-1978, N.M. Collins, 1q BMNH. THAILAND. Chiang Mai, iii-1975, D. Jackson, 1w BMNH.

***Gnamptogenys palamala* sp. n.**

(Fig. 32)

Diagnosis. Mandibular dorsum mostly smooth with scattered punctulae, masticatory margin separated from internal margin by sharp angle, the masticatory and internal margins diverging from each other. Tergite of abdominal segment 4 with basal half

longitudinally strigose and bulging in lateral view, apical half transversely strigose and straight in lateral view.

Type material. Holotype worker. Malaysia, Sarawak, Fourth Division, Gunung Mulu Natl. Pk., P.E. Hammond & J.E. Marshall, v-viii-1978, BM 1978-49. Deposited in BMNH. Paratype. One worker on the same pin as holotype, deposited in BMNH.

Worker. Metrics. [Holotype] Paratype ($n = 1$): HL [1.51] 1.78, HW [1.29] 1.32, ML [0.77] 0.80, SL [1.35] 1.45, ED [0.25] 0.28, WL [2.06] 2.24 mm. CI [0.85] 0.74, SI [1.05] 1.10, MI [0.51] 0.61, OI [0.19] 0.21. Head with subparallel lateral margins in frontal view, posterior margin medially straight with lateral lobes slightly projecting posterad; anterior margin of clypeus forms obtuse angle with median blunt point, lamella not well developed; cephalic vertex with carina that borders posterior margin, joining both occipital lobes; frons densely foveolate, almost areolate, with fine longitudinal sulcus extending posterad of frontal triangle and ending at eye height; clypeus posteromedially foveolate, anteriorly longitudinally striate; mandibular dorsum mostly smooth with scattered punctulae, masticatory margin with low denticles and separated from internal margin by sharp angle, the two margins diverging from each other; scape longitudinally strigulose and punctate; occipital lamella angular at both ends.

Anteroventral margins of pronotum form sharp point in lateral view; anteroventral margin of anepisternum with smooth and prominent carinae; katepisternum wedge shaped; mesosoma densely foveolate; promesonotal suture brief; mesosoma with evenly convex dorsal margin curving posterad to peg like

propodeal denticle in lateral view, then briefly concave before becoming convex again. Petiolar node evenly convex, areolate in lateral view; ventral process forming narrow, anteriorly placed lobe; postpetiolar dorsum with dense round foveolae anteriorly, posteriorly becoming less dense and oval; sternum medially smooth; tergite of abdominal segment 4 with basal half longitudinally strigose and bulging in lateral view, apical half transversely strigose and straight in lateral view. Fore coxae with low to prominent transverse strigulae in lateral view; fore tarsus opposite of strigil with row of stout setae. Head, mesosoma, petiole, and gaster reddish to dark brown; mandibles, antennae, legs brown.

Queen and male. Unknown.

Comments. The shape of the mandibles, the smooth mandibular dorsum, and the dorsal bulge of the fourth abdominal tergite make this species easy to determine. The type locality is a mixed dipterocarp forest.

Etymology. The species name is a compound epithet derived from the feminine Latin nouns for “shovel,” *pala*, and “jawbone,” *mala*. It alludes to the shovel-like mandibles of this species.

***Gnamptogenys paso* sp. n.**

(Fig. 33)

Diagnosis. Head with sinuate lateral margins in frontal view, slightly concave near eyes, convex anterad. Anterior margin of clypeal lamella converging toward median

blunt point, laterally bluntly angular. Mesosomal dorsum mostly smooth with scattered foveolae laterally, plus scattered shallow patches of longitudinal undulations. Petiolar node with dorsal margin higher posterad than anterad in lateral view; anterior margin straight and vertical, dorsal margin broadly convex, posterior margin steeply descending.

Type material. Holotype worker. Malaysia, Negeri Sembilan, Pasoh Forest Reserve, iii-1994, M. Brendell, K. Jackson, L. Ficken. Deposited in BMNH.

Worker. Metrics. [Holotype] Paratypes ($n = 3$): HL [1.75] 1.71-1.76, HW [1.52] 1.43-1.51, ML [0.92] 0.91-1.00, SL [1.59] 1.61-1.62, ED [0.33] 0.29-0.31, WL [2.48] 2.44-2.50 mm. CI [0.61] 0.83-0.88, SI [1.05] 1.07-1.13, MI [0.61] 0.64-0.66, OI [0.22] 0.20-0.21. Head with lateral margins sinuate in frontal view, slightly concave near eyes, convex anterad; posterior margin concave, anterior margin of clypeal lamella converging toward median blunt point, laterally bluntly angular; frons strigulose-punctate, strigulae continuing onto cephalic sides; clypeus longitudinally strigulose; scape with variable smooth and strigulose areas, most strigulae present apically; occipital lobe present; occipital lamella convex, parallel sided. Mesosoma mostly foveolate in lateral view, pronotal background sculpture mostly smooth dorsally, strigulose ventrally and on mesopleuron; pronotum with anterodorsal margin strigulose-punctate, anteroventrally bluntly angular, humeral angle not lamellate; mesosomal dorsum mostly smooth with scattered foveolae laterally, plus scattered, shallow longitudinal undulations; anterodorsal metapleuron mostly smooth, posteroventral metapleuron longitudinally strigulose; propodeal

dorsum with more foveolae and strigulae, propodeal declivity mostly smooth, with triangular denticles.

Petiolar dorsum mostly smooth with scattered foveolae, node with dorsal margin higher posteriorly than anteriorly in lateral view, anterior margin straight and vertical, dorsal margin broadly convex, posterior margin steeply descending; ventral petiolar process forms anteriorly projecting triangular lobe; postpetiolar dorsum mostly smooth with scattered shallow punctae, anterolaterally with oblique strigulae; sternum mostly smooth with lateral and posterolateral strigulae; fourth abdominal tergite mostly smooth with scattered punctulae, sternum smooth. Fore coxa transversely strigulose in lateral view, especially along posterior half; fore tarsus opposite strigil with row of stout setae; metacoxal tooth straight with posterior flange. Dorsum of thorax and abdominal segments 1-4 with few, scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster ferruginous-brown; mandibles, antennae, legs ferruginous.

Queen and male. Unknown.

Comments. This species comes close to *G. binghamii* in the key. *G. binghamii* can be separated from *G. pasci* by its smaller size (HL < 1.5; WL < 2.0 mm) and evenly convex petiolar node when seen laterally, as well as the lamellate humeral angle. The head of the holotype is detached and separately mounted on the same pin as the body.

Etymology. The species name is derived from the name of the type locality, Pasoh Forest Reserve, and is assumed to be feminine.

Additional specimens examined. MALAYSIA. **Selangor:** Ulu Gombak, 15km NNE Kuala Lumpur, 3°20'N 101°45'E, 220m, vii/ix-1992, F. Ito, FI92MG-23, 2w NMKL;

Ulu Gombak, 15km NNE Kuala Lumpur, 3°20'N 101°45'E, 220m, vii/ix-1992, F. Ito, FI92MG-121, 1w MCZC, 1w MIZA.

Gnamptogenys posteropsis (Gregg)

(Fig. 34)

Stictoponera posteropsis Gregg, 1951:77, Figs. 1, 3. Holotype queen: [Indonesia], Sumatra, Lampong, Wai Lima (Karny) (MCZC) [Examined].

Gnamptogenys posteropsis (Gregg); Brown, 1958:229. Placed in *Gnamptogenys*.

Diagnosis. Eye subglobulose and situated one-half its diameter or less from the vertex in lateral view; postpetiolar sternum with V-shaped anterior process and longitudinal median keel extending from process to just beyond posterior sternal margin, forming angular lamellate projection.

Worker. Metrics. ($n = 3$): HL 1.09-1.74, HW 0.92-1.35, ML 0.54-0.90, SL 0.89-1.51, ED 0.17-0.26, WL 1.53-2.49 mm. CI 0.78-0.88, SI 0.97-1.12, MI 0.59-0.67, OI 0.19-0.20. Head with straight lateral margins in frontal view, posterior margin concave with posterolateral projecting occipital lobes, anterior margin of clypeal lamella slightly sinuate with convex median projection; clypeus usually longitudinally strigulose with shallow median sulcus, occasionally transversely strigulose or mostly smooth with scattered punctae; frons mostly with round to oval foveolae; vertex posteriorly bordered by transverse carina that joins occipital lobes;

eye situated one-half its diameter or less from vertex; scape longitudinally strigulose; mandibular dorsum mostly longitudinally strigose with scattered prominent costae, masticatory margin slightly denticulate; occipital lobe projects posteroventrad in lateral view.

Mesosomal dorsum with uniformly distributed round to oval foveolae, intervening cuticle smooth; humeral angle lamellate; promesonotal suture weakly impressed, discernible only medially; anepisternum relatively narrow; metanotal sulcus vaguely impressed; mesosoma with very broadly convex dorsal margin in lateral view, mostly foveolate, especially propodeum; propodeal declivity bordered by triangular lamella that surrounds declivity, declivity mostly smooth except for median raised area. Petiolar dorsum densely foveolate, ventral process subquadrate in lateral view; postpetiolar dorsum with round to slightly oval foveolae, not as dense as on mesonotum, posterior margin scrobiculate; sternum with V-shaped anterior process and longitudinal median keel extending from process to just beyond posterior sternal margin, keel occasionally medially effaced, posteriorly forming angular projection; dorsum of abdominal segment 4 longitudinally costate, laterally foveolate; presternite of fourth abdominal sternite with bluntly pointed posteromedian directed lobe that hangs over broad, deep transverse sulcus with smooth cuticle on 3/4 anterior part of sternite, posterior fourth longitudinally strigulose; presternal lobe hook shaped in lateral view. Fore coxa strigose laterally; fore tarsus opposite strigil with row of setae, basal seta stoutest. Dorsum of thorax and abdominal segments 1-4 with abundant erect hairs. Head, mesosoma, petiole, and gaster reddish to dark brown; mandibles, antennae, legs light brown to brown.

Queen. Metrics ($n = 1$): HL 1.80, HW 1.42, ML 0.87, SL 1.52, ED 0.32, WL 2.73 mm. CI 0.79, SI 1.07, MI 0.61, OI 0.23. Pronotum densely foveolate laterally, medially either foveolate or mostly smooth; mesonotum longitudinally rugulose-punctate; anepisternum foveolate to longitudinally rugulose with scattered foveolae; propodeum densely foveolate.

Male. Unknown.

Comments. This striking species cannot be mistaken for any other *Gnamptogenys*. The posteriorly placed eyes, the keel on the gaster, and the deep transverse sulcus on the anterior margin of the fourth abdominal sternite suggest specialized predatory habits. Labels from some of the specimens examined indicated that some came from leaf-mold berlesate and rainforest or were taken while foraging on vegetation.

Specimens examined. INDONESIA. **Sumatera Selantan:** Lampung, Wai Lima, 12-xi-1921 #114, Karny, 1q MCZC. MALAYSIA. **Sabah:** Sandakan Kolopsis #5, 60m, 12-iii-1983, B. Hauser, 1w BMNH; Danum Valley, xi-1986, P. Eggleton, 1w BMNH; Danum Valley, west trail, 100m, 22-viii-1997, C. Brühl, 1w MIZA, Danum Valley, west trail, 100m, 19-viii-1997, C. Brühl, 1w MIZA; Tawau Hills Pk., 24 km NNW Tawau, 4/17'N 117/54'E, 6-x-1996, F. Ito, FI96-531, 1w MIZA; Poring Hot Springs, 900m, 12-v-1987, D. Burckhardt & I. Löbl, 1w BMNH. **Sarawak:** Kampong Segu, 20 mi SW Kuching, 4-vi-1968, RWT-68.289, 1w ANIC; confl. Sun Oyan and Mujong Rivers, E Kapit, 50m, 18-v-1994, I. Löbl & D. Burckhardt #5a, 1w BMNH. **Pahang:** Ringlet, 1250m, ravine #20, 26-iii-1993, I. Löbl & Calame, 1w BMNH; Cameron Highlands, Trail 9, 1400m, 27-iii-1993, I. Löbl & Calame #21, 1w BMNH. **Selangor:** Ulu Gombak, vii-x-1992, F. Ito, FI92MG-446, 3w MIZA, 1w

ANIC. PHILIPPINES. **Laguna**: 28km S Real, 300m, 14/40'N 121/36'E, 4-ix-1978, B.B. Lowery, 1w ANIC; Los Baños, Mt. Makiling, 500m, 14/10'N 121/11'E, 27-viii-1978, B.B. Lowery, 1w ANIC; Mt. Makiling, nr. summit, ii-1968, R.A. Morse, 1w MCZC. **Negros Oriental**: Dumaguete, Camp 1927, J.W. Chapman, 1w MCZC; Dumaguete, 2-v-1928, J.W. Chapman, 1q USNM; Dumaguete, Camp 6-iv-1927, J.W. Chapman, 2w USNM; Dumaguete, C. Lookout, 457m, 1949, J.W. Chapman, 2w MCZC.

***Gnamptogenys scalpta* sp. n.**

(Fig. 35)

Diagnosis. Propodeal declivity mostly smooth with strigulae along lateral margins and two diverging, posteromedian crests, declivity with broad lamella surrounding its posterolateral margins, propodeal denticles absent. Petiolar node convex with anterior margin longer than posterior margin in lateral view; ventral process subquadrate, slightly more projecting anterad than posterad, with dorsum foveolate over transverse striae; postpetiolar dorsum with punctae over transversely striate ground sculpture anteriorly, becoming longitudinal posteriorly.

Type material. Holotype worker. Malaysia, Sabah, Poring Hot Springs, 600m, 10-v-1987, I. Löbl & D. Burckhardt 19a. Deposited in BMNH.

Worker. Metrics. Holotype: HL 1.35, HW 1.20, ML 0.74, SL 1.23, ED 0.20, WL 1.94 mm. CI 0.89, SI 1.03, MI 0.62, OI 0.17. Head with broadly convex lateral

margins in frontal view, posterior margin concave, anterior margin of clypeal lamella sinuate, with median blunt point; frons longitudinally strigulose with abundant round to oval punctae; clypeus longitudinally strigulose with median shallow sulcus; scape longitudinally carinate; occipital lamella narrow, bluntly angular at both ends. Mesosoma mostly foveolate-striate in lateral view; mesosomal dorsum with round to oval foveolae on smooth to striate cuticle; pronotum with posteromedian striate area devoid of foveolae; promesonotal suture impressed as transverse line; mesonotum lacking foveolae medially, mostly smooth with weak curves to transverse striae; mesopleural suture scrobiculate; anterodorsal metapleuron smooth; propodeal dorsum densely foveolate, laterally with scalloped foveolae, propodeal declivity mostly smooth with strigulae along lateral margins and two diverging posteromedian crests, with broad lamella surrounding posterolateral propodeal margin, denticles absent.

Petiolar node dorsum transversely foveolate-striate, with anterior margin longer than posterior margin in lateral view, ventral petiolar process subquadrate, projecting slightly more anterad than posterad; postpetiolar dorsum with punctae in shallow elongate depressions that become deeper posterad, ground sculpture transversely striate along anterior half, becoming longitudinal on posterior half; posterior margin with narrow strigulose band; dorsum of abdominal segment 4 mostly smooth with scattered punctae, each puncture coinciding with small striate patch, mostly obliquely strigulate in lateral view, sternum strigulose. Fore coxa transversely striate in lateral view; fore tarsus opposite strigil with row of stout setae; metacoxal tooth relatively long and straight. Dorsum of thorax and abdominal segments 1-4 with scattered erect

to subdecumbent hairs. Head, mesosoma, petiole, and gaster dark brown; mandibles, antennae, legs brown.

Queen and male. Unknown.

Comments. This species and *G. helisa* have fine striations on the body, but *G. helisa* is a larger species (HL > 1.0; WL > 2.2 mm), with mostly smooth scapes, and the anterior margin of its clypeal lamella converges to a median lobe, while the lamellar margin in *G. scalpta* is sinuate, not converging so directly. The petiolar node in *G. helisa* is not evenly convex when seen laterally but higher posterad than anterad, its subpetiolar process is shaped as an anteriorly projecting narrow lobe, and it has small but distinct propodeal denticles.

Etymology. The species name is derived from the Latin, *scalptus*, meaning “scratch” or “engrave,” and alludes to the fine striations on the body of this species.

***Gnamptogenys toronates* sp. n.**

(Fig. 36)

Diagnosis. Frons and mesosoma mostly smooth with scattered foveolae. Petiolar node slightly higher anterad than posterad in lateral view, sculpture mostly smooth with scattered punctae; postpetiolar dorsum mostly smooth with scattered foveolae.

Type material. Holotype worker. Malaysia, Sabah, Crocker Range, 19-v-87, D. Burckhardt & I. Löbl 31a. Deposited in BMNH.

Worker. Metrics. Holotype: HL 1.72, HW 1.38, ML 0.83, SL 1.41, ED 0.28, WL 2.31 mm. CI 0.80, SI 1.02, MI 0.60, OI 0.20. Head with straight lateral margins in frontal view, posterior margin convex, posterolaterally ending with denticle-like projections, anterior margin of clypeal lamella sinuate, with concavities laterad of median convexity and lateral angles; frons mostly smooth with scattered foveolae; clypeus longitudinally strigulose with median raised area laterally bound by ridges that extend from lateral edges of lamella, extending posterad to anterior edge of frontal lobes; fine longitudinal sulcus extends posterad from frontal triangle to just posterad of eye level in frontal view; occipital lamella with angular posterior and anterior ends in lateral view; scape mostly smooth with scattered piligerous punctae; mandibular dorsum longitudinally strigulose-punctate.

Mesosoma mostly smooth with scattered foveolae, promesonotal suture brief, transverse; anepisternum roughly subquadrate; metanotal sulcus impressed as fine transverse line; mesosoma with broadly convex dorsal margin in lateral view, joining propodeal declivity through broad convexity; propodeal declivity mostly smooth; petiolar dorsum mostly smooth with scattered punctae, slightly higher anterad than posterad in lateral view, ventral process narrow and lobe like in lateral view, projecting anterad. Postpetiolar dorsum mostly smooth with scattered foveolae, foveolae elongate towards posterior margin, posterior margin with brief transverse striae, sternum with median area of transverse rugae; dorsum of abdominal segment 4 longitudinally costulate with piligerous depressions between costae. Fore coxa transversely strigose laterally, fore tarsal base opposite strigil with single stout seta and fine comb apically. Metacoxal tooth triangular, straight, tapering apically.

Queen and male. Unknown.

Comments. *G. costata* may be confused with *G. toronates*, but *G. costata* has the propodeal spiracle nearer to the propodeal dorsum than *G. toronates* when seen laterally and the declivitous and dorsal propodeal margins separate at the denticle. In *G. toronates* the propodeal denticles are posterad of the break between both propodeal margins. In *G. costata* the subpetiolar process does not form an acutely pointed lobe without a posterior angle as in *G. toronates*.

Etymology. The species name is a compound epithet derived from the Latin words for “bulge,” *torus* (m.), and “buttocks,” *natis* (f.). It alludes to the mostly smooth sculpturing compared with other species of *Gnamptogenys* that have a costulate fourth abdominal tergite.

***Gnamptogenys treta* sp. n.**

(Fig. 37)

Diagnosis. Scape mostly smooth with scattered piligerous punctae; occipital lobe absent; subpetiolar process projecting anterad as sharply pointed triangular lobe; sternum of fourth abdominal segment mostly smooth with sparse punctae; metacoxal tooth low and triangular.

Type material. Holotype worker. Malaysia, Sabah, 7km N Tembunen, 700m, 20-v-1989, I. Löbl & D. Burckhardt 32a. Deposited in BMNH. Paratype. One worker in the BMNH with the same data as the holotype.

Worker. Metrics. Holotype: HL 1.43, HW 1.18, ML 0.86, SL 1.34, ED 0.22, WL 2.08 mm. CI 0.83, SI 1.14, MI 0.73, OI 0.19. Head subquadrate in frontal view, widest anterad, lateral margins convex, posterior margin concave, anterior margin of clypeal lamella medially triangular with bluntly angular sides; frons and vertex densely foveolate; clypeus longitudinally strigulose with strigulae extending onto lamella; scape mostly smooth with scattered piligerous punctae; occipital lobes absent; occipital lamella well developed, convex. Pronotum foveolate, humeral angle small; anepisternum cuneiform, mostly smooth with scattered punctae; katapisternum foveolate with rugosity along posteroventral margin; metapleuron smooth anterodorsally, posteroventrally strigulose-punctate; propodeal declivity mostly smooth with transverse strigulae anterad; mesosomal dorsum foveolate, without transverse sutures, with median longitudinal smooth area. Mesosoma with convex dorsal pronotal margin in lateral view, mostly flat mesometanotum, convex dorsal propodeal margin and concave declivity. Petiolar node with subpetiolar process projecting anterad as sharply pointed triangular lobe in lateral view; postpetiolar dorsum foveolate, depressions becoming progressively smaller and less numerous posterad, sternum mostly smooth; dorsum of abdominal segment 4 mostly smooth with scattered punctulae, sternum mostly smooth with sparse punctae. Fore coxa transversely strigulose in lateral view; fore tarsus opposite strigil with row of stout setae; metacoxal tooth low, triangular. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster ferruginous brown; mandibles, antennae, legs ferruginous.

Queen and male. Unknown.

Comments. This species is similar to *G. pasci* and *G. binghamii* in the key. It may be further separated from *G. pasci* by the larger size (HL > 1.6; WL > 2.3 mm) of *G. pasci*. Also, the petiolar node of *G. pasci* has a very broad dorsal margin, higher posterad than anterad, and the subpetiolar process has a posterior blunt angle. *G. treta* is slightly larger than *G. binghamii*, which has occipital lobes and a lamellate humeral angle.

Etymology. The species name alludes to its foveolate cuticle and is derived from the Greek for “perforated,” *tretos*.

epinotalis group

Worker diagnosis. Scape length not surpassing median cephalic margin; eye reduced (OI 0.07-0.13). Katepisternum distinctly delimited by strongly marked mesopleural suture forming arching continuous groove with mesometapleural suture; propodeal spiracle separated less than one spiracular diameter from declivitous margin in lateral view, usually at apex of small tubular extensions, occasionally projecting beyond declivitous margin. Petiole erect in lateral view, anterior and posterior margins mostly straight and slightly convergent dorsad; length of dorsal margin less than anterior margin.

Worker description. Head wedge shaped in dorsal view, wider posterad than anterad; lateral margins broadly convex, posterior margin concave; occipital lobe absent, occipital ridge present, low, not laminate; vertex with reduced (mostly

smooth) sculpturing relative to frons, vertex separated from frons by relatively sharp angle (sculptured and more evenly curved in *G. crenaticeps*); frons mostly with rugulose-punctate rows that slightly diverge posterad, punctae usually flat bottomed in cross section; frons with longitudinal carinulae; dorsal lobe of torulus partially fused to ventral surface of frontal lobe but still distinct as separate sclerite; scape gradually widened apically, scape length not surpassing median cephalic margin (SI 0.78-0.92); background sculpturing mostly smooth with abundant piligerous punctulae, no strigulae, and abundant erect to suberect pilosity of uniform length along posterior margin in dorsal view; third antennal segment longer than wide; lateral margin of frontal lobe in dorsal view broadly convex, dorsal surface flat; eye reduced (OI < 0.15), with few ommatidia; dorsal mandibular surface mostly smooth with sparse, shallow punctae; masticatory border denticulate, with distinct ridge defining narrow, parallel-sided sector along basal margin, sometimes extending entire length of masticatory border; clypeal surface convex in all directions, forming separate convexity from frons in lateral view; anterior margin convex, lamella well developed.

Mesosomal dorsal margin broadly convex in lateral view, humeral angle not lamellate; ventral pronotal margin mostly straight, with bordering sulcus; promesonotal suture reduced, at most present as brief transverse impression; metanotal sulcus absent (except *G. epinotalis*); anepisternum posteriorly continuous with metapleuron, not separated by distinct suture or groove though sculpturing may differ from metapleuron; katepisternum distinctly delimited by strongly marked mesosomal suture forming single arching, continuous groove with mesometapleural

suture; anterior margin with broad, shallow sulcus; declivitous propodeal face mostly smooth, propodeal spiracles separated by less than one spiracular diameter from declivitous margin in lateral view, usually at apex of small tubular extensions, occasionally projecting beyond declivity.

Petiole erect in lateral view, anterior and posterior margins mostly straight and slightly convergent dorsad; length of dorsal margin less than anterior margin; anterior crest present, medially reduced (totally absent in *G. luzonensis*); subpetiolar process subquadrate laterally (triangular in *G. crenaticeps*), with anteroventral corner usually projecting ventrally more than posterior corner; process wedge shaped in ventral view, its anterior end pointed and posterior end bifurcate, with a median longitudinal groove; petiolar spiracle below anterolateral process; postpetiolar ventral margin broadly convex in lateral view; postpetiolar anterior and dorsal margins straight in lateral view, separated by convexity, process in anterior view convex to V-shaped, ventrally concave, with lateral convexities; presternite and pretergite of fourth abdominal segment without stridulitrum. Dorsum of thorax and abdominal segments 1-4 usually with scattered erect to subdecumbent hairs. Basal fore tarsus dorsally smooth with punctulae, concavity with single stout seta; apex of second protarsal segment with four stout setae; denticle present on metacoxal dorsum.

Included species: *G. atrata*, *G. cribrata*, *G. epinotalis*, *G. luzonensis*, *G. major*, *G. malaensis*, *G. sila*.

Comments. This species group is made up of seven small species found from Southeast Asia to Melanesia and includes the smallest known *Gnamptogenys*. The cuneiform ventral edge of the subpetiolar process is the definitive apomorphy for this

clade. They also have the eyes more reduced (CI 0.03-0.07) than any other group, though some overlap may occur with the larger values. They share with the Neotropical species *G. striatula* the densely punctulate antennal scapes. These species were previously placed in *Rhopalopone*, a group erected by Emery (1897) for *G. epinotalis* until it was synonymized by Brown (1958) as part of *Gnamptogenys*. Wheeler (1924) published a key for the species of *Rhopalopone* known at that time. Ergatoid queens are known in *G. luzonensis* and *G. malaensis*, while the queens of *G. cribrata* and *G. epinotalis* are normal, winged queens. Internal characters are based on dissections of *G. cribrata* and *G. relictata*.

Key to the workers of the *epinotalis* group in the Old World

1. Dorsum of fourth abdominal tergite mostly longitudinally costulate- or strigulose-punctate 2
- Dorsum of fourth abdominal tergite mostly smooth with scattered punctae or punctulae; costulae, if present, are limited to a narrow band along the posterior margin 3
2. Fourth abdominal tergite with longitudinal strigulose-punctate sculpturing usually extending anterad throughout its whole length; postpetiolar tergite transversely strigulose-punctate (Solomon Islands) *malaensis* (Mann)
- Fourth abdominal tergite with parallel longitudinal costulae usually not extending anterad more than one-half its length; postpetiolar tergite mostly smooth with

- scattered punctae (western Malaysia to New Guinea, Philippines)
- *cribrata* (Emery) (in part)
3. Postpetiolar tergite longitudinally costulate and with scattered punctae (Borneo)
- *sila* sp. n.
- Postpetiolar tergite either punctate or foveolate with mostly smooth cuticle between each depression; at most a narrow band of longitudinal striae may be present along posterior margin 4
4. Opening of propodeal spiracle elongate, almost slitlike (New Guinea)
- *major* (Emery)
- Opening of propodeal spiracle rounded, or slightly ovaloid at most 5
5. Declivitous propodeal face without a posterolateral ridge or denticle; WL more than 1.00, HL more than 0.81 mm (Sulawesi) *atrata* sp. n.
- Declivitous propodeal face with a posterolateral ridge or denticle sharply delimiting it from the lateral face; WL less than 1.00, HL less than 0.81 mm 6
6. Metanotal sulcus present (New Guinea) *epinotalis* (Emery)
- Metanotal sulcus absent 7
7. Propodeal dorsum with longitudinal grooves separated by flattened carinulae, some scattered punctae may be present, especially laterally; punctae on postpetiolar dorsum tend to be evenly abruptly impressed and not scalloped (Philippines) *luzonensis* (Wheeler)
- Propodeal dorsum not as above, either strigulose-punctate, punctate, or areolate; punctae on postpetiolar dorsum are scalloped, abruptly impressed anterad and

gradually sloping posterad (western Malaysia to New Guinea, Philippines)

..... *cribrata* (Emery) (in part)

***Gnamptogenys atrata* sp. n.**

(Fig. 38)

Diagnosis. Head, mesosoma, petiole, and gaster black; mandibles, clypeal lamella, antennae, legs brown. Anterior margin of clypeal lamella medially converging to form blunt obtuse angle. Propodeal declivity without posterolateral ridge or denticle sharply delimiting it from lateral propodeal face.

Type material. Holotype worker. Indonesia, Sulawesi Utara, 1000m, G. Mogogonipa, 24-ix-1986 (No collector data on the labels). Deposited in BMNH.

Paratypes. Three workers in BMNH, 1w in MIZA from holotype series.

Worker. Metrics. [Holotype] Paratypes ($n = 2$): HL [0.89] 0.91, 0.93; HW [0.71] 0.73, 0.75; ML [0.44] 0.43, 0.43; SL [0.63] 0.66, 0.68; ED [0.05] 0.08, 0.09; WL [1.16] 1.14, 1.11 mm. CI [0.81] 0.81, 0.80; SI [0.89] 0.91, 0.92; MI [0.62] 0.58, 0.58; OI [0.07] 0.11, 0.12. Head with anterior margin of clypeal lamella converging to form blunt obtuse angle in frontal view; clypeus longitudinally strigulose with median smooth area; clypeal lamella translucent, mostly smooth with sparse low strigulae. Pronotal dorsum with shallow piligerous punctae, each with one side deeper than other, roughly arranged in arches; rest of mesosomal dorsum mostly

smooth medially, laterally punctate; pronotum strigulose-punctate laterally, punctae relatively shallow, arranged in arches; promesonotal suture feebly impressed; katepisternum strigose, anepisternum mostly smooth; mesopleural suture very broad with transverse ridges and strigulae; metapleuron relatively smooth anterodorsad and longitudinally costulate posteroventrad; lateral propodeal surface mostly smooth, propodeal dorsum slightly scabrose, mostly smooth medially; propodeal declivity mostly smooth, posterolateral ridge or denticle lacking; declivitous propodeal margin slightly convex in lateral view, propodeal spiracle mounted on tubular prominence that extends beyond declivitous margin; mesosoma in lateral view with very broadly convex dorsal margin.

Petiolar dorsum mostly smooth, sparsely punctate, punctae becoming larger laterally; postpetiole laterally with scalloped foveolate, postpetiolar dorsum sparsely punctate, posterior margin with brief longitudinal strigulae; fourth abdominal tergite sparsely punctulate, posterior margin with brief longitudinal striae; fourth abdominal sternite punctate over smooth ground sculpture. Fore coxa transversely strigulose; metacoxal tooth triangular. Dorsum of thorax and abdominal segments 1-4 with abundant erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster black; mandibles, antennae, legs, and apex of propodeal spiracles and clypeal lamella brown.

Queen and male. Unknown.

Comments. This is the largest-bodied member of the *epinotalis* group and besides *G. major* the only other species that is predominantly black in coloration. It is also the only species lacking ridges or denticles on the posterolateral corners of the propodeal

declivity. *G. major* has a more triangular-shaped petiolar node in lateral view and an evenly convex margin on the clypeal lamella.

Etymology. The species name is derived from the Latin word for “dressed in black,” *atratus*, and alludes to the predominant body color of this ant.

***Gnamptogenys cribrata* (Emery)**

(Fig. 39)

Rhopalopone cribrata Emery, 1900a:311. Syntype workers: New Guinea (MCSN)
[One syntype examined].

Ectatomma (Mictoponera) diehlii Forel, 1901a:372. Syntype workers: Borneo,
Sarawak (Haviland) (MHNG) [Examined] **Syn. nov.**

Rhopalopone dammermani Wheeler, W.M., 1924:240. Holotype worker by
monotypy: Indonesia, Sebesi Island. (Dammerman) (MCZC) [Examined]. **Syn.
nov.**

Gnamptogenys cribrata (Emery); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Mesosomal dorsum varies from mostly smooth with punctae to longitudinally strigulose-punctate to densely punctate, usually with longitudinal median smooth area extending from posterior pronotum to part of propodeal dorsum; dorsal postpetiolar surface with scalloped punctae, not strigulose. Dorsum of fourth abdominal segment mostly smooth with scattered scalloped punctulae, frequently

with longitudinal costulae that extend anterad from posterior margin up to three-fourths the length, usually less, of tergite.

Worker. Metrics ($n = 10$): HL 0.62-0.72, HW 0.48-0.58, ML 0.24-0.30, SL 0.40-0.51, ED 0.03-0.06, WL 0.68-0.89 mm. CI 0.73-0.81, SI 0.82-0.90, MI 0.49-0.57, OI 0.07-0.11. Anterior margin of clypeal lamella usually with bluntly angular sides in frontal view and slight convex median projection, median projection variable as well as lateral angles; clypeus longitudinally strigulose with broad median smooth longitudinal sulcus, sometimes carinulate. Lateral pronotal face longitudinally strigulose-punctate, frequently with smooth ventral strip; mesopleuron strigulose; metapleuron posteroventrally strigulose, anterodorsally depressed and mostly smooth; mesosomal dorsum varies from punctate over smooth ground sculpture to longitudinally strigulose-punctate to densely punctate (especially on propodeum), usually with longitudinal median smooth area extending from posterior pronotum to part of propodeal dorsum; promesonotal suture reduced to brief, feebly impressed line; metanotal sulcus usually absent, rarely present as vaguely impressed very fine line; propodeal declivity ranging from smooth to longitudinally strigulose, with or without low posterolateral denticles or lobes; propodeal dorsal margin meets declivitous margin through single convexity or blunt angle in lateral view, lateral propodeal face mostly smooth.

Petiolar dorsum ranging from mostly smooth to densely punctate, node punctate in lateral view; postpetiolar dorsum mostly smooth with abundant shallow piligerous punctae forming scalloped surface, each depression with abruptly impressed anterior margin and gradually sloped posterior margin; sternum usually transversely

strigulose-punctate to densely punctate, sometimes punctate over mostly smooth ground sculpture; postpetiole punctate in lateral view, with each puncture more deeply impressed anterad than posterad; dorsum of abdominal tergite 4 similar to postpetiole but with finer, sparser depressions, frequently with longitudinal costulae that extend anterad from posterior margin up to three-fourths the length, usually less, of tergite; fourth abdominal sternite punctate over smooth to strigulose ground sculpture. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster brown; mandibles, antennae, legs ferruginous brown; lighter-colored specimens frequently found.

Queen. Metrics ($n = 1$): HL 0.67, HW 0.54, ML 0.27, SL 0.46, ED 0.11, WL 0.82 mm. CI 0.80, SI 0.85, MI 0.50, OI 0.20. Pronotum varies from punctate with scabrosity to strigulose-punctate in lateral view, anterior surface punctate with smooth cuticle between punctae; anepisternum punctate with undulations or strigulae; katepisternum longitudinally strigulose; mesoscutum longitudinally rugose-punctate, medially mostly impunctate; metanotum strigulose-punctate; propodeal declivity with more longitudinal strigulae than worker; lateral propodeal surface strigulose. Petiole more compressed than in worker.

Male. Unknown.

Comments. When Wheeler (1924:240) described *G. dammermani*, he compared it to *G. malaensis* and separated the two species based on the slight size and color differences of *G. dammermani*, as well as the presence of propodeal denticles. The examined syntype of *G. diehlii* is lighter colored than that of *G. dammermani* and has overall less sculpturing, but darker-colored specimens (previously considered *G.*

diehlii) are known from Thailand. The syntype of *G. diehlii* has a prominent spiracle on the fourth abdominal segment, but the conspicuousness of the spiracle seems to be an effect of the lighter coloring, and intermediate stages have been found in specimens previously considered *G. dammermani*. The development of the propodeal denticles, lobes, or ridges varies and does not correlate with any other potentially diagnostic character.

Compared with the forms known as *G. dammermani* and *G. diehlii* the syntypes of *G. cribrata* have more regular costulate sculpturing on the clypeus and the anterior margin of the clypeal lamella is more evenly convex, with much reduced lateral angles as well as a reduced median lobe. *G. cribrata* also has a very reduced anterior shelf on the petiole when seen laterally. The costulae are partially effaced in a specimen from Manus Island, and the same exemplar has an anterior petiolar shelf. Other specimens have the longitudinal clypeal strigulae much more regular and uniformly parallel, a condition closely approaching the regular carinulae in the forms known as *G. cribrata*. The extent of development of the anterior lobe of the clypeal lamella as well as the lateral angles of the lamella will vary. Intermediate morphologies can be found in ants previously regarded as *G. dammermani*. In short, no characters were found that could justify keeping *G. dammermani*, *G. diehlii*, and *G. cribrata* as different species from each other.

The lighter-colored specimens of *G. cribrata* may look superficially like *G. epinotalis* because of their body color, but *G. epinotalis* has uniformly round punctae on the postpetiole that are not scalloped. Other characters of *G. epinotalis* not present in *G. cribrata* are a narrow sulcus around the katepisternum, a metanotal sulcus, and

longitudinal costulae on most of the posterior end of the lateral mesosomal face. *G. cribrata* keys out along with *G. luzonensis* in the last couplet of the key. See Comments under *G. luzonensis* for additional differences between the two species in the Philippines. No ergatoid queens were seen among the four queens examined (from northern Borneo) of this species; all were either winged or previously alated individuals. This is the most widespread species of the *epinotalis* group and also the most commonly collected. Most of the specimens were found in forested areas beneath logs, one was in bamboo leaf mold, and another was from a soil core.

Specimens examined. INDONESIA. **Jawa Barat:** Bogor, 29-X-1973, B. Bolton, 1w BMNH, 6w LACM; Kalimantan, Gunung Palung Natl. Pk., Cabang Panti Res. Sta., 100-400m, 1/15'S 110/5'E, 15/vi-15/viii-1991, Y.J. Suhardjono, 1q MCZC. **Seram:** above Haruru, near Masohi, 50-150m, 18-iii-1981, W.L. Brown, 1w MCZC. MALAYSIA. **Kedah:** Gunong Jerai rainforest, 100-550m, 1-ix-1982, 3w ANIC. **Kelatan:** Temangh, forest reserve, 4-xi-1963, D.H. Murphy, Berlesate 114, 1w ANIC. **Johore:** Kahang, Kluang Road, mile 18, 18-viii-1962, D.H. Murphy, Berlesate 7, 2w ANIC; **Sabah:** Crocker Range Natl. Pk., Kota Kinabalu-Tambunan road, Km 60, 17-v-87, D. Burckhardt & I. Löbl, 1270m, BMNH; Gunong Silam, 810 m, 1983, R. Leakey, BMNH; Kibongol Valley, 7km N Tambuna, I. Löbl, D. Burckhardt, BMNH; Labuk Road, ex Sandakan (Lungmanis), 12/13-vi-1968, R.W. Taylor 68.476, 1w ANIC; Poring Hot Springs, 900m, 12-v-1987, D. Burckhardt & I. Löbl 22a, 3w BMNH; Sepilok Forest Reserve, nr. Sandakan, 12-vi-1968, R.W. Taylor 68.451, 2w ANIC; Tawau, 11-xi-81, J. Waage, BMNH; Tawau, Quoin Hill, 750 ft, 16-19-1968, R.W. Taylor 68.614, 2w ANIC. **Sarawak:** Fourth Division,

Gunung Mulu Natl. Pk., Roy. Geog. Soc. Exped., Long Palau lowland rainforest, in rotten trunk, 23-ix-1977, B. Bolton, 1w BMNH; Fourth Division, Gunung Mulu Natl. Pk., Kerangas forest, vi-1978, N.M. Collins, 1w MCZC, 3w BMNH; confl. Sun Oyan and Mujong Rivers, E Kapit, 50m, 18-v-1994; I. Löbl & D. Burkhardt 5a, 2w 1q BMNH; 12km E Bau, 20m, 14-v-1994, riparian forest, I. Löbl & D. Burkhardt 4a, 3w BMNH; Gunung Matang, 20km E Kuching, 200m, 26-v-1994; I. Löbl & D. Burkhardt 12, 2w BMNH; Kampong Segu, 20mi SW Kuching, 4-vi-1968, R.W. Taylor 68.293, 5w ANIC; Fourth Division, Gunung Mulu Natl. Pk., Roy. Geog. Soc. Exped., Kerangas, v-viii-1978, P.M. Hammond & J.E. Marshall, 3w BMNH; Semengoh Forest Reserve, 11mi SW Kuching, 2/3-vii-1968, R.W. Taylor 68.779, 1w ANIC; Semengoh Forest Reserve, 11mi SW Kuching, 28/31-v-1968, R.W. Taylor 68.202, 5w 1q ANIC. PAPUA NEW GUINEA. **Morobe**: lower Busu River, Huon Peninsula, v-17-1955 #1058, E.O.Wilson, 2w MCZC. **Manus**: Bismarck [Manus] Island, Lorengau, 20-vi-1962, Noona Dan Exped. 61-62, 1w ANIC. PHILIPPINES. **Negros Oriental**: Dumaguete, Camp 4-11-1931, J.W. Chapman 14, 5w MCZC. SINGAPORE. nr. Pierce Reservoir, 26-v-68, D.H. Murphy, BMNH; Pierce Reservoir, 27-v-1968, R.W. Taylor 68.103, 3w ANIC. THAILAND. **Trang**: 07/35'N 99/46'E, Khao Chong Nature Education Centre, 21/24-vii-1996, R. Snelling & Sonthichai, 3w LACM.

***Gnamptogenys epinotalis* (Emery)**

(Fig. 41)

Rhopalopone epinotalis Emery, 1897:550. *nomen nudum*. Without description.

Rhopalopone epinotalis Emery, 1900a:311. Syntype workers, queen: New Guinea, Paumomu River (Loria) (MCSN) [Examined].

Gnamptogenys epinotalis (Emery); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. General color yellowish brown. Mesosoma with abundant short, erect standing hairs in lateral view; metanotal sulcus present; sutures surrounding katepisternum narrow and fine; katepisternum, lateral propodeal face, and most of metapleuron with fine, longitudinal, parallel carinulae; metapleuron mostly longitudinally striate to costulate; propodeal declivity mostly smooth with sparse punctae and posterolateral low rounded lobes. Petiolar node with bluntly convex dorsal margin in lateral view.

Worker. Metrics ($n = 3$): HL 0.50-0.58, HW 0.41-0.45, ML 0.24-0.25, SL 0.33-0.41, ED 0.04-0.04, WL 0.62-0.76 mm. CI 0.78-0.82, SI 0.80-0.91, MI 0.54-0.59, OI 0.09-0.09. Head with subparallel lateral margins in frontal view, anterior margin of clypeus generally convex, lamella bluntly angular laterally with slight median convex projection; clypeus longitudinally strigulose with median longitudinal smooth area. Pronotum densely punctate along dorsal half in lateral view, ventral half mostly smooth with sparse punctae and brief longitudinal strigulae present along posterior margin; pronotal dorsum with rugulae arching around anterior margin, medially longitudinal; anepisternum longitudinally strigulose anterad, posterad mostly smooth; katepisternum strigulose, not significantly elevated over surrounding cuticle,

circumscribing sutures very fine; metapleuron mostly longitudinally striate to costulate; mesosoma with very broadly convex to almost flat dorsal margin in lateral view, metanotal sulcus well impressed and scrobiculate; mesosomal dorsum posterad of mesonotum medially mostly smooth, laterally and toward posterior propodeum strigulose-punctate; dorsal propodeal margin meeting declivitous margin through convexity, becoming relatively straight afterward at spiracular height; lateral propodeal face strigulose-punctate, propodeal declivity mostly smooth with sparse punctae and posterolateral low rounded lobes. Petiolar node with flat dorsal margin in lateral view; postpetiole laterally densely punctate, sternite strigulose-punctate, posteriorly thinning out somewhat; abdominal tergite 4 laterally punctulate, punctulae becoming less dense posterad, sternite smooth with some punctae. Dorsum of thorax, and abdominal segments 1-4 with dense mat of short, erect standing hairs, besides longer, scattered erect to subdecumbent hairs. Coloration yellowish brown.

Queen. Metrics ($n = 1$): HL 0.60, HW 0.48, ML 0.26, SL 0.42, ED 0.13, WL 0.83 mm. CI 0.79, SI 0.88, MI 0.56, OI 0.28. Pronotum laterally punctate, mostly smooth posterad; mesometapleuron longitudinally strigulose; mesoscutum with longitudinal, parallel strigulae and rows of punctae especially laterally; scutellum mostly smooth medially, laterally strigulose, axillae strigulose-punctate; lateral propodeal face strigulose-punctate; propodeal declivity mostly smooth with some transverse strigulae medially.

Male. Unknown.

Comments. *G. epinotalis* and *G. luzonensis* are both among the smallest *Gnamptogenys*, but *G. epinotalis* has a metanotal sulcus that is lacking in *G.*

luzonensis. The propodeum of *G. luzonensis* may have partially effaced sculpture, but longitudinal strigulae and foveolae are usually present. Sutures around the katepisternum in *G. luzonensis*, and most other species of the *epinotalis* group, tend to be wider and deeper compared with other Old World *Gnamptogenys* clades and with a slight elevation of the katepisternum over the anepisternum and metapleuron. The petiolar node in *G. epinotalis* seems to be more bluntly convex in shape than in other species of the *epinotalis* group. The dense layer of short hairs on the body is rare for Old World *Gnamptogenys*, though *G. sila* almost approaches the condition in *G. epinotalis*. The specimens studied were found in irregular galleries in the earth under a stone (Brown 1958).

Specimens examined. PAPUA NEW GUINEA. **Morobe:** Huon Peninsula, Mongi watershed, Ebabaang, 13/1400m, iv-16/18-1955, E.O. Wilson 831 (3w BMNH; 3w 1q MCZC, 1w ANIC, 1w MIZA); Paumomu River, L. Loria, 1w MCSN.

***Gnamptogenys luzonensis* (Wheeler)**

(Fig. 42)

Rhopalopone luzonensis Wheeler, W.M., 1929:30. Syntype workers, queen:

Philippines, Luzon Island, Los Baños (MCZC) [Examined].

Gnamptogenys luzonensis (Wheeler); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Clypeal lamella bluntly angular laterally and medially projecting as blunt, very obtuse angle; propodeal declivitous face mostly with faint longitudinal undulations. Petiolar node shaped as apically truncated triangle in lateral view.

Worker. Metrics ($n = 6$): HL 0.52-0.59, HW 0.43-0.47, ML 0.23-0.30, SL 0.38-0.41, ED 0.03-0.06, WL 0.65-0.72 mm. CI 0.78-0.92, SI 0.82-0.88, MI 0.52-0.65, OI 0.07-0.13. Head with anterior clypeal margin mostly convex in frontal view, lamella laterally bluntly angular and medially projecting as obtuse blunt angle; clypeus with posteromedian longitudinal carinulae, laterally rugulose-punctate, mostly smooth anteromedially; vertex mostly smooth with anterior punctate margin and brief posteromedian longitudinal strigulae; eye approximately four ommatidia in diameter. Pronotal dorsum longitudinally strigulose-punctate, medially impunctate with shallow strigulae; promesonotal suture absent or weakly impressed; lateral pronotal face dorsally longitudinally strigulose to undulate with punctae, ventrally mostly smooth; anepisternum undulate with some punctae; katepisternum longitudinally strigulose; metapleuron posteroventrally with longitudinal carinulae, anterodorsally depressed, mostly smooth; mesometanotum ranging from strigulose to medially smooth with strigulose-punctate sculpturing limited to sides and toward propodeum; propodeal declivity mostly with faint longitudinal undulations, posterolaterally with low triangular ridge, lateral propodeal face longitudinally strigulose. Petiolar node forms apically truncated triangle in lateral view; postpetiolar dorsum mostly smooth with abundant piligerous punctae, punctae usually sparser posterad; postpetiole strigulose-punctate in lateral view, sculpturing denser anterad than posterad; abdominal tergite 4 dorsally like postpetiole but with smaller depressions; fourth

abdominal sternite mostly smooth laterally with scattered, scalloped punctae. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster ferruginous brown; mandibles, antennae, legs ferruginous.

Queen. Metrics ($n = 1$): HL 0.61, HW 0.54, ML 0.28, SL 0.45, ED 0.08, WL 0.78 mm. CI 0.82, SI 0.89, MI 0.55, OI 0.55. Ergatoid. Pronotal dorsum with arching rugulose-punctate sculpturing; mesoscutum with median narrow band of longitudinal carinulae, laterally longitudinally strigulose; scutellum smooth; propodeum rugulose-punctate; mesometapleuron and lateral propodeal face longitudinally strigulose. Punctae on postpetiolar dorsum shallower and smaller in diameter posterad.

Male. Unknown.

Comments. This species is similar in appearance to *G. epinotalis*; see the discussion under *G. epinotalis* for differences between the two species. The only other known species of the *epinotalis* group from the Philippines is *G. cribrata*, which usually has a dark brown mesosoma and a rectangular-shaped petiolar node in lateral view. The posterior mesosomal sides of *G. cribrata* have more strigulae and undulations, compared with the mostly smooth to longitudinally carinulate cuticle in *G. luzonensis*. The punctae on the postpetiole of *G. cribrata* are abruptly impressed anterad and gradually slope posterad compared with the uniformly impressed punctae in *G. epinotalis*. *G. cribrata* is on average larger, but there is some overlap at the higher range of dimensions for *G. cribrata*. Only ergatoid queens are known for this species.

Specimens examined. PHILIPPINES. **Negros Oriental:** Dumaguete, 11-6-1949, J.W. Chapman, 3w 1q MCZC; Luzon: Los Baños, 1w MCZC; Los Baños, Mt. Makiling, 14/10'N 121/11'E, 27-viii-1978, B. Lowery, rainforest. ANIC ants vial 55.146, 2w ANIC, 1w MCZC.

***Gnamptogenys major* (Emery)**

(Fig. 40)

Rhopalopone major Emery, 1901:154. Syntype workers: New Guinea, Sattelberg (Biró) (MCSN) [Examined].

Gnamptogenys major (Emery); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Clypeus longitudinally costulate; metanotal sulcus present; petiolar node slightly triangular with bluntly rounded apex in lateral view; opening of propodeal spiracle elongate, almost slitlike. Body black; antennae, legs, and mandibles brown.

Worker. Metrics. Syntype ($n = 1$): HL 0.95, HW 0.83, ML 0.42, SL 0.70, ED 0.08, WL 1.27 mm. CI 0.87, SI 0.85, MI 0.50, OI 0.09. Anterior clypeal margin evenly convex in dorsal view; clypeus longitudinally costulate; eyes 3 ommatidia in width and 4-5 in length. Mesosomal dorsum with longitudinal strigulae mixed with sparse piligerous punctae, strigulae denser posterad; pronotum longitudinally costulate dorsad and ventrally mostly smooth in lateral view; promesonotal suture weakly impressed; metanotal sulcus present; katapisternum densely strigose; metapleuron

fairly smooth and shining, longitudinal costulae present over bulla; dorsal propodeal margin meets declivitous margin through blunt angle in lateral view, declivity with slight convexity caused by spiracle; propodeal spiracle elongate in lateral view, almost slitlike with horizontal longitudinal axis. Petiolar node slightly triangular with bluntly rounded apex in lateral view; dorsum of postpetiole longitudinally rugulose-punctate; postpetiolar sternite weakly strigulose, anterior process with anterior triangular cleft in ventral view; tergite of fourth abdominal segment similar to postpetiolar dorsum but with smaller punctures. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body black; antennae, legs, and mandibles brown.

Queen and male. Unknown.

Comments. This is the only known species of *Gnamptogenys* with elongate propodeal spiracles, instead of the rounded spiracles typical for all other species. The nearest relative with elongate to slit-shaped propodeal spiracles is the Neotropical genus *Ectatomma* F. Smith, but the spiracles in *Ectatomma* have a vertical longitudinal axis versus a horizontal axis for *G. atrata*. *G. major* bears some resemblance to *G. atrata*, having similar coloration and dimensions. Both are the largest-bodied species of the *epinotalis* group, but the clypeal lamella of *G. atrata* has a medially angular anterior margin, and its petiolar node is rectangular shaped in lateral view.

Specimen examined. PAPUA NEW GUINEA. **Morobe:** Sattelberg [Sattelburg, 6° 29'S 147° 46'E], L. Biró, 1w MCSN.

***Gnamptogenys malaensis* (Mann)**

(Fig. 43)

Rhopalopone malaensis Mann, 1919:281. Syntype workers: Solomon Islands, Malaita Island, Auki (Mann) (MCZC) [Examined].

Gnamptogenys malaensis (Mann); Brown: 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Cephalic posterior margin concave with shallow median notch in frontal view, anterior clypeal margin uniformly convex. Postpetiolar dorsum rugose-punctate (usually transversely oriented), slightly smoother medially; abdominal sternite 4 mostly smooth with round punctae.

Worker. Metrics ($n = 5$): HL 0.68-0.71, HW 0.53-0.55, ML 0.26-0.32, SL 0.47-0.49, ED 0.06-0.07, WL 0.79-0.89 mm. CI 0.75-0.80, SI 0.89-0.91, MI 0.47-0.60, OI 0.11-0.13. Posterior cephalic margin with shallow median concave notch in frontal view, anterior clypeal margin uniformly convex; clypeus medially with longitudinally costulae that extend onto lamella, laterally rugulose-punctate, with broad smooth sulcus just posterad of mandibular insertion; vertex mostly smooth with shallow punctae laterally. Lateral pronotal face with low longitudinal strigulae; anepisternum mostly smooth with some punctae, frequently separated by impressed line or abrupt elevation from depressed, mostly smooth anterodorsal metapleural surface; katepisternum and posteroventral metapleuron longitudinally strigulose; mesosomal dorsum longitudinally rugulose-punctate, mostly impunctate medially; promesonotal suture appears as fine transverse line of variable length; sculpture on mesonotum

sometimes smooth; propodeal declivity laterally smooth with median longitudinal carinulae, posterolateral ridge lacking or weakly developed, propodeal dorsal margin joins straight declivitous margin through blunt obtuse angle in lateral view. Postpetiolar dorsum rugose-punctate, slightly smoother medially; postpetiole rugulose-punctate to areolate in lateral view; fourth abdominal tergite dorsally longitudinally rugulose-punctate, medially impunctate, laterally longitudinally strigulose with scattered punctae; fourth abdominal sternite mostly smooth with round punctae. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Head, mesosoma, petiole, and gaster brown; mandibles, antennae, legs ferruginous brown.

Queen. Metrics ($n = 1$): HL 0.75, HW 0.60, ML 0.29, SL 0.51, ED 0.10, WL 0.89 mm. CI 0.80, SI 0.86, MI 0.49, OI 0.16. Ergatoid. Pronotal dorsum with arching rugulose-punctae; pronotum laterally with low diagonal to longitudinal strigulae and scattered punctae; anepisternum either smooth or strigulose; katepisternum longitudinally strigulose; metapleuron anterodorsally smooth with weak strigulae, posteroventrally longitudinally strigulose; mesoscutum longitudinally rugulose-punctate; scutellum with longitudinal or diagonal low undulations; lateral propodeal face densely areolate, propodeal dorsum transversely strigulose.

Male. Unknown.

Comments. This is the only species of the *epinotalis* group known from the Solomon Islands. The only other species of the *epinotalis* group with extensive longitudinal parallel sculpturing on the fourth abdominal tergite is *G. cribrata*. In that species the sculpturing consists of more regularly parallel costulae and rarely extends over half

the dorsal surface of the tergite, and the postpetiole is mostly smooth with scattered punctae, not rugulose-punctate. The type series from Malaita Island came from beneath the bark of a dead tree.

Specimens examined. SOLOMON ISLANDS. **Central Province:** Russell Island, Yandina, 15-viii-1966, P. Greenslade 23520, ANIC vial 32.21, 3w ANIC. **Malaita Province:** Malaita Island, Auki, W.M. Mann, 4w MCZC. **Western Province:** Vella Lavella Island, 7-v-1966, P. Greenslade 22859, 3w LACM, 8w 1q ANIC; Kolombangara Island, near Kuzi, 3/9-ix-1965, P.N. Lawrence, Roy. Soc. Exped., ANIC vial 32-20, 2w 1q ANIC; New Georgia, Munda, 15-ii-1966, P. Greenslade 22349, 2w ANIC; Vangunu Island, 10-vi-1966, P. Greenslade 23148, ANIC ants vial 32.22, 2w ANIC.

Gnamptogenys sila sp. n.

(Fig. 44)

Diagnosis. Vertex with small posteromedian area of fine areolae, anterior margin of clypeal lamella sinuate, with median convexity, lamella rounded at extreme lateral margins; mesosoma and postpetiole with round, well impressed, flat-bottomed punctae; postpetiolar tergite rugulose-punctate laterally.

Type material. Holotype worker. Malaysia, Sabah, Gunong Silam, 330m, 1983, R. Leakey (A9/72). Deposited in BMNH. Paratypes. Three workers in the BMNH from the same series as the holotype.

Worker. Metrics. Holotype: HL 0.55, HW 0.45, ML 0.23, SL 0.39, ED 0.03, WL 0.65 mm. CI 0.82, SI 0.87, MI 0.51, OI 0.07. Head with anterior margin of clypeal lamella sinuate in frontal view, medially convex and rounded at extreme lateral ends; frons mostly rugulose-punctate with large flat-bottomed punctae; cephalic surface ventrad of eyes more strigulose than punctate; posteromedian surface of vertex finely areolate; clypeus with longitudinal strigulae and median broad sulcus. Mesosoma with very broadly convex dorsal margin in lateral view, forming blunt angle with broadly concave propodeal declivity; pronotum laterally rugose-punctate; katepisternum strigulose, anepisternum rugulose-punctate; mesosomal dorsum longitudinally rugulose-punctate; promesonotal suture vestigial; metapleuron and lateral propodeal surface strigulose with sparse punctae, metapleuron with small smooth area, slightly depressed below surrounding cuticle; propodeal declivity mostly strigulose with prominent posterolateral carina, propodeal spiracle opening not projecting beyond declivitous margin.

Lateral face of petiole strigulose; postpetiolar tergite mostly rugulose-punctate, punctae disappearing posteromedially, sternite irregularly rugulose-punctate; abdominal tergite 4 mostly smooth, with low longitudinal strigulae and undulations, sparsely punctate, punctae becoming smaller and diminishing posterad, narrow row of scrobiculate sculpture parallel to pretergite present; sternite of fourth abdominal segment strigulose, mostly punctate with low longitudinal strigulae or undulations. Fore coxae transversely strigulose in lateral view, metacoxal tooth triangular. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent

hairs, besides abundant short standing hairs. Head, mesosoma, petiole, and gaster brown; mandibles, antennae, legs ferruginous yellow.

Queen and male. Unknown.

Comments. This species is unusual in having punctae that are more or less round, uniformly well impressed and flat bottomed throughout its body. Such depressions are found in other species of the *epinotalis* group but are usually limited to the head. The areolate area on the vertex of *G. major* is unique among species of *Gnamptogenys*, which usually have a few striae or scattered punctae on the vertex but no areolae.

Etymology. The species name is derived from the name of the type locality, Gunong Silam, and is assumed to be feminine.

***laevior* group**

Worker diagnosis. Head subrectangular, with parallel to subparallel lateral margins in dorsal view; vertex flattened, mostly smooth, separated from frons by blunt angle; scape widens apically, cross section flattened, scape usually not surpassing median cephalic margin; third antennal segment wider than long; eye slightly convex in cross section, almost flattened. Propodeum unarmed, lateral propodeal face not separated from metapleuron by sulcus; dorsal margin of petiolar node convex in lateral view; metacoxal tooth always present.

Worker description. Head subrectangular in dorsal view, with parallel to subparallel lateral margins (convergent in *G. delta*), posterior margin concave to broadly convex,

anterior clypeal margin straight or slightly concave, never strongly convex; vertex flattened, mostly smooth, separated from frons by blunt angle, occipital ridge present; occipital lobe present, very low and broadly convex, with lamella; ground sculpture on head mostly smooth, with round to oval foveolae; frons with median longitudinal area of mostly smooth cuticle; dorsal lobe of torulus separated from frontal lobes and close to base of torulus; frontal lobe broadly convex, its dorsal surface flat; scape widened apically, cross section flattened, scape length usually not surpassing median cephalic margin, if so, then by less than one apical width (SI 0.74-1.05); scape mostly smooth with punctulae and no pubescence; third antennal segment wider than long; eye not reduced in diameter, cross section slightly convex, almost flattened, ommatidia relatively large; mandibular chewing border crenulate, cross section cuneiform and thick, especially basally. Palpal formula 3,2.

Humeral angle present, never lamellate; pronotum with longitudinal sulcus present along ventral margin in lateral view; basisternal lobe short, apex bluntly rounded, ventral margin convex in lateral view; prosternal process with posteriorly projecting lobe, apically bluntly bidentate, tapering ventrally in posterior view; ridges widely separated by lobe and slightly projecting beyond ventral basisternal surface; furcasternum with posterodorsal convexity and ridge; lateral lobes of endosternum with narrow base. Mesosomal dorsum devoid of sutures or sulci, though occasionally very fine, vague transverse impressions hint of promesonotal suture, mesosomal dorsum generally with median longitudinal area of mostly smooth cuticle; mesometapleural suture well impressed; mesopleural suture weakly to well impressed, forming angle with mesometapleural suture; sulcus between metapleuron

and propodeum forming arching row of irregularly shaped depressions; propodeal spiracle separated from declivity by more than one spiracular diameter in lateral view; propodeum unarmed, mostly smooth, surface relatively flat. Mesosoma with slightly convex, almost straight dorsal margin in lateral view; mesosoma box shaped, with broadly convex lateral surfaces, subparallel in cross section.

Dorsal margin of petiolar node convex in lateral view, with anterior, dorsal, and posterior margins not distinctly separated from each other, node longer than high, node mostly smooth, occasionally undulated, with round to oval foveolae; petiolar spiracle situated below anterolateral process; subpetiolar process in lateral view variable in shape, narrow and lamellate in ventral view; petiolar node longer than wide in dorsal view, anterior ridge present; postpetiolar dorsum with sparse punctae or foveolae; postpetiolar ventral process forms two contiguous convexities or bluntly angular triangles with brief longitudinal rugosities in ventral view, never with median carina; fourth abdominal segment without stridulitrum, dorsum mostly smooth. Most of body with little pilosity, some dense pilosity present on apical third and fourth antennal segments; dorsum of thorax and abdominal segments 1-4 usually with scattered erect to subdecumbent hairs. Fore tarsal dorsal surface mostly smooth, no pubescence, little pilosity; concavity opposite strigil with single stout seta; apex of second fore tarsal segment with four stout setae; fore tarsal segments 2-4 slightly longer than wide; metacoxal tooth always present, usually triangular with broad base (peg like in *G. biloba*).

Included species: *G. biloba*, *G. chapmani*, *G. delta*, *G. fistulosa*, *G. hyalina*, *G. lacunosa*, *G. laevior*, *G. leiolabia*, *G. pertusa*, *G. polytreta*, *G. rugodens*.

Comments. This group has eleven species that are relatively uniform in general aspect and are distributed throughout Southeast Asia, from Thailand eastward to Sulawesi and the Philippines. The easternmost record is a single specimen of *G. laevior* recorded from Gunung Klabat on northern Sulawesi. The dominant body sculpture for species of the *laevior* group are round foveolae over a smooth ground cuticle. This group is the least setose compared with other Old World taxa. The description of the prosternal characters is based on dissections of *G. laevior*, the only species for which enough material was available to permit dissecting specimens.

The apomorphies defining this clade are the widened scapes and almost flattened, very broadly convex eyes. This group shares several characters with some New World species of *Gnamptogenys*, such as *G. mordax*, including flattened eyes, smooth dorsal surface on the basal protarsus, shortened smooth scape that fails to reach the posterior cephalic border when laid back, and as the general elongate aspect of the body. The mandibles in the *laevior* group are more robust and thicker in cross section than in other Old World clades. *G. mordax* also has robust mandibles, but in *G. mordax* the mandibular cross section is even thicker, and in a frontal view their mandibles have become elongated in a way unknown in any Old World *Gnamptogenys*.

Key to workers of the *laevior* group

1. Fourth abdominal sternite completely or at least laterally sculptured, either strigulose or colliculate, or both (Figs. 47a,b) (western Malaysia to Sulawesi, Philippines) *laevior* Forel
- Fourth abdominal sternite mostly smooth, with scattered punctae or foveolae (Fig. 47c) 2
2. Clypeal lamella in frontal view with its anterior margin forming a blunt median angle (Fig. 48a) 3
- Anterior margin of clypeal lamella shaped otherwise: mostly convex to almost straight or sinuate (Figs. 48b,c) 4
3. Sculpturing on median clypeus and mandibular dorsum with rugosities and punctae (Borneo) *lacunosa* sp. n.
- Sculpturing on median clypeus and mandibles mostly smooth, mandibles with scattered punctae (western Malaysia) *delta* sp. n.
4. Median clypeus delimited from lateral areas, either by distinct raised crests that extend anterad from frontal lobes or by being abruptly elevated; sculpturing on median clypeus and mandibular dorsum reduced, tending to smooth, mandibles with some punctae (Fig. 49b) 5
- Distinct crests do not delimit a median clypeal area, such crests, if present, not distinct from surrounding rugosities; sculpturing on median clypeus and mandibles variable, usually with rugosities and punctae (Fig. 49a) 7

5. Subpetiolar process subquadrate, with a distinct posterior angle (Fig. 56a) (northern Borneo, Philippines) *leiolabia* sp. n.
- Subpetiolar process in lateral view projecting anterad, either triangularly or as a lobe, without a posterior angle (Figs. 50a, 54a) 6
6. Head in lateral view with clypeal margin forming a distinct angle (Fig. 50a); in dorsal view with a row of depressions along anterior clypeal border and posterior border of lamella (Borneo) *biloba* sp. n.
- Lateral clypeal margin convex, not forming an angle (Fig. 54a); anterior clypeus almost totally smooth, lacking a row of depressions (Singapore) *hyalina* sp. n.
7. Occipital lamella in lateral view protuberant, both ends with blunt angles or sharp curvatures (Figs. 59a, 60a) 8
- Occipital lamella not conspicuously protuberant, generally evenly convex, at most just one end may have a blunt angle (Figs. 51a, 53a) 9
8. Mandibles with deep rugosities on posterior half, evident even in lateral view (Fig. 60a); petiolar process subquadrate (western Malaysia) *rugodens* sp. n.
- Mandibles mostly with sparse punctae and a few low rugosities basally, the mandibular margin forming an even, continuous curve (Fig. 59a); petiolar process shaped as an anteriorly projecting convex lobe (Thailand to western Malaysia) *polytreta* sp. n.
9. Clypeal lamella in frontal view with a very broadly convex, almost straight anterior margin, its anterior half with opaque scabrose roughening that contrasts with the posterior shining cuticle (Borneo) *pertusa* sp. n.

- Anterior margin of clypeal lamella convex to broadly convex, with its entire surface shining even though it may present fine rugosities or depressions 10
- 10. Propodeal spiracle elevated on a low barrel-like prominence above surrounding cuticle (Fig. 53a) (Philippines) *fistulosa* sp. n.
- Propodeal spiracle not raised above the surrounding sculpture (Fig. 51a) (western Malaysia to Borneo, Philippines) *chapmani* Brown

***Gnamptogenys biloba* sp. n.**

(Figs. 49b, 50)

Diagnosis. Clypeus anteromedially smooth, laterally bound by convex crest that extends anterad from each frontal carina; mandibular dorsum mostly smooth; subpetiolar process forms anteriorly projecting lobe, with long concave posterior margin. Metacoxal tooth peglike.

Type material. Holotype worker. Borneo, Mt. Tibang, 1400m, Mjöberg. Deposited in BMNH.

Worker. Metrics. HL 0.99, HW 0.82, ML 0.45, SL 0.67, ED 0.21, WL 1.32 mm. CI 0.83, SI 0.82, MI 0.56, OI 0.26. Head with subparallel lateral margins in frontal view, anterolaterally with brief, straight to slightly concave margin, forming obtuse angle with lateral cephalic margin; frontal carina straight, frontal lobe convex, elevated convex ridge extends anterad from frontal lobe, defining median clypeal smooth area; clypeus posteriorly strigulose, transverse row of punctae separates

clypeal lamella from rest of clypeus, anterior margin of lamella convex; clypeus laterally strigulose, mostly smooth at extreme lateral end; mandible edentate, dorsum smooth with sparse punctae; head laterally with occipital lamella mostly straight anterad, posteriorly convex. Pronotal dorsum posteromedially smooth with foveolae anterolaterally and anterad, humeral angle raised slightly above rest of surrounding surface, pronotum laterally foveolate, ventrally smooth to slightly undulate; anepisternum subquadrate, mostly smooth with some foveolae, dorsal margin concave; katepisternum mostly smooth with posterior strigulae; metapleuron mostly smooth with ventral longitudinal strigulae.

Petiole irregularly foveolate in lateral view, subpetiolar process forms anteriorly placed, short projecting lobe, with long concave posterior margin; postpetiole dorsolaterally with scalloped foveolae, deeper and wider anterad than posterad; postpetiolar sternite mostly smooth; postpetiolar sternal margin straight between anterior process and posterior convexity in lateral view; fourth abdominal tergite with lateral scallopings. Fore coxae smooth in lateral view; metacoxal tooth peglike. Sides of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Mesosomal dorsum devoid of standing hairs. Body mostly ferruginous.

Queen and male. Unknown.

Comments. This species shares with *G. hyalina* and *G. leiolabia* the two elevated clypeal ridges that define a median depression with effaced sculpturing. No other species of the *laevior* group have this trait, which defines a clade made up of these three species. Both of the other species have triangular metacoxal teeth. In *G. hyalina* the clypeal sculpturing is almost glabrous, while in *G. biloba*, and to a lesser degree

in *G. leiolabia*, there still are some irregularly shaped foveolae and faint strigulae on the clypeus. Among these species the clypeal ridges are most developed in *G. biloba*. *G. leiolabia* is quite small (HL < 0.70; WL < 1.00 mm) compared to *G. biloba*. *G. delta* also tends toward smoother cuticle on the clypeus and mandibles, but it lacks the pair of clypeal ridges characteristic of *G. leiolabia*. The compound eyes are normally flattened in the *laevior* group, but they are more flattened in *G. biloba* than in any of the other species. The type locality, Mt. Tibang, is in south central Sarawak in the Nieuwenhuis Range.

Etymology. The species name is derived from a conjugation of the Latin word for “lobe,” *lobus* (m.), and the Latin prefix, *bi*, meaning “two.” It alludes to the pair of clypeal ridges that are so prominent in this species.

Gnamptogenys chapmani Brown

(Fig. 51)

Gnamptogenys chapmani Brown, 1958:305. Holotype worker: Philippines, Negros Oriental, Cuernos Mountain (Chapman) (USNM) [Examined].

Diagnosis. Head with straight, slightly convergent sides in frontal view; occipital lamella evenly convex in lateral view, lacking abrupt angles; posterior clypeal margin with lateral ridges enclosed by lateral foveolae, clypeal ridges converge posteriorly, running parallel briefly before meeting or fading on frons; petiolar node with broadly convex dorsal margin in lateral view.

Worker. Metrics ($n = 21$): HL 0.60-0.84, HW 0.42-0.66, ML 0.23-0.39, SL 0.32-0.56, ED 0.12-0.19, WL 0.73-1.16 mm. CI 0.69-0.81, SI 0.75-0.88, MI 0.52-0.69, OI 0.25-0.35. Head with broadly convex subparallel sides in frontal view; frons ranging from densely foveolate to mostly smooth with irregular rows of foveolae that become denser and more regular laterally, fine median line sometimes impressed from posterior clypeal margin to mid eye height, frons usually mostly smooth; clypeus posteromedially smooth to longitudinally strigulose, strigulae extending onto lamella, posterior clypeal margin with lateral ridges enclosed by lateral foveolae, ridges converge posteriorly, running parallel briefly before fading on frons, or meeting; anterior margin of clypeal lamella mostly convex, with or without slight median convexity; occipital lamella convex, without abrupt angles in lateral view.

Pronotum laterally mostly smooth, usually with scattered punctae dorsally, low longitudinal strigulae or undulations may be present along posterior margin, anteroventral pronotal margins form blunt angle; mesopleuron mostly smooth with scattered punctae, mesopleural sculpture variably impressed; metapleuron mostly smooth and flat, with longitudinal strigulae posteroventrally; propodeum smooth or with low strigulae laterally plus variable amount of foveolae, dorsal and declivitous propodeal margins joined by sharply rounded convexity or blunt angle in lateral view. Dorsum of mesosoma and petiole mostly smooth, foveolae present laterally, sometimes strigulae present laterally; petiolar node foveolate in lateral view, dorsum mostly smooth; subpetiolar process variable, from subquadrate to forming rounded lobe or triangle; postpetiole tergite foveolate over smooth ground sculpture, each depression deeper anteriorly than posteriorly, and progressively smaller in diameter

posterad; fourth abdominal tergite laterally with less punctae than postpetiole, some concentrated along posterior edge; fourth abdominal tergite smooth with scattered punctulae, brief strigulae sometimes present along posterior margin. Fore coxa mostly smooth with low transverse strigulae posterad. Dorsum of thorax and abdominal segments 1-4 with abundant erect to subdecumbent hairs. Body ferruginous brown to brown, legs and antennae lighter colored than body.

Queen. Metrics ($n = 2$): HL 0.78, 0.66; HW 0.61, 0.51; ML 0.32, 0.28; SL 0.52, 0.41; ED 0.19, 0.20; WL 1.22, 0.99 mm. CI 0.77, 0.77; SI 0.86, 0.80; MI 0.53, 0.55; OI 0.31, 0.39. Mesosomal dorsum mostly smooth with sparse foveolae, foveolae on pronotum denser; mesoscutum with faint longitudinal undulations and brief longitudinal fine sulci; mesopleural suture well impressed with minute transverse crests; metapleuron mostly strigulose with small smooth area. Petiolar node with evenly convex dorsal margin in lateral view, curvature not as broad as in worker.

Male. Unknown.

Comments. Brown (1958) described *G. chapmani* from specimens gathered in different localities. A study of the type material revealed that the worker and female taken on 27 April 1924 represent a different species (*G. leiolabia*) from the series of workers taken on 19 March 1924, which include the holotype of *G. chapmani*. Additional specimens mentioned by Brown (1958) from Romblon Island, Philippines, were not examined, but his discussion of intraspecific differences corresponds to differences between *G. chapmani* and *G. leiolabia*. The following characters described by Brown (1958) as intraspecific variation are actually attributes of *G. leiolabia*: narrower head (CI 0.70-0.76) and petiole, smaller and sparser

foveolae, and the angular propodeal declivity relative to the mesosomal dorsum. Thus, the queen of *G. chapmani* described in Brown (1958) corresponds to *G. leiolabia*. The most easily discernible difference between the two species is the median clypeal area; in *G. leiolabia* it is mostly smooth down to the lamella, which is broadly concave, almost straight. This median area is bounded by two raised longitudinal crests that stretch from next to the anterior edge of each frontal lobe down to the lateral borders of the lamella.

G. chapmani is relatively widespread, but the amount of specimens in museums is meager. Specimens vary in the degree of foveolate sculpturing, posteromedian clypeal sculpturing, the angle formed by the ventral and anterior pronotal margins in lateral view, the angle formed by the dorsal and declivitous propodeal margins in lateral view, the shape of the subpetiolar process, and size. When two character states were well defined in some specimens other characters always merged into a continuity, making separation arbitrary. The altitude of the type locality is reported in Brown (1958) as 600m.

Specimens examined. INDONESIA. **Jawa Barat:** Mt. Halimun, ~1000m, 4-ix-96, F. Ito, FI96-267, 4w MIZA, 1w BMNH, 1w MCZC, 1w ANIC. MALAYSIA. **Pahang:** Cameron Highlands, Gunung Jasar Trail 11, 1550m, 24-iii-1993, I. Löbl & Calame #18b, 1w 1q BMNH, 2w BMNH; Cameron Highlands, Trails 4, 13, 1500m, 23-iii-1993, I. Löbl & Calame #15, 1w 1q MCZC, 1w MIZA; Genting Highlands, Awana, 1150m, 3-iv-93, I. Löbl & Calame #27b, 1w BMNH. **Sabah:** Poring Hot Springs, Langanan Falls, 150m, 12-v-1987, I. Löbl & D. Burckhardt, 2a. 1w BMNH; Poring Hot Springs, 500m, 7-v-1987, D. Burckhardt & I. Löbl, 2w 1q BMNH; mi 43

Labuk Road, ex Sandakan (Lungmanis), 13-vi-1968, R.W. Taylor, acc. 68.527, 2w ANIC. **Sarawak:** Fourth Division, Gunung Mulu Natl. Pk., Camp 5, P.M. Hammond, J. Marshall, v-viii-1978, BM 1978-49, 3w BMNH; confl. Sun Oyan and Mujong Rivers, E. Kapit, 50m, 18-v-1194 #5a, I. Löbl & D. Burckhardt. 1w BMNH. **Selangor:** Upper Gombak Valley nr. Kuala Lumpur, 1500ft [457m], 13-vii-68, RW Taylor 68.848, ANIC ants vial 6.222, 2w ANIC. PHILIPPINES. **Negros Oriental:** Cuernos Mt., iii-19-1924, 1w USNM. THAILAND. **Petchburi:** Kaeng Krachen Natl. Pk., 19-xi-1985, I. Löbl & D. Burckhardt, 3w BMNH, 1w ANIC, 1w MCZC, 1w MIZA.

***Gnamptogenys delta* sp. n.**

(Fig. 52)

Diagnosis. Head with lateral margins anteriorly convergent in frontal view, forming acute angle continuous with external mandibular margin; clypeal lamella triangular with rounded anteromedian lobe. Propodeal declivity with punctulae along lateral margin, centrally mostly smooth. Foveolae and punctae glazed, without sharp edges.

Type material. Holotype worker. Malaysia, Pahang, Ringlet, 1250m, ravine no. 20, 26-iii-1993, I. Löbl & Calame. Deposited in MHNG.

Worker. Metrics. Holotype: HL 0.76, HW 0.63, ML 0.41, SL 0.51, ED 0.18, WL 1.07 mm. CI 0.84, SI 0.81, MI 0.65, OI 0.28. Head with anteriorly convergent lateral margins in frontal view, clypeal lamella triangular with anterior median lobe; round

to oval foveolae present on frons, foveolae denser laterally, forming ill-defined posteriorly diverging rows; scape with subdecumbent hairs along dorsal margin; clypeus with a slightly elevated median area, mostly smooth with lateral irregular depressions and sparse punctae on lamella; mandible edentate, mostly smooth, sparsely punctate, with faint strigulae on base; occipital lamella gradually raising from cephalic surface along both ends in lateral view, minute angle present on anterior end.

Mesosoma with abundant foveolae on pronotum in lateral view, intervening space narrower than diameter of depressions except for smooth longitudinal strip parallel to groove along ventral margin; anepisternum rhomboid, mostly smooth with several punctae; katepisternum mostly smooth with low rugulae, plus few foveolae; metapleuron mostly smooth anterad, posteriorly strigulose with some punctae; propodeal declivity with series of punctulae along outer margin, centrally mostly smooth with brief longitudinal strigulae around foramen; mesosomal dorsum with median longitudinal, mostly smooth strip; with sparse foveolae forming ill-defined longitudinal rows laterally.

Petiolar node foveolate in lateral view, ventral process subquadrate with concave ventral margin; postpetiole laterally foveolate, deeper and wider anterad than posterad; sternal margin of postpetiole with a brief concavity formed by anterior process in lateral view, followed by straight margin, abruptly convex at posterior margin; postpetiolar dorsum with sparse, shallow piligerous punctae. Fore coxa laterally smooth. Dorsum of thorax and abdominal segments 1-4 with abundant erect

to subdecumbent hairs. Body brown; legs, antennae, and mandibles ferruginous brown.

Queen and male. Unknown.

Comments. Other species of the *laevior* group with a smooth to almost glabrous sculpturing on the median clypeus and mandibles are *G. biloba*, *G. hyalina*, and *G. leiolabia*. These species can be separated from *G. delta* by the presence of two distinct longitudinal ridges that extend from the anterior end of the frontal carinae down to the anterior clypeal margin, a feature lacking in *G. delta*. These species also have the clypeal lamella with a broadly convex anterior margin, not angular as in *G. delta*.

Etymology. The outline formed by the head and mandibles of *G. delta* is strikingly triangular in dorsal view, consequently the species name is derived from the Greek word for “triangular,” *delta*.

***Gnamptogenys fistulosa* sp. n.**

(Fig. 53)

Diagnosis. Clypeus posteriorly with lateral irregular depressions, posteriorly mostly smooth with thin, longitudinal extension of relatively smooth cuticle; mesometapleuron and lateral propodeal surfaces mostly smooth, propodeal spiracle

on rounded prominence above surrounding cuticle; petiolar dorsal margin evenly convex in lateral view.

Type material. Holotype worker. Philippines, Luzon, Lagunas, Mt. Makiling, 250m, 28-x-1966, L.D. Uhler. Deposited in MCZC. Paratypes. Two workers from the same nest series as the holotype, deposited in MCZC.

Worker. Metrics: [Holotype] Paratypes ($n = 2$): HL [0.75] 0.81, 0.81; HW [0.59] 0.61, 0.60; ML [0.40] 0.35, 0.35; SL [0.51] 0.51, 0.51; ED [0.18] 0.20, 0.18; WL [1.09] 1.08, 1.05 mm. CI [0.79] 0.75, 0.74; SI [0.86] 0.83, 0.86; MI [0.67] 0.58, 0.59; OI [0.31] 0.33, 0.31. Head with broadly convex, semiparallel sides in frontal view, anterior clypeal margin convex; clypeus posteromedially mostly smooth, laterally enclosed by irregular depressions, smooth area tapering posteriorly, sometimes extending to frons, lamella with brief longitudinal strigulae; frons with foveolae arranged in irregular longitudinal rows; fine, longitudinal impressed line extends from posterior clypeal margin to just beyond frontal lobes; frontal lobe smooth and flat; mandible sharply convex basally, dorsally with elongate punctae; occipital lamella evenly convex in lateral view.

Pronotum with anterior and ventral margins meeting through blunt, obtuse angle in lateral view, ventral margin slightly sinuate, with sparse foveolae present on upper two-thirds, bottom third mostly smooth, brief longitudinal strigulae present on posterior margin; promesonotal suture vestigial; mesopleuron mostly smooth, anteroventral sulcus of katepisternum broad and deep, posteroventrally with several tightly grouped foveolae; mesopleural suture with transverse ridges; metapleuron and lateral propodeum mostly smooth, with few depressions or strigulae present;

propodeal spiracular opening elevated on rounded prominence, dorsal propodeal margin meets declivity through blunt angle in lateral view, declivitous margin broadly convex.

Mesosomal and petiolar dorsum mostly smooth, sparsely foveolate, most foveolae situated laterally and along anterior pronotal margin; petiolar node with evenly convex dorsal margin in lateral view, ventral process subquadrate; postpetiolar sternite mostly broadly convex to almost straight in lateral view, convex ventrad of anterior process, abruptly convex at posterior margin; postpetiolar dorsum mostly smooth with sparse foveolae, most foveolae anterolaterally situated. Abdominal tergite 4 with sparse punctae anterolaterally, dorsum mostly smooth with few punctulae. Fore coxa laterally mostly smooth. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body light brown, extremities ferruginous.

Queen and male. Unknown.

Comments. This species can be confused with *G. chapmani* because of the similar size, subquadrate subpetiolar process, convex anterior margin of the clypeal lamella, and a blunt angle formed by the anterior and ventral pronotal margins in lateral view. The propodeal spiracle in *chapmani* is not elevated, as in *fistulosa*, and this can also be used to separate these two species.

Etymology. The species name is derived from the Latin adjective, *fistulosus*, “full of holes,” and alludes to the foveolate sculpturing.

***Gnamptogenys hyalina* sp. n.**

(Fig. 54)

Diagnosis. Head in lateral view with compound eye small and occipital lamella gradually curving from cuticular surface along its anterior edge and abruptly ending at the posterior angle. The clypeus with median glabrous area delimited on each side by longitudinal ridges, mandible mostly smooth with sparse punctulae.

Type material. Holotype worker. Singapore, Bukit Timah Nature Reserve, 15-ii-1967, D.H. Murphy, Ab2-10. ANIC ants vial 32.16. Deposited in ANIC. Paratype. One paratype on the same pin as the holotype, also in ANIC.

Worker. Metrics. [Holotype] Paratype: HL [1.06] 1.03, HW [0.75] 0.71, ML [0.42] 0.42, SL [0.77] 0.74, ED [0.18] 0.18, WL [1.51] 1.47 mm. CI [0.70] 0.69, SI [1.03] 1.05, MI [0.56] 0.59, OI [0.25] 0.25. Head with subparallel sides in frontal view; foveolae on head with intermediate areas larger than their diameters, foveolae become denser laterally; anterior margin of clypeal lamella convex; anteromedially glabrous, laterally bound by two ridges that project anterad from frontal carina and form sides of lamella; head with occipital lamella gradually rising from cuticular surface anterad but abruptly angular posteriorly in lateral view. Pronotum laterally with round to oval, irregularly spaced foveolae; mesopleuron mostly smooth (sometimes slightly undulate) with few foveolae; metapleuron smooth and shining anterad with transverse strigulae posterad; mesosomal dorsum mostly smooth and shining with widely spaced punctae, usually separated by more than their diameters,

propodeal declivity with arching smooth lateral strip in oblique frontal view and brief longitudinal depressions surrounding foramen.

Petiolar node mostly smooth with sparse foveolae; subpetiolar process triangular and anteriorly projecting; postpetiolar dorsum mostly smooth with sparse foveolae, their diameters less than those on petiolar node, anterolaterally with deep foveolae that fade out and decrease in diameter posterad; fourth abdominal sternite very broadly convex, almost straight, in lateral view; abdominal tergite 4 mostly smooth with sparse punctulae. Fore coxae smooth and shining in lateral view. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body brown; legs, antennae, and mandibles ferruginous brown.

Queen and male. Unknown.

Comments. Other species that could be confused with *G. hyalina* because of the smooth mandibles and clypeus are *G. leiolabia* and *G. biloba*. The three species share the same clypeal configuration (see Comments for *G. biloba*) and may constitute a small monophyletic group. The other two species have some rugosity on the clypeus in contrast to the strikingly smooth and polished surface of *G. hyalina*. *G. leiolabia* is smaller (HL < 0.70; WL < 1.00 mm) than *G. hyalina* and *G. biloba* has the lateral clypeal ridges more protuberant and the metacoxal tooth shaped as a peg and not triangular. The type specimens were collected in degraded coastal hill forest on granite. One label describes the specimens as coming from a small colony in dry bracket fungus on a log.

Etymology. The species name is derived from the Greek adjective, *hyalinus*, meaning “of glass,” and alludes to the polished clypeal and mandibular sculpturing.

***Gnamptogenys lacunosa* sp. n.**

(Figs. 47c, 48a, 55)

Diagnosis. Pronotum laterally with rugosities along posterior margin, mesosomal dorsum with low longitudinal strigae, evenly foveolate. Petiolar node with dorsal margin relatively evenly convex in lateral view; postpetiolar tergite mostly smooth with sparse punctae or punctulae in lateral view.

Type material. Holotype worker. Malaysia, Sabah, Crocker Range, 1600m, 18-v-1987, I. Löbl & D. Burckhardt. Deposited in MHNG. Paratypes. Two workers in BMNH from the holotype nest. Two workers in BMNH, 1w in MIZA from Malaysia, Sabah, Kinabalu, 1560-1660m, 24-iv-1987, I. Löbl & D. Burckhardt, 30a.

Worker. Metrics. [Holotype] Paratypes ($n = 5$): HL [0.91] 0.85-0.96, HW [0.70] 0.64-0.71, ML [0.41] 0.36-0.42, SL [0.60] 0.58-0.67, ED [0.22] 0.19-0.24, WL [1.23] 1.13-1.30 mm. CI [0.77] 0.74-0.76, SI [0.86] 0.86-0.95, MI [0.59] 0.55-0.64, OI [0.31] 0.32-0.34. Head with subparallel, broadly convex sides in lateral view, posterolateral corners bluntly angular; frons foveolate; clypeus longitudinally strigulose, strigulae extend onto lamella, with median area raised above rest of clypeus, not delimited by crest or abrupt slopes; anterior margin of lamella slightly scabrose, ending in median blunt point; mandibular dorsum strigulose-punctate, lateral margin straight, not sinuate; occipital lamella evenly convex in lateral view, posterior end more curved. Pronotum laterally with anterior and ventral margins separated by blunt angle, side foveolate with low longitudinal strigulae, strigulae

more concentrated along posterior margin; anepisternum smooth with few punctae; katepisternum with low strigulae and foveolae, especially ventrally, anteroventral flange bordered by deep and broad sulcus, posterior ventral edge of katepisternum laterally raised, higher than metapleuron; mesopleural suture impressed as transverse line or series of contiguous depressions; propodeum with dorsal and declivitous margins forming blunt obtuse angle in lateral view, spiracle slightly elevated, sculpture strigulose-foveolate; mesosomal dorsum evenly foveolate, interspersed with low longitudinal strigae.

Dorsum of petiolar node sparsely foveolate, mostly smooth, laterally foveolate-strigulose; subpetiolar process convex, projecting anterad; postpetiole laterally with broadly convex dorsal margin, ventral margin broadly convex after process, not sinuate; postpetiole smooth with sparse punctae on anterior one-third or less of tergite, sparse and shallow punctulae posteriorly, some strigulae present around spiracle; postpetiolar dorsum mostly smooth with sparse punctae, abdominal tergite 4 sparsely punctulate. Fore coxae transversely strigulose. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body ferruginous brown; antennae, legs ferruginous.

Queen and male. Unknown.

Comments. Most species of the *laevior* group have a mostly smooth longitudinal median band on the mesosoma and frons, in contrast to the regularly foveolate sculpturing of *G. lacunosa*. Some specimens of *G. polytreta* have a bluntly angular anterior clypeal lamella margin. Besides differences stated in the key, *G. polytreta* can be separated by the foveolae that cover over half of the postpetiolar tergite in

lateral view and a very broadly convex dorsal petiolar node margin. The angle formed between the dorsal and declivitous propodeal margins in lateral view is not as obtuse in *G. polytreta* as it is in *G. lacunosa*, approaching nearly a right angle in *G. polytreta*. The coarsely strigose mandibular base of *G. lacunosa* may approximate that of *G. rugodens*, but the rugosities are deeper in *G. rugodens*, which has a wider (HW > 0.75 mm) and broader (CI > 0.80) head and relatively smaller eyes (OI < 0.25).

Etymology. The species name is derived from the Latin term for “hole” or “opening,” *lacuna* (f.), and alludes to the depressions formed by the ant's foveolate cuticle.

***Gnamptogenys laevior* (Forel)**

(Figs. 47a-b, 57a-b)

Ectatomma (*Stictoponera*) *laevius* Forel, 1905:7. Holotype worker by monotypy:

Java, Tjibodas (Kraepelin) (MHNG) [Examined].

Stictoponera laevior (Forel); Emery, 1911:48. Placed in genus *Stictoponera*.

Stictoponera laevior var. *avia* Forel, 1912a:98. Syntype workers: Java, Nongkodjjar

[not examined]. Synonymized by Brown, 1954b:2.

Gnamptogenys kalabit Brown, 1958:308. Holotype: Sabah, Kalabit Country

(Mjöberg) (MCZC) [Examined]. **Syn. nov.**

Gnamptogenys laevior (Forel); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Anterior margin of clypeal lamella medially projecting as small lobe or very obtuse angle; anterior and ventral pronotal margins usually form pointed angle in lateral view; subpetiolar process usually subquadrate or forming anteriorly projecting lobe with posterior angle. Fourth abdominal sternite with extensive strigose to strigulose sculpturing; fourth abdominal tergite with narrow band of transverse strigulae; colliculate sculpturing usually present, especially on mesosomal sides, petiole and parts of gaster.

Worker. Metrics ($n = 15$): HL 0.86-1.23, HW 0.62-0.90, ML 0.37-0.52, SL 0.55-0.81, ED 0.16-0.25, WL 1.16-1.60 mm. CI 0.72-0.82, SI 0.86-0.95, MI 0.53-0.63, OI 0.19-0.34. Head parallel sided in frontal view; posterolateral margins angular to sharply pointed; foveolae on dorsum range from dense, with diameters larger than intervening space, to dispersed, with diameters equal to or less than intervening space; small smooth area present behind frontal lobes; background sculpturing mostly smooth, occasionally with longitudinal strigulae or brief, faint longitudinal striae; frontal lobe mostly smooth with elongate foveolae; median clypeus longitudinally punctate-strigulose, strigulae extend to posterior half of clypeal lamella, rest of lamella smooth, anterior margin of lamella medially projecting as small lobe or open obtuse angle; mandibular dorsum mostly smooth with sparse punctae, base strigulose, strigulae extending up to posterior half, mandibular dorsal surface basally convex; occipital lamella not conspicuously protuberant in lateral view, evenly convex.

Pronotum with anteroventral margins forming angle in lateral view, humeral angle with broad posterior sulcus, pronotal sides foveolate, intervening areas either smooth, colliculate or strigulose or with rows of colliculae; anterior pronotal face usually with transverse strigulae or colliculae, pronotal dorsum can be densely foveolate and with arching strigulae; anepisternum smooth with sparse punctae; katepisternum with broad anteroventral sulcus, ventral third foveolate and elevated, rest smooth to colliculate or strigulose; metapleuron mostly smooth with colliculate to strigulose posterior end; propodeum laterally smooth to slightly undulating with sparse foveolae or punctae, spiracles at same level or slightly raised above rest of integument; propodeal dorsal and declivitous margins in lateral view joined through variably curving convexity, never angular; mesosomal dorsum with mostly smooth median longitudinal strip.

Sides of petiolar node foveolate with intervening space smooth to colliculate; subpetiolar process subquadrate in lateral view or forms anteriorly projecting lobe with posterior angle; sides of postpetiolar tergite foveolate, anterior depressions deeper and wider than posterior ones, intervening cuticle smooth to colliculate, colliculae usually present ventrally; abdominal tergite 4 mostly smooth with sparse punctulae plus varying degrees of ventral strigulae or colliculae in lateral view; sternite posterolaterally with band of minute strigulae or colliculae. Fore coxae with transverse strigae ranging from rough to partially effaced anteriorly. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body brown to dark brown, extremities lighter.

Queen. Metrics ($n = 2$): HL 1.15, 1.22; HW 0.91, 0.95; ML 0.54, 0.51; SL 0.74, 0.82; ED 0.27, 0.31; WL 1.71, 1.75 mm. CI 0.79, 0.78; SI 0.82, 0.87; MI 0.59, 0.53; OI 0.29, 0.33. Pronotum foveolate; mesoscutum with anterior shiny area, posteriorly strigulose-foveolate or only foveolate; axillae rugulose-foveolate; scutellum with median smooth or sparsely foveolate area, laterally foveolate. Propodeal declivity posteriorly smooth, anterior margin finely rugulose.

Male. See Brown (1958:308).

Comments. This widespread species is variable in size and sculptural features compared with other members of the *laevior* group. It is usually easily distinguished from other *laevior* group members by the strigulose to colliculate sculpturing on the fourth abdominal sternite. All other species have mostly smooth sculpturing with scattered foveolae. In *G. laevior* the degree of coverage of minute rounded elevations forming the colliculate areas can vary from very widespread throughout the body of the ant to present only on the fourth abdominal sternite. Specimens completely lacking minute rounded elevations can be found on the Malay Peninsula, Greater Sundas, northern Borneo, and Sulawesi. Though these specimens were on average smaller than those with minute rounded elevations, some specimens with minute rounded elevations fall within their size range. The single record from Sulawesi (not included in "metrics" above) is smaller (HL 0.82; HW 0.59; WL 1.07 mm) than most *G. laevior* and has a more evenly convex anterior clypeal margin as well as a convex petiolar process without a posterior angle and with no colliculate areas.

The clypeal lamella varies from a medially projecting blunt angle with convergent straight sides, to a feebly medially projecting convexity, with straight to

slightly sinuate sides; sometimes one side is straight and the other is slightly concave in the same specimen. The clypeal lamella is evenly convex in specimens from Sulawesi and the Philippines. In frontal view the posterolateral cephalic corners can have the occipital lamella forming a small denticulate point. This feature depends on the degree of development of the lamella, which varies geographically, and on how frontal the view of the head is. Specimens from Luzon Island have smaller and more dispersed cephalic foveolae, with finer strigulae on the clypeus; the anterior pronotal margin lacks transverse strigulae, and the mesosomal sides tend to be smooth. Specimens from the Malay Peninsula have denser foveolae on the head with longitudinal low strigulae and patches of striae along the posterior edges of the foveolae.

Brown (1954b) included *G. laevior* in his treatise of the *coxalis* group of *Stictoponera* in which the only information provided was the characterization of *G. laevior* as a “small, slender shining species” and the justification of the synonymy of *G. avia* based on its being a teneral specimen. The specimen of *G. avia* he examined was apparently not the type but a worker from Poendjak, Java, identified by Forel. In his 1958 revision he did not see a type of *G. laevior* but based his concept of the species from “satisfactory evidence.” This also explains why Brown (1958) made no reference to *G. laevior* when comparing features of *G. kalabit* with other *Gnamptogenys* in his description of *G. kalabit*. An examination of the *G. kalabit* holotype as well as other specimens from the same nest series did not reveal any clear-cut difference from *G. laevior*. In his description of *G. avia* Forel (1912a) described two males that he assigns to this species even though they were not

associated with any of the females. The larvae of *G. laevior* are described in Wheeler and Wheeler (1952:122-123, pl. 3, figs. 1-8) as *Stictoponera* sp.

Specimens examined. INDONESIA: **Jawa Barat**: Gunung Gede, 75km SSE Jakarta, 6/47'S 106/59'E, i-1991, F. Ito FI91-6, 2w MIZA; same data, FI91-16, 4w MIZA; same data FI91-28, 4w MIZA; same data, FI91-119, 4w MIZA.

Undetermined Java: Poendjak, 7-vii-1920, 1w MCZC; Tjibodas, 1500m, 6/7-vi-1972, W.L. Brown, 4w MCZC. **Sulawesi Utara**: SW slope Mt. Klabat, 400-600m,

13/19-vi-1972, W.L. Brown, 1w MCZC. **Sumatera Barat**: Sukarami, nr. Padang 1/5-i-1992, F. Ito FI92-119, 4w MIZA. **Undetermined Sumatra**: Bang Rakal, NGS

SI Exped., 1937, Mann, 15w 2q USNM. MALAYSIA: **Pahang**: Cameron Highlands, 22-iii-1984, Rougemont, 1w BMNH; Sungei Simei Falls, Cameron Hills [= Highlands], 25/28-iii-1977, T. Jaccoud & P. Marcuard leg, 1w ANIC; Cameron

Highlands, 1550m, Gunung Jasar Trail 11, I. Löbl & Calame, 24-iii-93, 6w BMNH; Ringlet, 1250m, ravine #20, I. Löbl & Calame, 26-iii-93, 6w BMNH. **Selangor**: Ulu

Gombak, 3/20'N 101/45'E, 220m, 15km NNE Kuala Lumpur, vii/ix-1992, F. Ito FI92MG-258, 2q 7w MIZA; same locality, 23-x-96, F. Ito FI96-642, 4w MIZA.

Sabah: mi 43 Labuk Road ex Sandakan (Lungmanis), 13-vi-68, rainforest berlesate, R.W. Taylor acc. 68.527, 1w ANIC; Tawau Hill, 6-x-1996, F. Ito FI96-534, 4w

MIZA; Telupid, 29-ix-1996, F. Ito FI96-437, 9w MIZA; Crocker Range, 1200m, 19-v-1987, D. Burckhardt & I. Löbl B1a, 6w 1q BMNH. **Sarawak**: confl. Sun Oyan and

Mujong Rivers, E Kapit, 50m, 18-v-1994, I. Löbl & D. Burckhardt #5a, 1w BMNH.

PHILIPPINES. **Laguna**: Los Baños, Mt. Makiling, below summit, 550m, 24-iv-1981, W.L. Brown, 4w MCZC.

Gnamptogenys leiolabia sp. n.

(Fig. 56)

Diagnosis. Scapes when laid back do not reach posterior cephalic margin by at least one apical width; clypeus and mandibular dorsum mostly smooth, almost glabrous; clypeus delimited laterally by low carinae that extend from ends of clypeal lamella; occipital lamella short in lateral view, with bluntly angular anterior and posterior ends.

Type material. Holotype worker. Malaysia, Sabah, Sebuga Forest Reserve near Sandakan rainforest, 9-vi-1968, R.W. Taylor 68.371. ANIC ants vial 6.216. Deposited in ANIC. Paratypes. One worker and queen deposited in ANIC, 1 worker in MCZC from same nest as holotype.

Worker. Metrics. [Holotype] Paratypes ($n = 3$): HL [0.66] 0.63-0.64, HW [0.46] 0.45-0.47, ML [0.26] 0.26-0.28, SL [0.37] 0.36-0.39, ED [0.14] 0.13-0.14, WL [0.84] 0.81-0.84 mm. CI [0.70] 0.71-0.72, SI [0.80] 0.77-0.86, MI [0.57] 0.55-0.62, OI [0.31] 0.28-0.32. Head with subparallel sides in frontal view, occipital corner sharply curved, not angular; frons mostly smooth with longitudinal strigulae; foveolae on frons denser laterally with some smooth patches, especially just dorsad of eye; clypeus mostly smooth down to lamella, with median area surrounded by two longitudinal crests that extend from next to anterior end of frontal lobes to lateral ends of clypeal lamella, each crest with convexity posterad of lamella, anterior margin of lamella straight; frontal lobe convex, longitudinally strigulose dorsally;

mandibular dorsum mostly smooth with scattered punctae, longitudinal strigulae sometimes present basally, external margin relatively straight; head with dorsal margin broadly convex in lateral view, except for small elevation at posterior end of frontal lobe and rounded clypeal angle; occipital lamella brief, convex, with bluntly angular anterior and posterior ends.

Ventral pronotal margin convex, laterally mostly smooth with sparse foveolae, foveolae denser dorsally, anteroventral margin raised, not bordered by deep sulcus; mesopleuron mostly smooth, anepisternum more foveolate than katepisternum; metapleuron mostly smooth with longitudinal strigulae ventrad; mesosoma with broadly convex dorsal margin in lateral view, forming blunt angle with propodeal declivity. Petiolar node broadly convex dorsally in lateral view, anterior shelf very brief, inclined, forming fine notch with node, posterior shelf present; subpetiolar process subquadrate; postpetiolar ventral margin straight to broadly convex just posterad of process in lateral view, postpetiolar tergite anterolaterally with large foveolae becoming shallower and smaller posterad, rest of postpetiole smooth with scattered punctae; fourth abdominal tergite smooth with scattered punctulae. Fore coxa smooth in lateral view. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body ferruginous brown, legs and antennae ferruginous.

Queen. Metrics ($n = 2$): HL 0.69, 0.71; HW 0.52, 0.54; ML 0.30, 0.32; SL 0.41, 0.43; ED 0.17, 0.19; WL 1.00, 1.02 mm. CI 0.75, 0.76; SI 0.79, 0.80; MI 0.57, 0.59; OI 0.32, 0.36. The first queen is from the same series as the holotype; the second

female is from the MCZC. Besides inherent caste characters, substantial differences from workers are denser foveolae and punctae on frons; elongated, smoother anepisternum; metapleuron with narrower smooth area; petiolar node more convex in lateral view.

Male. Unknown.

Comments. Specimens of this species were examined by Brown (1958) and were considered variants of *G. chapmani* (see Comments for *G. chapmani*). The paratype queen of *G. chapmani* is actually a female of *G. leiolabia*. *G. chapmani* is most easily separated from *G. leiolabia* by its clypeal structure, which is longitudinally strigulose, and the medially bluntly protruding lamella. *G. chapmani* also lacks the lateral ridges that extend anteriorly from the frontal lobes and define the sides of the clypeal lamella as in *G. leiolabia*. The predominantly smooth clypeus of *G. leiolabia*, with a median area bound by two crests, points at close affinities with *G. biloba* and *G. hyalina* (see Comments for *G. biloba*). *G. biloba* and *G. hyalina* are considerably larger (HW > 0.80; WL > 1.00 mm) than *G. leiolabia*. The posterior median clypeal area in *G. hyalina* is much smoother, almost glabrous, while the clypeal ridges in *G. biloba* are much more protuberant and the metaxcoaxal tooth is peglike and not triangular. The holotype series is labeled as coming from rotten logs in rainforest, and the Gunung Matang specimen came from mixed dipterocarp forest.

Etymology. The species name is derived from a conjugation of the Greek *leios*, meaning “smooth,” and the Latin *labium* (n.), “lip.”

Additional specimens examined. MALAYSIA. **Sabah:** Sepilok Forest Reserve nr. Sandakan, 10-vi-1968, R.W. Taylor 68.386, ANIC ants vial 6.214, 2w BMNH. **Sarawak:** Gunung Matang, 20km E Kuchin, 200m, 26-v-1994, I. Löbl & D. Burckhardt #12, 1w BMNH. PHILIPPINES. **Negros Oriental:** Cuernos Mts., J.W.C.'s Camp, 27-iv-1924, J.W. Chapman, 1w 1q MCZC.

***Gnamptogenys pertusa* sp. n.**

(Figs. 48c, 58a,b)

Diagnosis. Mandible with swollen base in frontal view; clypeal lamella translucent, with broadly convex anterior margin; subpetiolar process subquadrate with sharp posterior angle in lateral view; propodeal declivity sharply defined laterally by low crests.

Type material. Holotype worker. Malaysia, Sabah, Borneo, mi. 45 Labuk Road, ex Sandakan (Lungmanis), 12/13-vi-1968, R.W. Taylor, acc. 68.502. Deposited in ANIC. Paratype. One callow worker on same pin as holotype, deposited in ANIC.

Worker. Metrics. [Holotype] Paratype: HL [0.70] 0.69, HW [0.55] 0.53, ML [0.31] 0.30, SL [0.43] 0.43, ED [0.15] 0.13, WL [0.97] 0.95 mm. CI [0.76] 0.77, SI [0.76] 0.81, MI [0.55] 0.55, OI [0.27] 0.25. Head with subparallel sides in dorsal view; foveolae on frons with intervening spaces broad or broader than average diameter of foveolae; clypeus with anteromedian smooth to undulated area, laterally with

longitudinal strigulae, lamella translucent with background lighting, anterior margin convex; mandible with convex bulging base; dorsally rugulose-punctate, apically mostly smooth; very small, broadly separated denticles present on chewing border; head with evenly convex occipital lamella in lateral view; posterodorsal mandibular margin with brief, mostly straight margin, then with pronounced convexity in lateral view.

Pronotum laterally foveolate along dorsal half, mostly smooth on ventral half, strigulae present along posterior edge; anepisternum rhomboid, smooth with some punctae; katepisternum mostly smooth, with shallow strigulae along anterodorsal corner; metapleuron and propodeum mostly smooth, longitudinal strigulae present along ventral area of metapleuron; propodeum foveolate, propodeal declivity sharply defined laterally by low crests. Dorsum of mesosoma and petiole sparsely foveolate, mostly smooth especially along longitudinal median strip; petiole with ventral process anteriorly convex in lateral view, ending in a posterior angle; postpetiole laterally with close and deep foveolae anterad, posteriorly becoming shallow and sparse; postpetiolar dorsum mostly smooth with sparse, shallow, piligerous punctae; fore coxa transversely strigulose along posterior half, smooth anterad. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body dark brown; legs, antennae, and mandibles ferruginous brown.

Queen and male. Unknown.

Comments. *G. pertusa* may be confused with *G. lacunosa* because of the angular anterior clypeal lamella margin and with *G. polytreta* because of the prominent

occipital lamella. *G. rugodens* also has these same traits, but the deep mandibular rugosities easily distinguish *G. rugodens*. *G. lacunosa* has more deeply strigulose sculpturing on the mandibular base than *G. pertusa*, and the mandibular base in *G. lacunosa* is not as bulging and convex as in *G. pertusa*. The dorsal margin of the petiolar node in *G. lacunosa* is more evenly convex, and the subpetiolar process is shaped as a rounded lobe; the postpetiolar tergite is mostly smooth in lateral view with punctae present on the anterior third or less. *G. polytreta* has a convex mandibular base but not as bulging as in *G. pertusa*, the subpetiolar process is triangular with a blunt posterior angle, and the dorsal margin of the petiolar node is more evenly convex. The node in *G. pertusa* has a sharper anterior curvature. The holotype of *G. pertusa* is decapitated, with body and head mounted on separate points.

Etymology. The species name is derived from the Latin adjective for “perforated,” *pertusus*, and alludes to the depressions of its foveolate sculpturing.

***Gnamptogenys polytreta* sp. n.**

(Figs. 48b, 49a, 59)

Diagnosis. Dorsum of head densely foveolate; oculomalar margin with low triangular projection; lateral mandibular margin slightly sinuate; clypeus convex with faint median convexity; occipital lamella protuberant and convex; anterior petiolar margin

broadly concave in dorsal view, without protuberant lateral lobes; anterior and posterior shelves of node form minute acute angles in lateral view with node margins.

Type material. Holotype worker. Malaysia, Pahang, Genting Highlands, Awana, 1150m, 3-iv-1993, I. Löbl & Calame #27b. Deposited in MHNG. Paratype. One worker in BMNH from Malaysia, Pahang, Genting Highlands, Awana, 1150m, 3-iv-1993, I. Löbl & Calame #27c.

Worker. Metrics. [Holotype] Paratype: HL [0.77] 0.77, HW [0.59] 0.59, ML [0.37] 0.35, SL [0.51] 0.51, ED [0.19] 0.20, WL [1.13] 1.15 mm. CI [0.76] 0.76, SI [0.87] 0.88, MI [0.63] 0.59, OI [0.33] 0.34. Head with lateral margin separated from posterior margin in frontal view by brief, broadly concave to straight margin; oculomalar margin divided by low triangular projection into longer posterior broad convexity and shorter broadly convex to almost straight anterior margin; frons evenly foveolate; frontal lobe dorsally smooth with shallow elongate depressions, posteriorly bordered by abrupt slope; clypeus posterolaterally strigulose-foveolate, medially with longitudinal strigulae extending to posterior half of clypeal lamella, low rounded ridge extends anterad from frontal lobe; lamella mostly smooth, anterior margin of lamella convex with slight median convexity; mandible slightly sinuate laterally, rugulose-punctate basally, apically mostly smooth with punctae; head with broadly convex dorsal margin in lateral view, interrupted by brief abrupt elevation of frontal lobes posterior margin; frontal lobe and clypeus each form broad convexities; occipital lamella convex and protuberant.

Pronotum laterally foveolate with low longitudinal undulations; mesopleuron mostly smooth with foveolae on anepisternum and particularly along ventral katepisternum; metapleuron triangular, tapering anterodorsally and diverging posteroventrally, anterior margin broadly convex, mostly smooth, longitudinally strigulose ventrally; propodeum undulate with irregular depressions, declivitous and dorsal margins form blunt, slightly obtuse angle in lateral view; mesosoma laterally with broadly convex dorsum, medially almost flat. Petiolar node dorsum mostly smooth with punctae, laterally foveolate; subpetiolar process triangular, projecting anteriorly; postpetiole mostly smooth, laterally foveolate, with anterior foveolae deeper and wider than posterior foveolae, dorsum sparsely punctate; ventral margin of postpetiole mostly straight after process in lateral view, convex posteriorly; fourth abdominal segment mostly smooth, dorsum sparsely punctate, punctae present along posterior margin. Fore coxae mostly transversely strigulose, smooth anteriorly. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body brown, antennae and legs ferruginous brown.

Queen and male. Unknown.

Comments. This species could be confused with *G. pertusa*, *G. lacunosa*, and *G. rugodens* as discussed under *G. pertusa*. *G. pertusa* has a very prominent mandibular base, forming a bulging convexity in frontal view, and its subpetiolar process is subquadrate in lateral view, with a sharp posterior angle. *G. rugodens* has a more evenly convex dorsal margin of the petiolar node and a relatively shorter declivitous margin to the propodeum compared with the dorsal margin in lateral view; it is also

larger bodied (HL > 0.85; HW > 0.65; WL > 1.25 mm) than *G. polytreta*. *G. lacunosa* has a more evenly convex dorsal petiolar node margin, the subpetiolar process forms a rounded lobe in lateral view, the lateral face of the postpetiolar tergite is mostly smooth with punctae on the anterior one-third or less, the dorsal and declivitous propodeal margins form a blunt obtuse angle, more open than in *G. polytreta*, and the mandibular base is more deeply strigulose in *G. lacunosa*.

Etymology. The species name is derived from the Greek terms *poly* (many) plus *treto*s (perforated). It alludes to the multiple depressions of its foveolate sculpture.

***Gnamptogenys rugodens* sp. n.**

(Fig. 60)

Diagnosis. Frontal lobe followed posteriorly by smaller convexity formed by frontal carina; each lateral cephalic margin just posterad of mandible forms small concavity followed by small triangular projection; mandibles deeply rugose, especially toward base. Propodeal declivitous margin very short compared with dorsal margin in lateral view.

Type Material. Holotype worker. Malaysia, Sarawak, Gunung Penrissen, 1000m, 23-v-1994, I. Löbl & D. Burckhardt legs, edge of primary forest #9a. Deposited in MHNG.

Worker. Metrics. Holotype: HL 0.94, HW 0.78, ML 0.42, SL 0.68, ED 0.18, WL 1.37 mm. CI 0.82, SI 0.87, MI 0.55, OI 0.23. Each lateral cephalic margin posterad of eye fairly straight in frontal view; briefly concave just anterad of eye, then mostly straight to broadly convex, followed by small triangular process; clypeal lamella laterally rounded and anteriorly straight, translucent, with reticulate etchings; frontal lobe convex followed posterad by smaller convexity formed by frontal carina; clypeus longitudinally strigulose posterad, sculpturing fading away anterad; mandibles edentate, deeply rugose basally; mandibular dorsal margin undulated basally in lateral view; occipital lamella medially straight, convex at both ends.

Pronotum laterally foveolate, foveolate-strigose posterad, smooth along ventral margin, anteroventrally bluntly angular; anepisternum undulate with punctae; katepisternum strigulose with irregular depressions along posterior margin, anterad smooth; metapleuron smooth, separated from propodeum by row of elongate foveolae that curve just below spiracle; propodeum with scattered foveolae; mesosoma with well developed humeral angle in lateral view. Petiolar node dorsum mostly smooth, sparsely foveolate, laterally densely foveolate, ventral process subquadrate; postpetiole laterally with deep anterior scalloping, slightly shallower posterad; postpetiolar sternite mostly smooth with shallow lateral foveolae, posterior margin with row of punctae; postpetiolar dorsum mostly smooth with sparse scalloped punctae, deeper anterad than posterad; fore coxa transversely strigose, smooth anterad. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body brown; mandibles, scapes, legs ferruginous brown.

Comments. The deeply rugose mandibles in *G. rugodens* are quite distinctive and find no parallel in any other species of *Gnamptogenys*, with the possible exception of *G. lacunosa*, which has a considerably rugose mandibular base, but the rugae are not as deep as in *G. rugodens*. *G. lacunosa* has a less prominent occipital lamella, the clypeal lamella has some minute sculpturing but not as finely scabrose, and its anterior margin is more convex; it is a smaller ant (HW < 0.75 mm), with relatively larger eyes (OI > 0.25) and narrower head (CI < 0.80). *G. polytreta* has prominent occipital lamella, as in *G. rugodens*, but differs in the more broadly convex dorsal margin of the petiolar node, a triangular subpetiolar process, and a relatively longer declivitous propodeal margin compared with its dorsal margin. It is also smaller bodied (HL < 0.85; HW < 0.65; WL < 1.25 mm) than *G. rugodens*.

Etymology. The species name is a compound epithet derived from the Latin words for “fold,” *ruga* (f.), and “tooth,” *dens* (m.) that alludes to the deep mandibular rugosities.

taivanensis group

Worker diagnosis. Scape strigulose-punctate, gradually widening apically, scape length surpassing posterior cephalic margin by at least one apical width (SI 0.89-1.05); eye reduced in diameter (OI 0.10-0.15) but with convex dorsal cross section,

not flattened; propodeal spiracle separated from propodeal declivity in lateral view by more than one spiracular diameter. Petiole in lateral view erect, anterior margin longer than dorsal margin; spiracle situated laterally on anterolateral petiolar corner, not below it.

Worker description. Head with convex lateral margins in frontal view, converging anterad, posteriorly wider than anteriorly, occipital ridge present; sculpture on head, including vertex, mostly rugulose-punctate; occipital lobes absent or present; frontal lobe dorsolaterally raised, dorsal lobe of torulus separate from frontal lobe and close to base of torulus, partially visible in frontal view; eye reduced in diameter ($OI < 0.16$), with convex, not flattened, dorsal cross section. Scape strigulose-punctate, gradually widening apically, scape length surpassing posterior cephalic margin by at least one but not more than two apical widths; scape with dense layer of short, erect pilosity of uniform length besides scattered longer hairs; first funicular segment approximately 1.2-1.5 times longer than wide. Anterior clypeal margin convex or with median lobe, shallow median longitudinal sulcus present (reduced in *G. sichuanensis*), lamella present; mandible dorsally striate-punctate; masticatory border denticulate, dorsal margin evenly convex in lateral view. Palpal formula 3,2.

Pronotum laterally with straight ventral margin lacking sulcus, anteroventrally bluntly angulose with a brief posteroventral lobe, humeral angle well developed; prosternal process with widely separated ridges, median lobe of process with apex entire, not cleft, not extending beyond prosternal ridges in ventral view; basisternal process relatively long; promesonotal suture distinct, interrupting sculpture medially;

anepisternum clearly delimited by sutures, approximately trapezoidal, not cuneiform; mesopleural suture wide, with transverse crests and ridges; mesometapleural suture distinct, well developed; suture between propodeum and metapleuron obsolescent; metanotal groove obsolescent; propodeal spiracle in lateral view separated from declivity by more than one spiracular diameter, propodeal declivity relatively flat and sculptured, propodeal lobes present or absent, propodeal denticles absent; mesosomal sculpturing mostly strigulose or strigulose-punctate, not smooth as in *laevior* group or *epinotalis* group; mesosomal dorsal margin mostly convex in lateral view.

Petiole erect in lateral view, anterior margin longer than dorsal margin, anterior shelf absent; anterior crest present but may be medially reduced; petiolar spiracle situated laterally on anterolateral petiolar corner, not below it; subpetiolar process of uniform width ventrally, laterally subquadrate; postpetiolar process V-shaped in anterior view, with brief median longitudinal crest. Fore tarsal base with row of stout setae opposite strigil, fore tarsal dorsum densely punctulate; apex of second protarsal segment with four stout setae and two slenderer setae; metacoxal dorsum with triangular tooth.

Included species: *G. panda*, *G. sichuanensis*, *G. sinensis*, *G. taivanensis*. **Dissected species:** *G. taivanensis*.

Comments. This small group of species is presently known only from southern China and Taiwan. Along with the *epinotalis* group they are the least variable in size and morphology. The presence of a stridulatory organ on the fourth abdominal pretergite is the defining apomorphy of this clade. The posterolateral ridges on the propodeal declivity are shared with the *coxalis* group.

***Gnamptogenys panda* (Brown)**

(Fig. 61)

Stictoponera panda Brown, 1948:263. Holotype worker: China, Szechwan [Sichuan],

Chao Kung Mt. (Brown) (MCZC) [Examined].

Gnamptogenys panda (Brown); Brown, 1958:228. Placed in *Gnamptogenys*.

Diagnosis. Head with occipital lamella forming blunt point in lateral view; anterior clypeal margin with median convex to bluntly pointed lobe; humeral angles prominent, upturned with parallel posterior convexity.

Worker. Metrics. [Holotype] Paratype: HL [1.28] 1.24, HW [1.14] 1.11, ML [0.61] 0.64, SL [1.12] 1.09, ED [0.12] 0.11, WL [1.70] 1.60 mm. CI [0.89] 0.90, SI [0.98] 0.98, MI [0.54] 0.54, OI [0.11] 0.10. Head with broadly concave posterior margin in frontal view; anterior margin of clypeus with convex to bluntly pointed median lobe; clypeus longitudinally strigulose with shallow median sulcus, laterally and posteriorly strigulose-punctate; frontal triangle oval, laterally bordered by arching sulcus; head with occipital lamella forming blunt point in lateral view. Humeral angle prominent, upturned with parallel posterior convexity, pronotal dorsum irregularly strigose, pronotum irregularly strigose laterally, lateroventrally convex, dull and granulate sculpture separated from shiny rugosity by longitudinal crest at height of mesopleural sulcus, promesonotal suture distinct; mesonotum longitudinally

strigulose; mesopleuron strigose, metapleuron longitudinally strigulose; propodeal declivity transversely strigulose, propodeal dorsum irregularly strigose. Mesosoma with convex dorsal margin in lateral view, pronotum slightly higher, with brief vertical drop to mesonotum, propodeal declivity concave.

Postpetiolar process forms two contiguous convexities in ventral view with brief posteromedian carinae; postpetiole and fourth abdominal sternite transversely strigulose-punctate, strigulae on side of fourth abdominal segment not as prominent as on dorsum; fore tarsal base with row of stout setae; procoxa laterally transversely strigulose. Dorsum of thorax and abdominal segments 1-4 with relatively short, scattered erect to subdecumbent hairs. Metacoxal tooth relatively low, apically parallel sided.

Queen and male. Unknown.

Comments. Brown (1948) described the type locality as the summit of a ridge near Chao Kung Mountain between 1524 and 2286m, 1.5 days travel on foot west of Guan Xian (Kuanshien). Guan Xian (31,00'N 103,37'E) is in Sichuan. The ants were found in bamboo humus on a ridge summit and were observed as moving slowing, freezing on disturbance. Brown (1958) mentioned seeing additional specimens of *G. panda*, but study of these specimens showed them to be *G. sichuanensis*. *G. panda* is also mentioned in Wu and Wang (1992, 1995). Wang (1992) reported this species from an altitude of 1050m in the Wuling Mountains of southwestern China. The altitude on the USNM specimen label is partially illegible, probably 6000 ft. The altitude on the holotype label is also partially illegible and may be 7000 ft.

The frontal triangle of *G. panda* is deeper than in *G. sichuanensis* and *G. taivanensis*. These two species have broader, more triangular metacoxal teeth than *G. panda* and more regularly shaped strigulae on the propodeal declivity. The relatively broad lateroventral granulose area on the pronotum of *G. panda* is not found in *G. sichuanensis* or *G. taivanensis*.

Specimens examined. CHINA. **Sichuan:** Chao Kung Mt., Guan Xian, 1829m[?], 4-xi-45, W.L. Brown, 1w USNM; Chao Kung Mt., 2134m[?], 4-xi-45, W.L. Brown, 1w MCZC.

***Gnamptogenys sichuanensis* sp. n.**

(Fig. 62)

Diagnosis. Occipital lobe well developed in lateral view, with thin, almost translucent lamella. Promesonotum longitudinally rugose-punctate; pronotal side and mesopleuron with parallel longitudinal strigae; postpetiolar dorsum anterad with anastomizing rugae.

Type material. Holotype worker. China, Szechwan [Sichuan], near Muping, 6000ft [1829m], July 1929, D.C. Graham leg. Deposited in USNM. Paratype. Same data as holotype, but Sichuan is spelled "Szechuen," 1 worker in MCZC.

Worker. Metrics. [Holotype] Paratype: HL [1.37] 1.35, HW [1.24] 1.23, ML [0.72] 0.71, SL [1.10] 1.13, ED [0.15] 0.16, WL [1.70] 1.78 mm. CI [0.91] 0.91, SI [0.89]

0.92, MI [0.58] 0.58, OI [0.12] 0.13. Head with posterior margin straight to weakly concave in dorsal view; anterior clypeal margin convex; clypeus anterolaterally with longitudinal strigulae, rugose-punctate posterad; frontal triangle U-shaped, with smooth bottom; longitudinal strigulae arch posterad over eyes becoming rugose-punctate laterally, frons laterally longitudinally strigulose, areolate toward vertex; posterior cephalic margin convex in lateral view; occipital lobes well developed, with thin, almost translucent lamella. Humeral angle well developed, not protuberant, without shallow posterior sulcus, laterally with longitudinal strigae separated by broad sulci, with anteroventral blunt angle and posteroventral rounded lobe; pronotal dorsum longitudinally rugose-punctate, rugae more continuous medially than laterally; promesonotal suture partially impressed, not breaking sculpture; mesopleuron longitudinally strigose, mesopleural suture well defined; mesosomal dorsum with dense longitudinal strigae, strigae irregular on propodeum; propodeum rugose-punctate, declivitous face with transverse carinae, rest smooth; mesosoma evenly convex until propodeal declivity in lateral view, declivity vertical, slightly convex.

Petiolar node rugose-punctate; subpetiolar process broadly triangular in lateral view, ventrally not cuneiform; postpetiolar dorsum with anterior anastomizing rugae, rugae diverging and less prominent posterad, posteromedially with arching strigulae, laterally with parallel strigae; sternite transversely strigose-punctate; postpetiolar process forms two contiguous convex lobes in ventral view, with median cleft and brief median carinae; fourth abdominal tergite with patches of longitudinal striae

centered around punctae on smooth background, posterior margin strigulose-striate; sternite transversely strigose. Fore coxae laterally transversely strigose; fore tarsal dorsum punctate, with abundant pilosity; basal concavity with row of stout setae; metacoxal tooth low, triangular. Dorsum of thorax and abdominal segments 1-4 with scattered erect to subdecumbent hairs. Body with abundant golden decumbent pilosity; body brown; legs, antennae, and mandibles ferruginous brown.

Queen and male. Unknown.

Comments. Brown (1958:300, Fig. 18) misidentified the present two specimens of *G. sichuanensis* as *G. panda*. The following traits serve to separate *Gnamptogenys* from China that could be confused with *G. sichuanensis*. *G. panda* is distinguished by the anteromedian irregular strigae on the pronotum, the irregularly strigose mesopleuron, and the more weakly impressed mesopleural suture. The postpetiolar strigae lack anterior anastomization and the lateral rugulae of the fourth abdominal segment are lower, not as prominent. *G. taivanensis* can be separated from *G. sichuanensis* by its lack of an occipital lobe and the presence of short propodeal denticles. The postpetiolar dorsum of *G. taivanensis* is mostly longitudinally strigulose-punctate compared with the posterior thinning of the rugulae into very low transverse to arching strigulae in *G. sichuanensis*. The dorsum of the second gastric segment of *G. taivanensis* is mostly smooth with abundant punctae and occasional traces of longitudinal striae.

Etymology. The species name is derived from the name of the province that contains the type locality: Sichuan.

***Gnamptogenys sinensis* Wu and Xiao**

Gnamptogenys sinensis Wu and Xiao, 1987:303, Figs 1-3. Holotype: China, Hunan, Daoxian (CFRB) [Not examined].

Diagnosis. Humeral angles forming distinct denticles.

Worker. Metrics ($n = 1$): HL 1.57, HW 1.52, SL 1.59, ED 0.16 mm. CI 0.97, SI 1.05, OI 0.11. Taken from Wu and Xiao (1987).

Comments. It was not possible to examine any specimens of this species. The description and figures in Wu and Xiao (1987) would place *G. sinensis* in the *taivanensis* group based on the shape of the petiole and the subpetiolar process and the small eyes. The type series consists of 6 workers deposited in the insect collection of the Forest Research Institute, Chinese Academy of Forestry in Beijing. The specimens were collected in Daoxian County of Hunan Province. This species is also mentioned in Wu and Wang (1992, 1995).

***Gnamptogenys taivanensis* (Wheeler)**

(Fig. 63)

Stictoponera taivanensis Wheeler, W.M., 1929:32. Holotype worker by monotypy: Taiwan, Funkiko (Silvestri) (MCZC) [Examined].

Gnamptogenys taivanensis (Wheeler); Brown, 1958:229. Placed in *Gnamptogenys*.

Diagnosis. Head lacking occipital lamella. Propodeal denticle present; postpetiolar dorsum with anterior strigae, fading posterad to mostly smooth punctate surface with scalloped ridges anterad of each puncture. Dorsum of second gastric segment mostly smooth, with punctae and occasional traces of longitudinal striae.

Worker. Metrics ($n = 4$): HL 1.25-1.32, HW 1.05-1.12, ML 0.60-0.63, SL 0.98-1.08, ED 0.11-0.17, WL 1.67-1.80 mm. CI 0.81-0.84, SI 0.93-0.99, MI 0.56-0.60, OI 0.10-0.15. Head with anterior clypeal margin bluntly angular medially in frontal view, frons rugose-punctate, except for median longitudinal strigulae; clypeus longitudinally carinate, with median shallow sulcus. Pronotum laterally strigose, humeral area angular, without raised crest; mesosomal dorsum mostly rugose-punctate, with longitudinal strigulae on median promesonotum; promesonotal suture distinct; meso- and metapleuron longitudinally strigose; propodeum laterally rugose-punctate; with short triangular denticles, propodeal declivity with transverse strigulae. Mesosoma in lateral view with convex dorsal margin, pronotum slightly higher than rest of mesosoma.

Petiole rugose-punctate; subpetiolar process triangular, broad; postpetiolar dorsum anteriorly strigose, fading posterad to mostly smooth, surface punctate with ridges around anterior edge of punctae, scalloped aspect, laterally reticulate-rugose; postpetiolar process forms two contiguous blunt angles with brief median carina that extends posteriorly in ventral view; postpetiolar sternite punctate, with low rugosity; fourth abdominal segment dorsum mostly smooth, punctate, with occasional traces of longitudinal striae. Fore coxa transversely strigulose in lateral view; metacoxal tooth

triangular, low; base of fore tarsus with row of stout setae. Dorsum of thorax and abdominal segments 1-4 with abundant erect to subdecumbent golden hairs. Body mostly ferruginous brown; antennae, legs, mandible lighter.

Queen and male. Unknown.

Comments. The examined type specimen bears a MCZ Cotype 20419 label, even though Wheeler (1929) explicitly stated the description was based on a single specimen. The original description fails to mention Silvestri as the collector. The type is a bit tattered, with many broken and appressed hairs, lacking a foreleg, several tarsi, and part of an antenna. The locality that figures on the type specimen label, Funkiko, is a Japanese name for Fen-chi-hu, which may also be spelled Fen-ch'i-hu. Unfortunately there are ten records for this name from Taiwan in the GEONet database. The only known *Gnamptogenys* from Taiwan, *G. taivanensis* could be confused with the following mainland species: *G. panda*, although this species has very distinctly angular occipital lobes, and *G. sichuanensis*, whose distinct occipital lobes form a convex, translucent lamella and whose postpetiolar dorsum has arching strigulae. Neither of these two species have propodeal denticles. Additional specimens of *G. taivanensis* were generously made available by Dr. Wu Wen-jer and Dr. C. Lien.

Specimens examined. TAIWAN. Funkiko, Silvestri, 1w MCZC; Ilan Hsien, 1100m, 24/44'N 121/12'E, 9-vi-1995, C.C. Lien, 1w ANIC, 1w BMNH, 1w LACM, 1w MIZA.

References

- Baroni Urbani, C., B. Bolton, and P.S. Ward. 1992. The internal phylogeny of ants. *Systematic Entomology*, 17:301-329.
- Bingham, C. T. 1903. The Fauna of British India, including Ceylon and Burma. Hymenoptera, Vol. II. Ants and Cuckoo-Wasps. Taylor and Francis, London. 506 pp.
- Bolton, B. 1990. Army ants reassessed: The phylogeny and classification of the doryline section. *Journal of Natural History*, 24:1339-1364.
- Bolton, B. 1994. Identification Guide to the Ant Genera of the World. Harvard University Press, Cambridge, Mass. 222 pp.
- Bolton, B. 1995a. A new general catalogue of the ants of the world. Harvard University Press, Cambridge, Mass. 504 pp.
- Bolton, B. 1995b. A taxonomic and zoogeographical census of the extant ant taxa. (Hymenoptera: Formicidae). *Journal of Natural History*, 29:1037-1056.
- Borgmeier, T. 1957. Myrmecologische Studien. I. *Anais de Academia Brasileira da Ciencias*, 29:103-128.
- Brown, W.L., Jr. 1948. A new *Stictoponera*, with notes on the genus (Hymenoptera: Formicidae). *Psyche*, 54:263-264.
- Brown, W.L., Jr. 1950. Morphological, taxonomic, and other notes on ants. *Wasmann Journal of Biology*, 8:241-250.
- Brown, W.L., Jr. 1952a. Contributions towards a reclassification of the Formicidae. I. Tribe Platythyreini. *Breviora*, Museum of Comparative Zoology, 6:1-6.
- Brown, W.L., Jr. 1952b. *Heteroponera* Mayr reinstated. *Psyche*, 59:70.

- Brown, W.L., Jr. 1953. Characters and synonymies among the genera of ants. Part I. *Breviora*, 11:1-13.
- Brown, W.L., Jr. 1954a. Systematic and other notes on some of the smaller species of the ant genus *Rhytidoponera* Mayr. *Breviora*, 33:1-11.
- Brown, W.L., Jr. 1954b. A review of the *coxalis* group of the ant genus *Stictoponera* Mayr. *Breviora*, Museum of Comparative Zoology, 34:1-10.
- Brown, W.L., Jr. 1958. Contributions towards a reclassification of the Formicidae. II. Tribe Ectatommini. *Bulletin of the Museum of Comparative Zoology*, 118:171-362.
- Brown, W.L., Jr. 1975. Contributions towards a reclassification of the Formicidae. V. Ponerinae, Tribes Platythyreini, Cerapachyini, *Cylindromyrmecini*, *Acanthostichini*, and *Aenictogitini*. *Search Agriculture*, 5(1):1-115.
- Brown, W.L., Jr. 1993. Two new species of *Gnamptogenys*, and an account of millipede predation by one of them. *Psyche*, 99:275-289.
- Brühl, C., G. Gunsalam, and K. Linsenmair. 1998. Stratification of ants in a primary rain forest in Sabah, Borneo. *Journal of Tropical Ecology*, 14:285-297.
- Carpenter, J. 1988. Choosing among multiple equally parsimonious cladograms. *Cladistics*, 4:291-6.
- Clark, J. 1930. New Formicidae, with notes on little known species. *Proceedings of the Royal Society of Victoria*, (n.s.) 43:2-25.
- Donisthorpe, H. 1932. On the identity of Smith's types of Formicidae (Hymenoptera) collected by Alfred Russell Wallace in the Malay Archipelago, with descriptions of two new species. *Annals and Magazine of Natural History*, (10)10:441-476.

- Emery, C. 1889. Formiche di Birmania e del Tenasserim raccolte da Leonardo Fea (1885-87). [part] *Annali del Museo Civico di Storia Naturale*, 27[=(2)7]:485-512.
- Emery, C. 1890. Studii sulle formiche della fauna neotropica. *Bullettino della Società Entomologica Italiana*, 22:38-80.
- Emery, C. 1895. Viaggio di Leonardo Fea in Birmania e regioni vicine. LXII. Formiche di Birmania del Tenasserim e dei Monte Carin raccolte da L. Fea. Parte II. *Annali del Museo Civico di Storia Naturale*, 34[=(2)14]:450-483.
- Emery, C. 1896. Clef analytique des genres de la famille des Formicides, pour la détermination des neutres. *Annales de la Société Entomologique de Belgique*, 40:172-189.
- Emery, C. 1897. Viaggio di Lamberto Loria nella Papuasias Orientale. XVIII. Formiche raccolte nella Nuova Guinea dal Dott. Lamberto Loria. *Annali del Museo Civico di Storia Naturale*, 38[=(2)18]:546-576.
- Emery, C. 1900a. Formicidarum species novae vel minus cognitae in collectione Musaei Nationalis Hungarici quas in Nova-Guinea, colonia germanica, collegit L. Biró. *Publicatio secunda. Természetráji Füzetek*, 23:310-338.
- Emery, C. 1900b. Formiche raccolte da Elio Modigliani in Sumatra, Engano e Mentawai. *Annali del Museo Civico di Storia Naturale*, 40[=(2)20]: 661-688.
- Emery, C. 1901. Formicidarum species novae vel minus cognitae in collectione Musaei Nationalis Hungarici, quas in Nova-Guinea, colonia germanica, collegit L. Biró. *Publicatio tertia. Természetráji Füzetek*, 25:152-160.

- Emery, C. 1902. Description d'une nouvelle espèce de fourmi du Brésil. Bulletin de la Société Entomologique de France, 1902:181.
- Emery, C. 1911. Hymenoptera. Fam. Formicidae. Subfam. Ponerinae. Genera Insectorum, 118:1-125.
- Forel, A. 1899. Formicidae. [part]. Biologia Centrali-Americana. Hymenoptera, 3:1-24.
- Forel, A. 1900. Les Formicides de l'Empire des Indes et de Ceylan. Part VII. Journal of the Bombay Natural History Society, 13:303-332.
- Farris, J. 1969. A successive approximations approach to character weighing. Systematic Zoology, 18:374-85.
- Forel, A. 1901a. Variétés myrmécologiques. Annales de la Société Entomologique de Belgique, 45:334-382.
- Forel, A. 1901b. Nouvelles espèces de ponerinae (Avec une nouveau sous-genre et une espèce nouvelle d'*Eciton*). Revue Suisse de Zoologie, 9:325-353.
- Forel, A. 1905. Ameisen aus Java. Gesammelt von Prof. Karl Kraepelin 1904. Mitteilungen aus dem Naturhistorischen Museum in Hamburg, 22:1-26.
- Forel, A. 1912a. Ameisen aus Java beobachtet und gesammelt von Edward Jacobson. III. Theil. Notes from the Leyden Museum, 34:97-112.
- Forel, A. 1912b. Einige neue und interessante Ameisenformen aus Sumatra etc. Zoologische Jahrbücher Supplement, 15:51-78.
- Forel, A. 1913. Wissenschaftliche Ergebnisse einer Forschungsreise nach Ostindien ausgeführt im Auftrage der Kgl. Preuss. Akademie der Wissenschaften zu Berlin von H. v. Buttel-Reepen. II. Ameisen aus Sumatra, Java, Malacca und Ceylon. Gesammelt von Herrn Prof. Dr. v. Buttel-Reepen in den Jahren

1911-1912. Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere, 36:1-148.

Forel, A. 1915. Fauna Simalurensis. Hymenoptera Aculeata, Fam. Formicidae. Tijdschrift voor Entomologie, 58:22-43.

Forel, A. 1917. Cadre synoptique actuel de la faune universelle des fourmis. Bulletin de la Société Vaudoise des Sciences Naturelles, 51:229-253.

Gobin, B. 1994. Dominance interactions and control of reproduction in the queenless ant *Gnamptogenys* sp. from Sulawesi. P. 286 in A. Lenoir, G. Arnold, and M. Lepage, eds., Les Insectes Sociaux. 12th Congress of the International Union for the Study of Social Insects. Publications Université Paris Nord.

Gobin, B., C. Peeters, and J. Billen. 1998a. Colony reproduction and arboreal life in the ponerine ant *Gnamptogenys menadensis*. Netherlands Journal of Entomology, 48:53-63.

Gobin, B., C. Peeters, and J. Billen. 1998b. Production of trophic eggs by virgin workers in the ponerine ant *Gnamptogenys menadensis*. Physiological Entomology, 23:329-336.

Gobin, B., C. Peeters, J. Billen, and E. Morgan. 1998. Interspecific trail following and commensalism between the ponerine ant *Gnamptogenys menadensis* and the formicine ant *Polyrhachis rufipes*. Journal of Insect Behavior, 11(3):361-369.

Gregg, R.E. 1951. Two new species of exotic ants. Psyche, 58:77-84.

Grimaldi, D., D. Agosti, and J. Carpenter. 1997. New and rediscovered primitive ants in Cretaceous amber from New Jersey, and their phylogenetic relationships. Novitates, 3208:1-43.

- Harris, R. 1979. A glossary of surface sculpturing. Occasional Papers in Entomology (Dept. Food & Agr., California), 28:1-31.
- Hölldobler, B. and E. Wilson. 1990. The Ants. Harvard University Press, Cambridge, Mass. 732 pp.
- Imai, H., W.L. Brown, Jr., M. Kubota, H.-S. Yong, and Y.P. Tho. 1984. Chromosome observations on tropical ants from western Malaysia. II. Annual Report. National Institute of Genetics, Japan, 34:66-69.
- Karavaiev, V. 1925. Ponerinen (Fam. Formicidae) aus dem Indo-Australischen Gebiet. Konowia, 4:69-81.
- Kugler, C. 1991. Stings of ants of the Tribe Ectatommini. Insecta Mundi, 5(3-4):153-166.
- Kugler, C. and W.L. Brown, Jr. 1982. Revisionary and other studies on the ant genus *Ectatomma*, including the description of two new species. Search Agriculture (Ithaca, N.Y.), 24:1-8.
- Lattke, J.E. 1990. Revisión del Género *Gnamptogenys* en Venezuela. Acta Terramaris, 2:1-48.
- Lattke, J.E. 1992. Revision of the *minuta*-group of the genus *Gnamptogenys*. Deutsche entomologische Zeitschrift, 39:123-129.
- Lattke, J.E. 1994. Phylogenetic relationships and classification in the Ectatommini (Hymenoptera: Formicidae). Entomologica Scandinavica, 25:105-119.
- Lattke, J.E. 1995. A revision of the ant genus *Gnamptogenys* in the New World. Journal of Hymenoptera Research, 4:137-193.

- Le Guillou, E.J.F. 1842. Catalogue raisonné des insectes hyménoptères recueillis dans le voyage de circumnavigation des corvettes l'Astrolabe et la Zélée. *Annales de la Société Entomologique de France*, 10:311-324.
- Maddison, W. and D. Maddison. 1997. *MacClade 3.07*. Sinauer Associates, Sunderland, Mass.
- Mann, W.M. 1916. The Stanford Expedition to Brazil, 1911, John C. Branner, Director. The ants of Brazil. *Bulletin of the Museum of Comparative Zoology*, 60:399-490.
- Mann, W.M. 1919. The ants of the British Solomon Islands. *Bulletin of the Museum of Comparative Zoology*, 63:273-391.
- Mann, W.M. 1921. The ants of the Fiji Islands. *Bulletin of the Museum of Comparative Zoology*, 64:401-499.
- Mayr, G. 1862. Myrmecologische Studien. *Verhandlungen der kaiserlich-königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 12:649-776.
- Mayr, G. 1884. [Untitled. Descriptions of eight new species.] Pp. 31-38 in Radoszkowsky, *Fourmis de Cayenne française*. *Trudy Russkago Entomologicheskago Obshchestva*, 18:30-39.
- Mayr, G. 1887. Südamerikanische Formiciden. *Verhandlungen der kaiserlich-königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 37:511-632.
- Menozzi, C. 1925. Nouvelles fourmis des Philippines. *Philippine Journal of Science*, 28:439-451.
- Roger, J. 1860. Die *Ponera*-artigen Ameisen. *Berliner entomologische Zeitschrift*, 4:278-312.

- Roger, J. 1861. Die *Ponera*-artigen Ameisen (Schluss). Berliner entomologische Zeitschrift, 5:1-54.
- Roger, J. 1863. Die neu aufgeführten Gattungen und Arten meines Formiciden-Verzeichnisses, nebst Ergänzung einiger früher gegeben Beschreibungen. Berliner entomologische Zeitschrift, 7:131-214.
- Santschi, F. 1922. Description de nouvelles fourmis de l'Argentine et pays limitrophes. Anales de la Sociedad Científica Argentina, 94:241-262.
- Santschi, F. 1929. Révision du genre *Holcaponera* Mayr. Zoologische Anzeiger, 82:437-477.
- Santschi, F. 1932. Résultats scientifiques du voyage aux Indes orientales néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. Hymenoptera. Formicidae. Mémoires du Musée Royal d'Histoire Naturelle de Belgique, 4:11-29.
- Shattuck, S. 1999. Australian Ants: Their Biology and Identification. C.S.I.R.O. Publishing, Canberra. 226 pp.
- Smith, F. 1857. Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A. R. Wallace. [part]. Journal and Proceedings of the Linnean Society of London, 2:42-88.
- Smith, F. 1858. Catalogue of Hymenopterous Insects in the Collection of the British Museum. Part VI. Formicidae. British Museum (Natural History), London. 216 pp.
- Snodgrass, R. 1956. Anatomy of the Honey Bee. Comstock Publishers, London. 334 pp.
- Swofford, D. 1998. PAUP* 4.0 Beta Version. Sinauer Associates, Sunderland, Mass.

- Tang, J., S. Li, E. Huang, B. Zhang, and Y. Chen. 1995. Hymenoptera: Formicidae. Economic Insect Fauna of China, 47:1-134.
- Torre-Bueno, J.R. 1989. The Torre-Bueno Glossary of Entomology (R. Schuh, ed.). New York Entomological Society, N.Y. 840 pp.
- Viehmeyer, H. 1916. Amesien von Singapore. Beobachtet und gesammelt von H. Overbeck. Archiv für Naturgeschichte, (A)81(8):108-168.
- Wang, M. 1992. Hymenoptera: Formicidae. Pp. 677-682 in F. Huang, ed., Insects of Wuling Mountains Area, Southwestern China. Science Press, Beijing. 777 pp.
- Ward, P.S. 1980. A systematic revision of the *Rhytidoponera impressa* group in Australia and New Guinea. Australian Journal of Zoology, 28:475-498.
- Ward, P.S. 1981. Ecology and life history of the *Rhytidoponera impressa* group. II. Colony origin, seasonal cycles, and reproduction. Psyche, 88:109-126.
- Ward, P.S. 1984. A revision of the ant genus *Rhytidoponera* in New Caledonia. Australian Journal of Zoology, 32:131-175.
- Ward, P.S. 1994. *Adetomyrma*, an enigmatic new ant genus from Madagascar, and its implications for ant phylogeny. Systematic Entomology, 19:159-175.
- Ward, P.S., B. Bolton, S. Shattuck, and W.L. Brown, Jr. 1996. A bibliography of ant systematics. University of California Publications in Entomology, 116:1-417.
- Wheeler, G.C. and J. Wheeler. 1952. The ant larvae of the subfamily Ponerinae - Part I. American Midland Naturalist, 48:111-144.
- Wheeler, G.C. and J. Wheeler. 1964. The ant larvae of the subfamily Ponerinae: Supplement. Annals of the Entomological Society of America, 57:443-462.

- Wheeler, G.C. and J. Wheeler. 1976. Supplementary studies on ant larvae: Ponerinae. Transactions of the American Entomological Society, 102:41-64.
- Wheeler, W.M. 1915. *Paranomopone*, a new genus of ponerine ants from Queensland. Psyche, 22:117-120.
- Wheeler, W.M. 1921. Chinese ants. Bulletin of the Museum Comparative Zoology, 64:529-547.
- Wheeler, W.M. 1923. Ants of the genera *Myopias* and *Acanthoponera*. Psyche, 30:175-192.
- Wheeler, W.M. 1924. Ants of Krakatau and other islands in the Sunda Strait. Treubia, 5:239-258.
- Wheeler, W.M. 1929. Ants collected by Professor F. Silvestri in Formosa, the Malay Peninsula and the Philippines. Bollettino dell' Laboratorio di Zoologia Generale e Agraria delle Reale Scuola Superiore d' Agricoltura, 24:27-64.
- Wheeler, W.M. 1930. A new *Emeryella* from Panama. Proceedings of the New England Zoological Club, 12:9-13.
- Wheeler, W.M. and W. Mann. 1914. The ants of Haiti. Bulletin of the American Museum of Natural History, 33:1-61.
- Wu, J. and C. Wang. 1992. Hymenoptera: Formicidae. Pp. 1301-1320 in J. Peng and Y. Lui, eds., Iconography of Forest Insects in Hunan, China. Hunan Scientific and Technical Publishing House, Hunan. 1473 pp.
- Wu, J. and C. Wang. 1995. The Ants of China. China Forestry Publishing House, Beijing. 214 pp.
- Wu, J. and G. Xiao. 1987. A new species of the genus *Gnamptogenys* from China. Scientia Silvae Sinicae, 23:303-305.

Revision of Gnamptogenys in Southeast Asia and Australasia

- Yamane, S. and A.R. Nona. 1994. Ants from Lambir Hills National Park, Sarawak. Pp. 222-226 in T. Inoue and A. Hamid, eds., Plant Reproductive Systems and Animal Seasonal Dynamics: Long-Term Study of Dipterocarp Forests in Sarawak. Center for Ecological Research, Kyoto University, Kyoto. 255 pp.
- Xu, Z. and W. Zhang. 1996. A new species of the genus *Gnamptogenys* (Hymenoptera: Formicidae: Ponerinae) from southwestern China. *Entomotaxonomia*, 18:55-58.

FIGURES

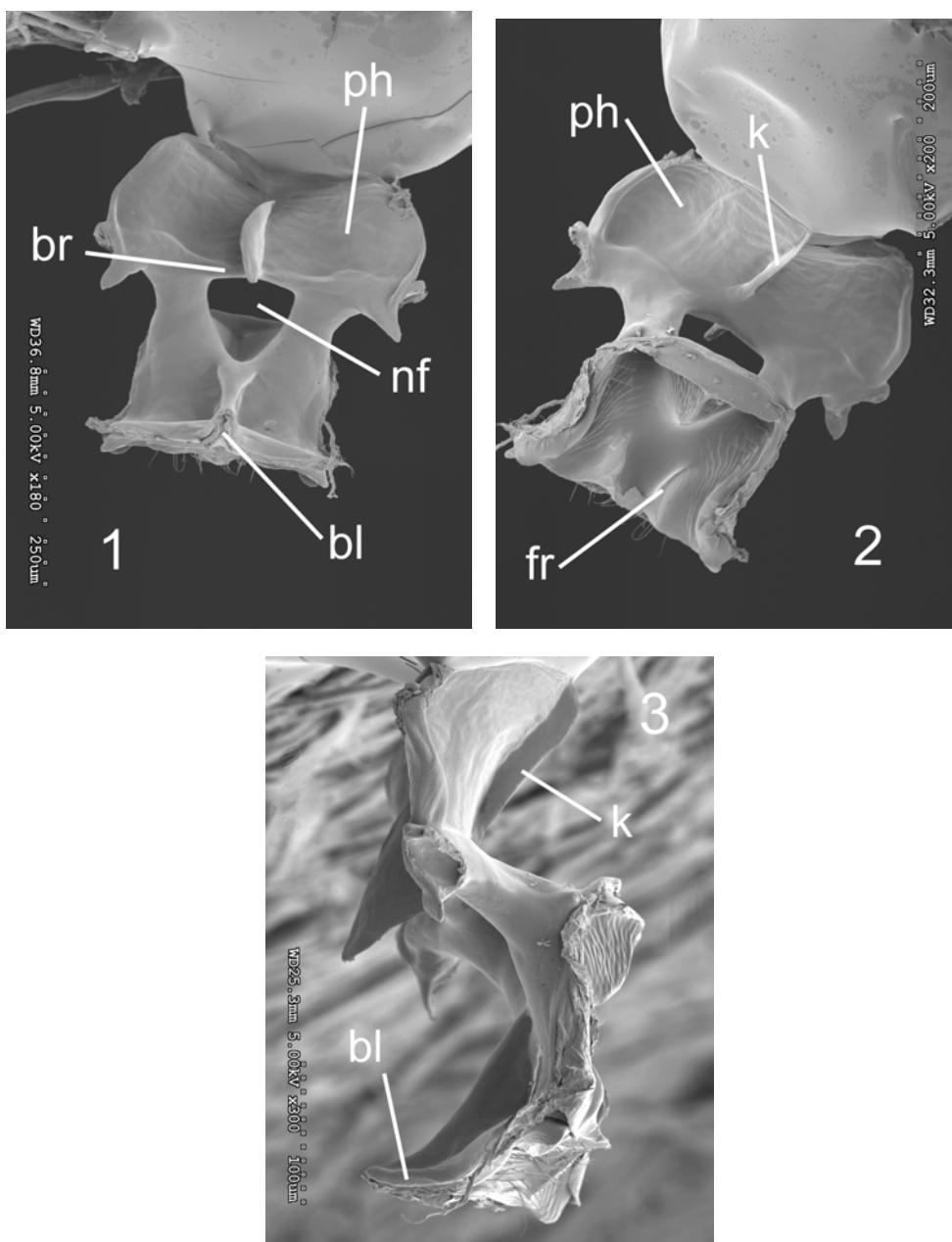


Fig. 1. Anterior view of prosternum of *Heteroponera dentinoda*: bl - basisternal lobe, br - endosternal bridge, nf - neural foramen, ph - phragma. **Fig. 2.** Posterior view of prosternum of *Heteroponera dentinoda*: fr - furcasternal ridge, k - keel, ph - phragma. **Fig. 3.** Lateral view of prosternum of *Heteroponera dentinoda*: bl - basisternal lobe, k - keel

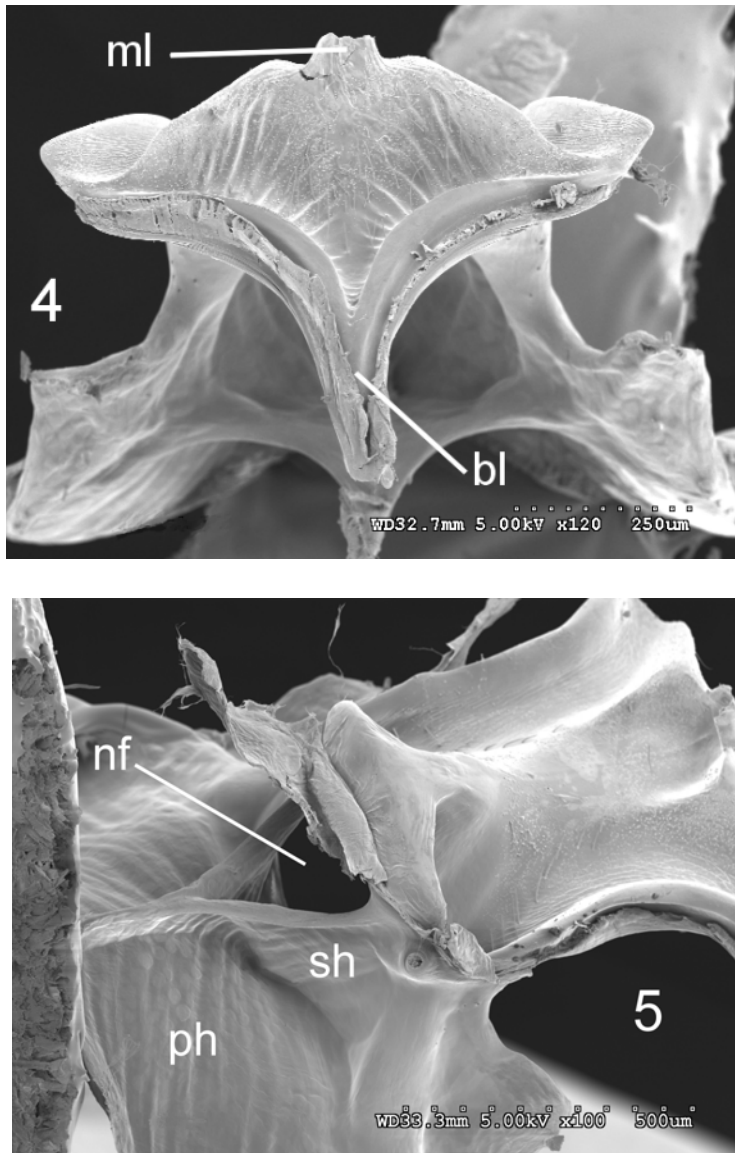


Fig. 4. *Gnamptogenys concinna*: ventral view of the basisternum. The basisternal lobe (bl) is pointing down, and the median lobe (ml) of the furcasternum is projecting up. **Fig. 5.** *Gnamptogenys concinna*: posterior view of the endosternum showing the sheath (sh) that surrounds the neural foramen (nf), ph - phragma.

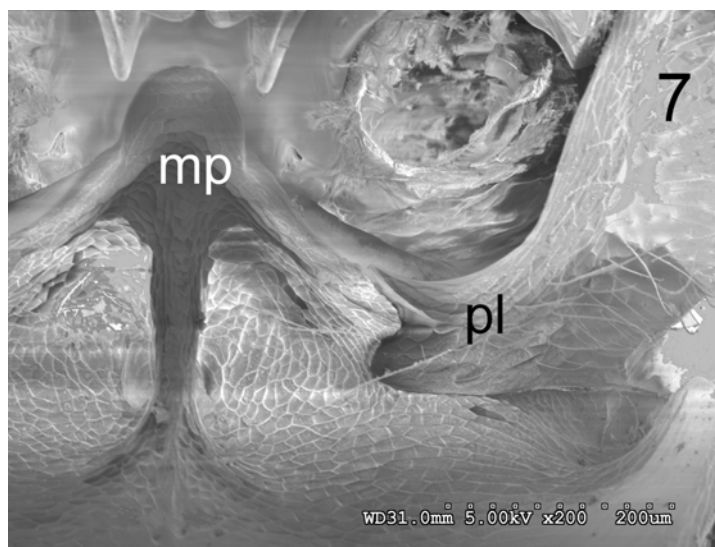
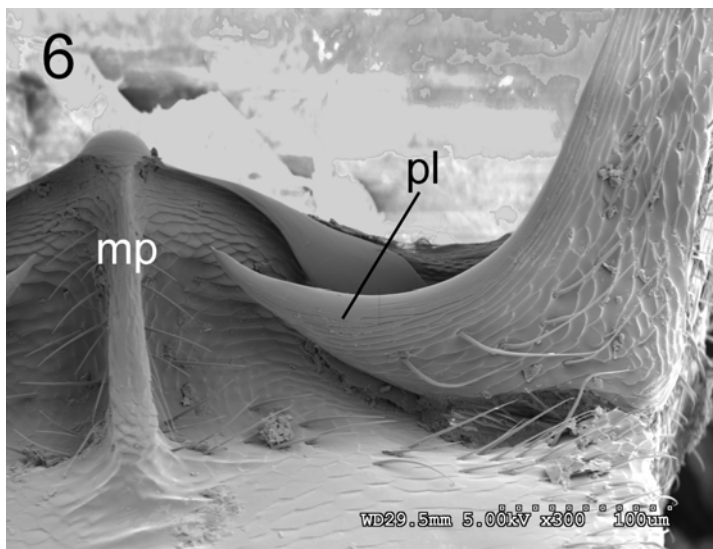


Fig. 6. Ventral view of left posterolateral pronotal lobe (pl) in *Heteroponera dolo*, which lies below the anterior mesosternal process (mp). **Fig. 7.** Ventral view of left posterolateral pronotal lobe (pl) in *Gnamptogenys costata*, which lies above and against the anterior mesosternal process (mp).

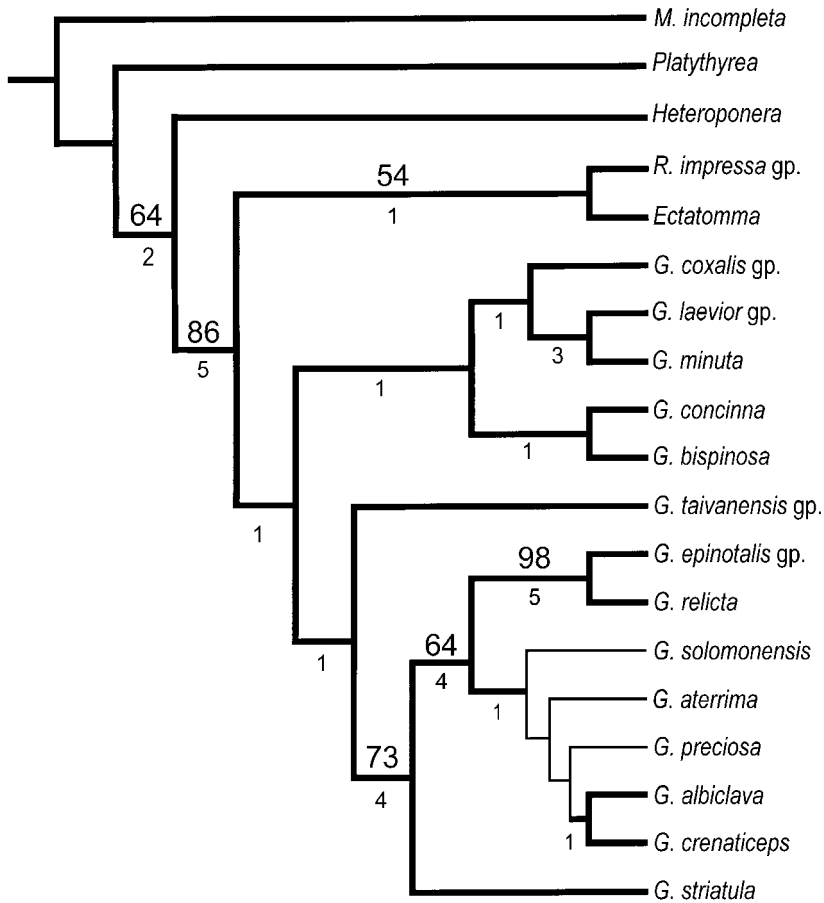


Fig. 8. Phylogeny of ectatommine taxa. One of the two most parsimoious (MP) trees chosen after successive approximations character weighting. Bootstrap values above 50% for the unweighted parsimony analysis are marked in larger numbers above the branch at the base of a clade, and the decay index is indicated by smaller numbers just beneath the branch. The thin branches collapse in a consensus of the MP trees.

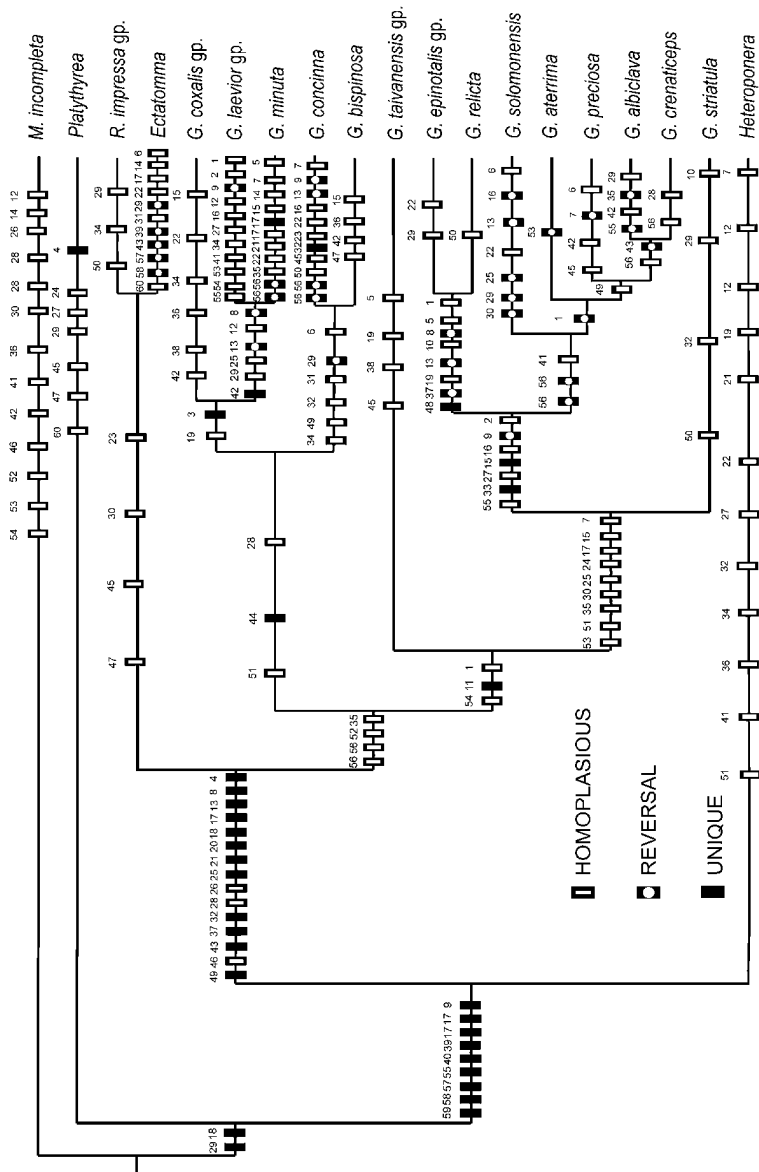
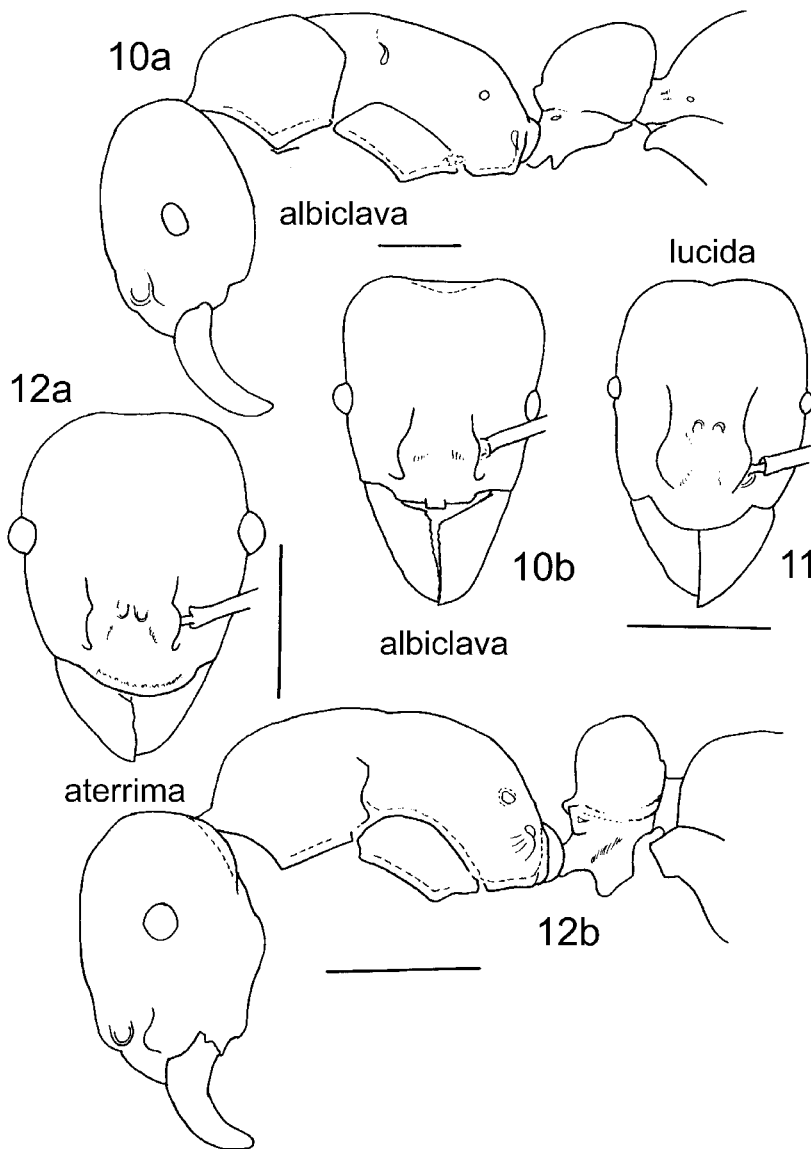


Fig. 9. One of the two most parsimonious (MP) trees chosen after successive approximations character weighting, with unambiguous character state changes marked on branches. There are other, equally parsimonious reconstructions of character state change for characters 10, 12, 13, 15, 21, 22, 26, 28, 32, 34, 40, 42, 46, and 51. The reconstruction shown here delays transformation in these characters.



10. *Gnamptogenys albiclava* worker (Guadalcanal, Solomon Islands): a - head and body in lateral view; b - head in frontal view. **Fig. 11.** *G. lucida* worker (Malaita, Solomon Islands): head in frontal view. **Fig. 12.** *G. aterrima* worker (Viti Levu, Fiji): a - head in frontal view; b - head and body in lateral view. Scale lines = 0.5mm.

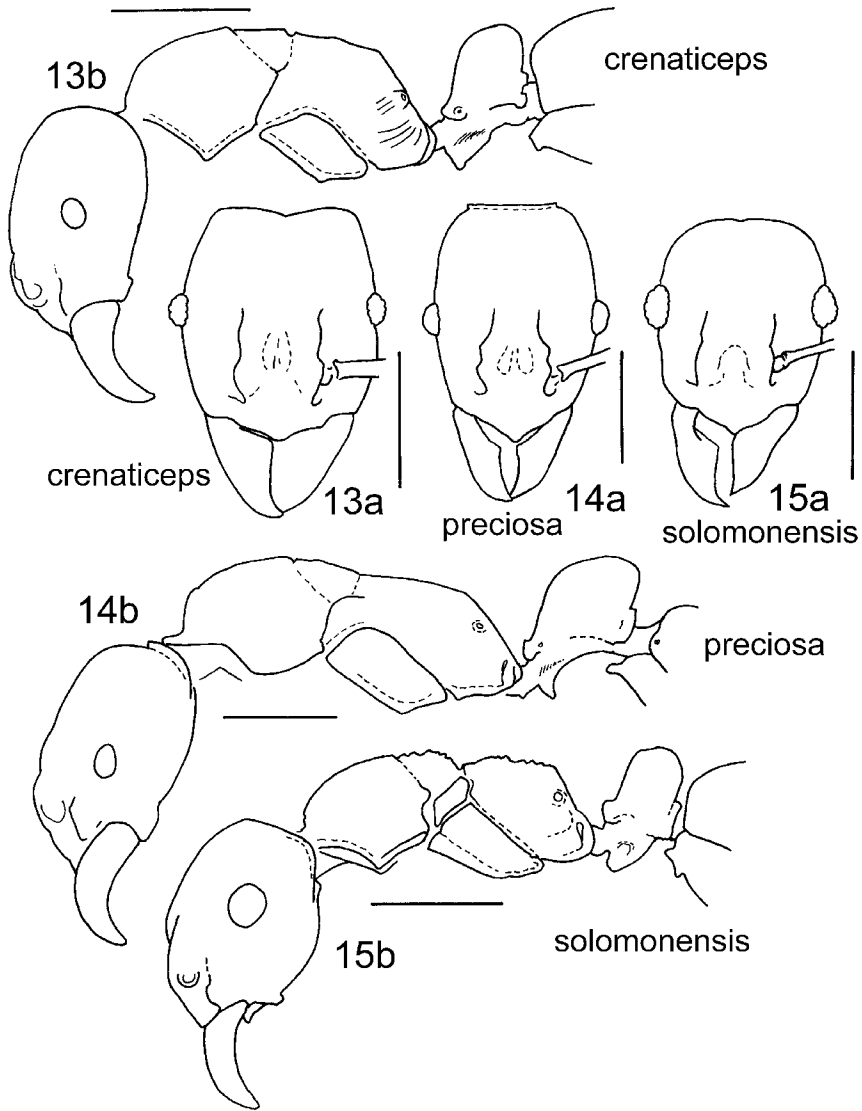


Fig. 13. *Gnamptogenys crenaticeps* worker (Isabel, Solomon Islands): a - head in frontal view; b - head and body in lateral view. **Fig. 14.** *G. preciosa* worker (Guadalcanal, Solomon Islands): a - head in frontal view; b - head and body in lateral view. **Fig. 15.** *G. solomonensis* worker (holotype): a - head in frontal view; b - head and body in lateral view. Scale lines = 0.5mm.

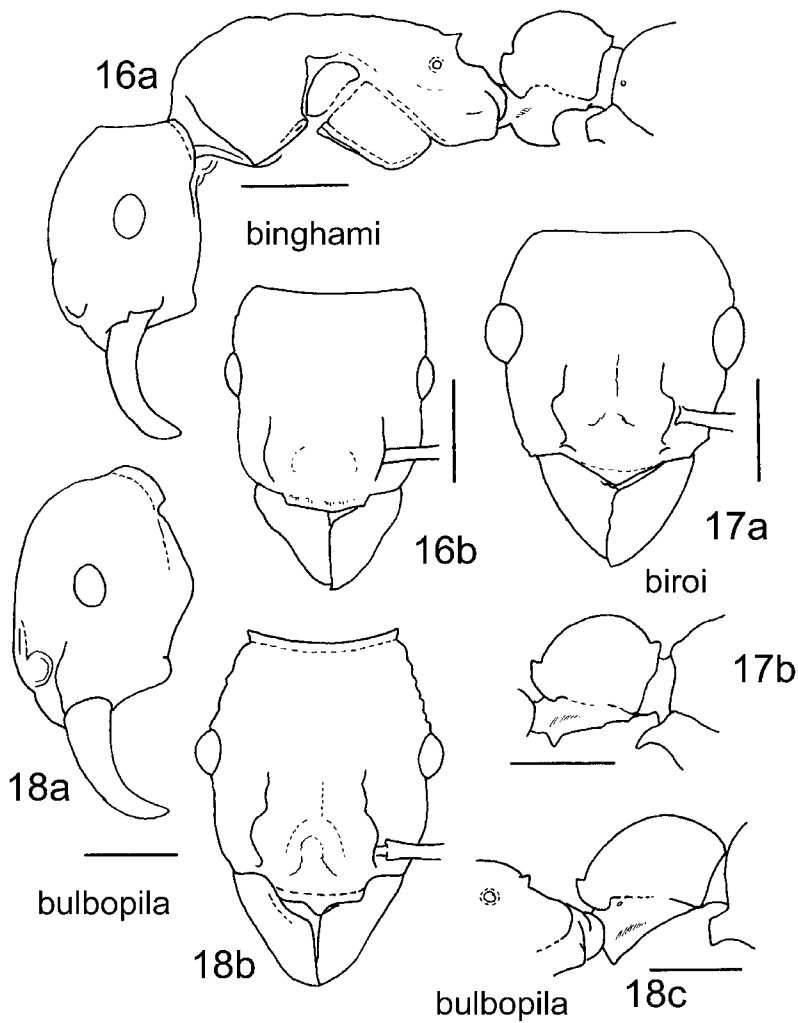


Fig. 16. *Gnamptogenys binghami* worker (western Malaysia): a - head and body in lateral view; b - head in frontal view. **Fig. 17.** *G. biroi* worker (New Guinea): a - head in frontal view; b - petiolar node in lateral view. **Fig. 18.** *G. bulbopila* worker (holotype): a - head in lateral view; b - head in frontal view; c - petiolar node in lateral view. Scale lines = 0.5mm.

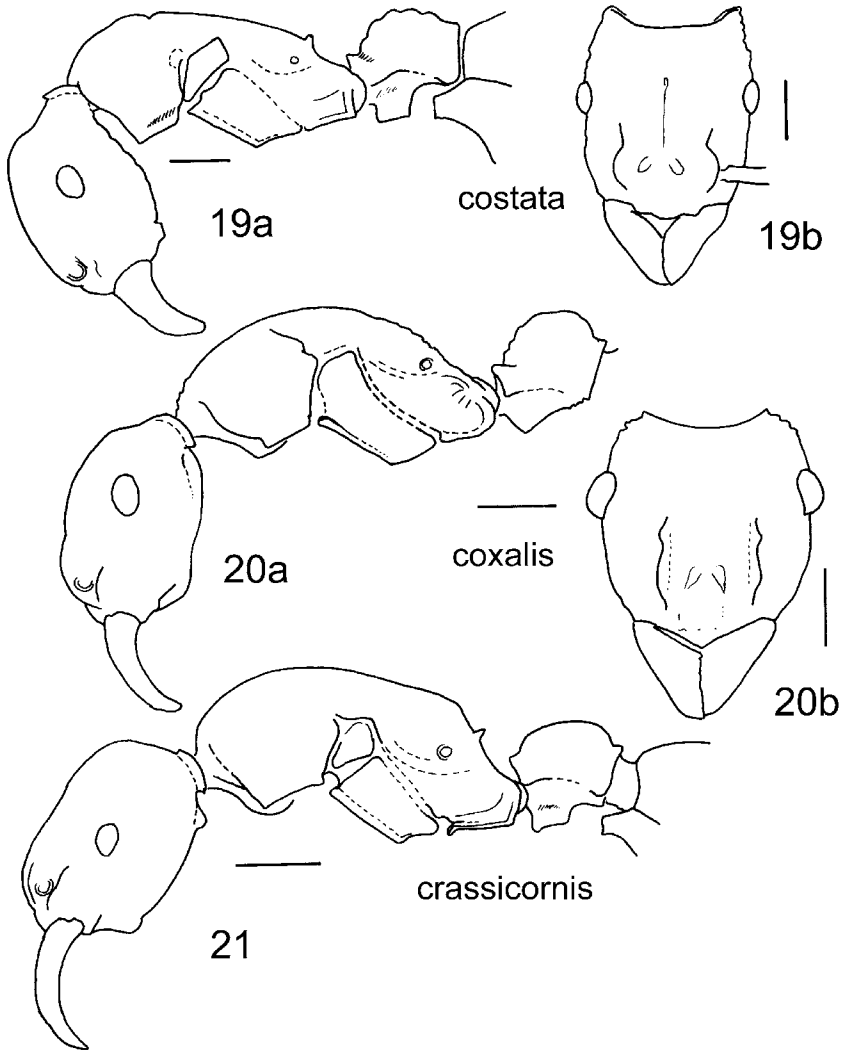


Fig. 19. *Gnaptogenys costata* worker (Borneo): a - head and body in lateral view; b - head in frontal view. **Fig. 20.** *G. coxalis* worker (Sri Lanka): a - head and body in lateral view; b - head in frontal view. **Fig. 21.** *G. crassicornis* worker (Java, Indonesia): head and body in lateral view. Scale lines = 0.5mm.

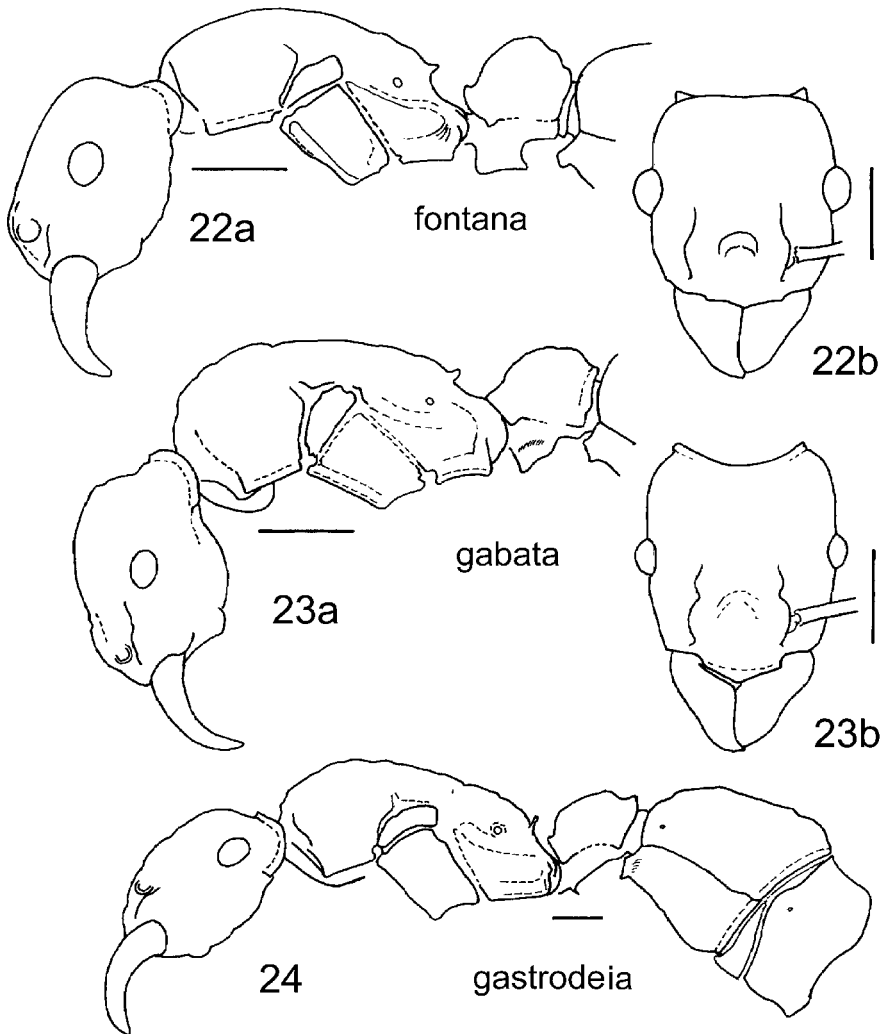


Fig. 22. *Gnamptogenys fontana* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 23.** *G. gabata* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 24.** *G. gastrodeia* worker (holotype): head and body in lateral view. Scale lines = 0.5mm.

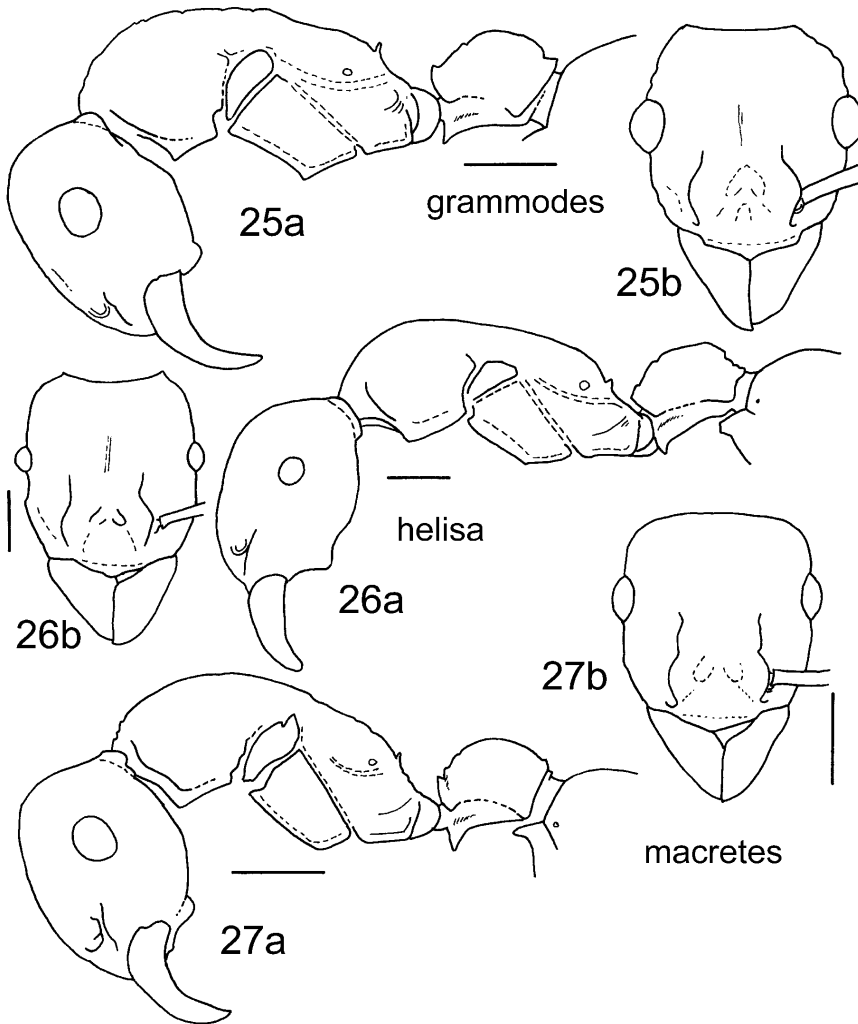


Fig. 25. *Gnamptogenys grammodes* worker (New Guinea): a - head and body in lateral view; b - head in frontal view. **Fig. 26.** *G. helisa* worker (Borneo): a - head and body in lateral view; b - head in frontal view. **Fig. 27.** *G. macretes* worker (New Guinea): a - head and body in lateral view; b - head in frontal view. Scale lines = 0.5mm.

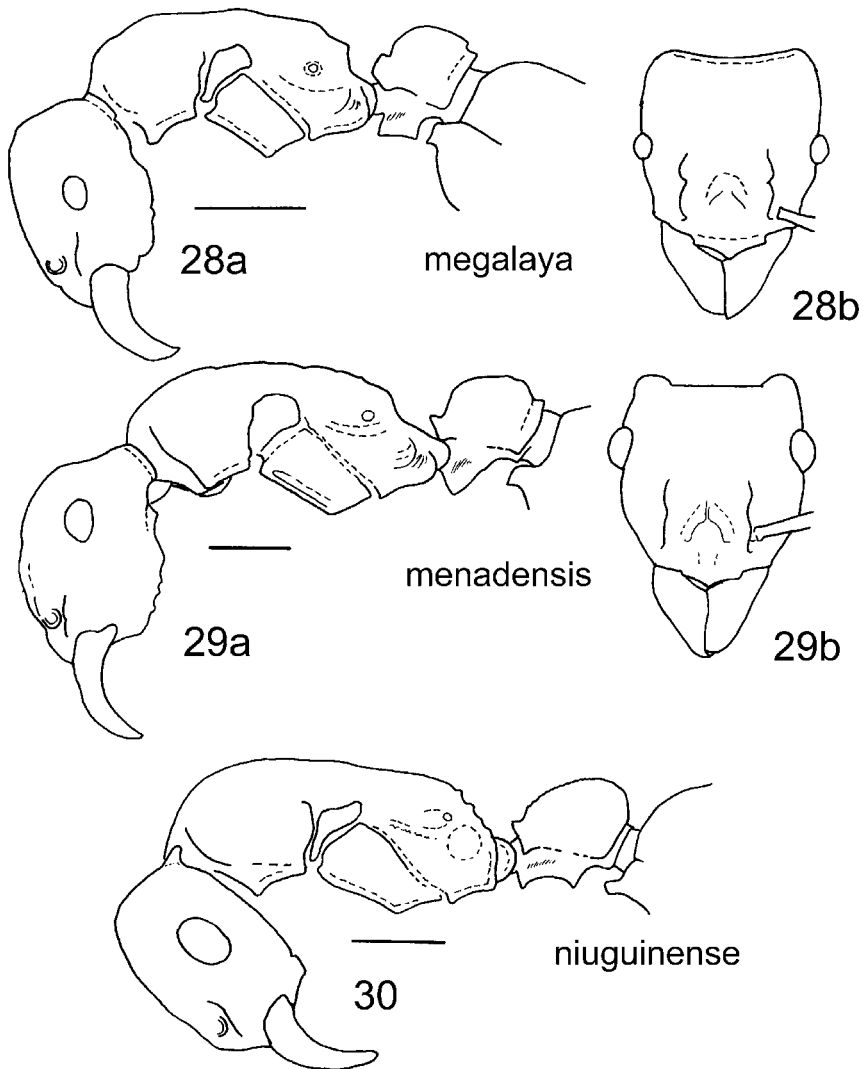


Fig. 28. *Gnamptogenys megalaya* worker (India): a - head and body in lateral view; b - head in frontal view. **Fig. 29.** *G. menadensis* worker (western Malaysia): a - head and body in lateral view; b - head in frontal view. **Fig. 30.** *G. niuginense* worker (New Guinea): head and body in lateral view. Scale lines = 0.5mm.

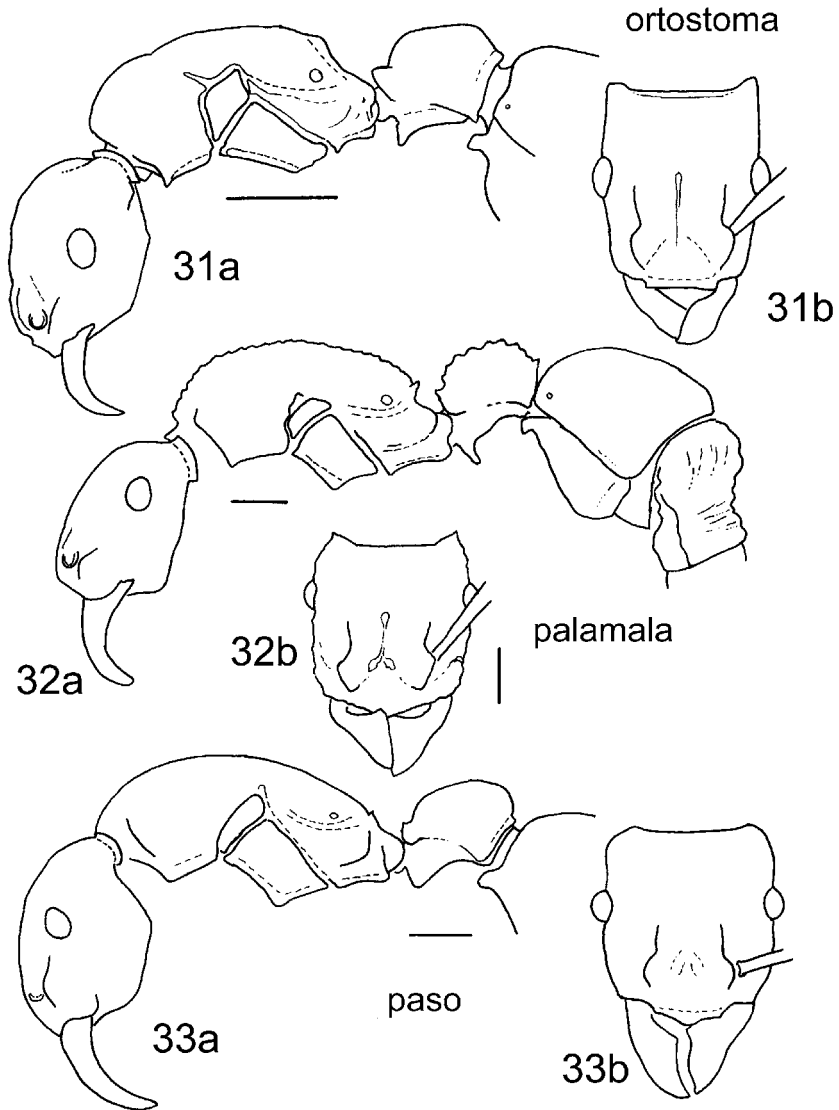


Fig. 31. *Gnampogenys ortostoma* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 32.** *G. palamala* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 33.** *G. paso* worker (western Malaysia): a - head and body in lateral view; b - head in frontal view. Scale lines = 0.5mm.

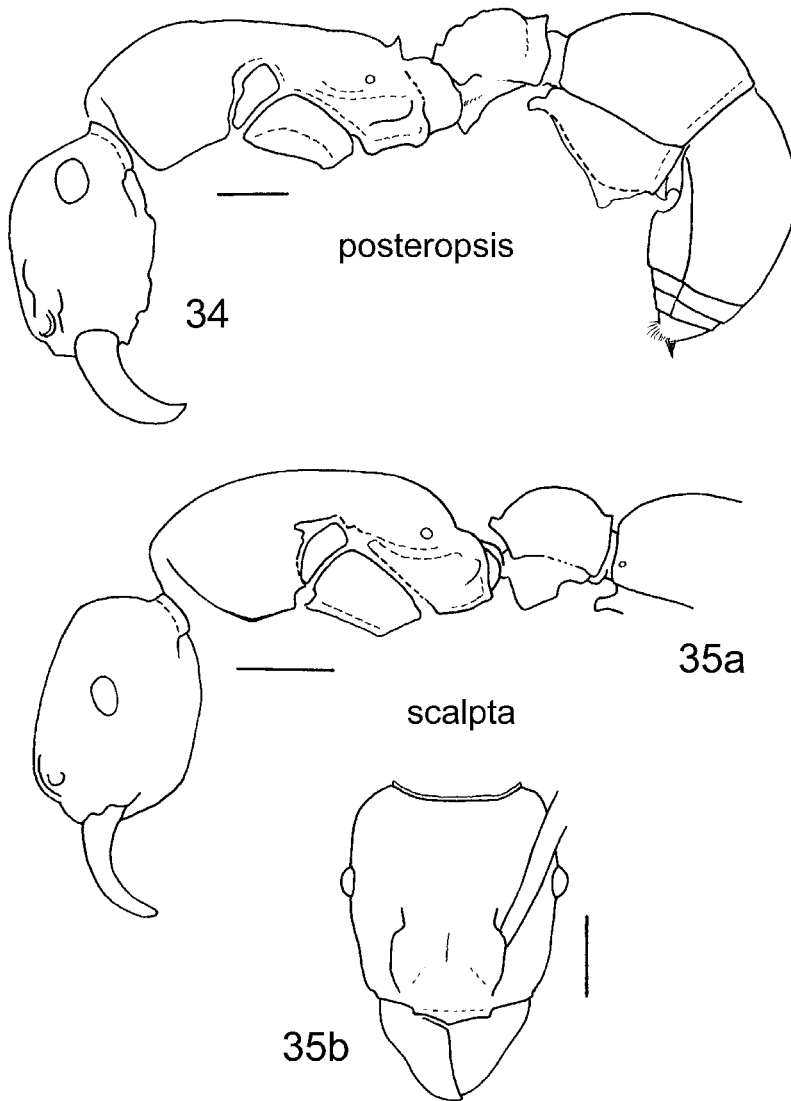


Fig. 34. *Gnamptogenys posteropsis* worker (western Malaysia): head and body in lateral view. **Fig. 35.** *G. scalpta* worker (Borneo): a - head and body in lateral view; b - head in frontal view. Scale lines = 0.5mm.

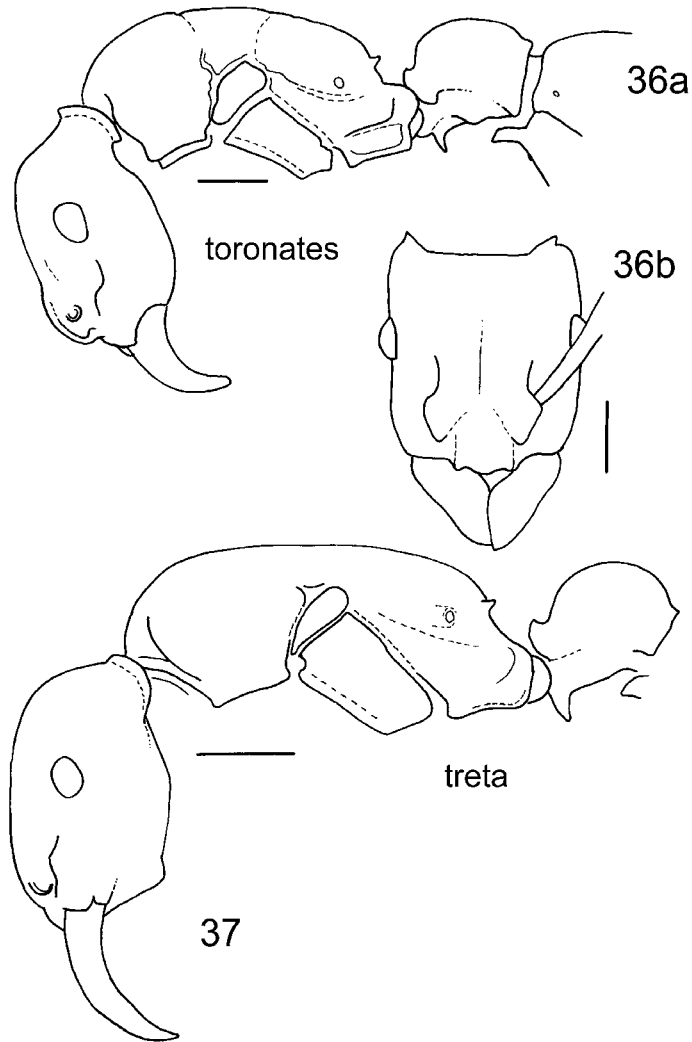


Fig. 36. *Gnamptogenys toronates* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 37.** *G. treta* worker (holotype): head and body in lateral view. Scale lines = 0.5mm.

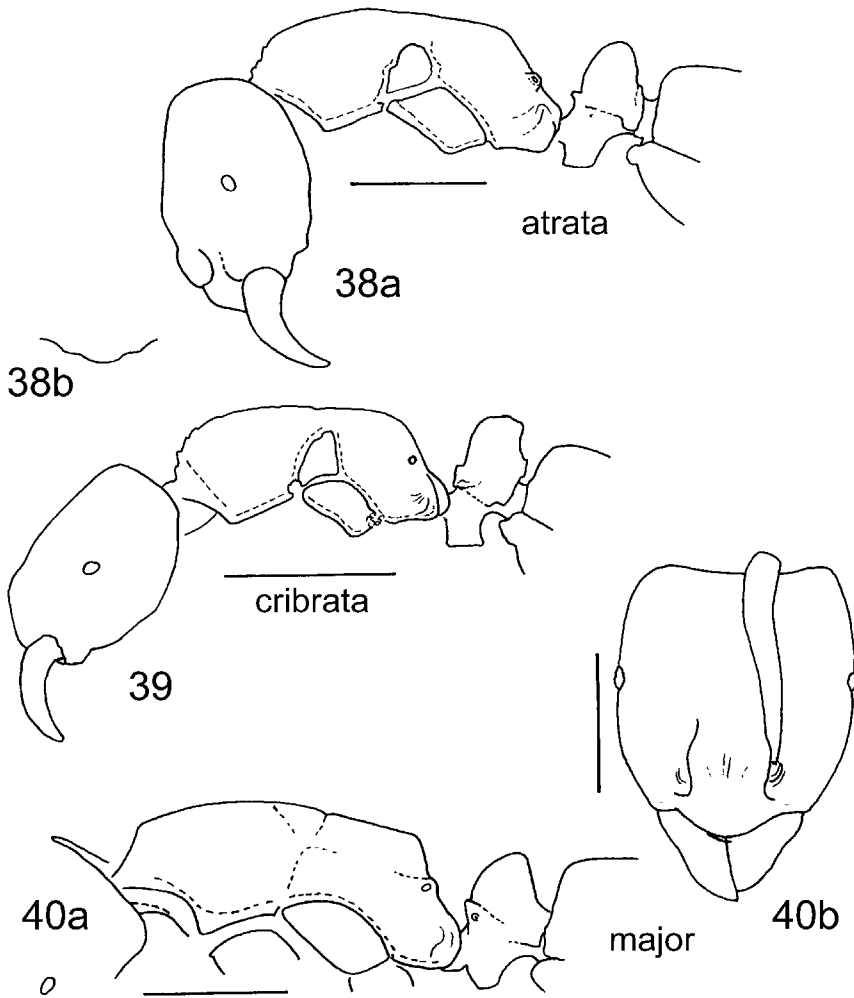


Fig. 38. *Gnamptogenys atrata* worker (Sulawesi): a - head and body in lateral view; b - clypeal lamella in frontal view. **Fig. 39.** *G. cribrata* worker (western Malaysia): body in lateral view. **Fig. 40.** *G. major* worker (New Guinea): a - mesosoma and petiole in lateral view; b - head in frontal view. Scale line = 0.5mm.

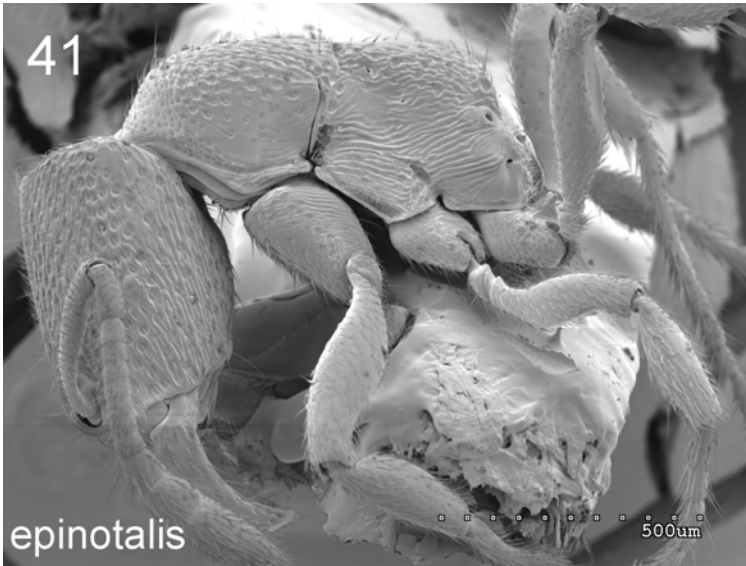


Fig. 41. *Gnamptogenys epinotalis* worker (New Guinea): head and body in lateral view. Petiole and gaster missing. **Fig. 42.** *Gnamptogenys luzonensis* worker (Luzon, Philippines): head and body in lateral view.

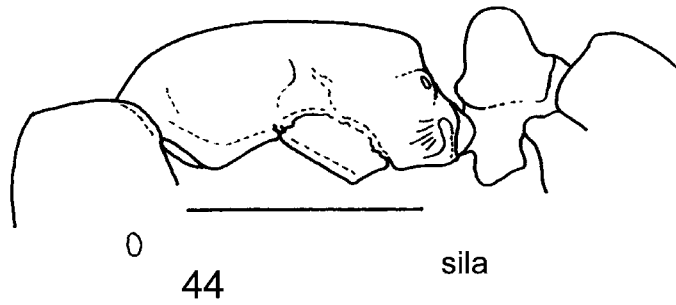
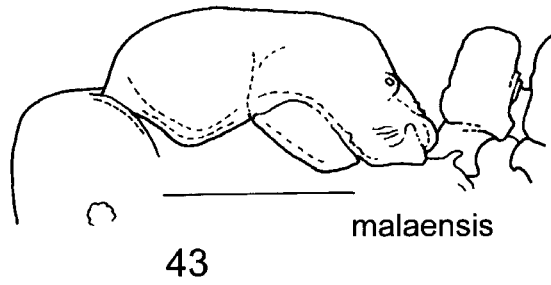


Fig. 43. *Gnamptogenys malaensis* worker (Vella Lavella, Solomon Islands): head and body in lateral view. **Fig. 44.** *G. sila* worker (Borneo): head and body in lateral view. Scale lines = 0.5mm.

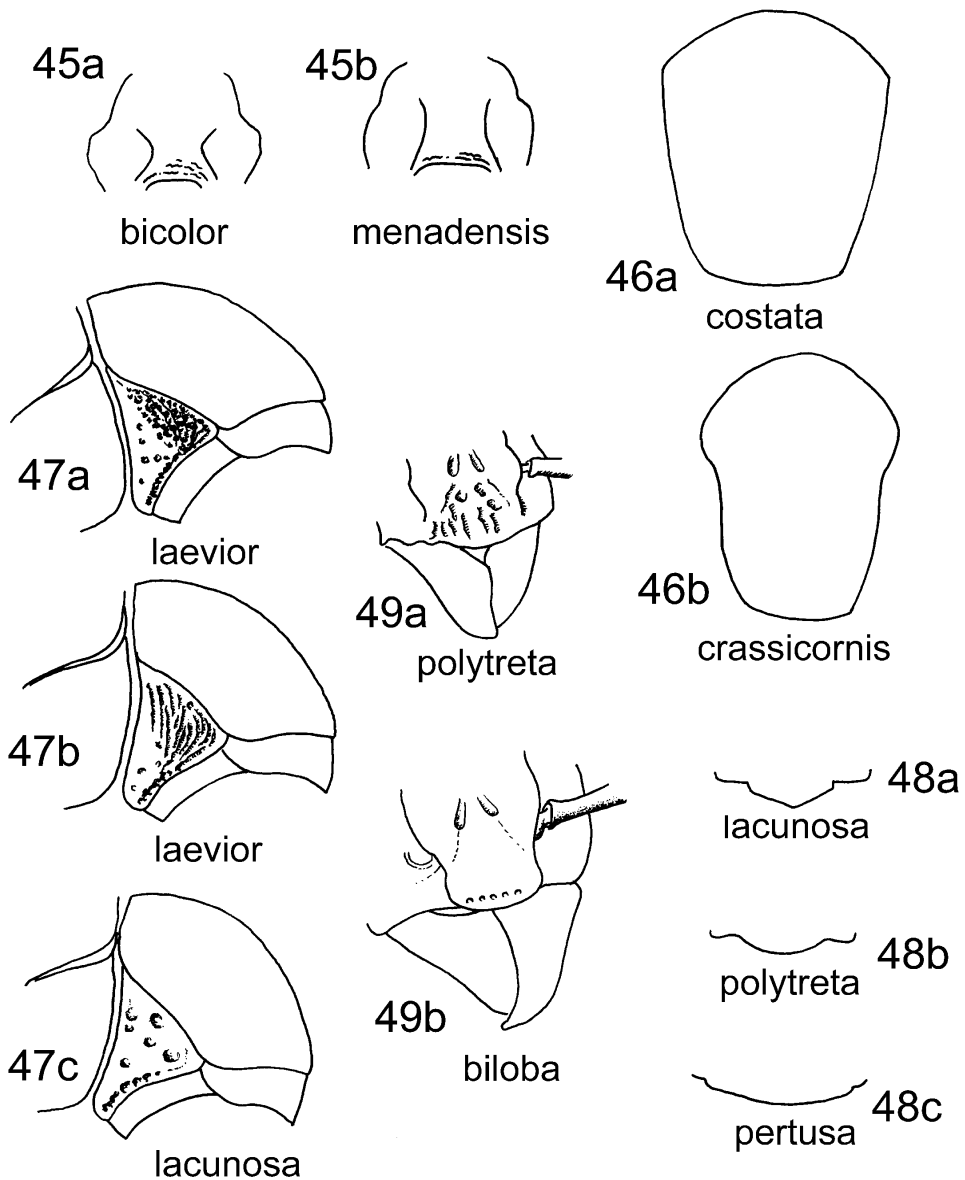


Fig. 45. Propodeal declivitous face of a - *bicolor*; b - *menadensis*, showing raised median area. **Fig. 46.** Dorsal view of fourth abdominal tergite of a - *costata*; b - *crassicornis*. **Fig. 47.** Oblique lateral view of fourth abdominal sternite of a, b - *laevior*; c - *lacunosa*. **Fig. 48.** Dorsal view of clypeal lamella of a - *lacunosa*; b - *polytreta*; c - *pertusa*. **Fig. 49.** Oblique frontal view of mandibular-clypeal configuration of a - *polytreta*; b - *biloba*. Figures not drawn to scale.

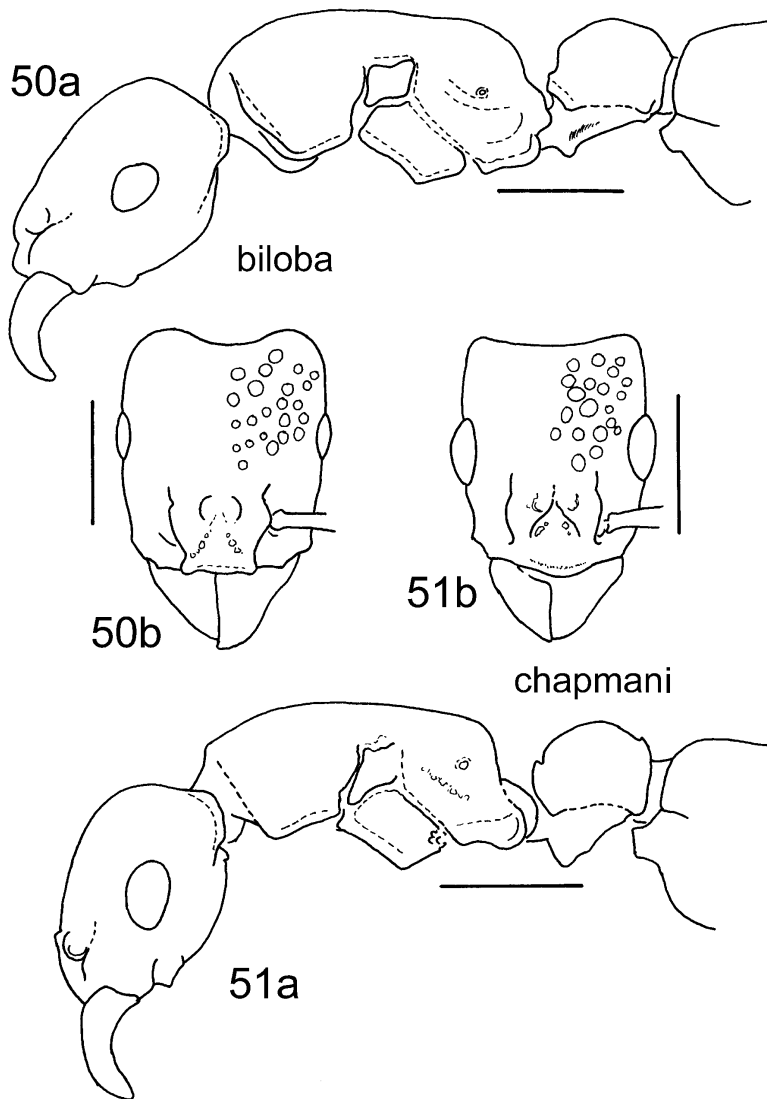


Fig. 50. *Gnamptogenys biloba* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 51.** *G. chapmani* worker (western Malaysia): a - head and body in lateral view; b - head in frontal view. Scale lines = 0.5mm.

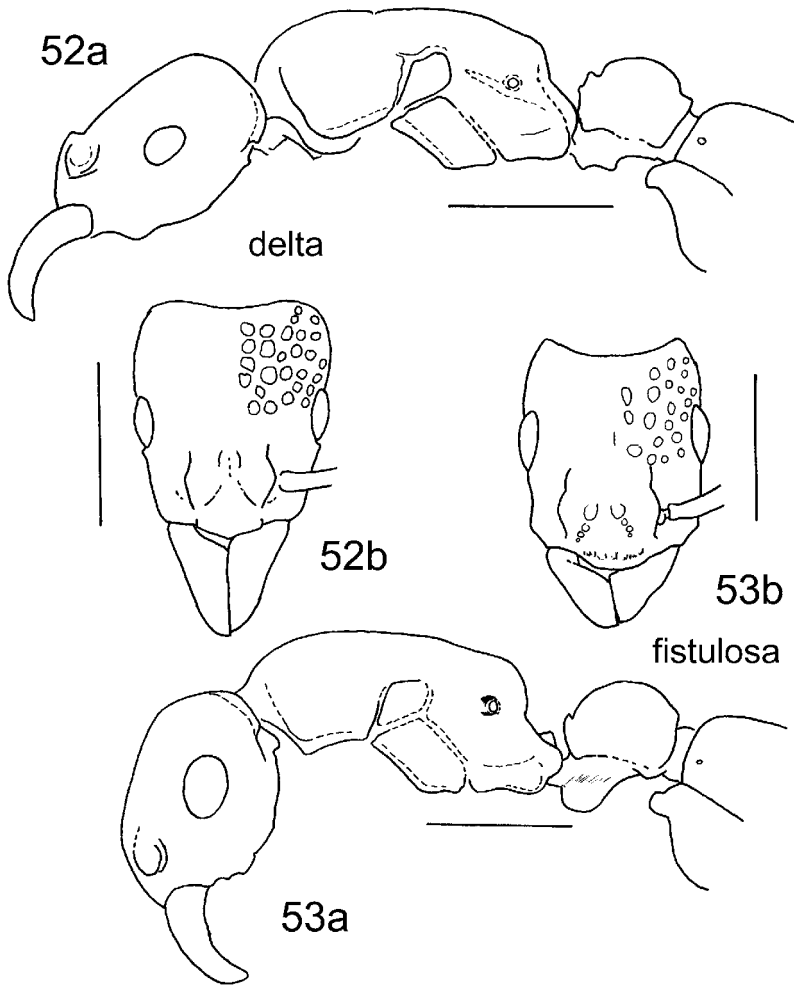


Fig. 52. *Gnampbogenys delta* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 53.** *G. fistulosa* worker (Luzon, Philippines): a - head and body in lateral view; b - head in frontal view. Scale lines = 0.5mm.

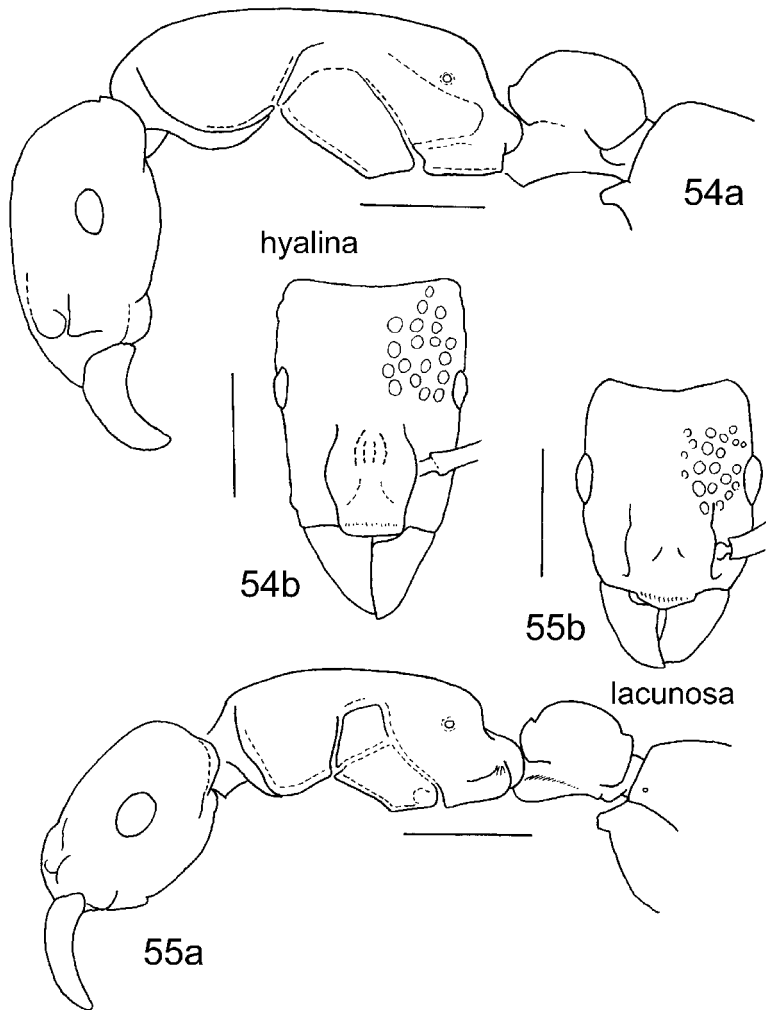


Fig. 54. *Gnamptogenys hyalina* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 55.** *G. lacunosa* worker (Borneo): a - head and body in lateral view; b - head in frontal view. Scale lines = 0.5mm.

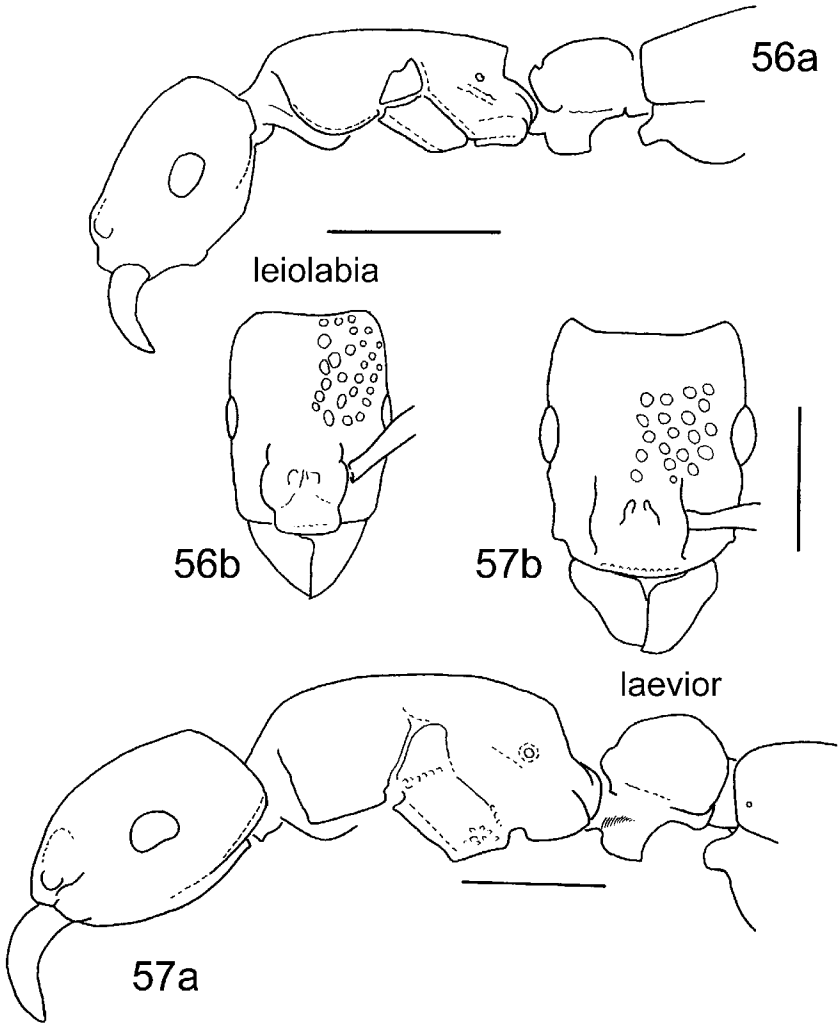


Fig. 56. *Gnamptogenys leiolabia* worker (Borneo): a - head and body in lateral view; b - head in frontal view. **Fig. 57.** *G. laevior* worker (Java, Indonesia): a - head and body in lateral view; b - head in frontal view. Scale lines = 0.5mm.

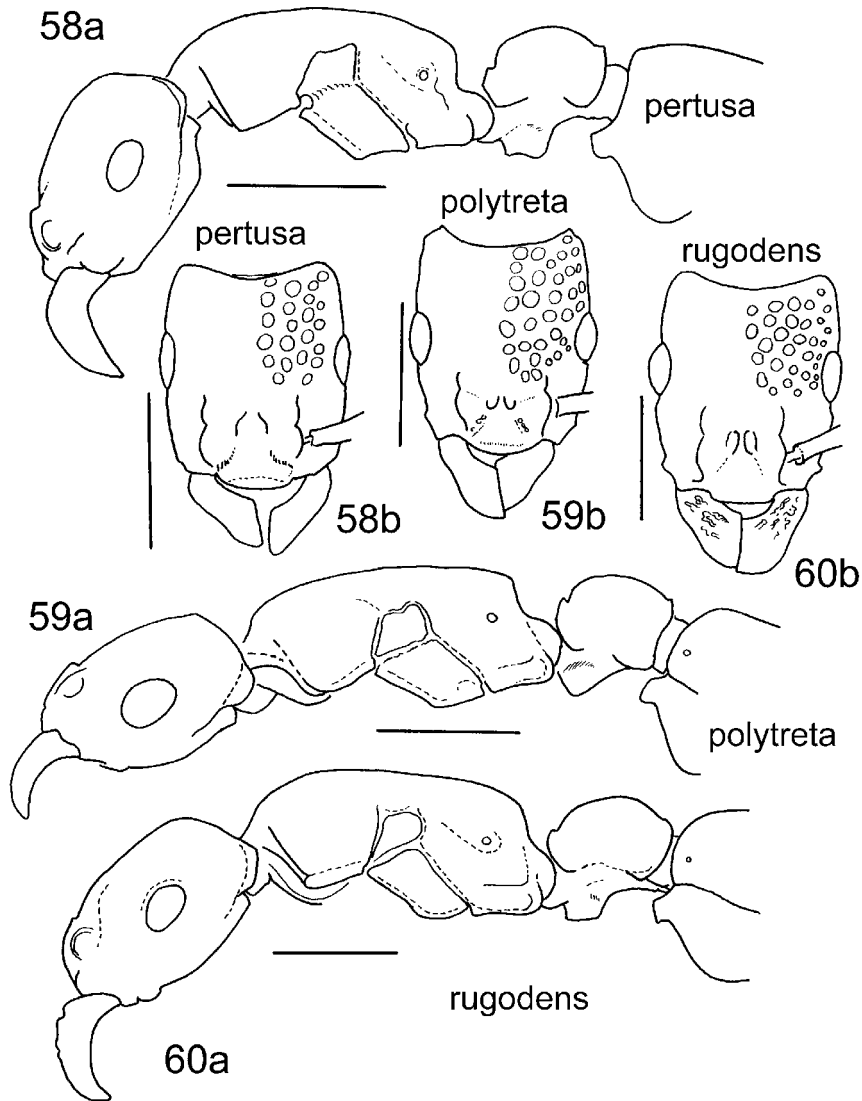


Fig. 58. *Gnamptogenys pertusa* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 59.** *G. polytreta* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 60.** *G. rugodens* worker (holotype): a - head and body in lateral view; b - head in frontal view. Scale lines = 0.5mm.

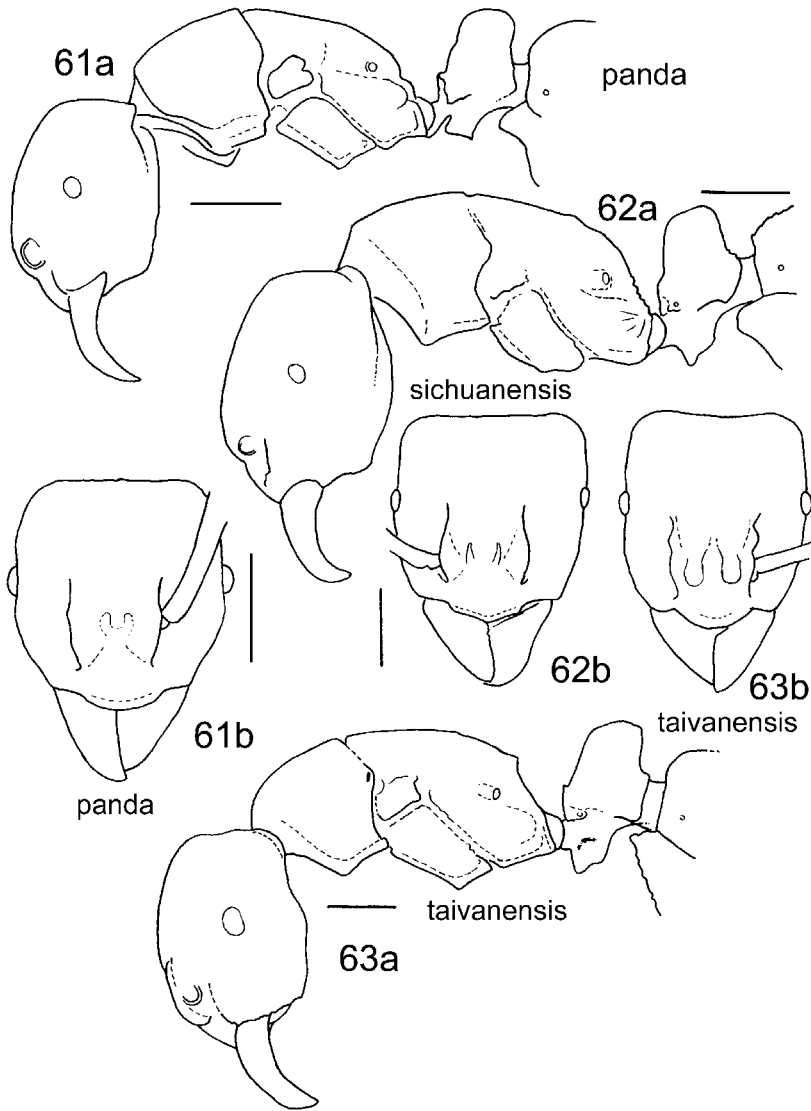


Fig. 61. *Gnampptogenys panda* worker (southern China): a - head and body in lateral view; b - head in frontal view. **Fig. 62.** *G. sichuanensis* worker (holotype): a - head and body in lateral view; b - head in frontal view. **Fig. 63.** *G. taivanensis* worker (Taiwan): a - head and body in lateral view; b - head in frontal view. Scale lines = 0.5mm.