Zootaxa 1769: 1–34 (2008)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Revision of the Termitinae with snapping soldiers (Isoptera: Termitidae) from New Guinea

THOMAS BOURGUIGNON[1], MAURICE LEPONCE[2] & YVES ROISIN[3]

[1]*Behavioral & Evolutionary Ecology, CP 160/12, Université Libre de Bruxelles (ULB), Avenue F.D. Roosevelt 50, B–1050 Brussels, Belgium. E-mail: thomas.bourguignon@ulb.ac.be – Phone: +32 26504525, fax: +32 26502445*

[2]*Biological Evaluation Section, Royal Belgian Institute of Natural Sciences (IRSNB/KBIN), Rue Vautier 29, B–1000 Brussels, Belgium. E-mail: Maurice.Leponce@naturalsciences.be – Phone: +32 26274358, fax: +32 26494825*

[3]*Behavioral & Evolutionary Ecology, CP 160/12, Université Libre de Bruxelles (ULB), Avenue F.D. Roosevelt 50, B–1050 Brussels, Belgium. E-mail: yroisin@ulb.ac.be – Phone: +32 26504512, fax: +32 26502445*

Table of contents

Abstract

Up to now, three described species of Termitinae with snapping soldier mandibles (the *Termes–Capritermes* group) were known from New Guinea: *Termes odontomachus* (Desneux), *Macrognathotermes errator* Miller and *Pericapritermes schultzei* (Holmgren). Here, we report the presence of seven additional species, among which three are new to science: *Pericapritermes parvus*, *P. pilosus* and *P. papuanus*. The other four, collected in southern Papuan savannas, were previously known from northern Australia: *Ephelotermes paleatus* Miller, *E. cheeli* (Mjöberg), *Lophotermes aduncus* Miller, and *L. brevicephalus* Miller. We reassign *T. odontomachus* to *Protocapritermes* Holmgren. Diagnostic characters and

Accepted by S. Kambhampati: 27 March 2008; published: 14 May 2008

illustrations are provided for all species. The Oriental affinities of the forest fauna of New Guinea and the similarities between Australian and New Guinean savannas are emphasized.

Key words: Isoptera, Termitinae, new species, Papuan Region, biogeography

Introduction

The Termitidae, sometimes called "higher termites," constitutes the most species-rich and ecologically diversified termite family. In New Guinea, the Termitidae are represented by two subfamilies: Nasutitermitinae and Termitinae. The former comprises fully nasute species that utilize chemical defence: soldiers squirt a glue on natural enemies through a long nose-like projection of their head capsule. In a recent monograph, 22 species of Nasutitermitinae were reported from New Guinea (Roisin & Pasteels 1996). Among the Termitinae, which in their present composition probably constitute a paraphyletic assemblage (Inward *et al.* 2007), the pantropical genera *Amitermes* and *Microcerotermes* possess soldiers with long, curved, piercing mandibles. The New Guinean species of both genera have recently been revised (Roisin 1990, Roisin & Pasteels 2000). Besides these two genera, the Termitinae are also represented in this region by several species whose soldiers are endowed with snapping mandibles. These soldiers have either near-symmetrical mandibles, as in *Termes* Linnaeus, or strongly asymmetrical ones, as in *Capritermes* Wasmann. They often have a conical frontal projection, but this projection can be very small or absent. Two smaller lateral tubercles can also be present at the base of the frontal projection. These termites are more or less specialized soil-feeders: for instance, among Australian genera, *Ephelotermes* is a wood/soil interface feeder, whereas *Macrognathotermes* and *Lophotermes* are certainly soil feeders (Tayasu *et al.* 1998). A few species build epigeal mounds but most nests are subterranean or established in abandoned or occupied mounds of other termites (Miller 1991).

Although Miller (1991) considered the *Termes–Capritermes* group of genera as a "branch" of the Termitinae, implying monophyly, he later suggested that snapping mandibles might be polyphyletic (Miller 1994, 1997). As to strongly asymmetrical mandibles, their polyphyletic evolution has long been considered probable (Hare 1937, Miller 1997, Noirot 2002). According to a recent molecular and morphological study encompassing representative genera from all over the world, snapping mandibles would indeed have evolved several times, and asymmetrical snappers would have appeared independently at least four times (Inward *et al.* 2007).

Termitinae with snapping soldiers are present throughout all tropical regions (Eggleton 2000). They are well represented in Australia, where 13 genera and 54 species are known (Miller 1991), and in Southeast Asia (Thapa 1982, Tho 1992, Eggleton 2000). The Australian symmetrical snappers probably constitute a monophyletic group closely related to *Termes*, whereas the asymmetrical snapper *Pericapritermes* pertains to a distant clade (Inward *et al.* 2007). Up to now, only three named species of termites with snapping soldiers have been recorded from New Guinea: *Termes odontomachus* Desneux, 1905, *Macrognathotermes errator* Miller, 1991, and *Pericapritermes schultzei* (Holmgren, 1911). In addition, Barrett (1965) reported a smaller, undescribed species of *Pericapritermes*. The present revision is primarily based on extensive collections carried out in New Guinea between 1978 and 1995. We recorded 10 species in 5 genera, among which 4 described species are reported from New Guinea for the first time and 3 species are new to science. This work concludes our series of monographic revisions of New Guinean Termitidae (Roisin 1990, Roisin & Pasteels 1996, 2000).

Material and methods

Material used. The material used in this study was mostly collected by J.M. Pasteels (hereafter JMP), Y. Roisin (YR) and M. Leponce (ML) in New Guinea and some neighboring islands. Other collectors are J.H. Barrett (JHB), D.A. Johnstone (DAJ) and F.R. Wylie (FRW). Geographical coordinates of the sampling localities are given in Appendix 1.

Characters used. This study is based on the morphology of soldiers, workers, and alates. Soldiers contain most of the important taxonomic information at the species level. The following characters are of major interest: size, general shape of the head, length and shape of mandibles, shape of postmentum, pilosity of head, shape of frontal projection. Alates, when available, give taxonomic information at the species level by the general shape of the head and pronotum. For workers, the anatomy of the digestive tract and the shape of the mandibles are useful characters at the generic level, whereas enteric valves give information at the species level. Descriptions of the digestive tube follow the nomenclature of Noirot (1995).

Measurements. The measurements used, detailed below, follow the guidelines of Roonwal (1970); they are also those used by Miller (1991).

Soldiers (Figs 1–3):

1. Head length to apex of frontal tubercle
2. Head length to anterolateral corner of the genae
3. Head depth with postmentum
4. Head depth without postmentum
5. Head maximum width
6. Head width at anterolateral corner of the genae
7. Distance between tips of lateral tubercles
8. Right mandible length
9. Left mandible length
10. Postmentum maximum width
11. Postmentum minimum width
12. Pronotum width

Imagoes (Fig. 4):

13. Length with wings
14. Length without wings
15. Head length to apex of the labrum
16. Head length to clypeofrontal suture
17. Head width with eyes
18. Eyes maximum diameter
19. Ocellus maximum diameter
20. Pronotum length
21. Pronotum width
22. Forewing length (with scale)
23. Forewing maximum width

Workers:

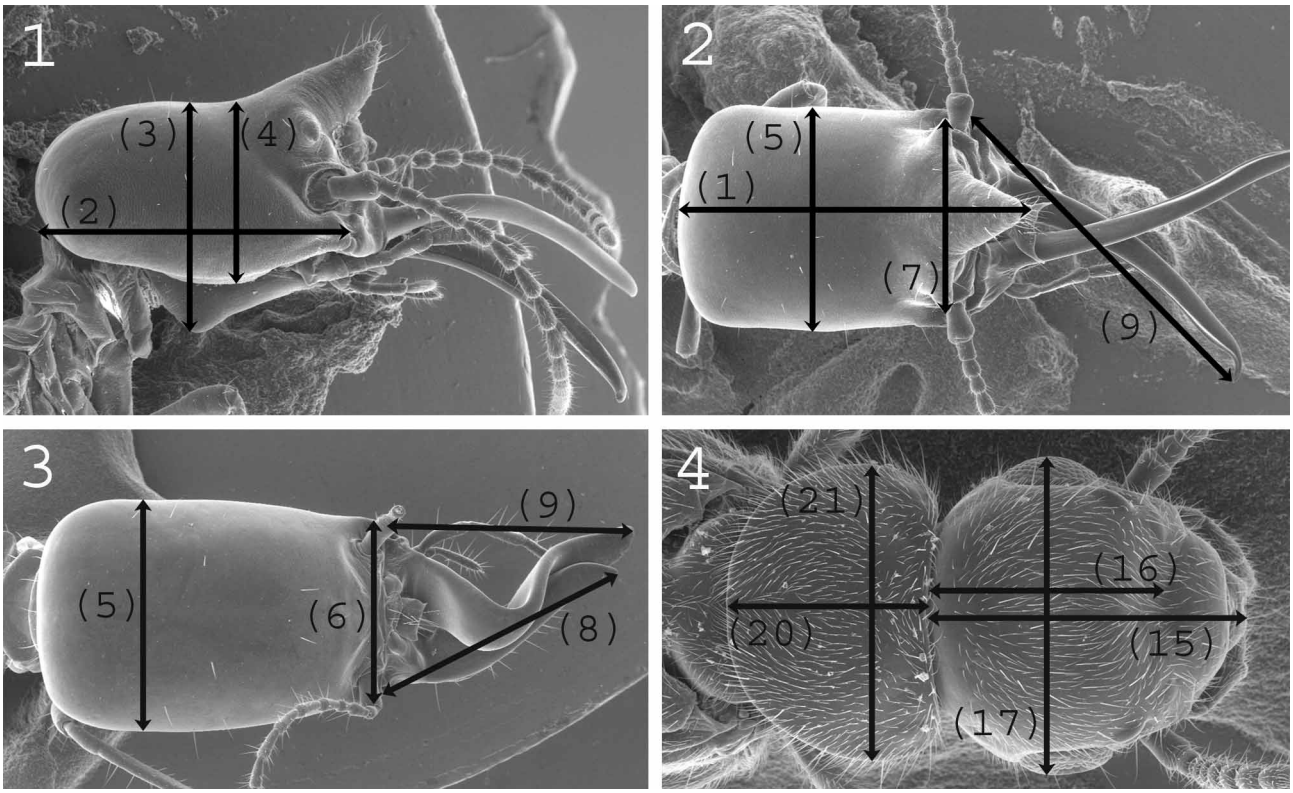
24. Head maximum width

For workers, the left mandible index (Emerson 1960) is the ratio between the distance separating the apical tooth from the fused first and second marginals, and the distance separating the fused first plus second marginals from the third marginal.

Illustrations. For scanning electron microscopy, specimens were dehydrated in a conventional ethanol series, impregnated for 24 h in hexamethyldisilazane, air dried and gold coated. Microphotographs were taken by a Philips XL 30 ESEM. For optical microscopy, enteric valve and mandibles of worker were dissected, dehydrated and mounted on slides in balsam.

Collections.

AMNH	American Museum of Natural History, New York, U.S.A.
ANIC	Australian National Insect Collection, Canberra, Australia
IRSN	Institut Royal des Sciences Naturelles, Brussels, Belgium.
MBBJ	Museum Zoologicum Bogoriense, Bogor, Indonesia.



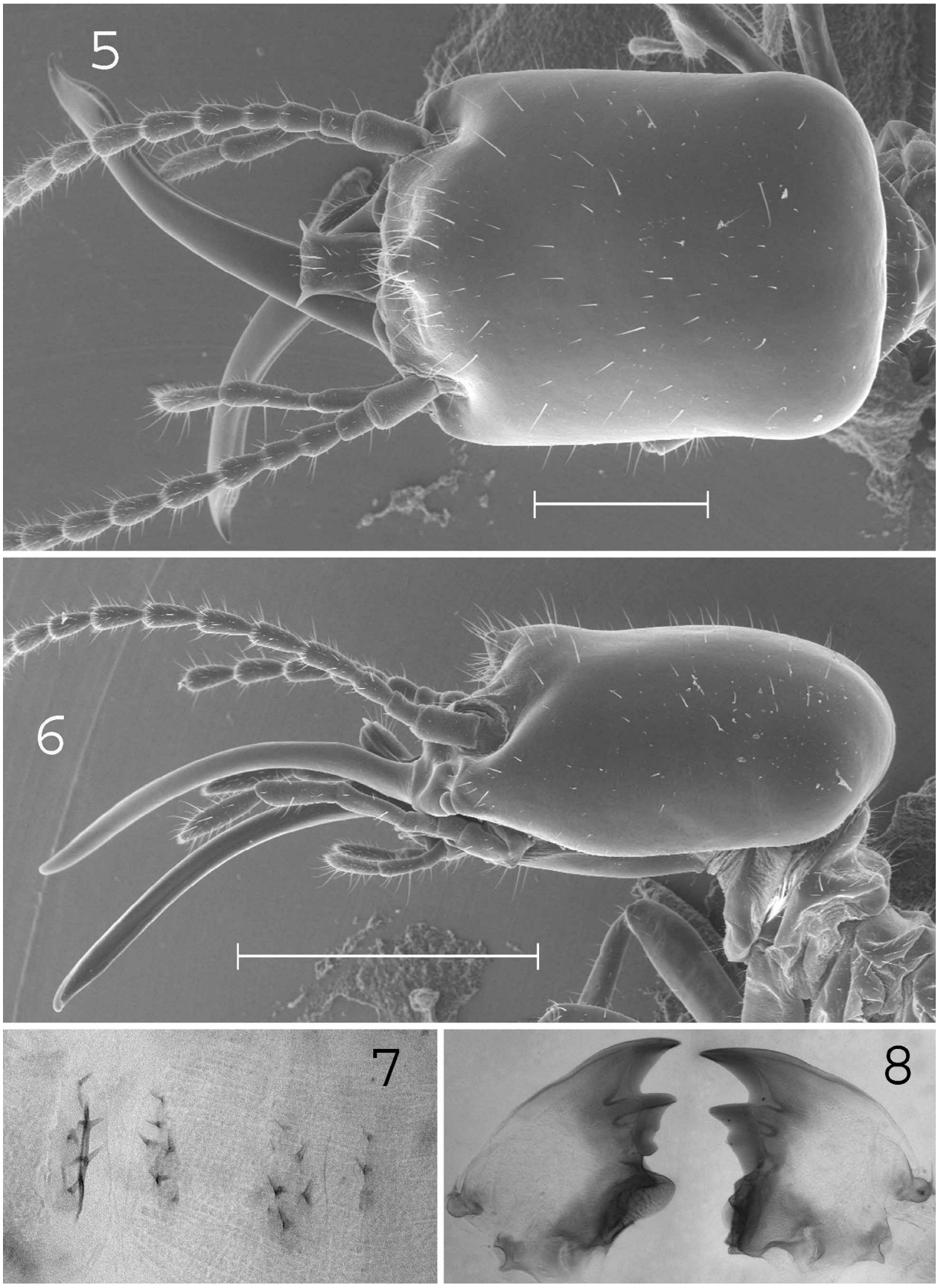
FIGURES 1–4. Measurements of soldiers: (1), head length to apex of frontal tubercle; (2), head length to anterolateral corner of the genae; (3), head depth with postmentum; (4), head depth without postmentum; (5), head maximum width; (6), head width at anterolateral corner of the genae; (7), distance between tips of lateral tubercles; (8), right mandible length; (9), left mandible length. Measurements of imago: (15), head length to apex of the labrum; (16), head length to clypeo-frontal suture; (17), head width with eyes; (20), pronotum length; (21), pronotum width.

Genus *Protocapritermes* Holmgren

Protocapritermes Holmgren, 1912: 108.
Type-species, fixed by monotypy: *Termes krisiformis* Froggatt, 1898.

Diagnosis. Soldiers of the genus *Protocapritermes* are characterized by their low frontal projection and lack of lateral tubercles (Figs. 5–6). Soldier mandibles moderately long and slender, almost symmetrical. Tibial spurs 3:2:2. Worker left mandible index: 0.8–1.2 (Fig. 8). Worker digestive tract with P3 subdivided into a small posterior section and a larger anterior one (Figs 59–60). Enteric valve weakly armed with short stout spines (Fig. 7). For a detailed description see Miller (1991).

Distribution. The type species of this genus occurs in coastal southeastern Australia (Watson & Abbey 1993: 138). The second species, discussed below, is known from New Guinea and from the Bismarck and Solomon Islands.



FIGURES 5–8. *Protocapritermes odontomachus*: 5, soldier head, dorsal; 6, soldier head, lateral; 7, enteric valve (4 cushions out of 6); 8, worker mandibles. Scale bars: 5, 0.5mm; 6, 1mm.

***Protocapritermes odontomachus* (Desneux), comb. nov.**
(Figs 5–8, 45–46, 59, 65)

Termes (*Eutermes*) *odontomachus* Desneux, 1905: 371.
Mirotermes odontomachus (Desneux).— Holmgren, 1911 : 462.
Termes odontomachus Desneux.—Snyder, 1949: 184.

Type material examined: syntypes. **PAPUA NEW GUINEA. IRSN collection.** *Morobe*. *Termes* (*Eutermes*) *odontomachus* Desneux, Sattelberg, 24.ix.1898, L. Biró.

Other material examined. PAPUA NEW GUINEA. Authors' collection. *East Sepik*. #PNGT71: Blup Blup Island, 16.vi.1981, JMP. – *Madang*. #PNGT32: Boisa Island, 3.xii.1978, JMP. #PNGT43: Laing Island, 14.xii.1978, JMP. #PNGT49: Yoro, 26.xii.1978, JMP. #PNGT246: Bogia, 4.iii.1983, JMP & YR. #PNGT273: Potsdam, 23.iii.1983, YR. #PNGT351: Potsdam, 17.v.1983, YR. #PNGT355: Sepen 2, 18.v.1983, YR. #PNGT367: Yoro, 20.v.1983, YR. #PNGT427: Guam River (bridge on Bogia–Josephstaal road), 29.x.1983, YR. #PNGT525: Kokun camp, 26.i.1984, YR. #PNGT531, 532: Yamu, 29.i.1984, YR. #PNGT686: Bunapae, 12.vi.1984, YR. #PNGT691, 692: Potsdam, 15.vi.1984, YR. #PNGT712: Guam River (bridge on Bogia–Josephstaal road), 23.vi.1984, YR. #PNGT750: Bunapae, 23.vii.1983, YR. #PNGT762: Potsdam, 26.vii.1984, YR. #PNGT794: Yoro, 25.viii.1984, YR. #PNGT804: Hansa Point, 3.ix.1984, YR. #PNGT817: Boisa Island, 6.ix.1984, YR. #PNGT895: Yoro, 22.ii.1985, JMP & YR. #PNGT1191: Bunapae, 21.iv.1988, YR. #PNGT1328: Braham Mission, 18.xi.1988, YR. – *Morobe*. #PNGT159: Mount Missim (alt. 1600m), 11.ii.1983, collected by JMP & YR. #PNGT160, 164: Mount Missim (alt. 1600m), 12.ii.1983, JMP & YR .#PNGT179: Wampit, 6.ii.1983, JMP & YR. #PNGT1094: Oomsis, 26.v.1987, YR. #PNGT1226: Bulolo, Manki Ridge (alt. 1350m), 18.v.1988, YR. – *Southern Highlands*. #PNGT1302: Pimaga, 16.x.1988, YR. – *Fly*. #PNGT1621: Nomad, 29.v.1990, YR & ML. #PNGT1623: Nomad, 31.v.1990, YR & ML. #PNGT1661: Nomad, 3.vi.1990, YR & ML. – *West Sepik*. #PNGT1730: Yapsiei, 10.iii.1994, YR & ML. #PNGT1741: Yapsiei, 11.iii.1994, YR & ML. – *New Ireland:* #PNGT602: Kolonoboi, 25.v.1984, JMP & YR. Lemakot: 30.v.1984, JMP & YR. #PNGT629: Lemakot, 30.v.1984, JMP & YR. – *Manus*. #PNGT662, 669, 672: 32 km from Lorengau on road to M'Bunai (approx. 2°06'S, 147°10'E), 4–6.vi.1984, JMP & YR. **ANIC.** *Morobe*. #10–9843: Bulolo, 12.vi.1961, J. Lake. #10–9911: Lae, 13.ix.1961, J.H. Ardley. #10–11021: Wau, 19.iv.1963, L. Clifford & JHB. #10–11039: Oomsis, 3.ix.1963, L. Clifford. – *Western Highlands*. #10–12512: Jimi, 18.ix.1968, FRW. – *New Ireland*. #10–12927: Namarodu, 29.iv.1969, B. Gray. **INDONESIA. Authors' collection.** *Irian Jaya*. #IRJT55: Pusppenssat (50 km from Nabire on Ilaga road): 15.xi.1995, YR.

Imago (Figs 45–46). Head capsule covered by many fine setae and by about 30 large scattered setae. Eyes prominent. Antennae 15-segmented. Pronotum wide and short. Measurements as in Table 1.

Soldier (Figs 5–6). Head elongated, slightly longer than wide, rectangular-shaped, covered by about 70 setae. Frontal projection reduced, bearing many setae. Labrum bearing about 10 setae, slightly elongated, with anterior corners drawn out into long points. Mandibles as long as head. Antennae 14-segmented. Postmentum flat. Measurements as in Table 2.

Worker (Figs 7–8). Monomorphic. Enteric valve, with 6 cushions of slightly unequal size, each with 3 to 7 long stout spines. Measurements as in Table 18.

Generic assignment. *Protocapritermes odontomachus* differs from *Termes* species by its soldier with shorter frontal tubercle and shorter mandibles, worker digestive tract with subdivided P3, enteric valve with few spines (Fig. 7). These characters suggest a close relationship with *P. krisiformis* (Fig. 60).

Diagnosis. This species can be distinguished from *P. krisiformis* by its shorter head and more prominent frontal tubercle in the soldier, and by its stronger enteric valve armature in the worker.

Distribution (Fig. 65). This species is common in New Guinean forests, where it was found up to 1700m a.s.l., but seems absent from the Papuan peninsula. It also occurs in New Ireland and on Manus Island, and was reported from the Solomon Islands (Harris & Brown 1958).

TABLE 1. Measurements (mm) of 4 male and 4 female imagoes from 2 colonies, plus 2 male and 2 female imagoes from the type colony of *Protocapritermes odontomachus.*

	Non-type male	Non-type female	Syntype male	Syntype female
Length with wings	8.82–11.05	9.00–9.66	/	/
Length without wings	5.06–5.57	5.46–5.59	4.56–4.90	5.34–5.64
Head length to apex of the labrum	1.07–1.10	1.08–1.11	1.13–1.14	1.14–1.20
Head length to clypeo-frontal suture	0.54–0.60	0.55–0.61	0.69–0.70	0.65–0.69
Head width with eyes	0.87–0.93	0.85–0.88	0.98–1.00	0.99–1.02
Eye maximum diameter	0.27–0.33	0.24–0.27	0.27–0.30	0.27–0.28
Ocellus maximum length	0.06–0.08	0.06–0.09	0.10–0.11	0.09–0.10
Pronotum length	0.41–0.53	0.42–0.49	0.48	0.48–0.50
Pronotum width	0.71–0.82	0.72–0.75	0.81	0.80–0.84
Forewing length	7.64–9.44	7.43–8.12	/	/
Forewing width	2.10–2.62	2.00–2.23	/	/

TABLE 2. Measurements (mm) of 33 soldiers from 11 colonies and 4 soldiers of the type colony of *Protocapritermes odontomachus.*

	Non-type	Syntypes
Head length to apex of frontal tubercle	1.18–1.53	1.52–1.56
Head length to anterolateral corner of the genae	1.35–1.72	1.66–1.75
Head depth with postmentum	0.66–0.88	0.86–0.90
Head depth without postmentum	0.73–0.97	0.97–1.01
Head maximum width	0.87–1.10	1.16–1.17
Pronotum width	0.52–0.72	0.66–0.71
Left mandible length	1.80–2.29	2.36–2.48
Postmentum minimum width	0.14–0.21	0.17

Genus *Ephelotermes* Miller

Ephelotermes Miller, 1991: 1178.
Type-species, by original designation: *Ephelotermes melachoma* Miller, 1991: 1178.

Diagnosis. The genus *Ephelotermes* is characterized by its well-developed frontal projection and the lack of lateral tubercles in the soldiers (Figs 9, 13). Tibial spurs 3:2:2 or 2:2:2. Monomorphic workers. Worker left mandible index usually > 1, sometimes slightly lower (Figs 12, 16). Enteric valve with cushions of two sizes distributed according to a triradial symmetry, with many small triangular spines (Figs 11, 15). Worker digestive tract with P3 subdivided into 3 sections, successively small – large – small (Fig. 61). Miller (1991) listed the following characters to distinguish between *Termes* and *Ephelotermes*: “Soldiers of *Ephelotermes* differ from the soldier *T. fatalis* in that the labrum is never elongated with long points but always relatively small, with short points or lacking points; the head capsule is always proportionally wider; and the mandibles are always more curved dorsoventrally”. For a detailed description see Miller (1991).

***Ephelotermes paleatus* Miller**
(Figs 9–12, 47–48, 66)

Ephelotermes paleatus Miller, 1991: 1188.

Type material examined: paratypes from type locality. **AUSTRALIA.** *Queensland*. Weipa, 9.xi.1978, L.R. Miller. ANIC #10–18368.

Other material examined. PAPUA NEW GUINEA. Authors' collection. *Fly.* #PNGT1467: Morehead, 27.iii.1989, YR & ML. #PNGT1578: Lake Murray, 24.v.1990, YR & ML.

Diagnosis. This species is easily recognised from congeners by its small size (Tables 3–4, 18) as well as by the downward projected postmentum of soldiers (Fig. 10). For additional description see Miller (1991). New Guinean specimens of this species slightly differ from Australian ones by the shape of the frontal projection, which is directed upwards. However, we judge this character insufficient to consider them as a distinct species.

Distribution (Fig. 66). We collected this species twice in Papua New Guinea, at Morehead and Lake Murray (Fly). It is also known from northern Queensland, Australia (Miller 1991, Watson & Abbey 1993: 102).

TABLE 3. Measurements (mm) of 1 queen of *Ephelotermes paleatus.*

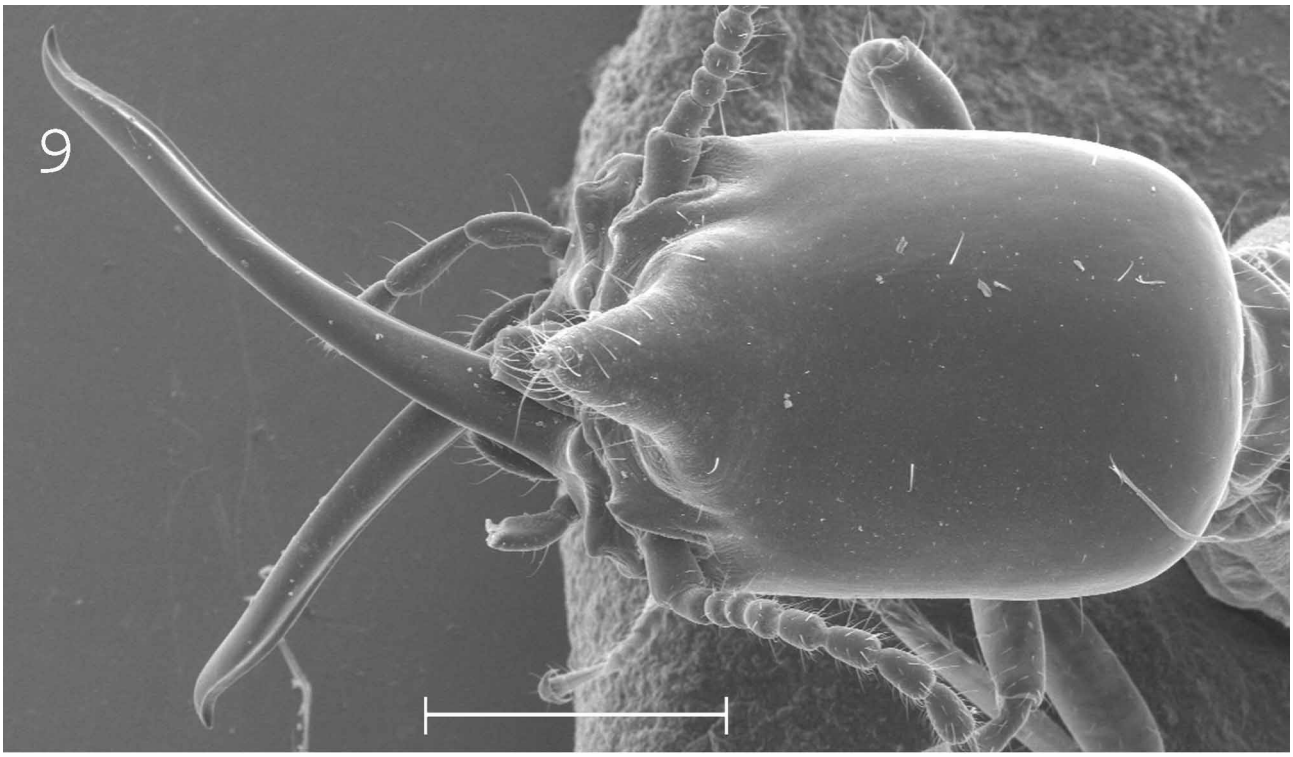
Length without wings	10.58
Head length to apex of the labrum	0.87
Head length to clypeo-frontal suture	0.50
Head width with eyes	0.74
Eye maximum diameter	0.20
Ocellus maximum length	0.10
Pronotum length	0.45
Pronotum width	0.70

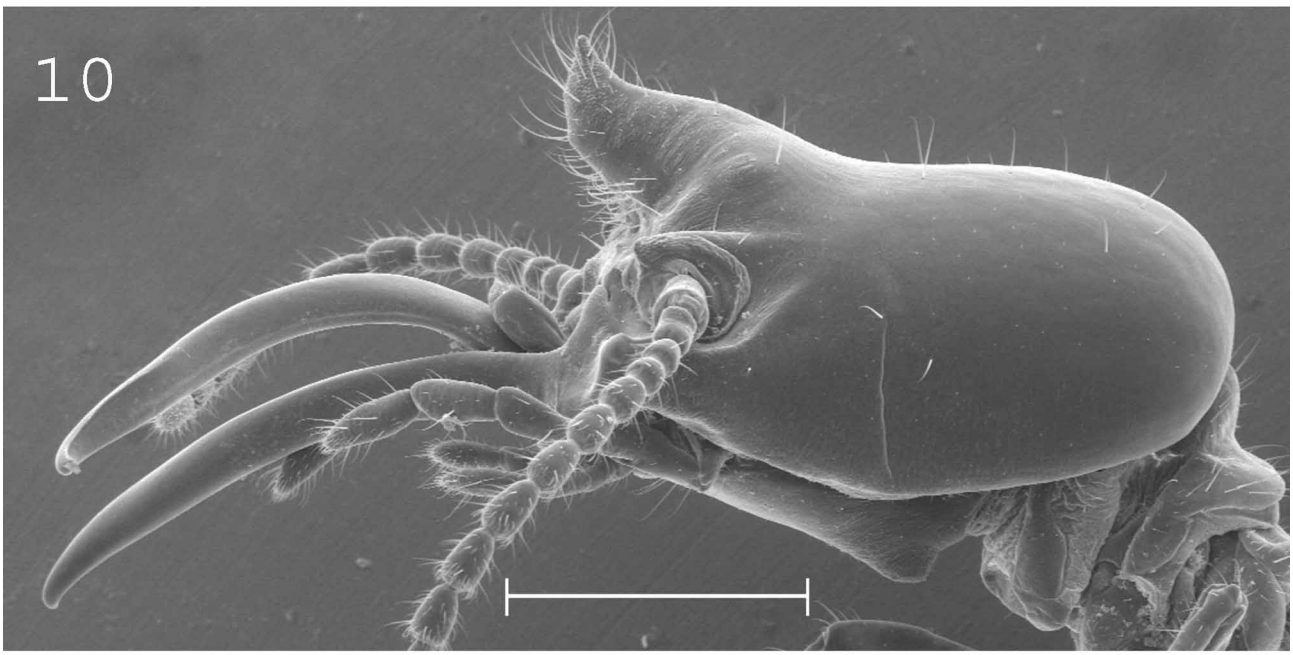
TABLE 4. Measurements (mm) of 12 soldiers from 2 colonies of *Ephelotermes paleatus.*

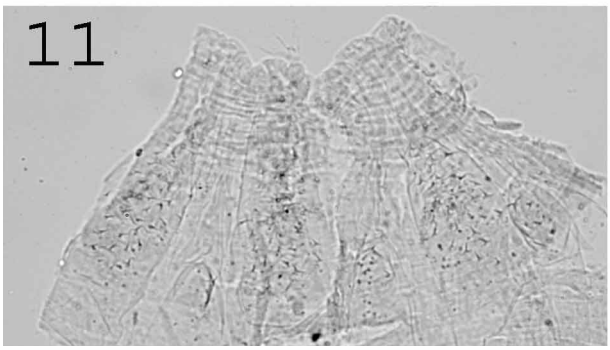
Head length to apex of frontal tubercle	0.99–1.12
Head length to anterolateral corner of the genae	0.91–1.02
Head depth with postmentum	0.45–0.57
Head depth without postmentum	0.57–0.71
Head maximum width	0.60–0.72
Pronotum width	0.38–0.46
Left mandible length	1.24–1.33
Postmentum minimum width	0.14–0.21

***Ephelotermes cheeli* (Mjöberg)**
(Figs 13–16, 49–50, 61, 66)

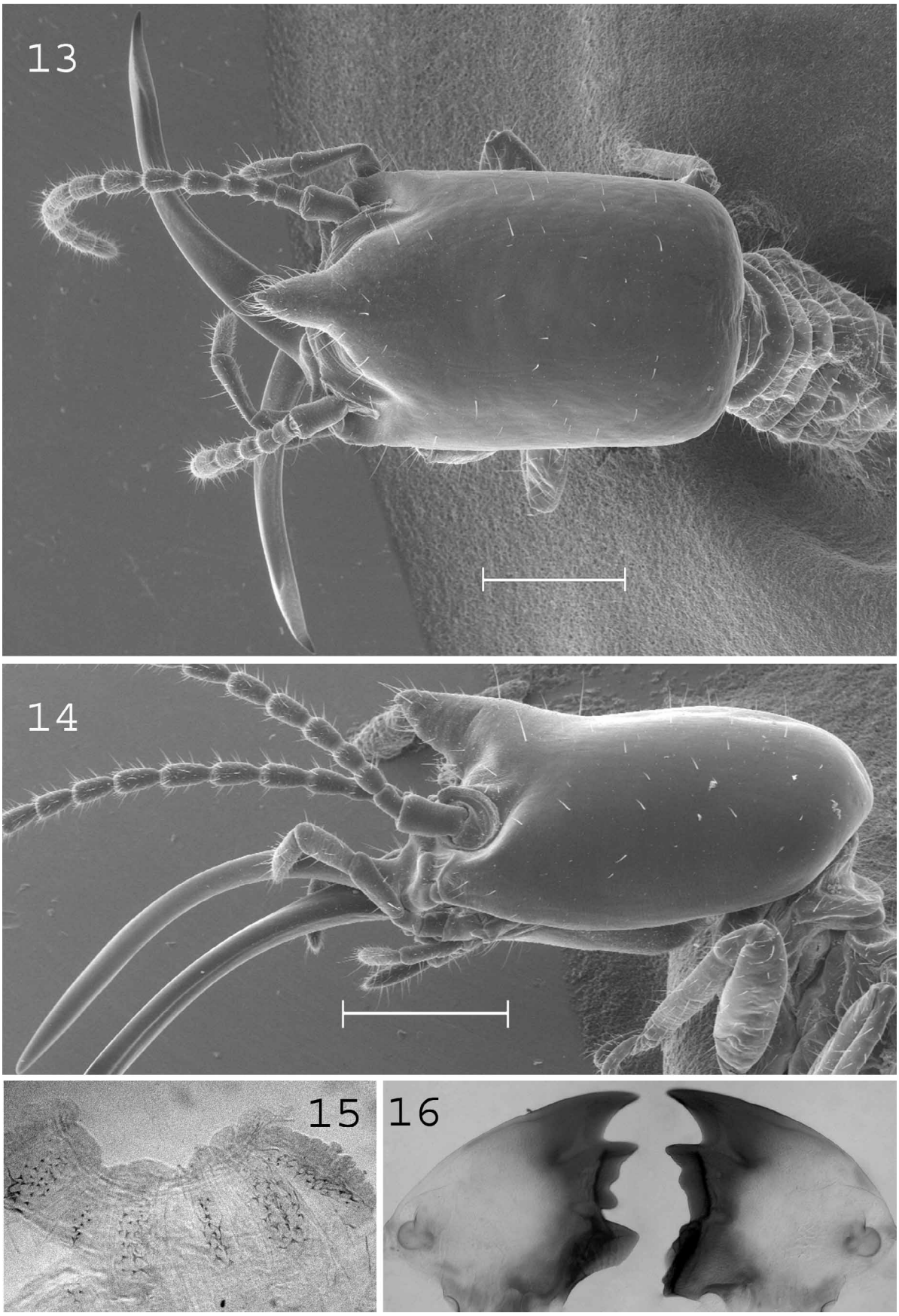
Mirotermes Cheeli Mjöberg, 1920: 95.
Ephelotermes cheeli (Mjöberg).—Miller, 1991: 1180.







FIGURES 9–12. *Ephelotermes paleatus*: 9, soldier head, dorsal; 10, soldier head, lateral; 11, enteric valve; 12, worker mandibles. Scale bars: 9, 10, 0.5mm.



FIGURES 13–16. *Ephelotermes cheeli*: 13, soldier head, dorsal; 14, soldier head, lateral; 15, enteric valve; 16, worker mandibles. Scale bars: 13, 14, 0.5mm.

Material examined. AUSTRALIA. ANIC. *Queensland.* #10–18434, Weipa, 2.xi.1978, collected and identified by L.R. Miller. **PAPUA NEW GUINEA. Authors' collection.** *Fly.* #PNGT1414: Morehead, 22.iii.1989, YR & ML. #PNGT1416: Morehead, 23.iii.1989, YR & ML. #PNGT1435, 1436: Morehead, 24.iii.1989, YR & ML. #PNGT1487, 1492: Wipim, 30.iii.1989, YR & ML. #PNGT1496: Wipim, 31.iii.1989, YR & ML. #PNGT1555, 1556: Lake Murray, 22.v.1990, YR & ML. #PNGT1565: Lake Murray, 23.v.1990, YR & ML. #PNGT1586: Lake Murray, 25.v.1990, YR & ML. #PNGT1655: Nomad, 2.vi.1990, YR & ML.

Diagnosis. This species can be easily distinguished from other ones of the genus by its large size (Tables 5–6, 18) and the short labrum of soldiers. For detailed descriptions see Mjöberg (1920), Hill (1942) and Miller (1991).

Distribution (Fig. 66). This species was collected 13 times in southern Papua New Guinea (Morehead, Wipim, Lake Murray and Nomad River) in both forests and savannas. It is also known from northern Queensland and Torres Strait islands (Miller 1991, Watson & Abbey 1993: 101).

TABLE 5. Measurements (mm) of 1 male and 5 female imagoes from 1 colony of *Ephelotermes cheeli.*

	Male	Female
Length with wings	7.67	7.03–7.48
Length without wings	4.30	3.88–4.32
Head length to apex of the labrum	0.91	0.78–0.87
Head length to clypeo-frontal suture	0.61	0.44–0.51
Head width with eyes	0.84	0.70–0.81
Eye maximum diameter	0.26	0.21–0.28
Ocellus maximum length	0.12	0.07–0.09
Pronotum length	0.47	0.36–0.46
Pronotum width	0.70	0.53–0.69
Forewing length	6.18	6.07–6.26
Forewing width	1.83	1.66–1.88

TABLE 6. Measurements (mm) of 27 soldiers from 9 colonies of *Ephelotermes cheeli.*

Head length to apex of frontal tubercle	1.28–1.79
Head length to anterolateral corner of the genae	1.20–1.55
Head depth with postmentum	0.60–0.80
Head depth without postmentum	0.69–0.89
Head maximum width	0.81–0.97
Pronotum width	0.46–0.68
Left mandible length	1.75–2.13
Postmentum minimum width	0.12–0.19

Genus *Lophotermes* Miller

Lophotermes Miller, 1991: 1212.
Type-species: *Lophotermes pectinatus* Miller, 1991: 1212.

Diagnosis. Soldiers of *Lophotermes* are usually characterized by well-developed frontal and lateral tubercles (Figs 17–18, 21–22); mandibles generally stout and longer than head capsule; antennae of 14 or sometimes 15

segments; labrum usually large; tibial spurs 3:2:2 or 2:2:2. Monomorphic workers. Worker left mandible index > 1.5, often > 2.0 (Figs 20, 24). Worker digestive tract with P3 subdivided into a small posterior section and a larger anterior one (Fig. 62). For a more complete description see Miller (1991).

Lophotermes aduncus Miller
(Figs 17–20, 65)

Lophotermes aduncus Miller, 1991: 1212.

Type material examined: paratypes. AUSTRALIA. ANIC. *Queensland.* #10–20450, 8 km SW of Cape Weymouth, 1.vii.1984, L.R. Miller.

Other material examined. PAPUA NEW GUINEA. Authors' collection. *Fly.* #PNGT1412: Morehead, 22.iii.1989, YR & ML. #PNGT1455: Morehead, 25.iii.1989, YR & ML. #PNGT1469: Morehead, 27.iii.1989, YR & ML.

Diagnosis. *L. aduncus* can be differentiated from congeners by the narrow frontal projection and lateral tubercles, and the short mandibles of its soldiers. Worker enteric valve with 6 cushions of equal size, with many small spines and long, curved ones in their distal part. For a detailed description see Miller (1991). Measurements as in Table 7 and 18.

Distribution (Fig. 65). *L. aduncus* was collected three times at Morehead, in Southern Papua New Guinea savannas. It is also known from various places in Queensland (Miller 1991, Watson & Abbey 1993: 110).

TABLE 7. Measurements (mm) of 12 soldiers from 3 colonies of *Lophotermes aduncus.*

Head length to apex of frontal tubercle	1.52–1.91
Head length to anterolateral corner of the genae	1.47–1.66
Head depth with postmentum	0.76–0.91
Head depth without postmentum	0.86–1.01
Head maximum width	1.10–1.19
Pronotum width	0.59–0.66
Left mandible length	1.54–1.74
Postmentum minimum width	0.14–0.20
Distance between tips of lateral tubercles	0.70–0.81

Lophotermes brevicephalus Miller
(Figs 21–24, 51–52, 62, 65)

Lophotermes brevicephalus Miller, 1991: 1214.

Type material examined: paratypes from type locality. AUSTRALIA. ANIC. *Queensland.* #10–18095, Weipa, 4.xi.1978, L.R. Miller.

Other material examined. PAPUA NEW GUINEA. Authors' collection. *Fly.* #PNGT1423: Morehead, 23.iii.1989, YR & ML.

Diagnosis. This species is related to *L. aduncus* and *L. pectinatus*. It is distinguished from the former by the longer mandibles and the downward projection of the postmentum of its soldiers (Figs 21–22) and from the latter by the smaller size and shorter head of its soldiers. Worker enteric valve with 6 cushions of alternating size, covered with many short spines. Measurements as in Tables 8–9 and 18.

Distribution (Fig. 65). *L. brevicephalus* was collected only once at Morehead (Fly), in southern Papuan savannas. It is also known from various places in Queensland (Miller 1991, Watson & Abbey 1993: 110).

TABLE 8. Measurements (mm) of 1 dealate male of *Lophotermes brevicephalus.*

Length without wings	4.82
Head length to apex of the labrum	1.01
Head length to clypeo-frontal suture	0.59
Head width with eyes	0.92
Eye maximum diameter	0.27
Ocellus maximum length	0.12
Pronotum length	0.52
Pronotum width	0.81

TABLE 9. Measurements (mm) of 8 soldiers from 1 colony of *Lophotermes brevicephalus.*

Head length to apex of frontal tubercle	1.50–1.65
Head length to anterolateral corner of the genae	1.36–1.45
Head depth with postmentum	0.75–0.83
Head depth without postmentum	0.96–1.01
Head maximum width	1.04–1.09
Pronotum width	0.55–0.60
Left mandible length	1.85–1.96
Postmentum minimum width	0.23–0.25
Distance between tips of lateral tubercles	0.81–0.91

Genus *Macrognathotermes* Miller

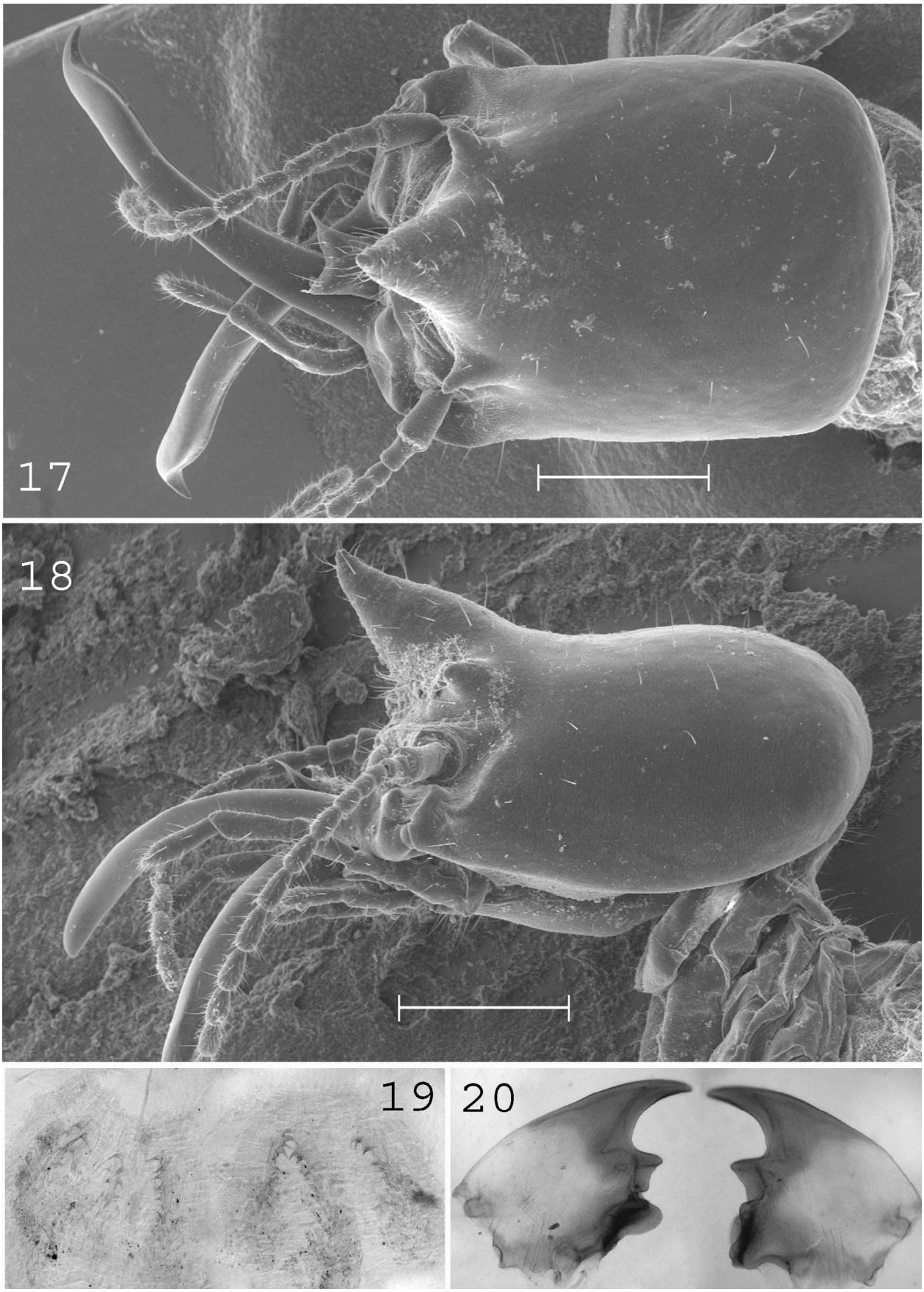
Macrognathotermes Miller, 1991: 1256.
Type-species, by original designation: *Macrognathotermes errator* Miller, 1991: 1256.

Diagnosis. Soldiers of this genus are characterized by the following characters (Figs 25–26): frontal projection well developed; lateral tubercles usually present, sometimes reduced or absent; mandibles very long and slender; postmentum projecting only slightly below the head capsule; antennae 14-segmented; tibial spurs 2:2:2. Monomorphic workers. Worker left mandible index > 1.5, usually > 2.0 (Figs 28). Enteric valve cushions of alternating size, slightly asymmetrical, with numerous small spines. Worker digestive tract with P1 enlarged, P3 subdivided into a posterior and an anterior section of the same size (Fig. 63). For additional description see Miller (1991).

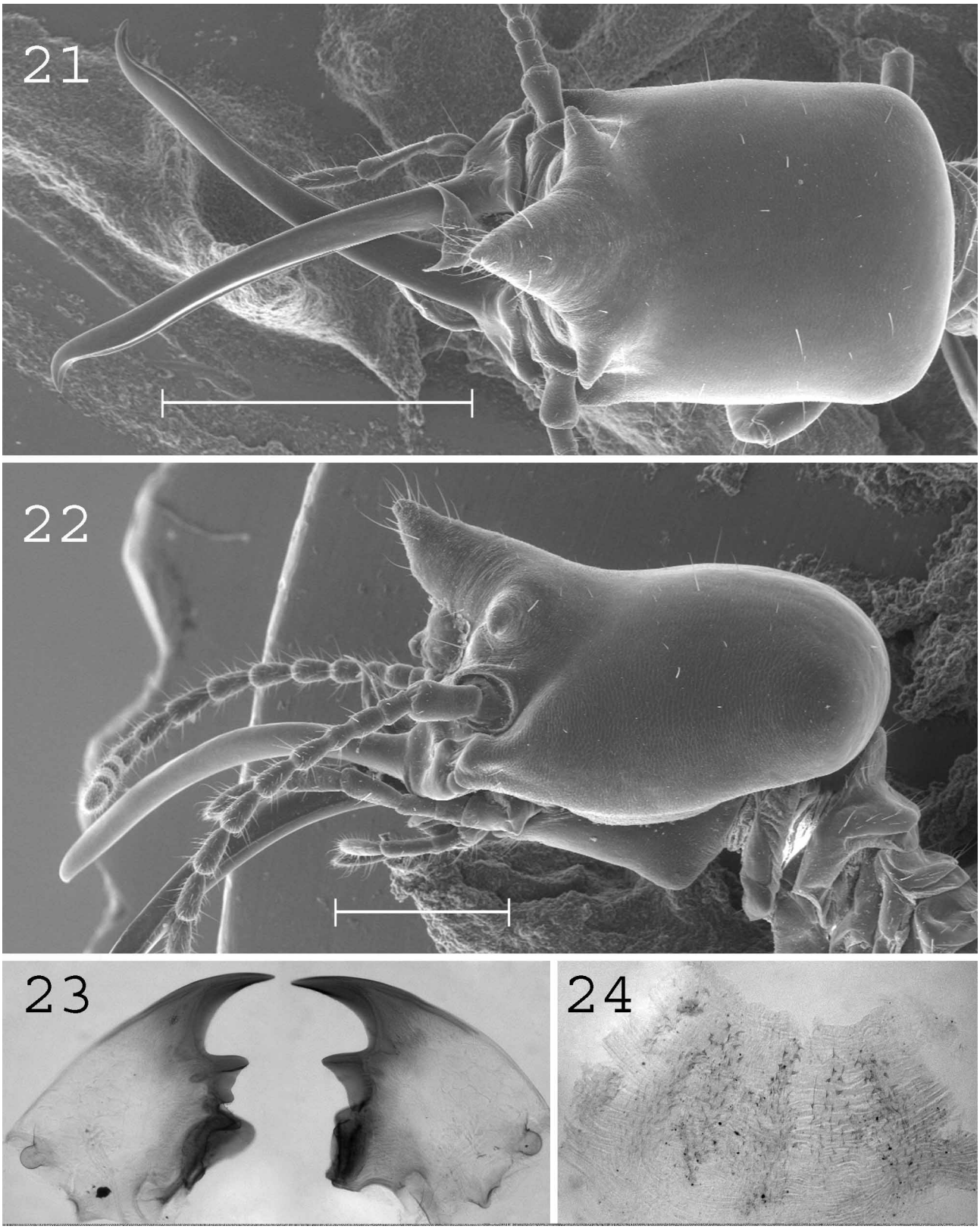
Macrognathotermes errator Miller
(Figs 25–28, 53–54, 63, 65)

Macrognathotermes errator Miller, 1991: 1258.

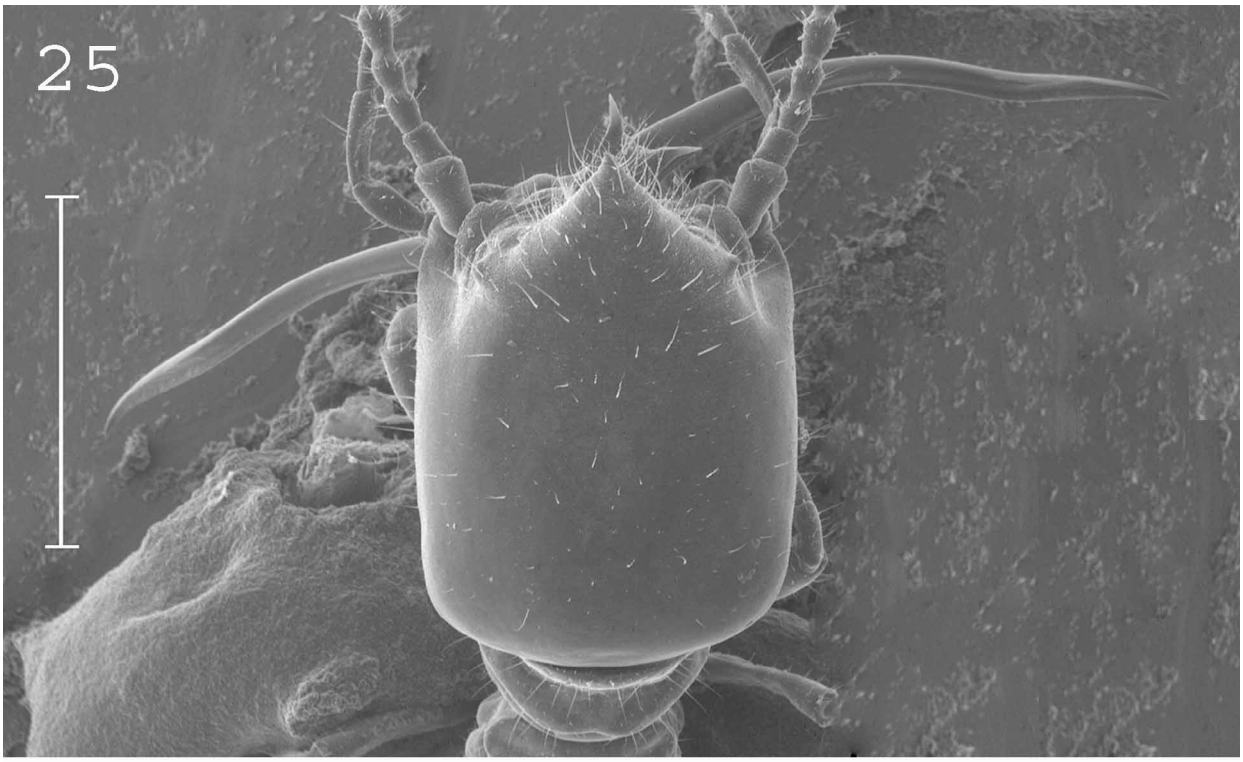
Type material examined: p**aratypes. AUSTRALIA. ANIC.** *Northern Territory.* #10–18280: Croker Island, 3.xi.1980, L.R. Miller.

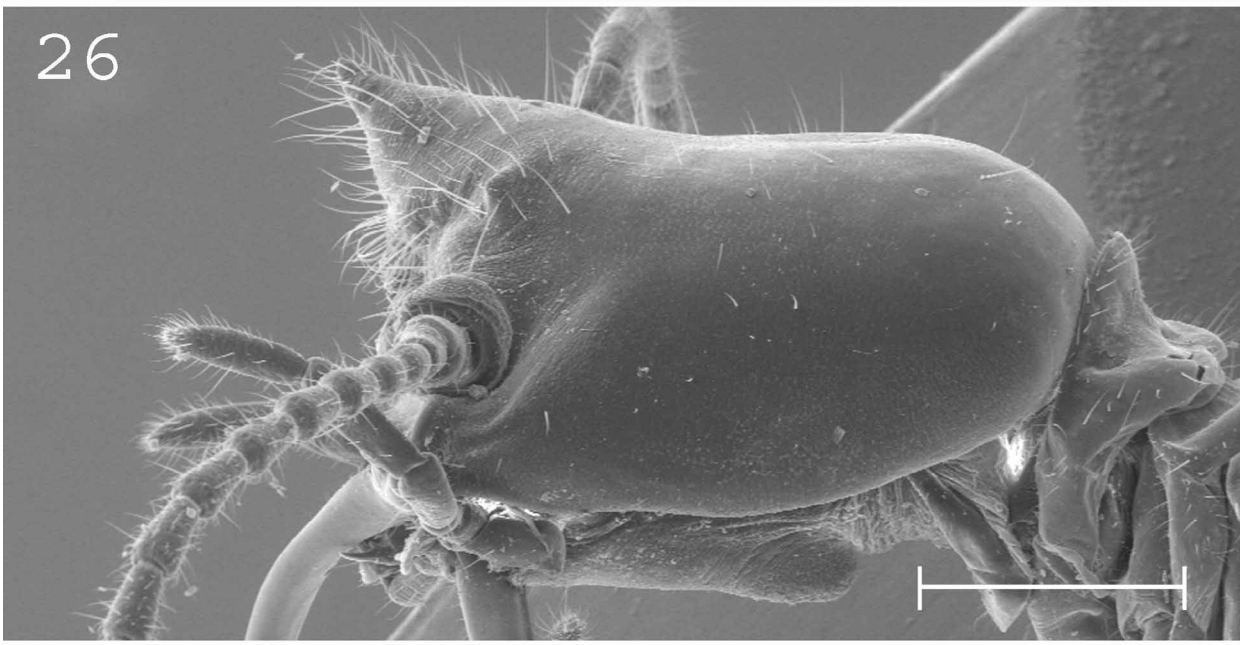


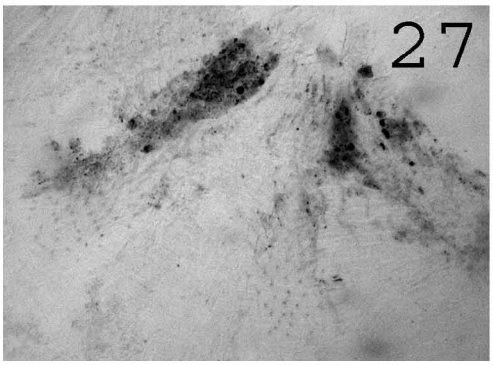
FIGURES 17–20. *Lophotermes aduncus*: 17, soldier head, dorsal; 18, soldier head, lateral; 19, enteric valve; 20, worker mandibles. Scale bars: 17, 18, 0.5mm.

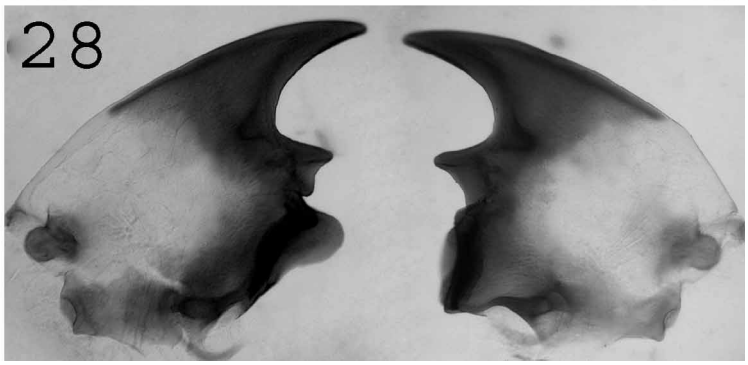


FIGURES 21–24. *Lophotermes brevicephalus*: 21, soldier head, dorsal; 22, soldier head, lateral; 23, worker mandibles; 24, enteric valve. Scale bars: 21, 1mm; 22, 0.5mm.









FIGURES 25–28. *Macrognathotermes errator*: 25, soldier head, dorsal; 26, soldier head, lateral; 27, enteric valve; 28, worker mandibles. Scale bars: 25, 1mm; 26, 0.5mm.

Other material examined. PAPUA NEW GUINEA. Authors' collection. *Fly.* #PNGT1408: Morehead, 22.iii.1989, YR & ML.

Diagnosis. Soldiers of this species (Figs 25–26) can be difficult to distinguish from *M. sunteri*. However, it has more prominent postmentum and lateral tubercles as well as longer and narrower frontal tubercle which is directed more forward (Miller 1991). For additional description see Miller (1991), for measurements see Tables 10–11 and 18. New Guinean specimens of this species differ from Australian ones in having a shorter frontal projection more lifted upward. Minor differences also exist in the shape of worker mandibles. However, we judge these differences insufficient to recognize two species. Moreover, Miller (1991) pointed out the great variation of form and size of this species along its geographical distribution.

Distribution (Fig. 65). We collected this species only once, at Morehead (Fly), in Southern Papuan savannas. This is about 22 km E of Rouku where it was previously recorded by Miller (1991). This species is also known from Queensland and Northern Territory (Miller 1991, Watson & Abbey 1993: 115).

TABLE 10. Measurements (mm) of 1 dealate male of *Macrognathotermes errator.*

Head length to apex of the labrum	1.30
Head length to clypeo-frontal suture	0.81
Head width with eyes	1.21
Eye maximum diameter	0.29
Ocellus maximum length	0.12
Pronotum length	0.73
Pronotum width	1.03

TABLE 11. Measurements (mm) of 3 soldiers from 1 colony of *Macrognathotermes errator.*

Head length to apex of frontal tubercle	1.40–1.48
Head length to anterolateral corner of the genae	1.25–1.34
Head depth with postmentum	0.72–0.76
Head depth without postmentum	0.92–0.98
Head maximum width	1.13–1.14
Pronotum width	0.67–0.72
Left mandible length	2.44–2.50
Postmentum minimum width	0.27–0.30
Distance between tips of lateral tubercles	0.73–0.77

Genus *Pericapritermes* Silvestri

Pericapritermes Silvestri, 1914: 134–135.
Type-species, by original designation: *Pericapritermes urgens* Silvestri, 1914: 135.

Diagnosis. *Pericapritermes* is the only genus in Papua New Guinea whose soldiers possess strongly asymmetrical mandibles. Left mandible strongly bent in the middle, without hook at tip or prominent basal projection and with rudimentary tooth in basal inner third. Right mandible bladelike, with tip usually pointed and bent outward anteriorly and inner apical margin straight. Labrum with anterior margin almost straight and anterolateral corners extended into short processes. Antennae with 14 articles. Tibial spurs 3:2:2. Middle tibia with one or two spines. Worker mandibles with apical teeth enlarged, left mandible with 1st and 3rd marginal

tooth distant (Figs 31, 35, 39, 43). Worker left mandible index: 0.4–0.6. For additional descriptions of imago and soldier, see Krishna (1968).

Worker digestive tract (Fig. 64). Gizzard narrow, separation with midgut badly visible. P1 slightly dilated. P3 large, undivided. P4 elongated and narrow, coming from the right to a central position in dorsal view. Enteric valve well developed. Six slightly asymmetrical cushions, with many short spines which appear triangular or spotlike when set flat on a slide. Smaller spines also present between cushions. An extensive armature of spines of various sizes is also present within P3.

Distribution. *Pericapritermes* species are broadly distributed from Africa to New Guinea throughout south and southeast Asia (Krishna 1968). Miller (1991) mentions a single record from northern Queensland.

Pericapritermes cf. *schultzei* (Holmgren)

(Figs 29–32, 67)

Capritermes Schultzei Holmgren, 1911: 462.
Pericapritermes schultzei (Holmgren). Krishna, 1968: 294.

Type material. We did not have the possibility to examine the type specimens of this species. They were presumably deposited in the Museum für Naturkunde, Humboldt Universität, Berlin, but could not be found there. Holmgren (1911) cites "Sepik (1570m über dem Meere, Nov. 1910, Schultze)" as collection data. In his report of the German–Dutch border expedition of 1910, Schultze actually mentions finding a new *Capritermes* on the top of the Peripatus mountain (Schultze Jena 1914: 74). As date and altitude correspond, the Peripatus summit (4°48'S, 141°10'E) should be considered as type locality for *P. schultzei* (Fig. 67).

Many samples from New Guinean hills or mountains are compatible with Holmgren's (1911) description, although variation in size and shape is substantial between, or sometimes within, colonies. Therefore, it is so far not possible to determine the limits of this species accurately. Provisionally, these series will be collectively labelled *P.* cf. *schultzei*.

Material examined. PAPUA NEW GUINEA. Authors' collection. *Morobe*. #PNGT196: Kaiapit, 20.ii.1983, JMP and YR. #PNGT1082: Bulolo, 22.v.1987, YR. #PNGT1231: Bulolo, Mt Susu Nature Reserve (alt. 1000m), 17.v.1988, YR. **ANIC.** *Southern Highlands*. #10–8583: Mendi, vii.1956, DAJ. #10–8621: Tari, xii.1955, DAJ. #10–8622: Mendi, xii.1955, DAJ. – *Eastern Highlands*. #10–11018: Asirangka (alt. 1650m), 1.ii.1963, JHB & Kenampi Rapoke; #10–11019: Namura, 3.i.1963, JHB, A.E. & E. Emerson. – *Morobe*. #10–14822: Bulolo, 4.xii.1973, FRW & P. Shanahan. **AMNH.** *Madang*. Wanuma (alt. 660m), 2.viii.1969, R. Zweifel.

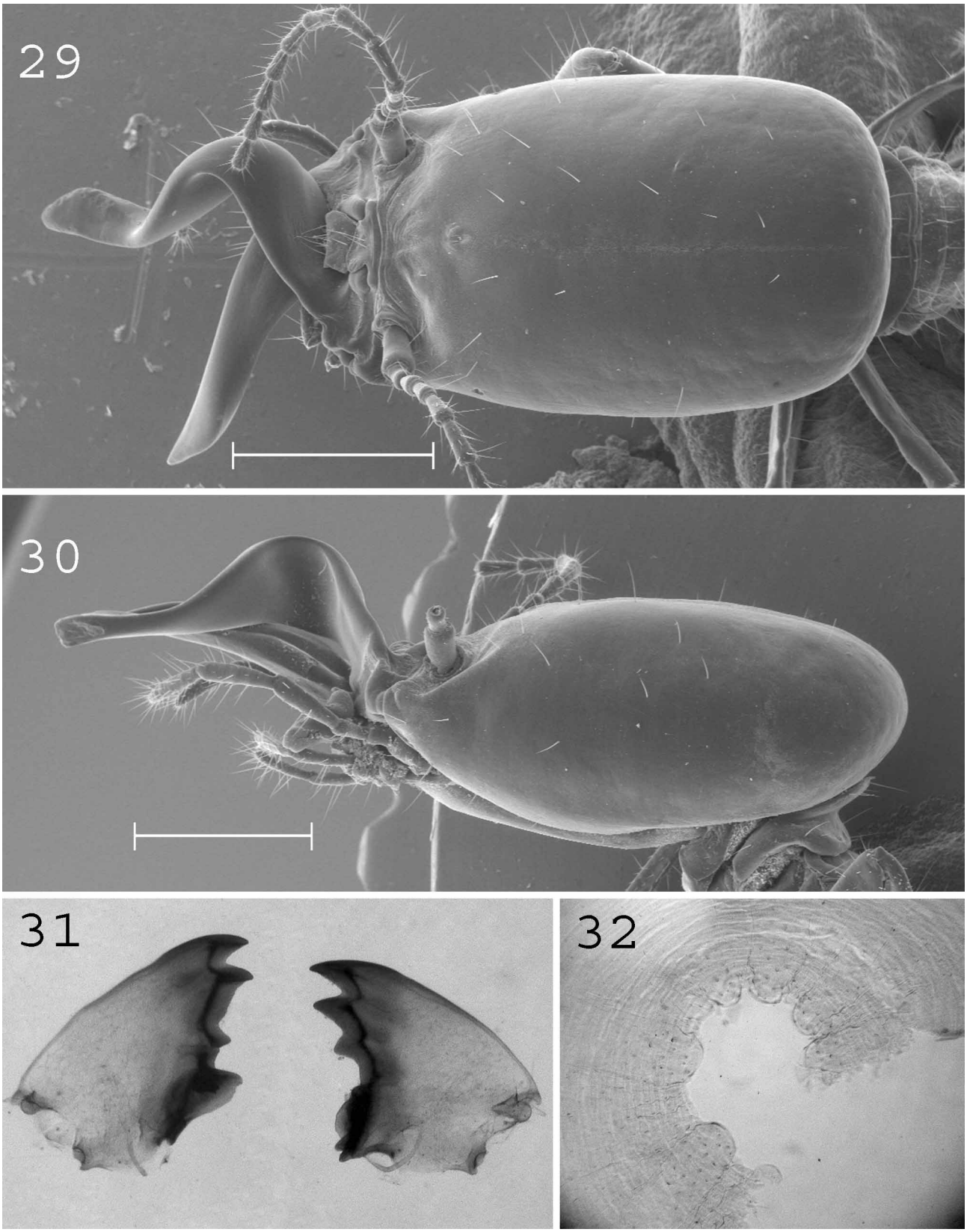
Diagnosis. Samples included in this group can be distinguished from congeners by their medium size and slightly hairy soldier head capsule (Figs 29–30), and by the worker enteric valve bearing very many small, spotlike spines (Fig. 32).

Imago. Unknown

Soldier (Figs. 29–30). Head capsule elongated, widest at the middle, rounded at corner, covered by 20 to 30 medium size setae. Frons flat, without hump. Fontanelle small, dotlike. Labrum short, with 4 setae at the apex. Postmentum narrow and elongated, with widest part 2.5 times wider than the narrowest part. Tip of right mandible pointed. Antennae 14-segmented. Thorax and abdomen fairly hairy. Measurements as in Table 12.

Worker (Figs 31, 32). Enteric valve well developed but not heavily armed, covered by many small spotlike spines. Measurements as in Table 18.

Distribution (Fig. 67). Samples included in this group were found mostly in hill forest in northern New Guinea and in the Highlands.



FIGURES 29–32. *Pericapritermes* cf. *schultzei* (sample from colony #PNGT1231, Bulolo): 29, soldier head, dorsal; 30, soldier head, lateral; 31 worker mandibles; 32, enteric valve. Scale bars: 29, 30, 1mm.

TABLE 12. Measurements (mm) of 23 soldiers from 7 colonies of *Pericapritermes* cf. *schultzei*.

	Non-type	Type (Holmgren 1911)
Head length to anterolateral corner of the genae	2.34–3.33	2.36
Head depth with postmentum	1.17–1.58	–
Head max width	1.42–1.89	1.48
Head width at anterolateral corner of the genae	1.14–1.48	–
Right mandible length	1.75–2.17	–
Left mandible length	1.77–2.21	–
Postmentum max width	0.41–0.59	–
Postmentum min width	0.17–0.23	–
Pronotum width	0.60–1.02	0.91

***Pericapritermes parvus* Bourguignon & Roisin, sp. nov.**
(Figs 33–36, 55–56, 67)

Holotype: INDONESIA. *Irian Jaya*. Authors' collection reference #IRJT165: soldier, Pusppenssat Irja (50 km from Nabire on Ilaga road): 26.xi.1995, YR. In the collection of the MBBJ.

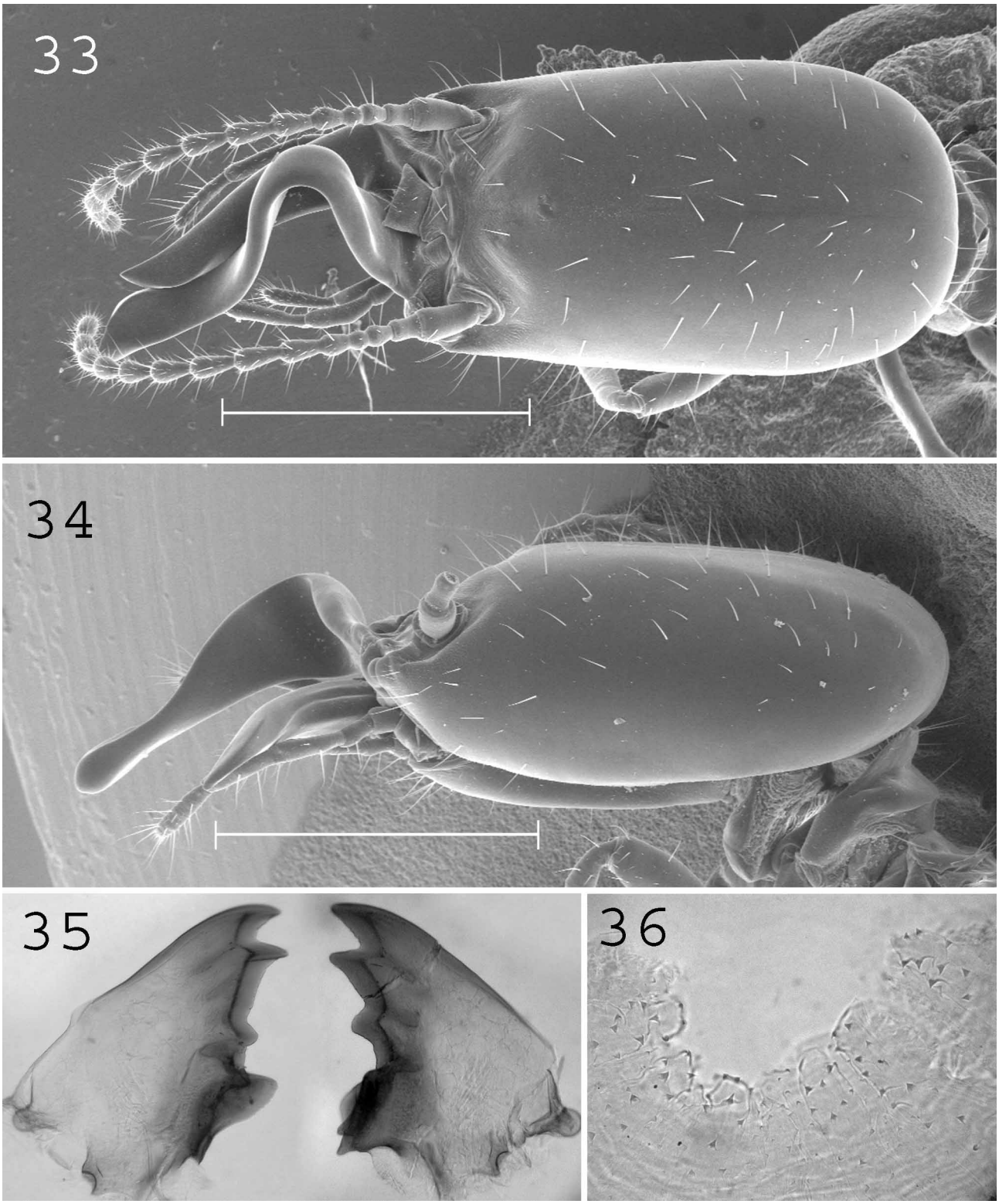
Paratypes: INDONESIA. *Irian Jaya*. Authors' collection reference #IRJT165 (same colony as holotype): alates, soldiers and workers. In the collections of the MBBJ and IRSN. **PAPUA NEW GUINEA. ANIC.** Enga. #10–11020: Baiyer River (alt. 1200m): 24.i.1963, JHB.

Imago (Figs 55–56). Entire body densely hairy. Head capsule covered by many short setae and few large setae. Eyes very large. Ocelli very large, close to the eyes but not touching them. Pronotum densely hairy, wider anteriorly than posteriorly. Antennae 15-segmented. Measurements as in Table 13.

TABLE 13. Measurements (mm) of 3 male and 1 female imagoes from 1 colony of *Pericapritermes parvus* **sp. nov.**

	Male	Female
Length with wings	10.95–11.79	11.41
Length without wings	5.67–6.42	6.03
Head length to apex of the labrum	1.25–1.37	1.30
Head length to clypeo-frontal suture	0.68–0.74	0.75
Head width with eyes	1.12–1.20	1.12
Eye maximum diameter	0.37–0.38	0.42
Ocellus maximum length	0.17–0.19	0.17
Pronotum length	0.49–0.53	0.54
Pronotum width	0.90–0.95	0.89
Forewing length	8.66–9.46	9.48
Forewing width	2.28–2.51	2.39

Soldier (Figs 33–34). Small size (Table 14). Head capsule elongated, rounded posteriorly, slightly narrower anteriorly than posteriorly, covered by about 60 long setae. Head rising vertically above the fontanelle, as is *Discupiditermes*. Labrum short, cover by some setae. Postmentum deep, narrow and elongated, with widest part less or more 2.5 times larger than the narrowest part. Antennae 14-segmented. Thorax and abdomen fairly hairy.



FIGURES 33–36. *Pericapritermes parvus* **sp. nov.** (type colony): 33, soldier head, dorsal; 34, soldier head, lateral; 35, worker mandibles; 36, enteric valve. Scale bars: 33, 34, 1mm.

Worker (Figs 35, 36). Enteric valve with cushions each covered by about 10 small triangular spines. Measurements as in Table 18.

Diagnosis. This species can be easily distinguished from other New Guinean species by its very small size and by the frons of the soldier showing a slight hump.

Distribution (Fig. 67). Known from 2 samples, one (type colony) from hill forest in Western Irian Jaya, one from the Baiyer River valley in the Papua New Guinea highlands.

Etymology. The specific epithet refers to little size of this species.

TABLE 14. Measurements (mm) of 7 soldiers from the type colony and 1 from colony ANIC #10–11020 of *Pericapritermes parvus* **sp. nov.**

	Type colony	ANIC #10–11020
Head length to anterolateral corner of the genae	1.69–1.84	1.77
Head depth with postmentum	0.80–0.87	0.90
Head max width	0.95–1.06	1.04
Head width at anterolateral corner of the genae	0.75–0.89	0.83
Right mandible length	1.13–1.30	1.30
Left mandible length	1.11–1.24	1.31
Postmentum max width	0.27–0.35	0.33
Postmentum min width	0.09–0.14	0.13
Pronotum width	0.46–0.52	0.53

***Pericapritermes pilosus* Bourguignon & Roisin, sp. nov.**
(Figs 37–40, 67)

Holotype: PAPUA NEW GUINEA. *Southern Highlands*. Authors' collection reference #PNGT1319: soldier, Pimaga, 19.x.1988, YR. In the collection of the IRSN. **Paratypes: PAPUA NEW GUINEA.** *Southern Highlands*. Authors' collection reference #PNGT1319 (same colony as holotype): soldiers and workers.

Diagnosis. This species is easily distinguished from other ones by the large size and the densely hairy head of soldiers.

Imago. unknown.

Soldier (Figs 37–38). Soldier of large size (Table 15). Head densely hairy, covered with many short setae, elongated, slightly rounded posteriorly, more than 2 times longer than wide. Fron flat. Labrum short, with few setae. Right mandible large, with tip not pointed. Postmentum narrow and elongated, with widest part 2.5 times larger than the narrowest part. Antennae 14-segmented. Entire body densely hairy.

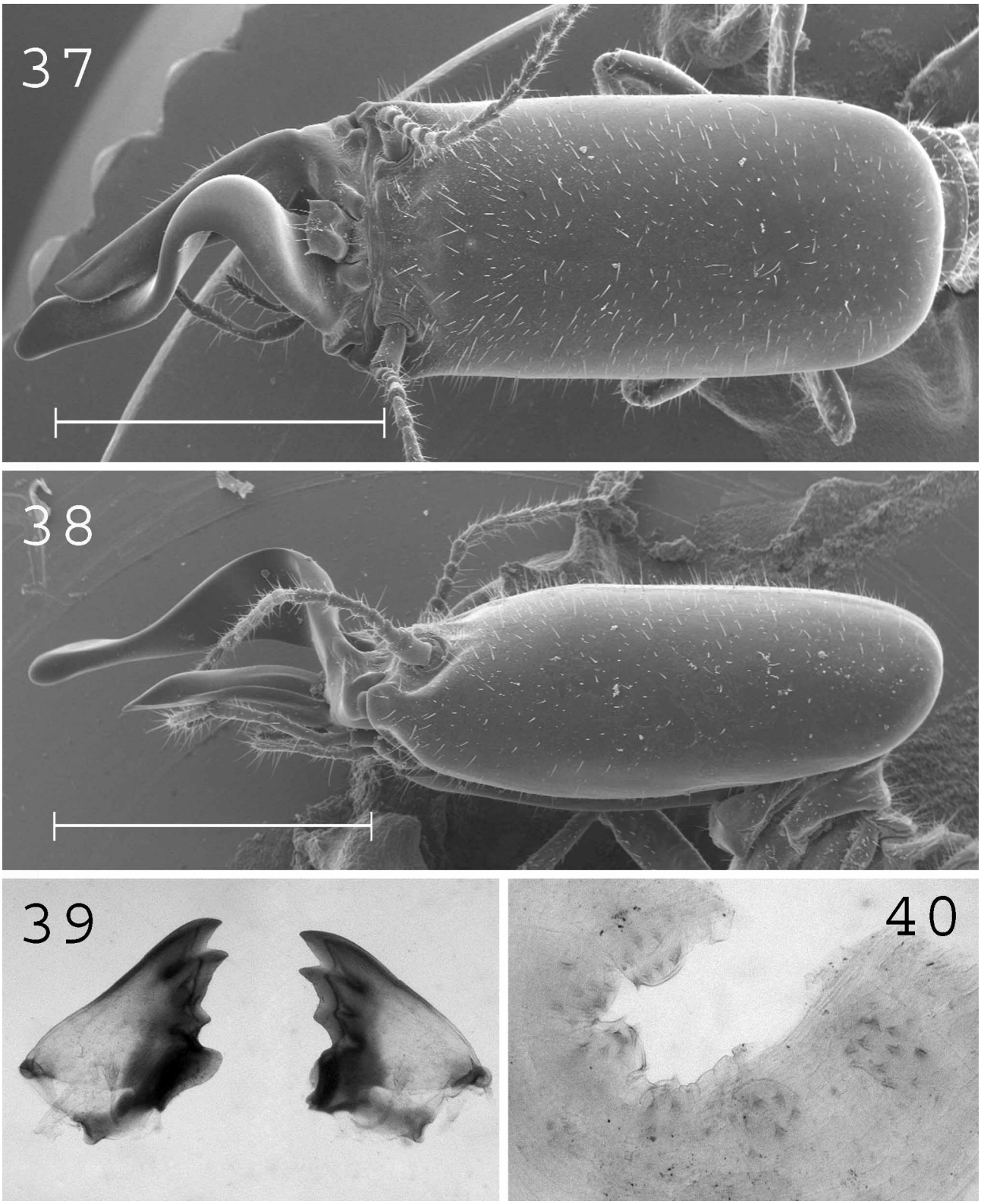
TABLE 15. Measurements (mm) of 6 soldiers from the type colony of *Pericapritermes pilosus* **sp. nov.**

Head length to anterolateral corner of the genae	3.72–3.81
Head depth with postmentum	1.51–1.57
Head max width	1.73–1.80
Head width at anterolateral corner of the genae	1.58–1.67
Right mandible length	2.08–2.21
Left mandible length	2.30–2.45
Postmentum max width	0.48–0.51
Postmentum min width	0.17–0.20
Pronotum width	1.01–1.04

Worker (Figs 39, 40). Enteric valve well developed, with cushions each covered by about 10 well sclerotized triangular spines. Measurements as in Table 18.

Distribution (Fig. 67). Only known from Pimaga, Southern Highlands.

Etymology. The specific epithet refers to the densely hairy head of the soldier.



FIGURES 37–40. *Pericapritermes pilosus* **sp. nov.** (type colony): 37, soldier head, dorsal; 38, soldier head, lateral; 39, worker mandibles; 40, enteric valve. Scale bars: 37, 38, 2mm.

***Pericapritermes papuanus* Bourguignon & Roisin, sp. nov.**
(Figs 41–44, 57–58, 64, 67)

Holotype: PAPUA NEW GUINEA. *Fly.* Authors' collection reference #PNGT1500: soldier, Wipim, 31.iii.1989, YR & ML. In the collection of the IRSN. **Paratypes: PAPUA NEW GUINEA.** *Fly.* Authors' collection reference #PNGT1500 (same colony as holotype): alates, soldiers and workers.

Diagnosis. This species is more similar to *Pericapritermes* cf *schultzei*. It can be distinguished from it by the head of the soldier, longer and more densely hairy, and by the enteric valve of the worker, with a stronger armature.

Imago (Figs 57–58). Head covered with many small setae and about 20 large setae. Large eyes. Ocelli large and close to eyes without touching them. Antennae 15-segmented. Pronotum and entire body covered with numerous setae. Measurements as in Table 16.

Soldier (Figs 41–42). Medium to large size (Table 17). Head twice longer than wide, moderately hairy, covered by setae of medium size. Frons flat. Labrum very short, with few setae. Right mandible large, with unpointed tip. Postmentum narrow and elongated, with widest part 2.5 times larger than the narrowest part. Antennae 14-segmented. Entire body moderately hairy.

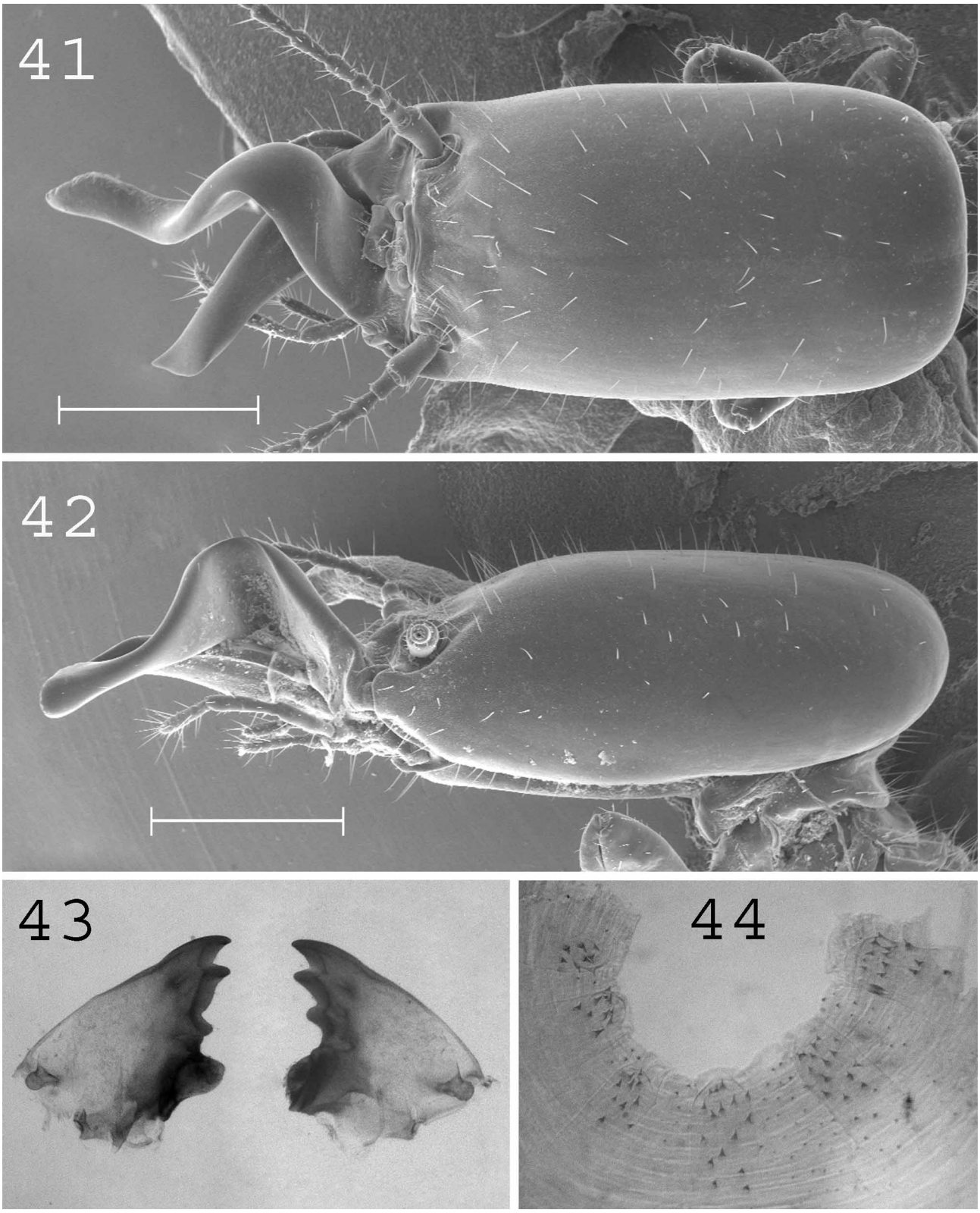
Worker (Figs 43, 44). Enteric valve well developed, with cushions each covered by about 15 well sclerotized triangular spines. Measurements as in Table 18.

TABLE 16. Measurements (mm) of 5 male and 1 female imagoes from the type colony of *Pericapritermes papuanus* **sp. nov.**

	Male	Female
Length with wings	12.3–13.3	13.5
Length without wings	6.06–6.85	6.88
Head length to apex of the labrum	1.36–1.53	1.43
Head length to clypeo-frontal suture	0.76–0.88	0.81
Head width with eyes	1.26–1.37	1.30
Eye maximum diameter	0.31–0.41	0.35
Ocellus maximum length	0.16–0.22	0.19
Pronotum length	0.55–0.63	0.54
Pronotum width	0.99–1.15	1.04
Forewing length	11.0–12.1	11.8
Forewing width	2.80–3.02	3.00

TABLE 17. Measurements (mm) of 5 soldiers from the type colony of *Pericapritermes papuanus* **sp. nov.**

Head length to anterolateral corner of the genae	3.04–3.28
Head depth with postmentum	1.34–1.44
Head max width	1.59–1.68
Head width at anterolateral corner of the genae	1.34–1.44
Right mandible length	1.79–1.92
Left mandible length	2.03–2.10
Postmentum max width	0.50–055
Postmentum min width	0.18–0.23
Pronotum width	0.83–0.90



FIGURES 41–44. *Pericapritermes papuanus* **sp. nov.** (type colony): 41, soldier head, dorsal; 42, soldier head, lateral; 43, worker mandibles; 44, enteric valve. Scale bars: 41, 42, 1mm.

Distribution (Fig. 67). Only known from Wipim (Fly) in the southern Papuan savannas.

Etymology. The specific epithet refers to the species' geographic origin (Papua New Guinea).

TABLE 18. Measurements (mm) of workers.

	Number of individuals measured	Number of colonies measured	Head width
Protocapritermes odontomachus	30	10	0.791–1.019
Ephelotermes paleatus	20	2	0.632–0.702
Ephelotermes cheeli	37	5	0.807–0.928
Lophotermes aduncus	20	2	0.812–0.890
Lophotermes brevicephalus	10	1	0.802–0.845
Macrognathotermes errator	10	1	0.870–0.953
Pericapritermes cf. *schultzei*	27	3	1.034–1.287
Pericapritermes parvus **sp. nov.**	10	1	0.880–0.943
Pericapritermes pilosus **sp. nov.**	10	1	1.209–1.239
Pericapritermes papuanus **sp. nov.**	10	1	1.077–1.181

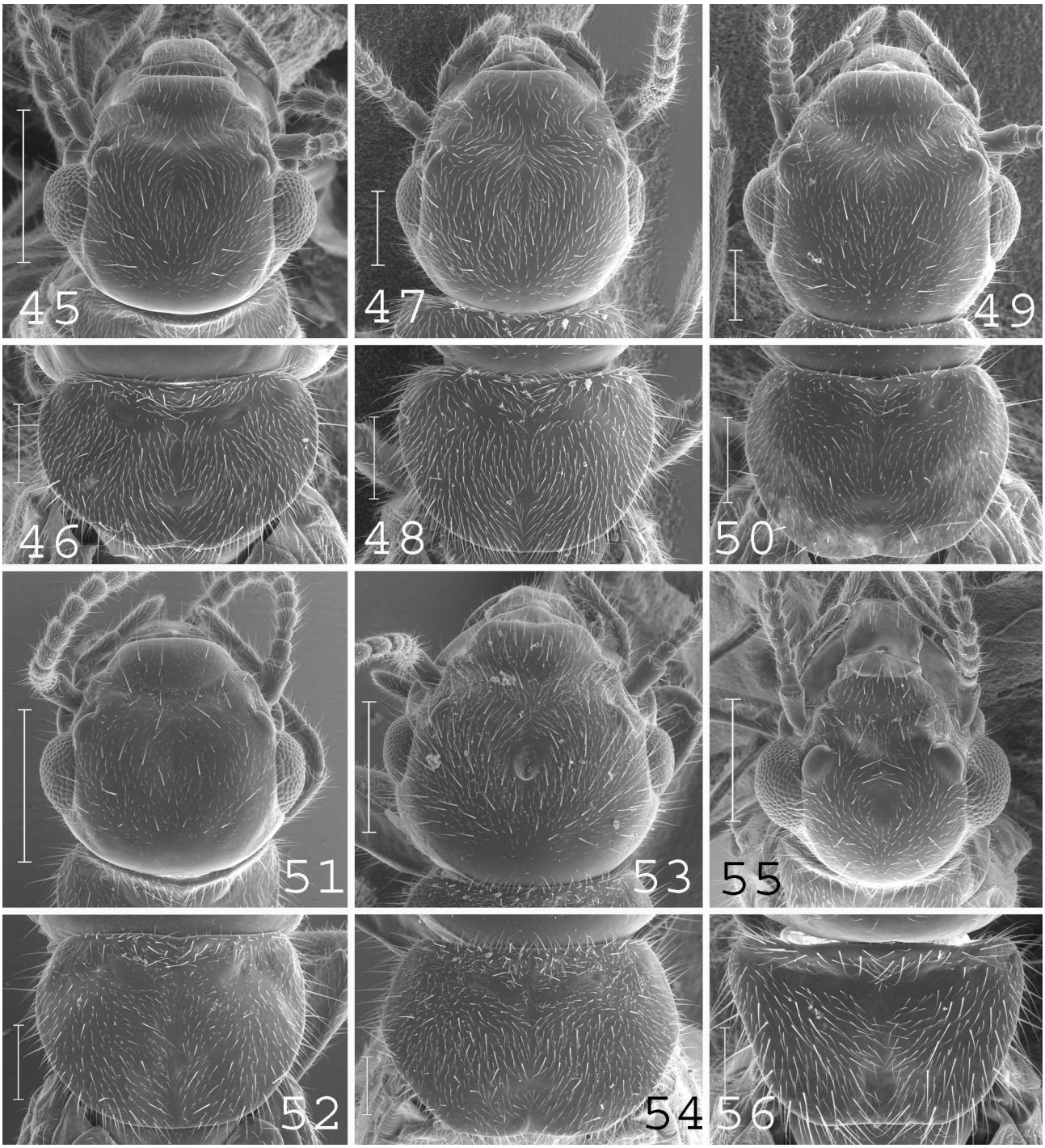
Key to New Guinean *Termes–Capritermes* species, based on the soldier

1. Mandibles strongly asymmetrical: left one almost straight, right one flattened and strongly curved (Fig. 33). No frontal projection ..... *Pericapritermes* 2
- Both mandibles elongated, almost symmetrical (Fig. 9) 5
2. Large species (head length > 3.5mm, Table 15), head with hundreds of small setae (Figs 37–38) ..... *P. pilosus*
- Smaller species (head length < 3.5mm), head with about 50 setae (Figs 41–42) or less 3
3. Small species (head length < 2mm, Table 14), frons with a small hump (Figs 33–34)..... *P. parvus*
   Medium sized species (head lengthr > 2mm, Tables 12, 15)..... 4
4. Head elongated, rectangular, covered by about 50 setae (Figs 41–42) ..... *P. papuanus*
- Head slightly elongated, covered by about 20 setae (Figs 29–30) ..... *P.* cf. *schultzei*
5. Lateral tubercles well developed (Figs 17, 21, 25)..... 6
- Lateral tubercles absent or reduced (Figs 5, 9, 13)..... 8
6. Frontal projection with many setae (Fig. 26); lateral tubercles low (Fig. 25) . *Macrognathotermes errator*
- Frontal projection with sparse setae (Figs 18, 22) lateral tubercles very prominent, horn-like (Figs 17, 21) ..... *Lophotermes* 7
7. Postmentum strongly projected downward (Fig. 22) ..... *L. brevicephalus*
- Postmentum not or slightly projected downward (Fig. 18) ..... *L. aduncus*
8. Frontal projection short, in profile reaching above antennal sockets (Fig. 6) ..... *Protocapritermes odontomachus*
- Frontal projection well developed, protruding in front of antennal sockets (Figs 10, 14) ...*Ephelotermes* 9
9. Soldier very small (head width < 0.75mm, left mandible length < 1.4mm; Table 4), postmentum projected downward ..... *E. paleatus*
- Soldier of medium size (head width > 0.8mm, left mandible length < 1.7mm; Table 6), postmentum without projection ..... *E. cheeli*

Discussion

Before this study, only four species of the *Termes–Capritermes* group were reportedly present in New Guinea (Hill 1942, Barrett 1965, Miller 1991). This low number contrasted with the rich faunas of neighbouring

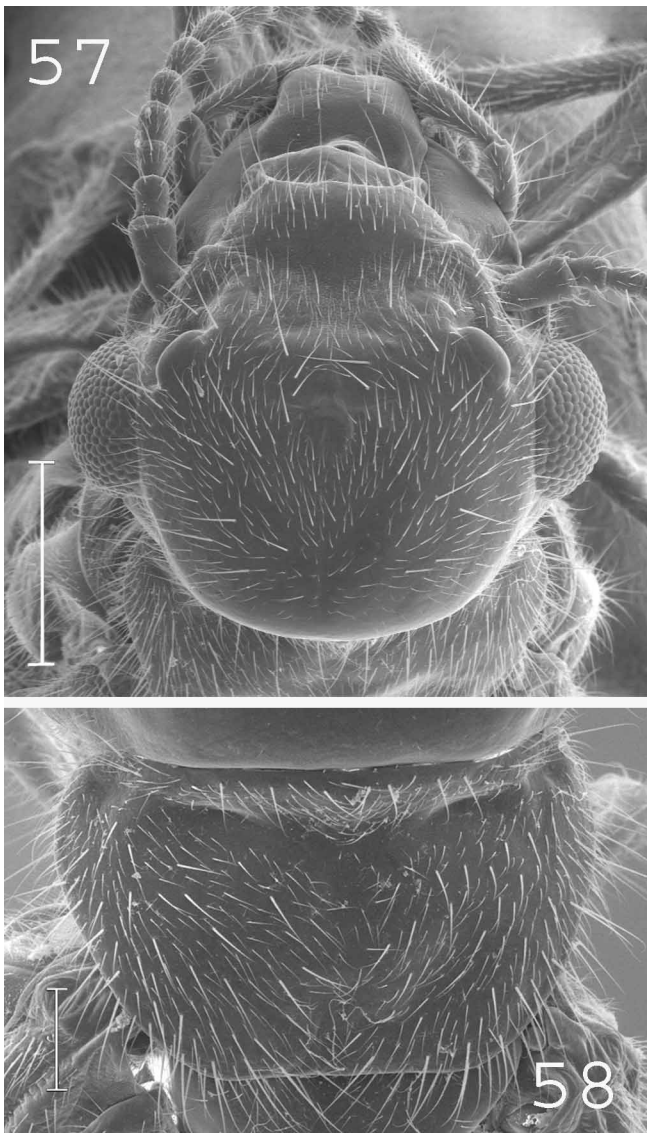
areas, such as Australia (53 species: Miller 1991), Malaysia (30 species: Tho 1992), or Sabah (19 species: Thapa 1982). The presence of additional species in New Guinea was therefore expected.



FIGURES 45–56. Alate. *Protocapritermes odontomachus*: 45, head; 46, pronotum. *Ephelotermes paleatus*: 47, head; 48, pronotum. *Ephelotermes cheeli*: 49, head; 50, pronotum. *Lophotermes brevicephalus*: 51, head; 52, pronotum. *Macrognathotermes errator*: 53, head; 54, pronotum. *Pericapritermes parvus* **sp. nov.**: 55, head; 56, pronotum. Scale bars: 46, 47, 48, 49, 50, 52, 54, 56, 0.2mm; 45, 51, 53, 55, 0.5mm.

Among the 10 species of the *Termes–Capritermes* group recorded in New Guinea, four have soldiers with asymmetrical snapping mandibles and belong to *Pericapritermes*. They are distributed throughout New Guinea, including in the Highlands. Some uncertainty remains as to the identification and distribution of *P. schultzei*. The series herein grouped within *P.* cf. *schultzei* may ultimately turn out to be a complex of species,

which evolved from populations isolated by mountain ridges. The other three species described herein are nonetheless well distinct from *P.* cf. *schultzei*. The small new species mentioned by Barrett (1965) is described as *P. parvus*, and the large species from southern Papua as *P. papuanus*. Finally, the Pimaga area yielded the most distinctive of all species, *P. pilosus*. With *Diwaitermes foi* and *Microcerotermes luluai* (Roisin and Pasteels 1996, 2000) this is the third new species of termite described from this area, which appears particularly rich in endemic taxa.



FIGURES 57–58. Alate. *Pericapritermes papuanus* **sp. nov.**: 57, head; 58, pronotum. Scale bars: 57, 0.5mm; 58, 0.2mm.

The remaining six species reported here have soldiers with near-symmetrical snapping mandibles. The most widespread species, also reported from the Solomon Islands (Harris and Brown 1958), was formerly known as *Termes odontomachus*. However, its low frontal projection and gut anatomy clearly distinguishes it from *Termes* species *sensu stricto*. These features led us to reassign it to the Australian genus *Protocapritermes*. The last five species belong to the genera *Ephelotermes*, *Lophotermes* and *Macrognathotermes*. These genera were all described by Miller (1991) from Australia. Recent analyses including *Ephelotermes* and *Macrognathotermes*, together with other Australian genera (*Cristatitermes*, *Paracapritermes* and *Xylochomitermes*), revealed that these genera are all part of a clade nested within the pantropical *Termes* genus (Inward *et al.* 2007), which suggests the occurrence of an adaptive radiation from primitive *Termes*-like colonizers of

Australian–New Guinean savannas. This also pinpoints the need for an extensive revision of *Termes* worldwide.

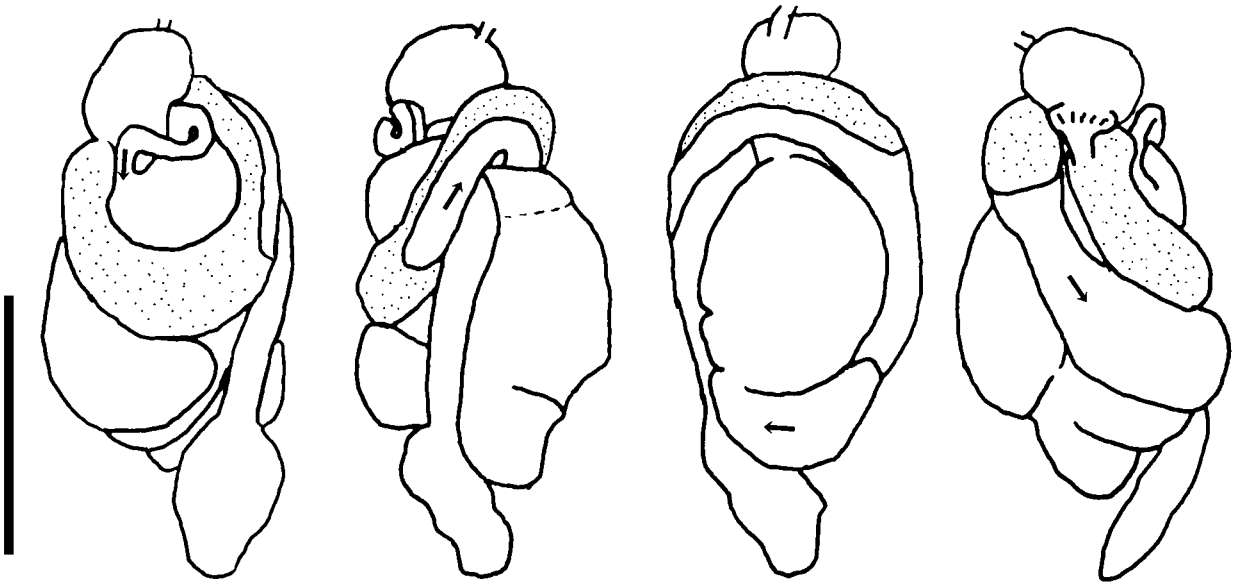


FIGURE 59. Worker digestive tract of *Protocapritermes odontomachus.* From left to right: dorsal view, right view, ventral view and left view. Mesenteron stippled. Arrows indicate the direction of transit.

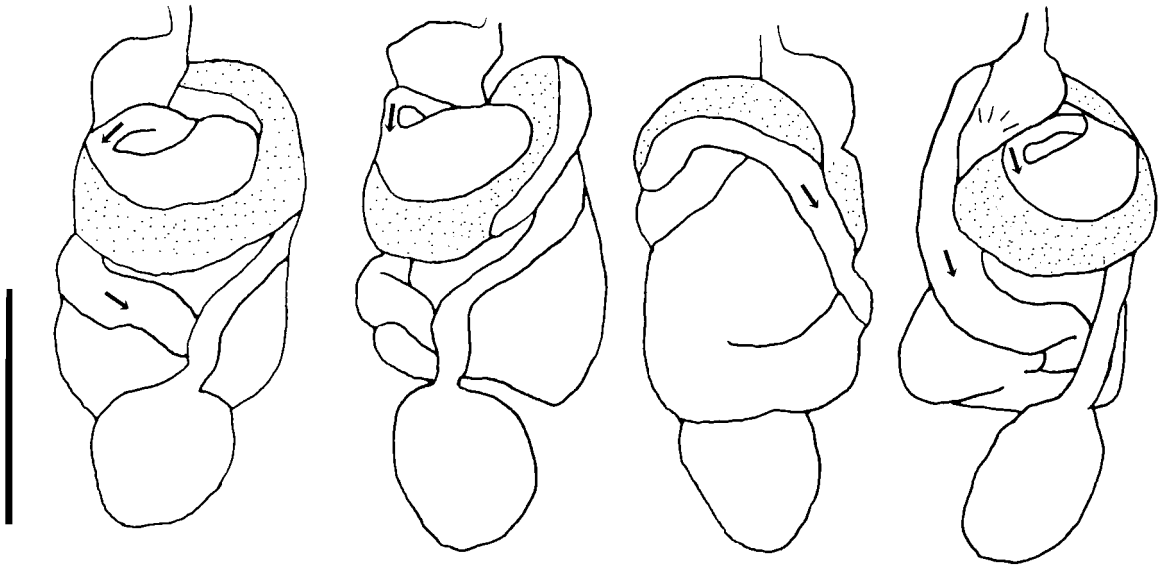


FIGURE 60. Worker digestive tract of *Protocapritermes krisiformis.* From left to right: dorsal view, right view, ventral view and left view. Mesenteron stippled. Arrows indicate the direction of transit.

The New Guinean fauna comprises species with Oriental and Australian affinities. Whereas New Guinean vertebrates generally have more affinities with Australian than with Oriental faunas (Pratt 1982, Ziegler 1982), an opposite trend is observed for invertebrates (Gressitt 1982). However, savannas of northern Australia and southern Papua New Guinea often harbor similar faunas (Gressitt 1982). This situation is illustrated by the five New Guinean species of *Lophotermes*, *Macrognathotermes* and *Ephelotermes*, which are also present in northern Australia (Miller 1991). Similarities between New Guinean and northern Australian savannas are also apparent from the distribution of other termitid genera (Roisin 1990, Roisin and Pasteels 1996, 2000).

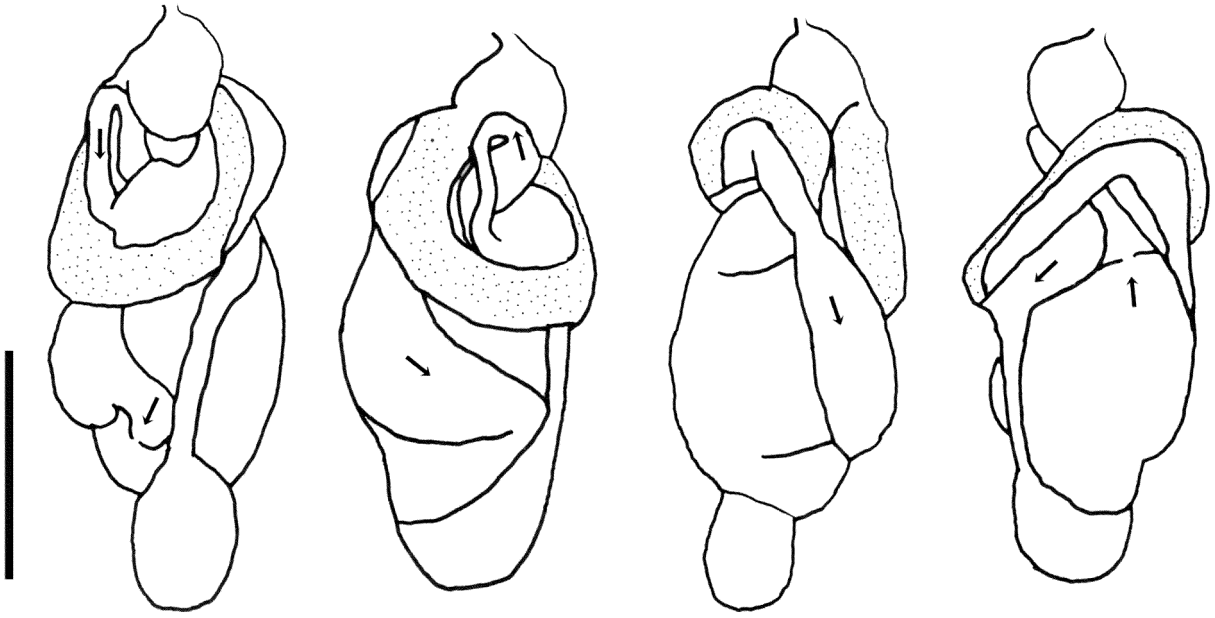


FIGURE 61. Worker digestive tract of *Ephelotermes cheeli.* From left to right: dorsal view, right view, ventral view and left view. Mesenteron stippled. Arrows indicate the direction of transit.

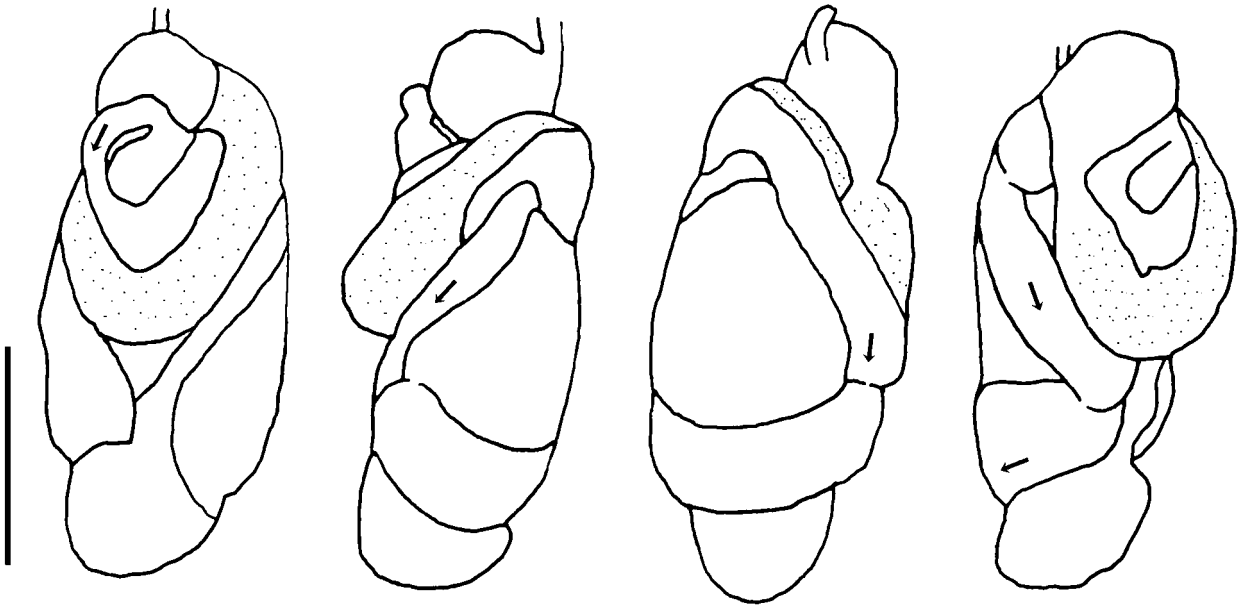


FIGURE 62. Worker digestive tract of *Lophotermes brevicephalus.* From left to right: dorsal view, right view, ventral view and left view. Mesenteron stippled. Arrows indicate the direction of transit.

Added to our previous revisions of *Amitermes* (3 species: Roisin 1990), the Nasutitermitinae (22 species in 6 genera: Roisin and Pasteels 1996), and *Microcerotermes* (10 species: Roisin and Pasteels 2000), the present monograph brings the number of New Guinea Termitidae taxa to 45 species in 13 genera. We expect these figures to reflect the overall richness of the island, although it is inevitable that some rare or locally distributed taxa escaped detection. Because our collecting effort in southern Papuan savannas was limited, additional Australian taxa are likely to be present there. As to the western half of New Guinea (Irian Jaya), it was also weakly explored and is therefore likely to conceal further taxa of Oriental origin, in the vein of the remarkable rhinotermitid genus *Termitogeton*, previously unknown east of Borneo, which was recently found

there (Parmentier and Roisin 2003). Yet, globally, the New Guinean Termitidae fauna appears poorer than that of neighboring regions, such as Peninsular Malaysia (27 genera: Tho 1992), Sabah (23 genera: Thapa 1982) or Australia (23 genera: Watson *et al.* 1998). This is understandable considering (1) the small area of New Guinean savannas compared to the Australian continent to which they were long connected by land, (2) and the relatively recent formation of northern New Guinea from accreted terranes, isolated from continental southeast Asia by sea water gaps (Hall 1998).

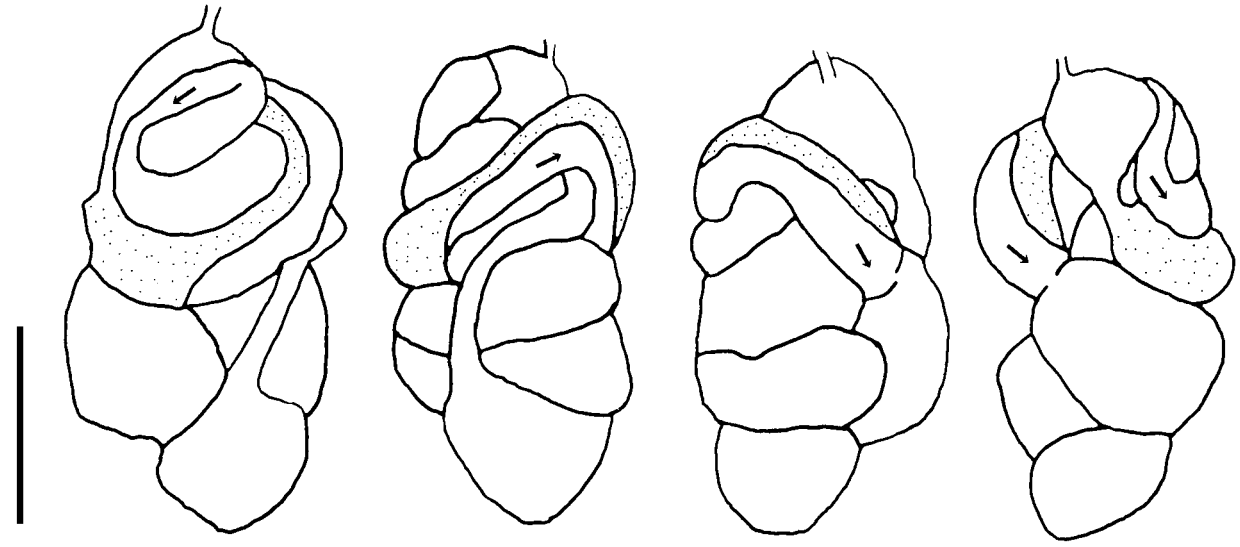


FIGURE 63. Worker digestive tract of *Macrognathotermes errator.* From left to right: dorsal view, right view, ventral view and left view. Mesenteron stippled. Arrows indicate the direction of transit.

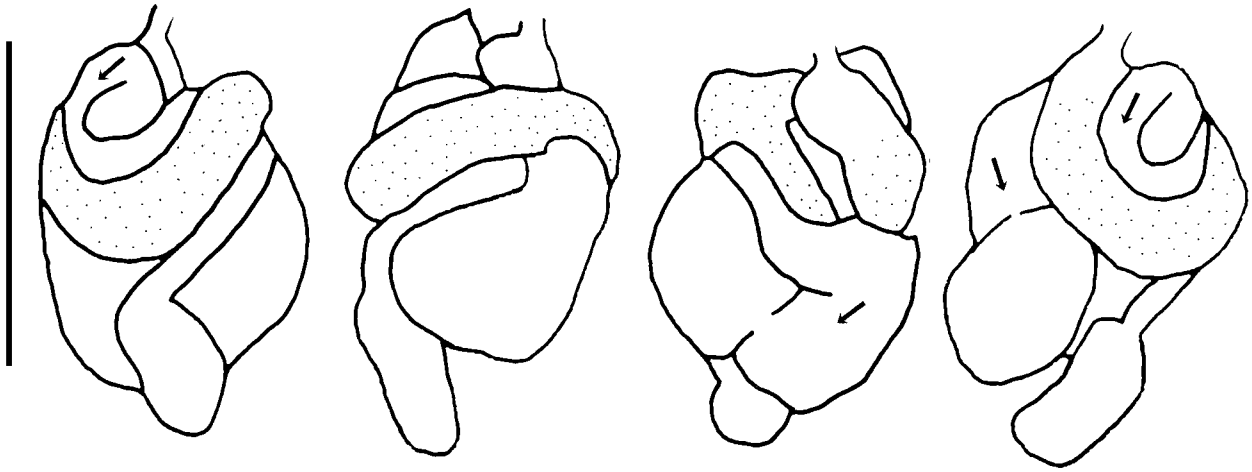


FIGURE 64. Worker digestive tract of *Pericapritermes papuanus* **sp. nov.** From left to right: dorsal view, right view, ventral view and left view. Mesenteron stippled. Arrows indicate the direction of transit.

Acknowledgments

We thank J. Křeček and J. Šobotník for their help and advice on the manuscript. J.M. Pasteels contributed to several collecting campaigns. J. Cillis provided technical assistance with SEM operation, and E. Terwinghe with optical microscopy. Financial support was provided by the Fund for Scientific Research (F.R.S.–FNRS), Belgium, through several grants and a FRIA predoctoral fellowship to T. Bourguignon.

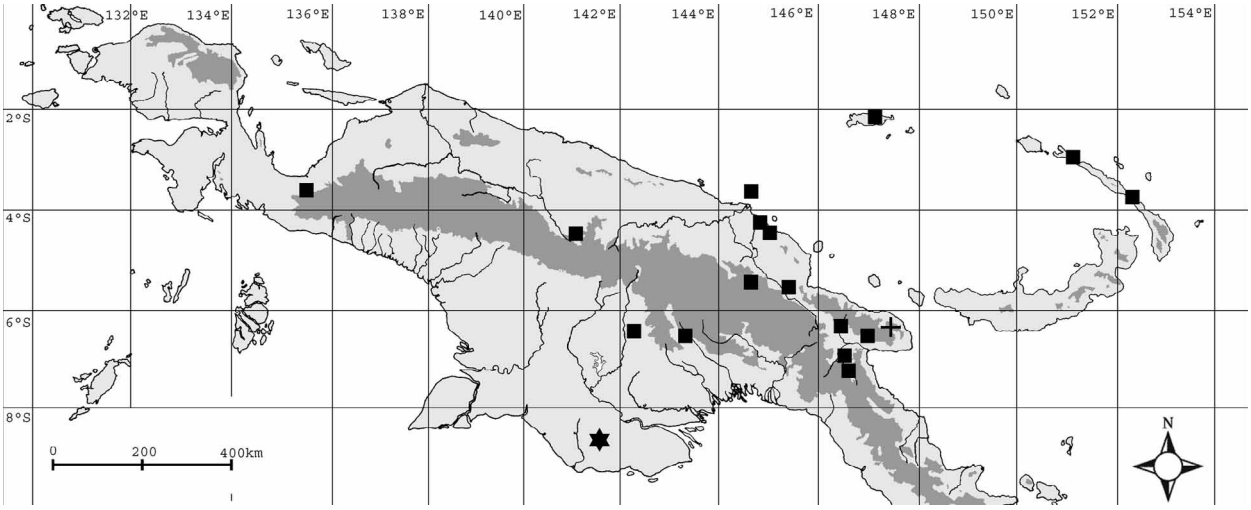


FIGURE 65. Known distribution in New Guinea and adjacent islands of: ■, *Protocapritermes odontomachus*; ★, *Lophotermes aduncus*, *Lophotermes brevicephalus*, *Macrognathotermes errator*. ✚, type locality of *Protocapritermes odontomachus*.

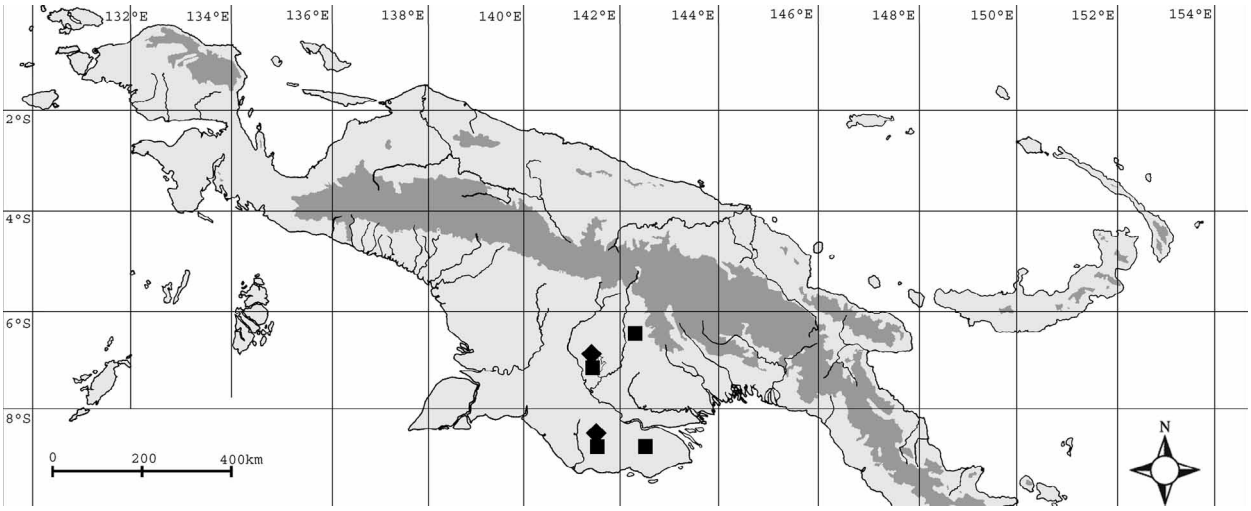


FIGURE 66. Known distribution in New Guinea of: ◆, *Ephelotermes paleatus*; ■, *Ephelotermes cheeli*.

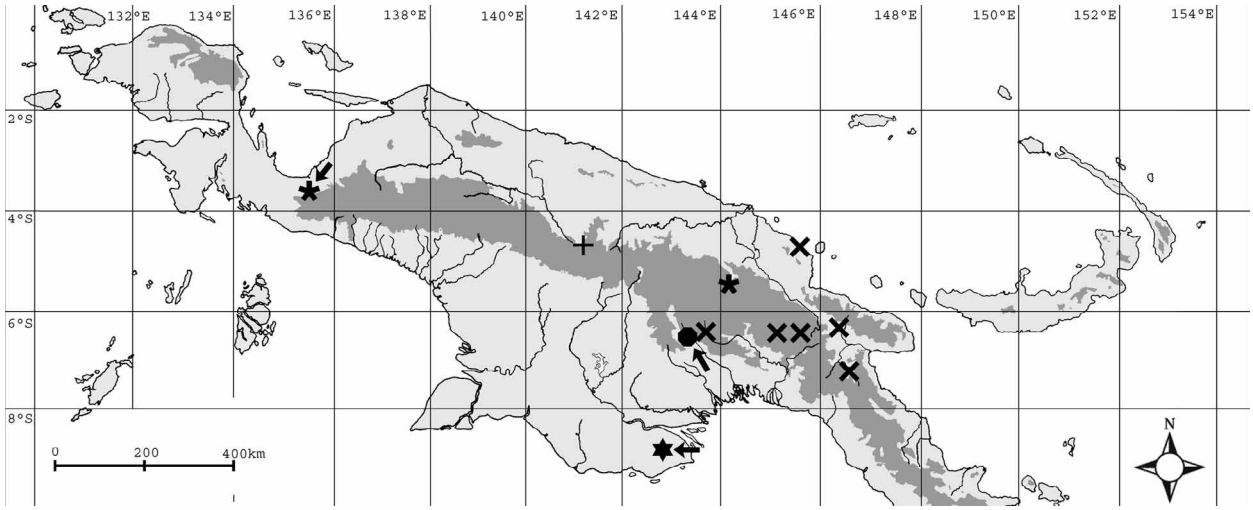


FIGURE 67. Known distribution of ✕, *Pericapritermes* cf. *schultzei*; ✶, *Pericapritermes parvus* **sp. nov.**; ●, *Pericapritermes pilosus* **sp. nov.**; ★, *Pericapritermes papuanus* **sp. nov.** Arrows indicate type localities. ✚, type locality of *P. schultzei*.

Bibliography

Barrett, J.H. (1965) The occurrence of termites in the New Guinea highlands. *Papua and New Guinea Agricultural Journal*, 17, 95–98.

Desneux, J. (1905) Isoptera of New Guinea collected by L. Biró. *Annales musei nationalis Hungarici*, 3, 367–377.

Eggleton, P. (2000) Global patterns of termite diversity. *In* T. Abe, D.E. Bignell and M. Higashi (Eds.), *Termites: Evolution, Sociality, Symbioses, Ecology*, Kluwer Academic Publishers, Dordrecht, pp. 25–51.

Emerson, A.E. (1960) New genera of termites related to *Subulitermes* from the Oriental, Malagasy, and Australian regions (Isoptera, Termitidae, Nasutitermitinae). *American Museum Novitates*, 1986, 1–28.

Froggatt, W.W. (1898) Australian Termitidae. Part III. *Proceedings of the Linnean Society of New South Wales*, 22, 721–758.

Gressitt, J.L. (1982) Zoogeographical summary. *In* Gressitt, J.L. (Ed.), *Biogeography and Ecology of New Guinea*, Junk, The Hague, pp. 897–918.

Hall, R. (1998) The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. *In* R. Hall, J.D. Holloway (Eds.), *Biogeography and Geological Evolution of SE Asia*, Backhuys, Leiden, pp. 99–131.

Hare, L. (1937) Termite phylogeny as evidenced by soldier mandible development. *Annals of the Entomological Society of America*, 37, 459–486.

Harris, W.V. & Brown, E.S. (1958) The termites of the Solomon Islands. *Bulletin of Entomological Research*, 49, 737–750.

Hill, G.F. (1942) *Termites (Isoptera) from the Australian Region.* C.S.I.R., Melbourne, 479 pp., 24 pl.

Holmgren, N. (1911) Neu-Guinea-Termiten. *Mitteilungen aus dem Zoologischen Museum in Berlin*, 5, 451–465.

Holmgren, N. (1912) Termitenstudien. *Kungliga Svenska Vetenskapsakademiens Händlingar*, 48 (4), 1–166.

Inward, D.J.G., Vogler, A.P., Eggleton, P. (2007) A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. *Molecular Phylogenetics and Evolution*, 44, 953–967.

Krishna, K. (1968) Phylogeny and generic reclassification of the *Capritermes* complex (Isoptera, Termitidae, Termitinae). *Bulletin of the American Museum of Natural History*, 138, 261–323.

Miller, L.R. (1991) A revision of the *Termes–Capritermes* branch of the Termitinae in Australia (Isoptera: Rhinotermitidae). *Invertebrate Taxonomy*, 4, 1147–1282.

Miller, L.R. (1994) Polyphyletic origins of the snapping mandibles and asymmetry, and the biogeography of some Termitinae (Isoptera: Termitidae). *In* A. Lenoir, G. Arnold and M. Lepage (Eds.), *Les Insectes Sociaux (12th Congress IUSSI)*, Paris: Université Paris Nord, p. 52.

Miller, L.R. (1997) *Systematics of the Australian Nasutitermitinae With Reference to Evolution Within the Termitidae (Isoptera)*. Ph.D. Dissertation, Australian National University, Canberra, A.C.T., 170 pp.

Mjöberg, E. (1920) Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia 1910–1913. 19. Isoptera. *Arkiv för Zoologi*, 12, 1–134.

Noirot, C. (1995) The gut of termites (Isoptera). Comparative anatomy, systematics, phylogeny. I. Lower termites. *Annales de la Société Entomologique de France (Nouvelle Série)*, 31, 197–226.

Noirot, C. (2002) The gut of termites (Isoptera). Comparative anatomy, systematics, phylogeny. II. Higher termites (Termitidae). *Annales de la Société Entomologique de France (Nouvelle Série)*, 37, 431–471.

Parmentier, D. & Roisin, Y. (2003) Caste morphology and development in *Termitogeton* nr. *planus* (Insecta, Isoptera, Rhinotermitidae). *Journal of Morphology*, 255, 69–79.

Pratt, T.K. (1982) Biogeography of birds in New Guinea. *In* Gressitt, J.L. (Ed.), *Biogeography and Ecology of New Guinea*, Junk, The Hague, pp. 815–836.

Roisin, Y. (1990) The termite genus *Amitermes* Silvestri in Papua New Guinea. *Indo-Malayan Zoology*, 6, 185–194.

Roisin, Y. & Pasteels, J.M. (1996) The nasute termites (Isoptera: Nasutitermitinae) of Papua New Guinea. *Invertebrate Taxonomy*, 10, 507–616.

Roisin, Y. & Pasteels, J.M. (2000) The genus *Microcerotermes* (Isoptera: Termitidae) in New Guinea and the Solomon Islands. *Invertebrate Taxonomy*, 14, 137–174.

Roonwal, M.L. (1970) Measurement of termites (Isoptera) for taxonomic purposes. *Journal of the Zoological Society of India*, 21, 9–66.

Schultze Jena, L. (1914) *Forschungen in Innern der Insel Neuguinea (Bericht des Führers über die wissenschaftlichen Ergebnisse der deutschen Grenzexpedition in das westliche Kaiser-Wilhelmsland 1910).* E.S. Mittler & Sohn, Berlin, 100 pp., 5 maps, 5 panoramas, 59 pl.

Silvestri, F. (1914) Contribuzione alla conoscenza dei Termitidae e termitofili dell' Africa occidentale. *Bollettino del Laboratorio di Zoologia Generale e Agraria, Portici*, 9, 1–146.

Snyder, T.E. (1949) Catalog of the termites (Isoptera) of the world. *Smithsonian Miscellaneous Collections*, 112, 1–490.

Tayasu, I., Inoue, T., Miller, L.R., Sugimoto, A., Takeichi, S. & Abe, T. (1998) Confirmation of soil-feeding termites (Isoptera; Termitidae; Termitinae) in Australia using stable isotope ratios. *Functional Ecology*, 12, 536–542.

Thapa, R.S. (1982) Termites of Sabah (East Malaysia). *Sabah Forest Record*, 12, 1–374.
Tho, Y.P. (1992) *Termites of Peninsular Malaysia*. Malayan Forest Records No. 36. Forest Research Institute Malaysia, Kepong, Kuala Lumpur, 224 pp.
Watson, J.A.L.. & Abbey, H.M. (1993) *Atlas of Australian Termites*. CSIRO Division of Entomology, Canberra, 155 pp.
Watson, J.A.L., Miller, L.R. & Abbey, H.M. (1998) Isoptera. *In* Houston, W.W.K. & Wells, A. (Eds.) *Zoological Catalogue of Australia*. *Vol. 23. Archaeognatha, Zygentoma, Blattodea, Isoptera, Mantodea, Dermaptera, Phasmatodea, Embioptera, Zoraptera*, CSIRO Publishing, Melbourne, pp. 163–250, 397–399, 401–402, 427–437.
Ziegler, A.C. (1982) An ecological check-list of New Guinea Recent mammals. *In* Gressitt, J.L. (Ed.), *Biogeography and Ecology of New Guinea*, Junk, The Hague, pp. 863–894.

Appendix 1. Geographical coordinates of sampling localities

Asirangka	6°20'S, 145°56'E
Awar	4°09’S, 144°51’E
Baiyer River	5°31’S, 144°08’E
Blup Blup Island	3°31'S, 144°36'E
Bogia	4°16’S, 144°58’E
Boisa Island	4°00’S, 144°58’E
Braham Mission	5°45'S, 145°22'E
Bulolo	7°12’S, 146°39’E
Bunapae	4°12’S, 144°41’E
Guam River	4°32’S, 144°58’E
Hansa Point	4°11’S, 144°54’E
Jimi	5°32’S, 144°34’E
Kaiapit	6°16’S, 141°16’E
Kokun camp	4°19’S, 144°38’E
Kolonoboi	3°31’S, 152°19’E
Lae	6°44’S, 147°00’E
Laing Island	4°11’S, 144°52’E
Lake Murray	6°48’S, 141°26’E
Lemakot	2°50’S, 151°12’E
Manus Island	2°06’S, 147°10’E (approx.)
Mendi	6°09'S, 143°39'E
Morehead	8°30’S, 147°40’E
Mount Missim	7°13'S, 146°49'E
Namarodu	3°43'S, 152°30'E
Namura	6°19'S, 145°47'E
Nomad	6°50’S, 142°00’E
Oomsis	6°41’S, 146°48’E
Pimaga	6°30’S, 143°31’E
Potsdam	4°13’S, 144°56’E
Sattelberg	6°29'S, 147°47'E
Sepen 2	4°11’S, 144°48’E
Tari	6°16'S, 145°11'E
Yamu	4°34’S, 144°37’E
Yapsiei	4°38’S, 141°06’E
Yoro	4°28’S, 145°12’E
Wampit	6°36’S, 146°45’E
Wanuma	4°54'S, 145°19'E
Wau	7°35'S, 146°45'E
Wipim	8°47’S, 142°52’E