Zootaxa 1892: 35–52 (2008)
www.mapress.com/zootaxa/

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

The Afrotropical ponerine ant genus *Phrynoponera* Wheeler (Hymenoptera: Formicidae)

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Abstract

The Afrotropical ponerine ant genus *Phrynoponera* is revised and a worker-based key to species presented. Five species are recognised of which two (*pulchella* and *transversa*) are described as new. Two new junior synonyms of the type-species *gabonensis* are established (*armata*, *heterodus*) and earlier synonymy of some infraspecific taxa is confirmed. The genus is redefined, with diagnoses of all castes and sexes. New and important characters of the genus are discussed.

Key words: *Phrynoponera*, Ponerinae, Ponerini, taxonomy

Introduction

The name *Phrynoponera* first appeared in a paper by Wheeler (1920), merely as a new genus-group name with the designation of an already described species as the type-species. A couple of years later Wheeler (1922) presented a formal description of the genus, a synopsis of newly discovered material from the Democratic Republic of Congo, mostly infraspecific taxa, and notes on a few previously described forms.

The description of the genus that Wheeler (1922) presented was adequate for its time, but superficial by modern standards and mistaken in several characters. First, Wheeler noted that the "stridulatory surface is well developed", which it is not. In fact, the stridulitrum is absent from all species except *pulchella*, where a vestigial and non-functional remnant is present. Second, he maintained that there was an "absence of any constriction between postpetiole [= first gastral segment] and gaster", when in fact differentiated presclerites are strongly developed on the second gastral segment but are specialised in form and usually concealed by the posterior portions of the sclerites of the first gastral segment. However, Wheeler did recognise that the apparent similarities between his *Phrynoponera* species and two Indian *Pachycondyla* (then *Bothroponera*) species, *P. bispinosa* (bispinose propodeum) and *P. rufipes* (denticulate dorsal margin of petiole), were superficial and possibly independently acquired. Each of these *Phrynoponera*-like species lack the extremely specialised morphology of the petiole sternite, helcium, and prora, as well as the characteristic 5-spinose petiole node, that are unique and consistent in the female castes of *Phrynoponera*.

Phrynoponera is a strictly Afrotropical member of the subfamily Ponerinae, tribe Ponerini, as diagnosed by Bolton (2003). Within the tribe, apomorphies of the *Odontomachus* genus group (*Anochetus*, *Odontomachus*) (Brown, 1976) and apomorphies of the *Plectroctena* genus group (*Loboponera*, *Psalidomyrmex*, *Plectroctena*) (Bolton & Brown, 2002) are absent. *Phrynoponera* apparently belongs in the mass of genus-group names that surrounds *Pachycondyla* and its synonyms, but the diagnosis below is unique to *Phrynoponera* and is not repeated in any other *Pachycondyla*-group member.

The species-rank taxonomy of the genus remained as Wheeler (1922) left it, until Brown (1950) reviewed

Accepted by J. Longino: 13 Aug. 2008; published: 6 Oct. 2008

some taxa, which resulted in the synonymy of a number of infraspecific names. Hence the genus has never before been investigated in its entirety, nor has its morphology been closely studied.

Five species are currently recognised in the genus, of which two, *bequaerti* and *gabonensis*, are widely distributed in the Afrotropical forest zone and are usually collected in leaf litter samples and pitfall traps. They nest in and under rotten wood, and sometimes directly in compacted soil. At least two species, *gabonensis* and *sveni*, will also nest in upright or fallen termitaries, but are by no means common in such places (Dejean, *et al*. 1996, 1997). *Phrynoponera* species are not generally considered to be termitophagous, but in truth their actual diet remains unknown, so termites may form a part of it. Individuals are not particularly numerous in litter samples. Belshaw & Bolton (1994) recorded the two species that occur in Ghana (*bequaerti*, *gabonensis*) as comprising only 0.08% of individuals in the leaf litter ant fauna. Beyond these few facts, nothing is known of their biology.

Measurements and indices

Measurements were taken using an optical micrometer, to the nearest 0.01 mm, on a Wild M5 microscope. All measurements are in millimetres.

Total Length (TL). The total outstretched length of the ant from the mandibular apex to the gastral apex.

Head Length (HL). The length of the head capsule excluding the mandibles, measured in full-face view in a straight line from the midpoint of the anterior clypeal margin to the mid-point of the posterior margin. In species where one or both of these margins is concave the measurement is taken from the midpoint of a transverse line that spans the apices of the projecting portions.

Head Width (HW). The maximum width of the head behind the eyes, measured in full-face view.

Cephalic Index (CI). HW divided by HL, × 100.

Scape Length (SL). The maximum straight-line length of the scape, excluding the basal constriction or neck.

Scape Index (SI). SL divided by HW, × 100.

Ocular Index (OI). Maximum diameter of eye divided by HW, × 100.

Pronotal Width (PW). The maximum width of the pronotum in dorsal view.

Weber's Length (WL). The diagonal length of the mesosoma in profile, from the point at which the pronotum meets the cervical shield to the posterior basal angle of the metapleuron.

Abbreviations of depositories:

AMNH	American Museum of Natural History, New York, U.S.A.
BMNH	The Natural History Museum (= British Museum, Natural History), London, U.K.
CASC	California Academy of Sciences, San Francisco, California, U.S.A.
DEUN	Dipartimento de Entomologia e Zoologia Agraria "Filippo Silvestri", Università di Napoli, Italy.
LACM	Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.
MCZC	Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland.
MNHN	Museum National d'Histoire Naturelle, Paris, France.
NHMB	Naturhistorisches Museum, Basel, Switzerland.
SELN	Station d'Écologie de Lamto, N'Douci, Côte d'Ivoire.
USNM	United States National Museum of Natural History, Washington, D.C., U.S.A.

Images

Digital colour images were created using a JVC KY-F75 digital camera and Syncroscopy Auto-Montage (v 5.0) software.

Genus *Phrynoponera*

Phrynoponera Wheeler

Phrynoponera Wheeler, W.M. 1920: 53. Type-species: *Bothroponera gabonensis* André, 1892: 50, by original designation. [Synonymy with *Pachycondyla* by Snelling, 1981: 389; revived from synonymy by Bolton, 1994: 156 (in key); Bolton, 1995: 42.]

Diagnosis of worker and queen (gyne)

Characters included in the diagnoses that are thought to be apomorphies are printed in italics.

Workers are known for all species; queens are known for all except *pulchella*.

1 Mandible with 3–8 teeth; without a basal pit but with a weak basal groove.

2 Masticatory margin of mandible somewhat oblique; basalmost tooth at the rounded basal angle; mandible at most subtriangular, usually the basal and external margins roughly parallel.

3 Palp formula 4,4.

4 Frontal lobes large but not hypertrophied; median portion of clypeus extends back between them as a narrow triangle, to beyond the midlength of the lobes. Frontal lobes do not overhang anterior clypeal margin in full-face view.

5 Antenna with 12 segments, gradually incrassate apically but without a differentiated club.

6 Metanotal groove vestigial to absent (worker caste only).

7 Metapleural gland orifice simple, posterolateral.

8 *Propodeum stoutly bispinose*.

9 Propodeal spiracle with orifice slit-shaped.

10 Mesosternal and metasternal processes present.

11 Mesotibia and metatibia each with two spurs; the anterior spur on each small, simple to barbulate, the posterior spur pectinate.

12 Pretarsal claws small and simple.

13 *Petiole surmounted by a high, stout scale that curves posteriorly over the base of the gaster and is armed dorsally with 5 long teeth or spines*.

14 Petiole sternite appears simple in profile, with a short anteroventral process that is followed by a feebly sinuate to weakly convex simple plate.

15 Sternite of petiole in posterior view very complex, see discussion below.

16 Prora apparently absent but actually unusually modified and concealed, see discussion below.

17 Gastral segment 2 (abdominal segment IV) with differentiated but unusual presclerites, see discussion below.

18 Gastral tergite 2 (abdominal tergite IV) with stridulitrum usually absent, rarely vestigial.

19 Queen (gyne) only: alate when virgin, very similar in size to conspecific workers, varying from slightly larger to slightly smaller. Head with three ocelli present and mesosoma with full complement of flight sclerites. Mesopleuron with a weak transverse sulcus (absent in workers). Jugal lobe present on hindwing.

In addition, workers of all known species have moderately large eyes (OI 19–27) and are strongly sculptured over the entire body. On the dorsal mesosoma the sculpture is coarse and usually consists of a coarse rugoreticulum, the spaces within the reticulum being depressed and concave. On the mesonotum the longitu-

dinal rugose component may predominate, with anastomoses reduced or absent, so that the coarse sculpture has a longitudinal trend. Pilosity is always dense, with numerous conspicuous suberect to erect setae on all dorsal surfaces of the head and body, and also on the scapes and tibiae. In full-face view the sides of the head, from the posterior corner to the clypeus, have many outstanding short setae present. Colour is basically black throughout the genus, but with a marked tendency for certain areas to be brown, reddish brown, red, or even yellowish. Such lighter areas usually include the anterior portion of the head capsule, the antennae and mandibles, the legs, and often the apices of the gastral tergites and around the metapleural gland; the entire head capsule and much of the body may be reddish. All species show variation in the extent and intensity of such paler areas and colour variation in the known species has no taxonomic value.

Discussion of female characters. Characters 8 and 13 above, in *italics*, are autapomorphic and together immediately differentiate *Phrynoponera* workers and queens from all other Ponerini. Characters 15 and 16 together are also highly diagnostic and are most probably also autapomorphic; some other characters have analogues developed convergently elsewhere in tribe Ponerini. Characters 1–19 together form an inclusive diagnosis that isolates *Phrynoponera* workers and queens from all other genera in the tribe.

6 The metanotal groove is absent in workers of most species. In some workers of *gabonensis*, the dorsolateral ends of the metanotal groove are faintly visible.

13 Petiole structure is unique to the genus. The apical armament of the scale consists of a median spine or thick tooth, on each side of which is a slightly to markedly smaller spine or tooth, and outside that on each side is a longer, stouter spine. A longitudinal carina runs along the dorsal surface of the median spine.

14 Ventral surface of petiole also appears simple in ventral view: the anterior prominence is followed by a simple plate, without secondary carinae or teeth, though the surface of the sternite is sculptured. The posterior margin of the plate is simple, feebly convex to almost transverse.

15 When the petiole is disarticulated from the helcium, the petiole sternite, in posterior view, is seen as very complex. In the posterior third of its length the sternite bifurcates into an externally visible broad and concave ventral plate and a slightly shorter internally projecting sclerite that is completely concealed by the external plate in normal view. The internal sclerite terminates in a thickened concave arc that forms the actual articulation with the helcium and is homologous with the articulation seen almost everywhere else in the Ponerini. The ventral margin of the arc has a deep excision that is more than semicircular, and the apices of the excision are acute. Within Ponerini similar modifications are seen only in *Asphinctopone* and the species of *Pachycondyla* that formerly constituted the genus *Brachyponera*. In the latter, however, the lower plate is much less developed than in *Phrynoponera* and appears as a posteriorly directed tooth in profile that is considerably lower than, and does not overlap and conceal, the internal sclerite. This difference in form of development implies convergence rather than genuine homology. *Asphinctopone* is otherwise so different morphologically that convergent acquisition of this one character is likely.

16 Viewed externally the first gastral tergite appears to lack a prora, but disarticulation of the helcium from the petiole reveals that a uniquely specialised prora is present. Very reduced, it is inserted between, and appears fused to, the ventral apices of the helcium tergite. In effect this makes the helcium double-chambered, with the upper chamber floored by the helcium sternite and the lower chamber floored by the prora. In Ponerini a similar modification is observed only in the former *Brachyponera* species, but the degree of development is not so advanced.

17 Presclerites of the second gastral segment are present but usually concealed by the tergite and sternite of the first, so that the gaster usually appears small, roughly globular and compact. If the gaster is slightly distended the presclerites become apparent, but are not of the usual form. Instead of a girdling constriction between pre- and postsclerites, the postsclerites are instead depressed slightly below the level of the presclerites and are followed by a shallow concavity of the surface.

18 Most species show no trace of a stridulitrum but in one (*pulchella*) there is a small, very roughly triangular, area anterodorsally on the presclerite of gastral tergite 2, at the midline, that has more regular transverse

fine costulae than are visible on either side of it and behind it. This appears to represent the last vestige of a non-functional stridulitrum. The sculpture is much more crude and coarse, and far more widely spaced, than that seen on a genuine stridulitrum, and the area does not scatter white light, as is frequently seen with a functional stridulitrum.

The metacoxal cavities of all species except *pulchella* are atypical for Ponerini. Within the tribe the usual condition of the cuticular annulus around the metacoxal cavities is to have a narrow straight suture medially that traverses the annulus from the metacoxal cavity to the petiolar foramen, so that the cuticular apices of the annulus are transverse, not pointed; and this is the condition in *pulchella*. In all other *Phrynoponera* species each end of the annulus terminates in a blunt point and the two points are separated by a small gap. As *pulchella* also plesiomorphically retains a vestige of the stridulitrum, and all of its petiolar teeth are more similar in size, it seems likely that this species is sister to the remainder of the genus, that its metacoxal annulus represents the condition of the ancestral "normal Ponerini" and that the remaining species in the genus have secondarily evolved narrowly open metacoxal cavities.

Diagnosis of male

Known only for *gabonensis*, previously undescribed.

1 Mandible very reduced, sublobate with a small apical tooth and a tiny basal denticle that is nothing more than an exaggeration of the basal angle.

2 Palp formula 6,4 (*in situ* count).

3 Frontal lobes absent; antennal sockets fully exposed.

4 Antenna with 13 segments, filiform.

5 Second funicular segment nearly three times longer than the short scape.

6 Eyes large, their inner margins shallowly evenly concave in the median third, not abruptly indented; ocelli prominent.

7 Notauli absent; mesoscutum with a short, narrowly triangular crest anteromedially.

8 Parapsidal grooves present.

9 Mesonotum with deep transverse groove between mesoscutum and mesoscutellum.

10 Epimeral lobe present, conspicuous.

11 Propodeal spiracle with orifice slit-shaped.

12 Mesotibia and metatibia each with two spurs, the anterior simple to barbulate, the posterior pectinate.

13 *Pretarsal claws coarsely bifid apically on all legs; the two teeth approximately the same length, inner tooth always slightly more stout than the outer.*

14 Hindwing with jugal lobe present.

15 *Apex of petiole node with a coarse triangular median tooth, on each side of which is a flat lamella that is angulate at the outer corners.*

16 Petiole in profile with an anteroventral tooth and a posteroventral long downcurved plate (appearing as a long curved tooth in absolute profile); *posterior free margin of plate is broadly excised medially.*

17 Prora apparently absent, modified as in worker and queen (see discussion below).

18 Gastral segment 2 (= abdominal segment IV) with a distinct girdling constriction between presclerites and postsclerites.

19 *Gastral tergite 5 (= abdominal tergite VII) with a posterolaterally directed large, broadly triangular, prominence on each side; these prominences very densely setose* (Fig. 4d).

20 Pygidium (= abdominal tergite VIII) with a long, strong, down-curved apical spine medially.

21 Hypopygium elongate-triangular.

22 Cerci (= pygostyles) present.

Discussion of male characters. Characters 13, 15, 19, and the second half of 16, in *italics*, are autapomorphic for *gabonensis* males; their presence is considered to be of genus rank and therefore assumed to be

universal within the genus. Character 17 is also highly diagnostic and most probably also autapomorphic. Characters 1–22 together form an inclusive diagnosis that isolates *Phrynoponera* males from all other genera in the tribe. As in the worker and queen some of the other characters are probably also apomorphies with convergent analogues elsewhere in Ponerini.

1 Reduced mandibles is a long-established apomorphy of male Ponerini (*e.g*. Bolton, 2003).

2 Bolton (2003) pointed out that in Ponerini dimorphism of palp formula between female castes and males was extremely common, with males characteristically having a higher PF count than females, suggesting this character may be an apomorphy of the tribe.

6 In many groups of Ponerini the inner margin of the eye is distinctly concave or suddenly indented in approximately its median third (*e.g*. Ogata, 1987; Yoshimura & Fisher, 2007).

13 A number of ponerine genera have the pretarsal claws with a preapical tooth in either the female castes, or in the male, or in both. Genera that have known males, and in which the females have simple claws and the males have toothed claws, include *Diacamma*, *Psalidomyrmex*, *Streblognathus*, some *Plectroctena*, some *Odontomachus*, and some groups within *Pachycondyla*. In all of these the preapical tooth is small compared to the apical and is some distance proximal of the apex, which is generally regarded as the plesiomorphic condition throughout the Formicidae. In *Phrynoponera* the preapical claws of the male are strongly bifid, with both components of about equal length; this condition is not otherwise known in the tribe. The condition is proposed as apomorphic for the genus.

15 The appearance of the dorsal apex of the petiole in the male is an obvious reduction of the condition universal in the female castes. The median tooth has a dorsal carina and a similar carina is visible on each side, close to the outer angle.

16 and 17 The ventral petiole and its articulation to the gaster are basically the same as in the female castes (see 15–16, above), but not as radically developed. The outer, posteroventral, plate of the petiole sternite is strongly curved downwards and has a V-shaped excision in its posterior margin, rather than being closely applied and convex apically as in the female castes. Because of this the inner, articulatory, sclerite of the sternite is visible in ventral view. The reduced prora, as in females, is inserted between the apices of the arched helcium tergite and is also visible in ventral view without disarticulation.

18 The girdling constriction between the presclerites and postsclerites of the second gastral segment is, in males, of the "normal ponerine" form and does not match the morphology of the female castes.

19 The presence of large, densely setose triangular prominences on the sides of the fifth gastral tergite is unique. Their function remains unknown though they are obviously sensory in nature.

The male morphology of *Phrynoponera* most closely resembles that of *Pachycondyla* (in the broad sense of Bolton, 1994, 1995; Yoshimura & Fisher, 2007), but in the latter several characters occur in a polymorphic condition. Characters common to *Phrynoponera* and *Pachycondyla* males include 1, 3, 4, 8, 9, 10, 12, 18, 20 and 22. Characters polymorphic in *Pachycondyla* males include 2, 6 (shape of inner margin of eye), 7, 11, 13 (claws simple or toothed, but not bifid) and 14. Characters 5 and 21 need further investigation through the tribe.

Synonymic synopsis of species

bequaerti Wheeler, 1922

gabonensis (André, 1892)

= *gabonensis* var. *striatidens* (Santschi, 1914)

= *armata* (Santschi, 1919) **syn. n.**

= *gabonensis* var. *robustior* (Santschi, 1919)

= *gabonensis* var. *esta* Wheeler, 1922

= *gabonensis* var. *fecunda* Wheeler, 1922
= *gabonensis* var. *umbrosa* Wheeler, 1922
= *heterodus* Wheeler, 1922 **syn. n.**

pulchella Bolton & Fisher **sp. n.**

sveni (Forel, 1916)

transversa Bolton & Fisher **sp. n.**

Key to species (workers)

1 With the head in full-face view the anterior clypeal margin with a roughly semicircular median excavation, the excavation flanked on each side by a projecting, bluntly tooth-like prominence (Figs 2d, 7d)....2
- With the head in full-face view the anterior clypeal margin medially shallowly convex to very shallowly and feebly concave; if the latter the shallow concavity rounds evenly into the margin on each side and is not flanked by projecting blunt tooth-like prominences.....3
2 With head in full-face view some or all of the vertex behind the level of the eyes with arched, transverse, subsulcate sculpture (Fig. 7d). (Gabon, Central African Republic) .....*transversa*
- With head in full-face view the vertex costulate, the costulae radiating outwards and posteriorly from the midline (Fig. 2d). (Ivory Coast, Ghana, Cameroun, Gabon, Central African Republic, Democratic Republic of Congo, Angola, Sudan, Uganda, Kenya) .....*gabonensis*
3 Much smaller species; HW <1.50, SL <1.20, PW < 1.20. Funicular segments 2–4 distinctly much broader than long (Fig. 1c). (Ghana, Cameroun, Gabon, Central African Republic, Democratic Republic of Congo) ..... *bequaerti*
- Much larger species; HW > 2.00, SL > 1.80, PW > 1.60. Funicular segments 2–4 at least as long as broad (Figs 5c, 6c) 4
4 First and second gastral tergites finely and very densely punctulate-shagreenate, matte and dull; both tergites with a dense pelt of appressed pubescence; longest standing setae on first tergite short, *ca* 0.22 (Fig 5a). Median spine on petiole only slightly longer than the intermediate spines between it and the outer pair (Fig. 5b). Head at least as broad as long, CI 100 or more; scape shorter, SI 78–80. (Kenya, Tanzania) ....*pulchella*
- First and second gastral tergites longitudinally costulate and reticulate-punctate; both tergites with sparse appressed pubescence; longest standing setae on first tergite longer, *ca* 0.36 (Fig. 6a). Median spine on petiole distinctly longer than the intermediate spines between it and the outer pair (Fig. 6a). Head slightly longer than broad, CI 95–98; scape longer, SI 87–91. (Cameroun, Gabon, Central African Republic, Democratic Republic of Congo)..... *sveni*

Species of *Phrynoponera*

***Phrynoponera bequaerti* Wheeler**
(Figures 1a–c)

Phrynoponera bequaerti Wheeler, W.M. 1922: 79, fig. 12. Holotype queen, DEMOCRATIC REPUBLIC OF CONGO: N'Gayu (= Ngayu), stomach *Bufo superciliaris* (*H.O. Lang*) (AMNH) [examined].

Worker (previously undescribed)**.** TL 5.0–5.7, HL 1.16–1.25, HW, 1.13–1.23, CI 96–101, SL 0.90–0.97, SI 75–81, PW 0.90–1.02, WL 1.66–1.90, maximum diameter of eye 0.28–0.32, OI 24–27 (20 measured).

Mandible smooth with scattered pits, usually with 4 teeth but very rarely with 3 or 5. Median portion of clypeus with anterior margin transverse to very shallowly concave, without a tooth-like cuticular prominence on each side. Cephalic dorsum finely and densely reticulate-rugose, the bases of the reticulae punctate. Funic-

ular segments 2–7 distinctly broader than long. Dorsum of mesosoma reticulate-rugose. Petiolar spines curve far back over the first gastral tergite; median spine at least three-quarters the length of the outer pair; intermediate spines much shorter and usually much more slender, often reduced and needle-like by comparison with the others. Gastral tergites 1–2 longitudinally costulae upon a reticulate-punctate ground sculpture; often with some anastomoses between the costulae. Colour varies considerably. In darkest forms the head and body are almost entirely black, with only the mandibles and legs reddish brown to red. From this there is a gradual increase in the amount of blackish red to dull red on most areas of the body until in the lightest colour forms the entire head is reddish, the legs are red and even the mesosoma, petiole and parts of the gaster are suffused with red.

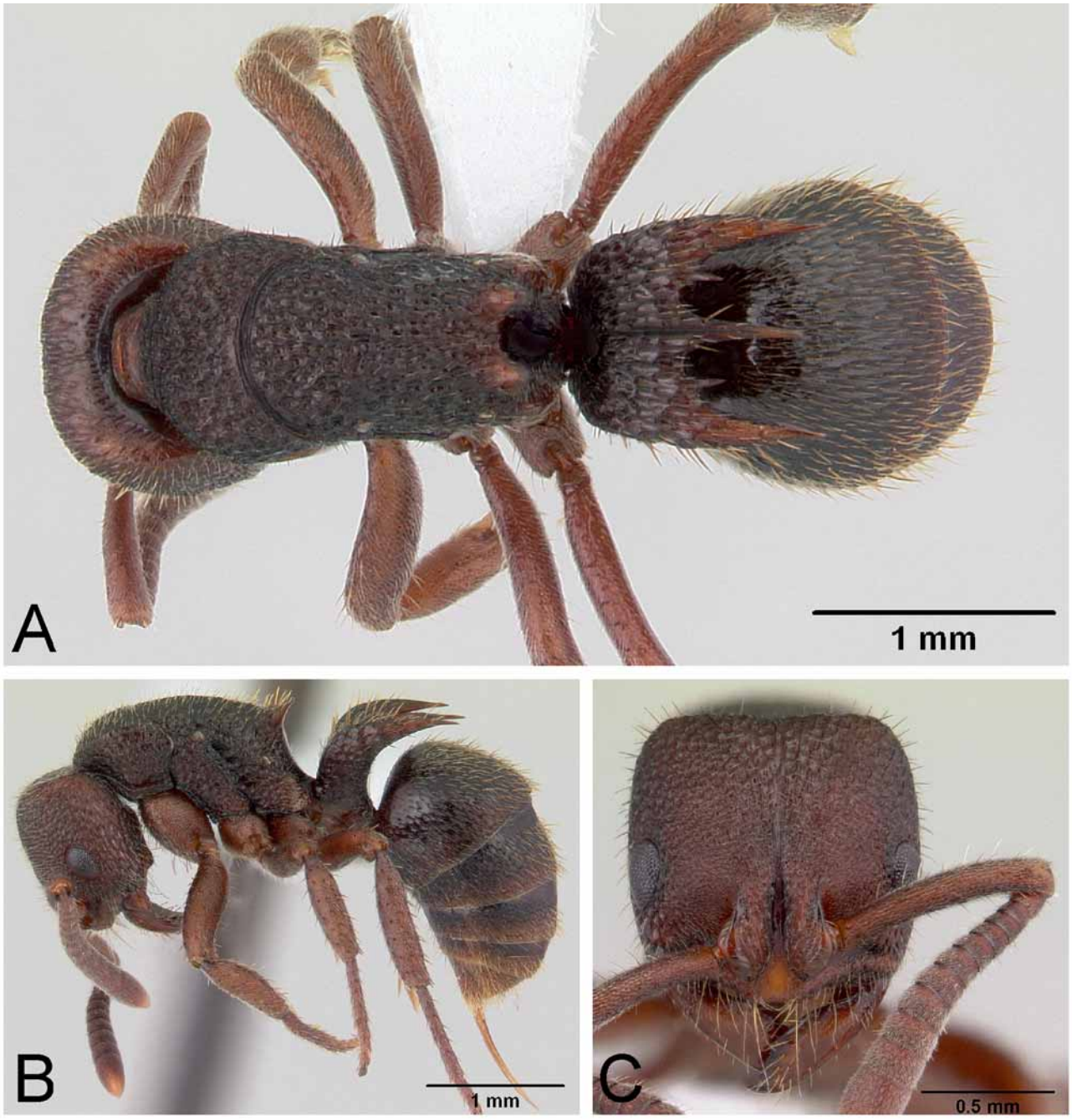

FIGURE 1. *Phrynoponera bequaerti* worker CASENT0411278: A, dorsal view of body; B, lateral view of body; C, full-face view of head.

Almost as common and widespread as *gabonensis* and by far the smallest species in the genus, *bequaerti* is easily recognised by its size, lack of clypeal teeth and short, broad funicular segments. The vast majority of the material examined was extracted from leaf litter samples, though occasional samples from rotten wood have been recorded. Unlike *gabonensis* and *sveni*, *bequaerti* has not been found in termitaries.

Material examined. Ghana: Tafo (*D. Leston*); Kade (*R. Belshaw*); Aiyaola For. Res. (*R. Belshaw*); Mamang River (*K. Yeo*). **Cameroun**: Mbalmayo (*N. Stork*); Res. Dja (*K. Yeo*); Prov. Sud-Ouest, Bimbia Forest, Limbe (*B.L. Fisher*); Korup, NW Mundemba (*B.L. Fisher*); Mnt Cameroon, Mapanja (*B.L. Fisher*); Prov. Sud, Res. de Faune de Campo, Ebodjé (*B.L. Fisher*); P.N. Campo, ESE Campo (*B.L. Fisher*); Res. Campo, Massif des Mamelles, E Ebodjé (*B.L. Fisher*); N'Kolo, Bondé Forest, SSE Elogbatindi (*B.L. Fisher*). **Gabon**: La Makandé, Forêt des Abeillies (*S. Lewis*); Plateau d'Ipassa (*J.A. Barra*); Makokou, CNRS (*W.H. Gotwald*); Prov. Woleu-Ntem, ESE Minvoul (*B.L. Fisher*); Prov. Estuaire, F.C. Mondah, NNW Libreville (*B.L. Fisher*); Prov. Ogooue-Maritime, Res. Monts Doudou, Doussala (*B.L. Fisher*); Res. Moukalaba, NW Doussala (*B.L. Fisher*). **Central African Republic**: Res. Dzanga-Sangha, Bayanga (*B.L. Fisher*); P.N. Dzanga-Ndoki, Lidjombo (*B.L. Fisher*); P.N. Dzanga-Ndoki, Mabéa Bai, NE Bayanga (*B.L. Fisher*). **Democratic Republic of Congo**: Epulu (*S.D. Torti*); N'Gayu (*H.O. Lang*).

***Phrynoponera gabonensis* (André)**
(Figures 2a–d, 3a–e, 4a–f)

Bothroponera gabonensis André, 1892: 50. Holotype worker, GABON: no loc. (*Mocquerys*) (MNHN) [examined]. [Combination in *Pachycondyla* (*Bothroponera*) by Emery, 1901: 45; in *Phrynoponera* by Wheeler, W.M. 1920: 53.]

Pachycondyla (Bothroponera) gabonensis var. *striatidens* Santschi, 1914: 315, fig. 4. Holotype worker, CAMEROUN: Victoria (*Silvestri*) (DEUN) [not seen; see note]. [Combination in *Phrynoponera* by Wheeler, W.M. 1922: 78; synonymy with *gabonensis* by Brown, 1950: 246; here confirmed.]

Pachycondyla (Bothroponera) armata Santschi, 1919: 82. Holotype worker, DEMOCRATIC REPUBLIC OF CONGO: Kitempuka (*Gérard*) (NHMB) [examined]. **Syn. n.** [Combination in *Phrynoponera* by Wheeler, W.M. 1922: 773.]

Pachycondyla (Bothroponera) gabonensis var. *robustior* Santschi, 1919: 82. Syntype worker, DEMOCRATIC REPUBLIC OF CONGO: Banalia, 12.xii., no. 96 (*Bequaert*) (NHMB) [examined]. [Combination in *Phrynoponera* by Wheeler, W.M. 1922: 774; synonymy with *gabonensis* by Brown, 1950: 246; here confirmed.]

Phrynoponera gabonensis var. *esta* Wheeler, W.M. 1922: 77. Syntype workers and queen, DEMOCRATIC REPUBLIC OF CONGO: Medje, stomach *Bufo superciliaris* (*H.O. Lang*); Medje, 27°15'E, 2°25'N, stomach *Bufo tuberosus* (no collector's name, presumably *Lang* or *Lang & Chapin*) (AMNH, MCZC, LACM) [examined]. [Synonymy with *gabonensis* by Brown, 1950: 246; here confirmed.]

Phyrnoponera gabonensis var. *fecunda* Wheeler, W.M. 1922: 78. Syntype workers and queen, DEMOCRATIC REPUBLIC OF CONGO: Akenge, 26°50'E, 2°55'N, stomach *Bufo polycercus, Bufo funereus* (H.O. *Lang*) (AMNH, MCZC, LACM) [examined]. [Synonymy with *gabonensis* by Brown, 1950: 246; here confirmed.]

Phrynoponera gabonensis var. *umbrosa* Wheeler, W.M. 1922: 78. Syntype workers, DEMOCRATIC REPUBLIC OF CONGO: Medje, stomach *Bufo polycercus* (*H.O. Lang*) (AMNH, MCZC) [examined]. [Synonymy with *gabonensis* by Brown, 1950: 246; here confirmed.]

Phrynoponera heterodus Wheeler, W.M. 1922: 78. Holotype queen, DEMOCRATIC REPUBLIC OF CONGO: Stanleyville, 25°10'E, 0°30'N (*Lang & Chapin*) (AMNH) [examined]. **Syn. n.**

Note. The holotype worker of *striatidens* is not in NHMB and therefore must be assumed to be in Silvestri's collection at DEUN, which is not currently available for examination. Among the large quantity of material examined the area of the mandible with striation was extremely variable, from entirely absent to complete, and the intensity of striation, when present, was also variable, thus Brown's synonymy of the name is confirmed here.

Worker. TL 7.8–10.2, HL 1.76–2.20, HW 1.76–2.12, CI 95–102, SL 1.38–1.76, SI 78–85, PW 1.44–1.76, WL 2.56–3.04, maximum diameter of eye 0.36–0.46, OI 19–23 (25 measured).

Mandible colour usually red, but quite commonly brownish red, brown or black, with all intermediate shades known; in teneral workers the mandibles may be yellow. Mandible usually smooth with scattered pits

but many samples show varying degrees of very fine striate sculpture on the apical half. Less commonly, more than half the mandible may be striate and sometimes the entire mandible is finely striate everywhere. Mandible usually with 4 or 5 teeth but some samples have 6 or 7 (7 in holotype); the maximum number recorded is 8 and some workers have different numbers of teeth on each mandible. Anterior clypeal margin

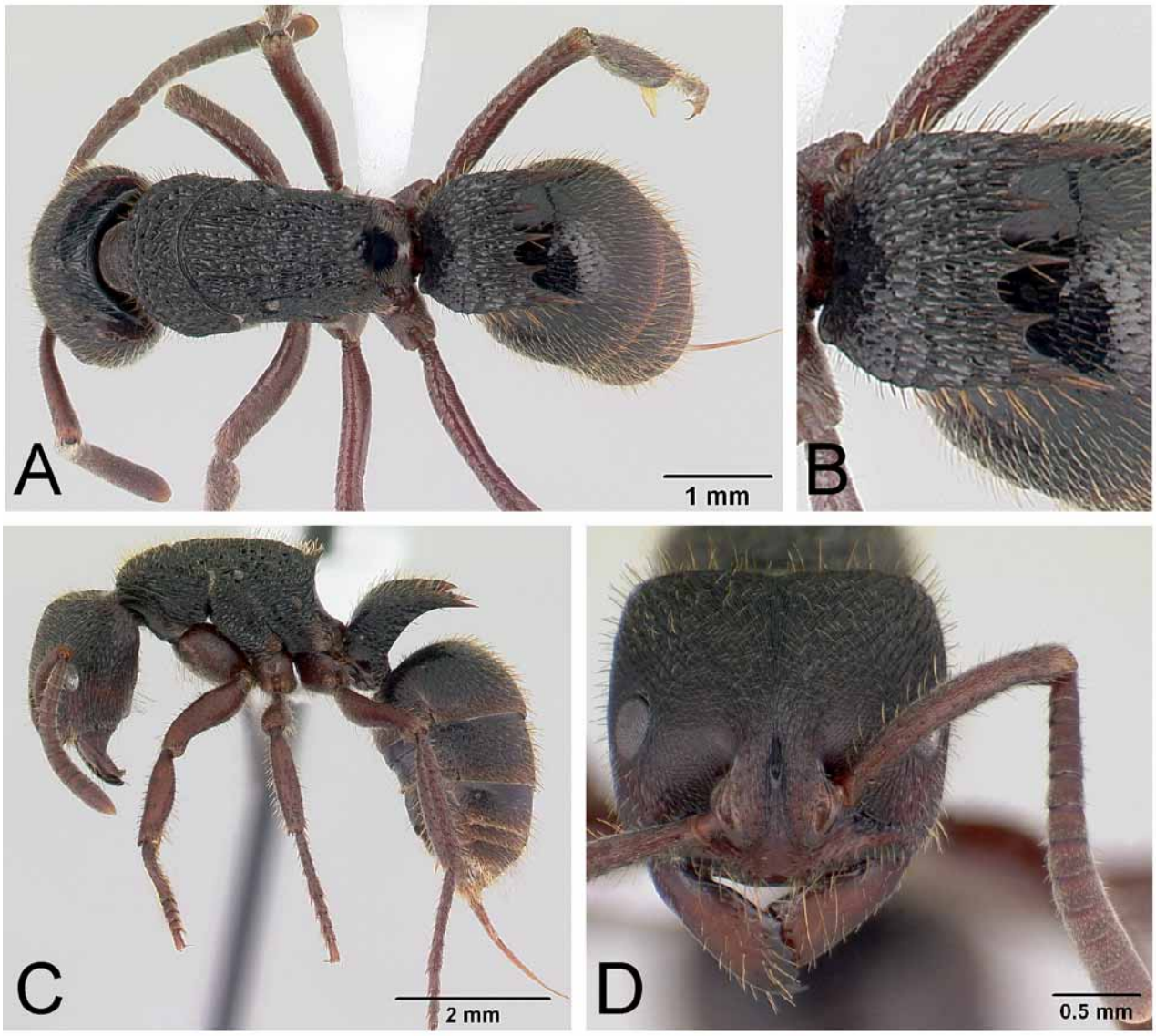

FIGURE 2. *Phrynoponera gabonensis* worker CASENT0178229: A, dorsal view of body; B, dorsal view of petiole; C, lateral view of body; D, full-face view of head.

with a conspicuous concavity medially and on each side of the concavity there is a blunt tooth or tooth-like prominence. Head capsule usually black but with the anterior portion and antennae brown to red. Sometimes the antennae are dark brown to blackish and sometimes the head capsule is entirely black or entirely reddish. Cephalic sculpture consists of costulae that may be uniform or broken, variable in coarseness of development, sometimes roughly longitudinal near the midline but otherwise radiating outwards and backwards on each side of the midline. Dorsal mesonotum usually reticulate-rugose, but frequently the rugular cross-meshes are weakened so that the sculpture has an overall longitudinal direction. Mesosoma generally black but varying patches or areas of red are frequent. Legs usually brown to red and distinctly lighter than the mesosoma, but in some they may be blackish. Gastral tergites 1–2 show much variation in density and intensity of sculpture. In the most weakly sculptured examples the tergites are glossy and almost smooth, only vaguely superficially reticulate-punctate. From this pattern the reticulate-punctate sculpture increases in density and intensity, so

that the surfaces become entirely covered in a sharply defined reticulate-punctate blanket and the tergal surfaces become less glossy. At any point in this sequence of increasing density of punctation small costulae may appear, first around the setal pits then more extensively between the pits. The costulae increase in density and extent, and become more obviously longitudinal and parallel, until in the most coarsely sculptured series the sculpture of the first and second gastral tergites is entirely of dense longitudinal costulae upon a reticulate-punctate ground-sculpture. The third gastral tergite is usually just reticulate-punctate, but in the most densely sculptured workers some longitudinal costulae may also appear on this sclerite. In general the form of the gastral sculpture is only slightly variable within nest samples, but the changes in sculpture outlined form a gradual and continuous sequence in which there are no obvious breaks. Posterior margins of the gastral sclerites are usually reddish (yellowish in tenerals), but in some the sclerites are entirely black.

All the synonyms listed above were based on workers, or workers and queens, except for *heterodus*, which was based on an isolated queen. All were founded on slight variations of colour and sculpture except for *heterodus*, which had a dental count at the higher end of the range seen in the species. The dental count of *heterodus* was reported as 7 by Wheeler (1922), but there are actually 6 teeth on the right mandible and apparently 7 on the left, which is mostly concealed by the overlapping right mandible. All of these characters are now known to be gradient and to lack taxonomic value at species-rank. Brown's (1950) summary dismissal of all the "varieties" was therefore justified. Many queens are now represented in collections and they exhibit the same gradient variations in colour, sculpture and dental count as are shown by the worker caste.

Males of this species, discussed above, originated in two series with the data: **Ghana**: Tafo, 11.vi.1970 *and* 26.vi.1970; respectively "in wet-rotten log" and "wet-rotten branch in leaf litter" (*B. Bolton*). In the first series the male was collected with both workers and queen, in the second with workers. Both are in BMNH and one specimen is in LACM.

P. gabonensis is the most common, widely distributed and frequently encountered member of the genus. Specimens are usually retrieved from leaf litter samples but also occur in pitfall traps. The species is known to nest in and under rotten wood, in compacted soil and in termitaries.

Material examined. Ivory Coast: Lamto (*J. Lévieux*); F.C.Haute Dodo (*K. Yeo*); F.C. Cavally (*K. Yeo*). **Ghana**: Tafo (*D. Leston*); Tafo (*B. Bolton*); Mt Atewa (*R.W. Taylor*); Mt Atewa (*D. Leston*); Bunso (*D. Leston*); Bunso (*R. Belshaw*); Mamang River (*K. Yeo*). **Cameroun**: Mbalmayo (*N. Stork*); Tissongo (*D. Jackson*); Nkoemvon (*D. Jackson*); Prov. Sud, P.N. Campo, ESE Campo (*B.L. Fisher*); Res. Campo, Massif des Mamelles (*B.L. Fisher*); Res. de Campo (*D.M. Olson*); Res. de Fauna de Campo, ESE Ebodjé (*B.L. Fisher*); Prov. Sud-Ouest, Bimbia For. (*B.L. Fisher*). **Gabon**: CNRS, Makokou (*W.H. Gotwald*); Makokou (*I. Lieberburg*); Prov. Estuaire, Pointe Ngombe, Ekwata (*B.L. Fisher*); F.C. Mondah, NNW Libreville (*B.L. Fisher*); Prov. Woleu-Ntem, ESE Minvoul (*B.L. Fisher*); Prov. Ogooue-Maritime, Res. Moukalaba, NW Doussala (*B.L. Fisher*); Res. Moukalaba, SW Doussala (*B.L. Fisher*); Res. Monts Doudou, NW Doussala (*B.L. Fisher*); Res. Monts Doudou (*S. van Noort*); WNW Doussala (*B.L. Fisher*). **Central African Republic**: Res. Dzanga-Sangha, NW Bayanga (*B.L. Fisher*); P.N. Dzanga-Ndoki, Mabéa Bai, NE Bayanga (*B.L. Fisher*); P.N. Dzanga-Ndoki, Lidjombo (*B.L. Fisher*). **Democratic Republic of Congo**: Kikwit (*A. Dejean*); Ituri For., vic. Epulu (*T. Gregg*); Epulu (*S.D. Torti*); Ituri For., Beni-Irumu (*N.A. Weber*); Walikale (*Ross & Leech*); Irangi, Luhoho Riv. (*Ross & Leech*); Ituri, Mont Hoyo (*Ross & Leech*); Akenge (*H.O. Lang*); Medje (*H.O. Lang*); N'Gayu (*H.O. Lang*); Gamangui (*H.O. Lang*); Avakubi (*H.O. Lang*); Stanleyville (*Lang & Chapin*); Bafwasende (*H.O. Lang*); Kitempuka (*Gérard*); Banalia (*Bequaert*). **Angola**: Dundo, Carrisso Park, R. Luachimo (no collector's name). **Sudan**: Imatong Mts, Equatoria (*N.A. Weber*); Lotti For. (*Myers*); Azza For. (*Myers*). **Uganda**: Kibale For. N.P., Kanyawara (*Quicke & Laurenne*); Lake Victoria, Nkosi I, S. Sesse (*G.D.H. Carpenter*); Zika Forest, nr Entebbe (*G. Arnold*). **Kenya**: Kakamega For., Kaunosi (*A. Loveridge*); Kakamega Distr., Isecheno Nat. Res., Isecheno (*R.R. Snelling*); Isecheno Forest Res. (*W. Okeka*); Kakamega Distr., Yala River For. Res. (*R.R. Snelling*); Kakamega Distr., Bunyangu Nat. Res., Salazar Circuit (*Snelling & Espira*).

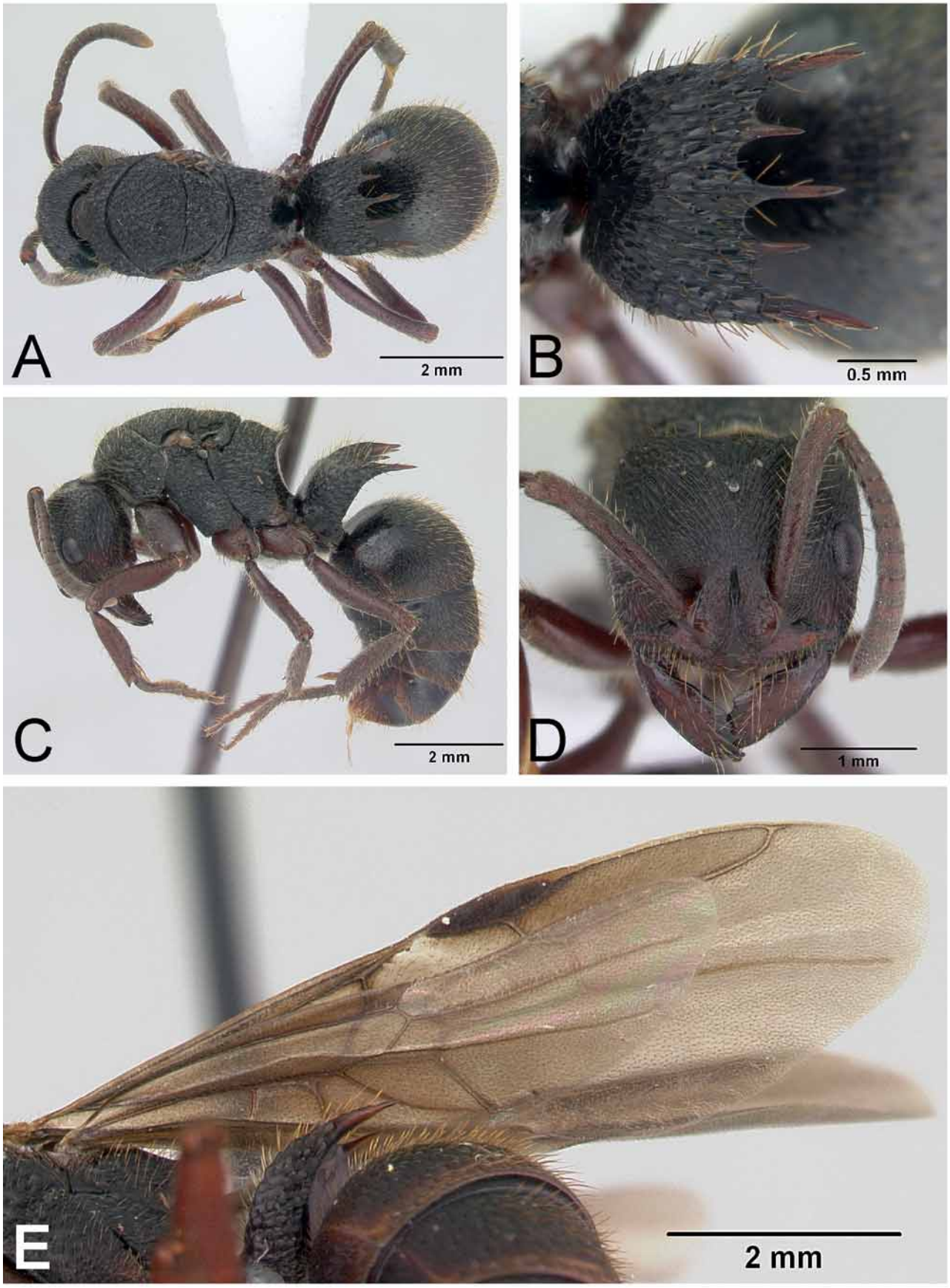

FIGURE 3. *Phrynoponera gabonensis* queen; CASENT0401945: A, dorsal view of body; B, dorsal view of petiole; C, lateral view of body; D, full-face view of head. CASENT0094797: E, lateral view of fore and hind wing.

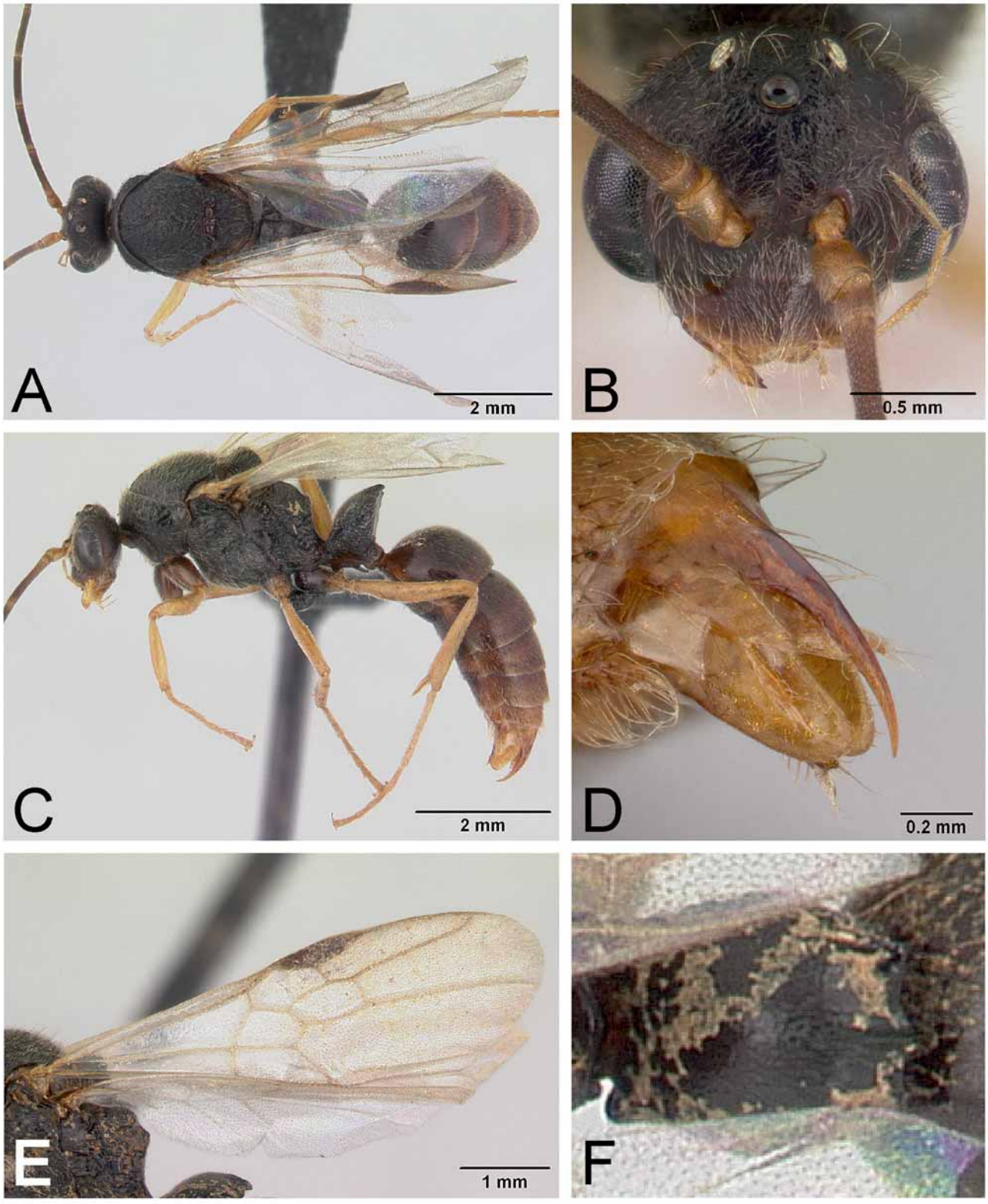

FIGURE 4. *Phrynoponera gabonensis* male; CASENT0178740: A, dorsal view of body; B, full-face view of head; C, lateral view of body; D, oblique lateral view of genitalia; CASENT0178202: E, lateral view of fore and hind wing; F, dorsal view of petiole.

***Phrynoponera pulchella* Bolton & Fisher sp. n.**
(Figures 5a–d)

Holotype worker. TL 11.1, HL 2.48, HW 2.56, CI 103, SL 2.04, SI 80, PW 2.04, WL 3.76, maximum diameter of eye 0.56, OI 22.

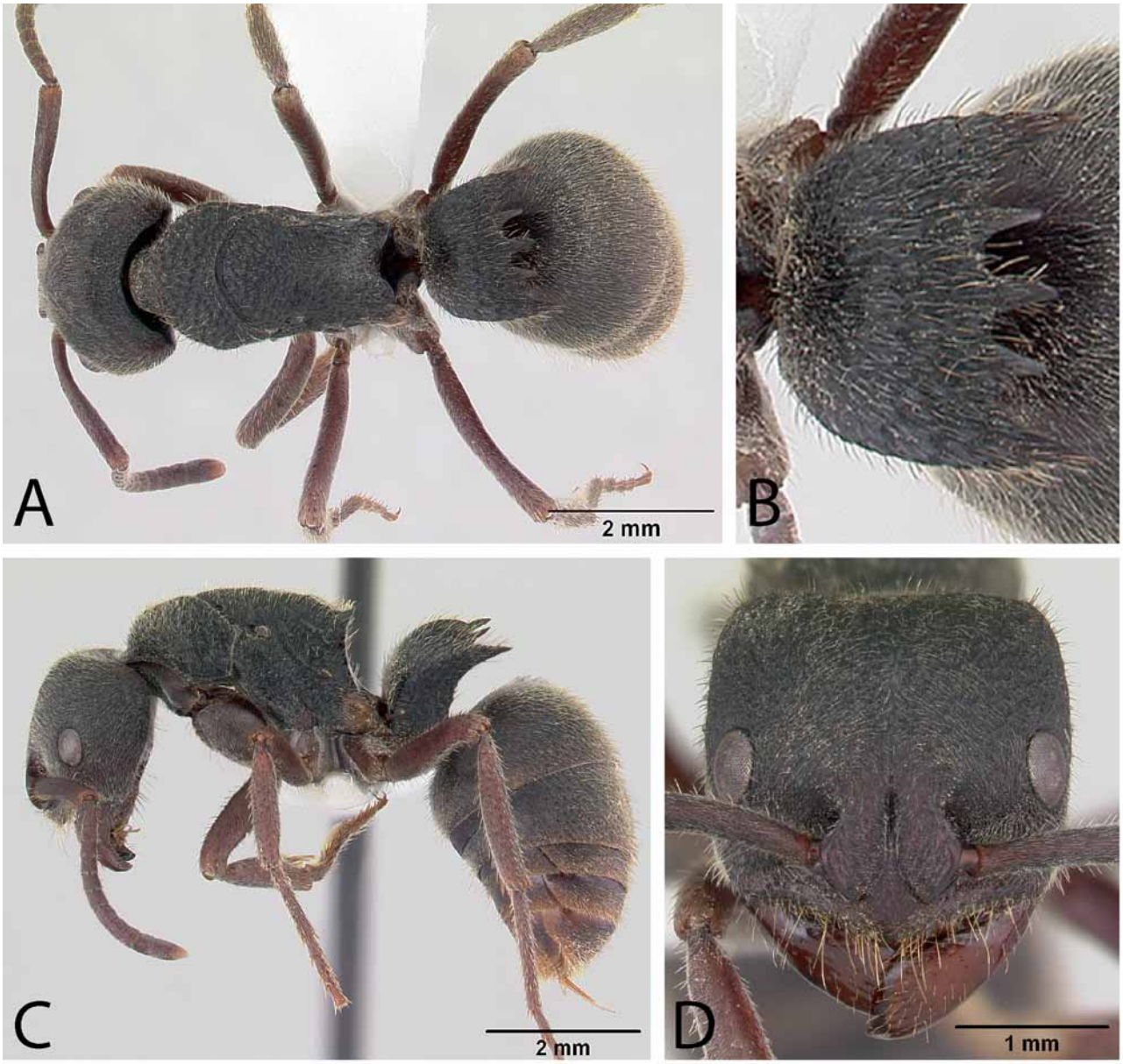

FIGURE 5. *Phrynoponera pulchella* paratype worker CASENT0178204: A, dorsal view of body; B, dorsal view of petiole; C, lateral view of body; D, full-face view of head.

Mandible smooth with scattered setal pits, with 5 teeth, the basal tooth no more than a broad angle. Median portion of anterior clypeal margin with a small and extremely shallow median indentation which rounds broadly and evenly into the clypeal margin on each side; without a prominent tooth on each side of the midline. Dorsum of head near midline very finely and very densely rugulose, the narrow rugulae predominantly longitudinal but with some fine anastomoses; spaces between rugulae extremely finely reticulate-punctate to shagreenate. More laterally on cephalic dorsum, and behind the eyes, the reticulae are wider though no more strongly defined. Dorsum of mesosoma coarsely, irregularly reticulate-rugose, spaces between reticulae shagreenate. Metanotal groove in dorsal view visible laterally but obliterated towards central area of dorsum. Median strip of propodeal dorsum with pubescence that is much more dense than anywhere else on dorsum of

mesosoma. Propodeal teeth in dorsal view short, broad at base and blunt apically. Petiole broad, width at base of spines *ca*. 2.00, surmounted by 5 spines that are all short and stout. Outer pair of petiolar spines the longest, broadly triangular and weakly divergent. Median spine only slightly longer than the flanking pair. Gastral tergites 1–3 shagreenate to extremely finely and densely reticulate-punctate, with scattered larger setal pits; tergites also densely clothed with subappressed to appressed pubescence. Setae on first gastral tergite suberect to subdecumbent, short, maximum length *ca*. 0.22.

Paratype workers. TL 11.5–12.0, HL 2.40–2.48, HW 2.40–2.62, CI 100–106, SL 1.92–2.04, SI 78–80, PW 1.88–1.96, WL 3.44–3.68, maximum diameter of eye 0.56–0.58, OI 22–23 (3 measured). As holotype but mandible with 3–5 teeth. In one specimen the left mandible has 5 teeth, the right mandible 3.

Holotype worker. Kenya: Kora Res., Tana River, 22.vii.1983, 0-100 m., no. 5c, *Acacia-Commiphora* scrub (*N.M. Collins & M. Ritchie*) (BMNH).

Paratypes: 9 workers (2 dissected, on same pin), with the same data (BMNH, CASC).

This large species is immediately identified by its unmodified clypeus, characteristic gastral sculpture, short stout petiolar spines and dense propodeal and gastral pubescence. It also retains traces of a stridulitrum, absent from all other known species.

Non-paratypic material examined. Kenya: Malindi Distr., Arabuko-Sokoke For. (*Snelling & Martins*). **Tanzania**: Mkomazi Game Res., nr Dindera Dam (*A. Russell-Smith*).

Phrynoponera sveni **(Forel)**

(Figures 6a–d)

Pachycondyla (Bothroponera) sveni Forel, 1916: 398. Syntype workers, DEMOCRATIC REPUBLIC OF CONGO: no loc. (*Kohl*) (MHNG) [examined]. [Combination in *Phrynoponera* by Wheeler, W.M. 1922: 80.]

Worker. TL 10.5–11.4, HL 2.20–2.36, HW 2.15–2.26, CI 95–98, SL 1.88–2.00, SI 86–91, PW 1.76–1.88, WL 3.20–3.48, maximum diameter of eye 0.52–0.58, OI 24–27 (7 measured).

Mandible with 4 teeth, smooth with scattered setal pits; some fine striation also may be present. Median portion of anterior clypeal margin shallowly convex to almost flat, lacking a prominent tooth on each side of the midline. Dorsum of head irregularly rugose to reticulate-rugose medially, the rugae sometimes smeared and confluent, chaotic rather than well defined. More laterally on dorsum the sculpture becomes more strongly reticulate-rugose, never with sharply defined costulae that radiate from the midline. Outer pair of petiolar spines very much longer than the median spine; intermediate spines slender and distinctly shorter than the median. Gastral tergites 1 and 2 finely longitudinally costulate on a reticulate-punctate background sculpture. Gastral tergite 3 reticulate-punctate only, or with a few feeble costulae present. Mesosoma, petiole and gaster with patches of cuticle that show dull metallic blue reflections.

All specimens examined had 4 teeth on the mandible, but because other species show some variation in this, individuals with 5 teeth are probably to be expected. Cephalic sculpture is coarse and disorganised. In some specimens the reticulate rugae are quite sharply defined everywhere, the reticulae becoming more broad towards the lateral margins. In others, the rugae near the midline are close-packed and blunted, the reticulae small, and the overall appearance is of coarse but chaotic sculpture. In some other species, blue metallic reflections are frequent on the propodeal declivity and elsewhere, but in *sveni* they are more widely distributed and appear always to be present. Samples of this species have been collected from rotten logs, in leaf litter samples, in pitfall traps, and from termitaries.

Material examined. Cameroun: Mvini (*A. Dejean*); Ottotomo (*A. Dejean*). **Gabon**: Prov. Ogooue-Maritime, Res. Monts Doudou, NW Doussala (*B.L. Fisher*). **Central African Republic**: Res. Dzanga-Sangha, NW Bayanga (*B.L. Fisher*); Dzanga-Ndoki, Lidjombo (*B.L. Fisher*). **Democratic Republic of Congo**: Medje (*Lang*); no loc. (*Kohl*); Kongolo (*A. Watsham*).

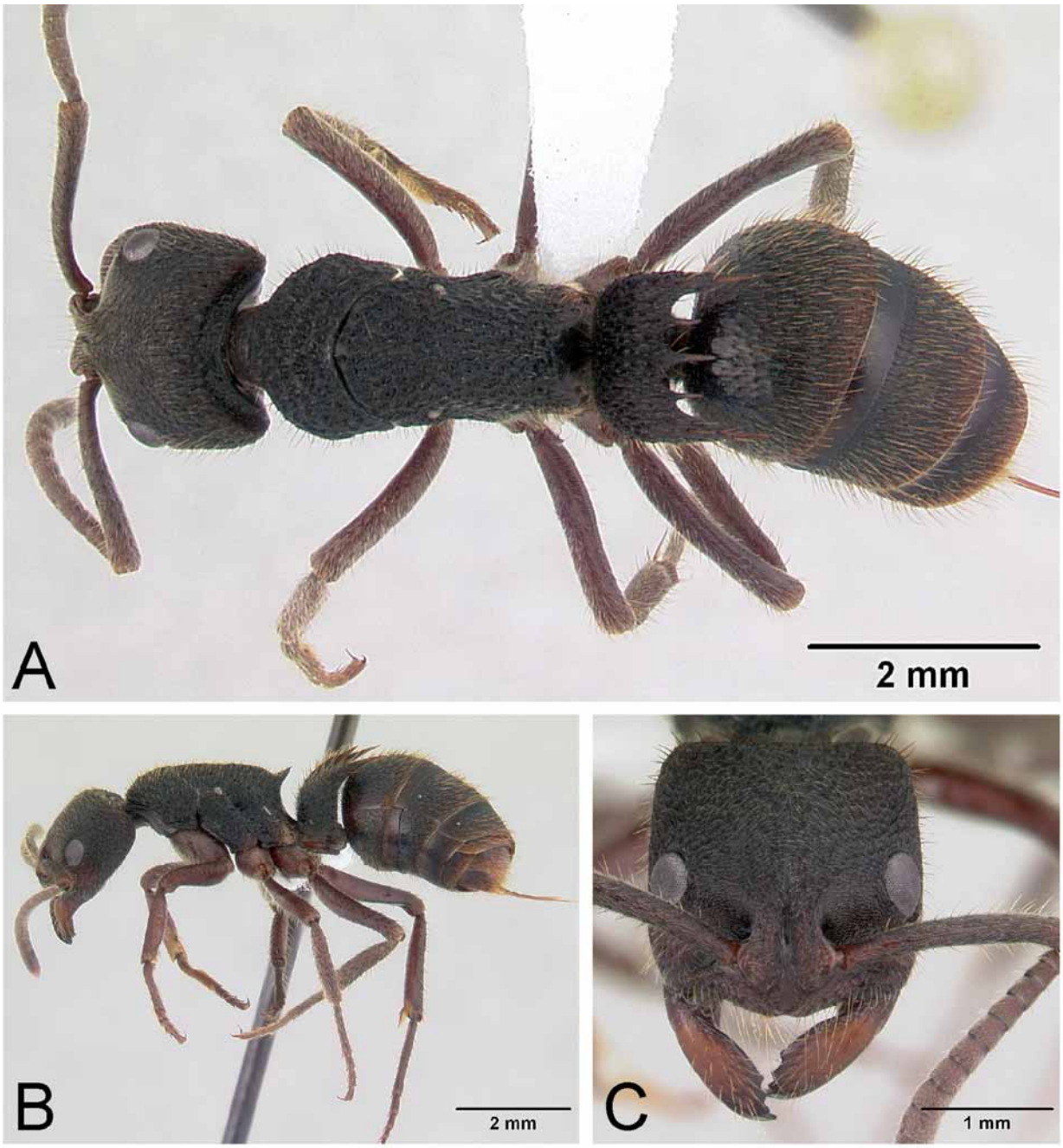

FIGURE 6. *Phrynoponera sveni* worker CASENT0417555: A, dorsal view of body; B, lateral view of body; C, full-face view of head.

Phrynoponera transversa **Bolton & Fisher sp. n.**
(Figures 7a–d)

Holotype worker. TL 9.6, HL 2.12, HW 2.08, CI 98, SL 1.66, SI 80, PW 1.76, WL 2.92, maximum diameter of eye 0.44, OI 21.

Four teeth on right mandible, 5 teeth on left; mandibles smooth with scattered pits. Anterior clypeal margin concave medially, the concavity flanked by a blunt tooth on each side. Dorsum of head transversely, concavely subsulcate from behind the level of the posterior margins of eyes to the posterior margin of the head. Posterior margin of head around midline very sharply defined, the midpoint of the vertex separated from the

occipital surface by an angle, the two surfaces not rounding together. Rugae on anterior pronotal dorsum transverse; pronotum reticulate-rugose posteriorly. Mesonotal rugae longitudinal; propodeal dorsum reticulate-rugose. Gastral tergites 1 and 2 longitudinally costulate on a densely reticulate-punctate ground sculpture. Gastral tergite 3 densely reticulate-punctate only.

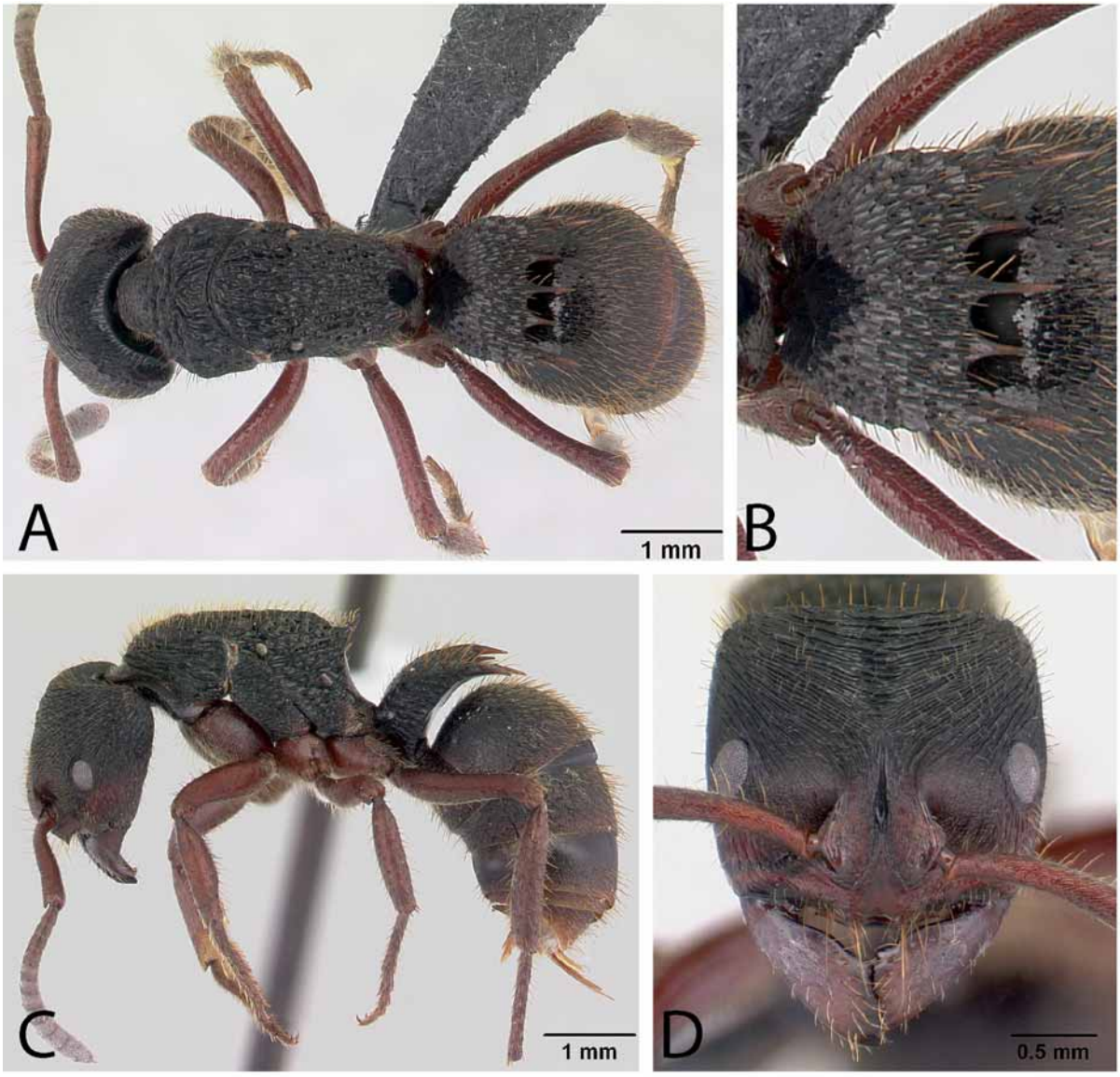

FIGURE 7. *Phyrnoponera transversa* holotype worker CASENT0178224: A, dorsal view of body; B, dorsal view of petiole; C, lateral view of body; D, full-face view of head.

Paratype workers. TL 9.5–9.8, HL 2.04–2.12, HW 1.96–2.12, CI 96–100, SL 1.60–1.68, SI 79–84, PW 1.68–1.80, WL 2.80–3.00, maximum diameter of eye 0.42–0.45, OI 20–22 (8 measured). The paratypes and non-paratypic material show the following variation. Mandible with 4–6 teeth, but typically with 5. Mandible usually completely smooth except for scattered pits but some workers with faint traces of weak striation between the pits in their apical halves. Extent of the transverse subsulcate sculpture on the head varies from almost the entire dorsum behind the level of the eyes, to a broad triangular posteromedian patch, but is always conspicuous. In some the mesonotal rugae have cross-meshes and are not so obviously longitudinal as in the type-series. The costulae on gastral tergites 1–2 are generally conspicuous, but in some they are very reduced or even absent.

Holotype worker. Gabon: Prov. Ogooue-Maritime, Res Monts Doudou, 24.5 km 303° WNW Doussala, 2°14.0'S, 10°23.9'E, 18.iii.2000, 630 m, #2276; code no. 2276(23)25; sifted litter (leaf mold, rotten wood), rainforest (*B.L. Fisher*) (CASC).

Paratypes: 7 workers with same data as holotype but code nos. 2276(7)16; 2276(22)23; 2276(26)28; 2276(33)17; 2276(40)28; 2276(41)22; 2276(50)20 (CASC).

This species is immediately distinguished by its modified clypeus and the presence of transverse sculpture on the dorsum of the head behind the level of the eyes. Like the type-series, most others were retrieved from leaf litter samples, but a couple of individuals were caught in pitfall traps.

Non-paratypic material examined. Gabon: Prov. Ogooue-Maritime, Res Monts Doudou, NW Doussala *(B.L. Fisher*); Res. Moukalaba, NW Doussala (*B.L. Fisher*). **Central African Republic**: P.N. Dzanga-Ndoki, Lidjombo (*B.L. Fisher*).

Acknowledgements

Our sincere thanks to the following people who loaned types and other material. Mr Paul Brown and Ms Christine Taylor (BMNH); Dr Daniel Burckhardt (NHMB); Dr James Carpenter (AMNH); Mr Stefan Cover (MCZC); Dr Bernhard Merz (MHNG); Dr Ted Schultz (USNM); Mr Roy R. Snelling (LACM); Dr Claire Villemant (MNHN); Dr Kolo Yéo (SELN). We also thank Chris A. Schmidt and Christian Rabeling for reviewing the manuscript.

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