



# Discovery of a new phragmotic species of the ant genus *Carebara* Westwood, 1840 (Hymenoptera, Formicidae) from Cambodia

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#### **Abstract**

Several phragmotic species in the ant genus *Carebara* Westwood, 1840 with a cephalic shield are known from the Old World, but species with an anteriorly truncated head seem to be unknown until now. A new species, resembling the phragmotic workers of the ant genus *Colobopsis*, is here described as *Carebara colobopsis* Hosoishi & Yamane, **sp. nov.**, based on major and minor worker found in Cambodia. This new species is similar to *Carebara acutispina* (Xu) and *C. obtusidenta* (Xu) in some important characters, but distinguished from the latter two by distinct metanotum and deep groove in front of metanotal disc in the major worker, and longer head and deep metanotal groove in the minor worker. This is the first confirmed record of a truncated phragmotic head in the major worker of the genus *Carebara*. We propose the *Carebara acutispina* species group to include all the three species, present a diagnosis of this group, and provide a key to species based on the major and minor worker castes.

#### **Keywords**

Ants, new species, phragmosis, Southeast Asia, taxonomy, truncated head

### Introduction

The ant genus Carebara Westwood, 1840 belongs to the tribe Crematogastrini of the subfamily Myrmicinae (Ward et al. 2015). The genus is distributed worldwide, mainly in tropical and subtropical regions, and contains more than 200 described taxa (Bolton 2022). The taxonomy of Carebara in the Afrotropical and Malagasy regions was remarkably improved in recent years (Fischer et al. 2014, 2015; Azorsa and Fisher 2018). In Asia, several taxonomic studies have been conducted for species of Japan (Terayama et al. 2014), China (Li and Tang 1986; Wu and Wang 1995; Zhou and Zheng 1997; Xu 2003; Zhou et al. 2006), Taiwan (Terayama et al. 2012), Thailand (Jaitrong et al. 2021), and India (Bharti and Kumar 2013). In contrast, little attention has been paid to the species of Southeast Asia except for Thailand, one of the species-rich areas for Carebara, especially for species previously included in the now synonymized Oligomyrmex and Pheidologeton. Species-level identifications are challenging due to a lack of comprehensive revisions of the genus in all the Old World except Madagascar (Fischer et al. 2015; Azorsa and Fisher 2018), although species with unique morphological characters have been described in smaller taxonomic treatments (e.g., Akbar and Bharti 2017; Jaitrong et al. 2021).

Among the unique morphological characters in ants, one of the most representative is 'phragmosis' (Wheeler 1927). Phragmosis is a method in which an animal defends itself in its burrow or nest by using its own modified body structure to plug the entrances. In ants (Formicidae), phragmosis is widely known from several genera, i.e. Blepharidatta Wheeler, Colobopsis Mayr, Cephalotes Latreille, Colobostruma Wheeler, Crematogaster Lund, Pheidole Westwood, Tetraponera Smith, and Carebara Westwood (Hölldobler and Wilson 1990; Fischer et al. 2015). Fischer et al. (2015) revised the African phragmotic Carebara species with a cephalic shield in a special major worker subcaste. Their examinations suggested that the phragmosis in Carebara is not always precisely displayed by major workers, but sometimes by ergatoid queens. Other phragmotic Carebara species are known from South Asia (Forel 1902, 1913; Sheela and Narendran 1997). Fischer et al. (2015) suggested that phragmosis in Carebara evolved independently in the Old World. In these cases, phragmotic workers have the same type of concave cephalic shield on the dorsal surface of the head. The cephalic shield is formed by the depressed dorsal surface of the head, clypeus and mandibles in the major worker subcastes of those species. Whereas an anteriorly truncated head, such as in Colobopsis, has not been reported for Carebara until now.

Recently, we examined *Carebara* specimens of a phragmotic species collected from a dry evergreen forest in Cambodia. The species is considered to be distinct and new to science in that its majors have an anteriorly truncated head, which clearly distinguishes it from other Asian species of *Carebara*. In this paper, we describe this new species based on the major and minor worker subcastes. It is similar to *C. acutispina* (Xu) and *C. obtusidenta* (Xu), which have been described from Yunnan Province, China (Xu 2003). In this paper the *Carebara acutispina*-group is established, and its diagnosis and a key to species are given based on the major and minor worker castes.

### **Methods**

Most observations were made on a Leica M205C stereomicroscope. Images were taken using a Canon EOS 50D with a Canon MP-E 65 mm 1–5 × Macro lens and a Leica DFC 450 digital imaging system, then processed using Combine ZM (Hadley 2010).

Specimens used in this study were collected during expeditions in Cambodia under the Memorandum of Understanding (MOU) between Japan and Cambodia, Kyushu University, Japan and the Forestry Administration, Cambodia, on cooperation concerning biological resources and information. The materials are shared between Cambodia and Japan, but the present materials are deposited in Japan, on indefinite loan from Cambodia. Type specimens were examined and/or deposited in the Institute of Tropical Agriculture, Kyushu University, Fukuoka, Japan (KUEC).

Measurements were made under a Leica M205C stereomicroscope using micrometers. All measurements are expressed in millimeters, recorded to the second decimal place. Measurements and morphological terminology follow Fischer et al. (2014) and Azorsa and Fisher (2018). Abbreviations of measurements and indices are as follows:

- HL head length: maximum length of head in full-face view between lines drawn across anterior margin of clypeus and lines drawn across the posterolateral corners of head;
- **HW** head width: width of head directly behind the eyes measured in full-face view;
- **SL** scape length: maximum scape length excluding basal condyle and neck;
- ML mandible length: the straight-line length of the mandible at full closure from the mandibular apex to the clypeal margin;
- **EL** eye length: maximum diameter of compound eye measured in oblique profile view;
- **EM** eye to mandible: distance from base of compound eye to the mandibular insertion, measured in profile view;
- **HD** head depth: maximum depth of head in profile view measured perpendicular to full-face view plane;
- WL Weber's length: diagonal length of mesosoma in profile view from the postero-ventral margin of the propodeal lobe to the anterior-most point of the pronotal slope, excluding the neck;
- **PSL** propodeal spine length: length of propodeal spine or posterodorsal corner of propodeum, measured from center of the propodeal spiracle to the tip of the spine of the posterodorsal corner of propodeum;
- PW pronotal width: maximum width of pronotum measured in dorsal view;
- **MFL** femur length: length of the profemur measured along its long axis in posterior view;
- **MFW** femur width: maximum width of the hind femur;
- MTL tibia length: maximum length of hind tibia;
- PTL petiole length: maximum length of petiole, measured in profile view;

**PTH** petiolar node height: maximum height of petiolar node measured in profile view from the highest (median) point of the node to the ventral outline;

**PNL** petiolar node length: maximum length of petiolar node measured in dorsal view;

**PTW** petiolar node width: maximum width of dorsal face of petiolar node measured in dorsal view;

**PSD** propodeal spiracle diameter: maximum length of propodeal spiracle in profile view:

**DPSD** distance from propodeal spiracle to declivity: minimum distance from posterior border of propodeal spiracle to declivity of propodeum;

PPL postpetiole length: maximum length of postpetiole measured in profile view;
 PPNL postpetiole node length: maximum length of postpetiole measured in dorsal view;

PPH postpetiole height: maximum height of the postpetiole measured in profile view from the highest (median) point of the node to the ventral outline. The measuring line is placed at an orthogonal angle to the ventral outline of the node;

PPW postpetiole width: maximum width of postpetiole measured in dorsal view;
 GL gaster length: maximum length of the gaster measured in profile view;
 GW gaster width: maximum width of the gaster measured in dorsal view;

CI cephalic index: 100\*HW/HL; MI mandibular index: 100\*ML/HL; SI scape index: 100\*SL/HL;

MLI metafemur length index: 100\*FL/HL;
PPLI postpetiole length index: 100\*PPL/PTL;
PPI postpetiole width index: 100\*PPW/PTW;
PSI propodeal spine index: 100\*PSL/HW.

### Results

## The Carebara acutispina-group

Carebara acutispina (Xu, 2003) Carebara colobopsis Hosoishi & Yamane, sp. nov. Carebara obtusidenta (Xu, 2003)

**Diagnosis.** The *Carebara acutispina* group can be distinguished from other Asian *Carebara* species by the following character conditions: (1) mandible with five teeth, but six teeth in the phragmotic major worker in *C. colobopsis*; (2) 9-segmented antennae; (3) posterolateral corner of head with a horn in major worker; (4) promesonotum convex in major worker; (5) developed propodeal spines; (6) propodeal declivity with lateral lamellae.

**Notes.** The members of this group are similar to *Carebara wheeleri* (Ettershank) in having features (2), (3) and (5), but can be distinguished from the latter by having the aforementioned feature (1). The species group is known from southern China and Cambodia, but has not been recorded from the neighboring regions (e.g., Vietnam, Thailand).

### Key to the Carebara acutispina-group species based on the major worker

The following key is partly based on Xu (2003).

Key to the Carebara acutispina-group species based on the minor worker

The following key is modified from Xu (2003).

## Carebara colobopsis Hosoishi & Yamane, sp. nov.

http://zoobank.org/62D5C172-3C04-477D-B7DC-6395F018250C Figs 1–3

**Type material.** KUEC; *Holotype* (major worker); CAMBODIA: Siem Reap Province, Local Forest Administration plot, 13°43'47"N, 104°02'38"E, 13. XII. 2012, S. Hosoishi leg., SH12-Cam-135 (collection code KUECANT031). – KUEC; *Paratypes*: 2

major workers (collection code KUECANT032, KUECANT033) (KUEC), 4 minor workers (collection code KUECANT034, KUECANT035, KUECANT036, KUECANT037) (KUEC), same data as holotype.

**Non-type material examined.** Three minor workers (collection code KUECANT038, KUECANT039, KUECANT040) (KUEC), same data as holotype.

**Diagnosis of worker.** Carebara colobopsis can be distinguished from the other species in the genus by the following characters: truncated head, posterolateral corner of head with a horn, 9-segmented antennae, distinct metanotum and deep metanotal groove, propodeal declivity with lamella laterally in the major worker subcaste; longer head, 9-segmented antennae, smooth surface of promesonotum, deep metanotal groove, propodeum armed with a long acute tooth, propodeal declivity with lamella and petiolar venter with lamella along its length in the minor worker subcaste.

**Measurements and indices.** Holotype major worker: HL 0.84; HW 0.63; SL 0.29; ML 0.22; EL 0.05; EM 0.22; HD 0.53; WL 0.68; PSL 0.13; PW 0.35; MFL 0.41; MFW 0.11; MTL 0.33; PTL 0.26; PTH 0.18; PNL 0.10; PTW 0.18; PSD 0.03; DPSD 0.06; PPL 0.15; PPNL 0.10; PPH 0.14; PPW 0.19; GL 1.06; GW 0.69; CI 75; MI 26; SI 34; MLI 49; PPLI 55; PPI 106; PSI 21. Paratype major workers (n = 2): HL 0.82–0.86; HW 0.63–0.64; SL 0.28–0.30; ML 0.20–0.21; EL 0.04–0.05; EM 0.22–0.23; HD 0.53–0.55; WL 0.71–0.72; PSL 0.13–0.14; PW 0.36–0.38; MFL 0.41–0.42; MFW 0.11–0.12; MTL 0.33–0.35; PTL 0.26–0.28; PTH 0.18–



Figure 1. Carebara colobopsis sp. nov., holotype major worker (KUECANT031). Body in profile view.

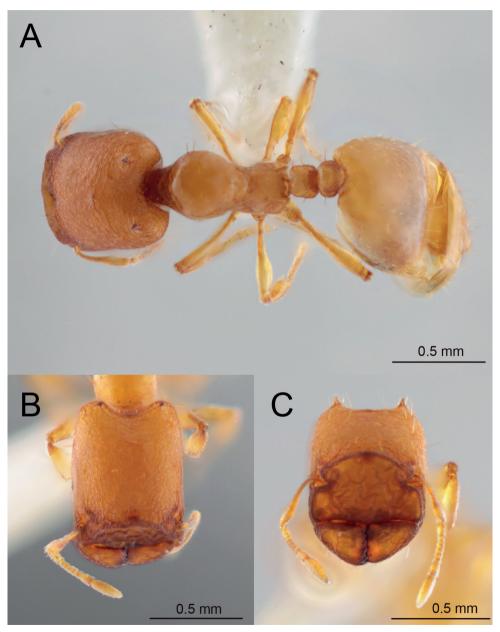
0.19; PNL 0.09–0.10; PTW 0.18–0.19; PSD 0.03–0.04; DPSD 0.06–0.07; PPL 0.14–0.15; PPNL 0.10–0.12; PPH 0.14–0.15; PPW 0.19–0.21; GL 1.00–1.39; GW 0.48–0.80; CI 73–76; MI 23–25; SI 33–35; MLI 48–50; PPLI 51–56; PPI 106–118; PSI 20–23. Paratype minor workers (n = 4): HL 0.36–0.38; HW 0.30–0.31; SL 0.23–0.24; ML 0.08–0.10; EL 0.01; EM 0.09–0.10; HD 0.21–0.22: WL 0.36–0.39; PSL 0.07–0.09; PW 0.17–0.18; MFL 0.23–0.24; MFW 0.05–0.06; MTL 0.18–0.19; PTL 0.15–0.16; PTH 0.10–0.11; PNL 0.06–0.07; PTW 0.06–0.07; PSD 0.01–0.02; DPSD 0.01–0.02; PPL 0.06–0.07; PPNL 0.06; PPH 0.06–0.07; PPW 0.08–0.09; GL 0.31–0.34; GW 0.22–0.26; CI 81–84; MI 22–26; SI 61–65; MLI 63–67; PPLI 41–46; PPI 118–139; PSI 26–28.

**Description of major worker.** Head, in full-face view, nearly rectangular, long, about 1.3 times as long as wide (CI 73-76), phragmotic with truncated anterior surface of head; posterior margin medially concave; posterolateral corner rounded; lateral margin straight to weakly convex. Posterolateral corner of head with a distinct, acute tooth resembling a horn. Supraclypeal area with deep transverse concavity located just behind posterior margin of clypeus. Clypeus entirely involved in phragmotic shield, margined throughout with continuous high rim; anterior margin medially and laterally very shallowly emarginate. Head, in profile view, gradually narrowed posteriad, with straight anterior margin; dorsal and ventral margins shallowly convex; anterior portion (phragmotic shield) separated from posterior portion by right-angled bent just in front of antennal socket. Ocelli absent. Compound eyes small, consisting of five to six ommatidia (EL 0.05). Mandibles in frontal view roughly triangular, taking part in round phragmotic shield; masticatory margin straight with six low and blunt teeth; basal margin shallowly convex; outer margin evenly curved. Antenna with nine segments; scape short (HL 0.82-0.86, SL 0.28-0.30, SI 33-35) not surpassing cephalic midlength, basally narrow and widening apicad; third to seventh antennal segments short, globular; apical two segments forming distinct club.

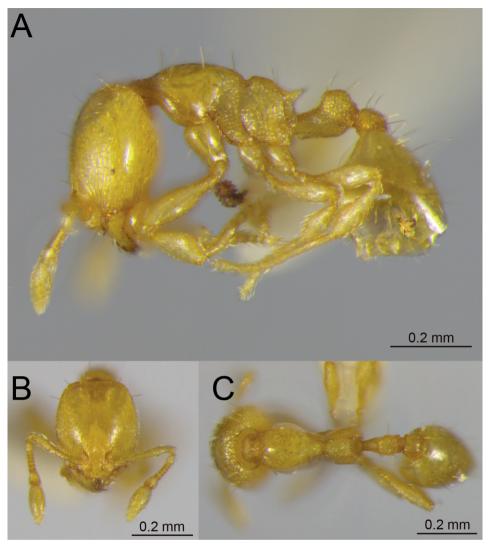
With mesosoma in dorsal view, pronotum globular, large, occupying most of mesosoma; mesonotum small, transverse, nearly as wide as propodeum; promesonotal suture faint; metanotum forming narrow, elevated band; dorsal face of propodeum wider than long; not defined from posterior declivity with carina; both dorsal and posterior faces flanked with high lamellae. In profile view, promesonotum high and dome-like; mesopleuron weakly differentiated into upper and lower portions; lower portion anteriorly and ventrally margined with carinae; metanotum separated from mesonotum and propodeum by deep furrows. Propodeum higher than long, with dorsal outline almost flat, armed at posterior angle with an angulate tooth posterodorsally directed; posterior margin lamellate; propodeal lobe triangular. Propodeal spiracle round and situated slightly above mid-height of sclerite, and slightly posterior to mid-length of sclerite; distance from propodeal spiracle to posterodorsal corner of propodeum (PSL 0.13–0.14) about four times the diameter of spiracle (PSD 0.03–0.04), and distance to declivity (DPSD 0.06–0.07) about twice the diameter of spiracle.

Petiolar node, in dorsal view, wider than long (PTW 0.18–0.19, PNL 0.09–0.10); petiolar peduncle long, longer than wide, widened posteriad. Postpetiolar node nearly

rectangular in outline, wider than long, slightly wider than petiolar node (PPW 0.19–0.21, PTW 0.18–0.19). Petiole, in profile view, longer than high (PTL 0.26–0.28, PTH 0.18–0.19) and with long peduncle; ventral outline of petiole nearly flat, anteriorly with subpetiolar process that is reduced to a small convexity; node differentiated



**Figure 2.** *Carebara colobopsis* sp. nov., holotype major worker (KUECANT031) **A** body in dorsal view **B** head in full-face view **C** close-up of cephalic shield.



**Figure 3.** *Carebara colobopsis* sp. nov., paratype minor worker (KUECANT034) **A** body in profile view **B** head in full-face view **C** body in dorsal view.

from peduncle by rather distinct flection; node apically blunt, with posterior outline convex and with similar inclination as anterior outline. Postpetiolar node rounded and lower than petiolar node.

Dorsal surface of head (frons and vertex) finely reticulate-rugose, with interspaces closely punctate; irregular short rugulae present just behind posterior margin of cephalic shield; posterior one-fourth of head dorsum with irregular transverse rugulae especially around horns; horn with longitudinal rugulae which extend to tip; dorsolateral face of head areolate-rugose. Upper two-thirds of phragmotic shield (mainly clypeus) finely shagreened and mat, with irregularly arranged stout rugulae.

In profile, lateral face of head closely and minutely punctate; posterolateral portion of cephalic dorsum finely areolate-rugose. Dorsum of mandibles (constituting lower one-third of phragmotic shield) with similar surface sculpture as in upper portion of phragmotic shield. Pronotum almost entirely smooth and shiny, with polka-dot pattern seen through transparent cuticle; narrowed anterior portion (neck) and anterolateral area closely punctate and mat to coriaceous. Mesonotum superficially punctate and rather shiny; mesopleuron generally smooth and shiny. Metanotum (elevated narrowly transverse sclerite) sparsely punctate and shiny; furrows flanking it anteriorly and posteriorly minutely punctate and mat; metapleuron entirely closely puncto-reticulate. Propodeum entirely puncto-reticulate including spines and lateral lamellae on declivity. Petiole and postpetiole closely puncto-reticulate except for posterior face of postpetiole weakly rugose and dorsal central portion of postpetiole smooth and shiny. Gaster smooth and shiny, with anterior narrowed portion striate.

Dorsal face of head with erect hairs sparsely, mixed with sparse appressed pubescence; anterior portion or cranium just behind phragmotic shield with three pairs of erect hairs (two pairs on supraclypeal area anteriorly and laterally, and one pair near antennal socket); lateral margin of head with few long hairs, and posterolateral corner of head around horn with suberect to curved hairs of various length. No visible hairs on cephalic shield. Outer margin of mandible with inconspicuous short appressed hairs; ventral face with erect or suberect hairs. Scape with appressed short hairs, without erect hairs. Promesonotum with less than ten long and fine erect hairs and sparse appressed pubescence. Propodeum often with a pair of suberect hairs. Petiole and postpetiole each with a pair of long suberect hairs and some decumbent hairs. Gaster with rather long appressed pubescence and long suberect hairs sparsely. Tibiae with decumbent hairs, without standing hairs. Body yellowish ferruginous; legs and parts of gaster, slightly lighter.

**Description of minor worker.** Head, in full-face view, long, about 1.2 times as long as wide (CI 81–84), weakly subrectangular and slightly narrowed anteriorly; posterior margin almost straight, posterolateral corners rounded, and lateral margins convex. Frontal lobes elongate, widened anteriad, covering antennal sockets; frontal carinae short, as long as frontal lobe, diverging posteriad, with anterior two-fifths thickened. Frontal triangle distinct, shallowly depressed. Clypeus posteriorly extends to level of anterior extremity of frontal carina, between lobes almost as wide as lobe. Median disk of clypeus with fine lateral carinae that diverge anteriad; anterior margin of clypeus widely shallowly emarginate, with roundly angulate lateral corners that are lamellate; the lamella extends entire length of lateral margin of median disk of clypeus. Eyes present, consisting of one ommatidium (EL 0.01). Mandibles with five teeth. Antennae with nine segments; scape fails to reach posterior margin of head (HL 0.36–0.38, SL 0.23–0.24, SI 61–65).

In dorsal view, pronotum large, longer than wide; main sclerite round with anterior margin nearly straight and lateral margin roundly convex; prescutum (neck) of pro-

notum rather wide, slightly less than two-thirds as wide as main sclerite. Mesonotum not clearly demarcated from pronotum, narrower than the latter, tapered posteriad. Metanotal groove distinct, transverse, laterally margined with carinae. Propodeal dorsum longer than wide, widened posteriad, with long spines slightly directed outwardly. In profile view, promesonotum moderately and roundly convex dorsally. Pronotum with distinctly defined prescutum. Mesopleuron clearly differentiated from pronotum and metapleuron, divided into upper and lower portions by type of sculpture; lower portion anteriorly margined with distinct lamella. Metanotal groove impressed. Propodeum not clearly demarcated from metapleuron, about 1.5 times as high as long, with distinct dorsal face declining posteriorly, spines long and acute, posterodorsally directed and ventrally equipped with lamella that continues along posterior margin of declivity; the latter portion of lamella inflated below. Propodeal lobe triangular; spiracle rounded and situated slightly above mid-height of sclerite, and close to posterior margin of propodeum; distance from propodeal spiracle to posterodorsal corner of propodeum (PSL 0.07–0.09) much longer than diameter of spiracle (PSL 0.01–0.02), and distance to declivity (DPSD 0.01-0.02) as large as diameter of spiracle.

With waist in dorsal view, petiolar node as wide as long (PTW 0.06–0.07, PNL 0.06–0.07), and postpetiolar node slightly wider than petiolar node (PPW 0.08–0.09, PTW 0.06–0.07). Postpetiole wider than long, slightly wider than petiole. In profile view, petiole longer than high (PTL 0.15–0.16, PTH 0.10–0.11) with relatively long peduncle; sternite ventrally equipped with lamella over its length and has almost straight outline. Petiolar node demarcated from anterior peduncle by distinct bent; its dorsum with flat outline, and longer than anterior slope and as long as posterior slope; posterior margin of node convex. Subpetiolar process forming a blunt denticle, its height measuring almost same as diameter of propodeal spiracle. Postpetiole much smaller and lower than petiole and globular; node weakly convex dorsally. Anterolateral corners of first gastral tergite distinctly tuberculate.

Dorsal surface of head including clypeus principally smooth, except for frontal lobe, lateral transverse area of clypeus and area between antennal socket and outer margin of head that are longitudinally rugose; anterior slope of clypeus punctate. Lateral and ventral faces of head principally smooth and shiny. Mandibles nearly smooth on dorsal face, superficially sculptured on laterobasal portion. Promesonotum smooth and shiny, except for prescutum (neck) of pronotum and posterior extremity of mesonotum puncto-reticulate. Lower portions of mesopleuron and metapleuron punctate; upper portions of mesopleuron and metapleuron smooth. Dorsal surface and posterior declivity (upper half) of propodeum densely punctate (punctures larger than those on mesopleuron); lower half of declivity smooth. Petiole and postpetiole densely punctate, except for dorsal central portion of postpetiole very weakly sculptured and shiny. Gastral tergites smooth and shiny except for presclerite of first tergite densely sculptured.

Dorsum of head with sparse appressed/decumbent short hairs and a few erect hairs; lateral margin and posterior margin of head sparsely with erect/suberect hairs.

Scape with short decumbent hairs. Outer margin of mandible with decumbent hairs. Mesosoma with four pairs of erect hairs, one pair on pronotum, two pairs on mesonotum, and one pair on propodeum. Petiole and postpetiole each with two pairs of erect/suberect hairs; gaster with sparse suberect hairs. Femora and tibiae with decumbent hairs. Color yellow.

**Remarks.** This species belongs to the *C. acutispina* group. In the major worker it is easily distinguished from the other Asian members of the genus by the combination of the following conditions: the anteriorly truncated head, posterolateral corner of head with a horn, 9-segmented antennae, distinct metanotal disc, deep groove in front of the disc, developed propodeal spines, and laterally lamellate propodeal declivity. Minor workers characteristically have lamellae on the venter of the petiole and on the lateral margins of the propodeal declivity (the lamella on the propodeal declivity involves propodeal spine and extends anteriad up to the anterior margin of the propodeal dorsum as a low carina), and sparse erect hairs on the body.

**Habitat.** The type series was collected from leaf litter in a lowland dry evergreen forest (Fig. 4).



**Figure 4.** Forest habitats on lowland dry evergreen forest, Siem Reap Province, Cambodia, the type locality of *Carebara colobopsis* sp. nov. (S. Hosoishi).

**Distribution.** This species is only known from the type locality in Cambodia. **Etymology.** The species name refers to the anteriorly truncated head of the major worker subcaste.

### Discussion

This is the first confirmed record of a truncated phragmotic head in the major worker of the genus *Carebara*. Among Asian *Carebara* fauna, the three species, *C. butteli* (Forel, 1913), *C. lamellifrons* (Forel, 1902) and *C. nayana* (Sheela & Narendran, 1997) are known as the phragmotic species with a depressed cephalic shield. Forel (1913) suggested that *C. butteli* is similar or conspecific to *C. lamellifrons*, but concluded that *C. lamellifrons* is different in having the developed rugulae on head, much less concave frons and occipital region not emarginated. In his paper, Forel (1913) established the subgenus *Lecanomyrma* of *Pheidologeton* based on a depressed cephalic shield in *C. butteli* (as *P. butteli*) and *C. lamellifrons* (as *P. lamellifrons*). Emery (1924) transferred the two species to *Aneleus* (*Lecanomyrma*). Ettershank (1966) treated them as members of the genus *Oligomyrmex*, then Fernández (2004) synonymized the genus *Oligomyrmex* under the genus *Carebara*.

The Afrotropical species *C. phragmotica* has a dimorphic major subcaste, one with the phragmotic head and the other with the regular head shape (Fischer et al. 2015). The regular major workers are so far unknown in *C. colobopsis*. Although our material is limited, all the major workers examined had an anteriorly truncated head. The regular major workers are also unknown for South Asian species, *C. butteli, C. lamellifrons* and *C. nayana*. Those incomplete collections are possibly due to the rarity of the phragmotic species (Fischer et al. 2015). The nest series samples might reveal the occurrence of the regular major workers in Asian phragmotic *Carebara* species in the future.

The phragmotic *Carebara* species seem to share several morphological trends (Table 1), but separated based on the antennal counts into three geographical members: Southeast Asian (*C. colobopsis*), South Asian (*C. butteli*, *C. nayana*, *C. lamellifrons*) and Afrotropical (the *Carebara phragmotica* species clade: *C. elmenteitae* (Patrizi, 1948); *C. lilith* Fischer, Azorsa & Hita Garcia, 2015; *C. phragmotica* Fischer, Azorsa & Hita Garcia, 2015). The number of antennal segments are considered one of the

<b>Table 1.</b> Character states of the phragmo	otic <i>Carebara</i> major	workers. Carebara	<i>lamellifrons</i> is not shown
here because the major worker caste is un	known.		

Species	Antennal	Horn on posterolateral	Metanotum	Propodeal	Propodeal	Reference
	segments	corner of head		spines	declivity	
Carebara colobopsis	9	present	present	present	lamellate	This study
Carebara nayana	11	present	?	present	?	Sheela and Narendran (1997)
Carebara butteli	11	present	?present	present	?lamellate	Forel (1913)
Carebara phragmotica	10	present	present	present	lamellate	Fischer et al. (2015)
Carebara elmenteitae	10	absent	present	present	lamellate	Fischer et al. (2015)
Carebara lilith	10	present	present	present	lamellate	Fischer et al. (2015)

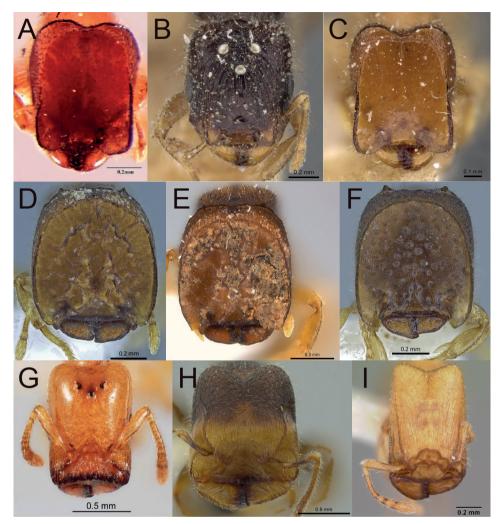
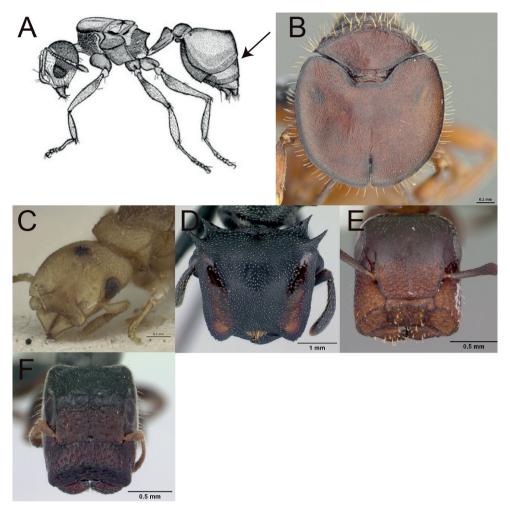


Figure 5. Phragmotic ants A Carebara nayana worker (Lubertazzi) B Carebara lamellifrons queen, CASENT0908890 (Zach Lieberman) C Carebara butteli worker, CASENT0908888 (Zach Lieberman) D Carebara phragmotica phragmotic major worker, CASENT0709550. Image from Fischer et al. (2015) E Carebara elmenteitae phragmotic major worker, CASENT0217087 (Erin Prado) F Carebara lilith phragmotic major worker, CASENT0709545. Image from Fischer et al. (2015) G Crematogaster cylindriceps queen. Image from Yamane et al. (2011) H Pheidole colobopsis worker, CASENT0619464 (Jeremy Pilllow) I Pheidole lamia worker, CASENT0104664 (April Nobile). www.AntWeb.org.

phylogenetically important characters in ants (e.g., Sparks et al. 2019). This suggests that the phragmotic mode of life evolved independently in different lineages, although a comprehensive phylogeny of *Carebara* has not been presented.

The truncated head shape in the major worker of *Carebara colobopsis* sp. nov. represents a type of phragmosis seen in ants, but is different from those found in the



**Figure 6.** Phragmotic ants (continued) **A** *Pheidole embolopyx* queen. Arrow indicates the phragmotic shield on gaster. Modified from Brown (1968) **B** *Blepharidatta conops* worker. Image from Brandão et al. (2015) **C** *Colobostruma leae* holotype queen (Steve Shattcuk) **D** *Cephalotes atratus* soldier worker, CASENT0178627 (April Nobile) **E** *Colobopsis cerberula* major worker, CASENT0104765 (April Nobile) **F** *Tetraponera phragmotica* major worker, CASENT0136420 (April Nobile). www.AntWeb.org.

Afrotropical (*C. elmenteitae*, *C. lilith*, *C. phragmotica*) and South Asian *Carebara* species (*C. butteli*, *C. lamellifrons*, *C. nayana*). The truncated area is composed of clypeus and mandibles in *C. colobopsis*, while it is the depressed dorsal surface of the cranium, clypeus and mandibles in the above-mentioned species. As mentioned earlier, phragmosis has been reported from several ant genera (Figs 5, 6, Table 2). The phragmotic head in *C. colobopsis* is similar to those in *Crematogaster cylindriceps* W. M. Wheeler, 1927, *Pheidole lamia* W. M. Wheeler, 1901, and *Tetraponera phragmotica* Ward, 2006 rather than those in other phragmotic *Carebara* species.

Subfamily	Taxon	Caste	Body parts used for	Distribution	Reference
·			phragmosis		
Myrmicinae	Carebara colobopsis	major worker	Clypeus, mandible	Southeast Asia (Cam- bodia)	This study
Myrmicinae	Carebara nayana	major worker	Cranium, clypeus, mandible	South Asia (India)	Sheela and Narendran (1997)
Myrmicinae	Carebara lamellifrons	queen	Cranium, clypeus	South Asia (India)	Forel (1902, 1913), Emery (1924)
Myrmicinae	Carebara butteli	major worker	Cranium, clypeus, mandible	South Asia (Sri Lanka)	Forel (1913), Emery (1924)
Myrmicinae	Carebara phragmotica	major worker	Cranium, clypeus, mandible	Africa (Kenya)	Fischer et al. (2015)
Myrmicinae	Carebara elmenteitae	major worker	Cranium, clypeus, mandible	Africa (Kenya)	Fischer et al. (2015)
Myrmicinae	Carebara lilith	major worker	Cranium, clypeus, mandible	Africa (Ivory coast)	Fischer et al. (2015)
Myrmicinae	Crematogaster cylin- driceps	queen	Clypeus, mandible	Southeast Asia (Ma- laysia)	Wheeler (1927), Yamane et al. (2011)
Myrmicinae	Pheidole colobopsis	major worker, queen	Cranium, clypeus, mandible	New World tropics	Mann (1916), Wilson (2003)
Myrmicinae	Pheidole lamia	major worker	Clypeus, mandible	United States, Mexico	Wheeler (1901), Wilson (2003)
Myrmicinae	Pheidole embolopyx	queen	Gaster	South America	Brown Jr (1968)
Myrmicinae	Blepharidatta conops	queen	Cranium, pronotum	New World tropics	Brandão et al. (2001)
Myrmicinae	Colobostruma leae	worker, queen	Cranium, clypeus, mandible	Australia	Wheeler (1927), Shattuck (2000)
Myrmicinae	Cephalotes	major worker, queen	Cranium	New World tropics	Oliveira et al. (2021)
Formicinae	Colobopsis	major worker, queen	Cranium (malar), clypeus, mandible	Palearctic, Oriental, Australian, New World (part)	Ward et al. (2016)
Pseudomyr-	Tetraponera	major worker,	Clypeus, mandible	Madagascar	Ward (2006)
mecinae	phragmotica	queen			

**Table 2.** Body parts used for phragmosis in ants.

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