



New ant species related to *Cerapachys sexspinus* and discussion of the status of *Yunodorylus* (Hymenoptera: Formicidae)

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Abstract

Three species related to the Chinese ant *Cerapachys sexspinus* (Xu, 2000) are described as new: *Cerapachys doryloides* n. sp. from Borneo, *C. eguchii* n. sp. from Vietnam, and *C. paradoxus* n. sp. from Borneo. Additionally, *Cerapachys sexspinus* is redescribed. A species-group diagnosis and a discussion of the group's affinities are provided, together with a key to species based on workers. All species are illustrated with photographs and a distribution map. It is recommended that the name *Yunodorylus* remain a synonym of *Cerapachys* until the taxonomy and phylogeny of the Cerapachyinae is better understood.

Key words: ants, Formicidae, dorylomorphs, Cerapachyinae, *Cerapachys*, *Yunodorylus*, taxonomy, key, new species

Introduction

In 2000, Xu introduced *Yunodorylus*, a new genus name in the Formicidae. He described a single species, *Y. sexspinus* from Yunnan province, China, and placed the genus in the subfamily Dorylinae. Due to a unique character combination seen in these ants, namely a one-segmented waist and general habitus reminiscent of doryline ants on the one hand and presence of modified, peg-like setae on the pygidium and absence of promesonotal suture on the other hand, he concluded that *Yunodorylus* may be an “interlink” in the evolution of Cerapachyinae and Dorylinae. However, Bolton (2003) synonymized the genus with *Cerapachys*, because its definition clearly includes apomorphies of the Cerapachyinae and the assumption that *Cerapachys* can only possess two waist segments is not true, as had already been shown in Bolton (1990).

Subsequently, *Cerapachys sexspinus* has been included in two important ant phylogenies, with ambiguous results. In Moreau *et al.* (2006) it appeared as sister group to *Sphinctomyrmex*, whereas in Brady *et al.* (2006) it appeared as sister group to an Aenictinae+Ectoninae clade.

The purpose of the present study is to describe the diversity of species related to *C. sexspinus* that has accumulated in collections since the original description, to provide a concise group diagnosis that can be related to other cerapachyines and to discuss group affinities based upon available data. An effort was undertaken to gain access to as much material of this group as possible. However, specimens collected in Thailand and reported as *C. sexspinus* by Jaitrong & Nabhitabhata (2005) have not been examined.

Measurements, terms, and material

Measurements were taken using Nikon SMZ 1500 and Wild M5A stereomicroscopes at 100X magnification with ocular micrometer. Color photographs were prepared using a Nikon SMZ 1500 stereomicroscope with a Nikon Coolpix 4500 digital photo camera (Figs. 1–8, 13–14) and Leica MZ 16 stereomicroscope with a JVC

digital video camera (Figs. 9–12). All images were processed using CombineZP freeware, and cleaned and adjusted using Adobe Photoshop.

HW	Head width: Maximum width in full face view. Since in this group eyes are absent, the measurement is taken across the widest point.
HL	Head length: Maximum length along midline in full face view, from the anteriormost part of the head (anterior edge of frontal lobes) to the posterior margin.
SL	Scape length: Maximum length measured without condyle and neck.
MH	Mesosoma height: In side view, maximum height measured from the lowermost point of mesopleuron (in front of middle coxa) to dorsal edge of mesosoma.
ML	Mesosoma length: In side view, maximum longitudinal distance from posteroventral corner of mesosoma to the farthest point on anterior face of pronotum, excluding the neck.
PrW	Pronotal width: Maximum width in dorsal view.
PW	Petiole width: Maximum width of abdominal segment II in dorsal view.
PL	Petiole length: Maximum length of abdominal segment II in dorsal view, measuring only the length of petiolar tergite.
III _{AW}	Third abdominal tergite width: Maximum width in dorsal view.
III _{AL}	Third abdominal tergite length: Maximum length in dorsal view, measuring only the length of posttergite, excluding pretergite III (helcium).
IV _{AW}	Fourth abdominal tergite width: Maximum width in dorsal view.
IV _{AL}	Fourth abdominal tergite length: Maximum length in dorsal view, excluding pretergite.
FFeW	Front femur width: Maximum width in side view.

All leg measurements below are taken as maximum length measured along extensor (outer) surface:

FFeL	Front femur length.
HFeL	Hind femur length.
FTiL	Front tibia length.
HTiL	Hind tibia length.
FBaL	Front basitarsus length.
HBaL	Hind basitarsus length.
CI	Cephalic index: $HL/HW \times 100$.
MI	Mesosomal index: $ML/MH \times 100$.
PI	Petiolar index: $PL/PW \times 100$.

Measurements of the holotype worker are given first, followed by ranges for all specimens measured, including the holotype. All measurements are given in millimeters.

Depositories:

BMNH	Natural History Museum, London, United Kingdom.
CASC	California Academy of Sciences, San Francisco, United States of America.
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, United States of America.
ISAS	Kunming Institute of Technology, Academia Sinica, Kunming, China.
KEPC	Katsuyuki Eguchi private collection, Nagasaki, Japan.
MLBC	Marek Borowiec private collection, Wrocław, Poland.
VNMN	Vietnam National Museum of Nature, Hanoi, Vietnam.

Two special terms used in this work are explained below.

The term '*parafrontal ridges*' is derived from Wilson's (1964) work on *Aenictus*, and is used for low lines running from lateral portions of clypeus laterad to antennal sockets, thus separating them from the genae. Such ridges are present in most Cerapachyini, but absent in many *Sphinctomyrmex*, all *Acanthostichus* and *Cylindromyrmex*.

'*Lateroclypeal tooth*' is here introduced for the modification of the lateral corners of the clypeus, which in cerapachyines can be variably developed, from being bluntly pointed to drawn into conspicuous teeth that project over the mandibles.

Characters of the species-group

In this contribution, an effort was taken to present a concise species-group diagnosis, enabling anyone working with *Cerapachys* material to distinguish these species from other groups. Modern species-group classification in Cerapachyinae is derived from work of Brown (1975), who recognized 18 informal groups in *Cerapachys*. However, he had not taken the diagnoses any further than providing very rudimentary remarks on characters such as number of antennal segments, size of the eyes, dorsolateral margination of various body parts, and geographical distribution. Apart from his preliminary key to species, he did not provide unique character combinations for each group that could constitute formal diagnoses. The present work included examination of a large amount of cerapachyine material in order to provide a good overview of characters relevant to diagnosing the *sexspinus* species-group.

Diagnosis of *sexspinus* species-group based on worker caste

Antennae with 11 or 12 segments.

Apical antennal segment not conspicuously enlarged, equal or little longer than two preceding.

Parafrontal ridges strongly reduced to absent (see note 1 below).

Two ridges present behind frontal carinae with medial impression between them.

Palp formula 2,2 (known in *sexspinus*, *paradoxus*).

Mandibles triangular, crenulate or with denticles, or elongated, with teeth.

Eyes in worker completely absent.

Ventrolateral margins of the head capsule reduced to weakly pronounced ridge.

Ocelli in workers absent.

Pronotum not marginate anterodorsally, pronotal collar not separated from dorsal surface.

Mesosoma, petiole and postpetiole not marginate dorsolaterally.

Waist of a single segment, abdominal segment IV with very broad presclerites and weak constriction between pre- and postsclerites (see note 2 below).

Fourth abdominal tergite not folding over sternite, and anterior portions of sternite and tergite are equally well visible in side view.

Spur formula 2(1s,1p),2(1s,1p) (see note 3 below).

Middle and hind basitarsi not widening distally, circular in cross-section.

Posterior flange of hind coxa not produced as raised lamella.

Metatibial glands with no discernible orifice, visible as a lighter, round to elongate patch of cuticle devoid of pubescence.

Pretarsal claws simple.

Polymorphic (see note 4 below).

Characters in italics are hypothetical autapomorphies of the group. They could not be seen in any other *Cerapachys* or other species of the Cerapachyinae available at the time of this study and are apparently unique for the whole subfamily.

Note 1. Absence of parafrontal ridges is characteristic of this group but can be observed in at least one species outside the group, namely Australian *Cerapachys edentatus* (Forel, 1900). However, this unrelated

species is easily distinguished by having 9 antennal segments and small abdominal segment III, differentiated as postpetiole. Many *Sphinctomyrmex* have parafrontal ridges reduced to absent. Since monophyly of both *Cerapachys* and *Sphinctomyrmex* is questioned (Brown 1975, Brady *et al.* 2006), at this point it is not possible to say how many times this feature appeared or disappeared in the subfamily.

Note 2. In *Cerapachys* the abdominal segments III and IV are externally separated by at least a girdling constriction between pre- and postsclerites of segment IV. Additionally, abdominal segment III may be of various sizes, in some species of *fragosus* and *typhlus* species-groups sensu Brown (1975) being much smaller and forming what can be called a postpetiole. The species-group discussed here is an exception, having a very weak impression between pre- and postsclerites IV. Illustrated description of this character throughout the Cerapachyinae was provided by Bolton (1990).

Note 3. In the original description of *C. sexspinus* (Xu, 2000), the tibial spur condition is described as single pectinate on middle and hind tibiae. The true condition is different, as all the specimens examined possess one simple and one broadly pectinate spur on both middle and hind tibiae. Bolton (2003) lists the following character states for spur formula in *Cerapachys*: 2p,2p; 2(1s,1b-p),2(1s,1p); 1s-b,1p; 1p,1p. The formula 1p,1p is the most common, occurring in, for example, the *antennatus*-group (containing the type species of the genus), the speciose *dohertyi-cribrinodis* species-group (sensu Brown 1975), and in most species with sides of petiole margined (the '*Phyracaces* lineage' of Brown [1975]). The spur formula 1s-b,1p is characteristic for apparently arboreal species related to *C. longitarsus* (Mayr, 1879). The unique spur formula 2p,2p is present in the aberrant *crawleyi*-group (see general discussion below).

Note 4. Of the species examined here, at least *eguchii*, *paradoxus*, and *sexspinus* exhibit considerable range of body size among workers. Only one specimen of *C. doryloides* has been examined, so nothing can be said about its polymorphism. A polymorphic worker caste is also present in some apparently not related, hitherto undescribed *Cerapachys* (author's unpublished data). Due to a limited amount of material, quantitative analysis of allometry and polymorphism is not attempted here but there seems to be continuous size variation, and allometry of various body parts is weakly pronounced.

No gynes or males are known thus far and the diagnosis is based solely on worker characters.

Key to species based on worker caste

1. Antennae 11-segmented. In side view, abdominal segment III (gastral I) is small and narrow compared to the following segment, with a rounded anterior face (Fig. 7). Malaysia (Sarawak) *paradoxus*
- Antennae 12-segmented. In side view, abdominal segment III (gastral I) is not clearly narrowed, having a well differentiated, perpendicular anterior face of both posttergite and poststernite (Figs. 2, 4–5, 10) 2.
2. Mandibles elongate with masticatory margins narrow and basal margin separated from anterior margin of clypeus by a wide gap at full closure (Fig. 13). Malaysia (Sarawak) *doryloides*
- Mandibles triangular with basal margins not separated from anterior margin of clypeus by a wide gap at full closure (Fig. 11–12, 14) 3.
3. Sides of mesosoma and petiole with microreticulum easily recognizable at 50X magnification. Subpetiolar process long, curved, and claw-like (Fig. 4). Vietnam *eguchii*
- Sides of mesosoma and petiole at 50X magnification appearing matted, not recognizable as microreticulum. Subpetiolar process smaller, with ventral margin drawn into a triangle directed slightly posteriorly (Fig. 10). China (Yunnan) *sexspinus*

Species accounts

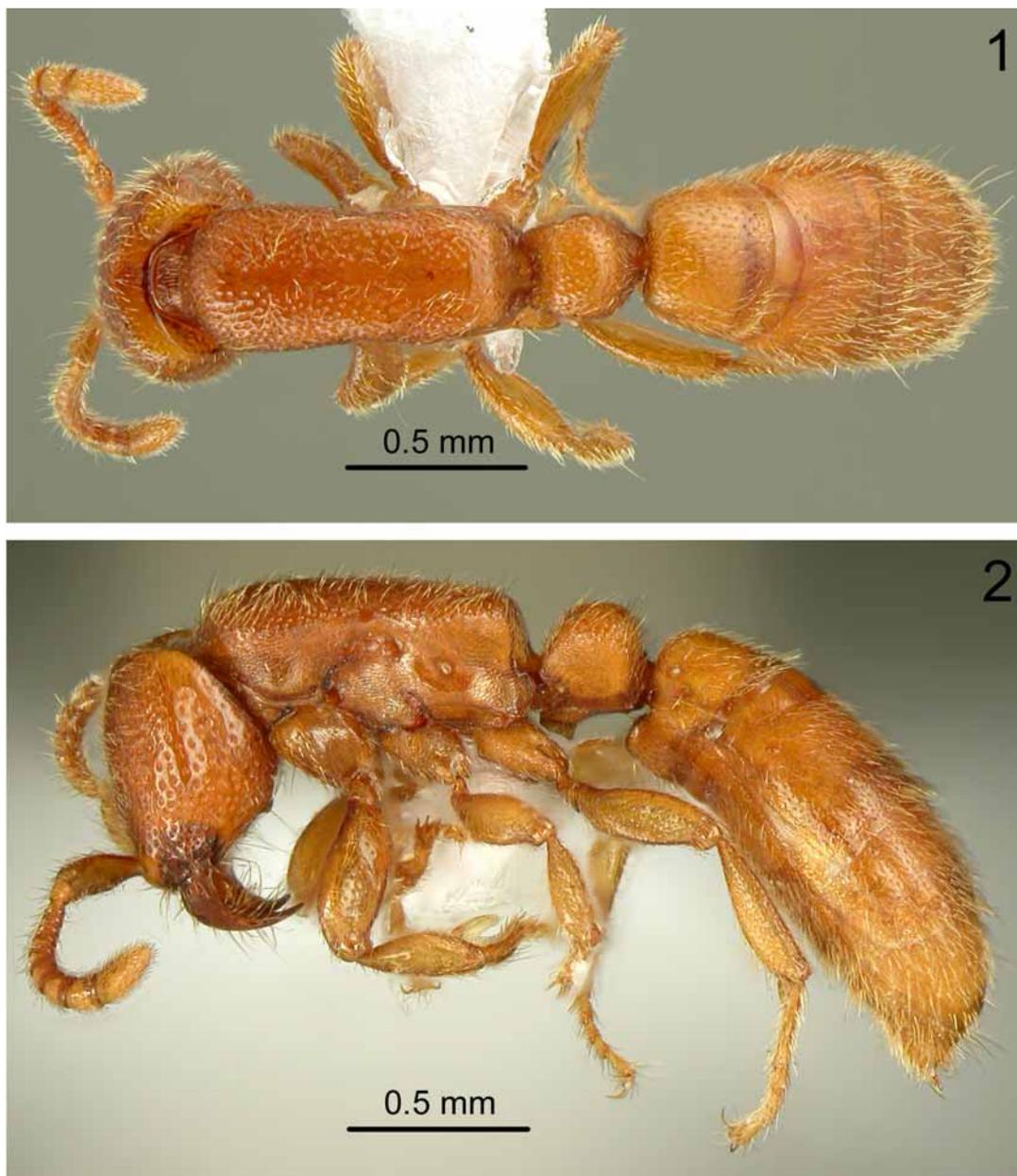
Cerapachys doryloides n. sp.

Figs. 1–2, 13

Holotype worker measurements: HW 0.62, HL 0.64, SL 0.32, MH 0.41, ML 0.95, PrW 0.42, PW 0.31, PL 0.30, IIIAW 0.45, IIIAL 0.35, IVAW 0.60, IVAL 0.41, FFeW 0.19, FFeL 0.45, HFeL 0.45, FTiL 0.37, HTiL

0.47, FBaL 0.23, HBaL 0.29, CI 103, MI 232, PI 97

Head almost as wide as long, widest at about midlength; sides parallel, slightly convex and converging anteriorly and posteriorly at about one fifth of head length; vertexal margin shallowly concave. Parafrontal ridges completely absent. Mandibles narrow and long; when closed, basal margin separated from anterior clypeal margin by wide gap. Basal margin long, meeting masticatory at obtuse angle; masticatory margin with two blunt teeth basally; remainder of margin elongated into broadly rounded apical tooth. Lateroclypeal tooth a small tubercle. Lateral portion of clypeus poorly developed, consisting only of semi-circular ridge surrounding antennal insertion. Antennae 12-segmented. Palp formula unknown.



FIGURES 1–2. *Cerapachys doryloides* n. sp., holotype worker; 1: dorsal view; 2: side view.

Mesosoma moderately stout, rectangular in dorsal view; dorsal surface flattened, bordered at the lateral sides by a distinct angle but with no margin. Openings of propodeal spiracles broadly oval, directed outwardly and upwardly at angle of 45°. Declivous face of propodeum immarginate above propodeal lobes. Propodeal lobes very small. Front femur short, very broad, and laterally compressed. Metatibial gland a whitish, elongate patch of cuticle, little longer than maximum width of hind tibia.

Petiole about as long as wide, with well developed dorsal and posterior faces. Subpetiolar process short and moderately broad; in side view with ventral margin sloping towards posterior end; translucent narrowing present along ventral margin, lamella gradually widening distally.

Abdominal tergite III wide relative to following segment, in side view the whole segment is robust, with developed anterior, perpendicular face.

Pygidial field small, weakly impressed with four teeth on each side.

Hypopygidium unarmed.

Mandibles sculptured with widely spaced punctures, interspaces shining. Head with regular punctures, spaced from about half of their diameter on dorsal and anterior lateral surfaces, to wider than diameter in posterior lateral section. Similar sculpture on dorsal surface of mesosoma with longitudinal stripe devoid of sculpturation in middle. All interspaces shining. Lateral sides of mesosoma microreticulate, only area around propodeal spiracle devoid of any sculpture and shining. Sides of petiole microreticulate.

Body pilosity composed of (1) dense, subdecumbent hairs present on head, mesosoma, and abdominal segments and (2) about one and half times longer, subdecumbent to suberect hairs present on the pronotal shoulders, propodeum, petiole, margins of gastral tergites. Outer surface of middle tibiae with two modified peg-like setae.

Color: yellowish-orange with brownish mandibles and genal areas around mandibular insertions.

Gyne and male unknown

Diagnosis and discussion. This species is most easily recognized by its peculiar falcate mandibles, unique in described workers of Cerapachyinae. These are elongate, somewhat resembling the condition observed in *Dorylus*, with the narrow masticatory margin equipped with two (excluding apical) well visible teeth and meeting the long basal margin at an obtuse angle, resulting in a wide gap between mandibles and clypeal margin at closure (Fig. 13).

Since only one specimen of this species was available for study, nothing can be said of individual variability and degree of worker polymorphism.

Material examined. Holotype worker. MALAYSIA: Sarawak, Bako National Park, near Kuching, rainforest, soil core, IV 1978 (*N.M. Collins*) [BMNH]

Cerapachys eguchii n. sp.

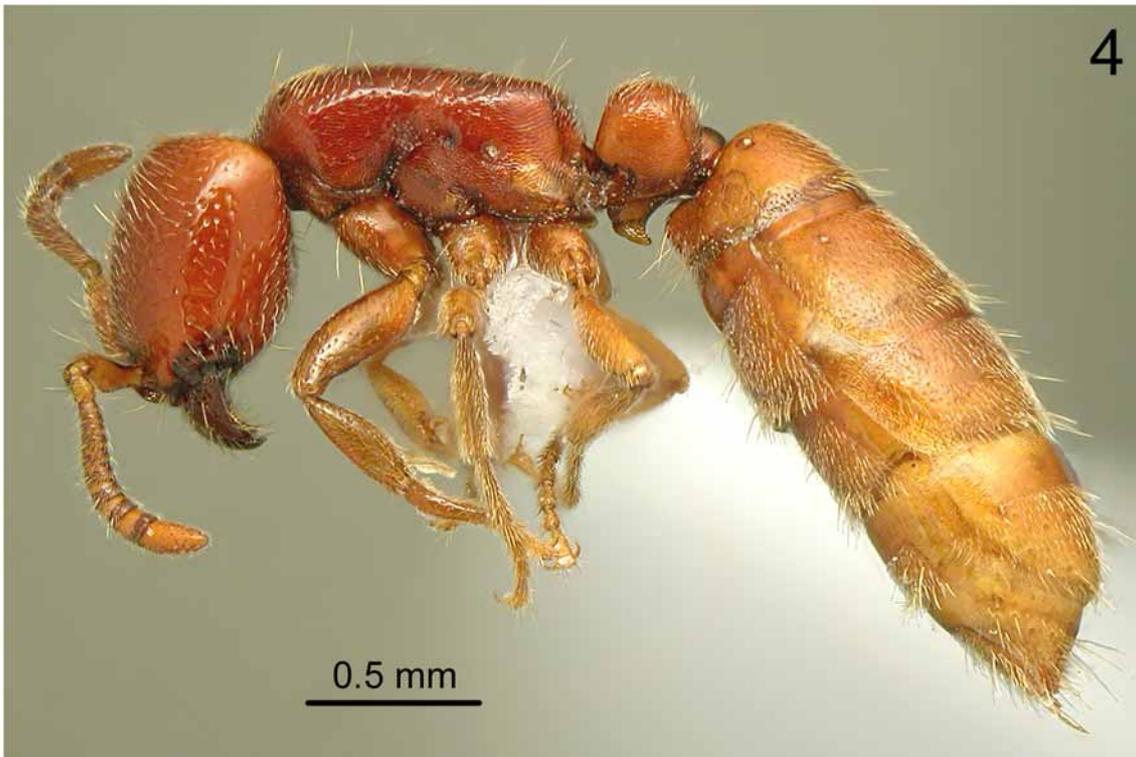
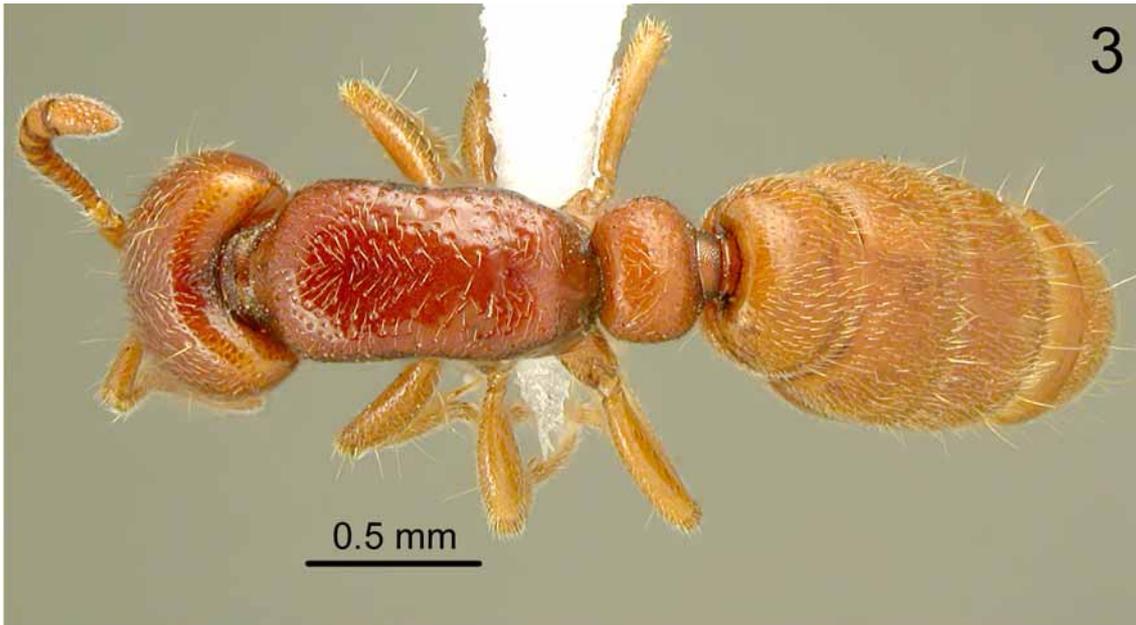
Figs. 3–5, 12

Holotype worker measurements: HW 0.70, HL 0.75, SL 0.35, MH 0.44, ML 0.94, PrW 0.53, PW 0.43, PL 0.31, IIIAW 0.57, IIIAL 0.37, IVAW 0.74, IVAL 0.38, FFeW 0.17, FFeL 0.50, HFeL 0.49, FTiL 0.40, HTiL 0.50, FBaL 0.22, HBaL 0.40, CI 107, MI 214, PI 72

Worker measurements: HW 0.50–0.76, HL 0.59–0.78, SL 0.29–0.35, MH 0.30–0.46, ML 0.70–0.98, PrW 0.34–0.56, PW 0.28–0.44, PL 0.22–0.31, IIIAW 0.39–0.60, IIIAL 0.25–0.37, IVAW 0.51–0.76, IVAL 0.28–0.40, FFeW 0.12–0.17, FFeL 0.35–0.50, HFeL 0.36–0.50, FTiL 0.30–0.40, HTiL 0.36–0.51, FBaL 0.19–0.25, HBaL 0.27–0.42, CI 103–115, MI 200–233, PI 64–79 [12 measured]

Head slightly longer than wide and widest slightly behind midlength; sides parallel, convex. Vertexal margin shallowly concave. Parafrontal ridges completely absent. Mandibles triangular; when closed, basal margin not separated from anterior clypeal margin by gap. Basal margin meeting masticatory at right angle; masticatory margin, excluding apical tooth, with triangular tooth followed by three smaller, triangular denticles; an additional, small denticle may be present distally on basal margin. Lateroclypeal teeth small, blunt and projecting slightly inwards. Antennae 12-segmented. Palp formula unknown.

Mesosoma moderately stout, rectangular in dorsal view; dorsal surface flattened, bordered at the lateral sides by a distinct angle but not marginate. Openings of propodeal spiracles irregularly circular, directed sideways. Declivous face of propodeum immarginate above propodeal lobes. Propodeal lobes well developed, broadly rounded. Front femur moderately short and broad, laterally compressed. Metatibial gland a whitish, elongate patch of cuticle, little longer than maximum width of hind tibia.



FIGURES 3–4. *Cerapachys eguchii* n. sp., paratype, large worker; 3: dorsal view; 4: side view.

Petiole wider than long, much so in large workers, with well developed dorsal and posterior faces. Subpetiolar process relatively narrow and long, drawn into claw-like structure recurved posteriorly; semi-translucent narrowing present as oval patch in middle of process.

Abdominal tergite III wide relative to following segment, in side view the whole segment is smaller than following, but with developed anterior, perpendicular face.

Pygidial field small, flattened with six to eight modified, peg-like setae on each side, arranged in two irregular rows.

Hypopygidium unarmed.

Mandibles densely sculptured with large, deep punctures and interspaces smooth and shining. Head with

regular punctures, ranging from very small to relatively large and deep, spaced from about once to three or more times their diameter. Similar sculpture on dorsal surface of mesosoma. All interspaces smooth and shining. Lateral sides of promesonotum with small punctures in upper part and microreticulate throughout except dorsal third; remaining mesosoma and sides of petiole finely microreticulate.

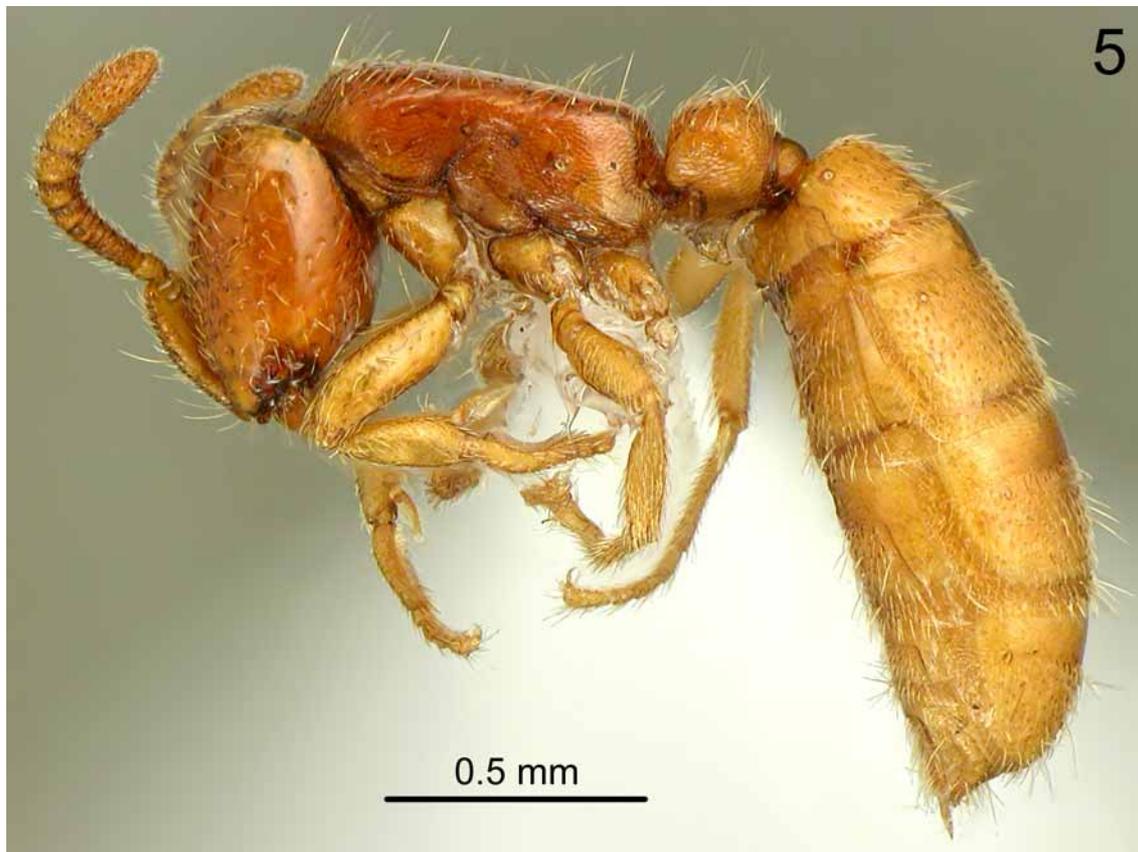


FIGURE 5. *Cerapachys eguchii* n. sp., paratype, small worker; side view.

Body pilosity composed of (1) dense, decumbent or subdecumbent hairs present on head, mesosoma, and abdominal segments and (2) moderately abundant, more than twice to four times longer than preceding, suberect or erect hairs present on head, mesosomal dorsum, petiole and posterior margins of gastral segments. Outer surface of middle tibiae without modified setae.

Color: in large workers head and mesosoma light chestnut-brown, remaining of body yellowish brown. Smallest workers lighter in color.

Gyne and male unknown

Diagnosis and discussion. This species shares most characters with *C. sexspinus*. *C. eguchii* can be fairly easily distinguished from it and all other species of the group by combination of color, sculpture and shape of subpetiolar process. The body is bicolored in *C. eguchii*, with head and mesosoma clearly darker than remaining of body. The lateral sides of mesosoma are sculptured with fine microreticulum, recognized easily at 50X magnification. The subpetiolar process rather long, forming a claw-like structure, curved posteriorly, and with semi-translucent narrowing in form of oval fenestra situated in the middle of the process (Fig. 4). *C. sexspinus* seems to have the body always unicolored, yellowish. The lateral sides of mesosoma are also microreticulate, but much more finely, so that under 50X magnification the surface appears matt with no individual lines of reticulation easily discernible. The subpetiolar process is shorter, not drawn into any spike, with ventral margin just evenly sloping towards the posterior end and a semi-translucent narrowing present along the ventral surface, except the anteriormost portion which is thick and opaque (Fig. 10).

Katsuyuki Eguchi (pers. comm.) informs that this species is locally not uncommon in Vietnam, nesting in soil, with colonies found under stones, and recorded from the following habitats: well-developed lowland evergreen/semi-evergreen forest influenced by a relatively strong dry season (Colony# Eg04-VN-748), and dwarf forest under a very dry climate (Eg12v07-03).

Material examined. Holotype, worker. VIETNAM: Dong Nai Province, S. Cat Tien National Park, forest behind the park's headquarters, ca. 160 m, Colony# Eg04-VN-748, 21 X 2004 (*K. Eguchi*) [VNMN]
Paratypes. 28 workers with the same data as holotype [BMNH, CASC, KEPC, MCZC, MLBC, VNMN]

Non-type material. 1 worker, VIETNAM: Ninh Thuan Province, Vinh Hai, Cau Gay village, 11°43'41"N 109°11'27"E, ca. 35 m, Colony# Eg12v07-03 12 V 2007 (*K. Eguchi*) [KEPC]

Cerapachys paradoxus n. sp.

Figs. 6–8, 14

Holotype worker measurements: HW 0.67, HL 0.68, SL 0.37, MH 0.46, ML 0.97, PrW 0.45, PW 0.27, PL 0.30, IIIAW 0.50, IIIAL 0.30, IVAW 0.70, IVAL 0.40, FFeW 0.19, FFeL 0.48, HFeL 0.46, FTiL 0.35, HTiL 0.43, FBaL 0.25, HBaL 0.30, CI 101, PI 111, MI 211

Worker measurements: HW 0.42–0.67, HL 0.49–0.68, SL 0.23–0.37, MH 0.30–0.46, ML 0.68–0.97, PrW 0.28–0.45, PW 0.19–0.27, PL 0.20–0.30, IIIAW 0.36–0.50, IIIAL 0.22–0.30, IVAW 0.45–0.70, IVAL 0.27–0.40, FFeW 0.12–0.19, FFeL 0.32–0.48, HFeL 0.27–0.46, FTiL 0.26–0.35, HTiL 0.27–0.43, FBaL 0.11–0.25, HBaL 0.14–0.30, CI 101–117, MI 202–227, PI 105–124 [6 measured]

Head almost as wide as long in the largest worker, in the smallest workers slightly longer than wide, and widest at about midlength; sides parallel, convex. Vertexal margin concave. Parafrontal ridges present but not raised, very low, reduced. Mandibles triangular; when closed, basal margin not separated from anterior clypeal region by gap. Basal margin long, meeting masticatory at right angle; masticatory margin with row of small denticles. In full face view, frontal lobes diverging laterally and confluent with lateral portions of clypeus. Lateroclypeal teeth very well developed, consisting of semi-translucent lamella overhanging mandibles; clypeus between teeth also lamellate and converging to frontal lobes medially. Antennae 11-segmented with apparent fusion resulting in 10 segments observed in one flagellum of the smallest specimen examined. Palp formula 2,2.

Mesosoma moderately stout, rectangular in dorsal view; dorsal surface flattened, bordered at the lateral sides by distinct angle but not marginate. Openings of propodeal spiracles irregularly circular, directed outwardly and upwards at angle of 45°. Declivous face of propodeum immarginate above propodeal lobes. Propodeal lobes well developed, broadly rounded. Front femur moderately short and broad, laterally compressed. Metatibial gland visible as small, broadly oval patch of lighter cuticle, diameter about fourth of maximum tibia width.

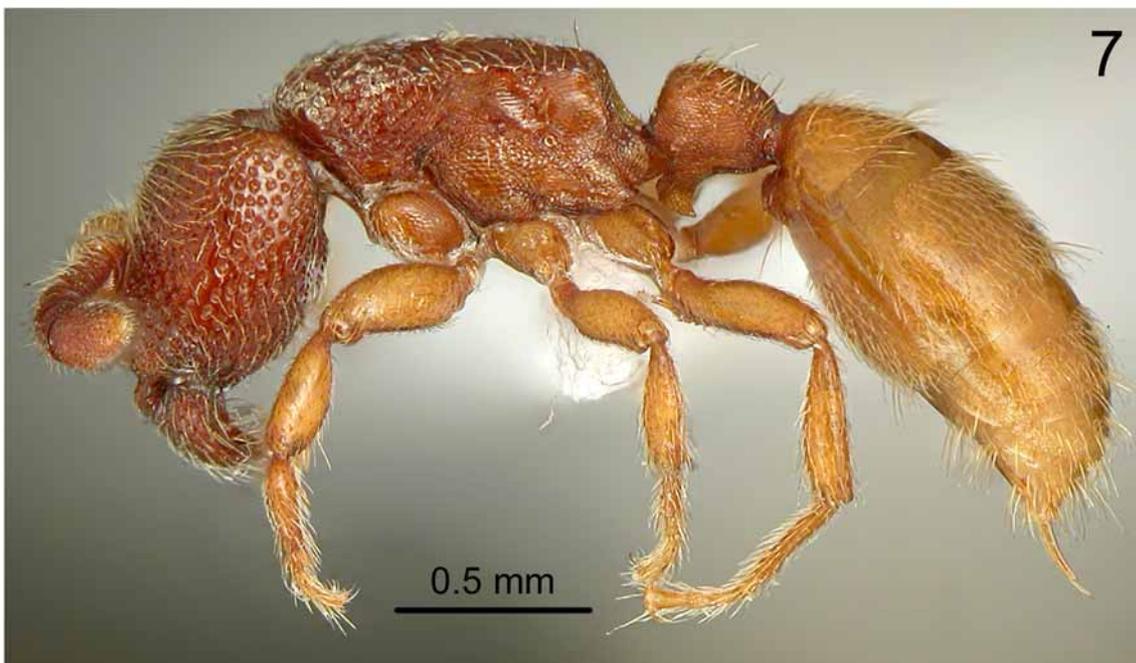
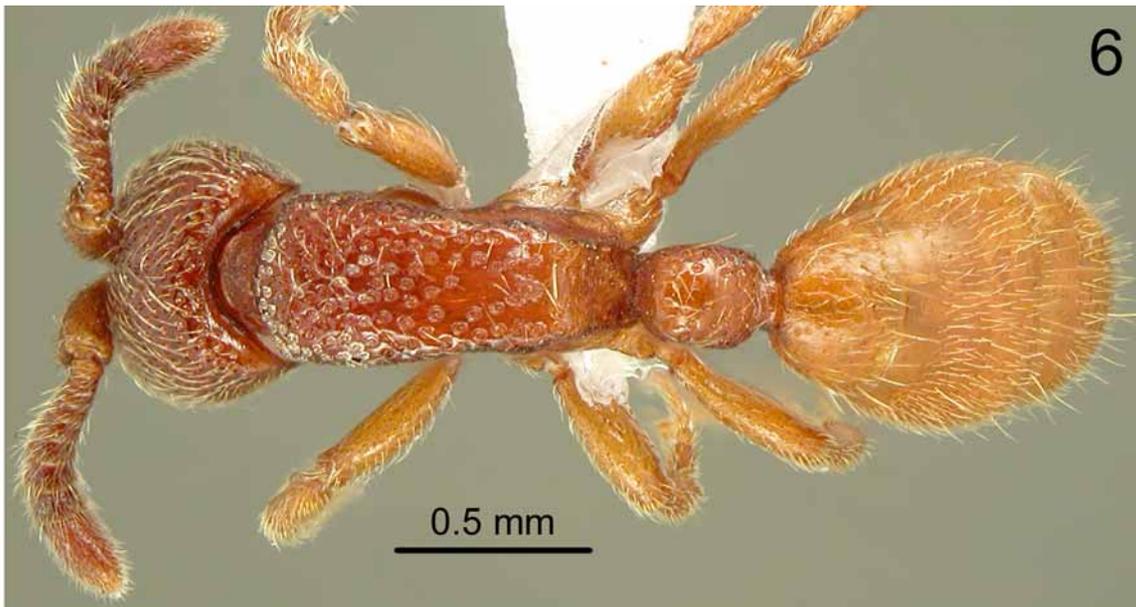
Petiole slightly longer than wide, with well developed dorsal face sloping gently posteriorly. Subpetiolar process relatively narrow and long; in side view with convex ventral margin and lamella forming broad angulate process.

Abdominal tergite III narrow relative to following segment, in side view the whole segment is small and anteriorly rounded.

Pygidial field small, weakly impressed, with six to eight teeth on each side.

Hypopygidium unarmed.

Mandibles densely sculptured with longitudinal striae and small punctures. Head with regular foveae, spaced from about one sixth to wider than their diameter. Similar sculpture on dorsal surface of mesosoma, but foveae somewhat smaller. All interspaces shining. Lateral sides of promesonotum with upper part foveolate, lower reticulate; remaining mesosoma with area above level of propodeal spiracle finely, longitudinally reticulate, and below that level (katapisternum, lower half of pronotal sides) reticulate. Sides of petiole similarly reticulate.



FIGURES 6–7. *Cerapachys paradoxus* n. sp., holotype, large worker; 6: dorsal view; 7: side view.

Body pilosity composed of (1) dense, subdecumbent hairs present on, head, mesosoma, and abdominal segments and (2) sparse, more than twice longer than preceding, mostly suberect hairs present on propodeum, petiole, posterior margins of gastral segments, and pygidium. Outer surface of middle tibiae with two or three modified, thick, peg-like setae.

Color: in larger workers bicolored with brownish antennae, mandibles, head and anterior mesosoma, posterior mesosoma and petiole lighter, legs and gaster yellowish. In smaller workers coloration similar or the whole body yellowish.

Gyne and male unknown.

Diagnosis and discussion. This species is aberrant in many characters as compared with others belonging to the group and thus easy to recognize. It is the only member of the group having 11-segmented antennae. The anterior margin of clypeus is conspicuously modified and drawn here into a semi-translucent lamella and laterally forming large, blunt teeth projecting over mandibles. Parafrontal ridges, however very low and

reduced, can be seen in this species, as opposed to the others in this group. The petiole is also quite special in having the dorsal surface sloping evenly into posterior end, thus not having well differentiated perpendicular posterior face. Abdominal segment III is unique by being very small compared to the following one, with narrow and rounded anterior faces, as opposed to clearly differentiated, perpendicular portion of tergites and sternites observed in other species. The sculpture of the head and dorsal mesosoma is strong, composed of closely spaced, regular, and umbilicate foveae.



FIGURE 8. *Cerapachys paradoxus* n. sp., paratype, small worker; side view.

The abdomen of this species is portrayed as fig. 18 in Bolton (1990).

Material examined. Holotype worker (topmost specimen of three on the pin). MALAYSIA: Sarawak, Gunung Mulu National Park, Kerangas forest, soil core, XII 1978 (*N.M. Collins*) [BMNH].

Paratypes. 3 workers with same data as holotype [BMNH].

Non-type material. 4 workers, MALAYSIA: Sarawak, Gunung Mulu National Park, 04°08'N 114°53'E, KE 07, 26 V 2006 (*D. Mezger*) [MCZC, MLBC].

Cerapachys sexspinus (Xu, 2000)

Figs. 9–11

Yunodorylus sexspinus Xu, 2000: 298–299. Figs 1–6. Holotype and paratype workers, CHINA: Yunnan province, Mengla county, Bubang village, 730 m, No. A97-2064, 17 VIII 1997, nest in soil, seasonal rainforest (*G. Zeng*); further paratype workers, Yunnan province, Mengla county, Longlin village, 1040 m, No. A98-775, 14 III 1998 (*G. Zeng*) [ISAS, MCZC] (MCZC paratypes examined).

Cerapachys sexspinus: Bolton 2003: 269. First combination in *Cerapachys*.

Cerapachys sexspenus: Jaitrong & Nabhitabhata 2005: 18. Incorrect subsequent spelling. Record in Thailand.

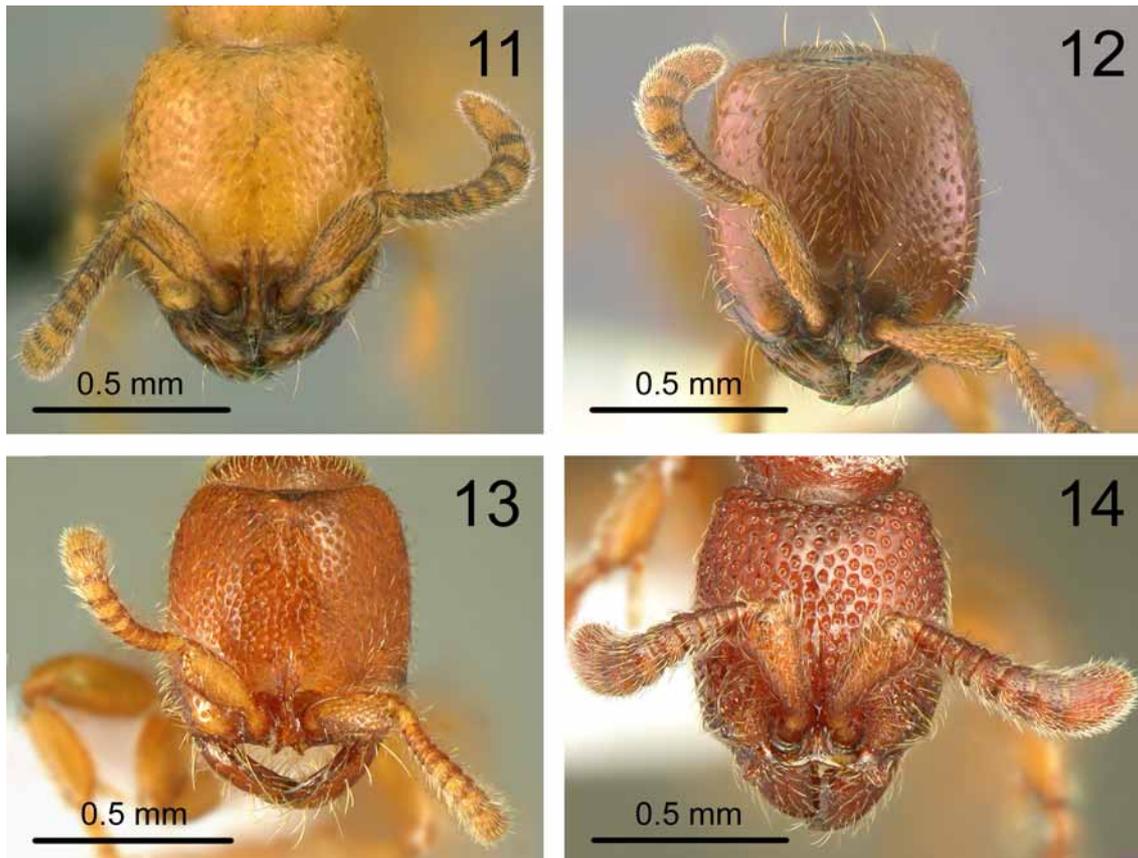
Worker measurements: HW 0.53–0.68, HL 0.63–0.74, SL 0.30–0.36, MH 0.38–0.44, ML 0.75–0.94, PrW 0.36–0.49, PW 0.29–0.36, PL 0.24–0.29, IIIAW 0.40–0.49, IIIAL 0.29–0.33, IVAW 0.53–0.64, IVAL 0.30–0.37, FFeL 0.38–0.46, HFel 0.36–0.45, FTiL 0.31–0.38, HTiL 0.38–0.48, FBaL 0.19–0.23, HBaL 0.28–0.35, CI 109–119, MI 197–214, PI 81–83 [2 measured]



FIGURES 9–10. *Cerapachys sexspinus* (Xu, 2000), paratype worker; 9: dorsal view; 10: side view.

Head slightly longer than wide and widest at about midlength; sides parallel, convex. Vertexal margin concave. Parafrontal ridges completely absent. Mandibles triangular; when closed, basal margin not separated from anterior clypeal region by gap. Basal margin meeting masticatory at right angle; masticatory margin with fine crenulation. Laterolypeal teeth small, blunt, and projecting forwards. Antennae 12-segmented. Palp formula 2,2 (after Xu 2000).

Mesosoma moderately stout, rectangular in dorsal view; dorsal surface flattened, bordered at lateral sides by distinct angle but not marginate. Openings of propodeal spiracles irregularly circular, directed sideways. Declivous face of propodeum immarginate above propodeal lobes. Propodeal lobes well developed, broadly rounded. Front femur moderately short and broad, laterally compressed.



FIGURES 11–14. Heads in frontal view, workers; 11: *Cerapachys sexspinus* (Xu, 2000), paratype; 12: *Cerapachys eguchii* n. sp., paratype; 13: *Cerapachys doryloides* n. sp., holotype; 14: *Cerapachys paradoxus* n. sp., holotype.

Petiole wider than long, with well developed dorsal and posterior faces. Subpetiolar process relatively narrow and short, simple with ventral margin straight, evenly sloping towards posterior end; semi-translucent narrowing present along posterior two thirds of ventral margin.

Abdominal tergite III wide relative to following segment, in side view the whole segment is smaller than following, but with developed anterior, perpendicular face (Fig. 10).

Pygidial field small, with five to nine modified, peg-like setae on each side, arranged in one or two rows. Number and arrangement of setae varying with worker size.

Hypopygidium unarmed.

Mandibles densely sculptured with large, deep punctures and interspaces smooth and shining. Head with large but shallow, regular punctures, spaced from about half to more than once their diameter. Similar sculpture on dorsal surface of mesosoma, with punctures more shallow. All interspaces smooth and shining. Lateral sides of promesonotum with small punctures in upper part and extremely finely microreticulate, appearing matt; remaining mesosoma and sides of petiole similarly microreticulate.

Body pilosity composed of (1) dense, decumbent or subdecumbent hairs present on head, mesosoma, and abdominal segments and (2) moderately abundant, twice to more than three times longer than preceding, mostly suberect hairs present on head, mesosomal dorsum, petiole and posterior margins of gastral segments. Outer surface of middle tibiae without modified setae.

Color: body unicolored, yellowish.

Gyne and male unknown.

Diagnosis and discussion. This species can be distinguished from *C. eguchii* by differences in color, sculpture and shape of subpetiolar process. See diagnosis and discussion under *eguchii* for more details.

Xu (2000) reports that this species constructs nests in soil with colonies ranging from 20 to 385

individuals, foraging probably in soil and under leaf litter. The habitats where this species has been found include seasonal rainforest, mountain rainforest, deciduous monsoon forest, and warm deciduous broad-leaved forest, ranging from 730 to 1280 m in elevation.

In addition to material examined by the author from Mengla county, Xu (2000) reports this species from two other localities in Yunnan: Menghai and Jinghong counties. It is unknown whether specimens mentioned from Thailand (Jaitrong & Nabhitabhata 2005) represent this species.

Material examined. Paratypes. 2 workers, CHINA: Yunnan province, Mengla county, Bubang village, 730 m, A97-2064, 17 VIII 1997 (G. Zeng) [MCZC]

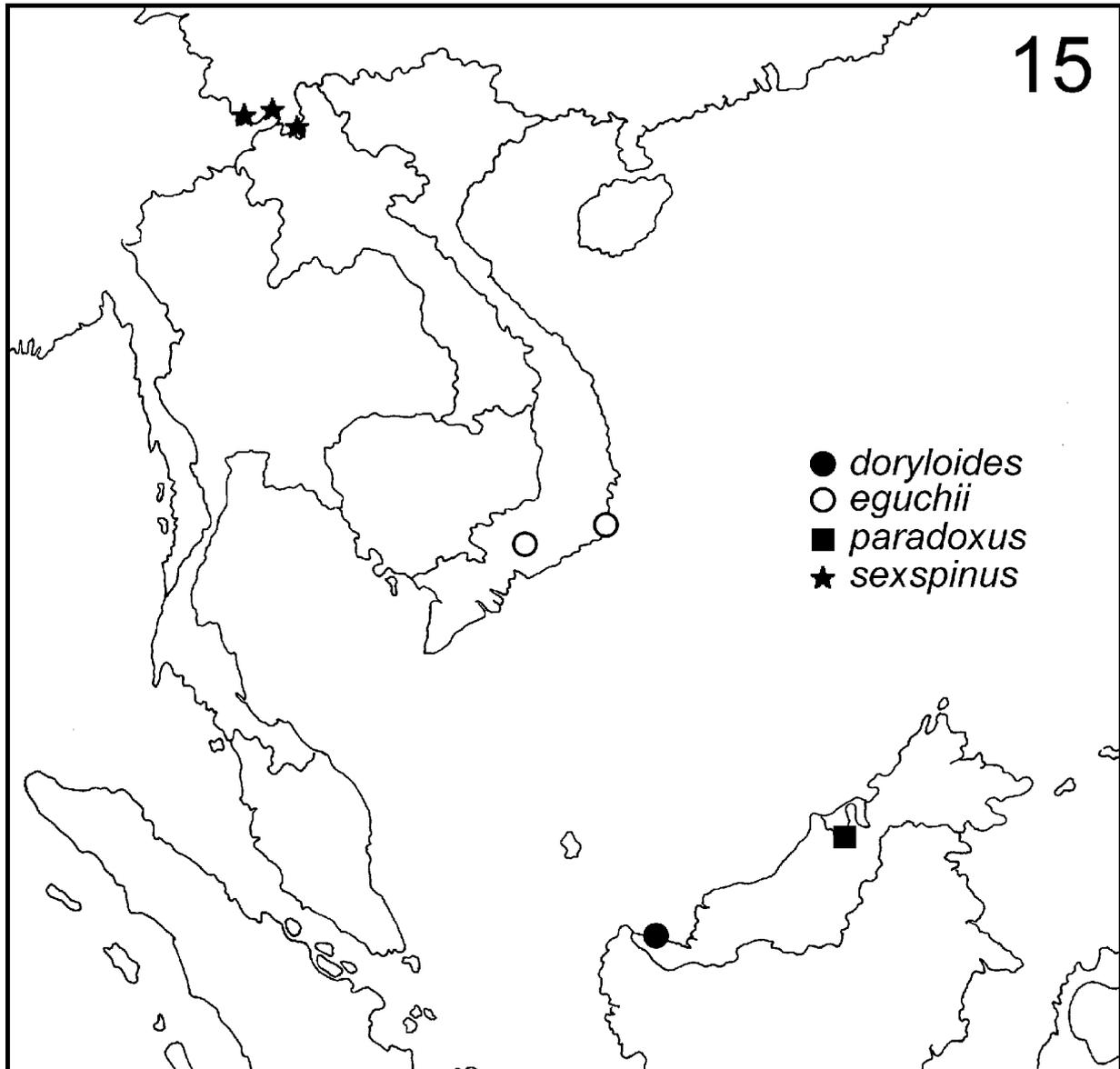


FIGURE 15. Species distribution map. Record of *Cerapachys sexspinus* (Xu, 2000) from Thailand by Jaitrong & Nabhitabhata (2005) is omitted.

General discussion

The original description of *Yunodorylus sexspinus* by Xu (2000) placed the newly established genus in Dorylinae on account of general habitus, single segmented waist, and polymorphic worker caste. However, due to certain characters found also in Cerapachyinae, namely triangular mandibles, modified peg-like setae

on pygidium, and absence of promesonotal suture, Xu concluded that the new genus may represent some evolutionary link between cerapachyines and dorylines. He also provided a key to the subfamily Dorylinae, incorporating and differentiating *Yunodorylus* and *Dorylus*. In 2003, Bolton synonymized *Yunodorylus* with *Cerapachys*, based on the fact that the genus diagnosis provided by Xu included defining characters of Cerapachyinae but did not include any characters that could account for placement in the Dorylinae: *Yunodorylus* lacks a defined promesonotal suture, large propodeal spiracle situated high and far forward, mesosomal endophragmal pit, and bidentate pygidium characteristic for Dorylinae and possesses an externally visible sting, which is reduced and non-functional in *Dorylus*. The only putative character shared by *Yunodorylus* and *Dorylus* and not found in cerapachyines then, would be the absence of propodeal lobes, which was stated in the original description. However, Bolton (2003) was able to examine two related species from Borneo (described here as *paradoxus* and *doryloides*), concluding that “*Yunodorylus*” species, contrary to Xu’s account, do possess propodeal lobes. Examination of *sexspinus* and other material in the course of this study confirms that all the species have propodeal lobes developed. Moreover, Bolton (2003) pointed out that he had already shown (Bolton 1990) morphoclinal reduction in constriction between abdominal segments III and IV among *Cerapachys*, leading to the condition observed in the *sexspinus*-group. Thus, he concluded (2003), there is nothing differentiating “*Yunodorylus*” from *Cerapachys* as this genus is currently understood. In addition to characters discussed above, Brady & Ward (2005) investigated the character of mesosomal endophragmal pit, universal in dorylines and absent in cerapachyines. These authors also recognized a thin comb of the metatibial spur as a synapomorphy of the clade of the true army ants (Aenictinae, Aenictogitoninae, Dorylinae, Ecitoninae) as opposed to the broadly pectinate comb observed in other dorylomorphs, including Cerapachyinae. Species of the *sexspinus*-group invariably have the metatibial spurs broadly pectinate, thus providing another character invalidating placement within Dorylinae.

Recently, two important phylogenies of the Formicidae derived from molecular data have been published (Moreau *et al.* 2006, Brady *et al.* 2006). Both included material of *Cerapachys sexspinus* in the analysis, concluding with different results. In Moreau *et al.* (2006) this species appears on the tree as *Yunodorylus* and constitutes the sister branch to *Sphinctomyrmex* species from Australia. In analysis by Brady *et al.* (2006) *Cerapachys sexspinus* appears sister to the clade of Aenictinae+Ecitoninae. However, in both studies these nodes were relatively weakly supported. On account of this fact and the strong morphological evidence discussed above, it seems highly improbable that this group is more closely related to the true army ants than to other cerapachyines. However, it is worth bearing in mind that the internal phylogeny of the Cerapachyinae is unresolved and recent studies suggest paraphyly of this subfamily (Brady & Ward 2005, Moreau *et al.* 2006, Brady *et al.* 2006).

Species in the *Cerapachys sexspinus*-group possess a unique character combination that could easily account for placement in a genus of their own, as compared with generic concepts in other ant groups. Although these species are very distinctive within *Cerapachys*, most notably by having a single segmented waist and unique spur formula, it seems premature to resurrect the genus name *Yunodorylus*. The genus *Cerapachys*, as presently understood, encompasses an enormous diversity of morphological traits (Brown 1975, Bolton 1990, Bolton 2003). For example, species related to *C. crawleyi* Wheeler, 1924 have quite exceptional morphology and at times have been placed in a genus of their own, *Chrysapace* Crawley, 1924. They also possess unique palp (5,3) and spur (2p,2p) formulas, and on this ground would deserve reviving their generic status. Therefore, until broader revision of genera and their status in the subfamily is attempted, rank change of the species-group discussed above would be an act of inconsequence. Full generic revision of the subfamily is beyond the scope of this study, and it is recommended that any changes at the generic level should be postponed until the internal phylogeny of the Cerapachyinae is better understood.

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References

- Bolton, B. (1990) Abdominal characters and status of the cerapachyine ants (Hymenoptera, Formicidae). *Journal of Natural History*, 24, 53–68.
- Bolton, B. (2003) Synopsis and Classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 370 pp.
- Brady, S.G., Ward, P. S. (2005) Morphological phylogeny of army ants and other dorylomorphs (Hymenoptera: Formicidae). *Systematic Entomology*, 30, 593–618.
- Brady, S.G., Schultz, T.R., Fisher, B.L., Ward, P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 18172–18177.
- Brown, W.L., Jr. (1975) Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cyliandromyrmecini, Acanthostichini, and Aenictogitini. *Search, Agriculture* (Ithaca, N. Y.), 5(1), 1–115.
- Crawley, W.C. (1924) Ants from Sumatra, with biological notes by Edward Jacobson. *Annals and Magazine of Natural History*, 9(13), 380–409.
- Forel, A. (1900) Ponerinae et Dorylinae d'Australie récoltés par MM. Turner, Froggatt, Nugent, Chase, Rothney, J.-J. Walker, etc. *Annales de la Société Entomologique de Belgique*, 44, 54–77
- Jaitrong, W., Nabhitabhata, J. (2005) A list of known ant species of Thailand. *The Thailand Natural History Museum Journal*, 1(1), 9–54.
- Mayr, G. (1879) Beiträge zur Ameisen-Fauna Asiens. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, 28, 645–686.
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B., Pierce, N.E. (2006) Phylogeny of the ants: diversification in the age of angiosperms. *Science*, 312, 101–104.
- Wheeler, W.M. (1924) On the ant-genus *Chrysapace* Crawley. *Psyche*, 31, 224–225.
- Wilson, E.O. (1964) The true army ants of the Indo-Australian area (Hymenoptera: Formicidae: Dorylinae). *Pacific Insects*, 6, 427–483.
- Xu, Z.-H. (2000) Two new genera of ant subfamilies Dorylinae and Ponerinae (Hymenoptera: Formicidae) from Yunnan, China. *Zoological Research*, 21, 297–302.