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The first subterranean ant species of the genus *Meranoplus* F. Smith, 1853 (Hymenoptera: Formicidae) from Vietnam

Первый подземный вид муравьев рода *Meranoplus* F. Smith, 1853 (Hymenoptera: Formicidae) из Вьетнама

V.A. Zryanin
В.А. Зрянин

Lobachevsky State University of Nizhni Novgorod, Gagarin Prospect, 23, build. 1, Nizhniy Novgorod 603950 Russia. E-mail: zryanin@list.ru
Нижегородский государственный университет им. Н.И. Лобачевского, пр. Гагарина, 23, корп. 1, Нижний Новгород 603950 Россия

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Ключевые слова: Hymenoptera, Formicidae, Myrmicinae, *Meranoplus*, новый вид, подземный образ жизни, оттесненные реликты, Вьетнам.

Abstract. A subterranean ant species of the subfamily Myrmicinae, *Meranoplus dlusskyi* **sp. n.**, is described based on workers recovered from a soil-core sample taken in a primary tropical monsoon forest of Southern Vietnam. Membership of the species in the genus *Meranoplus* F. Smith, 1853 is confirmed by all key characters including 9-merous antennae with 3-merous club and the structure of the sting apparatus, but unique characteristics, reflecting evolutionary trends toward a subterranean existence, are found. These include an almost complete reduction of eyes, an obsolete promesonotal shield, shortened appendages, depigmentation of cuticle and its superficial sculpture. Significant difference from all described species of the genus is the palp formula 3.3 vs. 5.3. No species with a subterranean lifestyle have hitherto been known in this genus. The presence of 5 mandibular teeth, absence of the clypeal armament, form of the propodeum, which constitutes part of the dorsal alitrunk (rather ancestral conditions) all suggest an early separation of the *M. dlusskyi* **sp. n.** lineage. The concept of ousted relicts is used for explaining the possible origin of this lineage and recent distribution of *Meranoplus* as a whole.

Резюме. Геобионтный вид муравьев подсемейства Myrmicinae, *Meranoplus dlusskyi* **sp. n.**, описывается по рабочим из почвенной пробы, взятой в первичном тропическом муссонном лесу Южного Вьетнама. Принадлежность вида к роду *Meranoplus* F. Smith, 1853 подтверждается по всем ключевым признакам, в том числе 9-члениковым антеннам с 3-члениковой булавой и структуре жалящего аппарата, но имеются специфические признаки, отражающие эволюционные тенденции к подземному образу жизни. Они включают почти полную редукцию глаз, зачаточный промезонотальный щит, укороченные придатки, депигментацию кутикулы и поверхностную скульптуру. Существенным отличием от всех остальных видов рода является формула щупиков 3.3 вместо 5.3. До сих пор виды с подземным образом жизни в этом роде были неизвестны. На основе вероятных плезиоморфий: 5 зубцов в мандибулах, отсутствие выростов наличника, форма проподеума, который образует часть спинной поверхности груди, можно предполагать раннее обособление филетической линии *M. dlusskyi* **sp. n.** Концепция оттесненных реликтов используется для объяснения возможного происхождения этой линии и современного ареала *Meranoplus* в целом.

Introduction

Several new myrmicine genera and species, which are of great interest in terms of phylogeny and biogeography, have recently been discovered from soil samples primarily in tropical rain forests [Bolton, 1988; Hosoishi et al., 2010; Zryanin, 2012]. Subterranean taxa are infrequently collected (sometime known only based on the type material) and often have distinctive morphological features such as vestigial eyes and depigmented yellowish body [Eguchi et al., 2006]. Of particular interest are subterranean ant species in the genera which are characterized mainly by ordinary lifestyles. Entering a new adaptive zone may have occurred in various groups at different evolution stages due to changes in environmental condition. In some cases species may be driven out to the periphery of an adaptive zone or area as a result of competition with more advanced forms [Darlington, 1966; Bolton, 1976, 1979; Fisher, 1997]. However, relict species can survive through specialization arising on the primitive basis. A possible example of such relicts is described in this paper as a new species of the genus *Meranoplus* F. Smith, 1853.

Meranoplus is a very distinctive myrmicine genus occurring throughout the Old World tropics with a unique protective morphology of the workers. Their diagnostic characteristics include the compact mesosoma with a promesonotal shield that overhangs the pleurae laterally and usually overhangs the propodeum posteriorly, deep antennal scrobes that extend above the eyes, and 9-segmented antennae with a 3-segmented club [Bolton, 2003]. When disturbed some species demonstrated "playing dead" behaviour (thanatosis): the ants retract their antennae into the scrobes, tuck their legs under the promesonotal shield, and lie motionless in a foetal position [Andersen, 2006]. Protective morphology and behaviour of slow-moving *Meranoplus* species (as in some other taxa such as *Cataulacus* F. Smith, 1853 and *Cephalotes* Latreille, 1802) are associated with foraging within the territories of aggressive, territorial species [Dornhaus, Powell, 2010]. In ant species that forage in narrow trophophoric field particularly in underground conditions such protective morphology is disadvantageous [Wilson, 1959].

Ecologically, the genus *Meranoplus* is rather homogeneous, represented mainly by species nesting in the soil and forage almost exclusively on its surface. However there known a registration of *M. castaneus* F. Smith, 1857 from emergent tree crown in a Bornean rainforest [Tanaka et al., 2012]. Furthermore, foragers of another rainforest-dwelling species, *M. mucronatus* F. Smith, 1857, on the bases of tree trunks during trophobiosis with hemipterans were observed [Maschwitz et al., 1987]. Hitherto species with a subterranean lifestyle in the genus *Meranoplus* were unknown. Most species of *Meranoplus* are omnivores, sometimes including seeds in the diet. The tendency to granivory exhibits maximum development in the Australian *M. diversus* group that includes 25 described species [Schödl, 2007]. *Meranoplus* species are known to recruit via pheromone trails laid from the base of the sting using secretions from their extremely large Dufour glands [Hölldobler, 1988; Billen et al., 2009].

The genus *Meranoplus* is currently represented by 88 described valid species [Bolton, 2015] mostly from the Australasian region (60 species), where the number of species is estimated at 400 [Andersen, 2007]. In other words, here is the center of diversity for the genus, but the center of its origin remains unknown. From the Ethiopian region have been recognized 8 species [Bolton, 1981], from Madagascar 4 species [Boudinot, Fisher, 2013]. So far, 16 species of *Meranoplus* have been described and revised from the Oriental zoogeographical region [Schödl 1998, 1999; Bharti, Akbar, 2014], but only *M. bicolor* (Guerin-Meneville, 1844) have been known from several localities in Vietnam [Dlussky, Radchenko, 1990; Eguchi et al., 2011; Zryanin 2011]. Taxonomy of *Meranoplus* is poorly understood, although in a provisional systematic review of Australian fauna Andersen [2006] has recognized 18 informal species groups within 7 putative radiations, which he treated as equivalent to subgenera. In a revision of Oriental *Meranoplus*, Schödl [1998] refused to identify species groups. Three species groups were allocated in the Ethiopian region [Bolton, 1981], as well the detailed diagnoses of 2 species groups including characters of males in a recent revision of *Meranoplus* from Madagascar were given [Boudinot, Fisher, 2013].

Below based on workers I describe a new species of *Meranoplus* from Vietnam, which is of interest for understanding the evolutionary history of the genus. Number of characters clearly distinguishes this species from all other known congeners and evidence of its hypogaeic lifestyle. Nevertheless, it has all synapomorphies of *Meranoplus* [for details see Bolton, 2003; Boudinot, Fisher, 2013] and should be included in this genus. A high degree of morphological and ecological differentiation of *Meranoplus* in Southeast Asia suggests the long-term evolution of the genus in this region.

Material and methods

Material for the description of the new species was obtained from soil-core samples in Dong Nai Culture and Nature Reserve (Dong Nai Province, Southern Vietnam). Ants were collected by taking soil cores (diameter 7.8 cm, depth 10 cm) and were extracted using Berlese funnels for 5 days. This site was covered by a primary tropical forest with 4 layers. The upper layer consisted mainly of Dipterocarpaceae and Irvingiaceae trees. The fresh litter (L horizon) consisted mainly of leaves of Dipterocarpus dyeri Pierre (about 10 cm thick). The F (decomposing litter) and H (well decomposed litter) horizons were absent. The soil is ferralitic.

Measurements (in millimeters) and indices generally follow Bolton [1981] and Schödl [1998, 1999, 2007], but total length (TL) was calculated as the sum of the lengths of body parts (HL and mandibles + WL + PTLL + PPLL + gaster length). This gives a somewhat higher value, but represents the real ratio of the overall sizes of ants in samples. Other abbreviations of morphometric measurements and indices are given below: HL – head length: maximum longitudinal distance from mid-point of occipital margin to mid-point of anterior clypeal margin, measured in full-face view; HW – head width: maximum width of head, measured in same view as for HL; SL – scape length: maximum length of antennal scape excluding the basal condylar bulb; PML – promesonotum length: length of promesonotum, measured from anterior mid-point of pronotum behind neck to mid-point of hind margin of mesonotum (posterolateral projections included); PW – pronotal width: maximum width of pronotum, measured posterior to base of antero-lateral pronotal angles in dorsal view; WL – Weber's length: in lateral view, diagonal length from anterior margin of pronotum (exluding neck) to posterior margin of propodeal lobe; PTLL – petiolar lateral length: length of petiole, measured in lateral view; PTLH – petiolar lateral height: height of petiole, measured in lateral view; PPLL – postpetiolar lateral length: length of postpetiole, measured in lateral view; CI – cephalic index: HW×100/HL; PMI – promesonotal index: PW×100/PML; PTI – petiolar index: PTLL×100/PTW; SI – scape index: SL×100/HW.

Images of whole ants and separate parts obtained using the Keyence VHX-1000 digital microscope and the Camscan MB2300 scanning electron microscope. Imaging obtained with the first microscope was performed using Helicon Focus 5.3 Pro from a series of source images taken by the Z-stack module. Corel Draw X3 and Adobe Photoshop CS2 were also used in image preparation.

The terminology for sting apparatus follows Kugler [1994, 1997], that for sculpture follows Harris [1979], and other terminology as in Serna and Mackay [2010].

The conclusion of genus affinity of the new species was performed using workers of type species *M. bicolor* which were collected by author in Nam Cat Tien (southern part of Cat Tien National Park), 40 km east of the point of discovery of the species described in the present article. Additionally, the descriptions of Ethiopian, Malagasy and Oriental species were used [in Bolton 1981, Boudinot, Fisher, 2013 and Schödl, 1998, 1999 respectively], as well as the images of workers in 3 planes that are available at www.antweb.org.

Abbreviations of the specimen depositories are:

IEBR – Entomological collection of the Institute of Ecology and Biological Resources (Hanoi, Vietnam);

BMNH – Natural History Museum (London, UK);

CASC – California Academy of Sciences (San Francisco, USA);

ZISP – Zoological Institute of the Russian Academy of Sciences (St. Petersburg, Russia);

ZMUM – Zoological Museum, Moscow State University (Moscow, Russia).

Taxonomy

Meranoplus dlusskyi Zryanin, **sp. n.**
(Figs 1–12)

Material. Holotype, worker: Vietnam, Dong Nai Province, Vinh Cuu District, Dong Nai Culture and Nature Reserve, 11°18′N / 107°04′E, lowland, on the plot "Dipterocarpus forest", 22.10.2011, soil core 1-5 (leg. A. Anichkin) (IEBR). Paratypes: 40 workers from the same locality, 22.10 and 21.12.2011 (leg. A. Anichkin), (BMNH, IEBR, CASC, ZISP, ZMUM and the personal collection of the author).

Description. Habitus of worker as illustrated (Figs 1–3). Head in full-face view subquadrate, slightly broadened posteriorly (trapezoid above antennal scrobes so that genae and temples are distinctly prominent), posterior outline broadly convex. Median portion of clypeus narrowing anteriorly, not projecting beyond apices of frontal lobes, the margin with an anteclypeal carina but without an apron as well without conspicuous prominence or denticle where the anterior margin meets the longitudinal carinae which bound the side of the median portion of the clypeus (Figs 4, 6). Labrum cleft medially. Frontoclypeal suture continuing anteriad to malar space and forming clypeomalar suture separating narrow premalar space from malar space, which also differs in sculpture (Fig. 4). Frons anteriorly delimited by faint but moderately large frontal triangle. Frontal carinae rather long, diverging from clypeus to vertex, sinuate. Frontal lobes distinct. Antennal scrobes conspicuous in full-face view, dorsally delimited by frontal carinae and ventrally by anteocular costulae. Ventral surface of head with several subocular rugae on each side (Fig. 5). Eyes strongly reduced, situated ventral to antennal scrobes and slightly posteriad between torulus and occipital margin, consisting of 1 or 2 ommatidia or 1 ommatidium in one eye but none in the other; in some specimens eyes completely absent. Mandibles triangular, possessing deep and proximal curved mandibular groove ventrally; masticatory

Figs 1–3. *Meranoplus dlusskyi* **sp. n.**, habitus of worker, holotype.
1 – lateral view; 2 – dorsal view; 3 – full-face view. Scales 0.5 mm.
Рис. 1–3. *Meranoplus dlusskyi* **sp. n.**, внешний вид рабочего, голотип.
1 – вид сбоку; 2 – вид сверху; 3 – вид спереди. Масштабная линейка 0.5 мм.

margin with 5 teeth; apical tooth largest, preapical tooth half size of apical, 3rd tooth smaller than preapical and 4th teeth, basal tooth smallest, sometimes obsolete. Strong swelling (denticle) present on ventral side of mandible beneath third tooth of masticatory margin (Fig. 6, arrows) as in other *Meranoplus* [Boudinot, Fisher, 2013]. Palp formula: maxillary 3, labial 3 (Fig. 5). 1st and 2nd segments of maxillary palps with distinctive silhouettes, suggesting formation of 2 segments due to partial and complete fusion [sensu Ettershank, 1966], respectively. Stipes of maxilla lacking a distinct transverse crest, which is visible as trace. Antennae 9-merous with 3-merous club. Scapes thicker in apical than in basal halves; club strongly incrassate, more than half the length of flagellum.

Mesosoma (alitrunk) compact, dorsally forming a promesonotal shield that is characteristic of *Meranoplus*, but it is obsolete (Figs 2, 7). Promesonotum very slightly wider than long. Anterior pronotal corners weakly projecting, blunt; lateral margins of pronotum subparallel, promesonotal suture absent, lateral mesonotal margins narrowed posteriorly and produced into small foliaceous projections. Mesopleuron well impressed (mesosoma constricted) receiving femora; metapleural gland scrobe superior to metacoxa, extending from metapleural gland bulla to mesopleural-coxal excavation (Fig. 8). Inferior carinula of this scrobe flanks metapleural gland slit dorsally that is very narrow; bulla is rather large, extended almost to propodeal spiracle. Propodeum (dorsopropodeum) and notopropodeal suture visible in dorsal view. Propodeal spines are short, wide at base and pointed to apex, divergent slightly outwards, with dorsomedian costa reaching notopropodeal suture. Lateropropodeum with a large tubulose spiracle that is accommodated into excavation on it and directed posteriorly. Internal margin of spiracle fused to the excavation, lateral margin free; from above lateropropodeal excavation limited by ridge-like anteropropodeal process. Posterior declivity of propodeum concave, descending to glabrous propodeal lobes. Articulatory excavation of petiole shallow, barely reaching a line spanning posteriormost points of metacoxal cavities. Legs comparatively short. Procoxa twice size of meso- or metacoxa, foretibia 2.3 times as long as wide. Meso- and metatibia without spurs. Pretarsus bearing two curved claws, without arolium.

Metasoma. Petiole sessile, tapered from base to crest, markedly higher than long; anterior and posterior faces meeting in an acute angle, but posterior face more gently sloping. Subpetiolar process present, laminar-lobose. Postpetiole wider than long, slightly wider than petiole, in profile nodiform, with relatively flat and oblique dorsal surface. Boundary between tergite and sternite visible only in helcium. Posttergite and poststernite of the postpetiole clearly fused (Fig. 12). Sternite of postpetiole projecting anteromedially into a subpostpetiolar process that forms with second cinctus a transverse cavity ventrally, where posterior margin of petiolar sternite are coupled. 1st gastral segment (Abd IV) occupying nearly 3/4 of gaster. 2nd helcium situated in excavation at base of postsclerites. In ventral view posttergite on each side of Abd IV markedly projecting anteriad to poststernite, broadly overlapping it. As in other *Meranoplus* species sting shaft relatively long, with dorsal flanges and spatulate lancets, large lancet valves and V-shaped furcula without dorsal arm (Fig. 9–11). Spiracular plate rectangular. Anterior apodeme without any process. Body of the quadrate plate very weakly sclerotized in lower part, anterodorsal corner blunt, but prominent. Posterior arm of oblong plate relatively long and massive. Anterior apodeme short and blunt. No postincision separates the posterior and ventral arms. Gonostylus oblong-triangular with acute apex, single-segmented.

In general, body with superficial sculpture; sculpture mainly alveolate on ventral surface of head, sides of mesosoma, all coxae and metasoma; postsclerites of 1st gastral segment more superficially and sparsely sculptured. Frons including frontal lobes with sparse longitudinal and slightly sinuate rugae (costulae), without meshes and with glabrate main surface. On vertex and sides of head rugae connected and forming partly areolate-rugulose sculpture with finely alveolate interspaces. Antennal scrobes also finely alveolate. Clypeus predominantly smooth and shiny. Sculpture of promesonotum obscure, as if erased. A similar condition observed also on other dorsal surfaces (propodeal declivity, petiole and postpetiole). Legs without marked sculpture, excluding coxae (see above). Scapes slightly rimose in basal halves; mandibles striate.

Pilosity consisting of short decumbent and subdecumbent hairs (30–80 μm long) and sparse longer (ca. 100 μm) suberect hairs. Longest hairs (150–160 μm) situated on median clypeus and on dorsum of petiole immediately below crest. Hairs whitish and more or less arcuate.

Generally, exposed cuticle exhibits depigmentation. Color of head, mesosoma, appendages, petiole and postpetiole dull yellow, mandibles (especially masticatory margin) darker. Gaster brown to dark-brown with yellowish-brown edges of sclerites; sometimes dark pigmentation reduced to a broad median band or entirely absent.

Gyne and male unknown.

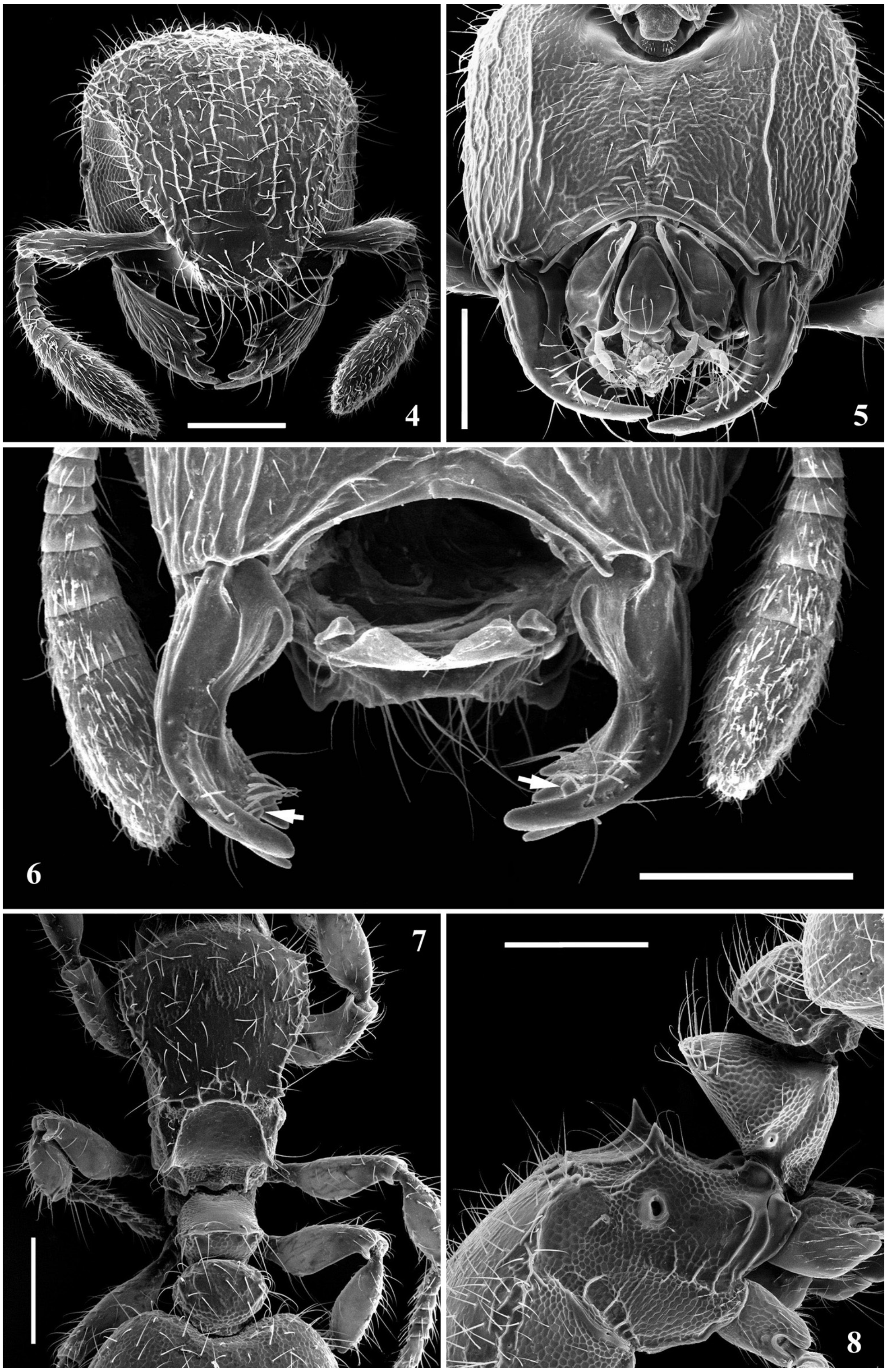
Measurements and indices. Holotype worker: TL 2.73, HL 0.6, HW 0.6, SL 0.33, PML 0.42, PW 0.45, PTLL 0.2, PTLH 0.28, PPLL 0.17, WL 0.65; CI 100, PMI 108, PTI 71, SI 56.

Paratype workers (n=30, mean ± standard deviation and variability in parentheses): TL 2.64±0.14 (2.28–2.98), HL 0.59±0.02 (0.53–0.63), HW 0.57±0.02 (0.52–0.6), SL 0.32±0.01 (0.28–0.33), PML 0.39±0.02 (0.33–0.42), PW 0.43±0.02 (0.37–0.47), PTLL 0.18±0.01 (0.15–0.2), PTLH 0.27±0.01 (0.25–0.3), PPLL 0.15±0.01 (0.12–0.17), WL 0.61±0.03 (0.53–0.67); CI 97±2.5 (91–100), PMI 110±2.4 (108–117), PTI 64±3.5 (59–71), SI 56±1.7 (53–59).

Diagnosis. Monomorphic subterranean myrmicine ants but with clearly size-variable workers (TL 2.3–3) that have vestigial eyes (0–2 ommatidia per eye) and reduced/obsolete promesonotal shield, depigmented cuticle with superficial sculpture and shortened appendages. Other important characteristics are: broad frontal carinae and well-defined antennal scrobes that extend above eyes, 9-merous antennae with 3-merous club, mandible with 5 teeth, sessile petiole with cuneate node, aculeus with dorsal flange and spatulate lancets. From all known species of the genus as defined by Bolton [1981, 2003] and Boudinot and Fisher [2013] *M. dlusskyi* **sp. n.** differs by palp formula 3.3 (5.3 in other species).

Etymology. The species is named to the memory of the famous Russian myrmecologist, Prof. Gennady M. Dlussky, whom the author considers as his first mentor in the study of ants.

Comments. At present, *Meranoplus dlusskyi* **sp. n.** is known only from Dong Nai Culture and Nature Reserve of Southern Vietnam. It is a very distinctive species within the genus. Specialized, autapomorphic conditions of its workers are presumably associated with an underground lifestyle. Partially they are a result of reduction and similar conditions are also seen in other genera of Myrmicinae that contain subterranean species. For example, the strong reduction of the eye is observed in the subterranean species of *Pheidole* Westwood, 1839, *Crematogaster* (*Orthocrema* Santschi, 1918), *Tetramorium* Mayr, 1855 etc. Reducing the number of segments in the maxillary palps may also be associated with adaptation to underground foraging. This possibility was pointed at the first time by Gotwald [1969]. In addition, the total depigmentation of cuticle, superficial sculpture, shortened and flattened tibiae and obsolete promesonotal shield indicates a hypogaeic lifestyle of *M. dlusskyi* **sp. n.**

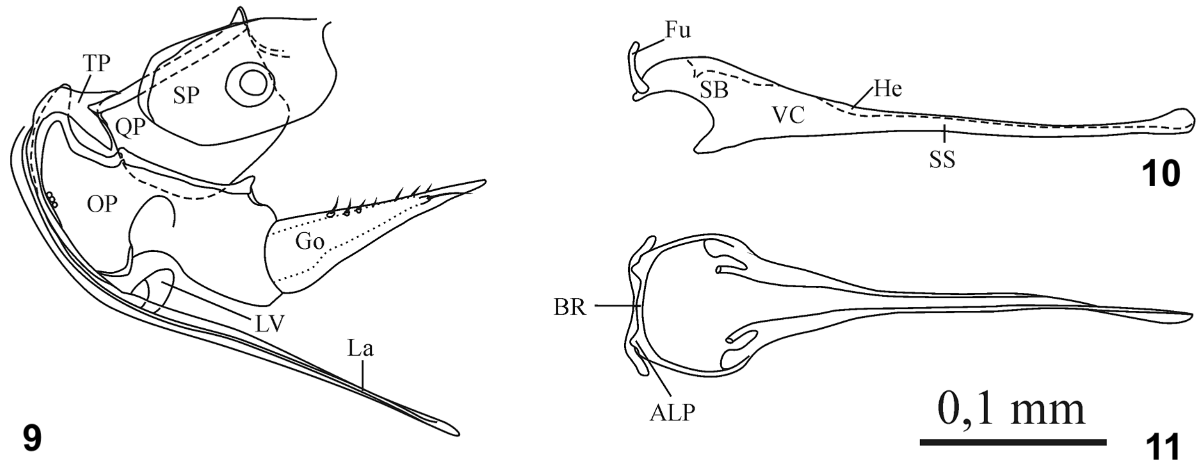


Figs 4–8. Morphological features of *Meranoplus dlusskyi* **sp. n.** workers.

4 – head, full-frons view; 5 – head, underside view; 6 – lower part of the head, underside view, labio-maxillary complex is removed (arrows point to the denticles beneath the 3rd tooth of mandibles); 7 – mesosoma and waist segments, dorsal view; 8 – same, lateral view. Scales 0.2 mm.

Рис. 4–8. Морфологические особенности рабочих *Meranoplus dlusskyi* **sp. n.**

4 – голова, вид спереди; 5 – то же, вид сзади; 6 – нижняя часть головы, вид сзади, лабио-максиллярный комплекс удален (стрелки указывают на зубчики под 3 зубцом мандибул); 7 – мезосома и сегменты стебелька, вид сверху; 8 – то же, вид сбоку. Масштабная линейка 0.2 мм.



Figs 9–11. Sting apparatus of worker in *Meranoplus dlusskyi* **sp. n.**
9 – lateral view; 10 – sting, lateral view; 11 – sting, ventral view. Abbreviations: ALP – anterolateral process, BR – basal ridge, Fu – furcula, Go – gonostylus, He – hemocoel, La – lancet, LV – lancet valve, OP – oblong plate, QP – quadrate plate, SB – sting bulb, SP – spiracular plate, SS – sting shaft, TP – triangular plate, VC – valve chamber.

Рис. 9–11. Жалящий аппарат рабочего *Meranoplus dlusskyi* **sp. n.**
9 – вид сбоку; 10 – жало сбоку; 11 – жало снизу. Сокращения: ALP – переднебоковой отросток, BR – базальный край, Fu – фуркула, Go – гоностиль, He – гемоцель, La – ланцет, LV – клапан ланцета, OP – продолговатая пластинка, QP – квадратная пластинка, SB – ампула жала, SP – дыхальцевая пластинка, SS – створка жала, TP – треугольная пластинка, VC – полость вальвы.

Nonetheless several features in *M. dlusskyi* **sp. n.** are associated with amplification of their functions. In this regard *M. dlusskyi* **sp. n.** workers differs from epigaeic species by the followed features (for comparison were used *M. bicolor* workers): 1) enlarged metapleural gland bulla, 2) deep and curved mandibular grooves that seem to be connected via mandalus with ducts of mandibular glands and 3) concentration of trichoid curvata sensillae [sensu Dumpert, 1972] on the much enlarged club segments of antennae. Probably these features are aimed at amplification of signal functions (namely of chemical signalization), important for underground lifestyle.

Tergosternal fusion [sensu Bolton, 1990] of postpetiole observed in the workers of *M. dlusskyi* **sp. n.** is also seen in the workers of *M. bicolor* (Fig. 13) and is a possible characteristic feature (synapomorphy) of the entire genus [but see Gotwald, 1969]. In studied specimens even after exposure to a hot caustic potash solution the postpetiole cannot be separated into tergite and sternite. So far, tergosternal fusion of postpetiole within Myrmicinae has been reported only in *Cephalotes*, *Procryptocerus* Emery, 1887, *Cataulacus* and *Myrmicaria* Saunders, 1842 [Bolton, 2003].

Discussion

Specialization for an underground lifestyle imposes a significant impact on the morphology of the worker caste of ants. Although some subterranean and leaf-litter myrmicine ants were recently described as the new genus-group taxa by the specialized morphological features of workers (*Secostruma* Bolton, 1988; *Tetheamyrma* Bolton, 1991; *Diaphoromyrma* Fernandez et al., 2009; *Tyrannomyrmex* Silva et al., 2009; *Kempfidris* Fernandez et al., 2014), a new species recognized in this study is a member of the genus *Meranoplus*. However, strongly hypogaeic species were hitherto unknown within *Meranoplus*, therefore the evaluation of taxonomic position and possible origin of *M. dlusskyi* **sp. n.** is of a particular interest.

Due to the presence of the above-considered apomorphies, the new species is strongly different from all known members of the genus and formally should be allocated in a separate species group. Moreover, the combination of *M. dlusskyi* **sp. n.** features actually does not reveal its relationship with other described species groups and even with putative radiations of *Meranoplus* [sensu Andersen, 2006]. Nevertheless, several conditions in *M. dlusskyi* **sp. n.** are most probably plesiomorphic, indicating an early separation of this phyletic line within the genus. These are the following characters: (1) the presence of 5 teeth in the masticatory margin of mandibles; (2) absence of clypeal armament; (3) shape of propodeum, which constitutes part of the dorsal alitrunk.

In various species of *Meranoplus* the number of teeth in the masticatory margin of mandibles ranges from three to five and all these variants were encountered in the Australian *M. diversus* group [Schödl, 2007]. Most species of this group have 3 or 4 teeth in masticatory margin of mandibles, but 5 teeth are found in only *M. mcarthuri* Schödl, 2007. Such variations along with the characteristic form of the clypeus may be due to adaptation to the granivory. The vast majority of other species of *Meranoplus* has 4 teeth in the mandibles. There are reasons to believe that this state derived from the mandibles with 5 teeth and reflects the general evolutionary trend among the Myrmicinae with triangular mandibles, expressed as the reduction in teeth number [Bolton, 2003]. *Meranoplus peringueyi* Emery, 1886, species of the *M. spininodis* group from the Ethiopian zoogeographical region [Bolton, 1981], Oriental *M. bellii* Forel, 1902 and *M. castaneus* [Schödl, 1998] as well as *M. dlusskyi* **sp. n.** have mandibles with 5 teeth. In all these species the basal (5th) tooth is the smallest, sometimes obsolete. In *M. levis* Donisthorpe, 1942 the basal tooth undergoes a further reduction (often absent).

When creating a preliminary system of Australian *Meranoplus* Andersen [2006] pointed to the distinctive feature of the *M. fenestratus* species group (putative radiation), which has an unusual clypeal structure for *Meranoplus*, lacking an acutely angled and often laterally toothed "apparent" anterior clypeal margin that projects well forward of the actual anterior clypeal margin. In other words, the clypeal armament typical for *Meranoplus* is absent in these species. The already mentioned *M. peringueyi*, *M. bellii*, *M. castaneus*, as well as *M. mayri* Forel, 1910 from Madagascar and *M. leveillei* Emery, 1883 from New Caledonia have a similar structure of clypeus [Andersen, 2006]. This state is considered plesiomorphic in the same sense as "conservative" in Rasnitsyn and Dlussky [1988]. In *M. dlusskyi* **sp. n.** the clypeus not projecting beyond the apices of the frontal lobes (Fig. 6) has not any armament. Consequently, in the structure of clypeus as well as the number of teeth in the mandibles the present new species is closer to the generalized (ancestral) type of *Meranoplus*.

The contraction of mesosoma is one of the clearest trends in the evolution of Myrmicinae [Dlussky, Fedoseeva, 1988]. With regard to *Meranoplus* it means that the presence of an extensively exposed dorsal part of propodeum that is clearly visible from above is undoubtedly plesiomorphic. In *M. dlusskyi* **sp. n.** this part compared with the rest of the mesosoma is significantly larger than in all other species of *Meranoplus*. The presence of a distinct dorsal face of the propodeum in *M. bellii*, *M. castaneus* and in the *M. spininodis* species group can also be regarded as a plesiomorphic trait. However, in some Australian species (for example, in *M. dimidiatus* gp.) the reduction of promesonotal shield evidently occurred when the mesosoma was already more compact, so their propodeum is virtually invisible from above.

The distribution of species with a set of postulated plesiomorphies at the edges of the *Meranoplus* range is in good agreement with the concept of ousted relicts [Darlington, 1966]. According to molecular data [Moreau et al., 2006], the *Meranoplus* clade split off at an early stage of diversification of Myrmicinae, therefore these ants were able to spread under conditions of low competitive pressure. Later the former area for *Meranoplus* in Africa and Asia has been reduced perhaps due to climate change and competition with more advanced species, such as *Tetramorium*, *Crematogaster* Lund, 1831, *Pheidole*, etc. For example, in South Asia most species are currently concentrated in the southern part of the Indian subcontinent and Sri Lanka, or confined to the mountain habitats [Schödl, 1998]. The *M. spininodis* species group and *M. peringueyi*, which are restricted to southern African savannahs [Bolton, 1981] can also be considered to be ousted relicts. In case of the ousted *M. dlusskyi* **sp. n.** a shift in adaptive zone also occurred. It is important to emphasize that the shift to the underground lifestyle in *Meranoplus* might have been possible only at an early stage of its evolution before the protective morphology characteristic of these ants appeared. This fact might indicate the formation of *Meranoplus* in the tropical forests and the main trend of its further evolution as the speciation in the humid-arid gradient. However, the entire history of this genus can be discussed when fossils of its ancestral lineage are found and when a more plausible phylogeny is revealed.

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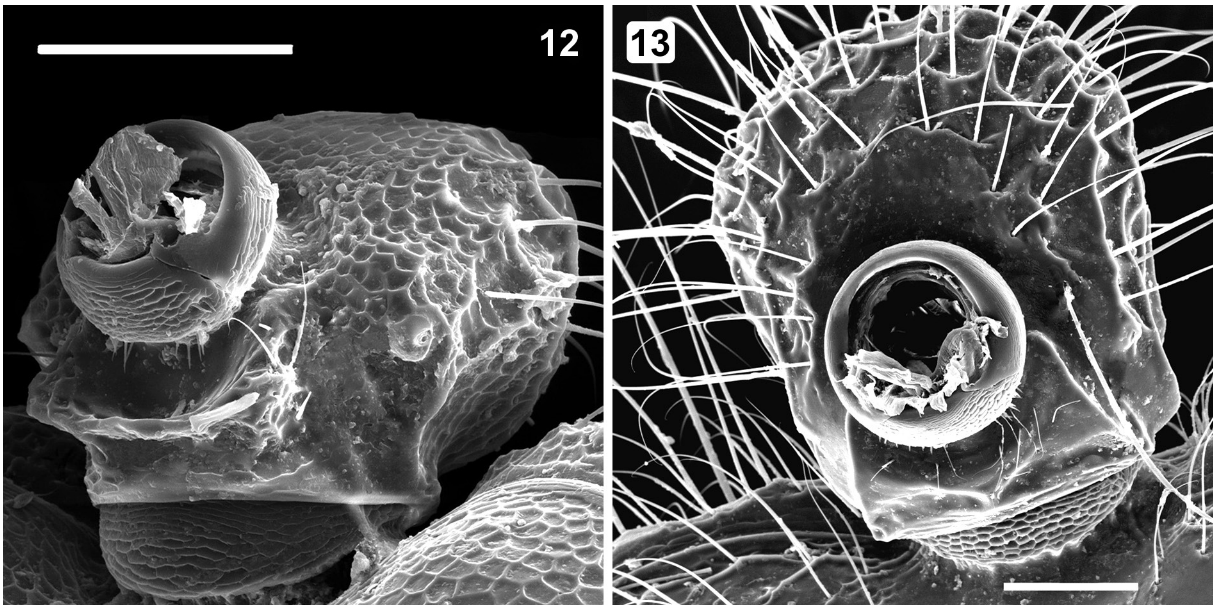

Figs 12–13. Postpetiole of workers in two species of *Meranoplus*.
12 – *M. dlusskyi* **sp. n.**; 13 – *M. bicolor*. Scales 0.1 mm.
Рис. 12–13. Постпетиоль рабочих двух видов *Meranoplus*.
12 – *M. dlusskyi* **sp. n.**; 11 – *M. bicolor*. Масштабная линейка 0.1 мм.

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