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A remarkable new species of *Leptogenys* Roger, 1861 (Hymenoptera: Formicidae) from Vietnam

Новый необычный вид *Leptogenys* Roger, 1861 (Hymenoptera: Formicidae) из Вьетнама

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Ключевые слова: Formicidae, Ponerinae, *Leptogenys*, новый вид, эргатоидные самки, параллельная эволюция, Вьетнам.

Abstract. The new large ant species of the subfamily Ponerinae, *Leptogenys leleji* **sp.n.**, is described from the Bi Dup-Nui Ba Nature Reserve (Lam Dong Province, South-Central Vietnam) based on a single worker and two ergatoid queens. This species is well distinguished from the other Vietnamese and Oriental congeners by general shape of the head, mandibles (the cranio-mandibular system) and especially by petiole which posterior apex in profile drawn out into a blunt tooth. The ergatoid queen is very similar to the worker except for the following features: body larger, dorsal propodeal margin more convex, petiole broader in dorsal view and gaster more voluminous than in the worker. Similar habitus including the shape of the petiole is known in some species group of *Leptogenys* from the New World, Africa and Australia. However, this similarity has arisen independently in each zoogeographical region as a result of the parallel evolution.

Резюме. Новый крупный вид подсемейства Ponerinae, *Leptogenys leleji* **sp.n.**, описан из природного заповедника Бидуп-Нуйба (провинция Ламдонг, Южно-Центральный Вьетнам) на основе рабочего и 2 эргатоидных самок. Этот вид хорошо отличается от остальных вьетнамских и ориентальных представителей рода общей формой головы, мандибул (кранио-мандибулярной системой) и особенно петиолем, задняя вершина которого в профиль вытянута в тупой зубец. Эргатоидная самка очень похожа на рабочего за исключением следующих особенностей: тело крупнее, спинной край проподеума более выпуклый, петиоль со спинной стороны шире и брюшко более объемное, чем у рабочего. Сходный облик, включая форму петиоля, известен в некоторых видовых группах *Leptogenys* из Нового Света, Африки и Австралии. Однако это сходство возникло независимо в каждом зоогеографическом регионе как результат параллельной эволюции.

Introduction

The ant genus *Leptogenys* Roger, 1861 is one of the pantropically distributed taxa of the subfamily Ponerinae, which currently includes 307 extant valid species or about a quarter of described species of Ponerinae [Bolton, 2016]. This genus is one of the ten largest ant genera of the world, and can serve as a model when discussing evolutionary success of the ponerine ants. Based on molecular phylogenetic analysis, Schmidt [2013] showed that *Leptogenys* is a monophyletic taxon within the *Odontomachus* genus group. The diversification of this group occurred probably in Africa between 40 and 30 Mya and had an explosive nature [Schmidt, 2013]. A modern species richness of *Leptogenys* has arisen probably due to the prey specialization, in particular, for isopods [Dejean, Evraerts, 1997; Lattke, 2011]. Indeed, prey specialization in *Leptogenys* is associated with significant changes of the cranio-mandibular system [Dlussky, Fedoseeva, 1988] that could explain much of the morphological diversity in this genus. On the other hand, a similar morphology in the different species groups may be the result of the parallel evolution. Some examples of parallelism within the genus were given elsewhere [Lattke, 2011]. Another interesting example is presented in this paper.

The two types of reproductives have so far been known in the genus: ergatoid queens and gamergates [Ito, Ohkawara, 2000; Peters, 2012]. According to Peters [2012] the term «ergatoid queens» should be used for all wingless reproductives that differ morphologically from workers. So far only three species of *Leptogenys* from the New World are known to have winged queens [Lattke, 2011]. Ergatoid queens in few species have the well-developed flight sclerites and/or three ocelli or the single median ocellus [Bharti, Wachkoo, 2013]. In most cases ergatoid queens are morphologically very similar to the workers, although may be identified by a large propodeum, relatively shorter and broader petiole, more voluminous gaster and some other features [Rakotonirina, Fisher, 2014]. Gamergates are morphologically identical to non-reproductive workers. In terms of ecology both ergatoid queens and gamergates ensure a strategy with rapid and less costly colony reproduction, i.e. colony fission. However, long-range dispersal capabilities are lost in colony fission

[Schmidt, 2013]. This may explain the high level of endemism within the genus. Predominance of ergatoid queens or gamergates in different clades within the genus may shed light on its phylogeny [Lattke, 2011]. However, in many species it is unknown whether ergatoid queens or gamergates is responsible for colony reproduction.

The fauna and taxonomy of *Leptogenys* are well understood in the Ethiopian region [Bolton, 1975], New World [Lattke, 2011] and Madagascar [Rakotonirina, Fisher, 2014], where in total more than a half of the known species has been described. The Oriental fauna of *Leptogenys* that includes about 100 species awaits a taxonomic revision, although the identification keys to species are now available for China [Xu, 2000; Zhou et al., 2012] and India [Bharti, Wachkoo, 2013]. A recent synopsis of *Leptogenys* of Vietnam includes 40 species [Eguchi et al., 2014], but most of them are presented therein as morphospecies and have not yet been identified based on careful examination of the type materials of Oriental species. It should be noted the problem of species boundaries in the genus [Lattke, 2011; Rakotonirina, Fisher, 2014]. For example, in the Cat Tien National Park (Dong Nai Province, South Vietnam) we collected 20 morphologically different representatives of *Leptogenys*. However, only 12 of them may be considered as «bonae species», the others may be complexes of two–three species or polytypic species which require further investigation better at the molecular level.

In the Bi Dup-Nui Ba Nature Reserve (Lam Dong Province, South-Central Vietnam) were found 90 ant species including eight species of *Leptogenys* [Zryanin, 2013]. One of them previously labeled as *Leptogenys* sp. [A] has unusual habitus among all the Oriental congeners. At the same time a combination of several features (shape of the cranio-mandibular system, the petiole, etc.) makes it similar to the representatives of the *L. conradti* species group from Africa, the *L. turneri* species group from Australia and some species of the *L. arcuata* clade from the Neotropics. That arouses a particular interest in terms of parallel morphological evolution in different phylogenetic lines of *Leptogenys* inhabiting the different continents. Description of this species and discussion of its unusual habitus are the main goals of this article.

Material and methods

Material for the description of the new species (one worker and two ergatoid queens) was obtained during the expedition of the Russian-Vietnamese Research and Technological Tropical Center in March — April 2008 in the Bi Dup-Nui Ba Nature Reserve. All specimens were collected by hand from the soil surface on very limited area near the Da Nhim River. This site can be characterized as the edge of a lower montane evergreen forest dominated by trees from the Fagaceae and Lauraceae families.

The terminology for morphological features generally follows Lattke [2011]. Measurements and indices also follow Lattke [2011], but for the petiole follow Rakotonirina and Fisher [2014]. All measurements were recorded to the nearest 0.001 mm using ZEN 2 software from the photos obtained using an Axiocam 105 color camera attached to a Stemi 2000C Carl Zeiss microscope. In the article measurements are rounded to the second decimal place and have the following abbreviations: HL — head length: midline length of the head capsule, measured in full-face view from the posterior margin to the anterior extremity of the clypeal margin; LCM — lateral cephalic margin: measured in the same plane as HL between the base of mandible and a line drawn across the posterior margin of the head; HW — head width: maximum width of head, measured in the same plane as HL; ML — mandible length: straight-line length of mandible, measured from the base at the insertion into the head capsule, to the apex; EL — eye length: maximum length of compound eye; SL — scape length: maximum length of the first antennal segment excluding the neck and basal condyle; PW — pronotal width: maximum width of pronotum in dorsal view; WL — Weber's length of the mesosoma (alitrunk): diagonal length, measured in lateral view from the anterior margin of the pronotum (excluding the collar) to the posterior extremity of the propodeal lobe; PNW — petiolar node width: maximum width of the node in dorsal view; PNH — petiolar node height: the height of the node in profile, measured vertically from the ventral margin at the junction between the ventral margin of the node and subpetiolar process to the dorsal border of the node; PNL — petiolar node length: maximum length of the node in dorsal view. Indices are expressed as a percentage, rounded to the nearest whole number and presented with following abbreviations: CI — cephalic index: HW×100/HL; SI — scape index: SL×100/HW; LNI — lateral petiolar node index: PNH×100/PNL; DNI — dorsal petiolar node index: PNW×100/PNL.

Multi-focused images of full-face view of the head, profile and dorsal view of the specimens were produced using Helicon Focus 5.3 Pro from a series of source photos (z-stacking) and cleaned with Adobe Photoshop CS5. For comparative purposes descriptions of selected species and species groups were used [in Bolton, 1975; Lattke, 2011; Rakotonirina, Fisher, 2014], as well as the images of specimens in three planes that are available at www.antweb.org (AntWeb v6.2.3).

Taxonomy

Leptogenys leleji Zryanin, **sp.n.**
Figs 1–5.

Material. Holotype, worker: Vietnam, Lam Dong Province, Lac Duong District, Bi Dup-Nui Ba Nature Reserve, near Long Lanh village, 12°10' N, 108°40' E, 1450 m a.s.l., 28.III.2008, leg. V. Zryanin (BD8). Paratypes: 2 ergatoid queens, same locality, 26.III and 23.IV.2008, leg. V. Zryanin (BD1, BD77). The holotype and one paratype are deposited in the collection of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), one paratype is deposited in the collection of the Zoological Museum of the Moscow Lomonosov State University.

Description. *Worker*, holotype. Measurements and indices: HL 2.18, LCM 1.45, HW 2.13, ML 1.88, EL 0.40, SL 2.10, PW 1.41, WL 3.70, PNH 1.08, PNL 1.34, PNW 0.83; CI 98, SI 99, LNI 81, DNI 62.

Habitus of worker as in Fig. 1. Head in full-face view markedly wider anteriorly than posteriorly, lateral and posterior margins forming continuous convexity, occipital

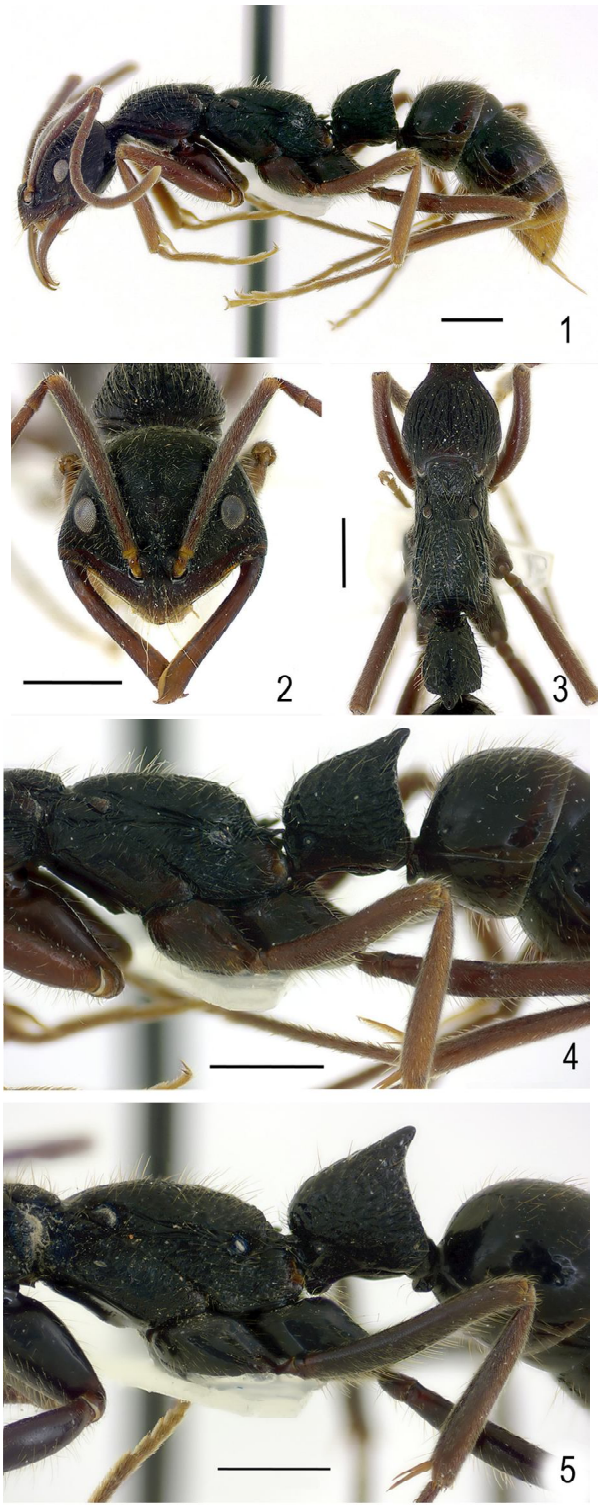

Рис. 1–5. *Leptogenys leleji* **sp.n.** 1–3 — рабочий, голотип, внешний вид сбоку (1); голова спереди (2); мезосома и стебелек сверху (3). 4–5 — часть мезосомы и петиоль сбоку: рабочий (4); эргатоидная самка (5). Масштабная линейка: 1 мм.

Figs 1–5. *Leptogenys leleji* **sp.n.** 1–3 — worker, holotype, habitus, lateral view (1); head, frontal view (2); mesosoma and petiole, dorsal view (3). 4–5 — part of the mesosoma and petiole in lateral view: worker (4); ergatoid queen (5). Scale bars: 1 mm.

carina distinct. Clypeus triangularly produced, with a blunt apex; anterior clypeal margin fringed with narrow translucent lamella, without peg-like setae medially; median longitudinal carina of clypeus sharp. Eyes large, weakly convex, placed dorsolaterally on head, their greatest diameter greater than maximal width of scape. Frontal groove shallow, extending to the level of posterior margin of eye. Mandibles long, feebly curved near bases, with only apical tooth and distinct crest along basal margin; blades in full-face view generally same width from the base to apex; a large gap formed between clypeus and mandible when fully closed (Fig. 2); basal groove indistinct. Palp formula: maxillary 4, labial 4. Antennal scape relatively short (SI 99). Basal flagellar (third antennal) segment elongate, markedly longer than neighboring antennal segments (the lengths of the segments 2–4: 0.35 mm, 0.53 mm, 0.38 mm).

Mesosoma (alitrunk) with deep and wide, transversally striate metanotal groove that divides dorsal outline of mesosoma into two distinct convexities in lateral view. Mesonotum wider than long, with markedly median impression on posterior half (Fig. 3); anteroventral mesopleural carina well-developed, forming small angular lobe anteriorly; epicnemial carina projected anteriorly into distinct laminate and angulate epicnemial process; anapleural sulcus divides mesopleuron into smaller anepisternum and larger katepisternum; mesometapleural suture well impressed. Metapleural-propodeal suture developed as ridge that extends from propodeal spiracle and broadened toward metathoracic spiracle; propodeal spiracle slit-like; bulla of metathoracic spiracle convex. Propodeum armed with triangular tooth at the level of spiracle; propodeal declivity with carina uniting apices of these teeth; area anteriad to the carina concave in cross-section, with mostly smooth and shining surface; area posteriad to the carina depressed as a broad transverse sulcus. Apex of protibia without setae; first protarsal segment with comb of stout setae opposite strigil; meso- and metatibial apex each with two apical spurs and several setae; posterior metacoxal swelling well developed; tarsal claws pectinate.

Petiole with convex anterior margin, and straight ascending dorsal margin in lateral view; both margins joined by convexity; dorsal margin ends in blunt pointed tooth that projects beyond posterior margin by almost one-fifth node length, tooth forms approximately 30-degree angle with longitudinal axis. Posterior margin of petiole in lateral view straight but not sinuate; posterior face flat and sharply margined laterally. Node longer than wide in dorsal view, its anterior margin little more than half of posterior margin (Fig. 3); cross-section of petiolar node at mid-length with convex sides. Subpetiolar process shaped as sub-rectangular tubercle with gentle posterior slope. Anterior and dorsal margins of first gastral (third abdominal) segment joined through a continuous convexity; constriction between first and second gastral segments well marked. Prora shaped as sharp, ventrally directed lobe at anteroventral angle of first gastral segment. Pygidium with indistinct median carina, hypopygium with a row of small setae close to base of sting.

Cephalic dorsum between and behind eyes mostly smooth and shinning, with shallow piligerous punctae; malar space and frontal area striate; clypeus with fine longitudinal to oblique striae, which are more pronounced antero-medially. Antennae covered with dense piligerous punctulae. Dorsal surface of mandible with fine striation. Propleuron and pronotal dorsum sulcate; mesopleuron mostly smooth and shining, katepisternum scrobiculate along mesometapleural suture; metapleuron sulcate to scrobiculate; dorsum of propodeum with irregular fovea and median sulcus; metanotal

groove with cross-ribs. Petiole scrobiculate, with rimose posterior face. Gaster smooth and shining.

Body with abundant suberect to erect hairs; apressed pubescence present on cephalic dorsum, antennae and legs. Longest hairs present on median lobe of clypeus.

Body colour mostly black to dark brown, with blue reflection of smooth surfaces. Antennae, mandibles, and legs mostly brown. Gastral apex and edges of last sclerites, base and apex of scape, crest on basal margin of mandible, last segments of tarsus dull yellow.

Queen (ergatoid). Measurements and indices (n = 2): HL 2.31–2.35, LCM 1.50–1.51, HW 2.23–2.35, ML 1.93–2.07, EL 0.45–0.46, SL 2.31–2.36, PW 1.49–1.55, WL 4.06–4.10, PNH 1.20–1.21, PNL 1.39–1.41, PNW 0.95–1.02; CI 96–100, SI 101–104, LNI 85–87, DNI 68–72.

Ergatoid queen is very similar to the worker except for the following features: body bigger, dorsal propodeal margin more convex compare to the worker (Figs 4, 5), petiole broader than in the worker in dorsal view and gaster more voluminous. In addition, hairs on dorsum of body are more abundant and appendages are darker than in worker.

Male. Unknown.

Diagnosis. This species is well distinguished from the other Vietnamese and Oriental congeners with a set of the following characters in the worker: cephalic capsule wider than long; anterior clypeal margin fringed with narrow translucent lamella; mandibles linear, a large gap formed between clypeus and mandible when fully closed; basal flagellar (third antennal) segment elongate; dorsum of body with standing hairs; propodeum with lateral teeth, posterior apex of petiole in profile drawn out into a tooth.

Etymology. The species is named in honor of the head of the Laboratory of Entomology (Institute of Biology and Soil Science, Vladivostok, Russia), Prof. Arkadiy S. Lelej, the authority of fauna and taxonomy of Hymenoptera.

Comments. A new species is well distinguished from the most of Oriental named congeners by general shape of the head, mandibles (the cranio-mandibular system) and especially by toothed petiolar node. At the same time a combination of these features makes it similar to the representatives of the *L. conradti* species group from the Ethiopian region [Bolton, 1975], the *L. turneri* species group from Australia [Taylor, 1988], as well as the *L. unistimulosa* and *L. ingens* species groups (both are included in the *L. arcuata* clade) from the Neotropics [Lattke, 2011]. However, there are significant differences between the new species and members of the listed species groups. They differ in the shape of clypeus and clypeal armament, especially the *L. turneri* group (former subgenus *Odontopelta* Emery, 1911). The members of *L. unistimulosa* species group have peg-like setae on clypeal apex and large hypostomal lobes. The *L. ingens* species group is characterized by the discrete kink of the median clypeal lobe and by the presence of well-developed lateral clypeal lobes. In *L. leleji* sp.n. the clypeus lacks denticles and prominent median lobe, its apex lacking peg-like setae, and the hypostomal lobes are absent, but narrow translucent lamella is present along lateral clypeal margins. In the *L. conradti* species group the clypeus has a rounded prominent median lobe, but lacks a fringing lamella. In *L. leleji* sp.n. the propodeum armed with well protruding triangular teeth, but in the listed species groups the propodeum unarmed. In addition, *L. leleji* sp.n. and the *L. turneri* species group have ergatoid queens, which are replaced by gamergates in the other species groups under consideration. Thus, the similarity of these species has arisen independently in each zoogeographical region as a result of the parallel evolution.

Discussion

As mentioned above, the prey specialization in *Leptogenys* is associated with significant changes of the cranio-mandibular system [Dlussky, Fedoseeva, 1988] and may be responsible for most of morphological diversity within the genus [Schmidt, 2013]. The characteristic prey of many representatives of *Leptogenys* are the oniscoid isopods as have been reported for the species from the New World, Africa, New Guinea, etc. [Dejean, Evraerts, 1997 and the references cited therein; Lattke, 2011]. These terrestrial crustaceans frequently constitute an important part of the soil fauna, but they are well protected from predators. In particular, they are able to roll themselves up or secrete adhesive proteinaceous compound as a defense mechanism against ants [Deslippe et al., 1995 cit. ex Lattke, 2011]. Thus, isopod-hunting *Leptogenys* species usually have curved, elongate, and narrow mandibles. The ants hunt isopods solitarily as a rule, and their hunting success positively correlates with the length of their mandibles [Dejean, Evraerts, 1997]. The lengthening of mandible is accompanied by a broadening of the anterior margin of the cephalic capsule, displacement of the compound eyes dorsolaterally on the head, certain changes in the shape of the clypeus. In general, these ants are characterized by the large body size of workers and small colony size (few dozen workers per family) [Lattke, 2011]. Most likely such morphological traits occurred independently in different species groups with the similar levels of social organization as a result of prey specialization. No data on the prey specialization of *L. leleji* sp.n. are available. However, the shape of its cranio-mandibular system closely resembles that of the actual specialists on terrestrial isopods (such as the species groups listed ones in the Comments). Rare occurrence of the new species (only three specimens were collected within a month of intensive sampling) indicates a small colony size and therefore a solitary hunting as in other specialists on isopods. Hence, it is possible to assume a similar prey specialization in *L. leleji* sp.n. that can explain its similarity with the congeners from other zoogeographical realms in the shape of cranio-mandibular system.

The similarity in the shape of petiole, i.e., having a toothed petiolar node, is more intriguing since the selective advantage of such petiole is difficult to explain. However, the petiole modifications in the *L. unistimulosa* species group from the Neotropics seem to provide a possible answer to the question. In the relatively small-sized species *L. peruana* Lattke, 2011 the petiolar node usually forms neither a tooth nor a lobe, or sometimes has a small blunt lobe that slightly overhangs the posterior petiolar margin. Conversely the large-sized species of this group (*L. paraensis* Lattke, 2011, for example) have the node apex with acutely sharp point that markedly overhangs posterior margin in lateral view.

In the *L. pubiceps* complex the shape of the node apex seems to be categorized into two trends: (A) a very modest posterior crest is formed; (B) a distinct blunt tooth is formed [Lattke, 2011]. Furthermore, in the *L. pubiceps* complex, the shape of petiole seems to be correlated to the structure of cranio-mandibular system. The species with the «trend A» petiole have the head that has subparallel lateral margins in dorsal view, is usually longer than broad, and has relatively narrow mandibles. On the other hands, the species with the «trend B» petiole vary in mandible thickness, and some of them will have the head that is wider anterad than posterad. In addition, the species with the «trend B» petiole tend to have the eyes more dorsolaterally situated than the species with the «trend A» petiole [Lattke, 2011]. These facts suggest that the toothed petiolar node is also one of the specializations for prey hunting or prey manipulation. Furthermore, it is worth noting that the petiolar tooth is more developed in large-sized species (also in the *L. ingens* and *L. conradti* species groups). This functional relation is assumed to have appeared independently in different *Leptogenys* species groups and to be typical for large solitary hunters including *L. leleji* sp.n.

In conclusion, one assumption could be made to explain the morphological distinction of *L. leleji* sp.n. from the other Oriental congeners. As far as the present author know, *L. modiglianii* Emery, 1900 is only one Oriental species which has the cranio-mandibular system similar to *L. leleji* sp.n., but *L. modiglianii* does not have a tooth on the petiolar node apex. This species has so far been known only from the type locality (Enggano Island, Indonesia). Meanwhile, species with the similar habitus are rather numerous in other zoogeographical regions. The reason may lie in the long evolutionary history of this genus in South East Asia. The long history implies more time for both speciation and extinction, and perhaps the species similar to *L. leleji* sp.n. are the relicts of previously more widespread and diverse group which has mostly been decimated by extinctions. The plesiomorphic character state of the predation of isopods in *Leptogenys* [Dejean, Evraerts, 1997] can serve as an additional argument, if the expected prey specialization of *L. leleji* sp.n. to be confirmed.

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