

A new species of *Haploperla* from China (Plecoptera, Chloroperlidae)

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Abstract

A new species of the genus *Haploperla*, *H. triangulata* **sp. n.**, is described and illustrated from specimens collected in Qinghai province, China. *Haploperla triangulata* is characterized by the epiproct mostly sclerotized and hairless, sub-triangular in dorsal view and blunt at tip; and by the aedeagus with two median elliptical lobes ventrally. The new species is compared with its most similar congeners, and diagnostic characters are presented.

Keywords

Stoneflies, species description, aquatic diversity

Introduction

The genus *Haploperla* Navás 1934 is mainly distributed in eastern Palaearctic and Nearctic regions, with only thirteen extant species reported (DeWalt et al. 2015). Only four Chinese species of *Haploperla* have been recorded from China, *Haploperla ussurica* Navás, 1934; *H. lepnevae* Zhiltzova & Zwick, 1971; *H. valentinae* Stark & Sivec, 2009; and *H. choui* Li & Yao, 2013 (Navás 1934, Zhiltzova and Zwick 1971, Stark and Sivec

2009, Li et al. 2013). Unknown specimens of *Haploperla* from Shuixia, Huangzhong county in Qinghai province were collected in August 2015, and identified as a new species. The types are deposited in the Insect Collection of Yangzhou University, Jiangsu. The species described in this contribution increases the number of known Chinese *Haploperla* taxa to five.

Materials and methods

All type specimens are preserved in 75% or 100% ethanol. Specimens were examined and illustrated using a Leica stereomicroscope-MZAPO. Images were taken using a Leica SZ45. The holotype of the new species is deposited in the Insect Collection of Yangzhou University, China.

Results

Haploperla triangulata sp. n.

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Figs 1–10

Type material. Holotype. 1 male, China: Qinghai province, Huangzhong county, Shuixia, 101°41.25'E, 36°82.46'N, 2590 m, 8 August, 2015, leg. Yu-Zhou Du. Paratype: 1 male and 7 females, the same locality and data as holotype, leg. Yu-Zhou Du, Zhi-Hou Li, Qiu-Yu Fan.

Diagnosis. This species is characterized by a pale head, a pale pronotum disc with median stripe and brown margins, and the abdominal terga 1–8 with a longitudinal stripe. Epiproct mostly sclerotized and hairless, sub-triangular in dorsal view with a blunt tip. Aedeagus ventrally with two median situated elliptical lobes.

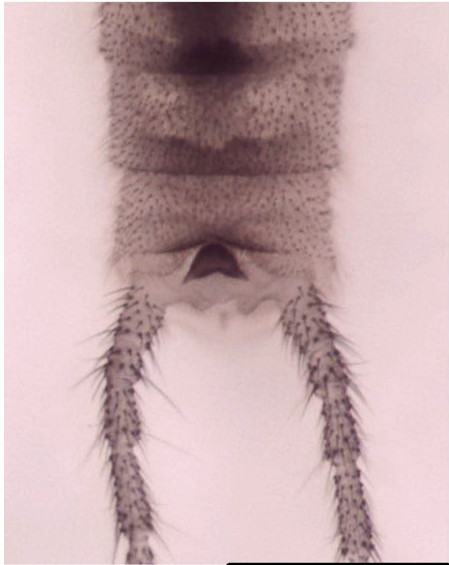
This new species is most similar to *H. valentinae* Stark & Sivec, 2009, known from Sichuan Province, China, but differs in the formation of the epiproct, which is mostly sclerotized and hairless in *H. triangulata* sp. n., whereas it is with sclerotized margins, membranous posterodorsal area and sparse patch of setae in *H. valentinae* (see Figs 13 and 17 in Stark and Sivec 2009). Besides, the subgenital plate of female is originating from tergum 8 to the posterior margin of tergum 9 in *H. triangulata*, while it's slightly produced as a small rounded lobe with long setae in *H. valentinae* (see fig. 15 in Stark and Sivec 2009). The details of the wing venation and aedeagus are not described for *H. valentinae*.

Adult habitus. Triocellate. General color light yellow patterned with dark brown. Head mostly pale yellow without any markings; compound eyes and ocelli black (Fig. 1). Pronotum hyaline, with median stripe and brown margins; meso- and metanota with dark brown W-shaped markings. Wings hyaline; Rs of both wings branched; A₃ of forewing fused with A₂ near base; anal field of hindwing small and folded with three



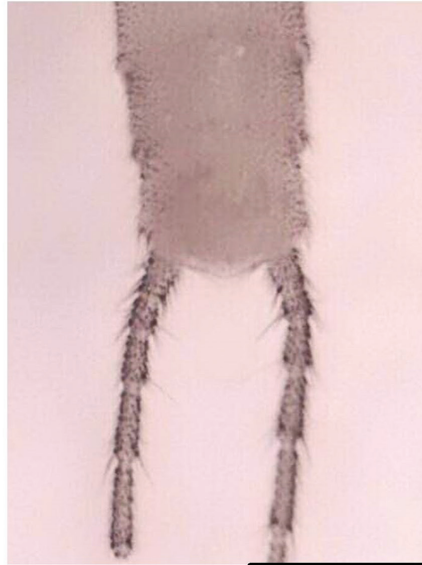
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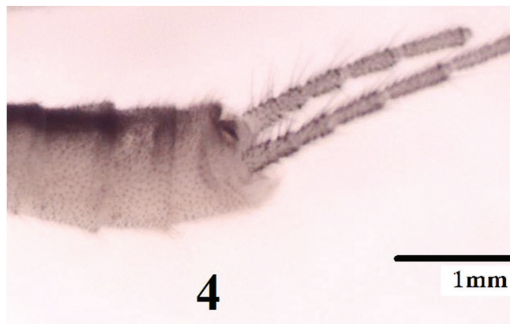
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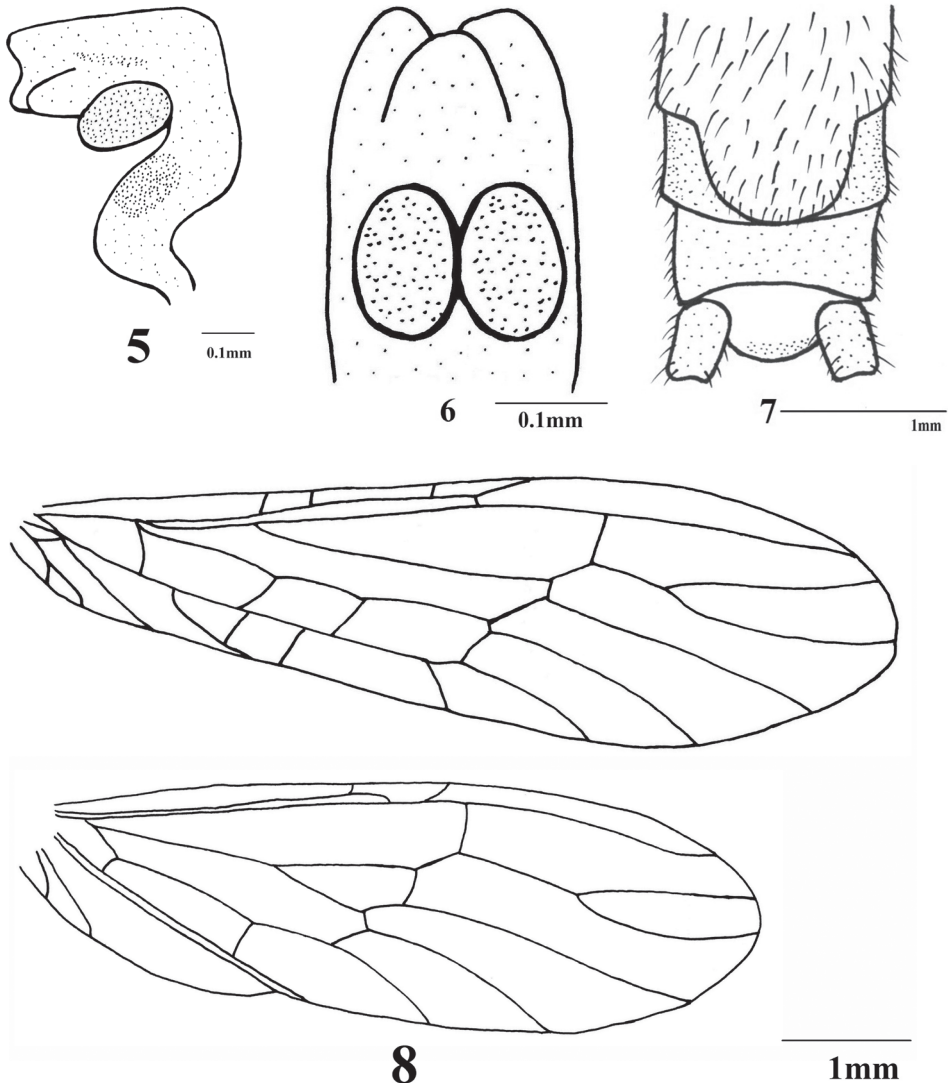
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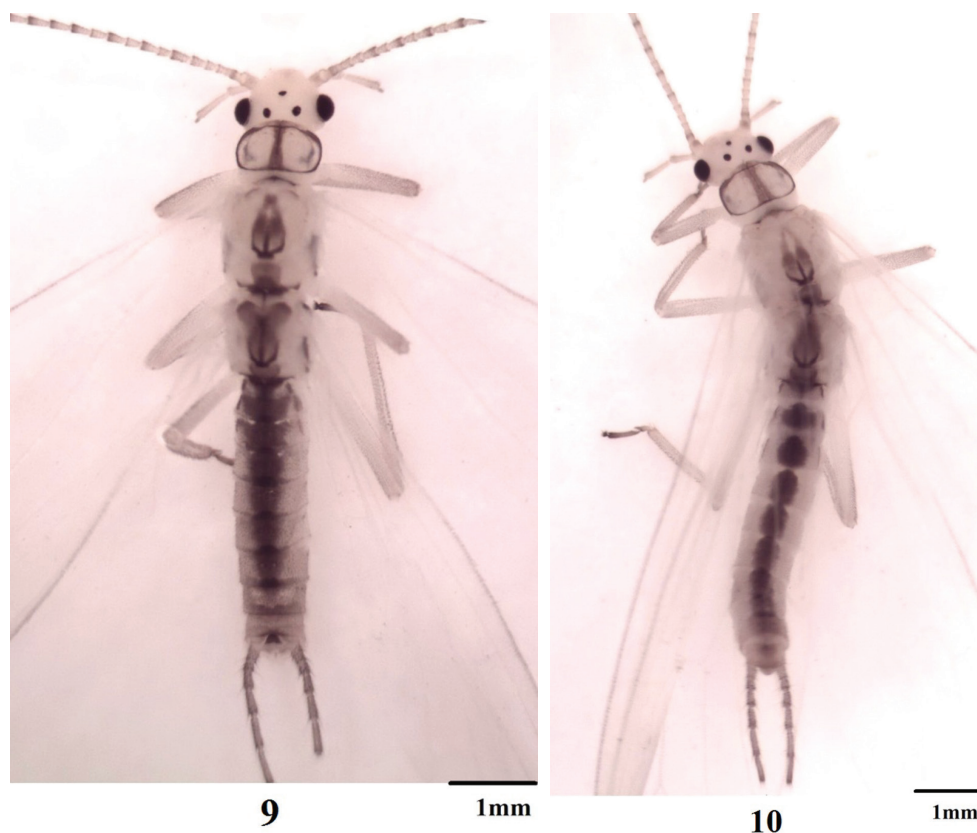
Figures 1–4. *Haploperla triangulata* sp. n. **1** Head and pronotum, dorsal view **2** Male terminalia, dorsal view **3** Male terminalia, ventral view **4** Male terminalia, lateral view.



Figures 5–8. *Haploperla triangulata* sp. n. **5** Aedeagus, lateral view **6** Aedeagus, ventroapical view **7** Female subgenital plate, ventral view **8** Wings.

veins (Fig. 8). Coxae, tibiae and femura pale, tarsi brown. Abdominal terga 1–8 with a medial wide stripe. Cerci yellowish-brown with long brown setae (Figs 9, 10).

Male. Forewing length 6.5–7.0 mm, hindwing length 5.5–6.0 mm. Posterior margin of tergum 9 dark and slightly concave, covered with fine hairs. Tergum 10 divided (Fig. 2). Subgenital plate arising from tergum 9 to tip of the abdomen, slightly tapering at tip (Fig. 3). Subanal process simple, pale and subtriangular in shape. Epiproct mostly sclerotized and hairless, sub-triangular in dorsal view with a blunt tip



Figures 9–10. *Haploperla triangulata*, sp. n. **9** Male habitus, dorsal view **10** Female habitus, dorsal view.

(Figs 2, 4). Aedeagus membranous and curved ventrally, ventrally with two median situated elliptical lobes, subapically with a plump lobe (Figs 5, 6).

Female. Forewing length 7.0–7.5 mm, hindwing length 6.0–6.5 mm. General pattern similar to males. Abdominal segments 1–8 with median brown strip (Fig. 10). Ventral surface and terminalia without markings. Subgenital plate distinct, originating from tergum 8 to the posterior margin of tergum 9; posterior margin slightly protruding, forming a blunt lobe (Fig. 7).

Etymology. The species epithet refers to the sub-triangular shape of the epiproct.

Distribution. China (Qinghai province).

Remarks. We describe a new species of the genus *Haploperla*, thereby increasing the total number of *Haploperla* species recorded in China to five. More *Haploperla* species are expected to be found in China in the future because the geographical conditions ensure suitable resources for stoneflies. More studies are needed to enrich our understanding of *Haploperla*.

Acknowledgments

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Description of two new species of bat fleas of the genus *Araeopsylla* (Siphonaptera) from Kenya and Madagascar with notes on miscellaneous bat fleas

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Abstract

The flea genus *Araeopsylla* Jordan and Rothschild, 1921 contains nine species distributed throughout the Palaearctic, Ethiopian and Oriental Regions primarily on molossid bats. A new species of bat flea, *Araeopsylla goodmani*, is described. This new species is represented by three females collected from one male specimen of the molossid bat *Chaerephon jobimena* Goodman & Cardiff, 2004 from Fianarantsoa Province, Madagascar. A second new species, *Araeopsylla smiti*, is described from one male from the Rift Valley, Kenya. It was collected from the molossid bat *Chaerephon bivittatus* (Heuglin, 1861). This represents the first record of *Araeopsylla* in Kenya. Previous records of *Araeopsylla* in the Malagasy region included *Araeopsylla martialis* (Rothschild, 1903) from Reunion Island and Madagascar. One hundred fifty-eight specimens (64♂, 94♀) of *A. martialis* were collected from 67 specimens (flea intensity of 2.4 fleas per host) of *Mormopterus jugularis* (Peters, 1865) across three provinces of Madagascar (Fianarantosa, Toamasina, and Toliara). *Mormopterus jugularis* is clearly a common host for *A. martialis*. *Dampfia grahami grahami* (Waterston, 1915) is also reported from *Eptesicus matroka* (Thomas & Schwann, 1905) which is the first record from this host species and the first time the genus *Dampfia* has been documented in Madagascar. Although *Lagaropsylla consularis* Smit, 1957 and *Lagaropsylla idae* Smit, 1957 have been reported in Madagascar previously, *Mops leucostigma* Allen, 1918 is a new host record for *L. idae*. The flea intensity of *L. idae* (64♂, 83♀) on 28 specimens of *M. leucostigma* was extremely high at 5.3 fleas per host. A key to the genus *Araeopsylla* is provided.

Keywords

Araeopsylla goodmani, *Araeopsylla smiti*, *Dampfia*, key, *Lagaropsylla*

Introduction

There are currently nine species represented in the flea genus *Araeopsylla* Jordan & Rothschild, 1921 (Lewis 2006). The distribution of *Araeopsylla* is wide-spread, extending across Africa, Madagascar, southern Europe, the Middle East, and Southeast Asia. Members of the genus primarily parasitize bats of the families Emballonuridae and Molossidae. Beaucournu and Fain (1983) and Beaucournu (2004) provided geographical and host lists for Ischnopsyllidae of continental Africa, while Beaucournu and Fontenille (1993) catalogued the fleas of Madagascar. Other papers include specific accounts of miscellaneous small collections of *Araeopsylla*. Although the genus has a broad geographical distribution, specimens are not commonly collected.

During the early 1970's, the author was associated with a project conducted by the late Hank W. Setzer, Department of Mammalogy, National Museum of Natural History that included the collection of small mammals and their ectoparasites across most of the African countries. The fleas collected were made available to the author and were studied for several years. During those early flea studies, the author recognized a new species of *Araeopsylla* and has maintained the single male specimen for 40+ years in anticipation that the female might be discovered. To date, no additional specimens of this species have been discovered.

The Field Museum of Natural History, Chicago, IL conducted mammal studies in Madagascar and also collected ectoparasites from those mammals. The fleas were provided to the author and they were subsequently identified and returned to the Field Museum. Among the material examined were three female specimens representing a new species of *Araeopsylla* and several new country and host records. These two new *Araeopsylla* taxa from Kenya and Madagascar will be described herein. Additional records of bat fleas from Ghana, Kenya, and Madagascar will also be documented and discussed.

Methods

Details of the genitalia of the whole mounted specimen of *A. smiti* (described below) were difficult to visualize. Therefore the specimen was photographed, dissolved off the microscope slide with xylene, dissected, and remounted in Canada balsam. Images were prepared using an Olympus BX61 Compound Microscope, Olympus CC12 digital camera accompanied with an Olympus Microsuite™ B3SV program. This system was also used to measure fleas in accordance with anatomical markers annotated in Hastriter and Eckerlin (2003). References to “flea intensity” implies the mean number of fleas from hosts that were positive for respective flea species. The primary types of *A. goodmani* and *A. smiti* were deposited in the Field Museum of Natural History (FMNH), Chicago, IL and the National Museum of Natural History, Washington, D.C., respectively. One paratype of *A. goodmani* (SMG-13344-2) was deposited in the FMNH collection and one paratype (SMG-13344-3) in the Brigham Young University flea collection (BYUC).

Madagascar records of bat fleas were extracted from data bases of the FMNH flea collections for which the author provided original species identifications. The additional species annotated herein were all retained in the FMNH flea collection (some mounted on microscope slides and others preserved in alcohol) with exception of those retained in the BYUC noted under “Material Examined” sections. For brevity, collectors are listed as: A. Kofi (AK), B.J. Hayward (BJH), C.B. Robbins (CBR), Fanja H. Rattrimomanarivo (FHR) and (RHF), Steve M. Goodman (SMG).

Results

Ischnopsyllidae

Ischnopsyllinae

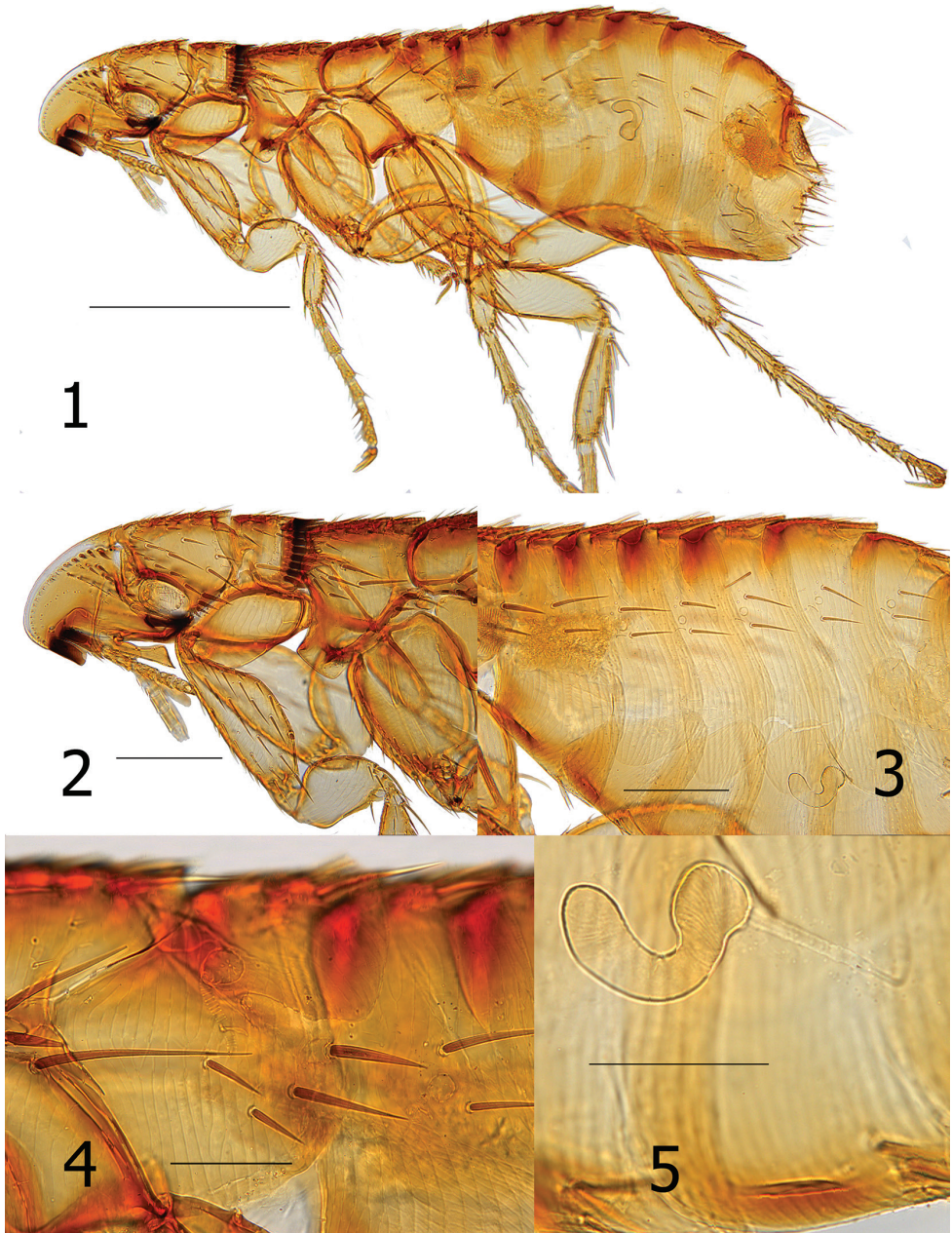
Araeopsylla goodmani Hastriter, sp. n.

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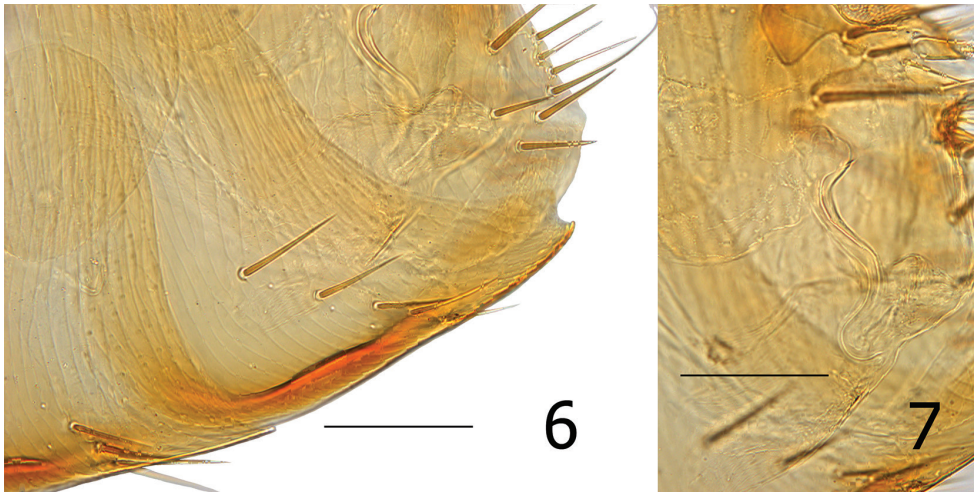
Figs 1–7

Diagnosis. Female distinguished from all other *Araeopsylla* species by the shape of the caudal margin of S-VII. The caudal margin lacks lobes but has a broad concave margin extending to near the ventral margin which terminates in a right angled lobe. The apex of the lobe has a small sinus (Fig. 6).

Description. Head. Frons smoothly rounded; frontal row of 19 setae, each successively stouter from oral angle to top of falx; more dorsal setae spiniform. Area between margin of frons and frontal row of setae clear, white, without surface structure except at extreme upper limit with one placoid pit. Eight minute setae post-frontal row and group of 10 mixed setae (spiniform, short and long) dorsal to row of eight setae. Of these, one seta adjacent to eye, very stout and long, extending beyond posterior margin of head. Gena darkly sclerotized, tapering to upturned apex. Eye vestigial, dark pigmented area merging with gena. Two genal teeth; anterior most tooth broader and blunter than posterior tooth. Pre-oral tuber divided into three portions; most posterior strongly hooked downward to pointed apex. Falx well demarcated. Post-antennal area with row of six stout setulae along dorsal margin of antennal fossa. Four rows of setae dorsal to setulae (4, 2, 3, 8); posterior main row without intercalaries and ventral four spiniform and grouped together (characteristic of the genus). Occiput with three dorsal incassations. Antennal scape with a few minute setae. Margin of pedicel with hyaline extension over first three segments of clavus; along margin of hyaline area are five or six fine long setae extending to seventh or eighth segment of clavus. Maxilla truncate; shaped like a trumpet at apex. Labial palpus of five segments (excluding bulbous palp-bearing segment); penultimate segment longer than other segments (all being quite short). Labial palpus extending about half length of fore coxa. Length of maxillary palpus similar to labial palpus. Galea and lacinia shorter than labial palpus (Figs 1–2).



Figures 1–5. *Araeopsylla goodmani* sp. n., holotype female (SMG-13344-1). **1** Overview of flea **2** Head and pronotum **3** Abdomen (note banding on terga and space between main rows of setae) **4** Metepimeron **5** Spermatheca (note banding on sterna). Scale: 500 μ (**1**); 200 μ (**2–3**); 100 μ (**5–6**).



Figures 6–7. *Araeopsylla goodmani* sp. n., holotype female (SMG-13344-1). **6** Sternum seven **7** Bursa copulatrix. Scale: 100 μ .

Thorax. Pronotum with 18–20 ctenidia; all shorter than length of pronotum. Ctenidia tapered to point, but not sharp at apex. Pronotum with main row of setae minute; more anterior scattered small setae and one long ventral seta. Each thoracic tergum with dorsal incassations. Twelve stout setae grouped over sclerotic dome of pleural rod. Pleural rod merges with sclerotic dome slightly behind middle of dome. Mesosternum truncate; metasternum diminished but oblique along margin. Metanotum with horizontal row of four setae near interface with dorsal incassations; one short spinelet at dorsal apex. Lateral metanotal area with one short and one long seta. Metepisternum with one long seta at dorsal margin. Four or five stout (nearly spiniform) setae below level of spiracle on metepimeron. Spiracle on metepimeron large and round (Fig. 4).

Legs. Upper portion of fore coxa very narrow; marginal row of six long setae on upper caudal margin. About 17–18 long lateral setae excluding marginals. All femora lacking lateral or mesal setae. Fore femorotibial joint with one long seta, Meso- and metafemorotibial joints each with two long setae. Lateral surface of fore tibia with six setae; meso- and metatibiae each with eight setae. Dorsal margin of fore tibia with about 10 dorsal notches; meso- (2, 2, 1, 2, 2, 1, 2, 2) and metatibiae (2, 2, 1, 2, 1, 1, 2, 2) each with eight dorsal notches. From proximal to distal, each succeeding tarsus shorter than preceding segment. Each distitarsomere with five lateral plantar bristles; proximal pair placed between second pair on plantar surface (Fig. 1, 4).

Unmodified abdominal segments. Spiracles round on T-II-VII; each segment with one dorsal incassation and heavily pigmented band extending below incassation. Terga each with one row of three small setae; single dorsal seta separated from two more ventral setae by large gap. One seta of each row located below spiracle. Heavy sclerotization on ventral surface of S-II–VII. Single row of setae on S-II–VI (1, 2, 2, 3,

3). One antensensilial bristle at margin of T-VII; with internal sclerotized incrassation at base of bristle. Two minute setae on each side of antensensilial bristle (Fig. 3).

Modified abdominal segments. Dorsal portion of T-VIII sclerotized cephalad to trumpet shaped spiracle; all setae below spiracle eight. About 14 setae grouped on apical portion of T-VIII. Caudal margin of S-VII concave to near ventral margin terminating in truncate lobe with small apical sinus. Ventral margin of S-VII with heavy sclerotization; with oblique row of four to six lateral setae (Fig. 6). Sternum eight reduced; without setae. Bursa copulatrix undulate; moderately sclerotized entire length (Fig. 7). Hilla of spermatheca more than twice length of bulga; bulga spherical with cribriform area at ventor. Junction of bulga and hilla hardly distinguishable (Fig. 5).

Dimensions. Female holotype: 2.2 mm, female average: 2.1 mm (n = 3), range: 2.0–2.2 mm.

Etymology. The new species epithet *goodmani* is named in honor of its collector, Dr. Steven M. Goodman, Field Museum of Natural History, Chicago, IL for his untiring efforts and excellent contributions to the field of mammalogy, specifically for his work on bats and small mammals in Madagascar from which these specimens were obtained.

Remarks. Although the respective male and female sexes of the two new flea species described in this paper were both collected from the bat genus *Chaerephon* representing two species [*Chaerephon bivittatus* (Heuglin, 1861) from Kenya and *Chaerephon jobimena* Goodman and Cardiff, 2004 from Madagascar], they do not represent the same species of flea. *Chaerephon bivittatus* and *C. jobimena* are allopatric in their distributions. Although there exists some sexual dimorphism among fleas, these females differ drastically from the male described below as *A. smiti*. Characteristics examined included major differences in the nature of the genal teeth, pre-oral tuber, pronotal comb, shape of the gena, variations in chaetotaxy of head and abdomen, and abdominal incrassations.

Araeopsylla lumareti Smit, 1958 (known only from the male sex) could potentially represent the male of this new species for which only females are known; however, this is doubtful based on their differences in hosts, morphology, and geographical remoteness. *Araeopsylla lumareti* is known only from the type locality in Cambodia from “bat guano” opposed to the occurrence of *A. goodmani* in Madagascar from *C. jobimena*, which is endemic to Madagascar. The frontal row of setae of males of *A. lumareti* are comprised of “small setae” and the occiput is “without marked dorsal incrassations” (Smit 1958). The frontal row setation of *A. goodmani* range from small setae to spini-form setae, the occiput is with marked dorsal incrassations, and the first genal tooth is much broader than that of *A. lumareti*. Based on these observations, I am confident that the male of *A. lumareti* does not represent the male counter-part of *A. goodmani*. Additional collecting of fleas from *L. jobimena* in Madagascar and from the temple of Angkor-Vat in Cambodia is needed to discover the males of *A. goodmani* and the females of *A. lumareti*.

Several species of the bat genus *Chaerephon* have yielded several bat flea species of the genus *Lagaropsylla* (Beaucournu 2004, Beaucournu and Fain 1983, Beaucournu

and Fontenille 1993, Beaucournu and Kock 1994a, and Klein and Uilenberg 1966), but this is the first record of *Araeopsylla* collected from the bat genus *Chaerephon* throughout Madagascar or tropical Africa.

Type material examined. Madagascar, Fianarantsoa Province: Isalo, 3.8 km NW Ranohira, along Namaza River (22°32'24"S, 45°22'48"E), *Chaerephon jobimena* ♂, 1 XII 2002, SMG, (SGM-13344-1, holotype ♀, SGM-13344-2, paratype ♀, FMNH) (SGM-13344-3, paratype ♀, BYUC).

***Araeopsylla smiti* Hastriter, sp. n.**

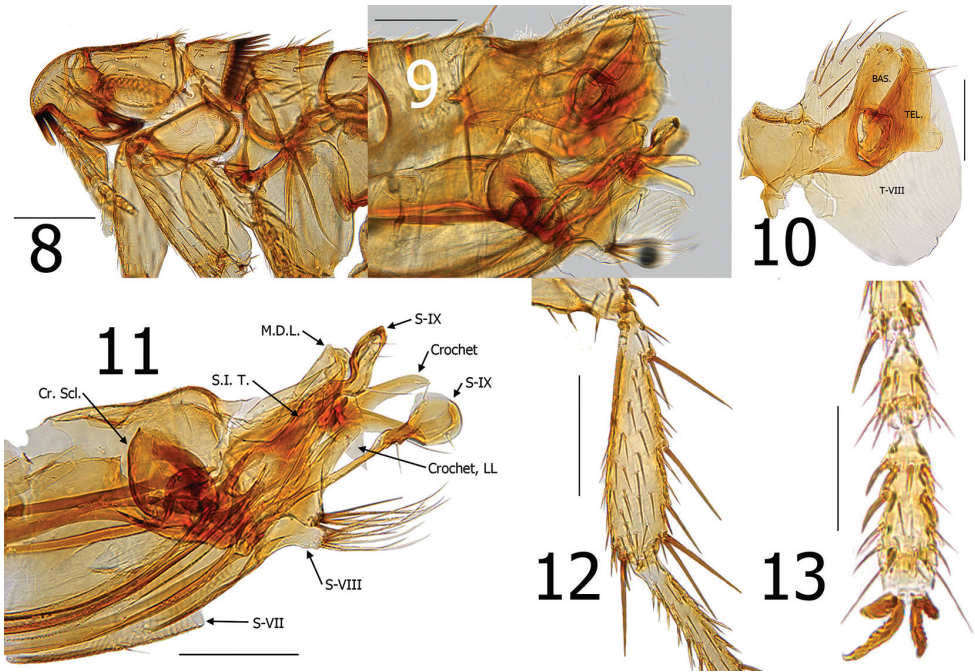
<http://zoobank.org/28BA81B1-6B62-4770-9A14-92E4F176A188>

Figs 8–13

Diagnosis. Distinguished from all other species of *Araeopsylla* by the details of the telomere and distal arm of S-IX. The telomere is acutely pointed at apex and has a broadly rounded lobe along its ventral margin (Fig. 10). The ventral lobe at the base of the distal arm of S-IX that is present in other *Araeopsylla* species is short, pencil-like and without an expanded lobe at its apex. The ventral lobe of the new species is drastically longer and adorned with an ornate apical lobe (Fig. 11). The eighth sternum, unlike all other species, has a lobe (paired) with tufts of long, coarse setae (Fig. 11).

Description. Head. Margin of frons gradually thickened from falx to oral angle. Frontal row of 9–10 minute setae. Area between frons and frontal row of setae with small punctate structures and two placoid pits. Area between frons and frontal row not white or clear, but moderately sclerotized. One placoid pit postad to frontal row of setae near base of genal tooth. Seven to eight minute setae postad to frontal row; group of 6–7 variable sized setae near ventral margin of antennal fossa. Eye fused into darkly sclerotized genal lobe. Genal lobe tapered and broadly rounded at apex; with minute apical tooth. Setae in occipital area rather randomly arranged. Five setulae along dorsal margin of antennal fossa; each as long as other randomly arranged setae in occipital area. Two small setae postad to antennal fossa in position of what is usually 4–5 spiniform setae in other *Araeopsylla* species. Apex of scape enlarged; three long setae along upper margin and three marginal setae at apex. Pedicel with several fine setae along apical margin; none extending beyond first segment of antenna. Clavus asymmetrical; not extending beyond margin of head. Five segmented labial palpus extended to 1/3 length of fore coxa. Proximal segment of five segmented labial palpus rather bulbous in form (Fig. 8).

Thorax. Pronotum with 26 ctenidia; each acutely pointed and only slightly shorter than length of pronotum. Setae on pronotum randomly arranged. Two dorsal and two ventral pseudosetae under mesonotal collar. Metanotum with three rows of setae; two marginal short, stout spinelets at dorsal apex of sclerite. Pleural rod nearly centrally attached to sclerotic dome. Ventral portion of metasternum lobed downward between coxae. Pleural arch absent. Metepisternum with squamulum and one long seta at dorsal margin. Metepimeron with nine setae; spiracle large and round.



Figures 8–13. *Araeopsylla smiti* sp. n., holotype male (BJH-5634). **8** Head and pronotum **9** Terminal segments, before dissection **10** Basimere, telomere, and eighth tergum **11** Aedeagus, eighth sternum, and distal arm of ninth sternum, (Cr. Scl. = Crescent Sclerite, LL = Lower Lobe, M.D.L. = Median Dorsal Lobe, S.I.T. = Sclerotized Inner Tube) **12** Hind tibia **13** Fourth and fifth segments of distitarsomere 2. Scale: 200 μ (**8–12**), 100 μ (**13**).

Legs. Fore coxa with ~40 lateral setae. Fore femur with 2 minute setae on mesal surface; none on lateral surface. Mesal surface of mesotibia with single row of five setae; multiple setae on lateral surface. Mesal surface of metatibia with single row of seven setae; multiple setae on lateral surface. Meso- and metatibiae with five well defined notches; two setae at each. Multiple single setae interspersed along margins between defined notches. Each tarsal segment longer than adjacent more distal segments on meso- and metatarsi. Five lateral plantar bristles on all distitarsomeres; first pair displaces between second pair. Two pre-apical plantar bristles on each distitarsomere (Figs 12–13).

Unmodified abdominal segments. Single spinelet on apex of T-I. Globular sclerotized incrustation at base of each terga (T-I–VII). Pigmented banding extends slightly ventrally from each incrustation. Each terga with single uninterrupted row of setae; one seta below level of each round spiracle. Single long antensensilial bristle. Ventral margin of each sternite is heavily sclerotized. Sternites II–III with one minute seta in row; S-IV–VI with two minute setae in each row.

Modified abdominal segments. Basimere without lobes or sinuses. Telomere with large lobe on lower ventral margin; a few fine setae along ventral margin of telomere above lobe. Tergum VIII encompassing basimere and telomere with all setae restricted to dorsal half of sclerite (Fig. 10). Sternum VIII with large lobe bearing tuft of long coarse setae. Crescent sclerite of aedeagus long, thin, and inverted so tectum is directed cephalad. Sclerotized inner tube straight, somewhat broad. Crochet with prominent truncate upper lobe and sharp ventral lobe. Distal arm of S-IX with sigmoid lobe similar to many bat species, but what is usually a small pencil-like lobe in other species, this lobe is greatly extended and expanded at its apex. The expansion bears two small setae at base of expansion, two setae on apico-dorsal surface, and one seta on ventral margin of expansion. A group of very fine hairs adorns the base of the ventral lobe of the distal arm of S-IX (Figs 9–11).

Etymology. Mr. F.G.A.M. Smit, during his long tenure at the British Museum, London was without doubt, a major contributor to our knowledge of the global flea fauna. It is thus fitting to name this flea *smiti* in his honor as a noun in apposition.

Remarks. This is the first record of the genus *Araeopsylla* occurring in Kenya, although the genus has been recorded throughout tropical Africa.

Type material. Holotype ♂, Kenya, Rift Valley, Maji Moto, 4.8 km W of Lake Harrington (00°16'00"S, 03°6'04"E), *Chaerephon bivittatus* (USNM Host 437-287), 25 VIII 1968, BJH-5634.

Araeopsylla martialis (Rothschild, 1903)

Ceratophyllus martialis Rothschild, 1903

Ischnopsyllus martialis Rothschild, 1906: 187–188

Araeopsylla martialis Jordan & Rothschild, 1921: 146; Hopkins and Rothschild 1956: 323–325; Lumaret 1962: 12; Klein and Uilenberg 1966: 53; Beaucournu and Fain 1983: 458, 460, 465; Beaucournu and Fontenille 1993: 79; Lewis 2006: 44; Marcus 1961: 190.

Remarks. Although *Araeopsylla* is generally collected only in very small numbers across its range, *A. martialis* is exceptional. Sixty-seven individual *M. jugularis* specimens yielded one or more specimens of *A. martialis*. These were collected in three provinces of Madagascar (Fianarantosa, Toamasina, and Toliara). A total of 158 (64♂, 94♀) specimens were harvested from the 67 specimens of *M. jugularis*, yielding a flea intensity of 2.4. One male specimen of *A. martialis* was collected from *Rousettus madagascanensis*. Other species of bats did not harbor *A. martialis*. Its occurrence on a *Rousettus* sp. is likely an accidental association.

Material examined (BYUC). Madagascar, Fianarantsoa Province: Fianarantsoa église FLM (21°27'32"S, 47°04'36"E), 1190 m, *M. jugularis* ♂, 18 XI 2004, FHR, 1♂, 1♀.

***Dampfia grahami grahami* (Waterston, 1915)**

Ischnopsyllus grahami Waterston, 1915: 115; Bedford 1932: 462.

Dampfia grahami grahami Smit 1954: 148–149; Smit 1955: 215–216; Hopkins and Rothschild 1956: 312; Marcus 1961: 184–187; Beaucournu 2004: 205.

Remarks. A total of 15 specimens (8♂, 7♀) was collected from four specimens of the Malagasy endemic *Neoromicia matroka* (Thomas & Schwann, 1905). This flea is not commonly collected and the only known existing records include the holotype ♂ from *Eptesicus capensis* = *Neoromicia capensis* (A. Smith, 1829) from Cape Town, South Africa, 3♀ specimens from Natal, and 2♀ from Orange Free State, South Africa (bat host species undetermined). *Neoromicia capensis* is widely spread across sub-Saharan Africa. Although not found in Madagascar, Goodman et al. (2012) considered *N. capensis* to be the closest ally and sister group to *N. matroka*. The current specimens represent a new country and host record and substantially increase the known number of specimens available for study. The hosts for *Dampfia* are thus far restricted to the family Vespertilionidae.

Material examined (BYUC). Madagascar, Toamasina Province: Andasibe, Ankazina (18°56'38"S, 48°24'46"E), 970 m, *Eptesicus matroka* (Thomas & Schwann, 1905) (RHF-58), 18 IX 2004, FHR, 1♀.

***Lagaropsylla consularis* Smit, 1957**

Lagaropsylla consularis Smit, 1957: 167, 1958: 242; Marcus 1961: 201; Smit 1968: 13; Hubbard 1969: 55; Ribeiro 1974: 143; Beaucournu and Fain 1983: 454–455; Beaucournu and Guiguen 1991: 129; Beaucournu and Fontenille 1993: 80; Beaucournu and Kock 1994b: 199, 1996: 164; Beaucournu 2004: 206; Lewis 2006: 48.

Remarks. *Lagaropsylla consularis* has been reported previously in Madagascar and is among the more common species in the genus, primarily parasitizing *C. pumilus*. *Chaerephon pumilus* has a broad range from Yemen to Senegal, south to South Africa and Madagascar. *Neoromicia somalicus* (Thomas, 1901) from which *L. consularis* was collected in Kenya, is also found in Madagascar. Reported primarily on molossid bats, *L. consularis* has also been documented on hipposiderid and vespertilionid bats (Beaucournu 2004 and Smit 1957).

Material examined (BYUC). Kenya: Rift Valley, Maji Moto, *Neoromicia somalicus* (USNM-436733), 23 XIII 1968, BJH-5592, 2♂, 2♀. **Madagascar, Toamasina Province:** Beforona, Bureau de Poste (18°53'21"S, 48°34'39"E), 560 m, *Chaerephon pumilus* ♂ (RHF-84), 21 IX 2004, FHR, 1♂, 1♀; same data except Anjiro village (18°53'40.31"S, 47°58'24.06"E), *C. pumilus* ♂ (RHF-502), 5 II 2005, 1♂, 1♀.

***Lagaropsylla hoogstraali* Smit, 1957**

Lagaropsylla hoogstraali Smit, 1957: 171–172, 1964: 44.

Lagaropsylla traubi Klein, 1967: 127–131; Smit and Wright 1978: 41; Lewis and Lewis 1990: 156. (Synonym).

Lagaropsylla hoogstraali Ribeiro, 1974: 144; Beaucournu and Fain 1983: 455; Beaucournu and Fontenille 1993: 79–80; Beaucournu 2004: 207; Lewis 2006: 48.

Remarks. *Lagaropsylla hoogstraali* has been documented in Angola, Rwanda, Sudan, Zaire and Madagascar. Although there are few collections of this flea, most have been collected from *Mops midas* (Sundevall, 1843), a broadly distributed bat in continental Africa and Madagascar. Ratrimomanarivo et al. (2007) concluded that the subspecific populations of *M. midas* in continental Africa and Madagascar were invalid. The flea *L. hoogstraali* occurring on *M. midas* in both regions would support the conclusions of Ratrimomanarivo et al. (2007).

Material examined (BYUC). Madagascar, Mahajanga Province: Ambondromamy, Cite de la Gendarmerie (16°26'03"S, 47°09'26"E), 50 m, *Mops midas miarensis* = *M. midas* ♀ (RHF-823), 13 III 2005, FHR, 1♂; same data except *M. midas* ♂ (RHF-824), 1♂; and *M. midas* ♂ (RHF-825), 1♀. **Toliara Province:** Sakaraha, EPP (22°54'26"S, 44°31'48"E). 480 m, *M. midas* ♂ (RHF-262), 20 X 2004, FHR, 1♀.

***Lagaropsylla idae* Smit, 1957**

Lagaropsylla idae Smit, 1957: 165–167; Marcus 1961: 196–199; Smit 1964: 44; 1968: 13–14.

Lagaropsylla setzeri Segerman, 1970: 3–5; Smit and Wright 1978: 43; Lewis and Lewis 1990: 139. (Synonym)

Lagaropsylla idae Ribeiro, 1974: 144; Beaucournu and Fain 1983: 455; Beaucournu and Guiguen 1991: 129; Beaucournu and Kock 1994b: 199, 1996: 164; Beaucournu 2004: 207; Lewis 2006: 48.

Remarks. Beaucournu (2004) suggested that *Mops condylurus* (A. Smith, 1833) is the principle host of *L. idae*. Specimens of *L. idae* in my collection from Ghana and Kenya were also collected from *M. condylurus*. This host is widely distributed across Africa but is not found in Madagascar. *Mops leucostigma*, endemic to Madagascar, is very closely allied to the mainland species *M. condylurus*. A total of 147 specimens (64♂, 83♀) to include those listed in the “Materials examined” section below and those preserved in alcohol in the FMNH was collected from 28 specimens of *M. leucostigma*, yielding a flea intensity of 5.3 fleas per host. An average of 5+ fleas per host is a very high flea intensity for any bat flea, as bat fleas in general, are usually found in extremely low numbers. *Mops leucostigma* is the preferred host of *L. idae* in Madagascar and it was not collected from any other bat species in Madagascar.

Material examined (BYUC). Ghana, Eastern Region: Teshi, Accra Plains (05°34"N, 00°00'6"W), *M. condylurus* (USNM-412535), 26 XI 1967, CBR-1931, 2♂; Volta, Denu (06°06'N, 00°10'9"E), *M. condylurus* (USNM-412667), 31 VIII 1967, AK-138, 1♂, 1♀. **Kenya, Eastern Region:** Mtoto Andei (02°41'S, 03°8'08"E), *Chaerephon pumilus* (Cretzschmar, 1830) (USNM-437019), 9 VII 1968, BJH-4846, 1♂; same data except *M. condylurus* (USNM-437225), BJH-4844, 1♀; Kiboko (02°12'S, 03°7'42"E), *M. condylurus* (USNM-437181), 4 VII 1968, BJH-4684, 1♂. **Kenya, Rift Valley:** Maji Moto, *Nycticeinops schlieffeni* (Peters, 1859) (USNM-436774), 24 VIII 1968, BJH-5610, 1♂, 2♀. **Madagascar, Toamasina Province:** Andasibe, Bureau du Poste (18°55'18"S, 48°25'18"E), 950 m, *Mops leucostigma* ♂ G.M. Allen, 1918 (RHF-13), 14 IX 2004, FHR, 1♀; Anjiro, Andranoalina (18°52'57"S, 47°58'15"E), 850 m, *M. leucostigma* ♂ (RHF-532), 7 II 2005, FHR, 1♂. **Toliara Province:** Sakaraha, Bureau Eau et Forets (22°54'34"S, 44°31'20"E), 470 m, *M. leucostigma* ♂ (RHF-202), 15 X 2004, FHR, 1♀, same data except *M. leucostigma* ♀ (RHF-206), 1♂; Andranovory, Hôpital (23°08'37"S, 44°08'41"E), 500 m, *M. leucostigma* ♂ (RHF-179), 13 X 2004, FHR, 1♂, same data except *M. leucostigma* ♂ (RHF-181), 1♀.

Key to the species of *Araeopsylla*

- 1 Males (*A. goodmani* sp. n., male unknown)..... 2
 1' Females (*A. lumareti* and *A. smiti* sp. n., females unknown)..... 11
 2(1) Acetabular bristles arranged on prominent long lobe of basimere (lobe longer than wide) 3
 2' Acetabular bristles along margin of basimere, not borne on lobe..... 6
 3(2) Ventral margin of telomere with a sinus and subtending lobe 4
 3' Ventral margin without a sinus or lobe 5
 4(3) Caudal margin of T-VIII truncate. Lobe on caudal margin of telomere rounded, not hooked downward (Cambodia) *phnomensis*
 4' Caudal margin of T-VIII narrowing to rounded lobe. Lobe on caudal margin of telomere hooked downward (Cambodia) *immanis*
 5(3') Ventral margin of telomere convex; dorsal margin concave (Cambodia) .. *lumareti*
 5' Ventral and dorsal margins nearly straight (Thailand) *elbeli*
 6(2') Apex of manubrium spatulate (Rwanda) *faini*
 6' Apex of manubrium not spatulate..... 7
 7(6') Basal lobe of distal arm of S-IX long and modified. Telomere acutely pointed at apex. Truncate lobe at apex of S-VIII with tuft of long, coarse setae (Kenya) *smiti* sp. n.
 7' Basal lobe of distal arm of S-IX short, without leaf-like apical lobe. Telomere rounded and blunt at apex. Sternum VIII without lobe bearing tuft of long setae..... 8
 8(7') Apex of manubrium sharp and turned downward. Sinus present above acetabular bristles on basimere (Kenya, Angola, Lesotho, South Africa)..... *scitula*

8'	Manubrium and basimere otherwise	9
9(8')	Crochet without hook-like lobes (Italy)	<i>gestroi</i>
9'	Crochet with hook-like lobes	10
10(9')	Basimere quadrate on dorso-apical margin. Telomere broadens towards apex and extends beyond apex of basimere (Réunion Island, Madagascar).....	<i>martialis</i>
10'	Basimere rounded on dorso-apical margin. Telomere somewhat parallel sided, rounded at apex, and sub equal in length to basimere (Egypt)	<i>wassifi</i>
11(1')	Hilla of spermatheca hardly longer than bulga (Thailand).....	<i>elbeli</i>
11'	Hilla distinctly longer than length of bulga.....	12
12(11')	Caudal margin of S-VII concave to margin of terminal truncate ventral lobe; ventral lobe with small sinus at apex (Madagascar).....	<i>goodmani</i> sp. n.
12'	Caudal margin of S-VII straight (not concave), or with lobes	13
13(12')	Bursa copulatrix rather straight; without sigmoid-like curves	14
13'	Bursa copulatrix not straight, but with various sigmoid-like curves.....	15
14(12')	Caudal margin of T-VIII slightly convex with vertical row of three short spiniform setae near apical margin of convexity. Spiracle VIII broadened at apex (Egypt).....	<i>scitula</i>
14'	Caudal margin of T-VIII more straight; without row of three spiniform setae. Spiracle VIII rounded at apex (Egypt).....	<i>wassifi</i>
15(13')	One closely arranged vertical row of six spiniform setae at caudal margin of T-VIII (Réunion Island, Madagascar)	<i>martialis</i>
15'	Chaetotaxy of caudal margin of T-VIII otherwise	16
16(16')	Caudal margin of S-VII without lobe (Cambodia).....	<i>phnomensis</i>
16'	Caudal margin of S-VII with lobe.....	17
17(16')	Apex of ventral margin of S-VII extends beyond dorsal lobe (Cambodia)	<i>immanis</i>
17'	Dorsal lobe projects beyond apex of ventral margin	18
18(17')	Dorsal lobe on caudal margin of S-VII broad, subtended by a broad shallow sinus (Italy).....	<i>gestroi</i>
18'	Broad angular lobe on margin of S-VII without subtending sinus (Rwanda) ..	<i>fain</i>

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A contribution to the knowledge of the mountain entomofauna of Mexico with a description of two new species of *Onthophagus* Latreille, 1802 (Coleoptera, Scarabaeidae, Scarabaeinae)

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Abstract

Recent intensive samplings carried out across the mountainous regions of El Pinal (Puebla, Mexico) have provided new insights into the main environmental factors that affect the geographic distribution of the scarabaeinae beetles of the Trans-Mexican Volcanic Belt above 2500 m a.s.l. This study is part of an ongoing project investigating the diversity and biogeography of copro-necrophagous beetles (Scarabaeinae, Aphodiinae, Geotrupinae and Silphidae) in the easternmost areas of the Trans-Mexican Volcanic Belt.

Previous experience allows us to propose a series of predictions that we expect will provide possible explanations for current distribution patterns observed in Scarabaeinae and other groups of insects found in the Trans-Mexican Volcanic Belt. This mountain range has a primarily biogeographic importance, limiting the Mexican High Plateau in the South and connecting the western and eastern Sierra Madre mountain chains, which are considered the most important routes for dispersal of mountain fauna of northern origin. The taxonomic and biogeographic study of the species collected so far in El Pinal (including *Onthophagus clavijeroi* **sp. n.** and *Onthophagus martinpierai* **sp. n.** described here), along with their possible relationships with other known species, allows us to answer the preliminary assumptions proposed.

Resumen

Con base en capturas intensivas realizadas en la montaña de El Pinal (estado de Puebla, México) se plantea un análisis de los factores que intervienen en la distribución geográfica de la fauna de montaña (en este caso Scarabaeinae) por encima de los 2500 m de altitud, en el Sistema Volcánico Transversal (SVT), principal cordillera dispuesta en sentido latitudinal de México y de toda América. Este artículo es parte de una serie de trabajos coordinados para estudiar los escarabajos coprófagos y necrófagos de la parte oriental del SVT.

La experiencia generada nos permite plantear una serie de premisas (Introducción) que se espera cumpla la distribución de la fauna de Scarabaeinae y de otros grupos en el SVT, cordillera de primera importancia biogeográfica, pues limita por el sur el Altiplano Mexicano (una península de Norte América) y une las dos principales cordilleras que se desarrollan N-S: las Sierras Madres Occidental y Oriental, las más importantes vías de penetración de la fauna de montaña de origen septentrional. Un análisis de las afinidades taxonómicas y biogeográficas de las colectas de Scarabaeinae en El Pinal (incluyendo dos especies nuevas de *Onthophagus* que se describen) nos permite dar respuesta en la Discusión a las premisas planteadas en la Introducción.

Keywords

Scarabaeinae, *Onthophagus*, mountain fauna, Mexican Transition Zone, Trans-Mexican Volcanic Belt

Palabras clave

Scarabaeinae, *Onthophagus*, fauna de montaña, Zona de Transición Mexicana, Sistema Volcánico Transversal

Introduction

Mexico is a country of vast mountain ranges. In tropical areas, these environmental conditions imply a rich and peculiar biota; the particular geographic position of Mexico and the extensive Mexican Transition Zone, which occurs between the Nearctic and Neotropical regions, emphasizes the biological exclusivity of this region.

The Mexican Transition Zone (hereafter referred to as MTZ) has been proposed by Halffter for insects and other groups of animals (e.g., Halffter 1987; Halffter 2003; Halffter et al. 2008), while Rzedowski introduced the concept of Megamexico, a phyto-geographic unit defined on the basis of distribution patterns observed in Mexican plants (Rzedowski 1991). The concept of the transition zone has also been utilized in general terms by Zunino and Zullini (2003: 66–68 and literature quoted therein). A biogeographical transition zone is a geographical area of biotic juxtaposition with a gradient of replacement and partial segregation between components, which are promoted by historical and ecological changes. During his travel across the Malay Peninsula between 1854 and 1862, A. R. Wallace had already realized the difficulty of delimiting clear biogeographical borders between the Oriental and Australian regions, a wide area with transitional characteristics, which is today known as Wallacea (see Ferro and Morrone 2014 for a very interesting and updated revision of biogeographic transition zones).

The transition occurs when biota of two different regions, the distribution areas of which have not been historically constrained by significant biogeographical barriers, meet and overlap within the same geographic area and time. If the transition character

remains temporally, this zone may harbour species of different geographical and evolutionary origins.

The mountain ranges of the MTZ play a fundamental role as a main route for the southward dispersal of northern fauna. Among the Mexican mountain ranges, the Trans-Mexican Volcanic Belt (hereafter referred to as TMVB) is the only one in the Americas with latitudinal development, intervening as central bridge between the western and eastern Sierra Madre mountain ranges (see Map 1).

Recently, Luna et al. (2007) provided a description of the geology, physical environment, as well as flora and fauna of the TMVB, presenting several biogeographic studies.

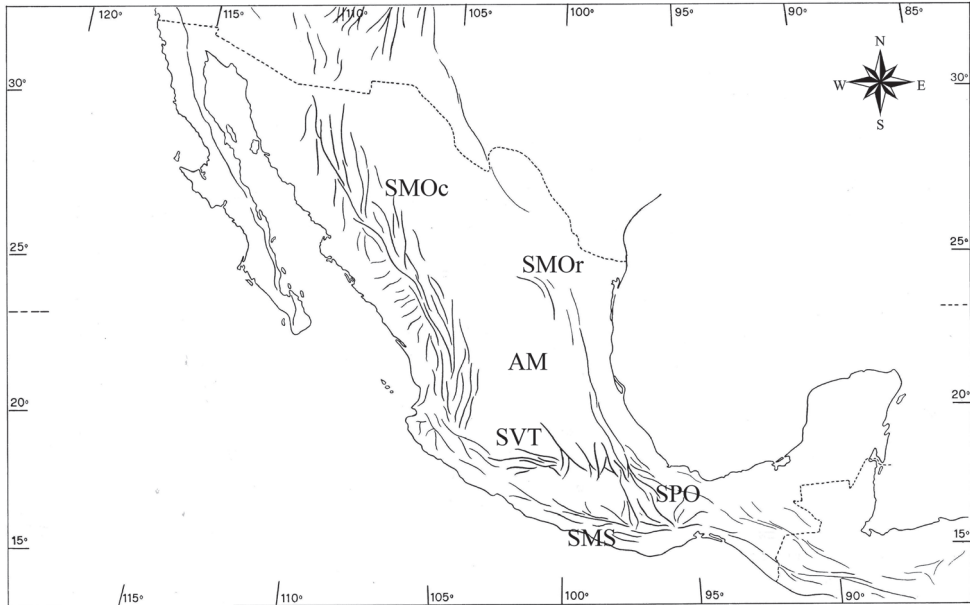
The TMVB features a series of mountain ranges and volcanoes that cross Mexico transversally between the parallels 18°30' and 21°30' W. The orogenesis of this area is widely accepted to result from the subduction of both the Rivera Microplate and northern border of the Cocos Plate under the southern boundaries of the North American Plate. Since the Early-Mid Miocene, the TMVB became an independent geological province because of the East-West rotation of the Transvolcanic Belt, as well as the change of type and composition of the main volcanic activities: silicious and explosive in the Sierra Madre Oriental, intermediate and eruptive in the TMVB (Ferrari et al. 2012).

Four main volcanic events that occurred over the last 19 million years contributed primarily to the formation of the TMVB, with the greatest volcanic activity recorded in the Quaternary. This volcanic eruption also involved the areas and locations investigated in this study, such as the mountains Pico de Orizaba, Cofre de Perote and La Malinche (see Torres-Miranda and Luna 2007 and other chapters in Luna et al. 2007).

The TMVB stretches for approximately 1000 km in length and, despite its current unity, the geological history of the areas lying east and west of the meridian 101° does not show any degree of continuity until the end of the Pliocene and Quaternary. Along with the geomorphology of the TMVB, the main stratovolcanoes of the central and eastern regions built up in the Upper Pleistocene (see Ferrari et al. 2012) are of great importance for explaining several biogeographic patterns, as well as vicariant events that occurred along the TMVB and are commonly represented within mountain lineages of northern origin. Initially, the lineages found only either in the western or eastern halves of the TMVB can be considered to be the oldest, with different biogeographic histories, as these are related to the Sierra Madre Occidental, the Sierra Madre del Sur or the Sierra Madre Oriental, respectively. On the other hand, lineages or species that are widely distributed across the entire TMVB can be considered the most recent ones, and show a succession of very closely related taxa.

Given its East-West orientation (Map 1) and dynamic geomorphological history, the TMVB is not only an important dispersal route for northern fauna with mountain adaptations, but is also an area characterized by a large number of vicariant events reported for many organisms as well as a high beta diversity (see Luna et al. 2007).

All of the results obtained to date are included in seven articles (including the present study), (Sanchez-Huerta 2015, Arriaga et al. 2016, Moctezuma et al., Skelley and Sanchez-Huerta, Sanchez-Huerta et al. A, Sanchez Huerta et al. B), two Master's dissertation (Moctezuma 2014, Sanchez-Huerta 2016) and a Doctoral thesis (Arriaga 2015).



Map I. Orographic systems mentioned in the text: SMOc: Sierra Madre Occidental; SMOr: Sierra Madre Oriental; AM: Mexican Plateau; SVT: Trans-Mexican Volcanic Belt; SMS: Sierra Madre del Sur; SPO: Puebla-Oaxaca Mountain System.

The initial predictions to be tested throughout these studies are as follows:

The entomofauna (especially Scarabaeinae) of the TMVB above 2500 m a.s.l. corresponds to the Paleo-American Distribution Pattern (see Halffter 1987, Halffter 2003, Halffter et al. 2008), that are northern lineages belonging to worldwide distributed genera with old penetration in the American continent. Within this distributional pattern, the Mountain Paleo-American sub-pattern, which includes lineages limited to the mountains of the MTZ, should take over.

The dispersal of lineages of the Mountain Paleo-American distribution pattern essentially occurs horizontally (Lobo and Halffter 2000), following a given altitudinal range and presenting dispersal events only under advantageous climatic conditions, whereas isolation and vicariant events appear under adverse climatic conditions, which are also responsible for the reduction of the area of distribution. Time represents a basic difference between horizontal and vertical colonization; vertical colonization requires the adaptation of lineages to new environmental conditions while horizontal colonization only requires dispersal.

The bioclimatic zones in mountainous areas experienced major altitudinal shifts during the Quaternary and Recent periods. The complex orography of the MTZ, especially that of the TMVB, along with the catathermal climatic periods, had strong effects on the high-altitude communities, which underwent a severe displacement toward the lowlands that were interconnected to a greater extent. Under the new environmental conditions, these biological elements found a favourable situation in which to spread horizontally. However, during anathermal periods, bioclimatic zones move

upward to higher elevations, with a consequent fragmentation of the distribution area of the species involved. These events are often followed by speciation processes associated with dynamic vicariance (see Zunino 2003: 161; Morrone 2009: 16).

Occasionally there are cases of vertical colonization, represented by upward dispersal from the lowlands. This dispersal event is expected to occur in species with the Paleo-American High Plateau Distribution sub-pattern (Halffter 2003). In some exceptional cases, some species of Neotropical affinity distributed on the Mexican High Plateau might penetrate the mountains, particularly at lower elevations.

Vertical movements are not expected on the southern slopes of the TMVB such as the Balsas and Tehuacán-Cuicatlán depressions, the fauna of which, adapted to warm and dry conditions, shows Neotropical affinity. The rare antiquity of the mountain El Pinal, but particularly the strong contrast in ecological conditions, has not favored the upward displacement of tropical species.

The dispersal-distribution pattern with predominantly horizontal distribution, observed in the TMVB and in Mexican mountain ranges in general, is completely different from the pattern found in the Andes (see Escobar et al. 2006, 2007) or on the Mexican mountains that are isolated within a tropical environment, such as Los Tuxtlas (Alvarado-Roberto 2014). In these cases, vertical colonization appears to be the more common distribution pattern, with the Neotropical fauna moving toward higher altitudes from the tropical lowlands.

In these tropical mountains with vertical colonization, the highest species richness occurs at intermediate elevations (at approximately 1500 to 1700 m a.s.l.), with rarefaction occurring at higher altitudes (Escobar et al. 2007). In the TMVB, which is colonized by fauna of northern origin, there is a representative number of species exclusive to high elevations that are not found at lower altitudes.

The species richness of Scarabaeinae on tropical mountains with vertical colonization is higher in wooded areas, as occurs in the surrounding lowlands (Escobar 2004, Escobar et al. 2007). As in Europe (see for example Errouissi et al. 2004, Jay-Robert et al. 2007), a higher number of Scarabaeinae species occur in opened or semi-opened areas in the TMVB, with a very low presence of species characteristic of forests and woodlands.

In this article, we describe two new *Onthophagus* species collected to date only in the westernmost mountains of the eastern sector of the TMVB (El Pinal). Phylogenetic and biogeographic relationships of both species are discussed, and our preliminary hypotheses on Scarabaeinae and other copro-necrophagous Scarabaeoidea of the TMVB are tested against the distribution patterns observed in these new *Onthophagus* and other species collected in the same sites.

Material and methods

Sampling was conducted on the westernmost mountains of the eastern sector of the TMVB (El Pinal, Puebla, Mexico). To date, the entomofauna of this area has been little studied compared to the tropical sector of the Mexican Transition Zone.

Copro-necrophagous beetles were collected using common pitfall traps baited with human and cow excrements, and squid. Collected specimens were processed at the Institute of Ecology (INECOL) in Xalapa.

The morphological study was carried out on multiple specimens belonging to the new species described here. In order to study the male and female genital organs, individuals were softened in hot water for approximately 20 minutes and their genitalia extracted. In males, the aedeagus was dissected for examination of the endophallic sclerotized structures of the internal sac. Genital structures of both sexes were cleared in a 10% KOH solution. Finally, the aedeagus, endophallic sclerotized pieces and vagina were either mounted on a paper-board with DMHF resin or preserved in microvials with glycerol.

Specimens collected during fieldwork were deposited in the following private and public collections (information regarding the repositories of holotypes and paratypes are provided with the species descriptions):

CNC	Canadian National Collection, Ottawa, Canada;
GH	Gonzalo Halffter collection, Xalapa, Mexico;
INECOL	Instituto de Ecología A. C., Xalapa, Mexico;
LD	Leonardo Delgado collection, Xalapa, Mexico;
MM	Miguel A. Morón, collection, Xalapa, Mexico;
MR	Michele Rossini collection, Pesaro, Italy;
MZ	Mario Zunino collection, Asti, Italy;
VM	Victor Moctezuma collection, Xalapa, Mexico.

Results

Onthophagus clavijeroi Moctezuma, Rossini & Zunino, sp. n.

<http://zoobank.org/74F35DE3-6094-48F3-948E-F0BB7992EA1D>

Material examined. Holotype: male pinned with genitalia in microvial. 1. Label Holotypus (in Spanish) “Mexico, El Pinal, Pue., at 0.3 km from Rincón, 2/VII/13, necrotrap 7n2, x- 97°53'59.8" W, y- 19°8'55.3", shrubby veg., 2704 m a.s.l., Moctezuma J.V.P. Col.” (1 ♂ GH). Paratypes: 1 ♂, same label as the holotype; 2 ♂♂, labeled “Mexico, El Pinal, Pue., at 0.3 km from Rincón, 2/VII/13, necrotrap 7n6, x- 97°54'1.1" W, y- 19°8'56.8", oak forest, 2710 m a.s.l., Moctezuma J.V.P. Col.”; 2 ♂♂, 1 ♀ labeled “Mexico, El Pinal, Pue., at 0.3 km from Rincón, 2/VII/13, necrotrap 7n7, x- 97°53'59.8" W, y- 19°8'54.3", oak forest, 2704 m a.s.l., Moctezuma J.V.P. Col.”; 1 ♀ labeled “Mexico, El Pinal, Pue., at 2.5 km from Rincón, 26/VI/13, necrotrap 5n1, x- 97°55'2.1" W, y- 19°7'46.6", oak forest, 2543 m a.s.l, Moctezuma J.V.P. Col.”.

Description. Holotype. Major male (Fig. 1). Length 9.4 mm, maximum width of pronotum 5.3 mm. Body dark-brown and dull with cupreous casts, antennal club dark grey, body covered with yellow and light setae. Clypeus transversally developed and pentagonal shaped, distinctly concave, with anterior margin widely curved at middle.



Figure 1. *O. clavijeroi* sp. n. major male.

Head with lateral margins slightly sinuate in proximity of clypeo-genal suture, genae with margins subparallel, genal suture distinct. Clypeal carina absent to very feebly indicated, frontal carina subtrapezoidal with anterior convexity and elevated at middle with a triangular tubercle, frons coarsely punctured, with short and light-yellow setae,

forward curved. Clypeus with strong and coarse punctures, punctuation almost confluent, some punctures with a long seta, few and shorter setae near the apex of clypeus. Posterior margin of pronotum with evanescent border, lateral margins straight to barely concave between anterior and median angles. Pronotal protuberance not regularly convex, pronotum distinctly sloped between median tubercles and anterior margin, pronotal protuberance obtusely trapezoidal, anterior tubercles absent, posterior tubercles strong and slightly forward than the middle of pronotum. Pronotal disc with irregular and coarse punctuation, punctures slightly elongated and crowded, pronotal surface between punctures clearly microsculptured, punctures with a long and light seta, pilosity shorter and scattered in proximity of apex of pronotal protuberance. Elytral striae impressed, bright and with medium-sized punctures well-spaced, interstriae flattened with finer punctuation than pronotum, every puncture bears a light-yellow seta, microsculpture evident. Pygidium dull and sericeous at the base, apically bright, pygidial surface with inconspicuous punctuation, punctures with a short and light seta, median and longitudinal part of pygidium bare and lacking significant punctures, microsculpture of pygidium reticular. Apex of pygidium with bigger, transversal and confluent punctures, microsculpture less evident. Foretibiae slender, distinctly curved and slightly wider at apex, apical spur with apex distinctly curved downward.

Parameres and endophallic sclerites: Figs 4–6.

Female (Fig. 3): Clypeus more elongated forward than in male, clypeal carina strong and evenly curved, frontal carina trapezoidal, lateral margins of clypeus straight, apex widely curved, clypeo-genal suture not indicated on lateral margin of the head. Lateral margins of pronotum curved, anterior pronotal protuberance ill-defined, disc of pronotum with two circular and flattened areas. Protibiae distinctly wider and less curved than in male. Female genitalia: Fig. 7.

Variation. Minor male (Fig. 2): Smaller than male, clypeus more distinctly trapezoidal, clypeal carina very weakly indicated and slightly swollen at middle, frontal carina reduced and lacking median tubercle, anterior pronotal protuberance ill-defined to absent, disc with two flattened and circular areas.

Derivatio nominis. We dedicate this species to Francisco Xavier Clavijero (Port of Veracruz, then New Spain, 9 September 1731 – Bologna, Italy, 2 April 1787), American naturalist who, together with his Chilean contemporary J. I. Molina, contested the ideas of Buffon and Pauw in their famous argument about the New World.

Synthesis of localities of the type material. MEXICO: State of Puebla, El Pinal mountain, Rincón Citlaltépetl at 0.3 km from Rincón Citlaltépetl, 2704–2710 m a.s.l.; Cerro El Pinal, Santa Isabel Tepezala at 2.5 km from Rincón Citlaltépetl, 2543 m a.s.l.

Type locality. Cerro El Pinal, Rincón Citlaltépetl, state of Puebla, Mexico.

Type deposit. Holotype and one paratype in the GH Collection. Six paratypes in the VM, MR, MZ and MM collections.

Affinities. *Onthophagus clavijeroi* belongs undoubtedly to the *chevrolati* group (Zunino and Halffter 1988), which is well represented in the MTZ mountains, particularly in the TMVB.



Figure 2. *O. clavijeroi* sp. n. minor male.



Figure 3. Female *O. clavijeroi* sp. n.



Figure 4. Aedeagus of *O. clavijeroi* sp. n.

Examination of the external morphology of *O. clavijeroi*, with special emphasis on the male and female genital organs, led us to consider that this new *Onthophagus* of El Pinal is closely related to the species included in the *fuscus* complex (Zunino and Halffter 1988), such as *O. fuscus* Boucomont and its subspecies (the nominotypic one, *O. f. mycetorum* Zunino & Halffter, *O. f. parafuscus* Zunino & Halffter and *O. f. canescens* Zunino & Halffter), *O. pseudofuscus* Zunino & Halffter and *O. semiopacus* Harold. The morphological pattern shared among these species appears to support their monophyletic origin, but a profound revision of the *fuscus* complex is required in order to properly address the identity of the polytypic *O. fuscus* and the internal systematics of the complex.

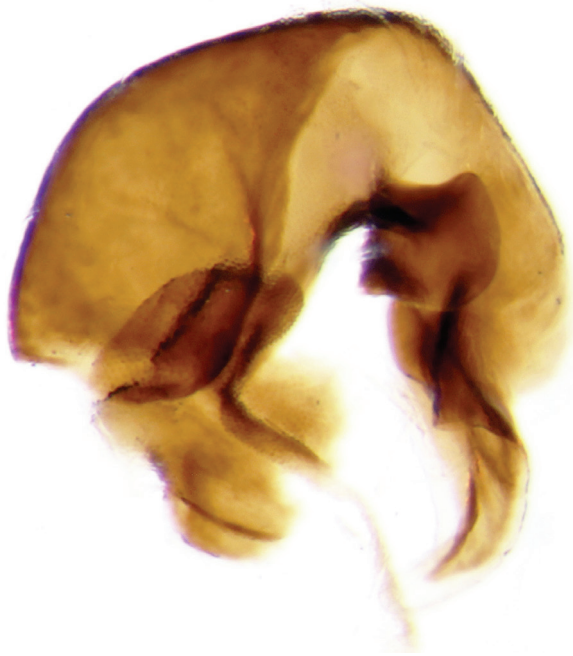


Figure 5. Copulatory lamella of *O. clavijeroi* sp. n.

The shape and orientation of the apices of the parameres of *O. clavijeroi* and *O. f. fuscus* are very similar (Fig. 4), but the general shape of the lamella copulatrix (Fig. 6), especially the shape and development of both the internal carina and right branch of the copulatory lamella, allow us to easily distinguish between the two species.

In the female, the ventral sclerotization of the vagina corresponds to the morphological pattern already found within the *fuscus* complex, although the cephalic branches appear noticeably less developed in *O. clavijeroi* (Fig. 7).

Distribution and ecology (Maps 2–3). The species and subspecies of the *fuscus* complex are distributed across the mountain ranges that delimit the Mexican High Plateau, including the Sierra Madre Occidental, the TMVB and the Sierra Madre Oriental, with one species in the Puebla-Oaxaca Mountain System (Map 2). According to Zunino and Halffter (1988), the *fuscus* complex occurs to the north of the Tropic of Cancer, on the continental side of the Sierra Madre Occidental at between 2400 and 3000 m a.s.l. and following the distribution pattern of *O. f. fuscus*. At the same latitude, but on the Pacific side of the same mountain range, *O. pseudofuscus* is found at 2000 m a.s.l. or higher.

As noted in other groups of organisms distributed across the Sierra Madre Occidental and westernmost areas of the TMVB, the distribution of the *fuscus* complex becomes discontinuous in the proximity of the southern part of the Durango State. This interruption may be due to several factors that are not exclusive of this region, such



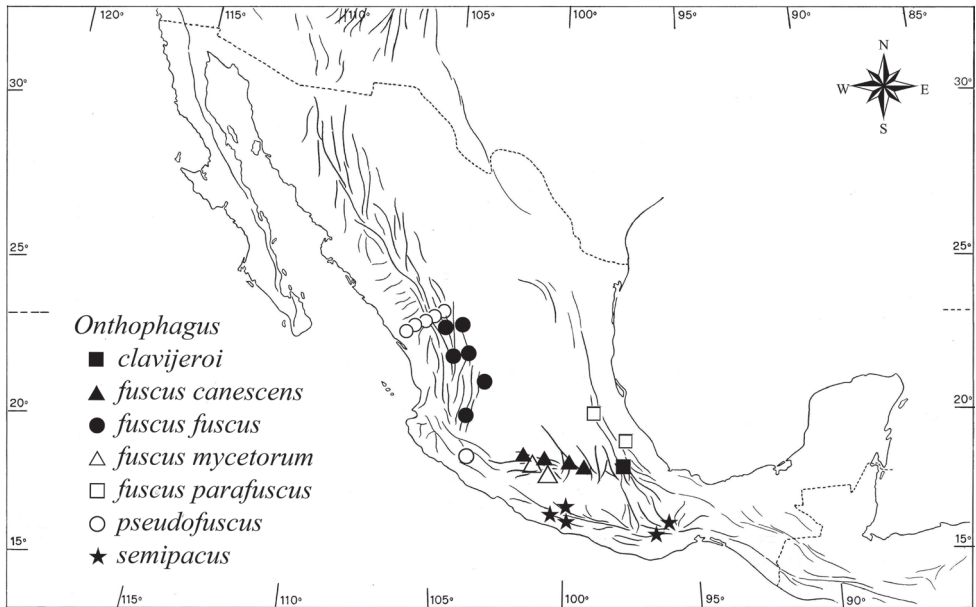
Figure 6. Accessory lamellae of *O. clavijeroi* sp. n.

as an interruption of geographic continuity caused by recent orographic movements, and probably the lack of beetle collection in one of the least studied mountainous areas of Mexico (to date, only one single and isolated capture of *O. pseudofuscus* has been reported for that area; see Map 2).

In the TMVB, the *fuscus* complex is represented by several subspecies of *O. fuscus*, such as *O. f. canescens* and *O. f. mycetorum* and *O. clavijeroi* (easternmost side of the TMVB). *Onthophagus f. parafuscus* is found in the southern part of the Sierra Madre Oriental. In addition to this U-shaped distribution across the mountain ranges that flank the Mexican High Plateau, *O. semiopacus* is found southward, in the southeastern part of the Puebla-Oaxaca Mountain System (Map 2).

It should be noted that recent cladistic analyses conducted by Gutiérrez-Velázquez (2013, unpublished data) support the monophyly of the *fuscus* complex.

The distribution of this complex, as well as its possible monophyletic origin, the taxonomic relationships among taxa and the geomorphological history of the moun-



Map 2. Distribution of *Onthophagus clavijeroi* and related species. Expanded from Zunino & Halffter 1988, including data from this study.

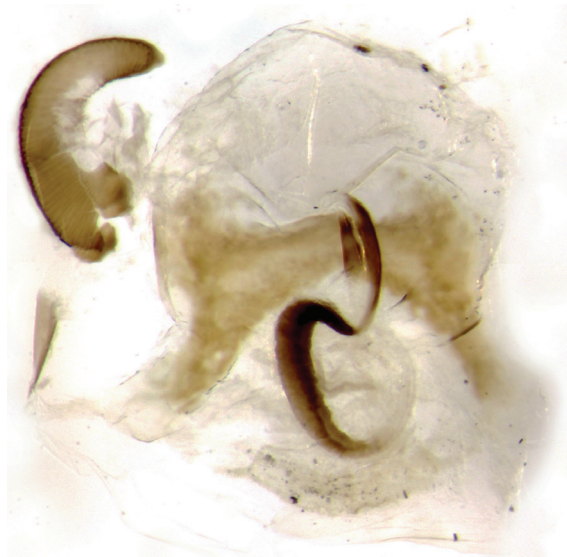
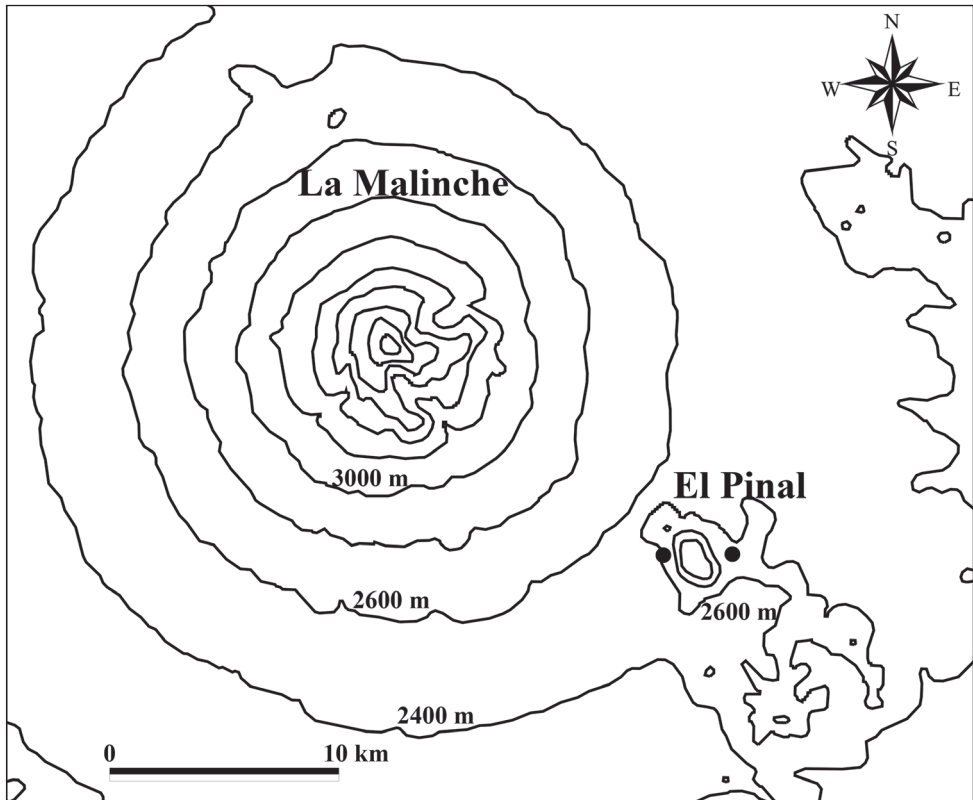


Figure 7. Genital apparatus of female *O. clavijeroi* sp. n.

tain ranges may support the hypothesis of a modern (Pleistocene to the present) distribution. To our knowledge, *O. clavijeroi* would represent a recent element within the *fuscus* complex, even considering that so far it is only known on mountains of relatively recent geological configuration.



Map 3. Collection sites for *Onthophagus clavijeroi* sp. n. (●). The two mountains mentioned in the text can be seen: La Malinche (4420 m a.s.l.) and El Pinal (3280 m a.s.l.).

El Pinal (3280 m a.s.l.) is associated with the mountain La Malinche (4461 m a.s.l., see Map 3) and its geological origin corresponds to the First Period of volcanic activity of La Malinche, which is estimated to have formed approximately 34 000 years ago, during the Late Pleistocene (Castro-Goeva and Siebe 2007). Further information on the Scarabaeinae of El Pinal is provided below in the Discussion.

Onthophagus clavijeroi was collected between 2543 and 2710 m a.s.l. in areas with primary and secondary oak forest and open habitats with shrubby vegetation and pastures. It was collected exclusively in traps baited with decaying squid. No specimens were collected in traps baited with human excrement or horse dung, nor by direct capture in other different excrement types. This implies that *O. clavijeroi* is likely to be necrophagous, a common feeding habit reported in various genera of Neotropical Scarabaeinae beetles, but one that is quite rare in American *Onthophagus*. It is possible that *O. clavijeroi* is also found in the nearby mountain of La Malinche, but systematic sampling using necrotraps remains to be carried out in that area.

***Onthophagus martinpierai* Moctezuma, Rossini & Zunino, sp. n.**

<http://zoobank.org/3E8D6AE4-9280-4266-826D-72CC4C8481AB>

Material examined. Holotypus ♂ labeled (In Spanish) “Mexico, El Pinal, Pue., at 2.5 km from Rincón, 23/VI/13, coprotrap 5h5, x- 97°55'7.1" W, y- 19°7'48.4" N, oak-pine forest, 2530 m a.s.l., Moctezuma J.V.P. Col.”. Paratypes: 4 ♀♀, with the same label as the Holotypus; 3 ♂♂, 3 ♀♀, labeled “México, El Pinal, Pue., a 2.5 km from Rincón, 23/VI/13, coprotrap 5c5, x- 97°55'3.5" W, y- 19°7'51.8" N, oak-pine forest, 2550 m a.s.l., Moctezuma J.V.P. Col.”; 4 ♂♂, 7 ♀♀, labeled “México, El Pinal, Pue., at 2.5 km from Rincón, 23/VI/13, coprotrap 5h1, x- 97°55'13" W, y- 19°7'52.9" N, oak-pine forest, 2530 m a.s.l., Moctezuma J.V.P. Col.”; 1 ♂, 1 ♀, labeled “México, El Pinal, Pue., at 2.5 km from Rincón, 23/VI/13, coprotrap 5h2, x- 97°55'11.4" W, y- 19°7'52" N, oak-pine forest, 2527 m a.s.l., Moctezuma J.V.P. Col.”; 1 ♀, labeled “México, El Pinal, Pue., at 0.3 km from Rincón, 24/VI/13, coprotrap 7c3, x- 97°54'5.8" W, y- 19°8'58.3" N, oak-pine forest, 2742 m a.s.l., Moctezuma J.V.P. Col.”; 3 ♀♀, labeled “México, El Pinal, Pue., at 0.3 km from Rincón, 24/VI/13, coprotrap 7h1, x- 97°53'53.9" W, y- 19°8'59" N, oak-pine forest, 2681 m a.s.l., Moctezuma J.V.P. Col.”; 2 ♀♀, labeled “México, El Pinal, Pue., at 0.3 km de Rincón, 5/VII/13, coprotrap 7h1, x- 97°53'53.9" W, y- 19°8'59" N, oak-pine forest, 2681 m a.s.l., Moctezuma J.V.P. Col.”; 2 ♀♀, labeled “México, El Pinal, Pue., at 0.3 km from Rincón, 24/VI/13, coprotrap 7h2, x- 97°53'55.8" W, y- 19°8'59.3" N, oak-pine forest, 2678 m a.s.l., Moctezuma J.V.P. Col.”; 1 ♂, 2 ♀♀, labeled “México, El Pinal, Pue., at 0.3 km from Rincón, 5/VII/13, coprotrap 7h2, x- 97°53'55.8" W, y- 19°8'59.3" N, oak-pine forest, 2678 m a.s.l., Moctezuma J.V.P. Col.”; 1 ♀, labeled “México, El Pinal, Pue., at 0.3 km from Rincón, 24/VI/13, coprotrap 7h3, x- 97°53'56.5" W, y- 19°9'1" N, oak-pine forest, 2674 m a.s.l., Moctezuma J.V.P. Col.”; 3 ♂♂, 2 ♀♀, labeled “México, El Pinal, Pue., at 0.3 km from Rincón, 5/VII/13, coprotrap 7h3, x- 97°53'56.5" W, y- 19°9'1" N, oak-pine forest, 2674 m a.s.l., Moctezuma J.V.P. Col.”; 2 ♂♂, 5 ♀♀, labeled “México, El Pinal, Pue., at 0.3 km from Rincón, 24/VI/13, coprotrap 7h4, x- 97°53'57.7" W, y- 19°9'2.4" N, oak-pine forest, 2673 m a.s.l., Moctezuma J.V.P. Col.”; 2 ♀♀, labeled “México, El Pinal, Pue., at 0.3 km from Rincón, 24/VI/13, coprotrap 7h7, x- 97°54'1.8" W, y- 19°9'6.6" N, oak-pine forest, 2684 m a.s.l., Moctezuma J.V.P. Col.”; 3 ♀♀, labeled “México, El Pinal, Pue., at 0.3 km from Rincón, 5/VII/13, coprotrap 7h7, x- 97°54'1.8" W, y- 19°9'6.6" N, oak-pine forest, 2684 m a.s.l., Moctezuma J.V.P. Col.”; 2 ♂♂, labeled “México, El Pinal, Pue., at 0.3 km from Rincón, 24/VI/13, C.D. human excrement, x- 97°53'59.3" W, y- 19°9'2.1" N, oak-pine forest, 2680 m a.s.l., Moctezuma J.V.P. Col.”.

Other material examined. Mexico: Hidalgo, Metztlán, 15 June 2005, 1♂, 1♀; México: Hidalgo, Metztlán, MSN, 22 June 2005, Verdú et al. col., 3♀♀; México: Hidalgo, Metztlán, MSN, 27 June 2005, 7♀♀.

Description. Holotype – Major male (Fig. 8). Length 5 mm, maximum width of pronotum 2.3 mm. Body black, dull and silky with cupreous-bronze casts, anten-

nal club black. Clypeal margin distinctly sinuate and slightly reflexed at the apex, head with lateral margins clearly sinuate in proximity of clypeo-genal suture, genal margin strongly widened and rounded, genal sutures evident. Clypeal carina feeble and evenly curved, frons with two aligned and transverse carinae clearly elevated and medially separated. Clypeal surface mostly flattened, slightly depressed near anterior margin, punctures fine and shallow on clypeal disc, strong and deeper near anterior margin, fronto-clypeal surface with scattered and irregular punctures, genae with few and stronger punctures, head surface with reticular microsculpture, some punctures are associated with short and yellowish setae.

Pronotum completely bordered, lateral and posterior margins evenly curved, anterior and superior side with a conical, tubercle-like protuberance. Pronotum with deep and setigerous punctures, some of them associated with a small and rounded granule on anterior margin, especially in proximity of anterior angles of pronotum; punctures less impressed near the posterior margin, reticular microsculpture evident. Elytral striae impressed, with simple to medium-sized punctures quite separated, interstriae almost flat, with small punctures associated with very tiny granules, less evident in females; same reticular microsculpture of pronotum. Pygidium with strong and dense punctures, punctuation smaller, shallower and less dense near base, pygidial surface with fine microsculpture, which is less evident at apex where pygidium appears shinier. Protibiae slender, elongated and apically strongly curved inward, inner margin wider at the apex, inner and apical angle with tuft of long, robust and yellowish setae; protibia with four external teeth well separated and distributed along apical half, external margin and intervals between external teeth serrated. Parameres and endophallic sclerites: Figs 10–12.

Variation. Minor male: Smaller than major males, clypeus more clearly trapezoidal, clypeal carina more evident, pronotal protuberance either absent or feebly indicated, foretibiae less elongated and curved at the apex, similar to those of the female.

Female (Fig. 9): Clypeus distinctly trapezoidal shaped and wider, clypeo-genal suture indicated by feeble depression on lateral margin of head, genae narrower, clypeal carina distinct and stronger than in male, frons with transversal carina slightly but clearly depressed at middle, clypeal punctuation stronger and evenly distributed. Pronotal protuberance either absent or very feebly indicated, protibiae shorter than in male and wider at apex, inner angle of the protibiae without tuft of setae, with few erected setae at most. Female genitalia: Fig. 13.

Derivatio nominis. We dedicate this new species to Fermín Martín Piera (Madrid, Spain, 7 July 1954–*ibid.*, 19 July 2001), entomologist and ecologist, who rescued modern Scarabaeoidology in Spain in the 1980s.

Synthesis of the localities of the type material. MEXICO: State of Puebla, El Pinal mountain (Rincón Citlaltépetl) at 0.3 km from Rincón Citlaltépetl, 2673–2742 m a.s.l.; El Pinal mountain (Santa Isabel Tepetzala) at 2.5 km from Rincón Citlaltépetl, 2530–2550 m a.s.l.

Type locality. El Pinal mountain, Santa Isabel Tepetzala, state of Puebla, Mexico.



Figure 8. *O. martinierai* male sp. n.



Figure 9. Female *O. martinierai* sp. n.



Figure 10. Aedeagus of *O. martinpierai* sp. n.

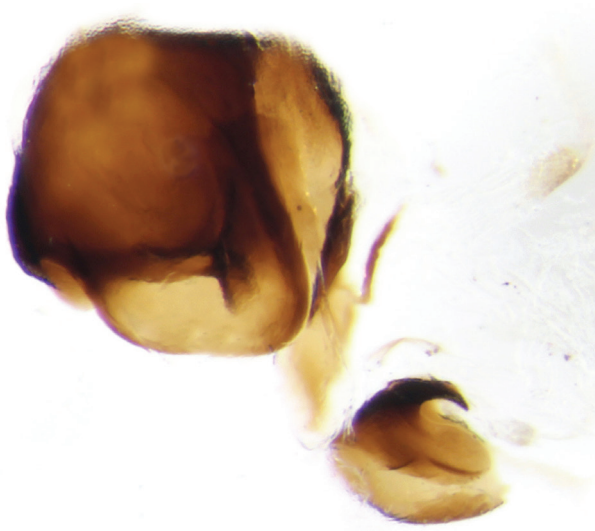


Figure 11. Copulatory lamella of *O. martinpierai* sp. n.



Figure 12. Accessory lamellae of *O. martinierai* sp. n.

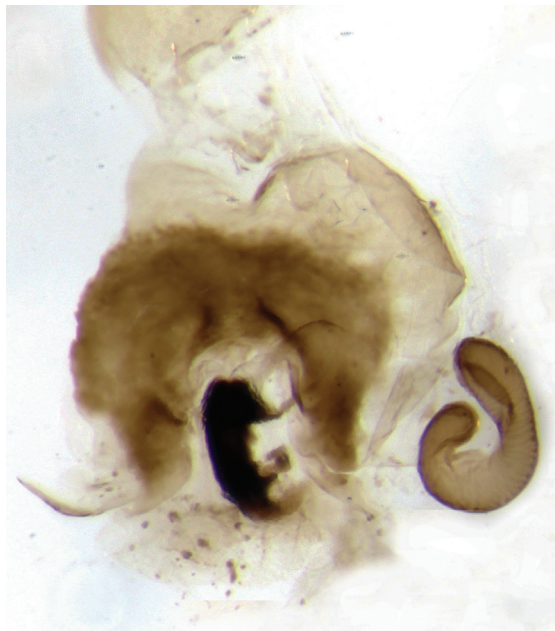


Figure 13. Genital apparatus of female *O. martinierai* sp. n.

Type repository: Holotype and five paratypes in the GH Collection. Paratypes in the collections of VM, MR, MZ, MM, CNC and LD collections.

Affinities. The morphology of *Onthophagus martinpierai* led us to include this new species of El Pinal in the *landolti* group (Zunino and Halffter 1997). This group is widely distributed from the southern border of Ontario (Canada) to the central regions of Amazonia (MR, unpublished data), with the highest diversity found in North America. To our knowledge, the *landolti* group may include several complexes of species (e.g. *lecontei-subopacus* complex, Howden and Génier 2004), the taxonomy and systematics of which require a profound revision.

This new species shares significant diagnostic characters, possible synapomorphic traits, with *O. dubitabilis* Howden & Génier and *O. mariozuninoi* Delgado, Navarrete & Blackaller. These include the shape of the frontal carina in the male, shape of the parameres (Fig. 10) and the shape of the copulatory lamella (the latter has not been published for *O. mariozuninoi*) (Fig. 11).

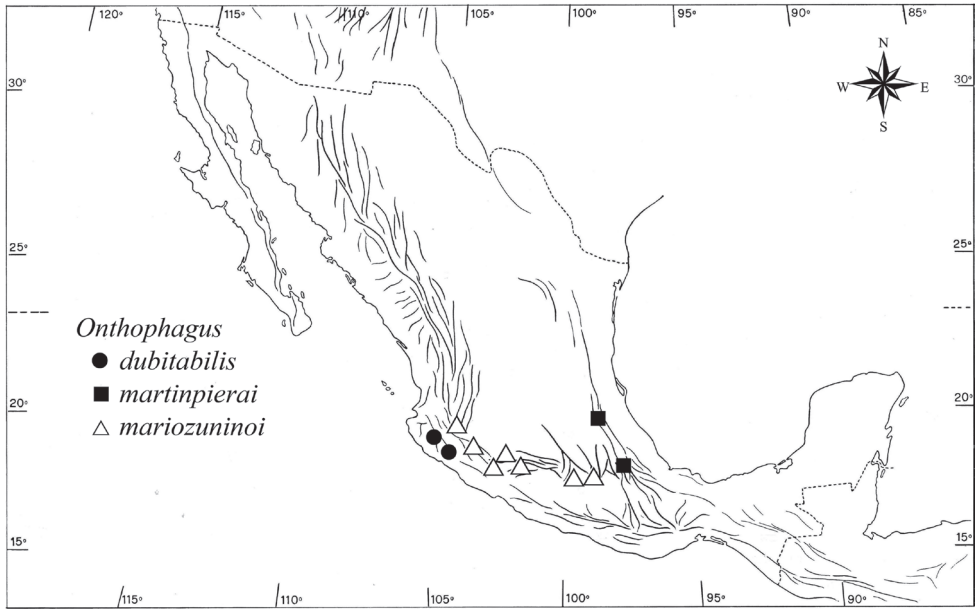
Distribution and ecology (Maps 4–5). *Onthophagus martinpierai*, *O. dubitabilis* and *O. mariozuninoi* seem to represent a new complex of species within the *landolti* group, occurring from the southern mountain range of the Sierra Madre Occidental and the nearby Sierra Madre del Sur, across the entire TMVB. As has been observed and proposed for the *fuscus* complex of the *chevrolati* group, these three species appear to show a modern distribution centred in the TMVB, with the occurrence in the southern Sierra Madre Occidental and eastern TMVB representing a secondary and more recent expansion of these species.

Onthophagus mariozuninoi is distributed from the south-eastern Sierra Madre Occidental (Tequila, Jalisco) and south-western TMVB (Atenquique, Jalisco) to the central-eastern part of the TMVB (Tlayacapan, Morelos) (Map 4). We provide Patzcuaro and Morelia, Michoacan, as geographic data additional to the known distribution of *O. mariozuninoi* (Delgado et al. 1993, Delgado 1997, Howden and Génier 2004).

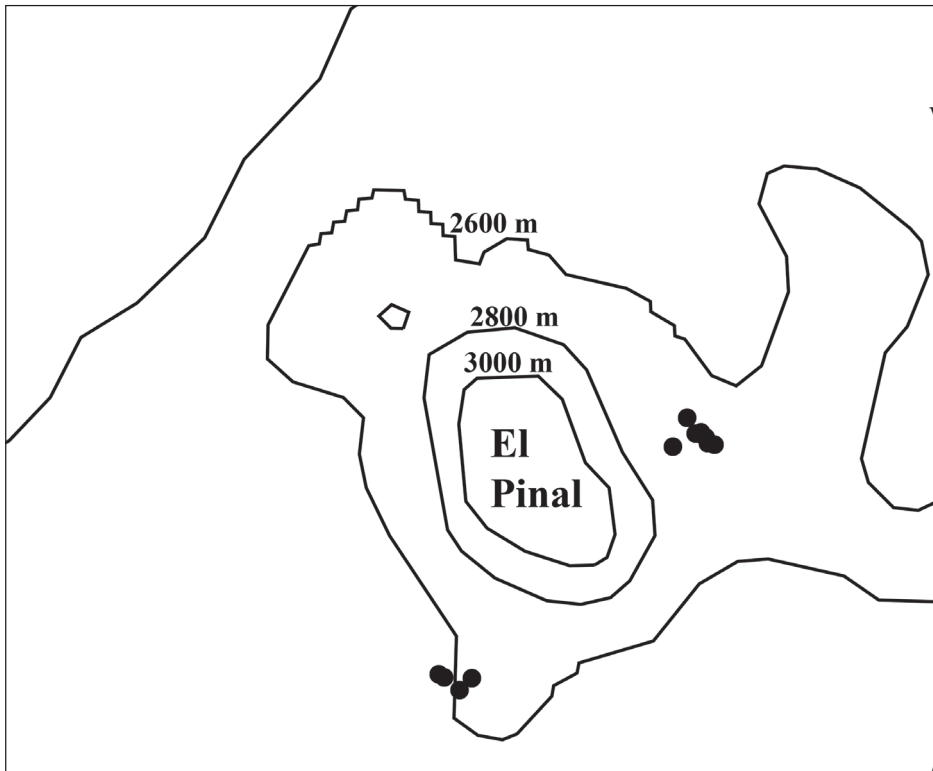
Onthophagus dubitabilis has been described by Howden and Génier (2004) for Autlán, Jalisco. We add two new records for this species: El Tapeiztle, Minatitlán Municipality, Colima, 2300 m a.s.l., pasture, 14-VIII-1989. L.E. Rivera col., 1 male; Laboratorio Natural Las Joyas de Manantlán, Sierra de Manantlán mountains, Jalisco, 8-IX-1987, L.E. Rivera and V. Bedoy col., 1 female. These new localities, along with that provided by Howden and Génier (2004), are located in the mountainous region of the Sierra de Manantlán, which is located in the south-western part of Jalisco and northern region of Colima. The Sierra de Manantlán forms part of the Sierra Madre del Sur.

Onthophagus martinpierai has been found in El Pinal, in the easternmost part of the TMVB, the same locality as *O. clavijeroi*. However, it is very likely this species also occurs in other localities across the central-eastern part of the TMVB (eastern limit of *O. mariozuninoi*'s distribution).

Onthophagus martinpierai has been collected both directly and using pitfall traps baited with human excrement and horse dung. The large number of specimens collected mainly with excrement suggests the coprophagous habit of this species. It was found in areas with secondary pine-oak forests with pastures between 2530–2742 m a.s.l.



Map 4. Distribution of *Onthophagus martinpierai* and related species.



Map 5. Collection sites for *Onthophagus martinpierai* (●) on the mountain El Pinal.

In contrast, *O. mariozuninoi* appears to be generalist since it has been collected in dog scats and pitfall traps baited with squid, even though the largest number of individuals has been captured on fungi. This species seems to occur between 1650–2370 m a.s.l. In Pátzcuaro, Michoacán, it was collected at 2150 m a.s.l. According to Delgado et al. (1993), this species is eurytopic and is found in mountain mesophilous and pine-oak forests. In Pátzcuaro, it was also collected in pine-oak forest.

The Sierra de Manantlán mountain range was originally a forested area, presenting distinct vegetation at different altitudes. *Onthophagus dubitabilis* has been collected in both mountain mesophilous forests and open habitats at between 1900–2300 m a.s.l.

Results and discussion

The Scarabaeinae beetles collected during our fieldwork in El Pinal belong to the genus *Onthophagus*. In addition to *O. clavijeroi* and *O. martinpiepai*, five more species have been found in the same localities: *O. chevrolati retusus* Harold, *O. incensus* Say, *O. lecontei* Harold, *O. mexicanus* Bates, and *O. bolivari* Moctezuma, Rossini & Zunino (a new species recently described in Arriaga et al. 2016).

As proposed at the beginning of this paper (prediction 1), species that occur above 2500 m belong to the Paleo-American Distribution Pattern. In the MTZ, the genus *Onthophagus* is a lineage of ancient penetration, showing high diversity in terms of both number of species and eco-geographic distribution. These characteristics can explain the ability of the genus to fit the Palaeo-American pattern in different ways. Only one specimen of *O. incensus* (a species very abundant at lower altitudes) has been collected at 2639 m. This species is distributed from Mexico to the northern regions of South America (Colombia and Venezuela) and associated with tropical conditions, although it also occurs in mountainous areas up to 2000 m a.s.l. This specimen was collected on the lowest part of El Pinal, in the same sampled area in which a large number of *O. mexicanus* was found, a species widely distributed on the Mexican High Plateau.

Among the lineages of *Onthophagus* (see Zunino and Halffter 1997) distributed across the southern High Plateau and foothills of the surrounding mountain ranges (Paleo-American Distribution on the High Plateau), two species have been found: *O. lecontei* (*landolti* group) and *O. mexicanus* (*mexicanus* group) (Zunino and Halffter 1997).

All of the remaining species, which constitute common elements of the scarabaeinae fauna of the TMVB, belong to the Mountain Paleo-American Distribution Pattern. *Onthophagus chevrolati retusus* is a very characteristic subspecies of the TMVB, reaching the highest elevation to date reported for Scarabaeinae in the MTZ (see Zunino and Halffter 1988). Indeed, this subspecies was found in the highest sampled locality of El Pinal (3017 m). *Onthophagus c. retusus* occurs in the eastern part of the TMVB, both in the Sierra Madre del Sur and in the Puebla-Oaxaca Mountain System.

Onthophagus clavijeroi and *O. martinpierai*, along with closely related species, occur in the central and western parts of the TMVB, a distribution pattern shared with *O. bolivari* (Arriaga et al. *in press*), the most abundant species of El Pinal, which was also collected on the mountain La Malinche.

El Pinal, a relatively recent and not particularly large mountainous formation, thus hosts representatives of the three main biogeographic patterns to which the genus *Onthophagus* corresponds across the MTZ. However, on older and higher mountains on the eastern side of the TMVB, the Mountain Palaeo-American distribution pattern will dominate above 2500 m.

Concerning prediction 2, it is important to emphasize that the species collected on El Pinal, as well as their close relatives, can be also found in western and eastern localities of the TMVB, including the Sierra Madre Oriental. As far as we could ascertain in this study, El Pinal appears to have been colonized from both the western and eastern sides, apart from with *O. lecontei* and *O. mexicanus*, which possibly arrived via vertical dispersion from the contiguous Mexican High Plateau. Instead, the remaining species (including *O. incensus*) appears to have adopted a horizontal distribution from the lower altitudes of the eastern TMVB.

The high level of endemism observed on El Pinal, quite unexpected on such a relatively small and recent mountain, may be the result of a recent vicariant event or due to the lack of intensive sampling in the central mountains of the TMVB and the nearby Puebla-Oaxaca Mountain System.

As indicated above, prediction 3 has been fully met, as has prediction 5. We could not test the fourth prediction because of the isolation of El Pinal on the northern side of the TMVB, as well as its lack of contact with the southern tropical depressions.

In accordance with the sixth preliminary hypothesis, the highest value of abundance and number of species were found at 2639 m. In contrast, sampling carried out at higher altitudes (2993 m) yielded a distinctly lower number of species and individuals: *Onthophagus c. retusus* and *O. bolivari* were the only species of the *chevrolati* group to be collected, with a few specimens (e.g., only one individual for *O. bolivari*). This altitudinal gradient firstly led us to suppose that some species and subspecies of the *chevrolati* group can reach the highest altitudes in the Mexican mountains. In other mountains of the TMVB, even *O. hippopotamus* Harold, a species of the *chevrolati* group associated with gopher nests, occurs at high elevations. Secondly, it is important to note that the altitudinal range between 3000–3100 m a.s.l. represents, with extreme rarefaction, the upper distributional limit of the mountain Scarabaeinae in the MTZ.

Regarding the seventh preliminary hypothesis, the *Onthophagus* of El Pinal are found in different types of mountain vegetation (e.g., opened and secondary forests, clearings etc.), with greatest abundance in areas dominated by plants that require high solar radiation. Furthermore, the presence and density of trees do not appear to affect the distribution of *Onthophagus* of El Pinal, in the way that they have been proved to be determinant in the tropical forest of the ZTM.

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Contributions to the knowledge of the genus *Horaeomorphus* Schaufuss (Coleoptera, Staphylinidae, Scydmaeninae) in mainland China

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Abstract

Five new species of the ant-like stone beetle genus *Horaeomorphus* Schaufuss (Scydmaeninae: Glandulariini) from China are described: *H. hainanicus* sp. n., *H. biwenxuani* sp. n., *H. pengzhong* sp. n., *H. hujiayaoi* sp. n. and *H. punctatus* sp. n. The previously unknown male of *H. chinensis* Franz, 1985 is now discovered, and its aedeagus and metatrochanter are illustrated. The latter species is newly recorded from Zhejiang. Three females from Guangxi are also recorded, but their identity remains unconfirmed until associated males become available. A key to *Horaeomorphus* of mainland China is included.

Keywords

Scydmaeninae, Glandulariini, *Horaeomorphus*, new species, new records, Oriental, China

Introduction

The Australo-Oriental genus *Horaeomorphus* Schaufuss currently comprises 59 species distributed in Malaysia, Singapore, Thailand, Nepal, Vietnam, Japan, continental China, Taiwan, Laos, the Philippines, Indonesia, Fiji, Australia, and Madagascar (Franz 1985; Jałoszyński 2002, 2003, 2004, 2006, 2009, 2012, 2014a, 2014b; Jałoszyński and Nomura 2004, 2008; Jałoszyński et al. 2007; Vít 2004); among them 21 Madagascan species were transferred from previous *Euconnus* (*Anthicimorphus*) together with the Australian type species of *Anthicimorphus*, but they should be treated as species *incertae sedis* within Glandulariini (Jałoszyński 2014b). Until now, only one species from mainland China has been described.

Among asian glandulariine (= former Cyrtoscydmini, see Newton 2015) genera, *Horaeomorphus* is characterized by the mesoventral intercoxal process being shorter and less elevated than the mesocoxae, the metaventral intercoxal process with two long spines projecting posteriorly, the presence of a small pit at the posteromesal margin of each supra-antennal tubercle, pronotal base with distinct median pit in addition to lateral pits, and each elytron with two foveae connected by a U-shaped groove extending anteriorly; many species have the male trochanters modified (Jałoszyński 2015).

Recent examination of unsorted material in our collection revealed five new species of *Horaeomorphus* from Hainan, Guangxi, Yunnan and Xizang. Moreover, during our recent expedition, two males of *H. chinensis* Franz, 1985 were discovered in the type locality, Fujian: Guadun (=Kuatun), which makes it possible to add a description of male characters. This species is also newly recorded from Zhejiang: Baishanzu. Three females from Guangxi are recorded; they belong to a group of species characterized by a strongly convex and broad body, but their identities remain unknown until associated males become available. A key to *Horaeomorphus* of mainland China is included.

Material and methods

All material treated in this study is housed in the Insect Collection of Shanghai Normal University, Shanghai, China (SNUC).

The collecting data are quoted verbatim. Each type specimen bears the following label: 'HOLOTYPE [red] (or PARATYPE [yellow]), ♂ (or ♀), *Horaeomorphus* + specific name sp. n., det. Zhou & Zhang, 2016, SNUC'.

The following abbreviations are applied: AeL—length of the median lobe of aedeagus in ventral view; AnL—length of the antennae; BL—length of the body (= HL + PL + EL); EI—elytral index (= EL / EW); EL—length of the elytra along the suture, from the base of scutellum to the apex; EW—maximum width of the elytra; HW—width of the head across eyes; HL—length of the head from the anterior clypeal margin to the occipital constriction; PL—length of the pronotum along the midline; PWb—width of the pronotum at base; PWm—maximum width of the pronotum; SpL—length of the spermatheca.

Taxonomy

Horaeomorphus chinensis Franz, 1985

Figs 1A, 6B–E, 6G–K

Horaeomorphus chinensis Franz, 1985: 116.

Material examined. 2 ♂♂, 4 ♀♀, labeled ‘China: Fujian Province, Wuyishan City [武夷山市], Tongmu Village [桐木村], Guadun [挂墩], 27°44'03"N, 117°38'40"E, decaying log, 1178m, 2.x.2015, Yan, Tu, Shen, Jiang & Zhou leg.’; 2 ♂♂, 2 ♀♀, labeled ‘China: Zhejiang, Lishui City [丽水市], Qingyuan Hsien [庆元县], Baishanzu [百山祖], Huangpi Swamp [黄皮湿地], 27°49'38"N, 119°11'29"E, decaying log, 1429m, 25.iv.2015, Song & Yan leg.’; 1 ♀, labeled ‘China: S.Zhejiang, Qingyuan, Mt nr. Liyang Village [栗洋村], 27°49'38"N, 119°11'22"E, leaf litter, sifted, 29.iv.2014, 990–1160m, Peng, Song, Yan & Yu leg.’

Description of male. Males (Fig. 1A) similar to females in external morphology, but metatrochanter (Fig. 6J) modified, with distal part protruded; slightly longer than half of metafemur, apex spiculate. BL 2.52–2.76 mm; HL 0.40–0.43 mm; HW 0.53–0.58 mm; AnL 1.05–1.17 mm, relative lengths of antennomeres: 1.0 : 0.9 : 1.4 : 1.1 : 1.1 : 1.0 : 1.0 : 1.0 : 1.1 : 1.1 : 2.0; PL 0.75–0.81 mm; PWb 0.46–0.52 mm; PWm 0.65–0.71 mm; EL 1.37–1.53 mm; EW 0.89–0.94 mm; EI 1.54–1.63.

Aedeagus (Fig. 6C–E) elongate, AeL 0.48 mm; endophallus (Fig. 6H–I) very complicated, with large bell-shaped central complex surrounded at each side by weakly sclerotized, elongate lateral structures; parameres (Fig. 6G) slender, longer than median lobe, each with three apical setae and two subapical setae.

Distribution. Eastern China: Fujian, Zhejiang (new provincial record).

Comments. *Horaeomorphus chinensis* shares many characters with several congeners: *H. punctifrons* Jałoszyński, 2006 (Malaysia: Pahang), *H. jeraianus* Jałoszyński, 2006 (Malaysia: Kedah), *H. jaechi* Jałoszyński, 2006 (Malaysia: Sarawak), *H. tiomanensis* Jałoszyński, 2006 (Malaysia: Tioman Is.), *H. caverniventris* Jałoszyński, 2006 (Malaysia: Pahang), *H. endauensis* Jałoszyński & Nomura, 2007 (Malaysia: Pahang), *H. imitator* Jałoszyński, 2009 (the Philippines: Mindanao), *H. solodownikovi* Jałoszyński, 2014 (Laos: Champasak), *H. sakishimanus* Jałoszyński, 2002 (Japan: Iriomote-jima and Ishigaki-jima islands), *H. hainanicus* sp. n. (China: Hainan) and *H. pengzhongii* sp. n. (China: Yunnan), all of them have elongate and convex habitus, the pronotum with three pits connected by a groove, the base of elytra barely wider than the basal margin of pronotum and protruded, recurved metatrochanters in males. Among these species, *H. hainanicus* sp. n. and *H. pengzhongii* sp. n. have a similar shape of the aedeagus, structures of endophallus and slender parameres each with two subapical setae, as those in *H. chinensis*. The character combination of the pronotum and elytra with a dense and distinct punctation, the recurved metatrochanters without expansions on their ventral margins in male, the parameres longer than median lobe and the structures of the endophallus can be used to distinguish *H. chinensis* from the two species mentioned above.



Figure 1. Habitus of *Horaeomorphus* species. **A** *H. chinensis*, male **B** *Horaeomorphus* sp., female. Scale bars: 1.0 mm.

Bionomics. Specimens from Guadun were collected by sifting material from an ant nest (Fig. 10B) in a relatively dry rotten trunk in a bamboo forest; four specimens from Baishanzu were collected from under bark of a rotten tree.

***Horaeomorphus* sp.**

Figs 1B, 6A, 6F

Material examined. 3 ♀♀, labeled ‘China: Guangxi Prov., Shangsi County [上思县], Shiwandashan [十万大山], alt. 300–400m, 23.iv.2011, Peng, Zhai & Zhu leg.’.

Description. Body (Fig. 1B) large, strongly convex, BL 2.48–2.51 mm; HL 0.37–0.38 mm; HW 0.50 mm; antennae (Fig. 6A) relatively short, AnL 0.99 mm; relative lengths of antennomeres: 1.0 : 0.8 : 1.2 : 1.0 : 1.0 : 0.9 : 0.9 : 0.9 : 1.0 : 1.0 : 2.2; PL 0.74–0.76 mm; PWm 0.59–0.61 mm; PWb 0.46–0.47 mm; EL 1.35–1.39 mm; EW 1.00–1.03 mm; EI 1.30–1.38.

Spermatheca (Fig. 6F) elongate, SpL 0.13mm; with longitudinal groove at middle.

Comments. These females have strongly convex and broadened elytra (EI 1.30–1.38), distance between humeral calli wider than the width of the pronotum at base, large and deep punctures sharply delimited from background in the center of pronotal disc and anterior third of elytra. The shape of the spermatheca is similar to that of *H. caverniventris* Jąłoszyński, 2006 (Malaysia: Pahang), but females of the Malaysian species are larger (2.79–3.12 mm). Therefore the three specimens almost certainly belong to a new species, but a male must be found for formal description.

Distribution. Southern China: Guangxi.

***Horaeomorphus hainanicus* D.-Y. Zhou & S.-J. Zhang, sp. n.**

<http://zoobank.org/754810B2-86FD-4684-8B7C-A4981F223105>

Figs 2, 4

Type material (20 ♂♂, 25 ♀♀). **Holotype:** CHINA: ♂, labeled 'China: Hainan, Ledong Hsien [乐东县], Jianfengling [尖峰岭] N.R., Mingfenggu [鸣凤谷], 18°44'30"N, 108°50'29"E, rainforest, decaying log from a colony termite nest, 995 m, 23.i.2015, Peng, Yin, Tu, Song, Shen, Zhou, Yan, Wang leg.'. **Paratypes:** 7 ♂♂, 14 ♀♀, same locality as holotype; 1 ♀, same locality as holotype, except 'alt. 950m, 30-IV-2012, PAN Y.H. & LI W. R. leg.'; 6 ♂♂, 7 ♀♀, labeled 'China: Hainan, Qiongzong Hsien [琼州县], Limu Mt [黎母山], nr. residence, path to peak, 19°10'04"N, 109°44'45"E, decaying log, 1000 m, 31.i.2015, Peng, Yin, Tu, Song, Shen, Zhou, Yan, Wang leg.'; 2 ♂♂, 1 ♀, same locality as previously except '01.ii.2015'; 1 ♂, 1 ♀, same locality as previously except 'nr. residence, 19°10'04"N, 109°44'45"E, decaying log, 625m, 29.i.2015'; 1 ♂, same locality as previously except 'path to Limu Temple, 19°08'09"N, 109°45'46"E, 580–760m, 29.i.2015, Peng, Yin, Tu, Song, Shen leg.'; 2 ♂♂, 1 ♀, labeled 'China: Hainan, Wuzhi Shan [五指山] N. R., nr.reservoir, 18°53'10"N, 109°36'11"E, 500m, 22.iv.2012, leaf litter, sifted, Peng& Dai leg.'.

Diagnosis. *Horaeomorphus hainanicus* can be readily separated from all other congeners by its moderately large (2.53–3.08 mm) and elongate body, fine punctuation on pronotal disc and elytra, rounded apices of metatrochanters in male, parameres each with 3–5 apical setae and two subapical setae, unique structure of endophallus and shape of spermatheca.

Description. Male. BL 2.77–3.08 mm; body (Fig. 2A) large, strongly convex, reddish brown, legs and palpi slightly lighter. Head broadest at large, finely faceted and moderately convex eyes, HL 0.40–0.48 mm, HW 0.58–0.68 mm; tempora rounded and slightly shorter than eye in dorsal view; vertex strongly transverse and weakly con-



Figure 2. Habitus of *Horaemorphus hainanicus* sp. n. **A** male **B** female. Scale bars: 1.0 mm.

vex, with pair of small but distinct pits located near posterior margins of supra-antennal tubercles; frons weakly convex; supra-antennal tubercles strongly raised. Punctuation on vertex and frons fine and inconspicuous; setae moderately long, sparse. Antennae (Fig. 4A) short, AnL 1.21–1.24 mm, relative lengths of antennomeres: 1.0 : 1.1 : 1.7

: 1.5 : 1.4 : 1.5 : 1.2 : 1.1 : 1.2 : 1.1 : 2.2. Pronotum inversely subtrapezoidal, widest near anterior third, PL 0.87–0.94 mm, PWm 0.72–0.81 mm, PWb 0.52–0.58 mm; anterior margin rounded, sides narrowing toward base; hind angles obtuse and blunt; posterior collar delimited from disc by deep and narrow transverse groove connecting three small pits. Punctuation on disc as fine as that on frons and vertex; dorsal surface glossy; setation moderately long. Elytra oval and elongate, moderately convex; widest near anterior third, narrowing toward apices. EL 1.50–1.66 mm, EW 0.92–1.04 mm, EI 1.59–1.63. Humeral calli distinct. Punctures more distinct than those on pronotum, sharply marked and separated by spaces 3–4× as wide as puncture diameters; setation moderately dense. Hindwings fully developed. Metatrochanter (Fig. 4I) modified, with distal part protruded and recurved; as long as half of metafemur, apex rounded. Aedeagus (Fig. 4B–D) elongate, AeL 0.53 mm; endophallus (Fig. 4F–G) very complicated, with large bell-shaped central complex surrounded at each side by weakly sclerotized, elongate lateral structures; parameres (Fig. 4E) slender, longer than median lobe, each with 3–5 apical setae and two subapical setae.

Female. Similar to male, with slightly smaller body and unmodified metatrochanter. BL 2.53–2.85 mm, HL 0.39–0.42 mm, HW 0.57–0.62 mm, AnL 1.11–1.20 mm, relative lengths of antennomeres: 1.0 : 1.1 : 1.5 : 1.4 : 1.4 : 1.3 : 1.1 : 1.1 : 1.2 : 1.2 : 2.2. PL 0.76–0.88 mm, PWm 0.63–0.74 mm, PWb 0.49–0.54 mm; EL 1.39–1.54 mm, EW 0.84–0.97 mm, EI 1.58–1.64, spermatheca (Fig. 4H) ovoid, slightly elongate, SpL 0.12 mm.

Comments. *Horaeomorphus hainanicus* is similar to many congeners (see comments at *H. chinensis*), and has a similar endophallic structures and the shape of spermatheca as *H. chinensis*. The relatively larger body (2.77–3.08 mm in males), the pronotal and elytral surface glossy, protruded metatrochanters with rounded apices and subtle differences in the endophallus can be used to readily separate this species from *H. chinensis*.

Bionomics. Specimens of the type series were collected from ant and termite nest material in rotten wood and under bark of standing rotten logs in rainforests of Hainan.

Distribution. Southern China: Hainan.

Etymology. The specific epithet refers to the province where the type locality of the new species lies.

***Horaeomorphus punctatus* D.-Y. Zhou & S.-J. Zhang, sp. n.**

<http://zoobank.org/B832FF57-E3B1-44C3-9D4F-87C3471AA98B>

Figs 3, 5

Type material (1 ♂, 1 ♀). **Holotype:** CHINA: ♂, labeled ‘China: Yunnan Prov., Yingjiang Hsien [盈江县], Xima [昔马], 1500–1650m, 20–22.v.2013, Wen-Xuan Bi leg.’. **Paratype:** 1 ♀, same locality as holotype.

Diagnosis. *Horaeomorphus punctatus* can be readily separated from all other congeners by its moderately large (2.07–2.36 mm) and stout body, broad pronotum with



Figure 3. Habitus of *Horaeomorphus punctatus* sp. n. **A** male **B** female. Scale bars: 0.5 mm.

a row of three pits connected by a shallow, barely notable groove; dense and coarse punctation on elytra, unmodified metatrochanters in male, aedeagal parameres lacking setae at apices and shape of spermatheca.

Description. Male. BL 2.36 mm; body (Fig. 3A) moderately large, flattened, dark reddish-brown, legs and palpi slightly lighter. Head broadest at large, finely faceted and moderately convex eyes, HL 0.34 mm, HW 0.46 mm; tempora shorter than eye in dorsal view, in anterior third nearly parallel, then strongly bent and in posterior third nearly transverse to long axis of head; vertex strongly transverse and weakly convex,

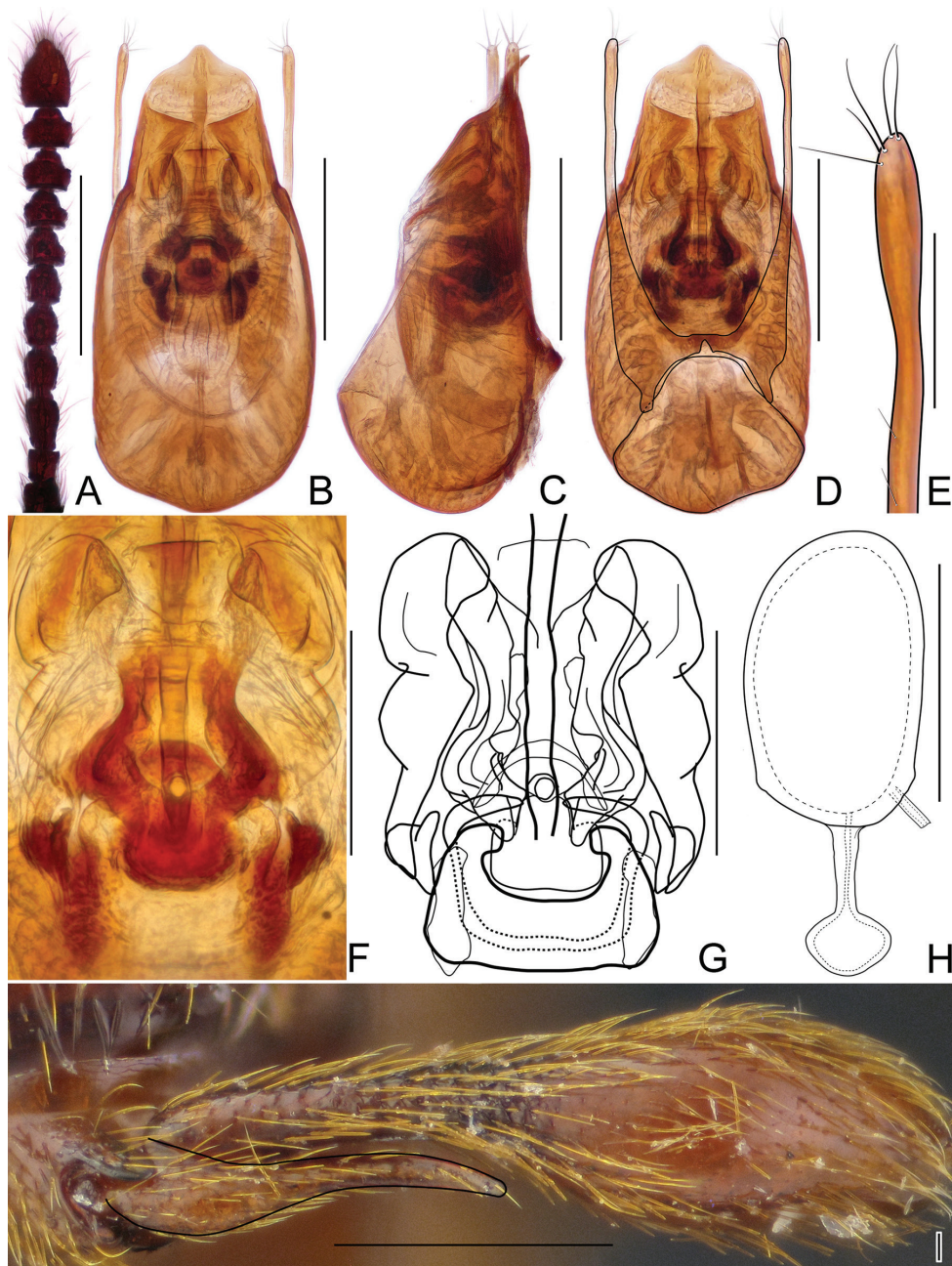


Figure 4. Diagnostic characters of *Horaeomorphus hainanicus* sp. n. **A** Left antenna of male, in dorsal view **B** Aedeagus, in ventral view **C** Same, in lateral view **D** Same, in dorsal view **E** Apical portion of paramere, enlarged **F** Endophallus, enlarged, in ventral view **G** Same, schematic **H** Spermatheca, in lateral view **I** Left metatrochanter of male, in ventral view. Scale bars: 0.5 mm (**A**); 0.2 mm (**B**, **C**, **D**); 0.04 mm (**E**); 0.1 mm (**F**, **G**, **H**); 0.3 mm (**I**).

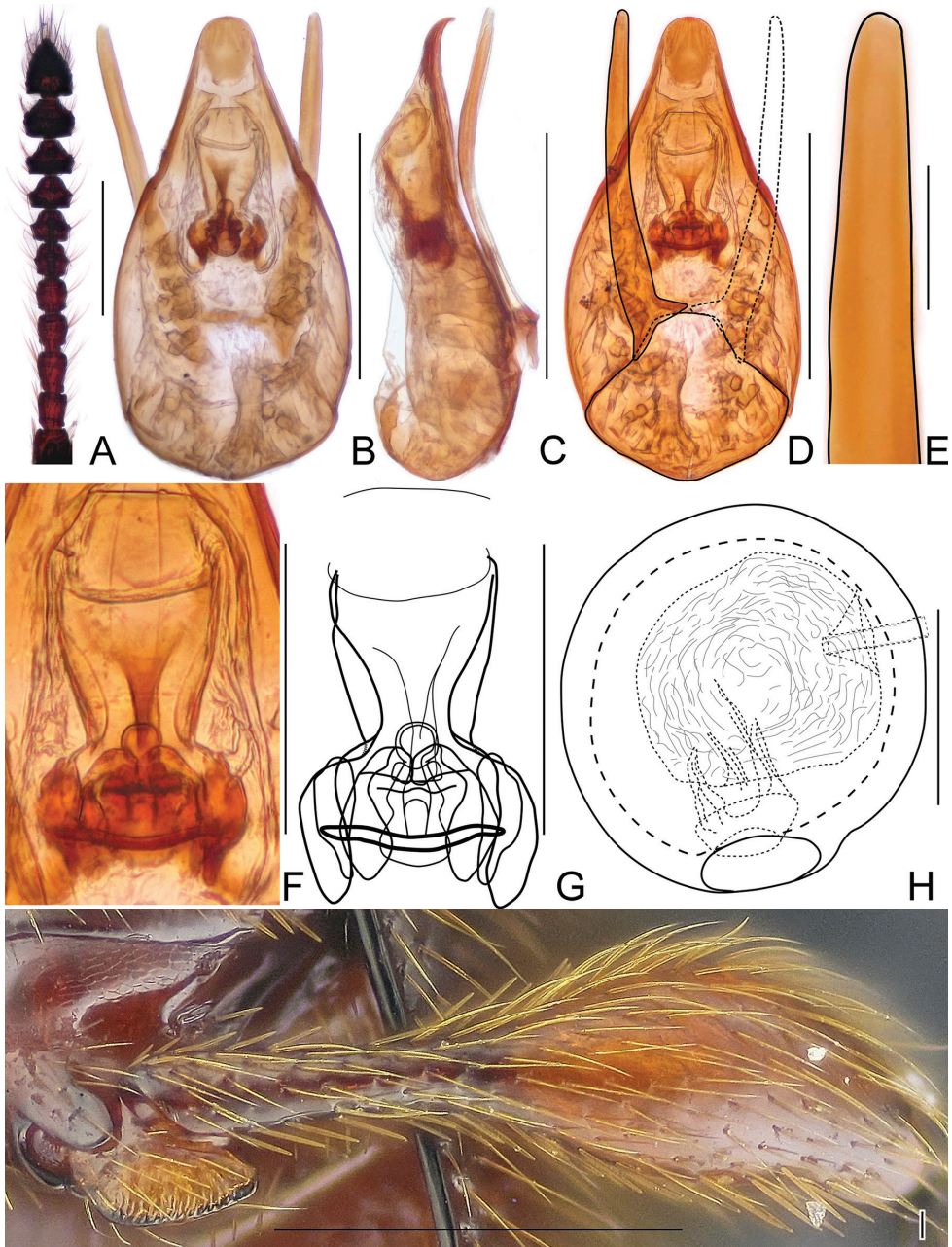


Figure 5. Diagnostic characters of *Horaemorphus punctatus* sp. n. **A** Left antenna of male, in dorsal view **B** Aedeagus, in ventral view **C** Same, in lateral view **D** Same, in dorsal view **E** Apical portion of paramere, enlarged **F** Endophallus, enlarged, in ventral view **G** Same, schematic **H** Spermatheca, in lateral view **I** Left metatrochanter of male, in ventral view. Scale bars: 0.3 mm (**A**); 0.2 mm (**B**, **C**, **D**); 0.03 mm (**E**); 0.08 mm (**F**, **G**); 0.04 mm (**H**); 0.3 mm (**I**).

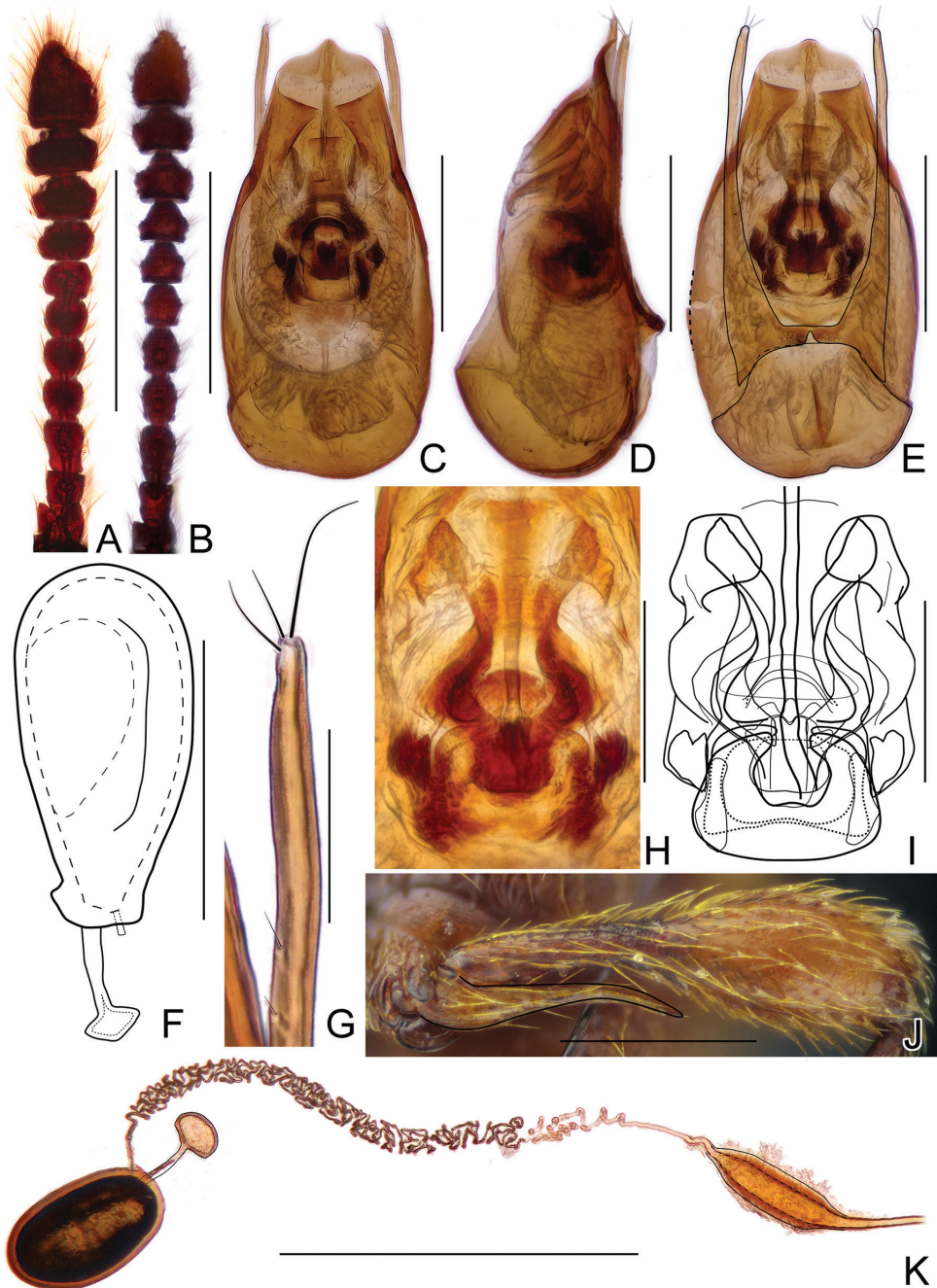


Figure 6. Diagnostic characters of *Horaeomorphus* species. (**A, F** *Horaeomorphus* sp. **B–E, G–K** *H. chinensis*) **A** Left antenna of male, in dorsal view **B** Left antenna of female, in dorsal view **C** Aedeagus, in ventral view **D** Same, in lateral view **E** Same, in dorsal view **F** Spermatheca, in lateral view **G** Apical portion of paramere, enlarged **H** Endophallus, enlarged, in ventral view **I** Same, schematic **J** Left metatrochanter of male, in ventral view **K** Spermatheca with bursa copulatrix, in lateral view. Scale bars: 0.5 mm (**A, B**); 0.2 mm (**C, D, E**); 0.1 mm (**F, H, I**); 0.04 mm (**G**); 0.3 mm (**J, K**).

with pair of small but distinct pits located near posterior margins of supra-antennal tubercles; frons weakly convex; supra-antennal tubercles strongly raised. Punctures on vertex and frons fine and inconspicuous; setation moderately long, sparse. Antennae (Fig. 5A) short, AnL 0.87 mm, relative lengths of antennomeres: 1.0 : 0.9 : 1.0 : 0.9 : 0.9 : 0.8 : 0.8 : 0.8 : 0.9 : 1.0 : 1.5. Pronotum broad, nearly circular, slightly longer than wide, widest at middle, PL 0.76 mm, PWm 0.72 mm, PWb 0.47 mm; posterior collar short, well delimited from disc by constriction and row of three shallow pits connected by shallow groove; punctation dense and coarse; setation moderately long. Elytra broad, flattened and distinctly impressed in middle at about anterior third; EL 1.26 mm, EW 0.84 mm, EI 1.50. Punctures coarse, more distinct than those on pronotum, sharply marked and separated by spaces as wide as diameters of punctures; setation long, moderately dense, erect to suberect. Hindwings fully developed. Metatrochanter (Fig. 5I) unmodified, with distinct ventral edge. Aedeagus (Fig. 5B–D) relatively slender, with median lobe strongly narrowing toward apex, AeL 0.57 mm; endophallus (Fig. 5F–G) relatively small and complicated, with sclerotized central portion and two moderately darkly sclerotized and curved structures; parameres (Fig. 5E) slender, minimally longer than median lobe, without apical setae.

Female. Similar to male, but with smaller body and less contractive pronotal base. BL 2.07 mm, HL 0.33 mm, HW 0.44 mm, AnL 0.75 mm, relative lengths of antennomeres: 0.8 : 0.8 : 0.9 : 0.8 : 0.7 : 0.7 : 0.6 : 0.7 : 0.6 : 1.0 : 1.2. PL 0.63 mm, PWm 0.58 mm, PWb 0.44 mm; EL 1.11 mm, EW 0.74 mm, EI 1.50, spermatheca (Fig. 5H) spherical, SpL 0.08 mm, with complicated internal structures.

Comments. *Horaeomorphus punctatus* is similar to *H. mesaios* Jałoszyński & Nomura, 2004 (Vietnam: Ninh Binh), *H. valdepunctatus* Franz, 1984 (Malaysia: Pahang), *H. sarawakensis* Franz, 1992 (W Malaysia) and *H. samosirensis* Jałoszyński, 2009 (Indonesia: Sumatra) in habitus, and is also very similar to *H. mesaios* in the shape of aedeagus and structures of endophallus; but it can be identified by its relatively large body (2.07–2.36 mm), the pronotum with three basal pits; unmodified metafemora, non-protruded metatrochanters in males and achaetous parameral apex.

Distribution. Southern China: Yunnan.

Etymology. The specific epithet refers to the coarse punctation of the elytra.

***Horaeomorphus pengzhongi* D.-Y. Zhou & S.-J. Zhang, sp. n.**

<http://zoobank.org/F7F96BFA-C563-45EF-AFCF-5F6539869D30>

Fig. 7

Type material (1 ♂). **Holotype:** CHINA: ♂, labeled ‘China: Yunnan, Baoshan City [保山市], Tengchong County [腾冲县], Mingguang Town [明光镇], Zizhi Village [自治乡], 25°18'24"N, 98°48'22"E, 1230 m, 24.vi.2013, Dai, Song& Peng leg.’.

Diagnosis. *Horaeomorphus pengzhongi* can be readily separated from all other congeners by its moderately large (3.00 mm) and elongate body, sparse and fine punctation on pronotal disc and elytra, protruded metatrochanter with expansion on its

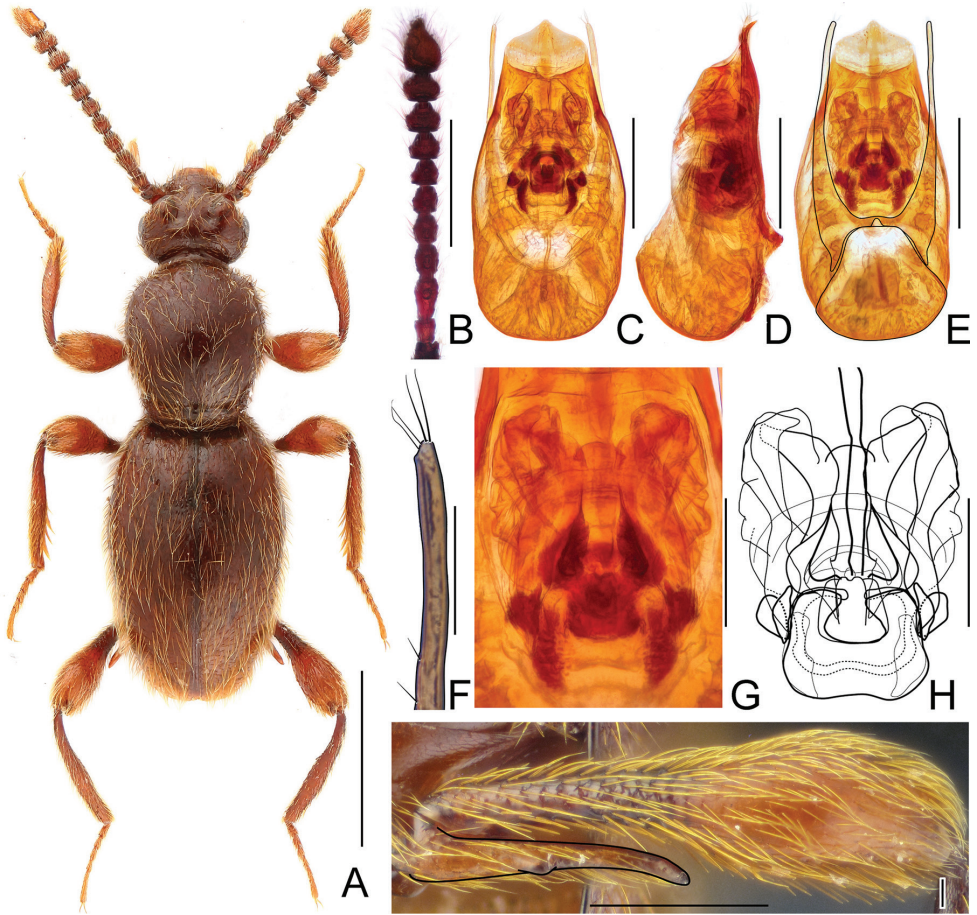


Figure 7. *Horaeomorphus pengzhongi* sp. n. **A** male, dorsal habitus **B** Right antenna of male, in dorsal view **C** Aedeagus, in ventral view **D** Same, in lateral view **E** Same, in dorsal view **F** Apical portion of paramere, enlarged **G** Endophallus, enlarged, in ventral view **H** Same, schematic **I** Left metatrochanter of male, in ventral view. Scale bars: 1 mm (**A**); 0.5 mm (**B**); 0.2 mm (**C, D, E**); 0.04 mm (**F**); 0.1 mm (**G, H**); 0.3 mm (**I**).

ventral edge in male, parameres each with four apical setae and two subapical setae and unique structures of endophallus.

Description. Male. BL 3.00 mm; body (Fig. 7A) large, strongly convex, reddish brown, legs and palpi slightly lighter. Head broadest at finely faceted and slightly convex eyes, HL 0.47 mm, HW 0.63 mm; tempora rounded, about as long as length of eye in dorsal view; vertex strongly transverse and weakly convex, with pair of small but distinct pits located near posterior margins of supra-antennal tubercles; frons weakly convex; supra-antennal tubercles strongly raised. Punctures on vertex and frons dense and coarse; setae moderately long, sparse. Antennae (Fig. 7B) short, AnL 1.31 mm, relative lengths of antennomeres: 1.0 : 0.8 : 1.8 : 1.4 : 1.1 : 1.1 : 1.0 : 1.1 : 1.2 : 1.1 : 2.2. Pronotum oval, convex, distinctly longer than wide, widest near anterior 2/5, PL 0.97 mm, PWm 0.79 mm, PWb 0.53 mm; anterior margin rounded, sides narrowing

toward base; hind angles obtuse and blunt; base with 3 large and deep pits connected by narrow groove. Punctuation on disc sparse and fine; dorsal surface glossy; setation moderately long. Elytra oval and elongate, moderately convex; widest near anterior 2/5, narrowing toward apices. EL 1.57 mm, EW 1.0 mm, EI 1.56. Humeral calli distinct. Punctures fine, more distinct than those on pronotum, separated by spaces 3–4× as wide as puncture diameters; setation moderately dense. Hindwings fully developed. Metatrochanter (Fig. 7I) modified, with distal portion straight and apical 1/7 recurved, as long as half of metafemur, with expansion on ventral margin, apex rounded. Aedeagus (Fig. 7C–E) elongate, AeL 0.53 mm; endophallus (Fig. 7G–H) very complicated, with large bell-shaped central complex surrounded at each side by weakly sclerotized, elongate lateral structures; parameres (Fig. 7F) slender, subequal in length to median lobe, each with four apical setae and two subapical setae.

Female. Unknown.

Comments. *Horaeomorphus pengzhongi* is similar to many congeners (see comments of *H. chinensis*); the relatively larger body (3.00 mm), elongated metatrochanters each with the ventral expansion in male, each paramere with two subapical setae and structures of endophallus are clearly different and can be used to identify this new species.

Distribution. Southern China: Yunnan.

Etymology. This species is dedicated to Zhong Peng, one of the collectors of the type specimen.

***Horaeomorphus biwenxuani* D.-Y. Zhou & S.-J. Zhang, sp. n.**

<http://zoobank.org/E5D8A881-C40E-4321-BAAE-415074D29AEF>

Fig. 8

Type material (1 ♂). **Holotype: CHINA:** ♂, labeled ‘China: Xizang Prov., Cuona County [措那县], Lexiang [勒乡], alt. 2500m, 15.vii.2012, Wen-Xuan Bi leg.’.

Diagnosis. *Horaeomorphus biwenxuani* can be readily separated from all other congeners by its moderately large (2.78 mm) and elongate body, small pronotum lacking basal groove, with a row of three dorsal pits, subtriangular metatrochanter with distal edge produced into a short acute spine, and slender aedeagus with a complicated and strongly asymmetrical endophallus.

Description. Male. BL 2.78 mm; body (Fig. 8A) large, slightly convex, dark reddish-brown, legs and palpi slightly lighter. Head broadest at large, finely faceted and moderately convex eyes, HL 0.41 mm, HW 0.58 mm; tempora rounded, about as long as length of eye in dorsal view; vertex strongly transverse and weakly convex, with pair of small but distinct pits located near posterior margins of supra-antennal tubercles; frons weakly convex; supra-antennal tubercles strongly raised. Punctuation on vertex and frons sparse, small but distinct; setae moderately long, sparse. Antennae (Fig. 8B) short, AnL 1.18 mm, relative lengths of antennomeres: 0.9 : 1.0 : 1.6 : 1.3 : 1.1 : 1.0 : 0.8 : 0.9 : 1.0 : 1.1 : 1.7. Pronotum short, longer than wide, widest slightly behind anterior fourth, PL 0.77 mm, PWm 0.65 mm, PWb 0.53 mm; pronotal margin rounded near anterior 2/3, then nearly

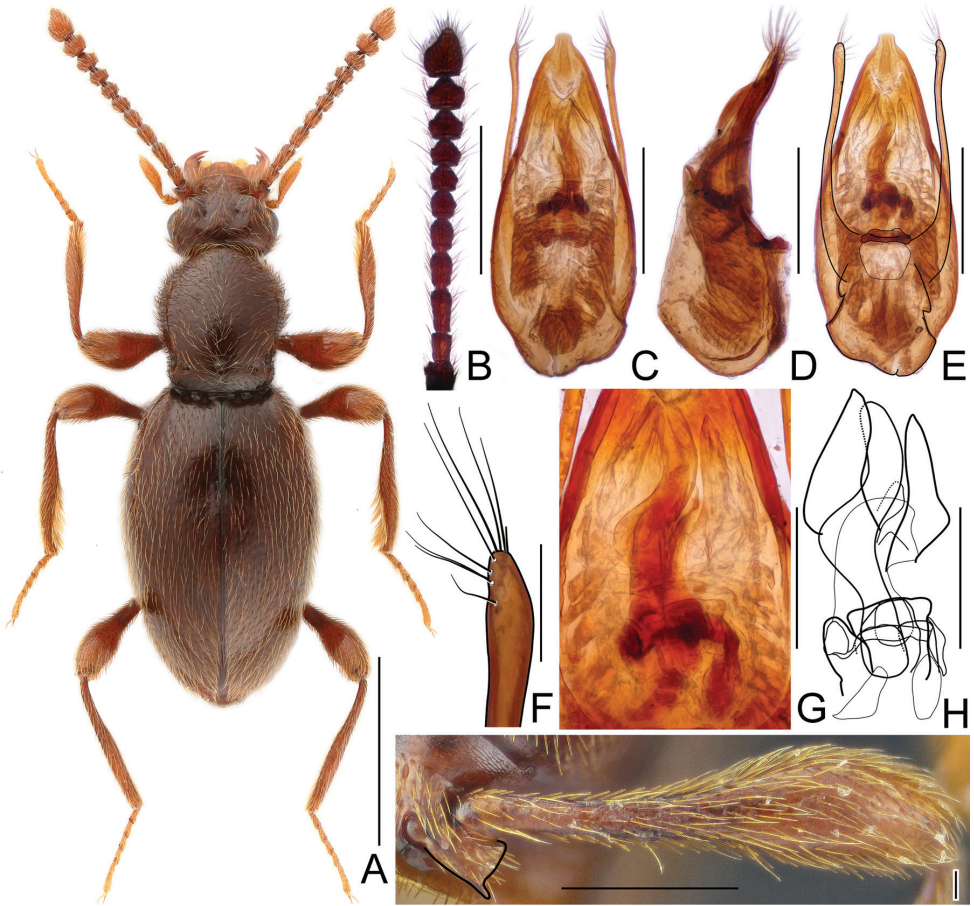


Figure 8. *Horaeomorphus biwenxuani* sp. n. **A** male, dorsal habitus **B** Left antenna of male, in dorsal view **C** Aedeagus, in ventral view **D** Same, in lateral view **E** Same, in dorsal view **F** Apical portion of paramere, enlarged **G** Endophallus, enlarged, in ventral view **H** Same, schematic **I** Left metatrochanter of male, in ventral view. Scale bars: 1 mm (**A**); 0.5 mm (**B**); 0.2 mm (**C, D, E**); 0.04 mm (**F**); 0.1 mm (**G, H**); 0.3 mm (**I**).

straight up to sub-basal constriction; base with row of three dorsal pits and pair of lateral impressions located in constriction. Punctuation on disc sparse and fine; dorsal surface glossy; setation moderately long. Elytra elongate, more convex than pronotum, distinctly impressed in middle at about anterior third; widest near anterior $2/5$, narrowing toward apices. EL 1.59 mm, EW 0.99 mm, EI 0.59. Humeral calli distinct. Punctures fine, more distinct than those on pronotum, sharply marked and separated by spaces 3–4× as wide as puncture diameters; setation moderately dense. Hindwings fully developed. Metatrochanter (Fig. 8I) short, subtriangular, distal edge produced into short acute spine. Aedeagus (Fig. 8C–E) slender, AeL 0.55 mm; endophallus (Fig. 8G–H) strongly asymmetrical, with curved axial component protruding from posterior complicated structure surrounded by two lateral Λ -shaped structures; parameres (Fig. 8F) very slender with broadened apical parts, slightly shorter than median lobe, each with nine apical and subapical setae.

Female. Unknown.

Comments. This new species with remarkably long legs has subtriangular metatrochanters in males, each with a sharp distal edge. This unique character can be found also in all four known Nepalese congeners: *H. obrus* Vít, 2004, *H. deharvengi* Vít, 2004, *H. himalayensis* Franz, 1974 and *H. nepalensis* Franz, 1973 (Franz 1974; Vít 2004), but so far has not been recorded in *Horaeomorphus* outside the Himalayas. However, a relatively small body (2.78 mm; among Himalayan species only *H. deharvengi* can be smaller than 3mm) and strongly asymmetrical endophallus are clearly different from characters of the Nepalese species. An asymmetrical endophallus also occurs in *H. deformatus* Jałoszyński, 2006 (W Malaysia: Kuala Terengganu), *H. pseudosabahensis* Jałoszyński, 2006 (E Malaysia: Sabah, Sarawak) and *H. minor* Jałoszyński, 2009 (the Philippines: Bukidnon, Mindanao), but its structure is distinctly different from that in *H. biwenzuani*.

Distribution. Western China: Xizang.

Etymology. This species is dedicated to Wen-Xuan Bi, who collected the type specimen.

***Horaeomorphus bujiayaoi* D.-Y. Zhou & S.-J. Zhang, sp. n.**

<http://zoobank.org/85FD7AC1-06A4-41EA-8F3D-B8A2E2FB221C>

Fig. 9

Type material (1 ♂). **Holotype:** CHINA: ♂, labeled ‘China: Guangxi Prov., Jinxiu County [金秀县], Mt.Lianhuashan [莲花山], alt. 1000–1150m, 30.vii.2011, Jia-Yao Hu leg.’.

Diagnosis. *Horaeomorphus bujiayaoi* can be readily separated from all other congeners by its moderately large (2.53 mm), short pronotum with five basal pits connected by a shallow groove, unmodified metatrochanters, median lobe of aedeagus with a blade-shaped, asymmetrical apex bent at an obtuse angle in relation to the long axis of aedeagus and asymmetrical parameres each with ten apical and subapical setae.

Description. Male. BL 2.53 mm; body (Fig. 9A) large, flattened, dark reddish-brown, legs and palpi slightly lighter. Head broadest at large, finely faceted, and moderately convex eyes, HL 0.36 mm, HW 0.50 mm; tempora rounded but not bent, about as long as length of eye in dorsal view; vertex strongly transverse and weakly convex, with pair of small but distinct pits located near posterior margins of supra-antennal tubercles; frons weakly convex; supra-antennal tubercles strongly raised. Punctuation on vertex and frons sparse, small but distinct; setae moderately long, sparse. Antennae (Fig. 9B) short, AnL 1.01 mm, relative lengths of antennomeres: 1.2 : 1.0 : 1.3 : 1.0 : 1.0 : 1.0 : 0.9 : 0.9 : 1.0 : 1.0 : 1.9. Pronotum inversely subtrapezoidal, flattened, longer than wide, widest near middle, PL 0.76 mm, PWm 0.61 mm, PWb 0.53 mm; anterior margin rounded; lateral margins rounded near anterior 2/3, then nearly straight up to sub-basal constriction; base with five pits connected by shallow groove. Punctuation on disc sparse and fine; dorsal surface glossy; setation moderately

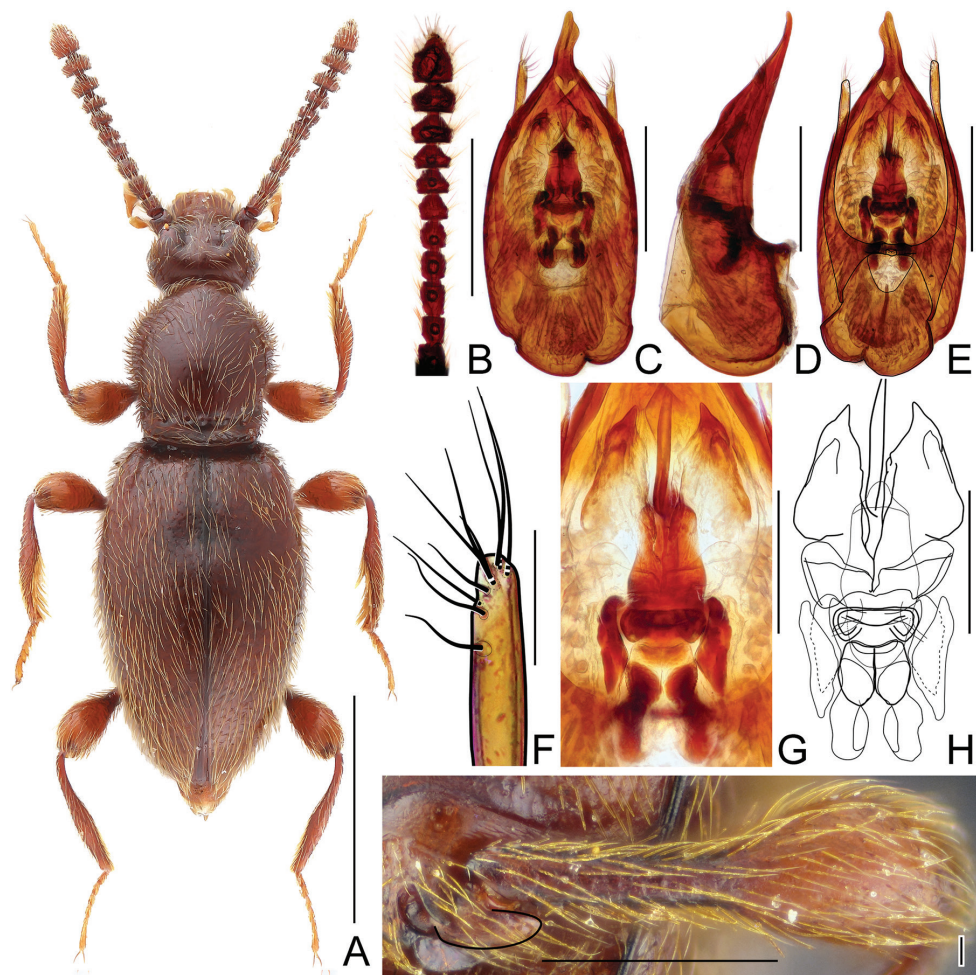


Figure 9. *Horaeomorphus hujiayaoi* sp. n. **A** male, dorsal habitus **B** Left antenna of male, in dorsal view **C** Aedeagus, in ventral view **D** Same, in lateral view **E** Same, in dorsal view **F** Apical portion of paramere, enlarged **G** Endophallus, enlarged, in ventral view **H** Same, schematic **I** Left metatrochanter of male, in ventral view. Scale bars: 1 mm (**A**); 0.5 mm (**B**); 0.2 mm (**C, D, E**); 0.04 mm (**F**); 0.1 mm (**G, H**); 0.3 mm (**I**).

long. Elytra elongate, more convex than pronotum, distinctly impressed in middle at about anterior third; widest slightly before middle, narrowing toward apices. EL 1.41 mm, EW 0.93 mm, EI 1.51. Humeral calli distinct. Punctures fine, more distinct than those on pronotum, especially on impressed area, sharply marked and separated by spaces 2–4× as wide as puncture diameters; setation moderately dense. Hindwings fully developed. Metatrochanter (Fig. 9I) unmodified. Mesotibiae slightly curved and with inner margin expanded near middle to form broad subtriangular tooth. Aedeagus (Fig. 9C–E) moderately elongate, median lobe with a strongly asymmetrical blade-shaped apex bent at obtuse angle in relation to long axis of aedeagus, AeL 0.59 mm; endophallus (Fig. 9G–H) with complicated system of variously sclerotized

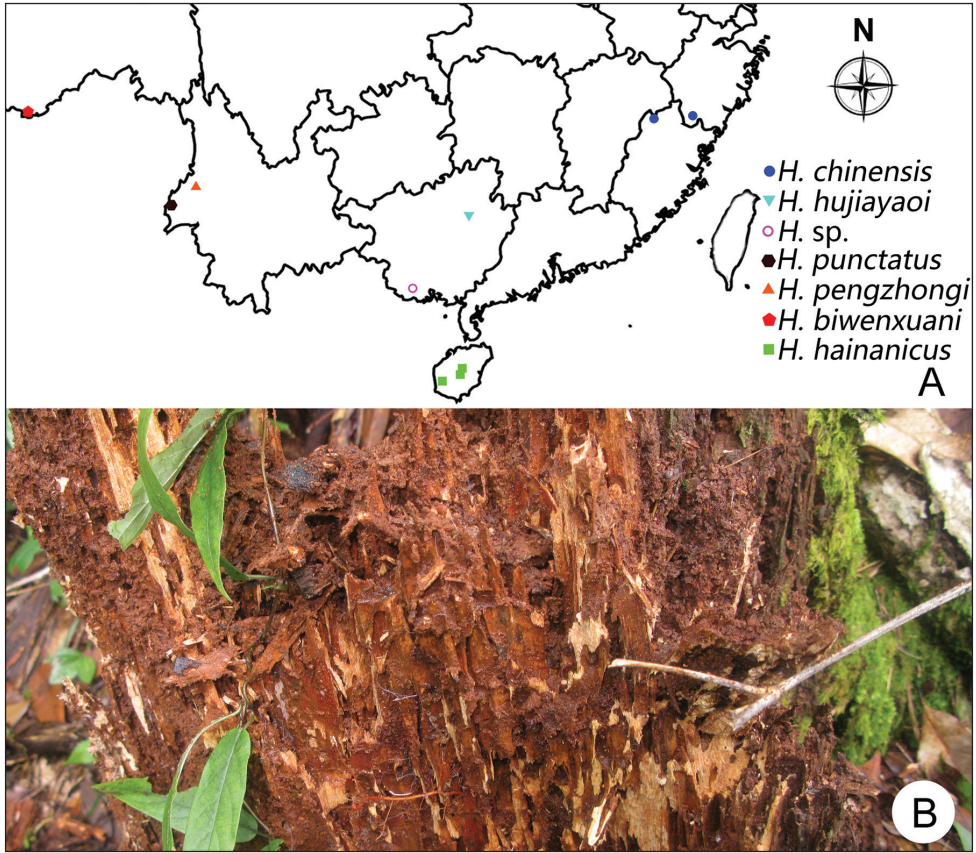


Figure 10. **A** Distribution of *Horaeomorphus* in mainland China **B** Habitat of *H. chinensis* at Guadun.

structures; parameres (Fig. 9F) asymmetrical, of unequal lengths, each with ten apical and subapical setae.

Female. Unknown.

Comments. This new species has the aedeagal median lobe with an apical blade-shaped projection bent to the left in ventral view and parameres of unequal lengths, characters shared with *H. obrus* Vít, 2004 (Nepal: Janakpur, Bagmati). *Horaeomorphus hujiayaoi* can be unambiguously separated from its Nepalese congener by the much smaller body (2.53 mm vs 4.3 mm in *H. obrus*) and different structures of the endophallus.

Distribution. Southern China: Guangxi.

Etymology. This species is dedicated to Jia-Yao Hu, who collected the type specimen.

Key to species of *Horaeomorphus* in mainland China

- 1 Basal pits on pronotum connected by a shallow and barely notable groove ...2
- Basal pits on pronotum connected by a deep and distinct groove..... 3

- 2 Pronotum broad, nearly circular; elytral punctures coarse, sharply marked and separated by spaces as wide as puncture diameters..... *H. punctatus* sp. n. (Yunnan: Yingjiang)
- Pronotum small; elytral punctation fine and sparse, elytra glossy *H. biwenxuani* sp. n. (Xizang: Cuona)
- 3 Pronotum with five basal pits..... 4
- Pronotum with three basal pits 5
- 4 Body slender and flattened, EI > 1.5 *H. bujiayaoi* sp. n. (Guangxi: Jinxiu)
- Body stout and convex, EI < 1.4 *H. sp.* (Guangxi: Shangsi)
- 5 BL < 2.5 mm; punctation of pronotal disc and elytra dense and coarse..... *H. chinensis* Franz, 1985 (N.Fujian, S.Fujian)
- BL > 2.5 mm; punctation of pronotal disc and elytra sparse and fine, surface glossy 6
- 6 Pronotum inversely subtrapezoidal, its lateral margins sharply bent at anterior third and strongly constricted near posterior fourth *H. hainanicus* sp.n. (Hainan)
- Pronotum oval, its anterior margin and lateral margins evenly rounded together *H. pengzhongi* sp.n. (Yunnan: Tengchong)

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Erratum

Zhou DY, Li LZ (2015) Discovery of the genus *Loeblites* Franz (Coleoptera: Staphylinidae: Scydmaeninae) in China, with description of a new species. Zootaxa 3986(3): 393–396. doi: 10.11646/zootaxa.3986.3.8

The generic name *Loeblites* occurs in the text in a miswriting as *Syndicus* (Page 394, figure caption, line 1).

A new species of Metopiinae (Hymenoptera, Ichneumonidae) parasitizing lepidopteran larvae in China

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Abstract

A new species of Metopiinae, *Trieces etuokensis* Sheng, **sp. n.**, is described and illustrated. Specimens were reared from two species of Lepidoptera: *Bazaria turensis* (Ragonot, 1887) (Pyralidae) from Balong, Dulan, Qinghai Province, and an unidentified psychid (Psychidae) from Mukainor, Etuoke, Inner Mongolia Autonomous Region, China. The new species is characterized by a yellow face and clypeus, fore and middle femora and hind tibia mainly black, antennae slightly longer than head and mesosoma combined, with 17 flagellomeres, occipital carina entirely absent, and the hind femur being compressed, 2.5 times as long as maximum width.

Keywords

Trieces, new species, *Bazaria turensis*, Pyralidae, Psychidae, China

Introduction

Trieces Townes, 1946 (Hymenoptera, Ichneumonidae, Metopiinae) comprises 68 species (Tolkanitz 2010, Yu et al. 2012), of which 13 are from the Eastern Palaearctic Region (Tolkanitz 2010). No species of *Trieces* have been reported from China to date. The genus is characterized mainly by areolet absent, mesopleural suture indistinct or

absent, lateral carina of first tergite weak or obsolescent, second tergite with complete median and sublateral longitudinal carinae, basal portion of sublateral longitudinal and median carinae of third tergite present, and epipleura of third to fifth tergites almost absent (Townes 1971, Gauld et al. 2002, Tolkanitz 1987, 2010).

The known hosts of *Triece* Townes mainly belong to the lepidopteran families Elachistidae (Bradley 1974), Geometridae (Petrice, et al. 2004), Tortricidae (Walley 1969) and Yponomeutidae (Gencer 2003, Yu et al. 2012).

Herein one new species of *Triece* is reported, reared from the pupae of *Bazaria turensis* (Pylalidae) and an unidentified psychid (Psychidae).

Materials and methods

Mature larvae of the host, *Bazaria turensis* (Ragonot, 1887) were collected on 28 August 2013 in a forest from where there had been an outbreak lasting at least three years, and brought to the laboratory. The forest is a shrubbery (Fig. 1) composed of *Nitraria tangerorum* Bobrov, *Lycium chinense* Miller var. *potaninii* (Pojarkova) A.M. Lu and *Kalidium foliatum* (Pallas) Moquin-Tandon, located in Dulan County, 36°09.65'N; 97°27.42'E, Qinghai Province. Mature larvae were maintained in a nylon cage at room temperature, and after pupating were stored individually in glass tubes (60 × 6 mm) with a piece of filter paper dipped in distilled water to maintain moisture and plugged tightly with absorbent cotton. After the emergence of moths and parasitoids was complete, remaining pupae were dissected to record their condition (i.e. status of moths, and parasitism).

Mature larvae of the psychid moth were collected in 16 September 2014 from a scrub where there had been an outbreak lasting at least fourth years, and brought to the laboratory. The scrub (Fig. 2) is composed of *Caragana intermedia* Kuang & H.C. Fu and located in Mukainor, 39°33.71'N; 108°40.24'E, Etuoke, Inner Mongolia Autonomous Region.

Images were taken using a Leica M205A Stereomicroscope with LAS Montage MultiFocus. Morphological terminology is mostly based on Gauld (1991).

Type specimens are deposited in the Insect Museum, General Station of Forest Pest Management (GSFPM), State Forestry Administration, People's Republic of China.

Results

Triece Townes, 1946

Triece Townes, 1946. Boletín de Entomología Venezolana, 5:60. Type-species: *Exochus texanus* Cresson.

Diagnosis. Interantennal process forming a triangular projection in front of antennal sockets. Anterior spur of mid tibia 0.25× to 0.65× length of posterior spur. Meso-



Figure 1. Habitat of *Trieces etuokensis* Sheng, sp. n. The shrubbery in Balong, Dulan County, Qinghai Province.



Figure 2. Habitat of *Trieces etuokensis* Sheng, sp. n. The scrub in Mukainor, Etuoke, Inner Mongolia Autonomous Region.

pleural suture indistinct or absent. Areolet absent. Lateral carina of first tergite weak or obsolescent. Second tergite with complete median and sublateral longitudinal carinae. Basal portion of sublateral longitudinal and median carinae of third tergite present. Epipleura of third to fifth tergites almost absent.

In Tolkanitz's (2010) key to the species of Palaearctic fauna, the new species can be inserted as follows:

- 14 (15) Head in dorsal view widened posteriorly behind eyes. Occipital carina obsolete. Metapleura as in Figs 3, 15. Face and clypeus of female reddish brown (Figs 5, 4). 2.7. (Male unknown). Russia (Amurskaya Province)....
..... *T. femoralis* Tolkanitz

- 15 (14) Head in dorsal view not widened posteriorly behind eyes, parallel-sided. Metapleura as in figs 3, 16. Occipital carina absent. Face, clypeus, and genae of female yellow **15(a, b)**
- 15a (15b) Antenna not longer than head and mesosoma combined; fore wing with vein 1cu-a slightly distal of 1-M, nearly interstitial; length of hind femur 2.2× its width; hind tibia reddish yellow; antennae reddish yellow. (Male unknown). Mongolia..... ***T. pumicatus* Tolkanitz**
- 15b (15a) Antenna longer than head and mesosoma combined; fore wing with vein 1cu-a distinctly distal of 1-M, distance between them 0.4× length of 1cu-a; hind femur distinctly compressed, 2.5× as long as maximum width; hind tibia mainly black; basal ventral profile of antennae red brown, basal dorsal profile blackish brown; apical portion brownish black. China (Inner Mongolia Autonomous Region) ***T. etuokensis* Sheng, sp. n.**

***Trieces etuokensis* Sheng, sp. n.**

<http://zoobank.org/23C8E597-4794-4069-B60C-665573C8159C>

Figs 3–12

Etymology. The specific name is derived from the holotype locality.

Material examined. Holotype female reared from pupa of unidentified psychid moth on 27 October 2014, CHINA: Mukainor, 1476m, Etuoke, Inner Mongolia Autonomous Region, Mao-Ling Sheng. Paratypes: 1 male, same data as holotype except 24 October 2014. 1 female reared from pupa of *Bazaria turensis* (Ragonot, 1887) on 2 October 2013, China: Balong, 2857m, Dulan, Qinghai Province, Mao-Ling Sheng.

Diagnosis. Malar space approximately as long as basal width of mandible. Ocular-ocellar line as long as diameter of posterior ocellus. Antenna slightly longer than head and mesosoma combined, with 17 flagellomeres. Occipital carina entirely absent. Metapleuron shiny, impunctate, lower posterior portion with distinct wrinkles. Hind femur compressed, 2.5× as long as maximum width. Face and clypeus yellow. Fore and middle femora and hind tibia mainly black.

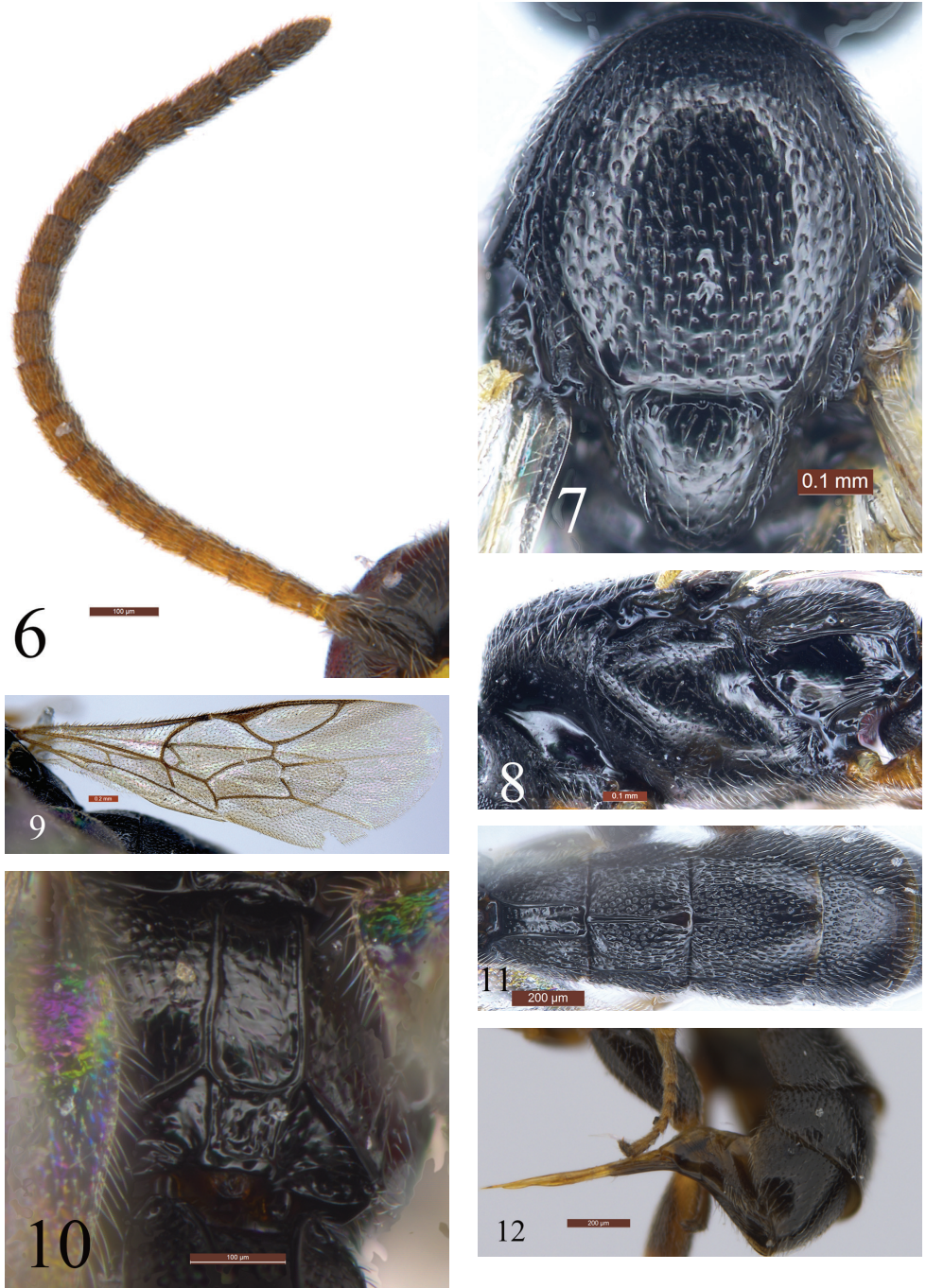
Description. Female. Body length approximately 2.8 mm. Fore wing length approximately 2.2 mm.

Head. Inner margins of eyes distinctly convergent downwards. Face (Fig. 4) with dense fine punctures, distance between punctures 0.2–0.5× diameter of puncture. Clypeus with denser punctures than that of face, distance between punctures approximately 0.2× diameter of puncture, apical portion slightly concave; apical margin almost truncate. Mandible small, weakly narrowed toward apex; upper tooth distinctly longer than lower tooth. Malar area flat, with fine punctures. Malar space approximately as long as basal width of mandible. Gena in dorsal view approximately as long as width of eye, almost smooth, with sparse, indistinct fine punctures, scarcely convergent posteriorly. Vertex (Fig. 5) and frons almost shiny, with indistinct fine punctures. Postocellar line 1.2× as long as ocular-ocellar line. Ocular-ocellar line approximately as long as



Figures 3–5 *Triecces etuokensis* Sheng, sp. n. Holotype. Female **3** Habitus, lateral view **4** Head, anterior view **5** Head, dorsal view. Scale bars: 0.5 mm (**3**); 0.1 mm (**4, 5**).

diameter of posterior ocellus. Upper portion of frons slightly convex, lower portion slightly concave. Antenna (Fig. 6) slightly longer than head and mesosoma combined, with 17 flagellomeres; each flagellomere longer than wide. First flagellomere 2.2× as long as maximum width, 1.1× as long as third flagellomere. Occipital carina absent.



Figures 6–12. *Trieces etuokensis* Sheng, sp. n. Holotype. Female **6** Antenna **7** Mesoscutum and scutellum **8** Mesosoma, lateral view **9** Fore wing **10** Propodeum **11** Tergites 1–4, dorsal view **12** Apical portion of metasoma, lateral view. Scale bars: 0.1 mm (**6, 7, 8, 10**); 0.2 mm (**9, 11, 12**)

Mesosoma. Lateral concavity of pronotum smooth, shiny, upper-posterior portion slightly rough, with dense shallow fine punctures. Epomia indistinct. Mesoscutum (Fig. 7) smooth, shiny, anterior portion slightly convex, posterior flat; with dense distinct punctures, distance between punctures 0.2–2.0× their diameter. Notaulus absent. Scutellum almost flat, shiny, with sparse, indistinct, fine punctures; lateral carina reaching apex. Postscutellum so short it resembles a transverse carina. Mesopleuron (Fig. 8) with sparse fine punctures. Speculum with fine indistinct punctures. Mesopleural fovea vestigial. Upper end of epicnemial carina reaching anterior margin of mesopleuron, at dorsal 0.75 of posterior margin of pronotum. Metapleuron almost flat, shiny, postero-dorsal portion with few hairs, lower posterior portion with distinct wrinkles. Juxtacoxal carina strong. Wings (Fig. 9) slightly infusate. Fore wing with vein 1cu-a strongly inclivous, distal to 1-M by about 0.4× length of 1cu-a. 2m-cu straight, distinctly inclivous, distal to 2rs-m by about 1.4× length of 2rs-m. Hind wing vein 1-cu 2.0× as long as cu-a. Hind femur compressed, 2.5× as long as maximum width. Hind tibia gradually widened apically. Posterior spur of hind tibia approximately 2.75× as long as anterior spur. Ratio of length of hind tarsomeres 1:2:3:4:5 is 2.8:1.2:1.0:0.8:1.6. Propodeum (Fig. 10) with strong apical transverse and complete longitudinal carinae. Pleural areas with dense, distinct, fine punctures. Area petiolaris with longitudinal wrinkles. Remainder of propodeum smooth, shiny, with indistinct fine punctures. Propodeal spiracle small, circular.

Metasoma (Figs 11, 12). First tergite approximately 0.75× as long as apical width, with dense punctures; median dorsal, dorsolateral, ventrolateral and sublateral longitudinal carinae complete; apical half with distinct median longitudinal carina. Second tergite (Fig. 11) 1.27× as long as apical width, densely punctate, median and sublateral carinae complete. Third tergite 0.78× as long as apical width; basal 0.7 with dense punctures, apical 0.3 with sparser punctures and smoother than basal 0.7; basal 0.4 with median longitudinal carina; basal 0.3 with lateral longitudinal carinae. Basal 0.6 of fourth tergite densely punctate, apical 0.4 shiny, gradually impunctate. Basal 0.4 of fifth tergite with dense punctures, apical 0.6 gradually impunctate. Ovipositor (Fig. 12) tapered from base to apex, with a large, shallow notch.

Color (Fig. 3). Black, except as follows. Face (Fig. 4) except upper median light brown spot, malar area and clypeus yellow. Maxillary and labial palpi yellow brown. Anterior profile of pedicel dark brown; basal ventral profile of antenna red-brown, basal dorsal profile darkish brown; apical portion brownish black. Anterior and posterior profiles of fore femur, tibia and tarsus, basal and apical portions of mid tibia, mid tarsus, all trochanters more or less, tegula brown to dark brown. Pterostigma (Fig. 9) blackish. Wing veins dark brown.

Male. Body length approximately 3.1 mm. Fore wing length approximately 2.5 mm. Antenna with 22 flagellomeres. Very similar to the female, except with hind first tarsomere yellow, apical portion pale brown yellow.

Hosts. One female was reared from pupa of *Bazaria turensis* (Ragonot, 1887) (Lepidoptera: Pyralidae). One female and one male were reared from unidentified species of Psychidae (Lepidoptera) collected as mature larvae but details of development and emergence unknown.

Host plants. *Caragana intermedia* Kuang & H.C. Fu (Leguminosae), *Nitraria tangutorum* Bobrov (Zygophyllaceae), *Kalidium foliatum* (Pallas) Moquin-Tandon (Amaranthaceae).

Remarks. This new species is similar to *T. pumicatus* Tolkanitz, 2010 and can be distinguished from the latter by the following combination of characters: antenna slightly longer than head and mesosoma combined, with 17 flagellomeres (female); fore wing with vein 1cu-a distinctly distal of 1-M, distance between them 0.4× length of 1cu-a; hind femur compressed, 2.5× as long as maximum width; lateral longitudinal carinae of tergite 3 distinct on anterior 0.3; fore and middle femora, hind tibia mainly black; basal ventral profile of antennae red brown, basal dorsal profile darkish brown; apical portion brownish black. The same characters for *Trieces pumicatus* Tolkanitz are as follows: antenna not longer than head and mesosoma combined, with 20 flagellomeres (female); fore wing with vein 1cu-a slightly distal of 1-M, nearly interstitial; length of hind femur 2.2× its width; lateral longitudinal carinae of tergite 3 vanishing behind its middle; fore and mid legs, hind tibia reddish yellow, fore and mid femora slightly darkened on outer side; antenna reddish yellow.

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Revision of the Malagasy *Camponotus edmondi* species group (Hymenoptera, Formicidae, Formicinae): integrating qualitative morphology and multivariate morphometric analysis

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Abstract

The Malagasy *Camponotus edmondi* species group is revised based on both qualitative morphological traits and multivariate analysis of continuous morphometric data. To minimize the effect of the scaling properties of diverse traits due to worker caste polymorphism, and to achieve the desired near-linearity of data, morphometric analyses were done only on minor workers. The majority of traits exhibit broken scaling on head size, dividing *Camponotus* workers into two discrete subcastes, minors and majors. This broken scaling prevents the application of algorithms that uses linear combination of data to the entire dataset, hence only minor workers were analyzed statistically. The elimination of major workers resulted in linearity and the data meet required assumptions. However, morphometric ratios for the subsets of minor and major workers were used in species descriptions and redefinitions. Prior species hypotheses and the goodness of clusters were tested on raw data by confirmatory linear discriminant analysis. Due to the small sample size available for some species, a factor known to reduce statistical reliability, hypotheses generated by exploratory analyses were tested with extreme care and species delimitations were inferred via the combined evidence of both qualitative (morphology and biology) and quantitative data. Altogether, fifteen species are recognized, of which 11 are new to science: *C. alamaina* sp. n., *C. androy* sp. n., *C. bevohitra* sp. n., *C. galoko* sp. n., *C. matsilo* sp. n., *C. mifaka* sp. n., *C. orombe* sp. n., *C. tafo* sp. n., *C. tratra* sp. n., *C. varatra* sp. n., and *C. zavo* sp. n. Four species are redescribed: *C. echinoploides* Forel, *C. edmondi* André, *C. ethicus*

Forel, and *C. robustus* Roger. *Camponotus edmondi ernesti* Forel, **syn. n.** is synonymized under *C. edmondi*. This revision also includes an identification key to species for both minor and major castes, information on geographic distribution and biology, taxonomic discussions, and descriptions of intraspecific variation. Traditional taxonomy and multivariate morphometric analysis are independent sources of information which, in combination, allow more precise species delimitation. Moreover, quantitative characters included in identification keys improve accuracy of determination in difficult cases.

Keywords

Allometry, *Camponotus*, exploratory data analysis, Madagascar, Malagasy region, multivariate statistics, morphometrics, taxonomy

Introduction

The ant genus *Camponotus* Mayr, 1861 is one of the most species-rich genera in the world, in the ranks of *Pheidole* (1002 species), *Strumigenys* (838 species), and *Tetramorium* (567 species) (Bolton 2015). It currently includes 1589 valid extant species and subspecies (Bolton 2015) distributed across the tropical and subtropical regions as well as the temperate zones (Bolton 1995). In the southwestern Indian Ocean region, 78 species and subspecies have been described in publications (e.g.: Roger 1863; André 1887; Forel 1891, 1897, 1914; Emery 1896, 1920; Santschi 1921; Wheeler 1922; Donisthorpe 1949); since 1949, no additional species have been described. Over the past two decades, however, the number of *Camponotus* samples has greatly increased thanks to recent intensive research surveys of ants in Madagascar and surrounding islands. A preliminary study (Fisher 1997) showed that *Camponotus* is one of the most diverse genera in the region. Its members occupy a wide variety of microhabitats across different terrestrial ecosystems in Madagascar and neighboring islands. This high diversity suggests that the genus is in great need of comprehensive taxonomic revision to improve the understanding and management of the region's biodiversity.

As stated by Brown (1973), the subgeneric classifications of *Camponotus* made by earlier ant taxonomists (e.g.: Emery 1896, 1920, 1925; Forel 1914; Santschi 1921; Wheeler 1922) were not useful because numerous unrelated taxa had been combined within many of these subgenera. An initial morphology-based study of the Malagasy *Camponotus* subgenera supported this view. For instance, Santschi (1921) created the subgenus *Myrmepinotus* Santschi for one species from Madagascar. In 1925, Emery transferred into this subgenus three other Malagasy species, all of which had previously been moved from three of the following subgenera: *Orthonotomyrmex* Ashmead (1906), *Myrmentoma* Forel (1912), *Myrmobrachys* Forel (1912), and *Myrmisolepis* Santschi (1921). These four species, when combined with the other new species included in the present study, may constitute unrelated groups of taxa in the subgenus *Myrmepinotus*. A few species might be more closely related to the species within *Myrmisolepis* of the afrotropical and Ethiopian regions than those of the Malagasy *Myrmepinotus*. To avoid following an unsupported subgeneric classification, we instead use a species group classification. The present study undertakes

a species-level taxonomic revision of the *Camponotus edmondi* species group of the Malagasy region.

More in-depth comparative taxonomic works, incorporating different sources of data to identify and recognize species, have been initiated in the region (e.g.: Fisher and Smith 2008; Yoshimura and Fisher 2012; Blaimer and Fisher 2013; Hita-Garcia and Fisher 2014; Rakotonirina and Fisher 2014). The present revision combines qualitative differences in morphological characters and multivariate statistical methods of recording morphometric measurement data to delimit and recognize species. Multivariate morphometric analysis combines (1) formation of species hypothesis by exploratory data analysis with (2) hypothesis testing through confirmative linear discriminant analysis (LDA). Not only has it proved efficient as a tool for assessing differences between similar ant taxa, but it also has helped unravel the cryptic diversity in different groups of ants using primary data on size measurements (Csősz et al. 2014; Seifert et al. 2014a, 2014b). The statistical investigation of morphological character variation among species, as is found in highly diverse genera like *Camponotus*, will provide independent information that helps assign individual specimens to a species, facilitate species recognition, and improve precision of species delimitation.

The *Camponotus edmondi* species group can be distinguished by the combination of the following characters: dorsolateral margin of propodeum marginate or extending into a sharp ridge, propodeal declivity usually concave, anterolateral corner of pronotum most often marginate, forecoxa larger than the width of mesopleuron, and usually propodeal dorsum abruptly sloping down to the insertion of the petiole. Our preliminary examinations conducted on the *edmondi* species group indicated that the group comprises a great number of morphologically similar species with highly polymorphic worker castes that are difficult to separate based on general qualitative traits alone. Thus, the *edmondi* species group is ideal for testing the value of combining qualitative morphology and morphometric methods. The current study tested whether multivariate morphometric analysis could clearly resolve species in the *edmondi* species group.

In this paper, 15 species of the *edmondi* species group are recognized on the basis of combined evidence of multivariate analyses of quantitative morphology and qualitative morphological data of worker caste. The use of multivariate morphometric analysis allowed the recognition of masked morphological traits that are useful in species delimitation. The application of conventional, morphology-based taxonomy in combination with multivariate morphometric study will reinforce the placement of taxonomic works as a basis for understanding and sustainably managing biodiversity.

Materials and methods

Abbreviation of depositories

CASC	California Academy of Sciences, San Francisco, CA, USA.
MHNG	Musée d'Histoire Naturelle, Geneva, Switzerland.
MNHN	Musée National d'Histoire Naturelle, Paris, France.

MSNG	Museo Civico di Storia Naturale “Giacomo Doria”, Genoa, Italy.
NHMB	Naturhistorisches Museum, Basel, Switzerland.
PBZT	Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar.
PSWC	P.S. Ward Collection, University of California at Davis, CA, USA
ZMHB	Museum für Naturkunde der Humboldt Universität, Berlin, Germany.

Materials

The present contribution includes all specimens of the *Camponotus edmondi* species group collected from the arthropod survey project conducted in Madagascar and surrounding islands in the Malagasy region by B.L. Fisher and the members of the Madagascar Biodiversity Center from 1992 through 2015. All pinned specimens examined in this study are available on the web portal AntWeb (<http://www.antweb.org>) and can be accessed using the unique identifying specimen code (e.g. CASENT0104547) assigned to specimen for each pin. Images are linked to their specimens via their unique specimen code, which is affixed to each pin (CASENT0002660).

A total of 292 specimens from 168 collecting events has been measured in this study (see Suppl. material 1). Due to the fact that samples from a single collecting event might not represent nest samples (colonies), but specimens mounted on one pin do, collection codes (BLF, MG, or ANTC numbers) were used as grouping factors in NC-clustering.

Methods

Morphological examinations were conducted to study patterns of morphological discontinuities and phenotypic similarity using a Leica MZ12 binocular microscope.

Digital color images of lateral and dorsal views of the entire body and full-face views of the head of each species were created using a JVC KY-75 or a Leica DFC450 digital camera with a Leica Z16 APO microscope and LAS (v3.8) software. These images are also available online on AntWeb (www.antweb.org) and are accessible using the unique identifying specimen code.

Distribution maps for all species were generated by importing specimen distribution records into the Diva GIS program (Hijmans et al. 2011). Older and type specimens with inadequate geographic coordinates were excluded from these maps.

Article 74 in the ICZN’s code states that the designation of a lectotype from syntype specimens which directly match the original description of a named species is necessary to stabilize the nomenclature. As a consequence, the phrase “present designation” is used to indicate a lectotype. New species epithets used in the present work are arbitrary combinations of letters and thus invariant, as are genitive nouns or nominative singular nouns in apposition.

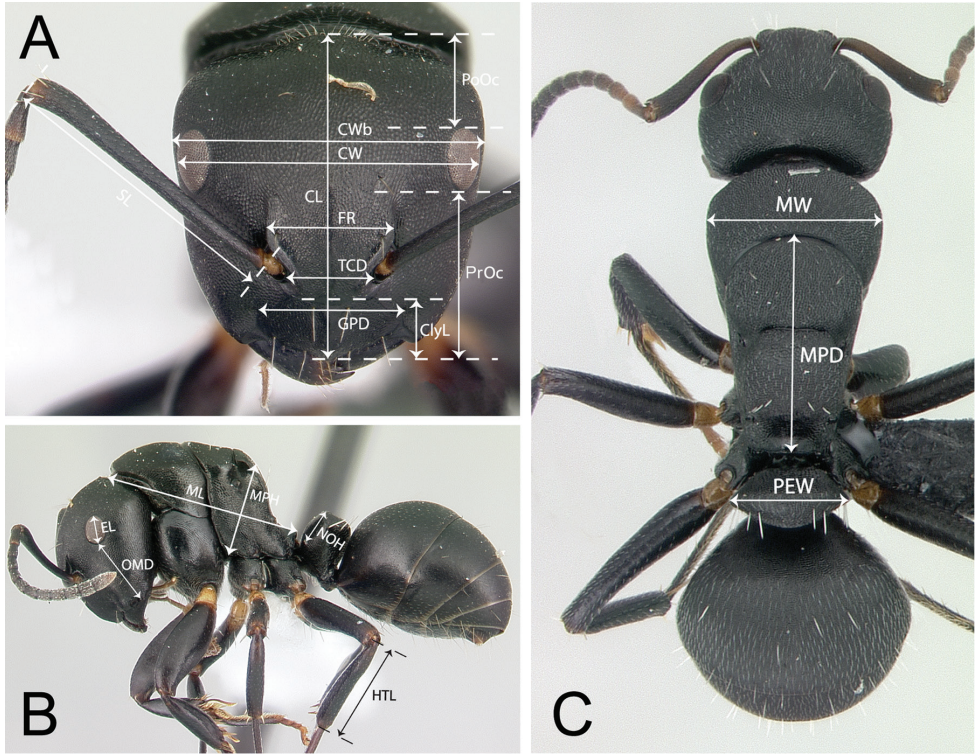


Figure 1. Illustrations of measurements for *edmondi* species group. **A** Head in full-face view **B** Body in lateral view **C** Body in dorsal view. See text for abbreviations.

Measurements

Morphometric measurements were taken using a Leica MZ 12 stereomicroscope equipped with a cross-scaled ocular micrometer and an orthogonal pair of micrometers. All measurements and indices are presented as arithmetic means and ranges are shown as minimum and maximum values in parentheses. Body size dimensions are expressed in millimeters (mm) and all values were rounded to the second decimal place.

The following 19 morphometric measurements were taken (Figure 1):

- 1) Maximum cephalic length (CL): The maximum midline length of the head in full-face view, measured from the midpoint of the posterior margin to the midpoint of the anterior margin of the clypeus.
- 2) Maximum cephalic width (CW): The maximum distance between the lateral margins of the compound eyes in full-face view.
- 3) Maximum head capsule width (CWb): The maximum width of the head excluding the compound eyes.

- 4) Postocular distance (PoOc): The distance between the posteromedian margin of the head and the level of the posterior margin of the compound eyes measured along the midline of the head in full-face view.
- 5) Preocular distance (PrOc): The distance between the anteromedian margin of the clypeus and the level of the anterior margin of the compound eyes measured along the midline of the head in full-face view.
- 6) Clypeal length (ClyL): the maximum midline length of the clypeus measured from the posterior margin to the anterior margin in frontal view, in which the anterior and posterior clypeal margins are aligned to same focus. Median concavity on either or both margins reduces the length of the clypeus.
- 7) Frontal carina distance (FR): The maximum distance between the frontal carinae.
- 8) Torular carina distance (TCD): The minimum distance between the torular arches that surround the antennal insertion.
- 9) Maximum tentorial pit distance (GPD): The greatest distance between the centers of the fossae located at or very close to the posterolateral margin of the clypeus.
- 10) Scape length (SL): Straight line length of the first antennal segment excluding the basal condyle.
- 11) Eye length (EL): Maximum diameter of the compound eye.
- 12) Oculo-mandibular distance (OMD): The smallest distance between the anterior margin of the compound eye and the mandibular insertion to the head.
- 13) Mesosoma width (MW): Maximum width of the pronotum in dorsal view, which in the *C. edmondi* group is also the maximum mesosomal width (hence “mesosoma width”).
- 14) Mesosoma length (ML): The longest median anatomical line that connects the posteriormost point of the propodeal lobe with the anteriormost point of pronotal collar; preferentially measured in lateral view, but if one of the reference points is not visible dorsal view may help.
- 15) Mesothoracico-propodeal distance (MPD): With the promesonotal suture and the anterior petiolar foramen margin in the same plane of focus in dorsal view, the maximum midline length between the promesonotal suture and the posteriormost point of the propodeal process dorsal to the petiolar insertion.
- 16) Mesothoracico-propodeal height (MPH): With the mesosoma in lateral view, the length of the line between the anteroventral corner of the mesopleuron, dorsal to the insertion of the mesocoxa, and the dorsalmost point of the propodeum that is crossed by the measured line. The line is perpendicular to the diagonal line of the mesosoma that connects the anteriormost point of the pronotal shield and the posteriormost point of the propodeal process dorsal to the petiolar insertion, in lateral view.
- 17) Maximum hind tibia length (HTL): Straight line length of the hind tibia measured from the constriction immediately before its proximal insertion to its distalmost point, excluding the bristles or spines.
- 18) Petiolar width (PEW): The maximum width of the petiole in dorsal view.
- 19) Petiolar node height (NOH): The maximum distance between the petiolar spiracle and the dorsalmost point of the petiolar node.
- 20) Cephalic size (CS): the arithmetic mean of CL and CWb.

Morphometric data analyses

The datasets

The datasets assessed in the present study consist of (1) the primary measurement data of the 19 morphological characters, which represent the general size of each individual specimen measured (See Table of basic measurements of the specimens in the Suppl. material 1), and (2) the ratios of measurements involving the comparison of one measured trait (variable) over another (CS) to show the body proportions or shape of the specimen (Table 1).

In the present taxonomic revision, multivariate statistical analysis of morphometric data was run to obtain information considered helpful in detecting species and to facilitate species delimitation decisions.

Data preparation

Nest-centroid clustering (NC-clustering) and linear discriminant analysis (LDA) do not require special data preparation, however, within-class linearity of correlation (linear scaling) for each trait is assumed.

Static trait allometry of variables for workers in the *edmondi* species group has been tested via pair-wise visual inspection of matrix scatterplots. Our results indicate the presence of broken, or sigmoid scaling, i.e. shifts in scaling resulting with different intercepts, steepness, or both, illustrated for CL for 12 of 19 characters, splitting workers into two remarkable subsets, minors and majors (see Figure 2). The broken scaling of traits and the different allometric properties of the subcastes prevented us from analyzing the two groups together. We selected minor workers for morphometric analyses, because these are more abundant in the material examined; 209 out of the 292 workers were minors based on scaling schemes and only 83 proved to be majors.

The Shapiro-Wilk W test was used to test for within-class normality after major workers were eliminated. No characters showed significant deviation from the normal distribution according to the W statistic, so each character can be considered normally distributed. In our statistical analyses we follow Csősz and Fisher (2015).

Generation of species hypotheses by exploratory data analyses

The classification hypothesis of samples, which is represented by the number of estimated clusters, was built using the exploratory analysis of continuous morphometric data technique. This technique uses an NC-clustering algorithm (Seifert et al. 2014a) that searches for discontinuities in the data and assembles all samples into clusters so that samples within clusters are similar and contrast with those in other clusters. This grouping technique transforms morphological differences

Table 1. Ratios of morphometric data for minors and majors of the species. Upper line: mean of ratios \pm standard deviation, lower line in square brackets: minimum and maximum values. Note: if only two specimens were available then minimum, maximum values are given.

Species	Worker castes	CS	CWb/CL	CW/CL	PoOC/CL	ClyL/CL	FR/CS	TCD/CS	GPD/CS	SL/CS
<i>alamaina</i>	minors (n = 52)	1.28 \pm 0.1 [0.99, 1.6]	0.83 \pm 0 [0.79, 0.91]	0.93 \pm 0 [0.89, 0.97]	0.23 \pm 0 [0.2, 0.27]	0.55 \pm 0 [0.53, 0.58]	0.3 \pm 0 [0.27, 0.33]	0.29 \pm 0 [0.27, 0.31]	0.46 \pm 0 [0.39, 0.5]	1.1 \pm 0 [1.02, 1.18]
	majors (n = 24)	1.98 \pm 0.2 [1.65, 2.22]	0.95 \pm 0 [0.87, 1]	0.91 \pm 0 [0.85, 0.95]	0.26 \pm 0 [0.24, 0.28]	0.52 \pm 0 [0.49, 0.55]	0.33 \pm 0 [0.31, 0.36]	0.26 \pm 0 [0.25, 0.28]	0.37 \pm 0 [0.35, 0.4]	0.75 \pm 0.1 [0.69, 0.89]
<i>androy</i>	minors (n = 11)	0.96 \pm 0.1 [0.87, 1.03]	0.8 \pm 0 [0.78, 0.83]	0.92 \pm 0 [0.9, 0.96]	0.2 \pm 0 [0.19, 0.22]	0.54 \pm 0 [0.53, 0.55]	0.31 \pm 0 [0.29, 0.32]	0.28 \pm 0 [0.27, 0.29]	0.48 \pm 0 [0.46, 0.51]	1.03 \pm 0 [0.97, 1.1]
	majors (n = 6)	1.67 \pm 0.1 [1.58, 1.74]	0.81 \pm 0 [0.8, 0.83]	0.8 \pm 0 [0.79, 0.81]	0.25 \pm 0 [0.24, 0.26]	0.57 \pm 0 [0.56, 0.58]	0.4 \pm 0 [0.38, 0.41]	0.28 \pm 0 [0.27, 0.29]	0.34 \pm 0 [0.32, 0.35]	0.69 \pm 0 [0.67, 0.71]
<i>betohitra</i>	minors (n = 9)	1.14 \pm 0.2 [0.99, 1.5]	0.81 \pm 0 [0.78, 0.85]	0.89 \pm 0 [0.82, 0.94]	0.2 \pm 0 [0.18, 0.21]	0.59 \pm 0 [0.57, 0.62]	0.34 \pm 0 [0.31, 0.38]	0.31 \pm 0 [0.3, 0.32]	0.48 \pm 0 [0.42, 0.51]	1.01 \pm 0.1 [0.84, 1.11]
	majors (n = 6)	1.48 \pm 0.1 [1.34, 1.59]	0.8 \pm 0 [0.79, 0.81]	0.83 \pm 0 [0.81, 0.86]	0.22 \pm 0 [0.21, 0.23]	0.6 \pm 0 [0.58, 0.63]	0.37 \pm 0 [0.35, 0.4]	0.29 \pm 0 [0.28, 0.31]	0.42 \pm 0 [0.4, 0.45]	0.81 \pm 0.1 [0.75, 0.91]
<i>echinoploides</i>	minors (n = 20)	1.51 \pm 0.1 [1.24, 1.67]	0.96 \pm 0 [0.94, 1]	0.96 \pm 0 [0.93, 1]	0.25 \pm 0 [0.23, 0.27]	0.56 \pm 0 [0.52, 0.6]	0.29 \pm 0 [0.26, 0.33]	0.27 \pm 0 [0.26, 0.29]	0.46 \pm 0 [0.43, 0.48]	0.95 \pm 0 [0.9, 1.05]
	majors (n = 2)	2.48, 2.67 [1.01, 1.02]	0.9 \pm 0 [0.87, 0.93]	0.88 \pm 0 [0.79, 0.9]	0.23 \pm 0 [0.21, 0.25]	0.55 \pm 0 [0.51, 0.51]	0.31 \pm 0 [0.28, 0.34]	0.39 \pm 0 [0.37, 0.41]	0.28 \pm 0 [0.27, 0.29]	0.44 \pm 0 [0.39, 0.46]
<i>edmondi</i>	minors (n = 15)	1.12, 1.47 [1.87, 0.1]	0.97 \pm 0 [0.94, 1]	0.89 \pm 0 [0.85, 0.92]	0.28 \pm 0 [0.27, 0.29]	0.51 \pm 0 [0.5, 0.53]	0.33 \pm 0 [0.32, 0.34]	0.39 \pm 0 [0.38, 0.4]	0.37 \pm 0 [0.35, 0.39]	0.72 \pm 0 [0.7, 0.75]
	majors (n = 8)	1.79, 1.95 [1.92, 2.58]	0.92 \pm 0 [0.87, 0.99]	0.84 \pm 0 [0.82, 0.86]	0.24 \pm 0 [0.21, 0.25]	0.57 \pm 0 [0.54, 0.59]	0.31 \pm 0 [0.29, 0.33]	0.25 \pm 0 [0.24, 0.26]	0.41 \pm 0 [0.37, 0.44]	1.14 \pm 0.1 [1, 1.26]
<i>ethicus</i>	minors (n = 11)	1.15 \pm 0.1 [0.93, 1.34]	0.97 \pm 0 [0.94, 0.99]	0.98 \pm 0 [0.96, 1.01]	0.23 \pm 0 [0.2, 0.25]	0.55 \pm 0 [0.53, 0.57]	0.29 \pm 0 [0.27, 0.31]	0.29 \pm 0 [0.28, 0.31]	0.46 \pm 0 [0.43, 0.49]	0.9 \pm 0.1 [0.81, 0.98]
	majors (unknown)	1.57 \pm 0.2 [1.32, 1.72]	1 \pm 0 [0.96, 1.03]	0.93 \pm 0 [0.9, 0.95]	0.3 \pm 0 [0.27, 0.31]	0.52 \pm 0 [0.5, 0.55]	0.31 \pm 0 [0.3, 0.32]	0.28 \pm 0 [0.27, 0.29]	0.4 \pm 0 [0.38, 0.42]	0.7 \pm 0 [0.65, 0.76]

Species	Worker castes	CS	CWb/CL	CW/CL	PoOC/CL	PrOo/CL	ClyL/CL	FR/CS	TCD/CS	GPD/CS	SL/CS
<i>matsilo</i>	minors (n = 11)	1.11 ± 0.1	0.9 ± 0	0.93 ± 0	0.21 ± 0	0.6 ± 0	0.32 ± 0	0.45 ± 0	0.31 ± 0	0.47 ± 0	0.91 ± 0
		[1, 1.33]	[0.88, 0.94]	[0.91, 0.95]	[0.18, 0.23]	[0.57, 0.62]	[0.29, 0.33]	[0.43, 0.47]	[0.3, 0.32]	[0.44, 0.49]	[0.87, 0.94]
	majors (n = 2)	[2.21, 2.29]	[0.96, 0.96]	[0.87, 0.88]	[0.28, 0.29]	[0.55, 0.55]	[0.34, 0.36]	[0.43, 0.43]	[0.3, 0.3]	[0.35, 0.36]	[0.59, 0.6]
<i>mifaka</i>	minors (n = 13)	1.15 ± 0.1	0.93 ± 0	0.92 ± 0	0.23 ± 0	0.56 ± 0	0.32 ± 0	0.41 ± 0	0.29 ± 0	0.47 ± 0	0.97 ± 0
		[1.05, 1.23]	[0.9, 0.95]	[0.9, 0.95]	[0.21, 0.25]	[0.54, 0.58]	[0.29, 0.34]	[0.4, 0.43]	[0.28, 0.31]	[0.45, 0.48]	[0.92, 1.02]
	majors (unknown)										
<i>oronobe</i>	minors (n = 2)	0.97, 1.06	0.88, 0.88	0.93, 0.94	0.23, 0.24	0.54, 0.56	0.3, 0.3	0.4, 0.41	0.28, 0.29	0.48, 0.49	1, 1.03
		1.82	0.98	0.91	0.3	0.5	0.32	0.4	0.28	0.38	0.67
	majors (n = 1)										
<i>robustus</i>	minors (n = 9)	2.21 ± 0.2	0.94 ± 0	0.86 ± 0	0.24 ± 0	0.57 ± 0	0.31 ± 0	0.35 ± 0	0.25 ± 0	0.44 ± 0	0.96 ± 0
		[1.88, 2.64]	[0.91, 0.98]	[0.84, 0.88]	[0.21, 0.27]	[0.54, 0.59]	[0.29, 0.33]	[0.34, 0.37]	[0.25, 0.26]	[0.43, 0.45]	[0.91, 1.02]
	majors (n = 9)	3.49 ± 0.3	1.01 ± 0	0.83 ± 0	0.28 ± 0	0.54 ± 0	0.33 ± 0	0.33 ± 0	0.23 ± 0	0.35 ± 0	0.69 ± 0
<i>tafo</i>		[2.84, 3.73]	[0.98, 1.02]	[0.81, 0.87]	[0.26, 0.3]	[0.52, 0.55]	[0.32, 0.34]	[0.31, 0.34]	[0.23, 0.24]	[0.32, 0.37]	[0.64, 0.77]
	minors (n = 8)	1.11 ± 0.1	0.93 ± 0	0.96 ± 0	0.21 ± 0	0.58 ± 0	0.3 ± 0	0.41 ± 0	0.29 ± 0	0.48 ± 0	1.05 ± 0.1
	majors (unknown)	[0.97, 1.26]	[0.91, 0.97]	[0.93, 0.99]	[0.19, 0.22]	[0.54, 0.59]	[0.28, 0.34]	[0.39, 0.42]	[0.28, 0.3]	[0.46, 0.5]	[0.96, 1.13]
<i>tratra</i>	minors (n = 8)	1.11 ± 0.1	0.93 ± 0	0.96 ± 0	0.21 ± 0	0.58 ± 0	0.3 ± 0	0.41 ± 0	0.29 ± 0	0.48 ± 0	1.05 ± 0.1
		[0.97, 1.26]	[0.91, 0.97]	[0.93, 0.99]	[0.19, 0.22]	[0.54, 0.59]	[0.28, 0.34]	[0.39, 0.42]	[0.28, 0.3]	[0.46, 0.5]	[0.96, 1.13]
	majors (n = 1)	1.58	0.99	0.91	0.3	0.52	0.32	0.37	0.26	0.4	0.75
<i>varatra</i>	minors (n = 16)	0.95 ± 0.1	0.92 ± 0	0.97 ± 0	0.22 ± 0	0.57 ± 0	0.3 ± 0	0.42 ± 0	0.29 ± 0	0.49 ± 0	1.01 ± 0
		[0.85, 1.11]	[0.83, 0.96]	[0.9, 1.03]	[0.2, 0.24]	[0.55, 0.59]	[0.28, 0.32]	[0.4, 0.45]	[0.26, 0.3]	[0.46, 0.52]	[0.93, 1.07]
	majors (n = 16)	1.46 ± 0.1	0.98 ± 0	0.93 ± 0	0.27 ± 0	0.51 ± 0	0.33 ± 0	0.41 ± 0	0.28 ± 0	0.4 ± 0	0.72 ± 0
<i>zavo</i>		[1.35, 1.62]	[0.95, 1]	[0.91, 0.98]	[0.24, 0.29]	[0.48, 0.55]	[0.3, 0.35]	[0.4, 0.43]	[0.25, 0.29]	[0.37, 0.42]	[0.66, 0.78]
	minors (n = 14)	1.12 ± 0.1	0.96 ± 0	0.97 ± 0	0.2 ± 0	0.57 ± 0	0.3 ± 0	0.41 ± 0	0.28 ± 0	0.48 ± 0	1.11 ± 0.1
		[1.02, 1.3]	[0.93, 1]	[0.93, 1]	[0.18, 0.23]	[0.54, 0.62]	[0.27, 0.33]	[0.39, 0.43]	[0.25, 0.3]	[0.44, 0.54]	[1, 1.22]
	1.74 ± 0.1	1.02 ± 0	0.92 ± 0	0.26 ± 0	0.54 ± 0	0.3 ± 0	0.39 ± 0	0.26 ± 0	0.39 ± 0	0.79 ± 0	
	[1.65, 1.81]	[1.01, 1.04]	[0.89, 0.94]	[0.24, 0.27]	[0.52, 0.55]	[0.29, 0.32]	[0.36, 0.42]	[0.25, 0.27]	[0.38, 0.39]	[0.76, 0.82]	

Table 1. Continued

Species	Worker castes	EL/CS	OMD/CS	MW/CS	PEW/CS	MPD/CS	HTL/CS	ML/CS	MPH/CS	NOH/CS
<i>alamaina</i>	minors (n = 52)	0.3 ± 0 [0.26, 0.32]	0.46 ± 0 [0.42, 0.49]	0.83 ± 0 [0.69, 0.89]	0.59 ± 0 [0.47, 0.66]	1.17 ± 0.1 [0.91, 1.26]	1.09 ± 0.1 [0.81, 1.23]	1.6 ± 0.1 [1.32, 1.67]	0.81 ± 0 [0.63, 0.87]	0.39 ± 0 [0.32, 0.46]
	majors (n = 24)	0.25 ± 0 [0.23, 0.27]	0.45 ± 0 [0.42, 0.47]	0.68 ± 0.1 [0.62, 0.91]	0.45 ± 0 [0.41, 0.5]	0.96 ± 0 [0.85, 1.08]	0.82 ± 0 [0.77, 0.93]	1.31 ± 0.1 [1.24, 1.45]	0.64 ± 0 [0.59, 0.72]	0.31 ± 0 [0.28, 0.35]
<i>androy</i>	minors (n = 11)	0.35 ± 0 [0.34, 0.38]	0.44 ± 0 [0.43, 0.46]	0.83 ± 0 [0.8, 0.85]	0.59 ± 0 [0.55, 0.63]	1.13 ± 0 [1.1, 1.16]	1.04 ± 0 [1, 1.09]	1.56 ± 0 [1.52, 1.6]	0.75 ± 0 [0.72, 0.79]	0.4 ± 0 [0.36, 0.49]
	majors (n = 6)	0.28 ± 0 [0.26, 0.29]	0.45 ± 0 [0.43, 0.46]	0.65 ± 0 [0.64, 0.66]	0.44 ± 0 [0.39, 0.48]	0.93 ± 0 [0.91, 0.95]	0.76 ± 0 [0.74, 0.77]	1.26 ± 0 [1.25, 1.27]	0.59 ± 0 [0.56, 0.63]	0.28 ± 0 [0.25, 0.32]
<i>bevohitra</i>	minors (n = 9)	0.3 ± 0 [0.27, 0.32]	0.47 ± 0 [0.45, 0.49]	0.7 ± 0 [0.61, 0.74]	0.4 ± 0 [0.38, 0.44]	1.06 ± 0 [0.97, 1.11]	1.08 ± 0 [0.96, 1.12]	1.54 ± 0.1 [1.43, 1.59]	0.73 ± 0 [0.65, 0.76]	0.4 ± 0 [0.34, 0.44]
	majors (n = 6)	0.27 ± 0 [0.26, 0.29]	0.49 ± 0 [0.47, 0.51]	0.62 ± 0 [0.6, 0.64]	0.35 ± 0 [0.34, 0.37]	0.98 ± 0 [0.95, 1.02]	0.95 ± 0 [0.9, 1.04]	1.39 ± 0 [1.35, 1.47]	0.62 ± 0 [0.58, 0.64]	0.35 ± 0 [0.31, 0.36]
<i>echinopluides</i>	minors (n = 20)	0.21 ± 0 [0.19, 0.24]	0.48 ± 0 [0.44, 0.52]	0.95 ± 0 [0.89, 1.01]	0.6 ± 0.1 [0.54, 0.74]	1.06 ± 0 [1, 1.11]	0.97 ± 0.1 [0.91, 1.18]	1.45 ± 0 [1.38, 1.51]	0.69 ± 0 [0.6, 0.76]	0.28 ± 0 [0.24, 0.32]
	majors (n = 2)	0.17, 0.17]	0.49, 0.49]	0.68, 0.73]	0.37, 0.43]	0.79, 0.81]	0.71, 0.72]	1.1, 1.18]	0.48, 0.58]	0.18, 0.18]
<i>edmondi</i>	minors (n = 15)	0.26 ± 0 [0.24, 0.28]	0.49 ± 0 [0.46, 0.51]	0.84 ± 0.1 [0.74, 1.03]	0.42 ± 0 [0.47, 0.68]	1.07 ± 0.1 [0.93, 1.42]	0.96 ± 0.1 [0.88, 1.29]	1.44 ± 0.1 [1.3, 1.51]	0.73 ± 0 [0.66, 0.81]	0.3 ± 0 [0.28, 0.34]
	majors (n = 8)	0.23 ± 0 [0.22, 0.24]	0.47 ± 0 [0.45, 0.5]	0.66 ± 0 [0.65, 0.68]	0.38 ± 0.47 [0.38, 0.47]	0.86 ± 0.1 [0.6, 0.94]	0.77 ± 0 [0.74, 0.81]	1.21 ± 0 [1.16, 1.25]	0.59 ± 0 [0.57, 0.61]	0.24 ± 0 [0.22, 0.27]
<i>ethicus</i>	minors (n = 11)	0.23 ± 0 [0.21, 0.25]	0.51 ± 0 [0.49, 0.53]	0.86 ± 0.1 [0.79, 0.95]	0.32 ± 0 [0.27, 0.36]	1.17 ± 0.1 [1.1, 1.27]	1.44 ± 0.1 [1.29, 1.56]	1.72 ± 0.1 [1.62, 1.86]	0.67 ± 0 [0.64, 0.72]	0.29 ± 0 [0.25, 0.34]
	majors (unknown)									
<i>galoko</i>	minors (n = 11)	0.24 ± 0 [0.23, 0.25]	0.47 ± 0 [0.43, 0.48]	0.85 ± 0 [0.79, 0.92]	0.49 ± 0 [0.47, 0.51]	0.95 ± 0 [0.89, 0.98]	0.83 ± 0 [0.78, 0.87]	1.33 ± 0.1 [1.24, 1.44]	0.64 ± 0 [0.59, 0.67]	0.27 ± 0 [0.24, 0.3]
	majors (n = 5)	0.21 ± 0 [0.19, 0.22]	0.46 ± 0 [0.46, 0.47]	0.72 ± 0 [0.7, 0.75]	0.41 ± 0 [0.37, 0.44]	0.87 ± 0 [0.84, 0.88]	0.72 ± 0 [0.71, 0.74]	1.17 ± 0 [1.13, 1.21]	0.56 ± 0 [0.52, 0.58]	0.24 ± 0 [0.21, 0.27]

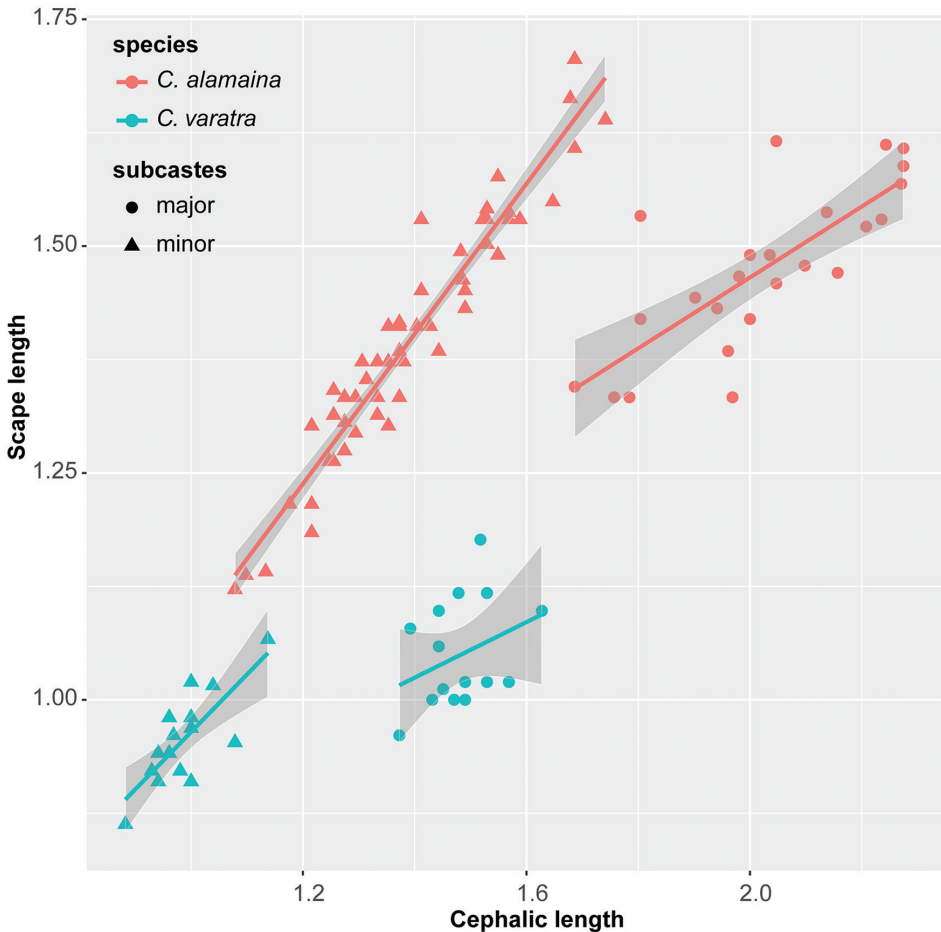


Figure 2. Broken scaling of a morphometric trait, scape length (SL) on cephalic length (CL) is illustrated in two species, *C. alamaina* (red) and *C. varatra* (blue). The scaling break splits the populations into two discrete phenotypes: minors (triangles) and majors (circles). The dark grey areas show confidence interval, the regression line is computed by linear model.

between nest samples into a distance matrix in linear discriminant space. The resulting linear discriminant scores are presented as a dendrogram within Euclidian space using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) distance method. Computations were run in R (R Core Team 2015). NC-clustering was run using packages *cluster* (Maechler et al. 2014) and *MASS* (Venables and Ripley 2002). To assess how reliable the same clusters are with a sub-sampled dataset, a bootstrap analysis was applied by running 100 iterations (method = “average,” method.dist = “Euclidean,” nboot = 100) using package *pvclust* (Suzuki and Shimodaira 2014).

Hypothesis testing by confirmatory LDA

The confirmative LDA was run repeatedly until the final classification, exhibiting the highest posterior probability values, was produced (Csősz et al. 2014). In addition, the technique was run as an iterative process until the minimum number of characters required to contribute to a desired level (>99%) of classification success was obtained (Seifert 2014a; Seifert et al. 2014b).

Each species was then described using qualitative and quantitative morphological characters of the worker castes (minor and major). An identification key to species is presented based on diagnostic characters of the workers. Morphological terminology follows Bolton (1994) and integument sculpture terminology follows Harris (1979).

Results and discussion

Synoptic list of species of the Malagasy *Camponotus edmondi* species group

alamaina Rakotonirina, Csősz & Fisher, sp. n.

androy Rakotonirina, Csősz & Fisher, sp. n.

bevohitra Rakotonirina, Csősz & Fisher, sp. n.

echinoploides Forel, 1891

edmondi André, 1887

= *edmondi* var. *ernesti* Forel, 1891 syn. n.

ethicus Forel, 1897

galoko Rakotonirina, Csősz & Fisher, sp. n.

matsilo Rakotonirina, Csősz & Fisher, sp. n.

mifaka Rakotonirina, Csősz & Fisher, sp. n.

orombe Rakotonirina, Csősz & Fisher, sp. n.

robustus Roger, 1863

tafo Rakotonirina, Csősz & Fisher, sp. n.

tratra Rakotonirina, Csősz & Fisher, sp. n.

varatra Rakotonirina, Csősz & Fisher, sp. n.

zavo Rakotonirina, Csősz & Fisher, sp. n.

Morphological diagnosis of the worker castes of *C. edmondi* species group

Although the majority of species in the *edmondi* species group are arboreal (13/15), a few species are terrestrial (i.e., build their nests in the ground, in rotten logs, and in dead tree stumps). Sometimes individual workers are found foraging on the forest floor or through leaf litter. Within a colony, two very different worker castes, minor and major workers (see Fig. 3), are observed in the group; between these extremes, various

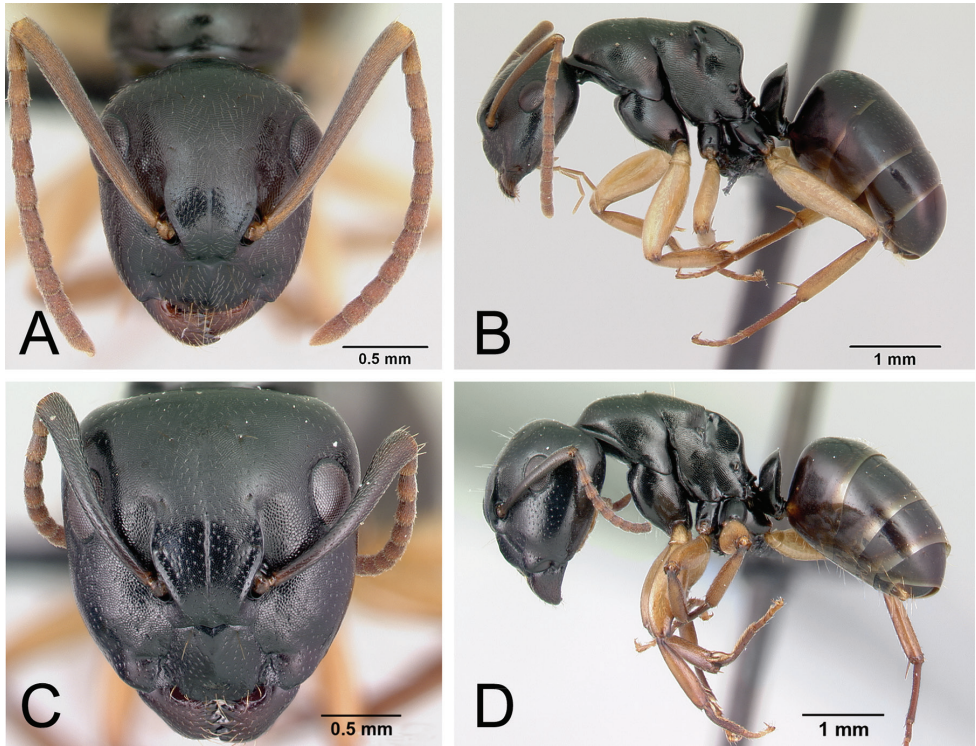


Figure 3. Head in full-face view and body in lateral view of the worker castes of *C. alamaina*. **A, B** minor worker (CASENT0499291) **C, D** major worker (CASENT0179431).

worker forms showing continuous morphological variation occur. The combination of the following features can be used to reliably diagnose the two extreme worker castes relative to other Malagasy species groups.

Minor worker

- 1) Mandibles triangular, masticatory margins armed with 6 teeth; basal margins smooth.
- 2) Palp formula 6,4; palps long with respect to head size.
- 3) Clypeus with straight (*C. ethicus*, *C. edmondi*), broadly convex, or medially triangular (*C. tafo*) anterior margin in full-face view; median notch present in the posterior margin.
- 4) Antenna with 12 segments; pedicel longer than the flagellum, length gradually reduced towards the penultimate antennomere; apical portion of the flagellum either lighter or darker in color than the basal portion; antennal scape variable in length.
- 5) Base of antenna inserted a good distance from posterior margin of clypeus, the distance at least as large as the maximum width of antennal scape.

- 6) Frontal lobe narrow and partially covering the antennal insertion; frontal carina extended posteriorly at about the level of anterior margin of the eyes in full-face view.
- 7) Compound eye large, located anterior to the midline of the head in profile view.
- 8) Head longer than broad; broader posteriorly; posterior margin convex.
- 9) Pronotum broad with very short anterior face, anterodorsally marginate to carinate; dorsolateral portion slightly to strongly marginate anteriorly; anterior and lateral faces rounding to the dorsum in *C. alamaina*.
- 10) Promesonotal suture present.
- 11) Metanotal groove vestigial or slightly impressed (*C. androy* and *C. bevohitra*) to strongly impressed.
- 12) Metapleuron anteroposteriorly compressed between mesopleuron and propodeum.
- 13) Propodeum generally marginate dorsolaterally; in lateral view, most of the dorsum abruptly sloping down to the insertion of the petiole; propodeum quadrate (*C. robustus*), with a pair of triangular extensions posteriorly (*C. ethicus* and *C. alamaina*).
- 14) Propodeal declivity slightly to strongly concave.
- 15) Propodeal lobe absent.
- 16) Metapleural gland lacking.
- 17) Procoxa large, maximum width larger than width of mesopleuron (or at least as large as 2/3 the width of the mesopleuro-propodeal surface together).
- 18) Tibial spur single and pectinate on mesotibia and metatibia.
- 19) Petiole generally flattened anteroposteriorly except in *C. echinoploides*; in profile, anterior margin convex and posterior margin either convex or straight; both faces either rounding or tapering dorsally.
- 21) Sculpture ranging from smooth and shiny superimposed with microreticulation to densely and finely reticulate-punctate or reticulate rugose.
- 22) Body color varying from light brown to black with lighter gastral segment and even lighter appendages (brown to depigmented yellow).

Major worker

Most of the features mentioned above for the minor caste are also characteristics of the major caste, except that the latter has the following characteristics: a bigger head, roughly as long as broad in full-face view; lateral cephalic margins gradually narrowed or abruptly converging (*C. echinoploides*) to the base of mandibles; posterior margin more or less straight; both palps and antennal scape short with respect to head size; antennal scape not surpassing posterior cephalic margin; anterior clypeal margin more or less straight; pronotum broad in dorsal view; in dorsal view, metanotum a narrow transverse ridge between metanotal groove and propodeum.

In the Malagasy region, the *C. edmondi* species group can be differentiated from other species of the genus by the combination of the following characters: dorsolateral margin of propodeum marginate or extending into a sharp ridge, propodeal decliv-

ity usually concave, anterolateral corner of pronotum most often marginate, forecoxa larger than the width of mesopleuron, and usually the propodeal dorsum abruptly sloping down to the insertion of the petiole.

Multivariate analysis of morphometrics

The NC-clustering dendrogram using row data revealed 15 clusters (Fig. 4), which are interpreted as 15 species in this revisionary work on the *edmondi* species group. In the dendrogram, three samples of *C. varatra* were placed in each of the following species: *C. mifaka*, *C. tafo*, and *C. tratra*, and one worker of *C. zavo* was embedded in *C. tafo*. The phenomenon may be ascribed to the large difference in sample size between those species: *C. varatra* (n=18), *C. zavo* (n=14), *C. mifaka*, *C. tafo* (n=8), and *C. tratra* (n=8), which hampers the correct placement of these lineages by the phenetic NC-clustering method. In addition, these species are very closely related and overlap in their morphometric and qualitative descriptions.

The 15-species hypothesis has been corroborated by confirmatory LDA at 99.06% (Table 2). Almost all of the species recognized in the present study were correctly classified: *C. alamaina* (100%), *C. androy* (100%), *C. bevohitra* (100%), *C. echinoploides* (100%), *C. edmondi* (100%), *C. ethicus* (100%), *C. matsilo* (100%), *C. mifaka* (100%), *C. orombe* (100%), *C. robustus* (100%), *C. tafo* (100%), *C. tratra* (100%),

Table 2. Classification matrix of species showing the classification success (percentage), the observed classification (rows) and the predicted classification (columns). Numbers in the matrix are specimen counts.

Species	Classification success (%)	<i>alamaina</i>	<i>androy</i>	<i>bevohitra</i>	<i>echinoploides</i>	<i>edmondi</i>	<i>ethicus</i>	<i>galoko</i>	<i>matsilo</i>	<i>mifaka</i>	<i>orombe</i>	<i>robustus</i>	<i>tafo</i>	<i>tratra</i>	<i>varatra</i>	<i>zavo</i>
<i>alamaina</i>	100.00	52														
<i>androy</i>	100.00		11													
<i>bevohitra</i>	100.00			9												
<i>echinoploides</i>	100.00				20											
<i>edmondi</i>	100.00					15										
<i>ethicus</i>	100.00						11									
<i>galoko</i>	90.91							10							1	
<i>matsilo</i>	100.00								11							
<i>mifaka</i>	100.00									13						
<i>orombe</i>	100.00										3					
<i>robustus</i>	100.00											9				
<i>tafo</i>	100.00												8			
<i>tratra</i>	100.00													8		
<i>varatra</i>	94.44													1	17	
<i>zavo</i>	100.00															14
Total	99.06	52	11	9	20	15	11	10	11	13	3	9	8	9	18	14

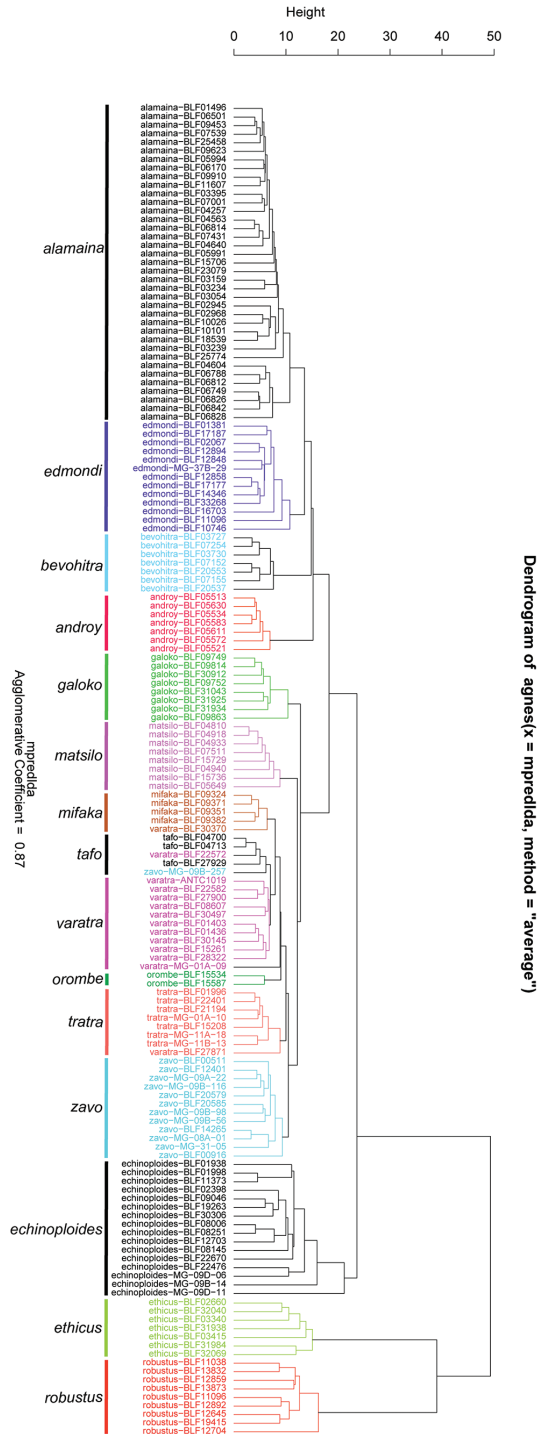


Figure 4. Dendrogram of NC-clustering of the *edmondi* species group. Label on the tip of the branch indicates the species name followed by the specimen code.

and *C. zavo* (100%). Only *C. varatra* and *C. galoko* show lower classification success scores of 94.44% and 90.91% respectively.

Two samples were misclassified by the cumulative LDA: a single individual observed in *C. varatra* sp. n. was classified as *C. tratra* sp. n. with posterior probability $p = 0.74$, and one of the 11 minor workers of *C. galoko* sp. n. was classified as *C. varatra* sp. n. with posterior probability $p = 0.76$. However, the low posterior probability values may indicate that these species are very closely related and overlap in their morphometric and qualitative descriptions.

Combining morphometry with other information for species definition

Taxonomy integrates multiple lines of evidence to better infer species boundaries. In the present study, information obtained from multivariate morphometric analysis constitutes one piece of evidence used to help indicate the presence of reproductive isolation. A few species in the *C. edmondi* group look very similar to each other and some species present significant morphological variation across their geographic distribution, requiring more independent information to achieve species resolution. As an example, the classification success of *C. galoko* is quite low because one sample was misclassified as *C. varatra*, but its status as a species is supported by qualitative morphological traits which were not included in the morphometric approach. Members of the former species are characterized by a densely and finely reticulate integument whereas those of the latter have imbricating sculpture. In addition, *C. galoko* is geographically distributed in the transitional humid forest in the northwest of Madagascar while *C. varatra* mostly occupies the eastern rainforest of the island.

In another case, two specimens of *C. zavo* and *C. varatra* are placed in the cluster of *C. tafo* based on NC-clustering analysis, suggesting that they should be grouped into one species. However, the separation of *C. tafo* is confirmed by biological data (see Distribution and biology in the Species account section) collected on its members, which have been found only in the rainforest canopy of Parc National Masoala. By contrast, the colony nests of *C. zavo* and *C. varatra* are built in dead twigs or branches slightly above the forest floor but never in the canopy. A similar species (*C. mifaka*), which contains one of the minor worker of *C. varatra*, generally nests in the ground under root mat layers.

In contrast to *C. varatra* and *C. zavo*, *C. alamaina* shows qualitative morphological character differences in the shape of the propodeum, the form of the petiolar node, and the color of the legs across its geographical distribution, but is grouped together in one cluster in the dendrogram (see discussion of the three variants in the species account). The grouping in the dendrogram shows no clear separation of the three variants and is supported by the gradual variation of the characters as many specimens are considered intermediate after assessment of numerous samples.

Two minor workers were misclassified by the cumulative LDA. Factors responsible for this are uncertain, but we might not have been able to measure the full range of worker forms representative of the species of concern in the *edmondi* species group. Because individual colonies of the species in the group show strong allometric variation

(polymorphism), the range of worker forms from the same nests should be considered in the study to obtain a more robust classification. Moreover, additional morphological characters should be included in the morphometric investigation.

Identification key to worker caste of the Malagasy *Camponotus edmondi* species group

The following key applies to both minor and major workers.

- 1 In profile, anterior margin of petiolar node convex and posterior margin more or less straight; propodeal spiracle located on lateral portion of propodeum, anterior to posterolateral margin of propodeum (Fig. 5A).....2
- In profile, anterior margin of petiolar node convex and posterior margin either convex or roughly triangular; propodeal spiracle located on declivitous surface or at posterolateral margin of the propodeum (Fig. 5B) 6

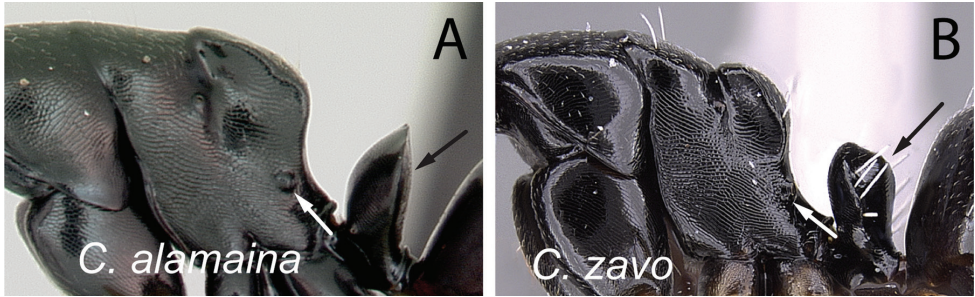


Figure 5. Mesosoma and petiolar node in profile. **A** *C. alamaina* (CASENT0499291) **B** *C. zavo* (CASENT0060041).

- 2 Larger species (CS: 1.882–3.725; CL: 1.961–3.686; ML: 3.098–4.667); body color uniformly black to dark brown (Fig. 6A)..... 3
- Smaller species (CS: 0.875–2.222; CL: 0.98–2.275; ML: 1.373–2.902); body bicolored, head and mesosoma black to dark brown, gaster and appendages lighter in color (dark brown to depigmented yellow) (Fig. 6B)..... 4

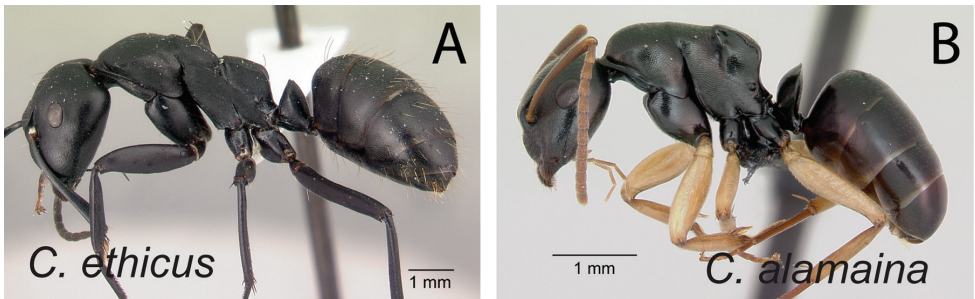


Figure 6. Individual minor worker in profile. **A** *C. ethicus* (CASENT0409948) **B** *C. alamaina* (CASENT0499291).

- 3 Level of the propodeal dorsum abruptly lower than level of the promesonotal dorsum; pronotal dorsum with few erect hairs; humeral angle extended anteriorly into a narrow ridge (Fig. 7A) ***ethicus***
- Level of propodeal dorsum not abruptly lower than level of promesonotal dorsum; pronotum covered with numerous erect hairs and pubescence; humeral angle slightly tuberculate, not extended into a narrow ridge (Fig. 7B) ***robustus***

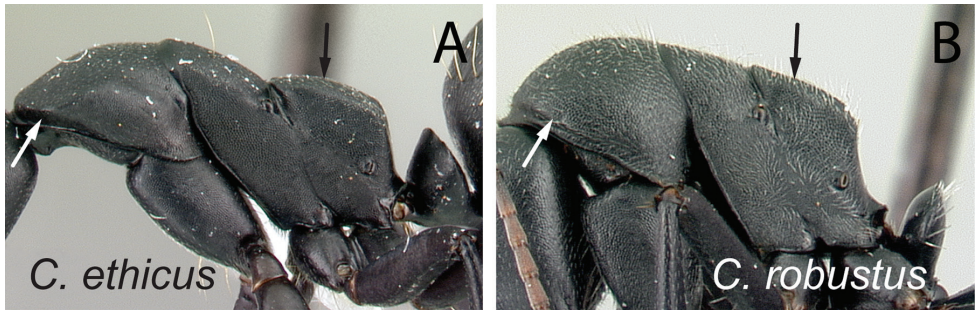


Figure 7. Lateral view of mesosoma. **A** *C. ethicus* (CASENT0409949) **B** *C. robustus* (CASENT0066723).

- 4 In profile, anterior margin of pronotum broadly rounding to the dorsum; dorsolateral and posterolateral margins of propodeum strongly carinate (Fig. 8A); somewhat larger species (CS: 0.991–2.222; CL: 1.078–2.275; ML: 1.62–2.902) ***alamaina***
- In profile, anterior margin of pronotum very short and indistinct, the cervical shield apparently joins the pronotal dorsum directly; at least posterolateral margin of propodeum not strongly carinate, but simply marginate or rounded (Fig. 8B); generally smaller species (CS: 0.875–1.739; CL: 0.98–1.922; ML: 1.373–2.235) **5**

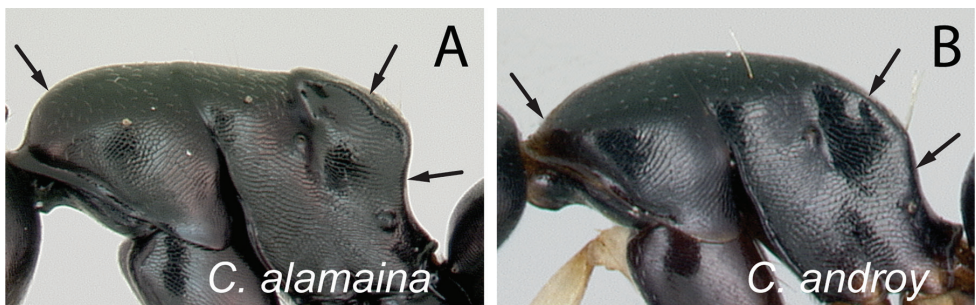


Figure 8. Mesosoma in lateral view. **A** *C. alamaina* (CASENT0499291) **B** *C. androy* (CASENT0453723).

- 5 In dorsal view, dorsolateral portion of propodeum with sharp carina, posterolateral margin marginate (Fig. 9A); in profile, width of mesopleuron, seen at the level of spiracle, about as large as that of lateral portion of propodeum; at least one pair of erect hairs present on propodeal dorsum ***androy***
- In dorsal view, dorsal face of propodeum rounded to lateral face, junction without sharp carina, and posterolateral margin rounded (Fig. 9B); in profile

mesopleuron, taken at spiracle level, much wider than lateral portion of propodeum; erect hairs lacking on propodeal dorsum *bevohitra*

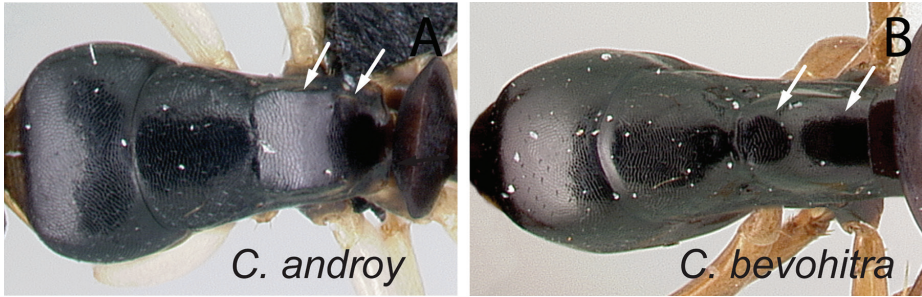


Figure 9. Mesosoma in dorsal view. **A** *C. androy* (CASENT0453723) **B** *C. bevohitra* (CASENT0437238).

- 6 In profile, propodeum strongly compressed anteroposteriorly, without clear distinction between dorsal margin and declivity (Fig. 10A); in dorsal view, mesonotum broad, at least twice as broad as long (Fig. 10B) 7
- In profile, propodeum not strongly compressed anteroposteriorly, propodeal dorsum and declivitous surface separated by blunt angle (Fig. 10C); in dorsal view, mesonotum narrow, less than twice as broad as long (Fig. 10D) 8

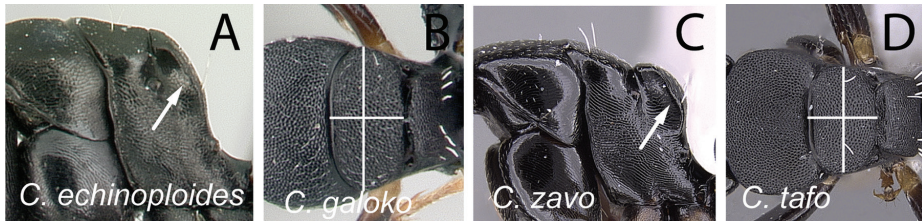


Figure 10. Mesosoma in lateral and dorsal views. **A** *C. echinoploides* (CASENT0409171) and **B** *C. galoko* (CASENT0178918) **C** *C. zavo* (CASENT0060041) and **D** *C. tafo* (CASENT0763608).

- 7 Posterodorsal corner of mesonotum raised into a bluntly rounded shield (Fig. 11A); somewhat larger species (CS: 1.235–2.667, 1.6; CL: 1.255–2.647, 1.625; ML: 1.843–2.922, 2.257) *echinoploides*
- Posterodorsal corner of mesonotum rounded, not forming an extended shield (Fig. 11B); somewhat smaller species (CS: 1–1.722, 1.265; CL: 0.961–1.725, 1.29; ML: 1.341–2.078, 1.623) *galoko*

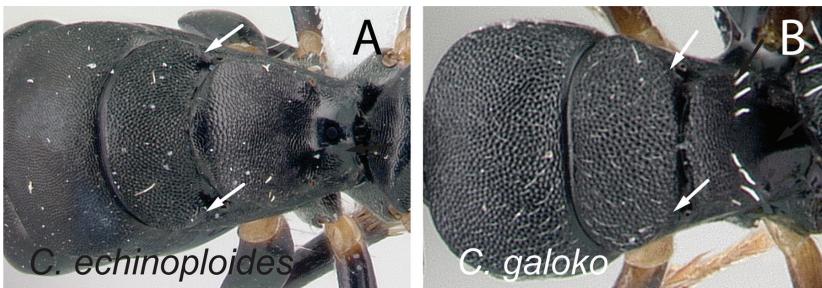


Figure 11. Mesosoma in dorsal view. **A** *C. echinoploides* (CASENT0409171) **B** *C. galoko* (CASENT0178918).

- 8 In profile, straight line connecting one end of dorsolateral carina of propodeum at the metanotal groove to the other end next to propodeal spiracle conspicuously longer than posterolateral margin of propodeum (Fig. 12A) *matsilo*
- In profile, straight line connecting one end of dorsolateral carina of propodeum at the metanotal groove to the other end next to the propodeal spiracle approximately as long as posterolateral margin of propodeum (Fig. 12B) ...9

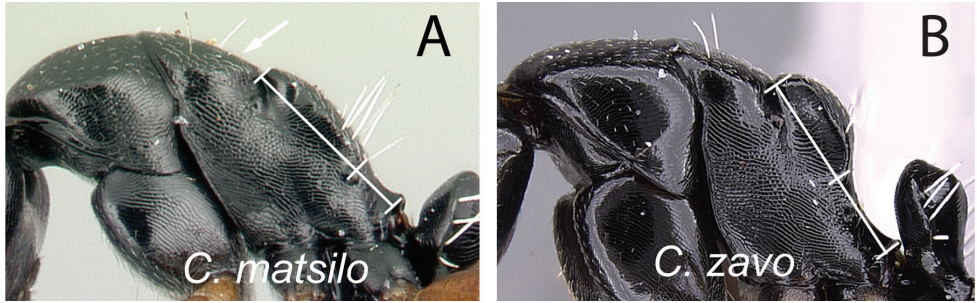


Figure 12. Mesosoma in lateral view. **A** *C. matsilo* (CASENT0121843) **B** *C. zavo* (CASENT0060041).

- 9 Dorsum of head and mesosoma densely and finely reticulate punctate (Fig. 13A) 10
- Dorsum of head and mesosoma smooth and shiny, superimposed by fine imbrication (Fig. 13B) 13

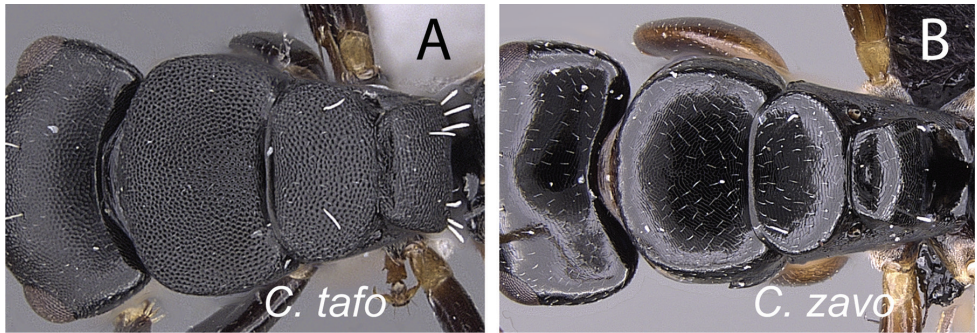


Figure 13. Head and mesosoma in dorsal view. **A** *C. tafo* (CASENT0763608) **B** *C. zavo* (CASENT0060041).

- 10 Dorsum of mesosoma with numerous erect hairs, pubescence conspicuous (Fig. 14A) *mifaka*
- Hairs lacking on dorsum of pronotum; a pair of hairs present on mesonotum; dorsum of propodeum covered with few erect hairs; hairs on propodeum mostly arise along the region separating dorsal surface and declivity; pubescence inconspicuous (Fig. 14B)..... 11

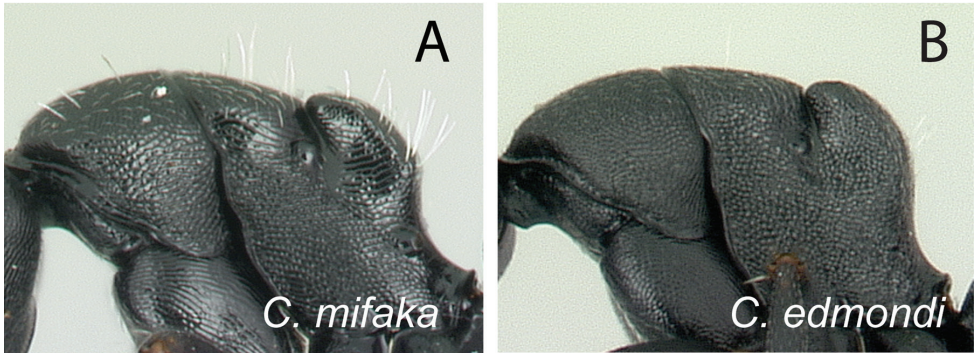


Figure 14. Mesosoma in lateral view. **A** *C. mifaka* (CASENT0217301) **B** *C. edmondi* (CASENT0136511).

- 11 Distance between meso-metapleural suture and dorsolateral margin of propodeum remains the same along the dorsolateral carina of propodeum (Fig. 15A); no distinct angle between dorsal margin of propodeum and declivity, both portions apparently forming a straight line *orombe*
- Distance between meso-metapleural suture and dorsolateral margin of propodeum variable, largest near the junction of dorsolateral carina and declivitous surface (Fig. 15B); blunt angle or convexity between dorsal margin of propodeum and declivity distinct..... 12

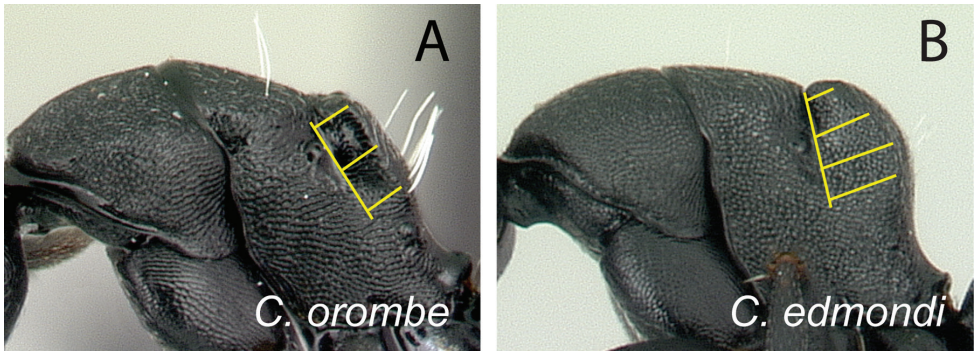


Figure 15. Mesosoma in lateral view. **A** *C. orombe* (CASENT0178923) **B** *C. edmondi* (CASENT0136511).

- 12 With mesosoma in dorsal view, lateral margins of mesonotum roughly straight and gradually converging posteriorly; width of propodeum at the metanotal groove less than half the maximum width of mesonotum (Fig. 16A); with head in full-face view, anteromedian margin of clypeus truncate..... *edmondi*
- With mesosoma in dorsal view, lateral margins of mesonotum convex and strongly converging posteriorly; width of propodeum at metanotal groove greater than half the maximum width of mesonotum (Fig. 16B); with head in full-face view, anteromedian margin of clypeus triangular..... *tafo*

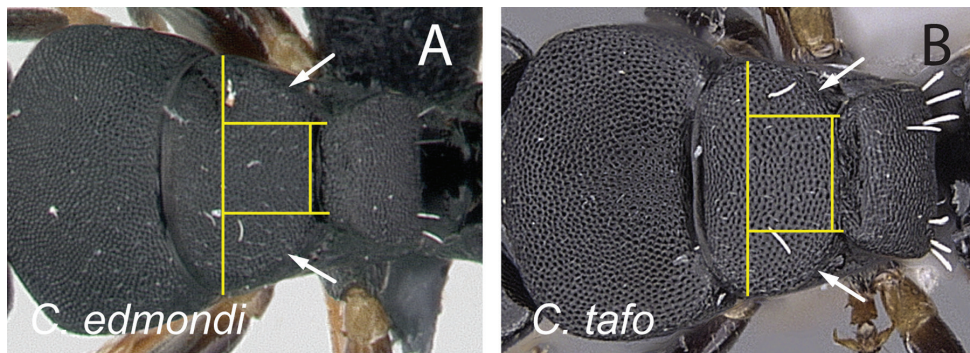


Figure 16. Mesosoma in dorsal view. **A** *C. edmondi* (CASENT0134980) **B** *C. tafo* (CASENT0763608).

- 13 In profile, mesonotal dorsum strongly sloping down to the level of propodeum, maximum length of mesonotum about as long as distance between metanotal groove and propodeal spiracle (Fig. 17A); in dorsal view, lateral margin of mesonotum not well defined and converging gradually towards metanotal groove (Fig. 17B); head and mesosoma brown *tratra*
- In profile, mesonotum slightly sloping down to the level of propodeum, maximum length distinctly shorter than distance between metanotal groove and propodeal spiracle (Fig. 17C); in dorsal view, lateral margin of mesonotum well defined and evenly convex, converging abruptly towards metanotal groove (Fig. 17D); head and mesosoma dark brown to black 14

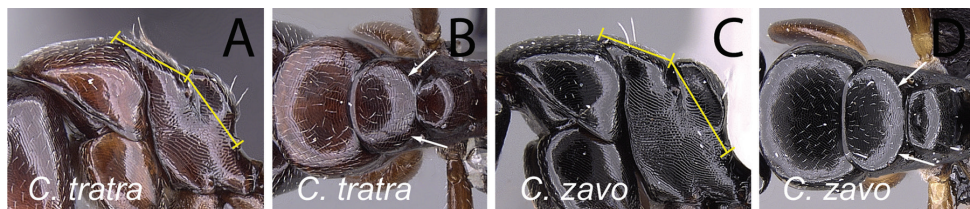


Figure 17. Mesosoma in profile and in dorsal view. **A, B** *C. tratra* (CASENT0763608) **C, D** *C. zavo* (CASENT0060041).

- 14 In profile, anterodorsal corner of pronotum extending anteriorly into narrow edge but dorsolateral portion not marginate, junction of dorsum to lateral surface always rounded; blunt angle between dorsal margin of propodeum and declivity distinct, or the junction between both portion rounded (Fig. 18A); antennal scape and gastral tergites I-III covered with abundant appressed pubescence (Fig. 18B) *zavo*
- In profile, anterodorsal corner of pronotum extending anteriorly into narrow edge and dorsolateral portion marginate; junction of dorsum to lateral surface

of pronotum sharply angulate; no distinct angle between dorsal margin of propodeum and declivity, both portions apparently forming a straight line (Fig. 18C); antennal scape and gastral tergites I-III with scattered appressed pubescence (Fig. 18D).....*varatra*

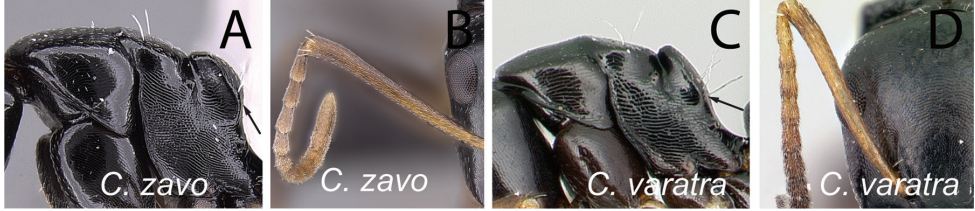


Figure 18. Mesosoma in lateral view and antennal scape in full-face view: **A,B** *C. zavo* (CASENT0060041) **C** *C. varatra* (CASENT0492888) and **D** *C. varatra* (CASENT0409723).

Species account of the Malagasy *Camponotus edmondi* species group

Camponotus alamaina Rakotonirina, Csősz & Fisher, sp. n.

<http://zoobank.org/CAEB7BC2-0095-4240-88EA-0019EAB8780B>

Figures 5A, 6B, 8A, 19, 34

Holotype worker. Madagascar, Province Mahajanga, Mahavavy River, 6.2 km 145° SE Mitsinjo, -16.05167, 45.90833, 20 m, gallery forest, ex dead branch above ground, 1–5 Dec 2002 (Fisher, Griswold et al.) collection code: BLF06982, specimen code: CASENT0481799 (CASC).

Paratype. 8 workers with same data as holotype but with the following specimen codes: CASENT0481797, CASENT0481798, CASENT0746987, CASENT0746988, CASENT0746989, CASENT0763743, CASENT0763744, CASENT0763745 (BMNH, MHNG, MNHN, MSNG, CASC).

Additional material examined. Form 1. MADAGASCAR: Province **Antananarivo:** Forêt de galerie, Telomirahavavy, 23.4 km NNE Ankazobe, -18.12167, 47.20627, 1520 m, disturbed gallery montane forest, (B.L. Fisher et al.) (CASC); Réserve Naturelle Sohisika, Sohisika 24.6 km NNE Ankazobe, -18.10322, 47.18692, 1464 m, gallery montane forest, (B.L. Fisher et al.) (CASC); Province **Antsiranana:** Forêt Ambato, 26.6 km 33° Ambanja, -13.4645, 48.55167, 150 m, rainforest, (B.L. Fisher) (CASC); Réserve Spéciale Manongarivo 17.3 km 218° SW Antanambao, -14.02167, 48.41833, 1580 m, montane rainforest, (B.L. Fisher) (CASC); Réserve Spéciale Manongarivo, 10.8 km 229° SW Antanambao, -13.96167, 48.43333, 400 m, rainforest, (B.L. Fisher) (CASC); Réserve Spéciale Ambre, 3.5 km 235° SW Sakaramy, -12.46889, 49.24217, 325 m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Réserve Spéciale Ankarana, 13.6 km 192° SSW Anivorano Nord, -12.86361, 49.22583, 210 m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Réserve Spéciale Ankarana, 22.9 km 224° SW Anivorano Nord, -12.90889, 49.10983, 80

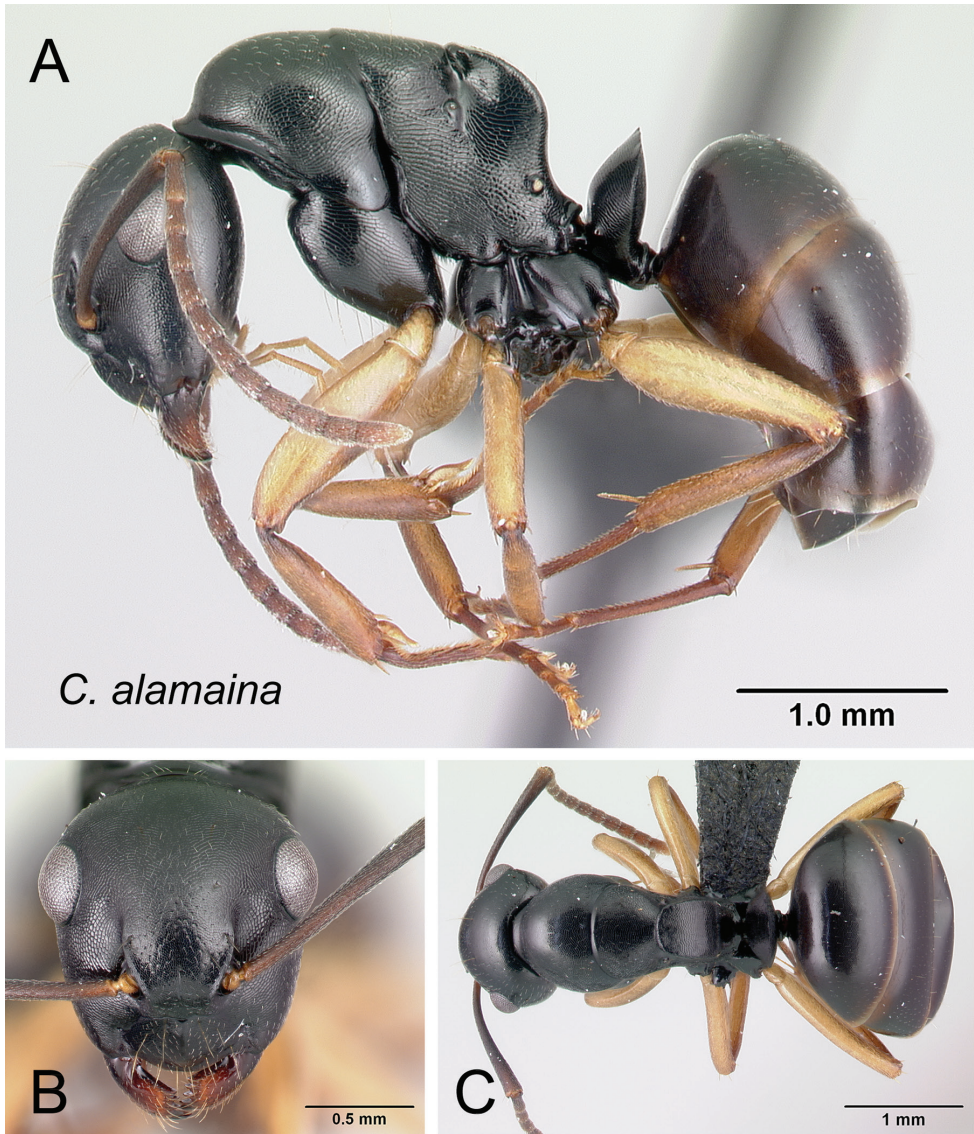


Figure 19. *Camponotus alamaina* minor worker CASENT0481799. **A** lateral view **B** head in full-face view **C** dorsal view.

m, tropical dry forest, (Alpert et al.), (Fisher, Griswold et al.) (CASC); Province **Fianarantsoa**: Southern Isoky-Vohimena Forest, $-22.68333, 44.83333, 730$ m, (Sylvain) (CASC); Forêt d'Analalava, 29.6 km 280° W Ranohira, $-22.59167, 45.12833, 700$ m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Province **Mahajanga**: Forêt Ambohimanga, 26.1 km 314° Mampikony, $-15.96267, 47.43817, 250$ m, tropical dry forest, (B.L. Fisher) (CASC); Forêt d'Anabohazo, 21.6 km 247° WSW Maromandia, $-14.30889, 47.91433, 120$ m, tropical dry forest, (Fisher, Griswold et

al.) (CASC); Forêt de Tsimembo, 11.0 km 346° NNW Soatana, -18.99528, 44.4435, 50 m, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Parc National Baie de Baly, 12.4 km 337° NNW Soalala, -16.01, 45.265, 10 m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Mahavavy River, 6.2 km 145° SE Mitsinjo, -16.05167, 45.90833, 20 m, gallery forest, (Fisher, Griswold et al.) (CASC); Parc National Ankarafantsika, Forêt de Tsimaloto, 18.3 km 46° NE de Tsaramandroso, -16.22806, 47.14361, 135 m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Parc National Namoroka, 16.9 km 317° NW Vilanandro, -16.40667, 45.31, 100 m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Parc National Namoroka, 17.8 km 329° WNW Vilanandro, -16.37667, 45.32667, 100 m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Parc National Namoroka, 9.8 km 300° WNW Vilanandro, -16.46667, 45.35, 140 m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Réserve d'Ankoririka, 10.6 km 13° NE de Tsaramandroso, -16.26722, 47.04861, 210 m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Réserve forestière Beanka, 50.2 km E Maintirano, -18.02649, 44.05051, 250 m, tropical dry forest on tsingy, (B.L. Fisher et al.) (CASC); Réserve forestière Beanka, 50.7 km E Maintirano, -17.88021, 44.46877, 140 m, tropical dry forest on tsingy, (B.L. Fisher et al.) (CASC); Réserve forestière Beanka, 52.7 km E Maintirano, -18.0622, 44.52587, 300 m, tropical dry forest on tsingy, (B.L. Fisher et al.) (CASC); Réserve forestière Beanka, 53.6 km E Maintirano, -18.04014, 44.53394, 272 m, tropical dry forest on tsingy, (B.L. Fisher et al.) (CASC); Parc National Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, -18.70944, 44.71817, 150 m, tropical dry forest on Tsingy, (Fisher-Griswold Arthropod Team) (CASC); Parc National Tsingy de Bemaraha, 2.5 km 62° ENE Bekopaka, Ankidrodra River, -19.13222, 44.81467, 100 m, tropical dry forest on Tsingy, (Fisher-Griswold Arthropod Team) (CASC); Parc National Tsingy de Bemaraha, 3.4 km 93° E Bekopaka, Tombeau Vazimba, -19.14194, 44.828, 50 m, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Province **Toliara**: 50 km N Morondava, -20.06667, 44.58333, in primary dry forest, (A. Pauly) (CASC); 6.1 km 182° S Marovato, -25.58167, 45.295, 20 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Beza-Mahafaly, 27 km E Betioky, -23.65, 44.63333, 135 m, tropical dry forest, (B.L. Fisher) (CASC); Fiherenana, -23.17694, 43.96083, 100 m, gallery forest, (Frontier Project) (CASC); Fiherenana, -23.22252, 43.88088, 65 m, degraded gallery forest, (Frontier Project) (CASC); Forêt de Beroboka, 5.9 km 131° SE Ankidranoka, -22.23306, 43.36633, 80 m, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Forêt de Kirindy, 15.5 km 64° ENE Marofandilia, -20.06915, 44.66042, 30 m, tropical dry forest, (B.L. Fisher et al.) (CASC); Parc National Tsimanampetsotsa, Mitoho Cave, 6.4 km 77° ENE Efoetse, 17.4 km 170° S Beheloka, -24.04722, 43.75317, 40 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Forêt de Tsinjoriaky, 6.2 km 84° E Tsifota, -22.80222, 43.42067, 70 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Forêt Vohidava 88.9 km N Amboasary, -24.24067, 46.28783, 500 m, spiny forest/dry forest transition, (B.L. Fisher et al.) (CASC); Mikea Forest, deciduous dry forest, -22.90367, 43.4755, 30 m, deciduous dry forest, (R. Harin'Hala) (CASC);

Mikea Forest, spiny forest, $-22.91333, 43.48222, 37$ m, spiny forest, (R. Harin'Hala) (CASC); Parc National Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, $-24.76389, 46.75167, 900$ m, montane rainforest, (Fisher-Griswold Arthropod Team) (CASC); Parc National Zombitse, 17.7 km 98° E Sakaraha, $-22.88833, 44.70167, 760$ m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Parc National Zombitse, 19.8 km 84° E Sakaraha, $-22.84333, 44.71, 770$ m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Réserve Privée Berenty, Forêt de Bealoka, Mandraré River, 14.6 km 329° NNW Amboasary, $-24.95694, 46.2715, 35$ m, gallery forest, (Fisher-Griswold Arthropod Team) (CASC); Réserve Privée Berenty, Forêt de Malaza, Mandraré River, 8.6 km 314° NW Amboasary, $-25.00778, 46.306, 40$ m, gallery forest, (Fisher-Griswold Arthropod Team) (CASC); Vohibasias Forest, 59 km NE Sakaraha, $-22.46667, 44.85, 780$ m, (Sylvain) (CASC).

Form 2. MADAGASCAR: Province **Mahajanga:** Parc National Baie de Baly, 12.4 km 337° NNW Soalala, $-16.01, 45.265, 10$ m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Réserve Spéciale Bemarivo, 23.8 km 223° SW Besalampy, $-16.925, 44.36833, 30$ m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Province **To-liara:** Forêt de Kirindy, 15.5 km 64° ENE Marofandilia, $-20.045, 44.66222, 100$ m, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC).

Form 3. MADAGASCAR: Province **Antsiranana:** Forêt d'Ampondrabe, 26.3 km 10° NNE Daraina, $-12.97, 49.7, 175$ m, tropical dry forest, (B.L. Fisher) (CASC); Forêt d'Analabe, 30.0 km 72° ENE Daraina, $-13.08333, 49.90833, 30$ m, littoral rainforest, (B.L. Fisher) (CASC); Forêt de Bekaraoka, 6.8 km 60° ENE Daraina, $-13.16667, 49.71, 150$ m, tropical dry forest, (B.L. Fisher) (CASC); Forêt de Binara, 7.5 km 230° SW Daraina, $-13.255, 49.61667, 375$ m, tropical dry forest, (B.L. Fisher) (CASC); Forêt d'Orangea, 3.6 km 128° SE Remena, $-12.25889, 49.37467, 90$ m, littoral rainforest, (Fisher, Griswold et al.) (CASC); Montagne des Français, 7.2 km 142° SE Antsiranana (=Diego Suarez), $-12.32278, 49.33817, 180$ m, tropical dry forest, (Fisher, Griswold et al.) (Alpert et al.) (CASC); Réserve Analamerana, 16.7 km 123° Anivorano-Nord, $-12.80467, 49.37383, 225$ m, tropical dry forest, (B.L. Fisher) (CASC); Réserve Analamerana, 28.4 km 99° Anivorano-Nord, $-12.74667, 49.49483, 60$ m, tropical dry forest, (B.L. Fisher) (CASC); Réserve Spéciale de l'Ankarana, 13.6 km 192° SSW Anivorano Nord, $-12.86361, 49.22583, 210$ m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Réserve Spéciale Ankarana, 22.9 km 224° SW Anivorano Nord, $-12.90889, 49.10983, 80$ m, tropical dry forest, (Fisher, Griswold et al.) (CASC).

Diagnosis. Anterior margin of petiolar node convex and posterior margin more or less straight; propodeal spiracle anterior to posterolateral margin of propodeum; head and mesosoma black to dark brown, gaster and appendages dark brown to yellow or light yellow; anterior margin of pronotum broadly rounding to the dorsum; dorsolateral and posterolateral margins of propodeum strongly carinate.

Description. Minor worker (Figs 5A, 6B, 8A, 19). In full-face view head longer than broad (CWb/CL: 0.79–0.91); lateral margin more or less straight, feebly converging toward base of mandibles and broadly rounding to the convex posterior margin. Anterior clypeal margin generally convex, posteromedian margin notched. Level of

posterior ocular borders generally located from posterior third to posterior fifth of head (PoOc/CL: 0.2–0.271); antennal scape somewhat long (SL/CS: 1.02–1.18), roughly its distal portion extending beyond rear border of head. Mandible subtriangular, apical margin armed with six teeth. In profile, anterior margin of pronotum broadly rounding to the dorsum; anterodorsal angle weakly marginate; junction of dorsum and sides of premesonotum rounded, without margination; dorsolateral margins of propodeum extending into sharp carina. In dorsal view, junction of mesonotum and propodeum laterally compressed; metanotal groove impressed. In profile, propodeal dorsum raised into a very short edge, descending feebly posteriorly and joining declivity by distinct angle; propodeal spiracle located anterior to posterolateral margin of propodeum. Maximum width of procoxa larger than width of meso-metapleuron. In profile, petiolar node anteroposteriorly flattened and tapered dorsally; anterior margin slightly convex and posterior margin more or less straight; dorsal margin straight or weakly excised medially. Constriction between abdominal segments III and IV lacking.

Dorsum of head, mesosoma, and petiole with imbricate sculpture; gaster with finer imbrication; mandible coriarius-punctulate. Pairs of erect hairs arranged as follows: three on clypeus, one near margin of frontal carina, at level of eyes, posterior portion of head, dorsum of mesonotum and propodeum. Two rows of sparse, erect hairs arranged on anterior and posterior portions of each of first three gastral tergites. Pubescence short and scattered on dorsum of body. Head, mesosoma and petiole black to dark brown; gaster, mandible, antenna, coxa and tarsus brown; rest of legs yellow.

Major worker. With characteristics of minor worker except the following divergent features: head subquadrate (CWb/CL: 0.87–1) in full-face view, posterior margin approximately straight; level of posterior ocular borders at about posterior fourth of head (PoOc/CL: 0.24–0.28); anterior clypeal margin straight and medially excised; antennal scape barely extending beyond rear cephalic border (SL/CS: 0.69–0.89); metanotum distinct between mesonotum and propodeum; dorsum of propodeum strongly inclined posteriorly and rounding into declivity; dorsal margin of petiolar node medially excised; few erect hairs present on dorsum of pronotum and more than one pair on mesonotum and propodeum.

Distribution and biology. *Camponotus alamaina* is a widespread species occurring mainly in the dry forest habitats in western Madagascar (Fig. 34). Members of the species are known also from the spiny forest and thickets of the south and southwest, the montane rainforest of the central plateau and the southeast, and the littoral forest of the north of the island. Although this species is both arboreal and terrestrial, its members commonly are found foraging on low vegetation and nesting in dead branches, twigs, or rot pockets above the ground. Nests sites also may be built in rotten logs or sticks, and rotting tree stumps.

Variant 1 (typical form) and variant 2 co-occur in the dry forests of the Réserve de Bemarivo and Parc National Baie de Baly.

Discussion. *Camponotus alamaina* is one of the common species in the *edmondi* group and displays remarkable morphological variation in the shape of the propodeum, form of the petiolar node, and color of the legs. Three different variants are rec-

ognized based on this morphological diversity, but gradually merge into one another across the geographic distribution of the species.

Variant 1. Workers are typical *Camponotus alamaina* and can be recognized by having dorsolateral and posterolateral margins of the propodeum that extend into sharp carinae, but the junction of the dorsum to the posterolateral portion is rounded or bluntly angulate and does not form a pair of teeth or tubercles laterally; in oblique profile view, the dorsal border of petiolar node is straight or slightly excised medially; and the legs are yellow.

Variant 2. This variant is known from Parc National Baie de Baly, Réserve de Bemarivo and Kirindy Forest near Marofandilia, and is characterized by the lateral projection into tubercles of the posterodorsal corner of the propodeum, the presence of numerous erect hairs on the dorsum of the propodeum, a much thicker petiolar node with a dorsal margin extending medially into a blunt tooth in frontal view, and a much darker-colored foreleg.

Variant 3. This variant expresses intermediate characters of the previous two variants, in that the posterodorsal corners of the propodeum are bidentate, the dorsal margin of petiolar node is slightly excised medially in frontal view, and the legs are yellow. Specimens of this variant have been collected from sites in the north of Madagascar, including Ankarana, Orangea, Montagne des Français, Binara, and Analabe.

The NC-clustering approach was used to detect these three variants, but the technique did not clearly reveal their existence. The members of each of the variants are scattered along the cluster of *C. alamaina*. More information from the robust molecular phylogenetics are needed in order both to decide whether the different variants constitute separate species and to study the ecological and evolutionary forces underlying these morphological variations.

***Camponotus androy* Rakotonirina, Csősz & Fisher, sp. n.**

<http://zoobank.org/0922743A-9E3D-4E33-A948-EB27C8FC9235>

Figures 8B, 9A, 20, 35

Holotype worker. Madagascar, Province Toliara, Réserve Spéciale de Cap Sainte Marie, 12.3 km 262° W Marovato, -25.58167, 45.16833, 200 m, spiny forest/thicket, ex dead twig above ground, 11–15 Feb 2002 (Fisher-Griswold Arthropod Team) collection code: BLF05583 specimen code: CASENT0453723 (CASC).

Paratype. 16 workers with same data as holotype but with the following specimen codes: CASENT0453722, CASENT0453725, CASENT0453726, CASENT0453727, CASENT0453728, CASENT0453729, CASENT0453730, CASENT0453731, CASENT0453732, CASENT0453734, CASENT0746981, CASENT0746982, CASENT0746983, CASENT0746984, CASENT0746985, CASENT0746986 (BMNH, MHNG, MNHN, MSNG, CASC).

Additional material examined. MADAGASCAR: Province **Toliara:** 3.4 km 190° S Marovato, -25.55972, 45.2825, 160 m, spiny forest/thicket, (Fisher-Griswold Ar-

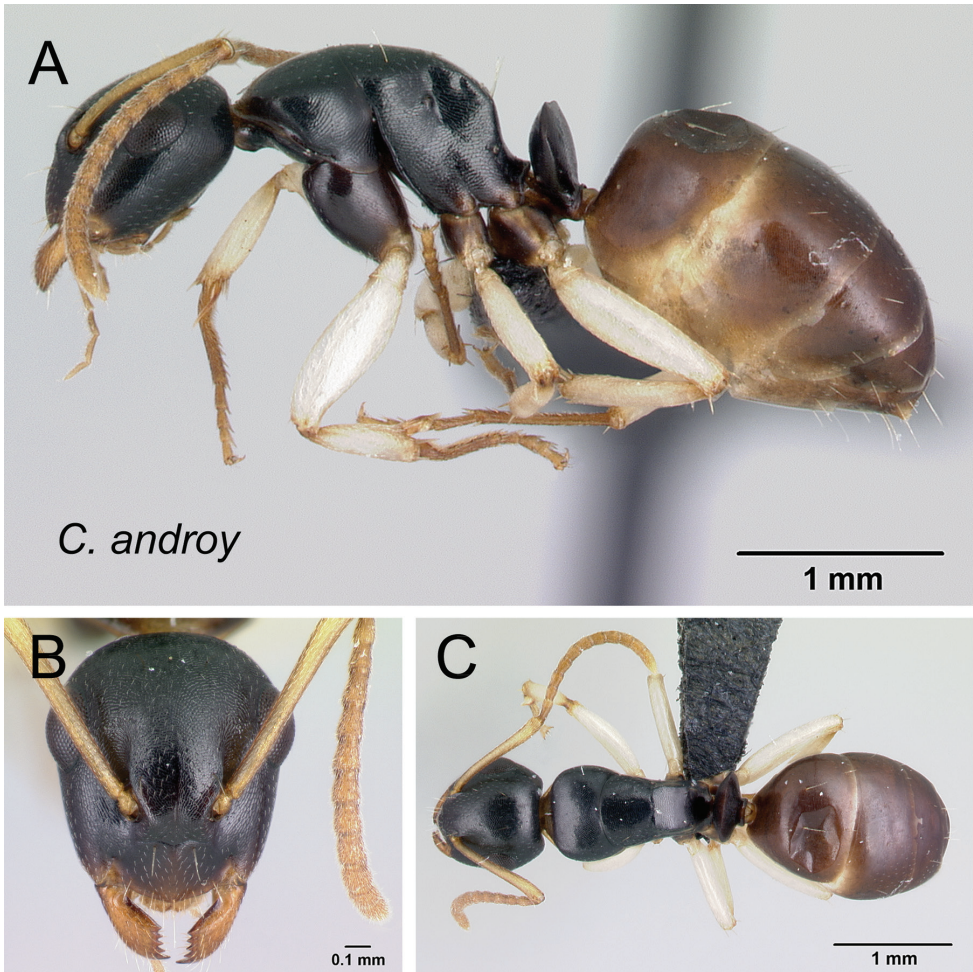


Figure 20. *Camponotus androy* minor worker CASENT0453723. **A** lateral view **B** head in full-face view **C** dorsal view.

thropod Team) CASC); Réserve Spéciale Cap Sainte Marie, 12.3 km 262° W Marovato, -25.58167, 45.16833, 200 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Réserve Spéciale Cap Sainte Marie, 12.3 km 262° W Marovato, -25.58167, 45.16833, 200 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC).

Diagnosis. Anterior margin of petiolar node convex and posterior margin more or less straight; propodeal spiracle placed anterior to posterolateral margin of propodeum; head and mesosoma black to dark brown, gaster and appendages dark brown to yellow or depigmented yellow; cervical shield joining pronotal dorsum directly; dorsolateral portion of propodeum with sharp carina, posterolateral margin marginate; in profile, width of mesopleuron about as large as that of lateral portion of propodeum; at least a pair of erect hairs present on propodeal dorsum.

Description. Minor worker (Figs 8B, 9A, 20). In full-face view head elongate (CWb/CL: 0.78–0.83), sides almost straight and rounding to the broadly convex posterior margin. Eyes protruding and large (EL/CS: 0.34–0.38), occupying more than one third of the side of the head; level of posterior ocular margin at posterior fifth portion of head (PoOc/CL: 0.19–0.22). Anteromedian margin of clypeus with blunt angle; posterior margin slightly notched medially. Mandible subtriangular, equipped with six teeth. Antennal scape relatively long, apical third portion surpassing rear cephalic margin (SL/CS: 0.97–1.1). Anterior face of pronotum very short, cervical shield directly joining pronotal dorsum. Anterodorsal angle and anterior portion of dorsolateral junction of pronotum marginate. In dorsal view, mesonotum almost as long as broad, width narrowing posteriorly; metanotal groove slightly impressed near sides and vestigial medially. In lateral view, width of mesopleuron, as seen at spiracle level, about as large as width of lateral portion of propodeum. Dorsolateral margin of propodeum extended into sharp carina; sides of propodeum and declivitous surface separated by sharp margination; propodeal dorsum sloping posteriorly and joining declivitous margin by blunt or rounded angle; propodeal spiracle on lateral portion of propodeum, located anterior to posterolateral margin of propodeum. Procoxa as wide as meso-metapleuron. In profile, petiolar node anteroposteriorly compressed; anterior margin convex and posterior margin more or less straight; dorsal margin medially excised. Constriction between abdominal segments III and IV absent.

Head, mesosoma, and petiolar node shining with imbricating sculpture; gastral tergite finely imbricate. Mandible with sparse piligerous punctures between smooth and shining surface. Number of pairs of erect hairs arranged as follows: three on clypeus, one near margins of frontal carinae, one at level of eyes, and one close to posterior margin of head; none on pronotum; one on mesonotum and propodeum at junction of dorsum and declivity; none on petiole. Two erect hairs on dorsum of anterior portion of first gastral tergite and four erect hairs on anterior and posterior portion of dorsum of two following gastral tergites. Pubescence sparse and short. Head and mesosoma black to dark brown; coxa, petiolar node and gaster brown to light brown; appendages proximally whitish-yellow (depigmented yellow) and apically light brown to yellow.

Major worker. With characteristics of minor worker except the following divergent features: posterior margin of head straight; lateral margin straight posteriorly and convex from anterior level of eyes to base of mandible; mandible robust with strong concavity near base of lateroventral portion and armed with eight teeth; level of posterior ocular margin at posterior fourth portion of head (PoOc/CL: 0.24–0.26); antennal scape reaching posterior cephalic border (SL/CS: 0.67–0.71); anterior portion of head with scattered shallow punctures. Pair of erect hairs arranged as: one or two on pronotum and propodeum, one on mesonotum.

Distribution and biology. *Camponotus androy* is restricted to the spiny bush and thicket of Marovato region and the Réserve Spéciale Sainte Marie in the extreme south portion of Madagascar (Fig. 35). Across these areas, between 20 m and 200 m of alti-

tude, colony nests have been generally established in dead twigs above the ground and rarely in rotten logs or dead tree stumps.

Discussion. Workers of *C. androy* might be confused with those of *C. bevohitra* in that they have a more or less straight posterior margin of the petiolar node, a very short anterior margin of pronotum and slightly carinate posterolateral margin of the propodeum. However, *C. androy* is characterized by a narrower mesopleuron, which is about as large as the width of the lateral portion of the propodeum; at least one pair of erect hairs is present on the propodeal dorsum. In *C. bevohitra*, the mesopleural width, taken at the level of the metanotal spiracle, is much larger than the width of the lateral portion of propodeum; the propodeal dorsum lacks erect hairs.

The taxonomic decision for *Camponotus androy* based on qualitative morphology-based study is corroborated by multivariate morphometric analysis. This species is classified correctly by confirmatory LDA at 100% success.

***Camponotus bevohitra* Rakotonirina, Csősz & Fisher, sp. n.**

<http://zoobank.org/6F93F122-9030-4D7F-B7A0-71ECA6CC88FF>

Figures 9B, 21, 36

Holotype worker. Madagascar, Province Antananarivo, Réserve Spéciale d'Ambohitantely, Forêt d'Ambohitantely, 20.9 km 72° NE d'Ankazobe, -18.22528, 47.28683, 1410 m, montane rainforest, ex dead twig above ground, 17–22 Apr 2001 (Fisher, Griswold et al.) collection code: BLF03727 specimen code: CASENT0437247 (CASC).

Paratype. 10 workers with same data as holotype but with the following specimen codes: CASENT0437237, CASENT0437238, CASENT0437239, CASENT0437240, CASENT0437241, CASENT0437243, CASENT0437244, CASENT0437245, CASENT0437246, CASENT0437248, (BMNH, MHNG, MNHN, MSNG, CASC).

Additional material examined. MADAGASCAR: Province **Antananarivo:** Forêt de galerie, Andranorovitra, 24.0 km NNE Ankazobe, -18.11243, 47.19757, 1491 m, disturbed gallery montane forest, (B.L. Fisher et al.) (CASC); Réserve Naturelle Sohisika, Sohisika 24.6 km NNE Ankazobe, -18.10322, 47.18692, 1464 m, gallery montane forest, (B.L. Fisher et al.) (CASC); Réserve Spéciale Ambohitantely, Forêt d'Ambohitantely, 20.9 km 72° NE d'Ankazobe, -18.22528, 47.28683, 1410 m, montane rainforest, (Fisher, Griswold et al.) (CASC); Province **Fianarantsoa:** Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, -20.59333, 46.56333, 1550 m, montane rainforest (Fisher, Griswold et al.) (CASC).

Diagnosis. Anterior margin of petiolar node convex and posterior margin more or less straight; propodeal spiracle placed anterior to posterolateral margin of propodeum; head and mesosoma black to dark brown, gaster and appendages dark brown to yellow or depigmented yellow; cervical shield joining pronotal dorsum directly; junction of dorsal face to lateral face of propodeum without sharp carina, posterolateral margin

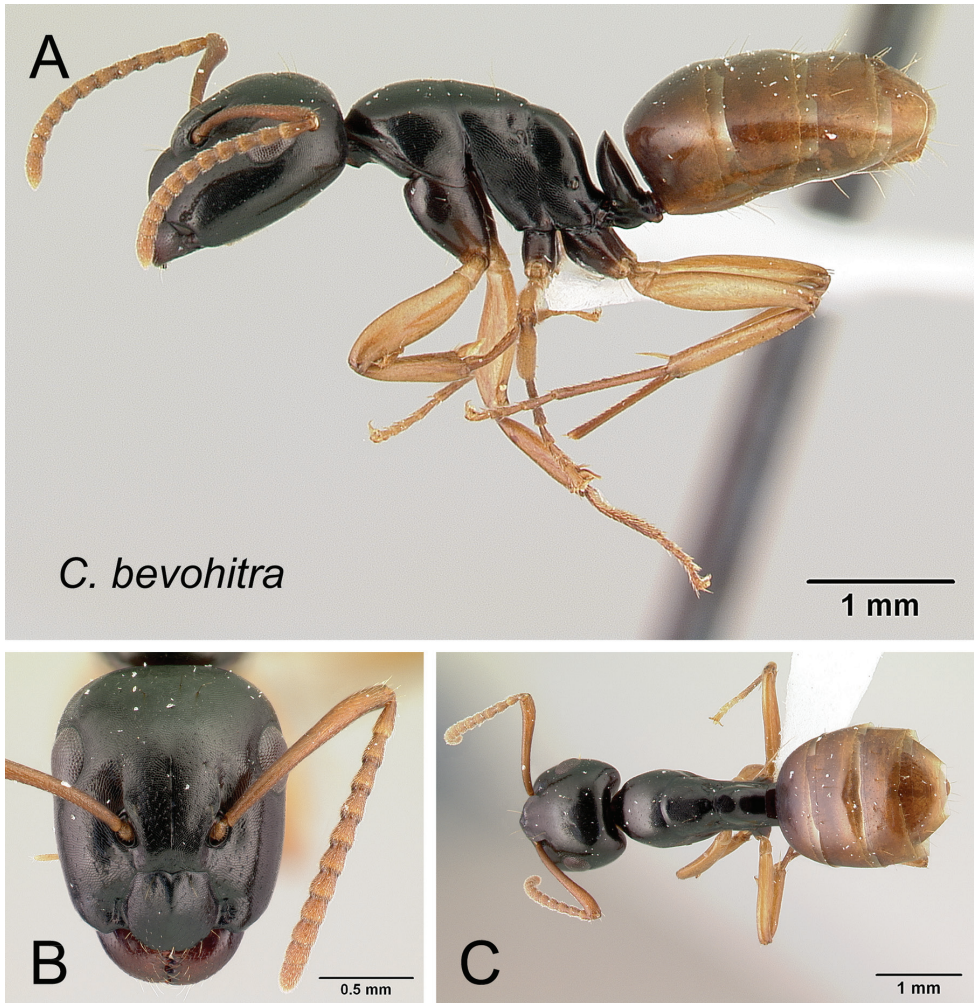


Figure 21. *Camponotus bevohitra* major worker CASENT0437238. **A** lateral view; **B** head in full-face view **C** dorsal view.

rounded; in profile mesopleuron much wider than lateral portion of propodeum; erect hairs lacking on propodeal dorsum.

Description. Minor worker (Fig. 9B). In full-face view head weakly longer than broad (CWb/CL: 0.78–0.85), posterior margin broadly convex; sides almost straight, their junction to posterior border concealed by eyes. Eyes large (EL/CS: 0.27–0.32) and strongly protruding, occupying roughly one third the side of head; level of posterior ocular margin at posterior fifth portion of head (PoOc/CL: 0.18–0.21). Antero-medial margin of clypeus straight; posteromedian margin slightly notched. Mandible subtriangular, armed with six teeth. Antennal scape relatively long (SL/CS: 0.905–1.109), more than apical third portion extending beyond posterior cephalic border. Promesonotal dorsum flattened; anterodorsal angle of pronotum and dorsolateral por-

tion of mesosoma bluntly marginate; posterolateral margin of propodeum rounding to declivitous surface. In dorsal view, mesonotum as long as broad, but sides converging posteriorly; mesonotum and propodeum laterally compressed at their junction; metanotal groove vestigial, represented by a transverse line. In lateral view, width of mesopleuron at the level of spiracle much wider than lateral portion of propodeum. Propodeal dorsum inclined posteriorly and rounding to declivitous margin; propodeal spiracle located anterior to posterolateral border of propodeum. Maximum width of coxa of foreleg as broad as meso-metapleuron width. In lateral view, petiolar node scale-like; anterior margin slightly convex and posterior margin more or less straight; dorsal margin straight or medially angulate. Junction between abdominal segments III and IV without constriction.

Dorsum of head, mesosoma shining with imbricate sculpture; gaster finely imbricate. Mandible coriarius-punctulate. Few erect hairs on clypeus and gastral tergites; one pair each near margin of frontal carina, on posterior cephalic portion, and on mesonotum. Erect hairs lacking from pronotum, propodeum, and petiolar node. Pubescence very scarce. Head, mesosoma, and petiole black to dark brown; gaster, mandible, antenna, coxa, and tarsus dark brown to brown; remainder of legs yellow.

Major worker (Fig. 21). With characteristics of minor worker with the exception of the following features: posterior margin of head straight and rounding to lateral margins; apical sixth portion of antennal scape surpassing posterior cephalic border (SL/CS: 0.753–0.852); metanotum visible between mesonotum and propodeum; sparse shallow punctures present laterally on head from level of anterior ocular margins and clypeus to base of mandible.

Distribution and biology. The distribution of *C. bevohitra* is limited to montane rainforest habitats in the central high plateau of Madagascar (Fig. 36). Specimens have been collected foraging on lower vegetation. The species nests in dead twigs or branches above the ground.

Discussion. See discussion of species differentiation under *C. androy*. In the present study, the definition of *C. bevohitra* based on both qualitative morphological analysis and morphometrics is congruent. The grouping shown by the morphometric dendrogram and confirmed by cumulative LDA at 100% success supports the existence of the species.

Camponotus echinoploides Forel

Figures 10A, 11A, 22, 37

Camponotus echinoploides Forel, 1891: 51. Holotype minor worker, Madagascar, 30 miles northwest Toamasina (=Tamatave) (O'swald), AntWeb CASENT0101379 (MHNG) [examined]. [Combination in *Camponotus* (*Myrmobrachys*): Forel 1914: 270; in *Camponotus* (*Orthonotomyrmex*): Emery 1920: 258; in *Camponotus* (*Myrmepinotus*): Santschi 1921: 312; Wheeler 1922: 1053; Emery 1925: 126; Bolton 1995: 97, 131].

Additional material examined. MADAGASCAR: Province **Antananarivo:** 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, -18.47333, 47.96, 1300 m, montane rainforest (Fisher, Griswold et al.) (CASC); Province **Antsiranana:** Réserve Spéciale Manongarivo, 14.5 km 220° SW Antanambao, -13.99833, 48.42833, 1175 m, montane rainforest, (B.L. Fisher) (CASC); Réserve Spéciale Manongarivo, 10.8 km 229° SW Antanambao, -13.96167, 48.43333, 400 m, rainforest (B.L. Fisher) (CASC); Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, -14.435, 49.76, 775 m, rainforest (B.L. Fisher) (CASC); Rés. Analamerana, 16.7 km 123° Anivorano-Nord, -12.80467, 49.37383, 225 m, tropical dry forest (B.L. Fisher) (CASC); Betaolana Forest, along Bekona River, -14.52996, 49.44039, 880 m, rainforest, (B.L. Fisher et al.) (CASC); Province **Fianarantsoa:** Parc National Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, Mount Papango, -23.83517, 46.96367, 940 m, rainforest (B.L. Fisher et al.) (CASC); radio tower, Ranomafana National Park, -21.25083, 47.40717, 1130 m, forest edge, mixed tropical forest, open area (M. Irwin, R. Harin'Hala) (CASC); JIRAMA water works near river, Ranomafana National Park, -21.2485, 47.45217, 690 m, open area near stream, (R. Harin'Hala) (CASC); Province **Mahajanga:** Réserve Spéciale Marotandrano, Marotandrano 48.3 km S Mandritsara, -16.28322, 48.81443, 865 m, transition humid forest, (B.L. Fisher et al.) (CASC); Province **Toamasina:** Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, -15.18833, 49.615, 470 m, rainforest, (Fisher, Griswold et al.) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, -15.28833, 49.54833, 600 m, rainforest (Fisher, Griswold et al.) (CASC); Parc National Mananara-Nord, 7.1 km 261° Antanambe, -16.455, 49.7875, 225 m, rainforest, (B.L. Fisher et al.) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, -18.80388, 48.40506, 1013 m, rainforest, (B.L. Fisher et al.) (CASC); Province **Toliara:** Forêt Classée Analavelona, 29.2 km 343° NNW Mahaboboka, -22.675, 44.19, 1100 m, montane rainforest (Fisher, Griswold et al.) (CASC).

Diagnosis. In profile, anterior and posterior margins of petiolar node convex; in profile, propodeum strongly compressed anteroposteriorly, without clear distinction between dorsal margin and declivity; in dorsal view, mesonotum three times as broad as long; posterodorsal corner of mesonotum raised into a bluntly rounded shield.

Description. Minor worker (Figs 10A, 11A, 22). In full-face view head as long as broad (CWb/CL: 0.94–1), broader posteriorly; posterior margin broadly convex, lateral margins roughly straight. Eyes larger relative to head size (EL/CS: 0.19–0.24), anterior level located at about posterior third of head (PrOc/CL: 0.52–0.6). Clypeus with broadly convex anterior margin and medially notched posterior margin. Mandible triangular, masticatory margin armed with six sharp teeth. Antennal scape slightly long (SL/CS: 0.9–1.05), distal half almost surpassing posterior cephalic margin. Pronotal dorsum flat, anteriorly projecting into narrow ridge; dorsum and lateral face separated by longitudinal margination. In dorsal view, mesonotum three times as broad as long, posterodorsal corner raised into bluntly rounded ridge. Propodeum strongly compressed anteroposteriorly and lacking a clear separation of the dorsal margin and

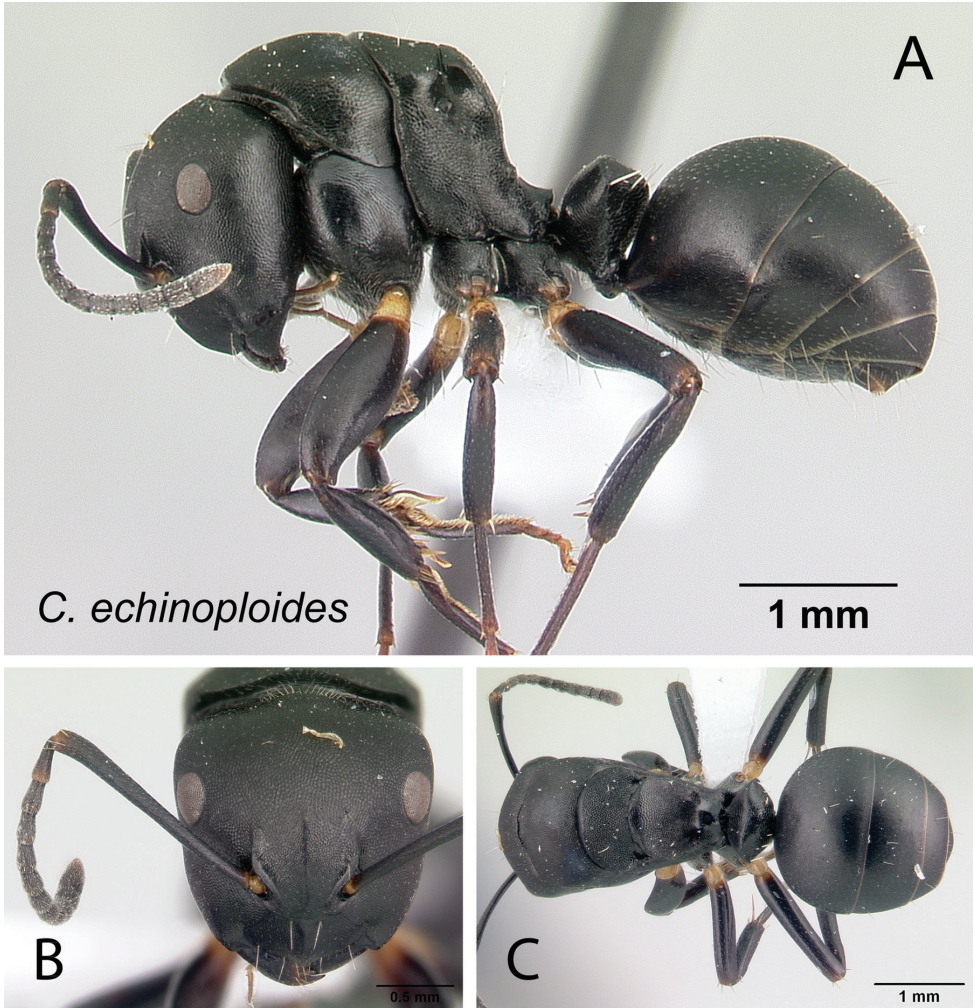


Figure 22. *Camponotus echinoploides* minor worker CASENT0409171. **A** lateral view **B** head in full-face view **C** dorsal view.

declivity. Propodeal spiracle located on posterior face of propodeum. Procoxa voluminous, maximum width as large as the combined width of meso-metapleuron and propodeal surface; femur of foreleg enlarged, twice as large as those of mid-leg and hind leg. Anterior and posterior margins of petiolar node convex. No constriction between abdominal segments III and IV.

Dorsum of head and mesosoma finely and densely reticulate punctate. Mandible finely and densely reticulate superimposed with scattered large punctures. Gastral segments covered with finely and densely reticulate punctate sculpture. Whitish erect hairs present as a pair on mesonotum and as two pairs near lateral margins of propodeum. Hairs lacking on pronotum. Whitish erect hairs present near lateral margins of

posterior face of petiolar node. Gastral segments with sparse and much shorter erect hairs and pubescence. Body color shining black; appendages black to dark brown basally, flagellum brown, trochanter and metatarsus light brown to yellow.

Major worker. Characteristics of minor worker, except: head in full-face view as long as broad (CWb/CL: 1.01–1.02), lateral margins almost parallel, but strongly converging near the base of mandibles. Eyes smaller relative to head size (EL/CS: 0.17), anterior level located roughly at mid-length of head (PrOc/CL: 0.51–0.51). Anterior clypeal margin truncate and posterior margin medially notched. Apical portion of antennal scape barely reaching posterior cephalic margin (SL/CS: 0.6–0.62). In dorsal view, mesonotum roughly twice as broad as long. Metanotum visible between metanotal groove and propodeum.

Distribution and biology. Endemic to Madagascar, *C. echinoploides* occupies the eastern rainforest (Fig. 37), areas with transitional northern rainforest, relict montane rainforest in the central plateau, and the southwest of the island. The fact that most of its members have been found foraging on low vegetation and nesting in dead branches above the ground suggests that *C. echinoploides* is arboreal.

Discussion. *Camponotus echinoploides* is mostly similar to *C. galoko*, but the latter has no extended shield rising from the posterodorsal corner of the mesonotum. The conventional taxonomic delimitation of *Camponotus echinoploides* is confirmed by the NC-clustering method. In addition, the recognition of the species is corroborated by confirmatory LDA at 100% classification success.

Camponotus edmondi André

Figures 14B, 15B, 16A, 23, 38

Camponotus edmondi André, 1887: 281. Lectotype minor worker, **present designation**, Toamasina (=Tamatave), Madagascar (E. André), AntWeb CASENT0101384 (MHNG) [examined]. [Combination in *Camponotus* (*Myrmobrachys*): Forel 1914: 270; in *Camponotus* (*Orthonotomyrmex*): Emery 1920: 258; Wheeler 1922: 1049; in *Camponotus* (*Myrmisolepis*): Santschi 1921: 310. in *Camponotus* (*Myrmepinotus*): Emery 1925: 127; Bolton 1995: 97, 131].

Camponotus edmondi var. *ernesti* Forel, 1891: 50. Syntype major worker, Madagascar, Toamasina Province, 30 miles northwest of Toamasina (=Tamatave) (O'Swald) [not examined]. [Combination in *Camponotus* (*Orthonotomyrmex*): Wheeler 1922: 1049; in *Camponotus* (*Myrmepinotus*): Emery 1925: 127; Bolton 1995: 97].

Syn. n.

Additional material examined. MADAGASCAR: Province **Antsiranana:** Forêt Ambanitaza, 26.1 km 347° Antalaha, –14.67933, 50.18367, 240 m, rainforest, (B.L. Fisher) (CASC); Forêt Ambanitaza, 26.1 km 347° Antalaha, –14.67933, 50.18367, 240 m, rainforest, (B.L. Fisher) (CASC); Vohemar, –13.37723, 50.0205, 25 m, cultivated land, (B.L. Fisher et al.) (CASC); Province **Fianarantsoa:** Manakara,

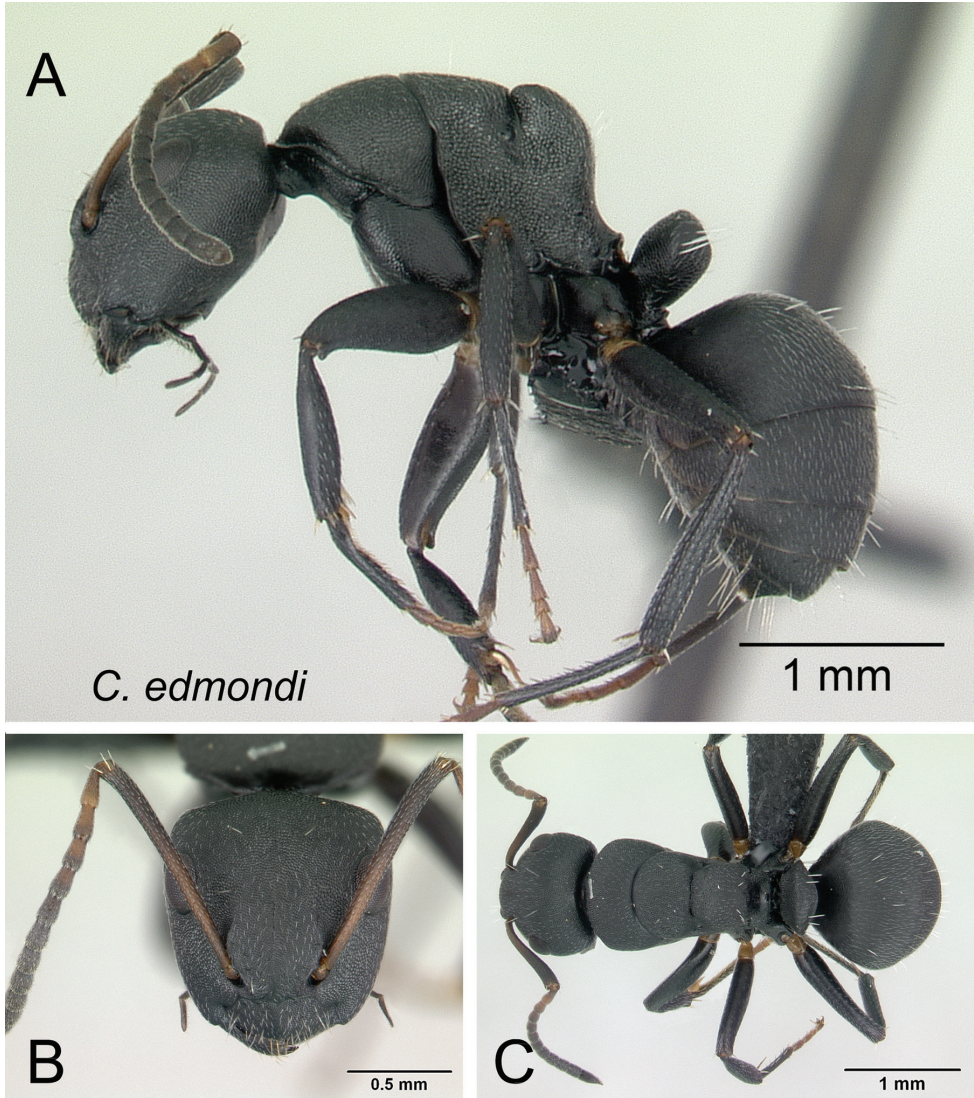


Figure 23. *Camponotus edmondi* minor worker CASENT0136511. **A** lateral view **B** head in full-face view **C** dorsal view.

–22.14817, 48.02267, 10 m, urban gardens, coastal *Casuarina equisetifolia*, (B.L. Fisher et al.) (CASC); Province **Toamasina**: Antongil Bay (Mocquerys) (MSNG); Brickaville, –18.82183, 49.07017, 24 m, urban/garden, (B.L. Fisher et al.) (CASC); Sainte Marie (MNHN); Ile Sainte Marie, Forêt Ambohidena, 22.8 km 44° Ambodifotatra, –16.82433, 49.96417, 20 m, littoral rainforest, (B.L. Fisher et al.) (CASC); Parcelle E3 Tampolo, –17.28104, 49.43012, 10 m, littoral forest, (Malagasy ant team) (CASC); Station Forestière Tampolo, 10 km NNE Fenoarivo Atsinanana, –17.2825, 49.43, 10 m, littoral rainforest, (B.L. Fisher) (CASC); Reserve Betampona, Camp

Vohitsivalana, 37.1 km 338° Toamasina, -17.88667, 49.2025, 520 m, rainforest, (B.L. Fisher et al.) (CASC); 11 km SE Ampasimanolotra, Brickaville, -18.9, 49.13333, 5 m, littoral rainforest, (P.S. Ward) (PSWC); Nosy Mangabe, -15.5, 49.76667, 5 m, littoral vegetation, (P.S. Ward) (PSWC); Province **Toliara**: 2.7 km WNW 302° Ste. Luce, -24.77167, 47.17167, 20 m, littoral rainforest, (B.L. Fisher) (CASC); Libanona beach, Tolagnaro, -25.03883, 46.996, 20 m, coastal scrub, (B.L. Fisher et al.) (CASC). **COMOROS: Anjouan**: Mount Ntringui, -12.19865, 44.41866, 740 m, montane forest, (B.L. Fisher et al.) (CASC); -12.18771, 44.35929, 65 m, coastal roadside, (B.L. Fisher et al.) (CASC); -12.18771, 44.35929, 65 m, coastal roadside, (B.L. Fisher et al.) (CASC); -12.30537, 44.45031, 500 m, along roadside, mango, banana, (B.L. Fisher et al.) (CASC); **Grande Comore**: Mouadja, -11.47435, 43.3004, 350 m, coastal scrub, (B.L. Fisher et al.) (CASC); Itoundzou, -11.63136, 43.30434, 635 m, secondary rainforest along roadside, (B.L. Fisher et al.) (CASC); Pidjani, -11.75447, 43.45148, 35 m, coastal scrub, (B.L. Fisher et al.) (CASC); Mouadja, -11.47435, 43.3004, 350 m, coastal scrub, (B.L. Fisher et al.) (CASC); **MAYOTTE**: Dapani, -12.96279, 45.15037, 135 m, rainforest, (B.L. Fisher et al.) (CASC); Reserve forestière Sohoa, -12.81237, 45.10476, 10 m, coastal dry forest, (B.L. Fisher et al.) (CASC); Mont Combani, -12.80632, 45.15314, 370 m, rainforest, (B.L. Fisher et al.) (CASC); Mont Benara, -12.87585, 45.15672, 425 m, rainforest, (B.L. Fisher et al.) (CASC); Baie de Tsingoni, -12.7926, 45.10764, 5 m, mangrove, coastal scrub, (B.L. Fisher et al.) (CASC); Mont Chongui, -12.95776, 45.13403, 470 m, rainforest, (B.L. Fisher et al.) (CASC); Mont Chongui, -12.95903, 45.13411, 380 m, rainforest, (B.L. Fisher et al.) (CASC); Mont Chongui summit, -12.99567, 45.13428, 550 m, rainforest, (B.L. Fisher et al.) (CASC); Coconi, DAF Campus, -12.83333, 45.13333, (R. Jocqué) (CASC); Dziani Karihani, -12.78333, 45.11667, forest (R. Jocqué & G. DeSmet) (CASC); Mont Combani, -12.80632, 45.15314, 370 m, rainforest, (B.L. Fisher et al.) (CASC).

Diagnosis. In profile, anterior and posterior margins of petiolar node convex; in profile, propodeal dorsum and declivitous surface separated by blunt angle; in dorsal view, mesonotum less than twice as broad as long; mesopleuron with propodeal surface distinctly wider together than lateral portion of pronotum; in profile, propodeal dorsum roughly as long as declivitous margin; dorsum of head and mesosoma densely and finely reticulate-punctate; erect hairs lacking on dorsum of pronotum; distance between meso-metapleural suture and dorsolateral margin of propodeum largest near the junction of dorsolateral carina to declivitous surface; in dorsal view, lateral margins of mesonotum roughly straight and gradually converging posteriorly; width of propodeum at the metanotal groove less than half the maximum width of mesonotum; in full-face view, anteromedian margin of clypeus truncate.

Description. Minor worker (Figs 14B, 15B, 16A, 23). Head elongate in full-face view (CWb/CL: 0.87–0.93), slightly diverging posteriorly; posterior margin convex medially and more or less straight near posterolateral corners; lateral margins slightly convex. Eyes larger relative to head size (EL/CS: 0.24–0.28), their anterior level located at about mid-length of head (PrOc/CL: 0.52–0.58). Anterior clypeal margin truncate;

posterior margin weakly notched medially. Mandible triangular, apical margin armed with six sharp teeth which reduce in size towards basal angle of the mandible. Antennal scape short (SL/CS: 0.89–1.06), apical third of its length surpassing posterior cephalic margin. Pronotum dorsally flat, anterodorsal angle marginate. In dorsal view, mesonotum less than twice as broad as long, posterodorsal corner rounded. In lateral view, propodeum not strongly compressed anteroposteriorly, dorsum strongly inclined posteriorly and separated with declivitous surface by blunt angle; mesopleuron with propodeal surface together distinctly wider than lateral portion of pronotum; propodeal dorsum and lateral surface separated by blunt margination; propodeal spiracle on declivitous surface. Coxa of foreleg larger than width of meso-metapleuron. In profile, anterior margin of petiolar node convex, posterior margin inclined posteriorly and then approximately vertically straight to posteroventral angle. Constriction between abdominal segments III and IV lacking.

Dorsum of head and mesosoma finely and densely reticulate punctate; lateral surfaces of head finely and densely reticulate punctate with much smaller punctures. Imbricate sculpture on gastral tergites. Mandible smooth and shiny with sparse piligerous punctures. Whitish hairs lacking on pronotum; several pairs on head dorsum from clypeus, frontal lobe to posterior portion of head; one pair on mesonotum; few pairs arranged transversely at mid-height of posterior face of propodeum; hairs arranged near lateral and dorsal borders of posterior face of petiolar node; scattered and much shorter erect hairs arranged near anterior and posterior margins of each gastral tergite; pubescence not abundant. Color of body, femur, and tibia black; trochanter and tarsi brown to light brown; antenna brown basally and dark brown apically.

Major worker. With characteristics of minor worker, except: head in full-face view feebly longer than broad (CWb/CL: 0.94–1) and slightly decreasing in width towards the base of mandibles; posterior margin slightly convex; sides broadly convex. Eyes smaller relative to head size (EL/CS: 0.22–0.24), their posterior level located roughly at posterior fourth of head (PoOc/CL: 0.27–0.29). Anterior margin of clypeus truncate and slightly concave. Antennal scape slightly extending beyond posterior cephalic margin. In dorsal view, metanotum visible between metanotal groove and propodeum. In profile, petiolar node much more flattened anteroposteriorly. Head with scattered piligerous punctures laterally near base of mandibles. Dorsum of pronotum with few pairs of whitish erect hairs.

Distribution and biology. *Camponotus edmondi* is known from Madagascar, Comore, and Mayotte Islands (Fig. 38). In Madagascar, it is generally distributed along the eastern littoral forests and in human-modified habitats. In neighboring islands, the species occurs also in coastal forests and disturbed forest habitats. Rarely is it found in rainforest between 130 m and 650 m of altitude. Foraging is done arboreally and nests sites are in dead twigs and branches above the ground.

Discussion. *Camponotus edmondi* looks similar to *C. orombe* and *C. tafo*, but for *C. orombe* there is no distinct angle separating the propodeal dorsum from the declivitous margin in profile, and the distance between the meso-metapleural suture and the dorsolateral margin of the propodeum remains the same along the dorsolateral

carina of the propodeum. As in *C. tafo*, the lateral margins of mesonotum are convex and converge strongly posteriorly while the width of the propodeum at the metanotal groove is more than half the maximum width of the mesonotum. *Camponotus mifaka* has numerous hairs on the dorsum of the mesosoma.

Camponotus edmondi ernesti was created by Forel (1891) because of its smaller body size, finer sculpture, and the shape of its propodeum. We were not able to examine the type specimen, but based on the observation of the specimens belonging to this subspecies, collected by Mocquerys in the Antongil Bay, and located at MSNG (Italy), there is no strong distinctive morphological traits between the members of the subspecies and those of *C. edmondi*. Therefore, *C. edmondi ernesti* is synonymized under *C. edmondi*. As *C. edmondi* is more or less widespread in the littoral forests of the Malagasy region, morphological variation within this species can be expected.

The identity of *C. edmondi* based on the traditional qualitative taxonomy has been detected by the multivariate morphometrics. The grouping of the samples of *C. edmondi* generated by NC-clustering method is corroborated by confirmatory LDA with a classification success of 100%.

***Camponotus ethicus* Forel**

Figures 6A, 7A, 24, 39

Camponotus ethicus Forel, 1897: 200. Lectotype minor worker, **present designation**, Madagascar, Antsiranana Province, Sakatia bay, Nosy Be (Voeltzkow), AntWeb CASENT0101389 (MHNG) [examined]. Paralectotypes: 2 workers and 2 males, of same data as lectotype, but worker and male respectively specimen coded as: CASENT0101388 and CASENT0101387 (MHNG); CASENT0101176 and CASENT0101177 (NHMB) [examined]. [Combination in *Camponotus* (*Myrmentoma*): Forel 1912: 92; in *Camponotus* (*Orthonotomyrmex*): Forel 1914: 273; Emery 1920: 258; Wheeler 1922: 1049; in *Camponotus* (*Myrmisolepis*): Santschi 1921: 310; in *Camponotus* (*Myrmepinotus*): Emery 1925: 127].

Additional material examined. MADAGASCAR: Province **Antsiranana:** Galoko chain, Mont Kalabenono, -13.64609, 48.67732, 937 m; -13.64179, 48.67282, 643 m; -13.63999, 48.67374, 498 m, rainforest, (B.L. Fisher et al.) (CASC); Réserve Spéciale d'Ambre, 3.5 km 235° SW Sakaramy, -12.46889, 49.24217, 325 m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Province **Mahajanga:** Forêt d'Anabohazo, 21.6 km 247° WSW Maromandia, -14.30889, 47.91433, 120 m, tropical dry forest, (Fisher, Griswold et al.) (CASC).

Diagnosis. Larger species (CS: 1.92–2.58; ML: 3.49–4.18) with uniformly black to dark brown body color; in profile anterior margin of petiolar node convex and posterior margin straight; level of the propodeal dorsum abruptly lower than level of the promesonotal dorsum; pronotal dorsum without numerous erect hairs; humeral angle extended anteriorly into a narrow ridge.

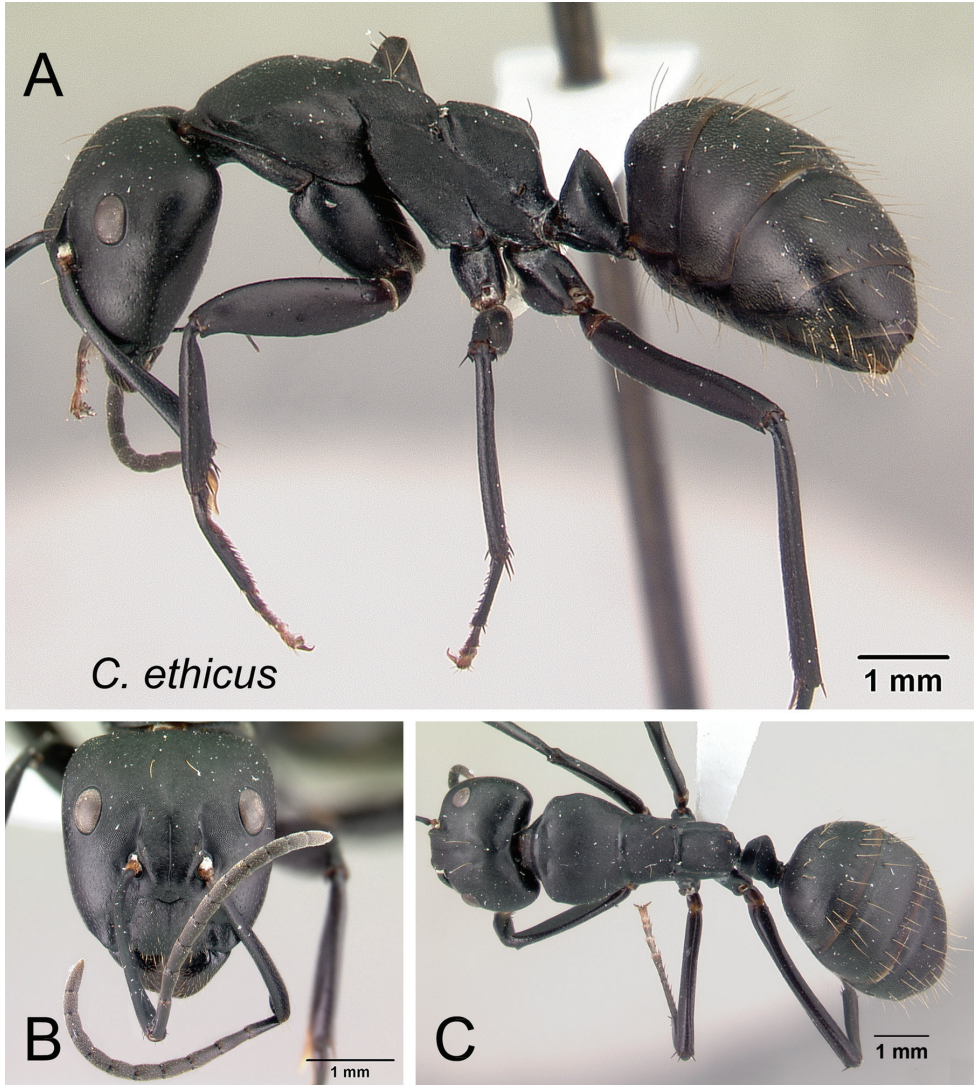


Figure 24. *Camponotus ethicus* minor worker CASENT0409948. **A** lateral view **B** head in full-face view **C** dorsal view.

Description. Minor worker (Figs 6A, 7A, 24). In full-face view head subquadrate (CWb/CL: 0.87–0.89), slightly diverging posteriorly; posterior margin more or less straight. Eyes not breaking lateral outline of head, their posterior level located at posterior fifth portion of head (PoOc/CL: 0.21–0.25). Anterior clypeal margin straight; posterior margin weakly notched medially. Mandible triangular, apical margin armed with six sharp teeth. Antennal scape long, apical half surpassing posterior cephalic margin. Pronotal dorsum flat, anterodorsal corner projecting anteriorly into narrow ridge; anterior margination present; pronotal dorsum and lateral portion anteriorly

separated by sharp margination. In dorsal view, mesonotum as long as broad; in profile, mesonotal dorsum inclined posteriorly and propodeal dorsum nearly horizontal and distinctly situated at lower level than promesonotum; mesopleuron and propodeal surface together distinctly longer than lateral portion of pronotum; propodeal dorsum almost horizontal and declivitous surface nearly vertical; propodeal spiracle located anterior to posterolateral margin of propodeum. Width of procoxa larger than width of mesopleuron. In profile anterior margin of petiolar node convex and posterior margin more or less straight. Constriction between abdominal segments III and IV lacking.

Dorsum of head and mesosoma with fine and dense imbrication. Imbricate sculpture much finer and denser on gastral tergites. Mandible imbricate and superimposed with sparse large punctures. Erect hairs lacking on pronotum; one pair present on mesonotum, propodeum near junction of dorsum and declivity, and upper level of lateral margin of petiole. Few pairs of erect hairs on head dorsum from clypeus and edge of frontal lobe to posterior portion of head; several scattered pairs organized transversely on anterior and posterior portions of each gastral tergite; pubescence short and reduced in number. Body coloration black; appendages dark reddish black.

Major worker. With characteristics of minor worker, except: head much more square (CL/CWb: 1.008–1.08); lateral margins slightly convex. Eyes located more anteriorly, their posterior level on posterior fourth of head (PoOc/CL: 0.227–0.252). One third of apical portion of scape extending beyond posterior cephalic margin. Scattered piligerous punctures present laterally on head from the level of anterior margin of eyes to near base of mandible.

Distribution and biology. Known from the dry forests of the Parc National Sahamalaza and the Reserve Spéciale Ambre, and the transitional rainforest of the Galoko Chain in the northwestern part of Madagascar (Fig. 39), *C. ethicus* is arboreal, forages most often on lower vegetation, and nests in dead branches above the ground.

Discussion. The lower level of the propodeal dorsum relative to the promesonotum and the larger body size combined with the dark color of the legs make *C. ethicus* easy to separate from *C. robustus* and the rest of the species in the *edmondi* group. The delimitation of *C. ethicus* based on qualitative morphology-based taxonomy is congruent with the classification hypothesis provided by the NC-clustering algorithm, strengthening its status as a species.

***Camponotus galoko* Rakotonirina, Csősz & Fisher, sp. n.**

<http://zoobank.org/0DE61664-AFA1-4B06-A0BF-542C74E29F20>

Figures 10B, 11B, 25, 40

Holotype worker. Madagascar, Province Antsiranana, Forêt de Binara, 9.1 km 233° SW Daraina, –13.26333, 49.60333, 650–800 m, rainforest, ex rotten log, 5 Dec 2003 (B.L. Fisher et al.) collection code BLF09814, specimen code CASENT0178918 (CASC).

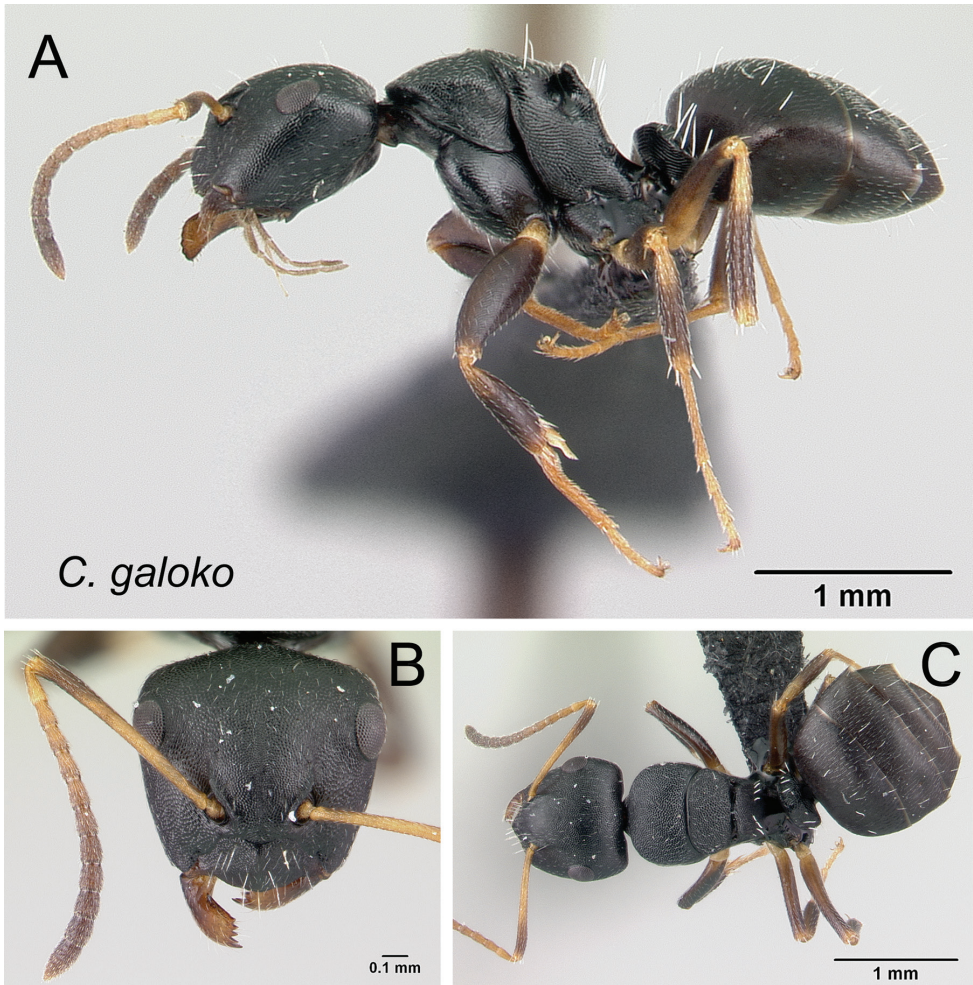


Figure 25. *Camponotus galoko* minor worker CASENT0178918. **A** lateral view **B** head in full-face view **C** dorsal view.

Paratypes. 8 workers same data as holotype but with the following specimen codes: CASENT0076246, CASENT0076247, CASENT0076248, CASENT0746972, CASENT0746973, CASENT0746974, CASENT0746975, CASENT0746976 (BMNH, MHNG, MSNG, CASC).

Additional material examined. MADAGASCAR: Province **Antsiranana:** Forêt de Binara, 9.1 km 233° SW Daraina, -13.26333, 49.60333, 650–800 m, rainforest, (B.L. Fisher) (CASC), Galoko chain, Mont Galoko, -13.5888, 48.72864, 980 m, montane forest, (B.L. Fisher et al.) (CASC); Galoko chain, Mont Galoko, -13.59358, 48.73157, 1100 m, montane forest, (B.L. Fisher et al.) (CASC); Galoko chain, Mont Kalabenono, -13.64609, 48.67732, 937 m, rainforest, (B.L. Fisher et al.) (CASC).

Diagnosis. In profile, anterior and posterior margins of petiolar node convex; in profile, propodeum strongly compressed anteroposteriorly, without clear distinction between dorsal margin and declivity; in dorsal view, mesonotum twice as broad as long; posterodorsal corner of mesonotum without extended shield.

Description. Minor worker (Figs 10B, 11B, 25). In full-face view head slightly longer than broad (CWb/CL: 0.94–0.99), slightly diverging posteriorly; posterior margin broadly convex, lateral margins roughly straight. Eyes larger relative to size of head (EL/CS: 0.23–0.25), their posterior level located at about posterior fourth of head (PoOc/CL: 0.2–0.25). Anterior clypeal margin transverse; posterior margin medially notched. Mandible triangular, apical margin armed with six sharp teeth, which reduce in size towards basal angle of the mandible. Antennal scape short (SL/CS: 0.81–0.98), one fourth of the length surpassing posterior cephalic margin. Pronotum flat dorsally, anteriorly projecting into narrow ridge; dorsolateral portion longitudinally marginate. In dorsal view, mesonotum twice as broad as long, posterodorsal corner rounded, without extended lobe; lateral margin convex and strongly convergent posteriorly. Propodeum strongly compressed anteroposteriorly, dorsal margin and declivity not distinctly separated; posterolateral portion extending laterally into sharp ridge. Propodeal spiracle on lower third of posterior face of propodeum. Maximum width of procoxa as large as the width of meso-metapleuron and propodeal surface together; femur of foreleg enlarged, twice as large as those of mid-leg and hind leg. Anterior and posterior margins of petiolar node convex. No constriction between abdominal segments III and IV.

Dorsum of head and mesosoma finely and densely reticulate punctate. Mandible finely and densely reticulate superimposed with scattered large punctures. Finer and denser reticulate punctures present on gastral tergites. Pronotum with a few pairs and mesonotum with one pair of whitish erect hairs; whitish hairs gathered at mid-height of posterior face of propodeum; whitish erect hairs present at mid-height of near lateral and on dorsal margins of posterior face of petiolar node; gastral segments with scattered and much shorter erect hairs; pubescence more abundant on gastral tergite than mesosomal dorsum. Integument shining black, antenna brown basally and darker apically; basal portion of mandible and leg dark brown, apical portion and trochanter light brown to yellowish-orange.

Major worker. Characteristics of minor worker, except: head in full-face view roughly as long as broad (CWb/CL: 0.96–1.03), lateral margins slightly convex and slightly converging near base of mandibles. Eyes smaller relative to head size (EL/CS: 0.19–0.22), their posterior level located roughly at posterior fourth of head (PoOc/CL: 0.27–0.31). Anterior margin of clypeus truncate and posterior. Antennal scape not extending beyond posterior cephalic margin. In dorsal view, metanotum visible between metanotal groove and propodeum. In lateral view, petiolar node more compressed anteroposteriorly. Lateral portion of head near base of mandible with sparse, large, piligerous punctures.

Distribution and biology. This species is known only from the transitional humid forests of the Daraina and Galoko chain in the north of Madagascar (Fig. 40). The data indicate that individual workers forage on lower vegetation, while nests are mostly found in dead twigs above the ground and rarely in rotten logs.

Discussion. *Camponotus galoko* is mostly similar to *C. echinoploides*, but the postero-dorsal corner of the mesonotum in the latter raises into a bluntly rounded shield. *Camponotus galoko* has a strongly anteroposteriorly flattened propodeum without a clear distinction between the propodeal dorsum and the declivity while the other species in the *edmondi* group have a propodeal dorsum and a declivitous surface separated by a blunt angle.

The taxonomic argument for *C. galoko* is strengthened by the congruence between the results of traditional qualitative morphology and the NC-clustering technique. However, the classification success is only 90.91%, because its one minor worker is misclassified as *C. varatra* by the confirmatory LDA with a low posterior probability of 0.76. This suggests that the entire range of minor worker forms of these species might not have been measured, and both species are closely related and have similar quantitative and qualitative morphology. Yet the two are distinguished by a morphological trait not easily incorporated into the morphometric approach. The dorsum of the head and mesosoma of *C. galoko* are densely and finely reticulate whereas those of *C. varatra* and *C. zavo* are smooth, shining, and superimposed by imbrication.

***Camponotus matsilo* Rakotonirina, Csósz & Fisher, sp. n.**

<http://zoobank.org/0364FA72-21E3-4C38-9944-AAA36894D9AA>

Figures 12A, 26, 41

Holotype worker. Madagascar, Province Toliara, Forêt Vohidava 88.9 km N Amboasary, -24.24067, 46.28783, 500 m, spiny forest/dry forest transition, ex dead twig above ground, 7 Dec 2006 (B.L. Fisher et al.) collection code BLF15725, specimen code CASENT0121843 (CASC).

Paratypes. 1 worker with same data as holotype but specimen coded as CASENT0178919 (CASC).

Additional material examined. MADAGASCAR: Province **Toliara:** Forêt Vohidava 88.9 km N Amboasary, -24.24067, 46.28783, 500 m, spiny forest/dry forest transition, (B.L. Fisher et al.) (CASC); Parc National d'Andohahela, Forêt d'Ambohibory, 1.7 km 61° ENE Tsimelaha, 36.1 km 308° NW Tolagnaro, -24.93 46.6455, 300 m, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Parc National d'Andohahela, Forêt de Manatalinjo, 33.6 km 63° ENE Amboasary, 7.6 km 99° E Hazofotsy, -24.81694, 46.61, 150 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Parc National de Zombitse, 19.8 km 84° E Sakaraha, -22.84333, 44.71, 770 m, tropical dry forest, (Fisher, Griswold et al.) (CASC); Réserve Spéciale de Cap Sainte Marie, 14.9 km 261° W Marovato, -25.59444, 45.14683, 160 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC).

Diagnosis. In profile, anterior and posterior margins of petiolar node convex; in profile, propodeal dorsum and declivitous surface separated by blunt angle; in dorsal view, mesonotum less than twice as broad as long; mesopleuron with propodeal surface together distinctly wider than lateral portion of pronotum; in profile, dorsolateral carina of propodeum much longer than its posterolateral margin.

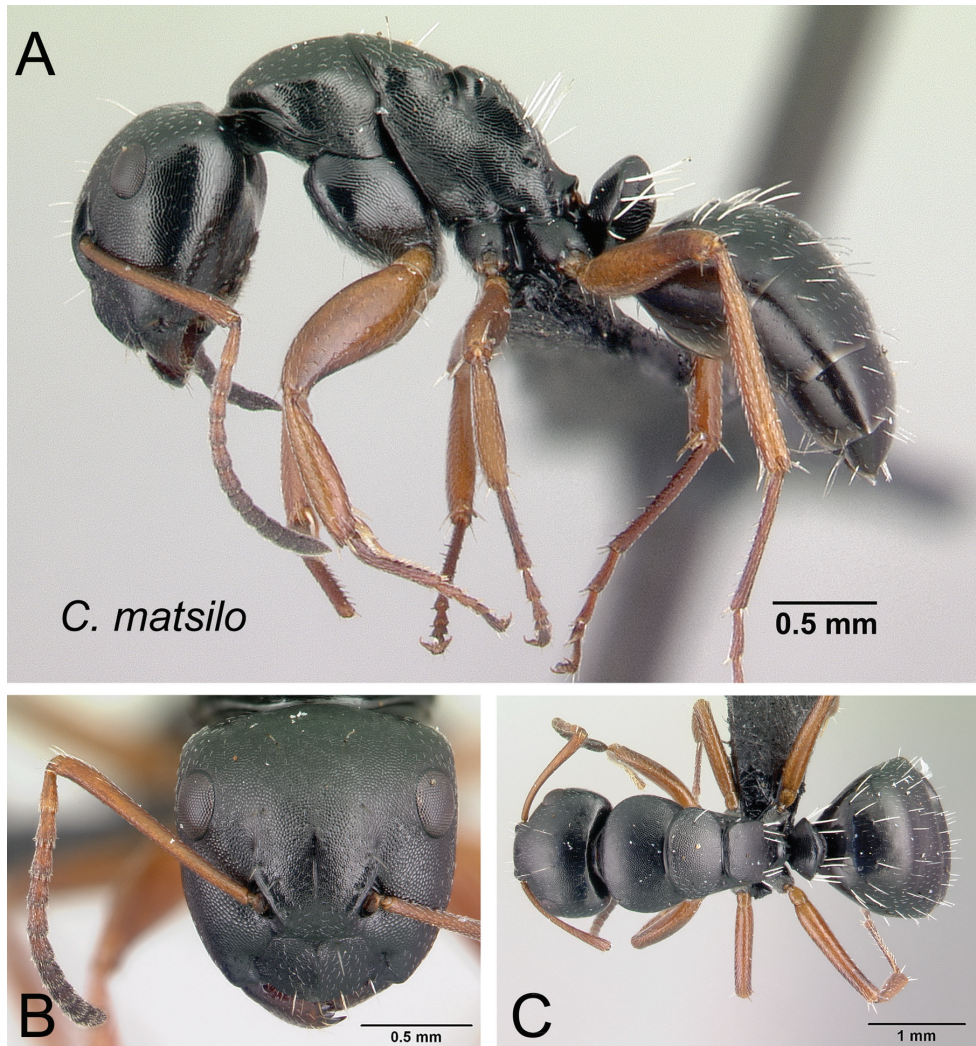


Figure 26. *Camponotus matsilo* minor worker CASENT0121843. **A** lateral view **B** head in full-face view **C** dorsal view.

Description. Minor worker (Figs 12A, 26). In full-face view head slightly longer than broad (CWb/CL: 0.88–0.94), lateral margins weakly convex and converging anteriorly; posterior margin feebly convex. Eyes located more on posterior portion of head (PoOc/CL: 0.18–0.23), posterior level of eyes at posterior fifth of head. Anteromedian margin of clypeus triangular; posterior margin weakly notched medially. Mandible triangular, masticatory margin armed with six teeth. Antennal scape short (SL/CS: 0.87–0.94), apical third portion roughly surpassing posterior margin of head. Pronotum flat dorsally, anterodorsal margin projecting anteriorly into narrow ridge; dorsum and sides of promesonotum separated by margination. In dorsal view, mesonotum narrow, less than twice as broad as long. In profile, mesopleuron and lateral

propodeal face together distinctly longer than lateral portion of pronotum; propodeal dorsum and declivitous surface separated by blunt angle. In profile, dorsolateral carina of propodeum much longer than declivity. Maximum width of procoxa larger than width of meso-metapleuron. In profile, anterior margin of petiolar node convex and posterior margin either convex or roughly triangular; propodeal spiracle located on declivitous surface or at posterolateral margin of the propodeum.

Dorsum of head and mesosoma finely and densely reticulate punctate. Gastral segments covered with fine and dense reticulation. Mandible finely and densely reticulate superimposed with scattered large punctures. Whitish erect hairs: several pairs of on dorsum of head; absent on pronotum, one pair on mesonotum, few pairs near dorsolateral margin of propodeum and at junction of dorsum and declivity, arranged on posterior face of petiolar node near lateral margins; organized transversely on anterior and posterior portions of each gastral tergite. Pubescence not abundant. Head, mesosoma, and petiole black; gaster dark brown; basal portion of antenna light brown to yellow and apical portion dark brown; trochanter to tip of tarsi light brown to yellow.

Major worker. With characteristics of minor worker, except: head much more subquadrate (CWb/CL: 0.96); eyes located roughly on posterior third of head capsule (PoOc/CL: 0.28–0.29); antennal scape not extending beyond posterior cephalic margin; inclination of propodeal dorsum much more vertical in profile. Head capsule microreticulate superimposed with scattered punctures in the anterior portion from the anterior level of eyes to base of mandibles. Mandibles smooth and shiny between sparse punctures. Two pairs of whitish erect hairs aligned at about the same level on posterior portion of head behind posterior level of eyes; three to four pairs on pronotum and five pairs on mesonotum. Mandible color much darker than other appendages.

Distribution and biology. Occurring in the south of Madagascar, the distribution of *C. matsilo* is ranging from the dry forest habitats of the PN Zombitse and the PN Andohahela through the transitional spiny forest of Vohidava to the spiny bush and thicket of Cap Sainte Marie in the extreme south (Fig. 41). In these habitats, the species mostly forages on low vegetation and its colonies are found frequently in dead twigs above ground.

Discussion. *Camponotus matsilo* can be easily separated from other species by the fact that its propodeal dorsum is distinctly longer than its propodeal declivity in lateral view.

The qualitative morphology-based study of this species agrees with the multivariate morphometric analysis to support the taxonomic determination for *C. matsilo*.

***Camponotus mifaka* Rakotonirina, Csösz & Fisher, sp. n.**

<http://zoobank.org/2A5DC5AD-5C2A-4BBE-B427-5ABD020752C7>

Figures 14A, 27, 42

Holotype worker. Madagascar, Antsiranana, Parc National de Marojejy, 25.4 km 30° NNE Andapa, 10.9 km 311° NW Manantenina, –14.445, 49.735, 2000 m, montane shrubland, ex root mat, ground layer, 24 Nov 2003 (B.L. Fisher et al.) collection code BLF09351, specimen code CASENT0217301 (CASC).



Figure 27. *Camponotus mifaka* minor worker CASENT0217301. **A** lateral view **B** head in full-face view **C** dorsal view.

Paratypes. 8 workers same data as holotype but with the following specimen codes: CASENT0486999, CASENT0487000, CASENT0487001, CASENT0746965, CASENT0746966, CASENT0746967, CASENT0746970, CASENT0746971 (BMNH, MHNG, MSNG, CASC).

Additional material examined. MADAGASCAR: Province **Antsiranana:** Parc National Marojejy, 25.4 km 30° NNE Andapa, 10.9 km 311° NW Manantenina, -14.445, 49.735, 2000 m, montane shrubland, (B.L. Fisher) (CASC).

Diagnosis. In profile, anterior and posterior margins of petiolar node convex; in profile, propodeal dorsum and declivitous surface separated by blunt angle; in dorsal view, mesonotum less than twice as broad as long; mesopleuron with propodeal sur-

face together distinctly wider than lateral portion of pronotum; in profile, propodeal dorsum roughly as long as declivitous margin; dorsum of head and mesosoma densely and finely reticulate punctate; dorsum of mesosoma covered with numerous erect hairs and pubescence.

Description. Minor worker (Figs 14A, 27). In full-face view, head elongate (CWb/CL: 0.9–0.95), diverging posteriorly; posterior margin slightly convex. Level of posterior ocular margins located generally on posterior fifth portion of head (PoOc/CL: 0.21–0.25). Anterior margin of clypeus straight; posterior margin medially notched. Mandible triangular, apical margin armed with six sharp teeth. Antennal scape relatively long (SL/CS: 0.92–1.02), more than one third of apical portion of antennal scape extending beyond posterior cephalic margin. Promesonotum slightly, broadly convex, dorsum and sides separated by margination; anterodorsal angle of pronotum projecting anteriorly into a ridge. In dorsal view, mesonotum less than twice as broad as long; posterodorsal angle without extended lobe. In lateral view, propodeum not strongly compressed anteroposteriorly; dorsal portion of propodeum raised and abruptly strongly sloping posteriorly; junction to declivity marked by blunt angle; dorsolateral portion of propodeum marginate, distance between meso-metapleural suture and dorsolateral margin of propodeum remaining the same along dorsolateral margin of propodeum; propodeal spiracle located on declivitous surface. Width of meso-metapleuron and propodeal lateral portion together noticeably greater than width of lateral portion of pronotum. In side view, maximum width of procoxa larger than width of meso-metapleuron. In profile, anterior and posterior margins of petiolar node convex. Junction of abdominal segments III and IV without visible constriction.

Dorsum of head anteriorly finely and densely reticulate punctate, the punctures deepening posteriorly. Mandible smooth and shining between scattered punctures. Mesosoma dorsum finely and densely reticulate punctate. Gastral tergites smooth and shining apart from shallow punctures from which erect hairs or pubescence arise. Pairs of whitish erect hairs numerous on dorsum of head and mesosoma; hairs randomly scattered on gastral tergites. Erect hair present on declivitous surface above propodeal spiracle. Near posterolateral margins to posterodorsal corner of petiolar node with a row of whitish erect hairs. Much shorter and sparse erect hairs organized transversely on anterior and posterior portions of each gastral tergite; pubescence reduced. Integument generally black; basal portion of legs dark brown and becoming lighter towards metatarsi; antennal scape basally brown and apically black to dark brown.

Major worker. With characteristics of minor worker, except: head larger relative to whole body size (ML/CS: 1.29–1.35); shape relatively subquadrate (CWb/CL: 0.93–0.95) with lateral margins slightly converging to base of mandibles; posterior margin more or less straight. Eyes positioned more on frontal portion of head, level of posterior ocular margins located approximately on posterior fourth portion of head (PoOc/CL: 0.23–0.25); mandible strong; one sixth of apical portion of antennal scape surpassing posterior cephalic margin (SL/CS: 0.92–0.96). Scattered punctures on dorsolateral portion of head near base of mandible.

Distribution and biology. Known only from the montane shrubland of the Parc National Marojejy (Fig. 42), *Camponotus mifaka* forages in leaf mold and rotten wood and nests under root mats in the ground.

Discussion. *Camponotus mifaka* might be confused with *Camponotus edmondi*, *C. orombe*, and *C. tafo* because of the dense and fine reticulate-punctate sculpture on the dorsum of the head and mesosoma; however, the latter three species have a reduced number of erect hairs on the dorsum of the mesosoma, particularly on the promesonotal dorsum.

Based on the information provided by the NC-clustering method, the cluster of *C. mifaka* contains one sample of *C. varatra*, but is classified successfully at 100% by LDA. The integration of this successful classification with the results from qualitative morphological study and biological evidence underscores the robustness of the taxonomic determination for this species. *Camponotus varatra* differs morphologically from *C. mifaka* by its imbricate sculpture and biologically by its nesting sites in dead twigs or branches above the ground.

***Camponotus orombe* Rakotonirina, Csósz & Fisher, sp. n.**

<http://zoobank.org/C02F05C1-3464-402D-BCA9-914AA06EADBD>

Figures 15A, 28, 43

Holotype worker. Madagascar, Province Toliara, Forêt Ivohibe 55.0 km N Tolagnaro, –24.569, 47.204, 200 m, rainforest, ex dead twig above ground, 12 Mar 2006 (B.L. Fisher et al.) collection code: BLF15534, specimen code: CASENT0178923 (CASC).

Paratypes. 3 workers, 1 worker same data as holotype but with specimen code CASENT0122867; 2 workers with the following data: Forêt Ivohibe 55.6 km N Tolagnaro, –24.56167, 47.20017, 650 m, rainforest, beating low vegetation, 12 Apr 2006, BLF15587 and CASENT0122787, BLF15628 and CASENT0121500 (BMNH, CASC).

Additional material examined. MADAGASCAR: Province **Toliara:** Forêt Ivohibe 55.0 km N Tolagnaro, –24.569, 47.204, 200 m, rainforest, (B.L. Fisher et al.) (CASC); Forêt Ivohibe 55.6 km N Tolagnaro, –24.56167, 47.20017, 650 m, rainforest, (B.L. Fisher et al.) (CASC).

Diagnosis. In profile, anterior and posterior margins of petiolar node convex; in profile, propodeal dorsum and declivitous surface separated by blunt angle; in dorsal view, mesonotum less than twice as broad as long; mesopleuron with propodeal surface together distinctly wider than lateral portion of pronotum; in profile, propodeal dorsum roughly as long as declivitous margin; dorsum of head and mesosoma densely and finely reticulate punctate; erect hairs lacking on dorsum of pronotum; distance between meso-metapleural suture and dorsolateral margin of propodeum not changing along the dorsolateral carina of propodeum.

Description. Minor worker (Figs 15A, 28). In full-face view head slightly longer than broad (CWb/CL: 0.88); lateral margins weakly convex and converging slightly

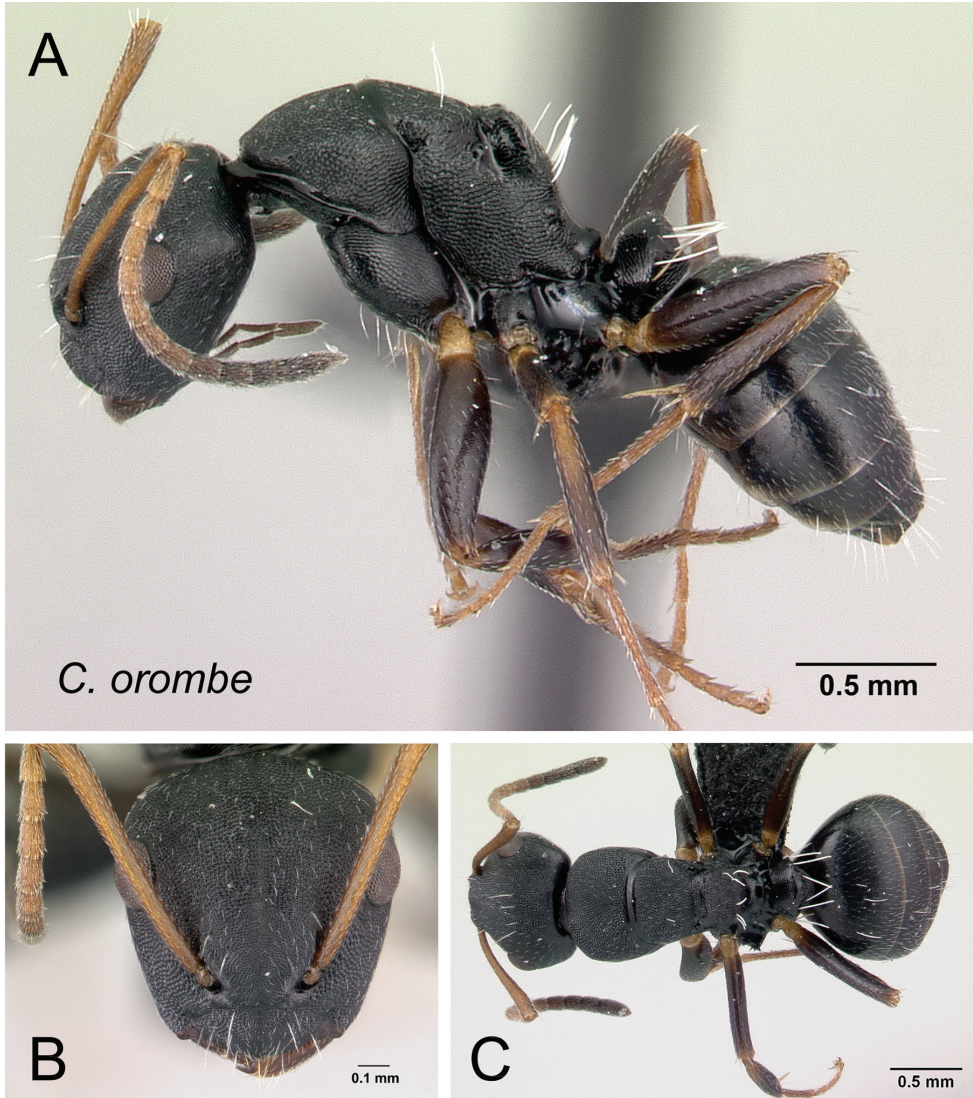


Figure 28. *Camponotus orombe* minor worker CASENT0178923. **A** lateral view **B** head in full-face view **C** dorsal view.

towards base of mandibles; posterior border broadly convex. Level of posterior ocular margins at about posterior fourth portion of head (PoOc/CL: 0.23–0.24). Anteromedian margin of clypeus with slightly blunt angle; posterior margin weakly notched. Mandible triangular, masticatory margin with six teeth. Antennal scape relatively long, distal portion almost extending beyond posterior border of head. In lateral view, pronotum dorsally flat, anterior margin projecting into narrow ridge; dorsolateral portion of promesonotum longitudinally marginate. In dorsal view, mesonotum less than twice as broad as long, posterodorsal corner without visible posterior lobe; lateral margin

convex and gradually converging to metanotal groove. In lateral view, propodeum strongly compressed anteroposteriorly, junction between dorsal margin and declivity not distinctly visible; ridge on posterolateral portion distinct; distance between meso-metapleural suture and posterolateral ridge of propodeum remaining the same along dorsolateral carina of propodeum. Propodeal spiracle on lower third of posterior face of propodeum. Maximum width of procoxa as large as width of meso-metapleuron and propodeal surface together. In lateral view, anterior margin of petiolar node convex; posterior margin sloping posteriorly to about mid-height and descending almost vertically to posteroventral angle. No constriction between abdominal segments III and IV.

Dorsum of head, mesosoma, and petiolar node with fine and dense reticulate punctures. Mandible with sparse piligerous punctures between smooth surfaces. Numerous pairs of whitish erect hairs on dorsum of head; one pair on mesonotum; numerous erect hairs arranged along junction of propodeal dorsum and declivity. No erect hair on declivitous surface above propodeal spiracle level. Posterior face of petiole with a row of four erect hairs near lateral margin and posterodorsal angle. Shorter and slender erect hairs organized transversely on anterior and posterior portions of each gastral tergite. Pubescence present on dorsum of head, mesosoma, petiole and gaster. Head, mesosoma, and petiole black in color; antennal scape and first five flagellar segments, mandible, trochanter, and tarsus yellow to light brown; gaster, apical portion of antennal segments, femur, and tibia dark brown.

Major worker. Similar to minor worker, but with the following divergent characters: in full-face view, head subquadrate (CWb/CL: 0.98), lateral borders almost parallel and converging strongly near base of mandibles; level of posterior margins of eyes located at about posterior third portion of head (PoOc/CL: 0.3). Anterior margin of clypeus medially excised; mandible robustly built; antennal scape barely surpassing posterior cephalic border. Anterior portion of pronotum not strongly marginate; in dorsal view, metanotum visible between metanotal groove and propodeum. Junction of dorsum and sides of propodeum more or less rounded; petiolar node more flattened anteroposteriorly.

Distribution and biology. *Camponotus orombe* is known only from a few individual workers collected from Ivohibe Forest between 200 m and 650 m of altitude in the southeast of Madagascar (Fig. 43). They were found foraging on low vegetation and nesting in dead twigs above the ground.

Discussion. *Camponotus orombe* can be confused to *C. mifaka*, but the latter has numerous erect hairs on the dorsum of its mesosoma. *Camponotus orombe* can be differentiated from *C. tafo* and *C. edmondi* by the fact that the propodeum of these two latter species is not strongly compressed anteroposteriorly and the distance between the meso-metapleural suture and the dorsolateral margin of the propodeum is largest near the junction of the dorsolateral carina and the declivitous surface.

In the morphometric dendrogram, *C. orombe* is represented by a successfully classified small cluster of three individual specimens that falls close to the cluster of *C. varatra*, *C. tafo*, *C. mifaka*, *C. zavo*, and *C. tratra*. Based on qualitative morphology, *C. varatra*, *C. zavo*, and *C. tratra* differ from *C. orombe* by the sculpture on the dorsum of

their head and mesosoma, which is imbricate or smooth and shiny with sparse piligerous punctures. This information supports the separation of *C. orombe* from the other three species.

***Camponotus robustus* Roger**

Figures 7B, 29, 44

Camponotus robustus Roger, 1863: 135. Lectotype minor worker, **present designation**, Madagascar (Humblot), AntWeb CASENT0101390 (MHNG) [examined]. Paralectotypes of 5 workers: 2 in the same pin as lectotype; 2 workers with the same data but specimen coded as CASENT0104621 and CASENT0104622 (ZMHB) [examined]. Combination in *Camponotus* (*Myrmentoma*): Forel 1912: 92; in *Camponotus* (*Orthonotomyrmex*): Forel 1914: 273; Emery 1920: 258; Wheeler 1922: 1049; in *Camponotus* (*Myrmisolepis*): Santschi 1921: 310; in *Camponotus* (*Myrmepinotus*): Emery 1925: 127; Bolton 1995: 120, 131].

Additional material examined. MADAGASCAR: Province **Antsiranana:** Forêt Ambanitaza, 26.1 km 347° Antalaha, -14.67933, 50.18367, 240 m, rainforest, (B.L. Fisher) (CASC); Forêt de Binara, 9.1 km 233° SW Daraina, -13.26333, 49.60333, 800 m, rainforest (B.L. Fisher et al.) (CASC); Makirovana forest, -14.10295, 50.01984, 90 m, rainforest (B.L. Fisher et al.) (CASC); Province **Fianarantsoa:** Réserve Forestière d'Agalazaha, Mahabo, 42.9 km 215° Farafangana, -23.19383, 47.723, 20 m, littoral rainforest, (B.L. Fisher et al.) (CASC); Réserve Spéciale Manombo 24.5 km 228° Farafangana, -23.01583, 47.719, 30 m, rainforest, (B.L. Fisher et al.) (CASC); Province **Toamasina:** Ile Sainte Marie, Forêt Ambohidena, 22.8 km 44° Ambodifotatra, -16.82433, 49.96417, 20 m, littoral rainforest, (B.L. Fisher et al.) (CASC); Parc National Mananara-Nord, 7.1 km 261° Antanambe, -16.455, 49.7875, 225 m, rainforest, (B.L. Fisher et al.) (CASC); Station Forestière Tampolo, 10 km NNE Fenoarivo Atsinanana, -17.2825, 49.43, 10 m, littoral rainforest, (B.L. Fisher) (CASC); Sahafina Forest 11.4 km W Brickaville, -18.81445, 48.96205, 140 m, rainforest, (B.L. Fisher et al.) (CASC); Mahavelona (Foulpointe), -17.66667, 49.5, in sandy forest (A. Pauly) (CASC); Forêt d'Analava Mandrisy, 5.9 km 195° Antanambe, -16.48567, 49.847, 10 m, littoral rainforest, (B.L. Fisher et al.) (CASC); Réserve Ambodiriana, 4.8 km 306° Manompana, along Manompana River, -16.67233, 49.70117, 125 m, rainforest, (B.L. Fisher et al.) (CASC); Parc National Masoala, 39.7 km 151° SSE Maroantsetra, -15.71333, 49.97167, 150 m, rainforest, (B.L. Fisher, H.J. Ratsirarson) (CASC); 11km SE Ampasimanolotra (= Brickaville), -18.9, 49.13333, 5 m, littoral rainforest (P.S. Ward) (PSWC).

Diagnosis. Larger species (CS: 1.882–3.725; ML: 3.098–4.666) with uniformly black to dark brown body color; in profile anterior margin of petiolar node convex and posterior margin straight; level of propodeal dorsum not abruptly lower than level of promesonotal dorsum; pronotum covered with numerous erect hairs and pubescence.

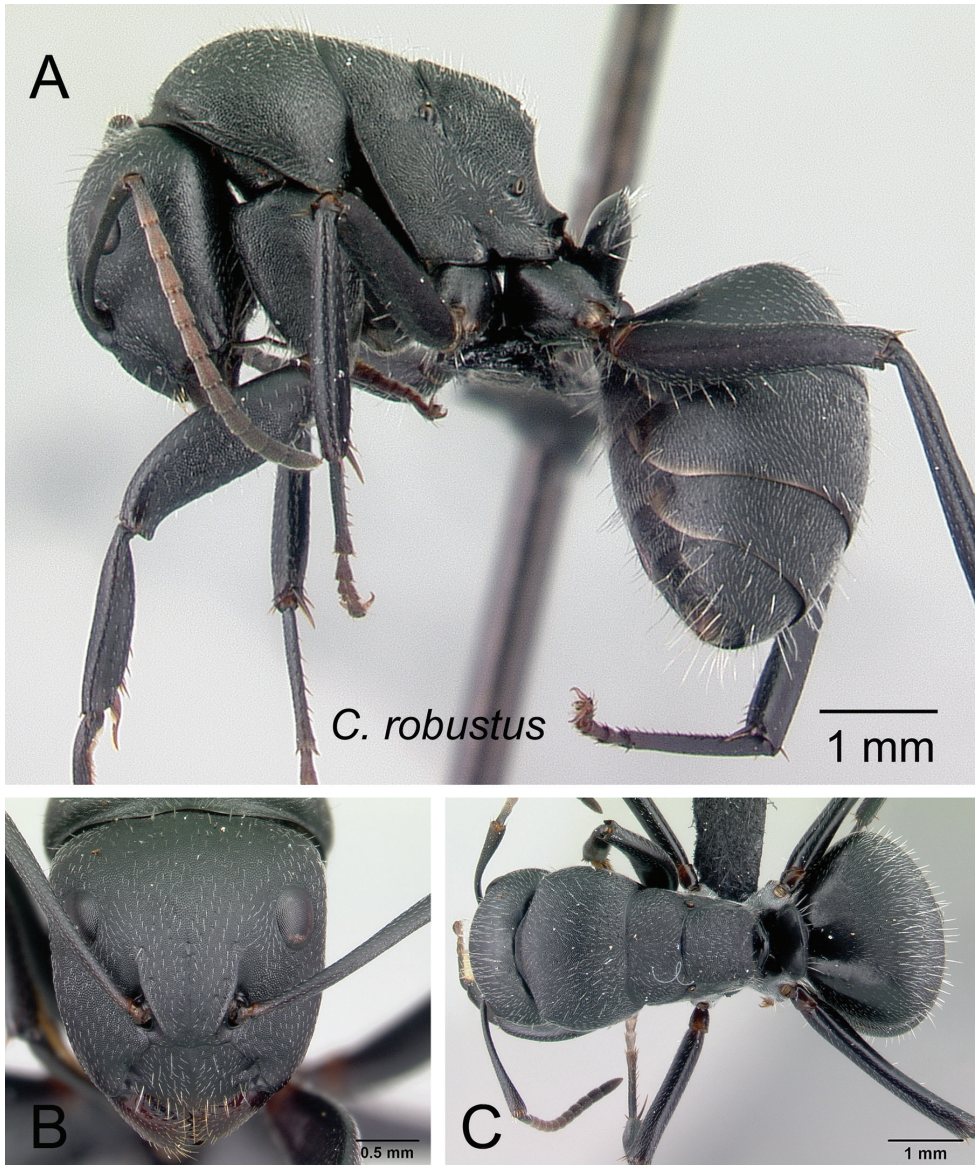


Figure 29. *Camponotus robustus* minor worker CASENT0066723. **A** lateral view **B** head in full-face view **C** dorsal view.

Description. Minor worker (Figs 7B, 29). In full-face view head rectangular and longer than broad (CWb/CL: 0.91–0.98); lateral margins nearly straight and slightly diverging posteriorly; posterior margin broadly convex. Eyes not breaking lateral outline of head, posterior level located at posterior fourth portion of head (PoOc/CL: 0.21–0.27). Anterior clypeal margin broadly triangular. Mandible triangular, apical margin armed with six teeth. More than apical third portion of antennal scape surpassing posterior cephalic margin. Anterodorsal corner of pronotum projecting anteriorly into narrow ridge;

anterior margination strong near corner and weak towards the center; pronotal dorsum rounding to lateral portion. In dorsal view, mesonotum broader than long. In lateral view, mesonotal dorsum slightly inclined posteriorly as is the propodeal dorsum, which joins the declivity at a blunt angle; mesopleuron and propodeal surface together distinctly longer than lateral portion of pronotum; propodeal spiracle located on lateral portion of propodeum anterior to posterolateral margin. Maximum width of procoxa larger than width of meso-metapleuron. In profile anterior margin of petiolar node convex and posterior margin more or less straight. Constriction between abdominal segments III and IV absent.

Dorsum of head, mesosoma, and gaster finely and densely reticulate rugose. Lateral portion of head finely and densely reticulate punctate. Mandible imbricate superimposed with punctures. Whitish yellow erect hairs numerous on head, mesosoma, and gaster. Petiole with erect hairs from lateral margins to posterodorsal angle. Pubescence abundant. Head, mesosoma, antennal scape, and distal portion of flagellum, femur, tibia, and basitarsus black; trochanter and metatarsi as well as basal portion of flagellum brown.

Major worker. With characteristics of minor worker, except: head broader than long (CWb/CL: 0.98–1.02); sides slightly convex and strongly converging towards base of mandibles. Eyes located more anteriorly, their posterior level on posterior third of head (PoOc/CL: 0.26–0.3). Antennal scape barely extending beyond posterior cephalic margin. Anteromedian portion of pronotum without margination. Lateral portion of head smooth and shining with scattered small punctures from which short hairs arise. Mandible with longitudinal striation near apical margin apart from fine imbrication and piligerous punctures.

Distribution and biology. *Camponotus robustus* occurs in the rainforests of eastern Madagascar, from Binara in the north to Ivohibe Forest in the south (Fig. 44). The species is both terrestrial and arboreal. Its workers forage individually on the forest floor, on lower vegetation, and in the canopy and nest in rotten logs, rotting tree stumps, or in dead branches above the ground.

Discussion. *Camponotus robustus* is similar to *C. ethicus*, but the latter has no erect hairs on the dorsum of the mesosoma and has a propodeal dorsum lower than the promesonotum. The remainder of the *edmondi* group can be distinguished from this species by their smaller size and yellow to brown legs.

Species delimitation of *C. robustus* based on traditional qualitative taxonomy is congruent with the grouping generated by the morphometric dendrogram and the species was classified correctly at 100% by the confirmatory LDA.

***Camponotus tafo* Rakotonirina, Csősz & Fisher, sp. n.**

<http://zoobank.org/9236C3BC-645D-44C1-BD20-5A416996BD84>

Figures 10D, 13A, 16B, 30, 45

Holotype worker. Madagascar, Toamasina Parc National de Masoala, 39.4 km 150° SSE Maroantsetra, –15.71, 49.97, 200 m, rainforest, canopy moss and leaf litter, 28 Nov–3 Dec 2001 (B.L. Fisher, H.J. Ratsirarson) collection code BLF04700 specimen code CASENT0763608 (CASC).

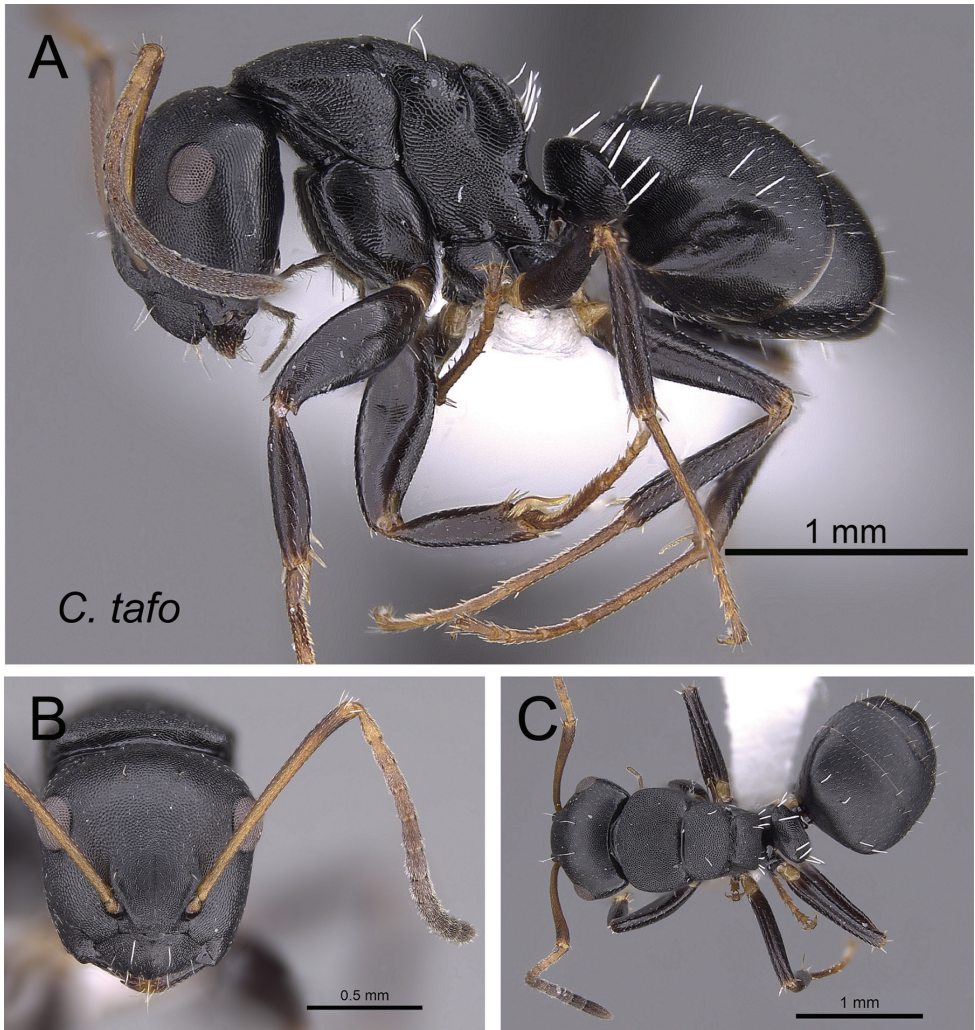


Figure 30. *Camponotus tafo* minor worker CASENT0763608. **A** lateral view **B** head in full-face view **C** dorsal view.

Paratypes. 4 workers same data as holotype but with specimen codes: CASENT0418183, CASENT0418184, CASENT0746968, CASENT0746969 (BMNH, MHNG, CASC).

Additional material examined. MADAGASCAR: Province **Toamasina:** Ankera-na Forest, $-18.40829, 48.82107, 750$ m, rainforest, (B.L. Fisher et al.) (CASC); Parc National Masoala, 39.4 km 150° SSE Maroantsetra, $-15.71, 49.97, 200$ m, rainforest, (B.L. Fisher, H.J. Ratsirarson) (CASC).

Diagnosis. In profile, anterior and posterior margins of petiolar node convex; in profile, propodeal dorsum and declivitous surface separated by blunt angle; in dorsal view, mesonotum less than twice as broad as long; mesopleuron with propodeal sur-

face together distinctly wider than lateral portion of pronotum; in profile, propodeal dorsum roughly as long as declivitous margin; dorsum of head and mesosoma densely and finely reticulate punctate; erect hairs lacking on dorsum of pronotum; distance between meso-metapleural suture and dorsolateral margin of propodeum largest near the junction of dorsolateral carina to declivitous surface; in dorsal view, lateral margins of mesonotum convex and strongly converging posteriorly; width of propodeum at metanotal groove greater than half the maximum width of mesonotum; in full-face view, anteromedian margin of clypeus triangular.

Description. Minor worker (Figs 10D, 13A, 16B, 30). In full-face view head about as long as wide (CWb/CL: 0.91–0.97), lateral margins roughly straight and slightly converging anteriorly; posterior margin broadly convex. Eyes located on posterior fifth portion of head (PoOc/CL: 0.19–0.22). Anteromedian margin of clypeus triangular; posterior margin weakly notched medially. Mandible triangular, apical margin armed with six teeth reducing in size towards basal angle of mandible. Antennal scape long, roughly the apical half of its length surpassing posterior cephalic margin. Pronotum flat dorsally, anterodorsal margin projecting anteriorly into narrow ridge; dorsum and sides of promesonotum separated by margination. In dorsal view, mesonotum less than twice as broad as long, posterodorsal corner rounded. In lateral view, propodeum not strongly compressed anteroposteriorly; propodeal dorsum strongly sloping posteriorly; junction to declivity marked by blunt angle; in dorsal view, mesonotum longitudinally narrow, less than twice as broad as long; width of meso-metapleuron and side of propodeum together distinctly much greater than width of side of pronotum; dorsolateral portion of propodeum bluntly marginate; propodeal spiracle located on declivitous surface. Maximum width of coxa of foreleg larger than width of meso-metapleuron. In profile, anterior face of petiolar node convex, posterior face sloping posteriorly and then descending vertically to posteroventral angle. Constriction between abdominal segments III and IV absent.

Dorsum of head and mesosoma finely and densely reticulate punctate. Imbricate sculpture on gastral tergites. Mandible finely and densely reticulate superimposed with scattered large punctures. Pronotum without whitish hairs; few pairs present on head dorsum from clypeus, and edge of frontal lobe to posterior portion of head; one pair on mesonotum; several pairs scattered on propodeal dorsum; petiolar node with whitish hairs arranged near lateral and dorsal borders of posterior face; scattered and much shorter erect hairs organized transversely on anterior and posterior portions of each gastral tergite; pubescence reduced. Body color black; antenna brown basally and dark brown apically; femur and tibia dark brown, trochanter and tarsi light brown.

Major worker. Unknown.

Distribution and biology. This species is known from the rainforest of Ankerana and the PN Masoala (Fig. 45). In Masoala, individual workers have been collected only from the moss and leaf litter of the canopy while at Ankerana one worker was collected from a Malaise trap, suggesting a preference for canopy microhabitat.

Discussion. *Camponotus tafo* is very similar to *C. edmondi*, but the latter is characterized by a mesonotum with lateral margins that are roughly straight and gradually

converge posteriorly in dorsal view. In *C. edmondi*, the width of the propodeum at the metanotal groove is less than half the maximum width of the mesonotum; with head in full-face view, anteromedian margin of clypeus is truncate.

From the NC-clustering dendrogram, *C. tafo* includes one sample of *C. varatra* and *C. zavo*, indicating that they are morphologically similar species. However, the confirmatory LDA successfully classified *C. tafo* at 100%, with no additional samples from other species included. According to the qualitative morphology method, *C. varatra* and *C. zavo* can be separated from *C. tafo* by their sculpture and nesting sites. In the two former species, the dorsum of the head and mesosoma is smooth and shining or imbricate. Their colony nests are built in dead twigs or branches slightly above the forest floor but never in the canopy. Thus, the separation of *C. tafo* from both species is sustained.

***Camponotus tratra* Rakotonirina, Csősz & Fisher, sp. n.**

<http://zoobank.org/DC902FCA-266A-42E6-9B57-DED5155930D8>

Figures 17A, 17B, 31, 46

Holotype worker. Madagascar, Province Toamasina, Parc National de Zahamena, Sahavorondrano River, –17.75257, 48.85725, 765 m, rainforest, beating low vegetation, 23 Feb 2009 (B.L. Fisher et al.) collection code: BLF22401, specimen code: CASENT0153055 (CASC).

Additional material examined. MADAGASCAR: Province **Antsiranana**, Makirovana forest, –14.17066, 49.95409, 225 m, rainforest, (B.L. Fisher et al.) (CASC); Parc National Montagne d’Ambre [1st campsite], –12.51444, 49.18139, 960 m, rainforest, (R. Harin’Hala) (CASC); Réserve Spéciale Manongarivo, 10.8 km 229° SW Antanambao, –13.96167, 48.43333, 400 m, rainforest, (B.L. Fisher) (CASC); Province **Fianarantsoa**: 1 km E of Isalo National Park Interpretive Center, –22.62667, 45.35817, 885 m, dry wash (R. Harin’Hala) (CASC); stream area, 900 m E of Isalo National Park Interpretive Center, –22.62667, 45.35817, 750 m, open area near stream, (R. Harin’Hala) (CASC); Province **Toamasina**: Parc National Zahamena, Sahavorondrano River, –17.75257, 48.85725, 765 m, rainforest, (B.L. Fisher et al.) (CASC); Province **Toliara**: Parc National Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, –24.7585, 46.85367, 275 m, rainforest, (B.L. Fisher et al.) (CASC).

Diagnosis. In profile, anterior and posterior margins of petiolar node convex; in profile, propodeal dorsum and declivitous surface separated by blunt angle; in dorsal view, mesonotum less than twice as broad as long; mesopleuron with propodeal surface together distinctly wider than lateral portion of pronotum; in profile, propodeal dorsum roughly as long as declivitous margin; dorsum of head and mesosoma smooth and shiny or imbricate; in profile, mesonotal dorsum strongly sloping down to the level of propodeum, maximum length of mesonotum about as long as distance between metanotal groove and propodeal spiracle; in dorsal view, lateral margin of mesonotum not well defined and converging gradually towards metanotal groove.

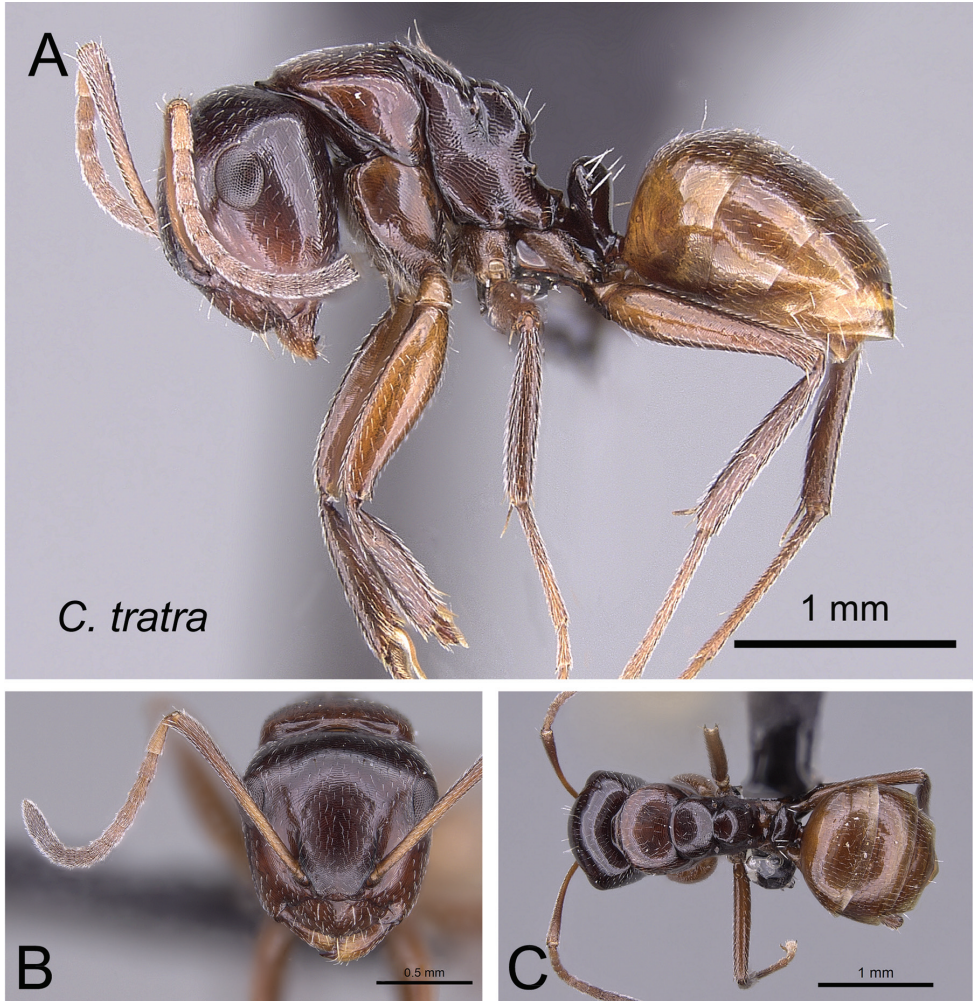


Figure 31. *Camponotus tratra* minor worker CASENT0153055. **A** lateral view **B** head in full-face view **C** dorsal view.

Description. Minor worker (Figs 17A, 17B, 31). In full-face view head roughly as long as broad (CWb/CL: 0.91–0.97), lateral borders more or less straight and weakly diverging posteriorly; posterior cephalic margin broadly convex. Level of posterior ocular margins located at less than posterior fifth portion of head (PoOc/CL: 0.19–0.22). Anterior clypeal margin broadly convex. Mandible triangular, armed with six teeth. Antennal scape relatively long (SL/CS: 0.96–1.13), apical half almost surpassing posterior cephalic border. Pronotal dorsum flattened, anterodorsal angle projecting anteriorly narrow edge; dorsolateral portion without margination. In dorsal view, mesonotum less than twice as broad as long; lateral margin of mesonotum not well defined and converging gradually towards metanotal groove; in lateral view, mesonotal dorsum inclined posteriorly and lowering level of propodeum; length of mesonotum about

as long as distance between metanotal groove and propodeal spiracle. In lateral view, dorsum of propodeum raised into a very short edge and then suddenly inclined posteriorly to join the declivitous surface. In lateral view, dorsolateral carina of propodeum weakly visible and roughly as long as declivitous margin; meso-metapleuron and lateral propodeal surface together distinctly broader than lateral portion of pronotum. Coxa of foreleg broad, maximum width greater than width of meso-metapleuron. In profile, anterior and posterior margins of petiolar node convex and rounding dorsal margin. Constriction between abdominal segments III and IV lacking.

Dorsum of head, mesosoma, petiolar node, and gastral tergite smooth and shining, superimposed with fine and dense imbrication and small punctures from which erect hairs and pubescence arise. Mandible sparsely punctulate. Pronotal dorsum without erect hairs; mesonotum with one pair, and propodeum with two or more pairs; erect hair lacking just above propodeal spiracle. Posterior face of petiolar node near lateral margin and posterodorsal angle with a row of four erect hairs; slender erect hairs arranged transversely on dorsum of petiolar node, on anterior and posterior portions of each gastral tergite. Body color generally brown, with much darker head, mesonotum, propodeum, and petiolar node.

Major worker. With characteristics of minor worker except for the following features: larger head (CS: 1.58) with straight rear margin; level of posterior margin of eyes located at about posterior third of head (PoOc/CL: 0.3); anterior clypeal margin transverse; antennal scape barely extending beyond posterior cephalic margin (SL/CS: 0.75); more robust mandible; two pairs or more of whitish erect hairs on dorsum of pronotum, mesonotum, and propodeum.

Distribution and biology. Known only from Madagascar, *Camponotus tratra* has a sparse but wide distribution from Parc National Montgne d'Ambre in the north through Makirovana Forest in the northeast and Réserve Spéciale Manongarivo in the northwest, to Parc National Zahamena in the central east and Parc National Andohahela in the southeast (Fig. 46). Workers of this species have been sampled most often from low vegetation and rarely from leaf litter and one nest was found in dead branches above the ground.

Discussion. *Camponotus tratra* is very similar to *C. zavo* and *C. varatra*, but the latter two species have a mesonotal dorsum slightly inclined posteriorly whose length is distinctly shorter than the distance between the metanotal groove and the propodeal spiracle in profile. Also, in the two latter species the lateral margins of the mesonotum are well defined and convex in dorsal view, converging strongly towards the metanotal groove.

The NC-clustering method groups all samples of *C. tratra* together in the dendrogram with a classification success of 100%. However, one specimen of *C. varatra* was placed in the *C. tratra* cluster and was misclassified by confirmatory LDA with a posterior probability of 0.74. This may be due to the fact that both species are very closely related and have some overlap in their morphometric and qualitative descriptions. However, as discussed above, these species can be distinguished based on few qualitative morphological traits, one of which was not captured by the multivariate morphometric analysis. In addition, biological data for *C. tratra* suggest that its nest

sites are arboreal and could be located higher in the vegetation strata. By contrast, *C. varatra* prefers nesting in dead branches above the ground or in lower vegetation.

***Camponotus varatra* Rakotonirina, Csósz & Fisher, sp. n.**

<http://zoobank.org/5A74DE4D-5942-4047-A47A-E1547BEC2424>

Figures 18C, 18D, 32, 47

Holotype worker. Madagascar, Province Fianarantsoa, Parc National de Ranomafana, Sahamalaotra River, 6.6 km 310° NW Ranomafana, -21.23667, 47.39667, 1150 m, montane rainforest, ex dead twig above ground, 31 Mar 2003 (Fisher, Griswold et al.) collection code: BLF08630, specimen code: CASENT0492888 (CASC).

Paratype. 1 dealate queen and 8 workers with same data as holotype but with the following specimen codes: CASENT0492886 (queen), CASENT0492887, CASENT0492889, CASENT0217289, CASENT0746977, CASENT0746978, CASENT0746979, CASENT0746980, CASENT0763748 (BMNH, MHNG, MSNG, CASC).

Additional material examined. MADAGASCAR: Province **Antananarivo:** Mandraka Park, -18.9019, 47.90786, 1360 m, montane shrubland, (B.L. Fisher et al.) (CASC); Province **Antsiranana:** 6.9 km NE Ambanizana, Ambohitsitondroina, -13.56667, 50, 1080 m, montane rainforest, (B.L. Fisher) (CASC); Ampasindava, Forêt d'Ambilanivy, 3.9 km 181° S Ambaliha, -13.79861, 48.16167, 600 m, rainforest, (Fisher, Griswold et al.), (CASC); Forêt de Binara, 9.1 km 233° SW Daraina, -13.26333, 49.60333, 650–800 m, rainforest, (B.L. Fisher) (CASC); Parc National Montagne d'Ambre [1st campsite], -12.51444, 49.18139, 960 m, rainforest, (R. Harin'Hala) (CASC); Sakaramy, 07 Km N of Joffre Ville, -12.33333, 49.25, 360 m, low rainforest in open area, Campsite 2 of Fisher, (R. Harin'Hala) (CASC); Province **Fianarantsoa:** Belle Vue trail, Ranomafana National Park, -21.2665, 47.42017, 1020 m, mixed tropical forest, (R. Harin'Hala) (CASC); Vatovavy Fitovinany Region, District of Ifanadiana, 12 km W of Ranomafana, -21.25083, 47.40717, 1127 m, forest edge, open area, (Rin'Ha, Mike) (CASC); Parc National de Ranomafana, Sahamalaotra River, 6.6 km 310° NW Ranomafana, -21.23667, 47.39667, 1150 m, montane rainforest, (Fisher, Griswold et al.) (CASC); radio tower, Ranomafana National Park, -21.25083, 47.40717, 1130 m, forest edge, mixed tropical forest, open area, (M.E. Irwin, R. Harin'Hala) (CASC); Ranomafana National Park, Talatakely area, 0.4 km WSW of Park Entrance -21.41667, 47.68333, 900 m, mixed tropical forest, (D.H. Kavanaugh) (CASC); 9 km ESE Ranomafana, nr. Ifanadiana, -21.28333, 47.53333, 600 m, (P.S. Ward) (PSWC); Province **Toamasina:** Andasibe National Park, botanic garden near entrance, West of ANGAP office, -18.92639, 48.40783, 1025 m, tropical forest, (M.E. Irwin, R. Harin'Hala) (CASC); 1 km SSW Andasibe (=Perinet), -18.93333, 48.41667, 920 m, rainforest edge, (P.S. Ward) (PSWC); Ankerana, -18.40636, 48.80254, 1108 m, montane forest, (B.L. Fisher et al.) (CASC); Ankerana, -18.40829, 48.82107, 750 m, rainforest, (B.L. Fisher et al.) (CASC); Ankerana, -18.4017, 48.80605, 1035 m,

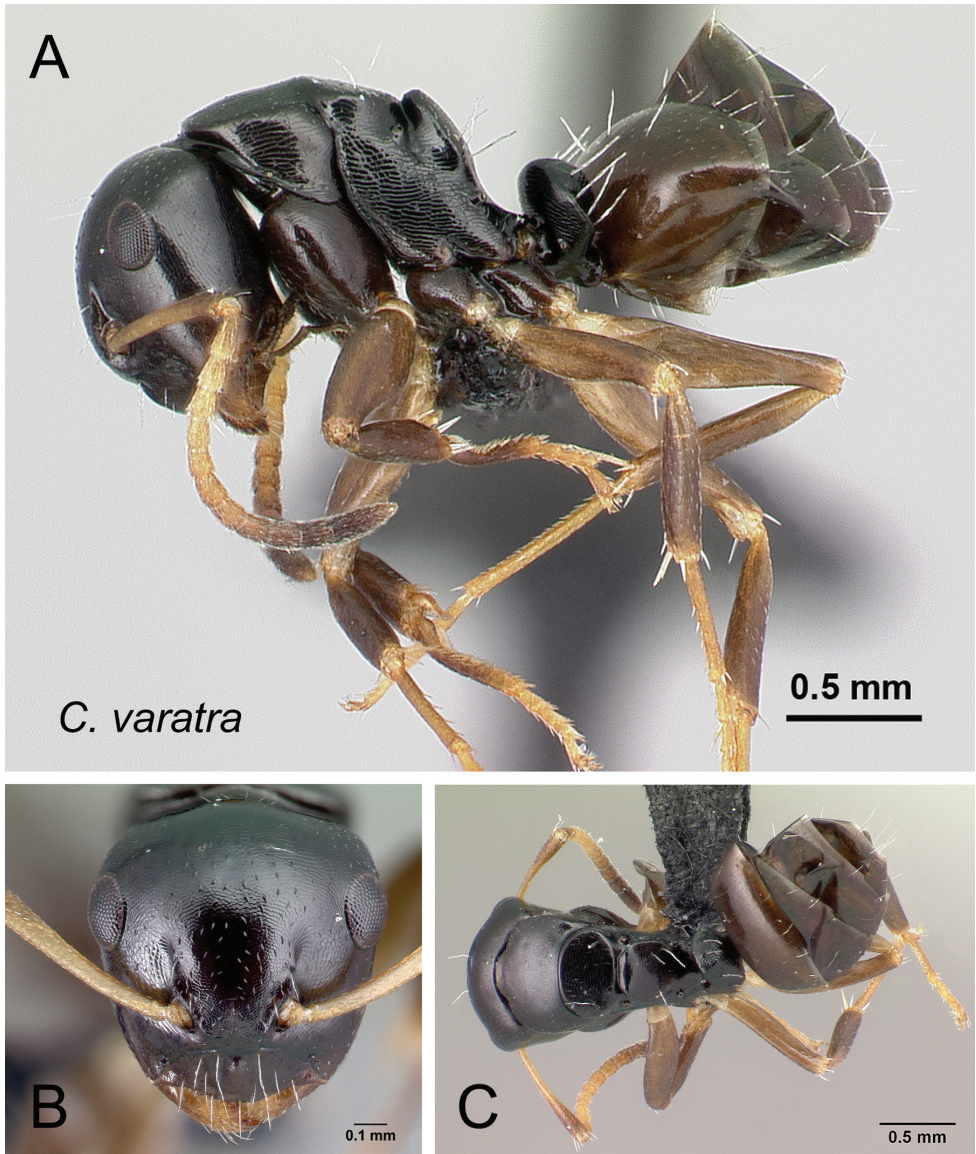


Figure 32. *Camponotus varatra* minor worker CAsENT0492888. **A** lateral view **B** head in full-face view **C** dorsal view.

montane forest, (B.L. Fisher et al.) (CASC); Betaolana Forest, along Bekona River, $-14.52996, 49.44039, 880$ m, rainforest, (B.L. Fisher et al.) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, $-18.80424, 48.40081, 968$ m, rainforest, (B.L. Fisher et al.) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, $-18.79944, 48.40375, 1016$ m, rainforest, (B.L. Fisher et al.) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, $-18.80438, 48.40735, 960$ m, rainforest, (B.L. Fisher et al.) (CASC); Corridor Forestier Analamay-Mantadia, Ambohibolakely,

–18.76131, 48.36437, 983 m, rainforest, (B.L. Fisher et al.) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, –18.76465, 48.41938, 1039 m, rainforest, (B.L. Fisher et al.) (CASC); 16 km S Moramanga, –19.8333, 48.23333, 950 m, roadside, (P.S. Ward) (PSWC); Didy, [–18.19833, 48.57833] forêt (A. Pauly) (CASC); Station Forestiere, Tampolo, 10 km NNE Fenoarivo Atsinanana, –17.2825, 49.43, 10 m, littoral rainforest, (B.L. Fisher) (CASC); Province **Toliara**: Parc National Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, –24.7585, 46.85367, 275 m, rainforest, (B.L. Fisher et al.) (CASC); Parc National Andohahela, 6 km SSW Eminiminy, –24.73333, 46.8, 330 m, rainforest, (P.S. Ward) (PSWC).

Diagnosis. In profile, anterior and posterior margins of petiolar node convex; in profile, propodeal dorsum and declivitous surface separated by blunt angle; in dorsal view, mesonotum less than twice as broad as long; mesopleuron with propodeal surface together distinctly wider than lateral portion of pronotum; in profile, propodeal dorsum roughly as long as declivitous margin; dorsum of head and mesosoma smooth and shiny or imbricate; in profile, mesonotum slightly sloping down to the level of propodeum, maximum length distinctly shorter than distance between metanotal groove and propodeal spiracle; in dorsal view, lateral margin of mesonotum well defined and evenly convex, converging abruptly towards metanotal groove; junction between dorsum and lateral surface of pronotum with sharp margination; no distinct angle between dorsal margin of propodeum and declivity; antennal scape and gastral segment with scattered appressed pubescence.

Description. Minor worker (Figs 18C, 18D, 32). In full-face view head slightly longer than broad (CWb/CL: 0.83–0.96), sides slightly convex and noticeably diverging posteriorly; posterior cephalic margin generally convex. Level of posterior ocular margins located around or less than posterior fourth portion of head (PoOc/CL: 0.2–0.24). Anterior clypeal margin broadly convex. Mandible triangular, armed with six teeth. Antennal scape relatively short (SL/CS: 0.93–1.07), apical third extending beyond posterior cephalic border. Promesonotal dorsum flattened, dorsal face joining lateral portion with margination; anterodorsal angle of pronotum extending anteriorly into narrow edge. In dorsal view, mesonotum less than twice as broad as long; lateral margin evenly convex and abruptly converging posteriorly. In lateral view, propodeal dorsum extending into very short edge and then sloping strongly posteriorly to join the declivitous surface without an angle. In lateral view, dorsolateral carina of propodeum roughly as long as declivitous margin; meso-metapleuron and lateral propodeal surface together distinctly broader than side of pronotum. In side view, mesonotal length shorter than distance between metanotal groove and propodeal spiracle. Width of procoxa greater than width of meso-metapleuron combined. In profile, anterior petiolar margin convex, posterior margin sloping posteriorly to mid-height and descending almost vertically to posteroventral angle. Junction between abdominal segments III and IV without constriction.

Dorsum of head, mesosoma, petiole, and gastral tergites smooth and shiny or with imbricating sculpture. Sparse shallow punctures present on lateral portion of head near base of mandible. Mandible with sparse piligerous punctures. Numerous pairs

of whitish erect hairs on dorsum of head arranged near lateral margin of clypeus and frontal carina to posteromedian portion of head. One pair of hairs on mesonotum and one to two pairs on propodeum at junction of its dorsum and declivity; pronotum and declivitous surface just above propodeal spiracle without erect hair. A row of four whitish hairs erected along near lateral margin and posterodorsal angle of posterior face of petiolar node. Anterior and posterior portions of each gastral tergite with transversely arranged, slender, erect hairs. Body with appressed, filiform, short pubescence; antennal scape covered with subdecumbent spatulate hairs. Body color generally black; gaster and appendages dark brown; basal portion of antenna, trochanter, and tarsus sometimes much lighter than remaining parts of appendages.

Major worker. Similar to minor worker, but differing in the following characters: head larger (CS: 1.35–1.62) and as long as broad (CWb/CL: 0.95–1), sides parallel to each other and suddenly converging to base of mandibles; posterior margin straight; small apical portion of antennal scape surpassing posterior margin of head (SL/CS: 0.66–0.78); level of posterior ocular margins at about posterior third of head (PoOc/CL: 0.24–0.29); mandible more robust; metanotum present between metanotal groove and propodeum; propodeal dorsum rounding to declivitous surface; one to two pairs of whitish erect hairs on pronotum, mesonotum, and propodeum.

Distribution and biology. The species is endemic to Madagascar, where it is mostly found in montane forest habitats and rarely in lowland rainforests and littoral forest areas (Fig. 47). Its colonies frequently have been collected from dead twigs above ground and occasionally from rotten logs and dead tree stumps.

Discussion. *Camponotus varatra* is separable from the similar species like *C. zavo* because the latter species has the following combination of characters: the junction of the dorsum to the lateral portion of the pronotum is rounded, the junction between the dorsal margin of the propodeum and the declivity is either rounded or with a blunt angle, and the antennal scape and gastral segment are covered with abundant appressed pubescence.

Based on morphometric analysis, members of *C. varatra* have been detected in the clusters of *C. mifaka*, *C. tafo*, and *C. tratra* in the dendrogram. The cause of this phenomenon is unclear, but one possibility is that these species are very similar in morphology and several quantitative traits can overlap. Also, a few differentiating morphological characters, such as sculpture and pilosity, cannot be integrated into a quantitative morphometric study. For *C. mifaka* and *C. tafo*, the sculpture on the dorsum of their head and mesosoma has dense and fine reticulate punctures. Biologically, these species inhabit root mats in the ground and moss with leaf litter in the canopy, respectively.

***Camponotus zavo* Rakotonirina, Csősz & Fisher, sp. n.**

<http://zoobank.org/9E5D4A34-7C31-427B-AE90-C5A19092CAB0>

Figures 5B, 10C, 17C, 17D, 18A, 18B, 33, 48

Holotype worker. Madagascar, Province Fianarantsoa, Forêt Classée Vatovavy, 7.6 km 122° Kianjavato, –21.4, 47.94, 175 m, rainforest, on low vegetation, 6–8 Jun 2005

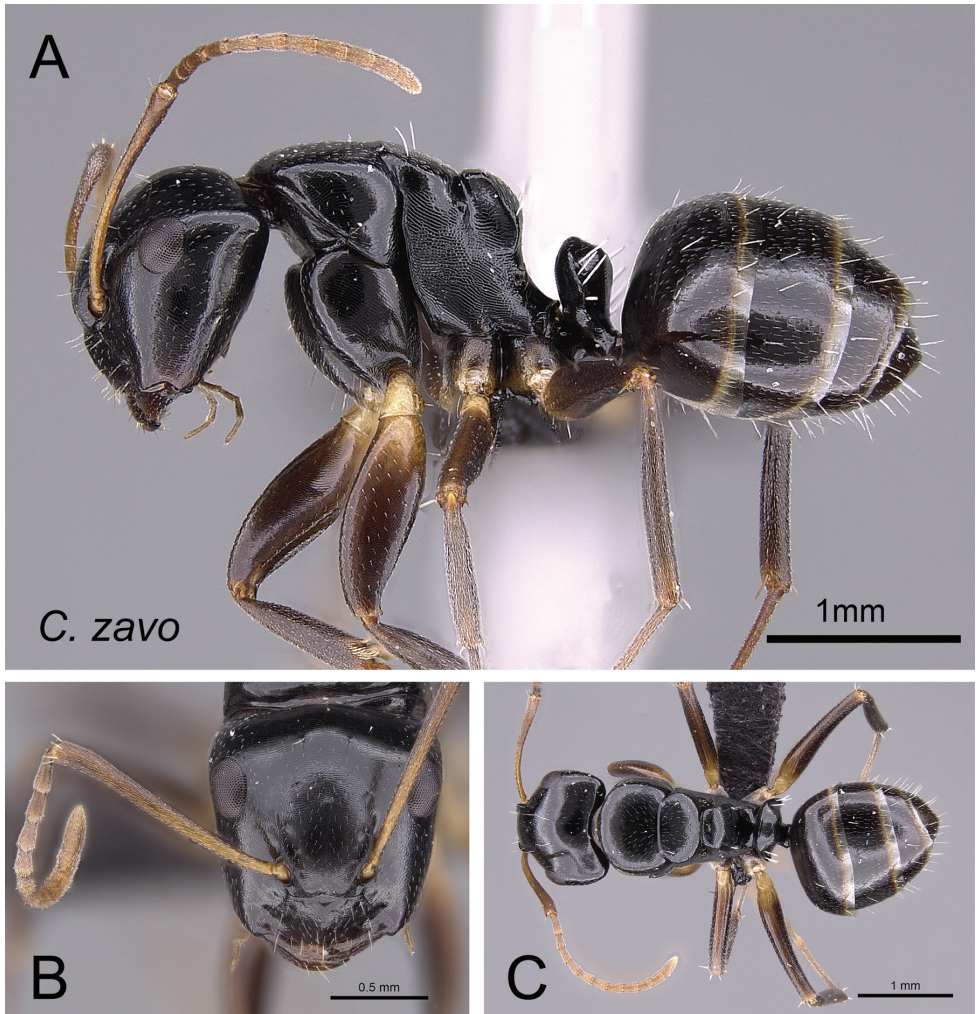
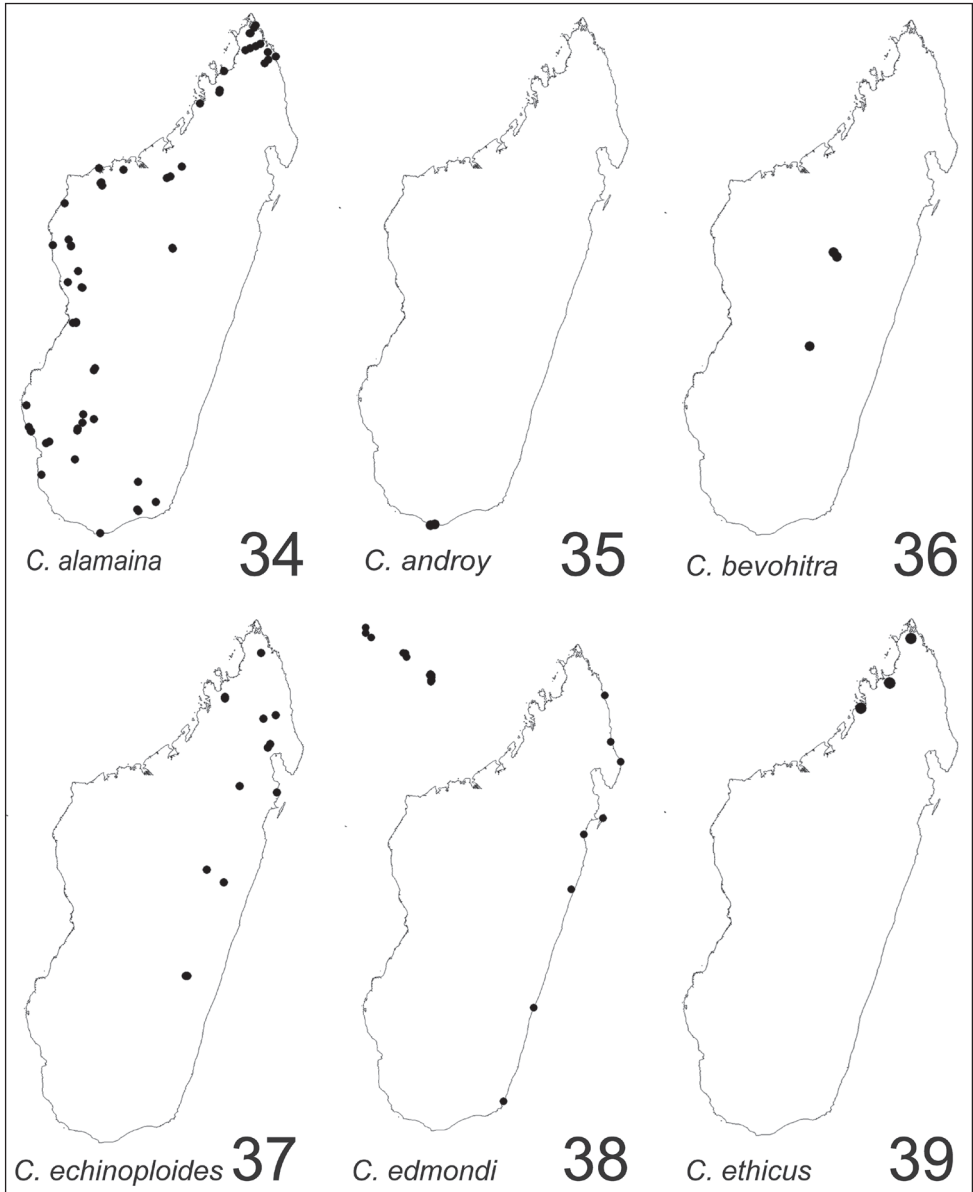


Figure 33. *Camponotus zavo* minor worker CASENT0060041. **A** lateral view **B** head in full-face view **C** dorsal view.

(B.L. Fisher et al.) collection code: BLF12401, specimen code: CASENT0060041 (CASC).

Paratype. 1 worker same data as holotype but with specimen code CASENT0060040 (CASC).

Additional material examined. MADAGASCAR: Province **Antananarivo:** Forêt de galerie, Telomirahavavy, 23.4 km NNE Ankazobe, $-18.12167, 47.20627$, 1520 m, disturbed gallery montane forest, (B.L. Fisher et al.) (CASC); Province **Antsiranana:** SAVA Region, District of Sambava, Marojejy National Park, 5 km W of Manantenina village, 1st Campsite (*Mantella*), $-14.43817, 49.774$, 487 m, low altitude rainforest, (Rin'Ha, Mike) (CASC); Province **Fianarantsoa:** 7.6 km 122° Kianjavato, Forêt Classée



Figures 34–39. Distribution maps of the *C. edmondi* species group in the Malagasy region.

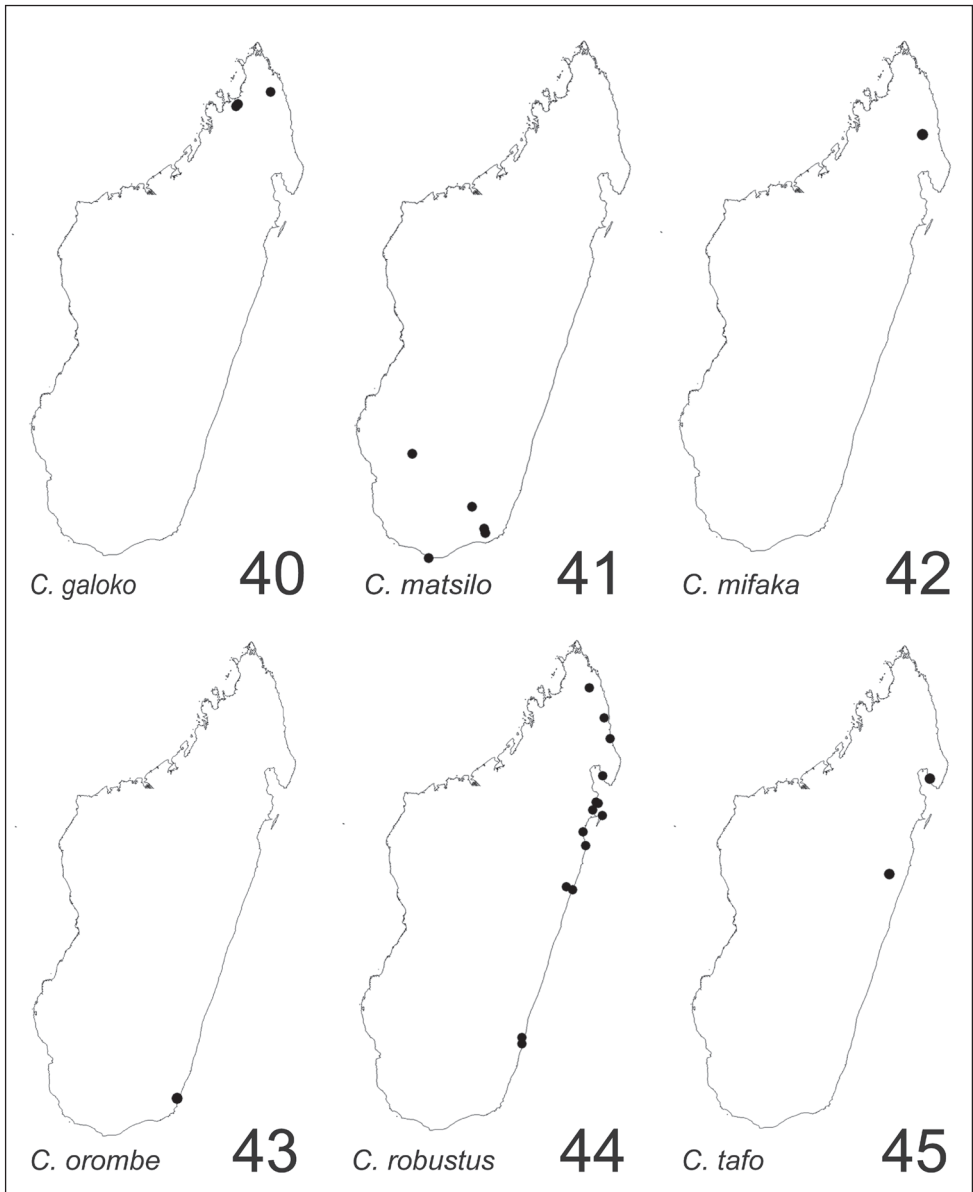
Vatovavy, $-21.4, 47.94, 175$ m, rainforest (B.L. Fisher et al.) (CASC); Vatovavy Fitovinany Region, District of Ifanadiana, 12 km W of Ranomafana, $-21.25083, 47.40717, 1127$ m, forest edge, open area, (Rin’Ha, Mike) (CASC); Forêt de Vevembe, 66.6 km 293° Farafangana, $-22.791, 47.18183, 600$ m, rainforest, transition to montane forest, (B.L. Fisher et al.) (CASC); radio tower, Ranomafana National Park, $-21.25083,$

47.40717, 1130 m, forest edge, mixed tropical forest, open area, (M.E. Irwin, R. Harin'Hala) (CASC); Vohiparara broken bridge, -21.22617, 47.36983, 1110 m, high altitude rainforest, (R. Harin'Hala) (CASC); Province **Toamasina**: 5.3 km SSE Ambanizana, Andranobe, -15.66667, 49.96667, 600 m, rainforest, (B.L. Fisher) (CASC); 7 km SE Andasibe National Park Headquarters, -18.96278, 48.45267, 1050 m, tropical forest, (M.E. Irwin, R. Harin'Hala) (CASC); Province **Toliara**: 13 km NW Enakara, Parc National Andohahela, -24.55, 46.8, 1150 m, montane rainforest, (B.L. Fisher) (CASC).

Diagnosis. In profile, anterior and posterior margins of petiolar node convex; in profile, propodeal dorsum and declivitous surface separated by blunt angle; in dorsal view, mesonotum less than twice as broad as long; mesopleuron with propodeal surface together distinctly wider than lateral portion of pronotum; in profile, propodeal dorsum roughly as long as declivitous margin; dorsum of head and mesosoma smooth, shiny, and superimposed by imbrication; in profile, mesonotum slightly sloping down to the level of propodeum, maximum length distinctly shorter than distance between metanotal groove and propodeal spiracle; in dorsal view, lateral margin of mesonotum well defined and evenly convex, converging abruptly towards metanotal groove; junction of pronotal dorsum to lateral surface always rounded; blunt angle between dorsal margin of propodeum and declivity distinct; antennal scape and gastral segment covered with abundant appressed pubescence.

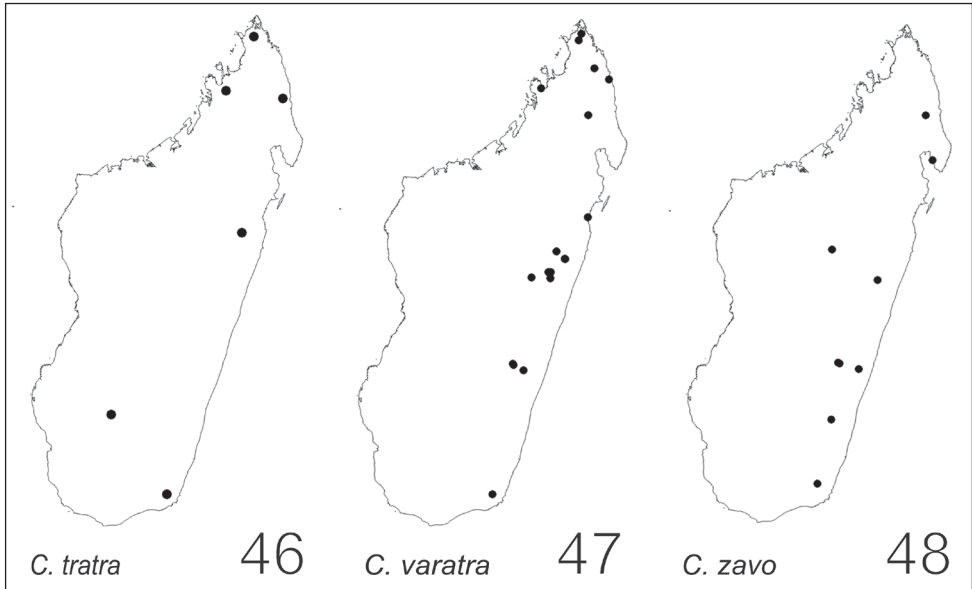
Description. Minor worker (Figs 5B, 10C, 17C, 17D, 18A, 18B, 33). In full-face view head subquadrate (CWb/CL: 0.93–1), sides approximately straight and slightly diverging posteriorly; posterior border medially convex and nearly straight towards corners. Level of posterior ocular margins located around or lower than posterior fifth portion of head (PoOc/CL: 0.18–0.23). Anterior clypeal margin straight. Mandible triangular, armed with six teeth. Antennal scape relatively long (SL/CS: 1–1.22), distal portion extending beyond posterior cephalic border. Anterodorsal angle of pronotum extending anteriorly into narrow edge, but dorsolateral portion without longitudinal margination, junction of dorsum to lateral surface rounded. In dorsal view, mesonotum narrow, less than twice as broad as long; lateral margin well defined and evenly convex, converging abruptly toward metanotal groove. In profile, propodeum not strongly compressed anteroposteriorly, propodeal dorsum with a short, more or less horizontal edge and suddenly sloping posteriorly to join the declivitous surface at a blunt angle. In profile, dorsolateral carina of propodeum as long as its posterolateral margin; width of mesopleuron and propodeal surface combined distinctly greater than width of lateral portion of pronotum. In profile, maximum length of mesonotum distinctly shorter than distance between metanotal groove and propodeal spiracle, which is located on declivitous surface. Maximum width of coxa of foreleg greater than width of meso-metapleuron combined. In profile, anterior margin of petiolar node convex and posterior margin inclined posteriorly until mid-height and descending almost vertically to posteroventral angle. Constriction between abdominal segments III and IV lacking.

Dorsum of head, mesosoma, petiole, and gastral tergites smooth and shiny with superimposed imbricating sculpture. Lateral portion of head near base of mandible with scattered shallow punctures. Mandible smooth and shining between sparse punc-



Figures 40–45. Distribution maps of the *C. edmondi* species group in the Malagasy region.

tures. Whitish erect hairs arranged as follows: several pairs on clypeus, three pairs on frontal carina, one pair at level of eyes and one pair on posterior portion of head dorsum; lacking on pronotum; one to two pairs on mesonotum; numerous hairs on propodeum arranged in a row along junction of propodeal dorsum and declivity; lacking on declivitous face just above spiracle; a few pairs arranged in a row near lateral margin



Figures 46–48. Distribution maps of the *C. edmondi* species group in the Malagasy region.

and posterodorsal angle of petiolar posterior face; sparse and slender erect hairs arranged transversely on anterior and posterior portions of each gastral tergite. Appressed pubescence present, abundant on antennal scape. Head, mesosoma, and petiole black; gaster dark brown; appendages brown to light brown.

Major worker. Similar to minor worker, but differing in the following characters: head slightly wider than long (CWb/CL: 1.01–1.04), posterior margin almost straight; antennal scape hardly surpassing posterior cephalic border (SL/CS: 0.76–0.82); level of posterior ocular margins at about posterior third portion of head (PoOc/CL: 0.24–0.27); mandible more robust with accentuated microreticulation basally and microreticulate punctate near apical margin; visible metanotum between metanotal groove and propodeum; one to two pairs of whitish erect hairs on pronotum and more on mesonotum and propodeum.

Distribution and biology. This species is widely distributed in eastern Madagascar and occupies a wide array of habitats ranging from lowland rainforest at 175 m of elevation to montane forest habitats up to 1520 m in elevation (Fig. 48). Foraging is carried out on lower part of vegetation and nests are built in dead twigs above the ground.

Discussion. *Camponotus zavo* is very similar to the sympatric species *C. varatra* in that in both, the integument is smooth and shining or imbricate and the lateral margins of the mesonotum are well-defined and evenly convex. However, *C. varatra* can be distinguished by the fact that it has no distinct angle separating the propodeal dorsum and the declivitous margin in lateral view and the dorsum and the lateral surface of the pronotum are separated by a sharp angle.

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Supplementary material I

Measurements of individual specimens

Authors: Jean Claude Rakotonirina, Sándor Csősz, Brian L. Fisher

Data type: specimens data

Explanation note: Basic measurements of individual specimens arranged by species code, collection code, and specimen code (unique identification number). See text for abbreviations.

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Capoeta coadi, a new species of cyprinid fish from the Karun River drainage, Iran based on morphological and molecular evidences (Teleostei, Cyprinidae)

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Abstract

As presently recognized, the genus *Capoeta* includes 24 species, nine of which are known to occur in Iran (*C. aculeata*, *C. capoeta*, *C. bubsei*, *C. damascina*, *C. fusca*, *C. heratensis*, *C. mandica*, *C. saadii* and *C. trutta*) and are distributed in almost all Iranian basins except Sistan and Mashkid. *Capoeta coadi* **sp. n.** is a new species from the Karun River, southern Iran, draining into the Arvand Rud (Shatt al-Arab) which drains into the Persian Gulf. It is distinguished from all other species of *Capoeta* by the combination of the following characters: elongate and usually cylindrical body; 8–9 branched dorsal-fin rays; last unbranched dorsal-fin ray weakly to moderately ossified and serrated along 1/3–2/3 of its length; scales small; 70–84 in lateral line (total); 12–17 scales between dorsal-fin origin and lateral line; 9–11 scales between anal-fin origin and lateral line; 26–32 circum-peduncular scales; 10–13 gill rakers on lower limb of first gill arch; 45–47 total vertebrae; one posterior pair of barbels; bright golden-greenish or silvery body coloration in life; length of the longest dorsal-fin ray 15–22% SL; head length 23–26% SL; mouth width 7–10% SL. *Capoeta coadi* is also distinguished from all other congeners in the Iranian drainages by fixed diagnostic nucleotide substitutions in the mtDNA COI barcode region and *cyt b*. It is nested in the *Capoeta damascina* species complex.

Keywords

Capoeta damascina species complex, COI, *Cyt b*, Persian Gulf, phylogenetic relationships

Introduction

The Middle East is a transition zone between three major biogeographic units, the Palearctic, the Afrotropical, and the Oriental realms. It served as an important crossroad of biotic exchange resulting in an outstanding biological diversity of freshwater fishes (Durand et al. 2002, Krupp et al. 2009). Lying between major drainages of the Nile in Africa to the west, the Indus in southern Asia to the east and the Caspian and Black Sea drainages to the north, the Tigris-Euphrates River drainage is the largest river system in the Middle East and has high fish diversity, especially in cyprinid fishes.

Capoeta Valenciennes in Cuvier and Valenciennes 1842 is an example of a cyprinid genus widely spread in the Middle East (Krupp and Schneider 1989). Being found in a wide range of habitats, species of this genus display considerable morphological variability (e.g., scale counts and colour pattern) and the extent of morphological plasticity and genetic variability remain to be determined. As a consequence, there has been considerable disagreement regarding the status of several species. However, *Capoeta* is considered monophyletic (Krupp 1985, Küçük et al. 2009).

Members of the genus *Capoeta* are cyprinids characterized by having an elongate, cylindrical body and a short dorsal fin. They have three to five unbranched and 5–9 branched dorsal-fin rays, the last unbranched ray being ossified and serrated. All species have three unbranched and 5 branched anal-fin rays. Scales are usually small. Mouth is inferior and the lower lip is covered with a horny sheath. One pair of barbels (rarely two) is present and the pharyngeal teeth are arranged in three rows. The shape of the mouth as well as the pharyngeal teeth are nearly identical in all species, which indicate their adaptation to the same mode of feeding. This combination of character states distinguishes *Capoeta* from all other cyprinids (Krupp 1985, Krupp and Schneider 1989).

As presently recognized, the genus *Capoeta* includes about 24 species (Eschmeyer and Fricke 2016) in different phylogenetic groups widely distributed in many river drainages and basins in southwestern Asia except the Arabian Peninsula (Alwan 2011, Levin et al. 2012). Levin et al. (2012) studied the phylogenetic relationships of the genus *Capoeta* based on complete mitochondrial gene for cytochrome *b* sequences obtained from 20 species from the overall range of the genus. Three main groups were detected: the Mesopotamian group (*Capoeta trutta* group), the Anatolian-Iranian group (*Capoeta damascina* group) and the Aralo-Caspian group (*Capoeta capoeta* group).

Members of the *Capoeta damascina* species group, characterized by having small scales, include *C. buhsei* Kessler, 1877, *C. caelestis* Schöter, Özuluğ & Freyhof, 2009, *C. damascina* (Valenciennes, 1842), *C. kosswigi* Karaman, 1969, *C. saadii* (Heckel, 1847), and *C. umbla* (Heckel, 1843) (Alwan 2011). Based on phylogenetic analyses of cytochrome *c* oxidase subunit I (COI) and the large subunit (LSU or 28S) ribosomal RNA gene sequences Alwan (2011) identified two main lineages within what we will refer to in this paper, as the “*C. damascina* species complex”. A western lineage is represented by *C. caelestis*, *C. damascina* and *C. umbla* and an eastern lineage represented by *C. buhsei*, *C. saadii*, and a new undescribed species.

Traditionally, *C. damascina* is recorded from Tigris, Mond, Kor, Esfahan, Dasht-e Kavir, Namak Lake, Kor River, Lake Maharlu, Persian Gulf (now Persis), Kerman-Na'in, Dasht-e Lut, Sirjan, Hormuz, and Hamun-e Jaz Murian basins in Iran (Nicol'skii 1899, Berg 1949, Kähsbauer 1964, Armantrout 1980, Rainboth 1981, Bianco and Banarescu 1982, Ghorbani Chafi 2000, Jalali et al. 2005, Esmaili et al. 2010, Bahrami Kamangar et al. 2012). Its distribution over such wide range of isolated water bodies, raises questions regarding the status of *C. damascina*. Currently, *C. damascina* s.l. represents a complex of closely related species with high intraspecific and comparatively low interspecific variation (Alwan 2011, Levin et al. 2012). Now, three species of *Capoeta* from Iranian water bodies are recognized as being members of *C. damascina* species complex group: *C. buhsei*, *C. saadii* (Iranian populations were considered as *C. damascina*) (see Alwan 2011, Levin et al. 2012), and a new undescribed species from the Karun (Karoun) River drainage. It is described here as a new species, *Capoeta coadi*.

Material and methods

After anaesthesia, fishes were either fixed in 5% formaldehyde, and stored in 70% ethanol, or directly fixed in 99% ethanol (for molecular studies). Measurements were made with a digital caliper and recorded to 0.01 mm. All measurements were made point to point, and never by projections. Methods for counts and measurements follow Hubbs and Lagler (1958) and Krupp (1983). Standard length (SL) was measured from the tip of the snout to the end of the hypural complex. The length of the caudal peduncle was measured from behind the base of the last anal-fin ray to the end of the hypural complex. The last two branched rays articulating on a single pterygiophore in the dorsal and anal fins are counted as "1½". The holotype is included in the calculation of means and SD.

Abbreviations used: SL, standard length; HL, lateral head length.

Abbreviations used for museum collections: Zoological Museum of Shiraz University, Collection of Biology Department, Shiraz, Iran (ZM-CBSU), the Senckenberg Research Institute and Natural History Museum (SMF: Frankfurt, Germany), and the private collection of Jörg Freyhof (FSJF: Fischesammlung J. Freyhof).

DNA extraction and PCR amplification protocol

For DNA sequencing, specimens were directly fixed in 99% molecular grade ethanol. Mitochondrial DNA was extracted using Salt method (Bruford et al. 1992). The standard vertebrate DNA barcode region of the COI (cytochrome c oxidase subunit 1) and cytochrome *b* (*cyt b*) were amplified using primer pairs named FishF1-5'TCAACCAACCACAAAGACATTGGCAC3' and FishR1-5'TAGACTTCTGGGTGGCCAAAGAATCA3' (Ward et al. 2005) and L14724-

5'GTGACTTGAAAAACCACCGTTG3' and H15915-5'CAACGATCTCCGGTTT-AGAAGAC3' (Xiao et al. 2001) or GluF- 5'AACCACCGTTGTATTCAACTACAA3' and H-15560 5'TAGGCRAATAGGAAR TATCA3' (Machordom and Doadrio 2001), respectively.

Purification and sequencing of the PCR products were conducted at Macrogen Korea Laboratories using the aforementioned primer sets.

Molecular data analyses

Data processing and sequence assembly was done in BioEdit 7.2.5 (Hall 1999); MEGA6 (Tamura et al. 2013) was used to create a DNA sequence alignment. No indications of unexpected stop-codons or nuclear copies of mitochondrial fragments occurred in any sequences. All generated DNA barcodes and *cyt b* were deposited in the NCBI GenBank. The most appropriate sequence evolution model for the given data was determined with Modeltest (Posada and Crandall 1998) as implemented in the MEGA6 software, treating gaps and missing data with the partial deletion option under 95% site coverage cut-off. The model with the lowest BIC (Bayesian Information Criterion) score is considered the best model to describe the substitution pattern for each gene. To explore species phylogenetic relationships, trees were generated using Maximum Likelihood analysis with 10,000 bootstrap replicates in RaxML 7.2.5 (Stamatakis 2006) under the GTR+G model of nucleotide substitution, with fast bootstrap and also Bayesian analysis (BA), using the Markov Chain Monte Carlo method (MCMC), with 6,000,000 generations under the most generalizing model (GTR+G+I) using Mr. Bayes 3.1.1 (Huelsenbeck and Ronquist 2001). Screening for diagnostic nucleotide substitutions was performed manually from the sequence alignment. As an appropriate outgroup to root the constructed phylogenetic hypothesis, we included the distantly related *Cyprinus carpio*.

Results

Morphological assessments

Capoeta coadi sp. n.

<http://zoobank.org/4B5B0984-0C65-4B6D-97CC-31245E179D13>

Figs 1–3

Holotype. ZM-CBSU Z190, 157 mm SL; Iran, Kohgiluyeh and Boyer Ahmad prov., Beshar (Bashar) River at Tale Gah village, Karun River drainage, 30°47'27"N, 51°25'13"E.

Paratypes. ZM-CBSU Z191, 6, 91–157 mm SL; same data as holotype. ZM-CBSU J520, 1, 107 mm SL; ZM-CBSU Z275, 12, 105–152 mm SL; Iran, Koh-



Figure 1. *Capoeta coadi* sp. n., ZM-CBSU Z190, holotype, 157 mm SL; Iran: Kohgiluyeh and Boyer Ahmad, Beshar River, Karun River drainage.

giluyeh and Boyer Ahmad prov., Beshar (Bashar) River at Tale Gah village, Karun River drainage, 30°47'27"N, 51°25'13"E. 15 December 2014, G. Sayyadzadeh, R. Khaefi, A. Khajehpanah. ZM-CBSU J526, 1, 98 mm SL; ZM-CBSU J533, 1, 114 mm SL; ZM-CBSU J535, 1, 97 mm SL; ZM-CBSU J540, 1, 67 mm SL; All from Iran, Kohgiluyeh and Boyer Ahmad prov., Beshar River at Tange sorkh, Karun River drainage, 30°26'14"N, 51°45'48"E. 24 July 2011, R. Zamaneian Nejad, S. Mirgheiasi, S. Ghasemian. ZM-CBSU J444, 2, 73–90 mm SL; ZM-CBSU J447, 2, 76–111 mm SL; ZM-CBSU J450, 1, 86 mm SL; ZM-CBSU J452, 1, 107 mm SL; ZM-CBSU J459, 2, 104–120 mm SL; ZM-CBSU J464, 1, 110 mm SL; all from Iran, Kohgiluyeh and Boyer Ahmad prov., Beshar River at Mokhtar village, Karun River drainage, 30°40'31"N, 51°31'26"E. 25 May 2011, R. Zamaneian Nejad.

Additional material. ZM-CBSU 7880–7881, 2, 96.69–158.12 mm SL; Iran, Fars prov., Sepidan city, Gorgu River, a tributary of Beshar River, north of Sepidan city, Karun River drainage, 30°21.283'N, 51°45.754'E. 2006. H.R. Esmacili, A. Teimori, M. Ebrahimi and A. Gholamhoseini. SMF 33337, 1, 48.86 mm SL; Iran, Lorestan prov., Hadi River between Zagheh and Polehoru, 33°31.138'N, 48°46.340'E. 04 March 2008. N. Alwan, K. Borkenhagen, M. Ghanbari Fardi and A. Kazemi. FSJF 2213, 11, 107.92–143.94 mm SL; Iran, Chaharmahal and Bakhtiari Prov., Sandgan River (Sandgan stream) at Sandgan, 31°15.692'N, 51°17.150'E. 19 April 2007, A. Abdoli and J. Freyhof. FSJF 2233, 2, 156.22–162.23 mm SL; Iran, Kohgiluyeh and Boyer Ahmad prov., Beshar River, 20 km northeast of Yasuj, 30°44.152'N, 51°29.522'E. 19 April 2007. A. Abdoli and J. Freyhof. SMF 30865, 1, 26.94 mm SL; Iran, Kohgiluyeh and Boyer Ahmad prov., Beshar River at Tang-e Sorkh, 30°27.680'N, 51°44.907'E. 28 November 2007, K. Borkenhagen, H. R. Esmacili and F. Wicker (in 96% alcohol). SMF 30871, 1, 28.34 mm SL; Iran, Kohgiluyeh and Boyer Ahmad prov., Beshar River at Tang-e Sorkh, 30°27.680'N, 51°44.907'E. 28 November 2007. K. Borkenhagen, H. R. Esmacili and F. Wicker (in 96% alcohol). SMF 33316, 7, 35.22–166.87 mm SL; Iran, Kohgiluyeh and Boyer Ahmad prov., Beshar River at Tang-e Sorkh, 30°27.680'N, 51°44.907'E. 28 November 2007, K. Borkenhagen, H. R. Esmacili and F. Wicker. SMF 30872, 1, 29.70 mm SL; Iran, Fars prov., Sepidan, Tang-e Tizab, 30°23.470'N, 51°46.710'E, 28 November 2007, K. Borkenhagen, H. R. Esmacili and F. Wicker (in 96% alcohol).



Figure 2. *Capoeta coadi* sp. n., paratypes: **a** ZM-CBSU Z191; 157 mm SL **b** ZM-CBSU Z192, 148 mm SL; Iran: Kohgiluyeh and Boyer Ahmad, Beshar River, Karun River drainage.

***Capoeta coadi* specimens used for molecular genetic analysis.** ZM-CBSU M1275, 1, Iran, Kohgiluyeh and Boyer Ahmad prov., Beshar River at Dehno village, Karun River drainage, 30°38'55"N, 51°37'05"E. 16 January 2014, H.R. Esmaili, G. Sayyadzadeh, H.R. Mehraban, M. Razbani. GenBank accession number: (COI: KU564296); ZM-CBSU M1447, 2, GenBank accession number: (COI: KU564297, KU564298; *cytb*: KU564303, KU564304) ZM-CBSU M1458, 2); Iran, Kohgiluyeh and Boyer Ahmad prov., Beshar River at Tale Gah village, Karun River drainage, 30°47'27"N, 51°25'13"E. 14 December 2013. G. Sayyadzadeh, A. Khajehpanah, R. Khaefi. GenBank accession number: (COI: KU564294, KU564295; *cytb*: KU564305, KU564306).

Diagnosis. *Capoeta coadi* sp. n. is distinguished from all other species of *Capoeta* by the following combination of characters: last unbranched dorsal-fin ray weakly to moderately ossified and serrated in 1/3–2/3 of its length; scales small, 70–84 total lateral line scales (84 in holotype), 12–17 scales between dorsal-fin origin and lateral line (16 in holotype), 9–11 scales between anal-fin origin and lateral line (11 in holotype), 26–32 encircling least circumference of caudal peduncle (31 in holotype); total gill rakers 14–18 (17 in holotype), 10–13 gill rakers on lower limb of first gill arch (12 in holotype); 45–47 total vertebrae; one posterior pair of barbels; length of the longest dorsal-fin ray 14.92–21.58% SL (18.90 in holotype); head length 22.87–26.33% SL (23.76 in holotype); mouth width 7.48–9.77% SL (8.65 in holotype); bright golden-greenish or silvery body coloration in life.



Figure 3. Live specimen of *Capoeta coadi* sp. n, Iran: Kohgiluyeh and Boyer Ahmad, Beshar River, Karun River drainage.

Description. General body shape and appearance are shown in Figs 1–3, morphometric data in Table 1 and meristic data are summarized in Tables 2–9. Body elongate and cylindrical; predorsal body profile smoothly convex with no marked discontinuity between head and body except when a nuchal hump is present in few specimens; greatest body depth at level of dorsal-fin origin; snout rounded (in 20 specimens) or pointed (in 14 specimens) and not size dependent; mouth inferior; lips slightly fleshy, especially at the mouth corners; lower lip covered with a sharp-edged horny sheath, its anterior margin straight in adult specimens and rounded to almost crescent-shaped in juveniles, with a considerable degree of individual variation.

Dorsal-fin origin anterior to pelvic-fin origin, its outer margin usually straight to concave with 3–5 unbranched and 8–9 branched rays (3 and 8 in holotype, respectively); last unbranched dorsal-fin ray weakly to moderately ossified, flexible and soft at the tip, serrated in 1/2–2/3 of its length (Fig. 4); pectoral fins not extending to pelvic-fin base; their outer margins usually slightly convex with 16–22 rays in total (19 in holotype) (Table 2); pelvic fins not extending to anal fin base, their outer margin straight or slightly convex and blunt with 7–11 rays in total (8 in holotype) (Table 2); pelvic axillary scale present; anal fin with 3 unbranched and 5 branched rays, outer margin straight or slightly convex; caudal fin forked with 16–19 branched rays (17 in holotype) (Table 3), its tip pointed and its upper lobe often longer than lower one.

Scales small, total lateral-line scales 70–84; 12–17 scales between dorsal-fin origin and lateral line (Table 4); 9–11 scales between anal-fin origin and lateral line (Table 4); 26–32 circum-peduncle scales (Table 5); ventral midline and pectoral region covered with deeply embedded scales of reduced size; gill rakers slightly hooked, total gill rakers 14–18 (10–13 gill rakers on lower limb) of first gill arch (Table 8–9); 45–47 total vertebrae; usually one posterior pair of barbels present (very rarely two, 1 out of 51 individual); pharyngeal teeth arranged in 3 rows in the following manner: 2.3.5–5.3.2 and very similar in shape to those of *C. damascina*; teeth in the main row spatulate or spoon-shaped and crowns flat, narrow and curved.

Table 1. Morphometric data of *Capoeta coadi* sp. n. (holotype ZM-CBSU Z190, and 33 paratypes), *C. bulsei* and *C. saadii*.

	Holotype		Paratypes (n=33)		<i>Capoeta bulsei</i> (n=27)		<i>Capoeta saadii</i> (n=20)		
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	SD
Standard length (mm)	157.64	110.67	67.23–157.64	110.67	74.30–149.30	112.56	51.31–231	109.30	
In percent of standard length									
Head length	23.76	24.5	22.87–26.33	24.5	21.47–25.98	23.56	24.28–29.62	26.84	1.32
Body depth at dorsal-fin origin	21.82	23.15	21.33–25.04	23.15	19.78–24.55	21.82	19.58–27.78	23.32	2.11
Predorsal length	49.07	50.23	47.75–53.43	50.23	48.85–55.05	51.59	44.33–55.12	51.93	2.51
Postdorsal length	54.13	57.53	54.13–63.19	57.53	48.20–60.13	55.24	50.79–59.64	55.06	2.60
Prenal length	72.45	72.8	70.22–76.14	72.8	71.34–76.34	74.01	69.37–78.38	75.61	2.07
Prepelvic length	53.74	52.84	50.22–55.90	52.84	50.17–56.64	53.58	51.23–61.21	56.22	2.36
Distance between pectoral and pelvic-fin origins	32.42	30.19	27.81–32.42	30.19	29.07–33.64	31.30	25.55–32.66	30.87	2.15
Distance between pelvic and anal-fin origins	21.48	21.12	19.31–23.17	21.12	19.90–23.65	21.60	18.32–23.41	20.83	1.56
Depth of caudal peduncle	10.37	10.65	10.03–11.61	10.65	8.58–10.84	10.05	8.98–11.15	10.43	0.60
Length of caudal peduncle	20.73	19.85	17.16–22.35	19.85	18.64–22.01	19.81	15.19–20.11	17.67	1.30
Dorsal-fin base length	12.71	14.41	12.27–16.17	14.41	11.75–15.28	13.51	10.46–14.39	12.98	1.11
Anal-fin base length	6.78	7.39	6.38–8.85	7.39	6.96–8.80	7.88	6.24–8.27	7.17	0.60
Pectoral-fin length	17.32	18.43	16.68–20.46	18.43	16.39–20.96	18.38	16.15–19.16	17.86	1.01
Pelvic-fin length	15.05	15.61	14.24–16.96	15.61	13.85–18.08	15.61	13.58–16.23	15.08	0.82
Length of the longest dorsal fin ray	18.90	19.57	14.92–21.58	19.57	16.42–21.22	18.78	16.35–21.53	19.03	1.47
Mouth width	8.65	8.63	7.48–9.77	8.63	6.49–8.89	7.87	6.51–9.38	8.1	0.73
In percent of head length									
Head depth at eye	56.88	54.21	49.05–61.87	54.21	48.01–56.63	67.01	49.17–57.97	65.47	3.96
Snout length	38.32	38.08	31.60–47.70	38.08	32.69–38.89	35.55	32.65–40.61	36.18	2.41
Postorbital distance	48.83	48.01	33.82–51.84	48.01	47.66–56.59	51.57	46.58–54.84	51.05	2.28
Interorbital width	40.04	38.19	34.62–42.81	38.19	33.88–41.49	37.15	30.90–40.16	35.57	2.70
Eye diameter	15.97	18.52	15.07–23.57	18.52	13.91–24.44	17.36	11.95–26.18	18.23	3.43
Maximum head width	60.53	59.60	51.75–66.89	59.60	57.83–69.68	62.76	47.38–59.00	54.62	3.39
Barbel length	15.14	16.25	13.30–20.20	16.25	15.66–24.60	19.71	13.34–24.64	18.11	2.73

Table 2. Number of pectoral and pelvic fin rays in examined *Capoeta* species.

	Pectoral fin rays										Pelvic fin rays				
	13	14	15	16	17	18	19	20	21	22	7	8	9	10	11
<i>C. buhsei</i>			2	10	4	6					2	14	10		
<i>C. coadi</i>				6	10	8	11	7	1	3	1	14	16	12	8
<i>C. mandica</i>	1	7	2	1							9	2			
<i>C. saadii</i>					3	12	4	1				9	10	1	
<i>C. trutta</i>		2	8	17	8	5						22	17	1	

Table 3. Number of branched caudal fin rays in examined *Capoeta* species.

Branched caudal fin rays	15	16	17	18	19	20
<i>C. buhsei</i>		3	21	3		
<i>C. saadii</i>		1	29	2	1	
<i>C. mandica</i>			2	8	1	
<i>C. trutta</i>	1	9	16	11	3	

Table 4. Number of scales above (between dorsal-fin origin and lateral line) and below (between dorsal-fin origin and lateral line) lateral line in examined *Capoeta* species.

	Above lateral line											Below lateral line										
	6	7	8	9	10	11	12	13	14	15	16	17	5	6	7	8	9	10	11	12	13	
<i>C. buhsei</i>								3	6	4	12						3	13	7	3	1	
<i>C. coadi</i>							1	9	9	15	15	1					11	20	18			
<i>C. mandica</i>							1	10								4	5	2				
<i>C. saadii</i>				1	2	1	8	7	1					2	4	3	9	2				
<i>C. trutta</i>			2	1	1	7	16	7	3	3						7	19	8	6			

Coloration. Live specimens. Dorsum and sides bright golden-green or silvery, darker dorsally and lighter below the lateral line; dorsal head bright golden-green or light pink-brown; dorsal, anal and caudal fins beige to light brown with light pink to red tinge; pectoral and pelvic-fins beige to light brown or golden with brown tinge on the first few rays (Fig. 3); few large black blotches present on the body of some specimens whereas small diffuse black spots are present only on the body of some juveniles (above the lateral line).

Preserved specimens. Dorsum, head and sides grey or brownish-grey dorsally and beige or yellow ventrally; dorsal and caudal fins dusky grey; pectoral, pelvic and anal fins white or beige with or without grey tinge; blotches and spots well discernible (Figs 1–2).

Sexual dimorphism. Breeding tubercles present in both sexes, being bigger and more pronounced in males. Tubercles present on the sides of the snout but may also cover the entire body surface, on and above the lateral line with one or two tubercles per scale but not on each scale, below the lateral line especially in the area above the anal fin and on the branched anal-fin rays; tip of anal fin reaching to or beyond the vertical of the caudal-fin base in females and to about 2/3 of the caudal peduncle in males.



Figure 4. Dorsal fins of *Capoeta coadi* sp. n. **a** ZM-CBSU J 444; 73 mm SL **b** ZM-CBSU Z195; 104 mm SL **c** ZM-CBSU Z192; 148 mm SL; Iran: Kohgiluyeh and Boyer Ahmad, Beshar River, Karun River drainage, to show size-dependent variability of the last simple dorsal-fin ray serration.

Table 5. Number of circum-pendicular scales in examined *Capoeta* species.

	19	21	22	23	24	25	26	27	28	29	30	31	32	33
<i>C. bubsei</i>							1	3	2	5	5	3	4	3
<i>C. coadi</i>							3	11	7	14	4	7	5	
<i>C. fusca</i>	1	6	2	4	1	1								
<i>C. mandica</i>								5	1	3	1			1

Table 6. Number of caudal-peduncle scales in examined *Capoeta* species.

	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>C. bubsei</i>								6	3	7	9	1	1
<i>C. coadi</i>					1	1	2	8	15	2	3	1	
<i>C. mandica</i>					4	2	4		1				
<i>C. saadii</i>					2	1	10	6	1				
<i>C. trutta</i>		1	1		2	3	5	14	8	1	4		1

Habitat and distribution. *Capoeta coadi* sp. n. occurs in medium-fast flowing rivers with usually gravel substrates and clear waters (Fig. 5). At the Beshar River sampling site, the river is about 25 m wide, with substrate consisting of coarse gravel and boulders, and fast-flowing and semi-transparent waters. The physicochemical parameters at the spot were: dissolved oxygen, 9.89 mg/L; total dissolved solids, 190.2 mg/L; salinity, 0.19‰; conductivity, 395 μ S/cm; pH: 8.5 and water temperature 23.4 °C. It is known only from the Karun River drainage, a system that constitutes the southeastern part of the Tigris-Euphrates River system.

Etymology. The new species is named after Brian W. Coad, a well-known ichthyologist for his valuable contribution to the knowledge of freshwater fishes of Iran.

Comparative remarks. The presence of one pair of barbels in *Capoeta coadi* sets the species apart from *C. antalyensis*, *C. baliki*, *C. banarescui*, *C. tinca*, and *C. heratensis*, all of which have two pairs of barbels based on data from Turan et al. (2006a) and this study. The new species is further distinguished from *C. antalyensis* by the presence of serrae on the last unbranched dorsal-fin ray (vs. absence) (Fig. 4), and by number of scales between dorsal-fin origin and lateral line (12–17 vs. 10–12 in *C. antalyensis*)



Figure 5. Beshar River at Taleh Gah village, Karun River drainage, type locality of *C. coadi*.

(Table 4), between anal-fin origin and lateral line (9–11 vs. 7), and by total number of the lateral-line scales (70–84 vs. 51–57) (Table 7). *Capoeta coadi* is distinguished from *C. banarescui* by number of scales between anal-fin origin and lateral line (9–11 vs. 8–9) (Table 4). Data for *C. antalyensis* and *C. banarescui* are from Turan et al. (2006a).

Capoeta coadi is distinguished from *C. mandica*, *C. erhani*, and *C. trutta* by having 10–13 gill rakers on the lower limb of the first gill arch (vs. 17–24 in *C. mandica*, 20–22 in *C. erhani* and 18–25 in *C. trutta* [data from Krupp 1985, Turan et al. 2008, Table 8]). The total number of gill rakers in *Capoeta coadi* specimens is 14–18 that is lower than in *C. mandica* (23–27), *C. barroisi* (28–30), *C. turani* (25–30) and *C. trutta* (21–31) [data from Turan et al. (2006b), Özuluğ and Freyhof (2008), and this study] Table 9. *Capoeta coadi* is further distinguished from *C. mandica* by having fewer pectoral fin rays (16–22 vs. 13–16) (Table 2). *Capoeta coadi* is distinguished from *C. bergamae*, *C. capoeta* and *C. sieboldii* by number of scales between dorsal-fin origin and lateral line (12–17 in *C. coadi* vs. 8–10 in *C. capoeta* and 9–11 in *C. sieboldii*); number of scales between anal-fin origin and lateral line (9–11 in *C. coadi* vs. 7–9 in *C. bergamae*, 6–10 in *C. capoeta* and 8–10 in *C. sieboldii*); total lateral line scales (70–84 in *C. coadi* vs. 48–66 in *C. capoeta* and 52–60 in *C. sieboldii*) [data from Banarescu 1999, Turan et al. 2006b, Tables 4, 7]. In addition to the presence of serrae on the unbranched dorsal-fin ray, *Capoeta coadi* is set apart from *C. caelestis* by the number of scales between the dorsal-fin origin and lateral line (12–17 in *C. coadi* vs. 10–13.5

Table 7. Number of lateral-line scales in examined *Capoeta* species.

	58	59	61	62	63	64	65	66	67	68	69	70	71	72	73
<i>C. bhubsei</i>														1	
<i>C. coadi</i>												2	1	2	6
<i>C. mandica</i>	1		1	2	1		2	1	2	1					
<i>C. saadii</i>			1				2	1	2	2	1	2	3	1	
<i>C. trutta</i>			1			2		1	3	1	5	4	2	2	2

	74	75	76	77	78	79	80	81	82	83	84	85	87	89
<i>C. bhubsei</i>	3		1	2	1	2		4	3	1	2	4	1	1
<i>C. coadi</i>	1	4	4	1	5	3	5	6	5	1	1			
<i>C. mandica</i>														
<i>C. saadii</i>			1	2	2									
<i>C. trutta</i>		5	3	2	4		2				1			

in *C. caelestis*); scales between anal-fin origin and lateral line (9–11 in *C. coadi* vs. 7–8 in *C. caelestis*); circum-peduncular scales (26–32 in *C. coadi* vs. 23–24 in *C. caelestis*) (Tables 4–5) and probably vertebral counts (45–47 in *C. coadi* vs. 44 in *C. caelestis*) [data from Schöter et al. 2009].

It is distinguished from *C. damascina* by having 11–13, modally 13, gill rakers on the lower limb of the first gill arch (vs. 12–18, modally 14–15) (Alwan 2011, Table 8). *Capoeta coadi* is clearly distinguished from *C. ekmekciae* by number of scales between dorsal-fin origin and lateral line (12–17 in *C. coadi* vs. 9–10 in *C. ekmekciae*); number of scales between anal-fin origin and lateral line (9–11 in *C. coadi* vs. 6–7 in *C. ekmekciae*) (Table 4); number of lateral line scales (70–84 in *C. coadi* vs. 55–61 in *C. ekmekciae*) [data from Turan et al. 2006b; Alwan 2011].

Capoeta coadi is distinguished from *C. kosswigi* by total number of gill rakers (Table 9): 14–18 in *C. coadi* vs. 19–28 in *C. kosswigi* (see Karaman 1969; Turan et al. 2006b; Turan 2008).

Capoeta coadi is distinguished from *C. mauricii* and *C. pestai* by having a weaker, thinner and less ossified last unbranched dorsal-fin ray in juveniles and adults and fewer scales between dorsal-fin origin and lateral line (12–17 in *C. coadi* vs. 18–22 in *C. mauricii* and 16–19 in *C. pestai* [data from Özüluğ and Freyhof 2008, Küçük et al. 2009]). It is further distinguished from *C. pestai* by the absence of spots on the body except in juveniles (vs. presence of many on the body [see Özüluğ and Freyhof 2008, Küçük et al. 2009]). *Capoeta coadi* is distinguished from *C. umbla* by total number of lateral line scales (70–84 vs. 86–104), number of scales between dorsal-fin origin and lateral line (12–17 vs. 18–24), number of scales between anal-fin origin and lateral line (9–11 vs. 11.5–15.5), and circum-peduncular scales (26–32 vs. 32–39) (see Alwan 2011, Tables 4–7).

Compared to other Iranian species of *Capoeta*, *C. coadi* has more scales and fewer gill rakers than *C. aculeata* (number of scales between dorsal-fin origin and lateral line:

Table 8. Gill rakers on the lower limb of the first gill arch in studied *Capoeta* species.

GR	8	9	10	11	12	13	17	18	19	20	22	24
<i>C. buhsei</i>	2	19	6									
<i>C. coadi</i>			1	9	19	20						
<i>C. mandica</i>							1	2	3	1	3	1

Table 9. Number of total gill rakers on the first gill arch in examined *Capoeta* species.

	12	13	14	15	16	17	18	21	22	23	24	25	26	27	28	31
<i>C. buhsei</i>	10	13	6													
<i>C. coadi</i>			1	7	14	6	5									
<i>C. mandica</i>										2	2	2	1	4		
<i>C. saadii</i>	1	9	6	1	2	1										
<i>C. trutta</i>								1	1	9	11	7	5	4	1	1

12–17 vs. 6–10; number of scales between anal-fin origin and lateral line: 9–11 vs. 5–8; circum-peduncular scales: 26–32 vs. 13–23; total number of lateral line scales: 70–84 vs. 36–52; caudal peduncle scales: 14–18 vs. 10–12; gill rakers on the lower limb of the first gill arch: 10–13 vs. 15–18 [data from Coad and Krupp 1994] and this study (Tables 4–9)). *Capoeta coadi* is distinguished from *C. fusca* by more total vertebrae (45–47 vs. 44), and more total lateral-line scales (70–84 vs. 40–62) (see Coad 2008, Johari et al. 2009).

Capoeta coadi differs from its sister species (see Figs 6–7), *C. buhsei* in having more gill rakers on lower limb of first gill arch (10–13 vs. 8–10), more gill rakers on the whole first gill arch (14–18 vs. 12–14, see Tables 8–9) and by depth of caudal peduncle in percent of standard length (10.03–11.61 vs. 8.58–10.84). *Capoeta coadi* is distinguished from another closely related species, *C. saadii* by having more scales below the lateral line (9–11 vs. 6–10, modally 9) (Table 4) and more circum-peduncular scales (26–32 vs. 23–28, modally 25–26) [data from Alwan (2011)].

Molecular phylogenetic assessments

We generated COI barcode and *cyt b* sequences for a total of 76 and 61 *Capoeta* specimens, respectively (Tables 10–11). Two phylogenetic approaches including Maximum Likelihood and Bayesian analyses for species of *Capoeta* are given in Figs 6–7. Tables 12–13 provide the diagnostic nucleotide substitutions found in the mtDNA COI barcode region and *cyt b*, respectively.

For inter-specific differences, the greatest pairwise genetic divergence between *C. coadi* and its congeners was found to be 6.5 by *C. erhani* and lowest by *C. buhsei* (0.4) for COI and greatest 9.7 by *C. mandica* and lowest (1.5) by *C. buhsei* for *cyt b* (Tables 14–15).

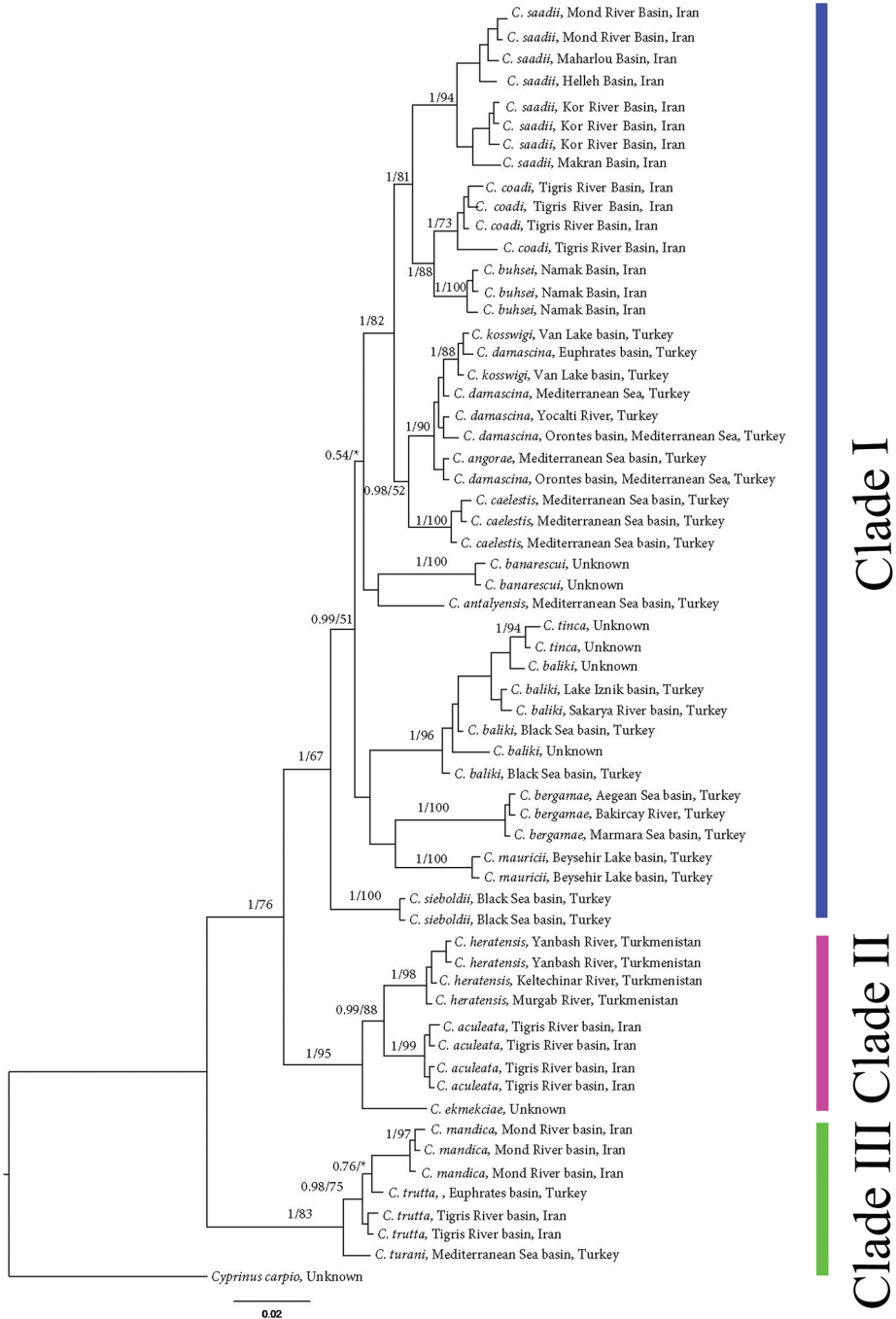


Figure 6. Bayesian tree inferred from *cyt b*. Numbers left of the slash, indicate the posterior probabilities of the Bayesian analysis, using MrBayes, while numbers right of the slash are the bootstrap support for 10,000 replicates in the Maximum Likelihood tree, using RaxML. Asterisks (*) indicate less than 50% Maximum Likelihood support for the node.

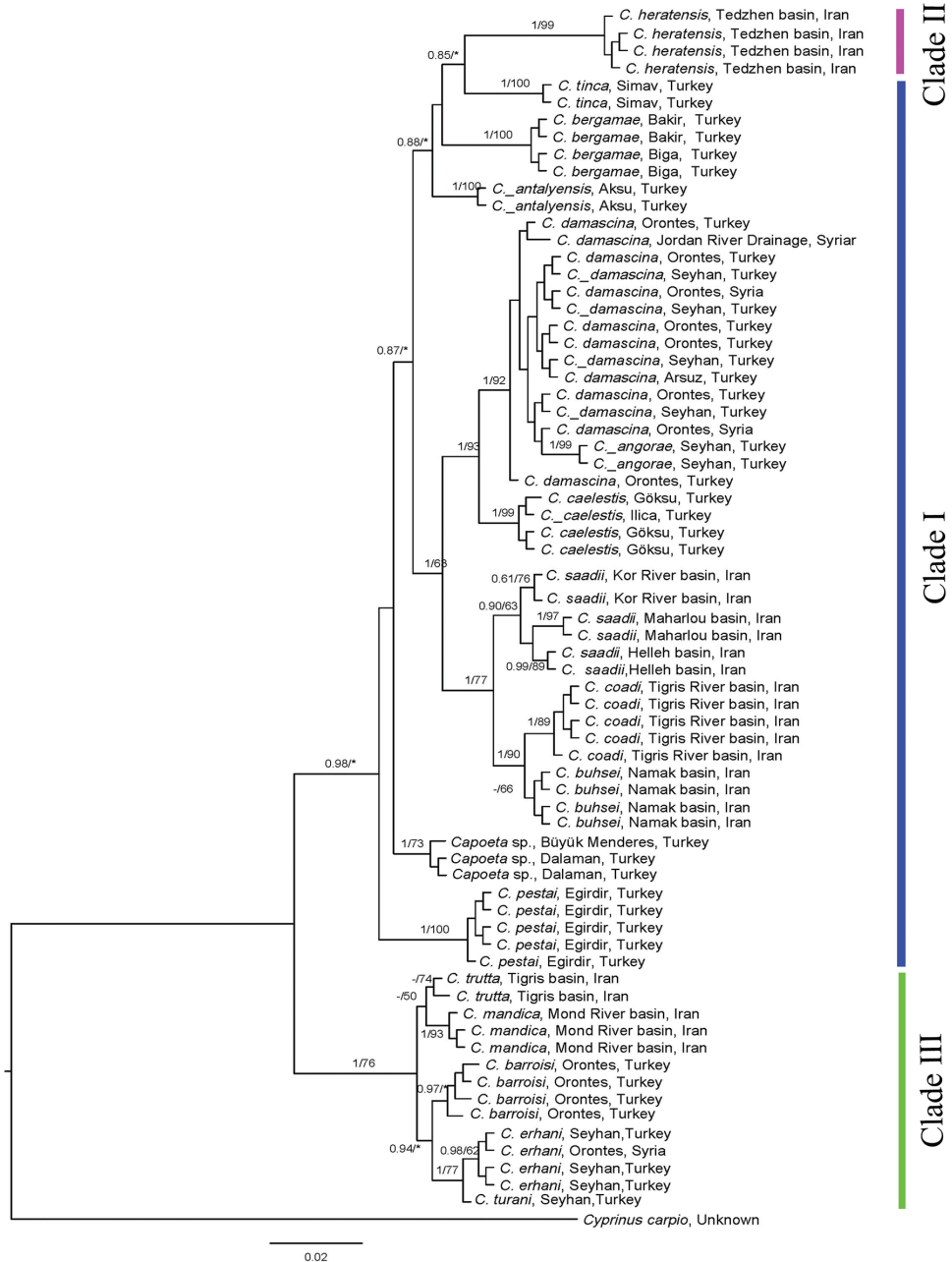


Figure 7. Bayesian tree inferred from COI. Numbers left of the slash, indicate the posterior probabilities of the Bayesian analysis, using MrBayes, while numbers right of the slash are the bootstrap support for 10,000 replicates in the Maximum Likelihood tree, using RaxML. Asterisks (*) indicate less than 50% Maximum Likelihood support and (-) indicates less than 0.50 Bayesian posterior probabilities for the node.

Table 10. List of species used for molecular analysis for *cyt b* (*present study, the ones without * are obtained from GenBank). *Cyprinus carpio* was considered as outgroup.

Species	Accession Number	Locality
<i>C. aculeata</i>	JF798267	Stream Sangan, Karun River basin, Tigris basin, Iran
<i>C. aculeata</i>	JF798264	Sevah River, Kor basin, Iran
<i>C. aculeata</i>	JF798266	Beshar River, Karun basin, Tigris basin, Iran
<i>C. aculeata</i>	JF798265	Sevah River, Kor basin, Iran
<i>C. angorae</i>	JF798268	Pozanti River, Mediterranean Sea basin, Turkey
<i>C. antalyensis</i>	JF798269	Boga Cayi River, Mediterranean Sea basin, Turkey
<i>C. baliki</i>	JF798272	Kizilirmak River, Black Sea basin, Turkey
<i>C. baliki</i>	JF798273	Biggest tributary of Kurtbog`azi dam lake, Sakarya River basin, Turkey
<i>C. baliki</i>	JF798275	Stream Cakirca, Lake Iznik basin, Turkey
<i>C. baliki</i>	GQ424019	Unknown
<i>C. baliki</i>	GQ424020	Unknown
<i>C. baliki</i>	JF798271	Kizilirmak River, Black Sea basin, Turkey
<i>C. banarescui</i>	GQ423987	Unknown
<i>C. banarescui</i>	GQ423988	Unknown
<i>C. bergamae</i>	JF798282	Bakacak stream, Marmara Sea basin, Turkey
<i>C. bergamae</i>	JF798280	Bakircay River, Turkey
<i>C. bergamae</i>	JF798281	Stream Guzelhisar, Aegean Sea basin, Turkey
<i>C. bubei</i>	JF798283	Taghra Rud stream, Namak Lake basin, Iran
<i>C. bubei*</i>	KU312369	Kordan River, Namak Lake basin, Karaj, Iran
<i>C. bubei*</i>	KU312370	Kordan River, Namak Lake basin, Karaj, Iran
<i>C. caelestis</i>	JF798336	Ilica stream, Gulf of Antalya, Mediterranean Sea basin, Turkey
<i>C. caelestis</i>	JF798286	Goksu River, Mediterranean Sea basin, Turkey
<i>C. caelestis</i>	JF798287	Kargi Cayi River, Mediterranean Sea basin, Turkey
<i>C. coadi*</i>	KU564303	Beshar River, Tigris River basin, Iran
<i>C. coadi*</i>	KU564304	Beshar River, Tigris River basin, Iran
<i>C. coadi*</i>	KU564305	Beshar River, Tigris River basin, Iran
<i>C. coadi*</i>	KU564306	Beshar River, Tigris River basin, Iran
<i>C. damascina</i>	JF798309	Karadut River, Euphrates basin, Turkey
<i>C. damascina</i>	JF798303	Stream Arsuz, Iskenderun Gulf basin, Mediterranean Sea, Turkey
<i>C. damascina</i>	JF798308	Yocalti River, Turkey
<i>C. damascina</i>	JF798306	Spring Incesu, Orontes basin, Mediterranean Sea, Turkey
<i>C. damascina</i>	JF798307	Yocalti River, Mediterranean Sea basin, Turkey
<i>C. ekmeckiae</i>	GQ424027	Unknown
<i>C. heratensis</i>	JF798319	Keltechinar River, Turkmenistan
<i>C. heratensis</i>	JF798318	Yanbash River, Turkmenistan
<i>C. heratensis</i>	JF798317	Yanbash River, Turkmenistan
<i>C. heratensis</i>	JF798316	Murgab River, Turkmenistan
<i>C. kosswigi</i>	JF798322	Deli Cayi River, Van Lake basin, Turkey
<i>C. kosswigi</i>	JF798323	Deli Cayi River, Van Lake basin, Turkey
<i>C. mandica*</i>	KU564307	Ghare Aghaj River, Mond River basin, Khaneh Zanian, Iran
<i>C. mandica*</i>	KU564308	Ghare Aghaj River, Mond River basin, Khaneh Zanian, Iran
<i>C. mandica*</i>	KU312375	Ghare Aghaj River, Mond River basin, Khaneh Zanian, Iran

Species	Accession Number	Locality
<i>C. mauricii</i>	JF798325	Eflatum spring, Beysehir Lake basin, Turkey
<i>C. mauricii</i>	JF798324	Sarioz stream, Beysehir Lake basin, Turkey
<i>C. saadii</i> *	KU564309	Ghare Aghaj River, Mond River basin, Firuzabad, Iran
<i>C. saadii</i> *	KU564310	Ghare Aghaj River, Mond River basin, Firuzabad, Iran
<i>C. saadii</i> *	KU564311	Saadii Tomb Spring, Maharlu basin, Iran
<i>C. saadii</i> *	KU312373	Helleh River, Helleh basin, KohmarSorkhi, Iran
<i>C. saadii</i> *	KU564312	Kor River, Kor basin, Kamfirouz, Iran
<i>C. saadii</i> *	KU564313	Kor River, Kor basin, Kamfirouz, Iran
<i>C. saadii</i>	JF798326	Rodan River, Makran basin, Iran
<i>C. saadii</i>	JF798327	Spring Golabii, 35 km north from Darab, Hormuz basin, Iran
<i>C. sieboldii</i>	JF798329	Kizilirmak River, Black Sea basin, Turkey
<i>C. sieboldii</i>	JF798330	Kelkit Cayi River, Black Sea basin, Turkey
<i>C. tinca</i>	GQ424008	Unknown
<i>C. tinca</i>	GQ424007	Unknown
<i>C. trutta</i>	JF798334	Dez River, Karun River basin, Iran
<i>C. trutta</i>	JF798333	Sultansuyu River, Euphrates basin, Turkey
<i>C. trutta</i>	JF798332	Gelal River, Ab e Seymareh, Tigris River basin, Iran
<i>C. turani</i>	JF798335	Çatkit River, Mediterranean Sea basin, Turkey
<i>Cyprinus carpio</i>	DQ868875	Unknown

Table II. List of species used for molecular analysis for COI (*present study, the ones without * are obtained from GenBank). *Cyprinus carpio* was considered as outgroup.

Species	Accession num.	Locality
<i>C. heratensis</i> *	KU564288	Gilas spring, Tedzen basin, Iran
<i>C. heratensis</i> *	KU564289	Gilas spring, Tedzen basin, Iran
<i>C. heratensis</i> *	KU564290	Gilas spring, Tedzen basin, Iran
<i>C. heratensis</i> *	KU564291	Bezangan Lake, Tedzen basin, Iran
<i>C. angorae</i>	KJ553074	Seyhan, Turkey
<i>C. angorae</i>	KJ552868	Seyhan, Turkey
<i>C. antalyensis</i>	KJ552850	Aksu, Turkey
<i>C. antalyensis</i>	KJ553025	Aksu, Turkey
<i>C. barroisi</i>	KJ553267	Orontes, Turkey
<i>C. barroisi</i>	KJ553245	Orontes, Turkey
<i>C. barroisi</i>	KJ552785	Orontes, Turkey
<i>C. barroisi</i>	KJ552810	Orontes, Turkey
<i>C. bergamae</i>	KJ553157	Bakir, Turkey
<i>C. bergamae</i>	KJ552877	Bakir, Turkey
<i>C. bergamae</i>	KJ553253	Biga, Turkey
<i>C. bergamae</i>	KJ553081	Biga, Turkey
<i>C. buhsei</i> *	KU312349	Kordan River, Namak Lake basin, Karaj, Iran
<i>C. buhsei</i> *	KU312350	Kordan River, Namak Lake basin, Karaj, Iran
<i>C. buhsei</i> *	KU564292	Roudbar River, Kavir basin, Iran

Species	Accession num.	Locality
<i>C. buhsei</i> *	KU564293	Roudbar River, Kavir basin, Iran
<i>C. caelestis</i>	KJ552856	Göksu, Turkey
<i>C. caelestis</i>	KJ553237	Illica, Turkey
<i>C. caelestis</i>	KJ553301	Göksu, Turkey
<i>C. caelestis</i>	KJ553030	Göksu, Turkey
<i>C. damascina</i>	KJ553080	Arsuz, Turkey
<i>C. damascina</i>	KJ553043	Orontes, Turkey
<i>C. damascina</i>	KJ552896	Orontes, Turkey
<i>C. damascina</i>	KJ553272	Orontes, Turkey
<i>C. damascina</i>	KJ552846	Orontes, Turkey
<i>C. damascina</i>	KJ552874	Ceyhan, Turkey
<i>C. damascina</i>	KJ552797	Orontes, Syria
<i>C. damascina</i>	KJ553202	Orontes, Syria
<i>C. damascina</i>	KJ553027	Ceyhan, Turkey
<i>C. damascina</i>	KJ553194	Ceyhan, Turkey
<i>C. damascina</i>	KJ552763	Ceyhan, Turkey
<i>C. damascina</i>	KJ552939	Jordan River Drainage, Syria
<i>C. damascina</i>	KJ553216	Orontes, Turkey
<i>C. damascina</i>	KJ553089	Orontes, Turkey
<i>C. erhani</i>	KJ552767	Ceyhan, Turkey
<i>C. erhani</i>	KJ552087	Ceyhan, Turkey
<i>C. erhani</i>	KJ552806	Ceyhan, Turkey
<i>C. erhani</i>	KJ553067	Ceyhan, Turkey
<i>C. mandica</i> *	KU564301	Ghare Aghaj River, Mond River basin, Khaneh Zanian, Iran
<i>C. mandica</i> *	KU564302	Ghare Aghaj River, Mond River basin, Khaneh Zanian, Iran
<i>C. mandica</i> *	KU312368	Ghare Aghaj River, Mond River basin, Khaneh Zanian, Iran
<i>C. pestai</i>	KJ553304	Egirdir, Turkey
<i>C. pestai</i>	KJ553138	Egirdir, Turkey
<i>C. pestai</i>	KJ552113	Egirdir, Turkey
<i>C. pestai</i>	KJ552841	Egirdir, Turkey
<i>C. pestai</i>	KJ552818	Egirdir, Turkey
<i>C. tinca</i>	KJ553229	Simav, Turkey
<i>C. tinca</i>	KJ553168	Simav, Turkey
<i>C. trutta</i> *	KU312352	Karkheh River, Tigris River basin, Seymareh, Iran
<i>C. trutta</i> *	KU312351	Gavi River, Tigris River basin, Illam, Iran
<i>C. turani</i>	KJ553224	Ceyhan Nehri, Turkey
<i>C. saadii</i> *	KU312358	Saadii Tomb Spring, Maharlou basin, Iran
<i>C. saadii</i> *	KU312395	Spring Pirbanoo, Maharlou basin, Iran
<i>C. saadii</i> *	KU312360	Helleh River, Helleh basin, KohmarSorkhi, Iran
<i>C. saadii</i> *	KU312361	Helleh River, Helleh basin, KohmarSorkhi, Iran
<i>C. saadii</i> *	KU564299	Kor River, Kor basin, Kamfiruz, Iran
<i>C. saadii</i> *	KU564300	Kor River, Kor basin, Kamfiruz, Iran
<i>C. saadii</i> *	KU312359	Kor River, Kor basin, Kamfiruz, Iran

Species	Accession num.	Locality
<i>C. coadi</i> *	KU564294	Beshar River, Tigris River basin, Iran
<i>C. coadi</i> *	KU564295	Beshar River, Tigris River basin, Iran
<i>C. coadi</i> *	KU564296	Beshar River, Tigris River basin, Iran
<i>C. coadi</i> *	KU564297	Beshar River, Tigris River basin, Iran
<i>C. coadi</i> *	KU564298	Beshar River, Tigris River basin, Iran
<i>Capoeta</i> sp.	KJ552935	Dalaman, Turkey
<i>Capoeta</i> sp.	KJ553011	Büyük Menderes, Turkey
<i>Capoeta</i> sp.	KJ552882	Dalaman, Turkey
<i>Cyprinus carpio</i>	DQ868875	Unknown

Table 12. Diagnostic nucleotide substitutions found in mtDNA COI barcode region of *Capoeta* species. Nucleotide position relative to *Cyprinus carpio* complete mitochondrial genome.

Species	6545	6620	6626	6665	6683	6713	6749	6758	6761	6770	6818	6845	6875	6887	6905	6986	6995	7076	7088
<i>C. buhsei</i>	C	A	A	T	G	G	T	C	G	G	G	A	A	C	C	G	A	G	T
<i>C. caelestis</i>	T	G	C	T	G	A	G	T	G	A	A	C	G	T	T	G	G	G	C
<i>C. coadi</i>	C	A	A	T	A	G	T	C	G	G	G	A	A	C	C	A	A	G	T
<i>C. damascina</i>	T	A	G	T	G	A	G	T	A	A	G	C	A	T	T	G	G	A	C
<i>C. saadii</i>	T	A	A	C	G	G	T	C	A	A	G	A	A	C	C	T	A	G	T

Table 13. Diagnostic nucleotide substitutions found in *cyt b* of *Capoeta* species. Nucleotide position relative to *Cyprinus carpio* complete mitochondrial genome.

Species	15430	15451	15457	15463	15472	15526	15550	15610	15670	15682	15760	15814	15925	16011	16027	16039	16045	16063
<i>C. buhsei</i>	C	G	T	A	A	G	G	T	G	T	G	G	G	C	C	A	G	C
<i>C. caelestis</i>	T	A	C	A	A	G	G	A	A	C	A	A	G	T	T	G	A	T
<i>C. coadi</i>	T	G	C	A	G	G	A	C	G	T	G	G	G	C	C	A	G	C
<i>C. damascina</i>	T	A	C	G	A	A	A	T	A	T	G	A	A	C	T	G	A	T
<i>C. saadii</i>	T	G	C	G	A	A	A	T	A	T	G	A	A	C	T	G	A	T

The two different phylogenetic analyses produced similar topologies. Both analyses produced a tree with 3 major clades (Figs 6–7). These included Clade I) *C. antalyensis*, *C. baliki*, *C. banarescui*, *C. bergamae*, *C. buhsei*, *C. caelestis*, *C. coadi*, *C. damascina* (*C. angorae* is a synonym [Alwan 2011]), *C. kosswigi*, *C. mauricii*, *C. pestai*, *C. saadii*, *C. sieboldii*, and *C. tinca*, Clade II) *C. aculeata*, *C. ekmeckciae*, and *C. heratensis*, and Clade III) *C. barroisi*, *mandica*, *C. trutta*, and *C. turani*.

The Iranian members of the *C. damascina* species complex, clustered together and formed the sister group to the other members in the complex. In these trees, samples of the *Capoeta coadi*, from Beshar River in Tigris River basin, form a well-supported monophyletic group, sister to *C. buhsei* in clade I.

Table 14. Mean genetic distance for *cyt b* between *Capoeta* species.

	<i>C. sieboldii</i>	<i>C. caelestis</i>	<i>C. mauricii</i>	<i>C. bergamae</i>	<i>C. baliki</i>	<i>C. antalyensis</i>	<i>C. tinca</i>	<i>C. banarescui</i>	<i>C. turani</i>	<i>C. trutta</i>	<i>C. bubsei</i>	<i>C. coadi</i>	<i>C. mandica</i>	<i>C. saadii</i>
<i>C. sieboldii</i>														
<i>C. caelestis</i>	3.8													
<i>C. mauricii</i>	5.1	4.6												
<i>C. bergamae</i>	5.3	5.4	4.8											
<i>C. baliki</i>	4.4	4.7	4.5	5.7										
<i>C. antalyensis</i>	4.3	4.1	4.1	4.9	4.6									
<i>C. tinca</i>	5.3	5.6	5.3	6.6	1.0	5.6								
<i>C. banarescui</i>	5.7	4.9	4.9	6.0	4.9	4.4	4.9							
<i>C. turani</i>	8.1	8.4	9.3	9.5	8.5	8.6	8.8	11.0						
<i>C. trutta</i>	8.7	8.7	9.1	9.9	9.1	9.2	9.4	10.9	1.2					
<i>C. bubsei</i>	4.3	2.6	4.1	5.6	4.3	4.0	5.1	4.7	9.3	9.5				
<i>C. coadi</i>	4.2	2.6	4.5	6.0	5.0	4.3	5.8	5.4	9.4	9.6	1.5			
<i>C. mandica</i>	8.5	8.8	9.0	9.9	8.7	9.5	9.2	11.4	1.5	1.1	9.6	9.7		
<i>C. saadii</i>	4.8	3.3	4.8	4.6	4.7	4.8	5.4	5.8	8.5	8.9	2.8	2.7	9.1	
<i>C. aculeata</i>	6.5	6.6	7.2	7.7	7.4	6.5	8.0	7.5	9.2	9.2	6.8	7.0	9.7	6.8

Discussion

Based on morphological and molecular results, *C. saadii* and *C. coadi* are distinct species in the *Capoeta damascina* species complex group formerly known as *C. damascina* in Iranian water bodies. Phylogenetic analyses recovered three main groups inside the genus *Capoeta*: the Mesopotamian group (*C. trutta* group), the Anatolian-Iranian group (*C. damascina* group) and the Aralo-Caspian group (*C. capoeta* group) which is in agreement with Levin et al. (2012). The genus *Capoeta* is monophyletic (Levin et al. 2012). Based on the previous published data, the *Capoeta damascina* species complex group diverged from the *C. capoeta* group about 9.1 MYA (95% CI: 6.4–10.9) in the Tortonian period (Levin et al. 2012). Iranian members of the *C. damascina* group (*bubsei*, *saadii* and *coadi*) formed a clade sister to other *C. damascina* species complex group members.

The populations of *Capoeta* from the Karun River drainage have long been considered as *C. damascina* (Esmaeili et al. 2010). However, it has been proposed that *C. damascina* might be restricted to the Damascus area in Syria. Most Iranian populations, referred to *C. damascina*, including Karun River population have been considered as *C. saadii* (Heckel, 1847) (Teimori et al. 2016). *Capoeta saadii* was originally described from Persepolis, Pulwar (Sivand) River, Kor River basin, Ruins, northeast of Shiraz,

Iran. It was considered as a synonym of *C. damascina* (Esmaeili et al. 2010) and as a valid species by Bianco and Bănărescu (1982), by Levin et al. (2012) and by Teimori et al. (2016). Based on morphological and molecular results presented here, *C. saadii* is a valid species closely related to *C. bubsei* (as proposed by Bianco and Bănărescu (1982) and to *C. coadi* yet is diagnosed from these species and from *C. damascina* (see Alwan 2011). *Capoeta saadii* is the least known species of the genus. It is not mentioned in the revision of the genus by Karaman (1969) who had no specimens available, but its position within the genus *Capoeta* and its close phylogenetic relationship to *C. coadi* and *C. bubsei* were demonstrated using many fresh specimens at our disposal, mostly from type localities.

Comparative materials used in morphological and molecular phylogenetic analyses

Morphological analyses

- Capoeta bubsei*: ZM-CBSU Z218-229, 12, 104-149 mm SL; Iran, Semnan prov., Kavir basin, Hableh Rud at Garmsar, 35°18'06"N, 52°24'57"E. 21 August 2011. H.R. Esmaeili, G. Sayyadzadeh, A. Gholamifard, R. Zamaniannejad. ZM-CBSU Z260-274, 15, 88–130 mm SL; Iran, Albourz prov., Kordan River at Karaj, 35°57'12"N, 56°50'18"E. 5 July 2014. M. Masoudi, R. Khaefi. H.R. Mehraban.
- Capoeta fusca*: ZM-CBSU Z197-211, 15, 50–78 mm SL; Iran, south Khorasan prov., Sharifabad Qanat at Birjand, 33°58'08"N, 59°17'03"E. 29 August 2011. H.R. Esmaeili, G. Sayyadzadeh, A. Gholamifard, R. Zamaniannejad.
- Capoeta mandica*: ZM-CBSU Z230-234, 5, 82-130 mm SL; Iran, Fars prov., Qareh Aghaj River at Khaneh Zanian, 29°41'13"N, 52°05'58"E. 30 May 2015. H. Zareian, A. Gholamhosseini, G. Sayyadzadeh. ZM-CBSU Z212-217, 6, 83-118 mm SL; Iran, Fars prov., Qareh Aghaj River at Kavar, 29°10'55"N, 52°41'32"E. 27 February 2015. G. Sayyadzadeh, M. Masoudi.
- Capoeta saadii*: ZM-CBSU Z136-146, 11, 78-121 mm SL; ZM-CBSU 2504, 1, 82 mm SL; ZM-CBSU 2508, 1, 69 mm SL; ZM-CBSU 2520-2521, 2, 51-62 mm SL; ZM-CBSU 2524-2528, 5, 113-231 mm SL; Iran, Fars prov., Ghadamgah spring, Doroodzan, 30°15'11"N, 54°25'32"E. 21 December 2003. H.R. Esmaeili, Biglari.
- Capoeta trutta*: ZM-CBSU E100-123, 24, 50-149 mm SL; Iran, Kermanshah prov., Gamasiab River, 34°23'31"N, 47°42'57"E. 27 September 2007. A. Teimori, A. Gholamhosseini, M. Ebrahimi, A. Gholamifard; ZM-CBSU C453-463, 11, 67-177 mm SL; ZM-CBSU C474-477, 4, 67–75 mm SL; ZM-CBSU C481, 76 mm SL; all from Iran, Khuzestan prov., Maroon River at Aghajari, 30°44'52"N, 49°54'59"E. 21 March 2008. H. Zareian.

Molecular phylogenetic analyses

- Capoeta buhsei*; ZM-CBSU M1299-1300, 2, Iran, Albourz prov., Kordan River at Karaj, 35°57'12"N, 56°50'18"E. 5 July 2014. M. Masoudi, R. Khaefi. H.R. Mehraban. GenBank accession number: (COI: KU312349, KU312350; *cytb*: KU312369, KU312370); ZM-CBSU M1289-1290, 2, Iran: Semnan Prov., Kavir basin, Roudbar River at Mehdishahr, 35°37'56"N, 53°20'41"E. 30 August 2011. H.R. Esmaeili et al., GenBank accession number: (COI: KU564292, KU564293).
- Capoeta heratensis*; ZM-CBSU M813-815, 3, Iran, Razavi Khorasan prov., Gilas spring, 36°36'55"N, 59°20'17"E. 25 August 2011. H.R. Esmaeili et al. GenBank accession number: (COI: KU564288, KU564289, KU564290). ZM-CBSU M816, 1, Iran, Razavi Khorasan prov., Bezangan Lake, Tedzen basin. 36°17'03"N, 60°24'18"E. 25 August 2011. H.R. Esmaeili et al. GenBank accession number: (COI: KU564291).
- Capoeta mandica*; ZM-CBSU M1433-1435, 3, Iran, Fars prov., Qareh Aghaj River at Khaneh Zanian, 29°41'13"N, 52°05'58"E. 30 May 2015. H. Zareian, A. Gholamhosseini, G. Sayyadzadeh. GenBank accession number: (COI: KU564301, KU564302, KU312368; *cytb*: KU564307, KU564308, KU312375).
- Capoeta saadii*; ZM-CBSU M1426-1427, 2, Iran: Fars prov. Kor River, at Kamfirouz, 30°25'2"N, 52°8'59"E. H. Zareian. 24 October 2015. GenBank accession number: (COI: KU564299, KU564300; *cytb*: KU564312, KU564313). ZM-CBSU M1421, ZM-CBSU1422-1425, 3, Iran, Fars prov., Qareh Aghaj River at Firuzabad, 28°41'31"N, 52°27'43"E. 25 April 2015. H. Zareian. GenBank accession number: (*cytb*: KU564309, KU564310, KU564311). ZM-CBSU M157, 1, Iran, Fars prov., Shiraz, Saadii Tomb, Maharlou basin, 29°37.348'N, 52° 34.934'E. R. Khaefi, 2009. GenBank accession number: (COI: KU312358). ZM-CBSU M825, M831, 2, Iran, Fars prov., Helleh River, Helleh basin, KohmarhSorkhi, S. Mirgheiasi, S. Ghasemian. 29°23'39"N, 52°09'49"E. GenBank accession number: (COI: KU312361, KU312360; *cytb*: KU312373). ZM-CBSU M822, 1, Iran, Fars prov., Qareh Aghaj River at Firuzabad, 29°07'34"N, 52°51'24"E. GenBank accession number: (*cytb*: KU564310). FSJF DNA-18 Iran: Fars prov.: spring Pirbanoo about 10 km south of Shiraz, 29°31'08"N, 52°27'55"E GenBank accession number: (COI: KU312395). FSJF DNA-22; Iran: Fars prov.: River Kor about 73 km north of Shiraz, 30°11'37"N, 52°27'56"E. GenBank accession number: (COI: KU312359).
- Capoeta trutta*; ZM-CBSU M583, 1, Iran: Ilam prov.; Gavi River at Mehran, H.R. Esmaeili, 13 November 2012, 33°39'18"N, 47°02'14"E. GenBank accession number: COI: KU312351; ZM-CBSU M593, 1, Iran, Ilam prov.; Seymareh River, H.R. Esmaeili, 13 November 2012, 33°38'17"N, 47°01'30"E. GenBank accession number: COI: KU312352.

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