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Six new species of dragon millipedes, genus *Desmoxytes* Chamberlin, 1923, mostly from caves in China (Diplopoda, Polydesmida, Paradoxosomatidae)

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Abstract

Six new species of *Desmoxytes* are described from southern China: *D. laticollis* **sp. n.**, *D. simplipoda* **sp. n.**, and *D. similis* **sp. n.**, all three from caves in Guangdong Province; *D. phasmoides* sp. n. also from a cave, and both epigean *D. spiniterga* **sp. n.** and *D. variabilis* **sp. n.**, the latter trio from Guangxi Zhuang Autonomous Region. A modified key to all 20 *Desmoxytes* species currently known to occur in China is given.

Keywords

Desmoxytes, new species, troglobite, key, southern China

Introduction

Millipedes in the genus *Desmoxytes* Chamberlin, 1923, belong to the tribe Orthomorphini, subfamily Paradoxosomatinae, family Paradoxosomatidae (Golovatch et al. 2012) and are often referred to as "dragon millipedes". This genus is conspicuous in its species generally showing a dragon-like appearance, with strongly wing-, spine- or antler-shaped paraterga. *Desmoxytes* was first revised by Golovatch and Enghoff

(1994), very recently reviewed by Likhitrakarn et al. (2015) to comprise 35 described species ranging from southeastern China south through Laos, Vietnam and Myanmar to southern Thailand and Western Malaysia. Only one species, *D. planata* (Pocock, 1895), has attained a nearly pantropical distribution through commerce.

The dragon millipede fauna of China has also been summarized, keyed and shown to contain 14 species, including all 11 congeners hitherto known from caves (Golovatch et al. 2010, 2012, Liu et al. 2014, Golovatch 2015). Most of the cavernicolous *Desmoxytes* look highly troglomorphic and show spiniform paraterga.

The following 14 species are currently known to occur in mainland China, arranged in alphabetic order:

D. cornutus Zhang & Li, 1982, from Guangxi, Guilin, Yangshuo.
D. draco Cook & Loomis, 1924, from Jiangxi, Jiujiang, Lushan Mountain.
D. eupterygota Golovatch, Li, Liu & Geoffroy, 2012, from two caves in Hunan, Chenzhou, Linwu.
D. getuhensis Liu, Golovatch & Tian, 2014, from two caves in Guizhou, Ziyun, Getuhe National Geopark.
D. lingulata Liu, Golovatch & Tian, 2014, from Guangxi, Guilin, Pingle, Chaotianyan.
D. longispina Loksa, 1960, from a cave in Guangxi (an exact locality unknown).
D. lui Golovatch, Li, Liu & Geoffroy, 2012, from a cave in Guangxi, Yongfu.
D. minutubercula Zhang, 1986, from Guangxi, Tianlin.
D. nodulosa Liu, Golovatch & Tian, 2014, from several caves in Guangxi, Hechi, Du'an.
D. parvula Liu, Golovatch & Tian, 2014, from Guangxi, Du'an, Xia'ao.
D. planata (Pocock, 1895), from a cave in Yunnan, Luxi, but actually nearly pantropical.
D. scolopendroides Golovatch, Geoffroy & Mauriès, 2010, from a cave in Guangxi, Huanjiang and several caves in Du'an.
D. scutigeroides Golovatch, Geoffroy & Mauriès, 2010, from several caves in Guangxi, Huanjiang and Du'an.
D. spinissima Golovatch, Li, Liu & Geoffroy, 2012, from a cave in Guangxi, Fuchuan.

The present paper describes another six new species of *Desmoxytes* from southern China, including four presumed troglobites. Three of the new species are the first to be recorded in Guangdong Province, whereas a further three are from Guangxi Zhuang Autonomous Region which alone has already been known to support seven troglobitic species. Altogether, 20 species of *Desmoxytes* have now been recorded from China.

Material and methods

The holotypes and a number of paratypes are deposited in the zoological collection of the South China Agricultural University, Guangzhou, China (SCAU), with some duplicates (paratypes) housed also in the Zoological Museum Alexander Koenig, Bonn,

Germany (ZFMK), and the Zoological Museum, State University of Moscow, Russia (ZMUM).

Observations and dissections were performed using an Olympus SZ51 stereo microscope. The line drawings were prepared with the help of an Olympus SZX12 stereo microscope and a camera lucida attached to the scope. The photographs were taken with Canon EOS 40D and 7D cameras, further processed using Adobe Photoshop CS5 software.

The methods and terminology used here are after Golovatch et al. (2012).

Taxonomic part

***Desmoxytes laticollis* sp. n.**
http://zoobank.org/9C11F333-5F13-4EBC-B111-2581CDB8D344
Figs 1A–B, 2–3

Holotype ♂ (SCAU), China, Guangdong, Qingyuan, Yingde Shi, Huanghua Xiang, Yanbei Cun, Cave Yangyan Dong, 24°18'32"N, 112°47'20"E, *ca* 450 m a.s.l., 2014-XII-30, leg. Mingyi Tian, Weixin Liu, Sunbin Huang & Xinhui Wang.

Paratypes. 13 ♂, 7 ♀ (SCAU), 1 ♂, 1 ♀ (ZMUM), 1 ♂, 1 ♀ (ZFMK), same locality and collecting data as the holotype.

Name. To emphasize the collum being the broadest segment; adjective.

Diagnosis. Keys out to the superficially most similar *D. eupterygota* Golovatch, Li, Liu & Geoffroy, 2012 (Liu et al. 2014), especially so concerning metatergal ornamentation and a condensed solenophore, but differs by the collum being the broadest segment, as well as the femora, postfemora and tibiae conspicuously clavate in both sexes.

Description. Length *ca* 26–27 mm (♂) or 28–29 mm (♀), width of midbody pro- and metazonae 2.0 and 2.5 (♂) or 2.2 and 2.5 mm (♀), respectively. Holotype 26 mm long, 2.0 and 2.5 mm wide on midbody pro- and metazonae, respectively, maximum width on collum 3.5 mm. In width, head < segment 8–16 < 5–7 < 4 < 3 < 2 < collum; starting with segment 17, body gradually tapering towards telson (Fig. 2). Live coloration rather uniformly yellowish to pallid (Fig. 1A–B). Head sparsely setose, epicranial suture distinct (Fig. 2A–B). Antennae long and slender, reaching back until posterior margin of segment 5 (♂) or middle of segment 4 (♀) when stretched dorsally; antennomeres 5 and 6 each with a compact apicodorsal group of bacilliform sensilla.

Body with 20 segments. Tegument (Fig. 2) very strongly shining, prozonae faintly microalveolate; surface below paraterga of collum and those of segments 2–4 finely microgranulate. Collum (Figs 2A, 3A) with at least 2+2 setae at front margin, another 1+1 setae in the middle, hardly visible; paraterga on collum particularly strongly developed, wing-shaped, lying a little below a rather convex collum; paraterga on segments 2–4 clearly elevated above dorsum, thereafter rather poorly-developed, relatively small and crest-shaped, lying slightly below level of a faintly convex dorsum until segment 18, vestigial and lying far below level of a strongly convex dorsum on segment 19

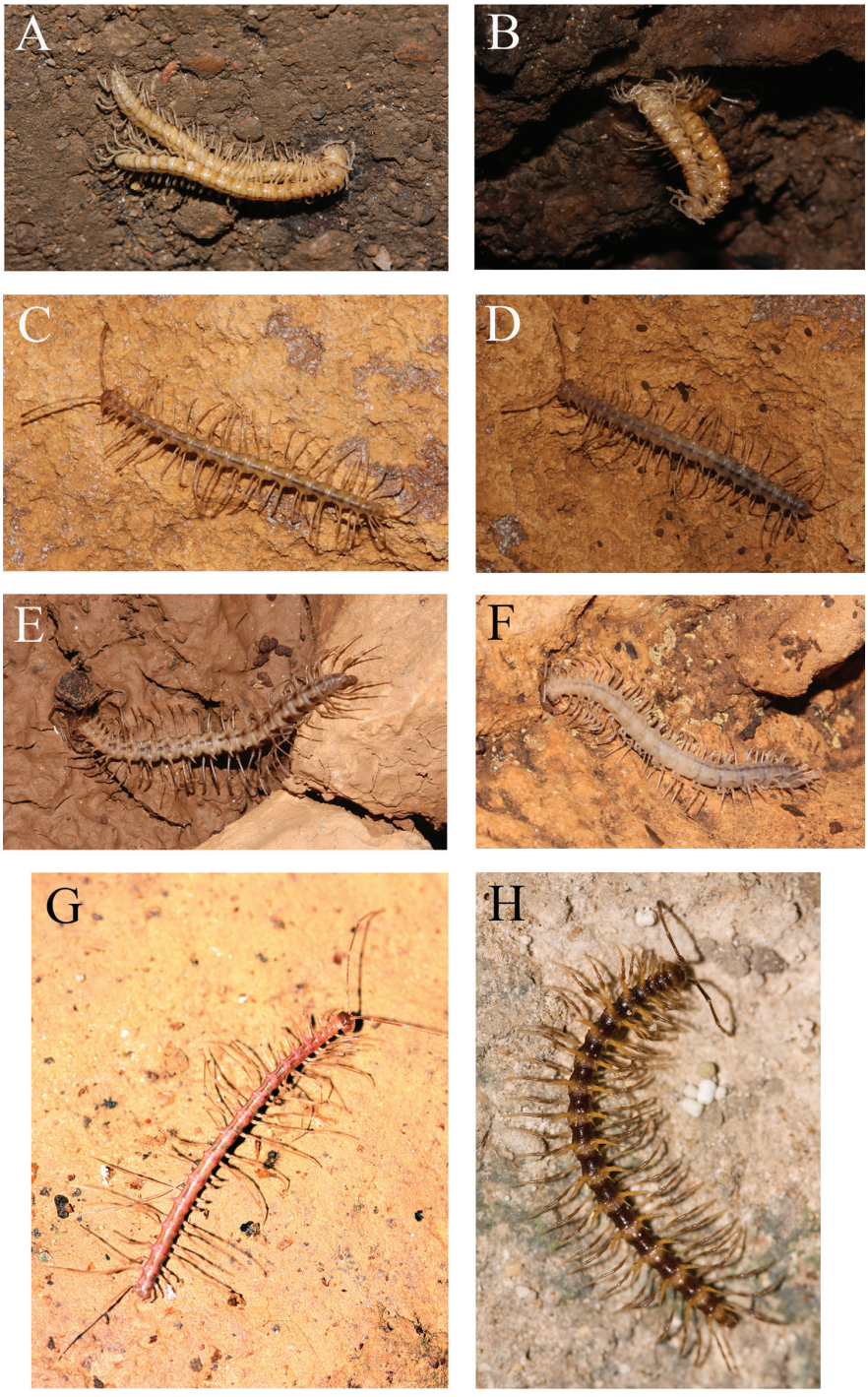

Figure 1. *In vivo* photographs. **A–B** a mating couple of *Desmoxytes laticollis* sp. n. **C–D** ♂ and ♀, *Desmoxytes simplipoda* sp. n. **E–F** 2 ♀, *Desmoxytes similis* sp. n. **G** ♂, *Desmoxytes phasmoides* sp. n. **H** ♂, *Desmoxytes variabilis* sp. n.

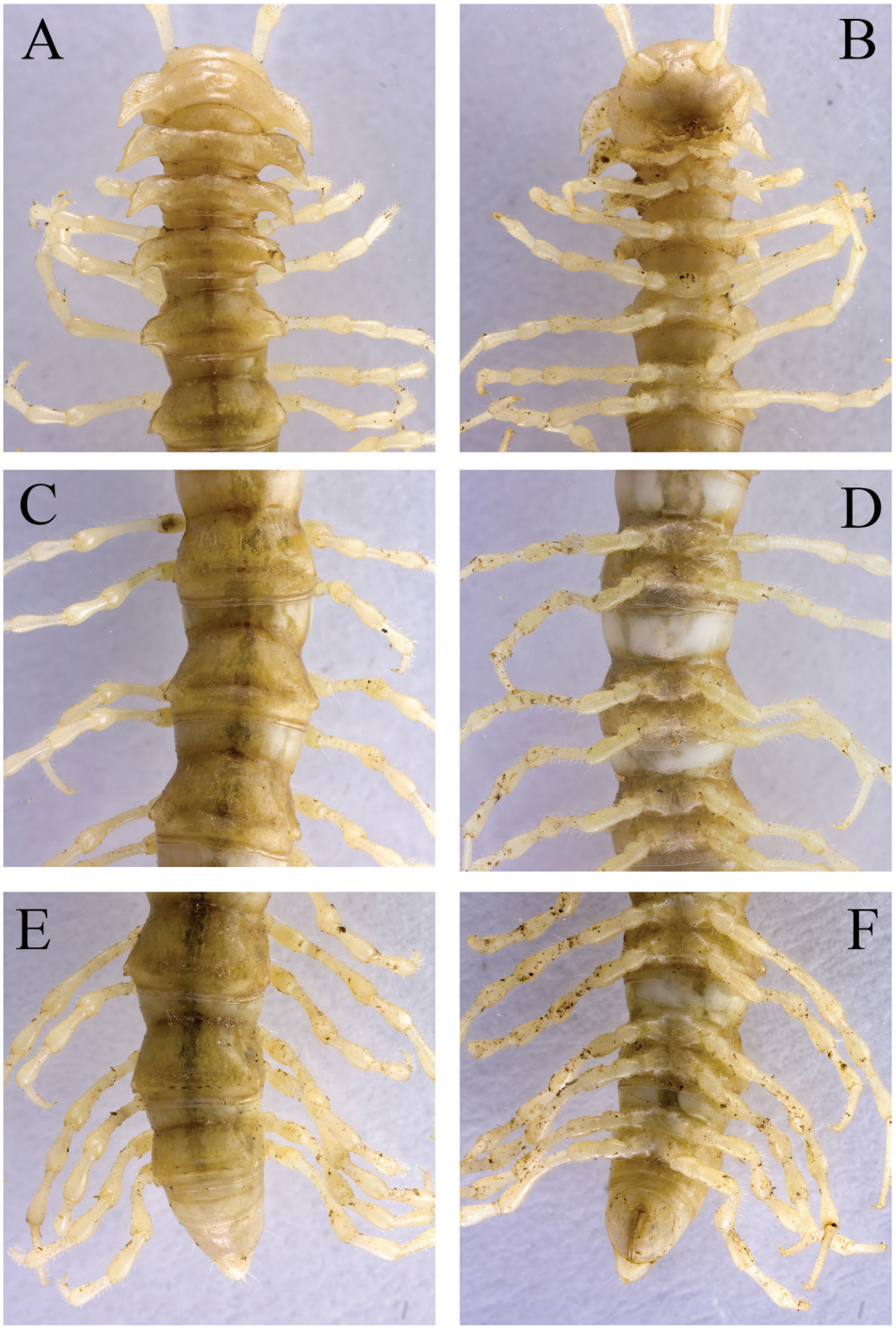

Figure 2. *Desmoxytes laticollis* sp. n., ♂ paratype from Cave Yangyan Dong. **A–B** anterior part of body, dorsal and ventral views, respectively **C–D** midbody segments, dorsal and ventral views, respectively **E–F** posterior part of body, dorsal and ventral views, respectively.

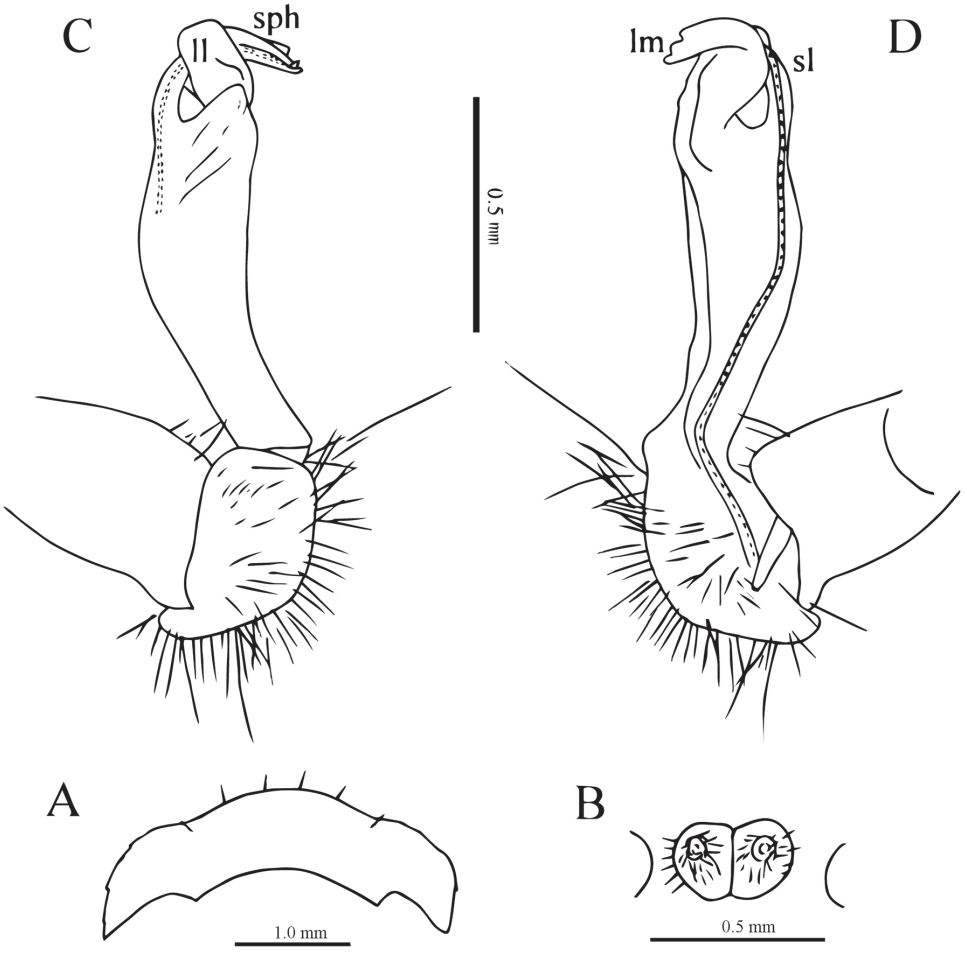

Figure 3. *Desmoxytes laticollis* sp. n., ♂ paratype from Cave Yangyan Dong. **A** collum, dorsal view **B** sternal processes between coxae 4, ventral view **C–D** right gonopod, lateral and mesal views, respectively.

(Fig. 2A, C, E); paraterga 1–4 with three especially strong denticles at lateral margin, two anterior of the denticles gradually disappearing towards segment 7, but caudalmost tooth persisting until segment 18 (Fig. 2A, C, E). Metaterga 2–4 each with 1+1 setae in anterior row; each of metaterga 5–19 additionally with 1+1 setae in posterior row, mostly poorly visible; paraterga a little more strongly developed in ♂ than in ♀, calluses very thin in poreless segments, slightly thicker in pore-bearing ones. Stricture between pro- and metazonae very narrow and deep. Ozopores entirely lateral, lying on top of caudal tooth on pore-bearing paraterga (Fig. 2A, C, E). Transverse sulcus evident and deep, smooth at bottom, reaching bases of paraterga on segments 7–16, incomplete (not reaching the bases of paraterga) in segments 5–6 and 17–18, vestigial in segment 19 (Fig. 2A, C, E). Epiproct subconical, clearly flattened dorsoventrally, mostly broad, subtruncate at a narrow apex, subapical lateral setae not borne on knobs

(Fig. 2E–F). Hypoproct subtrapeziform, clearly emarginate at caudal margin, caudal setae distinctly separated (Fig. 2E–F). Pleurosternal carinae poorly-developed, only visible on segments 2 and 3 both in ♂ and ♀. Axial line missing.

Sterna sparsely setose, nearly flat, cross-impressions shallow, axial groove being especially superficial (Fig. 2B, D, F). A pair of paramedian, densely setose, low cones between ♂ coxae 4 (Figs 2B, 3B). Legs 1 short, following ones growing slightly, but increasingly long and slender towards telson, midbody legs *ca* 2.5 (♂) or 2.0 (♀) times as long as body height; femora, postfemora and tibiae conspicuously clavate distad, neither tarsal brushes nor adenostyles in ♂ and ♀ (Fig. 2).

Gonopods (Fig. 3C–D) suberect. Coxite short, subcylindrical, sparsely setose distodorsally, nearly 1/3 as long as telopodite. Prefemur densely setose, almost half as long as acropodite. Femorite long, slightly curved ventrad. Solenophore (**sph**) clearly condensed and divided into a large rectangular lobe on lateral side (= lamella lateralis, **ll**) and a distinct coiled part on mesal side (= lamella medialis, **lm**). Seminal groove running entirely on mesal side of femorite before entering onto a short, but evident and flagelliform solenomere (**sl**), the latter lying between **ll** and **lm**.

Remark. Because of the pallid tegument and remarkably elongated antennae and legs, this species is most probably a troglobite.

***Desmoxytes simplipoda* sp. n.**
http://zoobank.org/AB383DC6-E76D-41D7-912F-6E75FC973DE0
Figs 1C–D, 4–5

Holotype ♂ (SCAU), China, Guangdong, Qingyuan, Yangshan Xian, Chengjia Xiang, Dabei Cun, Cave Kuangzhanyan, 24°46'28"N, 112°48'16"E, *ca* 140 m a.s.l., 2014-XII-28, leg. Mingyi Tian, Weixin Liu, Sunbin Huang & Xinhui Wang.

Paratypes. 1 ♂, 6 ♀ (SCAU), same locality and collecting data as the holotype.

Name. To emphasize the legs being simple, devoid of modifications; adjective.

Diagnosis. Using the latest key (Liu et al. 2014), this new species keys out to the superficially most similar *D. longispina* (Loksa, 1960), especially so due to spiniform paraterga and a condensed solenophore, but differs by the legs being devoid of modifications.

Description. All characters as in *D. laticollis* sp. n., except as follows.

Length *ca* 28–29 mm (♂) or 31–33 mm (♀), width of midbody pro- and metazonae 1.8 and 4.0 (♂) or 2.5 and 4.5 mm (♀), respectively. Holotype 29 mm long, 1.8 and 4.0 mm wide on midbody pro- and metazonae, respectively. In width, head < segment 2–4 < collum < 5–16. Coloration (Fig. 1C–D) varying from dark brownish to nearly pallid, anterior part of body a little darker than posterior part. In holotype, head, as well as dorsal and both lateral sides of metaterga dark brownish; prozonae, paraterga, sterna, and legs pallid to yellowish (Fig. 4); apices of antennomeres 6 and 7 dark brownish (Fig. 1C–D). Antennae very long and slender, reaching back until posterior margin of segment 6 (♂) or segment 5 (♀) when stretched dorsally.

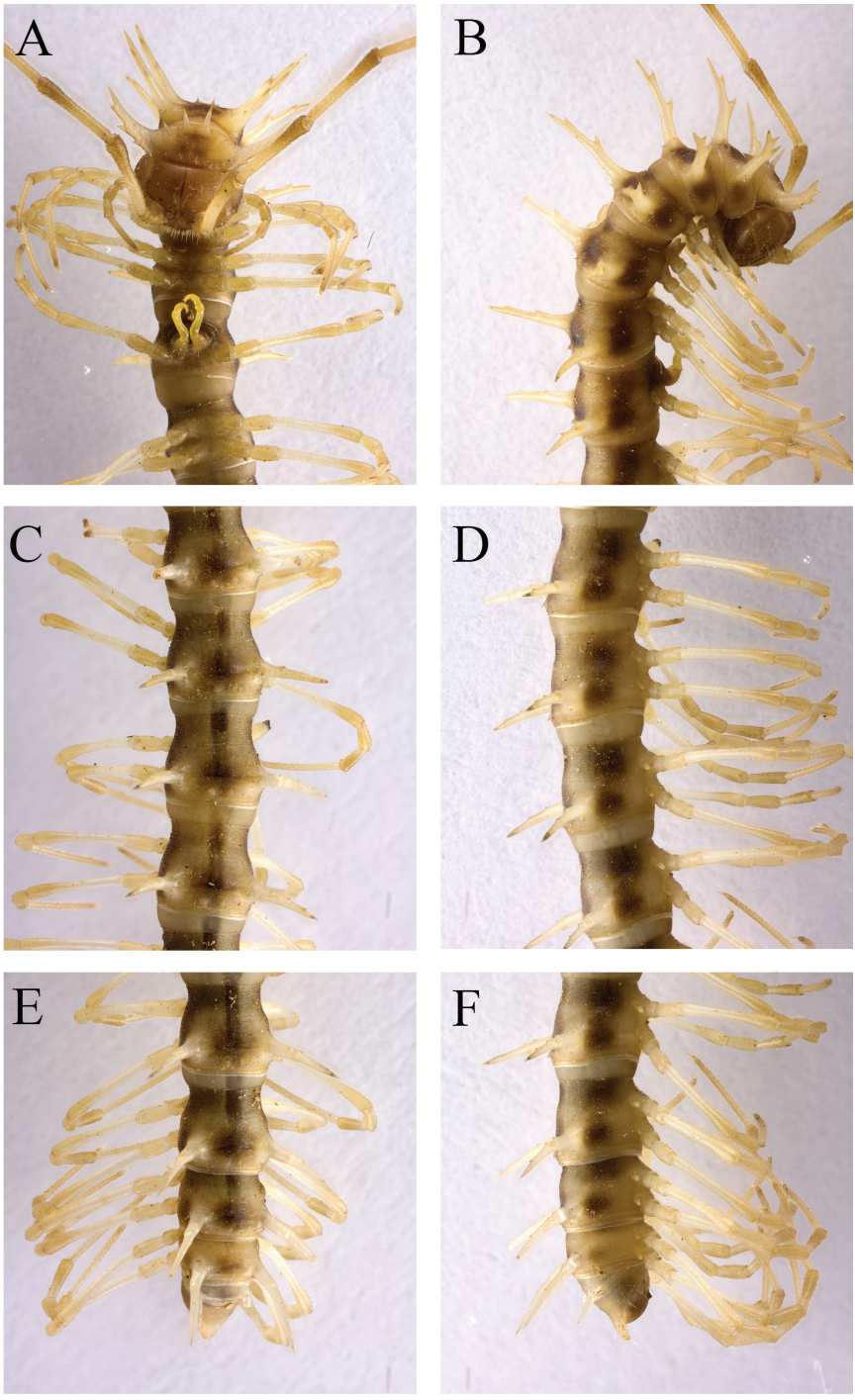

Figure 4. *Desmoxytes simplipoda* sp. n., ♂ holotype from Cave Kuangzhanyan. **A–B** anterior part of body, ventral and sublateral views, respectively **C–D** midbody segments, dorsal and lateral views, respectively **E–F** posterior part of body, dorsal and lateral views, respectively.

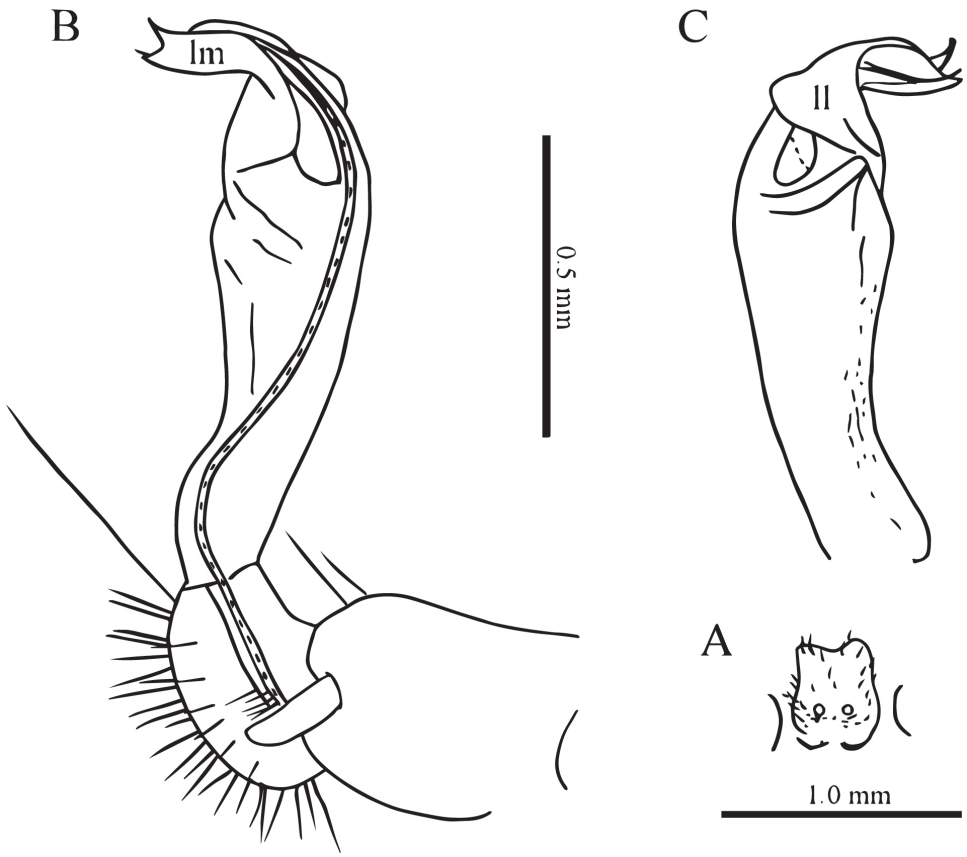

Figure 5. *Desmoxytes simplipoda* sp. n., ♂ holotype from Cave Kuangzhanyan. **A** sternal process between coxae 4, ventral view **B–C** entire right gonopod and its distal half, mesal and lateral views, respectively.

Prozonae very delicately microalveolate, metazonae rather finely shagreened and microgranulate (Fig. 4). Collum (Fig. 4A) with 3+3 evident setigerous spinules at fore margin, at least 1+1 much smaller spinules in the middle and 2+2 strongly enlarged spines (paramedian spines being larger than others) at posterior margin; following metaterga 2–18 showing a pattern of smaller 2+2 posterior spinules with invariably obliterated setae (paramedian two spinules a little larger, the other two located at base of each paratergum), while metaterga 19 with 1+1 posterior spinules (Fig. 4C, E). Paraterga (Fig. 4) very strongly developed, spiniform, on collum with four evident anteromarginal denticles; all following paraterga long, straight, also spiniform, about as high as metatergal height in ♂, a little shorter in ♀; paraterga 2–18 with 2–3 evident denticles frontally. Paraterga 2–9 directed more dorsad than laterad, nearly erect above dorsum; following paraterga directed a little caudad, but ending up clearly above dorsum. Ozopores conspicuous, located a little above first denticle from lateral side of pore-bearing paraterga (Fig. 4B–F). Transverse sulcus present on segments 2–19, but complete and reaching bases of paraterga only on segments 6–15 (Fig. 4C, E).

Sterna sparsely setose, cross-impressions evident. A large, median, sparsely setose process with two small pores at base between ♂ coxae 4 (Figs 4B, 5A). Legs devoid of modifications (Fig. 4A–B), *ca* 2.8–3.0 (♂) or 2.5 (♀) times as long as midbody height.

Gonopods (Fig. 5B–C) simple. Coxite stout, about 1/3 as long as telopodite. Prefemur short, less than half the length of acropodite. Femorite long, suberect. Solenophore strongly condensed and divided into a large subtriangular lamella lateralis (**ll**) and a terminally evidently bifid lamella medialis (**lm**).

Remark. Judging by the extremely elongated antennae and legs, this species seems to be a troglobite.

***Desmoxytes similis* sp. n.**
http://zoobank.org/3E252D45-5DE5-4F32-B3A6-9F855E84A437
Figs 1E–F, 6–7

Holotype ♂ (SCAU), China, Guangdong, Qingyuan, Yingde Shi, Qingkeng Zhen, Bangjiao Cun, Cave Bangjiao Dong, 24°25'09"N, 112°57'16"E, *ca* 230 m a.s.l., 2014-XII-29, leg. Mingyi Tian, Weixin Liu, Sunbin Huang & Xinhui Wang.

Paratypes. 1 ♂, 4 ♀ (SCAU), 1 ♂, 1 ♀ (ZFMK), same locality and collecting data as the holotype.

Name. To emphasize the particular similarities to *D. simplipoda* sp. n.; adjective.

Diagnosis. This species seems to be especially similar to *D. simplipoda* sp. n., from Yangshan, Qingyuan, Guangdong, but differs by the setose process between ♂ coxae 4 showing a large pore and the lamella medialis of the gonopod solenophore a small lobule at about midlength.

Description. All characters as in *D. simplipoda* sp. n., except as follows.

Length *ca* 25–26 mm (♂) or 27–29 mm (♀), width of midbody pro- and metazonae 1.5 and 4.0 (♂) or 2.5 and 4.5 mm (♀), respectively. Holotype 26 mm long, 1.5 and 4.0 mm wide on midbody pro- and metazonae, respectively. In width, head < collum < segment 2–8 < 9–16. Coloration rather uniformly light brownish to pallid (Figs 1E–F, 6).

Paraterga of collum (Fig. 6A–B) directed laterad; following paraterga 2–18 directed dorsad and a little caudad; paraterga 19 directed caudad, but all paraterga ending up clearly much above dorsum (Fig. 6). Transverse sulcus very vague, only traceable in segments 3–18 (Fig. 6B, D, F).

A large, median, setose process with a large central pore at bottom between ♂ coxae 4 (Fig. 7A). Legs devoid of modifications, about 2.5 (♂) or 2.0 (♀) times as long as midbody height.

Gonopods (Fig. 7B–C) short. Coxite less than 1/3 the length of telopodite. Prefemur about half as long as acropodite. Femorite very short, slightly enlarged distad. Solenophore strongly condensed and divided into a large subtriangular lamella lateralis (**ll**) and a terminally evidently bifid lamella medialis (**lm**), the latter with a very small lobule (**l**) at about midlength.

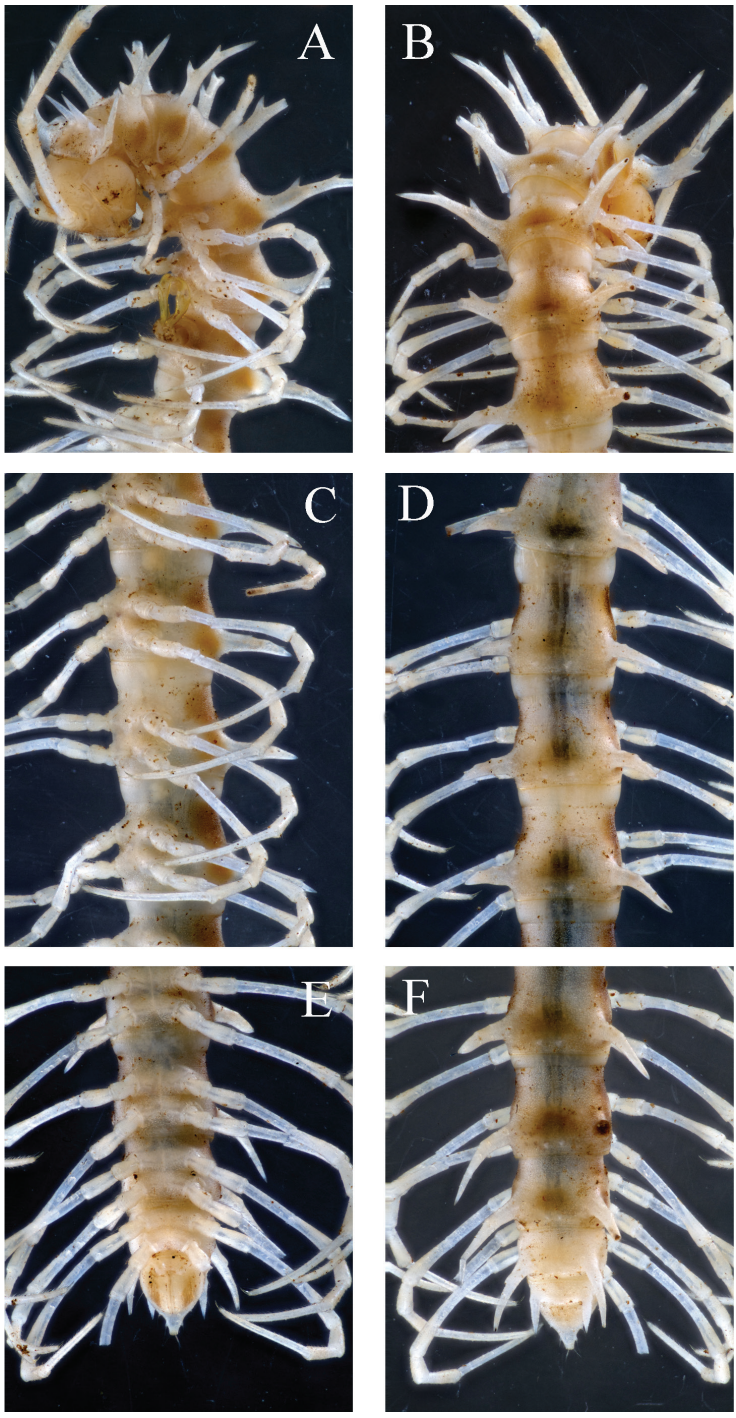

Figure 6. *Desmoxytes similis* sp. n., ♂ holotype from Cave Bangjiao Dong. **A–B** anterior part of body, subventral and dorsal views, respectively **C–D** midbody segments, subventral and dorsal views, respectively **E–F** posterior part of body, ventral and dorsal views, respectively.

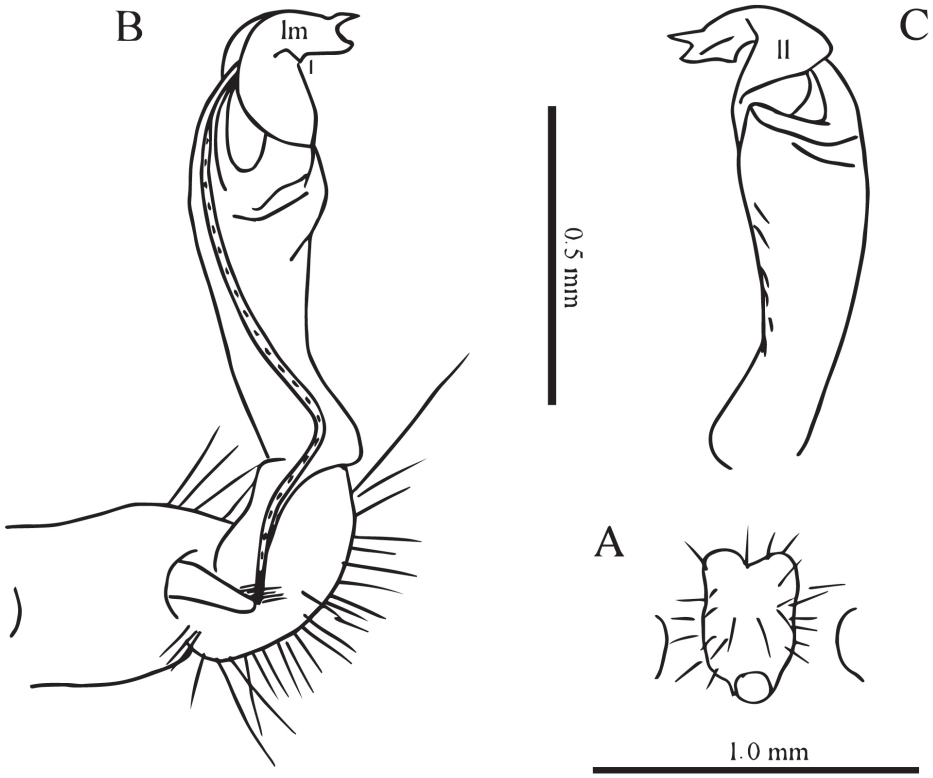

Figure 7. *Desmoxytes similis* sp. n., ♂ paratype from Cave Bangjiao Dong. **A** sternal process between coxae 4, ventral view **B–C** entire left gonopod and its distal half, mesal and lateral views, respectively.

Remarks. This species seems to be very similar to *D. simplipoda* sp. n., from Yangshan, Qingyuan, Guangdong. The only differences are outlined in the above diagnosis. Because of the nearly pallid tegument and extremely elongated antennae and legs, this species seems to be a troglobite.

***Desmoxytes phasmoides* sp. n.**
http://zoobank.org/258D7BBE-ECB2-4123-A03A-390B70438280
Figs 1G, 8–9

Holotype ♂ (SCAU), China, Guangxi, Baise, Lingyun Xian, Jiayou Zhen, Yangli Cun, Cave Fengliu Dong, 2015-VI-9, leg. Mingyi Tian, Weixin Liu, Xinhui Wang & Mingruo Tang.

Paratypes. 1 ♂, 1 ♀ (SCAU), 1 ♂ (ZFMK), same locality and collecting data as the holotype.

Name. To emphasize that superficially this new species somewhat resembles a stick insect, Phasmatodea; noun in apposition.

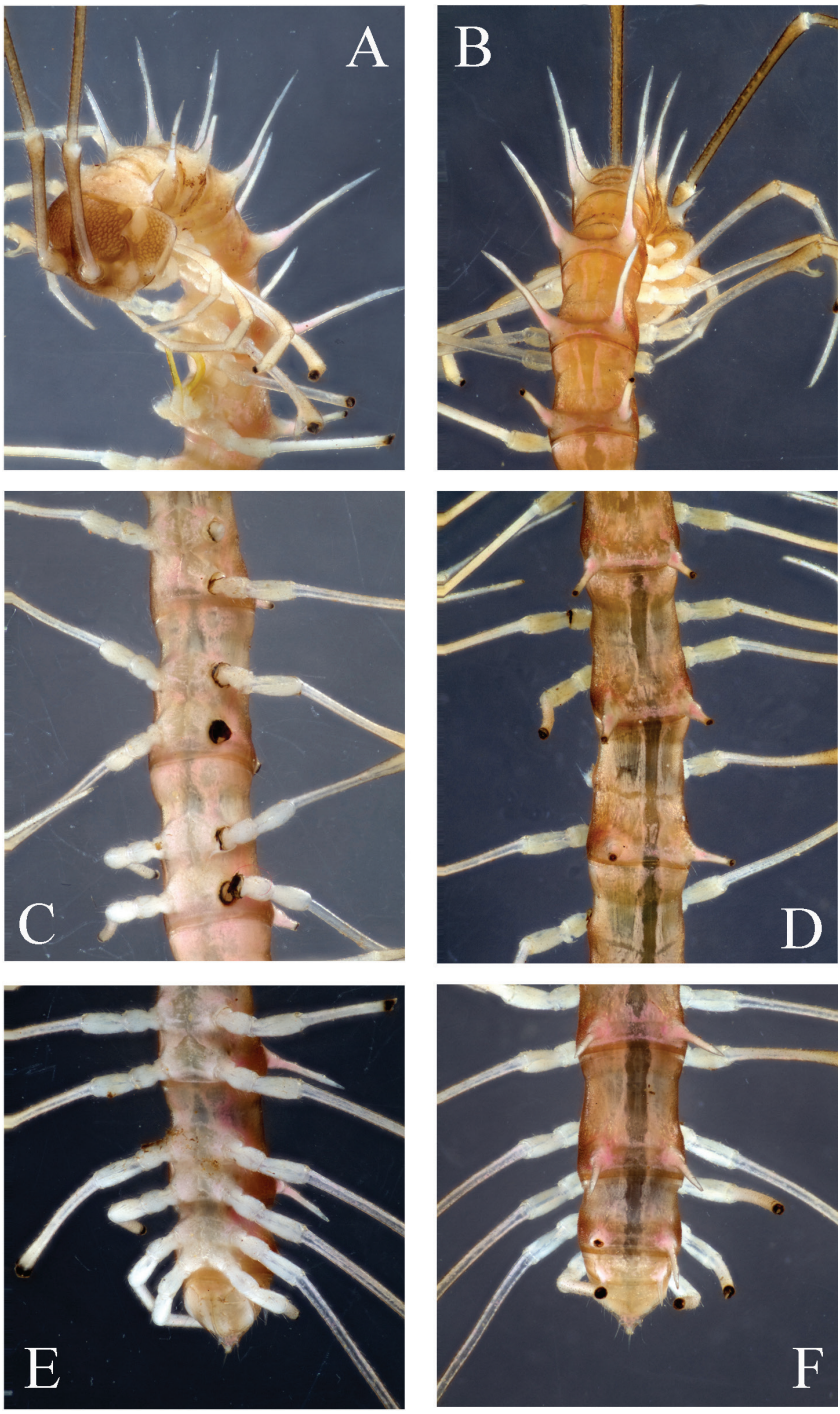

Figure 8. *Desmoxytes phasmoides* sp. n., ♂ paratype from Cave Fengliu Dong. **A–B** anterior part of body, subventral and dorsal views, respectively **C–D** midbody segments, ventral and dorsal views, respectively **E–F** posterior part of body, ventral and dorsal views, respectively.

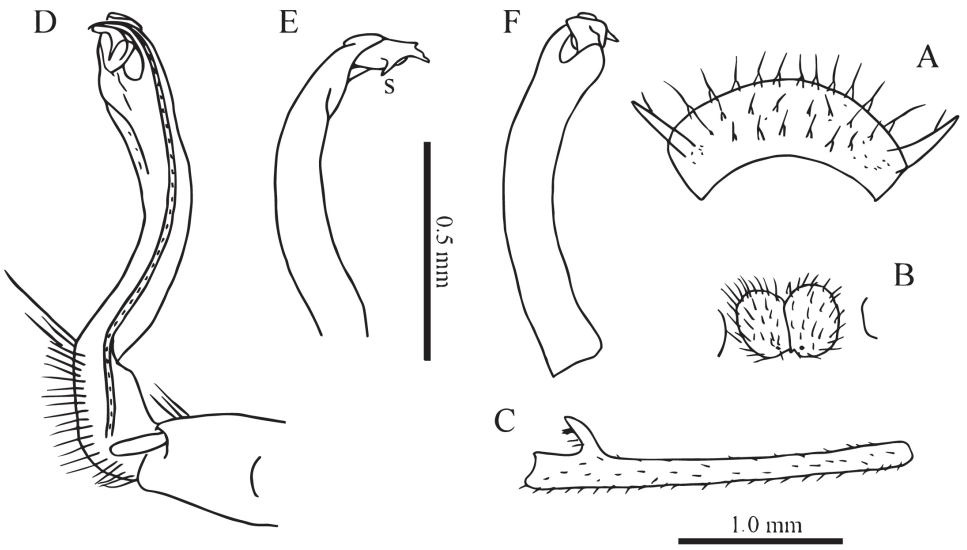

Figure 9. *Desmoxytes phasmoides* sp. n., ♂ paratype from Cave Fengliu Dong. **A** collum, dorsal view **B** sternal processes between coxae 4, ventral view **C** femur 6, front view **D–F** entire right gonopod and its distal half, mesal, ventral and lateral views, respectively.

Diagnosis. Keys out to the superficially most similar *D. minutubercula* Zhang, 1986 (Liu et al. 2014), especially so due to long spiniform paraterga and a particularly condensed solenophore, but differs by a pair of rounded, setose processes present between ♂ coxae 4 and the gonopod lamella medialis showing a distinct spine.

Description. All characters as in *D. laticollis* sp. n., except as follows.

Length of both sexes *ca* 27–29 mm, width of midbody pro- and metazonae 1.3–1.5 and 2.8–3.0 mm, respectively. Holotype 29 mm long, 1.5 and 3.0 mm wide on midbody pro- and metazonae, respectively. In width, segment 2–4 < collum < head < 5–7 < 8–18. Coloration rather uniformly light brownish, some metaterga and bases of paraterga pinkish (Fig. 1G). Antennae very long and slender, reaching back until posterior margin of segment 8 (7) (♂) or 6 (♀) when stretched dorsally.

Tegument shining and smooth, prozonae faintly microalveolate; metazonae finely microgranulate (Fig. 8). Collum (Fig. 8A) with at least 6+6 anterior, 4+4 (5) intermediate and 3+3 posterior setigerous spines; paraterga on collum spiniform, directed dorsolaterad, with a setigeous spine anteriorly at distal 1/3 (Figs 8A, 9A). Metaterga 2–4 each with 4+4 anterior, 3+3 intermediate and 5+5 posterior setigerous tubercles; metaterga 5–19 with a pattern of 5+5 setigerous tubercles anteriorly, these occasionally arranged in two transverse rows, as well as 4+4 between paraterga and at least 5+5 setigerous tubercles at posterior margin. Paraterga 2–18 (Fig. 8) extremely long, straight, spiniform, simple, usually with 2–3 very small setigerous denticles on lateral side; only paraterga 19 directed caudad. Ozopores inconspicuous, lying at base of pore-bearing paraterga on lateral side (Fig. 8D). Transverse sulcus incomplete, present on segments 6–18 (Fig. 8B, D, E).

Sterna modestly setose, cross-impressions very shallow (Fig. 8C, E). A pair of paramedian, rounded, setose processes between ♂ coxae 4 (Fig. 9B). Legs long and slender, midbody legs *ca* 4.5 (♂) or 3.5 (♀) times as long as body height; ♂ femur 6 with a very evident apophysis at distal 1/4 (Fig. 9C).

Gonopods (Fig. 9D–F) subfalcate. Coxite very short, less than 1/3 as long as telopodite. Prefemur short, less than half as long as acropodite. Femorite rather long, curved ventrad. Solenophore highly condensed, divided into a small, rectangular lamella lateralis and a simple lamella medialis, the latter with a distinct spine (**s**) at about midlength; solenomere very short and flagelliform.

Remark. Because of the pallid tegument and extremely elongated antennae and legs, this species may well be a troglobite.

***Desmoxytes spiniterga* sp. n.**
http://zoobank.org/9D8F7BAF-4AB7-43F4-BD54-2B5A8F1925EA
Figs 10–11

Holotype ♂ (SCAU), China, Guangxi, Hechi, Huanjiang Xian, near Cave Gui Dong II, Secondary forest, litter, Berlese extraction after sifting, 2007-V-18, leg. Louis Deharveng & Anne Bedos (CHIgx07-18-17).

Paratype. 1 ♂ (SCAU), same locality and collecting data as the holotype.

Name. To emphasize the metaterga showing very evident, spiniform, setigerous paraterga; adjective.

Diagnosis. Keys out to the superficially most similar *D. draco* Cook & Loomis, 1924 (Liu et al. 2014), judging from the ornamentation of metaterga, but differs by legs showing no modifications, in the metaterga supplied with more numerous setigerous spines, as well as the rather short femorite of the gonopod and the clearly coiled solenophore (cf. Kraus 2012).

Description. All characters as in *D. laticollis* sp. n., except as follows.

Length *ca* 11 mm (holotype) or 12 mm (paratype), width of midbody pro- and metazonae 0.5 and 1.8 mm, respectively. In width, head < collum < segment 2–4 < 5–16. Coloration brownish to yellowish (Fig. 10). Antennae very long and slender, reaching back until posterior margin of segment 6.

Prozonae faintly microalveolate; metazonae rather microgranulate and shagreened. Collum (Fig. 10A) with 4+4(5) anterior, 2+2 intermediate and 2+2 posterior setigerous spines; following metaterga 2–8 with 3+3 anterior and 3(4)+3(4) posterior setigerous spines; in metaterga 9–18 increasingly more numerous, with a pattern of 3(4)+3(4) anterior, 2–4+2–4 middle (behind transverse sulcus) and 5(4)+5 posterior setigerous spines, in posterior row lateral one or two spines being much larger than others; metatergum 19 with the same spination pattern, but setigerous tubercles smaller and similar in size. Paraterga (Figs 10A, 11A) very strongly developed, antler-shaped, usually three-branched, paraterga on collum with two branches; paraterga 2–8 directed more dorsad than laterad; paraterga 9–18 directed laterad, but clearly ending up above

Figure 10. *Desmoxytes spiniterga* sp. n., ♂ paratype from near Cave Gui Dong II. **A–B** body, dorsal and ventral views, respectively.

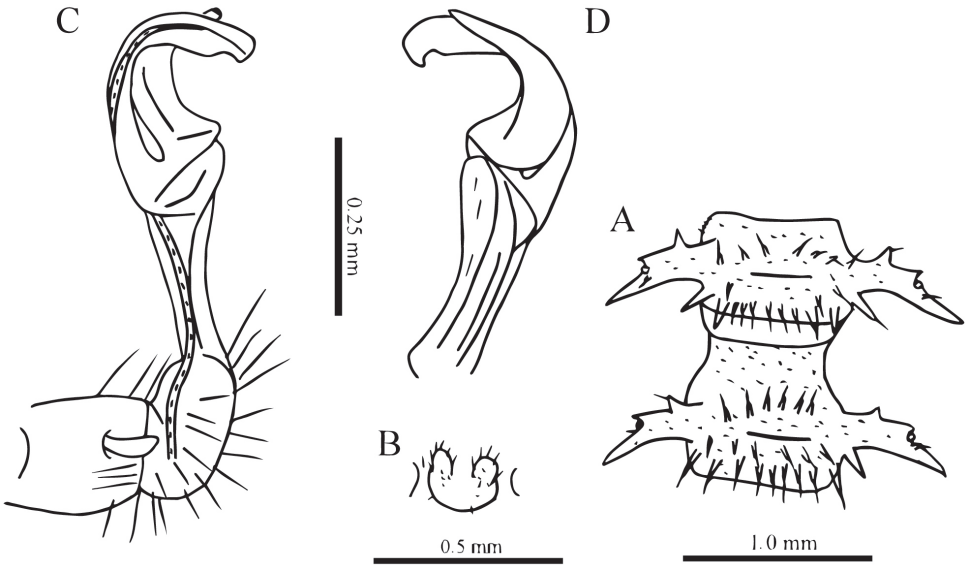

Figure 11. *Desmoxytes spiniterga* sp. n., ♂ paratype from near Cave Gui Dong II. **A** segments 9**–**10, dorsal view **B** sternal processes between coxae 4, ventral view **C–D** entire left gonopod and its distal half, mesal and lateral views, respectively.

dorsum, each with an additional small denticle at last incision; paraterga 19 directed caudad. Ozopores normal, lying at base of last incision of paraterga (Fig. 11A). Transverse sulcus present on segments 3–18, incomplete (Figs 10A, 11A).

Sterna moderately setose, cross-impressions shallow (Fig. 10B). A pair of paramedian processes between ♂ coxae 4 (Figs 10B, 11B). Legs without modifications, midbody legs *ca* 2.8 times (♂) as long as body height.

Gonopods (Figs 10B, 11C–D) with coxite about 1/3 as long as telopodite. Prefemur almost half as long as acropodite. Femorite short and slender, slightly enlarged distad. Solenophore clearly coiled and divided into a large spiniform lamella lateralis and a very distinct and coiled lamella medialis. Solenomere relatively long.

Remark. Compared to cave-dwelling congeners, this species is much smaller and darker.

***Desmoxytes variabilis* sp. n.**
http://zoobank.org/F5F0F547-D6D8-4B91-8DF3-7988C32E1822
Figs 1H, 12–14

Holotype ♂ (SCAU), China, Guangxi, Hechi, Fengshan Xian, Fengcheng Zhen, Cave Huoji Dong, 24°28'32"N, 107°03'28"E, *ca* 500 m a.s.l., 2015-VIII-3, leg. Jujian Chen, Xinhui Wang & Mingruo Tang.

Paratypes. 2 ♂, 3 ♀ (SCAU), same locality and collecting data as the holotype. 2 ♂, 1 ♀ (SCAU), 1 ♂, 1 ♀ (ZFMK), same County, Zhaiya Xiang, Laying Cun,

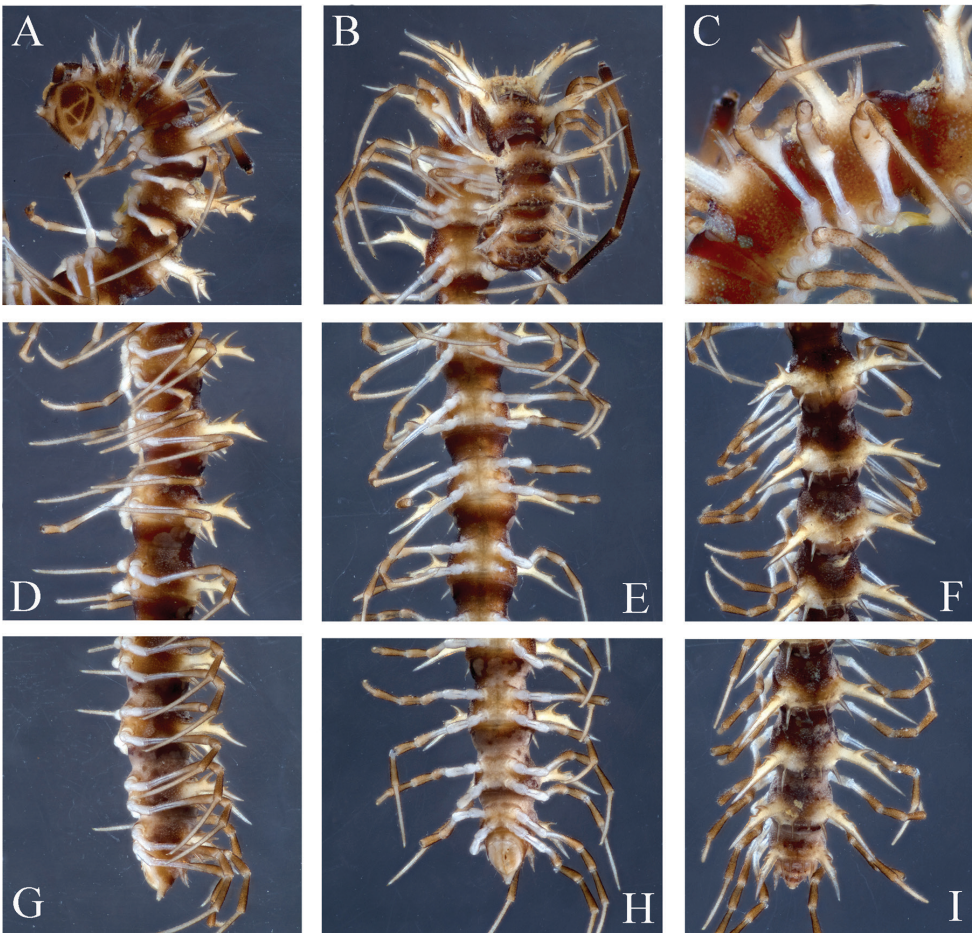

Figure 12. *Desmoxytes variabilis* sp. n., ♂ holotype from Cave Huoji Dong. **A–B** anterior part of body, lateral and ventral views, respectively **C** legs 5–7, ventral view **D–F** midbody segments, lateral, ventral and dorsal views, respectively **G–I** posterior part of body, lateral, ventral and dorsal views, respectively.

Cave II Dong, 2015-VIII-4, leg. Jujian Chen, Xinhui Wang & Mingruo Tang. 3 ♂, 2 ♀ (SCAU), same County, Jinya Xiang, Hangdong Cun, Cave I Dong, 2014-VI-14, leg. Mingyi Tian, Weixin Liu, Haomin Yin & Xiaozhu Luo. 3 ♂, 2 ♀ (SCAU), Lingyun Xian, Sicheng Zhen, Wuzhishan, Cave Qianlongya, 2015-VI-10, leg. Mingyi Tian, Weixin Liu, Xinhui Wang & Mingruo Tang. 1 ♂, 1 ♀ (SCAU), Bama Xian, Yandong Xiang, Namen Cun, Cave Baiyan Dong, 2015-VIII-3; 3 ♂, 2 ♀ (SCAU), Tian'e Xian, Bala Xiang, Gandong Cun, Cave number VIII Dong, 2015-VIII-8. leg. Jujian Chen, Xinhui Wang & Mingruo Tang. 3 ♂, 3 ♀ (SCAU), China, Guangxi, Hechi, Huanjiang Xian, Mulun, way to Mashan Dong, 2007-V-21, leg. Louis Deharveng & Anne Bedos (CHIgx07-21-02). 2 ♂, 1 ♀ (SCAU), China, Guangxi, Hechi, Huanjiang Xian, near Midong Cun, 2007-V-23, leg. Louis Deharveng & Anne Bedos (CHIgx07-23-05).

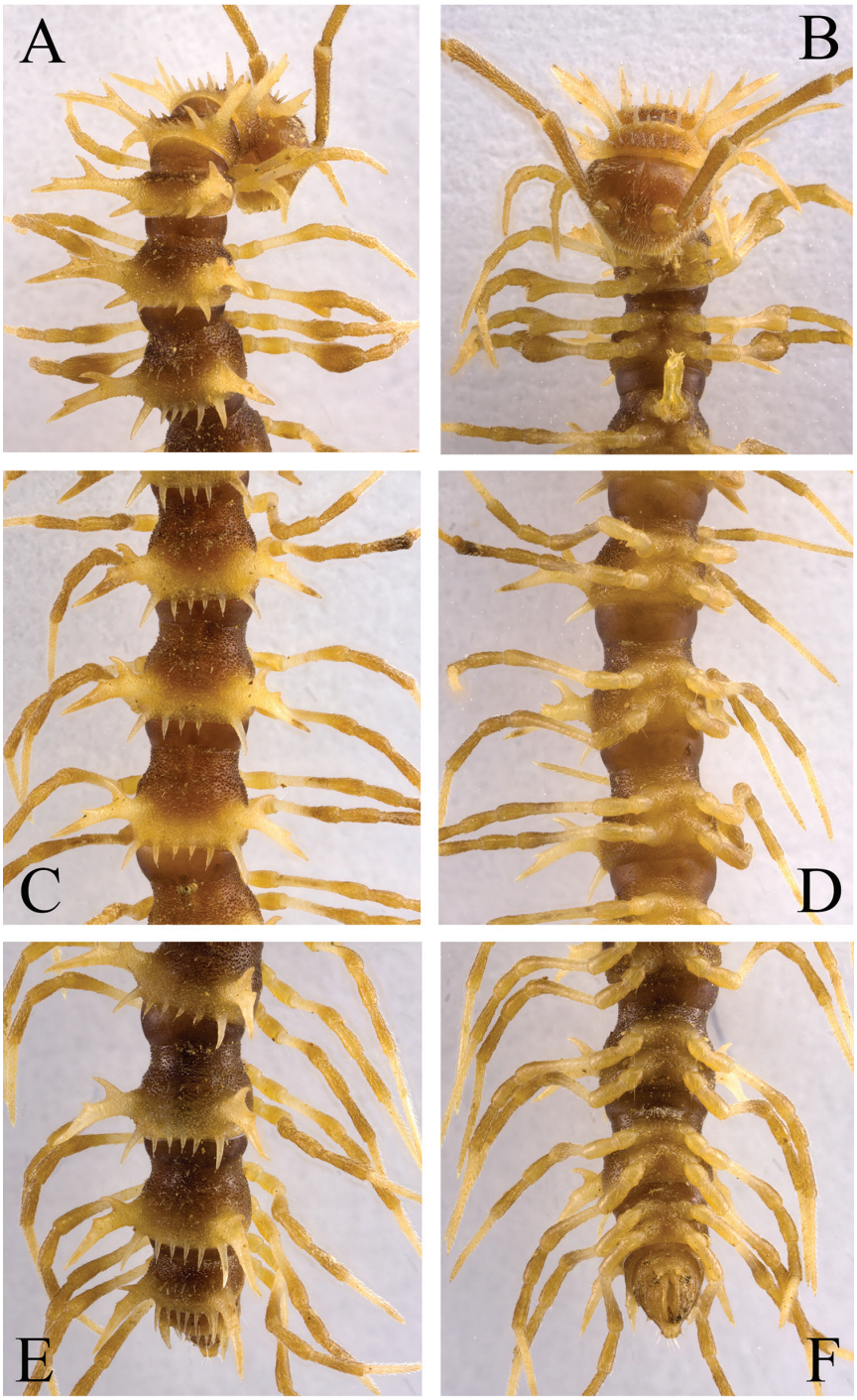

Figure 13. *Desmoxytes variabilis* sp. n., ♂ paratype from near Midong Cun. **A–B** anterior part of body, dorsal and ventral views, respectively **C–D** midbody segments, dorsal and ventral views, respectively **E–F** posterior part of body, dorsal and ventral views, respectively.

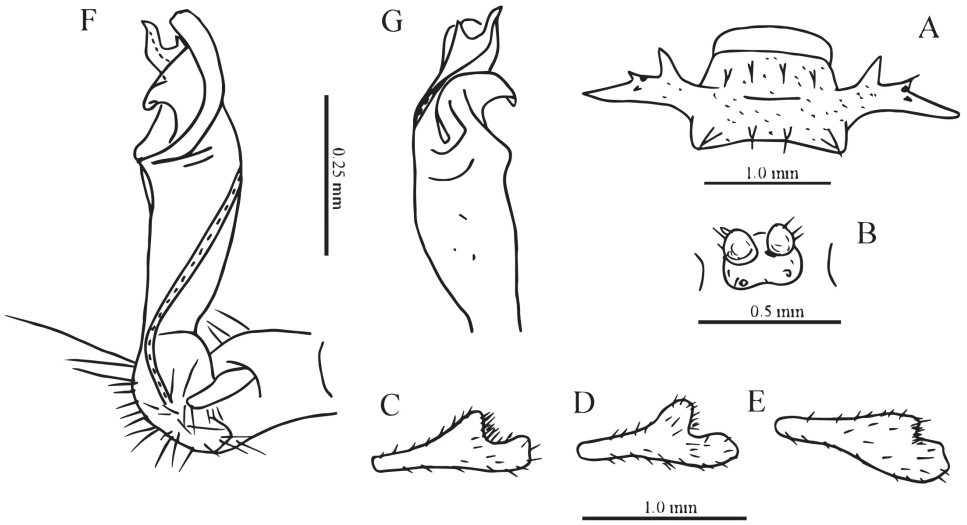

Figure 14. *Desmoxytes variabilis* sp. n., ♂ paratype from Cave Huoji Dong. **A** segment 10, dorsal view **B** sternal processes between coxae 4, ventral view **C–E** femora 5–7, front view **F–G** entire right gonopod and its distal half, mesal and lateral views, respectively.

Name. To emphasize the metaterga showing a variable pattern of setigerous spines; adjective.

Diagnosis. This species seems to be especially similar to *D. nodulosa* Liu, Golovatch & Tian, 2014, from Cave II, Xiao'ao Xiang, Du'an Xian, Hechi, Guangxi, because both share very close patterns of metatergal ornamentation and particularly stout gonopods, but differs by the metaterga showing a variable pattern of setigerous spines, and the particularly complex gonopod solenophore.

Description. All characters as in *D. laticollis* sp. n., except as follows.

Length *ca* 17–21 (♂) or 20–24 mm (♀), width of midbody pro- and metazonae 1.0–1.2 and 2.8–3.8 (♂) or 1.5–1.8 and 3.0–4.0 mm (♀), respectively. Holotype 19 mm long, 1.0 and 2.8 mm wide on midbody pro- and metazonae, respectively. In width, head < collum < segment 2–4 < segment 5–16. Coloration (Figs 1H, 12, 14–15) varying from dark to light brownish; paraterga and posterior parts of metaterga finely yellow-brownish. Antennae long and slender, reaching back until posterior margin of segment 5 (♂) or segment 4 (♀) when stretched dorsally (Fig. 12A–B).

Prozonae faintly microalveolate; metazonae rather microgranulate and shagreened. Collum (Figs 12B, 13B) with 4+4 (or 5+5) anterior and 2+2 (or 3+3) posterior setigerous spines. Metaterga 2–18 (Figs 12–13) each with 2+2 (or 3+3) anterior and 2+2 (or 3+3) posterior setigerous spines, lateral spine of posterior row being much larger than others; metatergum 19 with 3+3 anterior and 2+2 posterior, similar, small, setigerous tubercles. Paraterga very strongly developed, antler-shaped, usually three-branched, each tip with an evident lateral seta (Figs 12–13). Paraterga of collum stout, two-branched; paraterga 2–5 directed more dorsad than laterad; paraterga 19 directed cau-

dad, horizontal, lying level to dorsum; paraterga 6–18 directed obliquely upwards at *ca* 45°, in ♂ ending up clearly above dorsum (Figs 12–13), but paraterga slightly lower, shorter, subhorizontal and lying level to dorsum in ♀. Ozopores conspicuous, located at last incision of poriferous paraterga (Fig. 14A). Transverse sulcus obscure on collum and metaterga 2–4; more evident, but incomplete on metaterga 5–17 (Figs 12–13).

Sterna sparsely setose, cross-impressions very shallow (Figs 12–13). A paramedian pair of separated, short, rounded, poorly setose processes between ♂ coxae 4 (Fig. 14B). Legs long and slender, *ca* 2.5–2.8 (♂) or 2.0–2.2 (♀) times as long as body height; ♂ femora 5–7 each with a conspicuously densely pilose apophysis ventrally at about midlength (Figs 12C, 13A–B, 14C–E).

Gonopods (Fig. 14F–G) very short. Coxite less than 1/3 as long as telopodite. Prefemur less than half the length of acropodite. Femorite stout, apically with a distinct sulcus. Solenophore quite complex and compact, divided into two well differentiated lobes, a higher, bipartite and apically acuminate lamina medialis, plus a lower and curved lamina lateralis; solenomere short and flagelliform.

Remark. This obviously troglophilic species is rather eurytopic, occurring both outside and inside caves. It shows a remarkably variable pattern of spination on collum and metaterga (Figs 12–13), but the gonopod structure remains stable.

A key to *Desmoxytes* species currently known to occur in China

(modified after Golovatch et al. 2012; Liu et al. 2014)

1 Paraterga spiniform (Figs 4, 6, 8) **2**
– Paraterga wing- (Fig. 2) or antler-shaped (Figs 10, 12–13) **11**
2 ♂ femora unmodified. Gonopod lamella medialis terminally evidently bifid **3**
– At least a pair of ♂ femora (6–7) humped ventrally **4**
3 Lamella medialis devoid of a small midway lobe (Fig. 5B–C) ..... ***D. simplipoda* sp. n.**
– Lamella medialis supplied with a small lobule at midlength (Fig. 7B–C) ..... ***D. similis* sp. n.**
4 At least ♂ femora 7 humped ventrally **5**
– Only ♂ femora 6 humped ventrally **6**
5 Only ♂ femora 7 very evidently humped ..... ***D. longispina***
– Both ♂ femora 6 and 7 evidently humped ..... ***D. spinissima***
6 Paraterga spiniform until segment 5, following paraterga very short, coni- to dentiform ..... ***D. lui***
– Paraterga spiniform, very long, about as long as body height in ♂ **7**
7 Adult body relatively small, length < 20 mm, epigean ..... ***D. parvula***
– Adult body much larger, length > 20 mm, mostly troglobites **8**
8 Metaterga 2–19 not only with normally arranged setigerous tubercles, but also with a row of similar tubercles along posterior margin **9**

– Only metaterga 2–4 with several transverse rows of setigerous spines, following metaterga generally smooth, without tubercles along posterior margin **10**

9 A pair of rounded setose processes between ♂ coxae 4 (Fig. 9A); gonopod lamella medialis with a distinct spine (Fig. 9D–E) ..... ***D. phasmoides* sp. n.**

– A pair of square setose processes between ♂ coxae 4 .....***D. minutubercula***

10 Gonopod postfemoral part sulcus evident, lamina lateralis with several small lobes; Guangxi ..... ***D. scutigeroides***

– Gonopod postfemoral part without sulcus, lamina lateralis simple; Guizhou.... .....***D. getuhensis***

11 Paraterga wing-shaped **12**

– Paraterga antler-shaped.....**15**

12 Collum the broadest segment (Figs 2A, 3A)..... ***D. laticollis* sp. n.**

– Collum narrower than midbody segments **13**

13 ♂ femora unmodified. Paraterga long and mostly subfalcate.... ***D. eupterygota***

– ♂ femora 5–6 or 6–7 humped. Paraterga stout and suberect **14**

14 Metaterga 2–19 with two transverse rows of setigerous spines. Gonopod telopodite suberect..... ***D. planata***

– Metaterga 9–19 with four transverse rows of setigerous spines. Gonopod telopodite subfalcate .....***D. scolopendroides***

15 ♂ femora unmodified .....***D. spiniterga* sp. n.**

– At least ♂ femora 6 humped.....**16**

16 Only ♂ femora 6 humped **17**

– ♂ femora 5–7 or 5–6 humped.....**18**

17 A pair of tongue-shaped sternal processes between ♂ coxae 5. Gonopod femorite stout and curved.....***D. lingulata***

– A pair of divergent sternal processes between ♂ coxae 5. Gonopod femorite elongated and suberect.....***D. cornutus***

18 Paraterga strongly and long branched, collum with 4+4 anterior and 1+1 posterior spines; Jiangxi .....***D. draco***

– Paraterga usually three-branched, collum with at least 4+4 anterior and 2+2 posterior spines, sometimes even more numerous; Guangxi.....**19**

19 Gonopod solenophore simple, solenomere separated at base from solenophore ..... ***D. nodulosa***

– Gonopod solenophore complex (Fig. 14F–G), with several lobes, solenomere sheathed by solenophore..... ***D. variabilis* sp. n.**

Conclusion

The family Paradoxosomatidae (Polydesmida) is among the largest in the entire class Diplopoda (nearly 200 genera and >950 species, amounting to about 60% of the total species diversity in the Oriental fauna), but it is highly uncharacteristic of caves.

Remarkably, *Desmoxytes* is the sole genus of Oriental paradoxosomatids that comprises numerous true cavernicoles (Golovatch 2015).

Now that *Desmoxytes* encompasses 41 described species, of which half derive from mainland China, a few observations seem to be noteworthy. Species group delimitation lies beyond the scope of the present paper, as it focuses only on the Chinese fauna. It also seems somewhat premature given the rapidly growing number of species described lately and certainly many more still to be found across China and Southeast Asia. However, superficially all *Desmoxytes* spp. that are presumed troglobionts are highly troglomorphic and have only been encountered in the karsts of southern China. Only among such congeners there are several that show remarkably long and spiniform paraterga, obviously an apomorphic troglomorphism.

The diversity of *Desmoxytes* as currently known may seem biased to cave-dwellers, in part because much of the collecting and taxonomic exploration efforts still focus on cavernicoles alone. Interestingly, however, in contrast to China, not a single troglomorphic species of *Desmoxytes* has been encountered in the numerous well-explored karsts of Thailand, Laos or Vietnam, even though epigean *Desmoxytes* are likewise very common and diverse in Indochina.

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RESEARCH ARTICLE

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Biofilm feeding: Microbial colonization of food promotes the growth of a detritivorous arthropod

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Abstract

Feeding on plant material is common among animals, but how different animals overcome the dietary deficiencies imposed by this feeding strategy is not well understood. Microorganisms are generally considered to play a vital role in the nutritional ecology of plant feeding animals. Commonly microbes living inside animal bodies are considered more important, but recent studies suggest external microbes significantly shape plant-feeding strategies in invertebrates. Here we investigate how external microbes that typically form biofilm on primary plant material affect growth rates in a terrestrial isopod species *Porcellio scaber*. We experimentally manipulated the amount of biofilm on three different primary diet sources and quantified growth and survival of individuals that fed on food with either a small or large amount of biofilm. In addition, we tested how dietary manipulation shapes the composition of bacterial communities in the gut. The presence of visible biofilm significantly affected the growth of isopods: individuals that fed on the primary diet source with a large amount of biofilm gained more mass than individuals feeding on a diet with marginal biofilm. Diet also significantly affected the bacterial gut community. The primary diet source mainly determined the taxonomic composition of the bacterial community in the isopod gut, whereas the amount of biofilm affected the relative abundance of bacterial taxa. Our study suggests that terrestrial isopods may cope with low-quality plant matter by feeding on biofilm, with decomposition of plant material by organisms outside of the feeding organism (here a terrestrial isopod) probably playing a major role. Future investigations may be directed towards the primary diet source, plant matter, and the secondary diet source, biofilm, and should assess if both components are indeed uptaken in detritivorous species.

Keywords

Plant feeders, microorganisms, diet quality, bacterial gut community, growth

Introduction

Plant material is the common food source for herbivorous and detritivorous animals, although it has low nutritional quality and is difficult to digest. While herbivores may not obtain enough nitrogen by feeding on living plants (Pierce and Berry 2011), the nutrient content of dead plant material is even lower for detritivorous species (Zimmer 2002a). Nevertheless, many herbivores and detritivores successfully consume plant material, but how they actually meet their nutritional requirements is still an unresolved question (but see Filipiak and Weiner 2014). Animals have employed different strategies to compensate for low-quality diet by simply processing more food per unit time (Woods 1999) or aggregate in social groups to have better access to food (Lihoreau et al. 2015). Herbivores benefit from mutualistic associations with symbionts that provide them with essential nutrients (e.g. aphids and amino acid requirements, Gunduz and Douglas 2009), and detritivorous species may profit from microbial colonization of dead plant material (Kautz et al. 2002; Zimmer 2002a; Zimmer et al. 2003). Another strategy used by wood boring beetles promotes a significant nutritional contribution of fungi that are ingested along with decomposed wood (Filipiak and Weiner 2014; Tanahashi et al. 2009). Beetles thus may cover their nutritional needs by feeding on an organism that itself lives on plant material.

Plant tissues are colonized by different microorganisms that often form multicellular complexes ranging from small aggregates to highly structured biofilms (Eberl et al. 2007). Biofilm can be defined as an assemblage of microbial cells that are enmeshed in a self-produced extracellular matrix (Davey and O'toole 2000). The biofilm matrix provides the mechanical stability of biofilms, mediates the adhesion to surfaces and association with interfaces, buffers biofilms from environmental conditions (Flemming and Wingender 2010) and may even serve as a nutrient source for biofilm-feeding animals due to its high content of polysaccharides (Lawrence et al. 2002). The formation and growth of biofilm may be affected by factors such as temperature, pH, nutrient availability on the substrate, or time (Else et al. 2003; Moghadam and Zimmer 2014; Rinaudi et al. 2006). The growth of biofilm is characterized by an initial rapid proliferation of microbial cells and increased microbial richness and diversity, which finally leads to the formation of a stable climax community (Davey and O'toole 2000; Douterelo et al. 2014). Microbial colonization of plant material also affects detritivore performance. Increased microbial activity and density may improve growth, survival and fecundity, and also enhance digestive processes in the gut (Kautz et al. 2000; Zimmer 1997b; 2002a). Although the role of biofilm as a nutritional source for detritivores has been recognized, the understanding of how diet shapes the microbial community composition within the digestive tract of a host animal is still poorly understood.

To test for the general role of biofilm as an important food source for detritivorous isopods, we experimentally manipulated the amount of biofilm. We offered a primary diet source *ad libitum*, but we replaced the diet either after two days or after eight days, which allowed biofilm to develop on the primary diet source for different periods of time (see Figure 1B). Even after 8 days the primary food pellet was not substantially

consumed indicating true *ad libitum* conditions with respect to primary food source for both, 2-day and 8-day groups. However, our feeding regime also resulted in a much larger amount of biofilm in the 8-day group from day two onwards, the day when the food pellet was replaced with a new one only in the 2-day treatment. We quantified the nutritional contribution of biofilm by determining the growth and survival rates of individuals of the terrestrial isopod species *Porcellio scaber* Latreille, 1804 that fed on three different primary diet sources, each overgrown by either low or high amount of biofilm. We also estimated microbial community composition in the gut for a subset of individuals by 16S metagenomics. We used the species *P. scaber* which is considered to feed on plant material and is generally described as a detritivore, though it preferentially feeds on a diet inoculated with microbes (Ihnen and Zimmer 2008). We tested the following predictions: i) a primary diet source with a large amount of biofilm improves the growth and survival of individuals compared to a primary diet source with a small amount of biofilm, and ii) a similar amount of biofilm, regardless of the primary diet source, promotes similar patterns of isopod growth and survival. Bacterial communities of biofilm are mainly shaped by the type of substrate (Li et al. 2014) and the formation of biofilm is also characterized by the proliferation of attached microbial cells and by changes in species composition (effect of time, Sauer et al. 2002). Therefore, we further predicted that iii) the primary diet source or iv) the amount of biofilm on the primary diet source, affect bacterial gut communities in terms of taxonomic composition and the relative abundance of particular taxa.

Materials and methods

Animals and dietary manipulation

Specimens of woodlice (*Porcellio scaber*) were collected in the summer of 2013 in Kraków, Poland. The locality is situated in the courtyard of an old building, where isopods were found under rocks, bricks, trash or decaying trees. Adult individuals (236 males) were randomly chosen, weighed to the nearest 0.01 mg (Mettler Toledo XP26, Greifensee, Switzerland) and kept individually in separate boxes (52 × 48 mm, 100 ml) containing wet sand and a piece of clay pot. Individuals were equally assigned to three primary diets: an artificial diet (AD), an artificial diet with a single faecal pellet of a conspecific individual (ADF), and a single ash leaf (L). As a comparison to a natural isopod food source (leaves) which could potentially differ in quality, we chose an artificial diet that contains a similar amount of cellulose (30%) and has a well-defined composition (see Appendix). Leaves and the "artificial diet" were always offered *ad libitum*. These three diets were split into two treatments (2- and 8-day) to obtain food either substantially overgrown by biofilm (8-day) or with marginal biofilm growth (2-day; see Fig. 1A for the scheme of experimental design). When food was renewed every 2 days, only marginally visible biofilm could develop, whereas when food was renewed every 8 days, clearly visible biofilm overgrew the primary food source. The amount of biofilm

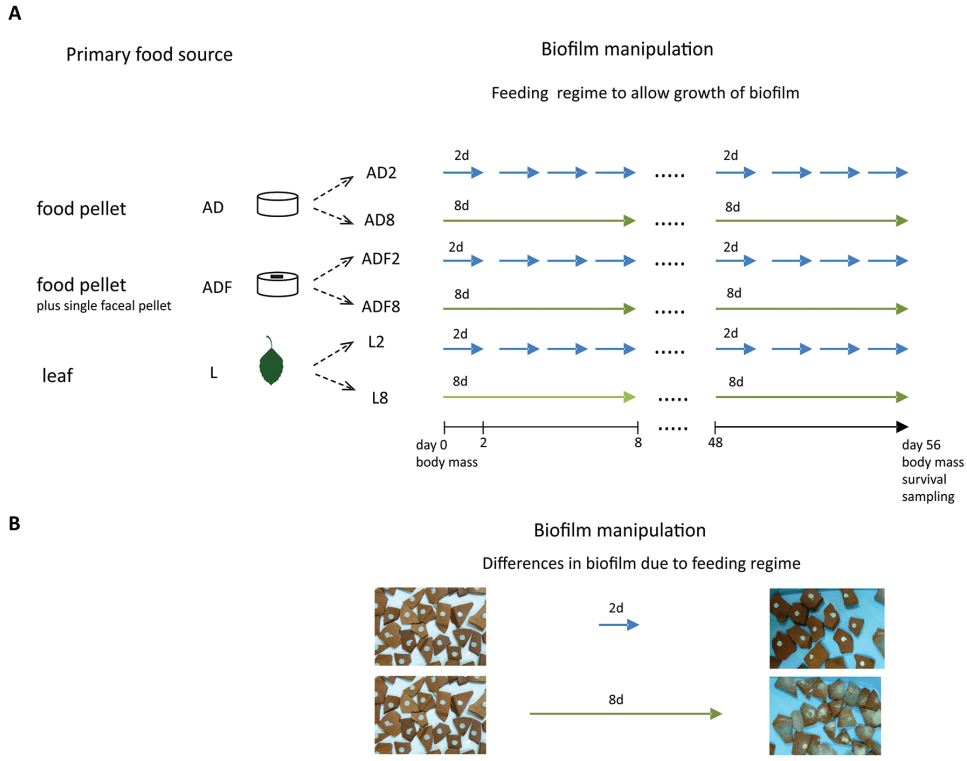

Figure 1. The scheme of the experimental design (**A**). The three primary diets: an artificial diet (AD), an artificial diet with a single faecal pellet of conspecific (ADF), and a single ash leaf (L) were split into two treatments (2d and 8d). With respect to these two treatments the food was renewed every 2 days or every 8 days to obtain food either substantially overgrown by biofilm or with marginal biofilm growth. Individuals were weighed at the beginning and the end of experiment. After final weighing, individuals were killed and the hindgut was dissected for molecular analyses. Part **B** shows fresh pellets of artificial diet (pictures left), which were renewed either every 2 days or every 8 days (pictures right).

could easily be verified visually (Fig. 1B) and was not quantified through other means. We expected that a longer incubation time (8 days) would promote the proliferation of microbial cells (Song and Leff 2006). Our experimental manipulation resulted in six experimental groups: AD2, AD8, ADF2, ADF8, L2 and L8. The boxes of the 8-day groups were opened every second day to mimic the disturbance in the 2-day groups during food changing. The ADF group was used to produce biofilm with a more natural (faeces-derived) bacterial community for terrestrial isopods, which often show coprophagous behaviour (Kautz et al. 2002). A single tiny faecal pellet (0.1-0.3 mg) was collected fresh from a box with individuals of *P. scaber* not used in the experiment. This stock population was fed with ash leaves and was collected at the same site as experimental animals. The faecal pellet was used to ensure that microorganisms from faeces would colonize the food and produce a biofilm. The details of diet composition and diet preparation are presented in the Appendix. Sixty adult isopods were placed

in experimental boxes sequentially in four blocks every week (240 in total). This gave forty isopods per experimental group. Individuals were weighed after four and eight weeks of growth.

Analyses of growth and survival

All data were tested for normality of distribution and homogeneity of variance prior to analyses. To examine the effect of diet on body mass increase, a generalized linear mixed model (GLMM) was used with diet source (AD, ADF, L) and amount of biofilm (2 days, 8 days) as fixed factors, and the interaction term between the two factors. The block of animals was a random factor, and the initial body mass was a covariate. Body mass increase was calculated as the difference between the initial body mass and body mass after two months.

The GLIMMIX procedure was used to analyse differences in survival rates. The model included survival as a binary response variable (survived or died within eight weeks) with diet source and amount of biofilm as fixed factors. The block of animals was a random factor, and the initial body mass was a covariate. All statistical analyses were performed with the SAS 9.4 statistical software package (SAS Institute Inc., Cary, NC, USA).

Bacterial community composition

Isopods were decapitated and the hindgut of each individual was dissected and stored in individual eppendorf tubes at -20 °C. Hepatopancreatic glands were not sampled as the bacterial community of *Porcellio scaber* is represented by resident symbiotic bacteria which are acquired from the environment during early life (Wang et al. 2007). Only two microbial species have been identified in the lumen of the hepatopancreas in *P. scaber*: *Candidatus* Hepatoplasma and *Candidatus* Hepatincola, which according to phylogenetic analyses cluster with Mycoplasmatales (Mollicutes) and Rickettsiales (α-Proteobacteria), respectively (Wang et al. 2004a; Wang et al. 2004b). Total DNA was extracted from the guts of 36 individuals (n = 6 per experimental group), and biofilm was scraped from the food samples (n = 2 per group) using the Wizard genomic DNA Purification kit (Promega). Amplification and Illumina sequencing of 16S DNA fragments was done following established protocols (Caporaso et al. 2010). The V4 variable region of bacterial and archaeal 16 ribosomal DNA was PCR amplified using primers 515f and 806r. The samples were indexed using a 12 bp barcode added to the 5' end of the 515f primer. For each sample, PCR reactions were done in triplicate and contained 1 µl of extracted DNA, 0.2 µM of each primer, 12.5 µl of PCR Multiplex kit (Qiagen) and PCR grade water added to a final volume of 25 µl. The PCR cycling programme was 94 °C for 15 min followed by 33 cycles of 94 °C for 45 s, 50 °C for 60 s, 72 °C for 90 s and a final extension step of 72 °C for 10 minutes. Two types of negative controls were included in each batch of PCR reactions: two extraction negative

controls (to guard against contamination at the DNA extraction step) and two PCR negative controls (to control for contamination during PCR). Amplicon libraries were pooled at equimolar ratios and sequenced on an Illumina MiSeq machine, producing 150 bp reads.

Further analyses were carried out in QIIME (Caporaso et al. 2010). The reads were demultiplexed, quality controlled and trimmed, retaining only reads with at least 75 bp of consecutive high quality bases. To assign reads to Operational Taxonomic Units (OTUs), we followed the open OTU picking workflow in QIIME using Greengenes version 13_8 as the reference database. The resulting BIOM table contained 468,881 reads with a mean of 9768 ± (SD) 1666 reads per sample. Diversity analyses were based on rarefaction to 6630 reads per sample (n = 36), which corresponded to the smallest per sample read number in our dataset. Two measures of microbial diversity were used: phylogenetic β- and α-diversity. To determine the similarity of the bacterial community between the individuals and between food samples (β-diversity), we used UniFrac metric distances which are based on the fraction of branch lengths shared between two communities within a phylogenetic tree constructed from 16S rRNA gene sequences from all communities being compared (Lozupone and Knight 2005). We used a qualitative and quantitative phylogenetic measure of β-diversity; unweighted UniFrac considers only the absence or presence of lineages (i.e., taxonomic composition), while weighted UniFrac directly accounts for differences in relative abundances of lineages within communities (Lozupone et al. 2007). Permutational MANOVA (Anderson 2001) was used to test for the effect of our experimental variables (diet source, amount of biofilm) on bacterial communities using both unweighted and weighted UniFrac distance metrics. For the measure of phylogenetic α-diversity (only gut community), a phylogenetic diversity tree (PD) was used to test for differences between experimental conditions using a two-way ANOVA with diet source, amount of biofilm and diet source x amount of biofilm as explanatory variables. The permutational MANOVA was computed using the Adonis function in the VEGAN package implemented in R. ANOVA was calculated with the SAS 9.4 statistical software package (SAS Institute Inc., Cary, NC, USA).

Results

Growth and survival

Mean initial body mass did not differ between the six experimental groups ($F_{5,240}$ = 1.4, p = 0.225) and was on average (±SD) 68±18 mg (AD2), 70±19 mg (AD8), 72±18 mg (ADF2), 64±23 mg (ADF8), 72±22 mg (L2) and 64±25 mg (L8), and had a negative effect on growth (Fig. 2, $F_{1,169}$ = 42.96, $p < 0.0001$). The final body mass increase differed significantly between the 2-day and 8-day groups ($F_{1,169}$ = 10.76, p = 0.001). Individuals on 8-day biofilm diets had a higher increase in body mass than individuals

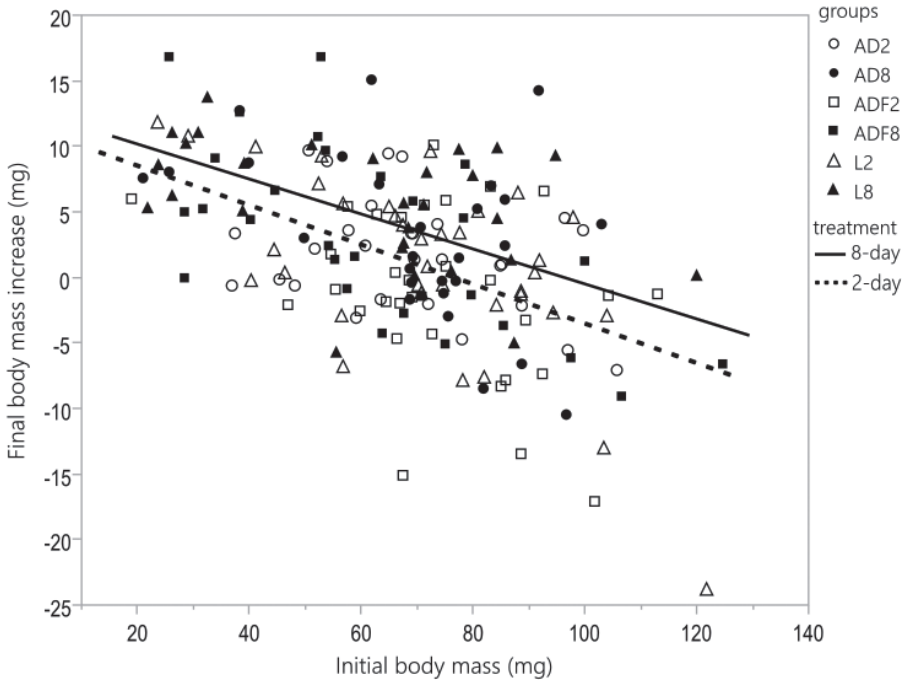

Figure 2. The relationship between initial body mass and the final body mass increase of woodlice feeding on the three primary diets (AD, ADF and L represent an artificial diet, an artificial diet inoculated with single faecal pellet, and leaves, respectively) either with small (2 days) or large (8 days) amount of biofilm. Regression lines represent the pooled data either for 2 or 8 days.

feeding on a diet with 2-day biofilm (Fig. 2 and Fig. 3A). Primary diet (AD, ADF, L) and the block of animals did not have a significant effect on body mass increase (Fig. 3B, diet source: $F_{2,169} = 2.63$, $p = 0.075$; block: $p = 0.189$). The interaction between diet source and amount of biofilm was not significant ($F_{2,169} = 0.47$, $p = 0.627$).

The number of surviving individuals was relatively high (out of the initial 40: AD2 = 31, AD8 = 29, ADF2 = 31, ADF8 = 31, L2 = 36, L8 = 28). Survival did not differ between experimental groups (diet source: $F_{2,230} = 0.54$, $p = 0.58$; amount of biofilm: $F_{1,230} = 2.91$, $p = 0.09$; diet source x amount of biofilm $F_{2,230} = 1.5$, $p = 0.74$). The initial body mass did not have a significant effect on survival ($F_{1,230} = 0.11$, $p = 0.74$).

Bacterial gut community composition

A total of 20 bacterial phyla and unclassified bacteria were detected in the guts of the isopod *Porcellio scaber* (n = 36). The majority of sequences belonged to *Proteobacteria* (84.1% of the classified sequences), *Bacteroidetes* (7.4%), *Actinobacteria* (3%), *Firmicutes* (1.9%), *Verrucomicrobia* (1.1%), *Cyanobacteria* (0.87%), *Tenericutes* (0.72%) and

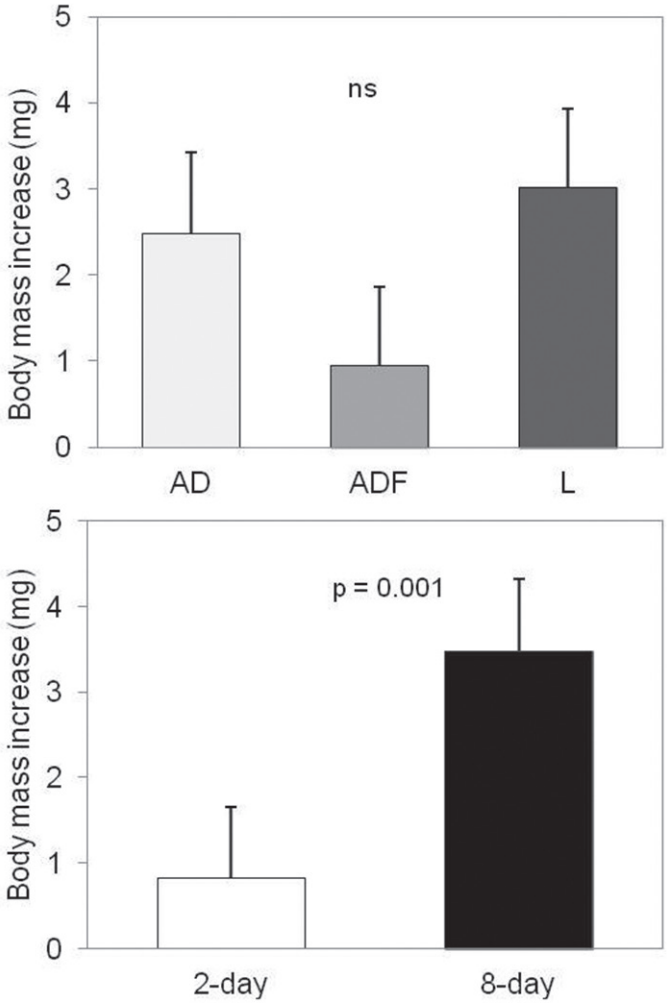

Figure 3. The effect of diet source (**A**) and amount of biofilm (**B**) on the final body mass increase of woodlice (least square means ± SE) after two months of growth (AD, ADF and L represent an artificial diet, an artificial diet inoculated with single faecal pellet, and leaves, respectively). Please note that isopods started at the average body mass of 68.5 mg.

unclassified bacteria (0.7%). At the bacterial class level, 18%, 2.1% and 64% of total sequences represented *Alpha-*, *Beta-* and *Gammaproteobacteria*, respectively. In phylum *Bacteroidetes*, 2.6%, 2.1% and 2% represented *Flavobacteriia*, *Sphingobacteriia* and *Saprospirae*, respectively. Phylum *Actinobacteria* was represented only by the class *Actinobacteria* (order *Actinomycetales*). The dominant class of *Firmicutes* was *Bacilli* (1.88%). *Verrucomicrobia* was represented by the class *Verrucomicrobiae* (0.78%) and *Spartobacteria* (0.35%). The dominant classes of *Cyanobacteria* and *Tenericutes* were *Chloroplast* (0.8%) and *Mollicutes* (0.72%).

Table 1. Percentage of sequence reads for dominant bacterial phyla (i.e., operational taxonomic units) of individuals *P. scaber* that fed on different diets (taxa which represented less than 0.01% of sequence reads were not included).

Bacteria phylum	Artificial diet	Artificial diet single faeces	Leaves	2-day biofilm	8-day biofilm
Actinobacteria	2.06	1.96	5.05	3.58	2.47
Bacteroidetes	8.97	8.12	5.24	11.25	3.63
Cyanobacteria	0.2	0.27	2.12	0.77	0.96
Firmicutes	3.8	1.76	0.1	1.55	2.23
Proteobacteria	83.28	85.16	83.95	79.96	88.3
Tenericutes	0.03	0.26	1.85	1.24	0.2
Verrucomicrobia	0.46	1.73	1.18	0.77	1.48
Other	1.09	0.51	0.67	0.7	0.64

The effect of dietary manipulation on bacterial composition in gut and on biofilm

The bacterial phylodiversity (measure of α-diversity) did not differ between gut samples (diet source: $F_{2,29} = 0.15$, $p = 0.863$; amount of biofilm: $F_{1,29} = 1.58$, $p = 0.219$; diet source x amount of biofilm: $F_{2,29} = 1.53$, $p = 0.233$). The analysis of similarity (measure of β-diversity) showed that the taxonomic composition of gut bacteria was significantly shaped by the primary diet source (PERMANOVA: unweighted UniFrac, $p = 0.001$). When the relative abundance of lineages was accounted for, the effect of primary diet source on bacterial composition became weaker (PERMANOVA: weighted UniFrac, $p = 0.057$). The amount of biofilm significantly affected the relative abundance of taxa (weighted UniFrac, $p = 0.047$) but not taxonomic composition (unweighted UniFrac, $p = 0.268$). This result suggests that the amount of biofilm affected the bacterial community quantitatively (relative abundance of taxa) rather than qualitatively (taxonomic composition). The largest differences in community structure between the 2-day and 8-day groups involved the bacterial phyla *Bacteroidetes* and *Proteobacteria*. Differences in taxonomic composition between experimental groups are presented in Table 1.

Despite the small sample size (n = 2 per diet group), we tested for differences in the bacterial communities of the different biofilms. The analysis of similarity showed that taxonomic composition on biofilm was affected by the primary diet source (PERMANOVA: unweighted UniFrac, $p = 0.002$). When the relative abundance of bacterial taxa was accounted for, the bacterial community differed between the 2-day and 8-day groups, although the effect was weak (PERMANOVA: weighted UniFrac, $p = 0.08$).

Discussion

Adult *Porcellio scaber* feeding on a diet overgrown by biofilm gained significantly more body mass than adults feeding on a diet with no visible biofilm. This finding was independent of the primary food source, i.e., the presence of a visible biofilm always

promoted higher growth rates. The higher growth rate in association with the provisioning of a large amount of biofilm was also accompanied by changes in bacterial gut community composition. Individuals that fed on 8- or 2-day biofilm differed in relative abundance of bacterial lineages but not in taxonomic composition. Individuals that consumed different primary food sources (both AD and ADF) differed in bacterial taxonomic composition which was further supported by analyses of the biofilm samples. Our results strongly support the hypothesis that biofilm can be of high nutritional benefit for the detritivore isopod *P. scaber*.

Leaf litter, which is a natural food source for detritivorous animals, is overgrown by biofilm composed of different fungal and bacterial species (Teuben and Roelofsma 1990) which can positively affect various life history traits. For example, high microbial activity of leaf litter positively affected the reproductive success and survival of various isopod species (Kautz et al. 2000; Rushton and Hassall 1983; Zimmer 2002b; Zimmer and Topp 1997). However, a positive impact of microbiota on isopod performance is not general. Some species such as *Oniscus asellus* may not depend on microorganisms when consuming low-quality detrital food sources (Zimmer and Topp 2000). In our study, survival did not differ between well-developed biofilm and marginal biofilm diets, but our experiment only lasted for two months, which might be too short to detect differences in survival rate based on the current sample size. Our results also show that faeces-colonizing microbiota did not increase the nutritive value of food as suggested by an earlier study (Hassall and Rushton 1982), questioning the nutritional role of coprophagy in terrestrial isopods (see also Kautz et al. 2002). Fungi are a common taxonomic group in biofilm associations and feeding on preferred fungal species increased the growth and reproduction of the Collembola species *Folsomia candida* and *Protaphorura armata* (Scheu and Simmerling 2004). We did not include fungi in our study since biodiversity of fungi is until today poorly known and the optimal DNA-based methods for its assessment are still debated (Kõljalg et al. 2013). The nutritional contribution of leaf litter biofilm has been generally attributed to the degradation of cellulose (Voriskova and Baldrian 2013; Zimmer and Topp 1997; 1999). Alternatively, the biofilm community may also provide limiting nutrients (Filipiak and Weiner 2014; Thompson et al. 2002; Zimmer and Topp 1998) or increase the consumption rate of feeding animals through indicating high-quality food sources (Zimmer et al. 2003). In our study, the greater mass increase of individuals feeding on diets with a high amount of biofilm suggests that the biofilm community improves the nutritional value of the primary food source. This may be facilitated indirectly through increased feeding rate of individuals and/or directly through digestion and utilization of microbial mass as an additional nutrient source. Thus, our results support a significant nutritional role of biofilm in the detritivore isopod *Porcellio scaber* (see also Zimmer and Topp 1998).

Diet is also considered to be one of the main factors determining the microbial gut community (Ley et al. 2008; Staubach et al. 2013). Our study showed that the bacterial community of the isopod gut was dominated by *Proteobacteria*, *Bacteroidetes*, *Actinobacteria* and *Firmicutes* which have also been identified as dominant phyla in various insect species, with *Proteobacteria* being predominant phyla in all insect guts

studied so far (Jones et al. 2013; Yun et al. 2014). Terrestrial isopods can harbour microorganisms in two morphologically and functionally distinct parts of the digestive tract, the hepatopancreas and the hindgut (Zimmer 2002a). Whereas resident bacterial symbionts in the hepatopancreas possibly contribute to cellulose hydrolysis, the hindgut community of transient microbes and fungi might serve as a source of food-limited nutrients (Zimmer and Topp 1998). Two bacterial symbionts appear in the hepatopancreas, *Candidatus* Hepatoplasma and *Candidatus* Hepatincola, but never occur together in a single specimen and the percentage of aposymbiotic individuals varies across studied populations (10% in a German and 70% in a French population of *P. scaber*, Zimmer 2006). The establishment and maintenance of a resident bacterial population in the hindgut is considered unlikely due to simple gut anatomy, the frequent renewal of the gut cuticle, and the short retention time of food (Kostanjšek et al. 2006). Furthermore, diversity in the gut bacterial community might also be affected by host identity (Dittmer et al. 2012), suggesting that not only diet but also some specific aspects of physiology or behaviour of the host may significantly shape the gut microbiota (Ye et al. 2014). The amount and variability of ingested food has been suggested to affect gut community composition; however, experimental demonstration is restricted to only two insect, two crustacean and three vertebrate species (Bertino-Grimaldi et al. 2013; Bolnick et al. 2014; Chandler et al. 2011; Dittmer et al. 2012; Turnbaugh et al. 2009). Wang et al. (2007) found that the bacterial community in the hepatopancreas of isopods differed between species living in semi-terrestrial, terrestrial and freshwater habitats. This suggests that the acquisition of hepatopancreatic symbionts in isopods might be the consequence of an evolutionary change in feeding habit. Our results show that the primary diet source significantly shaped the taxonomic composition of the bacterial community of the isopod gut, although it did not directly affect the growth rate. Since microbial community composition is better reflected by microbial activity, it is microbial biomass (i.e., nutrients) rather than activity that determines the importance of microbes for detritivore isopods. Because growth was mainly affected by the amount of biofilm which was expected to differ in total abundance of bacterial and fungal cells (Figure 1B, Song and Leff 2006), the quantity rather than the diversity of gut microbes affect isopod growth rates. In addition, different bacterial community structures in the 2-day and 8-day groups show that bacterial communities responded to our experimental manipulation (i.e., time for biofilm development on the primary diet source). Our results suggest that feeding on biofilm composed of a variety of bacterial taxa helps to meet the nutritional requirements of *P. scaber* and thus enables it to subsist on a low-quality terrestrial diet. Fungi may likely contribute to this effect, however we did not quantify this contribution.

Conclusion

A combination of experimental, molecular and life-history analyses revealed that biofilm may represent an important food source for the terrestrial isopod *Porcellio scaber*.

Plant feeding animals may solve their nutritional dilemma by associations with micro-organisms within the digestive system that enhance the digestibility of plant material and/or act as a direct food source. Alternatively, as suggested here, these animals could feed on micro-organisms that grow on the plant material. Future studies may be directed towards the separation of the uptake of plant material from the consumption of biofilm growing on the plant material by different herbivorous and detritivorous species. Such an understanding may contribute to the ongoing discussion about the separation of herbivory and detrivory in nature (see also Farmer and Dubugnon 2009). Many of these species may actually be "biofilmivors" that achieve a nutritionally balanced diet through the utilization of biofilm.

Concerning the multi-organism nature of biofilm, future studies may benefit by covering a wider range of the taxa that compose biofilm, including protists and fungi. It would not be surprising if the varied decompositional potential of different plant taxa determine the value and importance of biofilm. Potentially, the ingested microorganisms themselves represent the main part of the processed food. Terrestrial isopods such as *P. scaber* may rely much less on internal microbes to provide key enzymes, but rather take advantage of external microbes that predigest different resources which then become the primary food source.

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Appendix

The composition of artificial diet (Zimmer 1997a) modified after (Carefoot 1984):

Minimum diet (dry mass %): casein 15%, cellulose 30%, starch 25%, sucrose 10%, maltose 5%, glucose 5%, lactose 5%, di-Potassium hydrogen phosphate 1.15%, magnesium sulphate anhydrous 0.65%, copper chloride dihydrate 0.2%, sodium dihydrogen phosphatemonhydrate 0.45%, sodium chloride 0.2%, calcium hydrogenphosphate 0.65%, calcium lactate pentahydrate 1.55%, iron citrate 0.15%.

The preparation of diet:

A small amount of agar was sprinkled into boiling water in a glass beaker. The ingredients for minimum diet were added to the beaker while keeping the fluid warm. After stirring, the diet was poured into a sterile, plastic Petri dish and kept at 4 °C. Small pellets of artificial diet were cut out with plastic pipette tips.

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Paguristione uniuropodus, a new genus and a new species of Pseudioninae infesting hermit crabs from China (Crustacea, Isopoda, Bopyridae)

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Abstract

Paguristione uniuropodus **gen. n.**, **sp. n.** infests *Paguristes* sp. in the East China Sea. *Paguristione* **gen. n.** differs from the closely related genera *Pseudione* and *Pagurion* by its females having indistinct lateral plates on the last two pleomeres and its male with a long tapering pleon of six pleomeres, lacking both pleopoda and uropoda.

Keywords

Paguristes, East China Sea

Introduction

Bopyrid isopods infesting hermit crabs belong to the subfamilies Pseudioninae (branchial parasites) and Athelginae (dorsoabdominal parasites). An, Markham and Yu (2010), An, Williams and Yu (2011) and An, Li and Markham (2013) have reported a total of eight bopyrid species infesting hermit crabs in the South China Sea. Markham (1992) recorded six species of bopyrids infesting hermit crabs in Hong Kong. Boyko (2004)

reported one such species from Taiwan. In Chinese waters as a whole, An (2006) reported ten species of bopyrids infesting hermit crabs. Currently, throughout Asia, 36 species are recorded infesting 48 hermit crabs from Asia (Table 1). Worldwide, McDermott, Williams and Boyko (2010) catalog 83 species of bopyrids infesting hermit crabs, of which 41 species in ten genera are branchial parasites. As hosts worldwide, 11 species of *Paguristes* are known to bear bopyrids (Table 2); their parasites, all branchially infesting members of the subfamily Pseudioninae, are in the genera *Asymmetrione*, *Pseudione*, *Parapagurion* and now the new genus *Paguristione*.

Specimens used in this study were collected from the East China Sea in 1958, and one of the authors (An 2006) examined the parasites and reported *Parapagurion glabra* sp. n. infesting *Paguristes* sp. in her doctoral dissertation (not a published work in the sense of the ICZN). Further examination shows that they represent a new species in a new genus. The name *Parapagurion glabra* is here entered into its synonymy.

Material and methods

Materials for this study originated from Chinese Comprehensive Oceanographic Survey. All materials examined have been deposited in the Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China (IOCAS). Specimens were viewed and drawn using a Zeiss Stemi SV Apo microscope.

Taxonomy

Family BOPYRIDAE Rafinesque-Schmaltz, 1815
Subfamily Pseudioninae R. Codreanu, 1967

***Paguristione* gen. n.**
http://zoobank.org/1076C4FA-D580-45AC-A918-B28C2D1FC396

Diagnosis. Female. All body segments distinct, almost symmetry. Rudimentary coxal plates present in first four segments. Marsupium complete. Oostegite 1 with simple tubercules on internal ridge. Palp of maxilliped with long setae. All pleomeres distinct. First three pleomeres with lateral plates and biramous pleopoda. Fourth and fifth pleomeres with biramous pleopoda, but lateral plates without lateral plates. Sixth pleomere without lateral plates, uropoda uniramous. Male. All segments distinct. First and last pereomeres respectively much broader than adjacent head and first pleomere. Pereopods of first pair smaller than those of following 3 pairs. Pleon elongate, of 6 distinct pleomeres. No pleopoda or uropoda.

Etymology. Combination of the genus name of its host, *Paguristes* and bopyrid genus name *Ione*. Gender feminine.

Type species. *Paguristione uniuropodus* sp. n., herein designated.

Table 1. Bopyrid isopods infesting hermit crabs in Asian waters.

Bopyrids	Hosts	Localities	References
Subfamily Pseudioninae			
Asymmetrione asymmetrica (Shiino, 1933)	*Clibanarius bimaculatus* (De Haan, 1849)	Japan	Shiino 1933
	Clibanarius merguiensis de Man, 1888	Thailand	Markham 1985a; Brunenmeister 1980
Asymmetrione sallyae Williams & Schuerlein, 2005	*Diogenes avarus* Heller, 1865	Singapore	Williams and Schuerlein 2005
Bopyrissa dawydoffi (Codreanu & Codreanu, 1963)	*Clibanarius merguiensis* de Man, 1888	Vietnam	Codreanu and Codreanu 1963
Bopyrissa liberorum Markham, 1985	*Clibanarius merguiensis* de Man, 1888	Thailand	Markham 1985a
Bopyrissa pyriforma (Shiino, 1958)	*Clibanarius bimaculatus* (De Haan, 1849)	Hong Kong	Markham 1982
	Diogenes edwardsii (De Haan, 1849)	Japan	Shiino 1958
Bopyrophryxus branchiabdominalis Codreanu, 1965	*Oncopagurus monstrosus* (Alcock, 1894)	Indonesia	Bourdon and Boyko 2005
	Paragiopagurus acutus (de Saint Laurent, 1972)	Philippines	Bourdon and Boyko 2005
	unidentified pagurid	Indonesia	Bourdon and Boyko 2005
Pagurion arrosor An, Li & Markham, 2013	*Dardanus arrosor* (Herbst, 1796)	China	An, Li and Markham 2013
Pagurion tuberculata Shiino, 1933	*Dardanus scutellatus* (H. Milne Edwards, 1848)	Japan	Shiino 1933
	Dardanus aspersus (Berthold, 1846)	China	An, Li and Markham 2013
Pagurocryptella holthuisi Boyko & Williams, 2010	*Solitariopagurus tuerkayi* McLaughlin, 1997	Japan	Boyko and Williams 2010
Parapagurion calcinicola Shiino, 1933	*Calcinus elegans* (H.Milne Edwards, 1836)	Japan	Shiino 1933
	Calcinus linapropodus Morgan & Forest, 1991	Japan	Shiino 1933
	Paguristes monoporus Morgan, 1987	Indonesia	Haig and Ball 1988
	Paguristes sp.	Thailand	Markham 1985a
	Pagurus aff. *hedleyi* or *kulkarnii*	Hong Kong	Markham 1992
Parapseudione lata Shiino, 1958	*Pagurus middendorffii* Brandt, 1851	Japan	Shiino 1958
Propseudione rhombicosoma Shiino, 1933	*Calcinus laevimanus* (Randall, 1840)	Japan	Shiino 1933
	Calcinus morgani Rahayu & Forest, 1999	Japan	Shiino 1933
Pseudione calcinii Shiino, 1958	*Calcinus latens* (Randall, 1840)	Japan	Shiino 1958
Pseudione clibanaricola Shiino, 1933	*Clibanarius bimaculatus* (De Haan, 1849)	Japan	Shiino 1933
Pseudione hyndmanni (Bate & Westwood, 1868)	*Pagurus* sp.	Japan	Shiino 1936
Pseudione intermedia Nierstrasz & Brender à Brandis, 1932	*Lophopagurus* (*Australeremus*) *triserratus* (Ortmann, 1892)	Japan	Shiino 1936
	Pagurus sp. ?	Japan	Nierstrasz and Brender à Brandis 1932
Pseudione kensleyi Williams & Schuerlein, 2005	*Clibanarius infraspinatus* Hilgendorf, 1869	Singapore	Williams and Schuerlein 2005

Bopyrids	**Hosts**	**Localities**	**References**
Pseudione nobili Nierstrasz & Brender à Brandis, 1923	*Trizocheles spinosus spinosus* (Henderson, 1888)	Indonesia	Nierstrasz and Brender à Brandis 1923
Pseudionella attenuata Shiino, 1949	*Pagurus* sp.	Japan	Shiino 1949
Pseudionella spiropaguri An, Li & Markham, 2013	*Spiropagurus profundorum* Alcock, 1905	China	An, Li and Markham 2013
	Spiropagurus spiriger (De Haan, 1849)	China	An, Li and Markham 2013
Parasymmetrione tuberculineata An, Markham & Yu, 2010	*Clibanarius corallinus* (H. Milne-Edwards, 1848)	South China Sea	An, Markham and Yu 2010
Asymmetrione globifera An, Markham & Yu, 2010	*Dardanus hessii* (Miers, 1884)	Beibu Gulf	An, Markham and Yu 2010
	Spiropagurus sp.	South China Sea	An, Markham and Yu 2010
Subfamily Athelginae			
Allathelges pakistanensis Kazmi & Markham, 1999	*Paguristes perspicax* Nobili, 1906	Pakistan	Kazmi and Markham 1999
Athelges akanoshimensis var. *tenuibranchiatus* Shiino, 1936	*Lophopagurus* (*Australeremus*) *triserratus* (Ortmann, 1892)	Japan	Shiino 1936
Athelges japonicus Shiino, 1958	*Pagurus constans* (Stimpson, 1858)	Japan	Shiino 1958
	Pagurus lanuginosus De Haan, 1849	Japan	Shiino 1958
	Pagurus middendorffii Brandt, 1851	Japan	Shiino 1958
Athelges sp.	*Trizopagurus strigatus* (Herbst, 1804)	Indonesia	Haig and Ball 1988

Table 2. Known bopyrids infesting *Paguristes* species with localities and references.

Bopyrids	Host	Type locality	References
Asymmetrione aequalis Pardo, Boyko & Mantelatto, 2009	*P. tomentosus* H. Milne Edwards, 1848	Peru	Pardo et al. 2009
Asymmetrione desultor Markham, 1975	*P. tortugae* Schmitt, 1933	Brazil	Bourdon 1979
Asymmetrione foresti (Bourdon, 1968)	*P. eremita* (Linnaeus, 1767)	Mediterranean	Bourdon 1968
Parapagurion calcinicola Shiino, 1933	*P. monoporus* Morgan, 1987	Indonesia	Haig and Ball 1988
	P. sp.	Thailand	Markham 1985a
Parapagurion imbricata Markham, 1978	*P. tortugae* Schmitt, 1933	Cuba	Markham 1978
Pseudione biacuta Bourdon, 1979	*P. robustus* Forest & de Saint Laurent, 1967	Uruguay	Bourdon 1979
Pseudione quasimodo Boyko & Williams, 2004	*P. grayi* Benedict, 1901	Bahamas	Boyko and Williams 2004
	P. invisisacculus McLaughlin & Provenzano, 1974	Bahamas	Boyko and Williams 2004
	P. anahuachis Glassell, 1938	Gulf of California	Brusca 1980
Allathelges pakistanensis Kazmi & Markham, 1999	*P. perspicax* Nobili, 1906	Pakistan	Kazmi and Markham 1999
Athelges pelagosae Babiç, 1912	*P. eremita* (Linnaeus, 1767)	Adriatic	Babiç 1912
Parathelges piriformis Markham, 1972	*P. oxyophthalmus* Holthuis, 1959	Colombia	Markham 1978
Parathelges whiteleggei Nierstrasz & Brender à Brandis, 1931	*P. monoporus* Morgan, 1987	Indonesia	Haig and Ball 1988
Pseudostegias otagoensis Page, 1985	*P. barbatus* (Heller, 1862)	New Zealand	Page 1985

***Paguristione uniuropodus* sp. n.**
http://zoobank.org/E7EECB56-131C-4682-825B-1CBE50B12DCE
Fig. 1

Parapagurion grabla An, 2006 (unpublished thesis): 30–31, fig. 8 (invalid name).

Material examined. Infesting *Paguristes* sp. Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China (IOCAS). Chinese Comprehensive Oceanographic Survey, East China Sea, Station 4081, 28°00'N, 128°30'E, 74m, 5 April 1958, Yulin Liao, coll. Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China (IOCAS). 1♀ holotype, CIEA408101; 1 ♂, allotype, CIEA408102.

Description of holotype female. Length 5.20 mm, maximal width 3.41 mm across third pereomere, head length 1.0 mm, head width 1.31 mm. Body distorted about 16° (Fig. 1A).

Head subelliptical, fully embedded in pereomere 1, with short frontal lamina completely across anterior margin. Eyes absent (Fig. 1A). Antennae with two articles and three articles respectively (Fig. 1C). Maxilliped (Fig. 1D, E) with prominent round articulating palp, that fringed on medial margin by sparse setae. Plectron short and blunt. Barbula (Fig. 1F) with 2 large sharp falcate projections on each side, medially unornamented.

Pereon broadest across third pereomere. First 3 pereomeres with coxal plates. Brood pouch completely enclosed by oostegites. First oostegite (Fig. 1G, H) with deep groove separating 2 articles externally; internal ridge bearing 4-7 simple projections; posterolateral point extending laterally. Pereopods rudimentary, not extending beyond margins of brood pouch, visible only ventrally; all pereopods with all articles distinct, of nearly same size and structure (Fig. 1I).

Pleon of 6 distinct pleomeres, first three produced into small lateral plates and bearing biramous pleopods; fourth and fifth pleomeres lacking lateral plates. Terminal pleomere greatly reduced and deeply embedded in fifth, bearing uniramous uropoda. All pleopodal rami produced into tapering points and progressively smaller posteriorly, extending to sides of pleon and leaving ventral surface of pleon uncovered.

Description of allotype male

Body outline suboval. Length 2.52 mm, maximal width across third pereomere, 1.05 mm, head length 0.30 mm, head width 0.42 mm, first pleomere width 0.50 mm, fifth width 0.20 mm. All segments distinct (Fig. 1J, K).

Head semicircular, broader than long, much narrower than first pereomere, distinctly separated from first pereomere and not at all embedded into it (Fig. 1J). Eyes absent. Antennae visible only ventrally, not extending to margins of head, of 3 and 4 articles respectively; second antenna with sparse short setae on terminal article (Fig. 1L).

Pereon smoothly rounded, slightly broadest across third pereomere. No midventral tubercles. All pereopods with all articles distinct. Pereopod 1 somewhat smaller than pereopods 2-4, those 3 pairs largest and all of about same size; pereopods 5-7 progressively smaller (Fig. 1M, N). Pereopods 1-4 bearing sharp extended dactyli, dactyli of pereopods 5-7 much reduced.

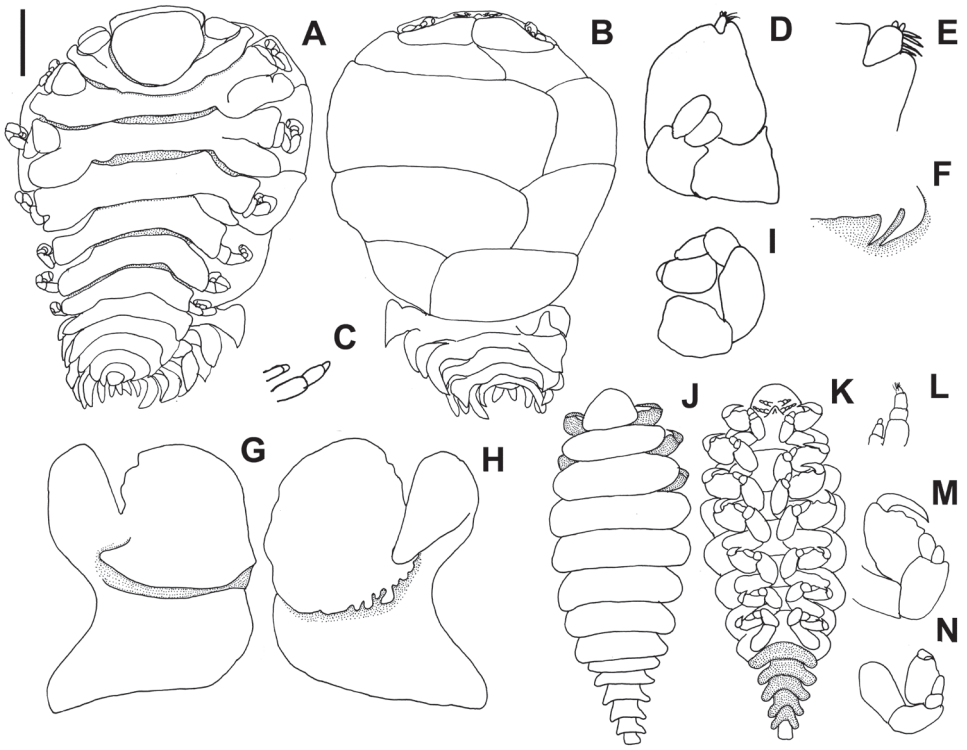

Figure 1. *Paguristione uniuropodus* sp. n. **A–I** holotype female **J–N** allotype male. **A** Dorsal view **B** Ventral view **C** Left antennae **D** Right maxilliped, external view **E** Palp of right maxilliped **F** Left side of barbula **G** Right oostegite 1, external view **H** Right oostegite 1, internal view **I** Pereopod 4 **J** Dorsal view **K** Ventral view **L** Left antennae **M** Pereopod 2 **N** Pereopod 7. Scale: 1.00 mm (**A, B**); 0.36 mm (**D**); 0.17 mm (**C, E**); 0.50 mm (**F–I**); 0.47 mm (**J, K**); 0.23 mm (L–M).

Pleon elongate, extending far posteriorly, of 6 distinct pleomeres deeply separated laterally, each markedly narrower than that before it; pleomere 1 abruptly narrower than last pereomere, it and pleomere 2 much shorter than pleomeres 2-6; every pleomere broadest across posterior edge. Pleopods and uropods completely absent, not even indicated by scars.

Etymology. Latin noun *uniuropodus*, referring to the uniramous uropoda of the female, used in apposition.

Remarks. The new genus differs from other closely similar hermit-crab-infesting genera *Pseudione*, *Pagurion* and *Parapagurion* thus: female with only rudimentary pleonal lateral plates (only first three pleomeres with small lateral plates) and uniramous uropoda, male with head and pleon abruptly narrower than contiguous pereomeres, first pereopod smaller than pereopods 2-4 and pleopodal appendages completely lacking. Females of *Pseudione* have distinct pleonal lateral plates on pleomeres 1-5; its males have pleopods, and their heads and pleons are smoothly narrower than the pereon. Females of *Pagurion* have distinct lamellar pleopodal appendages on all pleomeres

1-6 and biramous uropoda; its males have equally width pereopods and uniramous pleopods. Females of *Parapagurion* are nearly symmetrical and bear well-developed lateral plates on pleomeres 1-5 and uniramous uropods; the first pereopods of the males are never smaller than the second ones.

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RESEARCH ARTICLE

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An unexpected new species of the genus *Pseudopoda* (Araneae, Sparassidae, Heteropodinae) from the Western Ghats in India

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Abstract

A new species of the genus *Pseudopoda* is described from India: *Pseudopoda ashcharya* **sp. n.** Males are characterised by the absence of the conductor and females are unique within the genus in having the lateral lobes of their epigyne fused. The systematic relationship of the new species is discussed referring to its isolated occurrence in the Western Ghats.

Keywords

Taxonomy, Huntsman Spiders, morphology

Introduction

Almost all members of the subfamily Heteropodinae as well as almost all species of the genus *Pseudopoda* exhibit a membranous conductor (Jäger 2001, 2002). Jäger et al. (2015) described the first *Pseudopoda* species without a conductor. *Pseudopoda wu* Jäger, Li & Krehenwinkel 2015 shows a small non-sclerotised patch at its tegulum, most likely the rest of an otherwise reduced conductor homologue. Jäger (2015) described five species from the Nat Ma Taung in Myanmar lacking a conductor entirely. Logunov and Jäger (2015) described another species without conductor from Vietnam: *P. ohne*. Males of the present new species lack a conductor and females show unique

characters as well. The species was found in the Western Ghats and far away from other *Pseudopoda* populations. This geographically unexpected finding is described as a new species and its systematic background is discussed.

Material and methods

The examined spiders are preserved in 70 % denatured ethanol, samples for molecular analyses are kept in 99.5 % pure ethanol. Examination and drawings were carried out with a Leica MZ 16 stereomicroscope with camera lucida attachment. Female copulatory organs were dissected and the sclerotised internal duct system was cleared in 96% DL-lactic acid ($C_3H_6O_3$). All measurements are in millimetres [mm]. Opisthosoma length means the length without petiolus and spinnerets. Leg formula, leg spination pattern and size classes follow Jäger (2001). Palp and leg lengths are listed as: total (femur, patella, tibia, metatarsus, tarsus). Arising points of tegular appendages in males are described as clock-positions of the left pedipalp in ventral view. In schematic illustration of the internal duct system the blind ending (glandular) appendage is marked with "T", the copulatory orifice with a circle, and the end of the fertilisation duct in direction of the *uterus externus* with an arrow. As in Jäger (2005: 88), slit sensilla close to the epigyne are generally considered as descriptive character. Colouration is described from specimens in ethanol.

Elevation is given in metres [m]. Maps were produced with DIVA-GIS version 7.5.0.

Abbreviations used in the text: dRTA – dorsal part/branch of RTA, DS – dorsal shield of prosoma, mya- million years ago, OS – Opisthosoma, PJ – numbers represent subsequent numbers of Sparassidae examined by the first author, RTA – retrolateral tibial apophysis, SD – serial number of tissue samples for molecular analyses, vRTA – ventral part/branch of RTA, I–IV – referring to leg numbers.

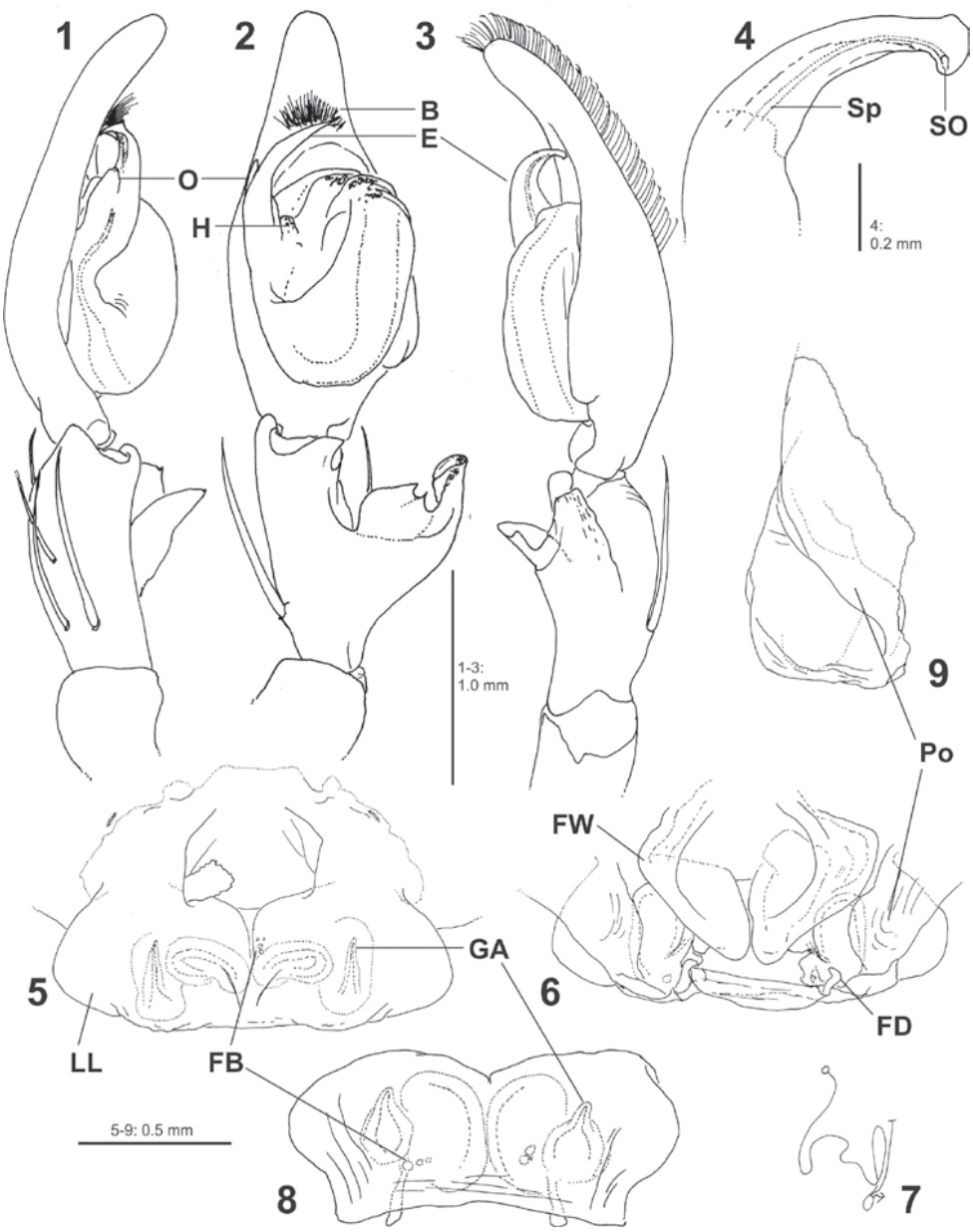
Museum collections (with curators): BNHS – Bombay Natural History Society, Mumbai, India (Rahul Khot), SMF – Senckenberg Museum, Frankfurt, Germany (Julia Altmann, Peter Jäger).

Results

***Pseudopoda* Jäger, 2000**

***Pseudopoda ashcharya* sp. n.**
http://zoobank.org/173F36B2-BC0B-4656-901B-29D79680A268
Figs 1–18

Type material. Holotype male, India, Maharashtra State, Devrukh, 17.068°N, 73.626°E [180 m elevation], leaf litter, 30 August 2013, PJ 3630, SD 1221 (SMF).



Figures 1–9. *Pseudopoda ashcharya* sp. n. from India, copulatory organs of male (**1–4** holotype) and female (**5–9** paratype). **1–3** Left male palp (**1** prolateral **2** ventral **3** retrolateral) **4** Embolus, retrolateroproximal **5** Epigyne, ventral **6** Vulva, dorsal **7** Schematic course of internal duct system, dorsal **8** Epigyne, posterior **9** Epigyne, lateral. **B** brush of setae close to embolus tip **E** embolus **FB** fusion bubbles **FD** fertilisation duct **FW** first winding of internal duct system **GA** glandular appendage **H** hump at base of embolus **LL** lateral lobe **O** embolic outgrowth **Po** sublobal pockets **Sp** spermophor **SO** spermophor opening.

Paratypes: 1 female, India, Maharashtra State, Guravwadi, 16.876°N, 73.645°E [100 m elevation], leaf litter, 2 September 2013, PJ 3631, SD 1222 (SMF). 1 male, India, Maharashtra State, Guravwadi, 16.876°N, 73.645°E [100 m elevation], leaf litter, S. Kulkarni leg., by hand, 15 August 2015, Sp. 316 (BNHS).

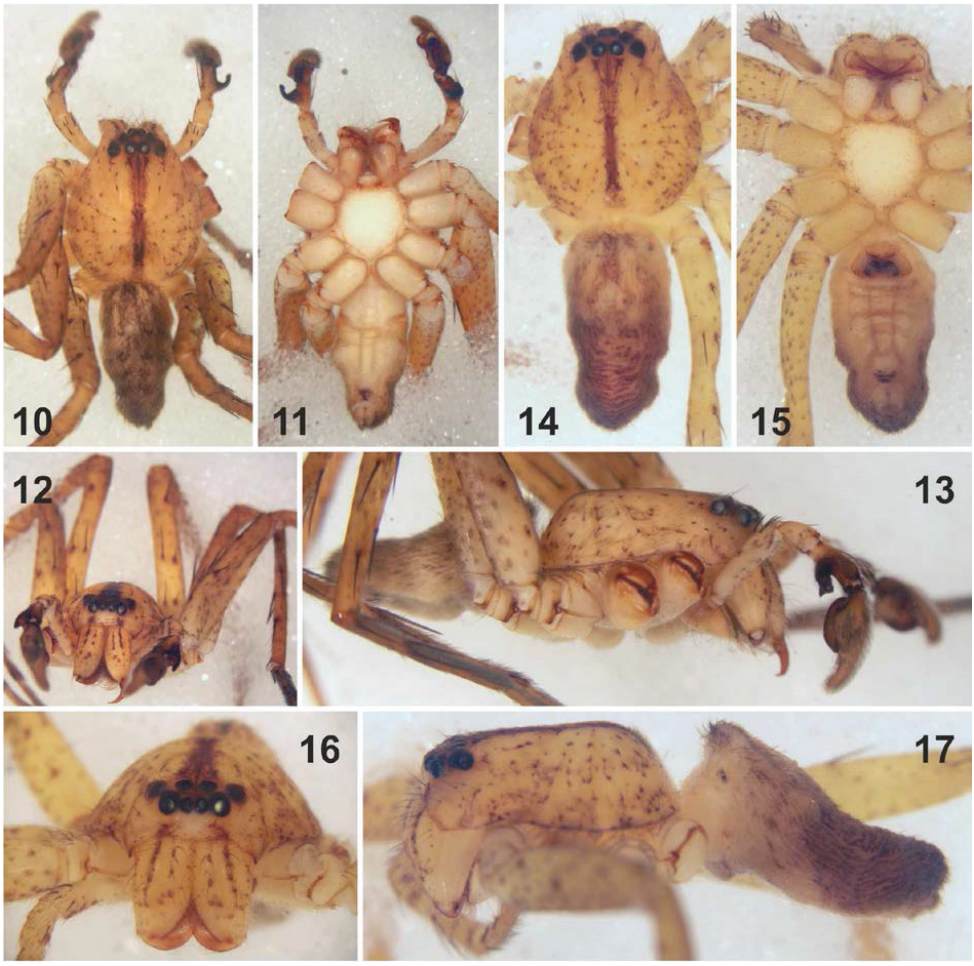
Etymology. The species name is taken from the Hindi, "ashcharya" meaning "surprise", referring to the unexpected occurrence of the genus *Pseudopoda* in the Western Ghats, more than 1400 km away from the closest congener; term in apposition.

Diagnosis. Small Heteropodinae, body length male 8.4, female 8.3. Males similar to those of *Pseudopoda* species described in Jäger (2015), *P. ohne* Logunov & Jäger 2015 and *P. wu* in having the conductor entirely reduced, most similar to *P. pingu* Jäger 2015, *P. wamwo* Jäger 2015 and *P. martinschuberti* Jäger 2015 in having the embolus roughly sickle-shaped in ventral view, but can be distinguished from these species by the mesal embolic outgrowth (Figs 1–4). Females may be recognised by the medially fused lateral lobes, the unique pointed glandular appendages and by the sublobal pockets (Figs 5–9).

Description. Male (holotype). DS length 4.3, width 3.8, anterior width 1.9, OS length 4.1, width 2.1. Eyes: diameters AME 0.22, ALE 0.35, PME 0.27, PLE 0.33; interdistances AME–AME 0.14, AME–ALE 0.05, PME–PME 0.17, PME–PLE 0.37, AME–PME 0.37, ALE–PLE 0.33, clypeus height at AME 0.49, at ALE 0.40. Spination: palp: 131, 11(small, distal)1, 2101; legs: femur I–II 323, III 322, IV 331; patella I–IV 101; tibia I–IV 2026; metatarsus I–II 1014, III 2025, IV 3036. Metatarsus IV ventrally with double row of bristles along entire length and with patch of bristles instead distal spine, I–III with scopula, without bristles. Leg formula: 2(14)3. Measurements of palp and legs: palp 6.0 (2.0, 0.8, 1.1., -, 2.1), leg I 19.7 (5.2, 2.1, 5.8, 4.9, 1.7), leg II 20.4 (5.5., 2.1, 6.0, 5.1, 1.7), leg III 15.8 (4.4, 1.7, 4.5, 3.9, 1.3), leg IV 19.7 (5.5, 1.6, 5.2, 5.7, 1.7). Promargin of chelicerae with 3 teeth, retromargin with 4 teeth; cheliceral furrow with ca. 15 denticles in patch close to anterior teeth; chelicerae with 1 bristle close to retromargin of fang base.

Palp as in diagnosis (Figs 1–4). Cymbium slender, with dorsal scopula in distal half, retrolateral bulge with small, proximad hump. RTA arising proximally to mesally, vRTA with 2 small pointed apices, dRTA with blunt end. Spermophor running submarginally retrolaterally, narrowing prolaterally when entering the embolus. Embolus arising from 9- to 10-o'clock-position from tegulum, with small hump at its base centrally, its widened tip situated close to a dense brush of setae at the proximal part of cymbium's tip.

Colouration (Figs 10–13): Light yellowish brown with brown markings. DS dotted, with narrow dark longitudinal band running from PME to posterior end of fovea and slightly darker lateral margins as well as indistinct submarginal band. Sternum, labium, gnathocoxae and coxae ventrally pale yellowish without pattern. Chelicerae yellowish brown with two distinct longitudinal bands frontally and one indistinct band laterally, in distal half with dots. Legs spotted, femora with additional spine patches. OS dorsally with alternating dark and light bands in anterior half and paired patches in posterior half; laterally spotted; ventrally with dark triangle in front of spinnerets.



Figures 10–17. *Pseudopoda ashcharya* sp. n. from India, habitus of male (**10–13** holotype) and female (**14–17** paratype) (**10, 14** dorsal **11, 15** ventral **12, 16** frontal **13, 17** lateral).

Female. DS length 4.0, width 3.4, anterior width 1.9, OS length 4.3, width 2.0. Eyes: diameters AME 0.19, ALE 0.32, PME 0.26, PLE 0.30; interdistances AME–AME 0.13, AME–ALE 0.05, PME–PME 0.15, PME–PLE 0.35, AME–PME 0.33, ALE–PLE 0.32, clypeus height at AME 0.49, at ALE 0.39. Spination: palp: 131, 101, 2121, 1014; legs: femur I–III 323, IV 321; patella I 001, III–IV 101; tibia I–IV 2026; metatarsus I–II 1014, III 2025, IV 3036. Metatarsus IV ventrally with double row of bristles along entire length and with patch of bristles instead distal spine, I–III with scopula, without bristles. Leg formula: 2413. Measurements of palp and legs: palp 5.4 (1.6, 0.8, 1.2, -, 1.8), leg I 15.4 (4.3, 1.8, 4.2, 3.7, 1.4), leg II 16.5 (4.7, 1.9, 4.5, 4.0, 1.4), leg III 12.7 (3.8, 1.5, 3.2, 3.0, 1.2), leg IV 15.8 (4.6, 1.5, 4.0, 4.2, 1.5). Promargin of chelicerae with 3 teeth, retromargin with 4 teeth; cheliceral furrow with 20–21 denticles in slightly elongated patch close to anterior teeth; chelicerae with 1 bristle close to retromargin of fang base. Palpal claw with 6 teeth.

Copulatory organ as in diagnosis (Figs 5–9). Epigyne wider than long, epigynal field without distinct anterior bands. Lateral lobes rounded at their posterio-lateral margin, protruding distinctly over epigastric furrow at about half of their length, with pockets between lateral parts and epigastric furrow; fused along the median line with indistinct external ledges and internal "fusion bubbles" (Jäger and Krehenwinkel 2015). Internal duct system with first winding bulging laterally, spermathecae situated postero-laterally. Fertilisation duct arising posteriorly from spermathecae, apical end antero-mediad.

Colouration (Figs 14–17): As in male but inner frontal band on chelicerae developed as row of dots, lateral band lacking.

Distribution. Known from two localities in the Western Ghats in India (Fig. 18).

Discussion

Pseudopoda species have been recorded from South, East and the north-western part of Southeast Asia (Fig. 18). Until now seven out of 120 species are known to have the conductor reduced (Jäger et al. 2015, Jäger 2015, Logunov and Jäger 2015). They are distributed in Yunnan, China and Chin State, Myanmar, as well as in Central Vietnam (Fig. 18). The present species is known from two localities in Maharashtra State, India. These are about 1,400 km away from the nearest occurrence of congeners in the Himalaya and more than 2,000 km from the closest locality with conductor-less congeners in Myanmar. The question is how this isolated occurence can be explained. The geological history of the Indian West coast indicates that the Western Ghats have

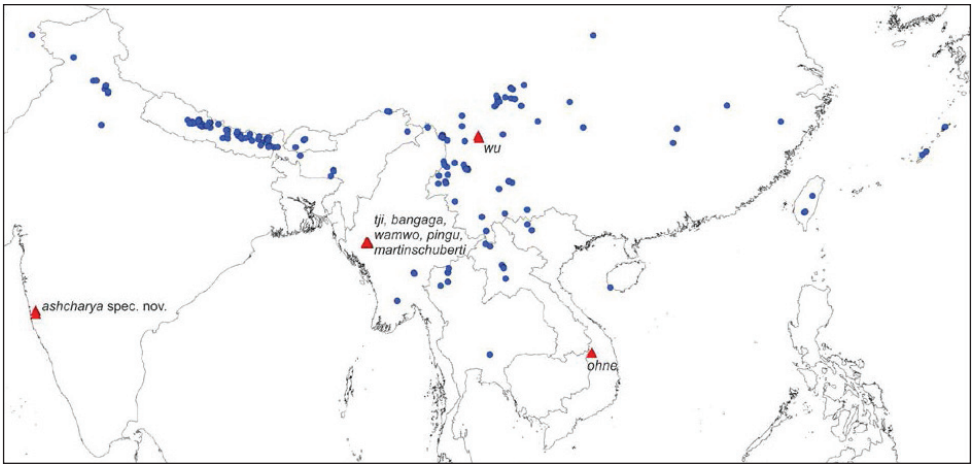


Figure 18. Distributional records of *Pseudopoda* species. Red triangles – species without conductor; blue circles – species with conductor.

been formed 150 mya during the break-up of Gondwana and came into being around 100 to 80 mya. This period was suggested as the time when the basal split within the Sparassidae occurred (Moradmand et al. 2014) rather than a time of diversifying within single genera like *Pseudopoda* (< 50 mya: Moradmand et al. 2014). During the same period (circa), the Indian raft was introduced to Asia allowing a passage for exchange of species (Conti et al. 2002). Most of India (except part of northwest) was covered by humid forest continuous with forests of South-east Asia, receiving high rainfall during 18–11 mya. The arrival of drier climate 5 mya onwards wiped out this wet zone isolating Western Ghats and parts of Eastern Ghats from the south and south-east Asian wet zones (Karanth 2003: fig. 3). When looking for other today's special criteria of the Western Ghats the annual precipitation of over 1000 mm might be one factor that could explain the isolated occurrence of *P. ashcharya* sp. n. Regions east of the Western Ghats have less than 200 mm annual rainfall which might represent a barrier for species adapted to moist and humid conditions. For this scenario it seems likely that the new species is a relict of a previously wider distribution range of the genus. However, the dis-junction in the distribution of *Pseudopoda ashcharya* sp. n. and its congeners from India and neighbouring countries might also be an artefact arising from lack of extensive survey in central and west Indian states.

From the morphology, males of the new species are apparently close to *Pseudopoda* species recently described from the southern Chin State in Myanmar. The conductor of species from both localities is reduced. Jäger (2015) considered a dense brush of setae as potential functional surrogate structure. This brush occurs in *P. ashcharya* sp. n. as well (Figs 1–2: B). Females, however, show a unique character within the entire genus: the lateral lobes are medially fused with "fusion bubbles" as indication for such an evolutionary event (Figs 5, 8: FB). Similarly, fused lateral lobes are known only from *Sinopoda* Jäger 1999 and to a lesser extent from *Bhutaniella* Jäger 2000. But the lack of other structures diagnostic for these latter two genera, such as for instance the epigynal pockets as well as the typical bifid and complex embolus in *Sinopoda* and *Bhutaniella* respectively make clear that the present species does not belong to either of these genera. The similarity of the male copulatory organ with those of other *Pseudopoda* species and the congruence of diagnostic characters according to the most recent diagnosis of the genus (Jäger et al. 2015) as well as similarities of other characters in the female copulatory organs and their congruence with diagnostic characters (Jäger 2001; here especially the course of the internal duct system as shown in fig. 82) let suggest placing the species in *Pseudopoda*.

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RESEARCH ARTICLE

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Tachysphex austriacus Kohl, 1892 and *T. pompiliformis* (Panzer, 1804) (Hymenoptera, Crabronidae) are a complex of fourteen species in Europe and Turkey

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Abstract

Tachysphex pompiliformis (Panzer, 1804) and *T. austriacus* Kohl, 1892 species subgroups belong to the *T. pompiliformis* species group, and both subgroups consist of morphologically similar species. The *T. austriacus* Kohl species subgroup comprises four species in Europe and Turkey. For this subgroup, differential diagnoses of *T. austriacus* and *T. prismaticus* Straka, 2005 are presented, and *T. hungaricus* **sp. n.** from Hungary and *T. smissenae* **sp. n.** from Spain, France and Turkey are described. The *T. pompiliformis* species subgroup consists of ten species from Europe and Turkey. For this subgroup, differential diagnoses of *T. ferrugineus* Pulawski, 1967 and *T. opacus* F. Morawitz, 1893, as well as the differential diagnosis and redescription of *T. pompiliformis*, are presented. *Tachysphex dimidiatus* (Panzer, 1809), *T. jokischianus* (Panzer, 1809) and *T. nigripennis* (Spinola, 1808) are resurrected from synonymy with *T. pompiliformis* and redescribed. Neotypes of *T. dimidiatus* (Panzer) and *T. nigripennis* (Spinola) are designed. *Tachysphex bohemicus* **sp. n.** from the Czech Republic; *T. cretensis* **sp. n.** from Crete, Greece; *T. nobilis* **sp. n.** from Bulgaria, the Czech Republic, Hungary, Poland, Slovakia and Turkey; and *T. punctipleuris* **sp. n.** from Bulgaria, Germany, Hungary, Italy, Slovenia and Turkey are described. Identification keys to all species from *T. pompiliformis* and *T. austriacus* species subgroups known from Europe and Turkey are presented.

Keywords

Hymenoptera, Apoidea, Crabronidae, *Tachysphex*, taxonomy, new species, description, Europe, Turkey

Introduction

Tachysphex pompiliformis (Panzer, 1804) and *T. austriacus* Kohl, 1892 species subgroups belong to the *T. pompiliformis* species group. *Tachysphex austriacus* Kohl has been considered to be a sister species to *T. pompiliformis* (Panzer) (Straka 2004). Later, *T. austriacus* Kohl, 1892 was recognized to be a cluster of closely related species different from *T. pompiliformis* (Panzer). Both species are now considered to belong to separate lineages and form two different species subgroups (Straka 2008). Only three species that were placed in the *T. pompiliformis* subgroup were recognized in the previous revision of *Tachysphex* in the Palearctic region (Pulawski 1971). Species from the *T. austriacus* subgroup were thought to be conspecific with *T. pompiliformis*. Most of the species from the *T. austriacus* subgroup were recently described or restored from synonymy. First, *T. austriacus* Kohl was resurrected and redescribed by Straka (2004). Subsequently, two other species were described and were considered to be related to *T. austriacus* Kohl: *T. prismaticus* Straka, 2005 and *T. stysi* Straka, 2008 (Straka 2005, 2008). Two new species that belong to the *T. austriacus* subgroup are described in the present study. In a revision of the Palearctic species (Pulawski 1971), only *T. pompiliformis* (Panzer), *T. ferrugineus* Pulawski, 1967, and *T. opacus* F. Morawitz, 1893 were recognized as valid; all other names from respective groups were considered to be junior synonyms. Subsequently, one additional species, *T. kaszabi* Tsuneki, 1972 from Mongolia, was described (Tsuneki 1972). Pulawski (1971) presented information on the extensive variability within *T. pompiliformis* (Panzer) species; however, no species recognition or change in taxonomy was made within this variable species until this time, except for the separation of species of the *T. austriacus* subgroup. In this study, ten species that belong to this subgroup are recognized in Europe and Turkey. Three species names are restored from synonymy, and four additional new species are described.

Methods

Material from the following institutions and private collections was examined:

BMNH British Museum, (Natural History), London, Great Britain (David Notton);
CSE Christian Schmid-Egger, Berlin, Germany;
IBER Institute of Biodiversity and Ecosystem Research, Sofia, Bulgaria (Toshko Ljubomirov);
JSPC Jakub Straka, Praha, Czech Republic;
HNHM Hungarian Natural History Museum, Budapest, Hungary (Sandor Csősz);
MRBC Martin Říha, Brno, Czech Republic;
NHMW Naturhistorisches Museum Wien, Wien, Austria (Manuela Vizek);
NJHC Niklas Johansson, Habo, Sweden
NMPC National Museum, (Natural History), Praha, Czech Republic (Jan Macek);
OLML Oberösterreichisches Landesmuseum, Linz, Austria (Fritz Gusenleitner);
POTC Piotr Olszewski, Toruń, Poland;

PTLC Pavel Tyrner, Litvínov, Czech Republic;
USMB Upper Silesian Museum, Bytom, Poland (Waldemar Żyła);
WAPC Werner Arens, Bad Hersfeld, Germany;
WSKC Wolfgang Schlaefle, Kaiseraugst, Switzerland;
ZIN Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (Yulia Astafurova);
ZKZC Zdeněk Karas, Zliv, Czech Republic; and
ZSM Staatliche Naturwissenschaftliche Sammlungen Bayerns, Zoologische Staatssammlung, Munich, Germany (Stefan Schmidt).

Morphological terms are used according to Bohart and Menke (1976) and Krombein and Pulawski (1994), except morphological description of volsella. There is volsellar corpus – the main part with setae on outer margin and a depression on inner side, which connecting volsella with gonocoxites; apical volsellar process – a thin process which bears setae on its outer margin, a row of setae continues from the corpus; dorsal volsellar process – the process, which can have various shapes and extending dorsally from the corpus. The following abbreviations are used in the morphological descriptions:

WML clypeus median lobe width
LCL clypeus maximum length
WCL clypeus width
LA3 length of antennal article III, dorsally
WA3 width of antennal article III, dorsoapically
LA5 length of antennal article V, dorsally
WA5 width of antennal article V, dorsoapically
WV vertex width
LV vertex length
MOD diameter of median ocellus
LF1 forefemur length
WF1 forefemur width, laterally

All of the newly described species were labeled in the following manner: "HOLOTYPUS ♂ or ♀, name of taxon sp. nov., J. Straka det. 2015" on a red card; neotypes were designated on red cards, and paratypes were designated on yellow cards. Exact label data are cited only for the holotypes. Separate lines on the labels are indicated with a slash "/", and separate labels are indicated with double slashes "//".

Results

Tachysphex austriacus species subgroup

Diagnosis of subgroup. The *Tachysphex austriacus* species subgroup belongs to the *T. pompiliformis* group, which is characterized by the following character combination: La-

brum flat; frons uniformly convex; scutum and mesopleuron finely reticulate or punctate, microsculptured or unsculptured among punctures; episternal ridge developed; tarsomeres V of mid and hind legs unmodified, straight ventrally and mildly convex dorsally; tarsomeres IV of the mid and hind legs distinctly emarginated and longer than wide; anal lobe of the hindwing small; sternum I without a longitudinal carina; sterna without distinct setal patches; pygidium triangular, narrowly truncate at the apex, with indistinct transverse carina, integument sparsely punctate, or without punctures in some species, interspaces between punctures finely sculptured to unsculptured. In males, the volsellar corpus is not separated from the dorsal process by constriction, and thus the corpus is extended to a process; aedeagus with distinct well-developed teeth, usually not more than 10 in number.

From the other species of the *T. pompiliformis* group, the *T. austriacus* species subgroup (species complex *sensu* Straka 2005) differs in having the following characters: glossa and galea short, galea as wide as long, apex densely setose; glossa shorter than galea; mesopleuron microsculptured, dull or slightly shiny, with or without punctures, punctures ill-defined when present, and with distinct interspaces; fore and midfemora uniformly sculptured throughout, with only small punctures and uniform interspaces; lateral parts of tergum II with variably sparse punctuation and shiny interspaces; and terga I-III with silvery apical fasciae (rarely absent). In the female, clypeus with lateral incisions and with shallow or absent median emargination. In the male, clypeus arcuate with conspicuous lip corner and forebasitarsus without rake. The *T. austriacus* species subgroup differs from the *T. pompiliformis* species subgroup by two consistent male characters. In the *T. austriacus* species subgroup, the forefemoral notch, slightly shiny to shiny, has no elevated plate and carinae on the margins and has distinct small setae on the surface; the setae on the volsellar apical process are uniformly directed ventrally (or nearly so). In the *T. pompiliformis* species subgroup, an elevated plate is present in the forefemoral notch with more or less distinct carinae on the margins; its surface appears nearly glabrous, finely or coarsely microsculptured; the ventral setae on the volsellar apical process are randomly directed. Characters for distinguishing females of *T. pompiliformis* and *T. austriacus* subgroups have not been identified so far.

Species included. *Tachysphex austriacus* Kohl, 1892; *T. hungaricus* sp. n.; *T. pekingensis* Tsuneki, 1971 (China); *T. prismaticus* Straka, 2005; *T. smissenae* sp. n.; and *T. stysi* Straka, 2008 (Central Asia).

Tachysphex austriacus Kohl, 1892

Figs 28, 38, 41, 50, 53, 62, 77, 86, 91

Type material. Holotype: ♀, Austria: Wien: Türkenschanze, 12.viii.1895, A. Handlirsch lgt. "12.8.95. / Handl. // Austr. inf. / Türkenschanz // austriacus / K. / det. Kohl Type", [handwriting, name of collector and word "det." printed]. Holotype in NHMW, examined.

Additional material examined. Czech Republic: Boh. centr., Lysá nad Labem env., 1 ♂, 1 ♀, 8. vi. 1950, A. Hoffer lgt., OLML; Mor. mer., Dolní Bojanovice, 1 ♂, 1 ♀, viii. 1942, A. Hoffer lgt., JSPC; Hodonín, 1 ♀, vii. 1942, A. Hoffer lgt., OLML; **Germany**:

Birkenheide env., 1 ♂, 2. vi. 1993, O. Niehuis lgt., JSPC; Ingelheim-nord, Mainz, 1 ♀, 24. vii. 1993, Ch. Schmid-Egger lgt., JSPC; Mallnow, Frankfurt an der Oder 13 km NNW, Brandenburg, 1 ♂, 24. vii. 2008, Ch. Schmid-Egger lgt., CSE; **Hungary**: Ör Sz. Miklós, Őrtilos Szentmihályhegy, Somogy, 1 ♀, 21. vi. 1920, Sajó lgt., HNHM; Kecskemét env., 1 ♀, 16. vii. 2006, J. Halada lgt., JSPC; Kecskemét, Nyomás, 1 ♀, 18. vii. 1962, Sólymosné lgt., HNHM; Kecskemét, puszta, 1 ♂, 23. 6. 1987, J. Halada, OLML; Oktatasi Központ, Fülophaza env., sand dunes, 1 ♀, 16. vii. 2013, J. Habermannová & J. Straka lgt., JSPC; Örkeny, puszta, 1 ♀, 16. viii. 2000, J. Straka lgt., 1 ♂, 7. vi. 2013, D.Benda, P.Bogusch & J.Straka lgt., JSPC; Ásotthalom Mcs., Szeged, 1 ♀, 3. vii. 1973, L. Móczár lgt., HNHM; **Kazakhstan**: Matay desert, Sarkand distr., 3 ♀♀, 25. vi. 1995, J. Halada lgt., OLML; **Mongolia**: Arvaykheer 137 km NE, Överkhangay prov., dunes, 4 ♂♂, 8 ♀♀, 2. vii. 2004, 6 ♀♀, 25. vii. 2004, J. Straka lgt., JSPC; Bayankhongor 2 km S, Bayankhongor prov., along Tüy Gol, 1 ♀, 10. vii. 2004, J. Straka lgt., JSPC; Ulaanbaatar 170km W, dunes, 1 ♀, 16. viii. 2007, J. Halada, JSPC; **Poland**: Kików, Malopolska Upland, 1 ♂, 2 ♀♀, 14. vii. 1996, R. Dobosz lgt., 9 ♂♂, 2 ♀♀, 19. vi. 1995, W.Żyła lgt., USMB, JSPC; Małkinia, 1 ♀, 14. vii. 1995, R. Dobosz lgt., USMB; Sierakowo, 1 ♂, 21. vi. 2011, P. Olszewski lgt., POTC; Toruń-Glinki, 1 ♀, 14. vi. 2011, P. Olszewski lgt., POTC; Toruń-poligon artyl., 1 ♀, 14. vi. 2011, P. Olszewski lgt., POTC; Wigry, Wigierski NP, 1 ♀, 5. viii. 2002, W. Żyła lgt., USMB; **Slovakia**: Chľaba 1.5km SE, 1 ♀, 5. viii. 2013, M. Říha lgt., MRBC; Chotín, 1 ♂, 12. vii. 1981, P. Tyrner lgt., PTLC, 1 ♀, 1. viii. 1960, 1 ♀, 30. vii. 1970, 1 ♀, 27. vii. 1974, 1♂, 13. vii. 1962, Z. Pádr lgt., 1♂, vi. 1977, M. Kocourek lgt., OLML, JSPC; Somotor, 1 ♂, vii. 1960, M. Kocourek lgt., OLML.

Diagnosis. *Tachysphex austriacus* is the type species of the *T. austriacus* species subgroup. *Tachysphex austriacus* Kohl differs from all other species from the subgroup in the following combination of characters: ♂, ♀: gena narrow, conspicuously converging behind compound eyes; scutum and scutellum sparsely punctate, punctures well developed and usually up to 1.5 diameter apart (more than that in some specimens); ventral part of mesopleuron densely punctate, punctures relatively large and well developed in comparison to other species; trochanters densely punctate; ♂: ventral volsellar setae in one line; ♀: clypeal lip with distinct irregular median emargination; clypeal bevel forming slightly convex to flat plate, but the transition between the clypeal basomedian area and the bevel is not angulated; forebasitarsal rake pale, with four apical spines.

Geographic Distribution. Austria, Czech Republic, Germany, Hungary, Kazakhstan, Mongolia, Poland and Slovakia.

Note. The holotype was redescribed by Straka (2004).

***Tachysphex hungaricus* sp. n.**
http://zoobank.org/A304520F-F80F-41AE-936D-FBDCF1436EEE
Figs 13, 36, 42, 54, 78, 79

Type material. Holotype: ♀, Hungary: "HU; Hungary, 8.vii.2006 / Örkeny, / 50km SE Budapest / J. Straka lgt., EtOH 96% // ZSM / HYM 23722". Holotype in NMPC. Paratype: Hungary: Pákozd env., pasture stepe, 1 ♀, 10. vi. 2015, M. Halada lgt., JSPC.

Diagnosis. The female of *Tachysphex hungaricus* sp. n. resembles *T. austriacus* Kohl, *T. prismaticus* Straka and *T. smissenae* sp. n. and also *T. jokischianus* Panzer and *T. punctipleuris* sp. n. from the *T. pompiliformis* species subgroup in the sculptures and shape of the clypeus. This new species is the most similar to *T. prismaticus*. They share a characteristic form of the clypeus with nearly angulated transition between the basomedian area and a nearly flat bevel; vertex punctures without interspaces medially and at least one diameter apart laterally; very short setae of frons, vertex and scutum, about 0.3 × MOD; and uniform microareolate sculpture of propodeal dorsum with longitudinal ridges all over. *Tachysphex hungaricus* sp. n. differs from *T. prismaticus* in its much denser punctation all over the body; its scutum, trochanters and terga are not sparsely punctate. Females of the *T. hungaricus* thus resemble species of the *T. pompiliformis* species subgroup, but differ from them in having the characters, which were specified as synapomorphies with *T. prismaticus* in their comparison. It is the form of clypeus, sculpture of vertex and propodeum and length of vertex setae.

Description of female (holotype). Body length: 8.2 mm.

Head. Clypeus conspicuously convex, highly elevated, its nearly angular top located slightly dorsally from clypeal midlength; basomedian area well developed, as densely and finely punctate as lateral section, with intermixed large punctures; bevel nearly flat, conspicuously declining, with few large punctures, much longer medially than laterally, but not reaching base of clypeus, bright shiny; lip very slightly arcuate to nearly straight, with median emargination and well developed lateral incisions, separated from bevel by distinct punctate groove, WML:LCL = 1.8, WCL:WML = 1.7. Supraclypeal area flat, finely, densely punctate, punctures ill-defined, interspaces between punctures finely microsculptured, dull. Supraantennal tubercle small, slightly elevated on inner side. Antenna relatively short, LA3:WA3 = 2.2, LA5:WA5 = 2.7. Frons irregularly, very densely punctate, punctures well defined, about half diameter apart, interspaces variable in size, slightly shiny; frontal median line ill defined, not impressed; frontal setae very short, about 0.3 × MOD. Vertex punctate, most punctures well defined, punctures without interspaces medially, but about one diameter apart laterally, punctures laterally slightly larger than medially, interspaces unsculptured, bright shiny. Vertex setae very short, semierect to apressed, about 0.3 × MOD; postocellar impression well developed, widely Y-shaped; vertex slightly wider than long; WV:LV = 1.3. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum with well defined punctures variable in size, less than one diameter apart, interspaces variable in size, shiny, setae gold-brown, about 0.5 × MOD or less. Mesopleuron coarsely microsculptured, with indistinct punctures evanescent in microsculpture; hypoepimeral area finely rugose to coarsely microsculptured, impunctate; ventral part of mesopleuron, with ill-defined punctures, one to less than one diameter apart, interspaces well developed, slightly shiny. Propodeal dorsum uniformly sculptured, very finely areolate with fine irregular longitudinal ridges on entire surface, dull; propodeal side regularly longitudinally ridged, ridges fine, but evenly developed all along, microsculptured, slightly shiny; posteromedial margin of dorsum elevated,

produced above marginal ridges, marginal ridges positioned nearly horizontally above groove on posterior side. Legs, including trochanters, densely punctate, punctures small; forebasitarsal rake pale yellowish, with three apical spines, one preapical spin and two other additional spines. Wings slightly infumate, yellowish, with brown veins.

Metasoma. Terga I-III with slightly developed, but distinct silvery apical fasciae, densely, very finely micropunctate, punctures ill-defined, evanescent in microsculpture, interspaces aciculate, slightly shiny; apical depressions shallow with indistinct micropunctures; sculpture of terga VI-V distinctly coarser than on previous terga, punctures denser, ill-defined, but large, one to less than half diameter apart, interspaces microsculptured, apical depression of tergum V coarsely microsculptured, with few scattered punctures. Pygidium of usual size, sparsely punctate, large and minute punctures intermixed, ill defined, but large punctures deep, interspaces nearly unsculptured, shiny. Central part of sternum II with several larger punctures, interspaces microsculptured, shiny; lateral part slightly shiny, densely micropunctate; remaining sterna with uniform sculpture similar to that on sternum II, but more or less reduced laterally.

Coloration. Large area in center of mandibles, terga and sterna I-III and base of tergum and sternum IV red. Distal tarsomeres, apex of pronotal lobe, ventral part of distal antennal segments, apex of clypeal bevel and tip of pygidium dark red. Tegulae reddish translucent. Apical parts of terga I-III slightly translucent. Remaining body parts all black.

Geographic distribution. Known only from Hungary.

Note. Male unknown.

Name derivation. The species is named after the country of origin.

Tachysphex prismaticus Straka, 2005

Type material. Holotype: ♂, Kazakhstan: "Kazakhstan 20km / SE Aksay env / 16. – 19. 6. 1992 / leg.K.Denes", printed label. Holotype in OLML, examined.

Diagnosis. *Tachysphex prismaticus* Straka resembles *T. austriacus* Kohl, *T. hungaricus* sp. n., and *T. smissenae* sp. n. in the shape of the clypeus and well developed punctures on the ventral part of the mesopleuron. It differs from the other species of the subgroup in the following character combination: ♂, ♀: mesopleuron rugose to densely punctate; venter of all trochanters with punctures several diameters apart, their interspaces unsculptured; all femora and tibiae black; ♂: volsella with large dorsal process; ventral volsellar setae in one line; ♀: clypeal lip with distinct irregular median emargination; clypeal bevel forming flat plate, separated from basomedian clypeal area by relatively sharp, more or less angulated transition; scutum and scutellum sparsely punctate, punctures up to two diameters apart at scutum center; forebasitarsal rake with four apical spines.

Geographic distribution. Kazakhstan, Kyrgyzstan and Turkey.

Note. Full description and all material is given in Straka (2005).

***Tachysphex smissenae* sp. n.**
http://zoobank.org/32C67CA4-285B-4AD8-88FF-8870428E866C
Figs 1, 14, 37, 43, 55, 81, 82, 92

Type material. Holotype: ♂, France: "F-(84) Bédoin, Sanddünen / 13 km NE Carpentras / v.d.Smissen leg.31.5.2000 // Tachysphex / austriacus / ♂ Kohl / Jakub Straka det.2006". Holotype in NMPC. Paratypes: **France**: Bédoin, 13 km NE Carpentras, sanddünen, 1 ♂, 31. v. 2000, 2 ♂♂, 3 ♀♀, 14. vi. 2001, 1 ♀, 21. vi. 2004, J. v. d. Smissen lgt., USMB, JSPC; **Spain**: Aranda de Duero, Burgos, 1 ♂, 11. vii. 1974, Z. Bouček lgt., BMNH; Segovia, 2 ♂♂, 28. vi. 1989, W. Schlaefle lgt., WSKC, JSPC; **Turkey**: Karakus Dagi centr., Isparta prov., 1 ♂, 11. vii. 2006, J. Halada lgt., JSPC.

Diagnosis. *Tachysphex smissenae* sp. n. resembles *T. hungaricus* sp. n. and *T. prismaticus* Straka in the shape of the clypeus: the limit between the basomedian area and the bevel appears angulated, although less so than in the other two species. This new species also has short setae (0.5 × MOD) on the frons, vertex and scutum, similar to the other two species. The sculpture of the propodeum, however, is coarser than in the other two species (it is areolate and not microareolate between longitudinal ridges), the sculptures of the whole body is coarser and denser and the vertex is normally sculptured, unlike *T. hungaricus*. The female differs from all other species of the *T. austriacus* and the *T. pompiliformis* subgroups by angulated shape of clypeus, sculpture of propodeum, short setae, gena robustly built, mesopleuron coarsely punctate, with relatively large and ventrally well developed punctures (similar to *T. austriacus*), terga densely punctate and posterior segments also coarsely punctate with apical depression of tergum V nearly impunctate and the pygidium relatively wide and shiny. The male has the forefemoral notch and the volsella typical for the subgroup (similar to *T. prismaticus* in shape), a conspicuously convex clypeus, which resembles that of the female (except the lip), densely and coarsely punctate terga and coarsely punctate mesopleuron, as in the female.

Description of male (holotype). Body length: 6.7 mm.

Head. Clypeus markedly convex, medially uniformly curved, top at clypeal midlength; basomedian area large, densely punctate; bevel well developed, nearly flat and declining, bright shiny, with several larger punctures; lip conspicuously arcuate, well developed medially, with well-developed, nearly rectangular, lateral corner, lip separated from bevel by distinct groove with large punctures; WML:LCL = 1.3, WCL:WML = 2.4. Supraclypeal area slightly concave with ill defined punctures in microsculpture, dull. Supraantennal tubercle small, slightly elevated on inner side. Antenna relatively short, LA3:WA3 = 1.6, LA5:WA5 = 2.1. Frons uniformly punctate, punctures well defined, one to less than half diameter apart, interspaces variable in size, shiny; frontal median line ill defined, punctate and slightly impressed. Vertex punctate, punctures well defined, with distinct, but small interspaces medially and about one diameter apart close to inner eye margin, punctures laterally slightly larger than medially, interspaces unsculptured, bright shiny. Vertex setae semierect, less than 0.5 × MOD long; postocellar impression well developed, relatively deep, but not sharply

delimited, obtusely V-shaped; vertex slightly wider than long; WV:LV = 1.4. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, most punctures less than half diameter apart, interspaces distinct, unsculptured, slightly shiny, setae about 1.0 × MOD or less. Mesopleuron coarsely punctate to rugose, punctures well defined in lower part and ventrally, but indistinct dorsally, interspaces small to absent, slightly shiny; hypoepimeral area densely punctate to uniformly rugose, dull. Propodeal dorsum coarsely sculptured with irregular longitudinal ridges, uniformly rugose to areolate between ridges; propodeal side longitudinally ridged, ridges well developed, interspaces slightly shiny; posteromedial margin of propodeal dorsum slightly elevated, marginal ridges nearly parallel above groove on posterior side. Legs densely punctate, punctures small; forefemoral notch small, but deep, nearly semicircular, shorter than distance that separates it from forefemoral base, central part of notch without microsculpture, with distinct small setae, shiny. Wings not infumated, with brown veins.

Metasoma. Terga I-III with silvery apical fasciae. Apical depressions of all terga shallow, with micropunctures. Terga I-III densely and distinctly micropunctate, punctures ill defined, interspaces microsculptured, slightly shiny to dull; sculpture of tergum IV-VII coarser than on other terga, also punctures denser. Sterna uniformly punctate, nearly like terga.

Coloration. Apical part of mandibles and terga I and II red. Distal tarsomeres, forefemoral notch, sternum I and base of sternum II dark red. Tegulae reddish translucent. Apical parts of all terga slightly translucent. Remaining body parts black.

Variation of males. Body length: 6.5–7.0 mm. Clypeus slightly to conspicuously convex medially. Forefemoral notch and all metasoma dark in some specimens.

Description of female. Body length: 7.6–8.2 mm.

Head. Clypeus conspicuously convex, highly elevated, its top slightly dorsally from clypeal midlength; basomedian area large, densely and finely punctate as in lateral section, with intermixed large punctures; bevel nearly flat, markedly declining, with few large, sparse punctures, much longer medially than laterally, not reaching base of clypeus, bright shiny; lip very slightly arcuate to nearly straight, with small median emargination and well developed lateral incisions, separate from bevel by distinctly punctate groove, WML:LCL = 1.7, WCL:WML = 1.8. Supraclypeal area slightly concave, very finely punctate, punctures ill defined, interspaces between punctures nearly unsculptured, shiny. Supraantennal tubercle small, slightly but distinctly elevated on inner side. Antenna relatively short, LA3:WA3 = 2.2, LA5:WA5 = 2.7. Frons densely, uniformly punctate, punctures well defined, about half diameter apart or less, interspaces variable in size, slightly shiny; frontal median line ill defined, punctate in dorsal half, indistinctly impressed; frontal setae very short, about 0.3 × MOD. Vertex punctate, punctures well defined, with distinct, but small interspaces medially and about one diameter apart close to inner eye margin, punctures laterally slightly larger than medially, interspaces unsculptured, bright shiny. Vertex setae very short, laterally semierect, about 0.5 × MOD, medially apressed, about 0.3 × MOD; postocellar impres-

sion well developed, widely Y-shaped; vertex slightly wider than long; WV:LV = 1.3. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, uniform in size, about half diameter apart (up to one diameter apart in some specimens), interspaces uniform in size, slightly shiny, setae about 0.5 × MOD or less. Mesopleuron coarsely punctate to rugose, punctures well defined in lower parts and ventrally, but indistinct dorsally, interspaces small to absent, slightly shiny; hypoepimeral area densely punctate, with punctures ill-defined, appearing uniformly rugose, dull; ventral part of mesopleuron with punctures well defined, interspaces shiny. Propodeal dorsum coarsely sculptured, uniformly rugose to areolate, with irregular longitudinal ridges; side longitudinally ridged, ridges well developed, interspaces slightly shiny; posteromedial margin of dorsum slightly elevated, marginal ridges nearly parallel, but turning ventrally and directed toward groove on posterior surface. Legs, including trochanters, densely punctate, punctures small; forebasitarsal rake pale yellowish, with reddish iridescence, with three apical spines, one preapical spin and two or three additional spines. Wings slightly yellowish, veins brown.

Metasoma. Terga I-III with silvery apical fasciae; densely and very finely micropunctate, punctures ill defined, evanescent in microsculpture, interspaces very finelly microsculptured, slightly shiny; apical depressions shallow, with indistinct micropunctures; sculpture of terga IV-V distinctly coarser than on previous terga, also punctures denser; terga IV-V coarsely punctate, punctures ill-defined, but large, one to less than half diameter apart, interspaces microsculptured, apical depression of terga IV and V coarsely microsculptured, apical depression of tergum IV very finely punctate, apical depression of tergum V with a few scattered punctures, slightly shiny, but coarsely microsculptured and dull in some specimens. Pygidium relatively wide, sparsely punctate, with large and minute punctures intermixed, large punctures well defined, deep, interspaces nearly unsculptured, shiny. Central part of sternum II with several larger punctures, interspaces microsculptured, shiny; lateral part slightly shiny, densely micropunctate; remaining sterna with uniform sculpture similar to that on sternum II, but more or less reduced laterally.

Coloration. Central part of mandibles and terga and sterna I-II red. Distal tarsomeres dark reddish. Tegulae brown translucent. Apical parts of terga I-III slightly translucent. Remaining body parts black.

Geographic distribution. France, Spain, Turkey.

Name derivation. The species is named in honor of the outstanding entomologist and collector of most of the type specimens, Jane van der Smissen.

Tachysphex pompiliformis species subgroup

Diagnosis of subgroup. The *Tachysphex pompiliformis* species subgroup differs from the *T. austriacus* species subgroup by two male characters. In the *T. pompiliformis* species subgroup, the surface of the forefemoral notch is microsculptured (very finely in

some species), slightly elevated, with a distinct carina on the inner margin, sometimes on the outer margin as well; and the setae on the lower surface of the forefemoral notch are hardly visible (magnification 50 ×). The ventral setae on the volsellar apical process are randomly directed. In the *T. austriacus* species subgroup, the forefemoral notch is slightly shiny to shiny, without an elevated plate and carinae on the margins and with distinct small setae on the surface; the setae on the volsellar apical process are uniformly directed ventrally (or nearly so). Characters for distinguishing females of *T. pompiliformis* and *T. austriacus* subgroups have not been identified so far. See the characterization under the diagnosis of the *T. austriacus* species subgroup.

Species included. *Tachysphex bohemicus* sp. n.; *T. cretensis* sp. n.; *T. dimidiatus* (Panzer, 1809); *T. ferrugineus* Pulawski, 1967; *T. jokischianus* (Panzer, 1809); *T. kaszabi* Tsuneki, 1972 (Mongolia); *T. nigripennis* (Spinola, 1808); *T. nobilis* sp. n.; *T. opacus* F. Morawitz, 1893; *T. pompiliformis* (Panzer, 1804); and *T. punctipleuris* sp. n.

***Tachysphex bohemicus* sp. n.**
http://zoobank.org/00DC3836-D9BD-485D-A2E4-C8591D94CD0C
Figs 2, 15, 29, 59, 63, 70, 80, 87, 93, 106

Type material. Holotype: ♂, Czech Republic: "CZ; Boh. bor., / 7.-19.vii.2013 / Okna, Doksy env. / J. Straka lgt., EtOH 96% // BC ZSM / HYM 24253". Holotype in NMPC. Paratype: 1 ♀, same locality as holotype, with label BC ZSM, HYM 24597.

Diagnosis. *Tachysphex bohemicus* sp. n. is most similar to *T. jokischianus* in having nearly impunctate apex of tergum V and wide pigydium with shiny surface. It also resamble *T. dimidiatus* in the overall sparsely micropunctate metasoma, which makes the appearance of metasomal sculptures more shiny than in other compared species from the *T. pompiliformis* species subgroup. The apex of the male volsella of the new species is sparsely setose and may resemble volsella of males from the *T. austriacus* species subgroup. Both sexes of *T. bohemicus* sp. n. are easily recognizable by a slightly prominent supraantennal tubercles, which are separated by punctate area; the tubercle is distinctly punctate on the top and nearly at all sides. This character is unique in the *T. pompiliformis* species subgroup. Like *T. jokischianus*, the apical depression of tergum V is nearly impunctate medially, but the terga are finely and sparsely punctate and the pygidium is basally microsculptured; the metasoma thus resembles that of *T. dimidiatus*, except for the apical depressions of all terga, which are very sparsely punctate and well impressed. *Tachysphex bohemicus* sp. n. possess an unusual combination of characters: the propodeum lack longitudinal ridges dorsally and laterally, the female clypeus is distinctly arcuate at apex and uniformly convex dorsally, and the male forefemoral notch is black, positioned more anteriorly than in the other species of the subgroup and its proximal margin is rounded and elevated over the distal margin.

Description of male (holotype). Body length: 7.3 mm.

Head. Clypeus uniformly convex, distinctly elevated in midlength; basomedian area large, densely, distinctly punctate; bevel small, decreasing toward clypeal lip, shiny,

sparsely punctate; lip uniformly, distinctly arcuate, not longer medially than laterally, with distinct lateral corner, lip separated from bevel by a groove; WML:LCL = 1.5, WCL:WML = 2.2. Supraclypeal area flat, distinctly punctate, punctures well defined, interspaces between punctures slightly shiny. Supraantennal tubercle small, rounded, distinctly punctate on top, nearly at all sides; area between the tubercles is also distinctly punctate, interspaces dull. Antenna relatively short, LA3:WA3 = 1.6, LA5:WA5 = 2.0. Frons uniformly punctate, punctures well defined, less than one diameter apart, interspaces variable in size, shiny; frontal median line inconspicuous, not impressed. Vertex sparsely punctate, punctures well defined, less than half to two diameters apart, interspaces slightly microsculptured, slightly shiny to dull. Vertex setae semierect medially, nearly erect close to inner eye margin, almost 1 × MOD long, postocellar impression large, and deep, but with ill defined margins, open widely U-shaped, sparsely punctate, punctures relatively large; vertex, WV:LV = 1.7. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, most punctures less than half diameter apart, interspaces distinct, anteriorly microsculptured, slightly shiny to dull, setae less than 1.0 × MOD long. Mesopleuron sparsely punctate anteriorly, posteriorly impunctate, interspaces microsculptured, dull; hypoepimeral area coarsely microsculptured, without distinct punctures, dull; ventral part of mesopleuron with small ill-defined punctures, interspaces finely microsculptured, slightly shiny. Propodeal dorsum coarsely, irregularly sculptured, longitudinally ridged only basally, irregularly ridged medially; propodeal side microsculptured, without longitudinal ridges, slightly shiny; posteromedial margin of dorsum inconspicuously elevated, marginal ridges inconspicuous, slightly ventromedially directed toward groove. Legs densely punctate, punctures small; forefemoral notch small, well developed, but not deep, positioned slightly anteriorly, shorter than distance that separates it from forefemoral base; proximal margin elevated over distal margin, but widely rounded; anterior and posterior side lined by well developed ledge, notch surface without distinct setae, slightly microsculptured, dull. Wings distinctly infumate, but not dark, with brown veins.

Metasoma. Silvery apical fasciae developed faintly on terga I-IV. Apical depressions of terga distinct, sparsely micropunctate, nearly like more anterior parts. Terga I-IV sparsely micropunctate, punctures ill defined, interspaces coarsely microsculptured, slightly shiny to dull; sculpture of terga IV-VII slightly more conspicuous than that of other terga, also densely punctate. Sterna uniformly punctate, nearly like terga. Volsella light brown, ventral setae pointing in various directions in medial part, but almost in one direction at apical process; apical process relatively sparsely setose; dorsal process large, wider than corpus; corpus lined with distinct ledge along base of setae on inner side of corpus.

Coloration. Apical part of mandibles, distal tarsomeres and terga I-III red. Forefemoral notch black. Tegulae reddish translucent. Apical parts of all terga slightly translucent. Remaining body parts black.

Description of female. Body length: 10.3 mm.

Head. Clypeus distinctly convex, top at clypeal midlength; basomedian area relatively large, more sparsely punctate and punctures larger than on lateral section, interspaces between punctures well developed, shiny, larger medially than laterally, punctures mostly less than one diameter apart; bevel large, distinctly convex, medially longer than basomedian area, laterally much shorter, obtusely triangular, with numerous large, sparse punctures, not reaching base of clypeus, shiny; lip distinctly arcuate, with small lateral incisions, without medial emargination, separate from bevel by punctate groove, WML:LCL = 1.6, WCL:WML = 1.9. Supraclypeal area flat, distinctly punctate, punctures well-defined, interspaces shiny. Supraantennal tubercle small, rounded, distinctly punctate on top, nearly at all sides; area between the tubercles is also distinctly punctate, interspaces dull. Antenna relatively short, LA3:WA3 = 2.3, LA5:WA5 = 2.6. Frons uniformly punctate, punctures well defined, about half diameter apart or less; frontal median line distinct, well impressed in lower frons. Vertex punctate, punctures well defined, less than half to one diameter apart, laterally finer and denser than medially, interspaces microsculptured, shiny. Vertex setae semierect mesally, nearly erect close to inner eye margin, shorter than 1 × MOD; postocellar impression deep, widely opened, V-shaped; vertex moderately wider than long; WV:LV = 1.4. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, most punctures less than half diameter apart, interspaces distinct, slightly shiny to shiny, setae less than 1.0 × MOD long. Mesopleuron distinctly punctate anteriorly, posteriorly impunctate, interspaces coarsely microsculptured, dull; hypoepimeral area coarsely microsculptured, without distinct punctures, dull; ventral part of mesopleuron with ill-defined punctures, interspaces finely microsculptured, slightly shiny. Propodeal dorsum coarsely irregularly sculptured medially, with few short longitudinal ridges basally, uniformly microsculptured, slightly shiny area developed posteromedially; propodeal side uniformly coarsely microsculptured, without longitudinal ridges, slightly shiny; posteromedial margin of dorsum inconspicuously elevated, marginal ridges inconspicuous, slightly ventromedially directed toward groove. Legs densely punctate, punctures small; forebasitarsal rake reddish, with two apical spines, one preapical spine, and two additional spines. Wings slightly infumate with brown veins.

Metasoma. Terga I-III with slightly developed but distinct silvery apical fasciae. Apical depressions of all terga well developed, very sparsely micropunctate. Terga I-III sparsely micropunctate, punctures ill-defined but distinct, interspaces microsculptured, slightly shiny; sculpture of tergum IV-V distinctly coarser than on previous terga, also slightly more densely punctate. Pygidium sparsely punctate, punctures variable, some ill defined, some well defined, but shallow, interspaces microsculptured medially, unsculptured laterally, slightly shiny to shiny. Central part of sternum II with several larger punctures, interspaces microsculptured, shiny; lateral part slightly shiny, densely micropunctate; remaining sterna with uniform sculpture similar to that on sternum II, but more or less reduced laterally.

Coloration. Central part of mandibles, distal tarsomeres, terga and sterna I-III red. Tegulae brown translucent. Apical parts of terga I-III slightly translucent. Remaining body parts black.

Geographic distribution. Known only from Czech Republic.

Name derivation. The species is named after the Bohemian part of the Czech Republic, where the type specimens were collected.

***Tachysphex cretensis* sp. n.**
http://zoobank.org/873850DC-225A-4948-B691-B76066553CA6
Figs 3, 44, 94, 104

Type material. Holotype: ♂, Greece, Crete: "GR,CRETE – SE / Kato Simi, ~ 1000m / 35°02'N,27°29'E / Sauša lg.,6.-12.V.03". Holotype in NMPC. Paratype: 1 ♂, same data as holotype.

Diagnosis. *Tachysphex cretensis* sp. n. is most similar to *T. pompiliformis* and *T. opacus*. They share a coarsely sculptured mesopleuron and the shape of the mandible is as in the latter species. The species is well recognizable by a coarsely sculptured dark body, four metasomal segments with silvery apical fasciae, the clypeal lip produced medially, the mandibular inner margin shallowly emarginated distally from the inner tooth, lacking any furrow, and a densely microsculptured forefemoral notch. The new species is probably endemic to the island of Crete, Greece.

Description of male (holotype). Body length: 8.1 mm.

Head. Mandibular inner margin shallowly emarginated distally from inner tooth, with no furrow. Clypeus uniformly convex, slightly elevated, top at clypeal midlength; basomedian area large, sparsely punctate, with nearly impunctate line medially; bevel convex, decreasing to clypeal lip, shiny, with several larger punctures; lip distinctly sinuate, conspicuously produced medially, with distinct lateral corner, lip separated from bevel by punctate groove; WML:LCL = 1.2, WCL:WML = 2.4. Supraclypeal area concave, sparsely punctate, punctures ill-defined, interspaces microsculptured, dull. Supraantennal tubercle distinctly elevated on inner side, shiny. Antenna relatively short, LA3:WA3 = 1.5, LA5:WA5 = 2.1. Frons uniformly finely punctate, punctures well defined, less than one diameter apart, interspaces variable in size, shiny; frontal median line distinct, narrow and finely impressed. Vertex finely and uniformly punctate, punctures well defined, one to less than one diameter apart, interspaces slightly microsculptured, slightly shiny. Vertex setae short, semierect medially, but nearly erect close to inner eye margin, less than 1 × MOD, postocellar impression distinct, shallow, punctate like rest of vertex, Y-shaped; vertex moderately wider than long; WV:LV = 1.4. Gena dorsally well developed.

Mesosoma. Scutum without anterior impression; scutum and scutellum densely punctate, punctures well defined, most punctures less than half diameter apart, interspaces distinct, microsculptured, slightly shiny, setae about 1.0 × MOD or less. Mesopleuron rugose to densely punctate, most punctures in ventral half well defined,

interspaces coarsely microsculptured to rugose, slightly shiny to dull; hypoepimeral area coarsely rugose, without distinct punctures, with irregular longitudinal ridges, dull; ventral part of mesopleuron with punctures large, relatively well defined, interspaces finely microsculptured, slightly shiny. Propodeal dorsum coarsely sculptured, with longitudinal ridges; side longitudinally ridged, ridges well developed, interspaces microsculptured, slightly shiny; posteromedial margin of dorsum insignificantly elevated, marginal ridges evanescent, directed ventromedially. Legs densely punctate, punctures small; forefemoral notch small but relatively deep, semicircular, shorter than distance that separates it from forefemoral base, proximal margin relatively sharp, but not distinctly elevated over distal margin; central part of notch slightly elevated, anterior and posterior margin lined by faint ledge, notch surface without distinct setae, coarsely microsculptured, dull. Wings moderately infumate, with brown veins.

Metasoma. Silvery apical faciae of terga I-IV distinctly developed. Apical depressions of all terga shallow, nearly as densely micropunctate as more anterior parts. Terga I-III densely and distinctly micropunctate, punctures ill defined, interspaces microsculptured, slightly shiny; sculpture of terga IV-VII coarser than on previous terga, also puncture denser. Sterna uniformly punctate, nearly like terga. Volsella brown, ventral setae pointing in various directions; apex with numerous setae; dorsal process about as wide as corpus.

Coloration. All body black, except central part of mandibles and terminal tarsomeres dark red. Tegulae brown translucent. Apical parts of all terga slightly translucent.

Geographic distribution. Known only from the island of Crete, Greece.

Note. Female unknown. Only two males have been collected so far.

Name derivation. The species is named after the island of Crete, Greece, where the specimens were collected.

Tachysphex dimidiatus (Panzer, 1809), restored from synonymy

Figs 4, 16, 22, 24, 30, 56, 60, 64, 71, 83, 95, 107

Larra dimidiata Panzer, 1809 (Heft 106: pl. 13), ♀. Type material lost. Type was probably from Germany.

Type material. Neotype: ♀, Germany: "Germany, BY, N of / Nürnberg, Tennenloher / Forst, 49,57'N 11.04 / leg. Schmid-Egger / 22.6.2008 by-te // Tachysphex / pompiliformis Panzer ♀ / det Schmid-Egger 2010 // ZSM / HYM 04855". Neotype in ZSM, present designation.

Additional material examined. Austria: Kapfenstein env., Steirmark, 1 ♂, 12. vi. 1989, J. Tiefenthaler lgt., OLML; Lechaue, Forchbach 1 km W, Tirol, A-lech3, 1 ♂, 23. vi. 2006, Ch. Schmid-Egger lgt., ZSM HYM 04856; Lechufer, Unter-Pinswang, Reutte 6km NW, Tirol, A-lech1, 1 ♂, 23. vi. 2006, Ch. Schmid-Egger lgt., ZSM HYM 04857; Mönchgraben, Ebelsberg, Oberösterreich, 1 ♀, 22. viii. 1948, F. Koller lgt., ZSM; **Czech Republic**: Boh. centr., Cihelna v Bažantnici, Praha-Hloubětín, 1

♂, 2 ♀♀, 7. vii. 1998, 1 ♂, 5 ♀♀, 17. viii. 1998, 5♂♂, 2 ♀♀, 22. vi. 1998, 7 ♂♂, 3 ♀♀, 2. viii. 1998, J. Straka lgt., JSPC; Divoká Šárka, Praha-Liboc, 1 ♀, 16. viii. 1998, 1 ♂, 10. vii. 1998, 1 ♂, 4. viii. 1998, J. Straka lgt., JSPC; Chvalské skály, Praha-H. Počernice, 1 ♀, 18. viii. 1998, J. Straka lgt., JSPC; Chvalský lom, Praha-H. Počernice, 1 ♀, 3. vi. 1998, 1 ♂, 1 ♀, 28. vi. 1998, 5 ♂♂, 1 ♀, 3. viii. 1998, J. Straka lgt., JSPC; Podbabské skály, Praha-Dejvice, 1 ♀, 5. vii. 2003, J. Straka lgt., JSPC; Radotínské údolí, Praha-Radotín, 1 ♀, 15. viii. 1998, J. Straka lgt., JSPC; Boh.mer., Chlum u Třeboně, lom Františkov, 1 ♂, 1 ♀, 29. vii. 2002, J. Halada lgt., JSPC; Boh.or., Bartoušov, sand quarry, 1 ♂, 28.-31. vii. 2015, J. Straka lgt., JSPC; Veská, Pardubice env., sand dune, 1 ♂, 1. vi. 2012, R. Tropek lgt., JSPC; Mor. mer., Mutěnice, 1 ♀, 12. viii. 1963, J. Strejček lgt., CSE; Velká Klajdovka NR, Brno-Líšeň, 3 ♂♂, 11. vi. 2014, M. Říha lgt., MRBC, JSPC; Mor. or., Krhová, clay quarry, natural reclamation, 1 ♀, 3.-5. viii. 2015, J. Straka lgt., CSE; Kurovice, lom, vápenec, přírodní rekultivace, 1 ♂, 3.-5. viii. 2015, J. Straka lgt., CSE; Rasová, sandstone quarry, 1 ♀, 4.-6. viii. 2015, J. Straka lgt., CSE; Žlutava, sandstone quarry, 1 ♀, 4.-6. viii. 2015, J. Straka lgt., JSPC; **Bulgaria**: Banitsa, 1 ♀, 31. vii. 2013, L. Toshkov lgt., IBER; Gorna Ribnitsa S, Maleshevska Planina, 1 ♂, 22. vi. 2007, T. Ljubomirov lgt., IBER; Gorno Kadiysko, Etropolska Planina, 4 ♂♂, 19. viii. 2008, T. Ljubomirov lgt. IBER; Gotsev Vruh W, Slavyanka Mts., 1 ♀, 2. ix. 2006, N. Simonov & M. L. Langourov lgt., IBER; Kameshtitsa reserve, 1 ♂, 30. vi. 2014, T. Ljubomirov lgt., IBER; Macedonia cotage W, Rila Mts., 1 ♂, IBER, CCDB-05716-H01; 1 ♂, CCDB-05716-H02, 1 ♂, CCDB-05716-H04, 28. viii. 2010, 1♂, 1 ♀, 31. vii. 2009, T. Ljubomirov lgt., IBER; Parangalitsa NW, Rila Mts., 2 ♀♀, 6. vii. 2007, 1 ♀, 27. viii. 2010, 1 ♂, 29. viii. 2010, 1 ♂, 12. vii. 2011, 1 ♂, 27. viii. 2011, 1 ♂, CCDB-05716-H10, 29. viii. 2011, 2 ♀♀, 18. vii. 2012, T. Ljubomirov lgt., IBER; Razdol, Maleshevska Planina, 6 ♂♂, 3 ♀♀, 27. vi. 2008, T. Ljubomirov lgt., IBER;Vodni Pad SE, 1 ♂, 18. viii. 2013, O. Todorov lgt., IBER; Vrah pek, Ilyov SE, Maleshevska Planina, 2 ♂♂, 1 ♀, 28. vi. 2008, T. Ljubomirov lgt., IBER; Chiša Kamenica, Pirin Mts., 4 ♂♂, 3 ♀♀, 11. viii. 2005, J. Straka lgt., JSPC; **France**: Valvignères, "Les Reynauds" Weinberge, 15 km SW Montélimar, 1 ♀, 18. vi. 2004, J. v. d. Smissen lgt., USMB; **Germany**: Breitbrunn/Ammersee, 1 ♂, 14. iv. 2005, Ch. Schmid-Egger lgt., CSE; Bretten, Diefenbach, Stromberg, Baden-Württemberg, S15, 1 ♂, 8. viii. 1990, Ch. Schmid-Egger lgt., CSE; Grafenau, 6km N, Bayern, Rie-1, 1 ♀, 23. vii. 2008, Ch. Schmid-Egger lgt., ZSM HYM 04854; Garmisch-Partenkirchen, Wiese E Vogelwarte, 1 ♀, 10. v. 2012, D. Doczkal lgt., ZSM, Lagerlechfeld 4 km NE, Bayern, 1 ♂, 5. viii. 2007, Ch. Schmid-Egger lgt., CSE; Mühltal, Starnberg, 1 ♂, 1♀, 6. vi. 1948, F. Stöcklein lgt., ZSM; Ochsenbach, Stromberg, Vaihingen/Enz, Baden-Württemberg, Ob5, 1 ♂, 8. viii. 1990, Ch. Schmid-Egger lgt., CSE; Starnberg, 1 ♂, 1 ♀, 16. vii. 1939, F. Stöcklein lgt., ZSM; Waldtruderinger Forst, Neuperlach, München, 1 ♂, 9. vi. 1998, J. Schuberth lgt., ZSM; **Italy**: Eita, Bormio 14 km SW, Valtellina, Lombardia prov.; 1 ♂, 9. vii. 2006, Ch. Schmid-Egger lgt., CSE; Lasa, Vinschgau 2 km N, Trentino-Alto Adige prov., 3 ♂♂, 8. vi. 2007, Ch. Schmid-Egger lgt., CSE; Lillaz, Valle d'Aosta, 14 km S Aosta, I-aoF, 1 ♂, 7. vii. 1995, Ch. Schmid-Egger lgt., CSE; Passo Gavia 3 km

N, Bormio 13 km SE, Lombardia prov., 5 ♀♀, 27. vii. 2007, Ch. Schmid-Egger lgt., CSE; Pondel, Aosta 8 km SW, Valle d'Aosta prov., 1 ♀, 4. viii. 1996, Ch. Schmid-Egger lgt., CSE; Tubre/Taufers, Vinschgau 1 km NE, Trentino-Alto Adige prov., 2 ♂♂, 1 ♀, 27. vii. 2007, Ch. Schmid-Egger lgt., CSE; Vetan, Aosta 9 km W, Valle d'Aosta prov., 1 ♂, 15. vi. 1996, P. Rosa lgt., CSE; Lanzada, Sondrio 11 km N, Lombardia, I-valD, 1 ♀, 9. vii. 2006, Ch. Schmid-Egger, ZSM HYM 11876; Partschins, Province of Bolzano - South Tyrol, 1 ♂, 20. vii. 1966, collector not indicated, ZSM; **Sweden**: Harghult, Ökna, 1 ♀, 25. v. 2009, Torrbacke lgt., NJHC; Persö, Eksjö, Småland env., 1 ♀, 7. vi. 2006, N. E. Johansson lgt., NJHC; **Switzerland**: Dräi, Centovalli, Tessin prov., 1 ♀, 22. viii. 2004, W. Schlaefle lgt., WSKC; Guarda, Engadin, Grisons prov., 1 ♂, 26. vii. 2007, W. Schlaefle lgt., WSKC; Chandolin/Siders, Wallis prov., 1 ♀, 18. vii. 1989, Perraudin lgt., CSE; La Punt, Engadin, Grisons prov., 1 ♂, 3 ♀♀, 25. vii. 2007, W. Schlaefle lgt., WSKC; La Punt, Engadin, Grisons prov., 3 ♂♂, 2 ♀♀, 21. vii. 2004, W. Schlaefle lgt., WSKC; Maggiadelta, 1 ♀, 15. vii. 2005, W. Schlaefle lgt., WSKC; Onsernonetal, 1 ♂, 1 ♀, 1. viii. 2003, W. Schlaefle lgt., WSKC. Specimens determined as *T. dimidiatus* aff.: **Bulgaria**: Kazanite E, Pirin Mts., 1 ♂, 31. viii. 2006, N. Simonov & M. L. Langourov lgt., IBER; Rozovo N, 1 ♂, 5. vii. 2012, T. Ljubomirov lgt., IBER; **France**: Col Chioula, Ax les Thermes, Pyrénées Mts., 1 ♀, 15. ix. 1987, Ch. Schmid-Egger lgt., CSE; Porte Puymorens, Pyrinees Mts., 1 ♀, 15. ix. 1987, Ch. Schmid-Egger lgt., CSE; Preste, Pic du Canigou, Pyrinees Mts., 3 ♀♀, 13. ix. 1987, Ch. Schmid-Egger lgt., CSE; **Greece**: Ano Trikala, Mt. Killini, Hellas 3 ♂♂, 30. v. 1995, 3 ♂♂, 23. vi. 1996, W. Arens lgt., WAPC; Meg. Tourla, Oros Parnon, Hellas, 1 ♂, 7. vii. 2007, W. Arens lgt., WAPC; Michas, Erymanthos, Achaea, 1 ♂, 23. vi. 1995, 3 ♂♂, 3 ♀♀, 10. vii. 1996, 3 ♂♂, 12. vi. 1997, 3 ♀♀, 27. vii. 1997, W. Arens lgt., WAPC; Oros Chelmos, Xerokambos, Hellas, 5 ♂♂, 3 ♀♀, 10. vi. 1997, W. Arens lgt., WAPC; Panahaikon Mts., Patras env., Achaea, 1 ♀, 4. vii. 2001, W. Arens lgt., WAPC; Panahaikon Mts., Patras env., Achaea, 1 ♂, 24. vi. 1995, 3 ♂♂, 1 ♀♀, 11. vii. 1996, W. Arens lgt., WAPC; Toriza-Prof. Ilias, Oros Taygetos, Hellas, 1 ♂, 8. vii. 1997, W. Arens lgt., WAPC; **Morocco**: Algou NE, 1 ♀, 22. v. 2013, T. Ljubomirov lgt., IBER; **Spain**: Ripoll 27km NE, Pirineos Orient, 2 ♂♂, 1. viii. 2011, J. Halada lgt., JSPC, ZSM HYM24312.

Diagnosis. *Tachysphex dimidiatus* (Panzer) is difficult to distinguish from *T. jokischianus* (Panzer), *T. pompiliformis* (Panzer) and *T. punctipleuris* sp. n. It is variable in most characters, and not a single character consistently differentiates it from the other species. It has the following combination of characters: ♀: The clypeus is markedly convex, the most elevated point is located between the clypeal midlength and the basal third. The clypeal bevel is distinctly triangular, it reaches the base of the clypeus in the middle, and separates the basomedian area into two parts; when the base of the clypeus is punctate, the punctures are larger and the distances between them are distinctly larger than on the lateral side of the basomedian area. The clypeal lip is arcuate or straight, without the medial anterior emargination even in fresh specimens. The vertex setae are semierect medially and nearly erect and slightly shorter than the MOD close to inner eye margin. The head is transversally oval in front view, with irregularly punctate frons.

The gena is robust. The dorsolateral cuticular projection of the propodeal spiracle is slightly arcuate to nearly straight, with the apex reddish transparent. The posteromedial margin of the propodeal dorsum is elevated and produced between the marginal ridges, the marginal ridges directed ventromedially toward the groove on the posterior surface. The propodeal side is longitudinally ridged; ridges anteriorly inconspicuous or absent. The propodeal dorsum often has inconspicuous, irregular longitudinal ridges. The punctures of the mesopleuron are exceptionally variable but usually small and inconspicuous. The terga are sparsely punctate, the punctures are ill defined. Apical depressions of tergum V densely microsculptured with micropunctures, densely punctate latereally. The pygidium is of usual size and distinctly microsculptured in most specimens. ♂: The clypeus is convex, conspicuously elevated in the basal half, continuously declining apically, the top at the clypeal midlength or in the basal half of the clypeus. The clypeal bevel is well developed, shiny. The gena is robust. The supraclypeal area is flat, the supraantennal tubercles are connected, slightly elevated ventromedially. The mesopleuron is distinctly punctate laterally and ventrally, the punctures are ill defined. When the interspaces between the punctures are distinct, then they are microsculptured, slightly shiny to dull. The forefemoral notch is relatively shallow, as long as the distance that separates it from the forefemoral base, central part slightly elevated and lined by a ledge on the anterior as well as the posterior margin. The propodeal side is variable but without basal ridges in most specimens. The posteromedial margin of the propodeal dorsum is elevated and produced between marginal ridges, which are directed ventromedially toward the groove on the posterior surface. The terga are sparsely micropunctate with variable interspaces between punctures.

Description of male. Body length: 5.0–8.0 mm.

Head. Mandibular inner margin with one rectangular tooth and distinct furrow next to tooth distally. Labrum flat. Clypeus convex, conspicuously elevated in basal half and continuously declining apically, top at clypeal midlength or in basal half of clypeus; basomedian area large, densely punctate, sparsely punctate medially in some specimens; bevel slightly convex to nearly flat, variable in size, shiny with several larger punctures; lip slightly arcuate, short, with small lateral incisions, lip separated from bevel by variable fine groove; WML:LCL = 1.3–1.5, WCL:WML = 2.2–2.3. Supraclypeal area flat, distinctly punctate, interspaces between punctures shiny to dull. Supraantennal tubercle small, slightly elevated on inner side. Antenna relatively short, LA3:WA3 = 1.5–1.6, LA5:WA5 = 1.9–2.1. Frons uniformly punctate, punctures well defined, less than one diameter apart, interspaces variable in size; frontal median line distinct, narrow, finely impressed. Vertex punctate, punctures well defined, less than half to one diameter apart, interspaces slightly microsculptured, shiny to slightly shiny. Vertex setae short, semierect medially, but nearly erect close to inner eye margin, less than 1 × MOD, postocellar impression distinct, shallow, open widely, V to Y-shaped; vertex moderately wider than long; WV:LV = 1.5-1.6. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, most punctures less than one diameter apart, interspaces distinct, unsculptured, shiny, setae about 1.0 × MOD. Mesopleuron

coarsely microsculptured, with or without distinct punctures; hypoepimeral area irregularly microsculptured, impunctate; ventral part of mesopleuron with punctures ill defined, but deep in some specimens, less than one diameter apart, interspaces shiny. Propodeal dorsum relatively finely, irregularly rugose, with irregular longitudinal ridges basally in some specimens; propodeal side irregularly longitudinally ridged, ridges variable, usually faint, or absent basally, microsculptured, dull; posteromedial margin of propodeal dorsum elevated and produced between marginal ridges, marginal ridges directed ventromedially toward groove on posterior surface. Legs densely punctate, punctures small; forefemoral notch relatively shallow, as long as distance that separates it from forefemoral base to proximal margin of notch, central part slightly elevated and lined by ledge on anterior as well as posterior margin, surface without distinct setae, microsculptured, dull. Wings slightly infumate with brown veins.

Metasoma. Terga I-III with silvery apical faciae. Apical depressions of all terga shallow, micropunctate. Terga I-III sparsely, finely micropunctate, punctures evanescent in microsculpture, slightly shiny; sculpture of tergum IV-VII coarser, than on previous terga, also punctation slightly denser. Sterna uniformly punctate nearly like terga. Volsella light brown, ventral setae pointing in various directions; dorsal process slightly wider than corpus in most specimens.

Coloration. Apical part of mandibles, tarsi, forefemoral notch, tegulae, terga and sterna I, II, and partly or all tergum III red. Apical parts of all terga and tegula translucent. Remaining body parts all black. Forefemoral notch very rarely black in specimens from high altitude mountains.

Description of female (neotype). Body length: 7.4 mm.

Head. Clypeus distinctly convex, top at clypeal midlength; basomedian area relatively large, densely punctate as lateral section; bevel large, distinctly convex, triangular, with sparse, large punctures, reaching base of clypeus, shiny; lip slightly arcuate, with lateral incisions, separate from bevel by punctate groove, WML:LCL = 1.7, WCL:WML = 1.8. Supraclypeal area flat, distinctly punctate, but shape of punctures ill defined, interspaces between punctures shiny to slightly shiny. Supraantennal tubercle small, slightly elevated on inner side. Frons uniformly punctate, punctures well defined, less than one diameter apart, interspaces variable in size; frontal median line distinct, narrow, well impressed. Vertex punctate, punctures well defined, less than half to one diameter apart, interspaces unsculptured, shiny. Vertex setae short, semierect medially, nearly erect close to inner eye margin, distinctly shorter than 1 × MOD; postocellar impression distinct, shallow, open, widely Y-shaped; vertex moderately wider than long; WV:LV = 1.5. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, half to one diameter apart, interspaces slightly microsculptured, shiny, setae about 1.0 × MOD. Mesopleuron coarsely microsculptured, without distinct punctures; hypoepimeral area irregularly microsculptured, impunctate; ventral part of mesopleuron with punctures ill defined, less than one diameter apart, interspaces shiny. Propodeal dorsum relatively finely, irregularly rugose, with few incomplete irregular, longitudinal ridges; propodeal side irregularly

and incompletely longitudinally ridged, ridges absent basally, microsculptured, dull; posteromedial margin of propodeal dorsum elevated and slightly produced between marginal ridges which are directed ventromedially toward groove on posterior surface. Legs densely punctate, punctures small; forebasitarsal rake reddish, with three apical spines, one preapical spine, and two additional spines. Wings slightly infumate with brown veins.

Metasoma. Terga I-III with silvery apical fasciae. Apical depressions of all terga shallow, with micropunctures evanescent in microsculpture. Terga I-III sparsely and finely micropunctate, punctures ill defined, interspaces microsculptured, shiny to slightly shiny; sculpture of tergum IV-V slightly coarser than on previous terga, also slightly more densely punctate. Pygidium sparsely punctate, punctures ill defined, interspaces microsculptured, slightly shiny. Central part of sternum II with several larger punctures, interspaces microsculptured, shiny; lateral part slightly shiny, densely micropunctate; remaining sterna with uniform sculpture similar to that on sternum II, but sculpture more or less reduced laterally.

Coloration. Central part of mandibles, three distal tarsomeres, terga and sterna I-III red. Tegulae brown translucent. Apical parts of terga I-III slightly translucent. Remaining body parts all black.

Variation of females. Extremely variable in most of characters. The clypeus is typically conspicuously elevated basally, with the top in the basal third; the bevel can be well separated from the clypeal base in some specimens, althouth infrequently. Vertex wider than long in large specimen and slightly wider than long in small specimens, WV:LV = 1.2–1.5. Antenna short, LA3:WA3 = 2.2–2.4, LA5:WA5 = 2.6–2.7.

Geographic distribution. Austria, Czech Republic, Bulgaria, France, Germany, Italy, Sweden and Switzerland. Specimens from mountains of Greece, Morocco and Spain probably also belong to this species.

Tachysphex ferrugineus Pulawski, 1967

Figs 96, 105

Type material. Holotypus: ♂, Turkey: Trabzon: Boztepe, 18.v.1962, K. M. Guichard and D. H. Harvey leg. Holotype in BMNH, examined in 2003.

Additional material examined. Georgia: Sairme, Caucasus, 1 ♀, 20. vii. 1983, Kadlec & Voříšek lgt., PTLC; **Russia**: Teberda, Karachay-Cherkessia, 1 ♀, 9. vi. 1978, W. J. Pulawski lgt., ZIN; **Turkey**: Trabzon: same data as holotype, 3 ♂♂, 1 ♀; Damar env., Artvin prov., 1 ♂, 1 ♀, 2. vii. 1997, P. Průdek & M. Říha lgt., JSPC; Samsun University campus, Samsun prov., 2 ♂♂, 4. vii. 2014, J. Barták & Kubík lgt., JSPC.

Diagnosis. *Tachysphex ferrugineus* Pulawski is easily recognizable by the body coloration, but in morphological characters and body sculpture it resembles *T. dimidiatus* (Panzer), *T. jokischianus* (Panzer), *T. pompiliformis* (Panzer) and *T. punctipleuris* sp. n. The species is similar to *T. stysi* Straka from central Asia in coloration, but *T. stysi* belongs to the *T. austriacus* species subgroup. *Tachysphex ferrugineus* Pulawski is largely

light red colored. All tibiae, tarsi and nearly all metasoma, except basal part of terga IV-VI in males and IV-V in females, are light red. The species is similar to *T. dimidiatus* in body morphology and sculpture but differs in the following characters: ♀: Supraantennal tubercle distinctly elevated, but supraclypeal area nearly flat. Gena inconspicuously developed but not short. Pygidium densely punctate, all coarsely microsculptured, dull. ♂: Gena dorsally inconspicuous. Vertex finely and densely punctate, and postocellar impression shallow. Forefemoral notch large, usually longer than the space that separates it from forefemoral base.

Geographic distribution. Georgia, Russia (Caucasus) and Turkey.

Note. Full description of the species is presented by Pulawski (1971).

***Tachysphex jokischianus* (Panzer, 1809), restored from synonymy**
Figs 5, 17, 23, 31, 39, 45, 51, 57, 61, 65, 72, 84, 88, 97

Larra Jokischiana Panzer, 1809 (Heft 106: pl. 15), ♀.

Type material. Holotype: ♀, no specific locality at the label but probably from Germany. Holotype by monotypy. "Coll. Sturm [printed] // Ca. // Larra / Jokischi / ana / Panz. [handwriting, card with black frame] // 54 [printed, red card] // Larra / Jokischiana / Panz. Typus / J. de Beaumont / det. 1955 [handwriting on pre-printed card with name of determinator and year] // Tachysphex ♀ / pompiliformis Pz. / J. de Beaumont / det. 1955 [handwriting on pre-printed card with name of determinator and year] // Typus Nr. / Zoologische / Staatsamlung / München. [printed, red card]". Holotype in ZSM, examined.

Additional material examined. Austria: Seefeld NW, Niederösterreich, 1 ♂, 19. v. 2015, M. Halada lgt., OLML; **Czech Republic**: Boh. bor., Počerady, ash coal deposit from power station, 1 ♂, 23. v. 2010, 1 ♂, 7. vi. 2010, 1 ♂, 1 ♀, 27. vi. 2010, 1 ♂, 1 ♀, 1. viii. 2010, R. Tropek lgt., JSPC; Boh. centr., Cihelna v Bažantnici, Praha-Hloubětín, 14 ♂♂, 1 ♀, 28. v. 1998, 6♂♂, 1 ♀, 22. vi. 1998, J. Straka lgt., JSPC; Černošice, 1 ♂, 30. v. 1968, Z. Pádr lgt., OLML; Divoká Šárka, Praha-Liboc, 1 ♂, 29. v. 1998, J. Straka lgt., JSPC; Heřmanův Městec, sandpit, 2 ♂♂, 1 ♀, 1. vii. 2012, 1 ♀, 1. viii. 2012, R. Tropek lgt., JSPC; Hrachovka, Praha-Troja, 1 ♀, 28. vi. 1998, J. Straka lgt., JSPC; Chvaletice, ash coal deposit, 1 ♂, 1. viii. 2012, R. Tropek lgt., JSPC; Chvalská navážka, Praha-H. Počernice, 1 ♂, 9. vii. 1997, 1 ♀, 22. viii. 1997, 2 ♂♂, 1 ♀, 6. vii. 1998, 1 ♀, 20. viii. 1998, J. Straka lgt., JSPC; Chvalský lom, Praha-H. Počernice, 1 ♀, 6. vii. 1998, J. Straka lgt., JSPC; Jenštejn, 4 ♂♂, 22. vi. 2001, Jos. Straka lgt., JSPC; Klánovický les, Praha-Klánovice, 1 ♂, 20. vi. 1998, J. Straka lgt., JSPC; Opatovice, ash coal deposit, 1 ♀, 1. vi. 2014, R. Tropek lgt., JSPC; Písečný vršek, Praha-Běchovice, 1 ♀, 2. vii. 1997, 5 ♂♂, 1 ♀, 6. vii. 1998, M. Kolísko & J. Straka lgt., JSPC; Písty, Nymburk env., sand dune, 1 ♀, 1. vii. 2012, 1 ♀, 1. viii. 2012, R. Tropek lgt., JSPC; Travčický les, Terezín env., 1 ♂, 6. viii. 1981, Z. Pádr lgt., OLML; Valy, 1 ♂, 7. viii. 1988, Odehnal lgt., OLML; Boh. mer., Blatná, sand

quarry, 1 ♂, 1998, P. Bogusch lgt., JSPC; Cep 1, sand quarry, 1 ♂, 4.-9. vi. 2013, 1 ♀, 1.-5. vii. 2013, R. Tropek, I. Černá, O. Čížek lgt., JSPC; Františkov, Chlum u Třeboně, 1 ♂, 29. vii. 2002, J. Halada lgt., JSPC; Hodějovice, 5 ♂♂, 1 ♀, 3. vi. 2015, 1 ♀, 2. viii. 2013, R. Tropek, I. Černá, O. Čížek lgt., JSPC; Plavsko, 1 ♂, 5. vii. 2013, R. Tropek, I. Černá, O. Čížek lgt., JSPC; Těšínov, 1 ♀, 2. viii. 2013, R. Tropek, I. Černá, O. Čížek lgt., JSPC; Slepičí vršek, Třeboňsko PLA, 1 ♂, 2 ♀♀, 6. viii. 1997, J. Straka lgt., JSPC; Vlkov, Třeboňsko PLA, 1 ♂, 6. viii. 1997, J. Straka lgt., 1 ♂, 1 ♀, 9. vi. 2013, R. Tropek, I. Černá, O. Čížek lgt., JSPC; Boh.occ., Starý lom, ash coal deposit from Prunéřov power station, 1 ♀, 26. vi. 2010, 1 ♀, 31. vii. 2010, R. Tropek lgt., JSPC; Tušimice, ash coal deposit from power station, 1 ♂, 6. vi. 2010, 2 ♂♂, 2 ♀♀, 26. vi. 2010, 1 ♀, 22. viii. 2010, R. Tropek lgt., JSPC; Boh. or., Plachta NR, Hradec Králové, 2 ♂♂, 1. vii. 1998, J. Straka lgt., JSPC; Veská, Pardubice env., sand dune, 1 ♂, 20. v. 2007, 1 ♀, 27. v. 2007, P. Bogusch lgt., 1 ♀, 1. viii. 2012, 3 ♂♂, 1 ♀, 1. vii. 2012, R. Tropek lgt., JSPC; Mor.mer., Bzenec env., 1 ♂, 18. vi. 1942, A. Hoffer lgt., 1 ♀, viii. 1963, M. Kocourek lgt., OLML; Bzenec env., Vojenské cvičiště NR, 1 ♀, 8. vi. 1997, M. Kolísko lgt., 1 ♀, 4. viii. 2015, J. Straka lgt., JSPC; Bzenec-přívoz, Bzenec env., 4 ♂♂, 31. v. 2002; J. Straka lgt., JSPC; Čučice 1 km S, 2 ♂♂, 1.-15.vii.2001, M. Říha lgt., MRBC; Dolní Bojanovice, 1 ♂, viii. 1941, A. Hoffer, OLML; Mistřín, 1 ♂, viii. 1942, A. Hoffer lgt., OLML; Pouzdřany, 1 ♂, 19. vi. 1970, J. Strejček lgt., OLML; Rohatec lgt., 1 ♂, vii. 1941, 2 ♀♀, vii. 1942; A. Hoffer, OLML; **France**: Falaise, 1 ♂,date and collector unknown, ZSM; Plateau du Coiron, 16 km NW Montélimar, 2 ♂♂, 24. vi. 2001, 2 ♂♂, 1 ♀, 11.-14 vii. 2002, 2 ♂♂, 1 ♀, 20. vi. 2004, J. v. d. Smissen lgt., USMB; Lachamp - Raphael W, D 122, 23 km NW Aubenas, 1 ♂, 2 ♀♀, 18. vi. 2004, 1 ♀, 29. vii. 2003, J. v. d. Smissen lgt., USMB; Cereste, Apt., Provence prov., 1 ♀, 9. ix. 1987, Ch. Schmid-Egger lgt., CSE; **Germany**: Allersberg, 1 ♂, 17. viii. 1956, Ettinger lgt., ZSM; Blankenförde, Mecklenburg-Vorpommern, mn-hex, 2 ♀, 7. vii. 2013, Ch. Schmid-Egger lgt., ZSM HYM 19879, ZSM HYM 19880; Blankensee, Lübeck, Schleswig-Holstein, 1 ♀, 18. vi. 1989, J. v. d. Smissen lgt., USMB; Brammerau, Nortorf, Schleswig-Holstein, 1 ♂, 1 ♀, 22. vii. 1995, J. v. d. Smissen lgt., USMB; Brünkendorf/Dannenberg, Niedersachsen, 3 ♂♂, 2. viii. 1995, J. v. d. Smissen lgt., USMB; Büchen, Schleswig-Holstein, 10 ♂♂, 10. vii. 1994, J. v. d. Smissen lgt., USMB; Damsdorf, Bornhöved 6km E, Schleswig-Holstein, 1 ♂, 18. vii. 1999, J. v. d. Smissen lgt., USMB; Eichholz, Lübeck, Schleswig-Holstein, 1 ♀, 25. vii. 1989, J. v. d. Smissen lgt., USMB; Friedrichsfeld, Mannheim, Baden-Württenberg, 1 ♂, 22. v. 1989, Ch. Schmid-Egger lgt., CSE; Friedrichsort, Kiel, Lehmgrube, 1 ♀, 1. vii. 1961, collector unknown, ZSM; Gabow, Bad Freienwalde 4km NE, gab, 1 ♀, 25. vi. 2001, Ch. Schmid-Egger lgt., CSE; Gemünda, Sesslach, Bayern, 2 ♂♂, 9. vii. 1994, J. v. d. Smissen lgt., USMB; Grissheim, Baden-Württemberg, gr, 1 ♂, 18. vii. 2012, Ch. Schmid-Egger, ZSM HYM 17628; Grissheim, Rhein, Freiburg 24 km SW, Baden-Württemberg, 1 ♀, 1. vii. 1999, J. v. d. Smissen lgt., USMB; Gudow, Schleswig-Holstein, 1 ♀, 1. ix. 1991, J. v. d. Smissen lgt., USMB; Ingolstadt, 1 ♀, 21. vii. 1948, H. Freude lgt., ZSM; Istein, Baden-Württenberg, 1 ♂, 26. vii. 1989, Ch. Schmid-Egger lgt., CSE; Klein Kühren/Dannenberg,

Niedersachsen, 1 ♂, 15. vi. 1996, 1 ♀, 10. viii. 1996, J. v. d. Smissen lgt., USMB; Laasche/Dannenberg, Niedersachsen, 3 ♂♂, 5 ♀♀, 19. vii. 1994, 12 ♂♂, 23. viii. 1994, J. v. d. Smissen lgt., USMB; Lenggries, Isarauen, 1 ♀, 27. vii. 2003, Ch. Schmid-Egger lgt., ZSM; Malk Göhren, Mecklenburg-Vorpommern, 2 ♂♂, 22. vii. 1997, J. v. d. Smissen lgt., USMB; Mallnow, Framkfurt an der Oder 13km NNW, Brandenburg, br-ma, 1 ♀, 22. vii. 2009, ZSM HYM 14826, 1 ♀, 26. vi. 2010, Ch. Schmid-Egger lgt., ZSM HYM 14825; Malsch, 1 ♀, 25. vi. 1967, R. Degen lgt., ZSM; Oldenburg 5km NW, Schleswig-Holstein, 1 ♀, 26. vii. 1997, 2 ♀♀, 4. viii. 1997, J. v. d. Smissen lgt., USMB; Putlos, Oldenburg, Schleswig-Holstein, 1 ♀, 29. vi. 1997, 1 ♀, 4. viii. 1997, J. v. d. Smissen lgt., USMB; Sandhausen, Heidelberg, Baden-Württenberg, 1 ♂, 20. v. 1989, Ch. Schmid-Egger lgt., CSE; Spreenhagen 4km W, Brandenburg, brsp, 1 ♂, 27. vi. 2011, Ch. Schmid-Egger lgt., ZSM HYM 14827; Steinenstadt, Baden-Württemberg, 1 ♂, 31. vii. 2005, W. Schlaefle lgt., WSKC; Zossen, Brandenburg, zos, 1 ♀, 14. vi. 2011, Ch. Schmid-Egger lgt., ZSM HYM 09867; **Hungary**: Dunatetétlen, saline lake, Kecskemét 45km SEE, 1 ♂, 17. vii. 2013, J. Habermannová, J. Straka lgt., JSPC; Hegyshalom N, 1 ♂, 1 ♀, 6. vi. 2015, M. Halada lgt., OLML; Kecskemét env., 1 ♂, 16. vii. 2006, J. Halada lgt., JSPC; Kesthely env., lime stone, 1 ♂, 1 ♀, 23. v. 2014, A. Astapenková, J. Habermannová, J. Straka lgt., JSPC; Kunpeszér env., sandy hill, 1 ♀, 7. vi. 2013, D. Benda, P. Bogusch & J. Straka lgt., JSPC; Kunszentmiklós env., salt marsh, 3 ♀♀, 16. vii. 2013, J. Habermannová, J. Straka lgt., JSPC; Örkeny, puszta, 5 ♂♂, 7. vi. 2015, 1 ♀, 27. vi. 2015, M. Halada lgt., OLML; Pákozd env., pasture stepe, 4 ♂♂, 18. vii. 2013, J. Habermannová, J. Straka lgt., JSPC, 6 ♂♂, 5 ♀♀, 10. vi. 2015, 7 ♂♂, 11 ♀♀, 25. vi. 2015M. Halada lgt., OLML, 1 ♂, 9. vi. 2013, D. Benda, P. Bogusch & J. Straka lgt., JSPC; Pusztavacs, sand dune, 1 ♂, 8. vi. 2015, M. Halada lgt., OLML; Súr 1km S, loes steppe, 1 ♀, 18. vii. 2013, J. Habermannová, J. Straka lgt., JSPC; Szenna, Kaposvár env., 1 ♀, 3. ix. 2007, W. Żyła, USMB; Velencei-tó env., steppe, 1 ♀, 9. vi. 2013, D. Benda, P. Bogusch & J. Straka lgt., JSPC; **Poland**: Białowieża forest, 1 ♂, 19. vii. 1995, R. Dobosz lgt., USMB; Borne Sulinowo, Baltic see coast, 1 ♂, 8. vii. 1997, Kaka lgt., USMB; Grabowiec, Małopolska Upland, 1 ♀, 18. vi. 1995, 2 ♂♂, 4 ♀♀, 12. vii. 1996, W. Żyła, USMB; Jastrzębia Góra, Władysławowo, Baltic see coast, 1 ♂, 16. vi. 1996, 1 ♀, 24. vi. 1996, R. Dobosz lgt., USMB; Kików, Malopolska Upland, 4 ♂♂, 2 ♀♀, 19. vi. 1995, 1 ♀, 14. vii. 1996, W. Żyła lgt., USMB; Kołczewo, Baltic see coast, 1 ♀, 10. vii. 2009, R. Dobosz lgt., USMB; Krzyżanowice, Malopolska Upland, 4 ♂♂, 16. vi. 1995, 1 ♂, 21. vi. 1995, W. Żyła lgt., 1 ♀, 30. vii. 1996, R. Dobosz lgt., USMB; Kuźnica, Baltic see coast, 1 ♂, 1 ♀, 25. vi. 1996, R. Dobosz lgt., USMB; Lubliniec, Upper Silesia, 1 ♂, 12. vi. 1994, R. Dobosz lgt., USMB; Osowo Stare, 1 ♂, 2 ♀♀, 12. viii. 1992, 1 ♂, 28. v. 1993, M. Bunalski lgt., USMB; Pasturka, Pińczów env., Małopolska Upland, 2 ♂♂, 19. vi. 1997, R. Dobosz, W. Żyła lgt., USMB; Ponice, Rabki, Beskid Zachodni, 1 ♀, 17. vii. 1997, W. Żyła lgt., USMB; Przedbórz, Małopolska Upland, 1 ♀, 2. viii. 2007, W. Żyła lgt., USMB; Smołdziński Las, Słowiński NP, 1 ♂, 29. vii. 2004, W. Żyła lgt., USMB; Sycyn Dolny, 2 ♂♂, 2 ♀♀, 22. vi. 1992, 1 ♂, 2 ♀♀, 28. vii. 1992, 1 ♀, 12. viii. 1992, M. Bunalski lgt.,

USMB; Szombierki, Bytom, 1 ♀, 29. v. 1993, W. Żyła lgt., USMB; Wisła, 1 ♀, 1. viii. 1994, 1 ♂, 8. viii. 1994, W. Żyła lgt., USMB; Władysławowo, 2 ♂♂, 2 ♀♀, 11. vi. 1993, 2 ♂♂, 1 ♀, 13. vi. 1993, 1 ♂,18. vi. 1993, R. Dobosz lgt., USMB; **Slovakia**: Abrod NR, Velké Leváre env., 1 ♀, 6. vii. 2008, J. Straka, P. Janšta, P. Šípek, D. Král lgt., JSPC; Chotín, 2 ♂♂, 3. viii. 1961, 1 ♂, 9. viii. 1961, 1 ♂, 12. vii. 1981, Z. Pádr lgt., 1 ♂, 15. vi. 1977, M. Kocourek lgt., 1 ♀, 26. vii. 1993, M. Halada lgt., OLML; Královský Chlmec, 3 ♂♂, 1 ♀, 25. vii. 1969, Z. Pádr lgt., OLML; Kúty 1 ♂, 9. vi. 1973, J. Strejček lgt., OLML; Lakšárska Nová Ves env., sandy area, 2 ♂♂, 13. vi. 2008, J. Straka lgt., JSPC; Somotor, 2 ♂♂, vii. 1959, M. Kocourek, OLML; Streda nad Bodrogom, 1 ♂, 26. vi. 1977, Z. Pádr lgt., OLML; Štúrovo, 1 ♀, vii. 1957, M. Kocourek lgt., 1 ♂, 24. vi. 1960, 1 ♂, 8. vi. 1964, Z. Pádr lgt., OLML; Velký Kamenec, 1 ♀, 14. vii. 1975, Z. Pádr lgt., OLML; **Sweden**: Dammersryet, Ravlunda, 1 ♂, 9. vii. 2011, N. E. Johansson lgt., NJHC; Gårdby, Öland isl., 1 ♀, 27. vii. 1998, collector unknown, USMB; Havängsdösen, Ravlunda, 1 ♂, 27. vi. 2011, N. E. Johansson lgt., NJHC; Lillesjö, Mörlunda env., 1 ♀, 27. vi. 2009, N. E. Johansson lgt., NJHC; Sandhajd, Fårö env., 2 ♂♂, 1 ♀, 10. vii. 2012, 1 ♀, 12. vii. 2012, N. E. Johansson lgt., NJHC; Sandviken, Gannelgarn env., 1 ♀, 9. vii. 2012, N. E. Johansson lgt., NJHC

Diagnosis. *Tachysphex jokischianus* (Panzer) is difficult to distinguish from *T. dimidiatus* (Panzer), *T. pompiliformis* (Panzer) and *T. punctipleuris* sp. n. It is exceptionally variable in most characters, and no single character differentiates it from the other morphologically similar species. It can be recognized by the following combination of characters: supraclypeal area with distinctly microsculptured interspaces between punctures, usually appearing dull. Gena dorsally robustly built. Mesopleuron, including hypoepimeral area, finely sculptured, punctures in lower parts of mesopleuron distinct but small. Propodeal dorsum usually lacking longitudinal ridges, if present, then only basally. Dorsolateral cuticular projection of propodeal spiracle arcuate to semicircular, with dark apex. Posteromedial margin of propodeal dorsum elevated but not produced between the marginal ridges, marginal ridges positioned nearly horizontally above groove on posterior side. Wings only slightly infumated to pale. ♀: Apical depression of terga IV and V finely microsculptured and impunctate or nearly so, contrasting with coarsely and densely punctate central part of these terga, punctures of terga IV and V well developed. Pygidium often wide, with convex, shiny surface (but not always). Tergum III all red or red laterally and basally, with black area apicomedially. ♂: Surface of supraclypeal area concave, supraantennal tubercle distinctly elevated ventromedially. Forefemoral notch light red, large, its longitudinal diameter usually longer than the space separating it from forefemoral base. Propodeal side densely and finely ridged basally in most specimens. Terga densely micropunctate.

Description of female (holotype). Body length: 7.2 mm.

Head. Clypeus distinctly convex, its top at clypeal midlength; basomedian area relatively large, as densely punctate as lateral section; bevel large, distinctly convex, as long as basomedian area laterally, slightly longer medially, obtusely triangular, with sparse large punctures, not reaching base of clypeus, shiny; lip slightly arcuate, with lateral in-

cision, separated from bevel by punctate groove, WML:LCL = 1.5, WCL:WML = 1.8. Supraclypeal area flat, distinctly punctate, punctures ill-defined, interspaces microsculptured, slightly shiny. Supraantennal tubercle small, slightly elevated on inner side. Both antennae broken off (only three segments present). Frons uniformly punctate, punctures well defined, about half diameter apart or less, most interspaces uniform in size; frontal median line distinct, narrow, finely impressed. Vertex finely punctate, punctures well defined, less than half to one diameter apart, laterally more sparsely punctate than medially, interspaces finely microsculptured, slightly shiny. Vertex setae short, semierect, slightly longer laterally than medially, about 0.5 × MOD; postocellar impression well developed, widely Y-shaped; vertex moderately wider than long; WV:LV = 1.5. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, less than half to one diameter apart, interspaces well developed, variable in size, microsculptured, slightly shiny, setae about 1.0 × MOD or less. Mesopleuron coarsely microsculptured, without distinct punctures; hypoepimeral area irregularly microsculptured without punctures; ventral part of mesopleuron with punctures ill defined, less than one diameter apart, interspaces small, slightly shiny. Propodeal dorsum relatively finely, regularly rugose, with few indistinct irregular, longitudinal ridges basally, dull, but slightly shiny posteromedially; propodeal side regularly longitudinally ridged, ridges inconspicuous basally, interspaces microsculptured, slightly shiny; posteromedial margin of propodeal dorsum elevated, but not produced between posterior marginal ridges, marginal ridges positioned nearly horizontally above groove on posterior surface. Legs densely punctate, punctures small; forebasitarsal rake light yellow with reddish opalescence at distal half, with three apical spines and two to three additional spines. Wings slightly infumate with brown veins.

Metasoma. Terga I-III with ill defined silvery apical fasciae. Terga I-III densely, finely micropunctate, punctures ill defined, interspaces microsculptured, slightly shiny; apical depressions shallow, with distinct micropunctures; sculpture of terga IV-V distinctly coarser than on previous terga, also slightly more densely punctate; tergum V coarsely punctate, punctures ill-defined, but large, half to one diameter apart, interspaces microsculptured, apical depression of tergum V very sparsely and finely punctate. Pygidium large, sparsely punctate, punctures large, ill defined, interspaces nearly unsculptured, shiny. Central part of sternum II with several larger punctures, interspaces microsculptured, shiny; lateral part slightly shiny, densely micropunctate; remaining sterna with uniform sculpture similar to that on sternum II, but more or less reduced laterally.

Coloration. Central part of mandibles, terga and sterna I-III red. Distal tarsomeres dark red. Tegulae reddish translucent. Apical parts of terga I-III slightly translucent. Remaining body parts black.

Variation of females. Very variable in sculpture, but finely sculptured over all body in most specimens except apical terga (in comparison to other species). Clypeal bevel reaching base of clypeus in some specimens, but well separated from the base in most.

Antenna short, LA3:WA3 = 2.2–2.4, LA5:WA5 = 2.6–2.7. Pygidium distinctly microsculptured, of usual width and dull in some specimens, but shiny and wide in most of specimens. Some specimens appear dark in coloration, with only terga I and II dark red and nearly all sternum II black. The most characteristic coloration of metasoma is as follows: segments I and II red, tergum III red basally and laterally, with larger or smaller black area apicomedially and sternum III basally red and apically dark.

Description of male. Body length: 5.6–8.7 mm.

Head. Mandibular inner margin with one distinct rectangular tooth and distinct furrow next to tooth distally. Clypeus slightly convex, uniformly curved, or more steeply declining ventrally than dorsally, top about in clypeal midlength; basomedian area very large, about two thirds of bevel or more, densely punctate; bevel small, slightly convex, shiny with several larger punctures; lip conspicuously arcuate or slightly sinuate, with small or large lateral corner, lip separated from bevel by distinct groove with large punctures; WML:LCL = 1.2–1.5, WCL:WML = 2.2–2.4. Supraclypeal area groove-like, concave, supraantennal tubercle distinctly elevated ventromedially; surface sparsely punctate, punctures ill defined, interspaces densely microsculptured, slightly shiny to dull. Antenna relatively short, LA3:WA3 = 1.5–1.6, LA5:WA5 = 1.9–2.1. Frons finely punctate, punctures well defined, one to less than half diameter apart, interspaces variable in size; frontal median line distinct, narrow, finely impressed. Vertex punctate, punctures well defined, less than one diameter apart, interspaces microsculptured, slightly shiny. Vertex setae short, semierect, less than 1 × MOD; postocellar impression well developed, open, widely Y-shaped; vertex wider than long; WV:LV = 1.4–1.5. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, most punctures less than half diameter apart, interspaces distinct, microsculptured, slightly shiny to dull, setae about 1.0 × MOD or less. Mesopleuron coarsely microsculptured with distinct or indistinct punctures in lower areas, most punctures ill defined, interspaces dull; hypoepimeral area coarsely microsculptured to finely rugose, dull; ventral part of mesopleuron with small, ill defined punctures, interspaces slightly shiny. Propodeal dorsum variably sculptured, irregularly ridged, areolate, or coarsely irregularly rugose, without distinct longitudinal ridges, short longitudinal ridges developed basally; propodeal side distinctly ridged, more densely and finely ridged basally than in the center in most specimens; posteromedial margin of propodeal dorsum elevated, but not produced between marginal ridges, marginal ridges positioned nearly horizontally above groove on posterior side. Legs densely punctate, punctures small; forefemoral notch light red and large, its diameter usually longer than space that separates it from forefemoral base, central part of notch slightly elevated, anterior and posterior margins lined by small distinct ledge, notch surface without distinct setae, microsculptured, dull. Wings slightly infumate, veins brown.

Metasoma. Terga I-III with silvery, apical fasciae. Apical depressions of all terga distinct, with micropunctures similar as on central part of terga. Terga I-III densely and distinctly micropunctate, punctures ill defined, interspaces microsculptured, slightly

shiny; sculpture of terga IV-VII slightly coarser and slightly more densely punctate than other terga. Sterna uniformly punctate nearly like terga.

Coloration. Apical part of mandibles, terga and sterna I and II and forefemoral notch red. Metasoma very variable in coloration; some specimens with only tergum I dark red, or terga I and II and sternum II basally red, or terga and sterna I-III equally red. Distal tarsomeres dark reddish. Tegulae brown to reddish. Apical parts of all terga and tegulae translucent. Remaining body parts black.

Geographic distribution. Austria, France, Germany, Hungary, Poland, Slovakia and Sweden.

Tachysphex nigripennis (Spinola, 1808), restored from synonymy

Figs 6, 18, 32, 46, 66, 89, 98, 103

= *Tachytes nigripennis* Spinola, 1808 (p. 260), ♀. Holotype or syntypes: Italy: "prope Genuam". Type material lost (de Beaumont 1952, 44).

Type material. Neotypus: ♀, Czech Republic: "CZ, Mor.mer. 30.vii.2008 / sandpit Bzenec-Přívoz I. / Bzenec env.; EtOH 96% [in bold] / Jakub Straka lgt. // ♀ *Tachysphex* / *nigripennis* / Spinola / Jakub Straka det. 2014 // ZSM / HYM 23693". Neotype in ZSM, present designation.

Additional material examined. Czech Republic: Boh. bor., Počerady, ash coal deposit from power station, 1 ♀, 27. vi. 2010, 1 ♀, 1. viii. 2010, R. Tropek lgt., JSPC; Střimická waste dump, Most env., 1 ♀, 30. vii. 2004, P. Tyrner lgt., JSPC; Boh. occ., Starý lom, ash coal deposit from Prunéřov power station, 1 ♂, 26. vi. 2010, R. Tropek lgt., JSPC; Mor. mer., Bratčice env., 1 ♂, 2 ♀♀, 21. vi. 2012, M. Halada lgt., JSPC; Bzenec-Přívoz, Bzenec env., sandpit, 1 ♀, 28. vi. 2012, M. Halada lgt., JSPC; **France**: Collias, W Pont du Gard, 16 km NE Nîmes, 1 ♀, 31. vii. 2003, J. v. d. Smissen lgt., USMB; Dieulefit (D547), 25 km E Montélimar, 1 ♂, 23. v. 2000, J. v. d. Smissen lgt., USMB; Prades 38km SW, Pyrénées Orient., 1 ♂, 22. vii. 2011, J. Halada lgt., JSPC; **Germany**: Speyer, sandy dune, Rhineland-Palatinate prov., 1 ♀, 26. vi. 2008, Reder lgt. et coll.; **Hungary**: Pusztavacs, sand dune, 3 ♂♂, 8. vi. 2015, 1 ♂, 1 ♀, 26. vi. 2015, M. Halada lgt., JSPC, OLML; **Italy**: St. Pierre, Valle d'Aosta prov., 1 ♂, 1. viii. 1997, Ch. Schmid-Egger lgt., CSE; **Kyrgyzstan**: Kashkasu env., Ala-Archa, 1 ♀, vii. 2000, 3 ♂♂, 7 ♀♀, vii. 2002, V. Gurko lgt., OLML; Malinovka, Ala-Archa riv., 1 ♂, 1 ♀, vii. 2000, V. Gurko lgt., JSPC; Ooru-say env., Ala-Archa, 1 ♀, vii. 2000, 1 ♀, vii. 2002, V. Gurko lgt., OLML; **Poland**: Toruń-Glinki, 1 ♀, 5. vii. 2011, P. Olszewski lgt., JSPC; **Slovakia**: Chotín, 1 ♂, 15. vii. 1967, A. Strejčková lgt., OLML; **Turkey**: Erzurum E, Erzurum prov., 1 ♂, 6. vii. 2000, M. Halada lgt., OLML; Hakkari env., 1 ♀, 17. ix. 1983, Ch. Schmid-Egger lgt., CSE; Mt. Gilo, Hakkari prov., 1 ♂, 15. viii. 1972, Kaniss lgt., ZSM.

Diagnosis. *Tachysphex nigripennis* (Spinola) is easily recognizable from the other species of the *T. pompiliformis* and *T. austriacus* species subgroups. It is generally dark

and coarsely punctate, and thus resembles *T. opacus* Morawitz and *T. pompiliformis* (Panzer). *Tachysphex nigripennis* (Spinola) is relatively well characterized species. It possesses an inconspicuous gena. The vertex is distinctly wider than long. The metasoma is coarsely punctate with densely micropunctate apical depressions. The mesopleuron is coarsely sculptured, rugose, or coarsely punctate, and the hypoepimeral area has more or less distinct longitudinal ridges. The metasoma has terga I-II dark red and a black sternum II. In females, the basomedian area of the clypeus is sparsely punctate; the pygidium is exceptionaly narrow, bright shiny and with inconspicuous lateral marginal carina. In males, the mandibular inner margin possesses one distinct rectangular tooth and a distinct furrow next to the tooth distally; the clypeal lip is distinctly arcuate, longest medially; the forefemoral notch is dark red but black in some specimens, with a shiny, nearly unsculptured surface; the dorsal process of volsella is larger than in species from the *T. pompiliformis* species subgroup.

Description of female (neotype). Body length: 8.9 mm.

Head. Clypeus distinctly convex, top at clypeal midlength; basomedian area relatively large, as sparsely punctate as lateral section, punctures small, ill-defined, interspaces variable, one to less than half diameter apart, shiny; bevel large, distinctly convex, triangular, with sparse large punctures, not reaching base of clypeus, shiny; lip distinctly sinuate, long medially, with poorly developed lateral incision, lip separate from bevel by punctate groove, WML:LCL = 1.7, WCL:WML = 1.8. Supraclypeal area flat, finely, sparsely punctate, punctures ill-defined, interspaces microsculptured, slightly shiny. Supraantennal tubercle small, slightly elevated on inner side. Antenna relatively short, LA3:WA3 = 2.5, LA5:WA5 = 3.1. Frons uniformly punctate, punctures well defined, less than one diameter apart, interspaces variable in size, microsculptured, slightly shiny; frontal median line distinct, narrow, finely impressed. Vertex finely, densely punctate, punctures well defined, one to less than half diameter apart, interspaces variable in size, coarsely microsculptured, slightly shiny. Vertex setae short, semierect medially, but nearly erect close to inner eye margin, less than 1 × MOD, postocellar impression distinct, shallow, open widely Y-shaped; vertex distinctly wider than long; WV:LV = 1.6. Gena dorsally short, converging directly behind eyes.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, less than one diameter apart, interspaces variable in size, microsculptured, slightly shiny, setae about 1.0 × MOD or less. Mesopleuron rugose, posteriorly coarsely microsculptured, without distinct punctures; hypoepimeral area iregularly rugose with indistinct irregular longitudinal ridges, impunctate; ventral part of mesopleuron sparsely punctate, punctures ill defined, one diameter apart, slightly shiny. Propodeal dorsum relatively regularly rugose, without longitudinal ridges, dull; propodeal side irregularly longitudinally ridged, microsculptured, dull; posteromedial margin of propodeal dorsum elevated, slightly produced between marginal ridges, marginal ridges positioned nearly horizontally above groove on posterior side. Legs densely punctate, punctures small; forebasitarsal rake dark reddish, with two apical spines, one preapical spin and one or two additional spines. Wings distinctly infumate, light brown, with brown veins.

Metasoma. Terga I-III with distinct but sparse silvery, apical faciae. Terga I-III densely micropunctate, with very large, but superficial, sparse punctures, micropunctures ill-defined, evanescent in micosculpture, faint, interspaces microsculptured, slightly shiny; apical depressions well developed, with distinct micropunctures; sculpture of terga III-V distinctly coarser than other terga, also more densely punctate; tergum V coarsely punctate, punctures ill defined, but large, half to one diameter apart, interspaces microsculptured, apical depression of tergum V distinctly, densely finely punctate. Pygidium distinctly narrower than in other related species, integument sparsely punctate, large and small punctures intermixed, punctures ill defined, interspaces nearly unsculptured, bright shiny. Central part of sternum II with several large punctures, interspaces microsculptured, shiny; lateral part slightly shiny, densely micropunctate; remaining sterna with uniform sculpture similar to that on sternum II, but more or less reduced laterally.

Coloration. Central part of mandibles, terga I-II and distal tarsomeres dark red. Tegulae brown translucent. Apical parts of terga I-III slightly translucent. Remaining body parts all black.

Variation of females: Body length: 7.0–10.1 mm. WML:LCL = 1.5–1.7, WCL:WML = 1.8–1.9. WV:LV = 1.5–1.6.

Description of male. Body length: 6.4–7.9 mm.

Head. Mandibular inner margin with one distinct rectangular tooth and distinct furrow next to tooth distally. Clypeus convex, slightly elevated, distinctly declining apically, top variably located between apical third and midlength; basomedian area large, sparsely punctate, more sparsely punctate medially in some specimens; bevel convex, decreasing toward clypeal lip, variable in size, reaching base of clypeus in most specimens, shiny, with several large punctures; lip distinctly sinuate, conspicuously produced medially, with more or less distinct lateral corner, lip separated from bevel by groove; WML:LCL = 1.2–1.3, WCL:WML = 2.3–2.4. Supraclypeal area slightly concave, distinctly punctate, punctures ill-defined, interspaces between punctures coarsely microsculptured, slightly shiny to dull. Supraantennal tubercle small, slightly elevated on inner side, shiny. Antenna relatively short, LA3:WA3 = 1.5–1.6, LA5:WA5 = 1.9–2.1. Frons uniformly punctate, punctures well defined, less than one diameter apart, interspaces variable in size; frontal median line distinct, narrow, finely impressed, or indistinct. Vertex uniformly, finely and densely punctate, punctures well defined, one to less than half diameter apart, interspaces variable in size, coarsely microsculptured, slightly shiny to dull. Vertex setae short, erect medially, but semierect close to inner eye margin, less than 1 × MOD, postocellar impression large, but shallow, open widely V to Y-shaped, densely punctate, punctures relatively small; vertex distinctly wider than long; WV:LV = 1.6. Gena dorsally inconspicuous.

Mesosoma. Scutum with shallow anterior impression, densely punctate, punctures well defined, most punctures less than half diameter apart, interspaces distinct, microsculptured, slightly shiny to dull, setae about 1.0 × MOD or less; scutellum slightly more sparsely punctate than scutum, punctures well defined, most punctures half to less than one diameter apart, interspaces shiny to slightly shiny. Mesopleuron rugose

to densely punctate, most punctures in ventral half well defined, interspaces coarsely microsculptured to rugose, dull; hypoepimeral area coarsely rugose, without distinct punctures, with distinct longitudinal ridges in most specimens, dull; ventral part of mesopleuron with small ill-defined punctures, interspaces finely microsculptured, slightly shiny. Propodeal dorsum coarsely sculptured, irregularly areolate to irregularly coarsely ridged, without longitudinal ridges except at very base; propodeal side longitudinally ridged, ridges well developed, ill defined in small specimens, interspaces microsculptured, dull; posteromedial margin of propodeal dorsum slightly elevated or not elevated, marginal ridges on posterior surface well developed, horizontal, or slightly directed toward propodeal groove medially. Legs micropunctate, punctures small; forefemoral notch large, deep, semicircular, about as long as distance that separates it from forefemoral base or slightly longer, proximal margin obtuse, not elevated over distal margin, central part of notch inconspicuously elevated, anterior and posterior margin lined by nearly indistinct ledge, notch surface without distinct setae, unsculptured, or very finely microsculptured, shiny. Wings infumate, with brown veins.

Metasoma. Silvery apical fasciae of terga I-III distinctly developed, but fasciae brown in specimens from eastern Turkey. Apical depressions of all terga shallow, densely micropunctate, nearly as densely as on tergal disk. Terga I-III densely and distinctly micropunctate, punctures ill defined, interspaces microsculptured, slightly shiny; terga IV-VII more coarsely and more densely punctate than previous terga. Sterna uniformly punctate nearly like terga.

Coloration. Apical part of mandibles red; terga I and II dark red; apex of sternum I and base of sternum II dark red in some specimens; distal tarsomeres dark red on ventral side; forefemoral notch dark red in most specimens, but black in some. Tegulae brown translucent. Apical parts of terga slightly translucent. Remaining body parts all black.

Geographic Distribution. Czech Republic, France, Germany, Hungary, Italy, Kyrgyzstan, Poland, Slovakie and Turkey.

Tachysphex nobilis sp. n.

http://zoobank.org/B19428FC-A83E-4E18-86BF-494F6EA075AC
Figs 7, 19, 33, 40, 47, 73, 99, 108

Type material. Holotype: ♀, Hungary: "HUNGARY centr. / ÖRKENY env. / 15.VI.2007 / P. Bogusch lgt. // ♀ Tachysphex / nobilis / sp.n. / Jakub Straka det.2009 // ZSM / HYM 23689". Holotype in ZSM. Paratypes: **Bulgaria**: Albena-Kraněvo, 1 ♀, 4. vii. 1978, Z. Pádr lgt., OLML; Asenovgrad env., 1 ♂, 15. vii. 1969, K. Deneš lgt., JSPC; Borika SW, Sredna Gora Mts., 1 ♂, 6. viii. 2010, T. Ljubomirov lgt., IBER; Konstantinovo N, 1 ♂, 26. vi. 2012, T. Ljubomirov lgt., IBER; Kurtovo Konare S, 1♂, 3. viii. 2012, T. Ljubomirov lgt., IBER; Pasarel NW, Isskar valey, 1 ♂, 2 ♀♀, 6. vi. 2009, T. Ljubomirov lgt., IBER; Slančev Brjag env., 3 ♀♀, 14. vii. 1971, 1 ♂, 2. vii. 1978, Z. Pádr lgt., OLML Z. Pádr lgt., OLML, 2 ♀♀, 10. vii. 1983, P. Tyrner lgt., PTLC, 1 ♀, 30. v. 1989, J. Halada lgt., OLML; Vlahi, 1 ♂, 3 ♀♀, 14. viii. 1993, M. Halada lgt.,

JSPC; Vlahinska Reka, Strouma valey, 1 ♂, 29. vi. 2008, T. Ljubomirov lgt., IBER; Sandanski env., 1 ♂, 13. vii. 1966, M. Kocourek lgt., OLML; **Czech Republic**: Mor.mer., Bzenec env., 1 ♂, 14. vi. 1942, 1 ♀, 21. vi. 1942, A. Hoffer lgt., OLML, JSPC; Vracov env., 1 ♀, 21. viii. 1942, A. Hoffer lgt., OLML; **Greece**: Petritsio SE, Strymon valley, Hellas prov., 1 ♀, 21. v. 2009, G. Ramel lgt., IBER; **Hungary**: Örkeny, puszta, 1 ♂, 18. v. 1985, J. Halada lgt., JSPC; Iszák, 1 ♀, 18. v. 1989, Z. Karas lgt., ZKZC; Sándorfalva env., 1 ♀, 19. v. 1988, Z. Karas lgt., ZKZC; **Poland**: Karwia, Władysławowo, Baltic see coast, 1 ♀, 24. vi. 1996, R. Dobosz lgt., USMB; Pasturka, Pińczów env., Malopolska Upland, 1 ♀, 10. vi. 1998, R. Dobosz lgt., USMB; Pustynia Błędowska, Gmina Klucze, 1 ♀, 30. vi. 1992, W. Żyła lgt., USMB; Sarbinowo, Baltic see coast, 1 ♀, 18. viii. 1995, J. Batleja lgt., USMB; Toruń-Glinki, 1 ♀, 14. vi. 2011, P. Olszewski lgt., JSPC; Wicie, Baltic see coast, 1 ♀, 18. vii. 2004, W. Żyła lgt., USMB; Wicie, Baltic see coast, 1 ♀, 23. vii. 2004, W. Żyła lgt., USMB; Wicie, Baltic see coast, 1 ♀, 28. vii. 2004, W. Żyła lgt., USMB; Wicie, Baltic see coast, 1 ♂, 1 ♀, 25. vii. 2004, W. Żyła lgt., USMB, JSPC; Wisełka env., Wolin, Baltic see coast, 1 ♂, 1 ♀, 25. vii. 1997, R. Dobosz lgt., USMB; Władysławowo, 1 ♂, 30. vi. 1993, R. Dobosz lgt., USMB; **Turkey**: Ahlat, near Van lake, 1 ♂, 14. vii. 1996, P. Tyrner, Voříšek lgt., PTLC; Çamardı, Niğde prov., 1 ♂, 13. vii. 1997, M. Halada lgt., OLML; Ilhara env., valley, Aksaray prov., 2 ♂♂, 13. vi. 2008, M. Obořil lgt., JSPC.

Additional material examined. Poland: Wisełka env., Wolin, Baltic see coast, 1 ♂, 25. vii. 1997, R. Dobosz lgt., USMB; **Turkey**: Ilhara env., valley, Aksaray prov., 1 ♂, 13. vi. 2008, M. Obořil lgt., JSPC.

Diagnosis. *Tachysphex nobilis* sp. n. is most similar to *T. bohemicus* sp. n. and *T. jokischianus* (Panzer) in having fine and dense body sculptures and sparsely punctate apical margin of tergum V in female. *Tachysphex nobilis* sp. n. is a characteristic and relatively easily recognizable species. It is generally slender in body, finely, densely punctate throughout, and possess an insignificantly convex clypeus, with the bevel small in the female and nearly absent in the male. Both sexes also have the gena dorsally inconspicuous, converging behind the compound eyes. The lateral emargination of the clypeal lip in the female is round, not angulated. The propodeal dorsum in the male has a finely sculptured longitudinal area posteromedially, which appears slightly shinier than the adjacent parts of the propodeum.

Description of female (holotype). Body length: 8.9 mm.

Head. Clypeus slightly convex, top at clypeal midlength; basomedian area cover majority of space of clypeus, as densely punctate as lateral section; bevel very small, slightly convex to flat, only about 2–3 × as long as clypeal lip, slightly longer medially than laterally, with few large punctures, ending far from base of clypeus, shiny; lip insignificanly arcuate to nearly straight, with faint lateral incision, separate from bevel by punctate groove, WML:LCL = 1.6, WCL:WML = 1.8. Supraclypeal area flat, finely and densely punctate, punctures ill defined, interspaces microsculptured, dull. Supraantennal tubercle small, slightly elevated on inner side. Frons uniformly, very densely punctate, punctures well defined, less than half diameter apart, interspaces uniform in size, dull; frontal median line distinct, shiny, not impressed. Vertex finely,

densely punctate, punctures well defined, half to less than half diameter apart, interspaces finely microsculptured, slightly shiny. Vertex setae short, semierect, about 0.5 × MOD; postocellar impression well developed, widely Y-shaped; vertex slightly wider than long; WV:LV = 1.2. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, less than half diameter apart, interspaces well developed and relatively uniform in size, microsculptured, slightly shiny, setae about 1.0 × MOD or less. Mesopleuron coarsely microsculptured, without distinct punctures; hypoepimeral area finely rugose with indistinct, longitudinal, irregular ridges, without punctures; ventral part of mesopleuron finely, densely punctate, with punctures ill defined, less than one diameter apart, interspaces small, slightly shiny. Propodeal dorsum relatively finely, regularly rugose, with short irregular longitudinal ridges basally, dull, posteromedially with transverse ridges on small longitudinal slightly shiny area; propodeal side regularly longitudinally ridged, ridges inconspicuous basally, microsculptured, dull; posteromedial margin of propodeal dorsum elevated, slightly produced between marginal ridges, marginal ridges positioned nearly horizontally above groove on posterior surface. Legs densely punctate, punctures small; forebasitarsal rake light reddish, with three apical spines, one preapical and one or two additional ones. Wings slightly infumate, yellowish, with brown veins.

Metasoma. Terga I-III with distinct silvery, apical faciae; terga I-II very densely and finely micropunctate, punctures ill-defined but distinct, interspaces microsculptured, slightly shiny; apical depressions well developed, with distinct micropunctures; sculpture of terga III-V distinctly coarser than on previous terga, also more densely punctate; tergum V coarsely punctate, punctures ill-defined, but large, half to one diameter apart, interspaces microsculptured, apical depression of tergum V very sparsely, finely punctate. Pygidium of usual size, sparsely punctate, punctures large, ill defined, interspaces microsculptured basally, but unsculptured in apical half, slightly shiny to shiny. Central part of sternum II with several large punctures, interspaces microsculptured, shiny; lateral part slightly shiny, densely micropunctate; remaining sterna with uniform sculpture similar to that on sternum II, but more or less reduced laterally.

Coloration. Central part of mandibles, terga and sterna I-III red. Distal tarsomeres are dark red. Tegulae brown translucent. Apical parts of terga I-III slightly translucent. Remaining body parts all black.

Variation of females: Body length: 7.2–9.0 mm. Antenna relatively short, LA3:WA3 = 1.9–2.1, LA5:WA5 = 2.9–3.0. In general, the species is not significantly variable in key characters. There is the usual variation in size dependent characters like the number of spins on foretarsal rake. The shape of the lateral emargination of the clypeal lip is one of a few variable characters; it can be well developed to nearly absent, but never angulated. The pygidium is slightly variable in width and sculpture; it is of usual shape in most specimens with distinct microsculpture, slightly shiny in basal half, but also wider and bright shiny in some specimens.

Description of male. Body length: 5.4–6.8 mm.

Head. Mandibular inner margin with one distinct rectangular tooth and distinct furrow next to tooth distally. Clypeus very slightly convex (appearing nearly flat), uni-

formly curved, top at about clypeal midlength; basomedian area dominant on clypeus, densely, uniformly punctate; bevel nearly or completely absent, reduced to shiny area ventromedially; lip arcuate or slightly sinuate, with small rectangular lateral corner, lip separated from bevel by distinct, punctate groove; WML:LCL = 0.9–1.2, WCL:WML = 2.2–2.4. Supraclypeal area groove-like, slightly concave, supraantennal tubercles slightly elevated ventromedially, circular; surface coarsely microsculptured with indistinct punctures, dull. Antenna relatively short, LA3:WA3 = 1.5–1.6, LA5:WA5 = 1.9–2.1. Frons finely punctate, punctures well defined, half to less than half diameter apart, interspaces relatively uniform in size; frontal median line distinct, narrow, finely or not impressed, shiny. Vertex finely punctate, punctures well defined, one to less than one diameter apart, interspaces microsculptured, slightly shiny to dull. Vertex setae short, semierect, less than 1 × MOD; postocellar impression distinctly impressed, but shallow, open widely V to Y-shaped; vertex moderately wider than long, WV:LV = 1.5. Gena dorsally inconspicuous.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, most punctures less than half diameter apart, interspaces distinct, microsculptured, slightly shiny to dull, setae about 1.0 × MOD or less. Mesopleuron coarsely microsculptured, with distinct or indistinct punctures in lower areas, most punctures ill defined, interspaces dull; hypoepimeral area coarsely microsculptured to finely rugose, dull; ventral part of mesopleuron densely punctate, punctures small ill defined, interspaces slightly shiny. Propodeal dorsum finely irregularly areolate to rugose, without longitudinal ridges, posteromedially with finely sculptured longitudinal area, which appears slightly shinier than adjacent areas; lateral surface of propodeum coarsely microsculptured, with or without ill defined longitudinal ridges, dull; posteromedial margin of propodeal dorsum elevated, but not produced between marginal ridges, marginal ridges positioned nearly horizontally above groove on posterior side. Legs densely punctate, punctures small; forefemoral notch light red and large, semicircular, its diameter is usually longer than distance that separates it from forefemoral base, central part of notch slightly elevated, anterior and posterior margins lined by small ledge, nearly indistinct in some specimens, notch surface without distinct setae, microsculptured, dull. Wings slightly infumate, veins brown.

Metasoma. Terga I-III with silvery apical faciae. Apical depressions of terga distinct, micropunctate similarly to that on tergal disk. Terga I-III densely, distinctly micropunctate, punctures ill defined, interspaces microsculptured, slightly shiny; sculpture of terga IV-VII slightly coarser than on previous terga, also punctures slightly denser. Sterna uniformly punctate, nearly like terga.

Coloration. Apical part of mandible, terga and sterna I-III and forefemoral notch red. Distal tarsomeres reddish. Tegulae brown to reddish. Apical parts of all terga and tegulae translucent. Remaining body parts all black.

Geographic distribution. Bulgaria, Czech Republic, Greece, Hungary, Poland and Turkey.

Name derivation. The species is named after its uniform sculptures. The species appears as a "noble" among other species of the *T. pompiliformis* species subgroup.

***Tachysphex opacus* F. Morawitz, 1893**
Figs 10, 11, 25, 34, 67, 74, 100

Material examined. Iran: Kherameh, Fars prov., 1 ♀, 24. i. 2013, E. Izadi lgt., IBER; Neyriz-Jaafarabad, Fars prov., ira-fa01, 1 ♂, 2 ♀♀, 7. ix. 2012, M. Khosroabadi lgt., CSE; **Kazakhstan**: Mangismlak, Kamysta (90 km Etaoutchik), 1 ♂, 8. v. 1962, Malkovskii, ZIN; **Kyrgyzstan**: Dzahal-Abad area, 2 ♂♂, 1 ♀, vi. 2000, V. Gurko lgt., JSPC, OLML; Kaltabulak road gorge, Transalai Mt. r., Alay prov., 1 ♀, 15. vii. 1998, I. Makogonova lgt., OLML; Kirghiz-Ata grg., Kitchik-Alai Mt., Nookat distr., 1 ♂, 25. vi. 1996, S. L. Zonstein lgt., JSPC; **Tajikistan**: Dushanbe env., 1 ♂, 15. vi. 1966, K. Deneš lgt., OLML; Gušari (Chuš-er), Gissar., 1 ♂, 26. vii. 1937, Gussakovskii, ZIN; Rushan 30 km N, Pamir Mts., 1 ♀, vii. 2000, V. Gurko lgt., JSPC; **Turkey**: Ahlat, near Van lake, Van prov., 1 ♀, 14. vii. 1996, P. Tyrner, Voříšek lgt., PTLC; Muradye 40km N, Van prov., 1 ♂, 5. vii. 2000, M. Halada lgt., OLML; **Uzbekistan**: Aman-Kutan pass., Zerevshan Mt., w. part, Samarkand prov., 1 ♀, 8. vi. 1995, S. L. Zonstein lgt., OLML; Bashkyzylsai river canyon, Tchatkal Mts., Parkent distr., 1 ♀, 5. viii. 1999, S. L. Zonstein lgt., OLML; Czirczik, Yangiyul District, 1 ♀, 28. v. 1994, J. Halada lgt., JSPC; Dzhizak vil., Douba 5km S, Turkest. Khrebet, Zaamin distr., 1 ♂, 13. vi. 1997, H. & R. Rausch lgt., OLML; Kainarsai, Ugam Mt. r., Bostanlik distr., 1 ♀, 24. vii. 1996, S. L. Zonstein lgt., OLML. Specimens determined as *T. opacus* aff.: **Jordan**: Petra 10km N, 1 ♂, 3. v. 1996, M. Halada lgt., OLML; **Kazakhstan**: Fabritchny, 40 km E Almaty, Zhambyl distr., 1 ♂, 9. vii. 1992, Jirousek lgt., JSPC; Ushtagan, Sauskan sands, Aktau 120km E, 1 ♀, 15. v. 2000, J. Matleuski lgt., JSPC; **Syria**: Damascus 40km NE, 2 ♂♂, 13. v. 1996, Mi. Halada lgt., OLML; Dibbin, Suwayda 30km S, 2 ♂♂, 17. v. 1996, Mi. Halada lgt., OLML; Homs 50km S, 1 ♀, 24. v. 1996, Mi. Halada lgt., OLML; Khabab, Damascus 60km S, 1 ♂, 14. v. 1996, Mi. Halada lgt., OLML; Marbij env., 1 ♂, 9. v. 1996, Mi. Halada lgt., OLML; Turkey: Çaykavak, Ulukışla, Niğde prov., 1 ♂, 30. v. 2001, M. Snížek lgt., OLML; Gürün 20km E, Malatya prov., 1 ♂, 10. vii. 1997, M. Halada lgt., OLML; Kengerlidüz, Hatay, 1 ♂, 17. v. 2008, M. F. Gürbüz lgt., IBER; Ürgüp 10km W, Nevşehir prov., 3 ♂♂, 15. vi. 1998, M. Halada lgt., OLML.

Diagnosis. *Tachysphex opacus* Morawitz is easily recognizable from other species of the *T. pompiliformis* and *T. austriacus* species subgroups. This species is generally dark and has coarsely sculptured mesopleuron and terga. Based on this characteristic, *T. opacus* resembles *T. nigripennis* (Spinola) and *T. pompiliformis* (Panzer). It differs from *T. pompiliformis* (Panzer) in having the gena inconspicuous and a sparsely punctate clypeal basomedian area. In the females, the metasoma has dark red terga I-II and a black sternum II, and the vertex is nearly as wide as long. In the males, the body is black, the mandibular inner margin is shallowly emarginated distally from inner tooth, with no furrow, the clypeal lip is nearly straight, the vertex is distinctly wider than long. In addition to the mentioned characters, the females of *T. opacus* Morawitz differ from *T. nigripennis* (Spinola) in having normal sized pygidium with microsculpture and

lacking a bright shine. The males differ in having a forefemoral notch microsculptured, dull, and the dorsal process of the volsella narrow.

Geographic distribution. China, Iran, Kazakhstan, Kyrgyzstan, Tajikistan, Turkey, and Uzbekistan. It is probably also distributed in Jordan, Lebanon and Syria.

Note. Holotype came from China (Uighur region). Type material not examined. The species was redescribed by Pulawski (1971).

***Tachysphex pompiliformis* (Panzer, 1804)**

Figs 9, 12, 20, 26, 35, 48, 52, 58, 68, 75, 85, 90, 101

= *Larra pompiliformis* Panzer, 1804 (Heft 89: pl. 13), ♀.

Type material. Holotype: ♀, no specific locality at the label, but probably from Germany. Holotype by monotypy. "Coll. Sturm [printed] // Stimmt / Larra / pompili - / formis / Panz. [handwriting, card with black frame] // 56 [printed, red card] // Larra / pompiliformis Panz. / Typus sec. Richards 1935 [handwriting] // Tachysphex ♀ / pompiliformis Pz. / J. de Beaumont / det. 1955 [handwriting on pre-printed card with name of determinator and year] // Typus Nr. / Zoologische / Staatsamlung / München. [printed, red card]". Holotype in ZSM, examined.

Additional material examined. Austria: Seefeld NW, Niederösterreich, 1 ♂, 19. v. 2015, M. Halada lgt., OLML; **Czech Republic**: Boh. occ., Tušimice, ash coal deposit from power station, 3 ♂♂, 26. vi. 2010, 1 ♂, 31. vii. 2010, ZSM HYM24250, 3 ♀♀, 22. viii. 2010, ZSM HYM24580, R. Tropek lgt., JSPC,; Mor. mer., Boleradice 1 km NE, 1 ♂, 10. vii. 2014, M. Říha lgt., JSPC; Bratčice env., 1 ♂, 21. vi. 2012, M. Halada lgt., JSPC; Čejč, 1 ♂, viii. 1963, Z. Pádr lgt., OLML; Gotberg, Popice 1.5km NE, 1 ♂, 25. v. 2014, ZSM HYM24595, M. Říha lgt., JSPC; Havraníky env., NP Podyjí, 1 ♂, 18. v. 2015, M. Halada lgt., JSPC; Morkůvky 1km NE, 1 ♂, 8. vii. 2014, M. Říha lgt., JSPC; **Bulgaria**: Martisganitsa cotage W, 1 ♂, 24. viii. 2013, T. Ljubomirov lgt., IBER; Milanovo W, 1 ♂, 7. vii. 2015, T. Ljubomirov lgt., IBER; Razdol, Maleshevska Planina, 2 ♂♂, 27. vi. 2008, T. Ljubomirov lgt., IBER; Rezhantsi env., 1 ♀, 9. viii. 2011, N. Simov lgt., IBER; Slančev Brjag env., 1 ♀, 18. vi. 1977, Z. Pádr lgt., 1 ♂, 29. vii. 1968, M. Kocourek lgt., OLML; Staroplaninets cotage SW, Etropolska Planina, 1 ♀, 24. viii. 2006, 1 ♂, 1 ♀, 1. vii. 2010, T. Ljubomirov lgt., IBER; Staroseltsi env., Isskar valey, 2 ♂♂, 28. v. 2011, T. Ljubomirov lgt., IBER; Trubatch, Razgradski heights, 1 ♀, 22. viii. 1999, K. Ivanov lgt., JSPC; **France**: St. Thomé, Font Just, 12 km SW Montélimar, 1 ♀, 14. vi. 2001, J. v. d. Smissen lgt., USMB; **Greece**: Ag. Petros, Meg. Tourla, Oros Parnon, Hellas, 1 ♀, 14. vii. 2006, 2 ♂♂, 24. vi. 2013, W. Arens lgt., WAPC; Ano Trikala, Mt. Killini, Hellas, 8 ♂♂, 24. vi. 2008, W. Arens lgt., WAPC; Meg. Tourla, Oros Parnon, Hellas, 1 ♀, 13. vii. 2006, 5 ♂♂, 23. vi. 2013, W. Arens lgt., WAPC; Michas, Erymanthos, Achaea, 1 ♀, 23. vi. 1995, 1 ♀, 10. vii. 1996, W. Arens lgt., WAPC; Prof. Ilias, Oros Taygetos, Hellas, 2 ♂♂, 28. vi. 2013, ZSM HYM24579, W. Arens lgt., WAPC, JSPC; Stymphalia, Hellas, 1 ♀, 15. vi. 1995, W. Arens lgt., WAPC; Toriza-

Prof. Ilias, Oros Taygetos, Hellas, 1 ♀, 11. vii. 2007, W. Arens lgt., WAPC; **Hungary**: Hegyshalom N, 2 ♂♂, 6. vi. 2015, M. Halada lgt., OLML; Kesthely env., lime stone, 1 ♂, 1 ♀, 23. v. 2014, A. Astapenková, J. Habermannová, J. Straka lgt., JSPC; Örkeny, puszta, 2 ♂♂, 27. vi. 2015, M. Halada lgt., JSC; Pákozd env., pasture stepe, 4 ♂♂, 10. vi. 2015, 2 ♂♂, 1 ♀, 25. vi. 2015, M. Halada lgt., JSPC; **Italy**: Coldrano, Vinschgau, Trentino-Alto Adige prov., 1 ♂, 8. vi. 2007, Ch. Schmid-Egger lgt., CSE; Lanzada, Sondrio 11 km N, Lombardia prov., 2 ♀♀, 9. vii. 2006, Ch. Schmid-Egger lgt., CSE; Lasa, Vinschgau 2 km N, Trentino-Alto Adige prov., 6 ♂♂, 3 ♀♀, 8. vi. 2007; Ch. Schmid-Egger lgt., CSE; Osis/Eyrs, Vinschgau, Trentino-Alto Adige prov., 4 ♂♂, 1 ♀, 8. vi. 2007, Ch. Schmid-Egger lgt., CSE; Pondel, Aosta 8 km SW, Valle d'Aosta prov., 3 ♂♂, 4. viii. 1996, P. Rosa lgt., CSE; Ponte in Valtellina, Sondrio 10 km E, Lombardia prov., 3 ♂♂, 9. vii. 2006, Ch. Schmid-Egger lgt., CSE; St. Pierre, Valle d'Aosta prov., 2 ♂♂, 1. viii. 1997, Ch. Schmid-Egger lgt., CSE; Tubre/Taufers, Vinschgau 1 km NE, Trentino-Alto Adige prov., 8 ♂♂, 2 ♀♀, 27. vii. 2007, Ch. Schmid-Egger lgt., CSE; Casali Santa Maria Maddalena N, 1 ♂, 22. vi. 2011, T. Ljubomirov lgt., IBER; Casali Santa Maria Maddalena NE, 6 ♂♂ 22. vi. 2011, T. Ljubomirov lgt., IBER, CCDB-12231-G09, CCDB-12230-A04, CCDB-12230-C01, CCDB-12232-B08, CCDB-12233-D06, CCDB-12233-F01; Ozein, 10km SW Aosta, I-aooz, 1 ♂, 19. viii. 1996, P. Rosa lgt., ZSM; Saint-Pierre, 16km W Aosta, Valle d'Aosta, I-aoB, 1 ♂, 8. vii. 1995, 1 ♀, 27. vi. 1996, Ch. Schmid-Egger lgt., CSE; Saint-Pierre, 6 km W Aosta, Valle d'Aosta, 2 ♂♂, 28. vi. 1999, J. v. d. Smissen lgt., USMB; Sarre, Aosta valey, 1 ♀, 1. viii. 2007, W. Schlaefle lgt., WSKC; Tartsch, Bolzano, 1 ♀, 28. vii. 1989, J. Tiefenthaler lgt., OLML; **Kyrgyzstan**: Ak-Buura ravine, Osh 45km S, Alai Mts., Osh prov., 1 ♂, 14. vii. 2014, Oistein Berg lgt., JSPC, ZSM HYM23639; Issik-Kul lake ost., Teplokljitchenka rg., 3 ♂♂, 3 ♀♀, viii. 2001, V. Gurko lgt., JSPC; Kashkasu env., Ala-Archa, 1 ♂, 9. vii. 2002, V. Gurko lgt., JSPC; Tchon-Aryk, Kirghizskyi Mts., 1 ♂, 11. vii. 2001, V. Gurko lgt., JSPC; **Portugal**: Armamar, Viseu distr., P-arn, 1 ♂, 1. viii. 2001, Ch. Schmid-Egger lgt., CSE; Gerês, Braga distr., P-ger, 2 ♂, 31. vii. 2001, Ch. Schmid-Egger lgt., CSE; **Slovakia**: Štúrovo, 1♂, 28. vii. 1959, 1 ♂, 18. vi. 1960, 1 ♀, 2. viii. 1960, 1 ♂, 15. viii. 1961, 1 ♀, 16. vii. 1962, 2 ♂♂, 1 ♀, 27. vii. 1962, Z. Pádr lgt., OLML, 1 ♀, 29. vii. 2002, J. Habarta lgt., JSPC; Somotor, 1 ♀, vii. 1958, M. Kocourek lgt., OLML; **Switzerland**: Leuk, Wallis prov., 1 ♀, 12. viii. 2011, W. Schlaefle lgt., WSKC, Mergoscia, Tessin prov., 1 ♂, 15. vii. 2011, W. Schlaefle lgt., WSKC; Monte Comino, Tessin prov., 1 ♀, 15. vii. 2007, 1♂, 11. vii. 2012, W. Schlaefle lgt., WSKC; Zeneggen, Wallis prov., 1 ♂, 15. vii. 2010, W. Schlaefle lgt., WSKC; **Turkey**: Dortiol, Amánus Mts., 4 ♂♂, 10. vi. 2008, M. Škorpík lgt., JSPC; Erzurum E, Erzurum prov., 2 ♂, 6. vii. 2000, M. Halada lgt., OLML; Esendere, Hakkari prov., 1 ♀, 21. vii. 1988, Ch. Schmid-Egger lgt., CSE; Ihara valey, Adana prov., 1 ♂, 13. vi. 2008, M. Kafka lgt., JSPC; Kasnak Mesesi, Isparta, 1 ♀, 28. vi. 2007, 1 ♀, 30. vi. 2007, 1 ♀, 8. ix. 2007, A. Bayindir lgt., IBER, 1 ♂, 6. viii. 2008, T. Ljubomirov, A. Bayindir, IBER; Kengerlidüz, Hatay, 1 ♀, 21. vii. 2007, M. F. Gürbüz lgt., IBER; Mitisin, Osmaniye prov., 1 ♂, 6. viii. 2008, T. Ljubomirov lgt., IBER; Muradiye, Van prov., 1 ♀, 3. vii. 2000, M. Halada lgt., OLML; Pazaryolu, Kumaşkaya, Erzurum prov., 1 ♂, 25. vi.

2014, T. Ljubomirov lgt., IBER; Pozantı, Adana prov., 1 ♂, 6. vii. 1984, Hladil lgt., OLML; Refahye 15km W, Erzincan prov., 1 ♀, 7. vii. 2000, M. Halada lgt., OLML; Salihli 35 km SEE, Manisa prov., 1 ♂, 30. vi. 2006, M. Halada lgt., JSPC; Samson University campus, Samson prov., 1 ♂, 4. vii. 2014, J. Barták, Kubík lgt., JSPC; Tekederesi env., Erzurum vil., 15 km SW, 2 ♂♂, 2. vii. 2001, M. Fikáček, J. Hájek, J. Straka lgt., JSPC; Yüksekova, Hakkari prov., 1 ♀, 22. vii. 1988, Ch. Schmid-Egger lgt., CSE.

Diagnosis. *Tachysphex pompiliformis* (Panzer) is difficult to distinguish from *T. dimidiatus* (Panzer), *T. jokischianus* (Panzer) and *T. punctipleuris* sp. n. It is exceptionally variable in most characters and no single character alone can differentiate it from morphologically similar species. This species is generally darker and more coarsely punctate than similar species. The metasoma is densely micropunctate, including apical depressions. The mesopleuron is coarsely sculptured, rugose, or coarsely punctate, and the hypoepimeral area has more or less distinct longitudinal ridges. In males, sternum II is often dark red to partly black, but tergum II is red; however, specimens with red metasomal segments I-III also occur. The terga are darker than in other species in some females, but this occurs less often. The forefemoral notch of the male is dark in most specimens. The gena is robust. The following combination of additional characters is also characteristic of this species: ♀: The clypeus is slightly convex, and the most elevated point is not well defined but located at about the clypeal midlength. The vertex setae are short and uniformly semierect both medially and laterally. The dorsolateral cuticular projection of the propodeal spiracle is arcuate to semicircular and usually dark. The propodeal dorsum and side are longitudinally ridged; the dorsum is coarsely sculptured, but the ridges are indistinct in some specimens. The forebasitarsal rake is reddish in fresh individuals, with two, well separated apical spines and one additional preapical spine. The wings are often but not always dark. ♂: The clypeus is coarsely punctate, the interspaces between the punctures large, approximately one diameter apart. The forefemoral notch is markedly carinated on the anterior and posterior margin. The volsella is dark, the dorsal process narrow, about as wide as the volsellar corpus basally.

Description of male. Body length: 5.3–7.8 mm.

Head. Mandibular inner margin with one rectangular tooth and distinct furrow next to tooth distally. Clypeus convex, slightly elevated and steeply declining ventrally, top in apical third or in midlength; basomedian area large, sparsely punctate, more sparsely punctate medially than laterally in some specimens; bevel convex, conspicuously decreasing toward clypeal lip, variable in size, shiny with several larger punctures; lip distinctly sinuate, conspicuously produced medially in most specimens, with distinct lateral corner, lip separated from bevel by variable groove; WML:LCL = 1.2–1.3, WCL:WML = 2.3–2.4. Supraclypeal area slightly concave, distinctly punctate, punctures ill-defined, interspaces microsculptured, dull. Supraantennal tubercle small, but distinctly elevated on inner side, shiny. Antenna relatively short, LA3:WA3 = 1.5–1.6, LA5:WA5 = 1.9–2.1. Frons uniformly punctate, punctures well defined, less than one diameter apart, interspaces variable in size; frontal median line distinct, narrow, finely impressed. Vertex punctate, punctures relatively large, well defined, less than half to

two diameters apart, interspaces slightly microsculptured, slightly shiny to dull. Vertex setae short, semierect medially, but nearly erect close to inner eye margin, less than 1 × MOD, postocellar impression distinct, shallow, sparsely punctate, punctures relatively large, open, widely V to Y-shaped; vertex slightly to moderately wider than long; WV:LV = 1.1-1.5. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, most punctures less than half diameter apart, interspaces distinct, microsculptured, slightly shiny to dull, setae about 1.0 × MOD or less. Mesopleuron rugose to densely punctate, most punctures in ventral half well defined, interspaces coarsely microsculptured to rugose, slightly shiny to dull; hypoepimeral area coarsely rugose, without distinct punctures, with distinct longitudinal ridges in most specimens, dull; ventral part of mesopleuron with punctures large, well defined (ill defined in small specimens), interspaces finely microsculptured, slightly shiny. Propodeal dorsum coarsely sculptured, longitudinally ridged, irregularly ridged, or areolate; side longitudinally ridged, ridges well developed, interspaces microsculptured, dull; posteromedial margin of dorsum slightly elevated or not elevated, marginal ridges fine, variably sinuous, horizontal, with ventromedially directed medially. Legs densely punctate, punctures small; forefemoral notch small, but relatively deep, semicircular, shorter than distance that separates it from forefemoral base, proximal margin relatively sharp, elevated over distal margin, central part of notch slightly elevated, anterior and posterior margins lined by faint ledge, notch surface without distinct setae, coarsely microsculptured, dull. Wings moderately infumate, but relatively pale in some specimens, veins brown.

Metasoma. Silvery apical faciae of terga I-III faintly developed, often absent. Apical depressions of all terga shallow, densely micropunctate, nearly as densely as more anterior parts. Terga I-III densely and distinctly micropunctate, punctures ill defined, interspaces microsculptured, slightly shiny; sculpture of terga IV-VII coarser than on previous terga, also punctation denser. Sterna uniformly punctate nearly like terga.

Coloration. Apical part of mandible red; terga I and II dark red, base of tergum II dark red in some specimens; apex of sternum I and base of sternum II dark red, infrequently specimens with three red metasomal segments also occur; distal tarsomeres dark red on ventral side; forefemoral notch black in most specimens, but dark red in a few. Tegulae reddish or brown translucent. Apical parts of all terga slightly translucent. Remaining body parts all black.

Description of female (holotype). Body length: 7.8 mm.

Head. Clypeus distinctly convex, top at clypeal midlength; basomedian area relatively large, more sparsely punctate and punctures larger than on lateral section, interspaces between punctures basolaterally small, but getting sparser in mesoventral direction, interspaces well developed, but punctures mostly less than one diameter apart; bevel large, distinctly convex, as long as basomedian area both laterally and medially, not triangular, with sparse large punctures, not reaching base of clypeus, shiny; lip slightly arcuate, with lateral incision, separate from bevel by punctate groove, WML:LCL = 1.6, WCL:WML = 1.8. Supraclypeal area flat, distinctly punctate, punctures ill-defined, interspaces between punctures shiny to slightly shiny. Supraanten-

nal tubercle slightly elevated on inner side. Antenna relatively short. Frons uniformly punctate, punctures well defined, about half diameter apart or less, interspaces slightly variable in size; frontal median line distinct, narrow, finely impressed. Vertex punctate, punctures well defined, less than half to one diameter apart, laterally sparser than medially, interspaces microsculptured, dull. Vertex setae short semierect, slightly longer laterally than medially, about 0.5 × MOD; postocellar impression distinct, shallow, V-shaped; vertex slightly wider than long; WV:LV = 1.3. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, less than half to one diameter apart, microsculptured, slightly shiny, setae about 1.0 × MOD or less. Mesopleuron coarsely microsculptured to finely rugose anteriorly, with indistinct punctures anteriorly; hypoepimeral area irregularly microsculptured to finely rugose, without punctures; ventral part of mesopleuron with punctures ill defined, less than one diameter apart, interspaces small, slightly shiny. Propodeal dorsum finely irregularly longitudinally ridged, interspaces rugose; propodeal side irregularly, but distinctly longitudinally ridged, ridges inconspicuous basally, interspaces microsculptured, dull; posteromedial margin of dorsum slightly elevated, marginal ridges directed ventromedially toward groove on posterior side. Legs densely punctate, punctures small; forebasitarsal rake reddish, with two apical spines, one preapical, and two additional ones. Wings slightly infumate, veins brown.

Metasoma. Terga I-III with silvery apical fasciae inconspicuously developed. Apical depressions of all terga shallow, with distinct micropunctures, on terga I-II evanescent in microsculpture. Terga I-III densely, finely micropunctate, punctures ill defined but distinct, interspaces microsculptured, slightly shiny; sculpture of tergum III-V distinctly coarser than on previous terga, also punctures slightly denser. Pygidium sparsely punctate, punctures ill defined, interspaces microsculptured, dull. Central part of sternum II with several large punctures, interspaces microsculptured, shiny; lateral part slightly shiny, densely micropunctate; remaining sterna with uniform sculpture similar to that of sternum II, but more or less reduced laterally.

Coloration. Central part of mandible, three distal tarsomeres, terga and sterna I-III red. Tegulae brown translucent. Apical parts of terga I-III slightly translucent. Remaining body parts all black.

Variation of females: Body length: 6.7–9.3 mm. WV:LV = 1.3–1.4. Antenna, LA3:WA3 = 2.2–2.4, LA5:WA5 = 2.6–2.7. Very variable in coloration and sculpture. The holotype female is among the specimens with the finest sculpture. The mesopleuron is coarsely punctate to coarsely rugose; the hypoepimeral area is longitudinaly ridged, but also coarsely and uniformly rugose in some specimens. The propodeal dorsum is longitudinaly ridged, but also coarsely and uniformly rugose in some specimens (usually the hypoepimeral area and the propodeal dorsum with a comparable sculpture). The abdominal segments I-III equally red or dark red, but also two, or just one tergite red, and then sterna darker than terga.

Geographic distribution. Austria, Czech Republic, Bulgaria, Germany, France, Greece, Hungary, Italy, Kyrgyzstan, Portugal, Slovakia, Switzerland and Turkey.

***Tachysphex punctipleuris* sp. n.**
http://zoobank.org/83E83A71-268C-4693-9238-EB074A4231B3
Figs 8, 21, 27, 49, 69, 76, 102

Type material. Holotype: ♂, Italy: "Italy Lombardia Valtellina, / Grosio 600 m NN 46,29 N / 10,26 E leg Schmid- / Egger 09.07.2006 I-valH // ♂ Tachysphex / pompiliformis (Pz.) / C form – punctate / Jakub Straka det.2008". Holotype in ZSM. Paratypes: **Austria**: Innsbruck, 1 ♀, 20. vi. 1920, E. Clément lgt., ZSM; **Bulgaria**: Dolni Pasarel N, Lozenska Planina, 1 ♂, 10. viii. 2010, T. Ljubomirov lgt., IBER; Etropole W, Etropolska Planina, 1 ♂, 1. vii. 2010, T. Ljubomirov lgt., IBER, CCDB-05716-A12; **Germany**: Badberg, Kaiserstuhl, Baden-Württemberg, bad, 1 ♀, 16. vii. 2011, Ch. Schmid-Egger lgt., ZSM HYM 14828; Grissheim, Baden-Württemberg, gr, 1 ♂, 16. vii. 2011, ZSM HYM 14830; 1 ♂, 18. vii. 2012, Ch. Schmid-Egger lgt., ZSM HYM 17629; **Hungary**: Apaj env., 1 ♂, 20.-22. vii. 2015, D. Benda lgt. et coll., ZSM HYM 24760; Kesthely, 1 ♀, 23. v. 2014, A. Astapenková, J. Habermannová, J. Straka lgt., JSPC; Kunszentmiklos env., 2 ♀♀, 16. vii. 2013, J. Habermannová, J. Straka lgt., JSPC; Pákozd env., pasture steppe, 2 ♂♂, 10. vi. 2015, 2 ♂♂, 25. vi. 2015, M. Halada lgt., ZSM HYM 24756, 1 ♂, 3.-6. vi. 2015, D. Benda, J. Straka lgt., ZSM HYM 24758, JSPC, OLML; Velencei-tó env., 1 ♀, 4.-9. vi. 2013, D. Benda, P. Bogusch, J. Straka lgt., 1 ♂, 23. v. 2014, A. Astapenková, J. Habermannová, J. Straka lgt., 1 ♂, 3.-6. vi. 2015, D. Benda, J. Straka lgt., ZSM HYM 24759, JSPC; **Italy**: Grosio, Valtellina, Lombardia prov., 3 ♂♂, 1 ♀, 9. vii. 2006, Ch. Schmid-Egger lgt., CSE; Monte/Castel, Veneto prov., I-venA, 1 ♂, 17. vii. 2011, Ch. Schmid-Egger lgt., ZSM HYM 14831; Osis/Eyrs, Vinschgau, Trentino-Alto Adige prov., 1 ♂, 8. vi. 2007, Ch. Schmid-Egger lgt., CSE; Rivera, Lignano, 1 ♂, 3. vii. 2015, M. Kafka lgt., JSPC; **Slovenia**: Narin, 1 ♂, 6. vii. 2015, M. Kafka lgt., JSPC; **Turkey**: between Güvern and Çerkes, 1 ♂, 18. vi. 2006, E. Scheuchl lgt., CSE.

Additional material examined. Bulgaria: Krushare E, 1 ♀, 6. vii. 2012, T. Ljubomirov lgt., IBER; Milanovo W, 1 ♂, 7. vii. 2015, T. Ljubomirov lgt., IBER; Dätzberg, Gellmersbach, Heilbronn, Baden-Württemberg, G2, 2 ♀♀, 20. vi. 1995, Ch. Schmid-Egger lgt., CSE; Keiserstuhl, Baden-Württemberg, 1 ♂, 19. viii. 1984, Ch. Schmid-Egger lgt., CSE; **Italy**: Eita 2 km N, Bormio 16 km SW, Valtellina, Lombardia prov., 1 ♂, 9. vii. 2006, Ch. Schmid-Egger lgt., CSE; Grosio, Valtellina, Lombardia prov., 1 ♂, 9. vii. 2006, Ch. Schmid-Egger lgt., CSE; Lago Rovine, Piemonte 26 km SW Cuneo, I-mari1, 1 ♂, 17. vi. 2009, Ch. Schmid-Egger lgt., CSE; San Benedetto Belbo, Province of Cuneo, 1 ♂, 15. vi. 2003, 1 ♂, 22. vii. 2008, 1 ♀, 25. viii. 2008, G. Pagliano lgt., ZSM; Sirino Mt., Basilicata prov., 1 ♂, 26. vi. 1998, M. Generani, P. L. Scaramozzino lgt., WSKC; Tartsch, Bolzano, 1 ♂, 28. vii. 1989, J. Tiefenthaler lgt., OLML; Terenten, Bolzano, 1 ♂, 1 ♀, 14.-28. ix. 1982, F. Parré lgt., OLML.

Diagnosis. *Tachysphex punctipleuris* sp. n. is difficult to distinguish from *T. dimidiatus* (Panzer), *T. jokischianus* (Panzer) and *T. pompiliformis* (Panzer). It is exceptionally variable in most characters, and no single character alone can distinguish this species

from the similar species. It possesses the following combination of characters: ♀: Clypeus slightly convex, the most elevated point not well defined, located approximately at clypeal midlength. Clypeal bevel variable, reaching the clypeal base in some specimens but well separated from it in others. Clypeal lip in fresh specimens sinuate, with ill-defined emargination medially. Vertex setae short, uniformly semierect medially as well as laterally. Postocellar impression well developed, deep, an open widely Y-shaped, or the posterior margin of the impression sinuous. Head nearly round, with uniformly, densely punctate frons. Gena robust. Punctures of mesopleuron variable but distinct and well defined in some specimens. Dorsolateral cuticular projection of propodeal spiracle arcuate to semicircular and usually all dark. Propodeal side uniformly longitudinally ridged, except in small specimens. Punctures of central part of tergum IV and V ill defined, interspaces between the punctures large, distinct, slightly shiny to shiny. Pygidium wide and shiny in most specimens, similar to *T. jokischianus* (Panzer). ♂: Clypeus slightly convex. Clypeal bevel large, densely punctate, interspaces between punctures small, punctures less than one diameter apart. Vertex approximately as wide as long. Gena robust. Supraclypeal area flat, supraantennal tubercle slightly elevated ventromedially. Mesopleuron laterally and ventrally distinctly punctate (punctures distinct also on hypoepimeral area in some specimens), punctures well defined, interspaces between the punctures distinct, slightly shiny to shiny on most parts. Forefemoral notch small, inconspicuously carinated, anterior carina distinct, black to dark red in coloration. Terga sparsely micropunctate, with variable interspaces between punctures. Volsella light brown, dorsal process basally wider than volsellar corpus.

Description of female. Body length: 6.4–9.2 mm.

Head. Clypeus distinctly convex, top at clypeal midlength; basomedian area relatively large, about two fifths of bevel in space, as densely, uniformly punctate as lateral section; bevel large, slightly convex, obtusely triangular, with sparse large punctures, reaching base of clypeus in some specimens, but distantly separated from it in others, shiny; lip slightly sinuate with small median emargination and with small, but well developed lateral incision with rectangular corner, lip separate from bevel by punctate groove, WML:LCL = 1.5–1.7, WCL:WML = 1.8. Supraclypeal area flat, densely and distinctly punctate, punctures ill-defined, interspaces between punctures shiny to slightly shiny. Supraantennal tubercle small, slightly elevated on inner side. Antenna relatively short, LA3:WA3 = 2.2–2.4, LA5:WA5 = 2.6–2.7. Frons uniformly punctate, punctures well defined, less than one diameter apart, interspaces variable in size; frontal median line distinct, narrow, well impressed. Vertex relatively uniformly punctate, punctures well defined, less than one diameter apart, interspaces between punctures relatively uniform in size, unsculptured, shiny. Vertex setae short, semierect everywhere, distinctly shorter than 1 × MOD; postocellar impression well developed, relatively deep, open widely Y-shaped to sinuous; vertex slightly to moderately wider than long; WV:LV = 1.2–1.6. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely punctate, punctures well defined, half to one diameter apart, interspaces slightly microsculptured, shiny, setae about 1.0 × MOD. Mesopleuron variable, dis-

tinctly, densely punctate, punctures well developed, interspaces microsculptured, slightly shiny to dull; in some specimens mesopleuron with ill-defined punctures, or with indistinct punctures in posterior and dorsal part; hypoepimeral area dull, with distinct punctures, or coarsely microsculptured, or finely longitudinally ridged, dull; ventral part of mesopleuron with punctures well developed in most specimens, less than one diameter apart, interspaces shiny. Propodeal dorsum relatively finely, irregularly rugose, but with distinct longitudinal ridges in some specimens; propodeal side irregularly, incompletely longitudinally ridged, ridges well developed in large specimens, completely absent in some small specimens, dull; posteromedial margin of propodeal dorsum slightly elevated, slightly produced between marginal ridges, marginal ridges directed ventromedially toward groove on posterior side. Legs densely punctate, punctures small; forebasitarsal rake pale reddish to yellowish, with three apical spines, one preapical spine, and two additional spines. Wings slightly yellowish, veins brown.

Metasoma. Terga I-III with silvery apical fasciae. Apical depressions of terga shallow, with micropunctures evanescent in microsculpture. Terga I-III sparsely, finely micropunctate, punctures ill defined, interspaces microsculptured, shiny to slightly shiny; sculpture of tergum IV-V slightly coarser than on previous terga, punctures slightly denser. Pygidium sparsely punctate, punctures ill defined, interspaces microsculptured, slightly shiny. Central part of sternum II with several large punctures, interspaces microsculptured, shiny; lateral part slightly shiny, densely micropunctate; remaining sterna with uniform sculpture similar to that of sternum II, but more or less reduced laterally.

Coloration. Central part of mandibles, three distal tarsomeres, terga and sterna I-III red. Tegulae brown translucent. Apical parts of terga I-III slightly translucent. Remaining body parts all black.

Description of male (holotype). Body length: 6.7 mm.

Head. Clypeus slightly convex, uniformly curved, top at clypeal midlength; basomedian area large, densely punctate; bevel small, slightly convex, shiny, with several large punctures; lip conspicuously arcuate, well developed medially, with small lateral corner, lip separated from bevel by distinct groove with large punctures; WML:LCL = 1.1, WCL:WML = 2.4. Supraclypeal area flat, distinctly punctate, interspaces between punctures shiny. Supraantennal tubercle small slightly elevated on inner side. Frons uniformly, finely punctate, punctures well defined, one to less than half diameter apart, interspaces variable in size; frontal median line distinct, narrow and finely impressed. Vertex punctate, punctures well defined, less than half to one diameter apart, interspaces unsculptured, shiny. Vertex setae short, semierect, less than 1 × MOD; postocellar impression well developed, relatively deep, open, widely Y-shaped; vertex moderately wider than long; WV:LV = 1.5. Gena dorsally well developed.

Mesosoma. Scutum without distinct anterior impression; scutum and scutellum densely, relatively finely punctate, punctures well defined, most punctures less than one diameter apart, interspaces distinct, unsculptured, shiny, setae about 1.0 × MOD or less. Mesopleuron distinctly punctate throughout, most punctures well defined,

interspaces finely microsculptured, slightly shiny; also hypoepimeral area densely punctate, interspaces microsculptured; ventral part of mesopleuron with punctures well defined, interspaces shiny. Propodeal dorsum coarsely sculptured, ridged and areolate; propodeal side longitudinally ridged, ridges well developed, microsculptured, dull; posteromedial margin of propodeal dorsum inconspicuously elevated, marginal ridges directed ventromedially toward groove on posterior side. Legs densely punctate, punctures small; forefemoral notch relatively shallow, small, shorter than distance that separates it from forefemoral base, central part of notch slightly elevated, anterior margin lined by faint ledge, posterior margin lined by shiny, nearly glabrous area, notch surface without distinct setae, microsculptured, dull. Wings slightly infumate, veins brown.

Metasoma. Terga I-III with silvery apical faciae. Apical depressions of terga shallow, micropunctate. Terga I-III sparsely, distinctly micropunctate, punctures ill defined, interspaces microsculptured, shiny; sculpture of tergum IV-VII coarser than on previous terga, punctures slightly denser. Sterna uniformly punctate nearly like terga.

Coloration. Apical part of mandibles, tegulae, terga and sterna I-III red; distal tarsomeres and forefemoral notch in center dark reddish. Apical parts of terga and tegula translucent. Remaining body parts all black.

Variation of males: Mandibular inner margin with one distinct rectangular tooth and distinct furrow next to the tooth distally. Antenna relatively short, LA3:WA3 = 1.5–1.6, LA5:WA5 = 1.9–2.1. Volsella light brown, ventral setae pointing in various directions; dorsal process slightly wider than corpus in most specimens. Sculpture of mesopleuron very variable, densely to sparsely punctate, punctures mostly well defined, but indistinct in some specimens. Propodeum coarsely to finely sculptured, with or without longitudinal ridges. Forefemoral notch often black.

Geographic distribution. Austria, Bulgaria, Germany, Hungary, Italy, Slovenia and Turkey.

Name derivation. The species is named after its punctate mesopleuron in most males.

Key to species of *T. austriacus* and *T. pompiliformis* subgroups of Europe and Turkey

♀♀

1a Gena dorsally inconspicuous, converging behind compound eyes (Figs 28, 32–34) **2**

1b Gena dorsally more robust (Figs 29–31, 35) **5**

2a Scutum and scutellum sparsely punctate, with large interspaces, punctures well developed, usually up to 1.5 diameter apart (more so in some specimens) (Fig. 38). Ventral part of mesopleuron with relatively large punctures, punctures and interspaces well developed (Fig. 50) ..... ***T. austriacus* Kohl**

2b Scutum and scutellum densely punctate, with small but distinct interspaces, punctures usually less than one diameter apart (only few interspaces larger

in some specimens) (Figs cf. 39, 40). Ventral part of mesopleuron densely punctate, punctures small, ill defined (Fig. cf. 51)..... **3**

3a Wing membrane light yellowish (Fig. cf. 105). Clypeus only slightly convex, bevel small, basomedian area densely punctate, as long as 2/3 of clypeal length (Fig. 19)..... ***T. nobilis* sp. n.**

3b Wing membrane infumate (Fig. 103). Clypeus distinctly convex, basomedian area about as long as bevel or shorter (Fig. 18) **4**

3c Character combination different..... **5**

4a Vertex distinctly wider than long (Fig. 32). Pygidium narrow (Fig. 89), interspaces between punctures unsculptured, bright shiny... ***T. nigripennis* (Spinola)**

4b Vertex about as long as wide or slightly wider than long (Fig. 34). Pygidium wider (Fig. cf. 90), densely microsculptured, dull ..... ***T. opacus* F. Morawitz**

5a Pygidium, mid- and hindtibiae light reddish (Fig. 105)... ***T. ferrugineus* Pulawski**

5b Pygidium and all tibiae dark **6**

6a Clypeus conspicuously elevated, transition between basomedian area and bevel relatively sharp, appearing angulated (Figs 13–14). Clypeal bevel flat, mirror-like shiny. Apical depression of tergum V impunctate medially (Figs 78, 81), sparsely, finely punctate laterally (Figs 79, 82), distinctly more shiny than basal part of tergum. Forebasitarsal rake pale, with three apical and one preapical spine 7

6b Clypeus less elevated, basomedian area sharply separated from bevel in sculpture, but gradually changing into one anoher in convexity (Figs 15–18, 20–21). Clypeal bevel convex, at least basally, shiny. Apical depression of tergum V punctate or impunctate laterally, hardly distinguishable from basal part in sculpture, equally dull (Fig. cf. 85). Forebasitarsal rake dark or pale, with three or two apical and one preapical spine..... **9**

7a Several punctures on scutum and trochanters about two diameters apart..... ..... ***T. prismaticus* Straka**

7b Punctures on scutum and trochanters less than one diameter apart..... **8**

8a Mesopleuron finely punctate, punctures less distinct, evanescent in microsculpture (Fig. 42). Vertex finely punctate, with punctures contiguous medially, laterally more than one diameter apart (Fig. 36) ..... ***T. hungaricus* sp. n.**

8b Mesopleuron coarsely punctate, punctures relatively large and well developed ventrally (Fig. 43). Vertex coarsely punctate, punctures medially separated by distinct interspaces, interspaces slightly larger laterally than medially (Fig. 37)..... ***T. smissenae* sp. n.**

9a Clypeal bevel distinctly triangular, reaching clypeal base at middle and separating basomedian area in two parts; when clypeal base punctate, punctures and interspaces larger than on lateral side of basomedian area (Figs 16, cf. 18, 21)..... **10**

9b Clypeal bevel distinctly separated from clypeal base by basomedian area, which is continuous from side to side, uniformly densely punctate, punctures much finer than on bevel (Figs 15, 17, 20) **14**

10a Clypeus markedly convex, most elevated point located between clypeal midlength and basal third of clypeus (Fig. 22). Vertex setae semierect medially, nearly erect, slightly shorter than 1 × MOD laterally. Dorsolateral cuticular projection of propodeal spiracle slightly arcuate to nearly straight, with apex reddish translucent..... ***T. dimidiatus*** **(Panzer)**

10b Clypeus less convex, most elevated point not well defined, but appearing located near clypeal midlength (Fig. 23). Vertex setae shorter, about 0.5 × MOD, uniformly semierect medially and laterally. Dorsolateral cuticular projection of propodeal spiracle arcuate to semicircular, usually all dark... **11**

11a Punctures of central part of terga IVand V small, ill defined; interspaces between punctures large, distinct, slightly shiny to shiny (Figs cf. 80, 83) **12**

11b Punctures of central part of terga IVand V larger, well defined, approximately 0.5–1.5 diameter apart, slightly shiny to dull (Figs 84, 85) **13**

12 Similar and variable species, difficult to distinguish:

12a Free margin of clypeus in fresh specimens sinuate, with small emargination medially (Fig. 21). Head appearing round in front view, frons uniformly, densely punctate. Vertex impression usually deeper. Dorsolateral cuticular projection of propodeal spiracle arcuate to semicircular, with dark apex. Propodeal side uniformly longitudinally ridged, except on small specimens. Punctures of mesopleuron variable, but more distinct and well developed in some specimens. Pygidium wider, slightly convex to partly flat and shinier in most specimens..... ***T. punctipleuris*** **sp. n.**

12b Free margin of clypeus in fresh specimens arcuate or straight, without emargination medially (Fig. 16). Head appearing transversally oval in front view, frons irregularly punctate. Vertex impression usually shallower. Dorsolateral cuticular projection of propodeal spiracle slightly arcuate to nearly straight, with apex reddish and transparent. Propodeal side longitudinally ridged, ridges anteriorly inconspicuous or absent. Punctures of mesopleuron variable, but usually smaller and less distinct. Pygidium narrower, convex and largely microsculptured in most specimens ..... ***T. dimidiatus*** **(Panzer)**

13a All mesopleuron coarsely sculptured (Figs cf. 44, cf. 46, cf. 48). Hypoepimeral area of mesopleuron, and propodeal dorsum longitudinally ridged (propodeal dorsum sometimes coarsely sculptured, with indistinct ridges) (Figs cf. 46, 58. Tergum V, including apical depression, densely, distinctly punctate (Fig. 85). Pygidium narrower, with microsculptured integument (Fig. 90)... ..... ***T. pompiliformis*** **(Panzer)**

13b Mesopleuron, including hypoepimeral area, finely sculptured (Fig. 45). Propodeal dorsum at most with basal ridges (Figs 57, 61). Apex of tergum V impunctate or finely, sparsely punctate (Fig. 84). Pygidium often wide, with convex and shiny surface (Fig. 88) ..... ***T. jokischianus*** **(Panzer)**

14a All mesopleuron coarsely sculptured (Figs cf. 44, cf. 46, cf. 48). Hypoepimeral area and propodeal dorsum and side longitudinally ridged (propodeal dorsum

sometimes coarsely sculptured, but ridges indistinct) (Figs cf. 46, 58. Tergum V, including apical depression, densely and distinctly punctate (Fig. 85). Forebasitarsal rake reddish in fresh individuals, with two, well separated apical spines and one preapical spine..... ***T. pompiliformis*** **(Panzer)**

14b Mesopleuron, including hypoepimeral area, punctate or finely sculptured (Fig. 45). Propodeal dorsum at most with basal ridges (Figs 56–57, 59–61). Apex of tergum V more sparsely and more finely punctate than in the central part (Figs 80, 83–84) **15**

15a Supraantennal tubercle rounded, distinctly punctate on top, in between and nearly at all sides; small impunctate area occurs only laterally (Fig. 106)..... ..... ***T. bohemicus*** **sp. n.**

15b Supraantennal tubercle prominent with relatively sharply delimited, shiny, nearly impunctate area laterally and at top (Figs 107, cf. 108) **16**

16a Apex of terga IV and V finely microsculptured, sparsely punctate to impunctate, contrasting with coarsely punctate central part of tergum IV, punctures of terga IV and V well developed (Fig. 84). Pygidium often wide, with distinctly convex, shiny surface (Fig. 88). Dorsolateral cuticular projection of propodeal spiracle arcuate to semicircular, with dark apex. Supraclypeal area with distinctly microsculptured interspaces between punctures, usually appearing dull (Fig. cf. 108). Propodeal dorsum without longitudinal ridges, ridged only basally, or with a few irregular ridges (Figs 57, 61)..... ..... ***T. jokischianus*** **(Panzer)**

16b Apex of tergum IV coarsely microsculptured, sparsely punctate (Fig. 83). Punctures of terga IV and V ill defined (Fig. 83). Pygidium of usual size, slightly convex, largely microsculptured, shiny at most in apical third (Figs cf. 87, 90). Dorsolateral cuticular projection of propodeal spiracle variable. Supraclypeal area with microsculptured interspaces between punctures but usually appearing shiny (Fig. 107). Propodeal dorsum variable but often with longitudinal ridges (Figs 56, 60) **17**

17 Similar and variable species, difficult to distinguish:

17a Clypeal free margin in fresh specimens sinuate, with small anterior emargination medially (Fig. 21). Head appearing round in front view, frons uniformly and densely punctate. Vertex impression usually conspicuous. Dorsolateral cuticular projection of propodeal spiracle arcuate to semicircular, with dark apex. Propodeal side uniformly longitudinally ridged, except in small specimens. Punctures of mesopleuron variable but more distinct and well defined in some specimens. Pygidium wider and shinier in most specimens..... ..... ***T. punctipleuris*** **sp. n.**

17b Clypeal free margin in fresh specimens arcuate or straight, without anterior emargination medially (Fig. 16). Head appearing transversally oval in front view, frons irregularly punctate. Vertex impression usually less conspicuous.

Dorsolateral cuticular projection of propodeal spiracle slightly arcuate to nearly straight, with apex reddish transparent. Propodeal side longitudinally ridged, ridges anteriorly inconspicuous or absent. Punctures of mesopleuron variable but usually smaller and ill defined. Pygidium narrow and largely microsculptured in most specimens..... ***T. dimidiatus*** **(Panzer)**

♂♂

1a Surface of forefemoral notch slightly shiny to shiny, without elevated plate and ledge on margins and with distinct small setae (Fig. 62). Setae on ventral part of volsella uniformly directed ventrally or nearly so (Figs 91–92). (*T. austriacus* species subgroup) **2**

1b Surface of forefemoral notch microsculptured (finely so in some species), slightly elevated, with distinct ledge on inner margin (also on outer margin in most species), without distinct setae (Figs 63–65, 68). Setae on ventral part of volsella directed randomly outward and inward (Figs 94–102). (*T. pompiliformis* species subgroup) **4**

2a Central part of scutum sparsely punctate, punctures more than one diameter apart (Fig. cf. 38)..... ***T. austriacus*** **Kohl**

2b Scutum densely punctate, puncture less than one diameter apart (Fig. cf. 39) **3**

3a Gena narrow (Figs cf. 25, cf. 28). Trochanteral venters with large, glabrous spaces between punctures. Ventral and lower part of mesopleuron coarsely punctate, punctures well defined. Vertex, propodeum and metasoma finely sculptured..... ***T. prismaticus*** **Straka**

3b Gena robust (Fig. cf. 27). Trochanters densely punctate. Ventral and lower part of mesopleuron coarsely punctate (Fig. cf. 43), punctures well defined. Vertex (Fig. cf. 37), propodeum (Fig. cf. 55) and metasoma coarsely sculptured..... ***T. smissenae*** **sp. n.**

3c Gena robust (Fig. cf. 27). Trochanters densely punctate. Ventral and lower part of mesopleuron finely and densely punctate, punctures ill defined (Fig. cf. 42). Vertex (Fig. 36), propodeum (Fig. 54) and metasoma finely sculptured.....Tentative position of unknown male of ***T. hungaricus*** **sp. n.**

4a Gena dorsally short, conspicuously converging behind compound eyes (Figs 25, cf. 32–34). Vertex distinctly wider than long..... **5**

4b Gena behind compound eyes more robust (Figs 24, 26–27). Vertex only slightly wider than long **8**

5a All tibia and tergum VII reddish (Fig. cf. 105)..... ***T. ferrugineus*** **Pulawski**

5b All tibia and tergum VII dark **6**

6a All clypeus densely punctate, clypeal bevel indistinct (Fig. 7). Two or three basal metasomal terga and sterna light red. Forefemoral notch large, light reddish (Fig. 73, cf. 65, cf. 72)..... ***T. nobilis*** **sp. n.**

6b Clypeal bevel distinct, sparsely punctate (Figs 1–6, 8–10). Metasoma black, or two basal terga dark red, sternum II almost always black. Forefemoral notch smaller, dark red, or black (Figs 66–67, 74) **7**

7a Forefemoral notch indistinctly microsculptured, shiny (Fig. 66). Clypeal lip wider than one third of clypeal width, projecting medially, its apical margin sinuate (Fig. 6). Mandibular inner margin with distinct small furrow distally of inner tooth (Fig. cf. 12) ..... ***T. nigripennis*** **(Spinola)**

7b Forefemoral notch densely microsculptured, dull (Fig. 67). Clypeal lip narrower, about as wide as one third of clypeal width, uniformly arcuate to nearly straight (Fig. 10). Mandibular inner margin shallowly emarginated distally of inner tooth, without furrow (Fig. 11) ..... ***T. opacus*** **F. Morawitz**

8a Supraantennal tubercle rounded, distinctly punctate on top, in-between and nearly at all sides; small impunctate area only laterally (Fig. 106) ..... ***T. bohemicus*** **sp. n.**

8b Supraantennal tubercle prominent, relatively sharply delimited, shiny, nearly impunctate area dorsally and laterally (Figs 107–108) **9**

9a Mesopleuron coarsely irregularly ridged (Figs 44, 48) or coarsely punctate (Fig. 49). Forefemoral notch black or dark red (Fig. 68) **10**

9b Mesopleuron finely sculptured (Figs cf. 45, cf. 47). Forefemoral notch light red (Figs 64–65, 69) **12**

10a Body black, silvery apical fasciae present on terga I-IV (Fig. 104) ..... ***T. cretensis*** **sp. n.**

10b At least basal metasomal terga red, silvery apical fasciae present on terga I-III **11**

11a Clypeus coarsely punctate, interspaces between punctures large, punctures about one diameter apart (Fig. 9). Clypel lip slightly arcuate (Fig. 9). Dorsal part of mesopleuron, especially hypoepimeral area more or less conspicuously longitudinally ridged (Figs cf. 44, 48). Forefemoral notch markedly carinated on both anterior and posterior margin (Fig. 68). Volsella dark, dorsal process narrow, about as wide as volsellar corpus (Fig. 101) ..... ***T. pompiliformis*** **(Panzer)**

11b Clypeus finely and densely punctate, interspaces between punctures small, punctures less than one diameter apart (Fig. 8). Clypeal lip conspicuously prominent (Fig. 8). Dorsal part of mesopleuron distinctly punctate, punctures well developed, hypoepimeral area also with punctures in some specimens (Fig. 49). Forefemoral notch small, inconspicuously carinated, carina well developed only on anterior margin (Fig. 69). Volsella light brown, dorsal process basally wider than volsellar corpus (Fig. 102) ..... ***T. punctipleuris*** **sp. n.**

12a Mesopleuron laterally and ventrally with well-defined punctures (punctures distinct also on hypoepimeral area in some specimens), interspaces distinct, light shiny to shiny on most parts (Fig. 49). Forefemoral notch small and relatively shallow, indistinctly carinated, carina well developed only on anterior margin (Figs 69, 76). Clypeal lip conspicuously prominent (Fig. 8) ..... ***T. punctipleuris*** **sp. n.**

12b Mesopleuron laterally and ventrally with ill-defined punctures, when interspaces distinct, then microsculptured, slightly shiny to dull. Forefemoral notch larger and deeper, distinctly carinated on anterior and posterior margin of notch (Figs cf. 63, 64–65). Clypeal lip of usual form, slightly arcuate (Fig. cf. 9) **13**

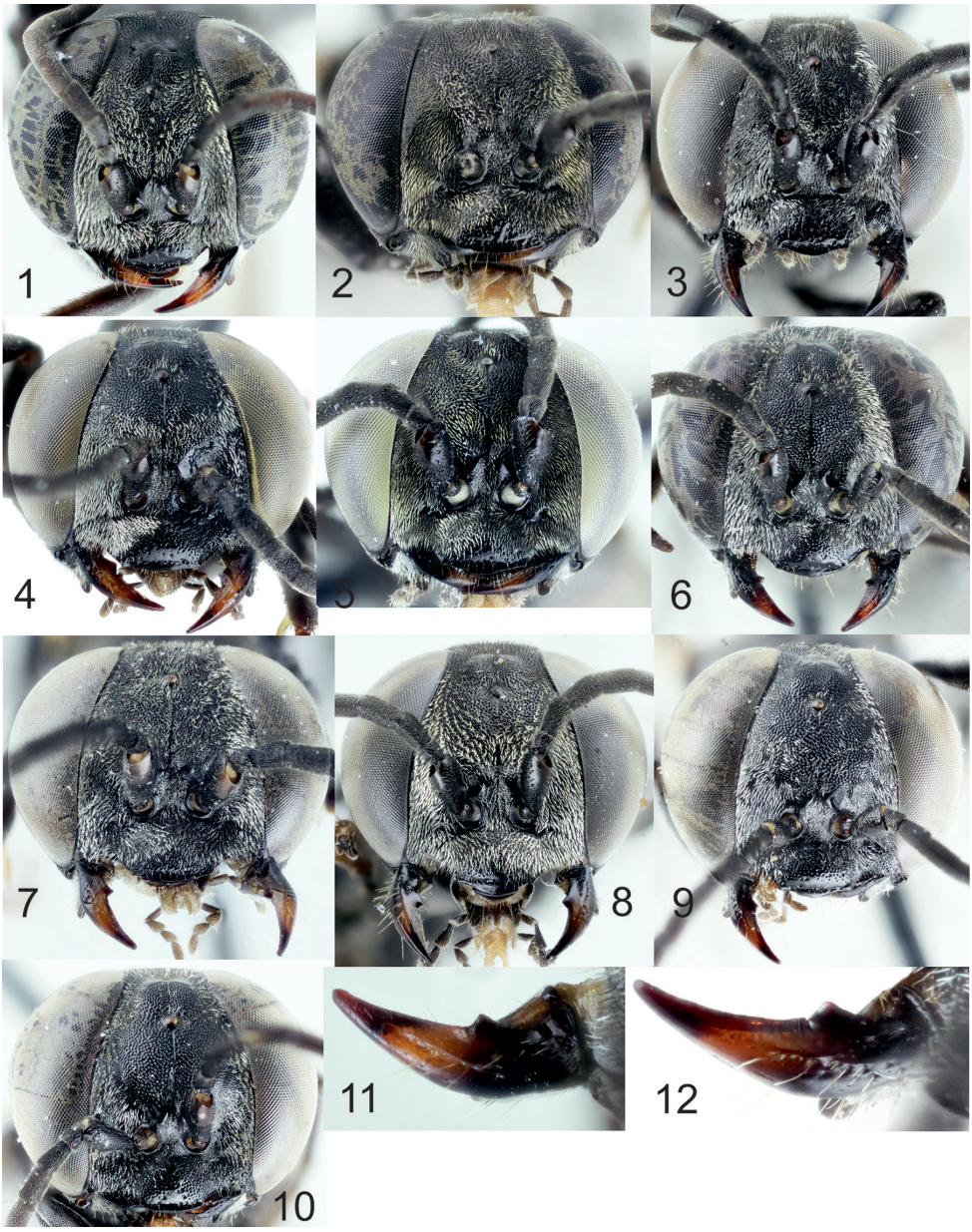
13a Supraclypeal area forming groove, supraantennal tubercle distinctly elevated ventromedially (Fig. cf. 108). Forefemoral notch light red, large, its diameter usually longer than distance that separates it from forefemoral base (Fig. 65). Propodeal side densely ridged basally in most specimens (Fig. cf. 45). Posteromedial margin of propodeal dorsum slightly elevated, with nearly parallel ridges that separate dorsum from groove on posterior surface (Fig. 61). Terga densely micropunctate ..... ***T. jokischianus* (Panzer)**

13b Supraclypeal area flat, supraantennal tubercle slightly elevated ventromedially (Fig. cf. 107). Forefemoral notch variable, usually smaller, light red to red (Fig. 64). Propodeal side variable but with ridges disappearing anteriorly in most specimens. Posteromedial margin of propodeal dorsum elevated and produced between ridges, ridges directed ventromedially toward groove on posterior surface (Fig. 60). Terga sparsely micropunctate with variable interspaces..... ***T. dimidiatus* (Panzer)**

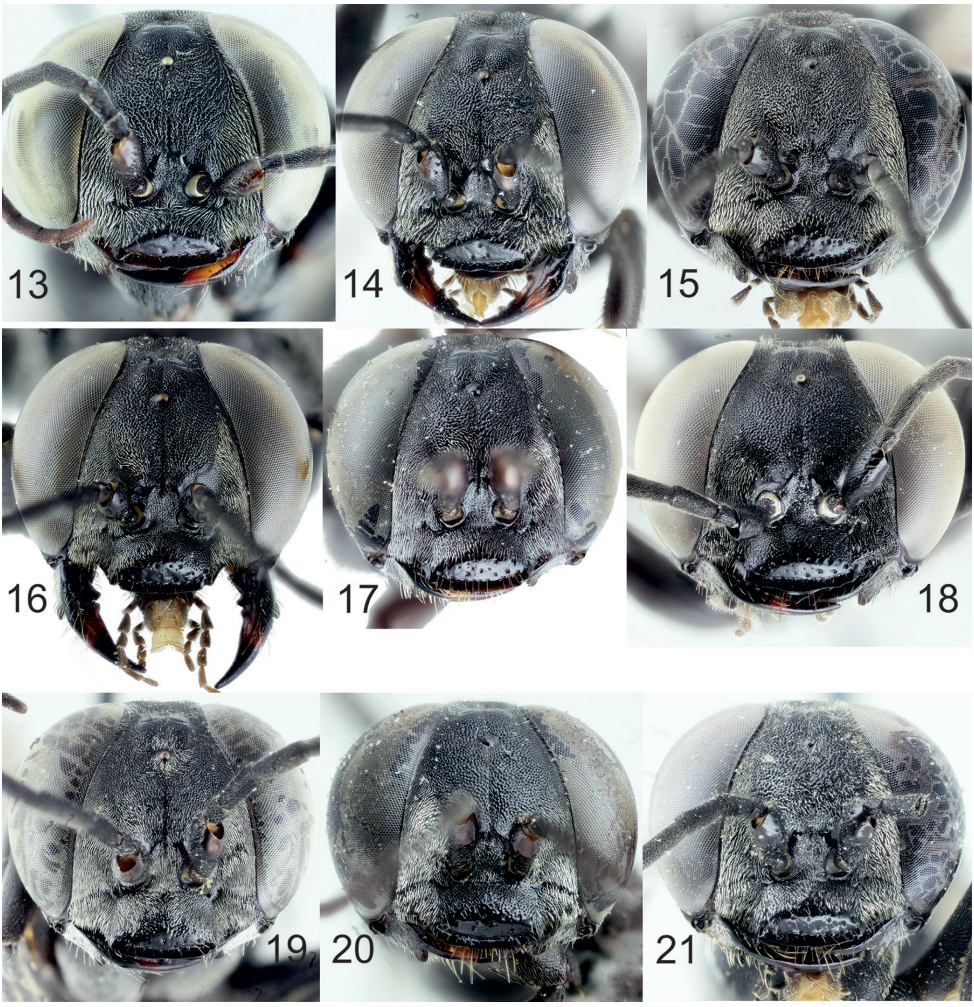
Discussion

Morphological variation in *T. pompiliformis* sensu Pulawski (1971) was found to be extensive (Pulawski 1971). Some species of this group have already been separated by Pulawski himself (Pulawski 1971) or later recognized as valid (Straka 2004, 2005). Present recognition of fourteen species and two species subgroups may appear surprising, but this variation is correlated with ecological and biogeographic data. Not all species are ubiquitous. Only two reach Scandinavia (*T. jokischianus* and *T. dimidiatus*). Some species occur predominantly on sandy or loess habitats (*T. jokischianus*, *T. nigripennis*, and *T. nobilis*). This uneven distribution have suggested the presence of different species within a group for a long time, validated in the present study. These species delimitations are supported by morphological characters.

Figures

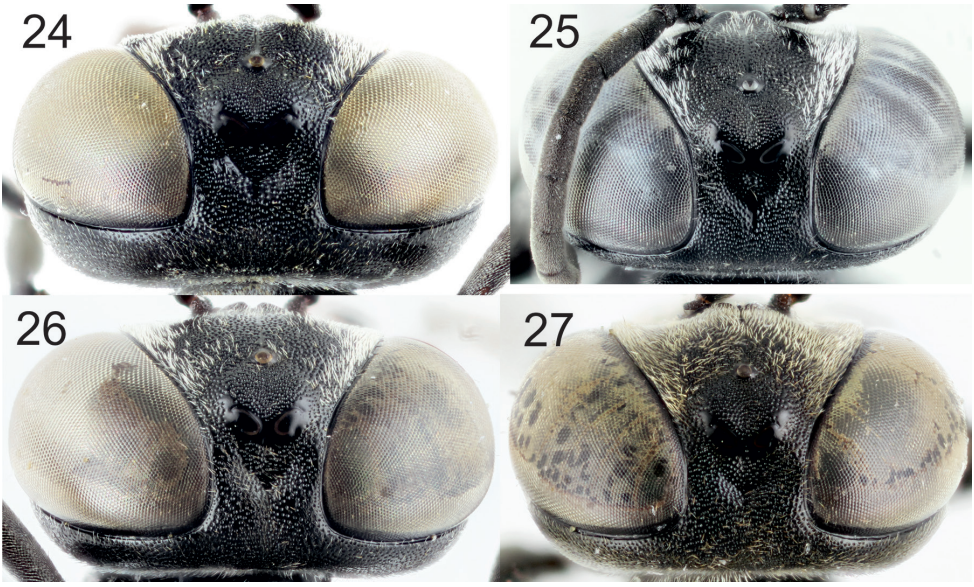


Figures 1–12. Head of male, front view, and mandibles. **1** *Tachysphex smissenae* sp. n. **2** *T. bohemicus* sp. n. **3** *T. cretensis* sp. n. **4** *T. dimidiatus* **5** *T. jokischianus* **6** *T. nigripennis* **7** *T. nobilis* sp. n. **8** *T. punctipleuris* sp. n. **9** *T. pompiliformis* **10** *T. opacus* **11** *T. opacus*, mandible, frontal view **12** *T. pompiliformis*, mandible, frontal view.

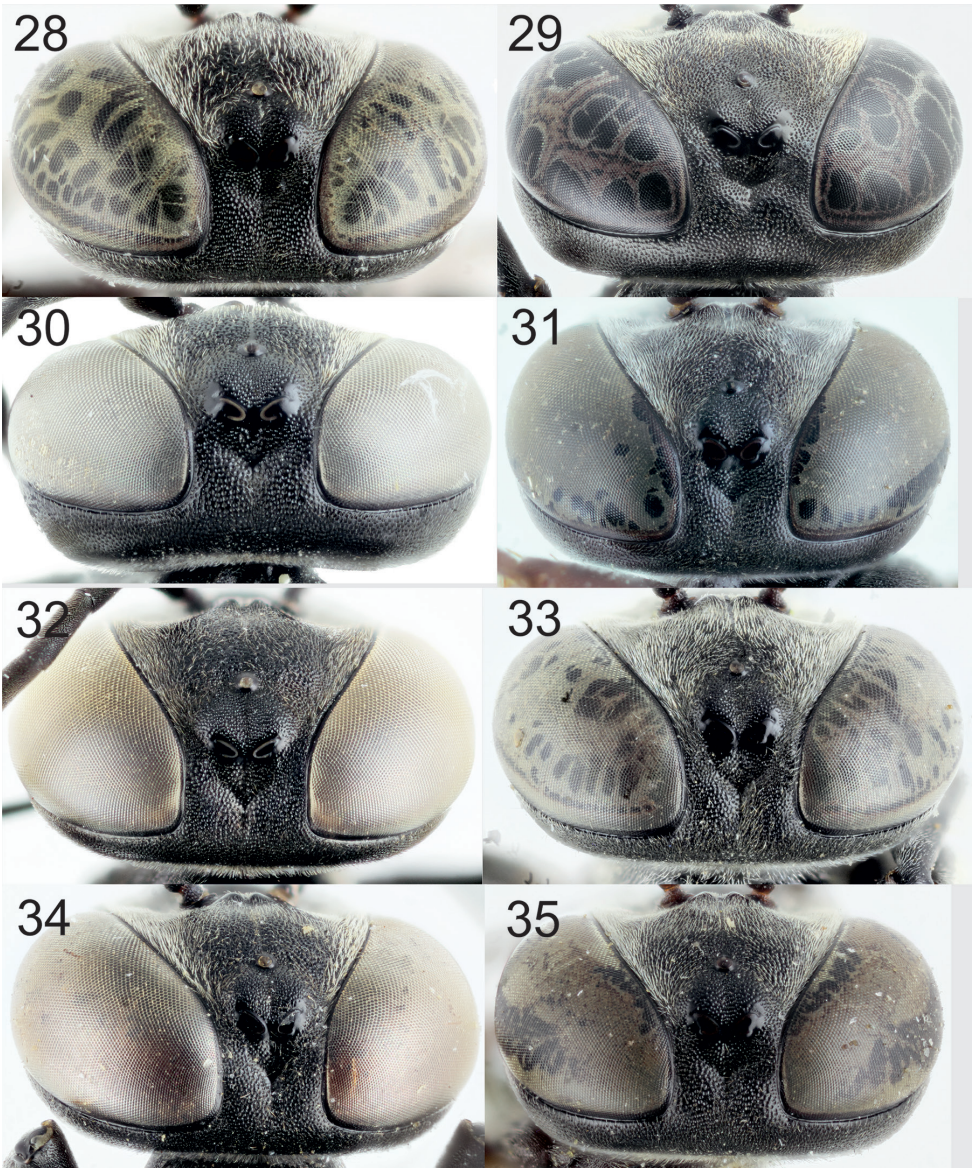


Figures 13–21. Head of female, front view. **13** *Tachysphex hungaricus* sp. n. **14** *T. smissenae* sp. n. **15** *T. bohemicus* sp. n., **16** *T. dimidiatus* **17** *T. jokischianus* **18** *T. nigripennis* **19** *T. nobilis* sp. n. **20** *T. pompiliformis* **21** *T. punctipleuris* sp. n.

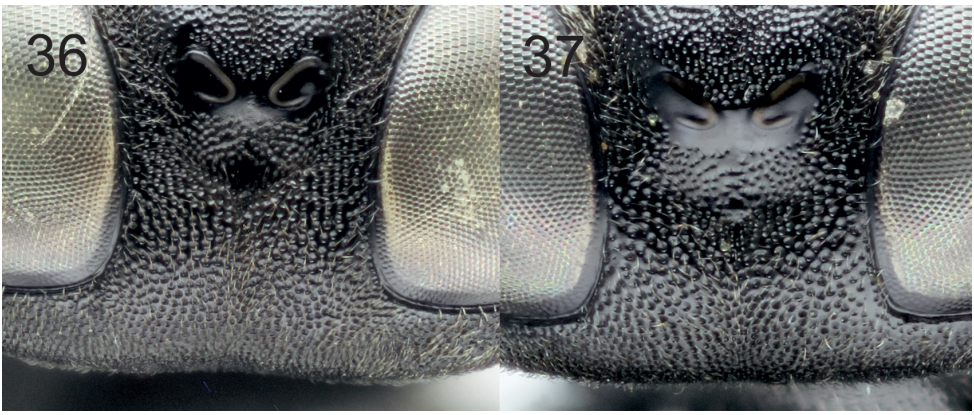
Figures 22–23. Head of female, lateral view of clypeus. **22** *Tachysphex dimidiatus* **23** *T. jokischianus*.



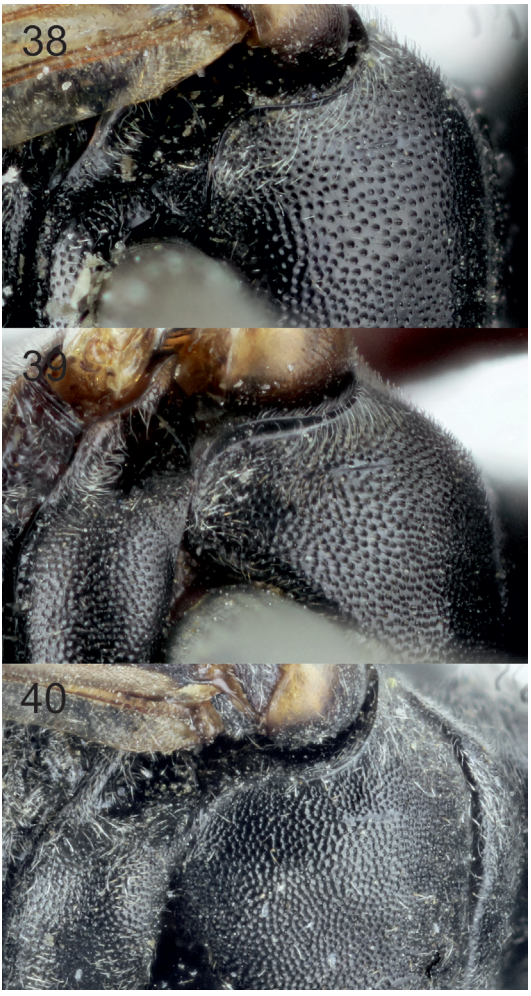
Figures 24–27. Gena of male. **24** *Tachysphex dimidiatus* **25** *T. opacus* **26** *T. pompiliformis* **27** *T. punctipleuris*.



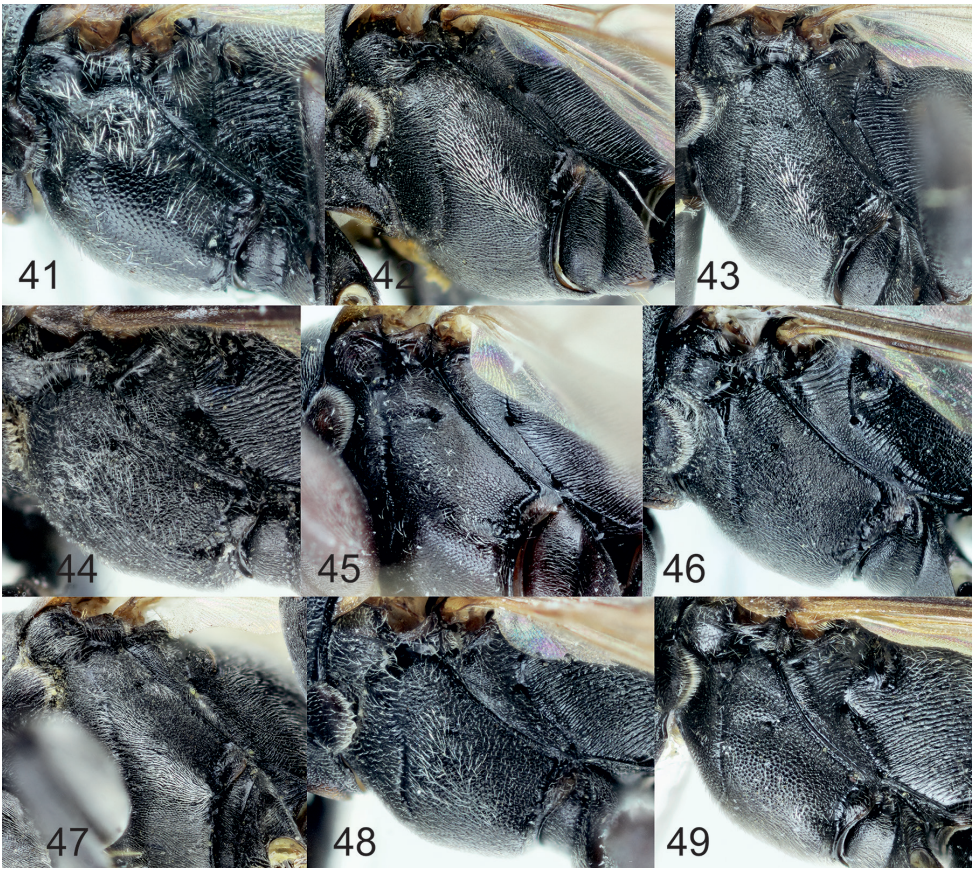
Figures 28–35. Gena of female. **28** *Tachysphex austriacus* **29** *T. bohemicus* sp. n. **30** *T. dimidiatus* **31** *T. jokischianus* **32** *T. nigripennis* **33** *T. nobilis* sp. n. **34** *T. opacus* **35** *T. pompiliformis*.



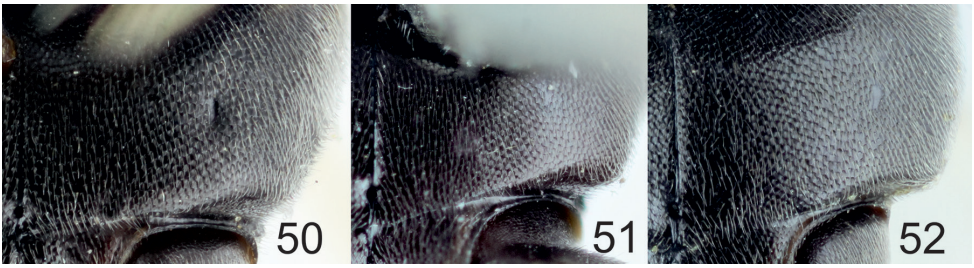
Figures 36–37. Vertex of female, detail. **36** *Tachysphex hungaricus* sp. n. **37** *T. smissenae* sp. n.



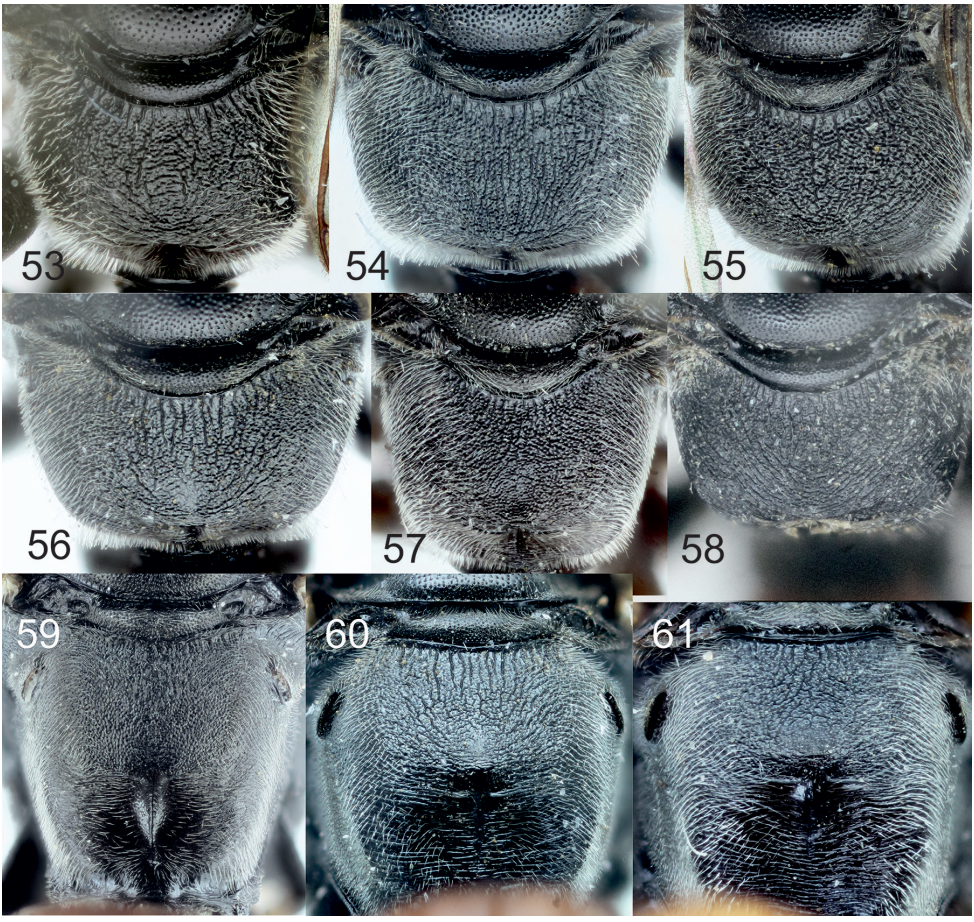
Figures 38–40. Scutum of female, dorsal view. **38** *Tachysphex austriacus* **39** *T. jokischianus* **40** *T. nobilis* sp. n.



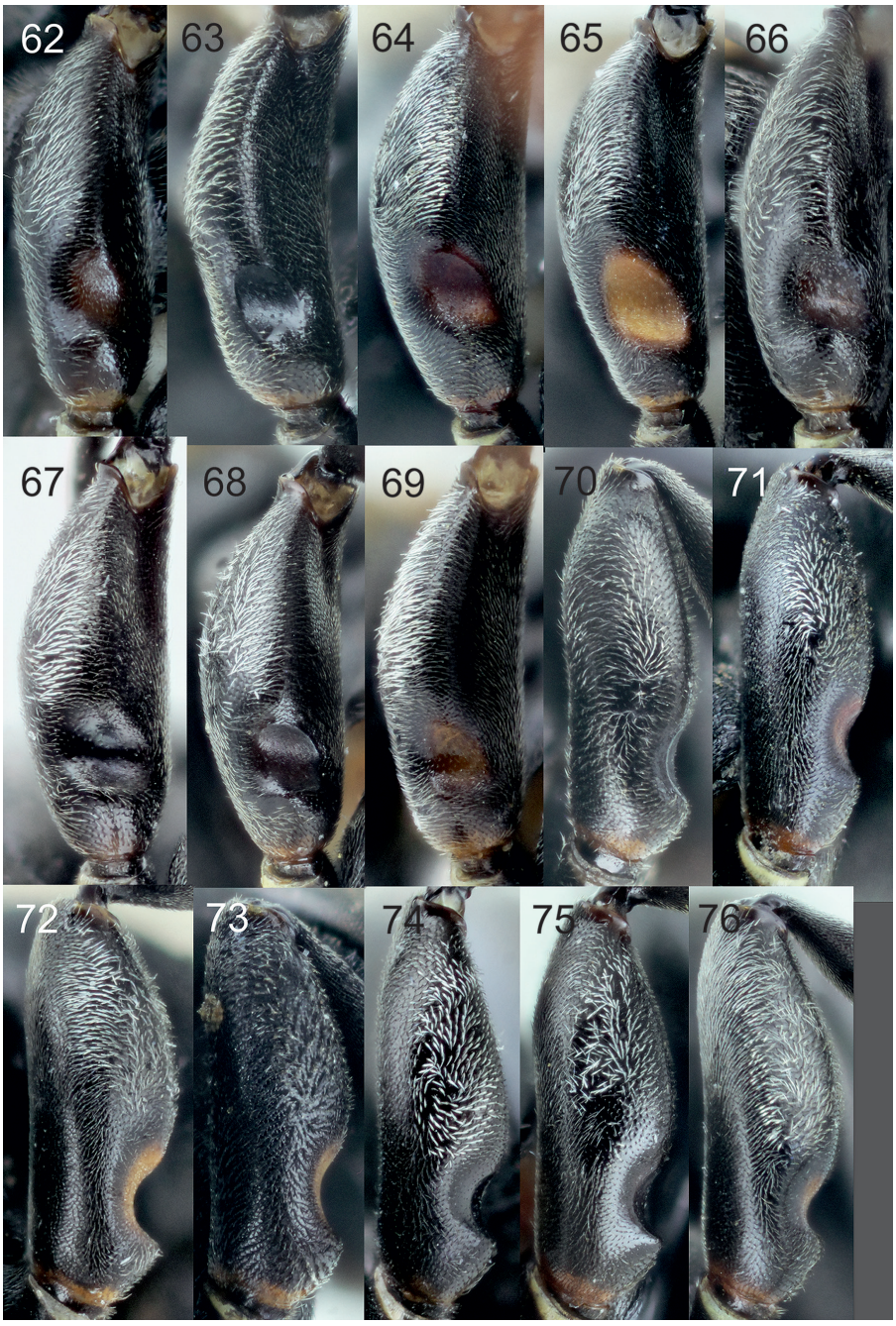
Figures 41–49. Mesopleuron, lateral view, sculptures. **41** *Tachysphex austriacus*, male **42** *T. hungaricus* sp. n., female **43** *T. smissenae* sp. n., female **44** *T. cretensis* sp. n., male **45** *T. jokischianus*, female **46** *T. nigripennis*, female **47** *T. nobilis* sp. n., female **48** *T. pompiliformis*, male **49** *T. punctipleuris* sp. n., male.



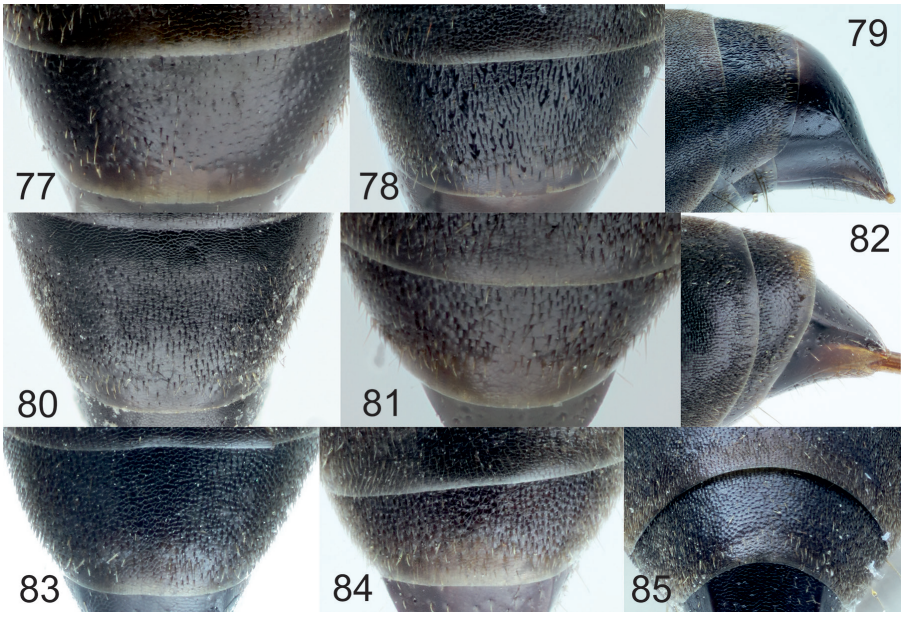
Figures 50–52. Mesopleuron, ventral view, sculptures, female. **50** *Tachysphex austriacus* **51** *T. jokischianus* **52** *T. pompiliformis*.



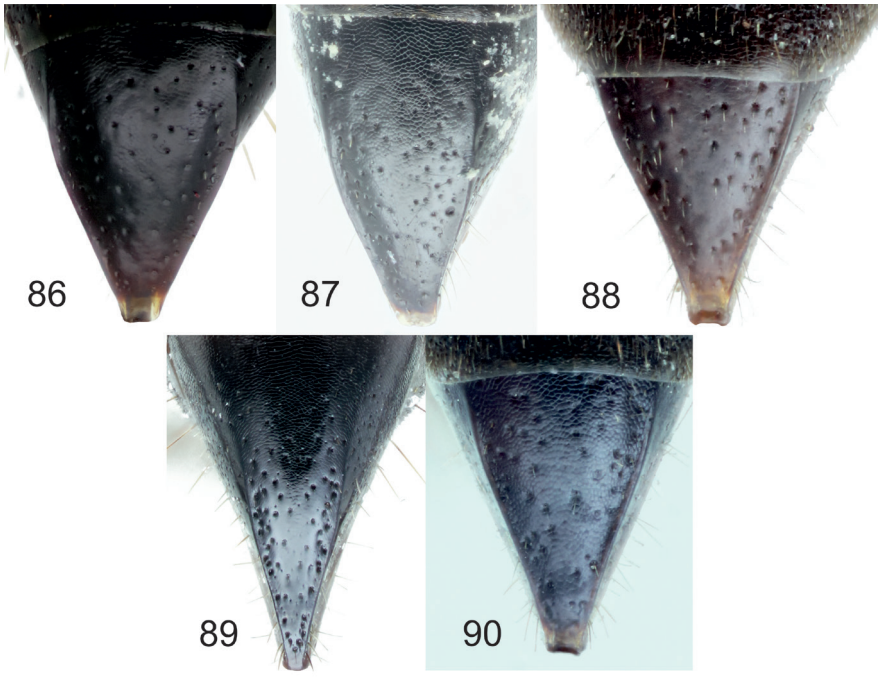
Figures 53–61. Propodeum, dorsal and posterior view, female. **53** *Tachysphex austriacus*, dorsal view **54** *T. hungaricus* sp. n., dorsal view **55** *T. smissenae* sp. n., dorsal view **56** *T. dimidiatus*, dorsal view **57** *T. jokischianus*, dorsal view **58** *T. pompiliformis*, dorsal view **59** *T. bohemicus* sp. n., posterior view **60** *T. dimidiatus*, posterior view **61** *T. jokischianus*, posterior view.



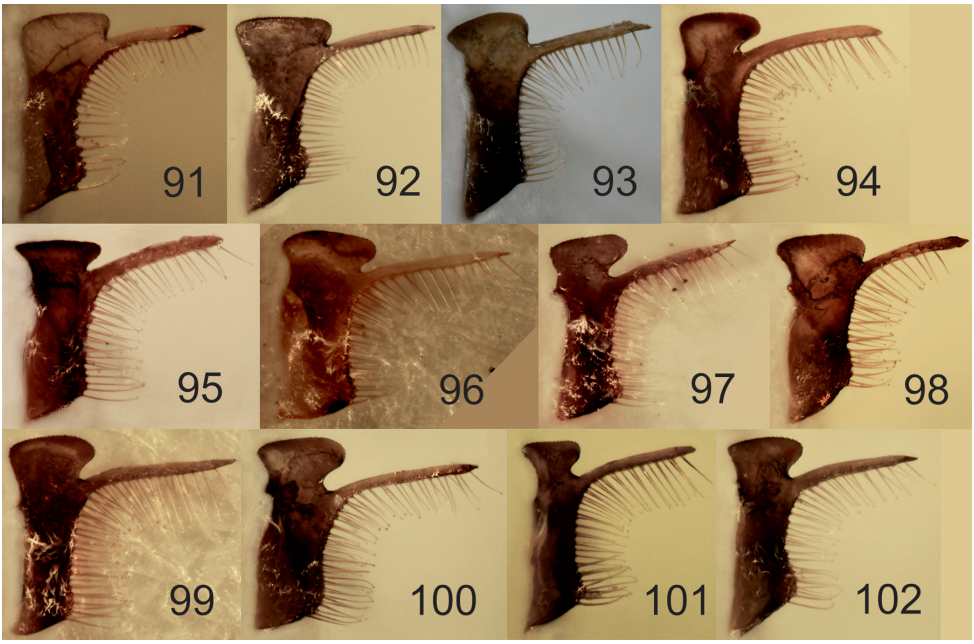
Figures 62–76. Forefemoral notch of male, ventral and lateral view. **62** *Tachysphex austriacus*, ventral view **63** *T. bohemicus* sp. n., ventral view **64** *T. dimidiatus*, ventral view **65** *T. jokischianus*, ventral view **66** *T. nigripennis*, ventral view **67** *T. opacus*, ventral view **68** *T. pompiliformis*, ventral view **69** *T. punctipleuris* sp. n., ventral view **70** *T. bohemicus* sp. n., lateral view **71** *T. dimidiatus*, lateral view **72** *T. jokischianus*, lateral view **73** *T. nobilis* sp. n., lateral view **74** *T. opacus*, lateral view **75** *T. pompiliformis*, lateral view **76** *T. punctipleuris* sp. n., lateral view.



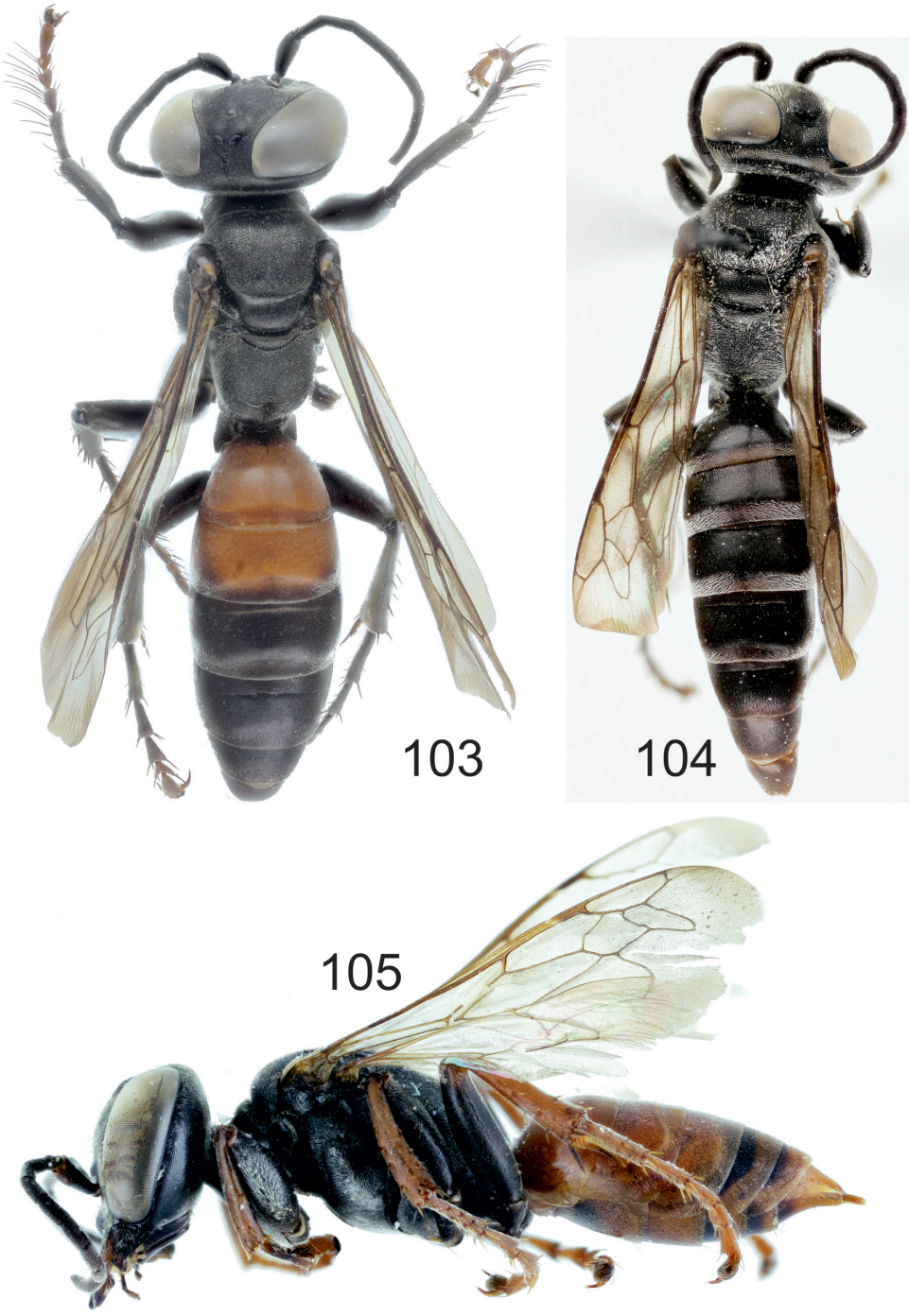
Figures 77–85. Tergum V, sculpture, female. **77** *Tachysphex austriacus*, dorsal view **78** *T. hungaricus* sp. n., dorsal view **79** *T. hungaricus* sp. n., lateral view **80** *T. bohemicus* sp. n., dorsal view **81** *T. smissenae* sp. n., dorsal view **82** *T. smissenae* sp. n., lateral view **83** *T. dimidiatus*, dorsal view **84** *T. jokischianus*, dorsal view **85** *T. pompiliformis*, posterior view.



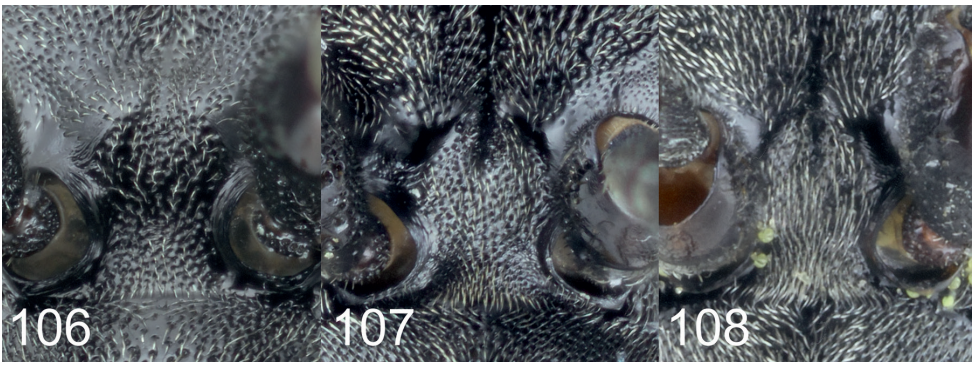
Figures 86–90. Pygidium, female. **86** *Tachysphex austriacus* **87** *T. bohemicus* sp. n. **88** *T. jokischianus* **89** *T. nigripennis* **90** *T. pompiliformis*.



Figures 91–102. Volsella, lateral view. **91** *Tachysphex austriacus* **92** *T. smissenae* sp. n. **93** *T. bohemicus* **94** *T. cretensis* sp. n. **95** *T. dimidiatus* **96** *T. ferrugineus* **97** *T. jokischianus* **98** *T. nigripennis* **99** *T. nobilis* sp. n. **100** *T. opacus* **101** *T. pompiliformis* **102** *T. punctipleuris* sp. n.



Figures 103–105. Habitus, dorsal and lateral view. **103** *Tachysphex nigripennis*, female, dorsal view **104** *T. cretensis* sp. n., male, dorsal view **105** *T. ferrugineus*, female, lateral view.



Figures 106–108. Supraantennal tubercles, frontal view. **106** *Tachysphex bohemicus* sp. n. **107** *T. dimidiatus* **108** *T. nobilis* sp. n.

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RESEARCH ARTICLE

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Description of two new species of the *Exocelina broschii*-group from Papua New Guinea, with revision and key to all representatives of this species group (Coleoptera, Dytiscidae, Copelatinae)

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Abstract

Two new species of *Exocelina* Broun, 1886 from Papua New Guinea are described herein: *E. mondmillensis* **sp. n.** and *E. pseudomarinae* **sp. n.** They are placed into the *E. broschii*-group based on the shovel/fork-like ventral sclerites of their median lobe. While the former has rather distinct combination of the morphological characters (inconspicuous dorsal punctation, thin apex of the median lobe and ventral sclerite of the median lobe with two tips of different length), the latter is very similar to already described species *E. marinae* (Shaverdo, Sagata & Balke, 2005). All described species of the group are revised and a key to their identification is provided. Important diagnostic characters (habitus, color, protarsomeres 4–5, median lobes, and parameres) are illustrated. Data on the distribution of all species of the group are given showing that its representatives occur only in Papua New Guinea and most of them are widely distributed in it central part.

Keywords

Exocelina broschii-group, Copelatinae, Dytiscidae, new species, Papua New Guinea

Introduction

This paper continues our previous studies on the New Guinea species of the genus *Exocelina* Broun, 1886 (Balke 1998, 1999; Shaverdo and Balke 2014; Shaverdo et al. 2005, 2012, 2013, 2014, 2016, submitted) and deals with one of the five species groups of New Guinea *Exocelina*, the *E. broschii*-group. This group was introduced by Shaverdo et al. (2005) for three species from Papua New Guinea (*E. broschii* (Balke, 1998), *E. hintelmannae* (Shaverdo, Sagata & Balke, 2005) and *E. marinae* (Shaverdo, Sagata & Balke, 2005)) and defined by the following apomorphy: shovel/fork-like ventral sclerite of the median lobe. Monophyly of the group was also supported by the phylogenetic analysis, based on molecular data (Toussaint et al. 2014).

Here, we provide a detailed diagnosis of the *E. broschii*-group, describe two new species, review the known species providing new faunistic data, and present a key to the species and map of their distribution.

We provided electronic resources for the species treated here in the form of species pages, which were automatically created by ZooKeys on the species-id.net portal with the publication of this article. This wiki engine based site provides for example high resolution art work and can be improved interactively should new data become available. By providing these resources, we hope to help creating a more user-friendly, sustainable taxonomy as suggested by Riedel et al. (2013).

Including the results of this work, 91 *Exocelina* species are described from New Guinea and 144 worldwide.

Material and methods

The present work is based on the material from the following collections:

BMNH	The Natural History Museum, London, UK
NARI	Papua New Guinea National Insect Collection, Port Moresby, PNG
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
ZSM	Zoologische Staatsammlung München, Munich, Germany

All specimen data are quoted as they appear on the labels attached to the specimens. Label text is cited using quotation marks. Comments in square brackets are ours. We extracted DNA and obtained DNA sequence data for some of the species/specimens, marked with individual DNA extraction numbers (e.g., "264 DNA M. Balke"). All types of the herein described species are provided with red labels. The female specimens, identification of which is difficult or sometimes impossible, were included in the type series only when collected with males of respective species and did not differ morphologically from them. If two or more morphologically similar species were collected together (i.e., males found together), their females were not included in the types series of the respective species but were instead mentioned under additional material. Species descriptions are based on the whole type series.

Some of the species treated herein are very similar to each other and, based on low overall genetic divergence, most likely also very recent (Toussaint et al. 2014). We have used constant morphological difference based on examined series as an indicator of interrupted gene flow and as an operational criterion to delineate biological species, but suggest that extensive population genetic work using genomic data might reveal many additional lineages that represent putative species in a highly structured geographic and geological setting.

Measurements were taken with a Wild M10 stereomicroscope choosing the smallest and the largest specimens within and among the populations. The following abbreviations were used: TL (total body length), TL-H (total body length without head), MW (maximum body width), and hw (handwritten). The number of ventral setae on the male protarsomere 5 is given for only one specimen of each species, which was mounted on a glass slide (see below) for drawing. This character was found not very useful for the species identification since it is possible to make a general statement of the setation pattern (short/long, dense/sparse) but not to count them with certainty at the magnification of normal dissecting scopes. The potential phylogenetic information content of this character will be studied in a further work.

Drawings were made with the aid of a camera lucida attached to a Leica DM 2500 microscope. For detailed study and drawing, protarsi, and genitalia were removed and mounted on glass slides with DMHF (dimethyl hydantoin formaldehyde) as temporary preparations. The drawings were scanned and edited, using the software Adobe Illustrator CS5.1. Arrangement of the figures follows the species descriptions.

The terminology to denote the orientation of the genitalia (ventral for median lobe and dorsal and external for paramere) follows Miller and Nilsson (2003). Left and right lobes of the ventral sclerite of the median lobe are indicated according figure view, not their original orientation. The terminology on the structure of the prosternum follows Larson et al. (2000). Administrative divisions of Papua New Guinea follow information from Wikipedia (2016).

Diagnosis of the *Exocelina broschii*-group sensu Shaverdo et al. (2005)

The representatives of the *E. broschii*-group share the following diagnostic characters:

- beetles small or middle-sized (TL-H 3.2–4.15 mm);
- habitus oblong-oval (broadest approximately at elytral middle), with rounded pronotal and elytral sides, body outline continuous;
- pronotum short, trapezoidal, with posterior angles not drawn backwards;
- coloration brown to piceous, mainly uniform, sometimes with paler head and pronotum and darker elytra;
- microreticulation and punctation of dorsal surface very fine to strongly impressed, so that beetles shiny to matt dorsally;
- metacoxae and abdominal ventrites 1–5 (and 6 in males) with thin, almost longitudinal striae/strioles;

– pronotum and elytra without striae or strioles;
– pronotum with lateral bead;
– male antennomeres not modified, antennomere 2 larger than antennomere 3;
– male protarsomeres 1–3 not expanded laterally;
– male protarsomere 4 cylindrical, narrow, with large anterolateral hook;
– male protarsomere 5 not modified: long and narrow, without expansion and concavity, ventrally with two sparse rows of relatively short setae;
– median lobe of aedeagus with continuous outline in ventral and lateral view;
– ventral sclerite of median lobe not deeply divided in the middle, apically forming a shovel/fork-like structure with two apices;
– apical part of median lobe with numerous setae;
– paramere without notch on dorsal side;
– paramere with long setae occupying whole dorsal side.

Checklist and distribution of the species of the *Exocelina broschii*-group

Representatives of this species group are recorded only from Papua New Guinea (PNG).

1.	*Exocelina broschii* (Balke, 1998)	PNG Madang, Eastern Highlands
2.	*Exocelina hintelmannae* (Shaverdo, Sagata & Balke, 2005)	PNG: Simbu, Eastern Highlands, Gulf
3.	*Exocelina marinae* (Shaverdo, Sagata & Balke, 2005)	PNG: Sandaun, Hela
4.	*Exocelina mondmillensis* sp. n.	PNG: Western Highlands, Enga, Madang
5.	*Exocelina pseudomarinae* sp. n.	PNG: Hela

Species descriptions

1. *Exocelina broschii* (Balke, 1998)

Figs 1–3, 8, 9A–E

Copelatus (*Papuadytes*) *broschii* Balke, 1998: 327; Nilsson 2001: 76 (catalogue).
Papuadytes broschii (Balke, 1998): Shaverdo et al. 2005: 270, 271 (notes, illustration).
Papuadytes broschii (Balke, 1998): Nilsson and Fery 2006: 56 (addition to catalogue).
Exocelina broschii (Balke, 1998): Nilsson 2007: 33 (comb. n.).
Exocelina undescribed sp. MB1520: Toussaint et al. 2014: Supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Madang Province, Finisterre Range, Moro, approximately 5°42'47.6"S; 146°03'40.1"E.

Type material studied. *Holotype*: male "Stn. No. 82", "NEW GUINEA: Madang Dist., Finisterre Mts. Moro.C.5550ft. 30.x.-15.xi.1964.", "M.E. Bacchus. B.M. 1965-120", "Holotypus" [red], "Copelatus broschii sp.n. Balke des. 1997" (BMNH). *Paratypes*: 4 males, 1 female with the same labels as the holotype, except for "Paratypus Copelatus broschii sp.n. Balke des. 1997" (BMNH, NHMW, ZSM).

Figures 1–3. Habitus and coloration of *Exocelina broschii* (Balke, 1998). **1** holotype **2** Madang, Simbai area, PNG 152, specimen with finer dorsal punctation **3** Madang, Simbai area, PNG 152, specimen with coarser dorsal punctation.

Additional material. Madang: 1 male "Stn. No. 82", "NEW GUINEA: Madang Dist., Finisterre Mts. Moro.C.5550ft. 30.x.-15.xi.1964.", "M.E. Bacchus. B.M. 1965-120", "Paratypus Copelatus broschii sp.n. Balke des. 1997" (BMNH) – although this specimen is with the paratype label, it is not included in the type material of the original description in Balke (1998). 17 males, 8 females "Papua New Guinea: Madang, Adalbert Mts., Sewan - Keki, 700m, 4.v.2006, 04.42.215S 145.25.154E, Balke & Manaono (PNG 51)" (NARI, NHMW, ZSM). 7 males "Papua New Guinea: Madang, Adalbert Mts., Keki, 850m, 4.v.2006, nr 04.42.300S 145.25.089E, Balke & Manaono (PNG 52)", one male with an additional green label "DNA M.Balke 1300" (NHMW, ZSM). 34 males, 35 females "Papua New Guinea: Madang, Adalbert Mts., below Keki, 790m, 5.v.2006, 04.42.300S 145.25.089E, Balke & Manaono (PNG 53)" (NARI, NHMW, ZSM). 14 males, 13 females "Papua New Guinea: Madang, Adalbert Mts., creek nr Keki, 790m, 28.xi.2006, 04.42.300S 145.25.089E, Binatang Boys leg. (PNG 53a)" (NHMW, ZSM). 4 males, 5 females "Papua New Guinea: Madang, Keki, Adalbert Mts., 400m, 29.xi.2006, 04.43.058S 145.24.437E, Binatang Boys, (PNG 119)" (NHMW, ZSM). 7 males, 6 females "Papua New Guinea: Madang, Keki-Sewan, Adalbert Mts., 700m, 30.xi.2006, nr 04.41.802S 145.25.460E Binatang Boys (PNG 120)" (NHMW, ZSM). 1 male "Papua New Guinea: Madang, Simbai area, 1800-2400m, 8.iii.2007, 05.12.693S 144.35.521E, Kinibel (PNG 151)" (ZSM). 24 males "Papua New Guinea: Madang, Simbai area, 1200m, 10.iii.2007, 05.13.389S 144.37.285E, Kinibel (PNG 152)" (NARI, NHMW, ZSM). 39 males "Papua New Guinea: Madang, Simbai area, 1200m, 11.iii.2007, 05.13.333S 144.37.611E, Kinibel (PNG 153)" (NARI, NHMW, ZSM). 10 males, 2 females "Papua New Guinea: Madang, Simbai - Mombeen, 1100m, 11.iii.2007, 05.12.876S 144.41.759E, Kinibel (PNG 154)" (NHMW, ZSM). **Eastern Highlands:** 4 males, 6 females "Papua New Guinea: Eastern Highlands, Bena Bridge, 1400m, 8.xii.2007, 06.10.781S 145.26.034E, Balke & Sagata (PNG 164)" (ZSM). 2 males "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 700m, 24.xi.2006, 05.52.754S 145.23.209E, Balke & Kinibel (PNG 109)", one of them with an additional green label "DNA M.Balke 1520" (ZSM). 1 male, 2 females "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 1200m, 24.xi.2006, nr 05.52.754S 145.23.209E, Balke & Kinibel (PNG 110)", one female with an additional green label "DNA M.Balke 1522" (ZSM). 8 males "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 800m, 24.xi.2006, 05.50.021S 145.24.664E, Balke & Kinibel (PNG 112)" (NHMW, ZSM). 18 males "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 750m, 25.xi.2006, 05.49.892S 145.24.491E, Balke & Kinibel (PNG 113)" (NARI, NHMW, ZSM). 3 males "Papua New Guinea: Madang, Akameku - Brahmin, Bismarck Range, 750m, 25.xi.2006, nr 05.49.307S 145.24.389E, Balke & Kinibel (PNG 114)" (NHMW, ZSM).

Females of doubtful identity. Eastern Highlands: 12 females "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 700m, 24.xi.2006, 05.52.754S 145.23.209E, Balke & Kinibel (PNG 109)" (ZSM). 24 females "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 800m, 24.xi.2006,

05.50.021S 145.24.664E, Balke & Kinibel (PNG 112)" (NARI, NHMW, ZSM). 15 females "Papua New Guinea: Eastern Highlands, Akameku - Brahmin, Bismarck Range, 750m, 25.xi.2006, 05.49.892S 145.24.491E, Balke & Kinibel (PNG 113)" (NHMW, ZSM). 25 females "Papua New Guinea: Madang, Akameku - Brahmin, Bismarck Range, 750m, 25.xi.2006, nr 05.49.307S 145.24.389E, Balke & Kinibel (PNG 114)" (NARI, NHMW, ZSM). These females are a mixture of two species: *E. broschii* and *E. damantiensis* (Balke, 1998). 19 males "Papua New Guinea: Madang, Simbai area, 1200m, 10.iii.2007, 05.13.389S 144.37.285E, Kinibel (PNG 152)" (NHMW, ZSM). These females are a mixture of two species: *E. broschii* and *E.* ?*damantiensis* (Balke, 1998). 53 females "Papua New Guinea: Madang, Simbai area, 1200m, 11.iii.2007, 05.13.333S 144.37.611E, Kinibel (PNG 153)" (NARI, NHMW, ZSM). These females are a mixture of three species: *E. broschii*, *E. simbaiarea* Shaverdo & Balke, 2014, and *E.* ?*damantiensis* (Balke, 1998).

Additions to the description (original description in Balke 1998, p. 327). *Size and shape*: Beetles small to medium-sized (TL-H 3.2–4.0 mm, TL 3.7–4.4 mm, MW 1.75–2.15 mm; holotype: TL-H 3.55 mm, TL 3.9 mm, MW 1.9 mm). *Male*: Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior row of 14 and posterior row of 5 short setae (Fig. 8A). Abdominal ventrite 6 with 3–6 lateral striae on each side. Median lobe with slightly curved apex in lateral view and more or less rounded in ventral view. Its ventral sclerite with almost equal, short apical lobes: left lobe broad or narrow (sometimes with broken apex, e.g., Fig. 9A) and right lobe short, relatively broad (Fig. 8B, C).

Variability: Beetles vary in size, kind of dorsal punctation (Figs 1–3), and shape of ventral sclerite of the median lobe (Fig. 9A–E). Dorsal punctation in great majority of the specimens is fine (Fig. 3), but some specimens have slightly coarser punctation, and very few (the types and one specimen from Simbai area, Madang, see Figs 1, 2) have distinct punctation, similar to that of *E. pseudomarinae* sp. n. There are populations (e.g., from Simbai area, Madang, and Akameku-Brahmin, Eastern Highlands) with the left lobe of the ventral sclerite of the median lobe very narrow (Fig. 9A, B). However, this character is not very stable even in one population. Taking into consideration the other different shapes of the ventral sclerite observed (Figs 8B, 9C–E) as well as the fact that it is differently sclerotized in different specimens and because of that is variable in shape, we treated all the material as *E. broschii*. Such variability in shape of the ventral sclerite of the median lobe is also characteristic for other species of this group (Figs 9, 10, 12).

Distribution. Papua New Guinea: Madang and Eastern Highlands Provinces (Fig. 14).

2. *Exocelina hintelmannae* (Shaverdo, Sagata & Balke, 2005)

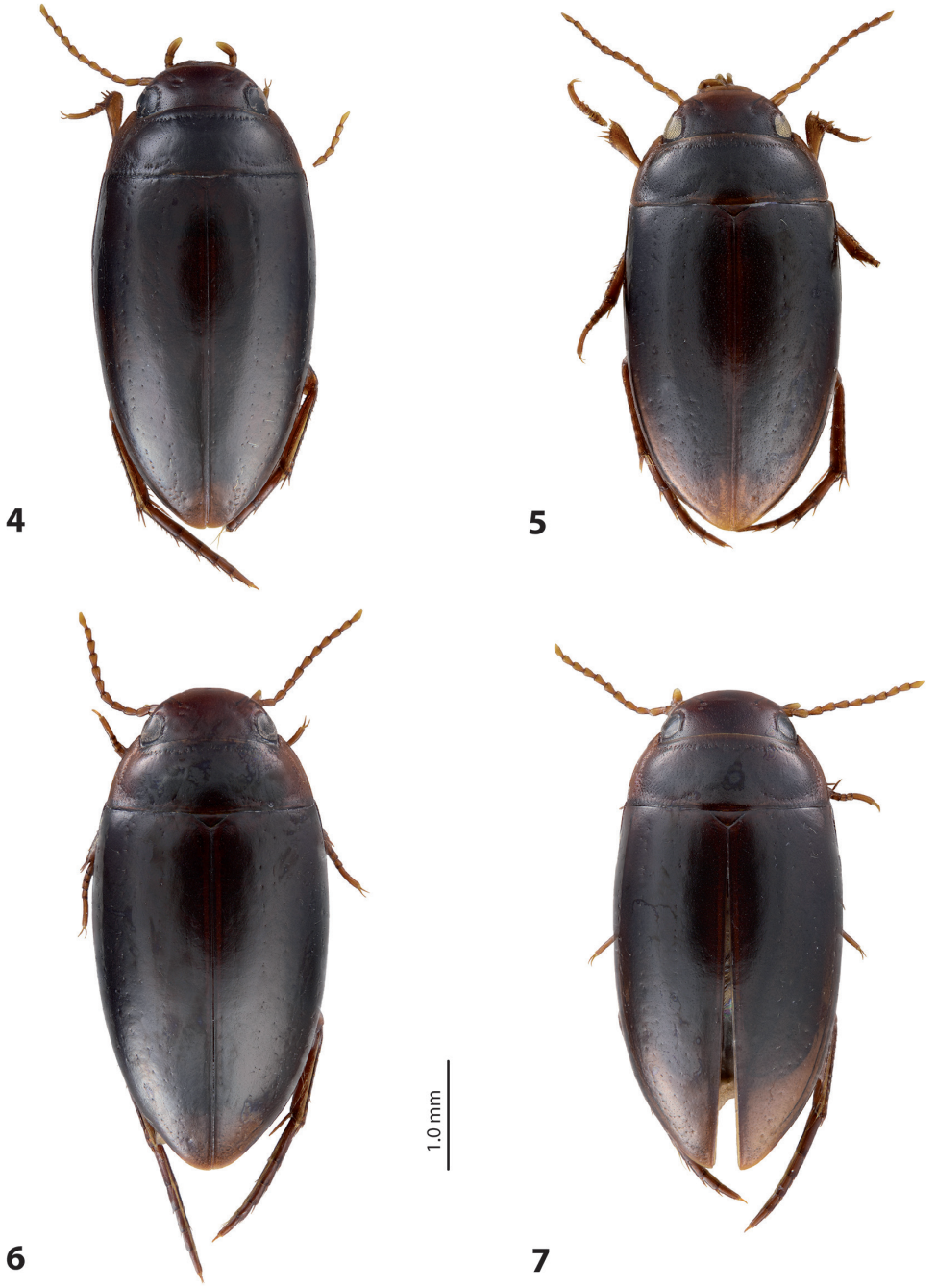
Figs 4, 9F, G

Papuadytes hintelmannae Shaverdo, Sagata & Balke, 2005: 272.
Exocelina hintelmannae (Shaverdo, Sagata & Balke, 2005): Nilsson 2007: 33 (comb. n.); Toussaint et al. 2014: Supplementary figs 1–4, tab. 2. (MB 1367).

Type locality. Papua New Guinea: border Simbu and Eastern Highlands Provinces, Crater Mountain, between Wara Sera Station and Herowana Village, Hulene River, approximately 06°43.4'S; 145°05.6'E.

Type material studied. *Holotype*: male "264 DNA M Balke" [green], "PNG Simbu / EHPr. Crater Mountain, Sera - Herowana, Wara Hulene, 1000 m, 16IX2002, Balke & Sagata (PNG 17)", "Holotypus Papuadytes hintelmannae sp.n. des. H. Shaverdo, K. Sagata & M. Balke, 2005" (BMNH). *Paratypes*: 1 male "256 DNA M Balke" [green], "PAPUA NEW GUINEA Simbu / EHPr. Crater Mountain, Wara Sera Station, 800 m, 14IX2002, Balke & Sagata (PNG 10)", "Paratypus Papuadytes hintelmannae sp.n. des. H. Shaverdo, K. Sagata & M. Balke, 2005" (NHMW). 1 male "260 DNA M Balke" [green], "PNG Simbu / EHPr. Crater Mountain, Sera - Herowana, upper Oh River, 1200 m, 15IX2002, Balke & Sagata (PNG 12)", "Paratypus Papuadytes hintelmannae sp.n. des. H. Shaverdo, K. Sagata & M. Balke, 2005" (NHMW).

Additional material. Simbu/EHL: 1 female "PAPUA NEW GUINEA: Simbu / EHPr. Crater Mountain, Wara Sera Station, 820m, 14IX2002, Balke & Sagata, (PNG 8)" (ZSM). 2 males, 6 females "Papua New Guinea: Simbu / EHP. Crater Mountain, Wara Sera Station, 800m, 14IX2002, Balke & Sagata, (PNG 009)" (ZSM). 17 males, 15 females "Papua New Guinea: Crater Mountain, Wara Sera Station, 800m, 14IX2002, Balke & Sagata, (PNG 010)" (NARI, NHMW, ZSM). 8 males, 9 females "PAPUA NEW GUINEA Simbu/EHP. Crater Mountain, Wara Sera Station, 800m, 14IX2002, Balke & Sagata, (PNG 10)" (NHMW, ZSM). 3 males, 4 females "Papua New Guinea: Simbu / EHP. Crater Mountain, Sera - Herowana, Wara Pima, 900m, 15IX2002, Balke & Sagata (PNG 011)" (ZSM). 7 males, 14 females "Papua New Guinea: Crater Mountain, Sera - Herowana, upper Oh river, 1200m, 15IX2002, Balke & Sagata (PNG 012)" (NHMW, ZSM). 1 male, 1 female "Papua New Guinea: Crater Mountain, Sera - Herowana, Jau river, 1100m, 15IX2002, Balke & Sagata (PNG 013)" (ZSM). 8 males, 7 females "Papua New Guinea: Crater Mountain, Sera - Herowana, Jau river, 1000m, 15IX2002, Balke & Sagata (PNG 015)" (NHMW, ZSM). 12 males, 10 females "Papua New Guinea: Simbu/EHP. Crater Mountain, Sera - Herowana, Hulene river, 1000m, 16IX2002, Balke & Sagata (PNG 017)" (NHMW, ZSM). 25 males, 33 females "Papua New Guinea: Simbu / EHP. Crater Mountain, Herowana, Yawasa River, 1200m, 17.IX.2003, Balke & Sagata (PNG 019)" (NARI, NHMW, ZSM). **Simbu:** 8 males, 13 females "Papua New Guinea: Supa Haia, 1032, 10.xi.2002, K. Sagata, (WB1)" (NHMW, ZSM). **EHL:** 1 male "Stn. No. 177a", "NEW GUINEA: E. Highland Dist., Wanatabe Valley. Nr. Okapa, c. 5000 ft. 5.ii.1965", "M.E. Bacchus. B.M. 195-120" (BMNH). **Gulf:** 30 males, 30 females "Papua New Guinea: Gulf, Marawaka, nr. Ande, 1000m, 10.xi.2006, 07.03.598S 145.4.375E, Balke & Kinibel (PNG 89)", one of them an additional green label "DNA M.Balke 1367" (NHMW, ZSM). 32 males, 35 females "Papua New Guinea: Gulf Province, Marawaka, Mala, 1400m, 11.xi.2006, 07.05.664S 145.44.467E, Balke & Kinibel, (PNG 90)" (NARI, NHMW, ZSM). 16 male, 12 females "Papua New Guinea: Gulf, Marawaka, Andakombe towards Morobe, 1100m,



Figures 4–7. Habitus and coloration of the holotypes. **4** *Exocelina hintelmannae* (Shaverdo, Sagata & Balke, 2005) **5** *E. marinae* (Shaverdo, Sagata & Balke, 2005) **6** *E. mondmillensis* sp. n. **7** *E. pseudomarinae* sp. n.

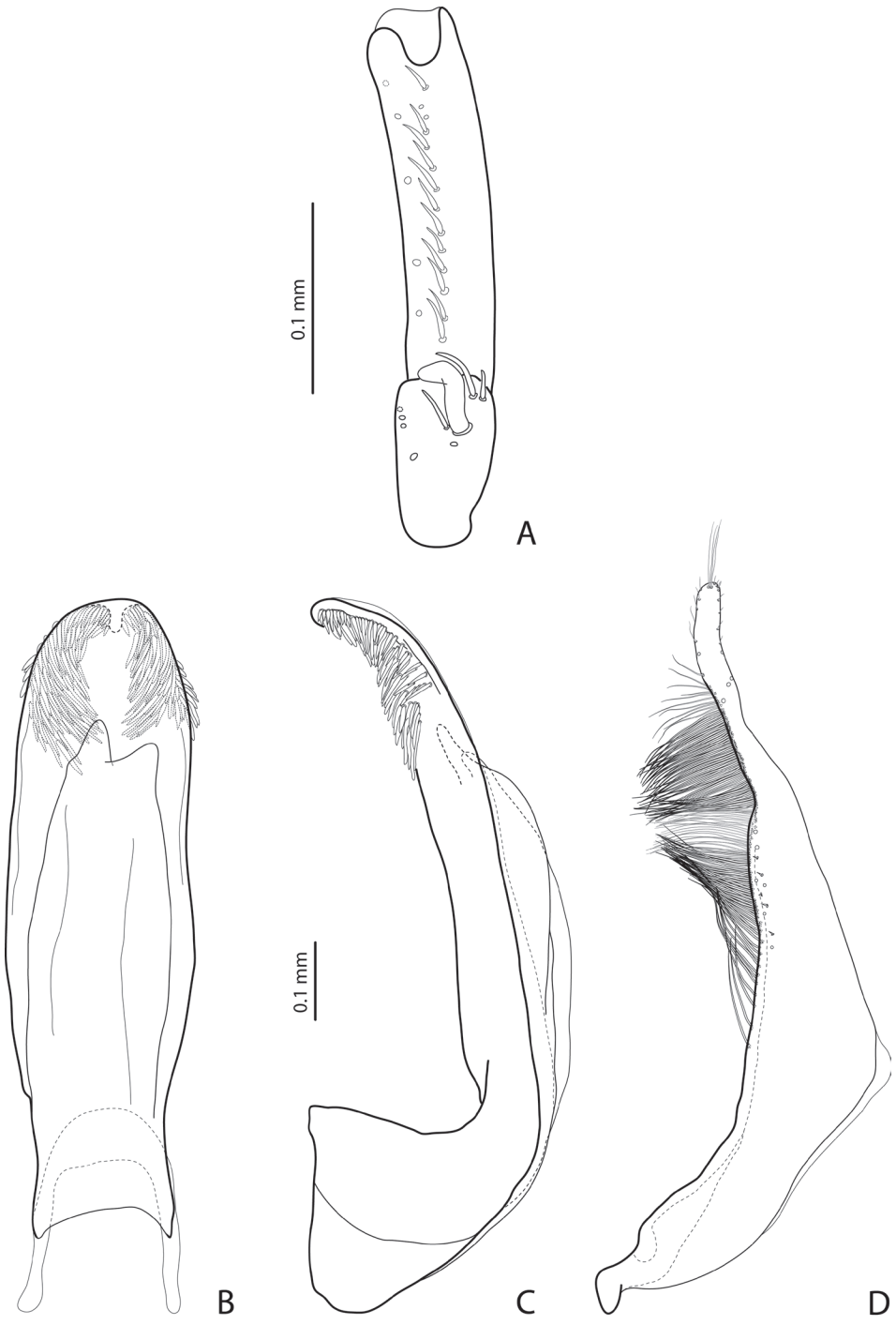


Figure 8. *Exocelina broschii* (Balke, 1998). **A** male protarsomeres 4–5 in ventral view (Madang, Simbai area, PNG 153) **B** median lobe in ventral view (paratype) **C** median lobe in lateral view (paratype) **D** paramere in external view (Madang, Simbai area, PNG 153).

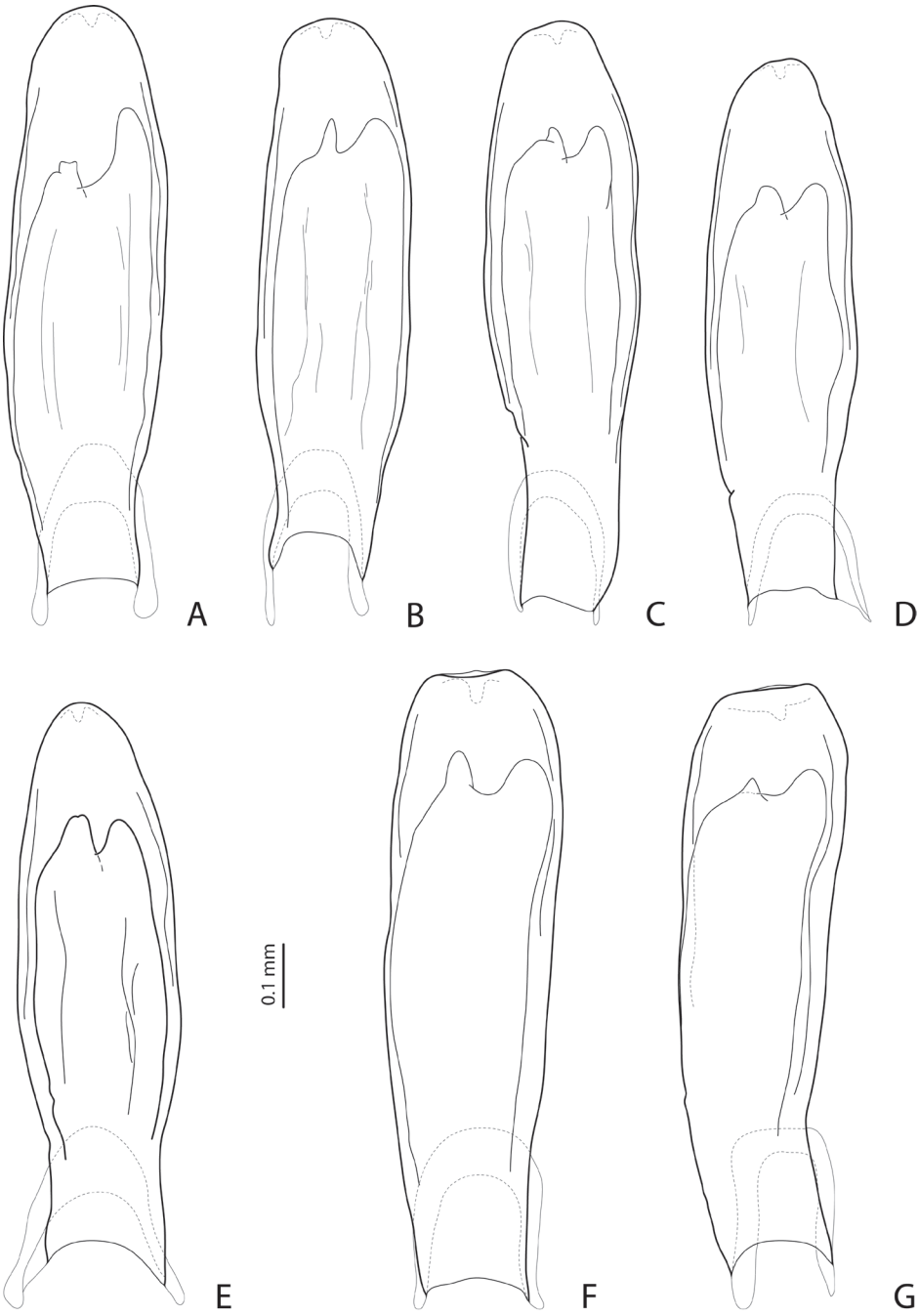


Figure 9. Lateral view of median lobe of **(A–E)** *Exocelina broschii* (Balke, 1998) and **(F, G)** *E. hintelmannae* (Shaverdo, Sagata & Balke, 2005). **A, B** Madang, Simbai area, PNG 153 **C** Madang, Adalbert Mts., Keki, PNG 52 **D** Madang, Adalbert Mts., below Keki, PNG 53 **E** Eastern Highlands, Bena Bridge, PNG 164 **F, G** Simbu/ Eastern Highlands, Crater Mountain, Sera-Herowana, Hulene River, PNG 017. Setae not shown.

12.xi.200, 07.09.766S 145.46.333E, Balke & Kinibel (PNG 92)" (NHMW, ZSM). 1 male, 3 females "Papua New Guinea: Gulf, Marawaka, Andakombe towards Morobe, 1500m, 12.xi.200, 07.10.413S 145.49.555E, Balke & Kinibel (PNG 93)", the male with an additional green label "DNA M.Balke 1362" (ZSM).

Additions to the description (original description in Shaverdo et al. 2005, p. 272). *Size and shape*: Beetles medium-sized (TL-H 3.4–4.15 mm, TL 3.75–4.55 mm, MW 1.8–2.2 mm; holotype: TL-H 3.9 mm, TL 4.3 mm, MW 2.05 mm), see Fig. 4.

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

Variability: Beetles vary in shape of the median lobe and its ventral sclerite: mainly shape and length of its left lobe (Fig. 9F, G).

Distribution. Papua New Guinea: Simbu, Eastern Highlands, and Gulf Provinces (Fig. 14).

3. *Exocelina marinae* (Shaverdo, Sagata & Balke, 2005)

Figs 5, 10

Papuadytes marinae Shaverdo, Sagata & Balke 2005: 272.

Exocelina marinae (Shaverdo, Sagata & Balke, 2005): Nilsson 2007: 34 (comb. n.); Toussaint et al. 2014: Supplementary figs 1–4, tab. 2 (*E. marinae* MB1291).

Type locality. Papua New Guinea: Sandaun Province, trail from Telefomin to Eliptamin.

Type material studied. *Holotype*: male "Papua N. G.: Sandaun Prov. Telefomin, 16.–17.5.1998 trail to Eliptamin 1700-1800 m; leg. Riedel", "Holotypus Papuadytes marinae sp.n. des. H. Shaverdo, K. Sagata & M. Balke, 2005" (NHMW).

Additional material. Sandaun: 4 males, 6 females "Papua New Guinea: Sandaun, Mianmin, 670m 20.x.2008, 4.53.292S 141.34.118E, Ibalim (PNG 191)", two males with additional green labels "DNA M.Balke 3733" and "DNA M.Balke 3734" (NHMW, ZSM). 2 females "Papua New Guinea: Sandaun, Mianmin (river), 990m, 23.x.2008, 4.54.570S 141.35.490E, Ibalim (PNG 192)", one of them with an additional green label "DNA M.Balke 3737" (ZSM). 1 male, 1 female "Papua New Guinea: Sandaun, Mianmin (pool), 990m, 23.x.2008, 4.54.570S 141.35.490E, Ibalim (PNG 193)", the female with an additional green label "M.Balke 3777 DNA" (ZSM). 2 males, 2 females "Papua New Guinea: Sandaun, Mianmin (river), 1080m, 24.x.2008, 04.55.780S 141.38.185E, Ibalim (PNG 195)", one male and one female with additional green labels "DNA M.Balke 3742" and "DNA M.Balke 3741", respectively (NHMW, ZSM). 1 male, 5 females "Papua New Guinea: Sandaun, Mianmin (pool), 1080m, 24.x.2008, 04.55.780S 141.38.185E, Ibalim (PNG 196)" (NHMW, ZSM). 1 female "Papua New Guinea: Sandaun, Mianmin (river), 700m, 21.x.2008, 04.52.858S 141.31.706E, Ibalim (PNG 197)" (ZSM). 1 female "Papua New Guinea: Sandaun, Mianmin area, >1000m, 26.xii.2009, Ibalim & Pius (PNG233)" (ZSM). 1 male, 5 fe-

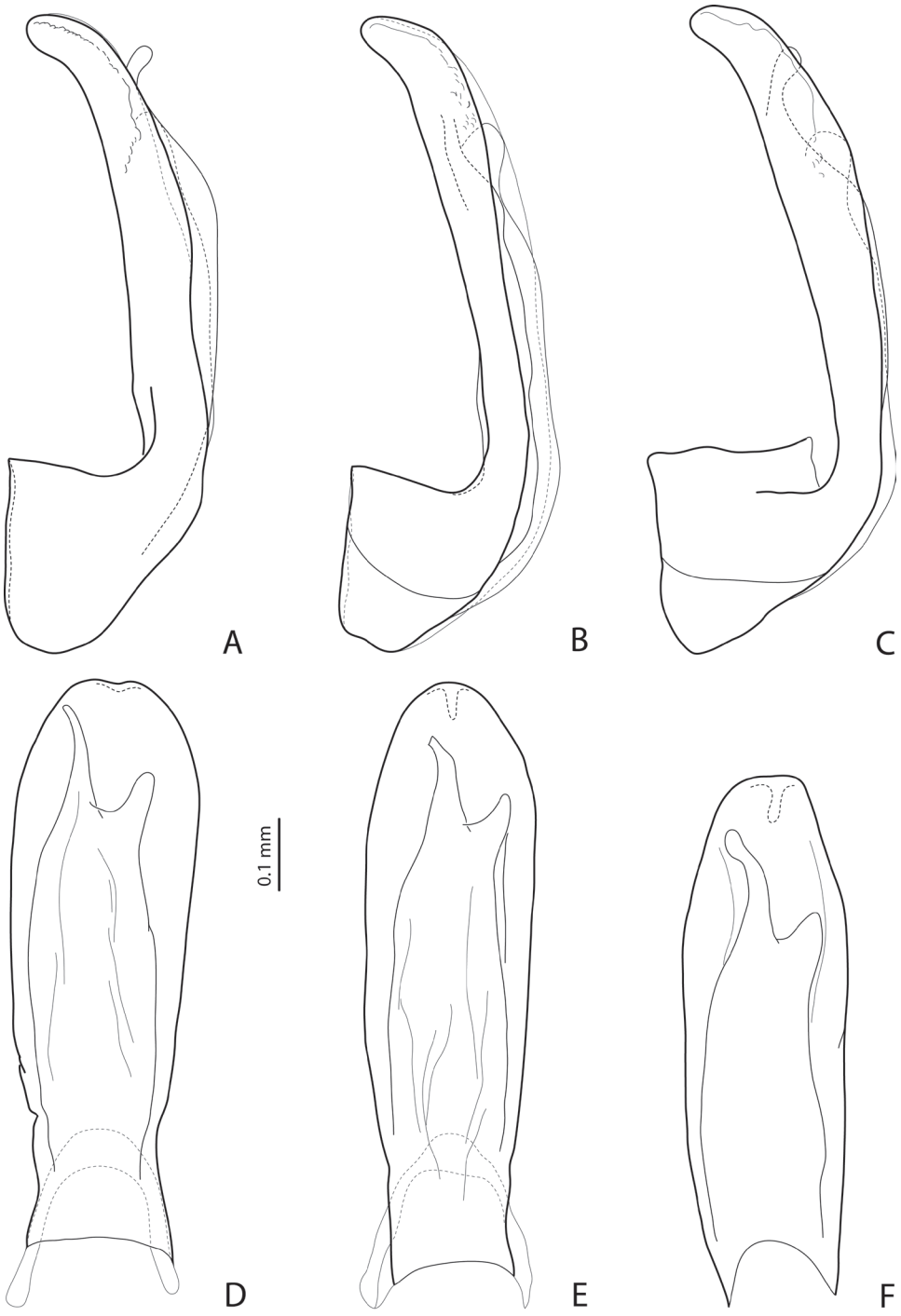


Figure 10. *Exocelina marinae* (Shaverdo, Sagata & Balke, 2005), lateral **(A–C)** and ventral **(D–F)** views of median lobe. **A, D** Sandaun, Mianmin, PNG 196 **B, E** Sandaun, Mianmin area, PNG 234 **C, F** Southern Highlands, Tari to Koroba, PNG 65. Setae not shown.

males "Papua New Guinea: Sandaun, Mianmin area, >1000m, 23.12.2009, Ibalim & Pius (PNG234)", the male with an additional label "DNA M.Balke 4934" (NHMW, ZSM). 8 males, 7 females "Papua New Guinea: Sandaun, Mianmin area, >600m, 13.i.2010, Ibalim & Pius (PNG235)", one male and one female with additional labels "DNA M.Balke 4938" and "DNA M.Balke 4931", respectively (NHMW, ZSM). 1 male "Papua New Guinea: Sandaun, Mianmin area, >600m, 13.i.2010, Ibalim & Pius (PNG236)" (ZSM). 1 male, 1 female "Papua New Guinea: Sandaun, Mianmin area, >700m, 14.i.2010, 0 4 54.540S 141 36.953E, Ibalim & Pius (PNG238)", the female with an additional label "DNA M.Balke 4933" (ZSM).

Hela: 1 male "Papua New Guinea: Southern Highlands, Tari to Koroba, 1600m, 15.v.2006, 05.46.500S 142.50.000E, Balke (PNG 65)", "DNA M.Balke 1291" [green] (ZSM).

Additions to the description (original description in Shaverdo et al. 2005, p. 270). *Male*: Median lobe with apex slightly curved in lateral view and more or less rounded in ventral view. Its ventral sclerite with unequal apical lobes: left lobe very long (very often with broken apex) and right lobe short, relatively narrow (Fig. 10).

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

Variability: Beetles small to medium-sized: for Mianmin populations: TL-H 3.3–3.55 mm, TL 3.6–3.95 mm, MW 1.75–1.95 mm; for the holotype (Telefomin): TL-H 3.6 mm, TL 4.1 mm, MW 1.9 mm (Fig. 5); for the specimen from Tari-Koroba: TL-H 3.85 mm, TL 4.25 mm, MW 2.15 mm. Also beetles vary in shape of the median lobe and its ventral sclerite as shown in Fig. 10.

Distribution. Papua New Guinea: Sandaun and Hela Provinces (Fig. 14). This species is mainly known from the south of Sandaun Province: Mianmin area. Based on the record from Tari-Koroba, we assume that the species occurs also further southeast.

4. *Exocelina mondmillensis* sp. n.

http://zoobank.org/810826A5-0AA1-47E6-9096-24D7EFC09805
Figs 6, 11, 12

Type locality. Papua New Guinea: Western Highlands Province, 5 km SE from Minj, Mondmill, 05°56.80'S, 144°39.90'E.

Type material. *Holotype*: male "Papua New Guinea: Western Highlands, Mondmill, 5 Km SE Minj, small pools near creek, 1741 m, 12.vi.2006, 05.56.801S 144.39.898E, John (PNG 77)" (ZSM). *Paratypes*: **Western Highlands:** 53 males, 80 females with the same labels as the holotype (NARI, NHMW, ZSM). 81 males "Papua New Guinea: Western Highlands, Kurumul, 6 Km SW Kudjip, small stream, 1580 m, 13.vi.2006, 05.53.426S 144.36.600E, John (PNG 78)", one of them with an additional green label "DNA M.Balke 1339" (NARI, NHMW, ZSM). 69 males "Papua New Guinea: Western Highlands, Mt. Hagen town area, 1600m, 7.xii.1994 05.49.745S 144.22.357E Balke & Kinibel (PNG 131)" (NARI, NHMW, ZSM).

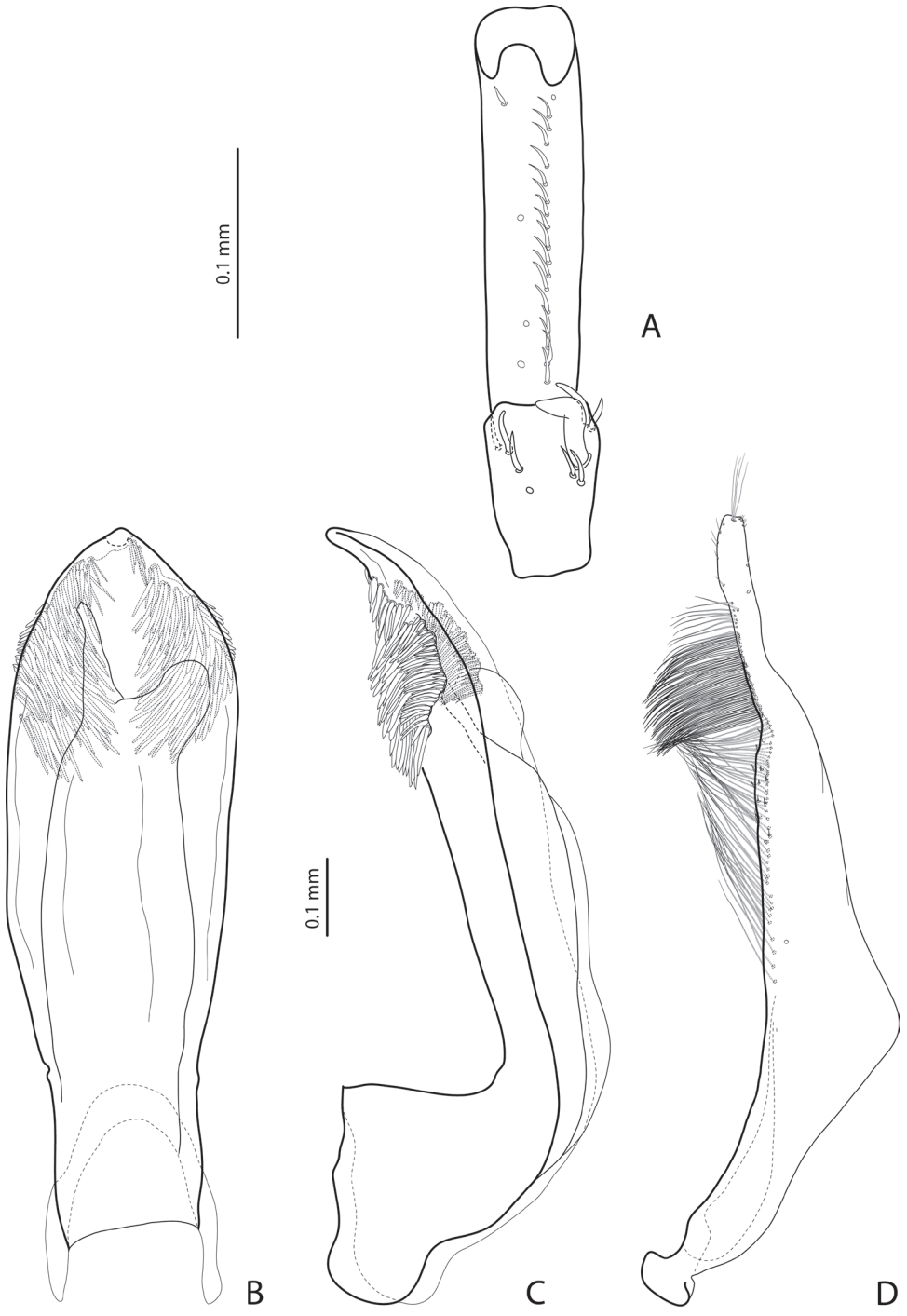


Figure 11. *Exocelina mondmillensis* sp. n., Western Highlands, Mondmill, PNG 77 **A** male protarsomeres 4–5 in ventral view **B** median lobe in ventral view **C** median lobe in lateral view **D** paramere in external view.

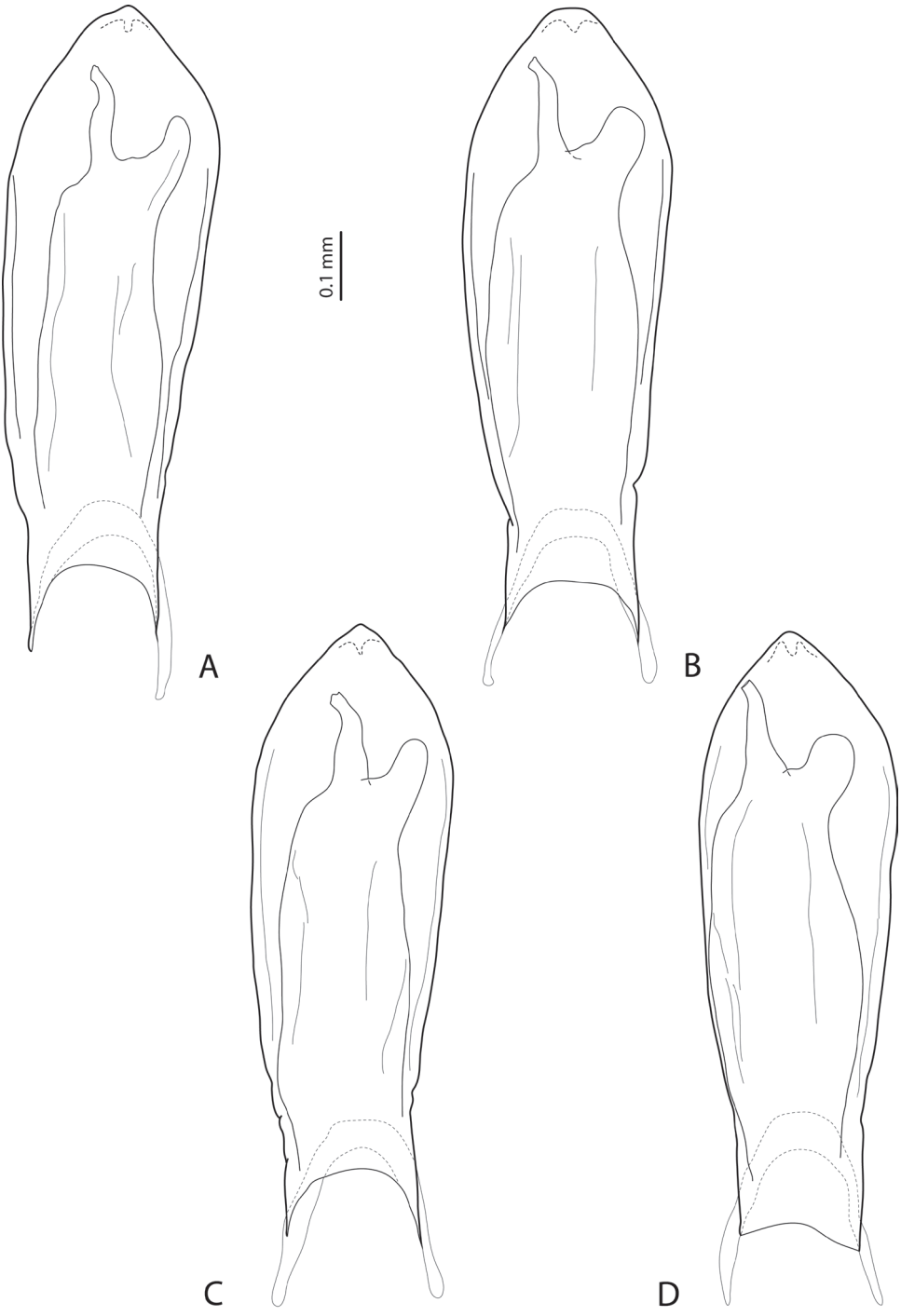


Figure 12. *Exocelina mondmillensis* sp. n., ventral view of median lobe. **A, B** Western Highlands, Mt. Hagen Town area, PNG 131 **C** Western Highlands, Gonzsidai-Sarup, PNG 144 **D** Enga, Anji, PNG 129. Setae not shown.

1 male, 1 female "Papua New Guinea: Western Highlands, Simbai, 1800-2000m, 26.ii.2007, 05.15.872S 144.32.717E, Kinibel (PNG 134)", the male with an additional green label "DNA M.Balke 3308" (ZSM). 9 males, 7 females "Papua New Guinea: Western Highlands, Simbai, Ineng River, 2000m, 27.ii.2007, 05.14.943S 144.32.818E, Kinibel (PNG 135)" (ZSM). 18 males, 21 females "Papua New Guinea: Western Highlands, Simbai, 2000m, 28.ii.2007, 05.15.174S 144.32.812E, Kinibel (PNG 136)" (NHMW, ZSM). 6 males, 1 female "Papua New Guinea: Western Highlands, Simbai, Fundum, 2000m, 1.iii.2007, 05.15.03S 144.30.867E, Kinibel (PNG 137)" (NHMW, ZSM). 23 males, 11 females "Papua New Guinea: Western Highlands, Simbai, 1800-2000m, 1.iii.2007, 05.14.276S 144.28.741E, Kinibel (PNG 138)" (NHMW, ZSM). 53 males "Papua New Guinea: Western Highlands, Simbai, Kairong River, 1850m, 2.iii.2007, 05.14.840S 144.28.457E, Kinibel (PNG 139)" (NHMW, ZSM). 4 males "Papua New Guinea: Western Highlands, Simbai - Jimi, 1500m, 2.iii.2007, 05.16.074S 144.27.886E, Kinibel (PNG 140)" (NHMW, ZSM). 1 male "Papua New Guinea: Western Highlands, Jimi, 1500m, 2.iii.2007, 05.16.335S 144.27.930E, Kinibel (PNG 141)" (ZSM). 18 males "Papua New Guinea: Western Highlands, Kundum, 1400m, 03.iii.2007, 05.16.096S 144.27.869E, Kinibel (PNG 142)" (NHMW, ZSM). 42 males "Papua New Guinea: Western Highlands, Lugup River, 1700m, 4.iii.2007, 05.17.237S 144.28.214E, Kinibel (PNG 143)" (NHMW, ZSM). 40 males "Papua New Guinea: Western Highlands, Gonzsidai-Sarup, 1700m, 4.iii.2007, 05.19.060S 144.28.671E, Kinibel (PNG 144)" one male with an additional green label "DNA M.Balke 3313" (NHMW, ZSM). 15 males "Papua New Guinea: Western Highlands, Above Sendiap, 1400m, 5.iii.2007, 05.19.774S 144.28.307E, Kinibel (PNG 145)" (NHMW, ZSM). 2 males "Papua New Guinea: Western Highlands, Jimi Valley, above Sendiap Station, 950m, 6.iii.2007, 05.20.587S 144.28.847E, Kinibel (PNG 147)" (ZSM). **Enga:** 17 males, 17 females "Papua New Guinea: Enga, nr Wabag, 1800m, 6.xii.2006, 05.30.124S 143.44.459E, Balke & Kinibel, (PNG 125)", one male with an additional green label "DNA M.Balke 1525" (NHMW, ZSM). 2 males "Papua New Guinea: Enga, nr Wapanamanda, 1700m, 6.xii.2006, 05.36.541S 143.52.559E, Balke & Kinibel (PNG 127)", one male with an additional green label "DNA M.Balke 1526" (ZSM). 8 males "Papua New Guinea: Enga, Wapanamanda, 1500m, 6.xii.2006, 05.38.105S 143.55.338E, Balke & Kinibel, (PNG 128)" (NHMW, ZSM). 12 males, 3 females "Papua New Guinea: Enga, Anji, 1900m, 6.xii.2006, 05.42.109S 143.55.635E, Balke & Kinibel, (PNG 129)" (NHMW, ZSM). **Madang:** 5 males, 14 females "Papua New Guinea: Madang, Keki, Adalbert Mts., 400m, 29.xi.2006, 04.43.058S 145.24.437E, Binatang Boys, (PNG 119)" (NHMW, ZSM).

Females of doubtful identity. Western Highlands: 142 females "Papua New Guinea: Western Highlands, Kurumul, 6 Km SW Kudjip, small stream, 1580 m, 13.vi.2006, 05.53.426S 144.36.600E, John (PNG 78)" (NARI, NHMW, ZSM). These females are a mixture of three species: *E. mondmillensis* sp. n., *E. edeltraudae* (Shaverdo, Hendrich & Balke, 2012), and *E. damantiensis* (Balke, 1998). 47 females "Papua New Guinea: Western Highlands, Mt. Hagen town area, 1600m, 7.xii.1994

05.49.745S 144.22.357E Balke & Kinibel (PNG 131)" (NARI, ZSM). These females are a mixture of two species: *E. mondmillensis* sp. n. and *E. edeltraudae*. 50 females "Papua New Guinea: Western Highlands, Simbai, Kairong River, 1850m, 2.iii.2007, 05.14.840S 144.28.457E, Kinibel (PNG 139)" (NARI, ZSM). 10 females "Papua New Guinea: Western Highlands, Simbai - Jimi, 1500m, 2.iii.2007, 05.1.074S 144.27.886E, Kinibel (PNG 140)" (ZSM). 7 females "Papua New Guinea: Western Highlands, Jimi, 1500m, 2.iii.2007, 05.16.335S 144.27.930E, Kinibel (PNG 141)" (ZSM). 33 females "Papua New Guinea: Western Highlands, Kundum, 1400m, 03.iii.2007, 05.16.096S 144.27.869E, Kinibel (PNG 142)" (ZSM). These females are a mixture of two species: *E. mondmillensis* sp. n. and *E. jimiensis* Shaverdo & Balke, 2014. 26 females "Papua New Guinea: Western Highlands, Gonzsidai-Sarup, 1700m, 4.iii.2007, 05.19.060S 144.28.671E, Kinibel (PNG 144)" (ZSM). These females are a mixture of two species: *E. mondmillensis* sp. n. and *E. edeltraudae*. 34 females "Papua New Guinea: Western Highlands, Lugup River, 1700m, 4.iii.2007, 05.17.237S 144.28.214E, Kinibel (PNG 143)" (NHMW, ZSM). 9 females "Papua New Guinea: Western Highlands, Above Sendiap, 1400m, 5.iii.2007, 05.19.774S 144.28.307E, Kinibel (PNG 145)" (ZSM). 9 females "Papua New Guinea: Western Highlands, Jimi Valley, above Sendiap Station, 950m, 6.iii.2007, 05.20.587S 144.28.847E, Kinibel (PNG 147) (ZSM). These females are a mixture of two species: *E. mondmillensis* sp. n. and *E. madangensis* (Balke, 2001). **Enga:** 10 females "Papua New Guinea: Enga, Wapanamanda, 1500m, 6.xii.2006, 05.38.105S 143.55.338E, Balke & Kinibel, (PNG 128)" (ZSM). These females are a mixture of two species: *E. mondmillensis* sp. n. and *E. madangensis* (Balke, 2001).

Diagnosis. Beetle medium-sized, brown to piceous, with reddish head and pronotal sides, shiny; median lobe with slightly curved downwards apex but thin in lateral view and ventral sclerite with two unequal apices (left one long, narrow and curved and right one short, broad and more or less rounded). The species is similar to *E. marinae* and *E. pseudomarinae* sp. n. in shape of the ventral sclerite of median lobe, but distinctly differs from them in having fine, inconspicuous punctation and weak microreticulation on the dorsal surface and a thin tip of the median lobe. From *E. broschii* and *E. hintelmannae*, it can be distinguished by the shape of the median lobe (thin apex) and its ventral sclerite (very long left lobe), and from the former also by finer elytral punctation.

Description. *Size and shape*: Beetle medium-sized (TL-H 3.5–4.1 mm, TL 3.9–4.5 mm, MW 1.8–2.2 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Head reddish brown to piceous, usually darker medially and posterior to eyes, sometimes almost uniform; pronotum with brown to piceous medially and reddish brown to brown sides; elytra brown to piceous, usually with narrow reddish sutural lines; head appendages and legs yellowish to reddish, legs distally darker, especially metathoracic legs (Fig. 6). Teneral specimen with coloration paler.

Surface sculpture: Head with dense punctation (spaces between punctures 1–3 times size of punctures), evidently finer and sparser anteriorly; diameter of punctures smaller than diameter of cells of microreticulation. Pronotum with much sparser and finer

punctation than head. Elytra with very sparse and fine punctation, almost invisible. Pronotum and elytra with weakly impressed microreticulation, dorsal surface shiny. Head with microreticulation stronger. Metaventrite and metacoxae distinctly microreticulate, metacoxal plates with longitudinal strioles and transverse wrinkles. Abdominal ventrites with distinct microreticulation, strioles, and very fine and sparse punctation.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct lateral bead and few setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 broadly rounded or slightly truncate.

Male: Antenna simple (Fig. 6). Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior row of 18 and posterior row of 4 short setae (Fig. 11A). Median lobe with thin apex, slightly curved in lateral view and pointed in ventral view. Its ventral sclerite with two unequal apices (left one long, narrow and curved and right one short, broad and more or less rounded). Paramere with subdistal setae denser and thicker than proximal setae (Fig. 11B–D). Abdominal ventrite 6 with 4–7 lateral striae on each side.

Holotype: TL-H 4.05 mm, TL 4.45 mm, MW 2.15 mm.

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

Variability: Beetles vary mainly in shape of the ventral sclerite of the median lobe as shown in Fig 12.

Distribution. Papua New Guinea: Western Highlands, Enga, and Madang Provinces (Fig. 14).

Etymology. The name refers to Mondmill, the type locality, where the species was found in great numbers. The name is an adjective in the nominative singular.

5. *Exocelina pseudomarinae* sp. n.

http://zoobank.org/60127776-664C-425F-962E-B40E1F9B7E74
Figs 7, 13

Exocelina undescribed sp. MB1287: Toussaint et al. 2014: Supplementary figs 1–4, tab. 2.

Type locality. Papua New Guinea: Hela Province, Tari, 05°50.38'S, 142°55.90'E.

Type material. *Holotype*: male "Papua New Guinea: Southern Highlands, Tari (trickle in gardenland), 1700m, 12.v.2006, 05.50.383S 142.55.901E, Balke (PNG 58)", "DNA M.Balke 1287" [green] (ZSM). *Paratypes*: 2 males, 1 female with the same labels as the holotype (NHMW, ZSM).

Diagnosis. Beetle medium-sized, brown to dark brown, with reddish head and pronotal sides, submatt; median lobe with apex strongly curved downwards in lateral view and ventral sclerite with two unequal apices (left one long, narrow and curved

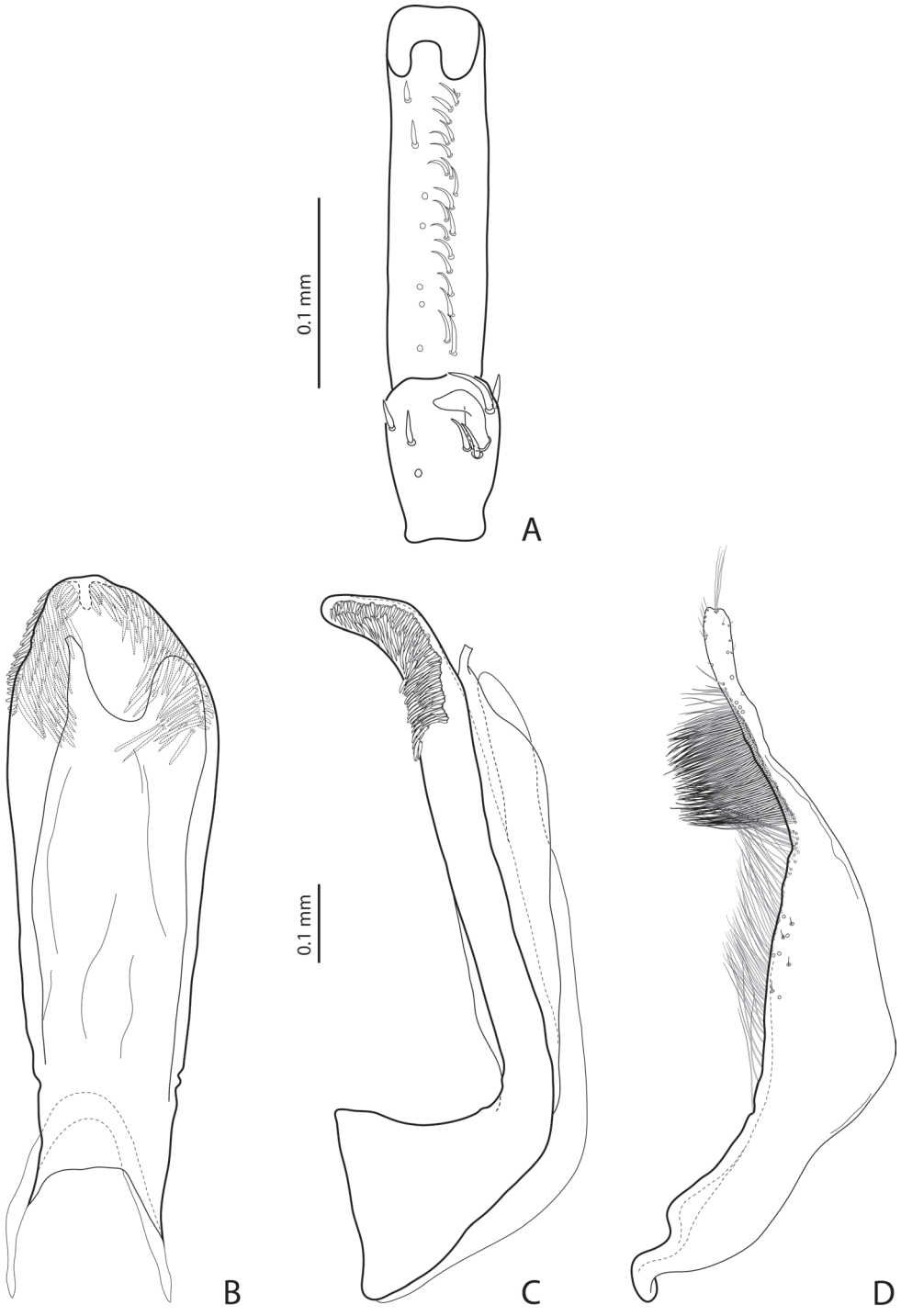


Figure 13. *Exocelina pseudomarinae* sp. n., Southern Highlands, Tari, PNG 58 **A** male protarsomeres 4–5 in ventral view **B** median lobe in ventral view **C** median lobe in lateral view **D** paramere in external view.

apically and right one short, broad and more or less strait). The species is similar to *E. marinae* Shaverdo, Sagata & Balke, 2005 from which distinctly differs in larger size, sparser and finer punctation and weaker microreticulation of the dorsal surface, and strongly curved apex of the median lobe, which is similar to that of *E. hintelmannae* Shaverdo, Sagata & Balke, 2005. The specimen of *E. marinae* from Tari-Koroba, though large in size and with the same distribution, has a distinctly stronger sculpture on the dorsal surface and a median lobe with only a slightly curved apex in lateral view and a narrower right lobe of the ventral sclerite. Therefore, it can be easily distinguished from *E. pseudomarinae* sp. n.

Description. *Size and shape*: Beetle medium-sized (TL-H 3.55–4.05 mm, TL 3.85–4.4 mm, MW 1.9–2.1 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Head reddish brown, brown to dark brown medially and posterior to eyes; pronotum with brown to dark brown medially (to piceous – narrow part on disc) and reddish brown sides; elytra brown to dark brown, sometimes with narrow reddish brown sutural lines; head appendages yellowish, legs yellowish to reddish, distally darker, especially metathoracic legs (Fig. 7). Teneral specimen with coloration slightly paler.

Surface sculpture: Head with very dense punctation (spaces between punctures 1–2 times size of punctures), evidently finer and sparser anteriorly; diameter of punctures smaller than diameter of cells of microreticulation or equal to it. Pronotum and elytra with punctation sparser and finer than on head, but very distinct. Pronotum and elytra with distinct microreticulation, dorsal surface submatt. Head with microreticulation stronger. Metaventrite and metacoxae distinctly microreticulate, metacoxal plates with longitudinal strioles and transverse wrinkles. Abdominal ventrites with distinct microreticulation, strioles, and sparse punctation, coarser on two last abdominal ventrites.

Structures: Pronotum with distinct lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct lateral bead and few setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 broadly rounded or slightly truncate.

Male: Antenna simple (Fig. 7). Protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior row of 20 and posterior row of 7 short setae (Fig. 13A). Median lobe with strongly curved apex in lateral view and more or less rounded in ventral view. Its ventral sclerite with two unequal apices (left one long, narrow and curved apically and right one short, broad and more or less strait). Paramere with subdistal setae denser and thicker than proximal setae (Fig. 13B–D). Abdominal ventrite 6 with 6–8 lateral striae on each side.

Holotype: TL-H 4.05 mm, TL 4.4 mm, MW 2.1 mm.

Female: Without evident differences in external morphology from males, except for not modified protarsi and abdominal ventrite 6 without striae.

Distribution. Papua New Guinea: Hela Province. This species is known only from the type locality (Fig. 14).

Etymology. The name points to similarity of the new species to *E. marinae*. The name is a noun in the nominative singular standing in apposition.

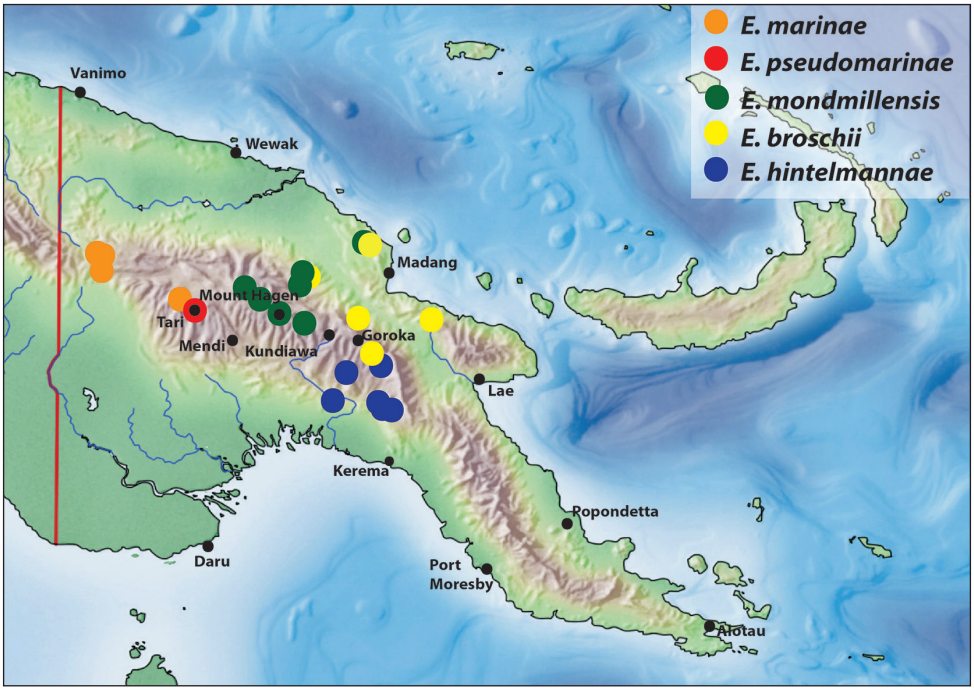


Figure 14. Map of Papua New Guinea showing distribution of species of the *Exocelina broschii*-group.

Key to species of the *Exocelina broschii*-group

The key is based mostly on male characters. In many cases females cannot be assigned to a species due to the similarity of their external and internal structures (for female genitalia see Figs 17a and 17b in Shaverdo et al. (2005)). Some species are rather similar in external morphology, therefore, in most cases, the male genitalia need to be studied for reliable species identification. Numbers in parentheses refer to the order of species descriptions given above.

1 Dorsal surface of the body matt, with strongly impressed microreticulation and dense coarse punctation or submatt, with finer microreticulation and punctation (Figs 5, 7). Median lobe with apex broad, slightly or strongly curved in lateral view and ventral sclerite with two apical lobes of different length and shape: left one long (it can be broken apically) and narrow and right one shorter and broader (Figs 10, 13).....**2**

– Dorsal surface of the body shiny, with distinctly weaker microreticulation and finer punctation (Figs 1–4, 6). Median lobe with apex thin, slightly curved in lateral view and ventral sclerite with two apical lobes of different length and shape (Figs 11B, 12) or with apex broad, slightly or strongly curved in lateral view and ventral sclerite with two apical lobes of more or less equal length and shape.....**3**

2 Dorsal surface of body matt, with strongly impressed microreticulation and dense coarse punctation (Fig. 5); apex of median lobe slightly curved in lateral view (Fig. 10D–F, fig. 12a in Shaverdo et al. (2005)).....(3) ***marinae***

– Dorsal surface of body submatt, with punctation evidently sparser and finer and microreticulation weaker (Fig. 7); apex of median lobe more strongly curved in lateral view (Fig. 13C).....(5) ***pseudomarinae* sp. n.**

3 Dorsal surface with very fine and sparse to moderately fine and dense punctation (Figs 1–3); median lobe with apex broad, slightly curved in lateral view and ventral sclerite with two more or less equal apical lobes (Figs 8, 9A–E) ...(1) ***broschii***

– Dorsal surface with very fine and sparse punctation (Figs 4, 6); shape of median lobe or its ventral sclerite different.....**4**

4 Median lobe with apex broad, strongly curved in lateral view, its ventral sclerite with two more or less equal tips (Fig. 9A–E, figs 3,13a in Shaverdo et al. (2005)) .....(2) ***hintelmannae***

– Media lobe with apex thin, slightly curved in lateral view, its ventral sclerite with two tips of different length: left one very long and narrow and right one shorter and broader, somehow rounded (Figs 11, 12).....(4) ***mondmillensis* sp. n.**

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We are grateful Dr. H. Schillhammer (Vienna) for the habitus photos and Prof. D. Bilton (Plymouth) for a linguistic review of the manuscript.

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RESEARCH ARTICLE

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Review of the Psychodinae from Mallorca, Spain, with description of *Pericoma unipennata*, sp. n. (Diptera, Psychodidae)

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Abstract

We review the Psychodinae of Mallorca, recognising fifteen species based on recent collections and available literature. Previously unpublished data is presented for eleven species, of which *Neoarisemus ibericus* Wagner, 1978, *Mormia tenebricosa* (Vaillant, 1954), *Clogmia albipunctata* (Williston, 1893), *Lepiseodina rothschildi* (Eaton, 1913), *Paramormia ustulata* (Walker, 1856), *Philosepedon pyrenaicus* Vaillant, 1974 and *Psychoda* (*Psycha*) *grisescens* Tonnoir, 1922 are first records for Mallorca. An old record of *Pericoma trifasciata* (Meigen, 1804) is considered doubtful. *Pericoma unipennata* **sp. n** is described and illustrated based on a male collected at Deía. Distributional data are reviewed for all newly recorded species. Based on the Psychodinae fauna, the zoogeographical affinities of Mallorca are briefly discussed.

Keywords

Moth flies, Balearic Isles, new species, faunistics, distribution, check list

Introduction

The Psychodidae (moth flies and sand flies) are a species-rich and widespread group of small insects mainly associated with humid habitats. The most thoroughly studied faunas of the group are found in Europe, from where more than 500 species have been described and new discoveries continue to be made (Wagner 2004, Wagner and Kvifte 2015). The most poorly studied moth fly faunas of Europe are those of the Iberian peninsula (Wagner 2001) and the Balearic islands of Spain.

The most thoroughly studied moth flies from the Balearic islands belong to the subfamily Phlebotominae, the sand flies. On Mallorca, the largest of the Balearic islands, phlebotomine sand flies have received much attention due to their significance in veterinary medicine as vectors of canine leishmaniasis. This disease is widespread and long established, to the point that some local dog breeds have evolved resistance to the parasite (Solano-Gallego et al. 2000). Four species of *Phlebotomus* and one of *Sergentomyia* have been recorded from the island, of which *Phlebotomus ariasi* Tonnoir, 1921 has been suggested as a doubtful record (Alcover et al. 2014).

Other subfamilies of Psychodidae have been studied far less. Wagner (1990) listed a single species, namely *Pericoma barbarica* Vaillant, 1955 based on Vaillant (1978). Wagner et al. (2002) further included a record of *Pericoma trifasciata* (Meigen, 1818), most likely based on a typographical error in Vaillant (1978). The *P. trifasciata* record was not mentioned by Wagner (2004), who instead listed *Psychoda minuta* Banks, 1894, *P. phalaenoides* (Linnaeus, 1758), *P.* (*Tineria*) *alternata* Say, 1824 and *P.* (*Tinearia*) *lativentris* Berdén, 1952 based on unpublished material (the latter two placed in *Tinearia* Schellenberg, 1803, treated by Wagner 2004 as a genus).

In the present study, we review existing records of Mallorcan Psychodinae and present new material for eleven species; seven of which are previously unknown from Mallorca. In addition, we describe *Pericoma unipennata* sp. n as new to science.

Material and methods

Specimens were collected mainly by sweep netting and with aspirators from vegetation near the presumed larval habitats and preserved in 70–100% alcohol. Male specimens were sorted, dissected and mounted on slides in euparal (material in coll. ZFMK and ZMUB) or Canada balsam (material in coll. RW). Morphological terminology is according to Quate and Brown (2004) and Kvifte (2014, 2015). The „median moveable appendage“ in Kvifte et al. (2013) is here recognised as a *parameral sclerite*. Measurements are given in μm with an accuracy of 3 μm; except wing length which is given in mm to an accuracy of 100 μm.

Both literature records and new material that we have examined are included in our present checklist. Tribe-level classification is given according to Duckhouse (1987), while genus-level taxonomy is according to Wagner (2004) except where noted otherwise in the text. Species recorded as new to Mallorca are marked with an asterisk (*).

The material is deposited in the following collections:

RW Private collection of Rüdiger Wagner, Kassel
ZFMK Alexander-König Zoologischer Forschungsmuseum, Bonn, Germany
ZMUB Entomology Collections, Dept. of Natural History, University Museum of Bergen, Bergen, Norway

Species list

Maruinini

* ***Neoarisemus ibericus* Wagner, 1978**

First record from Mallorca. Puigpunyant, 39.6167°N, 2.5167°E, 6.x.1981, H. Malicky leg. 1♂ (RW).

Remarks. Previously only recorded from the type locality in northern Spain.

Mormiini

* ***Mormia tenebricosa* (Vaillant, 1954)**

First records from Mallorca. Calobra, 39.85°N, 2.8°E, 9.v.1978, 90 m a.s.l., H. Malicky leg. 1♂ (RW);

Deiá, town fountain, 39.748072°N, 2.643385°E, 8.ii.2015, G.Kvifte, M. Stokkan & C. Garcia leg. 1♂ (ZFMK);

Puigpunyent, 39.62°N, 2.85°E, 12.v.1978, 200m a.s.l., H. Malicky leg., 1♂; same but 1.X.1979, 6 ♂♂; same but 6.x.1979, 6♂♂ (all RW);

South slope of Piug Major, north of Soller, 39.783°N, 2.767°E, 7.–9.v.1978, 700 m a.s.l., H. Malicky leg. 2♂♂ (RW).

Remarks. Previously known from France, mainland Spain, Italy, Morocco and Algeria (Vaillant 1974). The generic and subgeneric classification of Mormiina is unstable and requires revision; therefore the placement in *Mormia* may change.

Paramormiini

* ***Clogmia albipunctata* (Williston, 1893)**

First records from Mallorca. Esporles, IMEDEA research center, 39.666438°N, 2.580863°E, 13.iv.2015, M. Stokkan leg. 1♀ (ZMFK);

E of Puigpunyent, 39.616667°N, 2.85°E, 1.x.1979, 200m a.s.l., H. Malicky leg. 1♀; same but 6.x.1979, 4♀♀ (all RW).

Remarks. A widespread near-cosmopolitan species, first recorded from Spain by Tonnoir (1920) under the synonym *Telmatoscopus meridionalis* (Eaton, 1894). Its biology is summarised in Boumans et al. (2009) and Ježek et al. (2012); for a review of its taxonomy see Ibañez-Bernal (2008).

* *Lepiseodina rothschildi* (Eaton, 1912)

First record from Mallorca. SW Pollensa, 39.8833°N, 2.9833°E, 3–5.x.1981, H. Malicky leg. 1♂ (RW).

Remarks. Placed in *Lepiseodina* Enderlein, 1937 (type species *Psychoda tristis* Meigen, 1830) by Ježek (1990) because of its asymmetric genitalia. The placement in *Clogmia* by Ježek (1984), Vaillant (1989) and Wagner (2004) may be a valid option to consider for the future when further character systems are explored.

Previous records are from Austria, Belgium, Czech Republic, France, Germany, Great Britain, Ireland and Slovakia (Oboňa and Ježek 2012).

* *Paramormia ustulata* (Walker, 1856)

First records from Mallorca. Banyalbufar, 39.691635°N, 2.514367°E, 25.x.2012, G.Kvifte leg. 1♂1♀ (ZMUB);

Pond west of Cala Figuera, 39.335635°N, 3.152597°E, 11.ii.2015, G.Kvifte leg, 1♂ (ZFMK).

Remarks. A widespread species or complex of species occurring in the Holarctic region. Ježek and Yağci (2005) list occurences from the following countries: Afghanistan, Algeria, the Azores, Belgium, Bosnia-Herzegovina, Bulgaria, the Canary Islands, China, Corsica, Czech Republic, Denmark, France, Germany, Great Britain, Greece, Hungary, Iran, Ireland, Israel, Italy, Macedonia, Madeira, Mongolia, Morocco, the Netherlands, Olanda island, Poland, Romania, Sardinia, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland, Tunisia, Turkey and the USA.

Pericomaini

Pericoma unipennata Kvifte, Stokkan & Wagner, sp. n.

http://zoobank.org/14619D1C-5A7E-4197-B99C-2C004DE54E83

Type material. Holotype male. Deiá, town fountain, 39.748072°N, 2.643385°E, 8.ii.2015, G.Kvifte, M. Stokkan & C. Garcia leg (ZMUB).

Diagnosis. *Pericoma unipennata* can be separated from all other *Pericoma* species on the presence of one feather-tipped and four spatulate tenacula on each surstylus, as well as the following combination of characters: parameral sheath with shallow U-sha-

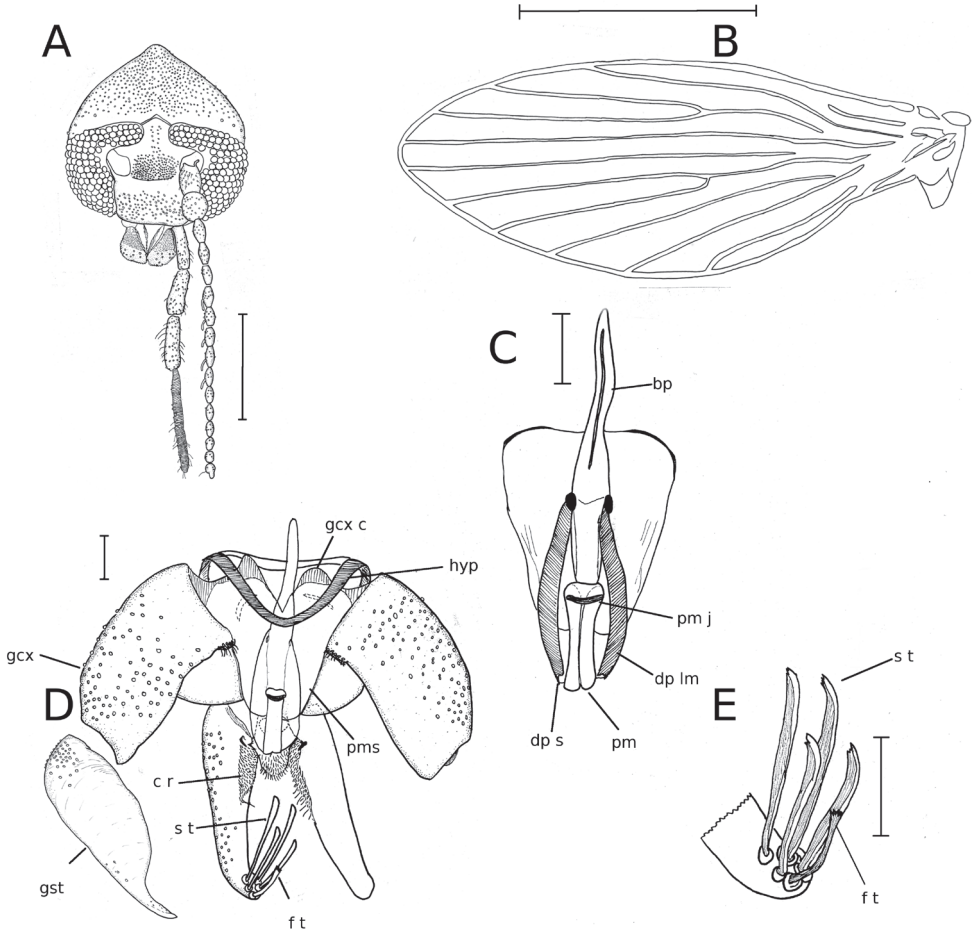

Figure 1. *Pericoma unipennata* sp. n., holotype male. **A** Head **B** Wing **C** Aedeagus **D** Male genitalia **E** Tenacula. The following abbreviations are used: bp – basiphallus, c r – cercal region, dp lm – distiphallic lateral margin, dp s – distiphallic spatula, f t – feathery tenacula, gcx – gonocoxite, gst – gonostyle, hyp – hypandrium, pm – parameral sclerite, pm j – parameral joint, pms – parameral sheath, s t – spatuliform tenacula.

ped apical indentation 1/6th as deep as width of parameral appendage base, gonostyle with narrow distal part 1/4th as long as broad basal part, distiphallic spatula with sclerotized side margins not converging apically, parameral appendage concave at lateral sides with distal 1/8th protruding over distiphallic spatula.

Description. Male (n=1). Head (Fig. 1A) longer than wide; vertex rounded with posterior lobe pointed, about half length of head; eyebridge comprising four rows of facets, separated by five facet diameters; interocular suture broadly V-shaped with median swelling; 7 supraocular setae present, 3 on ventral side and 4 on dorsal side; frontal scar patch inversely T-shaped, reaching level of uppermost facet row of eyebridge; clypeus subrectangular, weakly concave at anterior margin, densely setose, not

protruding in front of level of eyes; palp with 4th segment fleshy, corrugated, length of palpus segments 93 : 106 : 129 : 231; labellum fleshy, micropilose with 11 larger setae; antennae with 14 fusiform flagellomeres; scape cylindrical, pedicel elongate globular to barrell-shaped; ascoids present on flagellomeres 4-8; flagellomere 14 with apiculus about as long as base of segment; length of antennal segments 69 : 63 : 48 : 45 : 45 : 42 : 42 : 42 : 42 : 42 : 36 : 36 : 33 : 27 : 24 : 36.

Thorax without accessory organs; mesonotum and scutellum covered in setae alveoli except on lateral margins; anepisternum and laterotergite covered with setae alveoli; coxae and trochanters with dorsal and ventral stripes of setae alveoli, mid coxa with apicoanterior setose projection; legs without special features;

Wing (Fig. 1B) 2.3 mm long, subovate, membrane without setation or infuscation; radial fork very slightly distad of medial fork, both slightly distad of CuA_2; C with two breaks; Sc weakly curved towards C; apical section of R_2 curved anteriorly; wing apex between R_4 and R_5; medial fork incomplete; apical section of CuA_2 curved posteriorly; jugum obtuse;

Genitalia (Fig. 1C, D) with hypandrium of even width; aedeagus (Fig. 1D) with basiphallus compressed laterally; distiphallus consisting of two phallomeres forming a spatula with sclerotized lateral margins, lateral margins not converging distally; parameral sheath fused with gonocoxites basally, distally narrowing to nearly half its width at base; distally with narrow median incision; parameral sclerite meeting distal section of basiphallus, jointed to parameral sheath with slightly curved transverse band-like sclerite; parameral sclerite half length of distiphallus, consisting of two fused sclerites which are concave laterally, median suture complete; gonocoxites (Fig. 1C) stout, reniform, parabasal process absent but setose field present near connection with parameral sheath; gonocoxal condyles apparently fused with parameral sheath, gonostyle (Fig. 1C) with basal four 5ths liver-shaped, stout, distal 5th pointed, weakly sinous; epandrium slightly wider than long, expanding distally, number of apertures not discernable in specimen, carrying sparse hairs on ventral surface; surstyli about as long as epandrium, with lateral inner third more weakly sclerotized and densely micropilose; apex of surstylus with five aseriate tenacula of which one apical is feathery at the apex, four subapical tenacula spatulate; hypoproct obtusely isosceles trapezoid, micropilose; epiproct oval, densely pilose.

Etymology. *unipennata* = with one feather; refers to the presence of a single feather-tipped and four spatulate tenacula on its surstyli.

Biology. The specimen was collected at a spring with many bryophytes growing in a seepage stream. Bryophyte material was collected and extracted, however, no psychodid larvae or pupae were found.

Pericoma barbarica Vaillant, 1955

New records. Calobra, 39.85°N, 2.8°E, 9.v.1978, 90m a.s.l., H. Malicky leg. 1 ♂ (RW);

Deiá, town fountain, 39.748072°N, 2.643385°E, 8.ii.2015, G.Kvifte, M. Stokkan & C. Garcia leg. 3♂♂ (ZMUB);

Esporles, Torrent de San Vic, 39.670459°N, 2.569193°E, 11.ii.2015, G.Kvifte leg. 1♂ (ZMFK);

Puigpunyent, 39.616667°N, 2.85°E, 15.v.1978, 200m a.s.l., H. Malicky leg. 12 ♂♂; same but 1.x.1979, 5 ♂♂; same but 6.x.1979, 2 ♂♂ (all RW);

South slope of Piug Major, north of Soller, 39.783333°N, 2.766667°E, 7.–9.v.1978, 700 m a.s.l., H. Malicky leg. 11♂♂ (RW).

Literature record. Vaillant (1978).

Remarks. This species was described from Algeria and subsequently recorded from Mallorca by Vaillant (1978). It also occurs in mainland Spain and in North Africa (Vaillant 1978).

Pericoma trifasciata (Meigen, 1818)

Literature record. Wagner et al. (2002).

Remarks. Vaillant (1978) wrote "[*Pericoma*] *trifasciata* ist ebenfalls gemein auf der Mallorca-Insel [...]" ("*trifasciata* is also common on the island of Mallorca") in the paragraph summarizing the geographical distribution of *Pericoma barbarica* Vaillant, 1955; this is probably a lapsus as Mallorca is not mentioned in the species account for *Pericoma trifasciata*. No other records are available in the literature prior to the listing by Wagner et al. (2002), which was based on Vaillant (1978). In Wagner (2004) and the present paper we deem the records from the Baleares to be doubtful and in need of verification through examination of specimens.

Psychodini

* *Philosepedon pyrenaicus* Vaillant, 1974

First records from Mallorca. Deiá, town fountain, 39.748072°N, 2.643385°E, 8.ii.2015, G.Kvifte leg. 1♂ (ZMFK);

Esporles, town fountain, 39.669519°N, 2.576953°E, 10.ii.2015, G.Kvifte leg. 1♂ (ZMFK);

Palma de Mallorca, 39.570725°N, 2.641432°E, 7.ii.2015, G.Kvifte leg. 3♂1♀ (2♂ ZMFK, 1♂1♀ ZMUB).

Remarks. The males recorded here were identified as *Philosepedon pyrenaicus* according to the key in Vaillant (1974) because of the eyes separated by three facet diameters, the wing "mittwinkel" 105° and the left phallomere of the aedeagus being longer than the right. However, the specimens differ in that the 1st flagellomere is longer than the combined length of the scape and pedicel, and the eyebridge is two facet rows wide at several points. We deem these differences not to be taxonomically meaningful, as the differences in proportions and eyebridge composition could be interpreted as interspecific variation.

***Psychoda* (*Psychodocha*) *cinerea* Banks, 1894**

Literature record. Wagner (2004)

New records. Cala Figuera, 39.332245°N, 3.166440°E, 11.ii.2015, G. Kvifte leg. 2♂♂ (ZMFK);

Deiá, town fountain, 39.748072°N, 2.643385°E, 8.ii.2015, G.Kvifte, M. Stokkan & C. Garcia leg. 1♂ (ZMUB);

Esporles, Torrent de San Vic, 39.670459°N, 2.569193°E, 10.ii.2015, G.Kvifte leg. 1♂ (ZMFK).

***Psychoda* (*Psychodocha*) *gemina* (Eaton, 1904)**

Literature record. Wagner (2004)

***Psychoda* (*Psychoda*) *phalaenoides* (Linnaeus, 1758)**

Literature record. Wagner (2004).

* ***Psychoda* (*Psycha*) *grisescens* Tonnoir, 1922**

First records from Mallorca. Esporles, Torrent de San Vic, 39.670459°N, 2.569193°E, 11.ii.2015, G.Kvifte leg. 1♂.

Remarks. Recorded from Algeria, Austria, Belgium, Bosnia-Herzegovina, Czech Republic, Denmark, the Faroe Islands, France, Germany, Great Britain, Greece, Hungary, Ireland, Italy, Morocco, the Netherlands, Norway, Slovakia, Slovenia, Sweden, Tunisia and Turkey (Andersen 1999, Ježek 2004, Ježek and Yağci 2005).

***Psychoda* (*Psychodula*) *minuta* Banks, 1894**

Literature record. Wagner (2004).

New record. Esporles, Torrent de San Vic, 39.670459°N, 2.569193°E, 10.ii.2015, G.Kvifte leg. 1♂.

***Psychoda* (*Tinearia*) *alternata* +Say, 1824**

Literature record. Wagner (2004).

New record. Esporles, town fountain, 39.669519°N, 2.576953°E, 10.ii.2015, G.Kvifte leg. 1♀ (ZMFK).

Remarks. *Tinearia* Schellenberg, 1803 was treated as a genus by Wagner (2004) following Ježek (1977). This species group is undoubtedly monophyletic, however based on morphology and some analyses of molecular data it appears to be deeply nested within *Psychoda* s.l. (Vaillant 1990, Espindola et al. 2012, Kvifte and Andersen 2012, Kvifte unpubl.). Inclusion of *Tinearia* as a subgenus within *Psychoda* would thus allow ease of identification of monophyletic units, whereas recognising *Tinearia* as a separate taxon would render *Psychoda* paraphyletic. For a discussion of the monophyly criterion in supraspecific taxonomy, see Komarek and Beutel (2006).

Psychoda (*Tinearia*) *lativentris* Berdén, 1952

Literature record. Wagner (2004)

Remarks. For genus taxonomy, see remarks under *Psychoda alternata* above.

Discussion

The material examined in the present study was collected opportunistically and does not reflect the diversity of suitable habitats on Mallorca. Nevertheless, a few preliminary conclusions about the diversity and zoogeographic affinities of the fauna can be made.

Most of the species encountered are widespread European, Holarctic or even cosmopolitan species (*Clogmia albipunctata*, *Paramormia ustulata*, *Psychoda* spp. and arguably *Lepiseodina rothschildi*). Four species appear to have more limited distributions as local West Mediterranean elements, namely *Neoarisemus ibericus*, *Mormia tenebricosa*, *Pericoma barbarica* and *Philosepedon pyrenaicus*. A single species, *Pericoma unipennata* sp. n., has yet to be recorded outside of Mallorca but may have been overlooked elsewhere.

Our records of *Neoarisemus ibericus* and *Philosepedon pyrenaicus* are the first since the original descriptions, which in both cases were based on very few specimens collected in Northern Spain: Montes Universales and the Pyrenees respectively. The records from Mallorca represent a major range extension for both species, suggesting them to be more widespread than previously expected and that they may have been overlooked elsewhere.

Both *M. tenebricosa* and *P. barbarica* have similar distribution patterns; occurring on the north and south coasts of the West Mediterranean. Both species appear widespread in North Africa, having been recorded from Morocco, Algeria and Tunisia (Vaillant 1974, 1978, Wagner 1987). They differ in their European distributions, with the range of *P. barbarica* extending northeast to the Pyrenees and *M. tenebricosa* reaching the Western Alps in southern France and Italy.

Vaillant (1974) mentions consistent minor morphological differences between adult males of *M. tenebricosa* in the North African and European populations, but refrained from using them to delimit species. We consider that these differences warrant further study as they may be evidence of cryptic species or ongoing speciation; DNA sequences will be useful in illuminating this question.

Pericoma unipennata sp. n. appears to be a member of the Mediterranean *Pericoma modesta* Tonnoir, 1922 species group as defined by Vaillant (1978, p. 226). In this group, *Pericoma modesta* has a wide Mediterranean distribution whereas *P. alhambrana* Vaillant, 1978, *P. graecica* Vaillant, 1978 and *P. motasi* Vaillant, 1978 are localized endemics in Southern Spain, Southern Balkan and the Romanian Carpathian mountains, respectively. The Psychodidae of the Iberian peninsula are too incompletely known to tell whether *Pericoma unipennata* sp. n. is an island endemic of the Balearic islands or whether it is more widespread in the Mediterranean region.

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