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Revision of the freshwater crabs of the *Johora tahanensis* (Bott, 1966) species group (Crustacea, Brachyura, Potamidae), with a key to the genus

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Abstract

The taxonomy of the potamid freshwater crabs of the *Johora tahanensis* (Bott, 1966) species group (Potamoidea) is revised. Seven species are recognised, all from Peninsular Malaysia and southern Thailand, three of which are described as new. The three new species were previously identified as *J. tahanensis* but can be distinguished by characters of the carapace, male first gonopod, and vulva. A revised key to the 18 recognised species of *Johora* Bott, 1966, is provided.

Keywords

Freshwater crab, new species, Peninsular Malaysia, Potamoidea, taxonomy, Thailand

Introduction

Six genera of potamid freshwater crabs are known from the Malay Peninsula (Peninsular Malaysia, Thailand south of the Isthmus of Kra, and Singapore): *Baccazia* Ng, 2018a, *Demanietta* Bott, 1966, *Gempala* Ng & Ahmad, 2016, *Johora* Bott, 1966, *Stoliczia* Bott, 1966, and *Terrapotamon* Ng, 1986a (see Ng 1988, 2018a, b; Yeo et al. 1999; Ng and Ahmad 2016; Ng 2018). *Gempala* and *Baccazia* are unusual in that the terminal lobe of their mandibular palp is bilobed whereas in the other genera (and all other potamids), the terminal lobe is simple (Ng and Ahmad 2016; Ng 2018a). *Stoliczia* and *Terrapotamon* are distinct in having only a short flagellum (often absent) on the exopod of the third maxilliped (Ng 1986a, 1988, 2004; Lhekhim and Ng 2016; Promdam et al. 2017). Members of *Demanietta* and *Johora* possess a simple terminal lobe on the mandibular palp and the exopod of the third maxilliped has a long flagellum. *Demanietta* is known from eastern Myanmar and Thailand, but reaches only to Phuket (Yeo et al. 1999; Ng 2018b); whereas *Johora* occurs from southernmost Thailand to Singapore (Ng 1988, 2004; Leelawathanagoon et al. 2005; Yeo et al. 2007).

Johora is one of the most diverse of these Malayan genera, with 15 known species: *J. aipooae* (Ng, 1986a), *J. counsilmani* (Ng, 1985), *J. gapensis* (Bott, 1966), *J. grallator* Ng, 1988, *J. gua* Yeo, 2001, *J. hoiseni* Ng & Takeda, 1992, *J. intermedia* (Ng, 1986b), *J. johorensis* (Roux, 1936), *J. murphyi* (Ng, 1986b), *J. punicea* (Ng, 1985), *J. singaporensis* (Ng, 1986b), *J. tahanensis* (Bott, 1966), *J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005, *J. thoi* Ng, 1990, and *J. tiomanensis* (Ng & Tan, 1984) (Ng 1987, 1988, 1990; Ng and Takeda 1992; Yeo 2001; Leelawathanagoon et al. 2005; Ng et al. 2008).

The phylogenetic study by Yeo et al. (2007) showed that *Johora* is a monophyletic genus but three subclades were discerned. One of these subclades is the *J. tahanensis* species group (with *J. tahanensis*, *J. hoiseni* and *J. thoi*), which is distributed from central to northern Peninsular Malaysia and southern Thailand (Yeo et al. 2007: fig. 1). The present study revises the taxonomy of the *J. tahanensis* species group, and three new species are recognised. The three new species have all originally been referred to *J. tahanensis* mainly because of their relatively large adult size and general shape of the G1 structure. Detailed comparisons show they are morphologically distinct, and with discreet distributions, and *J. tahanensis* s. str. is not a wide-ranging species in Peninsular Malaysia. The *J. tahanensis* species group now contains seven species, including *J. thaiana* and the three new species described here. A revised key to all *Johora* species is also provided.

Materials and methods

Measurements provided are of the maximum carapace width and length (in millimetres), respectively. The abbreviations G1 and G2 are used for the male first and second gonopods, respectively. The terminology used follows Ng (1988), Guinot et al. (2013) and Davie et al. (2015). The Malay words Pulau, Gunung and Sungei are used for island, mountain and river, respectively. Material examined is deposited in the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (**ZRC**).

A full description is given for *Johora tahanensis*; for all other taxa, only diagnoses are provided.

Systematics

Family Potamidae Ortmann, 1896
Subfamily Potamiscinae Bott, 1970 sensu Yeo and Ng (2004)

Genus *Johora* Bott, 1966

Type species. *Potamon* (*Potamon*) *johorense* Roux, 1936, by original designation.

Comparative material. *Johora johorensis* (Roux, 1936): 1 male, 1 female, 1 juvenile (ZRC 2019.1054), Sungei Pulai, Gunung Pulai, Pulai, clear waters, sandy, and large rock substrate; shallow to waist deep waters with low vegetation cover on sides, in forest, 1°35'31.1"N, 103°31'10.7"E, Johor, coll. BY Lee et al., 23 June 2019. *Johora intermedia* Ng, 1986b: holotype male (19.8 × 15.1 mm) (ZRC 1984. 6529), stream near Bentong, Pahang, ca. 3°27'36"N, 101°53'31"E, ca. 600 m a.s.l., coll. Tweedie MWF, 12 July 1935; paratypes 26 males, 13 females, 17 juveniles (ZRC 1984. 6530–6585), same data as holotype; 7 males, 4 females, 1 juvenile (ZRC 1989.2171–2182), Gombak Forest, Selangor, coll. Ng PKL, 9 June 1987; 2 males, 2 females, 1 juvenile (ZRC 2001.1002), stream at Engkabau Trail, river tract, Forest Research Institute of Malaysia (FRIM), forest reserve, Kepong, Selangor, coll. Leong TM et al., September 2000; 3 males (ZRC 2003.0327), Sungei Kroh and Engkabau Trail, stream in Forest Research Institute of Malaysia (FRIM), Kepong, Selangor, coll. Leong TM & Lim KKP, 22–27 November 2002; 3 males (ZRC 2001.2283), Genting Highlands, Pahang, coll. Leong TM, 24 October 2001; 1 female (ZRC 2013.1819), Genting Highlands, Pahang, coll. Barlow HS, 9 April 2013; 2 males, 2 females (ZRC 2018.0690), Genting Tea Estate, Pahang, 3°21'24.9"N, 101°47'42.2"E, 670 m, coll. Barlow HS, 2000s**;** 4 males (ZRC 2002.242), in roadside seepage, on road to Jeriau Falls, Fraser's Hill, Pahang, coll. Leong TM, 24 February 2002; 2 males (ZRC 2016.003), under rocks, first stream on road towards Raub, descending from Fraser's Hill, Pahang, coll. Lai JCY, 6 December 2015; 2 males (ZRC 2020.0073), shaded stream along road, Fraser's Hill, Jalan Telekom, Pahang, 3.715485, 101.747604, coll. Lai JCY, December 2015; 1 male, 1 juvenile female (ZRC 2016.0002), Jeriau Falls, Fraser's Hill, Pahang, coll. Lai JCY & Hogg AH, 5 December 2015; 1 male (ZRC 2020.0354), Jeriau Falls, Fraser's Hill, Pahang, coll. Hogg AH, 30 May 2016. *Johora gapensis* (Bott, 1966): 2 males, 2 females (ZRC 1995.349), in shallow leaf litter stream, The Gap, Fraser's Hill, coll. Lim KKP, 9 June 1990; 1 male (ZRC 2002.0587), Gunung Bunga Buah, Genting Highlands, 3°22'30.0"N, 101°44'23.7"E, Pahang, coll. Lim KKP, 4 July 2002; 1 male (ZRC 2020.0074), along path to main waterfall, Jerijau Waterfall, Fraser's Hill, Pahang, 3.724534, 101.714471, coll. Lai JCY, December 2015. All locations in Peninsular Malaysia. For material of other *Johora* species, see Ng (1985, 1987, 1990), Ng and Takeda (1992), Yeo et al. (1999), Yeo (2001) and Leelawathanagoon et al. (2005).

Remarks. Members of the *J. tahanensis* species group are distinct from the nominate species group (*J. johorensis*, *J. gapensis*, *J. tiomanensis*, *J. counsilmani*, *J. intermedia*,

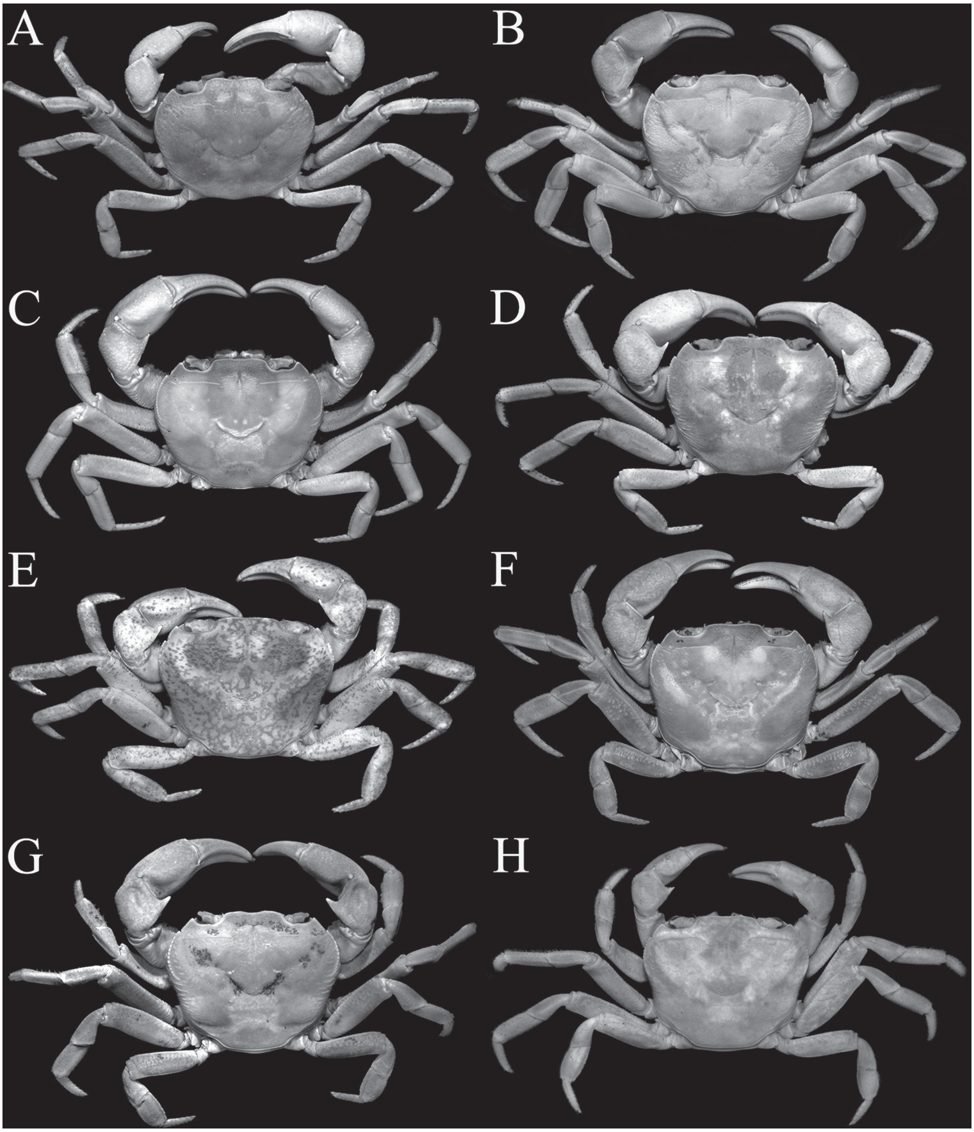

Figure 1. Overall dorsal view **A** *Johora intermedia* Ng, 1986, holotype male (19.8 × 15.1 mm) (ZRC 1984.6529), Pahang **B** *J. tahanensis* (Bott, 1966), male (30.7 × 25.5 mm) (ZRC 1984.6795), Pahang **C** *J. thoi* Ng, 1990, holotype male (41.2 × 33.3 mm) (ZRC 1989.2249), Terengganu **D** *J. hoiseni* Ng & Takeda, 1992, holotype male (25.1 × 21.1 mm) (ZRC 1984.6673), Kelantan **E** *J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005, paratype male (22.2 × 18.6 mm) (ZRC 2006.0052), Thailand **F** *J. booliati* sp. nov., holotype male (34.6 × 30.0 mm) (ZRC 2020.0072), Pahang **G** *J. erici* sp. nov., holotype male (38.3 × 32.0 mm) (ZRC 2020.0360), Perak **H** *J. michaeli* sp. nov., holotype male (22.7 × 19.2 mm) (ZRC 2010.0047), Terengganu.

J. murphyi and *J. singaporensis*) (sensu Yeo et al. 2007) and can be distinguished by the following suite of characters: the epibranchial tooth is prominent, clearly demarcated from the external orbital tooth by a distinct cleft (Fig. 2B–H); the frontal margin is relatively wide (Fig. 2B–H); the epigastric cristae are prominently anterior of the postorbital cristae (Fig. 2B–H); the postorbital crista is sharp and prominent, with the lateral part clearly reaching at least the beginning of the cervical groove (Fig. 2B–H); the lateral margins of the posterior margin of the epistome are obliquely sloping (Fig. 3B–H); the third maxilliped is covered with dense, long setae, and the merus and ischium are proportionately longer (Figs 3B–H, 4B); the male pleon is proportionately more elongate with somite 3 relatively less wide (Figs 5B–H, 6D, 7D); the G1 terminal segment is long to very long and often covered with numerous setae (e.g., Fig. 8A); and the adult female pleon is ovate (Fig. 13B–H). For members of the *J. johorensis* species group, the epibranchial tooth is usually lower and demarcated from the external orbital tooth by a shallow or narrow cleft (Fig. 2A); the frontal margin is relatively less wide (Fig. 2A); the epigastric cristae are only slightly anterior of the postorbital cristae (Fig. 2A); the postorbital crista is uneven and not sharp and do not clearly extend to the cervical groove (Fig. 2A); the lateral margins of the posterior margin of the epistome are horizontal and subparallel with the frontal margin (Fig. 3A); the setae on the third maxilliped are shorter and usually less dense, and in the smaller taxa, the merus and ischium are proportionately shorter (Figs 3A, 4A); the male pleon is broadly triangular with somite 3 relatively wider (Fig. 5A); the G1 terminal segment is short to long (e.g., Ng, 1987: figs 2F, I, 3A, 6D); and the adult female pleon is almost round (Fig. 13A).

In recent years, the structure of the vulva has proven useful in potamid taxonomy for some groups, but for *Johora* species, its morphology appears to be relatively conservative. The one exception is *J. thoi*, where the lateral sternal vulvar cover projects obliquely anteriorly as a large triangular plate (Fig. 14C), quite different from the simpler structures of congeners (Fig. 14A, B, D–H).

The molecular study by Yeo et al. (2007) tested three members of the *J. tahanensis* species group: "*J. tahanensis*" from Perak (ZRC 1995.268), *J. hoiseni* from Kelantan (ZRC1984.6674–6755, ZRC 1984.7683–7687), and *J. thoi* from Terengganu (ZRC 2001.1167), with the taxa coming out in one clade. The "*J. tahanensis*" from Perak (ZRC 1995.268) is here reidentified as a new species, *J. erici* sp. nov.

The last key to the genus was constructed in 1988 and in view of the additional species described since, there is a necessity to update this, and a revised key is presented here.

***Johora tahanensis* Bott, 1966**

Figures 1B, 2B, 3B, 4B, 5B, 8A–D, 12B, 13B, 14B

Potamiscus (*Johora*) *johorensis tahanensis* Bott, 1966: 495 (part), pl. 21 fig. 15.
Stoliczia (*Johora*) *johorensis tahanensis* – Bott 1970: 181 (part), pl. 50 fig. 50.
Johora tahanensis – Ng 1987: 33 (part), fig. 9A; Ng 1988: 42 (part), fig. C, F; Ng and Takeda 1992: 107 (part); Ng 2004: 321; Ng and Yeo 2007: 102; Ng et al. 2008: 163; Cumberlidge et al. 2009: table.
Stoliczia johorensis tahanensis – Takeda 1987: 92, pl. X (center).

Material examined. 13 males (largest 27.2 × 22.9 mm), 13 females (largest 24.4 × 21.0 mm), 4 juveniles (ZRC 1984.6764–6793), Kuala Tahan, Taman Negara National Park, Pahang, coll. Tweedie MWF, April 1940; 1 male (30.7 × 25.5 mm), 2 females (ZRC 1984.6795–6797), rivulet of Sungei Tahan, Kuala Tahan, Taman Negara National Park, Pahang, coll. Alfred ER, 23 March 1956; 1 male (ZRC 1989.2086), Changah Siveh, Sungei Tahan, Taman Negara National Park, Pahang, coll. Alfred ER, 3 March 1948; 1 female (ZRC 1989.3749), Jenka, Sungei Tekam, Pahang, 4°13'N, 102°39'E, coll. Lim RP, 19 March 1981; 1 young male, 1 female (ZRC 1989.2144–2145), from University of Malaya collections, 1960s; 2 juveniles (ZRC 1989.3358–3359), station F63/20, tributary of Sungei Telom (= Sungei Telum), Pahang, coll. University of Malaya, 9 March 1963; 1 female (ZRC 1989.3686), coll. University of Malaya, no date. All locations in Peninsular Malaysia.

Diagnosis. Adult carapace width to length ratio 1.16–1.19 (Figs 1B, 2B, 12B); dorsal surface gently convex in frontal view, not inflated (Fig. 3B); frontal margin almost straight (Fig. 2B); suborbital, pterygostomial and sub-branchial regions rugose, pterygostomial region covered with dense setae (Fig. 3B); epigastric cristae distinct, distinctly anterior to sharp postorbital cristae, postorbital cristae with lateral edges low, joining lateral margin through oblique striae (Fig. 2B); external orbital tooth separated from epibranchial tooth by distinct cleft, epibranchial tooth sharp, distinct (Fig. 2B); anterolateral margin distinctly convex (Fig. 2B); posterolateral margin gently sinuous to almost straight, distinctly converging towards gently convex, entire posterior carapace margin (Fig. 2B); posterior margin of epistome with triangular median triangle, lateral margin obliquely sloping (Fig. 3B); outer surfaces of third maxillipeds with dense, long stiff setae; ischium subrectangular, with shallow median oblique groove (Figs 3B, 4B); ambulatory legs not elongate, length to width ratio of merus of fourth ambulatory leg 2.7–2.8 (Figs 1B, 12B); G1 subterminal segment gradually tapering from broad proximal part to slender distal part, without distinct shelf-like structure along gently concave outer margin; terminal segment gently curved outwards (from median part of sternum), ca. half length of subterminal segment, surface with numerous short setae (Fig. 8A–C); G2 slightly longer than G1, distal segment long, about half length of basal segment (Fig. 8D). Female pleon longitudinally ovate; somites 3–6 progressively narrower; telson subtriangular (Fig. 13B). Vulvae large, on anterior half of sternite 6, slightly pushing into suture with sternite 5, lateral sternal vulvar cover semicircular (Fig. 14B).

Description of male. Carapace subrectangular broader than long, width to length ratio 1.16–1.19; dorsal surface gently convex in frontal view (Figs 1B, 2B, 3B). Frontal margin almost straight; frontal region, dorsal surface, lateral parts of anterolateral and branchial regions rugose, covered with small granules and striae; regions clearly indicated, median H-shaped gastro-cardiac groove deep; cervical grooves broad, shallow; suborbital, pterygostomial and sub-branchial regions rugose, covered with dense setae (Figs 2B, 3B). Epigastric cristae distinct, marked by transverse striae, not cristate, separated by median groove; postorbital cristae sharp, prominent, positioned distinctly posterior to and separated from epigastric cristae, lateral edges reaching beginning of cervical groove, reaching lateral margin through series of short, oblique striae (Figs 1B, 2B). Frontal

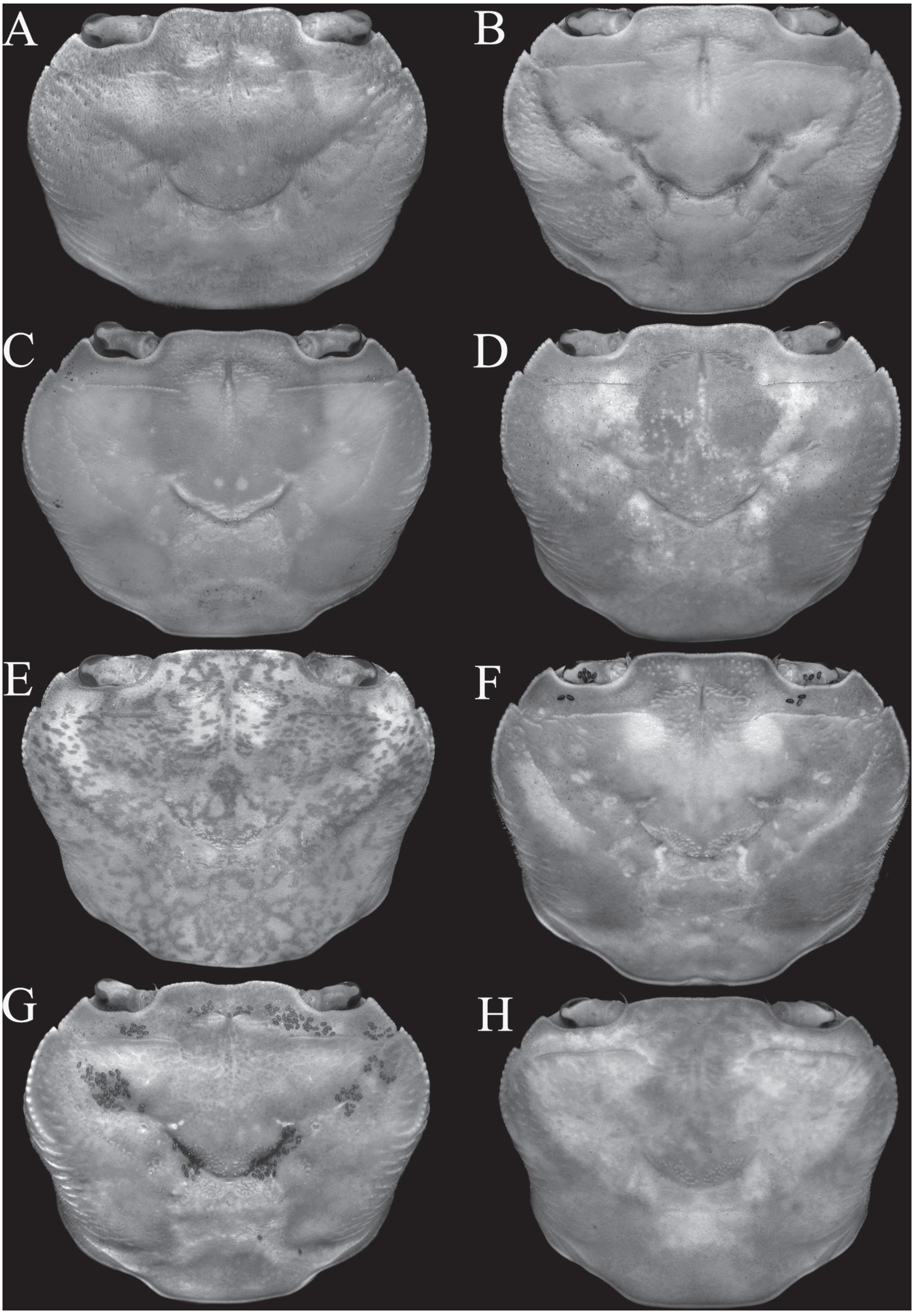

Figure 2. Dorsal view of carapace **A** *Johora intermedia* Ng, 1986, holotype male (19.8 × 15.1 mm) (ZRC 1984.6529), Pahang **B** *J. tahanensis* (Bott, 1966), male (30.7 × 25.5 mm) (ZRC 1984.6795), Pahang **C** *J. thoi* Ng, 1990, holotype male (41.2 × 33.3 mm) (ZRC 1989.2249) Terengganu **D** *J. hoiseni* Ng & Takeda, 1992, holotype male (25.1 × 21.1 mm) (ZRC 1984.6673), Kelantan **E** *J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005, paratype male (22.2 × 18.6 mm) (ZRC 2006.0052), Thailand **F** *J. booliati* sp. nov., holotype male (34.6 × 30.0 mm) (ZRC 2020.0072), Pahang **G** *J. erici* sp. nov., holotype male (38.3 × 32.0 mm) (ZRC 2020.0360), Perak **H** *J. michaeli* sp. nov., holotype male (22.7 × 19.2 mm) (ZRC 2010.0047), Terengganu.

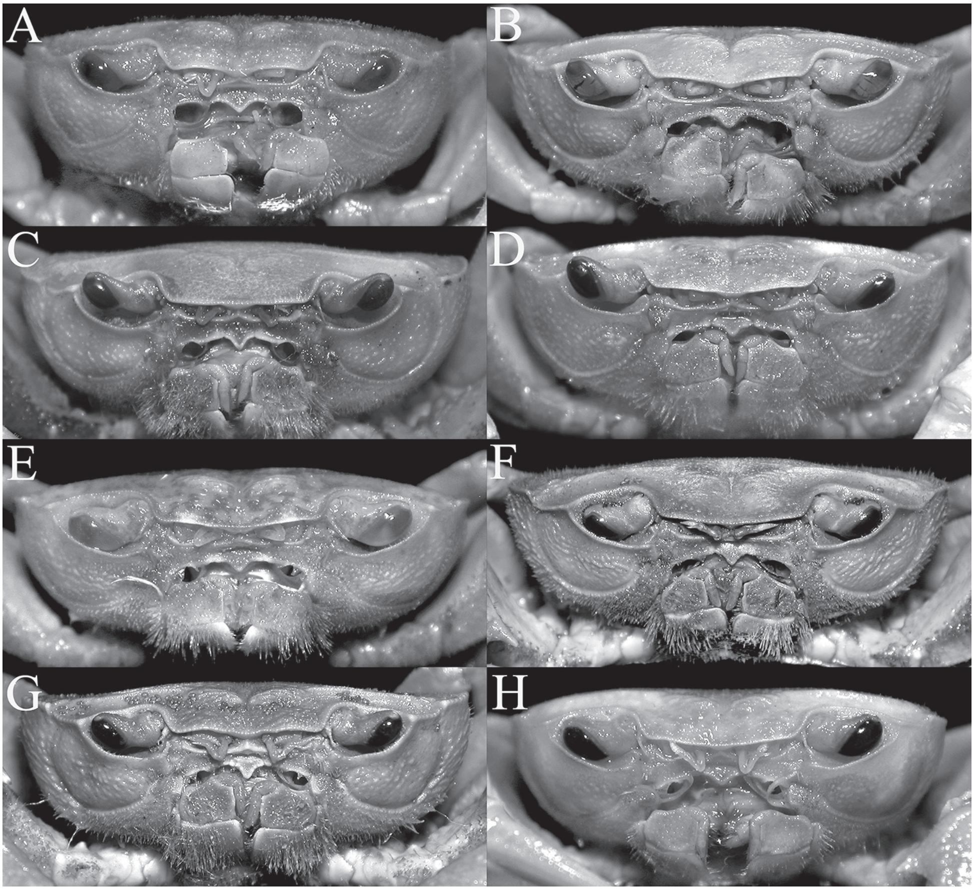

Figure 3. Frontal view of cephalothorax **A** *Johora intermedia* Ng, 1986, holotype male (19.8 × 15.1 mm) (ZRC 1984.6529), Pahang **B** *J. tahanensis* (Bott, 1966), male (30.7 × 25.5 mm) (ZRC 1984.6795), Pahang **C** *J. thoi* Ng, 1990, holotype male (41.2 × 33.3 mm) (ZRC 1989.2249), Terengganu **D** *J. hoiseni* Ng & Takeda, 1992, holotype male (25.1 × 21.1 mm) (ZRC 1984.6673), Kelantan **E** *J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005, paratype male (22.2 × 18.6 mm) (ZRC 2006.0052), Thailand **F** *J. booliati* sp. nov., holotype male (34.6 × 30.0 mm) (ZRC 2020.0072), Pahang **G** *J. erici* sp. nov., holotype male (38.3 × 32.0 mm) (ZRC 2020.0360), Perak **H** *J. michaeli* sp. nov., holotype male (22.7 × 19.2 mm) (ZRC 2010.0047), Terengganu.

margin entire; separated from supraorbital margin by rounded angle (Fig. 2B). External orbital tooth triangular, outer margin twice length of inner margin; epibranchial tooth sharp, distinct, separated from anterolateral margin by distinct cleft (Figs 1B, 2B). Anterolateral margins convex, cristate, granulated (Fig. 2B). Posterolateral margin gently sinuous to almost straight, distinctly converging towards gently convex, entire posterior carapace margin (Figs 1B, 2B). Orbits subovate; eye filling up most of orbital space; ocular peduncle relatively short, stout; cornea large, pigmented (Fig. 3B). Supraorbital margin concave, entire (Fig. 2B). Suborbital margin concave, complete, cristate

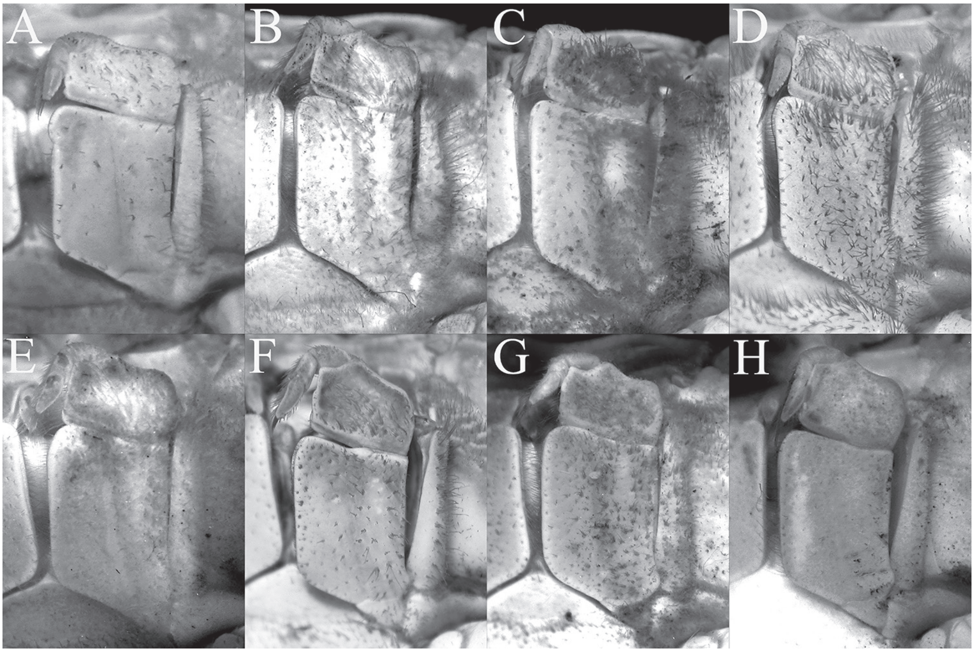

Figure 4. Left third maxilliped **A** *Johora intermedia* Ng, 1986, holotype male (19.8 × 15.1 mm) (ZRC 1984.6529), Pahang **B** *J. tahanensis* (Bott, 1966), male (30.7 × 25.5 mm) (ZRC 1984.6795), Pahang **C** *J. thoi* Ng, 1990, holotype male (41.2 × 33.3 mm) (ZRC 1989.2249), Terengganu **D** *J. hoiseni* Ng & Takeda, 1992, holotype male (25.1 × 21.1 mm) (ZRC 1984.6673), Kelantan **E** *J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005, paratype male (22.2 × 18.6 mm) (ZRC 2006.0052), Thailand **F** *J. booliati* sp. nov., holotype male (34.6 × 30.0 mm) (ZRC 2020.0072), Pahang **G** *J. erici* sp. nov., holotype male (38.3 × 32.0 mm) (ZRC 2020.0360), Perak **H** *J. michaeli* sp. nov., holotype male (22.7 × 19.2 mm) (ZRC 2010.0047), Terengganu.

(Fig. 3B). Antennules short, folding transversely in narrow fossa; antennae very short, not reaching cornea of eyes (Fig. 3B). Posterior margin of epistome with triangular median lobe; lateral part obliquely sloping, with 2 distinct concave margins (Fig. 3B). Mandibular palp with 3 distinct articles, terminal article single lobed.

Third maxillipeds covering most of buccal cavity when closed; surfaces of merus, ischium and exopod with numerous long stiff setae; ischium subrectangular, with shallow median oblique groove; merus subquadrate, slightly wider than long, anteroexternal angle not expanded; exopod slender, reaching half length of merus, with long flagellum (Figs 3B, 4B).

Chelipeds asymmetrical (Fig. 1B). Anterior margin of basis-ischium smooth; margins of merus rugose, uneven; inner margin lined with dense setae. Outer surface of carpus rugose, inner distal angle with sharp tooth (Fig. 1B). Outer surfaces of chelae rugose; chela stout (Fig. 1B). Fingers of chela almost straight, longer than palm; cutting edges of both fingers with variously sized teeth and denticles; fingers of slightly smaller chela similar (Fig. 1B).

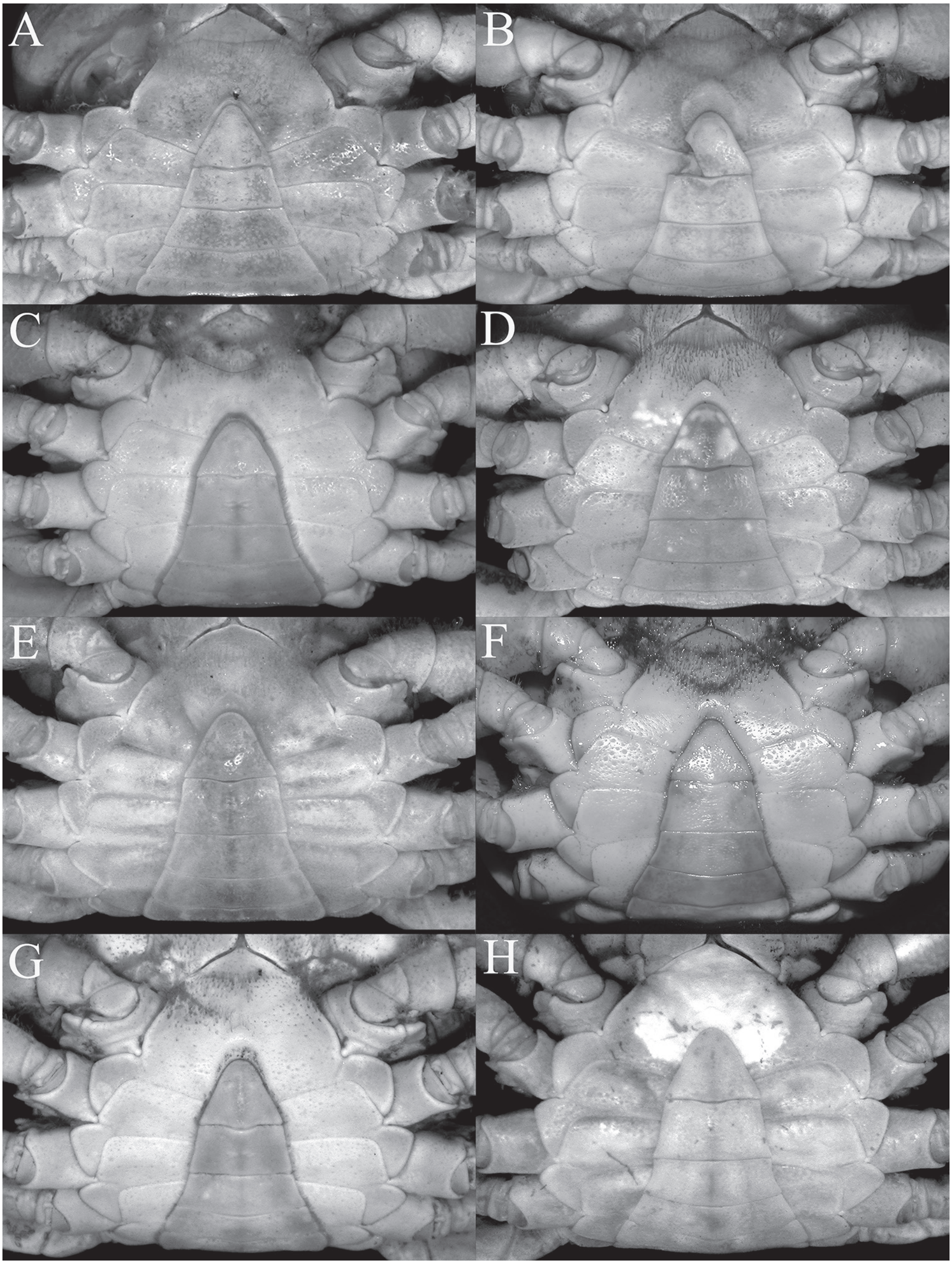

Figure 5. Anterior thoracic sternum and pleon **A** *Johora intermedia* Ng, 1986, holotype male (19.8 × 15.1 mm) (ZRC 1984.6529), Pahang **B** *J. tahanensis* (Bott, 1966), male (30.7 × 25.5 mm) (ZRC 1984.6795), Pahang **C** *J. thoi* Ng, 1990, holotype male (41.2 × 33.3 mm) (ZRC 1989.2249), Terengganu **D** *J. hoiseni* Ng & Takeda, 1992, holotype male (25.1 × 21.1 mm) (ZRC 1984.6673), Kelantan **E** *J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005, paratype male (22.2 × 18.6 mm) (ZRC 2006.0052), Thailand **F** *J. booliati* sp. nov., holotype male (34.6 × 30.0 mm) (ZRC 2020.0072), Pahang **G** *J. erici* sp. nov., holotype male (38.3 × 32.0 mm) (ZRC 2020.0360), Perak **H** *J. michaeli* sp. nov., holotype male (22.7 × 19.2 mm) (ZRC 2010.0047), Terengganu.

Ambulatory legs not elongate, length to width ratio of merus of fourth ambulatory leg 2.7–2.8; second pair longest, fourth pair shortest (Fig. 1B). Surface of merus gently rugose, dorsal margin weakly cristate, slightly uneven, appears serrated, without subdistal spine or tooth; carpus rugose with short setae; propodus laterally flattened, margins with short setae; dactylus gently curved, setose, margins with short spines (Fig. 1B).

Thoracic sternum (notably sternites 3, 4) with shallow pits to smooth (Fig. 5B). Sternites 1, 2 completely fused to form triangular plate with convex margins; separated from sternite 3 by distinct, gently concave suture lined with short setae; sternites 3, 4 completely fused except for shallow oblique depression between sternites, lined with short stiff setae (Fig. 5B); sutures between sternites 4/5, 5/6, 6/7 medially interrupted; suture between sternites 7, 8 complete; deep longitudinal groove on sternite 8 extending to most of sternite 7. Penis on condyle of coxa of fourth ambulatory leg. Sternopleonal cavity deep, reaching to imaginary line connecting submedian parts of cheliped coxae (Fig. 5B). Male pleonal locking tubercle relatively large, low, round, positioned on posterior edge of sternite 5, just adjacent to sternite 6.

Pleon triangular, all somites, telson free; telson triangular, lateral margins almost straight to gently sinuous; somite 6 subtrapezoidal, distinctly wider than long, lateral margins gently sinuous; somites 3–5 trapezoidal, gradually decreasing in width; somites 1, 2 subrectangular, narrow, very wide, reaching to bases of coxae of fourth ambulatory legs, thoracic sternite 8 not visible when pleon closed (Fig. 5B).

G1 subterminal segment gradually tapering from broad proximal part to slender distal part, without distinct shelf-like structure along gently concave outer margin; terminal segment gently curved outwards (from median part of sternum), ca. half length of subterminal segment, surfaces with numerous short setae (Fig. 8A–C); G2 slightly longer than G1, distal segment long, about half length of basal segment (Fig. 8D).

Female. Similar to male in most non-sexual features; chelipeds symmetrical or only slightly asymmetrical (Fig. 12B). Pleon longitudinally ovate, covering most of thoracic sternal surface, all somites and telson free; somites 3–6 progressively narrower; telson subtriangular (Fig. 13B). Vulvae large, covering anterior half of sternite 6, slightly pushing into suture with sternite 5, lateral sternal vulvar cover semicircular (Fig. 14B).

Remarks. Ng and Takeda (1992: 108) discussed the taxonomy of *J. tahanensis* at length, showing that the material from two parts of Taman Negara National Park in Malaysia belonged to two species and that the type series is mixed. Bott (1966, 1970) and Ng (1987, 1988) had regarded them as one taxon, incorrectly noting that the G1 structure was variable. The holotype of *J. tahanensis* was from Kuala Tahan in the state of Pahang, in the southern part of the national park, and the G1 of this specimen (in the Senckenberg Museum, Frankfurt) as well as the topotypic material we have from that location has a terminal segment which is gently curved (Fig. 8A). Material from the northern part of the park from the adjacent state of Kelantan had a G1 terminal segment that is straight (Fig. 8E). Ng and Takeda (1992) showed that the G1 differences of the Pahang and Kelantan specimens are consistent and the Kelantan material was referred to a separate species, *J. hoiseni*.

The material reported as "*J. tahanensis*" by Ng and Takeda (1992: 108) from and around Fraser's Hill in Selangor and Pahang should be now referred to *J. booliati* sp. nov. (see remarks for this species).

Distribution. *Johora tahanensis* is known from the tributaries around Sungei Tahan in southern Pahang, at the southern part of Taman Negara National Park (Fig. 15). It lives among rocks and submerged vegetation in the relatively fast flowing streams in the forest.

Conservation. The species is not under any immediate threat as it is found in Malaysia's oldest and largest national park. Ng and Yeo (2007) treated *J. tahanensis* s. str. as vulnerable as it is not known from a relatively wide geographic area but it was reappraised and regarded as of least concern in Cumberlidge et al. (2009).

***Johora thoi* Ng, 1990**

Figures 1C, 2C, 3C, 4C, 5C, 6, 9A–H, 12C, 13C, 14C

Johora thoi Ng, 1990: 305, figs 1, 2; Ng 2004: 321; Ng and Yeo 2007: 102; Ng et al. 2008: 163; Cumberlidge et al. 2009: table.

Material examined. ***Holotype*:** male (41.2 × 33.3 mm) (ZRC 1989.2249), Telok Kalong Besar, Pulau Redang, Terengganu, ca. 5°46'7"N, 103°01'38"E, coll. Tho YP, 8 March 1989. Others: 1 male (ZRC 1989.3758), in freshwater stream, Telok Kalong Besar, Pulau Redang, Terengganu, coll. Saw LG, 1 August 1989; 1 male (ZRC 1989.3740), Telok Kalong Besar, Pulau Redang, Terengganu, coll. Saw LG, 1 August 1989; 1 male, 1 female (ZRC 1996.2085), site 5, stream behind Pasir Panjang, Pulau Redang, Terengganu, Lim KKP et al., 25 June 1992; 1 male (ZRC 1996.2087), Pulau Redang, Terengganu, Lim KKP et al., 23 June 1992; 3 males (ZRC 1996.2086), site 7, stream behind Telok Kalong Besar, Pulau Redang, Terengganu, coll. Lim KKP et al., 25 June 1992; 6 males, 2 females, 1 juvenile (ZRC 2001.1167), from freshwater rocky stream, East Coast forest trail, ca. 1.2–1.6 km from Pasir Panjang to Telok Dalam, Pulau Redang, Terengganu, coll. Tan HH and Koh LL, 20 June 2001. All locations in Peninsular Malaysia.

Diagnosis. Adult carapace width to length ratio 1.19–1.24 (Figs 1C, 2C, 6A, B, 12C); dorsal surface gently convex in frontal view, not inflated (Figs 3C, 6C); frontal margin almost straight or slightly sinuous (Figs 2C, 6B); suborbital, pterygostomial and sub-branchial regions rugose, pterygostomial region covered with dense setae (Figs 3C, 6C); epigastric cristae distinct, distinctly anterior to sharp postorbital cristae, postorbital cristae with lateral edges low, not joining lateral margin (Figs 2C, 6B); external orbital tooth separated from epibranchial tooth by prominent cleft, epibranchial tooth sharp, distinct (Figs 2C, 6B); anterolateral margin distinctly convex (Figs 2C, 6B); posterolateral margin gently sinuous to almost straight, distinctly converging towards gently convex, entire posterior carapace margin (Figs 2C, 6B); posterior margin of epistome with triangular median triangle, lateral margin obliquely sloping

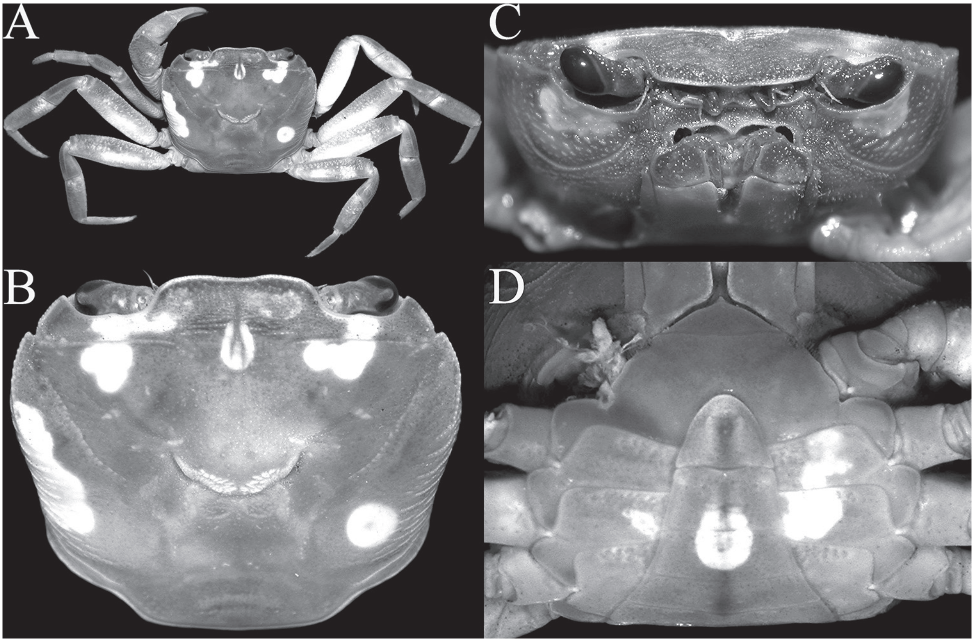

Figure 6. *Johora thoi* Ng, 1990, male (21.1 × 17.7 mm) (ZRC 2001.1167), Terengganu **A** overall dorsal view **B** dorsal view of carapace **C** frontal view of cephalothorax **D** anterior thoracic sternum and pleon.

(Figs 3C, 6C); outer surfaces of third maxillipeds with dense, long stiff setae; ischium subrectangular, with shallow median oblique groove (Figs 3C, 4C); ambulatory legs relatively longer, length to width ratio of merus of fourth ambulatory leg 3.0–3.2 (Figs 1C, 6A, 12C); G1 subterminal segment with broad proximal part, tapering suddenly to slender distal part, with distinct shelf-like structure along outer margin; terminal segment straight, long, slender, subequal in length to subterminal segment, surfaces with scattered short setae (Fig. 9A–C, E–G); G2 shorter than G1, distal segment long, about two-thirds length of basal segment (Fig. 9D, H). Female pleon ovate; somites 3–6 progressively narrower; telson semi-circular (Fig. 13C). Vulvae large, on anterior half of sternite 6, adjacent to suture with sternite 5, lateral sternal vulvar cover triangular, partially overlapping sternite 5 (Fig. 14C).

Remarks. This is one of the largest species of *Johora* and is rivalled in size only by *J. tiomanensis* and *J. counsilmani* from Pulau Tioman. The G1 structure of *J. thoi* is distinctive and consistent, the long and straight terminal segment being evident even in small subadult specimens (Fig. 9E–G). The only other species with superficially similar G1s are *J. singaporensis* and *J. michaeli* sp. nov. from Singapore and mainland Terengganu, respectively. In these species, however, the G1 terminal segment is prominently shorter, being only two-thirds or less the length of the subterminal segment (Fig. 9I–K; Ng 1987: fig. 8A, B).

Distribution. *Johora thoi* is endemic to Pulau Redang, the largest island in the Redang Archipelago, a group of nine islands about 25 km off the northeastern coast

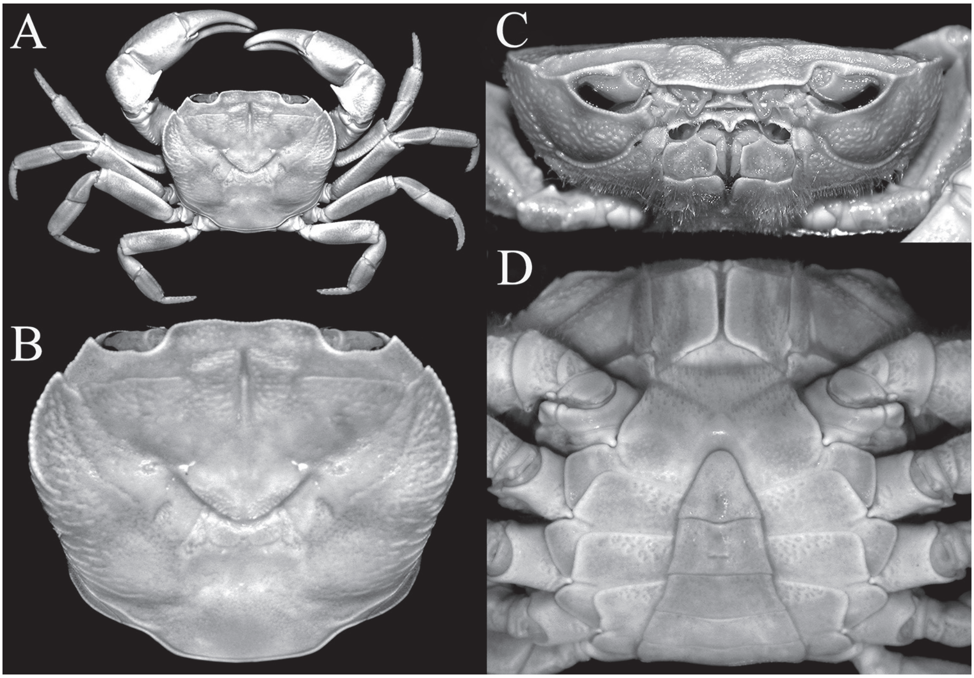

Figure 7. *Johora erici* sp. nov., male (41.2 × 33.8 mm) (ZRC 1995.0269), Kelantan **A** overall dorsal view **B** dorsal view of carapace **C** frontal view of cephalothorax **D** anterior thoracic sternum and pleon.

of Peninsular Malaysia. The species has been recorded from most parts of the island, including its highest point (359 m), occurring in all clean waters there (Fig. 15). It lives under rocks and can be found along the stream banks at night.

Conservation. Although the entire Redang Archipelago is a marine park, the forests are not fully protected, and development of the land for tourism and excessive freshwater use are concerns. As the species is only known from one island only 7 km long and 6 km wide, it is treated as endangered by Ng and Yeo (2007), but Cumberlidge et al. (2009) noted it was vulnerable at best as the area is technically protected.

Johora hoiseni Ng & Takeda, 1992

Figures 1D, 2D, 3D, 4D, 5D, 8E–H, 12D, 13D, 14D

Potamiscus (*Johora*) *johorensis tahanensis* Bott, 1966: 495 (part), fig. 32 (not *Stoliczia* (*Johora*) *johorensis tahanensis* Bott, 1966 s. str.).

Stoliczia (*Johora*) *johorensis tahanensis* – Bott 1970: 181 (part), pl. 40 fig. 57; Ng and Tan 1984: 172, fig. 7 (not *Stoliczia* (*Johora*) *johorensis tahanensis* Bott, 1966).

Johora tahanensis – Ng 1987: 33 (part), fig. 9B–K; Ng 1988: 42 (part), fig. 18A, B, D, E, G (not *Stoliczia* (*Johora*) *johorensis tahanensis* Bott, 1966).

Johora hoiseni Ng & Takeda, 1992: 108, figs 2, 3; Ng 2004: 321; Ng and Yeo 2007: 100; Ng et al. 2008: 163; Cumberlidge et al. 2009: table.

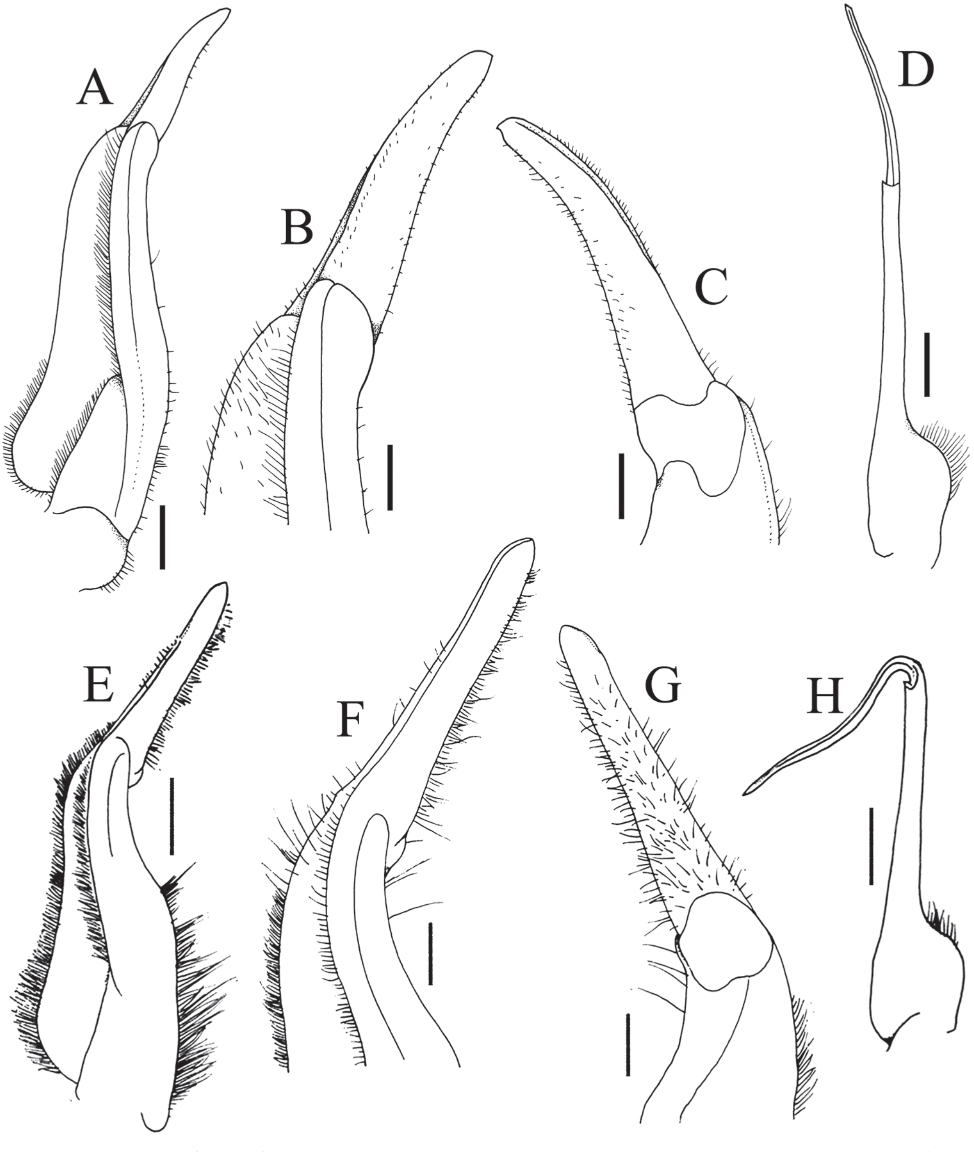

Figure 8. A–D *Johora tahanensis* (Bott, 1966), male (30.7 × 25.5 mm) (ZRC 1984.6795), Pahang **E–H** *J. hoiseni* Ng & Takeda, 1992, holotype male (25.1 × 21.1 mm) (ZRC 1984.6673), Kelantan **A, E** left G1 (ventral view) **B, F** distal part of left G1 (ventral view) **C, G** distal part of left G1 (dorsal view) **D, H** left G2 (ventral view) **E–H** after Ng and Takeda (1992: fig. 3B, D–F). Scale bars: 1.0 mm (**A, D, E, H**); 0.5 mm (**B, C, F, G**).

Material examined. ***Holotype*:** male (25.1 × 21.1 mm) (ZRC 1984.6673), stream entering Sungei Galas, near Gua Madir, Taman Negara National Park, Kelantan, ca. 4°51'30"N, 102°03'23"E, coll. Tweedie MWF, August 1939. Paratypes: 53 males, 13 females (ZRC 1984.6674–6755), same data as holotype. Others: 3 males, 18 females (ZRC 1984.7683–7687), stream entering Sungei Galas, near Gua Madir, Taman

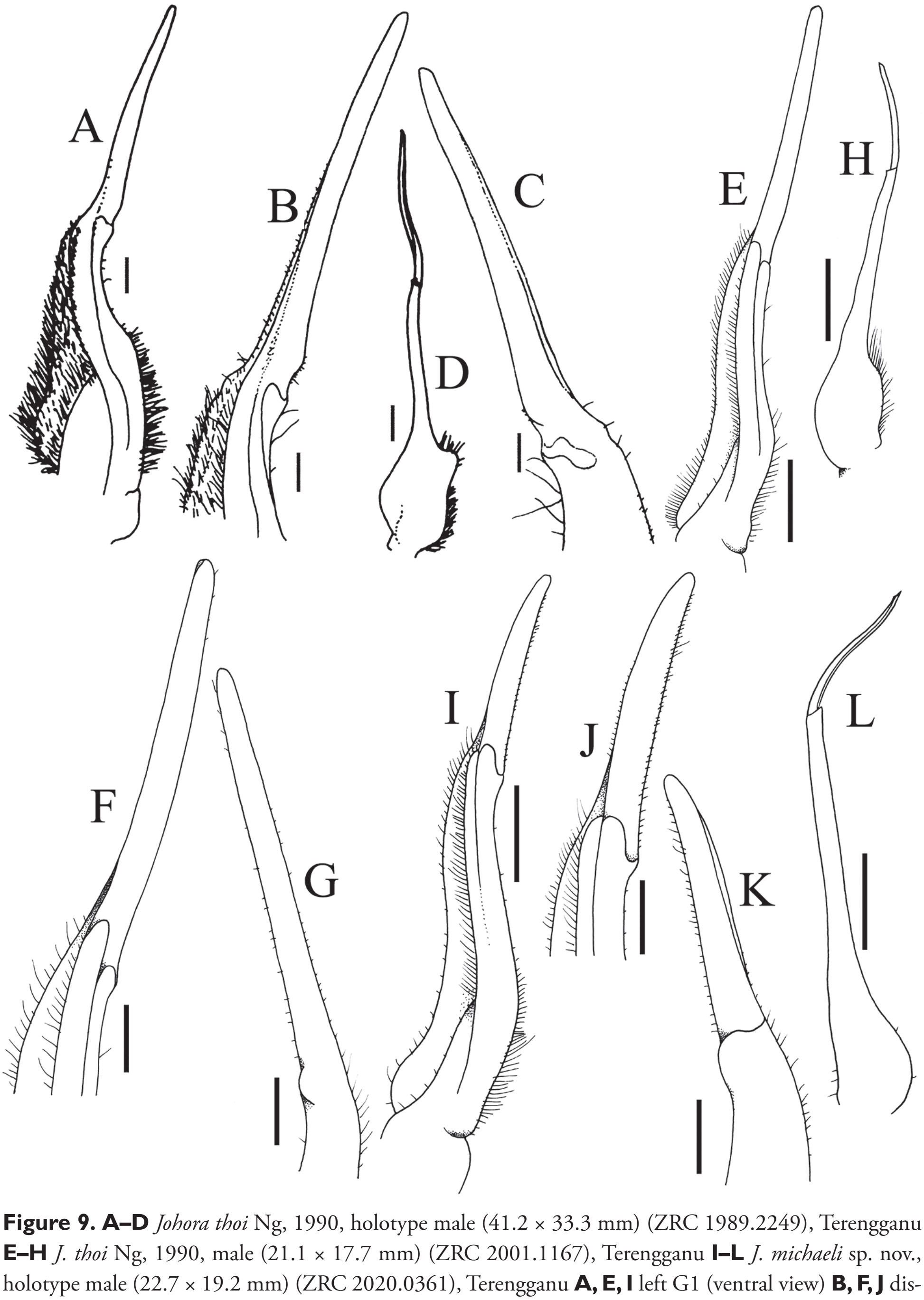

Figure 9. A–D *Johora thoi* Ng, 1990, holotype male (41.2 × 33.3 mm) (ZRC 1989.2249), Terengganu **E–H** *J. thoi* Ng, 1990, male (21.1 × 17.7 mm) (ZRC 2001.1167), Terengganu **I–L** *J. michaeli* sp. nov., holotype male (22.7 × 19.2 mm) (ZRC 2020.0361), Terengganu **A, E, I** left G1 (ventral view) **B, F, J** distal part of left G1 (ventral view) **C, G, K** distal part of left G1 (dorsal view) **D, H, L** left G2 (ventral view) **A–D** after Ng (1990: fig. 2A, C–E). Scale bars: 1.0 mm (**A, D, E, H, I, L**); 0.5 mm (**B, C, F, G, J, K)**.

Negara National Park, Kelantan, ca. 4°51'30"N, 102°03'23"E, coll. Tweedie MWF, August 1939; 2 males, 5 females (ZRC 1989.3617–3623), Pahang or Kelantan?, no other data. All locations in Peninsular Malaysia.

Diagnosis. Adult carapace width to length ratio 1.16–1.19 (Figs 1D, 2D, 12D); dorsal surface gently convex in frontal view, not inflated (Fig. 3D); frontal margin slightly sinuous to almost straight (Fig. 2D); suborbital, pterygostomial and subbranchial regions rugose, pterygostomial region covered with dense setae (Fig. 3D); epigastric cristae distinct, distinctly anterior to sharp postorbital cristae, postorbital cristae with lateral edges low, joining lateral margin through oblique striae (Fig. 2D); external orbital tooth separated from epibranchial tooth by distinct cleft, epibranchial tooth sharp, distinct (Fig. 2D); anterolateral margin gently convex (Fig. 2D); posterolateral margin medially concave to sinuous, gently converging towards gently convex, entire posterior carapace margin (Fig. 2D); posterior margin of epistome with triangular median triangle, lateral margin obliquely sloping (Fig. 3D); outer surfaces of third maxillipeds with dense, long stiff setae; ischium subrectangular, with shallow median oblique groove (Figs 3D, 4D); ambulatory legs not elongate, length to width ratio of merus of fourth ambulatory leg 2.7–2.8 (Figs 1D, 12D); G1 subterminal segment with broad proximal part, tapering suddenly to slender distal part, with distinct shelf-like structure along outer margin; terminal segment straight, ca. two-thirds length of subterminal segment, surfaces with numerous short setae (Fig. 8E–G); G2 slightly longer than G1, distal segment long, about half length of basal segment (Fig. 8H). Female pleon ovate; somite 3 less wide than somite 4, somites 4–6 progressively narrower; telson semicircular (Fig. 13D). Vulvae large, on anterior half of sternite 6, slightly pushing into suture with sternite 5, lateral sternal vulvar cover semicircular (Fig. 14D).

Remarks. Ng and Takeda (1992) showed that the G1 differences of the material that had been identified as "*J. tahanensis*" by Bott (1966, 1970; Ng 1987, 1988) belong to a distinct species, *J. hoiseni* (see remarks for *J. tahanensis*).

Distribution. *Johora hoiseni* is known from the drainages near Gua Musang in Kelantan, in the northwestern part of Taman Negara National Park (Fig. 15).

Conservation. The species is not under any immediate threat as it is found in Malaysia's oldest and largest national park. Ng and Yeo (2007) treated the species as endangered as it is only known from a relatively small geographic area but Cumberlidge et al. (2009) listed it as of least concern as it is in a protected area.

Johora thaiana Leelawathanagoon, Lheknim & Ng, 2005

Figures 1E, 2E, 3E, 4E, 5E, 10A–D, 12E, 13E, 14E

Johora thaiana Leelawathanagoon, Lheknim & Ng, 2005: 60, figs 1, 2; Cumberlidge et al. 2009: table.

Material examined. ***Paratypes*:** 1 male (22.2 × 18.6 mm) (ZRC 2006.0052), Huai Sam Sop, Ko Lok River Basin, Ban Ba La, 140 m above sea level, 5.71583°N, 101.83917°E, Wang District, Narathiwat Province, southern Thailand, coll. Lheknim V, 14 July 1999; 1 female (21.0 × 17.4 mm) (ZRC 2006.0053), Sirindthron Waterfall, Ban Ba La, 300 m above sea level, 5.8°N, 101.82083°E, Wang District, southern Thailand, coll. Lheknim V, 15 July 1999.

Diagnosis. Adult carapace width to length ratio 1.10–1.21 (Figs 1E, 2E, 12E); dorsal surface gently convex in frontal view, not inflated (Fig. 3E); frontal margin almost straight (Fig. 2E); suborbital, pterygostomial and sub-branchial regions rugose, pterygostomial region covered with dense setae (Fig. 3E); epigastric cristae distinct, distinctly anterior to sharp postorbital cristae, postorbital cristae with lateral edges low, not joining lateral margin (Fig. 2E); external orbital tooth separated from epibranchial tooth by distinct cleft, epibranchial tooth sharp, distinct (Fig. 2E); anterolateral margin distinctly convex (Fig. 2E); posterolateral margin medially concave, distinctly converging towards gently convex, entire posterior carapace margin (Fig. 2E); posterior margin of epistome with triangular median triangle, lateral margin obliquely sloping (Fig. 3E); outer surfaces of third maxillipeds with dense, long stiff setae; ischium subrectangular, with shallow median oblique groove (Figs 3E, 4E); ambulatory legs not elongate, length to width ratio of merus of fourth ambulatory leg 2.7–2.8 (Figs 1E, 12E); G1 subterminal segment gradually tapering from broad proximal part to slender distal part, without distinct shelf-like structure along gently concave outer margin; terminal segment almost straight, ca. half length of subterminal segment, surfaces with numerous short setae (Fig. 10A–C); G2 longer than G1, distal segment long, about two-thirds length of basal segment (Fig. 10D). Female pleon ovate; somites 3–6 progressively narrower; telson semicircular (Fig. 13E). Vulvae large, on anterior half of sternite 6, slightly pushing into suture with sternite 5, lateral sternal vulvar cover semicircular (Fig. 14E).

Remarks. The G1 structure of *J. thaiana* most closely resembles that of *J. hoiseni* in that the terminal segment is straight; but their subterminal segments differ. In *J. thaiana*, the subterminal segment gradually tapers from the broad proximal part to a slender distal section, without a shelf-like structure along the outer margin (Fig. 10A); in *J. hoiseni*, the distal part of the subterminal segment becomes slender more abruptly, resulting in distinct shelf-like structure on the outer margin (Fig. 8E). Biogeographically, the type localities of *J. thaiana* are less than 20 km from the *J. erici* sp. nov. in Jeli, Kelantan; but their carapace features and G1s differ markedly (Figs 2E, 10A–C versus Figs 2G, 7B, 11A–C, E–G).

Distribution. *Johora thaiana* is known from the forest tributaries in southern Thailand, near the Malaysian border at Kelantan (Fig. 15). Its distribution is adjacent to that of *J. erici* sp. nov. which lives in the highlands of northern Malaysia.

Conservation. The species has so far only been found in protected forests in southern Thailand and is not under any immediate threat; Cumberlidge et al. (2009) list it as of least concern.

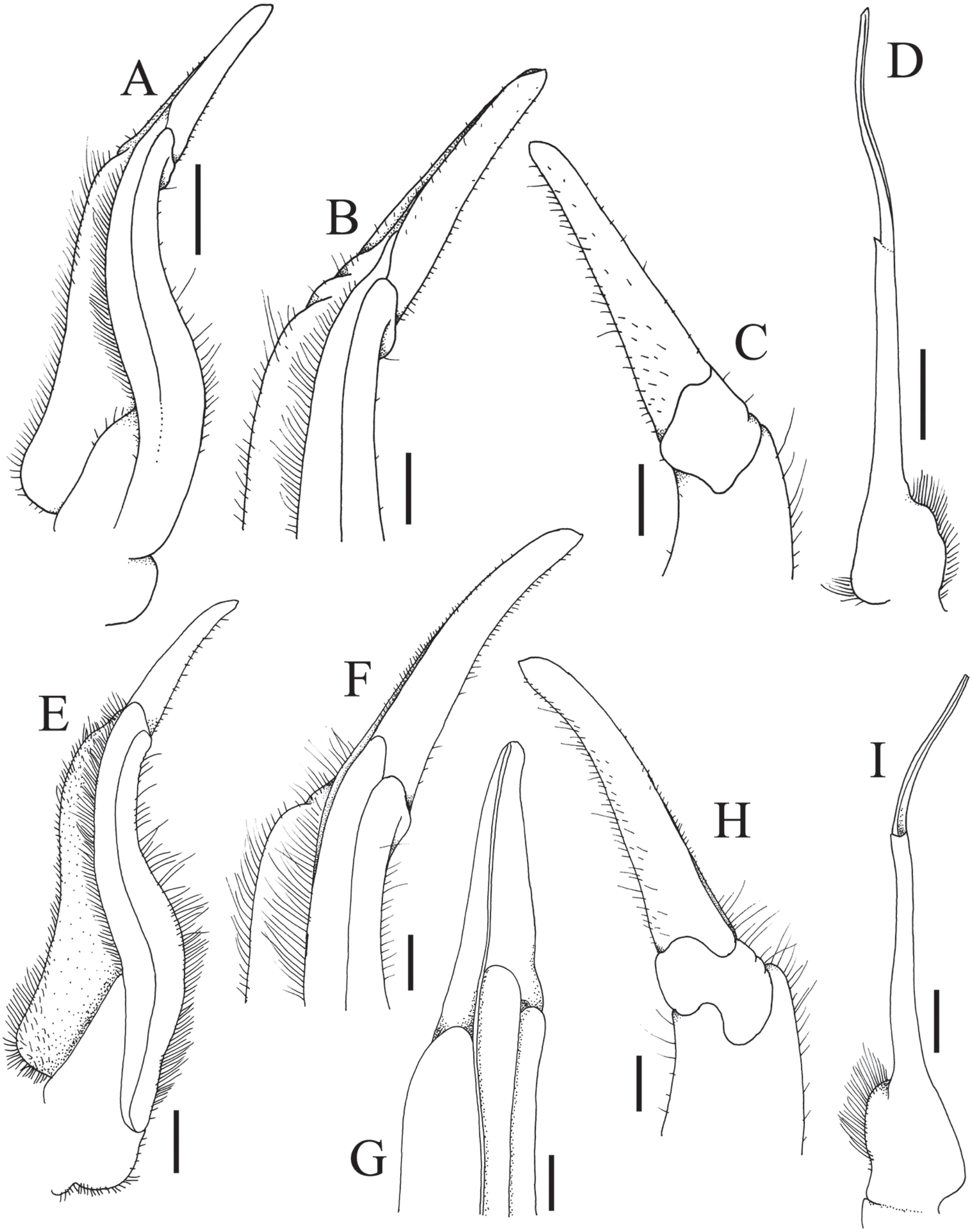

Figure 10. A–D *Johora thaiana* Leelawathanagoon, Lheknim & Ng, 2005, paratype male (22.2 × 18.6 mm) (ZRC 2006.0052), Thailand **E–I** *J. booliati* sp. nov., holotype male (34.6 × 30.0 mm) (ZRC 2020.0072), Pahang **A, E** left G1 (ventral view) **B, F** distal part of left G1 (ventral view) **C, H** distal part of left G1 (dorsal view) **G** distal part of left G1 (mesial view) **D, I** left G2 (ventral view). Scale bas: 1.0 mm (**A, D, E, I**); 0.5 mm (**B, C, F–H**).

Johora booliati **sp. nov.**

http://zoobank.org/8A3C9173-A7A5-4559-92D7-A548453C6688

Figures 1F, 2F, 3F, 4F, 5F, 10E–I, 12F, 13F, 14F

Johora tahanensis – Takeda & Ng, 1992: 107 (part); Ng 1995: 249 (part) (not *Stoliczia* (*Johora*) *johorensis tahanensis* Bott, 1966).

Material examined. ***Holotype*****:** male (34.6 × 30.0 mm) (ZRC 2020.0072), stream next to house, under rocks, in old farmland and secondary forest, Bukit Tinggi village, west side of northbound Karak Highway, ca. 480 m a.s.l., Bentong District, Pahang, 3°22'3.0396"N, 101°48'50.994"E, coll. July 2016. Paratype: 1 female (40.4 × 34.4 mm) (ZRC 1995.270), in shallow stream with leaf litter, The Gap, Fraser's Hill, 853 m a.s.l., Pahang, ca. 3°41'29"N, 101°44'56"E, coll. Lim KKP, 1 June 1990; 1 juvenile male (10.5 × 9.1 mm) (ZRC 2020.0364), under rocks, first stream on road towards Raub, descending from Fraser's Hill, Pahang, coll. Lai JCY, 6 December 2015. All locations in Peninsular Malaysia.

Diagnosis. Adult carapace width to length ratio 1.15–1.17 (Figs 1F, 2F, 12F); dorsal surface gently convex in frontal view, not inflated (Fig. 3F); frontal margin almost straight (Fig. 2F); suborbital, pterygostomial and sub-branchial regions rugose, pterygostomial region covered with dense setae (Fig. 3F); epigastric cristae distinct, distinctly anterior to sharp postorbital cristae, postorbital cristae with lateral edges low, joining lateral margin through oblique striae (Fig. 2F); external orbital tooth separated from epibranchial tooth by distinct cleft, epibranchial tooth sharp, distinct (Fig. 2F); anterolateral margin gently convex (Fig. 2F); posterolateral margin gently sinuous to almost straight, gently converging towards sinuous posterior carapace margin with shallow median indentation (Fig. 2F); posterior margin of epistome with triangular median triangle, lateral margin obliquely sloping (Fig. 3F); outer surfaces of third maxillipeds with dense, long stiff setae; ischium subrectangular, with shallow median oblique groove (Figs 3F, 4F); ambulatory legs not elongate, length to width ratio of merus of fourth ambulatory leg 2.7–2.8 (Figs 1F, 12F); G1 subterminal segment with broad proximal part, tapering relatively suddenly to slender distal part, with low shelf-like structure on outer margin; terminal segment gently curved outwards (from median part of sternum), less than half length of subterminal segment, surfaces with numerous short setae (Fig. 10E–H); G2 slightly longer than G1, distal segment long, about half length of basal segment (Fig. 10I). Female pleon ovate; somite 3 less wide than somite 4, somites 4–6 progressively narrower; telson semi-circular (Fig. 13F). Vulvae large, on anterior half of sternite 6, slightly pushing into suture with sternite 5, lateral sternal vulvar cover semi-circular (Fig. 14F).

Etymology. The species is named after an old friend and mentor, the late Dr Lim Boo Liat (1926–2020), one of Malaysia's most eminent biologists and naturalists. In a remarkable career spanning 70 years, he has contributed immensely to biodiversity and conservation science in Malaysia; more importantly, he has inspired, mentored, and trained many generations of biologists, many who now lead science in Malaysia and Singapore.

Remarks. The large adult size of *J. booliati* sp. nov. and *J. erici* sp. nov. (carapace width in excess of 25 mm) with the pronounced epibranchial teeth allies them with *J. tahanensis* s. str., *J. hoiseni*, *J. thaiana*, *J. thoi*, *J. tiomanensis*, and *J. counsilmani* (the last two being endemic to Pulau Tioman, Peninsular Malaysia).

Johora booliati and *J. erici* resemble *J. tahanensis*, *J. hoiseni*, and *J. thaiana* in the carapace shape and general features. Their G1 structures, however, are different. In *J. booliati* and *J. erici*, the G1 subterminal segment is proportionately more elongate and the terminal segment is relatively shorter (Figs 10E–H, 11A–C, E–G), and significantly, the terminal segment has only scattered short setae (versus subterminal segment shorter with the terminal segment longer and the surface of the latter more densely covered with short setae in *J. tahanensis* (Fig. 8A–C). Both *J. hoiseni* and *J. thaiana* have relatively straight G1 terminal segments which are prominently setose (Figs 8E–G, 10A–C).

Johora booliati and *J. erici* can be distinguished from *J. tiomanensis* and *J. counsilmani* by their carapace being relatively more quadrate in shape (width to length ratio less than 1.2) and the adult carapace is distinctly wider than long (width to length ratio 1.3–1.4) in *J. tiomanensis* and *J. counsilmani*. In addition, the epigastric cristae of *J. booliati* and *J. erici* are distinctly anterior to the postorbital cristae and separated by a gap with the entire postorbital cristae sharp (Figs 2F, G, 7B) while in *J. tiomanensis* and *J. counsilmani*, the epigastric cristae are only slightly anterior of the postorbital cristae and separated only by striae (cf. Ng and Tan 1984: figs 1A, 2A; Ng, 1985: fig. 3). Most significantly, the G1 terminal segments of *J. booliati* and *J. erici* are proportionately stouter and less curved (Figs 10E–H, 11A–C, E–G); in *J. tiomanensis* and *J. counsilmani*, it is distinctly slenderer, more elongate and strongly curved (cf. Ng and Tan 1984: fig. 3a–c; Ng 1985: figs 2a, c, e, 4a–c). *Johora booliati* and *J. erici* differ from *J. thoi* in possessing slightly shorter ambulatory legs (length to width ratio of merus of fourth leg 2.7–2.8 versus 3.0–3.2), the lateral carapace surfaces are relatively more rugose, and the distinctly shorter and gently curved G1 terminal segment (Figs 10E–H, 11A–C, E–G); in *J. thoi*, this structure is diagnostic, being very elongate and straight (Fig. 9A–C, E–G).

The G1 structure of *J. booliati* closely resembles that of *J. erici*, with the terminal segments similar in shape and proportions. The G1 subterminal segments of the two species, however, differ in form, with that of *J. booliati* forming a shelf-like structure along the outer margin (Fig. 10E) while in *J. erici*, the tapering of the segment is gradual, and no shelf is visible (Fig. 11A, E). The carapaces of the two species are different in adult males and females. In *J. booliati*, the carapace has a more quadrate form because the anterolateral margin is only gently convex, even in the largest male and the posterolateral margin is straighter and gently converging, with the posterior carapace margin medially indented (even in females) (Fig. 2F). In *J. erici*, the carapace appears more ovate, with the anterolateral margin distinctly convex, and the posterolateral margin is medially concave and strongly converging, and the posterior carapace margin is entire (Figs 2G, 7B).

The G1 structure of *J. booliati* and *J. erici* is superficially similar to that of *J. murphyi* from southern Peninsular Malaysia, notably in the shape of the G1 terminal and subterminal segments (Ng 1986b: fig. 14a, b; 1987: fig. 6D, E; 1988: fig. 16D, E), but differs in having the distal part of the terminal segment more rounded and less sharply tapering (Figs 10E–H, 11A–C, E–G). The G1 of *J. booliati* is also similar to *J. intermedia*, which has a wide distribution in central Peninsular Malaysia. The G1 terminal segment of *J. booliati* and *J. erici*, however, is relatively stouter and less curved, and the subterminal segment narrows along the distal third to form a neck-like structure with the terminal segment (Figs 10E–H, 11A–C, E–G) (versus the G1 terminal segment is more curved and tapers to a slender tip with only the distalmost part of the subterminal segment distinctly narrowed to form a broad cleft in *J. intermedia*, cf. Ng 1987: figs 3A–D, G–J, 4A–D, F, G, I, J; 1988: fig. 15D–F; Ng and Takeda 1992: fig. 1A–E). It is also noteworthy that both *J. murphyi* and *J. intermedia* are smaller species than *J. booliati* and *J. erici*, with adults not reaching carapace widths of 25 mm.

Ng and Takeda (1992: 107) had specimens from Fraser's Hill as well as adjacent areas (Sungei Gumut, Peretak, Selangor, 3°36'53.3"N, 101°44'40.4"E; Sungei Sum [probably Sungei Sum Sum], near Genting Highlands, Pahang, 3°20'42.2"N, 101°51'12.0"E; Ulu Teranum, Teras, Pahang, 3°44'12.6"N, 101°47'29.5"E) which they identified as "*J. tahanensis*". On the basis of geography, they are probably all *J. booliati* as defined here.

Distribution. *Johora booliati* sp. nov. is known from highland streams in the central highlands of Pahang (Genting Highlands, Bukit Tinggi and Fraser's Hill) (Fig. 15). The distribution of *J. booliati* overlaps with those of *J. intermedia* and *J. gapensis*, and we can expect the taxa to be found together. One juvenile male of *J. booliati* (10.5 × 9.1 mm, ZRC 2020.0364) was in fact collected with two adult males of *J. intermedia* at Fraser's Hill (ZRC 2016.003).

Conservation. The conservation status for *J. booliati* is not known as its actual distribution is not known. For the moment, it is known only from a 30 km stretch of hills along the Central Highlands of Peninsular Malaysia, in the area of Fraser's Hill, Genting Highlands and Bukit Tinggi. This area is not protected, and in this context, the species should be categorised as vulnerable for the time being (see Cumberlidge et al. 2009).

***Johora erici* sp. nov.**

http://zoobank.org/881E59DF-ACD2-4E4B-91A1-F9CE77725965
Figures 1G, 2G, 3G, 4G, 5G, 7, 11, 12G, 13G, 14G

Johora tahanensis – Ng 1995: 249 (part), fig. 1; Yeo et al. 2007: 257 (not *Stoliczia* (*Johora*) *johorensis tahanensis* Bott, 1966).

Material examined. ***Holotype*:** male (38.3 × 32.0 mm) (ZRC 2020.0360), Tasek Temengor, south of Banding, Sungai Halong, Perak, colI. Lim KKP and Tan HH, 1–4 November 1993. ***Paratypes*:** 1 male (23.9 × 20.0 mm), 3 females (largest 32.8 × 26.9 mm) (ZRC 1995.268), same data as holotype. Others: 1 male (41.2 × 33.8 mm) (ZRC 1995.0269), in logged forest, Hutan Simpanan, Gunung Basor, Sungai Long, off Sungai Pergau, Jeli, Kelantan, 457 m a.s.l., coll. Davison GWH, August 1986.

Diagnosis. Adult carapace width to length ratio 1.20–1.22 (Figs 1G, 2G, 7A, B, 12G); dorsal surface gently convex in frontal view, not inflated (Figs 3G, 7C); frontal

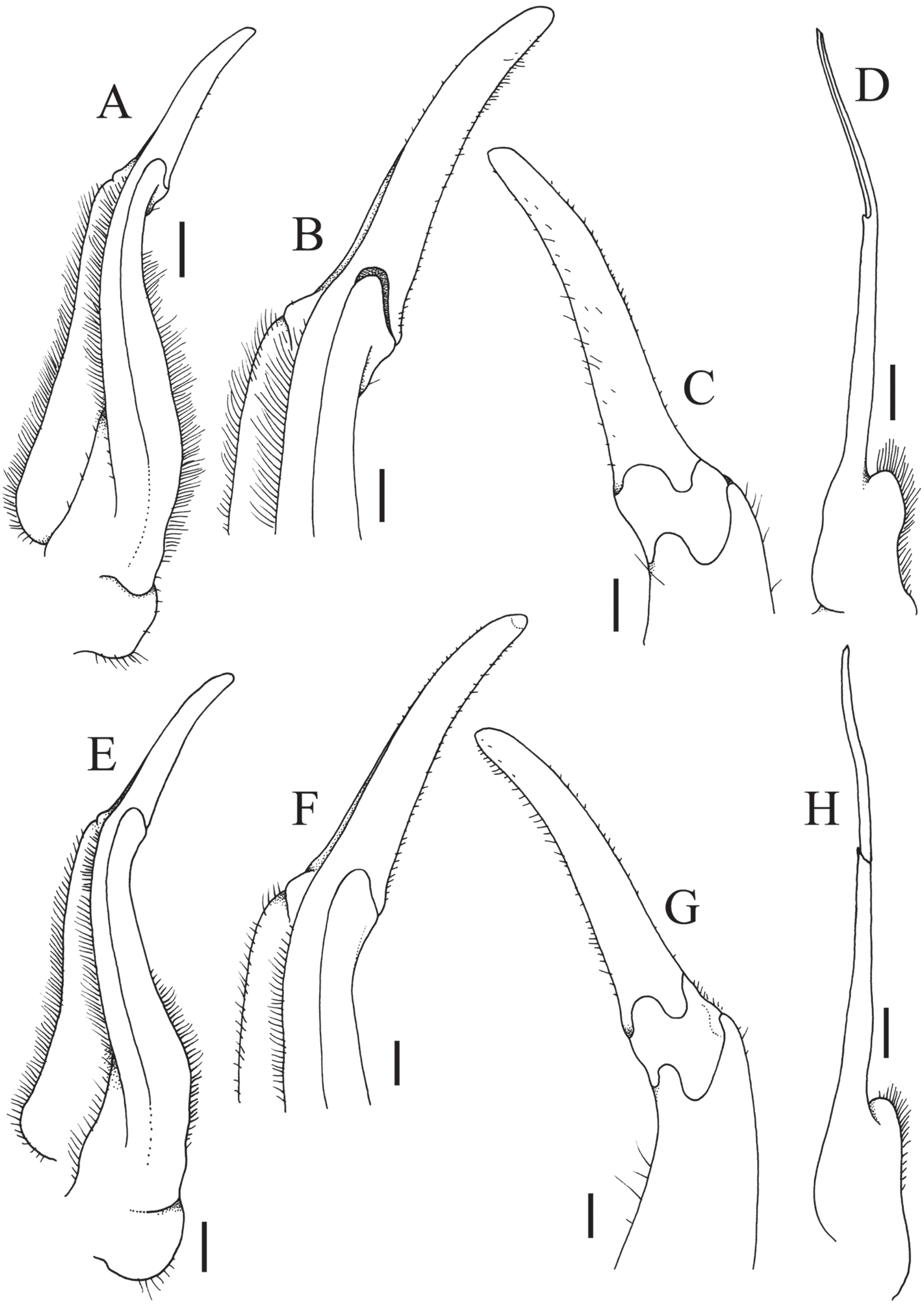

Figure 11. A–D *Johora erici* sp. nov., holotype male (38.3 × 32.0 mm) (ZRC 2020.0360), Perak **E–H** *J. erici* sp. nov., male (41.2 × 33.8 mm) (ZRC 1995.0269), Kelantan **A, E** left G1 (ventral view) **B, F** distal part of left G1 (ventral view) **C, G** distal part of left G1 (dorsal view) **D, H** left G2 (ventral view). Scale bars: 1.0 mm (**A, D, E, H**); 0.5 mm (**B, C, F, G**).

margin sinuous (Figs 2G, 7B); suborbital, pterygostomial and sub-branchial regions rugose, pterygostomial region covered with dense setae (Figs 3G, 7C); epigastric cristae distinct, distinctly anterior to sharp postorbital cristae, postorbital cristae with lateral edges low, joining lateral margin through oblique striae (Figs 2G, 7B); external orbital tooth separated from epibranchial tooth by distinct cleft, epibranchial tooth sharp, distinct (Figs 2G, 7B); anterolateral margin distinctly convex (Figs 2G, 7B); posterolateral margin sinuous or with shallow median concavity, distinctly converging towards gently convex, entire posterior carapace margin (Figs 2G, 7B); posterior margin of epistome with triangular median triangle, lateral margin obliquely sloping (Figs 3G, 7C); outer surfaces of third maxillipeds with dense, long stiff setae; ischium subrectangular, with shallow median oblique groove (Figs 3G, 4G, 7C); ambulatory legs not elongate, length to width ratio of merus of fourth ambulatory leg 2.7–2.8 (Figs 1G, 7A, 12G); G1 subterminal segment gradually tapering from broad proximal part to slender distal part, without distinct shelf-like structure along gently concave outer margin; terminal segment gently curved outwards (from median part of sternum), ca. half length of subterminal segment, surfaces with short setae (Fig. 11A–C, E–G); G2 slightly longer than G1, distal segment long, about half length of basal segment (Fig. 11D, H). Female pleon ovate; somites 3–6 progressively narrower; telson semi-circular (Fig. 13G). Vulvae large, on anterior half of sternite 6, adjacent to suture with sternite 5, lateral sternal vulvar cover semi-circular (Fig. 14G).

Etymology. The species is named after the first post-independence director of the National Museum of Singapore (the renamed Raffles Museum) (1967–1973), the late Eric Alfred. A very active freshwater ichthyologist, he collected many of the freshwater crabs in the museum. Eric was a good friend and provided wise counsel and help even years after he stepped down and took over the directorship of the Singapore Maritime Museum.

Remarks. Ng (1995: 250) commented that the G1 terminal segment of the males from Perak “seems to be somewhat longer and more slender” compared to typical *J. tahanensis* but incorrectly attributed it to variation. The differences are actually consistent, and it is here recognised as a separate species, *J. erici* sp. nov. See remarks for *J. booliati* sp. nov. for differences with allied taxa.

Distribution. *Johora erici* sp. nov. is known thus far only from highland streams in northern Perak and Kelantan (Fig. 15).

Conservation. The conservation status for *J. erici* is unclear as we have too few specimens, although it appears to have a relatively wide range in the mountains. It should be best categorised as data deficient for the time being (see Cumberlidge et al. 2009).

Johora michaeli sp. nov.

http://zoobank.org/4CA305BB-71CF-49E5-9559-24BB4019660C
Figures 1H, 2H, 3H, 4H, 5H, 9I–L, 12H, 13H, 14H

Material examined. ***Holotype***: male (22.7 × 19.2 mm) (ZRC 2020.0361), waterfalls at rock pools, ca. 5 minutes walk upstream from chalets, Sekayu Waterfall,

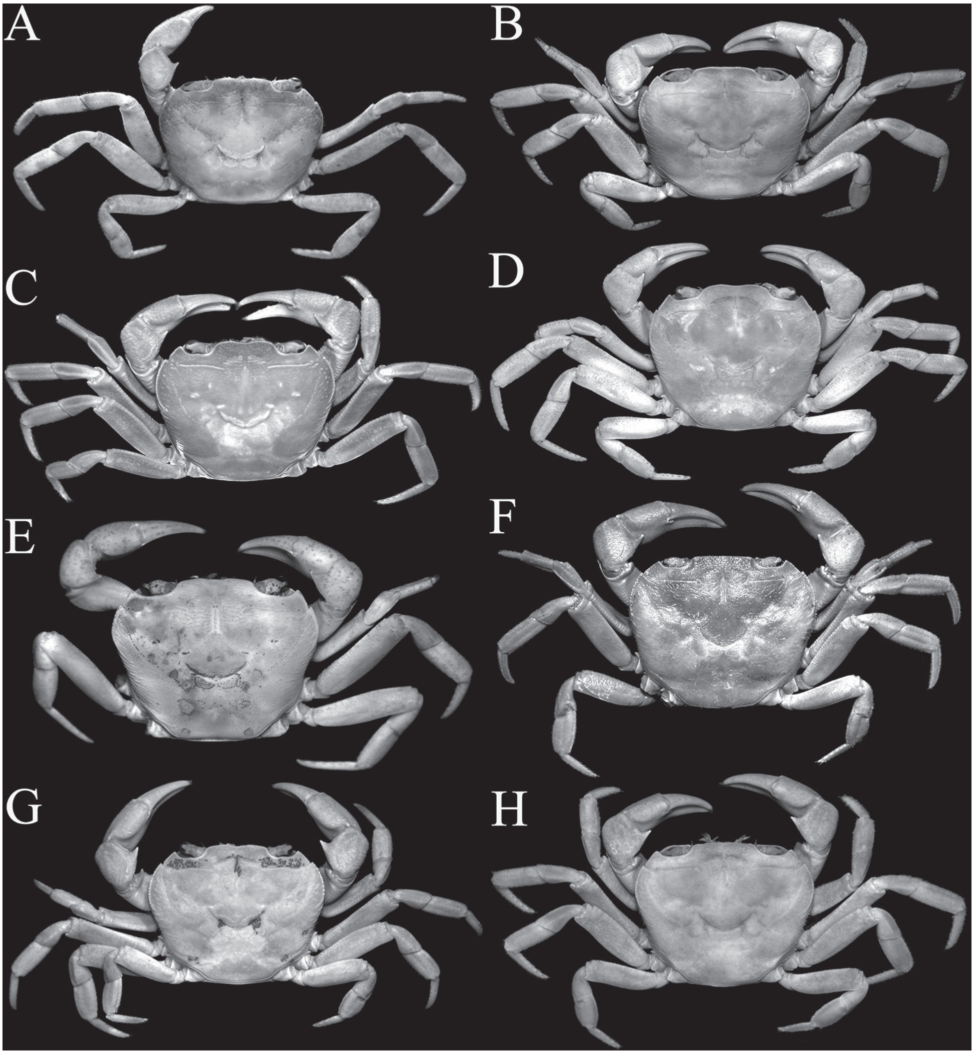

Figure 12. Overall dorsal view **A** *Johora intermedia* Ng, 1986, female (17.9 × 14.7 mm) (ZRC 2001.1002), Selangor **B** *J. tahanensis* (Bott, 1966), female (24.4 × 21.0 mm) (ZRC 1984.6765), Pahang **C** *J. thoi* Ng, 1990, female (31.7 × 25.5 mm) (ZRC 2001.1167), Terengganu **D** *J. hoiseni* Ng & Takeda, 1992, paratype female (22.1 × 19.0 mm) (ZRC 1984.6675), Kelantan **E** *J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005, paratype female (21.0 × 17.4 mm) (ZRC 2006.0053), Thailand **F** *J. booliati* sp. nov., paratype female (40.4 × 34.4 mm) (ZRC 1995.270), Pahang **G** *J. erici* sp. nov., paratype female (32.8 × 26.9 mm) (ZRC 1995.268), Perak **H** *J. michaeli* sp. nov., paratype female (29.9 × 25.0 mm) (ZRC 2010.0047), Terengganu.

4°59'35"N, 102°56'50"E, Terengganu, coll. Tan HH, 21 October 1998. Paratype: 1 female (29.9 × 25.0 mm) (ZRC 2010.0047), same data as holotype. Others: 1 female (30.8 × 25.2 mm) (ZRC 1984.6794), Gunung Padang, Terengganu, 4°50'55.7"N, 102°52'1.9"E, coll. Hislep JSA, 1952. All locations in Peninsular Malaysia.

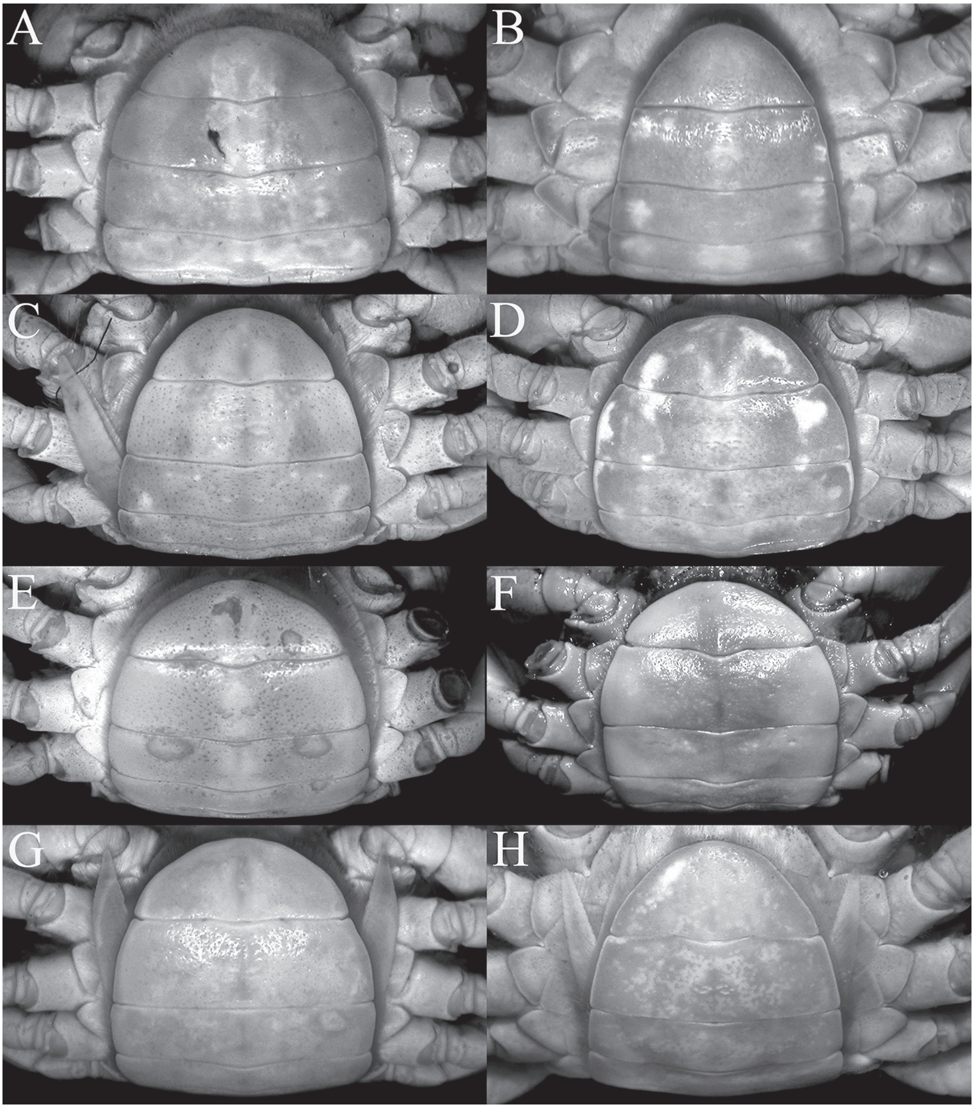

Figure 13. Female pleon **A** *Johora intermedia* Ng, 1986, female (17.9 × 14.7 mm) (ZRC 2001.1002), Selangor **B** *J. tahanensis* (Bott, 1966), female (24.4 × 21.0 mm) (ZRC 1984.6765), Pahang **C** *J. thoi* Ng, 1990, female (31.7 × 25.5 mm) (ZRC 2001.1167), Terengganu **D** *J. hoiseni* Ng & Takeda, 1992, paratype female (22.1 × 19.0 mm) (ZRC 1984.6675), Kelantan **E** *J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005, paratype female (21.0 × 17.4 mm) (ZRC 2006.0053), Thailand **F** *J. booliati* sp. nov., paratype female (40.4 × 34.4 mm) (ZRC 1995.270), Pahang **G** *J. erici* sp. nov., paratype female (32.8 × 26.9 mm) (ZRC 1995.268), Perak **H** *J. michaeli* sp. nov., paratype female (29.9 × 25.0 mm) (ZRC 2010.0047), Terengganu.

Diagnosis. Adult carapace width to length ratio 1.20–1.22 (Figs 1H, 2H, 12H); dorsal surface gently convex in frontal view, not inflated (Fig. 3H); frontal margin almost straight (Fig. 2H); suborbital, pterygostomial and sub-branchial regions rugose, pterygostomial region covered with dense setae (Fig. 3H); epigastric cristae distinct,

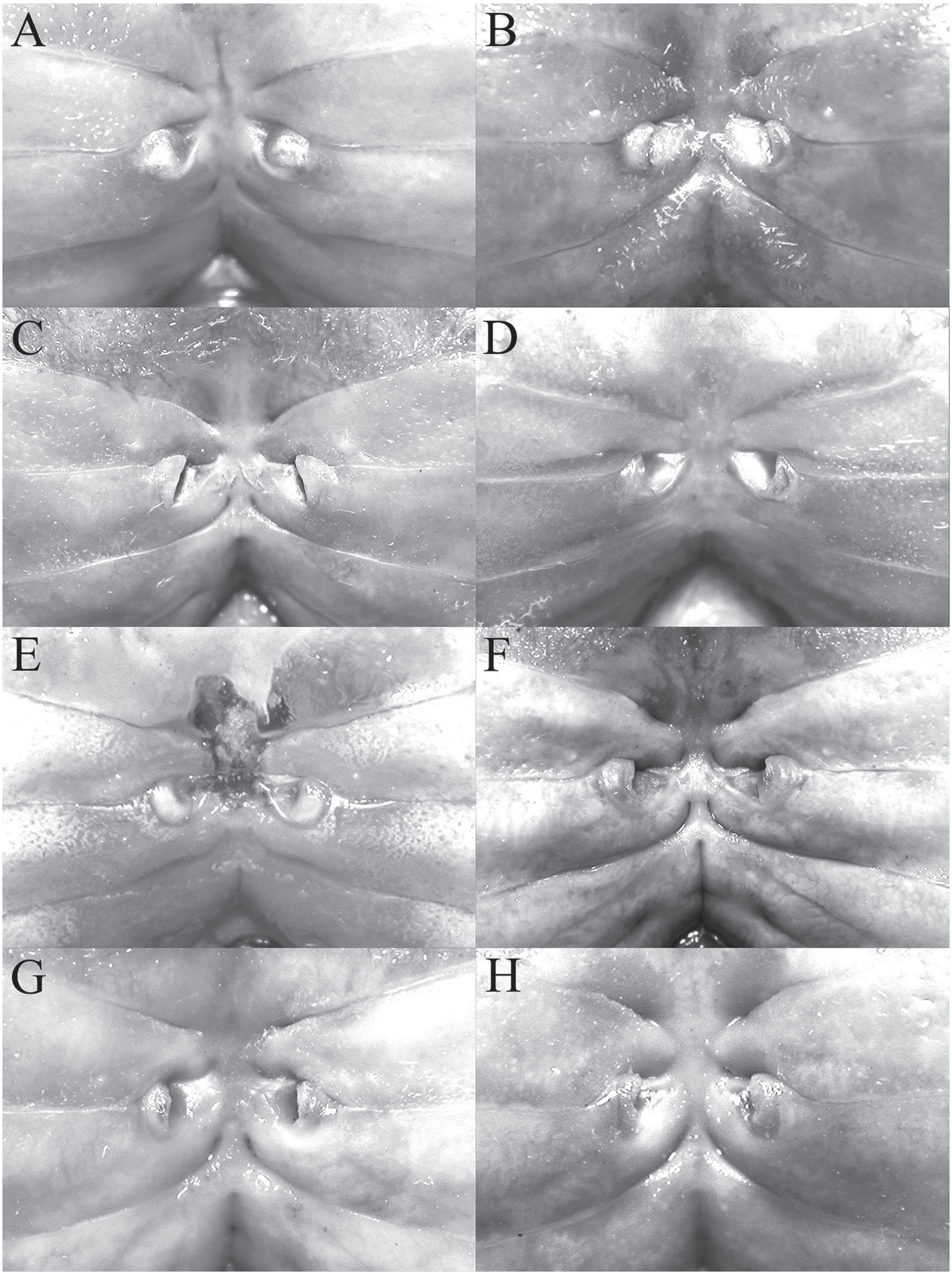

Figure 14. Sternopleonal cavity and vulvae **A** *Johora intermedia* Ng, 1986, female (17.9 × 14.7 mm) (ZRC 2001.1002), Selangor **B** *J. tahanensis* (Bott, 1966), female (24.4 × 21.0 mm) (ZRC 1984.6765), Pahang **C** *J. thoi* Ng, 1990, female (31.7 × 25.5 mm) (ZRC 2001.1167), Terengganu **D** *J. hoiseni* Ng & Takeda, 1992, paratype female (22.1 × 19.0 mm) (ZRC 1984.6675), Kelantan **E** *J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005, paratype female (21.0 × 17.4 mm) (ZRC 2006.0053), Thailand **F** *J. booliati* sp. nov., paratype female (40.4 × 34.4 mm) (ZRC 1995.270), Pahang **G** *J. erici* sp. nov., paratype female (32.8 × 26.9 mm) (ZRC 1995.268), Perak **H** *J. michaeli* sp. nov., paratype female (29.9 × 25.0 mm) (ZRC 2010.0047), Terengganu.

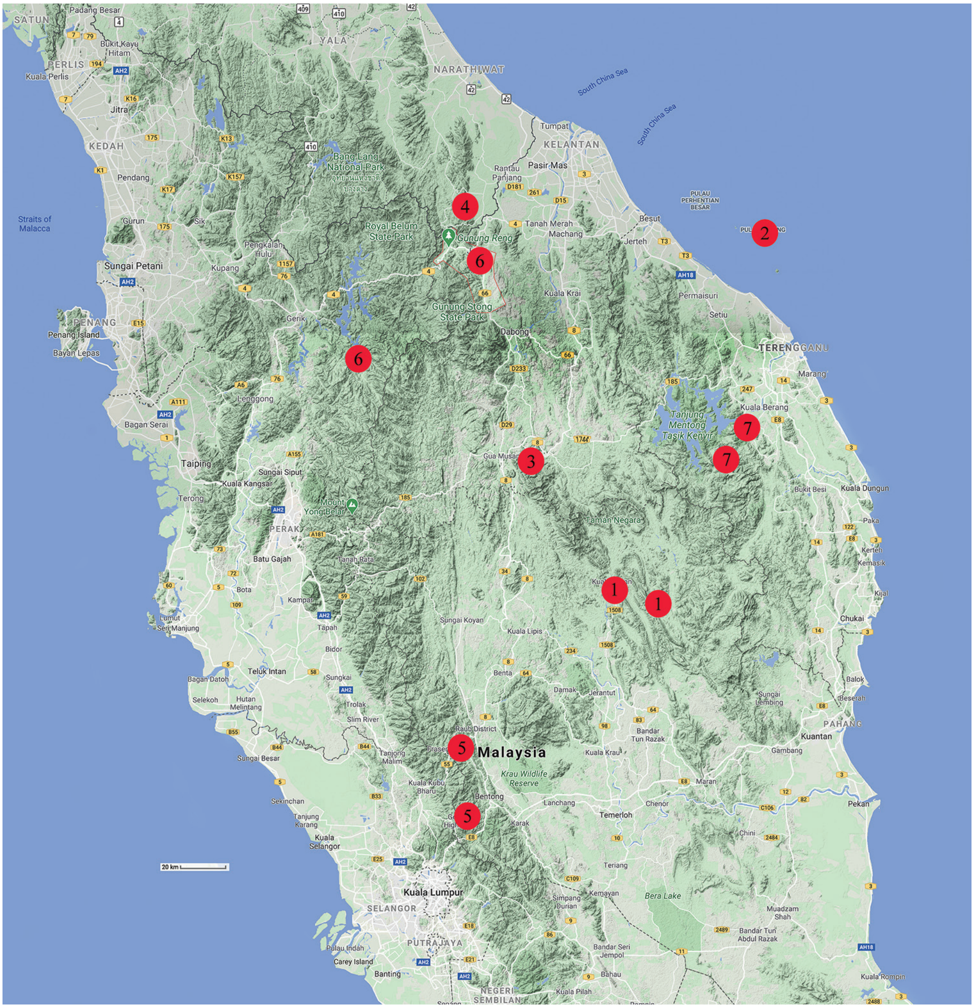

Figure 15. Distribution of species of the *Johora tahanensis* species group **1** *J. tahanensis* (Bott, 1966) **2** *J. thoi* Ng, 1990 **3** *J. hoiseni* Ng & Takeda, 1992 **4** *J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005 **5** *J. booliati* sp. nov. **6** *J. erici* sp. nov. **7** *J. michaeli* sp. nov. Map data 2020 Google.

distinctly anterior to sharp postorbital cristae, postorbital cristae with lateral edges low, not joining lateral margin (Fig. 2H); external orbital tooth separated from epibranchial tooth by distinct cleft, epibranchial tooth sharp, distinct (Fig. 2H); anterolateral margin distinctly convex (Fig. 2H); posterolateral margin with median concavity or sinuous, distinctly converging towards gently convex to almost straight, entire posterior carapace margin (Fig. 2H); posterior margin of epistome with triangular median triangle, lateral margin obliquely sloping (Fig. 3H); outer surfaces of third maxillipeds with long stiff setae; ischium subrectangular, with shallow median oblique groove (Figs 3H, 4H); ambulatory legs not elongate, length to width ratio of merus of fourth ambulatory leg 2.7–2.8 (Figs 1H, 12H); G1 subterminal segment gradually tapering from broad proximal part to slender distal part, without distinct shelf-like structure along gently concave outer margin; terminal segment almost straight, slightly curved outwards (from median part of sternum), ca. two-thirds length of subterminal segment, surfaces with scattered short setae (Fig. 9I–K); G2 subequal in length to G1, distal segment long, about one-third length of basal segment (Fig. 9L). Female pleon ovate; somites 3–6 progressively narrower; telson subtriangular (Fig. 13H). Vulvae large, on anterior half of sternite 6, adjacent to suture with sternite 5, lateral sternal vulvar cover subtruncate (Fig. 14H).

Etymology. The species is named after the last director of the Raffles Museum (1946–1967), the late Michael Tweedie, an intrepid collector of interesting animals from Malaysia. The author had the pleasure of knowing him, finally meeting him when the refreshed museum opened as the ZRC in 1988; and even after many years since retiring, he retained his great passion for his crabs, snakes, and fish.

Remarks. The holotype male of *Johora michaeli* sp. nov. is not fully adult and it is clear that it can grow larger, with the adult females reaching 30 mm in carapace width. The G1, however, remains diagnostic, with the terminal segment elongate and almost straight (Fig. 9I–K). While this somewhat resembles that of *J. thoi* which is known from the nearby island of Pulau Redang, that of *J. michaeli* is distinctly less elongate and slender, being only about two-thirds the length of subterminal segment. Specimens of *J. thoi* even smaller than the type of *J. michaeli* remain the same G1 terminal segment shape and proportions of adults (Fig. 9E–G) so the differences observed here are independent of size. The vulva of *J. thoi* is diagnostic, the lateral sternal vulvar cover being triangular in shape (Fig. 14C); it is subtruncate in *J. michaeli* (Fig. 14H). The general shape of the G1 terminal segment somewhat resembles that of *J. tahanensis* s. str. (Fig. 8A–C), it is clearly straighter and slenderer in *J. michaeli* (Fig. 9I–K). It is also unlike that of *J. hoiseni* which has a proportionately and even straighter G1 terminal segment (Fig. 8E–G).

The G1 of *J. michaeli* also resembles that of *J. singaporensis* but the terminal segment in this species is longer (Ng 1987: fig. 8A, B). In any case, the carapace of *J. singaporensis* is quite different from that of *J. michaeli* as it is a member of the *J. johorensis* species group (see remarks for the species group under remarks for the genus).

One large female (ZRC 1984.6794) had been collected from Gunung Padang, which is relatively close to the type locality in Sekayu Falls. Both are part of the same mountain system east of Lake Kenyir in Terengganu.

Distribution. *Johora michaeli* sp. nov. is known so far only from highland streams in central Terengganu (Fig. 15).

Conservation. The conservation status for *J. michaeli* should be regarded as vulnerable as it is known from a relatively well protected area that is not subject to development (see Cumberlidge et al. 2009).

Key to species of *Johora*

1 Carapace with anterolateral margins strongly convex, branchial regions appear gently swollen, external orbital tooth very acutely triangular; length of flagellum of third maxilliped exopod subequal to width of merus; G1 very stout, terminal segment cone-shape, tapering to relatively sharp tip (Pahang, Malaysia) .... ***Johora aipooae* (Ng, 1986a)**

– Carapace with anterolateral margins gently convex, branchial regions not swollen, external orbital tooth broadly triangular; flagellum on third maxilliped exopod longer than width of merus; G1 slender, variable shapes **2**

2 Frontal regions narrow, appear compressed, frontal margin slightly below level of external orbital tooth in dorsal view; postorbital cristae sharp, extending to epibranchial tooth as one structure; ambulatory legs especially, very long, length of merus more than 5 times maximum width (highlands, above 750 m a.s.l., Pulau Tioman, Malaysia) .... ***Johora grallator* Ng, 1988**

– Frontal region not distinctly narrow, frontal margin level with external orbital tooth; postorbital cristae sharp or low, never extending to epibranchial tooth, if joining always through series of interrupted striae; ambulatory legs not prominently elongate, length of merus less than 4.5 times maximum width **3**

3 Epigastric cristae just slightly anterior of and almost confluent with or indistinctly separated from postorbital cristae; postorbital cristae distinct not high, usually more prominent along median part of carapace, becoming uneven or breaking up into striae and granules laterally, not clearly reaching cervical groove **4**

– Epigastric cristae prominently anterior of and clearly separated from postorbital cristae; postorbital cristae high, sharp along entire length to cervical groove **12**

4 Dorsal carapace surface usually smooth, striae when present very low, at most with scattered very short setae; G1 terminal segment very slender, hook-shaped, subterminal segment neck-like with stout base; carapace and appendages purplish-red or uniformly orange in life (Pulau Tioman, Malaysia)......**5**

– Dorsal carapace surface with scattered granules and striae especially along lateral margins, usually with numerous short stiff setae; Gl terminal segment relatively stouter, various shapes, subterminal segment stout; carapace and appendages brown with patches of pale orange in life (Pulau Tioman and rest of Malay Peninsula) **6**

5 Ambulatory legs relatively shorter, stouter (dactylus of second leg 5.9–7.5 times longer than broad; second ambulatory leg merus 3.5–4.0 times longer than broad); purplish-red in life (lowland species, 100–300 m a.s.l., Pulau Tioman, Malaysia).. ***Johora punicea* (Ng, 1985)**

– Ambulatory legs relatively slenderer (dactylus of second leg 11.4–15.0 times longer than broad; second ambulatory leg merus 4.3–4.4 times longer than broad); purplish-red in life (montane species, ca. 900 m a.s.l., highlands, Pulau Tioman, Malaysia) .... ***Johora gua* Yeo, 2001**

6 Large species (adult carapace width 30–45 mm); adults with anterolateral margin strongly convex; frontal and anterolateral regions covered with numerous granules and striae (Pulau Tioman, Malaysia) **7**

– Small species (adult carapace width 22–23 mm); adults with anterolateral margin gently convex; frontal and anterolateral regions covered with scattered granules and striae (mainland Peninsular Malaysia).....................................**8**

7 Adult G1 terminal segment prominently hook-shaped, evenly tapering to tip, longer than half length of subterminal segment, surfaces almost smooth or with low flap, indistinct cleft between terminal and subterminal segments (western Pulau Tioman, Malaysia).... ***Johora tiomanensis*** **(Ng & Tan, 1984)**

– Adult G1 terminal segment slightly sinuous along distal half, shorter than half length of subterminal segment, with distinct flap on distal part of upper margin, distinct broad cleft between terminal and subterminal segments (eastern Pulau Tioman, Malaysia) .... ***Johora counsilmani*** **(Ng, 1985)**

8 G1 straight, slender, terminal segment rod-shaped, as long as subterminal segment, medium size species (Singapore)...... ***Johora singaporensis*** **Ng, 1986b**

– G1 bent in varying degrees between terminal and subterminal segment, terminal segment shorter than subterminal segment, tapered, downcurved and hook-shaped, small to large species (Malaysia) **9**

9 G1 terminal segment gently but distinctly upcurved (Gunong Pulai, Johor, Malaysia) ....***Johora johorensis*** **(Roux, 1936)**

– G1 terminal segment straight or hook-shaped..**10**

10 G1 terminal segment prominently curved, sickle-shaped, strongly bent, longer than half length of subterminal segment (Central Highlands, Malaysia) ....***Johora gapensis*** **(Bott, 1966)**

– G1 terminal segment gently curved, hook-shaped, obliquely bent, half or less than half length of subterminal segment **11**

11 G1 terminal segment curved, about half length of subterminal segment, with broad cleft between terminal and subterminal segments (Gunong Panti and adjacent highlands, Malaysia) ....***Johora murphyi*** **Ng, 1986b**

– G1 terminal segment slightly curved, tapered, less than half length of subterminal segment, wide ranging subspecies (Selangor, Negeri Sembilan, eastern Pahang, northern Johor, Malaysia)................***Johora intermedia*** **Ng, 1986b**

12 G1 terminal segment straight to almost straight, long, rod-like, at least two-thirds length of subterminal segment **13**

– G1 terminal segment straight to curved and hook-shaped, never as long as subterminal segment...**14**

13 Ambulatory legs relatively longer, length to width ratio of merus of fourth ambulatory leg 3.0–3.2; G1 terminal segment very long, slender, subequal to length of subterminal segment, even in young males (Pulau Redang, Malaysia) ....***Johora thoi*** **Ng, 1990**

– Ambulatory legs relatively shorter, length to width ratio of merus of fourth ambulatory leg 2.7–2.8; G1 terminal segment almost straight, about two-thirds length of subterminal segment, even in young males (Terengganu, Malaysia) .... ***Johora michaeli* sp. nov.**

14 G1 terminal segment gently curved outwards **15**

– G1 terminal segment straight or nearly so.. **17**

15 Adult posterior carapace margin with shallow median indentation; G1 subterminal segment with broad proximal part, tapering relatively suddenly to slender distal part, with low shelf-like structure on outer margin (Bukit Tinggi, Genting Highlands and Fraser's Hill, Malaysia) .... ***Johora booliati* sp. nov.**

– Adult posterior carapace margin gently convex, entire; G1 subterminal segment gradually tapering from broad proximal part to slender distal part, without distinct shelf-like structure along gently concave outer margin (Pahang, Kelantan and Perak, Malaysia).. **16**

16 Frontal margin almost straight; G1 subterminal segment relatively stouter, terminal segment proportionately shorter, stouter (Pahang) .... ***Johora tahanensis* (Bott, 1966)**

– Frontal margin sinuous; G1 subterminal segment relatively slenderer, terminal segment proportionately longer, slenderer (Kelantan and Perak, Malaysia) .... ***Johora erici* sp. nov.**

17 G1 terminal segment with margins subparallel or gently converging for most of length, tip straight to gently curving upwards (Kelantan, Malaysia) .... ***Johora hoiseni* Ng & Takeda, 1992**

– G1 terminal segment distinctly tapering, forming conical structure, distal part slightly curved (southern Thailand) .... ***J. thaiana* Leelawathanagoon, Lheknim & Ng, 2005**

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The bees of the family Halictidae (Hymenoptera) described by Ferdinand Morawitz from the collection of Aleksey Fedtschenko

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Abstract

The type specimens of the family Halictidae, described by Ferdinand Morawitz from the collection of Aleksey Fedtschenko deposited in the Zoological Museum of the Moscow State University and in the Zoological Institute, Russian Academy of Sciences, St. Petersburg (Russia), are critically reviewed. Precise information with illustrations of types for 43 taxa is provided. Lectotypes are here designated for the following seven nominal taxa: *Halictus aprilinus* Morawitz, 1876, *H. cingulatus* Morawitz, 1876, *H. laevinodis* Morawitz, 1876, *H. limbellus* Morawitz, 1876, *H. nasica* Morawitz, 1876, *H. rhynchites* Morawitz, 1876 and *H. vulgaris* Morawitz, 1876.

Keywords

Anthophila, Apiformes, lectotypes, Palaearctic Region, taxonomy

Introduction

More than 140 years ago (1876), the second part of Ferdinand Morawitz's critical study on the bees collected by the Aleksey Fedtschenko 1869–1871 Expeditions in "Turkestan" was published. In the prior volume, "Apidae genuinae" (1875), Morawitz treated

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a total of 255 species of numerous genera, of which many species were described as new. In this second part, "Andrenidae" (1876), the remaining bees were dealt with, including the species of the difficult genera *Andrena*, *Halictus* and *Hylaeus*, totalling 183 species (Pesenko and Astafurova 2003). The species treatments are of a high professional standard, the localities are precisely documented (A. Fedtschenko 1871, O. Fedtschenko 1874, Baker 2004, Kuhlmann 2005, Dathe and Proshchalykin 2017) and the type series have been carefully conserved over a long period, generally in the collections of the Zoological Museum of the Moscow State University, Moscow, Russia (ZMMU) and in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZISP). To this day, these remain some of the most important manuscripts on bees of this region.

The entomological literature uses various, often obscure, terms and names for Central Asian regions and countries. The term "Turkestan" has a particularly special use in entomology, widely adopted by Morawitz (1875, 1876), Dalla Torre (1896), Meade-Waldo (1923) and in other fundamental papers, regardless of its imprecise assignment to countries (Proshchalykin and Dathe 2018).

The territory of Central Asia, described as the "Western Regions" (Xi Yui) in Chinese sources, was referred to in the Russian and European historiography of the 18th and early 19th Centuries as Lesser Bukharia, as opposed to Greater Bukharia, where the Bukhara Khanate was situated. In Europe, these lands came to be referred to in the 18th and 19th Centuries as Turkestan, i.e. "the Land of Turks," which was the original Iranian name for the territory east of Fergana and Bukhara where nomadic Turkic tribes roamed. Subsequently, when the Turkic tribes occupied the enormous territory from the Caspian Sea to Lop Nor, the name Turkestan acquired a new meaning, so broad that it was deemed necessary to distinguish such areas as Western—Bukhara, or Russian Turkestan – and Eastern or Chinese Turkestan (Murzayev 1957). According to current views, Fedtschenko's "Turkestan" comprises the countries Uzbekistan, Tajikistan, Kyrgyzstan and southern parts of Kazakhstan.

The family Halictidae is represented in Morawitz's 1876 publication by four genera (*Nomioides* Schenck, 1866, *Halictus* Latreille, 1804, *Sphecodes* Latreille, 1804 and *Nomia* Latreille, 1804), comprising 73 species (Nos. 327–399). Only 30 species were previously known, while the remaining 43 were newly described (*Nomioides* – 2 species; *Halictus* – 36, *Sphecodes* – 2, *Nomia* – 2) (Table 1). Few of these taxa were mentioned in subsequent publications, remaining enigmatic for decades. Since the 1930s, V. Popov [ZISP] based his studies on the taxonomy and ecology of the Central Asian bee fauna using these collections. Popov involved other mellitologists in his research, so that specimens also reached specialists in other European museums. For example, P. Blüthgen took part in such work on *Halictus* and published several taxonomic papers, based on the Fedtschenko collection (Blüthgen 1931a, 1934a, 1955, Popov 1935).

The second attempt to recognise the true type material of Fedtschenko's Halictidae was made by K. Warncke, a teacher in Dachau (Germany), who visited ZMMU from 26.03.1975 to 01.04.1975 (Dathe and Proshchalykin 2017). He worked his way

Table 1. The nominal taxa of Fedtschenko's Halictidae, described by F. Morawitz, and their current status.

N	Species name	Sex	Current status	Depositaries of types
1.	*Halictus albitarsis*	♀	Homonym	LT (ZMMU); PLT (ZISP/ZMMU)
2.	*Halictus annulipes*	♀	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
3.	*Halictus aprilinus*	♀	Valid	LT, PLT (ZMMU)
4.	*Halictus atomarius*	♀	Valid	LT, PLT (ZISP)
5.	*Halictus cariniventris*	♂	Valid	LT, PLT (ZMMU)
6.	*Halictus cingulatus*	♀	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
7.	*Halictus croceipes*	♀, ♂	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
8.	*Halictus desertorum*	♀	Valid	LT (ZMMU)
9.	*Halictus determinatus*	♀	Homonym	LT (ZMMU); PLT (ZISP/ZMMU)
10.	*Halictus equestris*	♀	Valid	LT (ZMMU)
11.	*Halictus ferghanicus*	♂	Synonym	LT (ZMMU); PLT (ZISP)
12.	*Halictus fucosus*	♂	Synonym	HT (ZMMU)
13.	*Halictus fulvitarsis*	♂	Valid	HT (ZMMU)
14.	*Halictus funerarius*	♀	Valid	LT (ZISP); PLT (ZISP/ZMMU)
15.	*Halictus fuscicollis*	♀	Valid	LT (ZMMU); PLT (ZISP)
16.	*Halictus hyalinipennis*	♀, ♂	Valid	LT (ZISP); PLT (ZISP/ZMMU)
17.	*Halictus laevinodis*	♀	Valid	LT (ZISP); PLT (ZMMU)
18.	*Halictus limbellus*	♀	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
19.	*Halictus longirostris*	♀, ♂	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
20.	*Halictus maculipes*	♀	Valid	LT (ZMMU)
21.	*Halictus melanarius*	♂	Valid	HT (ZMMU)
22.	*Halictus minor*	♀	Valid	LT (ZISP); PLT (ZISP/ZMMU)
23.	*Halictus modernus*	♀	Valid	HT (ZMMU)
24.	*Halictus nasica*	♀, ♂	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
25.	*Halictus nigrilabris*	♂	Valid	LT (ZMMU); PLT (ZISP)
26.	*Halictus nigripes*	♂	Homonym	LT (ZMMU); PLT (ZISP/ZMMU)
27.	*Halictus obscuratus*	♀	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
28.	*Halictus palustris*	♀	Valid	LT (ZMMU); PLT (ZISP)
29.	*Halictus pectoralis*	♀	Homonym	HT (ZMMU)
30.	*Halictus picipes*	♀	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
31.	*Halictus rhynchites*	♀, ♂	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
32.	*Halictus scutellaris*	♀	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
33.	*Halictus sogdianus*	♀	Synonym	LT, PLT (ZMMU)
34.	*Halictus trifasciatus*	♀	Homonym	LT (ZMMU)
35.	*Halictus varipes*	♀, ♂	Synonym	LT, PLT (ZMMU)
36.	*Halictus vulgaris*	♀	Synonym	LT (ZMMU); PLT (ZISP/ZMMU)
37.	*Sphecodes nigripennis*	♀	Synonym	LT, PLT (ZMMU)
38.	*Sphecodes pectoralis*	♀	Valid	LT, PLT (ZMMU)
39.	*Sphecodes rufithorax*	♀, ♂	Synonym	LT (ZMMU); PLT (ZISP/ZMMU)
40.	*Nomia edentata*	♀, ♂	Valid	LT (ZMMU); PLT (ZISP/ZMMU)
41.	*Nomia rufescens*	♀	Valid	LT (ZMMU)
42.	*Nomioides parviceps*	♂	Valid	NT (ZISP)
43.	*Nomioides turanica*	♀, ♂	Valid	LT, PLT (ZISP/ZMMU)

Comment. LT – lectotype, PLT – paralectotype/s, NT – neotype.

through the drawers containing the Fedtschenko material and labelled specimens of all nominal taxa found there as "Lectotypen." Thereby, certain specimens from some groups of bees (*Hylaeus*, *Andrena*, *Anthidium* etc.) received a red label with the inscription "Lectotypus Warncke 1975." However, of all Fedtschenko's Halictidae described by Morawitz, only five specimens received such labels: *Sphecodes nigripennis* Morawitz, 1876, *S. pectoralis* Morawitz, 1876, *S. rufithorax* Morawitz, 1876, *Nomia edentata* Morawitz, 1876 and *N. rufescens* Morawitz, 1876 (Figs 32A, 33B, 34E, 35F, 36A). All other type specimens were left without nomenclatural status labels.

In his publication on the genus *Halictus*, which appeared seven years later (Warncke 1982), only the sex and locality for each lectotype is cited, for example: "*Halictus limbellus* Mor. / ♀ Lectotypus / Samarkand." The selected specimen is not further individually identified and data on syntypes and paralectotypes are completely missing from the text. Thus, of the twenty seven designated lectotypes, fifteen are either invalid or unnecessary (when the type series includes only the holotype) and require corrections by subsequent authors (Pesenko 1986a, Ebmer 1997, current publication).

In the 1980's, Yu. Pesenko continued the study of Halictidae in the Fedtschenko's collection of the ZISP and ZMMU, designating lectotypes for seven of Morawitz's nominal taxa in the genera *Halictus*, *Nomia* and *Nomioides* (Pesenko 1983, 1984, 1986a).

As a part of a detailed types inventory of the ZISP collection, all primary types of Halictidae, including seven species described by F. Morawitz from the collection of A. Fedtschenko, are being progressively photographed and catalogued (Astafurova and Proshchalykin 2018, 2019, 2020). The present paper is the first complete, illustrated summary of all species of the family Halictidae, described by F. Morawitz from the collection of A. Fedtschenko, an invaluable reference for researchers across this region who otherwise could not easily assign names to these difficult bees.

Materials and methods

All of the material listed below was examined for this study. In the following list, the taxa are treated in alphabetical order of the names used in the original descriptions. Each entry includes the name of the taxon in its original combination, the complete reference to the original description of the species (including the original combination and spelling of the name and the author, year and page of the description) and a list of type specimens present in the collections of the ZMMU and ZISP. The data from each label are separated by two slashes (//). Square brackets are used for English translations and when information is added to specimen label information (e.g. geographical coordinates) or published data (e.g. current name of an old place name; affiliation to a present-day country). Photographs were made using a combination of a stereomicroscope Olympus SZX10 and a digital camera (Olympus OM-D and Canon EOS70D).

Illustrations were obtained by montaging from an image series that covers different focal planes into a single in-focus image with the Helicon Focus 6. The final illustrations were post-processed for contrast and brightness using Adobe® Photoshop® software.

The classification and current species status for *Halictus* and *Lasioglossum* follow Michener (2007) and Ascher and Pickering (2020), for *Sphecodes* follow Astafurova et al. (2018a, b, 2019), for Nomiinae follow Astafurova (2014) and for Nomioidinae follow Pesenko (1983).

Taxonomy

List of species

Subfamily Halictinae
Genus *Halictus* Latreille, 1804

1. *Halictus albitarsis* Morawitz, 1876
Figure 1

Halictus albitarsis Morawitz, 1876: 217 (key to females), 246, ♀.

Type locality. Samarkand (Uzbekistan).

Published (original) locality. Uzbekistan: Samarkand, Tashkent.

Lectotype. ♀, designated by Warncke 1982: 117, <golden circle> // 21.[III.1869] // Самаркандъ [Uzbekistan, Samarkand, 39°39'N, 66°57'E] // *Halictus albitarsis* Mor., [N]372 [handwritten by F. Morawitz] // *Lasioglossum Evylaeus albitarsis* Mor., ♀ = lectotype, det A.W. Ebmer 1993 // Syntypus Lectotypus <red label> [ZMMU].

Paralectotypes (12 ♀)**.** 6 ♀, 11.[III.1871], 24., 25.[V.1871] // Ташкентъ [Tashkent] // [N]372; 1 ♀, 23.[III.1871] // Ташкентъ [Tashkent] // [N]372 // *Halictus albitarsis* Mor., F. Morawitz det. [handwritten by F. Morawitz] [ZMMU]; 1 ♀, <golden circle>, 11.[III.1871] // Ташкентъ [Tashkent] // *albitarsis* Mor., Typ. [handwritten by F. Morawitz]; 3 ♀, 11.[III.1871] // Ташкентъ [Tashkent] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] //*Halictus albitarsis* Mor. [handwritten by F. Morawitz]; 1 ♀, 11.[III.1871] // Ташкентъ [Tashkent] // Paralectotypus *Halictus albitarsis* Mor., design. Warncke, [19]82 <identical red label on each paralectotype specimens, labelled by Yu. Astafurova> [ZISP].

Current status. *Lasioglossum* (*Sphecodogastra*) *leucopymatum* (Dalla Torre, 1896), replacement name for *Halictus albitarsis* Morawitz, 1876 (nec *Hylaeus albitarsis* Schenck, 1853, nec *Halictus albitarsis* Cresson, 1872).

Remarks. The secondary designation of the lectotype by Ebmer 1995: 585 is unnecessary.

Description of male. Ebmer 1995: 585.

Distribution. Kazakhstan, Turkmenistan, Uzbekistan, Afghanistan (Ebmer 1995).

2. *Halictus annulipes* Morawitz, 1876
Figure 2

Halictus annulipes Morawitz, 1876: 217 (key), 221, ♀.

Type locality. Karatyube Mt., 15 km S Samarkand (Uzbekistan).

Published (original) locality. Uzbekistan: Samarkand, Karatyube Mt. (= 15 km S Samarkand).

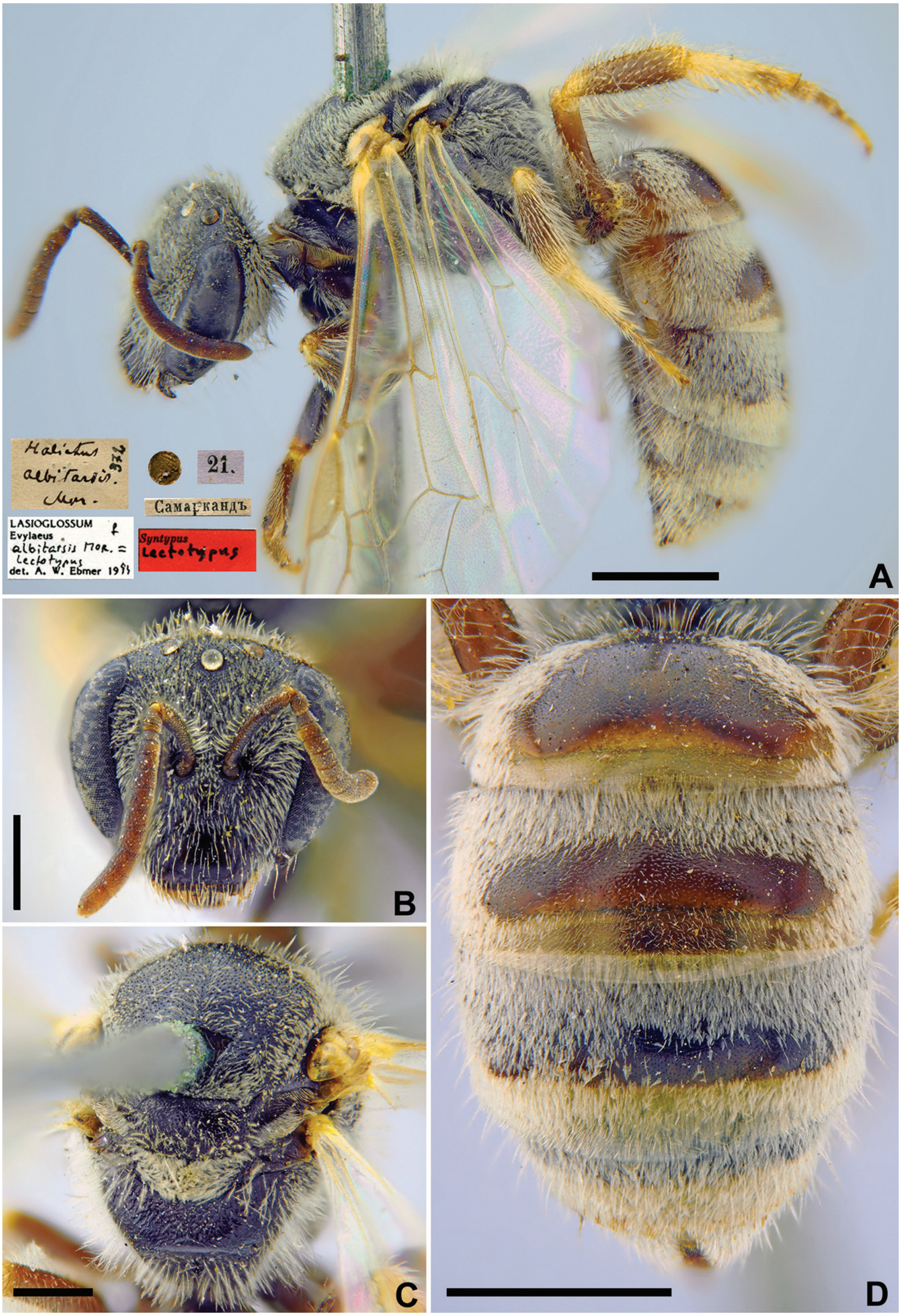

Figure 1. *Halictus albitarsis* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm (**A, D**), 0.5 mm (**B, C**).

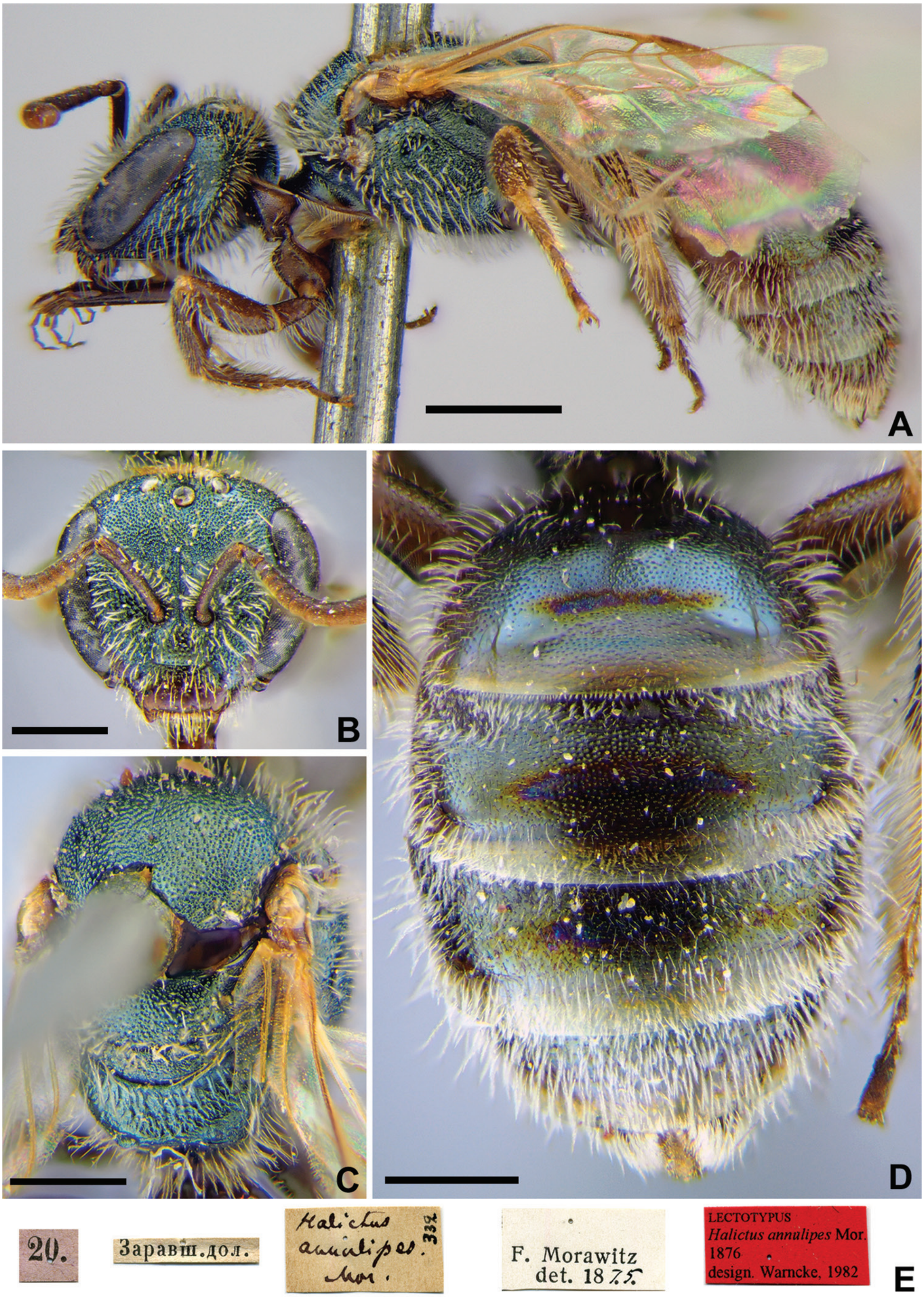

Figure 2. *Halictus annulipes* Morawitz, 1876, lectotype, female **A** habitus, lateral view **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view **E** labels. Scale bars: 1.0 mm (**A**), 0.5 mm (**B–E**).

Lectotype. designated by Warncke 1982: 81, ♀, 20[.V.1869] // Зеравшан.[ская] дол.[ина] [Uzbekistan, Zeravshan River valley, Karatyube Mt., 39°30'N, 66°52'E] // *Halictus annulipes* Mor., [N]332 [handwritten by F. Morawitz] // F. Morawitz det. 18.7.5. // Lectotypus *Halictus annulipes* Mor. 1876, design. Warncke, 1982 <red label, labelled by Yu. Astafurova> [ZMMU].

Paralectotypes (2 ♀)**.** 1 ♀, 17. [V.1869] // Самаркандъ [Uzbekistan, Samarkand] // [N]332 // *H. annulipes* F. Morawitz det. 1875 [ZMMU]; 1 ♀, 20[.V.1869] // Зеравшан.[ская] дол.[ина] [Zeravshan River valley] // *annulipes* Mor. Typ. [handwritten by F. Morawitz] // Paralectotypus *Halictus annulipes* Mor., 1876, design. Warncke, 1982 <identical red label on each paralectotype specimen, labelled by Yu. Astafurova> [ZISP].

Current status. *Lasioglossum* (*Dialictus*) *annulipes* (Morawitz, 1876).

Remarks. Description of male. Kohl 1905: 238, as *Halictus metopias* Vachal (synonymised by Warncke 1975: 89).

Distribution. Bulgaria, Armenia, Turkey, Russia (North Caucasus), Afghanistan, Iran, Tajikistan, Uzbekistan, Kazakhstan, Pakistan (Astafurova and Proshchalykin 2017, Ascher and Pickering 2020).

3. *Halictus aprilinus* Morawitz, 1876

Figure 3

Halictus aprilinus Morawitz, 1876: 216 (key), 228, ♀.

Type locality. Kattakurgan (Uzbekistan).

Published (original) locality. Uzbekistan: Katty-Kurgan.

Lectotype (designated here). ♀, <golden circle>, 28. [IV.1869] [Uzbekistan, Kattakurgan, 39°53'N, 66°15'E] // ♀ // *H. aprilinus* n. sp., ♀, F. Morawitz det., typus [handwritten by F. Morawitz] // Lectotypus *Halictus aprilinus* Mor., design. Astafurova et Proshchalykin, 2020 <red label> [ZMMU].

Paralectotypes. 3 ♀, 28. [IV.1869] // Каттыкурганъ [Kattakurgan] // [N]343 // Paralectotypus *Halictus aprilinus* Mor., design. Astafurova et Proshchalykin, 2020 <red label> [ZMMU].

Current status. *Lasioglossum* (*Sphecodogastra*) *aprilinum* (Morawitz, 1876).

Remarks. Warncke (1982: 76) did not designate the lectotype, but only wrote "Typus Mus. Moskau".

Description of male. Blüthgen 1925a: 119, as *Halictus inexspectatus* (synonymised by Blüthgen 1931a: 212).

Distribution. Southern Kazakhstan, Turkmenistan, Uzbekistan, Mongolia, China (Xinjiang) (Pesenko 2007, Murao et al. 2017).

4. ***Halictus atomarius*** **Morawitz, 1876**

Figure (see Astafurova and Proshchalykin 2018: 11, figs 7a–e).

Halictus atomarius Morawitz, 1876: 218 (key), 254, ♀.

Type locality. Tashkent (Uzbekistan).

Published (original) locality. Uzbekistan: Tashkent.

Lectotype. ♀, designated by Ebmer 1985: 290, 8.[VIII.1870] // Ташкентъ [Uzbekistan, Tashkent, 41°18'N, 69°16'E] // *Halictus atomarius* Mor. [handwritten by F. Morawitz] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] / / Syntypus <red label> // *Lasioglossum Evylaeus atomarium* (Mor.), ♀, Lectotypus, det. A.W. Ebmer 1985 // Lectotypus <red label> [ZISP].

Paralectotype. 1 ♀, 8.[VIII.1870] // Ташкентъ [Tashkent] // *Halictus atomarius* Mor. [handwritten by F. Morawitz] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] [ZISP].

Current status. *Lasioglossum* (*Evylaeus* s.l.) *politum atomarium* (Morawitz, 1876) (subspecies status according to Ebmer 1988b: 667).

Remarks. Description of male. Bytinski-Salz and Ebmer 1974: 211, as *Lasioglossum politum* ssp. *aramaeum* Ebmer 1974 (synonymised by Ebmer 1985: 290).

Distribution. Egypt, Palestine, Syria, Jordan, Israel, Turkey, Iran, Central Asia (Bytinski-Salz and Ebmer 1974, Warncke 1982, Pesenko 2007).

5. ***Halictus cariniventris*** **Morawitz, 1876**

Figure 4

Halictus cariniventris Morawitz, 1876: 220 (key), 226, ♂.

Type locality. Osh (Kyrgyzstan).

Published (original) locality. Uzbekistan: Samarkand, Dzhyuzak [=Jizzakh], Sokh; Kyrgyzstan: Osh.

Lectotype. ♂, designated by Blüthgen 1955: 19, 1.[VIII.1871] // Ошъ [Kyrgyzstan, Osh, 40°32'N, 72°47'E] // *Halictus cariniventris* Mor., [N]341 [handwritten by F. Morawitz] // Lectotypus *Halictus cariniventris* Mor., design. Blüthgen <red label, labelled by Yu. Astafurova> [ZMMU].

Paralectotypes (4 ♂)**.** 2 ♂, 4., 7.[VII.1869] // Самарканд [Samarkand] // [N]341; 2 ♂, 18., 22.[VII.1870] // Джюзакъ [Dzhyuzak] // [N]341 // Paralectotypus *Halictus cariniventris*, design. Blüthgen <identical red labels on each paralectotype specimen, labelled by Yu. Astafurova> [ZMMU].

Current status. *Halictus* (*Mucoreochalictus*) *pollinosa cariniventris* Morawitz, 1876 (subspecies status according to Ebmer 1988b: 578).

Remarks. The lectotype designation by Warncke (1982: 138) is unnecessary.

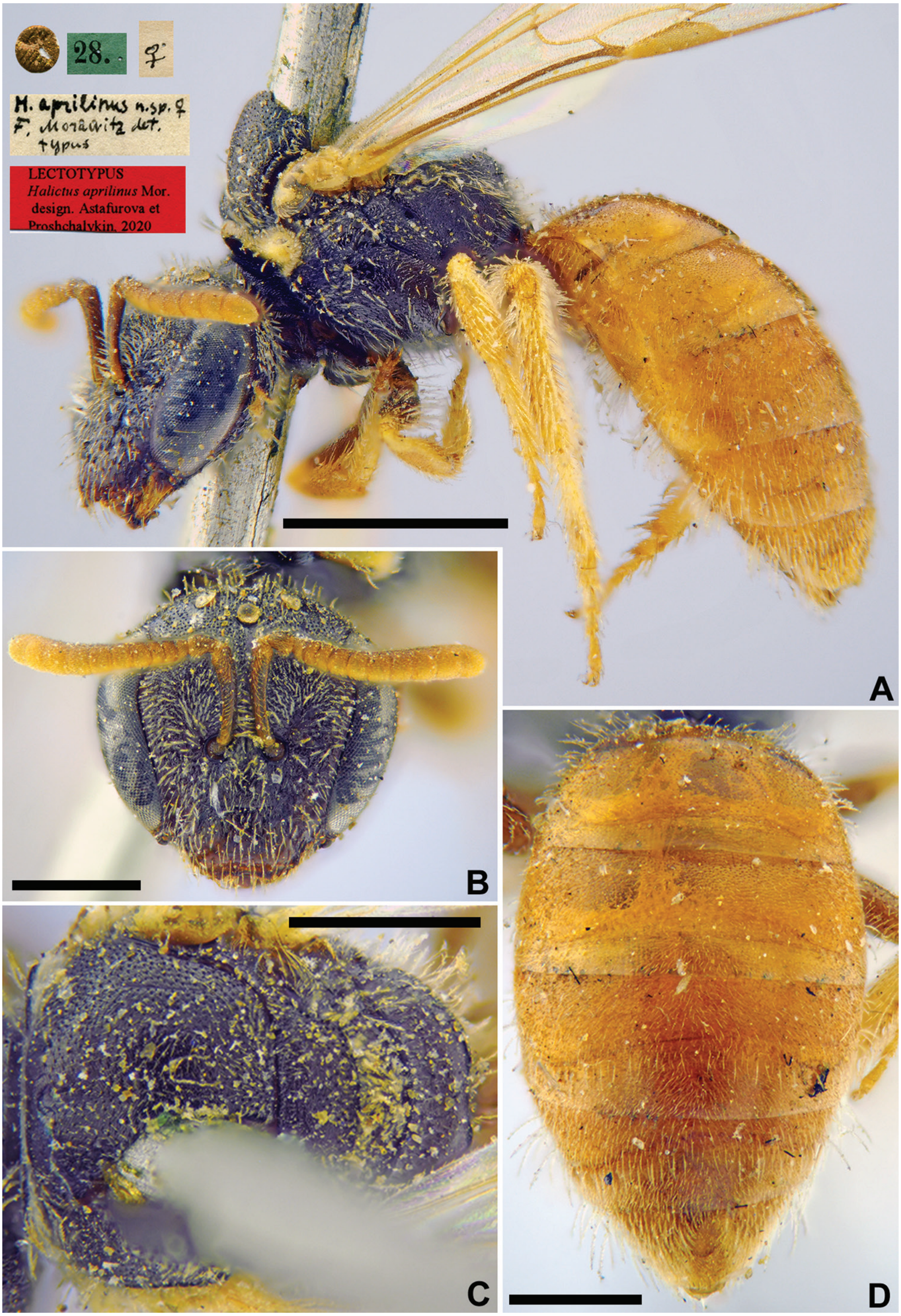

Figure 3. *Halictus aprilinus* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm (**A**), 0.5 mm (**B–D**).

Figure 4. *Halictus cariniventris* Morawitz, 1876, lectotype, male **A** habitus, lateral view **B** metasoma, dorsal view **C** head, frontal view **D** mesosoma, dorsal view **E** labels. Scale bars: 1.0 mm.

Description of female: Strand 1921: 314, as *Halictus cariniventris* var. *creticola* (synonymised by Ebmer 1988b: 578).

Distribution. Europe (except north), Russia (European part, except north), Turkey, Israel, Iran, Afghanistan, Pakistan, Central Asia, Mongolia, North China (Pesenko 2006a, Astafurova and Proshchalykin 2017).

6. *Halictus cingulatus* Morawitz, 1876

Figure 5

Halictus cingulatus Morawitz, 1876: 218 (key), 245, ♀.

Type locality. Samarkand (Uzbekistan).

Published (original) locality. Uzbekistan: Samarkand, Dzham [near Samarkand], Aksay [near Samarkand].

Lectotype (designated here). ♀, 18.[III.1869] // Самаркандъ [Uzbekistan, Samarkand, 39°39'N, 66°57'E] // *Halictus cingulatus* Mor., [N]371 [handwritten by F. Morawitz] // Lectotypus *Halictus cingulatus* Mor., design. Astafurova et Proshchalykin, 2020 <red label> [ZMMU].

Paralectotypes (22 ♀)**.** 11 ♀, 27., 28. [II. 1869], 18., 21. [V. 1869] // Самаркандъ [Samarkand] // [N]371; 1 ♀, 12.[V.1969] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, Dzham] // [N]370; 1 ♀, 16.[V.1969] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, Aksay] // [N]370 [ZMMU]; 1 ♀, the same labels, but 21.[V.1869] [ZMMU]; 1 ♀, <golden circle> // 18.[V.1869] // Самаркандъ [Samarkand] // *cingulatus* Mor. Typ. [handwritten by F. Morawitz]; 1 ♀, 18.[III.1869] // Самаркандъ [Samarkand] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz]; 1 ♀, 20.[III.1869] // Самаркандъ [Samarkand] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *Halictus cingulatus* Mor., ♀, CoType, F. Morawitz det. [handwritten by F. Morawitz]; 1 ♀, 27.[III.1869] // Самаркандъ [Samarkand] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz]; 1 ♀, 16.[III.1869] // Самаркандъ [Samarkand] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *Halictus cingulatus* Mor., ♀, F. Morawitz det. [handwritten by F. Morawitz]; 1 ♀, 30.[III.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, Samarkand] // *Halictus cingulatus* Mor. [handwritten by F. Morawitz]; 2 ♀, 12.[III.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, Samarkand] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // Paralectotypus *Halictus cingulatus* Mor., design. Astafurova et Proshchalykin, 2020 <identical red labels on each paralectotype specimen> [ZISP].

Current status. *Lasioglossum* (*Sphecodogastra*) *cingulatum* (Morawitz, 1876).

Remarks. Male unknown.

The lectotype designation by Warncke (1982: 116) is invalid because he labelled none of the eleven females from Samarkand deposited in ZMMU.

Distribution. South Kazakhstan, Central Asia, Pakistan (Ebmer 1995, Murao et al. 2017).

7. *Halictus croceipes* Morawitz, 1876

Figure 6

Halictus croceipes Morawitz, 1876: 217 (key to ♀), 220 (key to ♂), 224, ♀, ♂.

Type locality. Yeri, Sughd Province (Tajikistan).

Published (original) locality. Kyrgyzstan: Taka; Uzbekistan: Karatyube [Mt., 15 km S Samarkand], Dzham Gorge, Urgut; Tajikistan: Iori.

Lectotype. ♀, designated by Ebmer 1997: 956, <golden circle> // 1.[VI.1869] // Заравш.[анская] дол.[ина] [Tajikistan, Zeravshan River valley, Iori (= Yeri), 39°30'N, 67°52'E] // *croceipes* Mor. Typ [handwritten by F. Morawitz] // *croceipes* Mor. Blüthgen det. 1935 // Lectotype <red label> // *Lasioglossum* (*Evylaeus*) *croceipes* (Mor.), ♀, Lectotypus, det. A.W. Ebmer 1974 [ZMMU].

Paralectotypes (6 ♀). 1 ♀, 20.[V.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, Karatyube] // *croceipes* Mor., [N]338 [handwritten by F. Morawitz] // *croceipes* Mor. Blüthgen det. 1935; 3 ♀, 8.[VIII.1871] // Така [Taka] // [N]338; 1 ♀, 13.[V.1869] // Джамское ущ. [Dzham Gorge] // [N]338 [ZMMU]; 1 ♀, 1.[VI.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, Iori] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *croceipes* Mor., Blüthgen det. 1935 // Paralectotypus *Halictus croceipes* Mor., design. Ebmer 1997 <identical red labels on each paralectotype specimen, labelled by Yu. Astafurova> [ZISP].

Current status. *Lasioglossum* (*Hemihalictus*) *croceipes* (Morawitz, 1876).

Remarks. The lectotype designation by Warncke (1982: 106) is invalid because there are two females in ZMMU from the Zeravshan River valley, neither with Warncke's lectotype label.

Distribution. Turkey, Iran, Afghanistan, Central Asia, Kazakhstan (Ebmer 1997, Murao et al. 2017).

8. *Halictus desertorum* Morawitz, 1876

Figure 7

Halictus desertorum Morawitz, 1876: 217 (key), 228, ♀.

Type locality. Kattakurgan (Uzbekistan).

Published (original) locality. Uzbekistan: Katty-Kurgan.

Lectotype. ♀, designated by Warncke 1982: 107, 28.[IV.1869] // Катты-Курганъ [Uzbekistan, Katty-Kurgan (=Kattakurgan), 39°53'N, 66°15'E] // *Halictus desertorum* Mor., [N]344 [handwritten by F. Morawitz] // Lectotypus *Halictus desertorum* Mor., design. Warncke <red label, labelled by Yu. Astafurova> [ZMMU].

Current status. *Halictus* (*Placidochalictus*) *desertorum* Morawitz, 1876.

Remarks. Description of male. Blüthgen 1929: 84, figs 9a, b.

Distribution. Turkey, southern Kazakhstan, Turkmenistan, Uzbekistan, Pakistan (Blüthgen 1929, Ebmer 1988a).

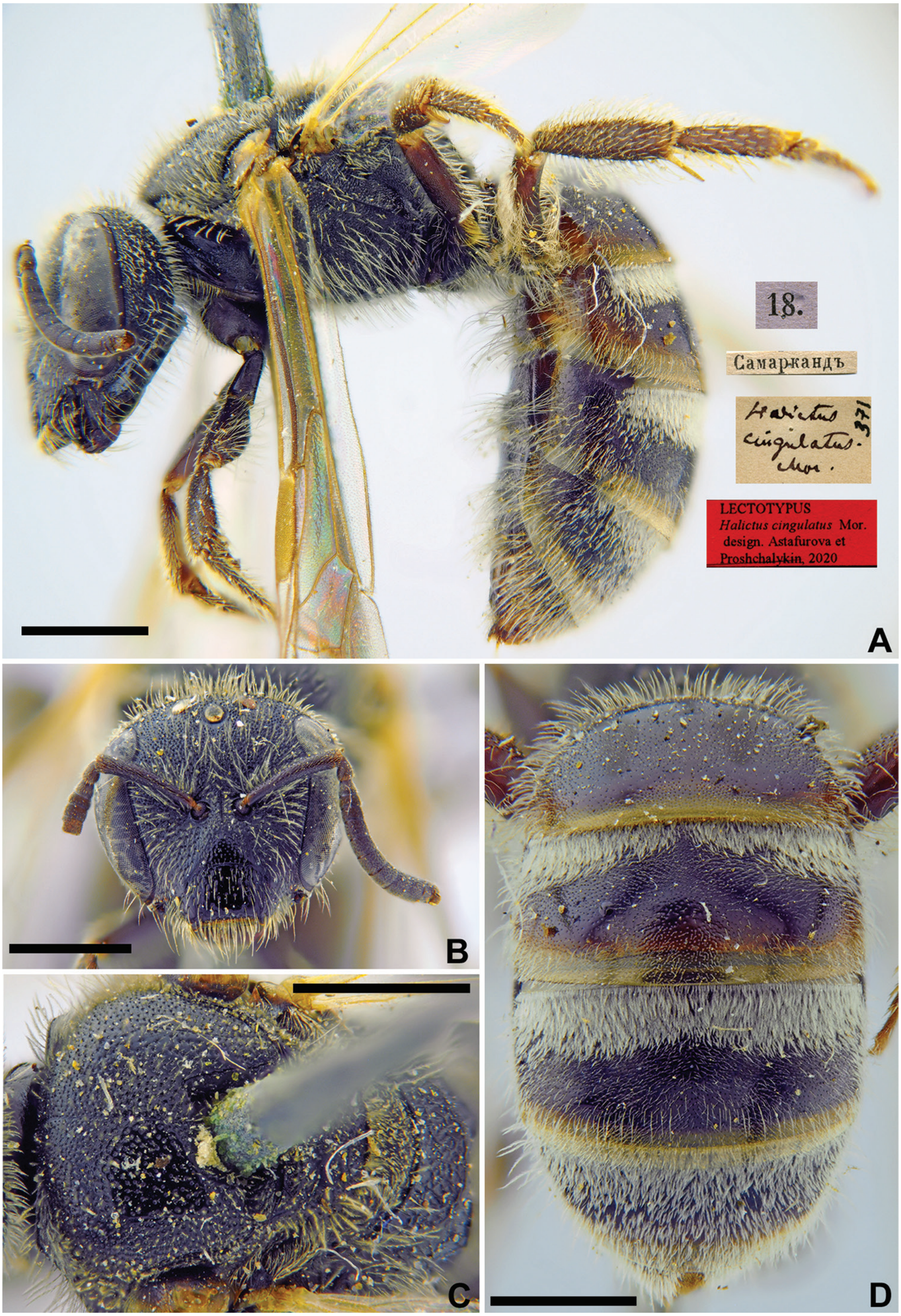

Figure 5. *Halictus cingulatus* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm.

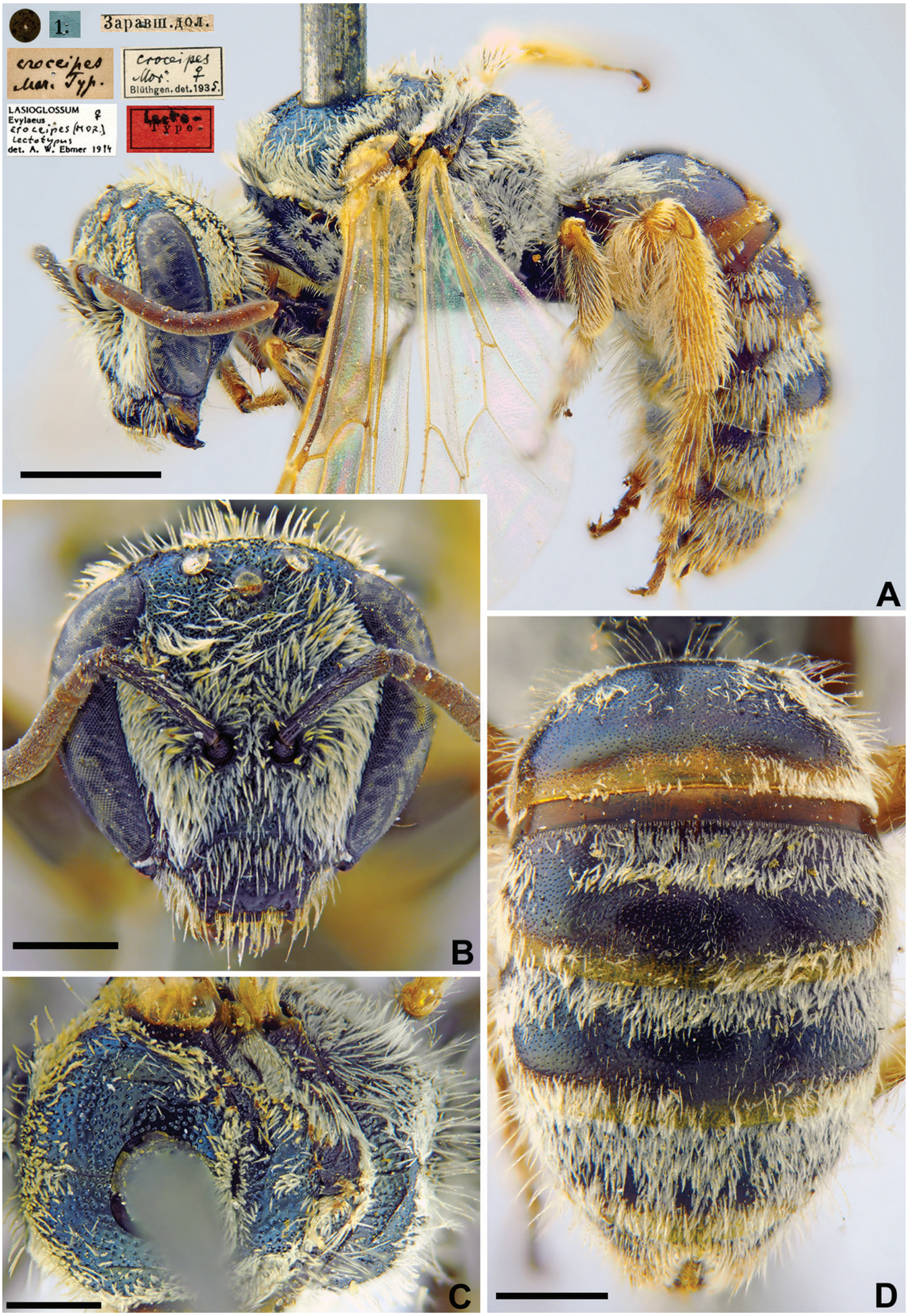

Figure 6. *Halictus croceipes* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm (**A, D**), 0.5 mm (**B, C**).

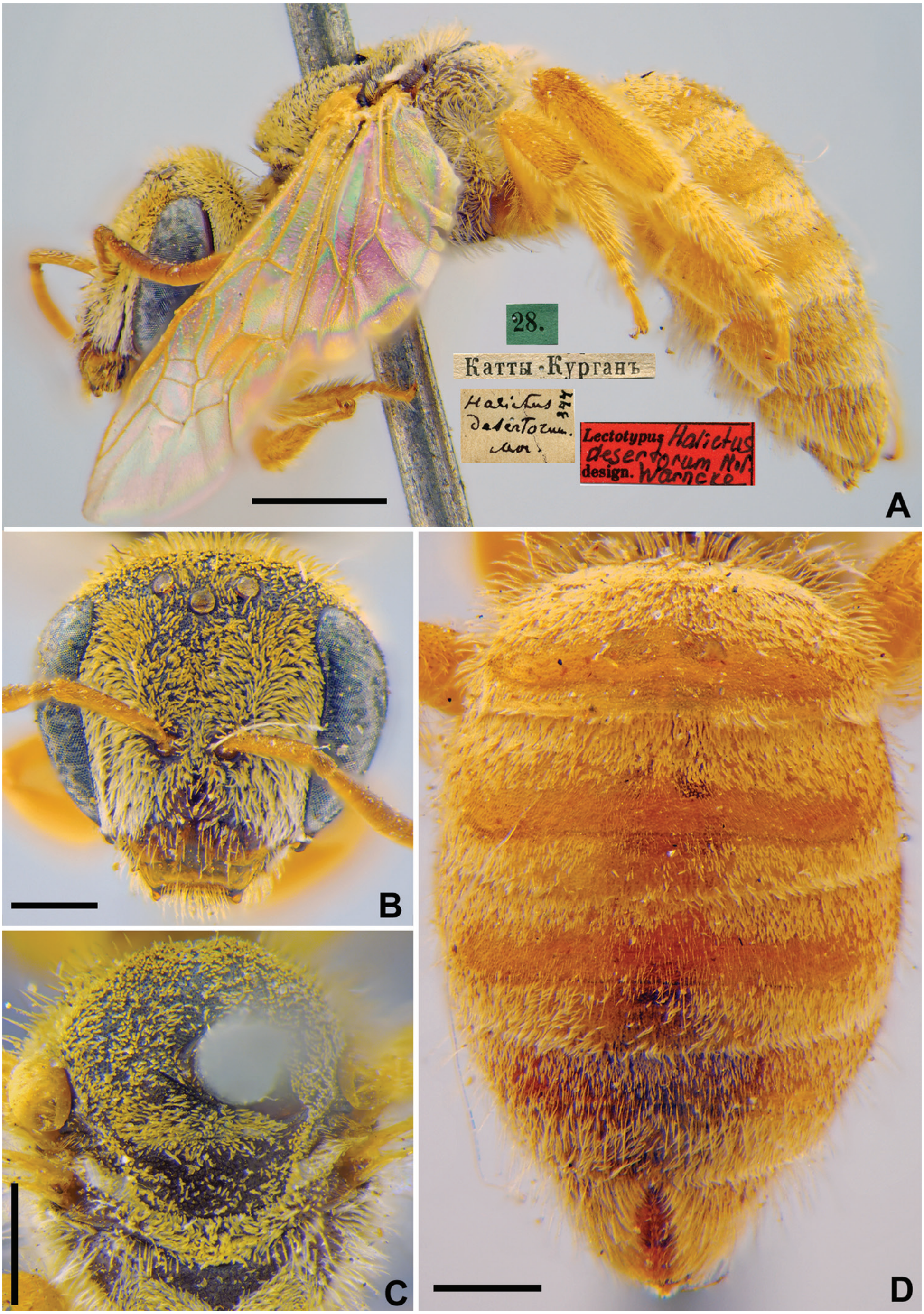

Figure 7. *Halictus desertorum* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm (**A**), 0.5 mm (**B–D**).

9. ***Halictus determinatus*** **Morawitz, 1876**

Figure 8

Halictus determinatus Morawitz, 1876: 217 (key), 233, ♀.

Type locality. 30 km SSE Samarkand, Sangu-dzhuman Pass (Uzbekistan).

Published (original) locality. Uzbekistan: "On the road to Sangy-Dzhuman [pass] and the Kulbasy Mountain".

Lectotype. ♀, designated by Pesenko 1984: 20, 25.[V.1869] // Сангы-Джуманъ [Uzbekistan, Sangu-dzhuman Pass, Zeravshan Ridge, 30 km SSE Samarkand, 39°27'N, 67°14'E] // *Halictus determinatus* Mor., [N]351 [handwritten by F. Morawitz] // Lectotypus *H. determinatus* Mor., ♀, design. Pesenko [1]981 <red label> [ZMMU].

Paralectotypes (6 ♀)**.** 3 ♀, the same label as in the lectotype; 1 ♀, 25.[V.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley] // [N]351 [ZMMU]; 2 ♀, Сангы-Джуманъ [Sangu-Dzhuman] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *determinatus* F. Mor., ♀ [handwritten by F. Morawitz] // Paralectotypus *H. determinatus* Mor., ♀, design. Pesenko [1]981 <identical red labels on each paralectotype specimen, labelled by Yu. Pesenko> [ZISP].

Current status. *Halictus* (*Platyhalictus*) *determinandus* Dalla Torre, 1896, replacement name for *H. determinatus* Morawitz, 1876 (nec *H. determinatus* Walker, 1871).

Remarks. Description of male. Ebmer 1980: 471, Fig. 1.

Distribution. A rare montane Central Asian species. Northern Afghanistan, eastern Uzbekistan, Tajikistan and Kyrgyzstan (Pesenko 2005a).

10. ***Halictus equestris*** **Morawitz, 1876**

Figure 9

Halictus equestris Morawitz, 1876: 217 (key), 242, ♀.

Type locality. Khozyay-Dun (Uzbekistan).

Published (original) locality. Uzbekistan: Khodzhaduk [= Khozyay-Dun].

Lectotype. ♀, designated by Warncke 1982: 105, 21.[V.1869] // Заравшан.[ская] дол.[ина] [Uzbekistan, Zeravshan River valley, Khozyay-Dun, 39°24'N, 67°01'E] // *Halictus equestris* Mor., [N]366 [handwritten by F. Morawitz] // Lectotypus *Halictus equestris* Mor., design. Warncke [19]82 <red label> [ZMMU].

Current status. *Lasioglossum* (*Lasioglossum*) *equestre* (Morawitz, 1876).

Remarks. Description of male. Morawitz 1876: 219 (key), 243, as *Halictus ferghanicus* (synonymised by Blüthgen 1926: 391).

According to the Fedchenko list (Baker 2004: 243), the locality given in Warncke's lectotype designation is in Uzbekistan, not Tajikistan.

Distribution. Turkey, Uzbekistan, Tajikistan, Kyrgyzstan, south-eastern Kazakhstan (Pesenko 1986a, Ascher and Pickering 2020).

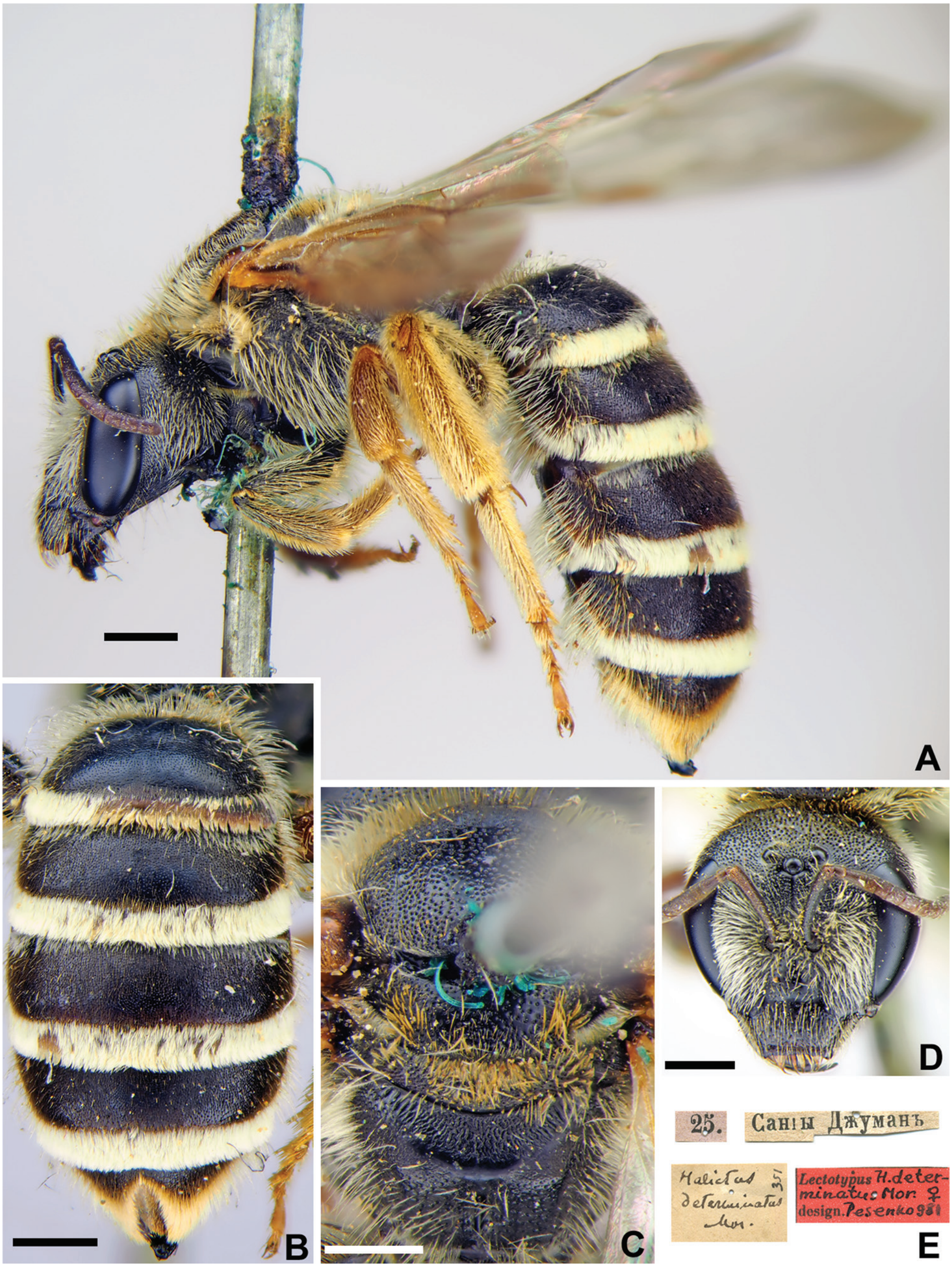

Figure 8. *Halictus determinatus* Morawitz, 1876, lectotype, female **A** habitus, lateral view **B** metasoma, dorsal view **C** mesosoma, dorsal view **D** head, frontal view **E** labels. Scale bars: 1.0 mm.

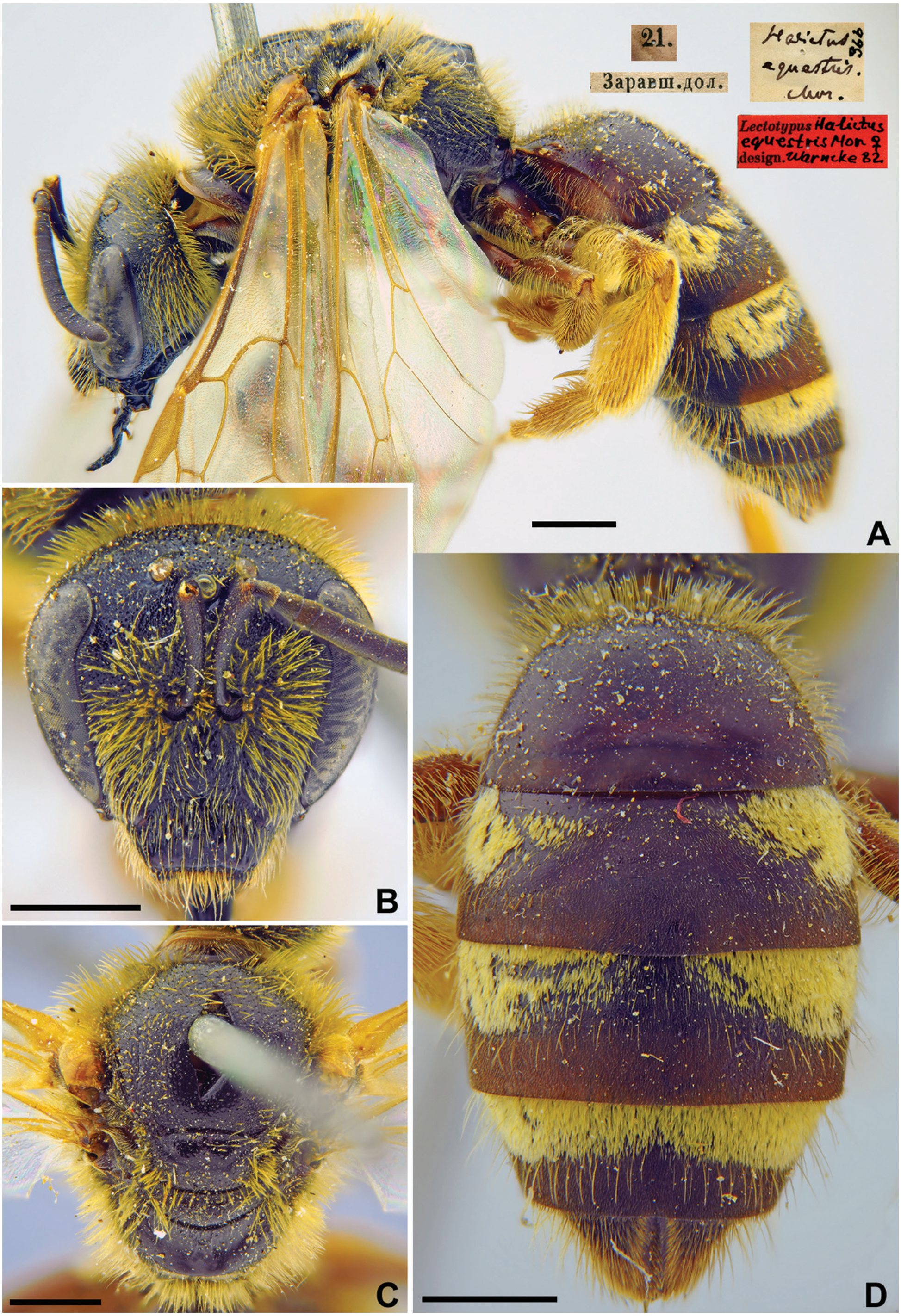

Figure 9. *Halictus equestris* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm.

11. *Halictus ferghanicus* Morawitz, 1876

Figure 10

Halictus ferghanicus Morawitz, 1876: 219 (key), 243, ♂.

Type locality. Shakhimardan (Uzbekistan).

Published (original) locality. Uzbekistan: near Shakhimardan.

Lectotype. ♂, designated by Warncke 1982: 105, <golden circle> // 6.[VII.1871] // Шагимарданъ [Shakhimardan in the Uzbek enclave in the territory of Kyrgyzstan, Alai Ridge; 39°58'N, 71°47'E] // *Halictus ferghanicus* Mor., [N]367 [handwritten by F. Morawitz] // Lectotypus *Halictus ferghanicus* Mor., ♂, design. Warncke [19]82 <red label, labelled by Yu. Pesenko > [ZMMU].

Paralectotypes (2 ♂)**.** 1 ♂, <golden circle> // 2.[VII.1871] // Шагимарданъ [Shagimardan] // *ferghanicus* Mor., Typ. [handwritten by F. Morawitz]; 1 ♂, 2.[VII.1871] // Шагимарданъ [Shagimardan] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *Halictus ferghanicus* M. [handwritten by F. Morawitz] // *Lasioglossum equestre* Mor., Pesenko det., 1985 // Paralectotypus, *Halictus ferghanicus* Mor., design. Warncke, [19]82 <identical red labels on each paralecotype specimen, labelled by Yu. Pesenko> [ZISP].

Current status. *Lasioglossum* (*Lasioglossum*) *equestre* (Morawitz, 1876) (synonymised by Blüthgen 1926: 391).

Distribution. See *Halictus equestris* Morawitz, 1876.

12. *Halictus fucosus* Morawitz, 1876

Figure 11

Halictus fucosus Morawitz, 1876: 219 (key), 230, ♂.

Type locality. 30 km SE Kozhatogai, Turkistan Province (Kazakhstan).

Published (original) locality. Uzbekistan: steppe between Tashkent and Syrdarya River.

Holotype. ♂, 18.[V.1871] // Степь м.[ежду] С.[ыр] д.[арьей] и Т.[ашкентом] [Kazakhstan, Turkistan Province, steppe between Syrdarya River and Tashkent, 30 km SE Kozhatogai, 41°47'N, 68°23'E] // *Halictus fucosus* Mor., [N]345 [handwritten by F. Morawitz] // *Halictus senilis* Evers. v. *fucosus* Mor., ♂, P. Blüthgen det. // Holotypus <red label> [ZMMU].

Current status. *Halictus* (*Argalictus*) *senilis* (Eversmann, 1852) (synonymised by Blüthgen 1922: 47).

Remarks. The lectotype designation of Warncke (1982: 148) is unnecessary as the species was described from a single male that was directly written about by Morawitz (1876: 231).

Distribution. North Africa, South and East Europe, Russia (south to Urals Mountains on the east), Caucasus, Turkey, Near East, Iraq, Iran, Afghanistan, Central Asia, Kazakhstan, Mongolia, China (Astafurova and Proshchalykin 2017).

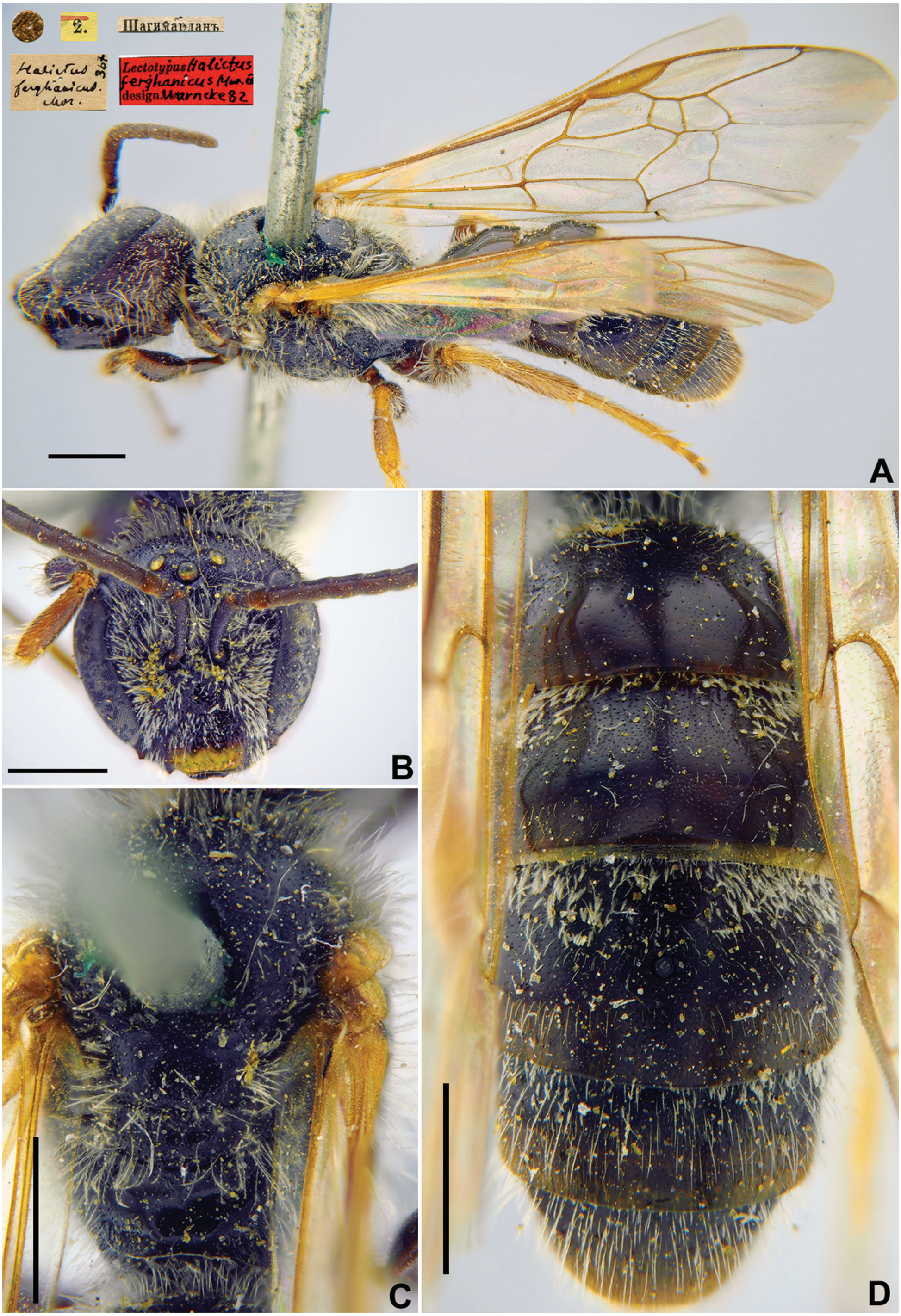

Figure 10. *Halictus ferghanicus* Morawitz, 1876, lectotype, male **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm.

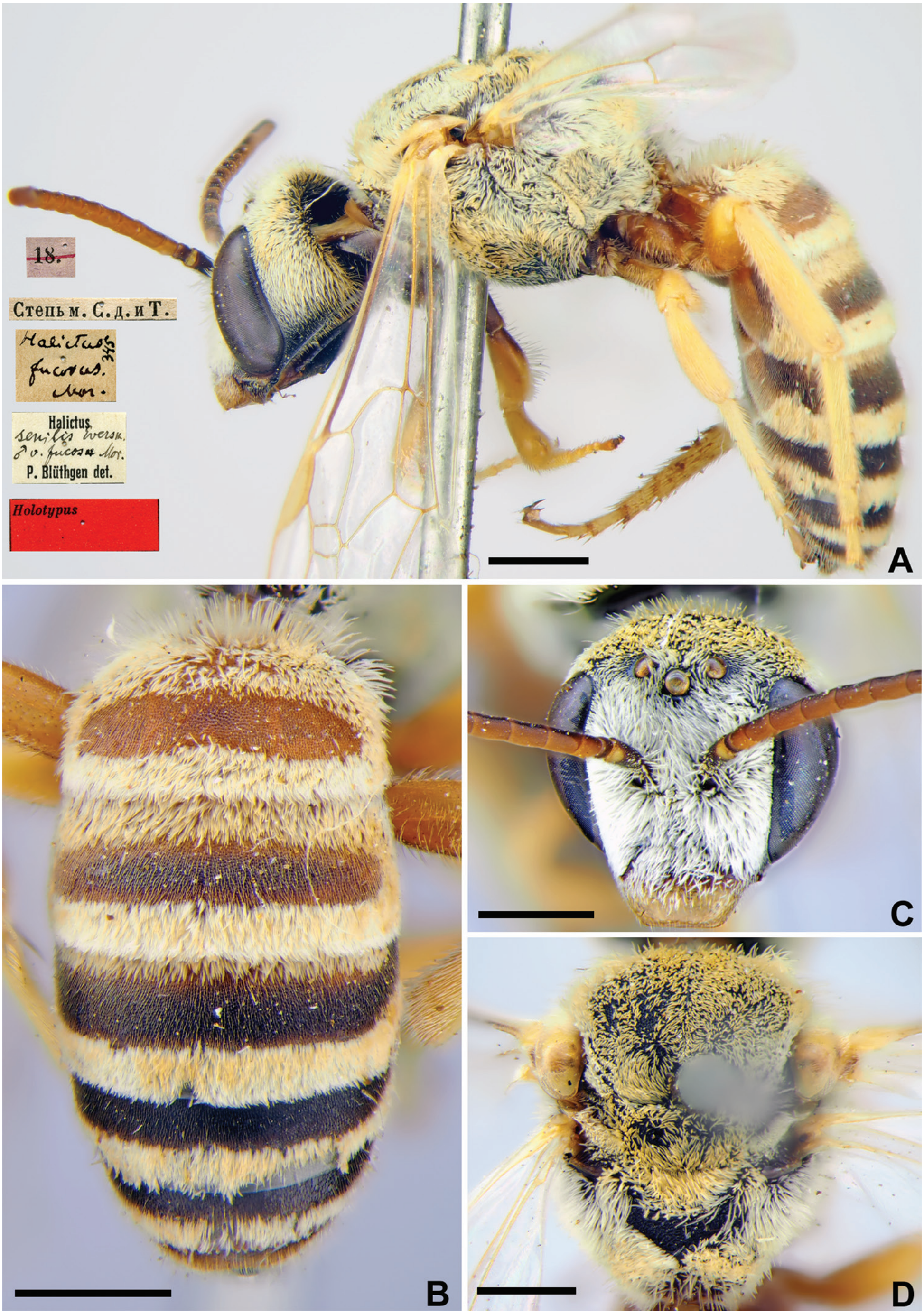

Figure 11. *Halictus fucosus* Morawitz, 1876, holotype, female **A** habitus, lateral view and labels **B** metasoma, dorsal view **C** head, frontal view **D** mesosoma, dorsal view. Scale bars: 1.0 mm.

13. *Halictus fulvitarsis* Morawitz, 1876

Figure 12

Halictus fulvitarsis Morawitz, 1876: 219 (key), 239, ♂.

Type locality. Khodzha-Chiburgan River (Tajikistan/Kyrgyzstan, not Uzbekistan as was indicated in Warncke 1982: 91).

Published (original) locality. Tajikistan/Kyrgyzstan: Khodzha-Chiburgan River.

Holotype. ♂, 26.[VI.1871] // Чибурганъ [Tajikistan/Kyrgyzstan: Khodzha-Chiburgan River (near Vorukh, ≈ 39°48'N, 70°41'E) // *Halictus fulvitarsis* Mor., [N]361 [handwritten by F. Morawitz] // Holotypus <red label> [ZMMU].

Current status. *Lasioglossum* (*Lasioglossum*) *fulvitarse* (Morawitz, 1876).

Remarks. Description of male. Blüthgen 1934b: 147.

The lectotype designation by Warncke (1982: 91) is unnecessary as the species was described from a single male that was directly written about by Morawitz (1876: 240).

Distribution. Tajikistan, Kyrgyzstan, Kazakhstan (Morawitz 1876, Pesenko 1986a, Murao et al. 2017).

14. *Halictus funerarius* Morawitz, 1876

Figure (see Astafurova and Proshchalykin 2020: 414, figs 11a–e).

Halictus funerarius Morawitz, 1876: 217 (key), 235, ♀.

Type locality. 30 km SSE Samarkand, Sangu-dzhuman Pass (Uzbekistan).

Published (original) locality. Uzbekistan: Sangu Dzhuman.

Lectotype. ♀, designated by Pesenko 1984: 21, <golden circle> // Сангы Джуманъ [Uzbekistan, Sangydzhuman Pass, 30 km SSE Samarkand, 39°22'N, 67°00'E] // 25.[V.1869] // *funerarius* Mor. Typ. [handwritten by F. Morawitz] // Lectotypus *H. funerarius* Mor., ♀, design. Pesenko [1]981 <red label> // Zoological Institute St. Petersburg INS_HYM_0000159 [ZISP].

Paralectotypes (8 ♀)**.** 8 ♀, the same label as in lectotype // Paralectotypus *H. funerarius* Mor. design. Pesenko [1]981 <red labels> [3 ♀ – ZISP; 5 ♀ – ZMMU].

Current status. *Halictus* (*Protohalictus*) *funerarius* Morawitz, 1876.

Distribution. A rare montane Central Asian species: Kazakhstan, Uzbekistan, Tajikistan, Western Kyrgyzstan, Iran, north-eastern Afghanistan and north-western China (Pesenko 2005a).

15. *Halictus fuscicollis* Morawitz, 1876

Figure 13

Halictus fuscicollis Morawitz, 1876: 217 (key), 229, ♀.

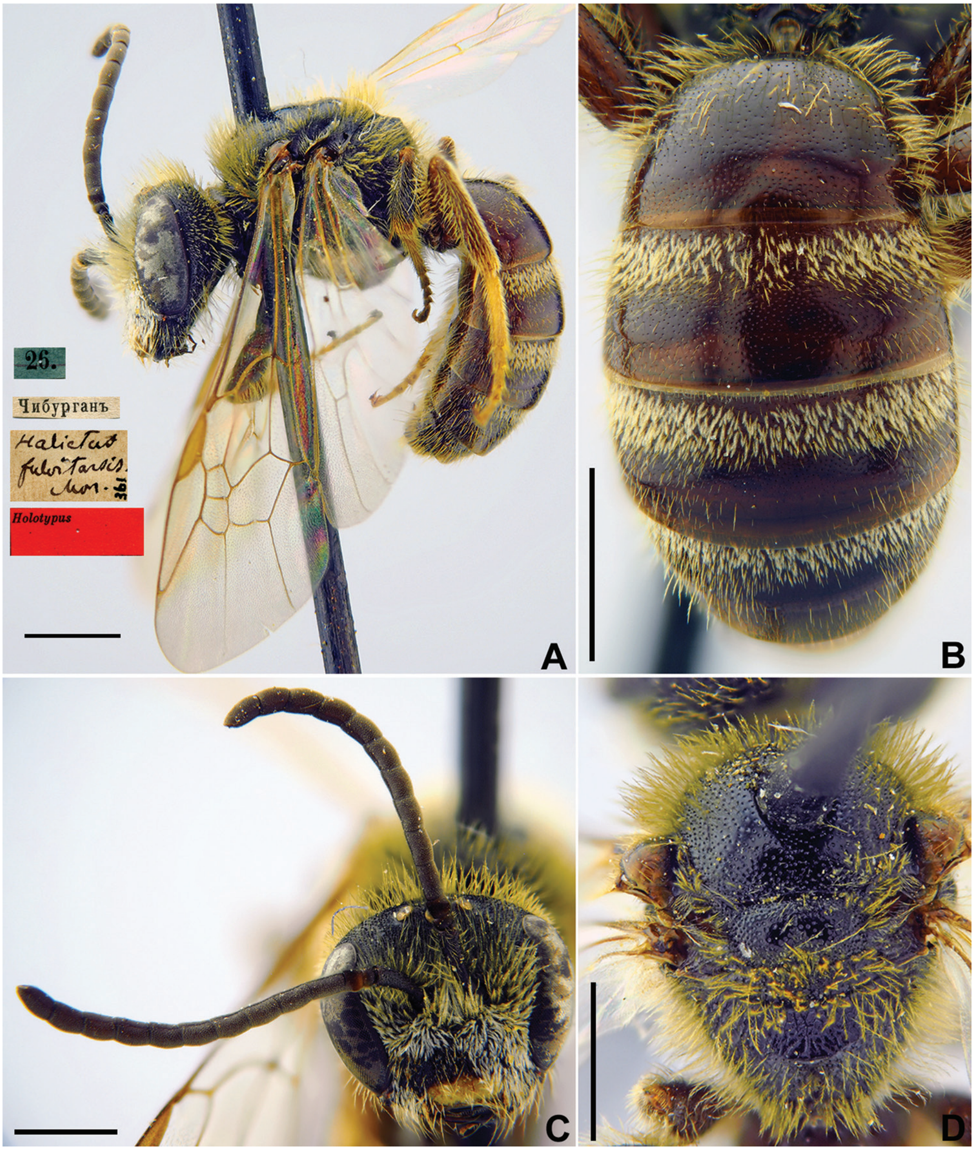

Figure 12. *Halictus fulvitarsis* Morawitz, 1876, holotype, female **A** habitus, lateral view and labels **B** metasoma, dorsal view **C** head, frontal view **D** mesosoma, dorsal view. Scale bars: 1.0 mm.

Type locality. 50 km NW Chardara, Kyzylkum Desert (Turkistan Province, Kazakhstan).

Published (original) locality. Kazakhstan: “Kyzyl-Kum Steppe, near Baybek”.

Lectotype. ♀, designated by Warncke 1982: 137, 30.[IV.1871] // Кизилъкумъ [Kazakhstan, Baybek Well, Kyzylkum Desert, ca. 50 km NW Chardara, ≈ 41°44'N, 67°54'E] // *Halictus fuscicollis* Mor., [N]345 [handwritten by F. Morawitz] // *Halictus Vestitohalictus fuscicollis* Mor., ♀, Lectotypus, design. A.W. Ebmer 1994 //

Figure 13. *Halictus fuscicollis* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 0.5 mm.

Lectotypus *Halictus fuscicollis* Mor., design. Warncke <red label, labelled by Yu. Pesenko> [ZMMU].

Paralectotype. 1 ♀, <golden circle> Kisilkum [handwritten by F. Morawitz] // *fuscicollis* Mor. Typ. [handwritten by F. Morawitz] // Paralectotypus <red label>, labelled by Yu. Astafurova [ZISP].

Current status. *Halictus* (*Placidochalictus*) *fuscicollis* Morawitz, 1876.

Remarks. Description of male. Morawitz 1894: 68, as *Halictus flavocallosus* (synonymised by Blüthgen 1931a: 214).

Distribution. Southern Kazakhstan, Turkmenistan, Iran, China (Xinjiang) (Morawitz 1876, 1894, Murao et al. 2017, Ascher and Pickering 2020).

16. *Halictus hyalinipennis* Morawitz, 1876

Figure (see Astafurova and Proshchalykin 2018: 23, figs 21a–e).

Halictus hyalinipennis Morawitz, 1876: 218 (key to females), 220 (key to males), 253–254, ♀, ♂.

Type locality. Tashkent (Uzbekistan).

Published (original) locality. Kazakhstan: Chardara, steppe between Tashkent and Syr-Darya; Uzbekistan: Dzhamsk Gorge, Dzhizmansk Gorge, Ulus, Dzham, Urgut, Keles, Samarkand, Soch, Shakhimardan, Uch-Kurgan; Kyrgyzstan: Alay, Osh, Gulsha, Taka.

Lectotype. ♀, designated by Astafurova and Proshchalykin 2018: 22, Ташкентъ [Uzbekistan, Tashkent, 41°18'N 69°16'E] // *hyalinipennis* F. Mor., ♀ [handwritten by F. Morawitz] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // Lectotypus *Halictus hyalinipennis* Morawitz, 1876, ♀, design. Astafurova & Proshchalykin 2018 <red label> [ZISP].

Paralectotypes (29 ♀, 10 ♂)**.** 1 ♀, Шагимарданъ [Shagimardan] // 3.[VII.1871] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz]; 1 ♂, Така [Taka] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz]; 1 ♀, 1 ♂, Сохъ [Sokh] // 29. [29.VI.1871] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz]; 1 ♂, Уч-Курганъ [Uch- Kurgan] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz]; 2 ♀, Ташкентъ [Tashkent] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] [ZISP]; 1 ♂, Ошъ [Osh] // 1.[VIII.1871]; 1 ♂, Самаркандъ [Samarkand] // 4.[VII.1869] // [N]384; 3 ♂, Самаркандъ [Samarkand] // 7.[VII.1869]; 2 ♀, Самаркандъ [Samarkand] // 3., 21.[III.1869]; 16 ♀, Ташкентъ [Tashkent] // 26., 27.[III.1871], 21., 23.[V.1871] and 1.,3.,5.,10.[VI.1871]; 1 ♀, Чардара [Chardara] // 27.[IV.1871]; 1 ♀, Учь-Курганъ [Uch-Kurgan] // 15.[VII.1871]; 2 ♂, Шагимарданъ [Shagimardan] // 2.[VII.1871] 5 ♀, Заравшан.[ская] дол.[ина] [Zeravshan River valley], 3., 11., 18., 23.[III.1871] // Paralectotypus *Halictus hyalinipennis* Morawitz, 1876, design. Astafurova & Proshchalykin 2018 <identical red labels on each paralectotype specimen> [ZMMU].

Current status. *Lasioglossum* (*Sphecodogastra*) *hyalinipenne* (Morawitz, 1876).

Distribution. Iran, Afghanistan, Kazakhstan, Uzbekistan, Kyrgyzstan, Tajikistan (Morawitz 1876, Ebmer 1974, Warncke 1982, Murao et al. 2017).

17. *Halictus laevinodis* Morawitz, 1876

Figure (see Astafurova and Proshchalykin 2018: 24, figs 23a–e).

Halictus laevinodis Morawitz, 1876: 218 (key to females), 248, ♀.

Type locality. 30 km SSE Samarkand, Sangu-dzhuman Pass (Uzbekistan).

Published (original) locality. Uzbekistan: Sangy Dzhuman.

Lectotype (designated here). ♀, <golden circle> // Сангы Джуманъ [Uzbekistan, Sangy-dzhuman Pass, 30 km SSE Samarkand, Zeravshan Ridge, 39°27'N, 67°14'E] // 25.[III.1869] // *laevinodis* Mor., Typ. [handwritten by F. Morawitz] // Lectotype *Halictus laevinodis*, design. Astafurova et Proshchalykin, 2020 <red label> [ZISP].

Paralectotypes (2 ♀)**.** 1 ♀, 25.[III.1869] // Сангы Джуманъ [Sangy Dzhuman] // *Halictus laevinodis* Mor. [handwritten by F. Morawitz]; 1 ♀ 25.[III.1869] // Сангы Джуманъ [Sangy Dzhuman] // [N]375 // Paralectotype *Halictus laevinodis*, design. Astafurova et Proshchalykin, 2020 <identical red labels on each paralectotype specimen> [ZMMU].

Current status. *Lasioglossum* (*Hemihalictus*) *laevinode* (Morawitz, 1876).

Remarks. Astafurova and Proshchalykin (2018: 23) indicated the lectotype specimen as «Holotype», but Morawitz (1876) did not directly indicate a single specimen and two specimens from the type series are deposited in ZMMU.

Description of male. Blüthgen, 1934b: 154, Fig. 3.

Distribution. Kazahkstan, Uzbekistan, Tajikistan, Kyrghyzstan, Afghanistan (Morawitz 1876, Blüthgen in Popov 1935, Ebmer 1980, Murao et al. 2017).

18. *Halictus limbellus* Morawitz, 1876

Figure 14

Halictus limbellus Morawitz, 1876: 218 (key), 249, ♀.

Type locality. Samarkand (Uzbekistan).

Published (original) locality. Uzbekistan: Samarkand; Tajikistan: Peti.

Lectotype (designated here). ♀, 5.[IV.1869] // Самаркандъ [Uzbekistan, Samarkand, 39°39'N, 66°57'E] // *Halictus limbellus* Mor., [N]377 [handwritten by F. Morawitz] // Lectotypus *Halictus limbellus* Mor., Astafurova et Proshchalykin, 2020 <red label> [ZMMU].

Paralectotypes (3 ♀)**.** 1 ♀, 5.[IV.1869] // Самаркандъ [Samarkand] // [N]377 // Typus <red label> [ZMMU]; 1 ♀, <golden circle> // 5.[IV.1869] // Самаркандъ [Samar-

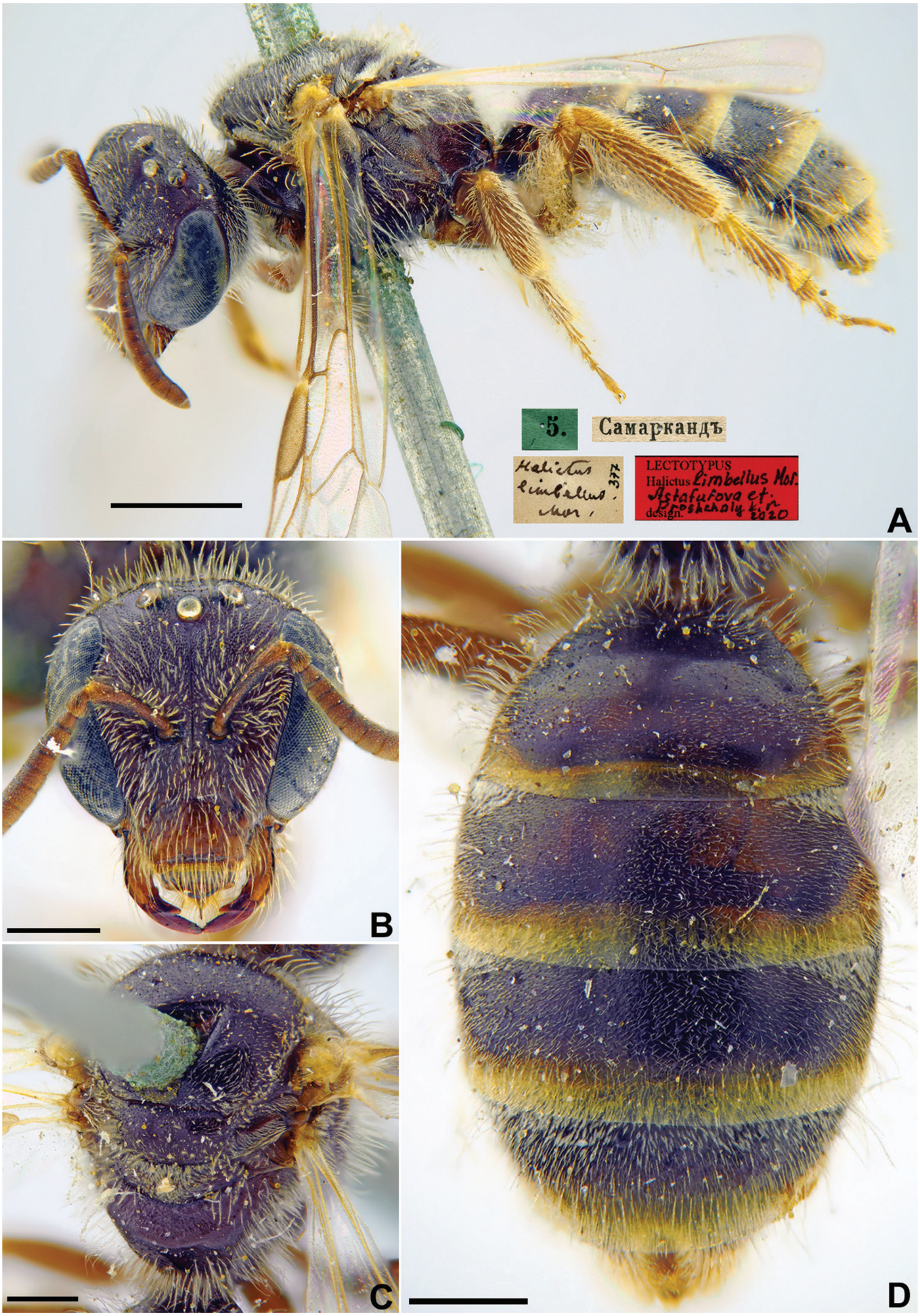

Figure 14. *Halictus limbellus* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm (**A**), 0.5 mm (**B–D**).

kand] // *Halictus limbellus* F. Mor., Typ. [handwritten by F. Morawitz]; 1 ♀, Самаркандъ [Samarkand] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *limbellus* Mor., Typ. [handwritten by F. Morawitz] // Paralectotypus *Halictus limbellus* Mor., Astafurova et Proshchalykin, 2020 <identical red labels on each paralectotype specimen> [ZISP].

Current status. *Lasioglossum* (*Hemihalictus*) *limbellum* (Morawitz, 1876).

Remarks. Description of male. Blüthgen 1930: 763.

The lectotype designation by Warncke (1982: 69) is invalid because he labelled no female of the two females from Samarkand deposited in ZMMU.

Distribution. Central and eastern Europe, Turkey, Caucasus, Russia (North Caucasus), Israel, Iran, Afghanistan, Tajikistan, Uzbekistan, Kazakhstan, China (Gansu) (Pesenko 2007, Astafurova and Proshchalykin 2017, Murao et al. 2017).

19. *Halictus longirostris* Morawitz, 1876

Figure 15

Halictus longirostris Morawitz, 1876: 216 (key to females), 219 (key to males), 236, ♀, ♂.

Type locality. Shakhimardan (Uzbekistan).

Published (original) locality. Uzbekistan: on the road to Sangy-dzhuman Pass, Shakhimardan; Tajikistan: Peti.

Lectotype. ♂, designated by Warncke 1982: 80, 3.[VII.1871] // Шагимарданъ [Shakhimardan in the Uzbek enclave in the territory of Kyrgyzstan, Alai Ridge; 39°58'N, 71°47'E] // *Halictus longirostris* Mor., [N]356 [handwritten by F. Morawitz] // Lectotypus *Halictus longirostris* Mor., design. Warncke [19]82 <red label, labelled by Yu. Astafurova> [ZMMU].

Paralectotypes (2 ♀)**.** 1 ♀, 25.[V.1869] // Сангы Джуманъ [Sangy Dzhuman] // [N]356; 1 ♀, 12.[VII.1870] // Фанъ [Fan] // [N]356 [ZMMU]; 1 ♀, 2.[VII.1871] // Шагимарданъ [Shagimardan] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *Halictus longirostris* Mor. [handwritten by F. Morawitz] // Paralectotypus *Halictus longirostris* Mor., design. Warncke < identical red labels on each paralectotype specimen, labelled by Yu. Astafurova> [ZISP].

Current status. *Lasioglossum* (*Hemihalictus*) *longirostre* (Morawitz, 1876).

Distribution. Greece, Israel, Lebanon, Turkey, Caucasus, Iran, Afghanistan, Central Asia, Kazakhstan, China (Xinjiang) (Murao et al. 2017, Niu et al. 2020).

20. *Halictus maculipes* Morawitz, 1876

Figure 16

Halictus maculipes Morawitz, 1876: 218 (key to females), 247, ♀.

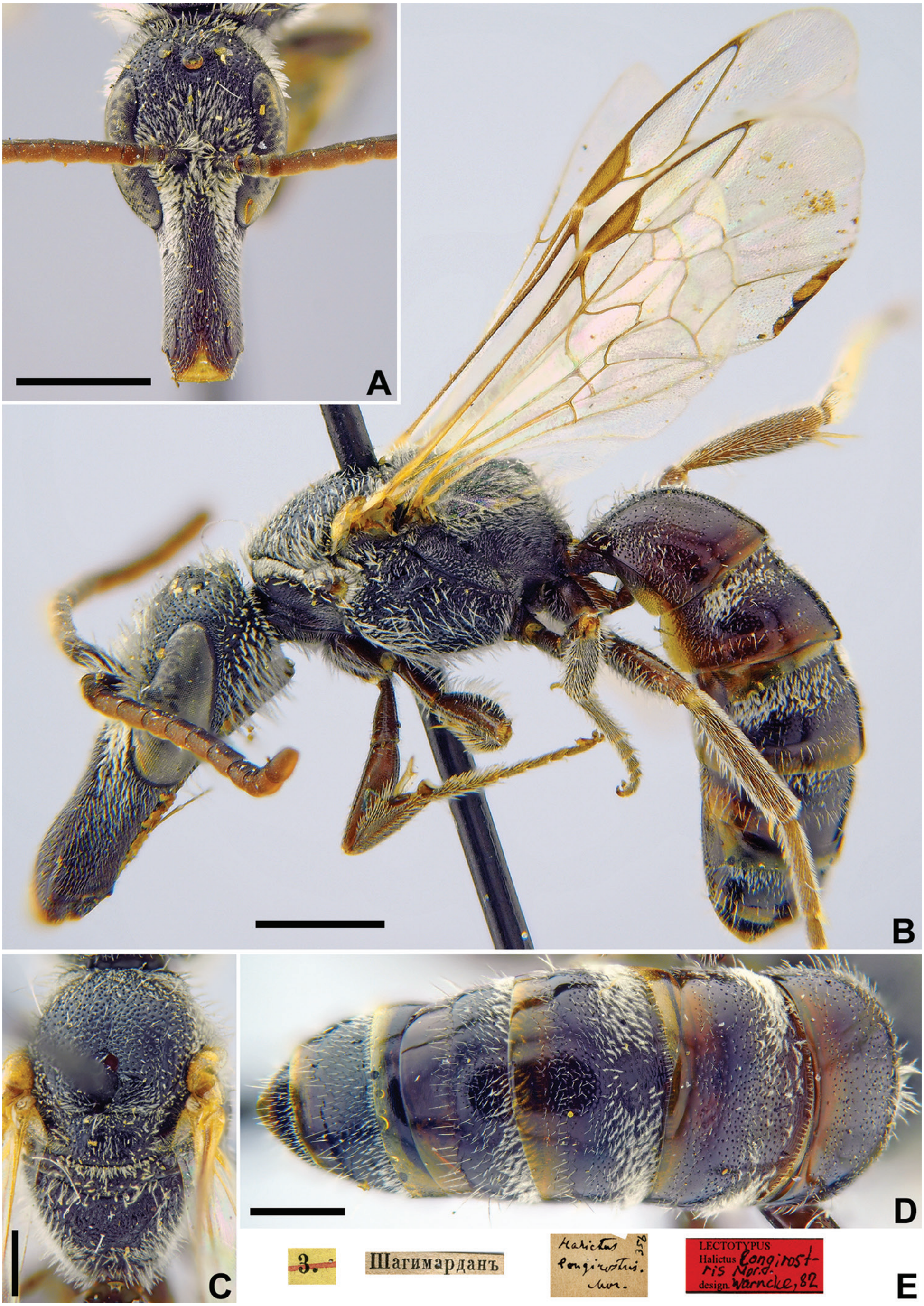

Figure 15. *Halictus longirostris* Morawitz, 1876, lectotype, male **A** head, frontal view **B** habitus, lateral view **C** mesosoma, dorsal view **D** metasoma, dorsal view **E** labels. Scale bars: 1.0 mm (**A, B**), 0.5 mm (**C, D**).

Type locality. Sokh District [Uzbekistan].

Published (original) locality. Kekh [Sokh District, Uzbekistan].

Lectotype. ♀ designated by Warncke 1982: 68, <golden circle> // 27.[VI.1871] // Сохъ [Uzbekistan, Sokh District, ≈ 39°57'N, 71°07'E] // *Halictus maculipes* Mor., [N]373 [handwritten by F. Morawitz] // Lectotypus *Halictus maculipes* Mor., design. Warncke <red label, labelled by Yu. Astafurova> [ZMMU].

Current status. *Lasioglossum* (*Hemihalictus*) *maculipes* (Morawitz, 1876).

Remarks. Male unknown.

Distribution. Turkey, Turkmenistan, Tajikistan, Uzbekistan, Iran, Afghanistan (Morawitz 1876, Ebmer 1984, 1986, Warncke 1982, Ascher and Pickering 2020).

21. *Halictus melanarius* Morawitz, 1876

Figure 17

Halictus melanarius Morawitz, 1876: 241, ♂.

Type locality. Shakhimardan (Uzbekistan).

Published (original) locality. Near Shakhimardan.

Holotype. ♂, 9.[VII.1871] // Шагимарданъ [Shakhimardan in the Uzbek enclave in the territory of Kyrgyzstan, Alai Ridge; 39°58'N, 71°47'E] // *Halictus melanarius* Mor., [N]364 [handwritten by F. Morawitz] // *Lasioglossum fallax* (Mor.) syn: *melanarium* (Mor.) det. A.W. Ebmer 1979 // Holotypus <red label> [ZMMU].

Current status. *Lasioglossum* (*Lasioglossum*) *fallax* ssp. *melanarium* (Morawitz, 1876) (subspecies status according to Ebmer 1998: 382).

Remarks. Description of female: Ebmer 1980: 493, Figs 12 and 13, as *Lasioglossum melan* Ebmer, 1980 (synonymised by Ebmer 1998: 382).

The lectotype designations by Ebmer (1980: 495) and by Warncke (1982: 91) were unnecessary as the species was described from a single male that was directly written about by Morawitz (1876: 241).

Distribution. Kazakhstan, Uzbekistan, Tajikistan, Kyrgyzstan, Afghanistan, Mongolia (Hovd) (Pesenko 2006b).

22. *Halictus minor* Morawitz, 1876

Figure (see Astafurova and Proshchalykin 2020: 418, figs 15a–e).

Halictus minor Morawitz, 1876: 217 (key), 233, ♀.

Type locality. 30 km SSE Samarkand, Sangu-dzhuman Pass (Uzbekistan).

Published (original) locality. Uzbekistan: Gus [near Urgut], Sangy-Dzhuman; Tajikistan: Pyandzhikent.

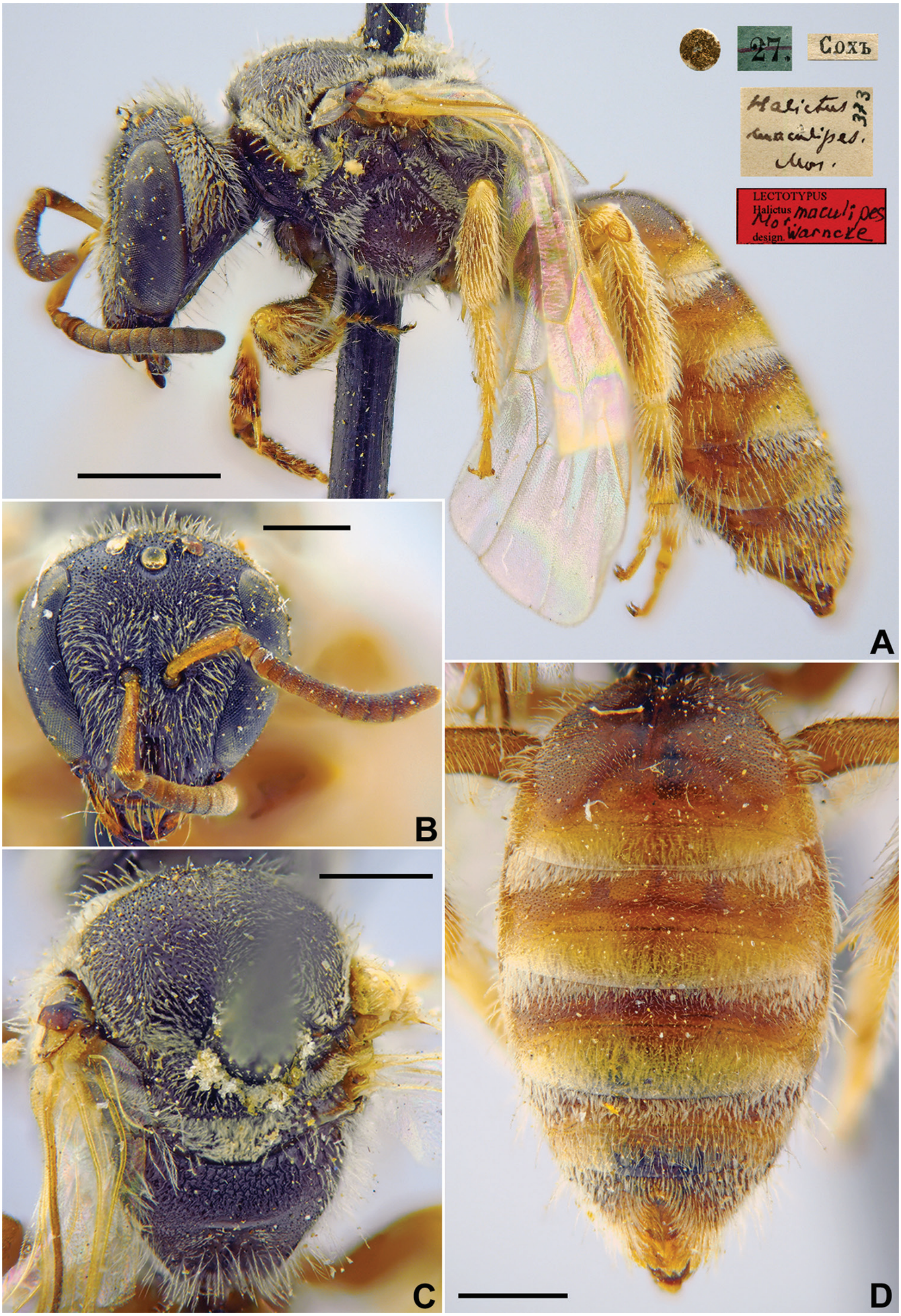

Figure 16. *Halictus maculipes* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm (**A**), 0.5 mm (**B–D**).

Figure 17. *Halictus melanarius* Morawitz, 1876, holotype, male **A** view habitus, lateral view and labels **B** head, frontal **C** genitalia, dorsal view **D** mesosoma, dorsal view **E** metasoma, dorsal view. Scale bars: 1.0 mm (**A, B, D, E**), 0.5 mm (**C**).

Lectotype. ♀, designated by Pesenko 1984: 23, <golden circle> // Сангы Джуманъ [Uzbekistan, Sangy-dzhuman Pass, 30 km SSE Samarkand, 39°20'N, 67°19'E] // 25.[V.1869] // *minor* Mor. [handwritten by F. Morawitz] // Lectotypus *H. minor* Mor., design. Pesenko, [1]981, ♀ <red label> // Zoological Institute St. Petersburg INS_HYM_0000164 [ZISP].

Paralectotypes (3 ♀)**.** 1 ♀, Сангы Джуманъ [Sangy Dzhuman] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *minor* Mor. [handwritten by F. Morawitz] // Syn.: *jarkandensis* Strand, ♀ // Paralectotypus *H. minor* Mor., design. Pesenko, [1]981, ♀ <red label >[ZISP]; 1 ♀, 25.[V.1869] // Сангы Джуманъ [Sangy Dzhuman] // *Halictus minor* Mor., [N]352 [handwritten by F. Morawitz]; 1 ♀, 24.[V.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, Gus] // [N]352 // Paralectotypus *H. minor* Mor., design. Pesenko, [1]981, ♀ <identical red labels on each paralectotype specimen> [ZMMU].

Current status. *Halictus* (*Platyhalictus*) *minor* Morawitz, 1876.

Remarks. Description of male. Blüthgen 1936: 295, fig. 11.

Distribution. Azerbaijan, Afghanistan, Iran, Kazakhstan, Central Asia, Altai, Pakistan, north-western and northern China, northern India (Pesenko 2005a, b).

23. *Halictus modernus* Morawitz, 1876

Figure 18

Halictus modernus Morawitz, 1876: 217 (key), 235, ♀.

Type locality. Samarkand (Uzbekistan).

Published (original) locality. Uzbekistan: near Samarkand.

Holotype. ♀, 5.[VII.1870] // Самаркандъ [Uzbekistan, Samarkand, 39°39'N, 66°57'E] // *Halictus modernus* Mor., [N]354 [handwritten by F. Morawitz] // Holotypus <red label> [ZMMU].

Current status. *Halictus* (*Lampralictus*) *modernus* Morawitz, 1876.

Remarks. The lectotype designation of Warncke (1982: 147) is unnecessary as the species was described from a single female that was directly written about by Morawitz (1876: 235).

Description of male. Ebmer 1984: 315, figs 3–5.

Distribution. Turkmenistan, Uzbekistan, Kyrgyzstan, Afghanistan, Pakistan (Pesenko 2005a).

24. *Halictus nasica* Morawitz, 1876

Figure 19

Halictus nasica Morawitz, 1876: 216 (key to females), 219 (key to males), 229, ♀, ♂.

Type locality. Samarkand (Uzbekistan).

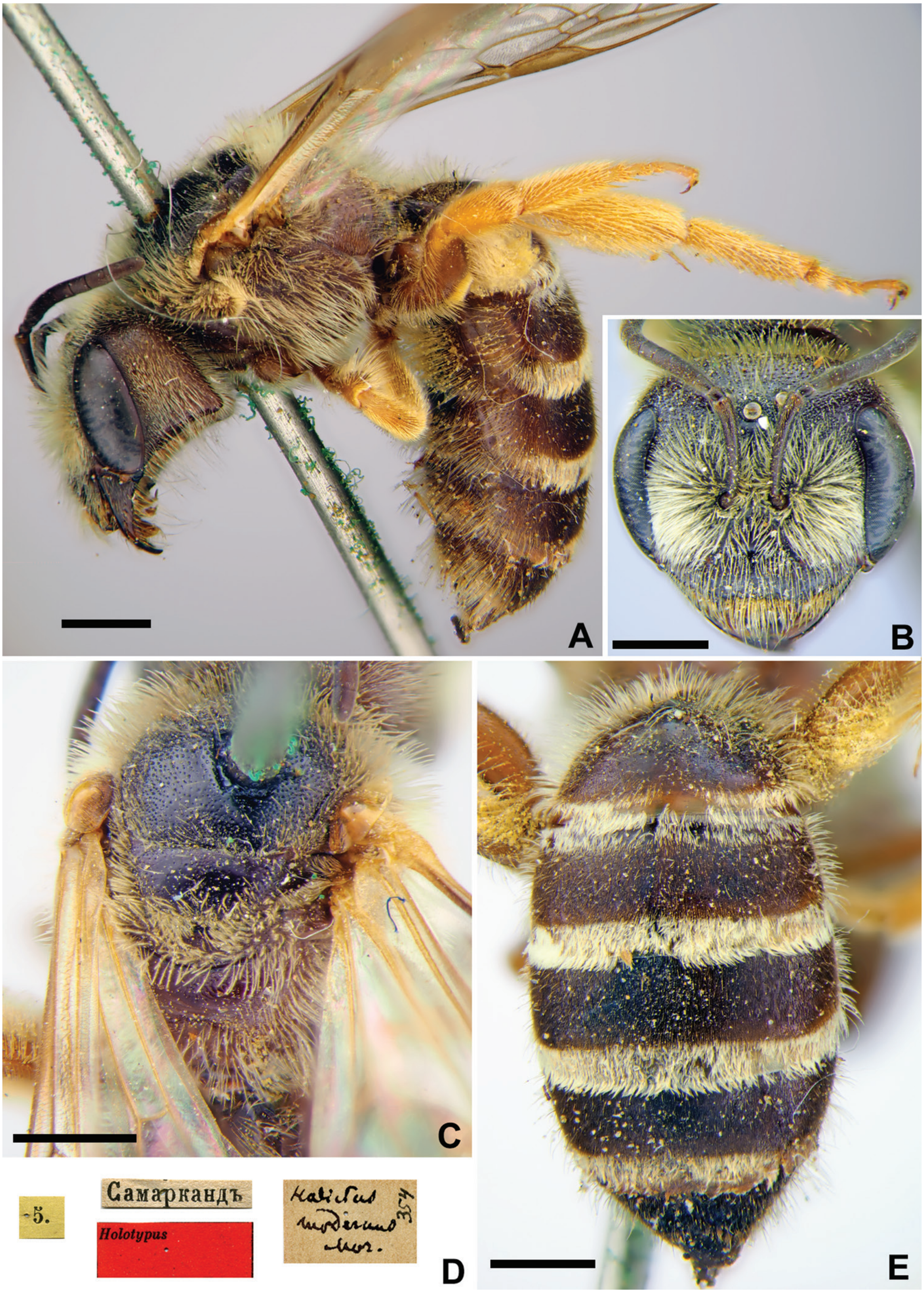

Figure 18. *Halictus modernus* Morawitz, 1876, holotype, female **A** habitus, lateral view **B** head, frontal view **C** mesosoma, dorsal view **D** labels **E** metasoma, dorsal view. Scale bars: 1.0 mm.

Published (original) locality. Southern Kazakhstan: Kysyl-Kum [desert] near draw-well Chakany; Uzbekistan: steppe between Katty-Kurgan and Ulus, Samarkand, Murzarabat, Chinaz, Sokh.

Lectotype (designated here). ♀, 9.[VI.1869] // Заравшан.[ская] дол.[ина] [Uzbekistan, Zeravshan River valley, near Samarkand, 39°39'N, 66°57'E] // *Halictus nasica* Mor., [N]346 [handwritten by F. Morawitz] // Lectotypus *Halictus nasica* Mor., design. Astafurova et Proshchalykin, 2020 <red label> [ZMMU].

Paralectotypes (28 ♀, 44 ♂)**.** 14 ♀, the same label as in the lectotype; 11 ♀, 2 ♂, 9., 13.[VI.1869], 4., 7.[VII.1869] // Самаркандъ [Samarkand] // [N]346; 12 ♂, 24.[VII.1870], 29.[VIII.1870] // Мурзарабадъ [Murzarabad] // [N]346; 1 ♀, 9 ♂, 28.[IV.1871] // Кизилъкумъ [Kizilkum] //[N]346; 17 ♂, 25.[VII.1870] // Чиназъ [Chinaz] // [N]346 [ZMMU]; 1 ♀, 28.[IV.1871] // Кизилъкумъ [Kizilkum] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *Halictus nasica* Mor. [handwritten by F. Morawitz]; 1 ♀, <golden circle> // 9.[VI.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, near Samarkand] // *nasica* Mor. Typ. [handwritten by F. Morawitz]; 3 ♂, 28.[VI.1871] // Сохъ [Sokh] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz]; 1 ♂, 9.[VI.1869] // Самаркандъ [Samarkand] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // Paralectotypus *Halictus nasica* Mor., design. Astafurova et Proshchalykin, 2020 <identical red labels on each paralectotype specimen> [ZISP].

Current status. *Halictus* (*Vestitohalictus*) *nasica* Morawitz, 1876.

Remarks. The lectotype designation by Warncke (1982: 138) is invalid because he labelled none of the 15 females from "valle Serafshan" deposited in ZMMU.

Distribution. Morocco, Kazakhstan, Uzbekistan, Turkmenistan, Iran, Afghanistan, Pakistan (Murao et al. 2017, Ascher and Pickering 2020).

25. *Halictus nigrilabris* Morawitz, 1876

Figure 20

Halictus nigrilabris Morawitz, 1876: 249, ♂.

Type locality. Sarafschan River valley, Yeri (Tajikistan).

Published (original) locality. Tajikistan: valley Sarafschan between Iori and Dashty-Kazy.

Lectotype. ♂, designated by Warncke 1982: 91, <golden circle> // 31.[V.1869] // Заравшан.[ская] дол.[ина] [Tajikistan, Zeravshan River valley, near Iori (= Yeri), 39°29'N, 67°53'E] // *Halictus nigrilabris* Mor., [N]378 [handwritten by F. Morawitz] // Lectotypus *Halictus nigrilabris* Mor. design. Warncke [1]982 <red label, labelled by Yu. Pesenko> [ZMMU].

Paralectotype. 1 ♂, Заравшан.[ская] дол.[ина] [Zeravshan River valley] // *Halictus nigrilabris* F. Morawitz [handwritten by F. Morawitz] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // Paralectotypus *Halictus nigrilabris* Mor., design. Warncke

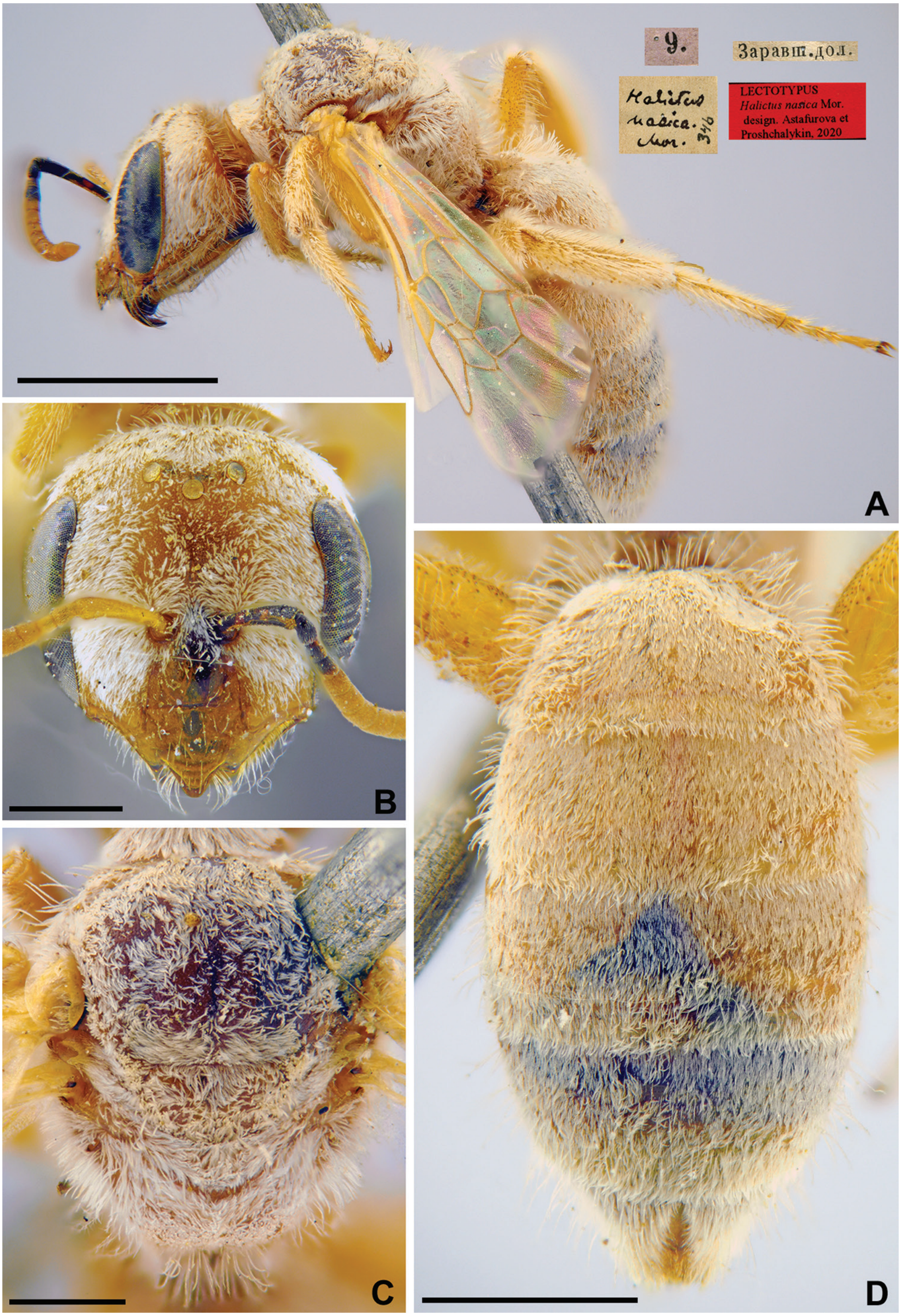

Figure 19. *Halictus nasica* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm (**A, D**), 0.5 mm (**B, C**).

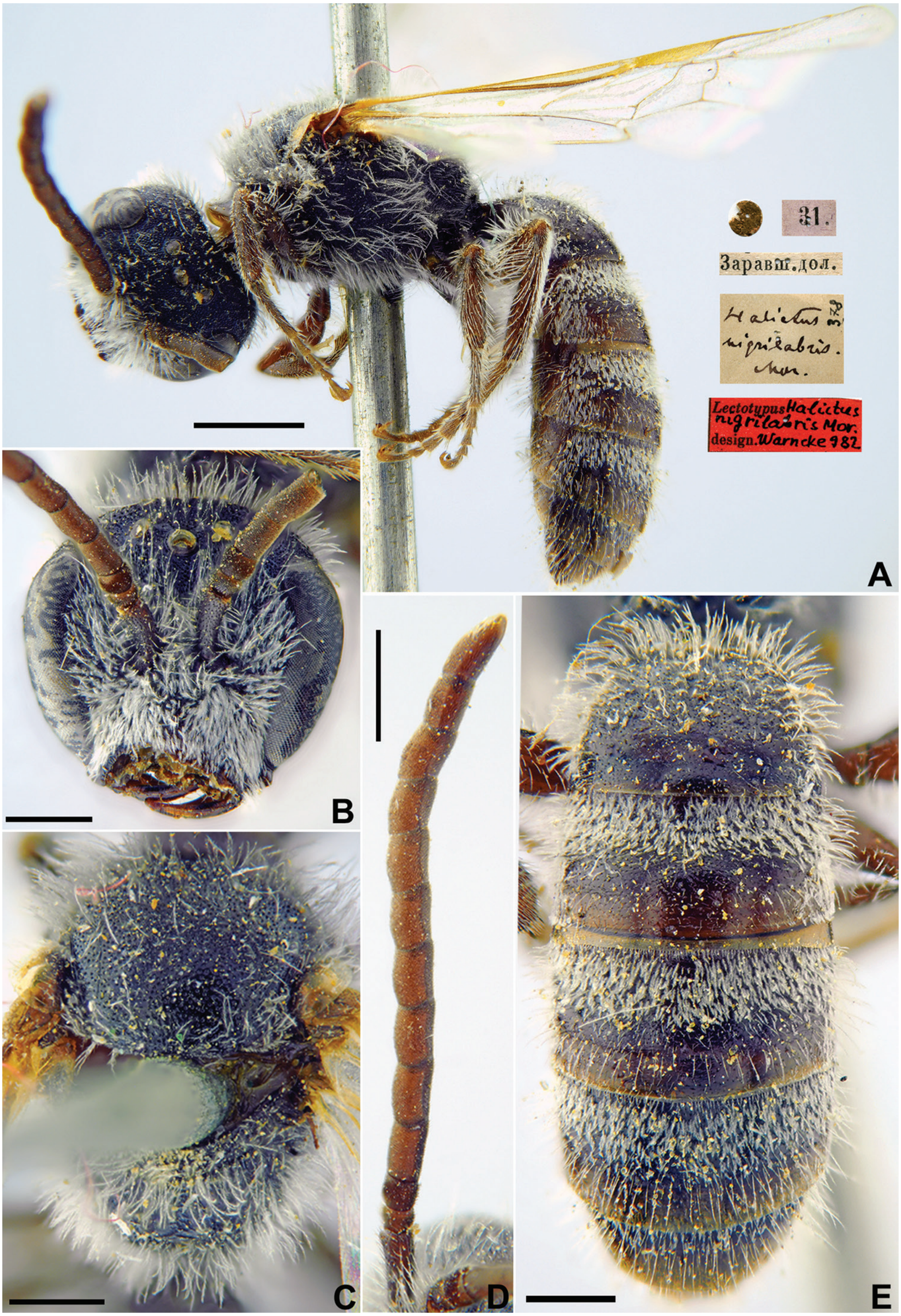

Figure 20. *Halictus nigrilabris* Morawitz, 1876, lectotype, male **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** antennae, dorsal view **E** metasoma, dorsal view. Scale bars: 1.0 mm.

[1]982 <red label, labelled by Yu. Pesenko> // Zoological Institute St. Petersburg, INS_HYM 0000076 [ZISP].

Current status. *Lasioglossum* (*Lasioglossum*) *nigrilabre* (Morawitz, 1876).

Remarks. Description of female. Blüthgen 1931b: 336, as *Halictus subprasinus* (synonymised by Ebmer 1978: 39).

Distribution. Iran, Afghanistan, Turkmenistan, Uzbekistan, Tajikistan, Kyrgyzstan (Blüthgen 1931b, Pesenko 1986a).

26. *Halictus nigripes* Morawitz, 1876

Figure 21

Halictus nigripes Morawitz, 1876: 251, ♂.

Type locality. Karazuk, vicinity of Shakhimardan (Uzbekistan).

Published (original) locality. Tajikistan: Iori George, Iskander River; Uzbek enclave in Kyrgyzstan: Karakazuk; Kyrgyzstan: Alay.

Lectotype. ♂, designated by Blüthgen 1934a: 302, 11.[VII.1871] // Каразукъ [Uzbekistan, Karazuk, vicinity of Shakhimardan 39°60'N, 71°50'E] // *Halictus nigripes* Mor., [N]380 [handwritten by F. Morawitz] // *nigripes* Mor., ♂, lecto-holotype, Blüthgen det. 1933 // Lectotypus *Halictus nigripes* Mor., design. Blüthgen [19]34 <red label> labelled by Yu. Astafurova [ZMMU].

Paralectotypes (3 ♂)**.** 1 ♂, 23.[VII.1871] // Алай [Alay] // [N]380 // *nigripes* Mor. ♂, Lecto-Paratype, Blüthgen det., 1933 [ZMMU]; 1 ♂, <golden circle> // 23.[VII.1871] // Алай [Alay] // *nigripes* Mor. Typ., [N]380 [handwritten by F. Morawitz]; 1 ♂, 22.[VII.1871] // Алай [Alay] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *Halictus nigripes* Mor. [handwritten by F. Morawitz] // Paralectotypus *Halictus nigripes* Mor., design. Blüthgen <identical red labels on each paralectotype specimen, labelled by Yu. Astafurova> [ZISP].

Current status. *Lasioglossum* (*Hemihalictus*) *melanopus* (Dalla Torre, 1896), replacement name for *Halictus nigripes* Morawitz, 1876 (nec *H. nigripes* Lepeletier, 1841).

Remarks. The specimens from Iskander and Iori George in the Morawitz type series are the holotype and paratypes of *Halictus pseudonigripes* Blüthgen, 1934.

Description of female: Vachal 1902: 229, as *Halictus attritus* (synonymised by Blüthgen 1934a: 301).

Distribution. Uzbekistan, Kyrgyzstan, Kazakhstan, Tajikistan, Afghanistan, China (Xinjiang) (Morawitz 1876, Murao et al. 2017, Ascher and Pickering 2020).

27. *Halictus obscuratus* Morawitz, 1876

Figure 22

Halictus obscuratus Morawitz, 1876: 218 (key), 245, ♀.

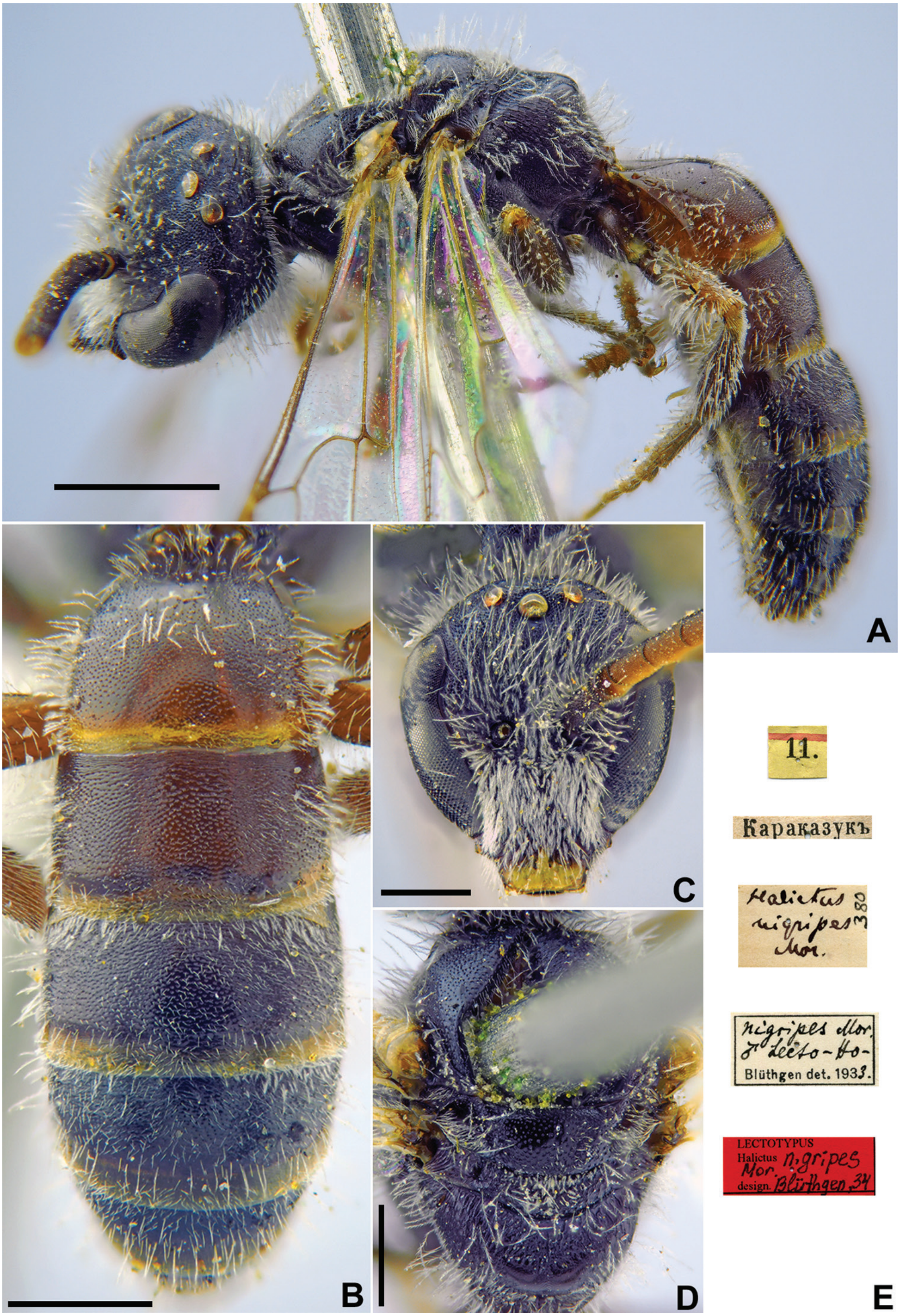

Figure 21. *Halictus nigripes* Morawitz, 1876, lectotype, male **A** habitus, lateral view **B** metasoma, dorsal view **C** head, frontal view **D** mesosoma, dorsal view **E** labels. Scale bars: 1.0 mm (**A**), 0.5 mm (**B–D**).

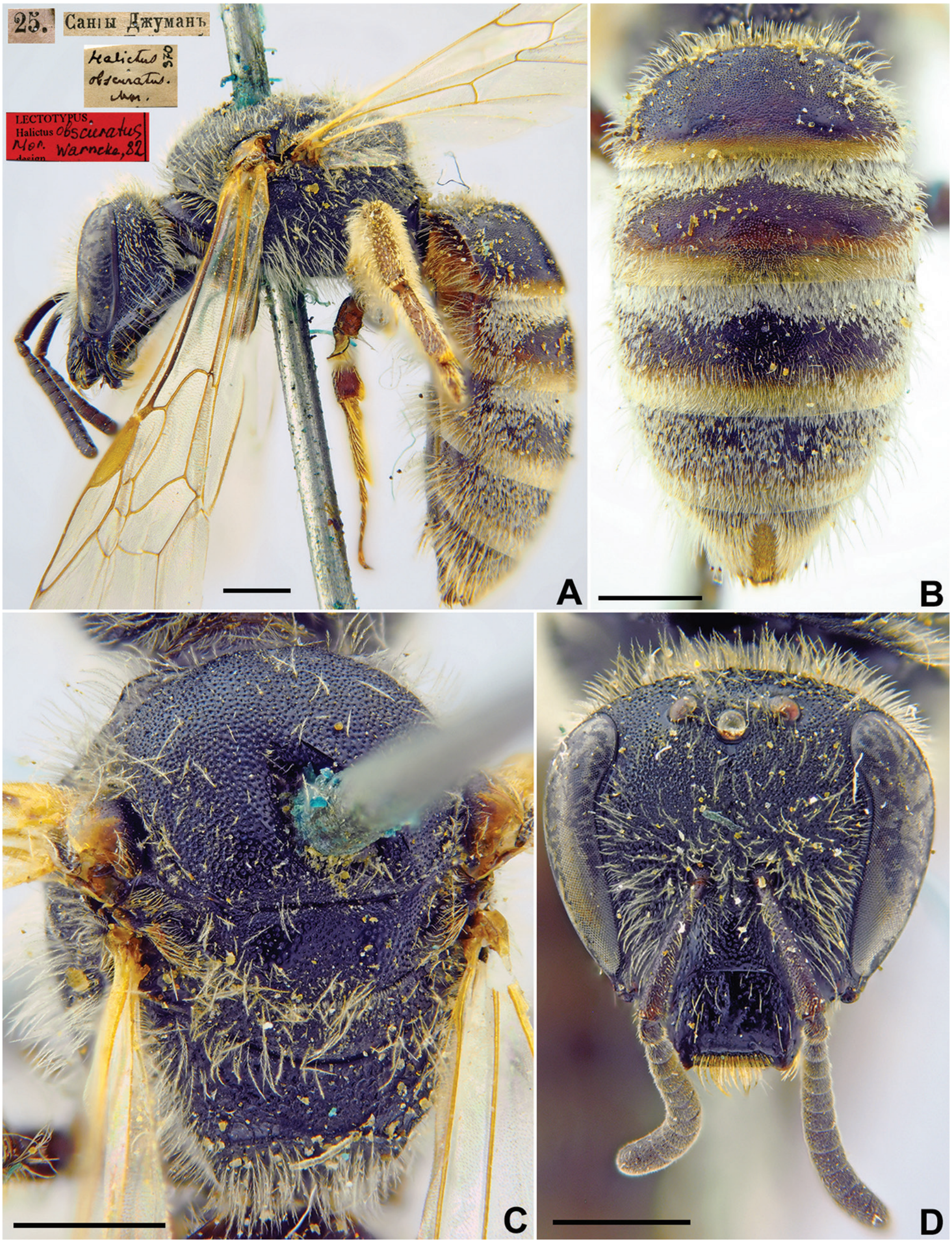

Figure 22. *Halictus obscuratus* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** metasoma, dorsal view **C** mesosoma, dorsal view **D** head, frontal view **E**. Scale bars: 1.0 mm.

Type locality. Sangy-dzhuman Pass, 30 km SSE Samarkand [Uzbekistan].

Published (original) locality. Uzbekistan: Samarkand, Aksay; Tajikistan: Iori Gorge, Varzaminor [=Ayni], Sangy-Dzhuman Pass.

Lectotype. ♀, designated by Warncke 1982: 116, 25.[V.1869] // Сангы Джуманъ [Uzbekistan, Sangy-dzhuman Pass, 30 km SSE Samarkand, 39°20'N, 67°19'E] // *Halictus obscuratus* Mor., [N]370 [handwritten by F. Morawitz] // Lectotypus *Halictus obscuratus* Mor., design. Warncke [19]82 <red label, labelled by Yu. Astafurova> [ZMMU].

Paralectotypes (7 ♀)**.** 1 ♀, 3.[IV.1869] // Самаркандъ [Samarkand] // [N]370; 1 ♀, 27.[II.1869] // Самаркандъ [Samarkand] // [N]370 // *obscuratus* [handwritten by F. Morawitz]; 1 ♀, [7.VI.1870] // Варзаминоръ [Varzaminor] // [N]370; 1 ♀, 16.[V.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, Aksay] // N[370]; 1 ♀, 2.[VI.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, Iori Gorge] // N[370]; [ZMMU]; 1 ♀, <golden circle> // 25.[V.1869] // Сангы Джуманъ [Sangy Dzhuman] // *obscuratus* Mor., Typ. [handwritten by F. Morawitz]; 1 ♀, Сангы Джуманъ [Sangy Dzhuman] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *obscuratus* Mor.[handwritten by F. Morawitz]; 1 ♀, Заравшан.[ская] дол.[ина] [Zeravshan River valley] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *Halictus obscuratus* F. Morawitz, ♀ [handwritten by F. Morawitz] // Paralectotypus *Halictus obscuratus* Mor., design. Warncke <identical red labels on each paralectotype specimen, labelled by Yu. Astafurova> [ZISP].

Current status. *Lasioglossum* (*Sphecodogastra*) *obscuratum* ssp. *obscuratum* (Morawitz, 1876).

Remarks. Description of male. Blüthgen 1923a: 277.

Distribution. Europe (except North), Cyprus, Azerbaijan, Russia (North Caucasus), Turkey, Syria, Jordan, Israel, Iran, Afghanistan, Central Asia, Kazakhstan (Astafurova and Proshchalykin 2017).

28. *Halictus palustris* Morawitz, 1876

Figure 23

Halictus palustris Morawitz, 1876: 217 (key), 234, ♀.

Type locality. Iskanderkul Lake (Tajikistan).

Published (original) locality. Tajikistan: "near Iskander-Kul Lake".

Lectotype. ♀, designated by Warncke 1982: 147, <golden circle> // 15.[VI.1870] // Искандеръ [Tajikistan, Iskanderkul Lake, Hissar Ridge, 39°04'N, 68°22'E] // *Halictus palustris* Mor., [N]353 [handwritten by F. Morawitz] // Lectotypus *Halictus palustris* Mor., ♀, design. Warncke [1]982 <red label>, labelled by Yu. Pesenko [ZMMU].

Paralectotype. 1 ♀, <golden circle> // 15.[VI.1870] // Искандеръ [Iskander] // *palustris* Mor., Typ. [handwritten by F. Morawitz] // Paralectotypus *H. palustris* Mor., ♀, design. Pesenko [1]981 <red label> [ZISP].

Current status. *Halictus* (*Tytthalictus*) *palustris* Morawitz, 1876.

Remarks. Description of male. Blüthgen 1936: 291.

Distribution. Kazakhstan, Uzbekistan, Tajikistan, Kyrgyzstan, China (Xinjiang) (Pesenko 1986b, Murao et al. 2017).

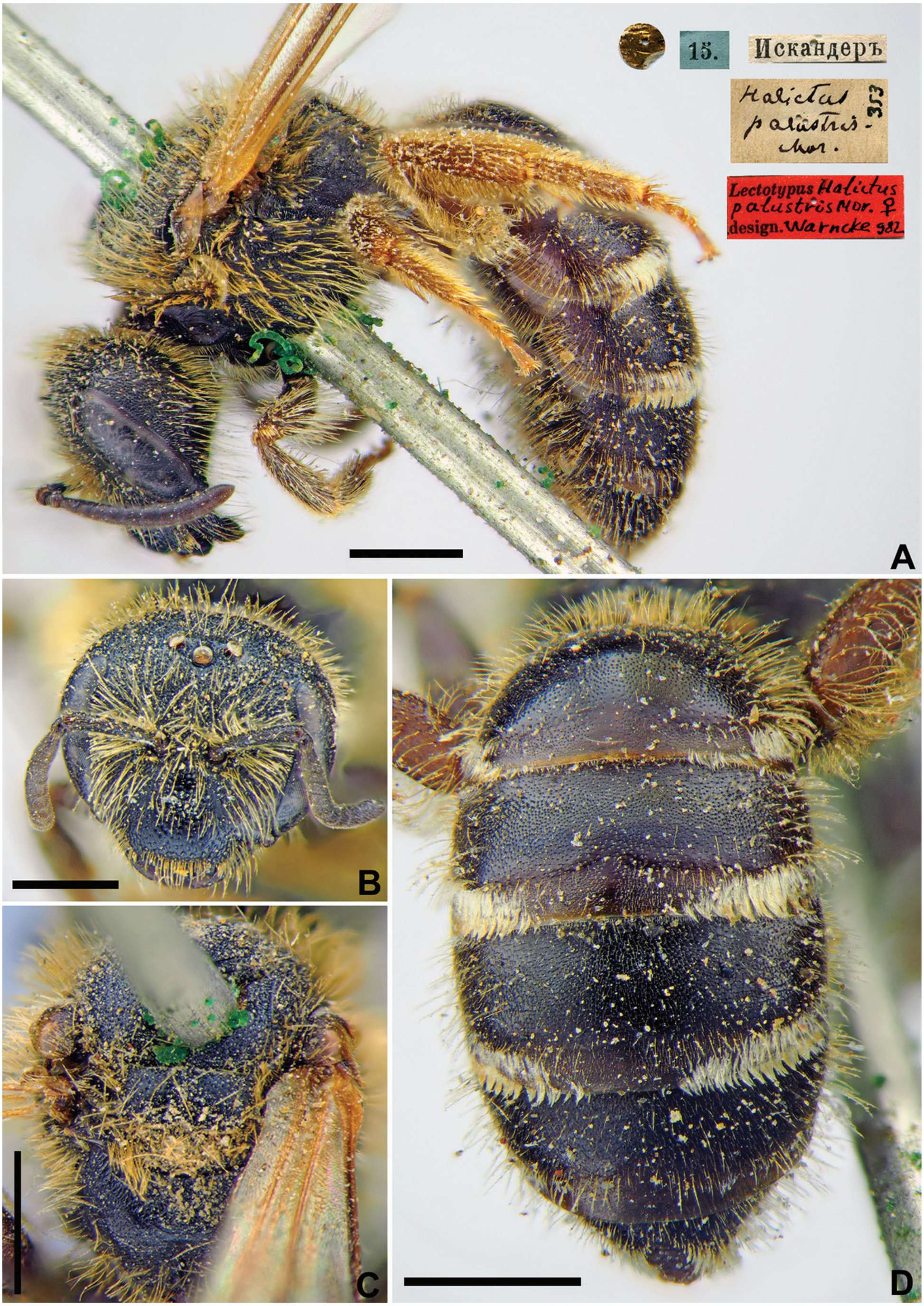

Figure 23. *Halictus palustris* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm.

29. *Halictus pectoralis* Morawitz, 1876
Figure 24

Halictus pectoralis Morawitz, 1876: 218 (key), 251, ♀.

Type locality. Gulcha (Kyrgyzstan).

Published (original) locality. Kyrgyzstan: Gulsha [Gulcha].

Holotype. ♀, 10.[VIII.1871] // Гульша [Kyrgyzstan, Gulcha, 40°19'N, 73°26'E] // *Halictus pectoralis* Mor., [N]381 [handwritten by F. Morawitz] // Holotype *H. pectoralis* Mor., 1876 <red label, labelled by Yu. Pesenko> [ZMMU].

Current status. *Lasioglossum* (*Hemihalictus*) *subaenescens* ssp. *asiaticus* (Dalla Torre, 1896), replacement name for *Halictus pectoralis* Morawitz, 1876 (nec *H. pectoralis* Smith, 1853) (subspecies status according to Ebmer 1997: 932).

Remarks. Description of male. Blüthgen 1923a: 271, as *Halictus proximus* (synonymised by Warncke 1975: 96).

The lectotype designation by Warncke (1982: 106) is unnecessary as the species was described from a single female that was directly written about by Morawitz (1876: 251).

Distribution. Egypt, Turkey, Near East, Iran, Azerbaijan, Central Asia, Mongolia (Hovd), China (Xinijang) (Ebmer 1997, Pesenko 2007).

30. *Halictus picipes* Morawitz, 1876
Figure 25

Halictus picipes Morawitz, 1876: 218 (key), 244, ♀.

Type locality. Zeravshan River valley (Tajikistan).

Published (original) locality. between Panjakent and Iori (Tajikistan).

Lectotype. ♀, designated by Pesenko 1986a: 138, 30.[V.1869] // Заравш.[анская] дол.[ина] [Tajikistan, Zeravshan River valley, between Panjakent and Iori (= Yeri)] // *Halictus picipes* Mor., [N]369 [handwritten by F. Morawitz] // Lectotype *Halictus picipes* Mor., ♀, design. Pesenko [1]985 <red label> [ZMMU].

Paralectotypes (3 ♀)**.** 1 ♀, the same label as in the lectotype [ZMMU]; 1 ♀, <golden circle>, the same label as in the lectotype; 1 ♀, Заравшан.[ская] дол.[ина] [Zeravshan River valley] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *Halictus picipes* Mor., ♀ [handwritten by F. Morawitz] // Paralectotypus *Hal. picipes* Mor., design. Pesenko [1]985 <identical red labels on each paralectotype specimen> [ZISP].

Current status. *Lasioglossum* (*Leuchalictus*) *picipes* (Morawitz, 1876).

Remarks. The lectotype designation by Warncke (1982: 111) is invalid because he labelled neither of the two females from “valle Serafshan” deposited in ZMMU.

Description of male. Blüthgen in Popov 1935: 362.

Distribution. Israel, Turkey, Iraq, Iran, Afghanistan, Turkmenistan, Uzbekistan, Tajikistan (Pesenko 1986a, Ascher and Pickering 2020).

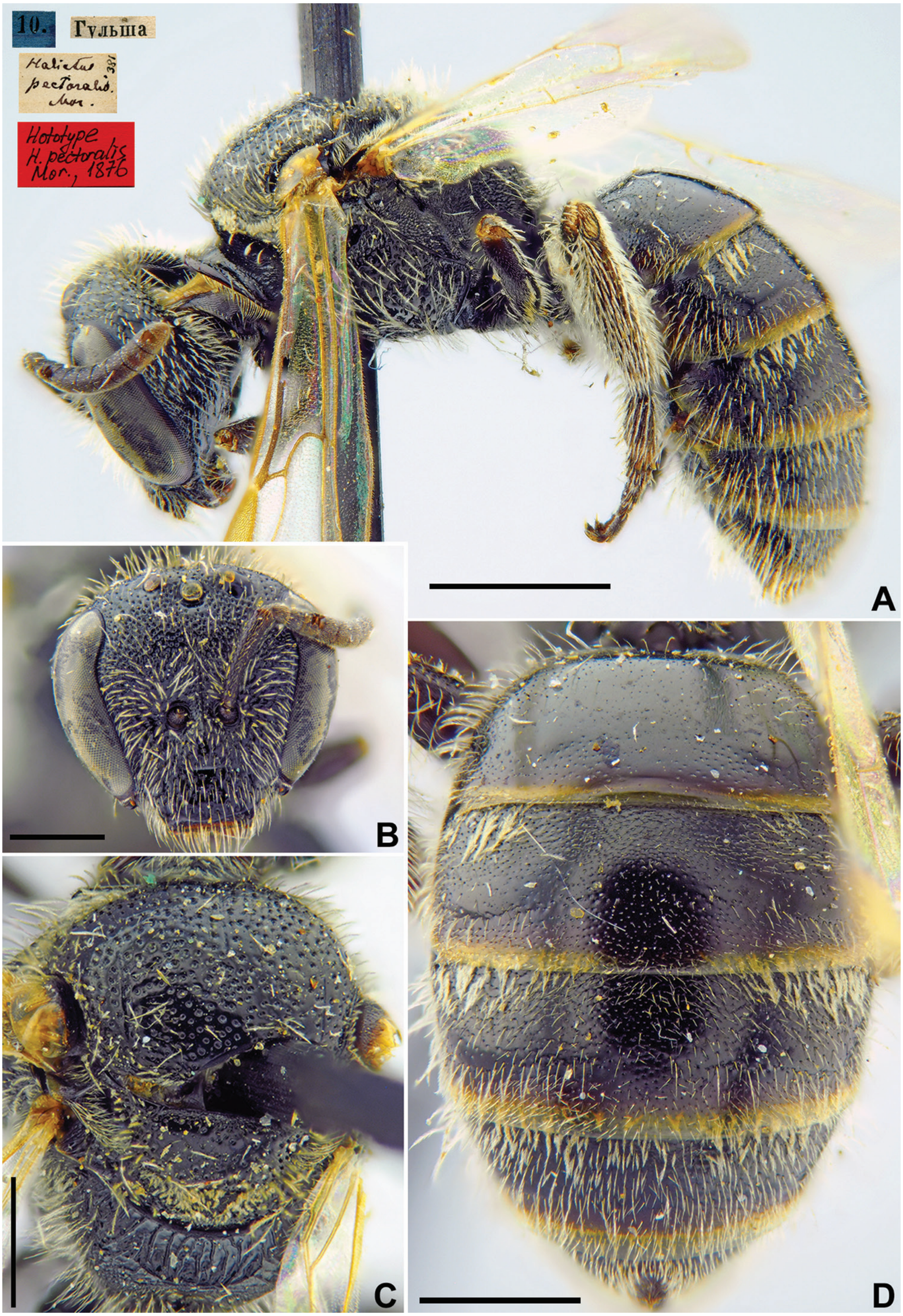

Figure 24. *Halictus pectoralis* Morawitz, 1876, holotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm (**A**), 0.5 mm (**B–D**).

Figure 25. *Halictus picipes* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm (**A, C, D**), 0.5 mm (**B**).

31. *Halictus rhynchites* Morawitz, 1876

Figure 26

Halictus rhynchites Morawitz, 1876: 217 (key to females), 220 (key to males), 222, ♀, ♂.

Type locality. Shakhimardan (Uzbekistan).

Published (original) locality. Usbekistan: Khodzha-Chiburgan gorge, near Shakhimardan Usbekistan]; Kyrgyzstan: Alay, Kichi-alay.

Lectotype (designated here). ♂, 7.[VII.1871] // Шагимарданъ [Shakhimardan in the Uzbek enclave in the territory of Kyrgyzstan, Alai Ridge, 39°58'N, 71°47'E] // [N]334 // Lectotypus *Halictus rhynchites* Mor., design. Astafurova et Proshchalykin, 2020 <red label> [ZMMU].

Paralectotypes (8 ♀, 5 ♂). 1 ♂, the same label as in a lectotype // *Halictus rhynchites* Mor., [N]334 [handwritten by F. Morawitz]; 1 ♀, 2 ♂, 26.[VI.1871] // Чибурганъ [Chiburgan] // [N]334; 1 ♀, 21.[VI.1871] // Чибурганъ [Chiburgan] // [N]334; 2 ♀, 28.[VII.1871] // Кичи-Алай [Kichi-Alay] // [N]334 [ZMMU]; 2 ♀, 1 ♂, Чибурганъ [Chiburgan] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *rhynchites* F. Mor. [handwritten by F. Morawitz]; 1 ♂, Кчи-Алай [Kchi-Alay] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *rhynchites* F. Mor. [handwritten by F. Morawitz]; 1 ♀, < golden circle> // 22.[VII.1871] // Алай [Alay] //*rhynchites* Mor., Typ. [handwritten by F. Morawitz]; 1 ♀, 22.[VII.1871] // Алай [Alay] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *Halictus rhynchites* Mor. [handwritten by F. Morawitz] // Paralectotypus *Halictus rhynchites* Mor., design. Astafurova et Proshchalykin, 2020 <identical red labels on each paralectotype specimen> [ZISP].

Current status. *Lasioglossum* (*Sphecodogastra*) *rhynchites* (Morawitz, 1876).

Remarks. The lectotype designation by Warncke (1982: 81) is invalid because he labelled neither of the two females from “Shakhimardan” deposited in ZMMU.

Distribution. Turkey, Afghanistan, southern Kazakhstan, Turkmenistan, Uzbekistan, Kyrgyzstan (Ebmer 1995, Murao et al. 2017).

32. *Halictus scutellaris* Morawitz, 1876

Figure 27

Halictus scutellaris Morawitz, 1876: 218 (key), 238, ♀.

Type locality. Bairkum (Chimkent Province, Kazakhstan).

Published (original) locality. Kazakhstan: Bayrakum [= Bairkum]; Tajikistan: Pendzhikent, Iori.

Lectotype. ♀, designated by Pesenko 1986a: 140, 4.[V.1871] // Байракумъ [Kazakhstan, Chimkent Province, Bairkum, Syr-Darya River, 42°05'N, 68°10'E] //

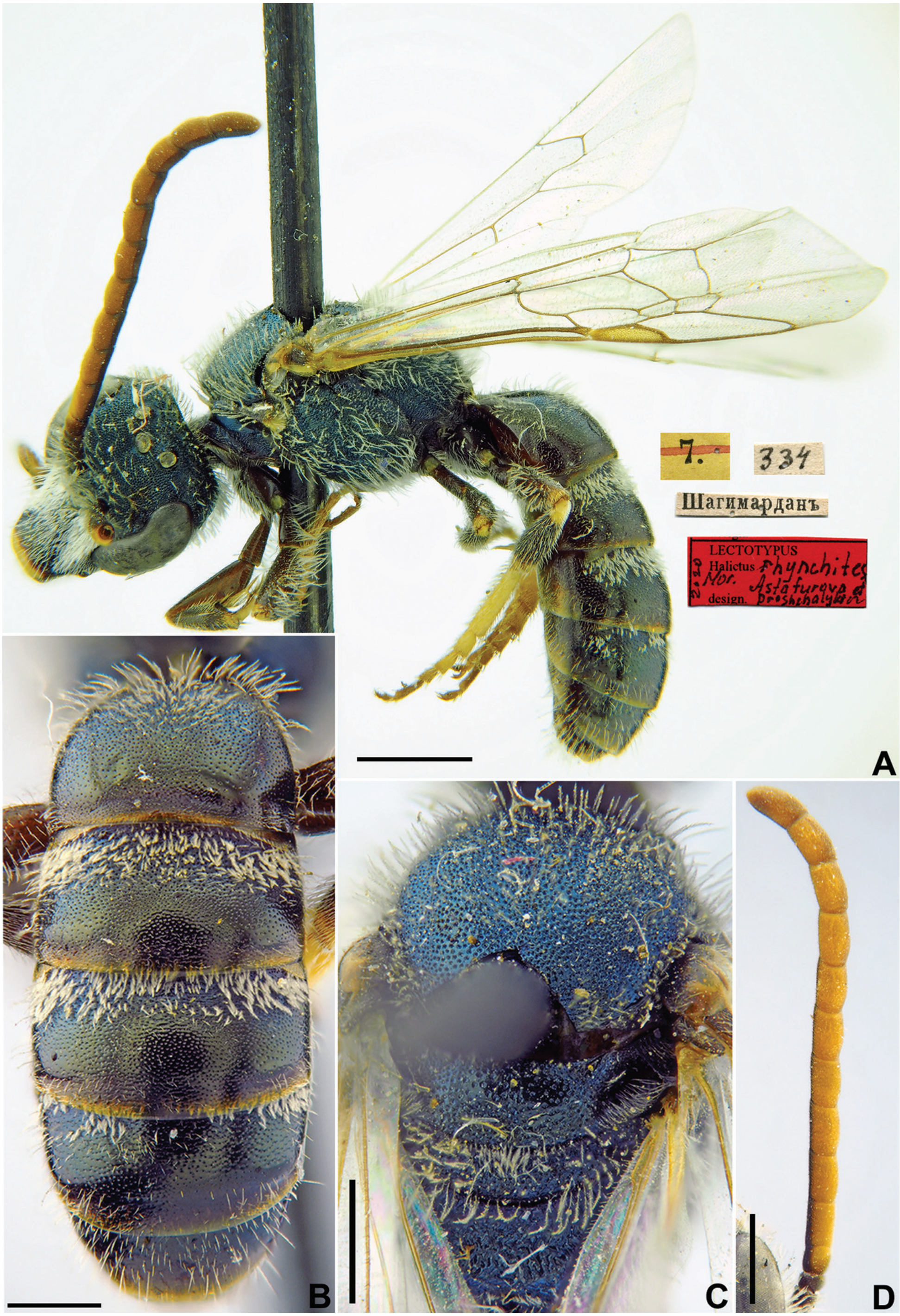

Figure 26. *Halictus rhynchites* Morawitz, 1876, lectotype, male **A** habitus, lateral view and labels **B** metasoma, dorsal view **C** mesosoma, dorsal view **D** antenna. Scale bars: 1.0 mm (**A**), 0.5 mm (**B–D**).

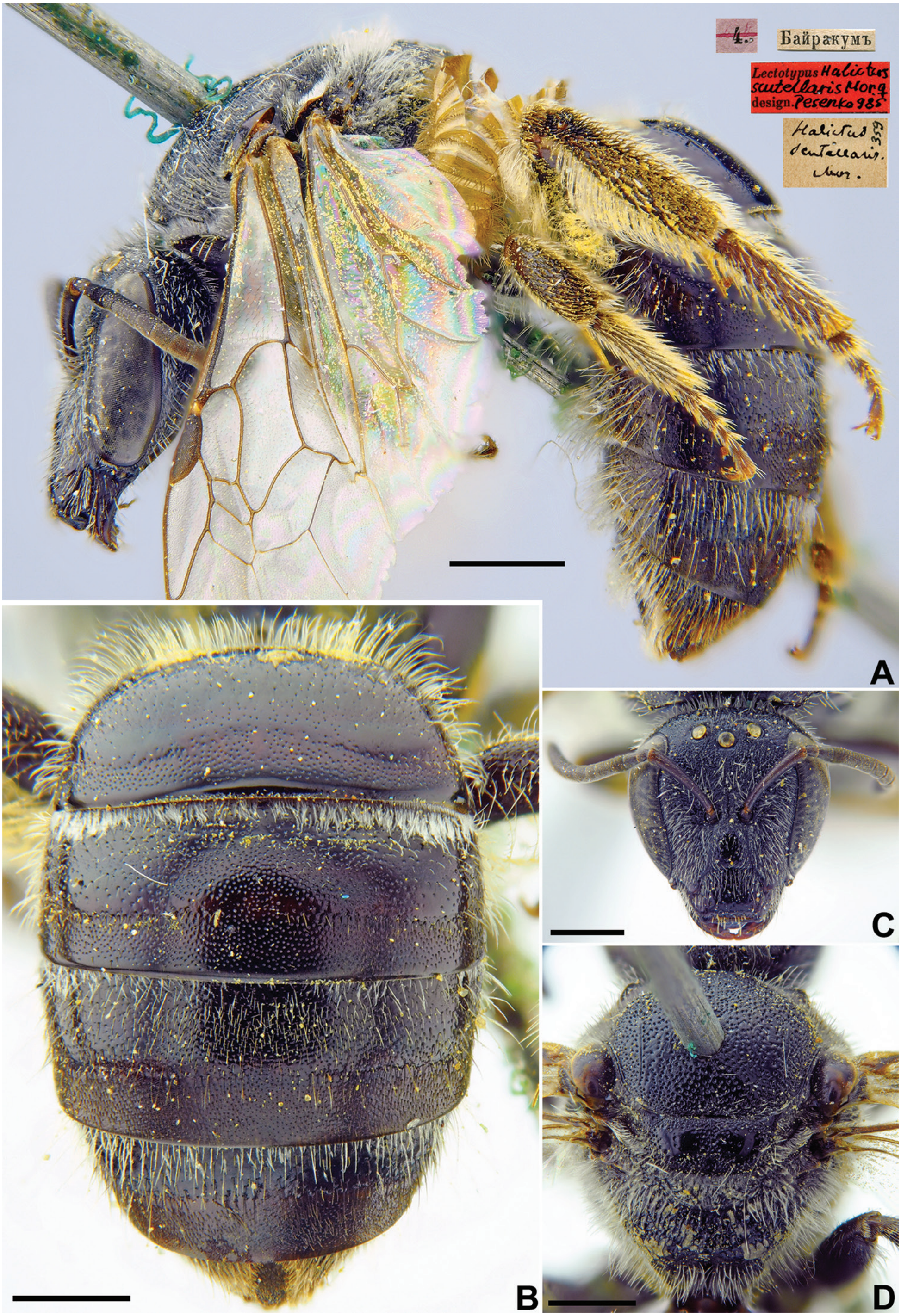

Figure 27. *Halictus scutellaris* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** metasoma, dorsal **C** view head, frontal view **D** mesosoma, dorsal view. Scale bars: 1.0 mm.

Halictus scutellaris Mor., [N]359 [handwritten by F. Morawitz] // Lectotypus *Halictus scutellaris* Mor., ♀, design. Pesenko [1]985 <red label> [ZMMU].

Paralectotypes (5 ♀). 1 ♀, the same label as in the lectotype; 1 ♀, 30.[V.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley, Iori] // N[359] [ZMMU]; 1 ♀, Байракумъ [Bayrakum] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *scutellaris* F. Mor., ♀ [handwritten by F. Morawitz]; 2 ♀, 4.[V.1871] // Байракумъ [Bayrakum] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // Paralectotypus *Hal. scutellaris* Mor., design. Pesenko [1]985 <identical red labels on each paralectotype specimen> [ZISP].

Current status. *Lasioglossum* (*Leuchalictus*) *scutellare* (Morawitz, 1876).

Remarks. Description of male. Blüthgen 1929: 53, as *Halictus scutellaris*.

The lectotype designation by Warncke (1982: 111) is invalid because he labelled neither of the two females from "Bayrakum" deposited in ZMMU.

Distribution. Southern Kazakhstan, Turkmenistan, Tajikistan, Kyrgyzstan, China (Xinnjiang) (Pesenko 1986a, Murao et al. 2017).

33. *Halictus sogdianus* Morawitz, 1876

Figures 28

Halictus sogdianus Morawitz, 1876: 216 (key), 227, ♀.

Type locality. Samarkand (Uzbekistan).

Published (original) locality. Uzbekistan: Samarkand, Dshyuzak [=Jizzakh], Iskander [River]; Kyrgyzstan: Osh.

Lectotype. ♀, designated by Blüthgen 1934a: 303, 7.[VII.1870] // Самаркандъ [Uzbekistan, Samarkand, 39°39'N, 66°57'E] // *Halictus sogdianus* Mor., [N]342 [handwritten by F. Morawitz] // *sogdianus* Mor., ♀, Lecto-Holotype, Blüthgen det. 1931 // Lecto-Type <red label> // Lectotypus *Halictus sogdianus* Mor., design. Blüthgen 1934 <red label> [ZMMU].

Paralectotypes (5 ♀)**.** 1 ♀, 21.[VI.1870] // Искандеръ [Iskander] // [N]342; 1 ♀, 2.[VIII. 1871] // Ошъ [Osh] // [N]342; 2 ♀, 4.[VII.1869] // Самаркандъ [Samarkand] // [N]342; 1 ♀, 18.[VII.1870] // Джюзакъ [Dzhyuzak] // [N]342 // Paralectotype *Halictus sogdianus* Mor. design. Blüthgen <identical red labels on each paralectotype specimen, labelled by Yu. Astafurova> [ZMMU].

Current status. *Halictus* (*Vestitohalictus*) *pulvereus* Morawitz, 1874 (synonymised by Ebmer 1988b: 576).

Distribution. Russia (European part, North Caucasus, Crimea), Cyprus, Turkey, Iran, Afghanistan, Central Asia, Mongolia, north-western China (Astafurova and Proshchalykin 2017).

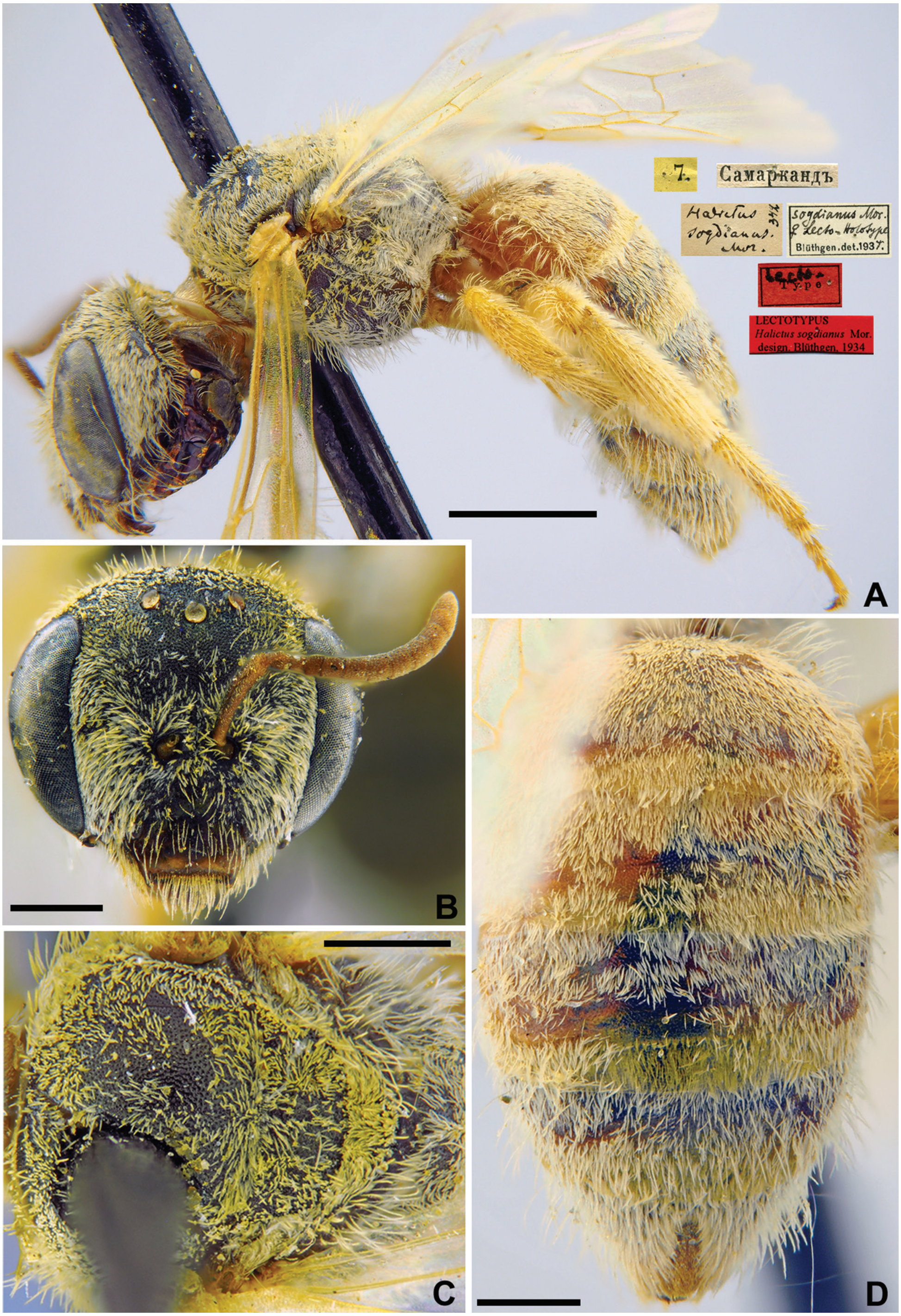

Figure 28. *Halictus sogdianus* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** metasoma, dorsal view **D** mesosoma, dorsal view. Scale bars: 1.0 mm (**A**), 0.5 mm (**B–D**).

34. *Halictus trifasciatus* Morawitz, 1876

Figure 29

Halictus trifasciatus Morawitz, 1876: 218 (key), 240, ♀.

Type locality. Bairkum (Chimkent Province, Kazakhstan).

Published (original) locality. Kazakhstan: Bayrakum.

Lectotype. ♀, designated by Warncke 1982: 90, <golden circle> // 4.[V.1871] // Байракумъ [Kazakhstan, Chimkent Province, Bairkum, Syr-Darya River, 42°05'N, 68°10'E] // *Halictus trifasciatus* Mor., [N]362 [handwritten by F. Morawitz] // Lectotypus *Halictus trifasciatus* Mor., design. Warncke [19]82 <red label, labelled by Yu. Pesenko> [ZMMU].

Current status. *Lasioglossum* (*Lasioglossum*) *lebedevi* Ebmer, 1972, replacement name for *Halictus trifasciatus* Morawitz, 1876 (nec *Hylaeus trifasciatus* Schenck, 1853).

Remarks. Male unknown.

Distribution. Southern Kazakhstan (Morawitz 1876, Mutao et al. 2017). The record from Azerbaijan (Aliyev et al. 2007) is doubtful and needs checking.

35. *Halictus varipes* Morawitz, 1876

Figure 30

Halictus varipes Morawitz, 1876: 217 (key to females), 220 (key to males), 223, ♀, ♂.

Type locality. Jizzakh (Uzbekistan).

Published (original) locality. Uzbekistan: Katty-Kurgan [= Kattakurgan], Dzhyuzak [= Jizzakh], Karatyube [= Karatepa near Samarkand], Urgut, Sangy-Dzhuman; Kyrgyzstan: near Osh.

Lectotype. ♀, designated by Blüthgen 1955: 17, 19.[VII.1870] // Джюзакъ [Uzbekistan, Dzhyuzak (= Jizzakh), 40°07'N, 67°51'E] // [N]337 // *Halictus varipes* Mor., ♀, Lecto-Holotype, P. Blüthgen det. // Typus <red label> // Lectotypus *Halictus varipes* Mor., 1876, design. Blüthgen, 1955 <red label> [ZMMU].

Paralectotypes (1 ♀, 2 ♂)**.** 1 ♂, the same labels as in the lectotype // *Halictus varipes* Mor. ♂, lecto-Paratype, Blüthgen det.; 1 ♂, the same label, but 14.[VII.1870] // *Halictus varipes* Mor. ♂, lecto-Holotype, Blüthgen det.; 1 ♀, 20. [VI.1869] // Катты-Курганъ [Katty-Kurgan] // *Halictus varipes* Mor. ♀, lecto-Paratype, Blüthgen det. // Paralectotype *Halictus varipes* Mor., design. Blüthgen 1955 <identical red labels on each paralectotype specimen, labelled by Yu. Astafurova> [ZMMU].

Current status. *Halictus* (*Seladonia*) *lucidipennis* Smith, 1853 (synonymised by Sakagami and Ebmer 1987: 326).

Distribution. Southern Palaearctic and Oriental Regions. North Africa, Israel, Arabian Peninsula, Turkey, Central Asia, Iraq, Iran, Afghanistan, Pakistan, Mongolia, north-western China, India, Nepal, Myanma,Thailand, Sri Lanka (Pesenko 2006a).

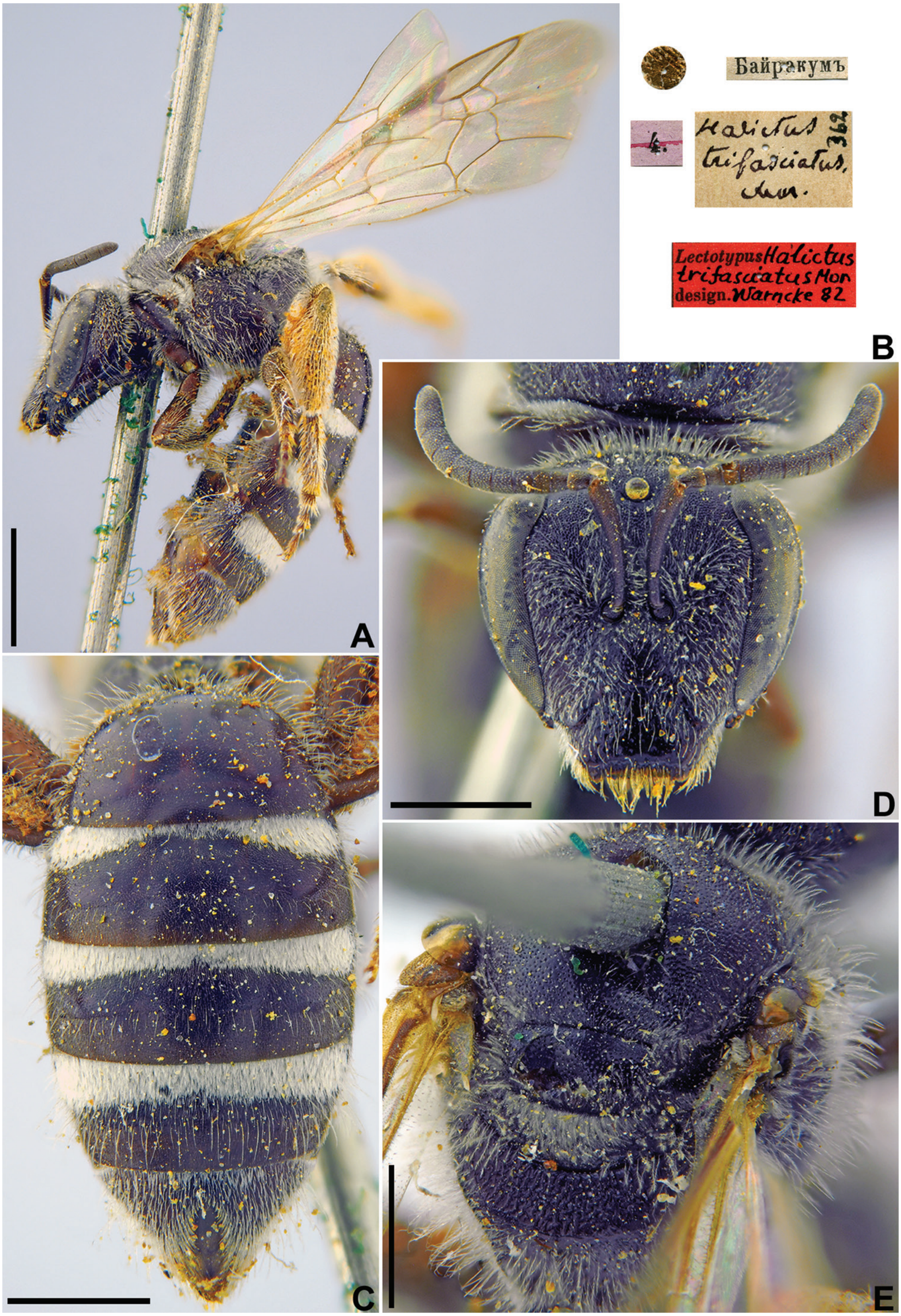

Figure 29. *Halictus trifasciatus* Morawitz, 1876, lectotype, female **A** habitus, lateral view **B** labels **C** metasoma, dorsal view **D** head, frontal view **E** mesosoma, dorsal view. Scale bars: 2.0 mm (**A**), 1.0 mm (**C–E**).

Figure 30. *Halictus varipes* Morawitz, 1876, lectotype, female **A** head, frontal view **B** habitus, lateral view and labels **C** metasoma, dorsal view **D** mesosoma, dorsal view. Scale bars: 1.0 mm (**B**), 0.5 mm (**A, C, D**).

36. *Halictus vulgaris* Morawitz, 1876

Figure 31

Halictus vulgaris Morawitz, 1876: 218 (key), 250, ♀.

Type locality. Samarkand (Uzbekistan).

Published (original) locality. Uzbekistan: Tashkent, Samarkand, Katty-Kurgan [Kattakurgan].

Lectotype (designated here). ♀, 3.[III.1869] [Uzbekistan, Samarkand, 39°39'N, 66°57'E// *Hylaeus* [sic!] *vulgaris* Mor., [N]379 [handwritten by F. Morawitz] // Lectotypus *Halictus vulgaris* Mor., design. Astafurova et Proshchalykin, 2020 <red label> [ZMMU].

Paralectotypes (257 ♀)**.** 26 ♀, 4., 20., 23., 30.[III.1869], 3., 11., 19.[IV.1869] // Самаркндъ [Samarkand]; 5 ♀, 28.[IV.1869] // Каттыкурганъ [Kattykurgan]; 222♀, 10., 11., 24., 26., 27., 28., [II.1871], 23., 24. [III.1871], 1., 2., 3., 5., 8., 10., 11.[IV.1871] // Ташкентъ [Tashkent] [ZMMU]; 1 ♀, 3.[IV.1871] // Ташкентъ [Tashkent] // к. Ф. Моравица // *Halictus vulgaris* Mor. [handwritten by F. Morawitz]; 1 ♀, 5.[IV.1871] // Ташкентъ [Tashkent] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz]; 2 ♀, 8.[IV.1871] // Ташкентъ [Tashkent] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz]; 1 ♀, 1.[IV.1871] // Ташкентъ [Tashkent] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // Paralectotypus, *Halictus vulgaris* Mor., design. Astafurova et Proshchalykin <identical red labels on each paralectotype specimen> [ZISP].

Current status. *Lasioglossum* (*Evylaeus*) *marginatum* (Brullé, 1832) (synonymised by Blüthgen 1926: 391).

Distribution. Europe (except North), North Africa, Caucasus, Russia (East of European part, North Caucasus), Turkey, Syria, Jordan, Israel, Iraq, Iran, Afghanistan, Pakistan, Central Asia, Kazakhstan, north India, Nepal (Astafurova and Proshchalykin 2017).

Remarks. The lectotype designation by Warncke (1982: 116) is invalid because he labelled none of the 222 females from Tashkent deposited in ZMMU.

Genus *Sphecodes* Latreille, 1804

37. *Sphecodes nigripennis* Morawitz, 1876

Figure 32

Sphecodes nigripennis Morawitz, 1876: 257, ♀.

Type locality. Shardara District of Turkistan Province (Kazakhstan).

Published (original) locality. Kazakhstan: coasts of Kosaral Lake; Uzbekistan: Khodzhaduk [= Khozyay-Dun].

Lectotype. ♀, designation by Warncke 1992: 30, 24.IV.1871 [the original blue data label was damaged] // Косаралъ [Kazakhstan, “Kosaral Lake”, Shardara (= Chardara) District of Turkistan (= South-Kazakhstan) Province, ≈ 41°10'N, 68°06'E] // *Sphecodes nigripennis* Mor. [handwritten by F. Morawitz] // Lectotypus, Warncke 1975 <red label> [ZMMU].

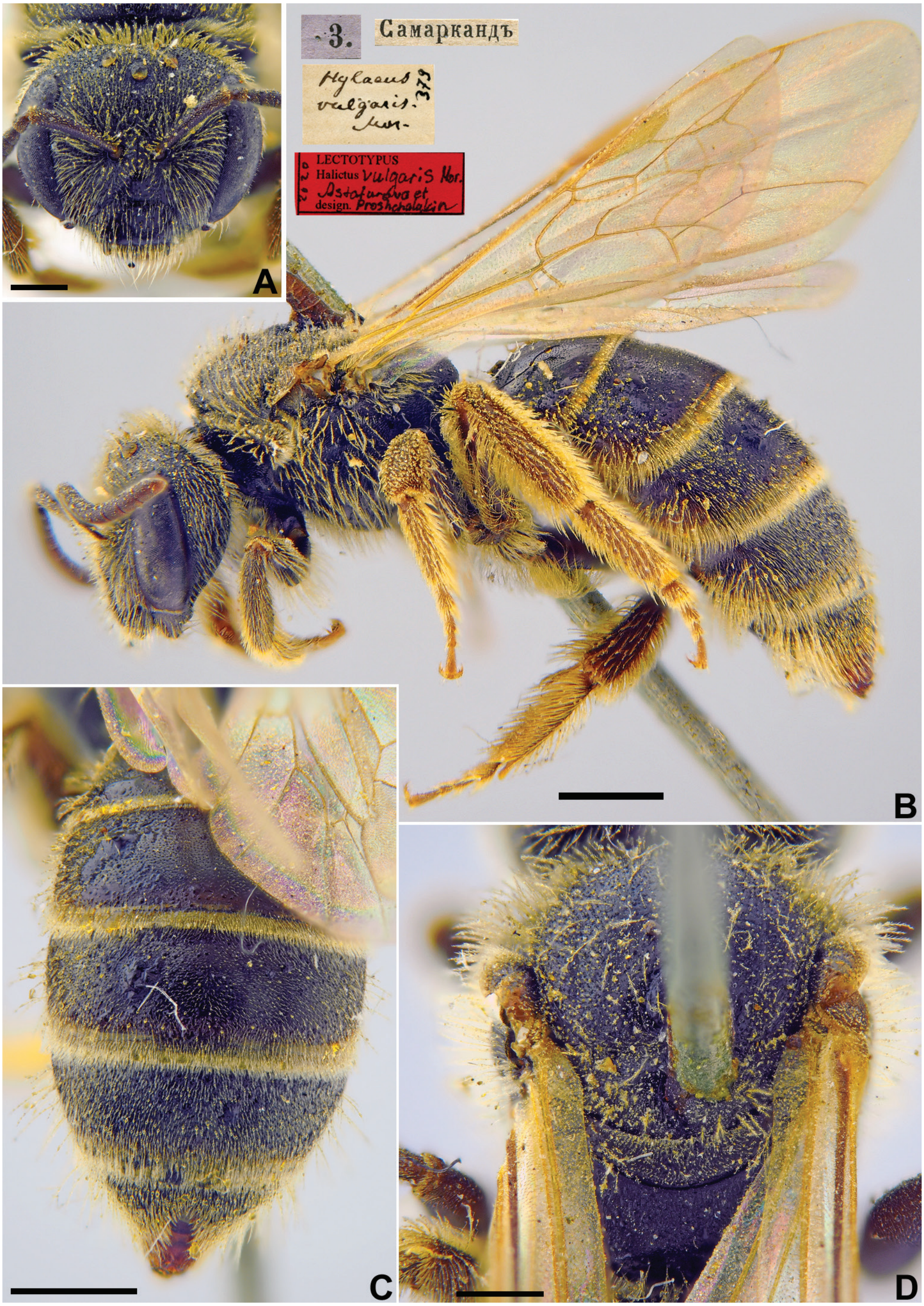

Figure 31. *Halictus vulgaris* Morawitz, 1876, lectotype, female **A** head, frontal view **B** habitus, lateral view and labels **C** metasoma, dorsal view **D** mesosoma, dorsal view. Scale bars: 1.0 mm (**B, C**), 0.5 mm (**A, D**).

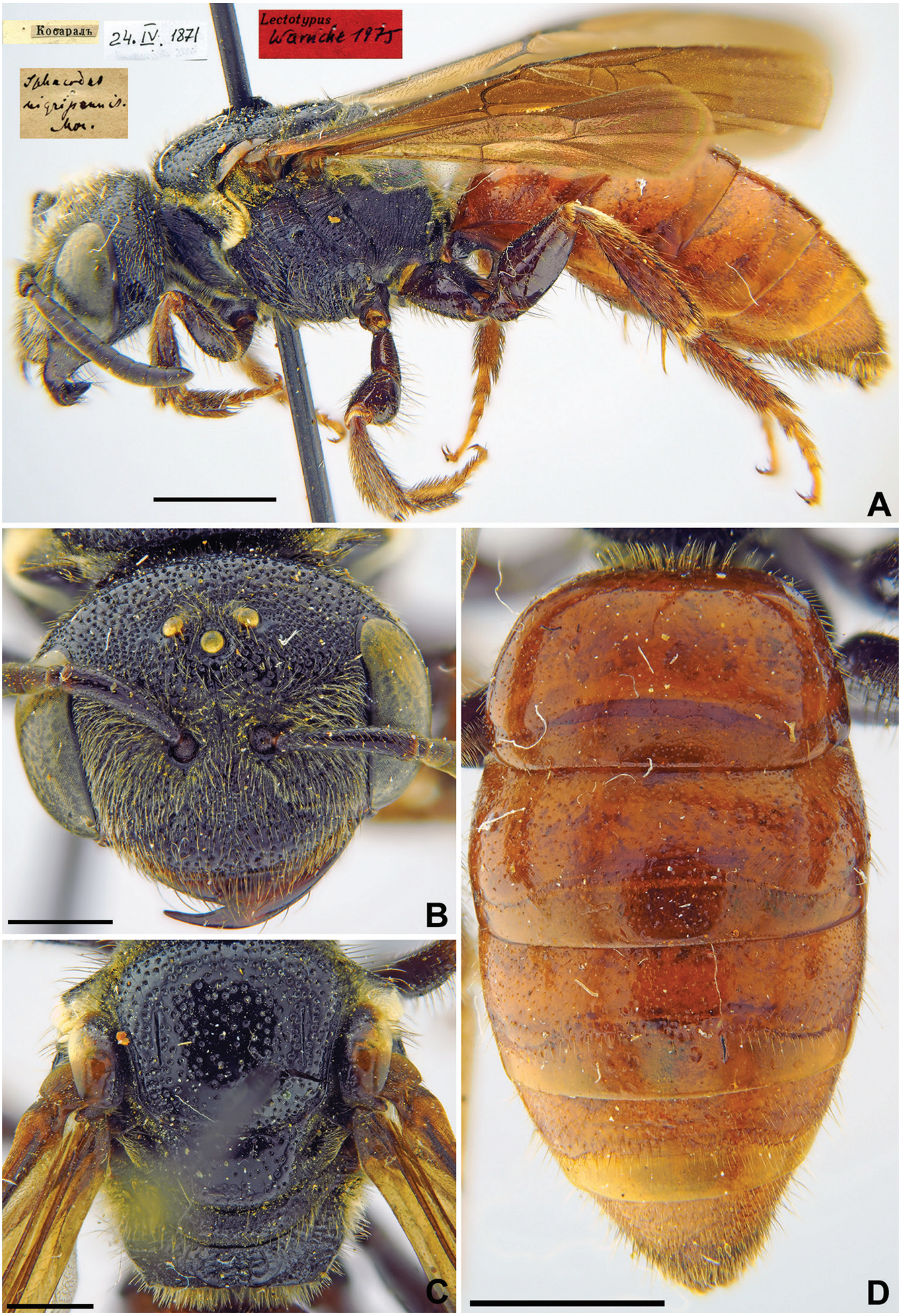

Figure 32. *Sphecodes nigripennis* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 2.0 mm (**A, D**), 1.0 mm (**B, C**).

Paralectotype. 1 ♀, 21.[V.1869] // Заравшан.[ская] дол.[ина] [Zeravshan River valley] // Paralectotype *Sphecodes nigripennis* Mor., design. Warncke <red label, labelled by Yu. Astafurova> [ZMMU].

Current status. *Sphecodes gibbus* (Linnaeus 1758) (synonymised by Blüthgen 1923b: 510).

Distribution. North Africa, Europe (north to 63°), Israel, Jordan, Russia (east to Yakutia), Turkey, Iran, Pakistan, Central Asia, Kazakhstan, Mongolia, NW China, India (Warncke 1992, Bogusch and Straka 2012, Astafurova et al. 2019).

38. *Sphecodes pectoralis* Morawitz, 1876

Figure 33

Sphecodes pectoralis Morawitz, 1876: 256, ♀.

Type locality. Shardara District of Turkistan Province (Kazakhstan).

Published (original) locality. Kazakhstan: coasts of Kosaral Lake; Kyzylkum [desert] near Chakany Well.

Lectotype. ♀, designation by Warncke 1992: 24, 24.[IV.1871] // Косаралъ [Kazakhstan, "Kosaral Lake", Shardara (= Chardara) District of Turkistan (= South-Kazakhstan) Province], ≈ 41°10'N, 68°06'E// *Sphecodes pectoralis* Mor. [handwritten by F. Morawitz] // Lectotypus, Warncke 1975 <red label> [ZMMU].

Paralectotype. 1 ♀, 28.[VI.1871] // Кызылъкумъ [Kyzylkum] // Paralectotype *Sphecodes pectoralis* Mor., design. Warncke <red label, labelled by Yu. Astafurova> [ZMMU].

Current status. *Sphecodes pectoralis* Morawitz, 1876.

Remarks. Description of male. Meyer 1919: 126, as *Sphecodes cristatus* sensu Meyer (non Hagens 1882) (see Blüthgen 1924: 475).

Distribution. South Kazakhstan, Central Asia, China (Gansu, Xinjiang) (Astafurova et al. 2018a, b, 2020).

39. *Sphecodes rufithorax* Morawitz, 1876

Figure 34

Sphecodes rufithorax Morawitz, 1876: 255, ♀, ♂.

Type locality. Bairkum (Chimkent Province, Kazakhstan).

Published (original) locality. Kazakhstan: Bayrakum [Bairkum]; steppe between Syr-Darya River and Tashkent.

Lectotype. ♀, designated by Warncke 1992: 24, 17. [V.1871] // Байракумъ [Kazakhstan, Chimkent Province, Bairkum, Syr-Darya River, 42°05'N, 68°10'E] // *Sphe-*

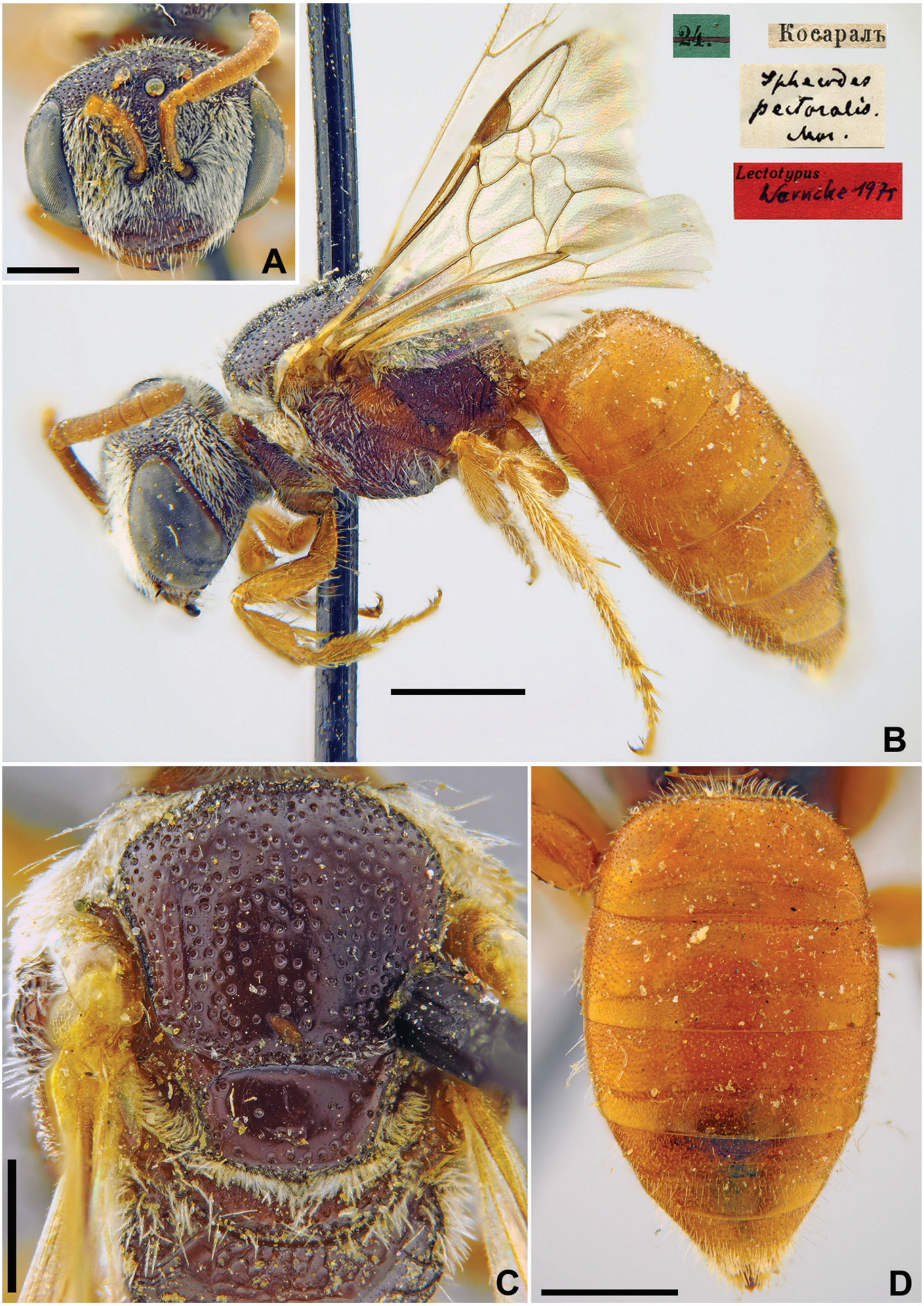

Figure 33. *Sphecodes pectoralis* Morawitz, 1876, lectotype, female **A** head, frontal view **B** habitus, lateral view and labels **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 2.0 mm (**B, D**), 1.0 mm (**A, C**).

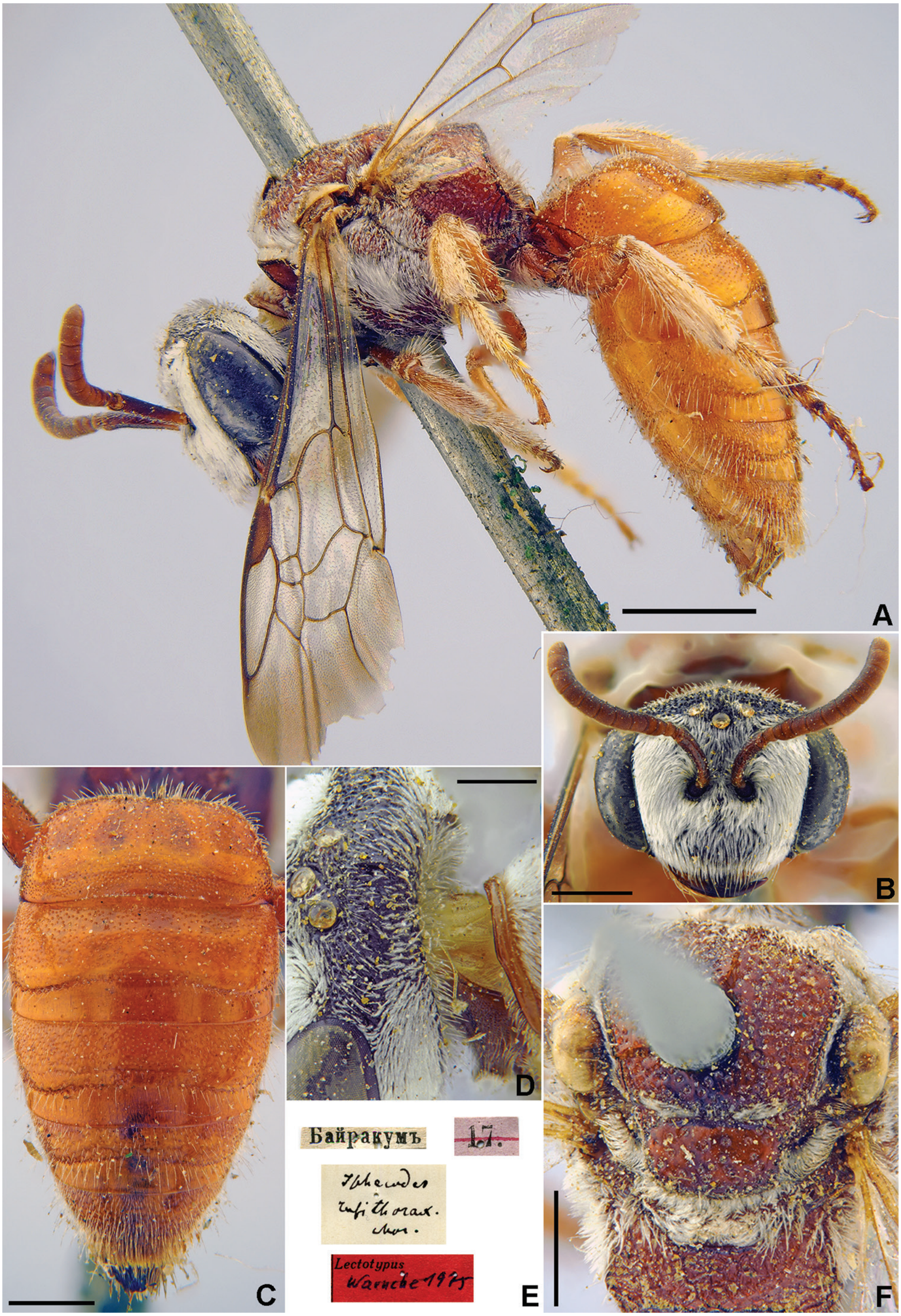

Figure 34. *Sphecodes rufithorax* Morawitz, 1876, lectotype, female **A** habitus, lateral view **B** head, frontal view **C** metasoma, dorsal view **D** vertex, dorso-lateral view **E** labels **F** mesosoma, dorsal view. Scale bars: 1.0 mm (**A–C, F**), 0.5 mm (**D**).

codes rufithorax F. Moraw., ♀ [handwritten by F. Morawitz] // Lectotypus Warncke, 1975 <red label> [ZMMU].

Paralectotypes (2 ♀, 1 ♂)**.** 1 ♀, Байракумъ [Bairkum] // кол.[лекция] Ф. Моравица [Collection of F. Morawitz] // *Sphecodes rufithorax* F. Moraw., ♀ [handwritten by F. Morawitz] // F. Morawitz det., Typ.; 1 ♀, 20.[V.1871] // Степь м.[ежду] С.[ыр] д.[арьей] и Т.[ашкентом] [Steppe between Syrdarya River and Tashkent] // *Sphecodes rufithorax* Mor., ♂ [handwritten by F. Morawitz] // Paralectotypus *Sphec. rufithorax* Mor., design. Warncke, [19]92 <red label, labelled by Yu. Astafurova> [ZMMU]; 1 ♀, the same labels [ZISP].

Current status. *Sphecodes olivieri* Lepeletier, 1825 (synonymised by Warncke 1992: 24).

Distribution. North Africa, the Arabian Peninsula, Israel, Jordan, South Europe, Russia (south of European part), Turkey, Caucasus, Iran, Pakistan, Central Asia, Kazakhstan, NW China (Astafurova et al. 2019).

Subfamily Nomiinae

Genus *Nomia* Latreille, 1804

40. *Nomia edentata* Morawitz, 1876

Figure 35

Nomia edentata Morawitz, 1876: 259, ♀, ♂.

Type locality. Jizzakh (Uzbekistan).

Published (original) locality. Uzbekistan: Samarkand, Dzhyuzak.

Lectotype. ♀, designated by Warncke 1976: 104, 20.[VII.1871] // Джюзакъ [Uzbekistan, Dzhyuzak (= Jizzakh), 40°07'N, 67°51'E] //*Nomia edentata* Mor. [handwritten by F. Morawitz] // Lectotypus, Warncke 1975 <red label> [ZMMU].

Paralectotypes (2 ♂)**.** 1 ♂, the same labels as in the lectotype // Paralectotypus, *Nomia edentata* Mor., design. Warncke <red label> [ZISP]; 1 ♂, 8.[VII.1869] // Самаркандъ [Samarkand] // Paralectotypus *Nomia edentata* Mor., design. Warncke <red label> [ZMMU].

Current status. *Pseudapis edentata* (Morawitz, 1876).

Distribution. North Africa, Saudi Arabia, Turkey, Azerbaijan, Kazakhstan, Central Asia, Iraq, Iran, Afghanistan, Pakistan, India (Astafurova 2014).

41. *Nomia rufescens* Morawitz, 1876

Figure 36

Nomia rufescens Morawitz, 1876: 261, ♀.

Type locality. Zeravshan River valley (Uzbekistan).

Published (original) locality. Uzbekistan: "Aykul Lake" in Zeravshan River valley.

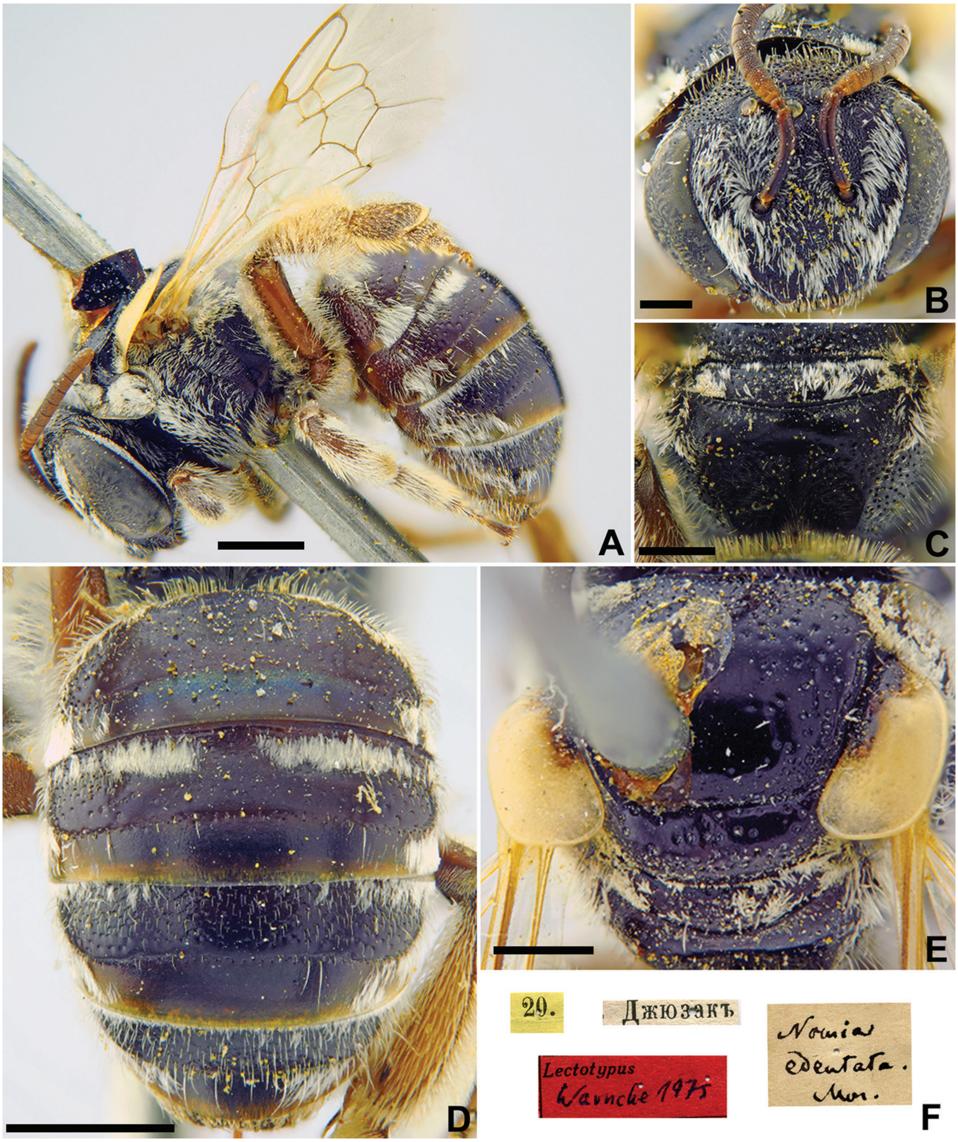

Figure 35. *Nomia edentata* Morawitz, 1876, lectotype, female **A** habitus, lateral view **B** head, frontal view **C** metapostnotum, dorsal view **D** metasoma, dorsal view **E** mesosoma, dorsal view **F** labels. Scale bars: 1.0 mm (**A, D**), 0.5 mm (**B, C, E**).

Lectotype. ♀, designated by Warncke 1976: 106, 5.[VIII.1869] // Заравш[анская]. дол.[ина] [Uzbekistan, Zeravshan River valley, Aykul Lake near Chelek, 39°56'N, 66°49'E] // *Nomia rufescens* Mor. // Lectotypus, Warncke 1975 <red label> [ZMMU].

Current status. *Pseudapis rufescens* (Morawitz, 1876).

Remarks. Description of male. Morawitz 1893: 79.

Distribution. Turkey, Central Asia, Kazakhstan (Astafurova 2014).

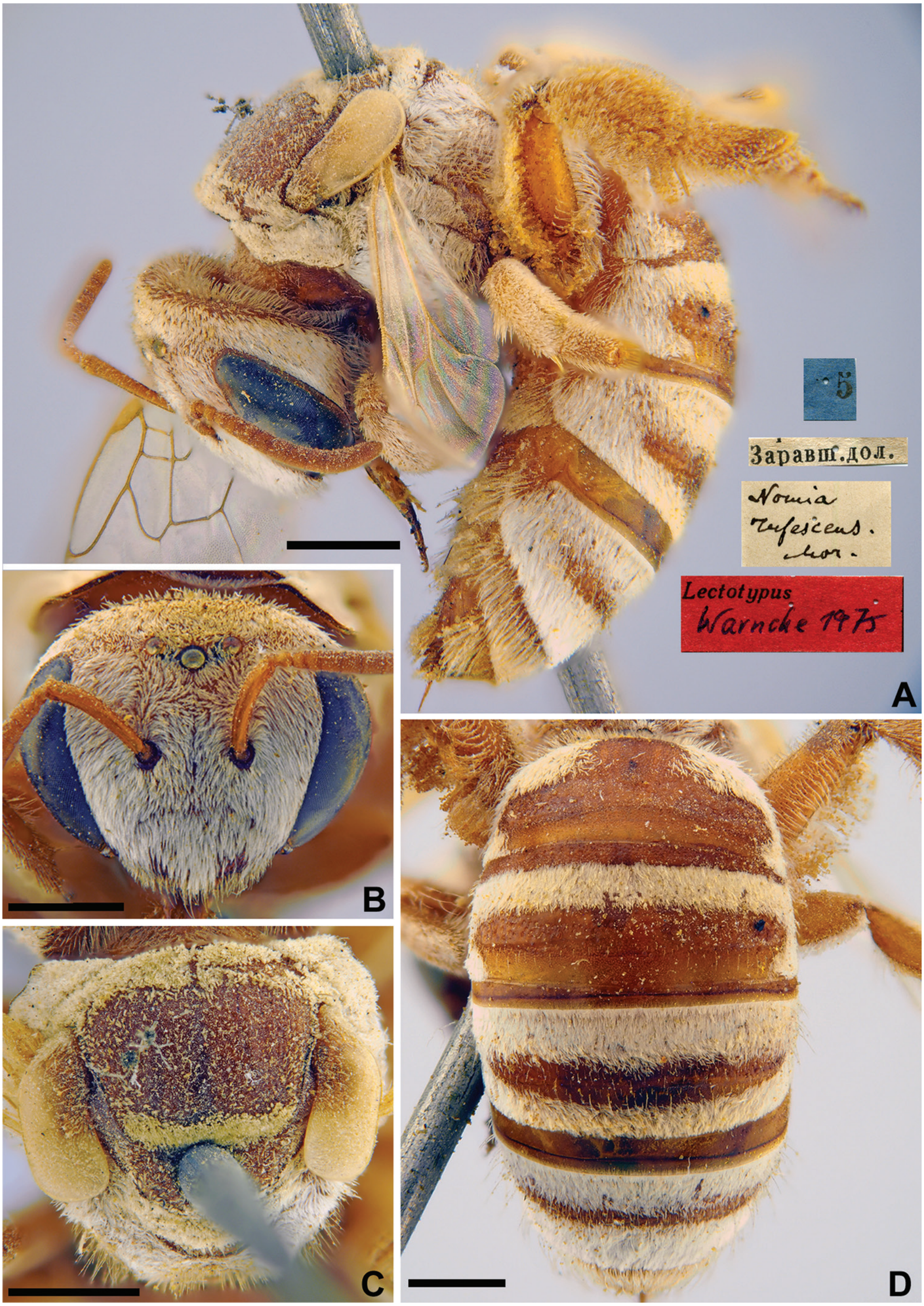

Figure 36. *Nomia rufescens* Morawitz, 1876, lectotype, female **A** habitus, lateral view and labels **B** head, frontal view **C** mesosoma, dorsal view **D** metasoma, dorsal view. Scale bars: 1.0 mm.

Subfamily Nomioidinae
Genus *Nomioides* Schenck, 1866

42. *Nomioides parviceps* Morawitz, 1876
Figure (see Astafurova and Proshchalykin 2019: 56, figs 51a–e)

Nomioides parviceps Morawitz, 1876: 215, ♂.

Type locality. Bairamali (Turkmenistan).

Published (original) locality. Uzbekistan: Samarkand.

Holotype. ♂, окр.[естности] Самарканда [Uzbekistan, Samarkand, 39°39'N, 66°57'E], 13.VI[1869], lost (also see Pesenko 1983: 168–170).

Neotype. ♂, designated by Pesenko 1983: 168, Байрам-Али Закасп.[ийская] обл.[асть] [Turkmenistan, Maryi Province, Bairamali, 37°37'N, 62°09'E], 14.VII.[1]928, В. Гуссаковский [V. Gussakovskij leg.] // *Nomioides conjungens* m., ♂, Blüthgen det. 1931 // Neotypus *Nomioides parviceps* Mor., ♂, design. Pesenko [1]980 [handwritten by Yu. Pesenko] <red label> // Zoological Institute St. Petersburg, INS_HYM_0000142 [ZISP].

Current status. *Nomioides* (*Nomioides*) *parviceps* Morawitz, 1876.

Remarks. Description of female: Blüthgen 1925b: 45, as *Nomioides conjungens* (synonymised by Blüthgen 1934c: 253).

Distribution. Asia Minor, Afghanistan, Armenia, Central Asia (Astafurova and Proshchalykin 2019).

43. *Nomioides turanica* Morawitz, 1876
Figure (see Astafurova and Proshchalykin 2019: 68, figs 62a–e).

Nomioides turanica Morawitz, 1876: 214, ♀, ♂.

Type locality. Samarkand (Uzbekistan).

Published (original) locality. Tajikistan: Murzarabat; Uzbekistan: Sokh, Samarkand.

Lectotype. ♂, designated by Pesenko 1983: 174, 5.[VII.1870] // Самаркандъ [Uzbekistan, Samarkand, 39°39'N, 66°57'E] // *turanica* Mor., Typ. [handwritten by F. Morawitz] // Lectotypus *Nom. turanica* Mor., ♂, design. Pesenko, 1976 // Zoological Institute St. Petersburg, INS_HYM_0000131 [ZISP].

Paralectotypes (5 ♂)**.** 1 ♂, 28.[VI.1871] // Сохъ [Sokh] // *Nomioides turanica* n. sp. F. Morawitz det.; 1 ♂, <gold circle> 8.[VII.1870] // Самаркандъ [Samarkand] // *Nomioides turanica* Mor. [handwritten by F. Morawitz] [ZMMU]; 3 ♂, Сохъ [Sokh] // к.[оллекция] Ф. Моравица [Collection of F. Morawitz] // *Nomioides turanica* Mor. // Paralectotypus ♂ *Nom. turanica* Mor., design. Pesenko, 1976 <identical red labels on each paralectotype specimen> [ZISP].

Current status. *Nomioides* (*Nomioides*) *turanicus* Morawitz, 1876.

Distribution. North Africa, Central Asia, Iran, Pakistan (Astafurova and Proshchalykin 2019).

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RESEARCH ARTICLE

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Stigmatopora harastii, a new species of pipefish in facultative associations with finger sponges and red algae from New South Wales, Australia (Teleostei, Syngnathidae)

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Abstract

A new species of pipefish, *Stigmatopora harastii* **sp. nov.**, is described based on the male holotype and two female paratypes, 136.3–145.5 mm SL, collected from red algae (sp.?) at 12 meters depth in Botany Bay, New South Wales (NSW), Australia. The new taxon shares morphological synapomorphies with the previously described members of *Stigmatopora*, including principle body ridges, fin placement, slender tail, and absence of a caudal fin. It is morphologically and meristically similar to *Stigmatopora nigra*, including snout length and shape, dorsal-fin origin on 6th–7th trunk ring, and lateral trunk ridge terminating on the first tail ring. *Stigmatopora harastii* **sp. nov.** is distinguished from its congeners, however, by characters of the head and first trunk ring, distinct sexual dimorphic markings on sides and venter of anterior trunk rings, and red background coloration in life. The new taxon can be further differentiated by genetic divergence in the mitochondrial COI gene (uncorrected p-distances of 9.8%, 10.1%, 10.7%, and 14.6%, from *S. argus*, *S. macropterygia*, *S. narinosa*, and *S. nigra*, respectively). The type locality is characterised by semi-exposed deep-water sandy areas interspersed with boulders, flat reefs, and an absence of seagrass beds, in which *S. harastii* has been observed living in facultative associations with a finger sponge and red algae at depths of 10–25 meters, compared to the shallow coastal and estuarine habitats preferred by the fucoid algae and seagrass-associating members of *Stigmatopora*. *Stigmatopora harastii* **sp. nov.** represents the fourth species of *Stigmatopora* recorded in temperate southern Australia.

Keywords
Botany Bay, COI, cryptobenthic, ichthyology, Jervis Bay, marine fish, morphology, South Pacific, Sydney, systematics, taxonomy

Introduction

The Syngnathidae contains over 300 species within 57 genera of predominantly small-bodied and cryptic marine fishes (Dawson 1985; Fricke et al. 2020; WoRMS Editorial Board 2020). The pipefishes assigned to *Stigmatopora* Kaup, 1853 currently comprise four species, which are restricted to southern Australia and New Zealand: *S. argus* Richardson, 1840, from New South Wales (NSW) to Western Australia, including Tasmania, and New Zealand; *S. nigra* Kaup, 1856, from Mooloolaba, Queensland to Shark Bay, Western Australia, including around Tasmania, and New Zealand; *S. macropterygia* Duméril, 1870 from New Zealand; and *S. narinosa* Browne & Smith, 2007, a South Australian endemic. The genus is distinguished from other family members by a combination of features that include fin placement, slender distally coiled prehensile tail, and absence of caudal fin. Dawson (1982) provided valuable data for differentiating the species on the basis of meristic and morphometric characters and sexual dimorphism in the ventral trunk markings, which was further discussed by Browne and Smith (2007). Members of the *Stigmatopora* form an abundant component of the ichthyofauna of shallow vegetated coastal and estuarine habitats in southern Australia and New Zealand, in which they associate with various species of fucoid algae and seagrass (Dawson 1982; Pollard 1984; Howard and Koehn 1985; Bell et al. 1992; Steffe et al. 1992; Ferrell et al. 1993; Connolly 1994; Pollard 1994; Jenkins et al. 1997; Kendrick and Hyndes 2003; Browne and Smith 2007; Browne et al. 2008; Parkinson and Booth 2016).

The present paper describes a new species of *Stigmatopora* from NSW, Australia that was first reported by underwater photographers (Oceantrek Diving Resort) in Jervis Bay in 2002, and subsequently observed in Shellharbour and Botany Bay. *Stigmatopora harastii* occurrs in semi-exposed habitats consistent for the Sydney Basin bioregion (Andrew 1999), which is markedly different from the shallow coastal and estuarine habitats typically preferred by the fucoid algae and seagrass associating members of *Stigmatopora* (Dawson 1985; Steffe et al. 1989; Browne and Smith 2007; Parkinson and Booth 2016).

Materials and methods

Type specimens (AMS I.49510-001, holotype, male; AMS I.47267, paratypes, two females) are deposited in the collections of the Australian Museum (AM).

Counts and measurements to the nearest 0.1 mm were taken from high resolution digital images of specimens using ImageJ (Rasband et al. 1997). Head and body measurements and morphometrics follow Short et al. (2018). External morphological characters were documented using a dissecting microscope and analyses of high-resolution digital images. Georeferenced locations for the type specimens of *S. harastii* use dWGS84 datum and were captured on GPS units.

DNA extraction, primers and PCR conditions, sequence alignment, and analysis of COI sequence data were performed following protocols described in Hamilton et al. (2017). A partial segment of mitochondrial cytochrome c oxidase subunit I (COI) DNA was sequenced from a 95% ethanol-fixed eye sample from a paratype collected from the type locality (AMS I.47267-001). COI sequence data was compared to the previously sequenced *Stigmatopora* species *S. argus*, *S. macropterygia*, *S. narinosa*, and *S. nigra*, respectively (available from Hamilton et al. 2017) in order to calculate genetic distances (uncorrected P distances) in MEGA v. 7.0.26 (Kumar et al. 2017).

Systematics

***Stigmatopora harastii* sp. nov.**

http://zoobank.org/CE61AAB9-3723-4B44-A025-1E8AE3486BD9

Figs 1–10

Type material. *Holotype*: AMS I.49510-001, male, 145.5 mm SL, collected from a scuba dive area locally referred to as "The Steps", Kamay Botany Bay National Park, Kurnell, Botany Bay, NSW, Australia, 34°00'07.9"S, 151°13'41.4"E, 13.5 m depth, 18 June 2020, by A. Trevor-Jones and D. Harasti.

***Paratypes*:** AMS I.47267, two females, 130.7 mm and 135.2 mm SL, collected from a scuba dive area known as "The Steps", Kamay Botany Bay National Park, Kurnell, Botany Bay, NSW, Australia, 34°00'07.9"S, 151°13'41.4"E, 12 m depth, 9 June 2017, by D. Harasti, R. Rodrigues, and A. Trevor-Jones.

Comparative material. *Stigmatopora nigra* AMS I.42611-009, Botany Bay, NSW, Australia, 03 Feb 2003, K. Parkinson; *Stigmatopra narinosa*, SAMA F10190, holotype, 150 mm SL, South Australia, Edithburg Pool, 35°05'S, 137°45'E, 31 Dec 2003. Published data was obtained for *S. argus*, *S. macropterygia*, *S. narinosa*, and *S. nigra* from Dawson (1982, 1985).

Diagnosis. *Stigmatopora harastii* differs from its congeners by the following combination of morphological characters: median ridge, distinct, low, present on dorsum of head and first trunk ring starting from the posterior third of the frontal, over the supraoccipital, to the anterior and posterior nuchal plates; opercular ridge prominent, complete, not angled dorsad; lateromedial ridge, distinct, low, present between opercle and pectoral fin base; dorsal-fin origin on 6th–7th trunk rings, subdorsal rings 19–20 (12 trunk rings + 7 or 8 tail rings); lateral trunk ridge ends on first tail ring. Colouration: red background colour; dorsum of snout with large, irregular pale white spots;

Table 1. Selected counts and morphometric measurements for *Stigmatopora harastii*. Abbreviations: SnD (snout depth), SnL (snout length), HL (head length), TrL (trunk length), TaL (tail length), SL (standard length).

Voucher	AMS I. 49510-001	AMS I.47267-001	AMS I.47267-002
Type	holotype	paratype	paratype
Gender	male	female	female
Trunk rings	18	18	18
Tail rings	68	70	71
Subdorsal rings	19	20	20
Dorsal-fin origin	7th trunk ring	6th trunk ring	7th trunk ring
Dorsal-fin rays	45	43	43
Pectoral-fin rays	18	13	13
SL (mm)	145.5	136.3	138.2
SnD/SnL	7.6	7.4	7.2
SnL/HL	63.2	65.5	64.5
SnL/TrL	36.1	39.3	35.8
HL/TrL	57.1	60.0	55.6
HL/SL	14.0	15.1	15.5
Trl/SL	24.5	25.2	27.9
Tal/SL	61.9	60.4	56.7

Figure 1. *Stigmatopora harastii*, preserved directly after collection, AMS I. 49510-001, holotype male, 145.5 mm SL **A** dorsal view **B** lateral view **C** ventral view; Australia: NSW, Botany Bay, Kurnell (photograph: Kerryn Parkinson).

sides of head and anterior trunk rings with large, irregular pale white spots or with diffuse pale white stripe; venter of first trunk ring with distinct red elongated spots in longitudinal row, almost forming a stripe, on midline present in male (AMS I. 49510-001); venter of anterior trunk rings pale red with a large cluster of distinct red spots extending posteriad from second trunk ring in male (AMS I. 49510-001), few scattered small red spots in females (AMS I.1.47267).

Description. General body shape as in Figs 1–6. Morphometric, meristic, and morphological characters listed in Table 1. Superior trunk and tail ridges continuous, not arched dorsad below the dorsal-fin base; lateral trunk ridge ends without deflection on the first tail ring; lateral tail ridge absent; inferior trunk and tail ridges continuous, the former largely located on the ventral portion of the trunk; dorsum of the trunk flat to slightly convex between superior ridges; trunk flat to slightly V-shaped ventrad, without a prominent median ridge; trunk compressed dorsoventrally and expanded

Figure 2. *Stigmatopora harastii*, preserved directly after collection, paratypes, female **A** AMS I.47267-001, 136.3 mm SL **B** AMS I.47267-002, 138.2 mm SL; Australia: NSW, Botany Bay, Kurnell (photograph: Kerryn Parkinson).

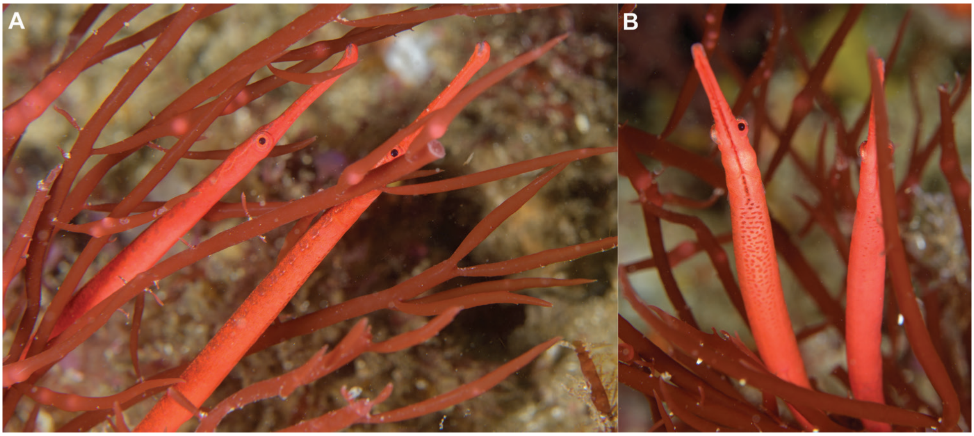

Figure 3. *Stigmatopora harastii* in situ, AMS I. 49510-001, holotype, male **A** (right individual) **B** (left individual); The Steps, Kurnell, Botany Bay, NSW, Australia, 13.5 meters depth, 18 June 2020. The male holotype was photographed with a paired female individual, which was not collected. Note the large cluster of distinct red spots extending posteriad on venter of anterior trunk rings in the male (photographs: Andrew Trevor-Jones).

laterad, especially in the females; tail slender, distally attenuated or thread-like. Snout long and slender; median dorsal snout ridge low, entire, failing to reach the interorbital, and ends just before vertical through nares; preorbital moderately broad, the nares well removed from anterior rim of orbit; interorbital broad, flat to slightly concave; median ridge, distinct, low, present on dorsum of head and first trunk ring starting from the posterior third of the frontal, over the supraoccipital, to the anterior and posterior nuchal plates; opercular ridge, prominent, complete, not angled dorsad; supraopercular ridges absent; opercle with or within a complete or incomplete longitudinal ridge, elsewhere ornamented with fine radiating striae; gill opening located above middle or posterior third of opercle; lateromedial ridge, distinct, low, present between

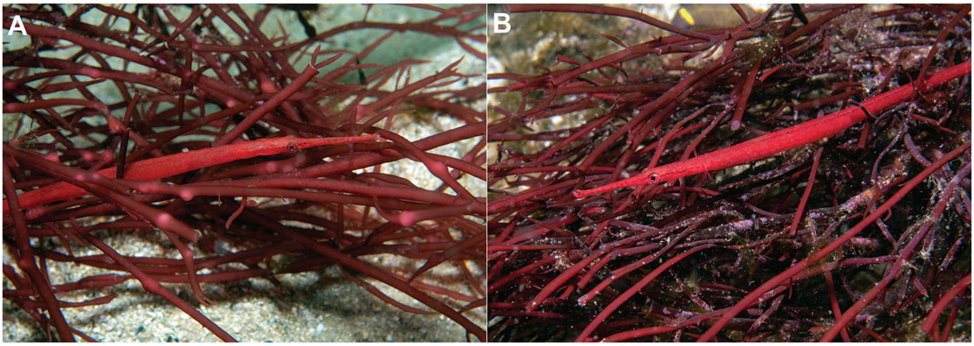

Figure 4. *Stigmatopora harastii* in situ, AMS I.47267 paratypes, female, The Steps, Kurnell, Botany Bay, NSW, Australia at 11–12 meters depth, 06 June 2017 (photographs: David Harasti).

cleithrum and pectoral fin base; principal body ridges low; head and body without spines, denticulations or dermal flaps; dorsal-fin origin on 6th–7th trunk rings, subdorsal rings 19–20 (12 trunk rings + 7 or 8 tail rings); lateral trunk ridge ends on first tail ring; anal-fin rays four; pouch plates absent; brood pouch under anterior portion of tail; pouch plates absent.

Colouration in life. In life, *S. harastii* exhibits red background colouration with unique colour patterns: dorsum of snout with large, irregular pale white spots; sides of head and anterior trunk rings with large, irregular pale white or red spots or with diffuse pale white markings; sexual dimorphic markings with venter of first trunk ring exhibiting distinct red elongated spots in longitudinal row on midline, almost forming a stripe, present in males (Figs 1, 3, 5); and venter of anterior trunk rings lighter than sides and dorsum with a large cluster of distinct red spots extending posteriad from second trunk ring in males (Figs 1, 3, 5) whereas few scattered small red spots are present in the females (AMS I.47267). In alcohol, head and body background colour typically uniformly pale red (Fig. 1). Fins hyaline.

Etymology. This species is named after David Harasti, one of the first to recognize *S. harastii* as being a new species, for recognition of his efforts towards conservation of Syngnathidae in Australia, and for being an aficionado extraordinaire of his beloved genus *Stigmatopora*. David has stated he counts green pipefish to fall asleep. Harasti's Pipefish and the Red Wide-bodied Pipefish are proposed here as the common names for *S. harastii.*

Distribution and habitat. *Stigmatopora harastii* is currently known to occur in central NSW, Australia from only three localities, including Botany Bay, Shellharbour, and Jervis Bay (Fig. 5). The paratypes and holotype described herein were collected separately at the scuba dive site referred to as The Steps between 2017 and 2020, respectively, at a depth of 11–12 meters at the southern entrance to Botany Bay, which is located within the Kamay Botany Bay National Park at Kurnell. The topography above and below the water at the type locality and the other localities is consistent for the Sydney Basin bioregion in the central eastern coast of Australia, which covers an area between Newcastle in the north to Bateman's Bay in the south (Andrew 1999),

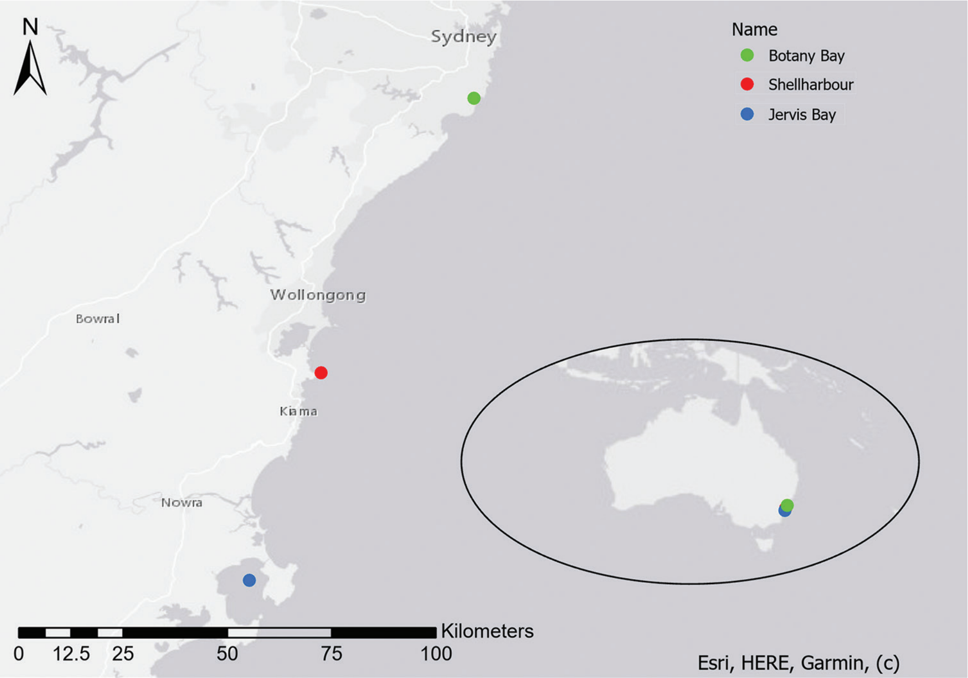

Figure 5. Distribution of *Stigmatopora harastii* in NSW, Australia. Type locality in green.

Figure 6. Aerial view of the scuba dive site The Steps, Kurnell, Botany Bay, NSW, Australia **A** shore and entrance **B** inshore boulders (photographs: Michael McFadyen).

and is comprised of weathered sandstone cliffs and flat intertidal platforms (Fig. 6). Subtidally, the rocky reefs typically have large undercut benches that are interspersed with large boulders and gutters. The underwater habitat closest to shore is composed of large boulders that are mostly devoid of sessile growth (Fig. 6), which is followed by sandy bottom at a depth of approximately 10–15 metres. At this depth, the sandy bottom is littered with large boulders, which are covered in prolific sessile growth,

Figure 7. *Stigmatopora harastii* in situ, male, The Leap, Kurnell, Botany Bay, NSW, Australia, 12 meters depth, 03 October 2018 (photograph: Andrew Trevor-Jones).

including ascidians, bryozoans, and sponges, and interspersed with beds of kelp (*Ecklonia*). Fucoid algae, and seagrass habitat comprising species that occur commonly in NSW coastal and estuarine areas such as *Posidonia australis* and *Zostera capricorni*, were recorded as absent. Along the sand edge of the entrance, small isolated clumps of red algae appearing to be of the family *Gracilariaceae* Nägeli, 1847, and possibly of the species *Crassiphycus secundatus* (Harvey) Gurgel, J.N. Norris & Fredericq, 2018, were attached to flat rocky substrate that was usually covered in sand. The red algae mostly appeared to occur at low densities as single or one to three adjoining clumps and widely dispersed throughout the habitat. Fluctuations in density of red algae was observed over many dives in the same area by the second author.

Single individuals or male-female pairs of *S. harastii* were observed to be closely associated with the red algae; however, they were infrequently detected and present in only one isolated clump of red algae among all the other clumps in the close vicinity. Multiple dives by the second author between the collection of the type specimens at The Steps in the area where the type specimens were collected, as well as at other nearby large areas with red algae did not consistently detect the presence of *S. harastii*. Most times individuals were absent or only a single individual was found, possibly suggesting fluctuations in the abundance of the red algae with which *S. harastii* associates. Individuals were oriented vertically or at an angle and extremely well-camouflaged within the red algae, the distal third of their tails clasped around single fronds. The habitat was subject to strong surge in which individuals of *S. harastii* and the red algae together

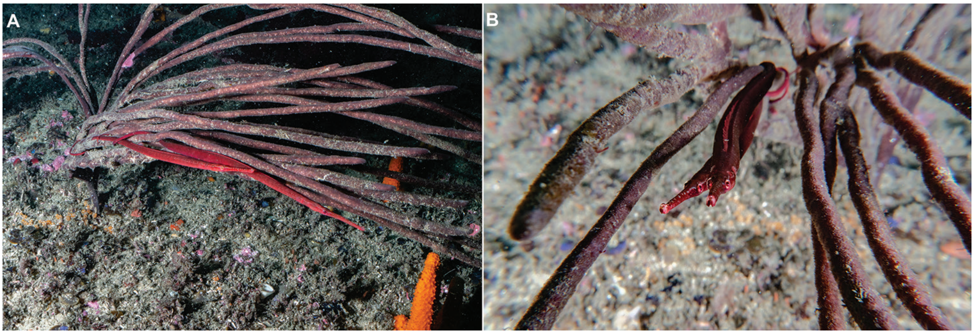

Figure 8. *Stigmatopora harastii* in situ, male-female pair **A** lateral view **B** anterior view, Minmi Trench, Botany Bay, NSW, Australia, 18 meters depth, 17 February 2019 (photographs: Duncan Heuer).

were observed swaying in unison with the surge (https://vimeo.com/229093467). The second author has observed on occasion active individuals swimming from one clump of red algae to another or feeding actively just outside the red algae. Feeding behaviour appears to be similar to other *Stigmatopora* species, with individuals darting out from the cover of their alga to capture food such as small copepods and shrimp. Individuals have been also observed nearby between the Steps and the dive site locally referred to as the Leap, one of which was associated with another species of red algae appearing to be of the genus *Gracilaria* Greville, 1830 (Fig. 7).

Stigmatopora harastii was also observed at the dive site locally referred to as the Minmi Trench, located at the northern headland of Botany Bay, that consists of a flattish reef with small to large boulders at about 16 meters depth, which then drops off to 22–23 meters depth. A male-female pair was observed associating with a finger sponge appearing to be a member of the family *Callyspongiidae* Laubenfels, 1936 at 18 meters depth (Fig. 8). Photographs of *S. harastii* were also taken on January 2017 at the locality referred to as The Gutter at Bass Point, Shellharbour, NSW at 18 meters depth (Fig. 9). A male individual exhibiting the characteristic dimorphic colour pattern on its ventral trunk was observed in red algae appearing to be of the same species observed at Kurnell (Fig. 9A–C). Additionally, a female individual (Fig. 9D) was observed associating with a clump of bubble red algae appearing to be of a different species of red algae of the genus *Gracilaria*.

Morphological comparisons. *Stigmatopora harastii* shares morphological synapomorphies with *S. argus*, *S. macropterygia*, *S. narinosa*, and *S. nigra*, including principle body ridges, dorsal-fin placement, distally attenuated, slender tail, and absence of caudal fin (Dawson 1982, 1985; Browne and Smith 2007). *Stigmatopora harastii* appears to be most similar to *S. nigra* (Dawson 1982: fig. 7) in meristics, snout length and shape, dorsal-fin origin on 6th–7th trunk ring, presence of a distinct median longitudinal ridge between the opercle and pectoral-fin base, and lateral trunk ridge terminating on the first tail ring (Table 2). Even though all members of *Stigmatopora* share similar meristic and morphometric characters (Table 2; Dawson 1982, 1985; Browne and Smith 2007), they can be morphologically distinguished on the basis of a distinct but low dorsal median ridge present on the dorsum of the head and first trunk ring (Dawson

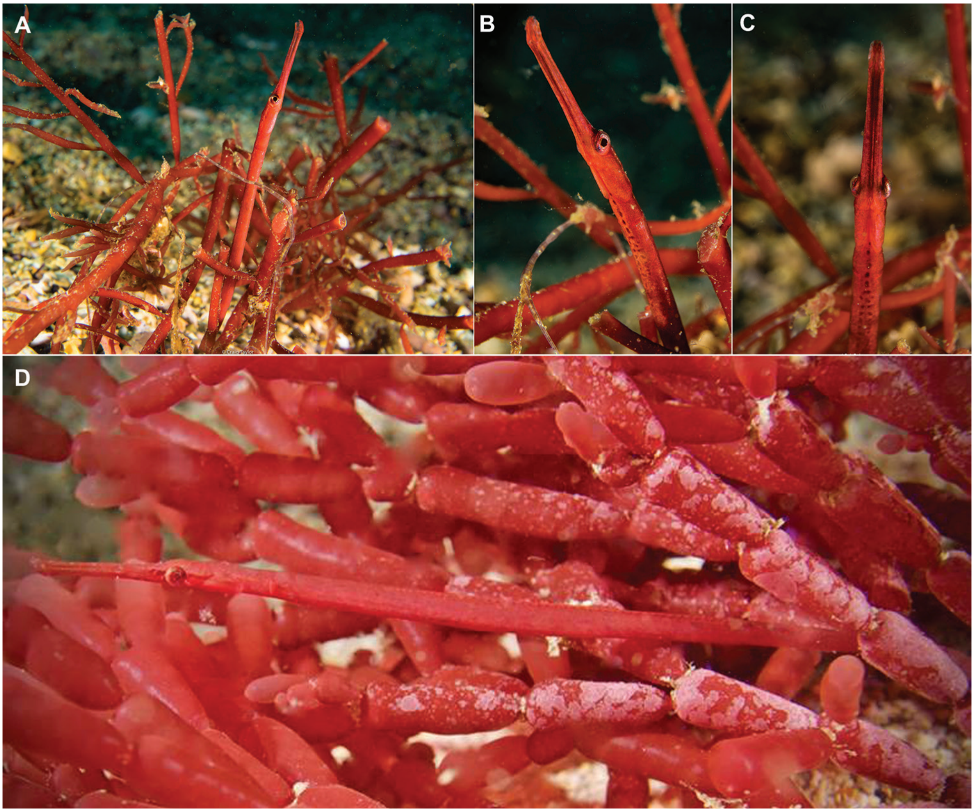

Figure 9. *Stigmatopora harastii* in situ **A–C** male **D** female, The Gutter, Bass Point, Shellharbour, NSW, Australia, 18 meters depth, 17 Feb 2017 (photographs: Craig Taylor).

1982, 1985; Browne and Smith 2007). In *S. harastii*, the dorsal median ridge extends from the posterior third of the frontal to the supraoccipital, anterior, and posterior nuchal plates (Fig. 10) (versus the posterior third of the frontal to the supraoccipital, anterior, and posterior nuchal plates, and first trunk ring in *S. nigra* [Fig. 10; Dawson 1982: fig. 7]; the anterior and posterior nuchal plates in *S. argus* [Dawson 1982: fig. 2]; absence of low dorsal median ridge on head an first trunk ring in *S. macropterygia*; restricted to the supraoccipital in *S. narinosa*). *Stigmatopora harastii* also differs from *S. argus* and *S. macropterygia* in the termination of the lateral trunk ridge on the tail ring (first tail ring vs. 8th–20th tail ring in *S. argus*; 22nd–35th tail ring in *S. macropterygia*) and the presence of a median longitudinal ridge between the opercle and pectoral-fin base (vs. absence of longitudinal ridge). *Stigmatopora harastii* is distinguished from *S. narinosa* in the shape of the snout (long vs. medium length, laterally flattened, and dorsally elevated) and the presence of the longitudinal ridge between the opercle and pectoral-fin base (vs. absence of longitudinal ridge).

Comparative colouration. The new species is most easily distinguished from *S. nigra* by features of the colour pattern in life (Figs 1–4, 6–9), including red background colour

Table 2. Comparison of morphological characters between *S. harastii* and other members of *Stigmatopora*.

	S. harastii	***S. nigra***	***S. argus***	***S. macropterygia***	***S. narinosa***
Data source	This study	Dawson, 1982	Dawson, 1982	Dawson, 1982	Browne & Smith, 2007
Trunk rings	18	16–19	16–23	21–22	18
Tail rings	68–71	67–79	78–91	85–92	68
Dorsal-fin rays	43–45	35–47	37–64	63–74	37–45
Pectoral-fin rays	13–18	11–16	13–18	15–19	12–13
Dorsal-fin origin	6th–7th	5th–7th	9th–13th	8th–10th	5th–7th
Lateral trunk ridge reaches	1st tail ring	Anal or 1st tail ring	8th–20th tail ring	22nd–35th tail ring	2nd tail ring
Snout length	long	long	long	long	medium, laterally flattened, dorsally elevated
Median dorsal ridge on head and first trunk ring	from frontal to posterior nuchal plate	from frontal to 1st trunk ring	from anterior to posterior nuchal plate	absent	supraoccipital
Longitudinal ridge between opercle and pectoral-fin base	present	present	absent	absent	absent

on the body (vs. base colour variably light brown to dark green in *S. nigra* [Fig. 11A, B]), and sexual dimorphic markings comprising (1) distinct red elongated spots in longitudinal row on midline, almost forming a stripe on venter of first trunk ring in the male and a smattering of red dots in the female (Figs 1–3, 6, 8B, C) (vs. small dots or striations crossing posterior area of snout, suborbital, and lower part of opercle on venter of head in *S. nigra* in the male and female [Fig. 11A, B; Dawson 1982: fig. 8]), and (2) a large cluster of distinct red spots extending posteriad from the second trunk ring on venter of the anterior trunk rings in the male and a smattering of red dots in the female (Figs 1–3, 7, 9B, C) (vs. presence of stripes between the trunk rings on the venter of all the trunk rings in *S. nigra*; pale stripes in the male, and dark stripes in the female, with the 2nd and 3rd trunk ring stripes darkest [Fig. 11A, B; Dawson 1982: fig. 8]). *Stigmatopora narinosa* exhibits two pairs of large black spots arranged in two rows, respectively, on venter of first trunk ring whereas dark transverse bands are present on the venter of each trunk and tail ring with anterior and dorsal margins of each ring white, forming thin white lines between each ring, resulting in appearance of a series of inverted saddles (Browne and Smith 2007). In contrast, *S. argus* and *S. macropterygia* exhibit no distinctive markings on venter of the head whereas venter of the trunk and tail in *S. argus* presents narrow dark bars between the rings on the whole trunk and anterior third of tail (vs. absence of markings on venter of trunk and tail in *S. macropterygia*; Fig. 11E; Dawson 1982).

Stigmatopora harastii, *S. nigra*, and *S. narinosa* share the presence of large, irregular pale white spots on dorsum of snout (vs. absence of white spots in *S. argus* and *S. macropterygia*). Finally, *S. harastii* and *S. nigra* share the presence of large, irregular pale white spots with scattering of small red dots, or diffuse pale white stripes, on sides of head and anterior superior trunk rings (vs. absence of colour markings on sides of

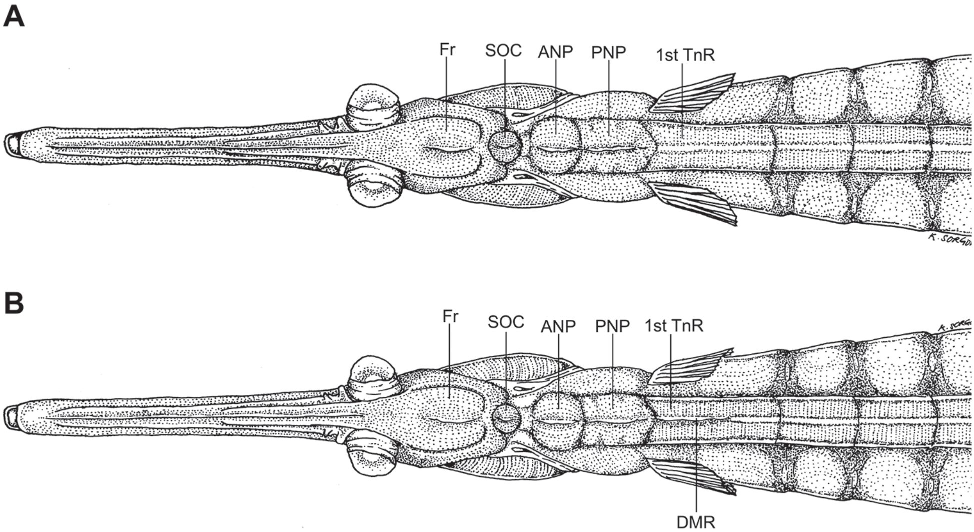

Figure 10. Comparison of the dorsal median ridge present on the head and first trunk ring in: **A** *S. harastii* and **B** *S. nigra*, AMS I.42611-009. Note the dorsal median ridge (DMR) extending into the first trunk ring in *S. nigra* versus ending on the posterior nuchal plate in *S. harastii*. Abbreviations: ANP, anterior nuchal plate; DMR, dorsal median ridge; Fr, frontal; PNP, posterior nuchal plate; SOC, supraoccipital; first TnR, first trunk ring (illustration by Kent Sorgon).

head and anterior superior trunk rings in *S. argus* and *S. macropterygia*). In contrast, *Stigmatopora narinosa* exhibits a camouflage pattern of brown and white diffuse colouration on sides of head.

Key to the species of *Stigmatopora*

1 Dorsal-fin origin on 5–7th trunk ring, lateral trunk ridge ends on anal, first, or second trunk ring **2**
– Dorsal-fin origin on 8th–13th trunk ring **5**
2 Snout long and slender **3**
– Snout shorter, laterally flattened, and dorsally elevated **4**
3 Red dots on venter of anterior trunk rings (male and female) .... ***Stigmatopora harastii***
– Black stripes on venter of anterior trunk rings (female) .... ***Stigmatopora nigra***
4 2 large transverse pairs of black dots on venter of trunk (female) .... ***Stigmatopora narinosa***
5 Lateral trunk ridge reaches 8th–23rd tail ring, black spots on dorsum and venter of trunk .... ***Stigmatopora argus***
– Lateral trunk ridge reaches 22nd–35th tail ring, no distinctive markings on venter of trunk .... ***Stigmatopora macropterygia***

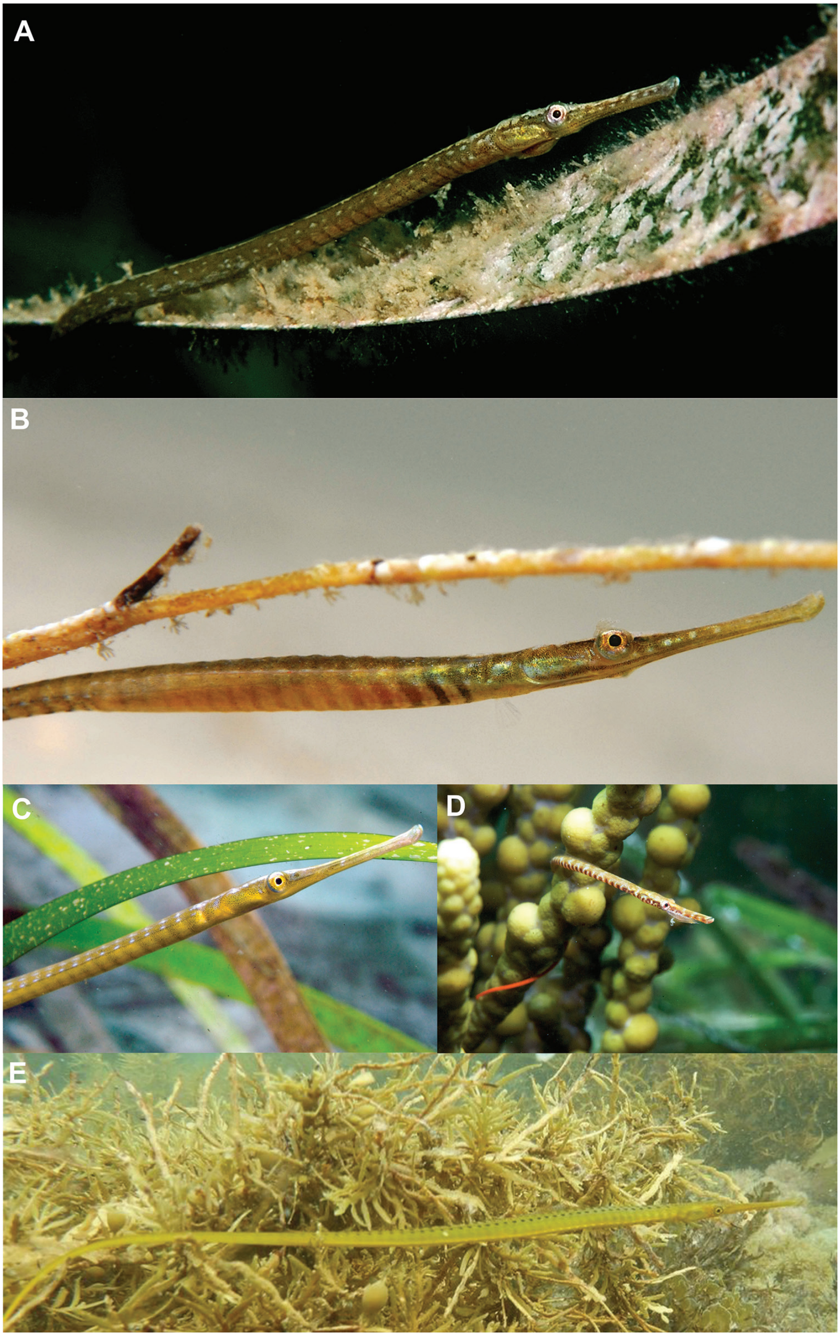

Figure 11. Fucoid algae and seagrass associating members of *Stigmatopora in situ* **A** *S. nigra*, male, Nelson Bay, NSW (photograph: David Harasti) **B** *S. nigra*, female, Port Hughes, Gulf St Vincent, South Australia (photograph: David Muirhead) **C** *S. argus*, Port Hughes, Gulf St Vincent, South Australia (photograph: Graham Short) **D** *S. narinosa*, Port Hughes, Gulf St Vincent, South Australia (photograph: Graham Short) **E** *S. macropterygia*, Winstones Cove, North Island, New Zealand (photograph: Nick Shears).

Habitat preferences

Stigmatopora harastii inhabits semi-exposed bay entrances and ocean embayments in which the underwater terrain is characterised by sandy areas interspersed with boulders and hard flat reefs. Fucoid algae, and seagrass species that occur commonly in NSW coastal and estuarine areas such as *Posidonia australis* and *Zostera capricorni*, were absent but were recorded within the shallow areas of the bays or in nearby adjacent bays (Larkum and West 1990; Bell et al. 1992; Creese et al. 2009; Griffiths 2010; Parkinson and Booth 2016). Individuals and pairs of *S. harastii* were observed in close association with a species of finger sponge appearing to a member of the family *Callyspongiidae* Laubenfels, 1936 (Fig. 7) and several different species of red algae appearing to be of the family Gracilariaceae in the genera *Crassiphycus* and *Gracilaria* (Figs 4, 5, 7, 8). *Stigmatopora harastii* was not observed associating with any of the other numerous species of small to large sponges or tunicates present on the sessile-rich boulders nor within the canopy kelp *Ecklonia radiata*.

The unique habitat associations of *S. harastii* with a finger sponge and red algae differ markedly from the fucoid algae and seagrass associating members of *Stigmatopora*. *Stigmatopora argus*, *S. narinosa*, *S. nigra*, and *S. macropterygia* inhabit sheltered seagrass and algal beds in bays and estuaries throughout southern Australia and New Zealand, respectively. In NSW, the congenerics *S. nigra* and *S. argus* occur in sympatry in seagrass beds and form an abundant component of the inshore ichthyofauna (Steffe et al. 1989; Parkinson and Booth 2016). However, these species were not observed at the three localities in which *S. harastii* was found, which is most likely due to the absence of preferred seagrass and fucoid algae habitat. Similarly, in South Australia, the congenerics *S. argus*, *S. narinosa*, and *S. nigra* occur in sympatry and form an abundant component of the inshore ichthyofauna in which *S. argus* generally prefers to associate with the large seagrass genus *Posidonia*, *S. nigra* with the smaller seagrass genus *Zostera*, and *S. narinosa* with the fucoid corkweed *Scaberia agardhii*, *Posidonia*, and *Zostera* (Dawson 1982; Browne and Smith 2007). During a survey of the ichthyofauna at Smith Bay, Kangaroo Island (https://www.ausocean.org/cp/smithbay), located south of the Fleurieu and Yorke Peninsulas, the first author has observed *S. nigra* in small beds of *Zostera* to depths of 25–30 meters. It was not observed associating with the small species of sponges nor small clumps of red algae of unknown identification that were recorded in the habitat, which is characterised by flat sandy areas with small beds of *Zostera*, clumps of red algae, sponges, and scallops. Lastly, the New Zealand endemic *S. macropterygia* has been recorded in canopy beds of *Ecklonia*, *Zostera* down to 10 meters depth, and fucoid algae of the genera *Carpophyllum* and *Cystophora* (Dawson 1982; G. Short 2017, pers. obs.).

COI Genetic Distances

Table 3 shows the genetic distance analysis at the COI gene (uncorrected p distances) between *S. harastii*, and the previously sequenced specimens of *S. argus* and *S. narinosa*

Table 3. Uncorrected genetic distances (*p*-distances) summary between *S. harastii* and other members of *Stigmatopora* based on cytochrome c oxidase I (COI) sequences analysed in this study.

	GenBank	Species	1	2	3	4	5
1	MK542828	*Stigmatopora harastii*					
2	KY066148	*Stigmatopora argus*	0.098				
3	MK552117	*Stigmatopora macropterygia*	0.101	0.054			
4	KY066149	*Stigmatopora narinosa*	0.107	0.115	0.115		
5	KY066150	*Stigmatopora nigra*	0.146	0.126	0.156	0.148	

(Hamilton et al. 2017) and the newly sequenced specimen of *S. macropterygia* from this study. *Stigmatopora harastii* differs from *S. argus* by 9.8%, from *S. nigra* by 14.6%, *S. narinosa* by 10.7%, and *S. macropterygia* by 10.1%. Reported mtDNA clock rates of approximately 1.2% per million years in marine teleosts (Reece et al. 2010) indicate divergence between *S. harastii* and *S. nigra* approximately 12.2 million years ago.

Discussion

Here we consider *S. harastii* as a valid species due to its morphological characters of the head, distinct sexual dimorphic markings on the ventral trunk rings, and genetic divergence from its congeners. We have identified a subtle but useful diagnostic morphological character consisting of a median dorsal ridge spanning the frontal, supraoccipital, and anterior and posterior nuchal plates that differentiate *S. harastii* from the superficially similar *S. nigra* (Figs 1, 9). In the previous diagnoses of *S. argus*, *S. macropterygia*, and *S. nigra* (Dawson 1982), the median dorsal ridge present on the neurocranial bones was cited, however its importance as a diagnostic character to differentiate between members of the genus was not recognised. The diagnosis of *S. narinosa* did not include this morphological character in the description (Browne and Smith 2007). Unequivocally, the most noticeable external features of *S. harastii* are the distinct sexual dimorphic red spotted markings on the ventral trunk rings in the male (Figs 1, 3, 6, 8), which differ markedly from the distinct markings exhibited on the ventral trunk rings by its congeners (Dawson 1982; Browne and Smith 2007). Typically, general body colouration in syngnathids is not considered a reliable feature for diagnosis (Lourie et al. 2016; Short et al. 2018), however, the presence of distinctive colour patterns on the venter of the anterior trunk rings is shared with the genus *Corythoichthys*, a sister species to *Stigmatopora* (Hamilton et al. 2017), in which all members bear diagnostic dark markings on the venter of anterior trunk rings that aid in their species identification.

The unique habitat associations of *S. harastii* with a finger sponge and red algae differ markedly from the fucoid algae and seagrass associating members of *Stigmatopora*. Even though no close association has been reported between fish and red algae in the literature until this study, Tyler and Böhlke (1972) documented 39 species of fish in the Caribbean known to have some association with sponges, and categorised sponge-dwelling fish as either (1) morphologically specialised obligate sponge dwellers, (2) morphologically unspecialised obligate sponge dwellers, (3) facultative sponge dwellers, or (4) fortuitous sponge dwellers. Facultative sponge dwellers in category 3 spend part of their lives on or in sponges, but have been observed in other types of habitat. Finally, fortuitous sponge dwellers in category 4 comprise a variety of families, all of which are known to occupy a wide variety of habitat types. The adult individuals of *S. harastii* that were observed during this study probably can be classified in category 3 as facultative finger sponge and red algae-dwellers, since *S. harastii* encountered at the type locality and other known localities only associates with one species of finger sponge (Fig. 7) and with at least three species of red algae (Figs 3, 4, 6, 8). It may prefer these habitat types since they provide many finger-like protuberances that allow for tail grasping and orienting their body in parallel to the finger sponge branches or red algae fronds, respectively, behaviours similarly seen in other members of *Stigmatopora* in fucoid algae and seagrass. *Stigmatopora harastii* has not been observed in the brown kelp *Ecklonia radiata* that is abundantly present near the red algae and finger sponge in their known localities, which may be due to the negative effects of the kelp canopy on feeding behaviour with respect to facilitating access in and out of the kelp habitat into the water column where they feed.

Other species of syngnathids form a component of the inshore ichthyofauna at the type locality where the authors and underwater photographers have recorded the following (1) seahorse species: *Hippocampus abdominalis*, *H. histrix*, *H. kelloggi*, and *H. whitei*; (2) pipefish species: *Festucalex cinctus*, *Heraldia nocturna*, *Lissocampus runa*, *Maroubra perserrata*, *Notiocampus ruber*, and *Trachyramphus bioarctatus*; (3) pygmy pipehorse species: *Idiotropiscis lumnitzeri*; and (4) weedy seadragon species: *Phyllopteryx taeniolatus*. *Hippocampus abdominalis*, *H. kelloggi*, and *H. whitei* have been observed associating with various species of sponges, as well as kelp and large tunicates (*Pyura spinifera*), and in a wide variety of habitat types at other localities in NSW (Harasti et al. 2010, 2012; Harasti 2014, 2015, 2017), including soft coral, seagrass, and shark nets, therefore placing them in category 4 as fortuitous habitat dwellers. Similarly, pairs of *Idiotropiscis lumnitzeri* has been observed on the large boulders using various species of sponges and soft corals as holdfasts, as well as bryozoans and calcified algae.

Habitat structural complexity plays an important role in shaping populations, community dynamics, and distribution of seagrass associating pipefish (Steffe et al. 1989; Connolly 1994; Jenkins et al. 1997; Jenkins and Wheatley 1998; Kendrick and Hyndes 2003; Curtis and Vincent 2005; Sanchez-Camara et al. 2006; Masonjones et al. 2010; Rose and Dixson 2010; Müller and Erzini 2017). *Stigmatopora harastii* likely has a wider distribution within NSW, southern Australia, and possibly New Zealand, where it remains undetected due to its preferred depth range, remarkable crypsis within its preferred habitat, and apparent low density of finger sponge and red algae occurring on the large boulders and flat rocky substrate, respectively. Its occurrence further north and south of central NSW may be confirmed by further sampling and by a better understanding of the distribution of the finger sponge and red algae with which it associates.

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RESEARCH ARTICLE

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A new species of *Pristimantis* (Amphibia, Anura, Strabomantidae) from the Pui Pui Protected Forest (central Peru), with comments on *Pristimantis albertus* Duellman & Hedges, 2007

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Abstract

We describe a new *Pristimantis* species from the eastern Andes, Región Junín, Peru following an integrative taxonomic approach. The description is based on three adult males (snout-vent length 25.7–28.8 mm) collected in two montane forests between 1615 and 1800 m a.s.l. in the Pui Pui Protected Forest and its close surroundings. The new species is mainly characterised by absence of tympanum, presence of inner tarsal fold, broad horizontal red band across iris, ventre mottled black and cream and ventral surfaces of thighs salmon and grey mottled. Amongst the Amazonian and montane forest *Pristimantis* that have the ventre and groin contrastingly black and cream mottled, *P. sinschi* **sp. nov.** is morphologically most similar to *P. lindae* and *P. ventrimarmoratus*. However, DNA barcoding revealed a clear distinction between these three species and placed *P. sinschi* **sp. nov.** as sister taxon of *P. lindae*. We designate a lectotype for *P. ventrimarmoratus* and restrict the type locality of this species to "El Topo, R. Pastaza, [Provincia Tungurahua,] E. Ecuador, 4200 feet". *Pristimantis albertus* and *P. sagittulus* are recorded for the first time in the Región Junín. Additional data on morphology and systematics are provided for *P. albertus*.

Keywords

Andes, anuran diversity, montane rainforests, *Pristimantis sinschi* sp. nov., *P. sagittulus*, *P. ventrimarmoratus*

Introduction

Faunal and taxonomic research provides the essential foundation and objectives for the effective conservation of biological diversity. The Pui Pui Protected Forest (PPPF) located in the eastern Andes of Peru (Provincias Chanchamayo, Jauja, Concepción and Satipo, Región Junín; Fig. 1) is a good example of a protected area with a rich, but until recently, practically unexplored fauna and flora. Any proposed inventories, taxonomic studies and conservation assessment of the local fauna and flora are of great importance for proper management of the protected area. Our recent herpetological surveys (first in the area) revealed that the amphibian and reptile fauna of the PPPF is remarkably diverse with a high degree of local endemism. We obtained new faunal records extending the known ranges of several species (e.g. *Euspondylus excelsum* Chávez, Catenazzi & Venegas, 2017: Lehr et al. 2018) and discovered nine taxa new to science (six anuran and one reptile species, two reptile genera; for example, Lehr and Moravec 2017; Lehr and von May 2017; Lehr et al. 2017b, c; Lehr et al. 2018; Moravec et al. 2018; Lehr et al. 2020). Nevertheless, it appears that our knowledge of the real species richness of the local amphibian and reptile fauna is still incomplete. Thorough genetic analyses of our collected *Pristimantis*, specimens from the PPPF revealed unrecognised taxa and new records for known taxa.

Herein, we describe a new species of *Pristimantis* Jiménez de la Espada, 1870 which phenotypically resembles *P. diadematus* (Jiménez de la Espada, 1875); *P. divnae* Lehr and von May, 2009; *P. eurydactylus* (Hedges & Schlüter, 1992); *P. lindae* (Duellman, 1978); *P. orcus* Lehr, Catenazzi & Rodríguez, 2009; and *P. ventrimarmoratus* (Boulenger, 1912). Furthermore, we provide the first records for *Pristimantis albertus* Duellman & Hedges, 2007 and *P. sagittulus* (Lehr, Duellman & Aguilar, 2004) for the Región Junín and additional data on systematics and morphology for *P. albertus*.

Material and methods

Morphological characters

The format for the description follows Lynch and Duellman (1997), except that the term dentigerous processes of vomers is used instead of vomerine odontophores (Duellman et al. 2006) and diagnostic characters are those of Duellman and Lehr (2009). Taxonomic classification follows Hedges et al. (2008), except that we followed Pyron and Wiens (2011) for family placement and Padial et al. (2014) for names of *Pristimantis* species groups. The holotype was fixed in 96% ethanol and stored in 70% ethanol. Liver tissue of the holotype was taken for genetic analyses. Sex and maturity of specimens were identified by observing secondary sexual characters (vocal slits) and gonads through dissections. Specimens were considered juveniles when gonads were

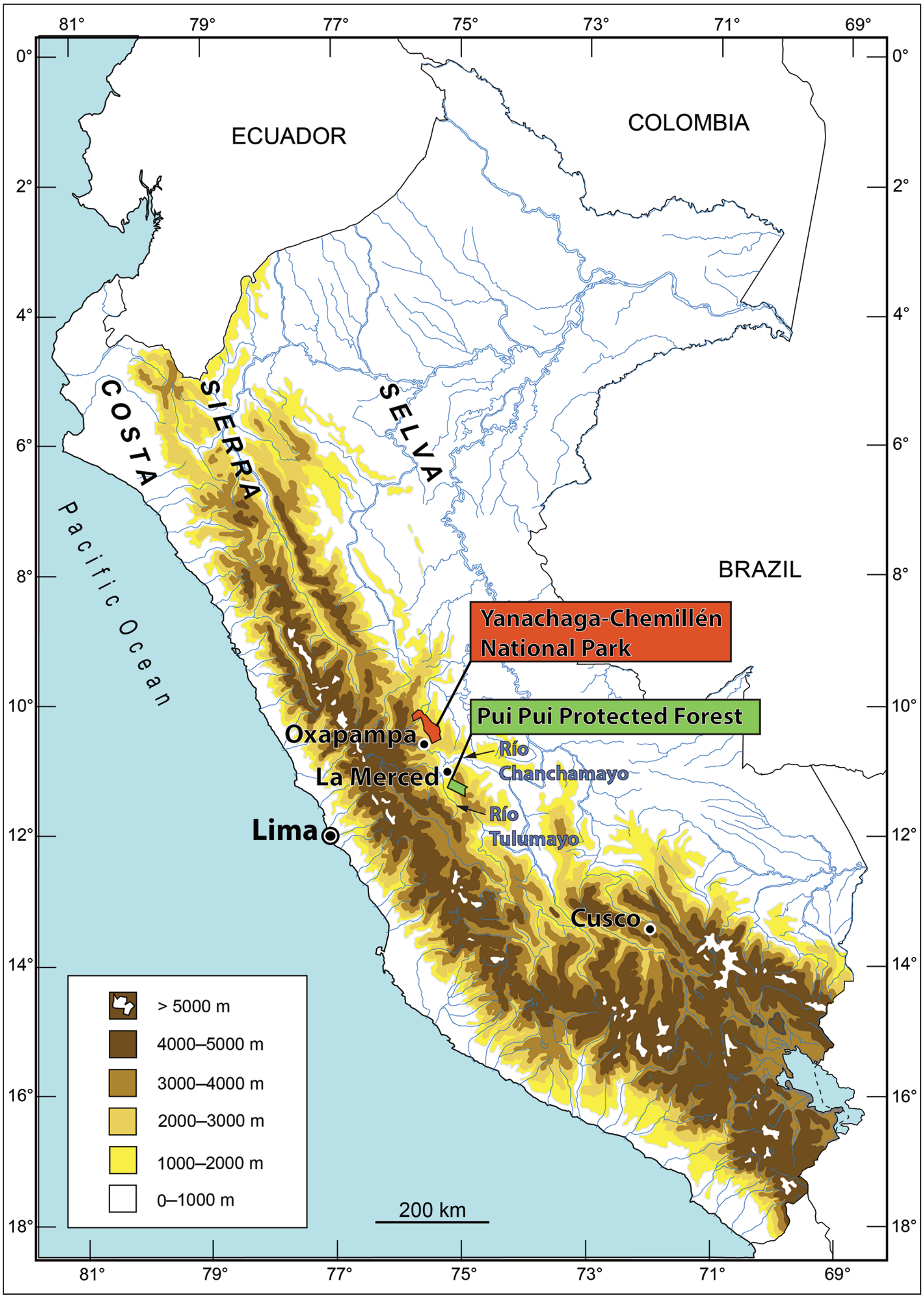

Figure 1. Map of Peru with the Yanachaga-Chemillén National Park (Region Pasco) and the Pui Pui Protected Forest (Region Junín).

too small to distinguish between sexes. We used maximum known SVL for males within a species to recognise smallest body size as recommended by Lehr and Coloma (2009). We measured the following variables to the nearest 0.1 mm with digital calipers under a stereomicroscope: snout-vent length (SVL, straight length distance from tip of snout to vent), tibia length (TL, distance from the knee to the distal end of the tibia), foot length (FL, distance from proximal margin of inner metatarsal tubercle to tip of Toe IV), head length (HL, from angle of jaw to tip of snout), head width (HW, at level of angle of jaw), horizontal eye diameter (ED), interorbital distance (IOD), upper eyelid width (EW), internarial distance (IND), eye-nostril distance (E-N, straight line distance between anterior corner of orbit and posterior margin of external nares) and horizontal tympanum diameter (TD). Fingers and toes are numbered preaxially to postaxially from I–IV and I–V, respectively. We compared the lengths of toes III and V by adpressing both toes against Toe IV; lengths of fingers I and II were compared by adpressing the fingers against each other. Drawings were made by EL using a stereomicroscope and a camera lucida. Photographs taken by JM and EL were used for descriptions of colouration in life.

Comparisons of congeners focused on phenotypically-similar species from Ecuador and Peru and those with close phylogenetic relationships as recovered in our trees. Information on species for comparative diagnoses was obtained from Duellman and Lehr (2009) and original species descriptions. For specimens examined, see paragraph Comparative specimens examined. Codes of collections are: QCAZ = Museo de Zoología of the Pontificia Universidad Católica del Ecuador; MUSM = Museo de Historia Natural Universidad Nacional Mayor de San Marcos, Lima, Peru; NMP-P6V = National Museum Prague, Czech Republic. Threat status was assessed using the IUCN criteria (2016).

Molecular analysis

Taxon sampling

Proceeding from our previous study (Lehr et al. 2017a), we included samples of various *Pristimantis* species collected by us in the Pui Pui Protected Forest (PPPF) during the surveys between 2012 and 2014 and from the area of nearby montane regions of the Cordillera Yanachaga. A list of the new genetically-investigated material and their GenBank accession numbers are presented in Table 1. For the final dataset, we retrieved additional sequences conspecific or presumably related with our samples from GenBank to show phylogenetic positions of our new material in relation to DNA sequences published earlier (most importantly in the review by Hedges et al. 2008). We also retrieved species known to occur in the Cordillera Yanachaga Region (Duellman and Hedges 2005, 2007) including holotypes of *P. albertus* Duellman & Hedges, 2007 and *P. stictogaster* Duellman & Hedges, 2005. For comparison of the new species with morphologically-similar *P. lindae* and *P. ventrimarmoratus*, we used DNA sequences obtained by Arteaga-Navarro et al. (2011) and von May et al. (2017). As outgroups,

Table 1. Names of taxa, museum numbers, field data and GenBank accession numbers of newly-genetically investigated material. For other abbreviations, see text. PPPF = Pui Pui Protected Forest.

Species	Museum number	Locality	Coordinates	Elevation (m)	Collectors; year	GenBank Accession number	
						16S	12S
P. sinschi sp. nov. (holotype)	MUSM 32733	PPPF, Peru	11°12'38.5"S, 74°57'28.9"W	1800	E. Lehr, J. Moravec; 2014	MW075408	MW075426
P. sinschi sp. nov.	NMP-P6V 75060	PPPF, Peru	11°12'38.5"S, 74°57'28.9"W	1615	E. Lehr, J. Moravec; 2014	MW075407	MW075425
P. albertus	NMP-P6V 76020	PPPF, Peru	11°07'37.2"S, 75°10'37.0"W	1970	E. Lehr, J. Moravec, J.C. Cusi, R. von May; 2013	MW075393	MW075414
P. albertus	NMP-P6V 76021	PPPF, Peru	11°07'37.2"S, 75°10'37.0"W	1970	E. Lehr, J. Moravec, J.C. Cusi, R. von May; 2013	MW075394	MW075415
P. cf. *stictogaster*	MUSM 32729	PPPF, Peru	11°12'38.5"S, 74°57'28.9"W	1700	E. Lehr, J. Moravec; 2014	MW075395	MW075417
P. cf. *stictogaster*	NMP-P6V 75061	PPPF, Peru	11°12'38.5"S, 74°57'28.9"W	1750	E. Lehr, J. Moravec; 2014	MW075396	MW075419
P. cf. *stictogaster*	MUSM 31173	PPPF, Peru	11°15'16.1"S, 74°53'30.7"W	1615	E. Lehr, R. von May; 2012	–	MW075416
P. cf. *stictogaster*	NMP-P6V 76024	PPPF, Peru	11°15'16.1"S, 74°53'30.7"W	1615	E. Lehr, R. von May; 2012	–	MW075418
P. cf. *malkini*	NMP-P6V 71199/2	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2001	MW075401	MW075423
P. cf. *malkini*	NMP-P6V 71199/4	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2001	MW075399	–
P. cf. *malkini*	NMP-P6V 71199/7	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2001	MW075397	–
P. cf. *malkini*	NMP-P6V 71199/9	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2001	MW075402	–
P. cf. *malkini*	NMP-P6V 73184/1	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2002	MW075400	MW075424
P. cf. *malkini*	NMP-P6V 73184/2	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2002	MW075398	–
P. diadematus	NMP-P6V 71172	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2001	MW075409	MW075420
P. cf. *lanthanites*	NMP-P6V 71203/1	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2001	MW075405	MW075421
P. cf. *lanthanites*	NMP-P6V 71203/2	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2001	MW075403	–
P. cf. *lanthanites*	NMP-P6V 71203/3	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2001	MW075404	–
P. cf. *lanthanites*	NMP-P6V 71203/4	Tarapoto, Peru	03°48'17"S, 73°24'19"W	95	J. Moravec; 2001	MW075406	–
P. cf. *olivaceus*	NMP-P6V 74067	Palmira, Bolivia	10°35'S, 65°44'W	150	J. Moravec; 2007	MW075410	MW075422
P. reichlei	NMP-P6V 74243/1	San Antonio, Bolivia	11°29'S, 68°52'W	250	J. Moravec; 2007	MW075411	MW075427
P. reichlei	NMP-P6V 74243/2	San Antonio, Bolivia	11°29'S, 68°52'W	250	J. Moravec; 2007	MW075413	–
P. reichlei	NMP-P6V 74243/3	San Antonio, Bolivia	11°29'S, 68°52'W	250	J. Moravec; 2007	MW075412	–

we used the strabomantid genera *Oreobates* Jiménez de la Espada, 1872 (*O. cruralis* (Boulenger, 1902)) and *Phrynopus* Peters, 1873 (*P. bracki* Hedges, 1990), retrieved from GenBank. The final dataset was composed of 134 samples of 49 nominal taxa, including the new species and outgroups. All sequences acquired from GenBank can be identified by the GenBank accession numbers as given in Fig. 2.

DNA extraction, PCR, sequencing and sequence alignment

Genomic DNA was extracted from tissues stored in 96% ethanol. A fragment of the mitochondrial gene for 16S rRNA (16S), which is commonly used in the amphibian DNA barcoding (Vences et al. 2012), was targeted using the primers 16SL1 and 16SH1 adapted or directly taken from Palumbi et al. (1991). For primer sequences and PCR conditions, see Moravec et al. (2009).

In the case of *Pristimantis ventrimarmoratus*, only the 12S sequence was available in the GenBank database. Therefore, for the purpose of comparison, a fragment of 12S rRNA (*12S*) was sequenced for the holotype of the new species and 13 other selected specimens (Table 1; at least one specimen per species). The 12S fragment was amplified using primers 12Sa (5'-AAACTGGGATTAGATACCCCACTAT – 3') and 12Sb (5'-GAGGGTGACGGGCGGTGTGT-3') and 12Sb (5'-GAGGGTGACGGGCGGTGTGT-3'), taken from Kocher et al. (1989), using the PCR protocol described in Moravec et al. (2009), with an annealing temperature of 48 °C. New sequences have been deposited in GenBank (MW075393–MW075427). The multiple sequence alignment was performed in Geneious 11.1.5 (Kearse et al. 2012), using implemented MUSCLE algorithm (Edgar 2004), producing a 710 bp-long concatenated alignment (incomplete matrix, 464 bp 16S and 246 bp 12S). Ambiguously-aligned positions were eliminated by Gblocks v0.91b under options for a less stringent selection (Castresana 2000).

Phylogenetic analysis

The Bayesian Inference (BI) was applied to construct a phylogenetic tree. First, the software PartitionFinder 2.1.1, using the PhyML algorithm (Lanfear et al. 2012), was used to find the best-fitting model for nucleotide evolution, which was the GTR+I+G model, based on both the Akaike and Bayesian information criteria. The same model was rated as best-fitting for both 16S rRNA and 12S rRNA under partitioned search setting. The BI analysis was run in MrBayes 3.2.7a (Ronquist et al. 2012) with two runs and four chains in each run for 6×10^6 generations, sampling every 100^{th} generation. Appropriate sampling was controlled by examining the stationarity of log-likelihood scores against the generation time using Tracer v1.6 (Rambaut et al. 2013; all parameters had an effective sample size > 1000) and convergence between the two simultaneous runs was confirmed by the convergence diagnostics of the average standard deviation of split frequencies and the potential scale reduction factor values. From the sampled trees, 25% were discarded as burn-in and a 50% majority-rule consensus tree was produced from the remaining post-burn-in trees. The posterior probabili-

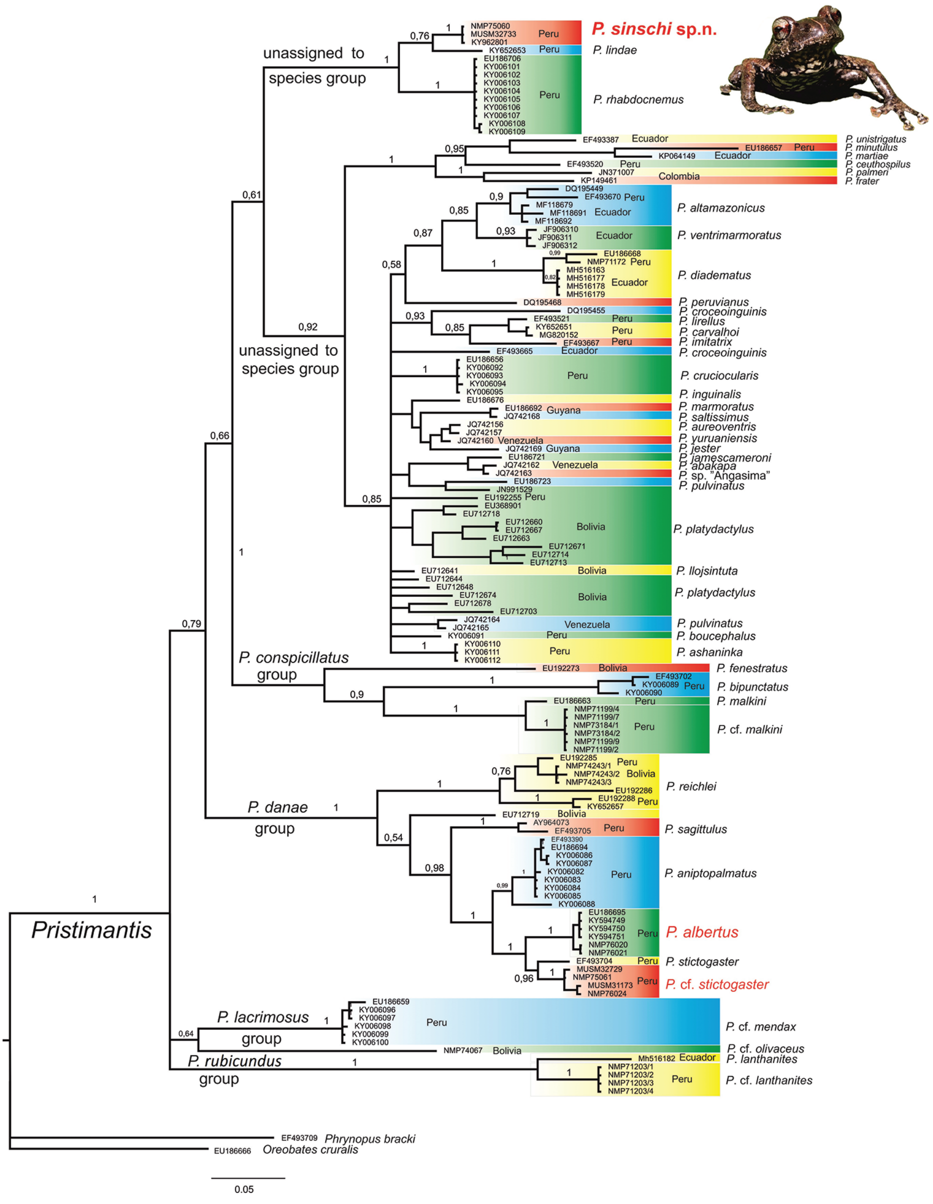

Figure 2. The Bayesian phylogenetic tree of selected South American *Pristimantis*; for taxon sampling design, see Material and Methods. Nodes with less than 50% of the post burn-in tree samples were collapsed. Posterior probability values (pp) given only for main lineages. The new species, *P. sinschi* sp. nov., is a member of a monophyletic clade, yet unnamed species Group, comprising species from Peruvian Cordillera Oriental – *P. lindae* and *P. rhabdocnemus*. The PPPF representatives of *P. danae* species Group form two distinct genetic lineages, one conspecific with *P. albertus* and the second closer to *P. stictogaster* (labelled as *P.* cf. *stictogaster*). Species-group names follow Padial et al. (2014). DNA sequences (for 12S rRNA and 16S rRNA) of taxa retrieved from GenBank are labelled by standard GenBank accession numbers (in cases where both 16S rRNA and 12S rRNA for the same specimen are under different accession numbers, taxon is labelled with 16S rRNA number), all other codes stand for our new material.

ties (pp) were calculated as the frequency of samples recovering any particular clade (Huelsenbeck and Rannala 2004). Genetic uncorrected *p*-distances were calculated in PAUP* (Swofford 2003).

Results

Molecular phylogenetic analyses

The obtained phylogenetic tree (Fig. 2) shows high support for six distinct evolutionary lineages within *Pristimantis* which are consistent with clades uncovered by Padial et al. (2014) and reconstructed also in our previous study (Lehr et al. 2017a). The newly-recognised species, *Pristimantis sinschi* sp. nov., belongs to a highly-supported clade (unassigned to any species group according to Padial et al. 2014) with *P. rhabdocnemus* and *P. lindae* as closest relatives (*P. lindae* in sister position). However, the average genetic uncorrected *p*-distance of 4.02% in the 16S barcode supports their status as separate species (Table 2).

Morphologically-similar species *P. ventrimarmoratus* (individuals from Ecuador, GenBank accession numbers: JF906310.1, JF906311.1 and JF906312.1) clusters within the species-rich clade comprising species from the Andes and the Guiana Shield, as well as lowland species from the intervening Amazon, with *P. altamazonicus* (Barbour & Dunn, 1921) and *P. brevicrus* (Andersson, 1945) as closest relatives (recently revalidated *P. brevicrus*, see Ortega-Andrade et al. 2017, is not in the tree, its position being verified separately). Average genetic uncorrected *p*-distance for 12S sequences between *P. ventrimarmoratus* and *P. sinschi* sp. nov. is over 10%. However, the situation concerning *P. ventrimarmoratus* is more complex and the exact identity of this species needs to be clarified. There are four syntypes of *Hylodes ventrimarmoratus* Boulenger, 1912: BMNH 1947.2.15.73 (formerly 1911.12.12.77) from "Chanchamayo, [Departamento Junín,] Peru, 2600 feet" and 1947.2.15.74–76 (formerly 1911.1.1.51–53) from "El Topo, R. Pastaza, [Provincia Tungurahua,] E. Ecuador, 4200 feet" (Duellman and Lehr 2009, Frost 2020). The Ecuadorian syntypes apparently belong to the sequenced Ecuadorian population of *Pristimantis ventrimarmoratus* because their locality lies between the collecting sites of the sequenced specimens (ca. 158 km SW of the locality of QCAR 41938 and QCAZ 42048 and ca. 176 km N of the locality of QCAZ 36403;

Table 2. Mean uncorrected genetic *p*-distance values of 16S rRNA barcode for species from the clade containing *Pristimantis sinschi* sp. nov. and for *P. albertus*–*P. stictogaster* clade within *P. danae* species Group.

	Species	1	2	3	4	5	6	7
1	*P. sinschi* sp. nov.	0.0000						
2	*P. lindae*	0.0402	0.0000					
3	*P. rhabdocnemus*	0.0535	0.0713	0.0136				
4	*P. albertus* GeneBank	0.1721	0.1691	0.1808	0.0000			
5	*P. albertus* this study	0.1721	0.1692	0.1809	0.0067	0.0000		
6	*P. stictogaster*	0.1611	0.1514	0.1720	0.0468	0.0497	0.0000	
7	*P.* cf. *stictogaster*	0.1585	0.1571	0.1745	0.0444	0.0472	0.0283	0.0023

see Arteaga-Navarro and Guayasamin 2011). Therefore, the Ecuadorian syntypes of *Hylodes ventrimarmoratus* can be regarded as the type specimens of *Pristimantis ventrimarmoratus* (Boulenger, 1912). Contrary to this, the Peruvian syntype of *Hylodes ventrimarmoratus* may be conspecific with *Pristimantis sinschi* sp. nov. It also originates from the Provincia Chanchamayo and displays unusual similarity to the new species (for comparison, see the photographs in Frenkel et al. 2018). To solve this taxonomic issue, we designate the syntype BMNH 1947.2.15.74 as the lectotype of *Hylodes ventrimarmoratus*. In consequence, the type locality of this taxon is "El Topo, R. Pastaza, [Provincia Tungurahua,] E. Ecuador, 4200 feet" (see the part Taxonomy).

The PPPF *Pristimantis* individuals, morphologically resembling *P. albertus*, belong to two separate lineages within the *P. danae* species Group. Specimens NMP-6V 76020-21 from the area of Rio Huatziroki are genetically very close to the holotype of *P. albertus* (KU 291675, GenBank accession number: EU186695; Duellman and Hedges 2007 – average uncorrected genetic *p*-distance = 0.6 %). Specimens MUSM 31173, 32729 and NMP-6V 75061, 76024 collected in the area of Río Bravo and surroundings of Nueva Florida (for coordinates, see Table 1) cluster more closely with *P. stictogaster* and we tentatively name them *P.* cf. *stictogaster*. The average genetic uncorrected *p*-distance between *P.* cf. *stictogaster* and holotype of *P. stictogaster* is 2.8% (Fig. 2, Table 2).

Taxonomy

Pristimantis ventrimarmoratus (Boulenger, 1912)

Hylodes ventrimarmoratus Boulenger, 1912

Designated lectotype (hoc loco): BMNH 1947.2.15.74

Paralectotypes. BMNH 1947.2.15.75 and BMNH 1947.2.15.76

Type locality. "El Topo, R. Pastaza, [Provincia Tungurahua,] E. Ecuador, 4200 feet"

Note. The fourth original syntype BMNH 1947.2.15.73 may be conspecific with *Pristimantis sinschi* sp. nov. but its accurate determination remains open.

Synonymy. *Eleutherodactylus ventrivittatus* Andersson, 1945; Type locality: "Ambitagua [= Abitagua], Rio Pastaza", Provincia Tungurahua or Pastaza, Ecuador (according to Frost 2020).

Pristimantis sinschi Lehr, Moravec & Kodejš, sp. nov.

http://zoobank.org/3E920AC3-5123-4B26-8B7A-84BBF3F5B68E
Figs 4–6, Tables 1–3
Suggested English name: Ulrich Sinsch's Rubber Frog
Suggested Spanish name: Rana cutín de Sinsch

Pristimantis sp. A – Lehr et al. (2017a)
Pristimantis sp. nov. – Lehr and Moravec (2017)

Holotype. MUSM 32733 (field number IWU 367), GenBank accession numbers MW075408 (16S rRNA) and MW075426 (12S rRNA), an adult male from the Pui Pui Protected Forest (11°12'38.5"S, 74°57'28.9"W; Figs 1, 3), 1800 m a.s.l., Distrito Pichanaqui, Provincia Chanchamayo, Región Junín, Peru, collected on 16 May 2014 by Edgar Lehr and Jiří Moravec.

Paratypes. Two adult males: NMP-P6V 75060 (field number IWU 359), GenBank accession numbers MW075407 (16S rRNA) and MW075425 (12S rRNA), collected at the type locality on 14 May 2014 by Edgar Lehr and Jiří Moravec. MUSM 31165 (field number IWU 123), GenBank accession number KY962801, collected at the entrance of the Pui Pui Protected Forest (11°15'16.1"S, 74°53'30.7"W; Figs 1, 3), 1615 m a.s.l., reached from Nueva Florida in ca. 8 hours walk on 1 May 2012 by Edgar Lehr, and Rudolf von May.

Generic placement. We assign this species to *Pristimantis*, based on our molecular data (Fig. 2) and general morphological similarity to other members of the genus.

Diagnosis. A new species of *Pristimantis* not assigned to any species group having the following combination of characters: (1) Skin on dorsum shagreen with many small subconical tubercles and a narrow, hairline mid-dorsal fold, skin on ventre areolate; discoidal and thoracic folds present; dorsolateral folds absent; (2) tympanic membrane and tympanic annulus absent; (3) snout short, rounded in dorsal and lateral views; (4) upper eyelid without enlarged tubercles; EW slightly shorter than IOD; cranial crests absent; (5) dentigerous processes of vomers present; (6) males without vocal slits; nuptial pads absent; (7) Finger I shorter than Finger II; discs of digits broadly expanded, elliptical; (8) fingers with lateral fringes; (9) small conical ulnar and tarsal tubercles present; (10) heel without conical tubercles; short inner tarsal fold present; (11) inner metatarsal tubercle ovoid, 3 times as large as outer; outer metatarsal tubercle small, ovoid; low, numerous supernumerary plantar tubercles; (12) toes with lateral fringes; basal toe webbing absent; Toe V longer than Toe III; toe discs slightly smaller than those on fingers; (13) in life, dorsal ground colouration greenish-grey, reddish-brown or brown with or without a hairline mid-dorsal tan stripe; canthal stripe absent, supratympanic stripe greyish-brown; groin black with cream blotches, anterior surfaces of thighs and ventral surface of shanks black; ventral surfaces of thighs salmon and grey mottled; ventre black and cream mottled; iris pale bronze with fine black vermiculation and broad median red band through pupil and a narrow black vertical streak from pupil across lower half of iris; (14) SVL in adult males 25.7–28.8 mm (n = 3), females unknown.

Comparison. Phylogenetically, *Pristimantis sinschi* and *P. lindae* from southern Peru (Región Cusco) are sister taxa. Both species have the dorsum shagreen with subconical tubercles, ventre areolate, dorsolateral folds absent, dentigerous processes of vomers, finger and toe discs expanded, fingers and toes with lateral fringes, tarsal folds, males with vocal slits and groin and ventre cream with black reticulations. However (characters for *P. sinschi* in parenthesis), *P. lindae* has a tympanum (absent), the single known male MUSM 26528 has nuptial pads (absent), ventral surfaces of thighs pale brown and grey mottled (salmon and grey mottled) and the iris with a median horizontal dark reddish-brown streak (red) (Duellman 1978).

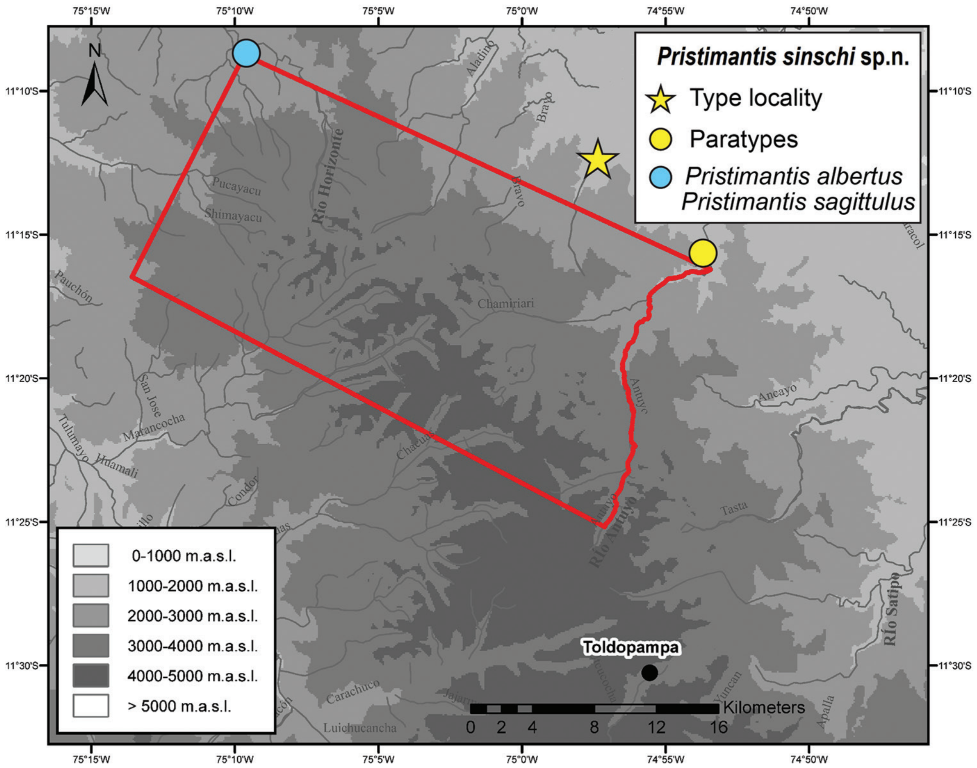

Figure 3. Pui Pui Protected Forest (red frame) with collecting sites of *Pristimantis sinschi* sp. nov. (yellow symbols) and *P. albertus* and *P. sagittulus* (blue symbol). Modified after Lehr et al. (2017).

Pristimantis sinschi is morphologically similar to five other *Pristimantis* (*P. diadematus*, *P. divnae*, *P. eurydactylus*, *P. orcus* and *P. ventrimarmoratus*) from the Amazonian lowlands and lower montane forests which have the ventre and groin contrastingly patterned in black and cream and an inner tarsal fold. However, *P. sinschi* is readily distinguished from its congeners (except for *P. ventrimarmoratus*) by lacking a tympanum and having the ventral surfaces of thighs orange brown and grey mottled. Characters for *P. sinschi* are in parenthesis in the following. Furthermore, *P. diadematus* has the ventral skin smooth (areolate), males with vocal slits (absent) and nuptial pads (absent) and the iris greenish-bronze with a median horizontal red streak or reddish-copper (pale bronze with fine black vermiculation and broad median horizontal red band) (Duellman and Lehr 2009). Male *P. divnae* have a much smaller SVL of 22.8–23.4 mm, n = 2 (25.7–28.8 mm, n = 3), scapular region with a W-shaped ridge (hour-glass shaped ridge) and iris golden with black reticulations and fine narrow black bars forming a cross or T (pale bronze with fine black vermiculation and broad median horizontal red band and a vertical streak at its lower half) (Lehr and von May 2009). Male *P. eurydactylus* lack vocal slits, have nuptial pads (absent), a maximum known SVL of 31.8 mm (28.8 mm, and scapular region with a W-shaped ridge (hour-glass shaped ridge) (Hedges and Schlüter 1992). Male *P. orcus* have nuptial pads present (absent), have a much smaller SVL of 20.0–25.1, n = 4 (25.7–28.8 mm, n = 3), the groin white or whitish-blue and black (groin black with cream blotches) and the iris gold with a copper tint and fine black reticulations (pale bronze with fine black vermiculation and broad median horizontal red band) (Lehr et al. 2009). *Pristimantis ventrimarmoratus* and *P. sinschi* both lack a tympanum and males are without vocal slits. However, male *P. ventrimarmoratus* have nuptial pads (absent), have a smaller SVL 17.8–25.5 mm, n = 8 (25.7–28.8 mm, n = 3) and the iris pale bronze with fine black flecks (pale bronze with fine black vermiculation and broad median horizontal red band) (Lynch and Duellman 1980).

Holotype description. Head slightly narrower than body, slightly wider than long; head length 42% of SVL; head width 44% of SVL; cranial crests absent; snout moderately long, rounded in dorsal and lateral views (Fig. 4A, B); eye-nostril distance 72% of eye diameter; nostrils slightly protuberant, directed dorsolaterally; canthus rostralis moderately long, broadly rounded in lateral view, weakly concave in dorsal view; loreal region weakly concave; lips rounded; upper eyelid each with several small subconical tubercles; upper eyelid width 86% of IOD; occipital and scapular region with several enlarged conical tubercles and with an hourglass-shaped fold from posterior margin of upper eyelid slightly passing the level of arm insertion; supratympanic fold short and narrow, extending from posterior margin of upper eyelid slightly curved to level of mouth corner; tympanic membrane and annulus absent; one conical postrictal tubercle present bilaterally. Choanae small, ovoid, not concealed by palatal shelf of maxilla; dentigerous processes of vomers oblique, moderately-sized, widely separated, each bearing four teeth; tongue discoidal, not notched posteriorly, covering entire floor of mouth, posterior fifth and lateral parts free.

Skin on dorsum and flanks shagreen with many small conical tubercles, dorsolateral folds absent, a narrow, hairline mid-dorsal fold present from snout towards cloacal sheath; skin on throat, chest and belly areolate; discoidal and thoracic folds present, weakly defined; cloacal sheath short.

Outer ulnar surface with four (left side) and three (right side) minute low tubercles; palmar tubercle partially divided distally; thenar tubercle ovoid; subarticular tubercles well defined, round in ventral view, conical in lateral view; supernumerary tubercles distinct, ovoid, subconical, approximately half the size of subarticular tubercles; fingers with narrow lateral fringes, much broader at base of fingers; Finger I shorter than Finger II; discs on digits of fingers broadly expanded (about 1.5 times width of digit proximal to disc), elliptical (Fig. 5A).

Hind limbs long, slender, tibia length 54% of SVL; foot length 51% of SVL; upper surfaces of hind limbs shagreen with many subconical tubercles; inner surface of thighs smooth, posterior and ventral surfaces of thighs areolate; heels without enlarged conical tubercles; outer surface of tarsus with scattered minute low tubercles; inner tarsal fold present, short and narrow, most distinct at its anterior third; inner metatarsal tubercle prominent, ovoid, three times the size of ovoid outer metatarsal tubercle;

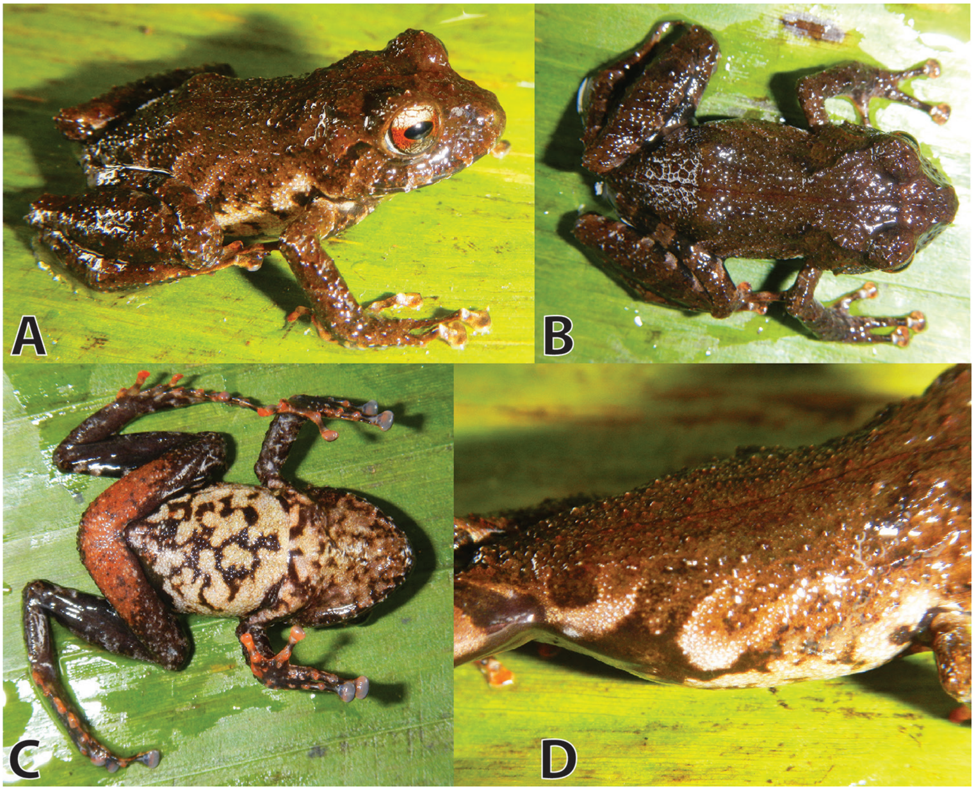

Figure 4. Life holotype (MUSM 32733, adult male, SVL 25.7mm) of *Pristimantis sinschi* sp. nov. in dorsal (**A**), dorsolateral (**B**), ventral (**C**) and lateral (**D**) views. Photos by E. Lehr.

subarticular tubercles well defined, round in ventral view, conical in lateral view; plantar supernumerary tubercles distinct, about half the size of subarticular tubercles; toes with narrow lateral fringes; basal webbing absent; discs broadly expanded, elliptical, less expanded than those on fingers; relative length of toes: 1 < 2 < 3 < 5 < 4; disc on Toe III reaching distal subarticular tubercle on Toe IV, disc on Toe V extends distal subarticular tubercle on Toe IV (Fig. 5B).

In life (Fig. 4), dorsum brown with narrow reddish-brown mid-dorsal stripe and weakly-defined reddish-brown interorbital bar; scapular region with widely-separated narrow dark greyish-brown X-shape (Fig. 4B); upper lip with two greyish-brown subocular bars and a greyish-brown supratympanic bar (Fig. 4A); arms and hind legs brown with diagonal black bars, finger and toe discs pale salmon; lower half of flanks cream, upper half of flanks with irregular-shaped dark brown diagonal stripes (Fig. 4A, D), groin and axilla black with cream blotches, posterior surface of thighs black, anterior surface of thighs with diagonal black bars interspaced with pale brown bars; throat greyish-cream with black mottling, chest and belly cream and black mottled, ventral surfaces of thighs salmon and grey mottled, arms and hind legs black and pale grey mottled, with hand and feet surfaces pale grey with palmar and plantar

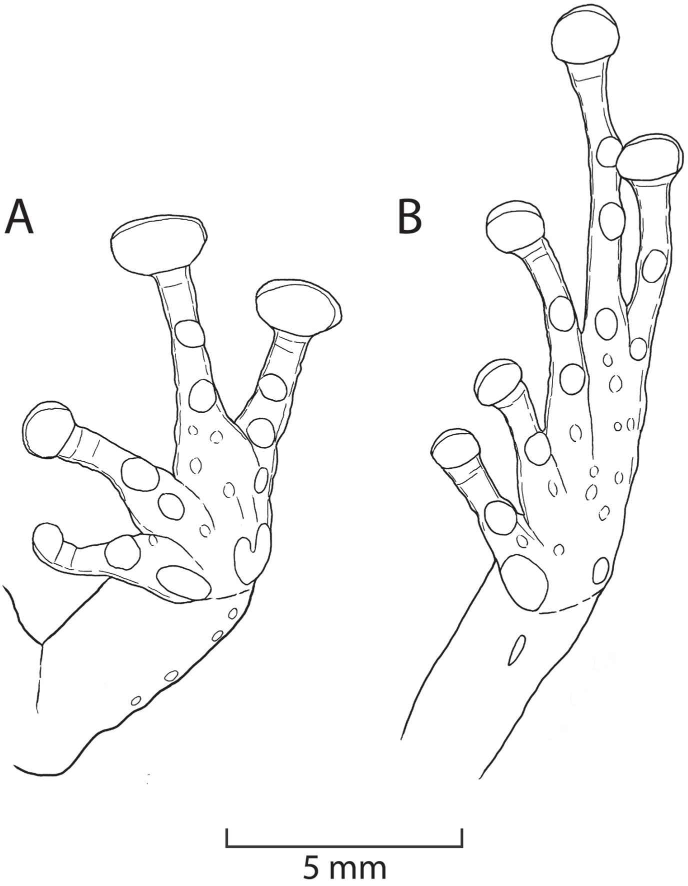

Figure 5. Ventral views of hand (**A**) and foot (**B**) of holotype of *Pristimantis sinschi* sp. nov. Drawings by E. Lehr.

tubercles salmon and discs of fingers I–II and discs of toes I–III salmon, other discs pale grey (Fig. 4C); iris pale bronze with fine black vermiculation and broad median red band through pupil and a narrow black vertical streak from pupil across lower half of iris (Fig. 4A).

In alcohol, general colouration pattern is as described for the holotype in life, except for brown which is pale brown, black which is dark brown, salmon which is cream and pale grey which is brown. Iris is pale grey.

Holotype measurements (in mm): SVL 25.7; TL 13.9; FL 13.0, HL 10.7; HW 11.2; ED 3.9; IOD 3.5; EW 3.0; IND 2.3; E-N 2.8.

Variation. All paratypes are similar to the holotype regarding morphology (see Table 3) and colouration pattern (Fig. 6). One specimen has a narrow tan mid-dorsal stripe from snout to cloaca (NMP-P6V 75060, Fig. 6D, E) and all specimens have short and narrow ridges on the anterior flanks (Fig. 6A, B, D, G). One uncollected specimen has a brownish-orange dorsal band (Fig. 6H) and the occipital region with prominent conical tubercles (Fig. 6G).

Figure 6. Variation of life male paratypes (**A–F**) and one uncollected specimen (**G–I**) of *Pristimantis sinschi* sp. nov. in dorsolateral, dorsal and ventral views **A–C** (MUSM 31165, SVL 25.8 mm) **D–F** (NMP-P6V 75060, SVL 28.8 mm) and **G–I** (uncollected). Photos by E. Lehr.

Distribution and natural history. *Pristimantis sinschi* is known from two localities in montane forest of the Pui Pui Protected Forest and its close surroundings in the eastern Andes between 1615 and 1800 m a.s.l. in the Región Junín (Figs 3, 7). The type locality is a primary montane forest with dense vegetation including ferns, tree ferns and epiphytes (bromeliads, mosses). All three frogs were found at night on the vegetation between 80 and 250 cm above ground. The holotype was found on a leaf of a tree fern at 250 cm aboveground, NMP-P6V 75060 was found on a leaf at 150 cm aboveground and MUSM 31165 was found on a leaf at 80 cm aboveground. In the Pui Pui Protected Forest, *Pristimantis sinschi* occurs syntopically with *P. albertus*; *P. ashaninka* Lehr & Moravec, 2017; *P. aniptopalmatus* (Duellman & Hedges, 2005); *P. bipunctatus* (Duellman & Hedges, 2005); *P. cruciocularis* (Lehr, Lundberg, Aguilar & von May, 2006), *P.* cf. *platydactylus* (Boulenger, 1903), *P. sagittulus* and *P.* cf. *stictogaster*. According to the sparse data available, we here classify *P. sinschi* as "Data Deficient" according to the IUCN Red List criteria.

Etymology. We dedicate this species to our colleague and friend Prof. Dr. Ulrich Sinsch in recognition of his important contributions to the South American and African herpetology. The specific epithet is used as a noun in apposition.

Figure 7. Collecting sites in montane forests of *Pristimantis sinschi* sp. nov. Type locality (**A, B**) in the close surrounding of the Pui Pui Protected Forest at 1800 m a.s.l. Second known locality (**C**) at the entrance of the Pui Pui Protected Forest at 1615 m a.s.l. Photos by J. Moravec (**A, B**) and E. Lehr (**C**).

Table 3. Measurements (in mm) of male type specimens of *Pristimantis sinschi* sp. nov. For abbreviations, see Material and methods.

Character	MUSM 32733	MUSM 31165	NMP-P6V 75060	Ranges followed by means and SD in parenthesis
SVL	25.7	25.8	28.8	25.7–28.8 (26.8 ± 1.8)
TL	13.9	14.2	15.6	13.9–15.6 (14.6 ± 0.9)
FL	13.0	13.0	14.6	13.0–14.6 (13.5 ± 0.9)
HL	10.7	10.7	11.5	10.7–11.5 (11.0 ± 0.5)
HW	11.2	11.4	11.8	11.2–11.8 (11.5 ± 0.3)
ED	3.9	3.5	3.8	3.5–3.9 (3.7 ± 0.2)
IOD	3.5	3.0	3.2	3.0–3.5 (3.2 ± 0.3)
EW	3.0	2.4	2.8	2.4–3.0 (3.1 ± 0.7)
IND	2.3	2.3	2.4	2.3–2.4 (2.3 ± 0.1)
N–E	2.8	2.6	2.8	2.6–2.8 (2.7 ± 0.1)

Pristimantis albertus Duellman & Hedges, 2007

Figs 8, 9, Table 4

Material. Five males: MUSM 31953, 31956, 31959; NMP-P6V 75067, 76021 (NMP-P6V 76021 GenBank accession numbers MW075394 (16S rRNA) and MW075415

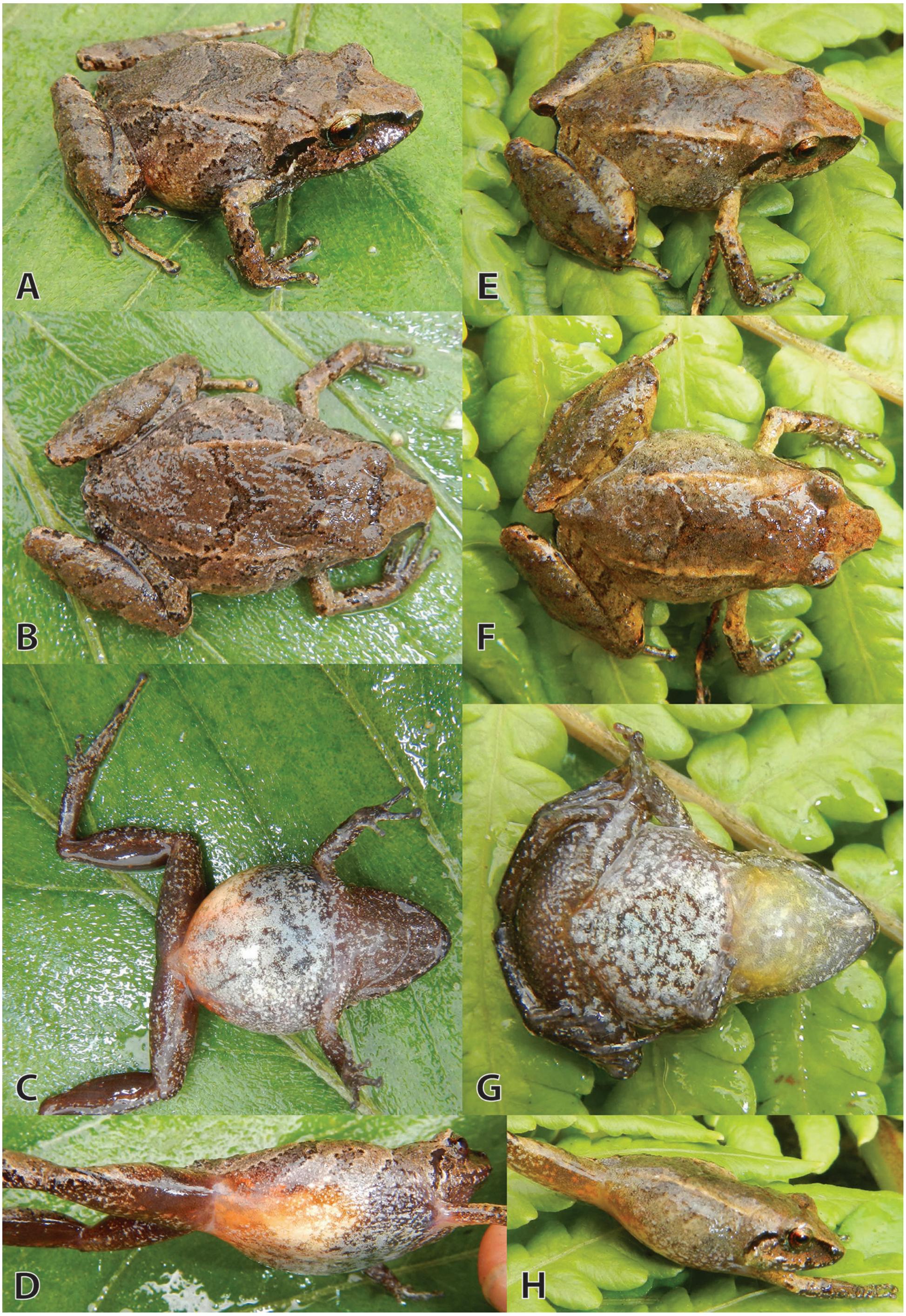

Figure 8. Life colouration of female (**A–D**, IWU 237, SVL 24.2 mm) and male (**E–H**, NMP-P6V 75067, SVL 15.5 mm) *Pristimantis albertus* in dorsolateral (**A, E**), dorsal (**B, F**), ventral **C, G**) and lateral (**D, H**) views. Photos by E. Lehr.

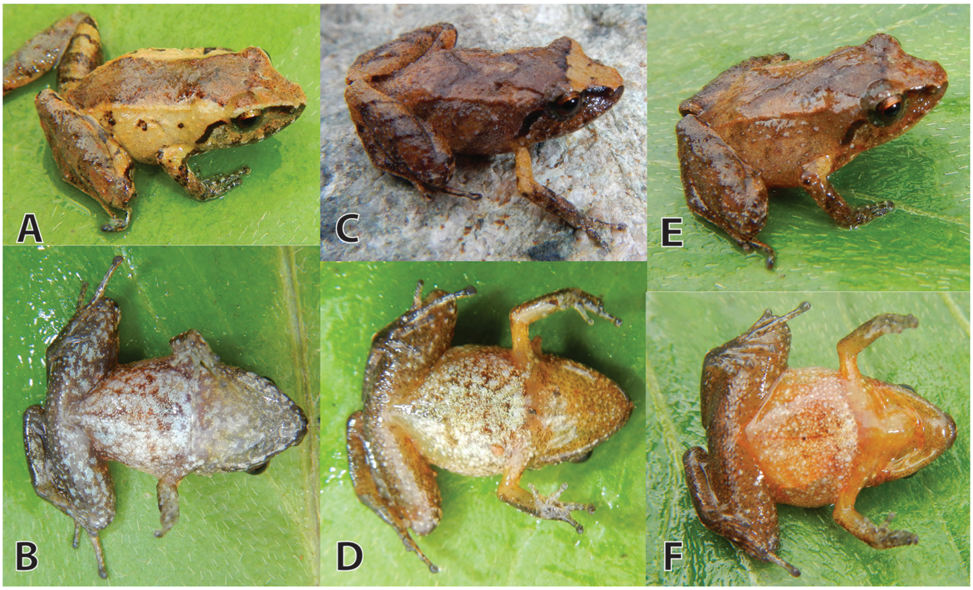

Figure 9. Colouration in life variation of males of *Pristimantis albertus* **A, B** (MUSM 31956, SVL 13.7 mm) **C, D** (IWU 257, SVL 13.4 mm) **E, F** (MUSM 31959, SVL 12.9 mm). Photos by E. Lehr.

(12S rRNA)), from the Pui Pui Protected Forest (Rio Huatziroki valley, 11°07'37.2"S, 75°10'37.0"W; Fig. 3), 1970 m a.s.l., Distrito Pichanaqui, Provincia Chanchamayo, Región Junín, Peru, collected on 13–16 June 2013 by Edgar Lehr, Jiří Moravec, Juan Carlos Cusi and Rudolf von May. Three females: MUSM 31957; NMP-P6V 75068, 76020 (NMP-P6V 76020 GenBank accession numbers MW075393 (16S rRNA) and MW075414 (12S rRNA), same locality and collecting data as the males.

Diagnostic characters. In general, the newly-collected and genetically-determined individuals of *Pristimantis albertus* correspond to the description of the type specimens. However, they differ in the following features: (1) discoidal fold is present, weakly defined (discoidal fold absent, according to Duellman and Hedges 2007); (2) dentigerous processes of vomers are present (absent, according to Duellman and Hedges 2007); (3) groin is orange in both sexes (Figs 8C, D, H, 9D, F), the orange colouration can continue to posterior parts of flanks and anterior parts of thighs, rarely the orange colouration is present in the axils (MUSM 31959).

Measurements (Table 4). The males are relatively small (SVL 12.9–19.5 mm, n = 5). All lack nuptial pads, but all have vocal slits, a distinct subgular vocal sack and, therefore, are regarded as adults. Females are represented by one adult (NMP-P6V 76020) and two subadult (MUSM 31957, NMP-P6V 75068) specimens. Snout-vent length of the adult female exceeds the size published for the type specimens (24.2 vs. 19.7–20.7 mm in Duellman and Hedges 2007).

Colouration of males in life (Fig. 9). The dorsal colouration resembles the colouration of the adult females. In one individual (MUSM 31956), the light brown

Table 4. Measurements (in mm) of *Pristimantis albertus*. For abbreviations, see Material and methods.

Character	NMP-P6V 75067	NMP-P6V 76021	MUSM 1953	MUSM 31965	MUSM 31959	NMP-P6V 76020	NMP-P6V 75068	MUSM 31957
SEX	M	M	M	M	M	F	F	F
SVL	15.5	13.4	19.5	13.7	12.9	24.2	14.3	14.6
TL	8.6	7.3	9.0	7.6	7.0	12.3	7.8	8.0
FL	6.5	5.6	8.1	6.2	5.6	10.2	6.0	6.1
HL	6.1	6.0	7.7	6.1	5.5	9.6	5.7	6.3
HW	5.9	5.3	7.4	5.5	5.1	9.1	5.4	5.6
ED	2.1	1.7	2.2	1.7	1.8	2.5	1.9	1.8
TY	0.7	0.6	0.9	0.7	0.6	1.2	0.6	0.6
IOD	1.9	2.1	2.3	1.8	1.8	2.8	1.8	2.0
EW	1.2	1.2	1.7	1.3	1.0	1.6	1.0	1.1
IND	1.9	1.8	2.3	1.9	1.7	2.9	1.9	1.8

colouration of the dorsum is sharply contrasting with the light tan flanks. The throat is brown with cream flecks, the belly is cream with brown mottling and the vocal sack is greenish-yellow.

Distribution and natural history. Our record of *Pristimantis albertus* from the PPPF lies ca. 65 km straight SE of the species type locality and represents the first record of this species for the Region Junín (Fig. 3).

Pristimantis sagittulus (Lehr, Aguilar & Duellman, 2004)

Material. One male: MUSM 31952, from the Pui Pui Protected Forest (Rio Huatziroki valley, 11°07'37.2"S, 75°10'37.0"W; Fig. 3), 1970 m a.s.l., Distrito Pichanaqui, Provincia Chanchamayo, Región Junín, Peru, collected on 14 June 2013 by Edgar Lehr, Jiří Moravec, Juan Carlos Cusi and Rudolf von May.

Distribution and natural history. Our record of *Pristimantis sagittulus* from the PPPF lies ca. 65 km straight SE of the species type locality (Lehr et al. 2004) and represents the first record of this species for the Region Junín (Fig. 3).

Comparative specimens examined

Pristimantis aniptopalmatus (1): Peru, Junín, buffer zone of the Pui Pui Protected Forest, 1970 m a.s.l., MUSM 33996, NMP-P6V 75055.

Pristimantis ashaninka (5): Peru, Junín: border of the Pui Pui Protected Forest, 1700 m a.s.l., MUSM 36517 (holotype), MUSM 32736, 32742, NMP-P6V 75063, 75064, all paratypes.

Pristimantis bipunctatus (1): Peru, Junín, buffer zone of the Pui Pui Protected Forest, 1970 m a.s.l., MUSM 31954.

Pristimantis lindae (3): Peru, Cusco: Alto Shima, 1785 m a.s.l., MUSM 26528, 26542; Alto Shima, 1790 m a.s.l., MUSM 26540.

Discussion

With the description of *Pristimantis sinschi*, the number of species in this genus known from Peru rises to 140 (AmphibiaWeb 2020), 13 of which (*P. albertus*, *P. aniptopalmatus*, *P. ashaninka*, *P. attenboroughi*, *P. bipunctatus*, *P. bounides*, *P.* cf. *platydactylus*, *P.* cf. *stictogaster*, *P. cruciocularis*, *P. humboldti*, *P. puipui*, *P. sagittulus* and *P. sinschi*) have been recorded inside the PPPF or its close surroundings. Comparison with the anuran list of the more intensively surveyed Yanachaga-Chemillén National Park (YCNP; see Angulo et al. 2016), which is located ca. 100 km NW of the PPPF, reveals that seven (54%) *Pristimantis* species occurring in PPPF are unknown from the YCNP. This leads us to the conclusion that the anuran fauna of the isolated PPPF area is characterised by an unusually high degree of local endemism and, therefore, deserves adequate protection. We predict that the amphibian and reptile species richness of the PPPF is much higher than is currently known because large parts remain unexplored.

The description of *Pristimantis albertus* was based on two adult females obtained by Hedges in 1987 from Rio San Alberto, 2.1 km E of Oxapampa (Provincia Pasco, Peru) at 1970 m a.s.l. (Duellman and Hedges 2007). It was assigned to the *Pristimantis danae* species Group (Hedges et al. 2008) and briefly accounted for by Duellman and Lehr (2009). Later, it was reported and documented with colour photographs from the Yanachaga-Chemillén National Park (Angulo et al. 2016). Samples of three newly-collected specimens of *P. albertus* were included in genetic analyses performed by Lehr and von May (2017) and Lehr et al. (2017b). Nevertheless, no additional data on the distribution or morphology of this species were published. Our series of eight specimens of *P. albertus* collected in the PPPF includes the first males of the species and consequently leads us to update the diagnostic and phenotypical characters of the species.

With a long, acuminate snout and a broad, longitudinal, red stripe on the posterior surfaces of the thighs, *Pristimantis sagittulus* can easily be distinguished from all its congeners. Previously, the species was only known from its type locality at San Alberto, the Yanachaga-Chemillén National Park and adjacent localities at elevations of 1970–2479 m a.s.l. in the Region Pasco (Duellman and Lehr 2009; Angulo et al. 2016).

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RESEARCH ARTICLE

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Hidden in plain sight: a new frog species of the genus *Blommersia* from the oceanic island of Mayotte, Comoros archipelago

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Abstract

The amphibian fauna of the western Indian ocean volcanic island of Mayotte is currently constituted by two species belonging to two genera of the anuran family Mantellidae: *Blommersia transmarina* and *Boophis nauticus*. These were recently described after intense fieldwork on the herpetofauna of the island. We here describe a third new species of frog from Mayotte, based on morphological and molecular data, that occurs in sympatry with the others and was utterly unnoticed until now. Genetic analyses of the16S rRNA gene, including all described and several undescribed species of the genus *Blommersia* from Madagascar and Mayotte, confirms that the new species is the sister species of *Blommersia transmarina*. Both species show apparent morphological differences as well as different life histories, ecology and genetics that confirm *Blommersia nataliae* **sp. nov.** as a new species. We propose an IUCN Red List status of Critically Endangered for *B. nataliae* **sp. nov.**

Keywords
Amphibia, Anura, *Blommersia nataliae* sp. nov., Comoros archipelago, Mantellidae, Mayotte

Introduction

The Mantellidae is a hyperdiverse family of frogs mostly endemic to Madagascar (Glaw and Vences 2006), with few representatives known from the Comoran island of Mayotte, an oceanic island separated from Madagascar by water depths of more than 3000 m. So far, one species of the genus *Boophis* and one species of the genus *Blommersia* were known from Mayotte (Vences et al. 2003), which have recently been described as *Blommersia transmarina* and *Boophis nauticus* (Glaw et al. 2019). Those species represent one of the best examples of dispersal across oceanic barriers, as their ancestors colonized Mayotte by oceanic dispersal from Madagascar circa 8–6 Mya (Vences et al. 2003; Crottini et al. 2012).

The genus *Blommersia* comprises eleven described frog species and constitutes a monophyletic radiation with at least six undescribed, genetically divergent lineages that may warrant species status, suggesting that the genus is likely more diverse than currently known (Vieites et al. 2009). Species in this genus are of small size and mostly terrestrial, occurring mainly in swamps, rice fields, paddy fields and other water bodies, which could be degraded, in open lands, as well as in dry and rain forests across Madagascar. They usually call during the night from perches, showing distinct advertisement calls that are diagnostic of each species, and some species are morphologically very similar. Like some Malagasy microhylids of the genus *Stumpffia*, which are miniaturized frogs of SVL from 8–9 mm (*S. contumelia*) to 28 mm (*S. staffordi*) (Rakotoarison et al. 2017), *Blommersia* species tend to miniaturization with the smallest species having snout-vent lengths (SVL) around 14–16 mm (*B. kely*, *B. sarotra*, *B. domerguei*) to ca. 26 mm (*B. wittei*) (Glaw & Vences, 2007). This trend towards miniaturization makes them a remarkable group to study diversification patterns and speciation mechanisms related to body size evolution.

In this context, the known species present on Mayotte offer an exciting opportunity to study the morphological and life history evolution of species that have evolved in isolation without the presence of other congeners for the last 5 or 6 million years. *Blommersia transmarina* evolved into a bigger body size than any other *Blommersia* from Madagascar, likely having undergone a process of moderate gigantism compared to the rest of *Blommersia* species (Santos-Santos et al. 2020). During fieldwork on the Comoran island of Mayotte to collect specimens of this *Blommersia* species, we discovered a second undescribed species of much smaller body size that occurs in syntopy. This raises several questions related to the origin and evolution of these two species. First, are they sister species or the result of two independent colonizations from Madagascar? Second, if they are sister taxa, how did the morphological and ecological diversification processes take place in isolation with empty niches available and without other potential frog competitors? In this study, we integrate morphological and genetic data to formally describe and name this new taxon, presenting the first data on its morphology, life history and ecology.

Materials and methods

Voucher collection

Individuals of *Blommersia transmarina* were located by tracking their calls during regular searches to localize calling males, as well as by visiting different types of water bodies and forests in Mayotte. Although this species calls during the night, the newly discovered one is much more secretive in terms of calling as no calls were ever heard in breeding places during reproduction. Individuals of the new species were found first on the forest ground mixed with *B. transmarina*, and later we discovered their breeding places where reproduction could be observed.

Individuals were euthanized using chlorobutanol, fixed in 90% ethanol, and preserved in 70% ethanol. Tissue samples were taken in the field and preserved in 99% ethanol or RNAlater for molecular studies. Preserved specimens are deposited at the Museo Nacional de Ciencias Naturales (**MNCN**), Madrid, Spain. Code DRV corresponds to D. Vieites' field numbers.

Morphological measurements

Morphological measurements were taken by D. Vieites, using a Vernier caliper, to the nearest 0.1 mm (Table 1): SVL (snout-vent length), HW (head width at its widest point), HL (head length measured from the tip of the snout to the maxillary commissure), ED (horizontal eye diameter), END (eye-nostril distance, measured from the anterior corner of the eye to the middle of the nostril), NSD (nostril-snout tip distance), NND (nostril-nostril distance), TD (horizontal tympanum diameter), HAL (hand length, measured from the base of the hand to the tip of the finger III), FORL (forelimb length, measured from the axilla to the tip of the finger III with forelimb extended), HIL (hind limb length, measured from the center of the cloaca to the tip of toe III), FOL (foot length, measured from the base of the inner metatarsal tubercle to the tip of toe IV), FOTL (foot length including tarsus), TIBL (tibia length, measured as the distance from the outer surface of the flexed knee to the heel/tibiotarsal inflection), FGL (femoral gland length), FGW (femoral gland width), FGD (minimal femoral gland distance from each other), and RHL (relative hindlimb length: point reached by the tibiotarsal articulation when the hindlimb is appressed along the body). RHL is coded as follows: when the hindlimb is appressed along the body the tibiotarsal articulation reaches the (1) anterior eye corner, (2) eye center, (3) between the eye and nostril, (4) nostril, (5) snout tip, (6) between the nostril and snout tip, and (7) passes the snout tip. Measurements of the type series of *B. wittei* were taken from Vences et al. (2010) and Pabijan et al. (2011).

Molecular analysis

DNA was extracted, and a fragment of 489bp of the mitochondrial 16S rRNA gene was amplified using primers 16S-AL and 16S-BH (see Vences et al. 2005). PCRs were per-

Table 1. Measurements of *Blommersia nataliae* sp. nov. and *B. transmarina* for comparison. See methods for abbreviations. The holotype of *B. nataliae* sp. nov. is shown in bold letters.

Species	Locality	Field number	MNCN catalog	Sex	SVL	HW	HL	TD	ED	END	NSD	NND	FORL	HAL	HIL	FOTL	FOL	TIBL	FGL	FGW	FGD	RHL
B. nataliae sp. nov.	Mont M'Sapere	DRV6854	MNCN50447	F	19.6	7.4	7.2	1.7	2.9	2	1.6	2.7	14	5.5	36	16	10	11				3
	Mont M'Sapere	DRV6855	MNCN50448	F	19.8	7.7	8.1	1.9	2.9	2	1.7	2.9	15	6	37	16	11	11				3
	Mont M'Sapere	DRV6869	MNCN50449	F	20.0	8.1	8.6	1.6	2.6	2	2	2.8	14	6	37	16	10	12				4
	Mont M'Sapere	DRV6868	MNCN50450	F	22.0	7	8.8	1.4	2.9	1.8	1.6	2.8	14	5.8	38	17	11	12				3
	Mont M'Sapere	DRV6808	MNCN50451	F	23.0	7.3	8.7	1.5	2.4	2.1	1.8	2.9	15	6.2	38	18	12	12				4
	Mont M'Sapere	DRV6862	MNCN50452	M	17.9	5.9	7	1.4	2.5	1.7	1.3	2.6	11	5	33	14	8.8	10	2	1.2	2.6	5
	Mont M'Sapere	DRV6857	MNCN50453	M	18.4	6.9	7.5	1.6	2.6	1.9	1.4	2.4	13	5.4	31	14	8.5	9.9	2.4	1.3		3
	Mont M'Sapere	DRV6861	MNCN50454	M	18.4	7.3	7.8	1.7	2.3	2	1.6	2.5	14	5.6	35	16	10	11	2.6	1.2		5
	Mont M'Sapere	DRV6859	MNCN50455	M	18.5	6.5	7.1	1.5	2.2	1.8	1.2	2.2	14	5.7	35	16	10	11	2	1.1		5
	Mont M'Sapere	**DRV6867**	**MNCN50456**	**M**	**18.6**	**6.3**	**7.5**	**1.5**	**2.8**	**2**	**1.4**	**2.4**	**14**	**5.4**	**33**	**15**	**9.7**	**10**	**3**	**1.8**	**2.3**	**3**
	Mont M'Sapere	DRV6863	MNCN50457	M	19.0	6.6	7.7	1.9	2.7	2.2	1.5	2.4	14	5.8	38	17	11	11	2.6	1.1		5
	Mont M'Sapere	DRV6860	MNCN50458	M	20.5	6.8	7.4	1.5	2.9	1.9	1.5	2.6	13	5.5	37	17	9.9	12	2.7	1.1	2.7	4
B. transmarina	Mont Choungi	DRV6835	MNCN50430	F	29.3	11	12	2.4	4	2.8	1.9	3.7	21	8.8	61	26	17	18				7
	Mont Combani	DRV6848	MNCN50431	F	26.0	9.1	10	2.4	3.5	2.7	1.9	3.3	20	7.8	52	22	14	16				7
	Mont Combani	DRV6805	MNCN50432	F	29.1	10	12	2.1	4.1	2.5	2	3.2	22	8.9	56	25	17	17				7
	Mont M'Sapere	DRV6813	MNCN50433	F	30.4	11	13	2.8	4.3	2.9	2	3.6	23	9.9	60	26	18	19				7
	Mont Bénara	DRV6831	MNCN50434	M	25.5	9.8	9	2.6	3.6	2.5	1.8	3	21	8.2	48	22	14	15	4.6	1.7		7
	Mont Bénara	DRV6832	MNCN50435	M	25.5	8.5	9.8	2.4	3.1	2.5	1.6	2.9	20	8.6	50.9	22	14	15	4.5	1.6	1.5	7
	Mont Bénara	DRV6833	MNCN50436	M	27.5	9.1	10	2.1	3.4	2.7	1.8	3	19	8.1	53	23	15	16	4.9	1.7		7
	Mont Bénara	DRV6841	MNCN50437	M	24.6	8.7	11	2.3	3.7	2.5	2.2	3.1	20	8.1	49	21	15	15	4.8	1.6	1	7
	Mont Bénara	DRV6838	MNCN50438	M	25.5	8.8	9.3	2.8	3.2	2.6	1.9	3	17	7.5	49	23	15	14	5	1.6		7
	Mont Bénara	DRV6836	MNCN50439	M	26.0	9.3	9.9	2.5	3.6	2.6	1.7	3	17	7.6	45	22	14	15	5.6	1.7	1.6	7
	Mont Combani	DRV6852	MNCN50440	M	24.5	8.4	9.7	2.1	3.4	2.2	1.4	3	16	6.4	47	21	13	15	3.8	1.5		7
	Mont Combani	DRV6819	MNCN50441	M	25.0	8.4	10	2.7	3.4	2.2	1.7	3.2	18	7.4	44	20	13	14	4.4	2		7
	Mont Combani	DRV6818	MNCN50442	M	26.0	8.8	9.4	2.4	3.5	2.8	1.7	3	19	7.8	49	24	14	15	4.6	1.7		7
	Mont Combani	DRV6806	MNCN50443	M	26.5	8.7	9.2	2.2	3.7	2.6	1.9	3.3	15	7.8	51	23	15	15	5.7	1.8	1	7
	Mont Combani	DRV6849	MNCN50444	M	27.0	9.4	12	2.4	3.9	2.5	2	3.6	18	8.6	46	23	16	15	4.5	1.6	1.6	7
	Mont Combani	DRV6850	MNCN50445	M	27.0	9.4	10	2.4	3.4	2.5	1.9	3.4	18	8.3	44	24	16	16	4.8	1.6		7
	Mont M'Sapere	DRV6807	MNCN50446	M	29.0	9.7	11	2.4	3.9	2.5	2.2	3.5	20	8.5	50	22	14	16	5.3	2	1.1	7

formed in 25 μL reactions using ca. 50 ng genomic DNA, 10 pmol of each primer, 15 nmol of each dNTP, 50 nmol additional MgCl2, and the Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM MgCl2, and 0.01% gelatin) and 1 U of standard Taq DNA polymerase. PCR conditions follow Vieites et al. (2006): an initial denaturation step at 94 °C for 90 s; 35 cycles at 94 °C for 30 s, annealing temperature two degrees below the melting temperature of each primer for 45 s, extension at 72 °C for 60 s; final extension of 10 min at 72 °C. PCR products were purified using spin columns in a robot before cycle sequencing. A 10 μL sequencing reaction included 1–2 μL of template, 1 μL of sequencing buffer, 2 μL of 2 pmol primer, 1.8 μL of ABI sequence mix (BigDye Terminator version 3.1 Sequencing Standard, Applied Biosystems) and 3.2–4.2 μL of water. The sequence reaction was 33 cycles of 10 s at 96 °C, 10 s at 50 °C and 4 min at 60 °C. These were subsequently resolved on a 3100 ABI automated sequencer. Sequences were aligned in Geneious v. 11.1.5 (https://geneious.com) using the Clustal-Wallis algorithm, and the alignment was corrected by eye resulting in a 492 bp alignment.

For phylogenetic analysis, we assembled a dataset of sequences for all *Blommersia* species available in GenBank that cover all described and several undescribed candidate species (Vieites et al. 2009; Vences et al. 2010; Pabijan et al. 2011). Maximum likelihood phylogenetic analysis was performed using the program RaxML (Stamatakis 2014) with 1000 bootstrap replicates and the GTR model. *Mantella laevigata* and *Guibemantis liber* were used as outgroups. Newly determined sequences' GenBank accession numbers correspond to the series MW025124–MW025133.

Results

Molecular phylogenetics

The recovered phylogenetic relationships between *Blommersia* species are shown in Fig. 1. We recovered three main clades within *Blommersia*: one constituted by *B. angolafa*, *B. grandisonae*, *B. sarotra* and *B. kely*, and five divergent undescribed lineages; the second constituted by *B. galani*, *B. dejongi*, *B. domerguei*, *B. blommersae* and *B. variabilis*; and a third clade constituted by *B. wittei*, an undescribed species resembling *B. wittei*, and two deep genetic lineages from Comoros. All the major clades had high bootstrap support with likelihood values higher than 99%. These two Comoroan lineages form a monophyletic group, having 4.3% divergence considering uncorrected pairwise 16S distances (21 substitutions), a value above the proposed 3% divergence in 16S typically used for recognition of distinct mantellid species (Vieites et al. 2009). One of them corresponds to the recently described *B. transmarina* as per sequence identity when compared to sequences provided by Vences et al. (2003) and Glaw et al. (2019). The other can be considered as a new candidate species, *Blommersia nataliae* sp. nov. This new candidate species shows 34 substitutions compared to *B. wittei* that results in an uncorrected pairwise divergence of 6.9 %, and there are 31 substitutions between *B. transmarina* and *B. wittei* that correspond to a 6.3% uncorrected pairwise distance.

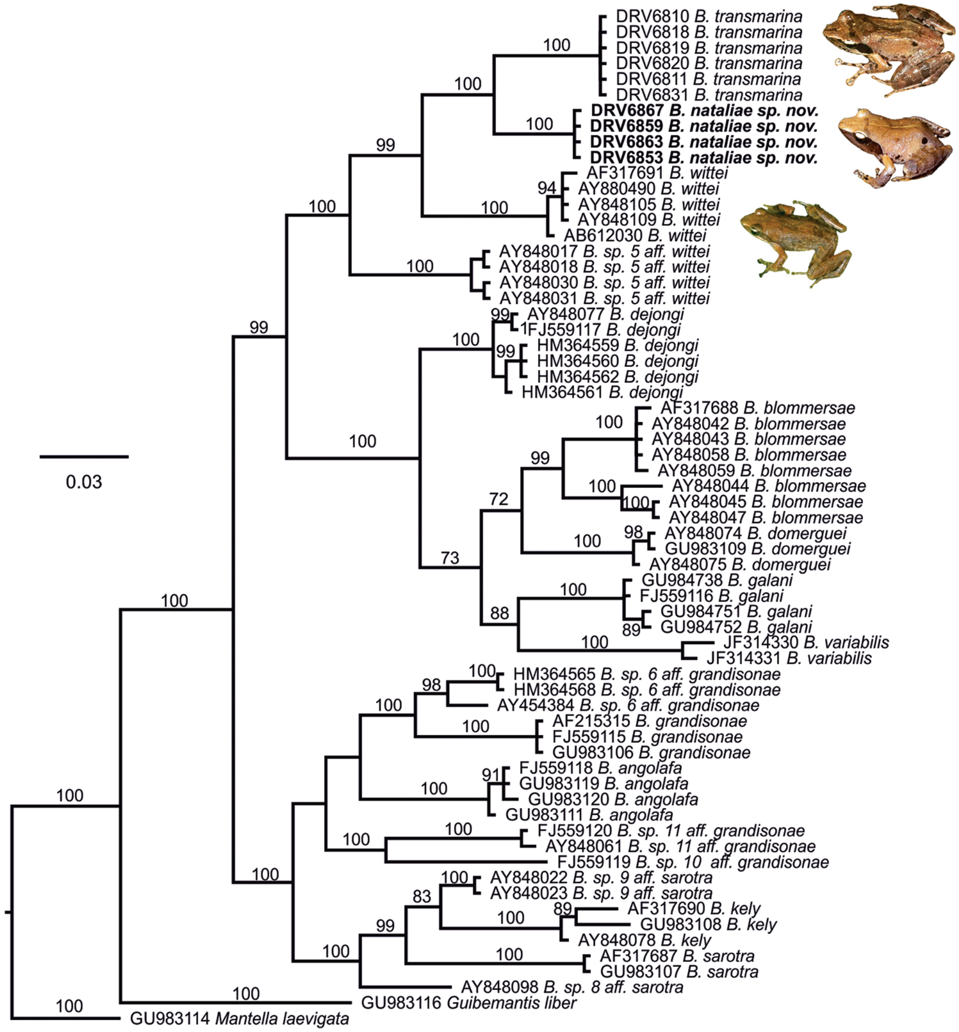

Figure 1. Maximum Likelihood phylogram of 16S rRNA relationships within *Blommersia*. Maximum Likelihood bootstrap support is shown above branches.

Taxonomy

The two *Blommersia* lineages from Mayotte differ from each other, and from other *Blommersia* species, by several morphological traits: (1) the shape, position, and size of the femoral glands (Figs 2–4), (2) the presence or absence and shape of vomerine teeth, (3) tympanum size, (4) the extent to which lateral metatarsalia are fused or separated only by webbing and webbing formulae, (5) tongue shape, (6) relative hindlimb length, and (7) adult body size. The two *Blommersia* occur syntopically on Mayotte's island and cannot be confused in the field with any other *Blommersia*.

Following an integrative taxonomic approach, morphological, genetic, life history, and biogeographic data support recognizing the newly discovered lineage on Mayotte as a new species under the evolutionary and biological species criteria. We therefore scientifically describe and name it here, providing a detailed description of adult morphology, intraspecific variation, and the first data on its life history and ecology.

Blommersia nataliae sp. nov.

http://zoobank.org/8D15676C-402C-417E-B185-5551C356CA44

Holotype. An adult male, left thigh muscle removed for genetic analyses. Original field number: "DRV6867, David R. Vieites collection". Museo Nacional de Ciencias Naturales catalog number: MNCN50456. Collected in a degraded forest with giant bamboo, in forest leaf litter at the Mont M'Sapere, island of Mayotte (French Overseas Department), Comoros archipelago, -12.7656°S, 45.1852°E 500 m a.s.l. the 25th November 2012 by D. Vieites and M. Peso Fernández.

Paratypes. Females DRV6808 (MNCN50451), DRV6854 (MNCN50447), DRV6855 (MNCN50448), DRV6868 (MNCN50450), DRV6869 (MNCN50449); males DRV6857 (MNCN50453), DRV6859 (MNCN50455), DRV6860 (MNCN50458), DRV6861 (MNCN50454), DRV6862 (MNCN50452), DRV6863 (MNCN50457), collected at the type locality at the Mont M'Sapere in 2012 by D. Vieites and M. Peso Fernández.

Etymology. Noun in the genitive case. D. Vieites and S. Nieto dedicate this species to their daughter Natalia Vieites Nieto, who has a birthmark resembling the beautiful conspicuous round moon-like brown spot characteristic of the species.

Diagnosis. Assigned to the genus *Blommersia* in the family Mantellidae and subfamily Mantellinae by a combination of (1) presence of femoral glands and absence of nuptial pads in males, (2) presence of intercalary elements between ultimate and penultimate phalanges of fingers and toes (verified by external examination and microCT scanning), (3) presence of a single subgular vocal sac in males, (4) small size (adult SVL < 30 mm), and (5) molecular data.

Within the genus *Blommersia*, *B. nataliae* sp. nov. is characterized by the following unique suite of morphological characters: (1) small adult body size (SVL 18–23 mm), (2) round femoral glands that are distantly separated in males, (3) inconspicuous vomerine teeth, (4) ovoid tongue, (5) tibiotarsal articulation reaching between the eye and the nostril when adpressed along the body. Furthermore, the new species is differentiated from all other species of *Blommersia* by a significant molecular genetic differentiation (≥ 4.3% uncorrected pairwise-distance in 16S).

Blommersia nataliae sp. nov. can be distinguished from all other described *Blommersia* species except *B. wittei* and *B. transmarina* by the presence of vomerine teeth (vs. absence) and having separated metatarsalia (vs. unseparated).

Blommersia nataliae sp. nov. can be distinguished from its syntopic sister taxon *B. transmarina* by its rounded, distantly separated femoral glands (versus oblong, less separated glands; Figs 2–3). Fig. 4 represents the relative femoral gland length versus the relative distance between the femoral glands' inner edges for both species and their sister taxon from Madagascar, *B. wittei*. *B. wittei* has an intermediate position between *B. nataliae* sp. nov. and *B. transmarina*; where *B. nataliae* sp. nov. presents rounded and shorter glands that are ca. two times more separated between each other than in *B. transmarina* (median FGD 2.6±0.2 mm vs. 1.3±0.3 mm, respectively) and ca. half shorter (median FGL 2.6±0.4 mm vs. 4.8±0.5 mm) (see also Figs. 2–3). *Blommersia nataliae* sp. nov. also differs from *B. transmarina* in having inconspicuous vomerine teeth versus well developed and showing a V shape, ovoid tongue (vs. bifid), shorter hindlimbs with tibiotarsal articulation reaching between the eye and the nostril (vs. surpassing well the snout when appressed along the body), less distinct inner metatarsal tubercle, webbing formula [1(1), 2i(1.75), 2e(1), 3i(2.5), 3e(2), 4i/e(3), 5(1.5) versus 1(1), 2i(1–1.5), 2e(0.5), 3i(1.5), 3e(1), 4i(2–2.5), 4e(1.5–2), 5(0.5)], and by showing a brown facial mask from the snout, under the loreal region, to the tympanum, and by the presence of (usually) one very conspicuous moon-like spot on the back of each flank, close to the pelvic region and the hindlimbs. From *B. wittei*, it differs in femoral gland dimensions and position (see Fig. 4), ovoid tongue (vs. bifid), slightly longer hindlimbs with tibiotarsal articulation reaching between the eye and the nostril (vs. reaching the anterior corner of the eye), less distinct inner metatarsal tubercle, webbing formula, and in coloration. *Blommersia wittei* has a proportionally smaller tympanum than both *B. nataliae* sp. nov. and *B. transmarina* (mean ratio TD/SVL 0.068±0.007, vs. 0.081±0.009 in *B. transmarina* and 0.080±0.010 in *B. nataliae* sp. nov.).

Description of the holotype (Fig. 2). Male specimen in good state of preservation. Part of the left thigh taken for genetic analyses. SVL = 18.6 mm. The body is slender; the head is slightly longer than wide but not wider than the body. Snout slightly pointed and rounded in lateral views with protuberant nostrils directed laterally, nearer to the tip of snout than to eye; canthus rostralis indistinct and straight; loreal region straight; tympanum distinct and rounded, with a diameter of 60% of the eye diameter; supratympanic fold present and slightly distinct behind the tympanum, but indistinct in its anterior part between the eye and the tympanum; tongue slender and ovoid, slightly notched posteriorly but not bifid; vomerine teeth present but very inconspicuous and very small, hard to see, and not grouped; maxillary teeth rudimentary; choanae rounded. The arms are slender with distinct, single subarticular tubercles, the inner and outer metacarpal tubercles distinct, the fingers without webbing, and the relative length of the fingers is 1<2<4<3; terminal finger discs are enlarged and nuptial pads absent. Hindlimbs are relatively robust; the tibiotarsal articulation reaches between the eye and the nostril when the hindlimb is appressed along the body; the lateral metatarsalia are separated; the inner metatarsal tubercle is small and the outer distinct; toe discs are enlarged, and the webbing between toes weakly developed [1(1), 2i(1.75), 2e(1), 3i(2.5), 3e(2), 4i/e(3), 5(1.5)]. The skin on the dorsal surface is smooth without folds or ridges. The ventral skin is uniformly smooth. Femoral glands are very distinct in life, as well as after ethanol preservation, in external view.

Figure 2. Dorsolateral and ventral views of the holotype of *Blommersia nataliae* sp. nov. DRV6867 (MNCN50456). Note the color and shape of the femoral glands which are a diagnostic character to distinguish it from its sister taxon *B. transmarina*.

Coloration of the Holotype (Fig. 2). In life, the overall color is creamy light brown with golden spots on the flanks, arms, and legs. It shows a thin yellowish line from the midpoint between the eyes to the vent. The legs are slightly darker brown and bands are visible. It shows a dark brown spot on the flanks and a characteristic larger moon-like spot on each flank's back close to the pelvic region and the hindlimbs. It presents a dark brown facial mask that covers from the snout, under the loreal region, to the tympanum (see Fig. 2). The loreal region, as well as the outer iris periphery, shows a thin golden-colored line. The pupil is black and the inner iris area dark brown, while the outer iris area is golden with dark reticulations. The throat is brownish. The belly is light brown with some whitish, silver, and gold spots. The femoral glands are oval with a yellowish coloration and 9–10 circular internal rounded structures. After eight years in preservative, the back shows a creamy brown coloration that gets lighter towards the sides of the body, but the golden spots and dorsal line are lost. Ventral coloration is light brown without evident golden spots. The moon-like brown spot in the posterior part of the flanks is still evident, as well as the small ones on the flanks behind the arms. The femoral glands are whitish.

Variation. The measurements of the holotype and paratypes are provided in Table 1. Sexual dimorphism is apparent in several characters: males present distinctive femoral glands, females are larger than males [males: median±SD SVL= 18.5±0.8 mm (min-max=17.9–20.5); females: 20±1.5 mm (min–max=19.6–23 mm)]. The color pattern is rather homogeneous, but females show an overall much creamier coloration than males, which are slightly darker. Both males and females show the characteristic brown rounded moon-like spot on the posterior flanks of the body, as well as some blotches on the lateral body sides behind the arms of variable size and shape. Vomerine teeth are more evident in specimen DRV6854 (MNCN50447), but only on one side of the vomer, and in DRV6855 (MNCN50448) and DRV6808 (MNCN50451) on both sides and more evident than in the holotype. Female DRV6855 (MNCN50448) lacks the moon-like blotch in the posterior side of the body, but shows a large circular one behind the arms. Female DRV6808 (MNCN50451) shows a similar pattern, but with a smaller blotch. Female DRV6868 (MNCN50450) shows a constellation of small rounded to irregular dark blotches from behind the arms to the inguinal region.

Natural history of *Blommersia nataliae* sp. nov. The species was found on the ground and in its breeding places: cut bamboo trunks filled with water (Fig. 5). There, we observed several males waiting for females to reproduce the night of 28th November 2012, with a temperature of 24.6 °C. No frogs were seen in the breeding places during the day. No call was ever heard during reproductive periods despite several attempts and leaving a digital recorder running for two hours at a breeding spot with active frogs at night, while *B. transmarina* and *B. nauticus* were calling. The clutches were placed on the bamboo's inner walls above the water, but only a few eggs seemed to be fertilized and showed embryonic development. We counted three clutches of 42, 43, and 22 eggs on the walls of cut bamboo trunks in November 2012 at Mont M'Sapere. Females seem to deposit several unfertilized eggs in the water that can serve as food for the tadpoles, but more research is needed to disentangle the species' reproductive strategy. Individuals were seen during the day on the ground in the forest leaf litter, mixed with

Figure 3. Dorsolateral and ventral views of *Blommersia transmarina* DRV6807 (MNCN50446), adult male collected at Mont M'Sapere in 2012 by D. Vieites and M. Peso Fernández. Note the shape and color of the femoral glands.

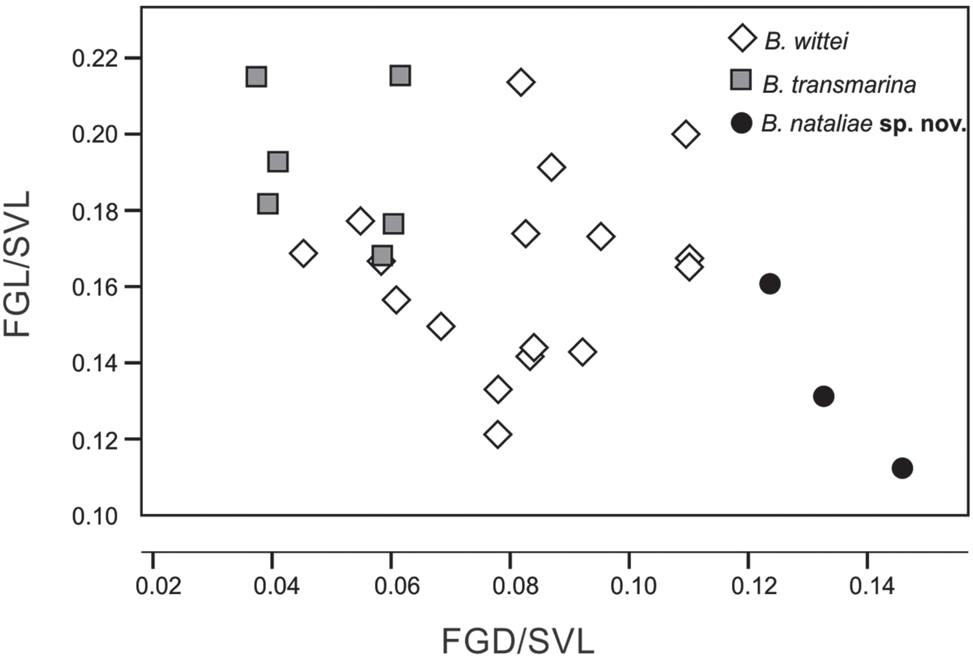

Figure 4. Scatterplot of relative femoral gland length (FGL/SVL ratio) and the relative distance between the inner edges of the femoral glands (FGD/SVL) in the two new species from Mayotte and their sister taxon *Blommersia wittei* from Madagascar. Measurements are based on Table 1; and for *B. wittei* on Vences et al. (2010) and Pabijan et al. (2011). Note the intermediate position of *B. wittei* between *B. transmarina* and *B. nataliae* sp. nov.

B. transmarina. No frogs were ever seen in other microhabitats like swamps, ponds, streams, or similar water bodies, where *B. transmarina* reproduces. The species reproduces during the rainy season if the bamboo holes are filled with water. We observed clutches and tadpoles in November–December 2012 and April 2014. In some years with little rain (e.g., November 2019), we observed the frogs, but all usual reproduction sites were empty of water with no clutches or tadpoles. The scarcity of rain may strongly affect this species in the near future, limiting its possibility to reproduce.

Distribution. Initially found on the slopes of Mont M'Sapere only where there is still forest present and giant bamboos, between 235 m a.s.l. and 409 m a.s.l. (2012, 2014, and 2019). In the 2014 expedition, we also found the new species at Mont Bénara (12.8712°S, 45.15614°E, 317 m a.s.l.) in a forested place with fewer bamboo stands available, but few specimens. It is possible that the species breeds in other microhabitats (e.g., tree holes) as in the places where it occurs at Mont Bénara there are not many bamboo stands available, but this hypothesis needs to be confirmed. After several trips and visits around the whole entire main island of Mayotte and surrounding islets, with very intense fieldwork, we have not found it anywhere else, and the habitat appears to be degraded for the species.

Figure 5. Photo of three specimens of *Blommersia nataliae* sp. nov. during reproduction in a cut bamboo trunk filled with water. On top of the picture, a male can be seen on top of a female, and another male is in the water on the left side of the trunk.

Conservation. The new species is only known from two localities and seems restricted to mountain areas where the forest is still present with giant bamboo stands. The area of occupancy is estimated to be less than 10 km^2 from the elevation range where it was observed (235 to 409 m a.sl.) and the remaining forest available at the Reserve Forestière de Majimbini (Mont M'Sapere) and the Reserve Forèstiere du Mont Benara (Dupuy et al. 2019). There are bamboo stands also at lower elevations in degraded forests, but we never detected the species there. The distribution range is extremely small, the habitat is increasingly degraded, the breeding places (broken bamboo trunks) not frequent, and the fact that the observed densities seem to be very low suggest to consider the species as Critically Endangered according to IUCN criteria, in need of urgent conservation actions considering the ongoing degradation of these forest habitats. The impacts of local harvesting of bamboos or fires are not known, but it seems critical for the conservation of the species. The introduction of the chytrid fungus in Mayotte could decimate this species as well as *B. transmarina* in a few years. The consequences of climate change, such as a reduction in rainfall that fills its reproductive sites, may strongly affect the species as well.

Discussion

For a long time, the Mantellidae was considered an endemic family of frogs to Madagascar, where it is highly diverse, with more than 220 species described so far. The presence of two amphibian mantellid species in Mayotte, a *Boophis* and a former *Mantidactylus* (now *Blommersia*), was known for a relatively long time (Vences et al. 2003; Glaw et al. 2019). A 2003 work showed that these represent different genetic lineages from Malagasy taxa (Vences et al. 2003), supporting the natural presence of mantellids in Mayotte, and suggesting two independent oceanic colonizations of Mayotte by oceanic dispersal. Despite intensive fieldwork in the Comoros archipelago (Hawlitschek et al. 2011), that materialized in a recently published distribution atlas of the amphibians and reptiles of Comoros (Augros 2019), nobody was aware until now of the presence of a third species of amphibian on Mayotte, which raises interesting questions about their origin and evolution in isolation from the rest of congeners in Madagascar.

Oceanic islands offer unique opportunities to study the evolution of ecological and morphological characters as new colonizers have few competitors and empty niches to exploit. In many cases, this leads to island radiations that show a wide range of ecological and morphological adaptations in small territories (e.g., Freed et al. 1987). There are not many cases of amphibian colonization of oceanic islands, being remarkable the case of the Guinean Gulf Islands where anurans and a caecilian were able to colonize from Africa (Measey et al. 2007; Bell et al. 2015a; 2015b), and the case of western Indian Ocean islands (Vences et al. 2003). The existence of two species of *Blommersia* frogs in Mayotte that are sister taxa and evolved in complete isolation from other *Blommersia* species offers a unique model system and opportunity to study the process of speciation from different perspectives, including the genetic, morphological, and ecological ones. Locals report small brown frogs in Mohéli, in forests north of Nioumachoua (G. Decalf pers. com.). Mohéli is another island of the Comoroan archipelago located west of Mayotte. This would suppose yet another oceanic dispersal event; however, these frogs have not been reported by locals for many years, and they are presumably extinct, pending further confirmation of its species identity and existence.

From the external morphological point of view, and comparing with their sister taxon *Blommersia wittei* from Madagascar (Table 1), *B. nataliae* sp. nov. and *B. transmarina* diverged in opposite directions. *Blommersia wittei* shows intermediate measurements between the two in most characters, being a typical small *Blommersia* species. *B. transmarina* has undergone a process of increase in body size, which can be considered towards a moderate gigantism compared to other *Blommersia*, being the largest *Blommersia* species known so far (Glaw et al. 2019; Santos-Santos et al. 2020). The overall aspect of *B. transmarina* more closely resembles other Mantellinae genera from Madagascar than a typical *Blommersia*, being bigger, more robust, and darker in coloration with proportionally longer and more robust legs. *Blommersia nataliae* sp. nov., on the contrary, has undergone a process towards miniaturization from their shared common ancestor, similar to other *Blommersia* species from Madagascar. We hypothesize that the ancestor of both species arrived in Mayotte and populations started to exploit available ecological niches, as they do not compete with the other frog species, *Boophis nauticus*, present on the island. In the ecological component, divergence happened in the selection of breeding habitats, with *B. transmarina* retaining the same ecology as *B. wittei*, but *B. nataliae* sp. nov. specializing in reproducing in bamboo trunks filed with water and maybe other cavities, leading to a specialized tadpole. Adaptation to different environments is also known from *Blommersia angolafa*, which is phytotelmic and reproduces in the water accumulated in fallen leaves (Andreone et al. 2010).

The different events of ecological and morphological release in Comoran species lead to their morphological divergence with an adult morphological pattern in *B. nataliae* sp. nov. that resembles other *Blommersia* from Madagascar that evolved towards miniaturization, whereas *B. transmarina* occupies the morphological space of other larger genera present in Madagascar (e.g., *Mantidactylus* or *Gephyromantis*). This offers a unique opportunity to explore the mechanisms of their morphological evolution in isolation.

In this study, we have followed an integrative taxonomic approach by incorporating morphological, genetic, and life history data, which supports the species status of this new taxon. Despite the effort to register mating calls from the new species, we never heard it in the field or in captivity, even when observing reproduction in front of us. This contrasts with *B. transmarina*, in which males are very active, calling at night everywhere, even at close distance. Hence, we could not include calls in the analyses, and the call of this species still needs to be determined.

The observed genetic divergence between Mayotte's two *Blommersia* species is above the values observed between other mantellid sister species (Vences et al. 2005; Vieites et al. 2009), and the morphological differences are clear. Both species have evolved in isolation and occur on a small island, with the actual range of *B. nataliae* sp. nov. being minimal. This, united to its particular breeding ecology and requirements for reproduction, the lack of suitable areas for reproduction, and its apparent low density and small population size, suggest that this species is threatened. We propose a category of Critically Endangered following IUCN criteria and predict that the species can disappear in parallel to the degradation of its environment if its remaining pockets of habitat are not well managed. In the last eight years, we have observed a loss of part of the bamboos in mid-elevation forests that are the only known breeding habitat of this species. Not all cut bamboo trunks are suitable for the species as they cannot hold water, so the current available breeding habitat is very scarce. Although giant bamboo stands occur at lower elevations, *B. nataliae* sp. nov. is not present there, so the management of the forest seems critical to ensure the survival of the species. *Blommersia transmarina* shows a different conservation situation since it can profit from degraded habitats, but it is more common in mountains and forested habitats.

Two other significant threats can also affect the conservation of the Comoran herpetofauna apart from habitat degradation. Warming of the western Indian Ocean is becoming more intense, with a higher likelihood of extreme climatic events (Ng et al. 2015), like droughts or cyclons, in this century. In 2016 and 2017, a severe drought affected the Comoros archipelago and Madagascar, with limited amphibian reproduction during the rainy season as wetlands were dry and the rain was scarce (pers. obs.). This scarcity of rain can severely affect *B. nataliae* sp. nov. as the microhabitats where it reproduces need to be filled up with water to allow reproduction. However, it could be counteracted with inexpensive conservation actions like filling them with water manually.

In contrast, *B. transmarina* is present in the typical *Blommersia* habitats: swamps, ponds, little brooks, roadside channels, and even water deposits, fountains, or buckets, occurring in both forest habitats as well as in very degraded areas. The breeding season can extend throughout the year as long as there is rain, as we observed clutches in spring, fall, and winter, although the main reproductive activity coincides with the rainy season. In captivity, they can reproduce all year round. The males of *B. transmarina* are very active in breeding grounds, calling from leaves, shrubs, low branches of trees or rocks, sometimes with frenetic activity. They even were even found calling in fountains of hotels during the night, so the potential impact of climate change may be less intense for this species. The introduction of the chytrid fungus, which so far has not been reported in Mayotte, could easily drive the three amphibian species known on the island to extinction as well.

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Supplementary material 1

Data descriptor for *Blommmersia nataliae* sp. nov.

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