

Review of the rare genus *Vanhornia* Crawford, 1909 (Hymenoptera, Proctotrupoidea, Vanhorniidae) with description of a new species from the Russian Far East

Alexander V. Timokhov¹, Sergey A. Belokobylskij²

¹ Department of Entomology, Lomonosov Moscow State University, Moscow 119234, Russia ² Zoological Institute, Russian Academy of Sciences, St. Petersburg 199034, Russia

Corresponding author: Sergey A. Belokobylskij (doryctes@gmail.com)

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Abstract

A brief review of the proctotrupoid genus *Vanhornia* Crawford is given. A new species, *Vanhornia yurii* **sp. nov.** from Primorskiy Territory, Russia, is described and illustrated. Photographic illustrations of *Vanhornia eucnemidarum* Crawford, 1909 (specimens from USA), *V. leileri* Hedqvist, 1976 (specimens from the Russian Far East) and *V. quizhouensis* (He & Chu, 1990) (holotype) are given. An identification key to all known species of *Vanhornia* is provided.

Keywords

Eastern Asia, key, new species, new distribution, Proctotrupoidea, Vanhorniidae

Introduction

The superfamily Proctotrupoidea is a diverse group of poorly studied parasitic Hymenoptera of ancient origin. The concept of Proctotrupoidea has changed considerably over the last few decades. After the exclusion of several taxa, Proctotrupoidea s. str.

is considered to include eight extant families. Along with the moderately abundant Proctotrupidae, there are much smaller but morphologically distinct families, namely Austroniidae, Heloridae, Pelecinidae, Peradeniidae, Proctorenyxidae, Roproniidae and Vanhorniidae (Sharkey 2007). Basal lineages, particularly Mesoserphidae, an extinct family, flourished already during the Jurassic, and proctotrupoid fossils are found in many deposits (Shi et al. 2013; Li et al. 2017). Given the rich paleontological history of the group and apparent morphological isolation of the extant families, most of them are considered to be relicts (Masner 1993).

Vanhorniidae is an enigmatic family of proctotrupoid wasps. The only genus of the family, *Vanhornia* Crawford, 1909, has included until now three extant species in the world fauna. The genus was erected for *V. eucnemidarum* Crawford, 1909, which is the type species by monotypy (Crawford 1909). The type species is widespread throughout North America (Smith 1995; Hogan et al. 2019; Kleiner et al. 2019) and has recently been doubtfully recorded in South Korea (Choi and Lee 2012). Another species of the genus, *V. leileri* Hedqvist, 1976, was described from two specimens collected in Sweden (Hedqvist 1976), the female holotype and a paratype reported as a male, although the latter has later been revealed to be a female lacking the ovipositor (Forshage et al. 2016). During the last decade, *V. leileri* was recorded from a few specimens in several countries of Central Europe, viz. Switzerland, Germany, France and the Netherlands (Baur et al. 2010; Artmann-Graf 2016; Belgers et al. 2020). This rare species is also known from the southern Russian Far East (Primorskiy Territory) (Kozlov 1998; Lelej 2012; Chemyreva 2019) and, thus has a vast, disjunctive range in the Palaearctic. He and Chu (1990) erected a genus *Sinicivanhornia* He & Chu, 1990 with the only species, *S. quizhouensis* He & Chu, 1990 based on a single female specimen collected in Guizhou Province, South China. Later, this genus was synonymised with *Vanhornia* (Kozlov 1998), and *V. quizhouensis* was recently recorded in Thailand (Artmann-Graf 2016). In addition, two undescribed species of *Vanhornia* are known from Oregon in the USA and Hokkaido in Japan (Masner 1993; Artmann-Graf 2016).

Members of this genus are medium-sized parasitoids (4.0–6.7 mm) and distinctly differ from other proctotrupoid wasps in a unique set of defining morphological features, namely the strong exodont mandibles, projecting downward and not meeting each other on midline; antennae attached very low on the frons, just above the clypeus; face extremely low; large metasomal carapace consisting of the syntergite (fused T2–T5) and synsternite (fused S2–S5 in females or S2–S6 in males); long exserted ovipositor, turned forward and at rest accommodated in the ventral median groove of the synsternite (Mason 1983; Naumann and Masner 1985).

Information of the biology of the genus remains scarce. Originally, the small type series of *V. eucnemidarum* was obtained from the larval chambers of an unidentified false click beetle (Coleoptera: Eucnemidae) (Crawford 1909). Subsequently, an eucnemid beetle, *Isorhipis ruficornis* (Say), has been specified as the host of *V. eucnemidarum*

in North America (Champlain 1922; Brues 1927; Deyrup 1985). In Sweden, *V. leileri* was also reared from an eucnemid host, *Hylis cariniceps* (Reitter) (Hedqvist 1976). Despite the fact that species of *Vanhornia* do not seem to have any economic importance as biological control agents of their rare hosts, investigations of this group of parasitic Hymenoptera are of great interest for Hymenoptera morphology and phylogeny (Castro et al. 2006; Hogan et al. 2019).

Study of materials from different regions of Russia revealed three additional records of *Vanhornia*. In this paper one of the specimens from the southern Russian Far East is described as a new species, and the other records provide new important information on the distribution of the trans-Palaearctic *V. leileri*.

The main aim of this study is to describe a new *Vanhornia* species from Eastern Palaearctic, to review all the known species of the genus of the world fauna, to prepare a new illustrated key for determination of *Vanhornia* species, and to discuss some of its morphological characters and distribution.

Material and method

The morphological terminology used in the present study follows Hymenoptera Anatomy Ontology (Yoder et al. 2010) and Mikó et al. (2007); surface sculpture terminology follows Harris (1979); terminology of wing venation follows Naumann and Masner (1985) and van Achterberg (1993). Traditional morphometric measurements were made from properly mounted specimens or from digital photographs (e.g. Popovici et al. 2013).

Photographs were obtained using a Leica M165 stereomicroscope equipped with a Leica DFC450 camera (Paleontological Institute RAS, Moscow) and with a Canon EOS 70D digital camera mounted on an Olympus SZX10 microscope (Zoological Institute RAS, St. Petersburg). Image stacking was performed using Helicon Focus 5.0. Final plates were prepared in Adobe Photoshop CS6.

The following abbreviations are used: **POL**, shortest distance between the lateral ocelli; **LOL**, shortest distance between the lateral ocellus and the median ocellus; **OOL**, shortest distance between the lateral ocellus and compound eye; **OD**, maximum ocellar diameter.

Institutional abbreviations:

ZISP Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia;
ZMMU Zoological Museum, Lomonosov Moscow State University, Moscow, Russia.

The holotype of *Vanhornia yurii* sp. nov. is housed in the Zoological Institute, Russian Academy of Sciences (St. Petersburg, Russia).

Taxonomy

Class Insecta Linnaeus, 1758

Order Hymenoptera Linnaeus, 1758

Family Vanhorniidae Crawford, 1909

Genus *Vanhornia* Crawford, 1909

Type species. *Vanhornia eucnemidarum* Crawford, 1909.

Taxonomic synopsis of *Vanhornia* species

Vanhornia eucnemidarum Crawford, 1909

Vanhornia leileri Hedqvist, 1976

Vanhornia quizhouensis (He & Chu, 1990)

Vanhornia yurii Timokhov & Belokobylskij, sp. nov.

Description

***Vanhornia yurii* Timokhov & Belokobylskij, sp. nov.**

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Figs 1, 2

Type material. *Holotype*, ♀, “RUSSIA, Primorskiy kray [Territory], Lazovsk. z-k [Lazovsky Nature Reserve], b. [bukhta = Bay] Proselochnaya, 21–25.VII.2008, Yu. Sundukov [coll.]” (ZISP).

Description. Female. Body length 3.9 mm; fore wing length 2.6 mm; antenna length 1.5 mm; ovipositor length 2.7 mm.

Head: In dorsal view 1.35 times as wide as its medium length, 1.3 times as wide as maximum width of mesoscutum; in lateral view 1.1 times as high as long; vertex distinctly roundly convex. Head behind eyes (dorsal view) weakly convex in anterior two-thirds, then weakly roundly narrowed. Vertex posteriorly without median longitudinal sulcus. Temple bulging, almost equal to transverse diameter of eye (dorsal view). Eyes suboval, slightly narrowed ventrally, bare. Ocelli weakly enlarged, arranged in obtuse triangle with base (POL) 1.5 times as large as its sides (LOL). POL almost 4.0 times OD, 1.6 times OOL. Occipital carina interrupted dorsally over wide distance, present laterally. Occiput dorsally with effaced vertical median sulcus. Frons distinctly widely convex medially, with small shallow but distinctly rounded submedian depression. Antennal scrobes present as shallow, smooth, subvertical oblique lateral furrows, without marginal carinae delimiting them from the central area of frons. Interantennal process present as obtuse low convex vertical cushion. Clypeal suture distinct and deep. Clypeus narrow and very wide, with two medio-lateral acuminate corners, distinctly concave medially and weakly concave laterally, about 5.0 times as wide as median



Figure 1. *Vanhornia yurii* sp. nov. (female, holotype) **A** habitus, dorsal view **B** mandible, antero-lateral view **C** head, lateral view **D** head, front view **E** head, dorsal view **F** antenna **G** mesosoma, dorsal view **H** mesosoma, lateral view **I** hind leg.

height. Malar space very short. Temple along its lower margin (between occipital carina and eye) with transverse crenulate narrow furrow. Mandible with four distinct and thick teeth and small additional tubercle on antero-lateral surface; apically two anterior teeth rather acuminate and two posterior teeth rounded and obtuse; anterior tooth distinctly separate from more closely situated three posterior teeth. Clypeus and base of mandibles covered by rather dense long whitish setae. Vertex and temple entirely in distinct but small, numerous and rather dense setiferous punctation; frons finely and sparsely punctate.

Antennae: Thickened, setiform, gradually weakly narrowed apically, 13-segmented, with very dense and short setosity. Scapus widened distally, 1.7 times as long as maximum apical width, about 2.5 times as long as subglobal pedicel. First flagellomere longest and widest, evenly widened towards apex, 2.6 times as long as its maximum width, 1.3 times as long as second flagellomere. Antennomeres A5–A9 elongate, uniform in length. Penultimate segment 2.0 times longer than wide, 0.75 times as long as apical segment; the latter weakly acuminate apically.

Mesosoma: Almost as high as wide, 2.1 times as long as maximum width (dorsal view), 1.9 times as long as maximum height (lateral view). Pronotal collar elongate, rugose-reticulate posteriorly and medially (dorsal view). Netrion almost spindle-shaped, smooth, distinctly delimited by complete and crenulate with rugosity netrion sulcus. Mesoscutum distinctly transverse, 1.5 times wider than medial length, weakly convex, almost entirely distinctly and rather densely (but fine and sparse posteriorly, including between notauli) punctate with short and pale setae. Notauli arcuate, deep, complete throughout, distinctly and rather sparsely crenulate, not widened posteriorly. Parapsidal lines present and narrow. Scutoscutellar (prescutellar) sulcus deep, curved, with seven rather narrow foveae separated by distinct high striae. Scutellum rather large, distinctly narrowed posteriorly, almost as wide anteriorly as its median length, posterior fifth of scutellum separated by deep and distinctly crenulate transverse curved mesoscutellar sulcus. Metanotum (dorsal view) medially with subsquare and coarsely rugose convex area, laterally coarsely and sparsely crenulate with rugosity. Mesopleuron in wide and mainly concave median area (femoral depression) smooth and bare, antero-ventrally with wide crenulation at short distance; mesopleural carina (anterior ridge of mesopleuron) sharp, rugulose-crenulate in antero-dorsal half, extending posteroventrad as low and effaced ridge to postpectal (ventral mesopleural) carina; speculum smooth; mesepimeral sulcus comprised of large subcircular foveae above and smaller transversely elongate foveae below; lower convex longitudinal area of mesopleuron anteriorly distinctly rugulose-punctate, finely and sparsely punctate posteriorly; mesodiscrimen wide, percurrent, foveolate, in sparse and coarse crenulation. Propodeum mostly coarsely reticulate-areolate; basally with two curved short medial keels and two long, oblique, posteriorly converging lateral keels, delimiting three rather small mainly smooth but rugose posteriorly basal areas; with complete high coarse transverse curved keel in posterior 0.4 of propodeum.

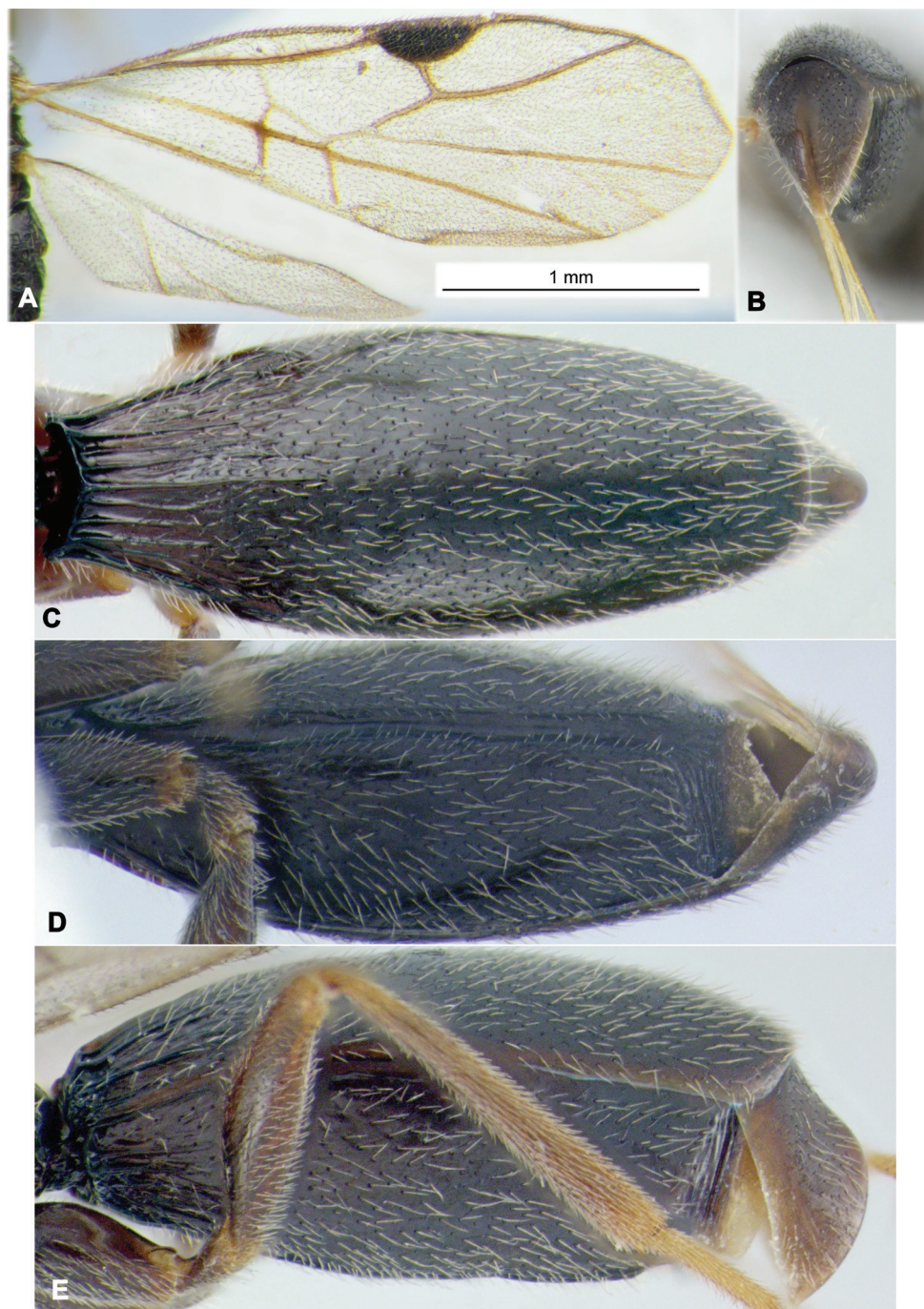


Figure 2. *Vanhornia yurii* sp. nov. (female, holotype) **A** wings **B** metasomal tergite 6, posterior view **C** metasoma, dorsal view **D** metasoma, ventral view **E** metasoma, lateral view.

Fore wing: About 3.0 times as long as maximum width, entirely in dense and dark setosity. Radial cell distinctly shortened, surpassed by postmarginal vein, 3.5 times as long as maximum width. Costal section of radial cell 1.4 times length of pterostigma, about 1.5 times distance from apex of radial cell to apex of wing. Apical (terminal) abscissa of radial vein (3-Rs) weakly curved basally and almost straight in distal half, 3.0 times as long as preceding abscissa of this vein (2-Rs). Medial cell small and narrow, strongly narrowed distally. Vein cu-a straight and interstitial to vein 1-M.

Legs: Slender. Hind femur distinctly narrowed basally and apically, 4.0 times as long as maximum width. Trochantelli absent on all legs. Tibial spurs short, their formula 1/2/2.

Metasoma: Narrow (dorsal view). Syntergite 2–5 (dorsal view) without any traces of fusion of tergites, 2.4 times as long as its maximum width; basally with high and coarse weakly curved transverse keel, medially and laterally with coarse longitudinal keels in basal quarter of syntergite, with several and rather sparse longitudinal striation on basal 0.2; remaining part of syntergite entirely in rather dense but fine setiferous punctation. Synsternite 2–5 with a percurrent deep, relatively narrow and almost smooth groove on midline, almost entirely in dense and fine setiferous punctation, upper smooth on narrow stripe, posteriorly in narrow area in dense, straight or weakly curved vertical striation. Cowled tergite 6 abruptly deflexed, mostly in sparse and fine setiferous punctation, almost smooth in anterior vertical third; in posterior view, rather narrow, subtriangular shape, strongly narrowed to lower margin and distinctly convex upper, 1.4 times as high as maximum width, with distinct median obtuse and smooth vertical bar. Ovipositor mostly exposed, slender and flexible, its visible part 0.7 times as long as body.

Colour: Body mainly black, metasoma with brown parts. Antenna black; mandibles mostly brown with black teeth; palpi light brown to brown. Legs brown to dark reddish brown, fore and middle tibiae and tarsi and hind tarsus yellow to partly brownish yellow. Tegula dark brown. Fore wing faintly infusate; sclerotised veins brown; pterostigma black. Ovipositor yellow.

Male. Unknown.

Comparative diagnosis. This new species is similar to *V. quizhouensis* (He & Chu, 1990) from China (Guizhou) (Fig. 3) and Thailand, but differs from it in having the vertex without median longitudinal sulcus (vs. such sulcus present), mesoscutum in fine, small and dense setiferous punctation (vs. punctation distinct, enlarged and rather sparse), scutoscuteellar (prescutellar) sulcus with seven narrow foveae (vs. only five foveae), vein cu-a in fore wing straight and interstitial to vein 1-M (vs. curved posteriorly and antefurcal); metasoma narrow, syntergite 2–5 in dorsal view 2.4 times as long as its maximum width (vs. 1.9 times).

The new species is also similar to the North American *V. eucnemidarum* Crawford, 1909 (Fig. 4), but differs from it in the scutoscuteellar (prescutellar) sulcus with seven narrow foveae (vs. only five foveae), metasoma narrow, syntergite 2–5 in dorsal view 2.4 times as long as its maximum width (vs. 1.86–2.07 times), femoral depression on

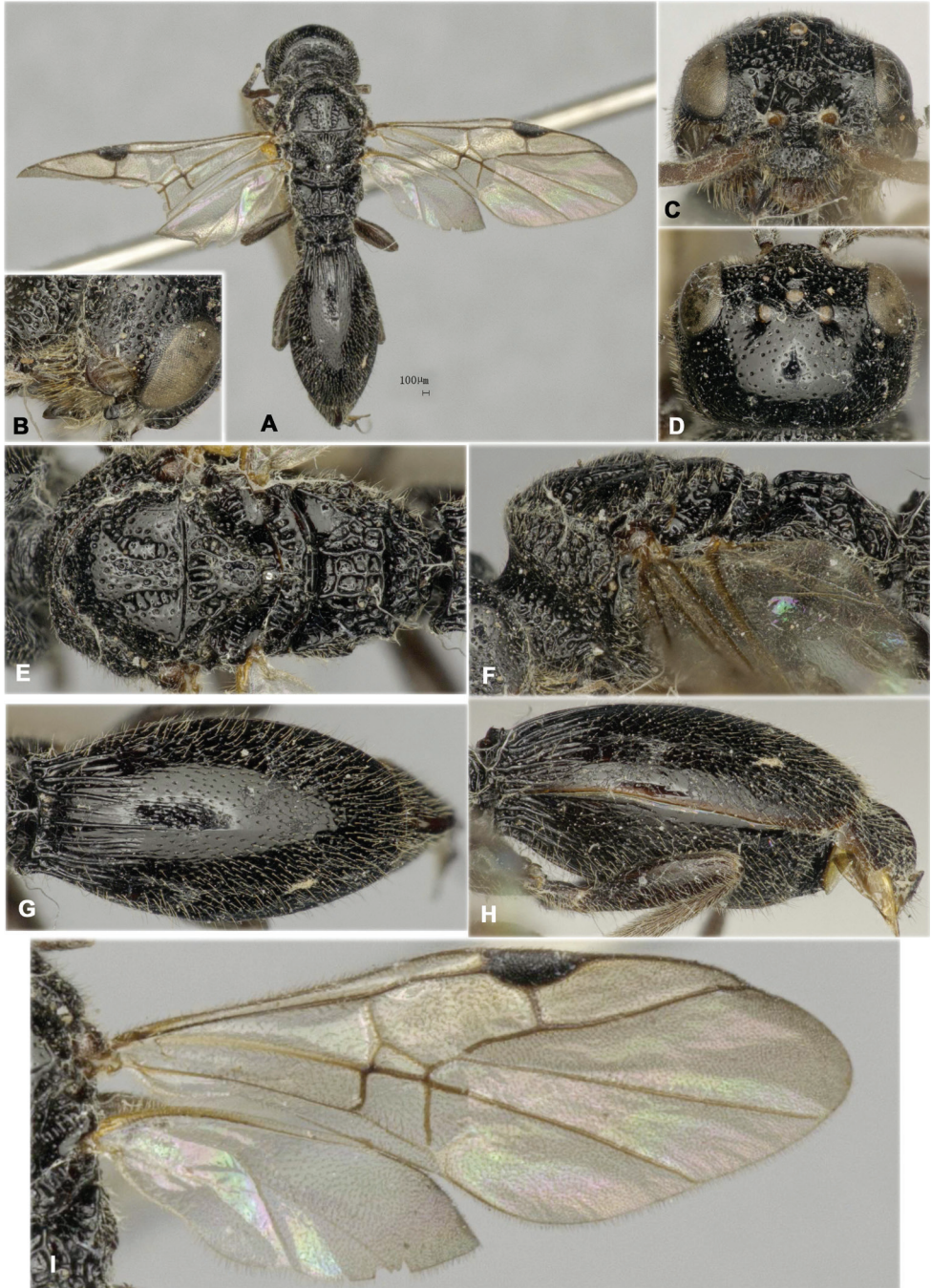


Figure 3. *Vanhornia quizhouensis* (He & Chu, 1990) (female, holotype) **A** habitus, dorsal view **B** mandible, ventro-lateral view **C** head, front view **D** head, dorsal view **E** mesosoma, dorsal view **F** mesosoma, lateral view **G** metasoma, dorsal view **H** metasoma, lateral view **I** wings.

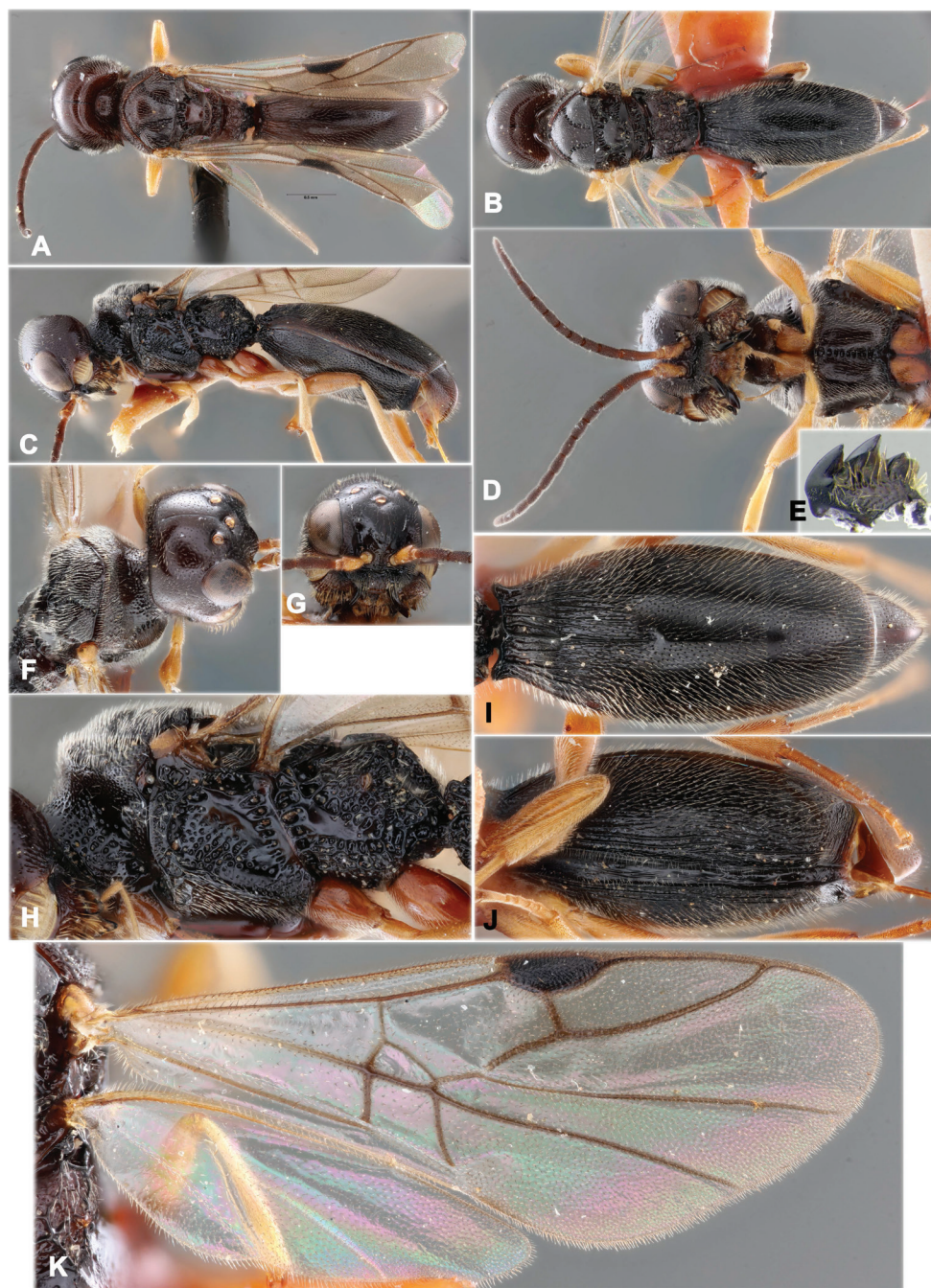


Figure 4. *Vanhornia eucnemidarum* Crawford, 1909 (female, specimens from USA) **A** habitus, dorsal view **B** body, dorsal view **C** body, lateral view **D** antennae, head and mesosoma, ventral view **E** right mandible, lateral view **F** head and mesoscutum, dorso-lateral view **G** head, front view **H** mesosoma, lateral view **I** metasoma, dorsal view **J** metasoma, ventral view **K** wings.

mesopleuron mostly smooth and with crenulation anteroventrally (vs. with areolation medially and without lower crenulation), vertex without median longitudinal sulcus (vs. sulcus extends back from anterior ocellus proceeding into occipital vertical median sulcus), as well as distribution, in the East Palaearctic (vs. North America).

Etymology. This species is named in honour of its collector, Dr Yuriy N. Sundukov, a Russian coleopterist and hymenopterist.

Distribution (Fig. 8). Russian Far East (Primorskiy Territory).

Remarks. According to the illustration (Choi and Lee 2012), the specimen found in South Korea could also belong to this species, but study of this specimen is necessary for correct confirmation of this suggestion.

Vanhornia leileri Hedqvist, 1976

Figs 5–7

Material examined (ZISP). RUSSIA • 1 ♀; Krasnoyarsk Territory, Krasnoyarsk, E bank [of Yenisey River], Stolby Res. Env., Laletina r., 300 m, 26.VII.2009, 55°57'43"N 92°46'48"E; YPT; K. Tomkovich leg. • 1 ♀; Primorskiy Territory, 128 km SSE of Dal'nerechensk, Pozhiga Village, 23.VII.1983; D. Kasparyan leg.; determined by M. Kozlov, 1998; re-determined by H. Bauer, 2015 • 1 ♂; Primorskiy Territory, 25 km NE of Spassk-Dal'niy, Siniy Ridge, forest, border of forest, 7.VII.2001; S. Belokobylskij leg.; determined by S. Belokobylskij, 2001; re-determined by H. Bauer, 2015 • 1 ♀; Primorskiy Territory, Vladivostok, Sedanka, forest, 26.VII.2001; S. Belokobylskij leg. • 1 ♀; Kuril Islands, NW of Kunashir Island, source of Zolotaya River, 250–550 m, 19.VIII.2013; Yu. Sundukov leg.

Male (first description). Body length 4.3 mm; fore wing length 3.0 mm. Antennomeres 4 and 5 noticeably and antennomere 6 only slightly modified, with narrow longitudinal ridges ventrally (Fig. 5G). Synsternite 2–6 below (Fig. 7C) without median longitudinal groove (this being with deep, rather wide and more widened anteriorly, crenulate groove for enclosing of open part of ovipositor in female: Fig. 7A). Cowled tergite 6 of metasoma (Fig. 7D) in posterior view less convex, without median vertical bar (in female median vertical obtuse and smooth bar present: Fig. 7B), suboval shape, almost straight in lower margin and convex upper, 1.6 times as wide as maximum height. Otherwise similar to female.

Distribution (Fig. 8). Sweden, France, Switzerland, the Netherlands, Germany, Russia (Krasnoyarsk Territory (new record), Primorskiy Territory, and Kuril Islands (new record)).

Vanhornia eucnemidarum Crawford, 1909

Fig. 4

Material examined (ZMMU). USA • 2 ♀♀; Virginia, Louisa Co., 4 mi S Cuckoo, 8–18.VI.1988; Malaise trap; J. Klope and D.R. Smith leg. • 1 ♀, South Carolina, Pickens Co., Wattacoo, 3.VI.1961; G. F. Townes leg.



Figure 5. *Vanhornia leileri* Hedqvist, 1976 (**A–F, H–K** female **G** male, specimens from Russian Far East) **A** habitus, lateral view **B** right mandible, lateral view **C** head, dorsal view **D** head, front view **E** head, lateral view **F** antenna **G** basal part of antenna **H** head, antero-lateral view **I** mesosoma, dorsal view **J** mesosoma, lateral view **K** metasoma and hind leg, lateral view.



Figure 6. *Vanhornia leileri* Hedqvist, 1976 (female, specimen from Russian Far East) **A** wings **B** metasoma, dorsal view **C** metasoma, lateral view.

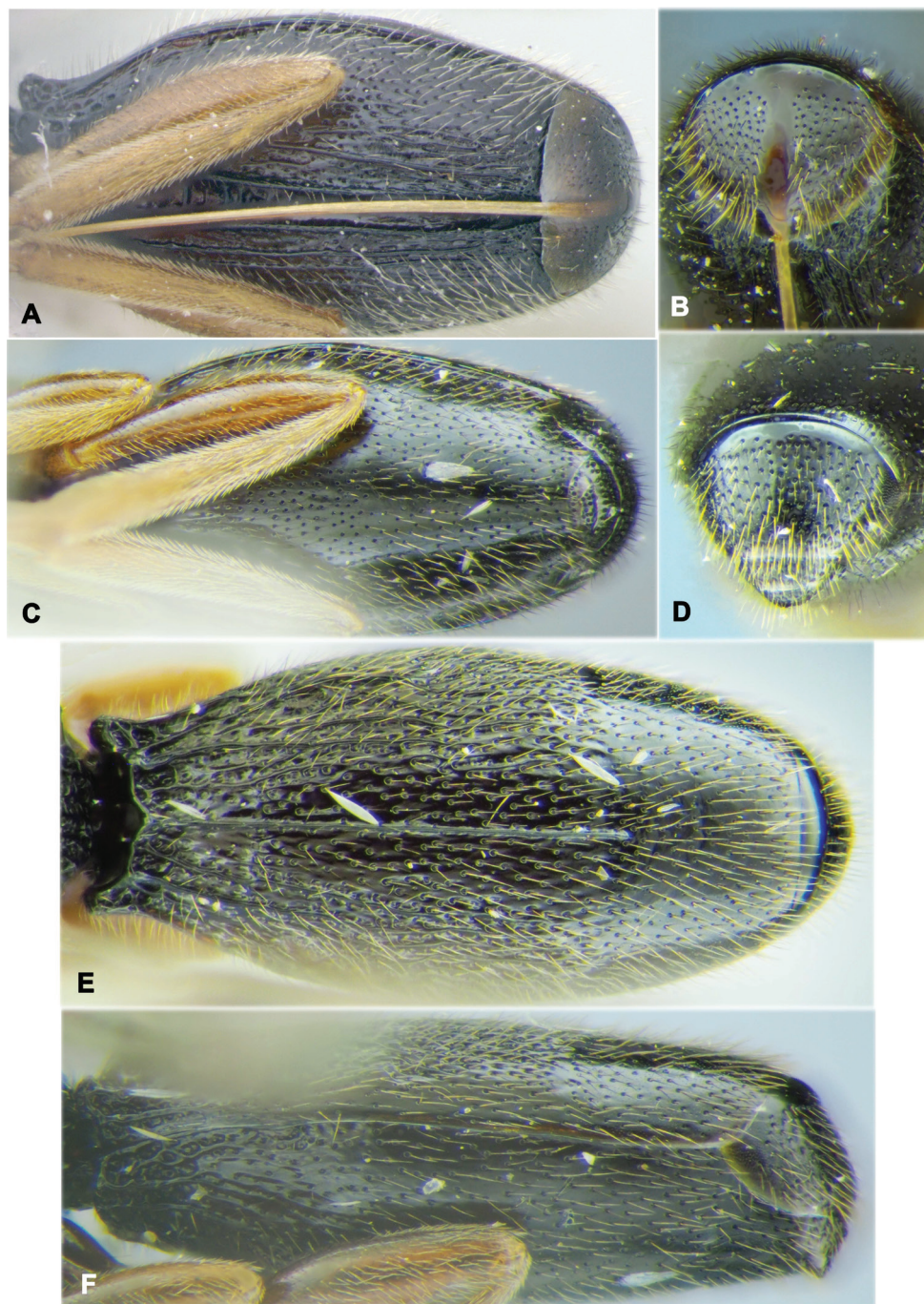


Figure 7. *Vanhornia leileri* Hedqvist, 1976 (**A, B** female **C–F** male, specimens from Russian Far East) **A, C** metasoma, ventral view **B, D** metasomal tergite 6, posterior view **E** metasoma, dorsal view **F** metasoma, lateral view.

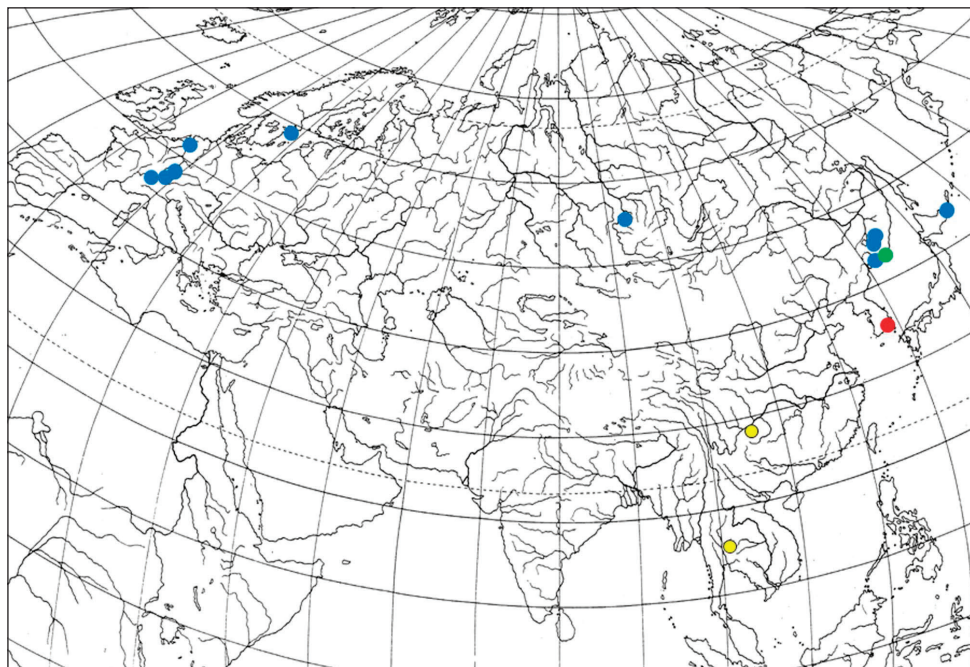


Figure 8. Map of distribution of *Vanhornia* in Eurasia. Green spot – *V. yurii* sp. nov., blue spots – *V. leileri*, yellow spots – *V. quizhouensis*, red spot – specimen from South Korea determined as *V. eucnemidarum* (Choi & Lee, 2012).

Key to *Vanhornia* species

- 1 Syntergite 2–5 striate in basal 0.7–0.8 (Figs 6B, 7E) ***V. leileri* Hedqvist**
- Syntergite 2–5 striate in basal 0.2–0.3 (Figs 2C, 3G, 4I)..... **2**
- 2 Scutoscuteellar (prescutellar) sulcus with seven foveae separated by prominent striae (Fig. 1G). Metasoma of female narrow, syntergite 2–5 (dorsal view) 2.4 times as long as its maximum width (Fig. 2C). Vertex without median longitudinal sulcus (Fig. 1E) ***V. yurii* Timokhov & Belokobylskij, sp. nov.**
- Scutoscuteellar (prescutellar) sulcus with five foveae separated by prominent striae (Figs 3E, 4A), or with six foveae and medial foveae indistinctly divided (Fig. 4B). Metasoma of female wide, syntergite 2–5 (dorsal view) 1.80–2.05 times as long as its maximum width (Figs 3G, 4I). Vertex at least with short median longitudinal sulcus (Figs 3D, 4F) **3**
- 3 Median longitudinal sulcus on vertex long and almost complete (Fig. 4F). Mesoscutum with dense setiferous punctation, punctures very small (Fig. 4A, B). Width of notaulus slightly increasing posteriorly (Fig. 4A, B). Vein cu-a of fore wing interstitial (Fig. 4K) ***V. eucnemidarum* Crawford**
- Median longitudinal sulcus on vertex very short and incomplete (Fig. 3D). Mesoscutum with sparse setiferous punctation, punctures small and large (Fig. 3E). Width of notaulus distinctly increasing posteriorly (Fig. 3E). Vein cu-a of fore wing antefurcal (Fig. 3I) ***V. quizhouensis* (He & Chu)**

Discussion

Vanhornia is a genus of rare and specialised parasitoids of remarkable appearance. *Vanhornia* is different from all other Proctotrupoidea in having exodont mandibles, which are generally rare in Hymenoptera. Exodont mandibles are characteristic of braconids in the large subfamily Alysiinae, which use them to cut their way out of the hosts' puparium (Tobias 1968; Wharton et al. 2006), and such mandibles are only occasionally found in some other braconid taxa (Wharton 1977; Mason 1991; Sharkey and Wharton 1994). Mymarommatoidea, an enigmatic group of small Proctotrupomorpha, also have mostly exodont mandibles (except in some extinct species), with their supposed function of rupturing the chorion of a putative host (Gibson et al. 2007). Likewise, the late instar larvae of several egg parasitoids are armed with powerful exodont mandibles to pierce the host egg chorion for allowing ventilation (Boivin 2010).

Rather intriguing is the similarity of the mouthparts of *Vanhornia* with those of some eucnemid larvae (its hosts), in particular those of Melasini, to which *Isorhipis ruficornis* belongs, also equipped with large, freely movable, exodont mandibles (Deyrup 1985; Muona and Teräväinen 2020). Based on this similarity, Deyrup (1985) speculated, though recognized it as unconvincing, of the origin of *Vanhornia* from much more flatter ancestors, who completed their development in the larval galleries, and not in the pupal cell of their hosts. In any case, like Deyrup (1985), we have to state that the adaptive value of the exodont mandibles of *Vanhornia* is still unknown, but perhaps it can use exodont mandibles to chew through wood, similar to their host larvae.

Although all species of *Vanhornia* have exodont mandibles, their shape is substantially different between certain species. Hedqvist (1976) described *V. leileri* as having 5 mandibular teeth. However he pointed out in the diagnosis that mandibles of this species have fewer teeth than *V. eucnemidarum*. He illustrated the mandible of *V. leileri* with four teeth, and the latter species with five, so an error clearly occurred (Hedqvist 1976: fig. 2B, D). In all specimens of *V. leileri* that we have studied, the mandibles are elongate, 1.5–1.6 times as long as their width at the base, and have five distinct teeth, the anterior tooth being small, but rather distinctly separated from the large second tooth (Fig. 5B). The mandible of the specimens of *V. eucnemidarum* studied by us is very wide and short, about 0.7 times as long as its basal width, with four distinct and thick teeth and a small additional tubercle on antero-lateral surface (Fig. 4E). It resembles that of *V. yurii* sp. nov., but the new species has a somewhat deeper notch between the two posterior teeth (Fig. 1B), thus making them more distinctly separated. In *V. eucnemidarum* and *V. yurii* sp. nov., the anterior mandibular tubercle may be hidden behind the medio-lateral corner of the clypeus depending on the position of the mandible. According to the original description, the mandible of *V. quizhouensis* is very wide, with four triangular teeth (He and Chu 1990).

Another morphological character making *Vanhornia* unique among the Proctotrupoidea is the presence of a netrion, a morphological trait that was not mentioned in the previous original descriptions of species of this genus (Crawford 1909; Hedqvist 1976; He and Chu 1990). The netrion is a posteroventral portion of the pronotum

delimited anteriorly by netrion sulcus and corresponds to the site of origin of the first flexor of the fore wing, and is well developed in all *Vanhornia* species. Other than in Vanhorniidae, a pronotal origin of the fore wing flexor is known only from Platygastroidea, and in all other Hymenoptera this muscle originates entirely from the mesopleuron (Mikó et al. 2007; Talamas et al. 2019).

The metasoma and ovipositor of *Vanhornia* are also very peculiar features. In *Vanhornia*, the heterogeneity of metasomal segments is especially pronounced among all Proctotrupoidea and is accompanied by the fusion of several sclerites into syntergites and synsternites, respectively. In *V. eucnemidarum* and *V. leileri*, the traces of fusion of metasomal tergites are barely discernible as areas with sparser pubescence (Figs 4I, 6B), whereas the syntergite is evenly punctate without any traces of fusion in *V. yurii* sp. nov. (Fig. 2C). The fusion of several metasomal sclerites is complemented by the reduction of metasomal spiracles, which is also a unique state for Proctotrupoidea s. str. (Naumann and Masner 1985). Only in *V. eucnemidarum* three minute pits are spaced at regular intervals along each side of the syntergite, which may be considered as vestiges of spiracles (Mason 1983). The ovipositor is extremely long, extruded, but very flexible, with weakly sclerotised third valvulae, transformed into the working element penetrating the substrate along with the first two pairs of valvulae. Investigation of the functional morphology of the ovipositor revealed that its external position in Vanhorniidae (as well as in Proctotrupidae) is a derived state (Rasnitsyn 1980). This type of ovipositor is adapted to attacking a concealed host and is no doubt unsuitable for drilling through hard wood. *Vanhornia* females have been observed to insert it into the cracks of logs or sticks using it like a probe to reach a potential host (Townes and Townes 1981; Deyrup 1985).

The presence of a set of peculiar morphological features implies a profound biological specialisation. However, biological information on *Vanhornia* is rather scarce. *Vanhornia eucnemidarum* is known as a parasitoid of *Isorhipis ruficornis* in North America (Champlain 1922; Brues 1927; Deyrup 1985) and *V. leileri* was reared from *Hylis cariniceps* in Sweden (Hedqvist 1976), with host species belonging to the subfamily Melasinae (Eucnemidae). Most of the false click beetles are associated with dead and rotting wood and are generally uncommon. If the assumption of the strict trophic relations of the parasitic wasps of the genus *Vanhornia* with eucnemids is true, it also explains the rare occurrence of these parasitoids. In Primorskiy Territory, Russia, 26 species of false click beetles of 18 genera have been recorded, and 22 species of them are found directly in the Lazovsky Nature Reserve (the type locality of *V. yurii* sp. nov.), all of them reported as rare (Gusakov 2009).

Species of the genus *Vanhornia* are found in the Nearctic (*V. eucnemidarum*) and Palearctic (*V. leileri* and *V. yurii* sp. nov.), and one species (*V. quizhouensis*) is found in the Oriental region (South China and Thailand). Of these, *V. eucnemidarum* is the most common. The other species are especially rare, including *V. leileri*, which has been known to date only from North, West and Central Europe and from the Russian Far East. Therefore, the new records of *V. leileri* in East Siberia (Krasnoyarsk Territory) and in the Kuril Islands on the one hand expand its range, and on the other hand partly close the huge distribution gap for this species (Fig. 8).

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