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The Pamphiliinae of the Russian Far East and Korea (Hymenoptera, Pamphiliidae)

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AKIHIKO SHINOHARA, KATJA KRAMP & ANDREAS TAEGER

THE PAMPHILIINAE OF THE RUSSIAN FAR EAST AND KOREA (HYMENOPTERA, PAMPHILIIDAE)

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Abstract

Four genera and 58 species of the web-spinning or leaf-rolling sawfly subfamily Pamphiliinae are recognized in the Russian Far East and Korea. *Pamphilius belokobylskiji* **sp. nov.** and *Pamphilius graciloides* **sp. nov.** are described from Primorskij Kraj (Russia) and Korea. *Pamphilius zinovjevi* Shinohara, 1988, is syn. nov. of *Pamphilius ussuriensis* Shinohara, 1988. Lectotypes are designated for *Lyda hilaris* Eversmann, 1847, *Lyda kumamotonis* Matsumura, 1912, *Lyda sapporensis* Matsumura, 1912, *Pamphilius virescens* Malaise, 1931, and *Neurotoma sibirica* Gussakovskij, 1935. *Pamphilius aucupariae* Vikberg, 1971, and *Pamphilius hilaris* (Eversmann, 1847) are newly recorded from Korea. Keys are given to separate the two tribes, four genera and 58 species. Additional collection records from Primorskij Kraj and Korea and photographs of all the species treated are given. The number of the specimens examined for each species, in total over 16000, is noted under the respective species. We undertook molecular analyses of the mitochondrial gene cytochrome c oxidase I (COI) for 597 specimens and of the nuclear gene sodium-potassium adenosine triphosphatase (NaK) for 271 specimens. Based on the results, we assess the monophyly of each supraspecific taxon and each intrageneric species group or subgroup and the hypotheses about their relationships. The tribe Neurotomini with its single genus *Neurotoma*, the tribe Pamphiliini and the genus *Onycholyda* are considered monophyletic with 99–100% UFBoot supports, whereas monophyly of the genus *Pamphilius* is not sufficiently supported by the COI results. The three available datasets, namely, morphology (Shinohara, 2002b), COI genes (present work) and NaK genes (present work), support three different hypotheses of relationships within the tribe Pamphiliini.

Key words: web-spinning sawflies, leaf-rolling sawflies, new species, new synonyms, new distribution records, keys, COI, NaK.

Introduction

The leaf-rolling or web-spinning sawfly family Pamphiliidae Cameron, 1890 was originally described as Pamphilina, a name covering the present superfamily Pamphilioidea (Springate 1999). The extant members of the family comprise about 300 described species distributed in the Holarctic and Oriental regions (Taeger *et al.* 2018) and are divided into two subfamilies, Cephalciinae and Pamphiliinae (Benson 1945; Beneš 1972b). The Pamphiliinae is represented by two tribes, six genera and over 190 species in the recent world fauna (Shinohara 2002b; Taeger *et al.* 2010; Shinohara & Wei 2012, 2016; Shinohara *et al.* 2018c; present work). Shinohara (2002b) reviewed the classification of this subfamily on a worldwide basis, giving a concise historical review and a list of all valid species. He also classified the world species in intrageneric species groups (and subgroups). The subfamily is most species-rich in East Asia (Shinohara 2004). Four genera and 51 species have been recorded in Japan (Shinohara 2019), four genera and 46 species in the Russian Far East (Sundukov & Lelej 2012) and four genera and 42 species in Korea (Lee *et al.* 2019), whereas five genera and 39 species are known in Europe (Lacourt 2020) and three genera and 29 species in North America (Smith 1979; Shinohara & Smith 1983). The known larvae of this subfamily are solitary or gregarious leaf-rollers or web-spinners on various angiosperms of the families Rosaceae, Betulaceae, etc., and they are usually monophagous or oligophagous. The species of the subfamily Cephalciinae are all associated with gymnosperms, mostly with the Pinaceae.

The present paper deals with the Pamphiliinae of the Russian Far East and Korea. The area of the Russian Far East covered in this work follows Belokobylskij & Lelej (2017, fig. 1) but does not include the Kurile Islands. It is a huge area, totalling 3,075,397 square kilometers (Wikipedia contributors 2021a, b), along the northeastern margin of the Eurasian continent and includes Kamchatka and Sakhalin. In its south, it borders with China and narrowly with North Korea and Japan. The southernmost part of the Russian Far East is Primorskij Kraj (164,700 square kilometers, Wikipedia contributors 2021a). North Korea covers 120,540 square kilometers (Wikipedia contributors 2021c) and South Korea100,339 square kilometers (Wikipedia contributors 2021d). Most of the material available for study comes from Primorskij Kraj (mostly from southernmost Vladivostok area) and South Korea (mostly from northeastern Odaesan and Sobaeksan areas and southern Jirisan area), which actually comprise only 8.0% of the whole areas of the Russian Far East and Korea. The Pamphiliinae of these areas were studied by many authors, including Takeuchi (1930, 1936a, 1938), Malaise (1931), Gussakovskij (1935), Beneš (1972a, b, 1974, 1976), Shinohara (1979, 1980, 1985a, b, 1987b, 1988a, b, 1991a, 1993, 1995, 1998, 2001, 2002b, 2004, 2005), Shinohara & Byun (1993), Shinohara & Lee (1997), Shinohara & Zhou (2006), Shinohara & Lelej (2007), Shinohara & Taeger (2007), Shinohara *et al.* (2018a) and Shinohara & Tripotin (2021a, b) (see Shinohara 2004 for a full historical review). This work was initially intended to present the results of taxonomic and faunistic studies of the material obtained in South Korea between 1987 and 2010 by A. Shinohara (AS) and in Primorskij Kraj in 2016 and 2017 by teams of the Senckenberg Deutsches Entomologisches Institut, Müncheberg, in cooperation with the Zoological Institute, Russian Academy of Sciences, St. Petersburg, and the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch of Russian Academy of Sciences, Vladivostok. The scope was subsequently enlarged to include a key to the pamphiliine species of these areas by revising and updating the key to the Russian Far Eastern species by Shinohara & Lelej (2007) and by adding the Korean species.

Here we present keys to two tribes, four genera and 58 species recognized in these areas and summarize the current knowledge about the distribution and host plants of each taxon. We also present the results of molecular analyses using the mitochondrial cytochrome c oxidase I (COI) and the nuclear sodium-potassium adenosine triphosphatase (NaK) genes and discuss their implications for the assessment of the monophyly and interrelationships of the supraspecific taxa and intrageneric species groups and the current interpretation of species.

Material and methods

This work is mainly based on the collection of the National Museum of Nature and Science, Tsukuba (NSMT), which contains over 30000 specimens of the Pamphiliinae representing about 90% of the valid species group taxa worldwide or 92% of the valid species group taxa from Eurasia, and the collection of the Senckenberg Deutsches Entomologisches Institut, Müncheberg (SDEI). Some type specimens are kept at the Hokkaido University, Sapporo (HU), the Naturhistoriska Riksmuseet, Stockholm (NHRS) and the Zoological Institute, Russian Academy

of Sciences, St. Petersburg (ZISP). We (mainly AS) have examined a total of 16235 specimens of the 58 species occurring in the area treated (506 *Neurotoma*, 18 *Chrysolyda*, 921 *Onycholyda* and 14790 *Pamphilius*), of which 4146 specimens (261 *Neurotoma*, 10 *Chrysolyda*, 152 *Onycholyda* and 3723 *Pamphilius*) are from the Russian Far East and Korea and the remaining 12089 specimens are from outside these areas, mostly from Japan. The number of specimens examined for each species is noted under respective species below. Morphological examinations were made with Olympus SZ60 and SZX7 stereo binocular microscopes. For general morphological terminology, we follow Viitasaari (2002a); for some specialized terminology of the sutures and crests on the head, and of the male genitalia we follow Shinohara (2002b).

Most of the photos were taken by A. Taeger (AT) at the SDEI with a Leica DFC 495 digital camera and a Leica M405 C stereo microscope or a Leica 9Si stereo microscope with an integrated camera. For diffuse illumination of the objects, the Leica LED5000 HDI was used on the Leica M405 C, while 3-4 photo spots (e.g., Ulanzi VL 49 RGB) were mostly used on the Leica 9Si. Composite images with extended depth of field were created from image stacks with the software CombineZP or Helicon Focus 7.6.4. and finally arranged and partly enhanced with Ulead PhotoImpact X3. The Microsoft Image Composite Editor (ICE) was used to stitch together images of large specimens. In some cases, photos were taken by AT and AS outside the SDEI using other photographic techniques. The composite images were also stored in their original size at figshare.com. The corresponding DOIs are listed in the treatment of the species. Additional photos that were not included in the plates of this work may be found under the corresponding DOIs.

For molecular work, genomic DNA of all specimens with the sample ID starting with "DEI-GISHym" was extracted at the SDEI by K. Kramp (KK), using the EZNA Tissue DNA Kit (Omega Biotek) according to the manufacturer's protocol and stored at -20 °C for later use. Typically, one or two legs were used for DNA extraction. DNA of samples with the sample ID starting with "NSMT" was extracted at NSMT and deposited in the Center for Molecular Biodiversity Research, NSMT. All PCRs of the specimens starting with "DEI-GISHym" and "NSMT" (including specimens already sequenced by Shinohara *et al.* 2016a, b, 2018b, 2019, except those marked with * in Table 1) were performed at the SDEI by KK. One mitochondrial and one nuclear region were used in the phylogenetic analyses, although the amplification of both genes was not possible for all individuals. For information on primers used for amplification and sequencing, and annealing temperatures, see Prous *et al.* (2019). The mitochondrial region used is a large fragment (1078 bp) of the cytochrome oxidase subunit I gene (COI). The fragment includes the entire standard barcode region (658 bp) of the animal kingdom (Hebert *et al.* 2003). The nuclear marker used is a fragment of the sodium/potassium-transporting ATPase subunit alpha (NaK). The NaK fragment amplified is a nearly complete sequence of its longest exon, 1654 bp. PCR products were purified with Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (Life Technologies, Darmstadt, Germany) and sequenced with an ABI3730XL sequencer using Big Dye v. 3.1 Terminator Kit (Thermo Fisher Scientific, Darmstadt, Germany) by Macrogen Europe (Amsterdam, Netherlands). Sequences were checked, manually edited using Geneious 9.1.2 (Kearse *et al.* 2012) and aligned using BioEdit 7.2.5 (Hall 1999). New sequences have been deposited in GenBank (Table 1).

Phylogenetic trees were calculated using the Maximum Likelihood method (ML) implemented in IQ-TREE 1.6.91 (Nguyen *et al.* 2015). The best-fitting models for the analyses were obtained by ModelFinder (Kalyaanamoorthy *et al.* 2017) and resulted in TVM+F+R5 for COI and TN+F+R3 for NaK. The ML analysis included 1,000 UFBoot (Ultrafast Bootstrap Approximation; Minh *et al.* 2013) replications using all sites. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved nucleotide sequences of 597 specimens for COI and 271 for NaK (Table 1). The pairwise proportion of differences per nucleotide sites (*p*-distance) between all sequences was calculated with MEGAX (Kumar *et al.* 2018) using the pairwise-deletion option (sites containing missing data or alignment gaps were removed from the analysis as the need arose). All codon positions were included. For all the trees in Figs 15, 16 and 137–161, UFBoot values are given only for 95% and above.

TABLE 1. List of sequences used for molecular analyses.

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
		ACANTHOLYDA			
Acantholyda aglaia	DEI-GISHym88081	ON016711 / *DEISY3931-19*	this work	ON016956	this work
Acantholyda angulata	CNCHYM 02016	HYCNC1511-11	BOLD	---	---
Acantholyda atrata	CNCHYM 02024	HYCNC1519-11	BOLD	---	---
Acantholyda atrata	CNCHYM 02025	HYCNC1520-11	BOLD	---	---
Acantholyda burkei	CNCHYM 02034	HYCNC2375-11	BOLD	---	---
Acantholyda burkei	CNCHYM 02035	HYCNC1521-11	BOLD	---	---
Acantholyda chicoutimiensis	CNCHYM 02021	HYCNC1516-11	BOLD	---	---
Acantholyda erythrocephala	BC ZSM HYM 10743	KC973746	Schmidt *et al.* 2017	---	---
Acantholyda erythrocephala	DEI-GISHym11062	KC975214	Schmidt *et al.* 2017	---	---
Acantholyda erythrocephala	DEI-GISHym15777	KC974085	Schmidt *et al.* 2017	---	---
Acantholyda erythrocephala	DEI-GISHym17886	KC974383	Schmidt *et al.* 2017	---	---
Acantholyda erythrocephala	DEI-GISHym88739	ON016719 / *DEISY4006-19*	this work	ON016959	this work
Acantholyda erythrocephala	MHV00103	MZ627386	Roslin *et al.* 2022	---	---
Acantholyda erythrocephala	tO7	KF936604	Malm & Nyman 2014	KF935899	Malm & Nyman 2014
Acantholyda flaviceps	BC ZSM HYM 03204	HQ563849	iBOL	---	---
Acantholyda flaviceps	BC ZSM HYM 16147	GBSYM1707-13	BOLD	---	---
Acantholyda flaviceps	MHV00104	MZ624911	Roslin *et al.* 2022	---	---
Acantholyda flaviceps	ZMUO.023956	MZ657227	Roslin *et al.* 2022	---	---
Acantholyda flaviceps	ZMUO.027937	MZ660652	Roslin *et al.* 2022	---	---
Acantholyda hieroglyphica	BC ZSM HYM 03209	HQ563851	BOLD	---	---
Acantholyda hieroglyphica	BC ZSM HYM 03211	KC973930	Schmidt *et al.* 2017	---	---
Acantholyda hieroglyphica	BC ZSM HYM 03240	HQ563864	iBOL	---	---
Acantholyda hieroglyphica	BC ZSM HYM 11387	KC975840	Schmidt *et al.* 2017	---	---
Acantholyda hieroglyphica	DEI-GISHym17037	KC974896	Schmidt *et al.* 2017	---	---

.....continued on the next page

TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Acantholyda hieroglyphica	DEI-GISHym17051	KC973576	Schmidt *et al.* 2017	---	---
Acantholyda hieroglyphica	FSYM-000082	MZ625264	Roslin *et al.* 2022	---	---
Acantholyda hieroglyphica	GL.2962	MZ623132	Roslin *et al.* 2022	---	---
Acantholyda hieroglyphica	MHV00105	MZ625504	Roslin *et al.* 2022	---	---
Acantholyda hieroglyphica	ZMUO.016336	MZ632898	Roslin *et al.* 2022	---	---
Acantholyda hieroglyphica	ZMUO.016337	MZ632005	Roslin *et al.* 2022	---	---
Acantholyda hieroglyphica	ZMUO.023641	FISYM337-15	BOLD	---	---
Acantholyda laricis	NSMT30572	ON016752	this work	ON016998	this work
Acantholyda nipponica	NSMT30556	---	---	ON016982	this work
Acantholyda nipponica	NSMT30568	ON016748	this work	ON016994	this work
Acantholyda parki	NSMT30867	ON016891	this work	ON017149	this work
Acantholyda posticalis pinivora	BC ZSM HYM 03205	KC974204	Schmidt *et al.* 2017	---	---
Acantholyda posticalis pinivora	BC ZSM HYM 03206	JN264369	iBOL	---	---
Acantholyda posticalis pinivora	BC ZSM HYM 03207	KC976107	Schmidt *et al.* 2017	---	---
Acantholyda posticalis pinivora	BC ZSM HYM 03208	HQ563850	iBOL	---	---
Acantholyda posticalis pinivora	BC ZSM HYM 09413	KC973065	Schmidt *et al.* 2017	---	---
Acantholyda posticalis pinivora	BC ZSM HYM 09414	KC975912	Schmidt *et al.* 2017	---	---
Acantholyda posticalis pinivora	BC ZSM HYM 09415	KC977059	Schmidt *et al.* 2017	---	---
Acantholyda posticalis posticalis	FSYM-000083	MZ627750	Roslin *et al.* 2022	---	---
Acantholyda posticalis posticalis	ZMUO.016338	MZ634042	Roslin *et al.* 2022	---	---
Acantholyda posticalis posticalis	ZMUO.016339	MZ629839	Roslin *et al.* 2022	---	---
Acantholyda posticalis posticalis	ZMUO.017853	MZ608478	Roslin *et al.* 2022	---	---
Acantholyda posticalis posticalis	ZMUO.017854	MZ608752	Roslin *et al.* 2022	---	---
Acantholyda pumilionis	BC ZSM HYM 03213	HQ563853	iBOL	---	---
Acantholyda pumilionis	BC ZSM HYM 03214	HQ563854	iBOL	---	---
Acantholyda pumilionis	BC ZSM HYM 03215	HQ563855	iBOL	---	---
Acantholyda pumilionis	BC ZSM HYM 10744	KC975161	Schmidt *et al.* 2017	---	---

.....continued on the next page

TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Acantholyda pumilionis	BC ZSM HYM 22137	BCHYM4942-14	BOLD	---	---
Acantholyda pumilionis	tK8	KF936565	Malm & Nyman 2014	KF935872	Malm & Nyman 2014
Acantholyda serbica	DEI-GISHym15776	KC976272	Schmidt *et al.* 2017	---	---
Acantholyda thalictra	DEI-GISHym32542	ON016686 / *DEISY1949-19*	this work	---	---
Acantholyda tsuyukii	NSMT30571	ON016751 / *DEISY2425-19*	this work	ON016997	this work
Acantholyda verticalis	CNCHYM 02071		BOLD	---	---
Acantholyda zappei	CNCHYM 02073		BOLD	---	---
		CEPHALCIA			
Cephalcia abietis	BC ZSM HYM 00153	HM376287	iBOL	---	---
Cephalcia abietis	BC ZSM HYM 07206	KC972706	Schmidt *et al.* 2017	---	---
Cephalcia alashanica	BC ZSM HYM 03221	KC975860	Schmidt *et al.* 2017	---	---
Cephalcia alashanica	BC ZSM HYM 03222	KC977044	Schmidt *et al.* 2017	---	---
Cephalcia alashanica	BC ZSM HYM 03223	KC972663	Schmidt *et al.* 2017	---	---
Cephalcia alashanica	BC ZSM HYM 09607	KC975640	Schmidt *et al.* 2017	---	---
Cephalcia alpina	BC ZSM HYM 09609	KC976437	Schmidt *et al.* 2017	---	---
Cephalcia alpina	DEI-GISHym11069	KC974537	Schmidt *et al.* 2017	---	---
Cephalcia alpina	DEI-GISHym18892	KC975087	Schmidt *et al.* 2017	---	---
Cephalcia alpina	DEI-GISHym18893	KC974724	Schmidt *et al.* 2017	---	---
Cephalcia alpina	DEI-GISHym18894	KC975884	Schmidt *et al.* 2017	---	---
Cephalcia alpina	FSYM-000087	MZ623852	Roslin *et al.* 2022	---	---
Cephalcia alpina	MHV00108	MZ625957	Roslin *et al.* 2022	---	---
Cephalcia alpina	ZMUO.019857	MZ629805	Roslin *et al.* 2022	---	---
Cephalcia alpina	ZMUO.019858	MZ629660	Roslin *et al.* 2022	---	---
Cephalcia alpina	ZMUO.027935	MZ658687	Roslin *et al.* 2022	---	---
Cephalcia annulicornis	BC ZSM HYM 03226	KC976408	Schmidt *et al.* 2017	---	---

.....continued on the next page

TABLE 1. (Continued)

Species	**Specimen ID**	COI	**Reference**	NaK	**Reference**
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Cephalcia annulicornis	BC ZSM HYM 10768	KC972711	Schmidt *et al.* 2017	---	---
Cephalcia annulicornis	DEI-GISHym11071	KC975599	Schmidt *et al.* 2017	---	---
Cephalcia annulicornis	DEI-GISHym11823	KC973522	Schmidt *et al.* 2017	---	---
Cephalcia arvensis	BC ZSM HYM 00156	HM376288	iBOL	---	---
Cephalcia arvensis	BC ZSM HYM 07209	KC974401	Schmidt *et al.* 2017	---	---
Cephalcia arvensis	BC ZSM HYM 09610	KC975773	Schmidt *et al.* 2017	---	---
Cephalcia arvensis	BC ZSM HYM 09611	KC974190	Schmidt *et al.* 2017	---	---
Cephalcia arvensis	BC ZSM HYM 09612	KC973530	Schmidt *et al.* 2017	---	---
Cephalcia arvensis	BC ZSM HYM 12721	BCHYM8921-15	BOLD	---	---
Cephalcia arvensis	BC ZSM HYM 15942	GBSYM1597-13	BOLD	---	---
Cephalcia arvensis	BC ZSM HYM 16143	GBSYM1703-13	BOLD	---	---
Cephalcia arvensis	BC ZSM HYM 16144	GBSYM1704-13	BOLD	---	---
Cephalcia arvensis	BC ZSM HYM 16145	GBSYM1705-13	BOLD	---	---
Cephalcia arvensis	BC ZSM HYM 17019	GBSYM2294-13	BOLD	---	---
Cephalcia arvensis	BC ZSM HYM 18790	GBCHA930-13	BOLD	---	---
Cephalcia arvensis	BC ZSM HYM 20292	BCHYM2337-14	BOLD	---	---
Cephalcia arvensis	DEI-GISHym11842	KC973676	Schmidt *et al.* 2017	---	---
Cephalcia arvensis	DEI-GISHym20315	KC975664	Schmidt *et al.* 2017	---	---
Cephalcia arvensis	MHV00107	MZ627105	Roslin *et al.* 2022	---	---
Cephalcia arvensis	tI5	KF936544	Malm & Nyman 2014	KF935854	Malm & Nyman 2014
Cephalcia arvensis	ZMUO.017855	MZ608985	Roslin *et al.* 2022	---	---
Cephalcia arvensis	ZMUO.027933	MZ660006	Roslin *et al.* 2022	---	---
Cephalcia arvensis	ZMUO.027934	MZ629373	Roslin *et al.* 2022	---	---
Cephalcia arvensis	ZMUO.029099	MZ631129	Roslin *et al.* 2022	---	---
Cephalcia californica	CNCHYM 02077	HYCNC1563-11	BOLD	---	---
Cephalcia californica	CNCHYM 02078	HYCNC1564-11	BOLD	---	---
Cephalcia distincta	CNCHYM 02161	HYCNC1647-11	BOLD	---	---

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Cephalcia distincta	CNCHYM 02162	HYCNC1648-11	BOLD	---	---
Cephalcia distincta	CNCHYM 02163	HYCNC1649-11	BOLD	---	---
Cephalcia erythrogaster	BC ZSM HYM 09613	KC974698	Schmidt *et al.* 2017	---	---
Cephalcia erythrogaster	BC ZSM HYM 09624	KC975265	Schmidt *et al.* 2017	---	---
Cephalcia erythrogaster	BC ZSM HYM 09625	KC976055	Schmidt *et al.* 2017	---	---
Cephalcia erythrogaster	BC ZSM HYM 10769	KC975572	Schmidt *et al.* 2017	---	---
Cephalcia erythrogaster	BC ZSM HYM 10770	KC974398	Schmidt *et al.* 2017	---	---
Cephalcia erythrogaster	BC ZSM HYM 16146	GBSYM1706-13	BOLD	---	---
Cephalcia erythrogaster	DEI-GISHym11066	KC974359	Schmidt *et al.* 2017	---	---
Cephalcia fascipennis	CNCHYM 02080	HYCNC1566-11	BOLD	---	---
Cephalcia fascipennis	CNCHYM 02082	HYCNC1568-11	BOLD	---	---
Cephalcia fascipennis	CNCHYM 02084	HYCNC1570-11	BOLD	---	---
Cephalcia frontalis	CNCHYM 02152	HYCNC1638-11	BOLD	---	---
Cephalcia frontalis	CNCHYM 02155	HYCNC1641-11	BOLD	---	---
Cephalcia fulva	BC ZSM HYM 09626	KC973655	Schmidt *et al.* 2017	---	---
Cephalcia fulva	BC ZSM HYM 09628	KC975485	Schmidt *et al.* 2017	---	---
Cephalcia fulviceps	CNCHYM 02156	HYCNC1642-11	BOLD	---	---
Cephalcia fulviceps	CNCHYM 02157	HYCNC1643-11	BOLD	---	---
Cephalcia fulviceps	CNCHYM 02158	HYCNC1644-11	BOLD	---	---
Cephalcia fulviceps	CNCHYM 02159	HYCNC1645-11	BOLD	---	---
Cephalcia hartigii	BC ZSM HYM 03241	HQ563865	iBOL	---	---
Cephalcia hopkinsi	DEI-GISHym32543	ON016687 / *DEISY1950-19*	this work	---	---
Cephalcia intermedia	DEI-GISHym11936	KC974279	Schmidt *et al.* 2017	---	---
Cephalcia isshikii	NSMT30566	ON016746 / *DEISY2420-19*	this work	ON016992	this work
Cephalcia lariciphila	BC ZSM HYM 03212	HQ563852	iBOL	---	---

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TABLE 1. (Continued)

Species	**Specimen ID**	COI	**Reference**	NaK	**Reference**
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Cephalcia lariciphila	BC ZSM HYM 03227	KC976539	Schmidt *et al.* 2017	---	---
Cephalcia lariciphila	BC ZSM HYM 03228	KC976285	Schmidt *et al.* 2017	---	---
Cephalcia lariciphila	BC ZSM HYM 03229	KC973153	Schmidt *et al.* 2017	---	---
Cephalcia lariciphila	BC ZSM HYM 03230	KC975913	Schmidt *et al.* 2017	---	---
Cephalcia lariciphila	BC ZSM HYM 10767	KC975406	Schmidt *et al.* 2017	---	---
Cephalcia lariciphila	BC ZSM HYM 10771	KC975817	Schmidt *et al.* 2017	---	---
Cephalcia lariciphila	BC ZSM HYM 10772	KC976979	Schmidt *et al.* 2017	---	---
Cephalcia provancheri	CNCHYM 02089	HYCNC1642-11	BOLD	---	---
Cephalcia provancheri	CNCHYM 02090	HYCNC1576-11	BOLD	---	---
Cephalcia provancheri	CNCHYM 02092	HYCNC1578-11	BOLD	---	---
Cephalcia semidea	CNCHYM 02094	HYCNC1580-11	BOLD	---	---
Cephalcia sp.	DEI-GISHym17559	ON016650 / *DEISY898-19*	this work	---	---
Cephalcia sp.	DEI-GISHym21862	ON016657 *DEISY1099-19*	this work	---	---
Cephalcia sp.	DEI-GISHym32034	ON016664 / *DEISY1785-19*	this work	ON016919	this work
Cephalcia sp.	DEI-GISHym32035	ON016665 / *DEISY1786-19*	this work	---	---
Cephalcia sp.	DEI-GISHym32039	ON016669 / *DEISY1790-19*	this work	ON016923	this work
Cephalcia sp.	DEI-GISHym32043	ON016673 / *DEISY1794-19*	this work	ON016927	this work
Cephalcia sp.	DEI-GISHym88018	ON016705 / *DEISY3910-19*	this work	ON016952	this work
Cephalcia sp.	DEI-GISHym88049	ON016709 / *DEISY3924-19*	this work	ON016955	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Cephalcia sp.	DEI-GISHym88082	ON016712 / *DEISY3932-19*	this work	---	---
Cephalcia sp.	DEI-GISHym88118	ON016713 / *DEISY3939-19*	this work	---	---
Cephalcia sp.	DEI-GISHym88119	ON016714 / *DEISY3940-19*	this work	---	---
Cephalcia sp.	DEI-GISHym88120	ON016715 / *DEISY3941-19*	this work	---	---
Cephalcia sp.	DEI-GISHym89796	ON016723	this work	ON016961	this work
Cephalcia sp.	NSMT30552	ON016736 / *DEISY2406-19*	this work	ON016978	this work
Cephalcia sp.	NSMT30741	ON016822 / *DEISY2573-19*	this work	ON017068	this work
Cephalcia sp.	NSMT30742	ON016823 / *DEISY2574-19*	this work	ON017069	this work
Cephalcia sp.	NSMT30743	ON016824 / *DEISY2575-19*	this work	ON017070	this work
Cephalcia sp.	tE8	KF936514	Malm & Nyman 2014	KF935826	Malm & Nyman 2014
Cephalcia sp.	tK7	KF936564	Malm & Nyman 2014	KF935871	Malm & Nyman 2014
		NEUROTOMA			
Neurotoma 027 China sp.	DEI-GISHym16393	KC975603	Schmidt *et al.* 2017	---	---
Neurotoma coreana	NSMT30596	ON016758 / *DEISY2432-19*	this work	---	---
Neurotoma crataegi	CNCHYM 02095	HYCNC1581-11	BOLD	---	---
Neurotoma crataegi	CNCHYM 02096	HYCNC1582-11	BOLD	---	---
Neurotoma crataegi	CNCHYM 02097	HYCNC1583-11	BOLD	---	---
Neurotoma crataegi	CNCHYM 02098	HYCNC1584-11	BOLD	---	---
Neurotoma fausta	BC ZSM HYM 03216	HQ563856	iBOL	---	---

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TABLE 1. (Continued)

Species	**Specimen ID**	COI	**Reference**	NaK	**Reference**
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Neurotoma fausta	BC ZSM HYM 11496	KC975963	Schmidt *et al.* 2017	---	---
Neurotoma fausta	BC ZSM HYM 20196	BCHYM2906-14	BOLD	---	---
Neurotoma fausta	DEI-GISHym11081	KC974827	Schmidt *et al.* 2017	---	---
Neurotoma fausta	DEI-GISHym15775	KC973244	Schmidt *et al.* 2017	---	---
Neurotoma iridescens	DEI-GISHym32050	ON016680 / *DEISY1801-19*	this work	ON016933	this work
Neurotoma iridescens	NSMT30565	ON016745 / *DEISY2419-19*	this work	ON016991	this work
Neurotoma mandibularis	DEI-GISHym11080	KC976444	Schmidt *et al.* 2017	---	---
Neurotoma mandibularis	DEI-GISHym15780	KC974200	Schmidt *et al.* 2017	---	---
Neurotoma nemoralis	BC ZSM HYM 03217	KC974531	Schmidt *et al.* 2017	---	---
Neurotoma nemoralis	BC ZSM HYM 03218	KC972758	Schmidt *et al.* 2017	---	---
Neurotoma nemoralis	BC ZSM HYM 03220	KC975556	Schmidt *et al.* 2017	---	---
Neurotoma nemoralis	BC ZSM HYM 11340	KC974446	Schmidt *et al.* 2017	---	---
Neurotoma nemoralis	BC ZSM HYM 20197	BCHYM2907-14	BOLD	---	---
Neurotoma nemoralis	DEI-GISHym11083	KC975271	Schmidt *et al.* 2017	---	---
Neurotoma nemoralis	DEI-GISHym11084	KC974521	Schmidt *et al.* 2017	---	---
Neurotoma nemoralis	DEI-GISHym16395	KC974604	Schmidt *et al.* 2017	---	---
Neurotoma nemoralis	NSMT30538	ON016726 / *DEISY2393-19*	this work	ON016966	this work
Neurotoma nemoralis	NSMT30726	ON016808 / *DEISY2558-19*	this work	ON017053	this work
Neurotoma nemoralis	tX1	KF936652	Malm & Nyman 2014	KF935938	Malm & Nyman 2014
Neurotoma saltuum	DEI-GISHym11082	KC974471	Schmidt *et al.* 2017	---	---
Neurotoma sibirica	DEI-GISHym32030	ON016660 / *DEISY1781-19*	this work	ON016915	this work
Neurotoma sibirica	DEI-GISHym32033	ON016663 / *DEISY1784-19*	this work	ON016918	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Neurotoma sibirica	DEI-GISHym32042	ON016672 / *DEISY1793-19*	this work	ON016926	this work
Neurotoma sibirica	DEI-GISHym32044	ON016674 / *DEISY1795-19*	this work	---	---
Neurotoma sibirica	DEI-GISHym32045	ON016675 / *DEISY1796-19*	this work	ON016928	this work
Neurotoma sibirica	DEI-GISHym32046	ON016676 / *DEISY1797-19*	this work	ON016929	this work
Neurotoma sibirica	DEI-GISHym32047	ON016677 / *DEISY1798-19*	this work	ON016930	this work
Neurotoma sibirica	DEI-GISHym32048	ON016678 / *DEISY1799-19*	this work	ON016931	this work
Neurotoma sibirica	DEI-GISHym32054	ON016684 / *DEISY1805-19*	this work	---	---
Neurotoma sibirica	DEI-GISHym32055	ON016685 / *DEISY1806-19*	this work	ON016937	this work
Neurotoma sibirica	NSMT30544	ON016731 / *DEISY2398-19*	this work	ON016971	this work
Neurotoma sibirica	NSMT30725	ON016807 / *DEISY2557-19*	this work	ON017052	this work
Neurotoma sibirica *	NSMT47743	LC126728	Shinohara *et al.* 2016a	---	---
		ONYCHOLYDA			
Onycholyda amplecta	CNCHYM 02103	HYCNC1589-11	BOLD	---	---
Onycholyda amplecta	CNCHYM 02104	HYCNC1590-11	BOLD	---	---
Onycholyda amplecta	tH9	KF936538	Malm & Nyman 2014	KF935849	Malm & Nyman 2014
Onycholyda armata	DEI-GISHym86268	ON016692 / *DEISY3438-19*	this work	ON016942	this work
Onycholyda armata	DEI-GISHym86314	ON016696 / *DEISY3449-19*	this work	ON016944	this work

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TABLE 1. (Continued)

Species	**Specimen ID**	COI	**Reference**	NaK	**Reference**
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Oncholyda armata	DEI-GISHym86315	ON016697 / *DEISY3450-19*	this work	ON016945	this work
Oncholyda decorata	NSMT30564	ON016744 / *DEISY2418-19*	this work	ON016990	this work
Oncholyda decorata	NSMT30591	ON016755 / *DEISY2429-19*	this work	ON017001	this work
Oncholyda esakii	NSMT30567	ON016747 / *DEISY2421-19*	this work	ON016993	this work
Oncholyda esakii	NSMT30781	ON016856 / *DEISY2613-19*	this work	ON017108	this work
Oncholyda esakii	NSMT30782	ON016857 / *DEISY2614-19*	this work	ON017109	this work
Oncholyda esakii	NSMT30783	ON016858 / *DEISY2615-19*	this work	ON017110	this work
Oncholyda esakii	NSMT30784	ON016859 / *DEISY2616-19*	this work	ON017111	this work
Oncholyda esakii	NSMT30798	ON016868 / *DEISY2628-19*	this work	ON017123	this work
Oncholyda esakii	NSMT30799	ON016869 / *DEISY2629-19*	this work	ON017124	this work
Oncholyda kumamotonis	NSMT30554	ON016737 / *DEISY2408-19*	this work	ON016980	this work
Oncholyda kumamotonis	NSMT30730	LC368500	Shinohara *et al.* 2018b	ON017057	this work
Oncholyda kumamotonis	NSMT30785	LC368501	Shinohara *et al.* 2018b	ON017112	this work
Oncholyda kumamotonis	NSMT30786	LC368502	Shinohara *et al.* 2018b	ON017113	this work
Oncholyda kumamotonis	NSMT30787	LC368503	Shinohara *et al.* 2018b	ON017114	this work
Oncholyda kumamotonis	NSMT30788	ON016860 / *DEISY2620-19*	this work	ON017115	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Oncholyda kumamotonis	NSMT30789	ON016861 / *DEISY2621-19*	this work	ON017116	this work
Oncholyda lucida	DEI-GISHym87674	ON016701 / *DEISY3817-19*	this work	ON016949	this work
Oncholyda lucida	NSMT30659	ON016780 / *DEISY2517-19*	this work	ON017014	this work
Oncholyda lucida	NSMT30668	LC368505 / *DEISY2523-19*	Shinohara *et al.* 2018b	ON017019	this work
Oncholyda lucida	NSMT30777	LC368506 / *DEISY2609-19*	Shinohara *et al.* 2018b	ON017104	this work
Oncholyda lucida	NSMT30778	LC368507 / *DEISY2610-19*	Shinohara *et al.* 2018b	ON017105	this work
Oncholyda lucida	NSMT30908	ON016909 / *DEISY2673-19*	this work	ON017167	this work
Oncholyda lucida	NSMT30909	ON016910 / *DEISY2674-19*	this work	ON017168	this work
Oncholyda luteicornis	CNCHYM 02107	HYCNC1593-11	BOLD	---	---
Oncholyda luteicornis	CNCHYM 02109	HYCNC1595-11	BOLD	---	---
Oncholyda luteicornis	CNCHYM 02110	HYCNC1596-11	BOLD	---	---
Oncholyda luteicornis	NSMT30969	ON016911 / *DEISY2675-19*	this work	ON017169	this work
Oncholyda minomalis	NSMT30669	ON016786 / *DEISY2524-19*	this work	ON017020	this work
Oncholyda minomalis	NSMT30670	ON016787 / *DEISY2525-19*	this work	ON017021	this work
Oncholyda minomalis	NSMT30671	ON016788 / *DEISY2526-19*	this work	ON017022	this work
Oncholyda minomalis	NSMT30693	ON016800 / *DEISY2547-19*	this work	ON017042	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Oncholyda minomalis	NSMT30776	ON016853 / *DEISY2608-19*	this work	ON017103	this work
Oncholyda multisignata	CNCHYM 02113	HYCNC1599-11	BOLD	---	---
Oncholyda nigritibialis	CNCHYM 02115	HYCNC1601-11	BOLD	---	---
Oncholyda nigritibialis	CNCHYM 02116	HYCNC1602-11	BOLD	---	---
Oncholyda nigritibialis	CNCHYM 02117	HYCNC1603-11	BOLD	---	---
Oncholyda nigritibialis	CNCHYM 02118	HYCNC1604-11	BOLD	---	---
Oncholyda nigritibialis	tK0	KF936557	Malm & Nyman 2014	KF935864	Malm & Nyman 2014
Oncholyda nigroclypeata	DEI-GISHym86743	ON016699 / *DEISY3511-19*	this work	ON016947	this work
Oncholyda rufofasciata	CNCHYM 02137	HYCNC1623-11	BOLD	---	---
Oncholyda rufofasciata	CNCHYM 02138	HYCNC1624-11	BOLD	---	---
Oncholyda rufofasciata	CNCHYM 02139	HYCNC1625-11	BOLD	---	---
Oncholyda rufofasciata	CNCHYM 02140	HYCNC1626-11	BOLD	---	---
Oncholyda rufofasciata	tG4	KF936526	Malm & Nyman 2014	KF935838	Malm & Nyman 2014
Oncholyda sertata	DEI-GISHym31245	ON016658 / *DEISY1700-19*	this work	---	---
Oncholyda sertata	DEI-GISHym31256	ON016659 / *DEISY1711-19*	this work	ON016914	this work
Oncholyda sertata	DEI-GISHym32031	ON016661 / *DEISY1782-19*	this work	ON016916	this work
Oncholyda sertata	DEI-GISHym32037	ON016667 / *DEISY1788-19*	this work	ON016921	this work
Oncholyda sertata	DEI-GISHym32053	ON016683 / *DEISY1804-19*	this work	ON016936	this work
Oncholyda sertata	DEI-GISHym86157	ON016690 / *DEISY3414-19*	this work	ON016940	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Oncholyda sertata	DEI-GISHym86310	ON016694 / *DEISY3445-19*	this work	---	---
Oncholyda sertata	GL.3070	FISYM093-14	BOLD	---	---
Oncholyda similis	DEI-GISHym87673	ON016700 / *DEISY3816-19*	this work	ON016948	this work
Oncholyda similis	NSMT30653	ON016777	this work	---	---
Oncholyda similis	NSMT30672	ON016789 / *DEISY2527-19*	this work	ON017023	this work
Oncholyda similis	NSMT30800	ON016870 / *DEISY2630-19*	this work	ON017125	this work
Oncholyda sitkensis	CNCHYM 02148	HYCNC1634-11	BOLD	---	---
Oncholyda sp.	NSMT30868	ON016892 / *DEISY2655-19*	this work	ON017150	this work
Oncholyda sp.	NSMT30890	---	---	ON017153	this work
Oncholyda tenuis	NSMT30795	ON016865 / *DEISY2625-19*	this work	ON017120	this work
Oncholyda tenuis	NSMT30796	ON016866 / *DEISY2626-19*	this work	ON017121	this work
Oncholyda tenuis	NSMT30797	ON016867 / *DEISY2627-19*	this work	ON017122	this work
Oncholyda trigaria	DEI-GISHym18062	KC974432	Schmidt *et al.* 2017	---	---
Oncholyda viriditibialis	DEI-GISHym32038	ON016668 / *DEISY1789-19*	this work	ON016922	this work
Oncholyda viriditibialis	DEI-GISHym32041	ON016671 / *DEISY1792-19*	this work	ON016925	this work
Oncholyda viriditibialis	DEI-GISHym88062	ON016710 / *DEISY3926-19*	this work	---	---
Oncholyda viriditibialis	DEI-GISHym89186	ON016720 / *DEISY4089-19*	this work	ON016960	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Onycholyda viriditibialis	NSMT30792	ON016862 / *DEISY2622-19*	this work	ON017117	this work
Onycholyda viriditibialis	NSMT30793	ON016863 / *DEISY2623-19*	this work	ON017118	this work
Onycholyda viriditibialis	NSMT30794	ON016864 / *DEISY2624-19*	this work	ON017119	this work
Onycholyda yezoensis	NSMT30779	ON016854 / *DEISY2611-19*	this work	ON017106	this work
Onycholyda yezoensis	NSMT30780	ON016855 / *DEISY2612-19*	this work	ON017107	this work
		PAMPHILIUS			
Pamphilius albopictus	DEI-GISHym32036	ON016666 / *DEISY1787-19*	this work	ON016920	this work
Pamphilius albopictus	DEI-GISHym86124	ON016689 / *DEISY3404-19*	this work	ON016939	this work
Pamphilius albopictus	MHV00115	MZ623848	Roslin *et al.* 2022	---	---
Pamphilius albopictus	NSMT30865	ON016889 / *DEISY2652-19*	this work	ON017147	this work
Pamphilius alnicola	NSMT30550	LC456280	Shinohara *et al.* 2019	ON016976	this work
Pamphilius alnicola	NSMT30899	ON016903 / *DEISY2667-19*	this work	ON017162	this work
Pamphilius alnivorus	NSMT30598	ON016759 / *DEISY2433-19*	this work	---	---
Pamphilius alnivorus	NSMT30717	ON016801 / *DEISY2549-19*	this work	ON017044	this work
Pamphilius alnivorus	NSMT30721	---	---	ON017048	this work
Pamphilius alternans	BC ZSM HYM 15186	GBSYM2076-13	BOLD	---	---
Pamphilius alternans	DEI-GISHym15778	KC972776	Schmidt *et al.* 2017	---	---

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius archiducalis	NSMT30601	ON016762 / *DEISY2436-19*	this work	---	---
Pamphilius archiducalis	NSMT30801	ON016871 / *DEISY2631-19*	this work	ON017126	this work
Pamphilius archiducalis	NSMT30904	ON016908 / *DEISY2672-19*	this work	ON017166	this work
Pamphilius aucupariae	NSMT30768	ON016845 / *DEISY2600-19*	this work	ON017095	this work
Pamphilius aucupariae	NSMT30769	ON016846 / *DEISY2601-19*	this work	ON017096	this work
Pamphilius aucupariae	NSMT30770	ON016847 / *DEISY2602-19*	this work	ON017097	this work
Pamphilius aucupariae	NSMT30861	ON016885 / *DEISY2648-19*	this work	ON017143	this work
Pamphilius aurantiacus	BC ZSM HYM 09417	KC974760	Schmidt *et al.* 2017	---	---
Pamphilius aurantiacus	BC ZSM HYM 10986	KC976100	Schmidt *et al.* 2017	---	---
Pamphilius aurantiacus	DEI-GISHym11119	KC973723	Schmidt *et al.* 2017	---	---
Pamphilius aurantiacus	DEI-GISHym17760	KC974314	Schmidt *et al.* 2017	---	---
Pamphilius aurantiacus	DEI-GISHym18896	KC976590	Schmidt *et al.* 2017	---	---
Pamphilius balteatus	BC ZSM HYM 04197	HQ955763	iBOL	---	---
Pamphilius balteatus	BC ZSM HYM 04198	KC975094	Schmidt *et al.* 2017	---	---
Pamphilius balteatus	DEI-GISHym12938	ON016646	this work	---	---
Pamphilius balteatus	DEI-GISHym21010	ON016654	this work	---	---
Pamphilius balteatus	FSYM-000086	MZ627362	Roslin *et al.* 2022	---	---
Pamphilius balteatus	GL.3111	FISYM233-14	BOLD	---	---
Pamphilius basilaris	NSMT30534	ON016725 / *DEISY2390-19*	this work	ON016963	this work

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TABLE 1. (Continued)

Species	**Specimen ID**	COI	**Reference**	NaK	**Reference**
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius basilaris	NSMT30586	ON016754 / *DEISY2428-19*	this work	ON017000	this work
Pamphilius belokobylskiji	DEI-GISHym88019	ON016706 / *DEISY3911-19*	this work	ON016953	this work
Pamphilius belokobylskiji	DEI-GISHym88121	ON016716 / *DEISY3942-19*	this work	ON016957	this work
Pamphilius belokobylskiji	DEI-GISHym88123	ON016718 / *DEISY3944-19*	this work	ON016958	this work
Pamphilius belokobylskiji	NSMT30766	ON016843 / *DEISY2598-19*	this work	ON017093	this work
Pamphilius belokobylskiji	NSMT30767	ON016844 / *DEISY2599-19*	this work	ON017094	this work
Pamphilius belokobylskiji	NSMT30866	ON016890 / *DEISY2653-19*	this work	ON017148	this work
Pamphilius benesi	NSMT30535	LC456281	Shinohara *et al.* 2019	ON016964	this work
Pamphilius benesi	NSMT30549	LC456282	Shinohara *et al.* 2019	ON016975	this work
Pamphilius benesi	NSMT30677	LC456283	Shinohara *et al.* 2019	ON017028	this work
Pamphilius benesi	NSMT30678	LC456284	Shinohara *et al.* 2019	ON017029	this work
Pamphilius benesi	NSMT30679	LC456285	Shinohara *et al.* 2019	ON017030	this work
Pamphilius benesi	NSMT30680	LC456286	Shinohara *et al.* 2019	ON017031	this work
Pamphilius benesi	NSMT30681	ON016792 / *DEISY2536-19*	this work	ON017032	this work
Pamphilius betulae	BC ZSM HYM 03261	KC976655	Schmidt *et al.* 2017	---	---
Pamphilius brevicornis brevicornis	DEI-GISHym17524	ON016649 / *DEISY879-19*	this work	---	---
Pamphilius brevicornis brevicornis	DEI-GISHym19820	KF642736	Malm & Nyman 2014	---	---
Pamphilius brevicornis brevicornis	DEI-GISHym88122	ON016717 / *DEISY3943-19*	this work	---	---

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TABLE 1. (Continued)

Species	**Specimen ID**	COI	**Reference**	NaK	**Reference**
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius brevicornis ibukii	NSMT30541	ON016728 / *DEISY2395-19*	this work	ON016968	this work
Pamphilius brevicornis ibukii	NSMT30720	ON016804 / *DEISY2552-19*	this work	ON017047	this work
Pamphilius brevicornis ibukii	NSMT30903	ON016907 / *DEISY2671-19*	this work	---	---
Pamphilius confusus	NSMT30600	ON016761 / *DEISY2435-19*	this work	---	---
Pamphilius confusus	NSMT30609	ON016766 / *DEISY2441-19*	this work	ON017003	this work
Pamphilius confusus	NSMT30610	ON016767 / *DEISY2442-19*	this work	ON017004	this work
Pamphilius confusus	NSMT30611	ON016768 / *DEISY2443-19*	this work	ON017005	this work
Pamphilius confusus	NSMT30612	ON016769 / *DEISY2444-19*	this work	---	---
Pamphilius confusus	NSMT30613	ON016770 / *DEISY2445-19*	this work	ON017006	this work
Pamphilius confusus	NSMT30614	ON016771	this work	ON017007	this work
Pamphilius confusus	NSMT30658	ON016779 / *DEISY2516-19*	this work	ON017013	this work
Pamphilius confusus	NSMT30740	ON016821 / *DEISY2572-19*	this work	ON017067	this work
Pamphilius coreanus	DEI-GISHym86267	ON016691 / *DEISY3437-19*	this work	ON016941	this work
Pamphilius coreanus	NSMT30753	ON016830 / *DEISY2585-19*	this work	ON017080	this work
Pamphilius coreanus	NSMT30857	LC126718 / *DEISY2644-19*	Shinohara *et al.* 2016a	ON017139	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius coreanus	NSMT30863	ON016887 / *DEISY2650-19*	this work	ON017145	this work
Pamphilius croceus	DEI-GISHym88000	ON016703 / *DEISY3904-19*	this work	ON016951	this work
Pamphilius croceus	NSMT30980	ON016912 / *DEISY2676-19*	this work	ON017170	this work
Pamphilius daisenus *	NSMT47832	LC158361	Shinohara *et al.* 2016b	---	---
Pamphilius daisenus *	NSMT47833	LC158362	Shinohara *et al.* 2016b	---	---
Pamphilius daisenus *	NSMT47834	LC158363	Shinohara *et al.* 2016b	---	---
Pamphilius daisenus *	NSMT47835	LC158365	Shinohara *et al.* 2016b	---	---
Pamphilius daisenus *	NSMT47836	LC158366	Shinohara *et al.* 2016b	---	---
Pamphilius daisenus *	NSMT47837	LC158367	Shinohara *et al.* 2016b	---	---
Pamphilius daisenus *	NSMT47905	LC158368	Shinohara *et al.* 2016b	---	---
Pamphilius daisenus *	NSMT47906	LC158369	Shinohara *et al.* 2016b	---	---
Pamphilius festivus	DEI-GISHym17755	KC974054	Schmidt *et al.* 2017	---	---
Pamphilius festivus	ZMUO.027931	MZ660035	Roslin *et al.* 2022	---	---
Pamphilius flavipectus	NSMT30599	ON016760 / *DEISY2434-19*	this work	---	---
Pamphilius flavipectus	NSMT30615	ON016772	this work	---	---
Pamphilius flavipectus	NSMT30616	ON016773	this work	---	---
Pamphilius flavipectus	NSMT30737	ON016818 / *DEISY2569-19*	this work	ON017064	this work
Pamphilius flavipectus	NSMT30738	ON016819 / *DEISY2570-19*	this work	ON017065	this work
Pamphilius fumipennis	DEI-GISHym11117	KC975328	Schmidt *et al.* 2017	---	---
Pamphilius fumipennis	DEI-GISHym19802	KF642755	Malm & Nyman 2014	---	---
Pamphilius fumipennis	DEI-GISHym20590	ON016653	this work	---	---
Pamphilius fumipennis	ZMUO.023646	FISYM342-15	BOLD	---	---

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius fumipennis	ZMUO.029379	MZ658636	Roslin *et al.* 2022	---	---
Pamphilius gracilis	NSMT30553	LC456287 / *DEISY2407-19*	Shinohara *et al.* 2019	ON016979	this work
Pamphilius gracilis	NSMT30559	LC456288 / *DEISY2413-19*	Shinohara *et al.* 2019	ON016985	this work
Pamphilius gracilis	NSMT30655	LC456289 / *DEISY2513-19*	Shinohara *et al.* 2019	ON017011	this work
Pamphilius gracilis	NSMT30676	LC456290 / *DEISY2531-19*	Shinohara *et al.* 2019	ON017027	this work
Pamphilius gracilis	NSMT30803	ON016873 / *DEISY2633-19*	this work	ON017128	this work
Pamphilius gracilis	NSMT30804	---	---	ON017129	this work
Pamphilius gracilis	NSMT30893	ON016897 / *DEISY2661-19*	this work	ON017156	this work
Pamphilius graciloides	DEI-GISHym88016	ON016704 / *DEISY3909-19*	this work	---	---
Pamphilius graciloides	NSMT30603	ON016764 / *DEISY2438-19*	this work	---	---
Pamphilius graciloides	NSMT30747	ON016826 / *DEISY2579-19*	this work	ON017074	this work
Pamphilius graciloides	NSMT30748	ON016827 / *DEISY2580-19*	this work	ON017075	this work
Pamphilius graciloides	NSMT30850	ON016875 / *DEISY2637-19*	this work	ON017132	this work
Pamphilius graciloides	NSMT30851	ON016876 / *DEISY2638-19*	this work	ON017133	this work
Pamphilius graciloides	NSMT30852	ON016877 / *DEISY2639-19*	this work	ON017134	this work
Pamphilius gyllenhali	BC ZSM HYM 01593	HM376318	iBOL	---	---

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius gyllenhali	BC ZSM HYM 10987	KC976674	Schmidt *et al.* 2017	---	---
Pamphilius gyllenhali	BC ZSM HYM 11579	KC975452	Schmidt *et al.* 2017	---	---
Pamphilius gyllenhali	DEI-GISHym17174	KC976422	Schmidt *et al.* 2017	---	---
Pamphilius gyllenhali	FSYM-000084	MZ625552	Roslin *et al.* 2022	---	---
Pamphilius gyllenhali	GL.3196	MZ626415	Roslin *et al.* 2022	---	---
Pamphilius gyllenhali	MHV00111	FISYN060-15	BOLD	---	---
Pamphilius gyllenhali	ZMUO.023647	MZ630383	Roslin *et al.* 2022	---	---
Pamphilius heecheonparki	NSMT30771	ON016848 / *DEISY2603-19*	this work	ON017098	this work
Pamphilius heecheonparki	NSMT30772	ON016849 / *DEISY2604-19*	this work	ON017099	this work
Pamphilius heecheonparki	NSMT30773	ON016850 / *DEISY2605-19*	this work	ON017100	this work
Pamphilius heecheonparki	NSMT30774	ON016851 / *DEISY2606-19*	this work	ON017101	this work
Pamphilius heecheonparki	NSMT30775	ON016852 / *DEISY2607-19*	this work	ON017102	this work
Pamphilius heecheonparki	NSMT30855	ON016880 / *DEISY2642-19*	this work	ON017137	this work
Pamphilius hilaris	DEI-GISHym88046	ON016707 / *DEISY3922-19*	this work	---	---
Pamphilius hilaris	NSMT30860	ON016884 / *DEISY2647-19*	this work	ON017142	this work
Pamphilius histrio	BC ZSM HYM 10988	KC975579	Schmidt *et al.* 2017	---	---
Pamphilius histrio	NSMT30547	LC126714 / *DEISY2401-19*	Shinohara *et al.* 2016a	---	---
Pamphilius histrio	ZMUO.017929	MZ630045	Roslin *et al.* 2022	---	---
Pamphilius hortorum	BC ZSM HYM 00160	GU706191	iBOL	---	---

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TABLE 1. (Continued)

Species	**Specimen ID**	COI	**Reference**	NaK	**Reference**
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius hortorum	BC ZSM HYM 10989	KC974137	Schmidt *et al.* 2017	---	---
Pamphilius hortorum	BC ZSM HYM 15182	GBSYM2072-13	BOLD	---	---
Pamphilius hortorum	BC ZSM HYM 15183	GBSYM2073-13	BOLD	---	---
Pamphilius hortorum	BC ZSM HYM 15184	GBSYM2074-13	BOLD	---	---
Pamphilius hortorum	BC ZSM HYM 15185	GBSYM2075-13	BOLD	---	---
Pamphilius hortorum	BC ZSM HYM 15187	GBSYM2077-13	BOLD	---	---
Pamphilius hortorum	BC ZSM HYM 15188	GBSYM2078-13	BOLD	---	---
Pamphilius hortorum	BC ZSM HYM 15983	GBSYM1733-13	BOLD	---	---
Pamphilius hortorum	BC ZSM HYM 15984	GBSYM1734-13	BOLD	---	---
Pamphilius hortorum	BC ZSM HYM 15985	GBSYM1735-13	BOLD	---	---
Pamphilius hortorum	BC ZSM HYM 20194	BCHYM2904-14	BOLD	---	---
Pamphilius hortorum	BC ZSM HYM 20195	BCHYM2905-14	BOLD	---	---
Pamphilius hortorum	DEI-GISHym12194	ON016645	this work	ON016913	this work
Pamphilius hortorum	DEI-GISHym12946	ON016647	this work	---	---
Pamphilius hortorum	DEI-GISHym12947	ON016648	this work	---	---
Pamphilius hortorum	DEI-GISHym16445	KC972882	Schmidt *et al.* 2017	---	---
Pamphilius hortorum	DEI-GISHym17750	KC973898	Schmidt *et al.* 2017	---	---
Pamphilius hortorum	DEI-GISHym17761	KC975129	Schmidt *et al.* 2017	---	---
Pamphilius hortorum	DEI-GISHym21846	ON016655 / *DEISY1092-19*	this work	---	---
Pamphilius hortorum	MHV00109	FISYN058-15	BOLD	---	---
Pamphilius hortorum	NSMT30548	ON016734 / *DEISY2402-19*	this work	ON016974	this work
Pamphilius hortorum	NSMT30560	ON016741 / *DEISY2414-19*	this work	ON016986	this work
Pamphilius hortorum	NSMT30660	ON016781 / *DEISY2518-19*	this work	ON017015	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius hortorum	NSMT30661	ON016782 / *DEISY2519-19*	this work	---	---
Pamphilius hortorum	ZMUO.027932	MZ659501	Roslin *et al.* 2022	---	---
Pamphilius hortorum	ZMUO.029378	MZ657764	Roslin *et al.* 2022	---	---
Pamphilius ignymontiensis	DEI-GISHym11123	KC977022	Schmidt *et al.* 2017	---	---
Pamphilius ignymontiensis	DEI-GISHym89949	ON016724	this work	ON016962	---
Pamphilius inanitus	DEI-GISHym15779	KC973678	Schmidt *et al.* 2017	---	---
Pamphilius inanitus	DEI-GISHym17043	KC975483	Schmidt *et al.* 2017	---	---
Pamphilius inanitus	DEI-GISHym19047	KF642762	Schmidt *et al.* 2017	---	---
Pamphilius inanitus	MHV00112	FISYN061-15	BOLD	---	---
Pamphilius inanitus	tK6	KF936563	Malm & Nyman 2014	KF935870	Malm & Nyman 2014
Pamphilius ishikawai *	NSMT47824	LC126719	Shinohara *et al.* 2016a	---	---
Pamphilius ishikawai *	NSMT47825	LC126720	Shinohara *et al.* 2016a	---	---
Pamphilius ishikawai *	NSMT47826	LC126721	Shinohara *et al.* 2016a	---	---
Pamphilius ishikawai *	NSMT47827	LC126722	Shinohara *et al.* 2016a	---	---
Pamphilius ishikawai *	NSMT47829	LC126723	Shinohara *et al.* 2016a	---	---
Pamphilius ishikawai *	NSMT47907	LC126724	Shinohara *et al.* 2016a	---	---
Pamphilius ishikawai *	NSMT47908	LC126725	Shinohara *et al.* 2016a	---	---
Pamphilius ishikawai *	NSMT47909	LC126726	Shinohara *et al.* 2016a	---	---
Pamphilius ishikawai *	NSMT47910	LC126727	Shinohara *et al.* 2016a	---	---
Pamphilius itoi	NSMT30557	ON016739 / *DEISY2411-19*	this work	ON016983	this work
Pamphilius itoi	NSMT30573	ON016753 / *DEISY2427-19*	this work	ON016999	this work
Pamphilius itoi	NSMT30718	ON016802 / *DEISY2550-19*	this work	ON017045	this work
Pamphilius itoi	NSMT30731	ON016812 / *DEISY2563-19*	this work	ON017058	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius itoi	NSMT30732	ON016813 / *DEISY2564-19*	this work	ON017059	this work
Pamphilius japonicus	NSMT30675	LC456291 / *DEISY2530-19*	Shinohara *et al.* 2019	ON017026	this work
Pamphilius japonicus	NSMT30692	LC456292 / *DEISY2546-19*	Shinohara *et al.* 2019	ON017041	this work
Pamphilius japonicus *	NSMT47971	LC456293	Shinohara *et al.* 2019	---	---
Pamphilius japonicus *	NSMT47972	LC456294	Shinohara *et al.* 2019	---	---
Pamphilius japonicus *	NSMT47973	LC456295	Shinohara *et al.* 2019	---	---
Pamphilius japonicus *	NSMT47974	LC456296	Shinohara *et al.* 2019	---	---
Pamphilius jucundus	DEI-GISHym20577	ON016651	this work	---	---
Pamphilius jucundus	DEI-GISHym20578	ON016652	this work	---	---
Pamphilius kamikochensis	DEI-GISHym87686	ON016702 / *DEISY3818-19*	this work	ON016950	this work
Pamphilius kamikochensis	NSMT30551	ON016735 / *DEISY2405-19*	this work	ON016977	this work
Pamphilius kamikochensis	NSMT30620	ON016776	this work	ON017010	this work
Pamphilius kamikochensis	NSMT30729	ON016811 / *DEISY2561-19*	this work	ON017056	this work
Pamphilius kashmirensis	DEI-GISHym19756	KF642668	Schmidt *et al.* 2017	---	---
Pamphilius komonensis	NSMT30673	ON016790 / *DEISY2528-19*	this work	ON017024	this work
Pamphilius komonensis	NSMT30674	ON016791 / *DEISY2529-19*	this work	ON017025	this work
Pamphilius komonensis	NSMT30683	ON016793 / *DEISY2537-19*	this work	ON017033	this work
Pamphilius komonensis	NSMT30684	ON016794 / *DEISY2538-19*	this work	ON017034	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius komonensis	NSMT30685	LC126715 / *DEISY2539-19*	Shinohara *et al.* 2016a	ON017035	this work
Pamphilius komonensis	NSMT30686	ON016795 / *DEISY2540-19*	this work	ON017036	this work
Pamphilius kontuniemii	BC ZSM HYM 22398	BCHYM5203-14	BOLD	---	---
Pamphilius kontuniemii	BC ZSM HYM 22399	BCHYM5204-14	BOLD	---	---
Pamphilius kontuniemii	BC ZSM HYM 22400	BCHYM5205-14	BOLD	---	---
Pamphilius kontuniemii	BC ZSM HYM 22401	BCHYM5206-14	BOLD	---	---
Pamphilius kontuniemii	DEI-GISHym11858	KC972932	Schmidt *et al.* 2017	---	---
Pamphilius kontuniemii	DEI-GISHym18897	KC976936	Schmidt *et al.* 2017	---	---
Pamphilius kontuniemii	DEI-GISHym18898	KC976064	Schmidt *et al.* 2017	---	---
Pamphilius kyutekparki	NSMT30754	ON016831 / *DEISY2586-19*	this work	ON017081	this work
Pamphilius kyutekparki	NSMT30755	ON016832 / *DEISY2587-19*	this work	ON017082	this work
Pamphilius kyutekparki	NSMT30854	ON016879 / *DEISY2641-19*	this work	ON017136	this work
Pamphilius kyutekparki	NSMT30864	ON016888 / *DEISY2651-19*	this work	ON017146	this work
Pamphilius leleji	DEI-GISHym32032	ON016662 / *DEISY1783-19*	this work	ON016917	this work
Pamphilius leleji	DEI-GISHym32051	ON016681 / *DEISY1802-19*	this work	ON016934	this work
Pamphilius leleji	DEI-GISHym86269	ON016693 / *DEISY3439-19*	this work	ON016943	this work
Pamphilius lethierryi	DEI-GISHym84935	ON016688 / *DEISY115-19*	this work	ON016938	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius lobatus	DEI-GISHym88047	ON016708 / *DEISY3923-19*	this work	ON016954	this work
Pamphilius lobatus	NSMT30542	ON016729	this work	ON016969	this work
Pamphilius lobatus	NSMT30690	ON016798	this work	ON017039	this work
Pamphilius lobatus	NSMT30691	ON016799	this work	ON017040	this work
Pamphilius lobatus	NSMT30763	ON016840	this work	ON017090	this work
Pamphilius lobatus	NSMT30764	ON016841	this work	ON017091	this work
Pamphilius lobatus	NSMT30765	ON016842	this work	ON017092	this work
Pamphilius lobatus	NSMT30856	ON016881	this work	ON017138	this work
Pamphilius lobatus	NSMT30862	ON016886	this work	ON017144	this work
Pamphilius marginatus	BC ZSM HYM 10990	KC974992	Schmidt *et al.* 2017	---	---
Pamphilius marginatus	DEI-GISHym11125	KC974859	Schmidt *et al.* 2017	---	---
Pamphilius masao	NSMT30539	ON016727	this work	ON016967	this work
Pamphilius masao	NSMT30558	ON016740	this work	ON016984	this work
Pamphilius masao	NSMT30722	ON016805	this work	ON017049	this work
Pamphilius masao	NSMT30733	ON016814	this work	ON017060	this work
Pamphilius masao	NSMT30734	ON016815	this work	ON017061	this work
Pamphilius masao	NSMT30900	ON016904	this work	ON017163	this work
Pamphilius masao	NSMT30901	ON016905	this work	ON017164	this work
Pamphilius montanus montanus	NSMT30894	ON016898	this work	ON017157	this work
Pamphilius montanus montanus	NSMT30895	ON016899	this work	ON017158	this work
Pamphilius montanus pulcher	NSMT30604	LC456278	Shinohara *et al.* 2019	---	---
Pamphilius montanus pulcher	NSMT30719	ON016803	this work	ON017046	this work
Pamphilius montanus pulcher	NSMT30749	LC456279	Shinohara *et al.* 2019	ON017076	this work
Pamphilius montanus pulcher	NSMT30853	ON016878	this work	ON017135	this work
Pamphilius nakagawai	NSMT30570	ON016750	this work	ON016996	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius nakagawai	NSMT30617	ON016774 / *DEISY2512-19*	this work	ON017008	this work
Pamphilius nakagawai	NSMT30618	ON016775	this work	ON017009	this work
Pamphilius nakagawai	NSMT30657	ON016778	this work	ON017012	this work
Pamphilius nakagawai	NSMT30666	ON016784	this work	ON017017	this work
Pamphilius nakagawai	NSMT30667	ON016785	this work	ON017018	this work
Pamphilius nakagawai	NSMT30735	ON016816	this work	ON017062	this work
Pamphilius nakagawai	NSMT30736	ON016817	this work	ON017063	this work
Pamphilius norimbergensis	BC ZSM HYM 03239	HQ563863	iBOL	---	---
Pamphilius ochreipes	CNCHYM 02124	HYCNC1610-11	BOLD	---	---
Pamphilius ochreipes	CNCHYM 02126	HYCNC1612-11	BOLD	---	---
Pamphilius ocreatus	CNCHYM 02119	HYCNC1605-11	BOLD	---	---
Pamphilius ocreatus	CNCHYM 02120	HYCNC1606-11	BOLD	---	---
Pamphilius ocreatus	CNCHYM 02123	HYCNC1609-11	BOLD	---	---
Pamphilius pacificus	CNCHYM 02129	HYCNC1615-11	BOLD	---	---
Pamphilius pallidus	DEI-GISHym32049	ON016679	this work	ON016932	this work
Pamphilius pallimacula	CNCHYM 02131	HYCNC1617-11	BOLD	---	---
Pamphilius pallipes	BC ZSM HYM 00161	HM376289	iBOL	---	---
Pamphilius pallipes	BC ZSM HYM 10991	KC975431	Schmidt *et al.* 2017	---	---
Pamphilius pallipes	DEI-GISHym17048	KC973591	Schmidt *et al.* 2017	---	---
Pamphilius pallipes	GL.3114	MZ626018	Roslin *et al.* 2022	---	---
Pamphilius pallipes	MHV00114	FISYN063-15	BOLD	---	---
Pamphilius pallipes	NSMT30756	ON016833	this work	ON017083	this work
Pamphilius pallipes	NSMT30757	ON016834	this work	ON017084	this work
Pamphilius pallipes	NSMT30758	ON016835	this work	ON017085	this work
Pamphilius pallipes	NSMT30759	ON016836	this work	ON017086	this work
Pamphilius pallipes	ZMUO.029465	MZ660574	Roslin *et al.* 2022	---	---

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius phyllisae	CNCHYM 02132	HYCNC1618-11	BOLD	---	---
Pamphilius planifrons	DEI-GISHym32040	ON016670	this work	ON016924	this work
Pamphilius planifrons	DEI-GISHym32052	ON016682	this work	ON016935	this work
Pamphilius rhoae	NSMT30858	ON016882	this work	ON017140	this work
Pamphilius sapporensis	NSMT30543	ON016730	this work	ON016970	this work
Pamphilius sapporensis	NSMT30563	ON016743	this work	ON016989	this work
Pamphilius sapporensis	NSMT30727	ON016809	this work	ON017054	this work
Pamphilius sp.	DEI-GISHym89664	ON016721	this work	---	---
Pamphilius sp.	DEI-GISHym89665	ON016722	this work	---	---
Pamphilius sp.	NSMT30869	ON016893	this work	ON017151	this work
Pamphilius sp.	NSMT30870	ON016894	this work	ON017152	this work
Pamphilius sp.	NSMT30891	ON016895	this work	ON017154	this work
Pamphilius sp.	tK9	KF936566	Malm & Nyman 2014	KF935873	Malm & Nyman 2014
Pamphilius sp.	tL1	KF936568	Malm & Nyman 2014	KF935874	Malm & Nyman 2014
Pamphilius stramineipes	DEI-GISHym19061	KF642747	Schmidt *et al.* 2017	---	---
Pamphilius stramineipes	NSMT30545	ON016732	this work	ON016972	this work
Pamphilius stramineipes	NSMT30546	ON016733	this work	ON016973	this work
Pamphilius sulphureipes sulphureipes	NSMT30606	ON016765	this work	---	---
Pamphilius sulphureipes sulphureipes	NSMT30750	ON016828	this work	ON016996	this work
Pamphilius sulphureipes sulphureipes	NSMT30751	LC126717	Shinohara *et al.* 2016a	ON016997	this work
Pamphilius sulphureipes sulphureipes	NSMT30752	ON016829	this work	ON016998	this work
Pamphilius sulphureipes sulphureipes	NSMT30859	ON016883	this work	ON017141	this work
Pamphilius sylvaticus	BC ZSM HYM 00162	GU706192	iBOL	---	---
Pamphilius sylvaticus	BC ZSM HYM 01607	GU706277	iBOL	---	---
Pamphilius sylvaticus	BC ZSM HYM 04215	HQ955765	iBOL	---	---
Pamphilius sylvaticus	BC ZSM HYM 10992	KC972898	Schmidt *et al.* 2017	---	---
Pamphilius sylvaticus	BC ZSM HYM 12666	BCHYM8866-15	BOLD	---	---

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TABLE 1. (Continued)

Species	**Specimen ID**	COI	**Reference**	NaK	**Reference**
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius sylvaticus	BC ZSM HYM 15979	GBSYM1729-13	BOLD	---	---
Pamphilius sylvaticus	BC ZSM HYM 15980	GBSYM1730-13	BOLD	---	---
Pamphilius sylvaticus	BC ZSM HYM 15981	GBSYM1731-13	BOLD	---	---
Pamphilius sylvaticus	BC ZSM HYM 16790	GBACU3205-13	BOLD	---	---
Pamphilius sylvaticus	BC ZSM HYM 17020	GBSYM2295-13	BOLD	---	---
Pamphilius sylvaticus	BC ZSM HYM 20260	BCHYM2305-14	BOLD	---	---
Pamphilius sylvaticus	CNCHYM 02144	HYCNC1630-11	BOLD	---	---
Pamphilius sylvaticus	DEI-GISHym17745	KC974210	Schmidt *et al.* 2017	---	---
Pamphilius sylvaticus	DEI-GISHym17746	KC975682	Schmidt *et al.* 2017	---	---
Pamphilius sylvaticus	DEI-GISHym17747	KC974775	Schmidt *et al.* 2017	---	---
Pamphilius sylvaticus	DEI-GISHym17748	KC976638	Schmidt *et al.* 2017	---	---
Pamphilius sylvaticus	DEI-GISHym19060	KF642725	Schmidt *et al.* 2017	---	---
Pamphilius sylvaticus	FSYM-000085	MZ625796	Roslin *et al.* 2022	---	---
Pamphilius sylvaticus	GL.2986	MZ626536	Roslin *et al.* 2022	---	---
Pamphilius sylvaticus	GL.3113	MZ625502	Roslin *et al.* 2022	---	---
Pamphilius takeuchii	NSMT30592	ON016756	this work	---	---
Pamphilius takeuchii	NSMT30593	ON016757	this work	---	---
Pamphilius takeuchii	NSMT30687	ON016796	this work	ON017037	this work
Pamphilius togashii	NSMT30602	ON016763	this work	ON017002	this work
Pamphilius tricolor	NSMT30896	ON016900	this work	ON017159	this work
Pamphilius tricolor	NSMT30897	ON016901	this work	ON017160	this work
Pamphilius tricolor	NSMT30898	ON016902	this work	ON017161	this work
Pamphilius tricolor	NSMT30902	ON016906	this work	ON017165	this work
Pamphilius ussuriensis	DEI-GISHym21853	ON016656	this work	---	---
Pamphilius ussuriensis	DEI-GISHym86348	ON016698	this work	ON016946	this work
Pamphilius vafer	BC ZSM HYM 10993	KC975774	Schmidt *et al.* 2017	---	---
Pamphilius vafer	BC ZSM HYM 15982	GBSYM1732-13	BOLD	---	---

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius vafer	tF8	KF936521	Malm & Nyman 2014	KF935833	Malm & Nyman 2014
Pamphilius vafer	ZMUO.019859	MZ630503	Roslin *et al.* 2022	---	---
Pamphilius vafer	ZMUO.029466	MZ659232	Roslin *et al.* 2022	---	---
Pamphilius varius	BC ZSM HYM 04210	HQ955764	iBOL	---	---
Pamphilius varius	DEI-GISHym17744	KC977081	Schmidt *et al.* 2017	---	---
Pamphilius varius	DEI-GISHym19821	KF642891	Schmidt *et al.* 2017	---	---
Pamphilius varius	DEI-GISHym86311	ON016695	this work	---	---
Pamphilius varius	FSYM-000125	MZ627387	Roslin *et al.* 2022	---	---
Pamphilius varius	GL.3112	MZ625201	Roslin *et al.* 2022	---	---
Pamphilius varius	GL.3115	MZ626741	Roslin *et al.* 2022	---	---
Pamphilius varius	NSMT30569	ON016749	this work	ON016995	this work
Pamphilius varius	NSMT30724	ON016806	this work	ON017051	this work
Pamphilius varius	NSMT30760	ON016837	this work	ON017087	this work
Pamphilius varius	NSMT30761	ON016838	this work	ON017088	this work
Pamphilius varius	NSMT30762	ON016839	this work	ON017089	this work
Pamphilius varius	NSMT30892	ON016896	this work	ON017155	this work
Pamphilius venustus	NSMT30555	ON016738	this work	ON016981	this work
Pamphilius venustus	NSMT30562	ON016742	this work	ON016988	this work
Pamphilius venustus	NSMT30728	ON016810	this work	ON017055	this work
Pamphilius venustus	NSMT30739	ON016820	this work	ON017066	this work
Pamphilius volatilis	NSMT30536	LC456272	Shinohara *et al.* 2019	ON016965	this work
Pamphilius volatilis	NSMT30561	LC456273	Shinohara *et al.* 2019	ON016987	this work
Pamphilius volatilis	NSMT30662	ON016783	this work	ON017016	this work
Pamphilius volatilis	NSMT30694	LC456274	Shinohara *et al.* 2019	ON017043	this work
Pamphilius volatilis	NSMT30723	LC456275	Shinohara *et al.* 2019	ON017050	this work
Pamphilius volatilis	NSMT30744	LC456276	Shinohara *et al.* 2019	ON017071	this work
Pamphilius volatilis	NSMT30745	LC456277	Shinohara *et al.* 2019	ON017072	this work

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TABLE 1. (Continued)

Species	Specimen ID	COI	Reference	NaK	Reference
		GenBank accession / *BOLD process ID*		**GenBank accession**	
Pamphilius volatilis	NSMT30746	ON016825	this work	ON017073	this work
Pamphilius volatilis	NSMT30802	ON016872	this work	ON017127	this work
Pamphilius volatilis	NSMT30805	ON016874	this work	ON017130	this work
Pamphilius volatilis	NSMT30806	LC158370	Shinohara *et al.* 2016b	ON017131	this work
Pamphilius zhelochovtsevi nipponicus	NSMT30688	ON016797	this work	ON017038	this work
Pamphilius zhelochovtsevi nipponicus	NSMT30689	LC126716	Shinohara *et al.* 2016a	---	---

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Results and discussion

Keys to the tribes, genera and species of the Russian Far East and Korea

Here we treat two tribes, four genera and 58 species recorded so far from the Russian Far East and Korea. As noted in the introduction, we follow Belokobylskij & Lelej (2017, fig. 1) for the definition of the Russian Far East, but the Kurile Islands are not included. In its broad sense, the Russian Far East may also include the Sakha Republic (Yakutia), the Republic of Buryatia and the Zabaykalsky Krai (Wikipedia contributors 2021a).

In a recent catalog of the Russian Hymenoptera (Sundukov 2017), we have noticed some erroneous distribution records from the Russian Far East (broad sense) and Korea. There is no evidence for the occurrence of the following five species in these areas.

Neurotoma saltuum (Linnaeus,1758)
Sundukov (2017) included the Korean Peninsula in the distribution of this species. As fully discussed by Shinohara (1980), this record is wrong. Shinohara *et al.* (2018a) and Lee *et al.* (2019) did not include this species in the Korean fauna. There is no evidence for the occurrence of this species in Korea.

Onycholyda lucida (Rohwer, 1910)
Sundukov (2017) included the Sakha Republic in the distribution of this species. The record of Kajmuk (1972) from Yakutia (also Verzhutskij 1981) was based on a misidentification of *Pamphilius balteatus* (Fallén, 1808) (Shinohara 1986c). Zhelochovtsev & Zinovjev (1995) and Shinohara & Lelej (2007) did not include *O. lucida* in the Russian fauna. *Onycholyda lucida* is endemic to Japan (Shinohara 2019, 2020).

Onycholyda minomalis (Takeuchi, 1930)
Sundukov (2017) noted "Russia: without regions (Taeger, Blank, 2011)" in the distribution of this species. This record is wrong, as explained under *O. yezoensis* below. There is no evidence for the occurrence of *O. minomalis* in Russia.

Pamphilius takeuchii Beneš, 1972
Sundukov & Lelej (2009, 2012) and Sundukov (2017) included Primorskij Kraj in the distribution of *P. takeuchii*. However, as discussed in detail by Shinohara (2013), the only known Russian specimen that was once determined as *P. takeuchii* (Beneš 1974) is the holotype of *P. croceus* Shinohara, 1986. *Pamphilius takeuchii* is endemic to Japan and not known from Russia (Shinohara & Zhou 2006).

Pamphilius venustus (Smith, 1874)
For the distribution of this species, Sundukov (2017) noted "Russia: FE (Shinohara, 1988b)", apparently referring to Shinohara's (1988b, P. 180) statement, "*P. venustus* (Smith) and *P. sapporensis* (Matsumura) from the Far East". Sundukov (2017) seems to have misunderstood "the Far East", which is much wider than "the Russian Far East". *Pamphilius venustus* is known only from Japan (Shinohara 2019, 2020).

Key to the East Asian tribes and genera of Pamphiliinae

1 (a) Head with lateral sutures divergent forward and not connected with antennal furrows (Fig. 1: 1a)
(b) Forewing with vein Sc1 absent (Fig. 1: 1b)
(c) Lancet with lamnium enlarged (Fig. 1: 1c). Neurotomini: 1 genus, 6 species. ... ***Neurotoma***, p.40 (key), p. 58
– (aa) Head with lateral sutures subparallel and connected with antennal furrows (Fig. 1: 1aa)
(bb) Forewing with vein Sc1 present (Fig. 1: 1bb)
(cc) Lancet with lamnium small (Fig. 1: 1cc). Pamphiliini: 3 genera ... **2**

2(1)
(a) Crossvein 1r-rs narrowed towards junction with R1 (Fig. 2: 2a).
(b) Legs black (Fig. 2: 2b, c).
(c) Hind tibia with two preapical spurs (Fig. 2: 2b, c). 1 species, ***C. leucocephala***. ... ***Chrysolyda***, p. 62
– (aa) Crossvein 1r-rs not narrowed towards junction with R1 (Fig. 2: 2aa).
(bb) Legs largely pale yellow (Fig. 2: 2bb, cc).
(cc) Hind tibia with three preapical spurs (Fig. 2: 2bb, cc). ... **3**

3(2)
(a) Anterior part of malar space with small, slightly depressed area bearing a row of recurved setae in female, and with large pit containing a long stout seta and several recurved setae in male (Fig. 2: 3a).
(b) Male: supraocular area with narrow, dull, densely pubescent patch (Fig. 2: 3b).
(c) Tarsal claws with acute basal lobe in addition to apical and one subapical teeth of subequal size (Fig. 2: 3c). 8 species. ... ***Onycholyda***, p. 41 (key), p. 62
– (aa) Anterior part of malar space without depressed area or pit bearing recurved setae in both sexes (Fig. 2: 3aa).
(bb) Male: supraocular area without narrow, dull, densely pubescent patch (Fig. 2: 3bb).
(cc) Tarsal claws with apical and one subapical teeth of subequal size and often with rounded basal lobe, but Asian species never with acute basal lobe (Fig. 2: 3cc). 43 species. ... ***Pamphilius***, p. 42 (key), p. 68

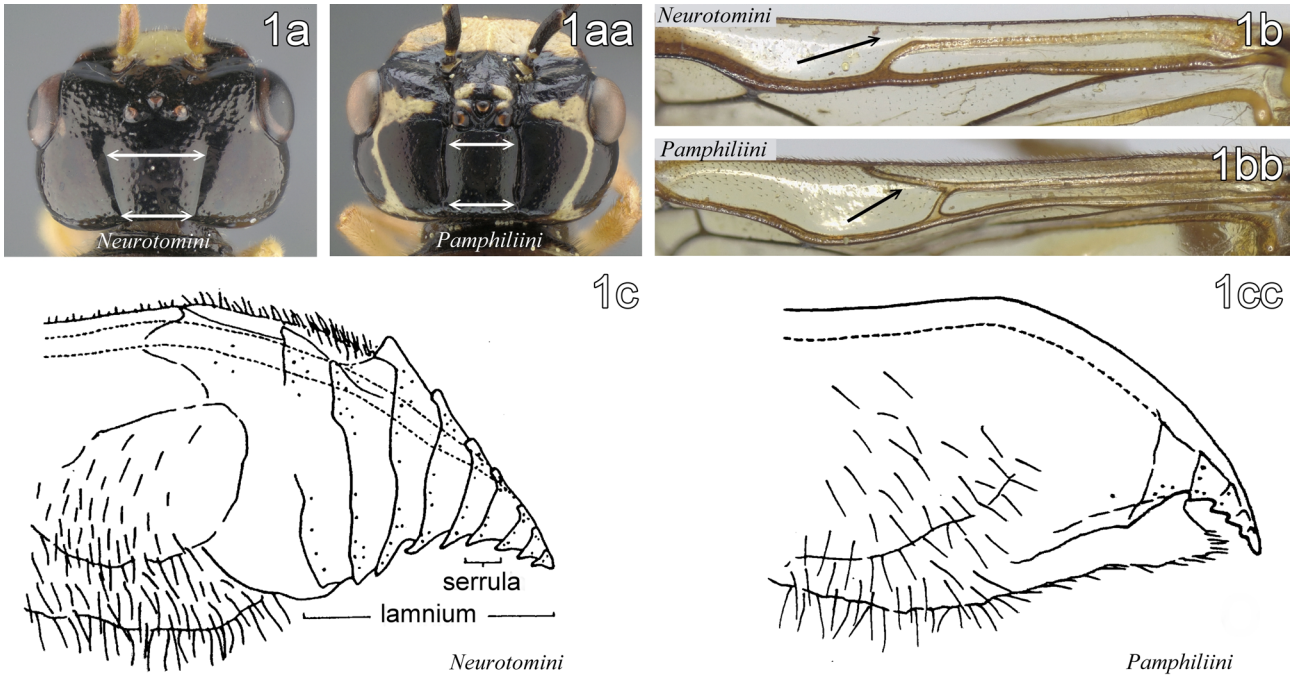


FIGURE 1. Key to tribes and genera 1



FIGURE 2. Key to tribes and genera 2

Key to the *Neurotoma* species of the Russian Far East and Korea

1 (a) Head covered with long hairs (Fig. 3: 1a,b; 2b; 2bb).
(b) Occipital carina blunt or inconspicuous (Fig. 3: 1a, b). ... **2**
– (aa) Head glabrous or nearly so except for sparsely pilose gena and clypeus (Fig. 3: 1aa, bb; 4a, b–5bb, cc).
(bb) Occipital carina sharply defined (Fig. 3: 1aa, bb). ... **3**

2(1)
(a) Abdomen without distinct bluish luster.
(b) Female: clypeus with large creamy white mark medially (Fig. 3: 2b).
(c) Male: head entirely black. ... ***N. atrata***, p. 58
– (aa) Abdomen with distinct bluish luster dorsally.
(bb) Female: clypeus with two large lateral creamy white marks (Fig. 3: 2bb).
(cc) Male: Head with large subtriangular mark on clypeus. ... ***N. coreana***, p. 59

3(1)
(a) Antenna with scape and pedicel usually entirely yellow in both sexes (see Fig. 3: 1aa, bb), scape at most with obscure blackish mark. ... ***N. iridescens***, p. 59
– (aa) Scape and pedicel mostly black in female (e.g., Fig. 3: 4aa, bb), at least scape black dorsally in male. ... **4**

4(3)
(a) Head (Fig. 3: 4a, b), thorax and abdomen richly marked with whitish yellow.
(b) Facial and frontoclypeal crests prominent, sharply carinate (Fig. 3: 4a, b). ... ***N. satoi***, p. 60
– (aa) Head (Fig. 3: 4aa, bb), thorax and abdomen with few pale-yellow marks.
(bb) Facial and frontoclypeal crests low, not sharply carinate (Fig. 3: 4aa, bb). ... **5**

5(4)
(a) Small species, female 7–9.5 mm, male 7.5–8.5 mm.
(b) Head entirely black in both sexes, except for sometimes obscure small spot at upper facial orbit (Fig. 3: 5b, c).
(c) Vertex and temple smooth, with shallow distant punctures (Fig. 3: 4aa, bb; 5b, c).
(d) Mesoscutellum and metascutellum entirely black in female.
(e) Cell C of forewing pilose all over. ... ***N. sibirica***, p. 60
– (aa) Large species, female 13 mm, male 12 mm.
(bb) Head with large pale yellow mark between antennae in female (Fig. 3: 5bb, cc), anterior surface mostly pale yellow in male.
(cc) Vertex and temple covered with dense, well-separated punctures (Fig. 3: 5bb, cc).
(dd) Mesoscutellum and metascutellum pale yellow in female.
(ee) Cell C of forewing glabrous, with some pilosity in apical posterior part. ... ***N. silla***, p. 61



FIGURE 3. Key to *Neurotoma* species

Key to the *Onycholyda* species of the Russian Far East and Korea

1 (a) Females. ... **2**
– (aa) Males. … **9**

2(1)
(a) All terga black, at most with narrow posterior margin pale, without orange areas. ... **3**
– (aa) Some terga largely orange… **6**

3(2)
(a) Fore, mid and usually hind femora largely marked with black.
(b) Head with clypeus widely yellow medially and frons almost entirely black (Fig. 4: 3b). … ***O. viriditibialis***, p. 66
— (aa) Femora entirely pale yellow or greenish yellow.
(bb) Head color pattern different (Fig. 4: 4a, b–5aa). … **4**

4(3)
(a) Anterior margin of clypeus pale yellow (Fig. 4: 4a, b).
(b) Median ocellus surrounded by large pale yellow mark (Fig. 4: 4a, b).
(c) Clypeus rather smooth, with inconspicuous surface microsculpture and sparse punctures. ... ***O. zinovjevi***, p. 67
– (aa) Anterior margin of clypeus with obscure pale yellow spot at middle or entirely black (Fig. 4: 4aa, bb, 5aa).
(bb)Pale yellow mark around median ocellus small, broken into four spots, posterior pair sometimes missing (Fig. 4: 4aa, bb, 5aa).
(cc) Clypeus dull, with distinct surface microsculpture. … **5**

5(4)
(a) Head color pattern Fig. 4: 4aa, bb (5a); pale yellow spot present on or behind facial crest.
(b) Trochanters pale.
(c) Sterna (3–) 4–6 with broad posterior margin pale yellow or greenish yellow. … ***O. armata***, p. 63
– (aa) Head color pattern Fig. 4: 5aa; pale yellow spot on facial crest usually missing.
(bb) Trochanters mostly black.
(cc) Sterna (3–) 4–6 entirely black, or with very narrow posterior margin pale yellow. … ***O. yezoensis***, p. 67

6(2)
(a) Mesoscutellum and metascutellum mostly or entirely black [in Chinese specimens mesoscutellum usually yellow marked]
(b) Wings distinctly yellowish, with veins mostly orange to pale brown.
(c) Head color pattern as in Fig. 4: 6c; left mandible bidentate (median tooth absent). … ***O. odaesana***, p. 65
– (aa) Mesoscutellum and metascutellum yellow.
(bb) Wings not distinctly yellowish, with veins mostly blackish brown.
(cc) Head color pattern different (Fig. 4: 7a, b; 8a; 8aa); left mandible tridentate (small median tooth present, Fig. 4: 7a, b). … **7**

7(6)
(a) Clypeus entirely black (Fig. 4: 7a, b), or with lateral parts and narrow anterior margin brownish. … ***O. nigroclypeata***, p. 64
– (aa) Clypeus anteriorly largely pale yellow (Fig. 4: 8a; 8aa). … **8**

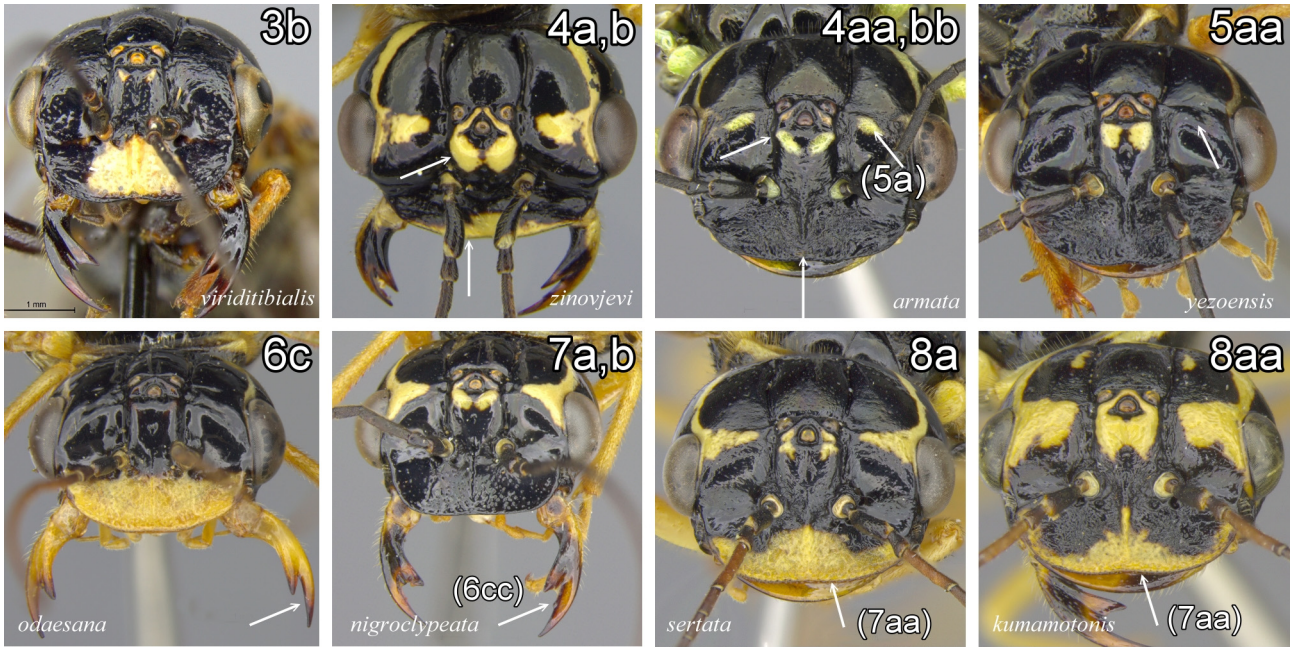


FIGURE 4. Key to *Onycholyda* species 1

8(7)
(a) Head color pattern as in Fig. 4: 8a.
(b) Abdominal tergum 3 usually entirely orange. … ***O. sertata***, p. 65
– (aa) Head color pattern as in Fig. 4: 8aa.
(bb) Abdominal tergum 3 usually with large black marking. … ***O. kumamotonis***, p. 64
9(1)
(a) Fore, mid and sometimes hind femora marked with black (Fig. 5: 9a). … ***O. viriditibialis***, p. 66
– (aa) All femora entirely pale yellow (trochantelli may be black marked). … **10**
10(9)
(a) Clypeus nearly flattened or with cup-shaped area medially, frontoclypeal crest absent ventrally (Fig. 5: 10a). … **11**
– (aa) Clypeus with entire frontoclypeal crest, medially divided into lateral halves (Fig. 5: 10aa). … **14**
11(10)
(a) Mesothorax below wings, including pectus, mostly or entirely pale yellow (Fig. 5: 11a).
(b) Left mandible bidentate (median tooth absent) (Fig. 5: 10a (11b)).
(c) Wings often distinctly yellowish or brownish, veins mostly orange to pale brown. … ***O. odaesana***, p. 65
– (aa) Mesothorax below wings darker, at least pectus mostly or entirely black.
(bb) Left mandible tridentate (median tooth present, Fig. 5: 11bb).
(cc) Wings not distinctly yellowish or brownish, veins mostly dark brown to blackish brown. … **12**
12(11)
(a) Abdomen with orange areas. … ***O. kumamotonis***, p. 64
– (aa) Abdomen without orange areas. ... **13**
13(12)
(a) Antennal scape completely yellow (Fig. 5: 13a).
(b) Mesoscutellum and metascutellum usually entirely black. … ***O. zinovjevi***, p. 67
– (aa) Antennal scape yellow, outer surface with black patch (Fig. 5: 13aa).
(bb) Mesoscutellum and metascutellum pale yellow. … ***O. armata***, p. 63
14(10)
(a) Abdomen with terga 4 and 5 orange (Fig. 14a). … ***O. nigroclypeata***, p. 64
– (aa) Abdominal terga entirely black or with only tergum 4 orange. … **15**
15(14)
(a) Stigma with basal 1/4 pale yellow (Fig. 5: 15a).
(b) Body length 7–9 mm.
(c) Abdominal terga always entirely black. … ***O. yezoensis***, p. 67
– (aa) Stigma with basal 1/3 pale yellow (Fig. 5: 15aa).
(bb) Body length 9–12 mm.
(cc) Abdomen often with tergum 4 orange. … ***O. sertata***, p. 65

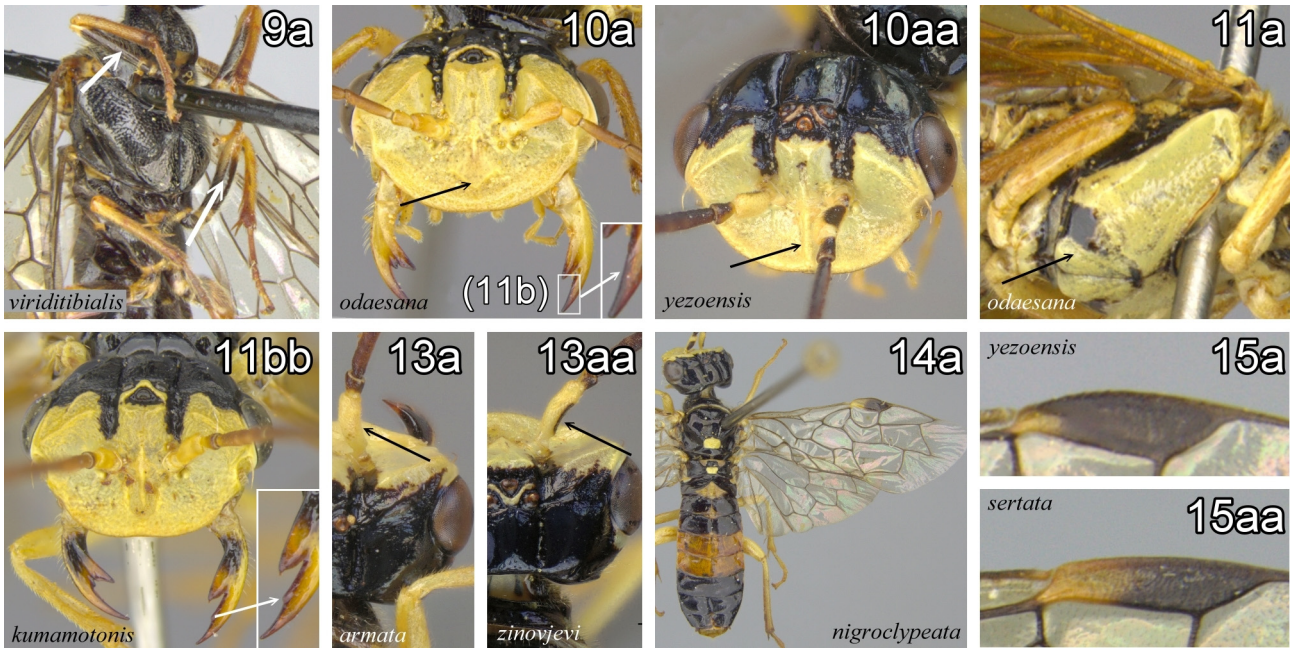


FIGURE 5. Key to *Onycholyda* species 2

Key to the *Pamphilius* species of the Russian Far East and Korea

1 (a) Females (unknown for *kimi* and *ochrostigma*). ... **2**
– (aa) Males (unknown for *albopictus*, *convexus*, *pallidus*, *pictifrons*, and *viridulus*). ... **43**

2(1)
(a) Flagellomere 1 1.0–1.5 × length of flagellomere 2 (Fig. 6: 2a). ... **3**
– (aa) Flagellomere 1 1.6–3.2 × length of flagellomere 2 (Fig. 6: 2aa). ... **20**

3(2)
(a) Upper part of head largely orange (see Fig. 6: 4a-c; 4aa-cc).
(b) Stigma yellow to orange in basal half and blackish in apical half (Fig. 6: 3b). ... **4**
– (aa) Upper part of head mostly black, black with pale yellow marks or largely pale yellow (Fig. 6: 3aa).
(bb) Stigma not as above, usually unicolorous pale or dark, or margins darker than middle (Fig. 6: 3bb). ... **5**

4(3)
(a) Upper head nearly impunctate and glabrous (Fig. 6: 4a-c).
(b) Upper frons below ocelli rather strongly convex, usually notched medially.
(c) Facial crest rather strongly convex. ... ***P. hilaris***, p. 74
– (aa) Upper head with large, distinct punctures and pilose (Fig. 6: 4aa-cc).
(bb) Upper frons below ocelli weakly convex, not notched medially.
(cc) Facial crest weakly convex. ... ***P. sapporensis***, p. 94

5(3)
(a) Antennal scape mostly or entirely yellow. ... **6**
– (aa) Antennal scape mostly or entirely black, at least largely black above. ... **8**

6(5)
(a) Cell C of forewing glabrous (Fig. 6: 6a).
(b) Ovipositor sheath very small, in lateral view about half as high as metatarsomere 1 long (Fig. 6: 6b).
(c) Paraantennal field glabrous.
(d) Terga 2–6 more or less marked with black basally. ... ***P. brevicornis brevicornis***, p. 71
– (aa) Cell C of forewing ventrally pilose (Fig. 6: 6aa).
(bb) Ovipositor sheath large, in lateral view almost as high as metatarsomere 1 long (Fig. 6: 6bb).
(cc) Paraantennal field pilose.
(dd) Terga 2–6 without black marking. ... **7**

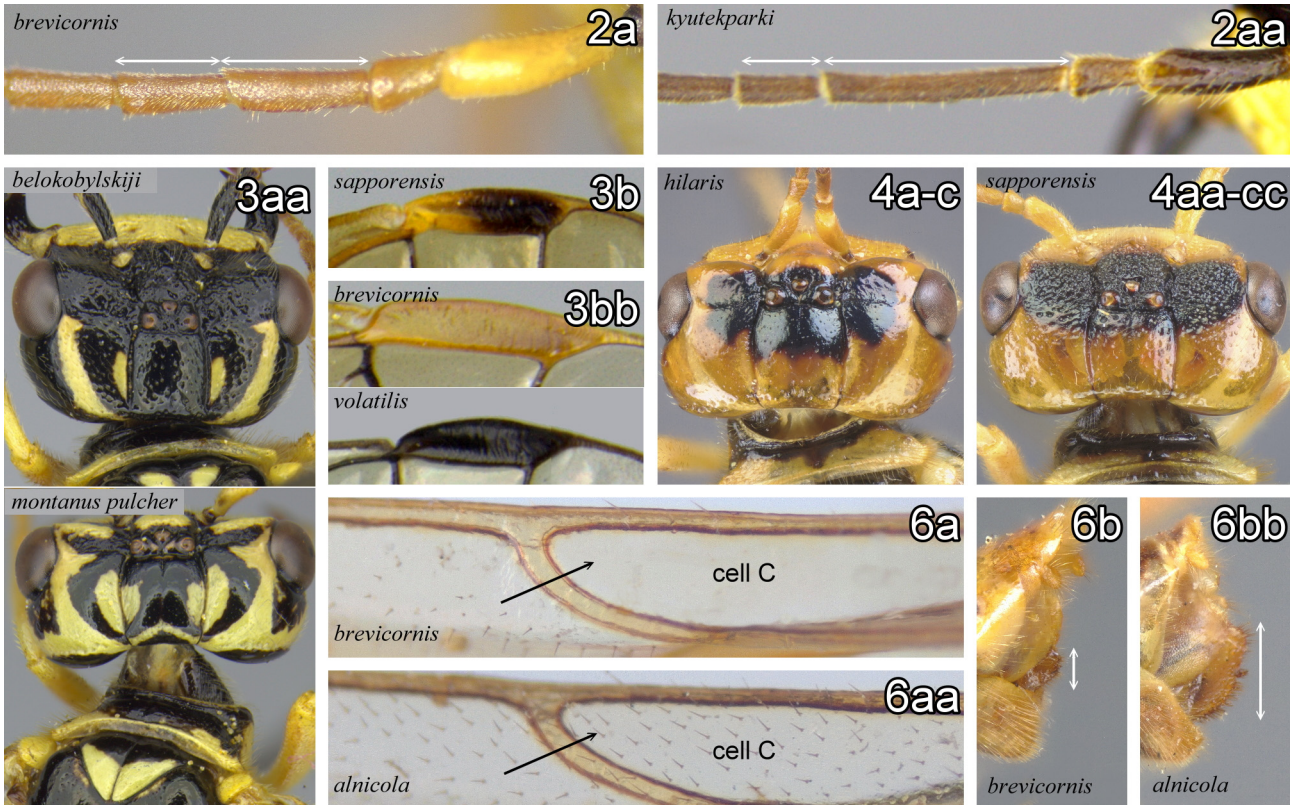


FIGURE 6. Key to *Pamphilius* species 1

7(6)

(a) Upper part of frons strongly swollen in front of ocelli (Fig. 7: 7a).
(b) Inner part of facial crest rounded, not distinctly carinate.
(c) Most of clypeus pale yellow (Fig. 7: 7c).
(d) Ovipositor sheath appendage large (Fig. 7: 7d). ... ***P. alnicola***, p. 78

– (aa) Upper part of frons moderately or weakly swollen in front of ocelli (Fig. 7: 7aa).
(bb) Inner part of facial crest more or less carinate.
(cc) Pale yellow area on clypeus limited to anterior half (Fig. 7: 7cc).
(dd) Ovipositor sheath appendage small (Fig. 7: 7dd). ... ***P. montanus pulcher***, p. 81

8(5)

(a) Abdomen mostly black above, without orange marking. ... **9**

– (aa) Abdomen with orange marking above. ... **16**

9(8)

(a) Fore femur yellow, basally marked with black. ... **10**

– (aa) Fore femur completely yellow without black marks. ... **12**

10(9)

(a) Upper frons without pale yellow mark (Fig. 7:10a).
(b) Pronotum entirely black.
(c) Abdomen entirely black. ... ***P. daisenus***, p. 79

– (aa) Upper frons with pale yellow mark (Fig. 7:10aa).
(bb) Posterior dorsolateral corners and ventral margin of pronotum pale yellow.
(cc) Abdomen with pale yellow marks ventrally. ... **11**

11(10)

(a) Stigma pale brown medially (Fig. 7: 11a).
(b) Mid and hind femora basally marked with black.
(c) Postocellar and postocular areas almost impunctate and glabrous (see Fig. 7: 10aa (11c)). ... ***P. ussuriensis***, p. 82

– (aa) Stigma mostly blackish brown, not pale brown medially (Fig. 7: 11aa).
(bb) Mid and hind femora yellow without black marks.
(cc) Postocellar and postocular areas with sparse small punctures and pilosity (Fig. 7: 11cc). ... ***P. graciloides***, p. 80

12(9)

(a) Upper head distinctly punctate and pilose (Fig. 7: 12a). ... **13**

– (aa) Upper head almost impunctate and glabrous (Fig. 7: 12aa). ... **14**

13(12)

(a) Malar space largely black (Fig. 7: 13a, b; 13c(13a)).
(b) Broad area along upper inner orbit somewhat rugose.
(c) Head color pattern as in Fig. 7: 13c.
(d) Body length 9.0–10.5 mm.
(e) Cell C of forewing ventrally pilose all over. ... ***P. planifrons***, p. 93

– (aa) Malar space almost completely pale (Fig. 7: 13aa, bb; 13cc (13aa)).
(bb) Broad area along upper inner orbit somewhat smooth.
(cc) Head color pattern as in Fig. 7: 13cc
(dd) Body length 8.0–9.5 mm.
(ee) Cell C of forewing entirely or mostly glabrous. ... ***P. rhoae***, p. 94

14(12)

(a) Cell C of forewing glabrous (compare Fig. 6: 6a).
(b) Antennal flagellum brown.
(c) Mesoscutal lateral lobe with large pale yellow mark.
(d) Abdomen ventrally black, with only posterior margins of sterna 3–6 and posterior part of each laterotergite pale yellow. ... ***P. convexus***, p. 79

– (aa) Cell C of forewing ventrally pilose (compare Fig. 6: 6aa).
(bb) Antennal flagellum blackish brown to black.
(cc) Mesoscutal lateral lobe without pale areas.
(dd) Ventral side of abdomen mostly pale yellowish or greenish. ... **15**

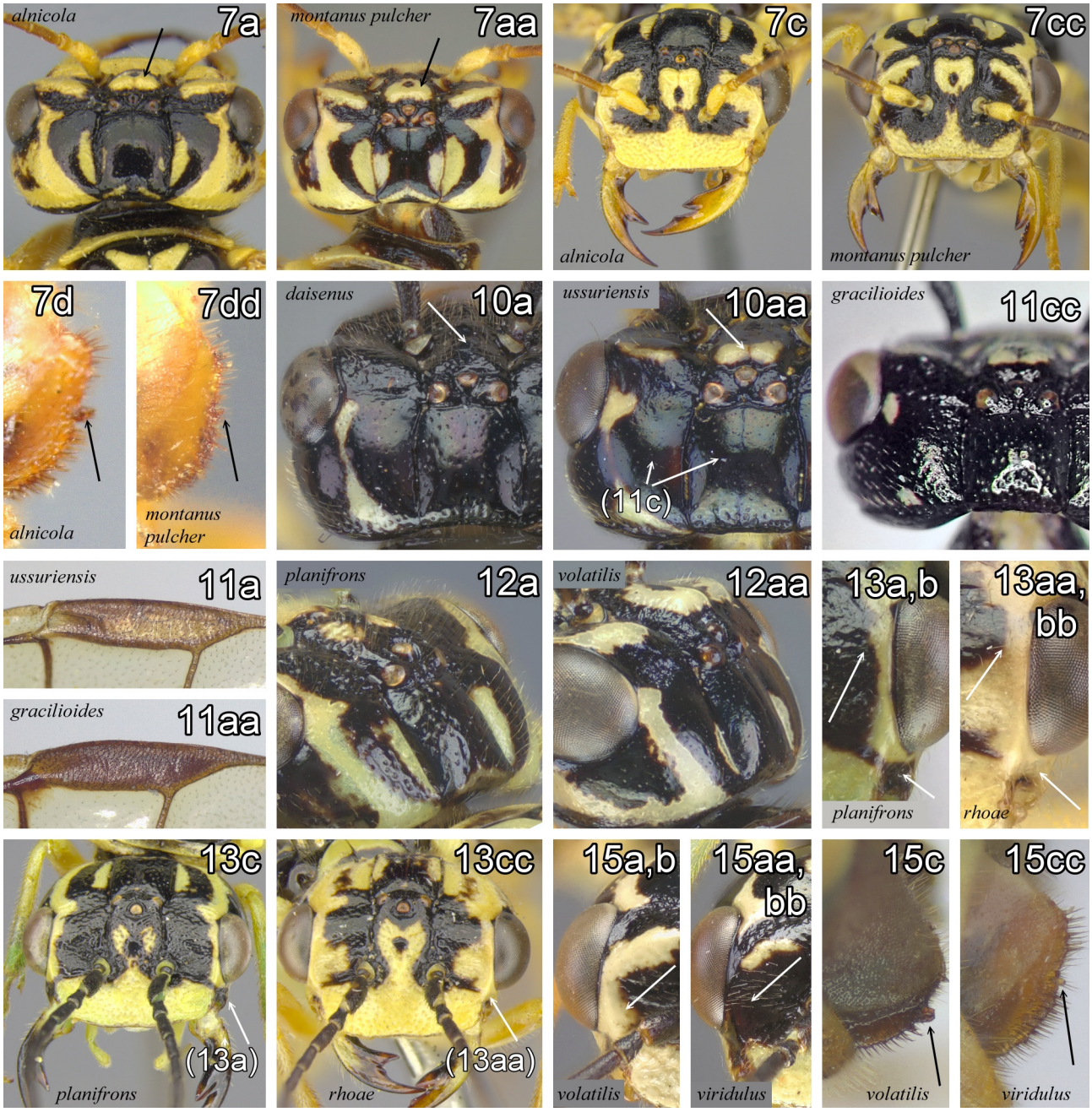


FIGURE 7. Key to *Pamphilius* species 2

15(14)

(a) Lower inner orbit with pale mark, usually connecting pale area on facial crest with pale area on malar space (Fig. 7: 15a, b).
(b) Upper part of frons and facial crest sparsely pilose (Fig. 7: 15a, b).
(c) Ovipositor sheath appendage large (Fig. 7: 15c).
(d) Body length 9.0–11.0 mm. ... ***P. volatilis***, p. 83

– (aa) Lower inner orbit without pale mark (Fig. 7: 15aa, bb).
(bb) Upper part of frons and facial crest rather densely pilose (Fig. 7: 15aa, bb).
(cc) Ovipositor sheath appendage small (Fig. 7: 15cc).
(dd) Body length 11.0 mm. ... ***P. viridulus***, p. 83

16(8)

(a) Postocellar and postocular areas almost impunctate and glabrous (compare Fig. 7: 12aa). ... **17**

– (aa) Postocellar and postocular areas distinctly punctate and pilose (compare Fig. 7: 12a). ... **18**

17(16)

(a) Head, thorax and abdomen largely pale. ... ***P. pallidus***, p. 82

– (aa) Head, thorax and abdomen largely black. ... ***P. benesi***, p. 79

18(16)

(a) Clypeus only anteriorly yellow (Fig. 8: 18a-c).
(b) Gena black with broad yellow stripe (Fig. 8: 18a-c).
(c) Paraantennal field smooth, ventral part almost impunctate (Fig. 8: 18a-c).
(d) Mesepisternum without yellow spot. (*P. stramineipes* partim) ... **38**

– (aa) Clypeus almost completely yellow (Fig. 8: 18aa-cc).
(bb) Gena completely black or with few yellow marks (Fig. 8: 18aa-cc).
(cc) Paraantennal field densely punctate (Fig. 8: 18aa-cc) or rugose (see Fig. 8: 19a (18cc)).
(dd) Mesepisternum usually with yellow spot laterally in posterior part. ... **19**

19(18)

(a) Paraantennal field rugose (Fig. 8: 19a).
(b) Gena rugose, rather mat (Fig. 8: 19b).
(c) Sterna 3–6 usually entirely or mostly pale yellow, sterna 2 and 7 basally black (Fig. 8: 19c). ... ***P. lobatus***, p. 92

– (aa) Paraantennal field densely punctate (Fig. 8: 18aa-cc (19aa)).
(bb) Gena sparsely punctate, shiny (Fig. 8: 19bb).
(cc) Sterna 3–6 basally black and apically yellow (amount of yellow increasing towards apex of abdomen), sternum 2 almost completely black, sternum 7 black with broad apical yellow margin (Fig. 8: 19cc). ... ***P. belokobylskiji***, p. 87

20(2)

(a) Clypeus entirely black, or with its narrow anterior margin pale yellow. ... **21**

– (aa) Clypeus with its anterior half or large median part or more extensive areas pale. ... **26**

21(20)

(a) Head, except for clypeus and gena, smooth, nearly impunctate and glabrous (Fig. 8: 21a).
(b) Abdomen almost entirely black, without orange marks. ... **22**

– (aa) Head distinctly punctate and pilose all over (Fig. 8: 21aa).
(bb) Abdomen marked with orange. ... **23**

22(21)

(a) Stigma yellow or pale green basally and black apically (Fig. 8: 22a).
(b) Cell C of forewing ventrally pilose anteriorly and glabrous posteriorly (Fig. 8: 22b). ... ***P. coreanus***, p. 76

– (aa) Stigma semi-translucent brown, darkened marginally (Fig. 8: 22aa).
(bb) Cell C of forewing ventrally densely pilose all over (Fig. 8: 22bb). ... ***P. sulphureipes sulphureipes***, p. 76

23(21)

(a) Head with only small postocular spot yellowish (Fig. 8: 23a). ... ***P. hortorum***, p. 90

– (aa) Head with entire postocular stripe and often narrow anterior margin of clypeus yellowish (see Fig. 8: 24a). ... **24**

24(23)

(a) Postocular stripe terminating anteriorly at dorsal corner of inner orbit, not extending along inner orbit (Fig. 8: 24a).
(b) Stigma usually pale brown medially and blackish brown marginally (compare Fig. 8: 22aa).
(c) Abdominal tergum 3 usually entirely black, at most with small orange spot at middle.
(d) Laterotergites largely black, each at least basally black. ... ***P. balteatus***, p. 87

– (aa) Postocular stripe extending anteriorly along inner orbit (Fig. 8: 24aa).
(bb) Stigma entirely blackish brown (Fig. 8: 25bb) or with pale brown area in basal median part (Fig. 8: 25b).
(cc) Abdominal tergum 3 largely orange.
(dd) Laterotergites mostly pale yellow or orange. ... **25**

25(24)

(a) Anterior margin of clypeus pale yellow (Fig. 8: 24aa(25a)).
(b) Stigma with pale brown area in basal median part (Fig. 8: 25b).
(c) Wings nearly hyaline or indistinctly stained with brown, veins at wing base mainly dark brown (see Fig. 8: 25b).
(d) Lateral black spots on abdominal terga 3–5 large (Fig. 8: 25d). ... ***P. itoi***, p. 91

– (aa) Anterior margin of clypeus usually entirely black (Fig. 8: 21aa(25aa)).
(bb) Stigma only with indistinct pale brown area in basal median part (Fig. 8: 25bb).
(cc) Wings distinctly stained with brown, veins at wing base mainly pale brown (see Fig. 8: 25bb).
(dd) Lateral black spots on abdominal terga 3–5 minute or missing (Fig. 8: 25dd). ... ***P. aucupariae***, p. 86

26(20)

(a) Upper head, frons and paraantennal field without distinct punctures, nearly or entirely glabrous (Fig. 8: 26a).
(b) Frons below ocelli and facial crest strongly convex (see Fig. 8: 26a). ... **27**

– (aa) Upper head, frons and paraantennal field distinctly punctate and pilose (Fig. 8: 26aa; in *P. varius* often upper head glabrous).
(bb) Frons below ocelli and facial crest less convex (see Fig. 8: 26aa; in *P. latifrons*, facial crest strongly convex). ... **33**

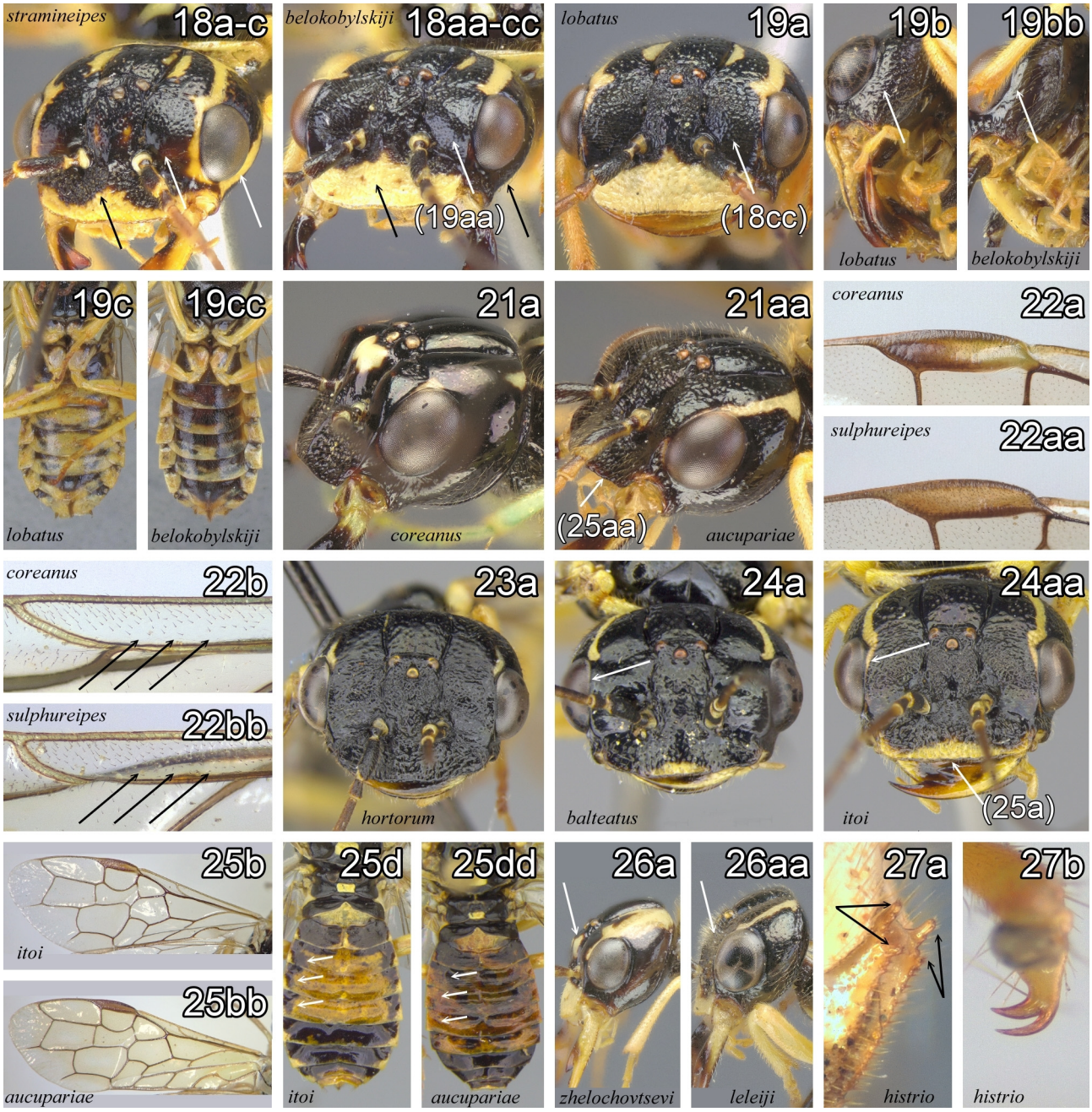


FIGURE 8. Key to *Pamphilius* species 3

27(26)

(a) Ovipositor sheath with two projections but without appendage (Fig. 8: 27a).

(b) Tarsal claws with inner tooth thicker and longer than outer tooth (Fig. 8: 27b). ... ***P. histrio***, p. 72

– (aa) Ovipositor sheath without projections and with appendage (compare Fig. 9: 31b; 31bb).

(bb) Tarsal claws with inner tooth various in thickness, as long as or shorter than outer tooth (compare Fig. 9: 40bb). ... **28**

28(27)

(a) Larger species, body length 13.0–15.5 mm.

(b) Head mostly brownish or orange with yellow marks, or yellow and orange with a large black marking on ocellar and postocellar areas (see Fig. 9: 28a, 28aa).

(c) Antennal scape entirely pale. ... **28***

– (aa) Smaller species, body length 8.0–11.0 mm.

(bb) Head black with pale yellow marks.

(cc) Antennal scape usually largely black. ... **29**

28*(28)

(a) Head and mesoscutum almost entirely orange with yellow marks (Fig. 9: 28a).
(b) Wings with distinct cloud in apical third.
(c) Abdomen with segments 1–5 orange, remaining segments mainly black with few yellow marks. ... ***P. croceus***, p. 69

– (aa) Head and mesoscutum with large black marks (Fig. 9: 28aa).
(bb) Wings without distinct cloud in apical third.
(cc) Abdomen ventrally yellow, dorsally orange, tergum 1 and narrow bases of terga 2–5 black. ... ***P. maximus***, p. 72

29(27)

(a) Abdomen dorsally with tergum 2 mostly black and tergum 6 often more or less pale; ventrally mainly yellow, at least sterna 3–6 posteriorly broadly yellow and sterna 2 and 7 posteriorly with narrow yellow margin. ... **30**

– (aa) Abdomen black with segments 2–5 almost completely orange to yellow, remaining abdomen mainly black, sterna 6 and 7 with posterior margin yellow (Fig. 9: 29a). (*P. kyutekparki* partim) ... **38**

30(29)

(a) Gena, frons and paraantennal fields entirely or mostly black (Fig. 9: 30a).
(b) Postocellar area with pale marking along lateral sutures very small or missing.
(c) Stigma pale with apical half or more extensive areas brownish (Fig. 9: 30c).
(d) Abdomen mostly black above, without orange marking. ... ***P. zhelochovtsevi zhelochovtsevi***, p. 77

– (aa) Gena, frons and paraantennal fields mostly pale (Fig. 9: 30aa, see Fig. 9: 32a, 32 aa).
(bb) Postocellar area with pale marking along lateral sutures very large.
(cc) Stigma pale, anterior margin usually darkened (Fig. 9: 30cc).
(dd) Abdomen with orange marking above (see Figs 31a, 31aa). ... **31**

31(30)

(a) Abdominal tergum 3 black (Fig. 9: 31a).
(b) Ovipositor sheath appendage large, knob-like (Fig. 9: 31b). ... ***P. tricolor***, p. 73

– (aa) Abdominal tergum 3 partly orange (Fig. 9: 31aa).
(bb) Ovipositor sheath appendage small and slender (Fig. 9: 31bb). ... **32**

32(31)

(a) Head mostly pale yellow, without black spot at posterolateral corner of eye (Fig. 9: 32a).
(b) Ovipositor sheath appendage directed downwards (see Fig. 9: 31bb). ... ***P. virescens***, p. 73

– (aa) Head with more black areas, with large black spot at posterolateral corner of eye (Fig. 9: 32aa).
(bb) Ovipositor sheath appendage directed backwards. ... ***P. pictifrons***, p. 72

33(26)

(a) Ovipositor sheath appendage large, short, thick, and rounded, without long setae (Fig. 9: 33a). ... **34**

– (aa) Ovipositor sheath appendage slender, various in size, with or without setae (see Fig. 9: 39a–aa). ... **36**

34(33)

(a) Cervical sclerite entirely black, rarely with obscure pale marking (Fig. 9: 34a). ... ***P. pallipes***, p. 93

– (aa) Cervical sclerite with distinct pale yellow marking (Fig. 9: 34aa). ... **35**

35(34)

(a) Ovipositor sheath appendage with dorsal and ventral margins subequal in length in lateral view (Fig. 9: 33a (35a)).
(b) Frons usually marked with pale yellow above level of toruli.
(c) Pale yellow marking on gena very often extending to occipital carina and connected with posterior end of postocular stripe. ... ***P. alnivorus***, p. 85

– (aa) Ovipositor sheath appendage with dorsal margin distinctly shorter than ventral margin in lateral view (Fig. 9: 33a (35aa)).
(bb) Frons with or without pale yellow marking above level of toruli.
(cc) Pale yellow marking on gena very often not extending to occipital carina and not connected with posterior end of postocular stripe. ... ***P. masao***, p. 93

36(33)

(a) Head black, with only postocular stripe and anterior margin of clypeus pale yellow. ... ***P. leleji***, p.91

– (aa) Head more richly pale-marked, at least clypeus mostly pale yellow and part of inner orbits, frons, or gena usually marked with pale yellow. ... **37**

37(36)

(a) Cervical sclerite and mesepisternum mostly or entirely black (compare Fig. 9: 34a). ... **38**

– (aa) Cervical sclerite and mesepisternum with large pale yellow areas (compare Fig. 9: 34aa). ... **39**



FIGURE 9. Key to *Pamphilius* species 4

38(18, 29, 37)

(a) Flagellomere 1 1.5–1.9 × length of flagellomere 2 (see Fig. 6: 2a).

(b) Stigma concolorous pale brown to brown. ... ***P. stramineipes***, p. 95

– (aa) Flagellomere 1 2.5–2.8 × length of flagellomere 2 (see Fig. 6: 2aa).

(bb) Stigma bicolored, pale yellow with various extent of blackish brown area posteroapically. ... ***P. kyutekparki***, p. 70

39(37)

(a) Ovipositor sheath appendage large, elongate and almost glabrous (Fig. 9: 39a). ... ***P. heecheonparki***, p. 89

– (aa) Ovipositor sheath appendage thin and setose (Fig. 9: 39aa). ... **40**

40(39)

(a) Facial crest strongly and roundly swollen, with distinct elongate depression laying just behind it extending from inner orbit to lateral ocellus (Fig. 9: 40a).

(b) Tarsal claws with inner tooth about as long as or slightly longer than outer tooth (Fig. 9: 40b). ... ***P. latifrons***, p. 75

– (aa) Facial crest not as above, and no distinct depression behind it (compare Fig. 9: 30a; 30aa).

(bb) Tarsal claws with inner tooth shorter than outer tooth (Fig. 9: 40bb). ... **41**

41(40)

(a) Inner orbit black, often with narrow fading pale yellowish stripe (Fig. 10: 41a, b).
(b) Frons usually without pale yellow spot (Fig. 10: 41a, b).
(c) Gena black with pale yellow spot at lower outer orbit.
(d) Mesoscutal lateral lobe usually without pale yellow marking.
(e) Cell C of forewing densely pilose all over. ... ***P. archiducalis***, p. 86

– (aa) Inner orbit usually broadly pale yellow (see Fig. 10: 42a-d; 42aa-dd).
(bb) Frons with or without pale yellow spot.
(cc) Gena usually mostly pale yellow.
(dd) Mesoscutal lateral lobe usually with pale yellow marking.
(ee) Cell C of forewing glabrous or sparsely pilose (in European specimens of *P. albopictus* often mostly pilose). ... **42**

42(41)

(a) Upper part of frons and facial crest with very dense, deep punctures, almost rugoso-reticulate (Fig. 10: 42a-d).
(b) Vertex distinctly punctate and pilose.
(c) Frons usually without distinct pale yellow marking.
(d) Pale yellow area on paraantennal field usually restricted to inner orbit. ... ***P. albopictus***, p. 84

– (aa) Upper part of frons and facial crest with sparse, shallow punctures (Fig. 10: 42aa-dd).
(bb) Vertex usually without distinct punctures, often glabrous.
(cc) Frons with large distinct pale yellow marking.
(dd) Paraantennal field often mostly pale yellow. ... ***P. varius***, p. 95

43(1)

(a) Flagellomere 1 0.9–1.6 × length of flagellomere 2. ... **44**

– (aa) Flagellomere 1 1.6–3.2 × length of flagellomere 2. ... **60**

44(43)

(a) Stigma yellow to orange in basal half and blackish in apical half (Fig. 10: 44a). ... **45**

– (aa) Stigma not as above, blackish to pale, frequently margins darker than middle (Fig. 10: 44aa). ... **46**

45(44)

(a) Upper head sparsely punctate or nearly impunctate and glabrous (Fig. 10: 45a-d).
(b) Upper frons below ocelli strongly convex, distinctly notched medially.
(c) Facial crest strongly convex.
(d) Pale colour of temple not extending to vertex. ... ***P. hilaris***, p. 74

– (aa) Upper head with large, distinct punctures and pilose (Fig. 10: 45aa-dd).
(bb) Upper frons below ocelli weakly convex, not notched medially.
(cc) Facial crest weakly convex.
(dd) Pale colour of temple extending to vertex and reaching lateral postocellar furrow. ... ***P. sapporensis***, p. 94

46(44)

(a) Antennal scape entirely yellow, at most with faint dark spot as in Fig. 10: 47a, b. ... **47**

– (aa) Antennal scape partly or entirely black. ... **53**

47(46)

(a) Upper frons strongly roundly swollen, medially notched (Fig. 10: 47a, b).
(b) Facial crest strongly swollen, rounded.
(c) Cell C of forewing entirely glabrous. ... ***P. brevicornis brevicornis***, p. 71

– (aa) Upper frons moderately or strongly swollen, not rounded (Fig. 10: 47aa, bb).
(bb) Facial crest strongly swollen and sharply carinate.
(cc) Cell C of forewing entirely pilose (only partly pilose or nearly glabrous in *P. benesi*). ... **48**

48(47)

(a) Genitalia with harpe broad, apical part with large half-membranous area (Fig. 10: 48a).
(b) Abdomen dorsally black, *and* mesepisternum ventrally (pectus) largely black (Fig. 10: 48b). ... ***P. ussuriensis***, p. 82

– (aa) Genitalia with harpe elongate, narrowed towards apex, apically without large half-membranous area.
(bb) Abdomen dorsally orange marked, *or / and* mesepisternum also ventrally largely pale (Fig. 10: 50a; 50aa). ... **49**

49(48)

(a) Abdomen without orange mark above (compare Fig. 11: 59aa). ... **50**

– (aa) Abdomen with orange marks at least on segments 4 and 5. ... **51**

50(49)

(a) Valviceps apically not curved outwards in dorsal view. ... **50***
(aa) Valviceps apically curved outwards in dorsal view. ... **52**

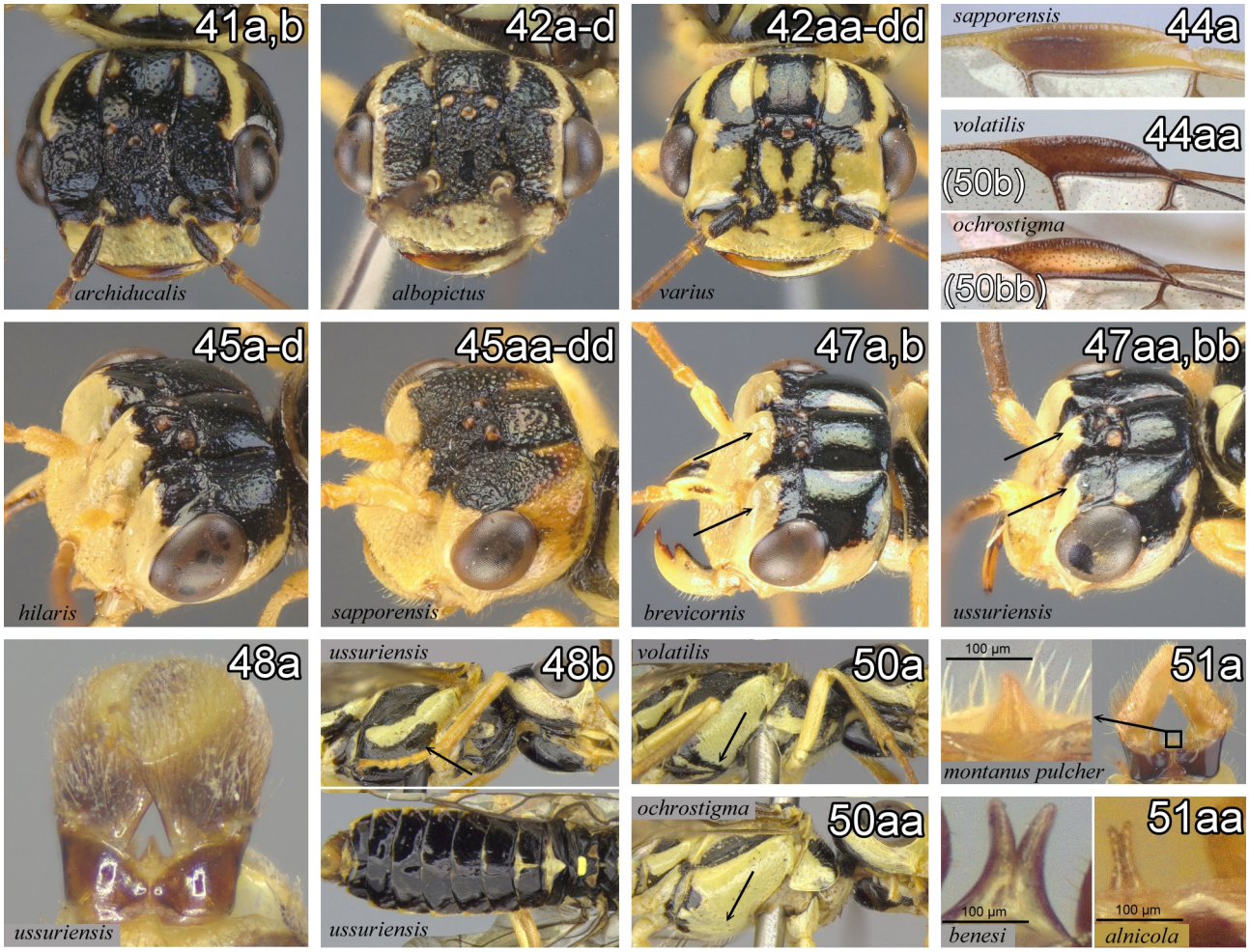


FIGURE 10. Key to *Pamphilius* species 5

50*(50)

(a) Ventral part of mesepisternum with large black area along outer margins of pectus and along median line (Fig. 10: 50a).

(b) Stigma uniformly blackish brown (Fig. 10: 44aa (50b)).

(c) Postocular stripe sometimes reduced or nearly missing, when present, its anterior apex not widened, usually more or less narrowed, and its posterior apex usually not connected with pale yellow area on gena.

(d) Postocular area beside lateral postocellar furrow black. ... ***P. volatilis***, p. 83

– (aa) Ventral part of mesepisternum including pectus mostly pale yellow, with narrow area along posterior margin black (Fig. 10: 50aa).

(bb) Stigma very pale brown, almost colorless, with broad margins blackish (Fig. 10: 44aa (50bb)).

(cc) Postocular stripe well developed, with its anterior apex more or less widened, not narrowed, and its posterior apex connected ventrally with pale yellow area on gena.

(dd) Postocular area often with small pale spot beside lateral postocellar furrow. ... ***P. ochrostigma***, p. 82

51(49)

(a) Valviceps apically not curved outwards in dorsal view (Fig. 10: 51a).

(b) Wings uniformly slightly stained with brown. ... ***P. montanus pulcher***, p. 81

– (aa) Valviceps apically curved outwards in dorsal view (Fig. 10: 51aa).

(bb) Wings usually clear hyaline, hindwing sometimes slightly brownish. ... **52**

52(50, 51)

(a) Body length 9.0–12.0 mm.

(b) Forewing with cell C ventrally pilose all over (see Fig. 6: 6aa).

(c) Abdominal terga 3 to 6 mostly and terga 7 and 8 medially orange, in dark specimens only terga 4 and 5 largely orange. ... ***P. alnicola***, p. 78

– (aa) Body length 8.0–10.0 mm.

(bb) Forewing with cell C glabrous with only sparse pilosity at apex and along anterior margin.

(cc) Abdominal terga 3 to 5 with small median orange marks or black. ... ***P. benesi***, p. 79

53(46)

(a) Postocellar and postocular areas impunctate and glabrous or sparsely punctate and pilose (Fig. 11: 53a, b).

(b) Facial crest strongly convex, rounded or sharply carinate. ... **54**

– (aa) Postocellar and postocular areas distinctly punctate and densely pilose (Fig. 11: 53aa, bb).

(bb) Facial crest moderately convex, rounded or very bluntly carinate. ... **56**

54(53)

(a) Body length 11.5–14.0 mm.

(b) Mainly pale species, dorsally with broad black marks (head Fig. 11: 53a, b-right), abdomen dorsally largely orange.

(c) Flagellomere 1 longer than 1.5 × length of flagellomere 2. ... ***P. maximus***, p. 72

– (aa) Body length less than 10.0 mm.

(bb) Mainly black species with yellow marks.

(cc) Flagellomere 1 shorter than 1.2 × length of flagellomere 2. ... **55**

55(54)

(a) Face pale yellow, only antennal furrows black (Fig. 11: 55a; see Fig. 11: 53a, b-left).

(b) Fore and mid femora entirely pale yellow, fore femur rarely with obscure black mark on posterior surface. ... ***P. graciloides***, p.80

– (aa) Face above toruli black, lower face yellow, clypeus with anterior margin black (Fig. 11: 55aa; see Fig. 11: 53a, b-middle).

(bb) Fore and mid femora basally black. ... ***P. daisenus***, p. 79

56(53)

(a) Mesepisternum anteriorly largely black, pectus completely black (Fig. 11: 56a).

(b) Flagellomere 1 1.4–1.6 × length of flagellomere 2. ... ***P. stramineipes***, p. 95

– (aa) Mesepisternum entirely or predominantly pale yellow, pectus at least partly pale yellow (Fig. 11: 56aa).

(bb) Flagellomere 1 1.0–1.4 × length of flagellomere 2. ... **57**

57(56)

(a) Genitalia with valviceps strongly expanding at apex (Fig. 11: 57a).

(b) Head color pattern as in Fig. 11: 57b. ... ***P. lobatus***, p. 92

– (aa) Genitalia with valviceps weakly expanding at apex (Fig. 11: 57aa).

(bb) Head color pattern as in Figs 11: 57bb and 58bb. ... **58**

58(57)

(a) Abdomen black and orange above, at least terga 3–5 largely orange (Fig. 11: 58a). ... ***P. belokobylskiji***, p. 87

– (aa) Abdomen black above, without orange areas or with small orange areas on terga 4–5 (see Fig. 11: 59a; 59aa). ... **59**

59(58)

(a) Abdominal terga 4 and 5 usually with small orange marks medially (Fig. 11: 59a).

(b) Facial crest rounded (Fig. 11: 59b).

(c) Flagellomere 1 1.1–1.3 × length of flagellomere 2.

(d) Body length 7.5–8.5 mm. ... ***P. rhoae***, p. 94

– (aa) Abdominal terga 4 and 5 without orange marks (Fig. 11: 59aa).

(bb) Facial crest bluntly carinate (Fig. 11: 59bb).

(cc) Flagellomere 1 1.0 × length of flagellomere 2.

(dd) Body length 8.5–9.0 mm. ... ***P. planifrons***, p. 93

60(43)

(a) Tarsal claws with inner tooth about as long as or shorter than outer tooth (Fig. 11: 60a). ...**61**

– (aa) Tarsal claws with inner tooth longer than outer tooth (Fig. 11: 60aa). ... **82**

61(60)

(a) Valviceps anchor-like in dorsal view (Figs 11: 61a). ... **62**

– (aa) Valviceps not anchor-like in dorsal view (e.g., Fig. 11: 61aa), or genitalia covered and valviceps not visible. ... **64**

62(61,79)

(a) Flagellomere 1 2.5–3.0 × length of flagellomere 2. ... ***P. varius***, p. 95

– (aa) Flagellomere 1 1.6–2.2 × length of flagellomere 2. ... **63**

63(62)

(a) Abdomen dorsally largely black.

(b) Valviceps short, inner margin of gonostipes concave, and inner margin of harpe nearly straight (see Fig. 11: 61a (63b)).

(c) Body length 7.0–10.5 mm. ... ***P. heecheonparki***, p. 89

– (aa) Abdomen dorsally orange above.

(bb) Valviceps longer, inner margin of gonostipes weakly convex, and inner margin of harpe concave (see Fig. 11: 61a (63bb))

(cc) Body length 10.5–13.0 mm. ... ***P. kimi***, p. 91

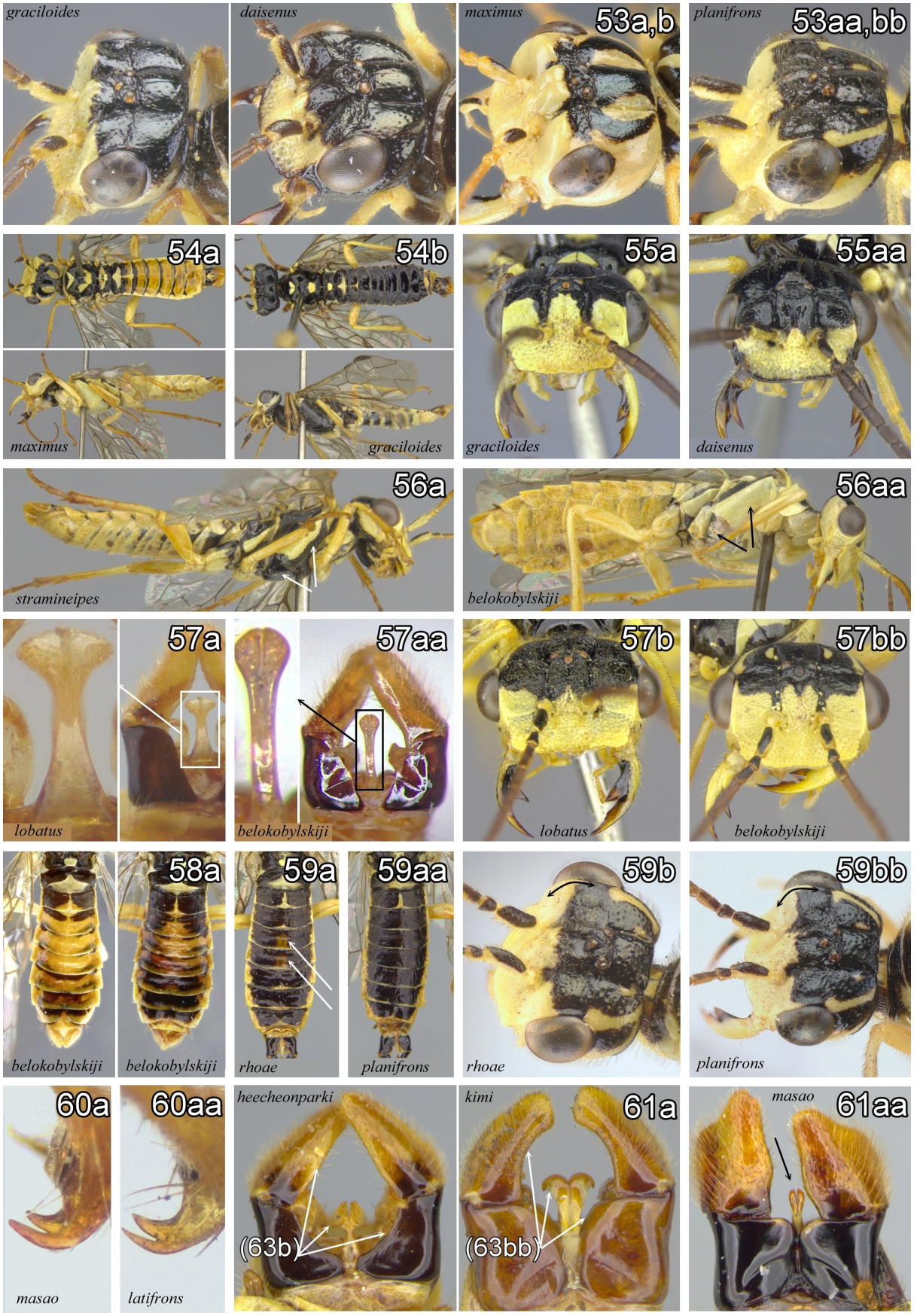


FIGURE 11. Key to *Pamphilius* species 6

64(61)

(a) Upper head and paraantennal field glabrous or sparsely pilose, with or without very sparse minute punctures, or with minute punctures and silky microsculpture (Fig. 12: 64a, b).

(b) Frons below ocelli and facial crest moderately to strongly convex (Fig. 12: 64a, b). ... **65**

– (aa) Upper head, frons and paraantennal field usually distinctly pilose, distinctly punctate (Fig. 12: 64aa, bb).

(bb) Frons below ocelli and facial crest weakly or moderately convex (Fig. 12: 64aa, bb). ... **72**

65(64)

(a) Abdomen black dorsally with only narrow lateral margins pale yellow (Fig. 12: 65a). ... **66**

– (aa) Abdomen dorsally with black, pale yellow and orange areas (Fig. 12: 65aa). ... **68**

66(65)

(a) Cell C of forewing entirely glabrous (compare Fig. 6: 6a).

(b) Head in frontal view with ventral part of paraantennal field strongly expanded laterally (Fig. 12: 66b).

(c) Pectus largely or entirely yellow (Fig. 12: 66c). ... ***P. zhelochovtsevi zhelochovtsevi***, p. 77

– (aa) Cell C of forewing ventrally pilose at least in anterior part (see Fig. 12: 67b; 67bb).

(bb) Head in frontal view with ventral part of paraantennal field not strongly expanded laterally (Fig. 12: 66bb).

(cc) Pectus entirely black (Fig. 12: 66cc). ... **67**

67(66)

(a) Stigma yellow basally and black apically (Fig. 12: 67a).

(b) Cell C of forewing ventrally pilose anteriorly and glabrous posteriorly (Fig. 12: 67b). ... ***P. coreanus***, p. 76

– (aa) Stigma semi-translucent brown, darkened marginally (Fig. 12: 67aa).

(bb) Cell C of forewing ventrally densely pilose all over (Fig. 12: 67bb). ... ***P. sulphureipes sulphureipes***, p. 76

68(65, 72)

(a) Upper frons moderately to strongly swollen, with distinct setiferous punctures (Fig. 12: 64a, b (68a)).

(b) Facial crest moderately convex, rounded or bluntly carinate, distinctly pilose dorsally.

(c) Cell C of forewing ventrally entirely pilose (compare Fig. 12: 67bb). ... ***P. kyutekparki***, p. 70

– (aa) Upper frons very strongly swollen, without distinct punctures (Fig. 12: 64a, b (68aa)).

(bb) Facial crest very strongly convex, usually carinate, glabrous.

(cc) Cell C of forewing entirely or partly glabrous (compare Fig. 6: 6a; Fig. 12: 67b). ... **69**

69(68)

(a) Upper head black without pale yellow marks (Fig. 12: 69a).

(b) Mesoscutal median lobe entirely black or with brownish marking.

(c) Wings strongly stained with dark brown (Fig. 12: 69c). ...***P. croceus***, p. 69

– (aa) Upper head black with extensive pale yellow areas (Fig. 12: 69aa; 71a; 71aa).

(bb) Mesoscutal median lobe with large pale yellow marking.

(cc) Wings not distinctly brownish (Fig. 12: 69cc). ... **70**

70(69)

(a) Abdominal terga 2 and 3 orange in posterior half (Fig. 12: 70d).

(b) Body length 11.5–14.0 mm.

(c) Antennal scape with broad black spot above (see Fig. 12: 69aa). ... ***P. maximus***, p. 72

– (aa) Abdominal terga 2 and 3 almost entirely black (Fig. 12: 65aa, 70dd).

(bb) Body length usually 7.0–11.0 (*P. histrio* up to13.0) mm.

(cc) Antennal scape entirely pale yellow or with dark spot above. ... **71**

71(70)

(a) Postocellar area with oblong yellow mark at lateral margin, anteriorly reaching transverse suture and extending inward along the suture, often fused at middle (Fig. 12: 71a). ... ***P. virescens***, p. 73

– (aa) Postocellar area completely black or with oblong yellow mark at lateral margin of postocellar area restricted to posterior part, not reaching transverse suture (Fig. 12: 71aa; see Fig. 13: 82a, c; 82aa, cc). ... **82**

72(64)

(a) Stigma pale yellow, with posteroapical part blackish (*P. kyutekparki* partim). ... **68**

– (aa) Stigma not as above, generally concolorous. ... **73**

73(72)

(a) Cell C of forewing pilose all over. ... **74**

– (aa) Cell C of forewing glabrous, if pilose, only partly. ... **78**

74(73)

(a) Head mostly black: postocular stripe reduced to small postocular spot, clypeus with only narrow anterior margin pale yellow, paraantennal field with only small spot along inner orbit pale yellow (Fig. 12: 74a). ... ***P. hortorum***, p. 90

– (aa) Head not so dark: postocular stripe entire, clypeus and paraantennal field largely pale yellow (Fig. 12: 74aa). ... **75**



FIGURE 12. Key to *Pamphilius* species 7

75(74)

(a) Head (Fig. 12: 75a) with inner dorsal part of paraantennal field and median part of frons mostly black, pale areas on paraantennal field and clypeus often separated by narrow black stripe, malar space and gena with large black areas.

(b) Mesoscutal median lobe entirely black. ... ***P. itoi***, p. 91

– (aa) Head (compare Fig. 12: 75aa) with anterior surface up to level of facial crests (including inner dorsal part of paraantennal field and median part of frons), malar space and lower gena usually mostly pale yellow.

(bb) Mesoscutal median lobe with large pale yellow spot. ... **76**

76(75)

(a) Thorax laterally and ventrally entirely black or nearly so (Fig. 13: 76a).

(b) Valviceps very long, distinctly bent downwards near base (Fig. 13: 76b). ... ***P. aucupariae***, p. 86

– (aa) Thorax laterally and ventrally with large pale yellow areas (Fig. 13: 76aa).

(bb) Valviceps not exceptionally long, not distinctly bent downwards near base (Fig. 13: 76bb). ... **77**

77(76)

(a) Gena and temple almost completely yellow (Fig. 13: 77a).

(b) Abdomen usually with only terga 4 and 5 largely dorsally orange. ... ***P. balteatus***, p. 87

– (aa) Gena and temple posteriorly largely black (Fig. 13: 77aa).

(bb) Abdomen with terga 3–5(–8) largely dorsally orange. ... ***P. archiducalis***, p. 86

78(73)

(a) Stigma blackish brown. ... ***P. leleji***, p. 91

– (aa) Stigma pale yellow to pale brown, margins often somewhat darker. ... **79**

79(78)

(a) Malar space completely yellow (compare Fig. 13: 77a; 77aa).

(b) Valviceps anchor-like in dorsal view. ... **62**

– (aa) Malar space often partly or entirely black (see Fig. 13: 81b; 81bb).

(bb) Valviceps not anchor-like in dorsal view. ... **80**

80(79)

(a) Valviceps short, directed backwards or downwards (Fig. 13: 80a). ... ***P. alnivorus***, p. 85

– (aa) Valviceps long, directed upwards (see Fig. 13: 81a; 81aa). ... **81**

81(80)

(a) Valviceps in dorsal view broadly inflated at apex, in lateral view narrow with lateral wall not flattened (Fig. 13: 81a).

(b) Species with less black markings (Fig. 13: 81b): malar space usually with dorsal half or more pale yellow, mesoscutal median lobe and mesoscutellum usually with large pale yellow spot, cervical sclerite usually entirely pale yellow ventrally and pectus frequently marked with pale yellow. ... ***P. masao***, p. 93

– (aa) Valviceps in dorsal view rather narrowly inflated at apex, in lateral view broad with posteroventral part of lateral wall broad and flattened (Fig. 13: 81aa).

(bb) Species with more black markings (Fig. 13: 81bb): malar space usually entirely black or with narrow pale yellow line along eye margin, mesoscutal median lobe usually entirely black or with small pale yellow spot, mesoscutellum usually with small pale yellow spot, cervical sclerite usually entirely black or with pale yellow spot, pectus almost always without pale yellow area. ... ***P. pallipes***, p. 93

82 (60, 71)

(a) Upper head distinctly pilose and punctate (Fig. 13: 82a, c).

(b) Pectus black (compare Fig. 13: 76aa).

(c) Antennal scape yellow with dark spot above (Fig. 13: 82a, c).

(d) Valviceps short, strongly bent ventrolaterally at apex in dorsal view (Fig. 13: 82d). … ***P. latifrons***, p. 75

– (aa) Upper head glabrous, with sparse minute punctures, with (Fig. 13: 82aa, cc) or without silky microsculpture.

(bb) Pectus mainly pale yellow (compare Fig. 10: 50aa).

(cc) Antennal scape entirely pale yellow (Fig. 13: 82aa, cc).

(dd) Valviceps long and slender in dorsal view (Fig. 13: 82dd). ... **83**

83(82)

(a) Tarsal claws with inner tooth longer than outer tooth (Fig. 13: 83a).

(b) Antenna relatively long (Fig. 13: 83b, c).

(c) Upper head smooth between punctures (Fig. 13: 83b, c). … ***P. histrio***, p. 72

– (aa) Tarsal claws with inner tooth shorter than outer tooth (Fig. 13: 83aa).

(bb) Antenna relatively short (Fig. 13: 83bb, cc).

(cc) Upper head with silky microsculpture between punctures (Fig. 13: 82aa, cc; 83bb, cc). ... ***P. tricolor***, p. 73

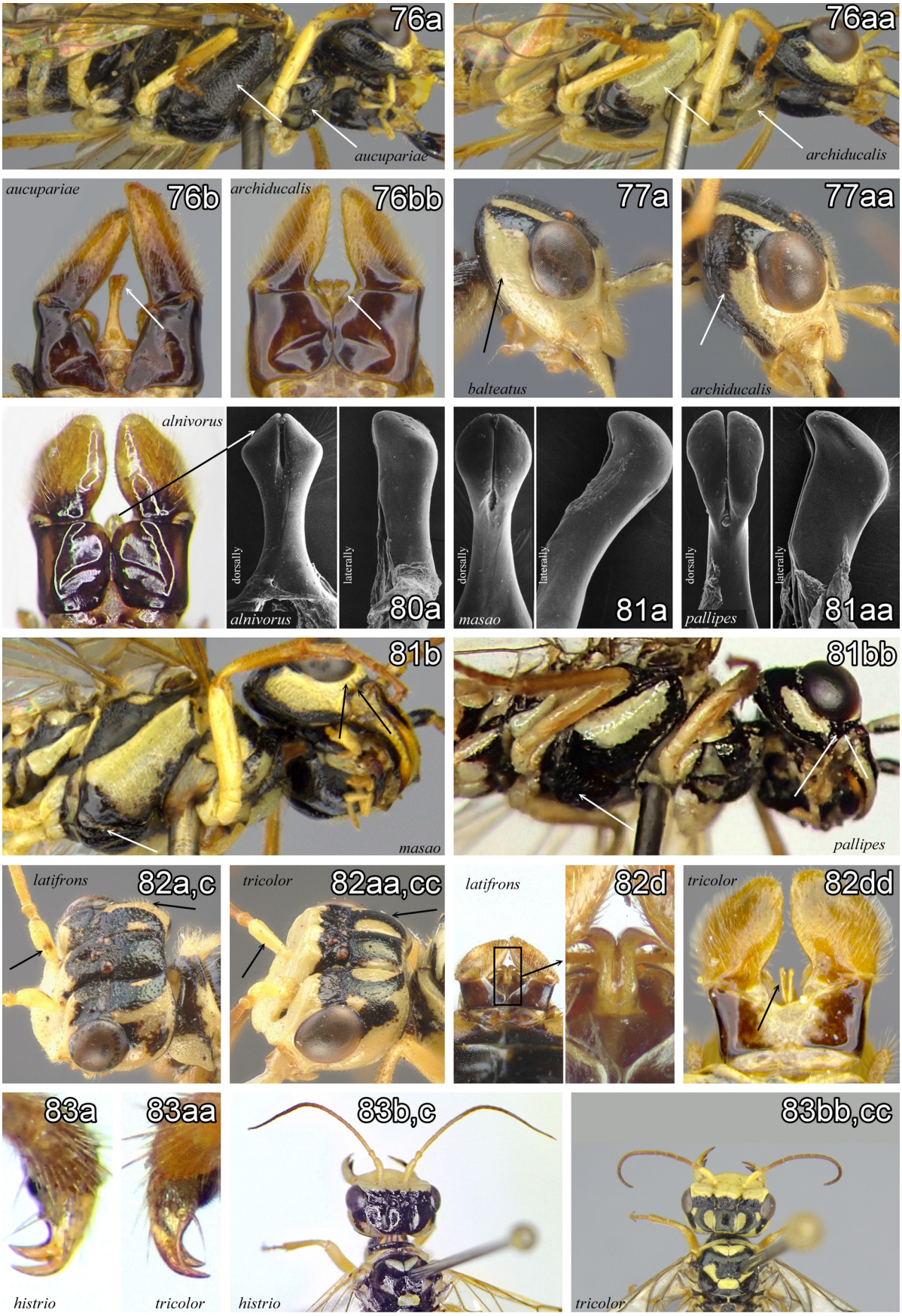


FIGURE 13. Key to *Pamphilius* species 8

Systematic account

Subfamily Pamphiliinae Cameron, 1890

The subfamily Pamphiliinae is represented by two tribes and six genera in the world, of which two tribes and four genera have been found in eastern Asia. Shinohara (2002b) discussed the taxonomy of this subfamily in detail, based mainly on adult morphology. His classification is generally followed here.

The monophyly of each of the Pamphiliinae, *Neurotoma*, Pamphiliini and *Onycholyda* was well supported by morphology (Shinohara 2002b, Fig. 14). In both COI and NaK analyses (present work, Figs 15, 16), these taxa were also retrieved as monophyletic.

Tribe Neurotomini Benson, 1945

The representatives of this tribe are characterized as follows (Shinohara 2002b): head with lateral sutures divergent forward and not connected with antennal furrows (Fig. 1: 1a); tarsal claws elongate (e.g., Figs 21h, 23h, 24h, 26h); forewing with vein Scl absent (Fig. 1: 1b); abdominal sternum 7 in female not strongly convex, with paired rounded ridges apically, enclosing rather small triangular marginal depression (fig. 4E–G in Shinohara 2002b); lancet with lamnium enlarged (Fig. 1: 1c).

Two postulated autapomorphies, the absence of vein Scl in the forewing and the enlarged lamnium of the lancet of the ovipositor, may support the monophyly of this tribe. In our molecular analyses using COI and NaK sequences (Figs 15, 16), *Neurotoma* was also retrieved as monophyletic with 100% UFBoot support.

The Neurotomini contains a single genus, *Neurotoma,* in the extant fauna.

Genus *Neurotoma* Konow, 1897

Neurotoma Konow, 1897a: 18.

See Taeger *et al.* (2010) for more synonymy.

The characters of this genus are as noted above for the tribe and this is regarded as a monophyletic group well supported by morphological and molecular evidence.

In this genus Shinohara (2002b) proposed six species groups, of which three (*N. fausta*, *N. mandibularis* and *N. nemoralis* groups) were included in our COI analysis and only one (*N. nemoralis* group) was included in the NaK analysis. In the COI tree (Fig. 137), the *N. mandibularis* group (*N. mandibularis* and *N. coreana*) was recovered as monophyletic with 100% UFBoot support, but this clade as well as *N. fausta* (representative of the *N. fausta* group) were within the paraphyletic assemblage of the *N. nemoralis* group (five species). Possibly, the *N. fausta* and *N. mandibularis* groups may form a group of specialized species within the more generalized, speciose, and heterogeneous *N. nemoralis* group.

This genus contains 23 species worldwide, including six species recorded from the Russian Far East and South Korea (Shinohara *et al.* 2018a). Of the six species, two belong to the *N. mandibularis* group and four to the *N. nemoralis* group.

The larvae of *Neurotoma* species feed on the host leaves, usually gregariously in webs. The known host plants are arborescent Rosaceae (*N. fausta* and *N. nemoralis* groups) and Fagaceae (*Quercus* spp.) (*N. satoi* and *N. mandibularis* groups).

Neurotoma atrata Takeuchi, 1930

(Figs 19, 20) (https://doi.org/10.6084/m9.figshare.11405028)

Neurotoma atrata Takeuchi, 1930: 8; Shinohara, 1980: 91; Shinohara & Okutani, 1983: 276; Shinohara, 1992b: 826; Shinohara & Byun, 1993: 79; Kim *et al.*, 1994: 216; Zhelochovtsev & Zinovjev, 1995: 397; Shinohara & Lee, 1997: 214; Shinohara,

2002b: 418; Shinohara, 2004: 262; Shinohara & Xiao, 2006: 285; Shinohara & Lelej, 2007: 927; Sundukov, 2009: 213: Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 82; Sundukov, 2017: 103; Shinohara *et al.*, 2018a: 595; Lee *et al.*, 2019: 7; Shinohara, 2019: 6; Shinohara, 2020: 8, 232; Shinohara & Tripotin, 2021b: 196.

Material examined. Eighteen specimens, including the type series. Eight specimens are from the Russian Far East and South Korea (Shinohara 1980, 1992b, Shinohara & Lee 1997, and Shinohara & Tripotin 2021b).

Distribution. Russian Far East (Primorskij Kraj), South Korea, Japan (Honshu), China (Zhejiang) (Shinohara & Xiao 2006).

Host plant. Fagaceae: *Quercus acutissima* Carruth. (Shinohara 1980).

Remarks. This is a rare species with no molecular data. With *N. coreana* Shinohara, 1980, and *N. sinica* Shinohara, 1980, it was included in the *N. atrata* subgroup of the *N. mandibularis* group by Shinohara (2002b).

Neurotoma coreana Shinohara, 1980

(Figs 21–22) (https://doi.org/10.6084/m9.figshare.11405034)

Neurotoma coreana Shinohara, 1980: 94; Shinohara & Byun, 1993: 79; Kim *et al.*, 1994: 216; Shinohara & Lee, 1997: 214; Shinohara, 2002b: 418; Shinohara, 2004: 262; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 82; Shinohara *et al.*, 2018a: 595; Lee *et al.*, 2019: 7; Shinohara & Tripotin, 2021a: 59.

Material examined. Fifty-two specimens, including the type series, all from South Korea (Shinohara 1980, Shinohara & Byun 1993, Shinohara & Lee 1997, Shinohara & Tripotin 2021a, present work). **New collection data: SOUTH KOREA: Gyeonggi-do**: 4♀7♂, Mt. Gwanggyosan, Suwon, 24. IV. 2000, H. S. Lee (NSMT). **Gangwon-do**: 9♀ (incl. NSMT 30596), Ucheon-myeon, Wuwon, Hoensong-gun, 17–19. V. 2000, A. Ishizuka (NSMT).

Distribution. South Korea.

Host plant. Unknown. Shinohara & Byun (1993) and Shinohara (2002b) suggested that *Quercus acutissima* is the host plant of this species (see also Lee *et al.* 2019), but this association has not been proved.

Remarks. This Korean endemic species is a member of the *N. atrata* subgroup of the *N. mandibularis* group (Shinohara 2002b). In the present molecular analysis using COI, where nine *Neurotoma* species were treated, *N. coreana* was sister to *N. mandibularis* with the minimum *p*-distance of 6.8%. The clade (*N. coreana* + *N. mandibularis*) was well supported by a 100% UFBoot value (Fig. 137).

Neurotoma iridescens (André, 1882)

(Figs 23–25) (https://doi.org/10.6084/m9.figshare.11405040)

Lyda iridescens André, 1882: 443.

Neurotoma iridescens: Konow, 1897a: 19; Gussakovskij, 1935: 160, 372; Takeuchi, 1938: 216; Kim, 1963: 278; Kim, 1970: 124, 716; Shinohara, 1980: 95; Shinohara & Okutani, 1983: 276; Achterberg & Aartsen, 1986: 23; Shinohara & Byun, 1993: 78; Kim *et al.*, 1994: 216; Zhelochovtsev & Zinovjev, 1995: 397; Taeger *et al.*, 1998: 100; Shinohara & Hara, 1999: 124; Shinohara, 2002b: 419; Shinohara, 2004: 262; Shinohara & Hara, 2005: 273; Shinohara & Lelej, 2007: 927; Sundukov, 2009: 213; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 82; Shinohara, 2013: 93; Sundukov, 2017: 103; Shinohara *et al.*, 2018a: 595; Lee *et al.*, 2019: 7; Shinohara, 2019: 6; Shinohara, 2020: 8, 231.

Material examined. About 130 specimens, including seven specimens from the Russian Far East and South Korea (Shinohara 1980, Shinohara & Byun 1993, present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (NSMT-I-Hym 28857), Valley of Tigrovaya River, 180 m alt., 12km N. of Partizansk, 4. VI. 1994, A. Shinohara (NSMT); 1♀ (Fig. 23, DEI-GISHym 12985), Komissarovo N, 130m, 45.000°N 131.788°E, 4. VI. 2016, K. Kramp, M. Prous & A. Taeger (SDEI); 1♀ (DEI-GISHym 32050), same data (SDEI).

Distribution. Russia (Primorskij Kraj, East Siberia), South Korea, northern and central Europe, Japan (Hokkaido, Kunashiri Is., Honshu, Shikoku, Kyushu) (Shinohara 1980).

Host plant. Rosaceae: *Cerasus* spp., *Sorbus* spp., *Crataegus chlorosarca* (Taeger *et al.* 1998; Shinohara & Hara 1999). Records of *Malus sieboldii* (Regel) Rehder and *Sorbaria sorbifolia* (L.) A. Braun (Lee *et al.* 2019) need confirmation.

Remarks. This is a widely distributed Palaearctic species showing some variation (Shinohara 1980). The two females from Russia and Japan in Figs 23 and 24 differ particularly in the surface microsculpture of the head. AS has examined about 130 specimens of this species mainly from Japan but also from Finland, Latvia, Turkey, Russian Far East and South Korea (collection data are partly given in Shinohara 1980 and National Museum of Nature and Science 2021) and found it difficult to recognize two or more distinguishable forms among the specimens. For molecular analysis, only one specimen each from Russia and Japan was available. They differed by 4.4% in COI and 0.8% in NaK sequences. These values were quite large, considering that the maximum intraspecific *p*-distance in *N. sibirica* from Russia and Japan was 2.0% (n=13) in COI and 0.1% (n=10) in NaK. Further genetic, morphological and bionomic approaches, particularly with more material for genetics, may reveal existence of multiple species within the current concept of *N. iridescens*, but we treat it as a single species for now.

The nearest relative of *N. iridescens* suggested by our molecular analysis was the European *N. nemoralis* (Linné, 1758), diverging by a minimum of 5.5% in COI and 1.8% in NaK, or the East Asian *N. sibirica*, diverging by a minimum of 6.0% in COI or 0.9% in NaK. In both COI and NaK trees (Figs 137, 152), however, *N. iridescens* and *N. sibirica* were sisters and *N. nemoralis* was sister to this clade, the topology supported by 97% or 100% UFBoot values. Shinohara (2002b) placed *N. iridescens*, *N. sibirica* and *N. nemoralis* in the *N. nemoralis* group, wherein *N. iridescens* was placed in the *N. saltuum* subgroup and *N. sibirica* and *N. nemoralis* in *N. nemoralis* subgroup. The minimum distance between specimens of *N. iridescens* and *N. saltuum* was 9.9% in COI. The intrageneric grouping in *Neurotoma* apparently needs a revision.

Neurotoma satoi Shinohara, 1980

(Figs 26, 27) (https://doi.org/10.6084/m9.figshare.11405046)

Neurotoma satoi Shinohara, 1980: 103; Shinohara & Byun, 1993: 79; Kim *et al.*, 1994: 216; Shinohara, 2002b: 419; Shinohara, 2004: 262; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 83; Shinohara *et al.*, 2018a: 595; Lee *et al.*, 2019: 7.

Material examined. Nine specimens (type series) from South Korea (Shinohara 1980).

Distribution. South Korea.

Host plant. Fagaceae: *Quercus acutissima* Carruth. (Shinohara 1980).

Remarks. This is a peculiar and very rare species known only from the type series collected in Suwon, South Korea in 1924–1932. Shinohara (2002b) placed it in the *N. satoi* group.

Neurotoma sibirica Gussakovskij, 1935

(Figs 28, 29) (https://doi.org/10.6084/m9.figshare.11405055)

Neurotoma sibirica Gussakovskij, 1935: 162, 372; Kim, 1963: 278; Verzhutskij, 1966: 27; Kim, 1970: 125, 716; Shinohara, 1980: 107; Shinohara & Okutani, 1983: 277; Shinohara, 1992b: 826; Shinohara & Byun, 1993: 78; Kim *et al.*, 1994: 216; Zhelochovtsev & Zinovjev, 1995: 397; Shinohara & Lee, 1997: 215; Shinohara & Hara, 1999: 123; Shinohara, 2002b: 419; Shinohara, 2004: 262; Shinohara & Hara, 2005: 273; Shinohara & Lelej, 2007: 927; Sundukov, 2009: 213; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 83; Sundukov, 2015: 249; Sundukov, 2017: 103; Shinohara *et al.*, 2018a: 595; Lee *et al.*, 2019: 7; Shinohara, 2019: 6; Shinohara, 2020: 8, 232.

Lectotype designation. Gussakovskij (1935) used a pair of specimens, a male and a female, for describing this species but did not designate a holotype. We hereby designate the female specimen (https://doi.org/10.6084/m9.figshare.16832095) in ZIL as a lectotype. It is labeled "Прим.[орская] обл.[асть]. Между Лазаревым и Чома у о-ва Чакмут, Солдатов, 31.VIII.911". According to Belokobylskij (pers. comm.), the locality is to be expected between Lazarev (52°11'42"N 141°27'43"E) and Bol'shoy Choma Island (52°23'29.9"N 141°12'24.0"E) [in Khabarovskij Kraj] near a spring or a river, as the collector V. K. Soldatov was an ichthyologist and insect collector. The date on the label corresponds to 13.IX.1911 in the Gregorian calendar.

Material examined. About 295 specimens, including the lectotype. A total of 183 specimens are from the Russian Far East and South Korea (Gussakovskij 1935; Shinohara 1980, 1992b; Shinohara & Byun 1993; Shinohara & Lee 1997; Shinohara & Taeger 2007; present work). **New collection data: RUSSIA: Primorskij Kraj**: 4♀2♂ (incl. DEI-GISHym 32030, 32042), Gornotajozhnoe, 1km E, 150 m, 43.694°N 132.168°E, 22. V. 2016,

K. Kramp, M. Prous & A. Taeger, RU010 (SDEI); 2♀, Arsenyev, Ski-Base Bodrost, 200m, 44.122°N 133.270°E, 25. V. 2016, K. Kramp, M. Prous & A. Taeger, RU017 (SDEI); 1♀, Arsenyev, Ski-Base Bodrost, 200m, 44.122°N 133.270°E, 26. V. 2016, K. Kramp, M. Prous & A. Taeger, RU018 (SDEI); 1♀, Arsenyev, Ski-Base Bodrost; 200 m. 44.122°N 133.270°E, 28. V. 2016; leg. K. Kramp, M. Prous & A. Taeger, RU021 (SDEI); 1♀, Yakovlevka 12km NW, 250m, 44.541°N 133.366°E, 27. V. 2016, K. Kramp, M. Prous & A. Taeger (SDEI); 2♀ (incl. DEI-GISHym 32046), Yakovlevka 10km NW, 250m, 44.523°N 133.392°E, 27. V. 2016, K. Kramp, M. Prous & A. Taeger, RU020 (SDEI); 1♀ (DEI-GISHym 32047), Taejka, 5 km SW, 170m, 44.050°N 133.177°E, 28. V. 2016, K. Kramp, M. Prous & A. Taeger (SDEI); 1♀ (DEI-GISHym 32045), 1♂(DEI-GISHym 12986, Fig. 29), 5♀, 5♂, Rettihovka, 170m, 44.182°N, 132.804°E, 29. V. 2016, K. Kramp, M. Prous & A. Taeger, RU023 (SDEI); 11♀ (incl. DEI-GISHym 32033, 32054), Rettihovka 9 km E, 170m, 44.178°N 132.877°E, 29. V. 2016, K. Kramp, M. Prous & A. Taeger RU024 (SDEI); 1♀ (DEI-GISHym 32055), Partizansk SSW, 140m, 43.073°N 133.074°E, 9. VI. 2016, K. Kramp, M. Prous & A. Taeger (SDEI); 3♀ (incl. DEI-GISHym 32048), Anisimovka W, 250m, 43.167°N 132.759°E, 13. VI. 2016, K. Kramp, M. Prous & A. Taeger, RU050 (SDEI); 2♀ (incl. DEI-GISHym 32044), Anisimovka 5 km SSE, 500m, 43.124°N 132.796°E, 15. VI. 2016, K. Kramp, M. Prous & A. Taeger RU052 (SDEI); 2♀ (incl. DEI-GISHym 12987, Fig. 28), Anisimovka, Gribanovka, 600m, 43.124°N 132.796°E, 15. VI. 2017, Taeger, Loktionov, Proshch., RU103 (SDEI); 1♀, Anisimovka 7 km S, Mt. Litovka; 1200 m, 43.102°N 132.786°E, 19. VI. 2017, leg. V. Loktionov, RU114 (SDEI); 1♀, Tigrovye N, 300 m, 43.205°N 132.911°E, 300m, 17. VI. 2017, leg. A. Taeger, M. Proshchalykin, T. Schmitt, V. Loktionov, RU108 (SDEI).

Distribution. Russia (East Siberia, "Amur", Khabarovskij Kraj, Primorskij Kraj, Sakhalin), North and South Korea, Japan (Hokkaido, Shikotan Is.) (Shinohara & Byun 1993), China (Inner Mongolia, Heilongjiang, Liaoning) (Shinohara & Byun 1993; Xiao & Chen 2005; Sundukov 2015).

Host plant. Rosaceae: *Sorbaria sorbifolia* (L.) A. Braun var. *stellipila* Maxim. (Shinohara 1980; Shinohara & Hara 1999). Records of *Populus tremula* L. and *Spiraea* sp. (Lee *et al.* 2019) need confirmation; the former is most probably erroneous.

Remarks. Adults of this species are locally abundant around *Sorbaria* bushes in the right season. The larvae are gregarious webspinners on this plant (Shinohara 1980; Shinohara & Hara 1999). The maximum *p*-distance between specimens from Russia and Japan was 2.0% (n=13) in COI and 1.2% (n=10) in NaK. The nearest neighbour, diverging by a minimum of 6.0% in COI and 0.9% in NaK, was *N. iridescens*. These two species formed a clade in the trees (Figs 137, 152), as discussed above.

Neurotoma silla Shinohara, Choi & Lee, 2018

(Figs 30, 31) (https://doi.org/10.6084/m9.figshare.16856284)

Neurotoma silla Shinohara, Choi & Lee, 2018a: 594, 596; Lee *et al.*, 2019: 7.

Material examined. Two specimens (types) from South Korea (Shinohara *et al.* 2018).

Distribution. South Korea.

Host plant. Unknown.

Remarks. This recently described species is known only from the female holotype and the male paratype, both from the northwestern part of Gyeongsangbuk-do, South Korea. No molecular data are available. It belongs to the *N. saltuum* subgroup of the *N. nemoralis* group as defined by Shinohara (2002b) (Shinohara *et al.* 2018a).

Tribe Pamphiliini Cameron, 1890

The representatives of this tribe are characterized as follows (Shinohara 2002b): head with lateral sutures subparallel and connected with antennal furrows (Fig. 1: 1aa); tarsal claws short (e.g., Figs 35h, 46h, 58g, 87h); forewing with vein Scl present (Fig. 1: 1bb); abdominal sternum 7 in female rather simply subconically swollen posteriorly, without paired ridges and triangular marginal depression (fig. 4K–M in Shinohara 2002b; *Onycholyda* exceptionally has paired rounded ridges and a very flat (in ventral view) subtriangular marginal depression or weakly sclerotized posterior margin, fig. 4H–J in Shinohara 2002b); lancet with lamnium small (Fig. 1: 1cc).

The tribe Pamphiliini is regarded as monophyletic. The characters listed above, except for the presence of the vein Sc1 in the forewing, are postulated as its autapomorphies. Our molecular analyses using COI and NaK genes also supported the monophyly of this tribe with UFBoot support of 100% (Figs 15, 16).

This tribe comprises five genera and 170 species in the recent world fauna (Taeger *et al.* 2010; Shinohara & Wei 2012, 2016; Shinohara *et al.* 2018c; present work). Here we treat three genera, *Chrysolyda*, *Onycholyda* and *Pamphilius*, containing 52 species as occurring in the Russian Far East and Korea. Of the three genera, *Chrysolyda* with only two world species and *Onycholyda* with 42 world species were considered monophyletic based on morphology (Shinohara 2002b). Our molecular analyses using the COI and NaK sequences also strongly supported the monophyly of *Onycholyda* with UFBoot support of 100% (Figs 15, 16). Molecular data for *Chrysolyda* and the two western Palaearctic genera, *Kelidoptera* Konow, 1897 and *Pseudocephaleia* Zirngiebl, 1937, were not available for the present study.

The monophyly or non-monophyly of *Pamphilius* and its relationship with *Onycholyda* should be clarified by further studies. Working on morphological characters, Shinohara (2002b) was not able to detect any autapomorphies for *Pamphilius*, and *Onycholyda* was retrieved as a sister group of all *Pamphilius* except for *P. sylvarum* and *P. basilaris* groups in his cladogram (fig. 11 in Shinohara 2002b; see Fig. 14 for an abbreviated version). In our NaK analysis, *Pamphilius* was recovered as monophyletic with UFBoot support of 99% and sister to *Onycholyda* (Fig. 16). In the COI analysis, *Pamphilius* was retrieved as paraphyletic and *Onycholyda* was a part of large assemblage of *Pamphilius* (supported by 97% UFBoot value) forming a sister group of *P. japonicus* (currently belonging to *P. sylvaticus* group) (Fig. 15). Therefore, the three available datasets, namely, morphology (Shinohara, 2002b, Fig. 14), COI genes (present work, Fig. 15) and NaK genes (present work, Fig. 16), supported three different hypothetical relationships.

Genus *Chrysolyda* Shinohara, 2002

Chrysolyda Shinohara, 2002b: 372.

This genus is well defined by the characters given in the key (see Shinohara 2002b and Shinohara & Wei 2012 for more details). Besides the type species, *C. leucocephala*, only one species, *C. yunshanica* Shinohara, 2012, from Hunan Province, China, is known. A postulated autapomorphy of this genus is the absence of the basal preapical spur of the hind tibia (Fig. 2: 2b, c). The host plants and immature stages are unknown.

Chrysolyda leucocephala (Takeuchi, 1938)

(Figs 17, 18) (https://doi.org/10.6084/m9.figshare.11402748)

Pamphilius leucocephalus Takeuchi, 1938: 219; Zinovjev, 1992: 56; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara & Lee, 1997: 216.

Chrysolyda leucocephala: Shinohara, 2002b: 374; Shinohara, 2004: 262; Shinohara & Lelej, 2007: 928; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 81; Sundukov, 2017: 103; Lee *et al.*, 2019: 7; Shinohara, 2019: 6; Shinohara, 2020: 9, 232.

Material examined. Eighteen specimens, including the type series. Ten specimens are from South Korea (Shinohara & Lee 1997).

Distribution. Russian Far East (Primorskij Kraj), South Korea, Japan (Hokkaido, Honshu, Kyushu) (Shinohara & Lee 1997).

Host plant. Unknown.

Remarks. This is a rare species with no molecular data. Zinovjev (1992) mentioned *Pamphilius leucocephalus* from Japan and southern Primorye without any collection data. We have not seen any specimens from Russia.

Genus *Onycholyda* Takeuchi, 1938

Pamphilius (*Onycholyda*) Takeuchi, 1938: 218.
Onycholyda: Beneš, 1972b: 385.

Onycholyda is a compact genus, well defined by the characters given in the key (see Shinohara 2002b for more details). Morphologically, this is regarded as a monophyletic group having the following autapomorphies: anterior part of malar space with setiferous area (female) or pit (male) (Fig. 2: 3a); supraocular area in male with narrow, dull, densely pubescent patch; facial crests in male developed, sharply carinate (e.g., Figs 34e, 39e, 43e); ventral inner surface of fore tibia with disconnected row of scale-like setae; tarsal claws with acute basal lobe (Fig. 2: 3c). The monophyly of this genus is also supported by our molecular analyses, as discussed above.

Shinohara (2002b) divided the world species of this genus into two species groups, the *O. amplecta* group and the *O. luteicornis* group, based on morphology. In our molecular work, 14 species of the *O. amplecta* group and five species of the *O. luteicornis* group were used for the COI analysis, and 10 species of the *O. amplecta* group and four species of the *O. luteicornis* group were used for the NaK analysis. In general, interspecific relationships were poorly resolved in our *Onycholyda* trees. In the COI analysis (Figs 138, 139), three Nearctic species of the *O. luteicornis* group (*O. luteicornis*, *O. nigritibialis* and *O. sitkensis*) formed a clade, though with only 61% UFBoot support, but two Palaearctic species of this species group (*O. armata* and *O. kumamotonis*) were rather distantly separated from them and located among the members of the *O. amplecta* group. In the NaK analysis (Fig. 153), the two Palaearctic species of the *O. luteicornis* group (*O. armata* and *O. kumamotonis*) were retrieved as monophyletic with 100% UFBoot support and the two Nearctic species of this species group (*O. luteicornis* and *O. nigritibialis*) were also retrieved as monophyletic with 95% UFBoot support, but these Palaearctic and Nearctic clades did not form a clade and were recovered among the members of the *O. amplecta* group. Thus, the result of our COI and NaK analyses did not support the dichotomous division of the genus into species groups advocated by Shinohara (2002b). On the other hand, it is interesting that in the COI tree all the 17 Nearctic specimens of six species were retrieved as a monophyletic group with 99% UFBoot support and each of the *O. amplecta* group (*O. amplecta*, *O. rufofasciata* and *O. multisignata*) and the *O. luteicornis* group (*O. luteicornis*, *O. nigritibialis* and *O. sitkensis*) formed a clade with low UFBoot support of 61%. The intrageneric relationships in *Onycholyda* still need a revision.

This genus is most diverse in warm temperate regions of eastern Asia. There are 42 valid species worldwide (Taeger *et al.* 2010; Shinohara & Wei 2012, 2016; Shinohara *et al.* 2018c), of which 32 occur in eastern Asia. In the Russian Far East and Korea, only eight *Onycholyda* species have been found, whereas ten species are known to occur in Japan and 19 species in China.

The larvae of *Onycholyda* species feed on the host leaves singly or gregariously in simple leaf-rolls or, when they become larger, often in webs. All known larvae feed on shrubby or herbaceous Rosaceae, except for one doubtful record of *Cornus* (Cornaceae) in North America (Middlekauff 1964; Shinohara *et al.* 2019). Most species are associated with the genus *Rubus* and a few with the genera *Filipendula* and *Agrimonia* (Middlekauff 1964; Shinohara 2002b; Shinohara & Wei 2010, 2016; Shinohara & Lee 2011; Shinohara *et al.* 2018b, c).

***Onycholyda armata* (Maa, 1949)**

(Figs 32–34) (https://doi.org/10.6084/m9.figshare.11405052)

Pamphilius armatus Maa, 1949: 37.

Onycholyda armata: Shinohara, 1985a: 349; Shinohara & Beneš, 1988: 806; Shinohara & Byun, 1993: 82; Kim *et al.*, 1994: 216; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2002b: 422; Shinohara, 2004: 262; Shinohara & Lelej, 2007: 929; Shinohara & Taeger, 2007: 32; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 83; Sundukov & Lelej, 2012: 108; Sundukov, 2017: 103; Lee *et al.*, 2019: 8.

Material examined. Twenty-eight specimens, including 26 specimens from the Russian Far East and South Korea (Shinohara & Beneš 1988; Shinohara & Byun 1993; Shinohara & Taeger 2007; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♂ (DEI-GISHym 86268), Arsenyev, Ski-Base Bodrost, 200m, 44.122°N 133.270°E, 25. V. 2016, K. Kramp, M. Prous & A. Taeger RU017 (SDEI); 1♀ (Fig. 33, DEI-GISHym 86315), 1♂ (DEI-GISHym 86314), Yakovlevka 12km NW, 250m, 44.541°N 133.366°E, 27. V. 2016, K. Kramp, M. Prous & A. Taeger RU019 (SDEI). **SOUTH KOREA: Gangwon-do**: 1♀, Mirugam (Bukdaesa), 1,300 m, Odaesan Mts., 4. VI. 2002, A. Shinohara (NSMT).

Distribution. Russia (Tomskaja Oblast', Khabarovskij Kraj, Primorskij Kraj), North and South Korea, China (Jilin).

Host plant. Unknown.

Remarks. The specimens recorded from Zhejiang Province, China, as *O. armata* by Shinohara & Xiao (2006) belong to *O. atra* Shinohara & Wei, 2016 (Shinohara & Wei 2016). In China, *O. armata* has been found only in the northeastern part (Jilin).

Morphologically, this species closely resembles *O. kumamotonis* particularly in having a comparatively long flagellomere 1 and a similar structure of the male clypeus. Shinohara (2002b) placed these two species in his *O kumamotonis* complex of the *O. luteicornis* subgroup of the *O. luteicornis* group. This placement was supported by our NaK analysis, where the nearest neighbour of *O. armata*, diverging by a minimum of only 0.2%, was *O. kumamotonis*, and *O. armata* and *O. kumamotonis* formed a clade with 100% UFBoot support (Fig. 153). However, in the COI analysis, the nearest neighbour, diverging by a minimum of 2.6%, was *O. viriditibialis,* with which *O. armata* formed a clade with 100% UFBoot support (Fig. 138). The maximum *p*-distance between three specimens of *O. armata* from Primorskij Kraj was 0.6% in COI and 0% in NaK.

It is interesting that the known distributions of *O. armata* and *O. kumamotonis* do not overlap. *Onycholyda armata* is a continental species and *O. kumamotonis* occurs only in Japan and Sakhalin.

Onycholyda kumamotonis (Matsumura, 1912)

(Figs 35, 36) (https://doi.org/10.6084/m9.figshare.11405067)

Lyda kumamotonis Matsumura, 1912: 75.

Onycholyda kumamotonis: Beneš, 1972b: 387; Shinohara, 1985c: 716; Shinohara, 1987a: 499; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2002b: 422; Shinohara, 2004: 262; Shinohara & Lelej, 2007: 929; Taeger *et al.*, 2010: 84; Sundukov & Lelej, 2012: 108; Sundukov, 2015: 249; Sundukov, 2017: 103; Shinohara, 2019: 7; Shinohara, 2020: 12, 236.

Onycholyda sp.: Shinohara & Okutani, 1983: 277.

Lectotype designation. Shinohara (1985d) treated a specimen in Matsumura's collection in HU as the holotype, stating "Matsumura (1912) described this species on the basis of a single female from Kiushu (Kumamoto)". However, Matsumura (1912) did not give the actual number of the specimens examined and thus the specimen is a syntype. Here we designate this specimen as a lectotype. It is labeled "Japan, Kumamoto, Matsumura, 7/18" (HU).

Material examined. About 355 specimens, including the lectotype. Two specimens are from the Russian Far East (Shinohara 1985d).

Distribution. Russia (Sakhalin), Japan (Hokkaido, Kunashiri Is., Honshu, ?Kyushu).

Host plant. Rosaceae: *Filipendula camtschatica* (Pall.) Maxim. (Shinohara & Okutani 1983; Shinohara 1985c).

Remarks. This species is not rare around *Filipendula camtschatica* bushes in Hokkaido, where two species of *Pamphilius*, *P. venustus* (Smith, 1874) and *P. sapporensis* (Matsumura, 1912) also occur together. These three pamphiliids are all associated with *Filipendula*.

In the COI analysis (Fig. 139), three specimens from Hokkaido (NSMT30554, 30788, 30789) and four specimens from Honshu (NSMT30730, 30785–30787) each formed a different cluster and the two clusters had a sister-group relationship supported by 100% UFBoot values. The maximum *p*-distance in the Hokkaido cluster was 0.2% and that in the Honshu cluster was 1%. The minimum *p*-distance between the Honshu and Hokkaido clusters was 2.2%. In the NaK tree (Fig. 153), the four Honshu specimens formed a cluster but the three Hokkaido specimens did not and, with the Honshu cluster, formed a polytomous clade, which was sister to *O. armata* (this clade, *O. kumamotonis* + *O. armata*, was supported by 100% UFBoot value). The maximum *p*-distance within *O. kumamotonis* was 0.4% and the nearest neighbour, diverging by a minimum of 0.2%, was *O. armata.* The Hokkaido and Honshu populations of *O. kumamotonis* certainly have some genetic divergence, but we will leave them as one species until more evidence of speciation becomes available.

Onycholyda nigroclypeata Shinohara, 1987

(Figs 37–39) (https://doi.org/10.6084/m9.figshare.11405073)

Pamphilius tenuis: Kim, 1970: 126, 717; Kim, 1980: 3. Not Takeuchi, 1938.

Onycholyda nigroclypeata Shinohara, 1987b: 649; Shinohara, 1992a: 502; Shinohara & Byun, 1993: 84; Kim *et al.*, 1994: 216; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara & Lee, 1997: 215; Shinohara, 2002b: 421; Shinohara, 2004: 262;

Shinohara & Lelej, 2007: 929; Shinohara & Taeger, 2007: 32; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 84; Shinohara & Lee 2011: 209; Sundukov & Lelej, 2012: 108; Sundukov, 2017: 103; Lee *et al.*, 2019: 8; Shinohara & Tripotin, 2021a: 60; Shinohara & Tripotin, 2021b: 196.

Material examined. Forty specimens, including the type series. Thirty-nine specimens are from the Russian Far East and North and South Korea (Shinohara 1987b; Shinohara & Byun 1993; Shinohara & Lee 1997; Shinohara & Taeger 2007; Shinohara & Tripotin 2021a, b; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (Fig. 38, DEI-GISHym 86743), Partizansk SSW, 140m, 43.073°N 133.074°E, 9. VI. 2016, K. Kramp, M. Prous & A. Taeger, RU044 (SDEI). **SOUTH KOREA: Gangwon-do**: 2♀1♂, Mirugam (Bukdaesa), 1,300 m, Odaesan Mts., 29. V.–1. VI. 1998, A. Shinohara (NSMT); 1♀, same locality, 2. VI. 2002, A. Shinohara (NSMT).

Distribution. Russia (Khabarovskij Kraj, Primorskij Kraj), North and South Korea, China (Heilongjiang) (Shinohara 1992a).

Host plant. Rosaceae: *Agrimonia pilosa* Ledeb. (Shinohara & Lee 2011).

Remarks. This species has much in common with *O. decorata* Shinohara, 1985, from Japan, in adult and larval morphology and host plant (Shinohara 1987b; Shinohara & Lee 2011). In our molecular analyses, the two species were also quite close, diverging by a minimum of 1.1% in COI and 0.3% in NaK. The two species formed a clade with 100% UFBoot support in both COI and NaK analyses (Figs 139, 153). However, we treat them as distinct species, because the differences between them (Shinohara 1987b) are small but quite constant.

The newly acquired female specimen from Russia (Fig. 38) has extensively orange-marked temples and vertex, but is otherwise not distinguishable from other specimens (Fig. 37) (Shinohara 1987b). The pale coloration of the head of this specimen is asymmetrical suggesting its aberrant nature (Fig. 38e).

Onycholyda odaesana Shinohara & Byun, 1993

(Figs 40, 41) (https://doi.org/10.6084/m9.figshare.11405079)

Onycholyda odaesana Shinohara & Byun, 1993: 83; Kim *et al.*, 1994: 216; Shinohara & Lee, 1997: 216; Shinohara & Xiao 2006: 288; Shinohara & Wei, 2012: 54; Shinohara & Wei, 2016: 307; Shinohara, 2002b: 423; Shinohara, 2004: 262; Paek *et al.*, 2010: 161; Taeger *et al.,* 2010: 84; Shinohara & Lee, 2011: 210; Lee *et al.*, 2019: 8; Shinohara & Tripotin, 2021a: 60.

Material examined. About 200 specimens, including the holotype. Nine specimens are from South Korea (Shinohara & Byun 1993; Shinohara & Lee 1997; Shinohara & Lee 2011; Shinohara & Tripotin 2021a; present work). **New collection data: SOUTH KOREA**: **Gangwon-do**: 1♂, Tokchomgogae, 510m, nr. Chuncheon, 28. V. 1996, A. Shinohara (NSMT); 1♂, Mirugam (Bukdaesa), 1,300 m, Odaesan Mts., 29. V.–1. VI. 1996, A. Shinohara (NSMT).

Distribution. South Korea, China (Gansu, Henan, Shaanxi, Anhui, Hunan, Zhejiang).

Host plant. Rosaceae: *Rubus adenophorus* Rolfe, *R. parvifolius* L. (Shinohara & Wei 2010; Shinohara & Lee 2011).

Remarks. This species was described from South Korea (Shinohara & Byun 1993) but later found across vast areas of southern China, where it is more commonly found (Shinohara & Wei 2012). It is a member of the *O. wongi* complex of the *O. wongi* subgroup of the *O. luteicornis* group. The *Onycholyda wongi* complex is represented by seven species (Shinohara *et al.* 2018c), all confined to southern China, except for *O. odaesana*. *Onycholyda odaesana* is the only Pamphiliidae known so far to occur both in southern China and Korea.

Onycholyda sertata (Konow, 1903)

(Figs 42, 43) (https://doi.org/10.6084/m9.figshare.11405088)

Pamphilius sertatus Konow, 1903: 37; Gussakovskij, 1935: 171.
Onycholyda sertata: Beneš, 1972b: 387; Achterberg & Aartsen, 1986: 26; Shinohara & Byun, 1993: 85; Kim *et al.*, 1994: 216; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2002b: 421; Shinohara, 2004: 262; Shinohara & Lelej, 2007: 929; Shinohara & Taeger, 2007: 32; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 84; Sundukov, 2017: 103; Lee *et al.*, 2019: 8.
Onycholyda rufofasciata: Beneš, 1972b: 388. Not Norton, 1869.
Onycholyda serrata [sic]: Sundukov & Lelej, 2012: 108.

Material examined. Forty specimens, including the lectotype (Blank *et al.* 1998). Thirty-one specimens are from the Russian Far East and North Korea (Shinohara & Byun 1993; Shinohara & Taeger 2007; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (DEI-GISHym 86157), Gornotajozhnoe, Dendrarium, 150m, 43.691°N 132.153°E, 21. V. 2016, K. Kramp, M. Prous & A. Taeger, RU009 (SDEI); 1♀ (DEI-GISHym 86310), Yakovlevka 12km NW, 250m, 44.541°N 133.366°E, 27. V. 2016, K. Kramp, M. Prous & A. Taeger, RU019 (SDEI); 1♀ (DEI-GISHym 32031), Arsenyev, Ski-Base Bodrost, 200m, 44.122°N 133.270°E, 30. V. 2016, K. Kramp, M. Prous & A. Taeger, in alcohol, RU026 (SDEI); 1♀ (DEI-GISHym 32053), Nakhodka 10 km ESE: Beregovoj, 30m, 42.788°N 133.030°E, 7. VI. 2017, K. Kramp, M. Prous & A. Taeger, in alcohol, RU040 (SDEI); 1♀ (DEI-GISHym 32037), Nikolaevka 5 km NNE, 140m, 43.137°N 133.249°E, 11. VI. 2017, K. Kramp, M. Prous & A. Taeger, in alcohol, RU047 (SDEI); 1♀, Sedanka, 80m, 43.210°N 131.995° E, 14. VI. 2017, A. Taeger, V. Loktionov & M. Proshchalykin, (Fig. 42, DEI-GISHym 12979); 2♀, Ussuri Nature Reserve, 150m, 43.644°N 132.346°E, 23. VI. 2017, A. Taeger, M. Proshchalykin, T. Schmitt, V. Loktionov, RU127 (SDEI).

Distribution. Northern Europe, across Siberia to Primorskij Kraj, North Korea, China (Jilin) (Shinohara & Taeger 2007).

Host plant. Rosaceae: *Filipendula ulmaria* (L.) Maxim. (Kangas & Syrjänen 1962). Record of *Spiraea* sp. (Kajmuk 1972; Verzhutskij 1981; Lee *et al.* 2019) needs confirmation.

Remarks. This is a widely distributed species associated with *Filipendula* (Kangas & Syrjänen 1962). It has much in common with *O. decorata* and *O. nigroclypeata* whose larvae feed on *Agrimonia* (Shinohara 2006; Shinohara & Lee 2011). In the COI tree (Fig. 139), *O. sertata* was retrieved as a sister of the clade represented by *O. decorata* and *O. nigroclypeata* but with 93% UFBoot support, which was not high enough to warrant credibility. The maximum *p*-distance within *O. sertata* (n=8) was 0.8% and the nearest neighbour, diverging by a minimum of 3.5%, was *O. decorata* and *O. viriditibialis.* The NaK tree was not well resolved among the species related to *O. sertata* (Fig. 153).

Onycholyda viriditibialis (Takeuchi, 1930)

(Figs 44, 45) (https://doi.org/10.6084/m9.figshare.11405106)

Pamphilius viriditibialis Takeuchi, 1930: 13; Kim, 1963: 278; Kim, 1970: 126.
Pamphilius tsherskii Gussakovskij, 1935: 178; Shinohara, 1986a: 271. (syn. of *viriditibialis*)
Onycholyda viriditibialis: Beneš, 1972b: 387; Shinohara, 1986a: 271; Shinohara & Byun, 1993: 82; Kim *et al.*, 1994: 216; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara & Lee, 1997: 215; Shinohara, 2002a: 189; Shinohara, 2002b: 421; Shinohara, 2004: 262; Shinohara & Lelej, 2007: 928, 929; Shinohara & Taeger, 2007: 34; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 85; Sundukov & Lelej, 2012: 108; Shinohara, 2013: 94; Sundukov, 2017: 103; Lee *et al.*, 2019: 8; Shinohara, 2019: 7; Shinohara, 2020: 10, 235; Shinohara & Tripotin, 2021a: 60; Shinohara & Tripotin, 2021b: 197.

Material examined. About 205 specimens, including the type series. Thirty-one specimens are from the Russian Far East and Korea (Shinohara 1986a; Shinohara & Byun 1993; Shinohara & Lee 1997; Shinohara & Taeger 2007; Shinohara & Tripotin 2021a, b; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (DEI-GISHym 32041), Partizansk SSW, 140m, 43.073°N 133.074°E, 9. VI. 2016, K. Kramp, M. Prous & A. Taeger, in alcohol, RU044 (SDEI); 1♀ (DEI-GISHym 32038), Anisimovka W, 250m, 43.167°N 132.759°E, 13. VI. 2016, K. Kramp, M. Prous & A. Taeger RU050 (SDEI).

Distribution. Russia (Primorskij Kraj), North and South Korea, Japan (Hokkaido, Honshu, Shikoku, Kyushu) (Shinohara 1986a).

Host plant. Rosaceae: *Rubus crataegifolius* Bunge, *R. microphyllus* L.f. (Hara & Shinohara 2017).

Remarks. *Onycholyda viriditibialis* was described from Japan (Takeuchi 1930). Shinohara (1986a) synonymized *Pamphilius tsherskii* Gussakovskij, 1935, described from Vladivostok, with this species, even though he noted a few very small colour pattern differences between them. In both COI and NaK trees (Figs 138, 153), the Russian and Japanese specimens formed separate clades, each with 100% UFBoot support. The Russian and Japanese clades together formed a clade with 100% UFBoot support in the COI tree (Fig. 138) but they did not form a clade in the NaK tree (Fig. 153). The maximum *p*-distance among the Russian specimens was 0.2% in COI (n=3) and 0% in NaK (n=2) and that among the Japanese specimens (n=4) was 0.9% in COI and 0% in NaK, whereas the minimum *p*-distance between the two populations was 1.2% in COI and 0.4% in NaK. Apparently, there is some

diversification among the geographically isolated populations, but here we treat all as a single species because we do not consider the observed differences sufficient to assume different species. The nearest neighbour was *O. armata* in COI analysis, diverging by a minimum of 2.6%, and *O. sertata* and *O. tenuis* in NaK analysis, diverging by a minimum of 0.5%.

The flight period of this species is long, from May to September, in South Korea (Shinohara & Tripotin 2021a, b) and also in Japan (Shinohara 1986a). The long flight period of adults is quite unusual for a pamphiliid, otherwise known only for the closely related *O. esakii* (Takeuchi, 1938). It is probably a result of polymodal adult emergence (Shinohara & Kojima 2009).

Onycholyda yezoensis Shinohara, 1987

(Figs 46, 47) (https://doi.org/10.6084/m9.figshare.11405091)

Anoplolyda minomalis: Takeuchi, 1936a: 62. Not Takeuchi, 1936, in part.
Onycholyda minomalis: Shinohara, 1985b: 349; Sundukov, 2017: 103; Taeger *et al.*, 2018. Not Takeuchi, 1936, in part.
Onycholyda yezoensis Shinohara, 1987a: 495; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2002b: 422; Shinohara, 2004: 262; Shinohara & Lelej, 2007: 929; Taeger *et al.*, 2010: 85; Sundukov & Lelej, 2012: 108; Sundukov, 2015: 249; Sundukov, 2017: 104; Shinohara, 2019: 7; Shinohara, 2020: 10, 235.

Material examined. About 40 specimens, including the type series. One specimen is from the Russian Far East (Shinohara 1987a).

Distribution. Russia (Sakhalin), Japan (Hokkaido, Kunashiri Is.) (Sundukov 2015).

Host plant. Rosaceae: *Rubus parvifolius* L. (Hara & Shinohara 2017).

Remarks. This species is similar to two Japanese species, *O. minomalis* (Takeuchi, 1930) and *O. similis* Shinohara, 1987, and a Chinese species, *O. atra* Shinohara & Wei, 2016 (Shinohara 1987a; Shinohara & Wei 2016). Molecular data are not available for *O. atra*, but we have COI and NaK sequences for *O. minomalis*, *O. similis* and *O. yezoensis* and they formed a clade with 100% UFBoot support in the COI and 99% UFBoot support in the NaK genes (Figs 139, 153). In the COI analysis, the two sequences of *O. yezoensis* differed by 0.1% and the nearest neighbour, diverging by a minimum of 2.3%, was *O. similis,* with which *O. yezoensis* formed a clade with 100% UFBoot support (Fig. 139). In the NaK analysis, the two sequences of *O. yezoensis* differed by 0.1% and the nearest neighbour, diverging by a minimum of 0%, was *O. similis*.

Takeuchi (1936a) first recorded this species as "*Anoplolyda minomalis*" (=*O. minomalis*) from Sakhalin. Shinohara (1985b), adopting a broader concept of *O. minomalis*, included Sakhalin in the distribution of *O. minomalis*. However, Shinohara (1987a) recognized three species in the previous concept of *O. minomalis* and described the species occurring in Hokkaido and Sakhalin as *O. yezoensis*, thus excluding Sakhalin from the distribution of *O. minomalis*. Zhelochovtsev & Zinovjev (1995) correctly understood this history and noted "*yezoensis* Shinohara, 1987 (= *minomalis* auct., in part). — EFE". Sundukov (2017) included *O. minomalis* in the Russian fauna, probably according to Shinohara (1985b) and neglecting Shinohara (1987a). Without further evidence, *O. minomalis* should be excluded from the list of the Russian fauna.

Onycholyda zinovjevi Shinohara, 1987

(Figs 48, 49) (https://doi.org/10.6084/m9.figshare.11405103)

Onycholyda zinovjevi Shinohara, 1987b: 644; Shinohara & Byun, 1993: 83; Kim *et al.*, 1994: 216; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2002b: 422; Shinohara, 2004: 262; Shinohara & Lelej, 2007: 929; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 85; Sundukov & Lelej, 2012: 108; Sundukov, 2017: 104; Lee *et al.*, 2019: 8; Shinohara & Tripotin, 2021a: 61.

Material examined. Thirteen specimens from the Russian Far East and South Korea, including the type series (Shinohara 1987b; Shinohara & Byun 1993; Shinohara & Tripotin 2021a).

Distribution. Russia (Primorskij Kraj), South Korea (Shinohara & Byun 1993).

Host plant. Unknown.

Remarks. This is a rare and little-known species, with no material available for molecular work.

Genus *Pamphilius* Latreille, 1803

Pamphilius Latreille, 1803: 303.
See Taeger *et al.* (2010) for more synonymy.

Pamphilius is a large and rather heterogeneous genus, characterized as follows: anterior part of malar space without setiferous area (female) or pit (male) (Fig. 2: 3aa); supraocular area in male without narrow, dull, densely pubescent patch; facial crests in male various in shape, nearly flattened, rounded or carinate (e.g., Figs 55e, 63e, 65e); ventral inner surface of fore tibia without disconnected row of scale-like setae; tarsal claws without acute basal lobe (e.g., Figs 56g, 74i, 89g). It is distinguishable from the related genera by the features given in the key (see Shinohara 2002b for more details), but as discussed above, the monophyly of this genus is uncertain based on both morphological and molecular data.

Based on morphology, Shinohara (2002b) divided the world species of this genus into 12 species groups, of which four major groups (*P. vafer*, *P. sylvaticus*, *P. alternans* and *P. histrio* groups) contained about 80% of all the species then known. Each of the remaining eight species groups contained only one to four species. The *P. ochreipes* group, represented by two Nearctic species, is here treated as a part of the *P. vafer* group. In the Russian Far East and Korea, the *P. inanitus*, *P. latifrons* and *P. sulphureipes* groups have been recorded in addition to the four major species groups.

For the molecular analyses of the present study, representatives of the seven species groups mentioned above, except for the *P. latifrons* group, and additionally the *P. basilaris* group, were used. The *Pamphilius basilaris* group contains two species associated with Juglandaceae from Japan and China (Shinohara 2003b; Shinohara *et al.* 2012). It has not been recorded from the Russian Far East and Korea, but the species group is likely to be found particularly in Korea.

The monophyly of each species group and the relationship among the species groups were discussed by Shinohara (2002b) based on morphology and will be examined further below in the light of the results of molecular analyses. Generally speaking, the monophyly of each species group was at least partly supported also by molecular data (see discussion under respective species group below) but the relationship among the species groups is still poorly clarified, as the hypotheses based on three different data sets (morphology, Fig. 14; COI sequences, Fig. 15; NaK sequences, Fig. 16) differ drastically (see also discussion under Pamphiliini above).

Pamphilius is distributed in the Holarctic region and contains 123 valid species and subspecies (Taeger *et al.* 2010; Shinohara & Wei 2012, 2016; present work), of which 43 are recorded for the Russian Far East and Korea.

The larvae of *Pamphilius* species feed on the host leaves singly or gregariously in simple leaf-rolls or in webs. Known host plants include Rosaceae (*Cerasus*, *Padus*, *Sorbus*, *Rosa*, *Rubus*, *Filipendula*, *Fragaria*, *Aruncus*, *Spiraea*, etc.), Betulaceae (*Alnus*, *Betula*, *Corylus*, *Carpinus*, etc.), Salicaceae (*Populus*, *Salix*), Spindaceae (*Acer*), Caprifoliaceae (*Lonicera, Macrodiervilla*), Adoxaceae (*Viburnum*), Fagaceae (*Quercus*), Cornaceae (*Cornus*), Juglandaceae (*Juglans*, *Platycarya*) and Saxifragaceae (*Astilbe*) (Shinohara 2002b, 2003b; Shinohara & Hara 2011; Shinohara & Kojima 2011; Shinohara *et al.* 2012, 2016a, b, 2019; Shinohara & Wei 2016). In some cases, distinct association between a species group and host plant family exists as noted under each species group below.

Pamphilius alternans group

The members of this species group are characterized as follows: clypeus entirely yellow; antenna with scape entirely yellow, in females sometimes marked with dark brown or entirely black; antennal flagellomere 1 2.2–3.0 × length of flagellomere 2; right mandible tridentate with incision between median and apical teeth distinct; left mandible tridentate with low middle tooth or bidentate with no middle tooth; forewing sometimes with brownish infuscated area and cell C pilose or glabrous; femora entirely pale, except in *P. lethierryi* subgroup. Ovipositor sheath appendage more or less pilose (Fig. 90g). Male genitalia: ventral arm of gonostipes with narrow plate-like process along proximal margin, developing inside gonocardo; inner margin of harpe roundly or angularly produced at base; apiceps broad; valviceps in lateral view rather short, apex directed above, ventral margin rounded, without conspicuous dorsoapical process.

Three subgroups (*P. alternans*, *P. komonensis* and *P. lethierryi* subgroups) containing 17 world species are known in the Palaearctic region (Shinohara 2002b; Shinohara & Zhou 2006). We recognized two species of the *P. komonensis* subgroup in the Russian Far East and Korea.

Twenty-seven sequences of nine species of three subgroups were treated in COI analysis and 15 sequences of six species of the same three subgroups were treated in NaK analysis. In the COI analysis (Fig. 140), the *P. alternans* subgroup (11 specimens of four species) was recovered as monophyletic with high UFBoot value (99%). Also, a part of the *P. komonensis* subgroup (*P. komonensis* Takeuchi, 1930 + *P. kyutekparki* Shinohara, 1991) and another part of the *P. komonensis* subgroup (*P. croceus* + *P. takeuchii*) are both retrieved as monophyletic, respectively, with 100% UFBoot value. These three clades form a monophyletic group (*P. alternans* group without *P. lethierryi* subgroup), but with low UFBoot support (78%) and unexpected inclusion in this clade of *P. norimbergensis* Enslin, 1917, which is currently placed in the *P. vafer* group (Shinohara 2002b). The only remaining specimen of the *P. alternans* group included in the COI analysis, namely, one sequence of the *P. lethierryi* subgroup, was recovered as sister to *P. histrio* (*P. histrio* group) but with very low UFBoot support (63%) in the remote part of the tree. Our COI analysis therefore did not support the monophyly of the *P. alternans* group (*P. alternans* + *P. komonensis* + *P. lethierryi* subgroups). The placement of *P. norimbergensis*, whose samples were not available for the NaK analysis, should be confirmed by further studies. In the NaK analysis (Fig. 154), the *P. alternans* group (three subgroups) and the *P. komonensis* subgroup (13 sequences of four species) were retrieved as monophyletic with high UFBoot support (99% and 100%, respectively). The *P. alternans* subgroup (one specimen available) was sister to the *P. lethierryi* subgroup (one specimen available) but with very low UFBoot support (30%).

Almost all recorded host plants for the members of this species group are Sapindaceae (*Acer*) (Shinohara 2002b). The only exception is the European *P. marginatus* feeding on Betulaceae (*Carpinus* and *Corylus*) (Taeger *et al.* 1998).

Pamphilius croceus Shinohara, 1986

(Figs 71, 72) (https://doi.org/10.6084/m9.figshare.11405169)

Pamphilius takeuchii: Beneš, 1974: 309, 313; Shinohara, 1979: 152; Zhelochovtsev & Zinovjev, 1995: 398; Sundukov & Lelej, 2009: 3; Sundukov & Lelej, 2012: 109; Shinohara, 2013: 99; Sundukov, 2017: 105. Not Beneš, 1972a, in part.

Pamphilius croceus Shinohara, 1986b: 425; Shinohara, 1991a: 56; Kim *et al.*, 1994: 217; Shinohara, 2002b: 424; Shinohara, 2004: 263; Shinohara & Zhou, 2006: 184; Shinohara & Lelej, 2007: 935, 942; Sundukov, 2009: 213; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 86; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 104; Lee *et al.*, 2019: 9; Shinohara & Tripotin, 2021a: 61.

Material examined. Fifty-eight specimens, including the holotype, all from the Russian Far East and Korea (Shinohara 1986b, 1991a; Shinohara & Zhou 2006; Shinohara & Tripotin 2021a; present work). **New collection data: RUSSIA: Primorskij Kraj**: 2♀ (Fig. 71, DEI-GISHym 88000, 88002), Sedanka, 80m, 43.210°N 131.995°E, 14. VI. 2017, A. Taeger, M. Proshchalykin & V. Loktionov (SDEI). **SOUTH KOREA: Gangwon-do**: 1♀45♂ (incl. NSMT 30980), Mirugam (Bukdaesa), 1300m, Odaesan Mts., 16–18. VI. 2010, A. Shinohara (NSMT).

Distribution. Russia (Primorskij Kraj), South Korea (Shinohara & Zhou 2006).

Host plant. Unknown.

Remarks. This species belongs to the *P. komonensis* subgroup of the *P. alternans* group (Shinohara 2002b; Shinohara & Zhou 2006) and is similar to *P. takeuchii* Beneš, 1972, from Japan. Beneš (1974) recorded *P. takeuchii* from Primorskij Kraj based on a female specimen from Suchan (= Partizansk), which was later designated as the holotype of *P. croceus* by Shinohara (1986b). No other specimens of *P. takeuchii* have been recorded from Russia. Although *P. takeuchii* was included in the lists of Russian sawflies (Zhelochovtsev & Zinovjev 1995; Sundukov & Lelej 2009, 2012; Sundukov 2017), it should be excluded from the Russian fauna as fully discussed by Shinohara (2013).

In both COI and NaK analyses (Figs 140, 154), *P. croceus* was recovered as sister to *P. takeuchii* with 100% UFBoot support. The two allopatric species are very close genetically, diverging by a minimum of 1.0% in the COI analysis and by a minimum of 0.4% in NaK analysis. The larvae of *P. takeuchii* feed on *Acer* spp. (Sapindaceae) solitarily rolling edge of a leaf. The larvae of *P. croceus* may also feed on these plants.

Pamphilius kyutekparki Shinohara, 1991

(Figs 90, 91) (https://doi.org/10.6084/m9.figshare.11405223)

Pamphilius jucundus: Kim, 1980: 3, pl. v, HYPA01. Not Takeuchi, 1930.

Pamphilius kyutekparki Shinohara, 1991a: 53; Kim *et al.*, 1994: 217; Zhelochovtsev & Zinovjev, 1995: 397; Shinohara & Lee, 1997: 216; Shinohara, 2002b: 424; Shinohara, 2004: 263; Shinohara & Zhou, 2006: 171; Shinohara & Taeger, 2007: 35; Shinohara & Lelej, 2007: 938, 942; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 88; Sundukov & Lelej, 2012: 109 ["*kyutekrarki*"]; Sundukov, 2017: 105; Lee *et al.*, 2019: 10; Shinohara & Tripotin, 2021a: 61.

Material examined. About 135 specimens, including the type series, all from the Russian Far East and Korea (Kim 1980; Shinohara 1991a; Shinohara & Lee 1997; Shinohara & Zhou 2006; Shinohara & Taeger 2007; Shinohara & Tripotin 2021a; present work). **New collection data: SOUTH KOREA: Gangwon-do**: 2♂ (NSMT 30754, 30755), Mirugam (Bukdaesa), 1,300 m, Odaesan Mts., 1. VI. 2008, A. Shinohara (NSMT); 1♀4♂ (incl. NSMT 30854, 30864), same locality, 30. V.–4. VI. 2009, A. Shinohara (NSMT); 2♀1♂, same locality, 11–16. VI. 2010, A. Shinohara (NSMT).

Distribution. Russia (Primorskij Kraj), South Korea.

Host plant. Unknown.

Remarks. This species belongs to the *P. komonensis* subgroup of the *P. alternans* group (Shinohara 2002b; Shinohara & Zhou 2006). *Pamphilius kyutekparki* is most closely related to the Japanese *P. komonensis* Takeuchi, 1930, though the two allopatric taxa are separated at least by the color pattern (Shinohara 1991a). In our molecular analysis using COI and NaK sequences, the two species were not clearly differentiated (Figs 140, 154). The host plant of *P. kyutekparki* is still unknown, but it is probably *Acer* (Sapindaceae), which is the host of *P. komonensis* (Shinohara & Okutani 1983).

Pamphilius basilaris group

The members of this species group are characterized as follows: antennal flagellomere 1 1.0–2.2 × length of flagellomere 2; right mandible tridentate with incision between middle and apical teeth much deeper than incision between basal and middle teeth; left mandible bidentate with middle tooth missing (figs 8C, 8D in Shinohara & Wei 2012); wings strongly infuscate in basal 3/2 and clear hyaline in apical 1/3 (figs 8A, 8F in Shinohara & Wei 2012); forewing with cell C glabrous, 1st abscissa of vein Rs very long and cell 1M small and short; femora entirely pale. Subgenital plate in male with large setose appendage. Ovipositor sheath appendage very large, pilose. Male genitalia: proximal ventral arm of gonostipes normal; apiceps simple, narrow; valviceps in lateral view rather short, apex directed upwards, ventral margin rounded, without conspicuous dorsoapical process.

Two species are known, *P. basilaris* Shinohara, 1982 from Japan and *P. lizejiani* Shinohara, 2012 (in: Shinohara & Wei 2012) from China. This species group has not been found in the Russian Far East and Korea, though it is likely to occur particularly in Korea. For the COI and NaK analyses, two sequences each of *P. basilaris* were used and they were retrieved as monophyletic with 100% UFBoot support in both analyses. In the COI tree (Fig. 141), *P. basilaris* was the sister group of the Nearctic *P. ocreatus* (*P. sylvaticus* group) and this pair was the sister group of *Onycholyda* but these relationships had low UFBoot support (75% and 64%, respectively). In the NaK tree (Fig. 155), the *P. basilaris* group was retrieved as the sister of the large clade represented by the speciose *P. vafer* and *P. sylvaticus* groups but this relationship was supported only by 87% UFBoot value. The affinity of this species group within *Pamphilius* or Pamphiliini is still unclear.

Among the Pamphiliidae, the members of this species group are unique in their association with Juglandaceae (*Juglans* and *Platycarya*) (Shinohara *et al.* 2012).

Pamphilius histrio group

The members of this species group are characterized as follows: upper part of head glabrous; facial crest in male very strongly swollen, rounded or very bluntly carinate; antennal flagellomere 1 1.0–2.5 × length of flagellomere 2; right mandible tridentate but incision between middle and apical teeth very shallow, or bidentate with only basal shoulder to apical tooth; left mandible tridentate with low middle tooth; wings hyaline, with dark marking only in *P.*

betulae subgroup; forewing with cell C glabrous; femora entirely pale. Ovipositor sheath and its appendage various in shape. Male genitalia (e.g., Figs 67g, h, 103g, h, 122g, h): proximal ventral arm of gonostipes normal; apiceps broad and flattened; valviceps in lateral view rather long, apex directed straight or below, ventral margin more or less concave, with conspicuous dorsoapical process.

Eleven known species, one represented by two subspecies, are classified into five subgroups (Shinohara 2002b). In the Russian Far East and Korea, six species of four subgroups have been found.

Twenty-four sequences of six species (four subgroups) were treated in the COI analysis and six sequences of two species (two subgroups) were treated in the NaK analysis. In the COI analysis (Fig. 142), the *P. brevicornis* and *P. gyllenhali* subgroups were each retrieved as monophyletic with 100% UFBoot support and they formed a clade with 99% UFBoot support. However, two other subgroups (*P. betulae* and *P. histrio* subgroups), though each recovered as monophyletic with 100% UFBoot support, did not form a monophyletic group with the *P. brevicornis* + *P. gyllenhali* subgroups. The sister group of the clade (*P. brevicornis* + *P. gyllenhali* subgroups) was the *P. inanitus* group with 91% UFBoot support and the *P. betulae* subgroup was retrieved as having the sister relationship with the clade ((*P. brevicornis* + *P. gyllenhali* subgroups) + *P. inanitus* group) but with low UFBoot value of 84%. The *P. histrio* subgroup was distant from the other three subgroups and had the sister relationship with the *P. lethierryi* subgroup of the *P. alternans* group with very low UFBoot support (63%). In the NaK analysis (Fig. 156), two species (belonging to the *P. brevicornis* and *P. gyllenhali* subgroups) were recovered as a clade with 100% UFBoot support. In conclusion, the monophyly and the sister relationships of the *P. brevicornis* and *P. gyllenhali* subgroups were strongly supported but the monophyly of the *P. histrio* group as a whole was not supported by the present analyses.

The known host plants of this species group are Salicaceae (*Salix* and *Populus*) and Betulaceae (*Betula*).

Pamphilius brevicornis brevicornis Hellén, 1948

(Fig. 66, ssp. *ibukii* Fig. 67) (https://doi.org/10.6084/m9.figshare.11405166)

Pamphilius histrio: Malaise, 1931: 63. Not Latreille, 1812.
Pamphilius histrio var. *brevicornis* Hellén, 1948: 40.
Pamphilius brevicornis: Kontuniemi, 1958: 94; Kontuniemi, 1965: 262; Beneš, 1972a: 47; Beneš 1974: 313; Achterberg & Aartsen, 1986: 38; Zhelochovtsev & Zinovjev, 1995: 397.
Pamphilius brevicornis brevicornis: Shinohara, 1995: 56; Shinohara, 2002b: 426; Shinohara & Lelej, 2007: 931, 940; Taeger *et al.*, 2010: 86; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 104; Lee *et al.*, 2019: 9.

See Shinohara (1995) for more references.

Material examined. Fifteen specimens, including 14 specimens from the Russian Far East and Korea (Shinohara 1995; present work). **New collection data: RUSSIA: Primorskij Kraj**: 2♀ (Fig. 66, DEI-GISHym 17524, 88122), Anisimovka 4 km W, 350m, 43.168°N 132.724°E, 19. VI. 2017, A. Taeger (SDEI). **SOUTH KOREA: Gangwon-do**: 2♀, Mirugam (Bukdaesa), 1,300 m, Odaesan Mts., 6. VI. 1996, A. Shinohara (NSMT).

Distribution. Northern Eurasia ranging from western and northern Europe to the Russian Far East (Kamchatka Kraj, Primorskij Kraj and Sakhalin) and South Korea (Shinohara 1995).

Host plant. Unknown, but probably *Betula* spp. [Betulaceae]. The Japanese subspecies, *Pamphilius brevicornis ibukii* Shinohara, 1995 (Fig. 67), is associated with *Betula ermanii*, *B. corylifolia* and *B. platyphylla* var. *japonica* (Shinohara & Kojima 2017).

Remarks. This is a widely spread Palaearctic species with two subspecies recognized by Shinohara (1995). The nominotypical subspecies originally described from Finland occurs in the Russian Far East and Korea. The maximum intrasubspecific *p*-distance within *P. brevicornis brevicornis* from Germany and Primorskij Kraj was 0.9% in COI (n=3) and the minimum distance to *P. brevicornis ibukii* from Japan is 1.9% in COI. This species (*P. brevicornis brevicornis* + *P. brevicornis ibukii*) was retrieved as sister to (*P. tricolor* + *P. gyllenhali*) in the COI tree with 99% UFBoot support (Fig. 142) and *P. brevicornis ibukii* was the sister of *P. tricolor* in the NaK tree with 100% UFBoot support (Fig. 156). This result agrees with the cladistic analysis based on morphology by Shinohara (1995), though *P. infuscatus* Middlekauff, 1964, *P. borisi* Beneš, 1974 and *P. virescens* Malaise, 1931, were not included in the molecular analysis. Shinohara (2002b) placed this species in his *P. brevicornis* subgroup of the *P. histrio* group. For another member of the *P. brevicornis* subgroup, *P. maximus* Shinohara, 1995, no molecular data were available.

Pamphilius histrio Latreille, 1812

(Figs 81, 82) (https://doi.org/10.6084/m9.figshare.16913065)

Pamphilius histrio Latreille, 1812: 689; Gussakovskij, 1935: 175, 375; Berland, 1947: 58; Beneš 1974: 313; Achterberg & Aartsen, 1986: 39; Shinohara, 1995: 48; Zhelochovtsev & Zinovjev, 1995: 397; Shinohara & Hara, 1997a: 193; Shinohara & Hara, 1999: 124; Shinohara, 2002b: 426; Shinohara, 2004: 263; Shinohara & Hara, 2005: 274; Taeger *et al.*, 2010: 87; Sundukov, 2017: 104; Lee *et al.*, 2019: 9; Shinohara, 2019: 9; Shinohara, 2020: 20, 249.

See Shinohara (1995) for more references.

Material examined. Forty-one specimens, including six specimens from Korea (Shinohara 1995).

Distribution. Europe, Kazakhstan, South Korea, Japan (Hokkaido).

Host plant. Salicaceae: *Populus tremula* (Stritt 1935), *Populus tremula* var. *davidiana* (Shinohara & Hara 1999, 2005) and ?*Populus nigra* (Midtgaard 1987).

Remarks. This species is widely spread in Eurasia but very rare in the Far East, known only from small series of specimens from Korea (Shinohara 1995) and Hokkaido, Japan (Shinohara & Hara 1997a, 1999, 2005). We have seen no specimens from the Russian Far East. This species is the sole representative of *P. histrio* subgroup of *P. histrio* group.

In our molecular analysis using COI (Fig. 142), the specimens of *P. histrio* formed a clade but it was rather distantly located from the clades represented by five other species of the *P. histrio* group (*P. brevicornis*, *P. gyllenhali*, *P. tricolor, P. betulae* and *P. festivus*). In the NaK analysis, *P. histrio* was not treated. The COI result was in line with the cladistic analysis based on morphology (Shinohara 1995), where *P. histrio* was situated remotely from the clade including the three species given above. The monophyly of the *P. histrio* group as a whole was not supported by our molecular study as noted in the remarks for the species group.

Pamphilius maximus Shinohara, 1995

(Figs 102, 103) (https://doi.org/10.6084/m9.figshare.11405256)

Pamphilius maximus Shinohara, 1995: 59; Shinohara, 2002b: 426; Shinohara, 2004: 263; Shinohara & Lelej, 2007: 935; Sundukov, 2009: 213; Taeger *et al.*, 2010: 88; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105; Lee *et al.*, 2019: 10.

Material examined. Thirteen specimens, including the type series, all from the Russian Far East and Korea (Shinohara 1995; present work). **New collection data: SOUTH KOREA: Gangwon-do**: 1♂, Mirugam (Bukdaesa), 1300m, Odaesan Mts., 29. V. 1998, A. Shinohara (NSMT); 11♂ (Fig. 103), same locality, 31. V. –4. VI. 2002, A. Shinohara (NSMT).

Distribution. Russia (Primorskij Kraj), South Korea (Shinohara 1995).

Host plant. Unknown.

Remarks. This is a large and light-colored species, so far known only from Primorskij Kraj and Korea. No molecular data are available. Shinohara (2002b) placed it in his *P. brevicornis* subgroup of *P. histrio* group.

Lee *et al.* (2019) gave *Populus* sp. as a host of this species without showing source of information. This record may have been based on Shinohara's (1995) statement, "the holotype female was found crawling on a leaf of *Populus* sp. (probably *P. davidiana*), which may be the host plant." Obviously, this statement was not a host record and the host is still unknown.

Pamphilius pictifrons Gussakovskij, 1935

(Fig. 110) (https://doi.org/10.6084/m9.figshare.11405271)

Pamphilius pictifrons Gussakovskij, 1935: 176, 379; Beneš, 1974: 299, 313; Shinohara, 1995: 49; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2002b: 426; Shinohara, 2004: 263; Shinohara & Lelej, 2007: 937; Taeger *et al.,* 2010: 90; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105.

See Shinohara (1995) for more references.

Material examined. Two specimens, including the holotype, from the Russian Far East (Shinohara 1995).

Distribution. Russia (Yakutia, Magadan Oblast) (Shinohara 1995).

Host plant. Unknown.

Remarks. Only two female specimens have been recorded for this species and the male is still unknown (Shinohara 1995). No molecular data are available. Shinohara (2002b) placed this species in his *P. pictifrons* subgroup in the *P. histrio* group. Sundukov (2017) noted "Host plant: ?*Rosa* spp. (Rosaceae)" but this host record, which is probably based on Verzhutskij (1981), is doubtful as discussed by Shinohara (1995).

Pamphilius tricolor Beneš, 1974

(Figs 121, 122) (https://doi.org/10.6084/m9.figshare.11405304)

Pamphilius tricolor Beneš, 1974: 301, 313; Shinohara, 1995: 50; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara & Zinovjev, 1996: 110; Shinohara, 2002b: 426; Shinohara, 2004: 263; Shinohara & Taeger, 2007: 38; Shinohara & Lelej, 2007: 936, 942; Shinohara & Hara, 2009: 295; Sundukov, 2009: 213; Taeger *et al.*, 2010: 91; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105; Lee *et al.*, 2019: 11; Shinohara, 2019: 12; Shinohara, 2020: 20, 250.

See Shinohara (1995) for more references.

Material examined. About 150 specimens, including the holotype. Ninety-six specimens are from the Russian Far East and Korea (Shinohara 1995; Shinohara & Zinovjev 1996; Shinohara & Taeger 2007; present work). **New collection data: SOUTH KOREA: Gangwon-do**: 1♀, Mirugam (Bukdaesa), 1300m, Odaesan Mts., 29. V.–1. VI. 1996, J.-W. Kim (NSMT).

Distribution. Russia (Urals, eastern Siberia, Sakha Republic, Kamchatka Kraj, Magadanskaya Oblast, Khabarovskij Kraj, Primorskij Kraj), South Korea, Japan (Hokkaido, Honshu) (Shinohara & Taeger 2007).

Host plant. Salicaceae: *Salix caprea* L. (Shinohara & Hara 2009).

Remarks. *Pamphilius tricolor* belongs to the *P. gyllenhali* subgroup of the *P. histrio* group (Shinohara 2002b) and is most closely related to the European *P. gyllenhali* (Dahlbom, 1835). These two allopatric species are similar morphologically, though distinguishable from each other, and share the same host plant and larval habits (Shinohara 1995; Shinohara & Hara 2009). The available COI data for the two species were retrieved as monophyletic with 100% UFBoot support, but the two species were not clearly differentiated within the clade (Fig. 142).

Pamphilius virescens Malaise, 1931

(Figs 130, 131) (https://doi.org/10.6084/m9.figshare.11405328)

Pamphilius virescens Malaise, 1931: 62; Gussakovskij, 1935: 174, 375; Verzhutskij, 1966: 27; Beneš, 1974: 303, 311; Shinohara, 1995: 55; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2002b: 426; Shinohara, 2004: 263; Shinohara & Lelej, 2007: 936, 942; Taeger *et al.*, 2010: 91; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 106; Lee *et al.*, 2019: 11; Shinohara, 2019: 12; Shinohara, 2020: 20, 249.

See Shinohara (1995) for more references.

Lectotype designation. Malaise (1931) described this species based on "2♂♂ und 2♀♀ aus Klutchi, Kamtchatka" but did not designate a holotype. We hereby designate the female labeled "Typus" in Malaise's collection (NHRS), as lectotype. It is labeled "Kamtschatka, Malaise" "Typus" "Pamphilius virescens Mal. Type Malaise det." "818". It was treated as the holotype by Beneš (1974) and Shinohara (1995) and fully redescribed by Beneš (1974).

Material examined. Thirteen specimens, including the lectotype, of which 12 are from the Russian Far East and South Korea (Shinohara 1995; present work). **New collection data: SOUTH KOREA: Gangwon-do**: 1♀, Mirugam (Bukdaesa), 1300m, Odaesan Mts., 1. VI. 2002, A. Shinohara (NSMT).

Distribution. Russia (Kamchatka Kraj, Irkutsk Oblast). South Korea. Japan (Hokkaido).

Host plant. Unknown.

Remarks. This species is known from a small number of specimens (Shinohara 1995) and no molecular data are available. It belongs to the *P. gyllenhali* subgroup of the *P. histrio* group (Shinohara 2002b). Lee *et al.* (2019)

gave *Salix* sp. as a host of this species without showing the source of information. Verzhutskij (1966) speculated that the host of *P. virescens* was *Salix*. As discussed by Shinohara (1995), this host record may be correct, but no decisive evidence is available.

Pamphilius inanitus group

The members of this species group are characterized as follows: upper part of head glabrous; facial crest in male very strongly swollen, very bluntly carinate; antennal flagellomere 1 0.9–1.4 × length of flagellomere 2; right mandible tridentate but incision between middle and apical teeth very shallow or bidentate with only basal shoulder to apical tooth; left mandible tridentate with low middle tooth; wings hyaline; forewing with cell C pilose; femora entirely pale. Ovipositor sheath appendage very small, pilose. Male genitalia (Fig. 80f, g): proximal ventral arm of gonostipes normal; apiceps short and narrow; valviceps in lateral view rather short, apex directed above, ventral margin more or less rounded, without conspicuous dorsoapical process.

Only two closely related species are known from the Palaearctic region (Shinohara 2002b), of which one, *P. hilaris*, occurs in the Russian Far East and Korea.

Six sequences of two species were treated in the COI analysis and one specimen of one species in the NaK analysis. In the COI analysis (Fig. 143), the *P. inanitus* group was retrieved as monophyletic with 100% UFBoot support and had a sister relationship (with 91% UFBoot support) with the clade composed of the *P. brevicornis* and *P. gyllenhali* subgroups of the *P. histrio* group. This clade (*P. inanitus* group + *P. brevicornis* and *P. gyllenhali* subgroups of *P. histrio* group) was the sister group of the *P. betulae* subgroup of the *P. histrio* group but with low UFBoot value of 84%. In other words, the *P. inanitus* group was placed within the *P. histrio* group. In the NaK analysis (Fig. 157), the *P. inanitus* group was recovered as the sister of the clade represented by the *P. histrio* and *P. sulphureipes* groups with 100% UFBoot support. The affinity of the *P. inanitus* group is still uncertain, but it appears closer to the *P. histrio* and *P. sulphureipes* groups, rather than to the *P. sylvaticus* group as suggested by Shinohara (2002b).

The larvae of this species group feed on Rosaceae (*Rosa*).

Pamphilius hilaris (Eversmann, 1847)

(Figs 79, 80) (https://doi.org/10.6084/m9.figshare.11405190)

Lyda hilaris Eversmann, 1847: 61.

Pamphilius hilaris: Gussakovskij, 1935: 170, 378; Shinohara, 1971: 25 ["*hiralis*"]; Beneš, 1974: 308, 313; Shinohara & Okutani, 1983: 277; Zhelochovtsev & Zinovjev, 1995: 397; Shinohara, 2002a: 189; Shinohara, 2002b: 431; Shinohara, 2004: 265; Shinohara & Taeger, 2007: 35; Shinohara & Lelej, 2007: 930, 940; Taeger *et al.,* 2010: 87; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 104; Shinohara, 2019: 9; Shinohara, 2020: 12, 243; Shinohara, 2021: 123.

Lectotype designation. Gussakovskij (1935) examined only one specimen in Eversmann's material ("Mir liegt nur das typische Stück von Eversmann vor") and Beneš (1972) treated it as the holotype. However, Eversmann's (1847) type material should be a syntype, because he did not mention the number of specimens he had for description. We hereby designate the specimen in ZISP as the lectotype. The head of the lectotype is missing. The abdominal segments 1–5 are yellow (Eversmann started counting the abdominal segments with 2, accordingly he wrote "segmentis 2–6 fulvis" in the original description). The lectotype is labelled as follows: "Spask Jun", "hilaris.", "Pamphilius hilaris Ev ♀ Gussakovskij det.", "село Спасское Оренбургской губ." (= village Spasskoe, oblast Orenburg, 52.017°N 56.567°E), "Lyda hilaris Ev. к. Эверсмана", golden circle, "Syntype Lyda hilaris Eversmann 1847 vide A. Taeger 2014", "DEI-GISHym 30352" (see https://doi.org/10.6084/m9.figshare.11405190).

Material examined. About 210 specimens, including the lectotype. Ten specimens are known from the Russian Far East and Korea (Shinohara & Taeger 2007; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (Fig. 79, DEI-GISHym 88046), Anisimovka 7 km S, Mt. Litovka, 1200m, 43.102°N 132.786°E, 19. VI. 2017, V. Loktionov (SDEI). **SOUTH KOREA: Gangwon-do**: 2♂, Mirugam (Bukdaesa), 1300m, Odaesan Mts., 31. V. 1992, A. Shinohara (Fig. 80, NSMT); 1♂, same locality, 29. V. 1993, A. Shinohara (NSMT); 1♂, same locality, 31. V. 1993, A. Shinohara (NSMT); 1♀ (NSMT 30860), same locality, 28. V. 2009, A. Shinohara (NSMT).

Distribution. Russia (Orenburg Oblast, Tomsk Oblast, Yakutia, Kamchatka Kraj, Khabarovskij Kraj, Primorskij Kraj, Sakhalin), China (Shaanxi), Japan (Honshu) (Shinohara & Lee 2010). South Korea (new record).

Host plant. Rosaceae: *Rosa multiflora* Thunb. (Shinohara 1971, 2021).

Remarks. This species belongs to the *P. inanitus* group (Shinohara 2002b) and is similar to the European *P. inanitus* both in morphology and life history, including the rose-feeding larva making a specialized leaf roll (Lorenz & Kraus 1957; Shinohara 1971, 2021). The female of the two species may be separated by the color pattern of the dorsal and lateral part of the head, which is mostly black in *P. inanitus* and mostly orange in *P. hilaris*. The previously undescribed male of *P. hilaris* is distinguished from the other East Asian congeners by the characters given in the key, whereas it is not separable for the moment from that of *P. inanitus*. Our molecular analysis, however, showed that the four European specimens of *P. inanitus* differed from the two Russian and Korean specimens of *P. hilaris* by a minimum of 4.2% in the COI sequences (Fig. 143), which was large enough for us to regard the two sets of specimens as belonging to different species.

The four male specimens from Korea listed above represent the first record of this species from the country.

Pamphilius latifrons group

The member of this species group is characterized as follows: upper part of head pilose; facial crest in male rather strongly swollen, bluntly carinate; antennal flagellomere 1 1.7–2.2 × length of flagellomere 2; right mandible bidentate with only basal shoulder to apical tooth; left mandible tridentate, but middle tooth low; wings hyaline; forewing with cell C glabrous; femora entirely pale. Ovipositor sheath appendage small, inconspicuous. Male genitalia (Fig. 93g): proximal ventral arm of gonostipes normal; apiceps very broad; valviceps rather long, bent outwardly and directed below, without conspicuous dorsoapical process.

Only one Palaearctic species is known (Shinohara 2002b), which occurs in the Russian Far East. It was formerly regarded as an isolated member of the *P. vafer* group (Beneš 1976) or the *P. histrio* group (Achterberg & Aartsen 1986). No molecular data are available. The larvae feed on Salicaceae (*Populus, Salix*).

Pamphilius latifrons (Fallén, 1808)

(Figs 92, 93) (https://doi.org/10.6084/m9.figshare.16923082)

Lyda latifrons Fallén, 1808: 226; Shinohara *et al.*, 2003: 34; Opinion, ICZN, 2005: 49.
Lyda maculosa Zaddach, 1866: 166.
Pamphilius latifrons: Kirby, 1882: 338; Konow, 1897a: 26, 32; Gussakovskij, 1935: 174, 375; Verzhutskij, 1966: 27; Beneš, 1976: 162; Achterberg & Aartsen, 1986: 40; Zhelochovtsev & Zinovjev, 1995: 397; Taeger *et al.*, 1998: 105; Shinohara *et al.*, 2003: 34; Shinohara, 2004: 265; Shinohara & Taeger, 2007: 35; Shinohara & Lelej, 2007: 939, 940; Taeger *et al.*, 2010: 88; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 104.
Pamphilius maculosus: Shinohara, 2002b: 429; Shinohara *et al.*, 2003: 34 (syn. of *latifrons*).

Material examined. Eight specimens, including one from the Russian Far East (Shinohara & Taeger 2007).

Distribution. Europe, Kazakhstan, East Siberia, Primorskij Kraj (Shinohara & Taeger 2007).

Host plant. Salicaceae: *Populus tremula*, *Salix caprea* (Taeger *et al.* 1998).

Remarks. This is a rare species, with only one collection record from the Russian Far East (Primorskij Kraj) (Shinohara & Taeger 2007). Shinohara (2002b) placed this species in his *P. maculosus* [=*latifrons*] group emphasizing its isolated position in the genus. No molecular data for this species are available.

Pamphilius sulphureipes group

The members of this species group are characterized as follows: upper part of head glabrous; facial crest in male very strongly swollen, bluntly carinate; antennal flagellomere 2 1.8–2.9 × length of flagellomere 1; right mandible tridentate but incision between middle and apical teeth shallow or bidentate with only basal shoulder to apical tooth; left mandible tridentate with low middle tooth; wings hyaline; forewing with cell C glabrous or pilose; femora en-

tirely pale. Subgenital plate in male without large setose appendage. Ovipositor sheath appendage slender subconical, pilose. Male genitalia (Figs. 70h, 120g, 136g, h): proximal ventral arm of gonostipes normal; apiceps narrow or broad; valviceps in lateral view rather short, apex directed upwards, ventral margin more or less rounded, without conspicuous dorsoapical process.

Five East Asian species, two represented by two subspecies, are included (Shinohara 2002b). Three species have been recorded in the Russian Far East and Korea.

Twenty sequences of four species were treated in the COI analysis and nine sequences of three species in the NaK analysis. In both analyses (Figs 144, 158), the *P. sulphureipes* group was retrieved as monophyletic with 100% UFBoot value. In both trees, the relationship ((*P. coreanus* + *P. sulphureipes*) + *P. zhelochovtsevi*) was supported by 99 or 100% UFBoot value on each node, and in the COI analysis, an additional species, *P. ishikawai* Shinohara, 1979*,* from Japan, was recovered as sister to the clade of the three species, again with 100% UFBoot support.

A host plant is known only for *P. ishikawai*, whose larvae are solitary leaf-rollers on Saxifragaceae (*Astilbe*) (Shinohara *et al.* 2016a). The other four members of this species group may also be associated with the plants of Saxifragaceae.

Pamphilius coreanus Takeuchi, 1938

(Figs 69, 70) (https://doi.org/10.6084/m9.figshare.11405181)

Pamphilius (*Anoplolyda*) *coreanus* Takeuchi, 1938: 225; Kim, 1970: 125.
Anoplolyda frontimacula Malaise, 1943: 126; Shinohara, 1981: 173 (syn. of *coreanus*).
Pamphilius frontimaculus: Shinohara, 1979: 152.
Pamphilius coreanus: Kim, 1963: 278; Shinohara, 1979: 155; Shinohara, 1993: 116; Kim *et al.*, 1994: 218; Zhelochovtsev & Zinovjev, 1995: 397; Shinohara & Lee, 1997: 215; Shinohara, 2002b: 425; Shinohara, 2004: 263; Shinohara & Lelej, 2007: 934, 941; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 86; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 104; Lee *et al.*, 2019: 9; Shinohara & Tripotin, 2021a: 61.

For more references, see Shinohara (1981).

Material examined. About 210 specimens, including the holotype, all from the Russian Far East and Korea (Takeuchi 1938; Malaise 1943; Shinohara 1979, 1993; Shinohara & Lee 1997; Shinohara & Tripotin 2021a; present work). **New collection data: RUSSIA**: **Primorskij Kraj**: 1♀, (Fig. 69, DEI-GISHym 86267), Arsenyev, Ski-Base Bodrost, 200m, 44.122°N 133.270°E, 25. V. 2016, K. Kramp, M. Prous & A. Taeger, RU017 (SDEI); 1♀, Arsenyev, Ski-Base Bodrost, 200m, 44.122°N 133.270°E, 26. V. 2016, K. Kramp, M. Prous & A. Taeger, RU018 (SDEI). **SOUTH KOREA**: **Gangwon-do**: 6♂, Mirugam (Bukdaesa), 1300m, Odaesan Mts., 29. V.–1. VI. 1996, A. Shinohara (NSMT); 1♀1♂, same locality, 6. VI. 1996, J.-W. Kim (NSMT); 4♂, same locality, 6–7. VI. 1997, A. Shinohara (NSMT); 4♂, same locality, 27–28. V. 1998, A. Shinohara (NSMT); 1♀, same locality, 31. V. 1998, H.-S. Lee (NSMT); 2♀29♂, same locality, 24. V.–3. VI. 2002, A. Shinohara (NSMT); 1♂ (NSMT 30753), same locality, 1. VI. 2008, A. Shinohara (NSMT); 2♂ (NSMT 30857, 30863), same locality, 31. V.–1. VI. 2009, A. Shinohara (NSMT); 1♀, Chuncheon, 23. V. 2002, H.-J. Kim (NSMT). **Jeollanam-do**: Mt. Nogodan, 1200m, Jirisan Mts., 26–28. V. 1997, A. Shinohara (NSMT).

Distribution. Russia (Khabarovskij Kraj, Primorskij Kraj), North and South Korea (Shinohara 1993).

Host plant. Unknown.

Remarks. This is a member of the *P. sulphureipes* group and most closely related to *P. sulphureipes*, as discussed above. The maximum intraspecific *p*-distance within *P. coreanus* from Primorskij Kraj and Korea was 0.2% in COI (n=4) and 0.4% in NaK (n=4) and the nearest neighbour was *P. sulphureipes sulphureipes*, diverging by a minimum of 3.0% in COI analysis and by a minimum of 0.9% in NaK analysis.

Pamphilius sulphureipes sulphureipes Kirby, 1882

(Figs 119, 120) (https://doi.org/10.6084/m9.figshare.11405298)

Pamphilius sulphureipes Kirby, 1882: 343; Gussakovskij, 1935: 178, 376; Beneš, 1974: 309, 313; Shinohara, 1979: 152; Kim *et al.*, 1994: 217; Zhelochovtsev & Zinovjev, 1995: 398; Paek *et al.*, 2010: 161.

P*amphilius viriditibialis* var. *aino* Takeuchi, 1936a: 62; Takeuchi, 1936b: 164 (syn. of *sulphureipes*).
Pamphilius sulphureipes sulphureipes: Shinohara, 1993: 113; Shinohara, 2002b: 425; Shinohara & Lelej, 2007: 934, 941; Taeger *et al.*, 2010: 90; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105; Lee *et al.*, 2019: 11.

See Shinohara (1979) for more synonyms and references.

Material examined. Sixty-three specimens, including the holotype, all from the Russian Far East and Korea (Beneš 1974; Shinohara 1979, 1993; present work). **New collection data: RUSSIA**: **Primorskij Kraj**: 1♀, Ussurijskij Reserve, 9–12. VI. 1995, A. Shinohara (NSMT). **SOUTH KOREA: Gangwon-do:** 3♂, Mirugam (Bukdaesa), 1300m, Odaesan Mts., 4–6. VI. 1996, A. Shinohara (NSMT); 12♂ (incl. NSMT 30606), same locality, 29. V.–4. VI. 2002, A. Shinohara (NSMT); 3♂ (NSMT 30751–3), same locality, 1. VI. 2008, A. Shinohara (NSMT); 6♂ (incl. NSMT 30859), same locality, 28. V.–5. VI. 2009, A. Shinohara (NSMT); 1♂, same locality, 11. VI. 2010, A. Shinohara (NSMT).

Distribution. Russia ("Amour, Siberia", Primorskij Kraj, Sakhalin), North and South Korea.

Host plant. Unknown.

Remarks. This is a member of the *P. sulphureipes* group (Shinohara, 1993). The maximum intraspecific *p*-distance within *P. sulphureipes sulphureipes* from Korea was 0.2% in COI (n=5) and 0.4% in NaK (n=4) and the nearest neighbour was *P. coreanus*, diverging by a minimum of 3.0% in the COI analysis and by a minimum of 0.9% in the NaK analysis.

Without giving the source of information, Sundukov & Lelej (2012) simply noted "larvae on *Rosa* (Rosaceae)" under the present subspecies. Most probably this is a lapsus. The closely related *P. ishikawai* from Japan is associated with *Astilbe* spp. (Saxifragaceae) (Shinohara *et al.* 2016a) and these are more likely host plants of *P. sulphureipes sulphureipes*.

Pamphilius zhelochovtsevi zhelochovtsevi Beneš, 1974

(Figs 135, 136) (https://doi.org/10.6084/m9.figshare.11405343)

Pamphilius zhelochovtsevi Beneš, 1974: 306, 313; Zhelochovtsev & Zinovjev, 1995: 398.
Pamphilius zhelochovtsevi zhelochovtsevi: Shinohara, 1993: 118; Shinohara & Lee, 1997: 218; Shinohara, 2002b: 425; Shinohara & Lelej, 2007: 935, 941; Taeger *et al.*, 2010: 91; Sundukov & Lelej, 2012: 110; Sundukov, 2017: 106; Lee *et al.*, 2019: 11.

Material examined. Thirty-one specimens, including the type series, all from the Russian Far East and Korea (Beneš 1974; Shinohara 1993; Shinohara & Lee 1997).

Distribution. Russia (Primorskij Kraj), South Korea.

Host plant. Unknown.

Remarks. This species was described from Primorskij Kraj by Beneš (1974) and later recorded from Korea by Shinohara (1993), who also described a Japanese subspecies, *P. zhelochovtsevi nipponicus* Shinohara, 1993, from Honshu. Sundukov (2015) newly recorded *P. zhelochovtsevi nipponicus* from Kunashiri and Shikotan Islands and noted "Larvae on *Rosa* (Shinohara 1993)" (original in Russian). *Pamphilius zhelochovtsevi nipponicus* has been recorded only from Honshu, not in Hokkaido, and the nominotypical subspecies is distributed in Primorskij Kraj and Korea (Shinohara 1993). The occurrence of this species (and subspecies) in southern Kuriles is not likely and needs confirmation. Sundukov's (2015) host record is inexplicable and erroneous because Shinohara (1993) never mentioned the host plant of *P. zhelochovtsevi nipponicus*, which is still unknown.

Molecular data were available only for Japanese specimens of *P. zhelochovtsevi nipponicus* (two COI sequences and one NaK sequence). In the COI analysis, the nearest neighbour was *P. sulphureipes sulphureipes*, diverging by a minimum of 3.4%, while in the NaK analysis, the nearest neighbour was *P. coreanus*, with the minimum distance of 1.5%. *Pamphilius zhelochovtsevi* is a member of the *P. sulphureipes* group (Shinohara 1993), which was retrieved as monophyletic with 100% UFBoot supports in our COI and NaK analyses (Figs 144, 158).

Pamphilius sylvaticus group

The members of this species group are characterized as follows: upper part of head pilose or glabrous; facial crest in male moderately to very strongly swollen, sharply carinate; antennal flagellomere 1 1.0–1.4 × length of flagellomere 2; right mandible bidentate with only basal shoulder to apical tooth; left mandible tridentate, but middle tooth low; wings hyaline; forewing with cell C glabrous or pilose; femora entirely pale or marked with black. Ovipositor sheath appendage usually large, pilose. Male genitalia (e.g., Figs 53g, h, 65g, h, 76g, h): proximal ventral arm of gonostipes normal; harpe large, outer basal part with long hairs; apiceps narrow, hooked at apex; valviceps in lateral view rather short, apex directed above, ventral margin more or less rounded, without conspicuous dorsoapical process, in dorsal view tapered toward pointed apex.

This species group contains 22 species, one with two subspecies, in the Holarctic region (Shinohara 2002b; present work). Eleven species are known to occur in the Russian Far East and Korea. Verzhutskij (1966) recorded *Pamphilius sylvaticus* (Linné, 1758) from the Baikal region based only on larvae. This may need confirmation. Popov (2015) also recorded *P. sylvaticus* from Yakutia.

A total of 86 sequences of 14 species were treated in the COI analysis and 43 sequences of nine species in the NaK analysis. In the COI analysis (Figs 15, 145–147), the *P. sylvaticus* group, except for *P. japonicus* and *P. ocreatus*, was recovered as monophyletic with UFBoot support of 95%. *Pamphilius japonicus* (six sequences available) was retrieved as forming the sister group of a large branch containing all *Pamphilius* (except for the *P. sylvaticus* group) and *Onycholyda*. While *P. japonicus* was placed in the *P. sylvaticus* group (Shinohara 1985a), it is a rather isolated species with an unusual host association with *Cornus* (Cornaceae) (Shinohara *et al.* 2019). *Pamphilius ocreatus* is a little-known Nearctic species and was recovered as the sister of the *P. basilaris* group with low UFBoot support of 75%, not close to the other species of the *P. sylvaticus* group. The systematic position of *P. japonicus* and *P. ocreatus* should be further investigated with more material. In the NaK analysis (Figs 16, 159), for which specimens of *P. ocreatus* were not available, the *P. sylvaticus* group, including *P. japonicus*, was retrieved as monophyletic with 100% UFBoot support.

The known host plants of the species of the *P. sylvaticus* group are Rosaceae (*Cerasus*, *Sorbus*, *Fragaria*, etc.), Betulaceae (*Alnus*, *Carpinus* and *Corylus*) and Cornaceae (*Cornus*).

Pamphilius alnicola Ermolenko, 1973

(Figs 52, 53) (https://doi.org/10.6084/m9.figshare.11405109)

Pamphilius alnicola Ermolenko, 1973: 24; Beneš, 1977: 263; Shinohara, 1985a: 327; Shinohara, 1988a: 318; Shinohara & Hara, 1993: 546; Shinohara & Hara, 2005: 274; Zhelochovtsev & Zinovjev, 1995: 397; Shinohara, 2001: 113, 115; Shinohara, 2002a: 189; Shinohara, 2002b: 429; Shinohara, 2004: 265; Shinohara & Hara, 2005: 274; Shinohara & Lelej, 2007: 931, 940; Taeger *et al.*, 2010: 86; Sundukov & Lelej, 2012: 108; Sundukov, 2017: 104; Shinohara, 2019: 8; Shinohara, 2020: 14, 244.

"*P*. sp. n.": Beneš, 1974: 313.

Material examined. About 85 specimens, including one specimen from the Russian Far East (Shinohara 1988a).

Distribution. Russia (Primorskij Kraj), Japan (Hokkaido, Shikotan Is., Honshu) (Shinohara 1988a).

Host plant. Betulaceae: *Alnus hirsuta* (Spach) Turcz. ex Rupr. (Shinohara & Hara 1993, 2005).

Remarks. Shinohara (1988a) gave a collection record of one female specimen from Primorskij Kraj (Tedjuche = Dal'negorsk district) and no additional specimens have been available from the continent. The species is uncommon throughout its distribution range. The larvae are gregarious leaf rollers on *Alnus* (Shinohara & Hara 1993).

This is a member of the *P. sylvaticus* group (Shinohara 1985a, 1988a, 2001, 2002b). The maximum intraspecific *p*-distance within *P. alnicola* is 0.5% in COI (n=2) and 0.1% in NaK (n=2). *Pamphilius alnicola* was retrieved as the sister of *P. montanus* Shinohara, 1985, with UFBoot support of 82% in the COI tree (Fig. 145), whereas it was retrieved as the sister of the clade consisting of *P. benesi* Shinohara, 1985, *P. pallidus* Shinohara, 1988, *P. volatilis* (Smith, 1874), *P. gracilis* Shinohara, 1985, *P. graciloides* **sp. nov.** and *P. montanus* with UFBoot support of 99% in the NaK tree (Fig. 159). In the distance data, the nearest neighbour of *P. alnicola* was *P. volatilis*, diverging by a minimum of 4.9% in the COI analysis and *P. montanus* and *P. volatilis* by a minimum of 0.6% in the NaK analysis.

Pamphilius benesi Shinohara, 1985

(Figs 64, 65) (https://doi.org/10.6084/m9.figshare.11405151)

Pamphilius benesi Shinohara, 1985a: 327; Shinohara, 1988a: 319; Shinohara & Hara, 1997b: 851; Shinohara, 2001: 108, 113, 116; Shinohara, 2002a: 189; Shinohara, 2002b: 429; Shinohara, 2004: 265; Shinohara & Hara, 2005: 274; Taeger *et al.*, 2010: 86; Shinohara, 2013: 94; Lee *et al.*, 2019: 9; Shinohara, 2019: 9; Shinohara, 2020: 14, 245.

Material examined. About 340 specimens, including the type series. Seventy-two specimens are from South Korea (Shinohara 2001).

Distribution. South Korea, Japan (Hokkaido, Honshu, Shikoku, Kyushu) (Shinohara 2001).

Host plant. Betulaceae: *Corylus sieboldiana* Blume var. *sieboldiana* (Shinohara & Hara 1997b, 2005).

Remarks. This species belongs to the *P. sylvaticus* group (Shinohara 1985a, 1988a, 2001, 2002b). From Korea, only a series of male specimens collected in 1992 and 1993 have been recorded (Shinohara 2001) and no material for molecular studies was available. The larvae are gregarious leaf rollers on *Corylus*.

The maximum intraspecific *p*-distance within *P. benesi* from Japan was 2.2% in COI (n=7) and 0.6% in NaK (n=7) and the nearest neighbour was *P. pallidus*, diverging by a minimum of 2.9% in the COI analysis, and by a minimum of 0.5% in the NaK analysis. In both COI and NaK trees (Figs 145, 159), *P. benesi* was the sister of *P. pallidus* with 100% UFBoot support.

Pamphilius convexus Shinohara, 1988

(Fig. 68) (https://doi.org/10.6084/m9.figshare.16934371)

Pamphilius convexus Shinohara, 1988a: 316; Zhelochovtsev & Zinovjev, 1995: 397; Shinohara & Lee, 1997: 218; Shinohara, 2001: 114; Shinohara, 2002b: 430; Shinohara, 2004: 265; Shinohara & Lelej, 2007: 933; Taeger *et al.*, 2010: 87; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 104; Lee *et al.*, 2019: 9.

Material examined. Five specimens, including the type series, all from the Russian Far East and South Korea (Shinohara 1988a; Shinohara & Lee 1997).

Distribution. Russia (Khabarovskij Kraj, Primorskij Kraj), South Korea (Shinohara & Lee 1997).

Host plant. Unknown.

Remarks. This species is known only from five specimens collected in the Russian Far East and South Korea (Shinohara & Lee 1997). Shinohara (1988a, 2002b) placed it in the *P. sylvaticus* group. No molecular data have been available for analysis.

Pamphilius daisenus Takeuchi, 1938

(Figs 73, 74) (https://doi.org/10.6084/m9.figshare.11405172)

Pamphilius daisenus Takeuchi, 1938: 221; Shinohara, 1985a: 332; Shinohara, 1988a: 319; Shinohara, 2001: 109, 114, 115; Shinohara, 2002b: 430; Shinohara, 2004: 265; Taeger *et al.*, 2010: 86; Shinohara *et al.*, 2016b: 123; Lee *et al.*, 2019: 9; Shinohara, 2019: 9; Shinohara, 2020: 16, 246; Shinohara & Tripotin 2021b: 197.

Material examined. Twenty-one specimens, including the holotype. Two specimens are from South Korea (Shinohara 2001; Shinohara & Tripotin 2021b).

Distribution. South Korea, Japan (Honshu) (Shinohara 2001).

Host plant. Rosaceae: *Aruncus dioicus* (Walter) Fernald var. *kamtschaticus* (Maxim.) H. Hara, *Spiraea japonica* L.f. (Shinohara *et al.* 2016b).

Remarks. This species was described from Honshu, Japan (Takeuchi 1938) and later recorded from Korea (Shinohara 2001; Shinohara & Tripotin 2021b). The larvae are oligophagous solitary leaf-rollers on *Aruncus* and *Spiraea* (Rosaceae) in Japan (Shinohara *et al.* 2016b). Molecular data are not available from the Korean specimens, but the eight COI sequences from the Japanese material formed a clade which was sister to *P. gracilis* + *P. graciloides* with 98 % UFBoot support (Fig. 145), diverging by a minimum of 4.9 % from both species.

***Pamphilius graciloides* sp. nov.**
(Figs 75, 76) (https://doi.org/10.6084/m9.figshare.11405232)

Pamphilius gracilis: Shinohara, 2001: 110, 114, 115; Shinohara, 2002b: 430; Shinohara, 2004: 265; Taeger *et al.*, 2010: 86; Lee *et al.*, 2019: 9. Not Shinohara, 1985a, in part.

Description. Female (Fig. 75). Length about 11.5 mm. Head black, with following pale yellow: linear mark along median anterior margin of clypeus, paired spots on frons, spot on upper margin of inner orbit, spot on posterior margin of postocular area, elongate spot on gena along lower outer orbit; mandible black, with outer basal part and subapical part pale yellow and apex dark rufous; antenna black. Thorax black, with following pale yellow: large spot on ventral margin of lateral pronotum, posterolateral corner of dorsal pronotum, tegula, posterior half of mesoscutal middle lobe, mesoscutellum, minute spot on anterodorsal corner of mesepisternum, metascutellum; legs pale yellow, with fore coxa (except for narrow apical margin), fore trochanter and basal half of fore femur (except for anterior surface of trochantellus), mid coxa (except for apical margin) and hind coxa (except for broad apical part) black. Wings hyaline, slightly tinted with blackish brown; veins and stigma black. Abdomen black, with outer margin of each laterotergite and posterior margin of each sternum (more broadly on sterna 4–7) pale yellow.

Frons rather strongly swollen; ocellar basin subtriangular, represented as broad furrow around median ocellus; upper frons not distinctly notched medially; frontoclypeal crest rather flat, rounded, swollen between antennal sockets; facial crest strongly convex, rounded. Upper part of head behind transverse and lateral transverse sutures smooth, weakly coriaceous, with sparse and small punctures; frons, area from facial crest to lateral transverse suture, and paraantennal field shallowly coarsely rugose; clypeus with distinct medium-sized punctures, with interspaces coriaceous medially and coarsely rugose laterally; gena coriaceous, with rather small, often ill-defined punctures; head covered with rather short silvery hairs before crassa. Antennae with 23 antennomeres; flagellomere 1 1.1 × length of flagellomere 2. Forewing with cell C pilose all over. Ovipositor sheath as in Fig. 75c; appendage large and elongate, setose apically.

Male (Fig. 76). Length about 8–10 mm. Head black; pale yellow are frontal surface before line connecting facial crests, minute spot at upper margin of inner orbit (sometimes missing) and most of gena and malar space (median part of malar space always black); mandible pale yellow, inner half usually black and apex dark rufous; scape pale yellow, with large black spot above; pedicel and flagellum blackish brown. Thorax black, with following pale yellow: large spot on ventral margin of lateral pronotum (sometimes small), posterolateral corner of dorsal pronotum (often narrowly), tegula, posterior half of mesoscutal middle lobe, mesoscutellum, broad anterior margin and large posterolateral spot on mesepisternum (often reduced or missing), metascutellum, and large spot on metepisternum; legs pale yellow, with most of coxae black; fore femur often obscurely marked with black posteriorly. Wings hyaline, slightly stained with blackish brown; veins and stigma black. Abdomen black, with most of laterotergites, broad posterior margin of each sternum and entire subgenital plate pale yellow. Genitalia black; harpe largely pale brown.

Structure generally similar to that of female. Frons very strongly swollen; ocellar basin often indistinct anteriorly; upper frons very shallowly notched medially; facial crest very strongly convex, bluntly carinate. Antennae with 22–23 antennomeres; flagellomere 1 1.0–1.1 × length of flagellomere 2 and slightly thinner in lateral view than the latter, with apex weakly oblique. Subgenital plate with apical margin broadly truncated. Genitalia as in Figs 76g, h; penis valve short and elongate-subtriangular seen from above.

Material examined. Eighteen specimens**. Holotype:** ♂ (Fig. 76), Mirugam (Bukdaesa), 1,300 m, Odaesan Mts., Gangwon-do, South Korea, 6. VI. 1996, A. Shinohara (NSMT). **Paratypes: RUSSIA: Primorskij Kraj**: 1♀ (DEI-GISHym 88016), Anisimovka 7 km S, Mt. Litovka, 1200m, 43.102°N 132.786°E, 16. VI. 2016, V. Loktionov (NSMT). **SOUTH KOREA: Gangwon-do**: 2♂, Mirugam (Bukdaesa), 1,300 m, Odaesan Mts., 6. VI. 1997, J.-W. Kim (NSMT); 1♂, same locality, 23. V. 2002, A. Shinohara (NSMT); 1♂, same locality, 29. V. 2002, A. Shinohara (NSMT); 4♂ (incl. NSMT 30603), same locality, 4. VI. 2002, A. Shinohara (NSMT); 2♂ (NSMT 30747, 30748), same locality, 26. V. 2008, A. Shinohara (NSMT); 1♂ (NSMT 30850), same locality, 27. V. 2009, A. Shinohara (NSMT); 1♂ (NSMT 30851), same locality, 31. V. 2009, A. Shinohara (NSMT); 1♂ (NSMT 30852), same locality, 4. VI. 2009, A. Shinohara (NSMT); 1♂, same locality, 5. VI. 2009, A. Shinohara (NSMT); 1♂, same locality, 13. VI. 2010, A. Shinohara (NSMT); 1♂, same locality, 17. VI. 2010, A. Shinohara (NSMT).

Distribution. Russia (Primorskij Kraj), South Korea.

Host plant. Unknown. The closely related Japanese species *P. gracilis* feeds on *Sorbus* (Shinohara & Hara 1992).

Etymology. The new specific epithet is *gracilis* plus a suffix, *-oides*, suggesting a species resembling *gracilis*.

Remarks. *Pamphilius graciloides* closely resembles *P. gracilis* Shinohara, 1985, from Japan and Shinohara (2001) recorded it as "*P. gracilis*" from South Korea. Because of the existence of recognizable, though small differences in colour pattern in both sexes and quite a large difference in COI sequences, we here treat the continental and Japanese populations as representing different species, *P. graciloides* and *P. gracilis*.

Shinohara (2001) discussed the variation of "*P. gracilis*" in detail and pointed out that the three Korean male specimens then available (now identified as *P. graciloides*) were darker in colour pattern than the 17 Japanese male specimens examined (*P. gracilis*). Examination of the additional 11 males from Korea listed above (*P. graciloides*) has shown that the differences in color pattern are fairly stable. The female of *P. graciloides* (only one Russian specimen available) is slightly different in colour pattern from those of *P. gracilis*, as shown below.

In the analysis of COI sequences (Fig. 145), each of *P. graciloides* and *P. gracilis* was retrieved as a clade with 100% UFBoot support and they formed a clade with 100% UFBoot support. The minimum distance (4.0%) between the two species was much larger than the interspecific distance between closely related congeners, such as *P. albopictus* and *P. kamikochensis* Takeuchi, 1930 (2.0%) or *P. benesi* and *P. pallidus* (2.9%). In the NaK analysis (Fig. 159), the available specimens of *P. graciloides* and *P. gracilis* were not separable but altogether formed a monophyletic group with 100% UFBoot support. *Pamphilius graciloides* and *P. gracilis* clearly show a large genetic differentiation in COI, though they are not clearly differentiated in NaK sequences.

The female of *P. graciloides* is similar to *P. gracilis*, but the base of the fore femur, including the trochantellus, is almost all black, and the mesepisternum has only a small pale yellow spot on the anterodorsal corner. In *P. gracilis*, the base of the fore femur is also blackish but the trochantellus is mostly pale yellow and the entire anterior margin of the mesepisternum is pale yellow. The male of *P. graciloides* has the mesepisternum mostly or entirely black with at most small pale-yellow marks and the malar space medially marked with black, whereas *P. gracilis* has the mesepisternum largely marked with pale yellow and the malar space entirely pale yellow. One specimen of *P. gracilis* from Shiga-kogen, Honshu, which was referred to by Shinohara (2001), has an exceptionally dark colour pattern and is almost indistinguishable from *P. graciloides*. The maximum intraspecific *p*-distance in *P. graciloides* was 0.8% in COI (n=7) and 0.2% in NaK (n=5).

Pamphilius montanus pulcher Shinohara, 1988

(Figs 104, 105) (https://doi.org/10.6084/m9.figshare.11405259)

Pamphilius pulcher Shinohara, 1988a: 311; Shinohara, 1991b: 113; Zhelochovtsev & Zinovjev, 1995: 398.
Pamphilius montanus pulcher: Shinohara, 2001: 106, 113, 115; Shinohara, 2002b: 430; Shinohara & Lelej, 2007: 932, 940; Taeger *et al.*, 2010: 89; Sundukov, 2017: 105; Lee *et al.*, 2019: 10; Shinohara, 2019: 11; Shinohara, 2020: 14, 244.

Material examined. Sixty specimens, including the type series. Forty-three specimens are from South Korea (Shinohara 1988b; present work). **New collection data: SOUTH KOREA: Gangwon-do**: 1♂ (NSMT 30749), Mirugam (Bukdaesa), 1300m, Odaesan Mts., 26. V. 2008, A. Shinohara (NSMT); 1♂ (NSMT 30853), same locality, 2. VI. 2009, A. Shinohara (NSMT). See Shinohara (1988a, 2001) for more collection data.

Distribution. Russia (Yakutia), South Korea, Japan (Hokkaido) (Shinohara 2001).

Host plant. Unknown.

Remarks. This is a member of the *P. sylvaticus* group defined by Shinohara (1985a, 2002b). Shinohara (1988a) described this subspecies as a full species but Shinohara (2001) treated it as a subspecies of *P. montanus* Shinohara, 1985.

In our molecular analysis, the maximum intrasubspecific *p*-distance among specimens from Korea and Hokkaido, Japan, was 1.5% in COI (n=4) and 0.2% in NaK (n=3). The minimum distance to the specimens of the nominotypical *P. montanus montanus* from Honshu, Japan, was 3.7% in COI and 0.1% in NaK. The nearest neighbour was *P. volatilis*, diverging by a minimum of 4.1% in the COI analysis, and *P. alnicola*, diverging by a minimum of 0.6% in the NaK analysis. In the COI tree (Fig. 145), each of *P. montanus*, *P. m. montanus* and *P. m. pulcher* was retrieved as monophyletic with UFBoot support of 100% and *P. montanus* was sister to *P. alnicola* with UFBoot support of 82%. In the NaK tree (Fig. 159), *P. m. montanus* (n=2) was retrieved as monophyletic with UFBoot support of 100%, but *P. m. pulcher* (n=3) was not, while all the specimens of *P. montanus* (n=5) formed a clade with UFBoot

support of 93% and the clade consisting of *P. gracilis* and *P. graciloides* was retrieved as sister to *P. montanus* with very low UFBoot support of 70%.

Pamphilius montanus pulcher is probably associated with *Sorbus* (Rosaceae) because the larvae of the nominotypical subspecies from Honshu, Japan, are gregarious web-spinners on *Sorbus commixta* Hedl. (Rosaceae) (Shinohara & Kojima 2011).

Pamphilius ochrostigma Shinohara, 2001

(Fig. 106) (https://doi.org/10.6084/m9.figshare.11405262)

Pamphilius ochrostigma Shinohara, 2001: 100, 115; Shinohara, 2002b: 430; Shinohara, 2004: 265; Taeger *et al.*, 2010: 89; Lee *et al.*, 2019: 10.

Material examined. Forty-four specimens (type series) from South Korea (Shinohara 2001).

Distribution. South Korea (Shinohara 2001).

Host plant. Unknown.

Remarks. This is a Korean endemic species known only from the males collected between 1989 and 1993 at the same locality. It belongs to the *P. sylvaticus* group and is close to *P. volatilis* and *P. benesi*, as discussed by Shinohara (2001). No molecular data are available.

Pamphilius pallidus Shinohara, 1988

(Fig. 107) (https://doi.org/10.6084/m9.figshare.11405265)

Pamphilius pallidus Shinohara, 1988a: 308; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2001:114; Shinohara, 2002b: 430; Shinohara, 2004: 265; Shinohara & Taeger, 2007: 38; Shinohara & Lelej, 2007: 932; Taeger *et al.*, 2010: 89; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105; Lee *et al.*, 2019: 10.

Material examined. Four specimens, including the type series, all from the Russian Far East and South Korea (Shinohara 1988a; Shinohara & Taeger 2007; present work). **New collection data: RUSSIA**: **Primorskij Kraj**: 1♀ (DEI-GISHym 32049), Komissarovo N, 130m, 45.000°N 131.788°E, 4. VI. 2016, K. Kramp, M. Prous & A. Taeger, RU035 (SDEI).

Distribution. Russia (Primorskij Kraj), South Korea.

Host plant. Unknown.

Remarks. *Pamphilius pallidus* was previously known only from three females from Primorskij Kraj and Korea (Shinohara & Taeger 2007). It is a member of the *P. sylvaticus* group (Shinohara 2002b). In our molecular study, the nearest neighbour was *P. benesi*, diverging by a minimum of 2.9% in the COI analysis and 0.5% in the NaK analysis. *Pamphilius pallidus* was retrieved as sister to *P. benesi* in both COI and NaK trees with 100% UFBoot support (Figs 145, 159).

The newly collected female (Fig. 107) is very pale; the black marks on the head are greatly reduced and the reddish (orange) colour of the abdominal dorsum (on the segments 2 to 5) has faded to dirty cream, with only a very faint tint of orange remaining. The male is still unknown.

Pamphilius ussuriensis Shinohara, 1988

(Figs 123–126) (https://doi.org/10.6084/m9.figshare.11405316)

Pamphilius ussuriensis Shinohara, 1988a: 314; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2001: 115; Shinohara, 2002b: 431; Shinohara, 2004: 265; Shinohara & Lelej, 2007: 940; Taeger *et al.*, 2010: 91; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105.

Pamphilius zinovjevi Shinohara, 1988a: 315; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2001: 111, 114; Shinohara, 2002b: 431; Shinohara, 2004: 265; Shinohara & Lelej, 2007: 933; Taeger *et al.*, 2010: 92; Sundukov & Lelej, 2012: 110; Sundukov, 2017: 106; Lee *et al.*, 2019: 12. **Syn. nov.**

Material examined. Ten specimens, including the holotypes of *P. ussuriensis* and *P. zinovjevi*, all from the Russian Far East and South Korea (Shinohara 1988a, 2001; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (Fig. 123, DEI-GISHym 12972), Samarka, Gordeyevskaya Mtn., 70 km N Chuguyevka, 250 m, 44.46N 134.13E, 29. V. 1993, leg. A. Taeger (SDEI); 1♂ (Fig. 124, DEI-GISHym 21853), Sikhote-Alin Reserve, Upper River Dzhigitovka, 44.970°N 136.080°E, 27. V. 2015, Sergeev (SDEI); 1♀ (Fig. 126a–c, DEI-GISHym 86348), Rettihovka 9 km E, 170m, 44.178°N 132.877°E, 29. V. 2016, K. Kramp, M. Prous & A. Taeger, RU024 (SDEI).

Distribution. Russia (Amurskaja Oblast', Primorskij Kraj), South Korea.

Host plant. Unknown.

Remarks. *Pamphilius ussuriensis* and *P. zinovjevi* were described from the holotypes only. The holotype of *P. ussuriensis* is a rather poorly preserved (discoloured) male specimen (Fig. 125) and that of *P. zinovjevi* is an exceptionally small female specimen (Fig. 126d–f; Shinohara 1988a). Shinohara (2001) examined five additional females of *P. zinovjevi* from Primorskij Kraj and South Korea and discussed the variation among them. *Pamphilius ussuriensis* was only known from the holotype male until now. The COI sequences of the newly obtained specimens of *P. ussuriensis* (a male, DEI-GISHym 21853, and a female, DEI-GISHym 86348, initially determined as *P. zinovjevi*) were retrieved as monophyletic with 100% UFBoot support (Fig. 146). Though the two specimens diverged by 1.8% in COI, it now seems reasonable to regard them as different sexes of the same species and here we propose to treat *P. zinovjevi* as a synonym of *P. ussuriensis*.

This species belongs to the *P. sylvaticus* group (Shinohara 2002b). Diverging by a minimum of 4.8% in the COI sequences, the nearest neighbour was *P. graciloides*, according to our molecular analysis. In the COI tree (Fig. 146), *P. ussuriensis* and *P. jucundus* (Eversmann, 1847) formed a monophyletic group with 99% UFBoot support.

Pamphilius viridulus Shinohara, 2001

(Fig. 132) (https://doi.org/10.6084/m9.figshare.11405331)

Pamphilius viridulus Shinohara, 2001: 102, 114; Shinohara, 2002b: 431; Shinohara, 2004: 265; Shinohara & Lelej, 2007: 933; Taeger *et al.*, 2010: 91; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 106.

Material examined. Two specimens (type series) from the Russian Far East.

Distribution. Russia (Primorskij Kraj).

Host plant. Unknown.

Remarks. Shinohara (2001) described *P. viridulus* based on two females, and these are still the only known specimens of this species. Shinohara (2001, 2002b) placed this species in the *P. sylvaticus* group. No molecular data for this species are available.

Pamphilius volatilis (Smith, 1874)

(Figs 133, 134) (https://doi.org/10.6084/m9.figshare.11405334)

Lyda volatilis Smith, 1874: 384.

Pamphilius smithii Kirby, 1882: 343.

Pamphilius volatilis: Gussakovskij, 1935: 180, 376; Beneš 1974: 308, 313; Shinohara & Okutani, 1983: 278; Shinohara, 1985a: 348; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2001: 114, 115; Shinohara, 2002a: 192; Shinohara, 2002b: 431; Shinohara, 2004: 265; Shinohara & Hara, 2005: 273; Shinohara & Lelej, 2007: 933, 940; Taeger *et al.*, 2010: 91; Sundukov & Lelej, 2012: 109; Shinohara, 2013: 96; Sundukov, 2017: 106; Lee *et al.*, 2019: 11; Shinohara, 2019: 12; Shinohara, 2020: 15, 245.

Material examined. About 1450 specimens, including the holotype, and 218 specimens from South Korea (Beneš 1974; Shinohara 1985a; National Museum of Nature and Science 2021; present work). **New collection data: SOUTH KOREA: Gangwon-do**: 4♂ (NSMT 30744–30802), Mirugam (Bukdaesa), 1300m, Odaesan Mts., 25–26. V. 2008, A. Shinohara (NSMT); 30♂, same locality, 27. V.–5. VI. 2009, A. Shinohara (NSMT); 11♂, same locality, 11–17. VI. 2010, A. Shinohara (NSMT).

Distribution. Russia (Primorskij Kraj), South Korea, Japan (Hokkaido, Honshu, Shikoku, Kyushu).

Host plant. Rosaceae: *Cerasus* spp., *Crataegus chlorosarca*.

Remarks. This species belongs to the *P. sylvaticus* group (Shinohara 1985a, 2002b). It is fairly common in Japan and apparently also in South Korea (1110 Japanese specimens and 177 Korean specimens recorded by National Museum of Nature and Science 2021) but only two specimens were recorded from Primorskij Kraj (Beneš 1974). In both the COI and NaK analyses (Figs 145,159), the 11 specimens from Japan and Korea were retrieved as monophyletic with 100% UFBoot support, though the intraspecific genetic variation was rather large. The maximum intraspecific *p*-distance was 2.4% in COI (n=11) and 0.5% in NaK (n=11). The nearest neighbour was *P. m. montanus* diverging by a minimum of 4.1% in the COI analysis and *P. alnicola* diverging by a minimum of 0.6% in the NaK analysis. In both COI and NaK trees (Figs 145, 159), *P. volatilis* was retrieved as sister to the clade *P. benesi* + *P. pallidus* but with low UFBoot support, 82% in COI and 45% in NaK.

The larvae are gregarious leaf-rollers on *Cerasus* and *Crataegus* (Rosaceae).

Pamphilius vafer group

The members of this species group are characterized as follows: upper part of head pilose; facial crest in male flattened to moderately swollen, rarely carinate; antennal flagellomere 1 1.0–3.9 × length of flagellomere 2; right mandible bidentate with only basal shoulder to apical tooth; left mandible tridentate with low middle tooth; wings hyaline; forewing with cell C glabrous or pilose; femora entirely pale (black-marked only in *P. nigrifemoratus*). Ovipositor sheath appendage various in shape, usually pilose. Male genitalia (e.g., Figs 57g, h, 59g, h, 78g, h, 89h, i): proximal ventral arm of gonostipes normal; apiceps various in shape; valviceps in lateral view rather long, apex directed downward, ventral margin usually more or less concave, without conspicuous dorsoapical process, in dorsal view distinctly swollen laterally at apex.

This is a large species group comprising 36 species in the Holarctic region (Shinohara 2002b, 2003a, 2005; Shinohara & Xiao 2006; Shinohara & Taeger 2007; present work). A total of 19 species are known from the Russian Far East and Korea. Shinohara (2002b) recognized ten subgroups. The Nearctic *P. ochreipes* group (Shinohara 2002b) has much in common with the *P. vafer* group and here we treat it as an additional subgroup of the latter.

Here we used 168 sequences of 31 species of ten subgroups (*P. albopictus*, *P. balteatus*, *P. heecheonparki*, *P. norimbergensis*, *P. ochreipes*, *P. pallimacula*, *P. stramineipes*, *P. togashii*, *P. vafer* and *P. varius* subgroups) for the COI analysis and 99 sequences of 24 species of seven subgroups (*P. albopictus*, *P. balteatus*, *P. heecheonparki*, *P. stramineipes*, *P. togashii*, *P. vafer* and *P. varius* subgroups) in the NaK analysis. In the COI analysis (Figs 15, 149–151), the *P. vafer* group, excluding *P. kashmirensis* Beneš, 1971, and *P. norimbergensis*, was recovered as monophyletic but with a low UFBoot value of 89%. *Pamphilius kashmirensis* and *P. norimbergensis* are little-known species, belonging to but rather isolated in the *P. vafer* group (Shinohara 2002b); their systematic position should be further studied with more material. In the NaK analysis (Figs 16, 160, 161), where *P. kashmirensis* and *P. norimbergensis* were not included, the *P. vafer* group was recovered as monophyletic with 99% UFBoot support. Within the *P. vafer* group, monophyly of each subgroup and relationships among the subgroups were not well resolved as detailed under the remarks on each species.

The known host plants of the species of the *P. vafer* group are Rosaceae (*Cerasus*, *Sorbus*, *Rosa*, etc.), Betulaceae (*Alnus* and *Betula*), Caprifoliaceae (*Lonicera* and *Macrodiervilla*), Adoxaceae (*Viburnum*) and Fagaceae (*Quercus*).

Pamphilius albopictus (Thomson, 1871)

(Figs 50, 51) (https://doi.org/10.6084/m9.figshare.15709641)

Lyda albo-picta Thomson, 1871: 312.

Lyda albopicta: André, 1881: 63 (syn. of *L. depressa* [=*P. vafer*]).

Pamphilius albopictus: Kirby, 1882: 337; Konow, 1897a: 25, 31 (syn. of *P. depressus* [=*P vafer*]); Kangas, 1961: 69; Kangas & Kangas, 1963: 267; Kangas & Kangas, 1965: 31; Beneš, 1976: 160; Achterberg & Aartsen, 1986: 36; Zhelochovtsev & Zinovjev, 1995: 397; Shinohara, 1998: 233; Taeger *et al.* 1998: 104; Shinohara, 2002b: 428; Shinohara, 2004: 264; Shinohara & Lelej, 2007: 940; Taeger *et al.,* 2010: 85; Sundukov & Lelej, 2012: 108; Sundukov, 2017: 104; Lee *et al.*, 2019: 8.

Pamphilius vafer: Malaise, 1931, p. 63 (not Linné, 1767, in part).

Pamphilius altaicus Gussakovskij, 1935: 187; Beneš, 1976: 160 (syn. of *P. albopictus*).

Pamphilius viridipes Achterberg & Aartsen, 1986: 45; Shinohara & Taeger, 1990: 95; Shinohara, 1998: 233 (syn. of *P. albopictus*).

See Shinohara (1998) for more synonyms and references.

Material examined. Sixty-one specimens, including the lectotype and 38 specimens from the Russian Far East and South Korea (Shinohara 1998; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (DEI-GISHym 32036), Zharikovo 4km N, 120m, 44.643°N 131.681°E, 3. VI. 2016, K. Kramp, M. Prous & A. Taeger, in alcohol, RU034 (SDEI); 1♀ (Fig. 51, DEI-GISHym 86124), Gornotajozhnoe 1km E, 150m, 43.694°N 132.168°E, 19. V. 2016, K. Kramp, M. Prous & A. Taeger, RU006 (SDEI). **SOUTH KOREA: Gangwon-do:** 1♀, Mirugam (Bukdaesa), 1300m, Odaesan Mts., 24. V. 2002, A. Shinohara (NSMT); 2♀ (incl. NSMT 30865), same locality, 28. V.–1. VI. 2009, A. Shinohara (NSMT).

Distribution. Europe across Siberia to Kamchatka Kraj and Primorskij Kraj, North and South Korea (Shinohara 1998).

Host plant. Rosaceae: *Padus avium* Mill. (Kangas 1961; Kangas & Kangas 1965).

Remarks. This is a widely distributed Eurosiberian species. It is probably thelytokous-parthenogenetic with no males (Shinohara 1998), a rare case in the Pamphiliidae. *Pamphilius albopictus* is one of the three species of the Pamphiliidae known to be associated with *Padus*. The other two are *P. kamikochensis* Takeuchi, 1930 from Japan and *P. padus* Shinohara, 2016, from Zhejiang Province, China (Shinohara & Wei 2016).

Shinohara (1998) proposed the *P. albopictus* subgroup of the *P. vafer* group to include *P. albopictus*, *P. kamikochensis* and *P. heecheonparki* Shinohara, 1998, from Korea and the Russian Far East, whereas Shinohara (2002b) recognized the *P. albopictus* subgroup (*P. albopictus* and *P. kamikochensis* only) and the *P. heecheonparki* subgroup (*P. heecheonparki* only). In our COI molecular analysis (Fig. 148), the *P. albopictus* subgroup *s. str.* (*P. albopictus*, *P. kamikochensis* plus subsequently described *P. leleji* Shinohara & Taeger, 2007) was retrieved as monophyletic with 100% UFBoot support and this clade was recovered as sister to *P. heecheonparki* with 89% UFBoot support. In the NaK analysis (Figs 160–161), both of the clades *P. albopictus* + *P. kamikochensis* and *P. heecheonparki* were recovered as monophyletic with 100% UFBoot support, but their relationships were not clearly resolved. The maximum intraspecific *p*-distance within *P. albopictus* was 0.8% in COI (n=4) and 0.2% in NaK (n=3) and the nearest neighbour was *P. kamikochensis*, diverging by a minimum of 2.2% in COI analysis and by a minimum of 0.4% in NaK analysis.

Pamphilius alnivorus Shinohara, 2005

(Figs 54, 55) (https://doi.org/10.6084/m9.figshare.11405118)

Pamphilius alnivorus Shinohara, 2005: 99; Shinohara & Hara, 2005: 275; Shinohara & Lelej, 2007: 937, 942; Sundukov, 2009: 213; Taeger *et al.*, 2010: 86; Sundukov & Lelej, 2012: 108; Sundukov, 2017: 104; Shinohara, 2019: 8; Shinohara, 2020: 23, 253.

Material examined. About 520 specimens, including the type series. Forty specimens are from the Russian Far East (Shinohara 2005; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (DEI-GISHym 21865), Sikhote-Alin Reserve: Blagodatnoe cordon, 44.953°N 136.547°E, 2. VI. 2016, M. Sergeev (SDEI).

Distribution. Russia (Yakutia, Khabarovskij Kraj, "Sikhote-alin", Primorskij Kraj, Sakhalin), Japan (Hokkaido, Kunashiri Is., Shikotan Is.) (Shinohara 2005).

Host plant. Betulaceae: *Alnus hirsuta* Turcz. and/or its variety, var. *sibirica* (Fischer) C. K. Sch., *Alnus japonica* (Thunb.) Steud. (Shinohara 2005; Shinohara & Hara 2005).

Remarks. *Pamphilius alnivorus*, *P. masao* Shinohara, 2005, and *P. pallipes* (Zetterstedt, 1838) belong to the *P. vafer* complex (Shinohara 2005) or the *P. vafer* subgroup of the *P. vafer* group (Shinohara 2002b), which comprises nine closely related Palaearctic species associated with *Alnus* and *Betula*. In our molecular study (Figs 148–151, 160, 161), the relationships of this group of species were poorly resolved. In the NaK analysis (Fig. 160), the two specimens of *P. alnivorus* from Japan did not even form a clade.

Pamphilius alnivorus is closest to *P. nakagawai* Takeuchi, 1930, occurring in Honshu, Shikoku and Kyushu, Japan, in morphology and bionomics (Shinohara 2005). The larva of *P. alnivorus* is a solitary leaf-roller on *Alnus*,

making a leaf-roll on the underside but oviposition is on the upperside (Type II of Shinohara 2005). The site of oviposition (upperside of a leaf) and direction of leaf-rolling (underside) in this species are quite peculiar, otherwise known only for the *Betula*-feeding species, *P. pallipes* (Shinohara 2005).

Pamphilius archiducalis Konow, 1897

(Figs 56, 57) (https://doi.org/10.6084/m9.figshare.11405121)

Pamphilius archiducalis Konow, 1897b: 249; Gussakovskij, 1935: 187, 378; Shinohara & Okutani, 1983: 277; Shinohara, 2002b: 428; Shinohara, 2004: 264; Shinohara & Hara, 2005: 275; Shinohara & Kojima 2006: 24; Shinohara & Taeger, 2007: 34; Shinohara & Lelej, 2007: 939, 942; Taeger *et al.*, 2010: 86; Sundukov & Lelej, 2012: 109; Shinohara, 2013: 94; Sundukov, 2015: 249; Sundukov, 2017: 104; Shinohara, 2019: 8; Shinohara, 2020: 22, 251.

Material examined. About 315 specimens, including the holotype. One specimen is from the Russian Far East (Shinohara & Taeger 2007).

Distribution. Russia (Sakhalin), Japan (Hokkaido, Shikotan Is., Honshu, Shikoku) (Shinohara 2013).

Host plant. Betulaceae: *Alnus hirsuta* (Spach) Turcz. ex Rupr., *Alnus matsumurae* Callier (Shinohara & Hara 1999, 2005; Shinohara 2005). Shinohara & Okutani's (1983) record of *Alnus viridis* (Chaix) Lam. et DC. subsp. *maximowiczii* (Callier) D. Löve is probably erroneous (Shinohara 2005).

Remarks. This species is known only from Sakhalin and Japan. The larva feeds on *Alnus* solitarily, rolling a leaf edge below. The egg is deposited on the underside of the leaf (Shinohara & Kojima 2006). Shinohara (2002b) placed this species in the *P. balteatus* complex of the *P. balteatus* subgroup, though our molecular analysis did not support the monophyly of this complex of species.

Pamphilius aucupariae Vikberg, 1971

(Figs 58, 59) (https://doi.org/10.6084/m9.figshare.11405133)

Pamphilius aucupariae Vikberg, 1971: 140; Achterberg & Aartsen, 1986: 37; Viitasaari, 2002b: 340; Shinohara, 2002b: 428; Vikberg, 2002: 444; Shinohara & Vasilenko, 2005: 33; Taeger *et al.*, 2006: 465; Taeger *et al.*, 2010: 86; Sundukov, 2017: 104.

Material examined. About 215 specimens, of which 210 are from Korea (present work). **New collection data: FINLAND:** 1♀, "Suomi EH: Pälkäne, ex larva, 23. 5. 1975, 17/74, leg. J. Kangas, *Sorbus aucuparia*" "*Pamphilius aucupariae* V. Vikberg, ♀, coll. J. Kangas" (NSMT); 1♀, "Suomi EH: Lammi, 30. V. 1967, leg. Kontuniemi" "Paratype, *Pamphilius aucupariae* sp. n., det. V. Vikberg, 1971" "From V. Vikberg, 14. III. 1983" (NSMT); 1♂, "Fennia 6798:354, Suomi EH: Pälkäne, ex larva, 31/5 1974, leg. J. Kangas" "*Pamphilius aucupariae* Vikberg, ♂, coll. Jaakko Kangas" "From V. Vikberg, 14. III. 1983" (NSMT). **SOUTH KOREA: Gangwon-do**: 1♂, Mirugam (Bukdaesa), 1300m, Odaesan Mts., 31. V. 1991, A. Shinohara (NSMT); 1♀8♂, same locality, 30–31. V. 1992, A. Shinohara (NSMT); 5♂, same locality, 29. V.–1. VI. 1996, A. Shinohara (NSMT); 1♂, same locality, 29. V.–1. VI. 1996, J.-W. Kim (NSMT); 1♂, same locality, 6. VI. 1996, A. Shinohara (NSMT); 13♂, same locality, 6. VI. 1996, J.-W. Kim (NSMT); 49♂, same locality, 26. V.–7. VI. 1997, A. Shinohara (NSMT); 4♂, same locality, 1–3. VI. 1997, J.-W. Kim (NSMT); 1♀26♂, same locality, 27. V.–1. VI. 1998, A. Shinohara (NSMT); 21♂, same locality, 24. V.–3. VI. 2002, A. Shinohara (NSMT); 3♂ (NSMT 30768–30770), same locality, 25. V.–1. VI. 2008, A. Shinohara (NSMT); 7♂ (incl. NSMT 30861), same locality, 27. V.–5. VI. 2009, A. Shinohara (NSMT); 2♂, same locality, 11. VI. 2010, A. Shinohara (NSMT). **Jeollanam-do**: 39♂, Jungsanri–Popkyesa, 1000–1300m, Jirisan Mts., 25–29. V. 1987, A. Shinohara (NSMT); 26♂, Mt. Nogodan, 1200m, Jirisan Mts., 4–5. VI. 1996, A. Shinohara (NSMT).

Distribution. Finland, Russia (Yakutia) (Shinohara & Vasilenko 2005). South Korea (new record).

Host plant. Rosaceae: *Sorbus aucuparia* L.

Remarks. This is a rare species previously known only from Finland and Yakutia, Russia (Shinohara & Vasilenko 2005). This is the first record from Korea. The larvae are gregarious web-spinners on *Sorbus* (Vikberg 2002). Another species of *Pamphilius*, whose larvae are gregarious web-spinners on *Sorbus*, is *P. montanus montanus* Shinohara, 1985, from Honshu, Japan (Shinohara & Kojima 2011). The larvae of these two species have not been differentiated.

The Korean specimens examined differ from the Finnish specimens in a darker colour pattern. In Korean females, the entire tergum 1, large areas on the terga 2 and 6 and the entire terga 7 and 8 are black and all the sterna are broadly black basally. In Finnish females, the entire tergum 1 and very narrow areas on the terga 2 and 6 to 8 are black and the sterna 2, 3, 6 and 7 are marked with black basally. In almost all males from Korea, the postocular stripe terminates at the corner of the upper inner orbits, whereas the postocular stripe extends ventrally along the inner orbits in the Finnish males (see fig. 2 in Vikberg 1971). In structural characters, no conspicuous differences have been found.

In our molecular analysis, the maximum intraspecific *p*-distance was 1.3% in COI (n=4) and 0.1% in NaK (n=4). The nearest neighbour was *P. balteatus* (Fallén, 1808), diverging by a minimum of 3.7% in the COI analysis, and *P. confusus* Shinohara, 2005, diverging by a minimum of 0.4%, in the NaK analysis. In the COI tree (Fig. 151), *P. aucupariae* branched off near the base of the *P. vafer* group and its affinities are unclear, whereas in the NaK tree (Fig. 161) it was retrieved as sister to *P. leleji* with UFBoot support of 98%.

Pamphilius balteatus (Fallén, 1808)

(Figs 60, 61) (https://doi.org/10.6084/m9.figshare.11405139)

Lyda balteata Fallén, 1808: 225.

Pamphilius balteatus: Konow, 1897a: 24, 31; Gussakovskij, 1935: 179, 376; Takeuchi, 1938: 222; Berland, 1947: 49; Kim, 1963: 278 ["*balteaetus*"]; Verzhutskij, 1966: 27; Kim, 1970: 126; Shinohara, 1985b: 459; Achterberg & Aartsen, 1986: 37; Kim *et al.*, 1994: 217 ["*balteaetus*"]; Zhelochovtsev & Zinovjev, 1995: 397; Taeger *et al.*, 1998: 104; Shinohara, 2002b: 428; Shinohara, 2004: 264; Shinohara & Hara, 2006: 159; Shinohara & Taeger, 2007: 35; Shinohara & Lelej, 2007: 938, 942; Sundukov, 2009: 213; Paek *et al.*, 2010: 161 ["*balteaetus*"]; Taeger *et al.*, 2010: 86; Sundukov & Lelej, 2012: 109; Sundukov, 2015: 249; Sundukov, 2017: 104; Lee *et al.*, 2019: 8; Shinohara, 2019: 8; Shinohara, 2020: 21, 250.

Material examined. About 50 specimens, including 26 specimens from the Russian Far Est and North Korea (Takeuchi 1938; Shinohara 1985b; Shinohara & Taeger 2007; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (DEI-GISHym 21845), Vladivostok, Botanical Garden, 43.224°N 131.993°E, 21. V. 2015, M. Sergeev (SDEI); 1♀, Rettihovka 9 km E, 170m, 44.178°N 132.877°E, 29. V. 2016, K. Kramp, M. Prous & A. Taeger, RU024 (Fig. 60, DEI-GISHym 12938).

Distribution. Europe, Siberia, Baikal region, Kamchatka Kraj, Primorskij Kraj, Sakhalin, North Korea, Japan (Takeuchi 1938; Shinohara 1985b; Sundukov 2017).

Host plant. Rosaceae: *Rosa* spp. (Taeger *et al.* 1998; Vikberg 2002; Shinohara & Hara 2006).

Remarks. This species is widely distributed in northern Eurasia. In Korea, it has been found only in Gosui [=Hapsu], Hakugan [=Paegam] and Tonai [=Tonae], all in Ryanggang-do, North Korea (Takeuchi 1938; Shinohara 1985b) and the confirmed host plants of this species are *Rosa* spp. (Taeger *et al.* 1998; Vikberg 2002; Shinohara & Hara 2006). Lee *et al.* (2019) included South Korea in the distribution of this species and Sundukov (2017) and Lee *et al.* (2019) gave *Fragaria*, *Prunus* and *Spiraea* as additional hosts without presenting new data or relevant references. These distribution and host records need confirmation.

In the key by Shinohara & Lelej (2007), *P. balteatus* will erroneously run to *P. itoi*, because *P. balteatus* is wrongly placed under couplet 19, whereas it should be placed under couplet 16 (then 18). This error has been corrected in the new key given above.

In our COI analysis (Fig. 148), six specimens from Germany, Finland and Primorskij Kraj formed a monophyletic group with 97% UFBoot support. The clade of *P. balteatus* (specimens from Germany, Finland and Primorskij Kraj) was retrieved as the sister group of the *P. thorwaldi* subgroup (*P. lobatus* Maa, 1950 + *P. planifrons* Beneš, 1976 + *P. belokobylskiji* **sp. nov.** + *P. rhoae* Shinohara, 1988) with 95% UFBoot support (Fig. 148).

Pamphilius belokobylskiji sp. nov.

(Figs 62, 63) (https://doi.org/10.6084/m9.figshare.16943245)

Pamphilius planifrons: Shinohara 1988b: 184; Kim *et al.*, 1994: 217; Shinohara, 2002b: 427; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 90. Not Beneš, 1976, in part.

Female (Fig. 62). Length about 11–12 mm. Head black, with following pale yellow: most of clypeus, narrow line along upper inner orbit (this line missing in one specimen, Fig. 62), continuing posteriorly as a rather broad postocular stripe extending from posterior inner corner of eye to crassa, crescent line along outer margin of lateral suture of postocellar area; mandible black, with outer basal part pale yellow and apex dark rufous; scape and pedicel black, with outer surface pale yellow; flagellum blackish brown, with outer surface paler, particularly the basal part. Thorax black, with following pale yellow: ventral part of lateral pronotum, broad posterolateral corner of dorsal pronotum, obscure mark on cervical sclerite, tegula, posterior part of mesoscutal middle lobe, mesoscutellum, large spot on lateral posterior part of mesepisternum, metascutellum, dorsal part of metepimeron; legs pale yellow, except for narrowly black coxal bases. Wings hyaline, distinctly stained with brown; veins blackish brown, with veins C and Sc yellowish, and base of vein 1A pale yellow; stigma dark yellow, marginally dark brown. Abdomen orange dorsally with terga 1 and 2 mostly, broad anterior margin (except for lateral margin and median interruption) of tergum 3, small lateral spot on each of terga 4 and 5, and most of more posterior terga black; narrow lateral margin (more broadly on more posterior segments) pale yellowish; abdomen pale yellow ventrally, with broad anterior part of each sternum black.

Frons swollen in dorsal aspect, somewhat concave below ocelli down to ill-defined median fovea; ocellar basin represented as a broad furrow around median ocellus; frontoclypeal crest rather flat, rounded, swollen between antennal sockets; facial crest moderately convex, very bluntly carinate. Upper part of head behind transverse and lateral transverse sutures smooth, with large, often ill-defined punctures; area from facial crest to lateral transverse suture coarsely rugose, outer part somewhat smoother, with large, rather shallow irregular punctures; frons almost reticulate, with coarse large deep punctures; paraantennal field with dense small punctures, transversely rugose, with only ventral part nearly impunctate along inner orbit; clypeus with distinct medium-sized punctures, with interspaces smooth medially and coarsely rugose laterally; gena weakly coriaceous, with rather small, often ill-defined punctures; head covered with rather long silvery hairs before crassa, except for nearly glabrous ventral part of paraantennal field. Antennae with 24–25 antennomeres; flagellomere 1 1.2–1.3 × length of flagellomere 2. Forewing cell C pilose all over. Ovipositor sheath as in Fig. 62g; appendage narrow-conical, setose medially and apically.

Male (Fig. 63). Length about 8.5–11 mm. Head black, with frontal surface below line connecting facial crests, broad postocular stripe, short crescent marking along outer margin of lateral suture of postocellar area (sometimes missing), entire gena and malar space pale yellow; mandible pale yellow with dark rufous apex; scape and pedicel pale yellow, with dorsal surface largely black (black area missing in one specimen); flagellum dark brown, with flagellomere 1 marked with black dorsally. Thorax black, with following pale yellow: most of lateral pronotum extending dorsally along posterior margin to cover broad posterolateral corner of dorsal pronotum, ventral half of cervical sclerite, tegula, posterior half of mesoscutal middle lobe, mesoscutellum, mesepisternum including pectus (except for black lateral spot along very narrowly black posterodorsal margin), broad posterior (dorsal) margin of mesepimeron, metascutellum, linear mark connecting inner ends of cenchri, metepisternum (except for ventral surface), dorsal half (except for anterior part) and posterior margin of metepimeron; legs pale yellow, except for narrowly black coxal bases. Wings hyaline, distinctly tinted with brown; veins blackish brown, with veins C and Sc yellowish, and base of vein 1A pale yellow; stigma dark yellow, marginally dark brown. Abdomen orange dorsally and pale yellow ventrally; dorsum with terga 1 and 2 mostly, broad anterior margin (except for lateral margin and median interruption) of each of terga 3 to 5, and terga 6 to 8 (except for broad lateral and posterior margins) black, and lateral margin (more broadly on more posterior segments), very narrow posterior margin (rather broadly on posterior segments) of each of terga 2 to 8, and tergum 10 wholly pale yellowish; venter with narrow anterior margin of sternum 2 black. Genitalia black; harpe and penis valve pale brown.

Structure generally similar to that of female. Antennae with 23–28 antennomeres; flagellomere 1 1.0–1.1 × length of flagellomere 2 and distinctly thinner in lateral view than the latter, with apex strongly oblique. Subgenital plate with apical margin broadly rounded. Genitalia as in Fig. 11: 57aa; penis valve very long and slender, valviceps not strongly produced laterally.

Material examined. 113 specimens. **Holotype:** ♂ (Fig. 63, DEI-GISHym 12942), RU: Primorskij Kraj: Anisimovka, Gribanovka 1km N, 450m, 43.126°N 132.797°E, 1. VII. 2017, Taeger, Loktionov, Proshch., RU150 (ZISP). **Paratypes: RUSSIA: Primorskij Kraj**: 14♂, Anisimov Pass, 400m, 5km E of Anisimovka, 6–7. VI. 1995, A. Shinohara (NSMT); 38♂, Pass, 500m, 28km NNW of Partizansk, 13–14. VI. 1995, A. Shinohara (NSMT); 2♂ (DEI-GISHym 88019, 88121), Anisimovka, Gribanovka 1km N, 450m, 43.126°N 132.797°E, 16. VI. 2017, A. Taeger

& M. Proshchalykin (SDEI); 6♂ (incl. DEI-GISHym 88123), Anisimovka, Gribanovka 1km N, 450m, 43.126°N 132.797°E, 1. VII. 2017, A. Taeger, M. Proshchalykin, T. Schmitt, V. Loktionov, RU150 (SDEI). **SOUTH KOREA: Gangwon-do**: 2♂ (described as *P. planifrons* by Shinohara, 1988b), Mirugam (Bukdaesa), 1300m, Odaesan Mts., 10–11. VI. 1987, A. Shinohara (NSMT); 8♂, same locality, 19–28. V. 1989, A. Shinohara (NSMT); 10♂, same locality, 31. V. –7. VI. 1991, A. Shinohara (NSMT); 1♂, same locality, 6. VI. 1991, J.-W. Kim (NSMT); 1♂, same locality, 30. V. 1992, A. Shinohara (NSMT); 1♀1♂, same locality, 29. V. –6. VI. 1996, J.-W. Kim (NSMT); 1♂, same locality, 6. VI. 1996, A. Shinohara (NSMT); 3♂, same locality, 27–30. V. 1998, A. Shinohara (NSMT); 1♀ (Fig. 62) 21♂, same locality, 23. V.–4. VI. 2002, A. Shinohara (NSMT); 2♂ (NSMT 30766, 30767), same locality, 26–27. V. 2008, A. Shinohara (NSMT); 1♂ (NSMT 30866), same locality, 1. VI. 2009, A. Shinohara (NSMT).

Distribution. Russia (Primorskij Kraj), South Korea.

Host plant. Unknown.

Etymology. This new species is named after Dr. Sergej A. Belokobylskij, who played an important role in bringing about the joint Russian-German expeditions in 1993 and 2016.

Remarks. This new species has much in common with *P. lobatus* Maa, 1950, *P. planifrons* Beneš, 1976, and *P. rhoae* Shinohara, 1988, which are the members of *P. thorwaldi* complex (Shinohara, 2002b). Shinohara (1988b) described the male of *P. belokobylskiji* as *P. planifrons*. These four species share punctate pilose heads with only moderately swollen upper frons and facial crests, short flagellomere 1 and a generally similar colour pattern, except for that of the abdomen. *Pamphilius belokobylskiji* is easily distinguished from *P. planifrons* and *P. rhoae* by the largely orange abdomen in both sexes, though the male genitalia of the three species are almost indistinguishable.

The female of *P. belokobylskiji* is very similar to that of *P. lobatus* and can be separated from it almost only by the different surface microsculpture of the head. In *P. belokobylskiji*, the broad area from the paraantennal fields (except for the ventral margin), frons, facial crests, ocellar area to the transverse and lateral transverse sutures is dull and rather shallowly rugose with mostly confluent and indistinct punctures (Fig. 8: 18aa-cc), whereas in *P. lobatus*, the area is dull and rugose and the punctures are dense and generally very distinct (Fig. 8: 19a). There may be some differences in colour pattern as shown in the key but the characters apparently overlap and are of only supplementary value for species distinction.

The male of *P. belokobylskiji* is also similar to that of *P. lobatus* in extragenital characters, but the narrow valviceps of *P. belokobylskiji* (Fig. 11: 57aa) is very different from the very broad valviceps of *P. lobatus* (Fig. 11: 57a). The differences in the surface microsculpture of the head, noted above for the females, also apply to the males. In male genitalic characters, *P. belokobylskiji* strongly resembles *P. planifrons* and *P. rhoae*, but the latter two species have no orange areas on the abdomen.

In our molecular analyses (Figs 149, 161), the *P. thorwaldi* complex was retrieved as monophyletic with 98% UFBoot support in COI and with 97% UFBoot support in NaK, but *P. belokobylskiji* was not clearly differentiated from the related species.

Pamphilius heecheonparki Shinohara, 1998

(Figs 77, 78) (https://doi.org/10.6084/m9.figshare.11405187)

Pamphilius heecheonparki Shinohara, 1998: 229; Shinohara, 2002b: 429; Shinohara, 2004: 264; Shinohara & Lelej, 2007: 939, 941; Sundukov, 2009: 213; Taeger *et al.*, 2010: 86; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 104; Lee *et al.*, 2019: 9.

Material examined. About 685 specimens, including the type series, almost all from the Russian Far East and South Korea (Shinohara 1998; National Museum of Nature and Science 2021; present work). **New collection data: SOUTH KOREA: Gangwon-do**: 4♀7♂ (incl. 30771–30775), Mirugam (Bukdaesa), 1300m, Odaesan Mts., 25. V.–1. VI. 2008, A. Shinohara (NSMT); 5♀86♂ (incl. NSMT 30855), same locality, 27. V.–5. VI. 2009, A. Shinohara (NSMT); 4♀38♂, same locality, 11–18. VI. 2010, A. Shinohara (NSMT).

Distribution. Russia (Irkutskaya oblast, Yakutia, Khabarovskij Kraj, Primorskij Kraj), North and South Korea (Shinohara 1998).

Host plant. Unknown. Many of the specimens from Odaesan Mts., South Korea, were swept from the foliage of *Padus* sp. (Rosaceae), which may possibly be a host plant of this species.

Remarks. This species is well characterized by the large elongate glabrous ovipositor sheath appendage (Fig.

77h) in the female and the anchor-like penis valve (Fig. 11: 61a) in the male. Shinohara (1998) included this species in his *P. albopictus* subgroup of the *P. vafer* group but later he (2002b) proposed the *P. heecheonparki* subgroup for this species alone.

In our molecular analysis, the six available COI sequences of this species from South Korea were identical and the maximum intraspecific *p*-distance among the six NaK sequences was 0.2%. The nearest neighbour was *P. kamikochensis* (a member of the *P. albopictus* subgroup), diverging by a minimum of 3.2% in the COI analysis and *P. masao* (members of the *P. vafer* subgroup) by a minimum of 0.5% in the NaK analysis. In the COI tree (Fig. 148), *P. heecheonparki* was retrieved as the sister group of *P. albopictus* + *P. kamikochensis* + *P. leleji* with 89% UFBoot support, whereas in the NaK tree (Fig. 161) *P. heecheonparki* was sister to the cluster of *P. stramineipes* + *P. togashii* (with only 58% UFBoot support) with very low UFBoot value of 42%.

Pamphilius hortorum (Klug, 1808)

(Figs 83–86) (https://doi.org/10.6084/m9.figshare.11405202)

Lyda hortorum Klug, 1808: 278.

Pamphilius hortorum: Kirby, 1882: 338; Konow, 1897a: 24, 31; Gussakovskij, 1935: 179, 376; Takeuchi, 1938: 224; Berland, 1947: 50; Verzhutskij, 1966: 27; Shinohara & Okutani, 1983: 278; Achterberg & Aartsen, 1986: 39; Zhelochovtsev & Zinovjev, 1995: 397; Taeger *et al.*, 1998: 105; Shinohara, 2002b: 428; Shinohara, 2004: 264; Shinohara & Taeger, 2007: 35; Shinohara & Lelej, 2007: 934, 942; Shinohara & Kojima, 2009: 407; Sundukov, 2009: 213; Taeger *et al.*, 2010: 87; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 104; Lee *et al.*, 2019: 10; Shinohara, 2019: 10; Shinohara, 2020: 17, 247.

Anoplolyda hortorum: Takeuchi, 1936a: 61.

Material examined. About 710 specimens, including 10 specimens from the Russian Far East and North Korea (Takeuchi 1936a; Shinohara 2002b; Shinohara & Taeger 2007; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♂, Lazovsky distr., upstream of Luk'yanov Log Creek, Malaise trap, 25. VI. 2008, Yu. Sundukov, YS034 (SDEI); 1♀ (DEI-GISHym 21846), Sikhote-Alin Reserve, Middle Kolume river, salty ground, forest, 45.500°N 135.900°E, 18. VI. 2015, M. Sergeev (SDEI).

Distribution. Europe, Siberia, Primorskij Kraj, Sakhalin, North Korea, China (Jilin), Japan (Shinohara 2002b, Shinohara & Yuan 2004, Sundukov 2017).

Host plant. Rosaceae: *Rubus* spp. (Shinohara & Kojima 2009).

Remarks. This is a widely distributed Palaearctic species and is not uncommon in Hokkaido, Japan (633 Japanese specimens recorded by National Museum of Nature and Science 2021), but it seems rare in the Russian Far East and Korea. In Korea, only one old female specimen labelled "Tonai [=Tonae, Ryanggang-do, North Korea], 23. VII. 1935, K. Takeuchi", has been recorded (Shinohara 2002b) and we have not seen any specimens or published collection records from South Korea. Lee *et al.*'s (2019) record of "Korea (South)" needs confirmation.

In our COI analysis (Fig. 151), the only specimen available from Primorskij Kraj formed a clade with northern European specimens from Finland and Norway with 100% UFBoot support and this clade was retrieved as sister to a clade of Japanese specimens with 98% UFBoot support; then, this clade of northern European and East Asian specimens was part of the polytomous clade with 100% UFBoot support mostly containing central European material from Germany and Switzerland. For the NaK analysis, only one Norwegian and three Japanese specimens were available and they formed a clade with 100% UFBoot support (Fig. 161). It is interesting that the East Asian specimens are genetically closer to the northern European specimens than to the central European specimens. This may have some connection with Benson's (1945) finding of pale (south) and dark (north) color forms in Britain and establishment of a new subspecies, *P. hortorum bicinctus* Benson, 1945, for the northern dark form, which occurs also in Sweden. The specimens from Primorskij Kraj (Fig. 83) and Japan (Fig. 84) are darker than the central European specimens and may agree with the diagnosis of *P. hortorum bicinctus*. We are not advocating the validity of Benson's subspecies, but the occurrence of morphologically and genetically similar populations in northern Europe and the Far East should be investigated with much more material from throughout the distribution range of the species.

Pamphilius itoi Shinohara, 1985

(Figs 87, 88) (https://doi.org/10.6084/m9.figshare.11405211)

Pamphilius itoi Shinohara, 1985b: 454; Shinohara & Hara 1995: 572; Zhelochovtsev & Zinovjev, 1995: 397; Shinohara, 2002a: 190; Shinohara, 2002b: 428; Shinohara, 2004: 264; Shinohara & Hara, 2005: 275; Shinohara & Lelej, 2007: 934, 942; Sundukov, 2009: 213; Taeger *et al.*, 2010: 88; Sundukov & Lelej, 2012: 109; Sundukov, 2015: 249; Sundukov, 2017: 105; Shinohara, 2019: 10; Shinohara, 2020: 18, 248.

Material examined. About 1610 specimens, including the type series, all from Japan. No specimens were available from the Russian Far East and Korea.

Distribution. Russia (Primorskij Kraj), Japan (Hokkaido, Kunashiri Is., Honshu) (Sundukov 2009).

Host plant. Betulaceae: *Alnus hirsuta* (Spach) Turcz. ex Rupr., *Alnus japonica* (Thunb.) Steud. (Shinohara & Hara 1995, 2005).

Remarks. This species is often commonly found in Hokkaido, Japan (1436 Japanese specimens recorded by National Museum of Nature and Science 2021), but only two females have been recorded from the continent (Primorskij Kraj, Russia, by Sundukov 2009). We have seen no specimens of this species from outside Japan.

In the molecular analysis using COI and NaK (Figs 149, 160), the specimens of this species (all from Japan) were retrieved as a clade belonging to a complex of rather poorly resolved *Alnus*- and *Betula*-feeding species of the *P. vafer* group, such as *P. alnivorus*, *P. confusus*, *P. flavipectus* Shinohara, 2005, *P. masao*, *P. nakagawai*, *P. pallipes*, *P. archiducalis* and *P. varius* (Serville, 1823).

Pamphilius kimi Shinohara, 1997

(Fig. 89) (https://doi.org/10.6084/m9.figshare.11405214)

Pamphilius kimi Shinohara, 1997: 227; Shinohara, 2002b: 429; Shinohara, 2004: 264; Taeger *et al.*, 2010: 88; Lee *et al.*, 2019: 10.

Material examined. Fifty-five specimens (type series) from South Korea (Shinohara 1997).

Distribution. South Korea.

Host plant. Unknown.

Remarks. *Pamphilius kimi* was described from a series of male specimens collected on the mountains of Gangwon-do, South Korea between 1992 and 1997 (Shinohara 1997). No additional collection records have been published and the females are still unknown. No molecular data for this species are available.

This is an isolated species in the *P. vafer* group and forms a subgroup of its own, the *P. kimi* subgroup (Shinohara 2002b). It is one of the three species of *Pamphilius* (*P. heecheonparki*, *P. varius* and *P. kimi*) whose males are characterized by the anchor-shaped penis valves. From *P. heecheonparki* and *P. varius*, *P. kimi* is distinguished by the arcuately concave inner margin of the harpe (Figs 11: 61a; 89h, i).

Pamphilius leleji Shinohara & Taeger, 2007

(Figs 94–96) (https://doi.org/10.6084/m9.figshare.11405220)

Pamphilius leleji Shinohara & Taeger, 2007: 35; Shinohara & Lelej, 2007: 938, 942; Taeger *et al.*, 2010: 88; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105.

Material examined. Twenty-three specimens, including the type series, all from the Russian Far East (Shinohara & Taeger 2007; present work). The holotype has been deposited in ZISP. **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (Fig. 95, DEI-GISHym 86269), Arsenyev, Ski-Base Bodrost, 200m, 44.122°N 133.270°E, 25. V. 2016, K. Kramp, M. Prous & A. Taeger, RU017 (SDEI); 1♀ (DEI-GISHym 32051), Komissarovo N, 130m, 45.000°N 131.788°E, 4. VI. 2016, K. Kramp, M. Prous & A. Taeger, in alcohol, RU035 (SDEI); 1♀ (DEI-GISHym 32032), Zolotaya Dolina E, 40m, 42.943°N 133.161°E, 10. VI. 2016, K. Kramp, M. Prous & A. Taeger, in alcohol, RU046 (SDEI); 1♀ (DEI-GISHym 21847), Sikhote-Alin Reserve: Middle Kolume river, salty ground, forest, 45.500°N 135.900°E, 18. VI. 2015, M. Sergeev (SDEI).

Distribution. Russia (Primorskij Kraj).

Host plant. Unknown.

Remarks. So far as is known, this species is endemic to Primorskij Kraj. In our molecular analysis, the maximum intraspecific *p*-distance was 0.2% in COI (n=3) and 0% in NaK (n=3). The nearest neighbour was *P. kamikochensis* (a member of the *P. albopictus* subgroup), diverging by a minimum of 3.1% in the COI analysis, and by a minimum of 0.8% in the NaK analysis. *Pamphilius leleji* was recovered as sister to the clade *P. albopictus* + *P. kamikochensis* with 100% UFBoot support in the COI tree (Fig. 148) but as sister to *P. aucupariae* with 98% UFBoot support in the NaK tree (Fig. 161).

Pamphilius lobatus Maa, 1950

(Figs 97–99) (https://doi.org/10.6084/m9.figshare.11405238)

Pamphilius lobatus Maa, 1950: 17; Shinohara, 1988b: 194; Kim *et al.*, 1994: 217; Shinohara & Lee, 1997: 220; Shinohara, 2002b: 427: Shinohara, 2004: 264; Shinohara & Taeger, 2007: 38; Shinohara & Lelej, 2007: 932, 940; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 88; Shinohara & Hara, 2011: 213; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105; Lee *et al.*, 2019: 10; Shinohara, 2019: 10; Shinohara, 2020: 15, 245; Shinohara & Tripotin, 2021a: 62; Shinohara & Tripotin, 2021b: 197.

Material examined. About 230 specimens, including 145 specimens from the Russian Far Est and South Korea (Shinohara 1988b; Shinohara & Lee 1997; Shinohara & Taeger 2007; Shinohara & Tripotin 2021a, b; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀, Lazovsky distr., upstream of Luk'yanov Log Creek, Malaise trap, 25. VI. 2008, Yu. Sundukov, YS034 (SDEI); 1♀ (Fig. 98, DEI-GISHym 88047), Anisimovka 7 km S, Mt. Litovka, 1200m, 43.102°N 132.786°E, 19. VI. 2017, V. Loktionov (SDEI). **SOUTH KOREA: Gangwon-do:** 1♂, Tokchomgogae, nr. Chuncheon, 22. V. 1992, A. Shinohara (NSMT). 1♂, Jingogae, 850m, Odaesan Mts., 2. VI. 1992, A. Shinohara (NSMT). 1♀2♂, Mirugam (Bukdaesa), 1300m, Odaesan Mts., 21–26. V. 1989, A. Shinohara (NSMT); 4♀6♂, same locality, 29. V.–2. VI. 1991, A. Shinohara (NSMT); 1♀2♂, same locality, 30. V.–2. VI. 1992, A. Shinohara (NSMT); 1♀1♂, same locality, 27–29. V. 1993, A. Shinohara (NSMT); 2♀1♂, same locality, 29. V.–6. VI. 1996, J.-W. Kim (NSMT); 2♀, same locality, 3–7. VI. 1997, A. Shinohara (NSMT); 2♂, same locality, 29–30. V. 1998, A. Shinohara (NSMT); 3♀8♂, same locality, 23. V.–4. VI. 2002, A. Shinohara (NSMT); 1♀2♂ (NSMT 30763–5), same locality, 27–30. V. 2008, A. Shinohara (NSMT); 4♀14♂ (incl. NSMT 30856, 30862), same locality, 27. V.–5. VI. 2009, A. Shinohara (NSMT); 1♀6♂, same locality, 11–18. VI. 2010, A. Shinohara (NSMT). **Jeollanam-do:** 1♂, Mt. Nogodan, 1200m, Chirisan Mts., 4–5. VI. 1996, A. Shinohara (NSMT); 1♀, same data, 26–28. V. 1997 (NSMT).

Distribution. Russia (Primorskij Kraj), China (Jilin), South Korea, Japan (Hokkaido, Honshu) (Shinohara & Taeger 2007).

Host plant. Caprifoliaceae: *Macrodiervilla middendorffiana* (Carriere) Nakai (Shinohara & Hara 2011).

Remarks. This species belongs to the *P. thorwaldi* complex of the *P. stramineipes* subgroup of the *P. vafer* group (Shinohara 2002b). The *P. thorwaldi* complex is represented by *P. lobatus*, *P. belokobylskiji*, *P. planifrons*, *P. rhoae* and *P. thorwaldi* Kontuniemi, 1946, and *P. lobatus* has the widest range of distribution among the East Asian members.

It should be noted that in the COI analysis (Fig. 149) nine sequences of this species were retrieved as two separate clades, the Japanese specimens (n=3) and the Korean and Russian specimens (n=6). The maximum *p*-distance among the Japanese specimens was 0.9% and that among the Korean and Russian specimens was 0.2% whereas the two sets of sequences diverged by a minimum of 2.7%. The last value is quite large as an intraspecific distance and comparable to the interspecific distance between closely related congeners, such as *P. albopictus* and *P. kamikochensis* (2.0%) or *P. benesi* and *P. pallidus* (2.9%). In the NaK analysis (Fig. 161), the Japanese and the continental clusters were not clearly differentiated. Here we treat the continental and Japanese populations as conspecific, though a fairly large geographical genetic diversification apparently exists between them.

Pamphilius masao Shinohara, 2005

(Figs 100, 101) (https://doi.org/10.6084/m9.figshare.11405247)

Pamphilius masao Shinohara, 2005: 55; Shinohara & Hara, 2005: 275; Shinohara & Lelej, 2007: 937, 942; Taeger *et al.*, 2010: 88; Sundukov & Lelej, 2012: 109; Sundukov, 2015: 250; Sundukov, 2017: 104; Shinohara, 2019: 10; Shinohara, 2020: 23, 253.

Material examined. About 3240 specimens, including the type series. Five specimens are from the Russian Far East (Shinohara 2005; present work). **New collection data: RUSSIA: Sakhalin**: 1♀, Matolozovo, 2–3. VII. 1991 (NSMT).

Distribution. Russia (Sakhalin), Japan (Hokkaido, Etorofu Is., Kunashiri Is., Shikotan Is.) (Shinohara 2005; Sundukov 2015).

Host plant. Betulaceae: *Betula ermanii* Cham., *Alnus maximowiczii* Call. (Shinohara 2005; Shinohara & Hara 2005).

Remarks. This species is a member of the *P. vafer* complex (Shinohara 2005) or the *P. vafer* subgroup of the *P. vafer* group (Shinohara 2002b), which is a complex of birch- or alder-feeding species having much in common morphologically and genetically (see also comments under *P. alnivorus*). The larva of *P. masao* is a solitary leaf-roller. The egg is laid on the upperside and the larval leaf-roll is also on the upperside of the leaf (Type III of Shinohara 2005). This character is known otherwise only for *P. confusus* and *P. flavipectus* from Japan (Shinohara & Kojima 2006).

Pamphilius masao is fairly common in montane birch forests in Hokkaido, Japan (2769 Japanese specimens recorded by National Museum of Nature and Science 2021), but only a few specimens were recorded from Sakhalin, Russia (Shinohara 2005).

Pamphilius pallipes (Zetterstedt, 1838)

(Figs 108, 109) (https://doi.org/10.6084/m9.figshare.11405268)

Lyda pallipes Zetterstedt, 1838: 355.

Pamphilius pallipes: Kirby, 1882: 337; Konow, 1897a: 25, 31; Gussakovskij, 1935: 185, 377; Berland, 1947: 56; Verzhutskij, 1966: 28; Achterberg & Aartsen, 1986: 43; Zhelochovtsev & Zinovjev, 1995: 398; Taeger *et al.*, 1998: 105; Shinohara, 2002b: 427; Shinohara, 2003a: 467; Shinohara, 2005: 40; Shinohara & Lelej, 2007: 937, 942; Taeger *et al.*, 2010: 89; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105; Lee *et al.*, 2019: 10; Shinohara & Tripotin, 2021a: 62.

Material examined. About 455 specimens, including the lectotype; 204 specimens are from the Russian Far East and Korea (Shinohara 2005; Shinohara & Tripotin 2021a; present work). **New collection data: SOUTH KOREA: Gangwon-do**: 4♀1♂ (incl. NSMT 30756–30759), Mirugam (Bukdaesa), 1300m, Odaesan Mts., 26. V.–2. VI. 2008, A. Shinohara (NSMT); 1♂, same locality, 28. V. 2009, A. Shinohara (NSMT).

Distribution. Europe, Iran, Siberia to Kamchatka Kraj and the continental part of the Russian Far East, northeastern China, North and South Korea (Shinohara 2005).

Host plant. Betulaceae: *Betula* spp., ?*Alnus* spp. (Taeger *et al.* 1998; Shinohara 2003a, 2005).

Remarks. This is a widely distributed Palaearctic species but not recorded from Japan (Shinohara 2003a, 2005). It belongs to the *P. vafer* complex (Shinohara 2005) or the *P. vafer* subgroup of the *P. vafer* group (Shinohara 2002b). The larva is a solitary leaf-roller, making a leaf-roll on the underside. The oviposition is on the upperside (Type II of Shinohara 2005). As noted under *P. alnivorus*, the site of oviposition (upperside of a leaf) and direction of leaf-rolling (underside) in this species and *P. alnivorus* are characteristic.

Pamphilius planifrons Beneš, 1976

(Figs 111, 112) (https://doi.org/10.6084/m9.figshare.11405274)

Pamphilius planifrons Beneš, 1976: 164; Shinohara, 1988b: 184; Shinohara, 2002b: 427; Shinohara, 2004: 264; Shinohara & Lelej, 2007: 932, 940; Taeger *et al.*, 2010: 90; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105; Lee *et al.*, 2019: 11.

Material examined. Eighteen specimens, including the holotype, all from the Russian Far East (Beneš 1976; Shinohara 1988, see comments below about the males; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♂, Ussurijskij Reserve, 21–26. V. 1994, A. Shinohara (Fig. 112, NSMT); 6♀, same locality, 9–12. VI. 1995, A. Shinohara (Fig. 111, NSMT); 2♀, same locality, 9–12. VI. 1995, A. Lelej (NSMT); 1♂, Okeanskaja, Vladivostok, 28. V. 1994, A. Shinohara (NSMT); 1♀, Anisimovka, 300m, 1. VI. 1994, A. Shinohara (NSMT); 1♀, Uglekamensk, 2. VI. 1994, A. Shinohara (NSMT); 2♀, Valley of Tigrovaja River, 180m, 12km N of Partizansk, 6. VI. 1994, A. Shinohara (NSMT); 1♀ (DEI-GISHym 32052), Arsenyev, Ski-Base Bodrost, 200m, 44.122°N 133.270°E, 25. V. 2016, K. Kramp, M. Prous & A. Taeger, RU017 (SDEI); 2♀ (DEI-GISHym 12992 & 32040), Zolotaya Dolina E, 40m, 42.943°N 133.161°E, 10. VI. 2016, K. Kramp, M. Prous & A. Taeger, in alcohol, RU046 (SDEI).

Distribution. Russia (Primorskij Kraj).

Host plant. Unknown.

Remarks. This species is a member of the *P. thorwaldi* complex of the *P. stramineipes* subgroup of the *P. vafer* group (Shinohara 2002b). Shinohara (1988b) recorded this species from South Korea based on two male specimens as *P. planifrons*. These two males actually belong to the new species *P. belokobylskiji* described above, and South Korea is here excluded from the distribution of *P. planifrons*. *Pamphilius planifrons* is most closely allied to *P. rhoae*, as discussed under the latter species. In the molecular analyses using COI and NaK sequences (Figs 149, 161), the relationships between *P. belokobylskiji*, *P. planifrons* and *P. rhoae* were poorly resolved.

Pamphilius rhoae Shinohara 1988

(Figs 113, 114) (https://doi.org/10.6084/m9.figshare.11405286)

Pamphilius rhoae Shinohara 1988b: 188; Kim *et al.*, 1994: 217; Shinohara & Lee, 1997: 218; Shinohara, 2002b: 427; Shinohara, 2004: 264; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 90; Lee *et al.*, 2019: 10; Shinohara & Tripotin, 2021: 62; Shinohara & Tripotin 2021b: 197.

Material examined. Seventy-two specimens, including the type series, all from South Korea (Shinohara 1988b; Shinohara & Lee 1997; Shinohara & Tripotin 2021a, b; present work). **New collection data: SOUTH KOREA: Gangwon-do**: 1♀, Tokchomgogae, 510m, nr. Chuncheon, 22. V. 1992, A. Shinohara (NSMT); 1♀, Sangwonsa, Odaesan Mts., 20. V. 1989, A. Shinohara (NSMT); 1♀ (NSMT 30858), same locality, 6. VI. 2009, A. Shinohara (NSMT); 1♀, Mirugam (Bukdaesa), 1300m, Odaesan Mts., 6. VI. 1996, J.-W. Kim (NSMT).

Distribution. South Korea.

Host plant. Unknown.

Remarks. This Korean species belongs to the *P. thorwaldi* complex of the *P. stramineipes* subgroup of the *P. vafer* group (Shinohara 2002b). It is very close to *P. planifrons* from Primorskij Kraj in morphology and genetics (Figs 149, 161). Although most of the known specimens can be identified by the characters given in the key, the two species may eventually be treated as local forms of the same species. Before synonymizing them, however, we still need more information about geographical variations and preferably also host plants and immature stages.

Pamphilius sapporensis (Matsumura, 1912)

(Figs 115, 116) (https://doi.org/10.6084/m9.figshare.11405283)

Lyda sapporensis Matsumura, 1912: 80; Takeuchi, 1930: 9 (syn. of *P. venustus* (Smith, 1874)).
Pamphilius rugosus Beneš, 1976: 165; Shinohara & Okutani, 1983: 278 (syn. of *P. sapporensis*).
Pamphilius sapporensis: Shinohara & Okutani, 1983: 278; Zhelochovtsev & Zinovjev, 1995: 398; Shinohara, 2002b: 427; Shinohara, 2004: 264; Shinohara & Taeger, 2007: 38; Shinohara & Lelej, 2007: 931, 940; Taeger *et al.*, 2010: 90; Sundukov & Lelej, 2012: 109; Sundukov, 2015: 250; Sundukov, 2017: 105; Shinohara, 2019: 11; Shinohara, 2020: 13, 243.

Lectotype designation. Matsumura (1912) described *Lyda sapporensis* without giving number of the specimens examined. Here we designate the male specimen labeled "Sahoro, 6/5" "29" "*Lyda sapporensis* n. sp. det. Matsumura" in Matsumura's collection (HU) as a lectotype. It is in poor condition and has the head and genitalia missing.

Material examined. About 545 specimens, including the lectotype, and two specimens from the Russian Far East (Shinohara 2002b; Shinohara & Taeger 2007).

Distribution. Russia (Sakhalin), Japan (Hokkaido, Shikotan Is.) (Shinohara & Taeger 2007).

Host plant. Rosaceae: *Filipendula camtschatica* (Pall.) Maxim. (Shinohara & Okutani 1983).

Remarks. Shinohara (2002b) placed this species in his *P. venustus* complex of the *P. stramineipes* subgroup of the *P. vafer* group. *Pamphilius sapporensis* has much in common with *P. venustus* in morphology, molecular data (see below) and host plants, and overlapping distributions of the two species in Hokkaido is interesting in clarifying their speciation history. The maximum intraspecific *p*-distance among the three Japanese specimens in *P. sapporensis* was 0.3% in COI and 0.1% in NaK and the nearest neighbour was *P. balteatus*, diverging by a minimum of 2.5% in the COI analysis, and *P. venustus* by a minimum of 0.8% in the NaK analysis. In the COI tree (Fig. 149), the relationship of *P. sapporensis* with other species was not well resolved, but in the NaK tree (Fig. 161), *P. sapporensis* was retrieved as the sister of *P. venustus* with 99% UFBoot support.

In Hokkaido, Japan, this species occurs together with two other *Filipendula*-associated pamphiliids, *P. venustus* (known from Hokkaido, Honshu and Shikoku) and *Onycholyda kumamotonis* (known from Sakhalin, Hokkaido, Kunashiri Is., Honshu and ?Kyushu). The largely orange upper part of head will easily distinguish *P. sapporensis* from the latter two species.

Pamphilius stramineipes (Hartig, 1837)

(Figs 117, 118) (https://doi.org/10.6084/m9.figshare.11405295)

Lyda stramineipes Hartig, 1837: 347.

Pamphilius stramineipes: Kirby, 1882: 337; Konow, 1897a: 25, 31; Gussakovskij, 1935: 184, 377; Berland, 1947: 53; Achterberg & Aartsen, 1986: 43; Shinohara, 1988b: 181; Shinohara & Hara, 1991: 734; Hara, 1993: 293; Zhelochovtsev & Zinovjev, 1995: 398; Taeger *et al.*, 1998: 105; Shinohara, 2002b: 427; Shinohara, 2004: 264; Shinohara & Hara, 2005: 275; Shinohara & Lelej, 2007: 938, 940; Taeger *et al.*, 2010: 90; Sundukov & Lelej, 2012: 109; Sundukov, 2017: 105; Shinohara, 2019: 11; Shinohara, 2020: 15, 245.

Anoplolyda pallipes: Takeuchi, 1936a: 61 (not Zetterstedt, 1838, in part).

For more references, see Shinohara (1988b).

Material examined. About 425 specimens, including two specimens from the Russian Far East (Shinohara 1988b).

Distribution. Europe, Armenia, Russia (Siberia, Sakhalin), Japan (Hokkaido, Etorofu Is., Kunashiri Is.) (Shinohara 1988b; Sundukov & Lelej 2012).

Host plant. Rosaceae: *Rosa* spp. (Hara 1993; Shinohara & Hara 2005). Records of other plants in Europe (*Crataegus*, *Fragaria*, *Rubus* and *Sanguisorba*, see Taeger *et al.* 1998) need confirmation.

Remarks. This species belongs to the *P. stramineipes* complex of the *P. stramineipes* subgroup of the *P. vafer* group (Shinohara 2002b). Shinohara (2002b) included *P. stramineipes*, *P. thorwaldi* and *P. venustus* complexes in his *P. stramineipes* subgroup, while our molecular analyses did not indicate a close relationship among the three species complexes. In our COI analysis (Fig. 151), the three specimens of *P. stramineipes* from Japan and Italy were retrieved as a monophyletic group (with 93% UFBoot support), which was sister (with 100% UFBoot support) to the clade of 26 specimens of *P. hortorum*. In the NaK analysis (Fig. 161), the two sequences of *P. stramineipes* from Japan formed a clade with 100% UFBoot support. This clade then came close to *P. togashii* and *P. heecheonparki*, but this relationship had low UFBoot supports of 42 and 58%.

Pamphilius stramineipes is a Palaearctic species widely spread from western Europe through Siberia and Sakhalin to Hokkaido, Japan. However, there are no collection records from other areas of the Russian Far East (e.g., Primorskij Kraj) and Korea.

Pamphilius varius (Serville, 1823)

(Figs 127–129) (https://doi.org/10.6084/m9.figshare.11405325)

Lyda varia Serville, 1823: 90.

Anoplolyda engelhardti Dovnar-Zapolskij, 1930: 93; Gussakovskij, 1935: 183, 381 (syn. of *P. varius*).

Pamphilius varius: Gussakovskij, 1935: 183, 381; Takeuchi, 1938: 223; Doi, 1938: 32; Berland, 1947: 55; Kim, 1963: 278;

Verzhutskij, 1966: 28; Kim, 1970: 126; Shinohara & Okutani, 1983: 279; Achterberg & Aartsen, 1986: 45; Kim *et al.*, 1994: 217; Zhelochovtsev & Zinovjev, 1995: 398; Taeger *et al.*, 1998: 106; Shinohara, 2002b: 428; Shinohara, 2004: 264; Shinohara & Hara, 2005: 276; Shinohara & Lelej, 2007: 940, 941; Sundukov, 2009: 213; Paek *et al.*, 2010: 161; Taeger *et al.*, 2010: 91; Sundukov & Lelej, 2012: 109; Sundukov, 2015: 250; Sundukov, 2017: 105; Lee *et al.*, 2019: 11; Shinohara, 2019: 12; Shinohara, 2020: 21, 251.

Anoplolyda vafer: Takeuchi, 1936a: 61. Not Linné, 1767.

For more synonyms and references, see Berland (1947) and Taeger *et al.* (2010).

Material examined. About 2460 specimens, including 1004 specimens from the Russian Far Est and South Korea (Takeuchi 1936a; National Museum of Nature and Science 2021; present work). **New collection data: RUSSIA: Primorskij Kraj**: 1♀ (Fig. 127, DEI-GISHym 86311), Yakovlevka 12km NW, 250m, 44.541°N 133.366°E, 27. V. 2016, K. Kramp, M. Prous & A. Taeger, RU019 (SDEI). **SOUTH KOREA: Gangwon-do**: 4♂ (incl. NSMT 30760–30762), Mirugam (Bukdaesa), 1300m, Odaesan Mts., 25–30. V. 2008, A. Shinohara (NSMT); 1♀28♂, same locality, 28. V.–5. VI. 2009, A. Shinohara (NSMT); 14♀1♂, same locality, 11–18. VI. 2010, A. Shinohara (NSMT).

Distribution. Europe, through Siberia to the Russian Far East (Kamchatka Kraj, Primorskij Kraj, Sakhalin, northern Kuriles), North and South Korea and Japan (Hokkaido, southern Kuriles, Honshu, Kyushu).

Host plants. Betulaceae: *Betula* spp., *Alnus incana* (Taeger *et al.* 1998; Shinohara & Hara 1999, 2005).

Remarks. This is a widely distributed northern Palaearctic species, often commonly found in birch forests on higher mountains in Korea and Japan. *Pamphilius varius* belongs to the *P. varius* subgroup of the *P. vafer* group (Shinohara 2002b). This species looks similar to the species of the *P. vafer* complex (Shinohara 2005) or the *P. vafer* subgroup of the *P. vafer* group (Shinohara 2002b), such as *P. alnivorus*, *P. masao* or *P. pallipes*, but the usually impunctate or sparsely punctate, almost glabrous upper part of head, the small and pilose ovipositor sheath appendage in the female and the characteristic anchor-shaped valviceps in the male genitalia (Fig. 129g, h) will easily separate *P. varius*. In our molecular analysis, however, available sequences of this species were not well resolved and did not even form a single cluster. It is interesting that the European (German and Finnish) specimens were retrieved as close to the Japanese (in-group distances 0.2–0.9% in Europe and distances between Europe and Japan 1.1–1.7%) and these were placed at a distance (3.7–5.3%) from the specimens from Primorskij Kraj and South Korea (in-group distances 0.1–1.3%, excluding one doubtfully identified larval specimen) in the COI analysis (Fig. 150). The genetic variations and affinities of this and the related species are still poorly understood.

Concluding remarks

We have recognized four genera and 58 species of Pamphiliinae from the Russian Far East and Korea. These are two-thirds of the world genera and about 30% of the world species. Of the 58 species, 34 (59%) occur in both areas, whereas ten species were not found in the Russian Far East and 14 species were not found in Korea. In other words, 48 species were recorded from the Russian Far East and 44 species from Korea. Four species (*P. pictifrons*, *P. viridulus*, *P. leleji* and *P. planifrons*) are known only from the Russian Far East (*P. pictifrons* also from the Sakha Republic) and six species (*N. coreana*, *N. satoi*, *N. silla*, *P. ochrostigma*, *P. kimi* and *P. rhoae*) are known only from Korea. Fifteen species are known only from the two areas combined except for *O. armata*, which is also recorded from Tomsk and northeastern China (Jilin), and *O. nigroclypeata*, which is also recorded from northeastern China (Heilongjiang). Therefore, the number of species currently regarded as endemic (nearly so for the two *Onycholyda* species mentioned above) to the Russian Far East and Korea is 25, or 43% of the 58 species recorded so far. The number of these apparently "endemic" species will certainly be reduced when more material becomes available, particularly from northeastern China. Twelve species have a broad Palaearctic distribution from Europe (one from Orenburg and one from the Urals) to the Far East, eight species further to Japan (one as a different subspecies). Twenty-nine species (50% of the 58 species recorded) are also known in Japan, three species (*P. brevicornis*, *P. sulphureipes* and *P. zhelochovtsevi*) in different subspecies. The pamphiliine fauna of the Russian Far East and Korea may be characterized by the rich representation of the *P. histrio* group (55% of the world species), *P. sulphureipes* group (60% of the world species), *P. sylvaticus* group (50% of the world species) and *P. vafer* group (53% of the world species).

Of the 48 species recorded from the entire Russian Far East (narrow sense, 3,075,397 square kilometers), 38

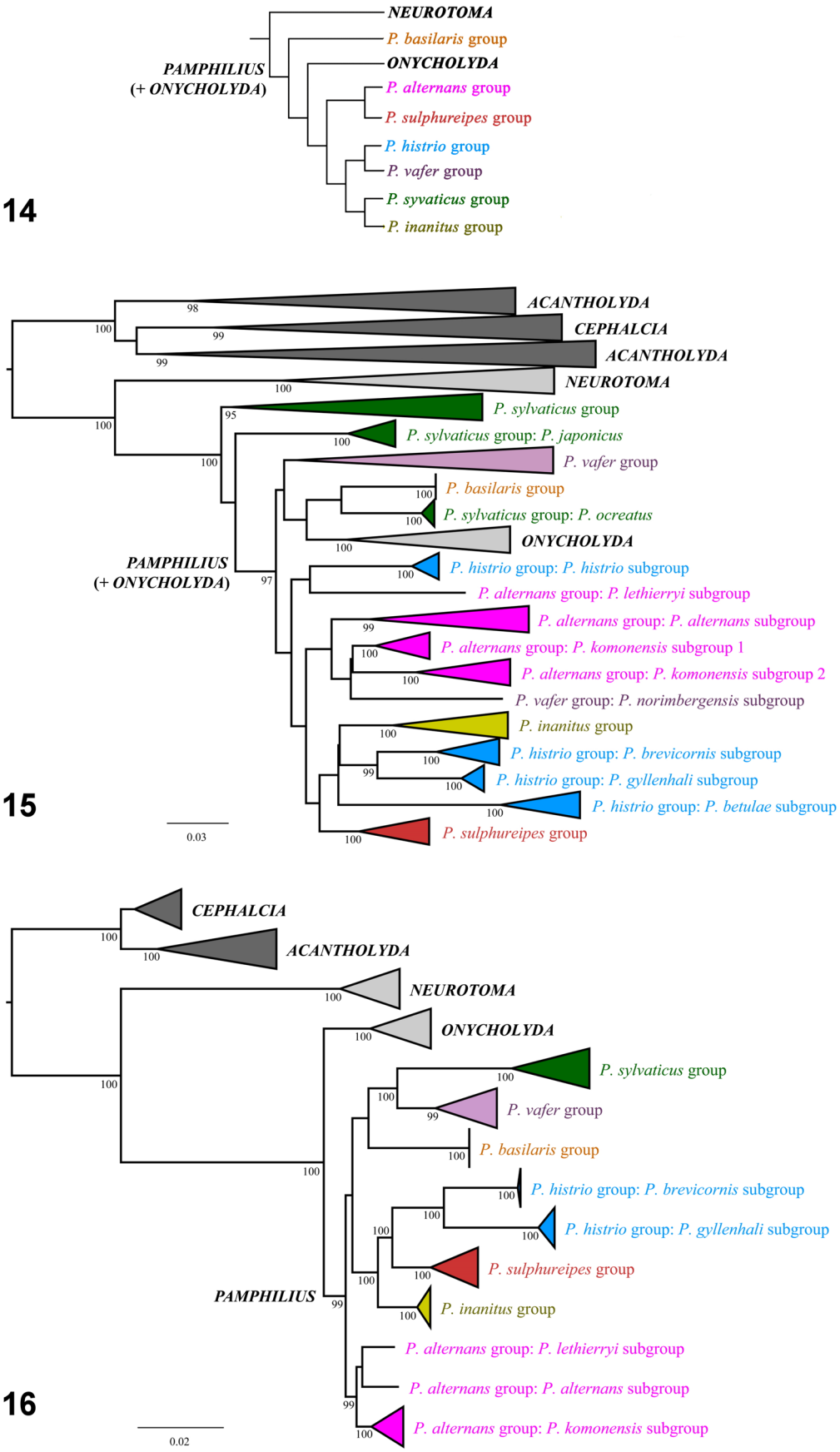
species (79%) occur in a comparatively small area of Primorskij Kraj (164,700 square kilometers, only 5.4% of the Russian Far East), while four others (*P. pictifrons*, *P. virescens*, *P. montanus pulcher* and *P. aucupariae*) are not known from Primorskij Kraj but known from Magadan Oblast and Kamchatka Kraj and from East Siberia and five others (*O. kumamotonis*, *O. yezoensis*, *P. archiducalis*, *P. masao* and *P. sapporensis*) are known in the Russian Far East only from Sakhalin, all of them otherwise occurring in Japan. The remaining species, *P. stramineipes*, is not known from Primorskij Kraj but is widely spread from Europe through Siberia to Sakhalin and Japan (Hokkaido). Of the 38 species known from Primorskij Kraj, 31 species (82%) occur also in Korea and 17 species (45%) occur also in Japan (three species in different subspecies), whereas three species (8%, *P. viridulus*, *P. leleji* and *P. planifrons*) are endemic to Primorskij Kraj.

Of the 44 species of Pamphiliinae recognized in Korea, three species, *O. sertata*, *P. balteatus* and *P. hortorum*, are known only from a few old specimens collected in the 1930s in the mountainous regions of North Korea (Shinohara 1985b, 2002b; Shinohara & Byun 1993). They have not been found in South Korea, though fairly thorough sampling has been made there. In South Korea, 41 species have been recorded, a great diversity if we consider the area of the country (100,339 square kilometers), which is much smaller than Primorskij Kraj (38 species in 164,700 square kilometers) or the entire Russian Far East (narrow sense, 48 species in 3,075,397 square kilometers). Japan has more species (51 species) but has a larger area (the four major islands have 364,805 square kilometers, Wikipedia contributors 2021e), with higher mountains, and its pamphiliine fauna has been very well investigated (Shinohara 2019, 2020). Future discovery of new or unrecorded pamphiliines is doubtless much more likely in South Korea than in Japan (Shinohara 2004). Of the 44 Korean species, 31 species (70%) occur also in Primorskij Kraj and 17 species (39%) occur also in Japan (three species in different subspecies), while six species (14%) are endemic to South Korea.

The current knowledge of the pamphiliine fauna of the Russian Far East and Korea is obviously biased by the availability of material. Most of the available material so far has been obtained from Vladivostok region in southern Primorskij Kraj and from a few mountainous areas (e.g. Odaesan and Jirisan mountains) in South Korea. From vast areas of the Russian Far East, except for southern Primorskij Kraj, and North Korea, material available for study is very limited. The host plants, immature stages and life histories of the Far East Russian and Korean Pamphiliinae are almost totally unknown. We are aware of only two papers on three Korean species (Shinohara 1980 on the host of *N. satoi* and Shinohara & Lee 2011 on the hosts and bionomics of *O. nigroclypeata* and *O. odaesana*) and no references at all concerning the Far East Russian species. Though relevant foreign information is available for species occurring also in Europe or Japan, data obtained in the Russian Far East and Korea are important for assessment of current interpretation of taxa and for recognition of possible geographic variations. Despite the limited availability of material from the Russian Far East and Korea, it is clear that these areas have a very rich pamphiliine fauna. Further sampling of the adults, particularly in the huge and little explored areas in the Russian Far East (other than Primorskij Kraj) and North Korea, will be needed for understanding the real diversity of the subfamily in this area.

In this work, we have made assessment of the existing morphology-based hypotheses of monophyly and relationships of the supraspecific taxa and species (sub)groups (Shinohara 2002b) by the molecular analyses using the mitochondrial COI and the nuclear NaK genes. The results of the analyses using three different data sets (morphology, Fig. 14; COI, Fig. 15; NaK, Fig. 16) agreed with each other and supported the monophyly of the subfamily Pamphiliinae, the tribe Neurotomini (the genus *Neurotoma*), the tribe Pamphiliini, the genus *Onycholyda*, and some species (sub)groups in the genus *Pamphilius* (e.g., *P. sulphureipes* group, see discussion under each species groups above). However, the monophyly of the genus *Pamphilius* was not supported by COI analysis and the intratribal relationships in the Pamphiliini is still poorly resolved (Figs 15, 16).

A potential reason for this is that COI barcoding is not suitable for use in phylogenetic reconstruction (Prous *et al.* 2017; Schmidt *et al.* 2017) and that analysis of additional nuclear genes is necessary for this purpose. Further, Patten *et al.* (2015) pointed out in their theoretical approach, that in haplodiploid species groups, a bias towards mitochondrial introgression is almost assured. In our COI data, we found several indications of this kind of introgression. For example, in one individual of *Acantholyda aglaia* Zhelochovtsev, 1968 (DEI-GISHym88081), 41 positions out of 1078 were found to be ambiguous, i.e. there were double peaks in chromatograms of both strands. Other examples are *Pamphilius kyutekparki* (NSMT30755) with 22 ambiguous positions and *P. volatilis* (NSMT30802) with 30 ambiguous positions, both out of 1078 bp in total. Additionally, the substitution rate in mitochondrial DNA is several-fold higher than in nuclear DNA (Ballard & Whitlock 2004, Lavrov 2007), which can also lead to different phylogenetic structures than reconstructed from nuclear analyses.



FIGURES 14–16: 14. Hypothesized relationships based on adult morphology in Pamphiliinae for several genera and species groups of *Pamphilius* (modified from Shinohara 2002b, only genera and species groups with molecular data are included). **15.** Condensed ML tree based on CO1 gene sequences. **16.** Condensed ML tree based on NaK gene sequences.

The present molecular analyses unfortunately did not include the material of three small, isolated genera, *Kelidoptera*, *Pseudocephaleia* and *Chrysolyda*. We certainly need much more work on morphology, bionomics and genetics based on more taxa for resolving the relationships within the Pamphiliini.

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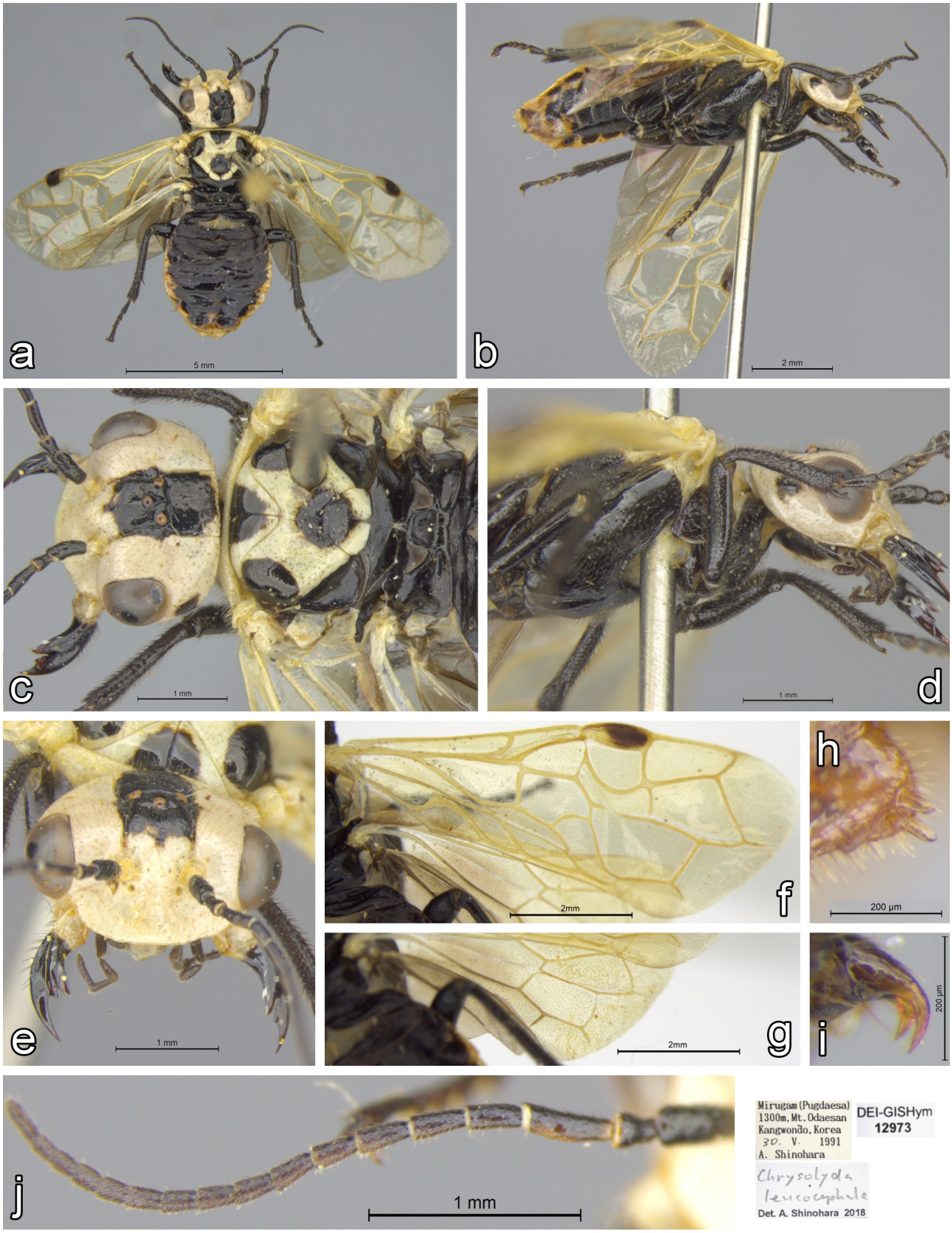


FIGURE 17. ***Chrysolyda leucocephala***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** fore wing, **(g)** hind wing, **(h)** sawsheath laterally, **(i)** claw, **(j)** antenna.

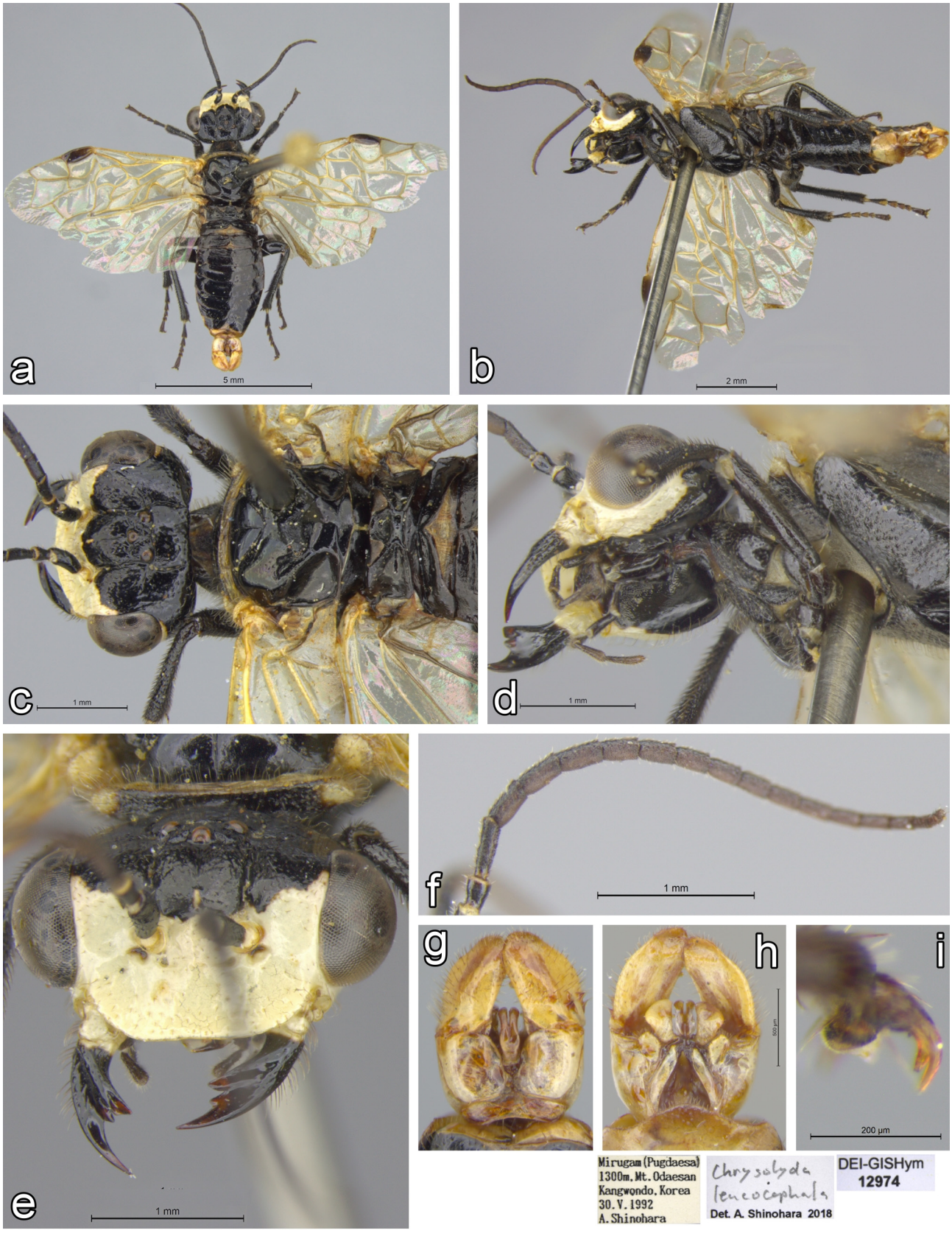


FIGURE 18. ***Chrysolyda leucocephala***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

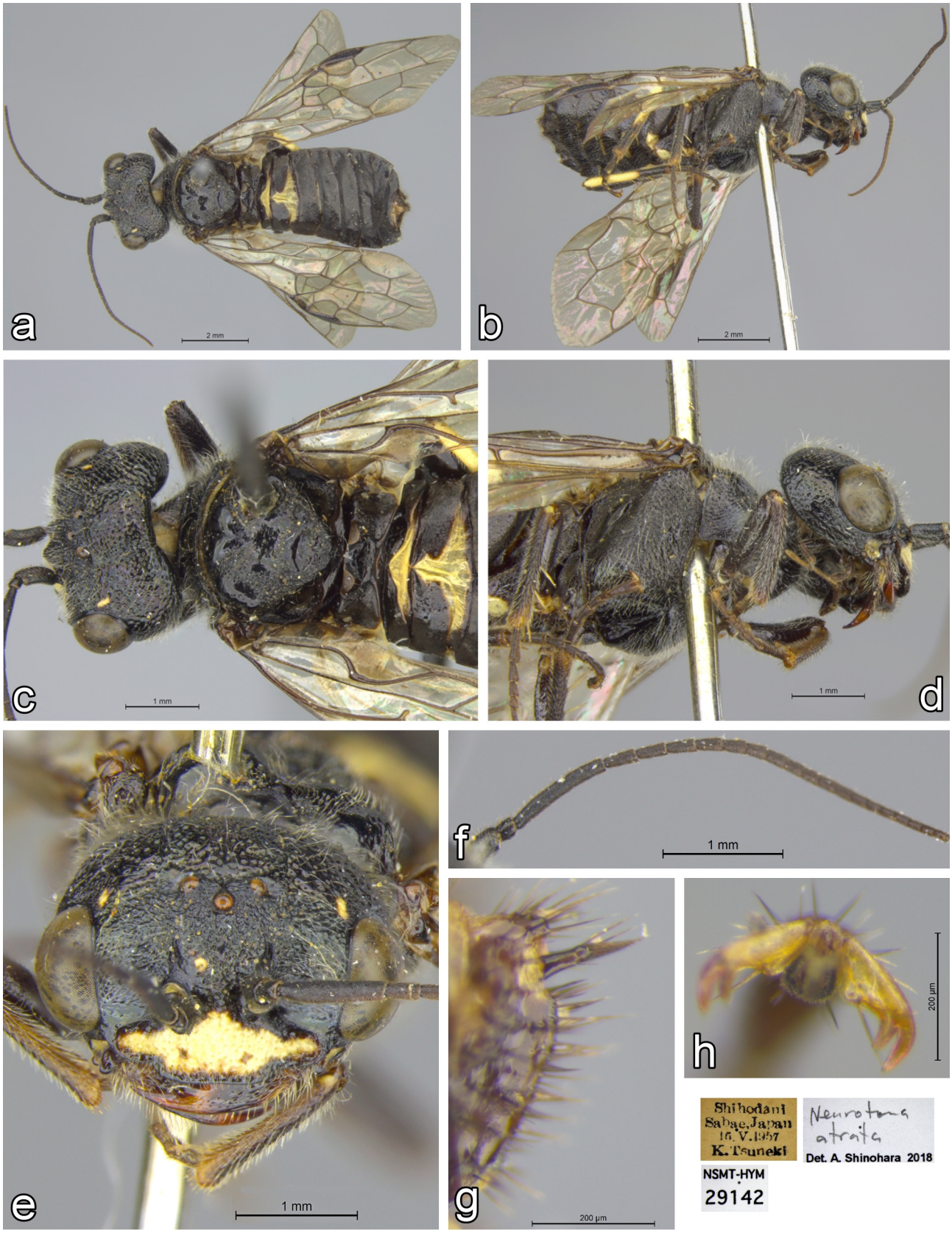


FIGURE 19. ***Neurotoma atrata***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

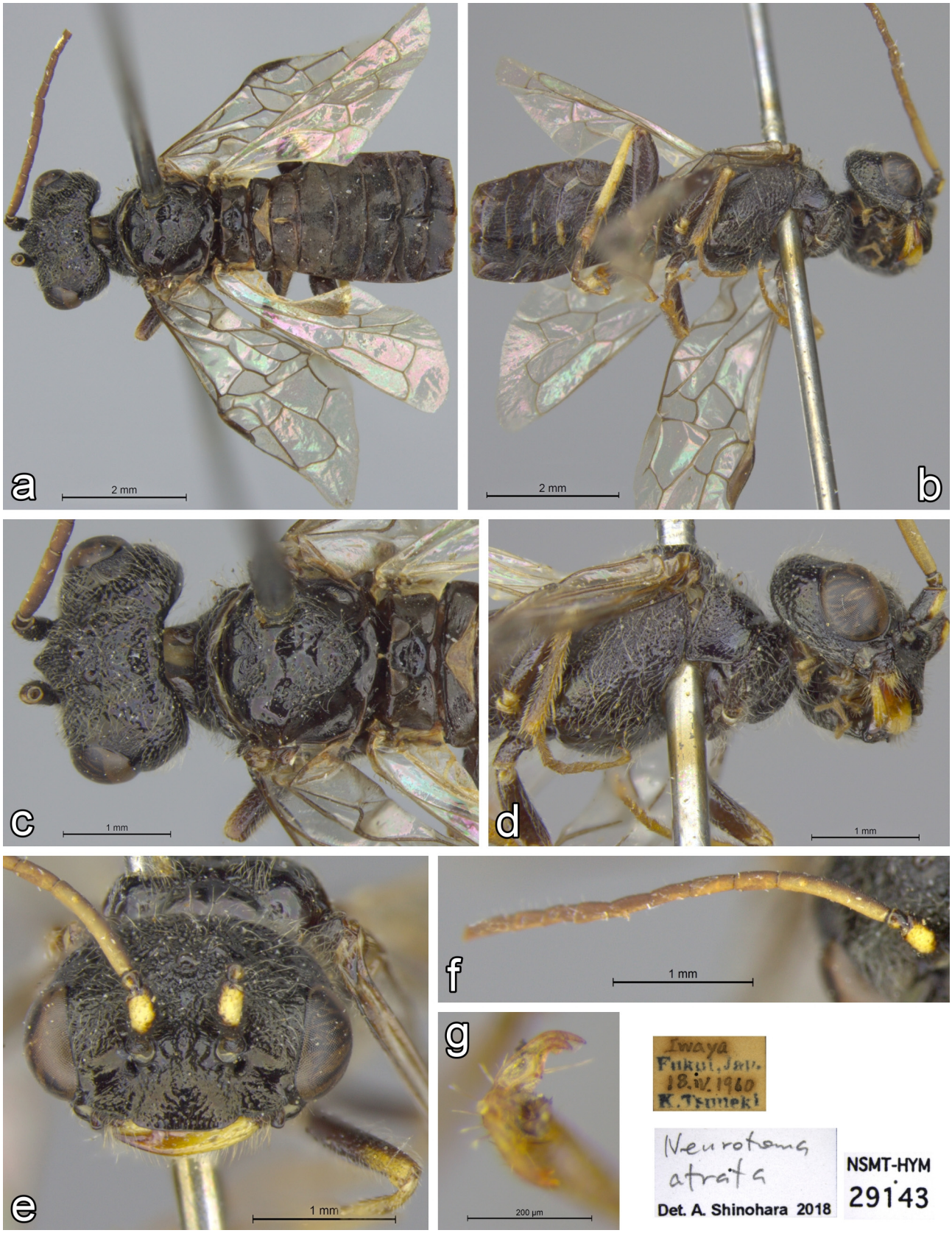


FIGURE 20. ***Neurotoma atrata***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw.

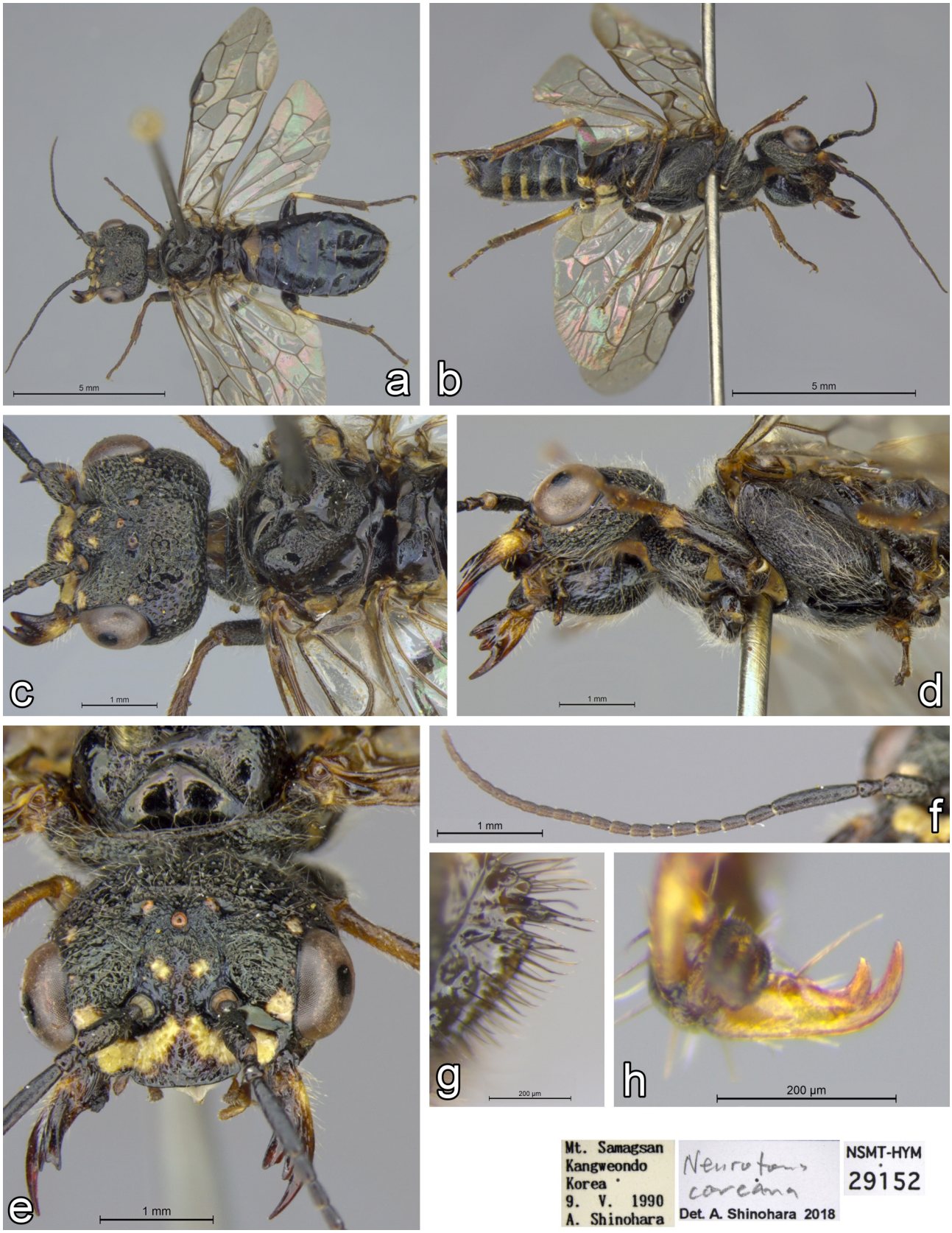


FIGURE 21. ***Neurotoma coreana***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

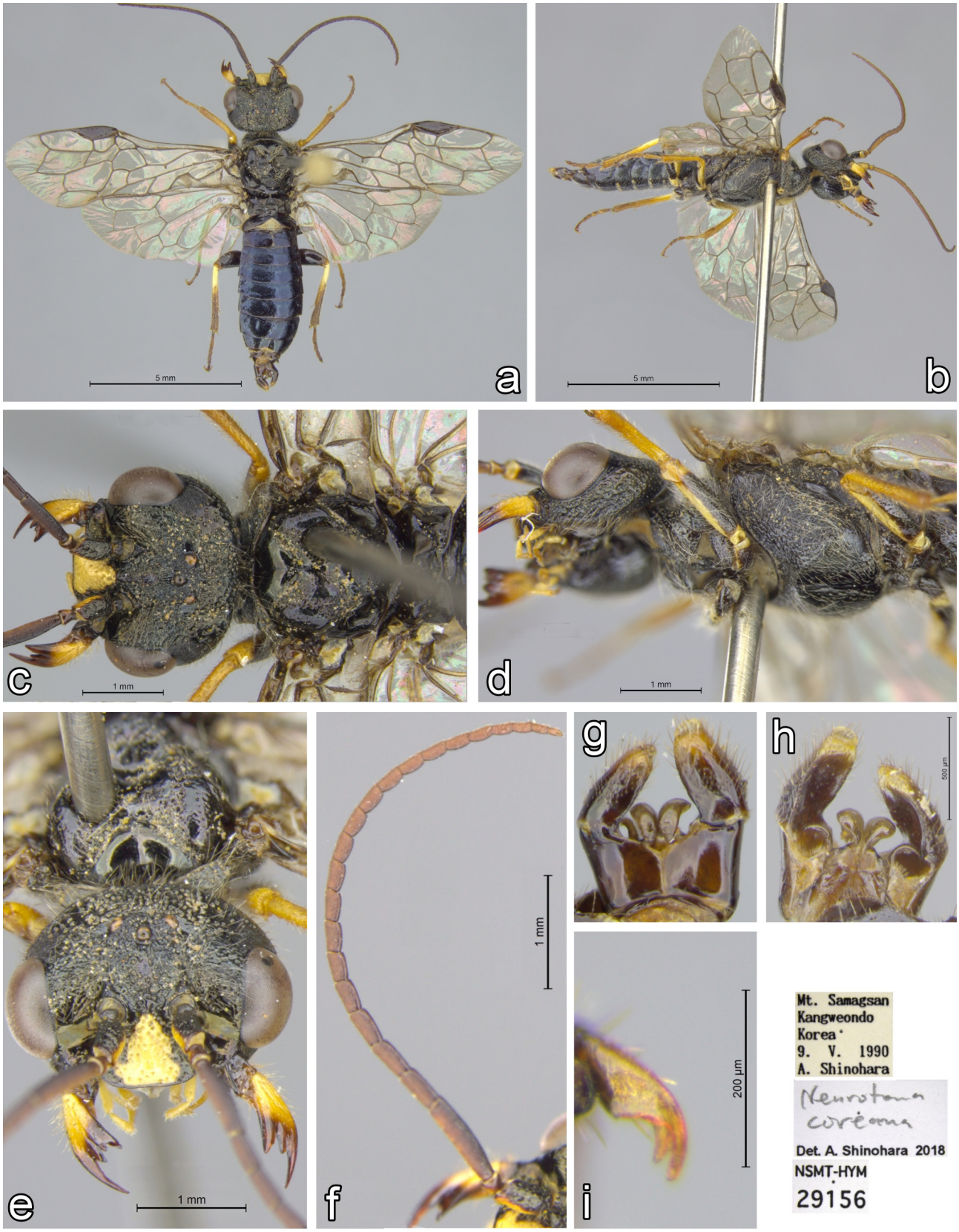


FIGURE 22. ***Neurotoma coreana***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

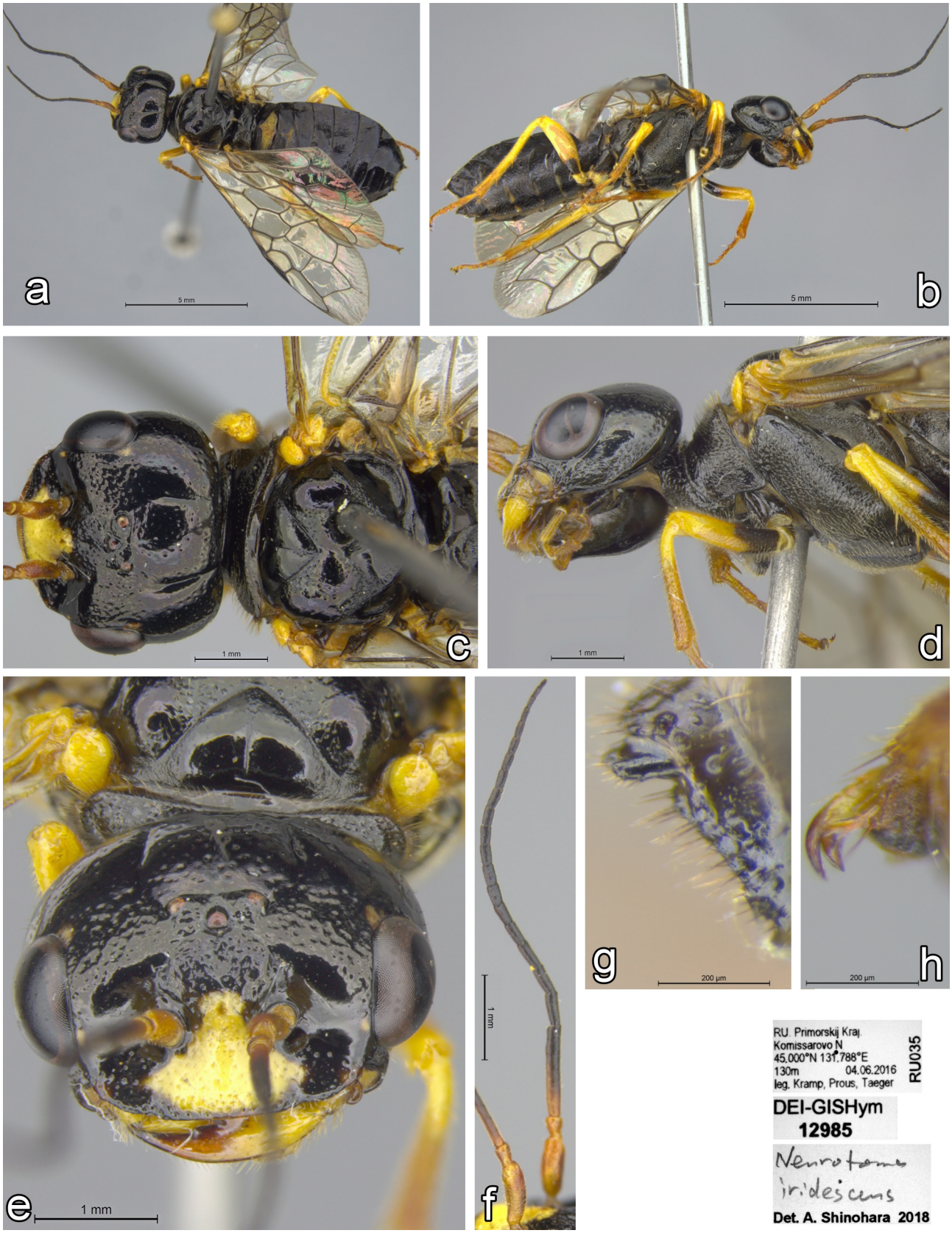


FIGURE 23. ***Neurotoma iridescens***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

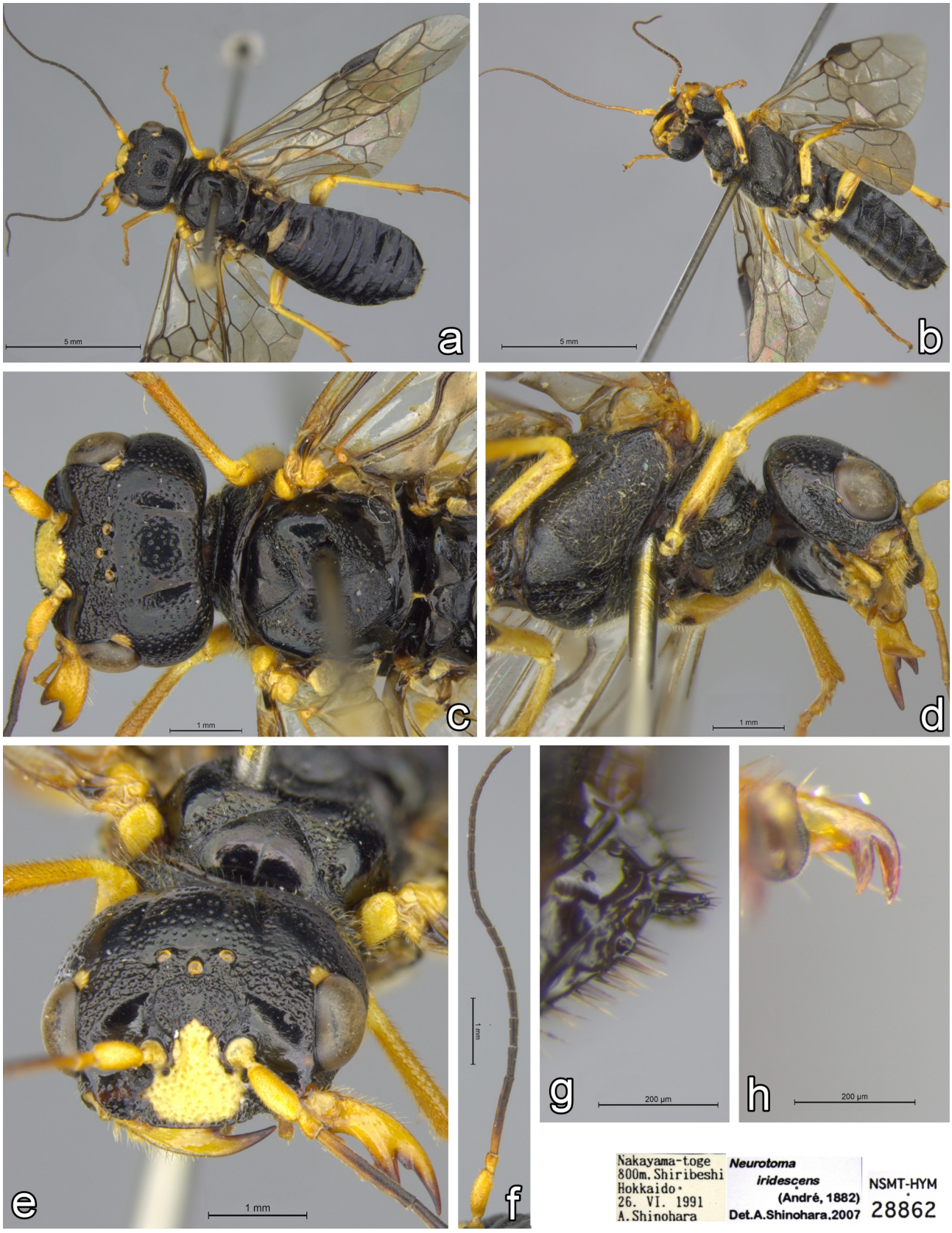


FIGURE 24. ***Neurotoma iridescens***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

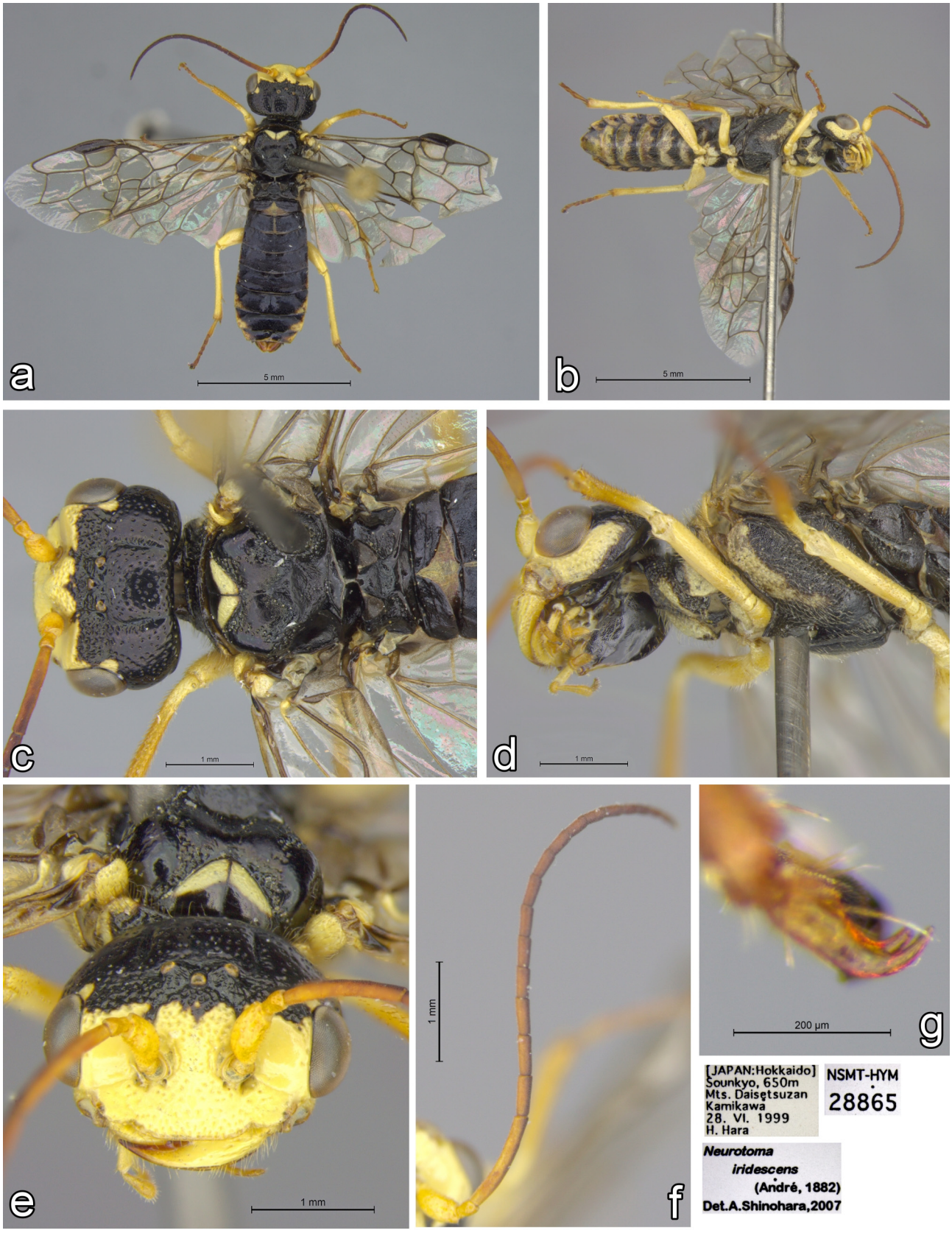


FIGURE 25. ***Neurotoma iridescens***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw.



FIGURE 26. ***Neurotoma satoi***, female, Korea (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

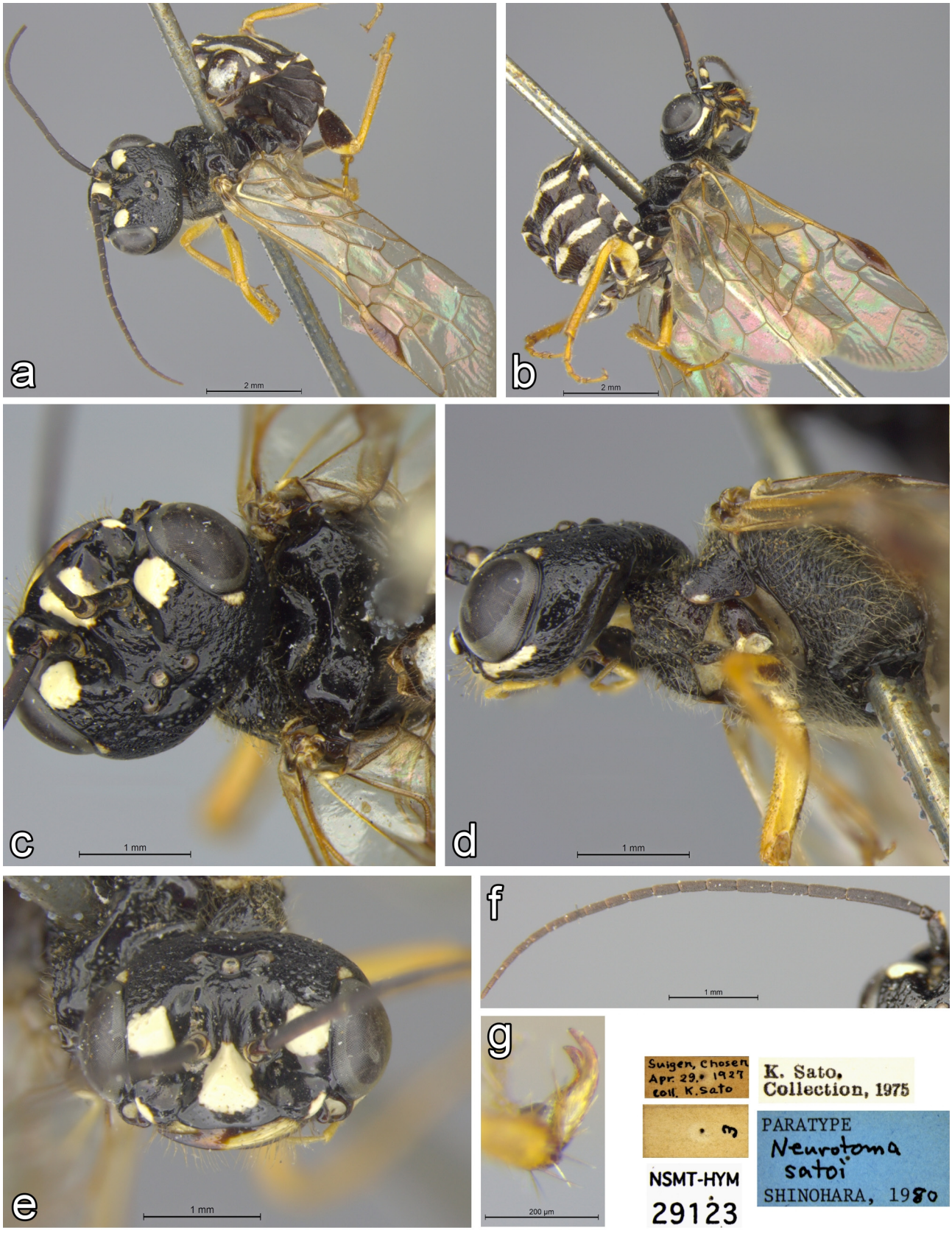


FIGURE 27. ***Neurotoma satoi***, male, Korea (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw.

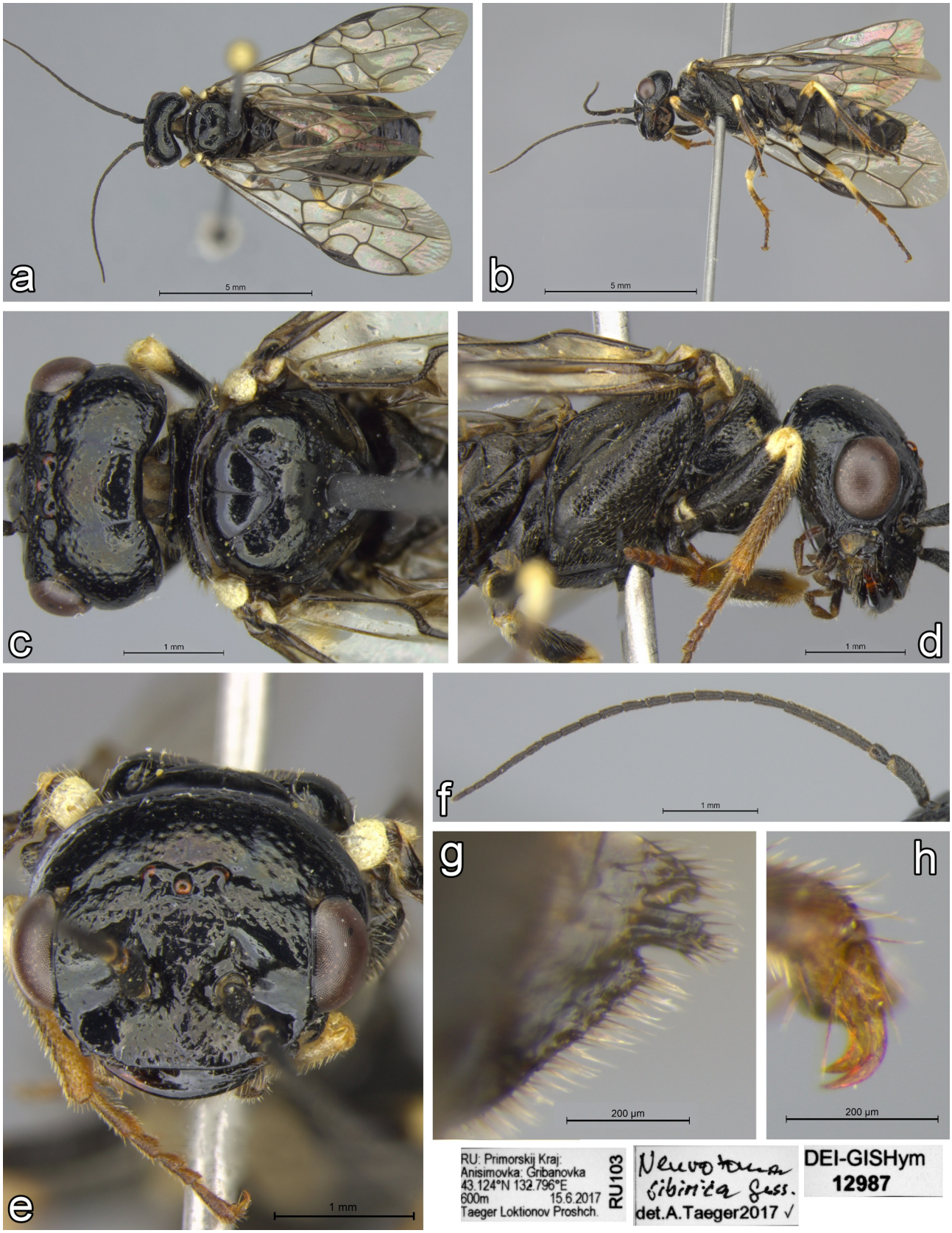


FIGURE 28. ***Neurotoma sibirica***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

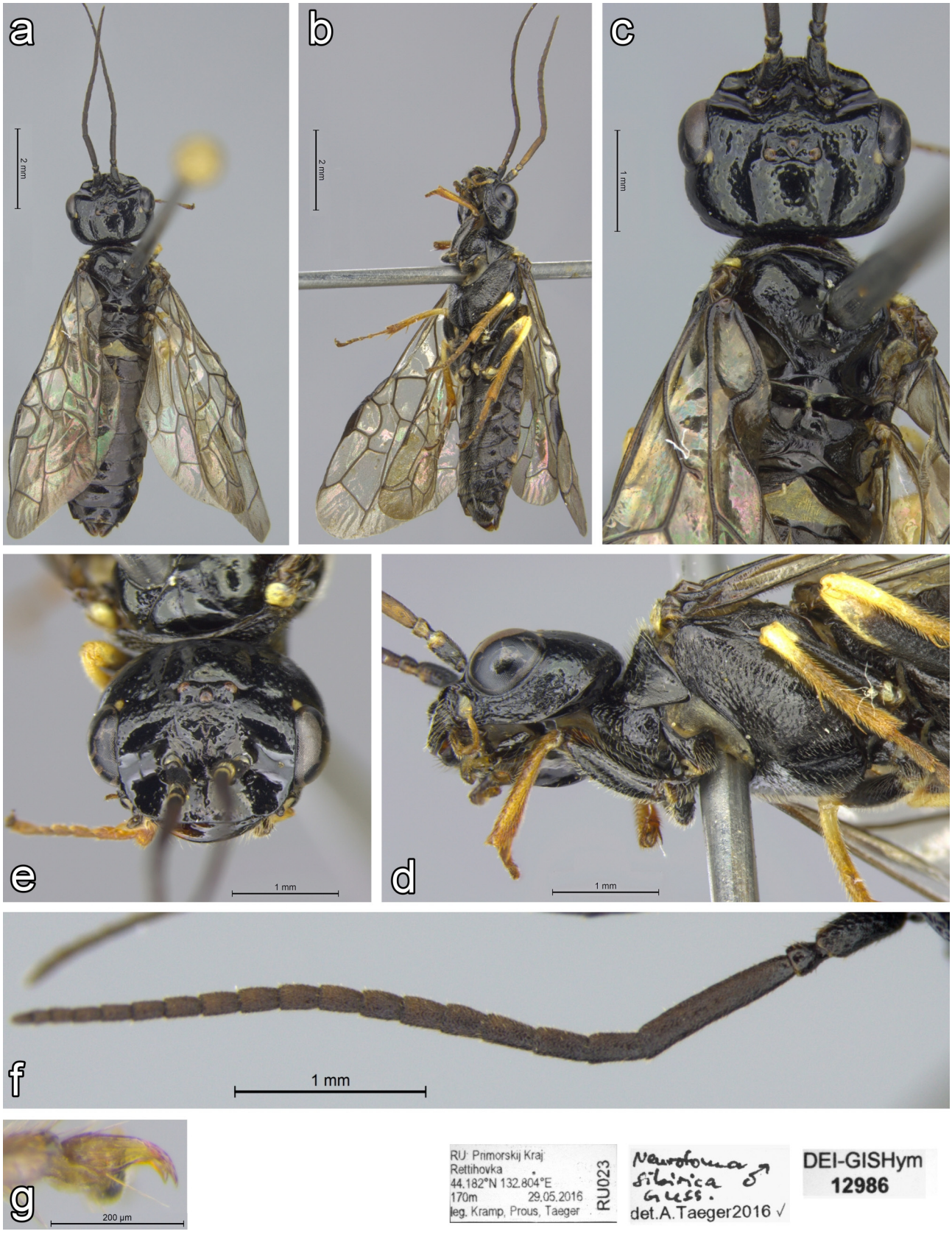


FIGURE 29. ***Neurotoma sibirica***, male, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw.

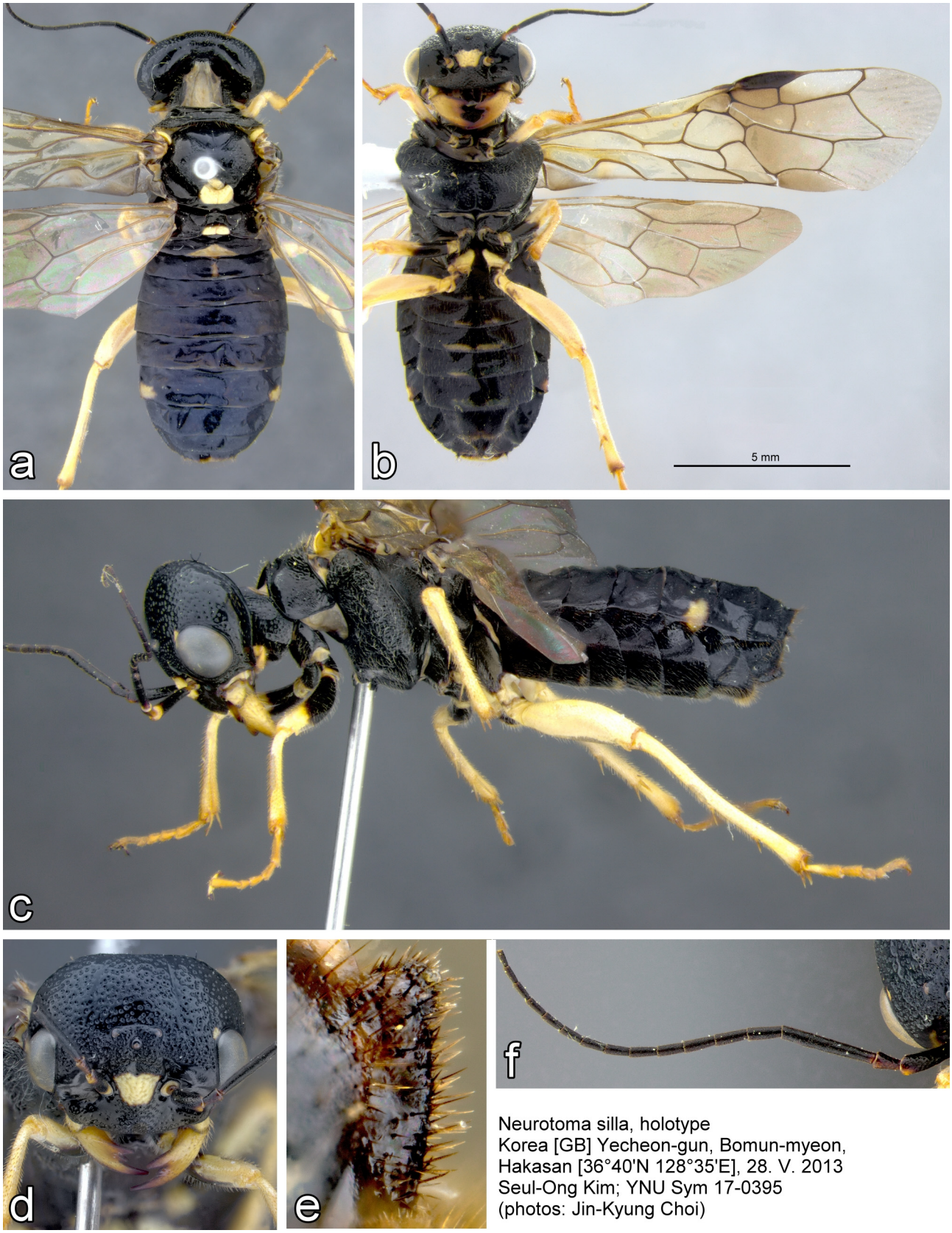
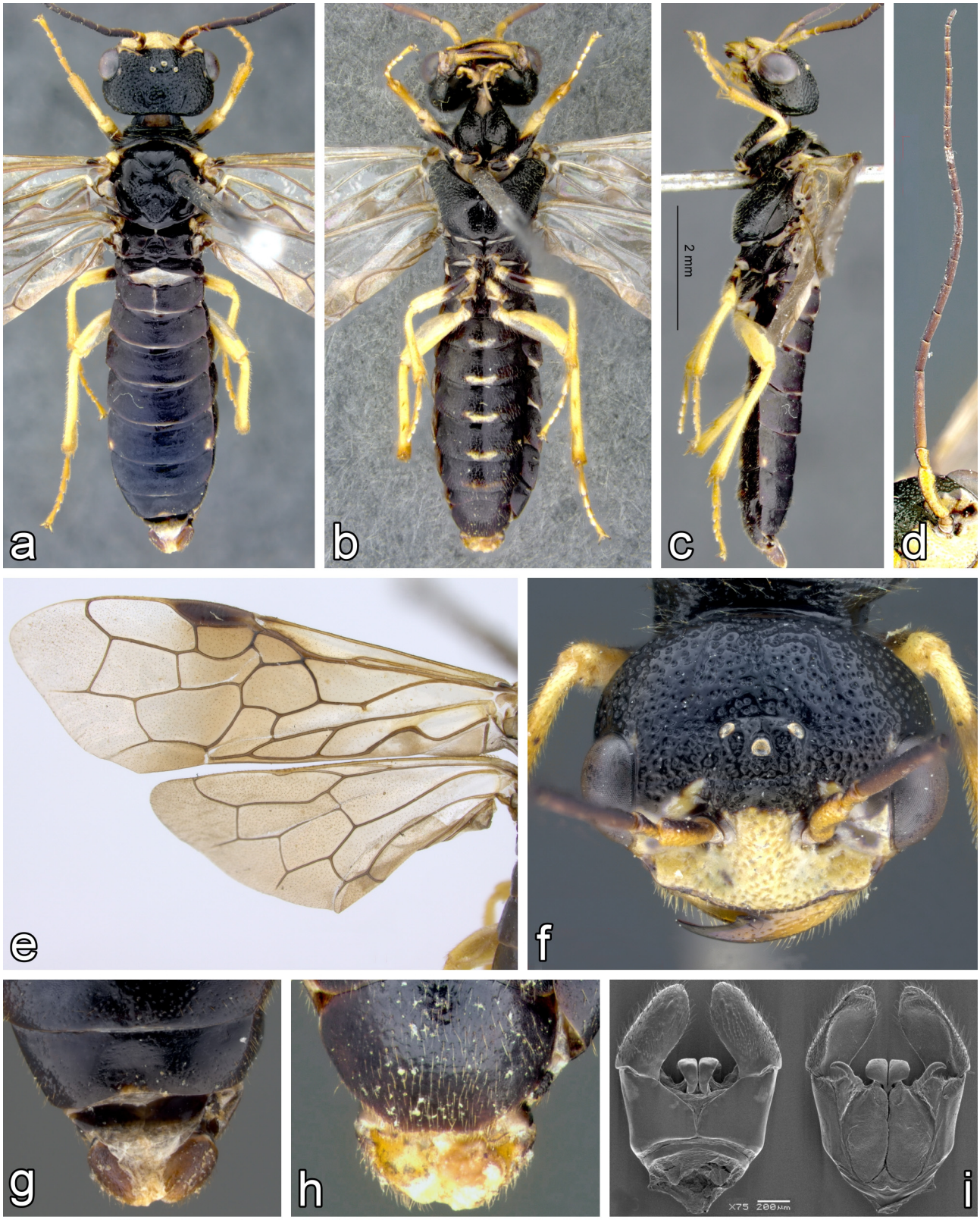


FIGURE 30. ***Neurotoma silla***, female, Korea (holotype) – **(a)** dorsally, **(b)** ventrally, **(c)** laterally, **(d)** face, **(e)** sawsheath laterally, **(f)** antenna.



Neurotoma silla, paratype. Korea: Mt. Undalsan (Gimryongsa)
[36°45'N 128°12'E, Mungyeong-si, Gyeongsangbuk-do] 26. V. 2000, coll. S. J. Suh; YNU Sym 17-0567

FIGURE 31. ***Neurotoma silla***, male, Korea – **(a)** dorsally, **(b)** ventrally, **(c)** laterally, **(d)** antenna, **(e)** wings, **(f)** face, **(g)** apex abdomen dorsally, **(h)** apex abdomen ventrally, **(i)** genitalia dorsally & ventrally.

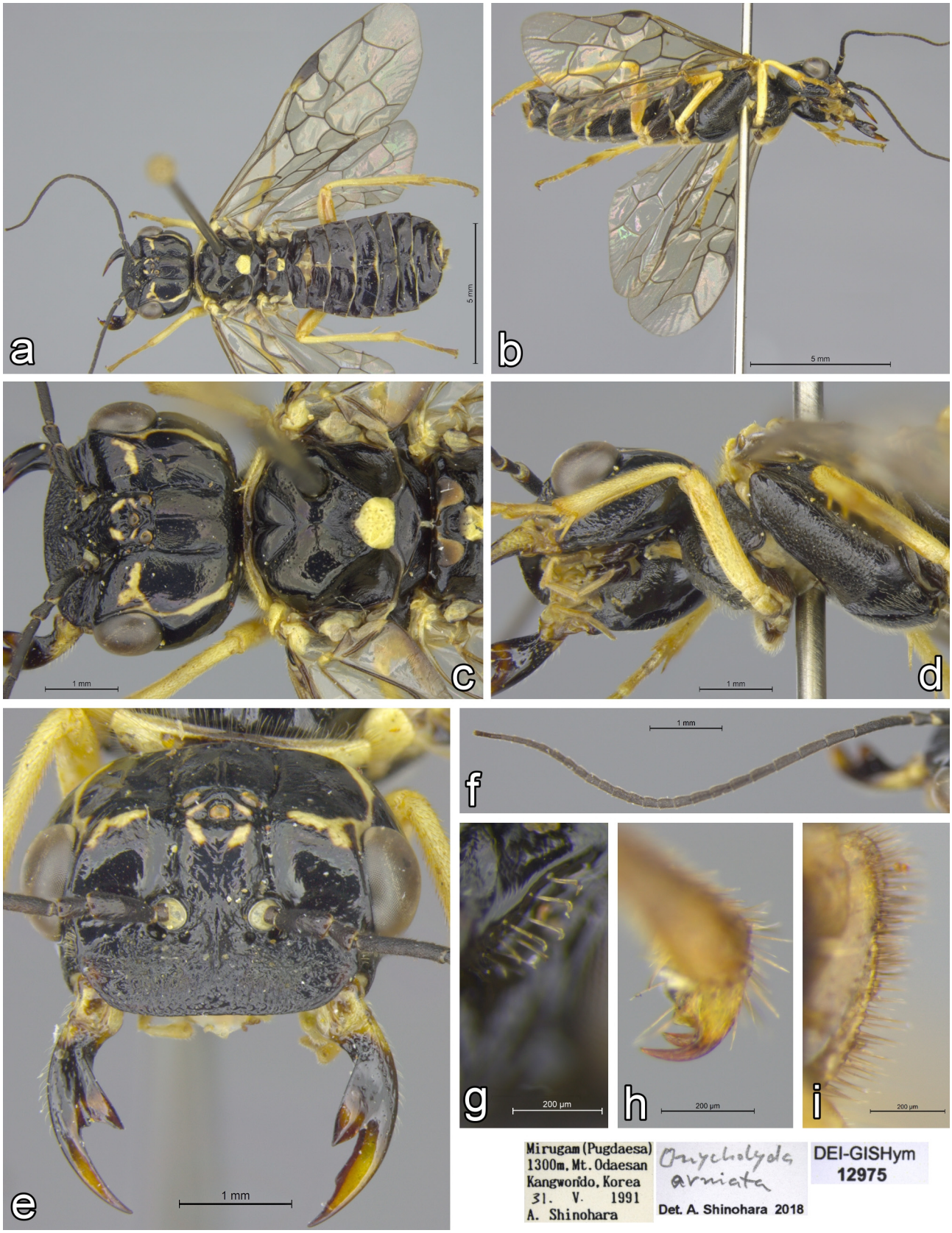


FIGURE 32. ***Onycholyda armata***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** malar space setae, **(h)** claw, **(i)** sawsheath laterally.

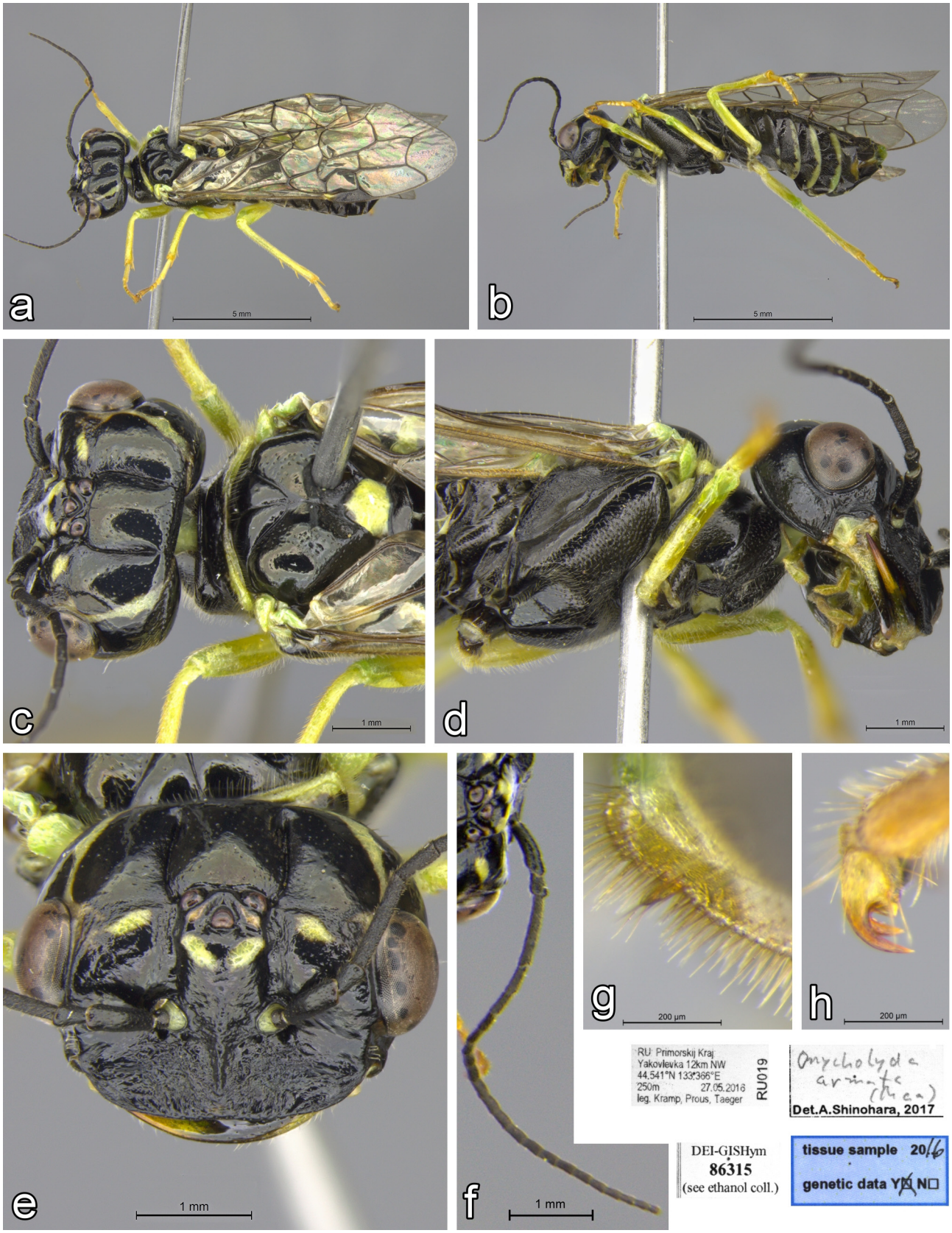


FIGURE 33. ***Onycholyda armata***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

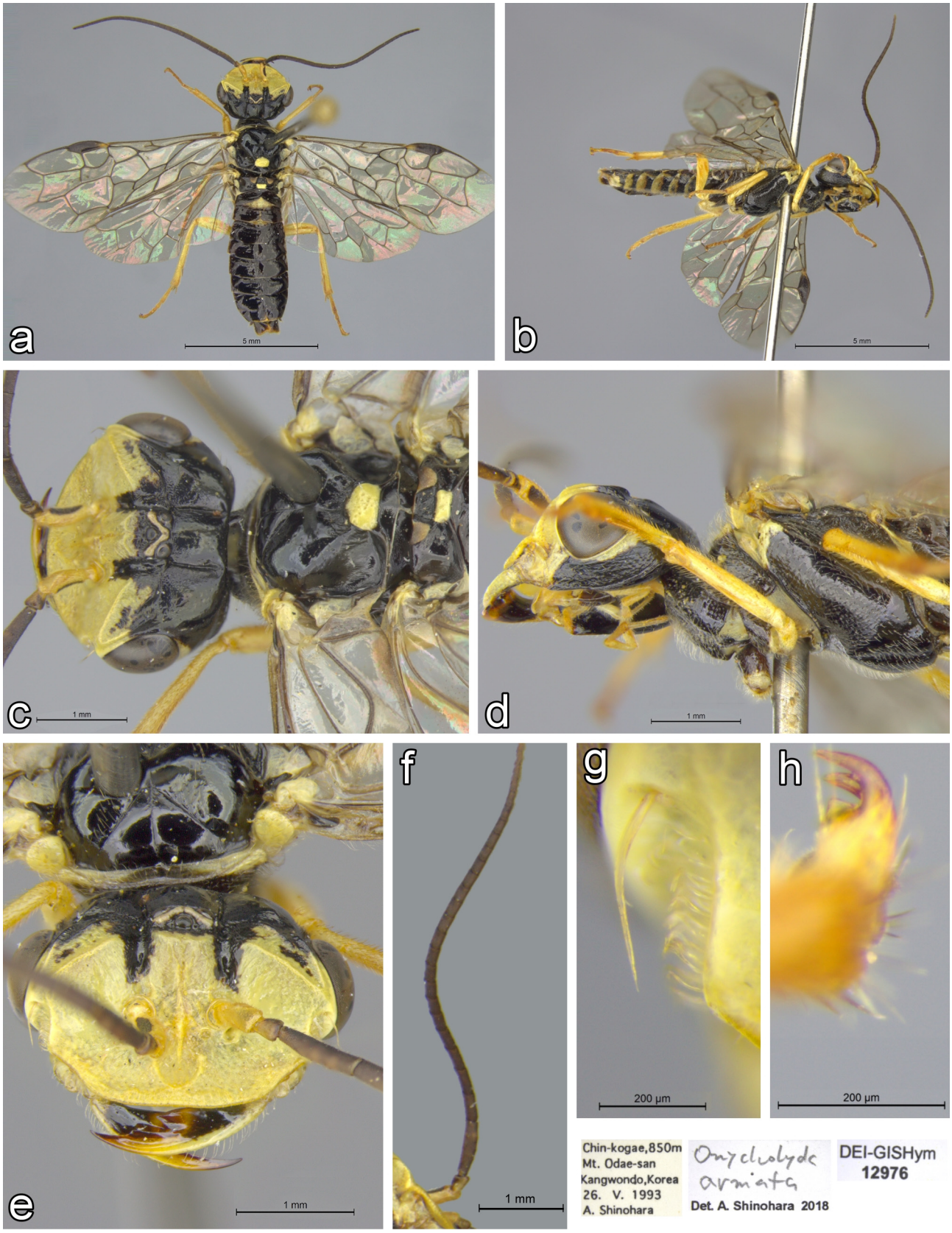


FIGURE 34. ***Onycholyda armata***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** malar space setae, **(h)** claw.

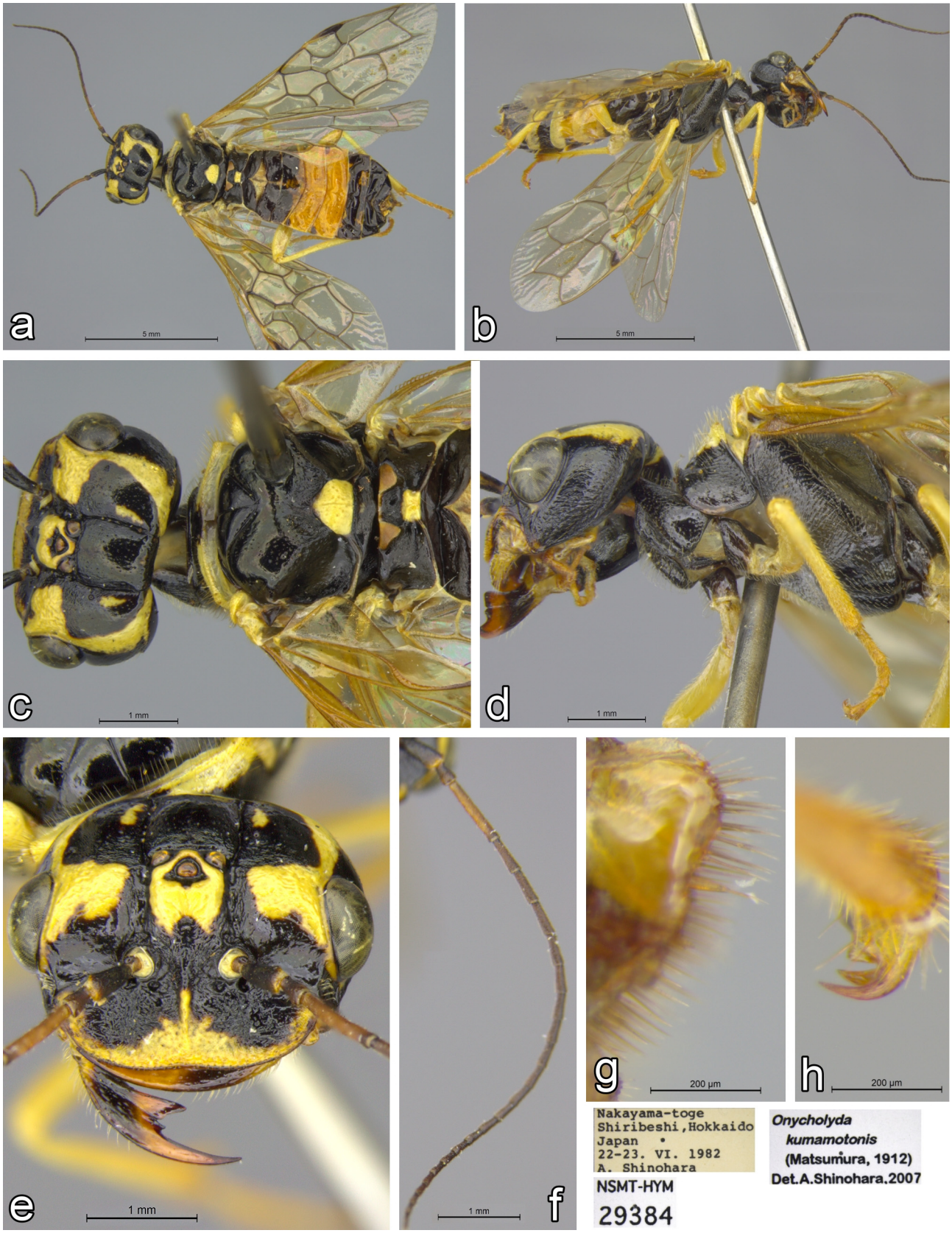


FIGURE 35. ***Onycholyda kumamotonis***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

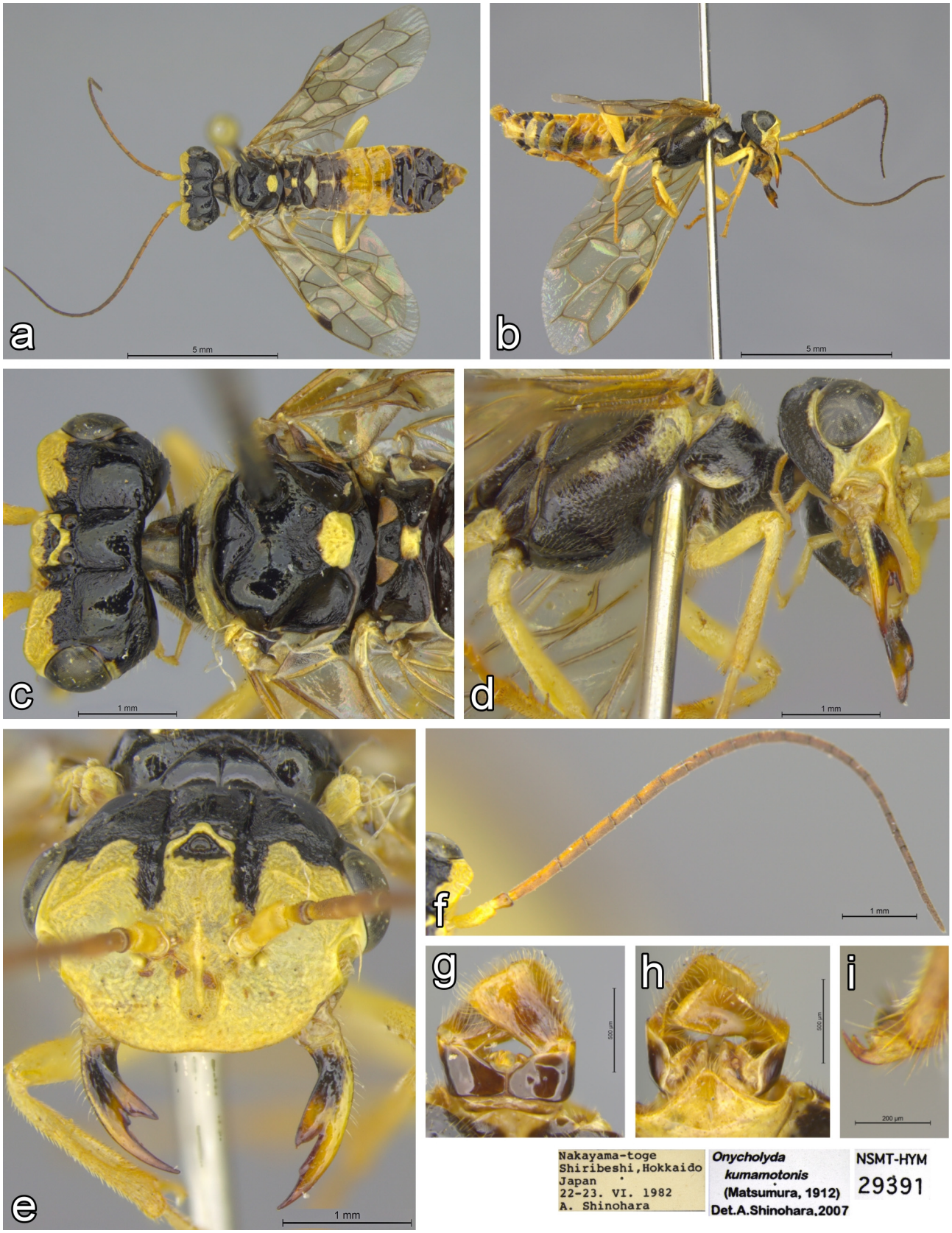


FIGURE 36. ***Onycholyda kumamotonis***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

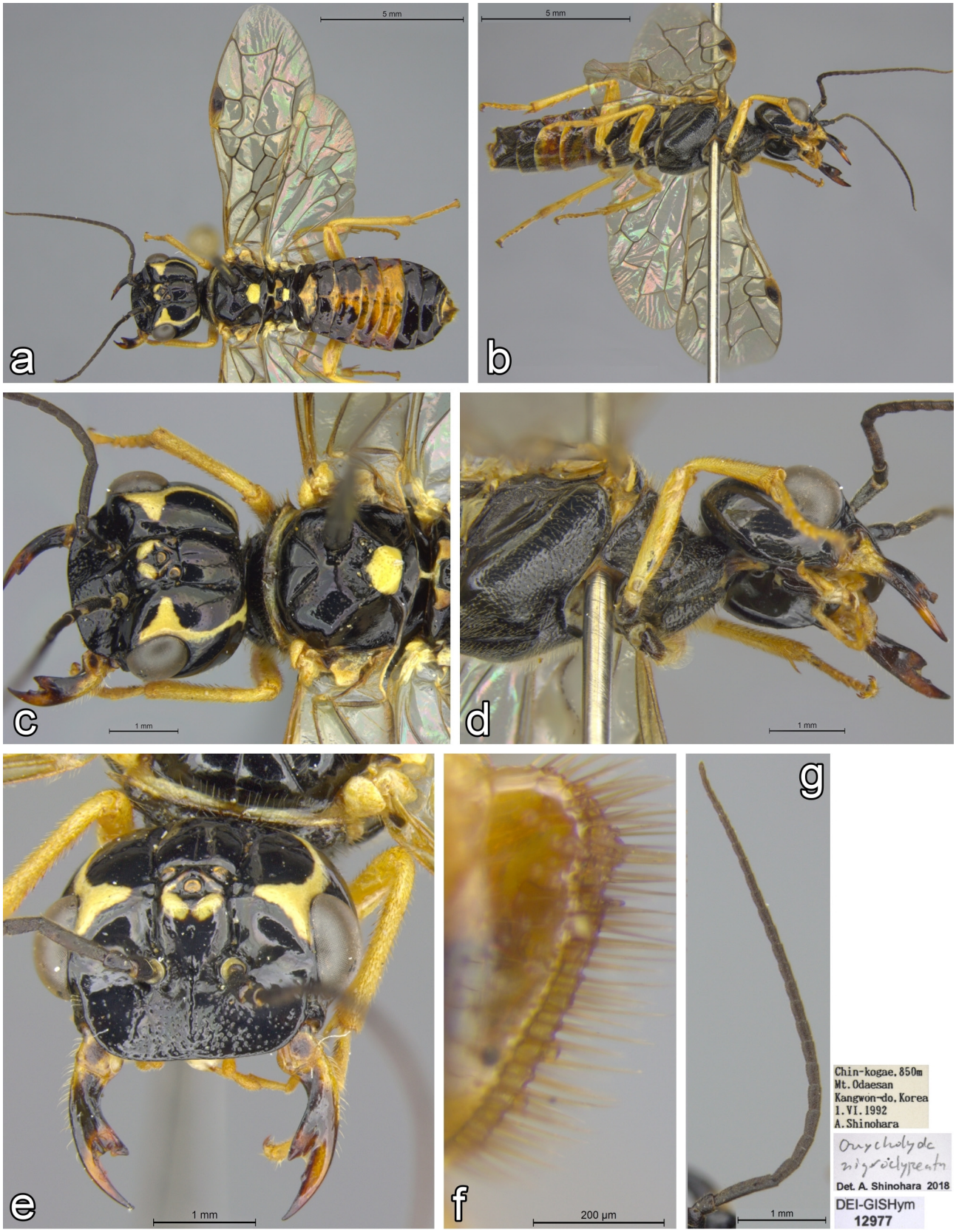


FIGURE 37. ***Oncholyda nigroclypeata***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** sawsheath laterally, **(g)** antenna.

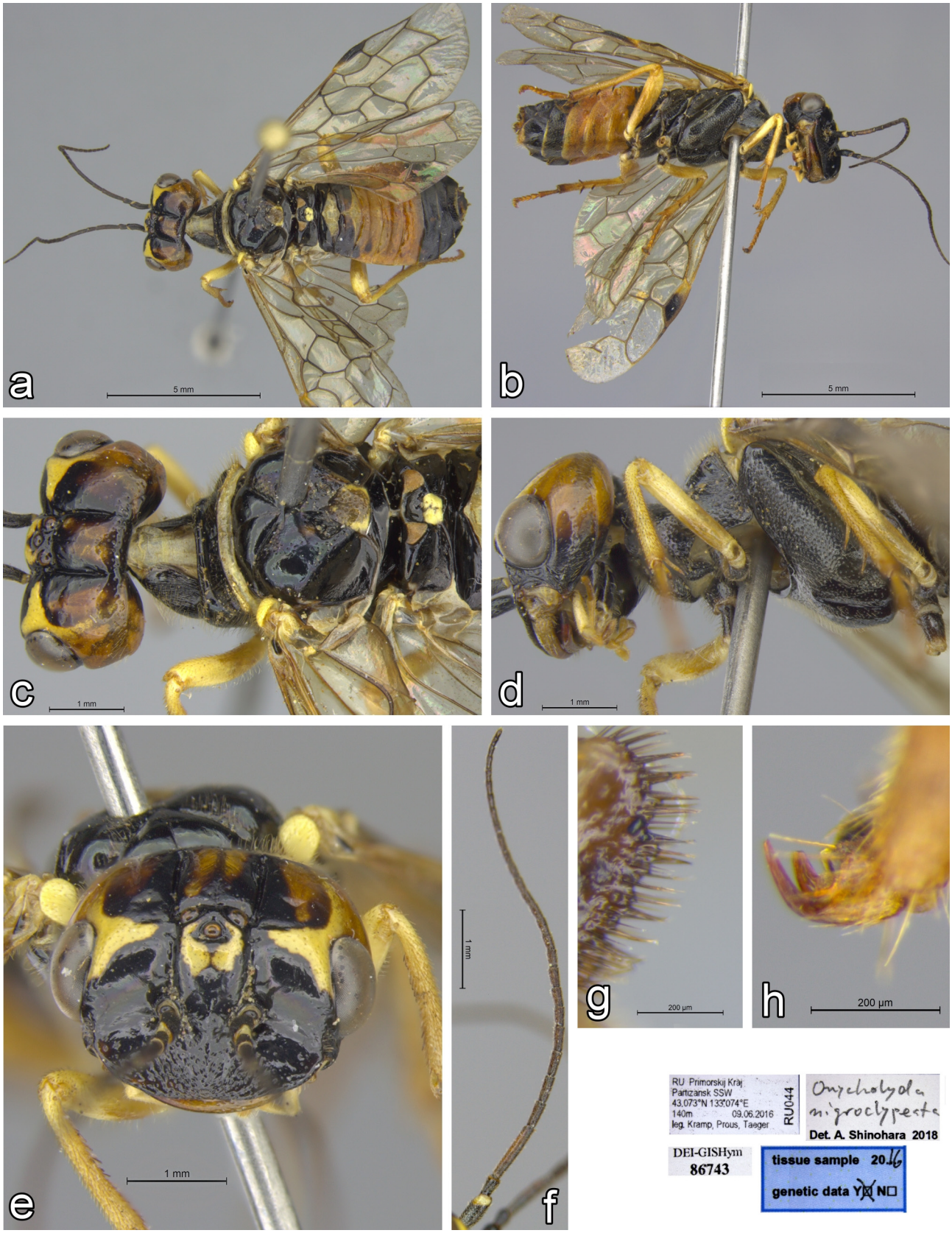


FIGURE 38. ***Oncholyda nigroclypeata***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

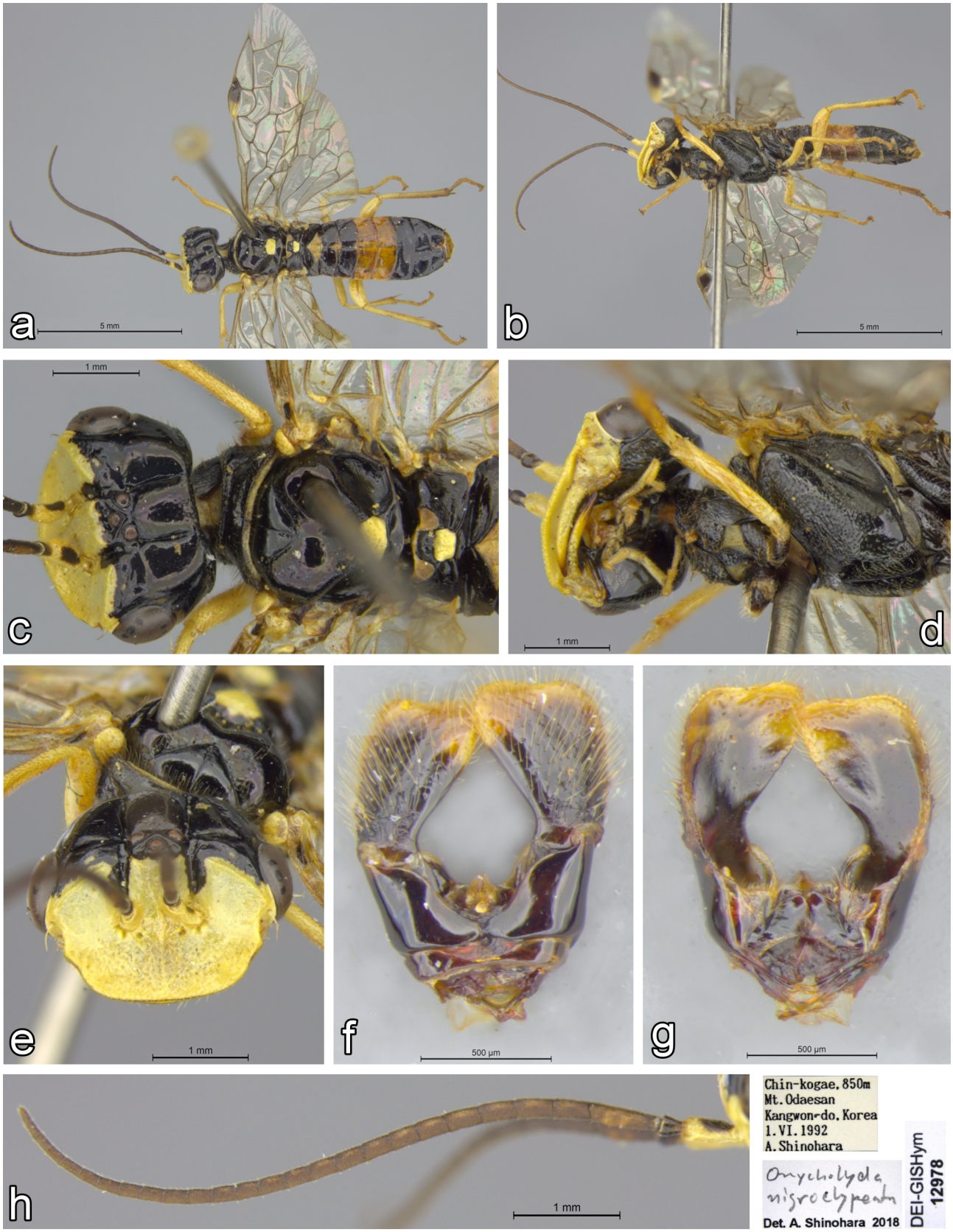


FIGURE 39. ***Onycholyda nigroclypeata***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** genitalia dorsally, **(g)** genitalia ventrally, **(h)** antenna.

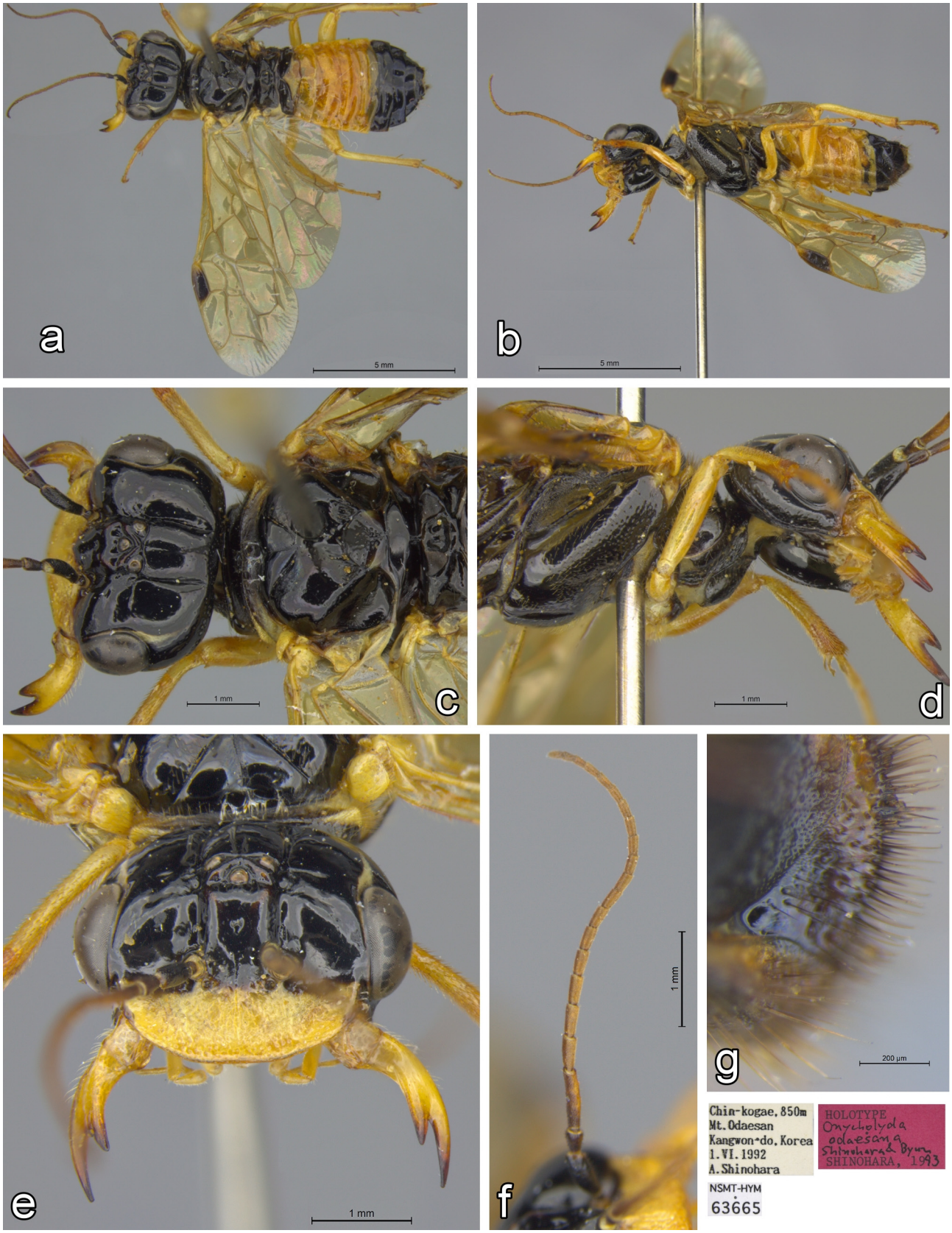


FIGURE 40. ***Oncholyda odaesana***, female, Korea (holotype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally.

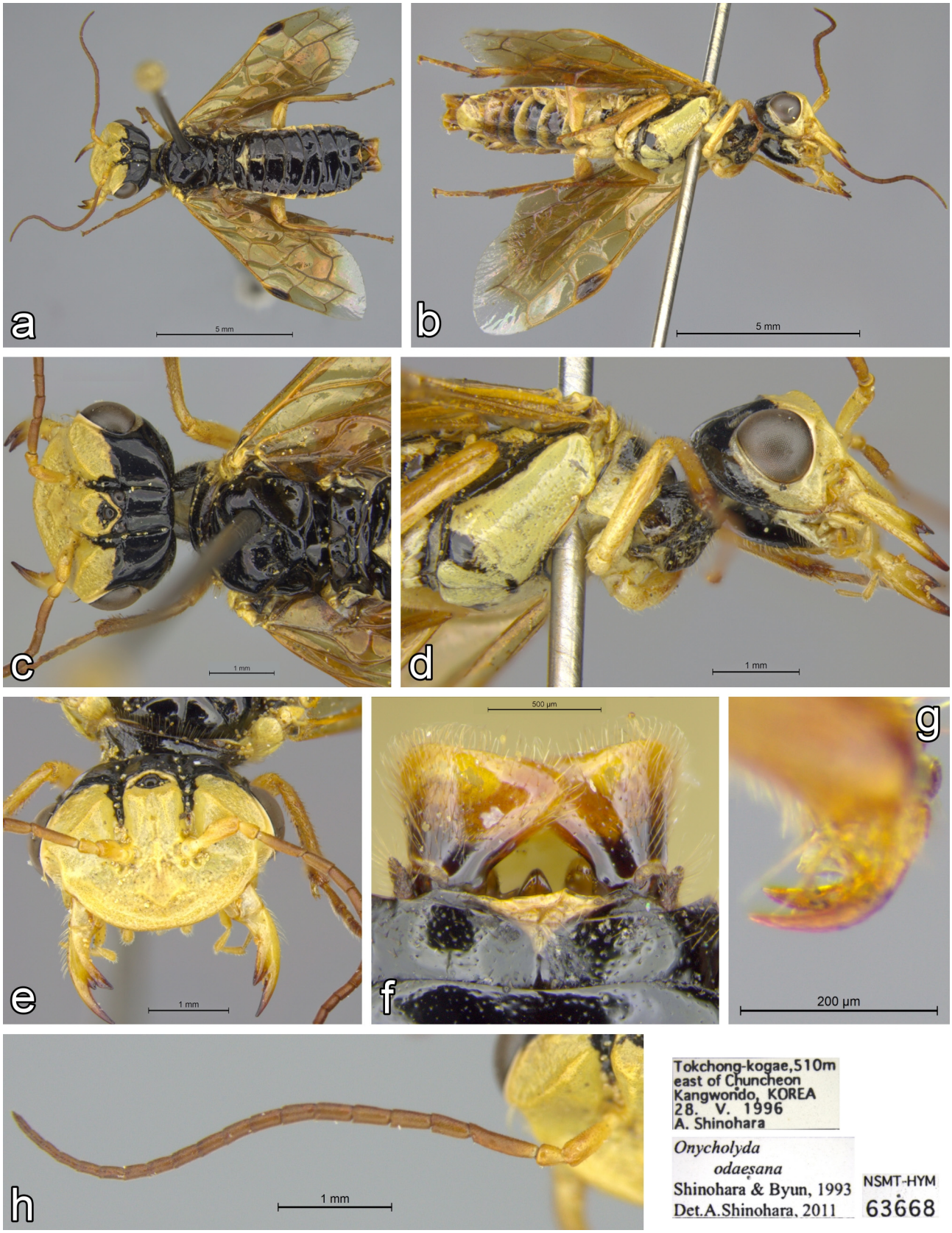


FIGURE 41. ***Onycholyda odaesana***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** genitalia dorsally, **(g)** claw, **(h)** antenna.

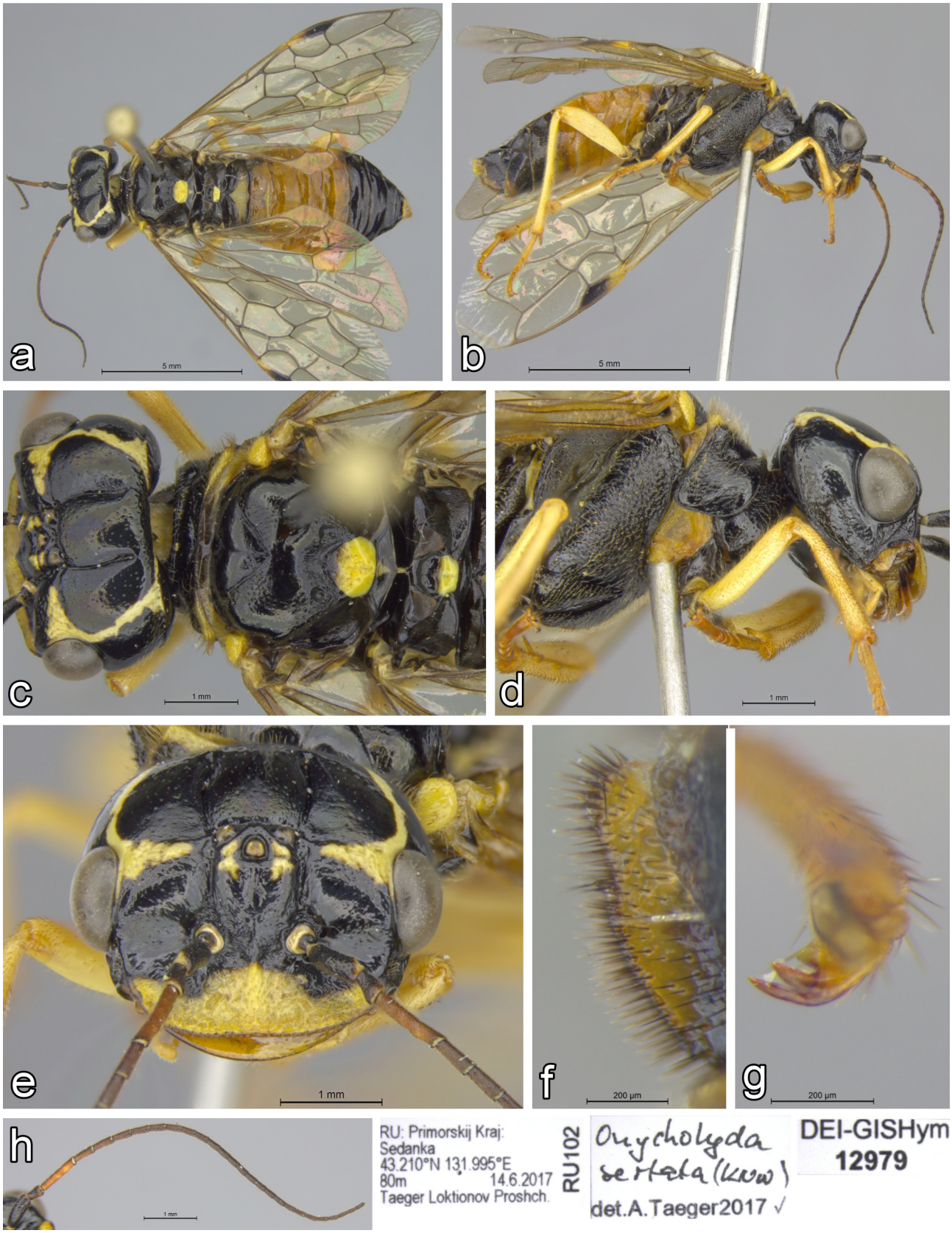


FIGURE 42. ***Onycholyda sertata***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** sawsheath laterally, **(g)** claw, **(h)** antenna.

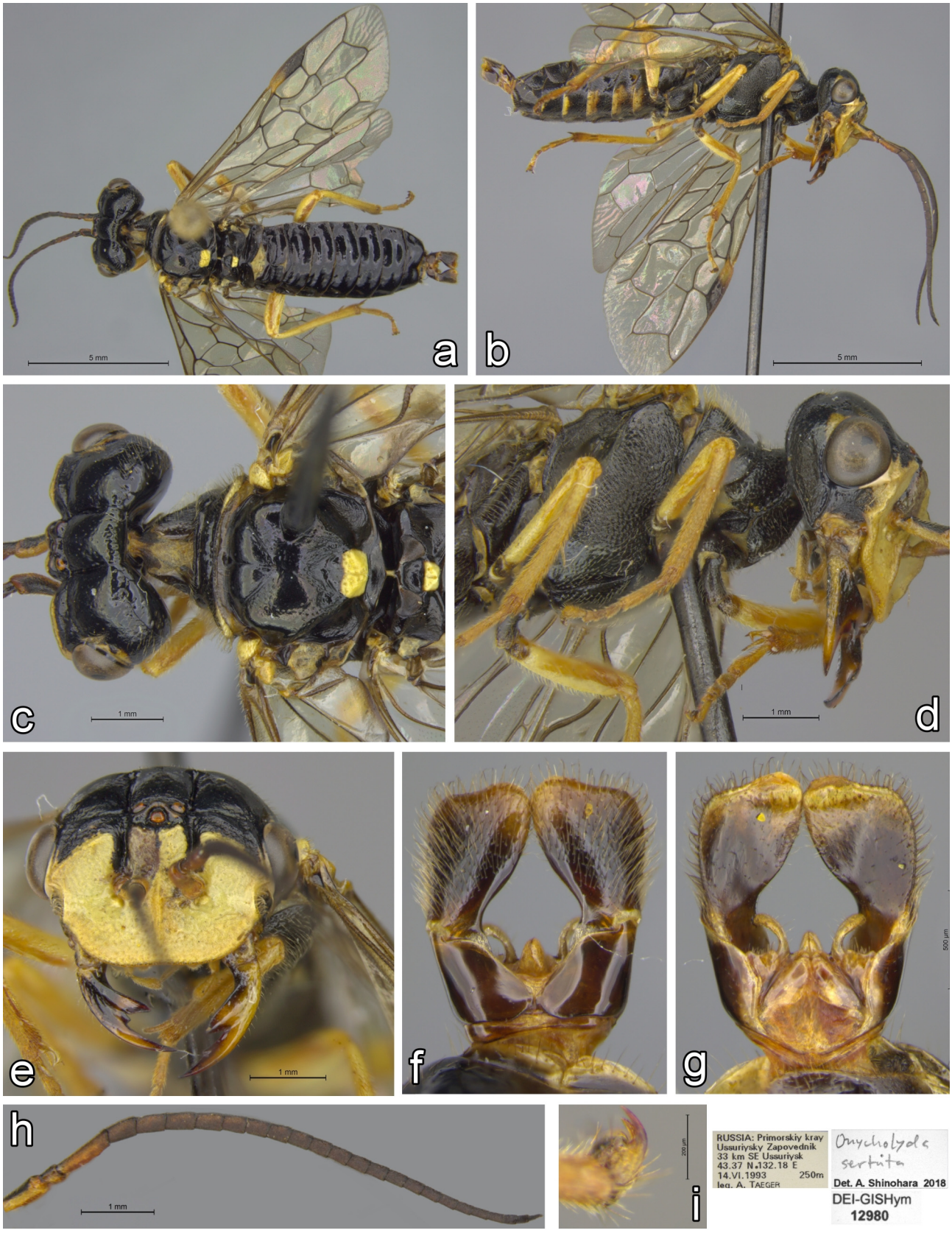


FIGURE 43. ***Oncholyda sertata***, male, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** genitalia dorsally, **(g)** genitalia ventrally, **(h)** antenna, **(i)** claw.

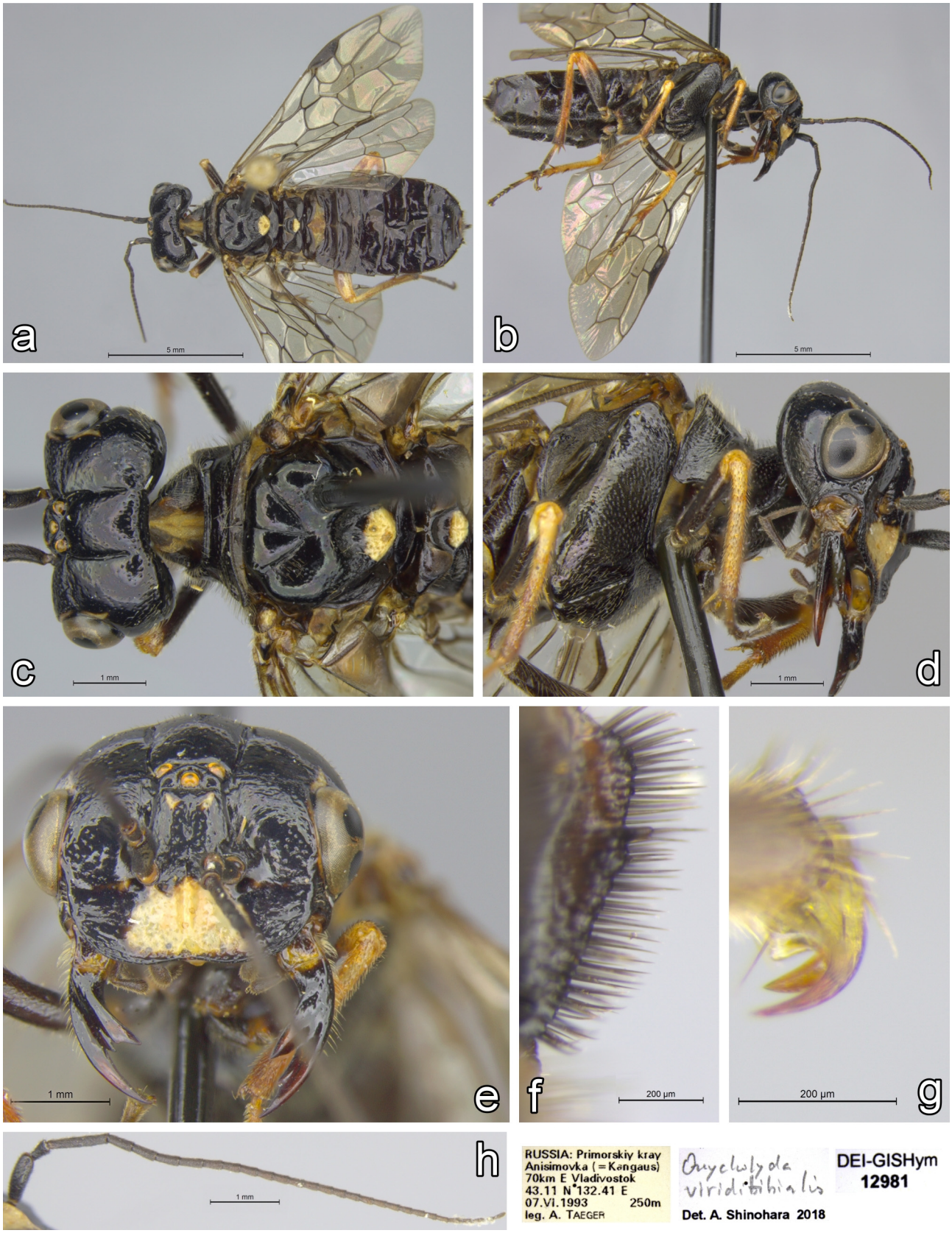


FIGURE 44. ***Onycholyda viriditibialis***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** sawsheath laterally, **(g)** claw, **(h)** antenna.

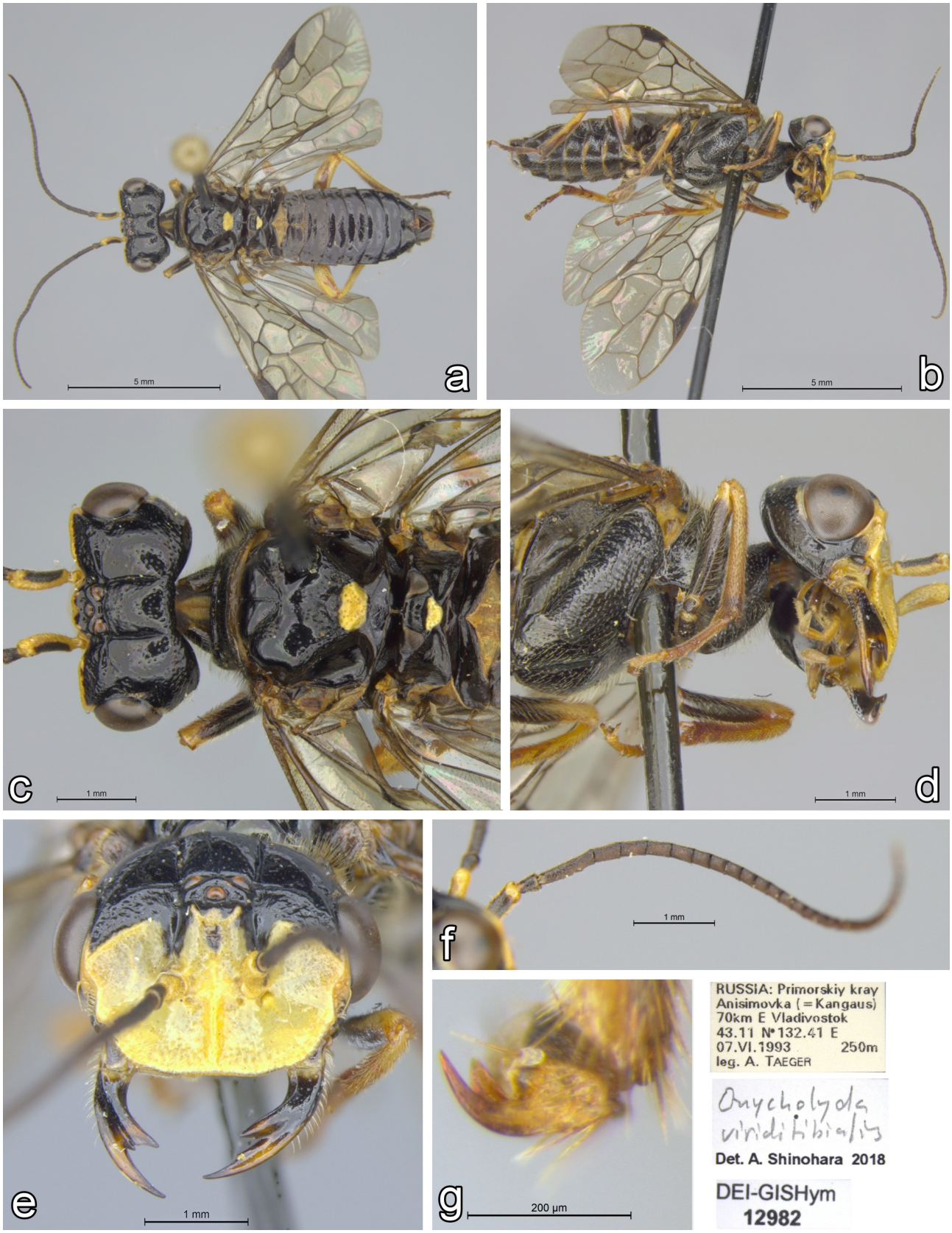


FIGURE 45. ***Onycholyda viriditibialis***, male, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw.

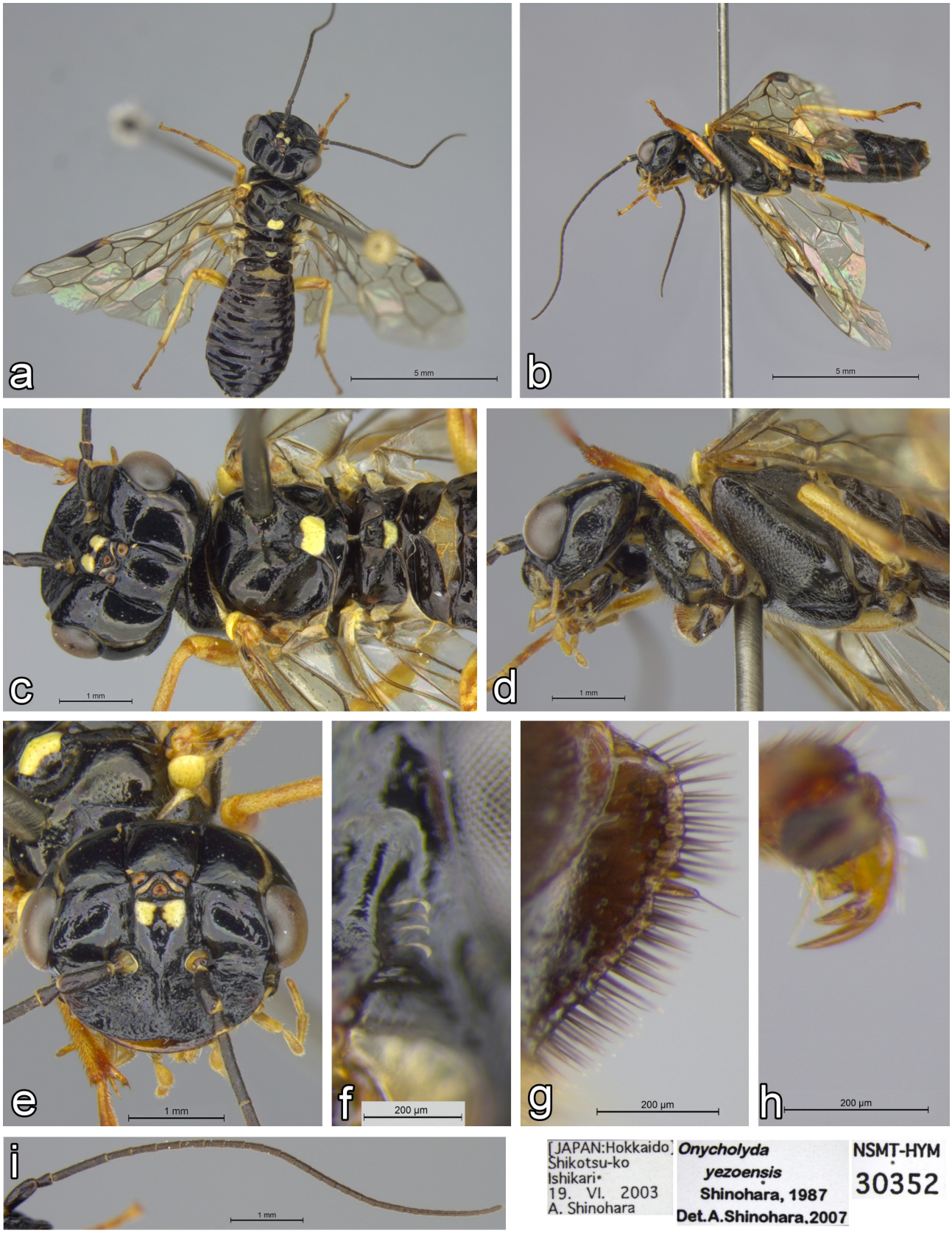


FIGURE 46. ***Onycholyda yezoensis***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** malar space setae, **(g)** sawsheath laterally, **(h)** claw, **(i)** antenna.



FIGURE 47. ***Onycholyda yezoensis***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw.

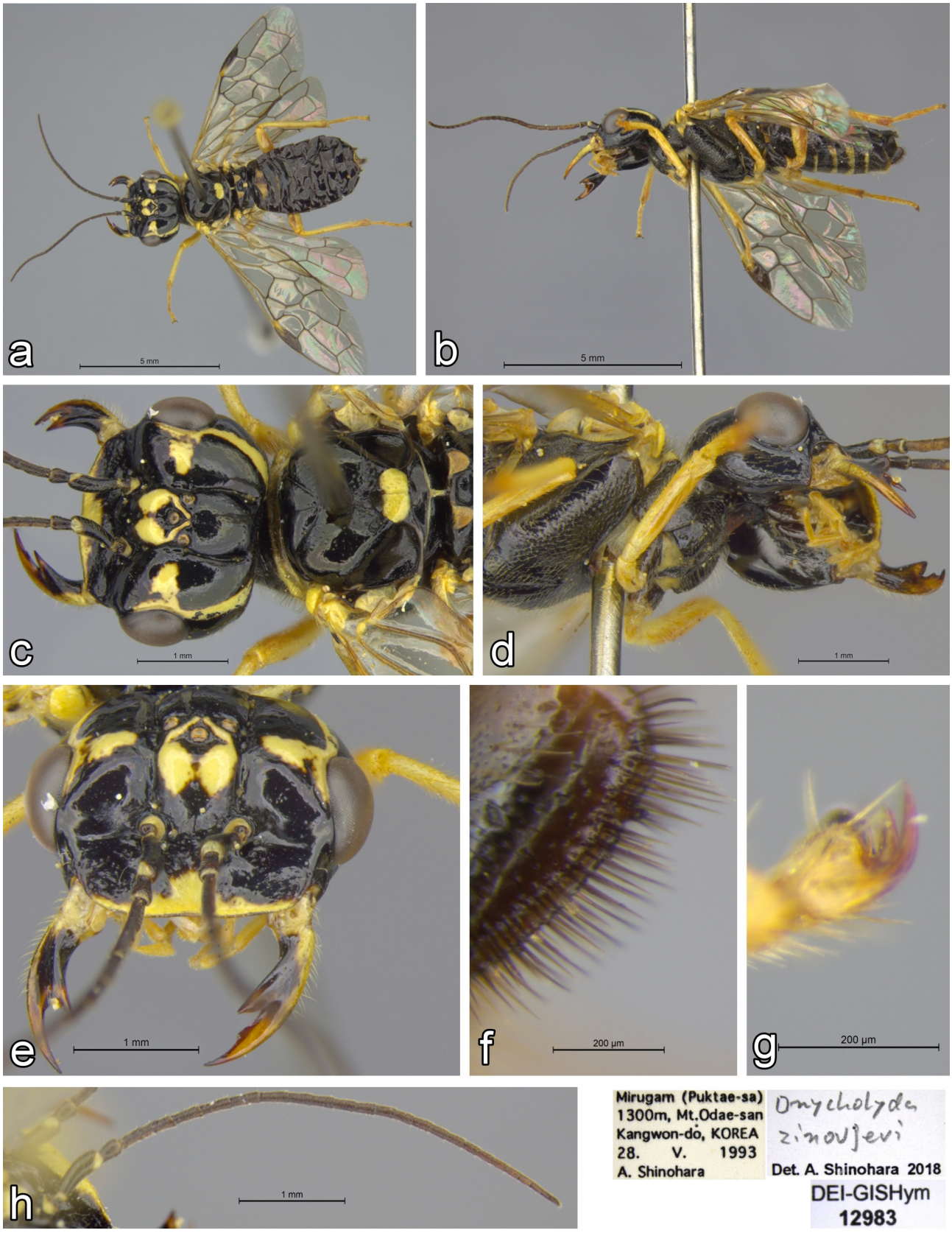


FIGURE 48. ***Onycholyda zinovjevi***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** sawsheath laterally, **(g)** claw, **(h)** antenna.

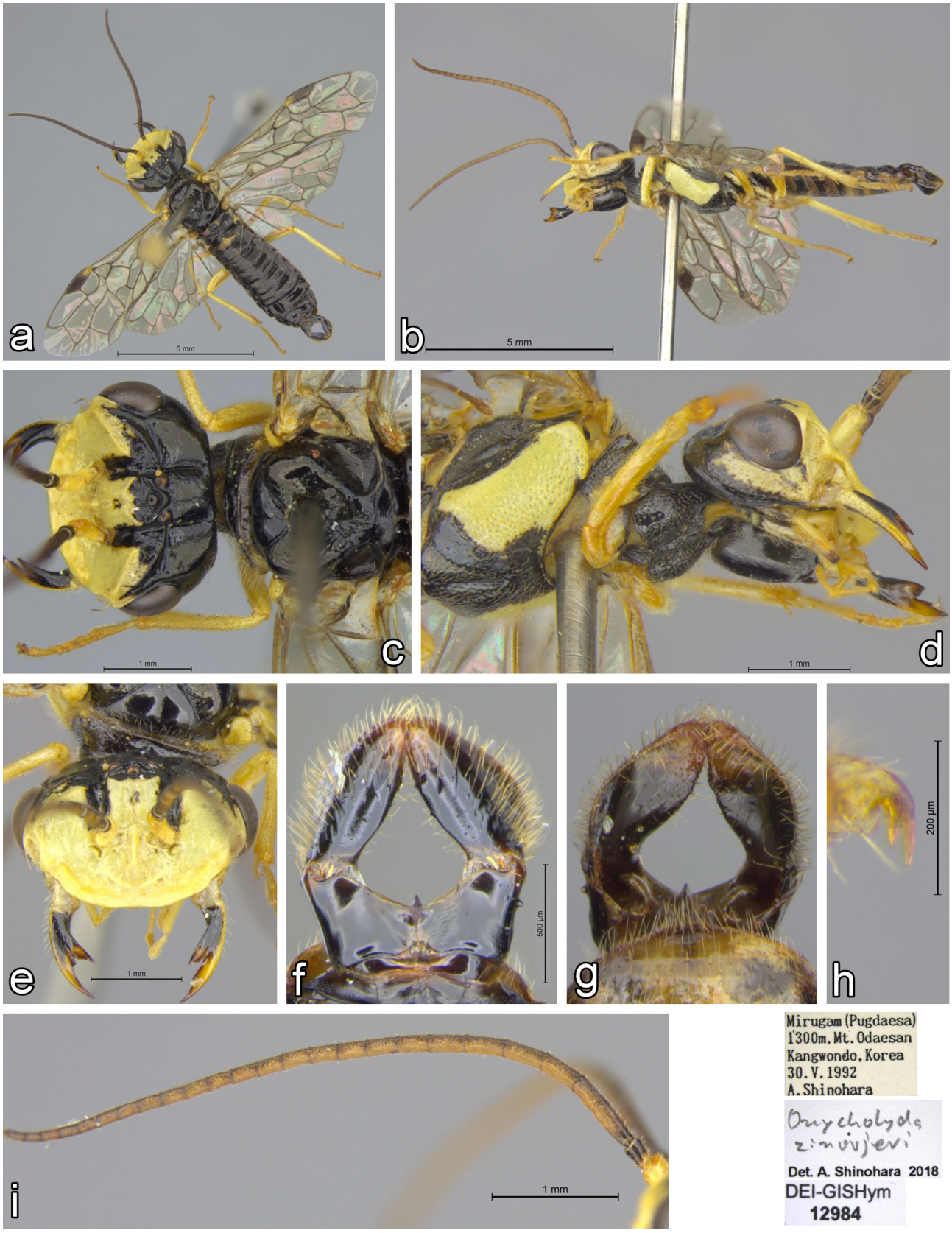


FIGURE 49. ***Onycholyda zinovjevi***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** genitalia dorsally, **(g)** genitalia ventrally, **(h)** claw, **(i)** antenna.

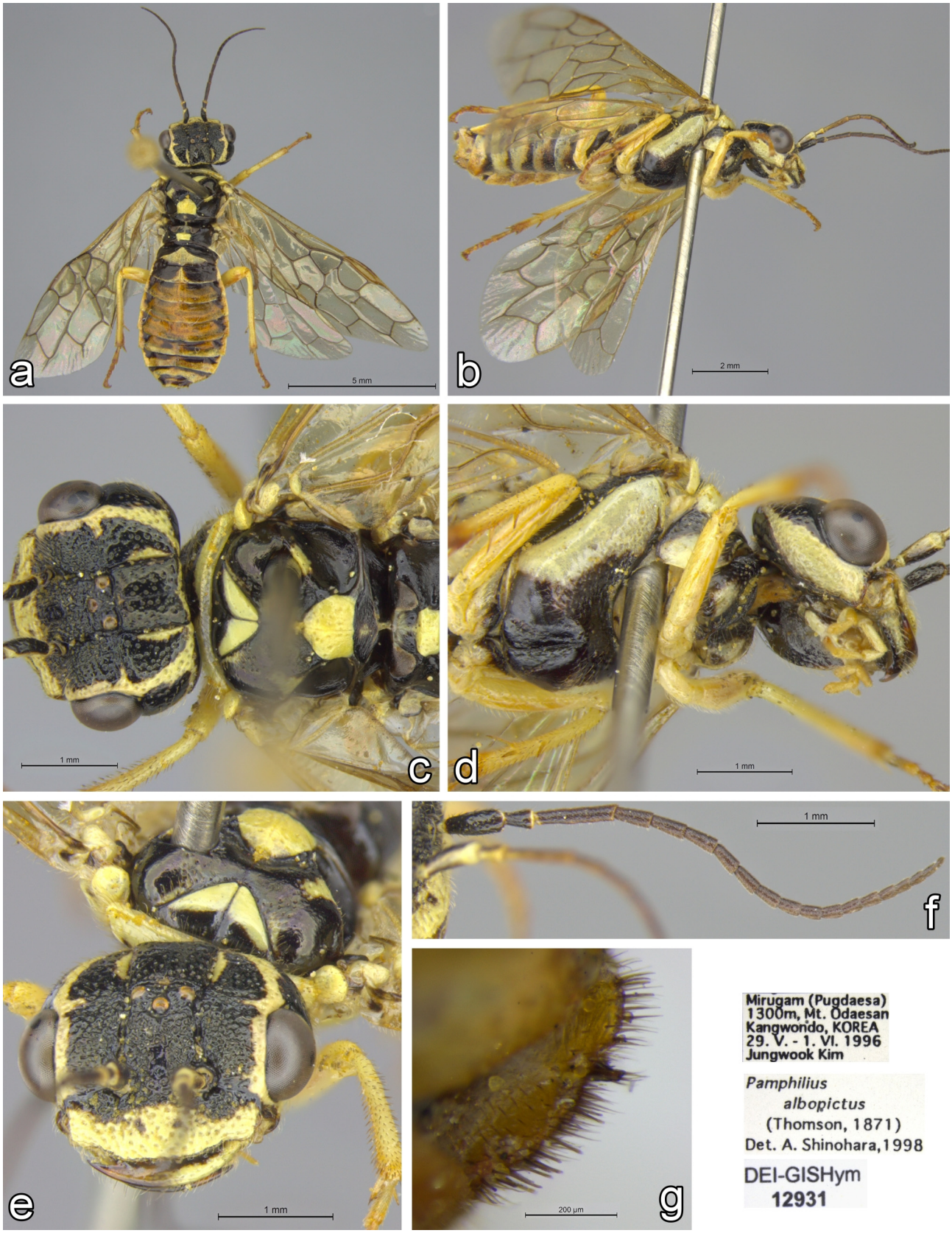


FIGURE 50. ***Pamphilius albopictus***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally.

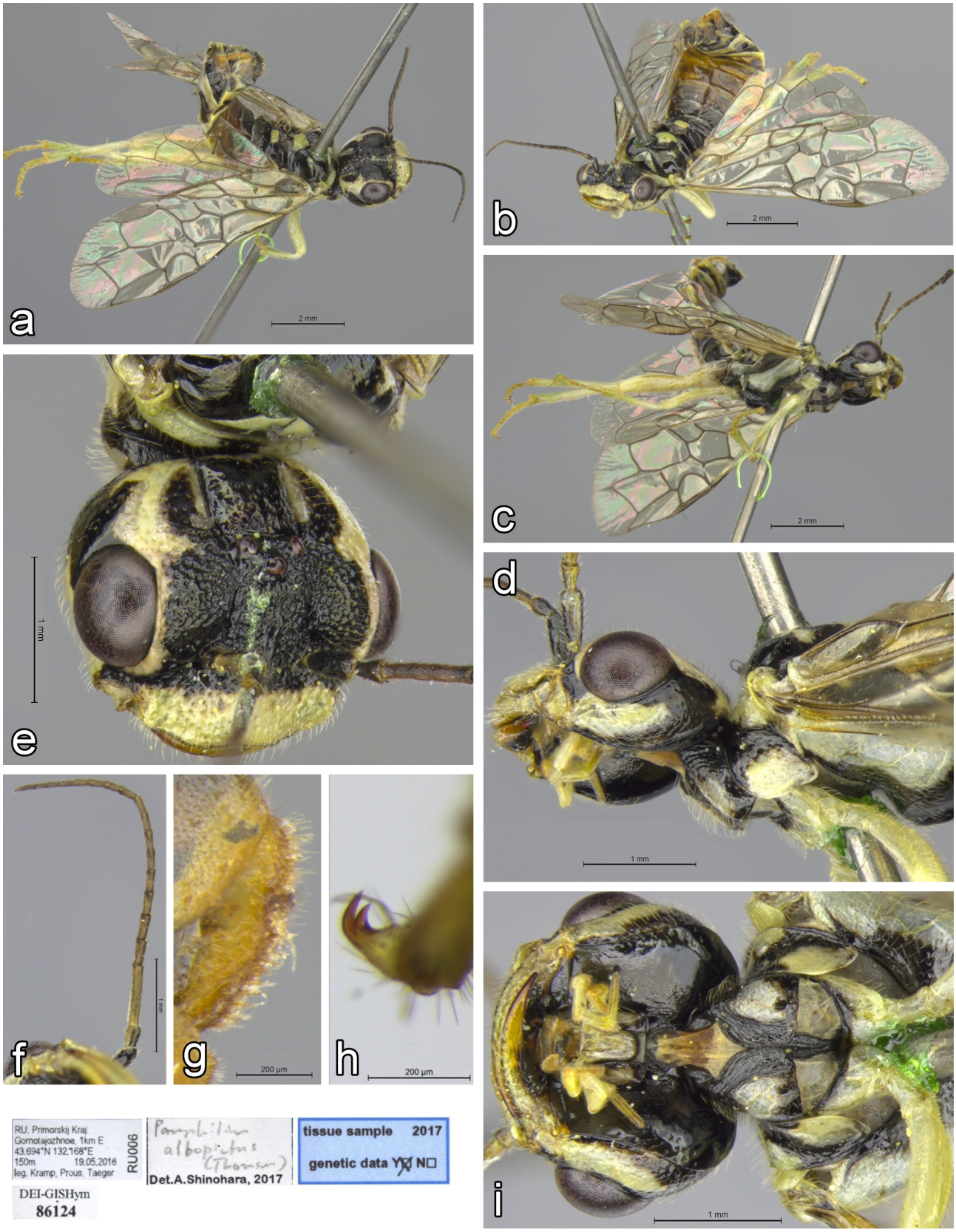


FIGURE 51. ***Pamphilius albopictus***, female, Russia – **(a)** laterodorsally, **(b)** anterodorsally, **(c)** lateroventrally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw, **(i)** head ventrally.

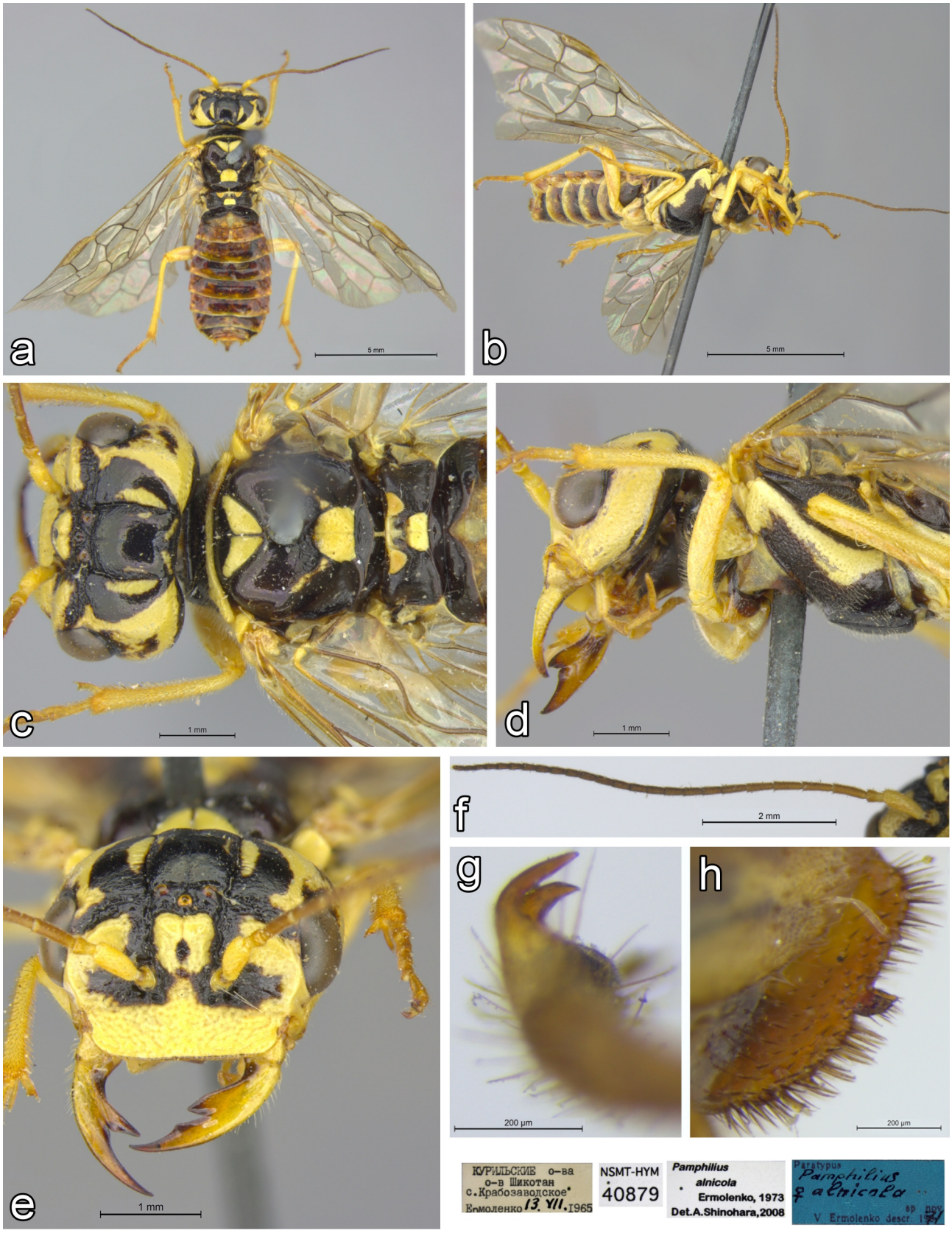


FIGURE 52. ***Pamphilius alnicola***, female, Kuriles (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** sawsheath laterally.

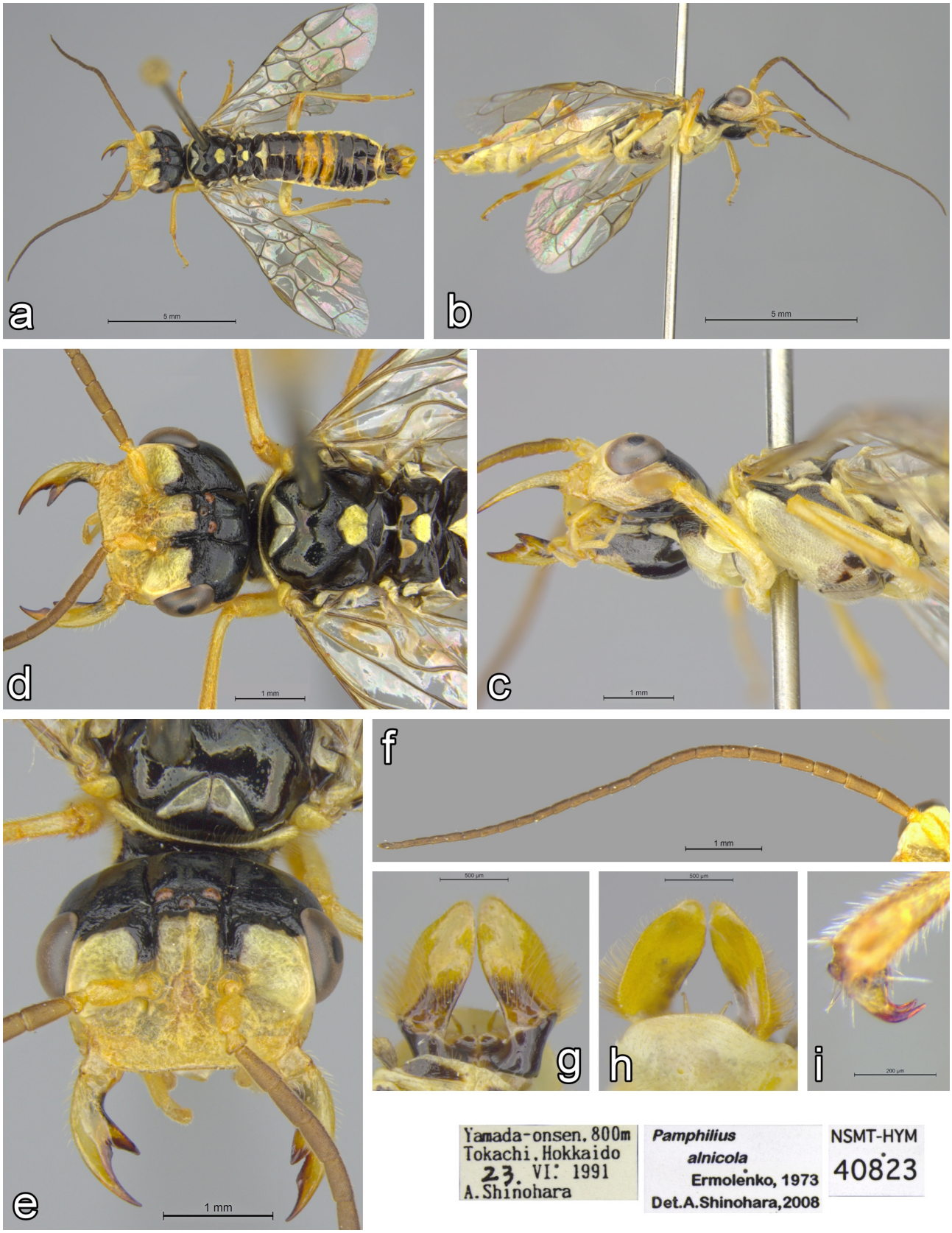


FIGURE 53. ***Pamphilius alnicola***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.



FIGURE 54. ***Pamphilius alnivorus***, female, Russia (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

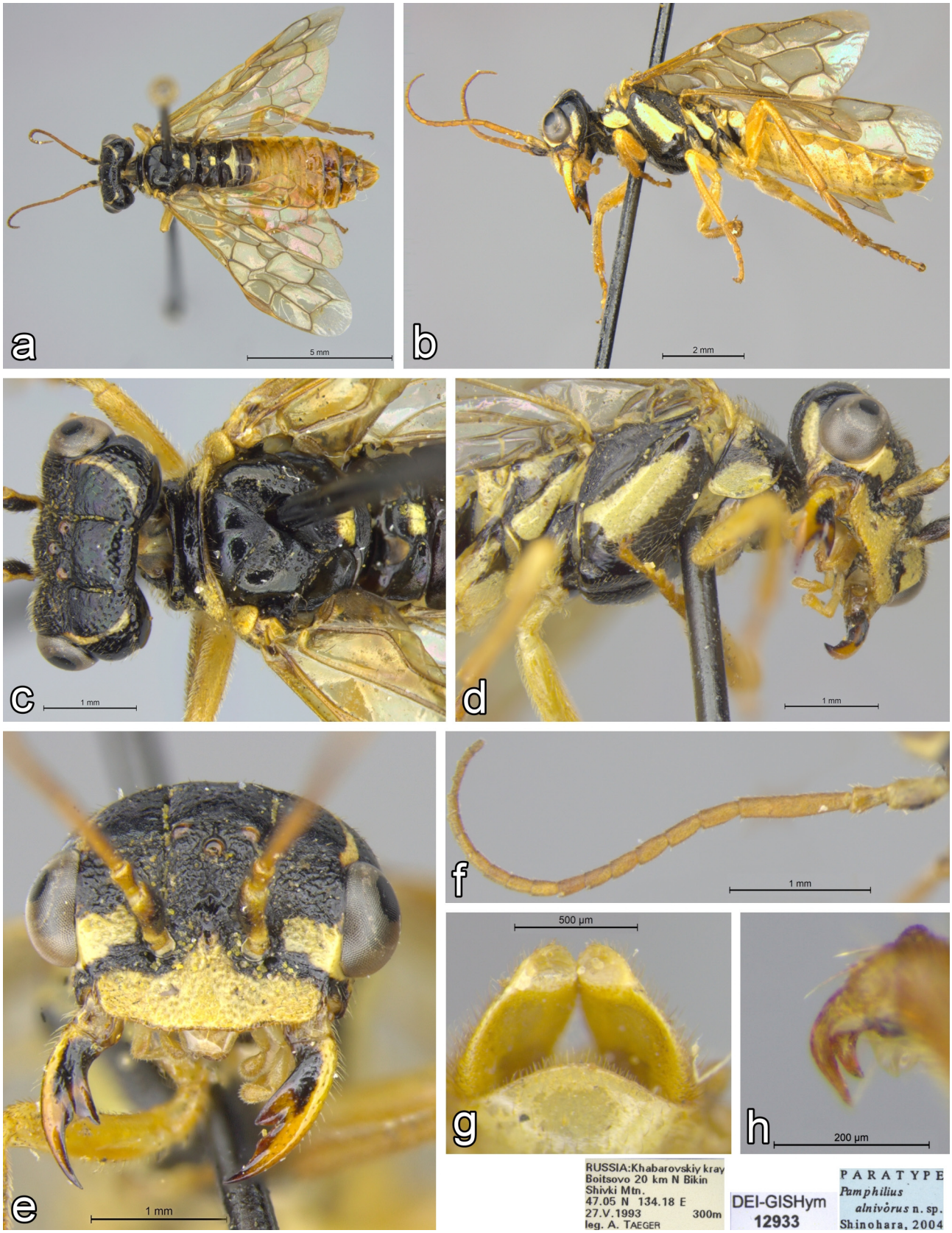


FIGURE 55. ***Pamphilius alnivorus***, male, Russia (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia ventrally, **(h)** claw.

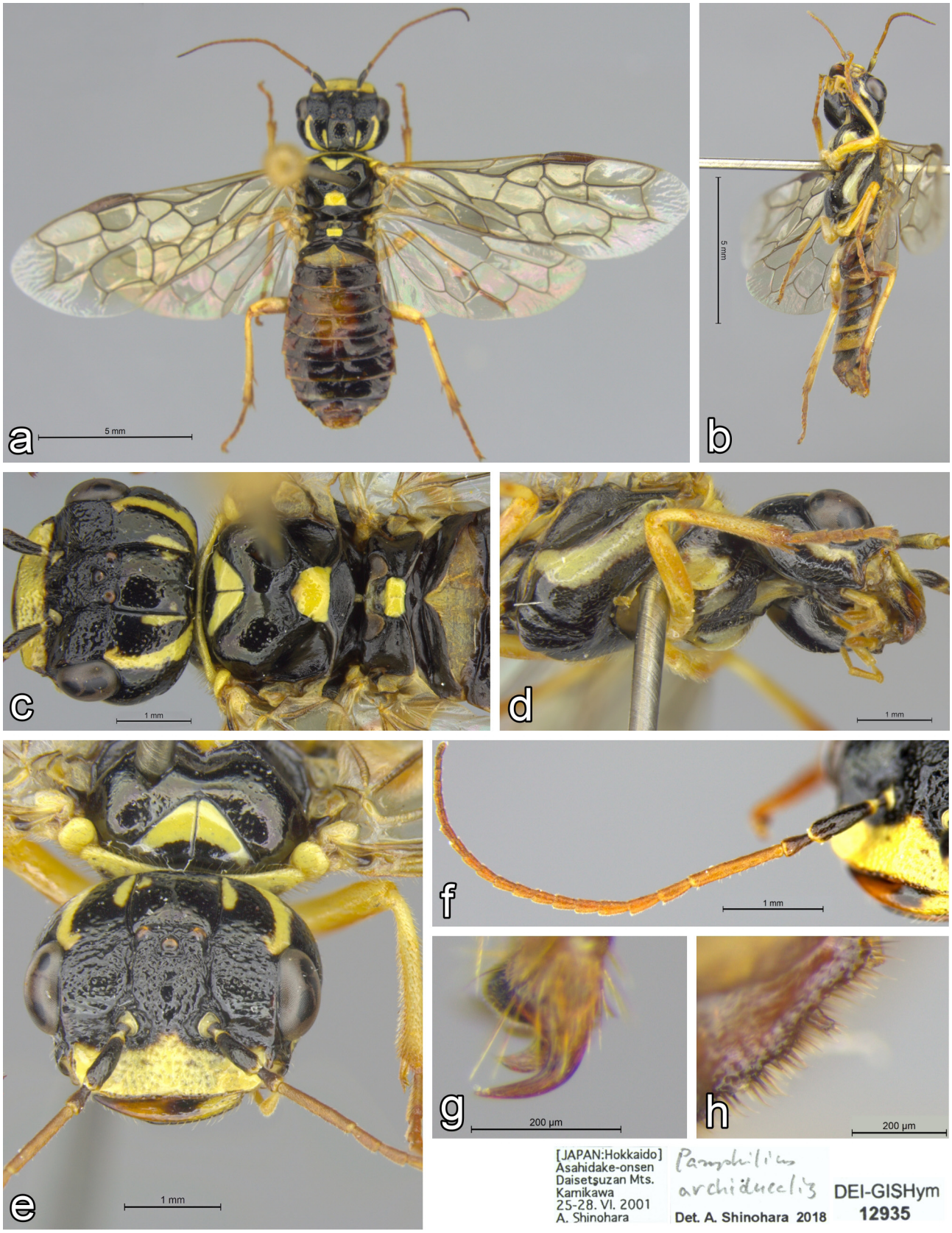


FIGURE 56. ***Pamphilius archiducalis***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** sawsheath laterally.

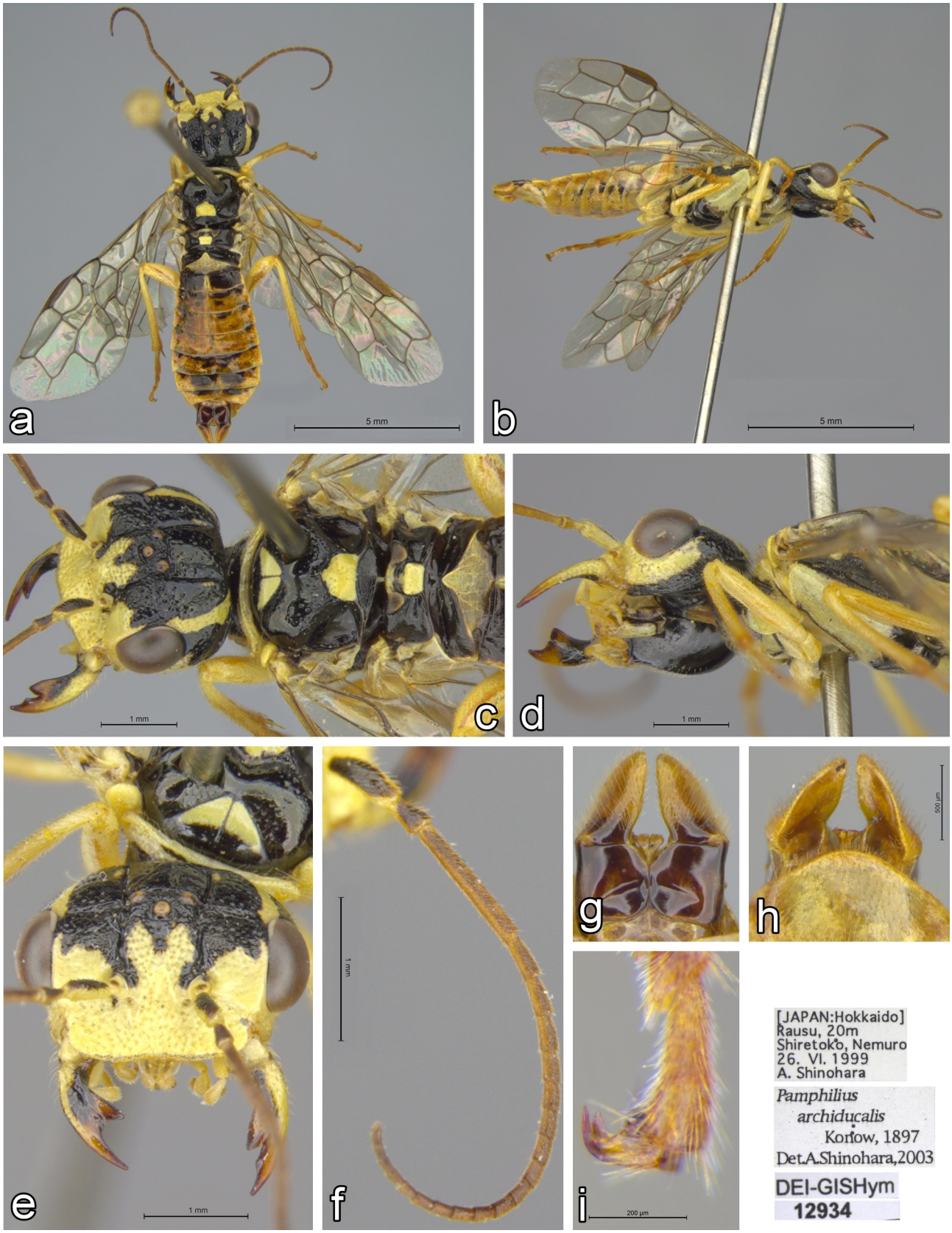


FIGURE 57. ***Pamphilius archiducalis***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

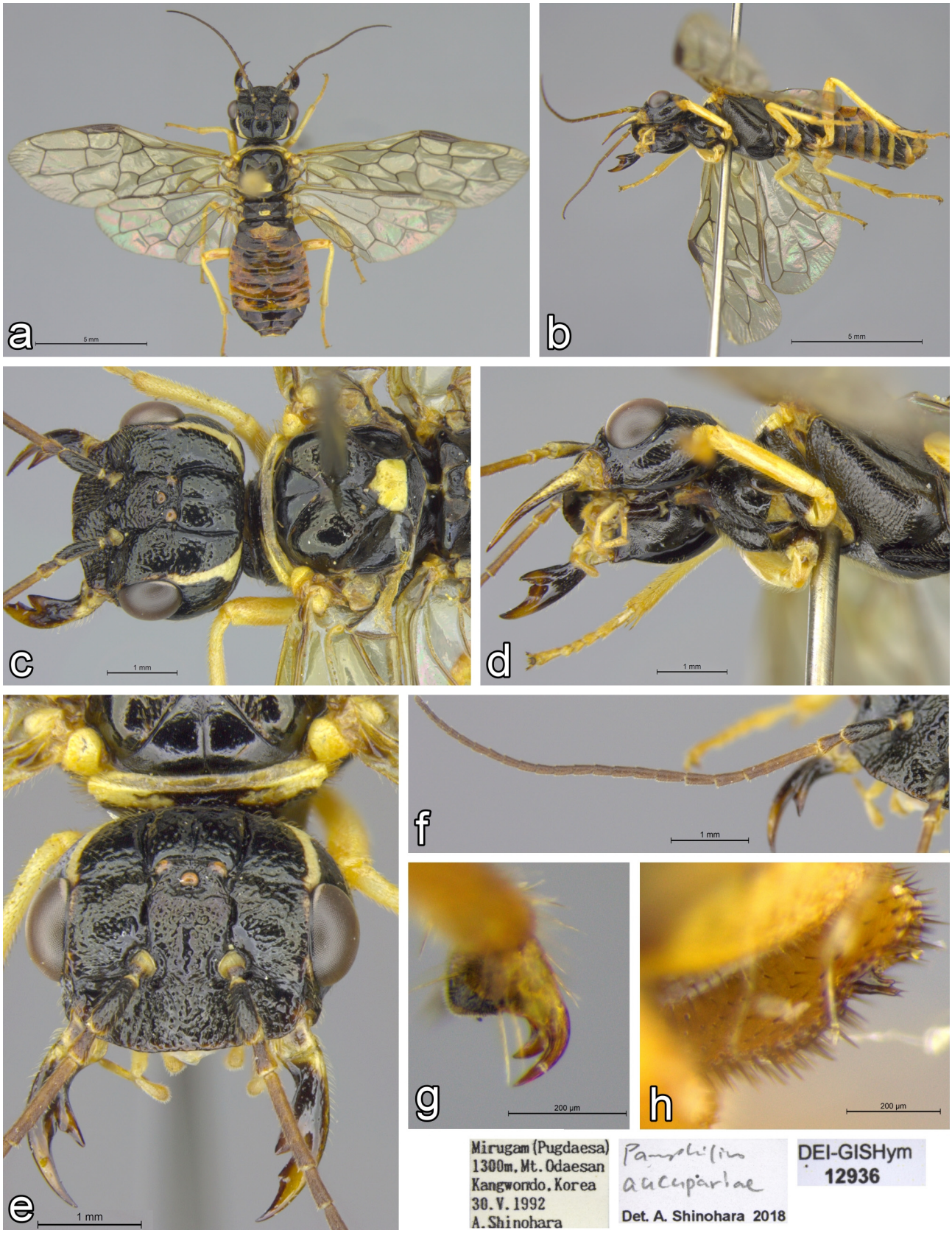


FIGURE 58. ***Pamphilius aucupariae***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** sawsheath laterally.

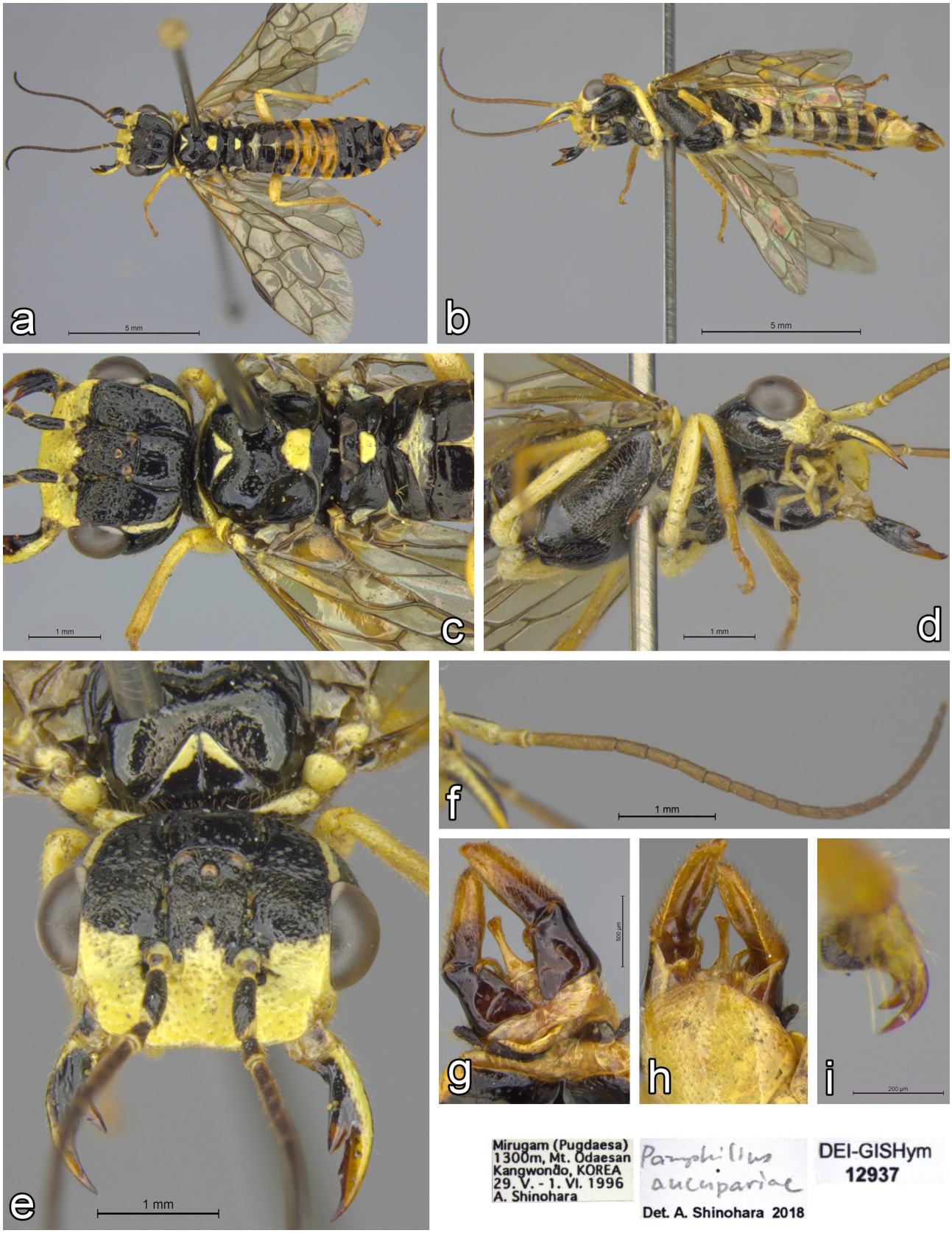


FIGURE 59. ***Pamphilius aucupariae***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

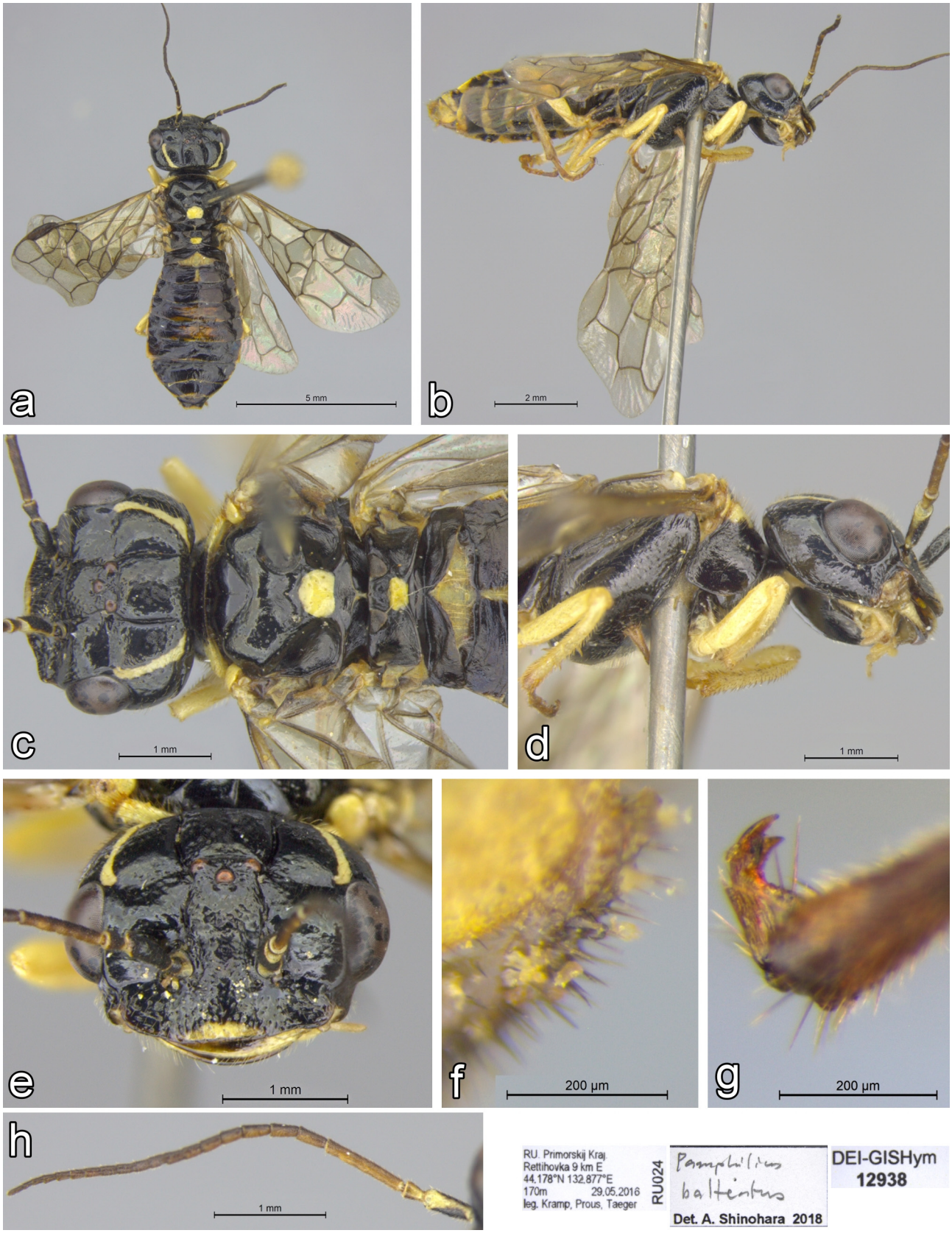


FIGURE 60. ***Pamphilius balteatus***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** sawsheath laterally, **(g)** claw, **(h)** antenna.

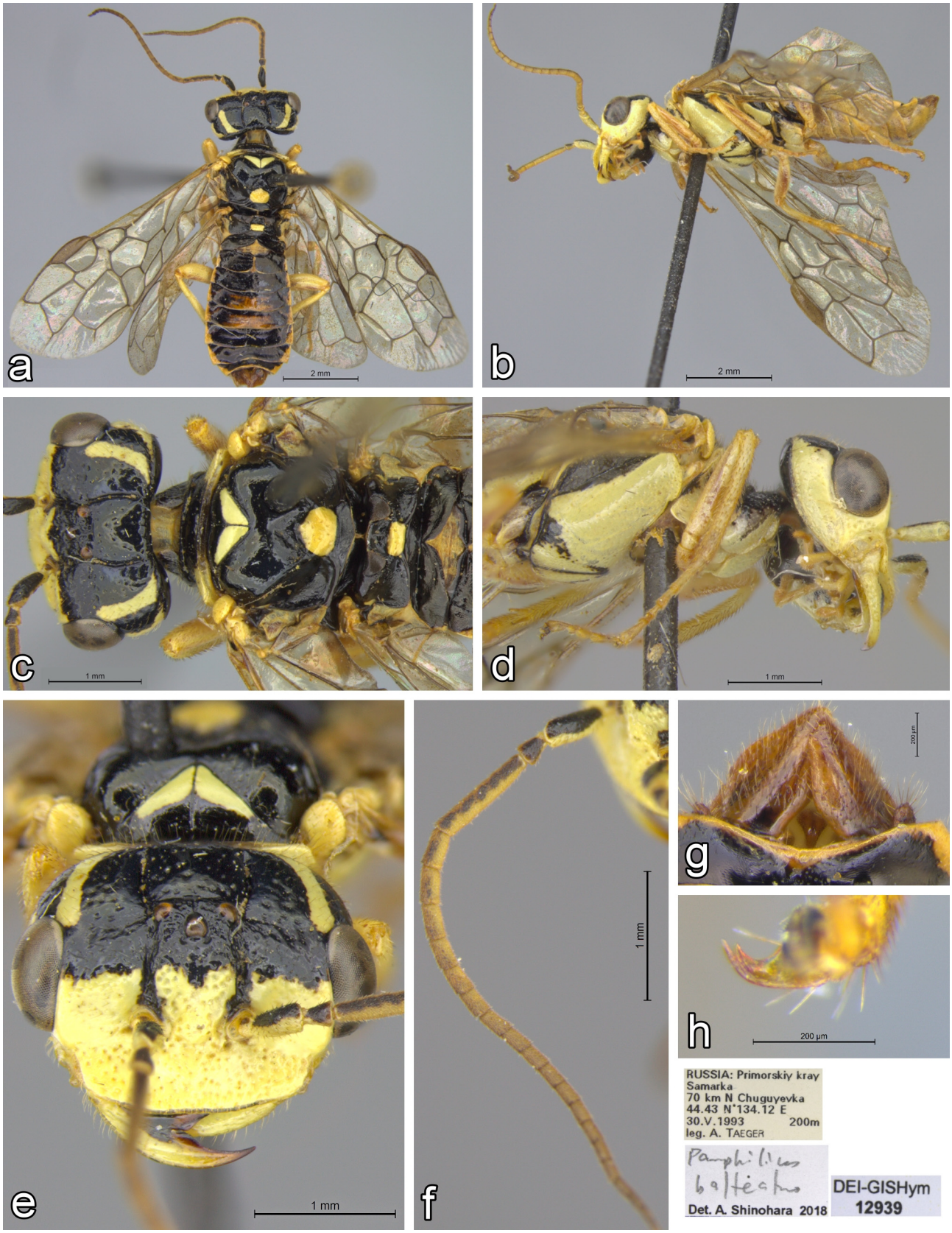


FIGURE 61. ***Pamphilius balteatus***, male, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** claw.

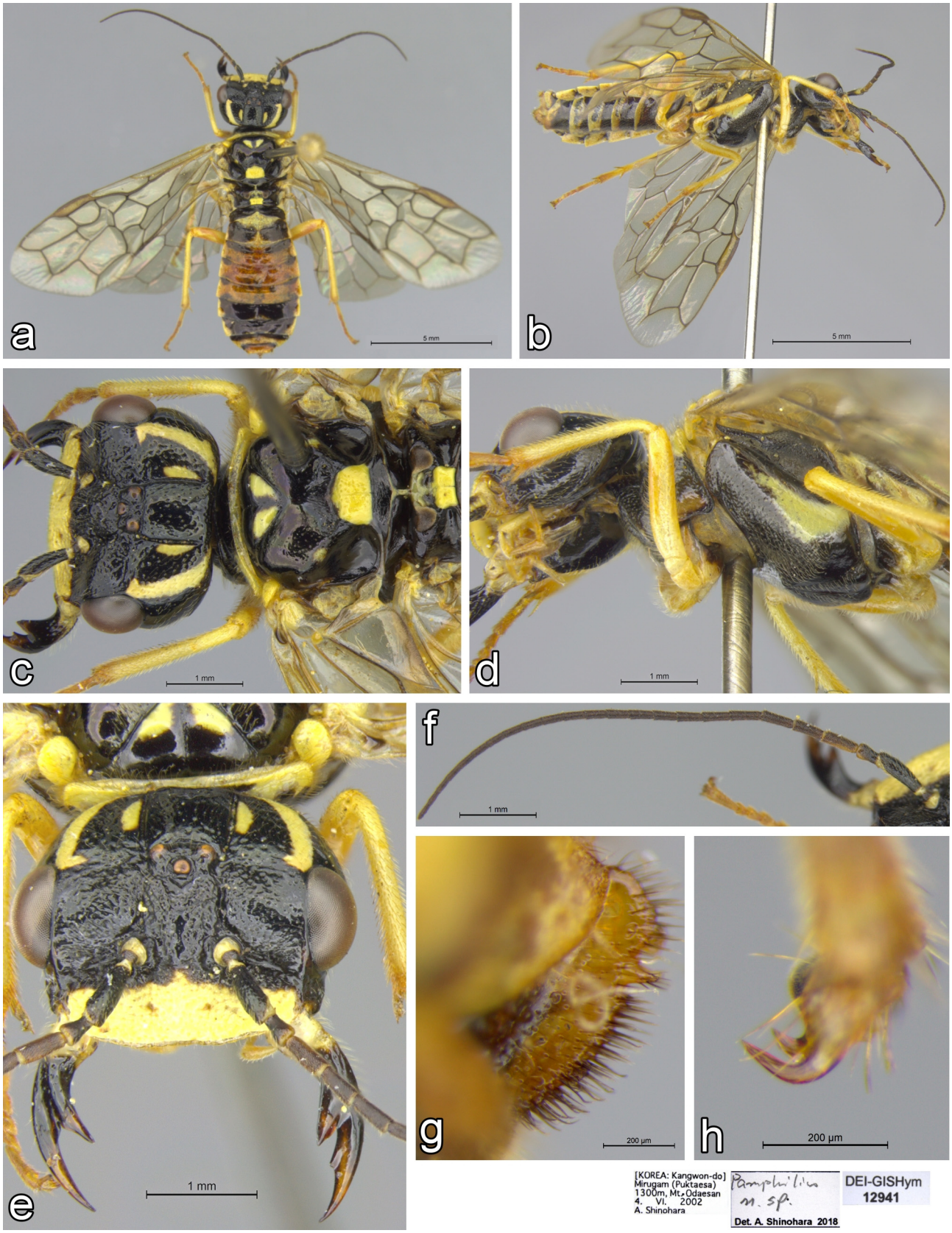


FIGURE 62. ***Pamphilius belokobylskii***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

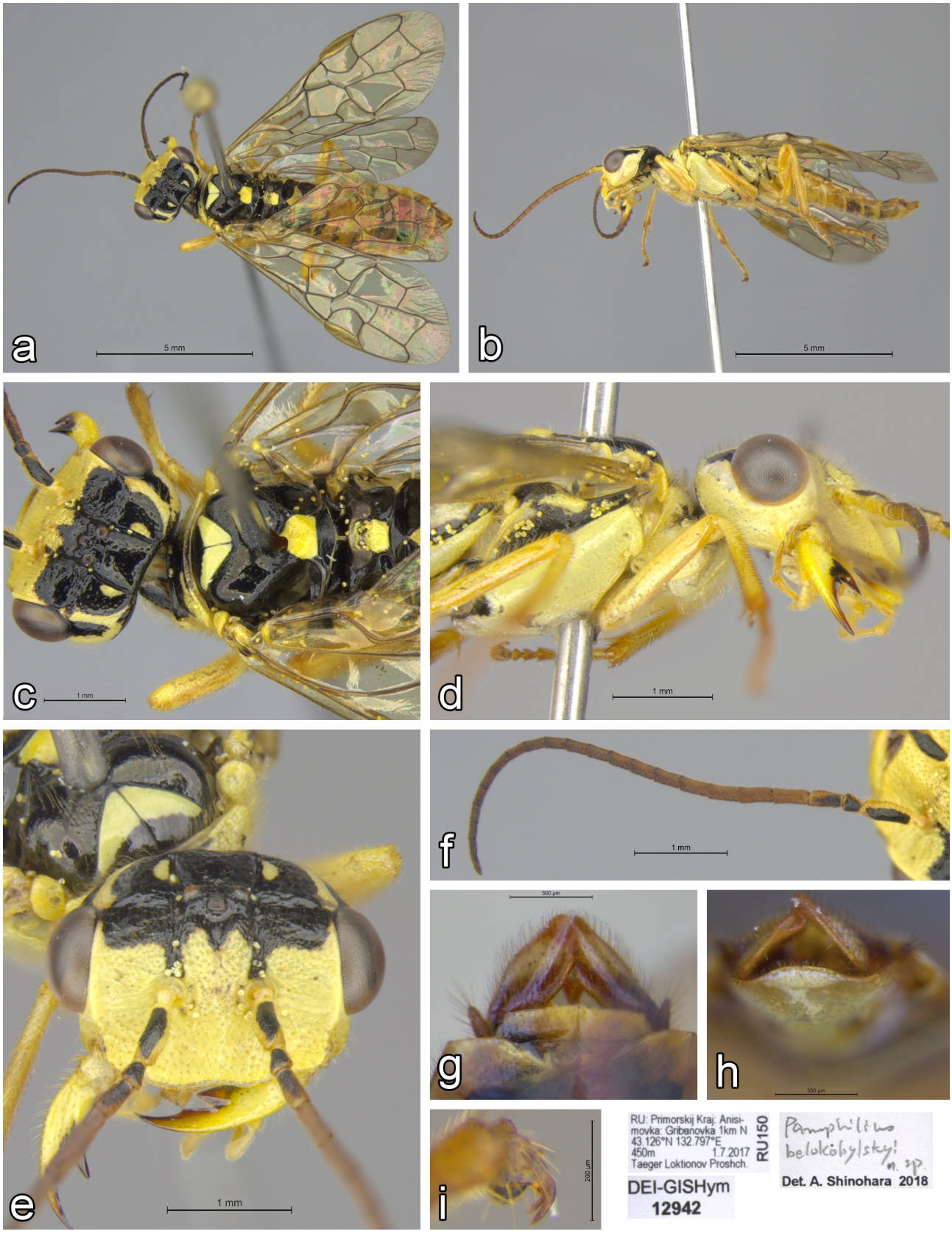


FIGURE 63. ***Pamphilius belokobylskii***, male, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

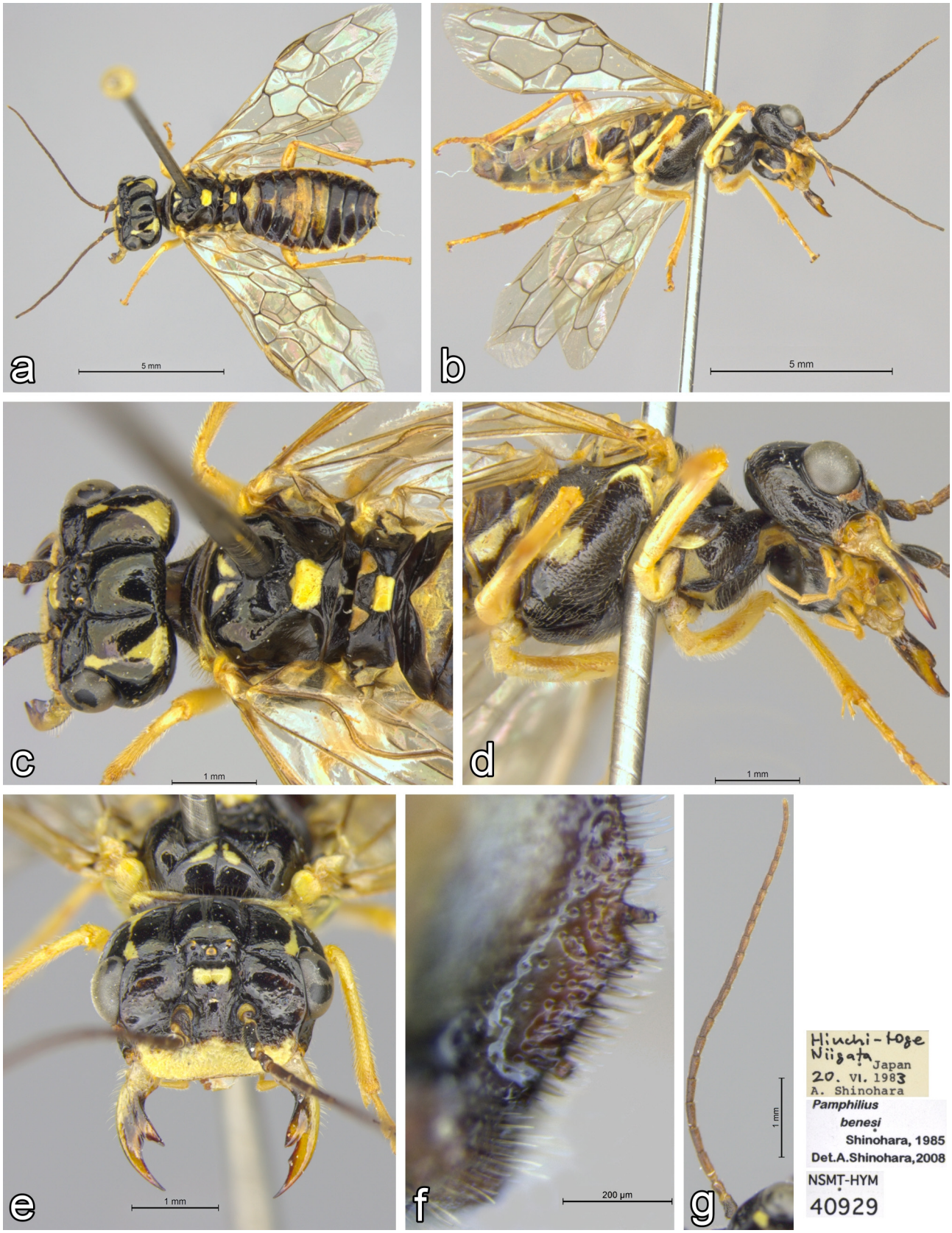


FIGURE 64. ***Pamphilius benesi***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** sawsheath laterally, **(g)** antenna.

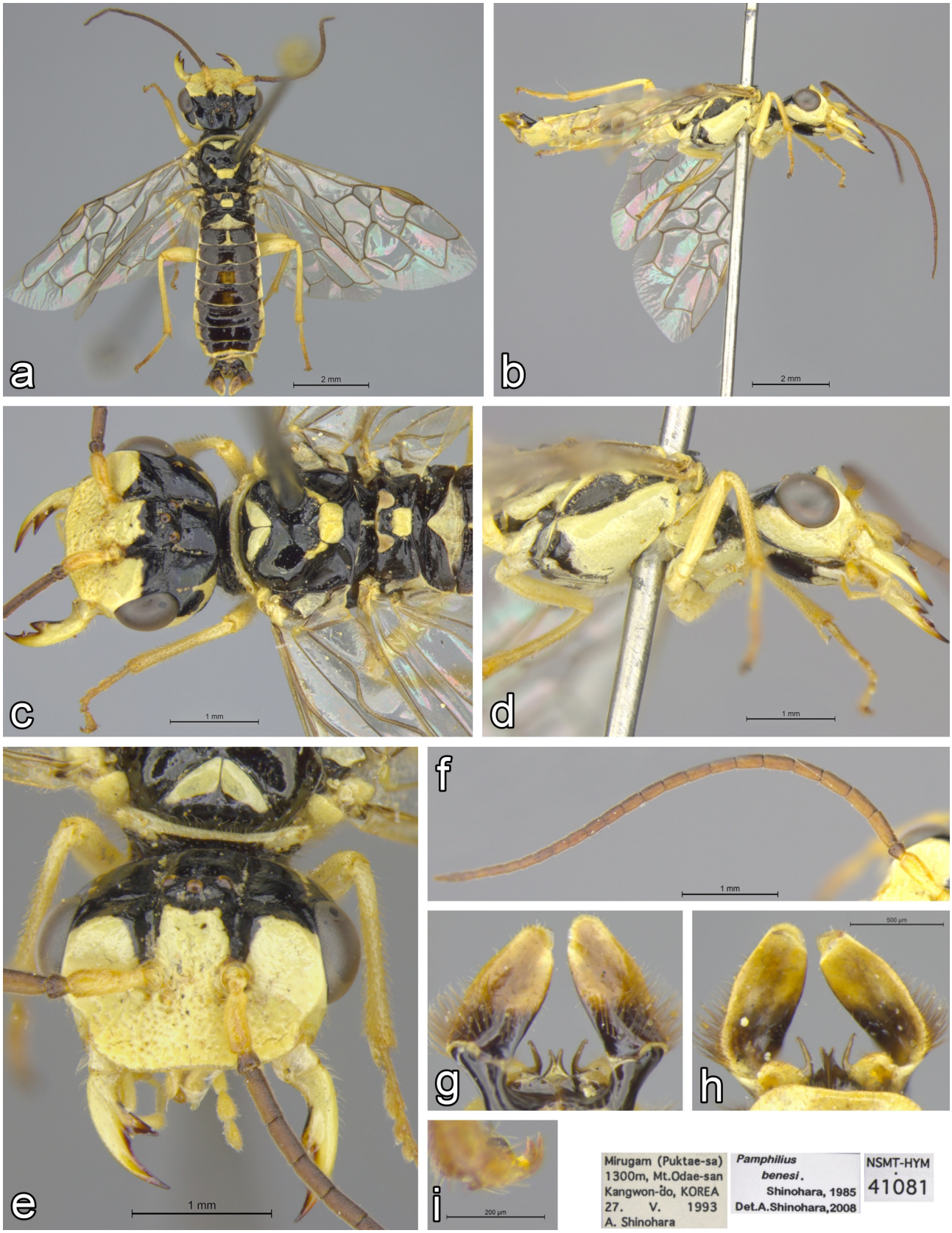


FIGURE 65. ***Pamphilius benesi***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

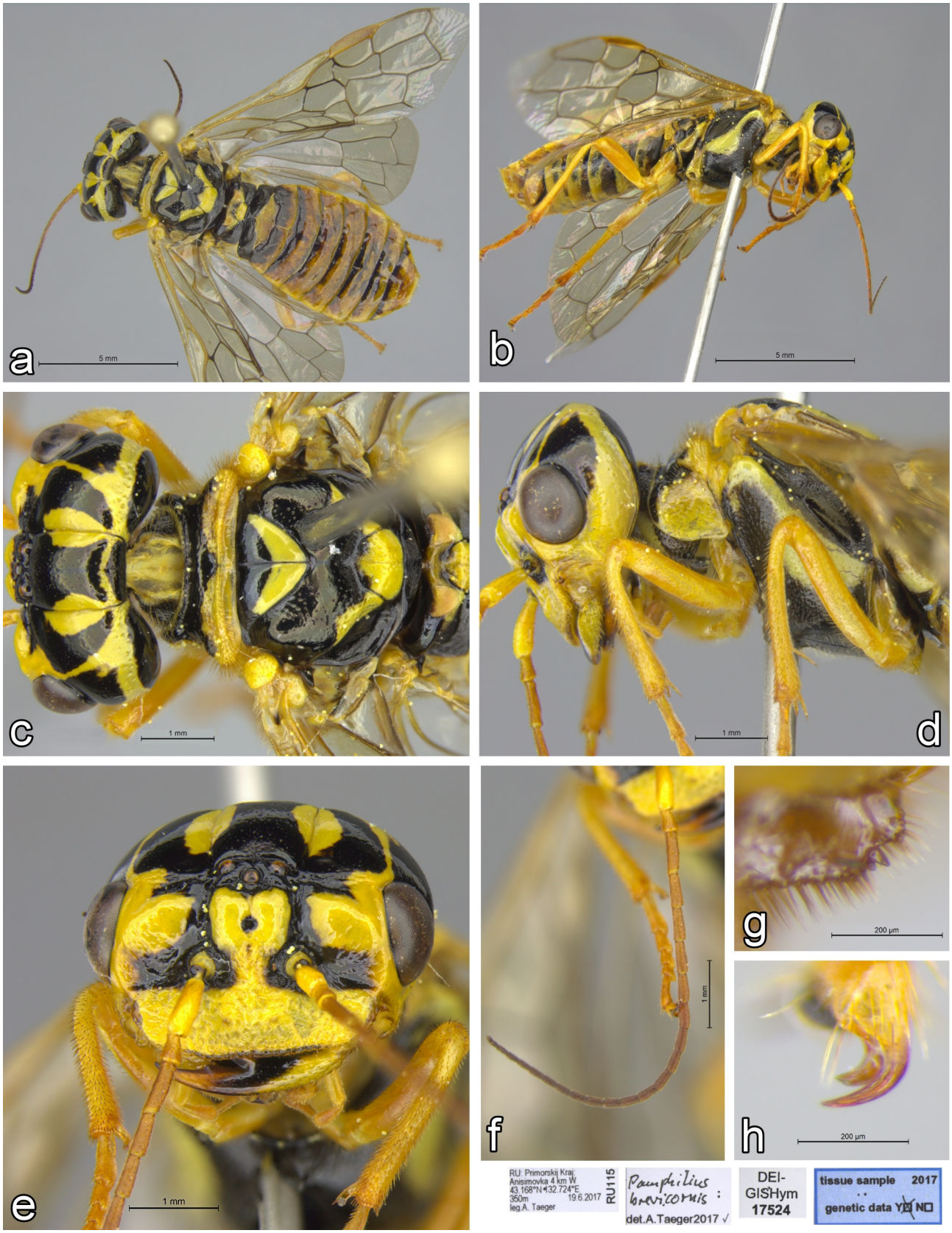


FIGURE 66. ***Pamphilius brevicornis brevicornis***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

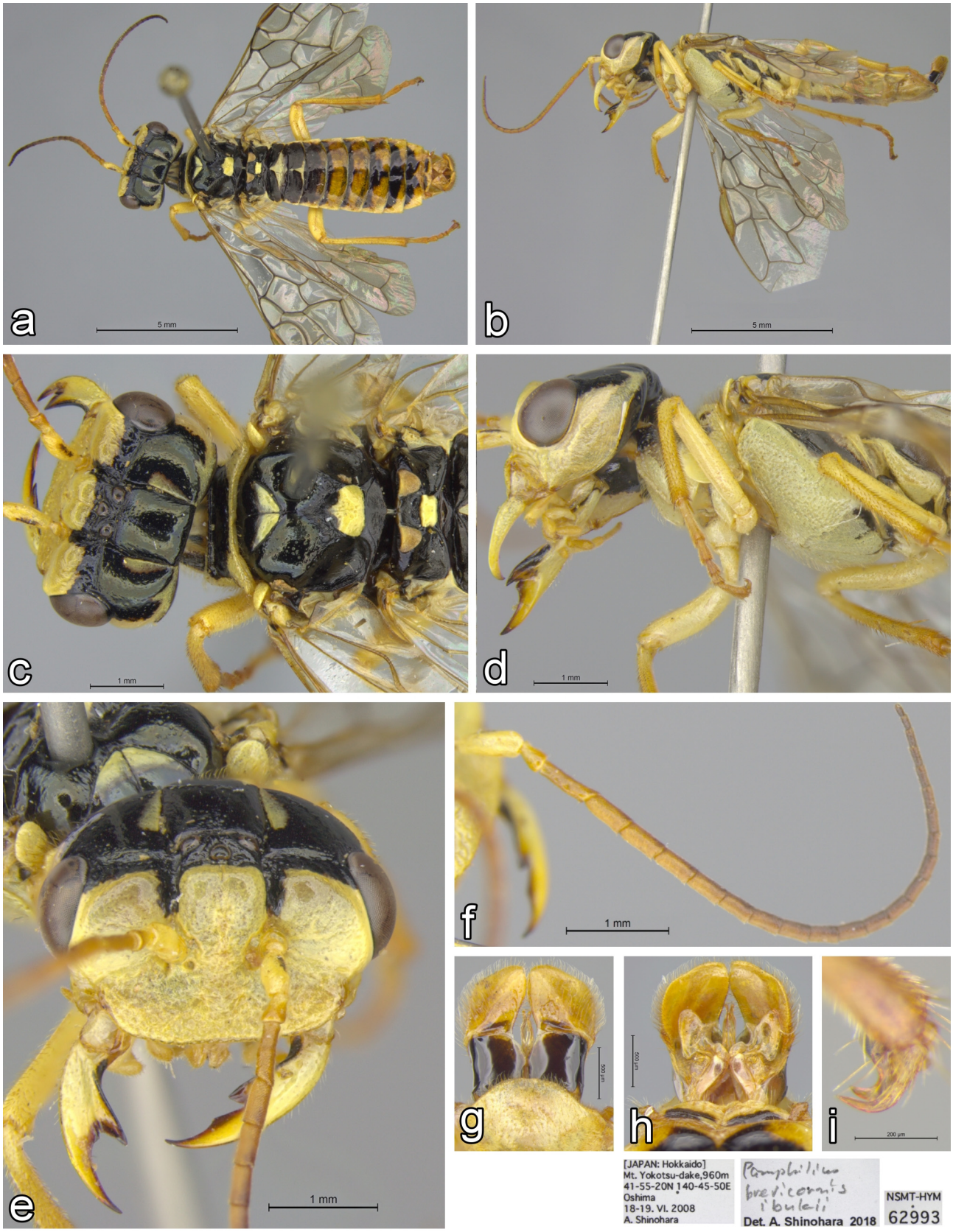


FIGURE 67. ***Pamphilius brevicornis ibukii***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

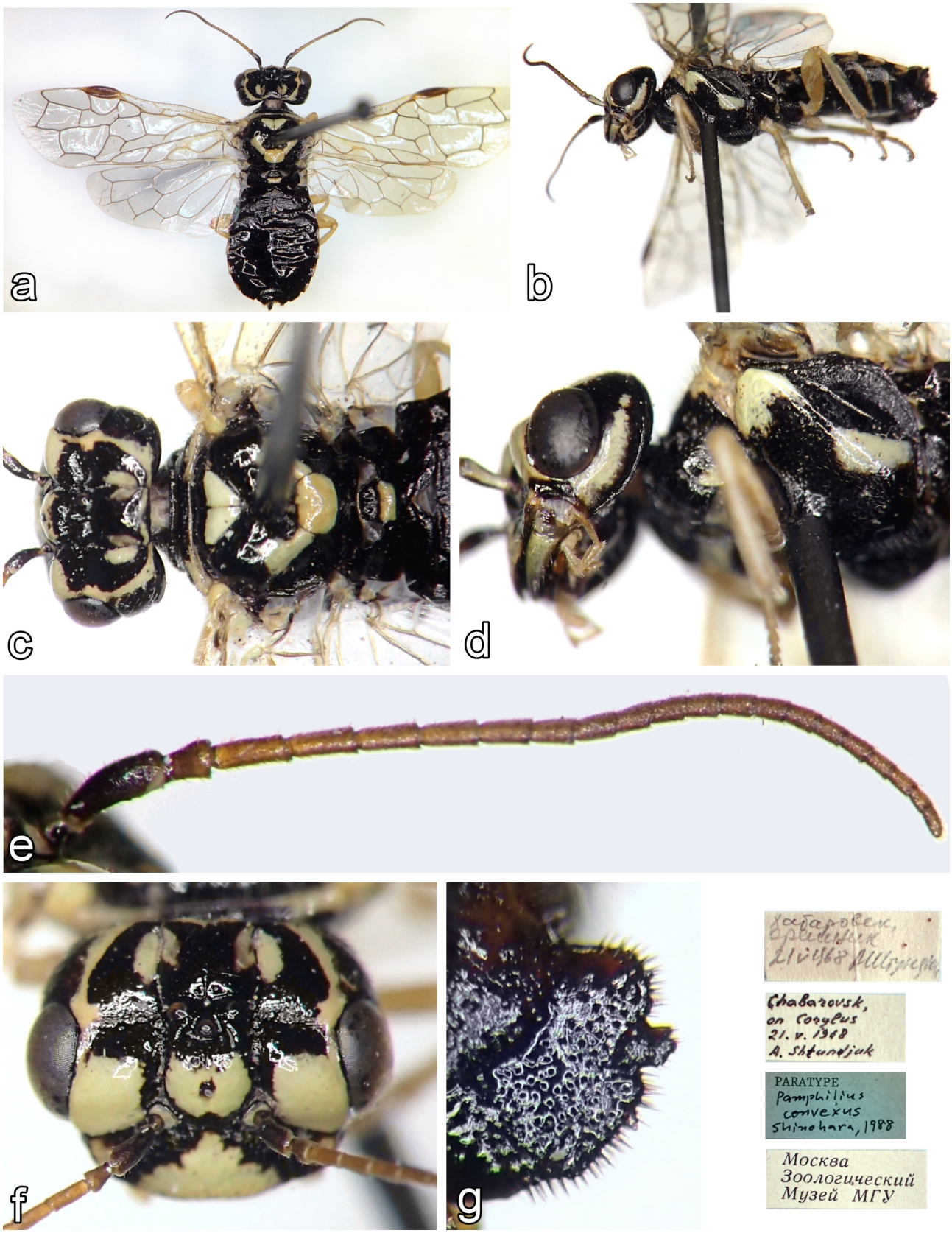


FIGURE 68. ***Pamphilius convexus***, female, Russia (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** antenna, **(f)** face, **(g)** sawsheath laterally.

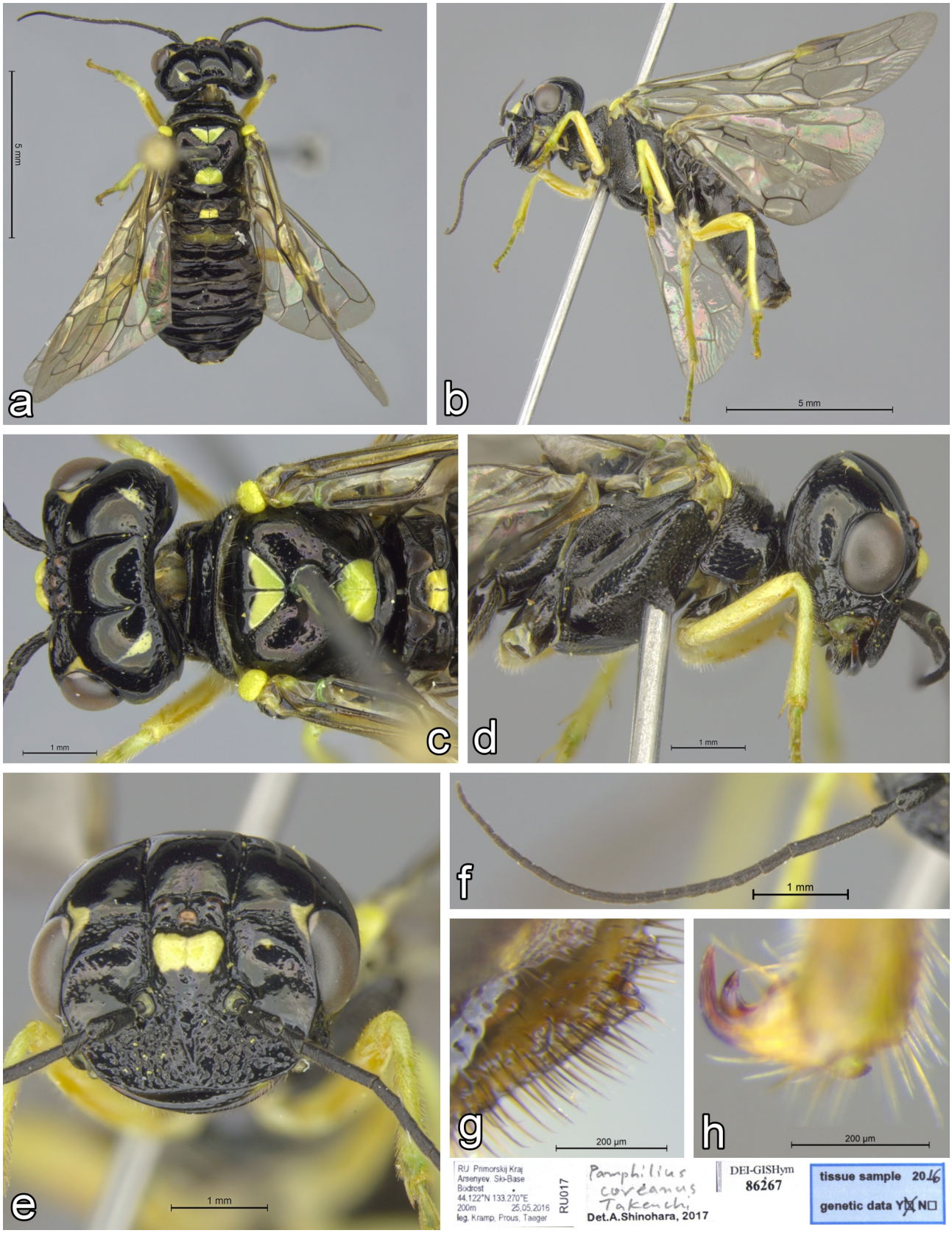


FIGURE 69. ***Pamphilius coreanus***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

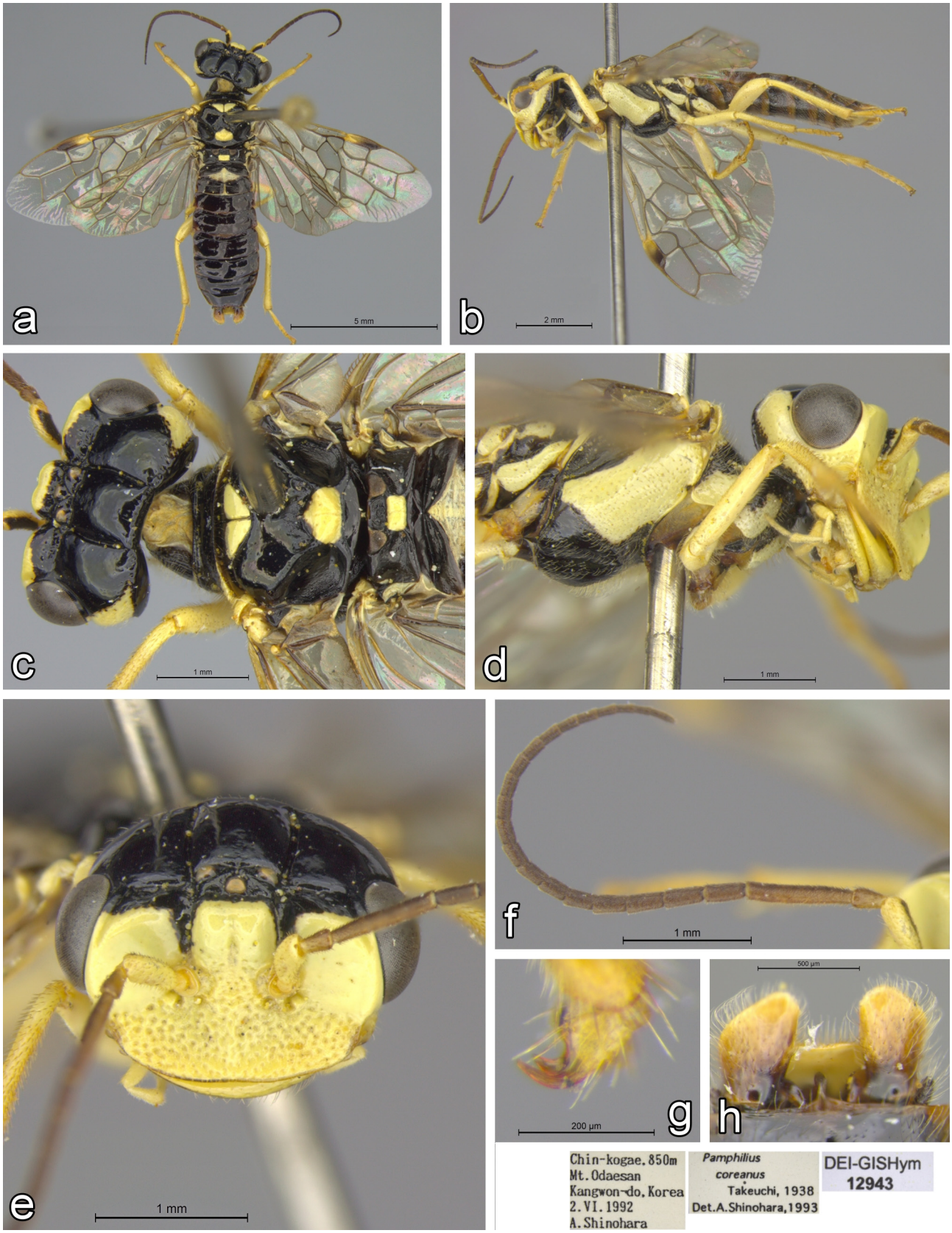


FIGURE 70. ***Pamphilius coreanus***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** genitalia dorsally.

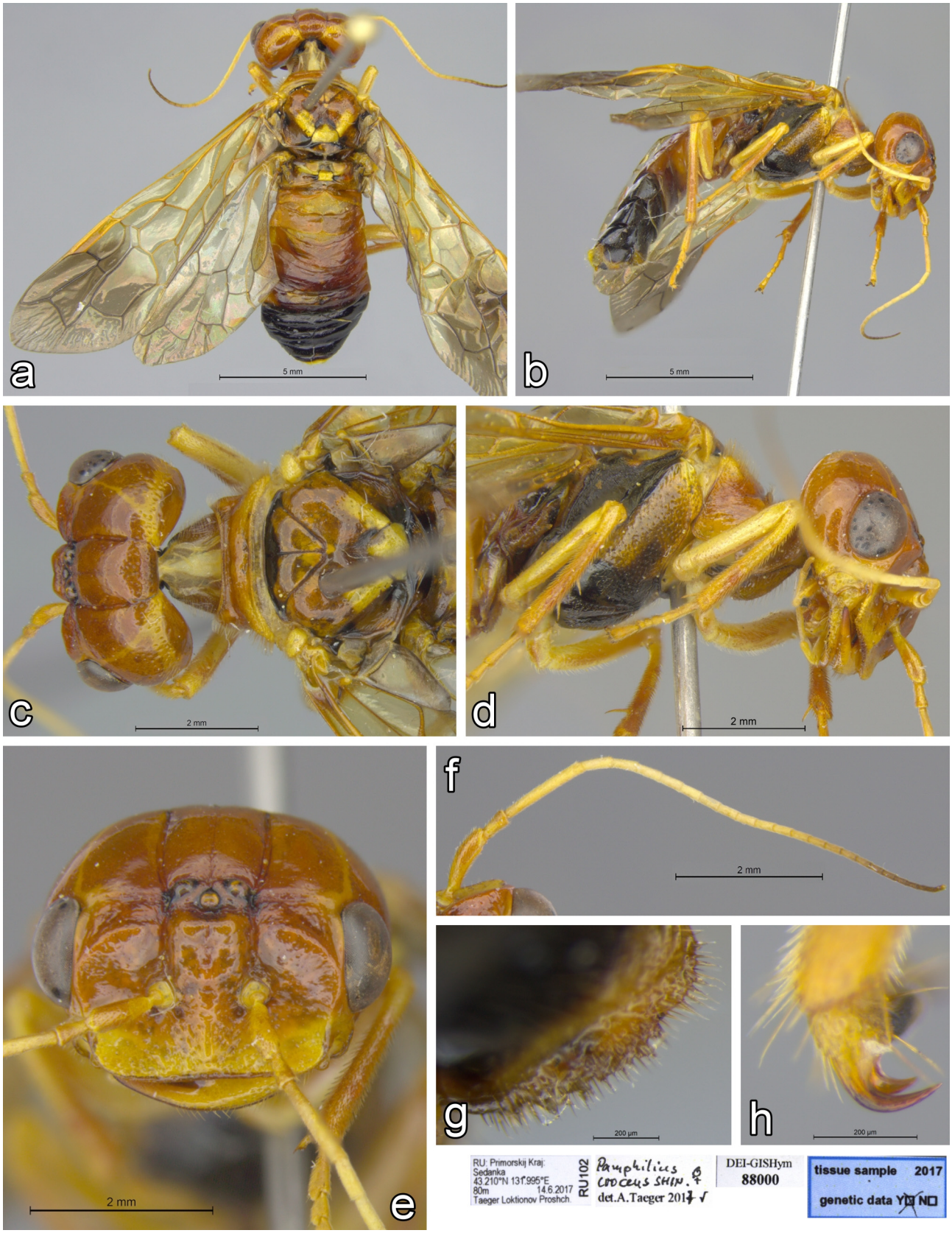


FIGURE 71. ***Pamphilius croceus***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

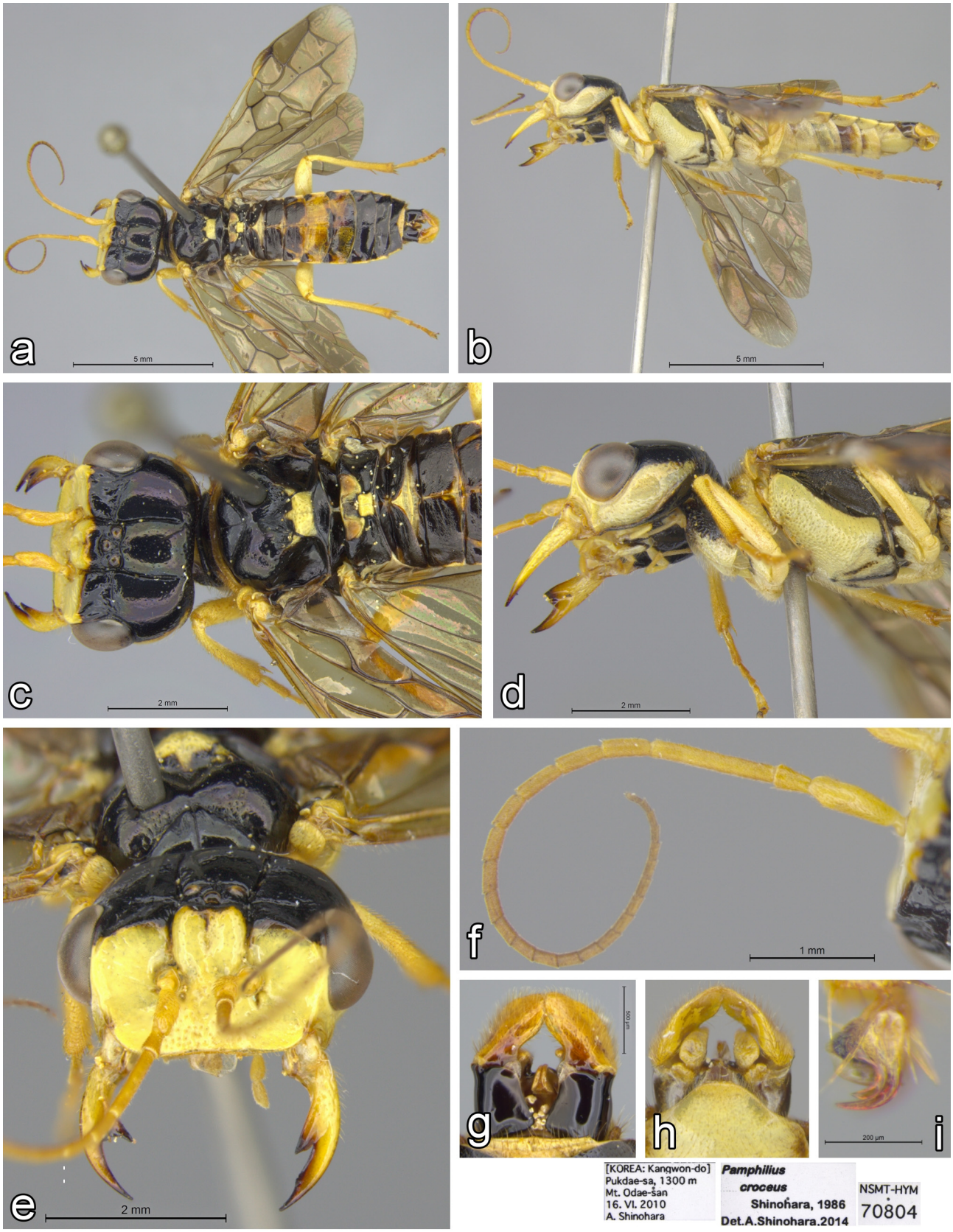


FIGURE 72. ***Pamphilius croceus***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

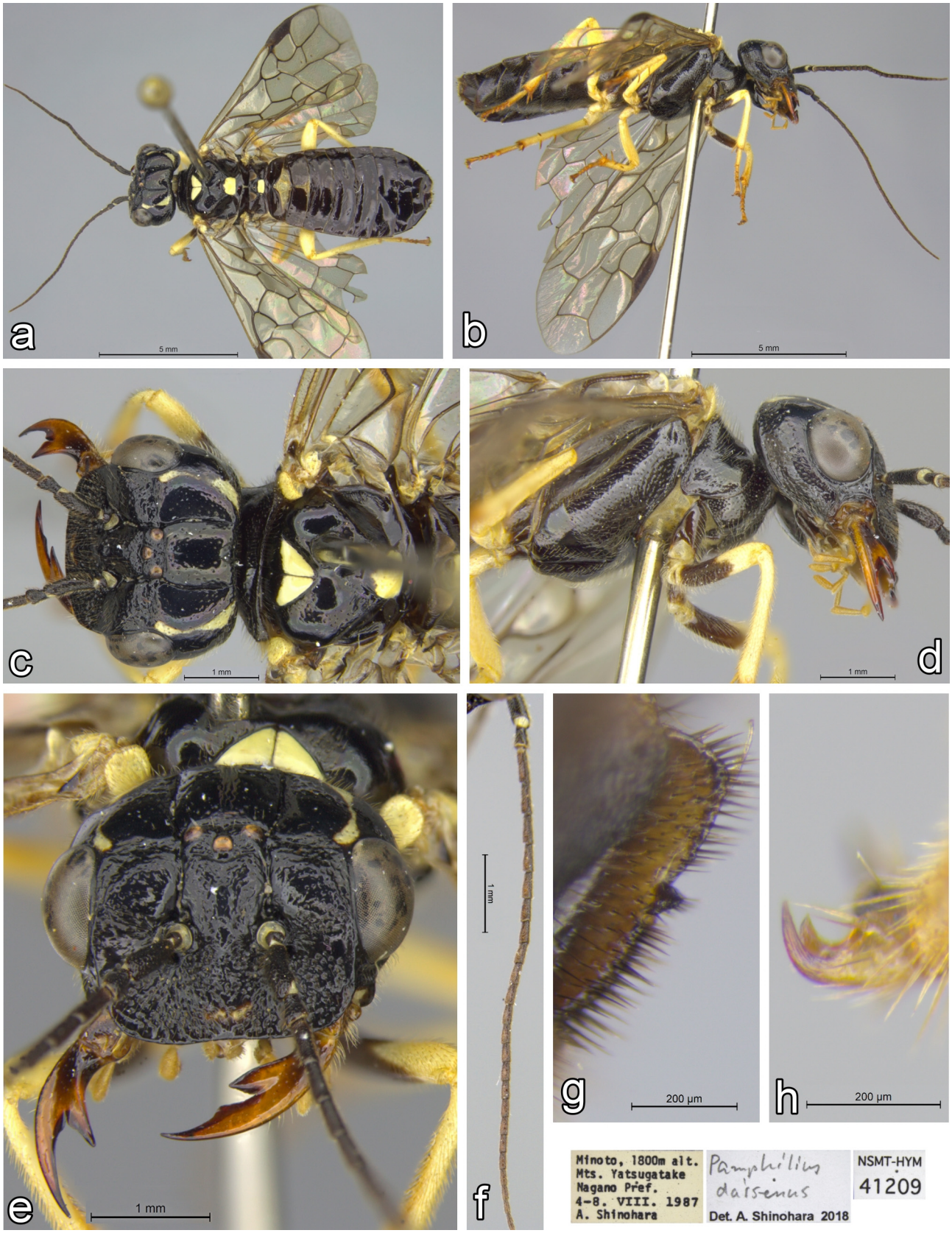


FIGURE 73. ***Pamphilius daisenus***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

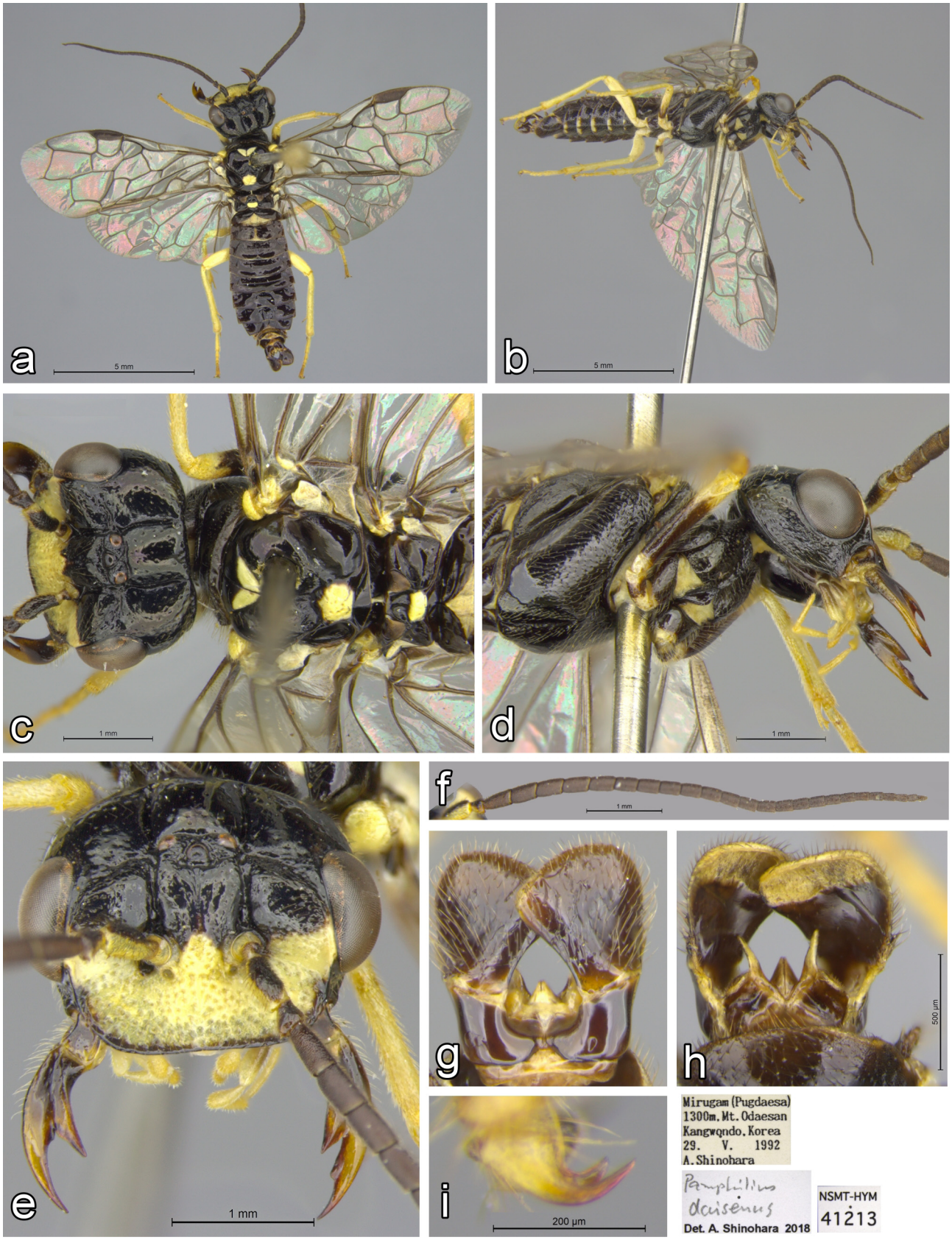


FIGURE 74. ***Pamphilius daisenus***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.



FIGURE 75. ***Pamphilius graciloides***, female, Russia (paratype) – **(a)** head & thorax dorsally, **(b)** head & thorax ventrolaterally, **(c)** sawsheath laterally, **(d)** face, **(e)** antenna, **(f)** fore wing.

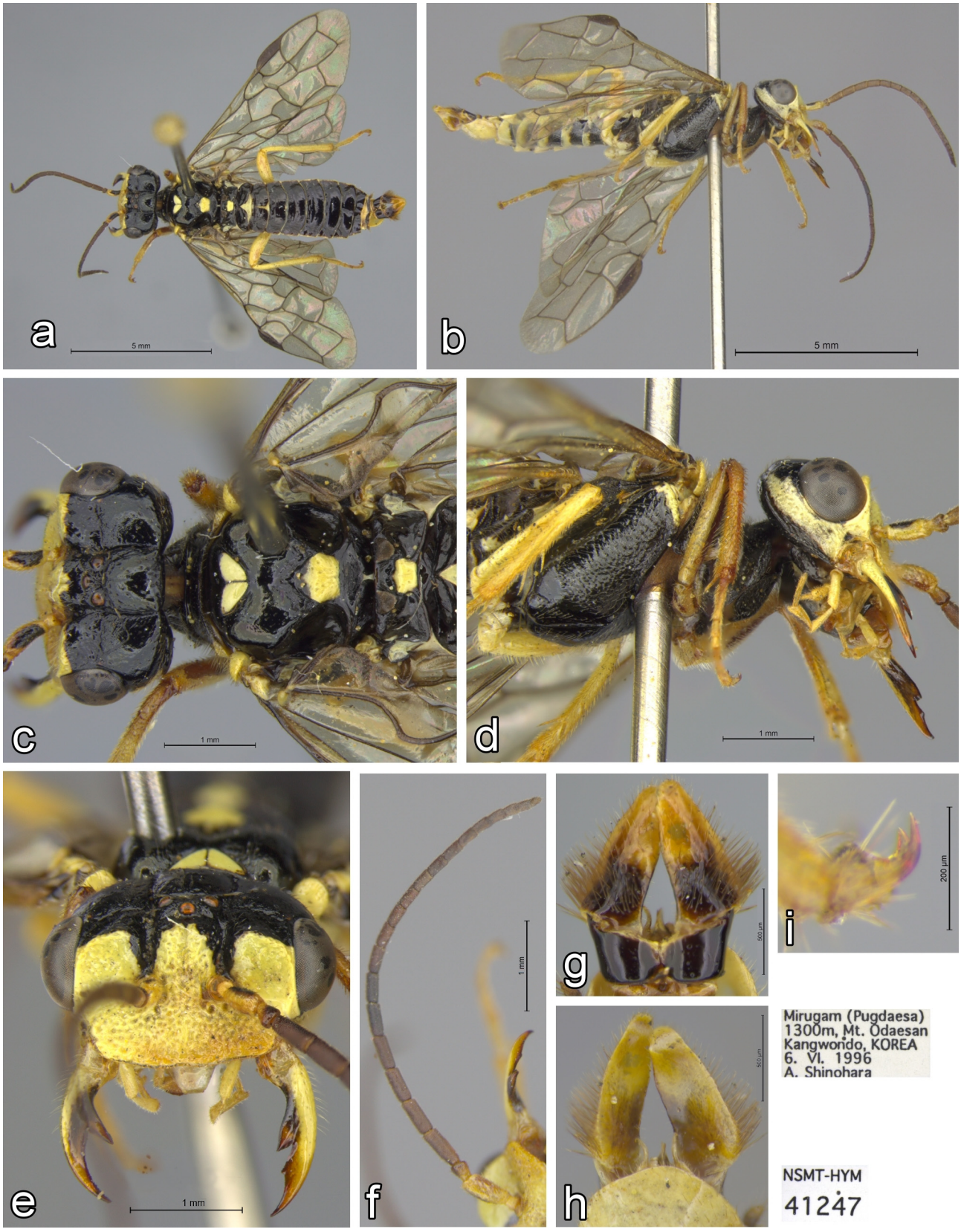


FIGURE 76. ***Pamphilius graciloides***, male, Korea (holotype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

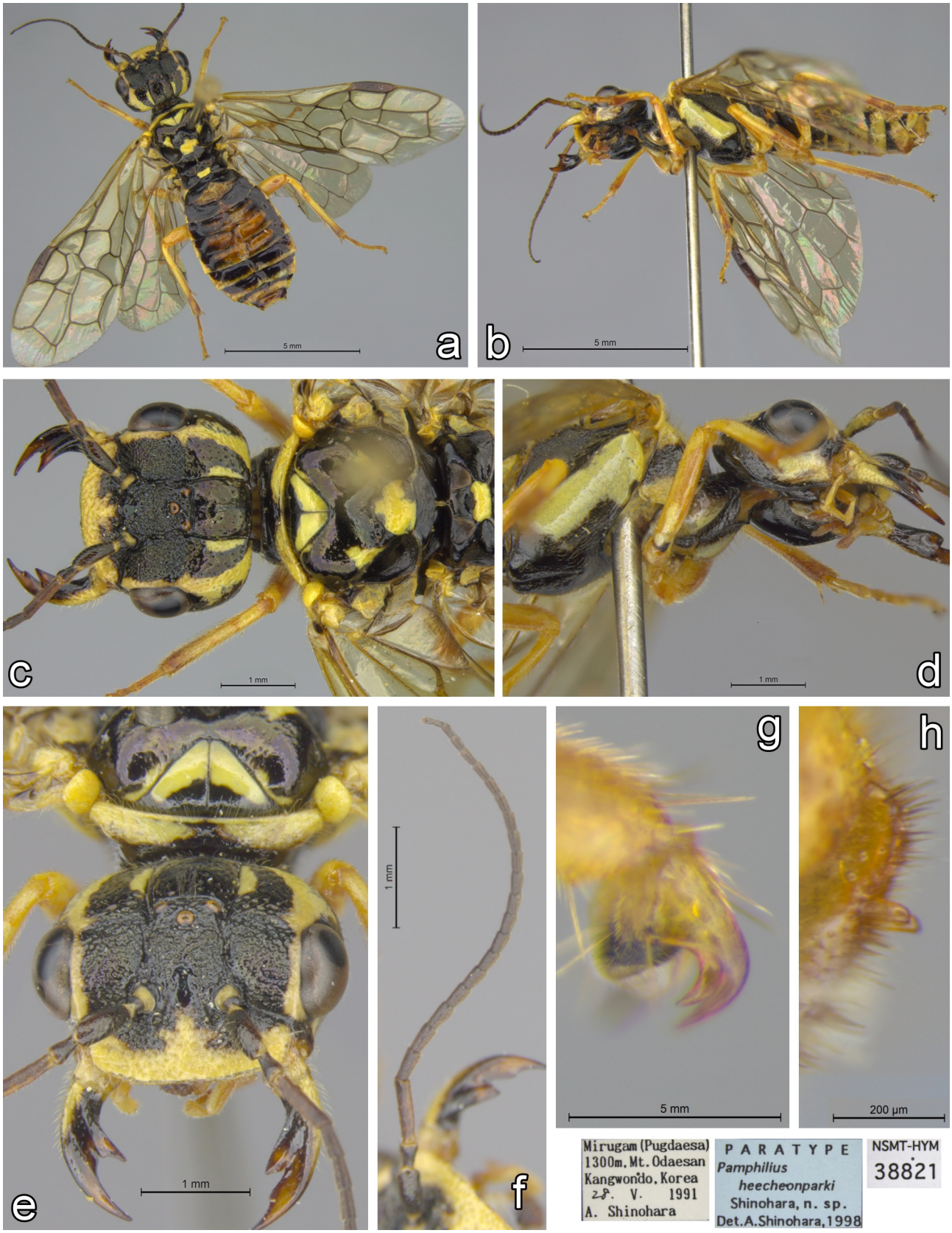


FIGURE 77. ***Pamphilius heecheonparki***, female, Korea (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** sawsheath laterally.

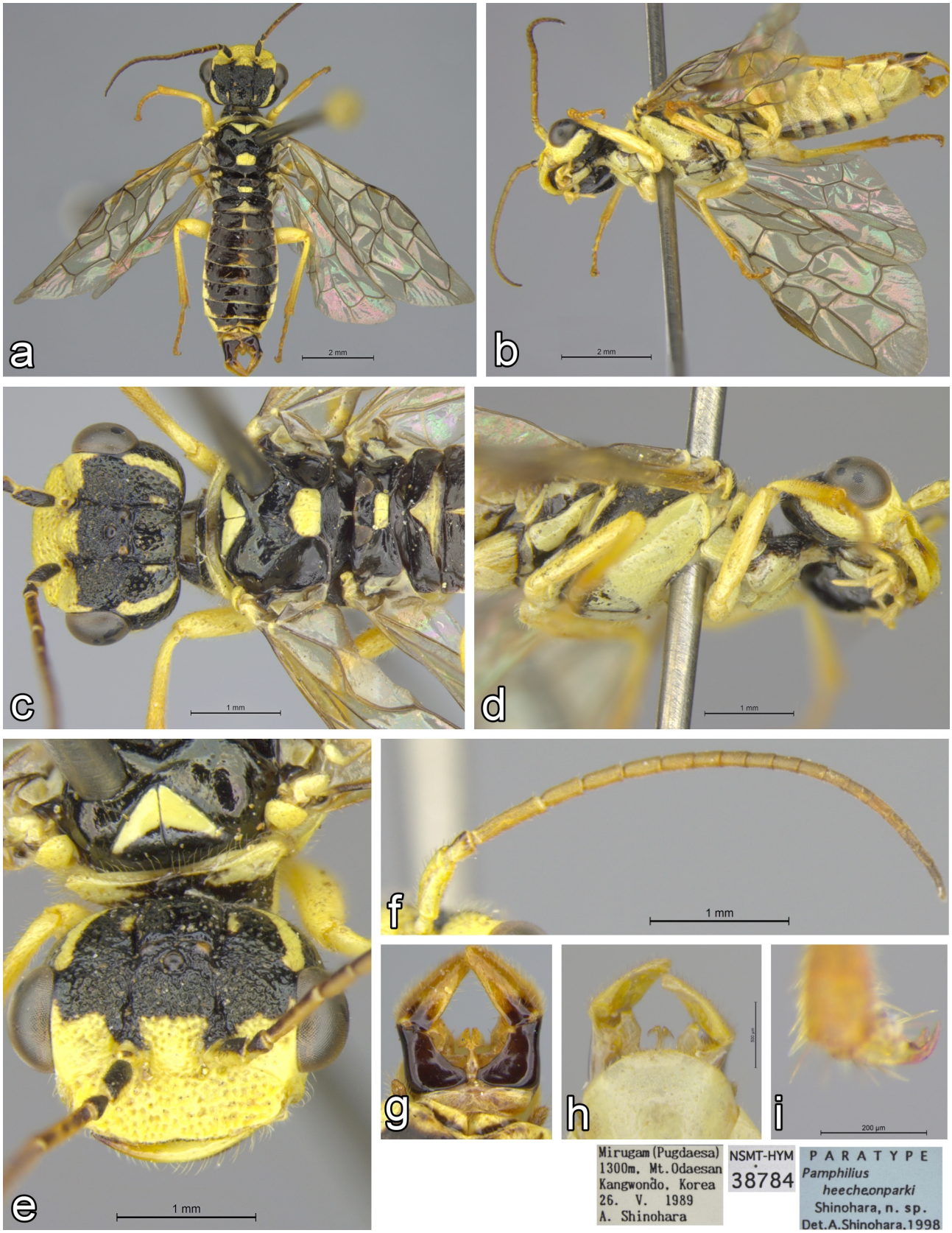


FIGURE 78. ***Pamphilius heecheonparki***, male, Korea (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

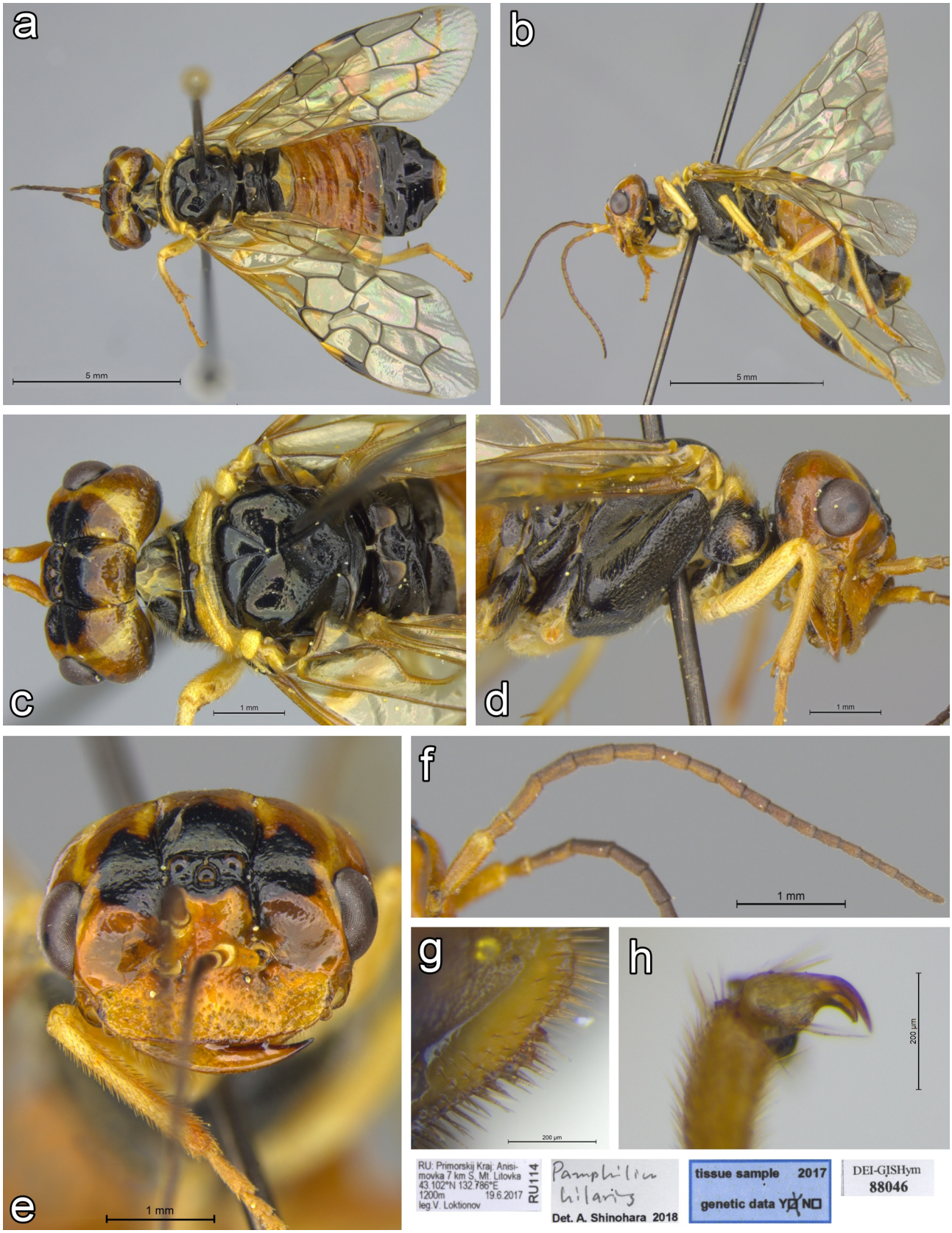


FIGURE 79. ***Pamphilius hilaris***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** fore wing, **(g)** sawsheath laterally, **(h)** claw.

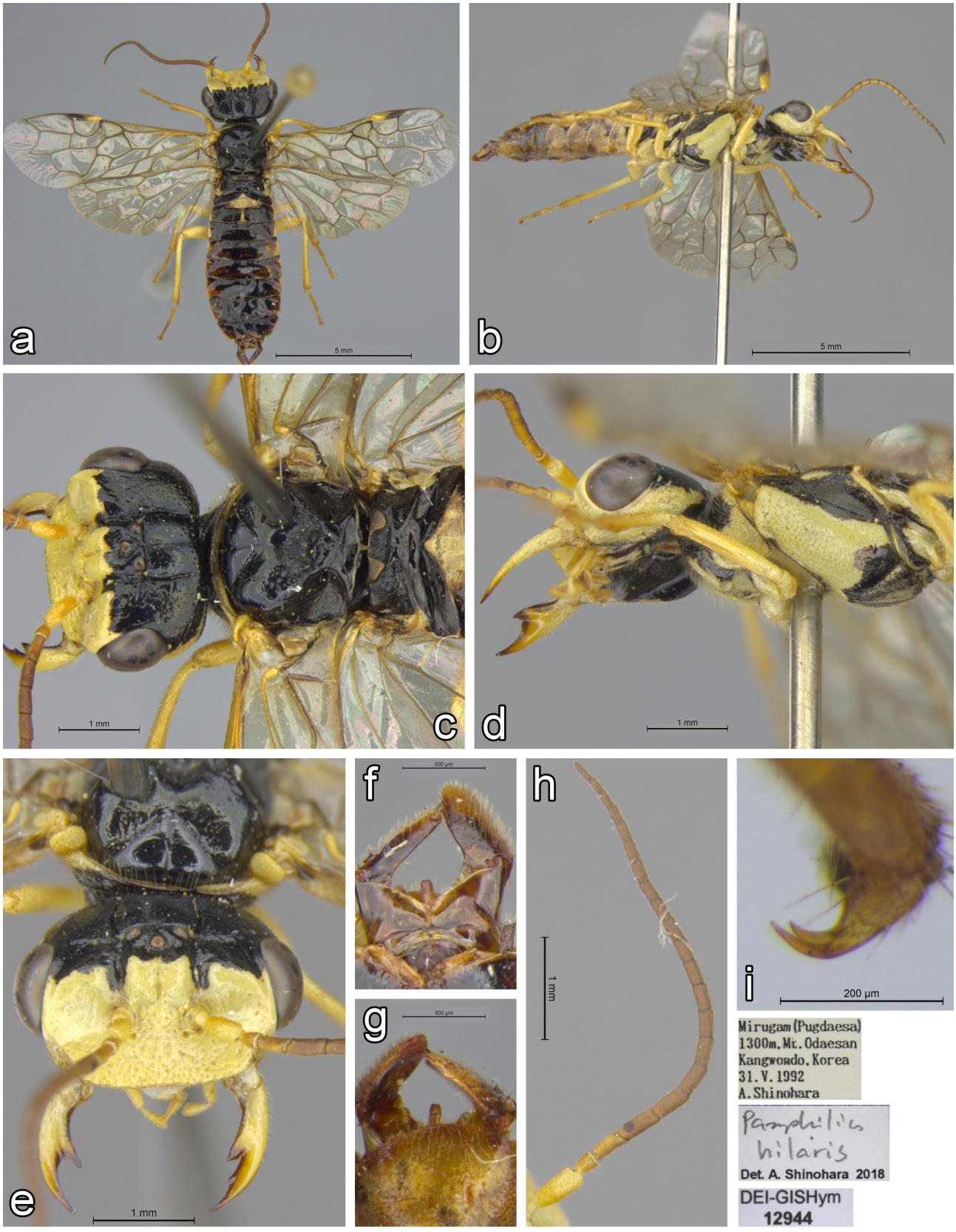


FIGURE 80. ***Pamphilius hilaris***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** genitalia dorsally, **(g)** genitalia ventrally, **(h)** antenna, **(i)** claw.

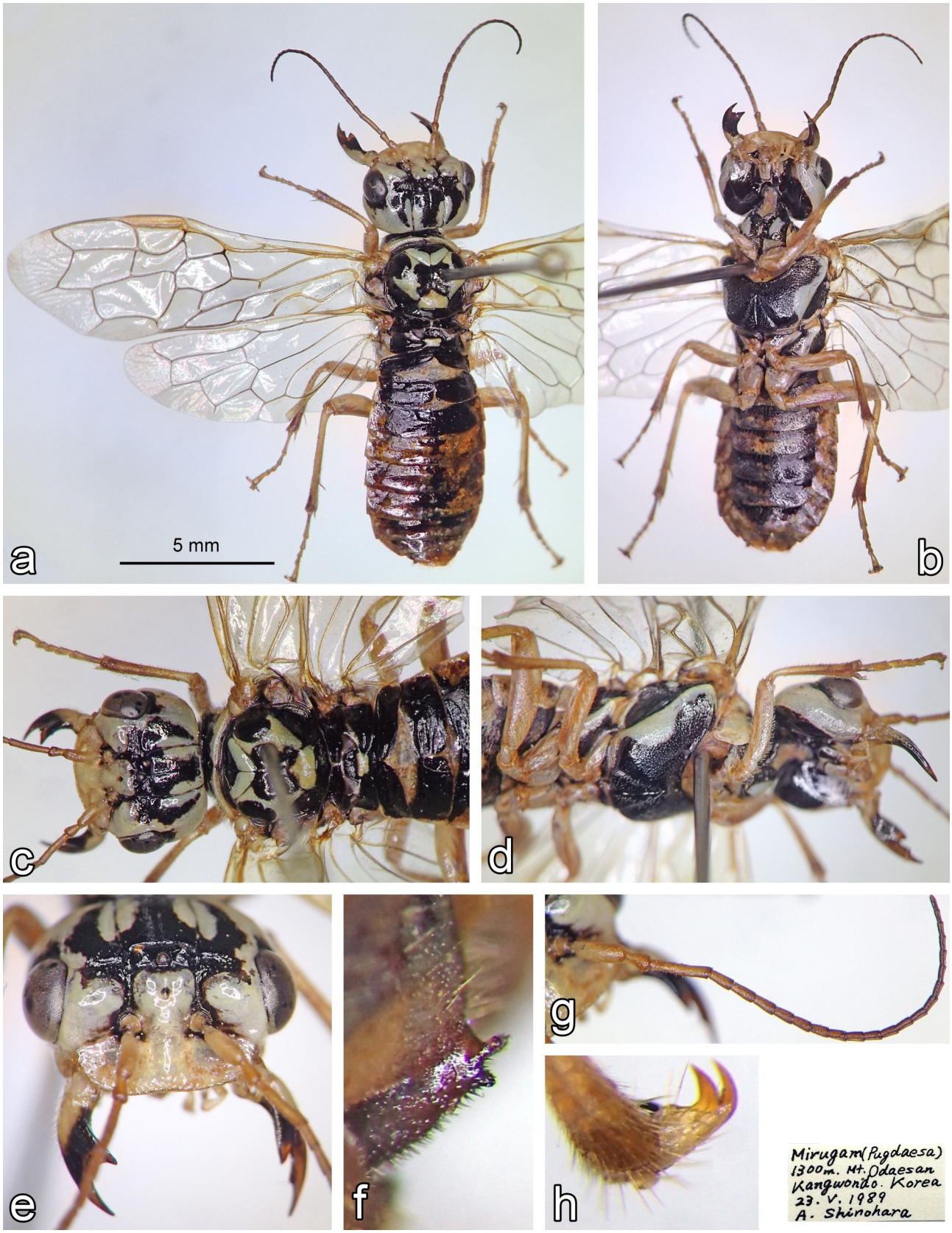


FIGURE 81. ***Pamphilius histrio***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** sawsheath laterally, **(g)** antenna, **(h)** claw.

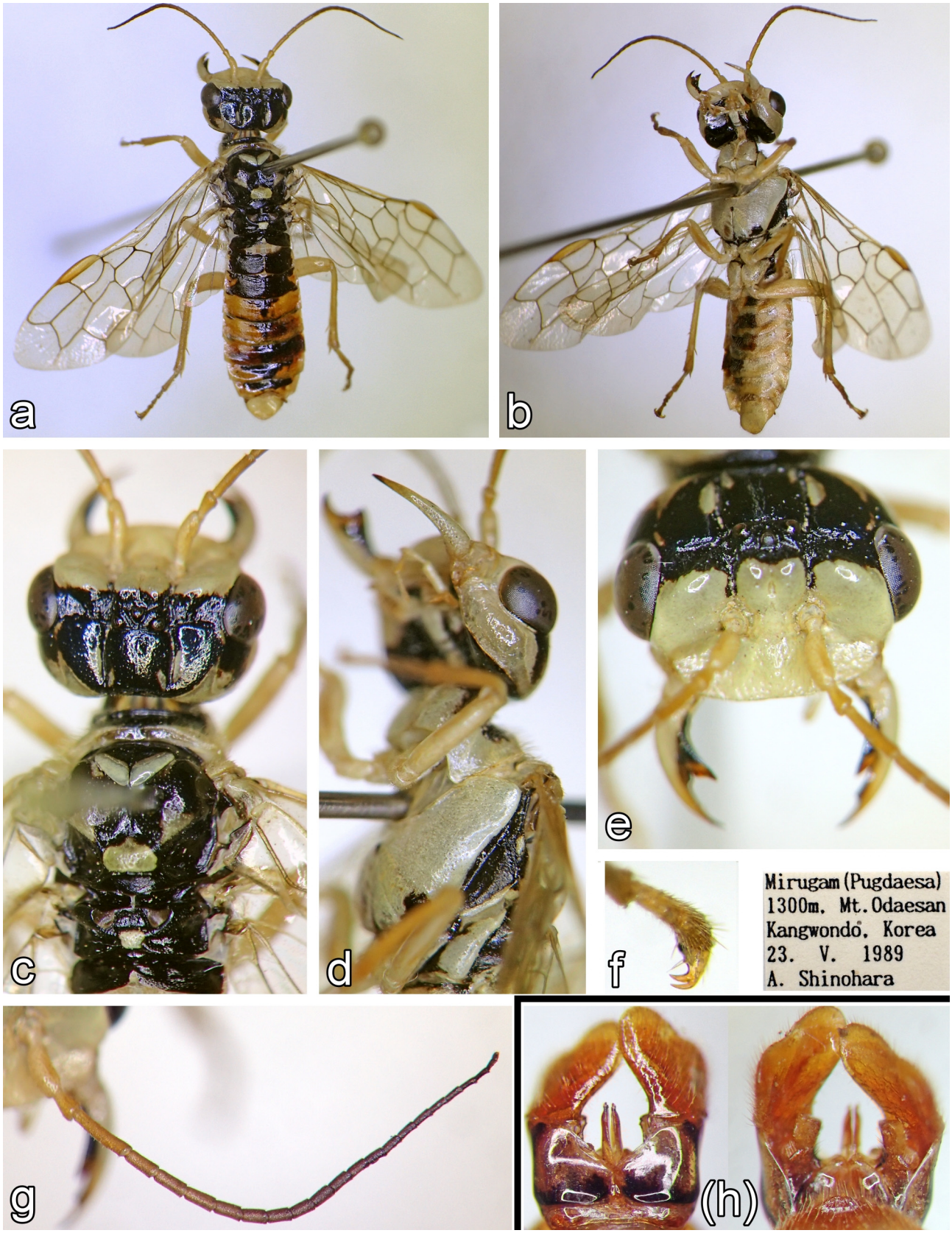


FIGURE 82. ***Pamphilius histrio***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** claw, **(g)** antenna, **(h)** genitalia dorsally & ventrally (specimen from Japan).

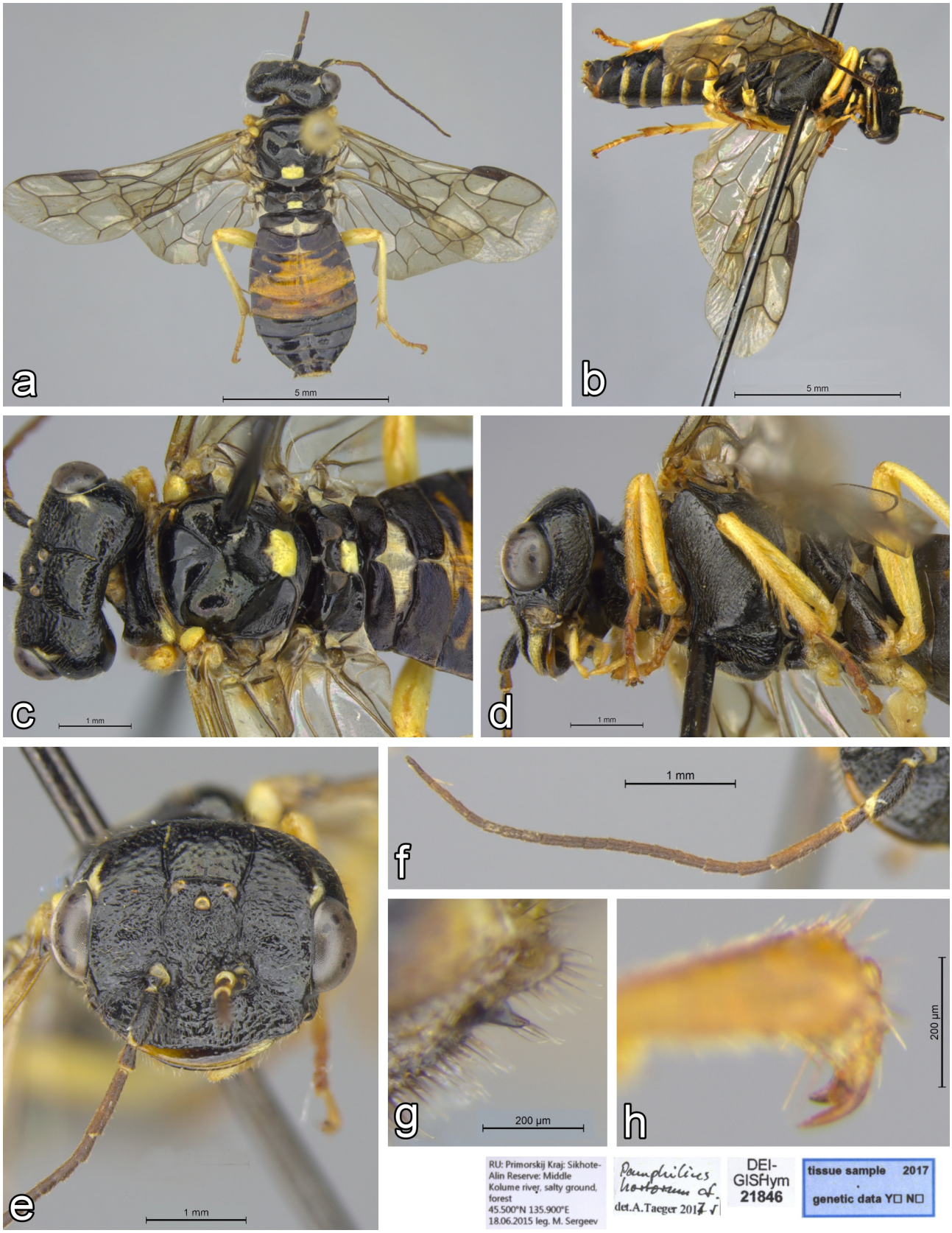


FIGURE 83. ***Pamphilius hortorum***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

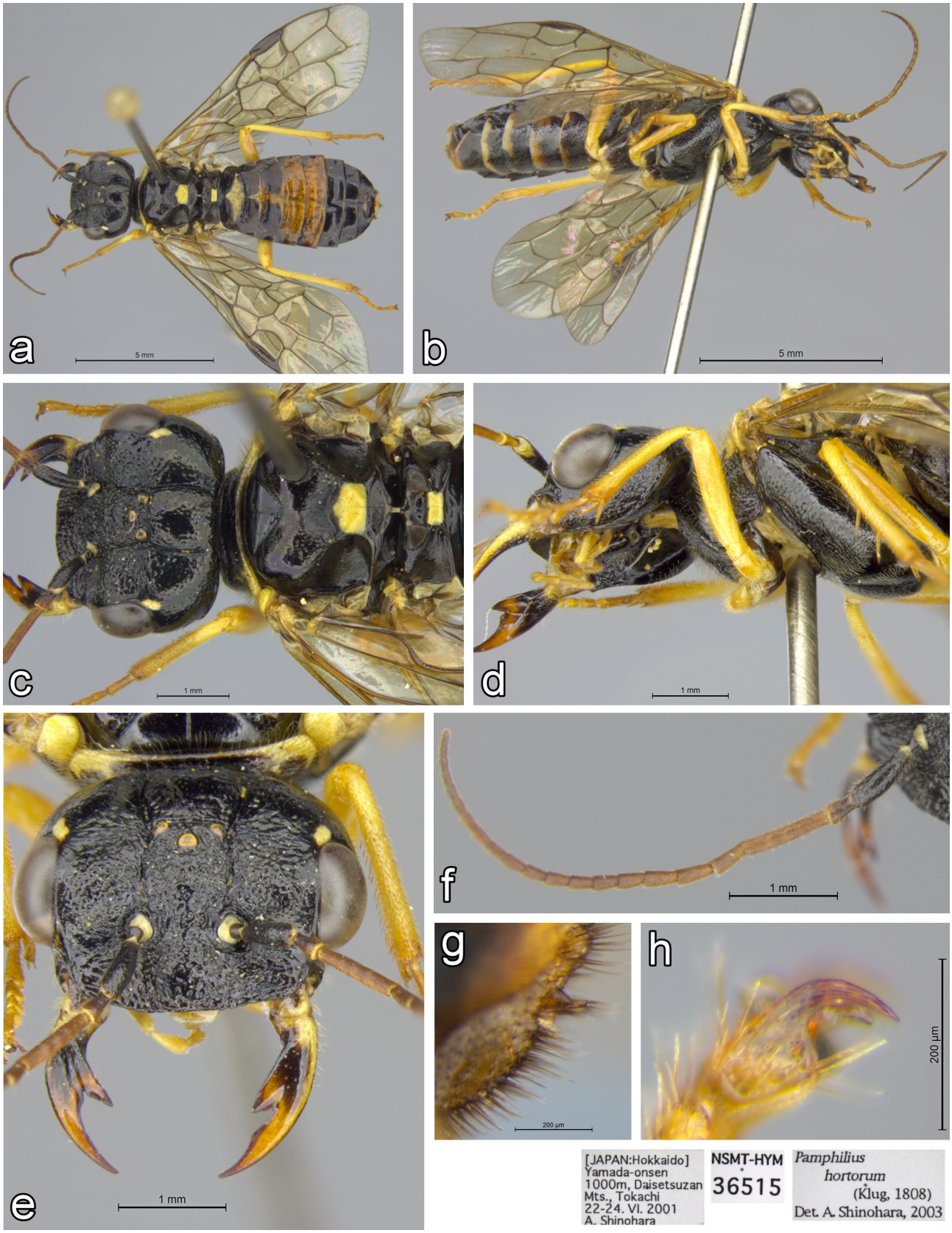


FIGURE 84. ***Pamphilius hortorum***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

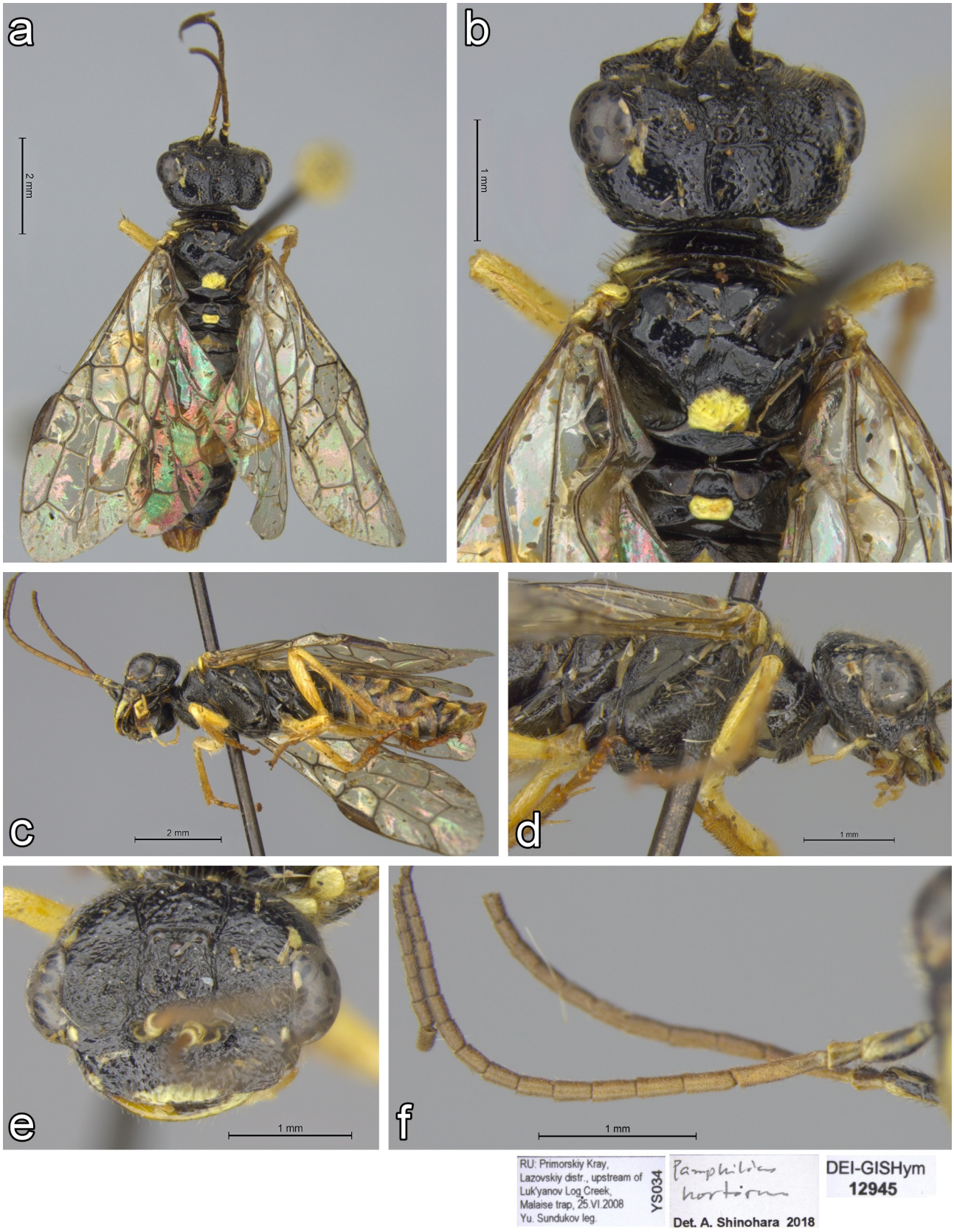


FIGURE 85. ***Pamphilius hortorum***, male, Russia – **(a)** dorsally, **(b)** head & thorax dorsally, **(c)** lateroventrally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna.

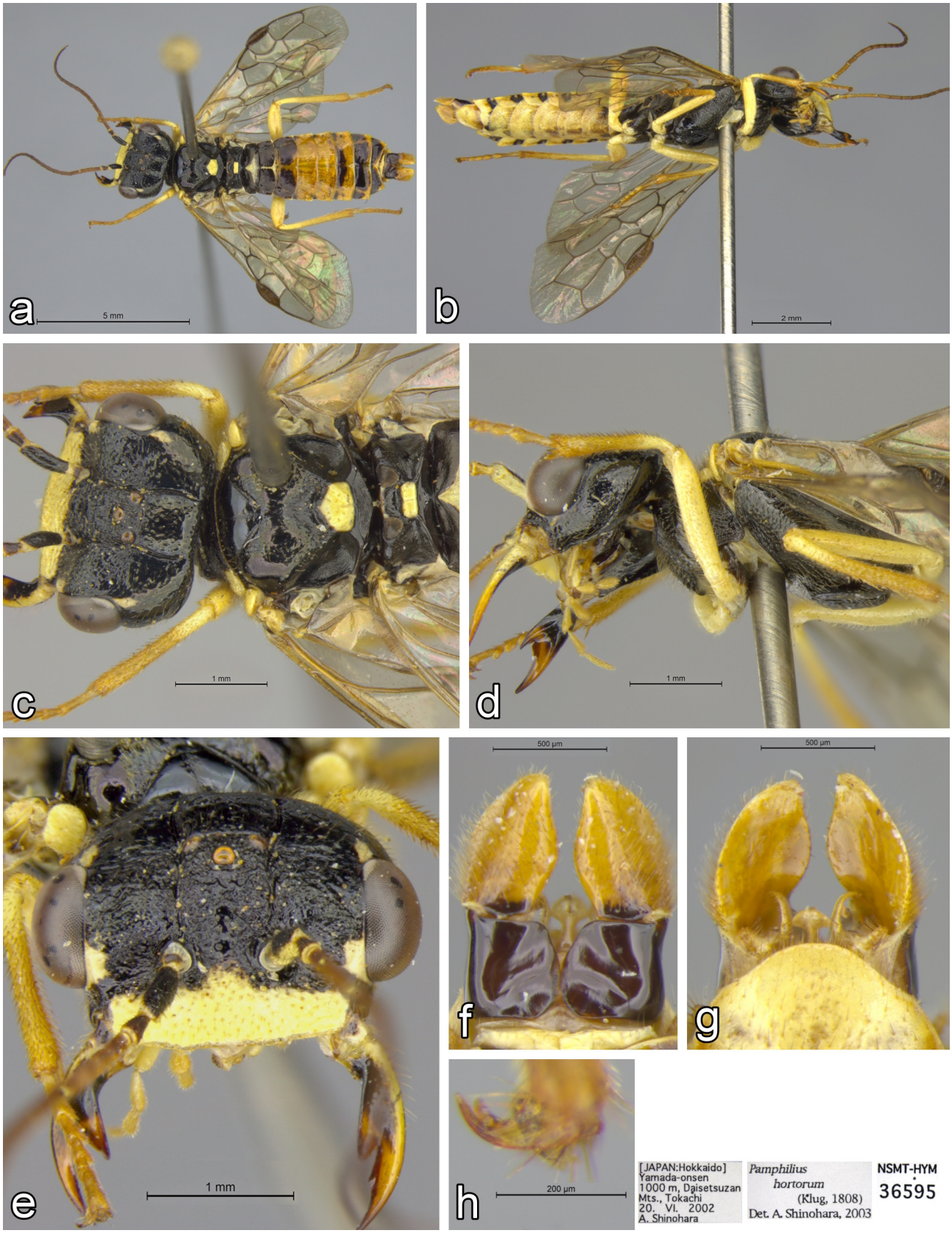


FIGURE 86. ***Pamphilius hortorum***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** genitalia dorsally, **(g)** genitalia ventrally, **(h)** claw.



FIGURE 87. ***Pamphilius itoi***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

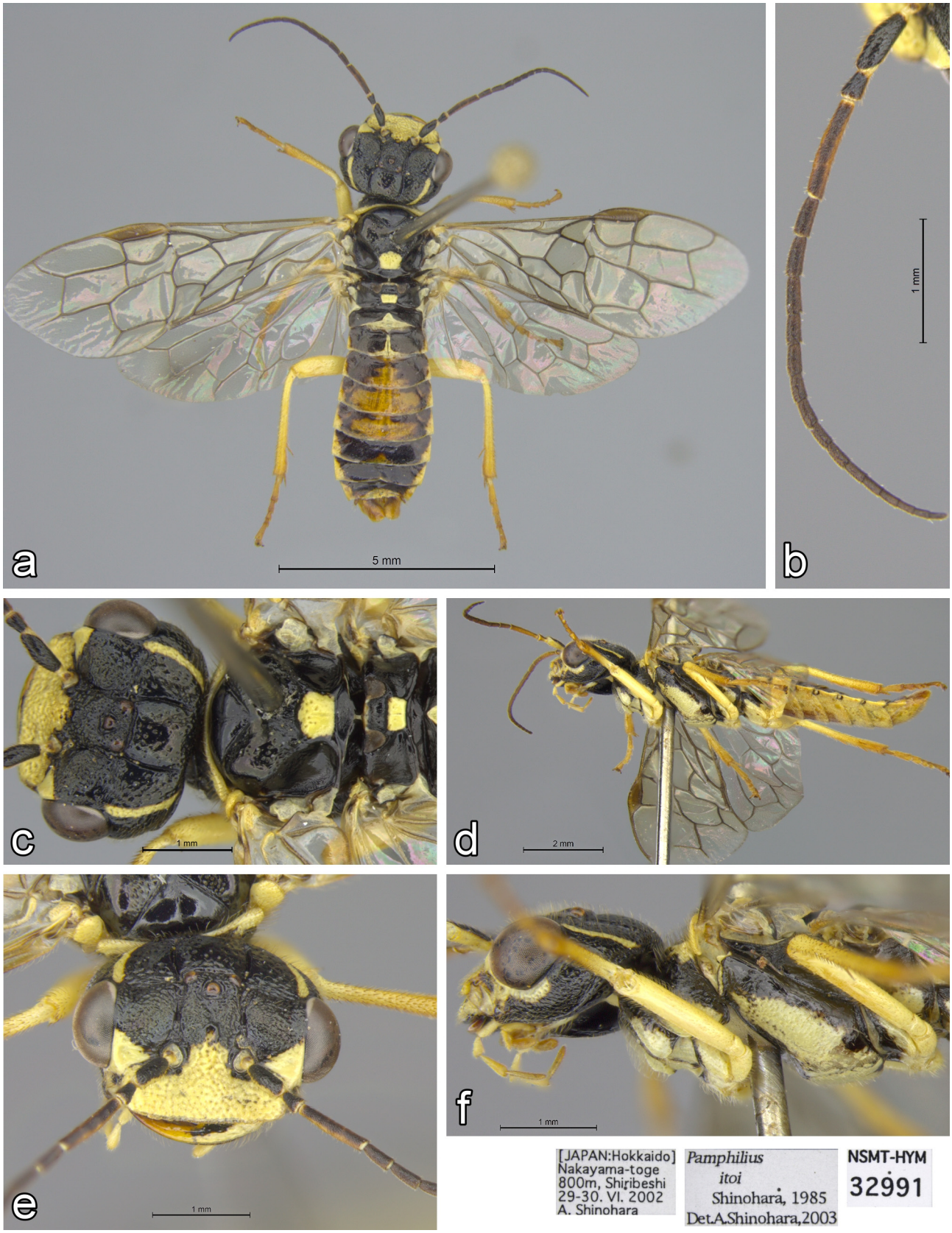


FIGURE 88. ***Pamphilius itoi***, male, Japan – **(a)** dorsally, **(b)** antenna, **(c)** head & thorax dorsally, **(d)** lateroventrally, **(e)** face, **(f)** head & thorax ventrolaterally.

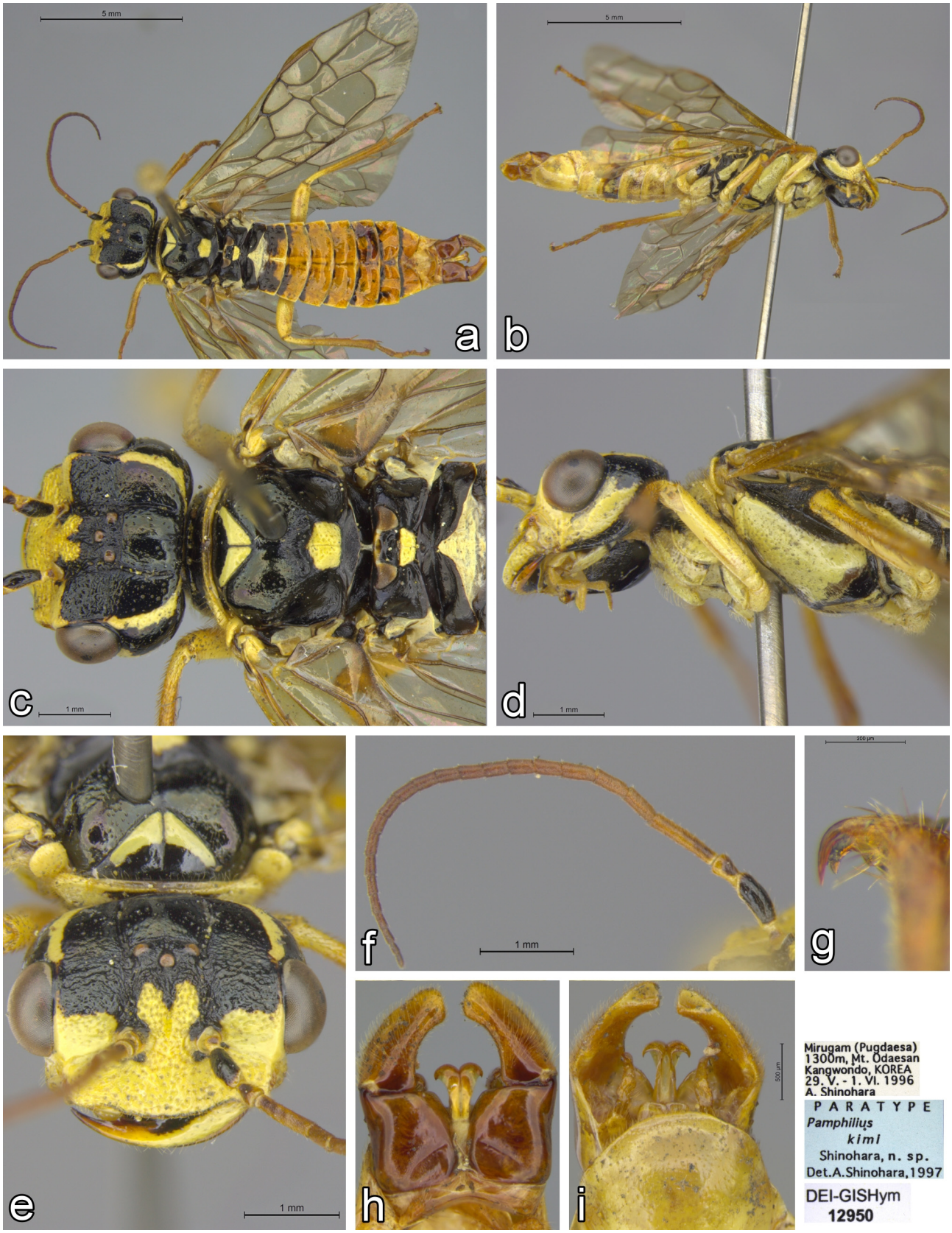


FIGURE 89. ***Pamphilius kimi***, male, Korea (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** genitalia dorsally, **(i)** genitalia ventrally.

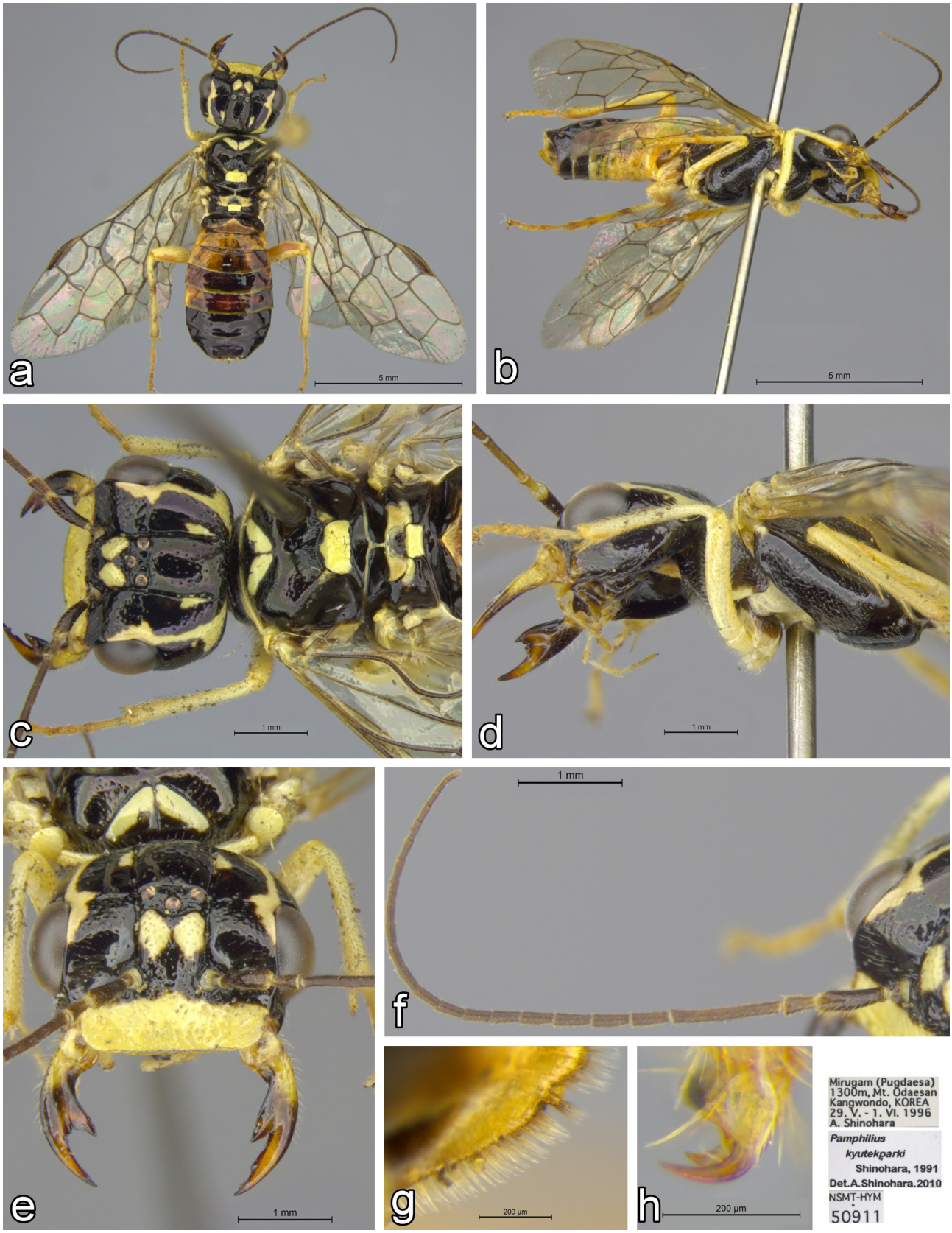


FIGURE 90. ***Pamphilius kyutekparki***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

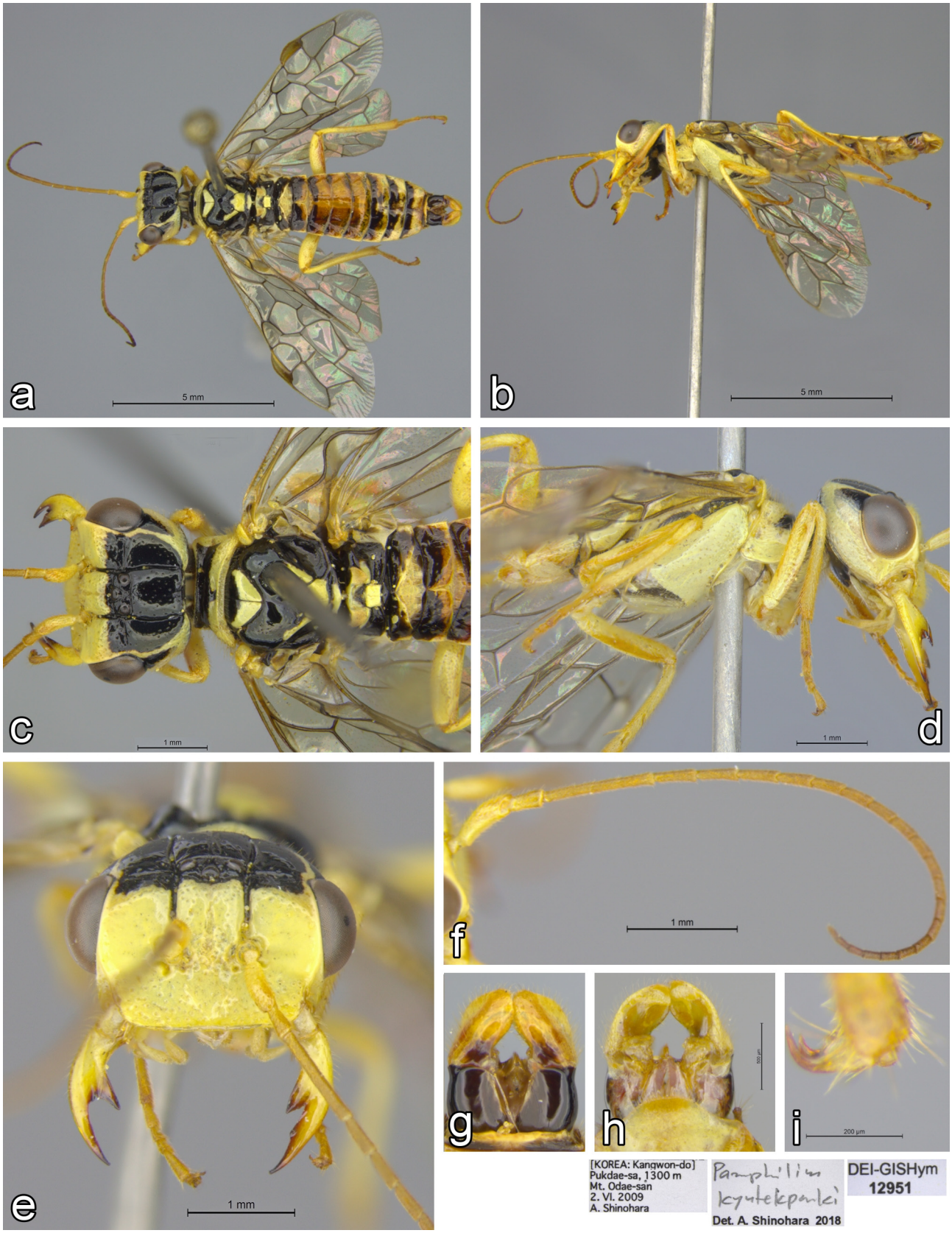


FIGURE 91. ***Pamphilius kyutekparki***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

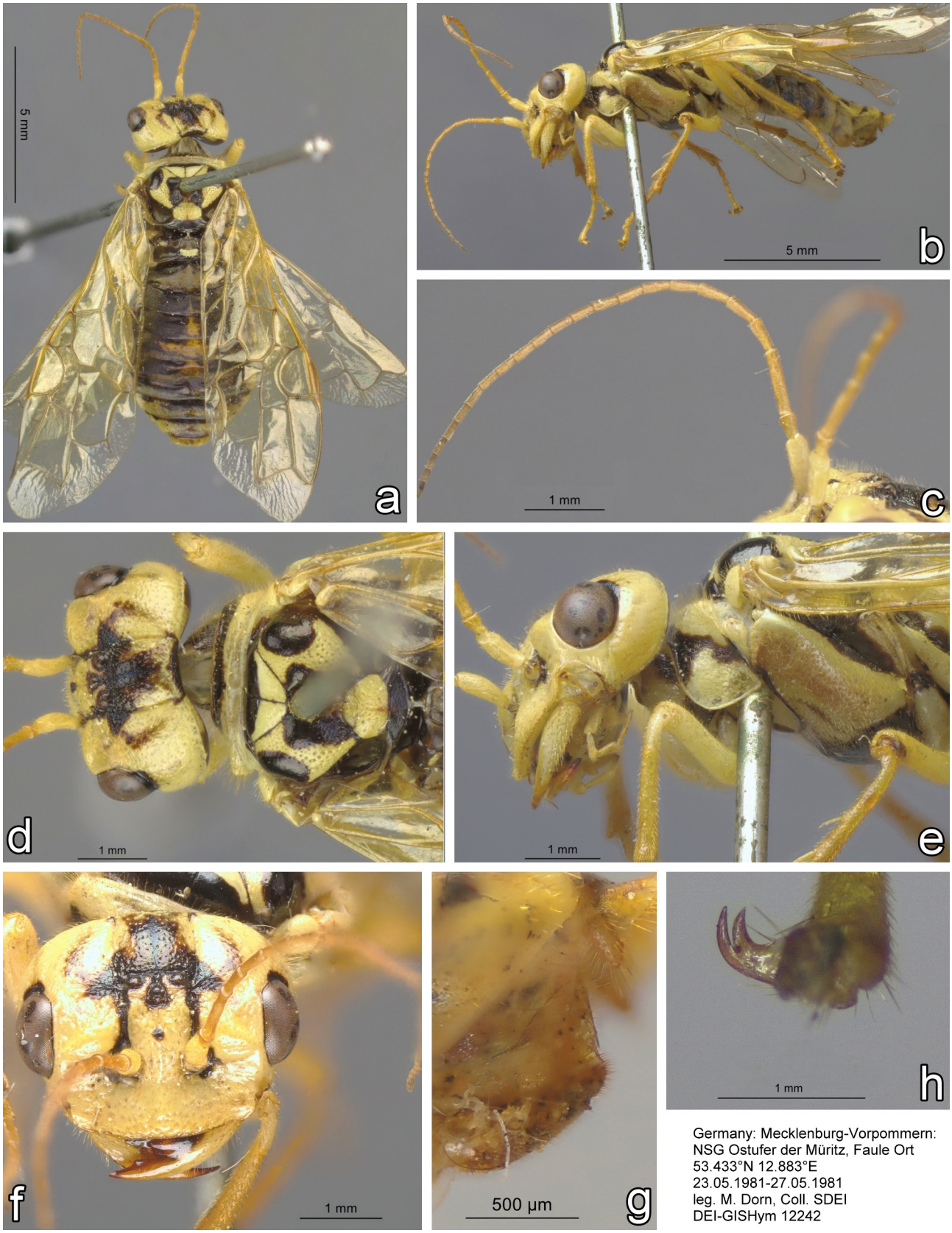


FIGURE 92. ***Pamphilius latifrons***, female, Germany – **(a)** dorsally, **(b)** lateroventrally, **(c)** antenna, **(d)** head & thorax dorsally, **(e)** head & thorax ventrolaterally, **(f)** face, **(g)** sawsheath laterally, **(h)** claw.

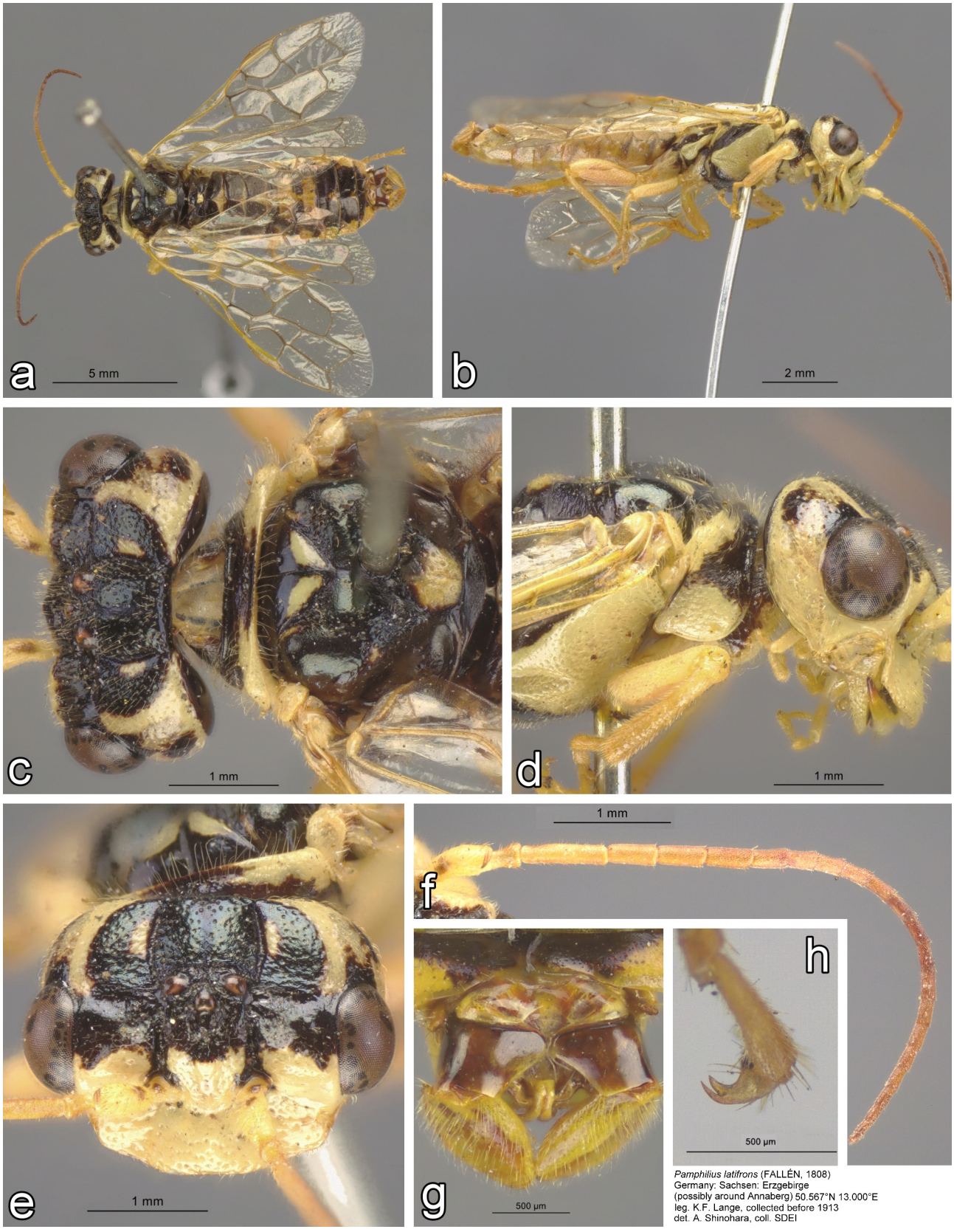


FIGURE 93. ***Pamphilius latifrons***, male, Germany – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** claw.

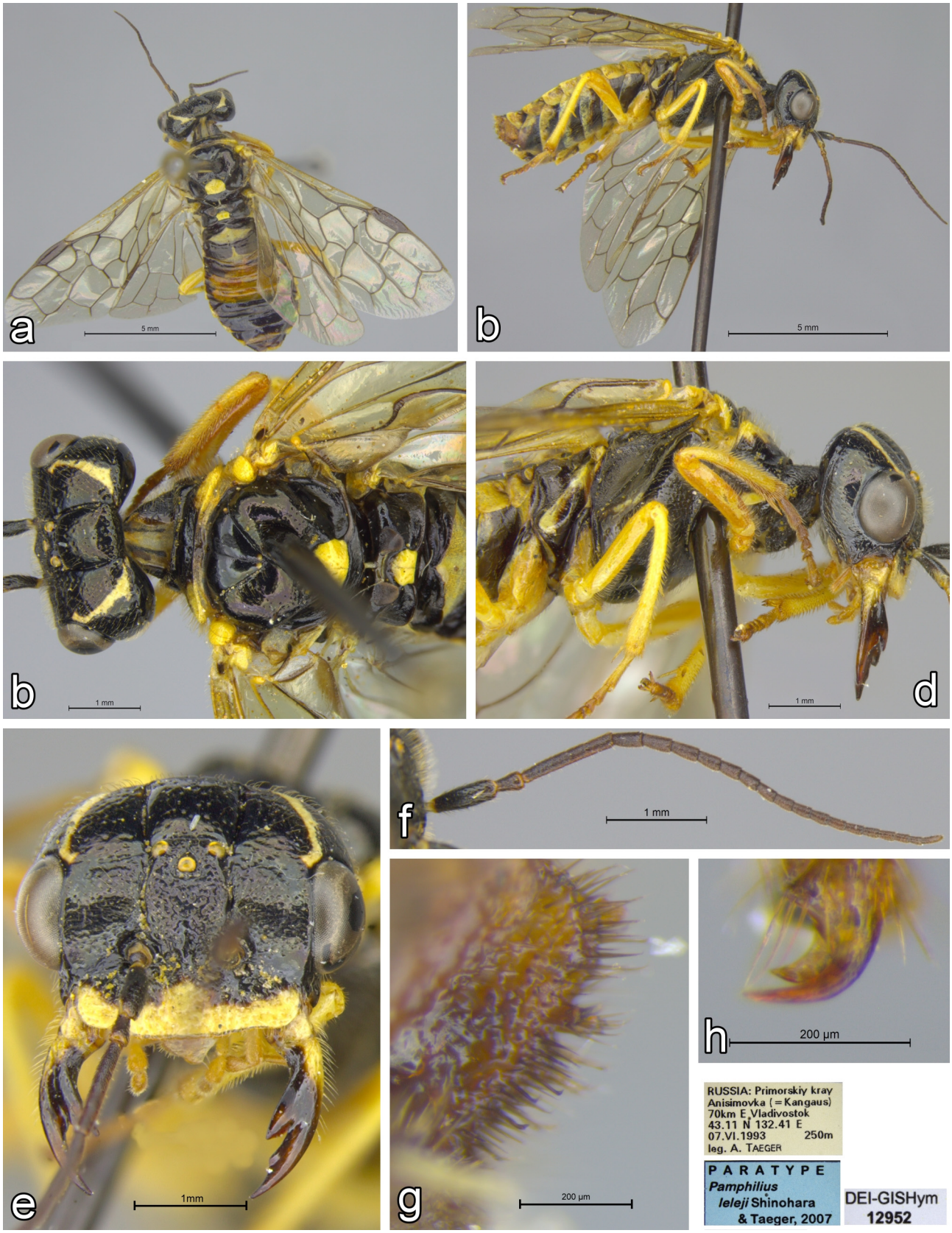


FIGURE 94. ***Pamphilius leleji***, female, Russia (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

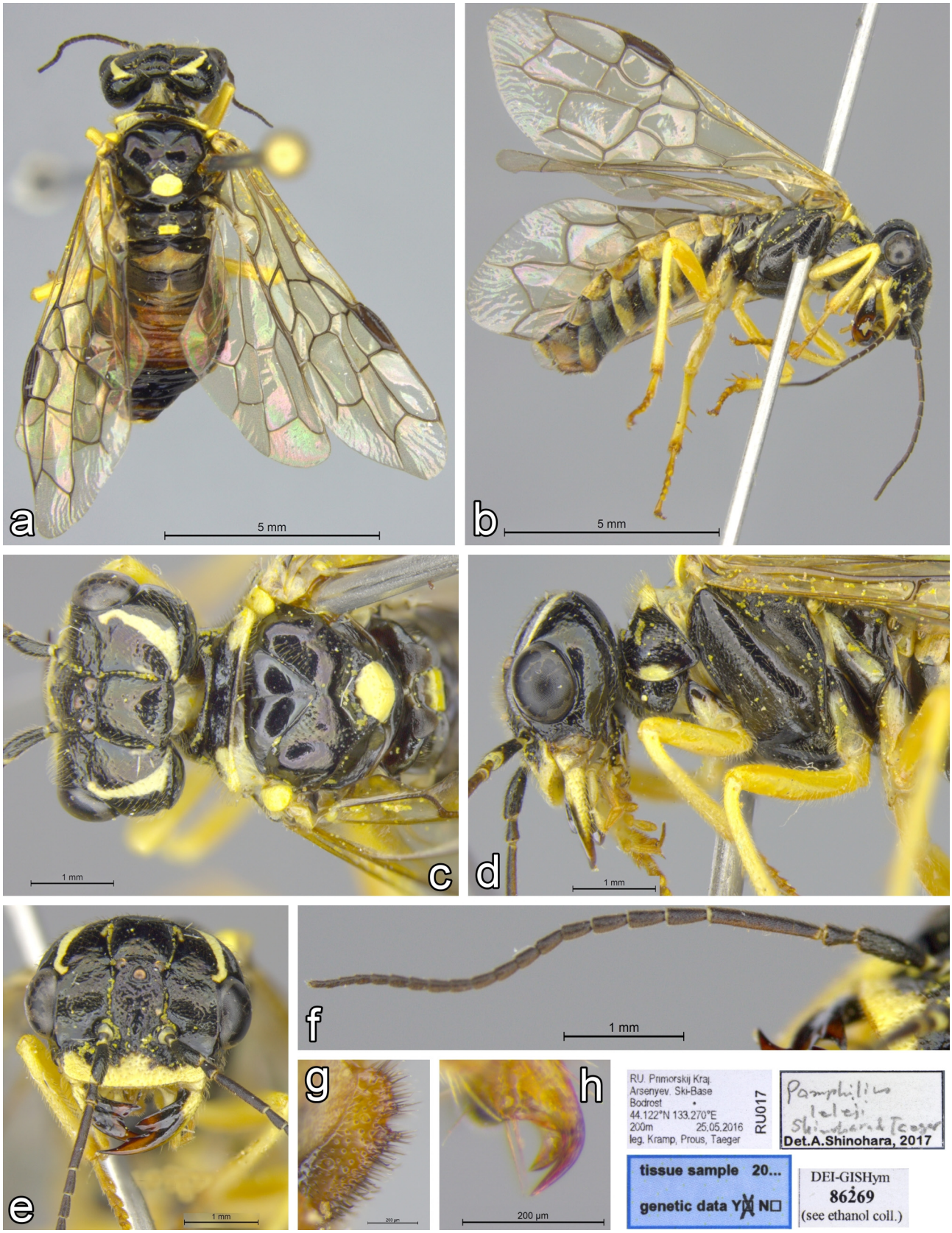


FIGURE 95. ***Pamphilius leleji***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

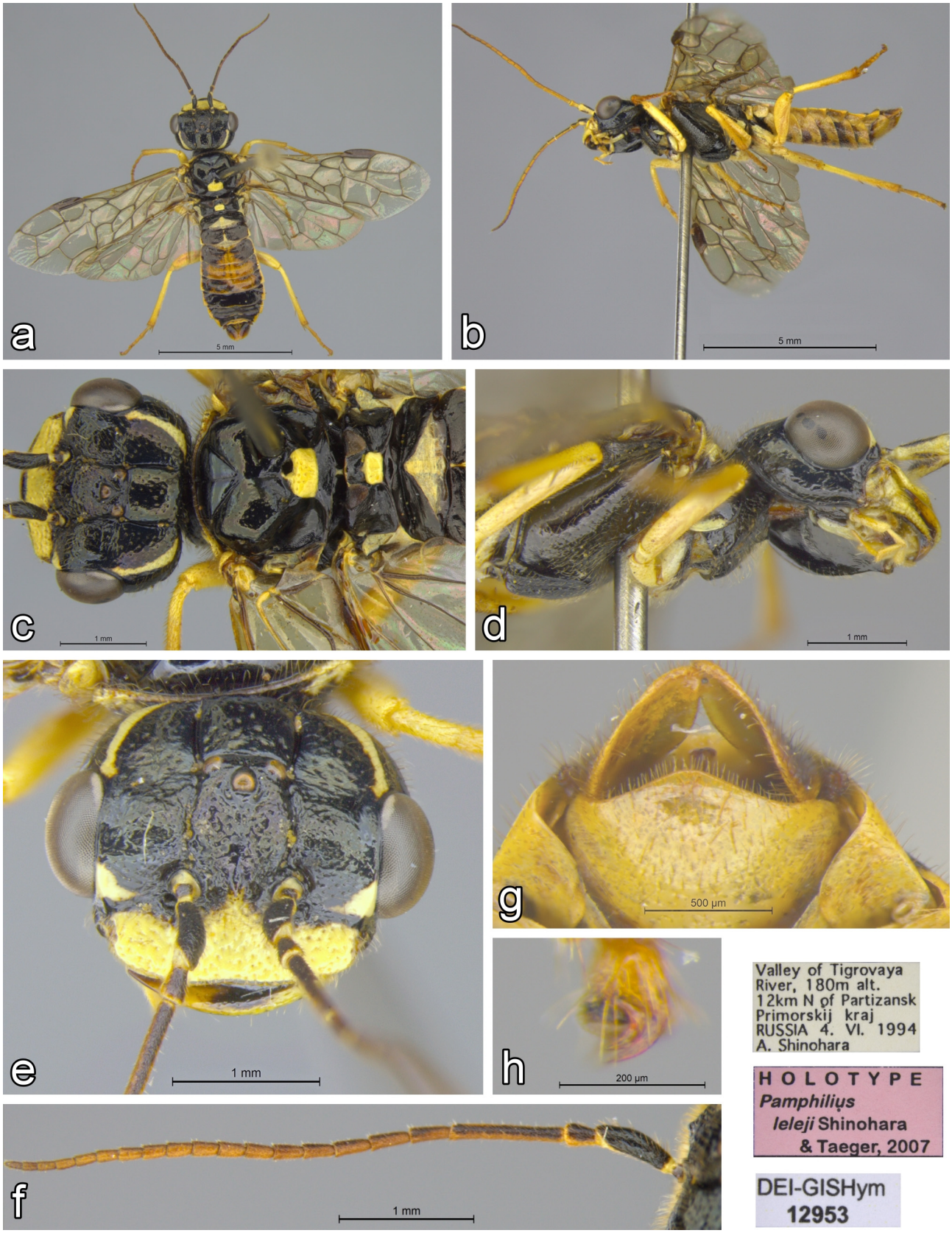


FIGURE 96. ***Pamphilius leleji***, male, Russia (holotype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** apex of abdomen ventrally, **(h)** claw.

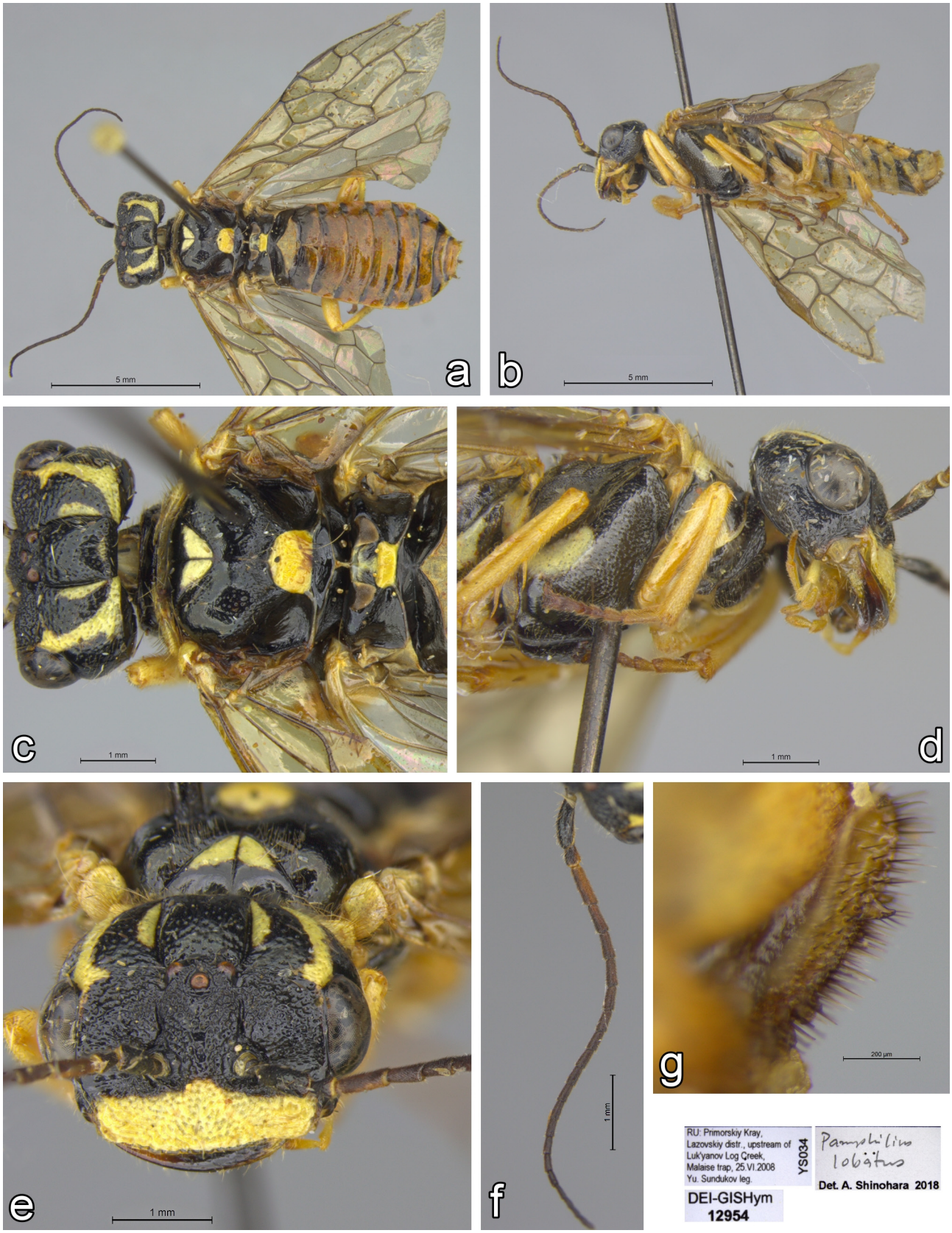


FIGURE 97. ***Pamphilius lobatus***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally.

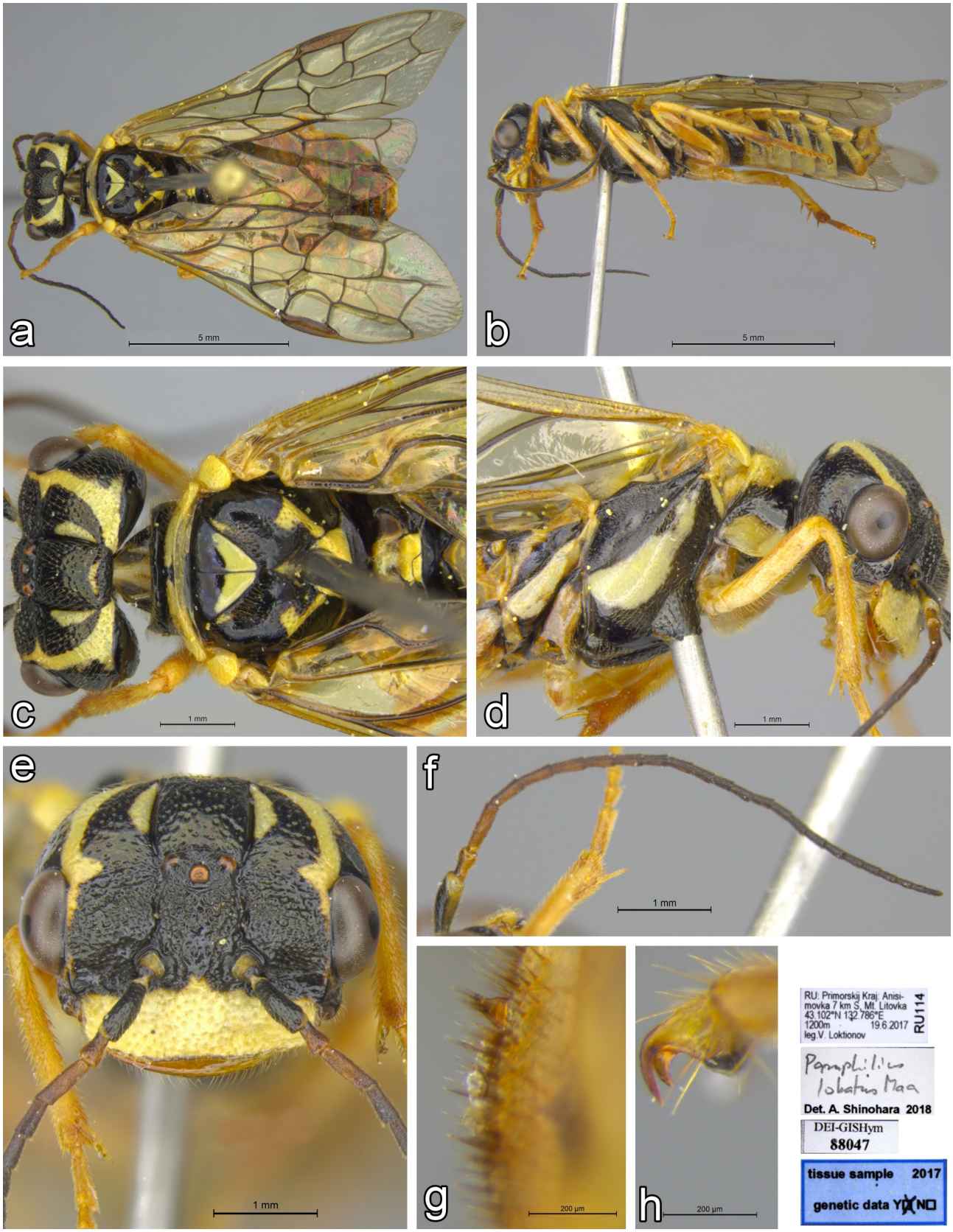


FIGURE 98. ***Pamphilius lobatus***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

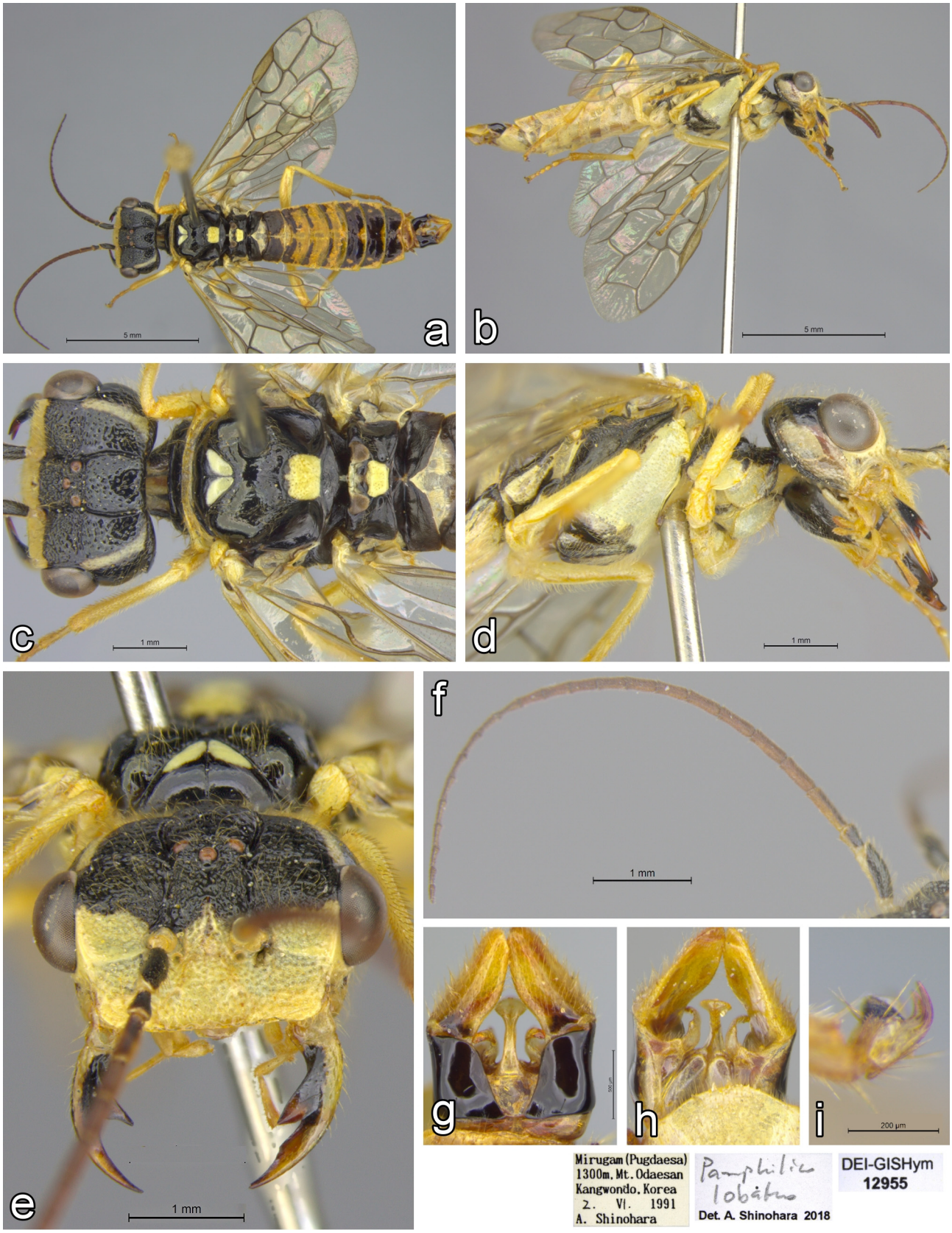


FIGURE 99. ***Pamphilius lobatus***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

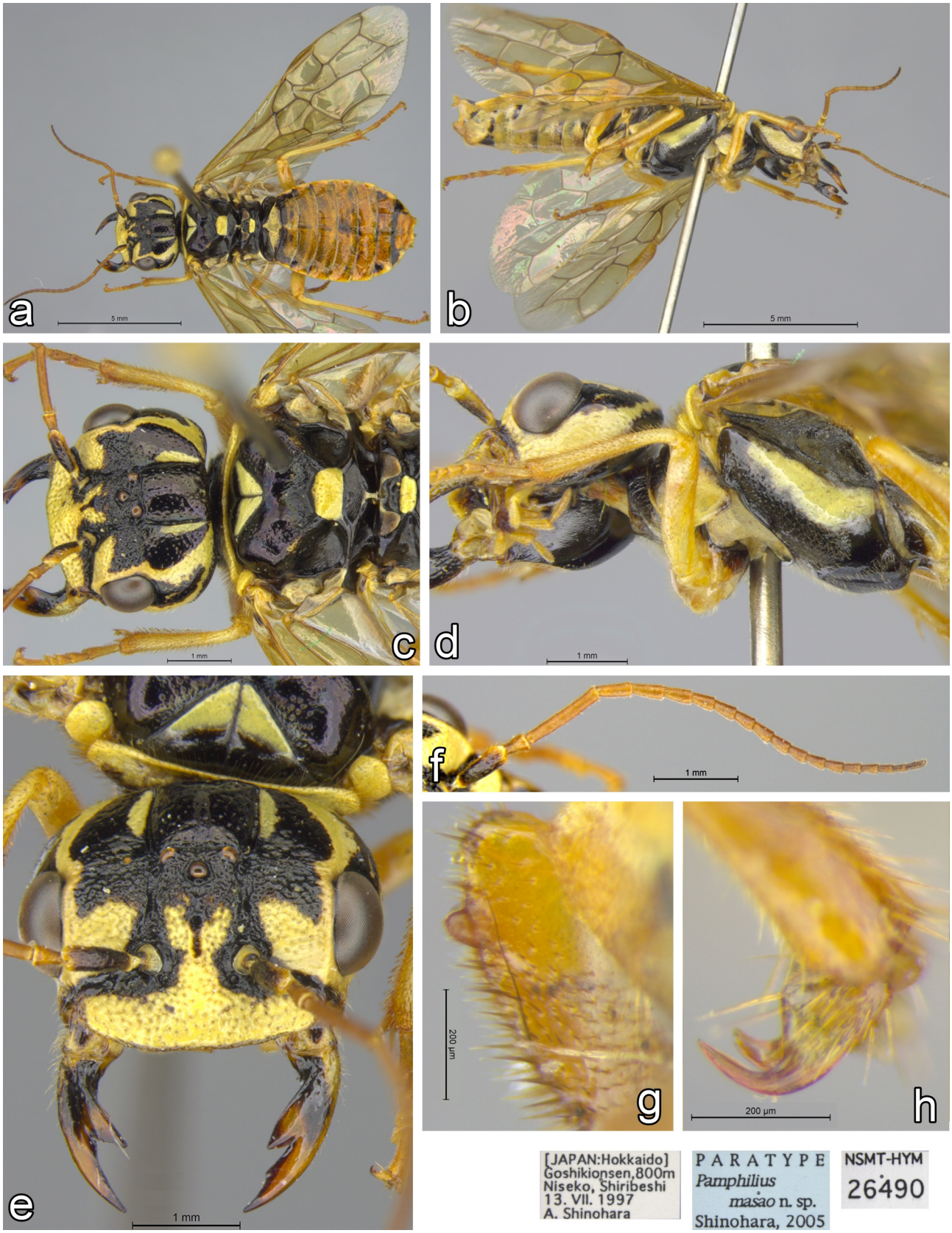


FIGURE 100. ***Pamphilius masao***, female, Japan (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

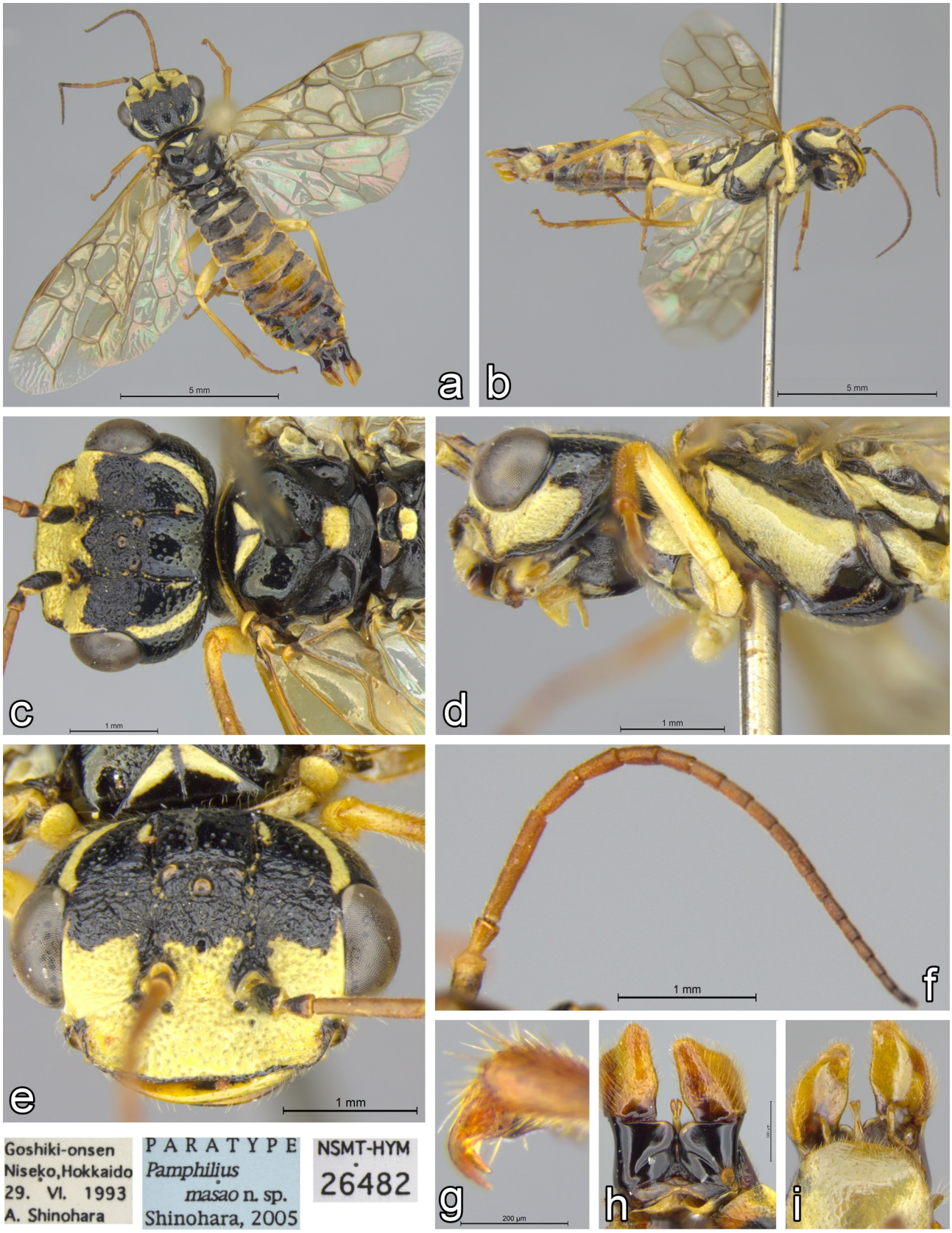


FIGURE 101. ***Pamphilius masao***, male, Japan (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** genitalia dorsally, **(i)** genitalia ventrally.

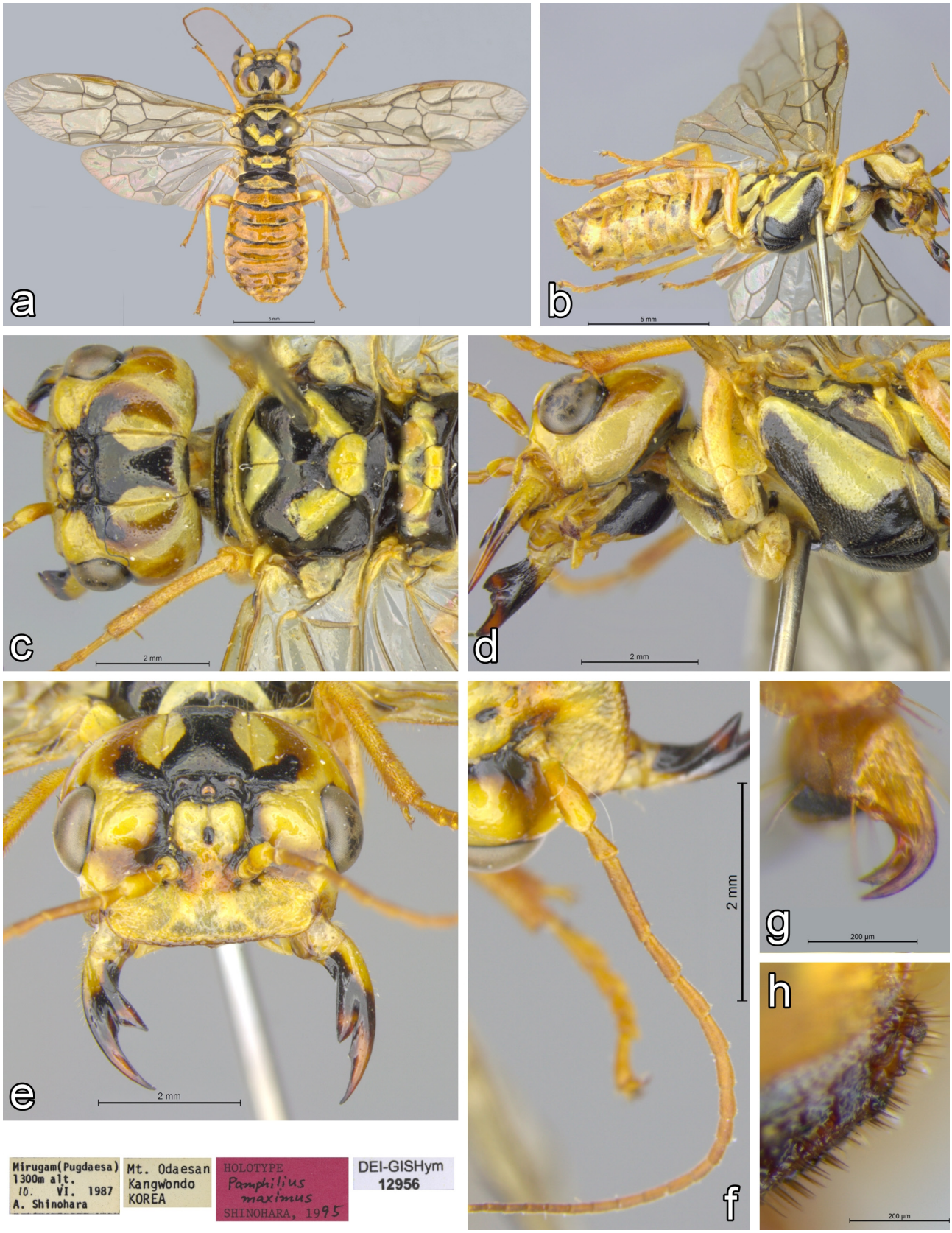


FIGURE 102. ***Pamphilius maximus***, female, Korea (holotype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** sawsheath laterally.

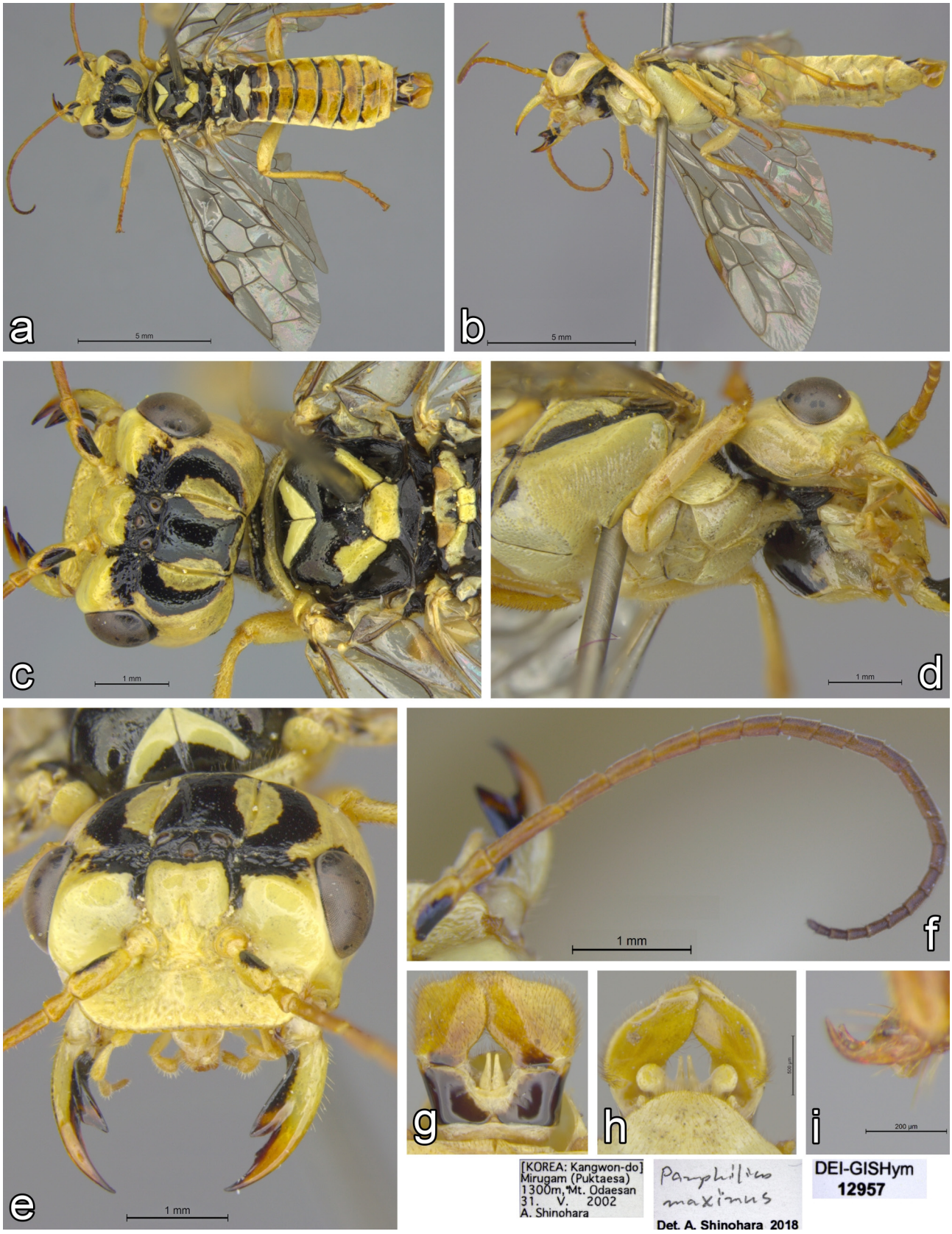


FIGURE 103. ***Pamphilius maximus***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

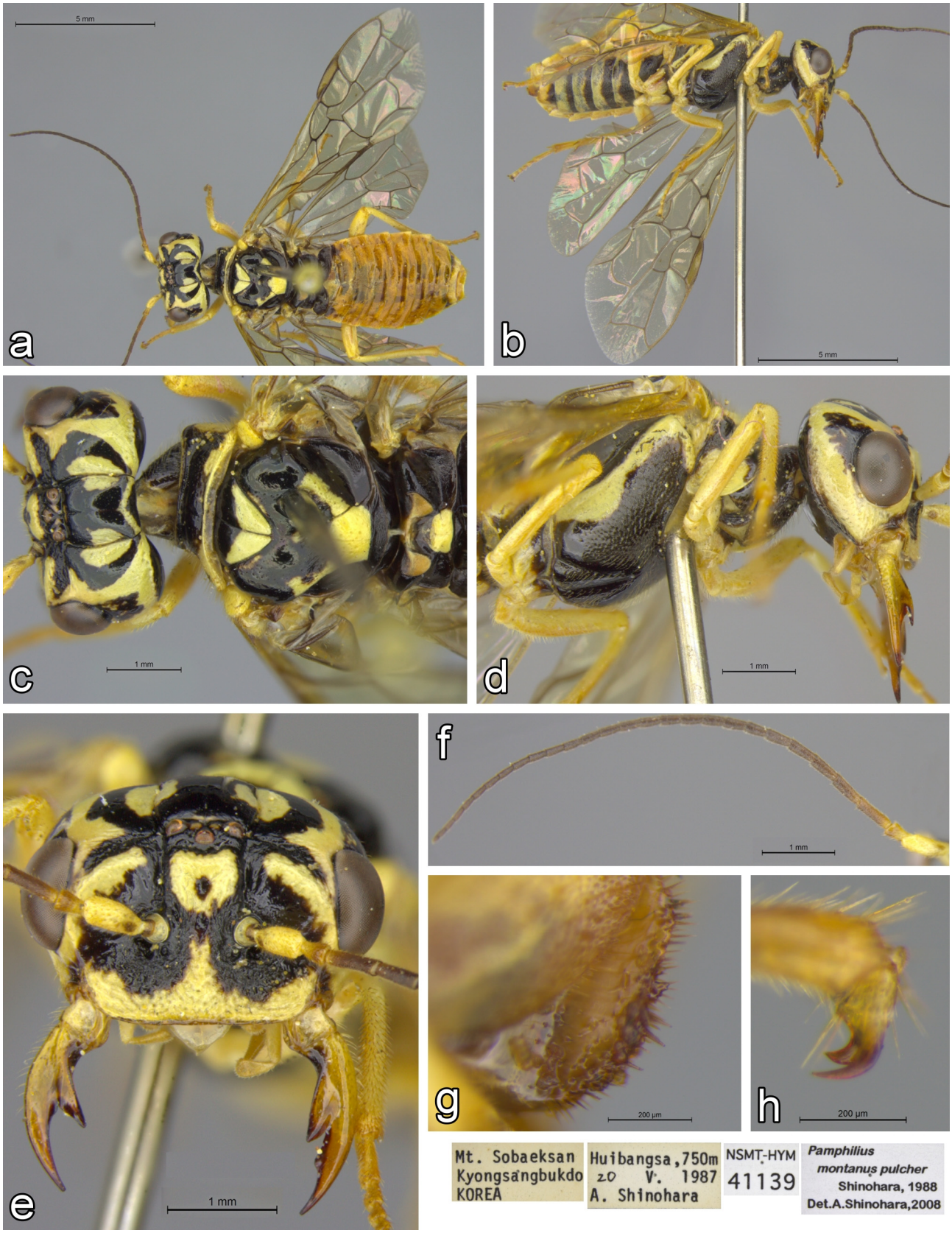


FIGURE 104. ***Pamphilius montanus pulcher***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

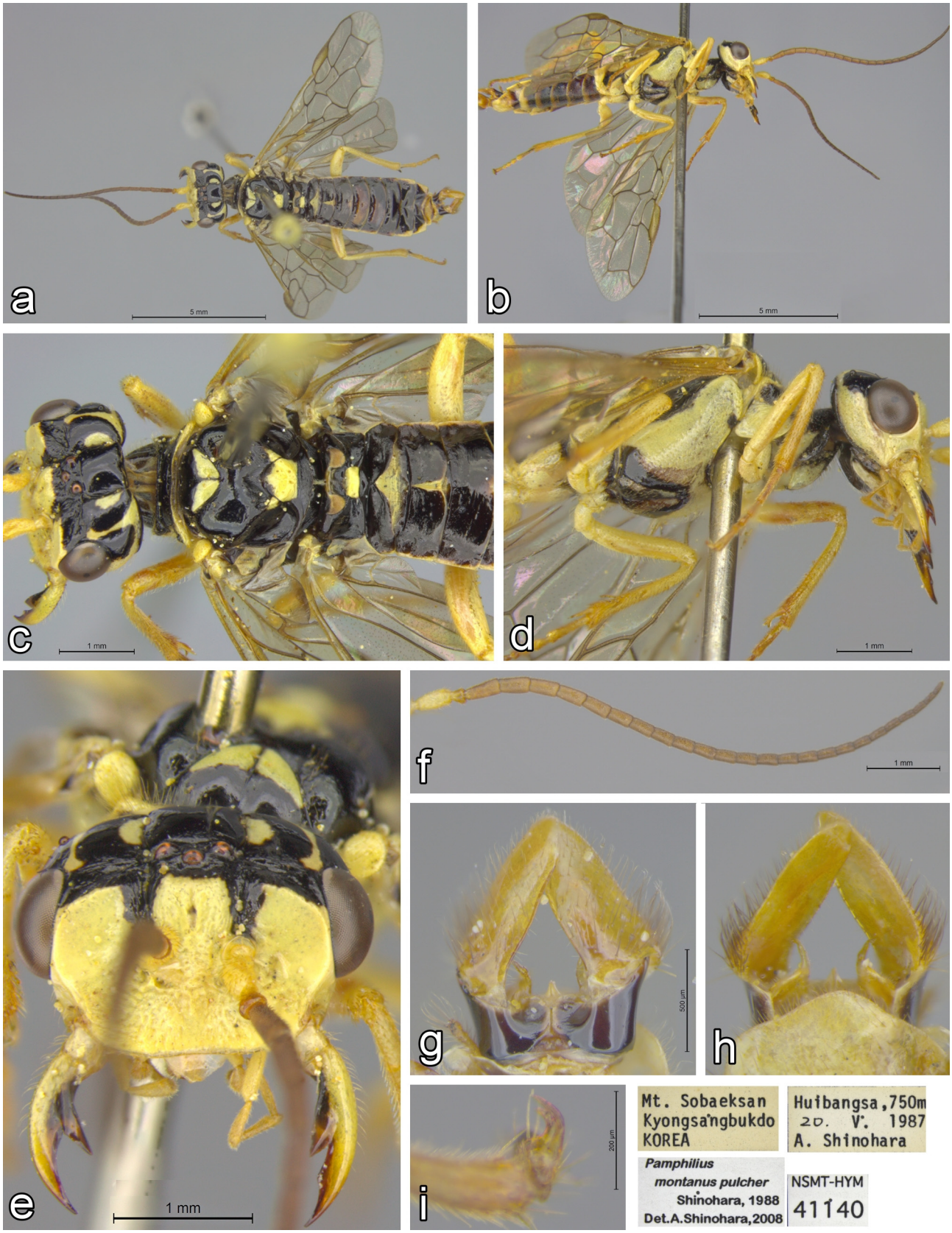


FIGURE 105. ***Pamphilius montanus pulcher***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

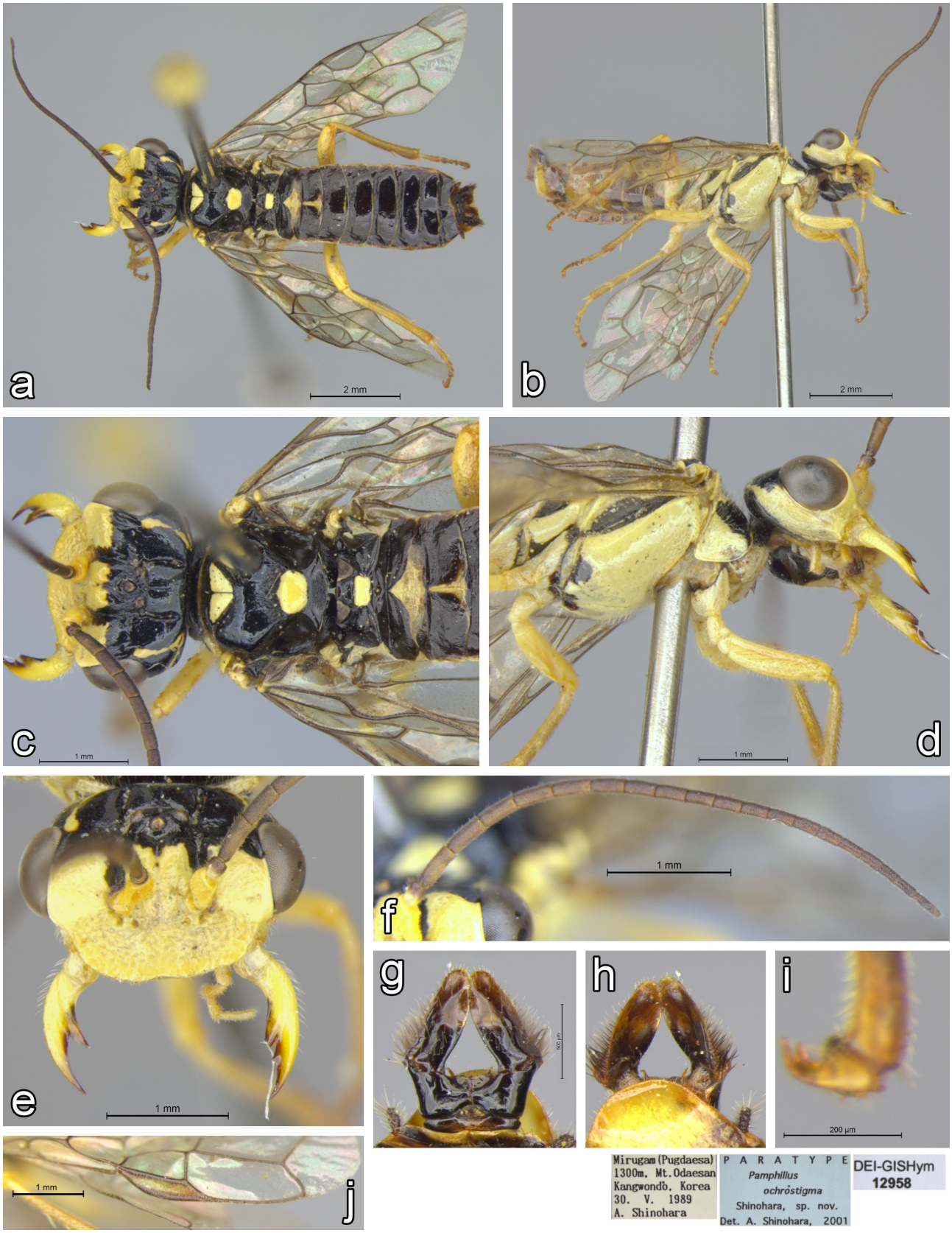


FIGURE 106. ***Pamphilius ochrostigma***, male, Korea (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw, **(j)** pterostigma.

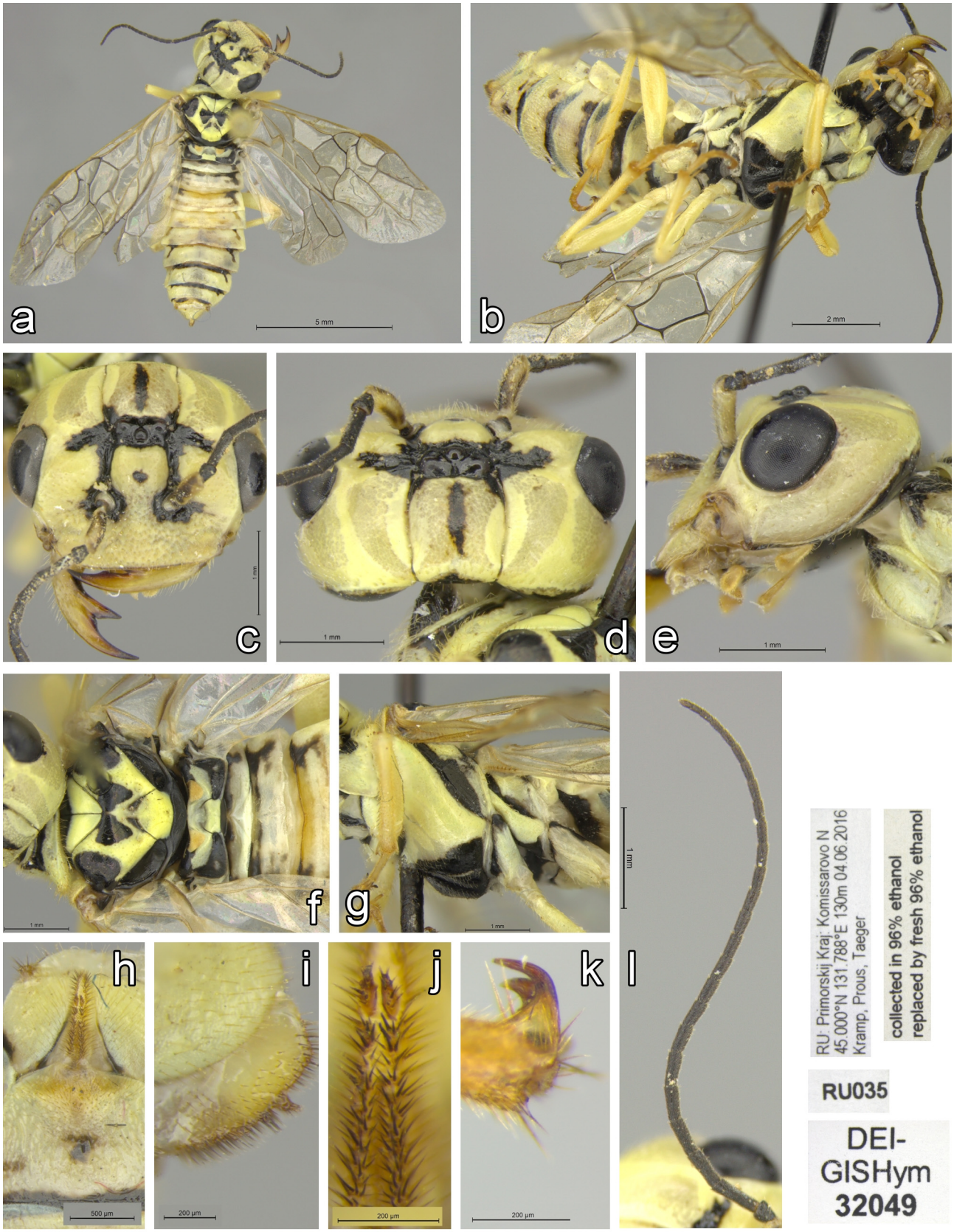


FIGURE 107. ***Pamphilius pallidus***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** face, **(d)** head dorsally, **(e)** head laterally, **(f)** thorax dorsally, **(g)** thorax laterally, **(h)** sawsheath ventrally, **(i)** sawsheath laterally, **(j)** sawsheath ventrally detail, **(k)** claw, **(l)** antenna.

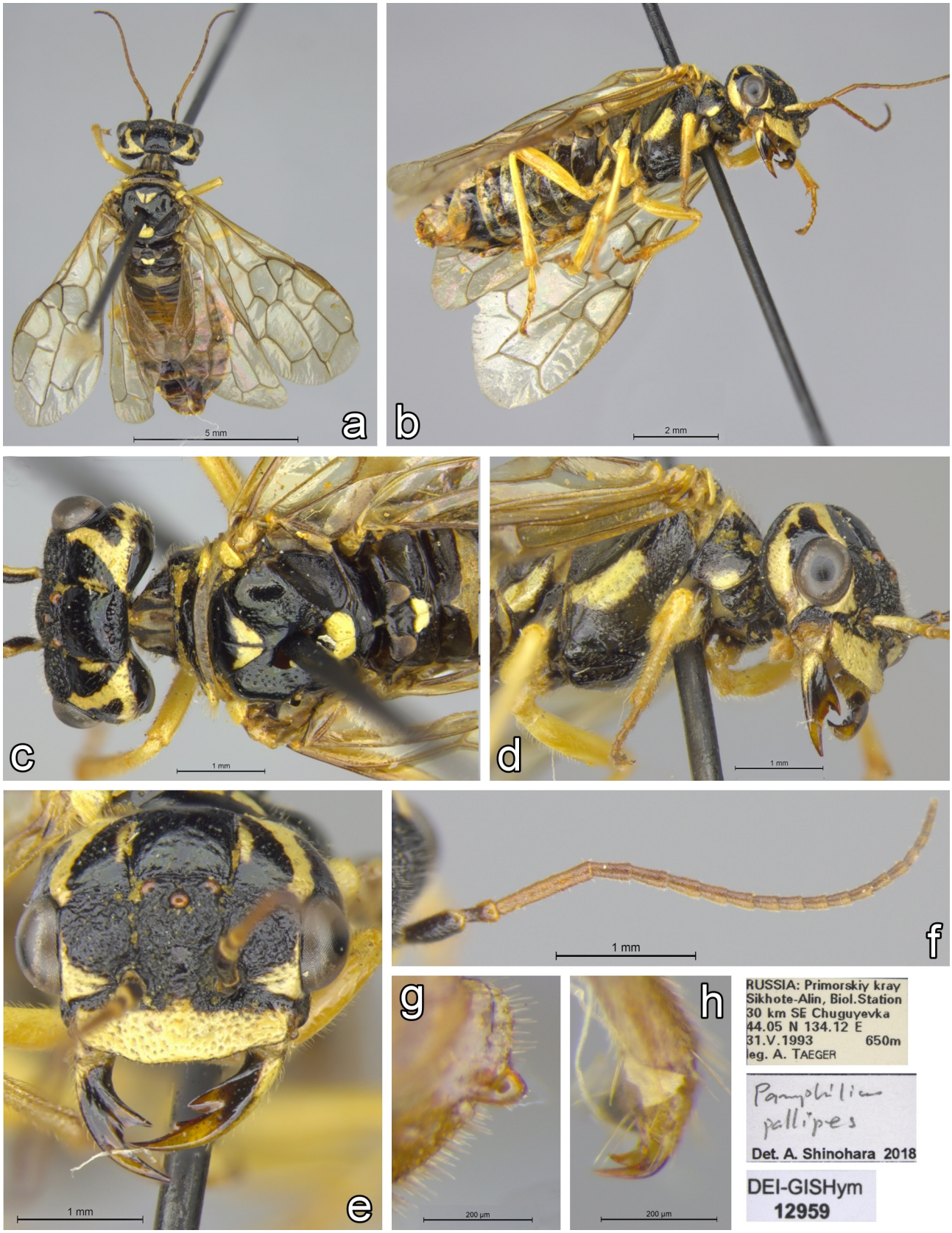


FIGURE 108. ***Pamphilius pallipes***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

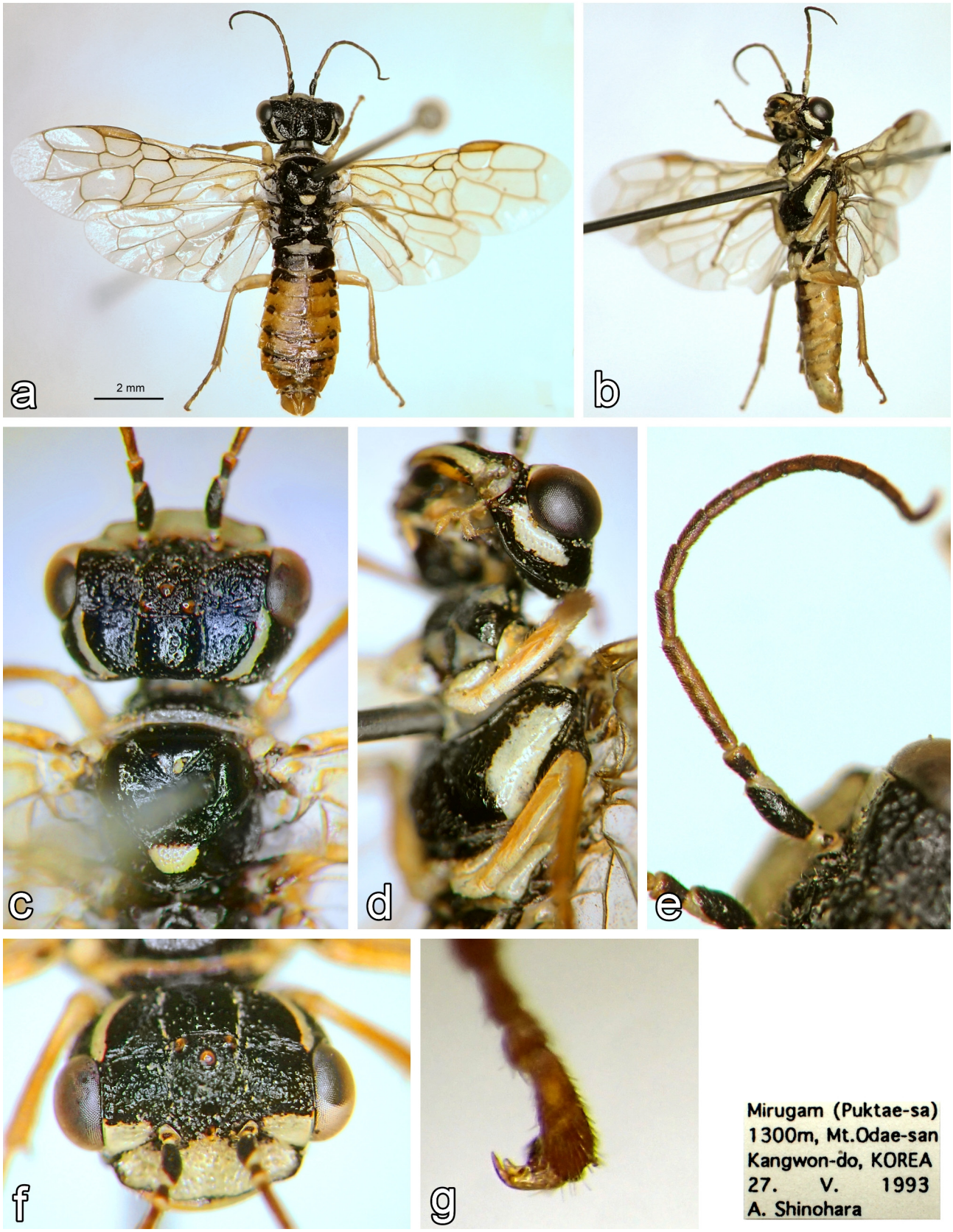


FIGURE 109. ***Pamphilius pallipes***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** antenna, **(f)** face, **(g)** claw.

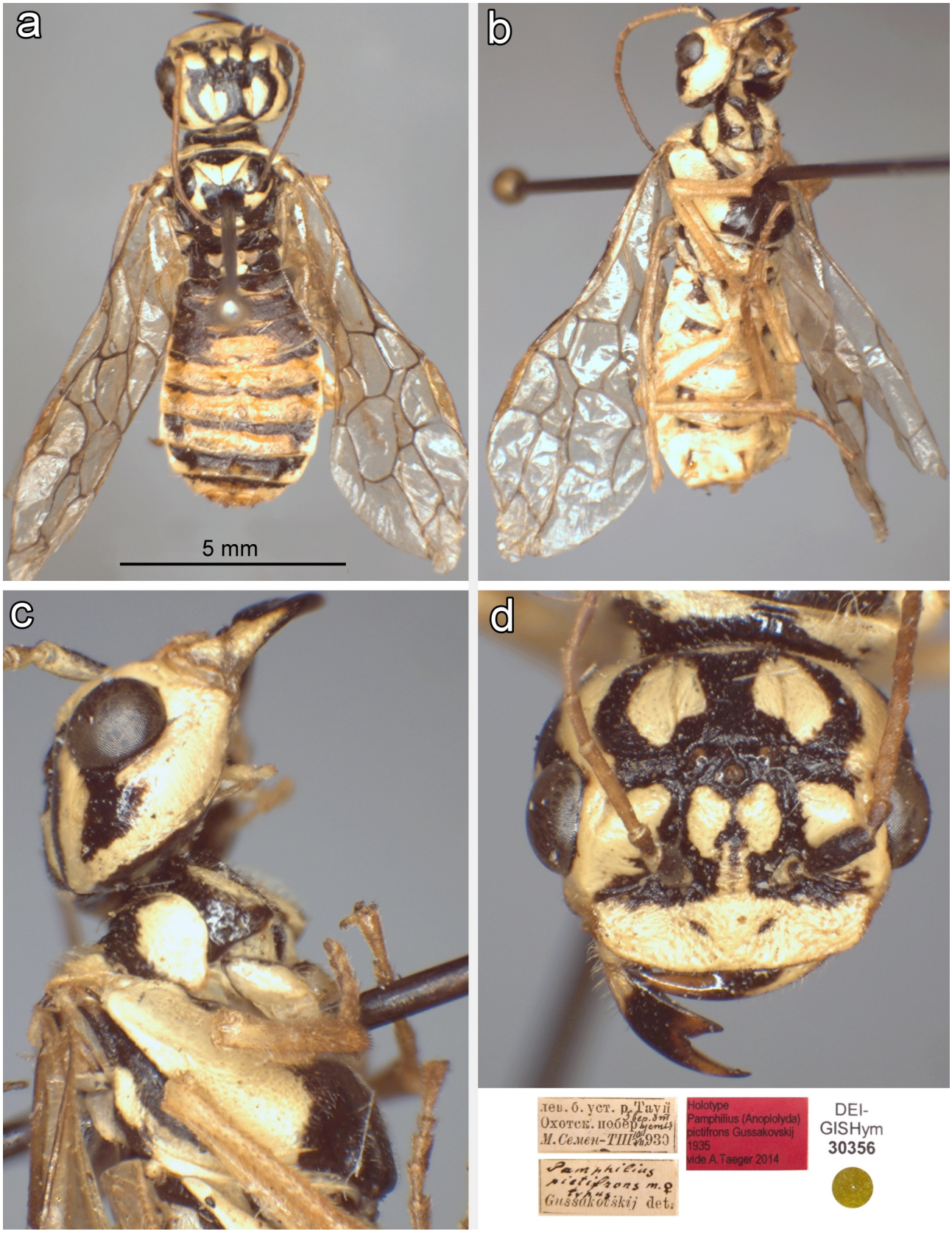


FIGURE 110. ***Pamphilius pictifrons***, female, Russia (holotype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax laterally, **(d)** face.

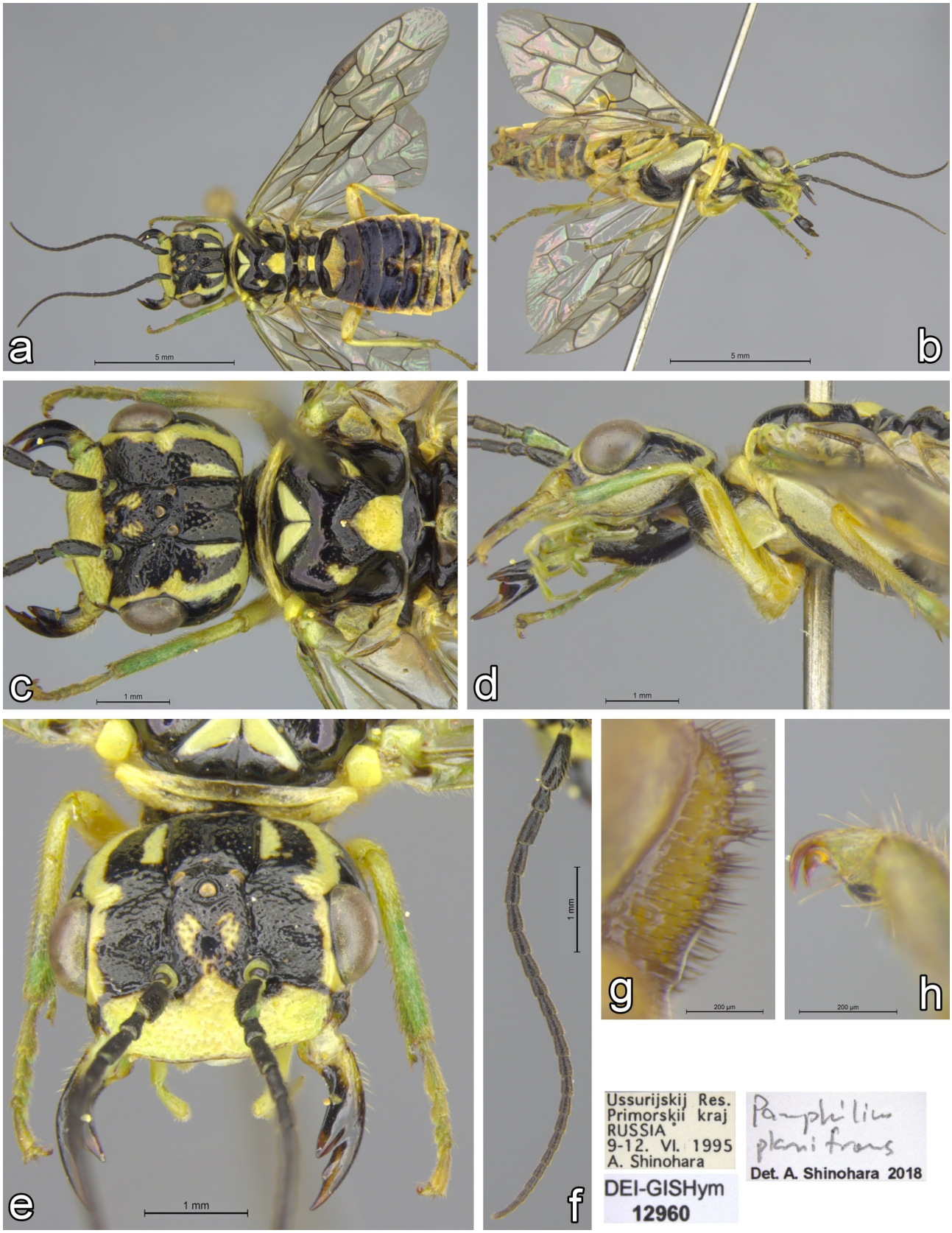


FIGURE 111. ***Pamphilius planifrons***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** , **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

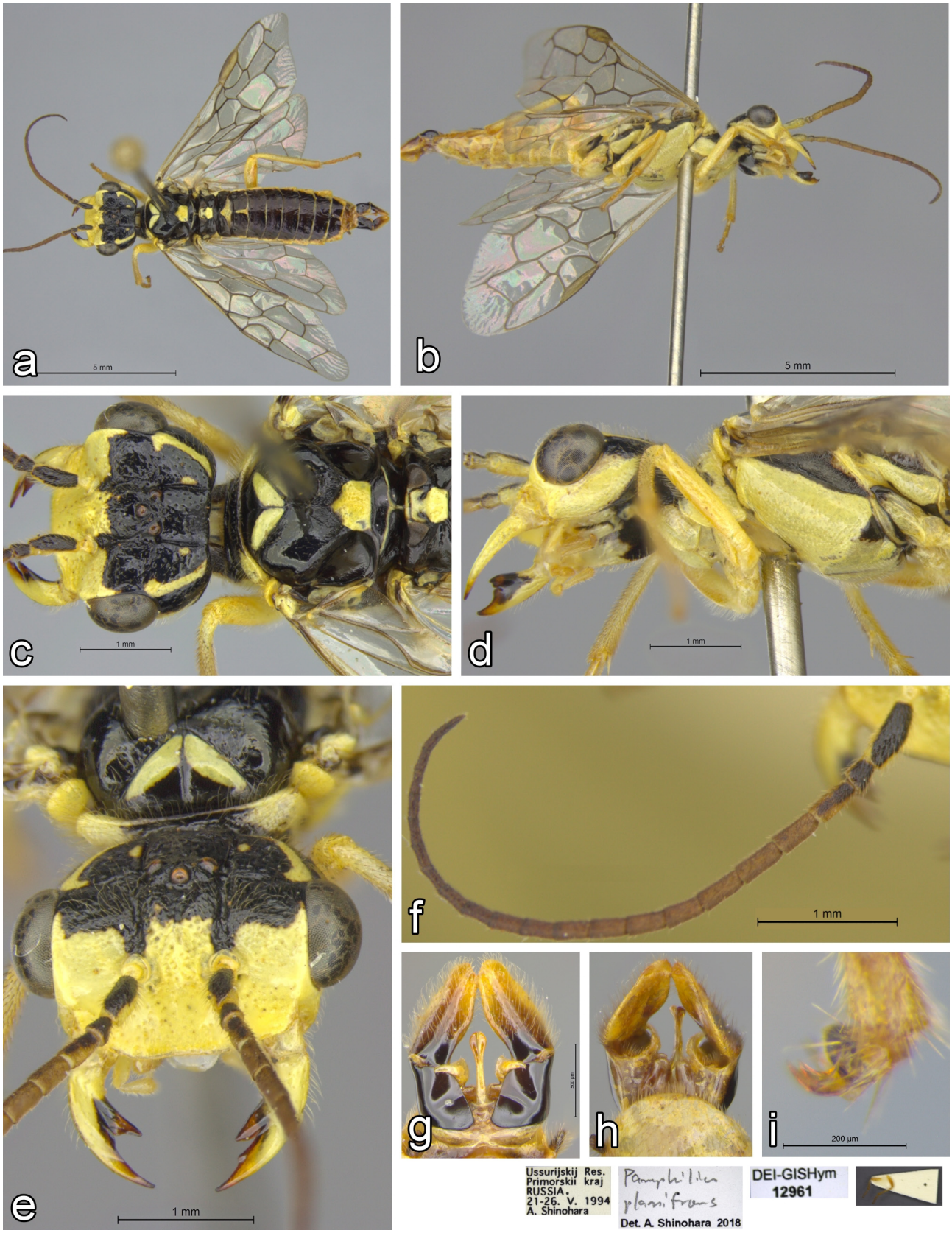


FIGURE 112. ***Pamphilius planifrons***, male, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

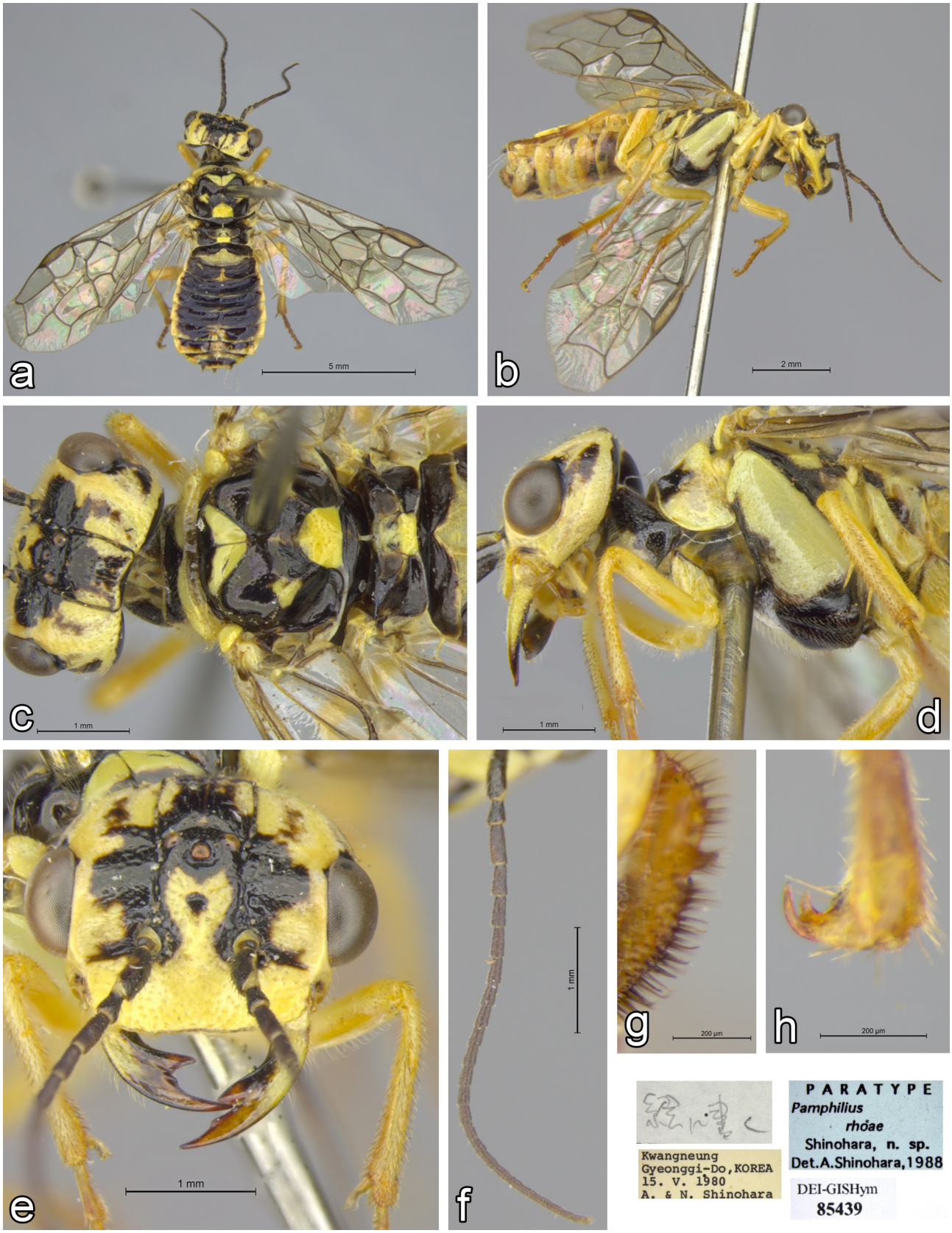


FIGURE 113. ***Pamphilius rhoae***, female, Korea (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

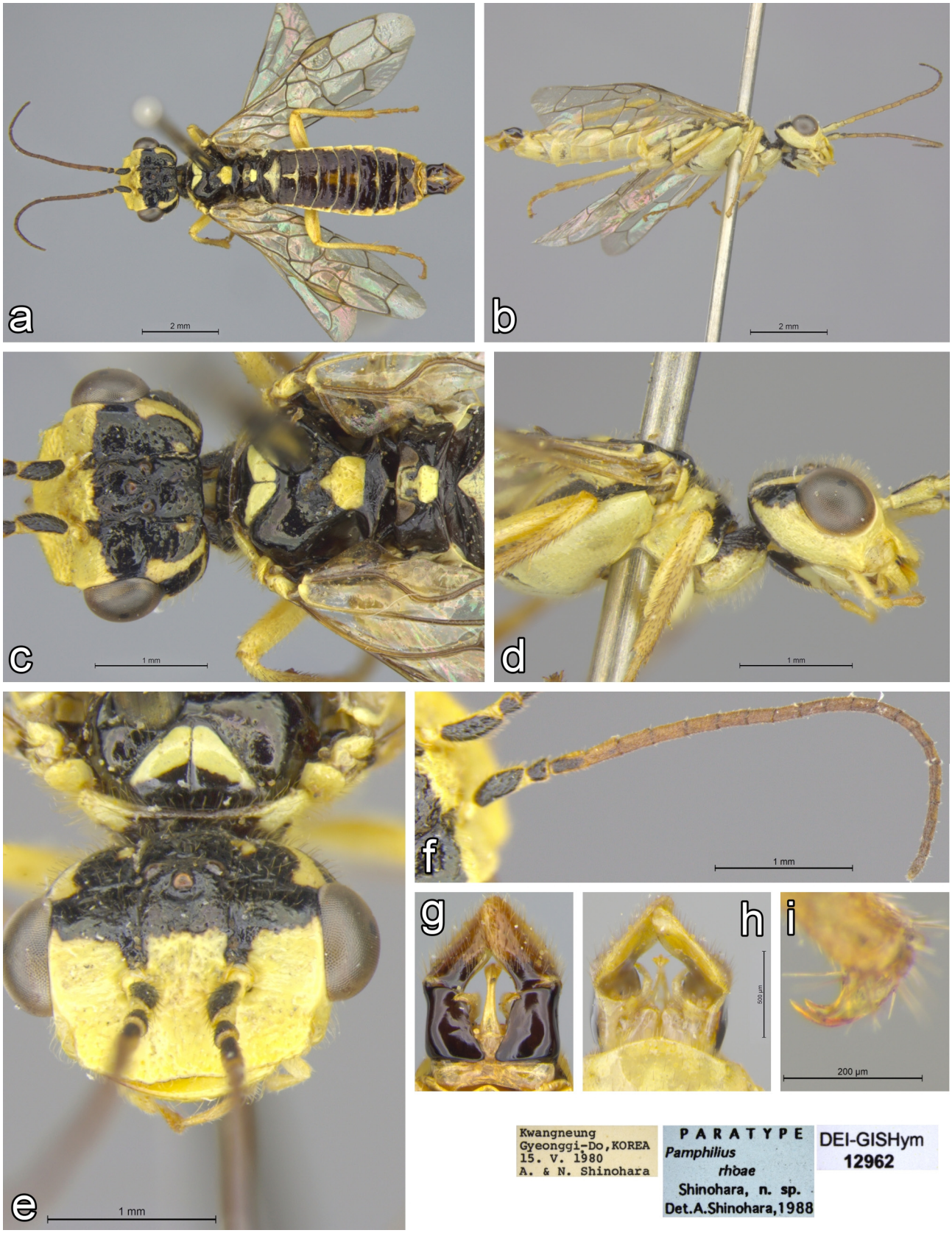


FIGURE 114. ***Pamphilius rhoae***, male, Korea (paratype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

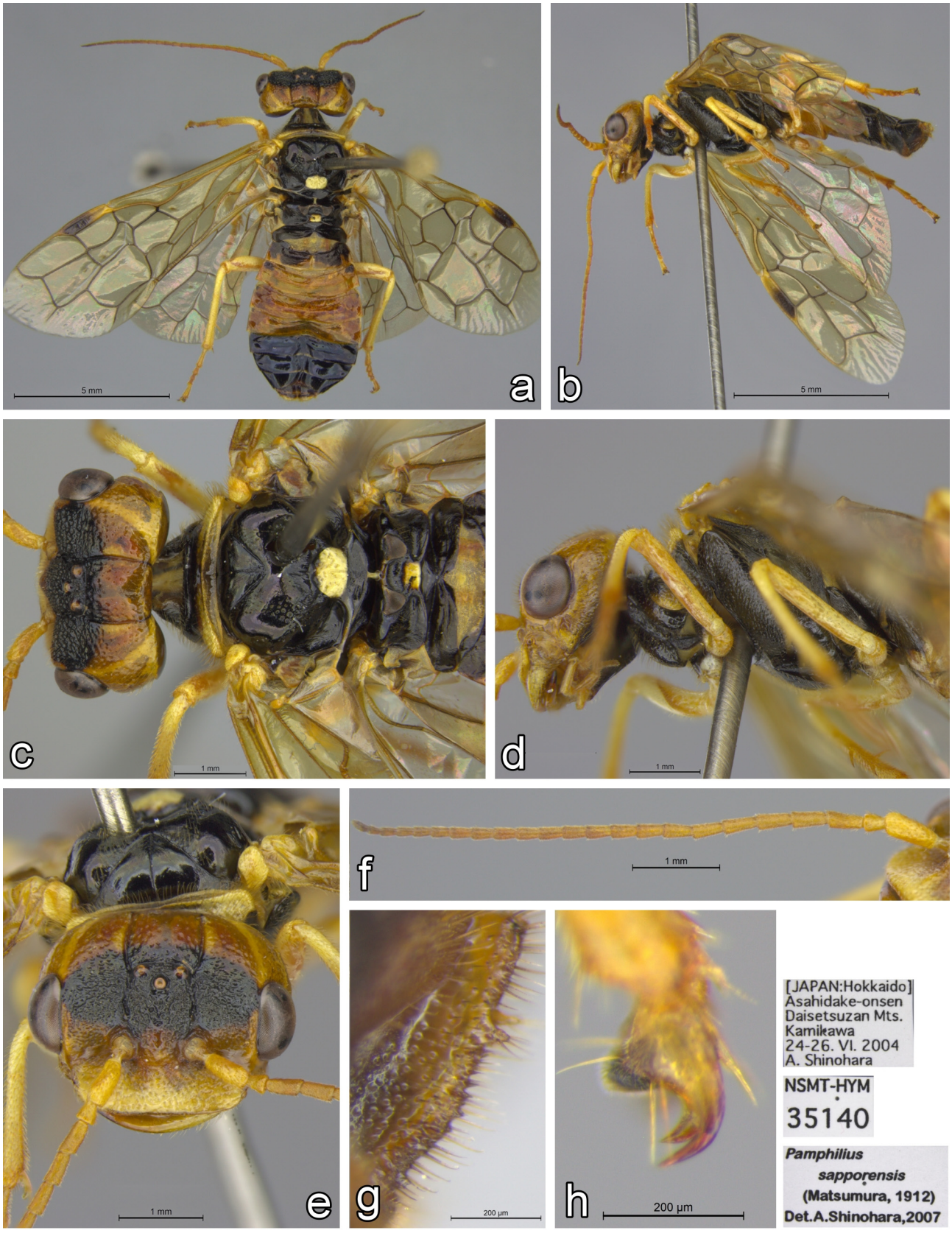


FIGURE 115. ***Pamphilius sapporensis***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

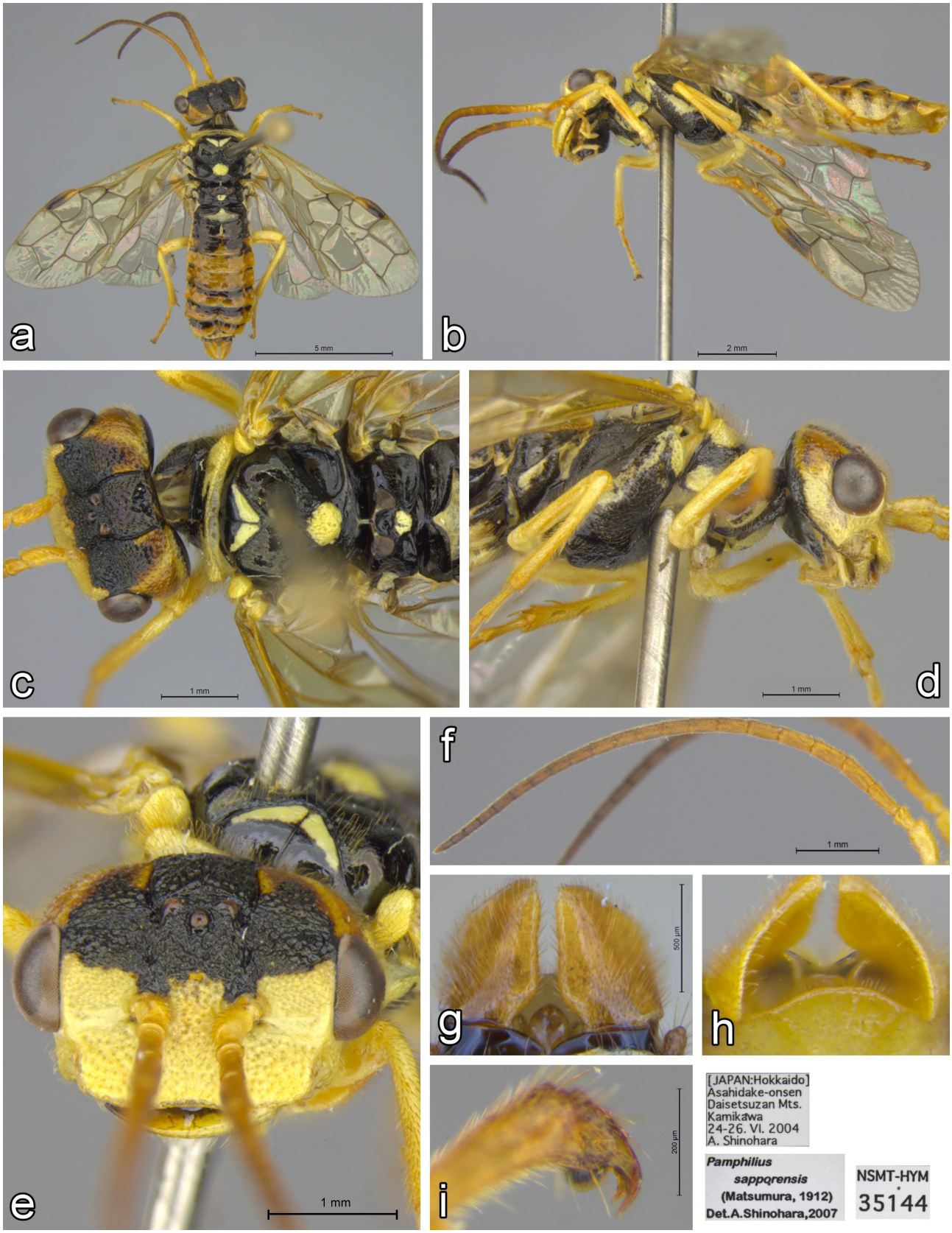


FIGURE 116. ***Pamphilius sapporensis***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** fore wing, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

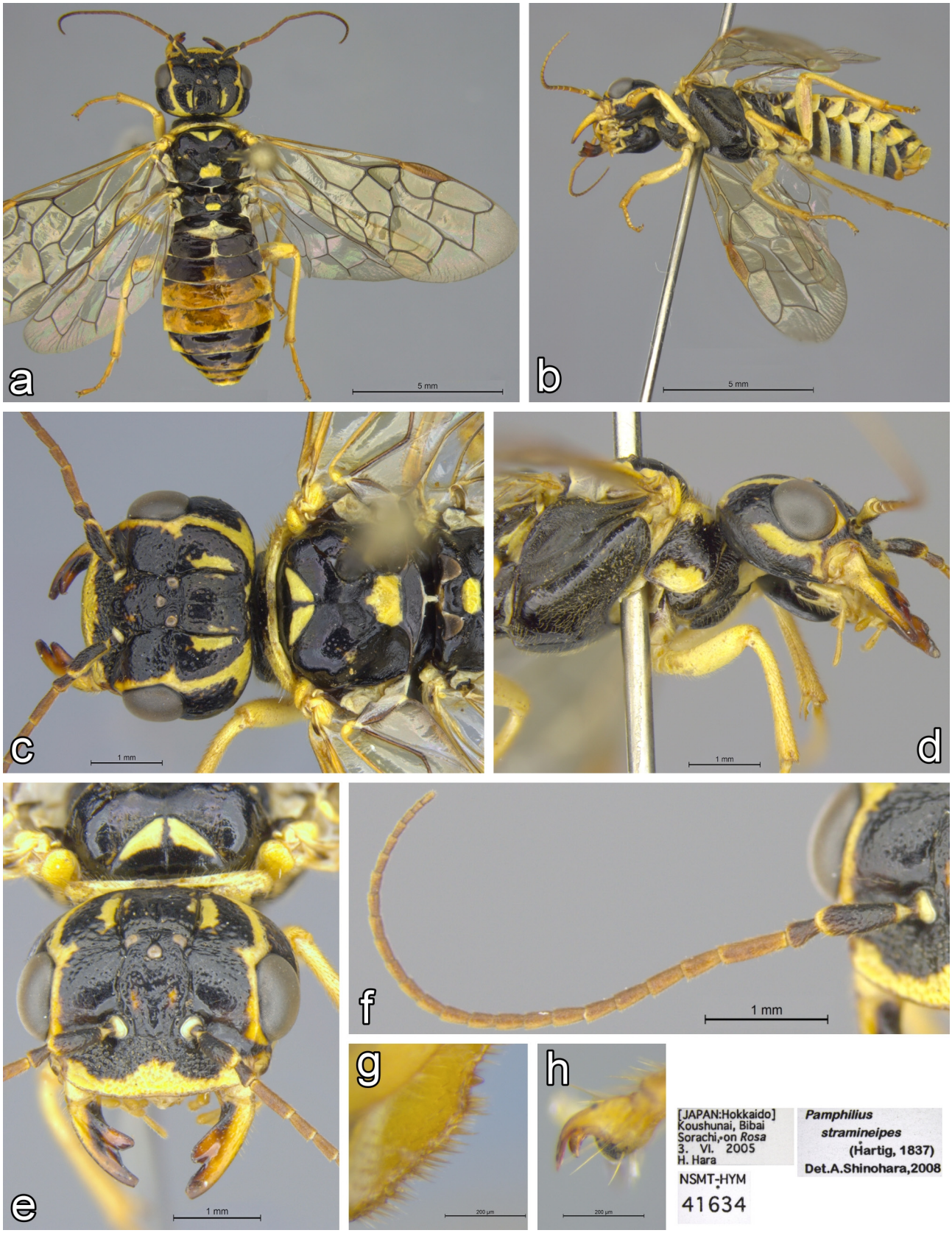


FIGURE 117. ***Pamphilius stramineipes***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

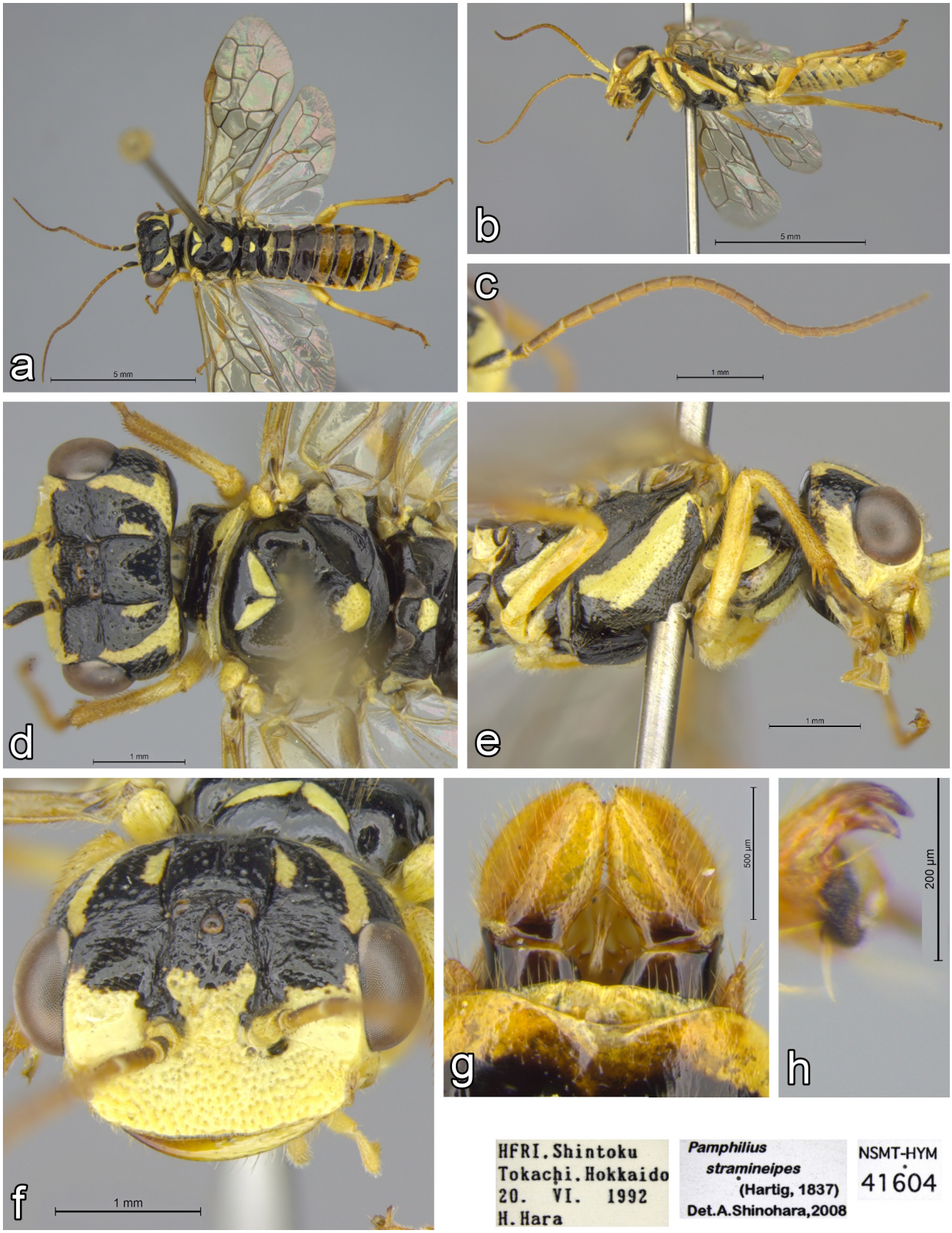


FIGURE 118. ***Pamphilius stramineipes***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** antenna, **(d)** head & thorax dorsally, **(e)** head & thorax ventrolaterally, **(f)** face, **(g)** genitalia dorsally, **(h)** claw.

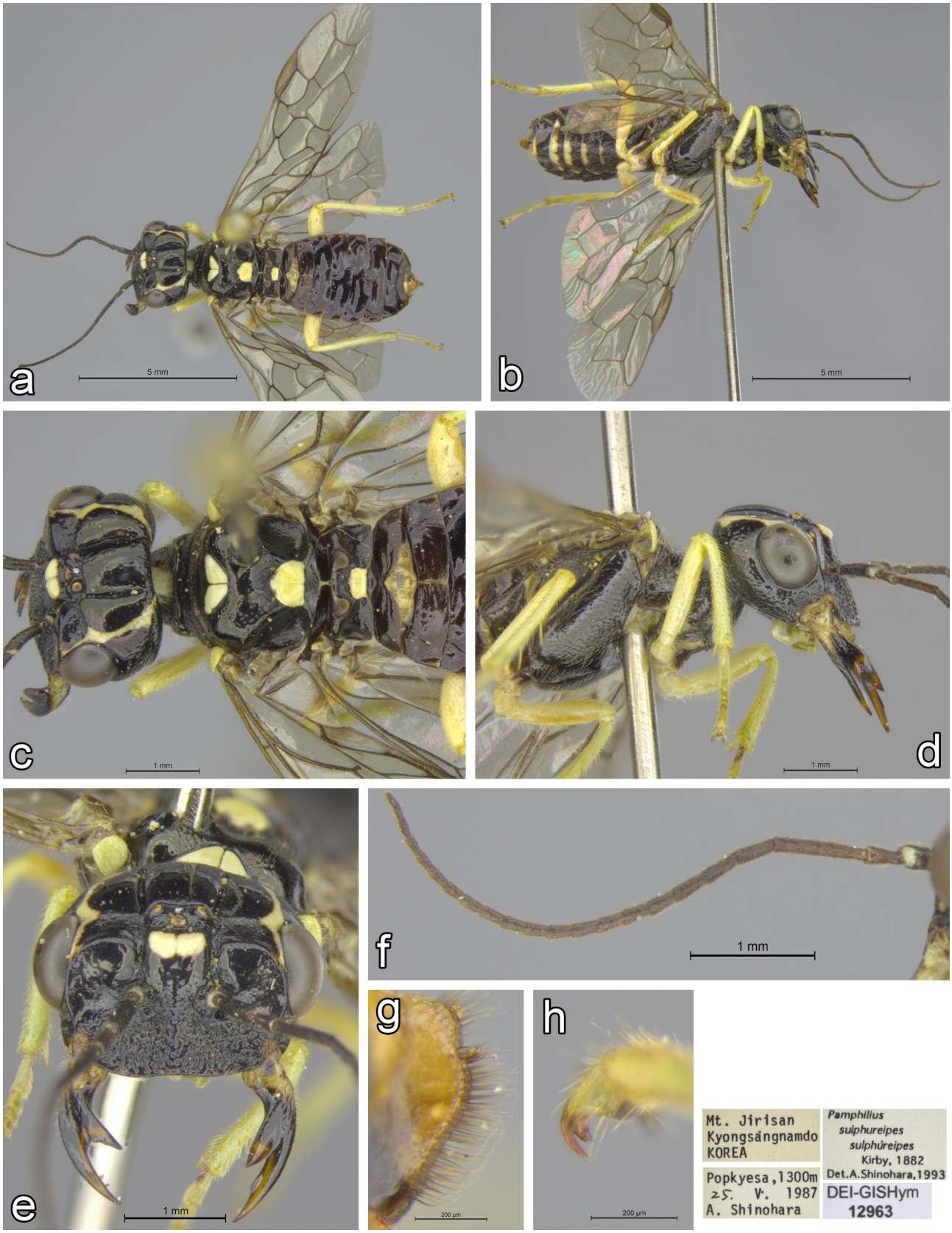


FIGURE 119. ***Pamphilius sulphureipes sulphureipes***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

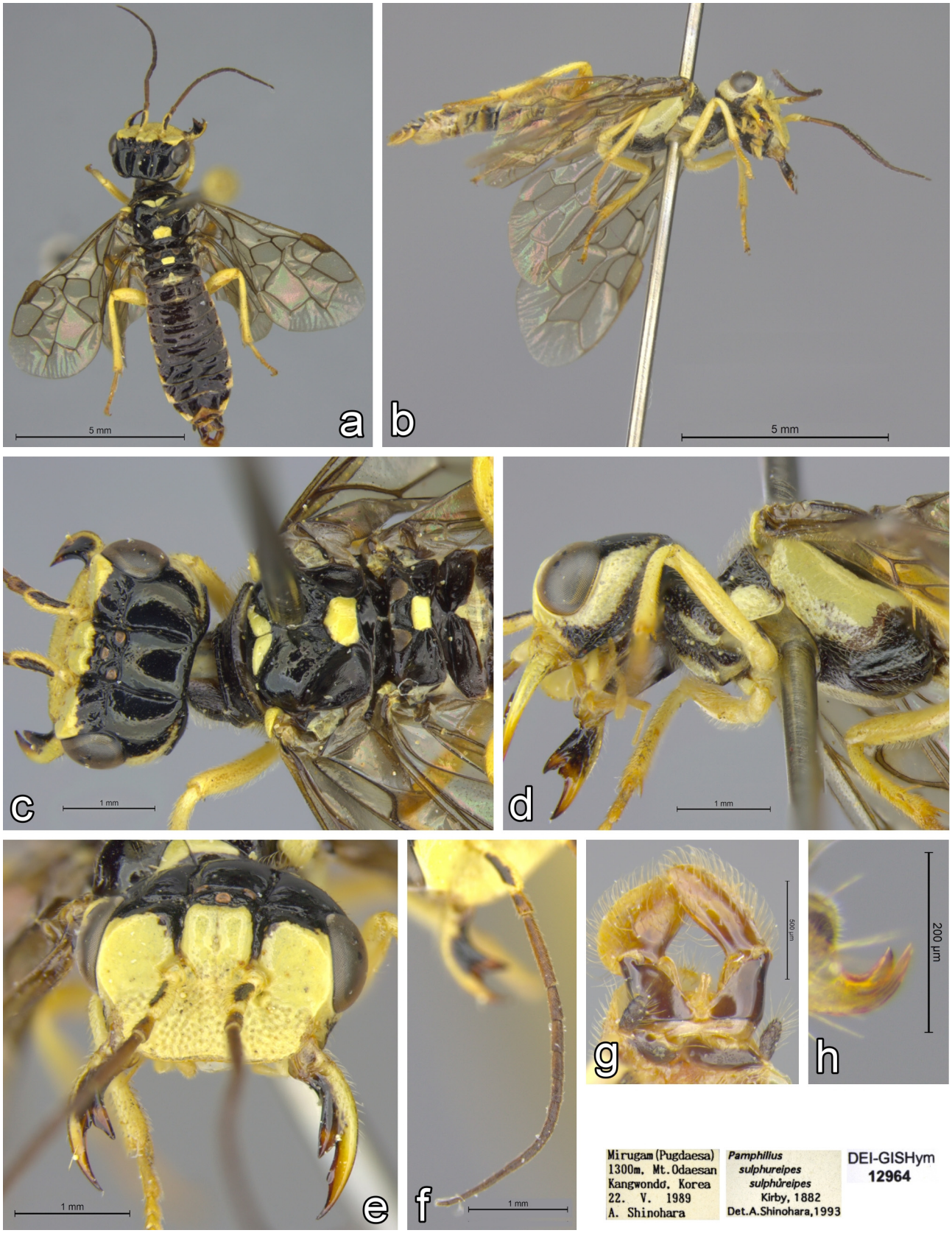


FIGURE 120. ***Pamphilius sulphureipes sulphureipes***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** claw.

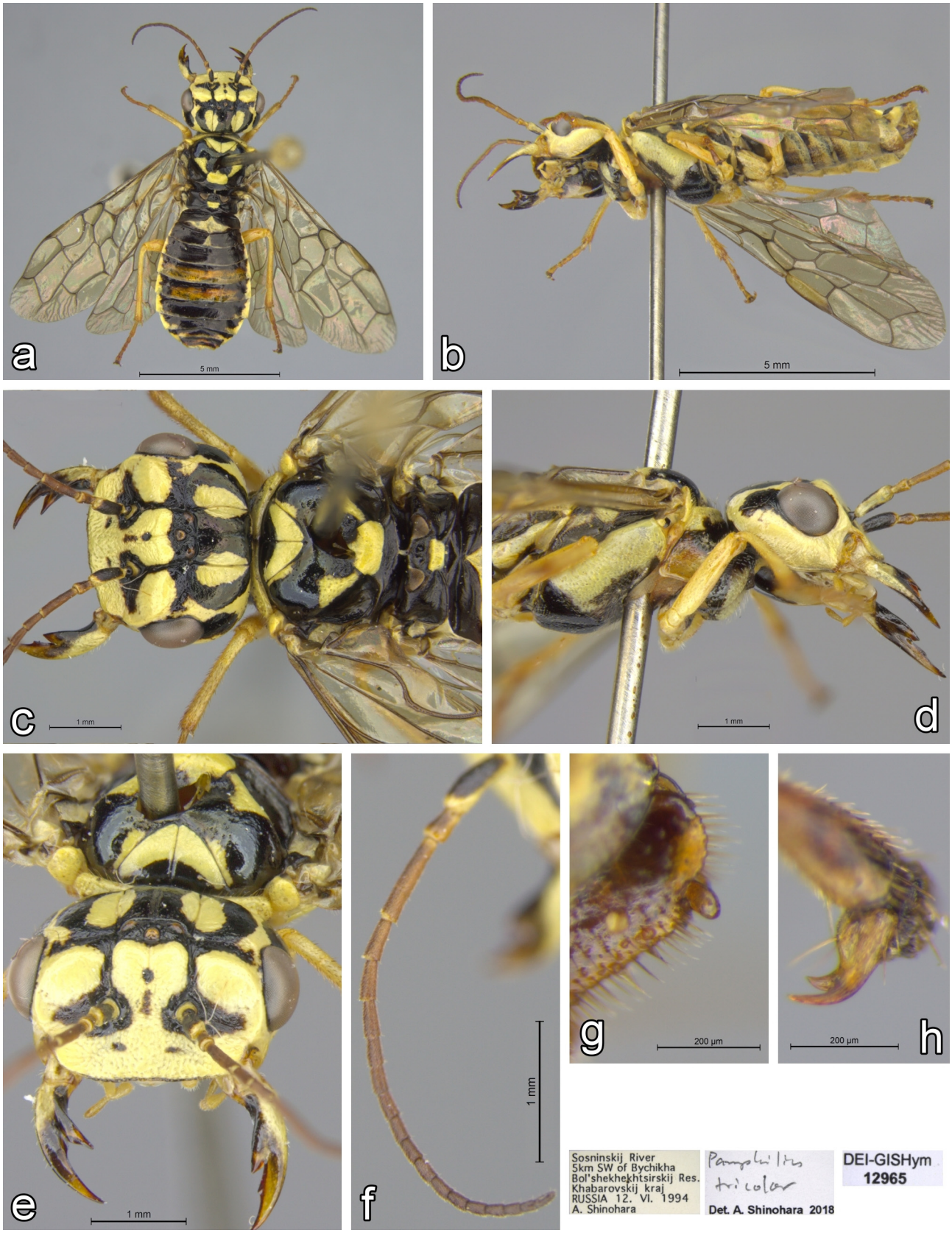


FIGURE 121. ***Pamphilius tricolor***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

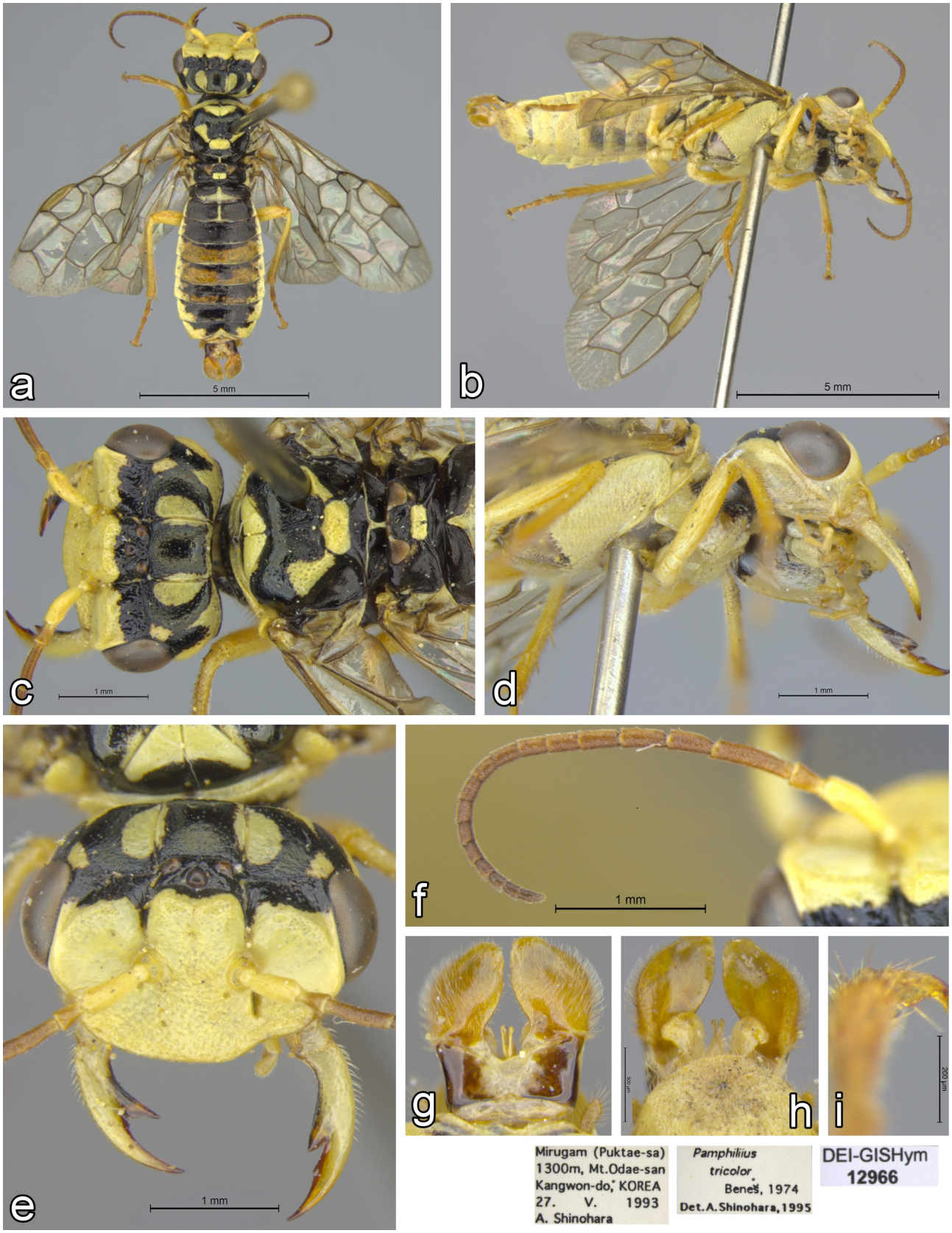


FIGURE 122. ***Pamphilius tricolor***, male, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

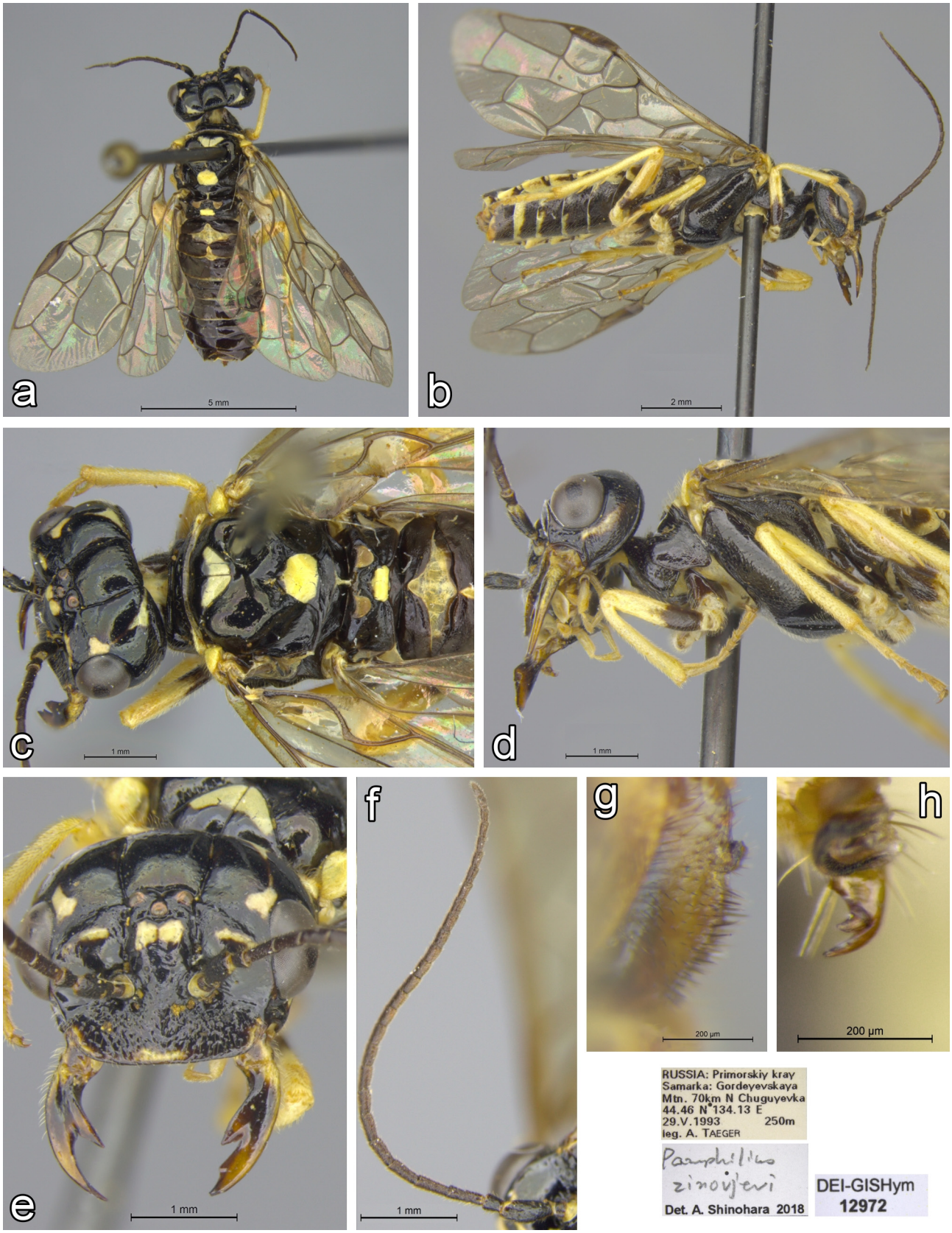


FIGURE 123. ***Pamphilius ussuriensis***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

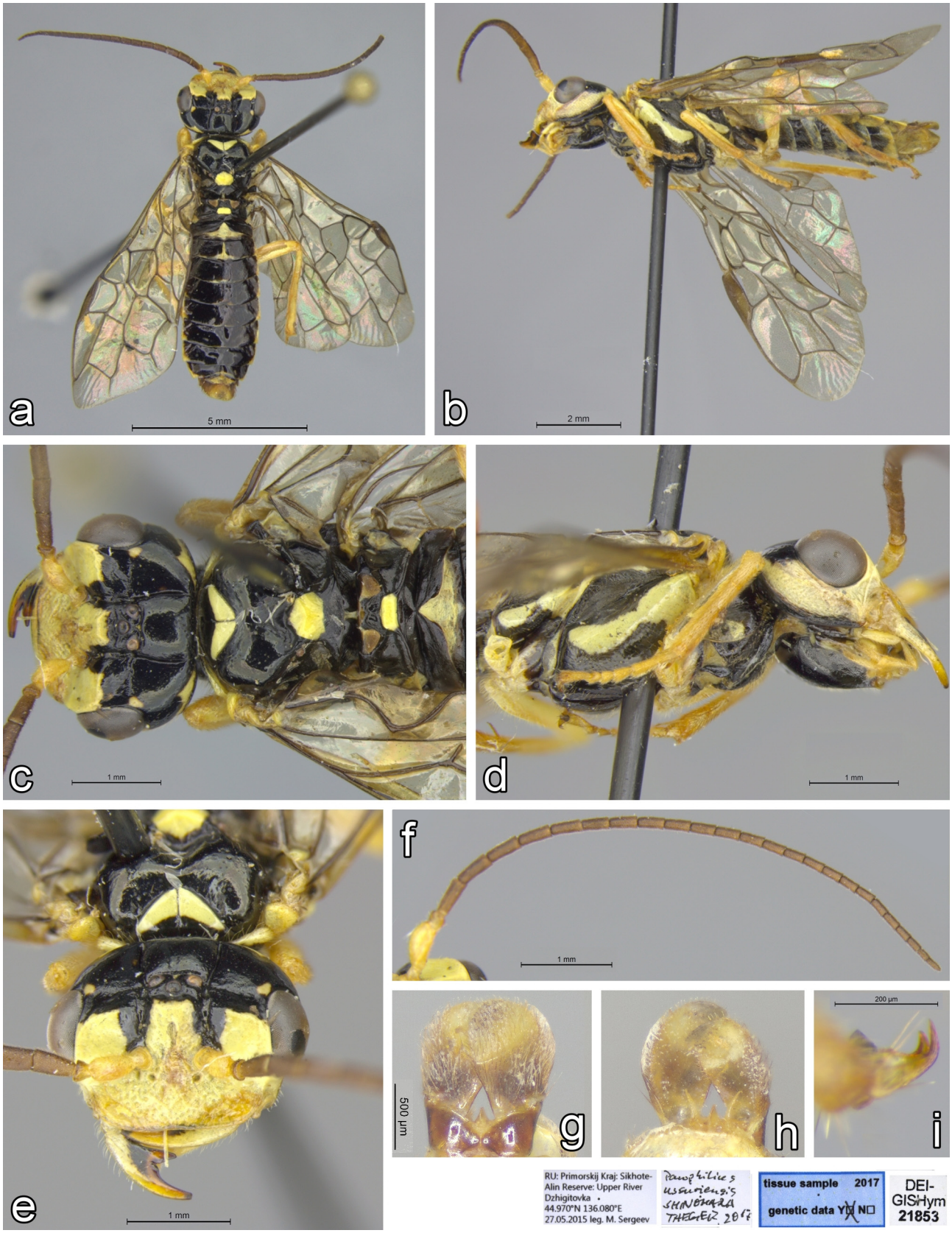


FIGURE 124. ***Pamphilius ussuriensis***, male, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

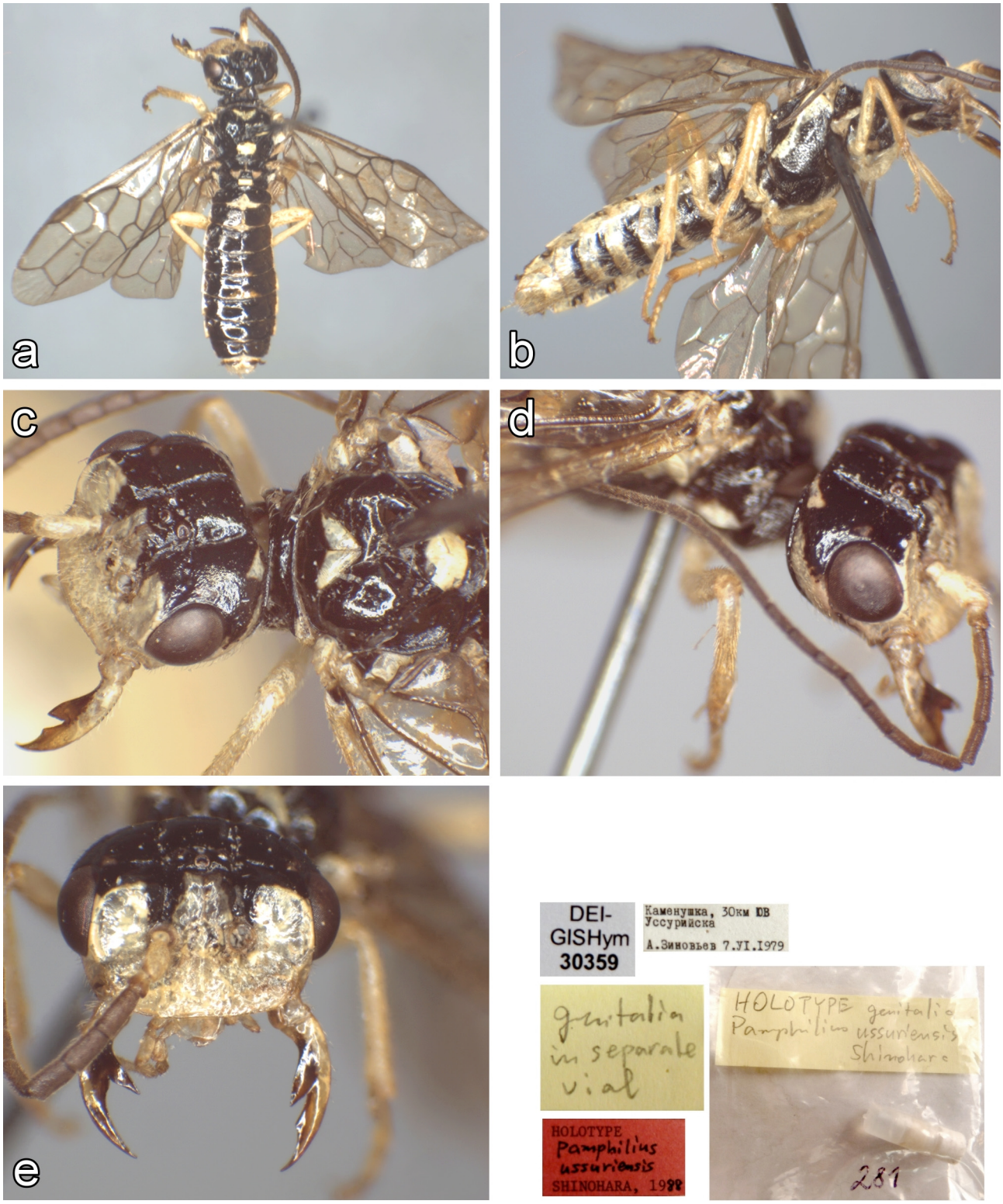


FIGURE 125. ***Pamphilius ussuriensis***, male, Russia (holotype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head antenna dorsolaterally, **(e)** face.



FIGURE 126. ***Pamphilius ussuriensis*** (specimen 86348 and holotype of *P. zinovjevi*), female, Russia – **(a)** head & thorax dorsally (86348), **(b)** head & thorax ventrolaterally (86348), **(c)** face (86348), **(d)** dorsally, **(e)** lateroventrally, **(f)** face.

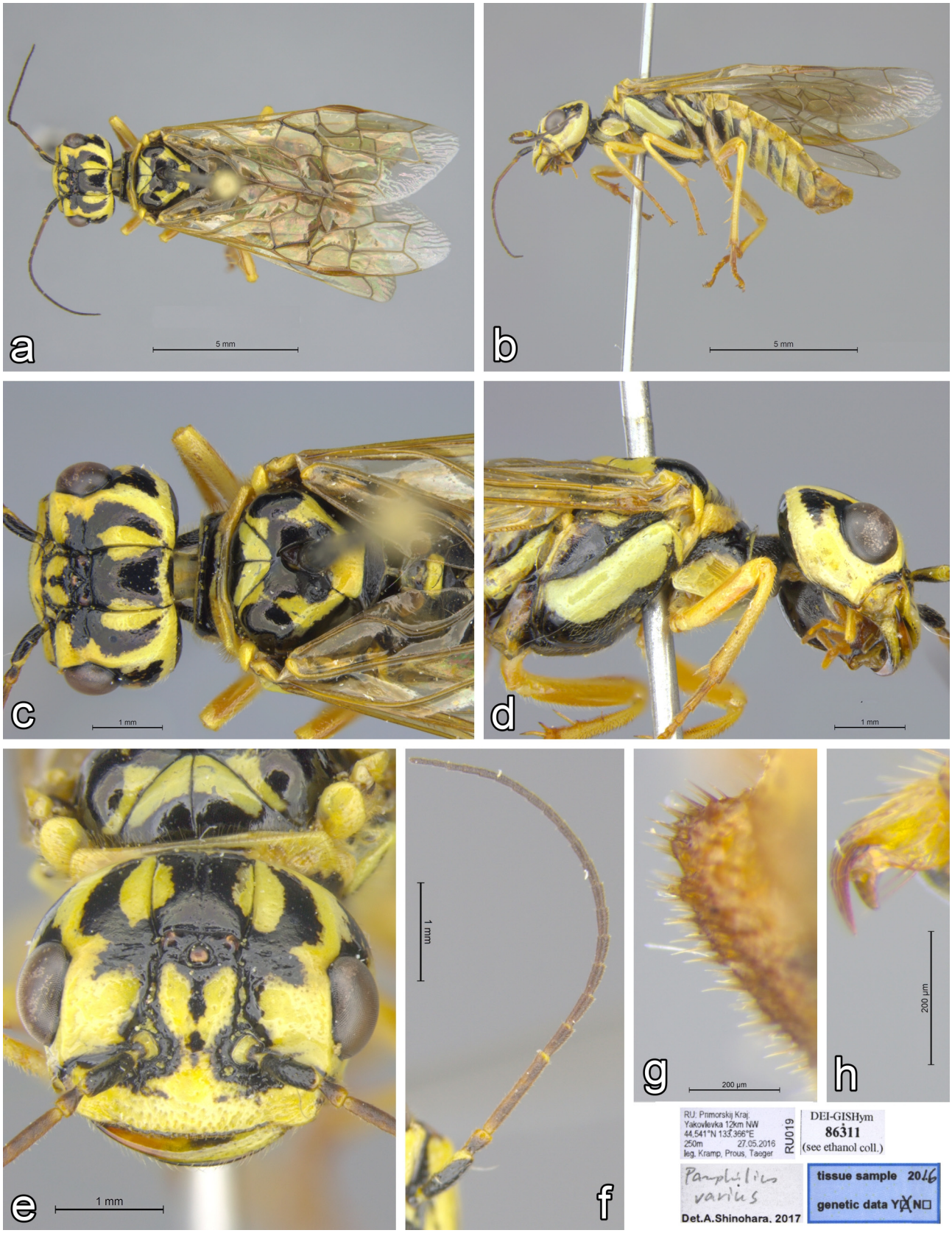


FIGURE 127. ***Pamphilius varius***, female, Russia – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

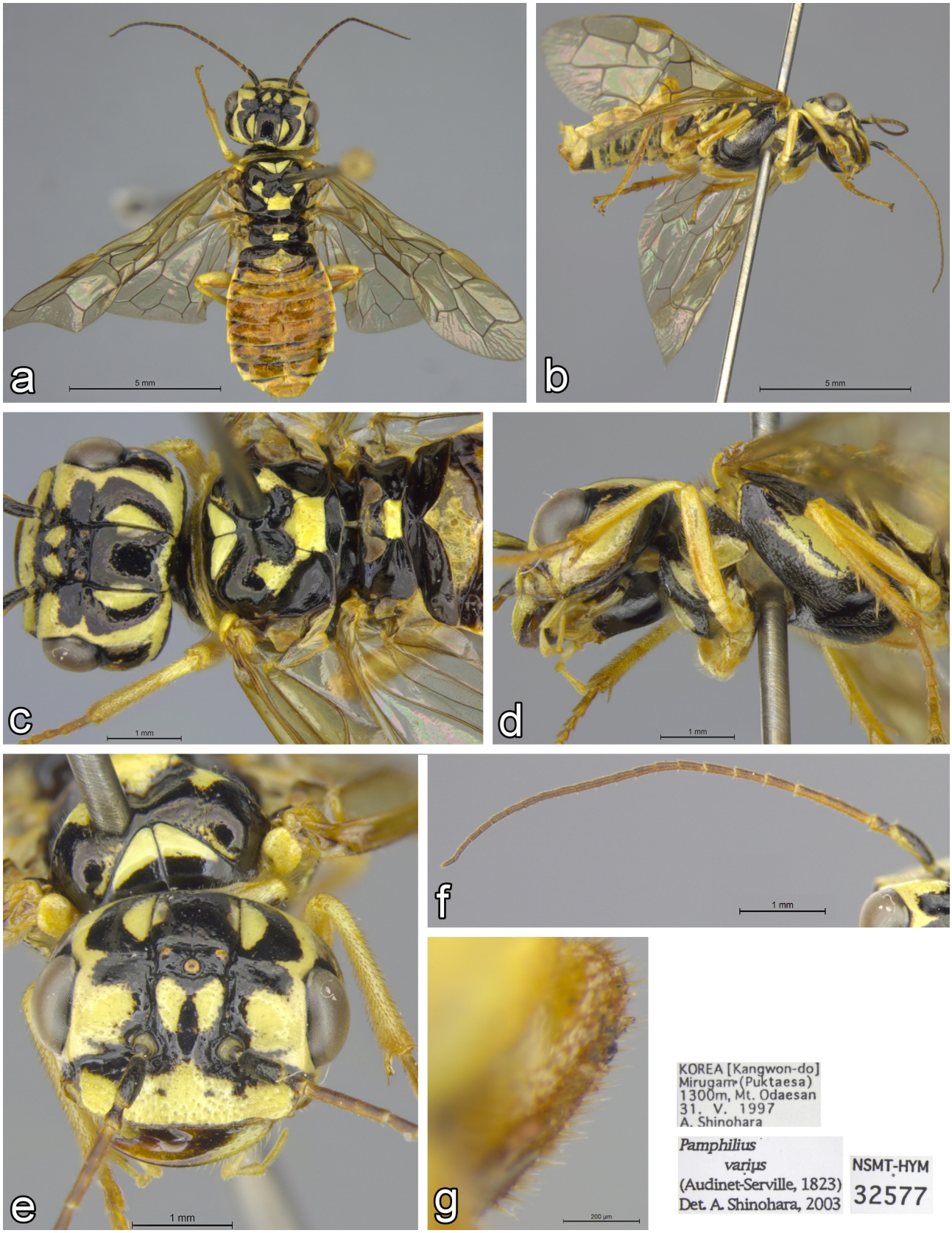


FIGURE 128. ***Pamphilius varius***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally.

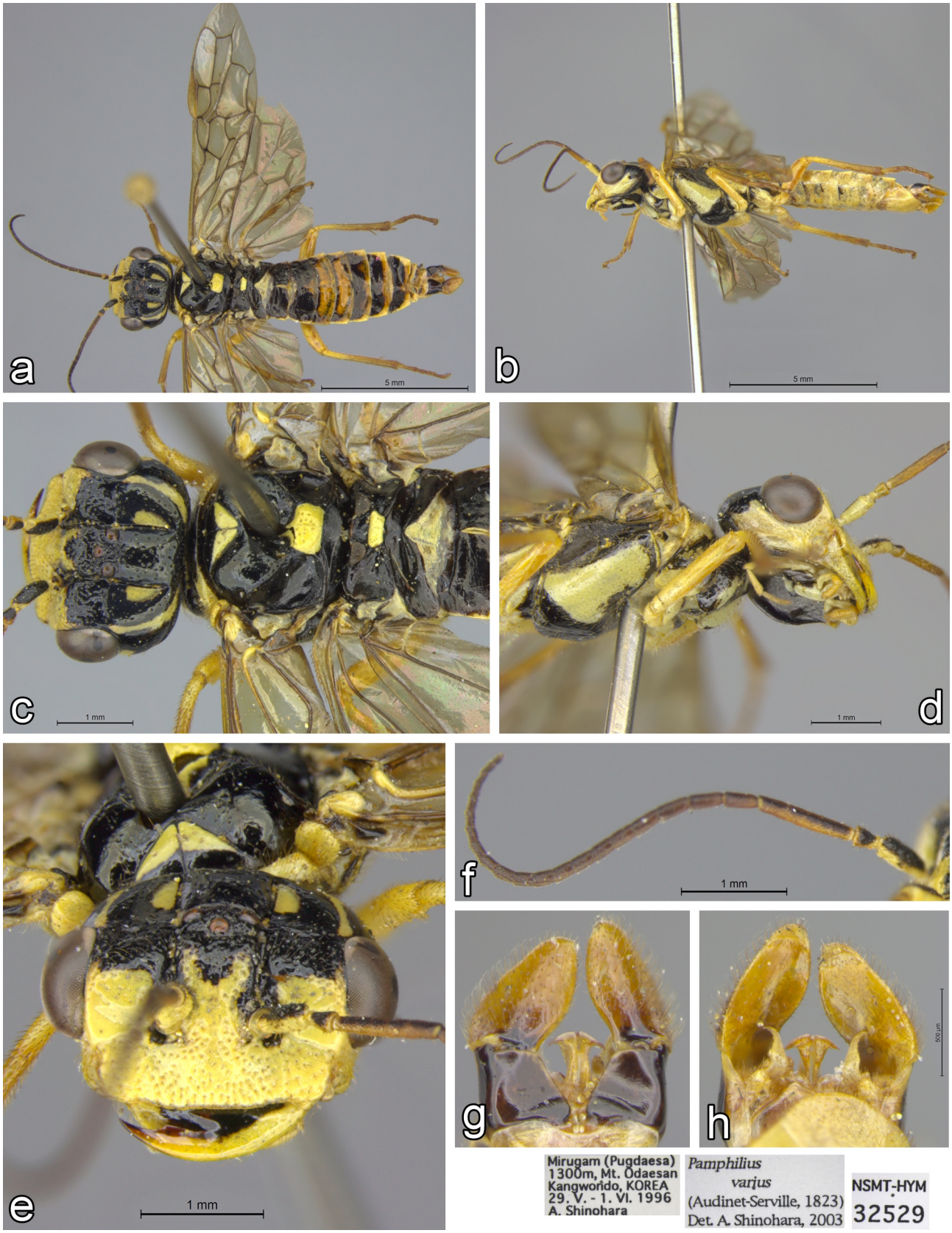


FIGURE 129. ***Pamphilius varius***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally.

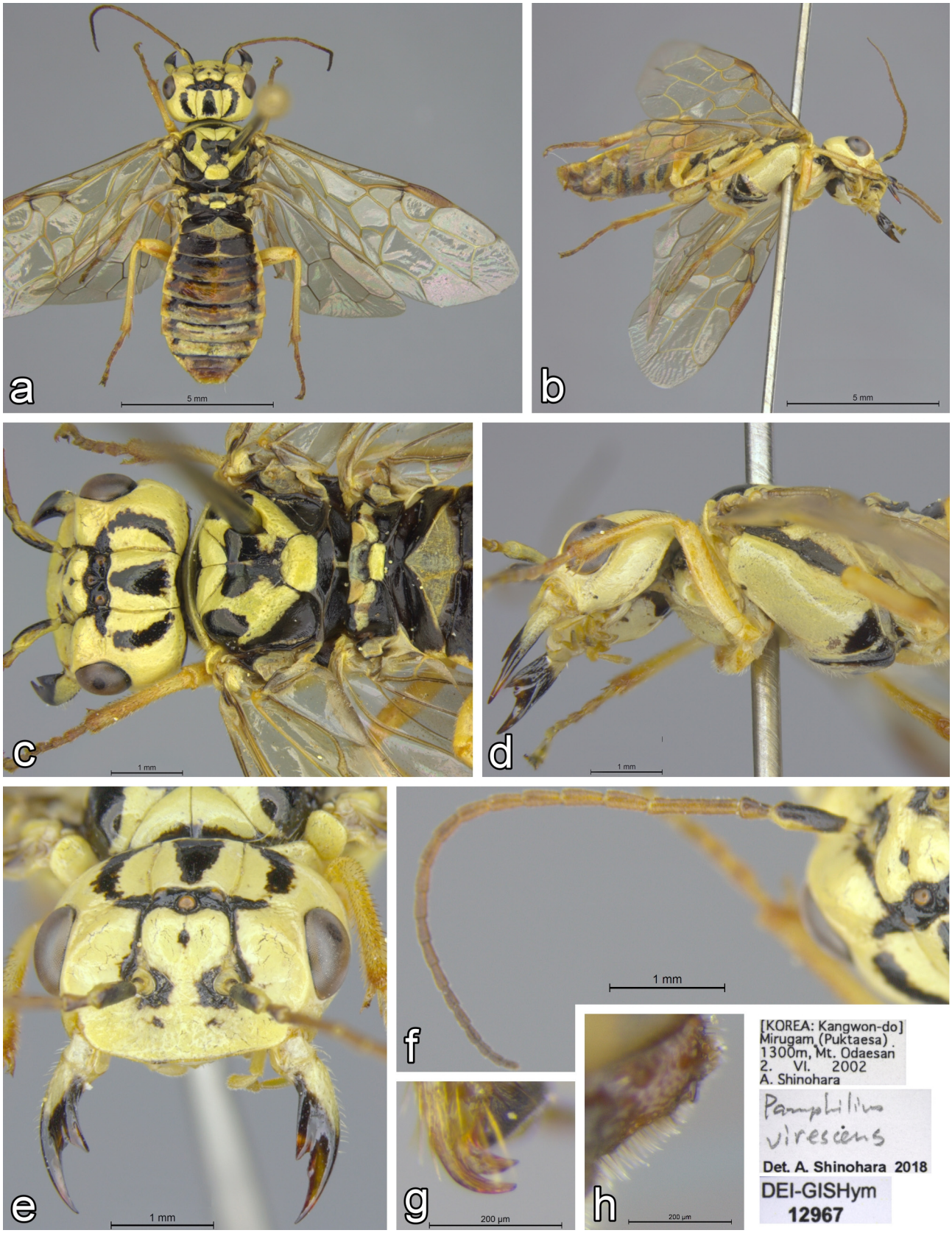


FIGURE 130. ***Pamphilius virescens***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** sawsheath laterally.

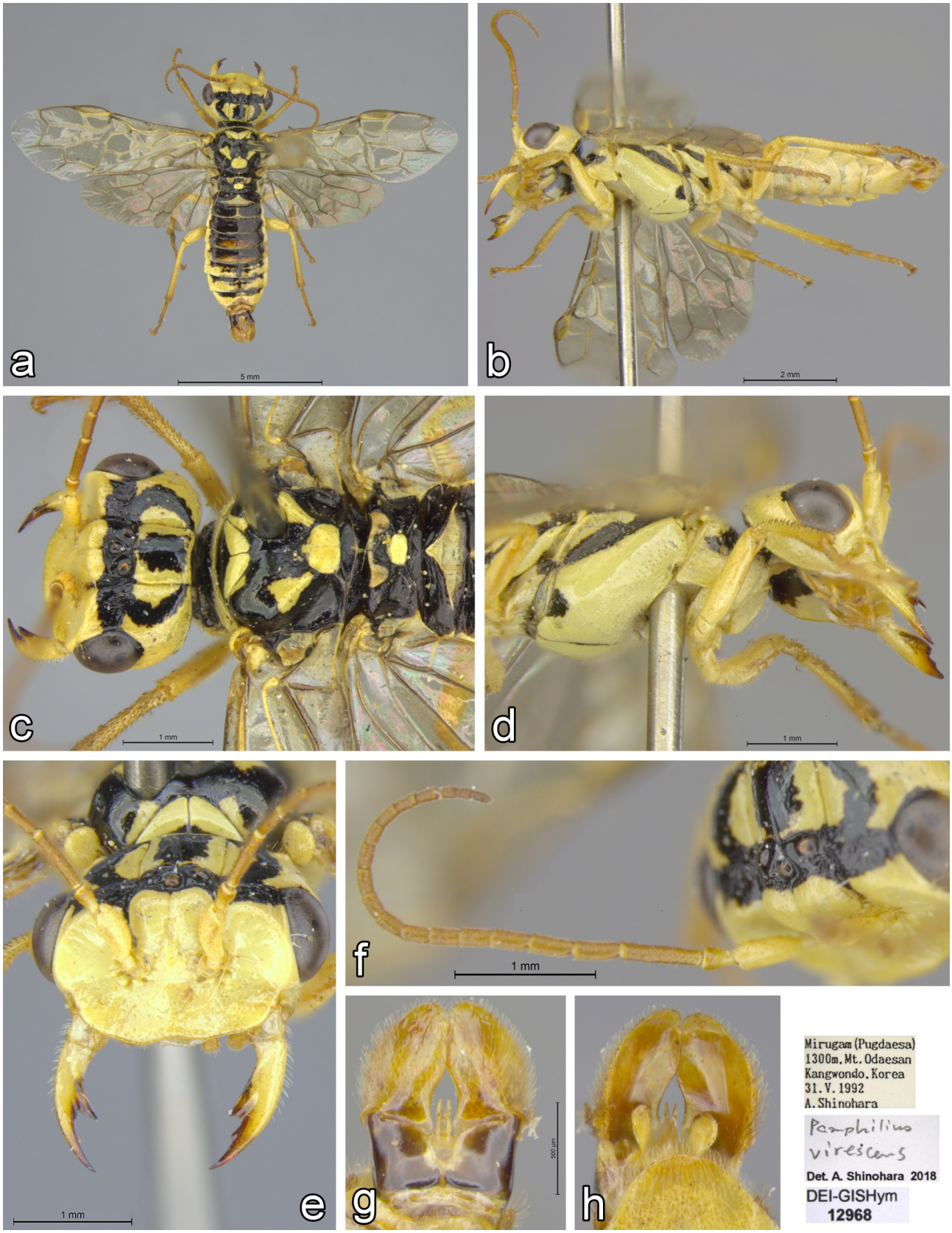


FIGURE 131. ***Pamphilius virescens***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally.

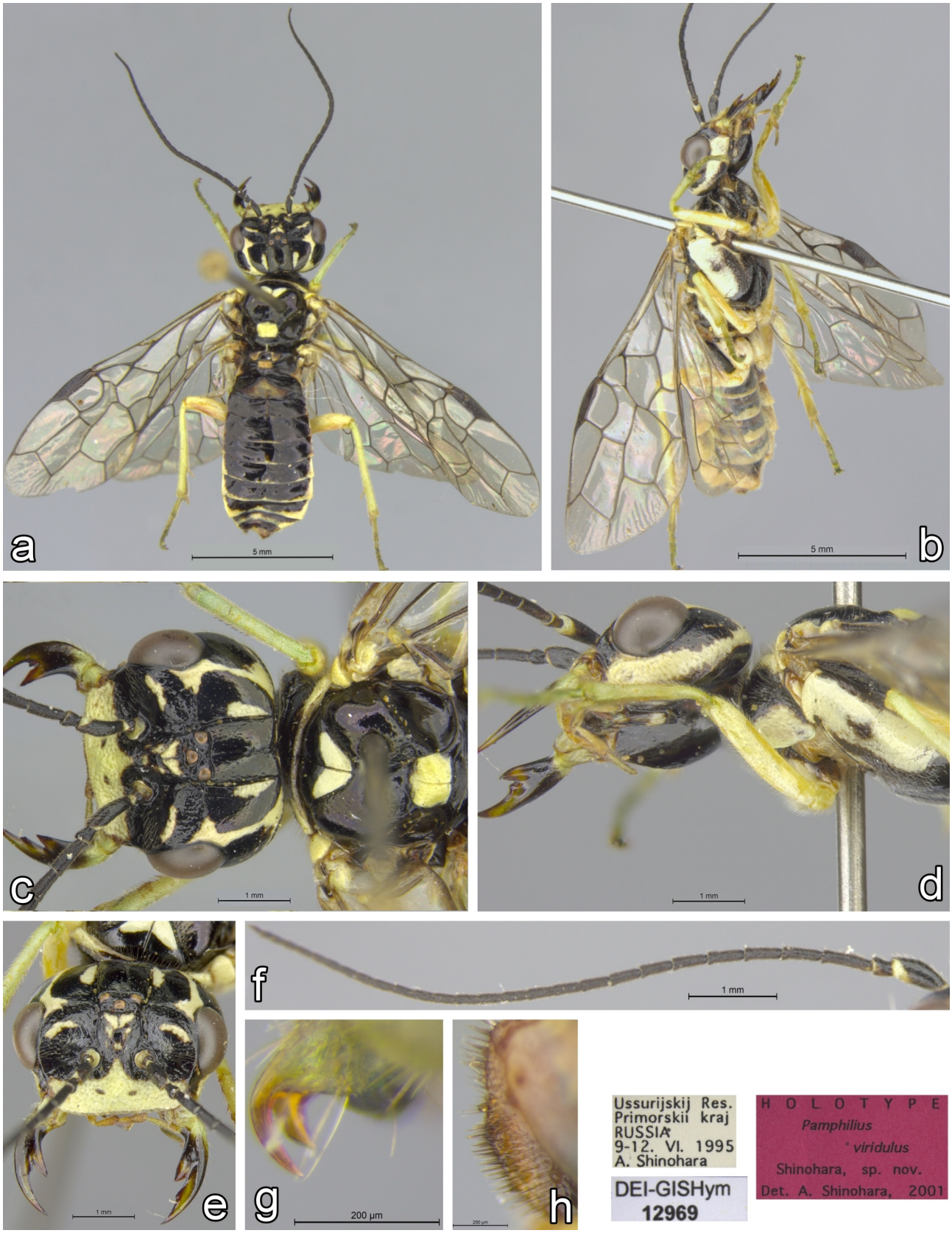


FIGURE 132. ***Pamphilius viridulus***, female, Russia (holotype) – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** sawsheath laterally.

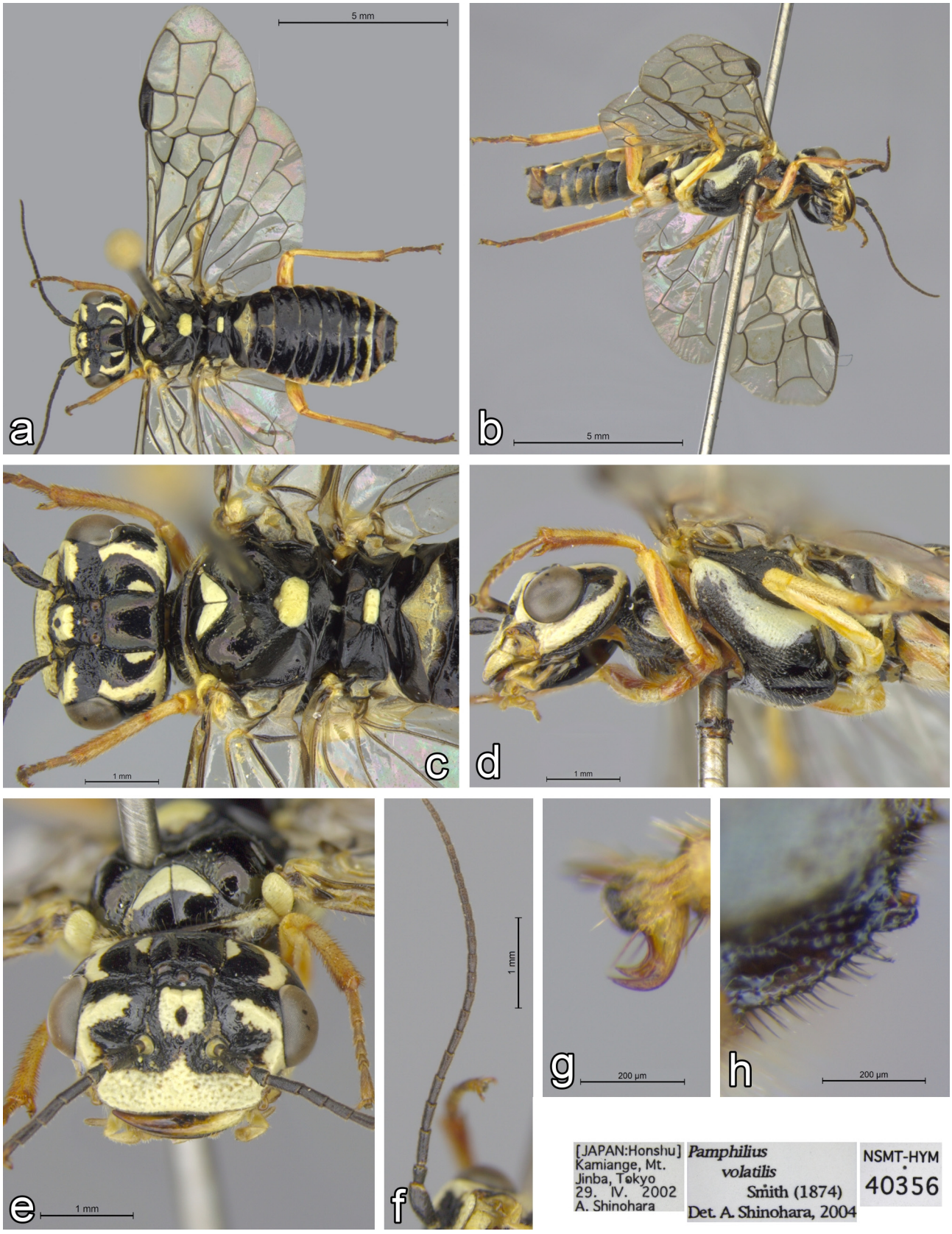


FIGURE 133. ***Pamphilius volatilis***, female, Japan – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** claw, **(h)** sawsheath laterally.

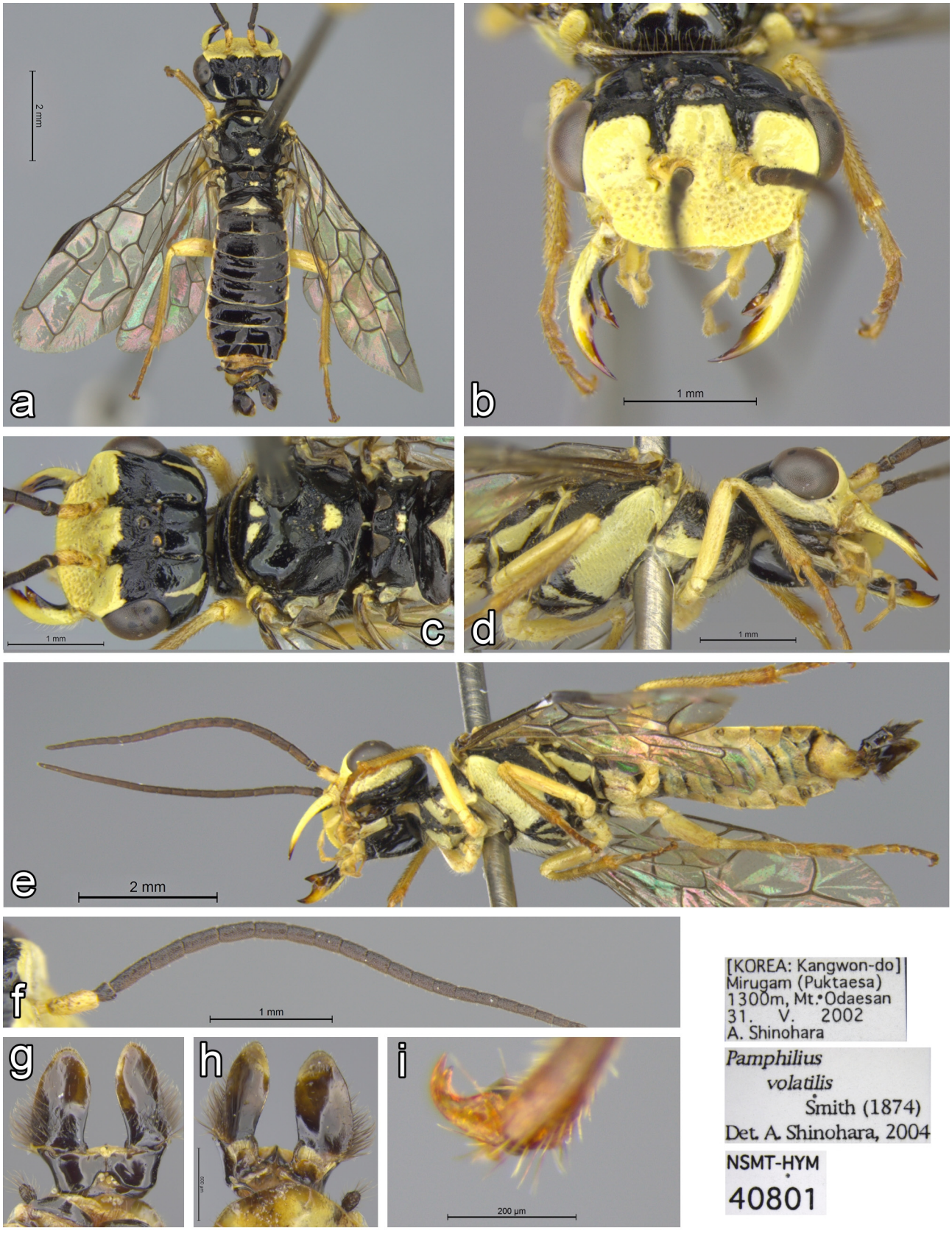


FIGURE 134. ***Pamphilius volatilis***, male, Korea – **(a)** dorsally, **(b)** face, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** lateroventrally, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

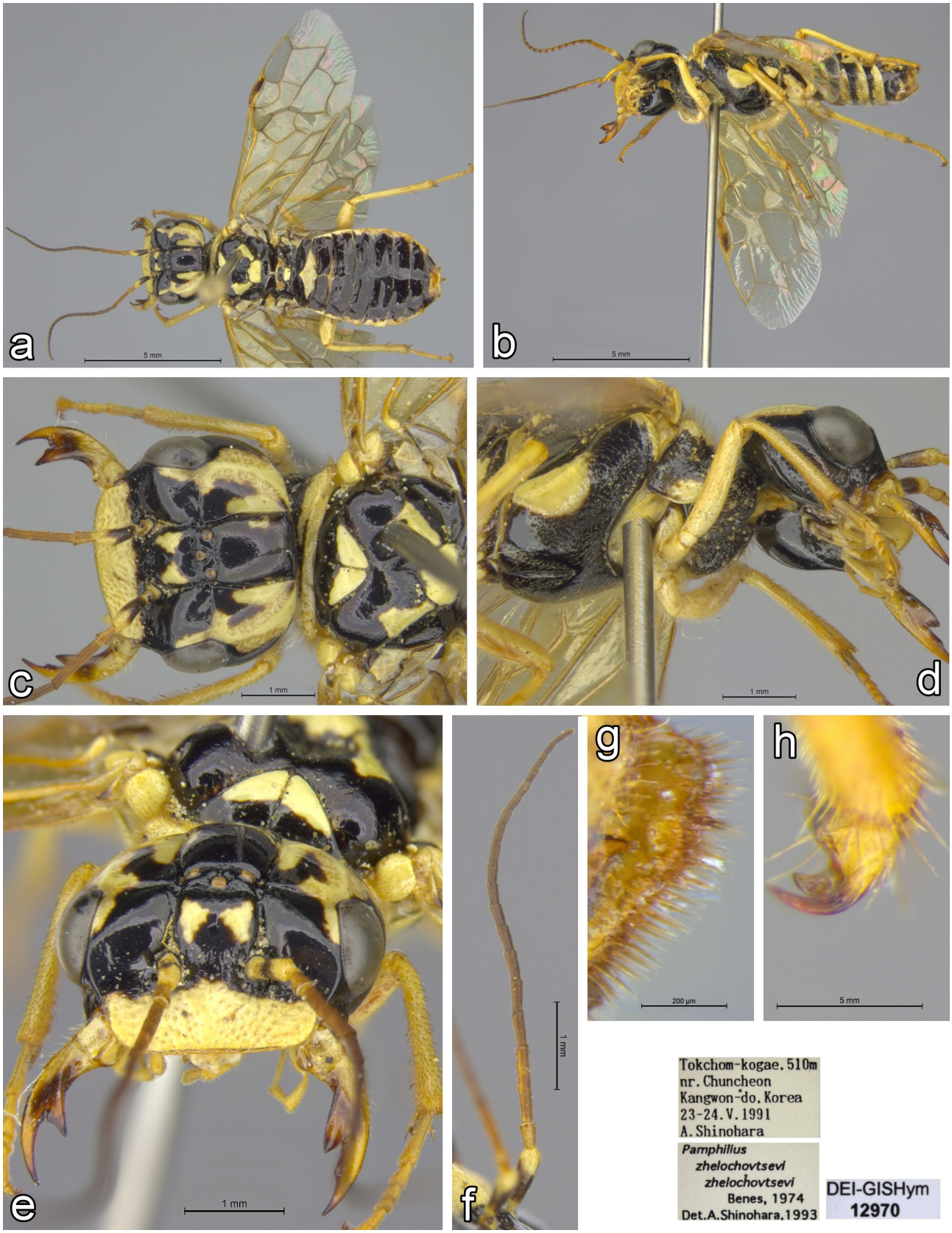


FIGURE 135. ***Pamphilius zhelochovtsevi***, female, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** sawsheath laterally, **(h)** claw.

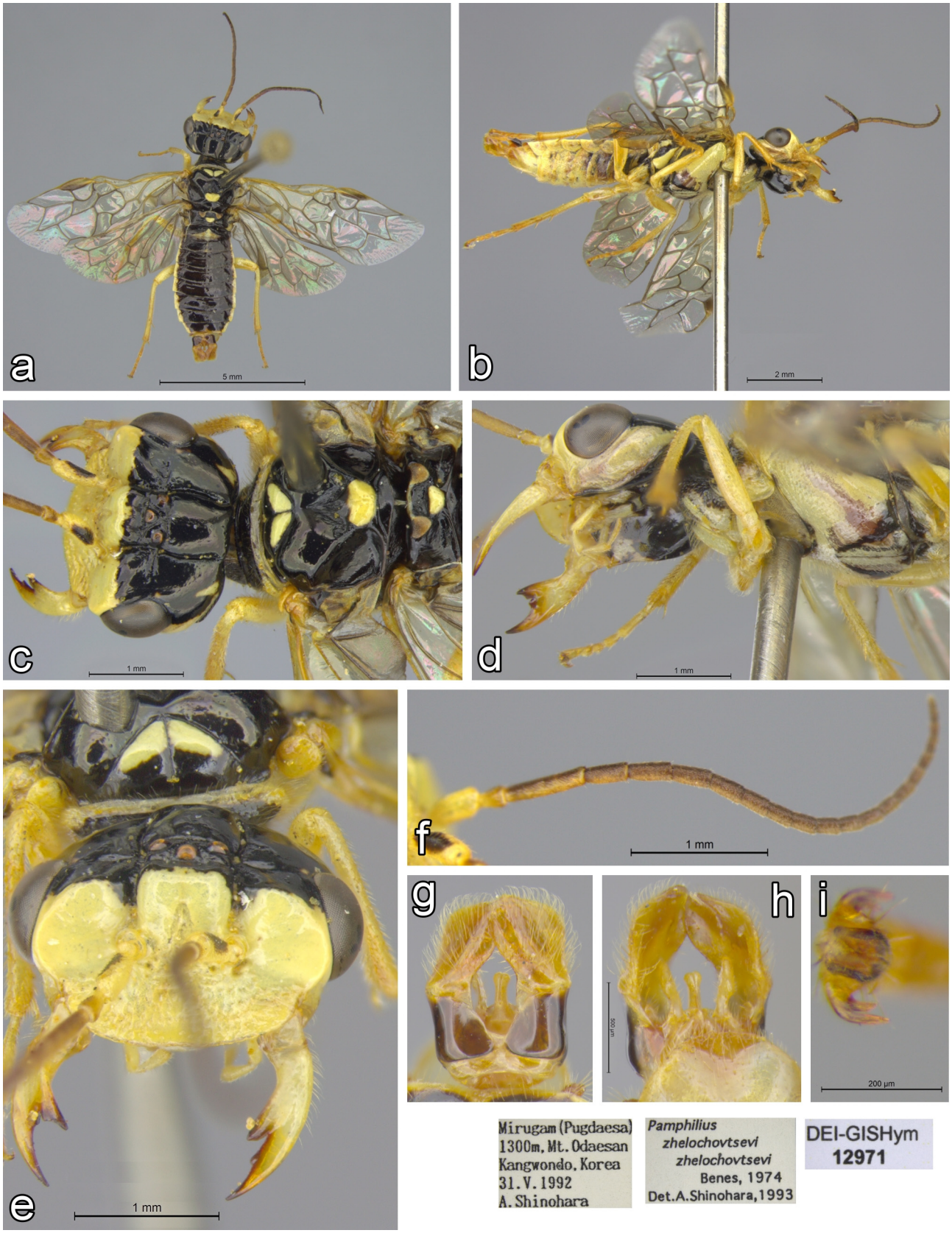


FIGURE 136. ***Pamphilius zhelochovtsevi***, male, Korea – **(a)** dorsally, **(b)** lateroventrally, **(c)** head & thorax dorsally, **(d)** head & thorax ventrolaterally, **(e)** face, **(f)** antenna, **(g)** genitalia dorsally, **(h)** genitalia ventrally, **(i)** claw.

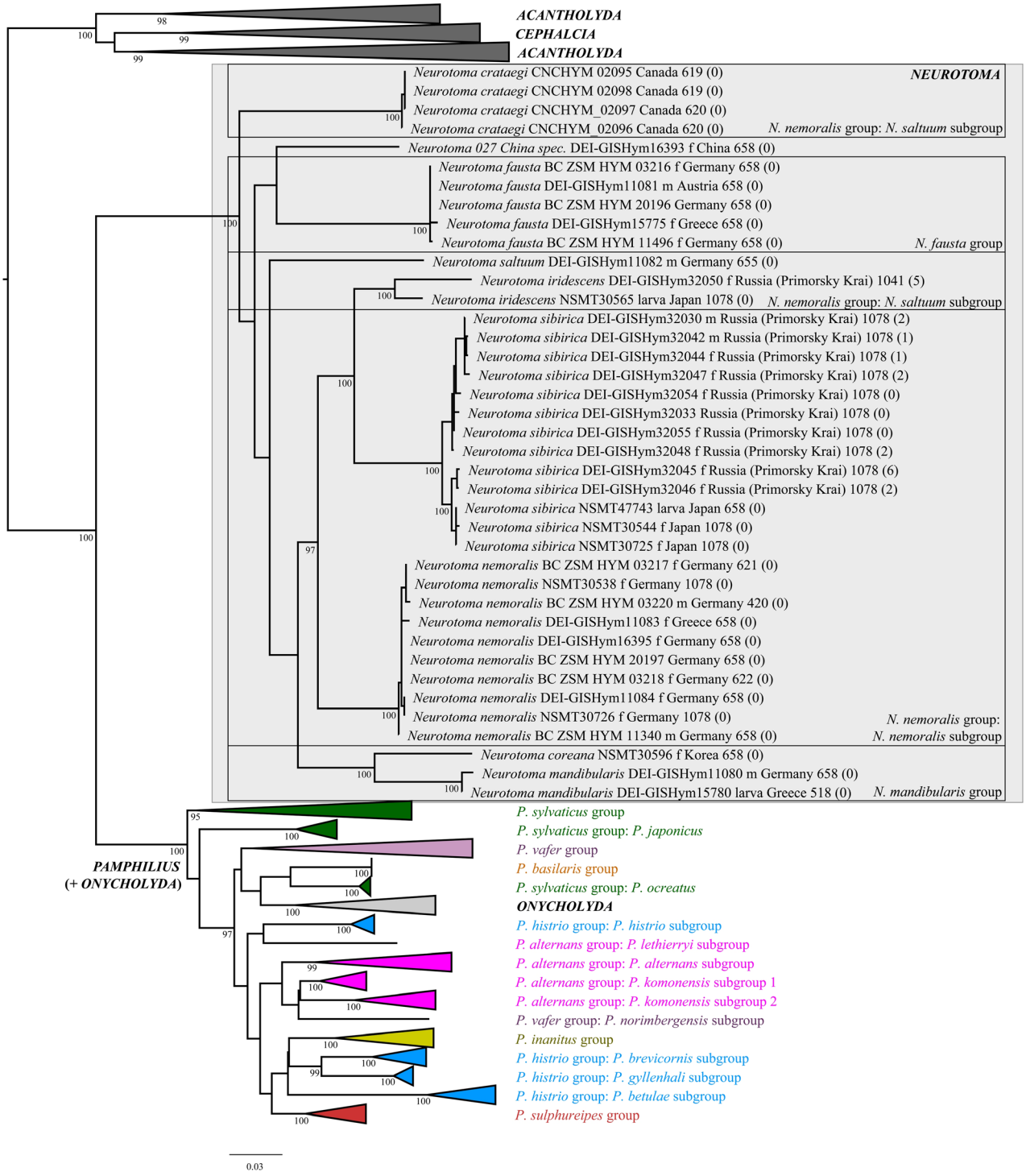


FIGURE 137. Condensed ML tree based on CO1 gene sequences, with details of *Neurotoma*.



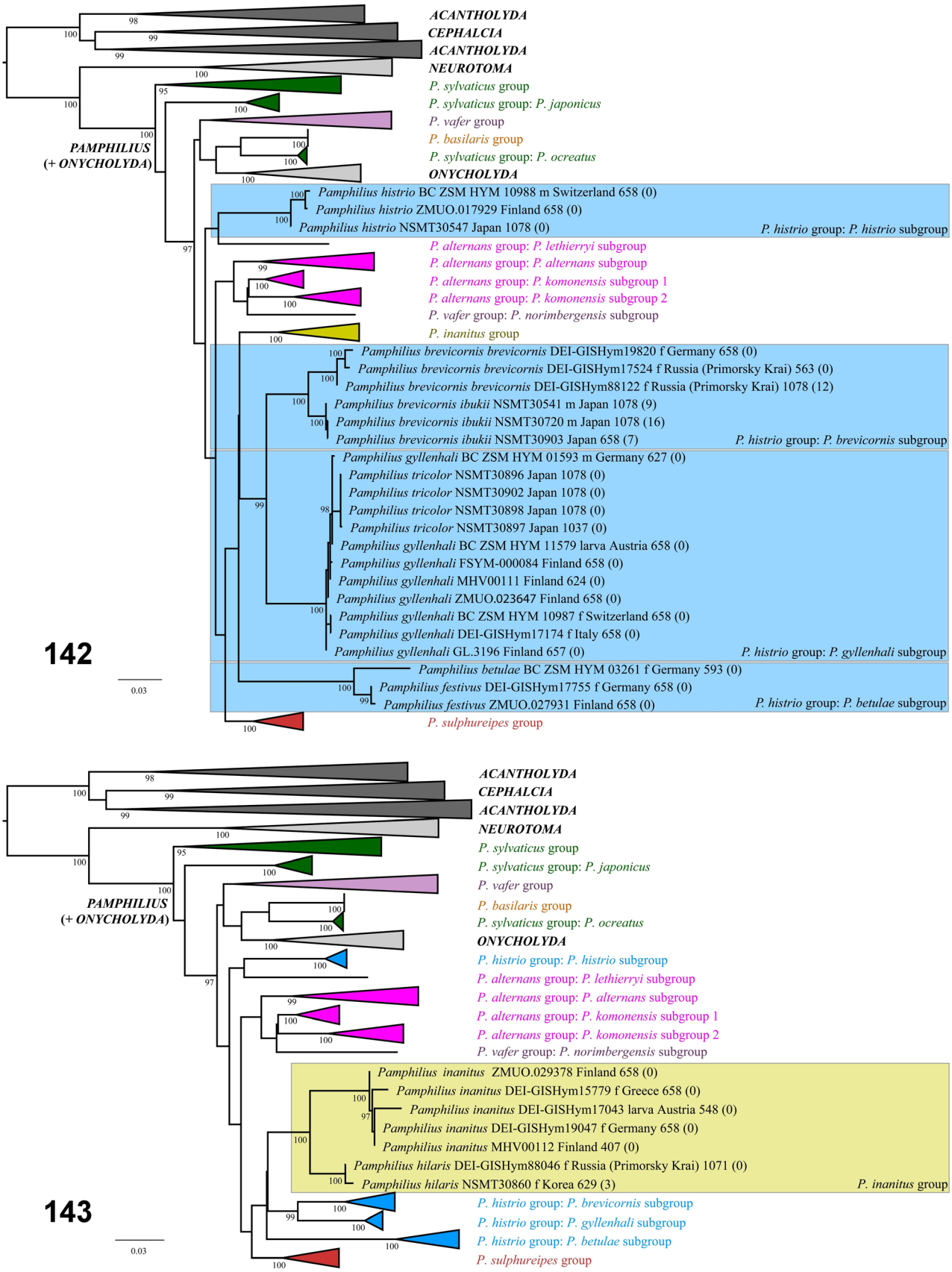
FIGURE 138. Condensed ML tree based on CO1 gene sequences, with details of *Onycholyda*, part 1.



FIGURE 139. Condensed ML tree based on CO1 gene sequences, with details of *Onycholyda*, part 2.



FIGURES 140–141: Condensed ML tree based on CO1 gene sequences, with details of *Pamphilius* **140.** *alternans* group. **141.** *basilaris* group.



FIGURES 142–143. Condensed ML tree based on CO1 gene sequences, with details of *Pamphilius* **142.** *histrio* group. **143.** *inanitus* group.

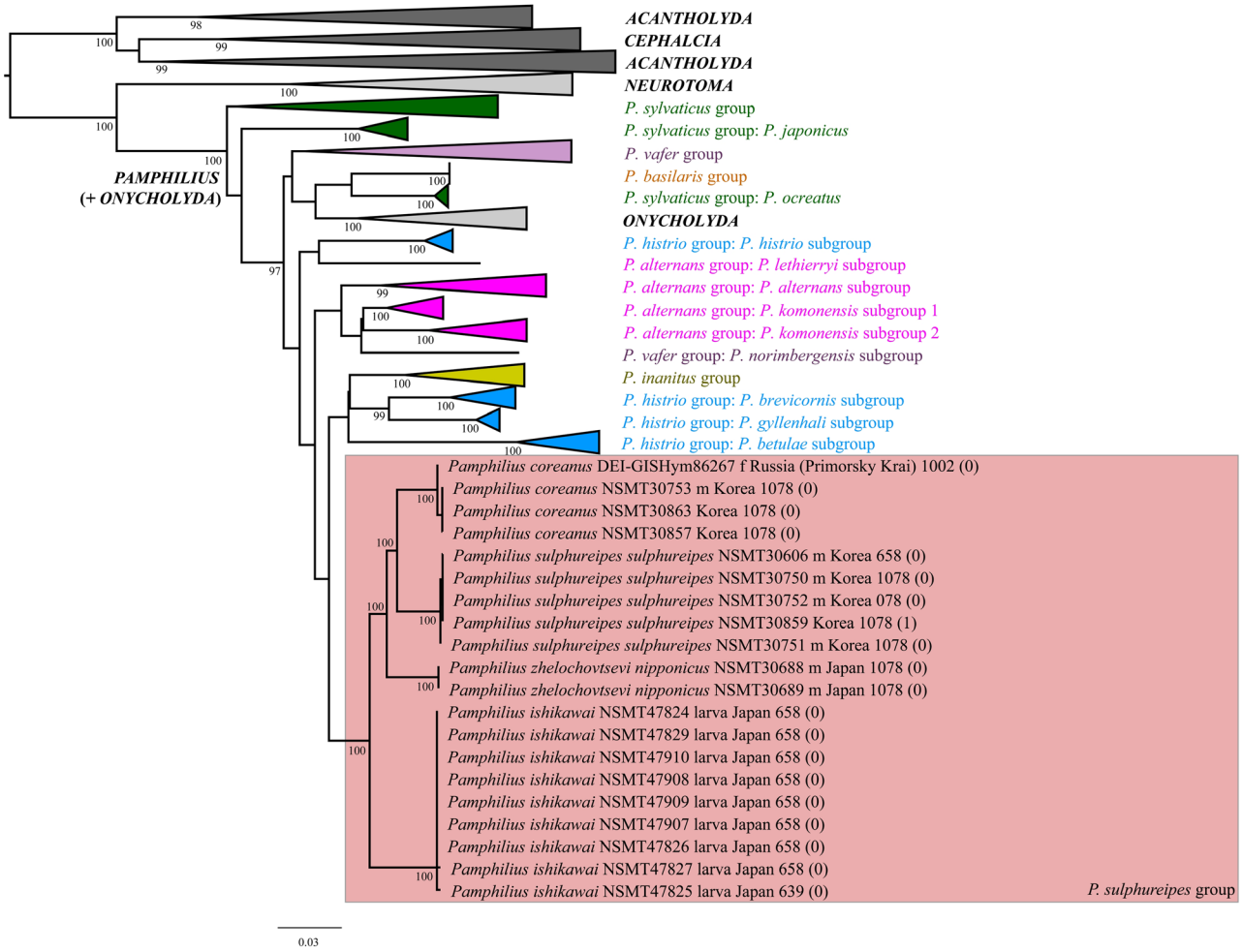


FIGURE 144. Condensed ML tree based on CO1 gene sequences, with details of *Pamphilius sulphureipes* group.



FIGURE 145. Condensed ML tree based on CO1 gene sequences, with details of *Pamphilius sylvaticus* group, part 1.



FIGURE 146. Condensed ML tree based on CO1 gene sequences, with details of *Pamphilius sylvaticus* group, part 2.

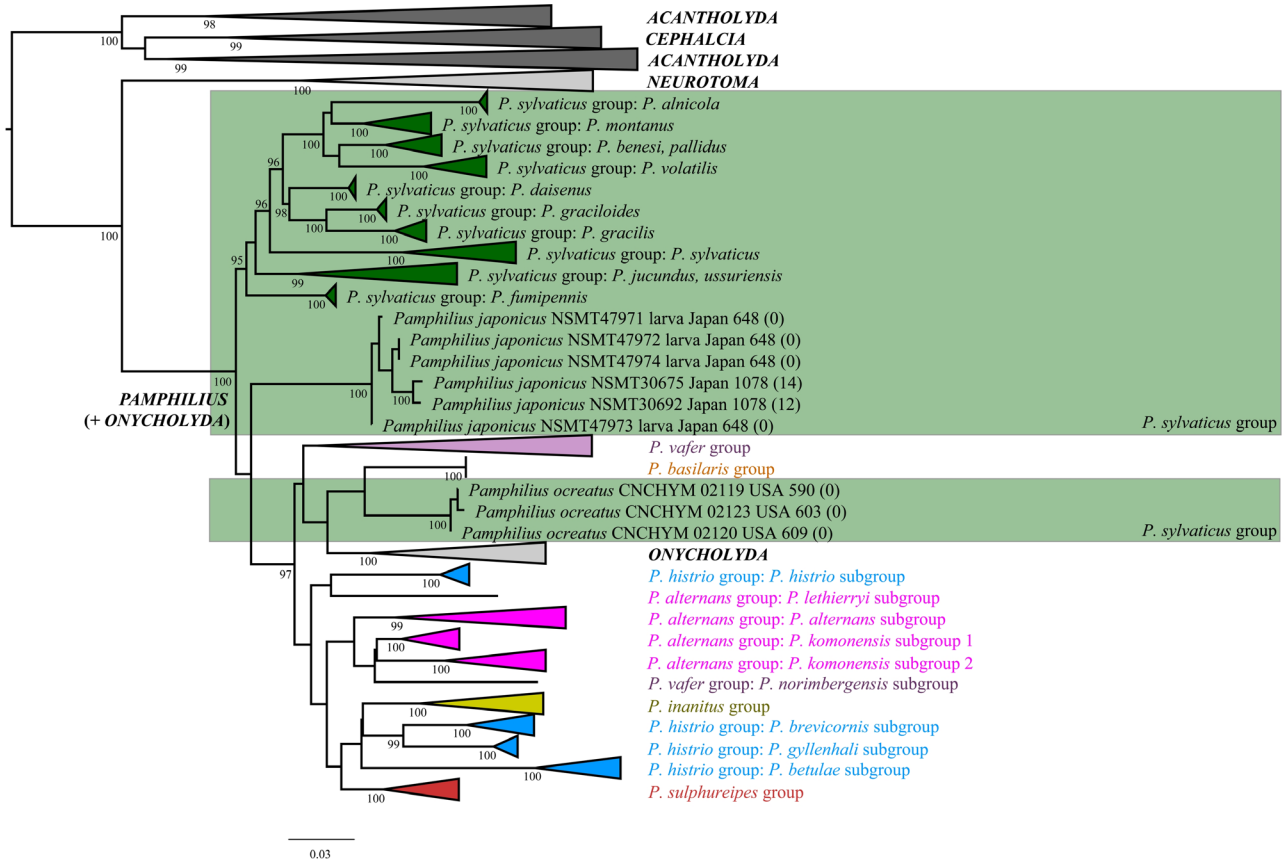


FIGURE 147. Condensed ML tree based on CO1 gene sequences, with details of *Pamphilius sylvaticus* group, part 3.

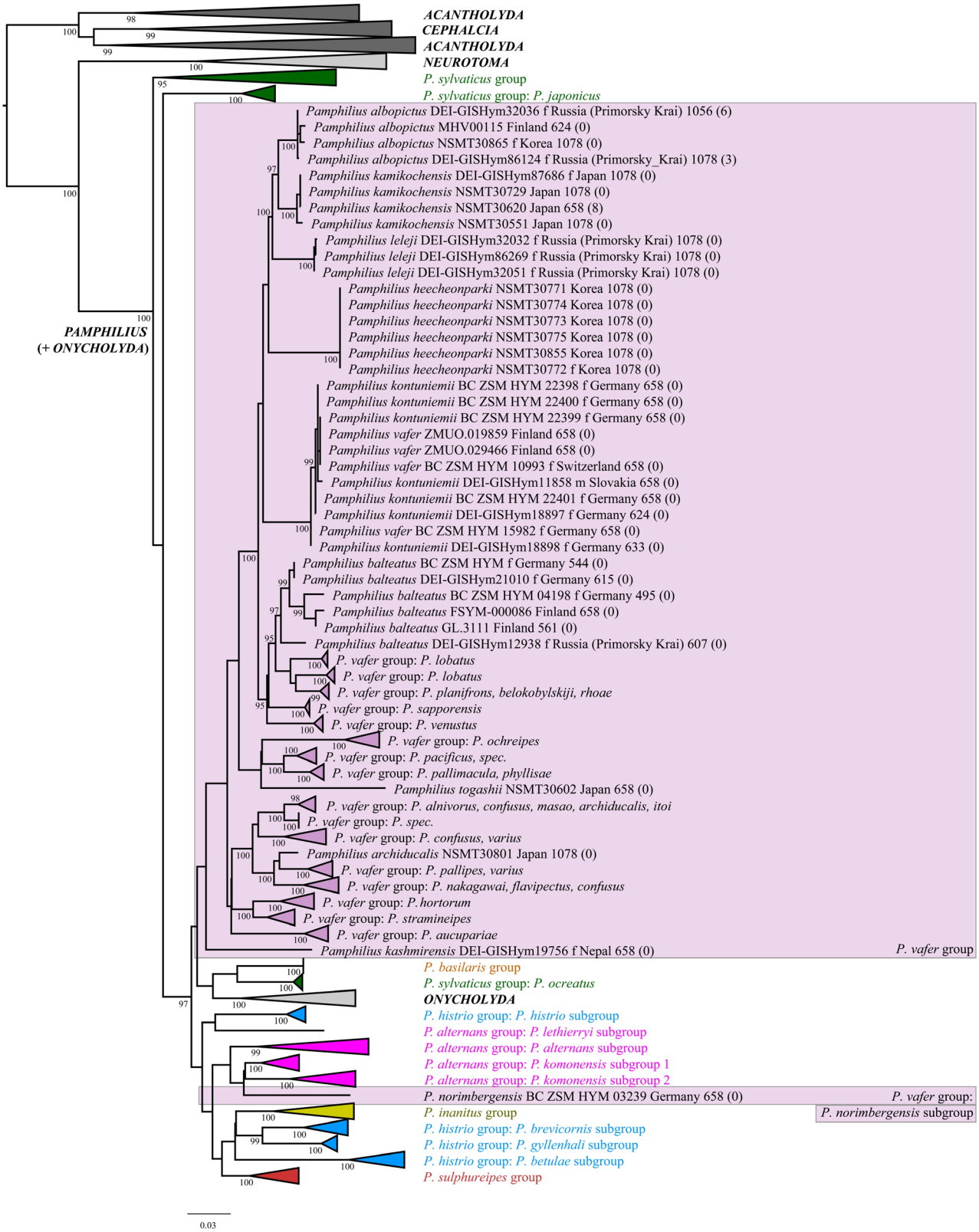


FIGURE 148. Condensed ML tree based on CO1 gene sequences, with details of *Pamphilius vafer* group, part 1.

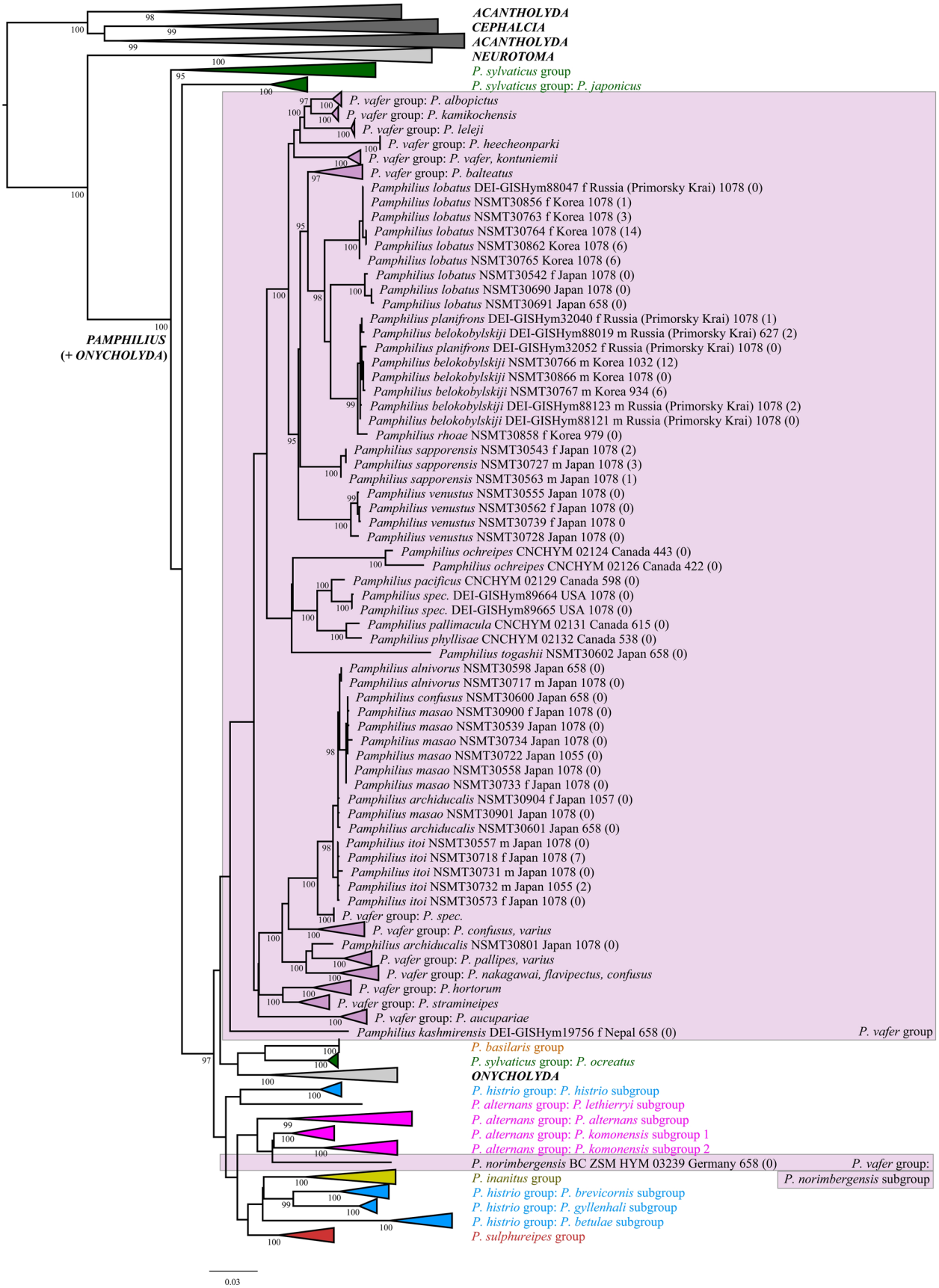


FIGURE 149. Condensed ML tree based on CO1 gene sequences, with details of *Pamphilius vafer* group, part 2.



FIGURE 150. Condensed ML tree based on CO1 gene sequences, with details of *Pamphilius vafer* group, part 3.

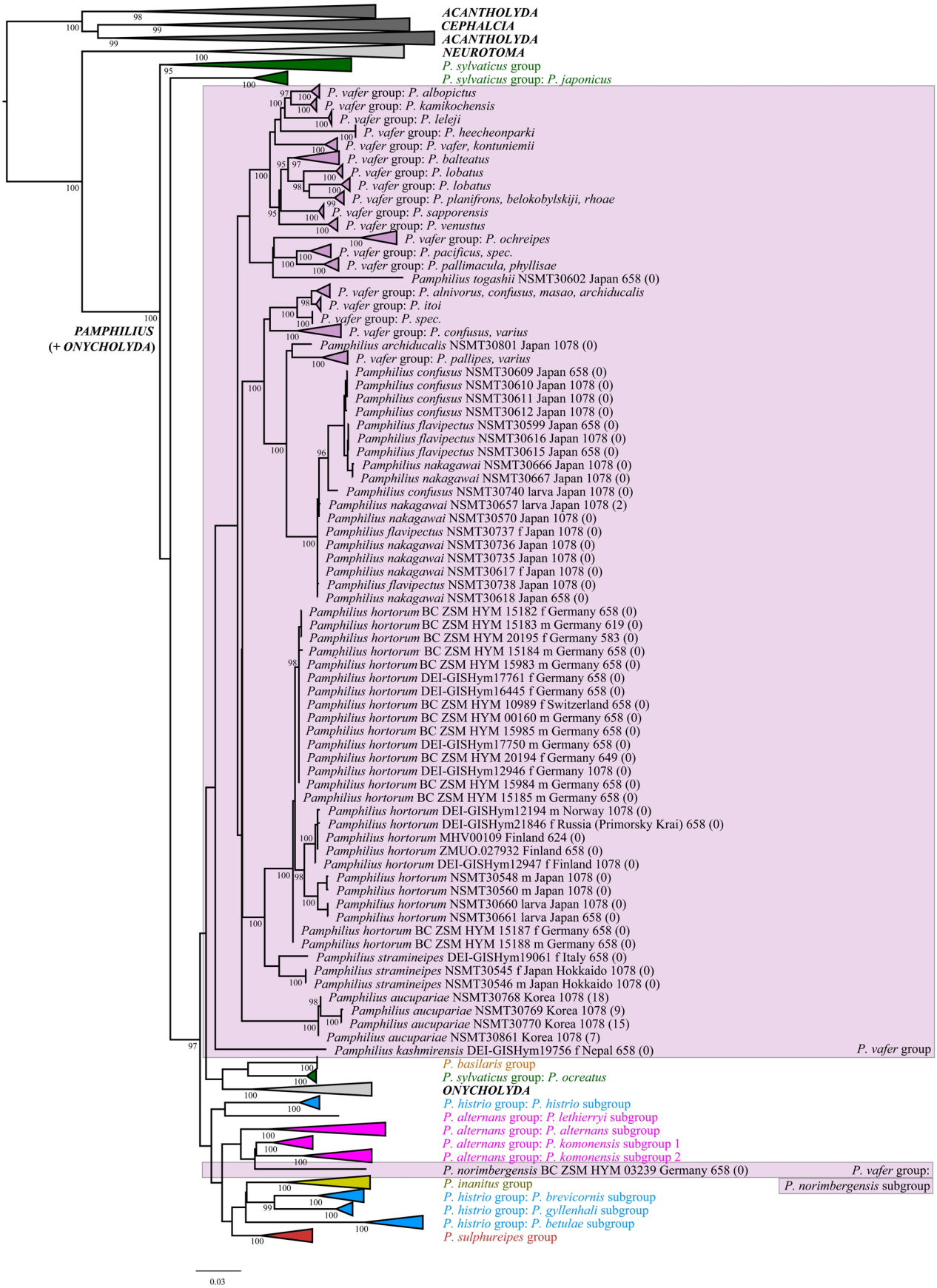


FIGURE 151. Condensed ML tree based on CO1 gene sequences, with details of *Pamphilius vafer* group, part 4.

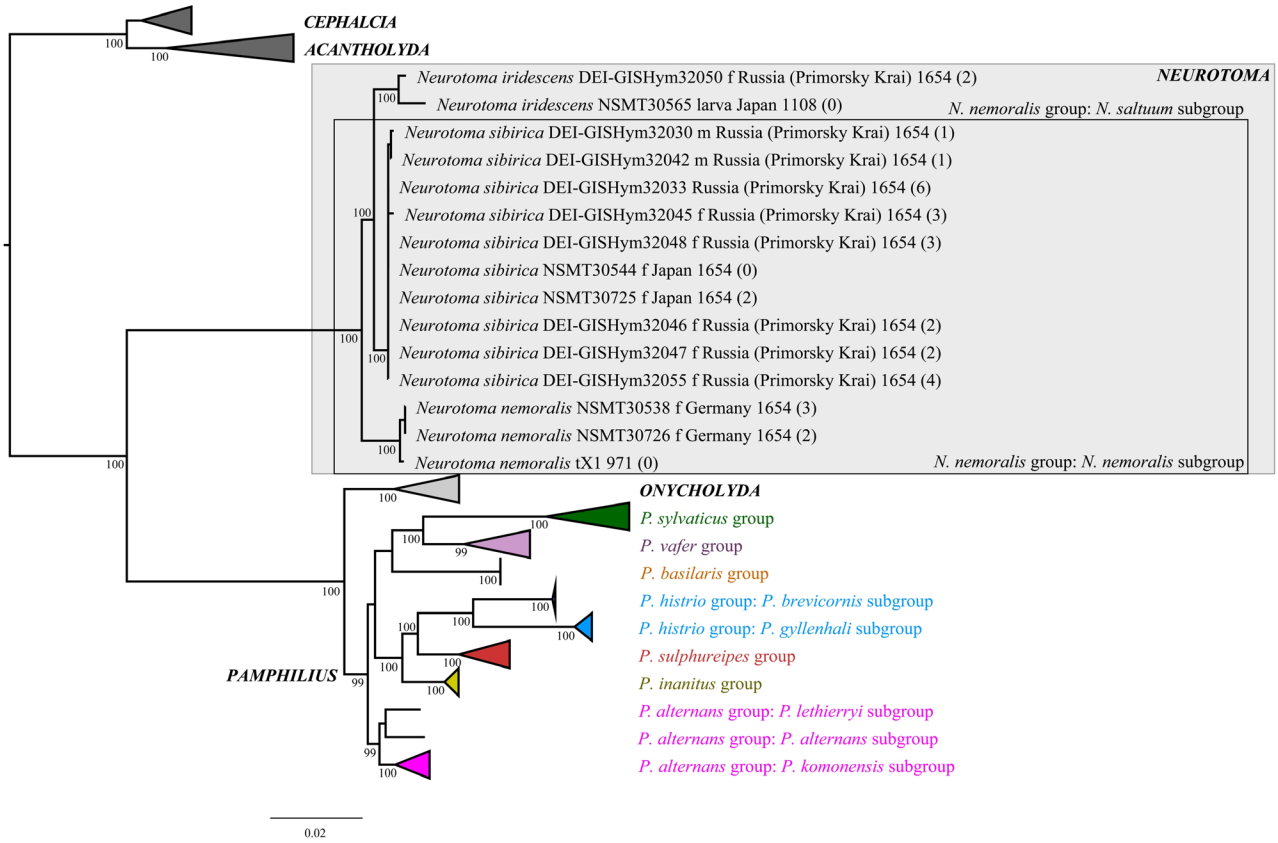


FIGURE 152. Condensed ML tree based on NaK gene sequences, with details of *Neurotoma*.

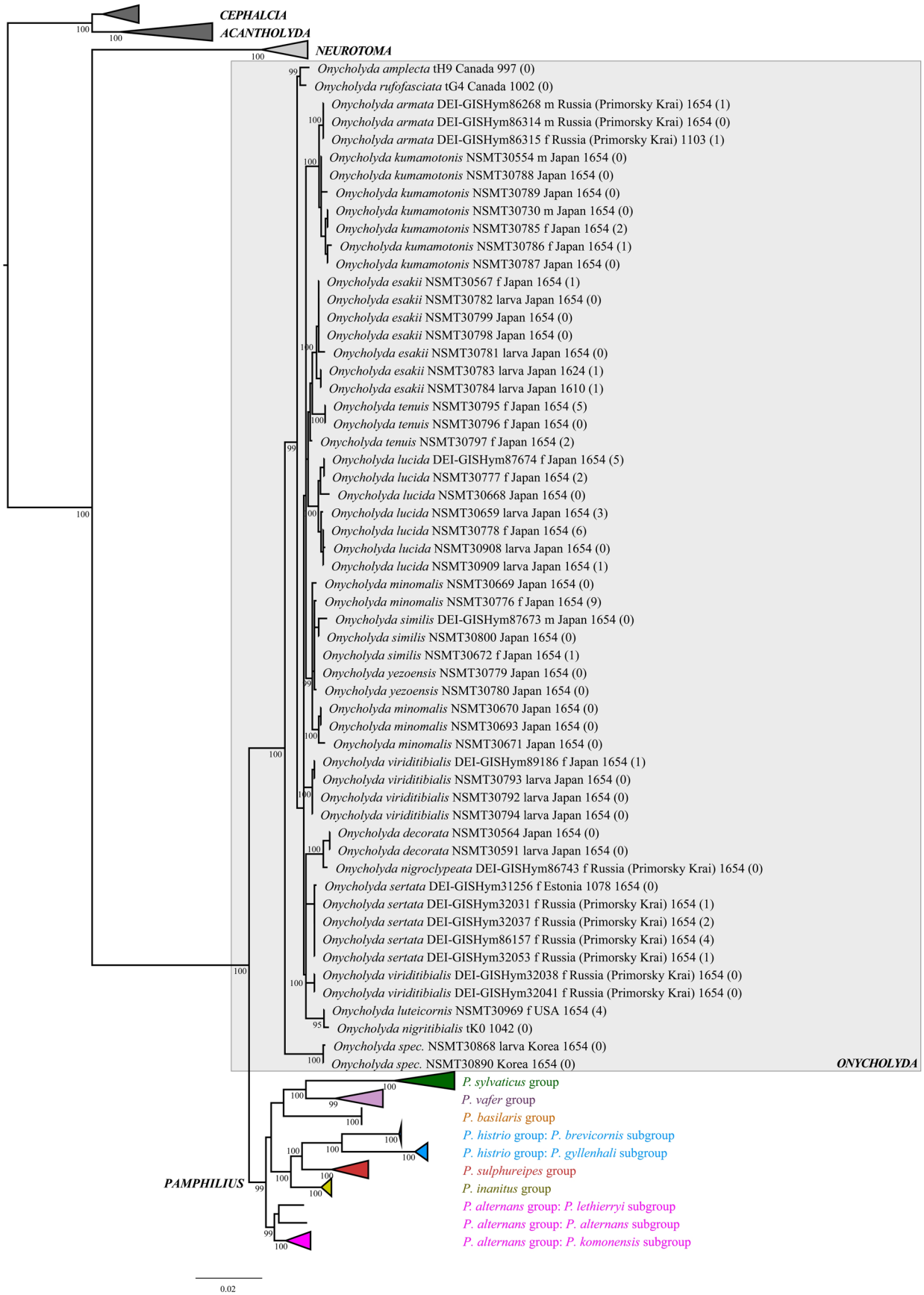
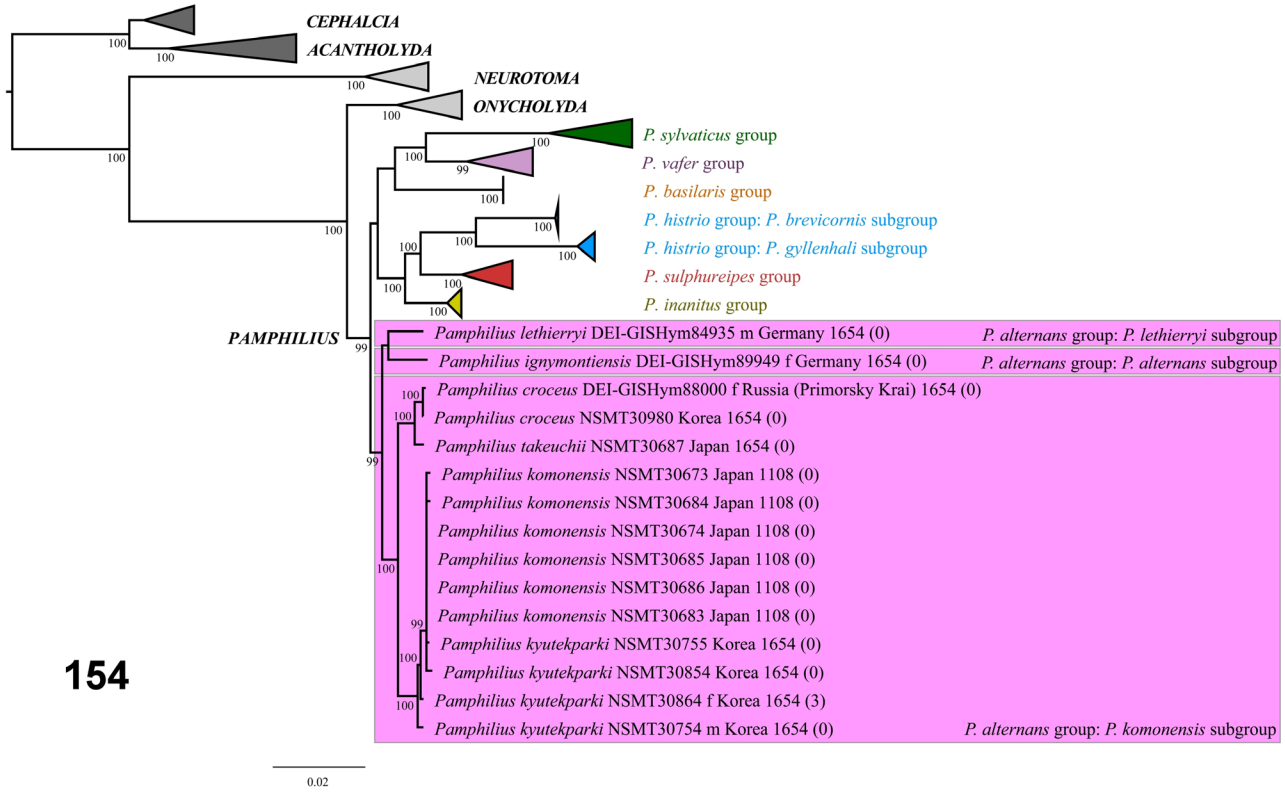
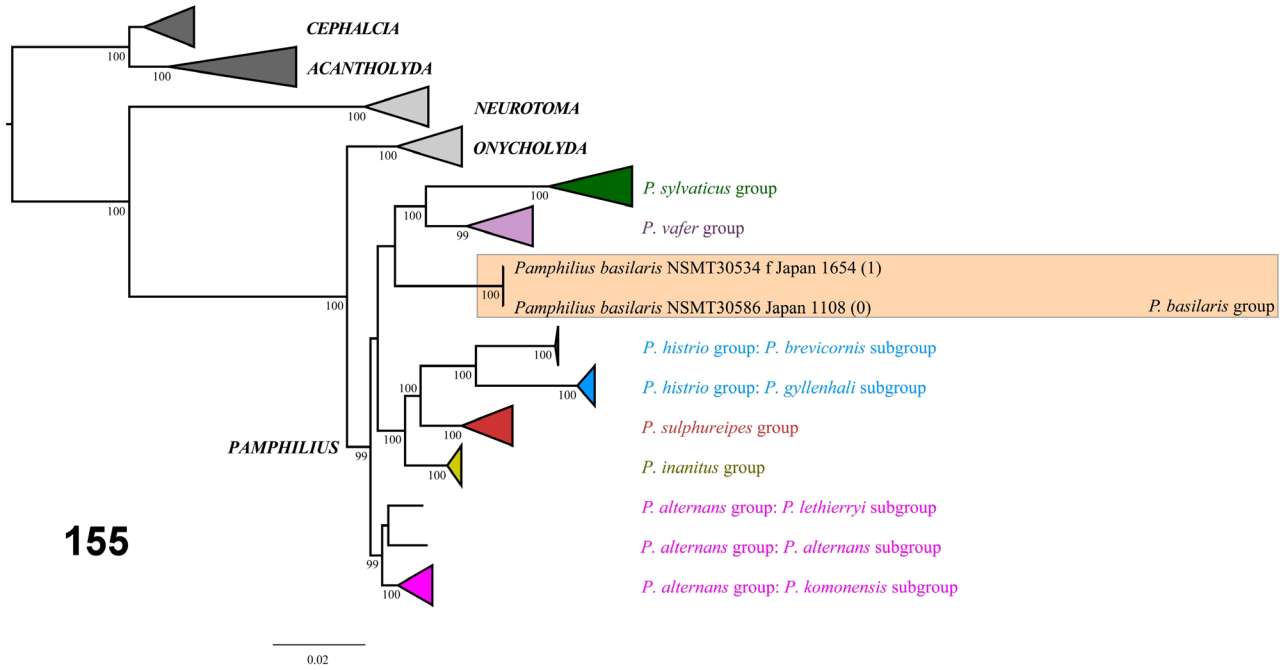
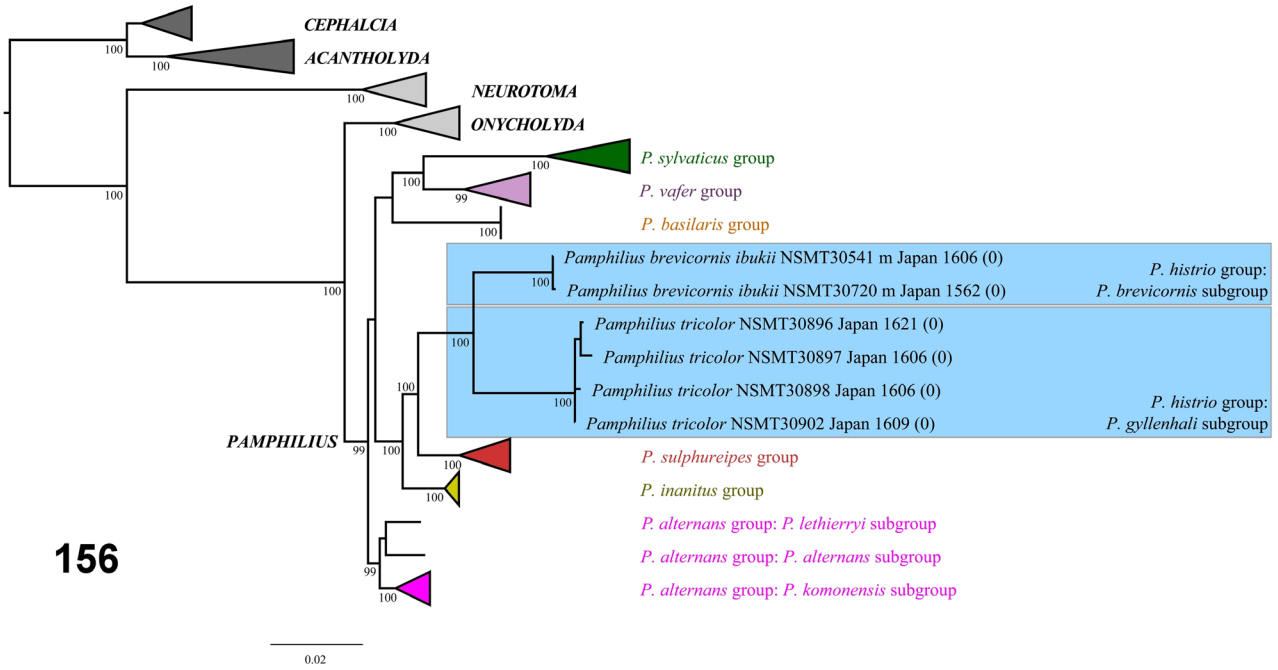


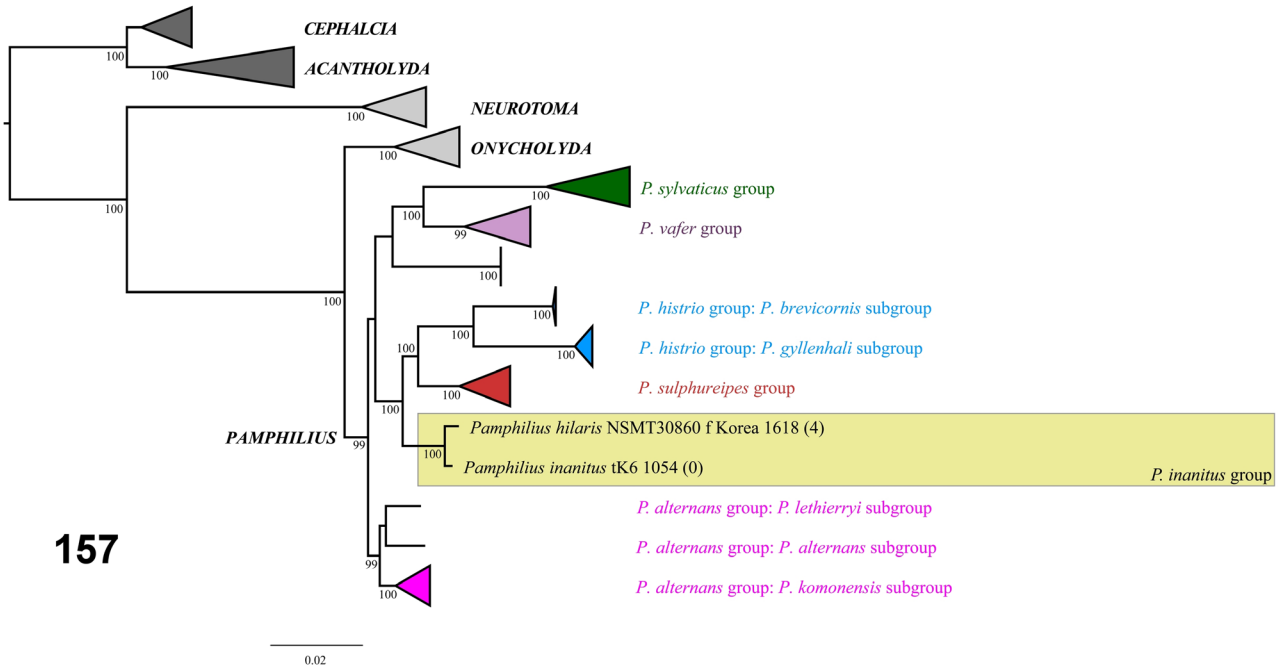
FIGURE 153. Condensed ML tree based on NaK gene sequences, with details of *Onycholyda*.





FIGURES 154–155: Condensed ML tree based on NaK gene sequences, with details of *Pamphilius* **154.** *alternans* group. **155.** *basilaris* group.





FIGURES 156–157: Condensed ML tree based on NaK gene sequences, with details of *Pamphilius* **156.** *histrio* group. **157.** *inanitus* group.

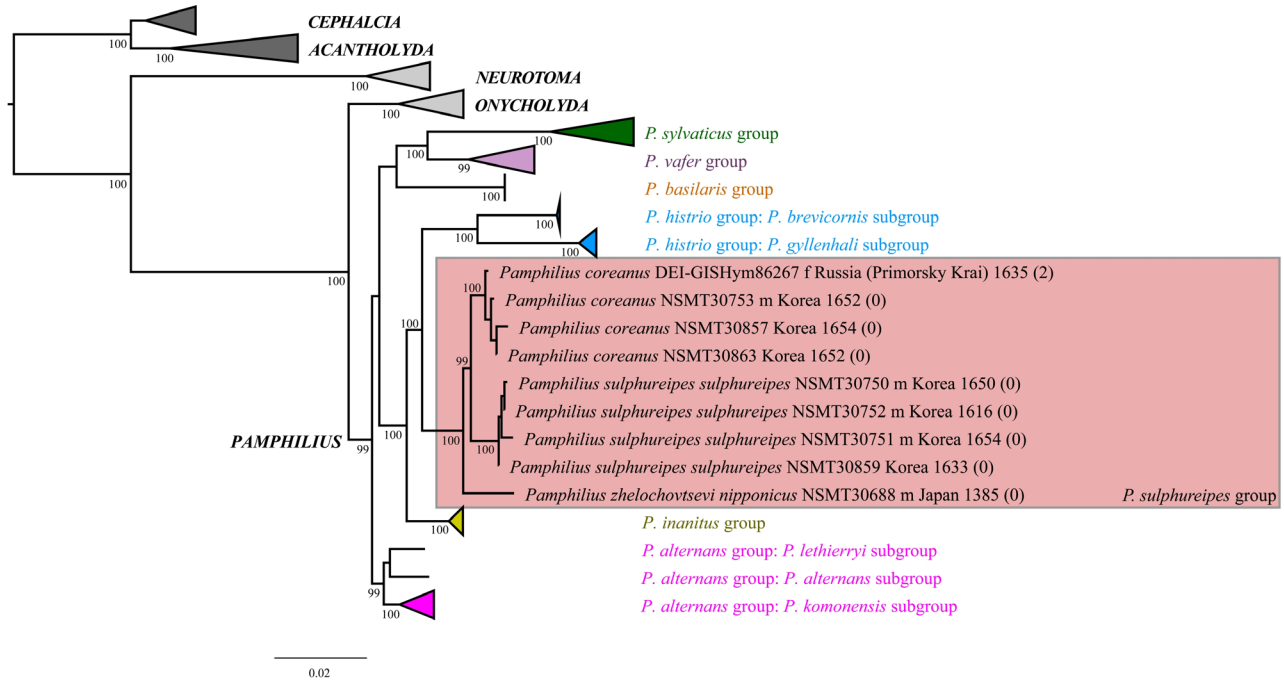


FIGURE 158. Condensed ML tree based on NaK gene sequences, with details of *Pamphilius sulphureipes* group.

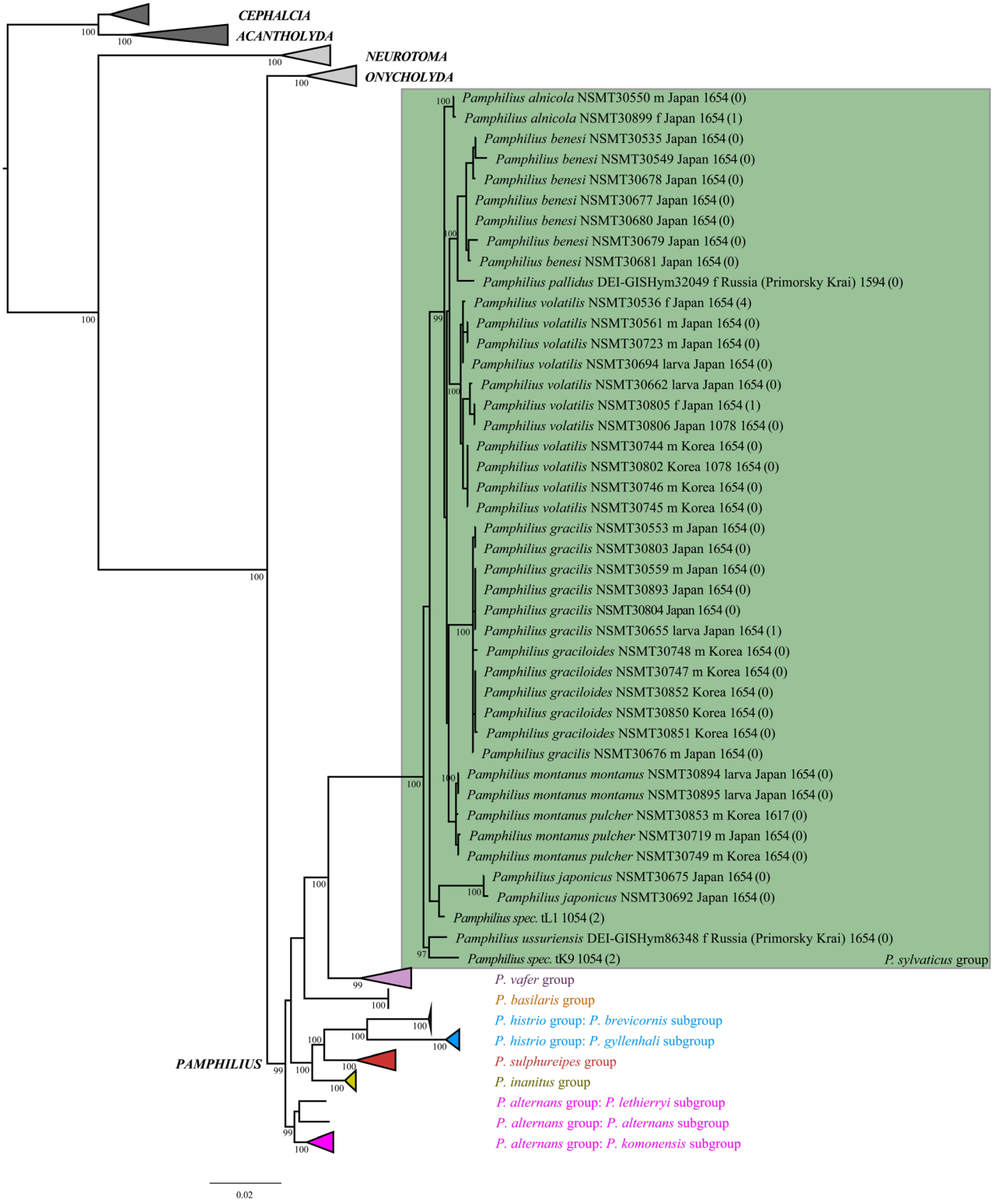


FIGURE 159. Condensed ML tree based on NaK gene sequences, with details of *Pamphilius sylvaticus* group.



FIGURE 160. Condensed ML tree based on NaK gene sequences, with details of *Pamphilius vafer* group, part 1.



FIGURE 161. Condensed ML tree based on NaK gene sequences, with details of *Pamphilius vafer* group, part 2.

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