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Monograph

Review of the genera and subgenera of the subtribe Aspilotina (Hymenoptera, Braconidae, Alysiinae), with a new illustrated key

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Abstract

The genera and subgenera of the subtribe Aspilotina are reviewed. A new illustrated key to all accepted supraspecies taxa is provided. *Grandilota* Fischer, 2002, **stat. nov.** is proposed as subgenus of *Aspilota* Foerster, 1863. *Carinthilota* Fischer, 1975, **syn. nov.** is synonymised with *Alitha* Cameron, 1906, **stat. nov.** and the latter is treated as subgenus of *Dinotrema* Foerster, 1863; *Eudinostigma* Tobias, 1986, **syn. nov.** is considered a synonym of *Dinotrema* Foerster, 1863. Moreover, the new subgenus *Pseudoprosapha* **subgen. nov.** (type species: *Dinostigma stenosoma* van Achterberg, 1988) is described. Additionally, *Synaldotrema* Belokobylskij & Tobias, 2002, **stat. nov.** is treated as a separate genus. The following new combinations are proposed: *Aspilota* (*Aspilota*) *ruficollis* Stelfox & Graham, 1950, **comb. nov.**, *Dinotrema* (*Alitha*) *lada* (Belokobylskij, 1998), **comb. nov.**, *D.* (*A.*) *longipennis* (Cameron, 1906), **comb. nov.**, *D.* (*A.*) *mavka* (Belokobylskij, 1998), **comb. nov.**, *D.* (*A.*) *parapsidalis* (Fischer, 1975), **comb. nov.**, *D.* (*A.*) *vechti* (van Achterberg, 1988), **comb. nov.**, *Dinotrema* (*Dinotrema*) *alox* (van Achterberg, 1988), **comb. nov.**, *D.* (*D.*) *entabeniense* (Fischer, 2009), **comb. nov.**, *D.* (*D.*) *latum* (Chen & Wu, 1994), **comb. nov.**, *D.* (*D.*) *planiceps* (Fischer, Tormos & Pardo, 2006), **comb. nov.**, *D.* (*D.*) *subpulvinatum* (Fischer, 2009), **comb. nov.**, *D.* (*Pseudoprosapha*) *stenosoma* (van Achterberg, 1988), **comb. nov.**, *D.* (*Synaldis*) *bienesae* (Fischer, Tormos & Pardo, 2006), **comb. nov.**, *D.* (*S.*) *fischeri* (Tobias, 1986), **comb. nov.**, *D.* (*S.*) *latistigma* (Fischer, 1962), **comb. nov.**, *D.* (*S.*) *planiceps* (Fischer, Tormos & Pardo, 2006), **comb. nov.**, *D.* (*Synaldis*) *cespitator* (Belokobylskij, 2004), **comb. nov.**, *D.* (*S.*) *perfidum* (Fischer, 1970), **comb. nov.**, *D.* (*S.*) *trematosum* (Fischer, 1967), **comb. nov.** and *Panerema fulvicornis* (Haliday, 1838), **comb. nov.**

Key words: Alysiini, *Aspilota* group, illustrated key, parasitoid of Diptera, Phoridae, re-descriptions

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Introduction

The parasitoid wasps of the subtribe Aspilotina Belokobyskij & Tobias, 2002 are the largest aggregation within the braconid tribe Alysiini (Hymenoptera: Braconidae: Alysiinae) with approximately 850 valid species worldwide (Yu et al.

2016). Specimens of this group are nearly always small, with a body length of 1.0–3.0 mm, and the body colour is predominantly dark brown to black.

Despite host-parasitoid relationships in the Alysiini are yet insufficiently known, already 29 families of cyclorrhaphous Diptera have been listed in the literature as their hosts. Most of them belong to the families Agromyzidae, Anthomyiidae, Calliphoridae, Drosophilidae, Muscidae, Phoridae, Sarcophagidae, and Tephritidae (Yu et al. 2016; Kostromina et al. 2016; Peris-Felipo and Belokobylskij 2018a), whose biological preferences vary from phytophagous to saprophagous and necrophagous. The members of the subtribe Aspilotina predominantly develop into larvae of the dipteran family Phoridae or humpbacked flies, which mainly feed on decaying organic matter (van Achterberg 1988). Other host records (e.g., of Agromyzidae and Drosophilidae) are mostly old and need reconfirmation, since Phoridae also consume insects from decaying organic matter.

Over the years, the genera included in this subtribe have changed statuses. For example, van Achterberg (1988) included the type species of *Synaldis* Foerster, 1863 in the genus *Dinotrema* Foerster, 1863. However, later publications by Fischer (1993a, 1993b), Belokobylskij (2002, 2004a, 2004b), Tobias (2003a, 2003b, 2004, 2006), and Peris-Felipo (Peris-Felipo et al. 2014a, 2014b; Peris-Felipo and Belokobylskij 2017) continued to consider *Synaldis* as a taxonomically valid genus separated from *Dinotrema* due to rather a stable diagnostic character, the complete absence of the vein 2-SR in fore wing and with the vein r not angled with vein 3-SR, resulting in a gently curved or straight vein. Groups based on the reduction of this vein (which is a wide-spread phenomenon in the subtribe Aspilotina) are likely derived lineages within a genus, and there is even no proof that all species included in e.g., *Synaldis* sensu stricto are belonging to the same lineage. Recently, Zhu et al. (2017) included *Synaldis* sensu stricto as subgenus of *Dinotrema* and synonymised *Adelphenaldis* Fischer, 2003 and *Regetus* Papp, 1999 with *Eusynaldis* Zaykov & Fischer, 1982, including the latter as a subgenus in *Aspilota* Foerster, 1863. In this paper, we review the generic status of the taxa within the subtribe Aspilotina and compile a new illustrated identification key to all accepted genera and subgenera.

Materials and methods

The revisions of the type species of the *Aspilota* group genera (= subtribe Aspilotina) carried out during many years and checking a large number of *Aspilota*, *Dinotrema*, and *Orthostigma* species allows us to recognise the main diagnosis characters to classify the almost 850 valid species worldwide. These characters are: paraclypeal fovea remained removed from or reaching the border of the eye; mandible without or sometimes with transverse carina; furrow between antennal socket and eye absent or present; notauli mainly absent in dorsal view or sometimes well developed; scutellum without or with transverse crenulated depression; position of the origin of the vein r; pterostigma almost not differentiated, very narrow, or sometimes well isolated and wide; vein 2-SR of fore wing present or absent; subbasal cell of hind wing distally closed or open; first subdiscal cell of fore

wing distally close or open; main cells of the hind wing closed or open; fore femur narrow and simple or wide and with tooth; first metasomal tergite with or without dorsope; second metasomal tergite entirely smooth or rarely sculptured basally; hypopygium not retracted under distal metasomal segments or sometimes strongly retracted.

For the terminology of morphological features, sculpture, and measurements (including for mandibles) see Peris-Felipo et al. (2014a); for wing venation nomenclature see van Achterberg (1993); for measurements of the marginal cell see Peris-Felipo and Belokobylskij (2017). The material was imaged using a Digital Keyence® VHX-2000 and Adobe Photoshop® imaging system.

The specimens examined are preserved in the entomological collections at the institutions listed below:

ANIC	Australian National Insect Collection (Canberra, Australia)
BMNH	The Natural History Museum (London, U.K.)
ENV	Entomological Collection of the University of Valencia (Valencia, Spain)
HNHM	Hungarian Natural History Museum (Budapest, Hungary)
MNHN	Museum National d'Histoire Naturelle (Paris, France)
NHMW	Naturhistorisches Museum (Vienna, Austria)
NHMB	Museum für Naturkunde (Berlin, Germany)
NHMD	Natural History Museum of Denmark (Copenhagen, Denmark)
NMA	Naturhistorisk Museum Aarhus (Aarhus, Denmark)
NMNH	Smithsonian National Museum of Natural History (Washington, U.S.A.)
PFEC	F.J. Peris-Felipo Private Entomological Collection (Basel, Switzerland)
QMBA	Queensland Museum (Brisbane, Australia)
RMNH	Naturalis Biodiversity Center (Leiden, The Netherlands)
ZISP	Zoological Institute of the Russian Academy of Sciences (St Petersburg, Russia)
ZSSM	Zoologische Staatssammlung München (München, Germany).

To establish the position and relationship between genera and subgenera, a multivariate statistical approach was used to build the cladogram (Table 1). Specifically, as the list of characters, plesiomorphic and apomorphic states, are attributes or qualitative variables, we performed a multiple correspondence analysis (MCA) (Greenacre 2017) to outline the relationship between the 17 characters. MCA builds a new set of latent variables (scores) which summarises the contained information in the variables and represent them in a geometric space. The analysis was conducted using R v. 4.4.1, with the FactoMineR (v. 2.11) and factoextra (v. 1.0.7) packages for MCA implementation and visualisation. We selected 10 scores, which accounted for at least 90% of the retained variability, effectively reducing the dimensionality from the original 17 plesiomorphic attributes to ten summary scores. Subsequently, we performed hierarchical clustering on these selected scores using Ward's procedure (Husson 2017), implemented through the cluster package (v. 2.1.6) in R. This clustering approach allowed us to identify groups of genera that share common characters. The combination of MCA and hierarchical clustering provided a robust framework for constructing the cladogram based on the shared attributes among the studied genera.

Table 1. The characters used for the cladogram construction.

Character	Plesiomorphic (0)	Apomorphic (1)
Furrow between antennal socket and eye	absent	present
Paraclypeal fovea	small to medium-sized	large and reaching eye border
Mandible	without transverse carina	with distinct submedial transverse carina
First flagellar segment	longer than second segment	equal to or shorter than second segment
Notauli	complete	posterior half absent
Scutellum	without depression posteriorly	with transverse depression posteriorly
Pterostigma	very slender	secondary widened
Vein r of fore wing originated	from the basal quarter of pterostigma	far from the base of pterostigma, arising near its middle
Subbasal cell of hind wing distally	closed	open
First subdiscal cell of fore wing distally	closed	open
Vein 2-SR of fore wing	present	absent
Hind wing cells	closed	open
Fore femur	simple without tooth	with wide ventral tooth
First tergite of metasoma	without dorsope	with dorsope
Hypopygium of metasoma	not retracted anteriorly under posterior tergites	distinctly retracted anteriorly under posterior tergites
Second tergite	smooth	sculptured
Clypeus	not protruding	protruding

Taxonomic part

Class Hexapoda Blainville, 1816
Order Hymenoptera Linnaeus, 1758
Family Braconidae Nees, 1811
Subfamily Alysiinae Leach, 1815
Tribe Alysiini Leach, 1815
Subtribe Aspilotina Belokobylskij & Tobias, 2002

The relation between the diagnostic characters has allowed the construction of a cladogram of the relationships in the Aspilotina (Fig. 1) in whose two main different linages are clearly distinguished from the beginning: *Aspilota* group and *Orthostigma* group. The *Aspilota* group linage consists of eight genera: *Apronopa* van Achterberg, 1980, *Aspilota* Foerster, 1863, *Dinostigma* Fischer, 1966, *Dinotrema* Foerster, 1863, *Leptotrema* van Achterberg, 1988, *Lysodinotrema* Fischer, 1995, *Panerema* Foerster, 1863, and *Synaldotrema* Belokobylskij & Tobias, 2002, stat. nov. Moreover, the genus *Aspilota* is formed by the subgenera *Aspilota* Foerster, 1863, sensu stricto, *Eusynaldis* Zaykov & Fischer, 1982, and *Grandilota* Fischer, 2002, stat. nov., while the genus *Dinotrema* contains the subgenera *Alitha* Cameron, 1906, stat. nov., *Dinotrema* Foerster, 1863 (sensu stricto), *Prosapha* Foerster, 1863, *Pseudoprosapha* subgen. nov., and *Synaldis* Foerster, 1863.

Orthostigma group contains three genera: *Cubitalostigma* Fischer, 1998, *Neorthostigma* Belokobylskij, 1998, and *Orthostigma* Ratzeburg, 1844. The latter is made up of four subgenera: *Africostigma* Fischer, 1995, *Orthostigma* Ratzeburg, 1844, sensu stricto, *Patrisaspilota* Fischer, 1995, and *Whartonstigma* Peris-Felipo, 2020. The distances between genera/subgenera generated from the multivariate statistical approach of the diagnostic characters are provided in Appendix 1.

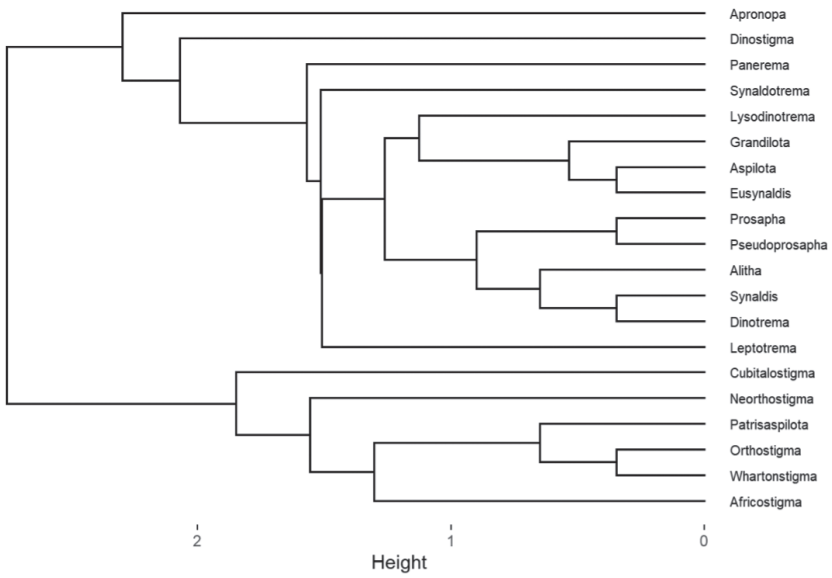

Figure 1. Subtribe Aspilotina cladogram based on the diagnostic characters from Table 1.

Synopsis of the genera and subgenera of the subtribe Aspilotina

Aspilota group

Genus *Apronopa* van Achterberg, 1980
Genus *Aspilota* Foerster, 1863
subgenus *Aspilota* Foerster, 1863, sensu stricto
subgenus *Eusynaldis* Zaykov & Fischer, 1982 (= *Regetus* Papp, 1999; *Adelphenaldis* Fischer, 2003)
subgenus *Grandilota* Fischer, 2002, stat. nov.
Genus *Dinostigma* Fischer, 1966
Genus *Dinotrema* Foerster, 1863 (Syn.: *Pterusa* Fischer, 1958; *Eudinostigma* Tobias, 1986, syn. nov.)
subgenus *Alitha* Cameron, 1906, stat. nov. (= *Carinthilota* Fischer, 1975, syn. nov.)
subgenus *Dinotrema* Foerster, 1863, sensu stricto
subgenus *Prosapha* Foerster, 1863
subgenus *Pseudoprosapha* subgen. nov.
subgenus *Synaldis* Foerster, 1863
Genus *Leptotrema* van Achterberg, 1988
Genus *Lysodinotrema* Fischer, 1995
Genus *Panerema* Foerster, 1863
Genus *Synaldotrema* Belokobylskij & Tobias, 2002, stat. nov.

Orthostigma group

Genus *Cubitalostigma* Fischer, 1998
Genus *Neorthostigma* Belokobylskij, 1998
Genus *Orthostigma* Ratzeburg, 1844
subgenus *Africostigma* Fischer, 1995
subgenus *Orthostigma* Ratzeburg, 1844, sensu stricto
subgenus *Patrisaspilota* Fischer, 1995
subgenus *Whartonstigma* Peris-Felipo, 2020

Subtribe Aspilotina Belokobyskij & Tobias, 2002

Aspilotina Belokobyskij and Tobias 2002: 2.

Aspilota group

Morphological diagnosis. See van Achterberg (1988).

Genus *Apronopa* van Achterberg, 1980

Apronopa van Achterberg, 1980: 75; Tobias 1986: 195; Fischer 1991: 8; Wharton 1994: 640; Belokobylskij 1998a: 169, 217; Belokobylskij and Tobias 2007: 10; Yu et al. 2016; Peris-Felipo and Belokobylskij 2018b: 144.

Type species. *Apronopa haeselbarthi* van Achterberg, 1980, by original designation (Figs 2, 3).

Material examined. ***Holotype*** (*Apronopa haeselbarthi*) Germany: • ♀, Dransfeld, B/L 2.vi.1966 (Haeselbarth leg.) (ZSSM). ***Paratypes*** (*Apronopa haeselbarthi*) Germany: • 1 ♀, 1 ♂, Schotten, Hessen, Fi., Streu, v.1967 (Haeselbarth leg.) (♀ in RMNH, ♂ in ZSSM).

Diagnosis. Mandible small, simple, robust, tridentate. Paraclypeal fovea short, remaining far from inner margin of eyes. Mesoscutum without medio-posterior pit; notauli absent in posterior half of mesoscutum; precoxal sulcus always present; propodeum smooth or with different types of sculpture and sometimes with longitudinal or transverse carinae. Marginal cell of fore wing never shortened; vein r originating approximately from basal quarter of pterostigma; vein 2-SR always present and distinctly sclerotized; veins m-cu and cu-a distinctly postfurcal; first subdiscal cell always closed postero-apically by CU1a vein. Metasoma of ♀ more or less distinctly compressed laterally. First metasomal tergite without dorsope; second tergite often longitudinally striate medially. Ovipositor sheath not longer than metasoma.

Remarks. This is a small genus with only three described species exclusively from the Palaearctic region (two of these species have an East Palaearctic distribution). Unfortunately, there is no data about its biology. *Apronopa* is characterised by three distinct diagnostic characters (van Achterberg 1980; Peris-Felipo and Belokobylskij 2018b): the dorsope of the first metasomal tergite are absent, the ovipositor has a distinct dorsal nodus subapically and the second metasomal tergite is sculptured basally (except in *A. levis* Papp, 2007). The combination of these features is unknown in other Aspilotina and supports well the separate generic status of this taxon.

Genus *Aspilota* Foerster, 1863

Figs 4–9

Aspilota Foerster, 1863: 268; Shenefelt 1974: 966; Wharton 1980: 84; van Achterberg 1988: 9; Chen and Wu 1994: 49; Belokobylskij 1998a: 218; Wharton 2002: 34; Yu et al. 2016.

Dipiesta Foerster, 1863: 268 (synonymised with *Aspilota* Foerster by Szépligeti (1904)).

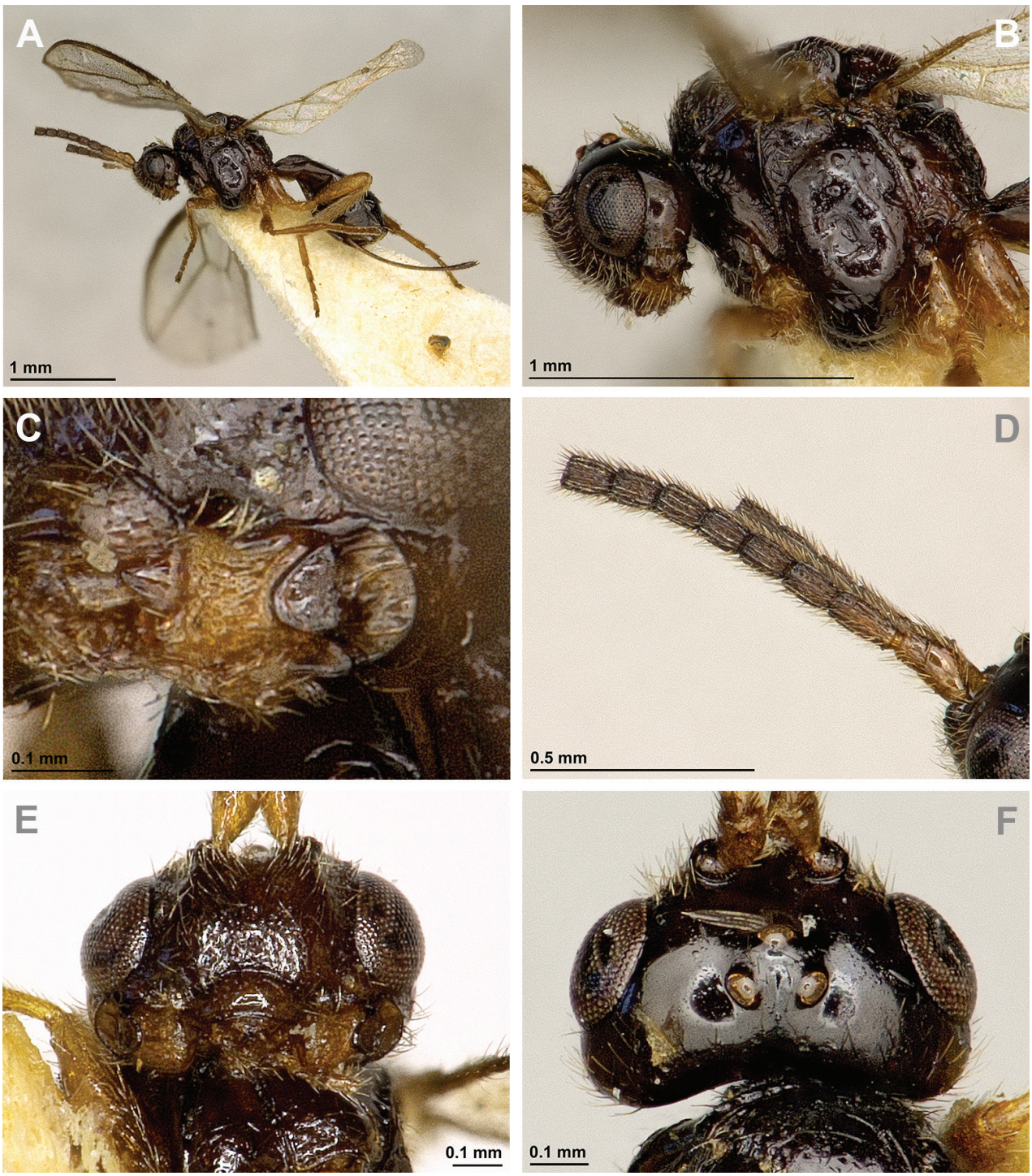

Figure 2. *Apronopa haeselbarthi* van Achterberg, 1980 (holotype, female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head, dorsal view.

Eusynaldis Zaykov & Fischer, 1982: 70; van Achterberg 1988: 9 (as synonym of *Aspilota* Foerster); Zhu et al. 2017: 19; Peris-Felipo and Belokobylskij 2019: 21.

Regetus Papp, 1999: 391; Fischer 2002: 101; Zhu et al. 2017: 19 (as synonym of *Aspilota* Foerster).

Grandilota Fischer, 2002: 103; Yu et al. 2016.

Adelphenaldis Fischer, 2003: 41; Peris-Felipo et al. 2012: 287; 2014b: 571; Yu et al. 2016; Zhu et al. 2017: 19 (as synonym of *Aspilota* Foerster).

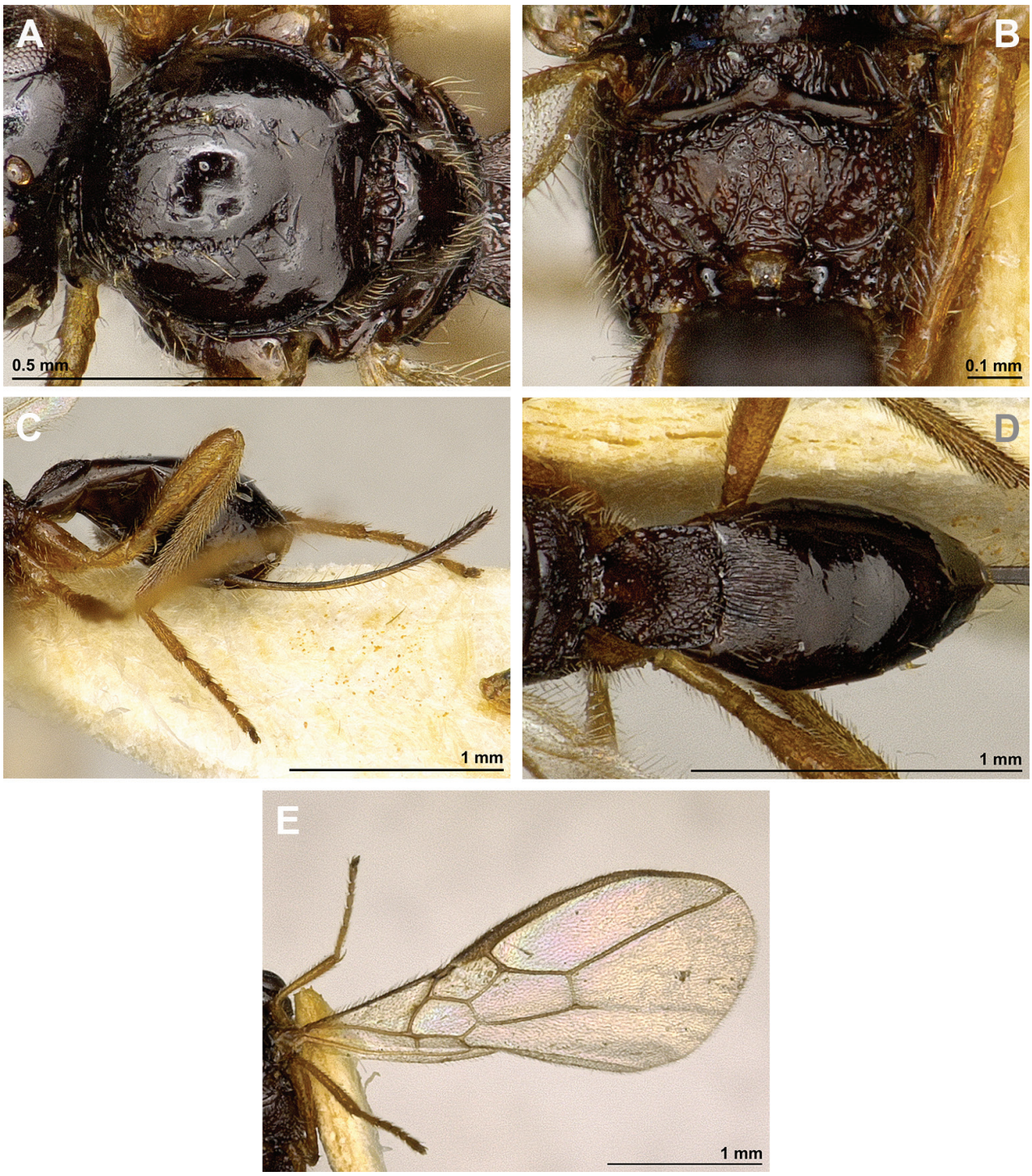

Figure 3. *Apronopa haeselbarthi* van Achterberg, 1980 (holotype, female) **A** mesonotum, dorsal view **B** propodeum **C** legs, metasoma and ovipositor, lateral view **D** metasomal tergites, dorsal view **D** fore wing.

Type species. *Alysia ruficornis* Nees von Esenbeck, 1834, by monotypy.

Diagnosis. Mandible small, simple, tridentate, often with upper (first) tooth diminished with respect to lower (third) tooth. Paraclypeal fovea large, reaching inner margin of eyes. Mesoscutum with or without medio-posterior pit; notauli present only in anterior part of mesoscutum; precoxal sulcus almost always present; propodeum smooth or more common with different types of sculpture and sometimes with longitudinal and/or transverse carinae, rarely forming areas.

In fore wing, marginal cell never shortened; vein r originating from basal quarter of pterostigma; vein 2-SR often present and usually distinctly sclerotised but absent in subgenus *Eusynaldis*; veins m-cu and cu-a postfurcal; first subdiscal cell always closed postero-apically by vein CU1a. In hind wing, subbasal cell usually closed. Metasoma of ♀ more or less distinctly compressed laterally; second tergite always smooth. Ovipositor sheath usually not longer than metasoma.

Remarks. Members of the genus *Aspilota* are frequently encountered as they are one of the most common genera among Alysiini wasps. It is mainly distributed in forested and humid areas of the Holarctic region and only a few species have been already recorded from other zoogeographic regions. This genus is undersampled in the tropics where their main hosts (Phoridae) have the greatest diversity.

Aspilota species are koinobiont endoparasitoids of larvae, mainly of the family Phoridae (Diptera). Previous reports established *Aspilota* as parasitoid of the families Anthomyiidae, Lonchaeidae, Muscidae, Platypezidae, Sarcophagidae, Syrphidae, and Tephritidae. However, these hosts need to be especially reconfirmed. The records of lepidopterous and hymenopterous larvae as hosts (families Erebidae, Bucculatricidae, Lasiocampidae, and Tortricidae, and family Tenthredinidae, respectively) are extremely doubtful because the known biology and perhaps were concerned to the Phoridae living in dead larvae of the species from these families.

The genus *Aspilota* contains three subgenera, *Aspilota* sensu stricto, *Eusynaldis* Zaykov & Fischer, 1982, and *Grandilota* Fischer, 2002.

Subgenus Aspilota Foerster, 1863, sensu stricto

Figs 4, 5

Aspilota Foerster, 1863: 268; Shenefelt 1974: 966; Wharton 1980: 84; van Achterberg 1988: 9; Chen and Wu 1994: 49; Belokobylskij 1998a: 218; Wharton 2002: 34; Yu et al. 2016.
Dipiesta Foerster, 1863: 265.

Type species. *Alysia ruficornis* Nees von Esenbeck, 1834, by monotypy.

Material examined. Numerous species from the Palaearctic, Nearctic, and Neotropical regions were reviewed (e.g., Peris-Felipo and Belokobylskj 2014; Peris-Felipo et al. 2016a, 2016b, 2016c, 2016d).

Remarks. This largest and easily recognised subgenus includes most of *Aspilota* species. *Pterusa ruficollis* (Stelfox & Graham, 1950) is returned to *Aspilota* as *A. ruficollis* Stelfox & Graham, 1950, comb. nov. after the revision of type because the paraclypeal fovea are wide and reaching the inner margin of the eyes. Its new generic position is also supported by Fischer's re-description of the species (Fischer 1972: 436).

Subgenus *Eusynaldis* Zaykov & Fischer, 1982

Eusynaldis Zaykov & Fischer, 1982: 70; Zhu et al. 2017: 19 (as subgenus); Peris-Felipo and Belokobylskij 2019: 21.
Regetus Papp, 1999: 391; Fischer 2002: 101; Zhu et al. 2017: 19 (as synonym).

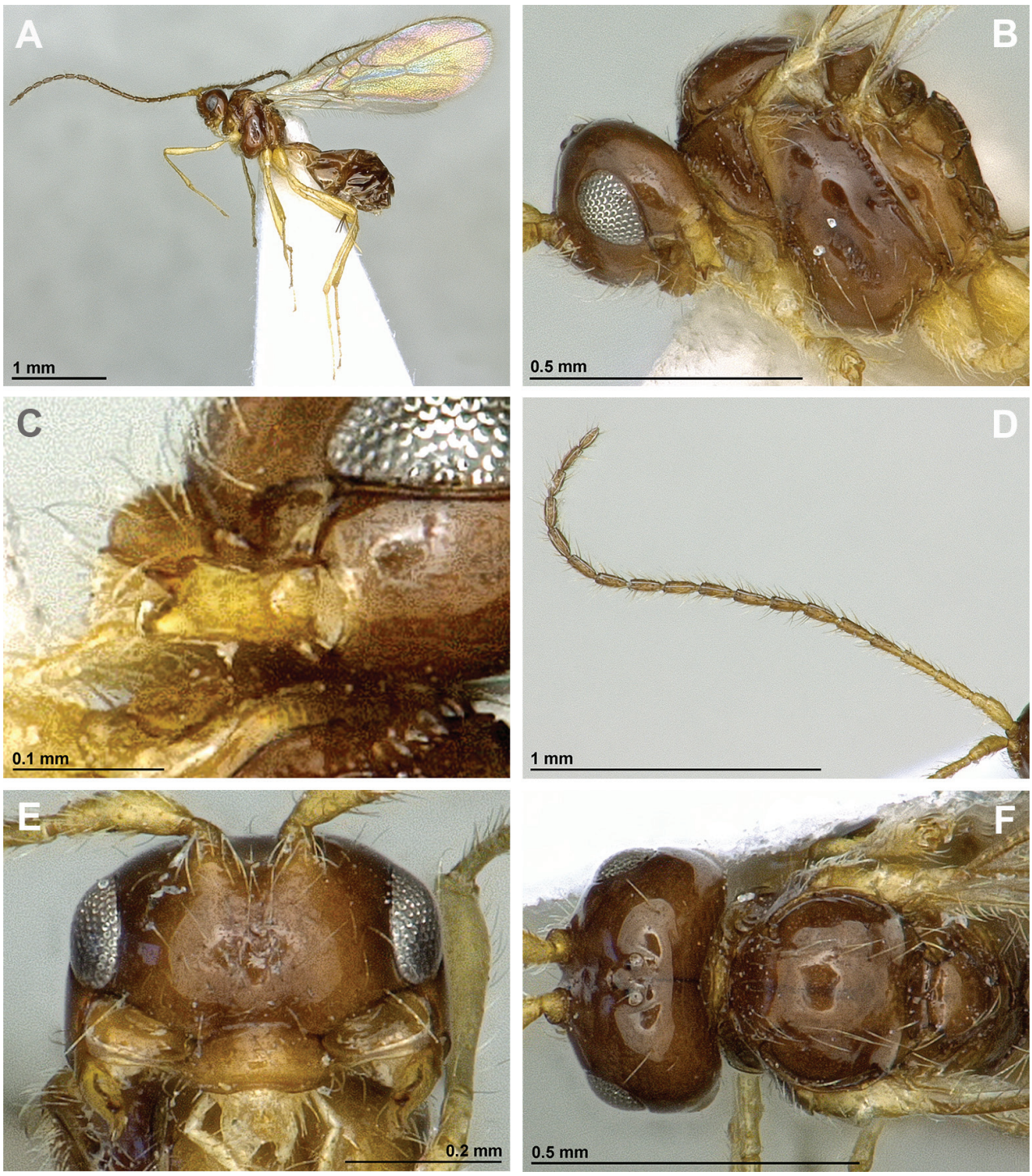

Figure 4. *Aspilota* (*Aspilota*) *ajara* Peris-Felipo, 2016 (holotype, female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head and mesonotum, dorsal view.

Adelphenaldis Fischer, 2003: 41; Peris-Felipo et al. 2012: 287; 2014b: 571; Yu et al. 2016; Zhu et al. 2017: 19 (as synonym).

Type species. *Eusynaldis varinervis* Zaykov & Fischer, 1972, by monotypy (Figs 6, 7).

Material examined. ***Holotype*** *Regetus balcanicus* [= *Aspilota* (*Eusynaldis*) *globipes*] Former Yugoslavia: • ♀, Kosovo, Mts. Sar, Brezovica, 900–1200 m, 20–23.v.1971 (Papp & Hortatovich leg.) (HNHM) [Hym. Typ. No. Mus. Budapest 7878].

Figure 5. *Aspilota* (*Aspilota*) *ajara* Peris-Felipo, 2016 (holotype, female) **A** propodeum **B** first metasomal tergite, dorsal view **C** legs, metasoma and ovipositor, lateral view **D** fore and hind wings.

Diagnosis. Subgenus *Eusynaldis* shares all diagnostic characters of *Aspilota* sensu stricto, except the absent vein 2-SR of the fore wing.

Remarks. *Regetus* Papp, 1999 and *Adelphenaldis* Fischer, 2003 are junior synonyms of *Eusynaldis* Zaykov & Fischer, 1982 because both taxa are characterised by the same diagnostic features (Zhu et al. 2017). Moreover, the study of the holotype of *Regetus balcanicus* Papp, 1999 (the type species of *Regetus*) showed this species to be a junior synonym of *Aspilota* (*Eusynaldis*) *globipes* (Fischer, 1962) (Peris-Felipo and Belokobylskij 2019).

Subgenus *Grandilota* Fischer, 2002, stat. nov.

Grandilota Fischer, 2002: 103; Yu et al. 2016.

Type species. *Grandilota kenyaensis* Fischer, 2002, by original designation (Figs 8, 9).

Material examined. ***Holotype*** (*Grandilota kenyaensis*). Kenya: • ♀, Mt. Elgon Natural Park, bamboo (Arundinaria alpine) thicket, 2740 m; swept. No. 496, 22.i.1992 (G. Varkonyl leg.) [Hym. Typ. No. Mus. Budapest 11673] (HNHM). ***Paratype*** (*Grandilota kenyaensis*) Kenya: • ♀, same label as holotype but [Hym. Typ. No. Mus. Budapest 11674] (HNHM).

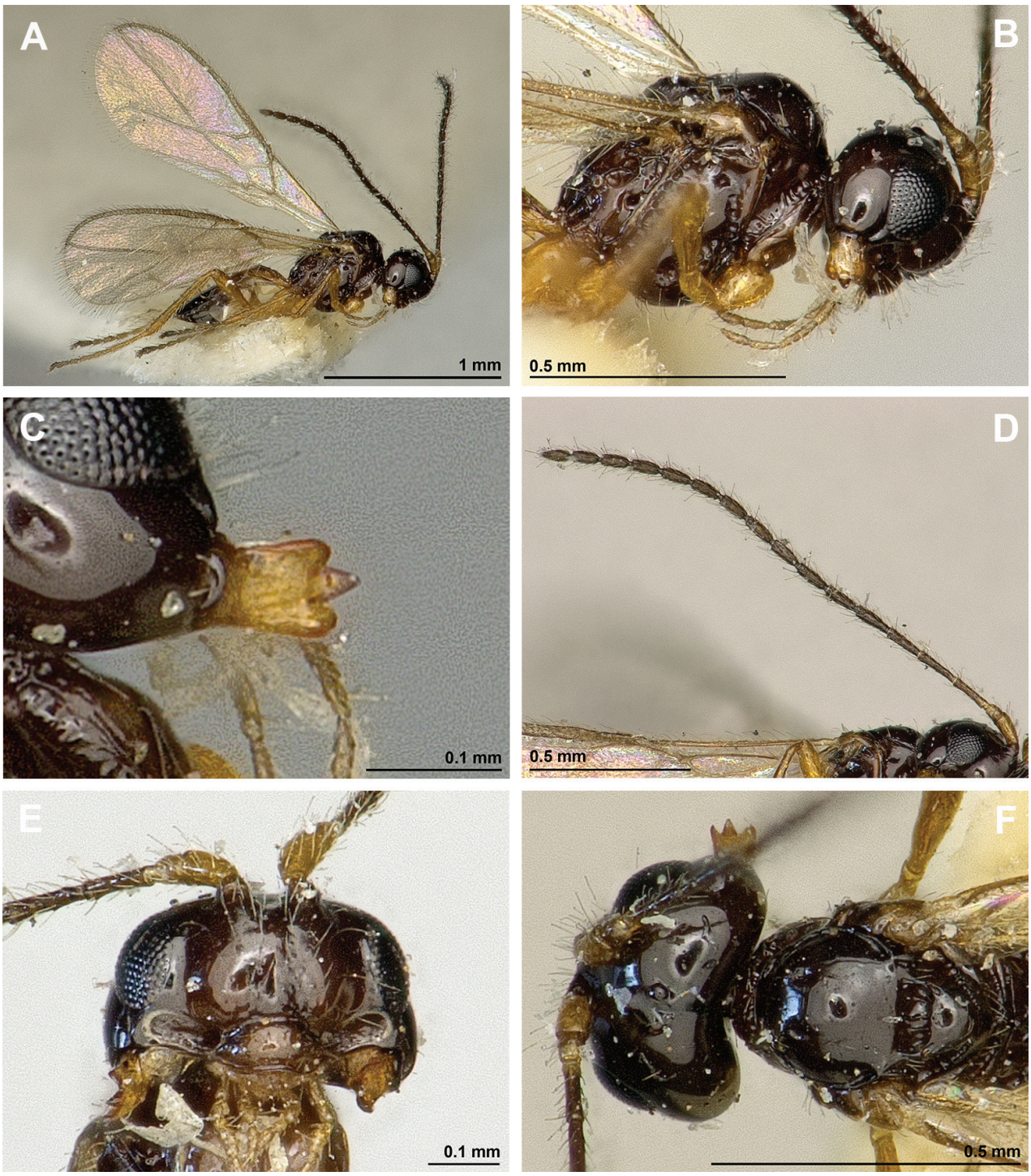

Figure 6. *Aspilota* (*Eusynaldis*) *varinervis* (Zaykov & Fischer, 1972) (holotype, male) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head and mesonotum, dorsal view.

Diagnosis. Mandible well developed, tridentate, with upper (first) tooth diminished to respect to lower (third) tooth. Paraclypeal fovea long, reaching inner margin of eyes. Mesoscutum without mesoscutal pit; notauli present only in anterior half of mesoscutum; precoxal sulcus present; propodeum with pentagonal areola, delineated by carinae. In fore wing, marginal cell reaching apex of wing; vein r originating from basal quarter of pterostigma; vein 2-SR present and sclerotised; veins m-cu and cu-a postfurcal; first subdiscal cell closed postero-apically

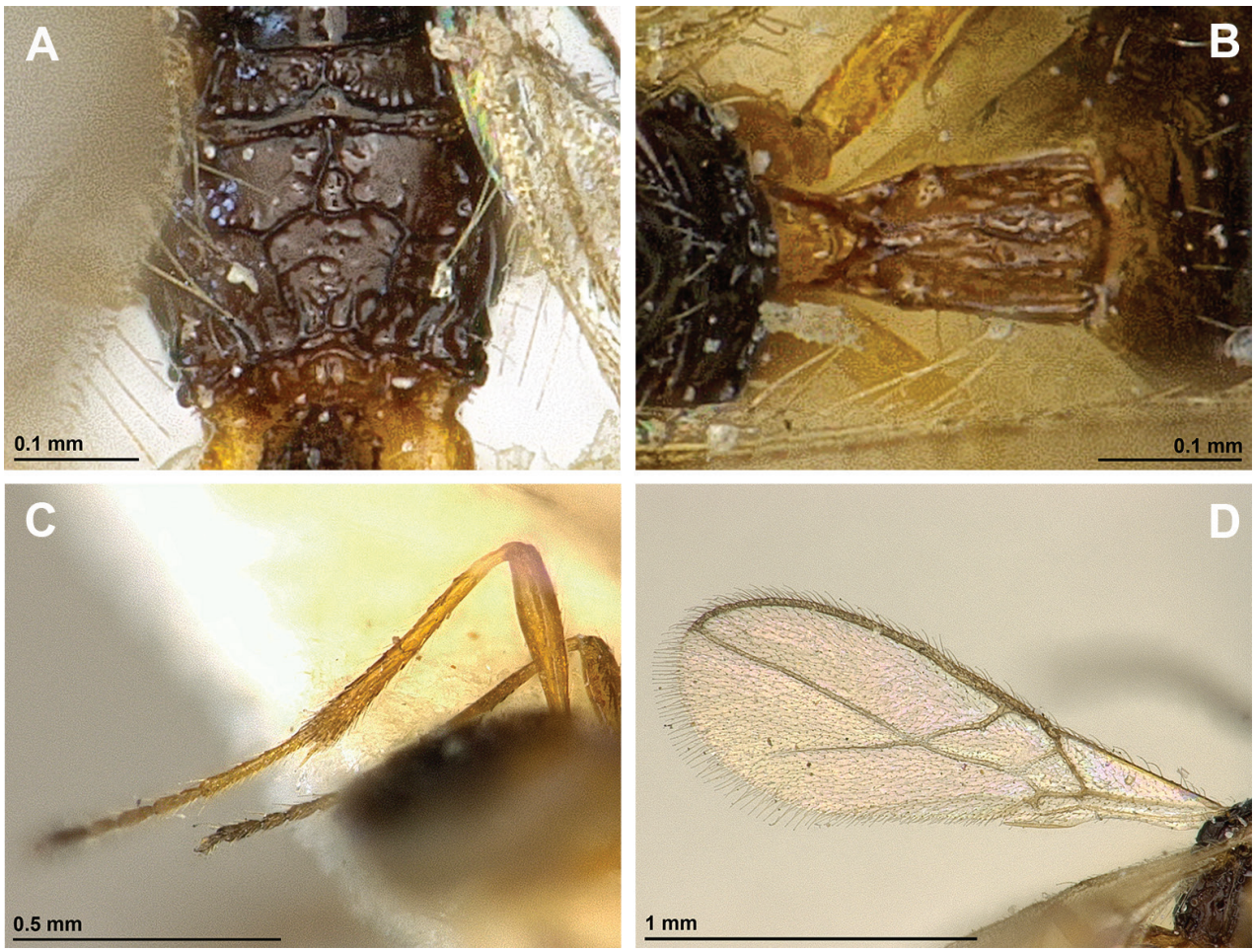

Figure 7. *Aspilota* (*Eusynaldis*) *varinervis* (Zaykov & Fischer, 1972) (holotype, male) **A** propodeum **B** first metasomal tergite, dorsal view **C** hind leg, lateral view **D** fore wing.

by CU1a vein. In hind wing, subbasal cell open. Metasoma of ♀ more or less distinctly compressed laterally. Ovipositor sheath not longer than metasoma.

Remarks. This subgenus has only one known species, *Aspilota* (*Grandilota*) *kenyaensis* Fischer, 2002, from Kenya and shares the main characters with *Aspilota* sensu stricto, however, the subbasal cell of the hind wing open distally (absent vein cu-a) and the wing membrane is pigmented, which distinguishes it at the subgeneric level.

Genus *Dinostigma* Fischer, 1966

Dinostigma Fischer, 1966: 182; Shenefelt 1974: 991; Wharton 1980: 38; van Achterberg 1988: 19; Yu et al. 2016.

Type species. *Dinostigma muesebecki* Fischer, 1966, by monotypy (Figs 10, 11).

Material examined. ***Holotype*** (*Dinostigma muesebecki*). United States Of America: • ♀, North East, Pa. [= Pennsylvania], No 9019, 6.vii.1912 (F. Johnson leg.) (NMNH).

Diagnosis. Mandible small, simple, tridentate. Paraclypeal fovea short, far from reaching inner margin of eyes. Mesoscutum without mesoscutal pit;

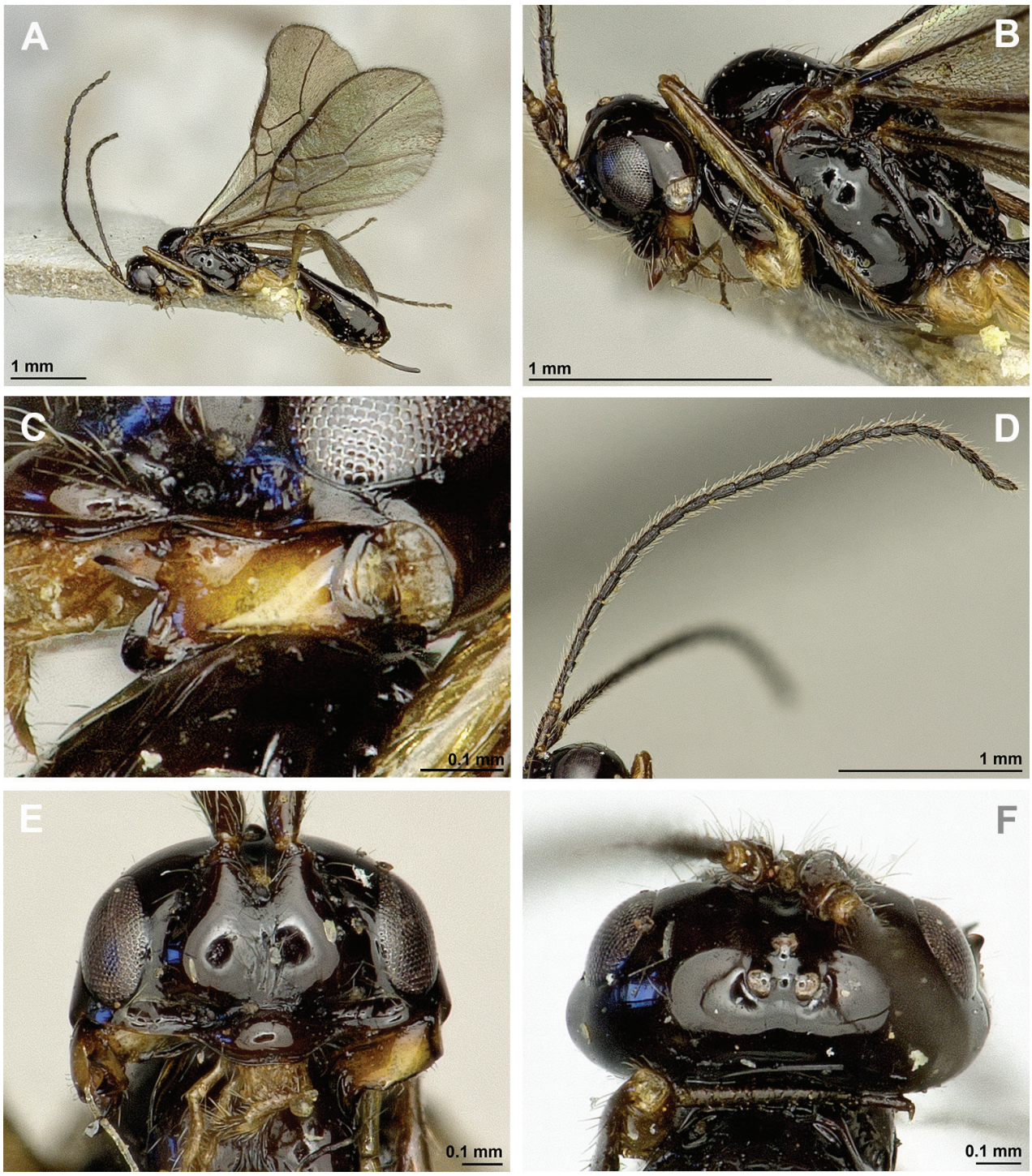

Figure 8. *Aspilota* (*Grandilota*) *kenyaensis* (Fischer, 2002), comb. nov. (holotype, female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head, dorsal view.

notauli present only in anterior part of mesoscutum; precoxal sulcus absent; propodeum always smooth; spiracles of propodeum large. In fore wing, marginal cell never shortened; vein r originating from basal quarter of pterostigma; vein 2-SR absent; vein cu-a postfurcal; first subdiscal cell open distally (without vein 2-1A). Hind wing with all cells open. Metasoma of ♀ more or less distinctly compressed laterally. Ovipositor sheath shorter than metasoma.

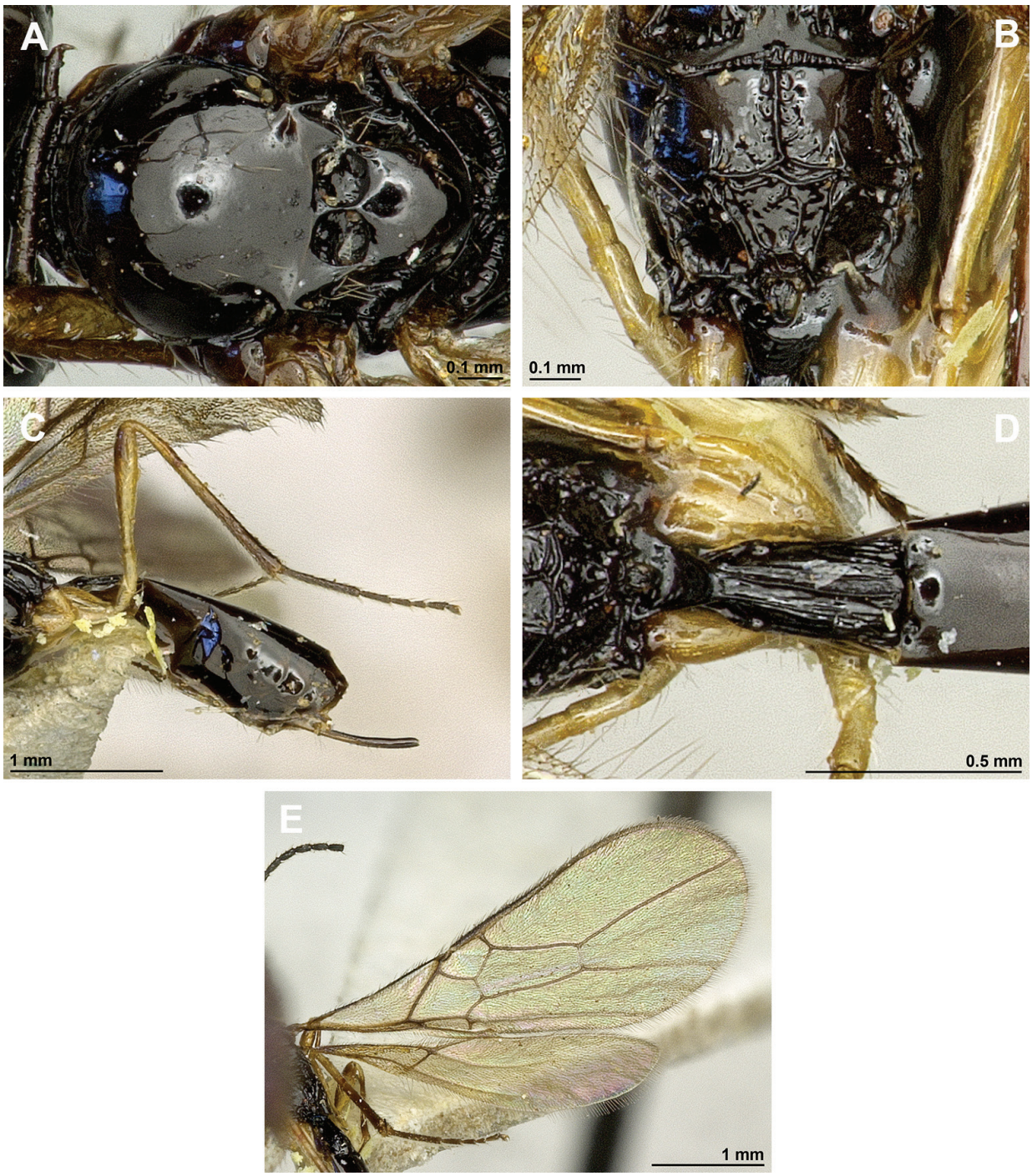

Figure 9. *Aspilota* (*Grandilota*) *kenyaensis* (Fischer, 2002), comb. nov. (holotype, female) **A** mesonotum, dorsal view **B** propodeum. **C** legs, metasoma and ovipositor, lateral view **D** first metasomal tergite, dorsal view **E** fore and hind wings.

Remarks. After careful revision of former *Dinostigma* and *Eudinostigma* (as subgenus of *Dinostigma*) species, only the type species of this genus, *Dinostigma muesebecki* Fischer, 1966, is retained in *Dinostigma*. The species *D. stenosoma* (van Achterberg, 1988) is transferred to the genus *Dinotrema* as a type species of the new subgenus, *Pseudoprosapha* subgen. nov. (see below), because this species has the first subdiscal cell of fore wing closed, the pterostigma broad and wider than vein r length, and all cells of the hind wing closed (*Dinotrema* (*P.*) *stenosoma* (van Achterberg, 1988), comb. nov.).

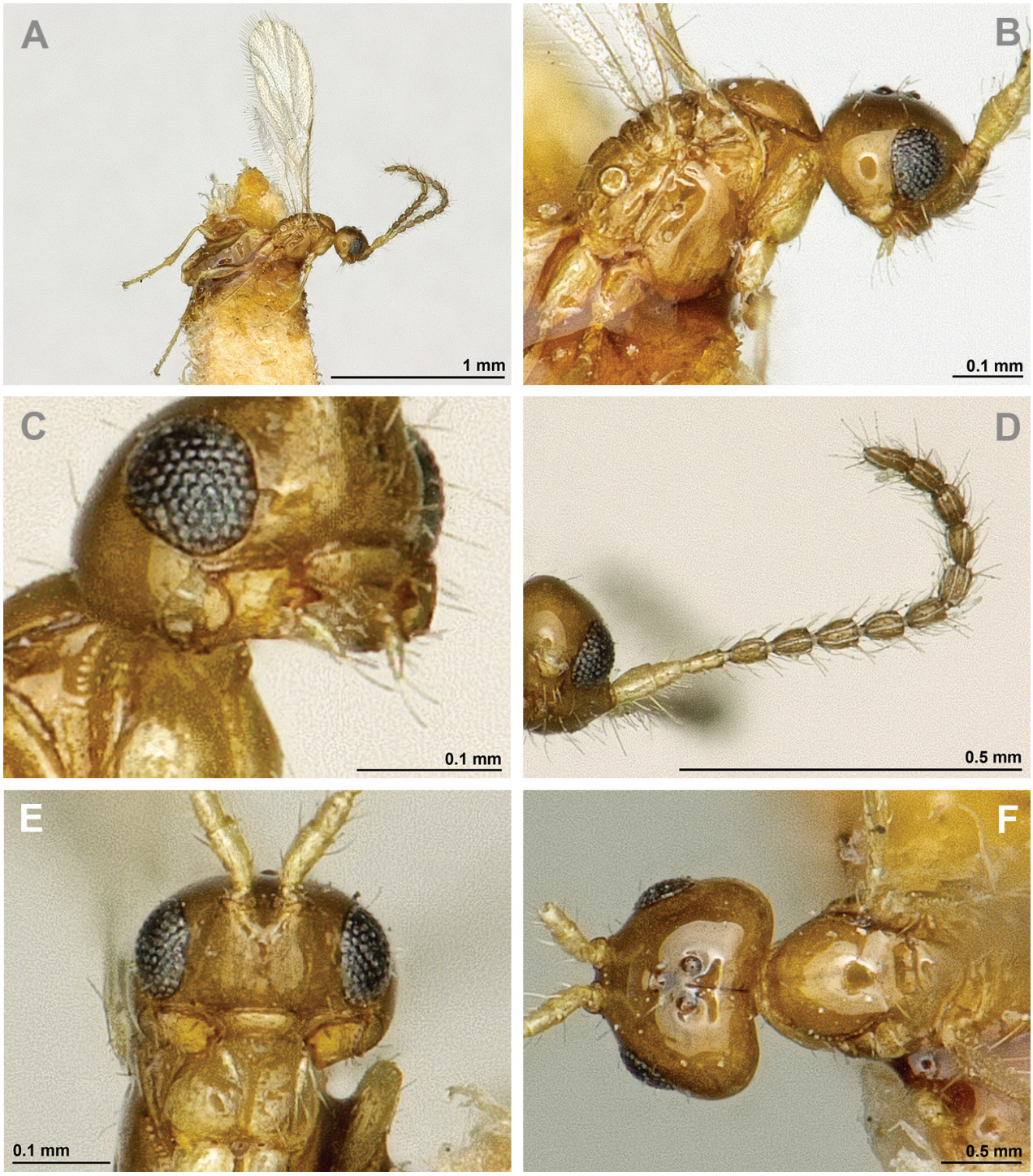

Figure 10. *Dinostigma muesebecki* Fischer, 1966 (holotype, female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head and mesonotum, dorsal view.

This genus is very close to the Oriental-Afrotropical *Lysodinotrema* Fischer, 1995, because both of them share, among others, such main diagnostic characters as simple tridentate mandible, short paraclypeal fovea, and mesoscutum without medio-posterior pit. However, the lack of closed cells in the hind wing in *Dinostigma* (present in *Lysodinotrema*), absence of vein 2-SR (present in *Lysodinotrema*), and absence of the precoxal sulcus (present in *Lysodinotrema*) are sufficient to separate both as different genera.

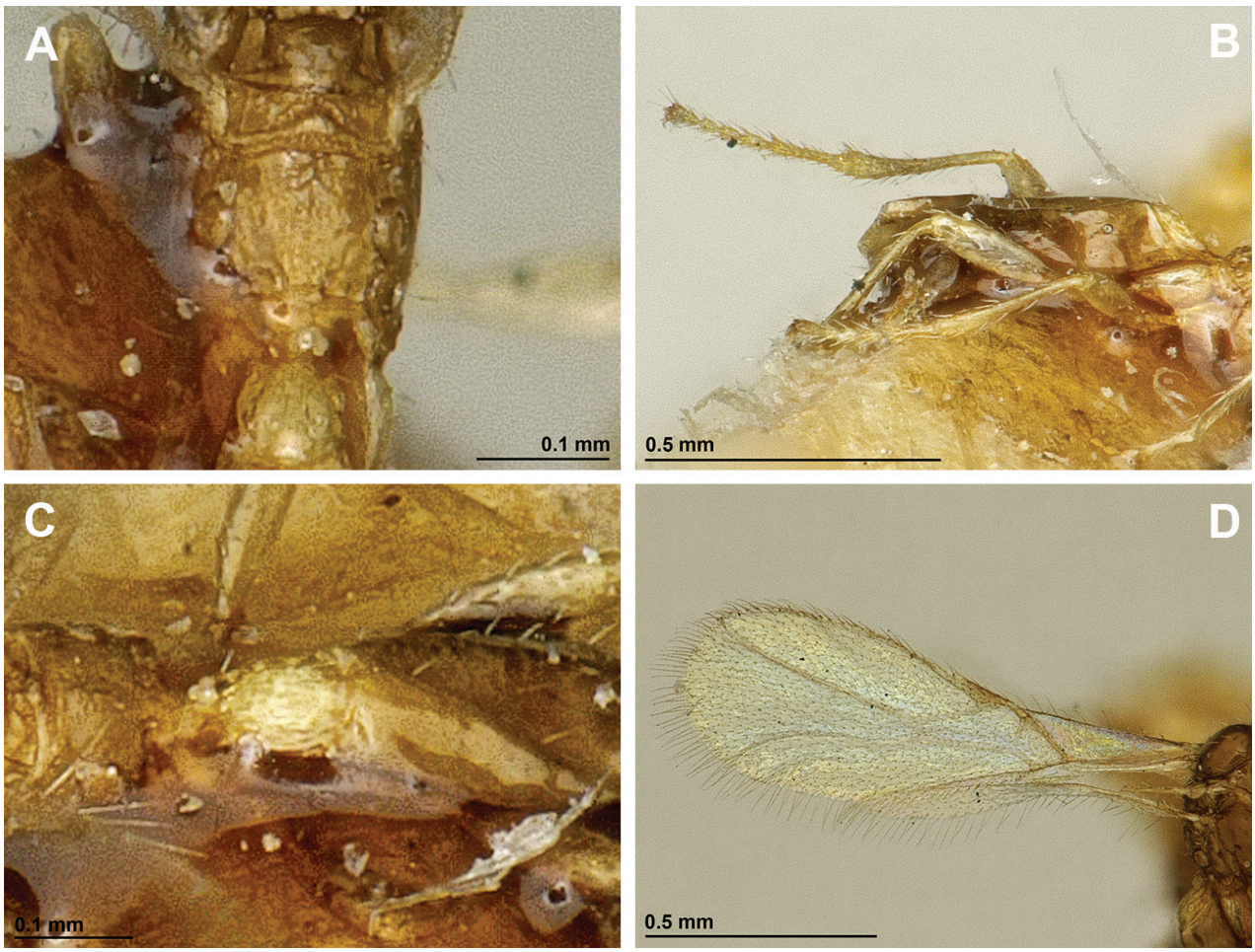

Figure 11. *Dinostigma muesebecki* Fischer, 1966 (holotype, male) **A** propodeum **B** legs, metasoma and ovipositor, lateral view **C** first metasomal tergite, dorsal view **D** fore and hind wings.

Genus *Dinotrema* Foerster, 1863

Figs 12–21

Dinotrema Foerster, 1863: 268; Wharton 1980: 84; van Achterberg and Bin 1981: 104; van Achterberg 1988: 19; Chen and Wu 1994: 69; Wharton 2002: 56; Tobias 2003a: 138; 2004: 468; 2006: 324; Peris-Felipo et al. 2014a: 10; Yu et al. 2016; Peris-Felipo and Belokobylskij 2018a: 4.

Coloboma Foerster, 1863: 268.

Spanomeris Foerster, 1863: 268.

Synaldis Foerster, 1863: 273; Fischer 1962: 1; 1971: 139; Tobias 1971: 199 (key); Shenefelt 1974: 1020; Tobias 1986: 123; Fischer 1993b: 567; Fischer 1997: 107; Belokobylskij 2002: 404; 2004a: 1991; 2004b: 935; Belokobylskij and Tobias 2007: 58; Fischer et al. 2008: 1461; Yu et al. 2016; Peris-Felipo and Belokobylskij 2017: 4.

Scotioneurus Provancher, 1886: 156.

Alitha Cameron, 1906: 28; Shenefelt 1974: 938; van Achterberg 1988: 9; Yu et al. 2016, stat. nov.

Pterusa Fischer, 1958: 14; Shenefelt 1974: 1108; van Achterberg 1988: 50; Belokobylskij 1998a: 170; van Achterberg and Vikberg 2014: 3 (as synonym of *Dinotrema* Foerster); Yu et al. 2016 (as valid genus).

Aspilota auct. p.p. Fischer 1972: 327; Shenefelt 1974: 966; Fischer 1976: 345.
Carinthilota Fischer, 1975: 311; Tobias 1986: 123; van Achterberg 1988: 9; Belokobylskij 1998a: 221; Fischer 2002: 102; Yu et al. 2016, syn. nov.
Eudinostigma Tobias, 1986: 244; van Achterberg 1988: 36; Fischer 1991: 12; Fischer et al. 2006: 831; Yu et al. 2016, syn. nov.

Type species. *Dinotrema erythropa* Foerster, 1863, by monotypy.

Diagnosis. Mandible small, simple, tridentate, often with upper (first) tooth diminished with respect to lower (third) tooth. Paraclypeal fovea short, not reaching more than half distance between clypeus and inner margin of eyes. Mesoscutum with or without mesoscutal pit; notauli usually present only in anterior part of mesoscutum, although in some species of the subgenus *Alitha* it is rather well developed and reaching or almost reaching mesoscutal pit; precoxal sulcus usually present, propodeum with different types of sculpture and sometimes with longitudinal and/or transverse carinae, rarely entirely smooth. In fore wing, marginal cell never shortened; vein r originating from basal quarter of pterostigma; vein 2-SR usually present and distinctly sclerotised or sometimes (subgenus *Synaldis*) absent or weakly developed and vein r not angled with vein 3-SR (van Achterberg 1988); veins m-cu and cu-a postfurcal; first subdiscal cell always closed postero-apically by CU1a vein. Venation of hind wing more or less reduced, sometimes without closed cells (Zhu et al. 2017). Metasoma of ♀ more or less distinctly compressed laterally. Ovipositor sheath usually not longer than metasoma.

Remarks. *Dinotrema* is the most complicated and largest genus within the tribe Alysiini with more than 440 known species, predominantly occurring in the temperate climatic regions (Peris-Felipo and Belokobyslkij 2018a). However, after studying a large amount of type material from different regions it should be possible to present a new generic classification, including the following subgenera: *Alitha* Cameron, 1906, stat. nov. (with *Carinthilota* Fischer as a new synonym), *Dinotrema* sensu stricto, *Prosapha* Foerster, 1863, *Pseudoprosapha* Peris-Felipo subgen. nov. and *Synaldis* Foerster, 1863 (with *Eudinostigma* Tobias as a new synonym).

A revision of *Eudinostigma* Tobias species was carried out for this reclassification. After careful study of the type species of *Eudinostigma* we consider it a synonym of *Dinotrema*. However, depending on the presence or absence of vein 2-SR of the fore wing, its species are divided between the subgenera *Dinotrema* and *Synaldis*. The main diagnostic characters of *Eudinostigma* are as follows: distinctly depressed head (resulting in antennal sockets situated at the upper level of eye and maximum width of head in dorsal view 1.6–2.4× width of mesoscutum), compressed mesosoma, and vein 2-SR of fore wing often absent (Tobias 1986; van Achterberg 1988). These characters also occur sometimes in *Dinotrema* species, e.g., among others, in *Dinotrema brevissimicorne* (Stelfox et Graham, 1948), *D. compressum* (Haliday, 1838), *D. parapunctatum* (Fischer, 1976), and *D. robertoi* Peris-Felipo, 2013.

The following species previously belonging to *Eudinostigma* are transfered to the subgenus *Dinotrema* sensu stricto: *D.* (*D.*) *alox* (van Achterberg, 1988), comb. nov.; *D.* (*D.*) *entabeniense* (Fischer, 2009), comb. nov.; *D.* (*D.*) *latum* (Chen & Wu, 1994), comb. nov.; *D.* (*D.*) *planiceps* (Fischer, Tormos & Pardo, 2006), comb. nov. and *D.* (*D.*) *subpulvinatum* (Fischer, 2009), comb. nov.. Moreover, four other *Eudinostigma* species are transferred to the subgenus *Synaldis*: *D.* (*S.*) *bienesae*

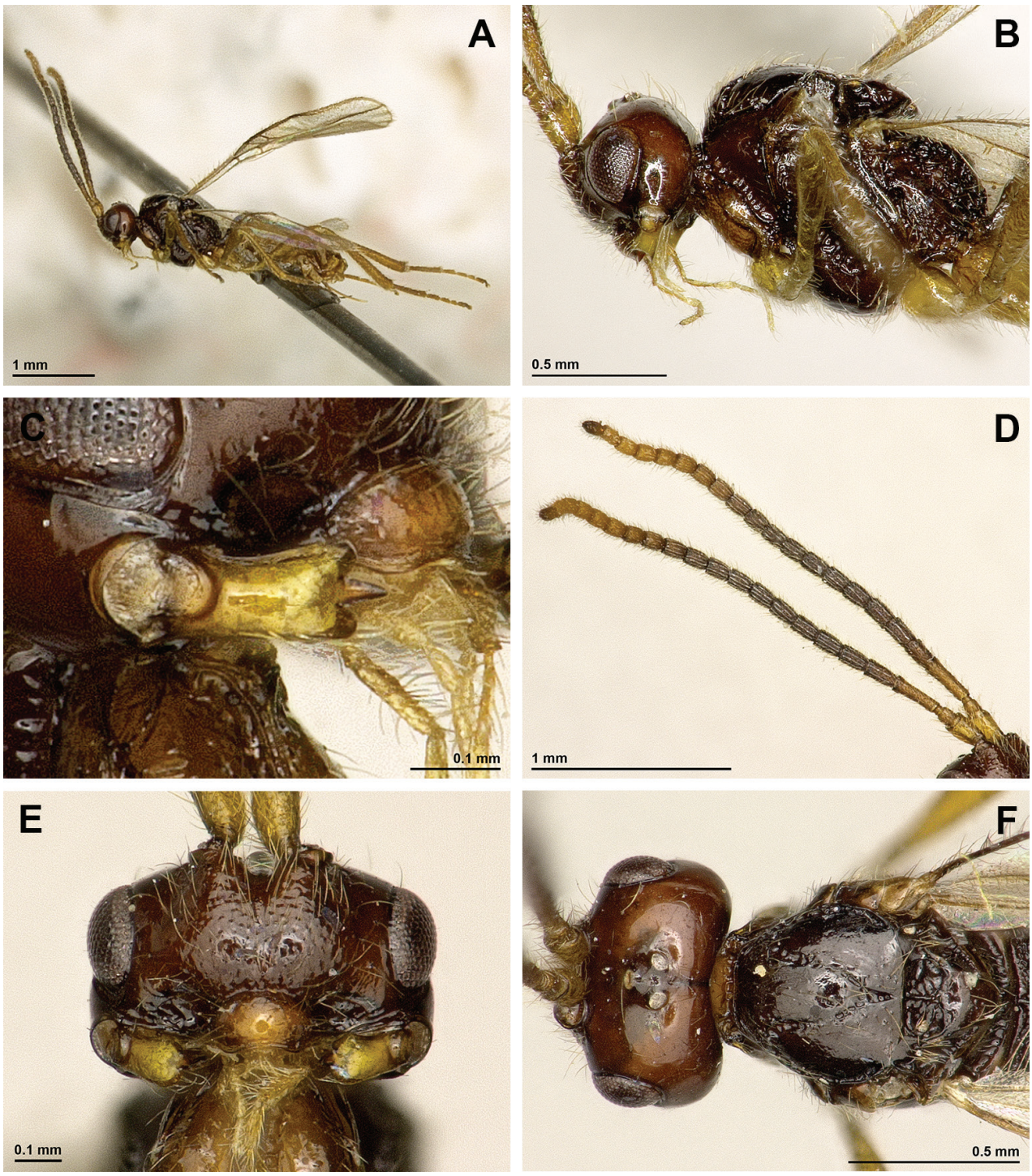

Figure 12. *Dinotrema* (*Alitha*) *parapsidalis* (Fischer, 1975), comb. nov. (holotype, female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head and mesonotum, dorsal view.

(Fischer, Tormos & Pardo, 2006), comb. nov., *D.* (*S.*) *fischeri* (Tobias, 1986), comb. nov. (type species of *Eudinostigma*), *D.* (*S.*) *latistigma* (Fischer, 1962), comb. nov., and *D.* (*S.*) *planiceps* (Fischer, Tormos & Pardo, 2006), comb. nov.

Furthermore, after studying the types of *Dinostigma* and *Eudinostigma* species, we consider the features of *Eudinostigma stenosoma* van Achterberg, 1988 (see below) enough different to transfer it to a new subgenus *Pseudoprosapha* subgen. nov.: *Dinotrema* (*Pseudoprosapha*) *stenosoma* (van Achterberg, 1988), comb. nov.

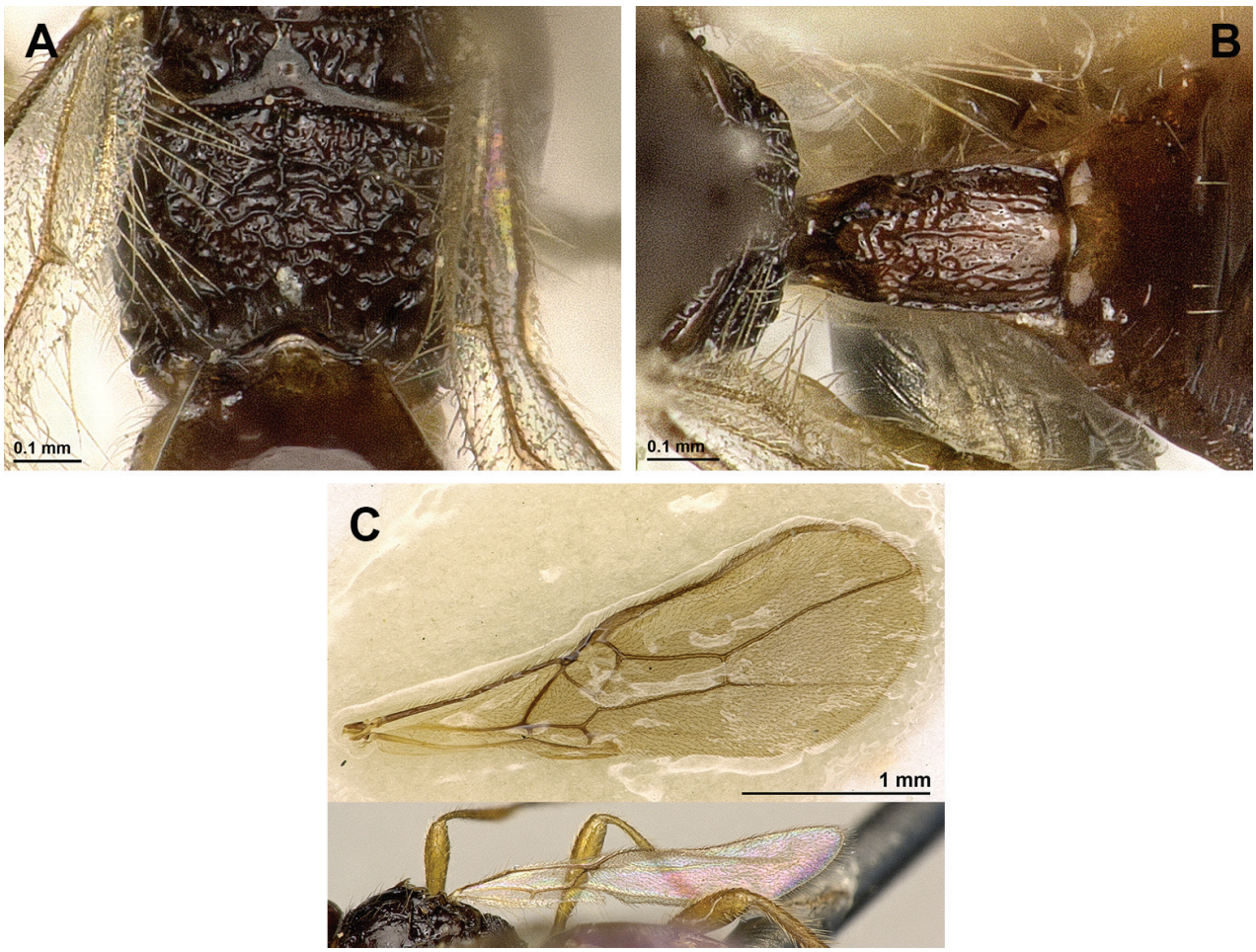

Figure 13. *Dinotrema* (*Alitha*) *parapsidalis* (Fischer, 1975), comb. nov. (holotype, female) **A** propodeum **B** first metasomal tergite, dorsal view **C** fore and hind wings.

In summary, five subgenera of the genus *Dinotrema* are recognised, *Alitha* Cameron, 1906, stat. nov., *Dinotrema* sensu stricto, *Prosapha* Foerster, 1863, *Pseudoprosapha* Peris-Felipo subgen. nov. and *Synaldis* Foerster, 1863.

Subgenus *Alitha* Cameron, 1906, stat. nov.

Alitha Cameron, 1906: 28; van Achterberg 1988: 9.
Carinthilota Fischer, 1975, syn. nov.

Type species. *Alitha longipennis* Cameron, 1906, by monotypy (lost).

Material examined. ***Holotype*** (*Carinthilota parapsidalis*) (Figs 12, 13) Austria: • ♀, Kärnten (88), 1 km O. Heft b(ei) Hüttenberg, 1000–1100 m, 25.viii.1973 (Fischer leg.) (NHMW). ***Holotype*** (*Carinthilota vechti*) The Netherlands: • ♀, Putten (Gld.), Malaise trap, 24–28.ix.1970 (J.v.d. Vecht leg.) (RMNH).

Diagnosis. This subgenus has all main characters of *Dinotrema* sensu stricto but differs from it by having the notauli more or less complete posteriorly, reaching or almost reaching the mesoscutal pit.

Remarks. Despite the loss of the type material of *Alitha* Cameron, 1906 described from South Africa (van Achterberg 1988) and thanks to the relative complete description of this genus given by Cameron (1906) and the additional comments by van Achterberg (1988), *Alitha* is considered a subgenus of *Dinotrema* (stat. nov.). Moreover, the genus *Carinthilota* Fischer, 1975 is considered a junior synonym of the subgenus *Alitha* (syn. nov.) because both share identical diagnostic characters. Unfortunately, so far only four Palaearctic and Oriental species are known and no studied specimens from the Afrotropical region.

The development of the notauli in *Alitha* species is highly variable: usually they are developed as rows of closely circular grooves more or less reaching the medio-posterior mesoscutal pit [*Dinotrema* (*A.*) *longipennis* (Cameron, 1906), comb. nov., *D.* (*A.*) *parapsidalis* (Fischer, 1975), comb. nov. and *D.* (*A.*) *vechti* (van Achterberg, 1988), comb. nov.] while the distal part of the notauli is more or less reduced in the two Eastern Palaearctic species [*D.* (*A.*) *lada* (Belokobylskij, 1998), comb. nov. and *D.* (*A.*) *mavka* (Belokobylskij, 1998), comb. nov.]. The variable development of the notauli supports our opinion that the presence of nearly complete notauli in several genera of *Aspilota* group (*Dinotrema* and *Orthostigma*) is an unsuitable generic character; at most it may be used provisionally at subgeneric level.

Subgenus *Dinotrema* Foerster, 1863, sensu stricto

Dinotrema Foerster, 1863: 268; Wharton 1980: 84; van Achterberg and Bin 1981: 104; van Achterberg 1988: 19; Chen and Wu 1994: 69; Wharton 2002: 56; Tobias 2003a: 138; 2004: 468; 2006: 324: Peris-Felipo et al. 2014a: 10; Yu et al. 2016; Peris-Felipo and Belokobylskij 2018a: 4.
Pterusa Fischer, 1958: 14; van Achterberg and Vikberg 2014: 1, 3.

Type species. *Dinotrema erythropum* Foerster, 1863, by original designation (Figs 14, 15).

Material examined (*Dinotrema* (*Dinotrema*) *erythropum*): England: • 1 female (paratype of *Aspilota praecipua*) and 1 male (paratype id.), Coll. Marshall Cornwall, Botusfleming (HNHM). Denmark: • 1 female, E-Jylland, Frisenborg, 28.vii.1986 (Munk leg.) (NMA). Finland: • 1 female, Sa. Valkeala, 6772:483, 28.vii.1977 (Koponen leg.) (NMA); • 1 female, same locality but, 29.vii.1977 (NMA). Hungary: • 1 female, Ugod, Somberek Hubertlak-Kórnyéle, 26–29.vi.1967 (Papp leg.) (HNHM). Luxembourg: • 2 females, Tratten, b. Murau Stmk. Coll Fulmek, 14.viii.1942 and 13.x.1954 (NHMW). Netherlands: • 1 female, Wijster (Dr.) opposite Biological Station, 22–30.ix.1975 (van Achterberg leg.) (RMNH). Spain: • 1 female, Valencia, 16.vii.1942 (NHMW).

Diagnosis. The main diagnostic characters of this subgenus are the short paraclypeal fovea which remain far from the eye margins, the pterostigma very narrow (linear) and vein 2-SR of fore wing present and more or less completely sclerotised.

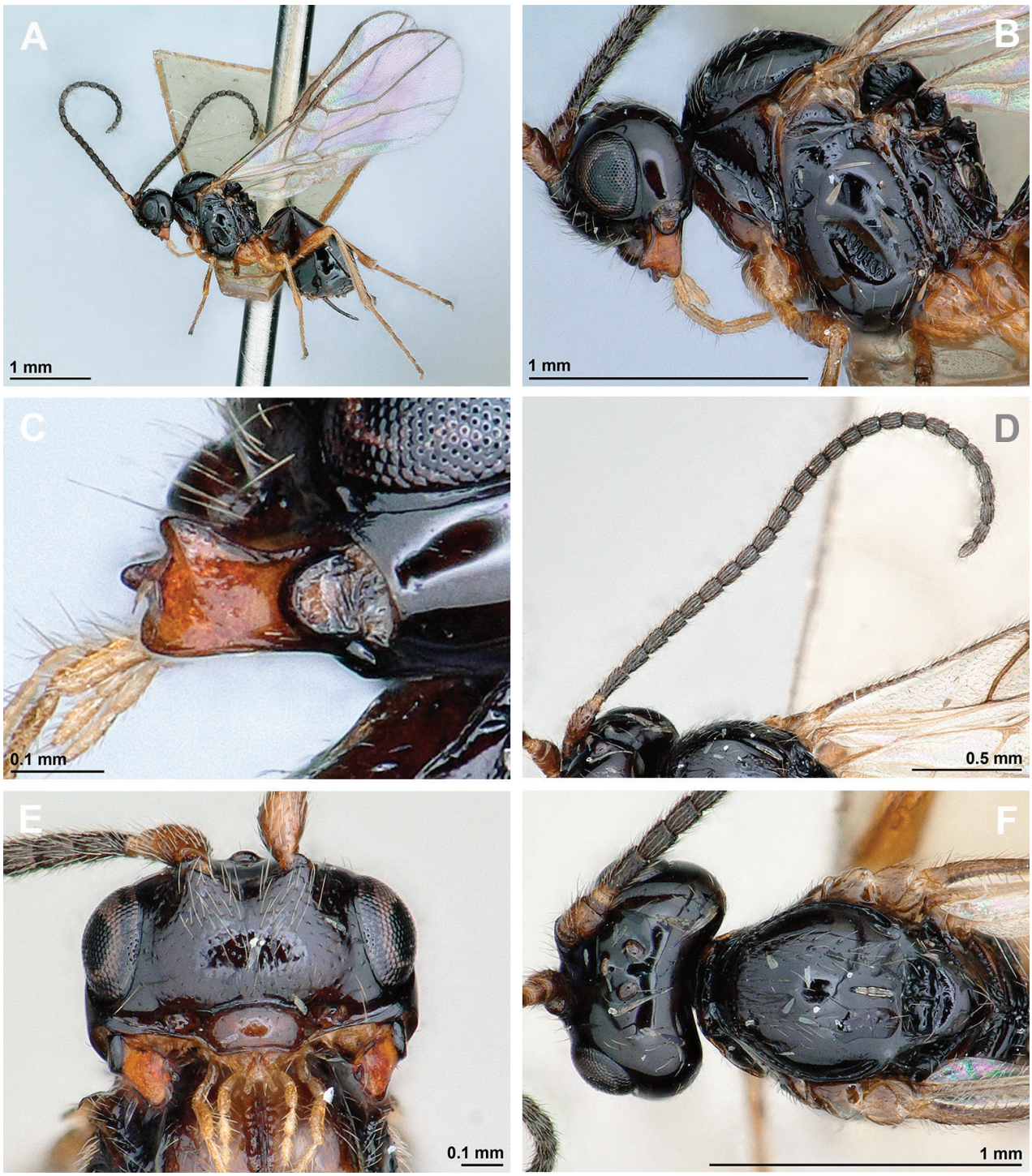

Figure 14. *Dinotrema* (*Dinotrema*) *erythropum* Foerster, 1863 (female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antennae **E** head, front view **F** head and mesonotum, dorsal view.

Remarks. This is the largest subgenus including the main part of *Dinotrema* species with approx. 440 species described worldwide (Peris-Felipo and Belokobyslkij 2018a). As shown by van Achterberg and Vikberg (2014), *Pterusa* Fischer, 1958 is a synonym of *Dinotrema* sensu stricto, because any differences are absent in females, and it is based only on the brachyptery of the males.

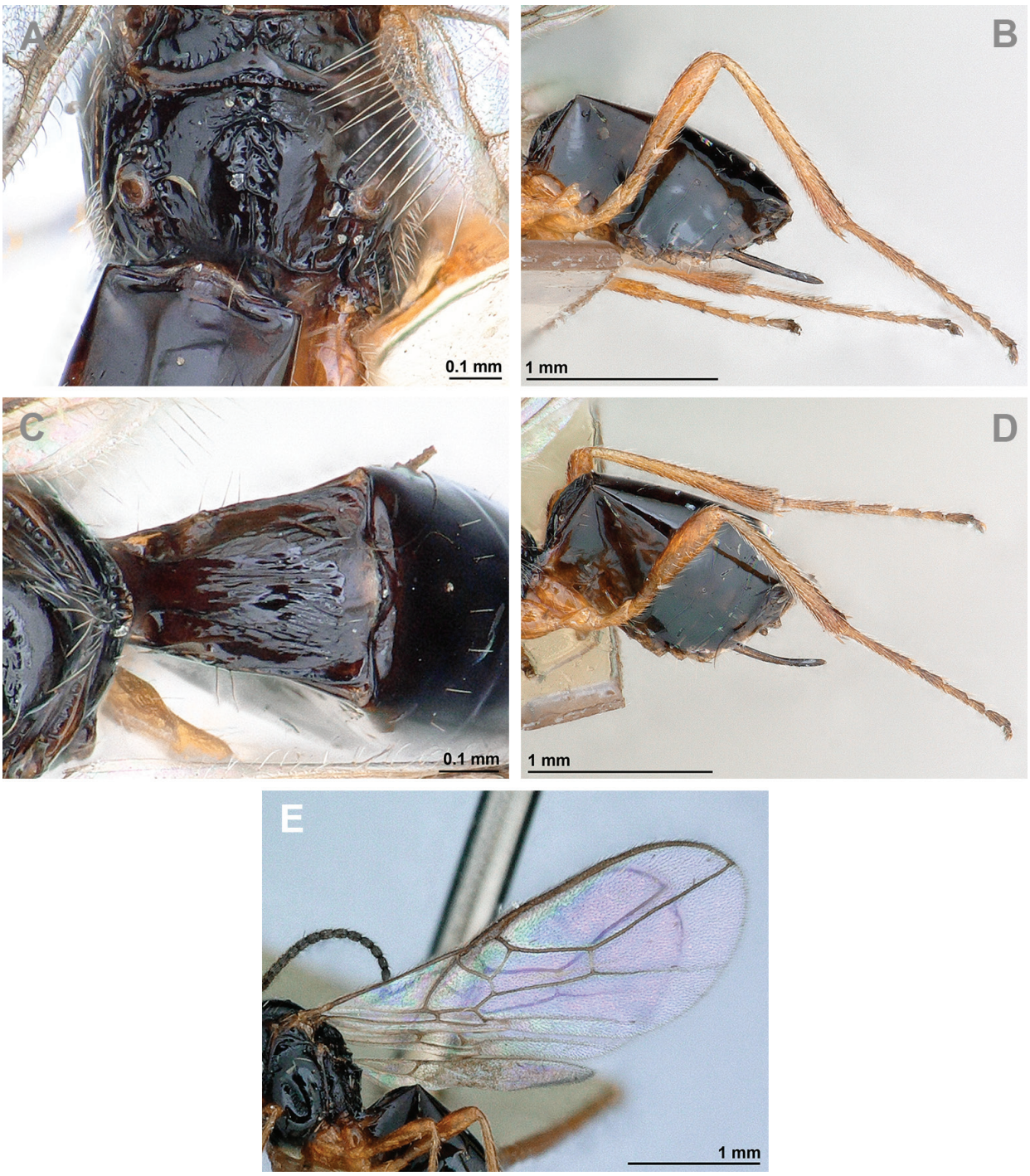

Figure 15. *Dinotrema* (*Dinotrema*) *erythropum* Foerster, 1863 (female) **A** propodeum, dorsal view **B** hind leg, lateral view **C** first metasomal tergite, dorsal view **D** metasoma and ovipositor, lateral view **E** fore and hind wings.

Subgenus *Prosapha* Foerster, 1863

Figs 16, 17

Prosapha Foerster, 1863: 263; Shenefelt 1974: 1018; Tobias 1986: 121.

Dinotrema (*Prosapha*) van Achterberg 1988: 88 (as synonym of *Dinotrema*); Tobias 2003b: 810; Belokobylskij and Tobias 2007: 11; van Achterberg and Vikberg 2014: 3; Yu et al. 2016.

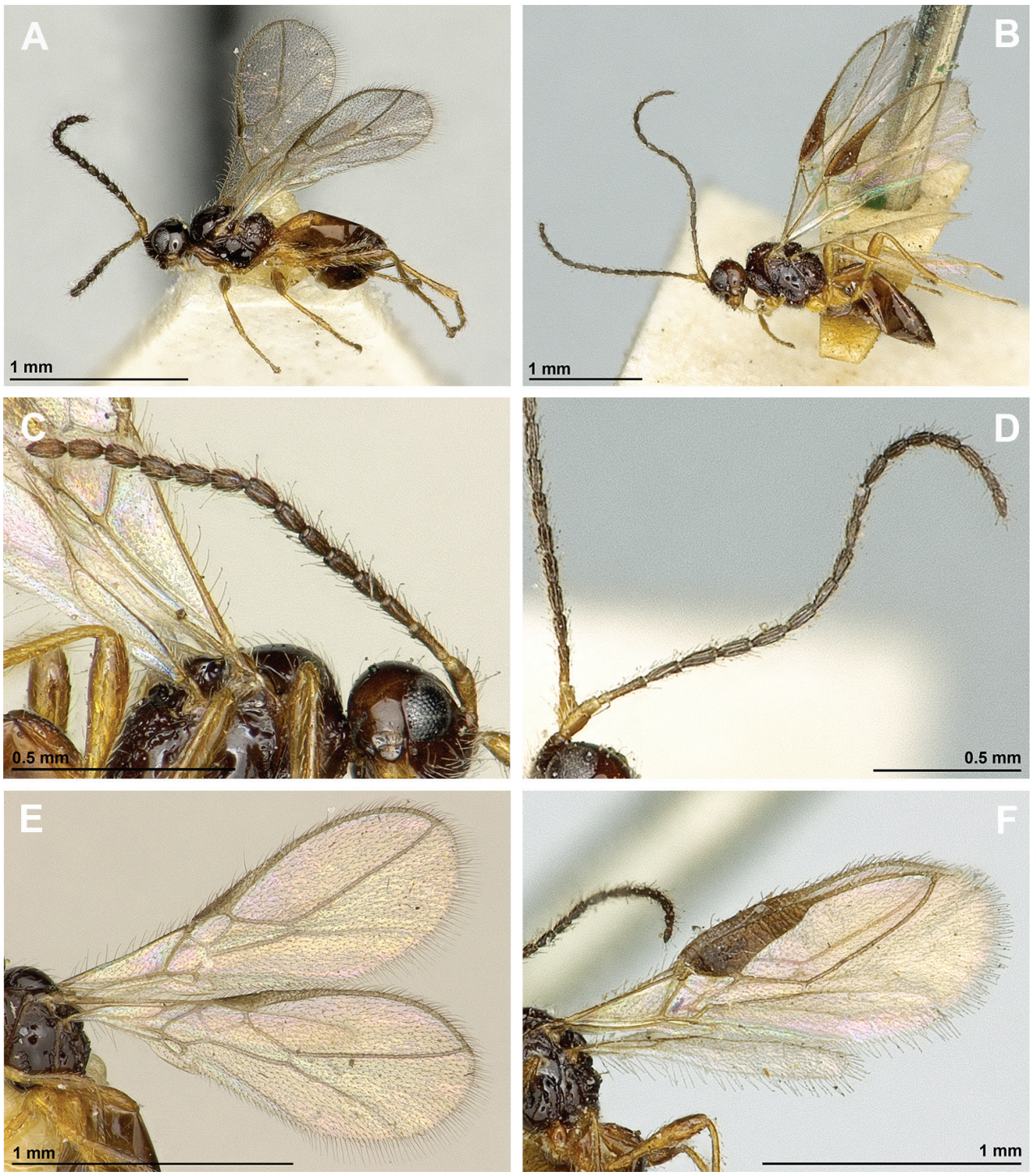

Figure 16. *Dinotrema* (*Prosapha*) *speculum* (Haliday, 1838) (**A, C, E:** female; **B, D, F:** male) **A, B** habitus, lateral view **C, D** antenna **E, F** fore and hind wings.

Type species. *Alysia speculum* Haliday, 1838, by original designation (Figs 16, 17).

Material examined (*Dinotrema* (*Prosapha*) *speculum*): Austria: • ♂, Spitzzicken, Burgenland, 24.viii.1959 (Fischer leg.) (NHMW). Russia: • 8 ♂, Leningradskaya Province, Tolmachevo, 23.viii.1960 (Tobias leg.) (ZISP); • 2 ♂, Novgorod Province, 20 km NW of Pestovo, 6.vii.1986 (Tobias leg.) (ZISP); • ♀, ibid, 15.viii.1990 (ZISP); • ♀, ibid, 27.vii.1999 (ZISP); • ♀, ibid, 1.viii.1999 (ZISP); • ♀, ibid, 5.viii.2001 (ZISP); • ♀, Volgograd Province, 10 km S of Novokhopersk,

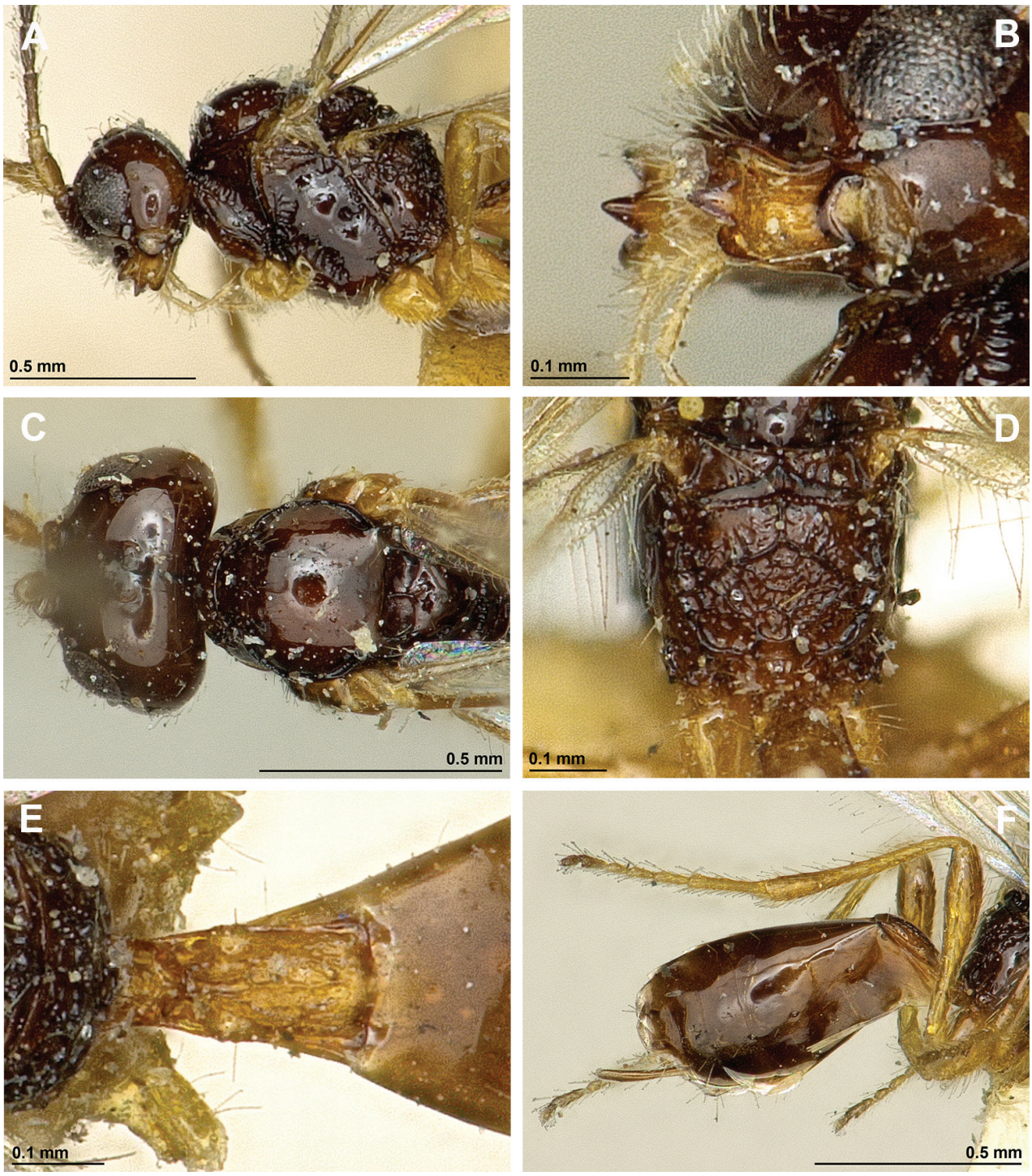

Figure 17. *Dinotrema* (*Prosapha*) *speculum* (Haliday, 1838) (female) **A** head and mesosoma, lateral view **B** mandible **C** head and mesonotum, dorsal view **D** propodeum **E** first metasomal tergite, dorsal view **F** legs, metasoma and ovipositor, lateral view.

10.vii.1977 (Tobias leg.) (ZISP); • ♂, Krasnodar Territory, Sochi, Lazarevskoe, 30.v.1988 (Tobias leg.) (ZISP); • ♂, Chelyabinsk Province, Ilmenskiy Nature Reserve, 17.vii.1958 (Tobias leg.) (ZISP).

Diagnosis. This subgenus shares the main characters of *Dinotrema* sensu stricto but differs by having, in the fore wing, the maximum width of pterostigma wider than vein r (especially in males) and vein 2-SR of fore wing always present.

Remarks. This subgenus includes five Palaearctic species: *D.* (*P.*) *comptum* Tobias, 2003, *D.* (*P.*) *pachysemoides* Tobias, 2003, *D.* (*P.*) *speculum* (Haliday, 1838), *D.* (*P.*) *tobiasi* (Fischer, 1994) and *D.* (*P.*) *ussuricum* Tobias, 2007. The status of *Prosapha* has been variable for a long time. Foerster (1863) described this genus based on the distinctive large, cuneiform and heavily sclerotised pterostigma of the male. Van Achterberg (1988) and Tobias (2003b) considered *Prosapha* species inside of *Dinotrema* based on their morphological similarity and because *Prosapha* females possess a narrower pterostigma weakly separated from the metacarp (1-R1). *Prosapha* species can be differentiated from *Pseudoprosapha* subgen. nov. by the presence of vein 2-SR (which is absent in *Pseudoprosapha*).

Pseudoprosapha Peris-Felipo, subgen. nov.

https://zoobank.org/5526942A-61D5-4085-B080-BCB05D629900

Type species. *Eudinostigma stenosoma* van Achterberg, 1988 (Figs 18, 19).

Material examined. ***Holotype*** (*Eudinostigma stenosoma*) Hungary: • ♂, Budapest, Biró, 21.ix.1927, "226" (RMNH).

Diagnosis. Mandible small, simple, tridentate, with upper (first) tooth diminished with respect to lower (third) tooth. Paraclypeal fovea short, length not more than half distance between clypeus and inner margin of eyes. Mesoscutum without medio-posterior pit; notauli present only in anterior part of mesoscutum; precoxal sulcus present; propodeum completely smooth. Marginal cell of fore wing never shortened; vein r originating from basal quarter of wide pterostigma; vein 2-SR absent; vein cu-a postfurcal; first subdiscal cell always closed postero-apically by vein CU1a. Hind wing with all cells closed. Metasoma of ♀ more or less distinctly compressed posteriorly. Ovipositor sheath not longer than metasoma.

Remarks. This new subgenus includes only a single species, *Dinotrema* (*Pseudoprosapha*) *stenosoma* (van Achterberg, 1988), comb. nov.. This subgenus shares with *Prosapha* the comparatively broad pterostigma (viz., wider than the length of vein r) and in female vein r + 3-SR forming a (nearly) straight line but differs by the loss of vein 2-SR (present in *Prosapha*), the depressed head (antennal sockets situated near the upper level of the eyes), the strongly compressed mesosoma and the very narrow clypeus. These differences make it worth to name a different subgenus for it.

Subgenus *Synaldis* Foerster, 1863

Synaldis Foerster, 1863: 273; Fischer 1962: 1; 1971: 139; Tobias 1971: 199 (key); Shenefelt 1974: 1020; Tobias 1986: 123; Fischer 1993b: 567; 1997: 107; Belokobylskij 2002: 404; 2004a: 1991; 2004b: 935; Belokobylskij and Tobias 2007: 58; Fischer et al. 2008: 1461; Yu et al. 2016; Peris-Felipo and Belokobylskij 2017: 4; Zhu et al. 2017: 61; Dias de Oliveira and Penteado-Dias 2024: 280.
Eudinostigma Tobias, 1986: 244, syn. nov.

Type species. *Bassus concolor* Nees, 1812, by original designation (lost) (Figs 20, 21).

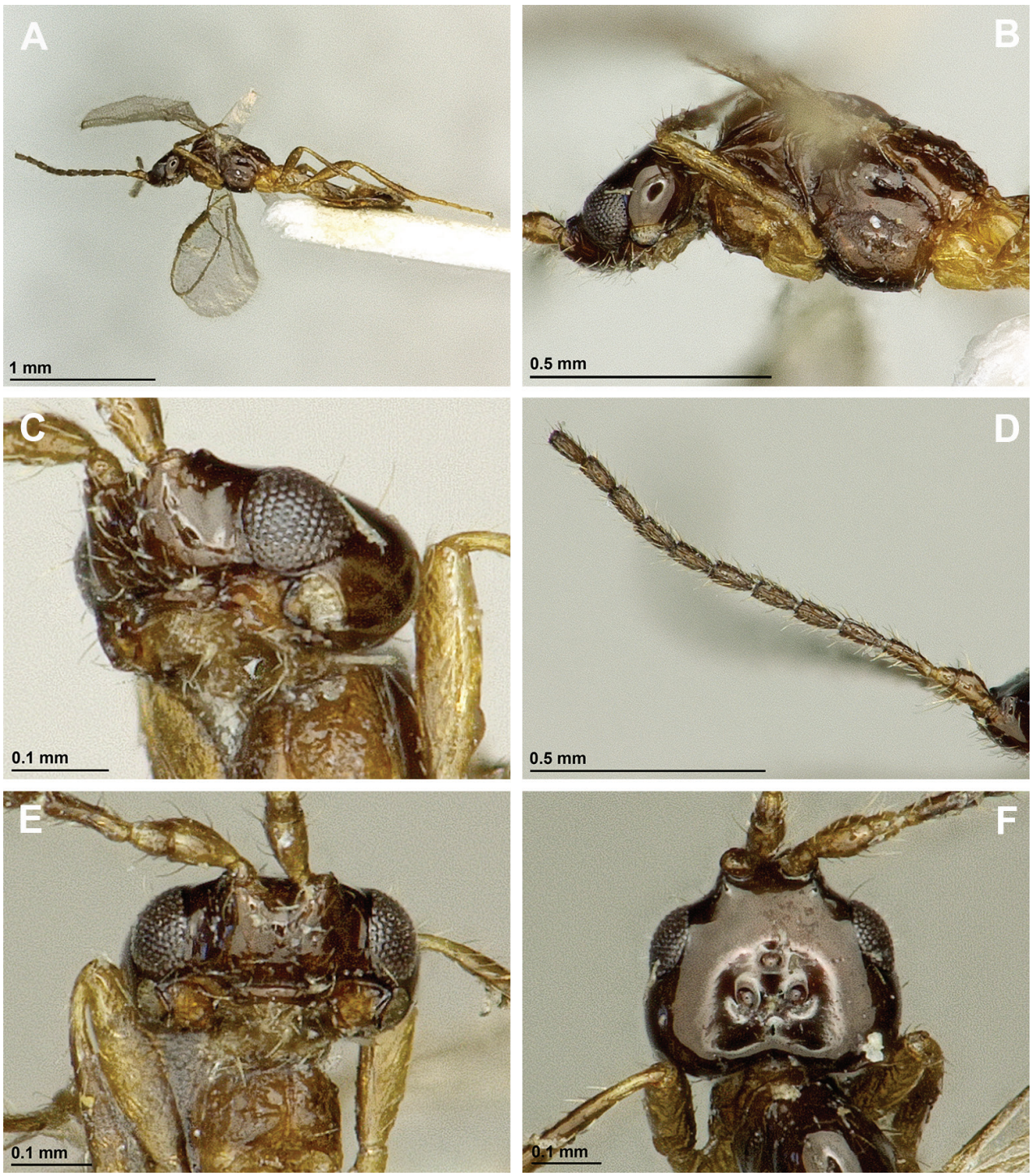

Figure 18. *Dinotrema* (*Pseudoprosapha*) *stenosoma* (van Achterberg, 1988), comb. nov. (holotype, male) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head, dorsal view.

Material examined. *Dinotrema* (*Synaldis*) *concolor*: Austria: • ♀, Mischerdorf, Burgenland, 5.ix.1956 (Fischer leg.) (NHMW); • ♀, Mischerdorf, Burgenland, 6.viii.1958 (Fischer leg.) (NHMW); • ♀, Spitzzicken, Burgenland, 5.ix.1956 (Fischer leg.) (NHMW). Hungary: • ♀, Nagyrákos, 6.vi.1985 (Rozner leg.) (HNHM). Slovakia: • ♀, Orosva Polhora, 25.vii.1988 (Podlussány leg.) (HNHM). *Dinotrema* (*Synaldis*) *cracipes* [= *Pterusa cracipes*]: ***Holotype***: Austria: • ♂, Wimpassing, Nieder-Österreich (Leitha-Gebirge), 2.v.1915 (Fischer leg.) (NHMW).

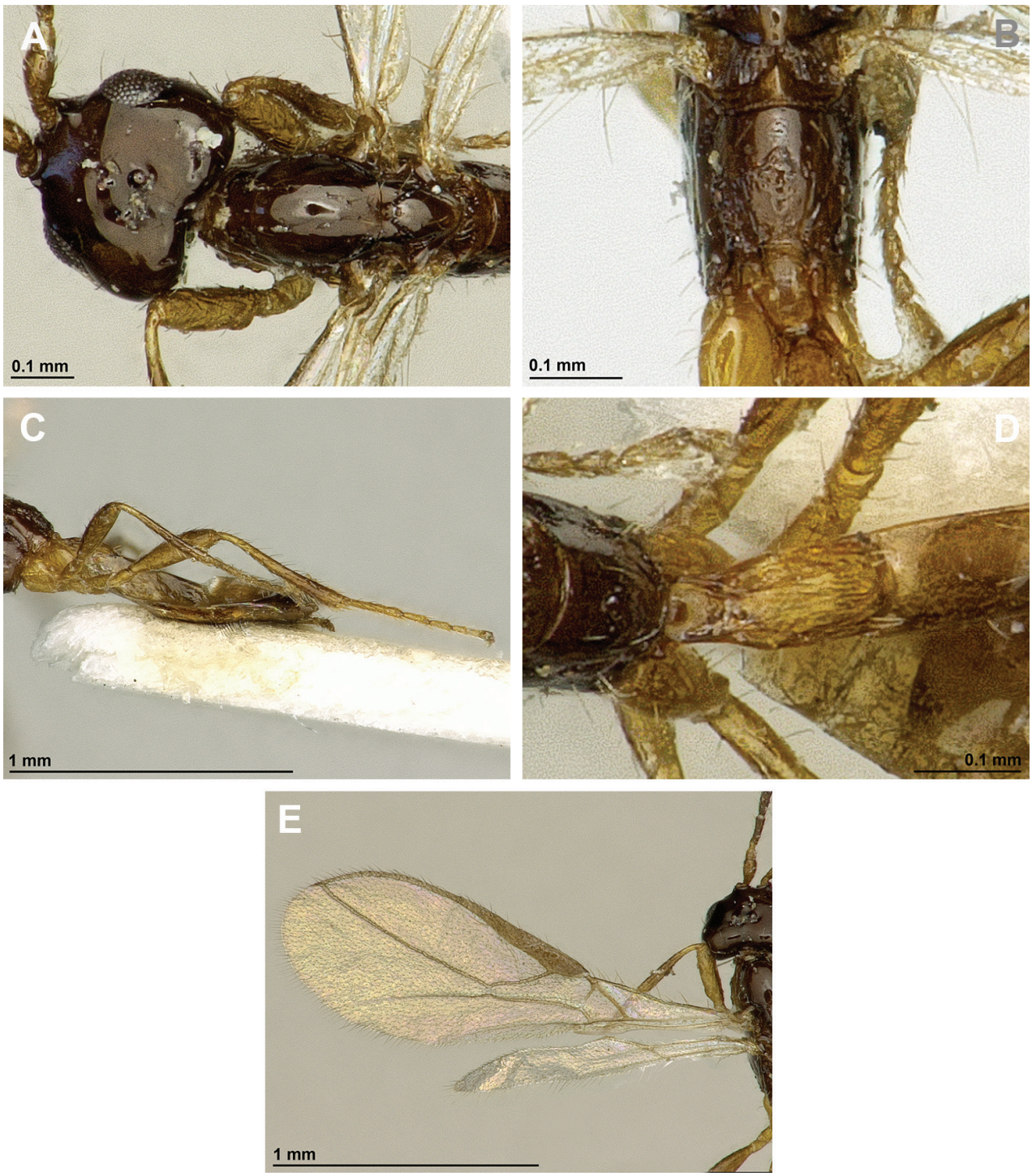

Figure 19. *Dinotrema* (*Pseudoprosapha*) *stenosoma* (van Achterberg, 1988), comb. nov. (holotype, male) **A** head and mesonotum, dorsal view **B** propodeum **C** legs and metasoma, lateral view **D** first metasomal tergite, dorsal view **E** fore and hind wings.

Diagnosis. The main characters of this subgenus are shared with *Dinotrema* sensu stricto, but it has vein 2-SR of fore wing absent.

Remarks. The status of *Synaldis* has been uncertain for a long time. Van Achterberg (1988) revised the genera of the *Aspilota* group and first synonymised this genus with the re-established *Dinotrema* based on the not enlarged paraclypeal fovea (the plesiomorphic state). As a result, the former

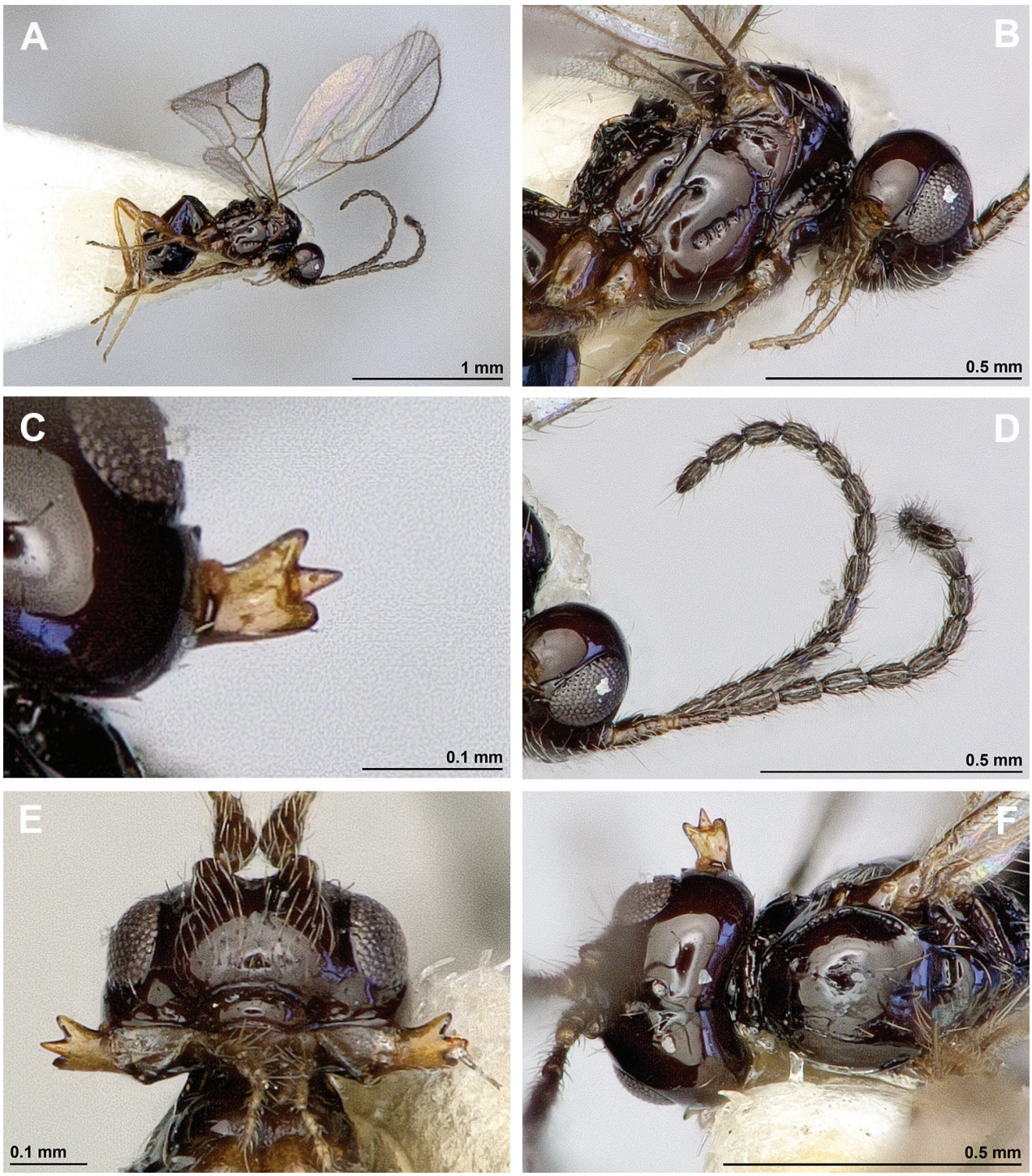

Figure 20. *Dinotrema* (*Synaldis*) *concolor* (Nees, 1812) (female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head and mesonotum, dorsal view.

Synaldis species were distributed among the genera *Aspilota* and *Dinotrema* according to the new used diagnostic feature, the size and position of the paraclypeal fovea. For some time, the synonymy of *Synaldis* was not accepted by several experts working on alysiine taxa (Fischer 1993a, 1993b; Papp 2001; Belokobylskij 2002; Peris-Felipo et al. 2014a). It is necessary to underline that the apomorphic feature of the subgenus, the complete reduction of vein 2-SR of the fore wing, is a peculiar evolutionary event which

Figure 21. *Dinotrema* (*Synaldis*) *concolor* (Nees, 1812) (female) **A** propodeum **B** legs, metasoma and ovipositor, lateral view **C** first metasomal tergite, dorsal view **D** fore and hind wings.

also resulted in the disappearance of the distinct break (corner) between veins r and 3-SR and this part is only gently and relatively widely curved. Such an apomorphic state of the wing venation might represent an important qualitative transformation and could support at least a subgeneric status of *Synaldis* (Belokobylskij 2002; Peris-Felipo and Belokobylskij 2014, 2017). However, the intermediate state is also known, both with the presence of non-sclerotised vein 2-SR and vein r not angled with vein 3-SR (e.g., *D.* (*D.*) *pulvinatum* (Stelfox & Graham) as depicted by van Achterberg 1988) or vein 2-SR entirely absent (e.g., *D.* (*S.*) *cespitator* (Belokobylskij, 2004), comb. nov.), *D.* (*S.*) *perfidum* (Fischer, 1970), comb. nov. (as depicted by Fischer 1970) and *D.* (*S.*) *trematosum* (Fischer, 1967), comb. nov. (as depicted by Fischer 1967) with vein r weakly angled with 3-SR). The variation of vein 2-SR from entirely absent to entirely present and non-sclerotised vein is aptly shown in *D.* (*D.*) *concinnum* (Haliday, 1838). Therefore, we agree with Zhu et al. (2017) to recognise *Synaldis* as a subgenus for convenience. Its position as separate genus likely will render the genus *Dinotrema* paraphyletic, and the loss of vein 2-SR occurred probably more than once in *Dinotrema* and is variable within some taxa as illustrated by *D. concinnum* (König 1972) and the type species of the genus *Synaldotrema* (Belokobylskij and Tobias 2002).

Genus *Leptotrema* van Achterberg, 1988

Leptotrema van Achterberg, 1988: 42; Chen and Wu 1994: 94; Belokobylskij 1998a: 219; Fischer 2002: 102; Yu et al. 2016.

Type species. *Aspilota dentifemur* Stelfox, 1943, by original designation (Figs 22, 23).

Material examined. (*Leptotrema dentifemur*) Denmark: • ♀, Stegelykke VG, 8–15.vii.1991 (Munk leg.) (PFEC). The Netherlands: • ♀, Putten (Gld.), Malaise trap, 26.ix–2.x.1973 (J.v.d. Vecht leg.) (RMNH).

Diagnosis. Mandible small, simple, tridentate, often with upper (first) tooth diminished with respect to lower (third) tooth. Paraclypeal fovea short, not reaching more than half distance between clypeus and inner margin of eyes. Mesoscutum with or without mesoscutal pit; notauli usually present only in anterior part of mesoscutum; precoxal sulcus usually present, propodeum with different types of sculpture and sometimes with longitudinal and/or transverse carinae, rarely entirely smooth. Fore femur has a distinct apomorphic character, viz., the presence of a large obtuse tooth (flange) or two or three small teeth. In fore wing, marginal cell never shortened; vein r originating from basal quarter of pterostigma; vein 2-SR usually present and distinctly sclerotised; veins m-cu and cu-a postfurcal; first subdiscal cell always closed postero-apically by vein CU1a. Metasoma of ♀ more or less distinctly compressed laterally. Ovipositor sheath usually not longer than metasoma.

Remarks. Only three rare *Leptotrema* species are known from the Palaearctic, Oriental and Australasian regions, *L. bovefemora* (Bhat, 1979), *L. dentifemur* (Stelfox, 1943) and *L. wilhelmense* Braet & van Achterberg, 2014. Wharton (2002) treated *Leptotrema* only as subgenus of *Dinotrema*, but some other experts (Fischer 2002; Belokobylskij and Tobias 2007; Braet and van Achterberg 2014) preferred to consider it as a valid genus based on its unique apomorphic character: the presence of the ventral tooth or teeth of the fore tibia. The study based on the main morphological characters show that *Leptotrema* deserves generic status.

Genus *Lysodinotrema* Fischer, 1995

Lysodinotrema Fischer, 1995: 717; Fischer 2002: 103; Yu et al. 2016.

Type species. *Lysodinotrema madli* Fischer, 1995, by original designation (Figs 24, 25).

Material examined. ***Holotype*** (*Lysodinotrema madli*) Madagascar: • ♀, Ste. Marie Flues Manandriana, 14–25.xi.1994 (Fischer leg.) (NHMW).

Diagnosis. Mandible small, simple, tridentate. Paraclypeal fovea short, remaining far from the inner margin of eyes. Mesoscutum without mesoscutal pit; notauli present only in anterior half of mesoscutum; precoxal sulcus present; propodeum mainly sculptured, without areola. In fore wing, marginal cell never shortened; vein r originating from basal quarter of pterostigma; vein 2-SR

Figure 22. *Leptotrema dentifemur* (Stelfox, 1943) (female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head and mesonotum, dorsal view.

present and sclerotised; veins m-cu and cu-a always postfurcal; first subdiscal cell completely open posteriorly and without vein 2-1A. Hind wing without closed cells. Metasoma of ♀ more or less distinctly compressed. Ovipositor sheath shorter than metasoma.

Remarks. This rare genus, with only three described species from the tropical areas (*L. madli* Fischer, 1995, *L. minimum* Fischer, 2004, *L. sarawakense*

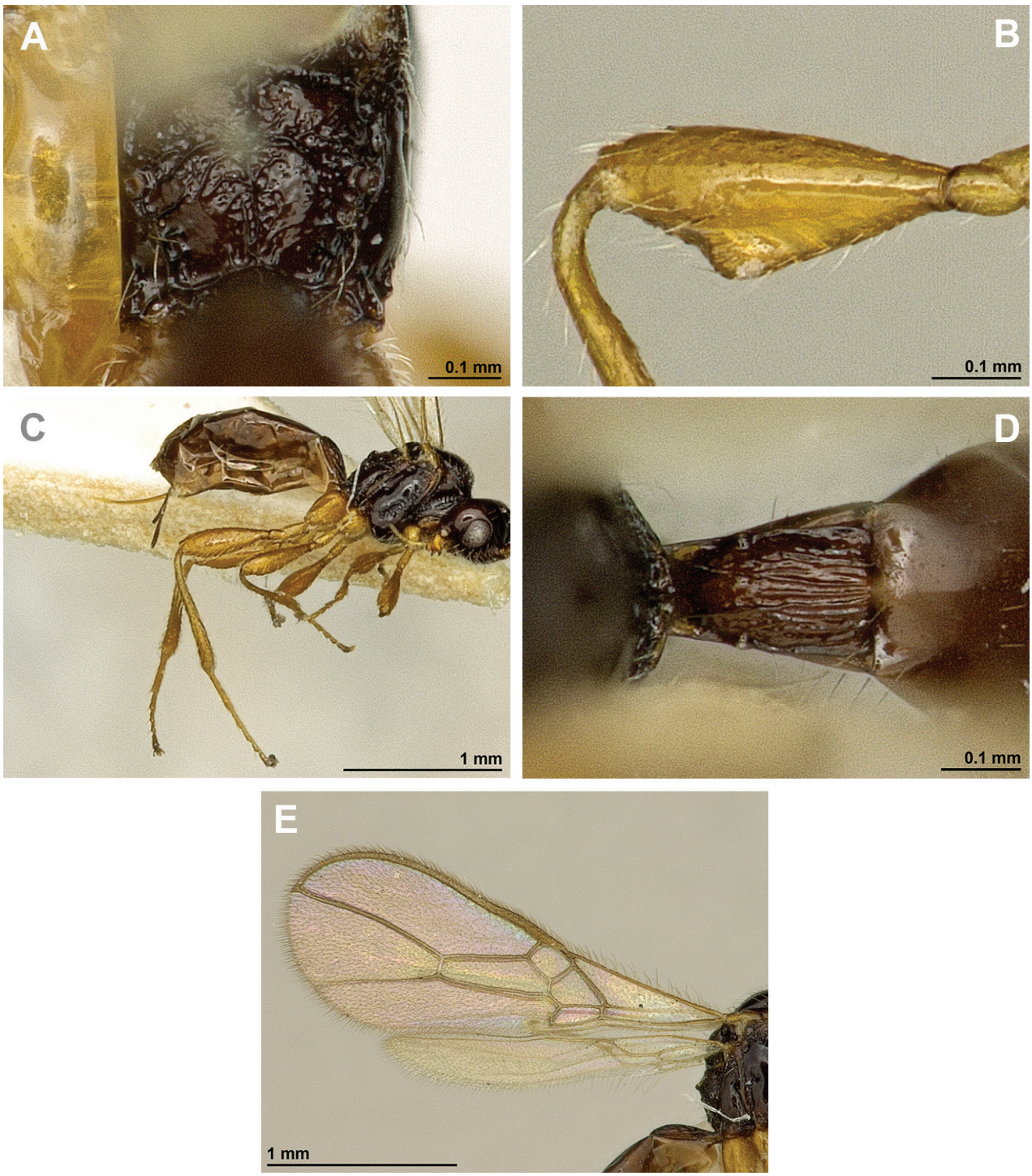

Figure 23. *Leptotrema dentifemur* (Stelfox, 1943) (female) **A** propodeum **B** fore femur, lateral view **C** legs, metasoma and ovipositor, lateral view **D** first metasomal tergite, dorsal view **E** fore and hind wings.

Fischer, 1995), is considered to be related with *Dinostigma* Fischer, 1966, because of sharing the open first subdiscal cell in the fore wing. However, the combination of closed cells in the hind wing (absent in *Dinostigma*), presence of vein 2-SR of fore wing (absent in *Dinostigma*) and of the precoxal sulcus (absent in *Dinostigma*) makes it possible to maintain *Lysodinotrema* as a valid genus.

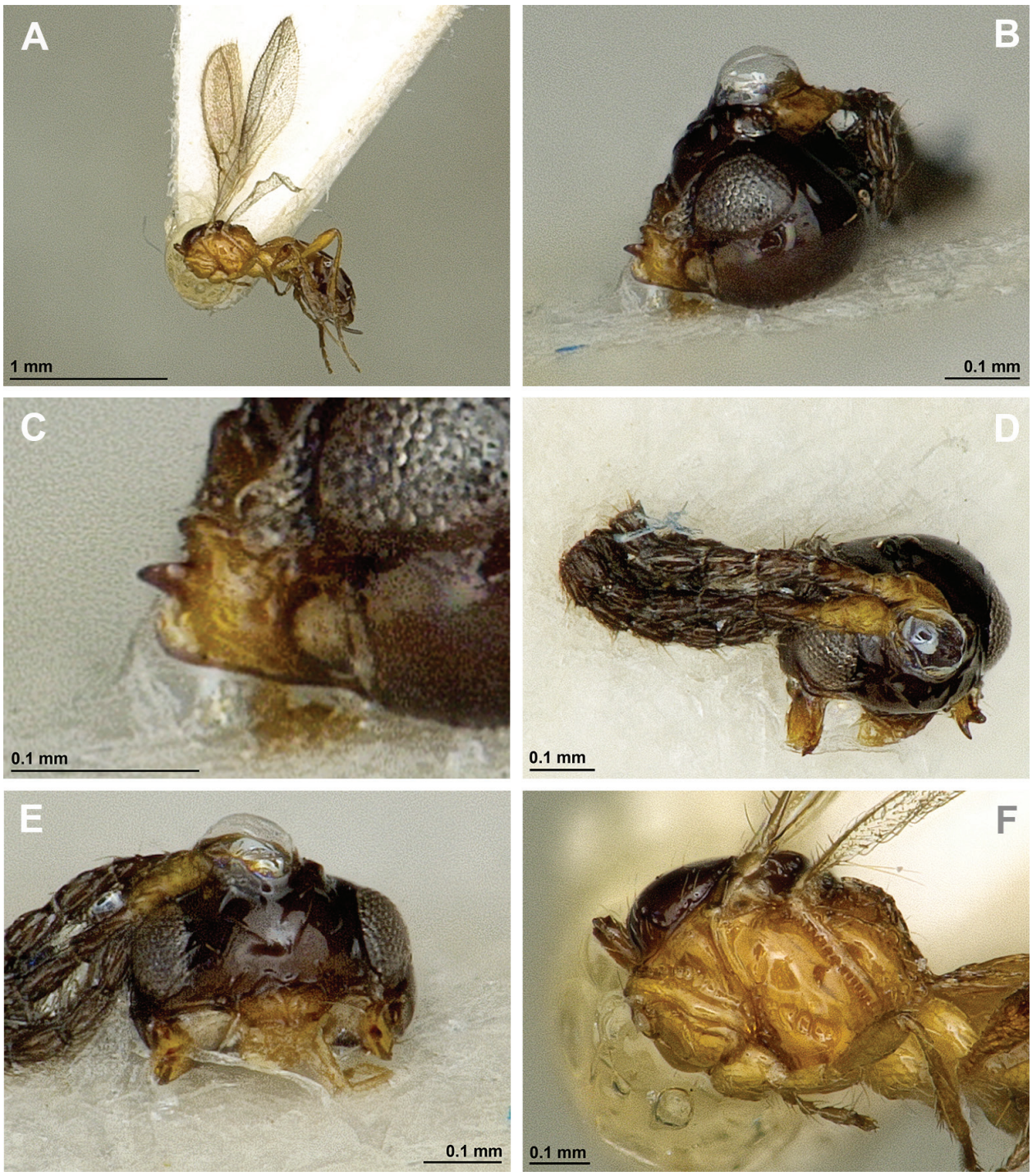

Figure 24. *Lysodinotrema madli* Fischer, 1995 (holotype, female) **A** habitus, lateral view **B** head, lateral view **C** mandible **D** antenna **E** head, front view **F** mesosoma, lateral view.

Genus *Panerema* Foerster, 1863

Panerema Foerster, 1863: 263; Szépligeti 1904: 203; van Achterberg 1988: 47; Fischer 2002: 102; Belokobylskij and Kula 2012: 43; van Achterberg and Vikberg 2014: 3; Yu et al. 2016.

Type species. *Panerema inops* Foerster, 1863, by original designation (lost) (Figs 26, 27).

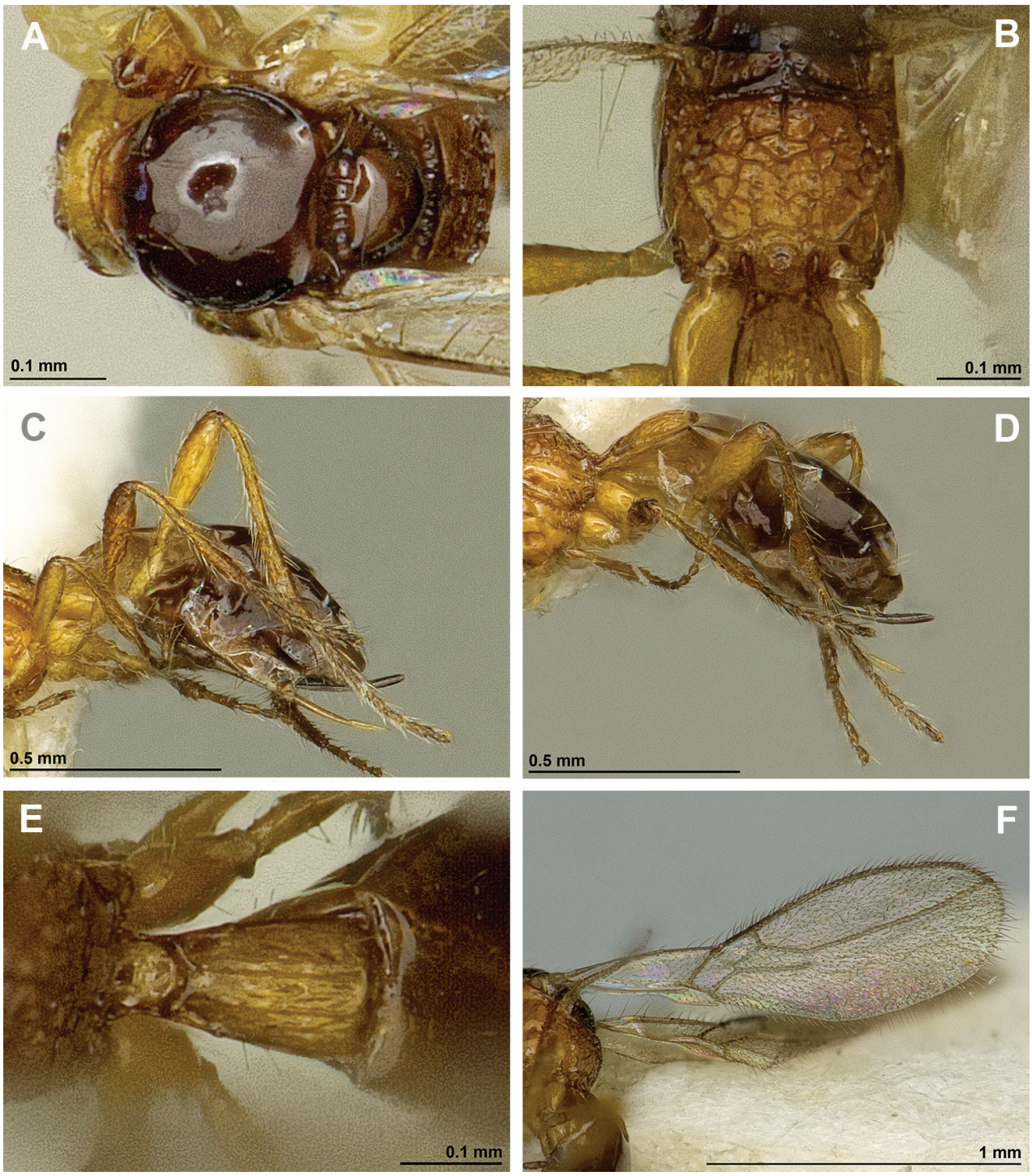

Figure 25. *Lysodinotrema madli* Fischer, 1995 (holotype, female) **A** mesonotum, dorsal view **B** propodeum **C** hind leg, lateral view **D** metasoma and ovipositor, lateral view **E** first metasomal tergite, dorsal view **E** fore and hind wings.

Material examined. (*Panerema inops*): Germany: • ♀, Zaarensee, Seggenwiese, 29.vi.1998 (v. Broen leg.) (PFEC). The Netherlands: • ♀, Cadier, 5.v.1975 (B. v. Aartsen leg.) (RMNH).

Diagnosis. Mandible small, simple, tridentate, often with upper (first) tooth diminished with respect to lower (third) tooth. Paraclypeal fovea short, not reaching more than half distance between clypeus and inner margin of eyes. Third antennal segment distinctly elongated. Mesoscutum with or without

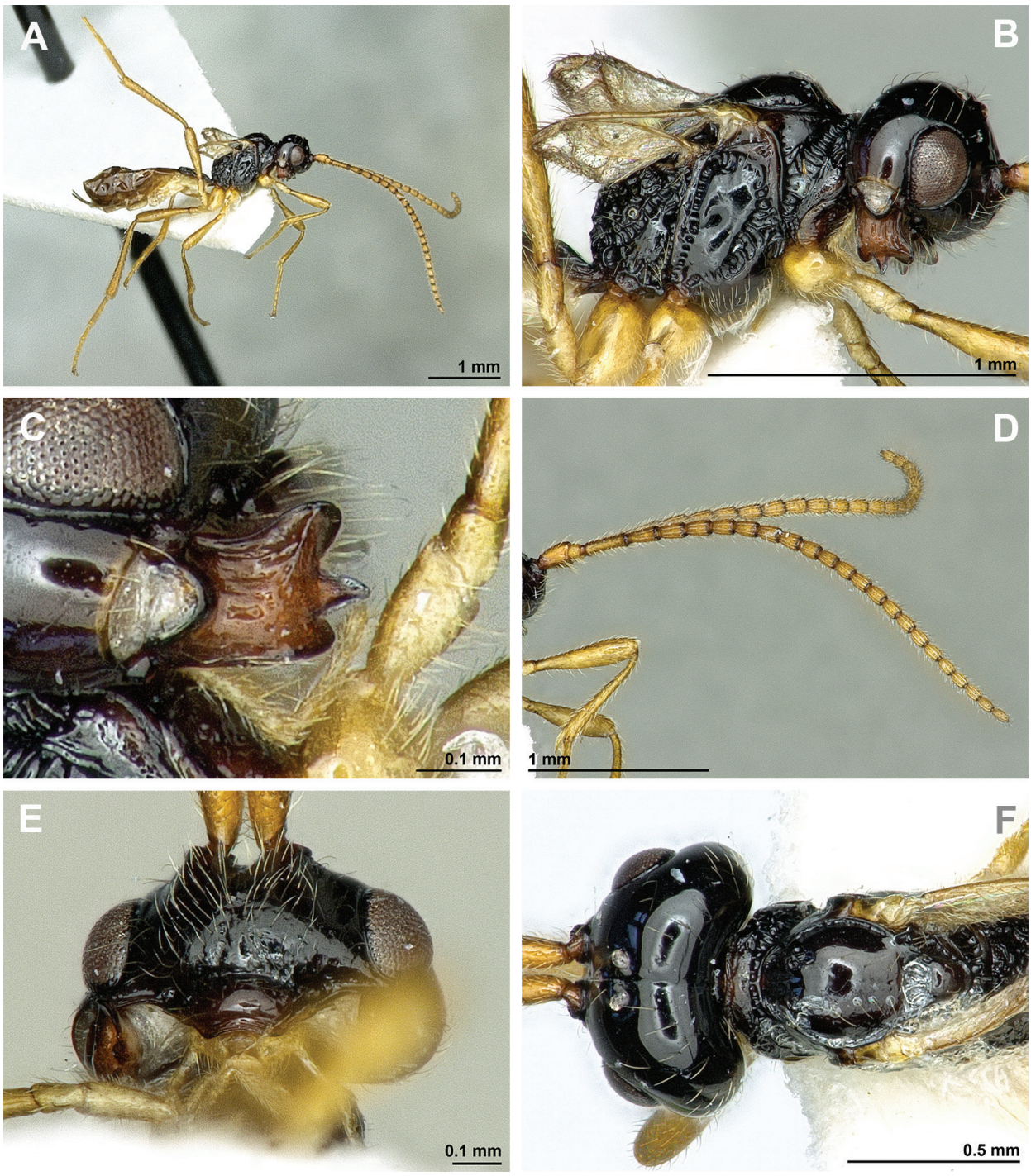

Figure 26. *Panerema inops* Foerster, 1863, comb. nov. (female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head and mesonotum, dorsal view.

mesoscutal pit; notauli usually present only in anterior part of mesoscutum. Scutellum with a transverse crenulate depression subposteriorly. Females are brachypterous with strongly reduced wings (commonly in this group of genera males are brachypterous but females macropterous). The preserved distal anterior veins in such wing are distinctly thickened, with veins r and 2-SR of the fore wing absent but hind wing with closed cells (van Achterberg 1988; Belokobylskij and Kula 2012). Metasoma of ♀ more or less distinctly compressed laterally. Ovipositor sheath usually not longer than metasoma.

Figure 27. *Panerema inops* Foerster, 1863, comb. nov. (female) **A** propodeum **B** first metasomal tergite, dorsal view **C** legs, metasoma and ovipositor, lateral view **D** fore wing.

Remarks. During many years, *Panerema* was considered as a valid genus (van Achterberg 1988; Fischer 2002; Belokobylskij and Tobias 2007; Belokobylskij and Kula 2012). As shown by van Achterberg (1988) despite its uncertain position of this taxon it has two synapomorphies, viz., the scutellum has a transverse crenulate depression subposteriorly and the third antennal segment is at least 1.5× longer than the fourth segment. The value of both characters is uncertain (although perhaps apomorphic), but the diagnostic character study carried out shows that *Panerema* deserves the status of genus due to its distance from other genera.

Genus *Synaldotrema* Belokobylskij & Tobias, 2002, stat. nov.

Synaldotrema Belokobylskij & Tobias, 2002: 3 (as subgenus of *Dinotrema* Foerster); Belokobylskij and Tobias 2007: 11; van Achterberg and Vikberg 2014: 3; Yu et al. 2016.

Type species. *Dinotrema* (*Synaldotrema*) *speciosum* Belokobylskij & Tobias, 2002, by original designation (Figs 28, 29).

Material examined. ***Holotype*** (*Dinotrema* (*Synaldotrema*) *speciosum*) Russia: • ♀, Primorskiy kray, 10 km SSW of Partizansk, border of forest, 12–13.

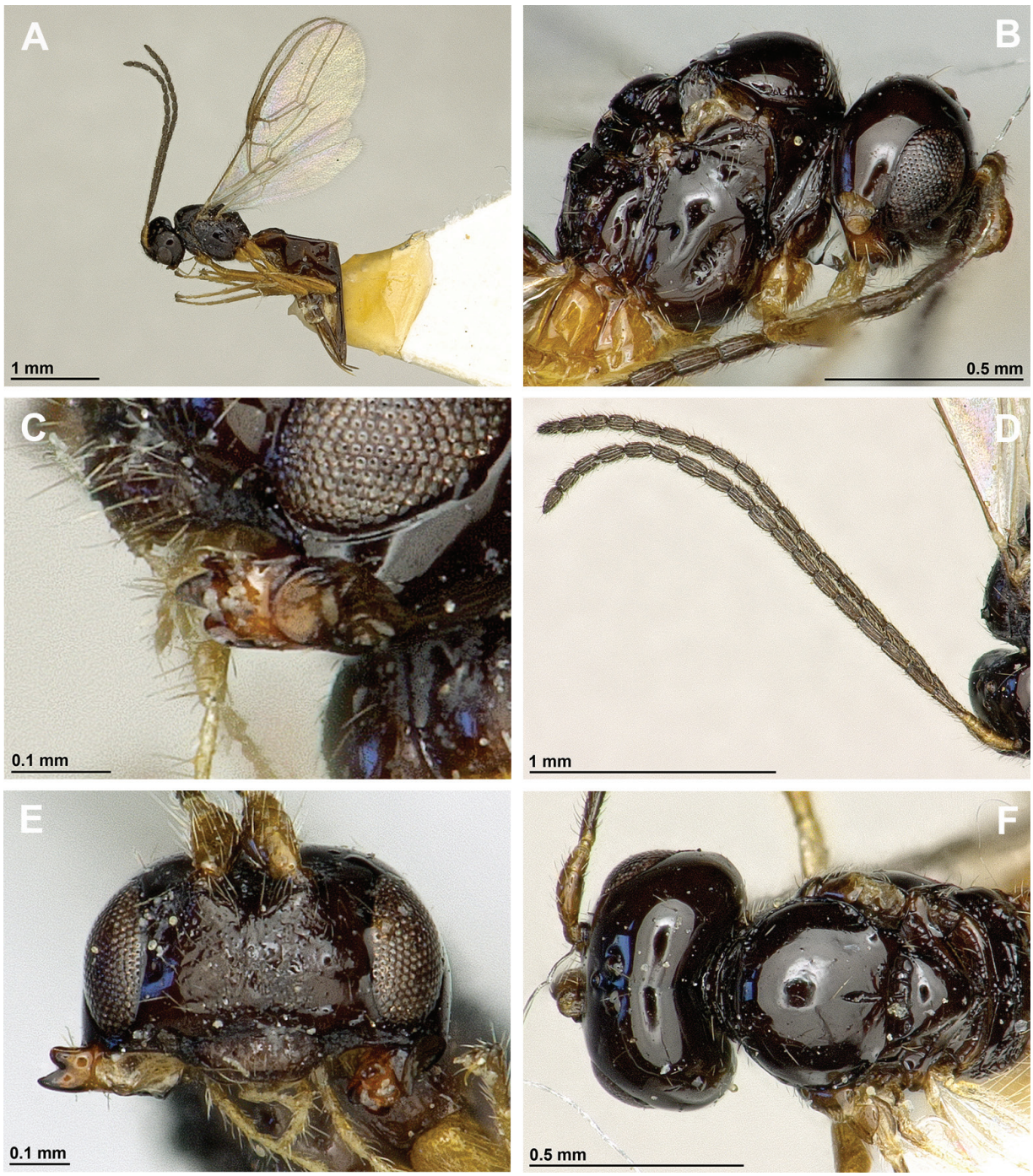

Figure 28. *Synaldotrema speciosum* Belokobylskij & Tobias, 2002, comb. nov. (holotype, female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head and mesonotum, dorsal view.

vii.1996 (S. Belokobylskij) (ZISP). ***Paratypes*** (*Dinotrema* (*Synaldotrema*) *speciosum*) Russia: • ♀, Primorskiy kray, 50 km N of Olga, mixed forest, 29.vii.1979 (S. Belokobylskij) (ZISP); • ♀, Primorskiy kray, Pogranichnyi District, Barabash-Levada, forest, 3–6.vi.1980 (S. Belokobylskij) (ZISP); • ♀, Primorskiy kray, 42 km S of Plastun, forest, 24.vi.1979 (S. Belokobylskij) (ZISP); • ♀, Republic of Tuva, 14 km E of Kyzyl, lowland of Ka Khem River, 31.v.1975 (D. Kasparyan) (ZISP).

Diagnosis. *Synaldotrema* Belokobylskij & Tobias shares the main characters of *Dinotrema* sensu stricto but differs by having the hypopygium of the female strongly retracted under the posterior tergites of metasoma and the fourth

Figure 29. *Synaldotrema speciosum* Belokobylskij & Tobias, 2002, comb. nov. (holotype, female) **A** propodeum **B** legs, metasoma and ovipositor, lateral view **C** first metasomal tergite, dorsal view **D** fore and hind wings.

tergite strongly elongated, ~ 2.5× longer than fifth tergite (vs approximately of equal length in *Dinotrema* s. str.).

Remarks. The type species of *Synaldotrema* (*D. speciosum* Belokobylskij & Tobias, 2002) has a variable vein 2-SR of the fore wing. This vein is usually present, but sometimes, mostly discoloured and its posterior half or sometimes entire vein 2-SR is absent (Belokobylskij and Tobias 2002). Previous studies showed that the value of the reduction of this vein illustrates well the subgeneric division (Belokobylskij and Tobias 2002), however the current diagnostic character study proved that retraction of hypopygium has enough value to consider *Synaldotrema* as a valid genus.

Orthostigma group

Genus *Cubitalostigma* Fischer, 1998

Cubitalostigma Fischer, 1998: 482; Fischer 2002: 100; Yu et al. 2016.

Type species. *Cubitalostigma reichli* Fischer, 1998, by monotypy (Figs 30, 31).

Material examined. ***Holotype*** (*Cubitalostigma reichli*) INDONESIA: • ♀, Sumatra, Aceh, Gunung Leuser Nat. Pk., Ketambe Res. Sta., 1° rainforest, Mature forest, Terrace 4 closed canopy, 400 m, 3°41'N, 97°29'E, Malaise trap W/pans, 1–30. xi.1989 (D.C. Darling leg.) (NHMW).

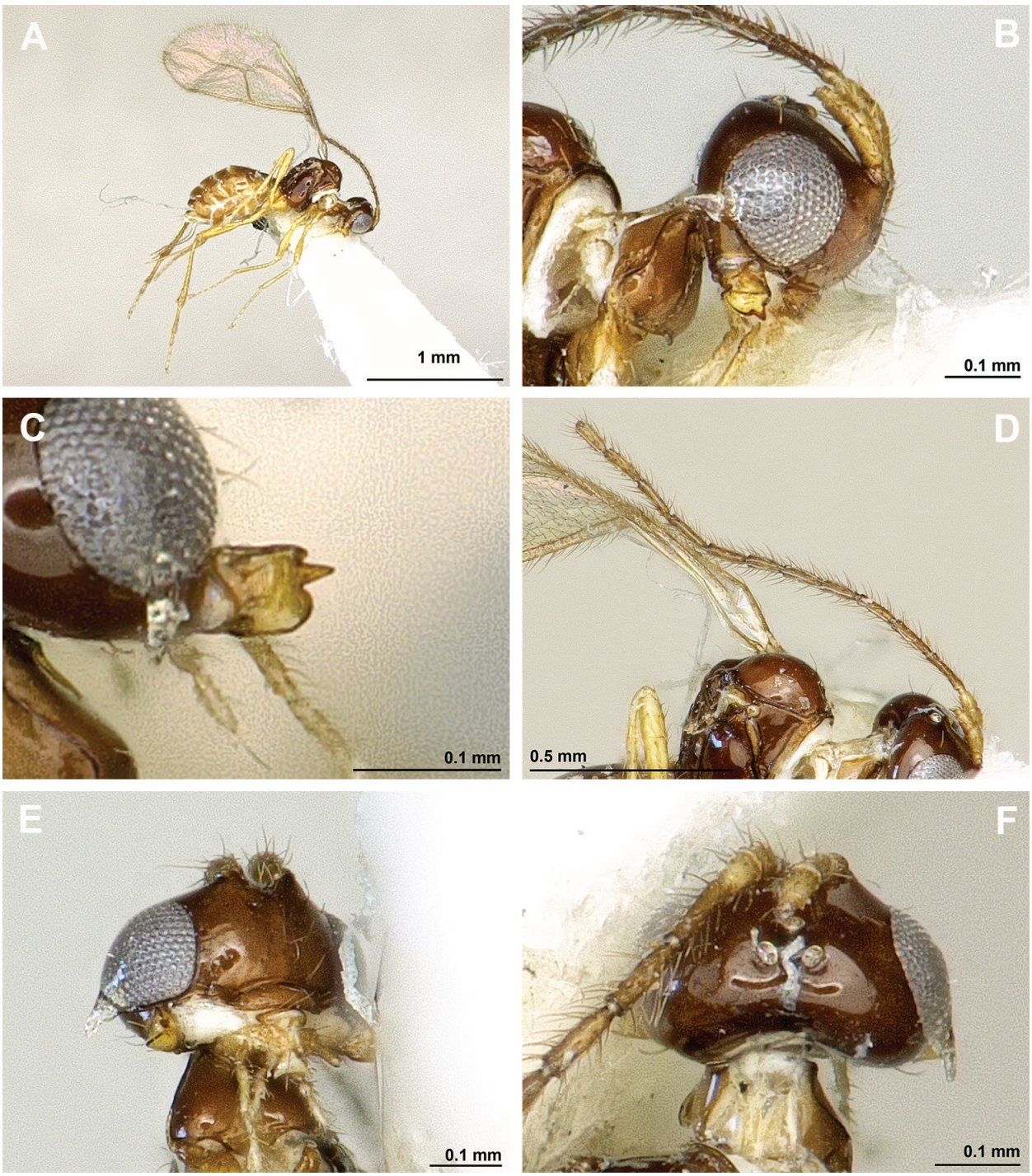

Figure 30. *Cubitalostigma reichli* Fischer, 1998 (holotype, female) **A** habitus, lateral view **B** head, lateral view **C** mandible **D** antenna **E** head, front view **F** head, dorsal view.

Diagnosis. Mandible small, simple, tridentate, with upper (first) tooth diminished with respect to lower (third) tooth, with complete submedial transverse curved carina. Paraclypeal fovea short, remaining far removed from edge of eyes. Mesoscutum without mesoscutal pit; notauli present only in anterior part of mesoscutum; precoxal sulcus always absent; propodeum smooth. In fore wing, marginal cell never shortened; vein r originating from almost middle of pterostigma; first submarginal cell very reduced; second submarginal cell widened; vein 2-SR present and well sclerotised; first subdiscal cell closed postero-apically by

Figure 31. *Cubitalostigma reichli* Fischer, 1998 (holotype, female) **A** mesosoma, lateral view **B** mesonotum, dorsal view **C** propodeum **D** legs, metasoma and ovipositor, lateral view **E** first metasomal tergite, dorsal view **D** fore and hind wings.

CU1a vein. Subbasal cell of hind wing minute but closed. Metasoma of ♀ distinctly compressed laterally. Ovipositor sheath shorter than metasoma.

Remarks. This is a peculiar monotypic genus with only the type species known from Indonesia. *Cubitalostigma* is characterised by the very aberrant venation of the fore wing, with vein r arising almost from the middle of the very narrow pterostigma, very far from its basal part. This is a unique character within the subtribe Aspilotina.

Genus *Neorthostigma* Belokobylskij, 1998

Neorthostigma Belokobylskij, 1998b: 9; Fischer 2001: 65; Wharton 2002: 91 (as subgenus); Belokobylskij and Tobias 2007: 10 (as valid genus); Yu et al. 2016; Belokobylskij et al. 2019: 215; Peris-Felipo et al. 2020: 33; Dias de Oliveira and Penteado-Dias 2023: 481.

Type species. *Neorthostigma eoum* Belokobylskij, 1998 (= *Aspilota macrops* Stelfox & Graham, 1951), by original designation (Figs 32, 33) [synonymised by Peris-Felipo et al. 2020].

Material examined. ***Holotype*** (*Aspilota macrops*) Ireland: • ♀, Sligo, S. shore of Lough Gill near Doonee Rock, 15.x.1937 (AWS leg.) [USNM #76022; USNMENT01569377] (NMNH). ***Holotype*** (*Neorthostigma eoum* (*= macrops*)) Russia: • ♀, Primorskiy kray, Anisimovka, forest, glades, 16.viii.1979 (S. Belokobylskij leg.) (ZISP). ***Paratypes*** (*Neorthostigma eoum* (*= macrops*)) Russia: • 2 ♀, Primorskiy kray, Spassk-Dal'niy, forest, glades, 16 and 22–23. viii.1995 (S. Belokobylskij leg.) (ZISP); • 1 ♀, Sakhalin Island, 10 km W of Aniva, mixed forest, 15.viii.1981 (S. Belokobylskij leg.) (ZISP). Japan: • 1 ♂, Fukuoka, Nogochi, Fukuoka-shi, 28.viii.1992 (V. Makarkin leg.) (ZISP).

Additional studied material. Norway: • 1 ♀, Oslo [AK], Maridalen, Dausjøen, Spruce forest, 5.vi–16.x.2010, 60.01234 N 10.787665 E, 160 m, Malaise trap, river outlet (Lars Ove Hansen leg.) (NHMO). Russia. Leningradskaya Province: • 1 ♀, Tolmachevo, mixed forest, 22.viii.1960 (V. Tobias leg), "*Aspilota macrops* Stelf., Tobias det. 1961" (ZISP). Primorskiy kray: • 1 ♀, 30 km E of Spassk-Dal'niy, forest, glades, 4.vi.1984 (S. Belokobylskij leg.) (ZISP); • 1 ♀, Nadezhdinskiy District, 15 km SSW of Nezhino, forest, 16–18.vii.1993 (S. Belokobylskij leg.) (ZISP); • 1 ♀, 30 km SE of Ussuriysk, forest, border of forest, 12–17.vii.2001 (S. Belokobylskij leg.) (ZISP); • 1 ♀, Vladivostok, Okeanskaya, forest, 25.vii.2001 (S. Belokobylskij leg.) (ZISP); • 1 ♀, Vladivostok, Sedanka, forest, border of forest, 30.vii.2001 (S. Belokobylskij leg.) (ZISP).

Diagnosis. Mandible small, tridentate, with very small and screwed upper tooth, with complete transverse and curved submedian carina. Paraclypeal fovea long, reaching or almost reaching inner margin of eyes. Mesoscutum always without mesoscutal pit; notauli present only in anterior half of mesoscutum; precoxal sulcus always developed; propodeum with wide and rather distinctly delineated by carina areola and with different types of sculpture but sometimes almost smooth. In fore wing, marginal cell never shortened; vein r originating from basal quarter of pterostigma; vein 2-SR always developed; veins m-cu and cu-a postfurcal; first subdiscal cell always closed postero-apically by vein CU1a. Metasoma of ♀ more or less distinctly compressed. Ovipositor sheath shorter than metasoma.

Remarks. Five described species are known: one from the Palaearctic region (widely distributed from Ireland to Japan), two from Papua New Guinea (Peris-Felipo et al. 2020) and two from Brazil (Dias de Oliveira and Penteado-Dias 2023). This genus is closely related to *Orthostigma* according to its specialised mandibles. Wharton (2002) treated *Neorthostigma* as a subgenus of *Orthostigma*. However, the combination of such important diagnostic characters such as the absence of eye-antennal socket sulcus, the

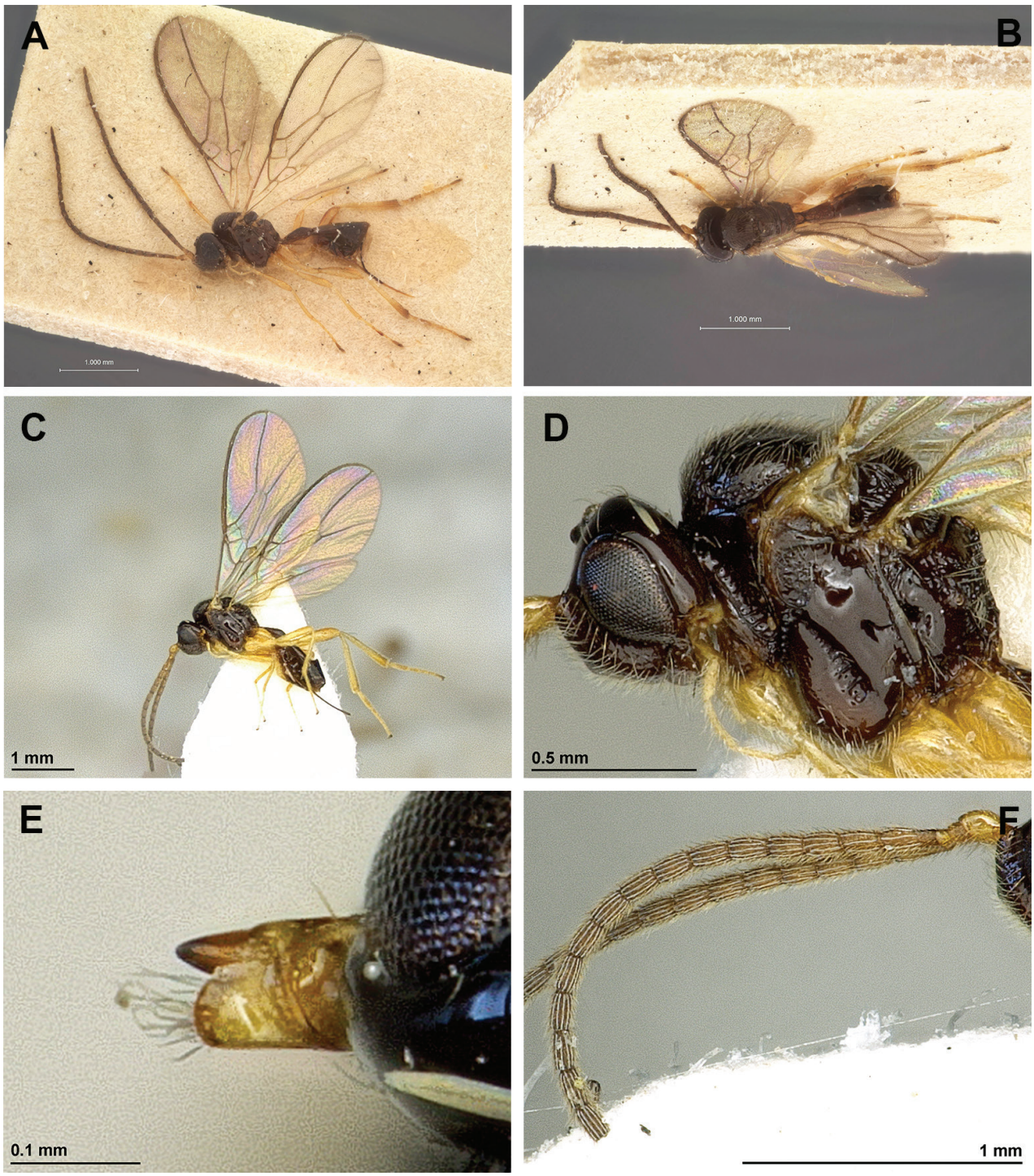

Figure 32. *Neorthostigma macrops* (Stelfox & Graham, 1951) (**A, B**: female, holotype of *A. macrops*; **C–F**: female, holotype of *Neorthostigma eoum*) **A, C** habitus, lateral view **B** habitus, dorsal view **D** head and mesosoma, lateral view **E** mandible **F** antenna.

large paraclypeal fovea reaching or almost reaching inner margin of eye, the usual absence of mesoscutal pit, the face and sometimes the mesoscutum entirely covered by dense setosity distinctly indicate a separate position of this taxon at the genus level (Belokobylskij et al. 2019; Peris-Felipo et al. 2020). Its hosts are still unknown.

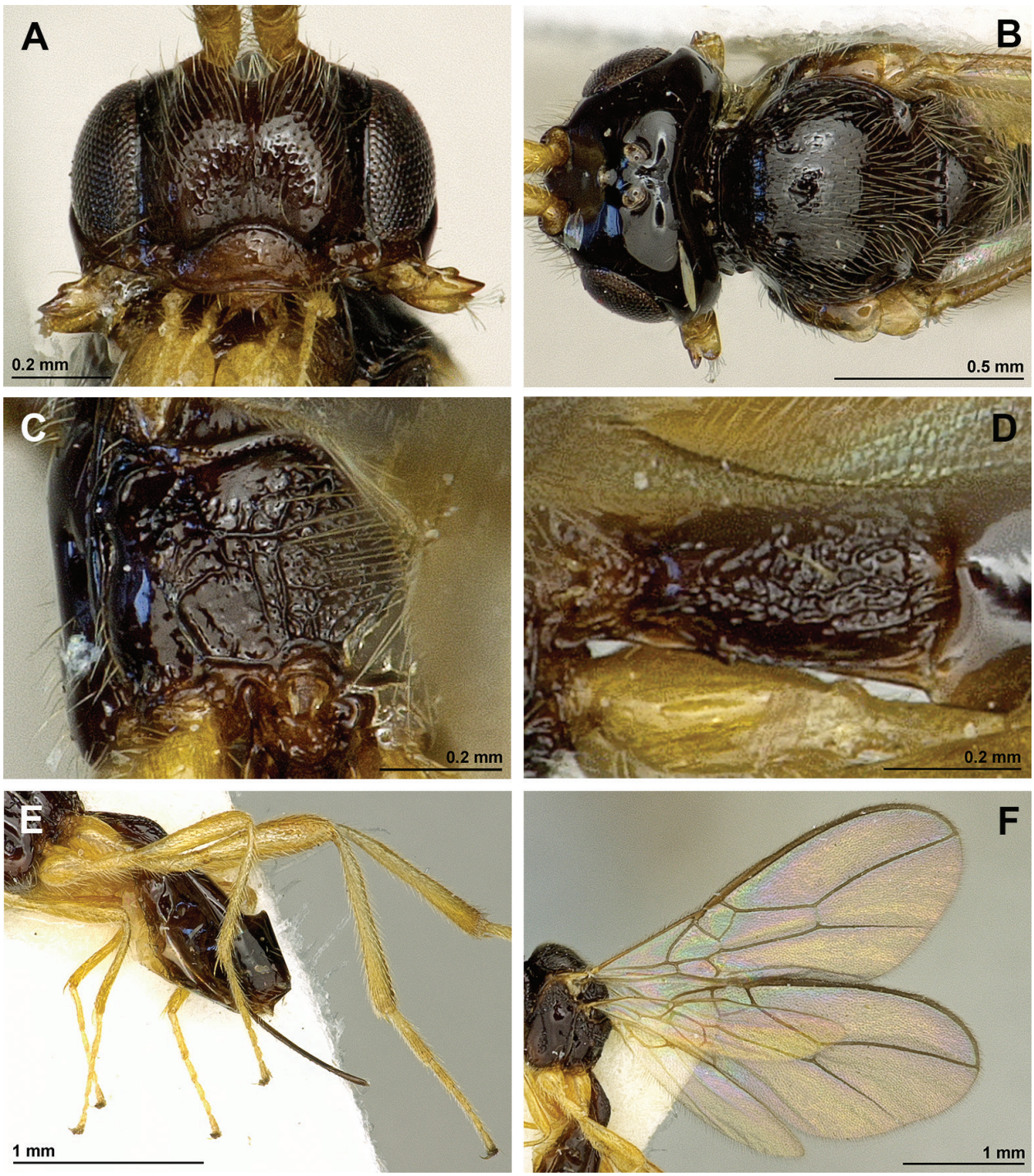

Figure 33. *Neorthostigma macrops* (Stelfox & Graham, 1951) (female, holotype of *Neorthostigma eoum*) **A** head, front view **B** head and mesonotum, dorsal view **C** propodeum, dorsal view **D** first metasomal tergite, dorsal view **E** hind leg, metasoma and ovipositor, lateral view **F** fore and hind wings.

Genus *Orthostigma* Ratzeburg, 1844

Figs 34–41

Orthostigma Ratzeburg, 1844: 53; Königsmann 1969: 2; Shenefelt 1974: 997; Wharton 1980: 85; Tobias 1986: 117; van Achterberg 1988: 44; Chen and Wu 1994: 99; Fischer 1995: 670; Belokobylskij 1998a: 209; Fischer 2002: 102; Wharton 2002: 91; Belokobylskij and Tobias 2007: 10; Yu et al. 2016; Zhu et al. 2017: 68.

Africostigma Fischer, 1995: 677 (as subgenus of *Orthostigma*); Yu et al. 2016; Peris-Felipo and Belokobylskij 2020: 411.

Patrisaspilota Fischer, 1995: 721; Fischer 2002: 102; 2004: 78; 2010: 636; Wharton 2002: 91 (as subgenus of *Orthostigma*); Yu et al. 2016; Peris-Felipo et al. 2019: 366; Peris-Felipo and Belokobylskij 2020: 412.

Whartonstigma Peris-Felipo in Peris-Felipo and Belokobylskij 2020: 412 (as subgenus of *Orthostigma*).

Type species. *Aphidius flavipes* Ratzeburg, 1844: 71, by monotypy.

Synonyms. *Delocarpa* Foerster, 1863; *Ischnocarpa* Foerster, 1863; *Patrisaspilota* Fischer, 1995; *Africostigma* Fischer, 1995; *Whartonstigma* Peris-Felipo, 2020.

Diagnosis. Mandible small, tridentate and with a wide ventral lobe as third tooth, with complete submedial transverse curved carina. Paraclypeal fovea short, far distant from inner margin of eyes. First flagellar segment usually longer or sometimes as long as second flagellar segment (slightly shorter in subgenus *Africostigma*). Mesoscutum usually with mesoscutal pit; notauli often present only in anterior part of mesoscutum, but in subgenus *Patrisaspilota* notauli almost reaching mesoscutal pit; precoxal sulcus always present; propodeum usually with different types of sculpture and sometimes with longitudinal or transverse carinae, rarely almost smooth. In fore wing, marginal cell never shortened; vein r originating from basal quarter of pterostigma; vein 2-SR usually distinctly sclerotised (but absent in subgenus *Whartonstigma*); veins m-cu and cu-a postfurcal; first subdiscal cell always closed postero-apically by vein CU1a. Metasoma of ♀ more or less distinctly laterally compressed. Ovipositor sheath usually not longer than metasoma.

Remarks. This genus includes more than 60 described species and is easily separated from other genera in the *Aspilota* group by the presence of the peculiar structure of mandible with complete transverse and curved submedial carina and usually wide lobe-shaped third tooth.

Currently four subgenera are recognised within this genus, *Africostigma* Fischer, 1995, *Orthostigma* sensu stricto, *Patrisaspilota* Fischer, 1995, and *Whartonstigma* Peris-Felipo, 2020 (Peris-Felipo and Belokobylskij 2020).

Subgenus *Africostigma* Fischer, 1995

Africostigma Fischer, 1995: 677 (as subgenus of *Orthostigma*); Yu et al. 2016; Peris-Felipo and Belokobylskij 2020: 411.

Type species. *Orthostigma* (*Africostigma*) *karkloofense* Fischer, 1995, by original designation (Figs 34, 35).

Material examined. ***Holotype*** (*Orthostigma* (*Africostigma*) *karkloofense*) South Africa: • ♀, Howick, Natal, Karkloof Forest, 19.ix.1963 (Haeselbarth leg.) (ZSSM).

Diagnosis. This Afrotropical subgenus includes two species from South Africa and shares the main diagnostic characters with *Orthostigma* but differs from all other subgenera by having the first flagellar segment of antenna shorter than the second one.

Figure 34. *Orthostigma* (*Africostigma*) *karkloofense* Fischer, 1995 (holotype, female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head, dorsal view.

Subgenus *Orthostigma* sensu stricto

Figs 36, 37

Orthostigma Ratzeburg, 1844: 53; Königsmann 1969: 2; Shenefelt 1974: 997; Wharton 1980: 85; Tobias 1986: 117; van Achterberg 1988: 44; Chen and Wu 1994: 99; Fischer 1995: 670; Belokobylskij 1998a: 209; Fischer 2002: 102; Wharton 2002: 91; Belokobylskij and Tobias 2007: 10; Yu et al. 2016; Zhu et al. 2017: 68; Peris-Felipo and Belokobylskij 2020: 412.

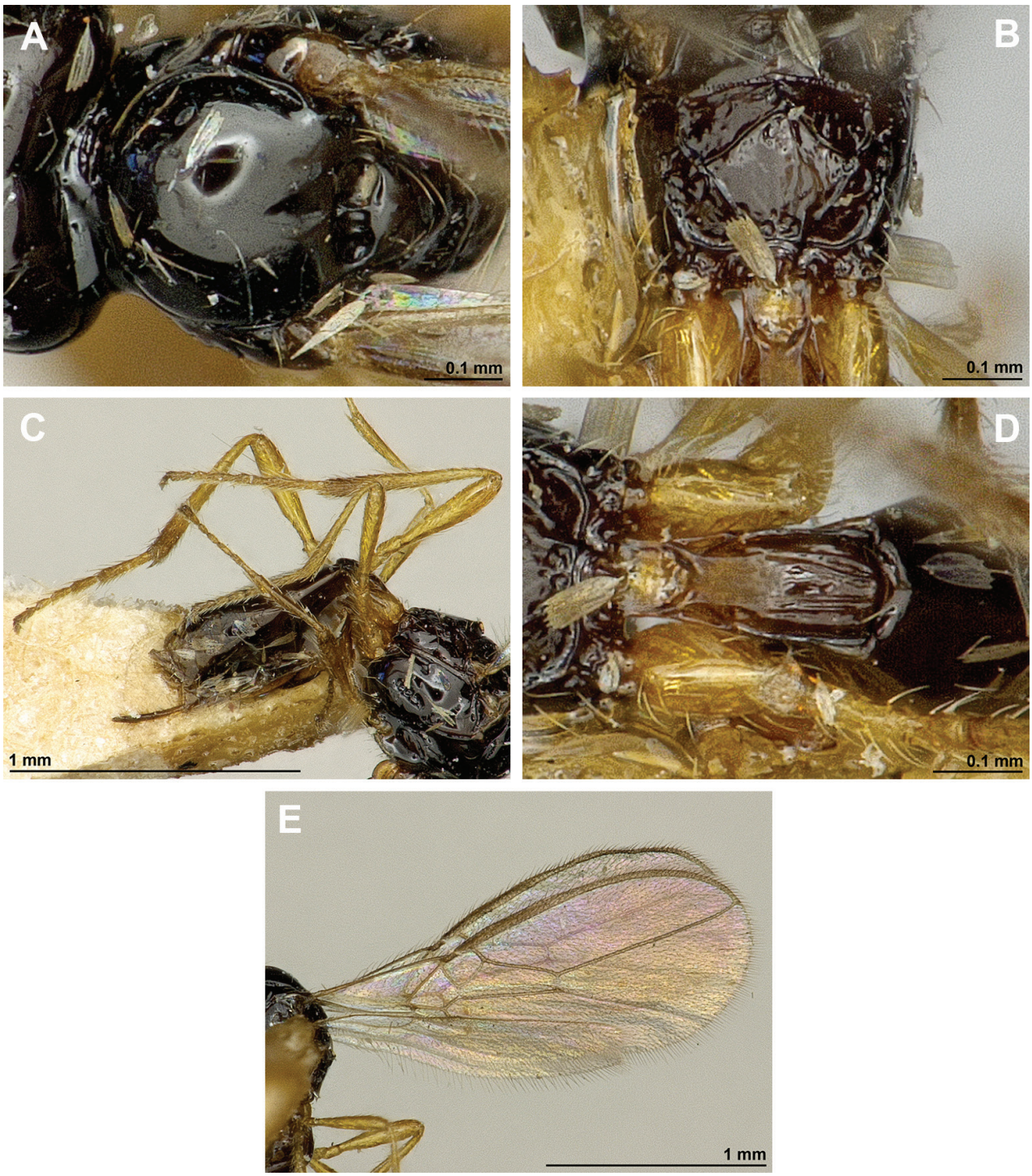

Figure 35. *Orthostigma* (*Africostigma*) *karkloofense* Fischer, 1995 (holotype, female) **A** mesonotum, dorsal view **B** propodeum **C** legs, metasoma and ovipositor, lateral view **D** first metasomal tergite, dorsal view **E** fore and hind wings.

Type species. *Aphidius flavipes* Ratzebrug, 1844, by monotypy.

Material examined. Several species from Palaearctic region were studied. For example:

– *Orthostigma beyarslani* Fischer, 1995: Spain: • ♀, Alicante, Torrevieja, Natural Park of Lagunas de la Mata-Torrevieja, 25.v.2004 (ENV).

– *Orthostigma laticeps* (Thompson, 1895): Spain: • ♀, Alicante, Alcoi, Natural Park of Carrascal de La Font Roja, 20.v.2004 (ENV).

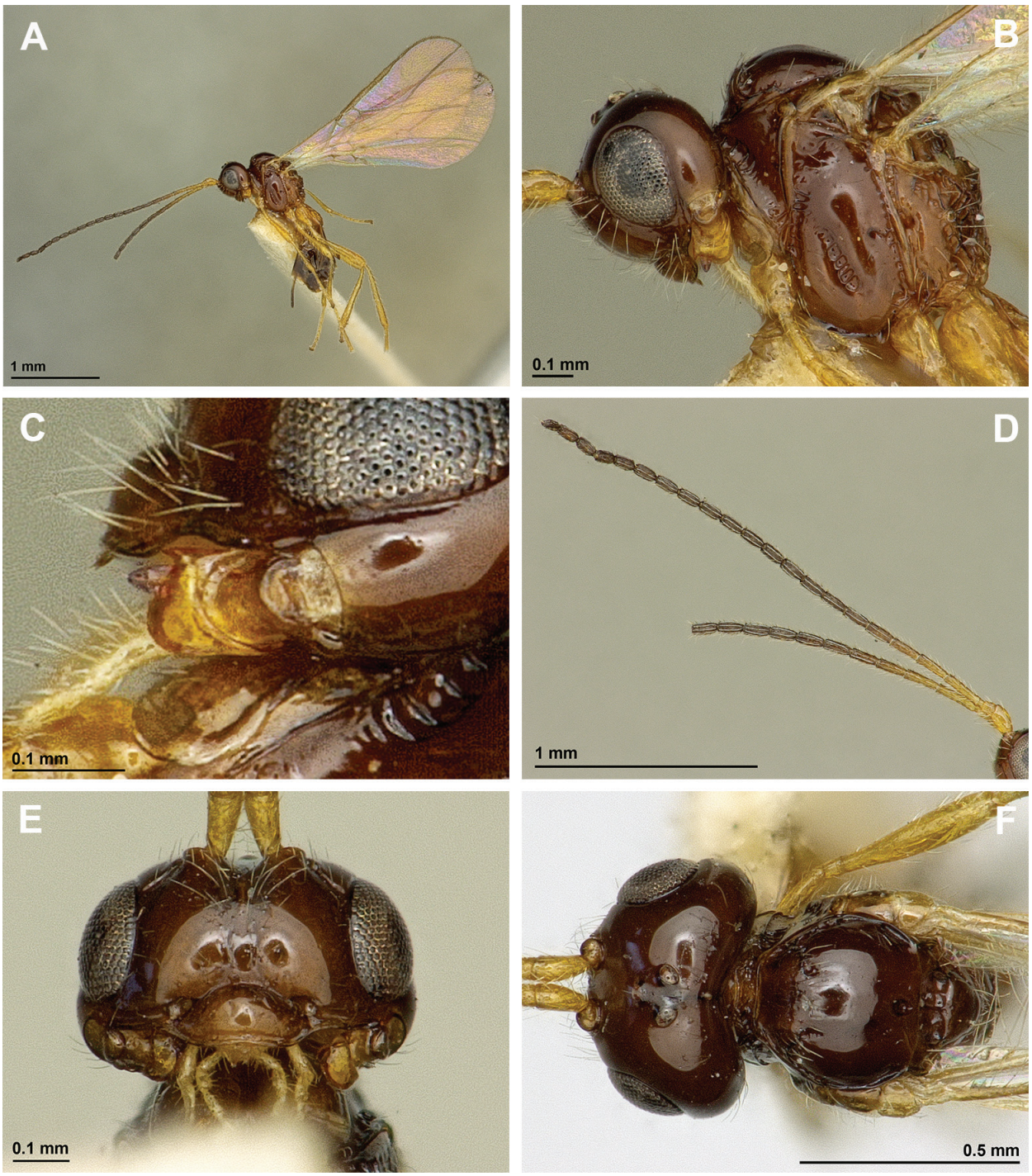

Figure 36. *Orthostigma* (*Orthostigma*) *mandibulare* (Tobias, 1962) (female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head and messonotum, dorsal view.

– *Orthostigma maculipes* (Haliday, 1838): Spain: • ♀, Castellon, Pobla de Benifassà, Natural Park of Tinença de Benifassà, 26.ix.2005 (ENV).

– *Orthostigma mandibulare* Tobias, 1962: Russia: Holotype: • ♀, Leningradskaya oblast'. Tolmachevo, border of forest near floodplain of Ostrovenka River, 19.viii.1960, Tobias [leg] (ZISP).

– *Orthostigma pumilum* (Nees, 1834): Spain: • ♀, Castellon, Pobla de Benifassà, Natural Park of Tinença de Benifassà, 17.vi.2004 (ENV).

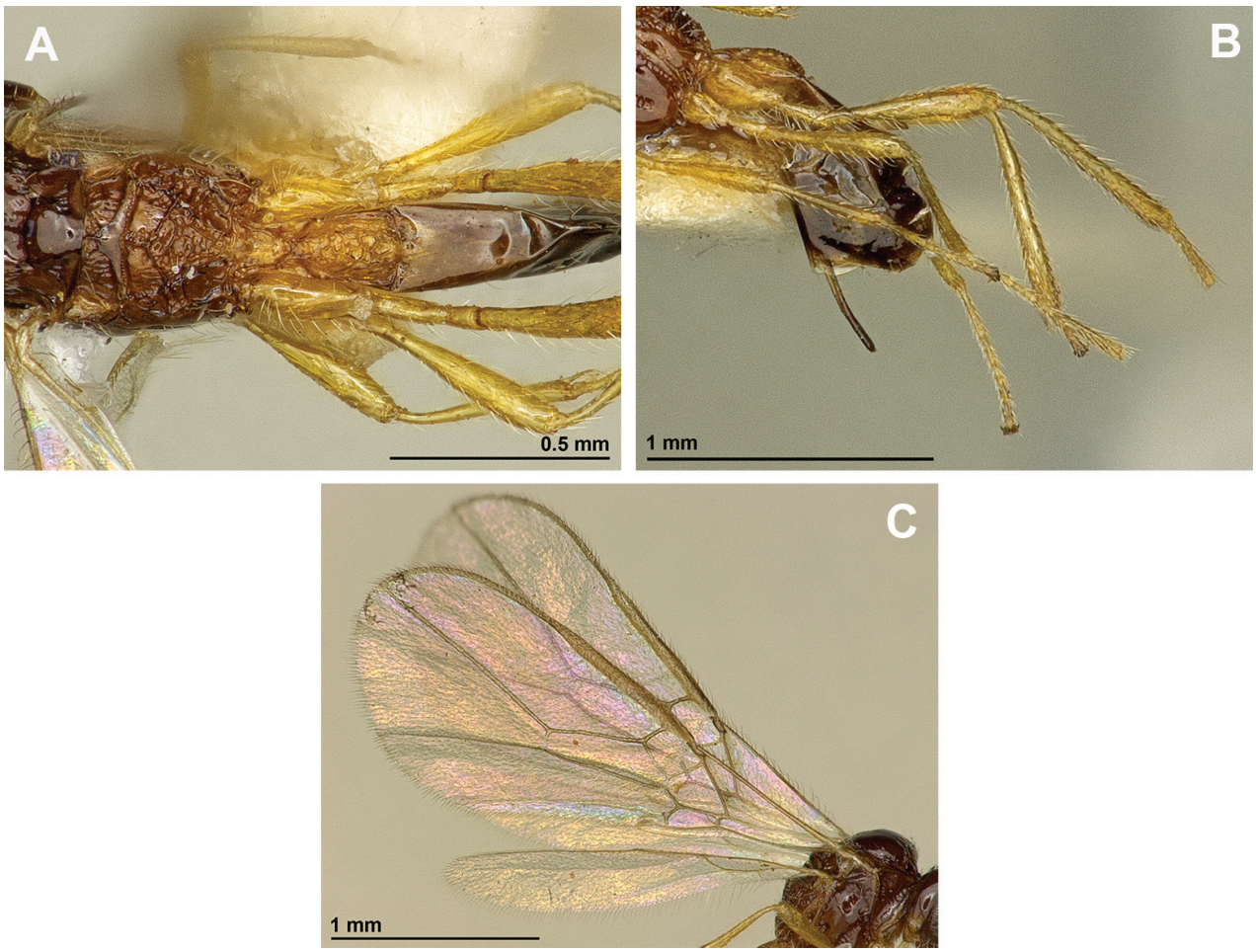

Figure 37. *Orthostigma* (*Orthostigma*) *mandibulare* (Tobias, 1962) (female) **A** propodeum, and metasomal tergites, dorsal view **B** legs, metasoma and ovipositor, lateral view **C** fore and hind wings.

– *Orthostigma sculpturatum* (Tobias, 1962): Spain: • ♀, Castellon, Pobla de Benifassà, Natural Park of Tinença de Benifassà, 28.viii.2006 (ENV).

Diagnosis. Main characters for the subgenus *Orthostigma* are the long first flagellar segment (longer than second segment), the notauli only anteriorly present on the mesoscutum and fore wing with vein 2-SR present and more or less distinctly sclerotised.

Remarks. This is the largest subgenus with about 60 known species from the Holarctic, Oriental, and Australasian regions.

Subgenus *Patrisaspilota* Fischer, 1995

Patrisaspilota Fischer, 1995: 721; Fischer, 2002: 102; 2004: 78; 2010: 636; Wharton 2002: 91 (as subgenus of *Orthostigma*); Yu et al. 2016; Peris-Felipo et al. 2019: 366; Peris-Felipo and Belokobylskij 2020: 412.

Type species. *Patrisaspilota memoranda* Fischer, 1995 (= *Orthostigma multicarinatum* Tobias, 1990) by original designation (Figs 38, 39). Synonymised by Peris-Felipo et al. 2019.

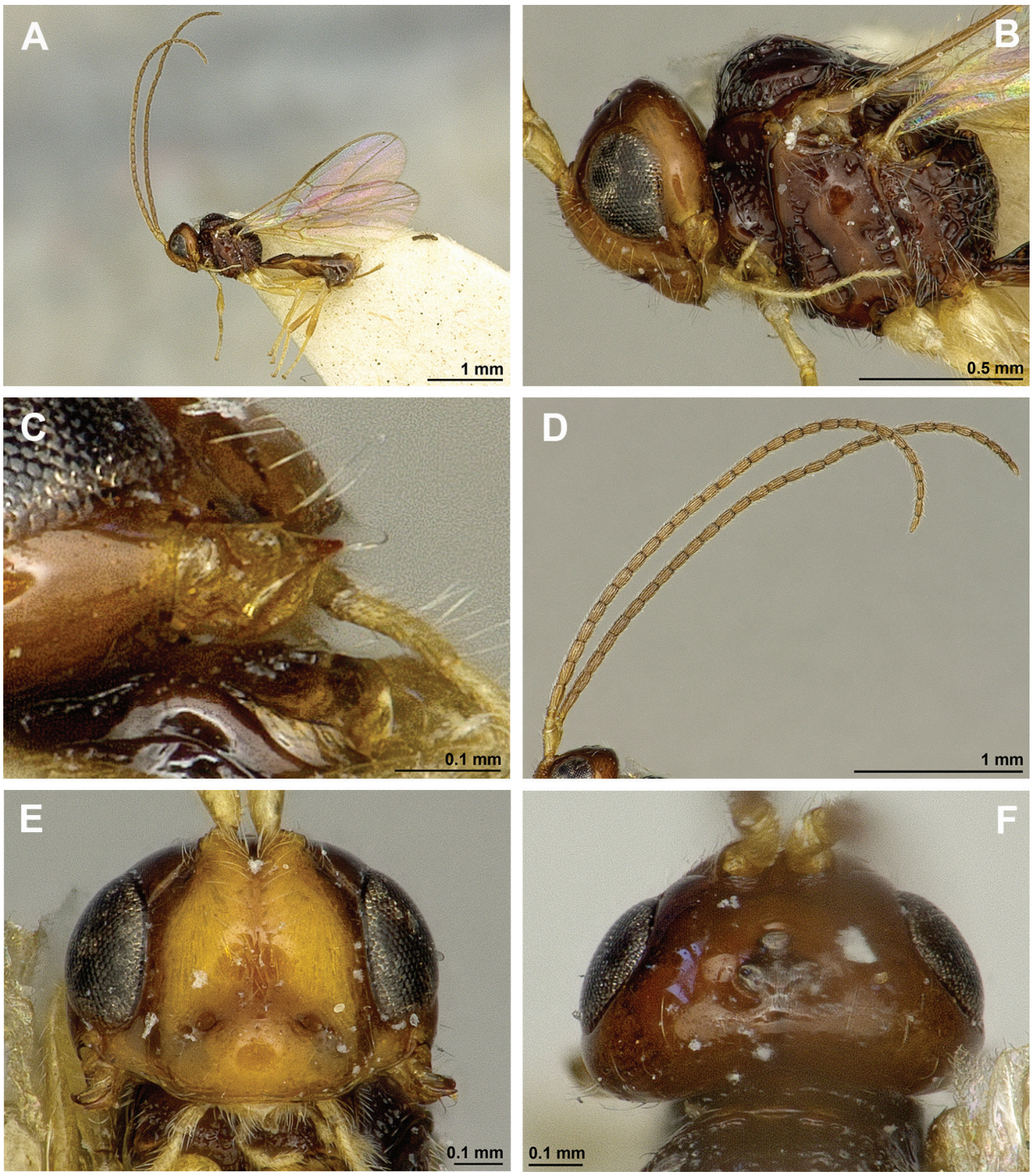

Figure 38. *Orthostigma* (*Patrisaspilota*) *multicarinatum* Tobias, 1990 (holotype, female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head, dorsal view.

Material examined. ***Holotype*** (*Orthostigma* (*Patrisaspilota*) *multicarinatum*) Vietnam: • ♀, Bathuok, 125 km W of Thanh Hoa, prov. Thanh Hoa, 26.i.1989 (B. Korotyaev leg.) (ZISP). ***Paratype*** (*Orthostigma* (*Patrisaspilota*) *multicarinatum*) Vietnam: • ♀, Vietnam, Tram Lap, 20 km N of Buon Luoi, prov. Gia Lai – Con Tum, 6.xii.1988 (Sharkov leg.) (ZISP).

Diagnosis. This subgenus shares the main characters of *Orthostigma* but has the notauli almost reaching the mesoscutal pit.

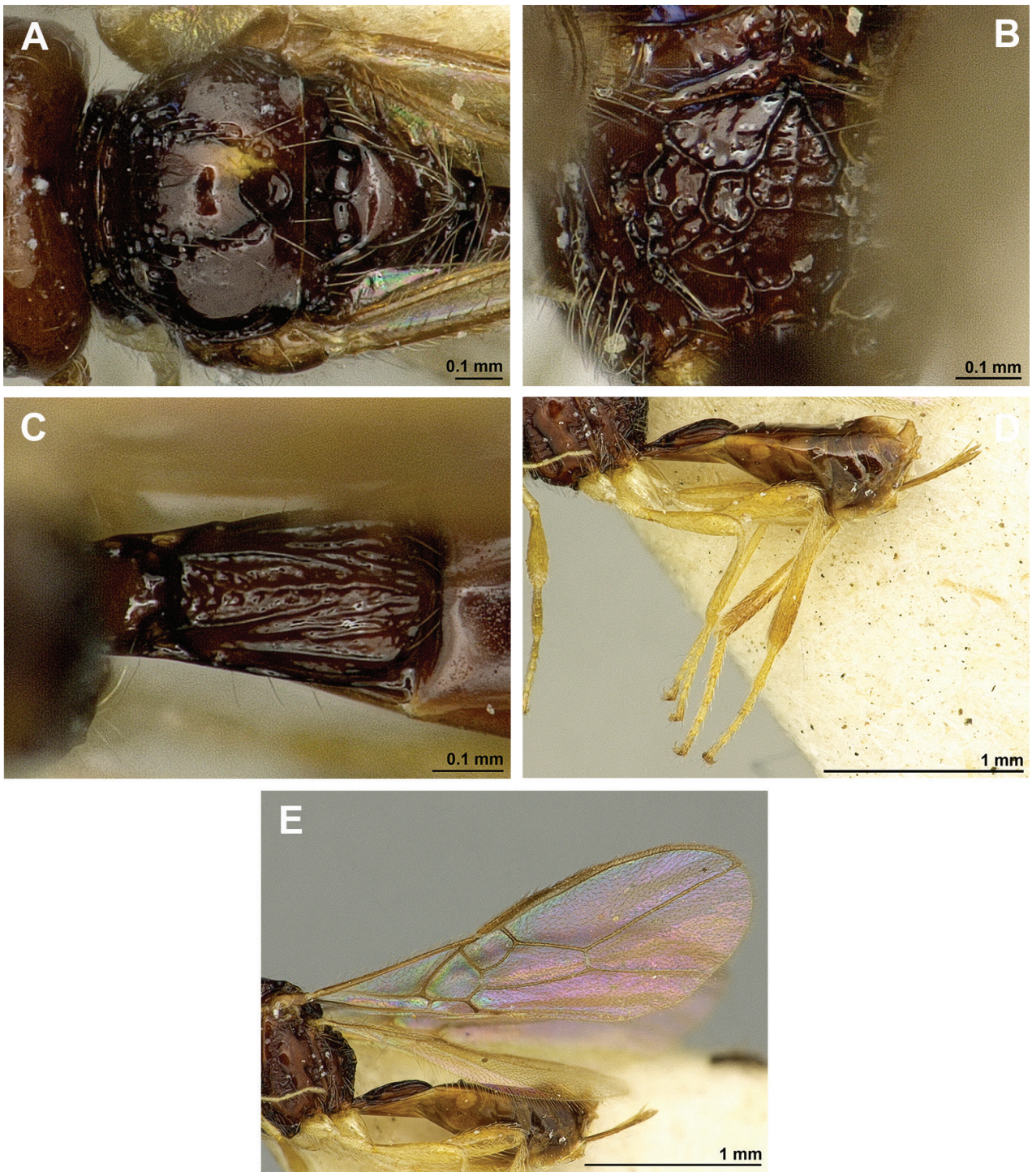

Figure 39. *Orthostigma* (*Patrisaspilota*) *multicarinatum* Tobias, 1990 (holotype, female) **A** mesonotum, dorsal view **B** propodeum **C** first metasomal tergite **D** legs, metasoma and ovipositor, lateral view **E** fore and hind wings.

Remarks. The four Oriental species of this subgenus share the almost completely developed notauli as in *Dinotrema* (*Alitha*). The notauli consist of a row of closely located large points more or less reaching the mesoscutal pit. The presence of such type of notauli in different genera of the subtribe Aspilotina (*Orthostigma* and *Dinotrema*) is obviously a parallelism and perhaps indicates the limited value of the character, viz., at least as subgeneric character.

Subgenus *Whartonstigma* Peris-Felipo, 2020

Whartonstigma Peris-Felipo in Peris-Felipo & Belokobylskij, 2020: 412 (as subgenus of *Orthostigma*).

Type species. *Orthostigma gallowagi* Wharton, 2002, by original designation (Figs 40, 41).

Material examined. ***Holotype*** (*Orthostigma* (*Whartonstigma*) *gallowagi*): Australia: • ♀, Queensland, Wongabel S. F., 6 km S of Atherton, 12.xi–1.xii.1983, Storey and Brown. M.T. (QMBA). ***Paratypes*** (*Orthostigma* (*Whartonstigma*) *gallowagi*): Australia: • 1 ♀, 1 ♂, same data as holotype [No.111581] (ANIC).

Diagnosis. Very similar to the subgenus *Orthostigma* sensu stricto but differs from it by the absence of vein 2-SR of the fore wing.

Remarks. This recently described subgenus includes four species from Australia and Papua New Guinea (Peris-Felipo and Belokobylskij 2020).

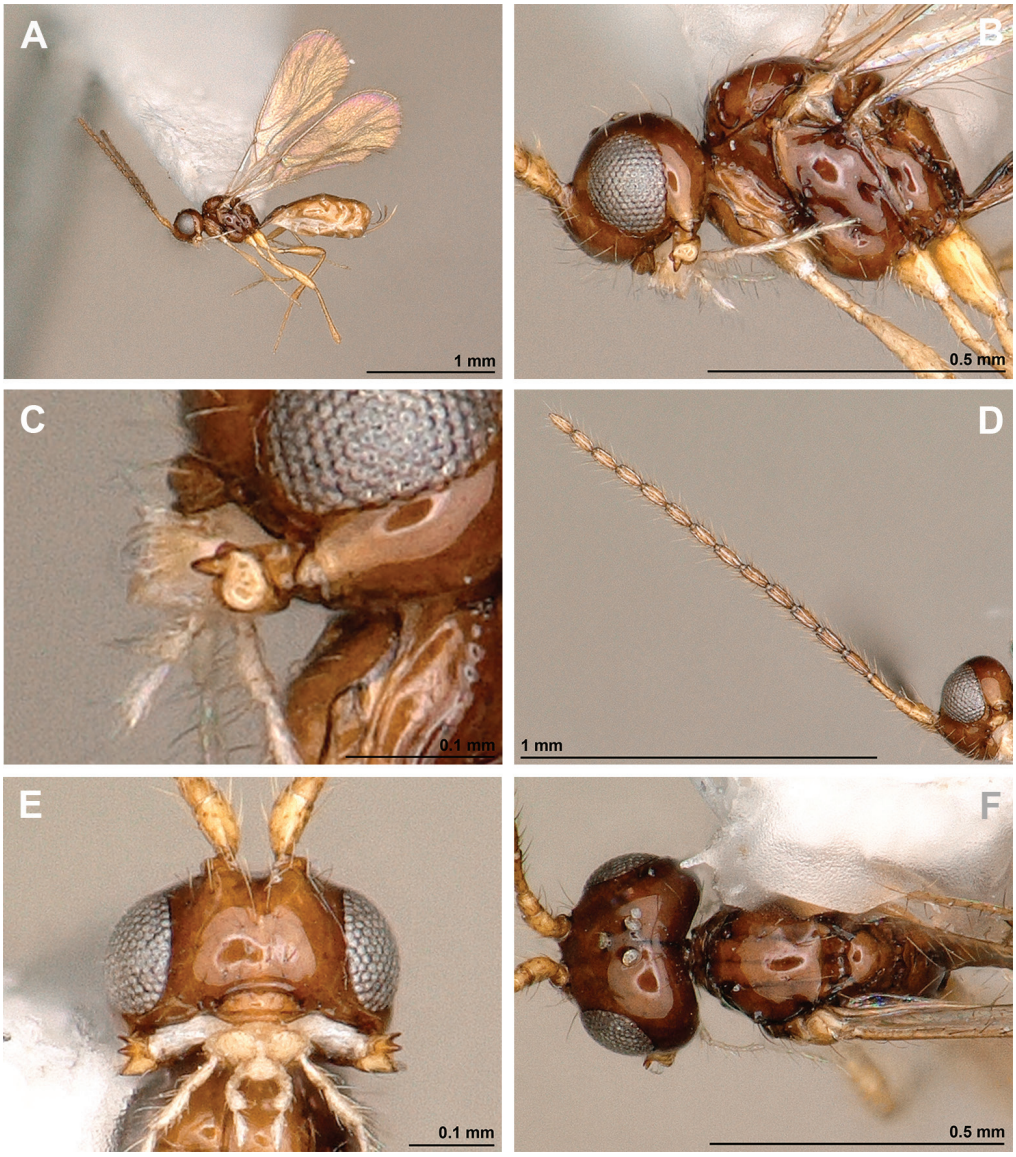

Figure 40. *Orthostigma* (*Whartonstigma*) *gallowagi* Wharton 2002 (holotype, female) **A** habitus, lateral view **B** head and mesosoma, lateral view **C** mandible **D** antenna **E** head, front view **F** head and mesonotum, dorsal view.

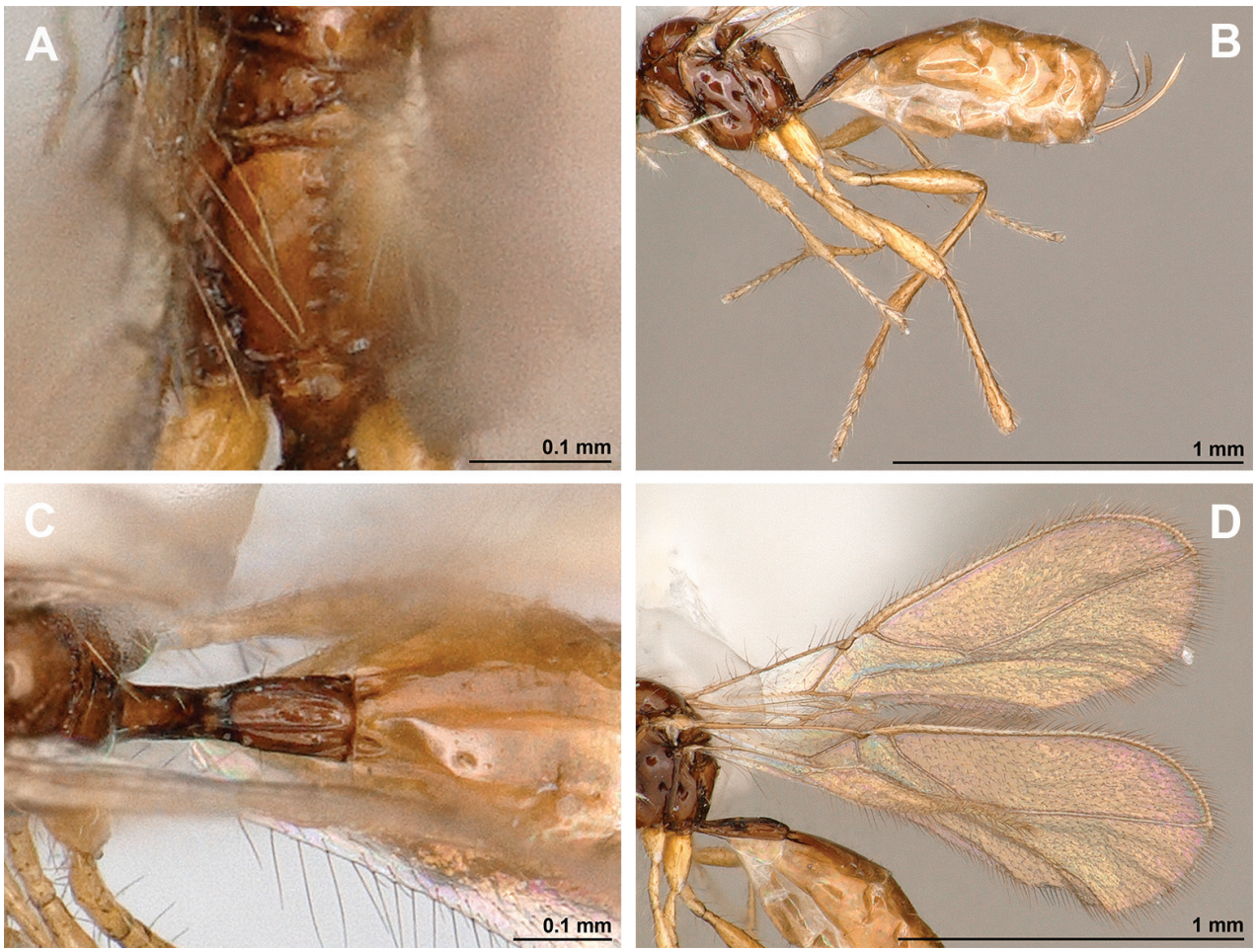

Figure 41. *Orthostigma* (*Whartonstigma*) *gallowagi* Wharton 2002 (holotype, female) **A** propodeum **B** legs, metasoma and ovipositor, lateral view **C** first metasomal tergite **D** fore and hind wings.

Key to subgenera and genera of the subtribe Aspilotina

1 First metasomal tergite without dorsope. Second metasomal tergite sculptured medio-basally (except in *A. levis*) (Fig. 42A) .....***Apronopa***

– First metasomal tergite always with dorsope. Second metasomal tergite always completely smooth (Fig. 42B) **2**

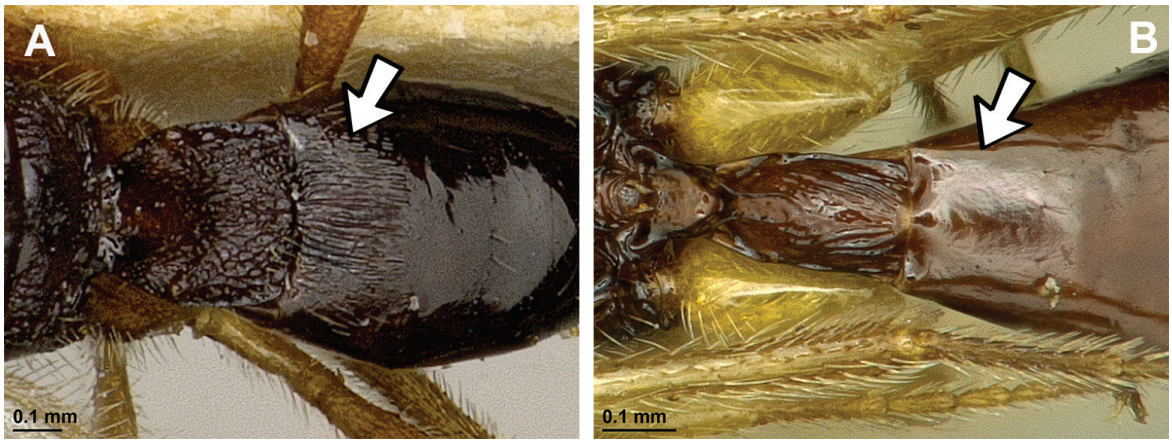

Figure 42. First and second metasomal tergites **A** second metasomal tergite sculptured [*Apronopa haeselbarthi* van Achterberg, 1980] **B** second metasomal tergite smooth [*Dinotrema* (*Dinotrema*) *katbergense* Peris-Felipo, 2016].

2(1) Mandible with distinct and curved transverse carina. Third tooth usually widest and often lobe-shaped (Fig. 43)..... [***Orthostigma* group**] **3**

– Mandible without curved transverse carina. Third tooth usually narrow and not lobe-shaped (Fig. 44) ..... [***Aspilota* group**] **8**

Figure 43. Mandible with distinct and curved transverse carina **A** *Orthostigma* (*Orthostigma*) *mandibulare* (Tobias, 1962) **B** *Orthostigma* (*Africostigma*) *karkloofense* Fischer, 1995 **C** *Neorthostigma macrops* (Stelfox & Graham, 1951).

Figure 44. Mandible without curved transverse carina **A** *Aspilota* (*Eusynaldis*) *varinervis* (Zaykov & Fischer, 1972) **B** *Dinotrema* (*Panerema*) *inops* (Foerster, 1863) **C** *Grandilota kenyaensis* Fischer, 2002.

3(2) Vein r of fore wing originating far from base of pterostigma (Fig. 45A). Combined first and second submarginal cells extremely enlarged..... ..... ***Cubitalostigma***

– Vein r of fore wing originating near base of pterostigma (Fig. 45B). Combined first and second submarginal cells not enlarged.....**3**

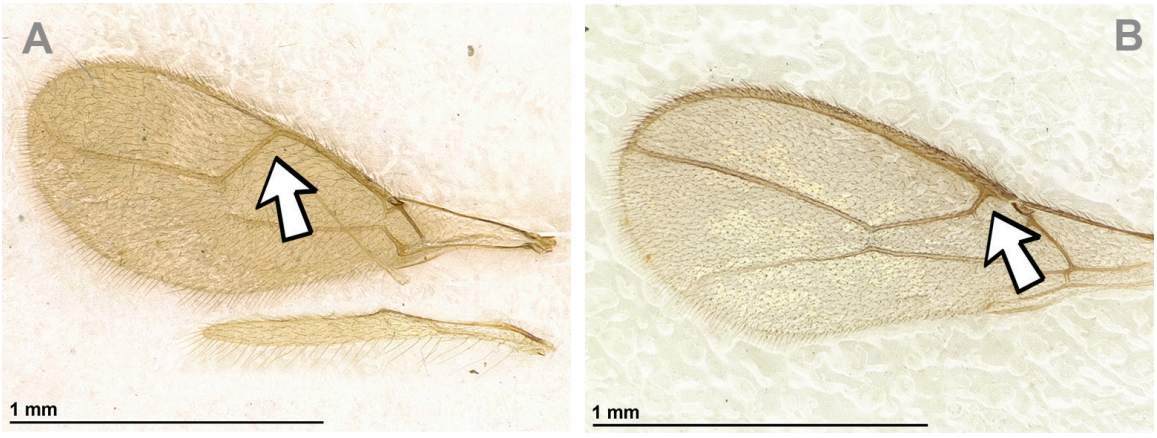

Figure 45. Fore wing **A** vein r originating from middle pterostigma [*Cubitalostigma reichli* Fischer, 1998] **B** vein r originating close to pterostigma base [*Dinotrema* (*Dinotrema*) *mareum* Peris-Felipo, 2013].

4(3) Paraclypeal fovea large and reaching or almost reaching inner border of eye (Fig. 46A). Furrow between antennal socket and inner margin of eye absent ..... ***Neorthostigma***

– Paraclypeal fovea smaller, reaching at most halfway distance between clypeus and eye (Fig. 46B). Furrow between antennal socket and inner margin of eye present ..... [***Orthostigma***] **5**

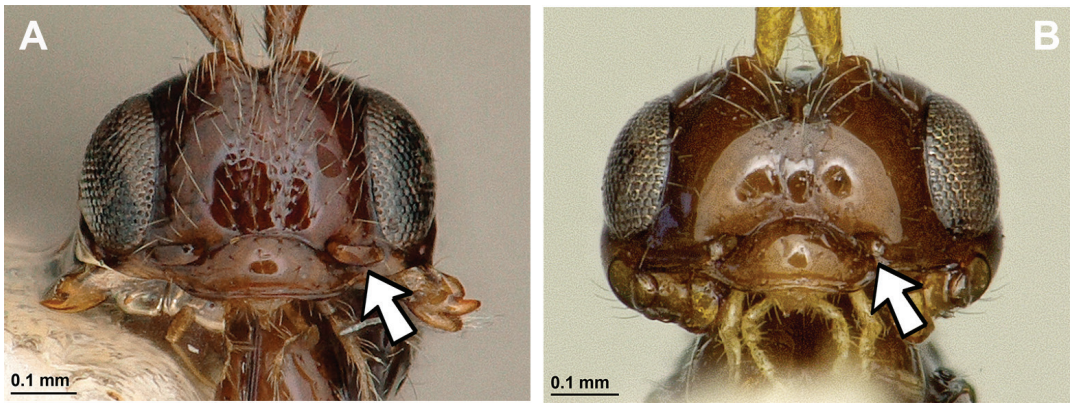

Figure 46. Paraclypeal fovea **A** paraclypeal fovea large and reaching border of eye [*Neorthostigma brachyclypeata* (Fischer, 1978)] **B** paraclypeal fovea comparatively small [*Orthostigma* (*Orthostigma*) *mandibulare* (Tobias, 1962)].

5(4) First flagellar segment shorter than second flagellar segment (Fig. 47A) ..... ***Orthostigma* (*Africostigma*)**

– First flagellar segment either as long as or longer than second flagellar segment (Fig. 47B, C) **6**

Figure 47. Basal segments of antenna **A** *Orthostigma* (*Africostigma*) *karkloofense* Fischer, 1995 **B** *Orthostigma* (*Patrisaspilota*) *multicarinatum* Tobias 1990 **C** *Orthostigma* (*Orthostigma*) *mandibulare* (Tobias, 1962).

6(5) Notauli present posteriorly and reaching mesoscutal pit (Fig. 48A) or nearly so ..... ***Orthostigma* (*Patrisaspilota*)**

– Notauli absent in posterior half of mesoscutum (Fig. 48B) **7**

7(6) Vein 2-SR present (Fig. 49A). Vein r distinctly angled with vein 3-SR ..... ***Orthostigma* (*Orthostigma*)**

– Vein 2-SR absent (Fig. 49B). Vein r + 3-SR gently curved ..... ***Orthostigma* (*Whartonstigma*)**

8(2) Paraclypeal fovea enlarged and reaching inner border of eye (Fig. 50A, B) ..... [***Aspilota***] **9**

– Paraclypeal fovea short, at most halfway distance between clypeus and inner border of eye (Fig. 50C) **11**

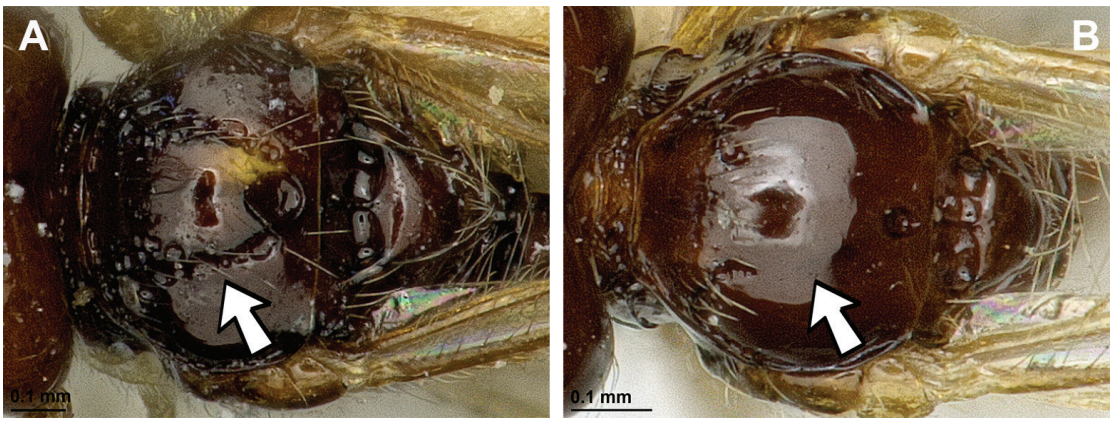

Figure 48. Mesoscutum in dorsal view **A** notauli complete [*Orthostigma* (*Patrisaspilota*) *multicarinatum* Tobias 1990] **B** notauli largely absent posteriorly [*Orthostigma* (*Orthostigma*) *mandibulare* (Tobias, 1962)].

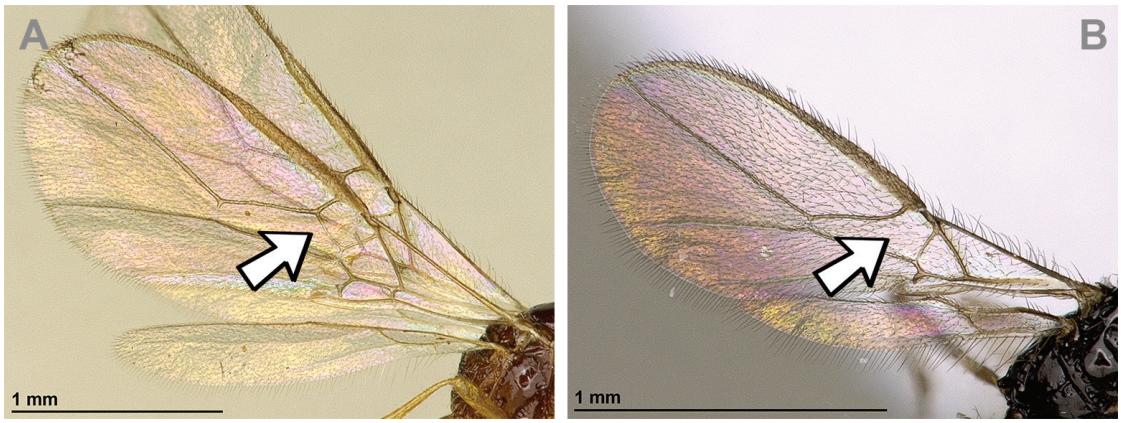

Figure 49. Submarginal cell of fore wing **A** vein 2-SR present [*Orthostigma* (*Orthostigma*) *mandibulare* (Tobias, 1962)] **B** vein 2-SR absent [*Orthostigma* (*Whartonstigma*) *longipede* Peris-Felipo, 2020].

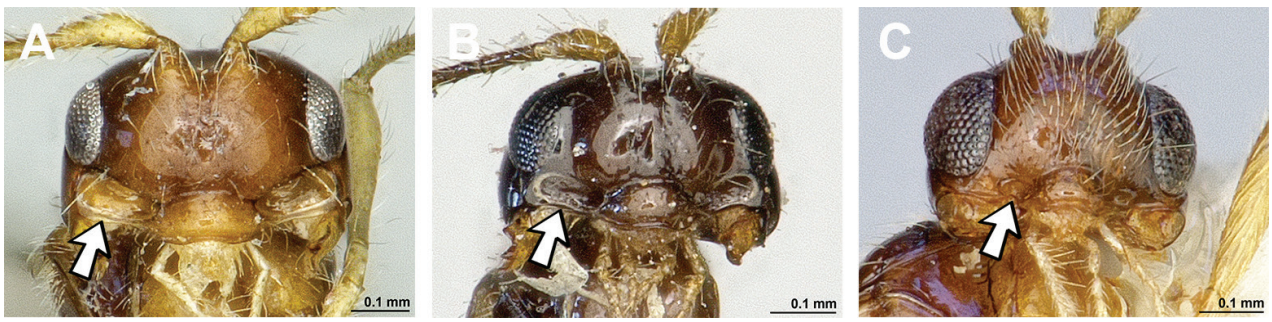

Figure 50. Paraclypeal fovea **A, B** paraclypeal fovea large and reaching border of eye [**A** *Aspilota* (*Aspilota*) *ajara* Peris-Felipo, 2016 **B** *Aspilota* (*Eusynaldis*) *varinervis* (Zaykov & Fischer, 1972)] **C** paraclypeal fovea short [*Dinotrema* (*Dinotrema*) *multiareolatum* Peris-Felipo, 2016].

9(8) Notauli complete and well developed in posterior half of mesoscutum, reaching to mesoscutal pit (Fig. 51A) .....***Aspilota* (*Alitha*)**

– Notauli absent in posterior half of mesoscutum (Fig. 51B, C).....**10**

10(9) Vein 2-SR of fore wing present (Fig. 52A). Angle between r and 3RSa present and distinct .....***Aspilota* (*Aspilota*)**

– Vein 2-SR of fore wing absent (Fig. 52B). Angle between r and 3RSa absent, resulting in a gently curved or almost straight vein ....***Aspilota* (*Eusynaldis*)**

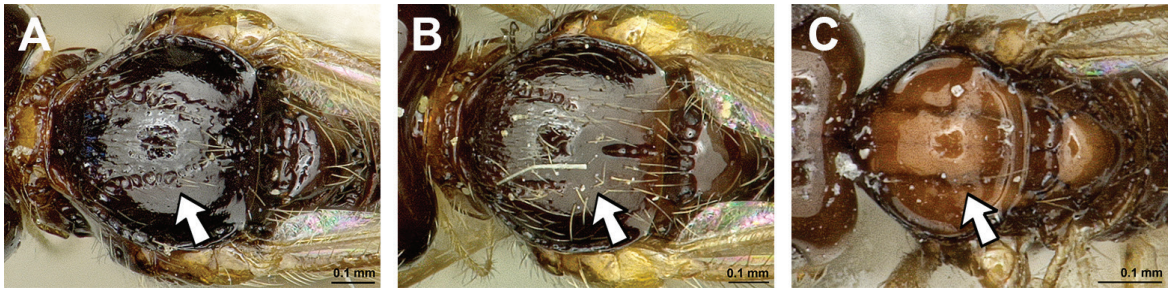

Figure 51. Mesoscutum in dorsal view **A** notauli well developed [*Dinotrema* (*Alitha*) *vechti* (van Achterberg, 1988)] **B, C** notauli incomplete [**B** *Dinotrema* (*Dinotrema*) *trastoae* Peris-Felipo, 2016 **C** *Dinotrema* (*Synaldis*) *baloghi* (Fischer, 1993)].

Figure 52. Submarginal cell of fore wing **A** vein 2-SR present [*Aspilota* (*Aspilota*) *flagimilis* Fischer, 1966] **B** vein 2-SR absent [*Aspilota* (*Eusynaldis*) *villemantae* Peris-Felipo, 2019].

11(8) Subdiscal cell of fore wing open posteriorly (Fig. 53A). Veins CU1b and 2-1A absent (Fig. 53B) **12**

– Subdiscal cell of fore wing completely closed posteriorly (Fig. 53C). Veins CU1b and 2-1A present (Fig. 53D) **13**

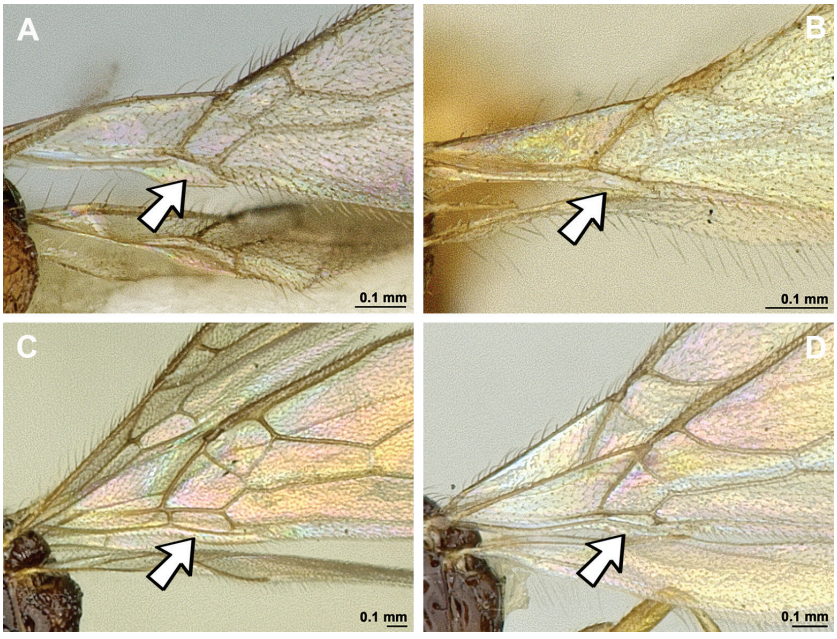

Figure 53. Subdiscal cell **A, B** completely open [**A** *Lysodinotrema madli* Fischer, 1995 **B** *Dinostigma muesebecki* Fischer, 1966] **C, D** completely closed [**C** *Dinotrema* (*Dinotrema*) *trastoae* Peris-Felipo, 2016 **D** *Dinotrema* (*Synaldis*) *longiflagellaris* Peris-Felipo, 2017].

12(11) Vein 2-SR of fore wing present (Fig. 54A). Precoxal sulcus present (Fig. 54C) ..... ***Lysodinotrema***

– Vein 2-SR of fore wing absent (Fig. 54B). Precoxal sulcus absent (Fig. 54D) ..... ***Dinostigma***

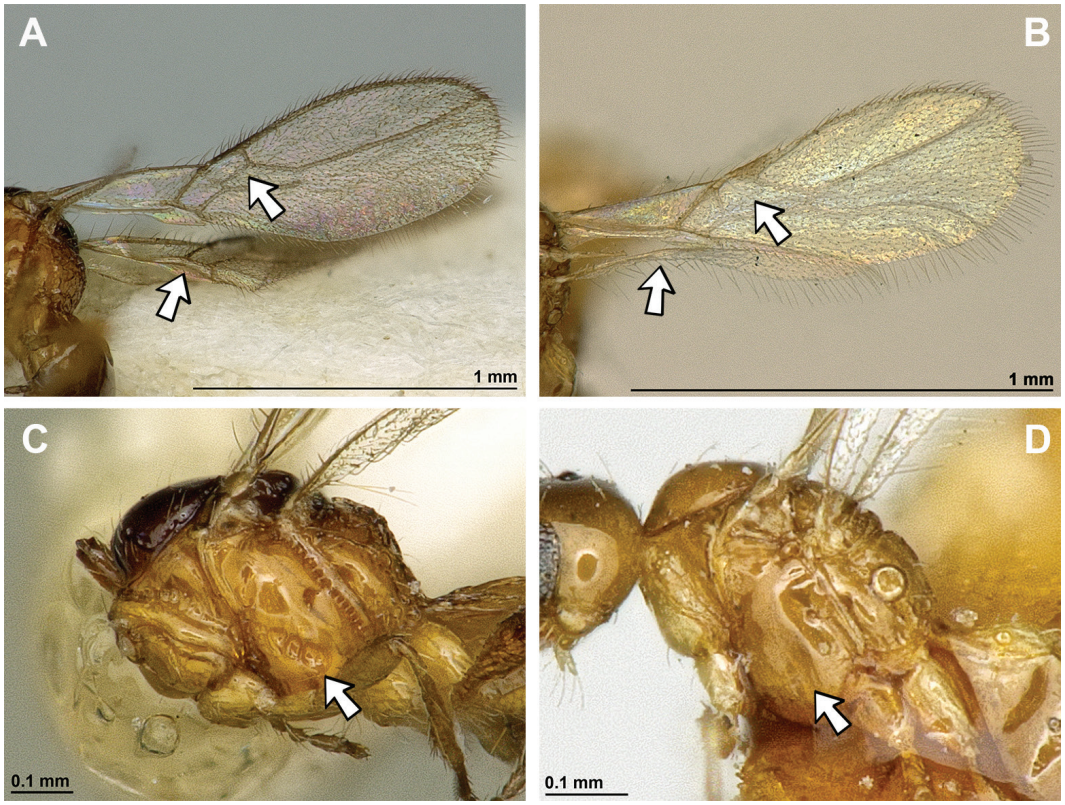

Figure 54. Fore wing and mesosoma **A** vein 2-SR of fore wing present and hind wing with closed cells [*Lysodinotrema madli* Fischer, 1995] **B** vein 2-SR of fore wing absent and hind wing without closed cells [*Dinostigma muesebecki* Fischer, 1966] **C** precoxal sulcus present [*Lysodinotrema madli* Fischer, 1995] **D** precoxal sulcus absent [*Dinostigma muesebecki* Fischer, 1966].

13(11) Fore femur with wide and obtuse ventral tooth (Fig. 55A) or with 2 or 3 small teeth ..... ***Leptotrema***

– Fore femur usual, without ventral teeth (Fig. 55B) **14**

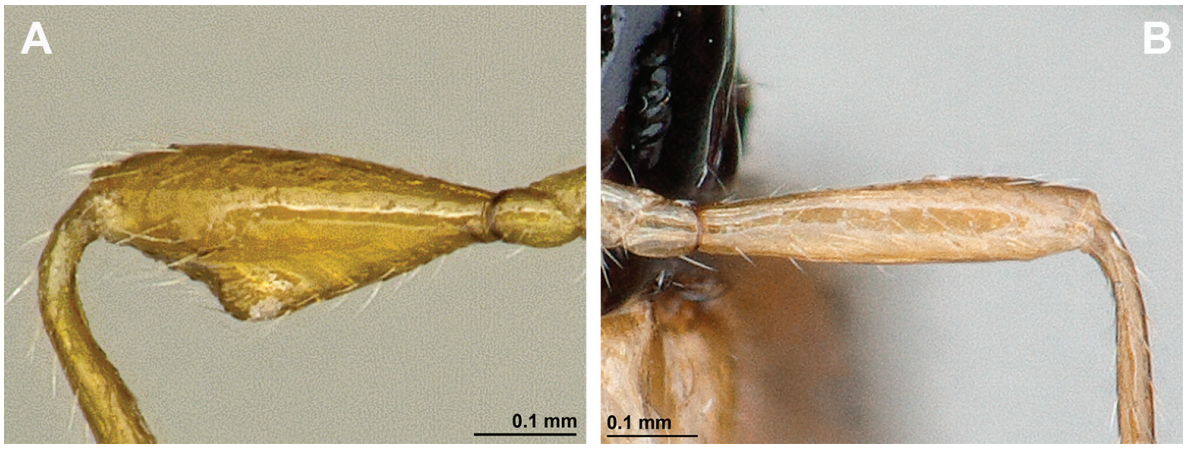

Figure 55. Fore femur **A** fore femur with ventral tooth [*Leptotrema dentifemur* (Stelfox, 1943)] **B** fore femur without ventral tooth [*Dinotrema* (*Dinotrema*) *alysiae* Munk & Peris-Felipo, 2013].

14(13) Metasoma with strongly retracted apical sternites under dorsal distally elongated tergites (Fig. 56A).....***Synaldotrema***

– Metasoma without strongly retracted apical sternites under distal tergites (Fig. 56B).....**15**

Figure 56. Metasoma, lateral view **A** metasoma with strongly retracted apical sternites [*Dinotrema* (*Synaldotrema*) *speciosum* Belokobylskij & Tobias, 2002] **B** metasoma without retracted sternites [*Dinotrema* (*Synaldis*) *soederlundi* (Fischer, 2003)].

15(14) Scutellum with transverse crenulate depression subposteriorly (Fig. 57A). Wing of female always strongly shortened and with partly thickened veins (Fig. 57B) .....***Panerema***

– Scutellum without transverse crenulate depression subposteriorly (Fig. 57C). Wing of female very rarely shortened and without thickened veins (Fig. 57D) ..... [***Dinotrema***]. **16**

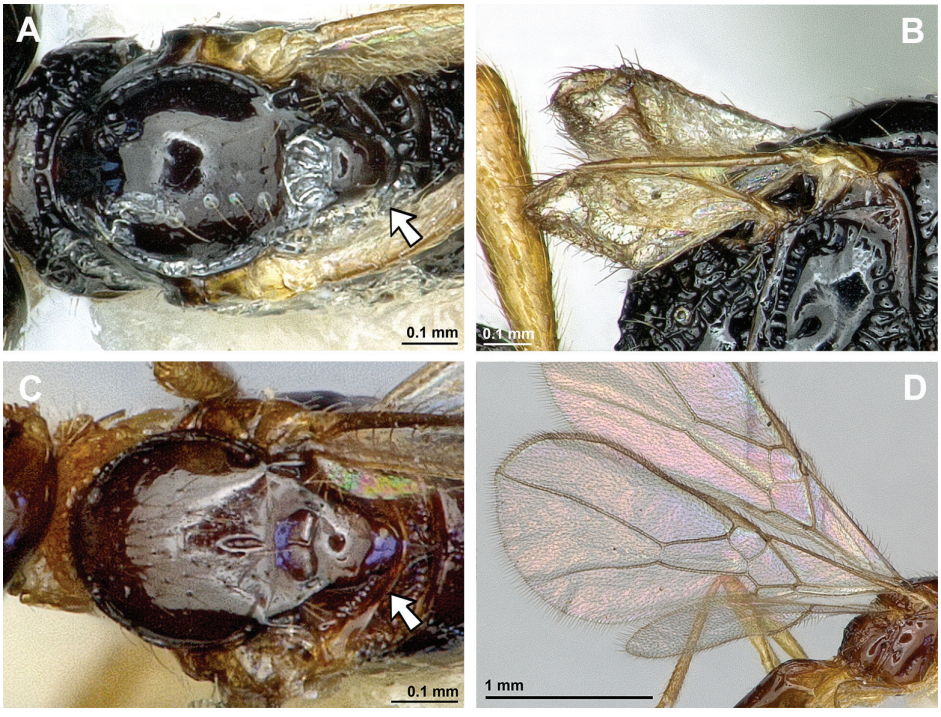

Figure 57. A scutellum with crenulate subposterior depression [*Dinotrema* (*Panerema*) *inops* (Foerster, 1863)] **B** shortened wings (female) [idem] **C** scutellum without crenulate [*Dinotrema* (*Dinotrema*) *multiareolatum* Peris-Felipo, 2016] **D** wings (female) depression [idem].

16(15) Pterostigma of fore wing narrow, its maximum width less than length of vein r (Fig. 58A) **17**

– Pterostigma of fore wing broad (especially in male), its maximum width larger than length of vein r (Fig. 58B) **18**

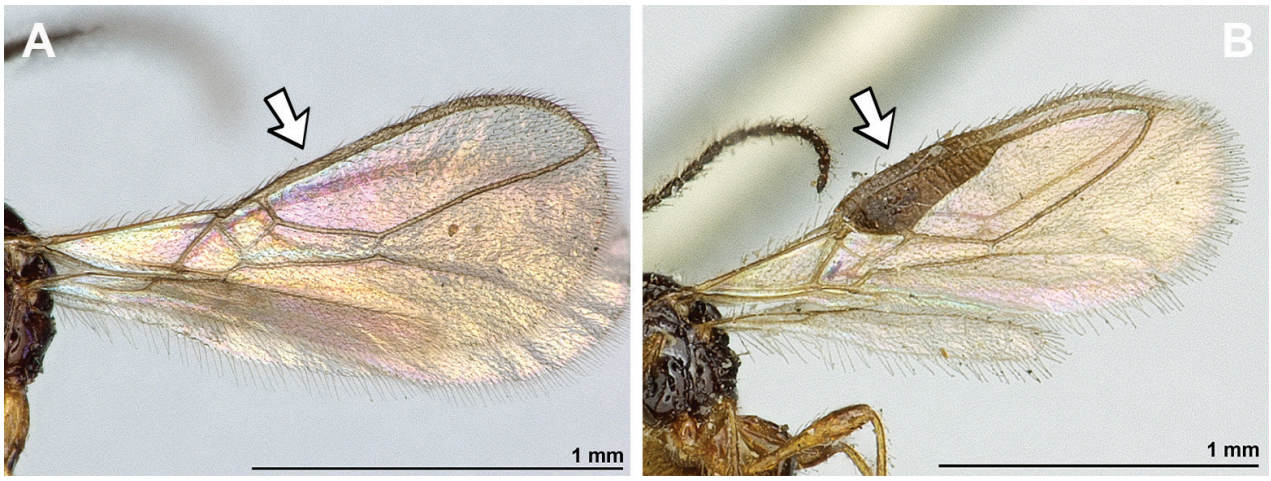

Figure 58. Fore wing **A** pterostigma narrow [*Dinotrema* (*Dinotrema*) *angusticorne* (Fischer, 1969)] **B** pterostigma broad [*Dinotrema* (*Prosapha*) *speculum* (Haliday, 1838)].

17(16) Vein 2-SR of fore wing present (Fig. 59A). Angle between veins r and 3-SR present and distinct ..... ***Dinotrema* (*Dinotrema*)**

– Vein 2-SR of fore wing absent (Fig. 59B). Angle between veins r and 3-SR absent and this part of veins connection only gently curved or straight..... ***Dinotrema* (*Synaldis*)**

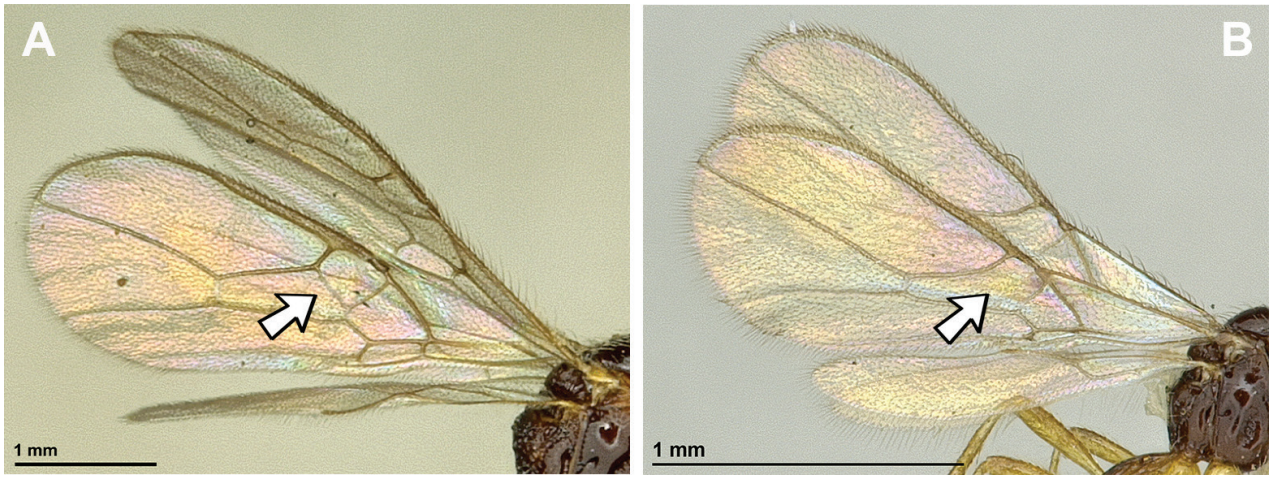

Figure 59. Fore wing **A** vein 2-SR present [*Dinotrema* (*Dinotrema*) *trastoae* Peris-Felipo, 2016] **B** vein 2-SR absent [*Dinotrema* (*Synaldis*) *longiflagellaris* Peris-Felipo, 2017].

18(16) Vein 2-SR of fore wing present (Fig. 60A). Angle between veins r and 3-SR present and distinct ..... ***Dinotrema* (*Prosapha*)**

– Vein 2-SR of fore wing absent (Fig. 60B). Angle between veins r and 3-SR absent and combined veins only gently curved or straight..... ***Dinotrema* (*Pseudoprosapha*)**

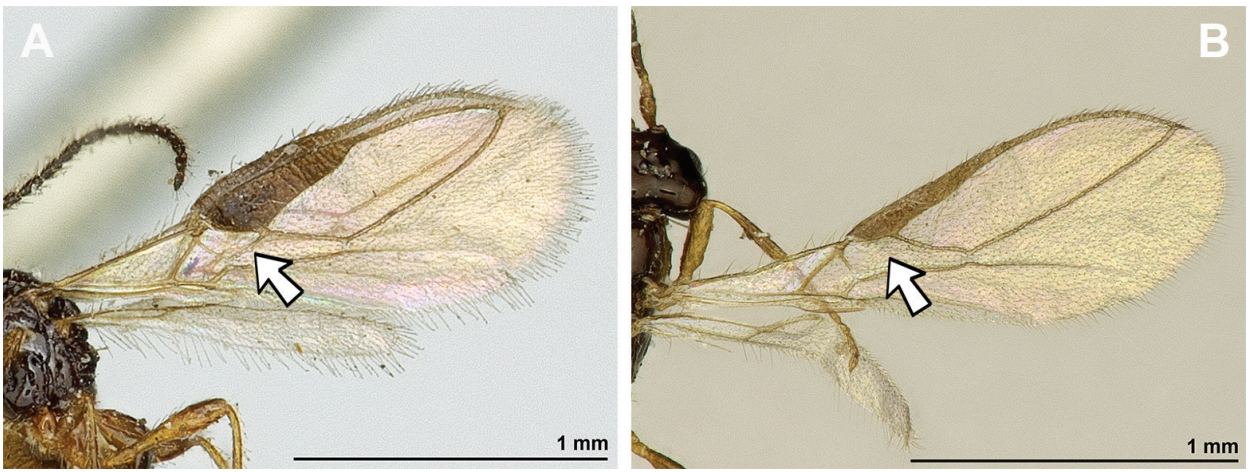

Figure 60. Fore wing **A** vein 2-SR present [*Dinotrema* (*Prosapha*) *speculum* (Haliday, 1838)] **B** vein 2-SR absent [*Dinotrema* (*Pseudoprosapha*) *stenosoma* (van Achterberg, 1988)].

Discussion

The alysiine belonging to the subtribe Aspilotina are a relatively homogeneous group of taxa with only a few available diagnostic characters for the determination of its genera and subgenera. This taxonomic group is characterised by several homoplesian features, which are developed parallel in different genera. The most important for identification of the generic diagnostic characters is the state of mandible (with or without a curved transverse carina): it is the most important character to separate *Orthostigma* and *Neorthostigma* from the other alysiine genera. The complete reduction of the vein 2-SR is an appreciable evolutionary event which is connected with the disappearance of the break (angle) between the veins r and 3-SR, and the connection between both veins is only gently curved or almost straight. In most cases it is distinct character state and useful for separation at least of subgenera (Belokobylskij 2002; Peris-Felipo et al. 2014a). The vein r of fore wing is generally situated near the base (in basal quarter) of pterostigma in practically all taxa of this group with only exception the Oriental *Cubitalostigma* where it arises almost from the middle of pterostigma. Besides this, the subdiscal cell of the fore wing is closed by veins 2-1A and CU1b in most of the genera. However, *Lysodinotrema* and *Dinostigma* have this cell open distally through the absence of the veins 2-1A and usually CU1b.

In the hind wing, sclerotised veins usually close the basal and subbasal cells. However, as an exception, there are species with no closed cells in the monotypic Nearctic genus *Dinostigma* (in the modern sense), *Lysodinotrema* and some very derived small species of the genus *Dinotrema*. Besides the wing venation characters, some other valuable features are found on the mesosoma. For example, the notauli are predominantly developed in the anterior subvertical third of the mesoscutum and absent in its posterior horizontal part, except in the subgenera *Orthostigma* (*Patrisaspilota*) and *Dinotrema* (*Alitha*), where they are complete or nearly so and rather well developed dorso-posteriorly. In addition to these characters, the variation of the propodeal sculpture from entirely smooth or smooth with delineated basolateral areas and often a large areola to entirely finely or coarsely rugose-reticulate and sometimes also with more or less visible delineated areola, shows a considerable intraspecific variation.

Hopefully, the revised classification for the subtribe Aspilotina presented in the current work will facilitate the identification of the genera and subgenera and will allow a better understanding of the character variability in this very complicate and speciose group of genera. Further revisions of this subtribe with use of molecular data will allow for a better insight in each of the genera and subgenera.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Appendix 1

Table A1. The distances between genera/subgenera generated from the multivariate statistical approach of the diagnostic characters.

Group	Genus/subgenus	Apronopa	Aspilota (Aspilota)	Aspilota (Eusynaldis)	Aspilota (Grandilota)	Dinostigma
Aspilota	***Apronopa***	0	1.750	1.800	1.836	2.347
Aspilota	***Aspilota* (*Aspilota*)**	1.750	0	0.347	0.416	1.764
Aspilota	***Aspilota* (*Eusynaldis*)**	1.800	0.347	0	0.565	1.680
Aspilota	***Aspilota* (*Grandilota*)**	1.836	0.416	0.565	0	1.638
Aspilota	***Dinostigma***	2.347	1.764	1.68	1.638	0
Aspilota	***Dinotrema* (*Alitha*)**	1.470	0.759	0.873	0.917	1.768
Aspilota	***Dinotrema* (*Dinotrema*)**	1.642	0.459	0.54	0.667	1.626
Aspilota	***Dinotrema* (*Prosapha*)**	1.742	0.729	0.679	0.942	1.425
Aspilota	***Dinotrema* (*Pseudoprosapha*)**	1.844	0.917	0.729	1.106	1.389
Aspilota	***Dinotrema* (*Synaldis*)**	1.706	0.608	0.459	0.794	1.547
Aspilota	***Leptotrema***	1.982	1.211	1.294	1.333	1.987
Aspilota	***Lysodinotrema***	1.895	0.994	1.087	0.758	1.194
Aspilota	***Panerema***	2.035	1.295	1.122	1.419	1.907
Aspilota	***Synaldotrema***	1.982	1.211	1.294	1.333	1.987
Orthostigma	***Cubitalostigma***	2.239	1.599	1.472	1.462	1.958
Orthostigma	***Neorthostigma***	2.244	1.352	1.398	1.459	2.234
Orthostigma	***Orthostigma* (*Africostigma*)**	2.172	1.500	1.557	1.595	2.179
Orthostigma	***Orthostigma* (*Orthostigma*)**	1.879	1.033	1.074	1.167	1.856
Orthostigma	***Orthostigma* (*Patrisaspilota*)**	1.762	1.242	1.317	1.367	2.009
Orthostigma	***Orthostigma* (*Whartonstigma*)**	1.933	1.105	1.033	1.242	1.785

Group	Genus/subgenus	Dinotrema (Alitha)	Dinotrema (Dinotrema)	Dinotrema (Prosapha)	Dinotrema (Pseudoprosapha)	Dinotrema (Synaldis)
Aspilota	*Apronopa*	1.470	1.642	1.742	1.844	1.706
Aspilota	*Aspilota* (*Aspilota*)	0.759	0.459	0.729	0.917	0.608
Aspilota	*Aspilota* (*Eusynaldis*)	0.873	0.540	0.679	0.729	0.459
Aspilota	*Aspilota* (*Grandilota*)	0.917	0.667	0.942	1.106	0.794
Aspilota	*Dinostigma*	1.768	1.626	1.425	1.389	1.547
Aspilota	*Dinotrema* (*Alitha*)	0	0.483	0.747	0.967	0.678
Aspilota	*Dinotrema* (*Dinotrema*)	0.483	0	0.502	0.723	0.347
Aspilota	*Dinotrema* (*Prosapha*)	0.747	0.502	0	0.347	0.47
Aspilota	*Dinotrema* (*Pseudoprosapha*)	0.967	0.723	0.347	0	0.502
Aspilota	*Dinotrema* (*Synaldis*)	0.678	0.347	0.470	0.502	0
Aspilota	*Leptotrema*	1.218	1.021	1.173	1.331	1.135
Aspilota	*Lysodinotrema*	0.998	0.878	1.082	1.247	1.002
Aspilota	*Panerema*	1.313	1.140	1.331	1.243	0.96
Aspilota	*Synaldotrema*	1.218	1.021	1.173	1.331	1.135
Orthostigma	*Cubitalostigma*	1.63	1.484	1.617	1.553	1.36
Orthostigma	*Neorthostigma*	1.646	1.501	1.63	1.724	1.555
Orthostigma	*Orthostigma* (*Africostigma*)	1.546	1.37	1.497	1.614	1.446
Orthostigma	*Orthostigma* (*Orthostigma*)	0.909	0.839	1.017	1.145	0.911
Orthostigma	*Orthostigma* (*Patrisaspilota*)	0.839	1.024	1.205	1.354	1.131
Orthostigma	*Orthostigma* (*Whartonstigma*)	1.023	0.905	0.999	1.017	0.839

Group	Genus/subgenus	Leptotrema	Lysodinotrema	Panerema	Synaldotrema	Cubitalostigma
Aspilota	*Apronopa*	1.982	1.895	2.035	1.982	2.239
Aspilota	*Aspilota* (*Aspilota*)	1.211	0.994	1.295	1.211	1.599
Aspilota	*Aspilota* (*Eusynaldis*)	1.294	1.087	1.122	1.294	1.472
Aspilota	*Aspilota* (*Grandilota*)	1.333	0.758	1.419	1.333	1.462
Aspilota	*Dinostigma*	1.987	1.194	1.907	1.987	1.958
Aspilota	*Dinotrema* (*Alitha*)	1.218	0.998	1.313	1.218	1.630
Aspilota	*Dinotrema* (*Dinotrema*)	1.021	0.878	1.140	1.021	1.484
Aspilota	*Dinotrema* (*Prosapha*)	1.173	1.082	1.331	1.173	1.617
Aspilota	*Dinotrema* (*Pseudoprosapha*)	1.331	1.247	1.243	1.331	1.553
Aspilota	*Dinotrema* (*Synaldis*)	1.135	1.002	0.960	1.135	1.360
Aspilota	*Leptotrema*	0	1.378	1.592	1.529	1.848
Aspilota	*Lysodinotrema*	1.378	0	1.465	1.378	1.528
Aspilota	*Panerema*	1.592	1.465	0	1.592	1.790
Aspilota	*Synaldotrema*	1.529	1.378	1.592	0	1.848
Orthostigma	*Cubitalostigma*	1.848	1.528	1.790	1.848	0
Orthostigma	*Neorthostigma*	1.85	1.773	1.926	1.850	1.885
Orthostigma	*Orthostigma* (*Africostigma*)	1.771	1.648	1.836	1.771	1.793
Orthostigma	*Orthostigma* (*Orthostigma*)	1.365	1.249	1.445	1.365	1.367
Orthostigma	*Orthostigma* (*Patrisaspilota*)	1.553	1.376	1.620	1.553	1.561
Orthostigma	*Orthostigma* (*Whartonstigma*)	1.450	1.337	1.306	1.450	1.230

Group	Genus/subgenus	Neorthostigma	Orthostigma (Africostigma)	Orthostigma (Orthostigma)	Orthostigma (Patrisaspilota)	Orthostigma (Whartonstigma)
Aspilota	*Apronopa*	2.244	2.172	1.879	1.762	1.933
Aspilota	*Aspilota* (*Aspilota*)	1.352	1.5	1.033	1.242	1.105
Aspilota	*Aspilota* (*Eusynaldis*)	1.398	1.557	1.074	1.317	1.033
Aspilota	*Aspilota* (*Grandilota*)	1.459	1.595	1.167	1.367	1.242
Aspilota	*Dinostigma*	2.234	2.179	1.856	2.009	1.785
Aspilota	*Dinotrema* (*Alitha*)	1.646	1.546	0.909	0.839	1.023
Aspilota	*Dinotrema* (*Dinotrema*)	1.501	1.37	0.839	1.024	0.905
Aspilota	*Dinotrema* (*Prosapha*)	1.63	1.497	1.017	1.205	0.999
Aspilota	*Dinotrema* (*Pseudoprosapha*)	1.724	1.614	1.145	1.354	1.017
Aspilota	*Dinotrema* (*Synaldis*)	1.555	1.446	0.911	1.131	0.839
Aspilota	*Leptotrema*	1.85	1.771	1.365	1.553	1.45
Aspilota	*Lysodinotrema*	1.773	1.648	1.249	1.376	1.337
Aspilota	*Panerema*	1.926	1.836	1.445	1.62	1.306
Aspilota	*Synaldotrema*	1.85	1.771	1.365	1.553	1.45
Orthostigma	*Cubitalostigma*	1.885	1.793	1.367	1.561	1.23
Orthostigma	*Neorthostigma*	0	1.63	1.126	1.354	1.194
Orthostigma	*Orthostigma* (*Africostigma*)	1.63	0	0.972	1.252	1.074
Orthostigma	*Orthostigma* (*Orthostigma*)	1.126	0.972	0	0.483	0.347
Orthostigma	*Orthostigma* (*Patrisaspilota*)	1.354	1.252	0.483	0	0.678
Orthostigma	*Orthostigma* (*Whartonstigma*)	1.194	1.074	0.347	0.678	0