



ILLUMINATING A DARK TAXON: REVISION OF EUROPEAN *Trichacis* FÖRSTER (HYMENOPTERA: PLATYGASTRIDAE) REVEALS A GLUT OF SYNONYMS

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Abstract

The parasitoid wasp genus *Trichacis* Förster is revised for Europe. Examination of historical and modern collections combined with DNA barcoding revealed the presence of only a single species in Europe, *Trichacis tristis* (Nees, 1834), redescribed here. Fourteen new synonymies are proposed for *T. tristis*: *T. abdominalis* Thomson, 1859 **syn.nov.**; *T. bidentiscutum* Szabó, 1981 **syn.nov.**; *T. didas* (Walker, 1835) **syn.nov.**; *T. fusciala* Szabó, 1981 **syn.nov.**; *T. hajduica* Szabó, 1981 **syn.nov.**; *T. illusor* Kieffer, 1916 **syn.nov.**; *T. nosferatus* Buhl, 1997 **syn.nov.**; *T. pisis* (Walker, 1835) **syn.nov.**; *T. persicus* Asadi & Buhl, 2021 **syn.nov.**; *T. pulchricornis* Szelényi, 1953 **syn.nov.**; *T. quadriclava* Szabó, 1981 **syn.nov.**; *T. remulus* (Walker, 1835) **syn.nov.**; *T. vitreus* Buhl, 1997 **syn.nov.**; *T. weiperti* Buhl, 2019 **syn.nov.**. Four species are transferred to *Amblyaspis* Förster: *A. afurcata* (Szabó, 1977) **comb. nov.**, *A. hungarica* (Szabó, 1977), **comb. nov.**, *A. pannonica* (Szabó, 1977) **comb. nov.**, and *A. tatika* (Szabó, 1977) **comb. nov.** Intraspecific variation, biological associations, and taxonomic history are discussed. DNA barcodes are provided and analyzed in the context of worldwide *Trichacis* and its sister genus *Isocybus* Förster.

Key words: DNA barcoding, Hessian fly, integrative taxonomy, *Mayetiola*, parasitoid wasps

Introduction

Trichacis Förster species are parasitoids of immature gall midges (Diptera: Cecidomyiidae) (Vlug 1995). The genus has been revised for the Nearctic (Masner 1983) and Neotropical (Arias-Penna *et al.* 2012) regions, but few species identification resources exist for *Trichacis* in Europe. The European fauna has never been revised, and many new species were described without sufficient comparison to existing species. Previous taxonomic work rarely included examination of type material, relying on superficial descriptions or making no comparison at all to the described fauna. As a result, the diagnoses tend to be absent or insufficient, the descriptions vague, and the keys outdated at best and largely unusable at worst.

DNA barcode identification is also not well-established for *Trichacis*. Although many specimens have been barcoded, relatively few are identified to genus, and none are identified to species. There are presently 267 BOLD (Barcode of Life Data System) records in eight BINs (Barcode Identification Numbers) identified as *Trichacis*, all from North America. A similarity search using known sequences suggests that there are hundreds of unidentified barcodes belonging to *Trichacis* in BOLD (Ratsnasingham & Hebert 2007).

At the beginning of this project, *Trichacis* contained 67 valid species described from the Neotropical (28), Palearctic (19), Nearctic (16), Indomalayan (2), Afrotropical (1), and Australasian (1) regions (Vlug 1995; Hymenoptera Online 2023). The species diversity of Neotropical and Nearctic *Trichacis* has been verified through revisionary work. Little has been published on *Trichacis* from Africa, Asia, or Australia, so we cannot presently draw conclusions about the species diversity in these regions.

Defining the generic limits of *Trichacis* is essential for assessing its diversity, as they determine which species

are included. *Trichacis* and *Isocybus* both have a tuft of setae in the center of the mesoscutellum, often in a pit or in a depression (Figs 1A, C). This distinctive character differentiates them from other Platygastriinae and suggests that they are sister taxa. This affinity is also supported by a phylogenetic analysis based on ultraconserved elements that retrieves these taxa as sisters, albeit with limited taxon sampling (Y. Miles Zhang *et al.*, unpublished data). *Isocybus* species tend to be large (> 5mm) with a blocky head and coarse sculpture on the frons (Fig. 1D), whereas species of *Trichacis* generally have a round or ovoid head, and the frons is smooth or finely sculptured, with transverse striae above the toruli (Figs 1B, D). These characters are mostly reliable for diagnosis in western Europe, where the fauna is relatively species-poor, but the head sculpture exhibits some intrageneric variation in other parts of the world. Assessment of both genera on a world scale is needed to clarify their boundaries. The present study represents the first taxonomic revision of *Trichacis* for Europe and employs an integrative approach to investigate its species diversity and advance an understanding of its relationship to *Isocybus*.

Material and methods

Morphology. Specimens were examined using light microscopy. Antennae were slide-mounted in euparal for closer inspection. Morphological character systems are based on Masner (1983) and Arias-Penna *et al.* (2012). Morphological terms generally follow Hymenoptera Anatomy Ontology (Yoder *et al.* 2010), except where no equivalent term exists. Term definitions and links are found in Supplemental File 1.

Photography. Photography was performed using a Macropod microphotography system with 10X and 20X Mitutoyo objective lenses, and image stacks were rendered in Helicon Focus. Post-processing (addition of scale bars and removal of stacking artifacts) was conducted in Adobe Photoshop. Images of primary types were deposited in Zenodo (Table 1), and images of molecular voucher specimens were deposited in BOLD (dataset DS-ISOTRIDE: *Isocybus* and *Trichacis* of Germany).

TABLE 1. Type status of *Trichacis* species described from Europe and Western Asia.

Original combination	Type depository	Image link
<i>Platygaster tristis</i> Nees, 1834	NHMW	https://doi.org/10.5281/zenodo.7681266
<i>Platygaster didas</i> Walker, 1835	NHMUK	https://doi.org/10.5281/zenodo.7681449
<i>Platygaster pisis</i> Walker, 1835	NHMUK	https://doi.org/10.5281/zenodo.7681458
<i>Platygaster remulus</i> Walker, 1835	NHMUK	https://doi.org/10.5281/zenodo.7681460
<i>Trichacis abdominalis</i> Thomson, 1859	NHRS (missing)	
<i>Trichacis opaca</i> Thomson, 1859	MZLU	https://flic.kr/p/KpNiCZ
<i>Trichacis illusor</i> Kieffer, 1916	type not found	
<i>Trichacis pulchricornis</i> Szelényi, 1953	type not found	
<i>Trichacis afurcata</i> Szabó, 1977	HNHM	https://doi.org/10.5281/zenodo.7681334
<i>Trichacis hungarica</i> Szabó, 1977	HNHM	https://doi.org/10.5281/zenodo.7681346
<i>Trichacis panonica</i> Szabó, 1977	HNHM	https://doi.org/10.5281/zenodo.7681352
<i>Trichacis tatika</i> Szabó, 1977	HNHM	https://doi.org/10.5281/zenodo.7681357
<i>Trichacis bidentiscutum</i> Szabó, 1981	type not found	
<i>Trichacis fusciala</i> Szabó, 1981	type not found	
<i>Trichacis hajduica</i> Szabó, 1981	type not found	
<i>Trichacis quadriclava</i> Szabó	type not found	
<i>Trichacis nosferatus</i> Buhl, 1997	ZMUN	https://doi.org/10.5281/zenodo.7681280
<i>Trichacis vitreus</i> Buhl, 1997	NHMD	https://doi.org/10.5281/zenodo.7681282
<i>Trichacis weiperti</i> Buhl, 2019	NME	https://doi.org/10.5281/zenodo.7681284
<i>Trichacis persicus</i> Asadi & Buhl, 2021	HMIM	

DNA barcoding. Fresh material was obtained for the project German Barcode of Life III: Dark Taxa using the methods outlined in Awad *et al.* (2021). Additional *Trichacis* records were identified from BOLD based on specimen photographs. Specimens of *Amblyaspis* Förster and *Isocybus* served as outgroups for the analysis. A total of 496 DNA barcode sequences were aligned using MUSCLE (Edgar 2004). Phylogenetic reconstruction was performed on the IQ-TREE web server (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016) with 0.4 perturbation strength and stopping rule at 150. ModelFinder (Kalyaanamoorthy *et al.* 2017) selected TIM2+F+I+G4 as the best model. Branch support was evaluated using SH-aLRT (Guindon *et al.* 2010) and 1000 ultrafast bootstrap replicates (Hoang *et al.* 2017). Species partitioning was evaluated with ASAP (Assemble Species by Automatic Partitioning) (Puillandre *et al.* 2021).

Institutional abbreviations

CNCI = Canadian National Collection of Insects, Ottawa, Canada
HMIM = Hayk Mirzayans Insect Museum, Tehran, Iran
HNHM = Hungarian Museum of Natural History, Budapest, Hungary
HVC = Henk Vlug personal collection, Scherpenzeel, Netherlands
MZLU = Biological Museum Lund University, Lund, Sweden
NHMD = Natural History Museum of Denmark, Copenhagen, Denmark
NHMUK = Natural History Museum, London, UK
NHMW = Naturhistorisches Museum Wien, Vienna, Austria
NHRS = Naturhistoriska Riksmuseet Sverige, Stockholm, Sweden
NME = Naturkunde Museum Erfurt, Germany
NMINH = National Museum of Ireland, Dublin, Ireland
OSUC = Ohio State University Collection, Columbus, USA
SMNS = State Museum of Natural History Stuttgart, Germany
ZMUN = Natural History Museum, University of Oslo, Norway

Results

Genus *Trichacis* Förster, 1856

Trichacis Förster, 1856: 108, 115. Type species *Platygaster pisis* Walker, 1835 by subsequent designation by Ashmead 1893: 294.

Diagnosis. Head smooth or finely sculptured with transverse striae above the toruli (Fig. 1E); female with three to five clavomeres (Fig. 2A) as opposed to six in *Isocybus* (Fig. 2C); OOL less than or equal to LOL (Fig. 1B, E); mesoscutellum with tuft of setae originating in a depression (Fig. 1A).

***Trichacis tristis* (Nees, 1834)**

(Figs 1A, B, E; 2A, B; 3; 4A–H; 5E–G)

Platygaster tristis Nees, 1834: 302, 303 (neotype NHMW).

Platygaster didas Walker, 1835: 240 (lectotype NMINH). **Syn. nov.**

Platygaster pisis Walker, 1835: 239 (lectotype NMINH). **Syn. nov.**

Platygaster remulus Walker, 1835: 239, 240 (lectotype NMINH). **Syn. nov.**

Trichacis didas (Walker, 1835). Förster 1856: 115 (generic transfer).

Trichacis pisis (Walker, 1835). Förster 1856: 115 (generic transfer).

Trichacis remulus (Walker, 1835). Förster 1856: 115 (generic transfer).

Trichacis tristis (Nees, 1834). Dalla Torre 1898: 480 (generic transfer).

Trichacis abdominalis Thomson, 1859: 79 (holotype NHRS, missing from pin). **Syn. nov.**

Trichacis opaca Thomson, 1859: 78, 79 (lectotype MZLU). Buhl & Notton 2009: 1700 (jr. syn. of *T. pisis*).

Trichacis illusor Kieffer, 1916: 564. **Syn. nov.**

Trichacis illusor fusca Kieffer, 1916: 565.

Trichacis illusor illusor Kieffer, 1926: 713, 714, Fig 294.

Trichacis pulchricornis Szélenyi, 1953: 484, 485. **Syn. nov.**
Trichacis bidentiscutum Szabó, 1981: 289, 290. **Syn. nov.**
Trichacis fusciala Szabó, 1981: 289. **Syn. nov.**
Trichacis hajduica Szabó, 1981: 288. **Syn. nov.**
Trichacis quadriclava Szabó, 1981: 290. **Syn. nov.**
Trichacis nosferatus Buhl, 1997: 97, Figs 13–16 (holotype ZMUN). **Syn. nov.**
Trichacis vitreus Buhl, 1997: 96, Figs 9–12 (holotype NHMD). **Syn. nov.**
Trichacis weiperti Buhl, 2019: 344, 345, Figs 9, 10 (holotype NME). **Syn. nov.**
Trichacis persicus Asadi & Buhl, 2021: 333–335, Fig. 1 (holotype HMIM). **Syn. nov.**

Description. Body length: 1.5–2.1 mm (n=10). Body color: dark brown to black. Antenna color: light brown to dark brown. Mandible color: light brown to dark brown. Leg color: yellow to dark brown. Coxa color: dark brown to black. Wing color: pale with brown markings basally, sometimes entirely pale. **Head.** Head shape: ovoid, slightly transverse. Sculpture of ocellar triangle: coriaceous. OOL:LOL: 1, or OOL slightly shorter than LOL. Mandibular sculpture: proximally striate. Mandibles: clasp-like, teeth equal in size. Sculpture of frons: smooth to coriaceous, sometimes with central keel indicated by a faint line. Number of epitorular striae: 5–7. Interantennal process: truncate. Clypeus: exposed, medial carina present below interantennal process. Ventral clypeal margin: straight. Number of clypeal setae: 8. Sculpture of gena: smooth along compound eye, sometimes faintly striate posteriorly; Hyperoccipital carina: present medially, attenuating laterally. Sculpture of vertex anterior to hyperoccipital carina: coriaceous to striate. Vertex posterior to hyperoccipital carina: slightly impressed medially, with whorled or striate sculpture. Occipital carina: incomplete, not extending ventrally to posterior articulation of the mandible. Setation of occiput: dense in ventral half. Projection on temples: absent. Distance between LO and HOC: 2 ocellar diameters.

Female antenna. A1 length: not surpassing vertex of head. Number of clavomeres: 4. Claval formula: 1-1-1-1.

Male antenna. A1 length: not surpassing vertex of head. A2–A5: cylindrical, A3 and A4 semi-appressed. Male sex segment (A4): not expanded, ventral portion flattened with minute longitudinal striae. A6–A10: cylindrical, setose, A10 longest. **Mesosoma.** Mesoscutum in lateral view: moderately arched. Antero-admedian line: present, faint. Notaulus: present, complete or nearly so. Sculpture of mesoscutum: reticulate-coriaceous, sometimes with smooth patches posteriorly. Setation of mesoscutum: moderate to dense, evenly or unevenly distributed. Parapsidal signum: indicated by a faint line. Cervical pronotal area: anteriorly smooth and glabrous. Shape of mesoscutum in lateral view: slightly flattened. Mesoscutellar setal patch: round to triangular, located in posterior half. Sculpture of mesopleuron: smooth, sometimes with very faint striae in dorsal half. Mesopleural carina: present anteriorly, incomplete. Fore wing length: surpassing metasoma. Fore wing marginal setae: very short, slightly longer on posterior distal margin.

Female metasoma. Metasoma length: approximately as long as head and mesosoma combined. Setation of pits on anterior T2 present. Shape of T1: transverse. Sculpture of T1: medially striate, lateral aspect obscured by dense setation. Sculpture of T2: smooth with a few striae between anterior pits. Sculpture of T3–T6: finely punctate. Felt fields: short, densely to sparsely setose. Sculpture of S2: smooth or finely punctate. **Male metasoma.** Metasoma length: slightly shorter than head and mesosoma combined, otherwise similar to female.

Diagnosis. *Trichacis tristis* (Figs 2A, B; 3) does not have any autapomorphic structures to easily distinguish it among the world fauna. The relatively extensive setation and sculpturing of the posterior vertex and mesoscutum (Fig. 3B, E) set it apart from many species in the Western Hemisphere, but a thorough diagnosis must rely on a combination of characters. The following diagnosis uses characters from the keys of Masner (1983) and Arias-Penna *et al.* (2012): temples unarmed; mandibles clasped; clypeus with 8 setae; interantennal process truncate; scape not surpassing vertex; posterior vertex with whorled or striate sculpture medially; hyperoccipital carina laterally weakened, surpassing line of inner eye margin and not merging with striae; internotal area sculptured at least anteriorly, moderately to densely setose; mesopleural carina incomplete; mesoscutellar setal patch round to triangular; fore wing usually with brown markings in proximal third (may be faint or faded), surpassing apex of metasoma in females.

Trichacis tristis is most similar to *T. virginiensis* Ashmead, 1893 and *T. celticola* Masner, 1983 in the Nearctic region. *Trichacis virginiensis* can be separated by the hooked interantennal process, which is simple in *T. tristis*, and by the strongly transverse head, which is only slightly transverse in *T. tristis*. *Trichacis celticola* has short fore wings, not surpassing the apex of the female metasoma, whereas the fore wings in female *T. tristis* extend well beyond the metasoma.

Distribution. *Trichacis tristis* is widespread in the Palearctic, ranging from Ireland to Japan, north to Scandinavia and south to the Mediterranean Sea.

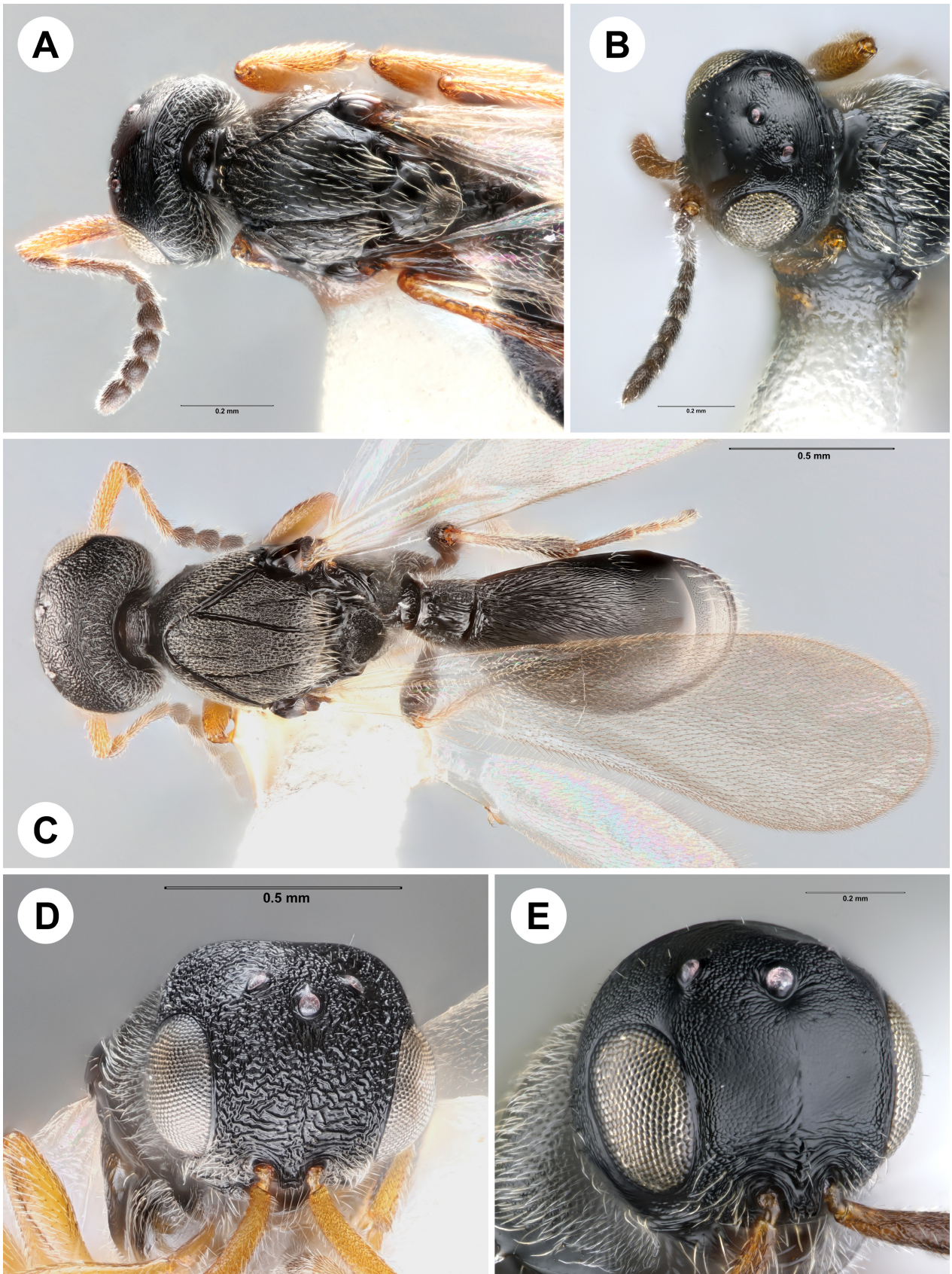


FIGURE 1. Genus-level characters of *Trichacis* and *Isocybus*. A–B. *Trichacis tristis* female, SMNS_Hym_Pla_000797; A. Dorsal head and mesosoma, showing broad aspect of clava; B. Dorsal head showing narrow aspect of clava; C. *Isocybus* female, dorsal habitus, SMNS_Hym_Pla_000880; D. *Isocybus* female, anterior head, SMNS_Hym_Pla_000851; E. *Trichacis tristis* female, anterior head, SMNS_Hym_Pla_000805.

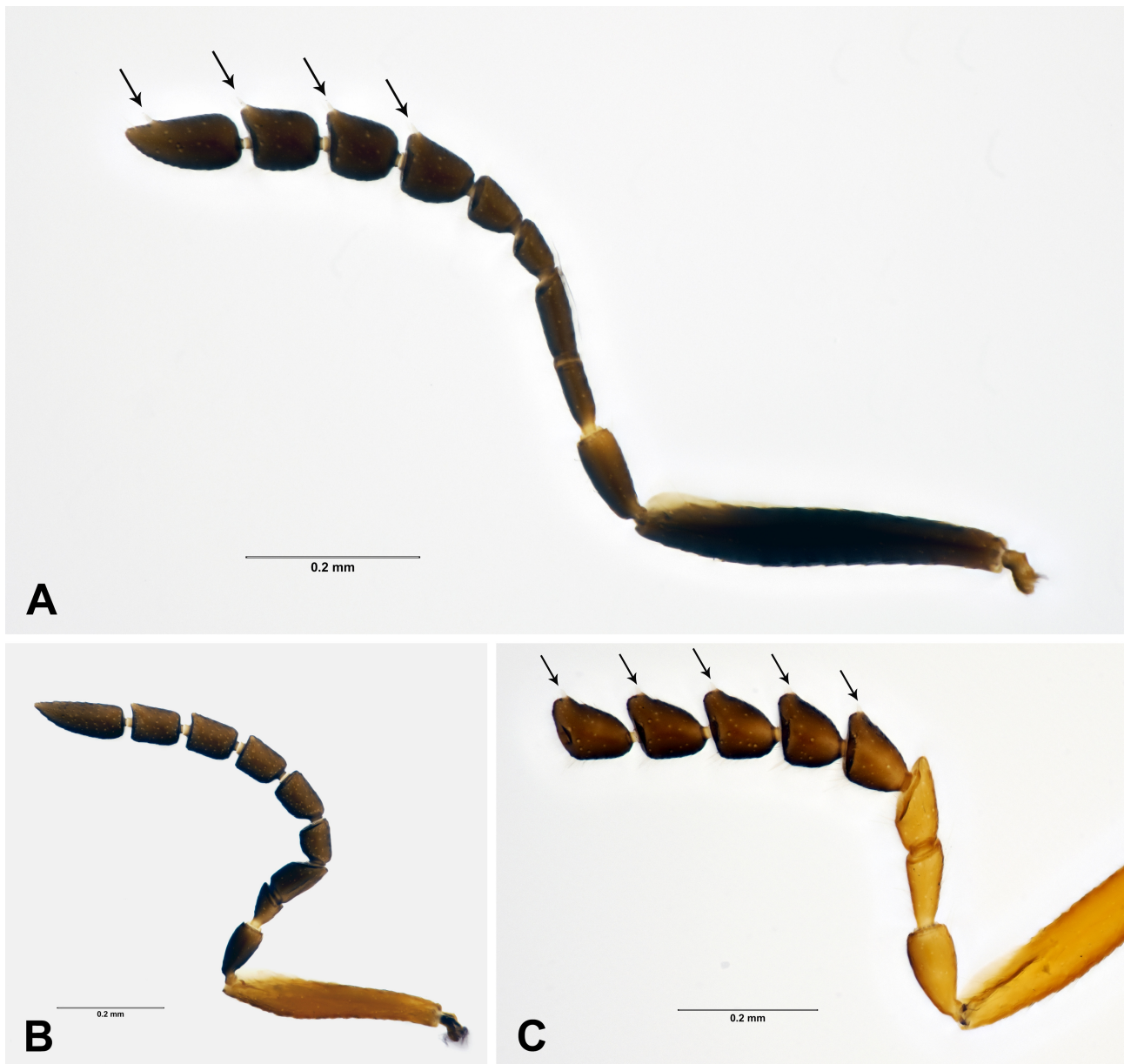


FIGURE 2. Antennae of *Trichacis* and *Isocybus*. A. *T. tristis* female, SMNS_Hym_Pla_000217; B. *T. tristis* male, SMNS_Hym_Pla_000220; C. *Isocybus* female (apical antennomere missing), SMNS_Hym_Pla_000870.

Biological associations. *Trichacis tristis* is associated with *Mayetiola destructor* (Say, 1817) and *M. avenae* (Marchal, 1895), both of which are herbivorous on grain crops and wild grasses (Poaceae). Embryonic and larval development of *T. tristis* (as *T. remulus*) were described and illustrated by Marchal (1906).

Type material examined. Neotype of *Platygaster tristis* ♀, GERMANY, original exemplar, NHMW-HYM-0005319 (NHMW). Lectotype of *P. didas* ♂, UNITED KINGDOM, London, NMINH_2018_11_18; lectotype of *P. pisis* ♂, London, NMINH_2018_11_24; lectotype of *P. remulus* ♂, London, NMINH_2018_11_25 (NMINH). Lectotype of *T. opaca* ♀, SWEDEN, Ringsjön, June, 2856:1-2 (MZLU). Holotype of *T. nosferatus* ♀, NORWAY, Tofteholmen, 7–31 July 1991, L.O. Hansen (ZMUN). Holotype of *T. vitreus* ♀, GREECE, Peloponnese, 5km S Monemvasia, 27 November 1983, G. Christensen, ZMUC 00021950 (NHMD). Holotype of *T. weiperti* ♀, GERMANY, Thuringia, Kyffhäuser, Steinhaleben, mixed oak forest, 230m, 26 June 1998, J. Weipert (NME).

Additional material examined. 1 specimen, AFGHANISTAN, Kabul, 9–11 April 1974, J. Papp; 1 specimen, ARMENIA, Tsakhador, 2000 m, 4 June 1980, J. Papp (HNHM). 1 ♀, AUSTRIA, Piesting, C. Tschek (NHMW). 1 ♂, BULGARIA, Kneja, reared from flies on wheat stalks, December 1960, Samfirov; 1 ♂, CROATIA, Laz, 10 June 1974, J. Papp (HNHM). 1 ♂, FRANCE, Meuse, Dompcevrin, 3–4 June 1985, M.J. Gliswit; 1 specimen,

Bitche, 21 June 1989, H. Vlug (HVC). 1 ♂, 4 ♀, **GERMANY**, North Rhine-Westphalia, Nationalpark Eifel, Helingsberg, May–June 2009, J. Esser, SMNS_Hym_Pla_000720, 721, 724, 726, 727; 1 ♂, Baden-Württemberg, Rems-Murr-Kreis, Aspach bei Backnang, forest, 15–30 April 2013, Krogmann *et al.*, SMNS_Hym_Pla_000729; 1 ♂, 5 ♀, Mecklenburg-Vorpommern, Rügen Island, Kniepow, 17–23 May 2015, F. Koch, SMNS_Hym_Pla_796–798, 804–806 (SMNS). 1 ♀, **GREECE**, Macedonia and Thrace Decentralized Administration, Macedonia Central Periphery, Kerkini Lake, 41.2258°N, 23.0845°E, 45m, March–April 2007, G. Ramel, OSUC 413928 (OSUC). 2 ♂, 2 ♀, **HUNGARY**, Ujszentmargita, 7 May 1975, J. Papp; 2 ♂, 3 ♀, Ujszentmargita, 21–25 April 1975, Hamorine & Marotine; 1 ♂, 1 ♀, Hortobagy, Zam, 16–18 June 1975, Kaszab & Mahunka; 7 ♀, Pécs, 6 May 1955, J.B. Szabó; 2 ♂, Tompa, 12 April 1960, Erdős (HNHM). 1 ♀, **IRELAND**, Glen of the Downs on Wicklow, 12 July 1983, H. Vlug; 1 ♀, **ITALY**, Fusine near Tarvisio, 11 August 1948, H. Vlug (HVC); 1 ♀, E. Graeffe, NHMW-HY♂0006911 (NHMW). 1 specimen, **MONGOLIA**, Central Aimak, Ulaanbaatar, Bogd Khan, 1650–1950m, 4 June 1966, Kaszab; 1 ♀, **ROMANIA**, Transylvania, Homoródkeményfalva, 8 May 1995, I. Rozner (HNHM). 1 ♂, 1 ♀, **SWEDEN**, Småland, Kronoberg, 4km N Hinnyerd, 56.6497°N, 13.5869°E, 7 July 1994, M. Söderlund, OSUC 45132, 45134 (OSUC). 3 ♀, **UNITED KINGDOM**, London, NHM Wildlife Garden, meadow, N51°29'45.6" W0°10'42.1", April–May 2013, Sivell *et al.* (NHMUK).

Remarks on intraspecific variation. European authors described *T. tristis* at least 15 times from England, Germany, Greece, Hungary, Iran, Italy, Sweden, and Norway (Figs 4A–H). This state of affairs is partially attributable to intraspecific variation, separation based on minute differences, and examination of small series. For example, *T. weiperti* (Fig. 4H) was treated as new based on antennomere measurements from a single specimen. Viewing angle can greatly influence measurement. Figures 1A–B illustrate the antenna of the same specimen at different angles, demonstrating the drastic difference. Antennomere measurements should only be taken in lateral view, preferably from antennae that have been removed from the head and mounted on a microscope slide. Antennomeres are also subject to allometric scaling and host-related variation (Johnson *et al.* 1987). Coloration is similarly unreliable and can vary with host species (Talamas *et al.* 2021), geographic region (Vlug 1985), or preservation history (Banks 1909). Buhl (1997) diagnosed *T. vitreus* (Fig. 4F) by its pale wings and legs, which likely faded in color during the 14 years between its collection and description. We have found no support for the description of species based solely on minor differences in coloration or antennomere size.

Cuticular sculpture is more useful for diagnosis, although this character is somewhat variable in *T. tristis*. The frons sometimes exhibits a longitudinal line or thin furrow ventral to the median ocellus as described in *T. pulchricornis* (Fig. 1E), and the mesopleuron sometimes exhibits very faint striations as described in *T. nosferatus* (Fig 3E, 4G). However, the mesopleural sculpture of *T. tristis* is always very smooth in comparison to the conspicuous striation found in *T. striata* Masner, 1983 (Fig. 4I). It should also be noted that description of new species from singleton specimens in poor condition, such as the holotype of *T. nosferatus* (Fig. 4G) is a poor choice, as it creates a challenge to observing characters of interest.

Remarks on additional synonymies. The Walker species of *Trichacis* (*T. didas*, *T. pisis*, and *T. remulus*) (Fig. 4C–E) were redescribed, illustrated, and keyed by Vlug (1985). He suspected that they were conspecific, with very slight variation in color and antennomere shape, but cautiously declined to take taxonomic action without examining more material. Similarly, Arnold Förster noted that he thought *T. didas*, *T. pisis*, and *T. remulus* were conspecific with *T. tristis*, based on original exemplars of these species received from their respective authors (unpublished label data, NHMW). Our morphological assessment of the types confirms the suspicions of both Vlug and Förster.

We did not locate the types of *T. abdominalis* Thomson, 1859 (Ringsjön, Sweden) and *T. illusor* Kieffer, 1916 (Trieste, Italy). However, the descriptions and geographic localities for both species match the morphology and distribution of *T. tristis*.

Trichacis persicus was described as being similar to *T. tristis*, but with minor differences in the proportions of the antennomeres. This diagnosis, the photographs provided in the description, and the locality (a wheat-producing region with agricultural fields visible in satellite photos), led us to conclude that *T. persicus* is a junior synonym of *T. tristis*.

Remarks on the Hungarian species of *Trichacis*. Gusztáv Szelényi worked as a plant protection entomologist in Hungary in the early to mid-20th century. His agricultural research led him to parasitoid taxonomy, including a few descriptions of Platygasteridae, one of which was *T. pulchricornis* Szelényi, 1953. The type of this species was not found in HNHM. However, other material from the type locality, Bátorliget, included no *Trichacis* species besides the common *T. tristis*. The description of *T. pulchricornis* is also consistent with our concept of *T. tristis*.

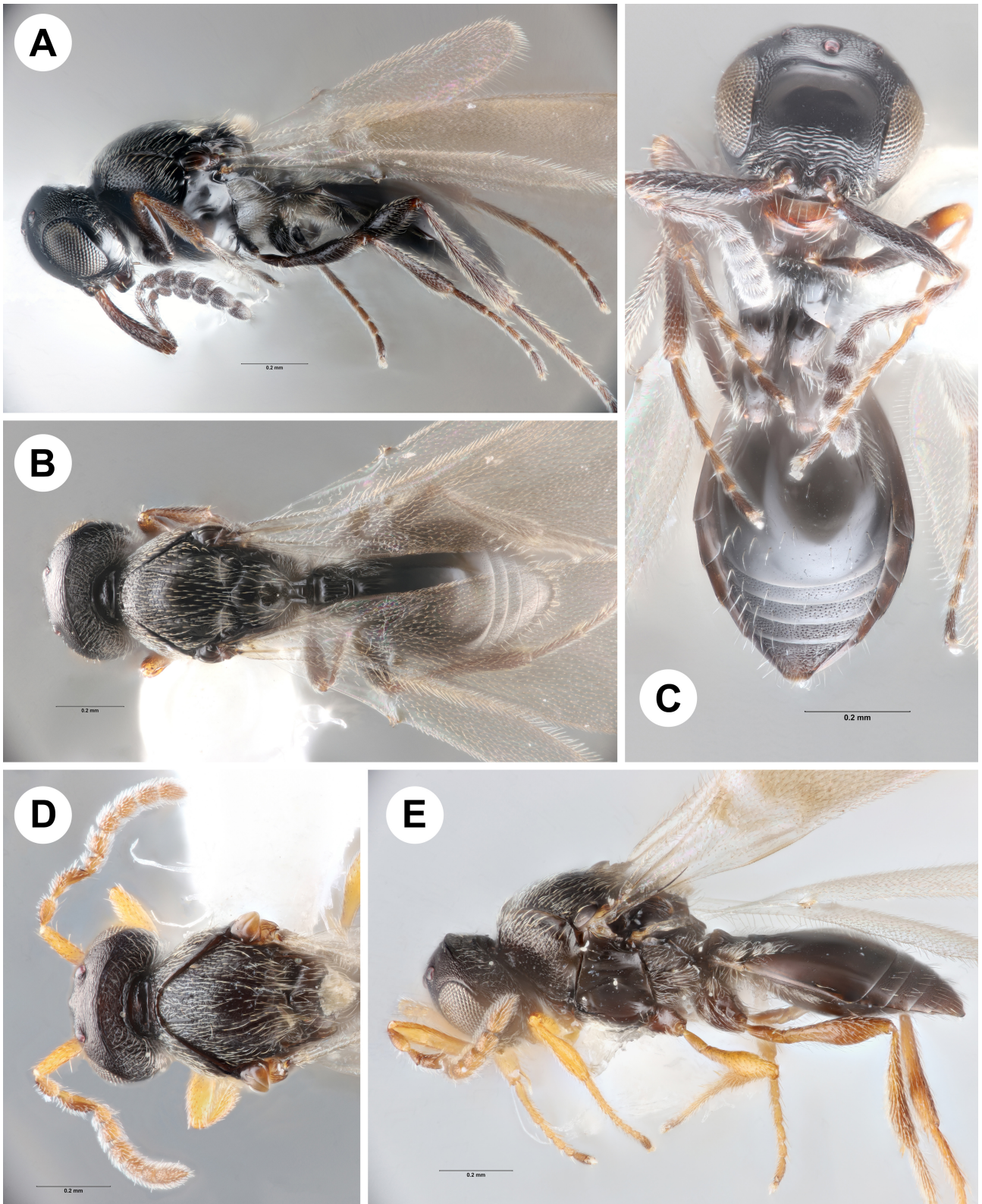


FIGURE 3. *Trichacis tristis*. A–B. Female, SMNS_Hym_Pla_000804; A. Lateral habitus; B. Dorsal habitus; C. Female, ventral habitus, SMNS_Hym_Pla_000720; D–E. Male, OSUC 45132; D. Dorsal head and mesosoma; E. Lateral habitus.

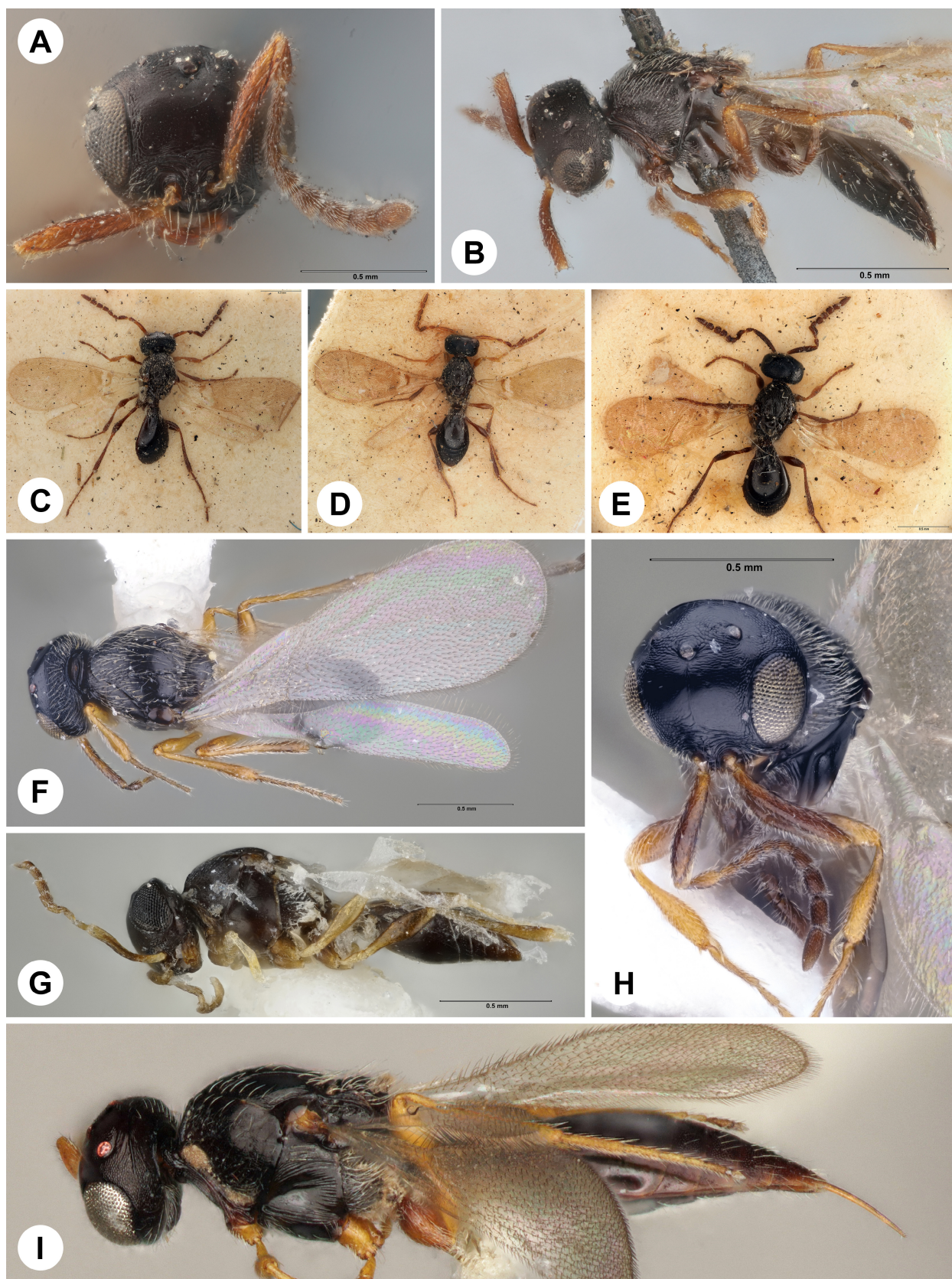


FIGURE 4. Selected type specimens of *Trichacis*; A. *T. tristis*, neotype female, anterior head; B. *T. tristis*, neotype female, lateral habitus; C. *Platygaster didas*, lectotype male, dorsal habitus; D. *P. pisis*, lectotype male, dorsal habitus; E. *P. remulus*, lectotype male, dorsal habitus; F. *T. vitreus*, holotype female, dorsal habitus; G. *T. nosferatus*, holotype female, lateral habitus; H. *T. weiperti*, holotype female, anterior head and antenna; I. *T. striata* Masner, holotype female, lateral habitus image by J. Mackey, CNCI.

János Barna Szabó was a prolific self-taught hymenopterist in Hungary in the mid-20th century. His knowledge of Platygastridae came primarily from one book: *Das Tierreich* volume 48 by Jean-Jacques Kieffer (1926) (Zoltán Vas, pers. comm.). The resulting taxonomic work therefore had limited perspective. It is clear from examination of Szabó's platygastriid collection that his generic concepts were sometimes inaccurate. Szabó described eight species of *Trichacis*, four of which were published in 1977 (*T. afurcata*, *T. hungarica*, *T. pannonica*, and *T. tatika*). The holotypes of these specimens, along with some other material determined by Szabó as *Trichacis*, belong to the genus *Amblyaspis* (Figs 5A–D), into which we now transfer them. It is likely that these are junior synonyms as well, but the chaotic state of species-level taxonomy in *Amblyaspis* does not allow for more specific determination at present.

Based on determination labels in HNHM, it appears that Szabó adopted the prevailing concept of *Trichacis* sometime after 1977. He published four species of *Trichacis* from Hortobágy National Park in 1981 (*T. bidentiscutum*, *T. fusciala*, *T. hajduica*, and *T. quadriclava*). These holotypes were not found in HNHM. However, examination of extensive material from the original collecting events yielded no evidence of any *Trichacis* species other than *T. tristis*, which was present in abundance (Figs 5E–G).

Furthermore, thorough examination of the platygastriid holdings at HNHM indicates that the *Trichacis* fauna of Hungary, like the rest of central Europe, includes only one species. We conclude that *T. pulchricornis*, *T. bidentiscutum*, *T. fusciala*, *T. hajduica*, and *T. quadriclava* are best treated as junior synonyms of *T. tristis*.

Genus *Amblyaspis* Förster, 1856

(Figs 5A–D)

Amblyaspis Förster, 1856: 107, 112. Type species *Platygaster tritici* Walker, 1835 by subsequent designation by Vlug 1995: 12.

Diagnosis. Mesoscutellum evenly setose, forming a cone in dorsal view (Figs 4B, C); antennal clava composed of articulated (A7–A8) and “semicompact” (A9–A10) segments (Fig. A).

Amblyaspis afurcata (Szabó, 1977), comb. nov.

(Fig. 5A)

Trichacis afurcata Szabó, 1977: 143, 144.

Type material examined. Holotype ♀, HUNGARY, Nadap, 13 November 1951, Kaszab (HNHM).

Amblyaspis hungarica (Szabó, 1977), comb. nov.

(Fig. 5B)

Trichacis hungarica Szabó, 1977: 143.

Type material examined. Holotype ♀, Soltvadkert, 15 April 1944, J. Balogh (HNHM).

Amblyaspis pannonica (Szabó, 1977), comb. nov.

(Fig. 5C)

Trichacis pannonica Szabó, 1977: 145

Type material examined. Holotype ♀, Kaposvár, September 1940 (HNHM).

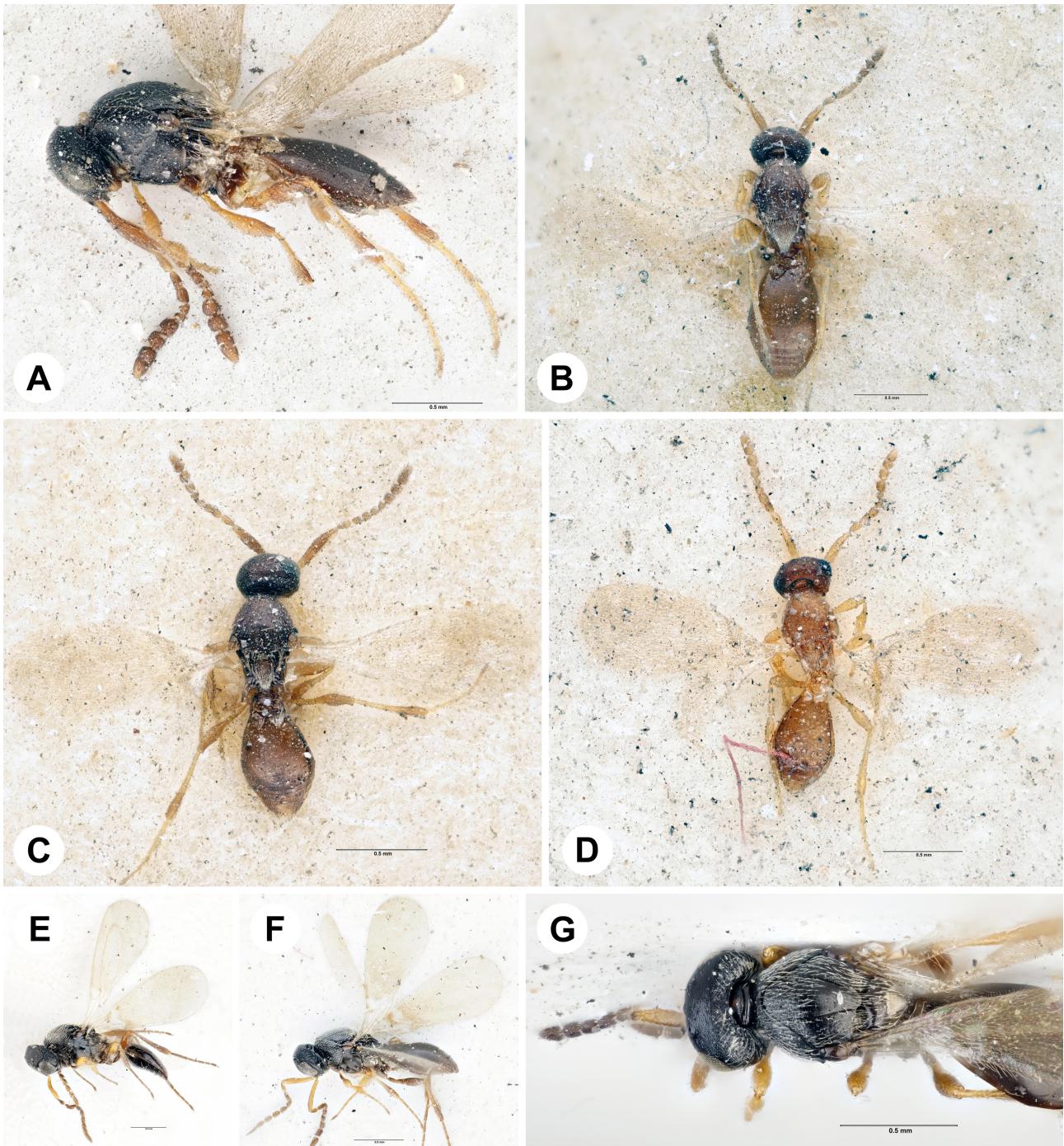


FIGURE 5. Specimens from HNHM. A. *Amblyaspis afurcata*, holotype female, lateral habitus; B. *Amblyaspis hungarica*, holotype female, dorsal habitus; C. *Amblyaspis pannonica*, holotype female, dorsal habitus; D. *Amblyaspis tatika*, holotype female, dorsal habitus; E. *T. tristis* male, lateral habitus, from collecting event of *T. hajduica*; F. *T. tristis* male, lateral habitus, from collecting event of *T. fusciala*; G. *T. tristis* female, dorsal habitus, from collecting event of *T. hajduica*.

***Amblyaspis tatika* (Szabó, 1977), comb. nov.**

(Fig. 5D)

Trichacis tatika Szabó, 1977: 145

Type material examined. Holotype ♀, Tatika, 12 September 1952, Kaszab (HNHM).

Molecular analysis. The ASAP analysis revealed that all 170 records from Europe were conspecific and formed

a clade with high support (Supplemental File 2). These records came from Belarus, Bulgaria, England, Germany, Finland, and Norway. Worldwide DNA barcode data from BOLD and GBOL indicated the existence of 11 to 13 species of *Trichacis* based on partitioning. The best ASAP score indicated the presence of 11 species, while the maximum likelihood tree recovered 13 distinct clades that could be considered putative species. Of the 13 putative species on the tree, seven species were recorded only from Canada, two species from Canada and the USA, one from Tennessee, one from Florida, and one from Honduras. Backbone support was low, although the resulting tree places *Isocybus* as sister to *Trichacis* (Fig. 6).

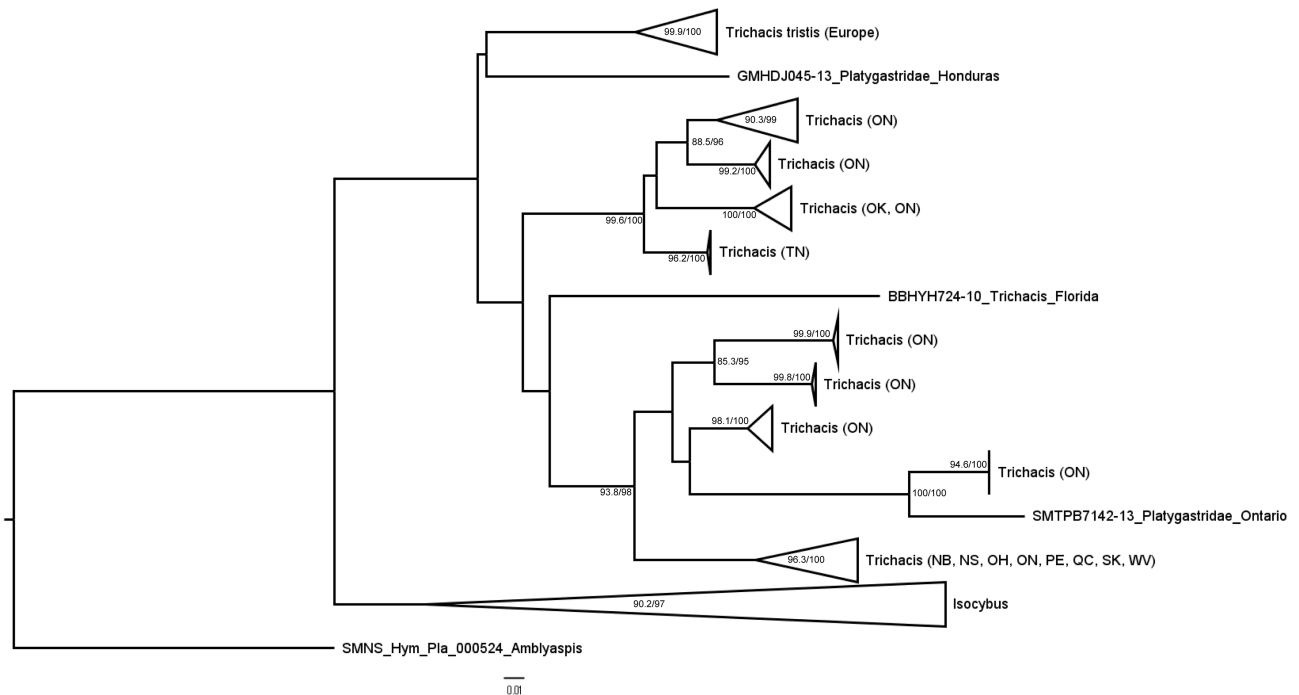


FIGURE 6. Maximum likelihood tree of all *Trichacis* barcodes available from BOLD and GBOL (n=496). Only significant branch supports are shown (SH-aLRT > 80 / ultrafast bootstrap > 95).

Discussion

The molecular analysis was congruent with the high species diversity of *Trichacis* in the Nearctic compared to the Palearctic region. Comparison between morphological and molecular species is not yet possible for the Neotropics due to a lack of publicly available sequences. However, the 28 species treated by Arias-Penna *et al.* (2012) are morphologically distinct, supporting the current status of the Neotropics as the region of highest *Trichacis* diversity. Backbone support and taxon sampling were not sufficient to test hypotheses about the biogeographic history of *Trichacis* or its relationship to *Isocybus*. The ability of DNA barcodes to elucidate deeper evolutionary processes is limited (Desalle & Goldstein 2019) and future phylogenetic work involving more genes as well as specimens from South America and East Asia will be needed to understand the evolutionary history of *Trichacis*.

There is no evidence that *T. tristis* is in Canada or the USA. This is somewhat surprising given its association with the Hessian fly, an invasive pest of wheat in North America (Schmid *et al.* 2018), and the tendency of other Palearctic platygastroid species to follow their hosts to the Nearctic (Gardner *et al.* 2013; Talamas *et al.* 2015; Cossentine *et al.* 2020; Birkmire *et al.* 2021; Talamas *et al.* 2021). Further investigations into the biology of *T. tristis* and *M. destructor* may provide insights into the mechanisms determining how and why certain parasitoid species become adventive in new regions and others do not.

At present, *T. tristis* is the only species of *Trichacis* for which the host is known. There are a few plant associations recorded for *Trichacis* outside of Europe (Vlug 1995). In North America, *T. cornicola* (Ashmead, 1893) was reared from *Cornus paniculata* Heritier (Cornaceae), *T. crossi* MacGown, 1989 from *Sphaeralcea* (Malvaceae), and *T. rufipes* Ashmead, 1893 from *Quercus* acorns (Fagaceae). In Brazil, *T. meridionalis* (Brues, 1910) was reared from *Acnistus* and *Cestrum* (Solanaceae).

Considering that *T. tristis* attacks a well-known agricultural pest with a long history of research, it is remarkable that no serious revision of the parasitoid has occurred. The discovery of 14 junior synonyms for *T. tristis* has significant implications for our taxonomic understanding. If a genus with such a robust link to human interests can be so neglected, what can we infer about other genera in Platygastrinae? Extrapolation would suggest that hundreds of synonymies have yet to be discovered by revisionary taxonomists in this one subfamily of Platygastroidea alone.

Although much of the diversity of Platygastridae remains undescribed, an accurate assessment of the Palearctic fauna is not possible without first resolving the excess of junior synonyms. Junior synonyms are a phenomenon to be expected because our knowledge at any given time will always be incomplete. The historical proliferation of synonyms is somewhat understandable, as many authors worked in isolation and international communication was far from the speed that we now enjoy. When taxonomic identification tools are insufficient, as has been the case with *Trichacis*, authors may be inclined to describe species as new rather than risk a misidentification. In other cases, the *mihi* itch (Evenhuis 2008) may be a factor. If the new species are described poorly, the superficial species impediment *sensu* Meier *et al.* (2022) is exacerbated, creating a feedback loop of chaos. Recognition and resolution of synonyms, as we have done for *T. tristis*, should therefore be considered a priority for taxonomic advancement that sustains research in biological control, faunistic studies, and insect conservation.

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References

- Arias-Penna, T.M., Masner, L. & Delsinne, T. (2012) Revision of the Neotropical species of *Trichacis* Foerster (Hymenoptera: Platygastroidea: Platygastridae), with description of 24 new species. *Zootaxa*, 3337 (1), 1–56.
<https://doi.org/10.11646/zootaxa.3337.1.1>
- Asadi-Farfar, M., Lotfalizadeh, H., Karimpour, Y. & Buhl, P.N. (2021) Discovery of the genera *Trichacis* Förster and *Piestopleura* Förster (Hymenoptera: Platygastroidea) in Iran with descriptions of three new species. *International Journal of Environmental Studies*, 78 (2), 332–340.
<https://doi.org/10.1080/00207233.2020.1723953>
- Ashmead, W.H. (1893) Monograph of the North American Proctotrypidae. *Bulletin of the United States National Museum*, 45, 1–472.
<https://doi.org/10.5479/si.03629236.45.1>
- Awad, J., Vasilița, C., Wenz, S., Alkarrat, H., Zimmermann, O., Zebitz, C. & Krogmann, L. (2021) New records of German Scelionidae (Hymenoptera: Platygastroidea) from the collection of the State Museum of Natural History Stuttgart. *Biodiversity Data Journal*, 9, e69856.
<https://doi.org/10.3897/BDJ.9.e69856>
- Banks, N. (1909) Directions for collecting and preserving insects. *United States National Museum Bulletin*, 67, 1–135.
<https://doi.org/10.5479/si.03629236.67.i>
- Birkmire, S., Penca, C., Talamas, E.J., Moore, M.R. & Hodges, A.C. (2021) *Psix striaticeps* (Dodd) (Hymenoptera, Scelionidae):

- an Old World parasitoid of stink bug eggs arrives in Florida, USA. In: Lahey, Z. & Talamas, E. (Eds.), *Advances in the Systematics of Platygastroidea III. Journal of Hymenoptera Research*, 87, 503–521.
<https://doi.org/10.3897/jhr.87.76191>
- Buhl, P.N. (1997) Four new species of Platygastriinae (Hymenoptera, Platygastriidae). *Entomofauna*, 18 (11), 93–100.
- Buhl, P.N. (2019) New species and notes on variation in Platygastriinae from Germany (Hymenoptera, Platygastriidae). *Entomofauna*, 40 (1), 337–346.
- Buhl, P.N. & Notton, D.G. (2009) A revised catalogue of the Platygastriidae of the British Isles (Hymenoptera: Platygastroidea). *Journal of Natural History*, 43, 1651–1703.
<https://doi.org/10.1080/00222930902993732>
- Cossentine, J.E., Brauner, A.M., Franklin, J.L., Robertson, M.C., Buhl, P.N., Blatt, S., Garipey, T., Fraser, H., Appleby, M., Grigg-McGuffin, K. & Mason, P.G. (2020) Parasitism and phenology of *Dasineura mali* (Diptera: Cecidomyiidae) in Canadian apple (Rosaceae) orchards. *Canadian Entomologist*, 152 (3), 355–373.
<https://doi.org/10.4039/tce.2020.15>
- Dalla Torre, C.G. (1898) *Catalogus Hymenopterorum. Vol. 5. Chalcididae et Proctotrupidae*. Engelmann, Leipzig, 668 pp. [in German]
- Desalle, R. & Goldstein, P. (2019) Review and interpretation of trends in DNA barcoding. *Frontiers in Ecology and Evolution*, 10, 1–11.
<https://doi.org/10.3389/fevo.2019.00302>
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32 (5), 1792–1797.
<https://doi.org/10.1093/nar/gkh340>
- Evenhuis, N.L. (2008) The “Mihi itch”—a brief history. *Zootaxa*, 1890 (1), 59–68.
<https://doi.org/10.11646/zootaxa.1890.1.3>
- Förster, A. (1856) *Hymenopterologische Studien. II. Heft. Chalcididae und Proctotrupidii*. Ernst ter Meer, Aachen, 152 pp. [in German]
- Gardner, W., Blount, J., Golec, J., Jones, W., Hu, X.-P., Talamas, E., Evans, R., Dong, X., Ray, C., Buntin, G., Gerardo, N. & Couret, J. (2013) Discovery of *Paratelenomus saccharalis* (Dodd) (Hymenoptera: Platygastriidae), an egg parasitoid of *Megacopta cribraria* F. (Hemiptera: Plataspidae) in its expanded North American range. *Journal of Entomological Science*, 48, 355–359.
<https://doi.org/10.18474/0749-8004-48.4.355>
- Guindon, S., Dufayard, J.-F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010) New algorithms and methods to estimate maximum likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology*, 59 (3), 307–321.
<https://doi.org/10.1093/sysbio/syq010>
- Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2017) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35 (2), 518–522.
<https://doi.org/10.1093/molbev/msx281>
- Hymenoptera Online (2023) Museum of Biological Diversity Public Database. Available from: <https://mbd-db.osu.edu/legacy/hol/root> (accessed 16 January 2023)
- Johnson, N.F., Rawlins, J.E. & Pavuk, D.M. (1987) Host-related antennal variation in the polyphagous egg parasite *Telenomus alsophilae* (Hymenoptera: Scelionidae). *Systematic Entomology*, 12 (4), 437–447.
<https://doi.org/10.1111/j.1365-3113.1987.tb00216.x>
- Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A. & Jermini, L.S. (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14, 587–589.
<https://doi.org/10.1038/nmeth.4285>
- Kieffer, J.J. (1916) Beitrag zur Kenntnis der Platygasterinae und ihrer Lebensweise. *Zentralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten*, 46, 547–592. [in German]
- Kieffer, J.J. (1926) *Das Tierreich. 48. Lieferung. Hymenoptera, Proctotrupoidea, Scelionidae*. Walter de Gruyter, Berlin/Leipzig, 885 pp. [in German]
<https://doi.org/10.1515/9783111432939>
- Macgown, M.W. (1989) A new species of *Trichacis* (Hymenoptera: Platygastriidae) from Texas, associated with *Sphaeralcea* (Malvaceae). *Entomological News*, 100 (1), 6–10.
- Marchal, P. (1906) Recherches sur la biologie et le développement des hyménoptères parasites: Les Platygasters. *Archives de Zoologie Expérimentale et Générale*, 4 (4), 485–640. [in French]
- Masner, L. (1983) Revision of the Nearctic species of *Trichacis* Foerster (Hymenoptera: Proctotrupoidea: Platygastriidae). *Canadian Entomologist*, 115, 1071–1093.
<https://doi.org/10.4039/Ent1151071-9>
- Meier, R., Blaimer, B.B., Buenaventura, E., Hartop, E., von Rintelen, R., Srivathsan, A. & Yeo, D. (2022) A re-analysis of the data in Sharkey *et al.*'s (2021) minimalist revision reveals that BINs do not deserve names, but BOLD Systems needs a stronger commitment to open science. *Cladistics*, 38, 264–275.
<https://doi.org/10.1111/cla.12489>

- Nees von Esenbeck, C.G. (1834) *Hymenopterorum Ichneumonibus Affinium, Monographiae, Genera Europaea et Species Illustrantes. Vol. 2.* J.G. Cottae, Stuttgart, 320 pp. [in Latin]
- Nguyen, L.T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274.
<https://doi.org/10.1093/molbev/msu300>
- Puillandre, N., Brouillet, S. & Achaz, G. (2021) ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources*, 21 (2), 609–620.
<https://doi.org/10.1111/1755-0998.13281>
- Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes*, 7, 355–364.
<https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- Schmid, R.B., Knutson, A., Giles, K.L. & McCornack, B.P. (2018) Hessian fly (Diptera: Cecidomyiidae) biology and management in wheat. *Journal of Integrated Pest Management*, 9 (1), 1–12.
<https://doi.org/10.1093/jipm/pmy008>
- Szelényi, G. (1953) *Trichacis pulchricornis* Szelényi spec. nov. In: Székessy, V. (Ed.), *Die Tier und Pflanzenwelt des Naturschutzgebietes Bátorliget und seiner Umgebung*. Adadémiai Kiadó, Budapest, pp. 484–485. [in German]
- Szabó, J. (1977) Durch Ausleseapparat erbeutete Zehrwespen aus der Gattung *Trichacis* Förster, 1856 (Hymenoptera: Proctotrupeoidea, Platygasteridae). *Folia Entomologica Hungarica*, 30 (1), 143–145. [in German]
- Szabó, J. (1981) Contributions to the platygasterid wasps of the Hortobágy National Park (Hymenoptera, Platygasteridae). In: Mahunka, S. (Ed.), *The Fauna of the Hortobágy National Park. Vol. 1.* Akadémiai Kiadó, Budapest, pp. 285–297.
- Talamas, E.J., Herlihy, M.V., Dieckhoff, C., Hoelmer, K.A., Buffington, M.L., Bon, M.-C. & Weber, D.C. (2015) *Trissolcus japonicus* (Ashmead) (Hymenoptera, Scelionidae) emerges in North America. *Journal of Hymenoptera Research*, 43, 119–128.
<https://doi.org/10.3897/JHR.43.4661>
- Talamas, E.J., Bremer, J.S., Moore, M.R., Bon, M.C., Lahey, Z., Roberts, C.G., Combee, L.A., McGathey, N., van Noort, S., Timokhov, A.V., Hougardy, E. & Hogg, B. (2021) A maximalist approach to the systematics of a biological control agent: *Gryon aetherium* Talamas, sp. nov. (Hymenoptera, Scelionidae). In: Lahey, Z. & Talamas, E. (Eds.), *Advances in the Systematics of Platygastroidea III.* *Journal of Hymenoptera Research*, 87, pp. 323–480.
<https://doi.org/10.3897/jhr.87.72842>
- Thomson, C.G. (1859) Sveriges Proctotruper. Tribus VII. Platygastriini. *Öfversigt af Kongliga Ventenskaps-Akademiens Förhandlingar*, 16, 69–87. [in Swedish and Latin]
- Trifinopoulos, J., Nguyen, L.T., von Haeseler, A. & Minh, B.Q. (2016) W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44 (W1), W232–W235.
<https://doi.org/10.1093/nar/gkw256>
- Vlug, H.J. (1985) The types of Platygastriidae (Hymenoptera, Scelionoidea) described by Haliday and Walker and preserved in the National Museum of Ireland and in the British Museum (Natural History) 2. Keys to species, redescriptions, synonymy. *Tijdschrift voor Entomologie*, 127 (9), 179–224.
- Vlug, H.J. (1995) Catalogue of the Platygastriidae (Platygastroidea) of the world (Insecta: Hymenoptera). *Hymenopterorum Catalogus*, 19, 1–168.
- Walker, F. (1835) On the species of *Platygaster*, &c. *The Entomological Magazine*, 3, 217–274.
- Yoder, M.J., Mikó, I., Seltmann, K.C., Bertone, M.A. & Deans, A.R. (2010) A gross anatomy ontology for Hymenoptera. *PLoS ONE*, 5 (12), e15991.
<https://doi.org/10.1371/journal.pone.0015991>