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Molecular analysis reveals *Latonius planus* Kononova to be a derived species of *Trissolcus* Ashmead

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Abstract

The monotypic genus *Latonius* Kononova, 1982 (Platygastroidea, Scelionidae), was described from a single female specimen collected in southern Ukraine. It somewhat resembles *Trissolcus* Ashmead but has a distinctive claval formula. The only species in the genus, *Latonius planus* Kononova, 1982, is lacking any details regarding biology, sexual dimorphism, intraspecific variability, or distribution. Based on recently collected specimens the present study clarifies the position of *Latonius* within the Telenominae, provides a comprehensive description accompanied by high quality images, and compares *Latonius* and *Trissolcus*. Five molecular markers were amplified, and sequences of *L. planus* were analyzed using a data set for the molecular phylogeny of Telenominae (Taekul et al. 2014) and a molecular phylogeny of *Trissolcus* (Talamas et al. 2019). We dissected the metasoma, tarsi, antennae, and ovipositor and performed SEM imaging. The genera *Latonius* and *Ioseppinella* Mineo, O'Connor & Ashe, 2010, are treated as junior synonyms of *Trissolcus* and the type species of *Latonius* and *Ioseppinella* are considered to be conspecific (**syn. nov.**).

Keywords

Ioseppinella serena, Mineo types, molecular systematics, Platygastroidea, Telenominae

Introduction

The subfamily Telenominae Thomson is one of the most successful groups of scelionid wasps for controlling pests of agriculture. Rearing data indicate that egg-parasitoid species in Telenominae show a clear pattern of host group specificity, being restricted to hosts from Hemiptera, Lepidoptera, Diptera, and Neuroptera (Austin et al. 2005; Taekul et al. 2014). Species of *Telenomus* Haliday and *Trissolcus* Ashmead target eggs of some important pentatomid pests including the genera *Bagrada* Stål, *Eurygaster* Laporte, *Halyomorpha* Mayr, and *Nezara* Amyot & Serville, as well as pests in other orders, e.g. *Lymantria dispar* (L.) (Lepidoptera, Erebidae) and *Tabanus* L. (Diptera, Tabanidae). Orr (1988) considered some platygastroids to be excellent biological control agents due to their efficient searching abilities, high reproductive rates, synchrony with host populations, and simple adult diets. Moreover, the simplicity of the rearing process for some species and their biology as egg parasitoids represent considerable advantages.

Telenominae contains more than 800 described species (various contributors, 2019). Johnson (1992) listed 14 genera in the subfamily: *Aradoctonus* Masner, *Bruchiola* Kieffer, *Eumicrosoma* Gahan, *Latonius* Kononova, *Mudigere* Johnson, *Nirupama* Nixon, *Paratelenomus* Dodd, *Phanuromyia* Dodd, *Phanuropsis* Girault, *Phlebiaporus* Kozlov, *Protelenomus* Kieffer, *Psix* Kozlov & Lê, *Telenomus* and *Trissolcus*. During the past two decades, the composition of the group has changed since several new genera have been described and others removed from Telenominae. New taxa include *Ioseppinella* Mineo, O'Connor & Ashe (Mineo et al. 2010), *Kozlotelenomus* Mineo, O'Connor & Ashe (Mineo et al. 2009a), *Paratrissolcus* Mineo, O'Connor & Ashe (Mineo et al. 2009b), *Rachelia* Mineo (Mineo 2004), *Televiggianus* Mineo (Mineo 2004). *Psix*, *Paratelenomus*, *Nirupama*, and *Mudigere* were excluded from Telenominae and placed in Scelioninae by Taekul et al. (2014). *Kozlotelenomus* and *Eumicrosoma* have since been treated as junior synonyms of *Trissolcus* and *Baeoneurella* Dodd, respectively (Talamas and Buffington 2015; Popovici et al. 2019). Apart from these extant genera, one genus – *Sinoprotelenomus* Zhang – was described to include a fossil species – *Sinoprotelenomus miocenicus* Zhang (Johnson et al. 2008).

The recognition of Telenominae is relatively straightforward based on some head and metasomal characters: sexually heteromerous antennae (10 or 11-merous in female and 12-merous in male), palpal formula with a reduced number of palpomeres (2:1, 2:0, 1:1, or 1:0), large laterotergites loosely attached to the sterna, absence of laterosternites, the second metasomal segment the longest, and a *Ceratobaeus*-type ovipositor (Masner 1976, 1993; Johnson 1988; Austin and Field 1997; Taekul et al. 2014; Popovici et al. 2017). However, these characters are not restricted to Telenominae; the large, loosely attached laterotergites can also be found in some Scelioninae (e.g. *Tiphodytes* Bradley, *Aradophagus* Ashmead, males of *Baeus* Haliday) and in some Platygastridae (e.g. *Fidiobia* Ashmead). The second tergite is the largest metasomal tergite in some *Gryon* Haliday and *Calliscelio* Ashmead (the species previously classified in *Yunkara* Galloway and *Xentor* Masner & Johnson), and essentially all Platygastridae.

Latonius was described as a monotypic genus with *Latonius planus* Kononova as the type species (Kononova 1982). Furthermore, it was described from a single female collected in the southern part of Ukraine. The original description of *Latonius* was repeated two more times, in Kozlov and Kononova (1983) and in Kononova (1992), but without any new information. *Latonius* otherwise appears only as a mention in Johnson (1984, 1985, 1992) and in two species lists (Pintureau 2012; Gramma et al. 2014). Specimens of *Latonius*, other than the holotype, have not been treated until recently, and this genus was not included in the molecular phylogeny of Telenominae performed by Taekul et al. (2014) due to a lack of specimens. Kononova (1982) considered *Latonius* to be related to *Aradophagus* because of the dorsoventrally depressed shape of the body, the antennal structure (clavomeres increase in size gradually and only slightly) and nearly colinear arrangement of the posterior and anterior ocelli [Kononova followed Ashmead (1893), Kieffer (1926), and Kozlov (1970), by including *Aradophagus* in Telenominae]. Based on the small size of the body, the number of the antennomeres, the pilosity of the wings, and the fore wing venation, Kononova placed *Latonius* close to *Telenomus*. She also considered that the genus was similar to *Protelenomus* based on the structure of the tarsi. Until now, the relationships of *Latonius* with other telenomine genera and its validity as a genus have been unclear. During a collecting expedition in southern France, we collected 5 fresh specimens of *Latonius*, providing an opportunity to shed light on the matter.

The aim of this study is to (1) comprehensively illustrate and redescribe *Latonius*, (2) compare it with other genera of Telenominae, and (3) establish if *Latonius* should be considered a valid genus. We also incorporated the molecular datasets of Taekul et al. (2014) and Talamas et al. (2019) to clarify its relationship with other Telenominae.

Materials and methods

Insects were collected using a triangular sweep net with a mesh screen over its opening as described in Noyes (1982) and Popovici et al. (2019). Specimens were preserved in 85% ethanol. All specimens were chemically dried using hexamethyldisilazane (Brown 1993; Heraty and Hawks 1998) and mounted on triangular black points to reduce glare during imaging. The photographs were taken at the CERNESIM facility of the "Al. I. Cuza" University of Iaşi using a Leica DFC-450 C camera on a Leica 205A stereomicroscope and a Leica LED5000 HDI dome illuminator. Extended focus images were produced with Zerene Stacker (PMax algorithm). For SEM images, a VEGA TESCAN SEM unit (HV = 30.00 kV; WD = 31.522 mm) was used. Final images were modified in Adobe Photoshop to enhance clarity. The maxillolabial complex was drawn in Adobe Illustrator based on photographs of the slide mounted parts. The female holotype, deposited in the collection of Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, was studied via photographs taken with a Leica Z16 APO stereomicroscope equipped with a Leica DFC 450 camera and aided with LAS Core software.

The type specimen of *I. serena* Mineo, O'Connor & Ashe, 2010, is deposited in the collection of Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy (MSNG). It was studied via images produced with Canon 90D + extension tube + 20× LWD microscope lens mounted on a macro-rail and illuminated with two speedlite flashes. The frames were merged with Zerene Stacker (PMax algorithm).

The antennae, wings, and legs from the left side of the body and the maxillolabial complex (MLC) were removed from one of the freshly collected specimens and mounted in Canada balsam on a microscope slide. Afterwards, the specimen, without MLC and appendages (antennae, legs, and wings), was coated with gold and used for SEM imaging. The same specimen was later boiled in a 10% solution of phenol in lactic acid for 30 minutes and rinsed in distilled water. Following these steps, the metasoma was dissected, with the tergites, sternites, and ovipositor mounted in Canada balsam on a microscope slide.

Two individuals were used for molecular analysis. DNA extraction was performed using the DNeasy Blood & Tissues Extraction Kit from Qiagen following the provided protocol with changes aimed at keeping the specimens intact and maximising the recovery of DNA (Cruaud et al. 2019). Five molecular markers were amplified: the mitochondrial protein coding gene Cytochrome C oxidase, subunit I and four nuclear genes: 18S rDNA, 28S rDNA, Elongation Factor 1α (F2 copy), and Wingless. The amplicons for the targeted genes were obtained by standard PCRs in 25 µl reaction volume. PCR reactions for COI, 18S rDNA, and 28S rDNA were conducted using 4 µl of DNA template. The PCR protocol was modified for EF-1α and Wingless to include 10 µl of DNA template. The amplification was carried out with the sets of primers listed in Table 1. Thermocycler conditions were set as specified in Table 2 and thermal cycles were repeated 40 times. For the reamplification of weak amplicons, we used 1 µl of purified PCR product as template and the number of cycles was set to 18; the rest of the PCR conditions remained unchanged. For COI we used two primer pairs and the resulting overlapping segments were assembled to obtain a sequence longer than the standard DNA barcode region.

The quality of all PCR products was evaluated by 1% agarose gel electrophoresis. PCR products were purified with polyethylene glycol (PEG) prior to sequencing. The use of For3 and Cho10 primers resulted, as expected, in the amplification of two regions of different sizes (~450 bp, ~600 bp) (Danforth et al. 1999). The 600 bp DNA fragment of interest was gel purified with the MinElute Gel Extraction Kit (Qiagen) following manufacturer's protocol. An additional PEG purification was performed to ensure that leftover salts did not inhibit the sequencing reaction. For Wingless, the PCR product appeared to be too short (400 bp) for PEG purification; therefore, it was gel purified using Zymoclean Gel DNA Recovery Kit following manufacturer's protocol. The samples were sequenced by Macrogen Europe (Amsterdam). Sequence proofing was completed with the Staden Package v.2.0.0: PreGAP v.4 and GAP v.4 software (Bonfield et al. 1995). Sequences are deposited in GenBank under the accession numbers MW549067 and MW549068 (COI); MW553725 (Wg); MW556696 and MW556697 (28S); MW556698 and MW556699 (18S); and MW583040 (Ef-1α).

Table 1. PCR primers.

Marker	Primer name	Direction	Primer sequence 5' to 3'	Reference
COI	LCO1490	Forward	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
	HCO2198	Reverse	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. (1994)
	COI_pF2	Forward	ACCWGTAATRATAGGDGGDTTTGGDAA	Kaartinen et al. (2010)
	COI_2437d	Reverse	GCTARTCATCTAAAWAYTTTAATWCCWG	Kaartinen et al. (2010)
18S rDNA	18Sb-441	Forward	AAATTACCCACTCCCGGCA	Heraty et al. (2011)
	18Sc-204-R	Reverse	GTTTCAGCTTTGCAACCAT	Viciriuc and Fusu (unpublished). Reverse complement of 18S a2.0 in Schulmeister (2003).
28S rDNA	D23F	Forward	GAGAGTTCAAGAGTACGTG	Park and O'Foighil (2000)
	28Sb	Reverse	TCGGAAGGAACCAGCTACTA	Whiting et al. (1997)
EF-1α	For3	Forward	GGNGACAAYGTTGGYTTCAACG	Danforth et al. (1999)
	Cho10	Reverse	ACRGCVACKGTYTGHCKCATGTC	Danforth et al. (1999)
Wingless	LepWg1	Forward	GARTGYAARTGYCAYGGYATGTCTGG	Brower and DeSalle (1998)
	LepWg2	Reverse	ACTNCGCRCACCARTGGAATGTRCA	Brower and DeSalle (1998)

Table 2. PCR conditions.

Amplified sequence	Thermocycler conditions
COI (LCO1490/HCO2198)	2' at 94 °C / 30" at 94 °C / 1' at 42 °C / 45" at 72 °C / 5' at 72 °C
COI (COI_PF2/COI_2437d)	2' at 94 °C / 30" at 94 °C / 1' at 45 °C / 45" at 72 °C / 5' at 72 °C
18S rDNA	2' at 94 °C / 30" at 94 °C / 1' at 55 °C / 45" at 72 °C / 5' at 72 °C
28S rDNA	2' at 94 °C / 30" at 94 °C / 1' at 55 °C / 1' at 72 °C / 3' at 72 °C
EF-1α	5' at 94 °C / 30" at 94 °C / 1' at 53 °C / 1' at 72 °C / 5' at 72 °C
Wingless	5' at 94 °C / 30" at 94 °C / 1'30" at 52,5 °C / 1' at 72 °C / 5' at 72 °C

Sequences were aligned in Mega-X v.10.0.5 (Kumar et al. 2018) with the data set for the molecular phylogeny of Telenominae obtained by Taekul et al. (2014) and with the data set for the molecular phylogeny of *Trissolcus* (Talamas et al. 2019) available from GenBank; for some GenBank sequences, untrimmed primer sequences were removed prior to the phylogenetic analysis. The EF-1α sequences were aligned with the MAFFT v.7 online service with the E-INS-i strategy (Kuraku et al. 2013; Katoh et al. 2019). Preliminary single gene analyses were performed to detect potential alignment errors (data not shown). Following this step, two sequences belonging to specimens of the *floridanus* group of *Telenomus* (OSUC 266768, OSUC 266774) were excluded from the EF-1α alignment because they were recovered within the outgroup. One sequence of *Telenomus podisi* Ashmead (OSUC 173850) was eliminated from the COI alignment because of the unusually long branch compared to the other *Te. podisi* sequences. Mesquite v.3.6 was used to create concatenated character matrices and generate .phy and .cfg files to be used in PartitionFinder2 (Guindon et al. 2010; Lanfear et al. 2012; Lanfear et al. 2017). We first delimited data blocks in the dataset by gene, and for protein-coding genes, by codon position. The intron sequences in EF-1α were treated as a separate data block. Afterwards the best partitioning scheme and models (Table 3) were selected with linked branch lengths and the greedy algorithm in PartitionFinder2. The alignments are available as Suppl. materials 5, 6.

We performed four analyses on the data set of Taekul et al. (2014): two Maximum Likelihood (ML) and two Bayesian Inference (BI) analyses. The ML analyses were

Table 3. Substitution models.

Latonius planus sequences included in the dataset provided by Taekul et al. (2014)			*Latonius planus* sequences included in the dataset provided by Talamas et al. (2019)		
Subset	**Best Model**	**Partition**	**Subset**	**Best Model**	**Partition**
1	TRNEF+I+G	18S	1	TRN+G	COI, 3rd position
2	SYM+I+G	28S	2	GTR+G	COI, 1st position
3	K81UF+G	COI, 3rd position	3	TVM+I+G	COI, 2nd position
4	GTR+I+G	COI, 1st position	4	TRNEF+I	Wingless, 1st and 2nd positions; 18S
5	TVM+I+G	COI, 2nd position	5	TVM+G	Wingless, 3rd position
6	TRN+I	Ef-1α exon, 1st position	6	TVMEF+I+G	ITS2
7	JC+G	Ef-1α exon, 2nd position	7	K80+G	28S
8	TRN+G	Ef-1α exon, 3rd position			
9	HKY+I+G	Ef-1α intron			

run using RAxML-HPC2 v.8.2.12 (Stamatakis 2014), using both the non-partitioned and the partitioned datasets, with 20 alternative runs. Support for the nodes of the best scoring tree was estimated with 1000 bootstrap iterations (Felsenstein 1985). Besides Felsenstein's bootstrap support, transfer bootstrap expectation values (TBE) were also calculated as this statistic gives higher support values for branches supported by moderate phylogenetic signal, but is not afflicted by falsely supported branches; a value above 70% is considered a good indication of support (Lemoine et al. 2018). TBE were obtained with the BOOSTER web application (https://booster.pasteur.fr/). Bayesian inference analyses were run using MrBayes v.3.2.7a, (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) using the non-partitioned and the partitioned datasets. We ran two parallel analyses with four chains each for a total of 2×10^7 generations, sampling every 100 generations. Convergence was assessed by examining trace files in Tracer v.1.7.1 (Rambaut et al. 2018) to assess convergence. The first 25% of the sampled trees were discarded as burn-in. All ML and BI analyses were performed on the online portal CIPRES Science Gateway v.3.3 (http://www.phylo.org; Miller et al. 2010). For both RAxML and MrBayes analyses on the non-partitioned data, the COI alignment was degenerated using the DEGENcoding platform http://www.phylotools.com (Regier et al. 2010; Zwick et al. 2012; Zwick 2013), similar to Taekul et al. (2014). All phylogenetic trees were edited in FigTree v.1.4.4. The final visual aspect of the trees was refined with Adobe Illustrator.

Results

Position of *Latonius* in the molecular phylogenies of Taekul et al. 2014 and Talamas et al. 2019

COI, 18S rDNA, and 28S rDNA sequences were successfully obtained for both specimens of *Latonius* (LatFr0605, LatFr0606), while the EF-1α and Wingless sequences were obtained for one specimen only (EF-1α for LatFr0605 and Wingless for LatFr0606). We obtained 871 bp for COI, 678 bp for 18S rDNA, 761 bp for 28S rDNA, 390 bp in two non-overlapping fragments for EF-1α and 357 bp for Wingless.

Our analyses of *L. planus* with the data set of Taekul et al. (2014) resulted in very similar topologies between the ML and BI trees. However, the results were very different between the partitioned and non-partitioned datasets. Both ML and BI analyses on the non-partitioned dataset with degenerated COI alignment produced a phylogenetic reconstruction similar to the one presented by Taekul et al. (2014) (Figure 1, Suppl. material 1) in which *Trissolcus* and *Telenomus* are monophyletic clades with PP of 70% and 91% respectively (BP of 47% and 61%, TBE of 88% and 98%, respectively). However, *Tr. thyantae* Ashmead is placed outside the "core clade", sister to a clade formed by *Trissolcus*, *Telenomus*, and *Baeoneurella*. *Latonius* is sister to a clade containing *Tr. basalis* (Wollaston), *Tr. hullensis* (Harrington), and *Tr. latisulcus* (Crawford) (92% PP, 40% BP, 82% TBE). The *Telenomus* species in the *crassiclava* group were not recovered in the same clade with the other *Telenomus* species, as in the original analysis, since they are actually *Phanuromyia* (Taekul et al. 2014).

Both ML and BI analyses on the partitioned dataset share very similar topologies (Suppl. materials 2, 3). In both trees *Trissolcus* includes *Latonius* and is paraphyletic relative to *Telenomus* + *Baeoneurella* with high support (100% PP, 99% BP, 100% TBE). However, it is branching more basally in the ML tree compared to the BI tree, with *Latonius* splitting just after *Tr. thyantae* and a clade formed by two species from the *thyantae* group.

Considering that *Latonius* was consistently retrieved inside *Trissolcus*, we performed additional partitioned phylogenetic analyses using the molecular dataset of *Trissolcus* (Talamas et al. 2019). In the ML and BI analysis (Figure 2, Suppl. material 4), *Latonius* is sister to *Tr. mitsukurii* (Ashmead) (86% PP, 69% BP, 100% TBE) and both are sister to *Telenomus* (76% PP, 34% BP, 100% TBE).

Redescription of the type species of *Latonius*: *Latonius planus* Kononova, 1982, with notes concerning its variability

***Latonius planus* Kononova, 1982**

Diagnosis. Antennal clava not distinctly wider than preceding flagellomeres; pretarsus enlarged with well-developed arolium; genal striae absent; maxillary palpus 1-segmented; subacropleural and prespecular sulci absent; mesoscutellar sculpture absent; metascutellum enlarged and smooth; body obviously dorsoventrally flattened.

Description. Female body length: 0.85–1.03 mm (n = 3). Body color: dark brown to black (Figures 10, 11).

Head. Color of radicle: brown. Length of radicle: less than width of clypeus. Color of A1–A6 in female: light brown to brown. Color of A7–A11 in female: brown. Clava: undifferentiated from preceding antennomeres. Ratio between width of 1st clavomere (A8) and A7: 1–1.1. Number of papillary sensilla on A7: 0. Claval formula: 1-1-1-1 (A8–A11) (Figure 5). Facial striae: absent. Number of clypeal setae: 6 (Figure 7). Number of mandibular teeth: 3. Size of mandibular teeth: the median tooth smallest, hardly visible (Figure 7). Microsculpture on gena directly above mandibular condyle: reticulate coriaceous. Shape of gena in lateral view: approximately the same width from vicinity

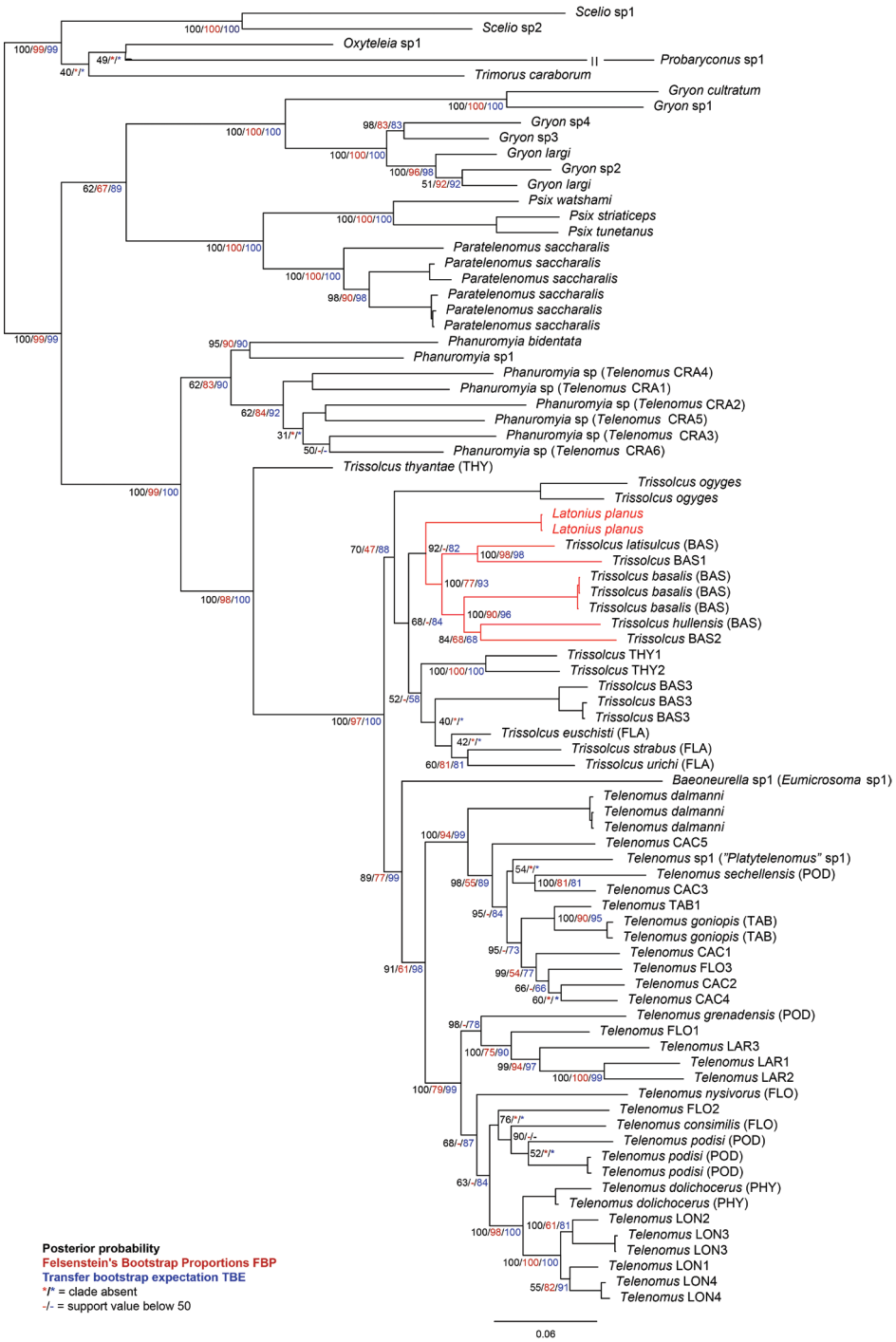


Figure 1. Phylogenetic reconstruction of the non-partitioned data set of Taekul et al. (2014) with a degenerated COI alignment, Bayesian analysis. Felsenstein's bootstrap support and transfer bootstrap expectation from the ML analysis were plotted besides the posterior probability.

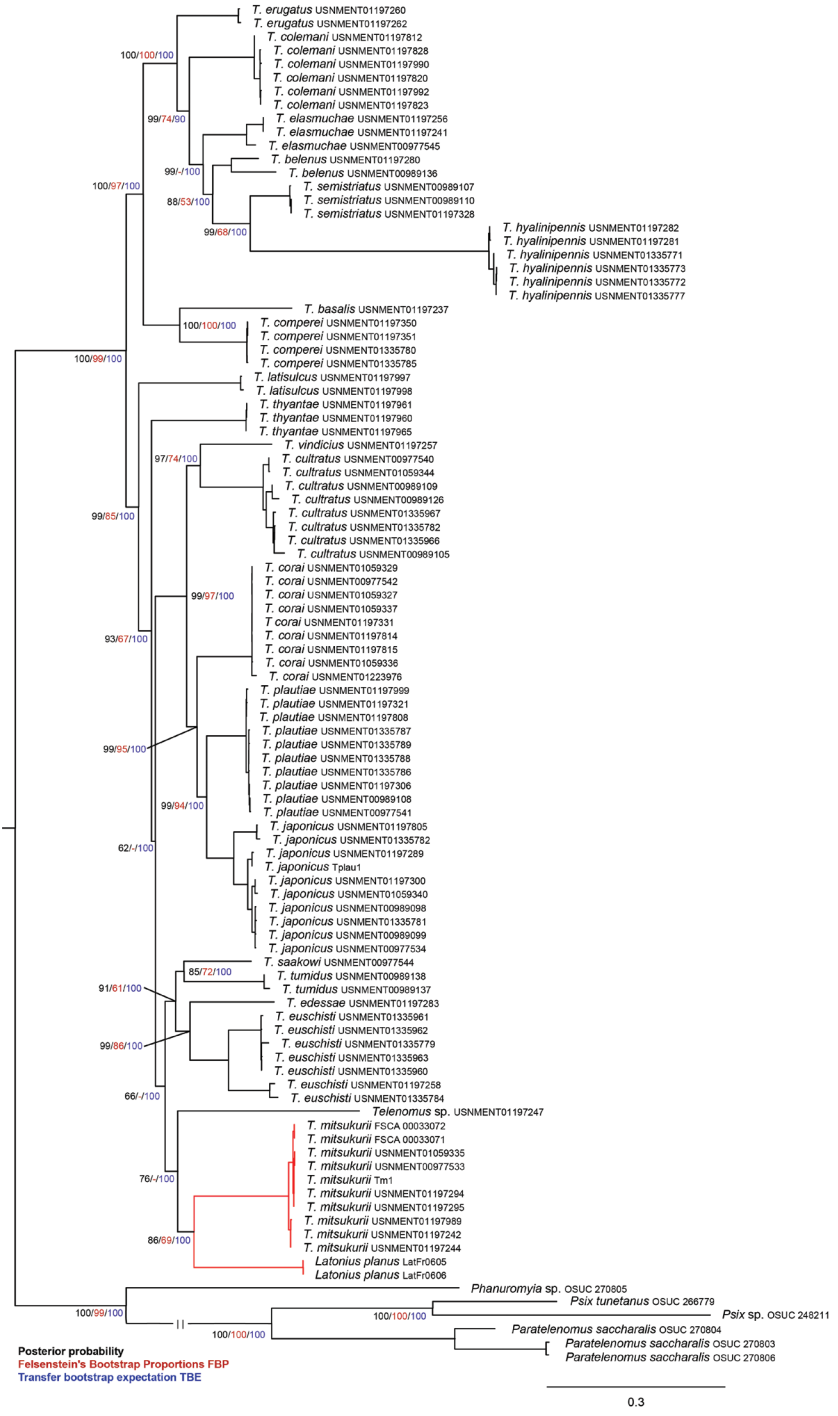
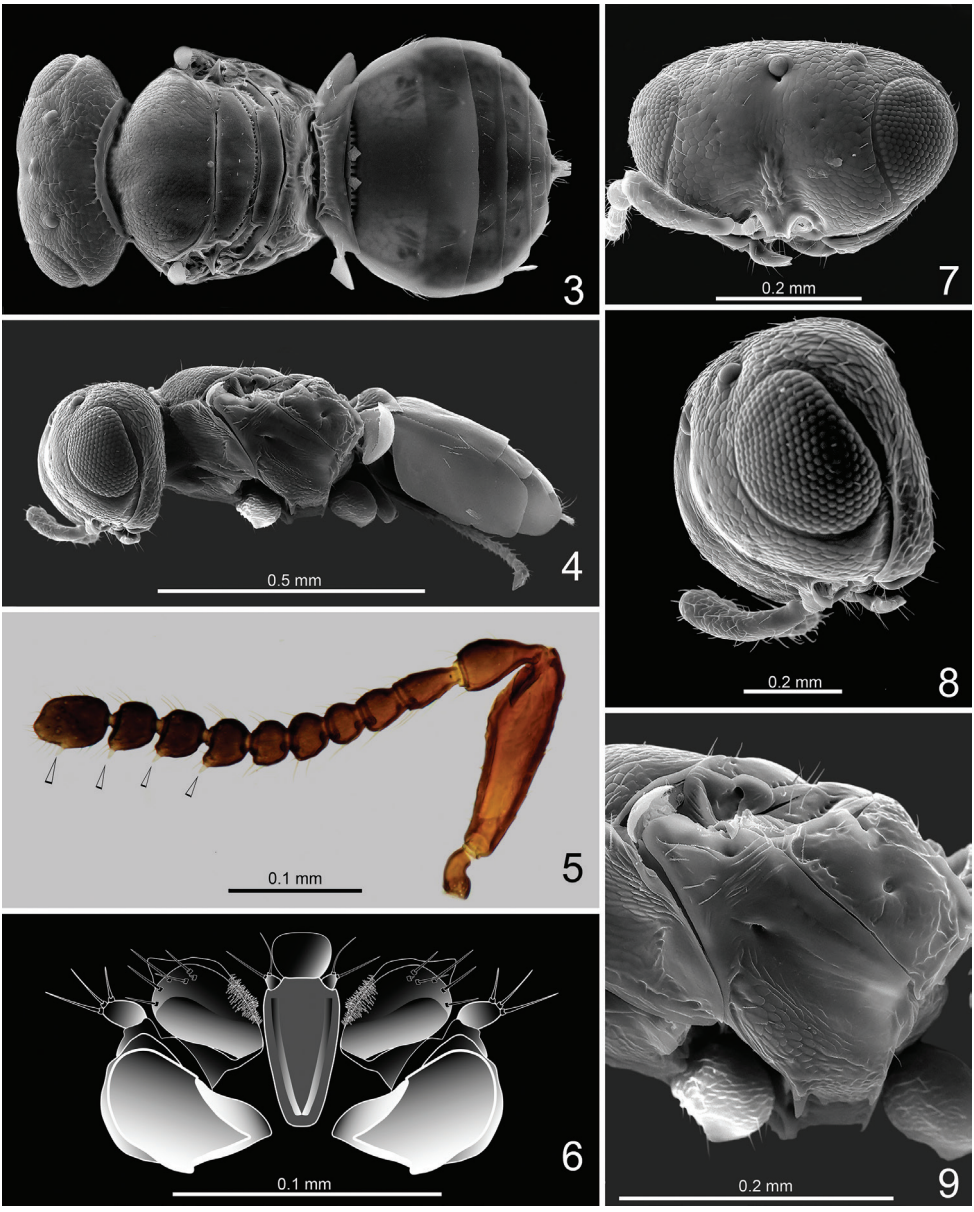


Figure 2. Phylogenetic reconstruction of the molecular data set of Talamas et al. (2019), ML analysis. Posterior probabilities from the BI analysis were plotted besides Felsenstein's bootstrap support and transfer bootstrap expectation.



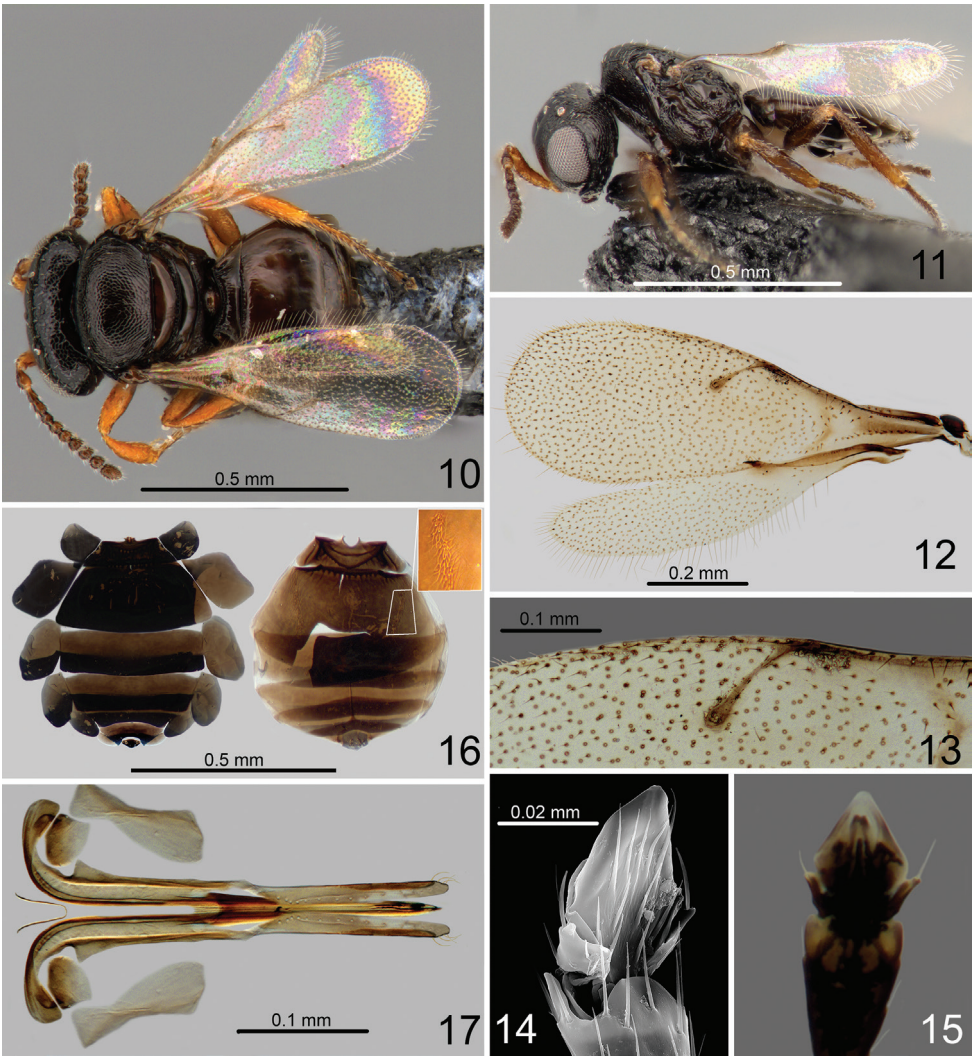
Figures 3–9. *Trissolcus planus* (female) **3** habitus, dorsal view (SEM) **4** habitus, lateral view (SEM) **5** female antenna **6** maxillolabial complex (composite drawing) **7** head, frontal view (SEM) **8** head, lateral view (SEM) **9** mesosoma, lateral view (SEM).

of lower eye margin to above mandibular condyle. Genal carina: present and extending dorsally to vicinity of lower eye margin. Malar striae: absent. Sculpture of malar sulcus: faintly present. Orbital furrow: uniform in width between midpoint of eye and malar sulcus (Figure 8). Macrosculpture of frons between antennal scrobe and anterior ocel-

lus: absent or faintly coriaceous. Preocellar pit: present, located within ocellar fovea. Setation of lateral frons: two rows of few (4–5) setae along the inner orbit and another few setae (4–6) on the dorsal half of lateral frons. Punctation of lateral frons: absent. Sculpture directly ventral to preocellar pit: present. Macrosculpture of lateral frons: well-defined coriaceous near antennal scrobe to imbricate coriaceous near the inner orbit (Figure 7). OOL: more than two times ocellar diameter. Hyperoccipital carina: absent. Anterior margin of occipital carina: crenulate (Figure 3).

Maxillolabial complex (Figure 6). Sculpture of posterior stipital sclerite: absent. Campaniform sensillum on 1st maxillary palpomere: absent. Trichoid sensilla on 1st maxillary palpomere: present apically. Number of maxillary palpomeres: 1. Lacinia: concealed. Mesal side of basal galeal sclerite: straight. Setae on apical edge of basal galeal sclerite: present. Lateral galeal crease: absent. Interstipital sclerite: absent. Lateral faces of prementum: not continuous posteriorly. Premental carinae: strip-like. Number of labial palpomeres: 1.

Mesosoma. Mesosoma: visibly depressed (two times as wide as high). Mesoscutum, mesoscutellum and metascutellum: in the same plane. Epomial carina: present. Macrosculpture of lateral pronotum directly anterior to netrion: coriaceous. Netrion sulcus: complete. Pronotal suprahumeral sulcus: hardly visible, faintly crenulated or undifferentiated from sculpture of dorsal pronotum (Figure 4). Number of episternal foveae: 3. Acropleural sulcus: present, developed. Subalar pit: present. Subacropleural sulcus: absent. Speculum: transversely strigose. Mesopleural pit: present, circular, not prolonged into a furrow. Mesopleural carina: absent. Sculpture of femoral depression: smooth. Patch of striae at posteroventral end of femoral depression: absent. Setal patch at posteroventral end of femoral depression: absent. Microsculpture of anteroventral mesopleuron: absent. Macrosculpture of anteroventral mesopleuron: imbricate coriaceous. Postacetabular sulcus: present as a furrow with no cells or crenulae. Setation of posteroventral metapleuron: absent. Sculpture of dorsal metapleural area: absent. Mesepimeral sulcus: present, weakly indicated, smooth. Posterodorsal metapleural sulcus: hardly visible, as a smooth line of foveae. Paracoxal sulcus in ventral half of metapleuron: absent. Anteroventral extension of metapleuron: not extending to base of mesocoxa. Metapleural epicoxal sulcus: present as coarse rugae (Figures 9, 11). Mesoscutal humeral sulcus: indicated by a narrow furrow. Median mesoscutal line: absent. Macrosculpture of mesoscutum: coriaceous. Mesoscutal suprahumeral sulcus: not visible. Parapsidal line: absent. Notaulus: absent. Median protuberance on anterior margin of mesoscutellum: absent. Shape of dorsal margin of anterior lobe of axillar crescent: rounded. Sculpture of anterior lobe of axillar crescent: oblique strigose. Posterodorsal margin of axillular carina: rounded. Macrosculpture of mesoscutellum: absent. Mesoscutellum: 3.4× as wide as long. Length of mesoscutellum / length of metascutellum: mesoscutellum 1.9× as long as metascutellum. Microsculpture on mesoscutellum: absent. Setation of posterior mesoscutellar sulcus: present. Form of metascutellum: transverse plate, 4.8× as wide as long. Metanotal trough: foveate, with a row of small foveae intercalated between two smooth areas. Metapostnotum: invaginated near lateral edge of metascutellum (Figures 3, 10). Length of postmarginal vein:



Figures 10–17. *Trissolcus planus* (female) **10** habitus, dorsal view **11** habitus, lateral view **12** fore and hind wings **13** fore wings venation **14, 15** arolium **16** metasoma with exposed tergites, sternites and latero-tergites (composite image) **17** ovipositor assembly (composite image).

around twice as long as stigmal vein. Basal vein: indicated as pigmented nebulous vein (Figures 12, 13). Color of legs: coxae dark brown to black, femora light to dark brown, and brown elsewhere (Figures 10, 11). Pretarsus: modified with atrophied claws, each bearing a long seta and hypertrophied arolium. Shape of arolium: rhomboidal (Figures 14, 15). Protarsus: 5th tarsomere as long as 4th and 3rd tarsomeres together, 1.6× as wide as 4th tarsomere and as wide as pretarsus.

Metasoma (Figure 16). Number of tergites: 7. Number of sternites: 6. Laterotergites: wide. Laterosternites: absent. Longitudinal striae on T1 posterior to basal costae:

present on anterior 2/3. Number of sublateral setae (on one side): 2. Setation of laterotergite 1: one seta. Longitudinal striation of T2: faintly present anteriorly. Setation of T2: present (4 setae). Setation of laterotergite 2: present. Posteriorly directed setae on medial S1: absent (Figures 3, 10).

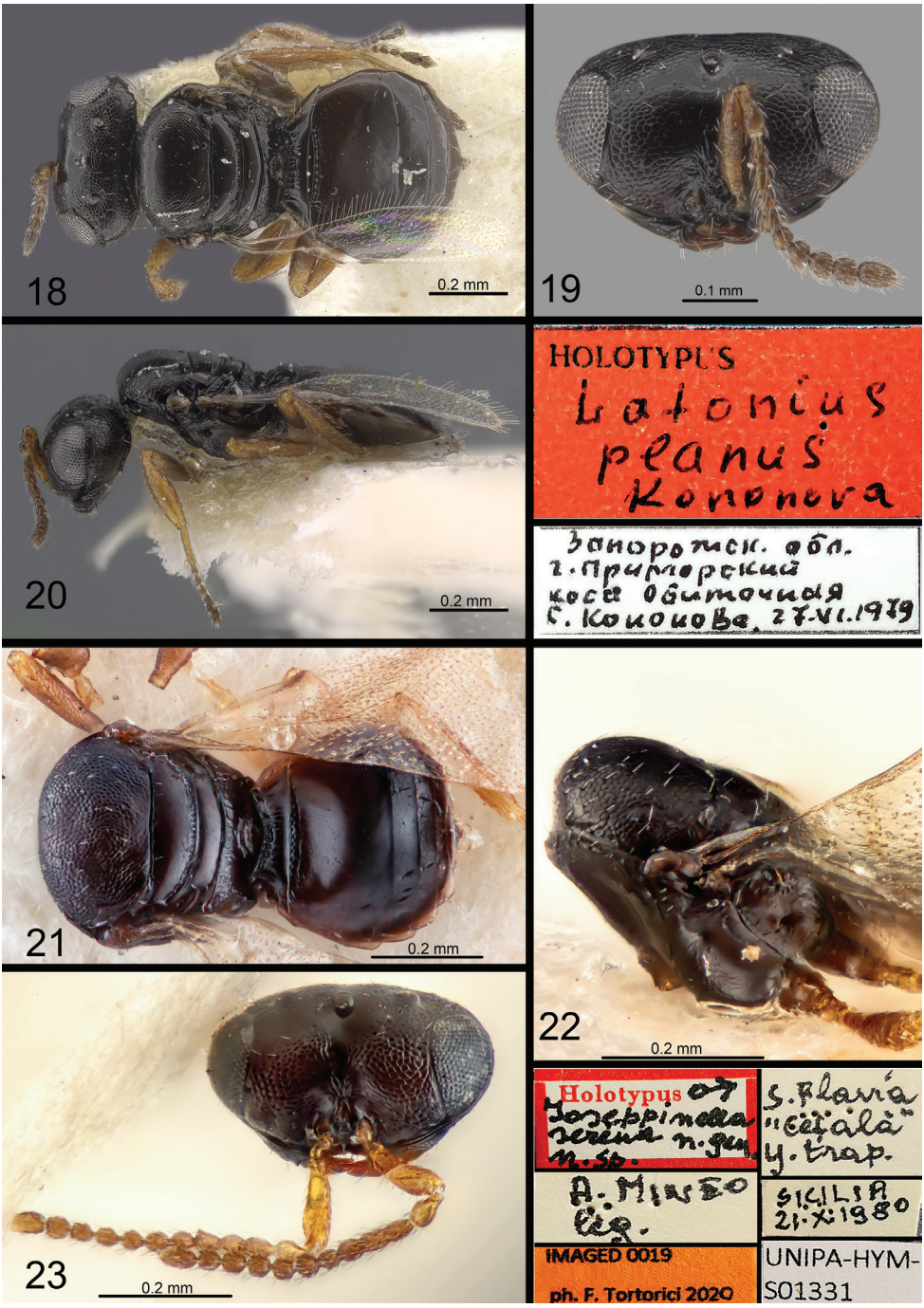
Ovipositor (Figure 17). Ovipositor system: *Ceratobaeus*-type. Proximal part of ventral membranous plate: present. Proximal arm: large, long and wide, 0.6× as long as third valvula. First valvifer: large, longest diameter 1.2× as long as width of proximal arm at the proximal end. Second valvula: simple. Third valvula: elongated, broad and heavily sclerotized distally, 0.4× as long as length of ovipositor. Lateral apodemes: present. Medial apodeme on S6: present.

Material examined. ***Holotype*** of *Latonius planus*: Ukraine: 1♀, "Запорожск. обл., г. Приморский, коса Обиточная, С. Кононова [Zaporizhzhia Oblast, Primors'kyi city, Obitochnaya bank, S. Kononova leg.], 27.VI.1979". ***Holotype*** of *Ioseppinella serena*: Italy: 1♂, "Sicilia, 21.X.1980, Santa Flavia, Cefala, y. trap [yellow trap in a citrus lemon orchard], A. Mineo leg.", UNIPA-HYM-S01331. ***Non type material*:** France: 5♀; Gard dep., Liouc; 43.89007N, 3.97897E; 135 m alt.; 5.IX.2018; glades in *Quercus* forest; screen sweeping; Fusu L. & Mitroiu M. leg.; Spain: 1♀ (specimen examined by L. Masner, but label data not available, CNC being closed due to the COVID pandemic).

Variability. Although most specimens of *Latonius* used in this study are from the same locality and likely belong to the same population, we found some morphological variation that does not appear to be size related: the genal carina is always present, but it can be well developed or faintly defined. The macrosculpture of the frons between the antennal scrobe and anterior ocellus can be well-defined or smooth, almost absent. The hyperoccipital carina is almost certainly absent, but in a specimen with the most evident sculpture, it can be imagined as an outline. The antero-admedian lines can be observed in two specimens but are absent in the other three. The femoral depression may be smooth or faintly striate. The postacetabular sulcus is present as a few superficial cells in only one specimen. The macrosculpture on the mesoscutum was observed to be coriaceous laterally but smooth centrally (internotaular area) and adjacent to the transscutal articulation in one specimen.

Comparison of the holotype with the original description

In the original description of *L. planus*, Kononova (1982) mentioned that the ocelli are nearly colinear. However, it can be seen on the holotype that this is not the case (Figure 18). Also, the striation on T2 is visibly reduced and was misinterpreted as absent (Figure 18). Some rather peculiar and interesting features are also specified, as well as illustrated: the seemingly undifferentiated female antennal clava (Figure 19), lack of any kind of sculpture on mesoscutellum and metascutellum, the rhomboidal shape of arolium (Figure 18), and the postmarginal vein being twice as long as the stigmal vein. The author also referred to the flattened body (Figure 20) and expanded arolium as discriminatory characters for the genus *Latonius*.



Figures 18–23. Holotype of *Latonius planus* (female) **18** habitus, dorsal view **19** head, frontal view **20** habitus, lateral; holotype of *Ioseppinella serena* (male) **21** mesosoma and metasoma, dorsal view **22** mesosoma, lateral view **23** head, frontal view.

Discussion

Telenominae is comprised of two "core genera": *Telenomus* and *Trissolcus*. Apart from these two speciose genera, there are several small genera, some of them monotypic (e.g. *Ioseppinella*, *Latonius*, *Paratrissolcus*, *Rachelia*), considered to be satellite taxa that may be derived from the two core genera. Johnson (1988) did not consider *Telenomus* or *Trissolcus* to be monophyletic, regarding *Trissolcus* as paraphyletic and *Telenomus* as polyphyletic. The phylogenetic study of Taekul et al. (2014) supports the assessment of Johnson (1988) concerning the monophyly of *Telenomus* and *Trissolcus*.

To resolve the paraphyly of *Trissolcus* retrieved by our partitioned analyses it would have to be divided into multiple genera. Considering the relative morphological homogeneity of the genus, and the difficulty of resolving relationships within the subfamily, we do not consider this to be prudent with our current understanding. To properly resolve the paraphyly of *Trissolcus*, one would have to increase and diversify the taxon sampling, as well as broaden the range of informative input provided by the molecular data. On the other hand, if we accept a monophyletic *Trissolcus* (excluding *Tr. thyantae*), as indicated by the non-partitioned analyses, with *Latonius* being placed well within the clade, we would have to rely on rather feeble bootstrap support and accept the morphological differences between *L. planus* and *Trissolcus* to be secondarily derived.

Morphologically, *Latonius* is an unusual scelionid in displaying a mixture of characters encountered in other genera of Telenominae. This is a typical situation for many monotypic genera erected with little regard for natural classification and without a phylogenetic assessment (Talamas and Buffington 2015). While trying to establish the relationships of *Latonius* with respect to the rest of Telenominae, we examined the holotypes of Mineo's monotypic telenomine genera. During this examination we observed that the male holotype of *Ioseppinella* is morphologically very close to *Latonius*. In a detailed inspection of the type species *I. serena* (Figures 21–23), we were not able to find any reliable characters that would separate it from the female holotype of *L. planus* except for the dimorphic antenna (Figure 23) and the extremely reduced striation on T1 (Figure 21). Therefore, we consider *I. serena* Mineo, O'Connor & Ashe, 2010, to be a junior synonym of *L. planus* Kononova, 1982 (syn. n.).

The presence of wide pretarsi with a well-developed arolium and a non-clubbed female antenna is a character that *Latonius* shares with *Protelenomus*. Veenakumari et al. (2019) did not mention the antenna without club as an apomorphy for *Protelenomus*. Nonetheless, images of the female antenna in *Protelenomus* provided by Veenakumari et al. (2019) revealed that there are species of this genus with clubbed antenna in females, but the club is not clearly differentiated by the size of the clavomeres (i.e., it is not abrupt). The female antenna in *Latonius* has 4 clavomeres, each with one papillary sensillum (antennal sensillar formula 1:1:1:1). In *Protelenomus*, Veenakumari et al. (2019) identified four or five clavomeres, depending on species, but they did not report the antennal sensillar formula in all examined species. Studying their photos, we observed that in *Protelenomus* species with four clavomeres, the antennal sensillar formula is 2:2:2:1 and in antennae with five clavomeres, the antennal sensillar formula is

2:2:2:2:1 or 1:1:1:1:1. Another observation was the correlation between the presence of two papillary sensilla per clavomere and the presence of the club: two papillary sensilla per clavomere were observed only in taxa with clubbed antennae. Hence, the antennal sensillar formula is a unique apomorphy for *Latonius* within Telenominae. This character (antennal sensillar formula) is highly variable within some Telenominae genera, e.g., *Telenomus*, *Trissolcus*, and *Protelenomus* (Bin 1981; Veenakumari et al. 2019).

The flattened body of *Latonius* is a feature found in many Telenominae and is likely a consequence of either a phoretic lifestyle, an adaptation for a peculiar shape of the host's eggs, or for the concealed microhabitats within which the eggs are laid. In this character, *Latonius* is convergent with species of *Baeoneurella*, with numerous species of *Telenomus* (from the *californicus* and *floridanus* groups), and even with some species of *Trissolcus* such as *Tr. sipius* (Nixon) and *Tr. sipioides* Johnson. A character shared by *Latonius* and flattened species of *Trissolcus* is the size and shape of the metascutellum – which seems to be a consequence of the flattening of the body. The clubbed antenna and the presence of the subacropleural and prespecular sulci appear not to be correlated with the shape of the body because these can be observed in *Tr. sipius* and *Tr. sipioides* despite their flattened body shape. The fact that the flattening of the body occurs in Platygastroidea multiple times in several rather distantly related genera was discussed by Popovici et al. (2019).

The 1:1 palpal formula in *Latonius* is not a common trait in Telenominae. Popovici et al. (2017) found this palpal formula in *Phanuropsis* and in one species of *Trissolcus* (most probably an aberrant specimen, because in *Trissolcus* the characteristic palpal formula is 2:1).

The shape of metasomal T2, in which the sclerite is wider than long, also suggests that *Latonius* is related to *Trissolcus*. However, the absence of the subacropleural sulcus and of the prespecular sulcus in *Latonius* separates these two genera. The ovipositor in *Latonius* is robust, very similar to the ovipositor in *Trissolcus* as described by Austin and Field (1997) but differs in the presence of the proximal part of the ventral membranous plate.

Analyzing the characters that distinguish *Latonius* from *Trissolcus*, it is easy to observe that these represent only simplifications (or reductions), or possibly some adaptive characters for a phoretic lifestyle (e.g. well-developed arolium). Many character states represented through reduction are usually characteristic of *Telenomus*, but occasionally can be observed in individual *Trissolcus* species. The loss of the subacropleural and prespecular sulci, typical of *Telenomus*, can also be noted in *Tr. exerrandus* Kozlov & Lê; the loss of sculpture of the mesoscutellum is observed in the large majority of species of *Telenomus* (except some species of, for example, the *floridanus* group), but this character state is also present in more than a few species of *Trissolcus* – e.g. *Tr. kozlovi* Rjachovskij, *Tr. occiduus* Johnson, *Tr. perepelovi* (Kozlov), *Tr. plautiae* (Watanabe), *Tr. semistriatus* (Nees von Esenbeck), *Tr. trophonius* (Nixon), *Tr. tumidus* (Mayr), *Tr. thyantae* Ashmead, *Tr. valkyria* Johnson & Talamas, *Tr. viktorovi* Kozlov, or it is very variable: from present to absent in *Tr. levicaudus* Talamas, *Tr. japonicus* (Ashmead), *Tr. flavipes* (Thomson), *Tr. oobius* (Kozlov) or in *Tr. scutellaris* (Thomson). Other examples of likely convergent reductive characters include reduction of the number of maxillary palpomeres in *Trissolcus* (Popovici et al. 2017) and reduction of the number of clavomeres. Most species of

Telenomus have four clavomeres (few exceptions with five, six, or even seven), whereas most species of *Trissolcus* have five clavomeres. However, there are a few species of *Trissolcus* with four clavomeres (e.g. *Tr. oobius* and *Tr. hyalinipennis* Rajmohana & Narendran).

These observations, correlated with molecular data, support the idea that *Latonius planus* is, in fact, an unusual, derived species of *Trissolcus*. We strongly suspect that the same is true concerning another phoretic group, the genus *Protelenomus*.

The requirement of monophyly is the only objective criterion that must be met by any taxon to be formally recognized, and for this reason we consider *Latonius* (including *Ioseppinella*) to be a junior synonym of *Trissolcus* (syn. nov.). Consequently, we here transfer the species *L. planus* to *Trissolcus* as *Trissolcus planus* (Kononova, 1982) comb. nov.

The newly proposed taxonomic arrangement will be:

***Trissolcus* Ashmead, 1893**

Trissolcus Ashmead, 1893: 138, 161. Type species: *Telenomus brochymenae* Ashmead by original designation.
Latonius Kononova, 1982: 76. Type species *Latonius planus* Kononova, 1982 by monotypy and original designation. syn. nov.
Ioseppinella Mineo, O'Connor & Ashe, 2010: 267. Type species *Ioseppinella serena* Mineo, O'Connor & Ashe, 2010 by monotypy and original designation. syn. nov.

Trissolcus planus (Kononova, 1982) comb. nov.

Latonius planus Kononova, 1982: 76. Holotype female.
Ioseppinella serena Mineo, O'Connor & Ashe, 2010: 267. Holotype male. syn. nov.

Following the incorporation of *Latonius* and *Ioseppinella* in *Trissolcus*, the diagnosis of the latter has to be extended with some new character states, as follows: body obviously dorsoventrally flattened; female antenna non-clubbed, with 4 clavomeres (antennomeres A8 to A11 with one papillary sensillum each); palpal formula 1:1; pretarsus with well-developed arolium.

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Supplementary material 1

Phylogenetic reconstruction on the non-partitioned data set of Taekul et al. (2014) with a degenerated COI alignment, ML analysis

Authors: Cristina Vasiliță, Ovidiu Alin Popovici, Elijah Talamas, Norman Johnson, Lubomir Masner, Francesco Tortorici, Lucian Fusu

Data type: phylogenetic

Link: https://doi.org/10.3897/jhr.87.63533.suppl1

Supplementary material 2

Phylogenetic reconstruction on the partitioned data set of Taekul et al. (2014), ML analysis

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Data type: phylogenetic

Link: https://doi.org/10.3897/jhr.87.63533.suppl2

Supplementary material 3

Phylogenetic reconstruction on the partitioned data set of Taekul et al. (2014), Bayesian analysis. Posterior probability indicated at nodes

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Data type: phylogenetic

Link: https://doi.org/10.3897/jhr.87.63533.suppl3

Supplementary material 4

Phylogenetic reconstruction on the molecular data set of Talamas et al. (2019), Bayesian analysis

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Data type: phylogenetic

Link: https://doi.org/10.3897/jhr.87.63533.suppl4

Supplementary material 5

Nexus alignment of the dataset from Taekul et al. (2014) including *Trissolcus planus*

Authors: Cristina Vasiliţa, Ovidiu Alin Popovici, Elijah Talamas, Norman Johnson, Lubomir Masner, Francesco Tortorici, Lucian Fusu

Data type: Nexus file

Link: https://doi.org/10.3897/jhr.87.63533.suppl5

Supplementary material 6

Nexus alignment of the dataset from Talamas et al. (2019) including *Trissolcus planus*

Authors: Cristina Vasiliţa, Ovidiu Alin Popovici, Elijah Talamas, Norman Johnson, Lubomir Masner, Francesco Tortorici, Lucian Fusu

Data type: Nexus file

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