



# The larva of the genus *Tolmerinus* Bernhauer described: does it help to reveal a sister-group for the rove beetle subtribe Anisolinina (Coleoptera: Staphylinidae: Staphylininae)?

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## Abstract

We provide a taxonomic description of the larva of the rove beetle *Tolmerinus fratumellitorum* Rougemont, 2017, identified through DNA barcoding. This is the first larval description for Anisolinina, the only subtribe whose sister group within the tribe Staphylinini remains unclear. While most phylogenetic hypotheses, especially molecular-based, suggest sister group relationships between Anisolinina and Staphylinina, conflicts remain, particularly when adult morphology is used for phylogeny reconstruction. Our attempt to use larval morphology for phylogeny reconstruction neither revealed a sister group for Anisolinina, nor unique synapomorphies for this subtribe. However, by mapping larval characters on the reference tree of Staphylinini, i.e., a phylogeny firmly established by phylogenomics in agreement with the adult morphology, we found unique larval synapomorphies to support the tribe Staphylinini and informal clade Staphylinini propria. We review all phylogenetic hypotheses ever proposed for a sister group of Anisolinina and discuss potential reasons for the poor phylogenetic signal in the larval characters alone. We stress some opportunities and challenges of using larval characters in phylogeny reconstructions.

## Key words

Barcoding, immature stages, morphology, phylogeny, Staphylinini, systematics

## 1. Introduction

The tribe Staphylinini is one of the biggest evolutionary radiations among rove beetles and even all insects. Recently, this group enjoyed extensive phylogenetic studies (Chatzimanolis 2014; Brunke et al. 2016; Chani-Posse

et al. 2018; Brunke and Smetana 2019; Cai et al. 2019, Chatzimanolis and Brunke 2019; Żyła and Solodovnikov 2019; Brunke and Chatzimanolis 2024; Reyes-Hernández et al. 2025) which, among many new insights, revealed

that one group of Staphylinini, the subtribe Anisolinina remains poorly understood. As of now, Anisolinina includes 15 genera and 227 extant species distributed worldwide. While its highest diversity is found in the Afrotropical and Oriental Regions, the subtribe is absent in the West-Palaeartic Region as well as in Australia and New Zealand (Newton 2022).

Originally, Anisolinina was established by Hayashi (1993) for four genera (*Amichrotus* Sharp, 1889, *Anisolinus* Sharp, 1889, *Hesperosoma* Scheerpeltz, 1965, and *Tympanophorus* Nordmann, 1837) after observing that the pronotum in these genera had an inferior marginal line not merging with the superior line at the prosternum, which was a condition different from that in *Philonthus* Stephens, 1829 (Philonthina), *Creophilus* Leach, 1819 and *Liusus* Sharp, 1889 (both Staphylinina), and *Xanthopygus* Kraatz, 1857 (Xanthopygina). Afterward, diagnosis of Anisolinina was re-defined several times, and characters including the club-shaped dilated second segment of the maxillary palpi with the asymmetrical insertion of segment 3, the ventral basal ridge of head extended anteriorly parallel to gular sutures (Smetana and Davies 2000), or the posterior half of mesoventrite with acute ridge not connecting with coxal cavities (Smetana and Davies 2000; Schillhammer 2004) were mentioned as diagnostic for this subtribe. Simultaneously, the composition of the subtribe was changing as can be traced in Herman (2001), Schillhammer (2002, 2004) and Hayashi (2003). Herman (2001) and Schillhammer (2004) included the genus *Tolmerinus* previously classified as Staphylinini incertae sedis. Schillhammer (2002, 2004) also criticized the characters proposed by Smetana and Davies (2000) as diagnostic for Anisolinina because they are only displayed in *Anisolinus* and *Amichrotus*. Hayashi (2003) transferred *Hesperoschema* Scheerpeltz, 1965 from Xanthopygina to Anisolinina. All these changes and ideas were proposed without phylogenetic analyses.

The subtribe Anisolinina was not sampled well in recent molecular or morphological phylogenetic studies of Staphylinini, either because it was not their main focus and (or) only a limited material was available (Table 1). As a result, putative synapomorphies of Anisolinina remain few and are still debatable. One of them is the presence of the accessory basal ridges on the abdominal tergites (Reyes-Hernández et al. 2025), a character also present in some members of Algonina, Philonthina, Staphylinina and Xanthopygina. Another putative synapomorphy seems to be the prepectus of the mesoventrite with an acute ridge on the posterior half, which does not connect the coxal cavities (Schillhammer 2004; Chani-Posse et al. 2018), but this character is present in some Philonthina and absent in some species of *Amichrotus* classified as part of Anisolinina (Brunke and Smetana 2019). Despite the lack of clear synapomorphies, the monophyly of Anisolinina has so far been revealed in all DNA-based studies that included multiple genera of the lineage (Brunke et al. 2016; Chani-Posse et al. 2018; Cai et al. 2019; Brunke and Smetana 2019), albeit sometimes only in the Bayesian analyses (Brunke et al. 2016; Chani-Posse et al. 2018). However, the sister group of

Anisolinina remains uncertain in all studies, especially in the morphological and total evidence phylogenies. The sister-group relationships of Anisolinina remained unresolved in the analyses by Żyła and Solodovnikov (2017) and Schillhammer and Brunke (2018). Chani-Posse et al. (2018), Brunke and Smetana (2019), Jensen et al. (2020), and Reyes-Hernández et al. (2025) revealed it as sister to Staphylinina, but Solodovnikov (2006b) revealed it as sister to Algonina, Li and Zhou (2011) to Philonthina, Solodovnikov and Newton (2005) to Tanygnathina, and Brunke et al. (2019) to Xanthopygina. Different sister group resolutions have been suggested by Solodovnikov and Schomann (2009), Solodovnikov et al. (2013), Brunke and Solodovnikov (2013) and Chatzimanolis and Brunke (2019). Molecular phylogenetic studies were less conflicting in this respect, supporting Staphylinina as the sister group to Anisolinina (Chatzimanolis 2014; Brunke et al. 2016; Chani-Posse et al. 2018; Brunke and Smetana 2019; Cai et al. 2019; Jenkins Shaw et al. 2020; Reyes-Hernández et al. 2025). Interestingly, Anisolinina is paraphyletic in recent phylogenomic dataset due to the position of *Tympanophorus*, but the authors argued that this issue could be caused by incomplete taxonomic sampling (Brunke and Chatzimanolis 2024).

Solodovnikov and Newton (2005), Pietrykowska-Tudruj et al. (2012) and Li and Tang (2024) were the only authors to use larval morphological characters for inferring backbone phylogenetic relationships within Staphylininae or Staphylinini, and only Solodovnikov and Newton (2005) included Anisolinina. This is a clear knowledge gap because in the holometabolous insects, larval morphology plays a special role in reconstructing the phylogeny, either alone or in combination with adult morphology (e.g., Crowson 1955; Lawrence and Newton 1982; Di Giulio et al. 2003; Lawrence et al. 2011). In particular, larval morphology is widely applied in establishing higher classification of Staphylininoidea (Beutel and Molenda 1997; Beutel and Leschen 2005), and to define subfamilies, tribes, and subtribes within the Staphylinidae (Ashe and Newton 1993; Ashe 2005; Clarke and Grebennikov 2009; Grebennikov and Newton 2009, 2012; Thayer 2000). Specifically for Staphylinini, larval morphology has been used in a few cases to evaluate the phylogenetic position of puzzling taxa (Solodovnikov and Newton 2005; Solodovnikov 2005; Pietrykowska-Tudruj et al. 2012; Pietrykowska-Tudruj et al. 2014a, b; Zhao and Solodovnikov 2023) where adult characters alone did not give a clear answer.

The rare use of larval characters for systematic purposes in Staphylinidae, despite their phylogenetic importance, is largely due to the still limited knowledge of staphylinid larvae. Only 7.0 % of genera and 1.4 % of species of the family have described larvae (Newton 1990b). Newton (1990b) indicated that the proportion of taxa with known larvae is dropping every year due to the continuous discovery of new species. More than 22,000 new species and 850 new genera of Staphylinidae have been described in the last 30 years (Newton 2022). In Staphylinini, larvae have been described or illustrated for only 18.7 % (41 out of 219) of the genera, as summarized in Table 2. For Anisolinina the only available information

**Table 1.** Published phylogenetic hypotheses for Anisolinina. Abbreviations: adult morphological characters (A), larval morphological characters (L), monophyletic (M), nM (non-monophyletic), maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI), sister to (+).

Reference	Taxon sampling for Anisolinina	Dataset	Monophyly test for Anisolinina, its sister group
<b>Morphological phylogenies</b>			
Solodovnikov and Newton 2005	<i>Diatrechus andohahelo</i> (adult) <i>Diatrechus</i> sp. (larva) <sup>1</sup>	100 (67 A + 33 L)	M, Anisolinina + (Staphylinina + (Xanthopygina + Philonthina)) in the A and L dataset. Anisolinina + Tanygnathinina in the L dataset. Both hypotheses were inferred by MP.
Solodovnikov 2006b	<i>Anisolinus tsuruqiensis</i> <i>Diatrechus andohahelo</i>	63 A	M, Anisolinina + (Philonthina + Staphylinina + Xanthopygina) in two conducted analyses; in strict consensus of MP with heuristic search; Anisolinina + Algonia in the MP unweighted pair-group method with arithmetic average tree.
Solodovnikov and Schomann 2009	<i>Anisolinus tsuruqiensis</i> <i>Tolmerinus</i> sp. <i>Tympanophorus puncticollis</i>	76 A	nM, <i>Anisolinus</i> + (Algonia + Xanthopygina + Philonthina + Hyptiomina). ( <i>Tolmerinus</i> and <i>Tympanophorus</i> ) + (Xanthopygina + Philonthina + Hyptiomina). <i>Anisolinus</i> sister to all other “Staphylinini propria” except Staphylinina. All relationships were inferred by MP.
Li and Zhou 2011	<i>Hesperosoma flavoterminalae</i>	104 A	Only a single genus of Anisolinina was included. Anisolinina + Philonthina in MP with poor support.
Solodovnikov et al. 2013	<i>Diatrechus andohahelo</i>	69 A	Only a single genus of Anisolinina was included. Anisolinina + (Staphylinina + (Philonthina + Xanthopygina)) in both BI and ML trees.
Brunke and Solodovnikov 2013	<i>Tolmerinus</i> sp. <i>Tympanophorus puncticollis</i>	80 A	nM, <i>Tolmerinus</i> + (Staphylinina + (Xanthopygina + Philonthina)) and <i>Tympanophorus</i> + this clade. The analysis was performed by MP.
Żyła and Solodovnikov 2017	<i>Tolmerinus</i> sp. <i>Tympanophorus puncticollis</i>	71 A	M, but sister group relationships remain unsolved. The analyses were performed by MP and BI.
<b>Molecular phylogenies</b>			
Chatzimanolis et al. 2010	<i>Tolmerinus</i> sp. <i>Tympanophorus</i> sp.	COI, TP, Wg, 28S	M, Anisolinina + Staphylinina in BI; nested inside Staphylinina + <i>Algon</i> clade in MP.
Chatzimanolis 2014	<i>Tolmerinus</i> sp. <i>Tympanophorus</i> sp.	ArgK, CAD, COI, TP, Wg, 28S	M, Anisolinina + Staphylinina. The analyses were performed by BI and ML.
Brunke et al. 2016	<i>Anisolinus</i> sp. <i>Hesperosoma pederseni</i> <i>Misantlius gebieni</i> <i>Pammegus ruficollis</i> <i>Tolmerinus</i> sp. <i>Tympanophorus</i> sp.	ArgK, CAD, COI, TP, Wg, 28S	M with high support in BI, but low support in ML. In both analyses Anisolinina + Staphylinina.
Żyła and Solodovnikov 2019	<i>Tolmerinus</i> sp.	ArgK, CAD, COI, TP, Wg, 28S	Only a single genus of Anisolinina was included. Anisolinina + Staphylinina in ML but without support.
Cai et al. 2019 <sup>1</sup>	<i>Anisolinus</i> sp. <i>Hesperosoma pederseni</i> <i>Misantlius gebieni</i> <i>Pammegus ruficollis</i> <i>Tolmerinus</i> sp. <i>Tympanophorus</i> sp.	ArgK, CAD, COI, TP, Wg, 28S	M, Anisolinina + Staphylinina in BI.
Jenkins Shaw et al. 2020	<i>Tolmerinus</i> sp.	ArgK, CAD, COI, TP, Wg, 28S	Only a single genus of Anisolinina was included. Anisolinina + Staphylinina in BI.
Tihelka et al. 2020 <sup>2</sup>	<i>Tolmerinus</i> sp.	ArgK, CAD, COI, TP, Wg, 28S	Only a single genus of Anisolinina was included. Anisolinina + Algonia, the analysis was performed under a site-heterogeneous CAT-GTR model.
Brunke et al. 2021	<i>Anisolinus</i> sp.	487 loci	Only a single genus of Anisolinina was included. Anisolinina + Staphylinina by ML.
Brunke and Chatzimanolis 2024	<i>Anisolinus</i> sp. <i>Tympanophorus puncticollis</i> <i>Hesperoschema</i> cf. <i>schoenmanni</i>	592 loci	nM, <i>Tympanophorus</i> strongly supports sister to all remaining Staphylinini propria in the sampling; the other two genera strongly supported topological conflict with Staphylinina.
Reyes-Hernández et al. 2025	<i>Anisolinus</i> sp.	531 loci	Only a single genus of Anisolinina was included. Anisolinina + Staphylinina in ML.
<b>Total evidence phylogenies</b>			
Chani-Posse et al. 2018	<i>Anisolinus</i> sp. <i>Hesperosoma pederseni</i> <i>Misantlius gebieni</i> <i>Pammegus ruficollis</i> <i>Tolmerinus</i> sp. <i>Tympanophorus</i> sp.	113 A + ArgK, CAD, COI, TP, Wg, 28S	M, Anisolinina + Staphylinina but only in BI, and no morphological characters were found to support this node.

Reference	Taxon sampling for Anisolinina	Dataset	Monophyly test for Anisolinina, its sister group
Schillhammer and Brunke 2018	<i>Tympanophorus</i> sp.	61 A + ArgK, CAD, COI, TP, Wg, 28S	Only a single genus of Anisolinina was included. The sister group relationships of Anisolinina remain unsolved. The analysis was performed by BI.
Brunke et al. 2019	<i>Tympanophorus</i> sp.	73 A + ArgK, CAD, COI, TP, Wg, 28S	Only a single genus of Anisolinina was included. Anisolinina + Xanthopygina. The analysis was performed by BI.
Chatzimanolis and Brunke 2019	<i>Misantlius gebieni</i> <i>Tolmerinus</i> sp.	91 A + ArgK, CAD, COI, TP, Wg, 28S	nM in BI tree, <i>Misantlius</i> + Staphylinina, and <i>Tolmerinus</i> + this clade. M in ML, Anisolinina + Staphylinina.
Brunke and Smetana 2019	<i>Diatrechus</i> sp. <i>Hesperosoma pederseni</i> <i>Misantlius gebieni</i> <i>Tolmerinus</i> sp. <i>Tympanophorus</i> sp.	67 A + ArgK, CAD, COI, TP, Wg, 28S	M in BI, ML and MP analyses, but without support. In all analyses Anisolinina + Staphylinina, with better support in BI and MP than in ML.
Jensen et al. 2020	<i>Anisolinus</i> sp. <i>Tolmerinus</i> sp.	89 A + ArgK, CAD, COI, TP, Wg, 28S	M with good support in BI, ML and MP analyses; Anisolinina + Staphylinina, with better support in BI and ML.

<sup>1</sup> Solodovnikov and Newton (2005) did not describe the larva of *Diatrechus* sp. but scored it in the phylogenetic data matrix.

<sup>2</sup> Cai et al. (2019) used both morphological and molecular data in their study. But for the morphological data they aimed to solve the tribal relationships within the subfamily Staphylininae, hence, the phylogenetic relationships within the tribe Staphylinini was not shown in their morphological analysis. Hence, Cai et al. (2019) was considered here in the section with molecular phylogenies.

<sup>3</sup> Tihelka et al. (2020) re-analyzed the data of Żyła and Solodovnikov (2019) and Cai et al. (2019) based on site-heterogeneous CAT-GTR model. However, they did not show the phylogenetic relationships within Staphylinini based on Cai et al. (2019). Hence, the dataset of Tihelka et al. (2020) considered in this table is the one from Żyła and Solodovnikov (2019).

**Table 2.** Review of the Staphylinini and Tanygnathinini larvae that have been described, illustrated, or scored in a phylogenetic analysis, the higher classification follows Reyes-Hernández et al. (2025). No larvae of Afroquediina (1 genus), Descarpentriellina (1 genus), Indoquediina (3 genera), Quelaestrygonina (1 genus), Valdiviodina (3 genera), Philothalpina (1 genus), and Ctenandropina (3 genera) have ever been described.

Taxa (in systematic order, alphabetically)	Reference
<b>Staphylinini</b>	
Acylophorina (10 genera)	
<i>Acylophorus</i>	Staniec 2005a, Pietrykowska et al. 2012 <sup>2</sup>
<i>Anaquedius</i>	LeSage 1984
Algonina (3 genera)	
<i>Algon</i>	Li and Tang 2024
Anisolinina (15 genera)	
<i>Diatrechus</i>	Solodovnikov and Newton 2005 <sup>2</sup>
<i>Tolmerinus</i>	In present study
Antimerina (1 genus)	
<i>Antimerus</i>	Solodovnikov and Newton 2010
Cyrtoquediina (9 genera)	
<i>Astrapaesus</i>	Pietrykowska-Tudruj et al. 2014b
<i>Sedolinus</i>	Solodovnikov 2006a
Erichsoniina (2 genera)	
<i>Erichsonius</i>	Topp 1978, Schmidt 1996, Solodovnikov and Newton 2005 <sup>2</sup>
Philonthina (73 genera)	
<i>Belonuchus</i>	Silvestri 1945
<i>Bisnius</i>	Paulian 1941, Pototskaya 1967, Kasule 1970, Boller 1983, Staniec and Pietrykowska-Tudruj 2010, Topp 1978
<i>Cafius</i> <sup>3</sup>	Paulian 1941, Pototskaya 1967, Kasule 1970, James et al. 1971, Coiffait, 1974, Moore 1975, Topp 1978, Jeon and Ahn 2005, 2007, 2014, Pietrykowska et al. 2012 <sup>2</sup> , Cai and Tang 2022
<i>Gabrius</i>	Paulian 1941, Jeannel and Paulian 1945, Pototskaya 1967, 1976, Kasule 1970, Coiffait, 1974, Topp 1978, Pietrykowska-Tudruj et al. 2019
<i>Hesperus</i>	Staniec 2004, Pietrykowska et al. 2012 <sup>2</sup>
<i>Neobisnius</i>	Topp 1978, Schmidt 1994a, Pietrykowska et al. 2012 <sup>2</sup> , Pietrykowska-Tudruj et al. 2019
<i>Philonthus</i>	Mulsant and Rey 1876, Xamheu 1900, Cerruti 1941, Paulian 1941, Jeannel and Paulian 1945, Smetana 1958, 1962, Szujecki 1965, Pototskaya 1966, 1967, Kasule 1970, Coiffait, 1974, Tawfik et al. 1976a, b, c, Moore 1977, Topp 1978, Boller 1983, Nekulisiyanu 1985, Byrne 1993, Kranebitter and Schatz 2002, Solodovnikov and Newton 2005 <sup>2</sup> , Chani-Posse 2006, Pietrykowska-Tudruj and Staniec 2006, Staniec and Pietrykowska-Tudruj 2007, 2008a, b, 2011, Pietrykowska et al. 2012 <sup>2</sup> , Sapieja et al. 2024, Li and Tang 2024
<i>Rabigus</i>	Staniec and Pietrykowska-Tudruj 2009

Taxa (in systematic order, alphabetically)	Reference
Quediina (14 genera)	
<i>Euryporus</i>	Kasule 1970, Pietrykowska et al. 2012 <sup>2</sup>
<i>Korgella</i>	Gusarov and Koval 2002
<i>Quedionuchus</i>	Pototskaya 1976
<i>Quedius</i>	Westwood 1838, Xambeu 1900, Voris 1939b, Paulian 1941, Smetana 1957, 1962, Pototskaya 1967, 1976, Frank 1969, Kasule 1970, Bordoni 1978, Topp 1978, Staniec 2003, Pietrykowska et al. 2012 <sup>2</sup> , Pietrykowska-Tudruj et al. 2014a, Hu et al. 2020
Staphylinina (51 genera)	
<i>Abemus</i>	Paulian 1941, Pototskaya 1967, Coiffait, 1974
<i>Creophilus</i>	Kemner 1912, Voris 1939a, Paulian 1941, Dajoz and Caussanel 1968, Kasule 1970, Coiffait, 1974, Pietrykowska et al. 2012 <sup>2</sup>
<i>Dinothenarus</i>	Paulian 1941, Pototskaya 1967, Coiffait, 1974, Boháč 1982, 1987, Solodovnikov and Newton 2005 <sup>2</sup>
<i>Emus</i>	Kemner 1912, Zhao and Solodovnikov 2023
<i>Eucibdelus</i>	Li and Tang 2024
<i>Hadropinus</i>	Shibata 1965
<i>Hadrotus</i>	Moore 1964
<i>Ocypus</i>	Paulian 1941, Pototskaya 1967, Kasule 1970, Coiffait, 1974, Orth et al. 1976, Topp 1978, Boháč 1982, 1987, Staniec et al. 2009, Pietrykowska et al. 2012 <sup>2</sup>
<i>Ontholestes</i>	Kemner 1912, Voris 1939a, Paulian 1941, Jeannel and Paulian 1945, Pototskaya 1967, Kasule 1970, Coiffait, 1974, Topp 1978
<i>Philetaerius</i>	Maruyama et al. 2013 <sup>4</sup>
<i>Platydracus</i>	Voris 1939a, Paulian 1941, Pototskaya 1967, Kasule 1970, Coiffait, 1974, Lesage 1977, Boháč 1982, Newton 1990a, Schmidt 1994b, Grebennikov and Newton 2009, Pietrykowska-Tudruj and Staniec 2012, Li and Tang 2024
<i>Saniderus</i>	Li and Tang 2024
<i>Staphylinus</i>	Kasule 1970, Coiffait 1974, Boháč 1982, Pietrykowska-Tudruj and Staniec 2012
<i>Tasgius</i>	Paulian 1941, Pototskaya 1967, Coiffait, 1974, Boháč 1982
<i>Thinopinus</i>	Böving and Craighead 1931
Xanthopygina (31 genera)	
<i>Nordus</i>	Chatzimanolis 2004, Grebennikov and Newton 2009 <sup>1</sup>
<i>Smilax</i>	Paulian 1941
<i>Triacrus</i>	Wasmann 1902
<i>Xanthopygus</i>	Quezada et al. 1970 <sup>4</sup> , Solodovnikov and Newton 2005 <sup>2</sup> , Grebennikov and Newton 2009 <sup>2</sup>
<i>Xenopygus</i>	Irmeler 1979
<b>Tanygnathinini</b>	
Amblyopinina (17 genera)	
<i>Edrabijs</i>	Timm and Ashe, 1989
<i>Heterothops</i>	Mulsant and Rey 1876, Paulian 1941, Pototskaya 1967, Drugmand 1988
<i>'Quedius' antipodum</i>	Pietrykowska et al. 2012 <sup>1</sup>
Hyptiomina (1 genus)	
<i>Holisus</i>	Solodovnikov and Newton 2005 <sup>2</sup>
Tanygnathinina (2 genera)	
<i>Atanygnathus</i>	Solodovnikov 2005, Solodovnikov and Newton 2005 <sup>1</sup> , Staniec 2005b
<i>Natalignathus</i>	Solodovnikov 2005
<sup>1</sup> As shown in Żyła and Solodovnikov (2019) and Jenkins Shaw et al. (2020), <i>Quedius antipodum</i> Sharp, 1886 in fact belongs to the subtribe Amblyopinina. Since it was not taxonomically moved from the genus <i>Quedius</i> yet, here it is referred as " <i>Quedius</i> " <i>antipodum</i> within Amblyopinina.	
<sup>2</sup> The larvae have only been scored in the phylogenetic analysis, not illustrated or described.	
<sup>3</sup> The generic concept of <i>Cafius</i> complex follows Yoo et al. (2021), which includes the former genera <i>Remus</i> and <i>Phucobius</i> .	
<sup>4</sup> Only a photo of a live specimen.	

on the larvae is limited to the characters scored in the morphology matrix in Solodovnikov and Newton (2005) for a larva of an unidentified species of *Diatrechus* Bernhauer, 1911 associated with the of adults *D. andohahelo* Lecoq, 2001 by co-occurrence.

In recent years, DNA barcoding has allowed for the efficient identification of larvae without time-consuming rearing experiments (e.g., Hu et al. 2020; Tokareva

et al. 2020). In 2021, a series of staphylinine larvae was collected with adults of *Tolmerinus fratumellitorum* Rougemont, 2017 in the course of the Taiwanese Leaf Litter Beetles Barcoding project (Hu et al. 2024). The identity of the larvae as *T. fratumellitorum* was confirmed by the DNA barcoding, making it the first known larva of *Tolmerinus* and the first undoubtedly identified larva of the subtribe Anisolina. Given the knowledge

gaps outlined above, we used this opportunity (1) to provide the detailed description of this larva for future morphology-based phylogenetic studies, (2) compare it with other known larvae of the Staphylininae, especially Staphylinini and (3) estimate whether larval morphology can clarify the phylogenetic position of Anisolinina.

## 2. Material and Methods

### 2.1. Specimen examination and illustrations

Specimens were examined using Leica® M205 C and DM750 microscopes. Habitus photos were taken by a Canon EOS 760D digital camera with a Canon MP-E65 macro lens or Olympus OM-D E-M1 digital camera with an Olympus M.Zuiko Digital ED 30mm F3.5 Macro lens. Other detailed photos were taken with a Leica MC170HD digital camera through a Leica® DM750 microscope. All the photos were stacked using the auto montage software Helicon Focus 7.0. After dissection, the adult specimens were mounted on cards or deposited in 75–95% ethanol. The larvae were killed, examined and preserved in 95% alcohol. Line drawings were prepared using the Clip Studio software, Adobe Illustrator CS5, and Adobe Photoshop CS5. The dots and gray areas are indicated for membranous parts and the cross-section.

### 2.2. Larval instars, morphological terminology and measurements

The first instar larvae are recognized by their less sclerotized body wall, smaller size, rounded head, and presence of only two spines on the tarsungulus. The second and third instars are very similar, both having a more sclerotized body wall, larger size, and slightly elongated head. However, the only difference between L2 and L3 might be the larger size of the head capsule in L3. The descriptions are primarily based on sequenced specimens, but other identical (thus conspecific) larvae found in the same or similar samples are also considered. The terminology for larval morphology follows Pietrykowska-Tudruj and Staniec (2012). Due to the fragmented knowledge of the Staphylinidae and Staphylinini larvae, we do not homologize all chaetotaxy elements in our descriptions to avoid an incorrect understanding of homology, which may lead to problems discussed by Solodovnikov (2007). Also, Hu et al. (2020) indicated that even within Staphylininae there are various approaches to describe chaetotaxy. At most, we attempted to make our description of chaetotaxy as compatible with other descriptions of contemporary workers as possible. The specimens were measured using a Leica MC170 HD digital camera with software LAS (Leica Application Suite Version 4.4.0, Leica, Wetzlar, Germany) through the computer. Measurement methods were modified from Pietrykowska-Tudruj and

Staniec (2012), as follows: Body length—from anterior margin of nasale to the end of pygopod, taken from dorsal view; Head length—from anterior margin of nasale to neck; Head width—maximal width; Pronotum length—along the median line; Pronotum width—maximal width; Mesonotum length—along the median line; Mesonotum width—maximal width; Metanotum length—along the median line; Metanotum—maximal width; Urogomphi length—maximal length of urogomphi; Abdominal segment X length—from its anterior margin to its posterior margin. All measurements are in millimeters and reported in the “mean (minimum-maximum)” format.

### 2.3. Depositories

FSHC – Fang-Shuo Hu collection, Yilan, Taiwan — NMNS – National Museum of Natural Science, Taichung, Taiwan (Bao-Cheng Lai) — NHMD – Natural History Museum of Denmark, Copenhagen, Denmark (Alexey Solodovnikov)

### 2.4. DNA barcoding

Genomic DNA was extracted from the adults of *T. fratrumelliotorum* and its putative larvae using the NautiaZ Tissue DNA Mini Kit (Nautia Gene Company, Taipei City, Taiwan) following the manufacturer’s protocol, but with adapted incubation times and temperatures (20 hours with T1 Buffer + proteinase K; stand at 25°C for 3 minutes after adding Elution Buffer). The 5’ fragment of the cytochrome oxidase I (cox1) mitochondrial gene was amplified using LCO1490 (GGTCAACAAATCATAAAGATATTGG) and HCO2198 (TAAACTTCAGGGTGACCAAAAATCA) primers (Folmer et al. 1994) with the following PCR protocol: 94°C for 3 mins, 40 × (94°C for 0:30 min, 47°C for 0:45 min, 72°C for 1:00 min), 72°C for 8 mins. The forward and reverse sequences were aligned and fitted to our primers. After alignment, the consensus sequences were checked for potential sequencing errors (ambiguous calls) and were manually edited. The forward and reverse sequences were assembled and edited in Geneious (v. 9.1). The matrix of genetic distances was calculated using Compute Pairwise model with MEGA X (Kumar et al. 2018) to provide accurate identification. The sequences were uploaded to the Barcode of Life Database (BOLD; Ratnasingham and Hebert 2007) under BOLD process IDs REICH008-25 to REICH012-25.

#### 2.4.1. Phylogenetic analysis

Our morphological phylogenetic analysis uses the dataset of Li and Tang (2024) that includes egg, larval and pupal characters, with larval characters of *T. fratrumelliotorum* added to represent the subtribe Anisolinina. Eggs and pupae are unknown for *T. fratrumelliotorum*, the egg and pupal characters of this species were not included (Table S1). The larvae of *Diatrechus* scored in Solodovnikov and Newton (2005) was not used here be-

**Table 3.** Pairwise nucleotide distance of sequence specimens of *T. fratrumelliotorum* based on *cox1* barcoding data.

Specimen ID	Stage	BOLD Process ID		1	2	3	
FS024L	Larva	REICH008-25	1				
FS025L	Larva	REICH009-25	2	0.010			
FS026L	Larva	REICH010-25	3	0.010	0.010		
FS027	Adult	REICH011-25	4	0.005	0.005	0.005	
FS028	Adult	REICH012-25	5	0.010	0.000	0.010	0.005

cause it was identified based on the syntopic collecting event of adults and larvae and because the character set in that paper is quite different from ours. In total, 41 species are included, representing the tribes and subtribes of Staphylininae for which larval specimens or descriptions are available for phylogenetic study. We included Arrowinini, Xantholinini, and Tanygnathinini as outgroups, and rooted the tree with Arrowinini. A total of 71 larval morphological characters defined by Li and Tang (2024) were coded for *T. fratrumelliotorum*. The character matrix is available in Table S1. Parsimony analyses under equal and implied weights (IWMP) was conducted using TNT 1.6 (Goloboff and Morales 2023) with the following parameters: a constant concavity ( $k$ ) equal to half the number of taxa ( $k = 20.5$ ; Goloboff and Arias 2019), memory set to hold 9,999 trees, 1,000 replicates, tree bisection-reconnection (TBR) branch swapping, 10 trees saved per replicate, and zero-length branches collapsed. The strict consensus tree is provided.

### 2.4.2. Character mapping

To explore the phylogenetic value of various larval characters we mapped our data matrix on two phylogenetic topologies. First, characters were mapped on our IWMP tree inferred from this matrix. Second, we mapped them on the reference topology, i.e. the one obtained in the phylogenomic study by Reyes-Hernández et al. (2025) which is largely consistent with the results of previous DNA-based phylogenetic studies (e.g., Brunke et al. 2016; Żyła and Solodovnikov 2019) and may be thus considered as the most robust phylogenetic hypothesis available to date. To perform our character mapping on that reference topology, first we pruned it to remove the taxa not represented in our larval dataset and then mapped characters from our matrix. In both cases we used WinClada ver. 2.0 (Nixon 2021) for character mapping, with character changes optimized unambiguously.

## 3. Results

### 3.1. Identification of larvae with DNA barcoding

The *cox1* barcoding fragment was sequenced from the two adults of *T. fratrumelliotorum* and three co-occurring putative larvae. The analysis shows that the sequences of

all specimens are nearly identical ( $d \leq 0.01$ ) (Table 3), confirming that the larvae are conspecific with the adults.

### 3.2. Larval description for *Tolmerinus fratrumelliotorum* Rougemont, 2017

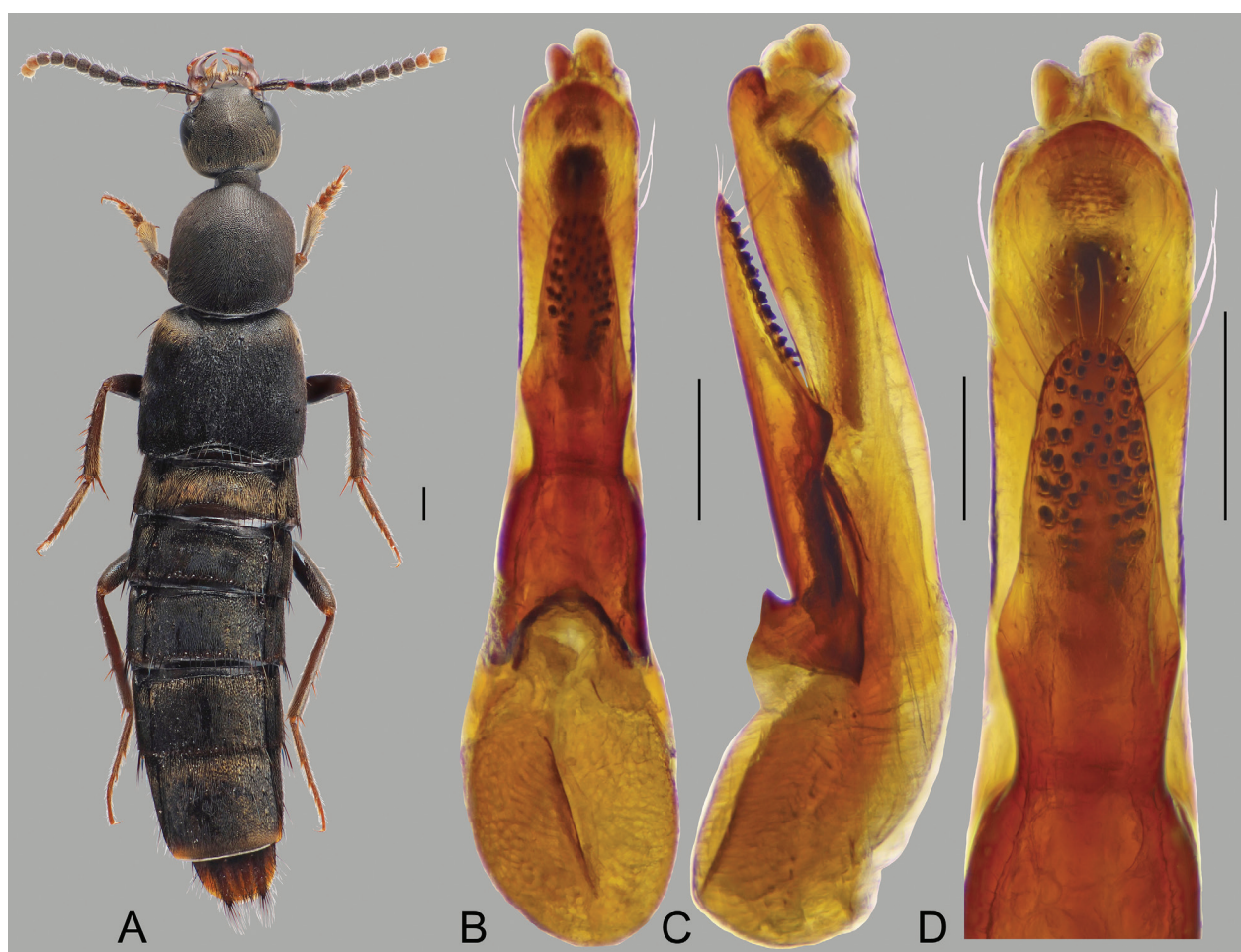
Figures 1–6

**Material examined. TAIWAN: Kaohsiung City:** Altogether the examined material includes eighteen larvae (three specimens of L1, thirteen specimens of L2 and two specimens of L3) and eight adults as follows: 5 adults (3 males and 2 females), Zuoying district (左營區), Banpingshan (半屏山), SW slope, 100 m, 22.694262, 120.305072, 9-22.vii.2021, M. Fikáček lgt. by squid-baited pitfall traps, TW2021-06d (FSHC, NMNS, NHMD); L2, 1 spec.; 3 female adults, Zuoying district (左營區), Banpingshan (半屏山), SW slope, 100 m, 22.694296, 120.305797, 22.vii.2021, M. Fikáček lgt. by sifting leaf litters, TW2021-06e (NHMD); L1, 1 spec., L2, 3 spec., L3, 1 spec., same locality as the previous one, 30.v.2023, BP8 (NHMD); L2, 3 spec.; L1, 1 spec., Zuoying district (左營區), Banpingshan (半屏山), SW slope, 90 m, 22.693469, 120.304979, 13.vi.2021, M. Fikáček lgt. by sifting leaf litters, TW2021-06 (NHMD); L1, 1 spec., L2, 2 spec., same locality as the previous one, 30.v.2023, BP10 (NHMD). **Nantou County:** L1, 1 spec., Huisun Forest reserve, track to Xiaochushan Mt., 24.0744602N, 121.0366337E, 1150 m, 16.viii.2021, Fikáček & Liang lgt. by sifting leaf litters, 21-08-HS1 (NHMD); L3, 1 spec., same locality and date as previous one, 21-08 HS1001-1 (extracted voucher, FS026L) (NHMD); L2, 1 spec., same locality and date as previous one, 21-08 HS1001-2 (NHMD); L1, 1 spec., Huisun Forest res., Wading trail, 24.0892139N, 121.0297836E, 700m, 17.viii.2021; Fikáček & Liang lgt. by sifting leaf litters (NHMD). **Taichung City:** L2, 3 spec., Wufeng, Beikeng Creek trail 24.045 120.7827, 410 m, 24 May 2023, FS Hu, YJ Chen, TW2023-018, lowland tropical forest with large accumulation of leaf litter and sparse understory, Taiwan Leaf Litter Beetles Project Additional specimens, WF1-08 (NHMD).

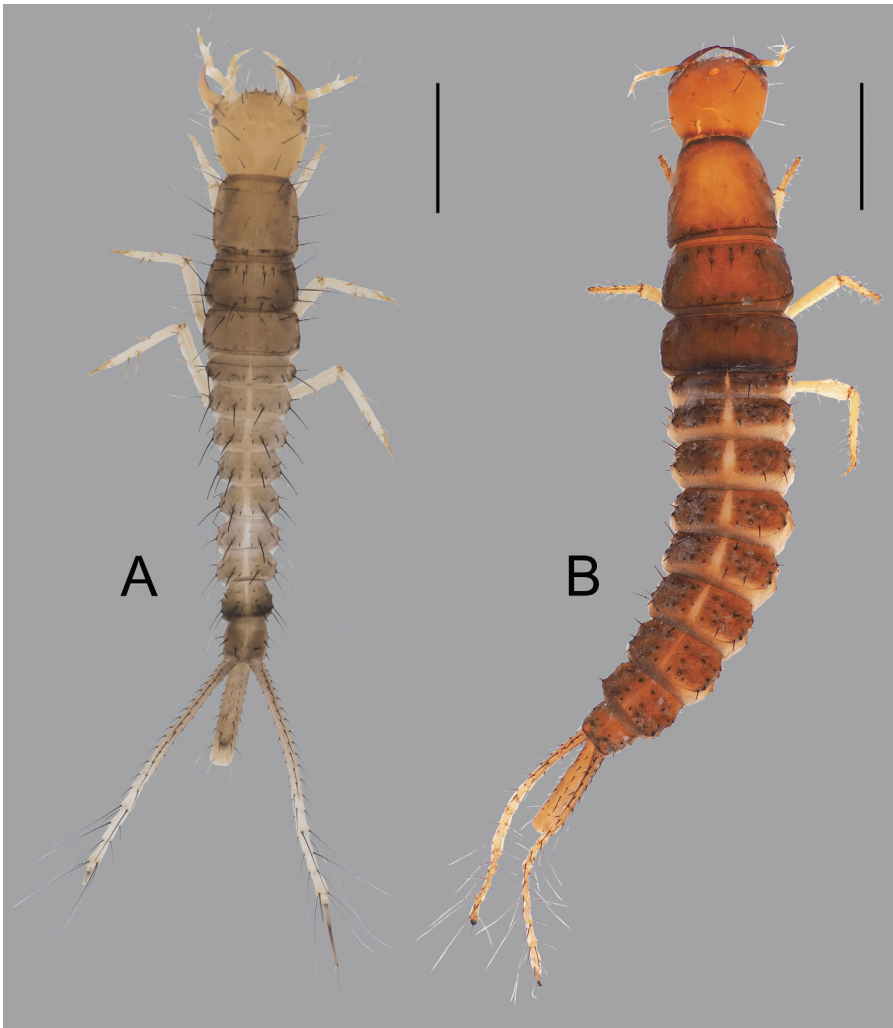
**Description of the third instar larva (L3). Measurements** (in mm,  $n = 2$ ): Body length: 12.21 (11.83–12.73); head width (HW): 1.43 (1.35–1.49); head length: 1.48 (1.38–1.53); pronotum width: 1.34 (1.27–1.42); pronotum length: 1.42 (1.33–1.52). — **Habitus:** Body slender, with relatively large head and long, slender legs, prothorax slightly wider than head, gradually wider posteriorly, mesothorax and metathorax slightly wider than prothorax and abdominal segments. Color: head and pronotum dark yellowish-brown, mandibles darker, thorax gradually darkening from mesonotum to metanotum, abdominal tergites I–IX same as metanotum, abdominal sternites

I–IX yellowish-brown. Antennae, maxillae, labium light yellowish-brown. Basal part of urogomphi and abdominal tergite and sternite X dark brown but slightly lighter than abdominal tergites I–X, apical part of urogomphi yellowish-brown. — **Head:** Head capsule weakly transverse, slightly expanded from base anteriorly, widest at stemmata level, with distinct pair of epicranial glands. Neck presents as distinct carina-delimited constriction. Each side of head with 4 pigmented stemmata in cluster, anterior two similar in size, slightly larger than upper-posterior one; lower-posterior one indistinct, almost indistinctive. Epicranium with five pairs of macro and five pairs of micro setae located symmetrically, divided by dorsal ecdysial line, two pairs of small pores located before epicranial dorsal setae, three pairs of posterior setae and one pair of posterior pores on posterior area; head chaetotaxy as in Fig. 3A. Nasale (Fig. 3C) with one pair of glandular pit and olfactory organs (F11), anterior margin of nasale with nine teeth, median tooth short, at same level as lateral teeth one, paramedian teeth longer than other teeth, lateral teeth two slightly shorter than paramedian teeth but longer than lateral teeth one and two, lateral teeth three short, slightly expanding to outer margin; setation on teeth symmetrical, with nine to ten pairs of macro setae and two to three pairs of micro setae. Head ventrally with 5 pairs of macro and 3 pairs of micro setae located

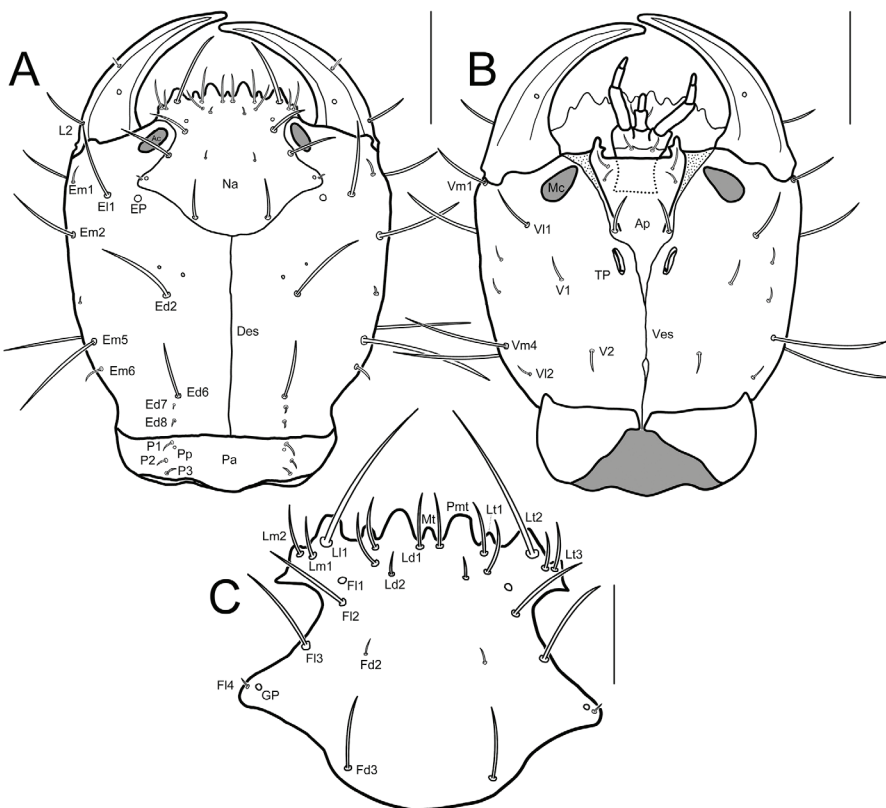
symmetrically, divided by ventral ecdysial suture (Fig. 3B). Apotome triangular, both sides anteriorly membranous, median part sclerotized, with narrow and long stalk extending beyond tentorial pits; one pair of macro setae in front of stalk, two pairs of micro setae anteriorly. Tentorial pits large and oval. Ventral ecdysial line with small median spindle-shaped sclerite near its middle. Antennae four-segmented, slender; segment I cylindrical, shorter than other segments; segment II longer than segment III, slightly swelled in anterior part; segment III longer than segment IV, distinctly swelled in middle of its inner part; segment IV more slender than other segments, slightly longer than segment I, membranous apically, with three solenidia in one cluster; segment II with three macro setae; segment III with three macro setae and with apically pointed sensory appendage, with one small pore in its inner part near sensory appendage, with one solenidium behind small pore (Fig. 4D). Mandibles slender, apically blunt, with one seta externally at base, two campaniform sensilla dorsally of which one located in 1/3 base of mandible in middle, another located in 1/2 from base at external margin; with one campaniform sensillum ventrally, located in 1/2 from base in middle (Fig. 4B). Maxillae with cardo slightly shorter than stipes, about 1.5 times wider than stipes, with one seta in anterior part of outer margin; stipes with nine setae, one on outer margin in mid-



**Figure 1.** The habitus and aedeagus of adult *Tolmerinus fratrumelliotorum*. **A:** Habitus; **B, D:** aedeagus in parameral view. **C:** aedeagus in lateral view. Scale bars: 0.5 mm.



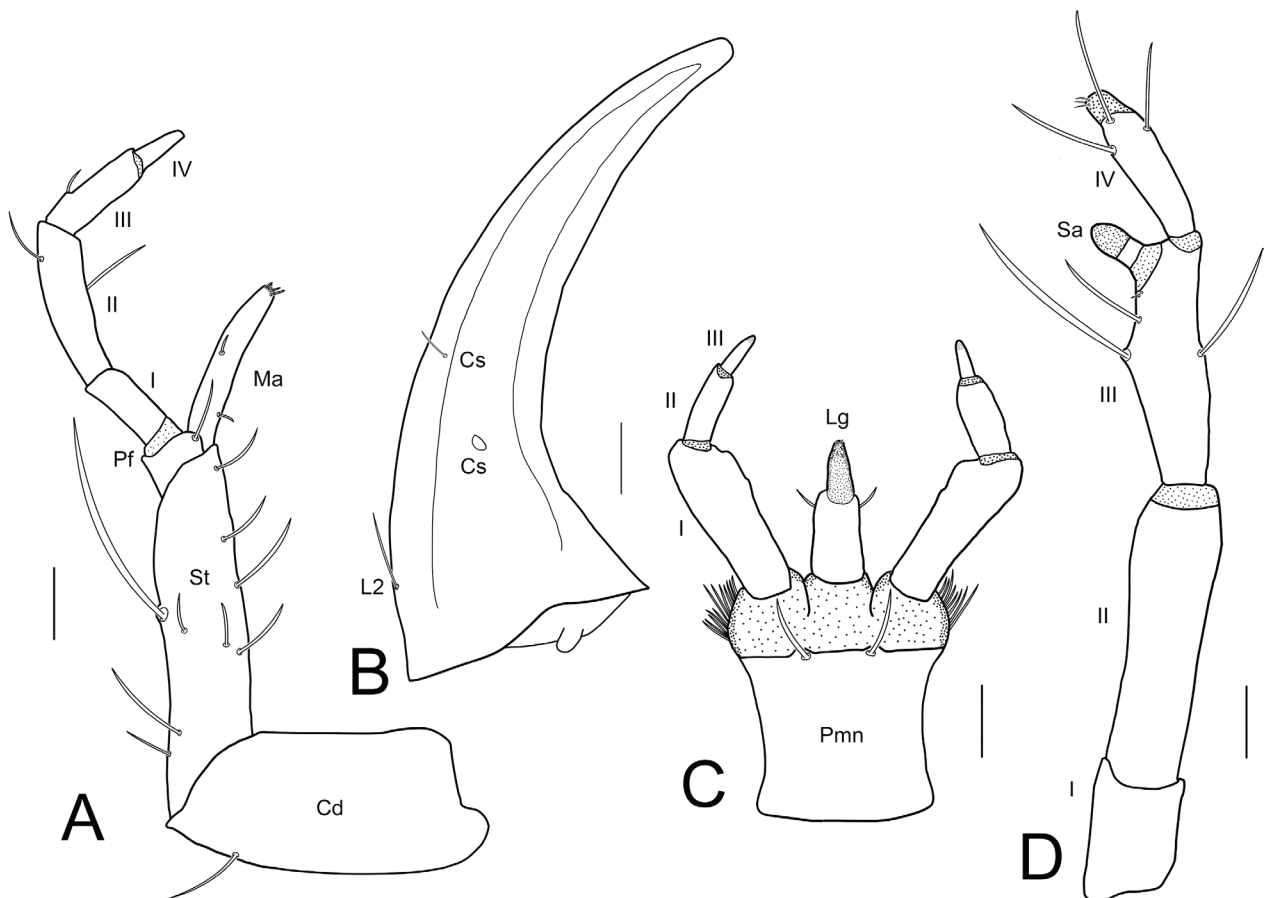
**Figure 2.** Habitus of first and third instars of larvae of *Tolmerinus fratrumelliotorum*. **A:** first instar. **B:** third instar. Scale bars: A, 1 mm; B, 2 mm.



**Figure 3.** Head and nasale of the third instar larva of *Tolmerinus fratrumelliotorum*. **A:** head in dorsal view. **B:** head in ventral view. **C:** nasale in dorsal view. Scale bars A, B: 0.5 mm; C: 0.2 mm. Abbreviations: Ap, apotome. Des, dorsal ecdysial suture. E, epicranial part. Ed, epicranialodorsal seta. Em, epicranial alomarginal seta. Ep, epicranial pore. Fl, frontal lateral seta. Fm, frontal marginal seta. Gp, glandular pit. L, lateral; Lt, lateral teeth. Mt, median tooth. Na, nasale. P, posterior part. Pmt, paramedian tooth. Pp, posterior pore. Tp, tentorial pit. V, ventral part. Ves, ventral ecdysial suture. V1, ventrolateral seta. Vm, ventral marginal seta.

dle distinctly longer than others, one near distinctly longer seta, two located near base of outer margin, two near middle of inner margin, another three evenly dispersed along with anterior part of inner margin; mala digitiform, slender and long, with two setae dorsally, one near base of inner margin, one near middle of outer margin, four solenidia in one cluster apically; palpifer with one seta dorsally, near inner margin; maxillary palps four-segmented, segments I, II and III almost equally wide, segment IV slightly narrower; segment II distinctly longer than others, segment III slightly longer than segment I, segment IV fusiform, shorter than other segments; segment II with two setae, one near middle of inner margin, another located in anterior part of outer margin, segment III with one pore, located near base of outer margin (Fig. 4A). Labium with well-sclerotized ventral side of prementum, slightly membranous anteriorly, with pair of setae apically located on anterior margin of well-sclerotized part; labial palps three-segmented, segment I distinctly longer and wider than segments II and III, segment II longer than segment III, segment III fusiform, shorter than other segments; ligula very long, can be divided into two halves, one half sclerotized with one pair setae in anterior part of outer margin, another half membranous with seven solenidia separated apically (Fig. 4C). — **Thorax:** Prothorax longer than wide, meso- and metathorax wider than long, mesothorax slightly longer than metathorax; protergite

with posterior carina, meso- and metatergite with anterior and posterior carinae. Thorax dorsally with mid-longitudinal ecdysial line. Thorax with simple macro or micro setae, without frayed setae (except on legs); chaetotaxy of pro-, meso-, and metanotum as shown in Fig. 5A. Cervicosternum large, triangular, with four pairs setae, two pairs near anterior suture of cervicosternum, one pair in middle of cervicosternum near ecdysial line, one pair on its posterior margin. Sternite of prosternal area trapezoid; with pair of setae near anterior margin (Fig. 5B). Spiracle oval. Legs (Fig. 5F) long and relatively slender; fore femora with about 22 spine-shaped setae, with longitudinal furrow medially, seven pairs of setae located along this furrow; foretibia with about 18 spine-shaped setae, 15 bifid setae located from its middle to anterior part in form of two or three clusters; tarsungulus with three spine-shaped setae (Figs 5C–D). — **Abdomen:** Abdominal segments with visible dark sclerites, with large or small frayed setae and long or short simple setae. Segment I with pair of paratergites and parasternites fused to each other. Segments II–VIII with pair of paratergites and pair of parasternites (Fig. 5D). Sternite I strongly reduced and of irregular shape, less sclerotized than other segments (Fig. 5E). Chaetotaxy of segment I simpler than more even serially homologous chaetotaxy on segments II–VIII (Fig. 5C–E). Segment IX with reduced chaetotaxy, without laterosclerites or ecdysial line. Segment X (pygopod) with



**Figure 4.** Head appendages of the third instar larva of *Tolmerinus fratrumelliotorum* in dorsal view. **A:** maxillary palps. **B:** mandible. **C:** labium. **D:** antenna. Scale bar: 0.2 mm. Abbreviations: Cd, cardo. Cs, dorsal sensillum. Lg, ligula. Ma, mala. Pf, palpifer. Pmn, prementum. Sa, sensory appendage. St, stipes.

about 24 relatively short spine-shaped setae dorsally and 16 relatively long spine-shaped setae ventrally, all setae located asymmetrically (Figs 6A–B). Urogomphi likely two-segmented (no complete specimen of mature larvae, the segmentation is inferred from early instars only), very long, at least four times as long as abdominal segment IX; first half of segment I straight, with about 30 relatively short setae; second half of segment II formed at least by eight cylindrical pseudosegments, each bearing three very long setae, these setae becoming gradually longer from base to apex of the segment (Fig. 6C).

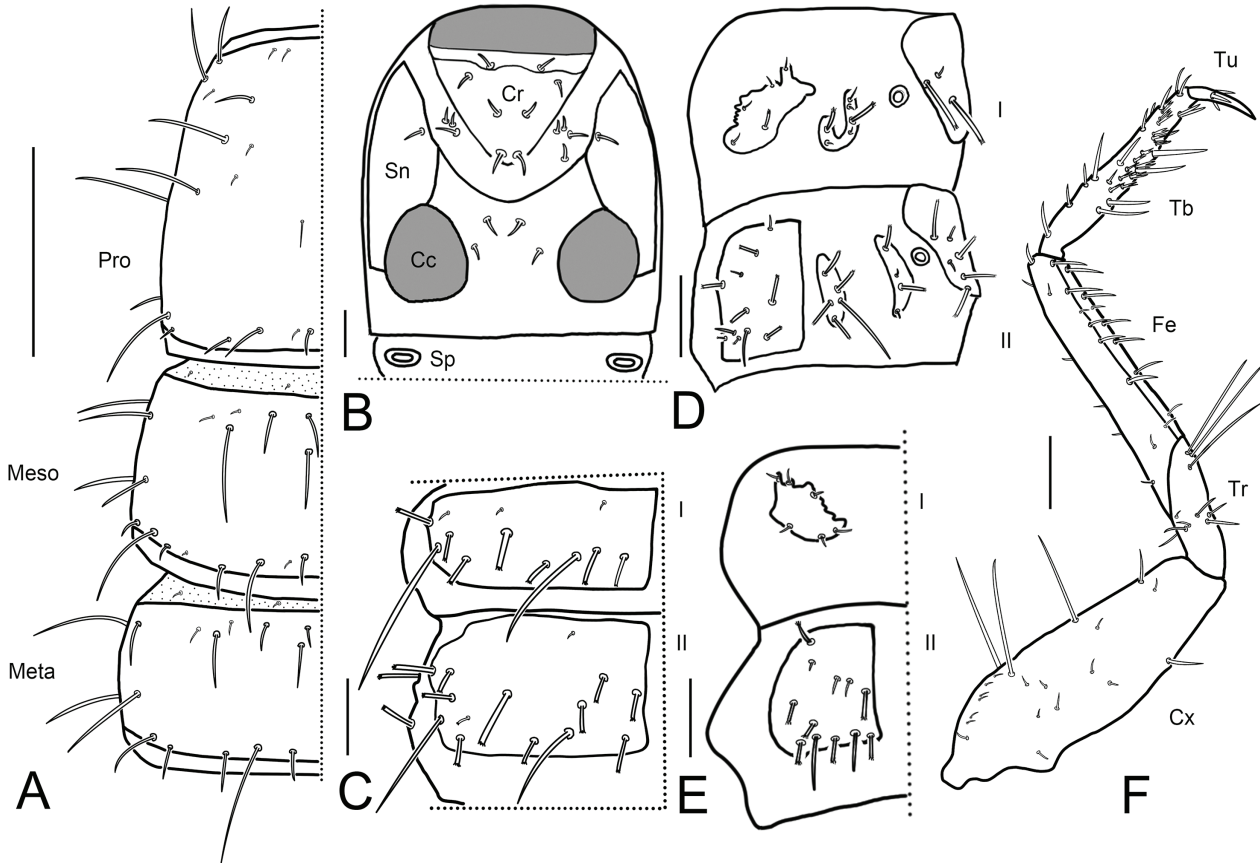
**The difference between larval instars. Measurements for the first instar larva (L1)** (in mm,  $n = 5$ ): Body length: 5.73 (5.24–6.29); head width (HW): 0.94 (0.92–0.98); head length: 0.77 (0.67–0.83); pronotum width: 0.91 (0.86–0.94); pronotum length: 0.67 (0.64–0.68). — **Measurements for the second instar larva (L2)** (in mm,  $n = 11$ ): Body length: 6.83 (6.10–7.38); head width (HW): 1.01 (0.93–1.05); head length: 0.91 (0.80–1.00); pronotum width: 0.84 (0.78–0.91); pronotum length: 0.86 (0.82–0.92).

L3 (see measurements above in the description) is larger than L1 and L2. The whole body of L1 is pale-yellow and less sclerotized than in L2 and L3. Habitus of L2 is similar to L3. Mandibles in L1 are relatively sharper and more sclerotized in the apical half of mandibles than

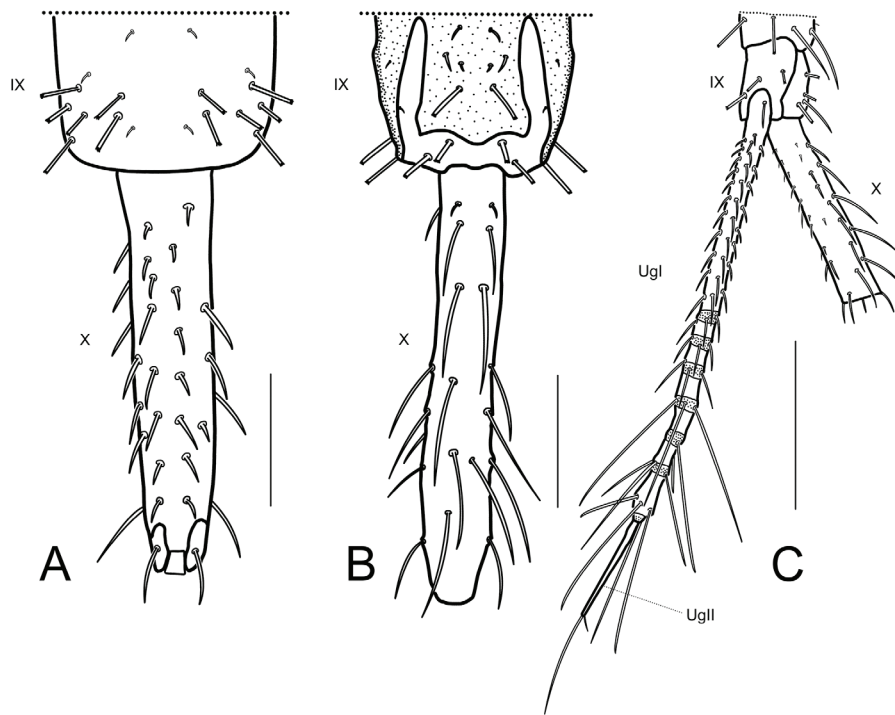
in L2 and L3. Apotome stalk absent in L1, but present in L2 and L3; ventral ecdysial lines of L1 very short without median spindle-shaped hole, L2 and L3 with median spindle-shaped hole on the second half of ecdysial line. The bifid setae of foretibia present in L2 and L3 but absent in L1. Tarsungulus with only two spines in L1, but three spines in L2 and L3.

**Biology.** Adults and larvae of *Tolmerinus fratumellitorum* were collected together from various habitats. In secondary forests with *Ficus*, they were found using squid-baited pitfall traps. In karst areas, they were collected by sifting through shallow leaf litter accumulations, which often included wood debris, fungi, and fallen fig fruits. In primary forests on slopes with sparse understory, the species was located by sifting through leaf litter accumulations, which may also contain fungi and mammal excrement. Additionally, the species was collected from small leaf litter accumulations in stony forests on mountain slopes. Interestingly, three sequenced specimens of *T. fratumellitorum* were contaminated by DNA of *Burmaniscus* isopods, which may indicate that *Tolmerinus* adults and larvae prey on terrestrial isopods.

**Distribution.** *Tolmerinus fratumellitorum* is known from the type specimens collected in Hong Kong, China (Rougemont 2017) and is now reported from Taiwan



**Figure 5.** Thorax, forelegs and abdominal segments I and II of the third instar larva of *Tolmerinus fratumellitorum*. **A:** thorax, in dorsal view. **B:** prothorax, in ventral view. **C:** abdominal segments I and II, dorsal view. **D:** same in lateral view proleg, in latero-ventral view. **E:** same in ventral view. Scale bars: A, 1 mm; B–E, 0.5 mm. Abbreviations: Cc, coxal cavity. Cr, cervicosternum. Fe, femora. Pro, prothorax. Meso, mesothorax. Meta, metathorax. Sn, sternite. Sp, spiracle. Tb, tibia. Tr, trochanter. Tu, tarsungulus.



**Figure 6.** Abdominal segments IX and X of the first and third instars larva of *Tolmerinus fratrutmelliotorum*. **A:** abdominal segments IX and X of third instar, in dorsal view. **B:** same in ventral view. **C:** same structures of first instar, in lateral view. Scale bars: 1 mm. Abbreviations: Ugl: urogomphi.

for the first time. Our data indicates that it may be widespread in Taiwan.

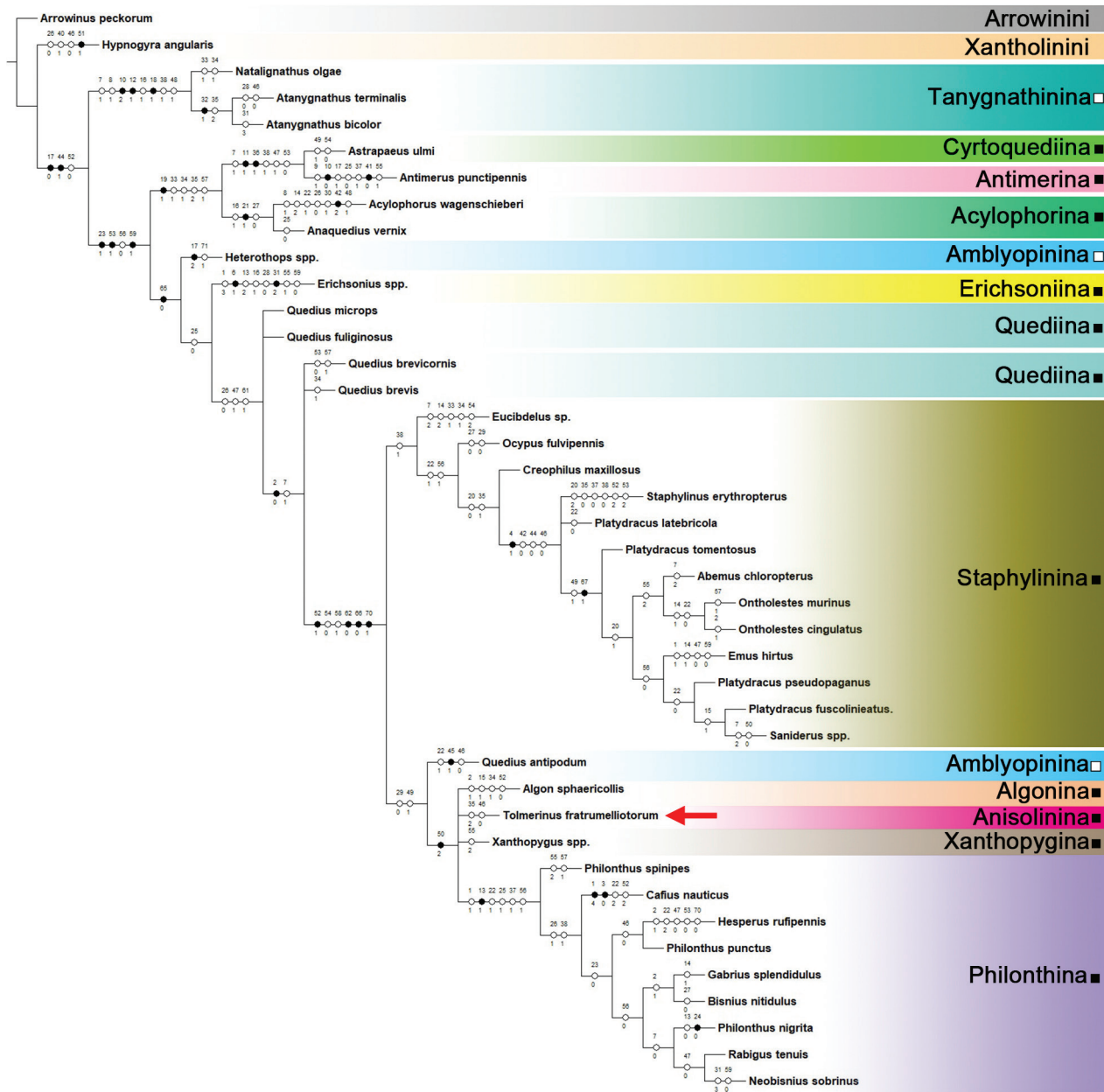
**Remarks.** Matějčiček and Boháč (2020) indicated *T. auronotatus* Fauvel, 1895 to occur in Taiwan, based on the catalogue of Herman (2001). However, Herman (2001) only listed the species for Myanmar. Therefore, *Tolmerinus fratrutmelliotorum* is at the moment the only species of the genus known in Taiwan. Additional species of *Tolmerinus* were collected by us during the Taiwanese Leaf Litter Beetles Barcoding project (Hu et al. 2024). The identifications of these species will be published in future papers.

### 3.3. Phylogenetic analysis

We obtained three most parsimonious trees from the IWMP analysis of immature characters, with a length of 233 steps. The topology of our strict consensus tree (Fig. 7) differs from the 50 % majority rule consensus tree in Li and Tang (2024) in the relationships among Quediina (*Quedius* Casey, 1915 spp.), Acylophorina (*Acylophorus* Nordmann, 1837 and *Anaquedius* Casey, 1915), Cyrtosquediina (*Astrapaeus* Gravenhorst, 1802) + Antimerina (*Antimerus* Fauvel, 1878), *Heterothops* Stephens, 1829 spp. (Amblyopinina), and *Erichsonius* Fauvel, 1874 spp. (Erichsoniina). Our strict consensus tree reveals that Anisolinina (represented by *Tolmerinus fratrutmelliotorum*) is not the sister group to Staphylinina as suggested by most previous molecular or adult morphology-based phylogenies. Instead, Anisolinina forms a clade with Algonina (*Algon* Sharp, 1874), Xanthopygina (*Xanthopygus* spp.) and Philonthina (represented by several genera) with unresolved relationships among all four subtribes. That big clade containing Anisolinina is sister

to '*Quedius*' *antipodum* (i.e., part of Amblyopinina). The subtribe Staphylinina is monophyletic and is sister to the latter clade containing Anisolinina and '*Quedius*' *antipodum*. In addition to the mentioned non-monophyly of Amblyopinina, this analysis does not reveal Quediina as monophyletic and it contradicts with the well-established backbone topology of Staphylininae and Staphylinini in intertribal and intersubtribal sister-group relationships. The tree topology in Fig. 7 shows a significant conflict with the rather well-established reference phylogeny of the group by Reyes-Hernández et al. (2025) in not resolving Staphylinini and Tanygnathinini as monophyletic sister tribes, not resolving monophyletic Quediina, Amblyopinina, and in other details.

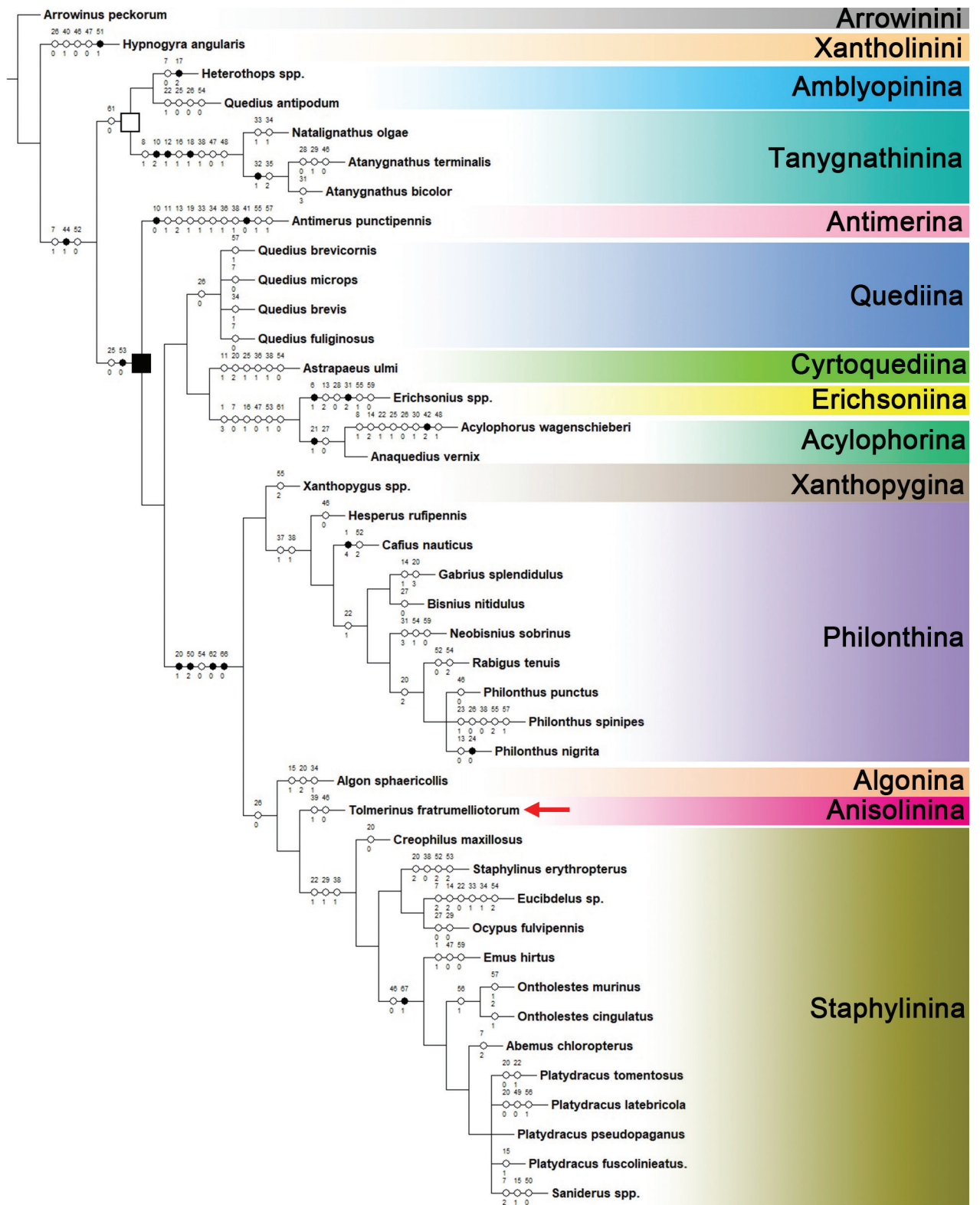
When we mapped characters of the immature stages onto the reference tree by Reyes-Hernández et al. (2025), expectedly, the tree became longer by having 275 steps. Also, no synapomorphies shared between Anisolinina and Staphylinina were found given this set of characters (Fig. 8). However, some synapomorphies were revealed in support of various other clades. For instance, the presence of spine-like setae on the dorsal side of the front tarsungulus (44/1) supports the sister group relationship between Staphylinini and Tanygnathinini, although this character is secondarily lost in the *Platydracus* group (Staphylinina). The tribe Staphylinini is supported by the chaetotaxy of the abdominal sternites II–VIII consisting only of the frayed or club-shaped setae (53/0), however, this character has secondary modifications in many ingroup taxa. The subtribe Tanygnathinina is supported by several characters: tentorial pits on the head capsule positioned posteriorly (10/2), the epicranial gland on the head is absent (12/1), and the main sensory appendage of the antennae with the sclerotized band absent (18/1). In Acylophorina, the digitiform sensory appendage on the maxillae is located anteriorly, closer to the apex (32/1).



**Figure 7.** Strict consensus tree reconstructed by parsimony analysis under implied weights (IWMP) using TNT for the immature morphological data of 41 taxa and 71 characters. Characters plotted using unambiguous optimization, their numbers indicated above the circles, their state numbers below the circles. Black character circles at tree branches represent unique synapomorphies, and white character circles indicate homoplasies; black squares after subtribal name indicate members of the tribe Staphylinini, white squares after subtribal name indicate members of the tribe Tanygnathinini. Character matrix from Li & Tang (2024), with addition of *Tolmerinus fratrumentorum* here.

The clade (i.e. Staphylinini propria) comprising Xanthopygina + Philonthina as sister to Algonina + (Anisolinina + Staphylinina) is supported by multiple characters, including the presence of setae on the inner margin of the second maxillary segment located in the middle (20/1); U-shaped lateral sclerites formed by abdominal paratergites and parasternites of segment I (50/2); the presence of

setiform projections on the pronotum of the pupa (62/0); and setiform cuticular processes on the sides of the abdominal segments of the pupa (66/0). The *Platydracus* group, as proposed by Brunke and Smetana (2019, 2020), is supported by the absence of terminal prolongations on segment IX of the pupa (67/1).



**Figure 8.** Reference phylogenetic tree of Staphylininae using our taxon sampling and topology from Reyes-Hernández et al. (2025). Characters plotted using unambiguous optimization, their numbers indicated above the circles, and state numbers below the circles. Black character circles at tree branches represent unique synapomorphies, white character circles indicate homoplasies, node marked by black square represents the tribe Staphylinini clade, node marked with white square represents the tribe Tanygnathini clade. Character matrix from Li & Tang (2024), with addition of *Tolmerinus frutumellitorum* here.

## 4. Discussion

### 4.1. Possible larval synapomorphy of Anisolinina and similarity to Staphylinina

One striking character of the *Tolmerinus* larva is very long urogomphi, with its second segment formed by multiple pseudosegments, each with very long setae. This form of urogomphi may represent a synapomorphy of Anisolinina, but it needs to be confirmed once larvae of other genera within the subtribe are studied. The character was not included in the character matrix of Solodovnikov and Newton (2005), so we cannot confirm it for *Diatrechus*, the only other genus of Anisolinina with known larvae. Long urogomphi are also found in some Philonthina, Staphylinina, and Xanthopygina, but pseudosegments are not present in these larvae. The *Tolmerinus* larva is generally similar to the larvae of Staphylinina, especially those from the *Ocypus* group, in the combination of 4 segmented of maxillary palps, 3 segmented of labial palps, presence of bifid setae on tibia forming a cluster, and 3 setae on tarsungulus. However, it can be distinguished by relatively slender and long legs, and paratergites and parasternites of the first abdominal segment merged into U-shaped lateral sclerites.

### 4.2. Shortage of data: missing egg and pupal morphology in Anisolinina

The sister-group relationships of Anisolinina with other lineages of Staphylinini remain unresolved based on characters of the immature stages, and none of such characters appear synapomorphic for the Anisolinina + Staphylinina clade suggested by other character systems. This may be due to the missing egg and pupal character data for Anisolinina, particularly as pupal characters have been highlighted as valuable for understanding phylogenetic relationships within Staphylinini (Staniec and Pietrykowska-Tudruj 2019; Li and Tang 2024). Notably, characters such as the dense band of aeropyles on the eggs (3/3) and the curved apical appendages on the pupae (69/1) were found to support the monophyly of Staphylinina in the unambiguously optimized tree by Li and Tang (2024). However, these characters were neither resolved as synapomorphies on our IWMP tree in Fig. 7, nor on the well-established reference phylogeny in Fig. 8.

### 4.3. Homoplastic characters in Cyrtosquediina and Antimerina

It is worth mentioning the issue regarding the relationship between *Cyrtosquediina* (*Astrapaeus*) and *Antimerina* (*Antimerus*). Pietrykowska-Tudruj et al. (2014b) found several synapomorphies shared by these two taxa, suggesting a close relationship and placing them

as a basal grade of Staphylinini, consistent with the hypothesis proposed by Brunke and Solodovnikov (2013). Both Li and Tang (2024) and our morphological analysis also found some synapomorphies between them. For instance, the presence of frayed or club-shaped setae on the head capsule (11/1) and numerous short setae on the protibia (36/1) are unique synapomorphies supporting this clade. This contradicts with molecular phylogenies that indicate that *Cyrtosquediina* and *Antimerina* are phylogenetically distant lineages (Żyła and Solodovnikov 2019; Reyes-Hernández et al. 2025), and that the above mentioned characters evolved independently in both groups. To clarify this, their examination has to be done under higher magnification or SEM (e.g., Staniec and Pietrykowska-Tudruj 2008a, figs 5–11), and more larvae have to be discovered and described, to detect possible minute difference that often exist if the same character state evolved independently. Because of the issues addressed in Solodovnikov (2007), a careful homology-based assessment of many similarly looking structures, especially chaetotaxy, is needed to properly evaluate their evolution.

### 4.4. Morphological synapomorphies of immature stages

Our analysis identifies 34 unique synapomorphies in the phylogenetic tree obtained by the analysis of the morphological matrix built for immature stages (Fig. 7) and 21 unique synapomorphies when the same character set is mapped on the reference phylogeny (i.e., the phylogenetic tree assessed through consistency with the adult morphological characters: Fig. 8). Most of the synapomorphies are the same in both trees where they support the same clades. However, two characters, chaetotaxy of abdominal sternites II–VIII consisting only of frayed or club-shaped setae (53/0) and the presence of setae on the middle of the inner margin of the second maxillary segment (20/1), are optimized as synapomorphies only in the reference tree. The character 53/0 supports the monophyly of the tribe Staphylinini which is well established with the multi-locus, phylogenomic, and adult morphology data; while the character 20/1 supports the monophyly of a large clade within Staphylinini, first well established in earlier phylogenies as “Staphylini propria”. Presumably, these two larval characters are phylogenetically important but their impact in the phylogenetic tree in Fig. 7 was outweighed by other characters, as discussed above for the characters 11/1 or 36/1. Similarly to characters 11 and 36, some other synapomorphies in the tree in Fig. 7, such as the digitiform sensory appendage on maxillae located anteriorly and closer to the apex (21/1), abdominal sternites II–VIII with both frayed or club-shaped setae and simple setae (53/1), pygopod moderately long (59/1), and the presence of cuticular processes on the sides of abdominal segment VIII in the pupa (65/0), appear to support sister group relationships among unrelated taxa. These characters likely need re-evaluation, before being used in phylogenetic analyses.

#### 4.5. Possible applications of larval characters for phylogenetic studies in Staphylininae

Recent practice shows that phylogenomics is the most efficient way for phylogeny reconstruction, including for Staphylininae (e.g., Brunke et al. 2021; Hansen et al. 2023; Reyes-Hernández et al. 2025). Even though larval characters are believed to be useful for phylogenetics of holometabolous insects and showed their utility in the phylogenetic studies of wider Coleoptera and Staphylinidae, they are difficult to observe and interpret, and they are missing for many genera and larger lineages. Many larval characters, especially chaetotaxy, require more in-depth morphological study before they are properly homologized and compared across taxa. Their understanding in taxonomic works, including those where very accurate and detailed comparative morphology has been done, may be still not sufficient to understand the homology. Additionally, our analysis shows that larval characters exhibit a high amount of homoplasy, making it difficult to accurately assess homologies. A similar case has been observed in other beetles (Archangelsky et al. 2020). Although phylogenomic data is powerful, systematic biases remain, such as compositional heterogeneity, missing data, branch-length heterogeneity, paralogy, heterotachy, and gene tree heterogeneity (Young and Gil-lung 2020). Morphological data can help identify such biases or determine which conditions are closer to reality (Wiens 2004). While there is no doubt that larval taxonomy is worthwhile for identification, larval characters also remain important for phylogenetic reconstruction if properly explored and described in the taxonomic literature, which is challenging.

### 5. Declarations

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## Supplementary Material 1

### Table S1

**Authors:** Hu F-S, Solodovnikov A, Fikáček M (2025)

**Data type:** .xlsx

**Explanation notes:** Data matrix used for the analyses.

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