

Research articleSubmitted: February 10th, 2020 - Accepted: April 4th, 2020 - Published: April 15th, 2020**Re-examination of the genus-level taxonomy of the pollen beetle subfamily Meligethinae – Part 1. *Sagittogethes* Audisio & Cline 2009 and allied genera; with description of a new genus (Coleoptera: Nitidulidae)**Meike LIU^{1,2}, Min HUANG², Andrew Richard CLINE³, Paolo CARDOLI⁴, Paolo AUDISIO⁴, Simone SABATELLI^{4,*}¹ College of Agriculture, Yangtze University - Jingzhou, Hubei, 434025 China - liumk2009@126.com² Key Laboratory of Plant Protection Resources and Pest Management of Ministry of Education, Entomological Museum, Northwest A&F University - Yangling, Shaanxi, 712100 China - huangmin@nwsuaf.edu.cn³ Plant Pest Diagnostics Center, California Department of Food & Agriculture - Sacramento (CA), USA - andrew.cline@cdfa.ca.gov⁴ Dipartimento di Biologia e Biotechnologie “Charles Darwin”, Sapienza Università di Roma - Viale dell’Università 32, I-00185 Rome, Italy - paolo.cardoli@gmail.com; paolo.audisio@uniroma1.it; simone.sabatelli@uniroma1.it

* Corresponding author

Abstract

Recent molecular and morphological data derived from members of the pollen-beetle subfamily Meligethinae suggest the need to separate the genus *Sagittogethes* Audisio & Cline, 2009, including species mostly distributed in Western Palaearctic areas, into two distinct (although related) genera, *Sagittogethes* and *Teucrogethes* **gen. n.** This new genus, comprising the Western European *Meligethes obscurus* Erichson, 1845 as its type species, includes less than ten species distributed between the Iberian Peninsula and North Africa westward, and China and Japan eastward. All inclusive species utilize members of the genus *Teucrium* L. (Lamiaceae: Ajugoideae) as larval host-plants. Morphological and bionomical information, and molecular data clearly demonstrate the necessity for updating the taxonomic position of the two clades. Based on molecular evidence, the new genus represents the sister-group of *Thymogethes* Audisio & Cline, 2009, while the sister-group relationships of the remaining *Sagittogethes* taxa with other Lamiaceae-associated genera of Meligethinae remain uncertain. Within the new genus, the relictual and rare Western Mediterranean species *T. minutus* (C.N.F. Brisout de Barneville, 1863) seems to occupy an isolated position.

Key words: molecular taxonomy, *Teucrogethes*, new genus, larval host-plants, pollen beetles, Lamiaceae, *Teucrium*.

urn:lsid:zoobank.org:D7BCE6E3-CEBC-41A9-9DE2-D9036D56B001

Introduction

Recently, the classification of Meligethinae underwent a broad-scale “revolution” in light of both molecular and morphological evidence, restricting the concept of several included genera (Audisio et al. 2009b), particularly the highly heterogeneous and previously polyphyletic genus *Meligethes* Stephens, 1830, which in the past possessed more than 500 species worldwide. The true *Meligethes*, as presently delimited (Audisio et al. 2009b), consists of more than 60 species, all associated with flowers of Rosaceae as larvae, predominantly occurring in the Eastern Palaearctic (Audisio et al. 2015; Liu et al. 2016, 2017, 2018), and closely related to the purported sister genus *Brassicogethes* Audisio & Cline, 2009, whose mostly Western Palearctic members are all associated with Brassicaceae (Audisio et al. 2003, 2005, 2006, 2011; De Biase et al. 2003, 2012;

Mancini et al. 2016; Liu et al. 2019). An upcoming paper will discuss the phylogeny of both these large groups, based on morphological and molecular data (Liu et al. unpublished data).

In a preliminary re-examination of genus-level taxonomy of Meligethinae (Audisio et al. 2009b), it was determined that further research combining integrated approaches was necessary to disentangle the intricate classification and phylogeny of the whole subfamily. Some genera have been, in fact, recently analyzed by our research group through an integrated approach combining morphological, molecular, and bionomical data of larval ecology (Sabatelli et al. 2020; Liu et al. 2019, and unpublished data). In this scenario of reciprocal reorganization of the original exploratory work (Audisio et al. 2009b), Sabatelli et al. (2020) recently demonstrated that molecular data strongly suggest to transition the distinct and relict

Western Mediterranean “*Thymogethes*” *grenieri* (C.N.F. Brisout de Barneville, 1872) into a new monotypic genus. This new genus is separated from true *Thymogethes* Audisio & Cline, 2009, as well as other related Meligethinae taxa. The description of this isolated genus will be accomplished in an upcoming manuscript.

The present contribution, as part of a series of analyses to test the monophyly of all recognized Meligethinae genera, is based on morphological and molecular data of adults, and larval bionomical data, involving members of the entire genus *Sagittogethes* Audisio & Cline, 2009 (Figs 1-2). *Sagittogethes* was believed to represent the sister-group of *Thymogethes* (Audisio et al. 2009b). The present work constitutes the first comprehensive species phylogenetic analysis of this mostly Western Palaearctic lineage.

The genus *Sagittogethes*

The genus *Sagittogethes* (Coleoptera: Nitidulidae, Meligethinae) was erected by Audisio & Cline (Audisio et al. 2009b), and subsequently treated by Lason & Gahari (2013), Audisio et al. (2014) and Sabatelli et al. (2020). The genus formally includes a moderate number of described species (little less than 30), all associated with Lamiaceae as larvae, and arranged in two well-defined species-groups (the *Sagittogethes umbrosus* and *S. obscurus* species-groups; Tables 3-4). Members are mostly distributed in the Western Palaearctic subregion, with a few taxa reaching the extreme NE Palaearctic (Central China and Japan) (Audisio et al. 2009b). The main biodiversity hotspots of this genus are the Southwestern Palaearctic, chiefly in central Mediterranean areas (in particular for members of the *obscurus* species-group), and in E Mediterranean and Anatolian areas (for members of the *umbrosus* species-group) (Kirejtshuk 1978, 1979, 1992; Jelínek & Spornraft 1979; Jelínek 1982; Audisio & Jelínek 1990; Audisio 1993; Jelínek & Audisio 2007; Liu et al. unpublished records). Larvae of all members of “*Sagittogethes*” (s.l.; i.e., *Sagittogethes* + *Teucrogethes* **gen. n.**) (Tables 3-4) are associated with flowers of Lamiaceae, including species in the genera *Salvia* L., *Prunella* L., *Glechoma* L., *Lallemantia* Fisch. & C.A. Mey., *Nepeta* L., and *Dracopcephalum* L. (for members of the *umbrosus* species-group: Table 3), whereas all members of the *obscurus* species-group (Table 4) appear to be exclusively associated with *Teucrium* L. (Audisio 1993; Audisio et al. 2009b).

Material and Methods

The whole material used for morphological and molecular analyses is stored in the P. Audisio’s collection, currently housed in the Zoological Museum, Sapienza Rome University, Rome, Italy (CAR-MZUR).

Morphological analyses

A matrix containing 28 morphological characters (61 to-

tal character states) of adults (Tables 1, 2) was used for all known 28 species of “*Sagittogethes*” (including two undescribed species from China; Tables 3 and 4). The four genera *Anthystrix* Kirejtshuk, 1980 (Audisio et al. 2009a; represented here by *A. longiclava*), *Brassicogethes* (Audisio et al. 2003, 2011; De Biase et al. 2012; Mancini et al. 2016; Liu et al. 2019; represented here by *B. aeneus*, *B. coracinus*, and *B. matronalis*), *Stachygethes* Audisio & Cline, 2009 (Audisio et al. 2009b; represented here by *S. ruficornis*), and *Thymogethes* (Audisio et al. 2009c, 2017; Sabatelli et al. 2020; represented here by *T. egenus*, *T. exilis*, and *T. gagathinus*) were selected as outgroups based on their variable affinities with members of “*Sagittogethes*” (Audisio et al. 2009b; Sabatelli et al. 2020). See the list below for complete nomenclatorial information on the analyzed species. Two additional bionomical characters (with four character states) were also analyzed combining available (published and unpublished) data on “*Sagittogethes*” larval ecology and host-plant relationships (Tables 1-4). Drawings of relevant diagnostic characters (Table 5) are provided in Figs 1-31. Refer to Audisio & Jelínek (1990) and to Audisio (1993) for additional figures of the included taxa and characters.

The morphological matrix was assembled with MES-QUITE version 3.51 (Maddison & Maddison 2018) and subsequently analyzed in TNT version 1.5 (Goloboff & Catalano 2016). Multistate characters were treated as unordered and zero-length branches were collapsed. Analyses were run as implicit enumeration under both equal and implied weights (concavity factor of 1 and higher). Bremer support values were calculated in TNT from 10,000 trees up to 10 steps longer than the shortest as obtained from a ‘traditional search’, using the ‘trees from RAM’ setting.

List of taxa compared on morphological base

(Outgroups in bold):

Anthystrix longiclava Kirejtshuk & Easton, 1988
Brassicogethes aeneus (Fabricius, 1775)
Brassicogethes coracinus (Sturm, 1845)
Brassicogethes matronalis (Audisio & Spornraft, 1990)
Stachygethes ruficornis (Marsham, 1802)
Thymogethes egenus (Erichson, 1845)
Thymogethes exilis (Sturm, 1845)
Thymogethes gagathinus (Erichson, 1845)
Sagittogethes astacus (Easton, 1957)
Sagittogethes ater (C.N.F. Brisout de Barneville, 1863)
Sagittogethes biondii (Audisio, 1988)
Sagittogethes devillei (Grouvelle, 1912)
Sagittogethes holzschuhi (Jelínek & Spornraft, 1979)
Sagittogethes incanus (Sturm, 1845)
Sagittogethes initialis (Kirejtshuk, 1979)
Sagittogethes interjectus (Jelínek & Spornraft, 1979)
Sagittogethes jordanis (Jelínek & Spornraft, 1979)
Sagittogethes kvaki (Kirejtshuk, 1977)
Sagittogethes maurus (Sturm, 1845)
Sagittogethes mus (Reitter, 1884)

Sagittogethes ovatus (Sturm, 1845)
Sagittogethes perceptus (Jelínek & Spornraft, 1979)
Sagittogethes pharetra (Easton, 1957)
Sagittogethes privus (Kirejtshuk, 1977)
Sagittogethes sp. n. (China)
Sagittogethes subater (Kirejtshuk, 1980)
Sagittogethes tauricus (Jelínek & Spornraft, 1979)
Sagittogethes umbrosus (Sturm, 1845)
Sagittogethes vomer (Kirejtshuk, 1978)
“*Sagittogethes*” *distinctus* (Sturm, 1845)
“*Sagittogethes*” *hladili* (Jelínek, 1982)
“*Sagittogethes*” sp. n. (China)
“*Sagittogethes*” *hoffmanni* (Reitter, 1871)
“*Sagittogethes*” *lindbergi* (Rebmann, 1940)
“*Sagittogethes*” *minutus* (C.N.F. Brisout de Barneville, 1863)
“*Sagittogethes*” *nuragicus* (Audisio & Jelínek, 1990)
“*Sagittogethes*” *obscurus* (Erichson, 1845)

Molecular analyses

DNA extraction, amplification and sequencing

In total, 14 adult specimens of *Sagittogethes*, *Teucrogethes*, *Brassicogethes*, *Stachygethes* and *Anthystrix* species, were field collected and directly killed and preserved in absolute ethanol. Twelve sequences of *Thymogethes*, previously provided by Sabatelli et al. (2020) were also used in the analysis. Table 6 lists the geographic details for each represented species. Species identifications were made using morphological characters detailed in Audisio (1993) and Audisio et al. (2009b). DNA was extracted from whole specimens following the salting out procedure described by Aljanabi & Martinez (1997). Partial sequences of the mitochondrial genes encoding for the cytochrome oxidase subunit 1 (COI) and 16S rRNA (16S) were amplified, using the primer pairs LC01490 5'-TCAACAAATCATAAAGATATTGG-3'; HC02198 5'-TAAACTTCAGGGTGACCAAAAATCA-3' (Folmer et al. 1994) and 16SA 5'-CGCCTGTTTATCAAAA CAT- 3'; 16SB 5'- CTCCGGTTTGA ACTCAGATCA- 3' (Simon et al. 1994). Amplifications were performed with the following general cycle conditions: initial denaturation at 96°C for three minutes, followed by 35 cycles of denaturation at 94°C for one minute, annealing at 54°-57°C for 40 seconds, 1-min. extension at 72°C and a last 7-min. Elongation step at 72°C. Reactions were performed in a 25µl volume containing (NH₄)₂SO₄ 16 mM, Tris-HCl 67 mM (pH 8.8 at 25°C), MgCl₂ 3 mM, 1 mM of each dNTP, 0.8 pmol of each primer and 1.25 units of Taq DNA polymerase. We used an MJ MINI Personal Thermal Cycler (BIO-RAD Laboratories, US) to perform PCR amplifications. The generated PCR products were purified with the Charge Switch PCR Clean-Up Kit (Invitrogen) and sent to an external sequencing service (Macrogen Inc.: www.macrogen.com). Sequences were edited and aligned with Geneious V. 9.1.6 (Kearse et al. 2012). A total of 28 new sequences are ready to be deposited in GenBank.

Molecular phylogeny and divergence time estimation

Bayesian inference (BI) and Maximum likelihood analysis (ML) were both performed on the concatenated mtDNA dataset using, respectively, MRBAYES v3.2.1 (Huelsenbeck & Ronquist 2001) and IQ-TREE (Nguyen et al. 2015) as implemented in W-IQ-TREE (Trifinopoulos et al. 2016). The BI analysis was performed by running 5,000,000 generations, with Markov chains sampled every 1,000 generations. A 10% burn-in was applied and the remaining trees were used to compute a 50 % majority rule consensus tree and posterior probabilities. Generalized Time-Reversible model with a proportion of invariable sites and heterogeneous substitution rates following a gamma distribution (GTR + I + G; Rodríguez et al. 1990) was selected as the best substitution model under the AIC criterion as implemented in JModelTest (Posada 2008). A ML phylogenetic reconstruction was performed running 1,000 ultrafast bootstrap replications (Minh et al. 2013) followed by 1,000 replications of assessment of branch supports with single branch tests with SH-like approximate likelihood ratio test. The best fitting model to analyze each partition was selected as for BI. COI genetic divergence between the lineages was estimated using MEGA 6 (Tamura et al. 2013) as reported in Table 7 (due to technical problems occurred during COI gene sequencing in “*Sagittogethes*” *minutus*, this species was excluded from the distance matrix).

To estimate cladogenetic events, an uncorrelated log-normal Bayesian molecular relaxed clock model and a Yule process prior were used on the mtDNA data set using the software BEAST v.1.8.0 (Drummond et al. 2012). Because of the lack of fossil records to calibrate the trees, we used as a prior, an average value of the COI substitution rate in a range between 1.5% and 3.54% divergence per MY, which represent values estimated for mitochondrial DNA in insects (Brower 1994; Farrell 2001; Papadopoulou et al. 2010; Pons et al. 2010) and previously used for a closely related group (Mancini et al. 2016; Sabatelli et al. 2020). Therefore, we applied an average rate of 0.0126 for molecular clock analysis. The analysis was independently performed three times, with 100 million generations and sampling of trees every 10,000 steps. The log files from the three runs were imported into TRACER v1.6 (Rambaut et al. 2014), to check the posterior distribution, ensuring the effective sample size (ESS) of each parameter in the combined trace file higher than 200. A maximum clade credibility tree was generated using TreeAnnotator v.1.8.2 (BEAST package), and visualized in FigTree v1.4.0

Combined morphological and molecular phylogenetic analyses

The combined molecular and morphological data set (concatenating both morphological and molecular matrices) was analysed under Bayesian inference (BI) using MRBAYES v3.2.1 (Huelsenbeck & Ronquist 2001). The mixed matrix contained three partitions, one for each gene

Table 1 – List of characters and character states used for morphological cladistic analysis. Reference drawings in Audisio (1993) and in Figs 1-31 herein.

-
1. Anterior edge of clypeus (observed dorsally)
(0) transversely truncate, (1) slightly to markedly emarginate
 2. Anterior edge of clypeus (observed frontally, if emarginated)
(0) without small bulge at middle, (1) with small bulge at middle
 3. Angle formed by temples and contiguous anterior portion of cervical region of head
(0) less obtuse ($< 140^\circ$), (1) markedly more obtuse ($> 140^\circ$)
 4. Circum-ocular furrows (occipital sulci on dorsal aspect of head) separating frons from dorsal portion of eyes
(0) present, (1) absent
 5. Inner edges of antennal furrows (ventral side of head)
(0) distinctly posteriorly convergent, (1) almost parallel-sided
 6. Shape of terminal maxillary palpomere (ventral view)
(0) $> 2.8\times$ as long as wide, (1) $< 2.5\times$ as long as wide
 7. Number of setae surrounding each side of the distal edge of antennomere 9
(0) ca. 12-16, (1) ca. 6-9
 8. Pronotal posterior angle shape
(0) almost right-angled, (1) obtuse to nearly bluntly rounded
 9. Pronotal microchetae on posterior edge of pronotum
(0) styloid, not campanulate, (1) hydroid, campanulate
 10. Notosternal sutures
(0) indistinct, not raised, (1) distinct, markedly raised at least anteriorly
 11. Elytral circumscutellar area
(0) with no aciculate and undulate transversal strigosity, (1) with at least traces of aciculate and undulate transversal strigosity
 12. Extension of inner borders of prosternal process
(0) borders terminate nearly at two thirds or three fourths of the prosternal process, (1) borders terminate at the posterior edge of the prosternal process
 13. Shape of prosternal process in both sexes (if completely bordered at sides)
(0) Markedly wider distad than at middle, (1) Scarcely wider distad than at middle
 14. Male metaventrite
(0) without raised bulges or tubercles, (1) with raised bulges or tubercles
 15. Extension of ventrally visible distal portion of metepimera
(0) metepimera terminates posteriorly largely before first ventrite axillary lines, (1) metepimera terminates posteriorly close to or slightly beyond first ventrite axillary lines
 16. Outer edge of protibiae
(0) simply crenulate, (1) with variable and usually asymmetrical teeth at least at distal third, (2) with 2 or 3 larger and acute usually symmetrical and nearly perpendicular teeth at distal third, separated by a series of smaller almost perpendicular teeth
 17. Elytral shape distad
(0) more or less arcuately truncate, (1) oval
 18. First abdominal ventrite
(0) without a more or less deep impression delimiting the outer angular portion of the “axillary line”, (1) with a more or less deep impression close to the outer angular portion of the “axillary line”
 19. First abdominal ventrite (if aedeagus apex more or less strongly widened before apex, and arrow-shaped)
(0) “axillary line” not deviating backwards, (1) “axillary line” slightly deviating backwards, (2) “axillary line” strongly deviating backwards
 20. Male last abdominal ventrite
(0) without raised bulges, tubercles, or carina (1) with large, medial predistal tubercle, or with subdistal transverse carina, (2) with large and obtuse bulge at middle
 21. Male apex of median lobe of aedeagus
(0) not widened before apex, (1) more or less strongly widened before apex, and usually arrow-shaped, (2) bottle-neck shaped before wider and arcuately truncate apex, (3) bottle-neck shaped before much wider and transversely truncate apex
 22. Male apex of median lobe of aedeagus
(0) without any minute median excision, (1) with minute median excision
 23. Male apex of tegmen (if apex of aedeagus bottle-neck shaped before wider and arcuately truncate apex)
(0) exhibiting maximum width distad, (1) exhibiting maximum width near middle

continued

24. Male tegmen (if apex of aedeagus more or less strongly widened before apex, and arrow-shaped)
(0) deeply and widely incised, (1) transversely widely truncate, only with minute median excision
25. Male tegmen (if apex of aedeagus more or less strongly widened before apex, and arrow-shaped)
(0) paramera more or less parallel-sided distad, or tegmen only minutely incised, (1) paramera widely and deeply incised, and distinctly divaricated distad
26. Male tegmen (pubescence on distal portions of paramera if notosternal sutures distinctly raised)
(0) distinct and more or less long, (1) indistinct and short
27. Female shape of ovipositor apex
(0) long styli present, (1) needle-shaped distad and styli absent
28. Female ovipositor (if needle-shaped distad and lacking styli)
(0) ca 2.0-2.1× as long as wide, (1) ca 3.5× as long as wide
29. Larval host-plant
(0) not Lamiaceae, (1) Lamiaceae
30. Larval host-plants (if Lamiaceae)
(0) Lamiaceae Nepeteae, (1) Lamiaceae Ajugoideae

Table 2 – Matrix of species and character states for morphological cladistic analysis. Character number and states correspond to the list in Table 1. Genera/colors combinations as in Table 7 and in Figs 32-35.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
<i>Anthystrix longiclava</i>	0	–	0	1	0	1	1	1	1	1	0	1	1	0	1	0	0	0	–	0	3	0	–	–	–	0	0	–	0	–	
<i>Brassicogethes aeneus</i>	0	–	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	–	0	0	0	–	–	–	–	0	–	0	–	
<i>Brassicogethes coracinus</i>	0	–	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	–	0	0	0	–	–	–	–	0	–	0	–	
<i>Brassicogethes matronalis</i>	0	–	0	0	0	0	0	0	0	0	0	0	–	0	0	0	0	0	–	0	0	0	–	–	–	–	0	–	0	–	
<i>Stachygethes ruficornis</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	0	1	1	0	0	–	0	0	0	–	–	–	–	0	–	1	0	
<i>Thymogethes egenus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0	1	–	2	0	1	–	–	–	–	1	0	–	1	0
<i>Thymogethes exilis</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	2	0	1	–	1	0	1	–	–	–	–	1	0	–	1	0
<i>Thymogethes gagathinus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0	1	–	1	0	1	–	–	–	–	1	0	–	1	0
<i>Teucrogethes distinctus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	0	1	2	0	1	–	0	2	1	0	–	–	0	1	0	1	1	
<i>Teucrogethes hladili</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	0	1	2	0	1	–	0	2	0	1	–	–	0	1	0	1	1	
<i>Teucrogethes hoffmanni</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	0	1	2	0	1	–	0	2	0	0	–	–	0	1	0	1	1	
<i>Teucrogethes lindbergi</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	0	1	2	0	1	–	0	2	0	1	–	–	0	1	1	1	1	
<i>Teucrogethes minutus</i>	1	0	0	1	1	1	1	1	1	1	0	1	1	0	1	2	0	1	–	0	0	0	–	–	–	0	0	0	1	1	
<i>Teucrogethes nuragicus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	0	1	2	0	1	–	0	2	0	0	–	–	0	1	0	1	1	
<i>Teucrogethes obscurus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	0	1	2	0	1	–	0	2	1	0	–	–	0	1	0	1	1	
<i>Teucrogethes</i> sp. n. (China)	0	–	0	1	1	1	1	1	1	1	0	1	1	0	1	2	0	1	–	?	?	?	?	?	?	?	?	1	0	1	1
<i>Sagittogethes astacus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes ater</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes biondii</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	2	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes devillei</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes holzschuhi</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	1	0	0	–	1	0	
<i>Sagittogethes incanus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	2	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes initialis</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes interjectus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	1	0	0	0	–	1	0	
<i>Sagittogethes jordanis</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes kvaki</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes maurus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	2	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes mus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes ovatus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes perceptus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes pharetra</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes privus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes subater</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes tauricus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	1	0	0	0	–	1	0	
<i>Sagittogethes umbrosus</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	2	1	1	0	–	0	0	0	0	–	1	0	
<i>Sagittogethes vomer</i>	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1	1	0	–	0	1	0	0	–	1	0	
<i>Sagittogethes</i> sp. n. (China)	0	–	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	0	1	0	–	0	0	0	?	?	1	0	

Table 3 – Genus *Sagittogethes* Audisio & Cline, 2009, updated list of included species.

Species	Distribution (<i>habitat</i>)	Larval host plant(s)
<i>Sagittogethes astacus</i> (Easton, 1957)	Japan (<i>forest clearings</i>)	unknown
<i>Sagittogethes ater</i> (C.N.F. Brisout de Barneville, 1863)	SE France, NE Italy, SE Europe (<i>xeric meadows, sunny rocky areas</i>)	<i>Salvia officinalis</i> L.
<i>Sagittogethes biondii</i> (Audisio, 1988)	NE Turkey (<i>mountain xeric areas, forest edges</i>)	<i>Salvia staminea</i> Montbr. & Aucher ex Benth.
<i>Sagittogethes devillei</i> (Grouvelle, 1912)	S Europe, N Turkey, Caucasus, NW Middle Asia (<i>high altitude xeric meadows</i>)	<i>Dracocephalum rujschiana</i> L. and <i>D. austriacum</i> L.
<i>Sagittogethes holzschuhi</i> (Jelínek & Spornraft, 1979)	S Turkey (E Taurus Chain) (<i>xeric meadows, sunny rocky areas</i>)	<i>Salvia hypargeia</i> Fisch. & Mey.
<i>Sagittogethes incanus</i> (Sturm, 1845)	Europe, N Africa, Near East (<i>xeric meadows, sunny rocky areas</i>)	<i>Nepeta</i> spp.
<i>Sagittogethes initialis</i> (Kirejtshuk, 1979)	E China (<i>forest edges, xeric meadows, sunny rocky areas</i>)	<i>Salvia przewalskii</i> Maxim.
<i>Sagittogethes interjectus</i> (Jelínek & Spornraft, 1979)	N Turkey (E Pontic Chain) (<i>high altitude xeric meadows, sunny rocky and gravel areas</i>)	<i>Lallemantia canescens</i> (L.) Fisch. & Mey.
<i>Sagittogethes jordanis</i> (Jelínek & Spornraft, 1979)	Pontic areas, Near East (<i>xeric meadows, sunny rocky areas</i>)	<i>Salvia</i> spp., especially <i>S. multicaulis</i> Vahl and <i>S. candidissima</i> Vahl
<i>Sagittogethes kvaki</i> (Kirejtshuk, 1977)	Middle Asia (<i>xeric meadows, sunny rocky areas</i>)	<i>Salvia</i> sp. (unidentified)
<i>Sagittogethes maurus</i> (Sturm, 1845)	Europe, Near East, Middle Asia, E Siberia (<i>meadows, forest edges, rocky areas</i>)	<i>Salvia</i> spp., especially <i>S. pratensis</i> L. and <i>S. nemorosa</i> L.
<i>Sagittogethes mus</i> (Reitter, 1884)	Japan (<i>forest edges</i>)	unknown
<i>Sagittogethes ovatus</i> (Sturm, 1845)	Europe, Caucasus (<i>shady forest edges, wet clearings</i>)	<i>Glechoma hederacea</i> L. and <i>G. hirsuta</i> Waldst. & Kit.
<i>Sagittogethes perceptus</i> (Jelínek & Spornraft, 1979)	W Iran (Zagros Chain) (<i>xeric meadows, sunny rocky areas</i>)	probably <i>Salvia</i> sp. (unidentified)
<i>Sagittogethes pharetra</i> (Easton, 1957)	Middle Asia, N Iran (<i>xeric meadows, sunny rocky areas</i>)	<i>Salvia</i> sp. (unidentified)
<i>Sagittogethes privus</i> (Kirejtshuk, 1977) *	Middle Asia, Near East (<i>xeric meadows, sunny rocky areas</i>)	<i>Salvia</i> spp., e.g., <i>S. staminea</i> M. & A. ex Benth., and <i>S. microstegia</i> Boiss. & Ball.
<i>Sagittogethes subater</i> (Kirejtshuk, 1980)	NE China, (<i>xeric meadows, sunny rocky areas</i>)	unknown
<i>Sagittogethes tauricus</i> (Jelínek & Spornraft, 1979)	E Pontic areas, Turkey, Caucasus, N Iran (<i>xeric meadows, sunny rocky areas</i>)	<i>Lallemantia iberica</i> (Bieb.) (L.) Fisch. & Mey., and <i>L. canescens</i> (L.) Fisch. & Mey.
<i>Sagittogethes umbrosus</i> (Sturm, 1845)	Europe, N Africa, Near East, W Russia (<i>forest clearings, meadows</i>)	<i>Prunella vulgaris</i> (L.) and <i>P. grandiflora</i> (L.) Scholler
<i>Sagittogethes vomer</i> (Kirejtshuk, 1978)	Circum-Pontic areas (<i>xeric meadows, steppic habitats</i>)	<i>Salvia aethiopsis</i> L.
<i>Sagittogethes</i> sp. n. cfr. <i>mus</i> **	Central China (Hubei) (<i>sunny rocky areas</i>)	unknown

* Actual uniformity of the Middle Asian and Anatolian populations of this taxon needs further analysis.

** The description of this new species, likely exhibiting a more close affinity to the Japanese *Sagittogethes mus*, had to be held over, due to the present-day availability of only one damaged male.

Table 4 – Genus *Teucriogethes* **gen. n.**, list of included species (previously treated as members of the *Sagittogethes obscurus* species-group).

Species	Distribution (<i>habitat</i>)	Larval host plant(s)
<i>Teucriogethes distinctus</i> (Sturm, 1845) (comb. n.)	Europe, Caucasus, Near East (<i>xeric meadows, sunny rocky areas</i>)	<i>Teucrium chamaedrys</i> L., <i>T. siculum</i> Rafin., <i>T. montanum</i> L.
<i>Teucriogethes hladili</i> (Jelinek, 1982) (comb. n.)	Turkey, Caucasus, Near East (<i>xeric meadows, sunny rocky areas</i>)	<i>Teucrium chamaedrys</i> L. ssp. <i>sinuatum</i> (Celak) Rech.
<i>Teucriogethes hoffmanni</i> (Reitter, 1871) (comb. n.)	Southern Palaearctic Region (North Africa to Japan) (<i>wet meadows, channel and river edges, wetlands</i>)	<i>Teucrium scordium</i> L.
<i>Teucriogethes lindbergi</i> (Rebmann, 1940) (comb. n.)	W Mediterranean areas, W Balkans (<i>xeric meadows, sunny rocky areas</i>)	<i>Teucrium flavum</i> L.
<i>Teucriogethes minutus</i> (C.N.F. Brisout de Barneville, 1863) (comb. n.)	SW Europe, North Africa, Crete Island (<i>xeric meadows, sunny rocky areas</i>)	<i>Teucrium polium</i> L., maybe also <i>T. luteum</i> (Mill.) Degen
<i>Teucriogethes nuragicus</i> (Audisio & Jelinek, 1990) (comb. n.)	Sardinia, Corsica (<i>xeric meadows, sunny rocky areas</i>)	<i>Teucrium massiliense</i> L., <i>T. polium</i> L.
<i>Teucriogethes obscurus</i> (Erichson, 1845) (comb. n.)	W Europe, North Africa (<i>forest edges, xeric meadows, sunny rocky areas</i>)	<i>Teucrium scorodonia</i> L., <i>T. chamaedrys</i> L.
<i>Teucriogethes</i> sp. n. cfr. <i>hladili</i> *	Central China (Hubei) (<i>sunny rocky areas</i>)	<i>Teucrium</i> sp. (unidentified)

* The description of this interesting new species, probably more closely related to the Anatolian *Teucriogethes hladili*, had to be held over due to the present-day availability of only one female.

and one for the morphological data. Generalized Time-Reversible model with a proportion of invariable sites and heterogeneous substitution rates following a gamma distribution (GTR+I+G) was selected for molecular data and Gamma-shaped rate variation for the morphological data is enforced with rates=gamma. As applied for molecular phylogeny the BI combined analysis was produced by running 5,000,000 generations, with Markov chains sampled every 1,000 generations. A burn-in of 10 % was applied and the remaining trees were used to compute a 50 % majority rule consensus tree and posterior probabilities.

Results

Morphological analyses

The cladistic analysis of the matrix (Table 2), constructed using implied weights, yielded several equally most parsimonious trees with poor statistical support. The strict consensus tree is in Fig. 32.

Despite the poorly supported results of the preliminary morphological analyses (considerably strengthened by molecular data, see below Fig. 33; output of a combined analysis of morphological and molecular data sets in Fig. 34), cladistic data clearly indicate the need to separate “*Sagittogethes*” into two distinct genera, with erection of a new genus to include all previous members of the “*Sagittogethes*” *obscurus* species-group. A series of characters (Table

5) clearly points towards the separation of these two clades, i.e., characters 14, 16, 18, 20, and 21 of the list in Table 1. The new genus, described below as *Teucriogethes* **gen. n.**, appears related to *Thymogethes* Audisio & Cline, 2009 (Audisio et al. 2009b; Sabatelli et al. 2020) (Fig. 32, 34) rather than to the remaining *Sagittogethes*. The new genus comprises less than ten species, including an undescribed new species from Central China (Hubei) (Liu et al. unpublished data; Table 4). However, other undescribed species could reasonably be expected from areas such as Caucasus, Iran, Middle Asia and Western China, where several endemic or subendemic species of *Teucrium* are known to occur (Li & Hedge 1994; Jamzad 2013). The actual phylogenetic position of the problematic “*Sagittogethes*” *minutus*, which, based on our preliminary morphological data, resulted in apparently paraphyletic *Thymogethes* (Fig. 32), is discussed below in a combined (morphological and molecular) analytical scenario (Fig. 34).

Molecular phylogeny and divergence time estimation

We obtained a COI fragment of 599 bp and a 16s fragment of 498 bp in length. These were concatenated, leading to a combined data set of 20 terminals and 1097 bp, which constituted the input for the BI and ML analyses. The selected evolutionary model was GTR + I + G for all genes. This model was then implemented for phylogenetic analyses in MrBayes and IQ-TREE. Phylogenetic trees resulting from the BI and ML analyses showed a concordant topology

Table 5 – Morphological and bionomical characters distinguishing *Sagittogethes* Audisio & Cline, 2009 and allied genera. Purported synapomorphies shared by *Teucrogethes* **gen. n.** and *Thymogethes* are in bold; whereas, authapomorphic characters of *Teucrogethes* **gen. n.** are underlined. Character numbers (cN) are derived from the list in Table 1. Additional character **00** refers to a different dimensional range of the species included in the three compared genera. Reference drawings may be found in Audisio (1993) and in Figs 1-31 herein.

cN	<i>Sagittogethes</i>	<i>Thymogethes</i>	<i>Teucrogethes</i> gen. n.
16	Outer edge of protibiae with variable and usually asymmetrical teeth at least in its distal third	Outer edge of protibiae with 2 or 3 large and acute usually symmetrical teeth at least in distal third, separated by a series of smaller teeth	Outer edge of protibiae with 2 larger and more or less acute usually symmetrical teeth at least in distal third, separated by a series of smaller teeth
18	First abdominal ventrite without a more or less deep impression delimiting the outer angular portion of the “axillary line”	First abdominal ventrite with a more or less deep impression close to the outer angular portion of the “axillary line”	First abdominal ventrite with a more or less deep impression delimiting the outer angular portion of the “axillary line”
11	Elytral circumscutellar area with no aciculate and undulate transversal strigosity	Elytral circumscutellar area with at least distinct traces of aciculate and undulate transversal strigosity	Elytral circumscutellar area with no aciculate and undulate transversal strigosity
1	Anterior edge of clypeus transversely truncate	Anterior edge of clypeus usually distinctly arcuately emarginate, with a small bulge at middle	Anterior edge of clypeus nearly always transversely truncate
14	Metaventrite in males usually with raised bulges or tubercles	Metaventrite in males usually with raised bulges or tubercles	Metaventrite in males without raised bulges or tubercles
20	Last abdominal ventrite in males usually with raised bulges or tubercles	Last abdominal ventrite in males usually with raised bulges or tubercles	Last abdominal ventrite in males always without raised bulges or tubercles
22	Apex of median lobe of aedeagus in males without any minute median excision	Apex of median lobe of aedeagus in males usually with minute median excision	Apex of median lobe of aedeagus in males usually with minute median excision
21	Apex of median lobe of aedeagus in males more or less strongly widened before apex, arrow-shaped	Apex of median lobe of aedeagus in males not widened before apex	Apex of median lobe of aedeagus in males usually bottle-neck shaped before wider and arcuately truncate apex
26	Pubescence on distal portion of paramera distinct and more or less long	Pubescence on distal portion of paramera barely distinct and short	Pubescence on distal portion of paramera distinct and more or less elongate
3	Angle formed by temples and contiguous anterior portion of cervical region markedly less obtuse (< 140°)	Angle formed by temples and contiguous anterior portion of cervical region markedly more obtuse (> 140°)	Angle formed by temples and contiguous anterior portion of cervical region markedly less obtuse (< 140°)
27	Ovipositor with more or less elongate styli	Ovipositor with more or less long styli	<u>Ovipositors mostly needle-shaped distad and lacking styli</u>
(00)	Middle- to large-sized pollen beetles (body length: 2.0-3.8 mm)	Small- to middle-sized pollen beetles (body length: 1.6-2.9 mm)	Small- to middle-sized pollen beetles (body length: 1.3-2.6 mm)
30	Larval host-plants Lamiaceae Nepetoideae Nepetinae (<i>Glechoma</i> , <i>Lallemantia</i> , etc.) or Salviinae (<i>Salvia</i>)	Larval host-plants Lamiaceae Nepetoideae Mentheae Menthinae (<i>Satureja</i> , <i>Thymus</i> , <i>Mentha</i> , etc.) or Nepetoideae Lavanduleae (<i>Lavandula</i>)	<u>Larval host-plants Lamiaceae Ajugoideae (<i>Teucrium</i> only)</u>

Table 6 – Species examined for molecular analyses, sample ID, and details of geographical data listed for each sample.

Species	Sample ID	Localities
<i>Sagittogethes initialis</i>	SIN1_1	China-Sichuan-Ganhaizi (Pond Lake)
<i>Sagittogethes maurus</i>	SMA1_1	Italy- Emilia Romagna- Parma University
<i>Sagittogethes pharetra</i>	SPH1_1	Iran- Mazandaran- Elborz- Valley above Gachsar
<i>Sagittogethes umbrosus</i>	SUM1_1	Italy- Lazio- Carpineto Romano
<i>Teucrogethes distinctus</i>	SDI1_1	Italy- Umbria- Amelia
<i>Teucrogethes hoffmanni</i>	SHO1_1	Turkey-Aksaray-Tuz Gölü, near Yenikent
<i>Teucrogethes minutus</i>	MS1_1	Italy- Calabria- Petrizzi
<i>Teucrogethes obscurus</i>	OB1_1	Spain-León-Isoba
<i>Anthystrix longiclava</i>	AL1_1	Republic of South Africa-Eastern Cape-Gamtoos Mouth
<i>Brassicogethes aeneus</i>	BAE13_3	Italy- Lazio- Pomezia- Borgo di Pratica di Mare
<i>Brassicogethes aeneus</i>	BAE13_4	Italy- Lazio- Pomezia- Borgo di Pratica di Mare
<i>Brassicogethes coracinus</i>	CR8_1	Turkey-Ardahan-road between Göle and Susuz
<i>Brassicogethes matronalis</i>	BMAT3_2	Italy- Lazio- Nemi- via della Radiosa
<i>Stachygethes ruficornis</i>	STRU1_1	Italy- Lazio- Nemi- via Francigena
<i>Thymogethes egenus</i>	TEG7_1	Georgia- Lagodeki- Kakheti
<i>Thymogethes egenus</i>	TEG8_1	Italy- Lazio- Lago Ripa Sottile
<i>Thymogethes exilis</i>	TEX1_1	Italy- Sardinia- Bruncu Spina
<i>Thymogethes exilis</i>	TEX2_1	Italy- Molise- Roccamandolfi
<i>Thymogethes gagathinus</i>	TGA1_1	Italy- Liguria- Quintiliano
<i>Thymogethes gagathinus</i>	TGA2_1	Italy- Lazio- Lago di Ripa Sottile

(Figure 33); only BI posterior probability values and ML bootstrap values exceeding 70% are shown as BI/ML. Our phylogram indicate the presence of two highly supported principal clades, corresponding to the true *Sagittogethes* species + *Stachygethes ruficornis* (BI = 0.97/ML=81) and the species currently ascribed to *Sagittogethes* but associated with members of the genus *Teucrium* L. (Lamiaceae: Ajugoideae) as larval host-plants (*Teucrogethes* **gen. n.**) + species belonging to genus *Thymogethes* (BI = 0.97/ML=70).

Divergence time estimates from BEAST are depicted in Fig. 35. The GTR model was transferred to the HKY (Hasegawa et al. 1985) model due to the low ESS values for some parameters in the analyses when applying the GTR model. With a calibration of 0.0126 substitutions/site per My, the split between the principal clades [*Sagittogethes* + *Stachygethes ruficornis*] and [*Teucrogethes* **gen. n.** + *Thymogethes*] is estimated to be approximately 6 Mya and the origin of the two clades can be traced back to ca. 5-6 Mya. However, molecular relationships and time divergence of *Sagittogethes* with members of the genus *Stachygethes* Audisio & Cline, 2009 (including several species associated with Lamiaceae Nepetoideae, such as *Stachys* L., *Ballota* L., *Marrubium* L., *Salvia* L., and others: Audisio & Cline 2009), as indicated in our preliminary analysis herein and summarized in Figs 33-35, may

be considered as an initial assessment in need of further analyses based on a wider set of taxa, especially among those known to share Lamiaceae as larval hosts (Audisio et al. 2009b).

Combined morphological and molecular phylogenetic analyses

Our combined data matrix included 37 taxa and 1127 characters (COI=1-599; 16s= 600-1097; morphology = 1098-1127). Of the 37 taxa, 21 taxa were scored only for morphology, 15 taxa were scored for morphology and molecular data. Results of the combined data set are summarized in Fig. 34. The BI topology retrieved the following well-supported clades: 1) the true *Sagittogethes* species + *Stachygethes ruficornis* (BI = 0.96) and 2) the species associated with members of the genus *Teucrium* L. (Lamiaceae: Ajugoideae) as larval host-plants (*Teucrogethes* **gen. n.**) + species belonging to genus *Thymogethes* (BI = 1).

Teucrogethes Audisio, Sabatelli, Liu & Cline, **gen. n.** (Figs 2, 6-9, 16-23, 27-29)

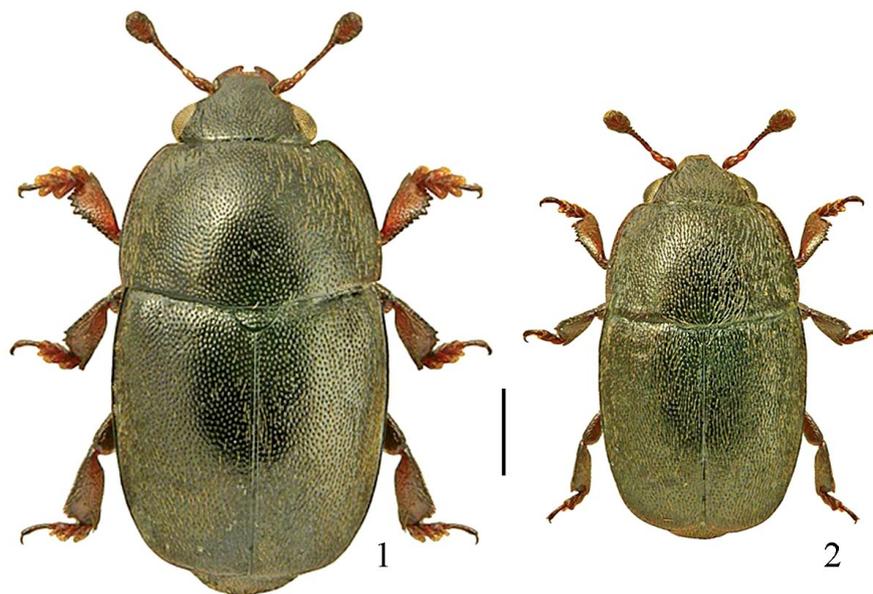
Diagnosis. Small-sized pollen beetles (body length 1.3-2.6 mm); protibiae with a couple of large perpendicular or moderately inclined and more or less acute teeth on outer

Table 7 – Matrix of COI K2Pmodel genetic divergence between the examined species, estimated using MEGA 6 (Tamura et al. 2013). Due to technical problems occurred during COI gene sequencing in “*Sagittogethes*” *minutus*, this species was excluded from the matrix. Genera/colors combinations as in Table 2 and in Figs 32-35.

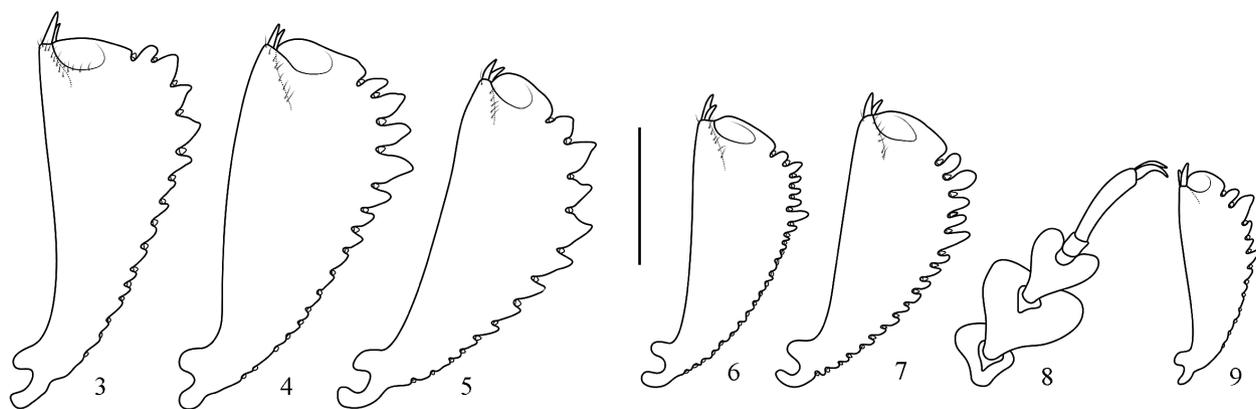
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 <i>Anthystrix_longiclava</i> 1_1																		
2 <i>Stachygethes_ruficornis</i> 1_1	0,167																	
3 <i>Brassicogethes_matronalis</i> 3_2	0,179	0,197																
4 <i>Brassicogethes_coracinus</i> 8_1	0,188	0,197	0,034															
5 <i>Brassicogethes_aeneus</i> 13_3	0,162	0,179	0,118	0,120														
6 <i>Brassicogethes_aeneus</i> 13_4	0,152	0,177	0,116	0,118	0,012													
7 <i>Thymogethes_gagathinus</i> 1_1	0,145	0,163	0,190	0,184	0,162	0,164												
8 <i>Thymogethes_gagathinus</i> 2_1	0,147	0,161	0,192	0,186	0,164	0,166	0,002											
9 <i>Thymogethes_egenus</i> 7_1	0,145	0,148	0,184	0,177	0,162	0,164	0,024	0,022										
10 <i>Thymogethes_egenus</i> 8_1	0,158	0,159	0,195	0,188	0,174	0,177	0,029	0,027	0,012									
11 <i>Thymogethes_exilis</i> 1_1	0,127	0,144	0,175	0,173	0,166	0,154	0,106	0,104	0,092	0,100								
12 <i>Thymogethes_exilis</i> 2_1	0,127	0,144	0,175	0,173	0,166	0,154	0,106	0,104	0,092	0,100	0,000							
13 <i>Teucrogethes_hoffmanni</i> 1_1	0,190	0,170	0,166	0,179	0,179	0,175	0,189	0,187	0,174	0,181	0,166	0,166						
14 <i>Teucrogethes_distinctus</i> 1_1	0,190	0,178	0,169	0,171	0,150	0,152	0,165	0,167	0,161	0,167	0,147	0,147	0,190					
15 <i>Teucrogethes_obscurus</i> 1_1	0,166	0,152	0,164	0,164	0,164	0,160	0,142	0,144	0,140	0,146	0,139	0,139	0,170	0,122				
16 <i>Sagittogethes_pharetra</i> 1_1	0,160	0,171	0,188	0,197	0,175	0,166	0,164	0,162	0,154	0,166	0,138	0,138	0,201	0,198	0,183			
17 <i>Sagittogethes_initialis</i> 1_1	0,150	0,153	0,147	0,158	0,168	0,160	0,148	0,142	0,152	0,128	0,128	0,154	0,166	0,145	0,130			
18 <i>Sagittogethes_maurus</i> 1_1	0,167	0,139	0,177	0,170	0,168	0,164	0,152	0,150	0,139	0,148	0,125	0,125	0,164	0,169	0,152	0,144	0,102	
19 <i>Sagittogethes_umbrosus</i> 1_1	0,129	0,124	0,166	0,172	0,166	0,162	0,129	0,127	0,127	0,131	0,112	0,112	0,157	0,166	0,139	0,131	0,102	0,111

edge, placed at distal third or distal two fifths (Figs 6-7, 9), separated by a series of 2-4 smaller and shorter teeth. Body usually rather parallel-sided and transversely convex, elongate, always uniformly dark brown to blackish, including peripheral dorsal margins of pronotum (Fig. 2). Legs usually uniformly dark brown to blackish, rarely brownish. Antennae dark brown, in some species with second and third antennomeres slightly paler, brownish. Pubescence on pronotum and elytra sparse, golden-yellow to silver, distinct but rather short, each individual seta distinctly shorter (ca. 0.70×) than 2nd antennomere. First abdominal ventrite with a more or less deep impression delimiting the outer angular portion of the “axillary line” (similar to Fig.

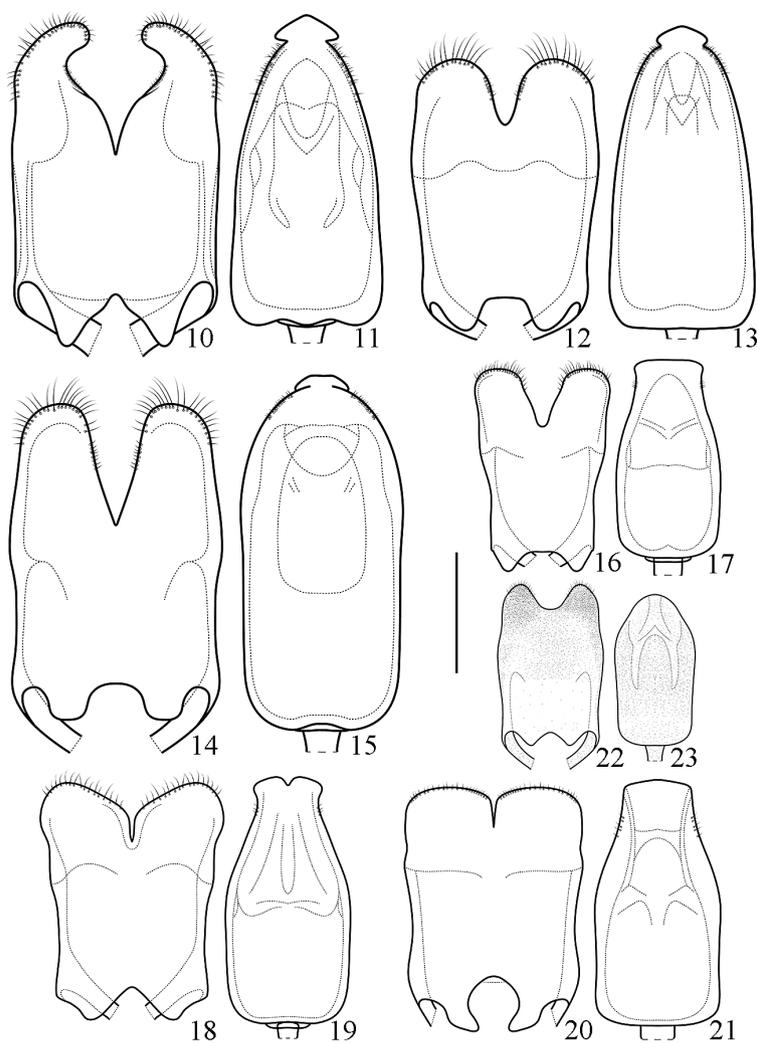
31). Metaventrite in both sexes without raised bulges or tubercles. Last abdominal ventrite in males always without raised bulges or tubercles. Elytra always without aciculate and undulate transverse strigosity, even on circumscutellar area. Protarsi in males usually strongly widened (Fig. 8). Apex of median lobe of aedeagus in males usually bottleneck shaped before the wider and arcuately truncate apex (Figs 17, 19, 21), obtusely rounded only in *T. minutus*: Fig. 23). Ovipositor almost always needle-shaped distad and lacking styli (Figs 27-28); the only exception being *T. minutus*: Fig. 29). Anterior edge of clypeus nearly always transversely truncate (the only exception is *T. minutus*, which exhibits a slightly emarginate edge). Larval host-



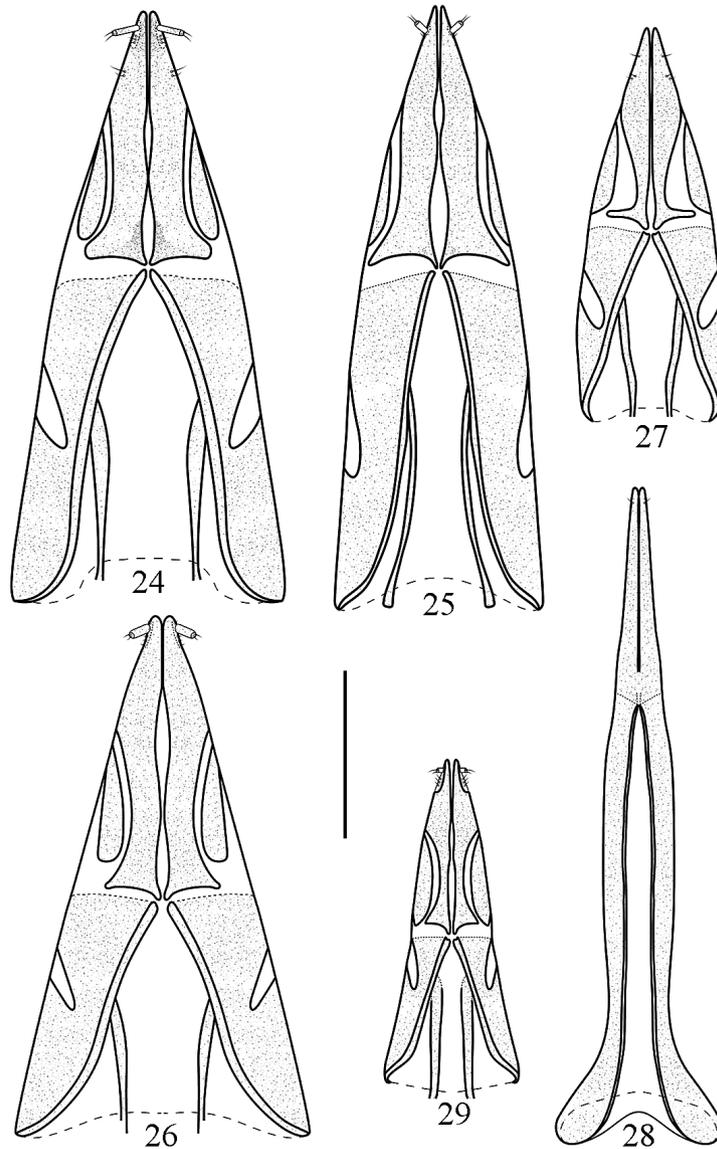
Figs 1-2 – Habitus of two representative species of *Sagittogethes* and of *Teucrogethes* **gen. n.** from Poland. **1**, male of *Sagittogethes umbrosus* (Sturm, 1845); **2**, female of *Teucrogethes distinctus* (Sturm, 1845), **comb. n.** Scale bar: 500 µm. Photos by Lech Borowiec.



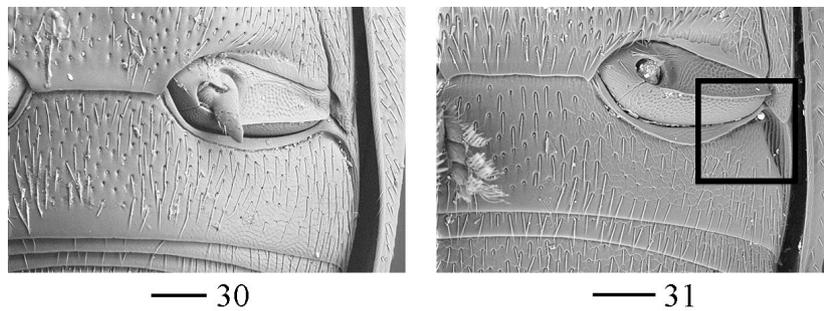
Figs 3-9 – Male front tibiae (in Fig. 8 male front tarsus) of some representative species of *Sagittogethes* and of *Teucrogethes* **gen. n.** from Italy (all species except *T. minutus*) and Spain (*T. minutus*). **3**, *Sagittogethes maurus* (Sturm, 1845); **4**, *S. ater* (C.N.F. Brisout de Barneville, 1863); **5**, *S. devillei* (Grouvelle, 1912); **6**, *Teucrogethes distinctus* (Sturm, 1845), **comb. n.**; **7**, *T. lindbergi* (Rebmann, 1940), **comb. n.**; **8**, *idem*, male front tarsus; **9**, *T. minutus* (C.N.F. Brisout de Barneville, 1863), **comb. n.** Scale bar: 0.2 mm. All drawings from Audisio (1993), modified.



Figs 10-23 – Male genitalia of some representative species of *Sagittogethes* and of *Teucrogethes* **gen. n.** from Italy (all species except *T. minutus*) and Morocco (*T. minutus*). **10-11**, *Sagittogethes maurus* (Sturm, 1845); **12-13**, *S. ater* (C.N.F. Brisout de Barneville, 1863); **14-15**, *S. devillei* (Grouvelle, 1912); **16-17**, *Teucrogethes hoffmanni* (Reitter, 1871), **comb. n.**; **18-19**, *T. distinctus* (Sturm, 1845), **comb. n.**; **20-21**, *T. lindbergi* (Rebmann, 1940), **comb. n.**; **22-23**, *T. minutus* (C.N.F. Brisout de Barneville, 1863), **comb. n.** Scale bar: 0.2 mm. All drawings from Audisio (1993), modified.



Figs 24-29 – Female genitalia of some representative species of *Sagittogethes* and of *Teucriogethes* **gen. n.** from Italy (all species except *T. minutus*) and Morocco (*T. minutus*). **24**, *Sagittogethes maurus* (Sturm, 1845); **25**, *S. ater* (C.N.F. Brisout de Barneville, 1863); **26**, *S. devillei* (Grouvelle, 1912); **27**, *Teucriogethes distinctus* (Sturm, 1845), **comb. n.**; **28**, *T. lindbergi* (Rebmann, 1940), **comb. n.**; **29**, *T. minutus* (C.N.F. Brisout de Barneville, 1863), **comb. n.** Scale bar: 0.2 mm. All drawings from Audisio (1993), modified.



Figs 30-31 – SEM photos of the “axillary” portion (black square in Fig. 31) of the first abdominal ventrite of some representative species of Meligethinae. **30**, *Afrogethes planiusculus* (Heer, 1841); an example of “simple”, not deeply impressed and plesiomorphic axillary area-type (as in *Sagittogethes*); **31**, *Thymogethes exilis* (Sturm, 1845); an example of deeply impressed and apomorphic axillary area-type (as in *Teucriogethes* **gen. n.**). Scale bar: 0.1 mm. Photos by S. Strika.

plants of all known species are represented by members of Lamiaceae/Ajugoideae (within the genus *Teucrium* only).

Type species:

Meligethes obscurus Erichson, 1845

Meligethes obscurus Erichson, 1845: 203.

Distribution. The eight thus far known species (7 described, 1 undescribed) range westward from North Africa and the Iberian Peninsula, eastward to Central China (Hubei) and Japan (Easton 1957a, b; Jelínek 1982; Audisio & Jelínek 1990; Kirejtshuk 1992; Audisio 1993; Jelínek & Audisio 2007; Audisio et al. 2009b; Liu et al. unpublished data).

Host-plants. All known species share Lamiaceae/Ajugoideae, genus *Teucrium* L., as larval host-plants (Audisio 1993; Audisio et al. 2009b; Liu et al. unpublished data).

Etymology. The specific epithet of this new genus is de-

rived from the Latin name *Teucrium* (the only known larval host plant genus) and *-gethes*, referring to the commonly used and shared ending of numerous genera of Meligethinae (Audisio et al. 2009b).

Taxonomic remarks. This new genus is similar in external shape to related genera *Sagittogethes* and *Thymogethes* (see Table 5). Some shared synapomorphies and molecular evidence (see below) point towards more close phylogenetic relationships between *Teucrogethes* **gen. n.** and *Thymogethes*, than to the true remaining *Sagittogethes* (Figs 32-35). The rare, relictual and deviating Western Mediterranean species *T. minutus* (C.N.F. Brisout de Barneville, 1863) seems to occupy an isolated and basal position within the genus (Figs 33-34), sharing some morphological characters (e.g., shape of median lobe of aedeagus and apex of ovipositor) with members of *Thymogethes* (Tables 2, 5; Fig. 32). On the other hand, this species clearly results embedded in the *Teucrogethes* clade, based on molecular evidence (Fig. 33).

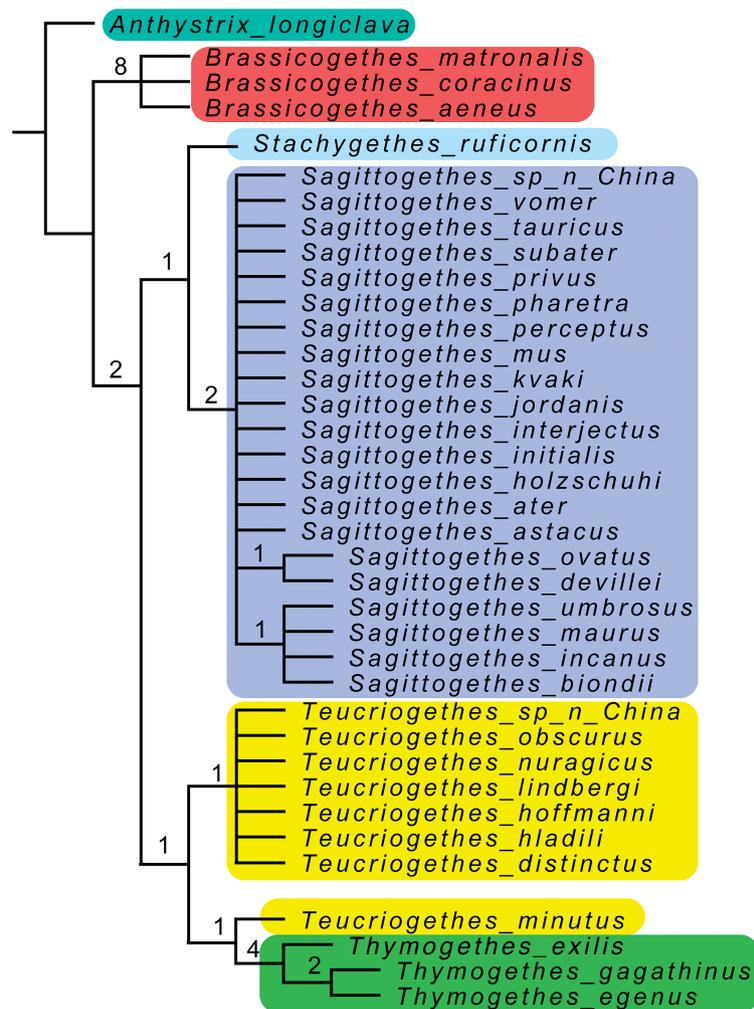


Fig. 32 – The strict consensus tree constructed on morphological characters via TNT. Numbers in bold above branches indicate Bremer support values (See Tables 1 and 2 for character list and matrix).

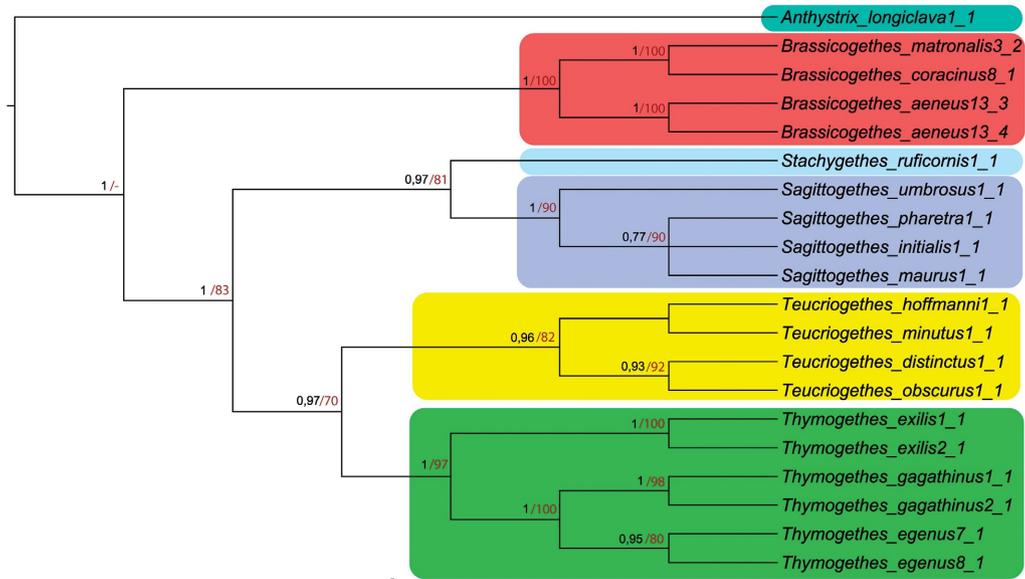


Fig. 33 – Phylogenetic interrelationships based on Bayesian inference (BI) performed using MrBayes and maximum-likelihood (ML) analyses performed using IQ-TREE. The final data matrix includes 20 terminals and 1097 aligned characters. The selected evolutionary model is GTR + I + G. See Table 6, for details on the examined specimens. Only BI posterior probability (black) values and ML bootstrap (red) values exceeding 70% are shown as BI/ML.

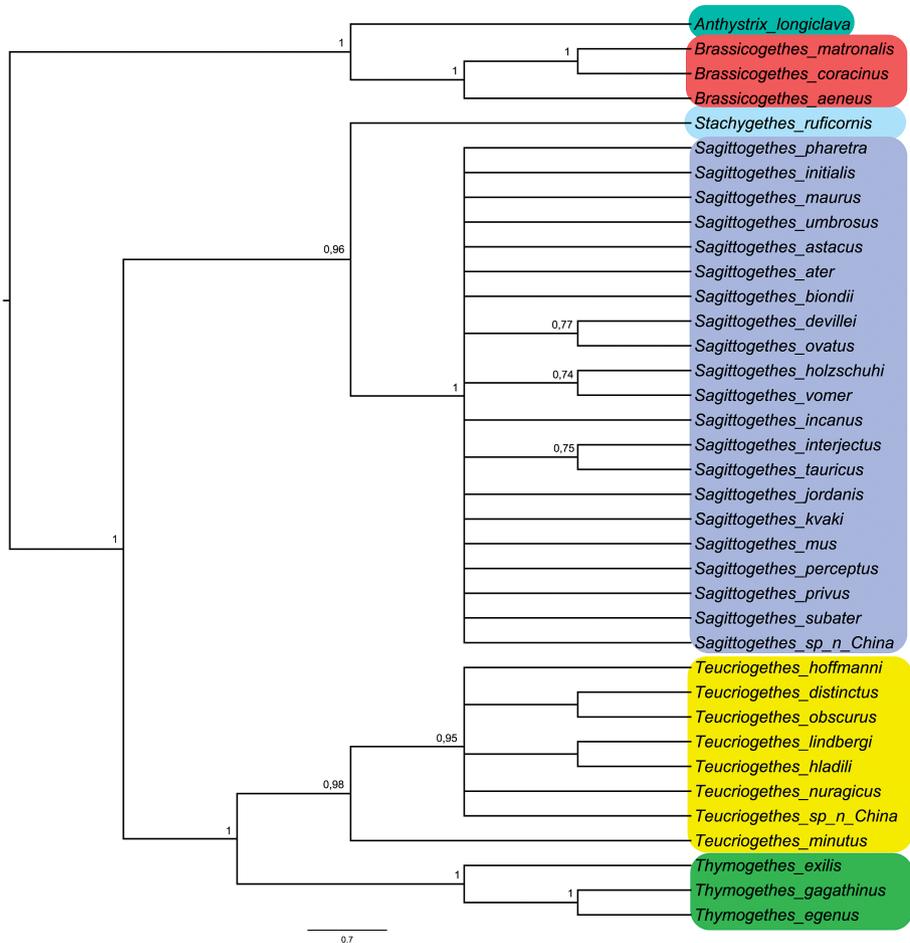


Fig. 34 – Bayesian inference (BI) consensus tree of the molecular and morphological characters combined analysis, performed using Mr-Bayes. Support values at nodes refer to BI posterior probabilities.

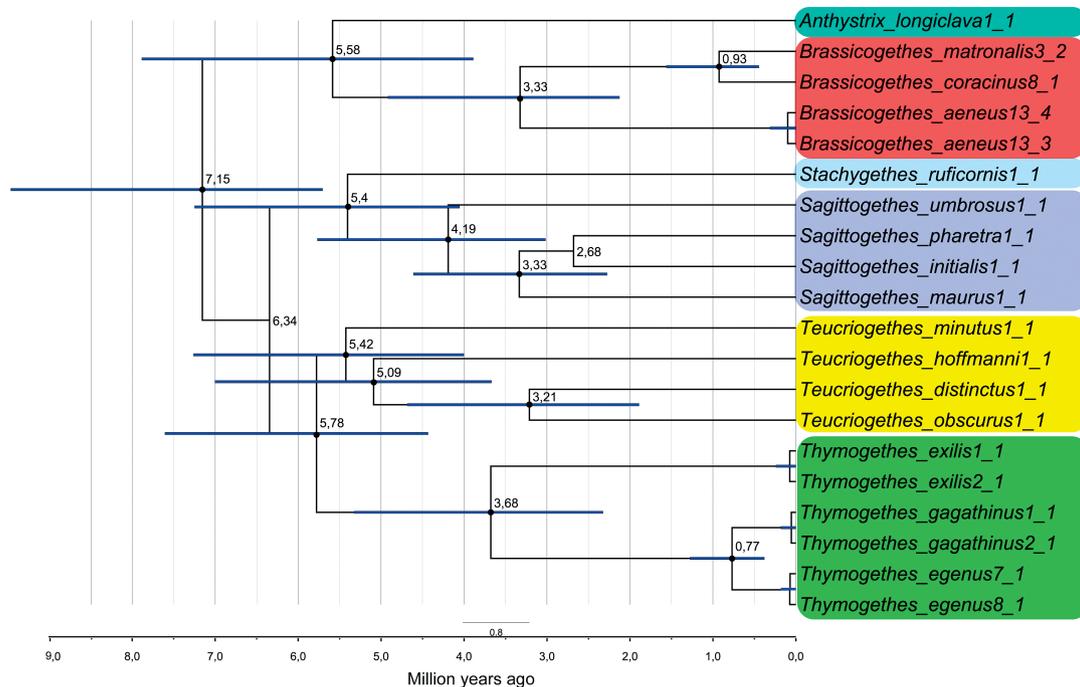


Fig. 35 – Time-calibrated phylogeny obtained with BEAST based on combined mitochondrial sequences (COI, 16S). Numbers at nodes, correspond to estimated age (Ma); bars represent highest posterior densities (95%) around mean date estimates. Nodes with black dots were supported with high posterior support (>95).

Conclusions

The combined evidence of both morphological and molecular analyses carried out on all members (based on morphology: Tables 1, 2, 5) or on some representative species (based on two molecular markers: Table 6) of the previously established genus *Sagittogethes* Audisio & Cline, 2009, suggest that this genus needs to be separated into two distinct (although related) genera, *Sagittogethes* and *Teucriogethes* **gen. n.** (Figs 32-35). The latter genus, possessing the Western European *Teucriogethes obscurus* (Erichson, 1845) as the type species, includes less than ten species distributed between the Iberian Peninsula and North Africa westwards, and China and Japan eastwards (Table 4). All inclusive species appear to use members of the genus *Teucrium* L. (Lamiaceae: Ajugoideae) as larval host-plants (Table 4). Based on both morphological and molecular evidence, the new genus appears to represent the sister-group of *Thymogethes* Audisio & Cline, 2009 (Figs 32-34). The sister-group relationships of the true remaining *Sagittogethes* with other Lamiaceae-associated genera of Meligethinae remain uncertain, and require further analyses. Within the new genus, the relict and rare Western Mediterranean species *T. minutus* (C.N.F. Brisout de Barneville, 1863) occupies an isolated position within the clade (Figs 32-35).

More detailed morphological analyses, including additional imaginal and larval stage characters in conjunction with more diverse molecular data (mitochondrial and

nuclear markers), is needed from material of all thus far known *Teucriogethes* species and related genera, to more finely resolve phyletic relationships of this small Meligethine clade.

Acknowledgements – This research was partially supported by the Fundamental Research Funds for Chinese Central Universities (Z109021305) and by funds from the State Administration of Foreign Experts Affair for Recruitment Program of High-end Foreign Experts (Popular Republic of China). The senior author (M.L.) thanks the China Scholarship Council for financial support for her stay in Rome (November, 2016–December, 2017) in collaboration with coauthor P.A. This research was also partially supported by funds from the Sapienza University of Rome, Italy (2018). The authors thank their colleague Lech Borowiec (Wrocław, Poland) for kind permission to use his beautiful pictures of Meligethinae from the site *Iconographia Coleopterorum Poloniae* (<http://www.colpolon.biol.uni.wroc.pl/index.htm>) (Figs 1-2). The authors also thank Sirio Strika and Lorenzo Costantini (Rome, Italy) for SEM pictures (Figs. 30-31), and our colleague Davide Badano (Genoa, Italy) for assistance in cladistic analyses and useful comments on a first version of this article.

References

- Aljanabi S.M., Martinez I. 1997. Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Research*, 25: 4692–4693.
- Audisio P. 1993. *Coleoptera Nitidulidae - Kateretidae*. Fauna d'Italia, vol. 32, Calderini ed., Bologna, XVI + 971 pp.
- Audisio P., Cline A.R., De Biase A., Antonini G., Mancini E.,

- Trizzino M., Costantini L., Strika S., Lamanna F., Cerretti P. 2009b. Preliminary re-examination of genus-level taxonomy of the pollen beetle subfamily Meligethinae (Coleoptera: Nitidulidae). *Acta Entomologica Musei Nationalis Pragae*, 49 (2): 341–504.
- Audisio P., Cline A.R., Lamanna F., Trizzino M., Antonini G., Mancini E., De Biase A. 2009a. Revision of the Southern African Pollen Beetle Genus *Anthystrix* (Coleoptera: Nitidulidae: Meligethinae). *Annals of the Entomological Society of America*, 102 (6): 998–1012.
- Audisio P., Cline A.R., Lason A., Jelínek J., Sabatelli S., Serri S. 2017. New species and records of pollen and sap beetles for Iran (Coleoptera: Kateretidae, Nitidulidae). *Zootaxa*, 4216 (4): 369–383.
- Audisio P., Cline A.R., Mancini E., Trizzino M., Avgin S.S., De Biase A. 2011. Four new Palaearctic *Brassicogethes* (Coleoptera, Nitidulidae, Meligethinae), and phylogenetic inference on the *B. coracinus* group. *Rendiconti Lincei*, 22: 235–268. Doi:10.1007/s12210-011-0126-4
- Audisio P., Cline A.R., Solano E., Mancini E., Lamanna F., Antonini G., Trizzino M. 2014. A peculiar new genus and species of pollen-beetle (Coleoptera, Nitidulidae) from eastern Africa, with a molecular phylogeny of related Meligethinae. *Systematics and Biodiversity*, 12 (1): 77–91. Doi: 10.1080/14772000.2013.877539
- Audisio P., De Biase A., Antonini G. 2003. A new exceptional *Meligethes* of the *M. aeneus* species-group from Western Alps and an updated key to identification of *M. aeneus* and allied species (Coleoptera: Nitidulidae: Meligethinae). *Insect Systematics and Evolution*, 34: 121–130.
- Audisio P., De Biase A., Antonini G., Mancini E., Özbek H., Gultekin L. 2005. Redescription and natural history of *Meligethes longulus* Schilsky, 1894, and provisional revision of the *M. coracinus* species-complex (Coleoptera, Nitidulidae, Meligethinae). *Italian Journal of Zoology*, 72: 73–85.
- Audisio P., De Biase A., Trizzino M., Mancini E., Antonini G. 2009c. A new species of *Meligethes* (Coleoptera: Nitidulidae: Meligethinae) of the *M. lugubris* complex from Sardinia. *Zootaxa*, 2318: 386–393.
- Audisio P., Jelínek J. 1990. Tassonomia e distribuzione geografica di *Meligethes obscurus* Auct., con descrizione di una specie nuova (Coleoptera, Nitidulidae). *Fragmenta entomologica*, 22(1): 75–85.
- Audisio P., Mancini E., De Biase A. 2006. A new species of the pollen-beetle genus *Meligethes* (Coleoptera: Nitidulidae) of the *M. aeneus* group from Greece, with review of the *M. subaeneus* complex. *Zootaxa*, 1275: 43–60.
- Audisio P., Sabatelli S., Jelínek J. 2015. Revision of the pollen beetle genus *Meligethes* Stephens, 1830 (Coleoptera: Nitidulidae: Meligethinae). *Fragmenta entomologica*, 46 (2014): 19–112. Doi: 10.4081/fe.2014.71
- Brower A.V.Z. 1994. Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA Evolution. *Proceedings of the National Academy of Sciences*, 91: 6491–6495.
- De Biase A., Antonini G., Mancini E., Audisio P. 2003. Molecular taxonomy of two sympatric sibling species of the pollen-beetle genus *Meligethes* (Coleoptera: Nitidulidae). *Zootaxa*, 190: 1–16.
- De Biase A., Antonini G., Mancini E., Trizzino M., Cline A.R., Audisio P. 2012. Discordant patterns in the genetic, ecological, and morphological diversification of a recently radiated phytophagous beetle clade (Coleoptera: Nitidulidae: Meligethinae). *Rendiconti Lincei, Springer*, 23: 207–215. Doi: 10.1007/s12210-012-0174-4
- Drummond A.J., Suchard M.A., Xie D., Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, 29: 1969–1973. Doi: 10.1093/molbev/mss075
- Easton A.M. 1957a. The *Meligethes* of Japan (Coleoptera: Nitidulidae). *Transactions of the Royal Entomological Society of London*, 109: 395–420. Doi: 10.1111/j.1365-2311.1957.tb00332.x
- Easton A.M. 1957b. The *Meligethes* (Col., Nitidulidae) of Afghanistan. *Entomologist's Monthly Magazine*, 92: 385–401.
- Erichson W.F. 1845: [I., II. Lieferungen]. Pp. 1–320. In: *Naturgeschichte der Insecten Deutschlands. Erste Abtheilung. Coleoptera. Dritter Band. Nikolaische Buchhandlung, Berlin*, vii + 968 pp. [(III Lief.) pp. 321–480 issued in 1846, (VI Lief.) pp. 801–968 in 1848].
- Farrell B.D. 2001. Evolutionary assembly of the milkweed fauna: Cytochrome oxidase I and the age of *Tetraopes* beetles. *Molecular Phylogenetics and Evolution*, 18: 467–478.
- Folmer O., Black M., Hoeh W., Lutz R., Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3(5): 294–299.
- Goloboff P.A., Catalano S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32: 221–238.
- Hasegawa M., Iida Y., Yan, T.A., Takaiwa F., Iwabuchi M. 1985. Phylogenetic relationships among eukaryotic kingdoms inferred from ribosomal RNA sequences. *Journal of Molecular Evolution*, 22(1): 32–38. Doi: 10.1007/BF02105802
- Huelsenbeck J.P., Ronquist F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17: 754–755.
- Jamzad Z. 2013. A survey of Lamiaceae in the flora of Iran. *Rostaniha*, 14(1): 59–67.
- Jelínek J. 1982. New and little known species of the genus *Meligethes* from Turkey and neighbouring countries (Coleoptera, Nitidulidae). *Türkiye Bitki Koruma Dergisi*, 5 [1981]: 201–214.
- Jelínek J., Audisio P. 2007. Family Nitidulidae. Pp. 459–491. In: Löbl I., Smetana A. (eds): *Catalogue of Palaearctic Coleoptera. Vol. 4: Elateroidea – Derontoidea – Bostrichoidea – Lymexyloidea – Cleroidea – Cucujoidea*. Apollo Books, Stenstrup, 935 pp.
- Jelínek J., Spornraft K. 1979. Die westpaläarktischen Arten der *umbrosus*-Gruppe der Gattung *Meligethes* Steph. *Mitteilungen der Münchner Entomologischen Gesellschaft*, 68: 1–11.
- Kearse M., Moir R., Wilson A., Stones-Havas S., Cheung M., Sturrock S., Buxton S., Cooper A., Markowitz S., Duran C., Thierer T., Ashton B., Meintjes P., Drummond A. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28 (12): 1647–1649.
- Kirejtshuk A.G. 1978. New species of the genus *Meligethes* Stephens (Coleoptera, Nitidulidae) from the USSR and review of the group of species related to *Meligethes umbrosus* Sturm. *Entomologicheskoye Obozrenie*, 57: 578–595 [in Russian].
- Kirejtshuk A.G. 1979. Novye vidy zhukov-blestyanok podsem. Meligethinae (Coleoptera, Nitidulidae) iz Aziatskoi chasti SSSR i sopredel'nykh territorii. [New species of coleopterous beetles of the subfamily Meligethinae (Coleoptera, Nitidulidae) from Asiatic regions of SSSR and adjacent territories]. *Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR*, 88: 50–68 [in Russian].
- Kirejtshuk A.G. 1992. 59, 61. Sem. Nitidulidae - Blestyanki. [Family Nitidulidae - Sap beetles.]. In: Ler P.A. (Ed.), *Note XXIX. Nauka, St. Petersburg*, pp. 114–210.
- Lason A., Gahari H. 2013. A checklist of the Kateretidae and Nitidulidae of Iran (Coleoptera: Cucujoidea). *Zootaxa*, 3746: 101–122.

- Li X-w., Hedge I.C. 1994. Flora of China—Lamiaceae. 17: 50–299.
- Liu M., Huang M., Cline A.R., Audisio P. 2018. New and poorly known *Meligethes* Stephens from China, with binomical data on some species (Coleoptera: Nitidulidae: Meligethinae). *Zootaxa*, 4392 (3): 546–566. Doi: 10.11646/zootaxa.4392.3.6
- Liu M., Huang M., Cline A.R., Sabatelli S., Audisio P. 2017. A new species of *Meligethes* Stephens from China and additional data on members of the *M. chinensis* species-complex (Coleoptera: Nitidulidae, Meligethinae). *Fragmenta entomologica*, 49 (1): 79–84.
- Liu M., Sabatelli S., Mancini E., Trizzino M., Huang M., Cline A.R., Audisio P. 2019. Rediscovery of *Brassicogethes salvan* (Coleoptera: Nitidulidae, Meligethinae) in the southwestern Alps. *Insect Conservation and Diversity*, 12: 80–87. Doi: 10.1111/icad.12317
- Liu M., Yang X.-K., Huang M., Jelinek J., Audisio P. 2016. Four new species of *Meligethes* from China and additional data on other species of the genus (Coleoptera: Nitidulidae: Meligethinae). *Zootaxa*, 4121 (2): 101–116.
- Maddison W.P., Maddison D.R. 2018. Mesquite: A Modular System for Evolutionary Analysis, Version 3.51 Available at <http://mesquiteproject.org> [accessed 12 June 2018].
- Mancini M., De Biase A., Cline A.R., Antonini G., Trizzino M., Clayhills T., Sabatelli S., Cerretti P., Audisio P. 2016. Morphological, genetic and host-plant diversification in pollen-beetles of the *Brassicogethes coracinus* group (Coleoptera: Nitidulidae: Meligethinae). *Rendiconti Lincei, Springer*, 27 (2): 321–339. Doi: 10.1007/s12210-015-0482-6
- Minh B.Q., Nguyen M.A.T., von Haeseler A. 2013. Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30 (5): 1188–1195.
- Nguyen L.-T., Schmidt H.A., Haeseler A., Minh B.Q. 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32: 268–274.
- Papadopoulou A., Anastasiou I., Vogler A.P. 2010. Revisiting the Insect Mitochondrial Molecular Clock: The Mid-Aegean Trench Calibration. *Molecular Biology and Evolution*, 27: 1659–1672.
- Pons J., Ribera I., Bertranpetit J., Balke M. 2010. Nucleotide substitution rates for the full set of mitochondrial protein-coding genes in Coleoptera. *Molecular Phylogenetics and Evolution*, 56: 796–807.
- Posada D. 2008. jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution*, 25: 1253–1256.
- Rambaut A., Suchard M., Xie D., Drummond A. 2014. Tracer v1. 6. Retrieved from <http://tree.bio.ed.ac.uk/software/tracer>.
- Rodríguez F., Oliver J.L., Marín A., Medina J.R. 1990. The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology*, 142: 485–501.
- Sabatelli S., Liu M., Badano D., Mancini E., Trizzino M., Cline A.R., Endrestøl A., Huang M., Audisio P. 2020. Molecular phylogeny and host-plant use (Lamiaceae) of the *Thymogethes* pollen beetles (Coleoptera). *Zoologica Scripta*, 49(1): 28–46.
- Simon C., Frati F., Beckenbach A., Crespi B., Liu H., Flook P. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87(6): 651–701.
- Tamura K., Stecher G., Peterson D., Filipowski A., Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729.
- Trifinopoulos J., Nguyen L.T., von Haeseler A., Minh B.Q. 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, 44 (W1): W232–W235.
- Trizzino M., Audisio P., Antonini G., De Biase A., Mancini E. 2009. Comparative analysis of sequences and secondary structures of the rRNA internal transcribed spacer 2 (ITS2) in pollen-beetles of the subfamily Meligethinae (Coleoptera, Nitidulidae): potential use of slippage-derived sequences in molecular systematics. *Molecular Phylogenetics and Evolution*, 51 (2): 215–226. Doi: 10.1016/j.ympev.2008.11.004