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Original Citation:

Availability:

This version is available at: 11577/3219150 since: 2018-03-05T17:28:15Z

Publisher:

ACADEMIC PRESS LTD ELSEVIER SCIENCE LTD, 24-28 OVAL RD, LONDON, ENGLAND, NW1 7DX

Published version:

DOI: 10.1111/cla.12181

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A total evidence phylogeny for the processionary moths of the genus *Thaumetopoea*
(Lepidoptera: Notodontidae: Thaumetopoeinae)

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Short running title: *Thaumetopoea* total evidence phylogeny

24 **Abstract**

25

26 Processionary moths belong to a group of about 100 species well known for their social behaviour
27 and their urticating systems. The genus *Thaumetopoea* s. lat. includes about 15 species and has been
28 divided into three genera (*Helianthocampa*, *Thaumetopoea* s. str., and *Traumatocampa*) in the last
29 revision, based on key morphological features of the adults and on the host plants of the larvae. We
30 performed a total evidence approach to resolve the phylogeny of the genus *Thaumetopoea* s. lat.,
31 analysing all valid taxa included in this group, plus a broad array of close relatives. *Thaumetopoea*
32 resulted monophyletic and supported by several apomorphies. Further subclades corroborated by
33 synapomorphies were identified. Our phylogeny suggests that *Thaumetopoea* must be regarded as a
34 single genus. The mapping of key life history traits on the total evidence tree allowed to sketch a
35 plausible identikit of the *Thaumetopoea* ancestor and to track the evolution of the genus. The ancestor
36 originated in the eastern Mediterranean area, and used broadleaves as host plants. Subsequently, a
37 switch to conifers occurred, just once, in a large subclade. The ancestor pupated in the soil, like
38 several current species, but in few taxa this trait was lost, together with the related morphological
39 adaptations.

40

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Introduction

Processionary moths belong to a group of insect herbivores well known since the ancient Greek and Roman times for their association with the host plants, their special behaviour, and their urticating and envenomation power (Roques and Battisti, 2015). All processionary moths are now included in Thaumetopoeinae, a clade of Notodontidae (Lepidoptera) (Miller, 1991; Zahiri *et al.*, 2011, 2013). In the past, this group was treated at family rank with three subfamilies: Thaumetopoeinae (mainly Palaearctic), Anaphinae (Afrotropical) and Epicominae (Australasian) (Kiriakoff, 1970). However, this view is now superseded by results obtained from morphological and molecular based phylogenetic analyses (Miller, 1991; Zahiri *et al.*, 2011, 2013). At present, Thaumetopoeinae account for 106 valid species split in 20 genera (Schintlmeister, 2013).

The processionary moths owe their name to the typical processions made by the larvae when they move in lines or groups to forage on trees or to pupation sites. A few species of processionary moths are plant pests and cause outbreaks on trees and shrubs of both broadleaves and coniferous trees and shrubs in Africa (Wagner and Cobbinah, 2013), Asia (Rahman and Chaudhry, 1992), Australia (Floater and Zalucki, 2000), and Europe (Jacquet *et al.*, 2012). All species are protected against vertebrate predators by urticating setae either as larvae or adults (Battisti *et al.*, 2017), and these setae may threaten animal and human health (Battisti *et al.*, 2011). In spite of these problems, in Africa some species are farmed for silk production or used as human food (van Huis, 2003; Schabel, 2006). Most information on life history and taxonomy concerning Thaumetopoeinae relates to the genus *Thaumetopoea*. Hübner ([1820], in 1816-[1826]) erected *Thaumetopoea* to include two species, namely *Phalaena processionea* Linnaeus, 1758, the type species associated with oaks in central and southern Europe, and *Bombyx pityocampa* [Denis & Schiffermüller], 1775, associated with pine in southern Europe and the Mediterranean. More taxa were added later and currently fifteen species are included in this genus (Table 1) (Schintlmeister, 2013). The Palaearctic species of *Thaumetopoea* have been reviewed by Agenjo (1941) and de Freina and Witt (1985, 1987). Agenjo (1941) maintained the split of the genus into the two subgenera *Thaumetopoea* and *Traumatocampa* done by Wallengren (1871) according to the absence/presence of a toothed protuberance on the frontal part of the head (crest) and of a foretibia claw (spine) in the adults (*sensu* Hogue, 1963) (Table 2), whereas de Freina and Witt (1985) raised *Traumatocampa* Wallengren, 1871 to the status of distinct genus. Furthermore, they erected the new genus *Helianthocampa* to accommodate only *Bombyx herculeana* Rambur, 1840 a species feeding on another group of host plants, which was previously included in *Traumatocampa* (Agenjo, 1941) (Table 2). Both revisions did not use a phylogenetic approach and the suggested taxonomic changes were not based on rigorous analyses corroborating the monophyly of their genera. In spite of that, the three genera were retained as valid in the most recent catalogue

105 of Notodontidae (Schintlmeister, 2013). However, a recent phylogeny based on nucleotide sequence
106 data on a subset of species indicated that the split of *Thaumatopoea* in three distinct genera is
107 untenable, and provided evidence for inclusion of all the species in a single genus *Thaumatopoea*
108 *s.lat.* until new revision (Simonato *et al.*, 2013).

109 We consider here all species of *Thaumatopoea s. lat.* occurring in the Palaearctic and Afrotropical
110 regions (Table 1). They extend altogether over an area ranging from the Atlantic coast of the Iberian
111 Peninsula to the Indian region of Jammu and Kashmir and from Scandinavia to southern Africa,
112 where the species are associated with very diverse habitats and host plants. Our analysis included all
113 taxa that were variously granted with independent status according to revisions and recent papers, for
114 a total of 21 taxa. As outgroups we selected 16 species of other Thaumetopoeinae, encompassing a
115 representative sample of the taxonomic diversity of the subfamily (Table 1, and Table S1)
116 (Schintlmeister, 2013). Thus the final data set contained 37 taxa included in seven genera. We
117 analysed morphological and molecular data separately and in combination. The major aim of our
118 research was to produce a robust phylogeny of *Thaumatopoea s. lat.*, to lay out a framework for a
119 thorough taxonomic revision of the genus. In addition, we aimed at tracking the origin of key life
120 history traits of the group to draw a plausible profile of the common ancestor of processionary moths
121 and to mark the main changes that led to the diversity currently shown by this group.

122

123 **Materials and methods**

124

125 *Taxonomic sampling*

126 The identification at species level of the specimens was done according to the dichotomous keys
127 provided by Agenjo (1941) and Kiriakoff (1970). When possible, the specimens were compared with
128 the types of various species. All the 15 species of *Thaumetopoea s. lat.* listed by Schintlmeister (2013)
129 were analysed. The very recently described *Thaumetopoea loxostigma* Hacker, 2016 could not be
130 included as the only extant specimen, viz. the holotype, was not available. According to the original
131 description, *T. loxostigma* is closely related to the *Thaumetopoea apologetica* – *Thaumetopoea*
132 *jordana* group (Hacker, 2016).

133 Five subspecies other than the nominotypical are currently recognised within *Thaumetopoea s. lat.*
134 (Schintlmeister, 2013), namely *T. apologetica abyssinica*, *T. herculeana judaea*, *T. processionea*
135 *pseudosolitaria*, *T. solitaria iranica*, and *T. pityocampa orana*. These taxa were included in our
136 analysis because they show peculiar habitus and/or separate geographical distributions, as well as
137 differences in habitat preference from the nominotypical subspecies (Kiriakoff, 1970). Finally, we
138 included in the analysis the informal taxon named by Kerdelhué *et al.* (2009) as *Thaumetopoea*
139 *pityocampa* ENA (Eastern-North African clade) as it markedly differs from nominal *T. pityocampa*
140 on genetic grounds. Further molecular data, provided by Simonato *et al.* (2013), support the view that
141 *T. pityocampa* ENA actually represents a distinct taxon.

142 The present study is based on the analysis of specimens deposited in the Department of Agronomy,
143 Food, Natural resources, Animals and Environment of the University of Padua; Museo Civico di
144 Zoologia of Rome; Museo di Zoologia - University of Rome ‘Sapienza’; Natural History Museum,
145 London; private collection of A. Schintlmeister (Dresden); Royal Belgian Institute of Natural
146 Sciences of Brussels; Royal Museum of Central Africa of Tervuren; The Bavarian State Collection
147 of Zoology of Munich and Witt Museum of Munich. The complete list of specimens analysed in this
148 paper is provided in Table S1.

149

150 *Specimens dissection and recording of morphological traits*

151 The abdomen was removed from the specimens listed in Table S1 and processed according to the
152 non-destructive dissection protocol described below, in order to prepare genitalia for successive
153 examination. The abdomens were digested overnight in an incubator kept at 37 °C, immersed, within
154 Eppendorf vial, in 180 µl of ATL buffer and 20 µl Proteinase K and mix. Before and after the
155 incubation the abdomens were vortexed at 350 rpm for 15’. Successively, the abdomen and the
156 solution were processed separately. The abdomens were dissected following the protocol given by
157 Robinson (1976). All forceps and scissors were sterilized before cutting each abdomen. Pipet tips

158 were discarded and changed every time. The genitalia and the abdomens were stained in saturated
159 chlorazol black (75% ethanol) for 30", soaked in absolute ethanol and eventually mounted on slides
160 with Euparal medium. All slides were labelled according to Robinson (1976). Legs and palps were
161 macerated in 10% KOH solution at 50°C for 5-10 minutes, cleaned in water, then stained and mounted
162 on slides as above.

163 All morphological observations were taken from pinned specimens of adult moths. Pictures of the
164 morphological characters were taken with a Canon Eos (600D) and a Lumix camera (DMC F200)
165 equipped with additional lens (DMW-LC55) using a led light chamber (Figs 1-3 and S3). Composite
166 focus-stacking images were produced from multiple images captured using AxioCam (MRc5),
167 software Axiovision SE64, (v4.9.1) mounted on a Lumar.v12 Zeiss (Carl Zeiss Microscopy GmbH;
168 Jena, Germany) stereomicroscope, and processed with Photoshop CS6 (v13.0) (Adobe System
169 Incorporated, San Jose, CA, USA). CorelDraw X5 (v15.1) (Corel Corporation, Ottawa, ON, Canada)
170 was used to create labels and drawings. Traits analysed in the present paper are listed in Figs 2, 3 and
171 S3.

172

173 *Molecular methods*

174 Parallel to the abdomen dissection of single specimens, the total DNA was extracted with QIAGEN©
175 DNeasy blood and tissue kit (Knölke *et al.*, 2005). This procedure did not provide always DNA
176 samples of good quality because of the very different level of tissue conservation of the studied
177 specimens. Thus, molecular analysis was restricted to the best preserved (for molecular purposes)
178 samples.

179 The DNA extracted during dissection of the genitalia was amplified with universal primers
180 (LCO1490/HCO2198) for the barcode portion of the mitochondrial gene *cox1* (Folmer *et al.*, 1994).
181 Extracts were concentrated with Amicon® Ultra-0.5 Centrifugal Filter Devices, in order to bring all
182 samples to a minimum detectable concentration for the amplification. Each Polymerase Chain
183 Reaction (PCR) contained: 2 µl DNA template ($\approx 15\text{ng}/\mu\text{l}$), 11.7 µl molecular biology grade water, 4
184 µl buffer (25 mM), 1.4 µl MgCl_2 (5X), 0.2 µl dNTPs mix (2 mM), 0.25 µl forward primer (10 µM),
185 0.25 µl reverse primer (10 µM), and 0.2 µl GoTaq G2 DNA Polymerase (5 U/µl) (Promega, Fitchburg,
186 WI, USA) in a total volume of 20 µl. The PCRs were performed on a Euroclone thermocycler under
187 the following conditions: (1) preheated lid at 105°C for 5 min; (2) 30 cycles: 94°C for 30 s, $48 \pm 3^\circ\text{C}$
188 for 45 s, and 72 °C for 45 s; (3) final extension at 72 °C for 5 min. The PCR products were visualised
189 by 1.5% agarose gel electrophoresis. A DNA template to negative and positive control reaction was
190 included in all experiments to test for contamination. PCR products were not obtained for some
191 species due to the poor quality of the extracted DNA.

192 PCR products were purified with ExoSap enzymes (ExoSAP-IT® - USB corporation) and sequenced
193 at the BMR Genomics company (Padua, Italy). The quality of the chromatograms was assessed with
194 the Chromas Lite program (<http://technelysium.com.au/wp/chromas/>). The final consensus sequence,
195 spanning about 650 base pairs, was assembled using the DNASTAR software (Lasergene® Madison,
196 WI).

197

198 *The data matrices*

199 One hundred and sixty-five morphological traits were studied in adult moths, divided as follows: head
200 (21), thorax (6), abdomen (9), male and female forewing (56), male and female hindwing (14), male
201 genitalia (59) (Appendix 1). No female genitalia data were included in the present analysis. The hard
202 decision to skip coding characters from the female genitalia was based on the circumstance that a
203 quick screening over representatives of the principal assemblages of *Thaumetopoea* (viz. *T.*
204 *proccessionea* and "*Traumatocampa*" *pityocampa*) essentially revealed differences in terms of relative
205 sizes of soft structures or in the degree of sclerotisation of pieces, and did not allow to fix definite
206 landmarks or boundaries. Consultation with two notodontid specialists (A. Schintlmeister and T.J.
207 Witt, pers. comm.) confirmed this view and pointed out that traits identified by Agenjo (1941) were
208 unreliable and largely a matter of artefact. It is also worth noting that Miller (1991), in his seminal
209 phylogenetic reconstruction of the Notodontidae, was able to code only 11 female genital characters
210 out of the whole family, whereas 23 were distinguished in the male ones. Further research, however,
211 is being planned to check whether or not the female genitalia may increase resolution of the
212 Thaumetopoeinae phylogeny, at least at the level of the most basal branches of the subfamily, which
213 at this stage were not the major focus of our study.

214 The traits included in the morphological matrix (hereafter named Thau.morph) were mostly those
215 used to identify genera and species of Thaumetopoeinae (Agenjo, 1941; Miller, 1991). The traits were
216 coded following the guidelines provided by Strong and Lipscomb (1999) and Sereno (2007). Thus,
217 'traits' and the 'variable of the traits' were coded as different characters, in order to split neomorphic
218 from transformational characters, providing a hierarchical order, and maintain the highest
219 phylogenetic signal (Lee and Bryant, 1999).

220 Morphological wings terminology mainly follows Heath and Emmet (1979) and Heppner (2008). The
221 genitalia terminology follows Berio (1985) and Steinmann and Zombori (1999). For other
222 morphological terminology refer to Fig.1.

223 The morphological matrix was built in Mesquite v3.04 (Maddison and Maddison, 2015) and exported
224 as nexus files for subsequent phylogenetic analyses.

225 The newly determined sequences were combined with previously available mitochondrial molecular
226 data (Simonato *et al.*, 2013) in order to create a single multigene data set. The alignment of the *cox1*

sequences was performed using the MAFFT program implemented in the pipeline TranslatorX (Abascal *et al.*, 2010). This alignment was concatenated with the mitochondrial sequences of Simonato *et al.* (2013) to produce a single multiple alignment (hereafter named Thau.DNA) spanning 6348 positions where unavailable genes were treated as missing data. The list of genes included in Thau.DNA is provided in Table S2.

A total evidence data matrix (hereafter named Thau.tot.comp) was produced by combining morphological and DNA data. The Thau.tot.comp set includes all 37 taxa analysed in this paper. In Thau.tot.comp combined morphological and molecular data are available for 18 species, only morphological traits are present for 18 taxa, and for *T. pityocampa* ENA only molecular data exist (Table S2). Unavailable characters were coded as missing data. Finally, a second total evidence data matrix (hereafter named Thau.tot.red) was created containing only the 18 taxa for which both DNA and morphological data were available.

Phylogenetic analysis

Parsimony analyses (MP) (Fig. S7) were performed with TNT software (v1.5-beta) (Goloboff *et al.*, 2008). The Thau.morph, Thau.DNA, Thau.tot.comp and Thau.tot.red sets were analysed according to the strategy described below. The ‘traditional search’ algorithm was activated with the following settings: General RAM of 1.0 Gbytes, memory set to hold 1,000,000 trees, setting 1,000 replicates with tree bisection-reconnection (Goloboff, 1999) branch swapping and saving 1,000 trees per replicate. Zero-length branches were collapsed. To evaluate clade support, Bremer support values (Bremer, 1994) were calculated in TNT from 10,000 trees up to 25 steps longer than the most parsimonious trees obtained from ‘traditional search’ using ‘trees from RAM’. A Bootstrap resampling (bt) (Felsenstein, 1985) under equal weights was carried out with ‘traditional search’ producing 10,000 replicates each of 1,000 random taxa addition; sub-replicates applying TBR, branch swapping and saving 1,000 trees per replication; resampling percentiles were calculated as frequency differences. Consistency index and retention index were calculated in Mesquite v3.04 (Maddison and Maddison, 2015).

The trait changes were mapped in WinClada software (Nixon, 2002) using the following settings: (1) optimization with unambiguous changes only.

Bayesian analysis (BI) were performed using MrBayes (x64, 3.2.5) (Ronquist *et al.*, 2012). The Thau.morph dataset was analysed under Mk1 model (Lewis, 2001) with the following settings: rates= gamma, and coding= variable. The GTR+I+G model was applied to Thau.DNA, and a combination of Mk1 model and GTR+I+G model was used for Thau.tot.comp and Thau.tot.red. Four Markov Chain Monte Carlo (MCMC) chains were run for 10 million generations and sampled every 1,000th

261 generation, with the first 25% of trees discarded as burn-in. Stationarity was considered to be reached
 262 when the average standard deviation of split frequencies was less than 0.005.
 263 Maximum likelihood analyses were done using the Iqtree v1.3.13 software (Nguyen *et al.*, 2015).
 264 Analyses on Thau.morph dataset were performed with Ordered and MK models (both
 265 +FQ+ASC+G4). The GTR+I+G model was applied to Thau.DNA. Finally, combinations of Ordered
 266 and MK models plus GTR+I+G were applied to Thau.tot.comp and Thau.tot.red sets.
 267 In every analysis, 50 independent tree searches were performed to minimize the possibility to be
 268 entrapped in a local minimum. Ultrafast Bootstrap support (Minh *et al.*, 2013) was calculated for
 269 every topology generated with Iqtree v1.3.13 program. In all analyses 10,000 replicates were
 270 performed.
 271 The following abbreviations are used in the Results section to describe statistical support to tree
 272 topologies: bt, standard bootstrap support, UFB= UltraFastBootstrap support, pp= posterior
 273 probability, and Bvs= Bremer value support.
 274 To evaluate alternative phylogenetic hypotheses, alternative topology tests were performed according
 275 to the Weighted Shimodaira and Hasegawa test (WSH) (Shimodaira and Hasegawa, 1999) and the
 276 Expected Likelihood Weights (ELW) test (Strimmer and Rambaut, 2002). The tests were done with
 277 the Iqtree v1.3.13 software (Nguyen *et al.*, 2015).
 278
 279 *Tracking the evolution of a selection of characters on the reference tree*
 280 The MP tree obtained from Thau.tot.comp set was used as reference topology to track the evolution
 281 of six selected characters of genus *Thaumatococcus*.
 282 Firstly, the evolutionary history of five larval morphological, ecological and biological traits (see the
 283 Traits description appendix for the coding strategy) was investigated. These traits are: (1) presence
 284 of urticating setae on larva; (2) pupation site; (3) larval seasonal feeding activity; (4) host plant group;
 285 (5) host plant family (Appendix 1). The tracking of the transformation pathways was performed with
 286 Mesquite 3.04 (Maddison and Maddison, 2015). The character history was traced by the ‘Ancestral
 287 reconstruction’ option based both on maximum parsimony (unordered characters) and the maximum
 288 likelihood method of Lewis (Lewis, 2001).
 289 The sixth trait investigated was the reconstruction of the biogeographical patterns of the
 290 *Thaumatococcus* species. This analysis was performed with the Statistical Dispersal-Vicariance (S-
 291 DIVA) (Yu *et al.*, 2010) (see Results, Fig. 6).
 292

Results

Morphology-based phylogenetic analysis

The MP tree (Length = 534; CI = 0.537; RI = 0.797) obtained from Thau.morph set is provided in Fig. 4 (see Fig. S4 for the outgroups). Nodes are supported by a variable number of apomorphies and homoplasious changes (Fig. 4; Table 3). The genus *Thaumetopoea* is monophyletic with strong statistical corroboration. The BI and ML topologies are mostly congruent with the MP tree with two noteworthy exceptions listed below.

The arrangement of the species belonging to clade O is different in the BI and ML (ORDERED+FQ+ASC+G4 evolutionary model) trees (Fig. 4; Fig. S5 and S7). In this alternative topology *T. bonjeani* and *T. pinivora* are sister species (clade W), a relationship that receives a very robust statistical support. Moreover, *T. libanotica* is sister taxon of clade W with high, even if not conclusive ($p < 0.95$), statistical corroboration (clade V; BI-pp = 0.93) (Fig. S5). *Thaumetopoea herculeana* is sister taxon of the J clade in the ML analysis based on the MK+FQ+ASC+G4 evolutionary model, but this relationship does not receive statistical corroboration (clade X) (Fig. 4; Fig. S6).

Finally, in all analyses based on morphology the current concept of *T. processionea* turned out as non-monophyletic, as the taxon *T. processionea pseudosolitaria* was recovered as sister to *T. solitaria*, although with no apomorphies supporting this relationship (Fig. 4; Figs. S5-S7).

The test performed on alternative phylogenetic hypotheses provided the results described below. The BI and ML trees topologies obtained from Thau.morph dataset are not rejected (ELW and WSH $p > 0.14$). Their parsimony scores (BI, Length = 543, CI = 0.528, RI = 0.790) (ML, Length = 541, CI = 0.530, RI = 0.791) are comparable with those of MP tree. The cladogram implying the monophyly of *T. processionea* species is not rejected (ELW and WSH > 0.12). This alternative tree exhibits parsimony scores (Length = 535, CI = 0.536, RI = 0.796) almost identical to those of the MP tree (see above).

Conversely, the placement of *T. herculeana* as sister taxon of clade B of Fig. 4 is rejected by ELW test ($p = 0.0306$) but not by WSH ($p = 0.3205$). The parsimony scores for this topology are worse than previous ones (Length = 544, CI = 0.528, RI = 0.789). This latter phylogenetic arrangement was tested because the placement of *T. herculeana* within *Thaumetopoea* is controversial in different analyses (see below).

328 *DNA-based phylogenetic analysis*

329 Availability of molecular data was restricted to 11 species of *Thaumetopoea* (Table S2), due to the
330 failure to obtain DNA for some taxa. The MP cladogram (Tree Length = 4491, CI = 0.492, RI =
331 0.492) obtained from Thau.DNA set (Fig. S8) shows phylogenetic relationships among
332 *Thaumetopoea* species, which are almost completely mirrored by the BI/ML tree (Fig. S9). This latter
333 topology identifies a statistically supported (1.00/95%) sister taxon relationship between *T.*
334 *apologetica* and *T. dhofarensis* not observed in the MP tree. The general arrangement of
335 *Thaumetopoea* species relationships in DNA trees broadly agrees with topologies obtained from
336 Thau.morph set (for complete details see Figs. S8-S9). However, the position of *T. herculeana* differs
337 from that obtained from Thau.morph dataset (see node L of Fig 4). In all the DNA-based trees *T.*
338 *herculeana* belongs to a very well supported clade, which contains also *T. solitaria* and *T.*
339 *processionea*. In particular, *T. herculeana* reveals a sister species relationship with *T. processionea*
340 with good statistical corroboration (Figs. S8-S9).

341 The BI/ML tree is not rejected by alternative topology tests (WSH, $p = 0.9868$; ELW, $p = 0.8529$).
342 The parsimony scores are Length = 4490, CI = 0.622 and RI = 0.492. The alternative topology
343 implying the placement of *T. herculeana* as recovered from Thau.morph set (Fig. 4) is rejected by
344 both ELW and WSH tests ($p < 0.0001$). MP scores for this tree (Tree Length = 4634, CI = 0.603, RI
345 = 0.449) are also markedly worse than the MP tree for what concerns the tree length.

346

347 *Total evidence phylogenetic analysis*

348 The MP tree obtained from Thau.tot.comp is shown in Fig. 5 (Tree Length = 5046, CI = 0.611, RI =
349 0.569) (see Fig. S10 for outgroups). The ML and BI trees obtained from the same data set are identical
350 (Fig. S11). Their topology differs from MP cladogram (Figs.5; Fig.S11) by the placement of *T.*
351 *jordana* and *T. dhofarensis*. These species are sister in the MP cladogram without bt and Bremer
352 support (clade J). Conversely, the alternative BI/ML arrangement receives ML-UFB support (clade
353 U) (Figs. 5 and S11). The vast majority of MP tree nodes receives strong statistical support and are
354 supported by apomorphies and/or homoplasious changes (Fig. 5). Therefore, both the genus
355 *Thaumetopoea* and most of its subclades receive statistical corroboration, but the placement of *T.*
356 *herculeana* is different from that observed in Fig. 4. Here this moth is sister to *T. processionea* and
357 this relationship receives very robust statistical support. Furthermore, both subspecies of the latter
358 cluster together to form a monophyletic group with strong statistical corroboration.

359 The analyses performed on Thau.tot.red, the total evidence data set without missing data, provide
360 topologies fully consistent with results obtained from Thau.tot.comp and are not detailed here any
361 further (see Figs. S12-S13).

362 The BI/ML tree obtained from Thau.tot.comp is not rejected by the topology statistical tests (ELW,
363 $p = 0.406$; and WSH, $p = 0.701$). The cladogram implying the placement of *T. herculeana* as sister
364 taxon of clade O of Fig. 5, which mirrors the placement of this species in the Thau.morph analysis
365 (clade L, Fig. 4), is fully rejected by both ELW and WSH tests ($p < 0.0001$).

366

367 *The evolution of life history traits of Thaumetopoea*

368 The evolutionary pathways of six life history traits were tracked along the MP tree obtained from
369 Thau.tot.comp (Fig. 5). The results of this analysis are summarized in Fig. 6 (see Figs. S14-S15 for
370 details). The inspection of Fig. 6 allows to outline some features that could have characterized the
371 common ancestor of current *Thaumetopoea* moths (clade A). According to Fig. 6, urticating setae
372 already characterized the larval stage of the ancestor of *Thaumetopoea*, which was active in summer,
373 and used angiosperms as host plants. However, it is unclear which group of angiosperms was the host.
374 Our reconstruction also suggests that the shift from angiosperms to gymnosperms as host plants
375 occurred only once (clade K). Pupation occurred preferably in soil. The ancestral area of the genus
376 was likely the Palearctic Region and successive colonization of the Afrotropics occurred once/twice
377 in *T. dhofarensis* and *T. apologetica*. Finally, the shift of the larval feeding from summer to winter
378 seems to have occurred in the common ancestor of clade L, and independently in *T. jordana*. The
379 reconstruction for the ancestral state of larval feeding activity at nodes G and K is ambiguously
380 resolved by both MP and ML methods. Thus it could be argued that the shift from summer to winter
381 occurred at node G (slightly preferred by MK1 ML evolutionary model) and successively a secondary
382 reversion to summer activity happened in most of the species of clade O. By considering the global
383 distribution of this character among *Thaumetopoea* species and the effect due to missing data on the
384 reconstruction, this latter interpretation is not very probable in our view.

385

386 Discussion

387

388 *Taxonomic inconsistencies*

389 The monophyly of *Thaumetopoea s. lat.* (clade A, Figs 4-5) is strongly supported in all our analyses,
390 thus corroborating previous studies based on a limited number of taxa (cf. Simonato *et al.*, 2013 and
391 references therein). The phylogenetic relationships within the genus are well resolved and generally
392 consistent with the available classification schemes (Agenjo, 1941; Kiriakoff, 1970), albeit with some
393 important exceptions. All our analyses, based on the combined dataset, identify a clade B (Fig. 5)
394 including the species traditionally assigned to *Thaumetopoea s. str.* (i.e., *T. processionea* and *T.*
395 *solitaria*), with the addition of *T. herculeana*. Thus, *Thaumetopoea s. str.* is retrieved as paraphyletic.
396 The remaining species of *Thaumetopoea* (clade G), which share a crested frons and a spine on
397 foretibia, form a group corresponding to the (sub)genus *Traumatocampa* (Agenjo, 1941) (Tab. 2.).
398 *Thaumetopoea herculeana* is quite mobile across our phylogenetic reconstructions, depending upon
399 the dataset used. This mirrors its variable taxonomic position, as it has been assigned either to
400 *Traumatocampa* due to the possession of a crested frons and the spine on foretibia (Agenjo, 1941; de
401 Freina and Witt, 1985, 1987) (see also Tab. 2.), or to its own, monotypic genus *Helianthocampa*
402 based upon larval host plant and adult morphology (de Freina and Witt, 1985). However, removing
403 *T. herculeana* from *Traumatocampa* would make this no longer monophyletic on morphological
404 grounds (see above Fig. 4).

405

406 *Circumscribing Thaumetopoea, Traumatocampa, and Helianthocampa: where should the tree be cut?*

407 The simultaneous presence of frontal crest and foretibia spine supports the monophyly of
408 *Traumatocampa sensu* Agenjo (i.e., clade E of Fig. 4) in our morphology-based analysis
409 (Supplementary material Figs. S4-S7). Frontal crest and foretibia spine have a clear adaptive
410 significance as these species spend the pupal stage deep into the soil (usually between 5 and 20 cm)
411 (Battisti *et al.*, 2015), and newly emerged adults use such anatomical structures to break through to
412 the surface (Démolin, 1969). In contrast, processionary moths that do not have frontal crest and
413 foretibia spine pupate either inside the tent (*T. processionea*) or in the litter (*T. solitaria*), but never
414 deep into the soil.

415 In contrast to morphology, both molecular and combined datasets recover *T. herculeana* as nested
416 within *Thaumetopoea s. str.* (clade B, Fig. 5), suggesting that the phylogenetic reconstruction is
417 influenced by a strong molecular signal. It must be noted here that for several taxa the DNA sequences
418 are represented solely by the barcoding portion of *coxI* gene (i.e. about 650 base pairs).

419 In the present paper we analysed only mitochondrial genes. Thus it could be argued that the DNA-
420 based placement of *T. herculeana* is biased by the origin of the selected markers and does not

421 represent a balanced molecular view. However, the same placement was obtained by Simonato *et al.*
 422 (2013), who worked on a DNA multi-genes alignment encompassing both mitochondrial and nuclear
 423 markers. Particularly important for our discussion, the positioning of *T. herculeana* (Fig. 5) was
 424 recovered also from a data set containing only the nuclear genes: *wingless*, *elongation-factor alpha*,
 425 and *photolyase* (Simonato *et al.*, 2013). This latter result strongly contradicts the hypothesis of the
 426 incorrect placement *T. herculeana* due to the mitochondrial origin of molecular markers. Thus,
 427 despite the limited gene sampling, compared to the 165 morphological traits, it appears that molecules
 428 alone, or in combination with morphology, support a close relationship between *T. herculeana* and
 429 *T. processionea*.

430 Considering the host plant associations, it seems likely that larvae of the ancestor of *Thaumetopoea*
 431 fed on angiosperms and that only later a drastic shift to gymnosperms occurred, as observed in clade
 432 K (Fig. 6). The reconstruction of the pupation strategy (Fig. 6) supports the view that the soil was
 433 probably the pupation site of the *Thaumetopoea* ancestor, even if the proportional likelihood is not
 434 conclusive (Fig. 6). It may thence be supposed that soil pupation made the processionary moths better
 435 suited to highly variable climatic conditions, such as for instance those occurring in the
 436 Mediterranean. Stiff frontal protuberances enabling emerging adults to dig themselves out of
 437 hardened soils, either associated with foretibia spines or not, are a common adaptation in several
 438 members of the allied family Noctuidae, particularly if living in arid environments, e.g. *Cardepi*,
 439 *Craterestra*, *Conicofrontia*, *Grotella*, *Aedophron* (e.g., Janse, 1939; Hogue, 1963; Berio, 1985;
 440 Matthews, 1991; Fibiger *et al.*, 2009), but none appears to be configured as those of *Thaumetopoea*
 441 *s. lat.* Thus, it is conceivable that early ancestors of *T. processionea* and *T. solitaria* independently
 442 lost both frontal crest and foretibia spine as a consequence of a change in their pupation strategy from
 443 soil to litter (*T. solitaria*) and to tent (*T. processionea*). To further substantiate this scenario, it is
 444 interesting to note that both *T. processionea* and *T. solitaria* show a pronounced median protuberance
 445 on the frons (Fig. 1), whereas in *Gazalina* and other genera of Thaumetopoeinae (e.g., *Anaphe*,
 446 *Epicoma*, *Hypsoides*, and *Ochrogaster*) the frons is flat. The same applies for the foretibia, as both *T.*
 447 *processionea* and *T. solitaria* show a pronounced distal edge (Fig. 1) recalling a “regressed” foretibia
 448 spine, which is pretty different from the flat distal edge shared by the remaining Thaumetopoeinae.
 449 This is suggestive of the absence of the toothed frontal crest in the two species as being non
 450 homologous to that of other genera examined and representing a secondary loss. The toothed crest
 451 would therefore be confirmed as a good autapomorphy defining the whole *Thaumetopoea*, not just
 452 the *Traumatocampa* branch as supposed by the early authors and corroborated by the morphological
 453 dataset alone. Maintained in *T. herculeana*, topology of the total evidence cladogram (Fig. 5) is in
 454 accordance with an independent regression of the crest in both *T. processionea* and *T. solitaria*. As a
 455 matter of fact, the crest of processionary moths is such a complex structure that following release of

the selection on the character it is more parsimonious to admit its loss as a result of some disruption in the underlying developmental gene machinery (e.g., Griffiths *et al.*, 1999; Hottes *et al.*, 2013; Stower, 2013) than assuming its independent evolution in *T. herculeana* and typical *Traumatocampa*.

The conifer feeding taxa: summer vs. winter

All our cladograms agree in reconstructing conifer feeding processionary moths (clade K, Fig. 6) as monophyletic. Monophyly of this clade has been strongly supported also by previous molecular studies (Simonato *et al.*, 2013). Conifer feeding processionary moths split into two subclades (L and O), each being characterized by a number of apomorphic character states (Fig. 5). Species included in clades L and O are also characterized by having different developmental strategies (Démolin, 1989) and diverging sexual pheromone composition (Frérot and Démolin, 1993). Clade L includes taxa whose larvae feed across winter ('winter species') while clade O those feeding across spring and summer ('summer species'). Clades L and O have been recovered as monophyletic in all our analyses, gaining strong statistical support. Clades differ in relation to host plants, as winter taxa usually feed on *Pinus* while summer taxa on *Cedrus*, although notable exceptions exist. In fact, *T. pityocampa* (Clade L) can develop on *Cedrus* as well as on other conifers (Battisti *et al.*, 2015) whereas *T. pinivora* (Clade O) feeds solely on *Pinus*, probably as a result of a host shift from a *Cedrus*-associated ancestor (Cassel-Lundhagen *et al.*, 2013).

The study of the evolution of seasonal feeding of *Thaumetopoea* larvae suggests that a change from summer to winter would have characterized the developmental strategy of the ancestor of clade K, thus triggering allochronic speciation events (e.g., Santos *et al.*, 2007). A winter feeding larval stage has several major advantages in temperate regions, such as a comparatively enemy- and competition-free space, although it can be constrained by winter cold (Battisti *et al.*, 2015). This adaptation, that involves several biochemical and physiological modifications, is a key to understand the response of *T. pityocampa* to former and current climate changes (Battisti *et al.*, 2005), which has likely contributed to the genetic population structure of this taxon (Kerdelhué *et al.*, 2009). Interestingly, under mild oceanic climatic conditions a winter population of *T. pityocampa* in coastal Portugal has recently shifted back to summer feeding, indicating that the trait has great adaptive value (Santos *et al.*, 2007, 2011).

Evolutionary history and conclusions

The study of the evolution of life history traits allows us to sketch an evolutionary scenario for *Thaumetopoea*. The Western Palaearctic Region, and the East Mediterranean-Middle East sub-region in particular, was likely the area from where this group started diversifying from an ancestor developing on angiosperms. It is likely that the host shift from angiosperms to gymnosperms that

characterized the ancestor of clade K (Figs. 5-6) occurred during the Tertiary and was further affected during the Quaternary glaciation events. Previous molecular work done on a subset of taxa indicated that the Messinian period is when major genetic diversification of species and clades happened (Salvato *et al.*, 2002; Simonato *et al.*, 2007; Kerdelhué *et al.*, 2009). Pines and cedar trees are documented to occur throughout that period in the West Palaearctic (Richardson, 1998; Qiao *et al.*, 2007), mainly in the mountains. This could have promoted the isolation of the insect populations and the speciation process, as it is evident for the cedar-feeding species in the summer clade (Basso *et al.*, 2016). As the host plant shift appears to be unique, it is not possible to reconstruct with precision its timing and location, although pines are the most likely candidates because of their large predominance in fossil remains of conifers (Richardson, 1998). The host shift drove speciation events on these plants, resulting now in the so-called ‘coniferous *Thaumetopoea*’ (Simonato *et al.*, 2013) (clade K) (Figs. 5-6), which comprise ten taxa spread mostly in the Mediterranean subregion. Conversely, the ancestors of clades B and H continued to rely on a very diverse number of angiosperms as host plants. A common trait shared by the latter groups is the colonization of dry areas of Middle East and Afrotropical region, which could have been facilitated by the plasticity in the life history. This is remarkably shown by *T. jordana*, which shifted to winter feeding, possibly driven by the necessity to escape from harsh conditions provided by Jordan valley in summer (Trough, 1954). The spread in the Afrotropical region would ultimately have been achieved by clade H radiating from the Middle East. It would be interesting to compare the special *Thaumetopoea* adaptation to climate and host plants with those of several other genera of Thaumetopoeinae occurring in Africa and Australasia in a number of different habitats, to come up with a comprehensive phylogenetic analysis of the whole group that could help to better understand the evolution of *Thaumetopoea*.

Acknowledgments

The authors warmly acknowledge the help of following people who provided useful suggestions and specimens for the analyses: M. Doganlar, P. Paolucci, A. Schintlmeister, M. Simonato, T. J. Witt. Thanks also to the curators of the Bavarian State Collection of Zoology of Munich Germany, Museo Civico di Zoologia of Rome Italy, Museo di Zoologia, ‘Sapienza’ University of Rome (Rome Italy), Royal Belgian Institute of Natural Sciences of Brussels Belgium, Royal Museum of Central Africa of Tervuren Belgium, Witt Museum (Munich Germany) for the opportunity to study their collections, and using their facilities, and finally to M. Ströhle and V. Zolotuhin for the DNA sequences of ‘African’ *Thaumetopoea*. Finally, we thank two anonymous reviewers for providing helpful comments to an early version of this paper. This work was supported by a grant to Enrico Negrisolò from Padua University (ex 60% 2012) and by a PhD grant from Padua University to Andrea Basso.

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 681

682 **Legend to the Tables**

683
684 **Table. 1.** List of Thaumetopoeinae taxa considered in this work.

685
686 **Table. 2.** Association of *Thaumetopoea s. lat.* species-group taxa to genera or subgenera by various
687 authors.

688
689 **Table. 3.** Indication of apomorphic characters and homoplasious changes of total evidence tree
690 showed in Fig. 4.

691
692 **Table. 4.** Indication of apomorphic characters and homoplasious changes of total evidence tree
693 showed in Fig. 5.

694
695

Table. 1.

Taxon	Author	Distribution	Host plants
<i>Thaumetopoea processionea processionea</i>	(Linnaeus, 1758)	Europe, Middle East	<i>Quercus</i> spp.
<i>Thaumetopoea processionea pseudosolitaria</i>	Daniel, 1951	South - Eastern Europe, Middle East	<i>Quercus</i> spp.
<i>Thaumetopoea solitaria iranica</i>	Agenjo, 1941	Middle East	<i>Pistacia</i> spp.
<i>Thaumetopoea solitaria solitaria</i>	(Freyer, 1838)	South - Eastern Europe, Middle East	<i>Pistacia</i> spp.
<i>Thaumetopoea herculeana herculeana</i>	(Rambur, 1837)	South - Western Europe, Northern Africa, Middle East	<i>Cistus</i> spp., <i>Erodium</i> spp., <i>Helianthemum</i> spp.
<i>Thaumetopoea herculeana judaea</i>	Bang-Haas, 1910	Middle East	unknown
<i>Thaumetopoea apologetica abyssinica</i>	Strand, 1911	Eastern Africa	<i>Maerua</i> spp.
<i>Thaumetopoea apologetica apologetica</i>	Strand, 1909	Southern and Eastern Africa	<i>Maerua</i> spp.
<i>Thaumetopoea dhofarensis</i>	Wiltshire, 1980	Middle East	unknown
<i>Thaumetopoea jordana</i>	Staudinger, 1887	Middle East	<i>Rhus tripartita</i>
<i>Thaumetopoea cheela</i>	Moore, 1883	Southern Asia	<i>Pinus</i> spp., or <i>Cedrus</i> spp.
<i>Thaumetopoea bonjeani</i>	Powell, 1922	North - Western Africa	<i>Cedrus atlantica</i>
<i>Thaumetopoea pinivora</i>	(Treitschke, 1834)	Central, Northern and Eastern Europe	<i>Pinus</i> spp.
<i>Thaumetopoea libanotica</i>	Kiriakoff & Talhouk, 1975	Middle East	<i>Cedrus libani</i>
<i>Thaumetopoea ispartaensis</i>	Doganlar & Avci, 2001	Middle East	<i>Cedrus libani</i>
<i>Thaumetopoea sedirica</i>	(Doganlar, 2005)	Middle East	<i>Cedrus libani</i>
<i>Thaumetopoea torosica</i>	(Doganlar, 2005)	Middle East	<i>Pinus brutia</i>
<i>Thaumetopoea pityocampa pityocampa</i>	([Denis & Schiffermüller], 1775)	Central Europe, Mediterranean region	<i>Cedrus</i> spp., <i>Pinus</i> spp.
<i>Thaumetopoea pityocampa orana</i>	(Staudinger, 1901)	North - Western Africa	<i>Pinus</i> spp.
<i>Thaumetopoea pityocampa ENA</i>	—	North - Eastern Africa	<i>Cedrus atlantica</i> , <i>Pinus halepensis</i>
<i>Thaumetopoea wilkinsoni</i>	Tams, 1925	Middle East	<i>Cedrus libani</i> , <i>Pinus</i> spp.
<i>Anaphe panda panda</i>	(Boisduval, 1847)	Central - Southern Africa	Polyphagous
<i>Anaphe panda infracta</i>	Walsingham, 1885	Central - Southern Africa	Polyphagous
<i>Anaphe venata</i>	Butler, 1878	Central - Southern Africa	Polyphagous
<i>Anaphe etiennei</i>	Schouteden, 1912	Central - Southern Africa	Polyphagous
<i>Epanaphe nigricincta</i>	(Hulstaert, 1924)	Central - Southern Africa	Polyphagous
<i>Epanaphe subsordida</i>	(Holland, 1893)	Central - Southern Africa	Polyphagous
<i>Epanaphe moloneyi</i>	(Druce, 1887)	Central - Southern Africa	Polyphagous
<i>Epanaphe carteri</i>	(Walsingham, 1855)	Central - Southern Africa	Polyphagous
<i>Gazalina apsara</i>	(Moore, 1859)	Southern Asia	Betulaceae, Fagaceae
<i>Gazalina chrysolopha</i>	(Kollar, 1844)	Southern Asia	Betulaceae, Fagaceae
<i>Gazalina transversa</i>	Moore, 1879	Southern Asia	Betulaceae, Fagaceae
<i>Hypsoides antsianakana</i>	(Oberthür, 1922)	Eastern Africa	Gentianaceae
<i>Hypsoides placidus</i>	(Oberthür, 1923)	Eastern Africa	Gentianaceae
<i>Ochrogaster lunifer</i>	Herrich-Schäffer, 1855	Australia	<i>Acacia</i> spp., <i>Corymbia</i> spp., <i>Eucalyptus</i> spp.
<i>Paradrallia punctigera</i>	Hulstaert, 1924	Central Africa	Fabaceae
<i>Paradrallia rhodesi</i>	Bethune-Baker, 1908	Central Africa	Fabaceae

Table. 2.

Taxon	Agenjo, 1941	de Freina & Witt, 1987	Simonato, 2013	Schintlmeister, 2013
<i>processionea processionea</i>	Thaumetopoea	Thaumetopoea	Thaumetopoea	Thaumetopoea
<i>processionea pseudosolitaria</i>	Thaumetopoea	—	Thaumetopoea	Thaumetopoea
<i>solitaria solitaria</i>	Thaumetopoea	Thaumetopoea	Thaumetopoea	Thaumetopoea
<i>solitaria iranica</i>	Thaumetopoea	—	Thaumetopoea	Thaumetopoea
<i>herculeana herculeana</i>	Traumatocampa	Helianthocampa	Thaumetopoea	Helianthocampa
<i>herculeana judaea</i>	Traumatocampa	—	Thaumetopoea	Helianthocampa
<i>apologetica abyssinica</i>	—	—	Thaumetopoea	Thaumetopoea
<i>apologetica apologetica</i>	—	—	Thaumetopoea	Thaumetopoea
<i>dhofarensis</i>	—	—	Thaumetopoea	Thaumetopoea
<i>jordana</i>	—	—	Thaumetopoea	Traumatocampa
<i>cheela</i>	—	—	Thaumetopoea	Thaumetopoea
<i>bonjeani</i>	Traumatocampa	Traumatocampa	Thaumetopoea	Traumatocampa
<i>pinivora</i>	Traumatocampa	Traumatocampa	Thaumetopoea	Traumatocampa
<i>libanotica</i>	Traumatocampa	—	Thaumetopoea	Traumatocampa
<i>ispartaensis</i>	—	—	Thaumetopoea	Traumatocampa
<i>seDIRica</i>	—	—	Thaumetopoea	Traumatocampa
<i>torosica</i>	—	—	Thaumetopoea	Traumatocampa
<i>pityocampa pityocampa</i>	Traumatocampa	Traumatocampa	Thaumetopoea	Traumatocampa
<i>pityocampa orana</i>	Traumatocampa	—	Thaumetopoea	Traumatocampa
<i>pityocampa</i> ENA	—	—	Thaumetopoea	—
<i>wilkinsoni</i>	Traumatocampa	—	Thaumetopoea	Traumatocampa

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Table. 3.

Node	Apomorphies	Homoplasious changes
A	17:0; 30:0; 36:0; 91:0; 102:1; 111:1; 129:1	37:3; 38:1; 74:0
B	29:3; 123:1	18:2; 24:2; 85:1
C	-	113:2; 115:2; 121:1; 133:1; 146:1; 150:1
D	28:3; 41:1; 86:1	37:2; 49:0; 64:0; 76:1; 79:1; 80:0; 82:0; 97:1; 163:1
E	2:0; 11:0; 26:0; 27:0; 112:0; 113:0	49:0; 64:0; 132:0
F	39:1; 42:1; 47:1	28:1; 31:1; 52:0; 60:1; 68:0; 81:3; 84:1; 104:1; 105:1; 135:1; 136:0; 157:2
G	-	132:2
H	8:2	74:0; 115:0
I	22:3; 101:1	106:0
J	29:1	24:0; 35:0; 89:1; 115:0; 133:1
K	-	82:0
L	50:1; 66:1; 112:1	33:1; 82:2; 100:1; 121:1
M	7:1; 8:0; 40:0; 48:0; 61:0; 94:1	12:0; 22:0; 29:0; 52:0; 68:0; 76:1; 96:1; 99:1; 103:1; 104:1; 115:2; 151:2
N	5:1; 28:2; 43:1; 49:2; 134:1	45:1; 140:1
O	138:1; 149:2	13:1; 103:1; 114:1; 150:1; 163:1
P	-	11:1; 12:2; 34:2; 88:1; 89:1
Q	-	10:0; 18:3; 37:3; 86:2; 103:1
R	71:1	9:0; 13:0; 44:0; 79:1; 81:1; 89:1; 147:3; 149:0; 151:0
S	-	18:1

698

699

Table. 4.

Node	Apomorphies	Homoplasious changes
A	15:1; 17:0; 23:1, 2; 30:0; 36:0; 64:0; 91:0; 129:1; 145:1	22:2,3; 38:1; 74:1; 107:0
B	29:3	14:0; 113:2; 115:2; 128:1
C	28:3	80:0; 82:0; 128:0; 133:1; 146:1; 150:1; 163:1
D	96:1	28:0; 99:1; 100:1
E	13:3	37:3; 49:1; 64:1; 81:1; 155:1
F	-	-
G	112:0; 113:0	2:0; 11:0; 26:0; 27:0; 78:2
H	4:0; 39:1; 42:1; 47:1; 151:0	18:3; 19:2; 52:0; 60:1; 68:0; 78:1; 81:3; 104:1; 135:1; 136:0; 137:3; 157:2
I	-	132:2
J	8:2	74:0; 115:0; 132:0
K	10:1	18:1; 23:0; 101:1; 131:0; 137:0
L	29:1	13:0; 24:0; 28:0; 35:0; 89:1; 97:1; 115:0; 161:1; 128:1; 133:1
M	10:2	34:2; 37:3; 82:0; 132:0
N	-	-
O	1:2; 15:2; 28:2; 43:1; 134:1; 145:0; 147:3	14:1; 33:1; 49:2; 50:1; 66:1; 100:1; 140:1
P	138:1	114:1; 128:4; 130:1; 163:1
Q	148:0	18:0; 101:0
R	-	10:0; 37:3; 86:2; 103:1
S	71:1	9:0; 13:0; 44:0; 79:1; 89:1
T	-	-

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701

702 **Legend to the Figures**

703

704 **Fig. 1.** Traits of *Thaumetopoea* spp.. a) Dorsal habitus and veins of wings; b) head traits. Frontal
705 protuberance or crest: c) *T. herculeana*, d) *T. apologetica*, e) *T. dhofarensis* / *T. jordana*, f) *T.*
706 *pityocampa*, g) *T. wilkinsoni*, h) *T. bonjeani*, i) *T. cheela*, j) *T. libanotica*, k) *T. ispartaensis* / *T.*
707 *sedirica*, l) *T. pinivora*, m) *T. processionea* / *T. solitaria*. Legs silhouette: n) foreleg of crested
708 *Thaumetopoea*, o) foreleg of non-crested *Thaumetopoea*, p) midleg / hindleg of *Thaumetopoea*.
709 Genitalia of *Thaumetopoea* spp.: q) front view, and r) lateral view.

710

711 **Fig. 2.** Taxa studied in this work. (a), *Thaumetopoea herculeana herculeana* - Algeria
712 (BMHN(E)_1378597); (b), *Thaumetopoea processionea* - France (BMHN(E)_1378609); (c),
713 *Thaumetopoea solitaria solitaria* - Cyprus (BMHN(E)_1378618); (d), *Thaumetopoea apologetica*
714 *apologetica* - Kenya (BMHN(E)_1378606); (e), *Thaumetopoea dhofarensis* - Oman (WITT_TH73);
715 (f), *Thaumetopoea jordana* - Palestine (ZSM_TH72); (g), *Thaumetopoea pityocampa pityocampa* -
716 Greece (BMHN(E)_1378583); (h), *Thaumetopoea wilkinsoni* - Cyprus (BMHN(E)_1378572). The
717 collection code associated to the specimen is provided in brackets (see Table S1). Scale bar = 1 cm.

718

719 **Fig. 3.** Taxa studied in this work. (a), *Thaumetopoea bonjeani* - Morocco (BMHN(E)_1378573); (b),
720 *Thaumetopoea cheela* ST - India (BMHN(E)_1378635); (c), *Thaumetopoea ispartaensis* - Turkey
721 (DAFNAE_TH30); (d), *Thaumetopoea libanotica* - Lebanon (BMNH(E)_1378640); (e),
722 *Thaumetopoea pinivora* - France (BMHN(E)_1378577); (f), *Thaumetopoea sedirica* PT - Turkey
723 (DAFNAE_TH29); (g), *Thaumetopoea torosica* PT - Turkey (DAFNAE_TH64). The collection code
724 associated to the specimen is provided in brackets (see Table S1). Scale bar = 1 cm.

725

726 **Fig. 4.** The most parsimonious tree (Length = 534, CI = 0.537, RI = 0.797) obtained from Thau.morph
727 dataset. Optimization: only unambiguous changes are mapped. Black circles, apomorphic characters;
728 white circles, homoplasious changes. Partial topologies show the differences observed in BI and ML
729 trees. MP-Bremer, Bremer support to the node; MP-bt, bootstrap support to the node; ML-ord-UFB,
730 ultrafast bootstrap support to the node (ordered model); ML-mk-UFB, ultrafast bootstrap support to
731 the node (unordered model); BI-pp, posterior probability support to the node.

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735

736 **Fig. 5.** The most parsimonious tree (Length = 504, CI = 0.611, RI = 0.569) obtained from
737 Thau.tot.comp dataset. Optimization: only unambiguous changes are mapped. Black circles,
738 apomorphic characters; white circles, homoplasious changes. Partial topology shows the difference
739 observed BI and ML trees. MP-Bremer, Bremer support to the node; MP-bt, bootstrap support to the
740 node; ML-ord-UFB, ultrafast bootstrap support to the node (ordered model); ML-mk-UFB, ultrafast
741 bootstrap support to the node (unordered model); BI-pp, posterior probability support to the node.

742
743 **Fig. 6.** The evolution of life history traits tracked of the MP tree obtained from Thau.tot.comp dataset.
744 The transformational pathways are provided for all terminal nodes plus selected internal nodes (for
745 full details see Figs. S14-S15). Maximum parsimony reconstructions are figured on the branch
746 leading to the selected node. Maximum likelihood reconstructions are provide only for ambiguous
747 results below the reference branch. Traits 1-5 were analysed with the Mesquite software. Trait 6 was
748 mapped with S-DIVA software.

749

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure S1. Species studied in this work. (a), *Thaumetopoea herculeana herculeana* - Algeria (BMHN(E)_1378597); (b), *Thaumetopoea processionea* - France (BMHN(E)_1378609); (c), *Thaumetopoea solitaria solitaria* - Cyprus (BMHN(E)_1378618); (d), *Thaumetopoea apologetica apologetica* - Kenya (BMHN(E)_1378606); (e), *Thaumetopoea dhofarensis* - Oman (WITT_TH73); (f), *Thaumetopoea jordana* - Palestine (ZSM_TH72); (g), *Thaumetopoea pityocampa pityocampa* - Greece (BMHN(E)_1378583); (h), *Thaumetopoea wilkinsoni* - Cyprus (BMHN(E)_1378572). The collection code associated to the specimen is provided in brackets (see Table S1).

Figure S2. Species studied in this work. (a), *Thaumetopoea bonjeani* - Morocco (BMHN(E)_1378573); (b), *Thaumetopoea cheela* ST - India (BMHN(E)_1378635); (c), *Thaumetopoea ispartaensis* - Turkey (DAFNAE_TH30); (d), *Thaumetopoea libanotica* - Lebanon (BMNH(E)_1378640); (e), *Thaumetopoea pinivora* - France (BMHN(E)_1378577); (f), *Thaumetopoea sedirica* PT - Turkey (DAFNAE_TH29); (g), *Thaumetopoea torosica* PT - Turkey (DAFNAE_TH64). The collection code associated to the specimen is provided in brackets (see Table S1).

Figure S3. Species studied in this work. (a), *Thaumetopoea apologetica abyssinica* - Abyssinia (BMHN(E)_1378622); (b), *Thaumetopoea herculeana judaea* - Palestine (BMHN(E)_1378602); (c), *Thaumetopoea pityocampa orana* - Algeria (BMHN(E)_1378565); (d), *Thaumetopoea solitaria iranica* - Persia (BMHN(E)_1378619); (e), *Thaumetopoea processionea pseudosolitaria* - Italy (ZSM_TH66); (f), *Gazalina apsara* - Pakistan (DAFNAE_TH77); (g), *Anaphe panda panda* - Tanzania (DAFNAE_TH78); (h), *Ochrogaster lunifer* - Australia (DAFNAE_TH85). The collection code associated to the specimen is provided in brackets (see Table S1).

Figure S4. The most parsimonious tree (Length= 534 , CI= 0.537, RI= 0.797) obtained from Thau.morph dataset. Optimization: only unambiguous changes are mapped. Black circles, synapomorphic characters; white circles, homoplasious changes. Partial topology shows the difference with ML and BI trees. MP-Bremer, Bremer support to the node; MP-bt, bootstrap support to the node; ML-ord-UFB, ultrafast bootstrap support to the node, with ordered model; ML-mk-UFB, ultrafast bootstrap support to the node, with unordered model; BI-pp, posterior probability support to the node.

Figure S5. Bayesian tree inferred from Thau.morph dataset. Values at the base of each clade correspond to posterior probabilities.

Figure S6. Maximum Likelihood tree ($-\ln=2971.8323$) inferred from Thau.morph dataset performed using MK+FQ+ASC+G4 evolutionary model. Values at the base of each clade correspond to bootstrap support.

Figure S7. Maximum Likelihood tree (-ln=2536.9751) inferred from Thau.morph dataset performed using ORDERED+FQ+ASC+G4 evolutionary model. Values at the base of each clade correspond to bootstrap support. Partial topologies on right of the main tree to visualize better the relationships in those cases.

Figure S8. Maximum Likelihood tree (-ln=27774.0440) inferred from Thau.DNA dataset performed using GTR+I+G4 evolutionary model. Values at the base of each clade correspond to bootstrap support (in blue) and posterior probabilities (in red).

Figure S10 The most parsimonious tree (Length= 5046 , CI= 0.611, RI= 0.569) obtained from Thau.tot.comp dataset. Optimization: only unambiguous changes are mapped. Black circles, synapomorphic characters; white circles, homoplasious changes. Partial topology shows the difference with ML and BI trees. MP-Bremer, Bremer support to the node; MP-bt, bootstrap support to the node; ML-ord-UFB, ultrafast bootstrap support to the node, obtained from ordered model; ML-mk-UFB, ultrafast bootstrap support to the node, obtained from unordered model; BI-pp, posterior probability support to the node.

Figure S11. Maximum Likelihood tree ($-\ln=30433.391857$) inferred from Thau.tot.comp dataset, performed using GTR+I+G4 evolutionary model for molecular partition and ORDERED+FQ+ASC+G4 evolutionary model for morphological partition. Values at the base of each clade correspond to bootstrap support (in blue) and posterior probabilities (in red).

Figure S12. Strict consensus of three most parsimonious trees inferred from Thau.tot.red dataset (TBR) (Length= 4658, CI= 0.641 , RI= 0.511). Values at the base of each clade correspond to bootstrap support (above) and Bremer support (below).

Figure S13. Maximum Likelihood tree ($-\ln=29835.0572$) inferred from Thau.tot.red dataset, performed using GTR+I+G4 evolutionary model with molecular partition and ORDERED+FQ+G4 evolutionary model with morphological partition. Values at the base of each clade correspond to bootstrap support (in blue) and posterior probabilities (in red). Partial topology in red-colour shows the difference with BI tree.

Figure S14. Mapping of biological and ecological traits for each species, reconstructed on reference tree applying maximum parsimony algorithm implemented in Mesquite software. Pie charts are enlarged on ambiguous ancestral nodes to increase clarity.

Figure S15. Mapping of biological and ecological traits for each species, reconstructed on reference tree applying maximum likelihood algorithm implemented in Mesquite software. Pie charts sections represent the proportional likelihood of each character state at the node and are enlarged on ambiguous ancestral nodes to increase clarity. Trait number 6 was mapped with S-DIVA software

Tab.S1A. Specimens examined in this work. List of collections where specimens are preserved: BMNH: Natural History Museum (formerly British Museum of Natural History), London UK. DAFNAE: Department of Agronomy, Food, Natural resources, Animals and Environment - University of Padua, Padua Italy. Private coll.: Private collection of A. Schintlmeister, Dresden Germany. RBINS: Royal Belgian Institute of Natural Sciences, Brussels Belgium. RMCA: Royal Museum of Central Africa, Tervuren Belgium. MCZR: Museo Civico di Zoologia, Rome Italy. MZUR: Museo di Zoologia, ‘Sapienza’ University of Rome, Rome Italy. WITT: Witt Museum, Munich Germany. ZSM: The Bavarian State Collection of Zoology, Munich Germany. HT= holotype, PT= paratype, ST= syntype.

N°	Ref. slides	Taxon	Locality	Ref. Specimens
1	Noto_2098	<i>Thaumetopoea apologetica abyssinica</i>	Ethiopia	BMNH_1378622
2	Noto_2099	<i>Thaumetopoea apologetica abyssinica</i>	Ethiopia	BMNH_1378623
3	Noto_2100	<i>Thaumetopoea apologetica abyssinica</i>	Ethiopia	BMNH_1378624
4	Noto_2101	<i>Thaumetopoea apologetica abyssinica</i>	Ethiopia	BMNH_1378625
5	Noto_298	<i>Thaumetopoea apologetica abyssinica</i>	Ethiopia	BMNH
6	Noto_2095	<i>Thaumetopoea apologetica apologetica</i>	Arabia	BMNH_1378605
7	Noto_2096	<i>Thaumetopoea apologetica apologetica</i>	Arabia	BMNH_1378607
8	Noto_2097	<i>Thaumetopoea apologetica apologetica</i>	Arabia	BMNH_1378603
9	Noto_297	<i>Thaumetopoea apologetica apologetica</i>	Uganda	BMNH
10	TH 4	<i>Thaumetopoea apologetica apologetica</i>	Zimbabwe	Private coll._#29.538
11	TH 5	<i>Thaumetopoea apologetica apologetica</i>	Zimbabwe	Private coll._#29.540
12	TH 56	<i>Thaumetopoea apologetica apologetica</i>	Zimbabwe	Private coll._#29.537
13	TH 57	<i>Thaumetopoea apologetica apologetica</i>	Zimbabwe	Private coll._#29.539
14	TH 58	<i>Thaumetopoea apologetica apologetica</i>	Tzaneen	Private coll._#29.541
15	TH 59	<i>Thaumetopoea apologetica apologetica</i>	South Africa	Private coll._#29.542
16	TH 6	<i>Thaumetopoea apologetica apologetica</i>	Namibia	Private coll._#29.543
17	TH 60	<i>Thaumetopoea apologetica apologetica</i>	Zimbabwe	Private coll._#29.544
18	Noto_2083	<i>Thaumetopoea bonjeani</i>	Morocco	BMNH_1378573
19	TH 18	<i>Thaumetopoea bonjeani</i>	Algeria - Tala Guilef	DAFNAE_TH18
20	TH 19	<i>Thaumetopoea bonjeani</i>	Algeria - Tala Guilef	DAFNAE_TH19
21	TH 20	<i>Thaumetopoea bonjeani</i>	Algeria - Tala Guilef	DAFNAE_TH20
22	TH 21	<i>Thaumetopoea bonjeani</i>	Algeria - Tizi Oujavoub	DAFNAE_TH21
23	TH 22	<i>Thaumetopoea bonjeani</i>	Algeria - Tizi Oujavoub	DAFNAE_TH22
24	TH 23	<i>Thaumetopoea bonjeani</i>	Algeria - Tizi Oujavoub	DAFNAE_TH23
25	Noto_2111	<i>Thaumetopoea cheela</i> ST	India	BMNH_1378635
26	TH 73	<i>Thaumetopoea dhofarensis</i>	Oman	WITT_TH73
27	TH 74	<i>Thaumetopoea dhofarensis</i>	Oman	WITT_TH74
28	Whiltshire_1911	<i>Thaumetopoea dhofarensis</i>	Oman	BMNH
29	Noto_2084	<i>Thaumetopoea herculeana</i>	Algeria	BMNH_1378597
30	Noto_2085	<i>Thaumetopoea herculeana</i>	Algeria	BMNH_1378596
31	Noto_2086	<i>Thaumetopoea herculeana</i>	Morocco	BMNH_1378599
32	Noto_2087	<i>Thaumetopoea herculeana</i>	Morocco	BMNH_1378600
33	Noto_2088	<i>Thaumetopoea herculeana</i>	Morocco	BMNH_1378601
34	TH 26	<i>Thaumetopoea herculeana</i>	Spain	DAFNAE_TH26
35	TH 33	<i>Thaumetopoea herculeana</i>	Spain	MZUR_TH33
36	TH 34	<i>Thaumetopoea herculeana</i>	Algeria	MZUR_TH34
37	Noto_2089	<i>Thaumetopoea herculeana judaea</i>	Palestine	BMNH_1378602
38	Noto_2090	<i>Thaumetopoea herculeana judaea</i>	Palestine	BMNH_1378638
39	TH 30	<i>Thaumetopoea ispartaensis</i>	Turkey - Isparta	DAFNAE_TH30

Tab.S1B. Continue from previous page.

N°	Ref. slides	Taxon	Locality	Ref. Specimens
40	TH 61	<i>Thaumetopoea ispartaensis</i>	Turkey - Isparta	DAFNAE_TH61
41	Noto_2080	<i>Thaumetopoea jordana</i>	Arabia	BMNH_1378574
42	Noto_2082	<i>Thaumetopoea jordana</i>	Jordan	BMNH_1378576
43	TH 72	<i>Thaumetopoea jordana</i>	Palestine	ZSM_TH72
44	Noto_2081	<i>Thaumetopoea jordana</i> *	Jordan	BMNH_1378575
45	Noto_2078	<i>Thaumetopoea pinivora</i>	France	BMNH_1378579
46	Noto_2079	<i>Thaumetopoea pinivora</i>	Poland	BMNH_1378578
47	TH 24	<i>Thaumetopoea pinivora</i>	Germany	WITT_TH24
48	TH 35	<i>Thaumetopoea pinivora</i>	Germany	MZUR_TH35
49	Noto_2073	<i>Thaumetopoea pityocampa orana</i>	Morocco	BMNH_1378569
50	Noto_2074	<i>Thaumetopoea pityocampa orana</i>	Tunisia	BMNH_1378567
51	Noto_2075	<i>Thaumetopoea pityocampa orana</i>	Algeria	BMNH_1378565
52	Noto_2076	<i>Thaumetopoea pityocampa orana</i>	Algeria	BMNH_1378566
53	Noto_2077	<i>Thaumetopoea pityocampa orana</i>	Algeria	BMNH_1378568
54	Noto_2064	<i>Thaumetopoea pityocampa pityocampa</i>	Portugal	BMNH_1378589
55	Noto_2065	<i>Thaumetopoea pityocampa pityocampa</i>	Portugal	BMNH_1378588
56	Noto_2066	<i>Thaumetopoea pityocampa pityocampa</i>	Algeria	BMNH_1378587
57	Noto_2067	<i>Thaumetopoea pityocampa pityocampa</i>	Majorca	BMNH_1378585
58	Noto_2068	<i>Thaumetopoea pityocampa pityocampa</i>	Republic of Macedonia	BMNH_1378584
59	Noto_2071	<i>Thaumetopoea pityocampa pityocampa</i>	Greece	BMNH_1378583
60	Noto_2072	<i>Thaumetopoea pityocampa pityocampa</i>	Greece	BMNH_1378582
61	Noto_2112	<i>Thaumetopoea pityocampa pityocampa</i>	France	BMNH_1378637
62	Noto_2113	<i>Thaumetopoea pityocampa pityocampa</i>	-	BMNH_1378563
63	TH 10	<i>Thaumetopoea pityocampa pityocampa</i>	Spain	DAFNAE_TH10
64	TH 12	<i>Thaumetopoea pityocampa pityocampa</i>	Italy	DAFNAE_TH12
65	TH 13	<i>Thaumetopoea pityocampa pityocampa</i>	Italy	DAFNAE_TH13
66	TH 17	<i>Thaumetopoea pityocampa pityocampa</i>	Italy	DAFNAE_TH17
67	TH 32	<i>Thaumetopoea pityocampa pityocampa</i>	Croatia	MZUR_TH32
68	TH 46	<i>Thaumetopoea pityocampa pityocampa</i>	Italy - Calbarina	DAFNAE_TH46
69	TH 47	<i>Thaumetopoea pityocampa pityocampa</i>	Italy - Calbarina	DAFNAE_TH47
70	TH 9	<i>Thaumetopoea pityocampa pityocampa</i>	Spain	DAFNAE_TH9
71	TH 27	<i>Thaumetopoea processionea</i>	Austria	WITT_TH27
72	Noto_1634	<i>Thaumetopoea processionea processionea</i>	France	BMNH
73	Noto_2091	<i>Thaumetopoea processionea processionea</i>	Hungary	BMNH_1378610
74	Noto_2092	<i>Thaumetopoea processionea processionea</i>	Switzerland	BMNH_1378611
75	Noto_2093	<i>Thaumetopoea processionea processionea</i>	France	BMNH_1378613
76	TH 36	<i>Thaumetopoea processionea processionea</i>	-	MZUR_TH36
77	TH 37	<i>Thaumetopoea processionea processionea</i>	Italy	MCZR_TH37
78	TH 63	<i>Thaumetopoea processionea processionea</i>	France	DAFNAE_TH63
79	Noto_2094	<i>Thaumetopoea processionea pseudosolitaria</i>	Macedonia	BMNH_1378612
80	TH 65	<i>Thaumetopoea processionea pseudosolitaria</i>	Republic of Macedonia	DAFNAE_TH65
81	TH 66	<i>Thaumetopoea processionea pseudosolitaria</i>	Italy - Sicilia	ZSM_TH66
82	TH 29	<i>Thaumetopoea sedirica</i> PT	Turkey - Sedir	DAFNAE_TH29
83	TH 31	<i>Thaumetopoea sedirica</i> PT *	Turkey - Sedir	DAFNAE_TH31
84	Noto_2105	<i>Thaumetopoea solitaria</i>	Cyprus	BMNH_1378618

*, specimens without genitalia

Tab.S1C. Continue from previous page.

N°	Ref. slides	Taxon	Locality	Ref. Specimens
85	Noto_2106	<i>Thaumetopoea solitaria</i>	Cyprus	BMNH_1378617
86	Noto_2107	<i>Thaumetopoea solitaria</i>	Iraq	BMNH_1378616
87	Noto_2108	<i>Thaumetopoea solitaria iranica</i>	Iran	BMNH_1378621
88	Noto_2109	<i>Thaumetopoea solitaria iranica</i>	Iran	BMNH_1378620
89	Noto_2110	<i>Thaumetopoea solitaria iranica</i>	Iran	BMNH_1378619
90	TH 3	<i>Thaumetopoea solitaria solitaria</i>	Pakistan	DAFNAE_TH3
91	TH 38	<i>Thaumetopoea solitaria solitaria</i>	Bulgaria	MCZR_TH38
92	TH 39	<i>Thaumetopoea solitaria solitaria</i>	Republic of Macedonia	MCZR_TH39
93	TH 64	<i>Thaumetopoea torosica</i>	Turkey - Adana	DAFNAE_TH64
94	TH 28	<i>Thaumetopoea torosica</i> *	Turkey - Isparta	DAFNAE_TH28
95	Noto_2104	<i>Thaumetopoea wilkinsoni</i>	Cyprus	BMNH_1378571
96	TH 11	<i>Thaumetopoea wilkinsoni</i>	Dishon - Israel	DAFNAE_TH11
97	TH 48	<i>Thaumetopoea wilkinsoni</i>	Israel - Dishon	DAFNAE_TH48
98	TH 49	<i>Thaumetopoea wilkinsoni</i>	Israel - Dishon	DAFNAE_TH49
99	TH 50	<i>Thaumetopoea wilkinsoni</i>	Israel - Western Negev	DAFNAE_TH50
100	TH 51	<i>Thaumetopoea wilkinsoni</i>	Israel - Western Negev	DAFNAE_TH51
101	TH 52	<i>Thaumetopoea wilkinsoni</i>	Israel - Judean Foothills	DAFNAE_TH52
102	TH 53	<i>Thaumetopoea wilkinsoni</i>	Israel - Judean Foothills	DAFNAE_TH53
103	TH 54	<i>Thaumetopoea wilkinsoni</i>	Israel - Southern Judean	DAFNAE_TH54
104	TH 55	<i>Thaumetopoea wilkinsoni</i>	Israel - Southern Judean	DAFNAE_TH55
105	Noto_2062	<i>Thaumetopoea wilkinsoni</i> ¹	Lebanon	BMNH_1378592
106	Noto_2063	<i>Thaumetopoea wilkinsoni</i> ¹	Lebanon	BMNH_1378593
107	Noto_2069	<i>Thaumetopoea wilkinsoni</i> ¹	Rhodes	BMNH_1378580
108	Noto_2070	<i>Thaumetopoea wilkinsoni</i> ¹	Rhodes	BMNH_1378581
109	Whiltshire_281	<i>Thaumetopoea wilkinsoni</i> HT	Cyprus	BMNH(E)_1378629
110	Noto_2102	<i>Thaumetopoea wilkinsoni</i> PT	Cyprus	BMNH_1378628
111	Noto_2103	<i>Thaumetopoea wilkinsoni</i> PT	Cyprus	BMNH_1378627
112	TH 75	<i>Anaphe etiennei</i>	DR of Congo	RMCA_TH75
113	Noto_271	<i>Anaphe panda</i>	South Africa	BMNH
114	TH 78	<i>Anaphe panda</i>	Tanzania	ZSM_TH78
115	TH 15	<i>Anaphe panda infracta</i>	Zambia	DAFNAE_TH15
116	TH 7	<i>Anaphe panda infracta</i>	DR of Congo	DAFNAE_TH7
117	TH 14	<i>Anaphe reticulata</i>	South Africa	DAFNAE_TH14
118	TH 76	<i>Anaphe venata</i>	DR of Congo	RMCA_TH76
119	TH 79	<i>Anaphe venata</i>	Congo da Lemba	RMCA_TH79
120	Noto_276	<i>Epanaphe (Anaphe) carteri</i>	Ghana	BMNH
121	Noto_275	<i>Epanaphe (Anaphe) moloney</i>	Zambia	BMNH
122	Noto_302	<i>Epanaphe (Anaphe) subsordida</i>	Nigeria	BMNH
123	TH 70	<i>Epanaphe carteri</i>	Angola	ZSM_TH70
124	TH 81	<i>Epanaphe maynei</i>	DR of Congo	RMCA_TH81
125	TH 69	<i>Epanaphe moloney</i>	Nigeria	ZSM_TH69
126	TH 80	<i>Epanaphe nigricincta</i>	Uganda	ZSM_TH80
127	Noto_278	<i>Epanaphe subsordida</i>	Cameroon	BMNH
128	TH 82	<i>Epanaphe subsordida</i>	DR of Congo	RMCA_TH82
129	TH 16	<i>Gazalina apsara</i>	Myanmar	WITT_TH16

¹, labelled as *T. pityocampa pityocampa* in BMNH; *, specimens without genitalia

Tab.S1D. Continue from previous page.

N°	Ref. slides	Taxon	Locality	Ref. Specimens
130	TH 67	<i>Gazalina apsara</i>	Myanmar	WITT_TH67
131	TH 77	<i>Gazalina apsara</i>	Pakistan	DAFNAE_TH77
132	TH 2	<i>Gazalina chrysolopha</i>	Pakistan	DAFNAE_TH2
133	TH 68	<i>Gazalina transversa</i>	Nepal	ZSM_TH68
134	TH 84	<i>Hypsoides antsianakana</i>	Madagascar	ZSM_TH84
135	TH 71	<i>Hypsoides placidus</i>	-	ZSM_TH71
136	TH 8	<i>Hypsoides antsianakana</i> *	Madagascar	DAFNAE_TH8
137	TH 85	<i>Ochrogaster lunifer</i>	Australia	DAFNAE_TH85
138	Noto_269	<i>Ochrogaster lunifer (Marane rubricorpus)</i>	Australia	BMNH
139	Noto_303	<i>Ochrogaster lunifer (ruptimacula)</i>	-	BMNH
140	Noto_270	<i>Ochrogaster lunifer (Teara contraria)</i>	Australia	BMNH
141	TH 83	<i>Paradrallia punctigera</i>	DR of Congo	RBINS_TH83
142	Noto_299	<i>Paradrallia rhodesi</i>	Zambia	BMNH
143	TH 1	<i>Paradrallia rhodesi</i>	Zambia	DAFNAE_TH1
144	TH 25	<i>Paradrallia rhodesi</i>	Zambia	DAFNAE_TH25

*, specimens without genitalia

Tab.S2. Mitochondrial genes used.

	<i>cox1-cox2-atp6-atp8-cox3</i>	partial <i>cob-nad1</i>	<i>nad4-nad5</i>
<i>Thaumetopoea processionea processionea</i>	HE963114	HE956699	HE864329
<i>Thaumetopoea solitaria solitaria</i>	HE963115	HE956700	HE864330
<i>Thaumetopoea herculeana herculeana</i>	HE963108	HE956693	HE864323
<i>Thaumetopoea apologetica apologetica</i> *	<u>LT614824</u>	—	—
<i>Thaumetopoea dhofarensis</i> *	<u>LT614825</u>	—	—
<i>Thaumetopoea bonjeani</i>	HE963107	HE956692	HE864322
<i>Thaumetopoea pinivora</i>	HE963111	HE956696	HE864326
<i>Thaumetopoea libanotica</i>	HE963110	HE956695	HE864325
<i>Thaumetopoea ispartaensis</i>	HE963109	HE956694	HE864324
<i>Thaumetopoea pityocampa pityocampa</i>	HE963112	HE956697	HE864327
<i>Thaumetopoea pityocampa</i> ENA	HE963113	HE956698	HE864328
<i>Thaumetopoea wilkinsoni</i>	HE963116	HE956701	HE864331
<i>Anaphe panda panda</i> *	HM892083	—	—
<i>Anaphe panda infracta</i> *	<u>LT614827</u>	—	—
<i>Epanaphe carteri</i> *	HM892014	—	—
<i>Gazalina chrysolopha</i> *	<u>LT614826</u>	—	—
<i>Hypsoides antsianakana</i> *	<u>LT614829</u>	—	—
<i>Ochrogaster lunifer</i>	AM946601	AM946601	AM946601
<i>Paradrallia rhodesi</i> *	<u>LT614828</u>	—	—

*, sequenced only the barcoding portion of *cox1*; —, not available; underline, sequences produced for the present work.

Tab.S3. Dataset content.

	morphology	cox1	cox2	cox3	atp6	atp8	cob	nad1	nad4	nad5
<i>Thaumetopoea processionea processionea</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea processionea pseudosolitaria</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea solitaria solitaria</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea solitaria iranica</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea herculeana herculeana</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea herculeana judaea</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea apologetica apologetica</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea apologetica abyssinica</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea dhofarensis</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea jordana</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea cheela</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea bonjeani</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea pinivora</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea libanotica</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea ispartaensis</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea sedirica</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea torosica</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea pityocampa pityocampa</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea pityocampa orana</i>	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea pityocampa</i> ENA	●	●	●	●	●	●	●	●	●	●
<i>Thaumetopoea wilkinsoni</i>	●	●	●	●	●	●	●	●	●	●
<i>Anaphe etiennei</i>	●	●	●	●	●	●	●	●	●	●
<i>Anaphe panda panda</i>	●	●	●	●	●	●	●	●	●	●
<i>Anaphe panda infracta</i>	●	●	●	●	●	●	●	●	●	●
<i>Anaphe venata</i>	●	●	●	●	●	●	●	●	●	●
<i>Epanaphe carteri</i>	●	●	●	●	●	●	●	●	●	●
<i>Epanaphe moloney</i>	●	●	●	●	●	●	●	●	●	●
<i>Epanaphe nigricincta</i>	●	●	●	●	●	●	●	●	●	●
<i>Epanaphe subsordida</i>	●	●	●	●	●	●	●	●	●	●
<i>Gazalina apsara</i>	●	●	●	●	●	●	●	●	●	●
<i>Gazalina chrysolopha</i>	●	●	●	●	●	●	●	●	●	●
<i>Gazalina transversa</i>	●	●	●	●	●	●	●	●	●	●
<i>Hypsoides antsianakana</i>	●	●	●	●	●	●	●	●	●	●
<i>Hypsoides placidus</i>	●	●	●	●	●	●	●	●	●	●
<i>Ochrogaster lunifer</i>	●	●	●	●	●	●	●	●	●	●
<i>Paradrallia punctigera</i>	●	●	●	●	●	●	●	●	●	●
<i>Paradrallia rhodesi</i>	●	●	●	●	●	●	●	●	●	●

● Complete data, ● Barcoding sequence (about 650 bases), ● Missing data.

Length of genes (bases). *cox1*: 1518 ca.; *cox2*: 679 ca.; partial *cox3*: 126 ca.; *atp6*: 165 ca.; *atp8*: 678 ca.; *cob*: 1062 ca.; *nad1*: 939 ca.; partial *nad4*: 490 ca.; *nad5*: 1509 ca.

Note. **Molecular markers coverage for the ingroup.** Ten of the 16 *Thaumetopoea* species possess the whole set of markers (8) with the total alignment spanning 6358 positions. Only the barcode-portion of *cox1* was sequenced for *Thaumetopoea apologetica* and *Thaumetopoea dhofarensis*. No molecular data available for *Thaumetopoea jordana*, *Thaumetopoea cheela*, *Thaumetopoea sedirica*, and *Thaumetopoea torosica*.