Critical re-examination of known purported fossil Bombycoidea (Lepidoptera)

Maria Heikkilä[1], Joël Minet[2], Andreas Zwick[3], Anna K. Hundsdoerfer[4], Rodolphe Rougerie[2], Ian J. Kitching[5]

[1] Finnish Museum of Natural History, Luomus, University of Helsinki, Finland

[2] Institut de Systématique, Évolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, EPHE, Sorbonne Université, Université des Antilles, Paris, France

[3] Australian National Insect Collection, CSIRO, Canberra, Australia

[4] Molecular Laboratory, Museum of Zoology, Senckenberg Natural History Collections Dresden, Dresden, Germany

[5] Natural History Museum, United Kingdom

Corresponding Author:

Maria Heikkilä[1]

Finnish Museum of Natural History, Luomus, P.O. Box 17, FI-00014 University of Helsinki, Finland Email address: maria.heikkila@helsinki.fi

Abstract

We critically re-examine 16 records of fossils currently assigned to the lepidopteran superfamily Bombycoidea, which includes the silk moths, emperor moths and hawkmoths. These records include subfossils, compression and impression fossils, permineralizations and ichnofossils. We assess whether observable morphological features warrant their confident assignment to the superfamily.

None of the examined fossils displays characters that allow unequivocal identification as Sphingidae, but three fossils and a subfossil (*Mioclanis shanwangiana* Zhang, Sun and Zhang, 1994, two fossil larvae, and a proboscis in asphaltum) have combinations of diagnostic features that support placement in the family. The identification of a fossil pupa as Bunaeini (Saturniidae) is well supported. The other fossils that we evaluate lack definitive bombycoid and, in several cases, even lepidopteran characters. Some of these dubious fossils have been used as calibration points in earlier studies casting doubt on the resulting age estimates. All fossil specimens reliably assigned to Bombycoidea are relatively young, the earliest fossil evidence of the superfamily dating to the middle Miocene.

Introduction

The superfamily Bombycoidea is mostly diversified in the intertropical region of the globe (Kitching and Rougerie *et al.* 2018) and includes the renowned moth families Sphingidae, Saturniidae and Bombycidae. Sphingids are large pollinators with excellent flying abilities, yet important prey for bats. The tobacco hornworm *Manduca sexta* (Linnaeus, 1763) is a common pest sphingid species causing considerable damage to tobacco, tomato, pepper, eggplant, and plantations of other crops. Saturniids include some of the largest moth species, most famous is the giant silk moth *Attacus atlas* with a wingspan of 25–30 cm. The domesticated silkmoth *Bombyx mori* Linnaeus, 1758 is a bombycid of great economic importance for silk production. Because these species have been extensively studied, they play a leading role in the fields of Lepidoptera genetics and physiology. Recently, a checklist reporting 6,092 species was provided by Kitching and Rougerie *et al.* (2018).

The Bombycoidea monophyly is corroborated by morphological and molecular data (Minet 1994; Lemaire & Minet 1998; Regier *et al.* 2008; Zwick *et al.* 2011; Hamilton *et al.* 2019). Based on molecular phylogenetics, changes were made to the higher-level classification in rapid succession. Regier *et al.* (2008) included Anthelidae in Bombycoidea (formerly Lasiocampoidea). Zwick (2008) synonymised the former family Lemoniidae with Brahmaeidae and re-established the bombycid subfamily Apatelodinae as a distinct family. Then Zwick *et al.* (2011) established Mirinidae and the former bombycid subfamilies Oberthueriinae and Prismostictinae as synonyms of Endromidae, and the former bombycine subfamily Phiditiinae as another distinct family. This resulted in the current classification that recognizes ten families in

62 Bombycoidea (Zwick *et al.* 2011; Kitching and Rougerie *et al.* 2018; Hamilton *et al.* 2019):
63 Anthelidae, Apatelodidae, Bombycidae, Brahmaeidae, Carthaeidae, Endromidae, Eupterotidae,
64 Phiditiidae, Saturniidae and Sphingidae.
65
66 Wahlberg *et al.* (2013) estimated a crown group age of 84 Ma for Bombycoidea, and Kawahara
67 *et al.* (2019) one of 80 Ma. However, the fossil record of Bombycoidea is considerably younger
68 than these estimates. The ages of the oldest fossils proposed to represent bombycoids are 53 Ma
69 for the specimen illustrated in Grande (2013), 47.8–41.2 Ma for fossilized Saturniidae cocoons
70 reported by Kuntz (2010, 2012), and 33.9±0.1 Ma for *Attacus? fossilis* Cockerell, 1914 (Sohn *et*
71 *al.* 2012). In the present work we provide arguments against the assertion that some of these
72 fossils represent lepidopterans (see below). The oldest trace fossils attributed to Sphingidae are
73 from the early Eocene (Roselli 1939; Genise 2013).
74
75 In the catalogue of fossil and subfossil Lepidoptera by Sohn *et al.* (2012, 2015), the number of
76 known fossil specimens placed in the superfamily Bombycoidea is estimated to be 53. However,
77 over 37 of these are permineralized cocoons from the same site in France and initially attributed
78 to Saturniidae, but later proposed to be pupation chambers of Hymenoptera (Kuntz 2015). A
79 purported saturniid fossil specimen not included in the catalogue by Sohn *et al.* is a compression
80 fossil from the Green River Formation figured in Grande (2013). Other fossils not included in
81 Sohn *et al.* 2012 include trace fossils (pupation chambers) found at several sites in Uruguay and
82 Argentina and attributed to Sphingidae (Genise *et al.* 2013; Genise 2017).
83
84 Some of the fossils listed under Bombycoidea in Sohn *et al.* (2012) have been used as calibration
85 points in divergence time analyses (e.g., Kawahara & Barber 2015). However, in many groups of
86 Lepidoptera the original identifications of fossil specimens are known to be based on superficial
87 similarity to modern species, not on apomorphies or reliable character combinations diagnostic
88 of the group in question. Therefore, trusting the original identifications can lead to erroneous
89 estimations on the age and historical biogeography of different groups of Lepidoptera. The
90 amount of new information on the morphology and systematics of Bombycoidea, and
91 Lepidoptera in general, has grown since the original description of many of the known fossils,
92 thus allowing critical review of their identification.
93
94 The study at hand is part on an international collaborative project with the aim of reviewing all
95 known fossil Lepidoptera. Reviews on the following groups have already been published:
96 Nepticulidae (Doorenweerd *et al.* 2015); Papilionoidea (De Jong 2017); Tortricidae (Heikkilä *et*
97 *al.* 2018a); Pyraloidea (Heikkilä *et al.* 2018b), Hepialoidea (Simonsen *et al.* 2019). The objective
98 of the present paper is to re-examine known fossil Bombycoidea and discuss the information
99 provided by reliably identified fossils of bombycoids towards our understanding of the
100 evolutionary history and biogeography of this group.
101

102

Materials & Methods

104

Institutional Abbreviations:

105	
106 ETH	ETH Zürich, Earth Science Collections, (= ETH Zürich, Erdwissenschaftliche
107	Sammlungen) Zurich, Switzerland
108 GPIT	Palaeontological Collection of Tübingen University (= Geologisch-
109	Palaeontologisches Institut Tübingen), Tübingen, Germany
110 GZG	Geoscience Centre of the University of Göttingen, Göttingen, Germany (=
111	Geowissenschaftliches Zentrum der Georg-August-Universität,
112	Geowissenschaftliches Museum) Göttingen, Germany
113 MfN	Museum für Naturkunde - Leibniz Institute for Evolution and Biodiversity,
114	Berlin, Germany.
115 MNHN	National Museum of Natural History, Paleontology (= Muséum National
116	d'Histoire Naturelle, Paléontologie), Paris, France
117 NHMUK	Department of Palaeontology, Natural History Museum, London, United
118	Kingdom.
119 NHUW	Museum of Natural History at University of Wroclaw (= Muzeum Przyrodnicze
120	we Wrocławiu), Wroclaw, Poland
121 NMK	National Museums of Kenya, Nairobi, Kenya
122 NMT	National Museum of Tanzania, Dar es Salaam, Tanzania
123 PFDL	Paleontological Fossil Depository (= 山东临朐山旺古生物化石保护管理所),
124	Linqu, Shandong, China
125 PIMUZ	Paleontological Institute and Museum, University of Zurich (= Paläontologisches
126	Institut und Museum, Universität Zürich), Zurich, Switzerland
127 ROMUT	Royal Ontario Museum, University of Toronto, Toronto, Canada
128 SF	Senckenberg Research Institute and Natural History Museum (= Senckenberg
129	Forschungsinstitut und Naturmuseum Frankfurt), Frankfurt, Germany
130 SFML	Shanwang Fossil Museum (= 山东临朐山旺古生物化石博物馆), Linqu,
131	Shandong, China.
132 SJCA	St. John's College, Agra, Uttar Pradesh, India
133 UCM	University of Colorado Museum of Natural History, Boulder, Colorado, U.S.A.
134 USNM	United States National Museum of Natural History, Washington, DC, U.S.A.

135

Specimens Examined:

137

138 The fossils are deposited in different institutions around the world and visiting all the collections
139 was not feasible. We were able to examine only two specimens in person: the compression fossil
140 tentatively identified as a saturniid by Grande (2013) and examined by MH at the USNM, and

141 the fossilized pupa identified as a bunaeine saturniid and examined by IJK when on loan to the
142 NHMUK. Many institutions do not allow sending specimens on loan. However, we were able to
143 obtain newly taken high-resolution photographs of several of the specimens to help us in our
144 assessments. In these cases, the curators of the collections and the photographers were instructed
145 as to the views and details we wished to see in close-up. We acknowledge that in such cases, and
146 in cases when the original specimen was not located and only information in the original articles
147 and figures was available to us, assessments could become more accurate when the original
148 specimens are found and/or can be examined first-hand. Even so, we consider that we have been
149 able to provide evidence and arguments for or against the placement of these fossils in
150 Bombycoidea.
151
152 In three cases the original publication did not include a detailed description and illustrations of
153 the specimen, and the depository was not stated. Therefore, we are unable to comment on the
154 veracity of the identifications. These fossils are listed in Results under the subheading "Fossils
155 not examined".
156
157 The age estimates of the fossils were taken from Sohn *et al.* (2012) unless stated otherwise.
158
159 **Specimen examination and character observation**
160
161 The identifications of the specimens were re-evaluated by scrutiny of the visible morphological
162 structures and assessing whether or not these provide compelling support. Explicit apomorphies
163 that would help identify a fossil as bombycoid with more certainty are few (Lemaire & Minet
164 1998: 321), and there are known exceptions to all these characters. They include:
165
166 1. Forecoxae distinctly fused anteriorly in last stage larvae (Figs. 25, 26 in Minet 1991; not so
167 however in Apatelodidae, Carthaeidae, most Anthelidae and certain Eupterotidae);
168
169 2. D1 setae on larval segment A8 arising from a middorsal scolus (sometimes absent or replaced
170 by a conical protuberance; convergent evolution in some non-bombycoid families, e.g., genus
171 *Entometa* Walker, 1855 in Lasiocampidae, several Notodontidae);
172
173 3. In the forewing venation, stem Rs1 + 2 closely parallel to stem Rs3 + 4 or fused to it (except
174 in most Anthelidae);
175
176 4. Loss of the spinarea (dense group of microtrichia), which is present, ventrally, at the base of
177 the forewing in many Lasiocampidae and indisputably belongs to the lepidopteran ground plan
178 (although also lost, through parallel evolution, in various groups of Lepidoptera).
179

180   5. A long mesothoracic parepisternal sulcus that reaches, or terminates near, the anapleural cleft;
181   this bombycoid autapomorphy is proposed here, based on information in Brock (1971: Figs 38b–
182   38d) and Minet (1994: 76). N.B., this sulcus had been regarded by Minet as a "lower sector" of
183   the precoxal suture ("lps") because of Brock's interpretation of the ditrysian mesopleurosternum.
184

185   If we compare, in the forewing, the common stem of Rs1 and Rs2 with that of Rs3 and Rs4, the
186   Rs1/Rs2 "forking point" is seen to lie distad of the Rs3/Rs4 forking point in many
187   Lasiocampoidea and Bombycoidea, but this trait cannot at present be regarded as a
188   synapomorphy of these superfamilies as it is may be absent from the lasiocampid ground plan
189   (Zolotuhin 2010: fig. 1, a Chionopsychinae) and from some bombycoid families (e.g.,
190   Apatelodidae). According to Hasenfuss (1999: 156), a possible synapomorphy of these two
191   superfamilies could be the presence, in the larval proleg, of two layers of "pad cuticle" in the
192   mesal region of the subcorona but this character remains to be verified more extensively in the
193   Bombycoidea, having been studied in only five bombycoid families. Unfortunately, another
194   supposed bombycoid autapomorphy in the male genitalia musculature (e.g., Minet 1994: 71) was
195   based on several misinterpretations in a paper by Kuznetzov & Stekolnikov (1985) and was thus
196   rejected some years ago (Zwick 2009).
197

198   Observing these characters in fossils is unlikely because of their often-fragmentary nature. In
199   addition, some of the characters of interest are extremely small or are rarely, if ever, preserved
200   because they are soft, unsclerotized structures. Because of these issues, we have also evaluated
201   whether combinations of homoplastic characters that are typically found in Bombycoidea could
202   be observed and tried to identify diagnostic characters of subgroups of Bombycoidea, such as
203   families or subfamilies.
204

205   ## Results

206   The fossils are discussed under four subheadings: *Fossils assigned to Bombycoidea with*
207   *reasonable certainty*; *Fossils possibly erroneously assigned to the Bombycoidea*; *Non-*
208   *lepidopteran fossil insect erroneously assigned to the Saturniidae* and *Fossils not examined*.
209   When these sections include several fossils, they are discussed from oldest to youngest.
210

211

212   **Fossils assigned to Bombycoidea with reasonable certainty:**
213

214   ***Mioclanis shanwangiana* Zhang, Sun and Zhang, 1994**
215   Fig. 1
216

217   **Excavation data:** China: Shandong, Linqu, Shanwang (Shanwang Formation); Langhian,
218   Middle Miocene.
219

Depository: PFDL Shandong, China (Holotype: SK000361). We have not been able to determine where the PFDL currently is.

Published illustrations: Zhang, Sun and Zhang (1994): 82, figs. 58, 59, pl. 10: 4 (drawings).

Preservation type and size: Full-body compression/impression fossil of adult moth. A dorsal view of the fossil, in which the wings are spread slightly overlapping either side of the body, and an interpretation of the visible wing venation were illustrated in Zhang *et al.* (1994). Forewing length: ca. 22.5 mm. Fragments of proboscis, antennal bases and legs visible. Sex indeterminate.

Comments: Assessment of this fossil is based on the illustrations and text in Zhang *et al.* (1994).

An estimated forewing length of 22.5mm and wingspan of 45–48 mm makes *Mioclanis* relatively small for a sphingid but similar in size to such genera as *Hemaris* Dalman, 1816 and *Macroglossum* Scopoli, 1777.

Zhang *et al.* (1994) noted a resemblance (but also some differences) between the fossil and moths of the extant genus *Clanis* Hübner, 1819 [erroneously attributed to "Walker" by Zhang *et al.* 1994], currently placed in the tribe Leucophlebiini (Sphingidae: Smerinthinae) (see Kitching and Rougerie *et al.*, 2018). Thus far, the only wing trait proposed as a smerinthine apomorphy is the constriction in the forewing, some distance before the tornus, of the space between the anal vein and the inner margin (Haxaire & Minet 2017: 111). However, this feature has been lost (= reversal) in some Smerinthinae (e.g., *Leucophlebia* Westwood, 1847: see Lemaire & Minet (1998: 339, fig. 18.5 I) and so its lack in *Mioclanis* does not exclude this genus from Smerinthinae.

Other characters consistent with a placement of *Mioclanis* in Sphingidae are:

Forewing veins Rs1 and Rs2 long-stalked (or entirely fused if the very short, free Rs1 branch is an artefact). Both conditions occur in Sphingidae but the former is less common, being confirmed only in some smerinthines (e.g., *Leucophlebia afra* Karsch, 1891; see Lemaire & Minet 1998: Fig. 18.5 I), *Callionima parce* (Fabricius, 1775) (Lima 1950: Fig. 86), *Manduca sexta* (Linnaeus, 1763) (Madden 1944: Fig. 9), *Agrius cingulata* (Fabricius, 1775) (Zimmerman 1958: Fig. 377), certain specimens of *Monarda oryx* Druce, 1896 (Haxaire & Minet 2017: 111) and, interestingly, Hemarini in Macroglossinae. In respect to the latter, according to the original description, the wings of *Mioclanis* are "translucent" (although it is not stated how this was determined), and so this character is consistent with *Hemaris* and *Cephonodes* Hübner, 1819.

259 *Stem Rs1+2 is separate from Rs3+4 but roughly parallel to it (and very close to it).* This is
260 consistent with the usual condition in Bombycoidea, in which these stems are either closely
261 parallel or fused together (Lemaire & Minet 1998: 321). The only bombycoid family that does
262 not have this feature is Anthelidae (except the antheline genus *Chelepteryx* Gray, 1835), in which
263 these stems are involved in the formation of an elongate areole and so not really approximated to
264 each other.

266 *Forewing discal cell narrow, with its upper angle more distal than its lower angle.* This is the
267 normal sphingid condition.

269 *Forewing vein M2 arises slightly closer to M3 than to M1 (i.e., discocellular m2-m3 = about ½*
270 *discocellular m1-m2).* This again is the normal sphingid condition, although M2 arises about
271 midway between M1 and M3 in *Callionima parce* (Lima 1950: Fig. 86). However, the condition
272 is widespread and also typical for Anthelidae and present in non-bombycoid families, e.g., some
273 Lasiocampidae, Erebidae and Satyridae.

275 *In both forewing and hindwing, m-cu crossvein long and in line with adjacent section of the*
276 *lower edge of the discal cell.* This character occurs in many Sphingidae but is relatively rare in
277 other moth families.

279 *Forewing anal vein distinctly arched upwards.* This is typical of most Sphingidae.

281 *Inner margin of forewing concave for much of its length.* This feature is found in certain
282 Sphingidae (e.g., *Hemaris fuciformis* (Linnaeus, 1758)).

284 *Hindwing veins Rs and M1 short-stalked.* This is typical of many Sphingidae but also occurs in
285 many other moth families.

287 *Hindwing discal cell small, elongate and roughly parallel to the costa.* This distinctive shape is
288 consistent with many Sphingidae (see, e.g., Heppner 1998: Figs 435 and 436).

290 *Hindwing crossvein (R) between subcosta and upper edge of discal cell beyond half length of*
291 *discal cell.* In *Mioclanis*, hindwing crossvein (R) between Sc and the upper edge of the discal
292 cell is more distal (beyond halfway) than in extant Sphingidae. However, although a crossing
293 point before halfway has been claimed as a sphingid apomorphy, it does also occur in other
294 bombycoids.

296 Several traits in *Mioclanis* disagree with the usual sphingid condition. Forewing vein Sc reaches
297 the costa much more distally than in most sphingids, where this vein does not extend beyond the
298 middle of the costa (e.g., Hodges 1971). However, there are a few known exceptions, e.g.,

299   *Leucophlebia afra* (Lemaire & Minet 1998: Fig. 339), *Agrius cingulata* (Zimmerman 1958: Fig.
300   377) and *Daphnis nerii* (Komai *et al.* 2011: Fig: II-39.3 E).

302   In *Mioclanis*, forewing vein R is shown as stalked with Rs1+2. This is never found in sphingids
303   as far as we are aware, where R arises separately from the leading edge of the discal cell around
304   the halfway point. R is stalked with elements of the radial sector in other bombycoids. However,
305   this may be an artefact of the drawing, given the apparent ambiguity in this region.

307   In *Mioclanis*, although Sc+R beyond the discal cell is closer to Rs than in many other moths, it is
308   not as close to it as in most extant Sphingidae (in which vein Sc+R is distinctly approximated to
309   the free section of Rs, at least for a short or very short distance – exceptions are rare but include
310   the closely related genera *Hemaris* and *Cephonodes*).

312   The wing shape of *Mioclanis* is closer to some Noctuoidea.

314   Overall, although many characters are consistent with *Mioclanis* being a sphingid, none is
315   unequivocal. Furthermore, one is completely contrary to *Mioclanis* being a sphingid (although
316   consistent with some other bombycoids) and another is inconsistent with superfamily
317   Bombycoidea. However, a comprehensive study of bombycoid wing venation is required to
318   ensure there are no exceptions. Thus, on balance, we consider that *Mioclanis* probably is a
319   sphingid but its placement within the family remains uncertain.

321   *Mioclanis* was used to provide a minimum age for the crown Smerinthini s.s. in the study by
322   Kawahara & Barber (2015) (as 16.1 ± 0.9 Ma) and Rougerie et al. (2022).

325   **Fossilized sphingid larva (silica or permineralization) illustrated and described in Zeuner**
326   **(1927)**
327   Fig. 2.

329   **Excavation data:** Germany: Baden–Württemberg, Münsingen, Böttingen b. Münsingen
330   ("Böttinger Marble"); Sarmatian, Late Middle Miocene. Excavation locality and age of deposit
331   taken from Zeuner (1927) and specimen label, but these differ from the information given by
332   Sohn *et al.* (2012).

334   **Depository:** GPIT. GPIT/HE/00071, NC/25/K/15. The counterpart and a silicone cast of the
335   larva are in the GPIT collection. The part of this specimen has not been located (I. Werneburg,
336   pers. comm. December 13, 2019).

338 **Published illustrations:** Zeuner (1927): 321, figs. 1–3, 5 (black and white photographs).
339 https://link.springer.com/content/pdf/10.1007%2FBF03160426.pdf
340
341 **Preservation type and size:** Silica or permineralization. Length: ca. 7 cm; greatest width: 1.4
342 cm. The larva has not been compressed and has left a concave cavity lined by a 1–2 mm thick
343 layer of "dough-like limestone" embedded in red limestone. The head is missing, but Zeuner
344 described the specimen as otherwise nearly complete and unusually well preserved, and with the
345 anterior part bent upwards. The cavities left by the thoracic legs are filled with aragonite and so
346 details cannot be observed. Details of abdominal and anal prolegs are also concealed. Zeuner
347 noted a cavity left by a slender anal scolus ("horn") and the anal plate is said to be relatively
348 large with a steep orientation.
349
350 **Comments:** According to Zeuner, the surface ornamentation and pleats (= "annulets") are
351 identical to those of extant sphingid larvae. He recognized two types of sphingid larvae: 1) those
352 in which the head capsule is rounded, the anterior three segments narrow abruptly, and the anal
353 plate is relatively small; and 2) those in which the head is dorsally pointed, the body segments
354 gradually narrow anteriorly, and the anal plate is large. Although the head of the fossil larva is
355 missing, Zeuner assigned the fossil to the latter group based on the gradually narrowing body
356 shape and a large, steep anal plate. Although annulets occur in several other lepidopteran
357 families (Peterson 1956), they are more numerous, 6–8 per segment, in Sphingidae, and this
358 condition is observed here. Furthermore, the presence of only a single median scolus on
359 abdominal segment 8 is also typical of Sphingidae, although there are exceptions (Scoble 1992;
360 Lemaire & Minet 1998). However, taken together, these two features, as well as its large size,
361 argue strongly for a placement of this fossil larva in Sphingidae, but *incertae sedis* because an
362 assignment to a subfamily is too speculative.
363
364
365 **Fossilized pupa from Laetoli discussed and illustrated by Kitching & Sadler (2011)**
366 Fig. 3.
367
368 **Excavation data:** Tanzania: Laetoli, Upper Laetoli Beds (Laetoli Fm.)/?Gelasian, Late Pliocene.
369 **Depository:** NMT (EP 352/03).
370
371 **Published illustrations:** Kitching & Sadler (2011): 551–552, figs. 20.1a–c, g–h (black and white
372 photographs).
373
374 **Preservation type and size:** Permineralization. Pupa, whole body male. Length 37 mm; width
375 15 mm; depth 11 mm. The authors describe the fossil as slightly compressed dorsoventrally. A
376 detailed description was given by Kitching & Sadler (2011).
377

Comments: Kitching & Sadler (2011) identified this fossil as a pupa of a saturniid moth in the tribe Bunaeini (Bunaeinae Bouvier, 1927 stat. rev., see Rougerie *et al.* 2022), a tribe exclusively Afrotropical in distribution. The authors compared the fossil with several extant species of Bunaeini. The closest resemblance was found to be with the pupa of *Cirina forda* (Westwood, 1849), although the fossil was not identified as this but a species near it. The authors also acknowledged that the reference material available at the NHMUK (twelve species from nine genera) was far from comprehensive and with many species not examined, there could be other species that fit equally well or better.

The characters that Kitching & Sadler (2011) stated as supporting placement of the fossil in Bunaeini include radial supporting struts around posterior margins of abdominal segments 2 and 3 dorsally and around the entire circumference of segment 7, and a pair of shallow L-shaped grooves on the dorsum of abdominal segment 10. The "radial supporting abdominal struts" match character 17 proposed as an autapomorphy of the tribe by Rougerie & Estradel (2008): junction zone between A2/A3, A3/A4, and A7/ A8–10 highly sclerotized with a row of numerous vertical grooves. Dorsal grooves (or more developed cavities) were found to be present in all the Bunaeini examined by Rougerie & Estradel (2008, their character 18), but also in most Micragonini and Urotini. In addition, the fossil pupa has the characteristic elevated crest on the posterior margin of A4-A6 (character 16 of Rougerie & Estradel 2008) found in the vast majority of Bunaeini and which is only observed outside Bunaeini in the genus *Usta* Wallengren, 1863 of tribe Urotini. It gives a unique aspect to the fossil pupa (as seen in fig. 20.1b of Kitching & Sadler), in which it appears more obvious than on the live pupa of *Cirina forda* illustrated in Kitching & Sadler.

In his paper on Bunaeini, Rougerie (2008) separated a group of four genera (*Pseudobunaea* Bouvier, 1927; *Athletes* Karsch, 1896; *Lobobunaea* Packard, 1901 and *Pseudimbrasia* Rougeot, 1962) based on the configuration of appendages on the cephalic mask of the pupa, and in particular the antennae being far from reaching the midline of the pupa. In contrast, in all other examined Bunaeini, including *Cirina*, the antennae reach the midline, with only the maxillae or small parts of thoracic legs visible. In Fig. 6, it is clear that the antennae of the fossil are short and the appendages are clearly visible (maxillae, legs), whereas in the illustrated *Cirina* pupa in Kitching & Sadler, the antennae clearly meet medially. These characters indicate that the fossil is not *Cirina*, and also exclude several other genera within the tribe.

Thus, while the identification of the fossil as Bunaeini is well supported, the genus-level identification needs further study.

In their divergence time study, Kawahara & Barber (2015) used this fossil to determine the minimum age of *Cirina forda* as 3.66 Ma.

418 **Proboscis of sphingid moth in asphaltum/tar sands (genus *incertae sedis*) in Churcher**
419 **(1966)**
420 Fig. 4.
421
422 **Excavation data:** Peru: Piura, Talara (Lobitos Tablazo Fm.); Late Pleistocene.
423
424 **Depository:** ROMUT. ROMIP30729
425
426 **Published illustrations:** Churcher (1966): 990, fig. 15 (black and white photograph).
427
428 **Preservation type and size:** Coiled structure interpreted as the haustellum (proboscis) of a
429 sphingid moth in black, asphalt-impregnated sandy matrix. The length of the structure is difficult
430 to assess because it is coiled, and some of the coils are hidden behind others. The diameter of the
431 coiled part of the structure (i.e., disregarding the basal (3 mm long) section) is ca. 4.2 mm. The
432 width of the coil at the base is ca. 0.8 mm. The haustellum seems to be at least 10 cm long (by
433 comparison with Recent Sphingidae having a coiled proboscis of a similar diameter).
434
435 **Comments:** The large diameter of this structure suggests it is indeed a coiled sphingid proboscis.
436 When coiled, the well-developed proboscides of several large Erebidae (Noctuoidea) have a
437 diameter of at most 3.5 mm (e.g., *Eudocima fullonia* (Clerck, 1764) and *Hypopyra megalesia*
438 Mabille, 1880). The estimated length of this fossil proboscis – 10–11 cm – suggests a position
439 within the Sphinginae, the only sphingid subfamily in which proboscides of this length have
440 been recorded (Miller, 1997).
441
442
443 **Fossil larva (silica or permineralization) reported by Leakey (1952) and identified as a**
444 **possible sphingid by Kitching & Sadler (2011)**
445 Fig. 5.
446
447 **Excavation data:** Kenya: South Nyanza, Rusinga and M'fwangano Islands in Lake Victoria
448 (Hiwegi Fm.)/Burdigalian, Early Miocene.
449
450 **Depository:** British-Kenya Miocene Expedition Collection, NMK. Accession No. KNMI-MW
451 261. The specimen was not located but a cast of it was found.
452
453 **Published illustrations:** Leakey (1952): 624, fig. 1 (black and white photograph).
454
455 **Preservation type and size:** Silica or permineralization. Whole body of a larva. The fossil has
456 retained the three-dimensional shape of the larva. Length 4 cm, width 0.7 cm.
457

Comments: Kitching & Sadler (2011) wrote "*Leakey (1952) illustrated an apparently large lepidopteran larva from the early Miocene deposits on Rusinga and Mfangano Islands in Lake Victoria, Kenya. The general smooth shape and secondary annulations of the body suggest this fossil may belong to the family Sphingidae (hawkmoths), although it lacks the anal horn typical of larvae of that family*".

The actual specimen was not located but we were able examine the cast of the fossil by means of 3D photogrammetry and colour photographic images provided by Job Kibii, Stephen Maikweki and Francis Muchemi (NMK), but have been unable to reach any more definite conclusions. A broken-off anal horn is unlikely in life (although they are sometimes bitten off in captivity when larvae are overcrowded and some species do lack them in the final instar), but it is possible the horn was broken off from the fossil, especially if the preparator was not expecting it. The short prolegs suggest it is a "macrolepidopteran" but the head appears large, relative to the prothorax rather than the body diameter, and the anal segment seems somewhat modified and deflected downward, features that suggest it could be Hesperiidae (D. Wagner, pers. comm. June 18, 2019). Furthermore, the anal prolegs are relatively small, which is not the condition normally found in Sphingidae, and the annulets, though present, are neither obvious nor numerous. Overall, therefore, while it remains possible that this fossil is a sphingid, other "macrolepidopteran" families cannot be ruled out and the family identification must be considered *incertae sedis*.

Fossils possibly erroneously assigned to the Bombycoidea:

Trace fossils of alleged sphingid or saturniid pupation chambers in the ichnogenus *Teisseirei* Roselli, 1939

Excavation data: Specimens interpreted as representing the ichnotaxon *Teisseirei* have been found in the Early Eocene Asencio Formation, Uruguay (see Genise 2014); localities of different Cenozoic ages in Argentina (Puerto Unzué Formation, Gran Salitral Formation, Sarmiento Formation, see Genise *et al.* (2013) and references therein, and the middle Miocene Collón Curá Formation at El Petiso, Chubut province, see Genise *et al.* 2022); and the Pliocene deposits at Laetoli, Tanzania (see Genise and Harrison (2018)).

Depository: The material examined by Genise *et al.* (2013) is deposited in the following collections: Colección de Icnología del Museo Argentino de Ciencias Naturales, Buenos Aires (MACN-Icn); Museo Paleontológico Egidio Feruglio Trelew, Chubut, Argentina (MPEF-Ic); and Colección Paleontológica de la Facultad de Ciencias, Montevideo, Uruguay (FCDPI). Material examined by Genise and Harrison (2018) is deposited in the Harrison collection; and the material examined by Genise *et al.* (2022) is in Ichnological Collection of the Museo Paleontológico "Egidio Feruglio", Trelew, Chubut province, Argentina (MPEF-IC).

498

499   **Published illustrations:** *Teisseirei barattinia* Roselli, 1939: Roselli (1939): 82, figs 29 and 30
500   (drawings); 84, fig. 31:7 (black and white photograph); Melchor *et al.* (2002): 25, fig. 12 A–E, I
501   (black and white photographs); Genise (2004): 431, fig. 3 b, c (black and white photographs);
502   Genise *et al.* (2013): 481, fig. 1 (colour photographs) https://doi.org/10.1111/let.12025; Genise
503   (2017): 346, fig. 13.25; 349, figs 13.28 a–d (colour photographs). *Teisseirei linguatus* Genise &
504   Harrison, 2018: 604, fig. 5 C–J (colour photographs); *Teisseirei barattinia* and *Teisseirei*
505   *paladinco* Genise & Cantil, 2022: Genise *et al.* (2022): 10–11, figs 7 A–I and 8 A (colour
506   photographs).

507

508   **Preservation type and size:** Trace fossils. There is some variation among the numerous
509   specimens of the *Teisseirei* ichnospecies, but in general they constitute of horizontal to sub-
510   horizontal chambers (enlargements of burrows) with a depressed, elliptical cross-section,
511   antechamber and multi-layered lining and inner surface covered in densely spaced sub-
512   rectangular or sub-triangular pits. On some of the chambers, a thin, discrete wall can be
513   observed. Internal casts of the chambers have also been found. For an amended diagnosis of the
514   ichnogenus *Teisseirei*, see Genise *et al.* (2022).

515

516   The size ranges of the several hundred chambers examined by Genise *et al.* (2013; 2022) and
517   Genise and Harrison (2018) were as follows: length - 1.9–9.1 cm; width - 0.9–4.9 cm; and height
518   - 0.75–3 cm. One exceptionally large chamber was 11.5 cm long and 7 cm wide. Genise *et al.*
519   (2013) suggested that the variation could be mostly taphonomic, but because the structures are
520   from different localities, it is also possible, even likely that different species produced them.

521

522   **Comments:** Originally, these structures (*"Teisseirei barattinia"*) were suggested to be pupation
523   chambers of Hymenoptera (Roselli 1939). Later, they were tentatively associated with
524   Coleoptera (Roselli 1987; Genise 2004). A new hypothesis that they were sphingid pupation
525   chambers was proposed by Genise *et al.* (2013), who made macro- and micromorphological
526   comparisons of these structures to pupation chambers burrowed by larvae of the modern
527   sphingid species *Manduca rustica* (Fabricius, 1775) and *Eumorpha labruscae* (Linnaeus, 1758),
528   and observed similarities. In particular, the authors emphasized the similarity in the distinct type
529   of multi-layered lining of the chambers, which they interpreted to be the result of the larva
530   packing soil dampened by liquid it had excreted. The densely pitted internal surface texture
531   visible in *Teisseirei barattinia* specimens was also found to be similar to that seen inside *M.*
532   *rustica* pupation chambers. The pits were interpreted to be imprints of thoracic legs. The authors
533   also hypothesized that the antechamber of *T. barattinia* and the hatch in modern pupation
534   chambers through which the adult emerges, could be comparable in function. Because pupation
535   in *M. rustica* and *E. labruscae* does not occur very deep in the soil, the trace fossils were
536   suggested to serve as indicators of uppermost horizons of palaeosols (Genise *et al.* 2013).
537   However, Genise *et al.* (2013) did note that in addition to Sphingidae, subterranean pupation

538   chambers are also known in other Lepidoptera, such as Noctuidae, Geometridae, and Saturniidae,
539   but the features and differences among these have not been thoroughly studied.
540
541   After the description of other ichnospecies in the ichnogenus *Teisseirei*, Genise *et al.* (2022)
542   amended the diagnosis of the ichnogenus and now attributed *Teisseirei* ichnospecies to the
543   pupation chambers of both Sphingidae and Saturniidae. Ichnotaxa are based on the fossilized
544   work of organisms but although the nomenclature of ichnotaxa resembles the conventional
545   Linnean system of classification, an ichnotaxon can include specimens that resemble each other
546   in morphology but those characteristics are not necessarily to be interpreted as evidence of a
547   shared most-recent common ancestor. The ichnogenus *Teisseirei* belongs in the ichnofamily
548   Coprinisphaeridae; other ichnogenera in that ichnofamily are attributed to Coleoptera, Hemiptera
549   and Hymenoptera (Genise 2004; Genise *et al.* 2022).
550
551   We consider that a ca. 2 cm long chamber, the minimum size mentioned by Genise *et al.* (2013),
552   is too small for a sphingid or a saturniid pupation chamber. According to Bell and Scott (1937:
553   341), the smallest known hawkmoth pupa (that of the Tiny Hawkmoth, *Sphingonaepiopsis*
554   *pumilio* (Boisduval, 1875)) is 20 mm long. They add that it lies in a "rough cocoon" that is not
555   subterranean – and this cocoon must necessarily be longer than 20 mm. Furthermore, to the best
556   of our knowledge, no recent Sphingidae or Saturniidae pupation chambers have "antechambers".
557   Thus, we consider it impossible at present to be certain that these pupation chambers were made
558   by sphingid or saturniid larvae specifically, rather than by the larvae of other lepidopteran
559   families (and possibly even other insect orders). There are hundreds of specimens placed in the
560   ichnogenus *Teisseirei*. It is possible that some of these fossil chambers are trace fossils produced
561   by Sphingidae or Saturniidae, but it is also entirely possible that most of them may eventually
562   prove not to be lepidopteran at all.
563
564
565   **Fossilized ovoid structures reported by Kuntz (2010, 2012)**
566
567   **Excavation data:** France: Alsace, North Middle Upper Rhine Graben, Bouxwiller quarry
568   (Bouxwiller Fm.); Lutetian, Middle Eocene.
569
570   **Depository:** The depository was not given in Kuntz (2012; 2015) but in Kuntz (2010) he implies
571   that such fossils are in several museum and private collections. Sohn *et al.* (2012) stated that the
572   specimens are deposited in "various institutes", but these were not listed. The exact number of
573   specimens is not given, but according to Kuntz (2012) there were hundreds. Of these, he
574   examined 37 specimens more closely.
575

576   **Published illustrations:** Kuntz (2010): figs 40–45 (photographs); Kunz (2012) (colour
577   photographs) https://asam67.org/ovoides-de-bouxwiller/; Kuntz (2015) (colour photographs)
578   https://asam67.org/bouxwiller-2015-les-ovoides-ont-de-nouveaux-parents/.
579
580   **Preservation type and size:** Permineralized ovoid structures proposed to be fossilized cocoons.
581   The length of the largest of these ovoid specimens ranges from 5.5 to 7 cm, and the diameter
582   from 2.5 to 3 cm. One extremity of these structures is rounded, the other pointed or flared. The
583   surface is uneven, with imprints likened to crossing silk fibers. Some specimens have a slight
584   dent in the middle of the long side along with a stronger calcification, possibly attesting a
585   horizontal position of the cocoon with respect to the ground. Many of these cocoons have an
586   opening, which Kuntz interpreted as the hole from which the adult moth had emerged. Some also
587   had smaller ovoid structures on their surfaces or possibly inside them (Kuntz 2012, fig. 7
588   https://asam67.org/ovoides-de-bouxwiller/), which he considered to be the pupae of parasitoids.
589
590   **Comments:** Sohn *et al.* (2012) listed these specimens in fossil Saturniidae following Kuntz
591   (2010 and 2012), who proposed that they were the cocoons of saturniid moths. The main
592   evidence he gave to support this view were the flared openings at one extremity of some of these
593   structures, which he interpreted as similar to the cocoons of Saturniidae such as *Saturnia pavonia*
594   (Linnaeus, 1758) in which the narrower, somewhat open anterior end has an internal ring of
595   apically convergent stiffer "bristles" that serve to prevent ingress of predators while facilitating
596   the emergence of the adult moth. In addition, the surface of the fossils seems to have an irregular,
597   slightly helical, striped pattern that is perpendicular to the long axis of the cocoon. Kuntz
598   considered this type of texture to be somewhat similar to that on cocoons spun by many recent
599   saturniids, with embossing on the surface formed by crossing silk fibers. However, in his 2015
600   publication, Kuntz concluded that these egg-shaped structures are more likely pupal chambers of
601   spider wasps, such as those of the genus *Pepsis* Fabricius, 1804 (Pompilidae) [guêpe géante].
602   The size, the apparent solidity and the more or less helical striation was proposed to support this
603   hypothesis, but the variable shape of the opening was problematic. Kuntz supposed the shape of
604   the opening could help in the attribution of these egg-shaped structures to an insect group, but he
605   also noted that the shape could be related to the stage of eclosion at the moment of fossilization.
606
607   We agree that these are most probably not fossilized lepidopteran cocoons.
608
609
610   ***Attacus? fossilis* Cockerell, 1914 [as cf. *Rothschildia fossilis* in Sohn *et al.* 2012]**
611   Fig. 6.
612
613   **Excavation data:** USA: Colorado, Teller County, Florissant Beds National Monument,
614   Florissant Formation; Late Priabonian, Late Eocene (33.9±0.1 Ma).
615

616   **Depository:** UCM. Holotype: UCM-8554.

617

618   **Published illustrations:** Cockerell (1914): 271, fig. 34 (drawing).

619

620   **Preservation type and size:** A compression fossil with what Cockerell (1914) interpreted as the
621   imprint of the apex of the forewing with veins of a large moth in the family Saturniidae (Fig. 6).
622   The fragment is 33 mm in length.

623

624   **Comments:** The fossil shows at least five more or less parallel arched lines, some of which are
625   incomplete. The distance between the arched lines is about 5 mm. There are no obvious stalked
626   or connate veins, and no traces of a wing pattern or scales. Cockerell (1914) interpreted the
627   parallel arched lines as veins, and the shorter line in the lower right of the fragment (as viewed in
628   fig. 8), more or less perpendicular to the longest vein, as a short segment of the wing margin (see
629   fig. 34 in Cockerell 1914). Cockerell considered the venation of the fossil to closely correspond
630   to that of the forewing of *Attacus dohertyi* Rothschild, 1895, and tentatively named the specimen
631   *Attacus? fossilis*. In the catalogue by Sohn *et al.* (2012), the specimen is referred to as cf.
632   *Rothschildia fossilis* following Schüssler (1933), who transferred "*fossilis*" from *Attacus* to the
633   genus *Rothschildia* Grote, 1896, probably because the former does not occur in the New World.
634   Below we attempt to reconstruct the reasons and characters that presumably led Cockerell to
635   assign the fossil to Saturniidae. We also evaluate whether these characters can reliably place the
636   fossil in this family.

637

638   The longest of the veins on the fossil was interpreted by Cockerell as vein "R5", (i.e., Rs4 in
639   current venation nomenclature), and he considered that the rather strongly curved shape of the
640   veins and the arrangement of Rs4 in relation to the short wing margin section resembled the
641   distal (apical) part of the forewing of certain Saturniidae. The strongly arched veins Rs4 and M1
642   indeed occur in the tribe Attacini but also in some *Antheraea* Hübner, 1819 (see fig. 92 in
643   Michener 1952) and several Arsenurinae (see, e.g., fig. 40 (*Caio richardsoni* (Druce, 1890), fig.
644   41 (*Rhescyntis pseudomartii* Lemaire, 1975) in Michener (1952), and figs 56, 57 and 126 in
645   Lemaire (1980)). The relatively greater distance separating Rs4 from the vein below (M1) could
646   also have been seen as a feature found in large Lepidoptera, such as saturniids. In addition, the
647   concave shape of the wing margin at the apex of Rs4 occurs occasionally in *Rhescyntis* Hübner,
648   1819 (Lemaire 1980: fig. 126) but practically never in *Antheraea* and *Rothschildia*. In contrast,
649   the oblique line of M2 (the short, incomplete vein below M1) would fit better with Saturniinae
650   (e.g., *Antheraea*) than with Arsenurinae.

651

652   We compared the veins on the fossil with those of several species of extant large saturniid moths
653   (those mentioned above and figures in Rougerie (2005)) by superimposing the fossil veins onto
654   illustrations of their forewing venation. In many cases the curvature of the veins was too strong
655   and did not correspond to that of the extant species. However, the curvature did follow more

656   closely the veins of the extant species of Attacini and *Antheraea*, but otherwise there was no
657   other obvious support for an assignment to the Saturniidae.
658
659   We also asked paleobotanist Dr Herbert Meyer (Florissant Fossil Beds National Monument,
660   Colorado, USA) and paleoentomologist Dr Conrad Labandeira (NMNH, Washington, D.C.,
661   USA) to examine a photograph of the fossil. They concluded that the imprint on the slab was
662   probably made by a leaf. This assessment was based on the observation that the line considered
663   by Cockerell to be a short segment of the wing margin was actually the thicker primary vein of a
664   leaf. The arched veins (Cockerell's R and M veins) were interpreted as secondary veins of the
665   leaf. The secondaries were also noted to merge into the primary and not end abruptly as would be
666   expected in an insect. Possible plant genera candidates could be *Staphylea* L., *Hydrangea* L., or
667   *Celastrus* L. (H. Meyer, pers. comm. November 14, 2016).
668
669   *Attacus? fossilis* was used as a calibration point in the divergence time analysis by Kawahara &
670   Barber (2015) to give a minimum age to the stem group of *Rothschildia* and *Saturnia* Schrank,
671   1802. The supporting information of their study stated that the fossil shares synapomorphies with
672   extant *Rothschildia* and *Saturnia*, a mistake the authors were not able to correct after the final
673   edits (A. Kawahara, pers. comm. June 14, 2015). Given the very different interpretations of the
674   fossil, we conclude that the identification is based on superficial similarity and additional
675   characters would be needed to place it reliably in Saturniidae (or any of the proposed plant
676   genera, for that matter).
677
678
679   **Compression-impression fossil of adult moth in Zhang (1989)**
680   Fig. 7
681
682   **Excavation data:** China: Shandong, Linqu, Shanwang (Shanwang Formation); Langhian,
683   Middle Miocene.
684
685   **Depository:** SFML. no. 820157).
686
687   **Published illustrations:** Zhang (1989): 94, pl. 20: 3 (black and white photo).
688
689   **Preservation type and size:** Compression-impression fossil of an adult moth. Poorly preserved.
690   Head, thorax, abdomen, left forewing and base of right forewing partly visible. Abdominal
691   segments with impressions of hair-like scales of reddish-brown colour. Some wing venation
692   visible on wings. Length of left forewing about 2.3 cm. Length of the preserved part of the body
693   is 25.2 mm. Width of abdomen at its widest part 1 cm.
694

695 **Comments:** Zhang (1989) identified the fossil as a sphingid based mostly on forewing
696 characteristics but noted that the genus and species cannot be determined. Zhang wrote that the
697 fossil has some similarities to moths in the genus *Clanis* Hübner, 1819 [misattributed to Walker
698 by Zhang (1989)] but did not elaborate on these. According to the original description by Zhang,
699 the forewing veins Rs3 and Rs4 [cited just as R and R] are stalked, M1 [cited as just M]
700 originates in the upper corner of the discal cell, and Sc, R, Rs1 and Rs2 [cited as Sc, R_1, R_2 and
701 R_3] are parallel and closely aligned. Five abdominal segments can be distinguished. However,
702 only part of the forewing venation is visible in the specimen and the above description by Zhang
703 is inaccurate. Importantly, vein M2 is straight and arises midway between M1 and M3, a
704 character that suggests this fossil differs from *Mioclanis shanwangiana* and may even not belong
705 to the Sphingidae (in which vein M2 arises closer to M3 than to M2; Lemaire & Minet (1998)).
706 The poor preservation of the specimen and lack of characters does not allow a reliable
707 identification of this specimen to superfamily level (or lower).
708
709
710 ***Sphingidites weidneri* Kernbach, 1967**
711 Fig. 8.
712
713 **Excavation data:** Germany: Lower Saxony, Willershausen am Harz /Piacenzian, Late Pliocene.
714
715 **Depository:** GZG. Holotype: GZG.W.03445 (old no. 596-11). The specimen has not been
716 located but is most certainly in the GZG collection (A. Gehler, pers. comm. June 26, 2018).
717 There is a typographical error in A. Straus's specimen number in Kernbach (1967) where it was
718 given as 3435. In the photograph presented in Kernbach's publication, the specimen number had
719 been cropped so that it cannot be completely seen. In the reproduction of the original photograph
720 presented in the present article (Fig. 8) this number is complete and reads 3445.
721
722 **Published illustrations:** Kernbach (1967): 108, fig. 11 (black and white photograph).
723
724 **Preservation type and size:** Whole body compression-impression fossil of a larva. Size not
725 given by Kernbach (1967).
726
727 **Comments:** Brauckmann *et al.* (2001) considered Kernbach's description of the genus
728 *Sphingidites* to be invalid because of the lack of a diagnosis. However, Sohn & Lamas (2013)
729 supported the interpretation that Kernbach intended this genus to accommodate fossil Sphingidae
730 whose association below family-level is not convincing and thus, as a collective genus, no type
731 species or diagnosis is required. A subsequent type designation had been provided by Clark *et al.*
732 (1971: 582) but this was also unnecessary because the type would have been automatically fixed
733 by monotypy. The circumscription of the genus is not affected by the type species designated by
734 Clark *et al.* (1971).

735

736 Kernbach (1967) interpreted the specimen to be probably a (prepupal) larva whose

737 transformation from larva to pupa had been disturbed. He reported the presence of several larval

738 segments and an anal horn. Some transverse lines are visible in the photograph that could be

739 interpreted as larval segments and a darker, narrow and short projection at one end of the fossil,

740 the possible anal horn, can be observed. However, because these characters are not very clear

741 and others cannot be made out, we agree with Kozlov (1988: 23, 55) and consider the

742 identification of this fossil as a sphingid to be uncertain. Indeed, it is very difficult to interpret

743 and possibly does not even represent a caterpillar.

744

745

746 ***Bombycites oeningensis* Heer, 1849**

747 Fig. 9.

748

749 **Excavation data:** Germany, Baden-Württemberg: Oeningen ("Molasseformation"), that is

750 Wangen (near Öhningen – see e.g., Cockerell 1915); Messinian, Late Miocene.

751

752 **Depository:** Heer (1849) wrote that the specimen is deposited at the University of Zurich and

753 according to Sohn *et al.* (2012) the holotype is in the PIMUZ. However, it is not in the PIMUZ

754 database (https://www.pim.uzh.ch/sammlung/db/index_en.php), which includes all published

755 specimens (C. Klug, PIMUZ, pers. comm., May 16, 2018). It was not found in the ETH Zürich,

756 Earth Science Collections (or database) either, where most holotypes described by Heer are

757 deposited (A. Mueller, pers. comm., June 19, 2018).

758

759 **Published illustrations:** The paper was first published as a separate in 1849 (Heer, 1849) but

760 also again the following year in Heer (1850). The same illustration (drawing) was included in

761 both publications: Heer, 1849: 183, pl. XIV: fig. 7; and Heer, 1850: pl. XIV, fig. 7. See

762 Biodiversity Heritage Library: https://biodiversitylibrary.org/page/2477621.

763

764 **Preservation type and size:** A compression-impression fossil of two very fragmentary adult

765 moths. According to Heer (1849), the abdomens and fragments of the wings are visible. One of

766 the abdomens is 3 lines (6.3 mm) wide and 6 lines (12.6 mm) long, the other 2.5 lines (5.25 mm)

767 wide and 5.5 lines (11.5 mm) long (1 line = 2.1 mm). Heer speculated that the wider abdomen

768 belonged to a female moth, the narrower to a male of the same species. No details of the wing

769 venation or wing shape can be made out.

770

771 **Comments:** Heer (1849) referred to these fossils as "Noctuo-Bombycida" and did not even

772 narrow the identification down further to "Bombyces".

773

774 Both Handlirsch (1908) and Kozlov (1988) placed the specimen in the category of Lepidoptera
775 *incertae sedis*. We agree with that assessment as no characters presented in the illustration or
776 described in the original publication enable placing of the moths in any lepidopteran superfamily.
777 Even the identification of the depicted impressions as moths is difficult. Handlirsch (1908) stated
778 "pupa" as the stage of the fossil, which is understandable because it is not obvious that the
779 illustration provided by Heer (1849, 1850) represents two adult moths.
780
781 The name "Bombycites" was first used by Latreille (1817: 561) for a suprageneric group
782 ("tribe") within recent "Phalaenae" (i.e., moths). It was proposed as a generic name – *Bombycites*
783 – by Heer (1849: 183), of which the type-species is the quite enigmatic *Bombycites oeningensis*
784 Heer, 1849 (Fletcher and Nye 1982). It was later used for a collective group aimed at
785 accommodating fossils proposed to be bombycoids but for which a genus-level identification is
786 not possible (Heer 1865; Sohn & Lamas 2013).
787
788
789 ***Bombycites buechii* Heer, 1865**
790 Fig. 10
791
792 **Excavation data:** Germany, Baden-Württemberg: Oeningen ("Molasseformation") (i.e.,
793 Wangen); Messinian, Late Miocene.
794
795 **Depository:** ETH, Zurich. Specimen barcode number: 0000000005466.
796
797 **Published illustrations:** Heer (1865): 397, fig. 310 (drawing).
798
799 **Preservation type and size:** Compression-Impression fossil of a larva (whole body). Length of
800 larva ~ 4 cm, width at widest part ~ 1.3 mm. The larva seems to be in lateral view.
801
802 **Comments:** The lack of details in the original description and diagnostic characters led Kozlov
803 (1988) to place the specimen in his list of Papilionida (i.e., Lepidoptera) incertae sedis. We agree
804 that the identification of this fossil as a bombycoid is very uncertain. It is possibly not even a
805 larva (there seems to be an elongate, tapering appendage (antenna ?) adjacent to it, but
806 admittedly not necessarily part of this fossil). In addition, there are no obvious prolegs. This is
807 perhaps not even an insect.
808
809
810 **Compression-impression fossil of wing scale tentatively assigned to a sphingid moth in by**
811 **George (1952)**
812

813   **Excavation data:** Pakistan: Punjab, Salt Range, Warcha and Jankush Nulla Gorges (Saline
814   Series dolomite); Late Eocene.
815
816   **Depository:** SJCA Uttar Pradesh; slide no. 16. We have been unable to reach the curator in
817   charge of the collection to request a new photograph of the specimen.
818
819   **Published illustrations:** George (1952): 88, fig. 55 (drawing). We have been unable to reach the
820   editors of this journal to request permission to reproduce the original image.
821
822   **Preservation type and size:** Compression/impression fossil of a wing scale of an adult moth.
823   The drawing shows a long and narrow scale, bent and folded close to its mid-length. The scale
824   has longitudinal striations, and the apex has three shallow subtriangular lobes. The total length is
825   described to be 640 micra [μm] and the width at the widest part about 64 micra [μm].
826
827   **Comments:** The author stated that "the unmistakable sphingid facies can be made out" but no
828   additional details to support this assessment were provided. No comprehensive study of
829   lepidopteran wing scales has yet been done and we are unaware of characters that would
830   unambiguously and definitively assign a wing scale to Sphingidae. We agree with Kozlov
831   (1988), who placed this specimen in the category of uncertain identifications.
832
833
834   **Fossilized scales and cuticular fragments in gut contents of fossil bats in Richter & Storch**
835   **(1980)**
836
837   **Excavation data:** Germany: Hesse, S Frankfurt, near Darmstadt, Messel oil shale-layers (Messel
838   Fm.); Early Lutetian, Middle Eocene.
839
840   **Depository:** SF.
841
842   **Published illustrations:** Richter & Storch (1980): 365, fig. 16, but see Comments below. We
843   have been unable to reach the editors of this journal to request permission to reproduce the
844   original image.
845
846   **Preservation type and size:** Fossilized scales and cuticular fragments of Lepidoptera in the gut
847   contents of fossilized bats. SEM images presented in Richter & Storch (1980) reveal that the
848   microstructure of the scales has been preserved well. Cuticular fragments are small and do not
849   contain diagnostic structures such as legs, antennae or larger hollow structures that have been
850   compressed. Association of the cuticular fragments with body parts is difficult, except for wing
851   fragments (double-layer of cuticle). These cuticular wing fragments show detailed sculpturing,

852   including a more or less dense cover of trichomes ("false hairs") in the case of lepidopteran
853   wings.
854
855   **Comments:** Sohn *et al.* (2012) stated that fig. 16 in Richter & Storch (1980: 365) could be a
856   possible sphingid scale, probably because it is very similar to the scales of modern Sphingidae
857   figured by Richter & Storch (1980: fig. 17). However, Richter & Storch said that this type of
858   scale, i.e., with inter-ridge perforations and cross-ridges, is typical of many lepidopteran families,
859   including Sphingidae, Noctuidae and Saturniidae. Assigning such lepidopteran scales to a
860   particular family is indeed difficult because such microstructure can be observed in many groups
861   of the lepidopteran clade Coelolepida (Lepidoptera with hollow scales) (Kristensen & Simonsen
862   2003; van Eldijk *et al.* 2018). In addition, the shape and structure of lepidopteran scales can vary
863   even on the same wing, and they are thus not very informative phylogenetically (Kristensen &
864   Simonsen 2003). Some of the scales in the gut contents are said to show similarities to those of
865   modern Cossidae, Micropterigidae and Eriocraniidae, the latter two of which are mostly diurnal,
866   unlike bats. The abundance of cuticular fragments with trichomes led Richter & Storch (1980:
867   365) to the conclusion that the dominant prey of these bats had been small, "primitive"
868   Lepidoptera, because wings with trichomes between scales are known from the families
869   Micropterigidae, Eriocraniidae and Hepialidae. There is no evidence that would indicate the
870   cuticular fragments or scales to belong to Sphingidae or any other bombycoid family. On the
871   contrary, based on the absence of certain scale types, Richter & Storch (1980: 364) even
872   concluded that Lasiocampidae were not part of the gut contents.
873
874
875   **Non-lepidopteran fossil insect erroneously assigned to Saturniidae by Grande (2013)**
876   Fig 11.
877
878   **Excavation data:** USA: Wyoming, Lincoln County, Green River Formation, Fossil Butte
879   Member, locality F; Ypresian, Eocene. According to Grande (2013), the fossil lake sediments
880   were deposited about 53–51 Ma.
881
882   **Depository:** Originally, the fossil was part of the private collection of the late Richard D.
883   Dayvault but was donated to the USNM in 2016 by his wife, Jalena Dayvault. USNM PAL
884   618360, part and counterpart labeled A and B.
885
886   **Published illustrations:** Grande (2013): 76, fig. 33 (colour photograph).
887
888   **Preservation type and size:** Compression fossil of a winged insect in lateral aspect. Forewing
889   length ~ 5 cm.
890

891   **Comments:** A closer inspection of the venation of this insect immediately reveals that it is not a
892   lepidopteran. There are more veins (crossveins, notably) than in the wings of either Trichoptera
893   or Lepidoptera (Fig. 11 B, close-up showing the crossveins). The venation is reticulate and
894   appears more similar to that of, e.g., Orthoptera or Neuroptera. We are currently unaware if any
895   progress regarding the identification of this fossil has been made. Mrs Jalena Dayvault, who
896   donated the specimen to the USNM, has expressed the wish that, if possible, the scientific name
897   to be given to this specimen should somehow incorporate 'Dayvault', in memory of her husband.
898   We will leave the description of this specimen to those with more knowledge of the group of
899   insects that it represents.
900
901
902   **Fossils of non-lepidopteran insects and a crustacean erroneously assigned to *Sphinx*:**
903   ***Myrmicium schroeteri* (Germar, 1839) [*Sphinx schroeteri* Germar, 1839 and *Sphinx snelleni***
904   **Weyenbergh, 1869] and the *Sphinx* larva illustrated by Weyenbergh (1869)**
905   Fig. 12
906
907   **Excavation data:** Germany: Upper Jurassic Solnhofen limestone deposits in Bavaria, Germany.
908   Altmühltal Formation, Tithonian (150.8 – 145.5 Ma).
909
910   **Depository:** *Sphinx snelleni* (Weyenbergh, 1869): 15396 and 15397; and "*Sphinx* larva" 15403
911   in Teylers Museum, Haarlem, The Netherlands. *Myrmicium schroeteri* (Germar, 1939):
912   MB.I.0860, Museum für Naturkunde Berlin, Germany.
913   https://portal.museumfuernaturkunde.berlin/detail/0d66f2851d77db8ebdf9.
914
915   **Published illustrations:** *Sphinx schroeteri* Germar, 1839: Schröter (1784) Plate III, fig. 16
916   https://zs.thulb.uni-
917   jena.de/rsc/viewer/jportal_derivate_00164692/NLKN_1784_Bd01_%200593.tif?logicalDiv=jpor
918   tal_jparticle_00152562 (drawing);
919   https://portal.museumfuernaturkunde.berlin/detail/0d66f2851d77db8ebdf9 (colour photograph) .
920   *Sphinx snelleni* Weyenbergh, 1869*:* Weyenbergh (1869): Plate I, fig. 9.
921   https://www.biodiversitylibrary.org/page/24004107 (drawing);
922   *Sphinx* larva: Weyenbergh (1869): Plate I, fig. 10.
923   https://www.biodiversitylibrary.org/page/24004107 (drawing) and Wikimedia Commons
924   https://commons.wikimedia.org/wiki/File:Myrmicium_snelleni_Teylers_museum.jpg (colour
925   photograph).
926
927   **Preservation type:** Compression fossils.
928
929   **Comments:** *Sphinx snelleni* was described by Weyenbergh (1869). The fossil is illustrated in
930   Plate I, fig. 9 of this publication along with another fossil labelled as a *Sphinx* larva (Plate I, fig.

931 10). The original description of *Sphinx snelleni* mentions a coiled proboscis (which is also
932 clearly shown in the corresponding figure: Pl. 1, Fig. 9), a trait that suggests that this taxon could
933 indeed belong to the Lepidoptera (perhaps even the Sphingidae). A curved structure is indeed
934 also visible in photographs of the specimen, but it is difficult to interpret whether it really is a
935 proboscis. After examination of the larval specimen, Handlirsch (1906) concluded that it was the
936 abdomen of a decapod (Crustacea). *Sphinx snelleni* was identified as a wood wasp of the
937 hymenopteran family Siricidae. However, it was later moved to Pseudosiricidae as a junior
938 synonym of what is now *Myrmicium schroeteri* (originally described as "*Sphinx schröteri*" by
939 Germar (1839)). For more references, see Sohn *et al.* (2012).
940
941
942 **Fossilized flower petal of *Nymphaea* tentatively interpreted as a sphingid larva by Nel &**
943 **Nel (1985)**
944
945 **Excavation data:** France: Les Figons, Aix-en-Provence / Rupelian, Oligocene.
946 Depository: MNHN. n°215 A
947
948 **Published illustrations:** Nel & Nel (1985) 126, figs. 11, 12.
949
950 **Preservation type and size:** Compression fossil. Length 2 cm.
951
952 **Comments:** Subsequently, the specimen and additional material were carefully reexamined by
953 Dr. André Nel. He concluded that they are fossilized water lily petals (Sohn et al. 2012; A. Nel,
954 pers. comm. 2.3.2023).
955
956
957 **Fossils not examined:**
958
959 **Sphingid in Baltic amber mentioned by Berendt (1830)**
960
961 **Excavation data:** Baltic Region (Baltic Amber, Prussian Fm.); Lutetian, Middle Eocene.
962
963 **Depository:** An important part of the Berendt amber collection is in the MfN, but the specimen
964 Berendt identified as "Sphinx" has not been located. There is no specimen in the MfN labelled as
965 such (T. Léger, pers. comm. June 20, 2019).
966
967 **Published illustrations:** none.
968

969 **Preservation type and size:** Specimen in Baltic amber. Berendt does not specify if the inclusion
970 in amber is an adult or a caterpillar. However, the way the text is written implies it is a
971 caterpillar. Condition and size unknown.
972

973 **Comments:** Berendt (1830: 36–37) mentioned a "Sphinx" in Baltic Amber. From the text it
974 cannot unambiguously be determined whether the specimen was an adult or caterpillar:
975 "*Lepidopteren finden sich am seltensten. Ich besitze nur einen Sphinx von bedeutender Grösse.*
976 *Kleine Raupen sieht man öfter*" (Translation: Lepidoptera are the rarest. I only own a single
977 Sphinx of significant size. Small caterpillars can be seen more often). The way the statement is
978 phrased implies that it is a caterpillar of significant size whereas the others he has seen are small.
979 Taken at face value, this fossil would represent the oldest evidence of Bombycoidea. However,
980 the identification cannot be confirmed because the specimen has not been located and is not
981 described in sufficient detail in the original publication. Kusnezov (1941: 69) possibly had access
982 to this specimen and identified the inclusion as a lepidopteran but did not suggest a lower-level
983 identification.
984

985

986 **Compression-impression fossil of a sphingid larva and a poorly preserved "Bombyx"**
987 **mentioned by Schöberlin (1888)**
988

989 **Excavation data:** Switzerland: Neuchâtel Canton, Oeningen ("Stinkschiefe")/Messinian, Late
990 Miocene.
991

992 **Depository:** The larva was originally in the [private?] Massmann Collection (Sohn *et al.* 2012),
993 but its current depository is unknown. The whereabouts of the poorly preserved "Bombyx" fossil
994 is not known either. We were unable to examine these specimens.
995

996 **Published illustrations:** none.
997

998 **Preservation type and size:** Compression/Impression fossil of a larva (whole body) and a
999 poorly preserved "Bombyx" fossil (2 species?). Size not given in Schöberlin (1888).
1000

1001 **Comments:** The author likened the size of the fossil larva to that of the larva of the extant
1002 species *Hemaris fuciformis* (Linnaeus, 1758). Because of the lack of details and illustrations in
1003 the original publication, and the unavailability of the specimens for closer examination, their
1004 assignment to Bombycoidea cannot be confirmed. In addition, back in 1888, "Bombyx" would
1005 have been used for any "Bombyces", i.e., including Bombycoidea (except Sphingidae),
1006 Notodontidae, Erebidae (subfamilies Lymantriinae and Arctiinae), Limacodidae, Zygaenidae and
1007 Psychidae. Thus, the mention of a "Bombyx" fossil does not necessarily mean that it belongs to

1008   Bombycoidea in the current sense, it could have been just about anything (see, e.g., Packard
1009   (1893) for an example of what was then considered to belong to "Bombyces").
1010
1011
1012   **Thoracic segment of *Aglia tau* (Saturniinae) larva in sieved residue (Lindberg, 1900).**
1013
1014   **Excavation data:** Finland: Lohja; Pleistocene.
1015
1016   **Depository:** not known.
1017
1018   **Published illustrations:** none.
1019
1020   **Preservation type and size:** First thoracic segment of larva. Size not known.
1021
1022   **Comments:** Lindberg (1900) gave credit for the identification of the specimen to Finnish
1023   entomologist, Enzio Reuter. According to the information in Lindberg (1900), the segment had
1024   well-preserved "strange" horn-like structures typical of *Aglia tau* (Linnaeus, 1758). These are
1025   probably the scoli found on the thoracic segments of early instar *Aglia* larvae. There are several
1026   recent species in the genus *Aglia* (Kitching and Rougerie *et al.* 2018) of which only *Aglia tau*
1027   occurs in present day Finland.
1028
1029   **Compression-impression fossil identified as *Sphinx* by Haase (1890)**
1030
1031   **Excavation data:** Excavation data or depository not known.
1032
1033   **Depository:** Originally in private collection of A. Assmann. According to information found
1034   online [https://en.wikipedia.org/wiki/August_Assmann, accessed 17.03.2020], the Assmann
1035   collection is nowadays in NHUW, Wrocław. However, the entomology collection at NHUW
1036   does not include compression/impression fossils, and Assmann's specimens are probably not in
1037   the collection of the NHUW paleontology department either, which has only vertebrates (M.
1038   Wanat, pers. comm. January 8, 2020).
1039
1040   **Published illustrations:** none.
1041
1042   **Preservation type and size:** Compression/Impression fossil. Size not known.
1043
1044   **Comments:** Haase (1890: 26) mentioned that he had seen a drawing of the specimen shown to
1045   him by Mr A. Assmann. According to Haase, Assmann had intentions to publish on the
1046   specimen. The location of the specimen was not given. Handlirsch (1908: 628) wrote that he was

1047 not able to locate it either and that to his knowledge Assmann's descriptions of these fossils were
1048 not published.

1049

1050

Discussion

1052 The re-examination of the 16 records shows that only five fossils can be placed in Bombycoidea
1053 with reasonable certainty — 4 to Sphingidae and 1 to Saturniidae. However, none of the 4 fossil
1054 sphingids displays unequivocal characters and their identification as Sphingidae is not 100%
1055 certain. This precludes their use as calibration points according to the criteria proposed by
1056 Parham *et al.* (2012). Furthermore, the use of some of the dubious fossils as calibration points in
1057 earlier studies (e.g., *Attacus? fossilis* in the study on the hawkmoth radiation by Kawahara &
1058 Barber (2015)) casts doubt on the resulting ages. New analyses with revised sets of fossils or
1059 calibration times would be welcome in these cases.

1060

1061 Although all known bombycoid fossils examined are relatively young, the oldest is *Mioclanis*
1062 *shanwangiana* from middle Miocene, the origin of the superfamily is expected to be significantly
1063 older. In studies focusing on all Lepidoptera, Wahlberg *et al.* (2013) and Kawahara *et al.* (2019)
1064 estimated a crown-group age of 84 Ma (95% HPD: 74-93) and 80 Ma (95% HPD: 70-90) for
1065 Bombycoidea, respectively. In a study on Saturniidae, Rougerie *et al.* (2022) estimated the stem
1066 age of the family to be in the early Cenozoic at about 63 Ma (95% HPD: 59-69 Ma). We note
1067 however that the estimate by Wahlberg *et al.* (2013) used time calibrations derived from a set of
1068 fossils that included some that have now been shown to be misidentified, while the selection of
1069 fossils in the studies by Kawahara *et al.* (2019) and Rougerie *et al.* (2022) were based on stricter
1070 criteria.

1071

1072 Unfortunately, bombycoid moths, as lepidopterans in general, are rare in the fossil record
1073 (Labandeira and Sepkoski, 1993; Sohn *et al.* 2012), and therefore, estimates of their age and
1074 evolution remain mostly based on the combination of molecular data and secondary calibrations.
1075 The probable reason for the scarcity of fossil Lepidoptera is that scales are water-repellent, thus
1076 preventing specimens from sinking to the bottom of water bodies where they would have been
1077 buried in sediment (Martínez-Declòs *et al.* 2004; Peñalver & Grimaldi 2006). A relatively high
1078 body-fat content of bombycoids may also increase buoyancy (Simonsen *et al.* 2019). The
1079 majority of fossil Lepidoptera are amber inclusions but nearly all of these are small moths (Sohn
1080 *et al.* 2015). Large moths are extremely rare as amber inclusions, and a reason may be that scales
1081 are relatively easily lost and doing so prevents big moths from getting trapped in amber. Large
1082 dead moths are also an attractive food source to scavengers and so may get spotted and eaten
1083 before they can be fossilized.

1084

1085

Conclusions

1087 Our study is a contribution to efforts to obtain a more reliable and accurate understanding of the
1088 evolutionary history and historical biogeography of Lepidoptera. We critically re-examined 16
1089 records of fossils currently assigned to the lepidopteran superfamily Bombycoidea, and assessed
1090 whether observable morphological features warrant their confident assignment to the
1091 superfamily.

1093 The study confirms that the identifications of many of the known fossil Bombycoidea were based
1094 on overall similarity to extant species and not apomorphies. None of the examined fossils
1095 displays characters that allow unequivocal identification as Sphingidae, but three fossils and a
1096 subfossil (Mioclanis shanwangiana Zhang, Sun and Zhang, 1994, two fossil larvae, and a
1097 proboscis in asphaltum) have combinations of diagnostic features that support placement in the
1098 family. The identification of a fossil pupa as Bunaeini (Saturniidae) is well supported. The other
1099 fossils that we evaluate lack definitive bombycoid and, in several cases, even lepidopteran
1100 characters.

1102 We can only hope that new discoveries of well-preserved fossil Bombycoidea will be made in
1103 the future and can reveal more on the evolutionary history of these moths and allow
1104 corroboration or critical revision of the current estimates of their ages.

Acknowledgements

1107 Daniil Aristov (Paleontological Institute, Russian Academy of Sciences), Chenyang Cai (Nanjing
1108 Institute of Geology and Palaeontology), Lance Grande (The Field Museum, Chicago), Jalena
1109 Dayvault, Alexander Gehler (GZG), Dale Greenwalt (Smithsonian Institution, NMNH), Talia
1110 Karim (UCM), Job Kibii (NMK), Christian Klug (PIMUZ), David Kohls, Conrad Labandeira
1111 (Smithsonian Institution, NMNH), Théo Léger (MfN), Stephen Maikweki (NMK), Finnegan
1112 Marsh (Smithsonian Institution, NMNH), Hebert Meyer and students (Florissant Fossil Beds
1113 National Monument), Sun Mingchang (SPFL), Francis Muchemi (NMK), Andreas Müller (ETH
1114 Zürich), Francis Ndiritu (NMK), André Nel (MNHN), Hossein Rajaei (State Museum of Natural
1115 History Stuttgart), Alexandr Rasnitsyn (Paleontological Institute, Russian Academy of Sciences),
1116 Michael Rasser (State Museum of Natural History Stuttgart), Anne Schulp (Teylers Museum,
1117 Haarlem); Jennifer Strotman (Smithsonian Institution, NMNH), Marek Wanat (NHUW), Ingmar
1118 Werneburg (GPIT), Huang Ying and Jukka Tabell, Tim de Zeeuw (Teylers Museum, Haarlem),
1119 David Zelagin (UCM).

References

1122 Bell, T.R.D. and Scott, F.B. 1937. Moths, vol. 5: Sphingidae 1–537. *In* Sewell, R.B.S. and
1123 Talbot, G. (eds) *The Fauna of British India*. Taylor and Francis, London, 537 pp.

1125 Berendt, G.C. 1830. *Die Insekten im Bernstein ein Beitrag zur Thiergeschichte der Vorwelt*.
1126 Nicolai, Danzig, 38 pp.

1127

1128 Brauckmann, C., Brauckmann, B. and Gröning, E. 2001. Anmerkungen zu den bisher
1129 beschrieben Lepidopteren aus dem Jung-Tertiär (Pliozän) von Willershausen am Harz.
1130 *Jahresberichte des Naturwissenschaftlichen Vereins Wuppertal* **54**, 31–41.

1131

1132 Brock, J.P. 1971. A contribution towards an understanding of the morphology and phylogeny of
1133 the ditrysian Lepidoptera. *Journal of Natural History* **5** (1), 29–102.

1134

1135 Churcher, C.S. 1966. The insect fauna from the Talara tar seeps, Peru. *Canadian Journal of*
1136 *Zoology* **44** (6), 985–993.

1137

1138 Clark, J., Cole, R., Fawcett, S., Green, M., Howcroft, J., Niedbala, S., Rawkins, K., Théobald, O.
1139 and Tobias, M. 1971. *The Zoological Record (1967). Vol. 104, 13. Insecta*. The Zoological
1140 Society of London, London, 704 pp.

1141

1142 Cockerell, T.D.A. 1914. Fossil Saturniidae. 271. *In* Packard, A.S. and Cockerell, T.D.A. (eds),
1143 Monograph of the Bombycine Moths of North America, Part III. Memoir of the National
1144 Academy of Science 12, 516 pp.

1145

1146 Cockerell T. D. A. 1915. Miocene fossil insects. *Proceedings of the Academy of Natural*
1147 *Sciences of Philadelphia* **66** (1914), 634–648.

1148

1149 De Jong, R. 2017. Fossil butterflies, calibration points and the molecular clock (Lepidoptera:
1150 Papilionoidea). *Zootaxa,* 4270, 1–63 https://doi.org/10.11646/zootaxa.4270.1.1

1151

1152 Doorenweerd C., Nieukerken, E.J. van, Sohn J.C. and Labandeira, C.C. 2015. A revised
1153 checklist of Nepticulidae fossils (Lepidoptera) indicates an Early Cretaceous origin. *Zootaxa,*
1154 3963, 295–334 https://doi.org/10.11646/zootaxa.3963.3.2.

1155

1156 Eldijk, T. van, Wappler, T., Strother, P.K., Weijst, C.M.H. van der, Rajaei, H., Visscher, H. and
1157 Schootbrugge, B. van de 2018. A Triassic-Jurassic window into the evolution of Lepidoptera.
1158 *Science Advances* **4** (1), e1701568 https://doi.org/10.1126/sciadv.1701568

1159

1160 Genise, J.F. 2003. Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols
1161 attributed to coleopterans, ants and termites. 419–453. *In* MCILROY, D. (ed.) *The Application of*
1162 *ichnology to palaeoenvironmental and stratigraphic analysis*. Geological Society, London,
1163 Special Publications, 228, 479 pp. https://doi.org/10.1144/GSL.SP.2004.228.01.21

1164

1165   Genise, J.F. 2017. Other insect trace fossils in paleosols: cicadas, chafers, weevils, and sphinx
1166   moths. 313–351. *In Ichnoentomology*. Insect Traces in Soils and Paleosols. Topics in Geobiology
1167   37. Springer International Publishing, Switzerland, 695 pp.
1168
1169   Genise, J.F., Farina, J.L. and Verde, M. 2013. *Teisseirei barattinia* Roselli 1939: the first sphinx
1170   moth trace fossil from palaeosols, and its distinct type of wall. *Lethaia*, **46**, 480–489.
1171
1172   George, V.P. 1952. On some arthropod microfossils from India. *Agra University Journal of*
1173   *Research*, **1**, 83–108.
1174
1175   Germar, E.F. 1839. Die versteinerte Insecten Solenhofens. *Nova Acta Leopoldina*, **19**, 187–222.
1176   https://play.google.com/books/reader?id=nXCIz9WoDdkC&pg=GBS.PA186&hl=fi&printsec=fr
1177   ontcover
1178
1179   Grande, L. 2013. *The Lost World of Fossil Lake: Snapshots from Deep Time*. The University of
1180   Chicago Press, Chicago and London, 425 pp.
1181
1182   Haase, E. 1890. Bemerkungen zur Palaeontologie der Insecten. *Neues Jahrbuch für Mineralogie,*
1183   *Geologie und Palaeontologie*, **2**, 1–33.
1184
1185   Hagen, H.A. 1862. Ueber die Neuropteren aus dem lithographischen Schiefer in Bayern.
1186   *Palaeontographica*, **10** (2), 96–145.
1187
1188   Hamilton, C.A., St Laurent, R.A., Dexter, K., Kitching, I.J., Breinholt, J.W., Zwick, A.,
1189   Timmermans, M.J.T.N., Barber, J.R. and Kawahara, A.Y. 2019. Phylogenomics resolves major
1190   relationships and reveals significant diversification rate shifts in the evolution of silk moths and
1191   relatives. *BMC Evolutionary Biology,* **19**, 182. https://doi.org/10.1186/s12862-019-1505-1
1192
1193   Handlirsch, A. 1906–1908. Die Fossilen Insekten und die Phylogenie der Rezenten Formen. Ein
1194   Handbuch für Paläontologen und Zoologen. Lieferung 4. Wilhelm Engelmann, Leipzig, 1430 pp.
1195   https://www.biodiversitylibrary.org/bibliography/34145;
1196   https://www.biodiversitylibrary.org/page/24524857
1197
1198   Hasenfuss, I. 1999. The adhesive devices in larvae of Lepidoptera (Insecta, Pterygota).
1199   *Zoomorphology*, **119**, 143–162.
1200
1201   Haxaire, J. and Minet, J. 2017. The systematic position of *Pentateucha*, *Monarda* and a
1202   Malagasy taxon misplaced in Smerinthinae (Lepidoptera Sphingidae Sphinginae). *Antenor*, **4** (2),
1203   107–113.
1204

1205 Heer, O. 1849. Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien,
1206 Vol. 2. Wilhelm Engelmann, Leipzig, 264 pp.

1208 Heer, O. 1850. Neue Denkschriften der allgemeinen Schweizerischen Gesellschaft für die
1209 gesammten Naturwissenschaften Band XI oder: Zweite Dekade. Band 1 mit XXII Tafeln. Druck
1210 von Zücher & Furrer, Zürich, 239 pp.

1212 Heer, O. 1865. Die Urwelt der Schweiz. Friedrich Schultheß, Zürich, 622 pp.

1214 Heikkilä M., Brown, J.W., Baixeras, J., Mey, W. and Kozlov, M.V. 2018. Re-examining the rare
1215 and the lost: a review of fossil Tortricidae (Lepidoptera). *Zootaxa,* 4394, 41–60.
1216 https://doi.org/10.11646/zootaxa.4394.1.2

1218 Heikkilä, M., Simonsen, T.J. and Solis, M.A. 2018. Reassessment of known fossil Pyraloidea
1219 (Lepidoptera) with descriptions of the oldest fossil pyraloid and a crambid larva in Baltic amber.
1220 *Zootaxa*, 4483, 101–127. https://doi.org/10.11646/zootaxa.4483.1.4

1222 Heppner, J.B. 1998. Classification of Lepidoptera. Part 1. Introduction. *Holarctic Lepidoptera*, 5
1223 (Suppl. 1): i–iv, 1–148 + 6 pp.

1225 Hodges, R.W. 1971. Sphingoidea (hawkmoths). *In* Dominick, R.B., Ferguson, D. C.,
1226 Franclemont, J. G., Hodges, R. W. and Munroe, E. G. (eds) The moths of America north of
1227 Mexico, **21**, R.B.D. Publications and E.W. Classey, London, 1–158 + xii pp. + 14 pls.

1229 Kawahara, A. Y. and Barber, J. R. 2015. Tempo and mode of antibat ultrasound production and
1230 sonar jamming in the diverse hawkmoth radiation. *PNAS,* **112** (20), 6407–6412.
1231 https://doi.org/10.1073/pnas.1416679112

1233 Kawahara, A. Y., Plotkin, D., Espeland, M., Meusemann, K., Toussaint, E. F. A., Donath, A.,
1234 Gimnich, F., Frandsen, P. B., Zwick, A., Dos Reis, M., Barber, J. R., Peters, R. S., Liu, S., Zhou,
1235 X., Mayer, C., Podsiadlowski, L., Storer, C., Yack, J. E., Misof, B. and Breinholt J. W. 2019.
1236 Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. *PNAS*, **116**
1237 (45) 22657–22663. https://doi.org/10.1073/pnas.1907847116

1239 Kernbach, K. 1967. Über die bisher im Pliozän von Willershausen gefundenen Schmetterlings-
1240 und Raupenreste. *Bericht der Naturhistorischen Gesellschaft zu Hannover*, **111**, 103–108.

1242 Kitching, I.J. and Sadler, S. 2011. Lepidoptera, Insecta. 549–554. *In* Harrison, T. (ed.)
1243 *Paleontology and Geology of Laetoli: Human Evolution in Context, Vol. 2: Fossil Hominins and*
1244 *the Associated Fauna.* Springer, Dordrecht, Heidelberg, London & New York, 600 pp.

1245

1246 Kitching, I.J., Rougerie, R., Zwick, A., Hamilton, C.A., St Laurent, R.A., Naumann, S.,
1247 Ballesteros Mejia, L. and Kawahara, A.Y. 2018. A global checklist of the Bombycoidea (Insecta:
1248 Lepidoptera) [with Suppl. Material 1: Global Bombycoidea checklist]. *Biodiversity Data*
1249 *Journal*, **6**, e22236. https://doi.org/10.3897/BDJ.6.e22236

1250

1251 Komai, F., Yoshiyasu, Y., Nasu, Y. and Saito, T. (eds) 2011. *A guide to the Lepidoptera of*
1252 *Japan*. Tokai University Press, Hadano, Kanagawa, xx + 1307 pp.

1253

1254 Kozlov, M.V. 1988. Paleontology of lepidopterans and problems of the phylogeny of the order
1255 Papilionida. 16–69. *In* Ponomarenko, A.G. (ed.) *The Mesozoic–Cenozoic Crisis in the Evolution*
1256 *of Insects*. Academy of Sciences, Moscow.

1257

1258 Kristensen, N.P. and Simonsen, T.J. 2003. Chapter 2. "Hairs" and scales. 9-22. *In* Kristensen,
1259 N.P. (ed.), *Lepidoptera, moths and butterflies, volume 2: Morphology, physiology, and*
1260 *development (Handbook of Zoology IV, 36)*. Walter de Gruyter, Berlin and New York, xii + 564
1261 pp.

1262

1263 Kunz, P. 2010. 30 ans déjà. *ASAM Bulletin*, **2010**, 39–45.

1264

1265 Kunz, P. 2012. Les temps forts de l'ASAM. Le Blog. Cocons, œufs, pupes et graines ou Révision
1266 des ovoïdes du Lutétien de Bouxwiller en Alsace – France. https://asam67.org/ovoides-de-
1267 bouxwiller/ [Blog post, accessed 18.11.2019]

1268

1269 Kunz, P. 2015. Les temps forts de l'ASAM. Le Blog. Bouxwiller 2015 : les ovoïdes ont de
1270 nouveaux parents! https://asam67.org/bouxwiller-2015-les-ovoides-ont-de-nouveaux-parents/
1271 [Blog post, accessed 18.11.2019]

1272

1273 Kuznetzov, V.I. and Stekolnikov, A.A. 1985. Comparative and functional morphology of the
1274 male genitalia of the bombycoid moths (Lepidoptera, Papilionomorpha: Lasiocampoidea,
1275 Sphingoidea, Bombycoidea) and their systematic position. *Trudȳ zoologicheskogo Instituta,*
1276 *Leningrad*, **134**, 3–48.

1277

1278 Kusnezov, N. 1941. *A Revision of Amber Lepidoptera*. Paleontological Institute, USSR Academy
1279 of Sciences, Moscow & Leningrad, 135 pp.

1280

1281 Leakey, L.S.B. 1952. Lower Miocene invertebrates from Kenya. *Nature*, **169** (4302), 624–625.

1282

1283 Lemaire, C. 1980. Les Attacidae américains. The Attacidae of America (=Saturniidae).
1284 Arsenurinae. C. Lemaire, Neuilly-sur-Seine, 199 pp. + 76 pls.

1285

1286 Lemaire, C. and Minet, J. 1998. Chapter 18. The Bombycoidea and their relatives. 321–353. *In*
1287 Kristensen, N.P. (ed.), *Lepidoptera, moths and butterflies, volume 1: Evolution, systematics, and*
1288 *biogeography (Handbook of Zoology IV, 35)*. Walter de Gruyter, Berlin and New York, 487pp.
1289

1290 Lima, A. Da Costa. 1950. *Insetos do Brasil, tomo 6: Lepidópteros (2a parte)*. Escola Nacional de
1291 Agronomia, Rio de Janeiro, 420 pp.
1292

1293 Madden, A.H. 1944. The external morphology of the adult tobacco hornworm (Lepidoptera,
1294 Sphingidae). *Annals of the entomological Society of America*, **37** (2): 145–160.
1295

1296 Martínez-Delclòs, X., Briggs, D.E.G. and Peñalver, E. 2004. Taphonomy of insects in carbonates
1297 and amber. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **203**, 19–64.
1298 https://doi.org/10.1016/S0031-0182(03)00643-6
1299

1300 Melchor, R.N., Genise, J.F. and Miquel, S.E. 2002. Ichnology, Sedimentology and paleontology
1301 of Eocene calcareous paleosols from a Palustrine Sequence, Argentina. *Palaios,* **17**, 16–35.
1302

1303 Michener, C.D. 1952. The Saturniidae (Lepidoptera) of the Western hemisphere. Morphology,
1304 phylogeny, and classification. *Bulletin of the American Museum of Natural History*, **98**, 335–
1305 501.
1306

1307 Minet, J. 1994. The Bombycoidea: phylogeny and higher classification (Lepidoptera: Glossata).
1308 *Entomologica scandinavica*, **25** (1), 63–88.
1309

1310 Nel, A. and Nel, J. (1985) À propos de chenilles et de chrysalides fossiles du stampien en France
1311 (Lepidoptera). *Alexanor*, 1, 3: 126–130.
1312

1313 Nieukerken, E.J. van, Kaila L., Kitching, I.J., Kristensen, N.P., Lees D.C., Minet, J., Mitter, C.,
1314 Mutanen, M., Regier, J.C., Simonsen, T.J., Wahlberg, N., Yen, S.-H., Zahiri, R., Adamski, D.,
1315 Baixeras, J., Bartsch, D., Bengtsson, B. Å., Brown, J. W., Bucheli, S. R., Davis, D. R., De Prins,
1316 J., De Prins, W., Epstein, M. E., Gentili-Poole, P., Gielis, C., Hättenschwiler, P., Hausmann, A.,
1317 Holloway, J. D., Kallies, A., Karsholt, O., Kawahara, A., Koster, S. J. C., Kozlov, M.,
1318 Lafontaine, J. D., Lamas, G., Landry, J. F., Lee, S., Nuss, M., Penz, C., Rota, J., Schmidt, B. C.,
1319 Schintlmeister, A., Sohn, J. C., Solis, M. A., Tarmann, G. M., Warren, A. D., Weller, S.,
1320 Yakovlev, R., Zolotuhin, V. and Zwick, A. 2011. Order Lepidoptera Linnaeus, 1758. In: Zhang,
1321 Z.-Q. (ed.), Animal biodiversity: an outline of higher-level classification and survey of
1322 taxonomic richness. *Zootaxa*, 3148: 212-221.
1323

Packard, A.S. 1893. Attempt at a new classification of the Bombycine Moths. *Journal of the New York entomological Society*, **1**, 6–11.

Parham, J.F., Donoghue, P.C.J., Bell, C.J., Calway, T.D., Head, J.J., Holroyd, P.A., Inoue, J.G., Irmis, R.B., Joyce, W.G., Ksepka, D.T., Patané, J.S.L., Smith, N.D., Tarver, J.E., Van Tuinen, M., Yang, Z., Angielczyk, K.D., Greenwood, J.M., Hipsley, C.A., Jacobs, L., Makovicky, P.J., Müller, J., Smith, K.T., Theodor, J.M., Warnock, R.C.M. and Benton, M.J. 2012. Best practices for justifying fossil calibrations. *Systematic Biology*, **61** (2), 346–359. https://doi.org/10.1093/sysbio/syr107

Peñalver, E. and Grimaldi, D.A. 2006. New data on Miocene butterflies in Dominican Amber (Lepidoptera: Riodinidae and Nymphalidae) with the description of a new nymphalid. American Museum Novitates, 3591, 1–17.

Peterson, A. 1956. *Larvae of Insects, an introduction to Nearctic species (3rd edition). Part I. Lepidoptera and plant infesting Hymenoptera*. Columbus, Ohio, 315 pp.

Richter, G. and Storch, G. 1980. Beiträge zur Ernährungsbiologie eozäner Fledermäuse aus der "Grube Messel". *Natur und Museum*, **110** (12), 353–367.

Ryckewaert, P., Razanamaro, O., Rasoamanana, E., Rakotoarimihaja, T., Ramavovololona, P. and Danthu, P. 2011. Les Sphingidae, probables pollinisateurs des baobabs malgaches. *Bois et Forêts des Tropiques*, **307** (1), 55–68.

Roselli, F.L. 1939. Apuntes de geología y paleontología uruguaya. Sobre insectos del Cretácico del Uruguay o descubrimiento de admirables instintos *constructivos de esa época. Boletín de la Sociedad Amigos de las Ciencias Naturales 'Kraglievich-Fontana',* **1**, 72–102.

Roselli, F.L. 1987. Paleoicnología. Nidos de insectos fósiles de la cubertura Mesozoica del Uruguay. *Publicaciones del Museo Municipal de Nueva Palmira*, **1**, 1–56.

Rougerie, R. 2005. *Phylogeny and biogeography of the Saturniinae (Lepidoptera: Bombycoidea, Saturniidae)*. PhD thesis. Muséum national d'Histoire naturelle, Paris, France. 530 pp. + 45 pls.

Rougerie, R., Cruaud, A., Arnal, P., Ballesteros-Mejia, L., Condamine, F., Decaëns, T., Elias, M., Gey, D., Hebert, P., Kitching, I.J., Lavergne, S., Lopez-Vaamonde, C., Murienne, J., Cuenot, Y., Nidelet, S. and Rasplus, J.-Y. 2022. Phylogenomics illuminates the evolutionary history of wild silkmoths in space and time (Lepidoptera: Saturniidae). bioRxiv preprint: https://www.biorxiv.org/content/10.1101/2022.03.29.486224v2 , accessed 27.02.2023.

1364 Rougerie, R. and Estradel, Y. 1998. Morphology of the preimaginal stages of the African
1365 emperor moth *Bunaeopsis licharbas* (Maassen and Weyding): phylogenetically informative
1366 characters within the Saturniinae (Lepidoptera: Saturniidae). *Journal of Morphology*,
1367 Supplement, **269**, 207–232.

1369 Schlotheim, E.F. von 1820. Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die
1370 Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und
1371 Pflanzernreichs der Vorwelt erläutert. Bekker'schen edit, Gotha, 457 pp.

1373 Schüssler, H. 1933. Saturniidae: 1. Subfam. Attacinae. In: Strand, E. (ed.), Lepidopterorum
1374 Catalogus. W. Junk, Berlin, 769 pp.

1376 Schöberlin, E. 1888. Der Oeninger Stinkschiefer und seine Insektenreste. Societas Entomologica,
1377 3(9), 68–69.

1379 Schröter, J.S. 1784. Neue Litteratur und Beyträge zur Kenntniß der Naturgeschichte vorzüglich
1380 der Conchylien und Foßilien, Vol. 1. Müller, Leipzig, 550 pp. https://zs.thulb.uni-
1381 jena.de/rsc/viewer/jportal_derivate_00164692/NLKN_1784_Bd01_%200001.tif?logicalDiv=jpor
1382 tal_jpvolume_00067117

1384 Scoble, M. J. 1992. The Lepidoptera: form, function and diversity. Oxford: Oxford University
1385 Press/Natural History Museum, 352 pp.

1387 Simonsen, T.J., Wagner, D.L. and Heikkilä, M. 2019. Ghosts from the past: a review of fossil
1388 Hepialoidea (Lepidoptera). *PeerJ* 7: e7982. http://doi.org/10.7717/peerj.7982

1390 Sohn, J.-C., Labandeira, C. and Davis, D. 2015. The fossil record and taphonomy of butterflies
1391 and moths (Insecta, Lepidoptera): implications for evolutionary diversity and divergence-time
1392 estimates. BMC Evolutionary Biology 15: Article 12 https://doi.org/10.1186/s12862-015-0290-8

1394 Sohn, J. C., Labandeira, C., Davis, D. and Mitter, C. 2012. An annotated catalog of fossil and
1395 subfossil Lepidoptera (Insecta: Holometabola) of the world. *Zootaxa*, 3286: 1–116.

1397 Sohn, J.-C. and Lamas, G. 2013. Corrections, additions, and nomenclatural notes to the recently
1398 published World catalog of fossil and subfossil Lepidoptera. Zootaxa, 3599 (4), 395–399.
1399 https://doi.org/10.11646/zootaxa.3599.4.8

1401 Wahlberg, N., WHEAT, C.W. & PEÑA, C. 2013. Timing and patterns in the taxonomic
1402 diversification of Lepidoptera (butterflies and moths). PLoS ONE 8, e80875.
1403 https://doi.org/10.1371/journal.pone.0080875

1404

1405   Weyenbergh, H., Jr. 1869. Sur les insectes fossiles du calcaire lithographique de la Bavière, qui

1406   se trouvent au Musée Teyler. *Archives du Musée Teyler*, 2, 247–294.

1407

1408   Zeuner, F.E. (1927) Eine Sphingidenraupe aus dem Obermiozän von Böttingen.

1409   Palaeontologische Zeitschrift, 8, 321–326.

1410

1411   Zhang, J. 1989. Fossil Insects from Shanwang, Shandong, China. Shandong Science Technology

1412   Publishing House, Jinan, 459 pp.

1413

1414   Zhang, J., SUN, B. and ZHANG, X. 1994. Miocene Insects and Spiders from Shanwang,

1415   Shandong. Science Press, Beijing, 298 pp., 42 pls.

1416

1417   Zimmerman, E.C. 1958. Insects of Hawaii, vol. 7: Macrolepidoptera. University of Hawaii Press,

1418   Honolulu, xiii + 542 pp.

1419

1420   Zolotuhin, V.V. 2010. A review of the genus *Chionopsyche* Aurivillius, 1909 with the

1421   description of a new species (Lepidoptera, Lasiocampidae: Chionopsychinae). *Atalanta,*

1422   *Würzburg*, 41 (3/4): 361-366, one col. pl.

1423

1424   Zwick, A. 2008. Molecular phylogeny of Anthelidae and other bombycoid taxa (Lepidoptera:

1425   Bombycoidea). Systematic Entomology 33, 190–209. https://doi.org/10.1111/j.1365-

1426   3113.2007.00410.x

1427

1428   Zwick, A. 2009. The principal structure of male genital sclerites and muscles of bombycoid

1429   moths, with special reference to Anthelidae (Lepidoptera: Bombycoidea). *Arthropod Structure &*

1430   *Development*, 38 (2): 147-161. https://doi.org/10.1016/j.asd.2008.07.006

1431

1432   Zwick, A., Regier, J.C., Mitter, C. and Cummings, M.P. 2011. Increased gene sampling yields

1433   robust support for higher-level clades within Bombycoidea (Lepidoptera). *Systematic*

1434   *Entomology*, 36: 31–43. https://doi.org/10.1111/j.1365-3113.2010.00543.x

Figure 1

Mioclanis shanwangiana Zhang, Sun and Zhang, 1994.

(A) Wings as in fossil. (B) Wings drawn separately. Drawings: Joël Minet (A & B); Maria Heikkilä (C). Redrawn after Zhang et al. (1994). Scale bars represent: 3 mm (A and B); 5 mm (C).
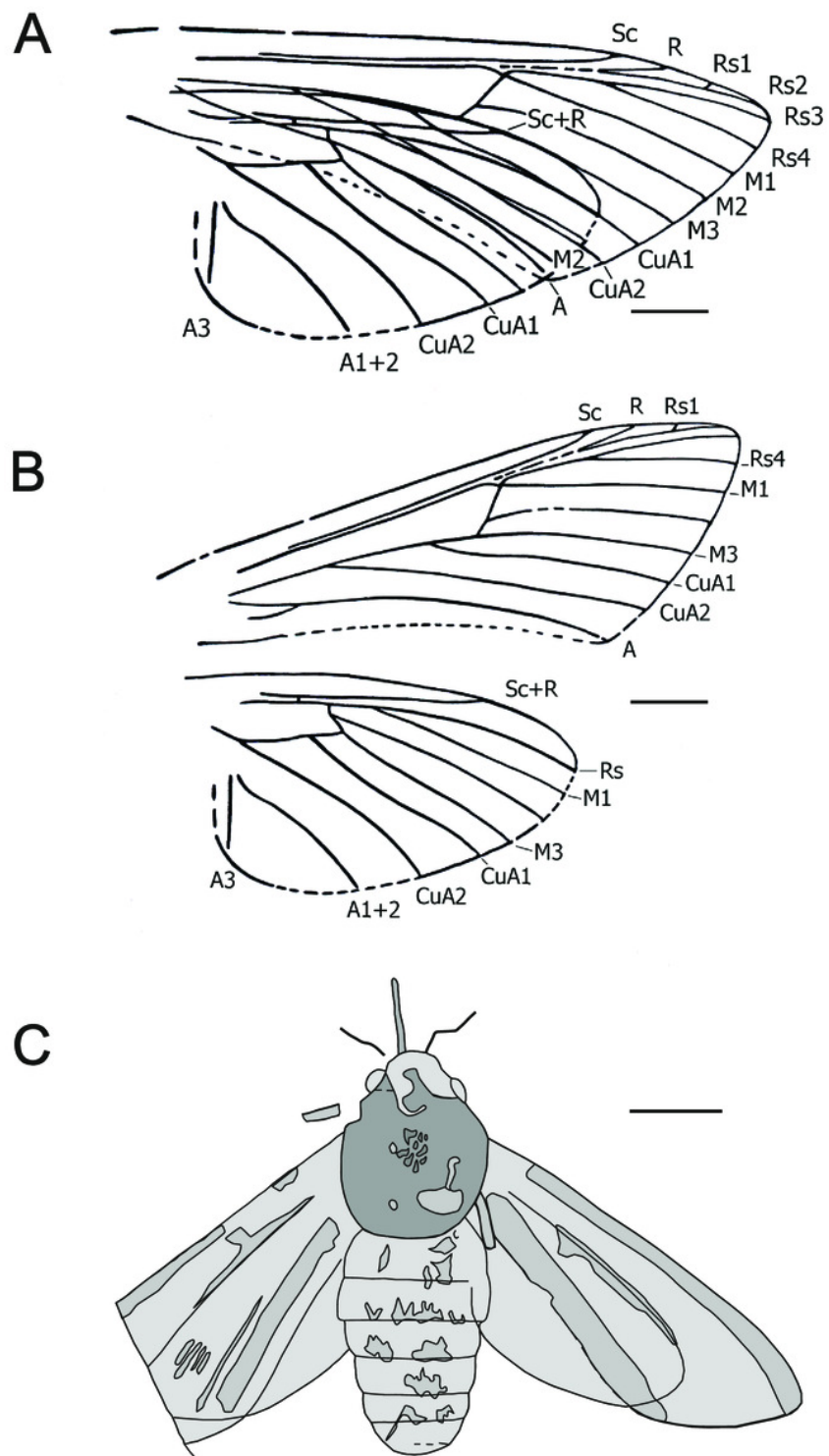
Figure 2

Counterpart and cast of the part of a fossilized sphingid larva (GPIT/HE/00071, NC/25/K/15).

The part has not been located at GPIT. All scale bars represent 1 cm. Photo credit: Hossein Rajaei, Staatliches Museum für Naturkunde, Stuttgart. Black and white photographs of the part and counterpart in Zeuner (1927).
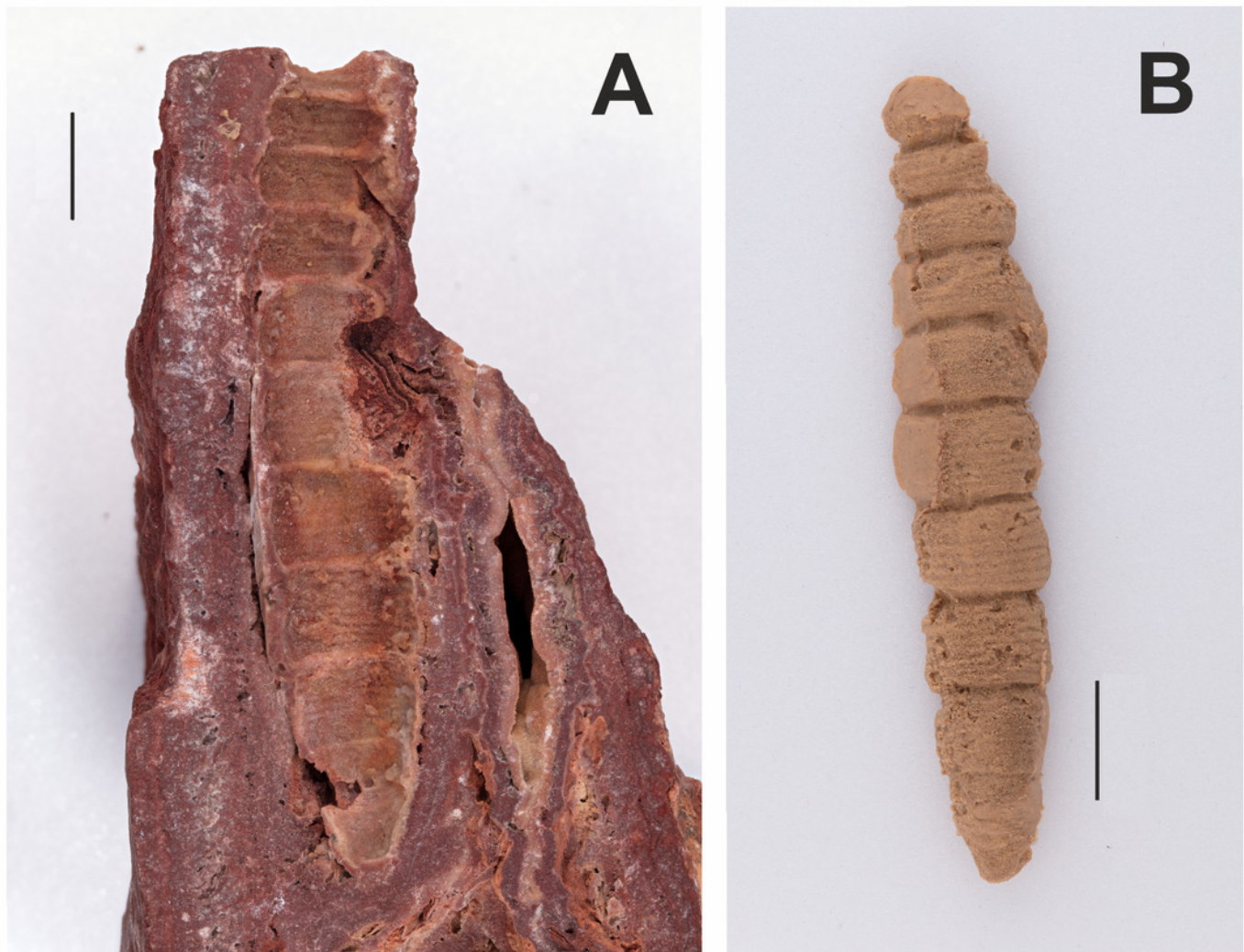
Figure 3

Fossilized pupa from Laetoli, Tanzania. (EP 352/03).

Late Pliocene. (A) Ventral view. Arrows pointing at antenna and labial palps. (B) Lateral view. (C) Dorsal view. (D) Oblique dorsal view of abdominal segment 10 showing the shallow L-shaped groove (arrow). (E) Posterior view showing radial supporting struts (arrow) around posterior margin of abdominal segment 7. (F) Close-up of mesonotal and metanotal calli. Scale bars represent: 5 mm (A-C). Photo credit. The Trustees of the Natural History Museum, London, UK.
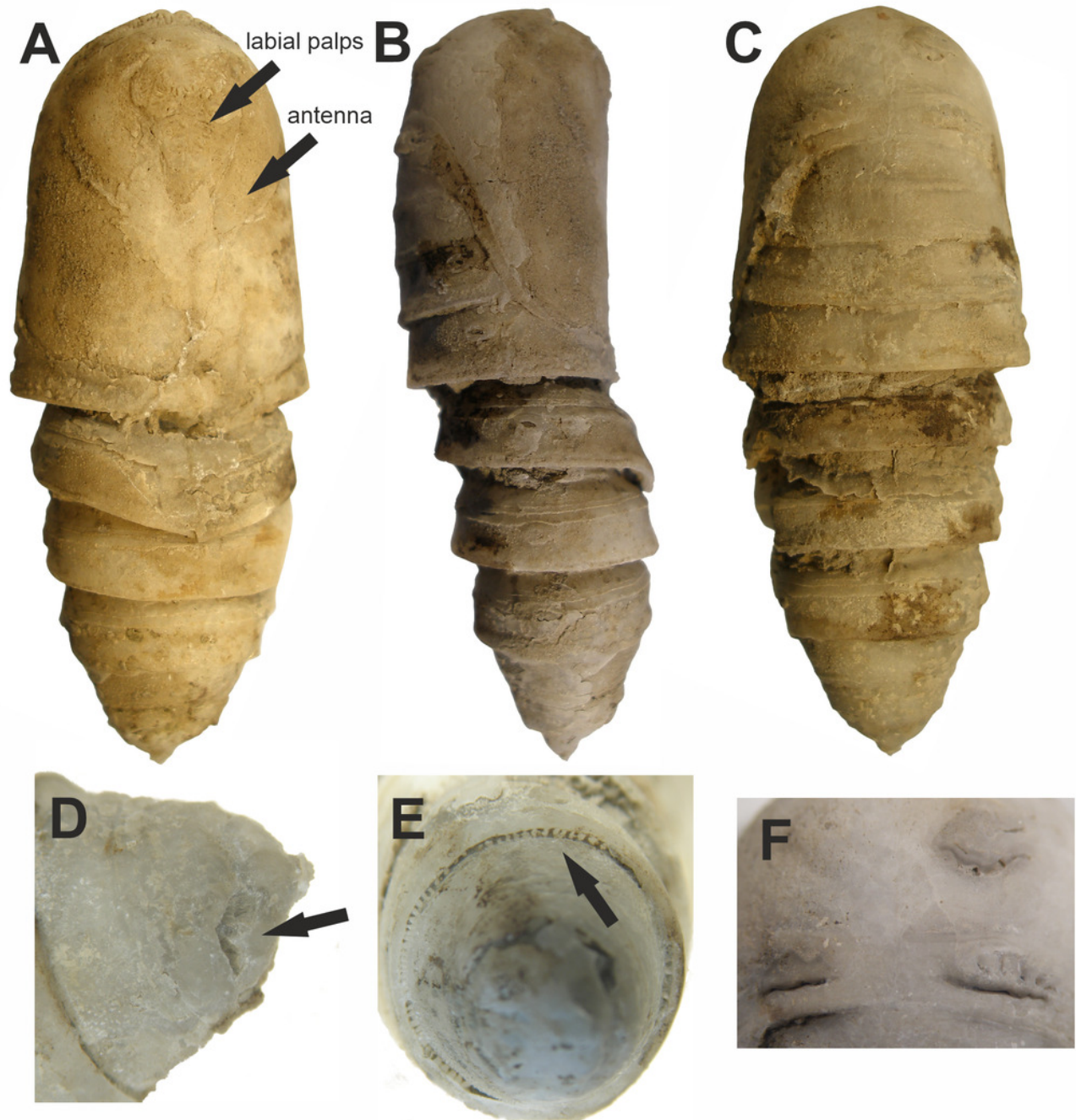
Figure 4

Proboscis of sphingid moth (right-hand lateral view). ROMIP30729. Talara Tar Pits, Talara, Peru.

Proboscis of sphingid moth (right-hand lateral view). ROMIP30729. Talara Tar Pits, Talara, Peru. © Royal Ontario Museum, Jean-Bernard Caron. Scale bars represents 1 mm.

Figure 5

Cast of fossil larva (KNMI-MW 261) reported by Leakey (1952) and identified as a possible sphingid by Kitching & Sadler (2011).

Cast of fossil larva (KNMI-MW 261) reported by Leakey (1952) and identified as a possible sphingid by Kitching & Sadler (2011). Fossil specimen not located. Photo credit: Job Kibii, NMK.

Figure 6

Attacus? fossilis Cockerell, 1914 [as cf. *Rothschildia fossilis* in Sohn *et al.* 2012]. UCM-8554.

Attacus? fossilis Cockerell, 1914 [as cf. *Rothschildia fossilis* in Sohn *et al.* 2012]. UCM-8554.

Photo credit: David Zelagin, UCM. Scale bar represents 5 mm.

Figure 7

(A and B) Compression-impression fossil of adult "sphingid" moth first illustrated in Zhang (1989). no. 820157.

(A and B) Compression-impression fossil of adult "sphingid" moth first illustrated in Zhang (1989). no. 820157. Photo: Sun Mingchang, SFML.
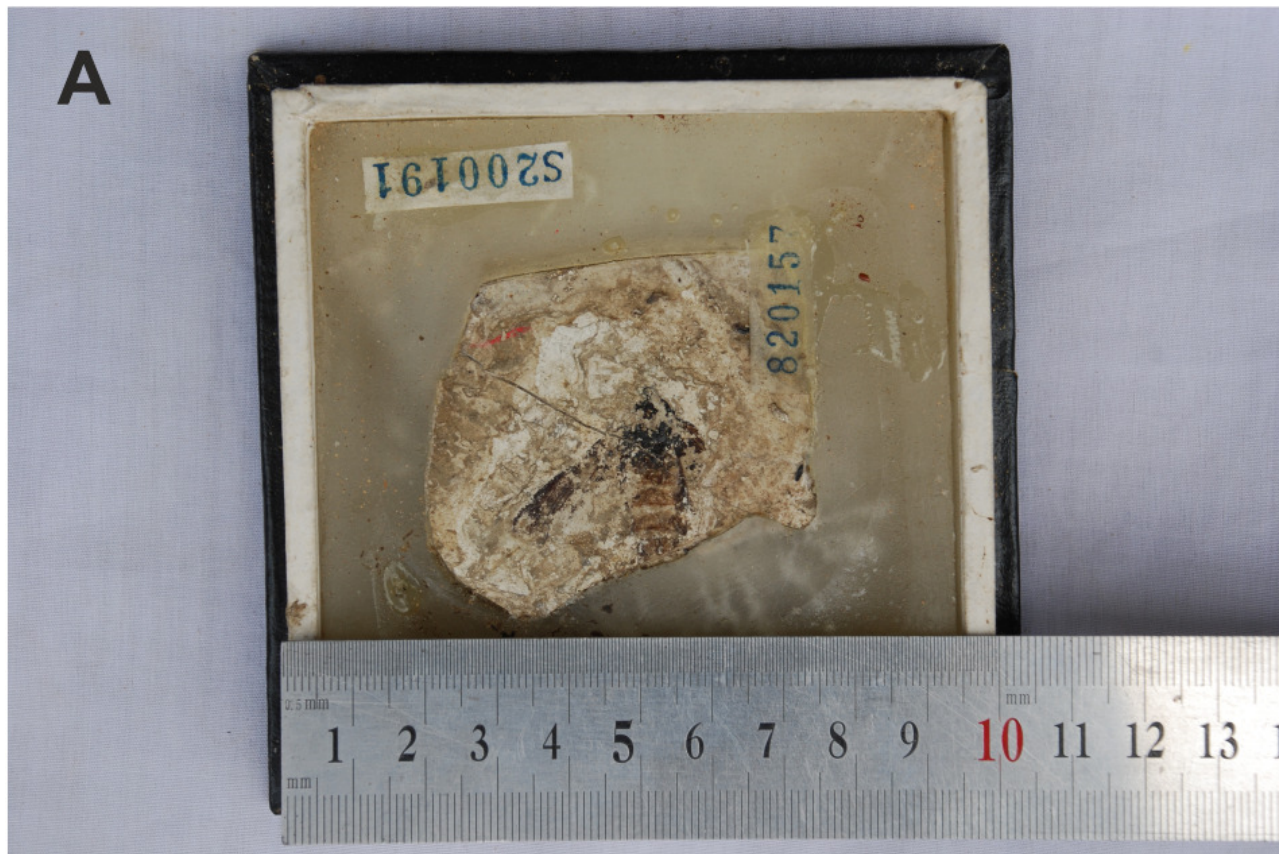
Figure 8

Sphingidites weidneri Kernbach, 1967. GZG.W.03445.

Photograph of the original photograph used in Kernbach´s article. Size not known. Photo credit: Alexander Gehler, GPUG.

Figure 9

Bombycites oeningensis Heer, 1849.

One of the abdomens is 3 lines (6.3 mm) wide and 6 lines (12.6 mm) long, the other 2.5 lines (5.25 mm) wide and 5.5 lines (11.5 mm) long (1 line = 2.1 mm). Photograph of illustration in original publication. The publication is no longer under copyright.

Figure 10

Bombycites buechii Heer, 1865. Specimen barcode number: 0000000005466.

Scale bar represents 2 mm. Photo credit: Earth Science Collections of ETH Zürich.

Figure 11

"Dayvault specimen". USNM PAL 618360.

(A) Compression fossil erroneously identified as a saturniid in Grande (2013). (B) Detail showing numerous crossveins. Scalebar represents 1 cm (A). Photo Credit: Alan Rulis, USNM.

Figure 12

Fossils of non-lepidopteran insects and a crustacean erroneously assigned to *Sphinx.*

(A) *Sphinx schroeteri* Germar,1839. MB.I.860. Photo downloaded from
https://portal.museumfuernaturkunde.berlin/ License: CC0. (B) Sphinx larva described in
Weyenbergh (1869). 15403. Photo credit: Teylers Museum, Haarlem, Netherlands. (C and D)
Sphinx snelleni Weyenbergh, 1869. 15396 and 15397. Photo credit: Teylers Museum,
Haarlem, Netherlands. All scale bars represent 1 cm.