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

Maria Heikkilä ^{Corresp., 1}, Joël Minet ², Andreas Zwick ³, Anna Hundsdoerfer ⁴, Rodolphe Rougerie ², Ian J. Kitching ⁵

¹ Finnish Museum of Natural History, Luomus, University of Helsinki, 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, London, United Kingdom

Corresponding Author: Maria Heikkilä Email address: maria.heikkila@helsinki.fi

We critically re-examine 17 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.

1 Critical re-examination of known purported fossil 2 Bombycoidea (Lepidoptera) 3 4 5 Maria Heikkilä¹, Joël Minet², Andreas Zwick³, Anna Hundsdoerfer⁴, Rodolphe Rougerie², Ian J. 6 7 Kitching⁵ 8 9 ¹ Finnish Museum of Natural History, Luomus, University of Helsinki, Finland ² Institut de Systématique, Évolution, Biodiversité (ISYEB), Muséum national d'Histoire 10 naturelle, CNRS, EPHE, Sorbonne Université, Université des Antilles, Paris, France 11

- ³ Australian National Insect Collection, CSIRO, Canberra, Australia
- ⁴ Molecular Laboratory, Museum of Zoology, Senckenberg Natural History Collections Dresden,
- 14 Dresden, Germany
- 15 ⁵ Natural History Museum, United Kingdom
- 16
- 17 Corresponding Author:
- 18 Maria Heikkilä¹
- 19 Finnish Museum of Natural History, Luomus, P.O. Box 17, FI-00014 University of Helsinki,
- 20 Finland Email address: maria.heikkila@helsinki.fi

21

22 Abstract

- 23 We critically re-examine 17 records of fossils currently assigned to the lepidopteran superfamily
- 24 Bombycoidea, which includes the silk moths, emperor moths and hawkmoths. These records
- 25 include subfossils, compression and impression fossils, permineralizations and ichnofossils. We
- 26 assess whether observable morphological features warrant their confident assignment to the
- 27 superfamily.
- 28
- 29 None of the examined fossils displays characters that allow unequivocal identification as
- 30 Sphingidae, but three fossils and a subfossil (Mioclanis shanwangiana Zhang, Sun and Zhang,
- 31 1994, two fossil larvae, and a proboscis in asphaltum) have combinations of diagnostic features
- 32 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
- 34 cases, even lepidopteran characters. Some of these dubious fossils have been used as calibration
- 35 points in earlier studies casting doubt on the resulting age estimates. All fossil specimens reliably
- 36 assigned to Bombycoidea are relatively young, the earliest fossil evidence of the superfamily
- 37 dating to the middle Miocene.
- 38 39

40 Introduction

- 41 The superfamily Bombycoidea is mostly diversified in the intertropical region of the globe
- 42 (Kitching and Rougerie et al. 2018) and includes the renowned moth families Sphingidae,
- 43 Saturniidae and Bombycidae. Sphingids are large pollinators with excellent flying abilities, yet
- 44 important prey for bats. The tobacco hornworm Manduca sexta (Linnaeus, 1763) is a common
- 45 pest sphingid species causing considerable damage to tobacco, tomato, pepper, eggplant, and
- 46 plantations of other crops. Saturniids include some of the largest moth species, most famous is
- 47 the giant silk moth *Attacus atlas* with a wingspan of 25–30 cm. The domesticated silkmoth
- 48 *Bombyx mori* Linnaeus, 1758 is a bombycid of great economic importance for silk production.
- 49 Because these species have been extensively studied, they play a leading role in the fields of
- 50 Lepidoptera genetics and physiology. Recently, a checklist reporting 6,092 species was provided
- 51 by Kitching and Rougerie *et al.* (2018).
- 52
- 53 The Bombycoidea monophyly is corroborated by morphological and molecular data (Minet
- 54 1994; Lemaire & Minet 1998; Regier *et al.* 2008; Zwick *et al.* 2011; Hamilton *et al.* 2019).
- 55 Based on molecular phylogenetics, changes were made to the higher-level classification in rapid
- 56 succession. Regier et al. (2008) included Anthelidae in Bombycoidea (formerly
- 57 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.*
- 59 (2011) established Mirinidae and the former bombycid subfamilies Oberthueriinae and
- 60 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
- reported by Kuntz (2010), and 33.9±0.1 Ma for *Attacus? fossilis* Cockerell, 1914 (Sohn *et al.*
- 71 2012). In the present work we provide arguments against the assertion that some of these fossils
- 72 represent lepidopterans (see below). The oldest trace fossils attributed to Sphingidae are from the
- 73 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,
- over 37 of these are permineralized cocoons from the same site in France and initially attributed
- 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
- points in divergence time analyses (e.g., Kawahara & Barber 2015). However, in many groups of
 Lepidoptera the original identifications of fossil specimens are known to be based on superficial
- similarity to modern species, not on apomorphies or reliable character combinations diagnostic
- of the group in question. Therefore, trusting the original identifications can lead to erroneous
- 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
- 85 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		
103	Materials &	& Methods
104		
105	Institutional	Abbreviations:
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	NMI	National Museum of Tanzania, Dar es Salaam, Tanzania
123	PFDL	Paleontological Fossil Depository (=山东临朐山肚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	TMH	Teylers Museum, Haarlem, The Netherlands.
134	UCM	University of Colorado Museum of Natural History, Boulder, Colorado, U.S.A.
135	USNM	United States National Museum of Natural History, Washington, DC, U.S.A.
136		
137	Specimens Ex	xamined:
138		

The fossils are deposited in different institutions around the world and visiting all the collectionswas not feasible. We were able to examine only two specimens in person: the compression fossil

141 tentatively identified as a saturniid by Grande (2013) and examined by MH at the USNM, and 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 144 145 assessments. In these cases, the curators of the collections and the photographers were instructed 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. 151 152 153 In three cases the original publication did not include a detailed description and illustrations of the specimen, and the depository was not stated. Therefore, we are unable to comment on the 154 155 veracity of the identifications. These fossils are listed in Results under the subheading "Fossils not examined". 156 157 158 The age estimates of the fossils were taken from Sohn et al. (2012) unless stated otherwise. 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: 165 166 167 1. Forecoxae distinctly fused anteriorly in last stage larvae (Figs. 25, 26 in Minet 1991; not so however in Apatelodidae, Carthaeidae, most Anthelidae and certain Eupterotidae); 168 169 170 2. D1 setae on larval segment A8 arising from a middorsal scolus (sometimes absent or replaced 171 by a conical protuberance; convergent evolution in some non-bombycoid families, e.g., genus Entometa Walker, 1855 in Lasiocampidae, several Notodontidae); 172 173 3. In the forewing venation, stem $Rs_1 + 2$ closely parallel to stem $Rs_3 + 4$ or fused to it (except in 174 175 most Anthelidae); 176 177 4. Loss of the spinarea (dense group of microtrichia), which is present, ventrally, at the base of the forewing in many Lasiocampidae and indisputably belongs to the lepidopteran ground plan 178 179 (although also lost, through parallel evolution, in various groups of Lepidoptera). 180

- 181 5. A long mesothoracic parepisternal sulcus that reaches, or terminates near, the anapleural cleft;
- this bombycoid autapomorphy is proposed here, based on information in Brock (1971: Figs 38b-
- 183 38d) and Minet (1994: 76). This sulcus had been regarded by Minet as a long "lower sector" of
- 184 the precoxal suture ("lps") because of Brock's interpretation of the ditrysian mesopleurosternum
- 185 (see Kristensen 2003 (Fig. 4.17) for a correct interpretation of this region).
- 186
- 187 If we compare, in the forewing, the common stem of Rs_1 and Rs_2 with that of Rs_3 and Rs_4 , the
- 188 R_{s_1}/R_{s_2} "forking point" is seen to lie distad of the R_{s_3}/R_{s_4} forking point in many Lasiocampoidea
- and Bombycoidea, but this trait cannot at present be regarded as a synapomorphy of these
- superfamilies as it is may be absent from the lasiocampid ground plan (Zolotuhin 2010: fig. 1, aChionopsychinae) and from some bombycoid families (e.g., Apatelodidae). According to
- 191 Chionopsychinae) and from some bombycoid families (e.g., Apatelodidae). According to
 192 Hasenfuss (1999: 156), a possible synapomorphy of these two superfamilies could be the
- 193 presence, in the larval proleg, of two layers of "pad cuticle" in the mesal region of the subcorona
- but this character remains to be verified more extensively in the Bombycoidea, having been
- 195 studied in only five bombycoid families. Unfortunately, another supposed bombycoid
- 196 autapomorphy in the male genitalia musculature (e.g., Minet 1994: 71) was based on several
- 197 misinterpretations in a paper by Kuznetzov & Stekolnikov (1985) and was thus rejected some
- 198 years ago (Zwick 2009).
- 199

200 Observing these characters in fossils is unlikely because of their often-fragmentary nature. In

- addition, some of the characters of interest are extremely small or are rarely, if ever, preserved
- because they are soft, unsclerotized structures. Because of these issues, we have also evaluated
- 203 whether combinations of homoplastic characters that are typically found in Bombycoidea could
- be observed and tried to identify diagnostic characters of subgroups of Bombycoidea, such as
- 205 families or subfamilies.

SPHINGIDAE

206

207 **Results**

- 208 The fossils are discussed under four subheadings: *Fossils assigned to Bombycoidea with*
- 209 reasonable certainty; Fossils possibly erroneously assigned to the Bombycoidea; Non-
- 210 *lepidopteran fossil insect erroneously assigned to the Saturniidae* and *Fossils not examined*.
- 211 When these sections include several fossils, they are discussed from oldest to youngest.
- 212
- 213

214 Fossils assigned to Bombycoidea with reasonable certainty:

- 215 216
- 217
- 218 The main distinctive traits of the Sphingidae were listed by Lemaire & Minet (1998: 344). Given
- that Brahmaeidae and Sphingidae are no longer regarded as sister groups, we propose to add the
- 220 following trait to the list of apomorphies that characterize the Sphingidae: in the hindwing

221 venation, Sc + R is approximated to the postdiscal section of Rs (an apomorphy also present, 222 through parallel evolution, in the Brahmaeidae). 223 224 1. Mioclanis shanwangiana Zhang, Sun and Zhang, 1994 225 Fig. 1. 226 227 **Excavation data:** China: Shandong, Lingu, Shanwang (Shanwang Formation); Langhian, 228 Middle Miocene. 229 Depository: PFDL Shandong, China (Holotype: SK000361). We have not been able to 230 determine where the PFDL currently is. 231 232 233 Published illustrations: Zhang, Sun and Zhang (1994): 82, figs. 58, 59, pl. 10: 4 (drawings). 234 Preservation type and size: Full-body compression/impression fossil of adult moth. A dorsal 235 view of the fossil, in which the wings are spread slightly overlapping either side of the body, and 236 an interpretation of the visible wing venation were illustrated in Zhang et al. (1994). Forewing 237 238 length: ca. 22.5 mm. Fragments of proboscis, antennal bases and legs visible. Sex indeterminate. 239 **Comments:** Despite considerable effort, we were unable to obtain more information on the 240 specimen. Assessment of this fossil is based on the illustrations and text in Zhang et al. (1994). 241 242 243 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 244 Macroglossum Scopoli, 1777. 245 246 247 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 248 al. 1994], currently placed in the tribe Leucophlebiini (Sphingidae: Smerinthinae) (see Kitching 249 and Rougerie et al., 2018). Thus far, the only wing trait proposed as a smerinthine apomorphy is 250 251 the constriction in the forewing, some distance before the tornus, of the space between the anal 252 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 253 254 (1998: 339, fig. 18.5 I) and so its lack in *Mioclanis* does not exclude this genus from 255 Smerinthinae. 256 257 Other characters consistent with a placement of *Mioclanis* in Sphingidae are: 258 Forewing veins Rs₁ and Rs₂ long-stalked (or entirely fused if the very short, free Rs1 branch is 259 260 an artefact). Both conditions occur in Sphingidae but the former is less common, being

261 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 262 sexta (Linnaeus, 1763) (Madden 1944: Fig. 9), Agrius cingulata (Fabricius, 1775) (Zimmerman 263 1958: Fig. 377), certain specimens of Monarda oryx Druce, 1896 (Haxaire & Minet 2017: 111) 264 265 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 266 determined), and so this character is consistent with Hemaris and Cephonodes Hübner, 1819. 267 268 269 Stem Rs_{1+2} is separate from Rs_{3+4} but roughly parallel to it (and very close to it). This is 270 consistent with the usual condition in Bombycoidea, in which these stems are either closely parallel or fused together (Lemaire & Minet 1998: 321). The only bombycoid family that does 271 272 not have this feature is Anthelidae (except the antheline genus *Cheleptervx* Gray, 1835), in which 273 these stems are involved in the formation of an elongate areole (= accessory cell) and so not 274 really approximated to each other. 275 276 Forewing discal cell narrow, with its upper angle more distal than its lower angle. This is the normal sphingid condition. 277 278 Forewing vein M_2 arises slightly closer to M_3 than to M_1 (i.e., discocellular m_2 - m_3 = about $\frac{1}{2}$ 279 *discocellular* m_1 - m_2). This again is the normal sphingid condition, although M₂ arises about 280 midway between M₁ and M₃ in *Callionima parce* (Lima 1950: Fig. 86). However, the condition 281 is widespread and also typical for Anthelidae and present in non-bombycoid families, e.g., some 282 283 Lasiocampidae, Erebidae and Satyridae. 284 285 In both forewing and hindwing, m-cu crossvein long and in line with adjacent section of the lower edge of the discal cell. This character occurs in many Sphingidae but is relatively rare in 286 287 other moth families. 288 289 *Forewing anal vein distinctly arched upwards.* This is typical of most Sphingidae. 290 291 Inner margin of forewing concave for much of its length. This feature is found in certain 292 Sphingidae (e.g., Hemaris fuciformis (Linnaeus, 1758)). 293 294 Hindwing veins Rs and M₁ short-stalked. This is typical of many Sphingidae but also occurs in 295 many other moth families. 296 297 Hindwing discal cell small, elongate and roughly parallel to the costa. This distinctive shape is consistent with many Sphingidae (see, e.g., Heppner 1998: Figs 435 and 436). 298 299

300 Hindwing crossvein (R) between subcosta and upper edge of discal cell beyond half length of discal cell. In *Mioclanis*, hindwing crossvein (R) between Sc and the upper edge of the discal 301 cell is more distal (beyond halfway) than in extant Sphingidae. However, although a crossing 302 point before halfway has been claimed as a sphingid apomorphy, it does also occur in other 303 304 bombycoids. 305 306 Several traits in *Mioclanis* disagree with the usual sphingid condition. Forewing vein Sc reaches the costa much more distally than in most sphingids, where this vein does not extend beyond the 307 middle of the costa (e.g., Hodges 1971). However, there are a few known exceptions, e.g., 308 309 Leucophlebia afra (Lemaire & Minet 1998: Fig. 339), Agrius cingulata (Zimmerman 1958: Fig. 310 377) and Daphnis nerii (Linnaeus, 1758) (Komai et al. 2011: Fig: II-39.3 E). 311 312 In *Mioclanis*, forewing vein R is shown as stalked with Rs_1+2 . This is never found in sphingids 313 as far as we are aware, where R arises separately from the leading edge of the discal cell around 314 the halfway point. R is stalked with elements of the radial sector in other bombycoids. However, this may be an artefact of the drawing, given the apparent ambiguity in this region. 315 316 317 In *Mioclanis*, although Sc+R beyond the discal cell is closer to Rs than in many other moths, it is not as close to it as in most extant Sphingidae (in which vein Sc+R is distinctly approximated to 318 the free section of Rs, at least for a short or very short distance – exceptions are rare but include 319 the closely related genera *Hemaris* and *Cephonodes*). 320 321 322 The wing shape of *Mioclanis* is closer to some Noctuoidea. 323 324 Overall, although many characters are consistent with *Mioclanis* being a sphingid, none is unequivocal. Furthermore, one is completely contrary to *Mioclanis* being a sphingid (although 325 326 consistent with some other bombycoids) and another is inconsistent with superfamily Bombycoidea. However, a comprehensive study of bombycoid wing venation is required to 327 328 ensure there are no exceptions. Thus, on balance, we consider that *Mioclanis* probably is a sphingid but its placement within the family remains uncertain. 329 330 331 *Mioclanis* was used to provide a minimum age for the crown Smerinthini s.s. in the study by 332 Kawahara & Barber (2015) (as 16.1 ± 0.9 Ma) and Rougerie et al. (2022). 333 334 335 2. Fossilized sphingid larva illustrated and described in Zeuner (1927) 336 Fig. 2. 337 Excavation data: Germany: Baden–Württemberg, Münsingen, Böttingen b. Münsingen 338 339 ("Böttinger Marble"); Sarmatian, Late Middle Miocene. Excavation locality and age of deposit



taken from Zeuner (1927) and specimen label, but these differ from the information given bySohn *et al.* (2012).

342

343 Depository: GPIT. GPIT/HE/00071, NC/25/K/15. The counterpart and a silicone cast of the
344 larva are in the GPIT collection. The part of this specimen has not been located (I. Werneburg,

345 pers. comm. December 13, 2019).

346

347 Published illustrations: Zeuner (1927): 321, figs. 1–3, 5 (black and white photographs).
348 https://link.springer.com/content/pdf/10.1007%2FBF03160426.pdf

349

350 **Preservation type and size:** Silica or permineralization. Length: ca. 7 cm; greatest width: 1.4 cm. The larva has not been compressed and has left a concave cavity lined by a 1-2 mm thick 351 layer of "dough-like limestone" embedded in red limestone. The head is missing, but Zeuner 352 353 described the specimen as otherwise nearly complete and unusually well preserved, and with the anterior part bent upwards. The cavities left by the thoracic legs are filled with aragonite and so 354 details cannot be observed. Details of abdominal and anal prolegs are also concealed. Zeuner 355 noted a cavity left by a slender anal scolus ("horn") and the anal plate is said to be relatively 356 357 large with a steep orientation.

358

Comments: According to Zeuner, the surface ornamentation and pleats (= "annulets") are 359 identical to those of extant sphingid larvae. He recognized two types of sphingid larvae: 1) those 360 in which the head capsule is rounded, the anterior three segments narrow abruptly, and the anal 361 362 plate is relatively small; and 2) those in which the head is dorsally pointed, the body segments gradually narrow anteriorly, and the anal plate is large. Although the head of the fossil larva is 363 missing, Zeuner assigned the fossil to the latter group based on the gradually narrowing body 364 shape and a large, steep anal plate. Although annulets occur in several other lepidopteran 365 366 families (Peterson 1956), they are more numerous, 6-8 per segment, in Sphingidae, and this condition is observed here. Furthermore, the presence of only a single median scolus on 367 abdominal segment 8 is also typical of Sphingidae, although there are exceptions (Scoble 1992; 368 Lemaire & Minet 1998). However, taken together, these two features, as well as its large size, 369 370 argue strongly for a placement of this fossil larva in Sphingidae, but incertae sedis because an assignment to a subfamily is too speculative. 371 372 373 374 3. Proboscis of sphingid moth in Churcher (1966) Fig. 3. 375

376

377 Excavation data: Peru: Piura, Talara (Lobitos Tablazo Formation); Late Pleistocene.

- 378
- 379 Depository: ROMUT. ROMIP30729

380 381 382	Published illustrations: Churcher (1966): 990, fig. 15 (black and white photograph).
383	Preservation type and size: Coiled structure interpreted as the haustellum (proboscis) of a
204	and moth in black against imprograded gandy matrix. The length of the structure is difficult
304	spiningia mourini ofack, aspirate-impregnated sandy matrix. The length of the structure is difficult
385	to assess because it is coned, and some of the cons are midden benind others. The diameter of the
386	coiled part of the structure (i.e., disregarding the basal (3 mm long) section) is ca. 4.2 mm. The
387	width of the coil at the base is ca. 0.8 mm. The haustellum seems to be at least 10 cm long (by
388	comparison with Recent Sphingidae having a coiled proboscis of a similar diameter).
389	
390	Comments: The large diameter of this structure suggests it is indeed a coiled sphingid proboscis.
391	When coiled, the well-developed proboscides of several large Erebidae (Noctuoidea) have a
392	diameter of at most 3.5 mm (e.g., Eudocima fullonia (Clerck, 1764) and Hypopyra megalesia
393	Mabille, 1880). The estimated length of this fossil proboscis $-10-11$ cm $-$ suggests a position
394	within the Sphinginae, the only sphingid subfamily in which proboscides of this length have
395	been recorded (Miller, 1997).
396	
397	
398	4. Fossil larva reported by Leakey (1952) and identified as a possible sphingid by Kitching
399	& Sadler (2011)
400	Fig 4
401	
402	Excavation data: Kenya: South Nyanza, Rusinga and M'fwangano Islands in Lake Victoria
403	(Hiwegi Formation): Burdigalian Farly Miocene
404	(Inwegi Formation), Durunganan, Larry Milocene.
405	Denositary: Pritich Kanya Miacana Expedition Collection NMK Accession No. KNMI MW
400	261. The specimen was not leasted but a cost of it was found
400	201. The specifien was not located but a cast of it was found.
407	Detricted Wester General Lesters (1052) , (24 fig. 1 (black and set its shots anoth)
408	Published mustrations: Leakey (1952): 624, fig. 1 (black and white photograph).
409	
410	Preservation type and size: Silica or permineralization. Whole body of a larva. The fossil has
411	retained the three-dimensional shape of the larva. Length 4 cm, width 0.7 cm.
412	
413	Comments: Kitching & Sadler (2011) wrote "Leakey (1952) illustrated an apparently large
414	lepidopteran larva from the early Miocene deposits on Rusinga and Mfangano Islands in Lake
415	Victoria, Kenya. The general smooth shape and secondary annulations of the body suggest this
416	fossil may belong to the family Sphingidae (hawkmoths), although it lacks the anal horn typical
417	of larvae of that family".
418	

419 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 420 and Francis Muchemi (NMK), but have been unable to reach any more definite conclusions. A 421 broken-off anal horn is unlikely in life (although they are sometimes bitten off in captivity when 422 423 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 424 prolegs suggest it is a "macrolepidopteran" but the head appears large, relative to the prothorax 425 rather than the body diameter, and the anal segment seems somewhat modified and deflected 426 downward, features that suggest it could be Hesperiidae (D. Wagner, pers. comm. June 18, 427 2019). Furthermore, the anal prolegs are relatively small, which is not the condition normally 428 found in Sphingidae, and the annulets, though present, are neither obvious nor numerous. 429 Overall, therefore, while it remains possible that this fossil is a sphingid, other 430 431 "macrolepidopteran" families cannot be ruled out and the family identification must be 432 considered incertae sedis. 433 434 SATURNIIDAE 435 436 Although Minet (1994: 83) proposed seven apomorphies for the characterization of the Saturniidae (e.g., tarsomere 4 of the foreleg sexually dimorphic, with a pair of distal, tooth-like 437 structures in the female), it should be noted that all of them belong to the imaginal stage. 438 439 440 5. Fossilized pupa discussed and illustrated by Kitching & Sadler (2011) 441 Fig. 5. 442 Excavation data: Tanzania: Laetoli, Upper Laetoli Beds (Laetoli Formation); ?Gelasian, Late 443 444 Pliocene. 445 446 **Depository:** NMT. EP 352/03. 447 448 Published illustrations: Kitching & Sadler (2011): 551–552, figs. 20.1a–c, g–h (black and white 449 photographs). 450 451 **Preservation type and size:** Permineralization. Pupa, whole body male. Length 37 mm; width 15 mm; depth 11 mm. The authors describe the fossil as slightly compressed dorsoventrally. A 452 453 detailed description was given by Kitching & Sadler (2011). 454 455 **Comments:** Kitching & Sadler (2011) identified this fossil as a pupa of a saturniid moth in the tribe Bunaeini (Bunaeinae Bouvier, 1927 according to Nässig et al. (2015) and Rougerie et al. 456 (2022)), a tribe exclusively Afrotropical in distribution. The authors compared the fossil with 457 458 several extant species of Bunaeini. The closest resemblance was found to be with the pupa of

459 *Cirina forda* (Westwood, 1849), although the fossil was not identified as this but a species near

460 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.
- 463

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

- 466 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):
- 469 junction zone between A2/A3, A3/A4, and A7/ A8–10 highly sclerotized with a row of

470 numerous vertical grooves. Dorsal grooves (or more developed cavities) were found to be

- 471 present in all the Bunaeini examined by Rougerie & Estradel (2008, their character 18), but also
- 472 in most Micragonini and Urotini. In addition, the fossil pupa has the characteristic elevated crest
- 473 on the posterior margin of A4-A6 (character 16 of Rougerie & Estradel 2008) found in the vast
- 474 majority of Bunaeini and which is only observed outside Bunaeini in the genus Usta Wallengren,
- 475 1863 of tribe Urotini. It gives a unique aspect to the fossil pupa (as seen in fig. 20.1b of Kitching
- 476 & Sadler), in which it appears more obvious than on the live pupa of *Cirina forda* illustrated in
- 477 Kitching & Sadler.
- 478

479 In his paper on Bunaeini, Rougerie (2008) separated a group of four genera (*Pseudobunaea*

- 480 Bouvier, 1927; Athletes Karsch, 1896; Lobobunaea Packard, 1901 and Pseudimbrasia Rougeot,
- 481 1962) based on the configuration of appendages on the cephalic mask of the pupa, and in
- 482 particular the antennae being far from reaching the midline of the pupa. In contrast, in all other
- 483 examined Bunaeini, including *Cirina*, the antennae reach the midline, with only the maxillae or
- 484 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
- 486 Kitching & Sadler, the antennae clearly meet medially. These characters indicate that the fossil is
- 487 not *Cirina*, and also exclude several other genera within the tribe.
- 488
- 489 Thus, while the identification of the fossil as Bunaeini is well supported, the genus-level
- 490 identification needs further study.
- 491

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

- 494
- 495 Fossils possibly erroneously assigned to the Bombycoidea:
- 496

497 6. Trace fossils of alleged sphingid or saturniid pupation chambers in the ichnogenus 498 *Teisseirei* Roselli, 1939

499

- 500 Excavation data: Specimens interpreted as representing the ichnotaxon *Teisseirei* have been
- 501 found in the Early Eocene Asencio Formation, Uruguay (see Genise 2014); localities of different
- 502 Cenozoic ages in Argentina (Puerto Unzué Formation, Gran Salitral Formation, Sarmiento
- 503 Formation, see Genise et al. (2013) and references therein, and the middle Miocene Collón Curá
- 504 Formation at El Petiso, Chubut province, see Genise *et al.* 2022); and the Pliocene deposits at
- 505 Laetoli, Tanzania (see Genise and Harrison (2018)).
- 506
- **Depository:** The material examined by Genise *et al.* (2013) is deposited in the following
- 508 collections: Colección de Icnología del Museo Argentino de Ciencias Naturales, Buenos Aires
- 509 (MACN-Icn); Museo Paleontológico Egidio Feruglio Trelew, Chubut, Argentina (MPEF-Ic); and
- 510 Colección Paleontológica de la Facultad de Ciencias, Montevideo, Uruguay (FCDPI). Material
- 511 examined by Genise and Harrison (2018) is deposited in the Harrison collection; and the material
- 512 examined by Genise *et al.* (2022) is in Ichnological Collection of the Museo Paleontológico
- 513 "Egidio Feruglio", Trelew, Chubut province, Argentina (MPEF-IC).
- 514

Published illustrations: *Teisseirei barattinia* Roselli, 1939: Roselli (1939): 82, figs 29 and 30

- 516 (drawings); 84, fig. 31:7 (black and white photograph); Melchor et al. (2002): 25, fig. 12 A–E, I
- 517 (black and white photographs); Genise (2004): 431, fig. 3 b, c (black and white photographs);
- 518 Genise *et al.* (2013): 481, fig. 1 (colour photographs) https://doi.org/10.1111/let.12025; Genise
- 519 (2017): 346, fig. 13.25; 349, figs 13.28 a–d (colour photographs). *Teisseirei linguatus* Genise &
- Harrison, 2018: 604, fig. 5 C–J (colour photographs); *Teisseirei barattinia* and *Teisseirei*
- 521 *paladinco* Genise & Cantil, 2022: Genise *et al.* (2022): 10–11, figs 7 A–I and 8 A (colour
- 522 photographs).
- 523

524 Preservation type and size: Trace fossils. There is some variation among the numerous

- 525 specimens of the *Teisseirei* ichnospecies, but in general they constitute of horizontal to sub-
- box horizontal chambers (enlargements of burrows) with a depressed, elliptical cross-section,
- 527 antechamber and multi-layered lining and inner surface covered in densely spaced sub-
- 528 rectangular or sub-triangular pits. On some of the chambers, a thin, discrete wall can be
- 529 observed. Internal casts of the chambers have also been found. For an amended diagnosis of the
- 530 ichnogenus *Teisseirei*, see Genise *et al.* (2022).
- 531
- 532 The size ranges of the several hundred chambers examined by Genise *et al.* (2013; 2022) and
- 533 Genise and Harrison (2018) were as follows: length 1.9–9.1 cm; width 0.9–4.9 cm; and height
- 0.75–3 cm. One exceptionally large chamber was 11.5 cm long and 7 cm wide. Genise *et al.*
- 535 (2013) suggested that the variation could be mostly taphonomic, but because the structures are
- 536 from different localities, it is also possible, even likely that different species produced them.
- 537

538 Comments: Originally, these structures ("Teisseirei barattinia") were suggested to be pupation chambers of Hymenoptera (Roselli 1939). Later, they were tentatively associated with 539 Coleoptera (Roselli 1987; Genise 2004). A new hypothesis that they were sphingid pupation 540 chambers was proposed by Genise et al. (2013), who made macro- and micromorphological 541 542 comparisons of these structures to pupation chambers burrowed by larvae of the modern sphingid species Manduca rustica (Fabricius, 1775) and Eumorpha labruscae (Linnaeus, 1758), 543 and observed similarities. In particular, the authors emphasized the similarity in the distinct type 544 of multi-layered lining of the chambers, which they interpreted to be the result of the larva 545 packing soil dampened by liquid it had excreted. The densely pitted internal surface texture 546 visible in *Teisseirei barattinia* specimens was also found to be similar to that seen inside M. 547 *rustica* pupation chambers. The pits were interpreted to be imprints of thoracic legs. The authors 548 also hypothesized that the antechamber of T. barattinia and the hatch in modern pupation 549 chambers through which the adult emerges, could be comparable in function. Because pupation 550 551 in *M. rustica* and *E. labruscae* does not occur very deep in the soil, the trace fossils were suggested to serve as indicators of uppermost horizons of palaeosols (Genise et al. 2013). 552 However, Genise et al. (2013) did note that in addition to Sphingidae, subterranean pupation 553 chambers are also known in other Lepidoptera, such as Noctuidae, Geometridae, and Saturniidae, 554 but the features and differences among these have not been thoroughly studied. 555

556

557 After the description of other ichnospecies in the ichnogenus *Teisseirei*, Genise *et al.* (2022)

amended the diagnosis of the ichnogenus and now attributed *Teisseirei* ichnospecies to the

559 pupation chambers of both Sphingidae and Saturniidae. Ichnotaxa are based on the fossilized

560 work of organisms but although the nomenclature of ichnotaxa resembles the conventional

- 561 Linnean system of classification, an ichnotaxon can include specimens that resemble each other
- 562 in morphology but those characteristics are not necessarily to be interpreted as evidence of a
- shared most-recent common ancestor. The ichnogenus *Teisseirei* belongs in the ichnofamily
- 564 Coprinisphaeridae; other ichnogenera in that ichnofamily are attributed to Coleoptera, Hemiptera
- and Hymenoptera (Genise 2004; Genise et al. 2022).
- 566

567 We consider that a ca. 2 cm long chamber, the minimum size mentioned by Genise *et al.* (2013),

is too small for a sphingid or a saturniid pupation chamber. According to Bell and Scott (1937:

569 341), the smallest known hawkmoth pupa (that of the Tiny Hawkmoth, *Sphingonaepiopsis*

- *pumilio* (Boisduval, 1875)) is 20 mm long. They add that it lies in a "rough cocoon" that is not
- subterranean and this cocoon must necessarily be longer than 20 mm. Furthermore, to the best
 of our knowledge, no recent Sphingidae or Saturniidae pupation chambers have "antechambers".
- 572 bi our knowledge, no recent springidae of Saturnidae pupation chambers have antechambers . 573 Thus, we consider it impossible at present to be certain that these pupation chambers were made
- 574 by sphingid or saturniid larvae specifically, rather than by the larvae of other lepidopteran
- 575 families (and possibly even other insect orders). There are hundreds of specimens placed in the
- 576 ichnogenus *Teisseirei*. It is possible that some of these fossil chambers are trace fossils produced
 - Peerl reviewing PDF | (2023:04:84528:1:1:NEW 26 Jun 2023)



577 by Sphingidae or Saturniidae, but it is also entirely possible that most of them may eventually prove not to be lepidopteran at all. 578 579 580 581 7. Fossilized ovoid structures reported by Kuntz (2010) 582 583 **Excavation data:** France: Alsace, North Middle Upper Rhine Graben, Bouxwiller quarry (Bouxwiller Formation); Lutetian, Middle Eocene. 584 585 **Depository:** The depository was not given in Kuntz (2015) but in Kuntz (2010) he implies that 586 such fossils are in several museum and private collections. Sohn et al. (2012) stated that the 587 specimens are deposited in "various institutes", but these were not listed. The exact number of 588 specimens is not given. 589 590 **Published illustrations:** Kuntz (2010): figs 40–45 (photographs); Kuntz (2015) (colour 591 photographs) https://asam67.org/bouxwiller-2015-les-ovoides-ont-de-nouveaux-parents/. 592 593 594 **Preservation type and size:** Permineralized ovoid structures proposed to be fossilized cocoons. The length of the largest of these ovoid specimens ranges from 5.5 to 7 cm, and the diameter 595 from 2.5 to 3 cm. One extremity of these structures is rounded, the other pointed or flared. The 596 surface is uneven, with imprints likened to crossing silk fibers. Some specimens have a slight 597 dent in the middle of the long side along with a stronger calcification, possibly attesting a 598 599 horizontal position of the cocoon with respect to the ground. Many of these cocoons have an opening, which Kuntz interpreted as the hole from which the adult moth had emerged. 600 601 Comments: Sohn et al. (2012) listed these specimens in fossil Saturniidae following Kuntz 602 603 (2010), who proposed that they were the cocoons of saturniid moths. The main evidence he gave to support this view were the flared openings at one extremity of some of these structures, which 604 he interpreted as similar to the cocoons of Saturniidae such as Saturnia pavonia (Linnaeus, 1758) 605 in which the narrower, somewhat open anterior end has an internal ring of apically convergent 606 607 stiffer "bristles" that serve to prevent ingress of predators while facilitating the emergence of the adult moth. In addition, the surface of the fossils seems to have an irregular, slightly helical, 608 striped pattern that is perpendicular to the long axis of the cocoon. Kuntz considered this type of 609 texture to be somewhat similar to that on cocoons spun by many recent saturniids, with 610 embossing on the surface formed by crossing silk fibers. However, in his 2015 publication, 611 Kuntz concluded that these egg-shaped structures are more likely pupal chambers of spider 612 613 wasps, such as those of the genus *Pepsis* Fabricius, 1804 (Pompilidae) [guêpe géante]. The size, the apparent solidity and the more or less helical striation was proposed to support this 614 hypothesis, but the variable shape of the opening was problematic. Kuntz supposed the shape of 615



the opening could help in the attribution of these egg-shaped structures to an insect group, but he 616 also noted that the shape could be related to the stage of eclosion at the moment of fossilization. 617 618 619 We agree that these are most probably not fossilized lepidopteran cocoons. 620 621 622 8. Attacus? fossilis Cockerell, 1914 [as cf. Rothschildia fossilis in Sohn et al. 2012] 623 Fig. 6. 624 Excavation data: USA: Colorado, Teller County, Florissant Beds National Monument, 625 Florissant Formation; Late Priabonian, Late Eocene (33.9±0.1 Ma). 626 627 Depository: UCM. Holotype: UCM-8554. 628 629 Published illustrations: Cockerell (1914): 271, fig. 34 (drawing). 630 631 **Preservation type and size:** A compression fossil with what Cockerell (1914) interpreted as the 632 imprint of the apex of the forewing with veins of a large moth in the family Saturniidae (Fig. 6). 633 The fragment is 33 mm in length. 634 635 **Comments:** The fossil shows at least five more or less parallel arched lines, some of which are 636 incomplete. The distance between the arched lines is about 5 mm. There are no obvious stalked 637 638 or connate veins, and no traces of a wing pattern or scales. Cockerell (1914) interpreted the parallel arched lines as veins, and the shorter line in the lower right of the fragment (as viewed in 639 fig. 8), more or less perpendicular to the longest vein, as a short segment of the wing margin (see 640 fig. 34 in Cockerell 1914). Cockerell considered the venation of the fossil to closely correspond 641 642 to that of the forewing of Attacus dohertvi Rothschild, 1895, and tentatively named the specimen Attacus? fossilis. In the catalogue by Sohn et al. (2012), the specimen is referred to as cf. 643 Rothschildia fossilis following Schüssler (1933), who transferred "fossilis" from Attacus to the 644 genus Rothschildia Grote, 1896, probably because the former does not occur in the New World. 645 646 Below we attempt to reconstruct the reasons and characters that presumably led Cockerell to 647 assign the fossil to Saturniidae. We also evaluate whether these characters can reliably place the 648 fossil in this family. 649 650 The longest of the veins on the fossil was interpreted by Cockerell as vein "R5", (i.e., Rs₄ in current venation nomenclature), and he considered that the rather strongly curved shape of the 651 veins and the arrangement of Rs₄ in relation to the short wing margin section resembled the distal 652 (apical) part of the forewing of certain Saturniidae. The strongly arched veins Rs₄ and M₁ indeed 653 occur in the tribe Attacini but also in some Antheraea Hübner, 1819 (see fig. 92 in Michener 654 655 1952) and several Arsenurinae (see, e.g., fig. 40 (Caio richardsoni (Druce, 1890), fig. 41

656 (*Rhescyntis pseudomartii* Lemaire, 1975) in Michener (1952), and figs 56, 57 and 126 in

- 657 Lemaire (1980)). The relatively greater distance separating Rs_4 from the vein below (M₁) could
- also have been seen as a feature found in large Lepidoptera, such as saturniids. In addition, the
- 659 concave shape of the wing margin at the apex of Rs_4 occurs occasionally in *Rhescyntis* Hübner,
- 1819 (Lemaire 1980: fig. 126) but practically never in *Antheraea* and *Rothschildia*. In contrast,
- the oblique line of M_2 (the short, incomplete vein below M_1) would fit better with Saturniinae
- 662 (e.g., *Antheraea*) than with Arsenurinae.
- 663
- 664 We compared the veins on the fossil with those of several species of extant large saturniid moths 665 (those mentioned above and figures in Rougerie (2005)) by superimposing the fossil veins onto 666 illustrations of their forewing venation. In many cases the curvature of the veins was too strong
- 667 and did not correspond to that of the extant species. However, the curvature did follow more
- 668 closely the veins of the extant species of Attacini and *Antheraea*, but otherwise there was no
- 669 other obvious support for an assignment to the Saturniidae.
- 670
- 671 We also asked paleobotanist Dr Herbert Meyer (Florissant Fossil Beds National Monument,
- 672 Colorado, USA) and paleoentomologist Dr Conrad Labandeira (NMNH, Washington, D.C.,
- 673 USA) to examine a photograph of the fossil. They concluded that the imprint on the slab was
- 674 probably made by a leaf. This assessment was based on the observation that the line considered
- by Cockerell to be a short segment of the wing margin was actually the thicker primary vein of a
- leaf. The arched veins (Cockerell's R and M veins) were interpreted as secondary veins of the
- 677 leaf. The secondaries were also noted to merge into the primary and not end abruptly as would be
- expected in an insect. Possible plant genera candidates could be *Staphylea* L., *Hydrangea* L., or
- 679 *Celastrus* L. (H. Meyer, pers. comm. November 14, 2016).
- 680
- 681 *Attacus? fossilis* was used as a calibration point in the divergence time analysis by Kawahara &
- Barber (2015) to give a minimum age to the stem group of *Rothschildia* and *Saturnia* Schrank,
- 683 1802. The supporting information of their study stated that the fossil shares synapomorphies with
- extant *Rothschildia* and *Saturnia*, a mistake the authors were not able to correct after the final
- edits (A. Kawahara, pers. comm. June 14, 2015). Given the very different interpretations of the
- 686 fossil, we conclude that the identification is based on superficial similarity and additional
- characters would be needed to place it reliably in Saturniidae (or any of the proposed plantgenera, for that matter).
- 689
- 690

691 9. Compression-impression fossil of adult moth in Zhang (1989)

- 692 Fig. 7.
- 693
- 694 Excavation data: China: Shandong, Linqu, Shanwang (Shanwang Formation); Langhian,
- 695 Middle Miocene.

696	
697	Depository: SFML. no. 820157.
698	
699	Published illustrations: Zhang (1989): 94, pl. 20: 3 (black and white photo).
700	
701	Preservation type and size: Compression-impression fossil of an adult moth. Poorly preserved.
702	Head, thorax, abdomen, left forewing and base of right forewing partly visible. Abdominal
703	segments with impressions of hair-like scales of reddish-brown colour. Some wing venation
704	visible on wings. Length of left forewing about 2.3 cm. Length of the preserved part of the body
705	is 25.2 mm. Width of abdomen at its widest part 1 cm.
706	
707	Comments: Zhang (1989) identified the fossil as a sphingid based mostly on forewing
708	characteristics but noted that the genus and species cannot be determined. Zhang wrote that the
709	fossil has some similarities to moths in the genus Clanis Hübner, 1819 [misattributed to Walker
710	by Zhang (1989)] but did not elaborate on these. According to the original description by Zhang,
711	the forewing veins Rs ₃ and Rs ₄ [cited just as R and R] are stalked, M ₁ [cited as just M] originates
712	in the upper corner of the discal cell, and Sc, R, Rs ₁ and Rs ₂ [cited as Sc, R ₁ , R ₂ and R ₃] are
713	parallel and closely aligned. Five abdominal segments can be distinguished. However, only part
714	of the forewing venation is visible in the specimen and the above description by Zhang is
715	inaccurate. Importantly, vein M ₂ is straight and arises midway between M ₁ and M ₃ , a character
716	that suggests this fossil differs from Mioclanis shanwangiana and may even not belong to the
717	Sphingidae (in which vein M_2 arises closer to M_3 than to M_2 ; Lemaire & Minet (1998)). The
718	poor preservation of the specimen and lack of characters does not allow a reliable identification
719	of this specimen to superfamily level (or lower).
720	
721	
722	10. Sphingidites weidneri Kernbach, 1967
723	
724	Excavation data: Germany: Lower Saxony, Willershausen am Harz; Piacenzian, Late Pliocene.
725	
726	Depository: GZG. Holotype: GZG.W.03445 (old no. 596-11). The specimen has not been
727	located but is most certainly in the GZG collection (A. Gehler, pers. comm. June 26, 2018). We
728	were able to examine a photograph of the original photograph by Adolf Straus, used by
729	Kernbach and published in the "Berichte der Naturhistorischen Gesellschaft Hannover" (1967).
730	There is a typographical error in A. Straus's specimen number in Kernbach (1967) where it was
731	given as 3435. In the photograph presented in Kernbach's publication, the specimen number had
732	been cropped so that it cannot be completely seen. The complete number is 3445.
733	
734	Published illustrations: Kernbach (1967): 108, fig. 11 (black and white photograph)
735	https://www.zobodat.at/pdf/Ber-Nathist-Ges-Hannover_111_0103-0108.pdf.

736	
737	Preservation type and size: Whole body compression-impression fossil of a larva. Size not
738	given by Kernbach (1967).
739	
740	Comments: Brauckmann et al. (2001) considered Kernbach's description of the genus
741	Sphingidites to be invalid because of the lack of a diagnosis. However, Sohn & Lamas (2013)
742	supported the interpretation that Kernbach intended this genus to accommodate fossil Sphingidae
743	whose association below family-level is not convincing and thus, as a collective genus, no type
744	species or diagnosis is required. A subsequent type designation had been provided by Clark et al.
745	(1971: 582) but this was also unnecessary because the type would have been automatically fixed
746	by monotypy. The circumscription of the genus is not affected by the type species designated by
747	Clark <i>et al.</i> (1971).
748	
749	Kernbach (1967) interpreted the specimen to be probably a (prepupal) larva whose
750	transformation from larva to pupa had been disturbed. He reported the presence of several larval
751	segments and an anal horn. Some transverse lines are visible in the photograph that could be
752	interpreted as larval segments and a darker, narrow and short projection at one end of the fossil,
753	the possible anal horn, can be observed. However, because these characters are not very clear
754	and others cannot be made out, we agree with Kozlov (1988: 23, 55) and consider the
755	identification of this fossil as a sphingid to be uncertain. Indeed, it is very difficult to interpret
756	and possibly does not even represent a caterpillar.
757	
758	
759	11. Bombycites oeningensis Heer, 1849
760	Fig. 8.
761	
762	Excavation data: Germany, Baden-Württemberg: Oeningen ("Molasseformation"), that is
763	Wangen (near Ohningen – see e.g., Cockerell 1915); Messinian, Late Miocene.
764	
765	Depository: Heer (1849) wrote that the specimen is deposited at the University of Zurich and
766	according to Sohn <i>et al.</i> (2012) the holotype is in the PIMUZ. However, it is not in the PIMUZ
767	database (https://www.pim.uzh.ch/apps/cms/pageframes/sammlung_db.php), which includes all
768	published specimens (C. Klug, PIMUZ, pers. comm., May 16, 2018). It was not found in the
769	ETH Zürich, Earth Science Collections (or database) either, where most holotypes described by
770	Heer are deposited (A. Mueller, pers. comm., June 19, 2018).
771	
770	rubinsneu mustrations: The paper was first published as a separate in 1849 (Heer, 1849) but
113	also again the following year in Heer (1850). The same illustration (drawing) was included in both publications: Hear, 1840; 182, al. XIV; fig. 7; and Hear, 1850; al. XIV; fig. 7; St
114 775	Dool publications: Heer, 1849: 185, pl. XIV: IIg. /; and Heer, 1850: pl. XIV, IIg. /. See
115	BIOUIVEISILY HERITAGE LIDFARY: <u>https://biodiversityilbrary.org/page/24//621</u> .

776

777 **Preservation type and size:** A compression-impression fossil of two very fragmentary adult moths. According to Heer (1849), the abdomens and fragments of the wings are visible. One of 778 the abdomens is 3 lines (6.3 mm) wide and 6 lines (12.6 mm) long, the other 2.5 lines (5.25 mm) 779 780 wide and 5.5 lines (11.5 mm) long (1 line = 2.1 mm). Heer speculated that the wider abdomen belonged to a female moth, the narrower to a male of the same species. No details of the wing 781 venation or wing shape can be made out. 782 783 784 Comments: Heer (1849) referred to these fossils as "Noctuo-Bombycida" and did not even 785 narrow the identification down further to "Bombyces". 786 787 Both Handlirsch (1908) and Kozlov (1988) placed the specimen in the category of Lepidoptera incertae sedis. We agree with that assessment as no characters presented in the illustration or 788 789 described in the original publication enable placing of the moths in any lepidopteran superfamily. Even the identification of the depicted impressions as moths is difficult. Handlirsch (1908) stated 790 "pupa" as the stage of the fossil, which is understandable because it is not obvious that the 791 792 illustration provided by Heer (1849, 1850) represents two adult moths. 793 794 The name "Bombycites" was first used by Latreille (1817: 561) for a suprageneric group ("tribe") within recent "Phalaenae" (i.e., moths). It was proposed as a generic name – Bombycites 795 - by Heer (1849: 183), of which the type-species is the quite enigmatic *Bombycites oeningensis* 796 Heer, 1849 (Fletcher and Nye 1982). It was later used for a collective group aimed at 797 798 accommodating fossils proposed to be bombycoids but for which a genus-level identification is not possible (Heer 1865; Sohn & Lamas 2013). 799 800 801 802 12. Bombycites buechii Heer, 1865 803 Fig. 9. 804 805 Excavation data: Germany, Baden-Württemberg: Oeningen ("Molasseformation") (i.e., 806 Wangen); Messinian, Late Miocene. 807 808 Depository: ETH. Specimen barcode number: 000000005466. 809 810 Published illustrations: Heer (1865): 397, fig. 310 (drawing). 811 812 **Preservation type and size:** Compression-Impression fossil of a larva (whole body). Length of larva ~ 4 cm, width at widest part ~ 1.3 mm. The larva seems to be in lateral view. 813

814

815 816 817 818 819 820 821 822	Comments: The lack of details in the original description and diagnostic characters led Kozlov (1988) to place the specimen in his list of Papilionida (i.e., Lepidoptera) incertae sedis. We agree that the identification of this fossil as a bombycoid is very uncertain. It is possibly not even a larva (there seems to be an elongate, tapering appendage (antenna ?) adjacent to it, but admittedly not necessarily part of this fossil). In addition, there are no obvious prolegs. This is perhaps not even an insect.
823	13. Compression-impression fossil of wing scale tentatively assigned to a sphingid moth by
824	George (1952)
825	
826	Excavation data: Pakistan: Punjab, Salt Range, Warcha and Jankush Nulla Gorges (Saline
827 828	Series dolomite); Late Eocene.
829	Depository: SJCA Uttar Pradesh; slide no. 16. We have been unable to reach the curator in
830	charge of the collection to request a new photograph of the specimen.
831	
832	Published illustrations: George (1952): 88, fig. 55 (drawing). We have been unable to reach the
833	editors of this journal to request permission to reproduce the original image.
834	
835	The drawing shows a long and narrow scale hant and folded close to its mid longth. The scale
030 927	has longitudinal strictions, and the appy has three shallow subtriangular lobes. The total longth is
838	described to be 640 micra [um] and the width at the widest part about 64 micra [um]
839	desenbed to be 646 miera [µm] and the width at the widest part about 64 miera [µm].
840	Comments: The author stated that "the unmistakable sphingid facies can be made out" but no
841	additional details to support this assessment were provided. No comprehensive study of
842	lepidopteran wing scales has yet been done and we are unaware of characters that would
843	unambiguously and definitively assign a wing scale to Sphingidae. We agree with Kozlov
844	(1988), who placed this specimen in the category of uncertain identifications.
845	
846	
847	14. Fossilized scales and cuticular fragments in gut contents of fossil bats in Richter &
848	Storch (1980)
849	
850	Excavation data: Germany: Hesse, S Frankfurt, near Darmstadt, Messel oil shale-layers (Messel
851	Formation); Early Lutetian, Middle Eocene.
852	Depositowy SE
000 851	Depository: Sr.
004	

Published illustrations: Richter & Storch (1980): 365, fig. 16, but see Comments below. We
have been unable to reach the editors of this journal to request permission to reproduce the

- 857 original image.
- 858

859 **Preservation type and size:** Fossilized scales and cuticular fragments of Lepidoptera in the gut contents of fossilized bats. SEM images presented in Richter & Storch (1980) reveal that the 860 microstructure of the scales has been preserved well. Cuticular fragments are small and do not 861 contain diagnostic structures such as legs, antennae or larger hollow structures that have been 862 compressed. Association of the cuticular fragments with body parts is difficult, except for wing 863 fragments (double-layer of cuticle). These cuticular wing fragments show detailed sculpturing. 864 including a more or less dense cover of trichomes ("false hairs") in the case of lepidopteran 865 866 wings.

867

868 Comments: Sohn et al. (2012) stated that fig. 16 in Richter & Storch (1980: 365) could be a possible sphingid scale, probably because it is very similar to the scales of modern Sphingidae 869 figured by Richter & Storch (1980: fig. 17). However, Richter & Storch said that this type of 870 scale, i.e., with inter-ridge perforations and cross-ridges, is typical of many lepidopteran families, 871 including Sphingidae, Noctuidae and Saturniidae. Assigning such lepidopteran scales to a 872 particular family is indeed difficult because such microstructure can be observed in many groups 873 of the lepidopteran clade Coelolepida (Lepidoptera with hollow scales) (Kristensen & Simonsen 874 2003; van Eldijk et al. 2018). In addition, the shape and structure of lepidopteran scales can vary 875 even on the same wing, and they are thus not very informative phylogenetically (Kristensen & 876 877 Simonsen 2003). Some of the scales in the gut contents are said to show similarities to those of modern Cossidae, Micropterigidae and Eriocraniidae, the latter two of which are mostly diurnal, 878 unlike bats. The abundance of cuticular fragments with trichomes led Richter & Storch (1980: 879 365) to the conclusion that the dominant prey of these bats had been small, "primitive" 880 881 Lepidoptera, because wings with trichomes between scales are known from the families Micropterigidae, Eriocraniidae and Hepialidae. There is no evidence that would indicate the 882 cuticular fragments or scales to belong to Sphingidae or any other bombycoid family. On the 883 contrary, based on the absence of certain scale types, Richter & Storch (1980: 364) even 884 885 concluded that Lasiocampidae were not part of the gut contents. 886 887 888 15. Non-lepidopteran fossil insect erroneously assigned to Saturniidae by Grande (2013) 889 Fig 10.

- 890
- 891 Excavation data: USA: Wyoming, Lincoln County, Green River Formation, Fossil Butte
- 892 Member, locality F; Ypresian, Eocene. According to Grande (2013), the fossil lake sediments
- 893 were deposited about 53–51 Ma.
- 894

Depository: Originally, the fossil was part of the private collection of the late Richard D. 895 Dayvault but was donated to the USNM in 2016 by his wife, Jalena Dayvault. USNM PAL 896 618360, part and counterpart labeled A and B. 897 898 899 Published illustrations: Grande (2013): 76, fig. 33 (colour photograph). 900 901 **Preservation type and size:** Compression fossil of a winged insect in lateral aspect. Forewing 902 length ~ 5 cm. 903 904 **Comments:** A closer inspection of the venation of this insect immediately reveals that it is not a lepidopteran. There are more veins (crossveins, notably) than in the wings of either Trichoptera 905 or Lepidoptera (Fig. 11 B, close-up showing the crossveins). The venation is reticulate and 906 appears more similar to that of, e.g., Orthoptera or Neuroptera. We are currently unaware if any 907 progress regarding the identification of this fossil has been made. Mrs Jalena Davvault, who 908 donated the specimen to the USNM, has expressed the wish that, if possible, the scientific name 909 to be given to this specimen should somehow incorporate 'Dayvault', in memory of her husband. 910 We will leave the description of this specimen to those with more knowledge of the group of 911 912 insects that it represents. 913 914 915 Fossils of non-lepidopteran insects and a crustacean erroneously assigned to *Sphinx*: 16. Myrmicium schroeteri (Germar, 1839) [Sphinx schroeteri Germar, 1839 and Sphinx 916 917 snelleni Weyenbergh, 1869] and the Sphinx larva illustrated by Weyenbergh (1869) 918 Fig. 11. 919 920 **Excavation data:** Germany: Solnhofen limestone deposits in Bavaria (Altmühltal Formation); 921 Tithonian (150.8–145.5 Ma), Upper Jurassic. 922 923 Depository: Sphinx snelleni (Weyenbergh, 1869): TMH. 15396 and 15397; and "Sphinx larva" 15403 in . Myrmicium schroeteri (Germar, 1939): MfN. MB.I.0860.. 924 925 926 Published illustrations: Sphinx schroeteri Germar, 1839: Schröter (1784) Plate III, fig. 16 927 https://zs.thulb.unijena.de/rsc/viewer/jportal derivate 00164692/NLKN 1784 Bd01 %200593.tif?logicalDiv=jpor 928 tal iparticle 00152562 (drawing); 929 https://portal.museumfuernaturkunde.berlin/detail/0d66f2851d77db8ebdf9 (colour photograph). 930 931 Sphinx snelleni Weyenbergh, 1869: Weyenbergh (1869): Plate I, fig. 9. https://www.biodiversitylibrary.org/page/24004107 (drawing); 932 933 Sphinx larva: Weyenbergh (1869): Plate I, fig. 10. 934 https://www.biodiversitylibrary.org/page/24004107 (drawing) and Wikimedia Commons

PeerJ	
-------	--

935	https://commons.wikimedia.org/wiki/File:Myrmicium_snelleni_Teylers_museum.jpg (colour
936	photograph).
937	
938	Preservation type: Compression fossils.
939	
940	Comments: Sphinx snelleni was described by Weyenbergh (1869). The fossil is illustrated in
941	Plate I, fig. 9 of this publication along with another fossil labelled as a <i>Sphinx</i> larva (Plate I, fig.
942 943	10). The original description of <i>Sphinx snelleni</i> mentions a coiled proboscis (which is also clearly shown in the corresponding figure: Pl. 1, Fig. 9), a trait that suggests that this taxon could
944	indeed belong to the Lepidoptera (perhaps even the Sphingidae) A curved structure is indeed
945	also visible in photographs of the specimen, but it is difficult to interpret whether it really is a
946	proboscis. After examination of the larval specimen, Handlirsch (1906) concluded that it was the
947	abdomen of a decapod (Crustacea). <i>Sphinx snelleni</i> was identified as a wood wasp of the
948	hymenopteran family Siricidae. However, it was later moved to Pseudosiricidae as a junior
949	synonym of what is now <i>Myrmicium schroeteri</i> (originally described as " <i>Sphinx schröteri</i> " by
950	Germar (1839)). For more references, see Sohn <i>et al.</i> (2012).
951	
952	
953	17. Fossilized flower petal of <i>Nymphaea</i> tentatively interpreted as a sphingid larva by Nel &
954	Nel (1985)
955	
956	Excavation data: France: Les Figons, Aix-en-Provence; Rupelian, Oligocene.
957	
958	Depository: MNHN. n°215 A
959	
960	Published illustrations: Nel & Nel (1985) 126, figs. 11, 12.
961	
962	Preservation type and size: Compression fossil. Length 2 cm.
963	
964	Comments: Subsequently, the specimen and additional material were carefully reexamined by
965	Dr. André Nel. He concluded that they are fossilized water lily petals (Sohn et al. 2012; A. Nel,
966	pers. comm. 2.3.2023).
967	
968	
969	Fossils not examined:
970	
971	Sphingid in Baltic amber mentioned by Berendt (1830)
972	
973	Excavation data: Baltic Region (Baltic Amber, Prussian Fm.); Lutetian, Middle Eocene.
974	

Depository: An important part of the Berendt amber collection is in the MfN, but the specimen 975 Berendt identified as "Sphinx" has not been located. There is no specimen in the MfN labelled as 976 such (T. Léger, pers. comm. June 20, 2019). 977 978 979 Published illustrations: none. 980 981 **Preservation type and size:** Specimen in Baltic amber. Berendt does not specify if the inclusion in amber is an adult or a caterpillar. However, the way the text is written implies it is a 982 caterpillar. Condition and size unknown. 983 984 985 Comments: Berendt (1830: 36-37) mentioned a "Sphinx" in Baltic Amber. From the text it cannot unambiguously be determined whether the specimen was an adult or caterpillar: 986 "Lepidopteren finden sich am seltensten. Ich besitze nur einen Sphinx von bedeutender Grösse. 987 988 Kleine Raupen sieht man öfter" (Translation: Lepidoptera are the rarest. I only own a single Sphinx of significant size. Small caterpillars can be seen more often). The way the statement is 989 phrased implies that it is a caterpillar of significant size whereas the others he has seen are small. 990 Taken at face value, this fossil would represent the oldest evidence of Bombycoidea. However, 991 992 the identification cannot be confirmed because the specimen has not been located and is not described in sufficient detail in the original publication. Kusnezov (1941: 69) possibly had access 993 to this specimen and identified the inclusion as a lepidopteran but did not suggest a lower-level 994 identification. 995 996 997 Compression-impression fossil of a sphingid larva and a poorly preserved "Bombyx" 998 mentioned by Schöberlin (1888) 999 1000 1001 Excavation data: Switzerland: Neuchâtel Canton, Oeningen ("Stinkschiefe")/Messinian, Late 1002 Miocene. 1003 1004 **Depository:** The larva was originally in the [private?] Massmann Collection (Sohn *et al.* 2012), 1005 but its current depository is unknown. The whereabouts of the poorly preserved "Bombyx" fossil is not known either. We were unable to examine these specimens. 1006 1007 1008 Published illustrations: none. 1009 1010 **Preservation type and size:** Compression/Impression fossil of a larva (whole body) and a 1011 poorly preserved "Bombyx" fossil (2 species?). Size not given in Schöberlin (1888). 1012 1013 **Comments:** The author likened the size of the fossil larva to that of the larva of the extant 1014 species Hemaris fuciformis (Linnaeus, 1758). Because of the lack of details and illustrations in

1015 1016 1017 1018	the original publication, and the unavailability of the specimens for closer examination, their assignment to Bombycoidea cannot be confirmed. In addition, back in 1888, "Bombyx" would have been used for any "Bombyces", i.e., including Bombycoidea (except Sphingidae), Notodontidae, Erebidae (subfamilies Lymantriinae and Arctiinae), Limacodidae, Zygaenidae and
1019 1020 1021	Psychidae. Thus, the mention of a "Bombyx" fossil does not necessarily mean that it belongs to Bombycoidea in the current sense, it could have been just about anything (see, e.g., Packard (1893) for an example of what was then considered to belong to "Bombyces").
1022 1023	
1024 1025	Thoracic segment of <i>Aglia tau</i> (Agliinae) larva in sieved residue (Lindberg, 1900).
1026 1027	Excavation data: Finland: Lohja; Pleistocene.
1028 1029	Depository: not known.
1030 1031	Published illustrations: none.
1032 1033	Preservation type and size: First thoracic segment of larva. Size not known.
1034 1035 1036	Comments: Lindberg (1900) gave credit for the identification of the specimen to Finnish entomologist, Enzio Reuter. According to the information in Lindberg (1900), the segment had well-preserved "strange" horn-like structures typical of <i>Aglia tau</i> (Linnaeus, 1758). These are
1037 1038 1039	probably the scoli found on the thoracic segments of early instar <i>Aglia</i> larvae. There are several recent species in the genus <i>Aglia</i> (Kitching and Rougerie <i>et al.</i> 2018) of which only <i>Aglia tau</i> occurs in present day Finland.
1040 1041 1042	Compression-impression fossil identified as <i>Sphinx</i> by Haase (1890)
1042 1043 1044	Excavation data: Excavation data or depository not known.
1045	Depository: Originally in private collection of A. Assmann. According to information found
1046	online [https://en.wikipedia.org/wiki/August Assmann, accessed 17.03.2020], the Assmann
1047	collection is nowadays in NHUW, Wrocław. However, the entomology collection at NHUW
1048	does not include compression/impression fossils, and Assmann's specimens are probably not in
1049	the collection of the NHUW paleontology department either, which has only vertebrates (M.
1050 1051	Wanat, pers. comm. January 8, 2020).
1052 1053	Published illustrations: none.
1054	Preservation type and size: Compression/Impression fossil. Size not known.

1055

1056 Comments: Haase (1890: 26) mentioned that he had seen a drawing of the specimen shown to
1057 him by Mr A. Assmann. According to Haase, Assmann had intentions to publish on the
1058 specimen. The location of the specimen was not given. Handlirsch (1908: 628) wrote that he was
1059 not able to locate it either and that to his knowledge Assmann's descriptions of these fossils were
1060 not published.

1061

1062 1063 **Discussion**

The re-examination of the 17 records shows that only five fossils can be placed in Bombycoidea
with reasonable certainty — 4 to Sphingidae and 1 to Saturniidae (see Supplemental Table S1).
However, none of the 4 fossil sphingids displays unequivocal characters and their identification

1067 as Sphingidae is not 100% certain. This precludes their use as calibration points according to the

criteria proposed by Parham *et al.* (2012). Furthermore, the use of some of the dubious fossils as
calibration points in earlier studies (e.g., *Attacus? fossilis* in the study on the hawkmoth radiation

1070 by Kawahara & Barber (2015)) casts doubt on the resulting ages. New analyses with revised sets

1071 of fossils or calibration times would be welcome in these cases.

1072

Although all known bombycoid fossils examined are relatively young, the oldest is *Mioclanis shanwangiana* from middle Miocene, the origin of the superfamily is expected to be significantly
older. In studies focusing on all Lepidoptera, Wahlberg *et al.* (2013) and Kawahara *et al.* (2019)
estimated a crown-group age of 84 Ma (95% HPD: 74–93) and 80 Ma (95% HPD: 70–90) for
Bombycoidea, respectively. In a study on Saturniidae, Rougerie *et al.* (2022) estimated the stem
age of the family to be in the early Cenozoic at about 63 Ma (95% HPD: 59–69 Ma). We note

1079 however that the estimate by Wahlberg *et al.* (2013) used time calibrations derived from a set of

- fossils that included some that have now been shown to be misidentified, while the selection of
 fossils in the studies by Kawahara *et al.* (2019) and Rougerie *et al.* (2022) were based on stricter
 criteria.
- 1083

1084 Unfortunately, bombycoid moths, as lepidopterans in general, are rare in the fossil record

1085 (Labandeira & Sepkoski, 1993; Sohn *et al.* 2012), and therefore, estimates of their age and

1086 evolution remain mostly based on the combination of molecular data and secondary calibrations.

- 1087 The probable reason for the scarcity of fossil Lepidoptera is that scales are water-repellent, thus
- 1088 preventing specimens from sinking to the bottom of water bodies where they would have been
- buried in sediment (Martínez-Declòs *et al.* 2004; Peñalver & Grimaldi 2006). A relatively high
 body-fat content of bombycoids may also increase buoyancy (Simonsen *et al.* 2019). The
- 1091 majority of fossil Lepidoptera are amber inclusions but nearly all of these are small moths (Sohn
- 1092 *et al.* 2015). Large moths are extremely rare as amber inclusions, and a reason may be that scales
- 1093 are relatively easily lost and doing so prevents big moths from getting trapped in amber. Large



1094 dead moths are also an attractive food source to scavengers and so may get spotted and eaten before they can be fossilized. 1095 1096 1097 Conclusions 1098 1099 Our study is a contribution to efforts to obtain a more reliable and accurate understanding of the 1100 evolutionary history and historical biogeography of Lepidoptera. We critically re-examined 16 records of fossils currently assigned to the lepidopteran superfamily Bombycoidea, and assessed 1101 1102 whether observable morphological features warrant their confident assignment to the 1103 superfamily. 1104 1105 The study confirms that the identifications of many of the known fossil Bombycoidea were based 1106 on overall similarity to extant species and not apomorphies. None of the examined fossils displays characters that allow unequivocal identification as Sphingidae, but three fossils and a 1107 1108 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 1109 1110 family. The identification of a fossil pupa as Bunaeini (Saturniidae) is well supported. The other 1111 fossils that we evaluate lack definitive bombycoid and, in several cases, even lepidopteran 1112 characters. 1113 1114 We can only hope that new discoveries of well-preserved fossil Bombycoidea will be made in the future and can reveal more on the evolutionary history of these moths and allow 1115 corroboration or critical revision of the current estimates of their ages. 1116 1117 **Acknowledgements** 1118 1119 Daniil Aristov (Paleontological Institute, Russian Academy of Sciences), Chenyang Cai (Nanjing Institute of Geology and Palaeontology), Lance Grande (The Field Museum, Chicago), Jalena 1120 1121 Dayvault, Alexander Gehler (GZG), Dale Greenwalt (Smithsonian Institution, NMNH), Talia Karim (UCM), Job Kibii (NMK), Christian Klug (PIMUZ), David Kohls, Conrad Labandeira 1122 1123 (Smithsonian Institution, NMNH), Théo Léger (MfN), Stephen Maikweki (NMK), Finnegan 1124 Marsh (Smithsonian Institution, NMNH), Hebert Meyer and students (Florissant Fossil Beds 1125 National Monument), Sun Mingchang (SPFL), Francis Muchemi (NMK), Andreas Müller (ETH 1126 Zürich), Francis Ndiritu (NMK), André Nel (MNHN), Hossein Rajaei (State Museum of Natural

- 1127 History Stuttgart), Alexandr Rasnitsyn (Paleontological Institute, Russian Academy of Sciences),
- 1128 Michael Rasser (State Museum of Natural History Stuttgart), Anne Schulp (Teylers Museum,
- 1129 Haarlem), Jennifer Strotman (Smithsonian Institution, NMNH), Marek Wanat (NHUW), Ingmar
- 1130 Werneburg (GPIT), Huang Ying and Jukka Tabell, Tim de Zeeuw (Teylers Museum, Haarlem),
- 1131 David Zelagin (UCM).
- 1132

1133 **References**

1134	Bell, T.R.D. and Scott, F.B. 1937. Moths, vol. 5: Sphingidae 1–537. In Sewell, R.B.S. and
1135	Talbot, G. (eds) The Fauna of British India. Taylor and Francis, London, 537 pp.
1136	
1137	Berendt, G.C. 1830. Die Insekten im Bernstein ein Beitrag zur Thiergeschichte der Vorwelt.
1138	Nicolai, Danzig, 38 pp.
1139	
1140	Brauckmann, C., Brauckmann, B. and Gröning, E. 2001. Anmerkungen zu den bisher
1141	beschrieben Lepidopteren aus dem Jung-Tertiär (Pliozän) von Willershausen am Harz.
1142	Jahresberichte des Naturwissenschaftlichen Vereins Wuppertal 54, 31–41.
1143	
1144	Brock, J.P. 1971. A contribution towards an understanding of the morphology and phylogeny of
1145	the ditrysian Lepidoptera. Journal of Natural History 5 (1), 29-102.
1146	
1147	Churcher, C.S. 1966. The insect fauna from the Talara tar seeps, Peru. Canadian Journal of
1148	<i>Zoology</i> 44 (6), 985–993.
1149	
1150	Clark, J., Cole, R., Fawcett, S., Green, M., Howcroft, J., Niedbala, S., Rawkins, K., Théobald, O.
1151	and Tobias, M. 1971. The Zoological Record (1967). Vol. 104, 13. Insecta. The Zoological
1152	Society of London, London, 704 pp.
1153	
1154	Cockerell, T.D.A. 1914. Fossil Saturniidae. 271. In Packard, A.S. and Cockerell, T.D.A. (eds),
1155	Monograph of the Bombycine Moths of North America, Part III. Memoir of the National
1156	Academy of Science 12, 516 pp.
1157	
1158	Cockerell T. D. A. 1915. Miocene fossil insects. Proceedings of the Academy of Natural
1159	Sciences of Philadelphia 66 (1914), 634–648.
1160	
1161	De Jong, R. 2017. Fossil butterflies, calibration points and the molecular clock (Lepidoptera:
1162	Papilionoidea). Zootaxa, 4270, 1–63 <u>https://doi.org/10.11646/zootaxa.4270.1.1</u>
1163	
1164	Doorenweerd C., Nieukerken, E.J. van, Sohn J.C. and Labandeira, C.C. 2015. A revised
1165	checklist of Nepticulidae fossils (Lepidoptera) indicates an Early Cretaceous origin. Zootaxa,
1166	3963, 295–334 <u>https://doi.org/10.11646/zootaxa.3963.3.2</u> .
1167	
1168	Eldijk, T. van, Wappler, T., Strother, P.K., Weijst, C.M.H. van der, Rajaei, H., Visscher, H. and
1169	Schootbrugge, B. van de 2018. A Triassic-Jurassic window into the evolution of Lepidoptera.
1170	Science Advances 4 (1), e1701568 https://doi.org/10.1126/sciadv.1701568
1171	
1172	Genise, J.F. 2003. Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols
1173	attributed to coleopterans, ants and termites. 419–453. In MCILROY, D. (ed.) The Application of

1174	ichnology to palaeoenvironmental and stratigraphic analysis. Geological Society, London,
1175	Special Publications, 228, 479 pp. https://doi.org/10.1144/GSL.SP.2004.228.01.21
1176	
1177	Genise, J.F. 2017. Other insect trace fossils in paleosols: cicadas, chafers, weevils, and sphinx
1178	moths. 313–351. In Ichnoentomology. Insect Traces in Soils and Paleosols. Topics in Geobiology
1179	37. Springer International Publishing, Switzerland, 695 pp.
1180	
1181	Genise, J.F., Farina, J.L. and Verde, M. 2013. Teisseirei barattinia Roselli 1939: the first sphinx
1182	moth trace fossil from palaeosols, and its distinct type of wall. Lethaia, 46, 480–489.
1183	
1184	George, V.P. 1952. On some arthropod microfossils from India. Agra University Journal of
1185	<i>Research</i> , 1 , 83–108.
1186	
1187	Germar, E.F. 1839. Die versteinerte Insecten Solenhofens. Nova Acta Leopoldina, 19, 187–222.
1188	https://play.google.com/books/reader?id=nXCIz9WoDdkC&pg=GBS.PA186&hl=fi&printsec=fr
1189	ontcover
1190	
1191	Grande, L. 2013. The Lost World of Fossil Lake: Snapshots from Deep Time. The University of
1192	Chicago Press, Chicago and London, 425 pp.
1193	
1194	Haase, E. 1890. Bemerkungen zur Palaeontologie der Insecten. Neues Jahrbuch für Mineralogie,
1195	Geologie und Palaeontologie, 2, 1–33.
1196	
1197	Hagen, H.A. 1862. Ueber die Neuropteren aus dem lithographischen Schiefer in Bayern.
1198	<i>Palaeontographica</i> , 10 (2), 96–145.
1199	
1200	Hamilton, C.A., St Laurent, R.A., Dexter, K., Kitching, I.J., Breinholt, J.W., Zwick, A.,
1201	Timmermans, M.J.T.N., Barber, J.R. and Kawahara, A.Y. 2019. Phylogenomics resolves major
1202	relationships and reveals significant diversification rate shifts in the evolution of silk moths and
1203	relatives. BMC Evolutionary Biology, 19, 182. https://doi.org/10.1186/s12862-019-1505-1
1204	
1205	Handlirsch, A. 1906–1908. Die Fossilen Insekten und die Phylogenie der Rezenten Formen. Ein
1206	Handbuch für Paläontologen und Zoologen. Lieferung 4. Wilhelm Engelmann, Leipzig, 1430 pp.
1207	https://www.biodiversitylibrary.org/bibliography/34145;
1208	https://www.biodiversitylibrary.org/page/24524857
1209	
1210	Hasenfuss, I. 1999. The adhesive devices in larvae of Lepidoptera (Insecta, Pterygota).
1211	Zoomorphology, 119 , 143–162.
1212	

1213 1214	Haxaire, J. and Minet, J. 2017. The systematic position of <i>Pentateucha</i> , <i>Monarda</i> and a Malagasy taxon misplaced in Smerinthinae (Lepidontera Sphingidae Sphinginae). <i>Antenor</i> , 4 (2)
1214	107_113
1210	107 115.
1210	Heer, O. 1849. Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien,
1218	Vol. 2. Wilhelm Engelmann, Leipzig, 264 pp.
1219	
1220	Heer, O. 1850. Neue Denkschriften der allgemeinen Schweizerischen Gesellschaft für die
1221	gesammten Naturwissenschaften Band XI oder: Zweite Dekade. Band 1 mit XXII Tafeln. Druck
1222	von Zücher & Furrer, Zürich, 239 pp.
1223	
1224	Heer, O. 1865. Die Urwelt der Schweiz. Friedrich Schultheß, Zürich, 622 pp.
1225	
1226	Heikkilä M., Brown, J.W., Baixeras, J., Mey, W. and Kozlov, M.V. 2018. Re-examining the rare
1227	and the lost: a review of fossil Tortricidae (Lepidoptera). Zootaxa, 4394, 41-60.
1228	https://doi.org/10.11646/zootaxa.4394.1.2
1229	
1230	Heikkilä, M., Simonsen, T.J. and Solis, M.A. 2018. Reassessment of known fossil Pyraloidea
1231	(Lepidoptera) with descriptions of the oldest fossil pyraloid and a crambid larva in Baltic amber.
1232	Zootaxa, 4483, 101–127. https://doi.org/10.11646/zootaxa.4483.1.4
1233	
1234	Heppner, J.B. 1998. Classification of Lepidoptera. Part 1. Introduction. Holarctic Lepidoptera, 5
1235	(Suppl. 1): i–iv, 1–148 + 6 pp.
1236	
1237	Hodges, R.W. 1971. Sphingoidea (hawkmoths). In Dominick, R.B., Ferguson, D. C.,
1238	Franclemont, J. G., Hodges, R. W. and Munroe, E. G. (eds) The moths of America north of
1239	Mexico, 21, R.B.D. Publications and E.W. Classey, London, 1–158 + xii pp. + 14 pls.
1240	
1241	Kawahara, A. Y. and Barber, J. R. 2015. Tempo and mode of antibat ultrasound production and
1242	sonar jamming in the diverse hawkmoth radiation. PNAS, 112 (20), 6407–6412.
1243	https://doi.org/10.1073/pnas.1416679112
1244	
1245	Kawahara, A. Y., Plotkin, D., Espeland, M., Meusemann, K., Toussaint, E. F. A., Donath, A.,
1246	Gimnich, F., Frandsen, P. B., Zwick, A., Dos Reis, M., Barber, J. R., Peters, R. S., Liu, S., Zhou,
1247	X., Mayer, C., Podsiadlowski, L., Storer, C., Yack, J. E., Misof, B. and Breinholt J. W. 2019.
1248	Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. PNAS, 116
1249	(45) 22657–22663. https://doi.org/10.1073/pnas.1907847116
1250	
1251	Kernbach, K. 1967. Über die bisher im Pliozän von Willershausen gefundenen Schmetterlings-
1252	und Raupenreste. Berichte der Naturhistorischen Gesellschaft zu Hannover, 111, 103–108.

1253	
1254	Kitching, I.J. and Sadler, S. 2011. Lepidoptera, Insecta. 549–554. In Harrison, T. (ed.)
1255	Paleontology and Geology of Laetoli: Human Evolution in Context, Vol. 2: Fossil Hominins and
1256	the Associated Fauna. Springer, Dordrecht, Heidelberg, London & New York, 600 pp.
1257	
1258	Kitching, I.J., Rougerie, R., Zwick, A., Hamilton, C.A., St Laurent, R.A., Naumann, S.,
1259	Ballesteros Mejia, L. and Kawahara, A.Y. 2018. A global checklist of the Bombycoidea (Insecta:
1260	Lepidoptera) [with Suppl. Material 1: Global Bombycoidea checklist]. Biodiversity Data
1261	Journal, 6, e22236. https://doi.org/10.3897/BDJ.6.e22236
1262	
1263	Komai, F., Yoshiyasu, Y., Nasu, Y. and Saito, T. (eds) 2011. A guide to the Lepidoptera of
1264	Japan. Tokai University Press, Hadano, Kanagawa, xx + 1307 pp.
1265	
1266	Kozlov, M.V. 1988. Paleontology of lepidopterans and problems of the phylogeny of the order
1267	Papilionida. 16–69. In Ponomarenko, A.G. (ed.) The Mesozoic–Cenozoic Crisis in the Evolution
1268	of Insects. Academy of Sciences, Moscow.
1269	
1270	Kristensen, N.P. 2003. Chapter 4. Skeleton and muscles: adults. 39-131. In Kristensen, N.P. (ed.)
1271	Lepidoptera, moths and butterflies, volume 2: Morphology, physiology, and development
1272	(Handbook of Zoology IV, 36). Walter de Gruyter, Berlin and New York, xii + 564 pp.
1273	
1274	Kristensen, N.P. and Simonsen, T.J. 2003. Chapter 2. "Hairs" and scales. 9-22. In Kristensen,
1275	N.P. (ed.), Lepidoptera, moths and butterflies, volume 2: Morphology, physiology, and
1276	development (Handbook of Zoology IV, 36). Walter de Gruyter, Berlin and New York, xii + 564
1277	pp.
1278	
1279	Kunz, P. 2010. 30 ans déjà. ASAM Bulletin, 2010, 39–45.
1280	
1281	Kunz, P. 2015. Les temps forts de l'ASAM. Le Blog. Bouxwiller 2015 : les ovoïdes ont de
1282	nouveaux parents! https://asam67.org/bouxwiller-2015-les-ovoides-ont-de-nouveaux-parents/
1283	[Blog post, accessed 18.11.2019]
1284	
1285	Kuznetzov, V.I. and Stekolnikov, A.A. 1985. Comparative and functional morphology of the
1286	male genitalia of the bombycoid moths (Lepidoptera, Papilionomorpha: Lasiocampoidea,
1287	Sphingoidea, Bombycoidea) and their systematic position. <i>Trudy zoologicheskogo Instituta</i> ,
1288	<i>Leningrad</i> , 134 , 3–48.
1289	
1290	Kusnezov, N. 1941. A Revision of Amber Lepidoptera. Paleontological Institute, USSR Academy
1291	of Sciences, Moscow & Leningrad, 135 pp.

1292

1293 1294	Leakey, L.S.B. 1952. Lower Miocene invertebrates from Kenya. Nature, 169 (4302), 624–625.
1295 1296 1297	Lemaire, C. 1980. Les Attacidae américains. The Attacidae of America (=Saturniidae). Arsenurinae. C. Lemaire, Neuilly-sur-Seine, 199 pp. + 76 pls.
1298	Lemaire, C. and Minet, J. 1998. Chapter 18. The Bombycoidea and their relatives. 321–353. In
1299 1300	Kristensen, N.P. (ed.), <i>Lepidoptera, moths and butterflies, volume 1: Evolution, systematics, and biogeography (Handbook of Zoology IV, 35)</i> . Walter de Gruyter, Berlin and New York, 487pp.
1301	
1302 1303 1304	Lima, A. Da Costa. 1950. Insetos do Brasil, tomo 6: Lepidopteros (2a parte). Escola Nacional de Agronomia, Rio de Janeiro, 420 pp.
1305 1306	Madden, A.H. 1944. The external morphology of the adult tobacco hornworm (Lepidoptera, Sphingidae). <i>Annals of the entomological Society of America</i> , 37 (2): 145–160.
1307	
1308 1309 1310	martinez-Deicios, X., Briggs, D.E.G. and Penaiver, E. 2004. Taphonomy of insects in carbonates and amber. <i>Palaeogeography, Palaeoclimatology, Palaeoecology</i> , 203 , 19–64. https://doi.org/10.1016/S0031-0182(03)00643-6
1311	
1312 1313	Melchor, R.N., Genise, J.F. and Miquel, S.E. 2002. Ichnology, Sedimentology and paleontology of Eocene calcareous paleosols from a Palustrine Sequence, Argentina. <i>Palaios</i> , 17 , 16–35.
1314	
1315 1316 1317	Michener, C.D. 1952. The Saturniidae (Lepidoptera) of the Western hemisphere. Morphology, phylogeny, and classification. <i>Bulletin of the American Museum of Natural History</i> , 98 , 335–501.
1318	Minst I 1004 The Dombysocides, about and higher classification (Lonidenterry Classete)
1319 1320 1321	Entomologica scandinavica, 25 (1), 63–88.
1321	Nässig W A Naumann S and Oberprieler R G 2015 Notes on the Saturniidae of the Arabian
1323	Peninsula with description of a new species (Lepidontera: Saturniidae) Nachrichten des
1324	entomologischen Vereins Apollo Frankfurt am Main NF 36 (1) 31–38
1325	
1326	Nel, A. and Nel, J. 1985. À propos de chenilles et de chrysalides fossiles du stampien en France
1327	(Lepidoptera). Alexanor, 1, 3: 126–130.
1328	
1329	Nieukerken, E.J. van, Kaila L., Kitching, I.J., Kristensen, N.P., Lees D.C., Minet, J., Mitter, C.,
1330	Mutanen, M., Regier, J.C., Simonsen, T.J., Wahlberg, N., Yen, SH., Zahiri, R., Adamski, D.,
1331	Baixeras, J., Bartsch, D., Bengtsson, B. Å., Brown, J. W., Bucheli, S. R., Davis, D. R., De Prins,
1332	J., De Prins, W., Epstein, M. E., Gentili-Poole, P., Gielis, C., Hättenschwiler, P., Hausmann, A.,

1333 Holloway, J. D., Kallies, A., Karsholt, O., Kawahara, A., Koster, S. J. C., Kozlov, M., 1334 Lafontaine, J. D., Lamas, G., Landry, J. F., Lee, S., Nuss, M., Penz, C., Rota, J., Schmidt, B. C., Schintlmeister, A., Sohn, J. C., Solis, M. A., Tarmann, G. M., Warren, A. D., Weller, S., 1335 Yakovlev, R., Zolotuhin, V. and Zwick, A. 2011. Order Lepidoptera Linnaeus, 1758. In: Zhang, 1336 1337 Z.-Q. (ed.), Animal biodiversity: an outline of higher-level classification and survey of 1338 taxonomic richness. Zootaxa, 3148: 212-221. 1339 1340 Packard, A.S. 1893. Attempt at a new classification of the Bombycine Moths. Journal of the New 1341 *York entomological Society*, **1**, 6–11. 1342 1343 Parham, J.F., Donoghue, P.C.J., Bell, C.J., Calway, T.D., Head, J.J., Holroyd, P.A., Inoue, J.G., 1344 Irmis, R.B., Joyce, W.G., Ksepka, D.T., Patané, J.S.L., Smith, N.D., Tarver, J.E., Van Tuinen, 1345 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 1346 1347 for justifying fossil calibrations. Systematic Biology, 61 (2), 346–359. 1348 https://doi.org/10.1093/sysbio/syr107 1349 1350 Peñalver, E. and Grimaldi, D.A. 2006. New data on Miocene butterflies in Dominican Amber 1351 (Lepidoptera: Riodinidae and Nymphalidae) with the description of a new nymphalid. American 1352 Museum Novitates, 3591, 1–17. 1353 1354 Peterson, A. 1956. Larvae of Insects, an introduction to Nearctic species (3rd edition). Part I. 1355 Lepidoptera and plant infesting Hymenoptera. Columbus, Ohio, 315 pp. 1356 1357 Richter, G. and Storch, G. 1980. Beiträge zur Ernährungsbiologie eozäner Fledermäuse aus der "Grube Messel". Natur und Museum, 110 (12), 353-367. 1358 1359 Ryckewaert, P., Razanamaro, O., Rasoamanana, E., Rakotoarimihaja, T., Ramavovololona, P. 1360 and Danthu, P. 2011. Les Sphingidae, probables pollinisateurs des baobabs malgaches. Bois et 1361 Forêts des Tropiques, **307** (1), 55–68. 1362 1363 1364 Roselli, F.L. 1939. Apuntes de geología y paleontología uruguaya. Sobre insectos del Cretácico 1365 del Uruguay o descubrimiento de admirables instintos constructivos de esa época. Boletín de la 1366 Sociedad Amigos de las Ciencias Naturales 'Kraglievich-Fontana', 1, 72–102. 1367 1368 Roselli, F.L. 1987. Paleoicnología. Nidos de insectos fósiles de la cubertura Mesozoica del 1369 Uruguay. Publicaciones del Museo Municipal de Nueva Palmira, 1, 1–56. 1370 1371 Rougerie, R. 2005. Phylogeny and biogeography of the Saturniinae (Lepidoptera: Bombycoidea, 1372 Saturniidae). PhD thesis. Muséum national d'Histoire naturelle, Paris, France. 530 pp. + 45 pls.

1373	
1374	Rougerie, R., Cruaud, A., Arnal, P., Ballesteros-Mejia, L., Condamine, F., Decaëns, T., Elias,
1375	M., Gey, D., Hebert, P., Kitching, I.J., Lavergne, S., Lopez-Vaamonde, C., Murienne, J., Cuenot,
1376	Y., Nidelet, S. and Rasplus, JY. 2022. Phylogenomics illuminates the evolutionary history of
1377	wild silkmoths in space and time (Lepidoptera: Saturniidae). bioRxiv preprint:
1378	https://www.biorxiv.org/content/10.1101/2022.03.29.486224v2, accessed 27.02.2023.
1379	
1380	Rougerie, R. and Estradel, Y. 1998. Morphology of the preimaginal stages of the African
1381	emperor moth Bunaeopsis licharbas (Maassen and Weyding): phylogenetically informative
1382	characters within the Saturniinae (Lepidoptera: Saturniidae). Journal of Morphology,
1383	Supplement, 269 , 207–232.
1384	
1385	Schlotheim, E.F. von 1820. Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die
1386	Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und
1387	Pflanzernreichs der Vorwelt erläutert. Bekker'schen edit, Gotha, 457 pp.
1388	
1389	Schüssler, H. 1933. Saturniidae: 1. Subfam. Attacinae. In: Strand, E. (ed.), Lepidopterorum
1390	Catalogus. W. Junk, Berlin, 769 pp.
1391	
1392	Schöberlin, E. 1888. Der Oeninger Stinkschiefer und seine Insektenreste. Societas Entomologica,
1393	3(9), 68–69.
1394	
1395	Schröter, J.S. 1784. Neue Litteratur und Beyträge zur Kenntniß der Naturgeschichte vorzüglich
1396	der Conchylien und Foßilien, Vol. 1. Müller, Leipzig, 550 pp. https://zs.thulb.uni-
1397	jena.de/rsc/viewer/jportal_derivate_00164692/NLKN_1784_Bd01_%200001.tif?logicalDiv=jpor
1398	tal_jpvolume_00067117
1399	
1400	Scoble, M. J. 1992. The Lepidoptera: form, function and diversity. Oxford: Oxford University
1401	Press/Natural History Museum, 352 pp.
1402	
1403	Simonsen, T.J., Wagner, D.L. and Heikkilä, M. 2019. Ghosts from the past: a review of fossil
1404	Hepialoidea (Lepidoptera). PeerJ 7: e7982. http://doi.org/10.7717/peerj.7982
1405	
1406	Sohn, JC., Labandeira, C. and Davis, D. 2015. The fossil record and taphonomy of butterflies
1407	and moths (Insecta, Lepidoptera): implications for evolutionary diversity and divergence-time
1408	estimates. BMC Evolutionary Biology 15: Article 12 https://doi.org/10.1186/s12862-015-0290-8
1409	
1410	Sohn, J. C., Labandeira, C., Davis, D. and Mitter, C. 2012. An annotated catalog of fossil and
1411	subfossil Lepidoptera (Insecta: Holometabola) of the world. Zootaxa, 3286: 1-116.
1412	

1413	Sohn, JC. and Lamas, G. 2013. Corrections, additions, and nomenclatural notes to the recently
1414	published World catalog of fossil and subfossil Lepidoptera. Zootaxa, 3599 (4), 395–399.
1415	https://doi.org/10.11646/zootaxa.3599.4.8
1416	
1417	Wahlberg, N., Wheat, C.W. and Peña, C. 2013. Timing and patterns in the taxonomic
1418	diversification of Lepidoptera (butterflies and moths). PLoS ONE 8, e80875.
1419	https://doi.org/10.1371/journal.pone.0080875
1420	
1421	Weyenbergh, H., Jr. 1869. Sur les insectes fossiles du calcaire lithographique de la Bavière, qui
1422	se trouvent au Musée Teyler. Archives du Musée Teyler, 2, 247–294.
1423	
1424	Zeuner, F.E. 1927. Eine Sphingidenraupe aus dem Obermiozän von Böttingen.
1425	Palaeontologische Zeitschrift, 8, 321–326.
1426	
1427	Zhang, J. 1989. Fossil Insects from Shanwang, Shandong, China. Shandong Science Technology
1428	Publishing House, Jinan, 459 pp.
1429	
1430	Zhang, J., Sun, B. and Zhang, X. 1994. Miocene Insects and Spiders from Shanwang, Shandong.
1431	Science Press, Beijing, 298 pp., 42 pls.
1432	
1433	Zimmerman, E.C. 1958. Insects of Hawaii, vol. 7: Macrolepidoptera. University of Hawaii Press,
1434	Honolulu, xiii + 542 pp.
1435	
1436	Zolotuhin, V.V. 2010. A review of the genus Chionopsyche Aurivillius, 1909 with the
1437	description of a new species (Lepidoptera, Lasiocampidae: Chionopsychinae). Atalanta,
1438	<i>Würzburg</i> , 41 (3/4): 361-366, one col. pl.
1439	
1440	Zwick, A. 2008. Molecular phylogeny of Anthelidae and other bombycoid taxa (Lepidoptera:
1441	Bombycoidea). Systematic Entomology 33, 190–209. https://doi.org/10.1111/j.1365-
1442	<u>3113.2007.00410.x</u>
1443	
1444	Zwick, A. 2009. The principal structure of male genital sclerites and muscles of bombycoid
1445	moths, with special reference to Anthelidae (Lepidoptera: Bombycoidea). Arthropod Structure &
1446	Development, 38 (2): 147-161. https://doi.org/10.1016/j.asd.2008.07.006
1447	
1448	Zwick, A., Regier, J.C., Mitter, C. and Cummings, M.P. 2011. Increased gene sampling yields
1449	robust support for higher-level clades within Bombycoidea (Lepidoptera). Systematic
1450	Entomology, 36: 31-43. https://doi.org/10.1111/j.1365-3113.2010.00543.x

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).



PeerJ

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

(A) Counterpart. (B) Cast. 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).



PeerJ

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.





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.



Manuscript to be reviewed





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 Lshaped 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.

Manuscript to be reviewed



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.



Manuscript to be reviewed



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 credit: Sun Mingchang, SFML.

Manuscript to be reviewed



Figure 8

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.



Bombycites buechii Heer, 1865. Specimen barcode number: 000000005466.

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

Manuscript to be reviewed



PeerJ reviewing PDF | (2023:04:84528:1:1:NEW 26 Jun 2023)

Figure 10

"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 and Maria Heikkilä.



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.

Manuscript to be reviewed

