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Reassessment of known fossil Pyraloidea (Lepidoptera) with descriptions of the oldest fossil pyraloid and a crambid larva in Baltic amber

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Abstract

The identifications of known fossils currently placed in the lepidopteran superfamily Pyraloidea are critically re-examined. Of the eleven fossils examined, only three are confirmed to show morphological characters supporting placement in the superfamily. These fossils include a crambid larva in Baltic Amber, *Baltianania yantarnia*, Solis **gen. n.** et **sp. n.** and the oldest known fossil pyraloid, *Eopyralis morsae* Simonsen, **gen. n.** et **sp. n.** The third fossil, *Glendotricha olgae* Kusnezov, 1941, displays apomorphic characters for Pyraloidea, but is shown to be an inclusion in copal, not Baltic amber as had been reported. Seven fossil specimens lack reliable characters and cannot be assigned to Pyraloidea with certainty: *Pyralites obscurus* Heer, 1856; *Pyralites preecei* Jarzembowski, 1980; *Petisca dryellina* Martins-Neto, 1998; three fossil larvae tentatively identified as Pyralidae by Zeuner (1931); and *Gallerites keleri* Kernbach, 1967. A possible fossil pyraloid in Mizunami amber could not be located in museum collections and available literature does not provide details to assess the validity of the identification. We discuss the contribution of the reliably identified fossils towards better understanding the evolutionary history of Pyraloidea.

Key words: Pyralidae, *Baltianania yantarnia*, copal, Crambidae, fossil record, *Eopyralis morsae*, *Gallerites keleri, Glendotricha olgae*, *Petisca dryellina, Pyralites obscurus, Pyralites preecei*

Introduction

With over 16,000 described species, Pyraloidea are one of the largest and ecologically most significant superfamilies of Lepidoptera (Munroe & Solis 1998; van Nieukerken *et al.* 2011). Pyraloidea are divided into two ecologically diverse families, Pyralidae and Crambidae (Minet 1982; Regier *et al*. 2012). Their larvae, in addition to feeding on most major groups of plants, include detritivores, coprophages, predators and parasitoids, and some lineages have immature stages adapted to aquatic life (Neunzig 1987; Solis 1997, 2008; Munroe & Solis 1998).

Despite being such a species-rich and a prominent group of insects, the fossil record of the superfamily is surprisingly meagre. Currently, only eleven fossils have been proposed to belong to this superfamily, some of them only tentatively (Sohn *et al.* 2012). This depauperate fossil record is part of a larger pattern of poor preservation of fossil Lepidoptera as compared, for example, to insects in the three other large orders: Coleoptera, Hymenoptera and Diptera (Kapoor 1981; Labandeira & Sepkoski Jr. 1993; Kristensen & Skalski 1998; Penney 2010). Lepidopterans are thought to rarely fossilize due to their relatively frail bodies, which are easily dismembered and destroyed during the fossilization process (Duncan 1997; de Jong 2017), and the characteristic dense cover of modified setae or scales preventing mineral-rich groundwater from penetrating the body cavities (Wagner *et al.* 1996; Martínez-Delclòs *et al.* 2004). In addition, size seems to matter. Microlepidoptera dominate the lepidopteran fossil record, possibly because the fossilization of larger insects may require even more exceptional conditions (de Jong 2017). The fossil record of Lepidoptera is also poor in terms of the number of specimens identified below ordinal level (Sohn *et al.* 2015); scales tend to hide external diagnostic characters that differentiate superfamilies,

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families, genera and species. Often the examination of internal characters, such as genitalia, is required to make detailed identifications in Lepidoptera, but they are seldom clearly visible in amber fossils and nearly never in compression fossils.

The correct identification of fossils is of great importance in studies exploring the evolutionary history of organisms. In recent years, fossils have also attracted more interest as studies based on molecular clock estimates of the time of divergence of different lineages of organisms have become very popular. These methods often use fossils as calibration points for a minimum age to diversification events. However, the identification of fossil Lepidoptera has often been based on superficial similarity to extant species and not on apomorphies or character combinations diagnostic of extant taxa (Kristensen & Skalski 1998; Sohn *et al.* 2012; Sohn *et al.* 2015). Incorrectly identified fossils can present a biased picture of the time frame and historical distribution of organisms, and if used, for example, in divergence time analyses, introduce error into the results.

The aims of this study are to critically re-examine the identification of known fossils currently placed in Pyraloidea and to explore whether the fossils can shed light on the evolutionary history of the superfamily. We discuss the reliability of the characters for the current identifications and assess whether some of these fossils can be used as calibration points in divergence time analyses. We also list characters diagnostic of the pyraloid families Pyralidae and Crambidae, which can be used in making more accurate identifications. This study is part of a large international effort to re-examine the reliability of the lepidopteran fossil record. Reviews of fossil Nepticulidae (Doorenweerd *et al.* 2015), Papilionoidea (de Jong 2017) and Tortricidae (Heikkilä *et al.* 2018) have already been published and others are in preparation.

Material and methods

Institutional abbreviations:

AMNH	American Museum of Natural History, New York, U.S.A.
NHMUK	Department of Palaeontology, Natural History Museum, London, United Kingdom.
DGUG	Department of Geoscience, University of Guarulhos (= Departamento de Geociências, Universidade de Guarulhos), São Paulo, Brazil.
GZG	Geoscience Centre of the University of Göttingen, Göttingen, Germany.
MFMJ	Mizunami Fossil Museum, Mizunami, Japan.
MGUH	Geological Museum, Natural History Museum of Denmark, University of Copenhagen (= Mineralogicum Geologicum Universitatis Hafniensis), Copenhagen, Denmark.
MHMM	Henrik Madsen Collection, Morsland Historical Museum (= Morslands Historiske Museum), Mors, Denmark.
NHMA	Natural History Museum Aarhus, Aarhus, Denmark.
OMNH	Osaka Museum of Natural History, Osaka, Japan.
PIMUZ	Paleontological Institute and Museum, University of Zurich (= Paläontologisches Institut und Museum, Universität Zürich), Zurich, Switzerland.
PIRAS	Paleontological Institute, Russian Academy of Sciences (= Палеонтологический институт РАН), Moscow, Russia.
SMNS	Stuttgart State Museum of Natural History (= Staatliches Museum für Naturkunde Stuttgart), Stuttgart, Germany.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

Abbreviations of authors' names:

MAS	M. Alma Solis
MH	Maria Heikkilä
TJS	Thomas J. Simonsen

Specimens examined. Sohn *et al.*'s (2012) catalogue of fossil and subfossil Lepidoptera listed eleven specimens assigned to Pyraloidea, two of these questionably placed in this superfamily. Seven of the fossils are adult moths, four are larvae.

Due to major morphological (Minet 1982) and molecular discoveries (Regier *et al.* 2012), the superfamily is at present divided into two families, Pyralidae and Crambidae. Pyralidae *sensu lato* was used until the 1980s and is equivalent to the Pyraloidea of today. Therefore, fossils identified as Pyralidae prior to these discoveries should be understood as Pyralidae in the broad sense. Three of the eleven fossils have been identified as belonging to the family Pyralidae (though one only questionably), and for two of these a subfamily has been proposed (Chrysauginae and Pyralinae). No family assignment has been proposed for the remaining eight fossils.

Of the eleven fossils, we were able to re-examine in detail one compression fossil and two amber fossils. The re-examination of the other eight fossils is based on the original publications describing these fossils, and when possible, new high-quality photographs obtained from the institutions holding the specimens.

Age of fossil specimens examined. The age estimates of the fossils follow those in Sohn *et al.* (2012) unless otherwise stated. The oldest fossil proposed to belong to Pyraloidea, *Eopyralis morsae* Simonsen **gen. n.** et **sp. n.** (MUGH 32064/DK188), is a compression fossil in a piece of cement diatomite from the Danish Fur Formation, which has been dated to the early Ypresian, Earliest Eocene (55–54 Ma) (Heilmann-Clausen & Surlyk 2006; Bonde *et al.* 2008; Pedersen & Pedersen 2012). The recently described oldest known fossil butterfly, *Protocoeliades kristenseni* de Jong, 2016 (Coeliadinae: Hesperiidae), is also from this formation. The second oldest fossil, *Baltianania yantarnia* Solis **gen. n.** et **sp. n.**, is a specimen in Baltic amber (Lutetian, Middle Eocene, 48.6 ± 0.2–40.4 ± 0.2 Ma). The compression fossil from England, *Pyralites preecei* Jarzembowski, 1980, is dated to late Priabonian, Late Eocene (33.9 ± 0.1 Ma). Three compression/impression fossils of larvae (SMNS Nr. 11; Nr. 15 and Nr. 19) from Germany are from the Burdigalian, Early Miocene (20.43–15.97 Ma). The compression/impression fossil of an adult moth also from Germany, *Gallerites keleri* Kernbach, 1967, is younger (Piacenzian, Late Pliocene, 2.588 Ma). *Pyralites obscurus* Heer, 1856, a compression fossil from France, and *Petisca dryellina* Martins-Neto, 1998, from Brazil have been dated to the Chattian–Aquitanian, Late Oligocene–Early Miocene boundary (23.03 Ma). One of the specimens, *Glendotricha olgae* Kusnezov, 1941, is in copal of unknown age and origin (see Results). In the original publication in which a specimen in Mizunami amber was mentioned, the age of the amber (also in the title) was given as Pleistocene (33,100 years old) (Schlee 1984). However, Dr. Y. Ando, curator of the Mizunami Fossil Museum, informed us in a personal communication that the amber inclusions in question are from the Middle Miocene (16 Ma) Shukunohora Formation, Mizunami Group. The Miocene age for the Shukunohora Formation in central Japan is based on the presence of mangrove pollen in the Shukunohora sandstone fascies (Saito *et al.* 1995). More detailed information on the excavation localities of the fossils is provided in the Results.

Character observation. We intend to verify whether the observable characters in the fossils warrant placement in Pyraloidea and subgroups thereof. The monophyly of Pyraloidea is strongly supported both by molecular and morphological evidence (Munroe & Solis 1998; Regier *et al.* 2012). The most prominent apomorphic character of adult pyraloid moths is abdominal tympanal organs that consist of tympanal chambers and conjunctiva (Minet 1982). However, this character is difficult to observe in fossils because the tympanal organs are located basoventrally on the abdomen (sternum II). They are composed of tympanal chambers, with the anterior "openings" facing toward the thorax. To externally study tympanal organs in freshly pinned extant specimens, it often requires lifting the abdomen slightly to get an unobstructed view. In dry, mounted specimens, the tympanal organs are visible only if the legs and wings do not obstruct the view. Additionally, maceration of the specimen in a KOH solution is necessary to observe details. In fossils, this is not possible and the tympanal organs can also be hidden by scales, legs, or folded wings. The tympanal organs are present in all Pyraloidea with some exceptions where they are very small (Minet 1991) or highly reduced (Solis 1998). Abdominal tympanal organs are also present in few other groups of Lepidoptera, notably in Geometroidea, but unlike pyraloids, geometroids lack scales at the base of the haustellum. The basally scaled haustellum is indeed another important character for identifying moths as pyraloids. Not all Pyraloidea have a well-developed haustellum, it can be reduced, and even absent (e.g. *Aglossa* Latreille, 1796 (Pyralinae)), but when present, the scaled base is an example of a useful character to identify moths trapped in amber. In very exceptional cases it can be visible in compression fossils. A scaled base of the haustellum is also present in a few other groups of moths (Gelechioidea, Adelidae, Tischeriidae, Choreutidae, Millieriidae), but these moths have attributes not found in Pyraloidea (see Davis 1998; Dugdale *et al.* 1998), and lack the paired abdominal tympana. In Pyraloidea, wing venation can also be useful; the hindwing Sc + R is approximated or anastomosed with Rs for some distance beyond the discal cell (Munroe & Solis 1998). Larval characters defining Pyraloidea include two prespiracular setae on the prothorax and three SV setae on abdominal segments 3–6 (Hasenfuss 1960; Neunzig 1987).

The division of the superfamily into two monophyletic families, Pyralidae and Crambidae, is also supported by ample morphological and molecular evidence (Minet 1982; Regier *et al.* 2012). Adult Pyralidae are defined by the following synapomorphies: bulla tympani closed; absence of a praecinctorium; forewing veins Rs2–Rs4 stalked or fused; and uncal arms are present (Minet 1982; Solis & Mitter 1992). In Crambidae the bulla tympani are open, the praecinctorium is present, vein Rs4 usually not stalked with Rs2+Rs3, and the uncus arms are absent. In amber fossils, the crambid praecinctorium could possibly be visible if not obscured by the metathoracic legs or folded wings. In pyralid larvae there is nearly always a sclerotized pinaculum ring at the base of the SD1 seta on A8, with the exception of, for example, *Etiella zinckenella* (Treitschke, 1832), or in laboratory reared larvae, e.g. *Galleria mellonella* (Linnaeus, 1758) (Solis 1999). Crambid larvae have a unisetose L group on A9, crochets in a complete or incomplete circle, and no pinaculum ring at the base of SD1 on A8 or any other segments (Hasenfuss 1960; Neunzig 1987).

Identification of fossil Pyraloidea to lower taxonomic levels, e.g. genus and species, can be difficult. Phylogenetic studies based on the morphology of the Pyralidae (Solis & Mitter 1992) and Crambidae (Solis & Maes 2002) illustrated that subfamilies currently are defined by a combination of characters using adult morphology [usually including genitalia], but some included genera can lack these characters. Many external and internal (e.g. genitalia) characters used in the past to define genera were also found to vary at the species-level in the Crambidae (Solis & Maes 2002) and Pyralidae (Solis & Mitter 1992). Larval characters can be useful in defining subfamilies (Hasenfuss 1960) or genera in some subfamilies of Crambidae such as Acentropinae [= Nymphulinae, with aquatic or semi-aquatic immatures] (Yoshiyasu 1985; Passoa 1988), but more research at the generic level is needed on the variation and distribution of these characters across subfamilies (Solis & Maes 2002).

Specimen examination. The compression fossil, *Eopyralis morsae* **gen. n.** et **sp. n.** (MGUH 32064), was examined and described by TJS at NHMA. To facilitate comparisons to current members of Pyraloidea, the fossil was compared to whole-body dissections of representatives of 12 Pyraloidea subfamilies from the collections in the NHMA (Table 1). The fossil and all dissections were studied under a WILD Heerbrugg 6-50x stereomicroscope. The fossil was photographed through the microscope using a Canon EOS 5D mk II and a general adapter. Micrographs were subsequently enhanced using the 'Auto Levels' option in Adobe Photoshop®.

TABLE 1. List of species dissected for comparison of *Eopyralis morsae* gen. n. et sp. n. with extant pyraloid taxa at the NHMA.

Family	Subfamily	Species	Dissection #
Pyralidae	Gallerinae	*Aphomia sociella* (Linnaeus, 1758)	TJS-NHMA 17-07
Pyralidae	Pyralinae	*Pyralis farinalis* (Linnaeus, 1758)	TJS-NHMA 17-08
Pyralidae	Phycitinae	*Zophodia grossulariella* (Hübner, 1809)	TJS-NHMA 17-09
Crambidae	Glaphyriinae	*Evergestis forficalis* (Linnaeus, 1758)	TJS-NHMA 17-01
Crambidae	Acentropinae	*Parapoynx stratiotata* (Linnaeus, 1758)	TJS-NHMA 17-02
Crambidae	Crambinae	*Agriphila inquinatella* (Denis & Schiffermüller, 1775)	TJS-NHMA 17-03
Crambidae	Spilomelinae	*Nomophila noctuella* (Denis & Schiffermüller, 1775)	TJS-NHMA 17-04
Crambidae	Schoenobiinae	*Schoenobius gigantella* (Denis & Schiffermüller, 1775)	TJS-NHMA 17-05
Crambidae	Scopariinae	*Scoparia aurundinata* (Denis & Schiffermüller, 1775)	TJS-NHMA 17-06
Crambidae	Pyraustinae	*Pyrausta purpuralis* (Linnaeus, 1758)	TJS-NHMA 17-10
Crambidae	Odontiinae	*Cynaeda dentalis* (Denis & Schiffermüller, 1775)	TJS-NHMA 17-11
Crambidae	Heliothelinae	*Heliothela wulfeniana* (Scopoli, 1763)	TJS-NHMA 17-12

The larva in Baltic amber, *Baltianania yartarnia* **gen. n.** et **sp. n.** (AMNH B-JH 131), was examined and described by MAS at USNM. The fossil larva was compared to extant larvae of the genera *Pyrausta* Schrank, 1802, *Achyra* Guenée, 1849, *Loxostege* Hübner, 1825, and *Anania* Hübner, 1823, of the Pyraustinae located at the USNM Pyraloidea larval collection. The fossil and all extant larvae were studied under a WILD Heerbrugg M3Z stereomicroscope. The fossil larva was photographed using the Visionary Digital® imaging system and minimally retouched with Adobe Photoshop®.

Glendotricha olgae Kusnezov, 1941 (no. 19), was originally part of the private collection of B. V. Miloradovitsch, Russia, but is now permanently deposited at the PIRAS. The examination of this fossil is based on the information and illustrations in the original publication by Kusnezov (1941) and examination of the specimen at PIRAS by MH and Prof. A. Rasnitsyn. The fossil was examined under a Leica stereomicroscope.

The examination of *Gallerites keleri* Kernbach, 1967 (GZG.W.13547) is based on high-quality photographs provided by Dr Alexander Gehler, GZG, and the original description (Kernbach 1967).

Pyralites obscurus Heer, 1856 was not found in the PIMUZ collection (pers. comm. Dr. C. Klug) or in the ETH (Swiss Federal Institute of Technology) collection where most of the Heer type specimens are (pers. comm. Dr. A. Müller). The examination of this fossil is based solely on the information provided in Heer (1856).

The examination of *Pyralites preecei* Jarzembowski, 1980 (BMNH I.8640) is based on the original description and illustration in Jarzembowski (1980) and photographs provided by Claire Mellish (NHMUK).

The examination of *Petisca dryellina* Martins-Neto, 1998 was also performed using the illustrations and text in the original publications.

The three impression fossils of larvae described by Zeuner (1931) were examined from recent high-resolution photographs provided by Dr Hossein Rajaei, SMNS.

The possible pyralid moth fossil in Mizunami amber (133B) was not found among the specimens deposited at the Mizunami fossil Museum where the other specimens listed in Hiura & Miyatake (1974) are (pers. comm. Dr. Y. Ando). The original publication listing this fossil specimen did not provide a description or illustrations, therefore we were unable to verify the identification.

For each of the fossil specimens examined we provide information regarding four features: 1) excavation locality and depository of the specimen; 2) previously published illustrations of the specimen; 3) description of the matrix (e.g. amber, compression/impression fossil or other) and condition of the specimen within the matrix; and 4) comments on the morphology and identification of the specimen.

Based on our observations and evidence provided in the literature, we group the fossils into two categories:

Fossils most likely Pyraloidea, possibly with family/subfamily assignment: These fossils show apomorphic characters or a character combination diagnostic of extant Pyraloidea (see above).

Fossils most likely not belonging to Pyraloidea or character evidence inconclusive for reliable assessment: These fossils are too poorly preserved to confirm presence of characters typical of Pyraloidea or such characters are not present.

Under each of the two categories, the fossils are discussed in chronological order, from oldest to youngest, and fossils of comparable age are in chronological order based on the year of publication.

Results

Fossils most likely Pyraloidea, possibly with family/subfamily assignment

Eopyralis Simonsen, gen. n.

(Figs 1–6)

Type species: *Eopyralis morsae* Simonsen, sp. n., by present designation.

Etymology. *Eo* = dawn (classic Greek), and *Pyralis*, Linnaeus, 1758, which is the type genus of Pyralidae, indicate that the fossil is the oldest known member of the family (at the time of description).

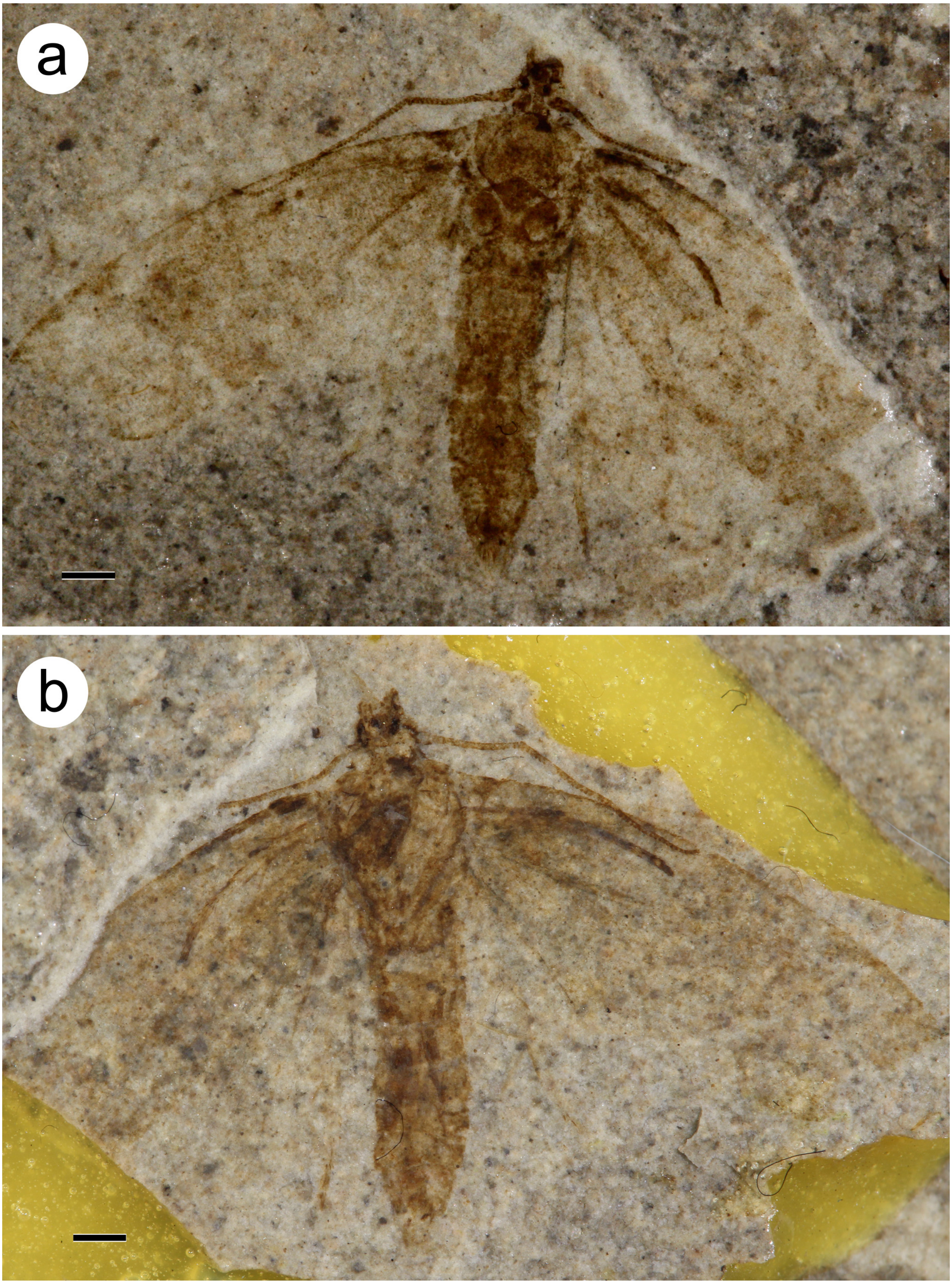

FIGURE 1. *Eopyralis morsae* Simonsen, **gen. et sp. n.** Overview. 1a: main part; 1b: counterpart. Scale bars = 1 mm. Photos: Thomas Simonsen.

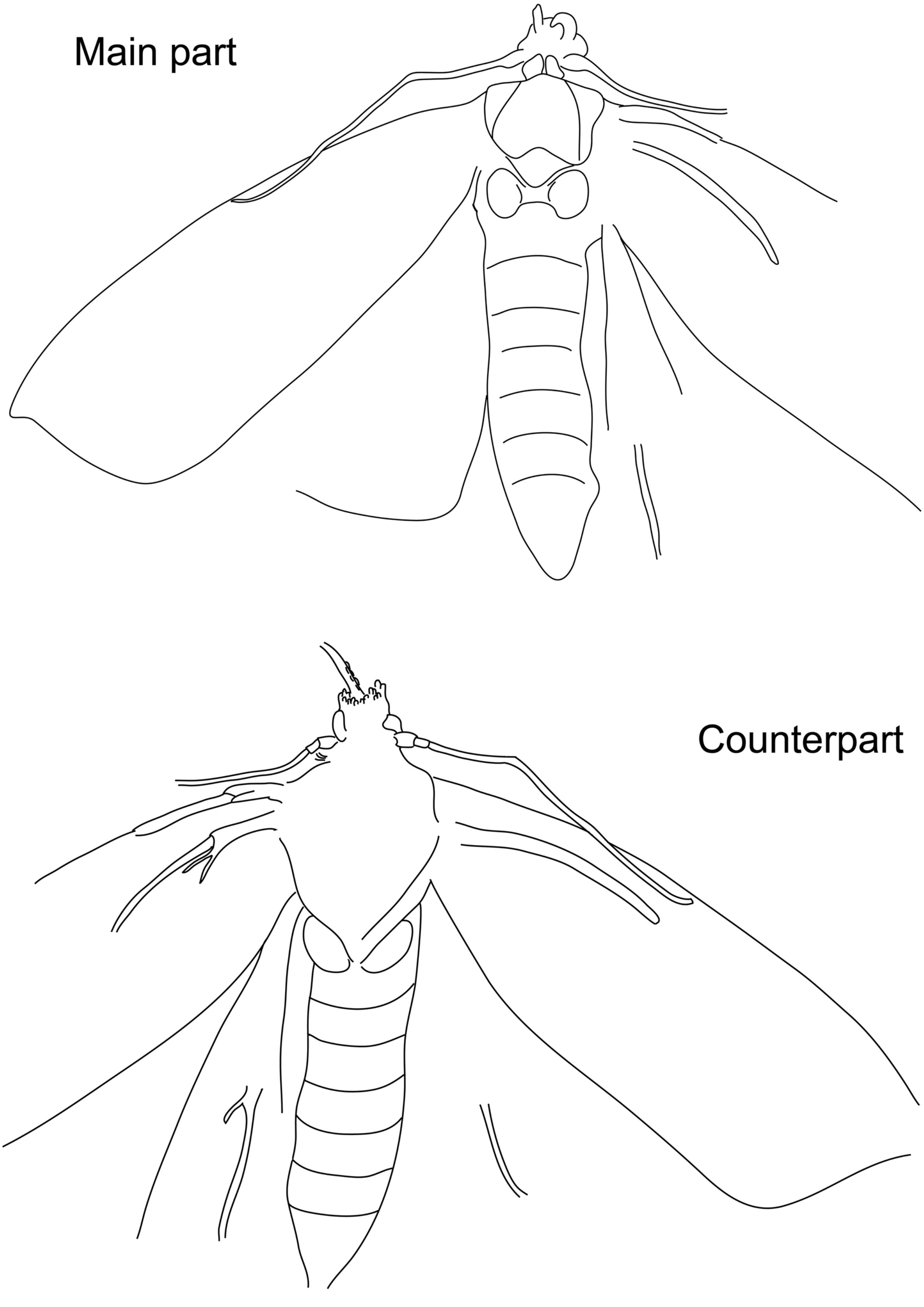

FIGURE 2. *Eopyralis morsae* Simonsen, **gen. et sp. n.** Drawings of the fossil in the main part (top), and counterpart (bottom). Illustrations: Thomas Simonsen.

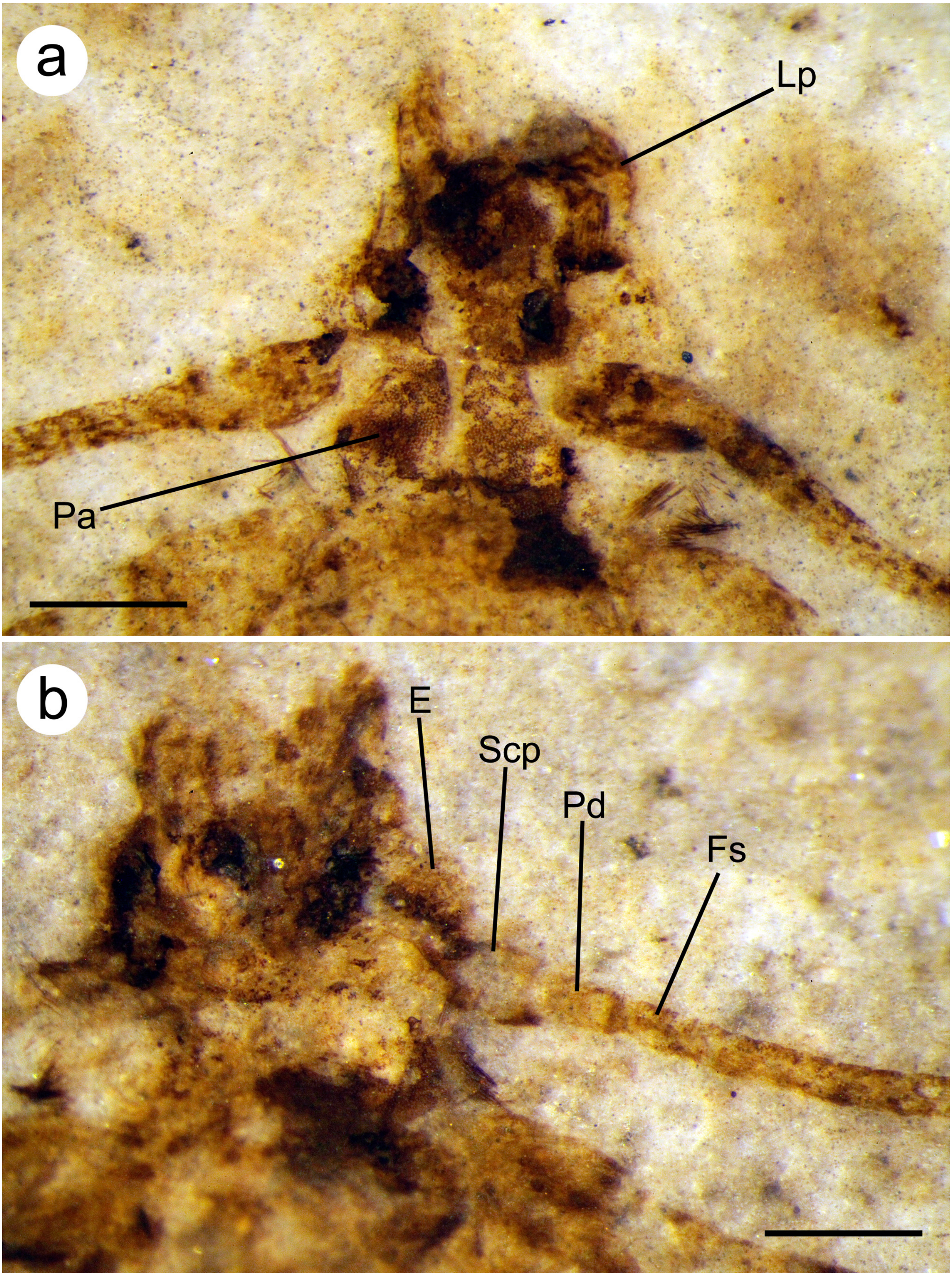

FIGURE 3. *Eopyralis morsae* Simonsen, **gen. et sp. n.** Head. 3a: main part; 3b: counterpart. Abbreviations: E, eye; Fs, antennal flagellum segment; Lp, labial palp; Pa, patagia; Pd, pedicel; Scp, scape. Scale bars = 1 mm. Photos: Thomas Simonsen.

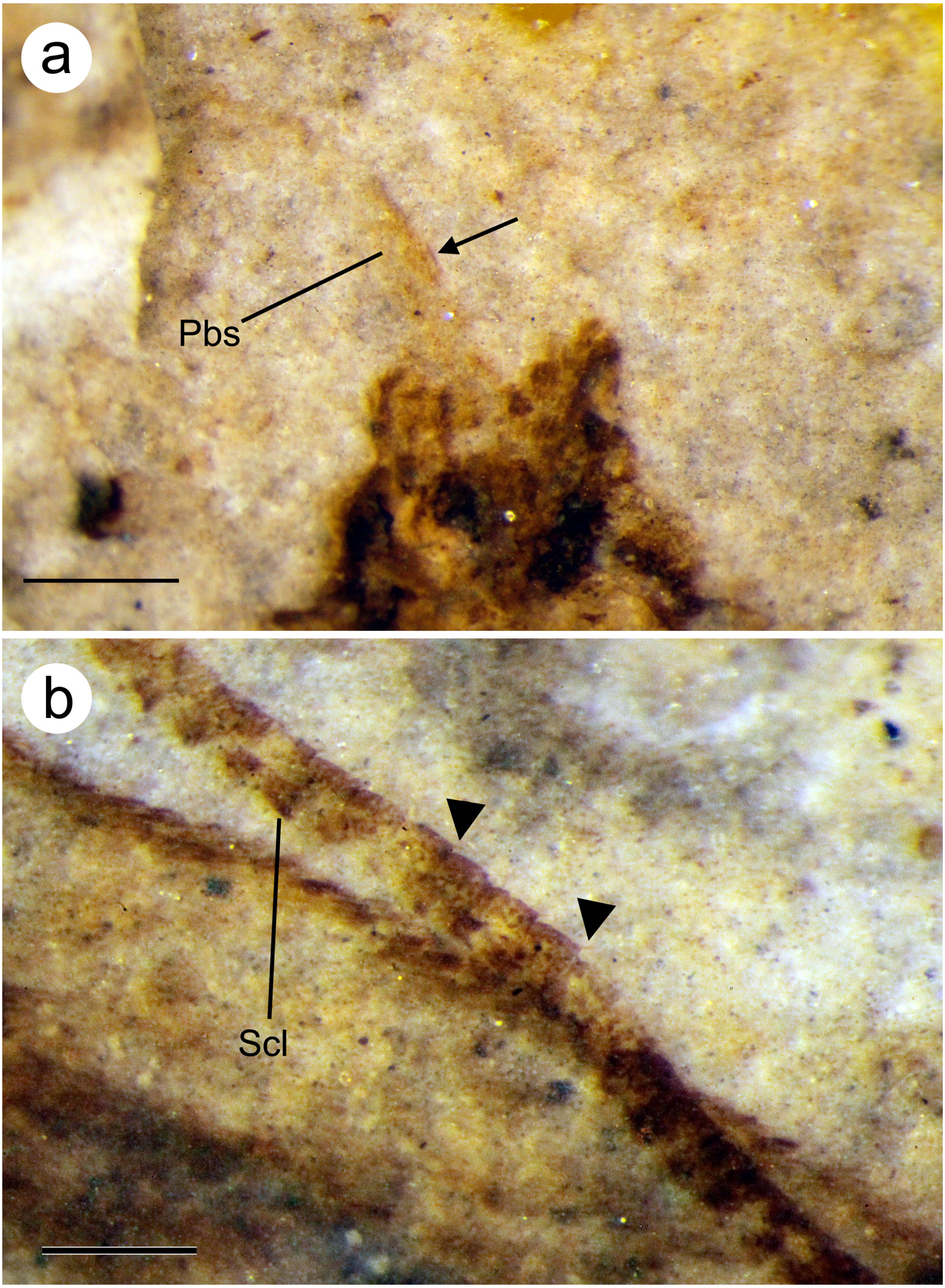

FIGURE 4. *Eopyralis morsae* Simonsen, **gen. et sp. n.** Details of haustellum and antenna (both from counterpart). 4a: Haustellum, note remnants of scales at the base (arrow); 4b: Antennal flagellum, note the small ventrodistal spines (arrowheads). Abbreviations: Pbs, proboscis; Scl, scales. Scale bars = 1 mm. Photos: Thomas Simonsen.

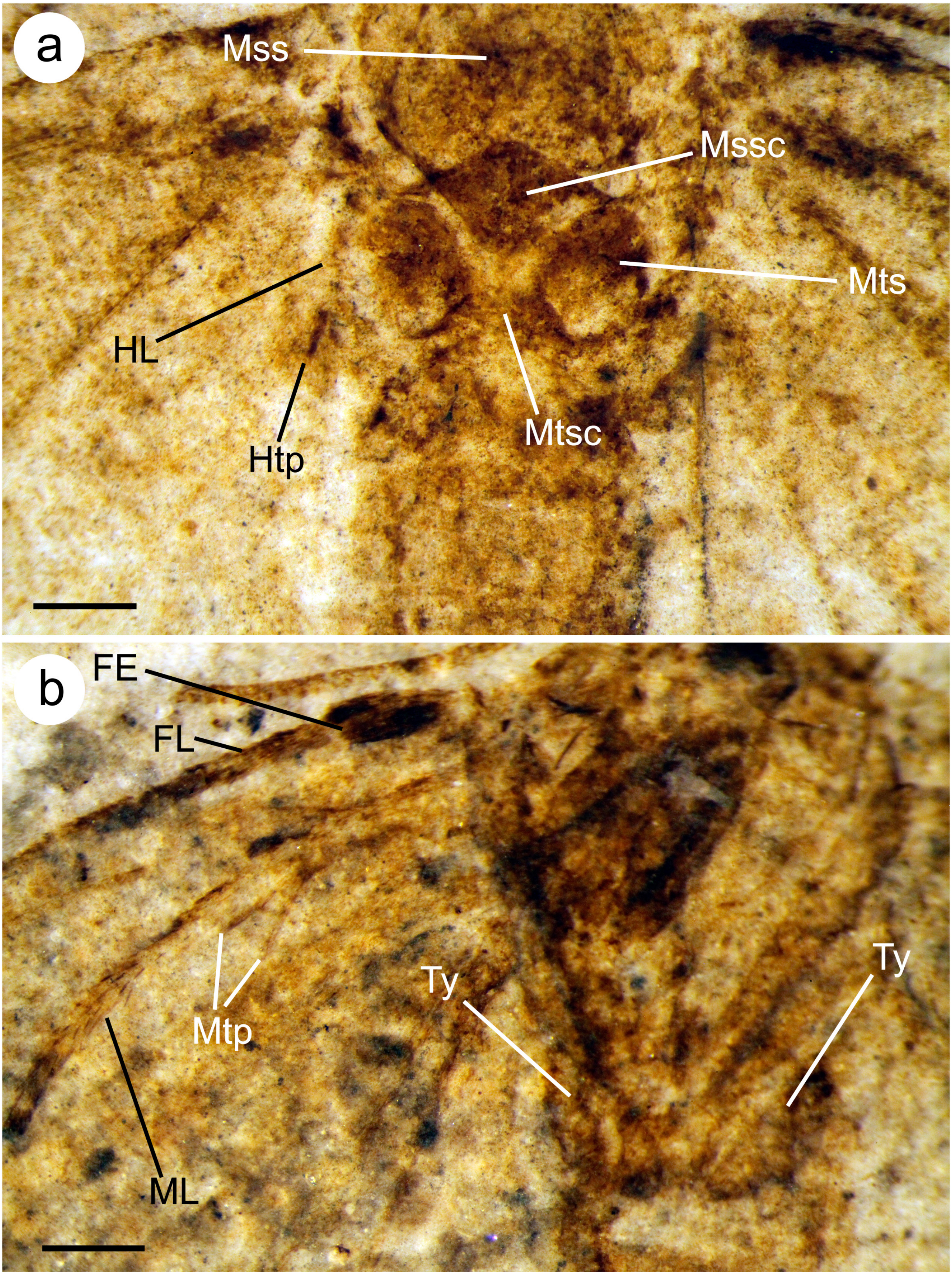

FIGURE 5. *Eopyralis morsae* Simonsen, **gen. et sp. n.** Thorax. 5a: main part; 5b: counterpart. Abbreviations: FE, foretibia epiphysis; FL, foreleg; HL, hindleg; Htp, hindtibia spurs; ML, midleg; Mtp, midtibia spurs; Mss, mesoscutum; Mssc, mesoscutellum; Mts, metascutum; Mtsc, metascutellum; Ty, tympana. Scale bars = 1 mm. Photos: Thomas Simonsen.

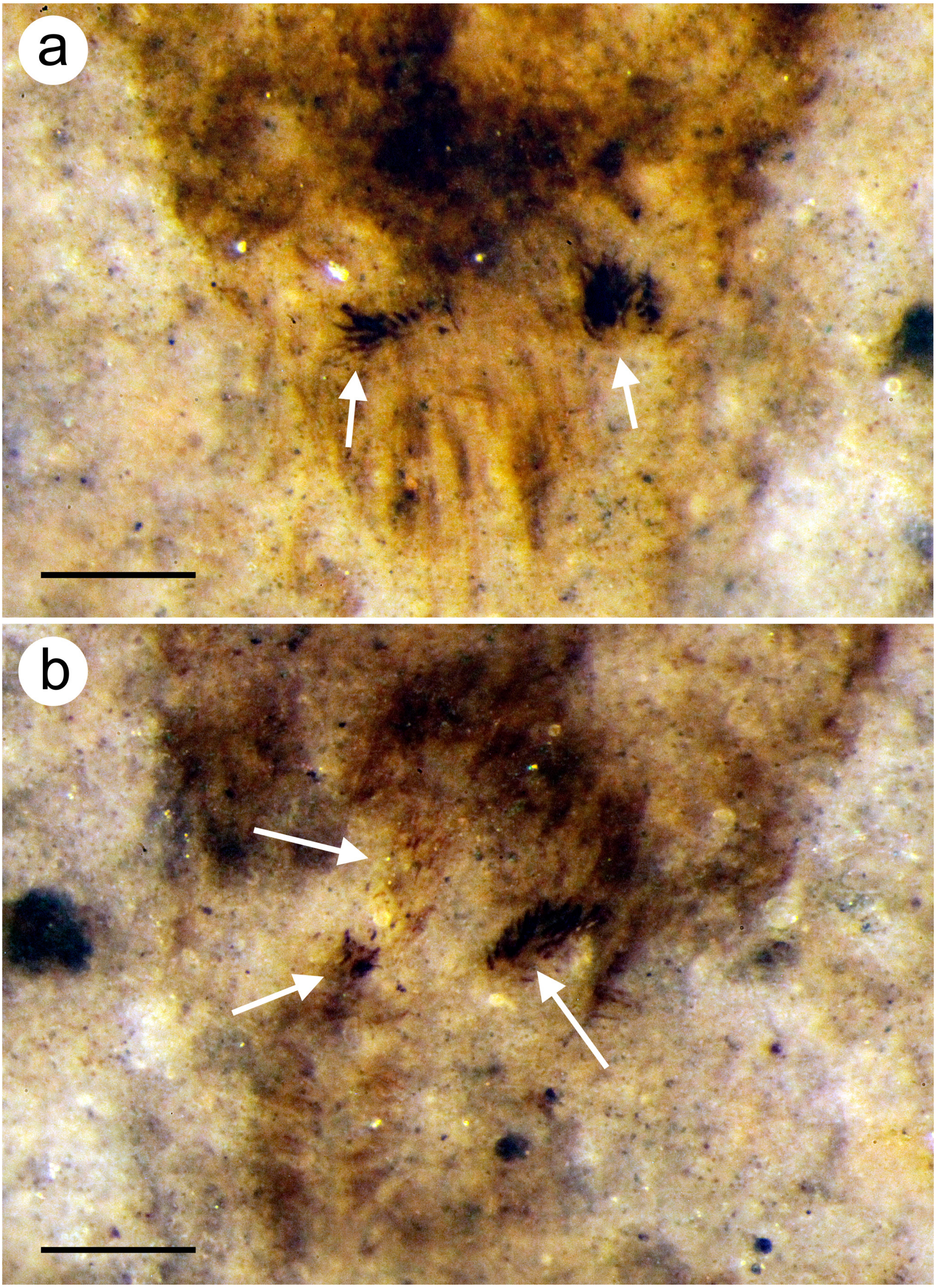

FIGURE 6. *Eopyralis morsae* Simonsen, **gen. et sp. n.** Abdomen: Postabdomen. 6a: main part; 6b: counterpart. The arrows indicate the structure we interpret to be either part of the male genitalia or secondary male structures of abdominal segment 8. Scale bars = 1 mm. Photos: Thomas Simonsen.

Diagnosis. Forewing characteristic, costal margin convex with small and pointed apex, overall wing shape subrectangular, with a broad and rounded tornus; patagia subtrapezoidal and clearly longer than broad; metascutum double-oval shaped. The wing shape with the pointed apex and broad, rounded tornus is to our knowledge unique in Pyralidae, justifying describing a new genus for the single specimen.

Description. *Head:* width (just before the antennae) 1.3 mm. Eyes large. Antenna with barrel-like scape, longer than broad; pedicel long and narrow, more than 2× longer than wide; flagellum thread-like, approximately half the length of the forewing; segments <1.5× longer than broad, with two transverse rows of dorsal scales, naked ventrally; at least some segments with a small ventrodistal 'spine' (probably a sensillum styliconicum). Palpi probably upturned (but not well preserved). Eyes large. Haustellum discernable, scaled at base.

Thorax: Forewing length 11 mm; forewing width 4 mm; forewing shape as in Diagnosis. Patagia prominent and clearly scaled/setose, otherwise as in Diagnosis. Foreleg with tibial epiphysis; midleg with two prominent distal tibial spurs, but no basal spurs visible; hindleg with visible basal spurs, so spur formula is either 0:2:2 or 0:2:4. Hindleg reaching at least the tip of abdomen. Mesoscutum large with deep basocentral indentation; mesoscutellum small and diamond-shaped. Metascutum as in diagnosis; metascutellum narrow and half-moon-shaped.

Abdomen: Paired tympanal organs present on A2; tympanal case suboval and apparently closed anteriorly; no secondary venula observable.

Male genitalia: The interpretation of this region is uncertain, but the specimen appears to have a narrow and triangular uncus with numerous small setae pointing towards the base of the abdomen. If this interpretation is correct, the presumed valvae extend just beyond the tip of the uncus and have dense, stout scales. An alternative interpretation is that the triangular structure and the dense stout scales are part of abdominal segment 8, and stout scales represent paired, composite scale brushes.

Eopyralis morsae **Simonsen, sp. n.**

(Figs 1–6)

Excavation locality and depository. Denmark: Jutland, Mors Island, Ejerslev Molergrav (Fur Fm., Cement Diatomite)/ early Ypresian, Early Eocene: ca. 54 Ma, Bonde *et al*. 2008). MGUH 32064 [previously: DK188]

Published illustrations. Bonde *et al.* 2008: 143 (photograph [as DK188]).

Condition. Compression fossil of a dorso-ventrally compressed adult moth (counterpart glued permanently onto main part). The larger block (which we here call the 'main part', 49 × 44 mm) has a smaller piece (which we here call the 'counterpart', 29 × 12 mm) glued permanently onto it. The two parts show slightly different details. Whole body; total head–body length 10.9 mm. Wings partly spread, wing venation not discernable. Overall relatively well-preserved: head, body, most of the wings present, fragments of fore-, mid- and hind legs visible. Head with well-preserved antennae; base of haustellum present. Thorax with some sclerites visible as described below. All legs at least partly present. Abdomen well preserved. Specimen probably a male as it has what appears to be a triangular uncus and densely setose valvae, *or* a distinct and triangular abdominal segment 8 with conspicuous composite hair brushes.

Etymology. The specific name refers to the Danish island (Mors) on which the fossil was found.

Diagnosis. As for genus.

Description. As for genus.

Comments: The paired tympanal organ at the base of the abdomen (Fig. 5, variably visible in both parts, most clearly in counterpart), and the probable scaled base of the haustellum (Fig. 4a, visible only in counterpart) clearly place the fossil in Pyraloidea. The rounded, and apparently anteriorly closed tympana clearly indicate placement within Pyralidae. The apparent absence of secondary venulae in association with the tympana indicate an association with the Phycitinae-Pyralinae-Epipaschiinae lineage within Pyralidae (Solis & Mitter 1992; Regier *et al.* 2012). The distinct patagia (Fig. 3a), which are subtrapezoidal and longer than broad, also indicate such a position as all studied current pyraloids have patagia, which are broader than long, but the studied Pyralinae and Phycitinae have patagia, which are only slightly broader than long. Furthermore, the studied Pyralinae have subtrapezoidal patagia. The suboval lateral halves of the metascutum (Fig. 5a) also indicate such a systematic position, as only the studied Phycitinae have rounded lateral halves of the metascutum—all other studied pyraloids have diamond-shaped or triangular lateral halves of the metascutum. Finally, if the structures described from the postabdomen (Fig. 6) are indeed composite scale brushes, this could indicate a close affiliation with Phycitinae, as such structures are found widespread and in a number of varieties in Phycitinae (e.g. Heinrich 1956; Horak 1997; Simonsen & Roe 2009; Roe *et al.* 2015). It is therefore possible that the fossil represents a stem group of the 'Phycitinae-Pyralinae-Epipaschiinae' clade as defined in Regier *et al.* (2012), or perhaps a stem group Phycitinae.

Baltianania **Solis, gen. n.**

(Fig. 7)

Type species: *Baltianania yantarnia* Solis, sp. n., by present designation.

Etymology. The generic name, *Baltianania,* is derived from the combination of the general locality, the Baltic Region, where the fossil was discovered, and its possible affinity to the crambid genus, *Anania* Hübner, 1823. The gender is feminine.

Diagnosis. Prothoracic setae D1 are 1.2 times closer together than XD 1 as in some extant species in *Loxostege* Hübner, 1825, but usually twice as close together in extant *Anania*; on abdominal segment 9, D2 of the two sides are on different pinacula, but are on a common shield-like pinaculum in most Pyraustinae; anal shield with SD2 twice as long as other setae on a slightly raised pinaculum.

Description. Length of larva 4.5–5.5 mm (the latter, if it were to be distended). Integument smooth. Pinacula present, flat in all segments (except with SD1 on A10), lacking dark black pigmentation. Instar unknown. *Head:* Examined dorsolaterally. Epicranial suture present. Adfrontal sutures not reaching occipital foramen. Antenna visible. P1 and L1 present. Stemmata present, only 3 seen dorsolaterally.

Thorax: *Prothorax:* Prothoracic shield without black pigmentation, segment membrane distended anteriorly. D1, D2, SD1, SD2, XD2 and XD1 present. Setae D1 are 1.2 times closer together than XD. Dark, elongated spots at base of setae. Two prespiracular setae (observed with ventral lighting). *Mesothorax and metathorax:* D1 and D2 present on individual, protruding, sclerotized pinacula. D1 anterodorsal to D2. SD1 and SD2 present on individual, protruding, sclerotized pinacula. SD2 anterodorsal to SD1 on mesothorax and anteroventral on metathorax; individual pinacula separate, not coalesced.

Abdomen: Abdominal segments 1–8: Pinacula of D1, D2, and SD1 sclerotized, dorsal setae D1, D2, and SD1 present. Larva in the ventral view appears to be twisted or distorted on A2–A4. On A3 and A4 the SV seta is determined by location with respect to SV1 on A2 and that no other setae were observed between it and the proleg. SD1 on abdominal segments 1–8 anterodorsal to spiracle on segments 3–7. Pinacula of D1 setae not fused on dorsum of segments. Spiracle barely visible on some segments, not visible in others. L1 present. Three SV setae on abdominal segments 3–6 (best seen on segment 6). Crochets in a penellipse (best seen in proleg 2). Crochet remnants appear to be uniordinal, but also appear thick enough to be biordinal or triordinal. Abdominal segments 1–7, D2 posterolateral to D1; abdominal segment 8, D2 parallel to D1. L1 and SV1 present. *Abdominal segment 9:* D2 setae on different pinacula; D2 posterodorsal, almost medially located from D1. SD1 posterolateral to D1. SD1 parallel to D2. L1 and SV1 present. *Abdominal segment 10:* D1, SD1, L1 in a triangle on the anterolateral corner of the anal shield. SD2 seta twice as long as other setae on a slightly raised pinaculum (also in extant *Anania* species, but this was not observed by Allyson (1981) who found no differences in this character among genera in Pyraustinae); D2 posteriorly located.

Baltianania yantarnia **Solis, sp. n.**

(Fig. 7)

Excavation locality and depository. Baltic Region, collected from Yantarny, Kaliningrad, Russia (Baltic Amber, Prussian Fm.)/Lutetian, Middle Eocene. AMNH B-JH 131.

Published illustrations. Grimaldi & Engel, 2005: 580, Fig. 13: 48 (identified as Pyralidae *sensu lato*) (colour photograph).

Condition. Larva in Baltic amber, whole body. Size of amber piece 26 × 19 mm. Larva excellently preserved dorsally, less so anteriorly and ventrally. Length of body 4.5–5.5 mm (the latter, if it were to be distended). Identified as Lepidoptera: caterpillar, det. D. Grimaldi.

FIGURE 7. *Baltianania yantarnia* Solis, **gen. et sp. n.** Length of larva 4.5–5.5 mm (the latter, if it were to be distended). Illustrations and photos: Taina Litwak.

Etymology. The specific name is derived from locality, Yantarny, where the fossil was discovered.

Diagnosis. As for genus.

Description. As for genus.

Comments. Most other fossils attributed to the Pyraloidea are adults, the possible pyraloid larvae mentioned by Zeuner (1931) being the exception. This is the fourth larval fossil attributed to Pyraloidea (as Pyralidae *sensu lato* in Grimaldi & Engel (2005)).

Kristensen & Skalski (1998) listed two autapomorphies for larval Lepidoptera: "Pleurostome elongated, craniocardinal articulation far behind mandibular base. Maxillary palp with fewer than 5 segments." Unfortunately, the larval head of this fossil is the least preserved area. The pleurostoma and maxillary palpi are not visible. But the fossil does have many other characteristics associated with lepidopteran larvae (Stehr 1987): a distinct head, chewing mouthparts (a clypeus or labrum visible), one pair of short antennae (1 antenna is visible), adfrontal areas (epicranial suture visible), a protruding labial spinneret (not visible), three pairs of thoracic legs (three of the pairs visible on the left side, and visible, but distorted on the right side), ten abdominal segments (visible) with crochet-bearing prolegs on abdominal segments 3, 4, 5, 6 and 10 (prolegs visible but damaged on the left side, only remnants of crochets visible on 3, 4, 5, 6; anal prolegs and crochets visible), and spiracles on the prothorax and abdominal segments 1–8 (not, or barely visible, best seen on abdominal segment 4).

The putative placement of this fossil specimen in the Pyraustinae is supported by the findings of the most thorough, comparative study of North American larvae, 19 pyraustine genera and 19 spilomeline genera (Allyson 1981; 1984 as Pyraustini and Spilomelini) and confirmed by Passoa (1985) in his larval study of Neotropical pyraustine genera. This fossil has the following characters as stated by Allyson (1981) and Passoa (1985): the pinacula bearing setae D and SD are not fused (fused in the Spilomelinae), the pinaculum bearing SD1 is not reduced on abdominal segments 2 and 7 (reduced in the Spilomelinae), setae V1 farther apart on abdominal segments 9 and 10 with a bandlike pinaculum (the latter not visible in the fossil), and seta L2 is not reduced on abdominal segments 1 to 8.

Glendotricha olgae Kusnezov, 1941

(Fig. 8)

Excavation locality and depository. In the original description the inclusion is reported to be in Baltic amber (Baltic Region, Prussian Fm./Lutetian, Middle Eocene), but Prof. A. Rasnitsyn has examined the specimen and concluded it is copal (pers. comm.). The specimen was formerly in the private collection of B. V. Miloradovitsch, Russia, but is now at the PIRAS, Moscow (no. 19).

Published illustrations. Kusnezov, 1941: 66, Figs 54–57 (drawings).

Condition. According to Kusnezov (1941) the adult male moth is in Baltic amber, but Prof. A. Rasnitsyn has informed us that his own observations strongly indicate that the inclusion is copal, and not amber: 1) he cut off a piece of the material and subjected it to 95% ethanol after which it became jelly-like and opaque; 2) unlike other inclusions treated by Kusnezov (1941), the surface of the inclusion containing *G. olgae* has since become densely cracked. These observations are consistent with subfossil resinites such as copal compared to amber (Szwedo 2002; Vávra 2009). The size of the copal piece is 16 × 20 mm. A fragment of the piece has broken off, but the inclusion has not been affected. The surface of the copal piece has a dense network of small cracks making the examination of the ventral side of the insect nearly impossible. Length of the body 5.1 mm. Length of forewing 5.0 mm. Both fore- and hind wings spread. The moth is nearly intact, but the labial palpi seem to be missing and the legs are broken off at the coxae. Fragments of the mid- and hind legs are preserved in the same piece of copal. The valvae of the male genitalia are partly visible.

Comments. Kusnezov saw close resemblance between the fossil moth and moths of the extant genus *Endotricha* Zeller, 1847 currently in the subfamily Pyralinae. As evidence of an affinity with *Endotricha,* he emphasized the similarities in genitalia characters and wing venation, in particular the anastomosis of the hindwing veins Rs and Sc+R.

The pyraloid apomorphy, the tympanal organs, is not mentioned in the original description of *Glendotricha olgae* and cannot be observed in the fossil. Kusnezov described the haustellum as smooth and without “lateral processes”, and no scales were drawn on the haustellum base in the illustration of the whole moth, or in that of the head only (his Figs 54 and 55). However, scales at the base of the haustellum are clearly visible in the fossil and can be seen in the photograph (Fig. 8b). An ocellus appears to be present, but the presence of chaetosemata is unclear. Veins Rs2–Rs4 in the forewing of the fossil moth share a common stem, which is the prevalent state in extant moths of the family Pyralidae—in Crambidae Rs4 is usually not stalked with Rs2–Rs3 (Munroe & Solis 1998). Additionally, the presence of a color pattern in the scales on the costa (recently discussed in the costa of the medial area for the Crambidae by Hayden (2013) and Minet (2015)) can be seen on the fossil. Pyralinae can be identified by alternating light and dark scales, specifically at the base of the wing. In extant *Endotricha*, basally there are three dark patches followed by a fourth longer patch, exactly as in the fossil.

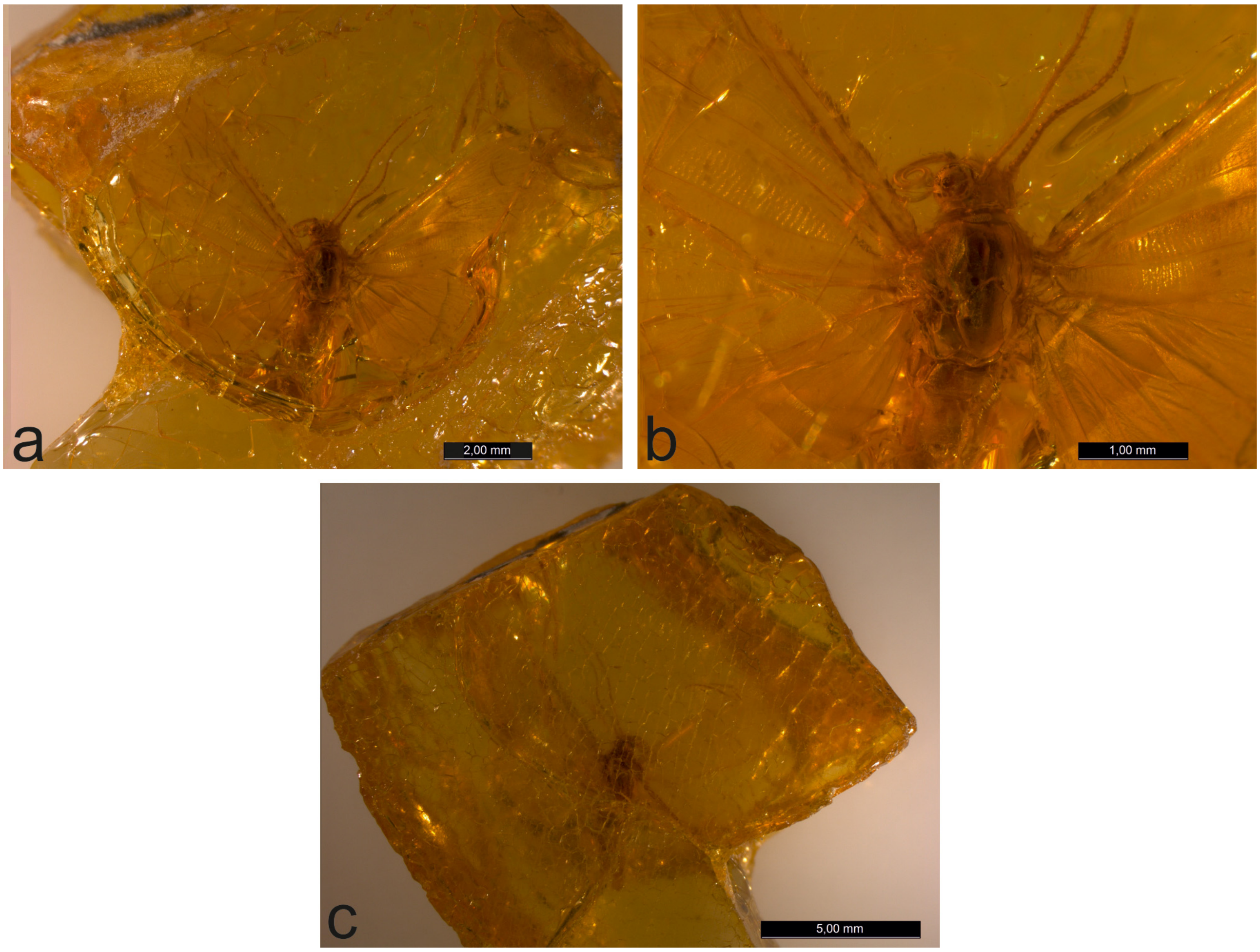

FIGURE 8. *Glendotricha olgae* Kusnezov, 1941 a. Dorsal view. b. Dorsal view of head and thorax. Note scaled base of haustellum. c. Ventral view with densely cracked surface of copal piece. Photos: Maria Heikkilä.

Solis & Shaffer (1999) found that the anastomosis of Rs and Sc+R is not a good character for tribal placement, but generally the venation of the fossil moth is a fit for the genus *Endotricha* in the Pyralinae. The wing venation is almost identical to that of *Endotricha flammealis* (Denis & Schiffermüller, 1775) figured by Whalley (1963, plate 12).

The fossil moth displays significant saccular processes on the valvae similar to those found in extant Endotrichini (see e.g. Solis & Shaffer (1999), p. 4, Fig. 3). There are other pyraloids with saccular processes, but not so sclerotized, and/or so prominent. The valvae are broad distally, which is true for almost all species in the genus *Endotricha* (Whalley, 1963). However, synapomorphies for the Endotrichini are present in the uncus-gnathal complex, which, unfortunately, are not visible in the fossil.

We conclude that the scaled base of haustellum and the wing venation indicate that this fossil moth is most likely a pyraline closely related to the genus *Endotricha*. Endotrichini seem to be very derived within the Pyralinae with respect to the genitalia, but not wing venation (see above), and, as a consequence, the genus was elevated to tribal rank. There are no comparative studies to support the tribal rank divisions in Pyralinae.

Fossils most likely not belonging to Pyraloidea or character evidence inconclusive for reliable assessment

Pyralites obscurus Heer, 1856
(Fig. 9)

Excavation locality and depository. France: Bouches-du-Rhône, Aix-en-Provence ("laminites lacustres")/ Chattian–Aquitanian, Late Oligocene–Early Miocene boundary. Whereabouts of the type unknown.

Published illustrations. Heer, 1856: pl. 2, Fig. 6 (drawing).

Condition: Compression/impression fossil of what appears to be an adult moth. The head and thorax are the most prominent features. Wings appear to be folded over the body. What seem to be the bases of the wings are in an unusual position, behind the thorax. According to Heer (1856) the whole length is 4 lines (8.5 mm), the length of the wings 2 ¾ lines (5.8 mm) and width at the rear 2 ⅛ lines (4.5 mm).

Comments. Although acknowledging that the specimen is very incomplete, Heer interpreted the fossil as a pyralid *sensu lato*. The preservation is indeed very poor and no details can be observed. We agree with Kozlov (1988) who regarded the identification of this fossil uncertain, and that there is nothing to indicate any lepidopteran superfamily relationship.

Determining whether a fossil genus was originally intended as a genus group name or a nominal genus can be difficult. In the present work we follow Sohn & Lamas (2013) who regarded fossil genera as nominal when authors had included statements on the diagnostic characters of the specimens in comparison with other fossil or extant genera. *Pyralites* Heer, 1856 falls into this category and was also treated as a nominal genus by Fletcher & Nye (1984: 131) with the type species, *Pyralites obscurus* Heer, 1856, fixed by monotypy (ICZN 1999: Article 68.3). In 1980, Jarzembowski described another fossil he placed in this genus (see below). We were not able to examine the actual specimen, but the illustration and description of the fossil in Heer (1856) do not provide convincing evidence to keep *Pyralites obscurus* in Pyraloidea. Therefore, we exclude it from the superfamily and consider it Lepidoptera *incertae sedis*.

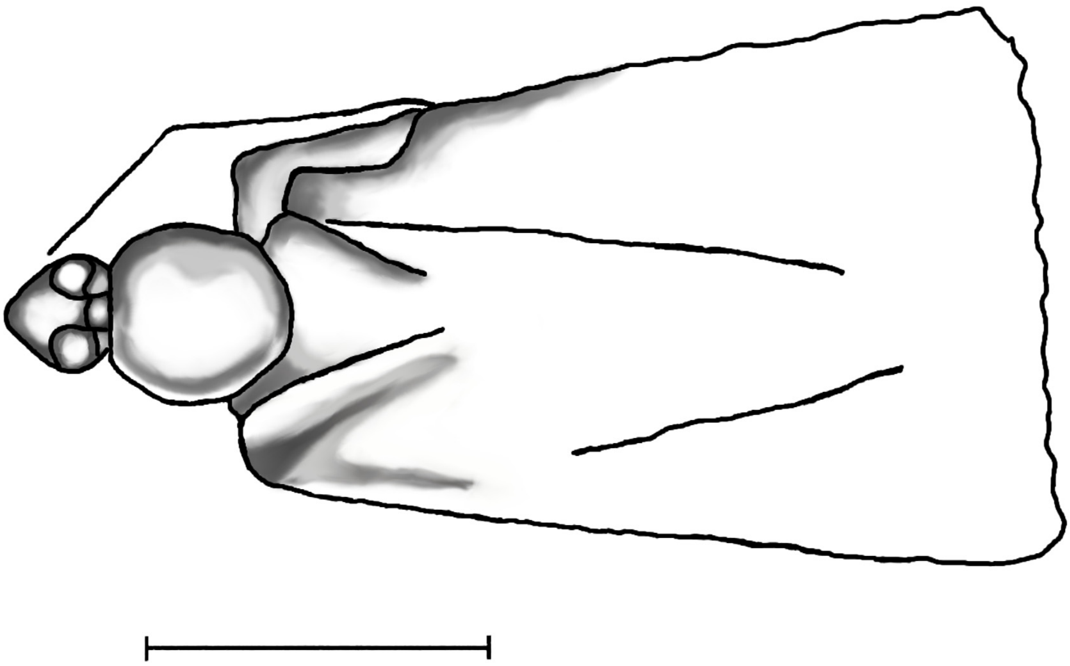

FIGURE 9. *Pyralites obscurus* Heer, 1856. Whole length of moth is 8.5 mm. Illustration: Anna Suuronen. Redrawn after Heer (1856).

Pyralites preecei Jarzembowski, 1980
(Fig. 10)

Excavation locality and depository. United Kingdom: England, Isle of Wight, Bembridge Marls (Bouldnor Fm.); late Priabonian, Late Eocene. NHMUK I.8640.

Published illustrations. Jarzembowski, 1980: 276, Fig. 69 (drawing).

Condition. Compression/impression fossil of a partially preserved adult moth. Head missing, thorax with traces of tegula and some sclerites visible, wing venation partly preserved and illustrated in Jarzembowski (1980). Length of mesothorax 3 mm, length of tegula 0.5 mm. The sex of the moth cannot be determined.

FIGURE 10. *Pyralites preecei* Jarzembowski, 1980. Length of mesothorax 3 mm. Photo: copyright NHM, London.

Comments. Jarzembowski (1980) placed the specimen in Pyralinae, in the fossil genus *Pyralites*, Heer 1856, but stated that a re-examination of *Pyralites obscurus* Heer, 1856 might require placing *P. preecei* in a separate genus.

According to Jarzembowski (1980) the wing venation of *Pyralites preecei* resembles that of certain genera in the tribe Pyralini. The affiliation with Pyralidae is based on the general habitus, the absence of the M vein in the cell, the closeness of M_2 to M_3 in both wings and the approximation of Sc + R to Rs in the hind wing beyond the discal cell. The first two vein M characters are not unique to Pyraloidea, but the latter wing vein character, the approximation of Sc + R to Rs in the hindwing, has been considered an apomorphy of the superfamily (most recently by Common 1990; Munroe & Solis 1998), and only the Pterophoridae "often have Sc + R of the hindwing anastomosing with Rs as in the Pyraloidea" (Munroe & Solis 1998). The approximation of Sc + R to Rs beyond the discal cell does, however, occur occasionally in some other groups of Lepidoptera (e.g. Drepanidae, see Minet & Scoble (1998: 303, Fig. 17.1 C)). Although the character could support an affinity with Pyraloidea, the fossil is very fragmentary and the other pyraloid apomorphies are not visible. Therefore, we prefer to be conservative and consider the identification of this fossil as a pyraloid uncertain.

There has been a purported difference in the condition of Sc + R in relation to Rs between Crambidae and Pyralidae (Minet 1982; Munroe & Solis 1998), but this character requires in-depth study at lower taxonomic levels.

Studies on the shape of the cross vein across the discal cell in the hind wing and/or the distribution of the different states across the Pyraloidea would also be needed. The cross vein in Jarzembowski's interpretation of the fossil is a basally, symmetrically, rounded vein that is similar to some phycitines (see multiple drawings in Heinrich (1956)), but it is clearly not a pyraline according to Solis & Shaffer (1999, see Figs 5 and 6), or an epipaschiine according to Solis (1993: Fig. 15), both with an asymmetrical cross vein.

The placement of *Pyralites preecei* in the same genus with *Pyralites obscurus* seems to have been based mostly on the round shape of the metascutellum (Jarzembowski 1980). It is likely that the two fossils are not congeneric and we doubt that closer examination of the specimens will add support to their belonging in the same genus. Due to lack of character evidence to warrant a place in Pyraloidea, we consider both fossils as Lepidoptera *incertae sedis*.

Petisca dryellina **Martins-Neto, 1998**

(Fig. 11)

Excavation locality and depository. Brazil: São Paulo, Tremembé City, near Padre Eternal, Fazenda Santa Fé (Tremembé Fm.); Chattian–Aquitanian, Late Oligocene–Early Miocene boundary. DGUG UnG/1T-83.

Published illustrations. Martins-Neto 1998: 63, Fig. 2D (drawing); 69, Plate III C (black and white photograph).

Condition. Compression fossil interpreted as a partly preserved forewing of an adult moth. Forewing length 3.5 mm.

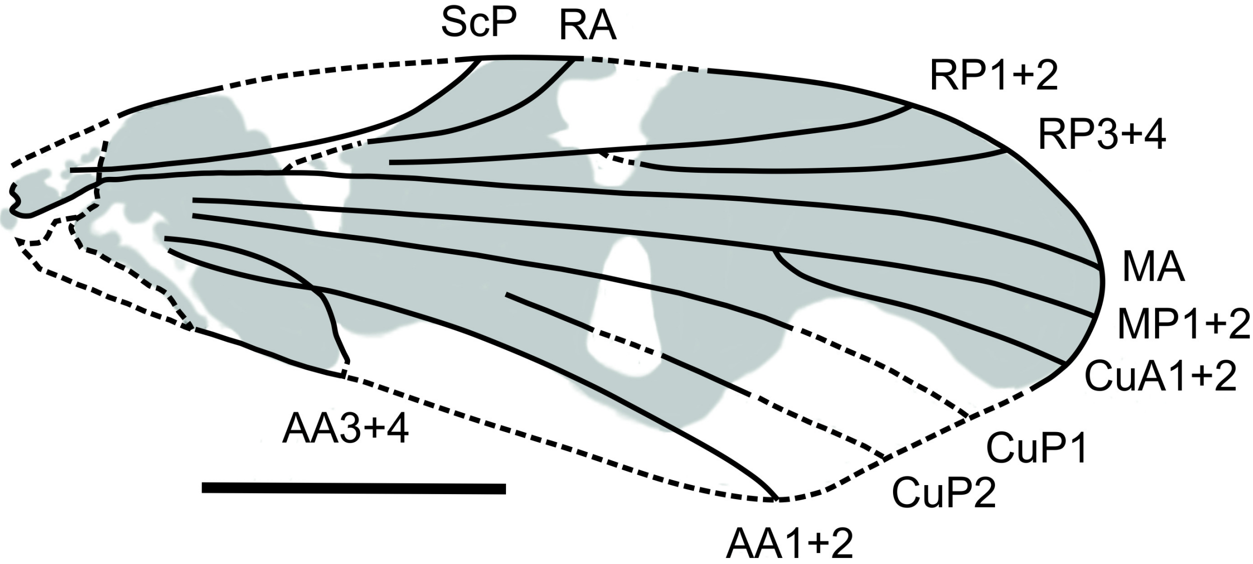

FIGURE 11. *Petisca dryellina* Martins-Neto, 1998. Length of wing: 3.5 mm. Illustration: Anna Suuronen. Redrawn after Martins-Neto (1998).

Comments. Martins-Neto (1998) saw a resemblance (but also differences) between the venation of the fossil moth and the venation of moths of the extant monobasic genus *Bradypophyla* Ihering, 1914 [*sic, Bradypophila*], Chrysauginae: Pyralidae. In particular, he considered the connectivity of the anal veins similar to the configuration found in this genus. The wing venation of *Bradypophila garbei* Ihering, 1914 is illustrated both by von Ihering (1914: 125) and Bradley (1982: 654), but the number and configuration of veins differ from each other and from that of *P. dryellina*. The connectivity of 3A and 2A also occurs in Galleriinae (e.g. Solis & Metz 2008) in Pyralidae, but not to our knowledge in the Phycitinae, Pyralinae, Epipaschiinae, or in Crambidae. We do not know about its occurrence in other lepidopteran superfamilies. The shape of the reconstructed wing of *P. dryellina* does not correspond to that of extant sloth moths and stored product galleriines. The illustration shows an anal angle to the forewing that does not exist in these extant moths. However, the photograph of the fossil wing (Martins-Neto 1998: 69) shows that the anal area of the wing is not well preserved, and the shape of the wing is not obvious. In Martins-

Neto's interpretation of the venation, the radial system of *P. dryellina* has only three veins and M_2 and M_3 are fused. In Pyralidae R_2, R_3, and R_4 are sometimes reduced to two veins or one vein (Munroe & Solis 1998). There are rare examples of R veins and M_2 and M_3 being fused in Phycitinae (e.g. *Cabnia* Dyar, 1904, see Heinrich (1956)), but it is not known to occur in Chrysauginae (see Cashatt 1968). According to Munroe & Solis (1998) the radial veins of male Chrysauginae are often stalked, but we are not aware of any chrysaugines with R veins completely fused. We conclude that the evidence is not very convincing and it does not support the placement of this fossil to the superfamily. The only wing visible does not have any characters known to be apomorphic of any extant group of pyraloids, and the most important diagnostic characters of Pyraloidea, the scaled base of the haustellum and the tympanal organs are not present.

Three fossil larvae tentatively identified as Pyralidae by Zeuner (1931)

(Fig. 12)

Excavation locality and depository. Germany: Baden–Württemberg, Esslingen, Randecker Maar ("dysodile beds")/Burdigalian, Early Miocene. SMNS Nr. 11; Nr. 15; Nr. 19.

Published illustrations. Zeuner, 1931: pl. 9, Fig. 6; pl. 11, Figs 3, 4 (black and white photographs).

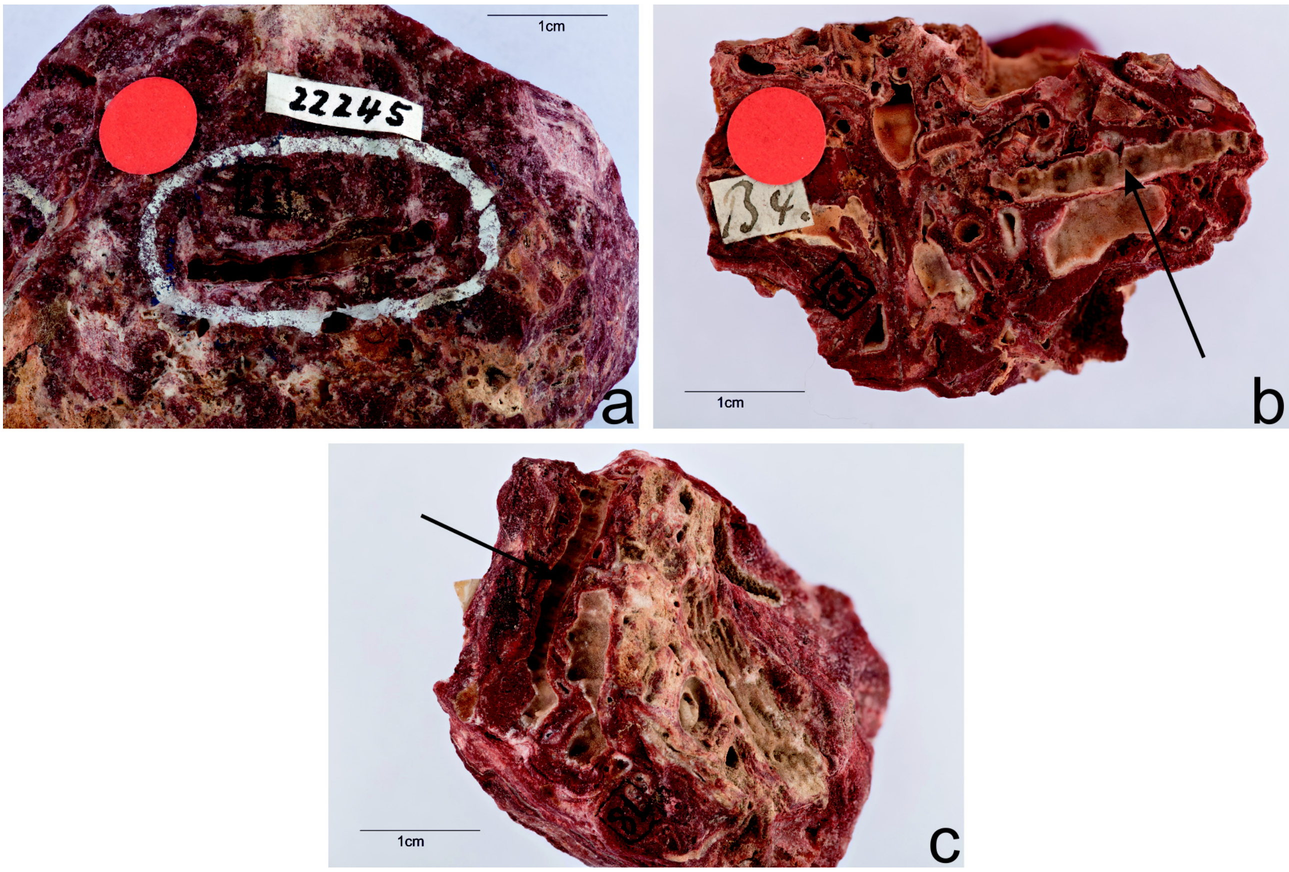

FIGURE 12. Three fossils tentatively interpreted as pyralid larvae by Zeuner (1931). a. Specimen Nr. 11, length of larva 20.3 mm.; b. Specimen Nr. 15, length of larva 22.5 mm.; c. Specimen Nr. 19 (indicated with arrow), length of larva 24.7 mm. The piece also includes specimen Nr. 18, an unidentified larva. Photos: Hossein Rajaei. Copyright: SMNS.

Condition. Three impression fossils interpreted as lepidopteran larvae. Fossil larva Nr. 11 is 20.3 mm long and evenly 2 mm wide. According to Zeuner (1931) sixteen legs can be observed. Fossil larva Nr. 15 is poorly preserved, based on the description only the underside of the larva from the third [thoracic] to the tenth segment [7th abdominal segment] remaining, the length being 22.5 mm, and width 3 mm. Fossil larva Nr. 19 is 24.7 mm long and 2.5–2.6 mm wide. It is preserved from the third [thoracic] segment on, and according to Zeuner's description, had sixteen feet (of which the impressions of the last pair of the thoracic legs and the prolegs can be observed).

Comments. Zeuner (1931) was not certain that the fossils belong to Pyralidae *sensu lato* and each identification is followed by a question mark. He identified larva Nr. 11 as a possible pyralid because he thought that such a thin larva could possibly belong to either Geometroidea or Pyralidae, but because the larva had sixteen legs it could not belong to the former. The identification of the larva Nr. 15 as a pyralid seems to be based on the preserved left side of segment 4 and the "callous thickening of this segment and the three- to four-fold pleatiness of the intersegmental skin". "Folds" of the larval integument have been considered diagnostic in some groups of Lepidoptera, such as Noctuidae and Geometridae (Stehr 1987), but in Pyraloidea folds of any distinction have not been observed (MAS personal observation). Zeuner (1931) identified fossil larva Nr. 19 as a pyralid *sensu lato* because according to him it had features characteristic of borers, but also strong legs indicating that the larva was capable of moving outside the food substance. Without a more detailed description, it is unclear what he meant exactly by "strong" legs and how these differ from those found in many other macrolepidoptera. To confirm a Pyraloidea affiliation setal characters of the prothorax and abdomen would have to be examined. Impressions of the very small setae are very unlikely to be visible in the fossil. We conclude that the identification of these fossil larvae as Pyraloidea is unfounded.

Gallerites keleri Kernbach, 1967

(Fig. 13)

Excavation locality and depository. Germany: Hesse, Brandenburg, Willershausen–Harz/Piacenzian, Late Pliocene. GZG.W.13547 (old no. 596-5).

Published illustrations. Kernbach 1967: 105, Fig. 6 (black and white photograph).

Condition. Compression fossil with whole body of an adult moth. The wings are folded and cover the abdomen (?) and legs. Forewings and one hindwing visible. The wings are 14 mm long and 4.5 mm wide. Some wing venation is visible. The antennae are filiform and 6.5 mm long. The sex of the moth cannot be determined.

FIGURE 13. *Gallerites keleri* Kernbach, 1967. Wings 14 mm long. Photo: GZG Museum / G. Hundertmark. Copyright.

Comments. Kernbach (1967) found that the visible features of the fossil moth resembled those of the genus *Galleria* Fabricius, 1798, currently in Galleriinae: Pyralidae. Carpenter (1992) doubted this placement, because the identification was based on a poorly preserved specimen and not a single character diagnostic of Pyraloidea was listed in the description.

A pyraloid affinity cannot be confirmed for this fossil specimen. Tympanal organs or a scaled base of haustellum are not visible. The wing venation seems to be lepidopteran, but is very partial and therefore is not informative. We agree with Carpenter (1992) that the identification of this specimen as a pyraloid is not based on reliable character evidence.

The type of the genus was subsequently fixed by monotypy (Clark *et al.* 1971: 582). *Gallerites* was treated as a nominal genus by Fletcher & Nye (1984: 62). It was also regarded as nominal by Sohn & Lamas (2013) because the author explicitly stated the diagnostic characters of this genus in comparison with other fossil or extant genera. Due to lack of character evidence, we here exclude *Gallerites keleri* Kernbach, 1967 from Pyraloidea and regard it as Lepidoptera *incertae sedis*.

Specimen not examined

Hiura and Miyatake, 1974: 389 (Pyralidae? sp.).

This specimen (133B) in Mizunami amber (Japan: Gifu Pref., Mizunami /Middle Miocene see Age of studied fossil Pyraloidea) was not found in the collection of the MFMJ, where the other specimens listed in Hiura & Miyatake (1974) are deposited (pers. comm. Y. Ando). No detailed information or illustrations were provided in the original publication. According to information in Sohn *et al.* 2012 it is a whole body fossil of an adult moth. We are unable to verify the identification.

Discussion and conclusions

With only eleven specimens, the known fossil record of Pyraloidea was poor to begin with, but the results of our review show that the number of fossils that can reliably be placed in this superfamily is actually even smaller. Only three of the ten fossils we were able to examine, either first-hand, from recent photographs, or using information provided by the original descriptions, show characters that convincingly support placement in Pyraloidea. The other seven fossils display characters that may be similar in appearance to characters found in certain extant pyraloids, but because the fossils are too fragmentary and therefore additional evidence not available, placement in Pyraloidea is unwarranted. All seven fossils are compression/impression fossils, which highlights the fact that only in very exceptional conditions can the apomorphic characters of Pyraloidea, adult or immature, be preserved in compression fossils. Scales, setae and crochets are microscopic in size and their preservation as visible and distinguishable features in compression fossils is extremely rare. The discernibility of internal characters, such as genitalia, or characters hidden by the dense scale vestiture, such as the abdominal hearing organs, is also infrequent in compression fossils. The preservation of details on *Eopyralis morsae* is therefore truly extraordinary. The fossils excavated from the Fur formation in the collections of the Fur Museum and the Fossil- and Mo-clay Museum include at least a thousand specimens that appear to be lepidopteran and are of comparable size to *Eopyralis morsae*. Many of these fossils could be of the same species or at least pyraloids, but unfortunately the preservation of details is too poor to make definitive identifications.

The apomorphic characters of both adult and immature pyraloids could be more easily observed in polished amber fossils. Micro-CT scanning could also potentially reveal internal characters. However, although most fossil Lepidoptera are inclusions in Baltic Amber (Sohn *et al*. 2015), the proportion of pyraloids in amber is extremely low. Currently the crambid larva, *Baltianania yantarnia*, described in the present study is the only confirmed pyraloid in Baltic Amber, *Glendoricha olgae* is the only known copal inclusion and an unconfirmed pyralid has been reported in Mizunami amber. Most of the known lepidopterans in amber are micromoths indicating that, at least in Lepidoptera, size may matter when it comes to preservation as intact amber inclusions. It could be easier for a smaller insect to be completely engulfed in resin than a larger one. The low proportion of pyraloids as amber inclusions cannot be explained by size because many species are very small (<1 cm in wing length). In addition, Pyraloidea are very diverse in their ecology and biology, and many species are found in habitats with resin producing trees. However, being entirely trapped in resin does not guarantee the preservation of the insect as it can also be destroyed during the drying process of the resin. In an experiment with butterflies, De Jong (2017) placed freshly caught adult butterflies in resin and made observations as the resin dried. After a year, the resin had dried and become very brittle destroying the butterfly inside. Museums and private collections include large numbers of fossil Lepidoptera in amber and a thorough examination will likely reveal some to be pyraloids.

The three fossils we consider securely placed in Pyraloidea are relatively young and do not contribute much new information to our understanding of the timing and biogeographical aspects of the evolutionary history of these moths or about the evolution of the hearing organs. Although *Eopyralis morsae,* dated at ca 54 Ma, offers the earliest evidence of the superfamily, the pyraloid lineage is probably much older. In a divergence time analysis, Wahlberg *et al.* (2013) estimated the pyraloid lineage to have originated ca 100 million years ago and the Pyralidae and Crambidae to have diverged ca 90 million years ago. Based on the observable characters, *Eopyralis morsae* is likely to belong to Pyralidae, and the split from the lineage of the sister group, Crambidae, had already occurred by then. However, at present, the crambid larva, *Baltianania yantarnia*, in Baltic amber dated to ca 44 Ma, is the earliest direct evidence we have of Crambidae. *Glendoricha* is possibly a pyraline, but a precise age and origin for it are currently not known, although copal is generally considered to be of Quaternary origin (e.g. Grimaldi & Engel 2005; Vávra 2009). The discordance between the fossil record and estimates based on molecular data and the molecular clock is a phenomenon that occurs throughout the Lepidoptera, but also in many other groups of organisms, e.g. Angiosperms (Magallón *et al.* 2015).

Our study confirms that the identifications of many of the known fossil Pyraloidea were based on overall similarity to extant species and not apomorphies. Such identifications are untenable and can lead to incorrect conclusions regarding the evolutionary history of organisms. The fossil record of Lepidoptera is poor, but because of the small number of specimens that are currently placed in one of the lepidopteran superfamilies, (less than a thousand (Sohn *et al.* 2015)), these identifications can be checked and updated. Revisions, such as the present work, are under way or have already been completed. We strongly encourage those describing new fossils, or reviewing manuscripts in which fossils are described, to use the same accuracy and care in reporting and documenting characters as when describing extant species.

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