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Thrips (Insecta: Thysanoptera) from the Insect Limestone (Bembridge Marls, Late Eocene) of the Isle of Wight, UK

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ABSTRACT: Thirty-two thrips fossils were studied from the Bembridge Marls, late Eocene of the Isle of Wight, S. England. Two extant families are recorded, Aeolothripidae with two species and Thripidae with three species. Described as new are *Sinaeolothrips* Shmakov gen. n. (*Aeolothrips brodiei* Cockerell, 1917, type species), *Aeolothrips jarzembowskii* Shmakov sp. nov (Aeolothripidae) and *Coccothrips hoffeinsorum* Shmakov, sp.nov.(Thripidae: Panchaetothripinae). The genus *Thrips* is tentatively recorded as fossil for the first time. Taxonomic composition of thrips is close to the Recent ones.

KEY WORDS: Terebrantia, Aeolothripidae, Thripidae, fossil thrips, new taxa.

The order Thysanoptera, or thrips (plural and singular), comprises approximately 5,000 known species of small insects with diverse life histories and habits. Most species feed on leaf, stem or flower tissues, though some feed on pollen or fungal hyphae, or are predatory. Some are likely to be significant pollinators (Lewis 1973; Ananthakrishnan 1984; Williams 2001). Behavioral studies over the last decades have revealed an unexpected diversity of rather sophisticated social behaviour, including even eusociality (Crespi & Mound 1997; Morris *et al.* 1999).

Thrips comprise a monophyletic group, well defined and easily recognisable, in the case of the winged adults, by narrow, straplike wings with reduced venation, and by the fringe of long setae ("cilia") surrounding the wing margins. Other synapomorphies of the order include tarsal segments reduced to one or two, with the pretarsus having claws reduced and uniquely possessing a small, eversible bladder (Heming 1971). Also, thrips have unusual development, wherein instars I and II are the "larva", an active, minute, wingless version of the adult typical of hemimetabolous insects. Instars III and IV (in Phlaeothripidae instar V as well) are quiescent and morphologically reduced, the "pupa" (Heming 2003).

The structure of thrips mouthparts is unique among insects. Thrips mouthparts comprise a mouthcone consisting of the labrum, labium, a pair of maxillary stipites and laciniae (the latter, so-called "stylets" and another stylet that is a slender left mandible (Reyne 1927; Mickoleit 1963; Mound 1971; Heming 1980, 1993). Unique to thrips is the loss of the right mandible, rendering the mouthcone asymmetrical. Thrips probe plant, fungal and animal tissues with their slender mouthparts, and suck out fluid contents. The structure and function of these mouthparts suggest they are related to the Hemiptera, but thrips plesiomorphically possess maxillary and labial palps, which all hemipterans have lost. The unusual development of thrips is similar to that of white flies (Aleyrodoidea) and male scale insects (Coccoidea), which may further reflect the close relationship of thrips to Hemiptera. Heming (2003) considered the unusual development in these orders to be convergent, since there are unique features of such in each order.

Thrips appear to be closely related to the extinct psocopteroid family Lophioneuridae, particularly to *Zoropsocus* Tillyard, 1935 (Hennig 1981; Zherikhin 2002). Zherikhin (2002) and some others have classified Lophioneuridae as thrips in an order Thripida (=Thysanoptera), with the suborders Lophioneurina and Thripina. Lophioneurids, and particularly *Zoropsocus*, possessed a reduced venation plesiomorphically similar to that of thrips and at least some are known to have had a narrow (albeit symmetrical) mouthcone (Vishniakova 1981). There are eight genera (possibly ten, depending on the classification) from the Permian of Australia, Russia and Kansas (Zherikhin 2002) and from the Jurassic and Cretaceous of Germany, Russia, China and Australia, including *Undacypha* Vishniakova, 1981, known both from rocks and Taimyr amber. Ansorge (1995) synonymised five Late Mesozoic genera under *Undacypha*. A bizarre genus, *Burmacypha* Zherikhin, 2000, was described from the Cretaceous amber of Myanmar. Besides the symmetrical mouthcone, lophioneurids are plesiomorphic in respect to true thrips in more complete venation, lack of a long marginal fringe on the wings, well-defined orbital sutures, and the unmodified legs. Thus, for this paper we use the traditional, more restricted treatment of Thysanoptera.

The Triassic thrips *Triassothrips virginicus* Grimaldi & Fraser (Cow Branch Formation: Carnian) and *Kazachothrips triassicus* Shmakov (Tologoy Formation: Carnian/Norian) were described from the Late Triassic of Virginia and Kazakhstan (Grimaldi *et al.* 2004). Jurassic thrips include *Liassothrips crassipes* (Martynov 1927) and *Karataothrips jurassicus* Sharov, 1972, both from the Late Jurassic of Kazakhstan (Karabastau Formation: Kimmeridgian). As found recently, *Liassothrips* may be a branch of primitive Tubulifera showing several specific features in antennae, mouthcone, forelegs and wings (Shmakov 2008).

By the Early Cretaceous, true thrips became much more abundant. The most diverse Mesozoic thrips occur in Cretaceous ambers, even though the only described ones come from the Early Cretaceous amber from Lebanon (zur Strassen 1973). Bhatti (1989) synonymised the families proposed by zur Strassen under the extant family Stenurothripidae, except for Jezzinothripidae zur Strassen, which was placed by Bhatti

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into the basal extant family Merothripidae. Diverse thrips occur in ambers from the Turonian of New Jersey (Grimaldi *et al*. 2000), Aptian of northern Spain (Alonso *et al*. 2000), and in amber of possible Cenomanian age from northern Myanmar (Burma) (Grimaldi *et al*. 2002).

In the Early Tertiary, thrips are found in many localities. The fauna of the Late Eocene Baltic amber is the best studied (Bagnall 1923, 1924a, b; Priesner 1924, 1929; Schliephake 1990, 1993, 1999, 2000, 2001, 2003). Schliephake (1997, 1999, 2000, 2001) has also described numerous new species and genera from the Saxonian amber of supposedly the same age. Several taxa have been described also from the late Eocene of the Isle of Wight in the UK (Cockerell 1917), and from the latest Oligocene of Rott (Schlechtendal 1887) and Enspel (Wedmann 2000) in Germany. All large living families, such as Aeolothripidae, Thripidae and Phlaeothripidae, are common and diverse there. The Late Tertiary thrips are poorly known. Few taxa are described from the Miocene of California (O'Neil 1957).

Thirty-two specimens of Thysanoptera were studied from the Insect Limestone of the Isle of Wight, UK. Of these, 19 are identified as members of Recent families Thripidae (six specimens) and Aeolothripidae (13 specimens), and 13 are left unidentified. Three genera are identified in Thripidae and two in Aeolothripidae.

The condition of all specimens is poor: antennae and legs are almost absent; wings are vastly incomplete or absent too. Therefore, all descriptions are not exhaustive.

The insects are preserved in concretions or tabular bands of very fine-grained micrite, known as Insect Limestone. The unit where these concretions/bands occur is known as the Insect Bed, which lies towards the base of the Bembridge Marls Member (Solent Group: Bouldnor Formation).

Gale *et al*. (2006) assumed that the Bembridge Marls are earliest Oligocene in age, but Hooker *et al.* (2007, 2009) say that the Insect Limestone is rather latest Eocene (Priabonian) in age, which is followed here.

Most of the specimens at The Natural History Museum, London (NHMUK) belong to the A'Court Smith (purchased 1877, 1883), P.B. Brodie (purchased 1898) and R.W. Hooley (purchased 1924) collections. They are labelled 'Gurnard Bay' or 'Gurnet Bay' (which is an old name for Gurnard Bay); however, Smith collected specimens all the way from West Cowes to Newtown River on the north-west side of the Isle of Wight. Most of the specimens probably came from Thorness Bay. Brodie and Hooley acquired parts of Smith's collection, so parts and counterparts of individual insects have turned up in all three collections. The parts and counterparts often have different numbers because they were registered at different times. An additional collection was recently discovered at the Sedgwick Museum, Cambridge by A. J. Ross. This collection has also yielded counterparts of specimens at the NHMUK, which indicates that this is another part of the Smith collection. A label with '1883' on it suggests that the Sedgwick Museum acquired this collection in 1883, the same year that the NHMUK purchased specimens from Smith.

Institutional repositories of specimens. NHMUK, Natural History Museum, London; MNEMG, Maidstone Museum & Bentlif Art Gallery, Maidstone; CAMSM, Sedgwick Museum of Earth Sciences, University of Cambridge.

1. Systematic palaeontology

Order Thysanoptera Haliday, 1836
Suborder Terebrantia Haliday, 1836
Family Aeolothripidae Uzel, 1895
Genus *Sinaeolothrips* Shmakov, gen. nov.

Derivation of name. After genus *Aeolothrips*. Gender masculine.

Type species. *Aeolothrips brodiei* Cockerell, 1917 (by monotypy and present designation).

Diagnosis. Wings are wider than in any other Aeolothripidae, except *Aeolothrips*, with complete venation including two longitudinal and five cross-veins. Pattern of venation is unique among Aeolothripidae.

Description. Head and prothorax transverse. Pterothorax longitudinal, with slightly rounded sides. All abdominal segments, except the last one, obviously transverse. All cross-veins straight, MCu slightly bent. Fringe is dense and long, about 0·65–0·7 of wing width.

Remarks. The genus is placed into Aeolothripidae because of characteristic venation with seven veins presented. It seems to be related to *Aeolothrips*; it differs from *Aeolothrips* by more primitive MCu position. Therefore, *Sinaeolothrips* might be the ancestor of *Aeolothrips*, the hypothesis deserving more close study.

Sinaeolothrips brodiei (Cockerell, 1917)
Text-fig. 1A, B; Plate 1, fig. 1
1917 *Aeolothrips brodiei* Cockerell, p. 381, fig. 5

Holotype. NHMUK I.8547, Brodie Collection; Insect Limestone, northwest Isle of Wight; headless body with pterothorax poorly preserved and tip of abdomen not visible, with no appendages, other than basally incomplete right forewing.

Other material. NHMUK I.9102, I.9133, I.9536, I.9991, Brodie Collection; NHMUK In.17401, Smith Collection; NHMUK In.24785, II.2855a, b, Hooley Collection; CAMSM X.50140.47b (TN98); all from the Insect Limestone, northwest Isle of Wight.

Description. Bases of veins R, R_1, Rs, base of M, MCu and Cu dark coloured. For measurements see Table 1.

Remarks. Vein coloration varies to an extent, but cross-strips are always absent.

Genus *Aeolothrips* Haliday, 1836
Aeolothrips jarzembowskii Shmakov, sp. nov.
Text-fig. 1C; Plate 1, fig. 2

Derivation of name. Named after palaeoentomologist Ed Jarzembowski.

Holotype. NHMUK In.25273, Hooley Collection; Insect Limestone, northwest Isle of Wight; almost complete body with head damaged, pterothorax structures not discernible, and abdominal tip invisible, with appendages lost except fore femur, middle leg and both forewings.

Paratypes. NHMUK I.9678, Brodie Collection, NHMUK In.17210, Smith Collection; Insect Limestone, northwest Isle of Wight.

Diagnosis. Forewings bearing two cross-colour strips, proximal one pale, incomplete, reaching wing fore margin; distal one complete, more distinct and broad, reaching both wing margins by bulges, with narrow spot near its middle.

Description. Head slightly transverse, prothorax highly transverse, pterothorax longitudinal, with obviously rounded sides. All abdominal segments except for last one strongly transverse. All cross-veins straight. Fringe wide, *c*.0·81–0·83 mm, as long as wing width. For measurements, see Table 2.

Remarks. Venation is typical of the genus, but the shape of wing cross-strips is apparently unknown in other congeners. On several wings, for example on left holotype forewing, distal strip is much paler between Rs and M, but distinct outside this section.

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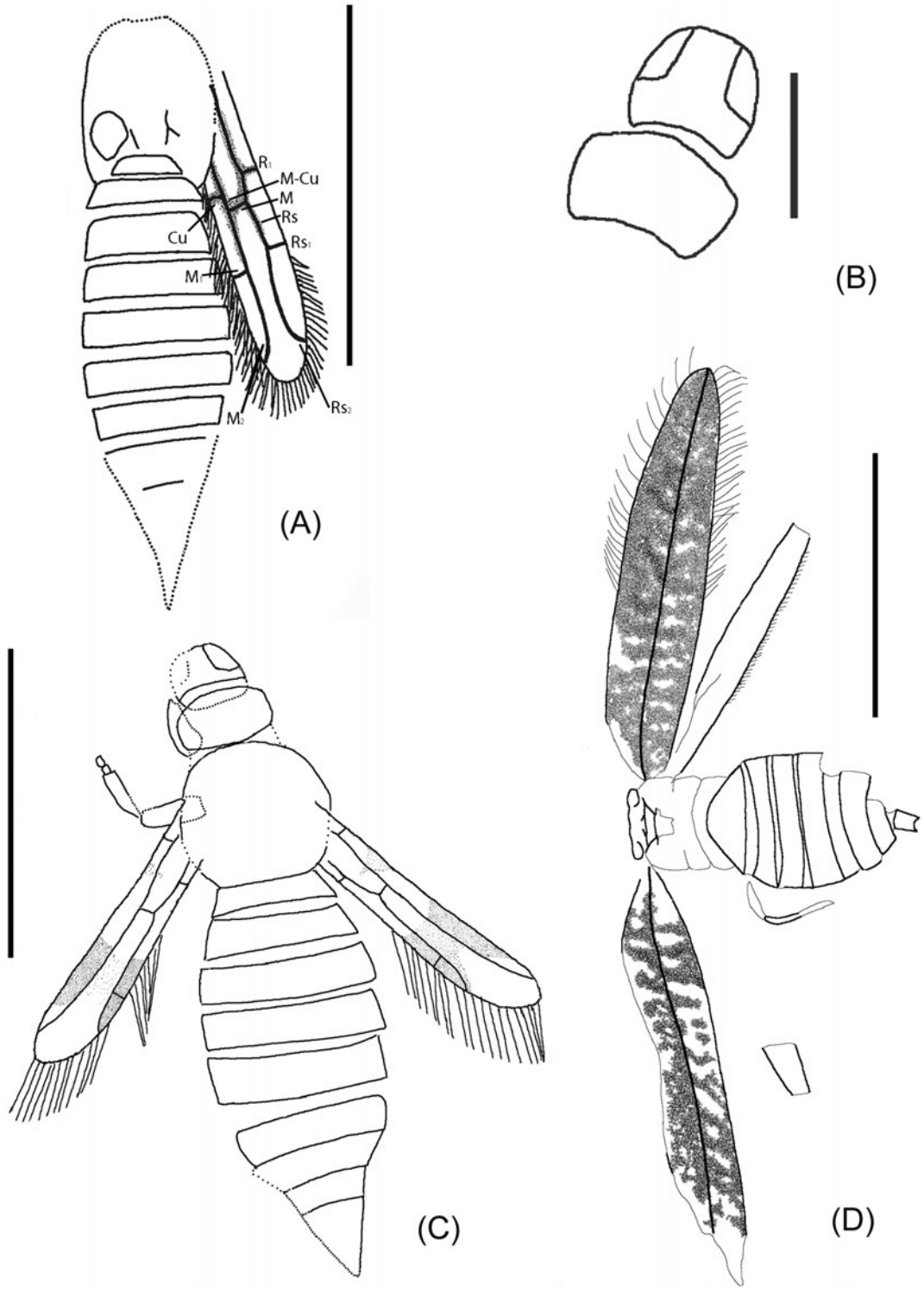

Text-figure 1 (A) *Sinaeolothrips brodiei* (Cockerell 1917), holotype, NHMUK I.8547, Insect Limestone, Bembridge Marls, Isle of Wight, England; Scale bar = 1 mm. (B) *Sinaeolothrips brodiei* (Cockerell 1917), NHMUK In.17401, head and prothorax; Scale bar = 0.25 mm. (C) *Aeolothrips jarzembowskii* Shmakov sp. nov., holotype, NHMUK In.25273; Scale bar = 1 mm. (D) *Coccothrips hoffeinsorum* Shmakov sp. nov., holotype, MNEMG 2007.12a [IL 64a]; Scale bar = 1 mm.

Family Thripidae Stephens, 1829
Subfamily Panchaetothripinae Bagnall, 1912
Genus *Coccothrips* Shmakov, gen. nov.

Derivation of name. After alternating wing wrinkles, similar to these on wings of the extant family Matsucoccidae (Hemiptera: Coccoidea).

Type species. *Coccothrips hoffeinsorum* Shmakov, sp.nov.

Diagnosis. Wings bear single central longitudinal vein, which reach tip of wings. Forewings covered by regular alternate wrinkles before and after the vein. Forewings are broad, lancet-like with weakly rounded tips. Hindwings are much narrower than forewings, without wrinkles.

Description. Prothorax and pterothorax transverse, with straight sides. Abdominal segments I–VII obviously transverse. Wing marginal setae are long even on front margin, but not

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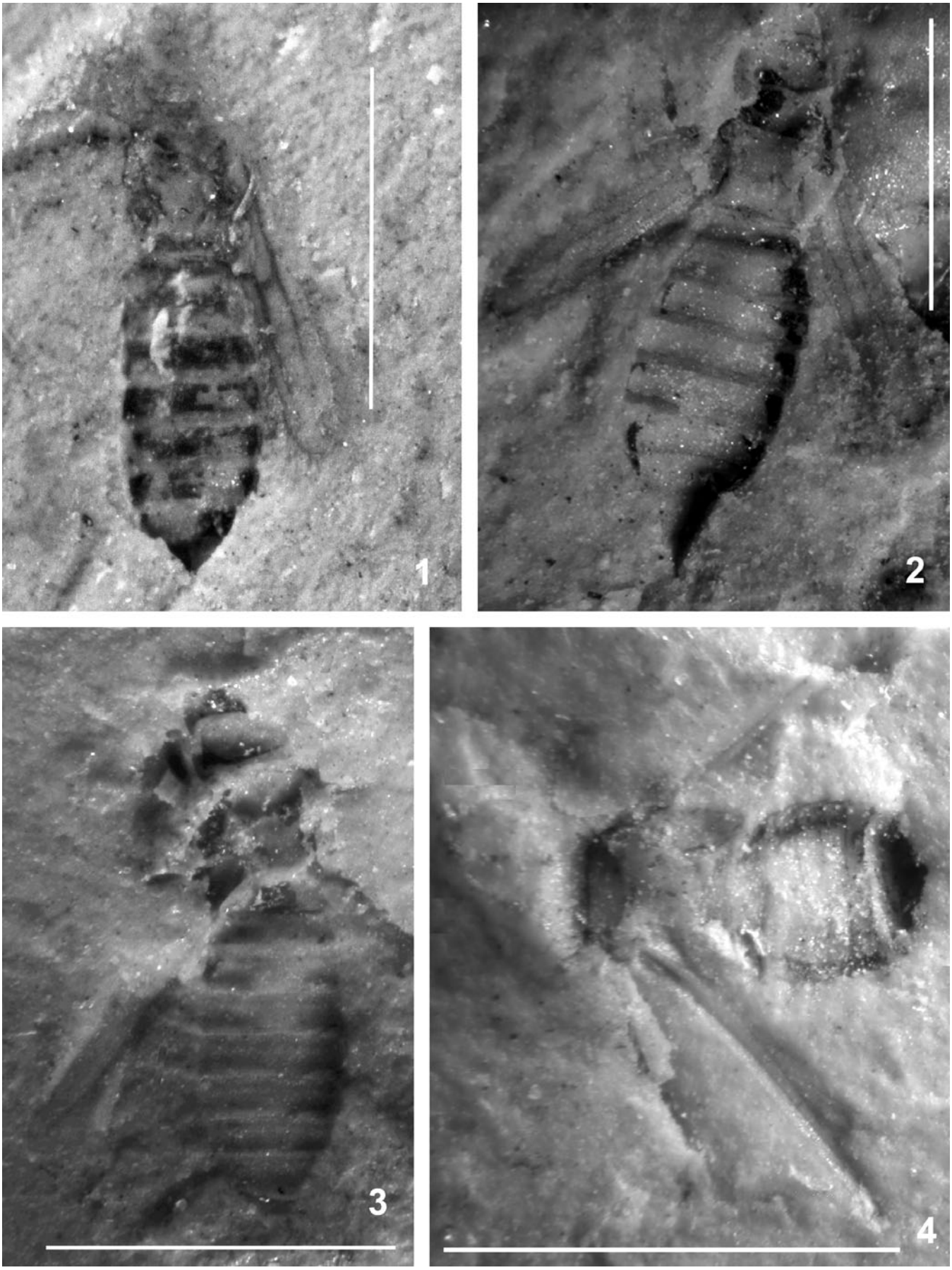

Plate 1 (1) *Sinaeolothrips brodiei* (Cockerell 1917), holotype, NHMUK I.8547, Insect Limestone, Bembridge Marls, Isle of Wight, England. (2) *Aeolothrips jarzembowskii* Shmakov, sp. nov., holotype, NHMUK In.25273. (3) ? *Thrips* sp., NHMUK I.9672. (4) Thripidae gen. sp. indet. 1, NHMUK I.9375. Scale bars = 1 mm.

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Table 1 Measurements and proportions of *Sinaeolothrips brodiei* (Cockerell, 1917).

Parts of body		Length (mm)	Width (mm)	Proportions (length/width)
Head		0.18	0.21-0.23	0.83
Prothorax		0.16–0.18	0.27–0.32	0.6–0.87
Pterothorax		0.47–0.52	0.37–0.41	1.28–1.4
Forewing		0.95–1.01	0.17–0.19	5.71–5.98
Abdomen tergite	I	0.05–0.06	0.19–0.2	0.25
	II	0.06	0.32–0.34	0.20
	III	0.10–0.12	0.35–0.39	0.31–0.33
	IV	0.09–0.12	0.37–0.38	0.26–0.27
	V	0.09–0.1	0.41	0.21
	VI	0.09–0.11	0.41–0.42	0.21
	VII	0.08–0.11	0.35–0.38	0.23
	VIII	0.11	–	–

Table 2 Measurements and proportions of *Aeolothrips jarzembowskii* Shmakov, sp. nov.

Parts of body		Length (mm)	Width (mm)	Proportions (length/width)
Head		0.12	0.23	0.52
Prothorax		0.17	0.31	0.57
Pterothorax		0.45	0.50	0.91
Forewing		1.01	0.15	6.71
Abdomen tergite	II	0.07	0.41	0.18
	III	0.12	0.50	0.25
	IV	0.12	0.57	0.21
	V	0.12	0.58	0.20
	VI	0.14	0.55	0.25
	VII	0.11	0.48	0.24
	VIII	0.10	–	–
	IX	0.09	–	–
Femur	fore	0.19	0.07	2.51
	middle	0.20	0.07	2.78
Tibia	middle	0.17	0.05	3.75

dense at front margin of forewing, without cross-setae on all wings.

Remarks. Most of diagnostic features, such as alternate wrinkles, shape of forewing and its great width with single vein only, are very uncommon for all thrips families. The species in question was placed into Thysanoptera because of the wings with single vein and marginal fringe. Such highly reduced venation is frequent for family Thripidae, in which all members of subfamily Panchaetothripinae have socketed wings and dorsal body surface.

Coccothrips hoffeinsorum Shmakov, sp. nov.
Text-fig. 1D; Plate 2, figs 1–4

Derivation of name. Named after Christel and Hans Hoffeins.

Holotype. MNEMG 2007.12a, b [IL 64a, b] Jarzembowski coll.; Insect Limestone, northwest Isle of Wight; body without head, with abdomen and prothorax damaged, pterothoracic structures discernible, with both hind legs incomplete, without tarsi. Forewings and one hindwing present; one forewing is almost complete, hindwing without apical part.

Paratype. NHMUK In.43474a, b, Hooley Collection; Insect Limestone, northwest Isle of Wight.

Description. All wings dark coloured, but there are more or less light strips at forewings following wrinkles from wing base even to tip. For measurements, see Table 3.

Remarks. Wings of NHMUK specimen are much less coloured than wings of MNEMG one; it may be caused by preservation or intraspecific variation.

Subfamily Thripinae Karny, 1921
Genus *Thrips* Linnaeus, 1758
?*Thrips* sp.
Plate 1, fig. 3

Material. NHMUK I.9349, I.9672, Brodie Collection; Insect Limestone, northwest Isle of Wight; almost complete body with legs and partial wings, with venation not visible.

Description. For measurements, see Table 4.

Remarks. Attribution to *Thrips* is based on the characteristic shape of head front surface between obvious prominent eyes and absence of any rugged sculpture on thorax and abdomen. Further identification is impossible at present because of the incomplete preservation of the material available.

Thripidae gen. sp. indet. 1
Plate 1, fig. 4

Material. NHMUK In.25324, II.2854, Hooley Collection; NHMUK I.9375, Brodie Collection; all from the Insect Limestone, northwest Isle of Wight; all with no preserved head, legs

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Plate 2 (1) *Coccothrips hoffeinsorum* Shmakov, sp. nov., holotype, MNEMG 2007.12a [IL 64a], Jarzembowski collection, Insect Limestone, Bembridge Marls, Isle of Wight, England. (2) *Coccothrips hoffeinsorum* Shmakov, sp. nov., holotype, MNEMG 2007.12b [IL 64b], Jarzembowski collection. (3) *Coccothrips hoffeinsorum* Shmakov, sp. nov., NHMUK In.43474a, Hooley Collection. (4) *Coccothrips hoffeinsorum* Shmakov, sp. nov., NHMUK In.43474b, Hooley Collection. Scale bars = 1 mm.

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Table 3 Measurements and proportions of *Coccothrips hoffeinsorum* Shmakov, sp. nov.

Parts of body		Length (mm)	Width (mm)	Proportions (length/width)
Prothorax		0.12	–	–
Pterothorax		0.40	0.36	1.10
Forewing		1.64	0.33	4.94
Abdomen tergite	IV	0.10	0.49	0.20
	V	0.08	0.50	0.16
	VI	0.09	0.50	0.18
	VIII	0.09	–	–
	IX	0.08	–	–
	X	0.09	0.07	1.27
Femur	hind	0.15	0.04	4.06
Tibia	hind	0.26	0.02	14.11

Table 4 Measurements and proportions of ?*Thrips* sp.

Parts of body		Length (mm)	Width (mm)	Proportions (length/width)
Head		0.09	0.16	0.57
Prothorax		0.14–0.15	0.24–0.26	0.57–0.58
Pterothorax		0.41–0.44	0.37–0.4	1.1–1.12
Forewing		1.12–1.15	0.10–0.11	10.57–11.05
Abdomen tergite	I	0.08	0.19	0.42
	II	0.09	0.36	0.27
	III	0.09	0.40	0.24
	IV	0.11	0.40	0.27
	V	0.10	0.41	0.24
	VI	0.09	0.41	0.24
	VII	0.09	0.34	0.28
	VIII	0.10	0.29	0.35
	IX	–	0.17	–
Femur	fore	0.09	0.03	2.77
	middle	0.13	0.03	3.96
Tibia	fore	0.14	0.05	3.03
	middle	0.12	0.03	3.68

Table 5 Measurments and proportions of Thripidae gen. sp. indet. 1.

Parts of body		Length (mm)	Width (mm)	Proportions (length/width)
Pterothorax		0.33	0.33	1.01
Forewing		0.80	–	–
Abdomen tergite	I	0.05	0.24	0.21
	II	0.06	0.33	0.17
	III	0.06	0.39	0.15
	IV	0.05	0.39	0.13
	V	0.05	0.39	0.14
	VI	0.05	0.37	0.14
	VII	–	0.31	–

or hind wings; pterothorax structures are not visible; all fore wings are incomplete at width, but one wing of NHMUK II.2854 is almost complete at length.

Description. For measurements, see Table 5.

Remarks. Specimens are determined as Thripidae, because of their narrow wings with reduced venation. They are placed in one group because of same size.

Thripidae gen. sp. indet. 2

Material. NHMUK I.10262, Brodie Collection; Insect Limestone, northwest Isle of Wight; deformed (much compressed) body with fore leg and partial forewing.

Description. Medial section of forewing highly pigmented, bearing light spots at wing midwidth. For measurements, see Table 6.

Remarks. Specimen is determined as Thripidae, because of its narrow wings with reduced venation.

2. Discussion

Aeolothrips is a worldwide predatory genus, preying on various phytophagous thrips, including *Thrips* species, also found in the Insect Limestone.

The identification of the genus *Thrips* is not certain because of the incomplete preservation: antennae and chaetotaxy are

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Table 6 Measurements and proportions of Thripidae gen. sp. indet. 2.

Parts of body		Length (mm)	Width (mm)	Proportions (length/width)
Head		0.09	–	–
Prothorax		0.14	–	–
Pterothorax		0.41	–	–
Forewing		1.12	0.10	–
Abdomen tergite	I	0.08	–	–
	II	0.09	–	–
	III	0.10	–	–
	IV	0.10	–	–
	V	0.10	–	–
	VI	0.09	–	–
	VII	0.09	–	–
	VIII	0.09	–	–
	IX	0.08	–	–
	X	0.12	–	–
Femur	fore	0.10	0.05	1.93
Tibia	fore	0.13	0.03	4.12

never seen; wings and thoracic structures are poorly preserved. The genus *Thrips* is phytophagous, mainly on herbaceous plants but sometimes on trees as well. It has a world-wide distribution, including subarctic and desert areas. The developmental optimum of the genus lies around 25°C (Ghabn 1948; Priesner 1960). Populations developing at higher temperatures are paler and smaller, and macropterous forms predominate; low temperatures have the reverse effect (Gentile & Bailey 1968). The fossils at hand are of more or less normal size and pigmentation, so providing the identification is correct, and given the mean duration of active ontogenesis (except egg stage) taking some 15–20 days, this makes it possible to hypothesise the environment with the temperature *c*. 25°C lasting for at least 15–20 days a year.

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4. References

Alonso, J. A., Arillo, E., Barro, N., Corral, J. C., Grimalt, J., Lopez, J. F., Lopez, R. F., Martinez-Delclos, X., Ortuno, V., Peñalver, E. & Trinca P. R. 2000. A new fossil resin with biological inclusions in Lower Cretaceous deposits from Alava (northern Spain, Basque-Cantabrian Basin). *Journal of Paleontology* **74**, 158–78.

Ananthakrishnan, T. N. 1984. *Bioecology of Thrips*. Oak Park, Michigan: Indira Publishing House. 233 pp.

Ansorge, J. 1995. Insekten aus dem oberen Lias von Grimmen (Vorpommern, Norddeutschland). *Neue Palaontologische Abhandlungen* **2**, 1–28.

Bagnall, R. S. 1912. On a new genus of Indian thrips (Thysanoptera) injurious to Turmeric. *Records of the Indian Museum* **7**, 257–60.

Bagnall, R. S. 1923. Fossil Thysanoptera I.—Terebrantia, part 1. *Entomologists' Monthly Magazine* **9**, 35–38.

Bagnall, R. S. 1924a. Fossil Thysanoptera, II. – Terebrantia, part 2. *Entomologists' Monthly Magazine* **10**, 130–33.

Bagnall, R. S. 1924b. Fossil Thysanoptera, III. – Terebrantia, part 3. *Entomologists' Monthly Magazine* **10**, 251–52.

Bhatti, J. S. 1989. The classification of Thysanoptera into families. *Zoology (Delhi)* **2**, 1–23.

Cockerell, T. D. A. 1917. New Fossil Insects from the Tertiary. *Proceedings of the US National Museum of Washington* **2181**, 381–85.

Crespi, B. J. & Mound, L. A. 1997. Ecology and evolution of social behavior among Australian gall thrips and their allies. *In* Choe, J. C. & Crespi, B. J. (eds) *Social Behavior in Insects and Arachnids*, 166–80. Cambridge, UK: Cambridge University Press. 195 pp.

Gale, A. S., Huggett, J. M., Pälike, H., Laurie, E., Hailwood, E. A. & Hardenbol, J. 2006. Correlation of Eocene–Oligocene marine and continental records: orbital cyclicity, magnetostratigraphy and sequence stratigraphy of the Solent Group, Isle of Wight, UK. *Journal of the Geological Society, London* **163**(2), 401–15.

Gentile, A. G. & Bailey, S. F. 1968. A revision of the genus *Thrips* in the New World with a catalog of the world species. *University of California Publications in Entomology* **1968**, 1–95.

Ghabn, A. A. E. 1948. Contributions to the knowledge of the biology of *Thrips tabaci* in Egypt. *Bulletin of Society Fouad I Entomology* **32**, 123–74.

Grimaldi, D., Shedrinsky, A. & Wampler, T. P. 2000. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey. *In* Grimaldi, D. (ed.) *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey*, 1–76. Leiden: Backhuys. 120 pp.

Grimaldi, D., Engel, M. S. & Nascimbene, P. C. 2002. Fossiliferous Cretaceous Amber from Myanmar (Burma): Its Rediscovery, Biotic Diversity, and Paleontological Significance. *American Museum Novitates* **3361**. 71 pp.

Grimaldi, D., Shmakov, A. S. & Fraser, N. C. 2004. Mesozoic thrips and early evolution of the order Thysanoptera (Insecta). *Journal of Paleontology* **78**(5), 941–52.

Haliday, A. H. 1836. An epitome of British genera, in the order Thysanoptera, with indications of a few species. *Entomological Magazine* **3**, 439–51.

Heming, B. S. 1971. Functional morphology of the thysanopteran pretarsus. *Canadian Journal of Zoology* **49**, 91–108.

Heming, B. S. 1980. Development of the mouthparts in embryos of *Haplothrips verbasci* (Osborn) (Insecta, Thysanoptera, Phlaeothripidae). *Journal of Morphology* **164**, 235–63.

Heming, B. S. 1993. Structure, function, ontogeny, and evolution of feeding in thrips (Thysanoptera). *In* Shaefer, C. W. & Leschen, R. A. B. (eds) *Functional Morphology of Insect Feeding,* 3–41. *Thomas Say Publications in Entomology*. Lanham, Maryland: Entomological Society of America. 237 pp.

Heming, B. S. 2003. *Insect Development and Evolution*. Ithaca, New York: Cornell University Press. 444 pp.

Hennig, W. 1981. *Insect Phylogeny*. Chichester: John Wiley and Sons. 514 pp.

Hooker, J. J., Collinson, M. E., Grimes, S. T., Sille, N. P. & Mattey, D. P. 2007. Discussion on the Eocene–Oligocene boundary in the UK. *Journal of the Geological Society, London* **164**(3), 685–88.

Hooker, J. J., Grimes, S. T., Mattey, D. P., Collinson, M. E. & Sheldon, N. D. 2009. Refined correlation of the UK Late Eocene–Early Oligocene Solent Group and timing of its climate history. *In* Koeberl., C. & Montanari, A. (eds) *The Late Eocene Earth –*

Hothouse, Icehouse, and Impacts. Geological Society of America Special Paper **452**, 179–95.
Karny, H. 1921. Zur Systematik der Orthopteroiden Insekten, Thysanoptera. *Treubia* **1**, 211–69.
Lewis, T. R. 1973. *Thrips. Their Biology, Ecology, and Economic Importance*. New York: Academic Press. 324 pp.
Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata* **1**, 538–41. Holmiae: Laurentii Salvii.
Martynov, A. V. 1927. Jurassic fossil insects from Turkestan. 7. Some Odonata, Neuroptera, Thysanoptera. *Bulletin de l'Academie des Sciences de l'URSS* **21**, 757–68.
Mickoleit, E. 1963. Untersuchungen zur Kopfmorphologie der Thysanopteren. *Zoologisches Jahrbuch (Anatomie)* **81**, 101–50.
Morris, D. C., Mound, L. A., Schwarz, M. P. & Crespi, B. J. 1999. Morphological phylogenetics of Australian gall-inducing thrips and their allies: the evolution of host-plant affiliations, domicile use and social behavior. *Systematic Entomology* **24**, 289–99.
Mound, L. A. 1971. The feeding apparatus of thrips. *Bulletin of Entomological Research* **60**, 547–48.
O'Neil, K.1957. Miocene arthropods from the Mojave Desert, California. *US Government Printing Office, Geological Survey Professional Paper* **294**(G), 251–55.
Priesner, H. A. 1924. Bernstein–Thysanopteren. *Entomologisches Mitteilungen* **13**, 130–51.
Priesner, H. A 1929. Bernstein-Thysanopteren II. *Bernstein Forschungen* **1**, 11–138.
Priesner, H. A 1960. *A monograph of the Thysanoptera of the Egyptian deserts*. Institut du Desert d'Egypte. Heliopolis : El-Mataria. 549 pp.
Reyne, A. 1927. Untersuchungen uber die Mundteile der Thysanopteren. *Zoologische Jahrbucher (Anatomie)* **49**, 391–500.
Schliephake, G. 1990. Beitrage zur Kenntnis fossiler Fransenflugler (Thysanoptera, Insecta) aus dem Bernstein des Tertiar. 1. Beitrag: Stenurothripidae. *Zoology (Delhi)* **2**, 163–84.
Schliephake, G. 1993. Beitrage zur Kenntnis fossiler Fransenflugler (Thysanoptera, Insecta) aus dem Bernstein des Tertiar. 2. Beitrag: Aeolothripidae (Melanthripinae) und Thripidae (Dendrothripinae und Thripinae). *Zoologisches Jahrbucher, Abteilung für Systematik, Okologie und Geographie der Tiere* **120**, 215–51.
Schliephake, G. 1997. Beitrage zur Kenntnis fossiler Fransenflugler (Thysanoptera, Insecta) aus dem Bernstein des Tertiar des Bitterfelder Raumes. 3. Beitrag: Thripidae, Panchaetothripinae. *Entomologische Nachrichten und Berichte* **41**, 66–67.
Schliephake, G. 1999. Fossil thrips (Thysanoptera, Insecta) of the Baltic (North and Baltic Sea) and Saxonian (Bitterfeldian) Tertiary amber from the collections of Hoffeins. *Deutsche Entomologische Zeitschrift* **46**, 83–100.
Schliephake, G. 2000. Neue Fransenflugler aus dem Baltischen und Bitterfelder Bernstein (Insecta: Thysanoptera). *Mitteilungen aus dem Geologisch – Palaontologischen Institut der Universität Hamburg* **84**, 219–29.
Schliephake, G. 2001. Thysanoptera (Insecta) of the Tertiary amber of the Museum of the Earth, Warsaw, with keys to the species of the Baltic and Bitterfeld amber. *Prace Muzeum Ziemi* **46**, 16–38.
Schliephake, G. 2003. Fossile Thysanoptera (Insecta) aus dem Baltishen Bernstein. *Mitteilungen aus dem Geologisch-Palaontologischen Institut der Universität Hamburg* **87**, 171–82.
Schlechtendal, D. 1887. Physopoden aus dem Braukohlegebirge von Rott am Siebengebirge. *Zeitschrift für Naturwissenschaften* **60**, 551–92.
Sharov, A. G. 1972. [On the phylogenetic relations of the order Thripida (Thysanoptera).] *Entomological Review* **54**, 854–58. [In Russian.]
Shmakov, A. S. 2008. [Jurassic thrips *Liassothrips crassipes* (Martynov, 1927) and its position in systematic of Thysanoptera (Insecta).] *Palaeontological Journal* **3**, 46–51. [In Russian.]
Stephens, J. F. 1829. Illustrations of British Entomology **1**, 355. London: Baldwin and Cradock.
Tillyard, R. J. 1935. Upper Permian insects of New South Wales. III. The Order Copeognatha. *Proceedings of the Linnean Society of New South Wales* **60**, 265–79.
Uzel, H. 1895. *Monographie der Ordnung Thysanoptera*. Konigratz: Tolman. 472 pp.
Vishniakova, V. N. 1981. [New Paleozoic and Mesozoic lophioneurids (Thripida, Lophioneurida).] *Proceedings of the Palaeontological Institute, USSR Academy of Science* **183**, 43–63. [In Russian.]
Wedmann, S. 2000. Die Insekten oberoligozanen Fossillagerstatte Enspel (Westerwald, Deutschland). *Mainzer Naturwissenschaftliches Archiv* **23**, 28.
Williams, G. A. 2001. Thrips (Thysanoptera) pollination in Australian subtropical rainforests, with particular reference to pollination of *Wilkiea huegeliana* (Monimiacea). *Journal of Natural History* **35**, 1–21.
Zherikhin, V. V. 2000. A new genus and species of Lophioneuridae from Burmese amber (Thripida [=Thysanoptera]: Lophioneurina). *Bulletin of the Natural History Museum (Geology)* **56**, 39–41.
Zherikhin, V. V 2002. Order Thripida Fallen, 1914 [*sic*] (=Thysanoptera Haliday, 1836). The thrips. *In* Rasnitsyn, A. P. & Quicke, D. L. J. (eds) *History of Insects*, 133–43. Dordrecht: Kluwer Academic Publishers. 517 pp.
Zur Strassen, R. 1973. Fossile Fransenflugler aus mesozoischem Bernstein des Libanon (Insecta: Thysanoptera). *Stuttgarter Beitrage zur Naturkunde* **256**, 1–51.

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