

HUBBARD

Fossil insects from the Lithographic Limestone of Montsech (late Jurassic-early Cretaceous), Lérida Province, Spain

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Synopsis

Fossil insects from the Lithographic Limestone (Upper Jurassic or Lower Cretaceous), Montsech, Lérida, Spain are described; their affinities and faunal significance are discussed. Seven orders of insects are represented (Ephemeroptera, Blattodea, Odonata, Hemiptera, Coleoptera, Diptera, Hymenoptera), three of which are previously unknown from this locality. The following six new species are described: *Mesopalingea lerida* gen. et sp. nov. (mayfly), *Artiocoblatta hispanica* (cockroach), *Condalia woottoni* gen. et sp. nov. (dragonfly), *Wonnacottella pulcherrima* gen. et sp. nov. (palaeontinid), *Chrysobotris* (?) *ballae* (buprestid beetle) and *Eobelus solutus* (eobelid weevil).

Introduction

The fossiliferous locality at Montsech has been known for many years: the first insects were described from the Lithographic Limestone by Meunier in 1902. Since then a number of collections have been made, the present paper being based on material collected by Dr H. W. Ball and Mr F. M. Wonnacott in 1955-60 and deposited in the British Museum (Natural History). The fossil insects are from a quarry in Lithographic Limestone 0.8 km south-west of Rubies (close to Santa Maria de Meyá) in the Sierra del Montsech, Lérida Province, north-east Spain (Figs 1-3). Some 50 m of strata are exposed and the succession has been described by Schairer & Janicke (1970).

The Lithographic Limestone is a facies development of the Caliza con Caráceas Formation (Garrido-Megias & Rios Aragües 1972) and was deposited in a lagoonal-lacustrine environment which became stagnant at times (Schairer & Janicke 1970). The limestone has usually been considered to be Upper Jurassic in age, but work on the Ostracoda (Brenner, Goldmacher & Schroeder 1974) has now shown that the upper part at Rubies is late Berriasian to early Valanginian, i.e. early Cretaceous. The Ostracoda associated with the insect remains have been determined by Dr R. H. Bate as belonging to the freshwater genera *Darwinula* and *Cypridea*: one, *Cypridea wicheri* Wolburg ranges from the Upper Purbeck to Wealden (Bate, *in litt.*), indicating an early Cretaceous age for associated insect material (In.59464).

The insects occur in a fine-grained, well-cemented brown limestone. They are preserved as impressions, more or less compressed, and frequently show traces of cuticle. They were collected from scree material and their exact stratigraphical positions are unknown.

The biota is summarized by Condal (1951), Calatayud *et al.* 1953, Teixeira (1954) and Brenner *et al.* (1974). Apart from insects it comprises Foraminifera, Porifera, Crustacea, Ostracoda, molluscan ichnofossils, fish, amphibia, reptiles and plant remains, the latter including Charophytes.

Insect fauna

Although some of the specimens collected by Ball and Wonnacott have been briefly discussed (Wootton 1972) the collection has not previously been studied in detail. Some of the insects from Montsech mentioned by earlier workers, for example the 'aculeate sphecoid' (Zeuner & Manning 1976: 155, Rasnitsyn 1980) have aroused controversy (Burnham 1978).



Fig. 1 Rubies Quarry, Lérída Province, Spain: general view. Photograph: H. W. Ball.

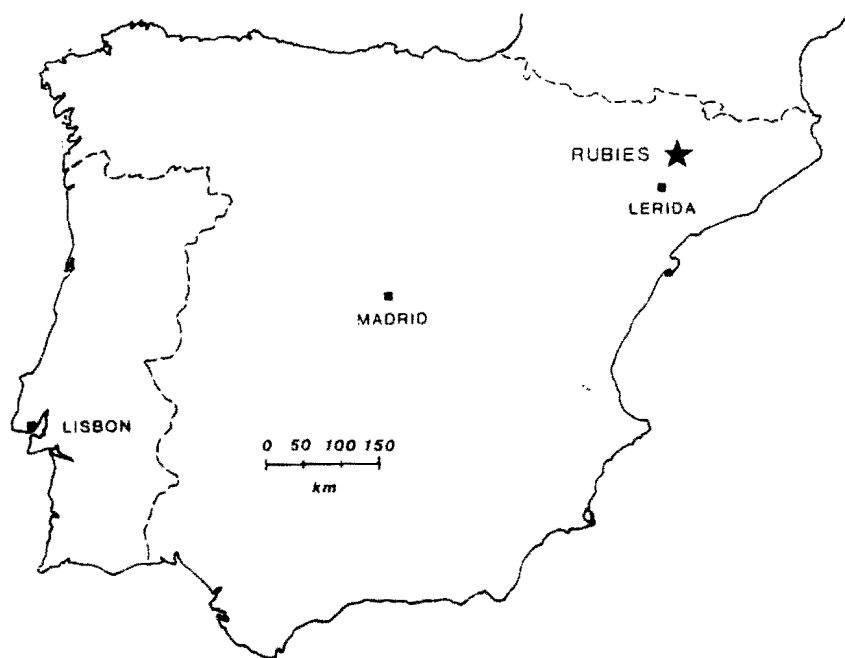


Fig. 2 Location map showing position of Rubies site.



Fig. 3 Lithograph

Wootton (unpublis
dae) at length and
Of the nine Ord
(Lepidoptera, Neu
remainder are sum

Ephemeropter
Blattodea:

Odonata:

Hemiptera:

Coleoptera:

Diptera:

Hymenoptera:



Fig. 3 Lithographic Limestone, Rubies Quarry, Lérida. Mr F. M. Wonnacott collecting.
Photograph: H. W. Ball.

Wootton (unpublished Ph.D. thesis, 1961) discussed one species (Hemiptera, Palaeontiniidae) at length and we have been fortunate in having access to his work.

Of the nine Orders of insects previously recorded from the Lithographic Limestone, two (Lepidoptera, Neuroptera *s.l.*) we consider to be based on incorrect determinations; the remainder are summarized below, with page numbers.

Ephemeroptera:	<i>Mesopalingea lerida</i> gen. et sp. nov.	384
Blattodea:	<i>Artitocoblatta colominasi</i> Meunier	387
	<i>A. hispanica</i> sp. nov.	388
Odonata:	<i>Condalia woottoni</i> gen. et sp. nov.	389
	<i>Palaeaeschna vidali</i> Meunier	391
Hemiptera:	<i>Wonnacottella pulcherrima</i> gen. et sp. nov.	392
	<i>Pachypsyche vidali</i> Meunier	391
	<i>Acocephalites breddini</i> Meunier	394
	<i>Aleyrodoidea</i> gen. indet.	394
	<i>Geocorisae</i> , gen. indet.	396
Coleoptera:	<i>Chrysobotris</i> (?) <i>ballae</i> sp. nov.	398
	<i>Buprestidae</i> gen. et sp. indet.	399
	<i>Eobelus solutus</i> sp. nov.	400
	<i>Curculionidea</i> , <i>incertae sedis</i>	400
Diptera:	<i>Stratiomyidae</i> gen. indet. (two species)	402
	<i>Sciomyzidae</i> gen. indet.	404
	uncertain affinities (two species)	404
Hymenoptera:	<i>Ephialtites jurassicus</i> Meunier	406
	<i>Ichneumonidae</i> gen. indet.	407
	Apocrita family indet.	408

The larva described as lepidopterous by Teixeira (1954: pl. 8, fig. 4) we consider probably dipterous but this is uncertain from the photograph. The dytiscid larva (Coleoptera) described by Condal (1951: 18) is an ephemeropteran nymph, while the sphecid (Hymenoptera, Aculeata) mentioned by Zeuner & Manning (1976: 155) we believe to be an ichneumonid wasp (p. 407). The various 'Neuroptera' mentioned by earlier workers are considered to be dipterous larvae (p. 403).

Systematic descriptions

Following the BM(NH) register number the letter (B) indicates the collection made by H. W. Ball & F. M. Wonnacott in 1960. The letter (W) indicates collections made by Wonnacott in other years.

Order EPHEMEROPTERA

Ephemeropteran adults have been recorded in Upper Carboniferous deposits (Chernova 1962), and from the Permian onward adult mayflies are found in many deposits (Wootton 1972); nymphal forms are less common in the fossil record. Kukalova (1968) described some Permian mayfly nymphs and Wootton (1972) mentioned the burrowing nymphs which are described below. Mayfly nymphs are the commonest insect fossils in the samples from Lérída, and although 19 nymphs were collected no adult mayfly was found.

Chernova (1977) described burrowing mayfly nymphs from the Siberian Jurassic in the families Palingeniidae and Bentiingiidae. McCafferty (1975) has described the burrowing nymphs of Recent species.

Superfamily EPHEMEROIDEA

Family PALINGENIIDAE Klapalek, 1909

This family is widespread in the Old World (Edmunds *et al.* 1976, McCafferty & Edmunds 1976), the nymphs being confined to fresh water. The nymphs described below are provisionally placed in this family, having similar mandibular structures which, in the Recent species, are important in the burrowing habit.

Genus *MESOPALINGEA* nov.

DIAGNOSIS. Palingeniid nymphs with broad flat mandibular tusks, toothed at the apex. Mandibles with two molar surfaces. Caudal filaments long, hairy.

NAME. *Meso* + *Palingea* (a Recent genus).

TYPE SPECIES. *Mesopalingea lerida* sp. nov.

Mesopalingea lerida sp. nov.

Figs 4, 6

1951 Dytiscid larva, Condal: 18; pl. 9, fig. 1.

DIAGNOSIS. As for genus.

NAME. Lérída Province, Spain.

DESCRIPTION. Nymph with broad, flat, mandibular tusks with inward pointing apical tooth on each tusk (Fig. 6). Outer margin of tusk with irregular edge formed by setal sockets (Fig. 4). Each tusk has large setal bases indicating that there were strong setae (not preserved).

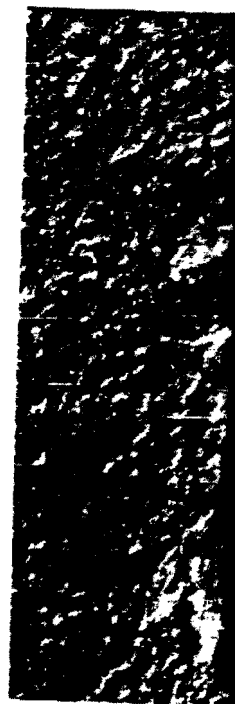


Fig. 4 *Mesopalingea lerida* sp. nov. Photographed (A) e - leg).

curved mandibles. Smaller setal sockets. Antennal base visible. Maxilla curved, pointed. Eyes, facets visible. Ocelli not visible. Wing pads with truncal segments. Cerci and caudal filaments long, hairy.

HOLOTYPE. In.59509 (B).

OTHER MATERIAL. In.59452 (B), In.59488 (B), In.59508 (W).

DIMENSIONS. Nymph.

DISCUSSION. Mandibles where the tusks assist in burrowing. *Mesopalingea* (Chernova) and *M. lerida* have mandibular tusks, which are not seen in the fossils. *M. lerida* and *M. lerida* have mandibular tusks, which are not seen in the fossils.

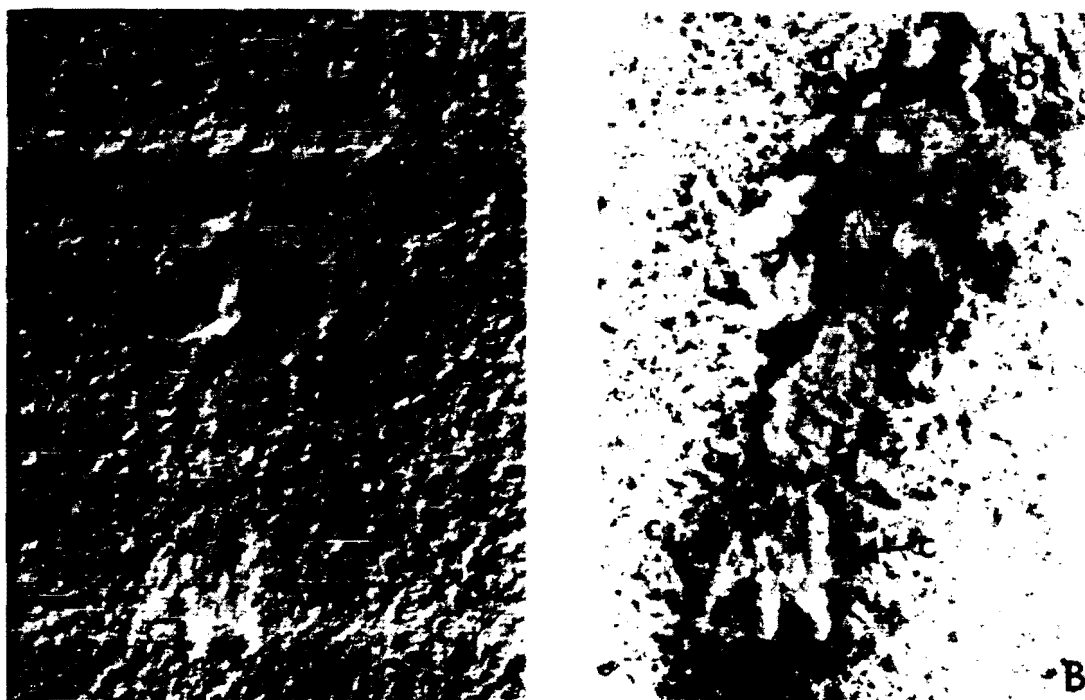


Fig. 4 *Mesopalingea lerida* gen. et sp. nov. (Ephemeroptera). Paratype. Nymph, In.49653, $\times 3$. Photographed (A) dry, (B) wet. (a - compound eye; b - tusk; c - cerci; d - terminal filament; e - leg).

curved mandibles have double molar surface. Frons slightly produced in front of head. Smaller setal sockets are present along inner margin of the tusks. Antennae missing, antennal base visible in some specimens. Hypopharynx with lateral paraglossae present. Maxilla curved, pointed; lateral palp not preserved. Head broad with laterally protruding eyes, facets visible in some specimens. Eyes separated by a short distance in mid-line on top of head. Ocelli not visible. Prothorax short, mesothorax longer, metathorax with distinct wing pads with truncated apex. Forelegs with enlarged hairy tibia, rest of legs lost. Abdomen 10-segmented, trace of lateral gills, shape indeterminate: possibly some styli on abdominal segments. Cerci and terminal filament long, hairy (Fig. 4).

HOLOTYPE. In.59509 (W). Fig. 6.

OTHER MATERIAL. In.44657 (W), In.49653 (W) (Fig. 4), In.49657 (W), In.59448 (B), In.59449 (B), In.59452 (B), In.59461 (B), In.59466 (B), In.59470 (B), In.59478 (B), In.59487 (B), In.59488 (B), In.59489 (B), In.59492 (B), In.59493 (B), In.59500 (B), In.59506 (W), In.59508 (W).

DIMENSIONS. Nymph, length 15-22 mm (depending on instar).

DISCUSSION. Mandibular tusks are characteristic of nymphs of several families of mayflies, where the tusks assisting in burrowing (Fig. 5). From the Jurassic palingenid *Mesopalingenia petersae* (Chernova 1977) the new species can be distinguished by the shape of the mandibular tusks, which are very broad in *lerida*. Even allowing for some compression in the tusks in the fossils, they are still wider than those of Recent species. Both *Mesopalingenia petersae* and *M. lerida* have an enlarged fore tibia.

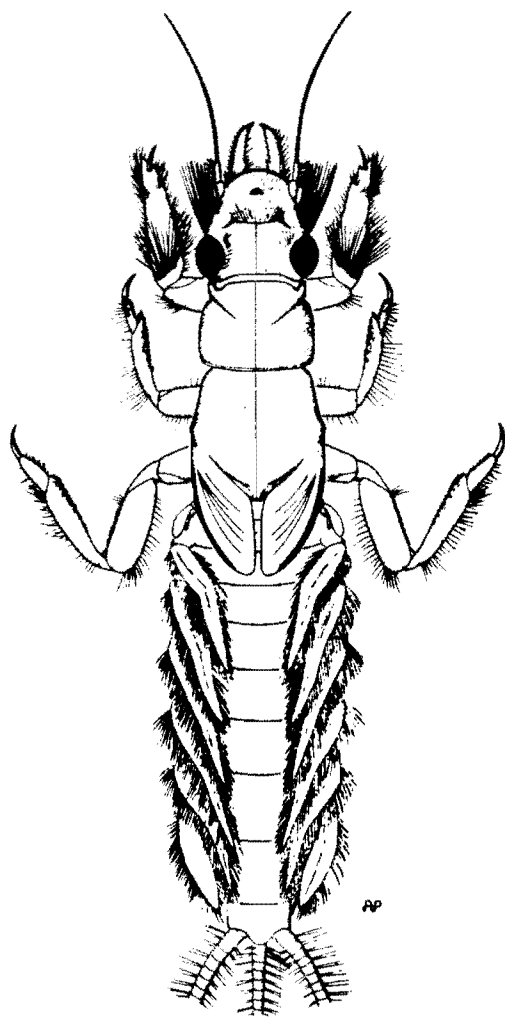


Fig. 5 Tusk-bearing Recent Ephemeroptera nymph, *Campsurus* sp., $\times 4$. After Edmunds *et al.* 1976: fig. 432.

The fossil nymphs occur in two size groups but there is no difference in the morphology of the two groups other than size. They are therefore considered to be two instars of a single species. Condal (1951: pl. 9, fig. 1) figured the nymph of *M. lerida* but regarded it (p. 18) as a dytiscid larva (Coleoptera).

From the fossils we had to decide if they represented the actual insects or only the exuviae (cast skin) of the nymphs. When a nymph moults, the old skin splits along the back but none of the fossils showed any trace of this split. Today the delicate exuviae often wash together in backwaters where they may collect in some numbers, although they do not usually remain intact for long. The fossil nymphs were found sporadically in the limestone and did not occur together in lenses (H. W. Ball, personal communication). Also, though they lacked appendages, many of the bodies were intact. The indications are therefore that they were not the exuviae but the actual insects.

Recent mayflies are essentially fresh-water insects and there is no reason to believe the Jurassic species were any different. The burrowing habit is a specialized adaptation found in a number of families (McCafferty 1975, 1979) and it is interesting to find it in the Jurassic. But mayflies have a long history, perhaps dating back to the Upper Carboniferous (Crowson *et al.* 1967).

Fig. 6 *Mesopalingea*
In. 5

Cockroaches are com
Meunier (1914) descr
the Lithographic Lime
(1951: fig. 4) figure
colominasi. From the
under the prothorax
recorded from the Li
cockroach specimens i

TYPE SPECIES. *Artitoco*

1914 *Artitocoblatta cole*
1951 ? Blattid, Condal:

MATERIAL. One incom

DIMENSIONS. 6.5 mm l

DISCUSSION. The costa
clearly visible. The c
Meunier's figures.

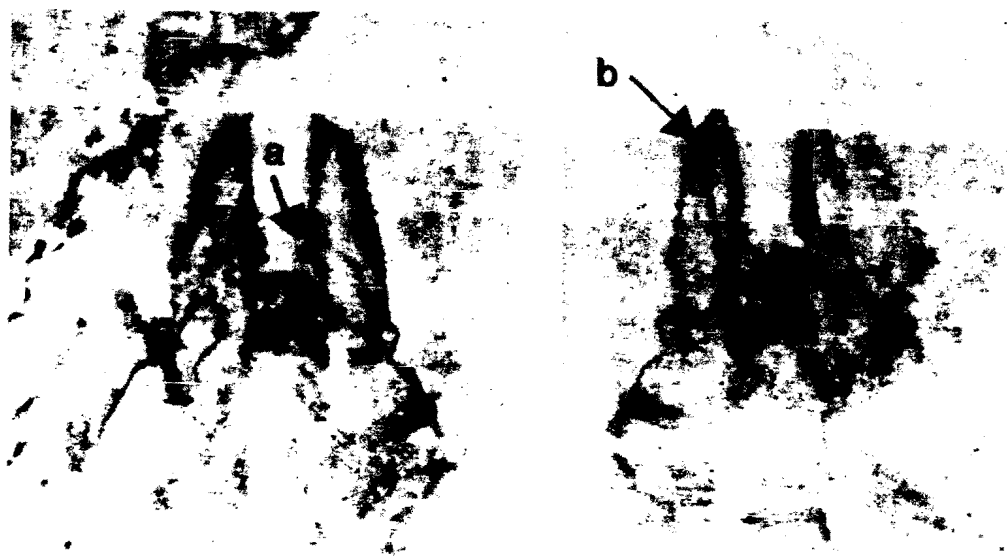


Fig. 6 *Mesopalingea lerida* gen. et sp. nov. (Ephemeroptera). Holotype. Head of nymph, In.59509, in part and counterpart, $\times 17$. (a - mandible; b - tusk).

Order BLATTODEA

Cockroaches are common in the fossil record from the Upper Carboniferous onwards. Meunier (1914) described an almost complete cockroach, lacking only the hind wing, from the Lithographic Limestone of Montsech, which he named *Artitocoblatta colominasi*. Condal (1951: fig. 4) figured another specimen from this deposit which he identified as *A. colominasi*. From the photograph this specimen seems to lack a head: perhaps it was crushed under the prothorax and so not visible. Teixeira (1954), in listing the plants and animals recorded from the Lithographic Limestone, included *A. colominasi*. There are four new cockroach specimens in the present collection.

Family MESOBLATTINIDAE Handlirsch, 1908

Genus *ARTITOCOBLATTA* Handlirsch, 1906

TYPE SPECIES. *Artitocoblatta gossii* (Scudder 1886), by monotypy. Upper Jurassic, U.K.

Artitocoblatta colominasi Meunier, 1914

1914 *Artitocoblatta colominasi* Meunier: 4; pl. 1, figs 1a, 2a, 3a.

1951 ? Blattid, Condal: pl. 9, fig. 2.

MATERIAL. One incompletely preserved forewing. In.59465 (B), part and counterpart.

DIMENSIONS. 6.5 mm long (incomplete).

DISCUSSION. The costal and radial veins are missing but the entire anal and median areas are clearly visible. The complete forewing was about 7 mm long and compares well with Meunier's figures.

Artitocoblatta hispanica sp. nov.

Fig. 7

DIAGNOSIS. Cockroach with short ovipositor in female.

NAME. 'Spanish'.

DESCRIPTION. Head, prothorax and forewings missing. Costal vein of hind wing short, upturned. Radial veins strongly upturned. Median veins closely parallel towards margin. Anal area large, folded over in fossil. Ovipositor valves clear, short; lateral lamellae slender. Cerci hairy. Part of leg visible showing spiny tibia. [Male unknown].

HOLOTYPE. In.59505 (W), part and counterpart. The only specimen. Fig. 7.

DIMENSIONS. Hind wing 6 mm. Abdomen 4.5 mm (excluding ovipositor). Cerci 2.5 mm.

DISCUSSION. Meunier's type figure of *A. colominasi* shows a female with the broad abdomen and typical shape of a Recent cockroach. Condal's (1951) specimen is also a female (Mrs J. Marshall, personal communication). Both resemble the majority of Recent cockroaches in lacking any trace of ovipositor lobes. *A. hispanica* has ovipositor lobes and is separated on the basis of this character. This is a structure which is very rare in Recent species but often well-developed in Palaeozoic and Mesozoic forms, where it may be much longer than in *A. hispanica*. The venation of the forewing is important for generic classification in fossil cockroaches and as this is missing in the only specimen of *A. hispanica*, it is only tentatively placed in the genus *Artitocoblatta* Handlirsch. There it is associated with broadly similar species (with ovipositors) described by Vishnyakova (1968) from the Jurassic of Karatau. *A.*



Fig. 7 *Artitocoblatta hispanica* sp. nov. (cockroach). Holotype. In.59505, $\times 13$. (a - cercus; b - ovipositor).

hispanica can be distinguished by the shape of the ovipositor lobes.

Judged on the size of the ovipositor, it is much larger than many Recent species.

Specimen no. 1 is the main diagnostic feature.

MATERIAL. In.59494.

Specimen no. 2 also shows the forewing showing typical venation.

MATERIAL. In.59459.

Condal (1951: pl. 9, fig. 10) shows a much larger (c. 10-8 mm) specimen has not been described.

The Lithographic Limestone is not related to the extant suborder Blattaria.

DIAGNOSIS. Anisoptera.

NAME. For Dr L. F. Condal.

TYPE SPECIES. *Condalia*.

DIAGNOSIS. As for genus.

NAME. For Dr Robert.

DESCRIPTION. A single specimen. Venation of hind wing showing only 4 antenodals (A₁, A₂, A₃, A₄) and an intercalary vein IR₃. The venation of the arculus not stalked.

HOLOTYPE. In.59491.

DIMENSIONS. Preserved length 10 mm.

DISCUSSION. Wootton (1968) placed *Libelluloidea*, an extinct suborder of Libellulidae, in the order Libellulidae.

hispanica can be distinguished from *A. asiatica* Vishnyakova by the shape and proportions of the ovipositor lobes and cerci.

Judged on the size of the hind wing, *A. hispanica* may well have been capable of flight like many Recent species of *Ectobius*.

Blattodea, *incertae sedis*

Specimen no. 1 is part of the forewing of a cockroach but is very incomplete and lacks the main diagnostic features for interpretation.

MATERIAL. In.59494 (B). 2.5 mm long (incomplete).

Specimen no. 2 also lacks the features used for generic interpretation but is part of the forewing showing typical intercalary veins of a cockroach.

MATERIAL. In.59459 (B). 3.5 mm long (incomplete).

Condal (1951: pl. 9, fig. 2) illustrates an almost complete cockroach which is not named. It is much larger (c. 10.8 mm long) than any currently known species from Lérida, but the original specimen has not been re-examined.

Order ODONATA

Suborder ANISOPTERA

The Lithographic Limestone of Lérida has yielded two species of dragonfly, both belonging to the extant suborder Anisoptera. One is an adult and the other is a nymph, but they are not related.

Family LIBELLULIDAE Latreille, 1802

Genus *CONDALIA* nov.

DIAGNOSIS. Anisopteran with four antenodals in the forewing.

NAME. For Dr L. Ferrer Condal.

TYPE SPECIES. *Condalia woottoni* sp. nov.

Condalia woottoni sp. nov.

Figs 8, 9

DIAGNOSIS. As for genus.

NAME. For Dr Robin J. Wootton.

DESCRIPTION. A single right forewing, well preserved except near apex where affected by a micro-fault. Venation as in Fig. 9. Nodus approximately two-thirds of wing length from base; only 4 antenodals (Ax), basal 2 stronger than distal 2. R_3 , R_4 and distal parts of primary intercalary vein IR_3 and MA sinuous; secondary intercalaries R_{spl} and M_{spl} reduced; sectors of arculus not stalked; no crossveins in cubital, bridge, and median spaces.

HOLOTYPE. In.59491 (B). The only specimen. Fig. 8.

DIMENSIONS. Preserved length of forewing 34 mm; maximum width 12.5 mm.

DISCUSSION. Wootton (1972) briefly referred to this fossil and identified it as belonging to the Libelluloidea, an extant superfamily of Anisoptera which is considered advanced, and is

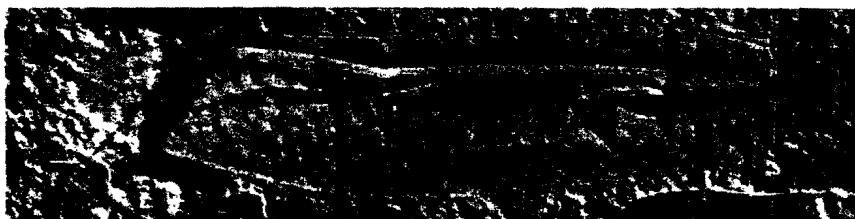


Fig. 8 *Condalia woottoni* gen. et sp. nov. (dragonfly). Holotype. Right forewing, In.59491. Counterpart, coated with ammonium chloride, $\times 2.75$.

otherwise unknown before the late Caenozoic. Zherikhin (1978) doubted this identification and determined the photograph received from Wootton as that of a gomphid. Pritykina (1980) awaited confirmation of the systematic placing of this fossil.

The forewing of *Condalia* is undoubtedly that of an anisopteran dragonfly. The triangle, subtriangle and supratriangle resemble those of the extant genus *Aethriamanta* (Libellulidae, Urotheminae) (Fraser 1957: fig. 59.2) but are also similar to those of the living *Onychogomphus* (Gomphidae, Gomphinae) (Fraser 1957: fig. 48) and extinct *Necrogomphus* (Handlirsch 1906–08: pl. 47, fig. 8). The small number of antenodals in *Condalia* is not typical of Anisoptera. Gomphidae have many more antenodals, although reduction of these cross-veins does occur in the Libellulidae: in *Macrodiplax* (Urotheminae) there are six antenodals in the forewing and five in the hindwing (Fraser 1957: fig. 58). In *Nannophya* (Libellulidae, Brachydiplactinae) there are four antenodals in the hindwing and there may be as few as five antenodals in the forewing. The arculus in *Nannophya* is advanced in lying between the first and second antenodals (Fraser 1957: 118), which is also the situation in *Condalia*. A study of the BM(NH) collection has failed to reveal any libellulid with only four antenodals in the forewing. The nodus in *Condalia* is distant from the wing base, as in *Macrodiplax* and some other Anisoptera, but not Gomphidae. *Condalia* also resembles Urotheminae in that the sectors of the arculus diverge from their origin and the distal antenodal is complete: however, in *Condalia* the primary antenodals do not appear to be reduced as in Urotheminae (Fraser 1957: 106).

If the reduction of the antenodals is a specialization of the Libellulidae within the Anisoptera then Wootton's identification is correct. The extreme reduction of antenodals in *Condalia* becomes a unique specialization, while the triangle remains in a primitive state. Hennig (1981: 352) doubted the identification of modern families of the Anisoptera in the Upper Jurassic, and it is conceivable that *Condalia* represents a specialized genus from the

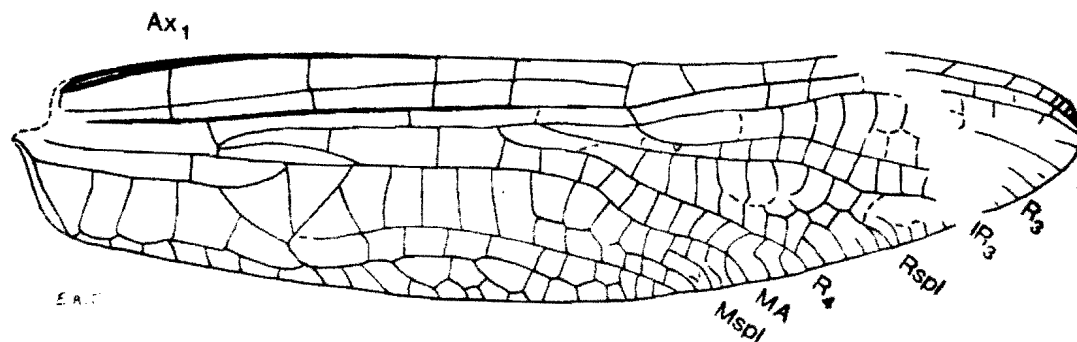


Fig. 9 *Condalia woottoni* gen. et sp. nov. (dragonfly). Right forewing, In.59491. Diagram of venation. $\times 4$.

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Anisoptera in the M

1914 *Palaeaeschna* v
1951 *Palaeaeschna* v

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Carpenter for the
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Examination of M
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buds in the text, but
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Condal (1951) de
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Mesozoic Odonat
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affinity with Anisoz

Condal (1951) rec
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The plant bugs from
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Calatayud *et al.* (
pl. 10, fig. 1) had
cannot comment on

The family is repre
described below; th
Wootton (1961, unj

stem-group of the Anisoptera. However, until further work is done on the evolution of the Anisoptera in the Mesozoic, Wootton's identification cannot be rejected.

Anisoptera, Family uncertain

Palaeaeschna vidali Meunier, 1914

1914 *Palaeaeschna vidali* Meunier: 122-123, 125-126; pl. 2.

1951 *Palaeaeschna vidali* Meunier; Condal: 12-13; pl. 3, figs 3-4.

This nymph was described by Meunier (1914) as a new genus and species of the extant family Aeshnidae. The depository of the only known specimen was not given. Meunier's illustrations provide no evidence for placing *Palaeaeschna* in the Aeshnidae or any other anisopteran family. A similar conclusion has been reached independently by Prof. F. M. Carpenter for the forthcoming part R (3) of the *Treatise on Invertebrate Paleontology* (personal communication). However, the slender form of the nymph suggests that it is an aeshnoid rather than a libelluloid.

Examination of Meunier's published figure and photographs suggests that the former is inaccurate. The two lateral grooves on the abdomen, clearly visible in Meunier's enlarged photograph, suggest that the nymph is in ventral aspect. His interpretation of the eyes is doubtful, especially when the nymph is viewed in its correct orientation. He refers to wing buds in the text, but does not show them in his illustrations. In living dragonfly nymphs the rudimentary wings are located dorsally. The evidence for an anal pyramid and nine abdominal segments is not clear.

Condal (1951) described some further material which he considered belonged to this species, but did not resolve the systematic problems.

Mesozoic Odonata include a number of extinct families based on adults and assigned usually to the now relict suborder Anisozygoptera. A few Mesozoic nymphs have also been referred to this suborder, although the published work on *Palaeaeschna* does not suggest any affinity with Anisozygoptera.

Condal (1951) recorded a second dragonfly nymph identified by Oustalet and figured by Zeiller (1902); from the published information, the specimen should be considered with the dipterous larvae (species 2, p. 403).

Order HEMIPTERA

The plant bugs from the Lithographic Limestone of Lérida are known from few specimens, and no aquatic Hemiptera have been recognized. Five species are described, each based on a single example, only two of which are in the same family. Two species are based on wings alone; the others include body material. There is considerable size difference between the largest and smallest species. The fossils probably represent occasional strays from the neighbouring vegetation.

Calatayud *et al.* (1953: pl. 9, fig. 3) illustrate a possible hemipteran which Condal (1951: pl. 10, fig. 1) had previously considered an isopod. We have not seen the specimen and cannot comment on its affinities.

Suborder HOMOPTERA

Superfamily CICADOIDEA

Family PALAEONTINIDAE Handlirsch, 1906

The family is represented by two species in the Lithographic Limestone, one of which is described below; the other species, *Pachypsyche vidali* (Meunier 1902) has been studied by Wootton (1961, unpublished).

Genus *WONNACOTTELLA* nov.

DIAGNOSIS. Palaeontinid differing from *Pachypsyche* Handlirsch, 1906, in possessing a narrower forewing and lacking venation between Rs and the anterior margin.

NAME. For Mr F. M. Wonnacott.

TYPE SPECIES. *Wonnacottella pulcherrima* sp. nov.

Wonnacottella pulcherrima sp. nov.

Figs 10, 11

1971 Palaeontinidae, Wootton: fig. f.

DIAGNOSIS. As for genus.

NAME. 'Very beautiful'.

DESCRIPTION. The species is known from a single right forewing. The triangular wing has a small clavus which has nearly split off from the remigium along the claval furrow. The anterior margin is indented where the nodal line reaches the margin. Venation as in Fig. 11: R and Rs unbranched, curved posteriorly near the nodal line. M branched dichotomously, M_{1+2} separating distad of M_{3+4} . Cross-vein r-m short. R, Rs and M fused basally. CuA 2-branched; CuP single, very close to claval fold. Clavus with two unbranched anal veins. Nodal line traceable as a crease across R and Rs to stem M_{1+2} where it continues along the vein to its origin. The line, now stronger and vein-like, then crosses to CuA, follows the latter for a short distance and then continues independently to CuP, reaching CuP a short distance before the distal end of the clavus. The membrane is pitted distad of the nodal line and smooth basad of the line. The costal sclerite is present at the wing base, consisting of a raised area with about 10 transverse grooves more or less incised.

HOLOTYPE. In.59486 (W). The only specimen. Fig. 10.

DIMENSIONS. Length 39 mm, width 16 mm.



Fig. 10 *Wonnacottella pulcherrima* gen. et sp. nov. (palaeontinid). Holotype. Right forewing, In.59486. $\times 3$. Arrow indicates costal sclerite.



Fig. 11 *Wonnacottella pulcherrima* sp. nov. (palaeontinid). Venation.

DISCUSSION. The forewing shape of *Wonnacottella* is distinct from *Sc* and *C* are not found as part of its course as in *Wonnacottella*.

Wootton (1961) described *Wonnacottella* (now *Wonnacottella*) as having the grooved areas of the sclerite when rubbed by the finger. This shows that in this species the sclerite is grooved: this sclerite is the costal sclerite. The grooved area is the costal sclerite: hence it was named.

Bekker-Migdisov (1961) described a form. One of these forms has a thickened anterior margin. *Wonnacottella* has a distinct basal fusion of R, Rs and M. The wing shape of *Wonnacottella* is distinct from Sphingidae: the anterior margin is known, are broad and triangular.

Wootton (1961) described a form comprising *Wonnacottella* (now *Wonnacottella*) which he considered as a development of the form described as separating at a single point, as discussed above. *Wonnacottella* (now *Wonnacottella*) Palaeontinidae (Wootton, 1961) anterior margin and shape.

In Wootton's genus *Wonnacottella* and from the illustration of the wing, the character.

The nodal line is a distinct feature of the wing of *Wonnacottella*. This line occurs in the wing of *Wonnacottella* and is suggested that the

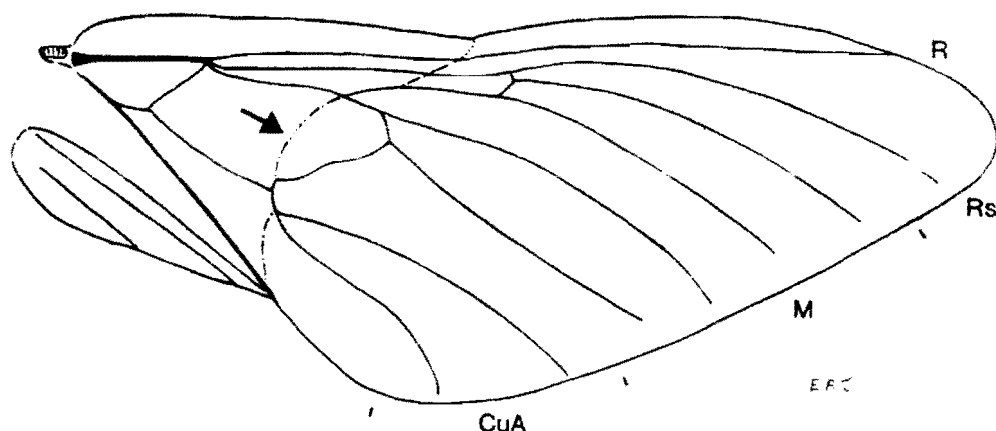


Fig. 11 *Wonnacottella pulcherrima* gen. et sp. nov. (palaeontinid). Right forewing. In.59486. Diagram of venation. $\times 3.3$. Nodal line arrowed.

DISCUSSION. The forewing of *Wonnacottella* is similar to that of *Pachypsyche* but is narrower. Sc and C are not free. m-cu leaves M_1 a little more basally, the nodal line follows M_{1+2} for part of its course and the clavus is apparently smaller.

Wootton (1961) suggested that the grooved area at the wing base of specimen In.59486 (now *Wonnacottella*) was a stridulatory file. He compared it with some extant cicadas where the grooved areas on the mesonotum are considered to be stridulatory files, producing sound when rubbed by the clavus. But examination of the file on *Chonosia crassipennis* Walker shows that in this species the anterior part of the costal sclerite at the wing base is also finely grooved: this sclerite is concerned with wing folding and not sound production (Myers 1928). The grooved area on the wing base of *Wonnacottella* is in the correct position for a costal sclerite; hence it was probably involved with flight and not in stridulation.

Bekker-Migdisova (1949) distinguished three groups of Palaeontinidae according to wing form. One of these, the Dipterygia, was characterized by narrow forewings with strengthened anterior margin which was considered a specialization for strong, rapid flight. *Wonnacottella* has a relatively narrow wing and the anterior margin is strengthened by the basal fusion of R, Rs and M; it can therefore be described as dipterygian (Wootton 1961). The wing shape of *Wonnacottella* resembles that of extant fast-flying moths of the family Sphingidae: the analogy is strengthened by the fact that the bodies of Palaeontinidae, where known, are broad like Sphingidae.

Wootton (1961) distinguished a group of late Jurassic-early Cretaceous Palaeontinidae comprising *Wonnacottella*, *Pachypsyche* and *Eocicada* (the last from the Solnhofen Limestone) which he considered to be 'clearly natural'. This group is characterized by the development of triangular forewings, with an extended anal angle, and R, Rs and M separating at a single point. This venational character is linked with narrowing of the forewing as discussed above, and narrow forewings appear to have arisen convergently in the Palaeontinidae (Wootton 1961). However, these particular modes of strengthening the anterior margin and the triangular wing form may well be unique specializations.

In Wootton's grouping only the genus *Eocicada* contains more than one included species, and from the illustrations it would appear that size difference is a useful interspecific character.

The nodal line in the forewing of extant cicadas separates the deformable and supporting zones of the wing in flight (Wootton 1981). Dimorphism of the membrane on either side of this line occurs in cicadas (Myers 1928) and is pronounced in *Wonnacottella*. Hinton (1948) suggested that the nodal line acts as a flexion line in the wing pads of the subterranean

nymphs of extant cicadoids, enabling them to move backwards. The nodal line is developed also in Hemiptera without subterranean nymphs, but Hennig (1981) suggests that the form of the line in adult cicadas might be linked with the distinctive nymphal habits of these insects. Myers (1928) considered the nodal line in Palaeontinidae to be cicada-like, but further investigation of Recent and fossil forms is clearly necessary.

Hennig (1981: 273-4) considered that a marginal membrane and a marginal (ambient) vein were characteristic of cicadoids. This is certainly true of all extant cicadoids, although Hennig did not mention the Palaeontinidae. In *Wonnacottella* the wing margin is well preserved but a marginal vein and membrane cannot be seen. From the figures in Wootton (1971), these characters appear to be present in early Palaeontinidae; Wootton's accompanying discussion suggests a sister-group relationship between Palaeontinidae and Mesogereonidae, and a marginal vein is definitely present in the latter family. The loss (or migration to the margin) of this vein thus seems a specialization within Palaeontinidae.

Extant cicadoids are plant feeders and closely associated with woodland habitats.

Superfamily **CICADELLOIDEA**

Family **CICADELLIDAE** Latreille, 1825

Genus **ACOCEPHALITES** Meunier, 1904

Acocephalites breddini Meunier, 1904

[for synonymy list see Metcalf & Wade, 1966: 36]

Evans (1956) says that the single forewing (tegmen) upon which this species is based 'resembles those of recent cicadellids in all essential features'. We have not seen the specimen and follow Evans' classification. Meunier (1904: figs 1-2) published a line drawing, and no new illustrations have appeared subsequently. Meunier figured only a single anal vein, which is unusual in cicadellid forewings. From the size of the forewing (4 mm long) the insect had a wing span of about 10 mm.

Superfamily **ALEYRODOIDEA** (?)

? *Bernaëid, incertae sedis*

Figs 12 (A-D), 13

DESCRIPTION. Body elongate, rounded anteriorly and posteriorly, and slightly convex, with traces of a marginal rim (Figs 12A, 13). The segmental divisions do not appear to intersect the body margin. Dorsal surface and margin of ventral surface with micro-processes ($1-2\mu$) which in places show a rough alignment (Fig. 12C). Thorax with some weak transverse furrows and strong meso-metathoracic suture. Abdomen with well-developed segmentation, comprising seven broad and one narrow divisions. Anal area elongate and situated in a depression (Figs 12B, C). Whole body area including anus with traces of chitin.

DIMENSIONS. Maximum length 0.9 mm; width 0.4 mm.

MATERIAL. In.60600 (W).

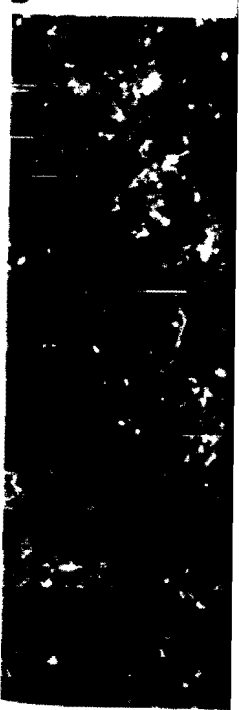
DISCUSSION. The fossil resembles the dorsal disc of an aleyrodoid 'pupa' case in the shape and relative flatness of the body with its unbroken, rimmed margin, the form of the dorsal anal area, the fact that obvious segmentation is confined to the central area, and its small size. The possibility that it is the immature stage of some other superfamily of insects or belongs in another class of arthropods has been considered. However, from the available

Fig. 12 Aleyrodid (whitefly)? Dorsal disc of pupa case, In.60600. A, $\times 67$ (arrow indicates anal area); B, hind end $\times 250$; C, lateral margin $\times 675$; D, anal area $\times 570$.



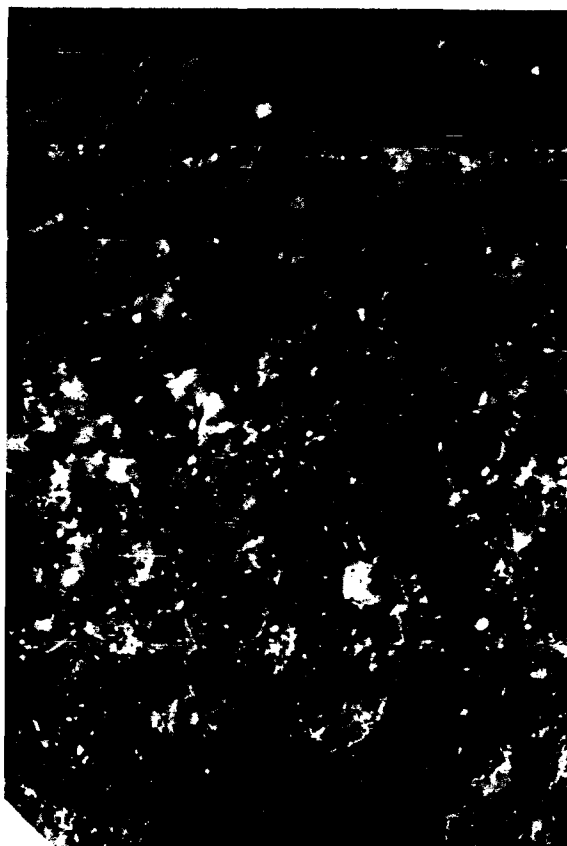
A

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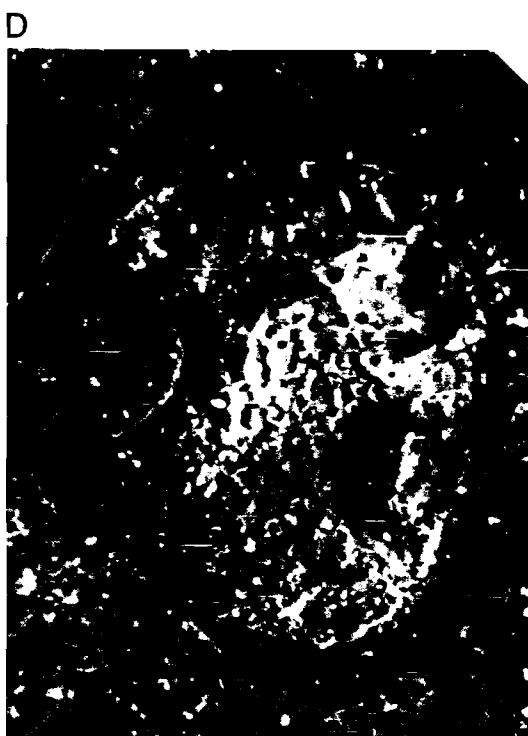




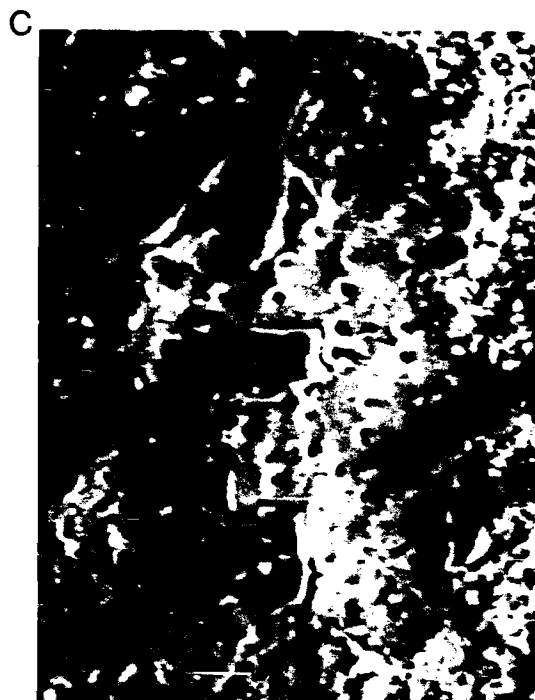
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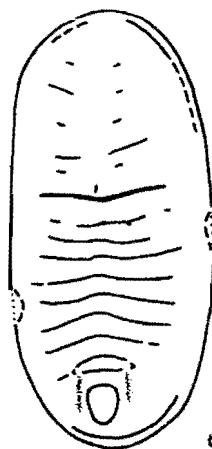


Fig. 13 Aleyrodid (whitefly)? Dorsal disc of pupa case. In.60600. Sketch, $\times 65$.

information it most closely resembles an aleyrodoid. Amongst the Insecta it shows some resemblance to Coccoidea (scale insects) but the ultrastructure is unlike the pores found in the latter.

Hitherto, the earliest known whiteflies have been adults occurring in Lebanese amber (Neocomian–Aptian) (Schlee 1970). These do not belong to any extant family or subfamily but to the stem group of the Aleyrodoidea (Schlee 1970). Zherikhin (1980) referred these fossils to a new family Bernaeidae. Immature whiteflies have not been reported previously from the Mesozoic: in extant species they are usually found on the undersides of angiosperm leaves, although a few occur on ferns (Woodward, Evans & Eastop 1970: 425).

Suborder HETEROPTERA

Division GEOCORISAE

[= Gymnocerata Fieber, 1851]

Geocorisae, incertae sedis

Fig. 14

DESCRIPTION. A single body (female) preserved in partial relief; eyes clearly preserved on head; pronotum apparently parallel-sided and slightly concave anteriorly; scutellum prominent, triangular; basal parts of forewings preserved with traces of weak venation; claval fold visible on left forewing; legs preserved as weak impressions in the body; wings and body covered with fine microtrichia aligned with the longitudinal axis of body.

DIMENSIONS. Body length 6.3 mm, width 2.1 mm.

MATERIAL. In.59495 (W).

DISCUSSION. The general form of the body is typical of the Heteroptera (*Geocorisae*); there is insufficient detail for family determination.

Order COLEOPTERA

Beetles are known in the fossil record from the Lower Permian. They are often abundant in deposits and are the commonest insect fossils in post-Permian times. Their strongly sclerotized structures, particularly the hardened elytra, are frequently fossilized.

Crowson (1975) summarized the evolutionary history of the Coleoptera with reference to the fossil record and comparative studies of extant species. Six beetles were found in

Lérida deposit, three any details. The remaining shows features of the only their outline shape.

The living Buprestidae in the temperate region Mesozoic (Crowson 1975) pattern, shape and extant buprestids and fossil buprestids had many Recent species.

The dytiscid larvae Lérida gen. et sp. nov.

Ponomarenko (1975) included, gives a detailed together with the we similarity to extant species which was obviously

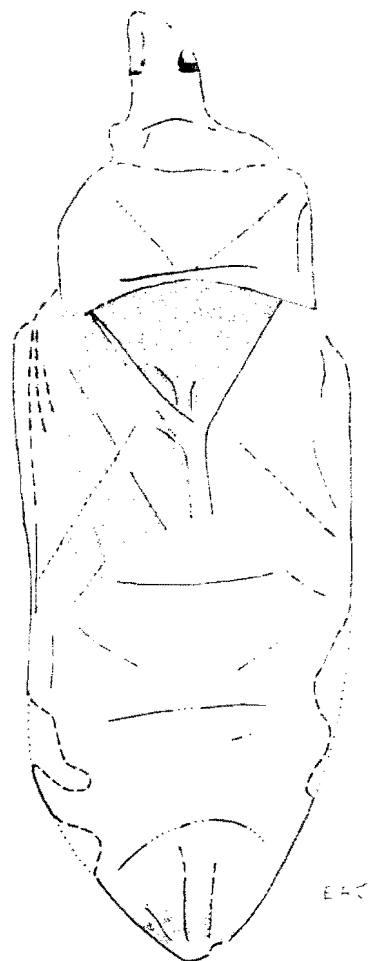


Fig. 14 Geocorisae bug. In.59495, $\times 20$.

Lérida deposit, three of them (the weevils) being mentioned by Crowson (1975) but without any details. The remaining three specimens are placed in the Buprestoidea. One clearly shows features of the family Buprestidae, while the other two are provisionally placed here: only their outline shape suggests Buprestoidea.

The living Buprestidae or Jewel Beetles are essentially a tropical group and less common in the temperate regions. Although there are references to possible buprestid beetles in the Mesozoic (Crowson 1975) the species described below is the first positive record. The pattern, shape and especially the spined apex of the abdomen are typical of some genera of extant buprestids and indicate an early evolution of this group of beetles. If the larvae of the fossil buprestids had similar habits to extant ones, then they may well have bred in plants; many Recent species breed in gymnosperms.

The 'dytiscid larva' figured by Condal (1951: pl. 9, fig. 1) is a nymph of *Mesopalingea lerida* gen. et sp. nov. (Ephemeroptera); see p. 384.

Ponomarenko (1977) deals with Mesozoic beetles and, although no Buprestidae are included, gives a detailed account of the weevils found in the Jurassic of the U.S.S.R. These, together with the weevils described below, are the earliest known and show a remarkable similarity to extant species. This suggests a much earlier evolution of this specialized group, which was obviously well developed by the Jurassic.

Superfamily BUPRESTOIDEA

Family BUPRESTIDAE Stephens, 1829

Genus *CHRYSOBOTRIS* Eschscholtz, 1829[= *Chrysobothris* auctt., incorrect subs. emend.]TYPE SPECIES. *C. chrysostigma* (Linn.), by subsequent designation of Westwood, 1838.

DIAGNOSIS. Elytra truncate; anal sternite deeply incised; fore femora with broad tooth.

Chrysobotris (?) *ballae* sp. nov.

Fig. 15

DIAGNOSIS. Buprestid with prominent pattern on elytra.

NAME. For Mrs H. W. Ball, who collected the specimen.

DESCRIPTION. Pronotum large, broad, apparently unmarked. Elytra with paler symmetrical patches, probably four on each elytron. The pattern is made up of a smooth oval spot subapically, a fairly regular, slightly rectangular spot anterior to this and then an elongate patch. Finally at the base of the elytron there is a small patch which is only preserved on one elytron. Apex of elytra pointed, with short, concave terminal margin. Outer margin curved, elytra slightly broader in basal half. Hindwings only faintly visible, about the same length as the elytra. Foreleg with broad tooth on fore femora, mid-leg with four heavily spined tarsal segments, tibia narrow. Abdomen with strongly sclerotized tergites. Apical sternites deeply incised with two lateral points. Head obscured, antennae lost.



15



16

Fig. 15 *Chrysobotris* (?) *ballae* sp. nov. (buprestid beetle). Holotype. In.59501, $\times 5$.Fig. 16 Buprestid beetle, species 1. In.59511, $\times 9$.

HOLOTYPE. In.59501

DIMENSIONS. Length

DISCUSSION. Although typical Buprestid, especially the shape of the rostrum, typical of most Recent species used in the generic classification of fossil, which can then not imply that we are dealing with a fossil.

C. ballae is similar to *C. chrysostigma* and bears a close resemblance to the pattern on the elytra of the species *Buprestis nana*. The elytra have deeply incised abdominal striae. *Phaenops*. The fossil is placed in the lateral margin of the rostrum for positive identification. It has the broad tooth on the fore femora.

The larvae of some

Although relatively small, they represent the same species.

DESCRIPTION. Head with a broad anterior margin, apical margin well sclerotized, apical margin preserved.

MATERIAL: In.59604

DIMENSIONS. Body length

DISCUSSION. These are placed in the fossil record.

The weevils are a group of specialized Coleoptera (Imms *et al.* 1970). They have larval stages. Many are gymnosperms, including abundant and varied species.

There is no problem of identification since many are collected; two are different genera. The diagnostic characters are the rostrum but in the third specimen

HOLOTYPE. In.59501 (B). The only specimen. Fig. 15.

DIMENSIONS. Length 15 mm. elytra 10 mm.

DISCUSSION. Although this is a well preserved specimen, it has not been possible to see the typical Buprestid transverse suture on the metasternum. The general shape, however, especially the shape of the apex of the abdomen and well-sclerotized abdominal segments, is typical of most Recent Buprestidae. But many of the smaller detailed structural characters used in the generic classification of Recent Buprestidae unfortunately cannot be seen in the fossil, which can therefore only be provisionally placed in the genus *Chrysobotris*. This does not imply that we consider *Chrysobotris* to have been fully developed by the Upper Jurassic.

C. ballae is similar in pattern to a number of extant species of Buprestidae (Schaefer 1949) and bears a close resemblance to a number of species in *Melanophila* and *Phaenops*. The pattern on the elytra may be due to coloured patches, as in the similarly-patterned Recent species *Buprestis novemmaculata* Linn., or may be the result of structural differences in the elytra. These may have been in the form of depressions in the elytra of the living insect. The deeply incised abdominal sternite occurs in Recent species of *Chrysobotris*, *Melanophila* and *Phaenops*. The fossil differs from Recent species in the genus in not having serrations along the lateral margin of the elytral apices. The head and scutellum are not well preserved for positive identification as a species of *Chrysobotris*, but the left fore femur of the specimen has the broad tooth-like projection which is characteristic of Recent species of *Chrysobotris*.

The larvae of some species of Recent *Chrysobotris* feed in gymnosperms.

Buprestidae: species 1

Fig. 16

Although relatively well preserved in outline these two specimens, which we believe represent the same species, do not show sufficient detail to identify their relationship.

DESCRIPTION. Head broad, antennae missing. Thorax roughly square. Elytra with curved anterior margin, apex truncate, some striae and punctures visible on the elytra. Abdomen well sclerotized, apex narrower. Tarsi spiny. Hindwing well developed, indistinctly preserved.

MATERIAL: In.59604 (W); In.59511 (W).

DIMENSIONS. Body length 9 mm; elytra 4 mm, width 1.5 mm.

DISCUSSION. These specimens are tentatively placed in the Buprestidae. They have the general shape of Buprestoidea and Elateroidea but because of the well-sclerotized abdomen are placed in the former superfamily.

Superfamily CURCULIONIDEA

The weevils are a group of beetles with an elongate snout or rostrum in many species. They are specialized Coleoptera and 'can in many respects be regarded as the most highly evolved' (Imms *et al.* 1970: 811). They are almost exclusively plant-feeders, both in the adult and larval stages. Many species feed inside seeds while others are associated with various gymnosperms, including cycads. According to Arnoldi (1977), weevils were the most abundant and varied group of Coleoptera-Polyphaga in the Upper Jurassic of Asia.

There is no problem in identifying the fossils as weevils but the family placing is more difficult since many of the diagnostic characters are indistinct. Three specimens were collected; two are probably the same species while the third is distinct and certainly a different genus. The position of the insertion of the antennae on the rostrum is an important diagnostic character of weevils. In one specimen the antennae are inserted towards the tip of the rostrum but in another they are inserted nearer the head. The antennae cannot be seen in the third specimen.

The earliest known fossil weevils, from the Triassic of the U.S.S.R. (Arnoldi 1977), are very similar to the fossil family Eobelidae. Although the three specimens described below resemble some of Arnoldi's figures, none shows clearly either of the two most distinctive features of the family, namely the strongly margined prothorax and the very steep frons (the latter resulting from the emergence of the rostrum horizontally from the lower part of the head capsule). Specimen In.49648 appears to have the antennae inserted at the base of the rostrum, whereas in all known Eobelidae they are inserted at or beyond the middle of the rostrum. If the antennal insertion is really basal, then this species will not fit into any known weevil family.

Family EOBELIDAE Arnoldi, 1977

Although many diagnostic characters of this family are obscured in the fossil, the general shape indicates it belongs here and it is provisionally placed in the genus *Eobelus*.

Genus EOBELUS Arnoldi, 1977

TYPE SPECIES. *Eobelus longipes* Arnoldi, by original designation. Upper Jurassic, U.S.S.R.

Eobelus solutus sp. nov.

Fig. 17

DIAGNOSIS. Eobelid-like weevil with long rostrum and well-sculptured elytra.

NAME. 'Without impediment'.

DESCRIPTION. This is larger than the problematic species described below and the antennae are clearly inserted towards the apex of the rostrum. The antennae have at least nine segments and the rostrum, even allowing for some compression, is broad. Only the margin of the eye is visible. The elytra have a broadly truncate anterior margin and are pointed posteriorly. The surface of the elytra is covered with fine hairs arranged in rows, and inserted into prominent hair-bases. The tibiae are very hairy.

HOLOTYPE. In.59510 (W). The only specimen. Fig. 17.

DIMENSIONS. Length 6.5 mm (excluding rostrum); rostrum 3.5 mm; femur 1.5 mm.

Curculionidea, incertae sedis

Weevil: species 1

Figs 18, 19

DESCRIPTION. Few details are visible on either specimen. Antennae probably inserted towards the base of the rostrum, segments indistinct. Rostrum slightly curved. Coxae broad, long. Tibiae hairy. Three tarsal segments ending in a bifurcate claw. Body rounded.

MATERIAL. In.49648 (W) (Fig. 19); In.49658 (W) (Fig. 18).

DIMENSIONS. In.49648: length 3.5 mm (excluding rostrum); rostrum 1.8 mm; hind femur 1 mm; hind tibia 1.2 mm. In.49658: body length 3 mm; rostrum 1.5 mm.

Order DIPTERA

While adult Diptera are known as fossils since the Triassic, their larvae are extremely rare in Mesozoic deposits. From the Cretaceous of Canada McAlpine (1970) described a possible Calypterate fly pupa while Brodie (1845) described the 'vermiform larva of a subaqueous

17

18

Fig. 17 *Eobelus* insertion of Figs 18-19 W. × 10; arrow.

dipterous insect identity of McAlpine's vermiform larva is either coleopterous from the Upper Cretaceous also described Brachycera larvae illustrated by Rohdendorf with the adult identification



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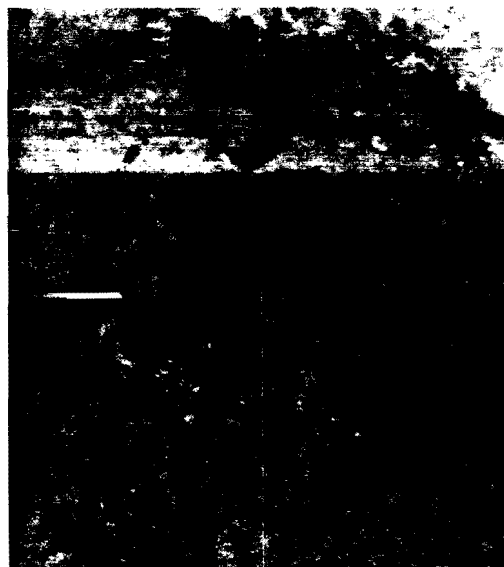


Fig. 17 *Eobelus solutus* sp. nov. (eobelid weevil). Holotype. In.59510. $\times 8$. Arrow indicates insertion of antenna.

Figs 18–19 Weevil. species 1. Fig. 18, In.49658. $\times 21$; arrow indicates rostrum. Fig. 19, In.49648, $\times 10$; arrow indicates insertion of antenna.

dipterous insect' from the Upper Jurassic of Britain. There is an element of doubt over the identity of McAlpine's dipterous pupa while an examination of Brodie's type-specimen of 'vermiform larva' in the BM(NH) shows it to have a distinct head and sickle-shaped jaws; it is either coleopterous or neuropterous. Bode (1953) described a number of larvae and pupae from the Upper Liassic of Germany. The larvae he identified as nematoceran Diptera. He also described an adult fly, placing it in the Asilidae (Diptera, Brachycera). None of the larvae illustrated by Bode resembles the Spanish specimens, which are the earliest known Brachycera larvae.

Rohdendorf (1964) in his '*Historical Development of the Diptera*' dealt almost exclusively with the adult stages. Larvae of Recent Diptera are not easy to identify and much of their identification is based on a lateral view of the cephalopharyngeal skeleton. While there is no

doubt of the dipterous nature of the Spanish specimens, further classification into families is difficult.

Larvae were described and illustrated from Lérida as early as 1902. Zeiller (1902: pl. 1, fig. 4) figured the larva of an insect which he considered to be Neuroptera (s.l.). We have examined the photograph and believe it to be a dipterous larva, showing the typical cephalopharyngeal skeleton, although we cannot place it in a family within the Diptera on the evidence available.

Condal (1951: pl. 5, figs 1, 3) figured insect larvae and quoted Oustalet as suggesting they were neuropterous (s.l.). The shape of the cephalopharyngeal skeleton shows clearly in Condal's pl. 5, fig. 1, which is similar to our species 2 (below). His pl. 5, fig. 3 shows a larva which Oustalet considered to be that of a dragonfly, but we think it is another typical dipterous larva, although less well preserved than most specimens in this formation.

Teixeira (1954) listed and figured the fossils from Lérida sent to him by Condal, but did not name them. The larva described as an 'aquatic coleopteran' (Teixeira 1954: pl. 8, fig. 5; not pl. 7, fig. 5 as in Teixeira's caption) is difficult to interpret from the photograph. Another larva is also illustrated in pl. 8, figs 4 (lower) and 4a: Teixeira considered it to be lepidopterous and compared it with the Sphingidae. He also compared the specimen with Condal's (1951: pl. 5, fig. 1) unnamed insect larva. We do not think these are lepidopterous: Condal's figure is clearly dipterous and we believe Teixeira's figure also represents a dipterous larva. From the size and shape we think it is similar to our stratiomyid species 2 below.

Eight positively identifiable dipterous larvae were collected at Montsech, and a further specimen may be dipterous but is poorly preserved. They represent several species which may well belong to unrelated genera. From the tentative identifications proposed below it appears that the larvae, if they had similar habits to Recent species, lived in a damp or fully aquatic, non-marine environment.

Suborder BRACHYCERA

Family STRATIOMYIIDAE Latreille, 1802

Dipterous larva: species 1

Fig. 20

DIAGNOSIS. Dipterous larva with the skin covered with minute plates, typical of the family Stratiomyidae.

DESCRIPTION. The minute plates are about the same size as some found on Recent Stratiomyidae larvae (Rozkošný 1973), with which these fossils have been compared. On the last segment of the larva there is a slight thickening which may represent the posterior spiracle. The mandibular sclerites have a hooked tip and appear as paired slender rods.

MATERIAL. In.59503 (W) (Fig. 20, part and counterpart), In.59475 (B), In.59484 (B).

DIMENSIONS. In.59503: length 14 mm, width 7 mm, mandibular sclerite 1.2 mm. In.59475: length 18 mm, width 6 mm. In.59484: length 16 mm, width 3.5 mm.

DISCUSSION. The broad similarity to Recent Stratiomyidae, particularly in the form of the surface sculpturing, is striking. Fossil Stratiomyidae adults are known from the Eocene/Oligocene and are very similar to Recent species, even having similar colour pattern. Many Recent Stratiomyidae larvae are aquatic and have a circle of hairs or two lobes on the posterior segment. The whole skin is rough or 'shagreened' and, in Recent species, the integument may be composed of hexagonal or oval plates which are of calcium carbonate. The function of this is not known but many species live in water rich in organic matter and thus with a low pH value. The calcium carbonate integument may well be an adaptation for survival in acid conditions which cannot be tolerated by other larvae not having this characteristic (McFadden 1967).

Fig. 20 Fly larva

Specimen In.59503. Specimen although an imago, marks at the posterior abdominal segment.

1902 Neuroptera
1951 Neuroptera
1954 Lepidoptera

DIAGNOSIS. Dipterous larva

DESCRIPTION. Typical of Recent Stratiomyidae and have a general appearance similar to previous specimens. The posterior mandibular sclerite and posterior spiracle.

MATERIAL. In.59503 (W)

DIMENSIONS. In.59503: length 14 mm, width 7 mm, mandibular sclerite 1.2 mm. In.59475: length 18 mm, width 6 mm. In.59484: length 16 mm, width 3.5 mm.

DISCUSSION. It is very similar to later instar or adult. In.59469: it is a dipterous larva with skin like modern Stratiomyidae.

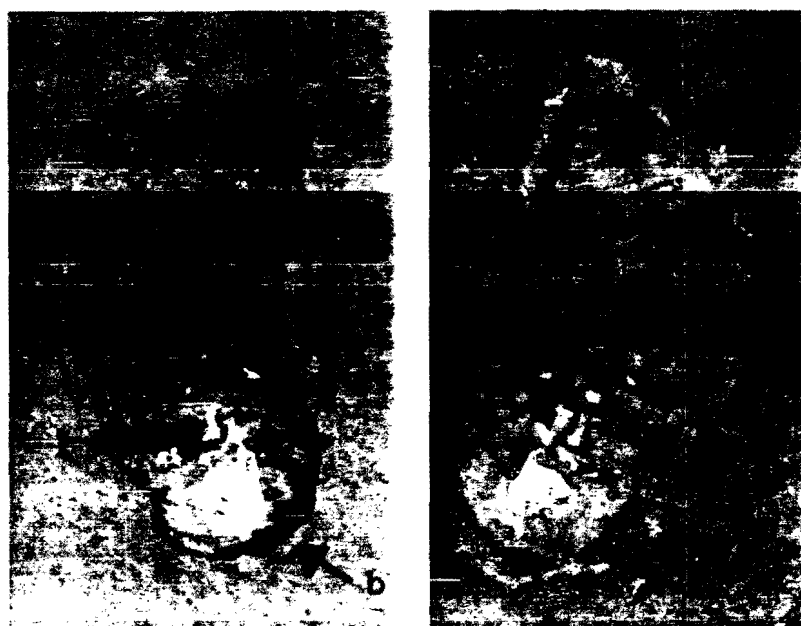


Fig. 20 Fly larva. Diptera species 1. In.59503, part and counterpart. $\times 4.5$. (a – mandibular sclerite; b – posterior spiracle).

Specimen In.59475 has the integument covered with minute plates and is broadly similar to In.59503. Specimen In.59484 is indistinct with no trace of the sclerotized mouthparts, although an impression of the cephalopharyngeal skeleton is visible. There are two small marks at the posterior end of the larva which may represent a short process on the last abdominal segment. This specimen is only tentatively associated with the previous two.

Dipterous larva: species 2

Fig. 21

- 1902 Neuróptero (= Odonata); Zeiller: pl. 1, fig. 4.
 1951 Neuróptero (= Odonata); Condal: pl. 5, fig. 1.
 1954 Lepidoptera larva; Teixeira: pl. 8, fig. 4a.

DIAGNOSIS. Dipterous larva with minute plates on the body, similar to Recent Stratiomyidae.

DESCRIPTION. The skin is heavily folded but the cover of minute platelets, broadly similar to Recent Stratiomyidae, is visible. The mandibular sclerites are longer than those of species 1 and have a gently curved apex. The preservation of this larva is not as good as some of the previous specimens and only a little surface detail can be seen, but there is a thickening on the posterior margin of the last abdominal segment which suggests that the larva had two posterior spiracles.

MATERIAL. In.59469 (B), In.49650 (W) (Fig. 21).

DIMENSIONS. In.59469: length 18 mm, width 5 mm, mandibular sclerite 3 mm (part and counterpart). In.49650: length 46 mm, width 13 mm, mandibular sclerite 6 mm.

DISCUSSION. It is difficult to tell if In.59469, which is larger than species 1 (In.59503), is a later instar or a different species. In.49650 is particularly large while being broadly similar to In.59469; it is included with the latter as species 2. All have the roughened ('shagreened') skin like modern Stratiomyidae.

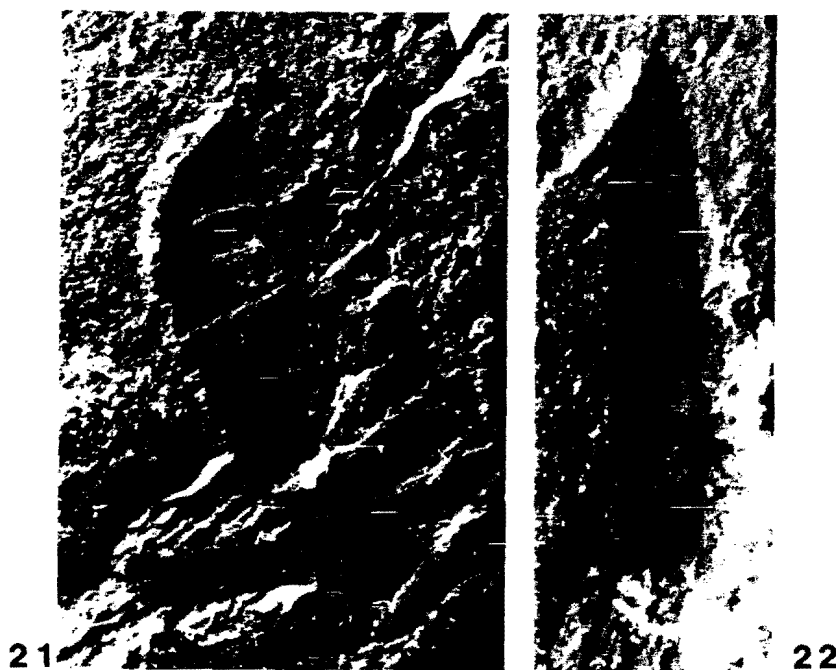


Fig. 21 Fly larva, Diptera species 2. In.49650, $\times 1.5$. Arrow indicates mandibular sclerite.
 Fig. 22 Fly larva, Diptera species 3. In.49656, $\times 4$.

Suborder CYCLORRHAPHA

Family SCIOMYZIDAE, *sensu* Hendel, 1902

Dipterous larva: species 3

Fig. 22

DIAGNOSIS. Dipterous larva with lateral tubercles on abdominal segments.

DESCRIPTION. Although the cephalic part is missing the shape is unmistakably dipterous. Clearly visible are three rows of tubercles on each side of the seven preserved segments and traces of tubercles (or spiracular structure?) on the last segment.

MATERIAL. In.49656 (W).

DIMENSIONS. Length 17 mm, width 5 mm (mandibular sclerite lost). Part and counterpart.

DISCUSSION. This larva is very similar to those of Recent species of *Dictya* (Sciomyzidae), a group of snail-killing flies with aquatic larvae (K.G.V. Smith, personal communication); the lateral processes are quite distinctive.

UNCERTAIN AFFINITIES

Dipterous larva: species 4

Fig. 23

DIAGNOSIS. Dipterous larva with long, slender mandibular sclerites.

DESCRIPTION. The long, slender mandibular sclerites are curved at the apex and both are clearly preserved. The body is covered with minute granules (smaller than the Stratiomyidae



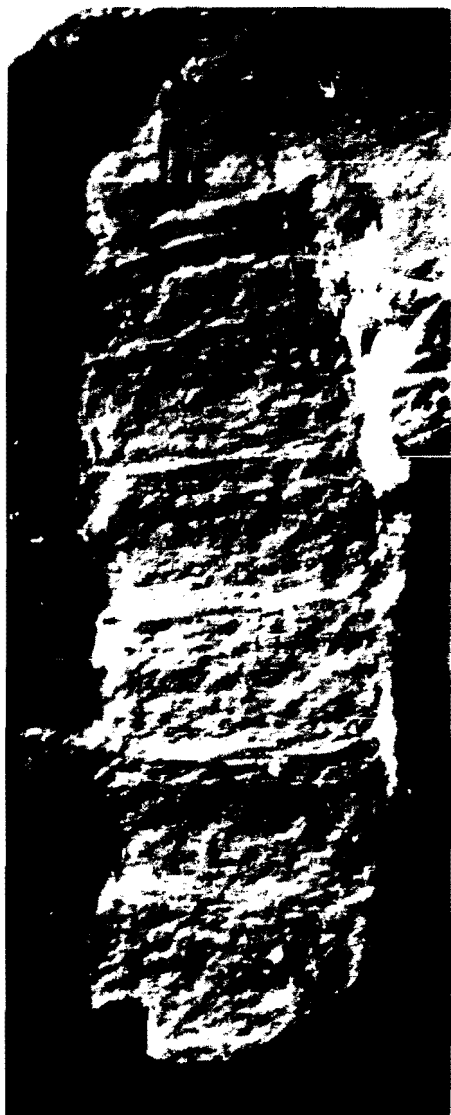
Fig. 23 Fly
 Fig. 24 Fly

platelets). On the faintly preserved

MATERIAL. In.594

DIMENSIONS. Length 4 mm, width 1 mm. Mandibular sclerite 4 mm

DISCUSSION. The sclerites are too close together on the segment; they may be of that of some R



23



24

Fig. 23 Fly larva, Diptera species 4. In.59455, $\times 5$. Arrow indicates mandibular sclerites.

Fig. 24 Fly larva, Diptera species 5. In.59467, $\times 6$.

platelets). On the fourth to eighth segments there are paired, round structures which are faintly preserved.

MATERIAL. In.59455 (B).

DIMENSIONS. Length 23 mm (excluding projecting mandibular sclerite), width 7 mm, mandibular sclerite 4 mm.

DISCUSSION. The lateral, round, paired, segmental structures along the body appear to be too close together, even allowing for compression, to be the two spiracles of a single segment; they may be short pseudopods. The general appearance of this larva is reminiscent of that of some Recent Ephydriidae or the aquatic muscid *Limnophora*. Further possibilities

are the larva of an aquatic member of the Dolichopodidae or Empididae. Although there is no sign on the specimens of the lateral or anal appendages even the possibility of it being the larva of one of the Athericidae should be considered (K. G. V. Smith, personal communication).

Dipterous larva: species 5

Fig. 24

DIAGNOSIS. Dipterous larva with minute surface granules.

DESCRIPTION. In this specimen the tip of the cephalopharyngeal skeleton is missing but at the base of it there is a short ridge at right angles to the sclerites which may be part of this cephalopharyngeal structure. On six of the body segments there are indistinct paired marks which could represent pseudopods. Further classification of this specimen is impracticable.

MATERIAL. In.59467 (B), part and counterpart.

DIMENSIONS. Length 17 mm, width 5 mm; mandibular sclerite lost.

Order HYMENOPTERA

Suborder STEPHANOIDEA

Family EPHIALTITIDAE Rohwer, 1920

Genus EPHIALTITES Meunier, 1903

TYPE SPECIES. *E. jurassicus* Meunier, by monotypy.

***Ephialtites jurassicus* Meunier, 1903**

Fig. 25

- 1903 *Ephialtites jurassicus* Meunier: 4, 9; fig. 1.
- 1951 *Ephialtites jurassicus* Meunier (*sic*); Condal: 55; pl. 3, fig. 2.
- 1954 *Ephialtites jurassicus* Meunier; Teixeira: 141.
- 1975 *Ephialtites jurassicus* Meunier; Rasnitsyn: 43.
- 1981 *Ephialtites jurassicus* Meunier; Hennig: 402.



Fig. 25 *Ephialtites jurassicus* Meunier (parasitic wasp). Holotype, $\times 4$. Specimen believed to be in Spain. After Meunier 1903: fig. 1.

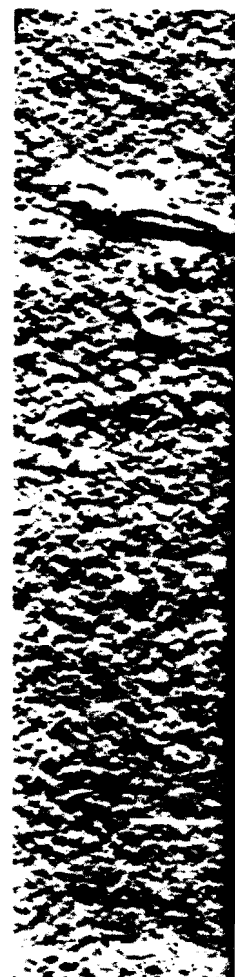


Fig. 26 Parasitic wasp, *Ephialtites jurassicus* Meunier.

The family Ephialtites (1975) to the Stepanov family. The published figure shows a long ovipositor and

In the introduction (155), reference is made to the Stepanov family. It had been considered that the Stepanov family had appeared in print.

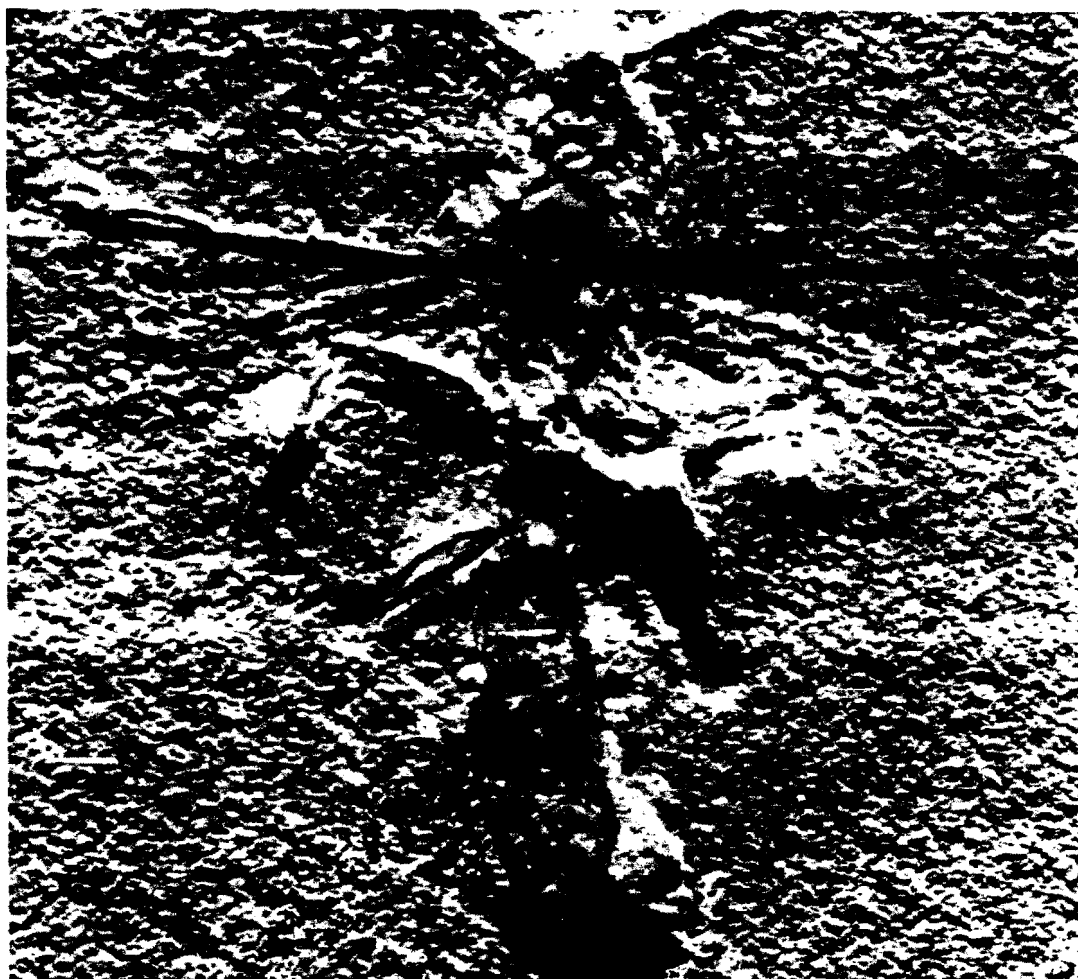


Fig. 26 Parasitic wasp, Ichneumonoidea. Part. $\times 6$. Specimen apparently lost; photograph: R. J. Wootton. (a - antenna; b - head; c - forewing costal margin; d - abdomen).

The family Ephialtitidae was described in the Ichneumonidea but transferred by Rasnitsyn (1975) to the Stephanoidea. We have not examined the original material but from the published figure there is no reason to doubt Rasnitsyn's interpretation. *E. jurassicus* has a long ovipositor and is much smaller (7.5 mm) than the apocritan wasp described below.

Suborder APOCRITA

Superfamily ICHNEUMONOIDEA

Ichneumonoidea, incertae sedis

Fig. 26

In the introduction by Morris to the monograph on fossil bees by Zeuner & Manning (1976: 155), reference is made to a sphecoid wasp fossil from the Jurassic of Lérida. This specimen had been considered by Manning as close to the ancestor of the bees. Burnham (1978: 119) commented on this, expressing some doubt about it. No other account of this specimen has appeared in print. The original specimen seen by Manning has not been re-examined but

through the kindness of Dr R. J. Wootton we have been able to study a series of photographs of the part and counterpart.

It is now considered more likely that this specimen is an ichneumonid wasp (M. Fitton & M. Day, personal communication). Fig. 26 is reproduced from Dr Wootton's photograph. The costal margin of the wing looks thickened, the antennae are long and the abdomen expanded. The insect was large (20 mm body length), bigger than most other known fossil ichneumonids known, and has the general appearance of the Recent *Opheltes glaucopterus* Linn. (a sawfly parasite), although it is not necessarily related to this species. The possible host-group of ichneumonids, sawflies, were certainly present from the early Triassic and are common in the Jurassic rocks of Asia (Rasnitsyn 1969). Currently the earliest known ichneumonid wasps are from the Lower Cretaceous (Rasnitsyn 1980).

SUPERFAMILY INDET.

Apocrita, incertae sedis

Fig. 27

Specimen In.60602 (W) is clearly a hymenopteran and certainly in the suborder Apocrita. Few details can be seen, although structures are visible on the tip of the abdomen. One hind-leg, showing possibly an enlarged femur, is present. The base of the forewing has been preserved (Fig. 27) but unfortunately not enough of it to place this specimen in a superfamily with confidence. What is preserved is similar to some extant sphecoids (Riek *et al.* 1970: fig. 37.31-2). The specimen (10 mm long) is longer than *Ephialtites*, but only half the size of the ichneumonid discussed above.

Discussion

At least two-thirds of the fifty fossil insects found in the Lérída deposit are aquatic nymphs or larvae, or adult insects derived from aquatic larvae.

It is interesting that all the aquatic juvenile forms found are either bottom-dwellers (Ephemeroptera) or perhaps in a few cases dwellers in thick aquatic vegetation (Diptera); none are powerful swimmers like Recent water-boatmen (Hemiptera) or water beetles (Coleoptera). Mobile aquatic adult insects may be absent because they could swim strongly against the current that swept in the juvenile forms, none of which can be classed as strong



Fig. 27 Wasp, Apocrita superfam. indet. In.60602, $\times 7.5$.

swimmers. This which form the environment with slightly damaged transported then in organic content at the edges of and are less frequent.

Cockroaches, with terrestrial might be found. For example, a aleyrodoid. So Orthoptera, which associated with would the Lepidoptera juveniles may have been in the water. Other groups may be randomly distributed consequently no mayfly nymphs. The presence of

Examination of there is small-scale no evidence of rock around the which would po

Fig. 28 Litho

swimmers. This presupposes that the insects were transported by water. The mayfly nymphs, which form the largest single group, are almost certainly derived from a fresh-water environment with a soft bottom in which they would have burrowed. The fossil nymphs are slightly damaged, which suggests they did not live at the site of deposition but were transported there. The Diptera larvae would in general require shallow non-saline water high in organic content; i.e. stagnant conditions. Many modern stratiomyid (Diptera) larvae occur at the edges of lakes or slow streams where the vegetation is rotting freely and accumulating, and are less frequent in running water.

Cockroaches, bugs, beetles and wasps are all insects which would be associated mainly with terrestrial vegetation and not dependent on close association with water, but equally might be found in vegetation near water. There is no size sorting of the terrestrial species. For example, among the Hemiptera there is a large palaeontinid as well as a small aleyrodoid. So far no Orthoptera or Lepidoptera have been found in the deposit. Orthoptera, which are common in many Toarcian (Lower Jurassic) deposits, would be associated with open bush country and would not necessarily be found near water; neither would the Lepidoptera. The absence of adult mayflies is particularly interesting. Aquatic juveniles may have been carried away from their original habitat, or deposition may have been in the wrong season for adults to be present – although the presence of adults from other groups makes this less likely. The insect remains in the Lithographic Limestone are randomly distributed (H. W. Ball, personal communication). Many are relatively intact and consequently not likely to have been carried far from the areas in which they lived. The mayfly nymphs are common and possibly lived in muddy water-courses entering the lagoon. The presence of some sizeable insects suggests a warm climate.

Examination of the individual pieces of rock on which fossil insects were found shows that there is small-scale lamination in an otherwise fine-grained and homogeneous limestone with no evidence of bioturbation and only a little current activity (Fig. 28). The surface of the rock around the fossil insects shows no signs of surface structures, infills or other evidence which would point to an exposed surface at any stage. The insect fauna includes a high

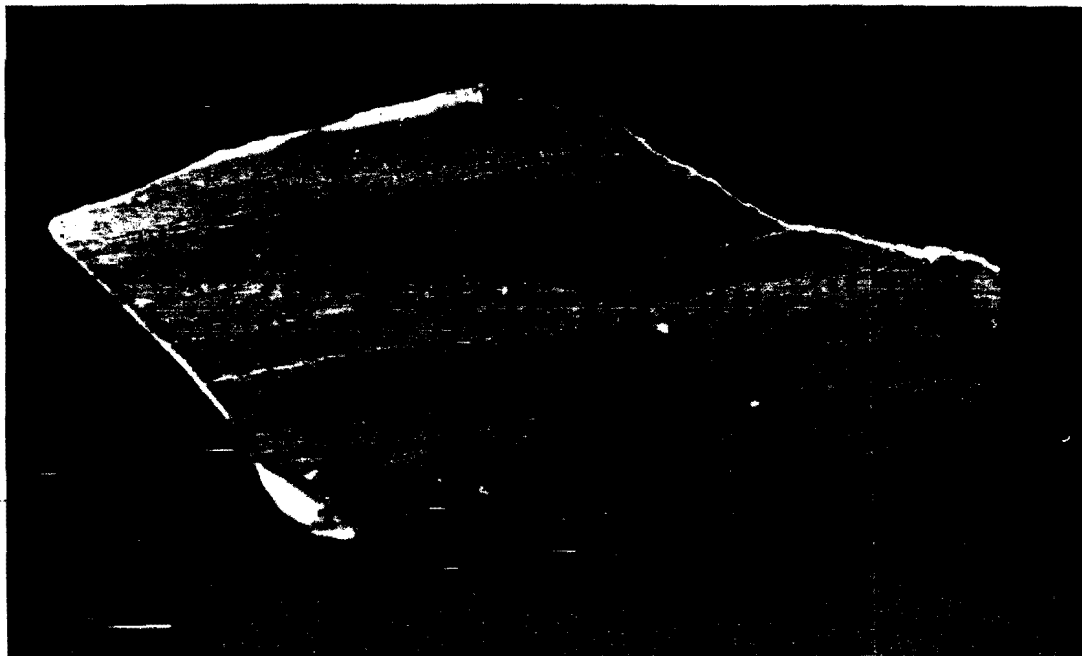


Fig. 28 Lithographic Limestone of Montsech: polished transverse section, $\times 2.5$. (In.59497).

proportion of the soft-bodied forms. This suggests the specimens were deposited under very tranquil and anaerobic conditions. The fossils occur infrequently in the rocks, not apparently concentrated into lenses, although none were actually collected *in situ* (H. W. Ball, personal communication). Very little plant debris is associated with the insects and this suggests either that they were brought in separately or that some sorting (perhaps based on differential rates of settling of the organic debris) has occurred.

Evidence presented by Shairer & Janicke (1970) suggests fossilization in water, completely undisturbed on the muddy bottom of a lake or lagoon. In several of the specimens, the wings are spread out horizontally and these are species where the living insect would have normally folded its wings when at rest. Cockroaches, for example, normally keep the hind wing tightly folded below the forewings when at rest whereas the fossil cockroach (Fig. 7, p. 388) clearly has its hind wings outstretched, suggesting that its wings were open when it flew or was blown into the depositional environment. Schairer & Janicke (1970: pl. 21) illustrate what appear to be the drag-marks of a washed-in dipterous larva.

The insect fossils were deposited sporadically on very fine calcareous mud, and that this mud was laid down in cycles can be inferred from the laminations (Fig. 28). The periodicity of the laminations is unknown. The incorporation of organic detritus is visualized as a gentle 'rain' of water-logged material; the insects are unlikely to have been deposited as the result of storms or flash-floods. The fineness of the sediment suggests off-shore deposition, or that only fine material normally entered the basin of deposition. Such tranquil conditions are more likely in deeper water.

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The following were very patient in answering our enquiries, often about very small fragments of insects: Dr P. C. Barnard, Dr J. Cox, Mr M. C. Day, Mr W. R. Dolling, Dr M. G. Fitton, Mr D. Hollis, Dr B. Levey, Miss C. M. F. von Hayek, Dr W. J. Knight, Dr R. J. Lincoln, Mrs J. A. Marshall, Mr J. H. Martin, Dr L. A. Mound, Mr R. D. Pope, Mr K. G. V. Smith, Mr R. T. Thompson, Dr D. J. Williams, Dr A. R. Woolley; to all we offer our thanks.

The photographs, unless otherwise stated, were taken by the Staff Photographer, British Museum (Natural History), the stereoscans by Mr D. Claugher. Original line drawings by E. A. Jarzembowski.

References

- Arnoldi, L. V. 1977. In Arnoldi, L. V., Zherikhin, V. V., Nikritin, L. M. & Ponomarenko, A. G., *Mezozoiskie Zhestokokrylye. Trudy paleont. Inst.*, Moscow, **161**: 1-203, 14 pls.
- Bekker-Migdisova, E. E. 1949. Mesozoic Homoptera of central Asia. *Trudy paleont. Inst.*, Moscow & Leningrad, **22**: 1-68, 1 pl.
- Bode, A. 1953. Die Insektenfauna des ostniedersächsischen Oberen Lias. *Palaeontographica*, Stuttgart, (A) **103**: 1-375, pls 1-15.
- Brenner, P., Goldmacher, W. & Schroeder, R. 1974. Ostrakoden und Alter der Plattenkalke von Rubies (Sierra de Monsech, Prov. Lérida, N.E. Spanien). *Nouvelles Jb. Geol. Paläont. Mh.*, Stuttgart, **1974** (8): 513-524.
- Brodie, P. B. 1845. *A history of the fossil insects in the Secondary rocks of England*. xviii + 130 pp, 11 pls. London.
- Burnham, L. 1978. Survey of social insects in the fossil record. *Psyche, Camb.*, Cambridge, Mass., **85**: 85-133.

Calatayud, D. 1953. Isona.

Chernova, O. (Chleniston) 1977. [D.] Jurassic of Paleont. J.

Condal, L. F. min. Esp.

Crowson, R. A. evidence. A

—, Rolfe, W. The Chelice (eds). The

Edmunds, G. F. Minneapolis

Evans, J. W. 1965-258.

Eschscholtz, J. Fraser, F. C. 1

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Handlirsch, A. 13 tabs, 14

Hennig, W. Chichester.

Hinton, H. E. 395-409.

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Kukalova, J. McAlpine, J. Can. Ent.

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— 1979. Eve (eds). Princ

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McFadden, M. Washington

Metcalf, Z. I (Suppleme

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Myers, J. G. 365-472.

Ponomarenko Pritykina, L. nasekomv

Rasnitsyn, A. 123, 184 p 1979].

- Calatayud, D. J. R. B., Alavedra, D. V. M., de Galvez-Canero, D. A., Luna, G. & de Benito, D. F. 1953. Isona (Lérida). *Mapa geol. España, 1:50,000* (expl. Hoja 290). 113 pp., pls 1-23. Madrid.
- Chernova, O. A. 1962. Otryad Ephemeroptera. In Rohdendorf, B. B. (ed.), *Osnovy Paleontologii* 9 (Chlenistonogie, Trakheinye i Khelitserovye): 55-64. Akademi Nauk SSSR, Moscow.
- 1977. [Distinctive new mayfly nymphs (Ephemeroptera: Palingeniidae, Behningiidae) from the Jurassic of Transbaikalia.] *Paleont. Zh.*, Moscow, 1977 (2): 91-96, pl. 10. [In Russian; Engl. transl. *Paleont. J.*, Washington, 11 (2): 221-226, pl. 10].
- Condal, L. F. 1951. Nuevos hallazgos en el jurásico superior del Montsech. *Notas Comun. Inst. geol. min. Esp.*, Madrid, 23: 45-62, pls 1-10.
- Crowson, R. A. 1975. The evolutionary history of Coleoptera as documented by fossil and comparative evidence. *Atti Congresso naz. ital. Ent.*, Florence, 10: 47-90.
- , Rolfe, W. D., Smart, J., Waterstone, C. D., Willey, E. C. & Wootton, R. J. 1967. Arthropoda: The Chelicerata, Pycnogonida, Palaeoisopus, Myriapoda, and Insecta. In Harland, W. B. et al. (eds), *The Fossil Record*: 499-528. London.
- Edmunds, G. F., Jensen, S. L. & Berner, L. 1976. *The Mayflies of North and Central America*. 330 pp. Minneapolis, Univ. Minnesota Press.
- Evans, J. W. 1956. Palaeozoic and Mesozoic Hemiptera (Insecta). *Aust. J. Zool.*, Melbourne, 4 (2): 165-258.
- Eschscholtz, J. F. von 1829. *Zoologischer Atlas* . . . (&c.), 1. Berlin.
- Fraser, F. C. 1957. *A reclassification of the order Odonata*. 133 pp. Sydney, R. Zool. Soc. N.S.W.
- Garrido-Megias, A. & Rios Aragües, L. M. 1972. Síntesis geológica del Secundario y Terciario entre los ríos Cinca y Segre. *Boln geol. min. Inst. geol. min. Esp.*, Madrid, 83: 1-47.
- Handlirsch, A. 1906-08. *Die fossilen Insekten und die Phylogenie der rezenten Formen*. ix + 1430 pp., 15 tabs, 14 figs, 51 pls. Leipzig.
- Hennig, W. 1981. *Insect phylogeny* (transl. Pont, A. with additional footnotes). xxii + 514 pp. Chichester.
- Hinton, H. E. 1948. On the origin and function of the pupal stage. *Trans. R. ent. Soc. Lond.*, 99: 395-409.
- Imms, A. D., Richards, O. W. & Davies, R. G. 1970. *A general textbook of Entomology* (9th edn). x + 886 pp. London.
- Kukalova, J. 1968. Permian mayfly nymphs. *Psyche, Camb.*, Cambridge, Mass., 75: 310-327.
- McAlpine, J. F. 1970. First record of a calyptate fly in the Mesozoic Era (Diptera: Calliphoridae). *Can. Ent.*, Ottawa, 102: 342-345.
- McCafferty, W. P. 1975. The burrowing mayflies of the United States (Ephemeroptera). *Trans. Am. ent. Soc.*, Philadelphia, 101: 447-504.
- 1979. Evolutionary trends among the families of the Ephemeroidea. In Pasternak, K. & Sowa, R. (eds), *Proc. II int. Conf. Ephemeroptera*, 1975: 45-49. Warsaw, Polska Akademia Nauk.
- & Edmunds, G. F. 1976. Redefinition of the family Palingeniidae and its implications for the higher classification of the Ephemeroptera. *Ann. ent. Soc. Am.*, Washington, 69: 486-490.
- McFadden, M. W. 1967. Soldierfly larvae in America north of Mexico. *Proc. U.S. natn. Mus.*, Washington, 121: 1-72.
- Metcalf, Z. P. & Wade, V. 1966. *General catalogue of the Homoptera: fossil Homoptera 1* (Supplement). v + 245 pp. Raleigh, North Carolina State Univ.
- Meunier, F. 1902. Un nuevo cicadido del Kimeridgense de la Sierra del Montsech, Provincia de Lérida (Cataluña). *Mems R. Acad. Cienc. Artes Barcelona*, 4 (18): 269-274, 1 pl.
- 1903. Nuevas contribuciones á la fauna de los himenópteros fósiles. *Mems R. Acad. Cienc. Artes Barcelona*, 4 (34): 4-12, 3 figs. [In Spanish and French].
- 1904. Sur une Cicadine du Kiméridgien de la Sierra del Montsech (Catalogne). *Feuille jeun. Nat.*, Rennes & Paris, 34: 119-121.
- 1914. Un Blático y una larva de Odonato del Kimeridgense de la Sierra del Montsech (Lérida). *Mems R. Acad. Cienc. Artes Barcelona*, 11 (9): 121-126, 2 pls.
- Myers, J. G. 1928. The morphology of the Cicadidae (Homoptera). *Proc. zool. Soc. Lond.*, 1928: 365-472.
- Ponomarenko, A. G. 1977. See Arnoldi, L. V. 1977.
- Pritykina, L. N. 1980. Otryad Libellulida. In Rodendorf, B. B. (ed.), *Istoricheskoe razvitie klassa nasekomykh. Trudy paleont. Inst.*, Moscow, 175: 128-134, figs 67-69.
- Rasnitsyn, A. P. 1969. [Origin and evolution of lower Hymenoptera.] *Trudy paleont. Inst.*, Moscow, 123. 184 pp., 8 pls. [In Russian; Engl. transl. U.S. Agricultural Research Service, Washington D.C., 1979].

- 1975. Vysshie pereponchatokrylye Mezozoya. *Trudy paleont. Inst.*, Moscow, 147: 1-132, pls 1-8.
- 1980. Otryad Vespida. In Rodendorf, B. B. (ed.), *Istoricheskoe razvitie klassa nasekomykh. Trudy paleont. Inst.*, Moscow, 175: 122-127, figs 62-66.
- Riek, E. F. et al. 1970. Hymenoptera. In Waterhouse, D. F. (ed.), *The insects of Australia*: 867-959. Melbourne (C.S.I.R.O.).
- Rodendorf, B. B. 1964. Istoricheskoe razvitie dvukrylykh nasekomykh. *Trudy paleont. Inst.*, Moscow, 100: 1-312.
- Rozkošný, R. 1973. The Stratiomyidae (Diptera) of Fennoscandia and Denmark. *Fauna ent. scand.*, Gadstrup, 1: 1-140.
- Schaefer, L. 1949. Les Buprestides de France: Famille LVI. *Miscnea ent.*, (Supp.), Paris. 511 pp., 25 pls.
- Schairer, G. & Janicke, V. 1970. Sedimentologisch-paläontologische Untersuchungen an den Plattenkalken der Sierra de Monsech (Prov. Lérida, N.E.-Spanien). *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, 135 (2): 171-189, pls 20-24.
- Schlee, D. 1970. Insekten fossilen aus der unteren Kreide - 1. Verwandtschaftsforschung an fossilen und rezenten Aleyrodina (Insecta, Hemiptera). *Stuttg. Beitr. Naturk.*, (A) 213: 1-72.
- Teixeira, C. 1954. La flore fossile des calcaires lithographiques de Santa Maria de Meyá (Lérida, Espagne). *Bolm Soc. geol. Port.*, Lisbon, 11: 139-152, pls 1-8.
- Vishnyakova, V. N. 1968. Mezozoiskie tarakany s naruzhnym yatsekladom i osobennosti ikh razmnozheniya (Blattodea). In Rodendorf, B. B., (ed.), *Yurskie nasekomye Karatau*: 55-86, pls 6-8. Moscow, Akademii Nauk SSSR.
- Woodward, T. E., Evans, J. W. & Eastop, V. F. 1970. Hemiptera. In Waterhouse, D. F. (ed.), *The insects of Australia*: 387-457. Melbourne (C.S.I.R.O.).
- Wootton, R. J. (1961). *Some Mesozoic Hemiptera*. Ph.D. thesis, Univ. of London (unpubl.).
- 1971. The evolution of Cicadoidea (Homoptera). *Int. Congr. Ent.*, Moscow (1968), 1: 318-319.
- 1972. The evolution of insects in freshwater ecosystems. In Clark, R. B. & Wootton, R. J. (eds), *Essays in Hydrobiology*: 69-82. University of Exeter.
- 1981. Support and deformability in insect wings. *J. Zool., Lond.*, 193: 447-468.
- Zeiller, R. 1902. Sobre algunas impresiones vegetales del Kimeridgense en Santa María de Meyá, provincia de Lérida (Cataluña). *Mems R. Acad. Cienc. Artes Barcelona*, (3) 4 (26): 345-356, pls 1-2.
- Zeuner, F. E. & Manning, F. J. 1976. A monograph on fossil bees (Hymenoptera: Apoidea). *Bull. Br. Mus. nat. Hist.*, London, (Geol.), 27 (3): 149-268, 4 pls.
- Zherikhin, V. V. 1978. Razvitie i smena Melovykh i Kainozoiskikh faunisticheskikh kompleksov (Trakheinye i Khelitserovye). *Trudy paleont. Inst.*, Moscow, 165: 1-197.
- 1980. Klass Insecta. In Menner, V. V. (ed.), *Razvitie i smena bespozvonochnykh na rubezhe Mezozoya i Kainozoya*: 40-97. Moscow, Nauka.