

**EARLY CRETACEOUS ZYGOPTEROIDS OF SOUTHERN ENGLAND,
WITH THE DESCRIPTION OF *CRETACOENAGRION ALLENI*
GEN. NOV., SPEC. NOV. (ZYGOPTERA: COENAGRIONIDAE;
"ANISOZYGOPTERA": TARSOPHLEBIIDAE, EUTHEMISTIDAE)**

E.A. JARZEMBOWSKI

Booth Museum of Natural History,
Dyke Road, Brighton, BN1 5AA, United Kingdom

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The remains of damselflies are infrequent in the early Cretaceous (Wealden) beds of south-east England but include some interesting forms: *Cretacoenagrion alleni* gen. n., sp. n. (Coenagrionidae) is one of the earliest records of this important extant family; "Mesozoic Anisozygoptera" include *Tarsophlebia?* sp. (Tarsophlebiidae) and *Euthemis* sp. (Euthemistidae), the latter comprising the only European and Cretaceous record of this extinct family. The infrequency of damselflies and lack of larval Odonata generally in the English Wealden is attributed to saline incursions into the basin of deposition.

INTRODUCTION

The remains of Odonata are frequent in the early Cretaceous Wealden Series of southern England, especially in the Weald Clay Group, and include Anisoptera, Zygoptera and Mesozoic Anisozygoptera (JARZEMBOWSKI, 1984; 1988a, 1988b). The remains are predominantly wing fragments of Anisoptera or Anisoptera-like forms although body parts also occur; Zygoptera (s.s.) constitute only 6% of the remains (JARZEMBOWSKI, 1987). The Wealden Zygoptera (Lestomorpha: PRITYKINA, 1980) include one of the earliest Coenagrionidae, *Cretacoenagrion alleni* gen. n., sp. n. This family was considered to be no older than the Miocene as recently as CARLE (1982), a difference of a 100 million years (Ma). At the present day, the suborder Anisozygoptera is represented only by two species in the Asian genus *Epiophlebia*; however, a number of extinct Mesozoic families have been placed in this suborder including Tarsophlebiidae (CARPENTER, 1954) and Euthemistidae (PRITYKINA, 1968). These families have

not been described previously from the Cretaceous of north-west Europe although they were reported briefly by JARZEMBOWSKI (1988a). Tarsophlebiidae are familiar Odonata from the Upper Jurassic Solnhofen Limestone of Bavaria (HANDLIRSCH, 1925) but Euthemistidae are otherwise known only as wings from the Upper Jurassic of Kazakhstan (Karatau; PRITYKINA, 1968).

I have followed PRITYKINA (1980) and treated these Odonata as damselflies, especially as CARLE (1982) considered tarsophlebiids to be zygopteroids and PRITYKINA (1968) believed Euthemistidae were related to Tarsophlebiidae.

The geology and palaeoenvironment of the Wealden beds have been summarised briefly by JARZEMBOWSKI (1988a) and are discussed in depth by ALLEN (in press).

With the exception of one specimen from the Wessex sub-basin (see below) the fossils are from the Weald of south-east England and are deposited in the Booth Museum of Natural History (B.M.o.N.H.) and British Museum (Natural History) (B.M.N.H.).

The drawing conventions follow JARZEMBOWSKI (1980) and for general venation abbreviations see Figure 12.

NEW WEALDEN ZYGOPTERA

Few, if any, true damselflies have been described yet from the Lower Cretaceous. Several specimens have been found in the Wealden, but only one is sufficiently well preserved for description.

COENAGRIONOIDEA

Coenagrionidae Kirby, 1890

CRETACOENAGRION GEN. N.

Coenagrionidae gen. n.; JARZEMBOWSKI, 1987; p. 47.

Type species. — *Cretacoenagrion alleni* sp. n.; Weald Clay, south-east England.

Etymology. — After Latin stem for Cretaceous and tropical extant genus.

Diagnosis. — An early Cretaceous species of Coenagrionidae with an open discoidal cell.

Species included. — Type species.

CRETACOENAGRION ALLENI SP. N.

Figures 1, 4a-b

For previous references see JARZEMBOWSKI, 1988a, p. 2.

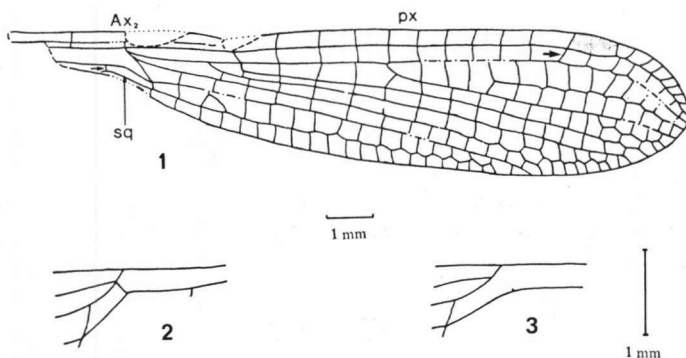
Material. — **Holotype:** B.M.o.N.H., 014884-5. — Clockhouse (Butterley) Brickworks, lat. 51°8'N, long. 0° 19'W. Lower Weald Clay, (?) late Hauterivian (WORSSAM, 1978).

Etymology. — After the Wealden sedimentologist Professor Perceval Allen F.R.S.

Diagnosis. — As for genus.

Description. — A single right wing is known. Venation as in Figure 1. Nine postnodals (Px): discoidal cell open basally; subquadrilateral (sq) present; 1A separates from posterior wing margin midway between primary antenodals (Ax 1-2) with anal crossing (Ac) slightly distal of point of separation; anal field with single row of cells. Wing membrane unpigmented; veins brown or black; pterostigma (p) elongate, brown, with brace vein (br).

Measurements (in mm). — Maximum length 14.6, width 3.1.



Figs. 1-3. Details of venation: (1) Wing venation of *Cretacoenagrion allenii* gen., sp. n., holotype (large and small horizontal arrows indicate Br and Ac, resp.); — (2) Normal discoidal cell in *Agriocnemis* (after FRASER, 1957); — (3) Aberrant discoidal cell in indeterminate agriocnemine, B.M.N.H.

Affinities and Remarks. — The Wealden fossil agrees with crown group Coenagrionoidea in that: (1) the wing is petiolate; — (2) the wing is hyaline; — (3) two antenodals are present; — (4) the arculus is aligned with Ax2; — (5) the postnodals (Px) are aligned with crossveins behind them; — (6) 1A is fused basally with the posterior wing margin; — and (7) IR3 and R4+5 arise nearer to the nodus than to the arculus.

It also agrees with extant Coenagrionidae in that: (1) 1A is present; — (2) CuP is present; — (3) the arculus is level with Ax2; — and (4) MA and IR3 are zig-zagged (distally).

It differs only in that the discoidal cell is closed in all crown group coenagri-

onoids, although in coenagrionids the cell has a sharply acute angle as in the fossil (DAVIES, 1981).

FRASER (1957, p.15) considered the discoidal cell to be the most important area of the Odonata wing for purposes of classification. An open discoidal cell, similar to that in the Wealden wing, is found in extant Zygoptera in *Hemiphlebia*

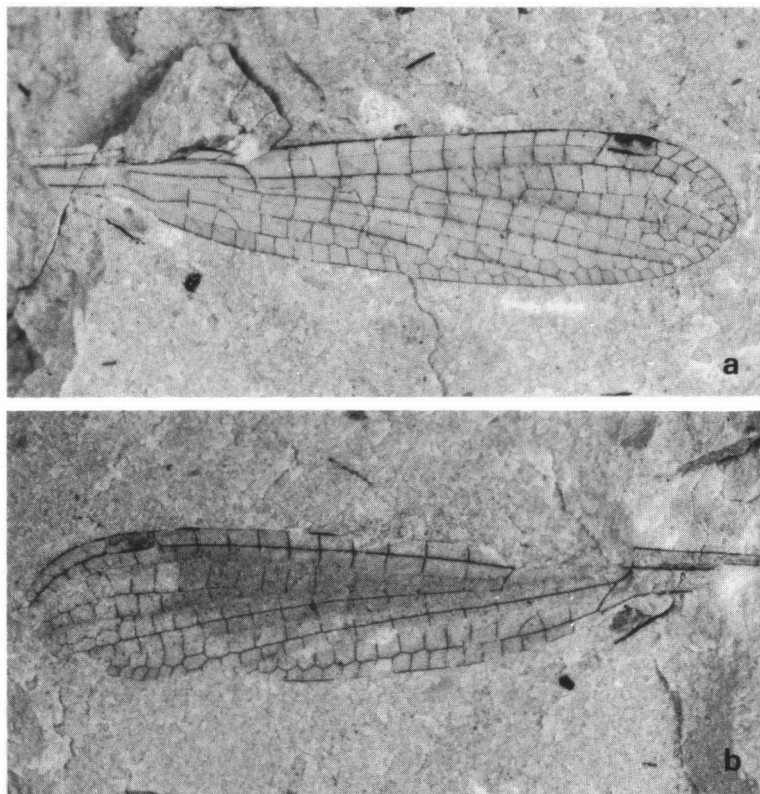


Fig. 4. *Cretacoenagrion alleni* gen. n., sp. n., part (a) and counterpart (b) of the holotype.

mirabilis Selys and *Chorismagrion risi* Morton (FRASER, 1957); it is also found in the extinct Jurassic Oreopteridae (PRITYKINA, 1968). Fraser considered an open discoidal cell to be a primitive (plesiomorphic) character, therefore this cell is no clue to the relationships of the Wealden fossil. Furthermore, the fossil is readily distinguished from *Hemiphlebia* in the number and position of the postnodals and the position of Ax2 (RODENDORF, 1962); from *Chorismagrion* in the position of the base of R4+5 (FRASER, 1957); and from

Oreopteridae in the more basal position of the nodus (PRITYKINA, 1968).

CARLE (1982) took the opposite view to Fraser: he considered that an open discoidal cell ("proximally open quadrangle" in his terminology) is an advanced character, though likely to arise independently in different zygoteroid groups. In Carle's interpretation, an open discoidal cell is an apomorphy due to parallelism, and again cannot be used to determine the relationship of the Wealden fossil.

Extant coenagrionids are reported to have closed discoidal cells, but I have observed an open cell in an unidentified species of *Agriocnemidinae* from Indonesia in the B.M. N.H. (T. Enim, 26-VII-1976). This raises the possibility that an open cell may occur occasionally as an aberration. In the *agriocnemidine* specimen, the cell is closed in three wings in the normal manner as in *Agriocnemis* (Fig. 2), but not in the right hindwing where it is open (Fig. 3). Close examination showed the presence of a small portion of the basal crossvein at right angles to CuP, Fig. 3). The Wealden fossil shows no trace of a basal crossvein and cannot be considered an aberration.

From the above discussion, the open discoidal cell serves to separate the Wealden fossil from other coenagrionids, but this character is of uncertain phylogenetic value. The Wealden wing agrees with *Coenagrionidae* in other venational characters and I am therefore placing it in this family. HENNIG (1981) considered it odd that no Mesozoic species of this family had been described because Fraser considered *Coenagrionidae* to be a comparatively primitive family of *Zygoptera*. The Wealden find answers Hennig's query and supports Fraser's view. If Fraser's interpretation of the discoidal cell is correct, then the Wealden specimen is not only one of the earliest, but also the most primitive coenagrionid wing currently known. However, if Carle's interpretation is correct, then the Wealden wing is already specialised and more primitive coenagrionids should turn up in the early Cretaceous, or even the Jurassic, with closed discoidal cells. RASNITSYN (1988) and DIMITRIEV & ZHERIKHIN (1988) have recently reported the family as occurring in the late Jurassic and a description is awaited with interest.

NEW WEALDEN "ANISOZYGOPTERA"

Two Wealden wings, one from the Weald Clay and one from the Durlston Formation, can be assigned to the extinct *Tarsophlebiidae*, and a third from the Weald Clay to the *Euthemistidae*. Cretaceous *Tarsophlebiidae* are otherwise known from a single record in the early Cretaceous of the U.S.S.R. (ZHERIKHIN, 1980). The only other record of *Euthemistidae* is from the Upper Jurassic of Kazakhstan (PRITYKINA, 1968). Pritykina considered this family to be related to *Tarsophlebiidae* and placed it in the same superfamily "*Tarsophlebiidae*", which should be changed to *Tarsophlebioidea* in accord with Recommendation 29A of the International Code of Zoological Nomenclature (3rd ed., 1985).

TARSOPHLEBIOIDEA

Tarsophlebiidae Handlirsch, 1906

TARSOPHLEBIA HAGEN, 1866

Type species. — *Heterophlebia eximia* Hagen, 1862; Upper Jurassic, Bavaria; cf. Figs 6, 8, 11.

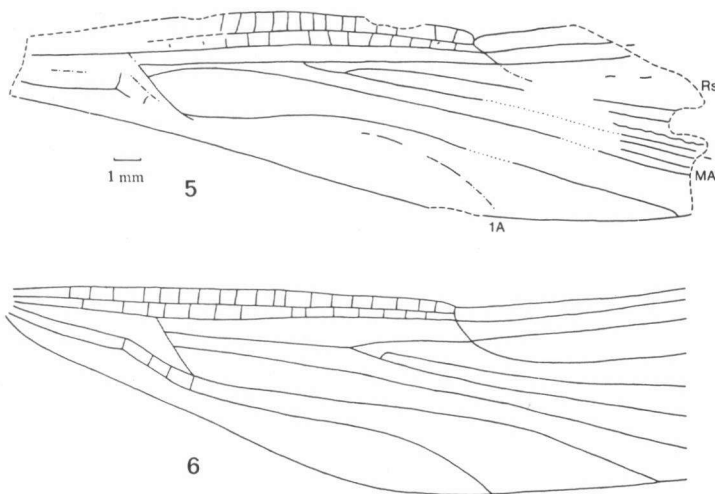
TARSOPHLEBIA? SP.

Figures 5, 7, 9

Material. — B.M. N.H., In. 64641, CLEMENTS (1969) Bed 175, Durlston Bay, lat. 50°36'N, long. 1°57'W; — B.M.o.N.H., 014886, Lower Weald Clay, same locality as *Cretacoenagrion alleni* gen. n., sp. n.

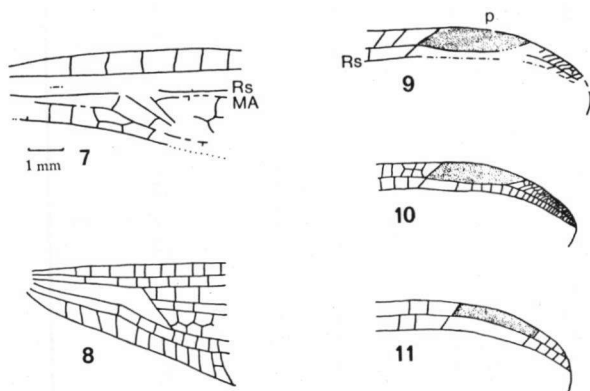
Affinities and Remarks. — The Wealden fossils are referred to Tarsophlebiidae because they show the following diagnostic wing features of the family: (1) the pterostigma is well developed (Fig. 9); — (2) the discoidal cell is merged with the medial cell, together forming a distinctly curved pointed area devoid of crossveins (Figs 5, 7); — and (3) vein 1A nearly reaches the middle of the posterior wing margin (Fig. 5) (RODENDORF, 1962).

The two late Jurassic genera in this family, *Tarsophlebia* Hagen and *Turanophlebia* Pritykina, differ in (1) the form of the discal cell in the hindwing; — (2)



Figs 5-6. Longitudinal venation and antennodorsals of forewings: (5) *Tarsophlebia*? sp., Weald Clay; — (6) *Tarsophlebia eximia* (Hagen), Solnhofen Limestone (after HANDLIRSCH, 1925), wing 33 mm long.

the width of the anal area; — and in (3) general density of venation (PRITYKINA, 1968). It is not possible to determine (1) in the Wealden material because only forewings are known. I am uncertain about (2) because the anal area is different in width in the fore and hindwings of *Tarsophlebia* (RODENDORF,



Figs 7-11. Forewing base (Figs 7-8) and pterostigmal areas (p) (Figs 9-11): (7, 9) *Tarsophlebia*? sp., Durlston Formation; — (8, 11) *Tarsophlebia eximia* (Hagen), Solnhofen Limestone (after HANDLIRSCH, 1925); — (10) *Turanophlebia martynovi* Pritykina, Upper Jurassic, Karatau (after PRITYKINA, 1968).

1962, fig. 165) as in many other Odonata and *Turanophlebia* is based on hindwings (PRITYKINA, 1968, 1977). RODENDORF (1962) considered that *Tarsophlebia* was distinguished by the presence of large cells in the centre of the wing around the branches of Rs, but this is also the case in *Turanophlebia* (PRITYKINA, 1968, fig. 14). With regard to (3), comparison of the hindwings of *Turanophlebia martynovi* (loc. cit.) and *Tarsophlebia eximia* (HANDLIRSCH, 1925, fig. 134) shows that there are more small cells in the apical part of the wing in the former than in the latter (Fig 10, 11). *T. martynovi* shows more small cells (i.e. a denser venation) in the subcostal area distal of the pterostigma than the specimen from the Durlston Formation (Fig. 9). I am therefore placing the Wealden material tentatively in the genus *Tarsophlebia*. The Wealdon wings are unusual in that MA is curved anteriorly in its basal portion (Figs 5, 7) and may belong to a distinct species. Unfortunately, HANDLIRSCH (1906-08) did not figure this venational feature in the various species briefly described by him.

Euthemistidae Pritykina, 1968

EUTHEMIS PRITYKINA, 1968

Type species. — *Euthemis multivenosa* Pritykina, Upper Jurassic, Karatau, U.S.S.R., cf. Fig. 13.

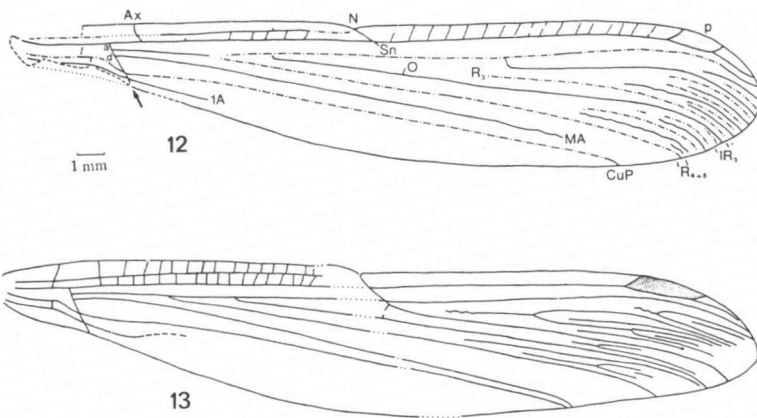
EUTHEMIS SP.

Figure 12

Material B.M.o.N.H., 014888-9. — Horizon and locality as *Cretacoenagrion allenii* gen. n., sp. n.

Affinities and Remarks — A unique forewing from the Weald Clay shows the following diagnostic wing features of this family (Fig. 12): (1) the wing is of "medium size"; — (2) the wing is narrow; — (3) the base of vein R4+5 is well separated from the base of vein IR3; — (4) the base of R4+5 is approximately midway between the base of IR3 and the arculus; — (5) there is a well-defined line of veins from R to the posterior wing margin in the basal part of the wing; — (6) the vena obliqua (O) is distal of the nodus (N); — (7) the discoidal cell is open; — and (8) vein 1A is short and weakly S-shaped.

PRITYKINA (1968) gave two other diagnostic family characters: there are two thickened complete antenodals in the vicinity of the arculus and numerous incomplete antenodals are present. In the Wealden specimen, some of the numerous incomplete antenodals are preserved, as well as a thickened complete antenodal (Ax) in the vicinity of the arculus as in *E. multivenosa* (cf. Fig. 13).



Figs 12-13. Longitudinal venation and antenodals: (12) *Euthemis* sp., Weald Clay, including postnodals (a: arculus, d: discoidal cell; arrow: line of veins from R to the posterior wing margin); — (13) *Euthemis multivenosa* Pritykina, Upper Jurassic, Karatau (after PRITYKINA, 1968).

PRITYKINA (1968) proposed the following generic characters for *Euthemis*: (1) 19-20 costal and subcostal antenodals are present which do not coincide; — (2) R3 commences from the posterior end of the subnodus (Sn); — (3) IR3 commences half way between the nodus (N) and arculus; — (4) R is joined to the posterior margin by three veins (arculus, part of 1A, and a crossvein from 1A to the posterior margin) which are thickened and form a line across the wing; — and (5) the anal area is less than a quarter of the wing length. Only a few antenodals are preserved in the Wealden specimen, and detailed comparison is therefore impossible, but they do resemble those of *E. multivenosa* (Figs 12, 13).

The posterior part of Sn and the basal portion of R3 are not preserved in the Wealden specimen, but could be contiguous (Fig. 12). Compared with *E. multivenosa*, the base of IR3 is a little nearer the nodus than the arculus in the Wealden specimen, but this is also the case in *Euthemis cellulata* PRITYKINA (1968, fig. 15) from Karatau.

Generic character (4) is the same as family character (5) and is present in the Wealden specimen.

Generic character (5) is difficult to observe because vein 1A merges distally with the numerous cells between vein CuP and the posterior margin of the wing in both the Wealden specimen and Pritykina's figures of the Karatau material. However, the recognisable part of 1A in both the Wealden specimen and *E. multivenosa* certainly extends to about a quarter of the wing length.

PRITYKINA (1968) described two species of *Euthemis* and distinguished them on: (1) the number of antenodal and postnodal crossveins; — (2) the general density of crossveins; — and on (3) the basal width of the median and cubital areas being combined. I cannot see the difference in (3) from Pritykina's figures. (1) and (2) are difficult to determine in the Wealden specimen because the crossveins are poorly preserved. However, about 17 postnodals (Px) may be discerned (Fig. 12) compared with 25 in *E. multivenosa* and 18 in *E. cellulata*. On the number of postnodals, the Wealden species is thus nearer to *E. cellulata*, and it also resembles the latter species in the position of the base of vein IR3 (see above). However, the Wealden wing is only 28 mm long compared with 48 mm in *E. multivenosa* and 45 mm in *E. cellulata*. It is outside the normal range of intraspecific size variation in Odonata (Mr S.J. Brooks, pres. comm.) and therefore probably represents a separate species. However, the discovery of a more detailed impression is awaited prior to formal naming.

CONCLUSION

The fossils found so far suggest that there would have been a diverse Odonata fauna in southern England in early Cretaceous times. However, larvae have not been recorded with certainty (JARZEMBOWSKI, 1987). ALLEN (1976, 1981) considered that the Wealden clay formations — which have yielded the Odonata

fossils — were often deposited during saline incursions into the Wealden basin. A dearth of local freshwater habitats would account for lack of larvae. The young stages possibly lived further north towards Londinia or even west towards Cornubia, land areas which supplied the Wealden freshwater run-off according to Allen. The predominance of dragonfly over damselfly remains (see Introduction) may reflect the former's greater ability for sustained flight away from larval habitats.

Early Cretaceous Zygoptera were previously hardly known. The discovery of *Cretacoenagrion alleni* gen. n., sp. n. may yet result in a re-appraisal of current views of Odonata phylogeny: the apparent absence of Coenagrionidae in the Mesozoic led CARLE (1982) to doubt the origin of crown group Odonata from Protozygoptera. The disappearance of "Mesozoic Anisozygoptera" from the fossil record by the end of the Lower Cretaceous remains an enigma. ZHERIKHIN (1980) suggested that these became rheophile, i.e. associated with fast-flowing waters, and thus moved into upland habitats where burial and fossilisation are unlikely. Extant Anisozygoptera are associated with rapid, stony streams (CORBET, 1962, p. 79, 145) but there is at present no evidence of a close relationship between *Tarsophlebia*, *Euthemis* and *Epiophlebia*. Perhaps the radiation of birds during the Cretaceous (FISHER, 1967) brought Odonata into contact with new aerial predators which led to selection and extinction.

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REFERENCES

- ALLEN, P., 1976. Wealden of the Weald: a new model. *Proc. Geol. Ass.* 86(4): 389-437.
 ALLEN, P., 1981. Pursuit of Wealden models. *J. geol. Soc. Lond.* 138: 375-405.
 ALLEN, P., Wealden Research — meditations on ways ahead. *Proc. Geol. Ass.* 100(4). — [In press].
 CARLE, F.L., 1982. The wing homologies and phylogeny of the Odonata: a continuing debate. *Soc. int. odonatol. rapid Comm.* 4: ix + 66 pp.
 CARPENTER, F.M., 1954. Extinct families of insects. In: C.T. Brues, A.L. Melander & F.M. Carpenter, Classification of insects. *Bull. Mus. comp. Zool. Harvard* 108: 777-827.
 CLEMENTS, R.G., 1969. Annotated cumulative section of the Purbeck Beds between Peveril Point and the Zig Zag Path, Durlston Bay. In: H.S. Torrens, [Ed.], International symposium on the British Jurassic. Excursion No. 1. Guide for Dorset and south Somerset, fig. A35a-d. Keele Univ.
 CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.
 DAVIES, D.A.L., 1981. A synopsis of the extant genera of the Odonata. *Soc. int. odonatol. rapid. Comm.* 3: 1-59.
 DMITRIEV, V. YU. & V.V. ZHERIKHIN, 1988. Izmeneniya raznoobraziya semeystv nasekomykh po dannym metodam nakoplenykh poyavlenii. In: A.G. Ponomarenko, [Ed.], Melovoi

- biotsenoticheskii krizis i evolyutsiya nasekomykh, pp. 208-15, Nauka, Moscow. — (Russ.).
- FISHER, J., 1967. Fossil birds and their adaptive radiation. In: W.B. Harland et al., [Eds], The fossil record, pp. 133-154, Geol. Soc. London.
- FRASER, F.C., 1957. *A reclassification of the order Odonata*. R. Zool. Soc. N.S.W., Sydney.
- HANDLIRSCH, A., 1906-1908. *Die fossilen Insekten und die Phylogenie der rezenten Formen*. Engelmann, Leipzig.
- HANDLIRSCH, A., 1925. Palaeontologie. *Handb. Ent.* 3: 117-306.
- HENNIG, W., 1981. *Insect phylogeny*. Wiley, Chichester.
- JARZEMBOWSKI, E.A., 1980. Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, southern England. *Bull. Br. Mus. nat. Hist. (Geol.)* 33(4): 237-293.
- JARZEMBOWSKI, E.A., 1984. Early Cretaceous insects from southern England. *Modern Geol.* 9: 71-93.
- JARZEMBOWSKI, E.A., 1987. *Early Cretaceous insects from southern England*. PhD thesis, Univ. Reading.
- JARZEMBOWSKI, E.A., 1988a. British dragonflies in the latter part of the age of dinosaurs. *J. Br. Dragonfly Soc.* 4(1): 1-8.
- JARZEMBOWSKI, E.A., 1988b. A new aeshnid dragonfly from the Lower Cretaceous of south-east England. *Palaeontology* 31(3): 763-769.
- PRITYKINA, L.N., 1968. Strekozy Karatau (Odonata). In: B.B. Rodendorf, [Ed.], Yurskie nasekomye Karatau, pp. 26-54, pls 1-5, Akad. Nauk SSSR, Moscow. — (Russ.).
- PRITYKINA, L.N., 1977. Novye strekozy iz nizhnemelovykh otlozheniy Zabaikalya i Mongolii. In: B.A. Trofimov, [Ed.], Fauna, flora i biostratigrafiya mezozoya i kaynozoya Mongolii, pp. 81-96, pls 1-4, Nauka, Moscow. — (Russ.).
- PRITYKINA, L.N., 1980. Otryad Libellulidae Laicharting, 1781. In: B.B. Rodendorf, [Ed.], Istoricheskoe razvitiye klassa nasekomykh, pp. 128-134, pl. 7, Nauka, Moscow. — (Russ.).
- RASNITSYN, A.P., 1988. Problema globalnogo krizisa nazemnykh biotsenozov v seredine melovogo perioda. In: A.G. Ponomarenko, [Ed.], Melovoi biotsenoticheskii krizis i evolyutsiya nasekomykh, pp. 191-207. Nauka, Moscow. — (Russ.).
- RODENDORF, B.B., 1962. Otryad Odonata. Strekozy. In: Rodendorf, B.B., [Ed.], Osnovy paleontologii, Vol. 9: Chlenistonogie, trakheinye i kheliterovy, pp. 73-85, Akad. Nauk SSSR, Moscow. — (Russ.).
- WORSAM, B.C., 1978. The stratigraphy of the Weald Clay. *Rep. Inst. geol. Sci.* 78(11): ii + 23 pp.
- ZHERIKHIN, V.V., 1980. Klass Insecta. Nasekomye. In: V.V. Menner, [Ed.], Razvitiye i smena bespozvonochnykh na rubezhe mezozoya i kaynozoya. Mshanki, chlenistonogie i glokozhiye, pp. 40-97, 168-175, Akad. Nauk SSSR, Moscow. — (Russ.).