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TWO NEW DRAGONFLIES FROM THE LOWER CRETACEOUS DEPOSITS OF WEST MONGOLIA (ANISOPTERA: SONIDAE FAM. NOV., CORDULIIDAE)

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Sona nectes gen. n., sp. n. (Sonidae fam. n.) and *Eocordulia cretacea* gen. n., sp. n. (Corduliidae: Gomphomacromiinae), based on ca 300 specimens from Lower Cretaceous localities in West Mongolia, are described and illustrated. The material is deposited in the Institute of Palaeontology, USSR Academy of Sciences, Moscow. Sonidae fam. n. is classified as being closer to Gomphidae than to other Aeshnoidea; some specific features of sonid larvae are considered as adaptations to a nectonic mode of life. Some aspects of the new taxa, ecology, geological and palaeogeographical distribution are briefly discussed.

INTRODUCTION

The main concepts on dragonflies from the beginning of the Early Cretaceous period (Neocom) in Eurasia have so far been based on palaeontological material from the Trans-Baikal region, Mongolia (PRITYKINA, 1977) and China (HONG, 1965; LIN, 1976; ZHOU & WEI, 1980), i.e. from areas within the limits of the East Asiatic province of the Indo-European palaeo-biogeographical region (VAHRAMEEV et al., 1970). In the last two years, the collection of Neocom dragonflies from the Trans-Baikal region and from East Mongolia has grown considerably; nevertheless, the complex has turned out to be sufficiently typical for the region as a whole.

To the West of this area, dragonflies have so far been practically unknown. There is only limited information on taxa of disputable Late Jurassic or Early Cretaceous age in Spain (MEUNIER, 1914; WOOTTON, 1972; cf. also WHALLEY & JARZEMBOWSKI, 1985) and in southwestern Egypt (SCHLÜTER &

HARTUNG, 1982), therefore, the Neocom dragonflies of West Mongolia, described below, are of special interest. The findings in West Mongolia are even more important because, as suggested by PONOMARENKO & POPOV (1980), at the beginning of the Early Cretaceous period West Mongolia was outside the limits of the East Asiatic province of the Indo-European region. Thus, the faunal complex from the territory of West Mongolia characterizes another, Central Asiatic, province of the region.

We had at our disposal about 300 remains of imagines and larvae, from three sites associated with the deposits of the Gurvan-Eren formation (Myangad, Khukh-Mort, Gurvan-Ereniy-Nuru), collected in 1970, 1976 and 1979 by the Joint Soviet-Mongolian Palaeontological Expedition.

The dragonfly remains are met with in grey and yellow argillites of a lacustrine genesis together with other insects, predominantly aquatic Diptera and Heteroptera. Most odonate fossils are those of young larvae, which are well preserved; ultimate instar larvae and imagines are rare and fragmentary. Practically the entire collection comes from Myangad. In Khukh-Mort we found a single larva and one imago conspecific with the mass species of Myangad, while in Gurvan-Ereniy-Nuru only the head of an imago (which could not be identified) was found.

DESCRIPTION OF THE NEW TAXA

Aeshnoidea

SONIDAE FAM. N.

Type genus — *Sona* gen. n.; Lower Cretaceous, West Mongolia.

Diagnosis: Imagines — Medium size; eyes globular, without tendency to recede laterally, though not touching each other; antennae 7-jointed; tarsi of all legs 3-jointed. Base of hind wing in the male strongly angulated and excised; triangle equilateral in the fore wing, elongated in the hind wing; anal veins with several long branches and small anal loop. Female ovipositor rudimentary, apparently with two pairs of valves. Inferior anal appendage of male simple, unforked.

Larvae — Labium flat, elongate; median lobe with deep but closed median cleft. Last instar larvae with all tarsi 3-jointed; internal surface of tibia and tarsus with large spines; pretarsal claws separate. Tibia and tarsus of young larvae with long hair fringe; tarsal segments consolidated; long claws fused for entire length. Anal pyramid absent; robust long paraprocts set widely apart and diverging sharply, approximately of the same length as the three last abdominal segments; epiproct and cerci short; laminae subanales open and well visible from above.

Genera included — Type genus.

Affinities — The general appearance of the adults, wing venation, shape of the appendices superiores and rudimentary ovipositor of Sonidae fam. n. suggest affinity with Gomphidae. At the same time, the new family is close to the rest of Aeshnoidea (in particular Aeshnidae), without Gomphidae, chiefly on account of the presence of 7-jointed antennae, 3-jointed tarsi, undivided appendix inferior and larval labium with median cleft. The distinguishing features of the sonid larvae are the peculiar shape, size and arrangement of the caudal appendages and the unusual structure of the legs, which are unlike any other aeshnoid larvae known to me. They resemble the larvae of the unrelated Hemeroscopidae from the Lower Cretaceous of Transbaikalia (PRITYKINA, 1977; cf. Fig. 21).

Remark — There is a possibility that ultimate instar larvae, similar to younger ones, are also characterized by well-developed hair fringes on the legs, but this delicate structure could not be detected in the few and fragmentary remains in our collection.

SONA GEN. N.

Type species — *Sona nectes* sp. n.; Lower Cretaceous, West Mongolia.

Etymology — Derived from the Mongol "*son*" — "*dragonfly*".

Diagnosis: Imagines — Primary antenodales without intervening secondaries; pterostigma braced, elongate and narrow; fork of RS symmetrical; no crossveins in triangle, supertriangle and subtriangle; Mspl absent or nearly so; anal loop consisting of one weakly bordered cell; Rspl present at least in the hind wing. Tibial spines short, all of similar length. Male tergite 10 with a clear medial concavity in the caudal half; superior appendages are twice as long as inferior appendage.

Larvae — Third antennal segment longest. Pro-, meso- and metaleg bases similarly distant from each other. Wing sheats parallel. Segment 10 half as long as segment 9; no dorsal spines; short lateral spines on abdominal segments 7 to 9; epiproct nearly as long as segment 10, but only 1/5 to 1/4 length of paraprocts.

Species included — Type species.

SONA NECTES SP. N.

Figures 1-20, 25-28

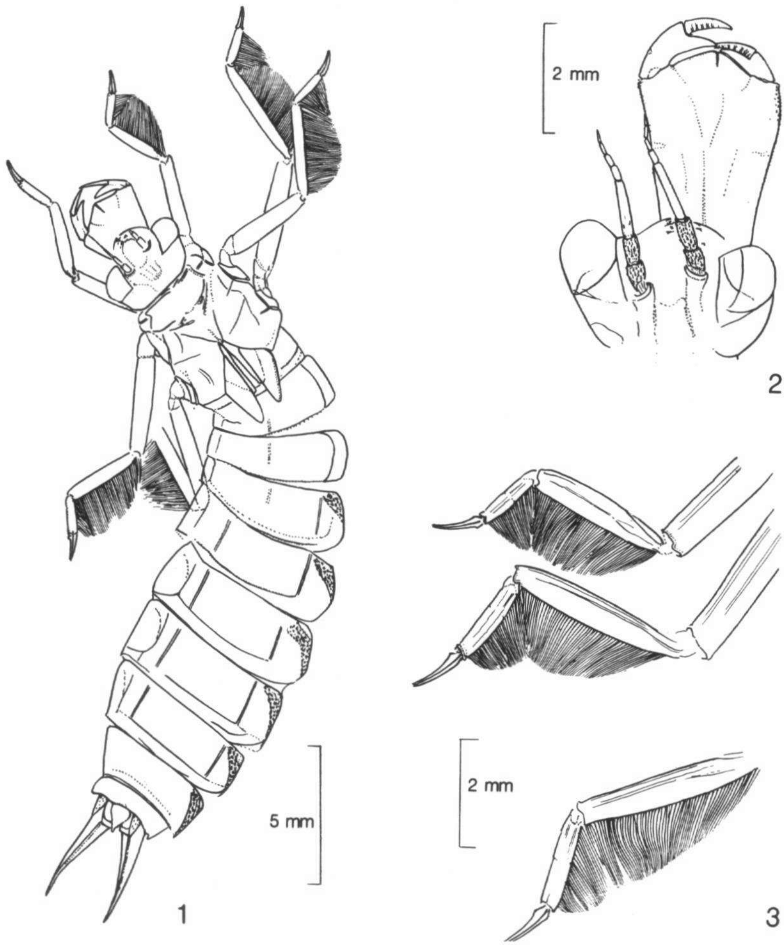
Material — **Holotype:** Collection of the Institute of Palaeontology, USSR (PIN) N 3152/2258, almost complete, well preserved young larva, obverse; Mongolia, Kobdo aimak, 8 km SE of Myangad somon, Myangad locality, section 221/17; L. Cretaceous, Neocom, Gurvan-Eren formation. — **Paratypes:** 14 specimens, PIN N 3152/74, 125, 135, 142, 2118, 2124, 2128, 2132, 2135, 2165, 2178, 2222, 2245, 2248 (imagines, ultimate and young instar larvae).

The collection from Myangad contains about 300 specimens referred to *S. nectes* sp. n.; among these are 17 imagines and 9 ultimate instar larvae; the rest are young larvae. Remains of the imagines and of ultimate instars are fragmentary and/or poorly preserved; most of the young larvae are complete and in fine condition.

One wing fragment and one larva of *S. nectes* were collected at Khukh-Mort by Dr P. Hosbayar in 1968 and Dr Yu. A. Popov in 1979: W. Mongolia, Gobi-Altai aimak, 40 km W of Khukh-Mort somon, between Shinlust-Ula and Tzakhir-Ula mountains; they are apparently of the same age and were recovered from the same formation as the holotype, coll. PIN N 3058/1 and 4.

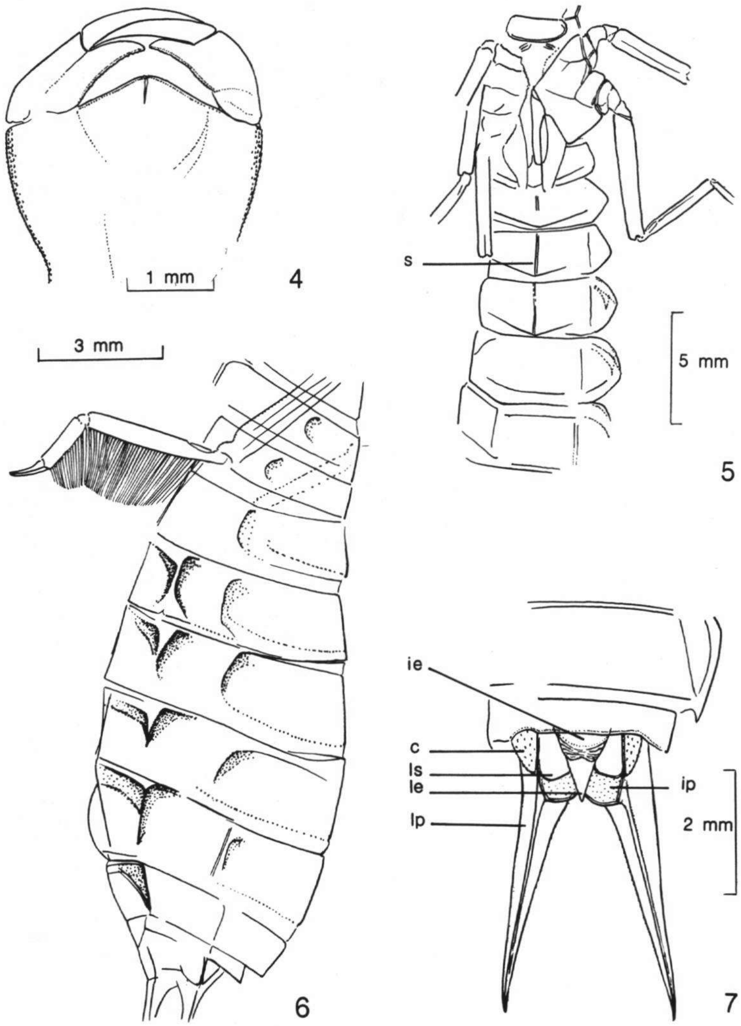
Etymology — From the Greek "*nectes*" — "*rower*".

Description: Imago (mainly hind wing) — At least 3-4 antenodals, at least



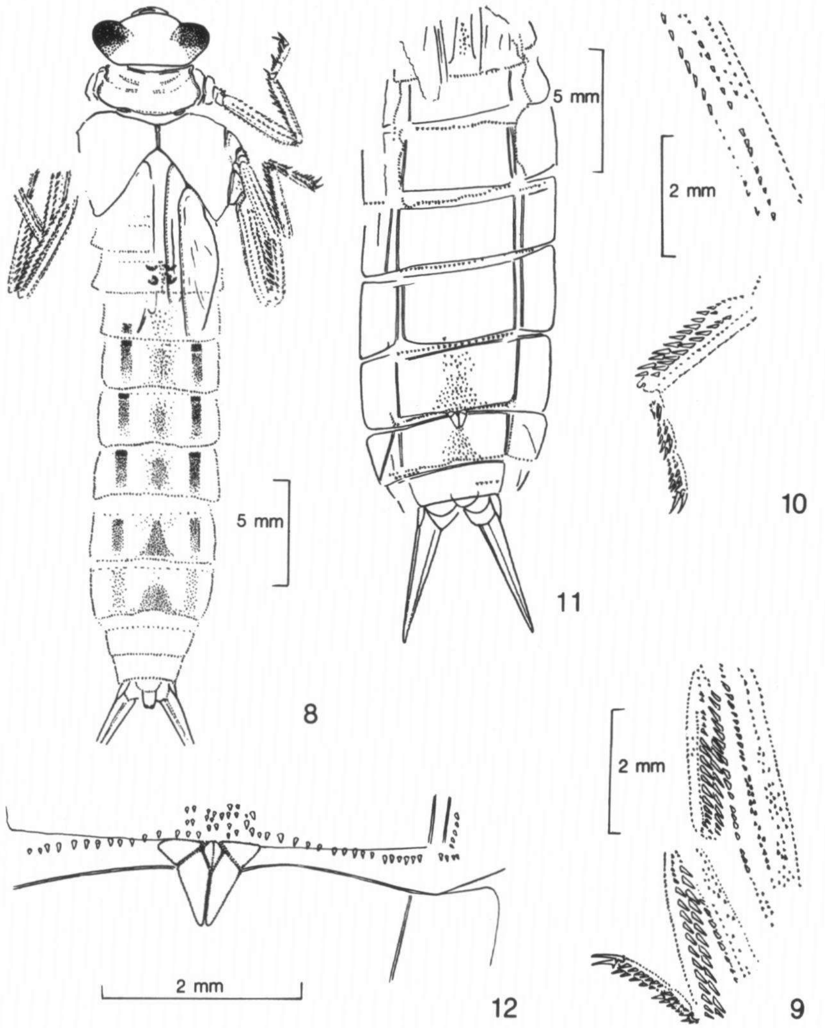
Figs 1-3. *Sona nectes* sp. n., young larvae, dorsal view; Lower Cretaceous, West Mongolia; (1) holotype, N 3152/2258, complete larva; — (2) paratype, N 3152/125, head with labium; — (3) paratype, N 3152/2178, leg fragments.

4-5 postnodals; pterostigma approximately 5 times as long as wide; 1 row of cells between R_3 and IR_3, but distal cell divided; between IR_3 and R_{4+5} at the level of vein o 2 rows of cells; distal parts of R_{4+5} and MA almost parallel, 2 or 3 rows of cells between them; distal side of hind wing triangle twice as long as proximal side; discoidal field parallel sided to nodus, there divergent, 3 cells adjacent to triangle in fore wing, 3 or 4 cells in hind wing; space between CuP and 1A not widened apically; 1A with 5 or 6 branches; 5-8 rows of cells between 1A and wing



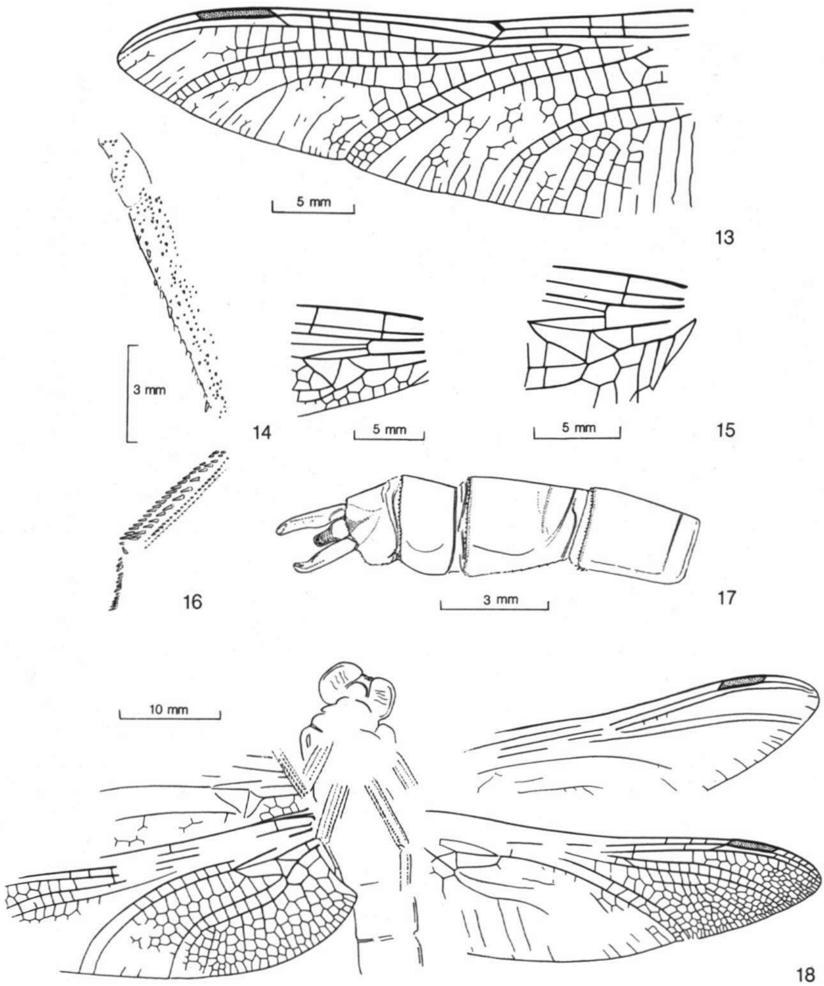
Figs 4-7. *Sona nectes* sp. n., young larvae, paratypes; Lower Cretaceous, West Mongolia: (4) N 3152/74, distal part of labium, dorsal view; — (5) N 3152/125, body fragment, dorsal view; — (6) N 3152/2245, decayed abdomen, showing lateral swellings at tergite and sternite, laterodorsal view; — (7) N 3152/135, abdominal end with apps, dorsal view. — (s: sulcus; — ie: imaginal epiproct; — le: larval epiproct; — c: cercus; — ls: lamina subanalis; — ip: imaginal paraproct; — lp: larval paraproct).

margin; anal triangle 3-celled; membranule covering 1/2 of proximal side of anal triangle in hind wing.



Figs 8-12. *Sona nectes* sp. n., ultimate instar larvae, paratypes; Lower Cretaceous, West Mongolia: (8) N 3152/2248, almost complete specimen, showing rudiment of copulatory apparatus and imaginal segment contours, larval segments are missing, dorsal view; — (9) the same, right middle and hind leg fragments; — (10) N 3152/2165, left hind leg fragment; — (11) N 3152/2222, abdomen, showing rudimentary ovipositor and partially imaginal segment contours, ventral view; — (12) the same, sternites 8 and 9 showing rudimentary ovipositor.

Ultimate instar larva — Wing sheaths extending almost to the end of segment 4; apex of the hind femora reaching the middle of segment 3; abdomen long,



Figs 13-18. *Sona nectes* sp. n., imago, paratypes; Lower Cretaceous, West Mongolia: (13) N 3152/2124, hind wing without base; — (14) N 3152/2132, fore wing fragment; — (15) N 3152/2128, hind wing fragment; — (16) N 3152/2135, leg fragment; — (17) N 3152/142, posterior end of abdomen with appendages, dorsolateral view; — (18) N 3152/2118, fragmentary body and wings, ventral view.

almost parallel sided from segments 5 to 8, there tapered; paraprocts straight, tapered evenly, nearly as long as the hind femora, with sharp tips.

Young larvae with wing sheaths extending to the middle of the 1st — middle of the 4th segment. Body surface bare. Eyes large, prominent; antennae nearly as long as posterior border of the head, or a little longer; 3rd antennal joint little longer than the rest of flagellum; mouth parts projecting forward. Labium long, extending backwards slightly beyond the middle of mesocoxae; distal half of postmentum roundly expanded laterally and bordered with minute spines; median lobe a low triangle; labial palps with apices pointed and slightly incurved; movable hook very robust, as long as, or a little longer than the external side of the palp from its base to the base of the movable hook. Prothorax distinctly narrower, synthorax wider than head. Legs moderately long; apex of hind femora reaching the middle of segment 3; femora, tibiae and tarsi straight, carinated, possibly a little flattened; pretarsal claws half as long as tarsus. Abdomen long, much wider than head; broadly upcurved lateral lobes on segments 3-8, therefore general outline of the abdomen when seen from above seems wavy; tergites 2-4 with medial sulcus; widest segments 6 and 7; segment 9 somewhat shorter than 8; lateral tergites and sternites furnished with rugged swellings. In many specimens the right or left lateral portion of segments is pressed against the sternites. (Possibly it was the normal posture of living larvae or else lateral portions of segments were oriented mainly ventrally, and were more or less movable about their mesal portions). Cerci as long as laminae subanales, covered with short hairs; male epiproct a little longer than cerci; paraprocts straight or slightly curved, gradually narrowing from base to apex, almost as long as hind femora, with sharp tips; their inner ribs contoured with short spines; epiproct and paraprocts bare.

Measurements (mm) — Imago: width of head including eyes 7, — length of fore wing 40-42, — length of hind wing 38-39, — greatest width of fore wing 11, — of hind wing 15. — Ultimate instar larva: length of abdomen 28-30, — of fore wing 12 or 13, — of paraproct 7 or 8. — Young larva with wing sheaths to the end of segment 2: width of head 4 or 5, — prothorax 2 or 3, — length of the fore wing 4 or 5, — of abdomen 23-26, — of paraproct 3 or 4.

Libelluloidea

CORDULIIDAE: GOMPHOMACROMIINAE

EOCORDULIA GEN. N.

Type species — *Eocordulia cretacea* sp. n.; Lower Cretaceous, West Mongolia.

Etymology — The generic name is made up of the Greek *"eos"* — *"early"*, and of *Cordulia*.

Diagnosis: Imagines — Moderately large. At least the hind wing with 2 primary antenodals (Ax_1, Ax_2) strongly differentiated, much more widely separated than secondaries, no other thickened antenodals; at least two distal antenodals of the 1st and the 2nd series do not coincide in the fore wing; pterostigma moderately long, approximately 3 times as long as wide; arculus between Ax_1 and Ax_2 and much closer to Ax_1 and much more proximal to the triangle in the hind wing; sectors of arculus arising separately, their bases widely spaced; hypertrian-

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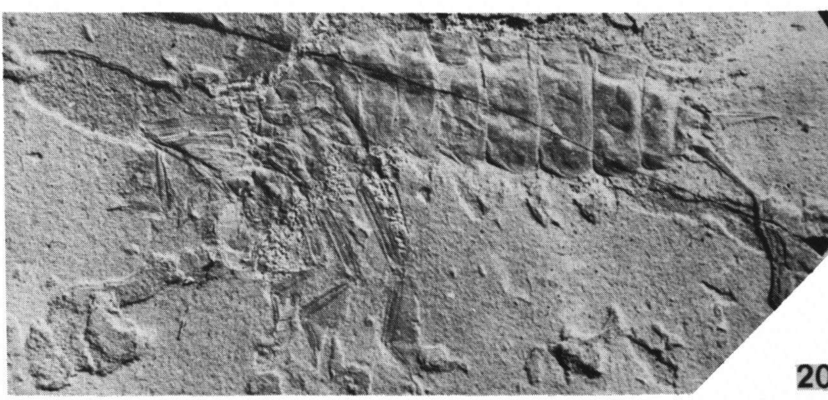

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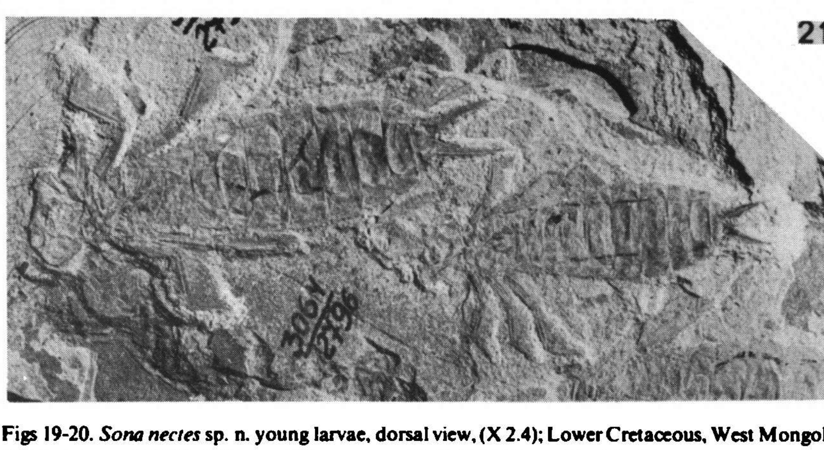


Figs 19-20. *Sona nectes* sp. n. young larvae, dorsal view, (X 2.4); Lower Cretaceous, West Mongolia: (19) holotype, N 3152/2258; — (20) paratype, N 3152/2178. — Fig. 21. *Hemeroscopus baissicus* Prit., two young larvae, dorsal view, (X 1.2); Lower Cretaceous, Zazinskaya formation, Baysa locality, Transbaikalia, original photograph of N 3064/2725, 2726.

gle and triangle of the hind wing free; distinct Rspl at least in the fore wing; discoidal field of the fore wing parallel sided to or beyond nodus, then slightly divergent; discoidal field of the hind wing divergent from the beginning; distinct Mspl present in both the wings; anal loop compact; anal triangle containing 3 cells, its distal side over 3 times as long as the costal one. Male abdomen slender, gradually attenuated towards the end; anal appendages long, superiors almost 3 times as long as segment 10 and a little longer than inferior appendage.

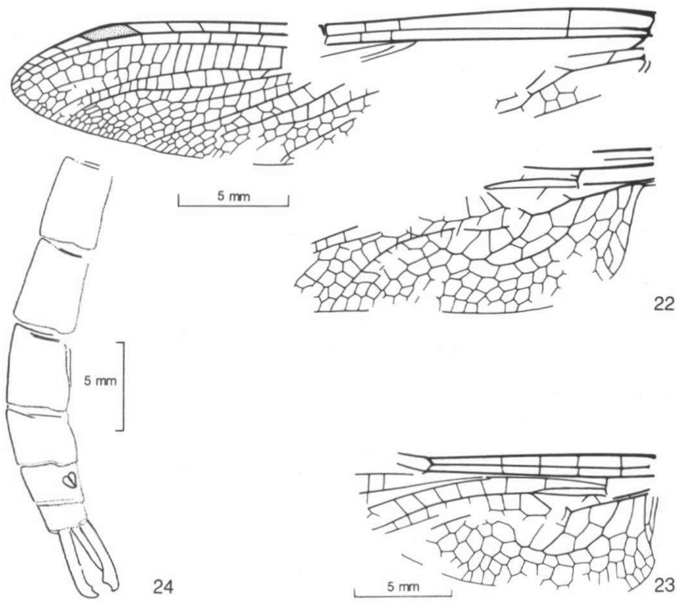
Species included — Type species.

Affinities — *Eocordulia* gen. n. differs from other Gomphomacromiinae mainly in the wider distance between sectors of arculus at their base, by the presence of Mspl in both wings and by a 3-celled anal triangle of the male hind wing.

EOCORDULIA CRETACEA SP. N.

Figures 22-24, 29

Material — **Holotype:** Coll. PIN N 3152/2121, three incomplete, poorly preserved female wings overlying each other, obverse and reverse; W. Mongolia, Kobdo aimak, 8 km SW of Myangad somon, Myangad locality, section 221/17; L. Cretaceous, Neocom, Gurvan-Eren formation. —



Figs 22-24. *Eocordulia cretacea* sp. n., Lower Cretaceous, West Mongolia: (22) holotype, N 3152/2121, ♀ fragmentary fore and hind wings; — (23) paratype, N 3152/2116, ♂ fragmentary hind wing; — (24) paratype, N 3152/2117, ♂, posterior end of abdomen with appendages, dorsal view.

Paratypes: 2 specimens from the same locality and section: N 3152/2116, fragment of male hind wing, and N 3152/142, incomplete male abdomen with caudal appendages (segments 1-3 lacking).

Description — Wing membrane hyaline; pterostigma light-coloured, overlying 1 or 2 veins; no less than 4 antenodals and postnodals in the marginal spaces of both wings; costal side of triangle longest, proximal side shortest in hind wing; discoidal field of hind wing starting with 2 cells, then broadening to between 10 and 12 cells at the wing border; 2 cu-a in both fore and hind wings; distal cu-a in the hind wing clearly distal to arculus; anal loop of female 6-celled, of male 4-celled with 2 cells at the base; 1A strongly curved.

Measurements (mm) — Length of female fore wing 31, — greatest width 6, — pterostigma 2.3, — greatest width of male hind wing 9, — length of male abdomen fragment (segments 4-10) 20, — length of superior anal appendages 6.

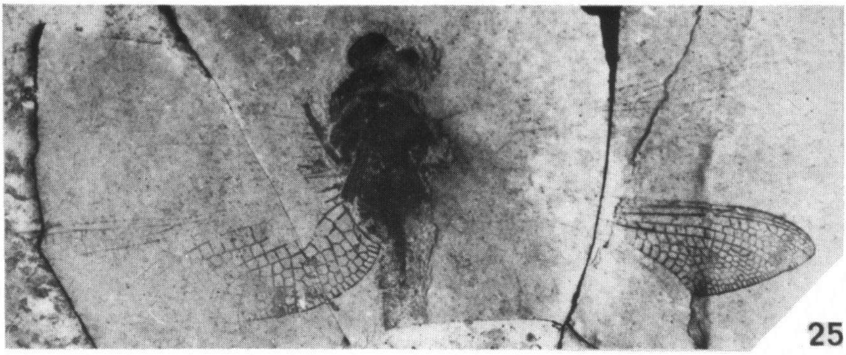
DISCUSSION AND CONCLUSIONS

As the Sonidae do not differ from gomphids in wing venation, the family status may seem doubtful and hence our classification requires some explanation.

When compiling identification keys for the families of Anisoptera, venational characters are often not given enough consideration. However, it is impossible to formulate such a key using only venational features. Usually specialists utilize body characteristics of adults and larvae, and probably such a spontaneous evaluation of distinctive characteristics is not accidental. As the experience with the fossil dragonflies shows, divergence of major branches of the genealogical tree has usually started with ecological divergence of larvae. Changes in adults, apart from the organs and structures connected with reproduction, were late, while transformations of the flying apparatus in a number of cases were less significant than any other changes. I assume that taxa at the beginning of their existence could not be distinguished by wing characters. Thus, I suggest that the Sonidae, as described above, should be considered as an example of an evolutionarily young family.

It is too early to argue about the time of the origin of the Sonidae. Detection in Jurassic deposits of wings with gomphid-like venation warns us not to come to the conclusion that sonids originated in the Cretaceous.

When the single stem diverged, the changes did not practically affect adult sonids, whereas in adult gomphids there was reduction in the number of joints of the antennae and tarsi, a tendency to lateral receding of the eyes, complication in the shape of the male caudal appendix inferior, while the valvae of the rudimentary ovipositor merged into a single lamina. In both phylogenetic branches the most significant changes occurred in the larvae. In gomphids, which preserved the primitive anal pyramid, the number of joints in the antennae and tarsi decreased and the medial cleft was reduced. In contrast, larvae of sonids preserved the number of antennal and tarsal joints typical for most dragonflies, as well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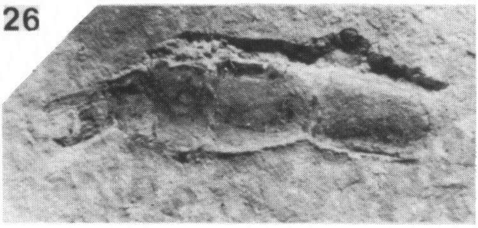


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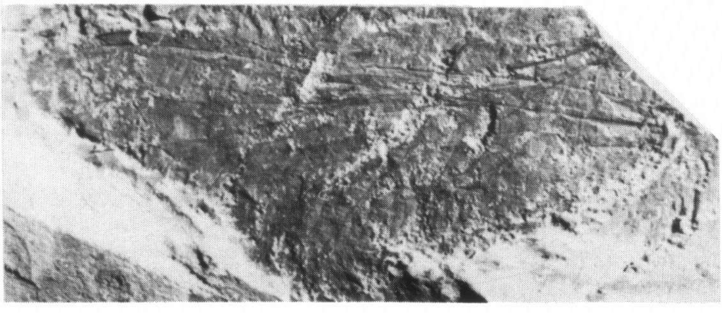
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as the cleft of the labium, while the caudal appendages and legs acquired an unusual structure.

Divergence of the families was probably primarily determined by specialization of the larvae for different habitats. Thus gomphids started to adapt to life in streams, whereas sonids apparently learned to cope with different habitats which are not characteristic for modern dragonflies. The abundance and good preservation of the sonid larvae allow us to study in detail their structure and, on this basis, to make assumptions concerning their possible mode of life.

Most probably young larvae of *Sona* were good swimmers. The large eyes allowed a large field of vision. The tarsi and tibia had a dense and long hair fringe, presumably an adaptation for swimming. At the same time, consolidation of the tarsal joints and the static character of the claws made the legs poorly fit for walking on the substratum. Another specific feature, undoubtedly associated with the nectonic way of life, is an unusual organization of the caudal appendages. *Sona* does not have the anal pyramid characteristic of Anisoptera. Strong, long paraprocts and the small epiproct are widely spaced and leave open the laminae anales, which usually cannot be seen in larvae with a normal anal pyramid. The paraprocts resemble the urogomphs of the aquatic beetle *Coptoclava* Ping (PONOMARENKO, 1975), and they probably performed a similar function, helping them attach to the surface film of water. The assumption about a nectonic way of life of the sonid larvae is also indirectly confirmed by the fact that they have been buried together with a mass of nectonic larvae and pupae of chaoborid mosquitos (Dr N.S. Kalugina, pers. comm.), their probable food source. Adult mosquitoes falling on the surface of the water would also be potential prey and their remains are also numerous in the layers containing dragonflies.

Adult larvae of *Sona* have probably covered considerable distances in search of a substratum suitable for ecdysis. Legs in these larvae are good for walking, with normal tarsi and claws and with spines developed as those of the imago.

Active movement in the open water is not usual for dragonfly larvae. That is why information about conditions that have produced this remarkable life form is of special interest. At present, the Mesozoic lakes and their biota are being successfully studied by Moscow palaeoentomologists. Major data on the Neocom lakes and their population are contained in the works of KALUGINA (1974, 1980), KALUGINA & PONOMARENKO (1980) and PONOMA-

Figs 25-28. *Sona nectes* sp. n., paratypes; Lower Cretaceous, West Mongolia: (25) N 3152/2118, (X 1.3), ♂ fragmentary body and wings, ventral view; — (26) N 3152/142, (X 3.8), ♂, posterior end of abdomen with appendages; — (27) N 3152/2222, (X 11.2), ultimate instar larva ovipositor, ventral view; — (28) N 3152/2248, (X 1.6), ♂ ultimate instar larva, dorsal view. — Fig. 29. *Eocordulia cretacea* sp. n., Lower Cretaceous, West Mongolia, holotype, N 3152/2121, (X 2.2), ♀, three fragmentary wings, overlying each other.

RENKO & POPOV (1980). It will be expedient to outline some of these data here.

The Mesophytic vegetation is not supposed to have prevented erosion of the earth's surface to any significant degree. Thus, even in a humid climate, landscapes similar to badlands could be widespread. At the beginning of the Early Cretaceous, due to weak regulation of the surface run-off, large areas of Mongolia were occupied by peculiar landscapes which never dried or were never grown over. Lakes associated with such landscapes were characterized by extreme instability of the hydrochemical and hydrological regime, by an extremely changeable shore line and, as one of the consequences, by extremely poor benthos with contrasting abundance of nectonic and pleistonic forms. These lakes did not have permanent near-water vegetation, while forest communities were far from their shores.

The absence of coastal vegetation probably explains the absence among the described dragonflies of forms with an endophytic ovipositor and the general qualitative poverty of the faunal complex, quite unexpected for a collection of 300 specimens.

Eocordulia cretacea sp. n. is the secondary element of this complex, represented by remains of adults only. Perhaps *Eocordulia* larvae lived in habitats other than those of *Sona* larvae. Indeed they might have been similar to the habitats of recent Gomphomacromiinae.

So far, fossil Corduliidae had only been known since the beginning of the Eocene (RIS, 1910). The discovery in the Neocom increases the age of the family by at least 80 million years and indicates that the range of the Gomphomacromiinae (provided our association is correct) in the geological past has been much wider than the present distribution. However, in the large odonate collection from the Neocom of Siberia and East Mongolia the corduliids are lacking. They are not known from younger than Neocom deposits of the Cretaceous period either. This shows how careful one should be when determining the age of a taxon using its first appearance in the palaeontological record. This first appearance is probably the beginning of bloom and wide settlement of a taxon rather than the beginning of its existence.

So far it has not been possible to prove clear continuity between the Early Cretaceous complex of West Mongolian dragonflies and the Late Jurassic odonate complex of the Central Asiatic palaeo-biogeographical province, evidenced in the Karatau (MARTYNOV, 1925, 1927; PRITYKINA, 1968, 1971). In the Karatau fauna there are species with a gomphid-like wing venation but, as noted above, there is not enough information about wing characters for distinguishing between fossil gomphids and sonids. Libelluloidea are entirely absent in the large Late Jurassic fauna complexes, not only of the Karatau but also of Solnhofen.

It is interesting to compare the complex of dragonflies from the Neocom of

West Mongolia with the complex of the same age from territories farther to the east. It is true though, that the large collection of dragonflies from the Neocom of Trans-Baikal region and East Mongolia has only partially been subject to a detailed taxonomic examination (PRITYKINA, 1977). The rest of the material has only been preliminarily identified. However, even these preliminary results are interesting. I relate them below, taking into account published data: Protozygoptera: Protomyrmeleontidae; Anisoptera: Aeshnidae, Petaluridae, Gomphidae (only larvae), Aktassiidae, Aeschnidiidae, Hemeroscopidae; Anisozygoptera: Tarsophlebiidae, Oreopteridae, Isophlebiidae and Stenophlebiidae.

Comparison shows that the isolation of the Neocom complex of West Mongolia from the fauna of the same age of more eastern territories is very significant; indeed there are no common families. Naturally, one can question whether or not the West Mongolian material is sufficiently representative to fully reflect the composition of the actual fauna. However, this way one cannot explain the absence of sonids and corduliids in eastern Asia. Here dragonfly fossils have been collected in several dozens of localities in different parts of the region, and the total size of the collection approaches 5000 specimens.

Traditionally, it is assumed that the presence of endemics of a high rank points to a biogeographical specificity of a region. In dragonflies, the faunas of West and East Mongolia are endemic on the family level, thus our data confirm the assumption of a palaeo-biogeographical border, which in the Neocom has divided the territories of West and East Mongolia.

It is interesting that, though sharply differing in systematic composition, the compared faunas have something in common in their ecological structure. In both cases dragonflies with nectonic larvae predominate, but sonids and their eastern analogs — hemeroscopids, are only remotely related (representatives of different Anisoptera superfamilies). This is probably one of the most illustrative examples of a parallel evolution in the history of the order.

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