THE LARVAE OF THE MESOZOIC FAMILY AESCHNIDIIDAE AND THEIR PHYLOGENETIC IMPLICATIONS (INSECTA, ODONATA, ANISOPTERA)

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ABSTRACT. Four giant dragonfly larvae are described from the Lower Cretaceous of China. Owing to the preservation of wing tracheal venation on the larval wing sheaths, they can be identified as the first undoubted larvae of the extinct Mesozoic family Aeschnidiidae. They are ultimate or penultimate male and female specimens, and a younger larva. The female larva has a very long ovipositor sheath. These larvae have an anisopteran anal pyramid and a very particular spoon-shaped labial mask, with a very narrow prementum and large palps with numerous teeth, suggesting possible affinities of the Aeschnidiidae with the Anisoptera Cavilabiata. The positions of other larvae formally attributed to the Aeschnidiidae are discussed, i.e. *Nothomacromia sensibilis* (Carle and Wighton, 1990), *Sona nectes* Pritykina, 1986, and the alleged larvae of *Hemeroscopus baissicus* Pritykina, 1977. They differ greatly from the true Chinese larval Aeschnidiidae, in the labial mask and female ovipositor, even if they show some similarities in the anal pyramid.

KEY WORDS: Insecta, Odonata, Aeschnidiidae, larval morphology, phylogenetic position, Lower Cretaceous, China.

THE Aeschnidiidae were one of the most diverse and most widely distributed dragonfly groups during the Late Jurassic and Early Cretaceous. About 25 species have been described from all continents, except North America, but nearly twice this number await description. The phylogenetic position of this group remains uncertain. After studying the adult characters, Nel *et al.* (1993) proposed to include them in the Anisoptera, close to the Cordulegastridae. Bechly (1997, 1998) considered them to be the sister group of the Anisoptera, within the Pananisoptera. Fleck (in prep.) shows that there is no clear evidence to support the division in Anisoptera and Pananisoptera. However, until recently, their larvae have been a complete mystery. Carle and Wighton (1990) regarded the larvae of Aeschnidiidae as unknown, even though they attributed the fossil dragonfly larva *Nothomacromia sensibilis* from the Lower Cretaceous of Brazil to the Aeschnidioidea. Nel *et al.* (1993) rejected the latter attribution as ill founded and therefore also considered the larva of Aeschnidiidae as unknown. Recently, Bechly (1997, 1998) and Bechly *et al.* (1998) regarded several Mesozoic dragonfly larvae with particular anal appendages, also including *Sona nectes* and *Nothomacromia sensibilis*, as potential larvae of the Aeschnidiidae. Because of the lack of common features of these larvae and the adult Aeschnidiidae, these attributions were still speculative. Zhang (1999*a, b*) described several Chinese Mesozoic larvae that he attributed to the Aeschnidiidae on the basis of the presence of a long larval ovipositor. In the present paper, we describe the first larvae unequivocally attributed to the Aeschnidiidae on the basis of the tracheal venation of the wing sheaths. The attributions of the other alleged aeschnidiid larvae are discussed.

The nomenclature of the dragonfly wing venation used in this paper is based on the interpretations of Riek (1976) and Riek and Kukalová-Peck (1984), as emended by Kukalová-Peck (1991), Nel *et al.* (1993) and Bechly (1996). The higher classification of fossil and extant Odonatoptera is based on the new phylogenetic system of Bechly (1996, 1997). The systematic analysis is based on the principles of consequent phylogenetic systematics (*sensu* Hennig 1966, 1969).

[Palaeontology, Vol. 45, Part 1, 2002, pp. 165–184]

SYSTEMATIC PALAEONTOLOGY

Order ODONATA Fabricius, 1793
Family AESCHNIDIIDAE Handlirsch, 1906

Larvae gen. et sp. indet.

Text-figures 1–15

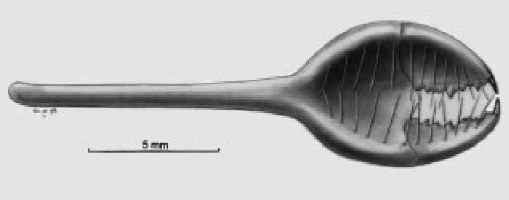
Material. Specimens MNHN-LP-R. 55203 (male, coll. Escuillié), MNHN-LP-R. 55218 (female, coll. Fleck), MNHN-LP-R. 55219 (two larvae, one male and one younger instar, coll. Escuillié), Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris.

Occurrence. Yixian Formation, near the village of Chaomidian, 25 km south-east of Beipiao City, western Liaoning Province, People's Republic of China. Upper Jurassic/Lower Cretaceous. Age uncertain. Dong and Guo (1996) considered it to be Late Jurassic. Smith *et al.* (1995) and Wellnhofer (1997) supposed it to be Early Cretaceous (Early Aptian). Zhang (1999*a*) indicated that it could be latest Jurassic rather than Early Cretaceous.

Diagnostic characters of the aeschnidiid larvae. The present diagnosis is based on the study of the Chinese larvae described. The tracheae of the hindwing sheaths have the same organisation as the adult wing veins (not observed by Zhang 1999*a, b*). The cerci are distinctly cordiform. The head is very small compared to the body length (character shared with some Gomphidae). The antennae of the last instar are very long (*c*. 9 mm) and filiform. This character is also present in some Libellulidae: Trameinae, e.g. *Trapezostigma* (antenna 6 mm long for a body length of 22 mm), and some Corduliidae, e.g. *Cordulia*, *Epitheca* and *Somathochlora* (antennae between 5·0 and 6·0 mm long for a body length between 19 and 30 mm). Zhang (1999*a*) indicated that the antenna is seven-segmented (plesiomorphy). The legs are very long and slender, with numerous hairs, which are not of natatorial type. The labial prementum is very long and narrow, with setae in its distal part. The well-developed spoon-shaped labial palp bears long setae, disposed in a corbicula, several acute teeth on its inner margin, and an apical movable hook. These setae could have had a function similar to that of the setae of the labial palps of some extant libellulids (e.g. *Leucorrhinia*, *Libellula*, *Sympetrum*) (Text-figs 1, 12). The late female larval instars have a very long ovipositor extending well beyond the apex of the anal pyramid, with well-developed valvulae V3 and V1, valvulae V2 not being visible and probably absent or very reduced; by contrast Zhang (1999*a*) opined that the ovipositor would be 'complete'.

Remarks. Zhang (1999*a*, pp. 813–814) noted in his diagnosis of the aeschnidiid family (based on the Chinese larvae he attributed to the genus *Aeschnidium* Westwood, 1854) several points that are debatable:

1. The larvae is 'of libelluloid type' ('Libelluloidea + Cordulegasteroidea') 'but body considerably elongated'. The larvae of the Cordulegastridae and Chlorogomphidae also have a very elongate body, thus this character is not discriminating.
2. The larvae have a prementum with a 'prominent median lobe'. We could not observe such a structure in our material. Zhang's specimen B97613 has a prominent median lobe (after Zhang 1999*a*, fig. 1A; 1999*b*, fig. 10a) but specimen B97611 does not have such a lobe (Zhang 1999*a*, fig. 1G; 1999*b*, fig. 11). These specimens may correspond to two different species or at least one of Zhang's drawings is partly wrong.
3. The larvae have 'wing rudiments usually strongly divergent, but in certain species' (*sic*, as Zhang considered that all these Chinese larvae belong to the same species) 'they lie parallel to one another'. This author added in his diagnosis of *Aeschnidium*, based on the same specimens, that the 'wing rudiments are obviously divergent'. In our material, there are specimens with parallel wing sheaths and another with strongly divergent wing sheaths, the divergence being clearly a result of taphonomic processes. It is more likely that the living larvae had parallel wing sheaths.
4. The larval eyes are 'clearly not touching each other' (Zhang's generic diagnosis). This is true for all the known odonatan larvae.



TEXT-FIG. 1. Reconstruction of the labial mask of an aeschnidiid larva.

5. Zhang added in the description of these larvae and adults that the larval postmentum and abdomen are 'cylindrical' and the adult body 'subcylindrical'. These characters remain uncertain because it is certainly not possible to observe the exact shape of these structures on this material because of compression.
6. He also indicated in the description that the female larval ovipositor is 'spathulate'. According to Zhang's photographs and the study of our material, the larval female ovipositor is clearly not spathulate nor apically broadened.
7. He noted that the larval prementum is 'shorter than labial palp'. This is not so in our female larva and it is not obvious in Zhang's (1999*a*, fig. 1A) material. It is frequently very difficult to determine the boundary between the prementum and the postmentum in fossil odonatan larvae. Thus, this character remains uncertain.
8. According to Zhang, the paraprocts are longer than the two last abdominal segments. In our material and in Zhang's (1999*a*, fig. 1G) illustration of specimen B97611, they are of nearly the same length (specific difference or phenomenon a result of the compression of the larvae?).

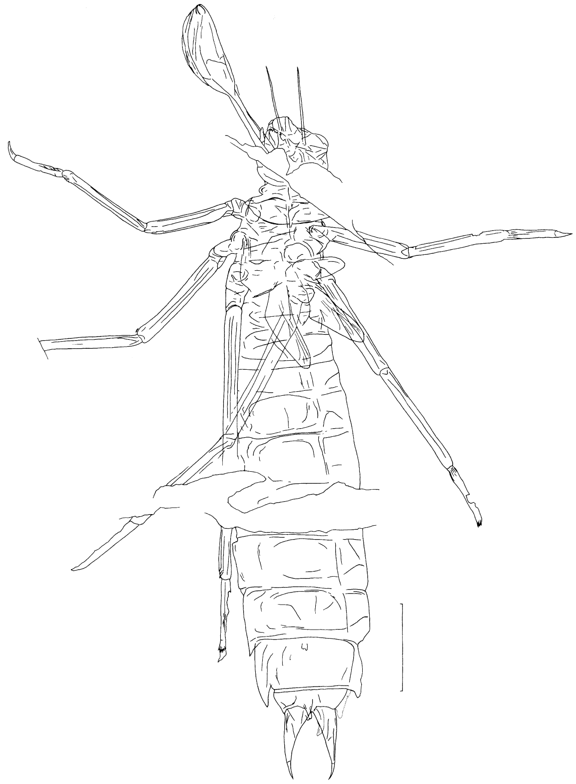
Descriptions

R. 55203 (male specimen, Text-figs 2–8). Imprint of a complete male larva of a late (probably ultimate) instar (Text-figs 2–3). Body length without anal pyramid, 68·7 mm. A very late instar is indicated by the very well-developed wing sheaths that reach beyond the middle of the fourth abdominal segment.

The male genital porus and genital valves are visible near the anterior margin of the ninth abdominal segment as a small disk, less than 1 mm wide. This tiny structure cannot correspond to the female ovipositor 'Anlage', considering the strongly hypertrophied ovipositor in female larval and adult Aeschnidiidae (Nel *et al.* 1993). The anal appendages are very well preserved and homologous with those of the extant Anisoptera (Text-fig. 4). The epiproct is bifid and relatively short (3·7 mm) compared to the paraprocts. Paraprocts 9·7 mm long, maximum width basally 2·5 mm, strongly arcuate (forceps-like), and with two longitudinal ridges ending in the outer margin somewhat before the apex. The apex of the paraproct is a very sharp and strongly chitinized spine 1·5 mm long. The paraprocts were certainly movable because they are asymmetrically placed in different positions on the various specimens. The cerci are slightly cordiform with a rather sharp apex, and 2·7 mm long, thus only slightly longer than the tenth abdominal segment, which is *c.* 2·3 mm long. The male projection above the epiproct is only partly preserved but it is very large, its visible part being about 2·1 mm long and 2·3 mm wide. Remains of the anal valvula are perhaps faintly visible below the male projection. A lateral spine is faintly visible on the ninth abdominal segment.

Prothorax with strong lateral spines. Forewing sheaths rather poorly preserved and partly hidden under the hindwing sheaths, about 15·5 mm, probably 16·5 mm long. Hindwing sheaths very well preserved, between 15·4 and 16·5 mm long (Text-fig. 5). Tracheae clearly visible and strongly resemble the unique pattern of the main veins in adult Aeschnidiidae, i.e. with a very transverse, long and narrow discoidal triangle, the typical antesubdiscoidal spaces in the anal area (pseudo-anal loops), a Mspl and a Rspl, the areas between MA and RP3/4 and between IR2 and RP2 distally widened, a very broad postdiscoidal area, and the typical cubito-anal area. Sheaths parallel and extending up to the distal part of the fourth abdominal segment. Since the wing sheaths are not flattened, and their inner margins are parallel and nearly touching each other, it is obvious that the specimen is not an exuvia, but a late instar larva that died well before the emergence.

The legs are very long (the hind legs extending up to the end of the abdomen), and not adapted to burrowing (Text-figs 6–8). Femorae and tibiae with at least two parallel longitudinal ribs, similar to *Nothomacromia sensibilis* (Carle



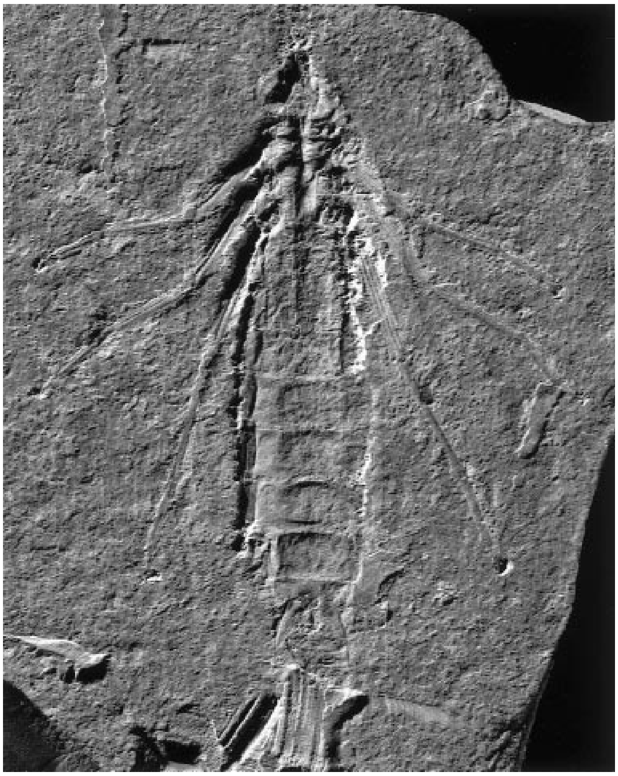
TEXT-FIG. 2. Habitus of specimen R. 55203; scale bar represents 10 mm.

and Wighton 1990). Metafemorae with two strong apical spines. There are long setae on the tibiae and tarsi. All of the tarsi are three-segmented, the third tarsomere being at least as long as the other two tarsomeres together. The last tarsal segment bears a row of strong setae at its apex. The apical claws are asymmetrical and 2·5–3·4 mm long. One of the two claws is distinctly broader than the other and bears a longitudinal median groove in which the other claw fits exactly. Obviously, these claws were movable (not fused as in *Sona*) because they are in different positions on the six legs. They may have acted as a kind of forceps to grasp plants or other supports. Length of the prothoracic leg, *c.* 36 mm, mesothoracic leg, *c.* 45 mm, metathoracic leg, *c.* 50 mm.

Abdomen *c.* 48 mm long, the anal pyramid being excluded, and 16·8 mm wide (width of ninth segment 13·3 mm). It was probably not flattened, but has been compressed. Nevertheless, the tergites are 10·1–12·6 mm wide, which may correspond to the original width of the abdomen. The ninth abdominal segment may have had two lateral spines, but they are not clearly visible.

Head very small compared to the body dimensions, *c.* 5 mm long and 8 mm wide. It is poorly preserved, and no clear structures can be identified. There are a few faint traces of the mouthparts (mandibles). The left labial palp is partly visible, bearing numerous setae. The antennae are not preserved.

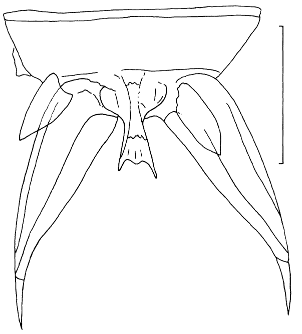
R. 55218 (female specimen, Text-figs 9-12). Imprint of a complete female larva of a late (probable ultimate) instar (Text-figs 9–10). Body length without anal appendages, 71·0 mm. A very late instar is indicated by the very well-developed wing sheaths that reach beyond the middle of the fourth abdominal segment. The female genital ovipositor is very well preserved, more than 29 mm long and 2·1 mm wide at the level of the tenth segment. It is more than three times longer than the paraprocts. The ovipositor is composed of two very visible pairs of valvulae, i.e. the lateral valvulae V3 and the ventral valvulae V1 *sensu* Pfau (1991). Length of the V3, 21·9 mm. V3 bears no apical constriction (rudiment of stylus *sensu* Asahina 1954), which strongly suggests that the egg laying was not endophytic, contrary to Zhang's (1999*a*) opinion. The base of V3 is clearly visible on ninth segment; V3 is basally widened, as in extant Anisoptera, except for female cordulegastrid larvae (with V1 hypertrophied) and other



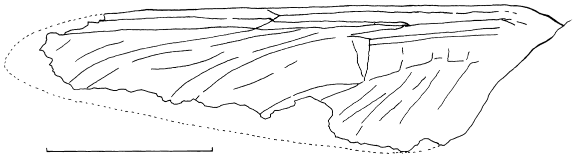
TEXT-FIG. 3. Photograph of specimen R. 55203, general habitus; scale bar represents 10 mm.

Exophytica. The base of V1 is at the junction between the ninth and the eight segments. The valvulae V2 are not visible; they are probably hidden by the other valvulae or absent. This hypertrophied ovipositor of Aeschnidiidae is not homologous with those of the Cordulegastridae because of the presence of the valvulae V3, contrary to the opinion of Nel *et al.* (1993). Thus it does not constitute a possible synapomorphy between Aeschnidiidae and Cordulegastridae.

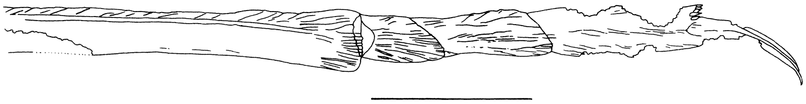
A very small undetermined structure, 1·2 mm long, is visible at the base of ninth segment. It could correspond to rudimentary V2 or to a mating aperture. This strongly hypertrophied ovipositor corresponds to that of the female adult



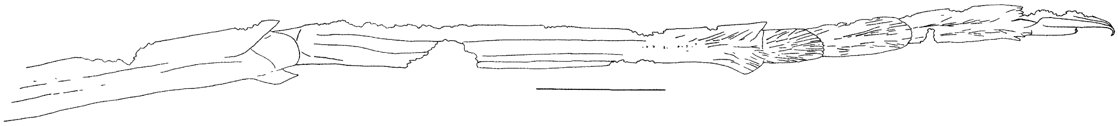
TEXT-FIG. 4. Anal pyramid of specimen R. 55203; scale bar represents 5 mm.



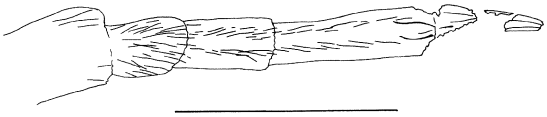
TEXT-FIG. 5. Hindwing sheaths of specimen R. 55203.



TEXT-FIG. 6. Right hind tibia and tarsi of specimen R. 55203.



TEXT-FIG. 7. Left hind leg of specimen R. 55203.



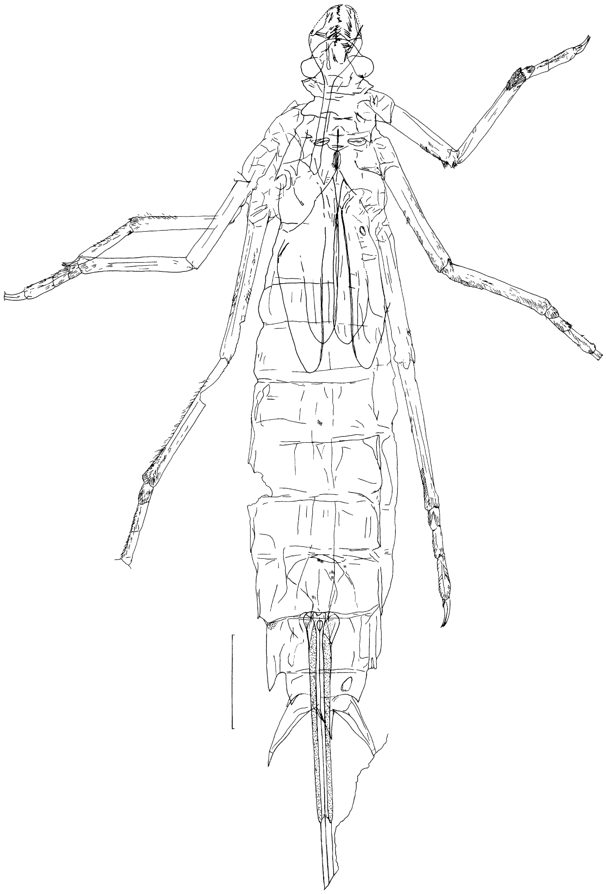
TEXT-FIG. 8. Left fore tarsi of specimen R. 55203. In each of the text-figures above the scale bar represents 5 mm.

Aeschnidiidae (Nel *et al.* 1993; cf. Bechly in press). The anal appendages are very well preserved and homologous with those of the extant Anisoptera. The epiproct is hidden under the ovipositor but it ends in a sharp spine (3·7 mm long), thus rather short compared to the paraprocts. Paraprocts 8·9 mm long, 2·5 mm wide basally, strongly arcuate (forceps-like), and with two longitudinal ridges ending in the outer margin somewhat before the apex. They are more open than in specimen R. 55203. The inner margin of the paraproct bears irregular small spines (Text-fig. 11), as in extant Aeshnidae (*Anax, Aeshna, Boyeria*). The apex of the paraproct is a very sharp and strongly chitinized spine 1·5 mm long. There is a sclerotized structure visible on the tenth segment, which could correspond to a moved cercus, 1·9 mm long.

The forewing sheaths are well preserved, 17·6 mm long, partly hidden under the hindwing sheaths, *c.* 18·0 mm. The hindwing sheaths are very well preserved, with the tracheae visible and strongly resembling the unique pattern of the main veins in adult Aeschnidiidae (see Text-fig. 9). The sheaths are parallel and extend up to the distal part of the fourth abdominal segment. Since the wing sheaths are not flattened, and their inner margins are parallel and close to each other, it is obvious that the specimen is not an exuvia but a late instar larva that died before the emergence.

The legs are very long but the hind legs do not extend up to the end of the abdomen, and were not adapted to burrowing. Femorae and tibiae with at least two parallel longitudinal ribs (similar to *Nothomacromia sensibilis*). There are long setae on the distal part of the femora, tibiae and tarsi. All of the tarsi are three-segmented, the third tarsomere being nearly as long as the other two tarsomeres together. At its apex the last tarsal segment bears a row of setae. The apical claws are 2·6–3·1 mm long but they look symmetrical, unlike those of the male specimen, but all are visible from their side. Length of prothoracic leg, *c.* 32 mm; mesothoracic leg, *c.* 38 mm; metathoracic leg, *c.* 48 mm.

The abdomen is *c.* 53 mm long, except for the anal appendages, and 16·2 mm in maximum width. It was probably



TEXT-FIG. 9. Habitus of specimen R. 55218; scale bar represents 10 mm.

not flattened, but has been compressed. Nevertheless, the tergites are 8·6–14 mm wide, which may correspond to the original width of the abdomen. The fifth–tenth abdominal segments have two lateral spines. Those of the ninth segment are very strong.

The head is very small compared to the body dimensions, *c.* 4·6 mm long and 8 mm wide. There are a few faint traces of the mouthparts (mandibles). The right antenna is partly visible. The eyes are 2·9 mm wide, and 2·8 mm apart. The labial mask is clearly visible. The postmentum is not visible; it is probably hidden by the premetum, which is very long and narrow, *c.* 14·7 mm long and 0·82 mm wide in its narrower part. The labial palps are 3·7 mm long and 2·7 mm wide. They bear numerous irregular teeth. The prementum and the palps bear long setae (Text-fig. 12). It is not possible to determine if there was a median cleft in the prementum.

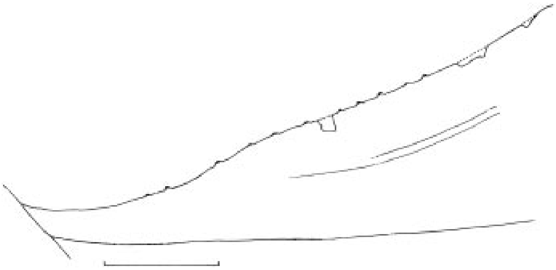
R. 55219 (large larva, Text-figs 13–14). Imprints of a complete male exuvia of a late (probably penultimate) instar and a younger larva. Body length without anal pyramid, 67·5 mm. The presence of well-developed wing sheaths reaching beyond the apex of the third abdominal segment supports the hypothesis that it is a very late instar. The epiproct is poorly preserved but smaller than the paraprocts. Paraprocts 8·5 mm long, basally 2·4 mm in maximum width, strongly arcuate (forceps-like), and with one longitudinal ridge ending in the outer margin somewhat before the apex, visible on the right paraproct. The apex of the paraproct is a very sharp and strongly chitinized spine 2·0 mm long.

The forewing sheaths are displaced and partly hidden under the hindwing sheaths. They are all well preserved, about 10·0 mm long (Text-fig. 13). Some tracheae are clearly visible and strongly resemble the unique pattern of the main

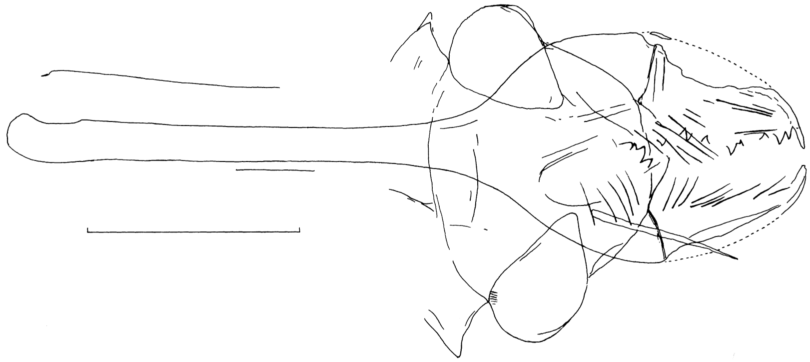
TEXT-FIG. 10. Photograph of specimen R. 55218, general habitus; scale bar represents 10 mm.

veins in adult Aeschnidiidae, i.e. with the areas between MA and RP3/4 and between IR2 and RP2 distally widened, and a very broad postdiscoidal area. It may be a penultimate exuvia because of the following characters: ratio between the wing sheaths and the body smaller than that of specimen R. 55203; labial mask displaced before the head; wing sheaths displaced; right metathoracic leg displaced to the left.

The legs are very long, even if the hind legs do not extend up to the end of the abdomen, and are not adapted to burrowing. Femorae and tibiae with at least two parallel longitudinal ribs. The hind tibiae and tarsi bear setae. These are not visible on the other legs. All the tarsi seem to be three-segmented, the third tarsomere being apparently at least as long as the other two tarsomeres together. Length of the prothoracic leg, *c*. 31·0 mm; mesothoracic leg, *c*. 37·0 mm; metathoracic leg, *c*. 45·0 mm.



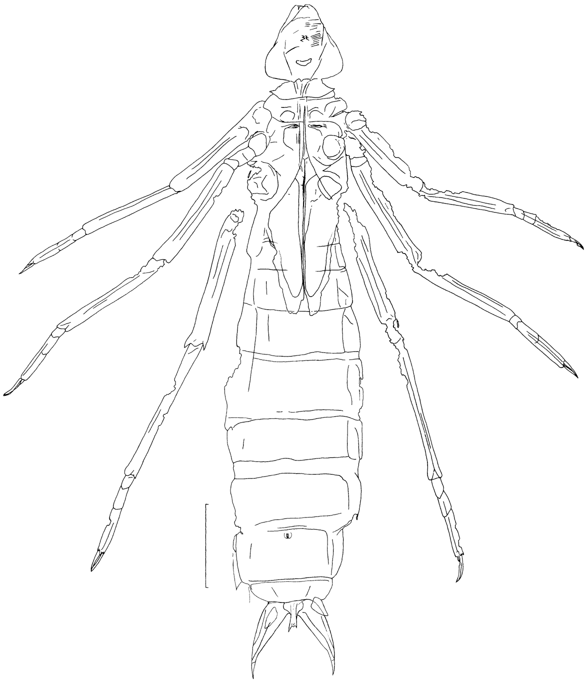
TEXT-FIG. 11. Detail of the right paraproct of specimen R. 55218; scale bar represents 1 mm.



TEXT-FIG. 12. Labial mask and head of specimen R. 55218; scale bar represents 10 mm.

Abdomen *c.* 48·5 mm long, the anal pyramid being excluded, and 15·0 mm wide. It was probably not flattened, but has been laterally compressed. The eighth and ninth abdominal segments bear two lateral spines, but they are poorly preserved. No ovipositor.

Head very small compared to the body dimensions, *c.* 6·7 mm long and 8·5 mm wide. It is poorly preserved, strongly compressed. No clear structures can be identified, except for the labial mask, the mandibles and perhaps a maxillary palp covering the proximal part of the prementum. Antennae faintly visible, very long (*c.* 9·0 mm) and filiform. Postmentum not visible. Premetum very long and narrow, *c.* 14·0 mm long, *c.* 1·0 mm wide in its narrowest part, and *c.* 3·7 mm wide in its widest part, with a longitudinal median furrow. Labial palps 5–6 mm long and less than 2·5 mm wide, but they are poorly preserved and their teeth and setae are not visible. It is not possible to determine if there was a median cleft in the prementum. The distal part of the prementum and labial palps are distinctly concave, spoon-like.



TEXT-FIG. 13. Habitus of specimen R. 55219, large larva; scale bar represents 10 mm.

TEXT-FIG. 14. Photograph of specimens R. 55219, general habitus; scale bar represents 10 mm.

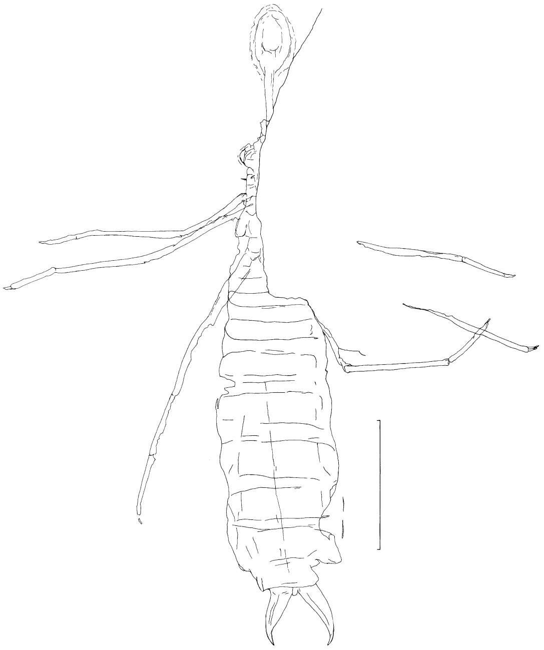
This larva could belong to a different species or genus, because its prementum is distinctly shorter and larger, and the paraprocts are thinner and more acute than those of specimens R. 55203 and R. 55218. Nevertheless, there can be strong morphometric differences between ultimate and penultimate instars of the same species of Aeschnidiidae.

R. 55219 (small larva, Text-fig. 15). This is very close to the large one. It is 17 mm long without anal pyramid. It has long, narrow legs (P1, 8·5 mm; P2, 10·0 mm; P3, 12·0 mm), strong forceps-like paraprocts *c.* 2·4 mm long. Epiproct very small. Cerci not visible. Typical spoon-shaped labial mask partly preserved, with a long and narrow prementum.

DISCUSSION

These larvae are remarkable because of their very large size. They are among the largest known dragonfly larvae. Only some isophlebiid larvae (*Samarura gigantea*) are nearly the same length (Pritykina 1985; Fleck and Nel in prep.), and some 'aeschnidiid-like' larvae from the Lower Cretaceous of Brazil nearly reach a similar size. The wing tracheation, which is identical to the highly derived wing venation of adult Aeschnidiidae, allows an undoubted attribution of these larvae to Aeschnidiidae. Zhang (1999*a*) attributed such larvae to the Aeschnidiidae on the basis of weaker evidence, i.e. the shape and size of the larval ovipositor, similar to that of the adult aeschnidiids. The female of several other Mesozoic groups (Tarsophlebioidea, Steleopteridae) also have long ovipositors. Zhang (1999*a*) supposed that the unknown tarsophlebiid larvae were of 'anisopteroid-type'. There is no evidence for this assumption. The Epiophlebiidae have 'anisopterid-type' larvae and the Isophlebiidae have 'zygopterid-type' larvae (Fleck in prep.).

Dong (1995) described an adult aeschnidiid species, *Sinaeschnidia cancellosa* from the same formation, which was synonymized with *Aeschnidium heishankowense* (Hong, 1965) by Zhang (1999*a*), who also described larvae very similar to those described here. This taxon, based on adult material, could



TEXT-FIG. 15. Habitus of specimen R. 55219, small larva; scale bar represents 5 mm.

correspond to these larvae, but there will never be any definite evidence to support this speculation, despite the opinion of Zhang (1999*a*, p. 819) who synonymized all the described Chinese adult and larva taxa with *Aeschnidium heishankowense* on the basis of the following arguments:

1. All of these dragonflies 'cannot be referred to more than one species because it is unlikely from the viewpoints of both taxonomy and ecology that, within a particular lake and geographic region, many large and predatory aquatic insects belonging to several species within a single genus coexisted'. This assumption is erroneous because several *Aeshna* spp. or *Sympetrum* spp. coexist very easily in a Western Palaearctic pond.
2. The 'near-ultimate instar female nymphs and female adults' have bodies of 'nearly the same length'. In all non-aeschnidiid Odonata, the adult body is longer than the last instar, and of course longer than the previous instar. Thus, it is impossible to be sure, *a priori*, of the fact that in aeschnidiids, the adult and larval bodies were, as a rule, of the same length.
3. The 'adult and larval eyes are widely separated'. In all other Odonata, even in species with adult eyes meeting, the larval eyes are separated.
4. The 'nymphs and adults are abundant, and dominate known odonate fossils' at the outcrop concerned. The abundance of both adult and larvae Odonata in the same outcrop does not prove that they 'belong to the same species'. Nel (1991) and Nel and Paicheler (1994) gave several counter-examples to this 'rule' of abundance.

Furthermore, if fossil adult specimens can be compared on the basis of wing-venation structures, the comparison between larva and adult dragonflies is much more difficult. For example, it is very difficult to discriminate the larvae of some modern *Aeshna* spp. or *Sympetrum* spp. from the same pond. Thus, we consider that Zhang's opinion is unsupported, at least concerning the synonymy of the larvae and, therefore, it is preferable not to attribute these larvae to any described adult Aeschnidiidae.

It is also impossible to attribute accurately these four larvae to the same genus or species. Even if the larger larvae are nearly the same size and general shape, they differ in the relative dimensions of the abdomen and hind legs, and in the shape of the epiproct. It is impossible to know if these differences are of sexual origin or not. The male epiproct of the extant *Epiophlebia superstes* is trifid and the female one is simple, similar to those of these aeschnidiid larvae.

The ovipositor of the female larva is nearly the same length as those of the adult female aeschnidiids described. In Cordulegastridae and Aeshnidae, the size of the adult ovipositor is between 1·5 times and more than twice that of the mature larva. If it were so for these aeschnidiids, the corresponding adult ovipositor would have been between 45 and 60 mm long, for a body length of between 67 and 80 mm. It is more likely to suppose that the mature larval ovipositor was nearly the same size as that of the adult ovipositor. Similarly, the abdomens of the ultimate larval instar and adult were probably of nearly the same size for Aeschnidiidae. Such an ovipositor was probably not endophytic but may have been adapted for egg laying in the mud or aquatic plant accumulations.

The very long and narrow labial prementum strongly suggests that these larvae did not live in, or on, the sediment, but in aquatic vegetation of standing water. This hypothesis is supported by the very long legs and the specialized structure of the tarsal claws.

The anal appendages of these larvae would have corresponded to the anisopteroid anal pyramid, since the paraprocts and epiproct are not developed as caudal gills but as spine-like movable appendages. A difference from the anal pyramid of extant Anisoptera is the hypertrophied forceps-like paraprocts that are much longer than the epiproct. Nevertheless, rather similar proportions between the paraprocts and the epiproct can be found in the extant aeshnid genera *Boyeria* and *Notoaeschna*. But the epiproct is shorter, half the length of the paraproct, in our aeschnidiid larvae, unlike in extant Aeshnidae. In *Epiophlebia*, the epiproct is half the length of the paraproct, but the paraprocts of *Epiophlebia* are strongly modified, not flat and hypertrophied like those of the aeschnidiids and Anisoptera.

Bechly (1996) considered that all the Mesozoic dragonfly larvae with hypertrophied and forceps-like paraprocts were related to the Sonidae (excluding the unrelated alleged adult sonids), which he considered as the sister-group of the Stenophlebiidae, but later he (Bechly 1997, 1998) and Bechly *et al.* (1998) synonymized the Sonidae with the Aeschnidiidae. The fossil larvae referred to the Aeschnidiidae are *Dissurus liauyuanensis* Hong, 1982, *D. quinquanensis* Hong, 1982, *Neimengogomphus dongwugaiensis* Hong, 1982, *Yixiangomphus labius* (Lin 1976), *Pseudosamarura largina* Lin, 1976 (all synonymized by Zhang 1999*a* with *A. heishankowense*), *Nothomacromia sensibilis* (Carle and Wighton 1990), *Sona nectes* Pritykina, 1986, and the alleged larvae of *Hemeroscopus baissicus* Pritykina, 1977. As we show below, comparison with the new Chinese material shows that the position of these taxa is more problematic than previously supposed.

REVIEW OF THE PREVIOUSLY DESCRIBED AESCHNIDIID LARVAE

The 'sonid' larvae (Sona nectes *Pritykina, 1986*)

Pritykina (1986) described *Sona nectes* and the monotypic family Sonidae from the Lower Cretaceous of West Mongolia. She mentioned the presence of about 300 specimens of which only 18 are adults while the rest are larvae at different stages. The holotype of *Sona nectes* is a well-preserved young larva.

Bechly (1996, 1997) and Bechly *et al.* (1998) argued that the larval Sonidae (including the holotype) are unrelated to the alleged adults and, therefore, restricted the taxon Sonidae to the particular larvae, and suggested a taxon for the adult dragonflies that were formerly attributed to Sonidae. Bechly *et al.* (1998) formally described *Proterogomphus krauseorum* within a gomphid family, Proterogomphidae.

Nevertheless, even restricted to the larvae of the original description, *Sona nectes* remains a problematical taxon. The holotype is a young larva, very similar in shape to our specimens. They share the hypertrophied paraprocts, a short epiproct, and three-segmented tarsi with strong, elongated, terminal claws. *Sona* differs from our material in having: (1) very long hairs on all tibiae and tarsi; (2) apparently fused tarsal claws; (3) distinctly shorter legs; (4) styliform instead of cordiform cerci; (5) more slender paraprocts.

Furthermore, the labial mask of the holotype of *Sona nectes* is very different from that of our Chinese aeschnidiid larvae. The premetum bears no setae. It is flat, large and comparatively short, instead of being setose, narrow and very long. The labial palp is flat, narrow and has only one strong apical tooth instead of being concave and bearing the numerous teeth of the Chinese material. Since there is no extant family of

Odonata with such variety in labial mask structure, these important differences suggest that the holotype of *Sona nectes* does not belong to the same family as the Chinese aeschnidiids.

The alleged ultimate instar of *Sona nectes* (figured in Pritykina 1986) differs considerably from the holotype of *Sona* in the following characters: straight paraprocts (similar to *Nothomacromia*) instead of being forceps-like; epiproct blunt, rectangular, instead of triangular or cordiform; head shape different; legs with short strong spines on femora, tibiae and tarsi, instead of fringes of long hairs on tibiae and tarsi; tarsal claws not elongated and not fused. Among extant larvae of Anisoptera there is no example with similar significant morphological differences between young and ultimate instars. Therefore, it is very likely that the alleged ultimate instars of *Sona nectes* correspond to a different genus and species. Furthermore, these alleged ultimate instars have very short legs, with tarsal claws very different from those of genuine aeschnidiid larvae.

The very small ovipositor of the alleged larger larvae of *Sona nectes* does not correspond to the very long ovipositor of the Chinese aeschnidiid larva. Pritykina (1986) based her description of *Sona* on about 250 specimens, and did not note a long ovipositor for any of them. Thus, these alleged ultimate larvae are probably not aeschnidiid.

The identification of the alleged larger larvae of *Sona nectes* as ultimate instars can be also contradicted by the length of the wing sheaths, which only reach up to the beginning of segment 4 (not extending almost to the end of segment 4 as erroneously stated by Pritykina 1986), while they reach the middle of segments 4–6 in ultimate instars of extant anisopteran larvae. Nevertheless, the abdomen of the alleged larger larvae of *Sona nectes* may have been deformed by fossilisation.

The fringe of hairs on the tibiae of the young larvae of Sonidae was interpreted by Pritykina (1977, 1986) as a swimming device, correlated with a nectic way of life that inspired her specific name for the species. Although such a function cannot be excluded, there are no known extant examples for nectic dragonfly larvae, but there are several extant examples of gomphid larvae with hairy legs that use these structures as a burrowing device. Furthermore a strikingly similar type of larva with nearly identical legs is known from the stonefly species *Perla marginata* (Plecoptera). Although its legs with dense fringes of hairs are used as a swimming device (Karny 1934, p. 124, fig. 80c, and pers. obs.), these perlids are not at all nectic, but benthic organisms. Therefore, we do not regard Pritykina's original interpretation as compelling, as already noted by Nel (1991) and Bechly *et al.* (1998).

'Sonid' larvae have a general habitus similar to those of the true Chinese aeschnidiids but comparison of the labial masks and ovipositors suggests that these larvae are probably not aeschnidiid. Therefore, it is necessary to be very prudent with the attribution of other similar larvae to the Aeschnidiidae.

The alleged Chinese 'aeschnidiid' larvae

All the described Chinese larvae attributed to the Aeschnidiidae are poorly described and figured in publications prior to Zhang's (1999*a, b*) work.

1. *Dissurus quinquanensis* Hong, 1982 (name emended to *D. quingquanensis* by Zhang, 1999*a*). Hong (1982*a*) described two dragonfly larvae from the Lower Cretaceous of China (Hebei), which he named *Dissurus quinquanensis* and *D. liauyuanensis*. Zhang (1999*a*, p. 824) indicated that *D. quinquanensis* bears no visible differences from *Yixiangomphus labius* (= *A. heishankowense*) 'despite the fact that its mask and epiproct are badly preserved and not clearly seen'. Zhang (1999*a*, p. 824) also indicated that the larva of *D. liauyuanensis* (name emended to *D. liaoyuanensis*) is a 'poorly known nymph', possibly referable to *Aeschnidium* cf. *A. heishankowense.*

The habitus of the larva of *D. quinquanensis* is similar to that of specimens R. 55203 and R. 55219. As there remains some doubt about the structure of the epiproct of *D. quinquanensis*, there is no direct evidence to regard specimen R. 55203 as conspecific with it. Furthermore, the type material of the *Dissurus* spp. figured by Hong (1982*a*) lacks a labial mask. This is one of the best characters for the attribution of a larva to the Aeschnidiidae other than the wing sheath tracheation when preserved, which is apparently not the case in this material. Thus, its attribution to the Aeschnidiidae remains uncertain, because, as noted above, there are larvae that superficially look like the true larvae of Aeschnidiidae but are probably not aeschnidiids (e.g. *Sona*).

2. *Yixiangomphus labius* (Lin, 1976), *Yixiangomphus* sp. (Hong 1982), and *Pseudosamarura largina* Lin, 1976. *Yixiangomphus* Lin, 1986 (a replacement name for the homonym *Archaeogomphus* Lin, 1976) looks, from the photograph of Lin (1976, pl. 2, fig. 5), to be nearly identical to our material, especially specimen R. 55219. Zhang (1999*a*) indicated that they also closely resemble the larvae he described and attributed to *A. heishankowense*. Hong (1982*a*) described two other dragonfly larvae from the Lower Cretaceous of China that he attributed to *Archaeogomphus*. Lin (1986) did not mention these specimens in his list of the species of *Yixiangomphus*. The exact status of the larvae described by Hong remains uncertain. All the *Yixiangomphus* and *Pseudosamarura* spp. have a labial mask that is very similar to those of our specimens (very long and narrow postmentum and prementum) and a trifid epiproct in the male (unknown in *Pseudosamarura*). Thus their attribution to the Aeschnidiidae is highly likely. Nevertheless, the drawings of both Lin and Hong are very poor and useless for specific comparison with our material. Zhang (1999*a*) did not provide any description or figure for this material.

(3) *Neimengogomphus dongwugaiensis* Hong, 1982 (name emended to *Neimenggolgomphus dongwugaiensis* by Zhang, 1999*a*). According to the figures in the original description (Hong 1982*b*), the larval holotype of this genus and species is similar to our specimen R. 55203. Zhang (1999*a*) indicated that this taxon is extremely similar to the larvae he described under the name of *A. heishankowense*. Unfortunately, he did not redescribe or figure them.

The type material of *Neimengogomphus* apparently lacks the labial mask and the wing sheath. Hence, its attribution to the Aeschnidiidae is not certain, even if highly probable, in particular because of the very similar anal appendages, female ovipositor, and the very long legs extending beyond the apex of the abdomen.

Note. All the genus and species name corrections proposed by Zhang (1999*a*) are unjustified, after article 32.5.1. in the fourth edition of the International Code of Zoological Nomenclature (1999): only inadvertent errors must be corrected, and incorrect transliteration or Latinization or use of an inappropriate connecting vowel, are not to be considered inadvertent errors.

Is Nothomacromia sensibilis *(Carle and Wighton, 1990) an aeschnidiid larva?*

Carle and Wighton (1990) described a very curious dragonfly larva from the Lower Cretaceous of Brazil (*Pseudomacromia sensibilis*) with two hypertrophied paraprocts, very long legs, and a gomphid-like mask. Carle (1995) replaced the homonymous generic name *Pseudomacromia* by *Nothomacromia*. Because of several alleged ‘primitive’ features that were believed to indicate a basal position in Anisoptera (like adult Aeschnidiidae), and because of an alleged lentic life style for this larva, Carle and Wighton (1990) suggested classification in a separate family, the Nothomacromiidae (= Pseudomacromiidae), within the superfamily Aeschnidioidea, which was regarded by these authors as a sister-group of the other Anisoptera. However, their arguments have been shown by Nel *et al.* (1993) and Bechly (1998) to be unconvincing, for the following reasons: (1) plesiomorphic similarities are invalid as evidence for phylogenetic relationship; (2) at least one of the alleged plesiomorphies of *Nothomacromia* represents an autapomorphy (‘petalurid-like palps’ after Carle and Wighton 1990; convergent with Petaluridae); (3) some of the alleged ‘primitive’ characters mentioned by Carle and Wighton (1990) as evidence for the basal position of Aeschnidiidae (e.g. poorly developed arculus, nodus and pterostigma, and presence of numerous intercalary veins) are, without doubt, autapomorphic reversals and not symplesiomorphies with ‘protodonates’ since these states do not belong to the ground-plan of the crown-group Odonata (see Bechly 1996, 1997); (4) the alleged lentic adaptation of these larvae is mere speculation and even improbable, since all aquatic insect larvae recovered from the Crato Formation are probably of allochthonous origin, having been washed in by adjacent streams.

This argument is very doubtful anyway, since there is no evidence whatever for lentic adaptations in the Aeschnidiidae; the lentic adaptations of *Nothomacromia* larvae, even if correct, could not indicate a close relationship with adult Aeschnidiidae. The long forceps-like appendages are formed by the paraprocts and not by the cerci (*contra* Carle and Wighton 1990). A further incorrect assumption of Carle and Wighton (1990) is the interpretation of the holotype of *Nothomacromia sensibilis* as a penultimate larval instar, because the wing sheaths seem to be insufficiently developed for this stage.

Bechly (1998) suggested that, in spite of all the doubtful arguments and incorrect statements, Carle and Wighton (1990) were right for the wrong reasons, not only concerning the basal position of Aeschnidiidae (also proposed by Bechly 1996, 1997), but also concerning the close relationship of *Nothomacromia* with Aeschnidiidae. The latter is suggested by circumstantial evidence that among the 241 known adult dragonflies from this locality, the seven specimens referable to the Aeschnidiidae might represent the corresponding adults for these strange larvae because nearly all other adult specimens belong to the crown-group Anisoptera (gomphoids, aeshnoids, libelluloids), for which such an unusual type of larva looks improbable, at least at first glance. Affinities with 'anisozygopteres' are unlikely because there are no adults known from this locality, which may not be a sampling artefact considering the large number of known specimens of adult dragonflies. Nevertheless, the future possibility of discovery of an 'anisozygopteran' cannot be excluded. We have recently described from the same formation the strange new aeshnoid family Liupanshaniidae (Bechly *et al.* in press). These very large dragonflies, known from the Cretaceous of China, Russia and Brazil, have very particular features in their wing venation, and could correspond to large larvae of an unknown type. These could be either sonid or nothomacromiid larvae. Only the discovery of a larva of *Nothomacromia* with the wing sheath tracheae preserved will allow us to classify these larvae definitively. Furthermore, the labial mask of *Nothomacromia*, as figured by Carle and Wighton (1990), is gomphid- or sonid-like, with a wide, flat, prementum and short, flat, palps with only one strong apical tooth, and thus very different from those of our larvae.

Bechly (1998) described giant 'aeschnidiid-like' larvae from the same locality that seem to be very closely related to *Nothomacromia sensibilis* because they share not only the hypertrophied paraprocts (straight rather than forceps-like), but also the spine-like epiproct and the lyre-shaped antennae. The latter character is highly derived and unique (lyre-shaped antennae are absent in *Sona* and our aeschnidiid larvae) and has to be regarded as a strong autapomorphy of *Nothomacromia*. At this locality there are larvae of this type of very different sizes that form a gradual morphocline from small *Nothomacromia*-like larvae to the above-mentioned giant larvae (body length without appendages varies from 14·3 to 63·5 mm). The only distinction of the big larvae from the small larvae, apart from their size, is the proportionally somewhat shorter legs and larger eyes. Both differences could be easily explained by allometric growth. It is very interesting that the small larvae always have poorly developed wing sheaths, while the giant larvae have well-developed wing sheaths that extend up to the end of the fifth abdominal segment. Consequently, it is highly probable that the giant larvae are simply later instars of *Nothomacromia sensibilis*.

This giant larva has a flat gomphid-like mask, which confirms the original drawing of Carle and Wighton. Therefore, the attribution of *Nothomacromia* to the Aeschnidiidae is contradicted by these great differences from our Chinese aeschnidiid larvae.

The *Nothomacromia* larvae also have very long paraprocts, between one-third and one-half the length of the abdomen (depending on the instar); very long wing sheaths relative to the abdomen, reaching the sixth segment (instead of the fifth segment in the Chinese aeschnidiids); and a very wide and short ninth segment (distinctly longer in the Chinese aeschnidiids). The head is of normal size compared to the body, instead of being very small. Furthermore, among the numerous larvae attributable to *Nothomacromia* that we have examined in various collections, none had a long ovipositor. It seems unlikely that all of these larvae were males. Thus, the female larvae of *Nothomacromia* probably did not have a long ovipositor, unlike the Chinese aeschnidiid larvae and probably all the female larvae of the various aeschnidiid species.

Are the alleged larvae of Hemeroscopus baissicus (sensu *Pritykina 1977*) *Aeschnidiidae*?

Bechly (1996) indicated that the larvae which have been attributed to *Hemeroscopus baissicus* by Pritykina (1977) are very similar to the holotype larva of *Sona nectes* since they not only share a similar general habitus, but also two highly derived characters, namely the dense fringe of hairs on the tibiae and forceps-like paraprocts. Pritykina (1986) regarded these similarities as convergences because the *Sona* larvae clearly possess a flat gomphid-like mask whereas the *Hemeroscopus* larvae have a spoon-shaped libelluloid-like mask and a libelluloid-like gizzard. After our recent re-examination of the reference material in Moscow, we suspected that the mask of the alleged hemeroscopid larvae could not be of the derived spoon-shaped libelluloid type, but of the plesiomorphic, flat gomphid type. Bechly *et al.* (1998)

therefore considered Pritykina's reconstruction of the alleged hemeroscopid larva as a 'chimaera' of two different species: one *Sona*-like species with hairly legs and forceps-like paraprocts, and one libelluloid-like species with a spoon-shaped mask and a bilaterally symmetrical gizzard. Because of this, Bechly *et al.* (1998) indicated that the reference larvae could be unrelated to the Hemeroscopidae, but very likely related to the Sonidae (young larvae), with which they share the very long hairs of the tibiae and tarsi as a possible unique synapomorphy. However, the alleged hemeroscopid larvae differ from *Sona* and our Chinese material in having dense fringes of hairs on the inner margin of the larval paraprocts (probable autapomorphy).

More recently, Huang and Nel (2001) have described very well-preserved new Chinese larvae that are undoubtedly attributable to the same alleged *Hemeroscopus* larvae. They clearly have a 'libellulid-type' mask (labial palps with smooth teeth, labial prementum broad and rather short), demonstrating that they correspond to a Libelluloidea. Thus, the alleged larvae of *Hemeroscopus* are clearly not related to the genus *Sona*. These larvae are associated with numerous adult hemeroscopids but, because of the lack of preservation of the wing trachae on these larvae, it is not possible to attribute them unquestionably to *Hemeroscopus*. Furthermore, their mask strongly differs from that of the known aeschnidiid larvae: labial palps with smooth teeth instead of strong and sharp teeth of the aeschnidiid larvae; and a labial prementum broader than that of the known aeschnidiid larvae. The variability of this last character within the Aeschnidiidae remains unknown. It may be highly variable within a given family [see, for example, the Lestidae *Chalcolestes viridis* (Van der Linden, 1825) and *Lestes macrostigma* (Eversmann, 1836), as figured by Aguesse 1968]. Nevertheless, the alleged larvae of *Hemeroscopus* are also probably not related to the Aeschnidiidae.

PHYLOGENETIC CONSIDERATIONS

Bechly (1996) considered that the Sonidae could be the sister group of the Stenophlebiidae, and together constitute the sister-group (Stenophlebioidea) of the Pananisoptera (=Aeschnidioptera + Anisoptera). This opinion was based on Pritykina (1986) who described an apparently reduced ovipositor (like adult Stenophlebiidae) in alleged ultimate instar larvae of *Sona nectes*, and assumed that the sonid larvae do not possess a true anal pyramid, which would have indicated a position in the basal stem-group of Anisoptera.

Our study suggests that there is no clear difference between the anal appendages of the aeschnidiid and sonid larvae and the anal pyramid of extant Anisoptera larvae. Thus, there is no more evidence in favour of a sister-group relationship between the Sonidae and the Stenophlebiidae. The stenophlebiid larvae are still unknown.

The polarity of the characters 'presence of hypertrophied forceps-like paraprocts' and 'paraprocts are more than twice as long as the epiproct' could be established by an outgroup comparison with the larva of Epiophlebiidae and Isophlebioptera, even though the larvae of other fossil stem-group representatives of Anisoptera (i.e. Stenophlebiidae, Heterophlebioptera and Liassogomphidae) are still unknown. According to the outgroup comparison with the Epiophlebiidae, the hypertrophied paraprocts of the putative larvae of the Aeschnidiidae would have to be regarded as derived. Nevertheless, elongated, forceps-like paraprocts are also present in '*Sona*' and '*Hemeroscopus*' larvae and in extant aeshnid larvae. They are even more obvious in a few extant aeshnid genera, like *Boyeria*, *Notoaeschna* and *Spinaeschna*. Thus, this character can be homoplastic or a plesiomorphy for the Anisoptera.

The polarity of the character 'paraprocts more than twice as long as the epiproct' is more difficult to establish because the epiproct of the larva of *Epiophlebia* is one-half the length of its paraprocts if measured in dorsal view. But the paraprocts of *Epiophlebia* are curved; thus, if we consider their real length, they are distinctly more than twice as long as the epiproct. Therefore, the character 'paraprocts more than twice as long as the epiproct' could be considered plesiomorphic. Nevertheless, the great differences in the shape of the anal appendages between *Epiophlebia* and the Aeshnidiidae and other Anisoptera render the homology of this character uncertain.

The known larvae of Isophlebioptera (e.g. *Dinosamarura* Pritykina, 1985) have a very long and slender abdomen like Zygoptera larvae, and zygopteroid anal appendages of the synlestid type; i.e. broad, leaf-like paraprocts and epiproct. The attribution of these larvae to the Isophlebioptera, proposed by Pritykina (1985), was doubted by Nel *et al.* (1993), but our recent re-examination of the type material demonstrated that the wing sheaths of these larvae show derived similarities of the tracheation with the wing venation of the adult Isophlebioptera (Fleck *et al.* in prep.). Furthermore, the only fossil adult dragonflies found in the relevant outcrops are large isophlebioids. They correspond to the large size of these larvae, which are the only dragonfly larvae found in these outcrops. Consequently, the attribution of these larvae to Isophlebioptera has to be regarded as certain. Their similarity to larvae of basal Zygoptera (e.g. Hemiphlebiidae and Synlestidae) is so striking that there can be hardly any doubt that the similarities (e.g. shape of the caudal gills) are based on homology. Since the wing venation of adult Isophlebioptera clearly demonstrates a phylogenetic position in the stem-group of Anisoptera (see Nel *et al.* 1993; Bechly 1996, 1997), the homologous similarities with Zygoptera must represent symplesiomorphies. These new results also influence the hypothetical phylogenetic position of Epiophlebiidae, which was previously regarded as the most basal clade of the anisopteroid lineage, even more basal than Isophlebioptera (Nel *et al.*, 1993; Bechly 1996). This hypothesis can no longer be regarded as convincing since the larvae of extant Epiophlebiidae share several highly derived characters with the larvae of extant Anisoptera: abdomen shortened and broadened; anal appendages developed as short valves around the anus (paraprocts and epiproct not developed as caudal gills); and strongly improved rectal respiration with tracheated folds as rectal gills. These character states are absent in Isophlebioptera (plesiomorphies), and represent strong possible synapomorphies for Epiophlebiidae and Anisoptera. The larvae of Heterophlebioptera and Stenophlebioptera are unknown, but the wing venation of the adults suggests that they are more closely related to the Anisoptera than the Isophlebioptera and Epiophlebiidae. Thus, *Epiophlebia* is not the 'best possible' outgroup for the polarization of the Anisoptera characters.

The epiproct and paraprocts of the Isophlebioptera larvae are nearly of the same size (Pritykina 1985; pers. obs.), which would confirm the interpretation of the character 'epiproct shorter than paraprocts' as a synapomorphy of the Anisoptera (+ Epiophlebiidae?), but it does not add information on the character 'epiproct distinctly shorter than half length of the paraprocts'. Furthermore, this discussion is based on comparison in a situation with rather distant outgroups. The larval structures of the Heterophlebiidae, Stenophlebiidae, and Liassogomphidae are still unknown. The assumption of a close phylogenetic relationship between the true aeschnidiid larvae and *Nothomacromia*, *Sona*, and the alleged *Hemeroscopus* larvae is contradicted by the great differences in the labial masks and ovipositors. The labial masks of *Hemeroscopus*, *Nothomacromia* and *Sona* are different from those of the 'real' Aeschnidiidae in that the prementum of the latter is very elongate and narrow and not broad and short. Also, the labial palps of our aeschnidiid larvae are spoon-like, unlike the flat palps of *Sona* and *Nothomacromia*. The spoon-like labial mask of the true aeschnidiid larvae would be a strong synapomorphy with the Anisoptera Cavilabiata. This hypothesis contradicts the possible relationships with the sonid and hemeroscopid larvae and the position of the Aeschnidiidae as a sister group of all Anisoptera.

Nevertheless, the assumption of Zhang (1999*a*) about a close similarity between aeschnidiid, libelluloid and cordulegastroid larvae is poorly supported. The characters of the aeschnidiid and libelluloid larvae are very different. The aeschnidiid larvae resemble more closely the cordulegastrids but their larval and female ovipositor are very different. They also resemble the aeschnid larval habitus (long slender legs, elongated flattened abdomen with lateral spine, very long paraprocts, large eyes).

The Aeschnidiidae have very strong autopomorphic structures in both adults and larvae, e.g. female larval and adult ovipositors, wing venation, adult abdomen, larval legs, larval prementum. All of these suggest that the larvae and adults were adapted to very particular biotas that remain almost unknown. Zhang (1999*a*) supposed that the aeschnidiid larvae were benthic animals, crawling over the substrate and burrowing into it with their clypeus. But how could they manage to extend their very long and thin mask? No recent benthic Odonata has a similar structure. On the contrary, modern burrowing Anisoptera larvae have a short, broad, strong mask. Zhang (1999*a*) also noted that these aeschnidiid larvae had an 'enormous grasping mask'. The mask of these larvae is not especially larger or broader than those of many Recent Anisoptera. Furthermore, because of their narrow prementum, they probably could not catch large prey.

It is possible that the spoon-shaped labial mask of the Chinese Aeschnidiidae is a result of an extraordinary convergence with the Cavilabiata because no Cavilabiata have a narrow prementum similar to that of the aeschnidiid larvae. In fact, the mask (more precisely the prementum) of these larvae strongly resembles that of some Zygoptera: Lestidae (*Lestes*). This suggests that convergences can occur in this structure.

In conclusion, either the true Aeschnidiidae and the *Nothomacromia*, *Sona*, and (less probably) the alleged *Hemeroscopus* larvae represent several very distinct groups, or specialized lineages within the Aeschnidioidea and correspond to family-level differences of the unknown adults. As there is no known Recent group with such differences in the labial mask and ovipositor, the second hypothesis is clearly less probable than the first. The possible attribution of the Aeschnidiidae to the Cavilabiata needs to be supported by further evidence. Therefore, this Mesozoic family may currently be regarded as true Anisoptera *incertae sedis*.

Note. Zhang (1999*a*, p. 823) dismissed the attribution of the Aktassiidae Pritykina, 1968 to the Petaluroidea proposed by Nel *et al.* (1998) and suggested that this family could be the sister group of Aeschnidiidae, within the Aeschnidioidea, on the basis of the putative synapomorphies 'a nearly equilateral (hindwing) discoidal triangle being as high as wide, not extended longitudinally' and presence of 'numerous crossveins in the cubito-anal area'. He did not argue against the synapomorphies proposed by Nel *et al.* for the Petaluroidea. Furtheremore, the hindwing discoidal triangle of the Aeschnidiidae is clearly transverse; it is not so for *Aktassia*, which has an elongate triangle. There are numerous crossveins in the cubito-anal area of all the anisopteran groups with a large and broad cubito-anal area. The Aeschnidiidae have several strong synapomorphies in the hindwing cubito-anal area (Nel and Martínez-Delclòs 1993). *Aktassia* has none of these synapomorphies. Therefore, we exclude the Aktassiidae from the Aeschnidioidea and restore them in the Petaluroidea.

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Typescript received 9 February 2000
Revised typescript received 4 January 2001