

# The discovery of aeschnidiid nymphs (Aeschnidiidae, Odonata, Insecta)

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**Abstract** Aeschnidiid nymphs are here first identified and described, and its phylogenetic relationship and bioecological characteristics are deduced. The nymphs known from China, Mongolia, Russia and Brazil and arranged in the family Aeschnidiidae are, in fact, unrelated to this group. All the known five Chinese species in four genera which were erected based on fossil nymphs and placed in the family Gomphidae may be transferred in Aeschnidiidae and merged into one alone, the *Sinaeschnidia cancellosa*. It is a geographically widespread species from the "Jehol biota" of East Asia and appeared in the latest Late Jurassic age.

**Keywords:** Jehol biota, Aeschnidiidae, dragonfly nymphs.

The extinct family Aeschnidiidae in the superfamily Aeschnidoidea of Anisoptera, Odonata is a primitive and specialized dragonfly group that lived only in the latest Late Jurassic (Lower Tithonian) to Early Cretaceous except for a single species, *Tauropteryx crassilovi* Pritykina, found in the earliest Late Cretaceous (Lower Cenomanian) at Crimea, Russia. It presented a diversification of sorts and a wide spread in geographical distribution at that time. Up to now, aeschnidiids with at least 25 species of 19 genera were described, all of which are based on the adult specimens respectively from Germany, England, Spain, Kazakstan, Russia, China, Australia, Brazil, and Egypt<sup>[1-5]</sup>.

Since the first species of Aeschnidiidae was discovered and described in the middle of the 19th century, none of its nymphs has yet been recovered. Nymphs play an important role for classifying the order Odonata at higher systematic ranks, and thus there have been different opinions about aeschnidiid assignment to superfamilies. It had been arranged respectively into Aeschnoidea<sup>[5-7]</sup>, Cordulegasteroidea<sup>[8,9]</sup>, and Aeschnidoidea<sup>[10]</sup> as well. Recently, however, some researchers announced that the aeschnidiid or aeschnidiid-like nymphs had been identified, and some discussions and descriptions of this dragonfly group have been issued<sup>[7,10,11]</sup>. But, the present author recently collected a large number of the real aeschnidiid nymphs from the non-marine sedimentary rocks of the Yixian Formation near Huangbanjiegou Village of Shangyuan Town in Beipiao City of Liaoning Province, China. These fossils have been able to be regarded as the nymphs of the species *Sinaeschnidia cancellosa* Ren beyond doubt, which will be synonymous of the species *Aeschnidium heishankowense* (Hong) comb. nov. (= *Sinaeschnidia heishankowensis* Hong<sup>[12]</sup>). The articles on discussion in detail of subdivision of the adult aeschnidiids will be soon published in other magazines. Making a comparison between them, the present author believes that those nymphs described by Chinese and foreign paleontologists cannot be placed in Aeschnidiidae, and thus, it is the first discovery and identification about aeschnidiid nymphs. The unique quality of preservation and the rich quantity of both sexual aeschnidiid nymphs ensured usefulness for revelation of its basic features, systematic position and phylogenetic relationship, subdivision between genera and species, bioecology, geological age, and geographical distribution as well.

## 1 Fundamental characteristics of nymphs

Nymphal diagnosis of the species *Sinaeschnidia cancellosa* Ren can now be given as follows.

Of libelluloid type but body considerably elongated, deplanately bucket-shaped, and covered with hairs at least on hind margins of abdominal segments. Antennae thin and long, 7-segmented. Clypeus strongly developed, armed with a tubercle at middle of its anterior margin. Eyes large, situated near fore margin of head, and convex dorso-laterally. Labial mark spoon-shaped, armed with long setae not only dorsally but also ventrally. Prementum widened apically and produced into a prominent median lobe, armed with a row of elongated setae on its lateral margins. Labial palp quite long and wide, possessing denticles on its inner and distal margins where without setae, outer margins narrow and flattened, and

movable end hooks small. Wing rudiments usually strongly divergent. Legs quite elongate, ambulatorial, covered without natatorial hairs, and with longitudinal ridges on femora and tibiae, tarsi 3-segmented (usually only single visible in most materials), and claws deeply cleft. Paraprocts robust, long, and cheliform, longer than the two last abdominal segments combined, each armed with wide median oncus. Cerci small and triangular. Epiproct oblong but with its posterior margin distinctly invaginating upwards. Female near penultimate instar with ovipositor complete, fully developed, and rather long (see the cover, figs. 1 and 2).

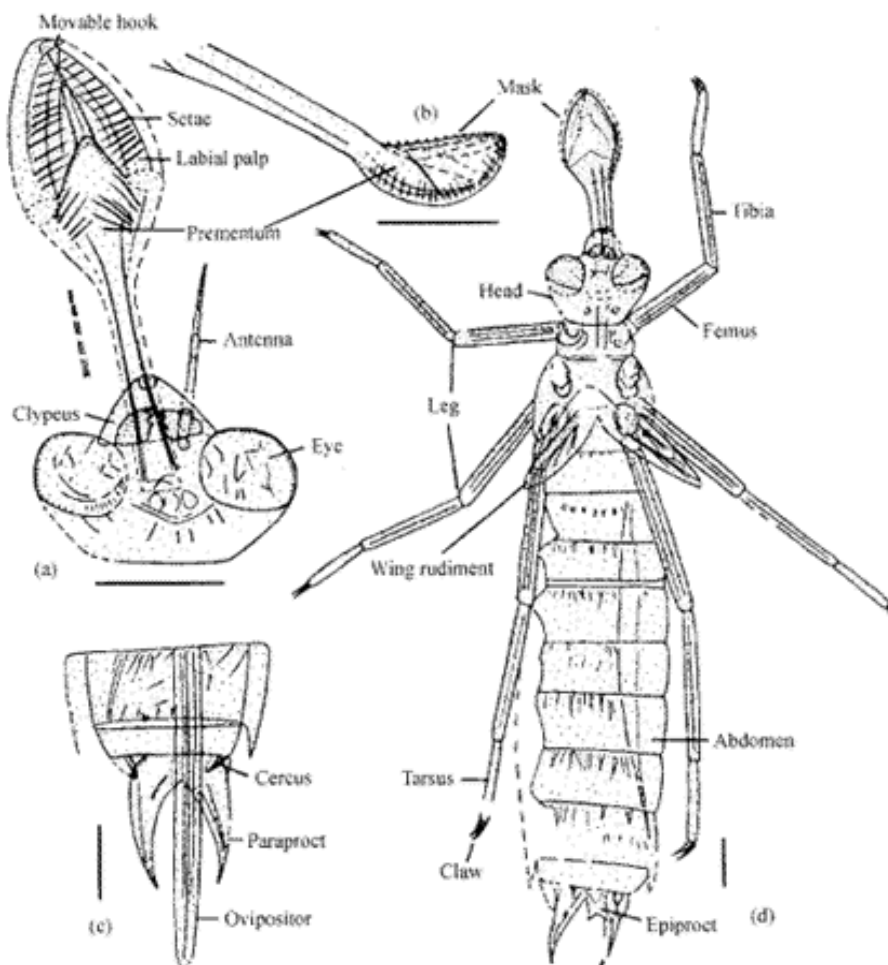


Fig. 1. *Sinaeschnidia cancellosa* Ren, young instar nymphs; (a) head (including labium), dorso-ventral aspect, B97611; (b) labial mask, B97619; (c) abdominal apex of female, dorso-ventral aspect, B97614; (d) male, dorso-ventral aspect, B97613. Scale bar = 5 mm.

## 2 Discussion

( ) Systematic position of nymphs. Odonates belong to hemimetabola. Although adults and nymphs share certain similarities in morphological characteristics to each other but their differences come to be rather obvious. However, it is very difficult to connect the nymphs with the adults in the living dragonflies not only at specific and generic levels but also at the familial rank when we have unknown their ontogenetic knowledge. In the extinct dragonflies of fossil materials this identification becomes hardly possible. But there is an exception to the *Sinaeschnidia cancellosa* Ren<sup>[5]</sup>, a real aeschnidiid species known from Upper Jurassic-Lower Cretaceous of China. Those near penultimate

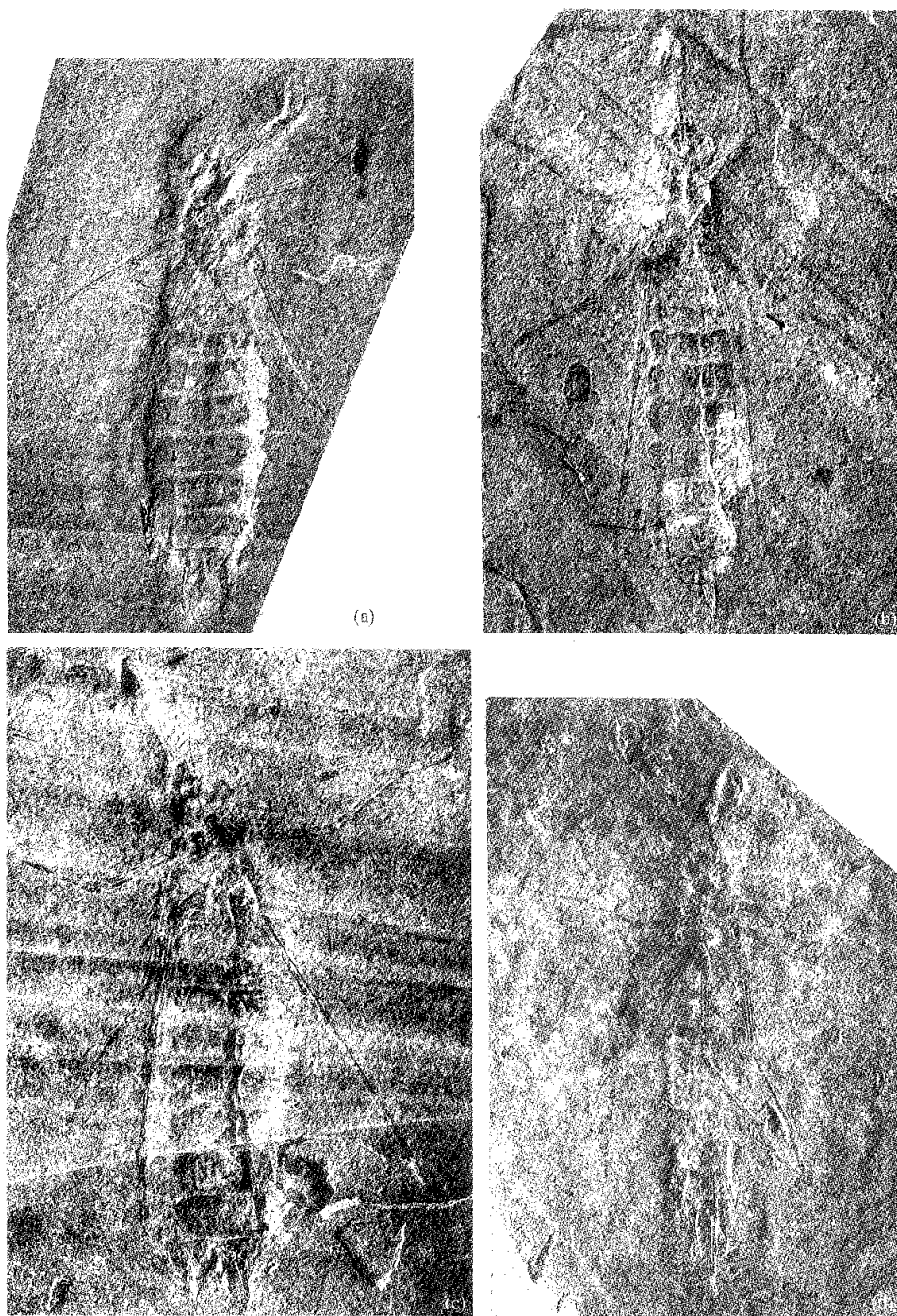


Fig. 2. *Sinaeschnidia cancellosa* Ren, young instar nymphs; (a) male, abdomen dorso-ventral aspect but with head and thorax lateral aspect,  $\times 1.3$ , B97619; (b) male, dorso-ventral aspect,  $\times 0.73$ , B97613; (c) male, dorso-ventral aspect,  $\times 0.95$ , B97611; (d) female, dorso-ventral aspect,  $\times 0.84$ , B97614.

instar female nymphs and female adults yielded in the Yixian Formation in Liaoning, China bear the hypertrophied ovipositors extremely resembling each other in shape and length (see figs. 1(c), 2(d) and 3). In addition, these nymphs and adults are one alone of dragonfly with so long ovipositors and are the archest in specimen number (belonging to the dominance species) among the known odonate fossil group at this locality (Huangbanjiegou Village), and thus both the two can be classified into the same species. It is quite evident that, based on the characteristics of nymphal mask, Aeschnidiidae cannot be placed in the Aeschnoidea. On the other hand, the new replenished proof is that the undoubted aeschnidiid nymphs possess close similarities to those of Cordulegasteroidea, but might be distinguished from the latter by the well-developed setae on ventral labial mask, the very long ovipositor, and the large pincer-like paraprocts as well. Hence the foundation of Aeschnidoidea might well be correct.



Fig. 3. *Sinaeschnidia cancellosa* Ren, female adult, dorso-ventral aspect,  $\times 0.83$ , B930040-2.

Those nymphs known from the Yixian Formation in Liaoning and the Chijinqiao Formation in Gansu Province, China had been named as *Yixiangomphus labius* (Lin)<sup>[13]</sup> (= *Archaeogomphus labius* Lin<sup>[14,15]</sup>; *Archaeogomphus* sp.<sup>[16]</sup>), and mistakenly assigned to the extant family Gomphidae. The present author had the opportunity to reexamine the type specimen of *Yixiangomphus labius* (Lin). The characterized nymph does not correspond to the figure drawn by the founder. It is based on a young female nymph, with abdomen dorso-ventrally preserved but head (including labial mask) and thorax nearly laterally. The labial mask is typically spoon-shaped undoubtedly, with certain portions damaged. Setae on ventral are probably bad-preserved and invisible. Antennae show thin and long, bad-preserved terminally but with basic six segments visible. Ovipositor extends from hind margin of the eighth abdominal segment, ends at hind margin of the tenth one. The ninth abdominal segment is armed with a pair of long lateral spines. Paraprocts show strongly developed, and appears in cheliform, with a broad crista on median portion. Epiproct becomes oblong but with its posterior margin distinctly invaginating upwards. Cerci are triangular. All the visible features come up to entire identity to that of *Sinaeschnidia cancellosa* Ren described in this paper, and then both the two can be conspecific.

The *Pseudosamarura largina* Lin known from Yixian Formation at Dakonpu in Yixian City of Liaoning Province, China is founded based on a single specimen on lateral aspect, with terminal half of abdomen missing. It was also incorrectly arranged to Gomphidae<sup>[14]</sup>. After reexamining the type specimen, the present author identifies its antennae being absent, labial mask showing lateral aspect. It

shares the fundamental characteristics wholly similar to that of *Yixiangomphus labius* (Lin), thus may be treated as *Sinaeschnidia* cf. *S. cancellosa* Ren.

*Dissurus qingquanensis* Hong (originally spelling the specific name *Dissurus qinquanensis*) was based on a single young male nymph known from the Chijinpu (=Chijinjiao) Formation at Xiagou Village in Jiudian City of Gansu province, China was regarded erroneously as the member of Gomphidae<sup>[16]</sup>. It bears no visible differences from *Yixiangomphus labius* (Lin) despite of its mask and epiproct, both of which are badly preserved and invisible. It could be also assigned to *Sinaeschnidia* cf. *S. cancellosa* Ren. Another species *Dissurus liaoyuanensis* Hong (originally spelling the specific name *Dissurus liauyuanensis*) known from Jingangshan (=the Yixian) Formation in Liaoyuan City of Liaoning Province, China belongs to a poorly-known nymph<sup>[15]</sup>, with head wanting, and terminal portion of abdomen damaged. It could reluctantly be dealt with as *Sinaeschnidia* cf. *S. cancellosa* Ren. However, until new information becomes available, the two species can only be considered the provisional members of the *Sinaeschnidia cancellosa* Ren.

The new genus and new species *Neimengolmphus dongwugaiensis* Hong (originally spelling the generic name *Neimenggolmphus* Hong) was erected by many nymph specimens collected from the Huliugou Formation (=lower part of Lisangou Formation) at Shilianji in Wulate, Neimenggol region, China and placed into the subfamily Gomphinae within Gomphidae<sup>[17]</sup>. All the materials lack nymphal heads. The type specimen is a young instar female nymph, with its ovipositor clearly visible according to the photograph provided by the paper<sup>[17]</sup>. All the derived characteristics are extremely similar to that of *Sinaeschnidia cancellosa* Ren, and thus may be taken for *Sinaeschnidia* cf. *S. cancellosa* Ren.

Meanwhile, it is puzzling that several larva remains discovered from the Laiyang Formation in Laiyang City of Shandong province, China had temporarily been classified into the *Sinaeschnidia heishankowensis* Hong<sup>[7]</sup>. It is difficult to see from the descriptions how they might be related to dragonflies, let alone the *Sinaeschnidia heishankowensis* Hong. Great deals of this sort of fossil larvae have recently been recovered by the present author from the identical locality and horizon. After examining these samples, the author confirms that they should belong to the order Diptera, and most likely related to the larvae of the family Syrphidae (flower flies) within the suborder Cyclorrhapha.

Some European specialists thought that there is a strong possibility that all the nymphs with forcep-like paraprocts of Nothomacromiidae, Hemeroscopidae, and Sonidae respectively from the Lower Cretaceous in Brizal, Mongolia and Russia belong to a common family Sonidae (s.str.), which might represent the nymphs of Stenophlebiodea or even more probably of the Aeschnidiidae<sup>[11,18]</sup>. Owing to the discovery of true aeschnidiid nymphs described herein, it is most likely that this conclusion is erroneous. Comparing Aeschnidiidae in the basic features of nymph with Nothomacromiidae (=Pseudomacromiidae)<sup>[10]</sup> and Sonidae<sup>[19]</sup>, the last two show that the labial mask is flat without setae on prementum and small labial palpi, and relatively large movable end hooks, a typical aeschnoid-shaped that clearly differs from the libelluloid-shaped labial mask of the former. Thus, both the two become estranged in relationships, and cannot be merged into single family. On the other hand, a single specimen of nymphal mask originally placed in the nymphs of Hemeroscopidae is probably related neither sonid and hemeroscopid nymphs. It belongs possibly to a genuine aeschnidiid nymph who has a close relationship to the *Leptaeschnidium latum* Pritykina<sup>[9]</sup>, an indisputable aeschnidiid representative founded according to adult hindwings from the identical locality in Trans Baikal of Russia. Perhaps both belong to the same species. But, this deduction remains to be confirmed by new fossil materials or the original author's further explanations.

Contrary to some paleoentomologists<sup>[11,18]</sup>, the present author believes that there is the strong possibility that the absolutely unique forcep-like paraprocts, considerably small epiproct and cerci, elongate body, long and strongly developed antennae appeared in many extinct families of the Anisoptera that represent an almost certainly plesiomorphic state, and reflect the evolutionary stage of this dragonfly group at that time. Meanwhile, it is possibly related to the features of the special paleoclimate and paleoecology during the Late Mesozoic age.

( ) Deduction of nymph biology and ecology. There at least are four nymphal instars of *Sinaeschnidia cancellosa* Ren to be distinguishable according to these specimens known from the Yixian Formation in Huangbanjiegou Village in Shangyuan Town of Beipiao City of Liaoning

Province, China, all of which are of young instar nymphs, the oldest belonging possibly to near penultimate. Various instar nymphs show clearly different in body in size, width, and length. The youngest is only 20 mm long and 11mm wide, whereas the oldest reaches 76 mm in length and 17 mm in width. Other structures are also greatly different, such as the labium, legs, paraprocts, and ovipositor, etc. in length and width. The epiproct and female ovipositor are hardly visible in the youngest nymphs. The longest ovipositor reaches 23 mm in length, and nearly as long as that of adult. The present author considers that all these fossils might be assigned into a single species, because it is hardly possible that, in a definite lake and geographic region, many huge and predatory aquatic insects who belong in several species within a single genus coexisted in the light of the viewpoint not only of taxonomy but also of ecology.

The abundance and good preservation of the specialized aeschnidiid nymphs allow us to make assumptions in detail concerning their possible habitats, mode of life as well as bionomic characteristics based on the fundamentals of functional morphology, ecological knowledge of the known, similar extant nymphs, and characteristics of taphonomy, etc. The nymph *Sinaeschnidia cancellosa* Ren most probably represents sprawlers who lived in the warm shallow lakes of low-energy fresh water, perching in root of vegetation on the bottom near shores of lake or river mouths. Comparing those neighbors of the great swimmers with these lacustrine insects, they seem to be not good at swimming, and usually crept on silt, and made a living of semi-swimming and semi-crawling. The well-developed clypeus arms with tubercle on middle of its anterior margin, presumably an adaptation for burrowing, even if that was so, perhaps they could descend in the silt and muck by raking it out from beneath with their clypeus, legs, and paraprocts. Then they kicked it up over their backs and hid themselves against observation, having only the large eyes, the aristiform antennae, the respiratory aperture at the tip of abdomen (invisible on the fossil specimens), and probably the strongly developed paraprocts exposed. In this case, so succeeded in staying hidden that they would be hardly seen by both their natural enemies and targets for hunting. Sometimes they lay in ambush, entirely inactive where main another aquatic insects lived. Their neighbors were probably nymphs of *Ephemeropsis trisetalis* Eichward (a mayfly species), larvae and imagoes of *Coptoclava longipoda* Ping (a beetle species) and of *Mesolygaeus laiyangensis* Ping (a bug species), other kind of aquatic bugs, wigglers of *Chironomapter gregaria* (Grabau) (a mosquito species), other species of nymph dragonflies, *Peipiaosteus* sp. (fish) and *Lycoptera* sp. (fish), etc. It is most likely that they hunted the wandering near of wigglers of *Chironomaptera gregaria* (Grabau), larvae or adults of *Mesolygaeus laiyangensis* Ping, young larvae of *Coptoclava longipoda* Ping, young nymphs of *Ephemeropsis trisetalis* Eichward, and even callow fishes invited a thrust of the enormous grasping mask. Their natural enemies might be the ferocious fishes, *Peipiaosteus* sp. and *Lycoptera* sp., meanwhile the young nymphs of *Sinaeschnidia cancellosa* Ren might be harassed and assaulted by the adults and near ultimate instar larvae of *Coptoclava longipoda* Ping, near ultimate instar larvae of *Ephemeropsis trisetalis* Eichward or other species of nymph dragonfly. They hid themselves in holes or burrows, and sometimes, they could crawled rapidly on bottom to escape from the enemy's attack. The long paraprocts of them whereas probably performed a function for predator deterrent.

( ) Distribution and geological age. Nymph *Sinaeschnidia cancellosa* Ren has been spotted from the Yixian Formation at the following localities: the Shangyuan in Beipiao, Dakangpu in Yixian, Dawangzhangzi in Lingyuan of Liaoning Province, the Chijinpu Formation at Xiagou in Qingquan of Gansu Province, the Huliugou Formation in Wulate of Neimenggol region, the Nanzhao Formation in Nanzhao of Henan Province. Adult *Sinaeschnidia cancellosa* Ren has been discovered from the Yixian Formation in Senjitu of Fengning, Hebei Province, the Laiyang Formation in Laiyang of Shandong Province, the Hangjiahu Formation at Yangjiaxie in Huzhou of Zhejiang Province, China as well as the Turga Formation in Trans Baikal of southern Siberia, Russia, besides the Yixian Formation in Shangyuan of Beipiao, Liaoning Province and the Chijinpu Formation at Xiagou in Qingquan of Gansu Province. These specimens have respectively been identified as the *Hebeiaeschnidia fengningensis* Hong<sup>[16]</sup>, *Sinaeschnidia heishankowensis* Hong, *S. huzhouensis* Zhou et Wei<sup>[20]</sup>, and *Sinaeschnidia* sp.<sup>[21]</sup> All of them would be merged into a single species *Aeschnidium heishankowense* (Hong) comb. nov., a revised specific name which will be issued in other papers. It leaves the question open that this

aeschnidiid adult appeared also in the Jiufutang Formation at Meileiyingzi in Kezuo, Liaoning Province, China and The Shahai Formation at Heishangou in Chifeng, Neimenggol region, China. The strata bearing the adult aeschnidiids need to make a reinvestigation.

Like the *Ephemeropsis trisetalis* Eichward, *Sinaeschnidia cancellosa* Ren represented another geographically widespread species within "Jehol biota", and appeared in almost throughout eastern Asia at that time. However, there has still been the focus of much discussion about the geological age among Chinese paleontologists. Different researchers regarded it as the Late Jurassic, Late Jurassic-Early Cretaceous, or Early Cretaceous, respectively. It is common knowledge that the determination of geological age for non-marine sedimentary rocks is decided mainly by the biostratigraphical information. It is quite evident that the most reliable and important way to solve this problem is based on a comparison between the creatures yielded in both terrestrial and marine deposits. Aeschnidiids possessed a short specific longevity, and the ability for rapid migration and evolution. Among them, two species within *Aeschnidium* Westwood, *Aeschnidium densum* (Hagen) and *Sinaeschnidia cancellosa* Ren (= *Aeschnidium heishankowense* (Hong)), were founded by well-preserved fossils, and enable us to make a comparison based on the advanced standards of modern insect classification. The former is known from the Lower Tithonian in Solnhöfen, Germany, and the latter distributed throughout "Jehol biota". If *Aeschnidium* Westwood originated from East Asia, it would be possible that the appearance of the Chinese species would not later than the Kimmeridgian. On the other hand, it would be most likely the oriental aeschnidiid moved from Europe to Asia. As they are characterized by long migrations and probably as so fast as the corresponding period birds and dinosaurs, the time that spent in the course of the migratory flight might be negligible during the geological past. But, a new species comes into being only after the change of the genes, and then it would take a considerably long time. Therefore, it is assumed that the appearance of *Sinaeschnidia cancellosa* Ren (= *Aeschnidium heishankowense* (Hong)) is slightly later than that of *Aeschnidium densum*, and the beginning of its existence is possibly from Middle or Upper Tithonian, that is to say, by the end of latest Late Jurassic age. The oldest aeschnidiid-bearing strata within the Yixian Formation in Hebei and Liaoning provinces, China could be regarded as the Upper Jurassic sediments. This is probably the interesting Chinese species extending itself into the beginning of the Early Cretaceous throughout eastern Asia. The exactly geological age for extinction of this species needs to make further investigation.

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