New Early Cretaceous pentatomorph bugs from China and the systematic position of Kobdocoridae

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Kobdocoridae is an extinct family of the infraorder Pentatomomorpha, mainly distributed in the Eurasia and currently comprise only nine species from seven genera in three locations. But, the systematic position of the Kobdocoridae has long been debated. Here we describe a new genus and species *Maculocris yixiani* Dai, Yao, & Ren, from the Lower Cretaceous Yixian Formation in Northeastern China. This new genus is characterized by eyes relatively small, contiguous with pronotum; triangular scutellum, clavus with margins converging towards apex and large rounded patterns on the hemelytra, distinguishing it from other genera within the family. Based on the discovery of new specimens, Kobdocoridae are characterized by having slender antennal segments with the first segment partially concealed dorsally on the head; an elongated labium reaching at least the hind legs; initially rounded scutellum, with some genera possessing large scutellum covering the hemelytra; a clavus reduced to a rod-like structure; the claval commisure absent; and a tarsus with three segments. These features are proposed to be closely related to Pentatomoidea, possibly as a stem group or sister taxon.

Key words: Insecta, Aradoidea, Pentatomoidea, fossil, Yixian Formation, Mesozoic.

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Introduction

The Pentatomomorpha is the second largest infraorder of the Heteroptera, subdivided into six superfamilies, namely Pentatomoidea, Coreoidea, Lygaeoidea, Pyrrhocoroidea, Aradoidea, and Idiostoloidea (Henry 1997; Weirauch et al. 2019; Schuh and Weirauch 2020). The fossil records of the Pentatomomorpha can be traced back to the Late Triassic, and throughout its long evolutionary history, numerous extinct groups have appeared, including Pachymeridiidae Handlirsch, 1906; Yuripopovinidae Azar et al., 2011; Mesopentacoridae Popov, 1986; Primipentatomidae Yao et al., 2013, and Kobdocoridae Popov, 1986 (Dai et al. 2022; Yao et al. 2012, 2013). Popov (1986) established Kobdocoridae based on specimens from the Lower Cretaceous of Mongolia and considered it to be the earliest fossil record of the Aradoidea (Popov 1986). Due to image data acquisition being limited at that time, the membrane with reticulate venation was not observed with enough details. Yao et al. (2012)

established Venicoridae based on numerous specimens from the Lower Cretaceous Yixian Formation of China (now considered synonym of Kobdocoridae), and conducted a phylogenetic analysis of the Pentatomomorpha. Their results showed that the monophyly of the Venicoridae was strongly supported. Subsequently, Du et al. (2016) also described two new species under Venicoridae based on specimens from northeastern China. Schuh and Weirauch (2020) summarized the fossil groups of the Heteroptera in their monograph, endorsing Popov's (1986) placement of Kobdocoridae within the Aradoidea and proposed that Venicoridae should be classified under the Idiostoloidea. More recently, Ryzhkova et al. (2023) re-examined the type specimen used by Popov (1986) to establish Kobdocoridae. Then, drawing on the original specimens from Khasurty, Russia, situated within the Mesozoic outcrops of the lower subformation of the Sangin Formation of the Gusinoe Ozero Group, which are Upper Jurassic and Lower Cretaceous, they analyzed and compared two groups from Mongolia and China. Their results proposed a synonymy of Kobdocoridae Popov, 1986, and Venicoridae Yao et al., 2012. Currently, there are 9 species in 7 genera within Kobdocoridae. They are: *Kobdocoris aradinus* Popov, 1986, from Mongolia; *Venicoris solaris* Yao et al., 2012, *Clavaticoris zhengi* Yao et al., 2012, *Halonatusivena shii* Du et al., 2016, *Halonatusivena nervosus* Du et al., 2016, from China; and *Khasoris yuripopovi* Ryzhkova, 2023, *Buryatocera beta* Ryzhkova, 2023, *Extralapis breviscutum* Ryzhkova, 2023, *Extralapis carens* Ryzhkova, 2023, from Russia.

A recent discovery in the Yixian Formation of Yixian County, Liaoning Province, China, has provided 10 impression fossil specimens (CNU-HET-LB2024010–2024019). These specimens display well-preserved bodies and have been identified as belonging to species of previously unknown genus of Kobdocoridae. Based on the new specimens discovered, we have summarized the characteristics of family Kobdocoridae and explored its systematic position.

Institutional abbreviations.—CNU, Capital Normal University, Beijing, China; STRC, Science and Technology Research Center of China Customs, Beijing, China.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:56A55AC4-FE32-4E85-BDE0-44058A572DEB.

Material and methods

The materials studied herein (CNU-HET-LB2024010– 2024019) come from the Yixian Formation. The Yixian Formation is primarily composed of volcanic materials, along with minor layers of sedimentary rocks that are abundant in fossils. The sedimentary sequence in this area is characterized by lacustrine sediments, mainly consisting of shale and tuff (Zhou et al. 2003; Xu et al. 2017). It was deposited during the early Aptian, Early Cretaceous, approximately 125 million years ago (Chang et al. 2017) This formation has yielded fossils of almost all known fossil groups of Pentatomomorpha, including the majority of the aforementioned extinct families and extant families, such as Cydnidae and Rhopalidae (Yao et al. 2007; Chen et al. 2015).

The specimens were examined and photographed using a Nikon SMZ25 dissecting microscope and a Nikon ECLIPSE Ni microscope, both fitted with a Nikon DS-Ri 2 digital camera system. The specimen was illustrated with the aid of a camera attached to the microscope. Morphological terminology mainly follows Schuh and Weirauch (2020).

Body length was measured along the midline from the apex of the head to the apex of the abdomen. Body width was measured at the maximum width of the body. The length of the fore wing was measured from its base to its apex. All measurements are given in millimeters.

Systematic palaeontology

Class Insecta Linnaeus, 1758 Order Hemiptera Linnaeus, 1758 Suborder Heteroptera Latreille, 1810 Infraorder Pentatomomorpha Leston et al., 1954 Family Kobdocoridae Popov, 1986 = Venicoridae Yao et al., 2012 Genus *Maculocris* Dai, Yao, & Ren. nov. *Zoobank LSID*: urn:lsid:zoobank.org:act:8C8D5ABA-3C0B-4B9E-8

EBF-1D08F56C5362.

Etymology: A combination of Latin *macula*, a spot and Classic Greek *coris*, true bug, in reference to the presence of the characteristic spots on the hemelytra. Masculine.

Type species: Maculocris yixiani Dai, Yao, & Ren sp. nov.; by mono-typy; see below.

Diagnosis.—As for the type species.

Remarks.—The new genus and *Clavaticoris* Yao et al., 2012, from the same locality, the two significantly differ in morphological characteristics: head pentagonal, with similar length and width (vs. the latter with a rectangular head, length greater than the width); second segment shorter than the last two segment combined (vs. second segment much greater than the last two segment combined); pronotum callosities present (vs. callosities absent); labium only extends to the metacoxae (vs. labium extending to the third abdominal segment); and the ovipositor long, bisecting the last four abdominal segments (vs. the ovipositor only bisecting the last three abdominal segments).

The new genus and Halonatusivena Du et al., 2016, are from the same locality, but are also the most morphologically similar. Both of them have pentagonal head with similar length and width; the length of the second segment is no longer than the sum of the last two segments; both have distinct callosities on the pronotum. These shared characteristics distinguish them from other genera within the family. Therefore, we believe that the new genus is more closely related to Halonatusivena. However, they can be distinctly differentiated based on the following characteristics: the new genus has a larger body size of about 20 mm (vs. medium-sized, less than 10 mm of *Halonatusivena*); eyes relatively small, anterior almost adjacent to margin of pronotum. (vs. compound eyes are larger and anterior distant from the margin of pronotum of Halonatusivena); the distance between the ocelli is greater than the distance from an ocellus to a compound eye (vs. ocelli are close together, with the distance between them smaller than the distance from an ocellus to a compound eye of *Halonatusivena*); scutellum punctate, triangulate without median trifurcate carina, covering party the clavus (vs. scutellum without puncture, with a approximately T-shaped carina, narrowing gradually towards the apex and not covering the clavus of Halonatusivena).

Stratigraphic and geographic range.—As for the type species.

Maculocris yixiani Dai, Yao, & Ren sp. nov.

Figs. 1-3.

Zoobank LSID: urn:lsid:zoobank.org:act:C2EC4776-4122-46EA-BE22-A3DFFF4B7DB4.

Etymology: Derived from the Yixian Formation, where it was discovered. *Type material*: Holotype CNU-HET-LB2024010, male, well preserved bodies, antennae and forewings. Paratypes: CNU-HET-LB2024011, male; CNU-HET-LB2024012–15 female; CNU-HET-LB2024016–19, male; well preserved bodies, labium, leges and ovipositor from the type locality and horizon.

Type locality: Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, China.

Type horizon: Yixian Formation, lower Aptian, Lower Cretaceous.

Diagnosis.—Body large (Fig. 1A). Head nearly rounded pentagonal, as long as wide (Fig. 2B). Eyes relatively small, anterior almost adjacent to margin of pronotum (Fig. 1A). Length of antennomere II less than the combined length of antennomere III and IV (Fig. 3B₄). Bucculae reaching at the midline of compound eyes, half the length of head (Fig. 2B). Labium reaching metacoxae (Fig. 1C). Ocelli situated closer to eyes than to each other (Fig. 2A). Pronotum impunctate; callosities well-developed, oval; posterior angles rounded (Fig. 2A). Scutellum punctate, triangular without sharp vertices, covered part of abdominal (Fig. 3C). Forewings corium with two rounded markings (Fig. 1A). Ovipositor long, bisecting the last four abdominal segments (Fig. 1C, D).

Description.—Body elongated, about 2.76 times as long as wide.

Head pentagonal, slightly shorter than pronotum, length about equal to width. Mandibular plates not projecting past midpoint of clypeus. Antenna four segments, slender, slightly shorter than half of body, antennomere I shortest, slightly exceeding the apex of head, antennomere II longest, antennomere III and IV subequal in length; antennomeres I–III subcylindrical, antennomere IV fusiform. Labium four-segmented, straight, appressed to venter, reaching metacoxae, labiomere II longest, 2.05 times as long as labiomere II, labiomere II–III subequal in length, labiomere IV shortest, tapering apically. Compund eyes relatively small, anterior almost adjacent to margin of pronotum. Ocelli present, closer to eyes than to each other, interocular gap narrower than the diameter of the ocelli.

Thorax smooth. Pronotum 1.56 times as wide as long, lateral margin convex, posterior angles feebly rounded. Pronotal collar and carinae absent. Pronotum with two large callosities on anterior area, callus broader than intercallus space. Scutellum subequilateral triangular; about 0.93 times as long as pronotum at midline, 0.85 times as wide as long.

Hemelytron poorly preserved, membrane venation not visible. Corium relatively small, almost 1/3 length of hemelytron. Corium with two obvious rounded markings, one



Fig. 1. Kobdocorid pentotomomorph bug *Maculocris yixiani* Dai, Yao, & Ren gen. et sp. nov. from the Lower Cretaceous Yixian Formation of Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, China. A. Holotype, male, CNU-HET-LB2024010. B. Paratype, male, CNU-HET-LB2024011. C. Paratype, female, CNU-HET-LB2024012. D. Paratype, female, CNU-HET-LB2024013. Scale bars 4 mm.

of oval shapes in 1/3 length middle of corium, the other one nearly circular and relatively small on posterior margin of corium. R, M and Cu fuse in the basal of corium. Clavus well developed, clavate, tapers from the base to the apex, claval commissure absent.

Legs slender. Femora stout, about 2 times as thick as corresponding tibiae. Hind legs longer than fore and mid legs, metafemur longest, about 1.28 times as long as mesofemur, about 1.09 times as long as profemur, metatibia longest, about 1.27 times as long as mesotibia, about 1.65 times as long as protibia. Tarsi three-segmented, second shortest, third tarsomeres 3.91 times the length of the second. Pulvilli present.

Abdomen oval, abdominal connexivum sternites II–VII visible, Ovipositor long, bisecting the last four abdominal segments, about 1/3 of body length (Table 1).

Stratigraphic and geographic range.—Yixian Formation, lower Aptian, Lower Cretaceous of Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, China.



Fig. 2. Line drawings of a kobdocorid pentotomomorph bug *Maculocris yixiani* Dai, Yao, & Ren gen. et sp. nov. from the Lower Cretaceous Yixian Formation of Northeastern China. **A**. Body in dorsal view. **B**. Head in ventral view. **C**. Forewing. **D**. Fore leg. **E**. Mid leg. **F**. Hind leg.

Table 1. Measurements (in mm) of Maculocris yixiani Dai, Yao, & Ren	
gen. et sp. nov. specimens.	

	Holotype CNU- HET-LB2024010	Paratype CNU- HET-LB2024011–19
Body length/width	19.65/7.11	17.11-20.35/5.73-8.05
Head length/width	2.69/2.56	2.33-3.23/2.26-2.56
Interocular space	2.70	2.48-2.83
Preocellar space	0.57	0.51-0.57
Antennal segments length	8.11	8.04-8.17
Labium segments length	_	7.20–7.36
Pronotum length/width	3.43/5.35	2.89-4.04/4.32-5.56
Scutellum length/width	3.18/2.93	2.77-3.63/4.32-5.56
Fore leg length	9.31	8.96–10.11
Middle leg length	9.38	9.12–10.57
Hind leg length	11.91	11.46–12.34
Male genitalia	2.56	2.38-2.56

Discussion

All species of Kobdocoridae have the reticulate venation on hemelytra membrane, which seems to be a rather unique feature in kobdocorids (Du et al. 2016). Unfortunately, in all ten specimens of Maculocris gen. nov., membranes of the forewing are poorly preserved. However, based on the following characteristics: (i) antennae inserted anteriad to anterior margin of eye; (ii) R, M, and Cu fused at the base of clavus; (iii) claval commissure reduced; (iv) the connexivum exposed completely; (v) acicular ovipositor well-developed, we assign the new genus to Kobdocoridae (Yao et al. 2012). The species of Kobdocoridae are known from three locations: Mongolia (Myangad, Lower Cretaceous, Gurvan-Eren Formation), Russia (Khasurty, Lower Cretaceous, Khasurty Formation), and China (Liaoning Province, Lower Cretaceous, Yixian Formation). Analysis of external morphological characteristics based on these locations revealed that individuals from Mongolia and Russia have a relatively wide pronotum, more



Fig. 3. Morphological details of kobdocorid pentotomomorph bug *Maculocris yixiani* Dai, Yao, & Ren gen. et sp. nov. from the Lower Cretaceous Yixian Formation of China. **A**. Holotype, male, CNU-HET-LB2024010; head (A₁), forewing (A₂). **B**. Paratype, male, CNU-HET-LB2024011; labium (B₁); ovipositor (B₂); tarsus (B₃); antennae (B₄). **C**. Paratype, female, CNU-HET-LB2024012; scutellum. Abbreviations: AI–IV, antennae I–IV; b, buccula; cal, callosities; cl, claw; lb1–4, labium 1–4; o, ocellus; pl, pulvillus; t1–3, tarsus 1–4. Scale bars A₁, B₃, C, 1 mm; 2 mm, B₁, B₂, A₂, B₄.

than twice as wide as long. In contrast, individuals from China have a noticeably longer pronotum, with a width only about 1.5 times the length, while other characteristics show no significant differences among the locations.

Currently, the taxonomic position of Kobdocoridae is controversial. When Popov et al. (1986) established Kobdocoridae, they considered its broad body and the morphology of the head and pronotum to be similar to those of Aradoidea. Yao et al. (2012) established Venicoridae (a synonym of Kobdocoridae) and found it to be a sister group to the entire Eutrichophora, rather than placing Kobdocoridae within Aradoidea. Schuh and Weirauch (2020) endorsed Popov's placement of Kobdocoridae within the Aradoidea and proposed that Venicoridae should be included in the Idiostoloidea. Ryzhkova et al. (2023) considered Venicoridae to be a synonym of Kobdocoridae and argued that Kobdocoridae should not be placed in Aradoidea, but does not specify which position (Table 2). Now, with the characterization of the new genus and species of of Kobdocoridae, we agree with Ryzhkova et al. (2023) and Yao et al. (2012) that Kobdocoridae should not be placed in Aradoidea. And, according to the characterization of the new specimen Kobdocoridae should be the stem group of Pentatomoidea. The reasons for this placement are outlined below.

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Taxonomic decision	Based on	References	
Venicoridae as synonym of Kobdodoridae; unknown higher classification		Ryzhkova et al. 2023	
Venicoridae as a sister group of Eutrichophora	phylogenetic analysis	Yao et al. 2021	
Kobdocoridae as a part of Aradoidea	body and head morphology	Schuh and Weirauch 2020	
Venicoridae as a part of Idiostoloidea	membrane and veins morphology		
Kobdocoridae as a part of Aradoidea	body, head, and pronotum morphology	Popov 1986	

It is widely accepted that Aradoidea should be placed in Pentatomomorpha and that they are the sister group to the remaining Pentatomomorpha (Henry 1997; Hua et al. 2008; Cassis and Schuh 2010; Tian et al. 2011; Yao et al. 2012; Wang et al. 2016; Weirauch et al. 2019). We agree that Aradoidea is placed in Pentatomomorpha and use that taxonomic decision. The morphological evidence available through phylogenetic analyses by Henrry (1997) supported the monophyly of the Aradoidea based on the following characteristics: (i) ocelli absent; (ii) first antennal segment short and stout; (iii) fourth antennal segment thickened and globose; and (iv) tarsus with two segments. Results from Yao et al. (2012) also supports the monophyly of Aradoidea based on: (i) flattened body; (ii) short labium, not extending posteriorly to forecoxae; (iii) mandibles and maxillae extremely elongated and coiled within head; and (iv) fourth antennal segment thickened and globose; (v) tarsus with two segments; and (vi) fungivory. The phylogenetic analysis of Weirauch et al. (2019) indicates that: (i) ocelli absent; (ii) stylets, inside head coiled; (iii) claval commissure absent, wings overlapping posterior to scutellum; (iv) coxae in each pair separated by 3-4 times coxal width; and (v) tarsus with two segments. While there are differences between conclusions of the morphology of antennae and labium, and whether the claval commissure exists, one stable character is the tarsi with two segments. However, based on published fossil records, all kobdocorid genera have tarsi with three segments. Furthermore, the absence of ocelli, the morphology of antennae and the length of labium, are also important characteristics supporting the monophyly of the Aradoidea. The Maculocris vixiani Dai, Yao, & Ren gen. et sp. nov. and Halonatusivena. nervosus Du et al., 2016, display significantly larger ocelli observed also in the Extralapis. carens Ryzhkova, 2023, and E. breviscutum Ryzhkova, 2023. Additionally, all kobdocorid species have slender antennal segments, with the first antennal segment not fully visible on the dorsal of the head, and the fourth antennal segment slender (vs. Aradoidea antennae short and stout, the first antennal segment fully exposed and the fourth segment thickened). The labium of species within Kobdocoridae is elongated, reaching at least to the base of the hind legs, in Clavaticoris zhengi Yao et al., 2012, it may even extend to the third abdominal segment (vs. the labium of Aradoidea species is typically shorter and thicker, not extending posteriorly to forecoxae). As above, Kobdocoridae lacks the synapomorphy of Aradoidea, exhibiting characteristics that are significantly different from Aradoidea in terms of the presence or absence of ocelli, the morphology of antennae, the length of labium, the number of tarsomeres, etc. Therefore, we conclude that Kobdocoridae should not be classified within Aradoidea.

Schuh and Weirauch (2020) suggested that Venicoridae (synonym of Kobdocoridae), with reticulate membrane veins, should be classified within the Idiostoloidea. However, having reticulate wing veins is not exclusive to the Idiostoloidea. For example, groups within the two super-

families Pentatomidae and Pyrrhocoroidea, which also belong to the Pentatomomorpha, exhibit reticulate wing veins (Du et al. 2016). Therefore, categorizing Venicoridae (synonym of Kobdocoridae) solely based on this feature as part of the Idiostoloidea is not sufficient evidence. Additionally, the characteristics of Venicoridae (Kobdocoridae) are very different from Idiostoloidea. For example, all species of Kobdocoridae have (i) the clavus reduced (vs. Idiostoloidea having the clavus wide and big); (ii) only a single vein 1A present on clavus (vs. veins 1A and 2A present on clavus); and (iii) the claval commisure absent (vs. the claval commisure present). In addition, in the Maculocris vixiani Dai, Yao, & Ren gen. et sp. nov. has the abdominal connexivum on segment VII present (vs. abdominal connexivum on segment VII being absent in Idostoloidea). The latter characteristics support the monophyly of the Idiostoloidea (Henry 1997; Yao et al. 2012). Therefore, we believe that Venicoridae (synonym of Kobdocoridae) should also not be classified within the Idiostoloidea.

Yao et al. (2012), while establishing the Venicoridae (a synonym of Kobdocoridae), conducted a phylogenetic analysis using 130 characteristics on 5 fossil groups and 34 extant groups within the Pentatomomorpha. The monophyly of Kobdocoridae received strong support; the group was found to be sister to the entire Eutrichophora. Yao et al. (2012) did not assigns Kobdocoridae to any specific superfamily but they argued that some characteristics of Kobdocoridae are more similar to the Pentatomoidea than to the Coreoidea. Based on the new fossil specimens studied herein, as well as a summary of the characteristics of all Kobdocoridae species, we agree with this point for the following reasons. First, all species within Kobdocoridae have rounded and blunt scutellum, with some genera having large scutellum that cover the hemelytra, and in new species the scutellum even reaches the third abdominal segment; the clavus is reduced into a rod-like structure. Second, only a single vein 1A is present on clavus, and the claval commisure absent. Next, the grooved scent peritreme is observed in Venicoris solaris Yao et al., 2012. The above characteristics are more similar to the Pentatomoidea than to the Coreoidea (which scutella are small, clavi are large, claval commissures are present, and scent peritreme not well-developed, often being auricle shape). Therefore, we suggest that Kobdocoridae may have a closer relationship with the Pentatomoidea than with Coreoidea. Although Kobdocoridae has also have some characters that are different from the extant Pentatomoidea such as a well-developed lanceolate ovipositor (vs. plate-like ovipositors in extant Pentatomoidea) and four-segmented antennae (vs. five-segmented antennae in Pentatomoidea), these two characters are considered to be of the ancestral type. Based on previous studies, the lanceolate ovipositor is considered an ancestral state for the Pentatomomorpha (Dupuis 1955, 1970; Scudder 1959; Schaefer and Ahmad 2000; Zhou and Rédei et al. 2020), and the four-segmented antenna is considered ancestral character for the Pentatomidae (Yao et al. 2012). It is suggested that the two distinct characteristics of Kobdocoridae are actually ancestral characters of the Pentatomoidea (in *Venicoris solaris* Yao et al., 2012, and *Clavaticoris zhengi* Yao et al., 2012, antennae are four-segmented, but with the pedicel notably longer, than the remaining antennal segments combined and a tendency towards re-segmentation of the pedicel). Therefore, the combination of characteristics in Kobdocoridae is closest to those of the Pentatomoidea, while also possessing some ancestral characteristics of the Pentatomoidea. Therefore, it is likely that Kobdocoridae is a stem group or sister taxon of Pentatomoidea.

Conclusions

A new genus and species, Maculocris vixiani Dai, Yao, & Ren gen. et sp. nov., of the Kobdocoridae is reported based on the impression fossil specimens from the Lower Cretaceous Yixian Formation in China. The report of it not only enriches the species diversity of Kobdocoridae, but also its characteristics, such as large ocelli; a relatively large scutellum extending to the third abdominal segment; the clavus reduced into a stick shape, with only vein 1A present; the claval commisure absent; and the tarsus with three segments, provide assistance in exploring the systematic position of Kobdocoridae. Based on this, we summarized several controversial views of previous scholars, namely whether Kobdocoridae belongs to Aradoidea, Idiostoloidea, or Pentatomoidea. After comparing the morphologies of all species of Kobdocoridae, it is believed that Kobdocoridae is a stem group or sister taxon of Pentatomoidea. Due to the limited number of Kobdocoridae species discovered so far, we have not conducted a phylogenetic analysis to verify the conjecture. This still requires more evidence to be found in the future to confirm the systematic position of Kobdocoridae.

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References

- Azar, D., Nel, A., Engel, M.S., Garrouste, R., and Matocq, A. 2011. A new family of Coreoidea from the Lower Cretaceous Lebanese amber (Hemiptera Pentatomomorpha). *Polish Journal of Entomology* 80: 627–644.
- Cassis, G. and Schuh, R.T. 2010. Systematic methods, fossils, and relationships within Heteroptera (Insecta). *Cladistics* 26: 262–280.

- Chang, S.C., Gao, K.Q., Zhou, C.F., and Jourdan, F. 2017. New chronostratigraphic constraints on the Yixian Formation with implications forthe Jehol Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology* 487: 399–406.
- Chen, X.T., Yao, Y.Z., and Ren, D. 2015. A new genus and species of Rhopalidae (Hemiptera: Heteroptera) from the Early Cretaceous of Liaoning Province, China. Zootaxa 4058 1: 135–40.
- Dai, R., Du, S.L., Ren, D., and Yao, Y.Z. 2022. New Cretaceous bugs from northeastern China imply the systematic position of Pachymeridiidae (Hemiptera: Heteroptera). *Insects* 13: 689.
- Du, S.L., Yao, Y.Z., and Ren, D. 2016. New fossil species of the Venicoridae (Heteroptera: Pentatomomorpha) from the Lower Cretaceous of Northeast China. *Cretaceous Research* 86: 2127.
- Dupuis, C. 1955. Les génitalia des Hémiptères Hétéroptères. (Génitalia externes des deux sexes; voies ectodermiques femelles). Mémoires du Muséum National d'Histoire Naturelle. Série A, Zoologie 6: 183–278.
- Dupuis, C. 1970. Heteroptera. In: S.L. Tuxen (ed.), Taxonomist's Glossary of Genitalia in Insects. 190–209. Munksgaard, Copenhagen.
- Henry, T.J. 1997. Phylogenetic analysis of family groups within the infraorder Pentatomomorpha (Hemiptera: Heteroptera), with emphasis on the Lygaeoidea. *Annals of the Entomological Society of America* 90: 275–301.
- Hua, J.M., Li, M., Dong, P.Z., Cui, Y., Xie, Q., and Bu, W.J. 2008. Comparative and phylogenomic studies on the mitochondrial genomes of Pentatomomorpha (Insecta: Hemiptera: Heteroptera). *BMC Genomics* 9: 1–15.
- Latreille, P.A. 1810. Considérations générales sur l'ordre natureldes animaux. composant les classes des crustacés, desarachnides, et des insectes. 444 pp. F. Schoell, Paris.
- Leston, D., Pendergrast, J.G., and Southwood, T.R.E. 1954. Classification of the terrestrial Heteroptera (Geocorisae). *Nature* 174: 91–94.
- Linnaeus, C. 1758. Systema naturae per regna tria naturaesecundum classes ordines, genera, species, cum characteribusdifferentiis synonymis, locis. Tomus I. Editio decimo, reformata. 824 pp. L. Salvius, Holmiae.
- Popov, Y.A. 1986. Peloridiina (= Coleorrhyncha) and Cimicina (= Heteroptera) [in Russian]. In: B.B. Rohdendorf (ed.), Insects in Early Cretaceous Ecosystems of Western Mongolia. Transactions of the Joint Soviet-Mongolian Palaeontological Expedition 28: 47–84.
- Ryzhkova, O.V., Yao, Y.Z., and Kopylov, D.S. 2023. New fossil Kobdocoridae (Heteroptera: Pentatomomorpha) from the Lower Cretaceous of Transbaikalia, Eastern Russia. *Cretaceous Research* 147 (1): 105509.
- Schaefer, C.W. and Ahmad, I. 2000. Cotton stainers and their relatives (Pyrrhocoroidea: Pyrrhocoridae and Largidae). *In*: C.W. Schaefer and A.R. Panizzi (eds.), *Heteroptera of Economic Importance*, 207–307. CRC Press, Boca Raton.
- Schuh, R.T. and Weirauch, C. 2020. True Bugs of the World (Hemiptera: Heteroptera). Classification and Natural History, 2nd Edition. 768 pp. Siri Scientific Press, Manchester.
- Scudder, G.G.E. 1959. The female genitalia of the Heteroptera: morphology and bearing on classification. *Transactions of the Royal Entomological Society of London* 111: 405–467.
- Tian, X.X., Xie, Q., Li, M., Gao, C.Q., Cui, Y., Xi, L., and Bu, W.J. 2011. Phylogeny of pentatomomorphan bugs (Hemiptera–Heteroptera: Pentatomomorpha) based on six *Hox* gene fragments. *Zootaxa* 2888: 57–68.
- Wang, Y.H., Cui, Y., Rédei, D., Baňař, P., Xie, Q., Štys, P., Damgaard, J., Chen, P.P., Yi, W.B., Wang, Y., Dang, K., Li, C.R., and Bu, W.J. 2016. Phylogenetic divergences of the true bugs (Insecta: Hemiptera: Heteroptera), with emphasis on the aquatic lineages: The last piece of the aquatic insect jigsaw originated in the Late Permian/Early Triassic. *Cladistics* 32: 404–407.
- Weirauch, C., Schuh, R.T., Cassis, G., and Wheeler, W.C. 2019. Revisiting habitat and lifestyle transitions in Heteroptera (Insecta: Hemiptera): Insights from a combined morphological and molecular phylogeny. *Cladistics* 35: 67–105.
- Xu, X., Zhou, Z.H., Sullivan, C., and Wang, Y. 2017. The Yanliao Biota: a trove of exceptionally preserved Middle–Late Jurassic terrestrial lifeforms. *In*: N.C. Fraser and H.-D. Sues (eds.), *Terrestrial Conservation*

Lagerstatten: Window into the Evolution of Life on Land, 131–168. Dunedin Academic Press, London.

- Yao, Y.Z., Cai, W.Z., and Ren, D. 2007. The first fossil Cydnidae (Hemiptera: Pentatomoidea) from the Late Mesozoic of China. *Zootaxa* 1388: 59–68.
- Yao, Y.Z., Cai, W.Z., Rider, D.A., and Ren, D. 2013. Primipentatomidae fam. nov. (Hemiptera: Heteroptera: Pentatomomorpha), an extinct insect family from the Cretaceous of north-eastern China. *Journal of Systematic Palaeontology* 11: 63–82.
- Yao, Y.Z., Ren, D., Rider, D.A., and Cai, W.Z. 2012. Phylogeny of the infraorder Pentatomomorpha based on fossil and extant morphology, with description of a new fossil family from China. *PLoS One* 7 (5): 37289.
- Zhou, Z.H., Barrett, P.M., and Hilton, J. 2003. An exceptionally preserved-Lower Cretaceous ecosystem. *Nature* 421: 807–814.
- Zhou, Y.Y. and Rédei, D. 2020. From lanceolate to plate-like: Gross morphology, terminology, and evolutionary trends of the trichophoran ovipositor. Arthropod Structure & Development 54: 100914.