

On the systematic position of *Circularva reichardti* Shcherbakov et Ponomarenko, 2023

О систематическом положении *Circularva reichardti* Shcherbakov et Ponomarenko, 2023

K.V. Makarov
К.В. Макаров

Moscow State Pedagogical University, Zoology & Ecology Department, Kibalchicha str. 6, build. 3, Moscow 129164 Russia. E-mail: kvmac@inbox.ru

Московский педагогический государственный университет, кафедра зоологии и экологии, ул. Кибальчица д. 6, корп. 3, Москва 129164 Россия.

KEY WORDS. *Circularva*, Coleoptera, Isopoda, Diplopoda, taxonomic position.

КЛЮЧЕВЫЕ СЛОВА. *Circularva*, Coleoptera, Isopoda, Diplopoda, таксономическое положение.

ABSTRACT. Based on a comparison of the structure of *Circularva reichardti* Shcherbakov et Ponomarenko, 2023 with the recent and fossil higher crustaceans and millipedes, a new interpretation of the taxonomic position of the genus *Circularva* Shcherbakov et Ponomarenko, 2023 is proposed as Eumalacostraca incertae sedis.

РЕЗЮМЕ. На основании сопоставления строения *Circularva reichardti* Shcherbakov et Ponomarenko, 2023 с рецентными и ископаемыми высшими ракообразными и многоножками предлагается новая трактовка таксономического положения рода *Circularva* Shcherbakov et Ponomarenko, 2023 как Eumalacostraca incertae sedis.

In September 2023, a paper by D.E. Shcherbakov and A.G. Ponomarenko appeared in the Russian Entomological Journal, describing a hygropetric beetle larva from the Middle Permian, related to Myxophaga. While reviewing and editing the manuscript, considerable debate arose among the reviewers and editors. The publication made the views of the authors publicly available, while the alternative point of view remained in the shadow. Below I shall briefly outline my opinion about the morphological peculiarities and systematic position of *Circularva* Shcherbakov et Ponomarenko, 2023.

Results

All information concerning the morphology of *Circularva* [Shcherbakov, Ponomarenko, 2023] is grouped in three obvious categories:

(a) Structures that are clearly observed and can be accurately interpreted. These are the number and shape of the dorsal sclerites, the number and location of ocelli

on each side of the head, the sculpture of the integument (rows of tubercles at the posterior margin of tergites), and the pleurites of the abdominal segments;

(b) Poorly distinguishable, unclear structures that cannot be accurately interpreted based on the visible organization. These are the several processes/appendages on the segments, the setae on tubercles in the posterior part of the tergites, and the abdominal sclerites. Their interpretation is based on the principle of taxonomic analogy, i.e. such that can be considered as spiracular gills, setiferous tubercles, sternites only if the fossil does belong to Coleoptera;

(c) Expected structures that are not visible on the impressions. First of all, such are the appendages of the head and body. Nothing is known yet as to how many and which antennae this creature may have had, nor how many legs could have been involved.

Since we do not know the set and structure of the appendages and legs of *Circularva*, we can confidently attribute it only to the Arthropoda, among which it could potentially have been related to both crustaceans and myriapods, as well as to hexapods (Figs 1–4). Let me consider these three hypotheses one by one.

Crustaceans are highly diverse in terms of the number of segments and their combinations into tagmata [Schram, Koenemann, 2021]. If this hypothesis is accepted, a complete coincidence of the segmentation of *Circularva* is to be found with one of the tagmosis variants of Isopoda, in which the thoracic region consists of seven segments, the abdominal region includes five free segments, and the sixth abdominal segment is merged with the telson (Fig. 2). Among the isopods, there are animals with an almost homonomous segmentation of the thoracic region, yet heteronomous segmentation with varying segment sizes is likewise very common

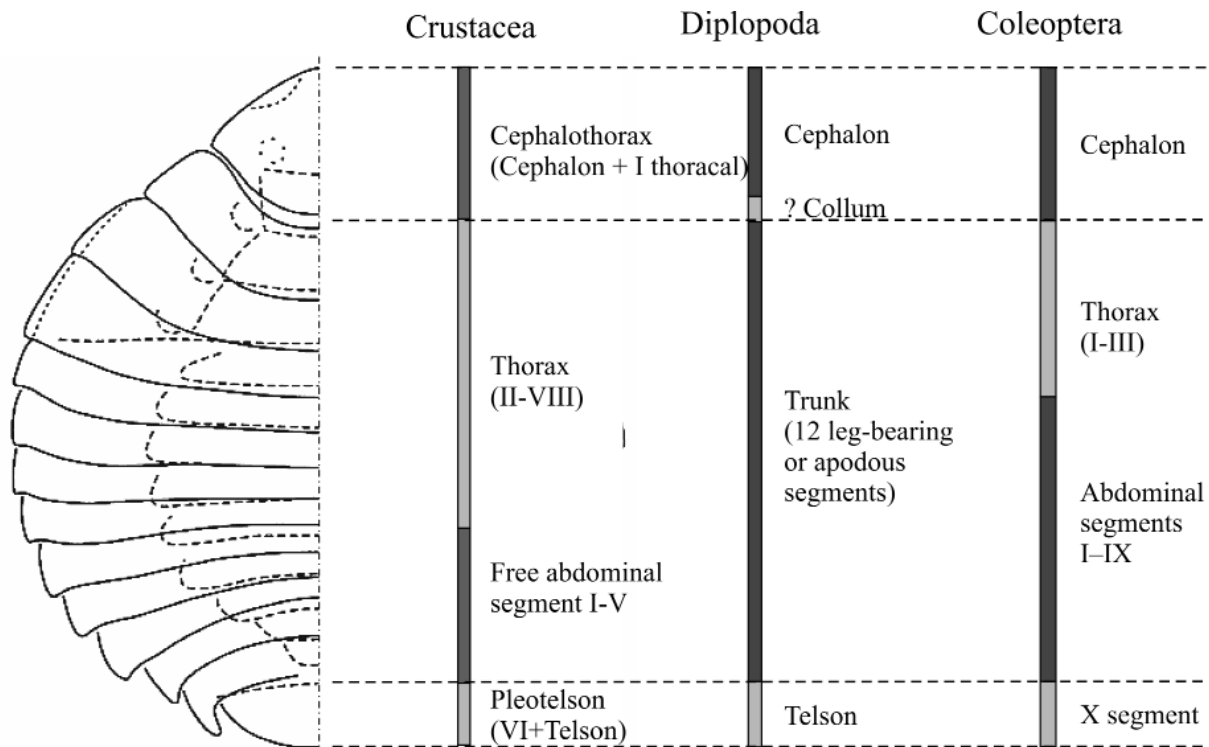
[Brandt, Poore, 2003]. The wide sternal region of *Circularva* is similar to that of Isopoda. The appendages of Isopoda are diverse and often specialized, this giving room to interpreting the unclearly distinguishable structures. Fossils of Isopoda have been known since the Carboniferous [Schram, Koenemann, 2021], this failing to contradict the age of *Circularva*.

Oniscomorpha forms are common among millipedes, or Diplopoda [Koch, 2015]. Modern Sphaerotheriida have 11 free trunk segments (segment XII is merged with the telson) and a telson [Wesener, 2015]. This resembles the tagmosis of *Circularva* (see Fig. 3), but requires at least two assumptions: (a) a weakly bound area at the base of the head must be interpreted as a collum, and (b) segment XII has not yet become fused with the telson in that primitive putative millipede. Millipedes of the superorder Oniscomorpha have well-developed pleurites [Blower, 1985], and their fossil representatives (Aminylspedida) are known from the Upper Carboniferous [Edgecombe, 2015]. The number of trunk segments in the fossil Oniscomorpha ranged from 13 to 15, supporting the diplopod hypothesis. However, in Diplopoda the sternites are usually narrow, which is not consistent with the impression. Besides this, Aminylspedida showed characteristic spines on the tergites [Lheritier

et al., 2023], these being absent from *Circularva*. Thus, the “diplopod” hypothesis is acceptable, but has obvious disadvantages compared to the “isopod” hypothesis.

The absence of wings, simple ocelli on the head, slightly enlarged first segments (interpreted as thoracic segments) and a ten-segmented abdomen (Fig. 4), all this suggests that *Circularva* is a Holometabola larva, probably Coleoptera. It seems important that the size differences between the thoracic and abdominal segments are very small: starting with the metathorax, their length is approximately the same and half the length of the prothorax (measured from the photograph in the original description). The rather narrow abdominal segments V–VII (0.3–0.4 the length of the prothorax) look strongly deformed in the photographs of the impression, while the following segments VIII–IX already show the normal length, which is half the prothorax length. Consequently, only thoracic segments I and II differ in size from the other segments and this trait is also common among Isopoda.

As shown above, the number of segments in *Circularva* satisfies the interpretation in favour of the “diplopod” hypothesis and corresponds very well to the “isopod” hypothesis. In addition, *Circularva* has several features that fail to fit well with the morphology of Coleop-



Figs 1–4. *Circularva reichardti* and interpretations of its morphology: 1 — *Circularva reichardti* Shcherbakov et Ponomarenko, 2023, drawing from the original description, left half, unclear structures not shown; 2–4 — putative tagmosis of *Circularva* due to hypotheses about its belonging to crustaceans, millipedes and coleopterans, respectively.

Рис. 1–4. *Circularva reichardti* и интерпретации её строения: 1 — *Circularva reichardti* Shcherbakov et Ponomarenko, 2023, рисунок из первоописания, левая половина, неясные структуры не показаны; 2–4 — предполагаемый тагмозис *Circularva* в рамках гипотез о её принадлежности к ракообразным, многоножкам и насекомым, соответственно.

tera larvae and, more generally, of Holometabola larvae in general. Firstly, they lack molting sutures, which are usually clearly visible on impressions, especially on the head, since the sutures often diverge when the head capsule is deformed. Secondly, *Circularva* had an unusually wide abdominal segment X. In Holometabola larvae, this segment usually assumes a locomotor function and has the shape of a tube, more or less strongly bent ventrally. Among the larvae of Coleoptera, no forms with such a wide segment X are known [Böving, Craighead, 1931; Costa *et al.*, 1988; Lawrence *et al.*, 1991, 2011]. Wide tergites in insect larvae are associated with the presence of dorsoventral and dorsopleural muscles. In Ectognatha, these muscle groups in segment X are greatly reduced. In the Zygentoma, two muscle pairs remain [Rousset, 1973] and in the Ephemeroptera, only one muscle pair is present [Birket-Smith, 1971], whereas in all Holometabola larvae whose anatomy has been studied, segment X comprises only longitudinal muscles [Kemner, 1913; Snodgrass, 1931; Berrios-Ortiz, Selander, 1979; Beutel, Hornschemeyer, 2002; Wipfler *et al.*, 2012; Yavorskaya *et al.*, 2015]. Therefore, the attribution of *Circularva* to Coleoptera, based on the structure of the last segment, is extremely unlikely.

To summarize, I believe that *Circularva* could not have been a coleopteran larva. Therefore, discussing its placement in the suborder Myxophaga and its similarities to the family Torridincolidae is meaningless. Most likely, that was a crustacean, but its attribution to Isopoda still remains unclear. Therefore, it seems rational to consider *Circularva* Shcherbakov et Ponomarenko, 2023 as an Eumalacostraca *incertae sedis*.

Discussion

Based on the above arguments, the authors of *Circularva*, when discussing its systematic position, appear to have chosen an almost incredible option from all possible ones. In addition to the lack of a careful morphological analysis, I see several logical mistakes as the reasons for the incorrect interpretation.

First, indirect evidence is allotted same weight as direct evidence. The statements concerning *Circularva* as a member of the suborder Myxophaga and the similarity to Torridincolidae are based only on a superficial habitual resemblance and some poorly discernible structures, which can be interpreted differently depending on the initial hypothesis about the taxonomic position of this fossil. In the absence of a sufficiently reliable evidence that *Circularva* belonged to Coleoptera, this approach creates the risk of false conclusions.

Secondly, the attitude to the plausible hypotheses is unequal. To give tribute to the authors, they do mention both Isopoda and Diplopoda in their paper. But this comparison consisted of two sentences and did not include an analysis of four tagmosis diversity in both those taxa with due care. On the contrary, the similarities and differences between *Circularva* and various coleopterans are discussed in detail, this inherently leading to skewed numbers of arguments put forth and thus not allowing

for the trueness of the “isopod” and “diplopod” hypotheses to be evaluated.

Thirdly, there is a discrepancy between the scales of evidence and the consequences of the acceptance of the “coleopteran” hypothesis. The assumption that *Circularva* belonged to Coleoptera generates two consequences: (a) it changes our notion about the age of the Coleoptera suborders and (b) it requires altering the well-grounded ideas about the abdominal structure of Coleoptera larvae. Is the indirect evidence the assumption of Shcherbakov and Ponomarenko is based upon sufficient for this?

It is beyond doubt that the problems resolved by palaeontologists are much more complicated than those faced by neontologists. Palaeontologists almost permanently have to deal with incomplete information, this making their inferences more hypothetical. However, this should not be a reason for premature conclusions and inattention to alternative hypotheses.

Acknowledgements. I am especially grateful to Olga Makarova and Sergei Golovatch (Moscow, Russia) for checking the English. I am grateful to Dmitry Shcherbakov for his critical reading of the manuscript and comments made.

References

- Berrios-Ortiz A., Selander R.B. 1979. Skeletal musculature in larval phases of the beetle *Epicauta segmenta* (Coleoptera, Meloidae) // Series Entomologica. Vol.16. P.1–114.
- Beutel R.G., Hornschemeyer T. 2002. Larval morphology and phylogenetic position of *Micromalthus debilis* LeConte (Coleoptera: Micromaltidae) // Systematic Entomology. Vol.27. P.169–190. <https://doi.org/10.1046/j.1365-3113.2002.00172.x>
- Birket-Smith J. 1971. The abdominal morphology of *Povilla adusta* Navas (Polymitarciidae) and of Ephemeroptera in general // Entomologica Scandinavica. No.2. P.139–160.
- Blower J.G. 1985. Millipedes: Keys and notes for the identification of the species // Synopses of the British fauna. New series No.35. Linnean Society of London, Estuarine and Brackish-water Sciences Association E. J. Brill/Dr. W. Backhuys. P.1–242.
- Böving A.G., Craighead F.C. 1931. An illustrated synopsis of the principal larval forms of the order Coleoptera // Entomol. Am. (N.S.). Vol.11. P.1–351.
- Brandt A., Poore G.C.B. 2003. Higher classification of the flabelliferan and related Isopoda based on a reappraisal of relationships // Invertebrate Systematics. Vol.17. No.6. P.893–923. <https://doi.org/10.1071/IS02032>.
- Costa C., Vanin S.A., Casari-Chan S.A. 1988. Larvas de Coleoptera do Brasil // Museu de Zoologia, Universidade de Sao Paulo, Brazil. 282 pp. 165 pl.
- Edgecombe G.D. 2015. Chapter 14. Diplopoda — Fossils // Minelli A. (ed.) Treatise on Zoology — Anatomy, Taxonomy, Biology. The Myriapoda. Vol.2. P.337–351
- Kemner A. 1913. Beiträge zur Kenntnis einiger schwedischen Coleopterenlarven. II. Das Analsegment und die Rektalschläuche einiger Carabidenlarven // Arkiv för Zoologi. Bd.8. Nr.13. S.1–23.
- Koch M. 2015. Chapter 2. Diplopoda — General morphology // Minelli A. (ed.) Treatise on Zoology — Anatomy, Taxonomy, Biology. The Myriapoda. Vol.2. P.7–67.
- Lawrence J., Hastings A., Dallwitz M., Paine T., Zurcher E. 1991. Beetle Larvae of the World: Descriptions, Illustrations, Identification, and Information Retrieval for Families and Sub-Families. CSIRO. CD-ROM + Manual.
- Lawrence J.F., Ślipiński A., Seago A.E., Thayer M.K., Newton A.F., Marvaldi A.E. 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae // Annales Zoologici. Vol.61. No.1. P.1–217. <https://doi.org/10.3161/000345411X576725>.

- Lheritier M., Perroux M., Vannier J., Escarguel G., Wesener T., Moritz L., Chabard D., Adriene J., Perriera V. 2023. Fossils from the Montceau-les-Mines Lagerstätte (305 Ma) shed light on the anatomy, ecology and phylogeny of Carboniferous millipedes // *Journal of Systematic Palaeontology*. Vol.21. No.1. P.1477–2019. <https://doi.org/10.1080/14772019.2023.2169891>
- Rousset A. 1973. Squelette et musculature des regions génitales et postgénitales de la femelle de *Thermobia domestica* (Packard). Comparaison avec la region génitale de *Nicoletia* sp. (Insecta: Apterygota: Lepismatida) // *International Journal of Insect Morphology and Embryology*. Vol.2. No.1. P.55–80. [https://doi.org/10.1016/0020-7322\(73\)90006-8](https://doi.org/10.1016/0020-7322(73)90006-8)
- Schram F.R., Koenemann S. 2021. Evolution and phylogeny of Pancrustacea: a story of scientific method. Oxford University Press. xii + 827 p. + 32 pl. <https://doi.org/10.1093/oso/9780195365764.001.0001>
- Shcherbakov D.E., Ponomarenko A.G. 2023. The first known fossil hydropetric beetle larva related to *Myxophaga* (Coleoptera) from the Permian of European Russia // *Russian Entomol. J.* Vol.32. No.3. P.261–270. <https://doi.org/10.15298/rusentj.32.3.02>
- Snodgrass R.E. 1931. Morphology of the insect abdomen. Part I. General structure of the abdomen and its appendages // *Smithsonian miscellaneous Collections*. No.85. P.1–128.
- Wesener T. 2015. Infraclass Pentazonia Brandt, 1833 // Minelli A. (ed.) *Treatise on Zoology — Anatomy, Taxonomy, Biology. The Myriapoda*. Vol.2. P.370–381.
- Yavorskaya M.I., Hörnschemeyer T., Beutel R.G. 2015. The head morphology of *Micromalthus debilis* (Coleoptera: Micromalthidae) — an archostematan beetle with an unusual morphology and a unique life cycle // *Arthropod Systematics & Phylogeny*. Vol.76. No.3. P.475–486. <https://doi.org/10.3897/asp.76.e31964>