

Reply to the Paper “Beutel *et al.* 2018. Is †Skleroptera (†*Stephanastus*) an order in the stemgroup of Coleopterida (Insecta)?”

Alexander G. Kirejtshuk^{a,b,*} and Andre Nel^b

^aZoological Institute of the Russian Academy of Sciences, Universitetskaya emb. 1, St. Petersburg, 199034, Russia

^bInstitut Systématique Evolution Biodiversité (ISYEB), Muséum national d’Histoire naturelle, CNRS, Sorbonne Université, EPHE, 57 rue Cuvier, CP 50, 75005 Paris, France.

E-mail: anel@mnhn.fr

*Corresponding author, e-mail: agk@zin.ru; kirejtshuk@gmail.com

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Abstract

The recent critical revision of the order Skleroptera by Beutel *et al.* (2018a) is considered. We show several defects in their interpretation, contradicted by the original descriptions and diagnosis (Nel *et al.*, 2013; Kirejtshuk & Nel, 2013). The main arguments of the initial interpretation of *Stephanastus polinae* Kirejtshuk et Nel, 2013 (Stephanastidae) and reasons for the proposal of the order Skleroptera (Kirejtshuk & Nel, 2013) are mentioned, together with reasons to reject the proposal of Beutel *et al.* (2018a, b). A comparison of Skleroptera with other neopteran orders is made. Lastly the problem of the position of *Umenocoleus* as a member of Coleopterida versus a roachoid is discussed, the first hypothesis being supported by synapomorphies which is not the case for the second.

Keywords

Coleopterida; Holometabola; Polyneoptera; Stephanastidae; Umenocoleidae; posmortal deformation; plesiomorphies and apomorphies in forewing venation

The description of a new order is a rather important event in entomology. It is understandable to examine the viewpoint of the original description. Recently three entomologists criticized the proposal of a new order Skleroptera (*Stephanastus polinae* Kirejtshuk et Nel, 2013), as sister group of the Coleopterida (Beutel *et al.* 2018a). Among them, Jarmila Kukalová-Peck is an experienced specialist in morphology and paleontology who made many important contributions in studies of fossils insects. Unfortunately, it seems that none of them has read the original description (Nel *et al.* 2013; Kirejtshuk & Nel 2013) enough attentively, and analyzed the photographs. Even they did not propose new drawings or photographs illustrating and supporting their

interpretation but only reproduced one of the Nel *et al.* (2013)'s drawings. Also they did not examine the type specimen, while this fossil is rather complicated to interpret, due to the overlapping wings. The writers of the critical paper also did not pay attention to the argumentation that the imprint of *Stephanastus polinae* Kirejtshuk et Nel, 2013 (Stephanastidae Kirejtshuk et Nel, 2013) certainly demonstrates a certain lateral compression of body because the attachments of the two visible wings are located at the same level, not at a great distance from the dorsal middle axis of body – see photographs in Nel *et al.* (2013) and Kirejtshuk & Nel (2013). These two wings are both forewings, but not a forewing and a hindwing of the same side of body, as supposed by Beutel *et al.* (2018a: 2), which is the crucial basis of their argumentation. The reasons to reject Beutel *et al.*'s hypothesis are as follows:

- First, these two wings are clearly identical in size, shape, venation, and relative positions. More precisely, these two wings have exactly the same lengths and their bases are superimposed, while in the case of a forewing and a hind wing of the same side, the base of the hind wing would have been on metathorax, thus slightly closer to abdomen than that of the forewing. Beutel *et al.* declared that “narrow separation of the bases of its [*Stephanastus*] ‘forewings’ is obviously an artefact, since the fore and hind wings combined are partly detached, shifted away from the body and the wing articulation mangled” (p. 5). But there is nothing showing that these two wings are detached from the body.

- Second, following Beutel *et al.* (2018a: 2)'s hypothesis of two wings of the same side of body, the convexities of the corresponding veins of these two wings would have been the same. It is clearly not the case because the two wings exposed on the studied specimen show an exact coincidence in their venations but clear inverted convexities of the corresponding veins. Beutel *et al.* (2018a) did not consider at all the problem of the relative convexities of the veins. Nel *et al.* (2013: Supplementary Information) clearly indicated that “One of the two forewings is preserved as a part while the second is a counterpart so that the veins appear with inverted convexity”. This fact is especially verifiable for the two identical CuA that are very easily identifiable because both have particular shape with the same small apical fork. The convex CuA of one wing was indicated by a white arrow while the ‘concave’ CuA of the second wing was indicated by a black arrow in Nel *et al.* (2013: Fig. 1b) to show this fact (see also Fig. 1). As a result, Beutel *et al.* (2018a) indicated that the “Due to the superposition with the hind wing, the radial sector, media, cubitus and analis of both wings are impossible to reconstruct. Only the costa, subcostal and radius are preserved well enough to provide information potentially relevant for an assignment to an insect order.” They did not take into their consideration the common fact that the venation can be reconstructed because it is possible to identify on the fossil all the veins (including M, CuA, CuP and first anal vein) of the two wings on the basis of their relative convexities and their relative distances. To achieve this during our study, we verified first that the distances between the corresponding veins of the two wings along a line perpendicular to their main axis in distal third of the wings were the same on the two wings (see Fig. 1), something that Beutel *et al.* (2018a) did not make. Thus, we could accurately identify the different veins ScP, R, M, CuA, CuP, and weak anal veins.

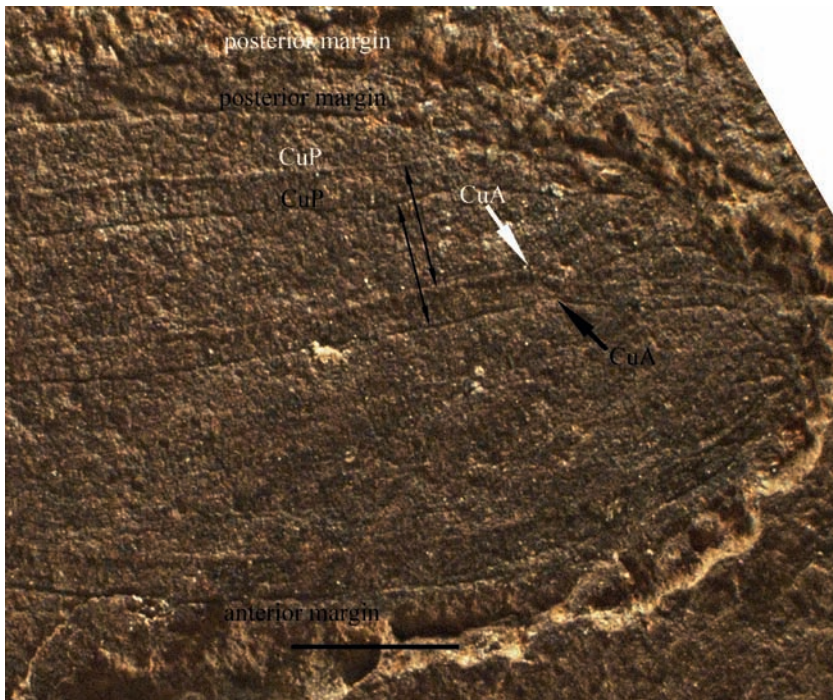


Fig. 1. *Stephanastus polinae* Kirejtshuk et Nel, 2013, holotype MNHN.A.49011, photograph of distal part of wings showing the convex veins CuA at their respective forks, while arrow convex CuA, black arrow ‘concave’ CuA; double arrows showing equal distances between veins of the two wings. Scale bar = 2 mm.

The hypothesis of Beutel *et al.* (2018a) is based on the following assumptions: “The authors [meaning Kirejtshuk and Nel] proposed that the specimen of †*Stephanastus* includes two overlapping forewings, held in life flexed in a lateral position as in orthopteroids, a condition they considered an autapomorphy. However, such wing preservation is highly unlikely. The seemingly “orthopteroid position” is most likely an artefact and due to lateral burial of the specimen. Parallel orientation of the veins indicates that the overlapped wing is almost certainly the folded hind wing, with the anal lobe flexed underneath, along the anal fold. The right fore- and hind wings are probably missing.” – However, an isomorphy between forewing and hindwing located on one side of body is impossible in insects with wings folding one pair beneath another because of morphological rules of congruence of closely approached pairs of wings. It is also impossible to imagine a postmortal deformation of a dorsoventrally compressed insect body, which could produce the imprint of *Stephanastus polinae* maintaining the isomorphy of venation of forewing and hindwing admitted by Beutel *et al.* (2018a) (but improbable after physical reasons – see above). Beutel *et al.* (2018a) indicated the presence of a folded anal ‘lobe’ of the alleged hindwing, but this structure is strictly imaginative, without any trace on the fossil itself. Beutel *et al.* (2018a) also indicated that they could see numerous crossveins on the photographs that Nel *et al.* (2013) proposed. But the direct exam of the type specimen of *Stephanastus polinae* and its

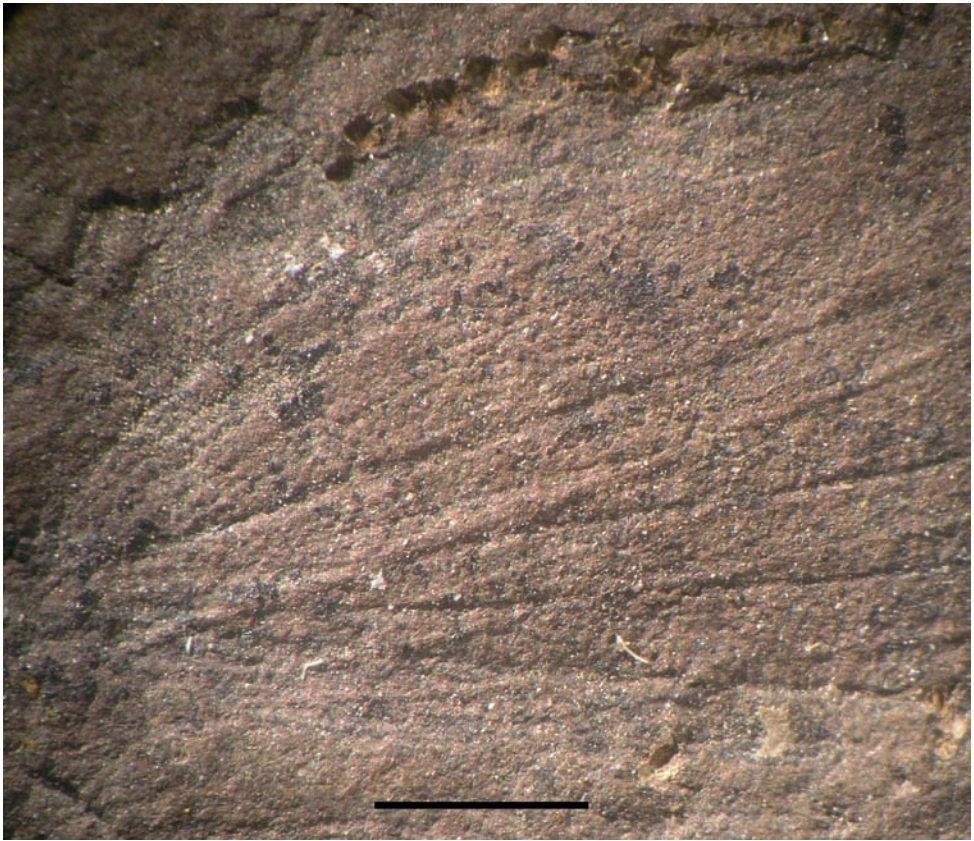


Fig. 2. *Stephanastus polinae* Kirejtshuk et Nel, 2013, holotype MNHN.A.49011, photograph of basal part of wings showing the reticulation. Scale bar = 2 mm.

photographs (Kirejtshuk & Nel 2013; Nel et al. 2013) show that there is no crossvein in the wing (some striations on the rock are visible but they overlap the main veins in apical part of wings). A reticulation and tegminisation is clearly visible (Fig. 2) (which are not characteristic of Polyneoptera, even if a tegminisation can occur in some Dicyoptera – see for instance: Nel *et al.*, 2014). Even the alleged presence of crossveins would not be an argument against a position in the stem Coleopterida because the character ‘presence of crossveins’ is clearly a plesiomorphy for beetles as it is shared by the whole clade Neuropterida, sister group of Coleopterida, and other Holometabola. Beutel *et al.* (2018a) indicated that the so-called ‘hind wing’ of *Stephanastus* has a “bowed vein with a series of short terminal branches resembling CuA” (p. 4), but this series of short branches are simply not there, CuA has only an apical fork and CuP is simple in both wings.

The apomorphic characters of holometabolans are difficult to define in structures available in compression fossils: Martynov (1925, 1938) grounded his divisions of Neoptera into three branches mostly on transformations in the jugal region of hindwings (evolutionary enlargement of this regions in these lineages had some parallelisms

and peculiar tendencies). Indeed *Stephanastus polinae* does not demonstrate hindwings at all. Nevertheless, the forewing venation of *Stephanastus* Kirejtshuk et Nel, 2013 shows the synapomorphies of the Coleopterida, visible in ‘archaic’ groups of Coleoptera (Kirejtshuk *et al.* 2013, 2016; Kirejtshuk & Nel 2016) rather than any other insect order, including the strongly reduced anal area that can be linked with that of Coleoptera. In particular, the forewing of Skleroptera shares with that of Coleoptera the sclerotization (synapomorphy among Holometabola); a simple and somewhat reduced Sc; a simple and concave RP; a convex RA; M less convex than R and CuA; M also simple; a long basal stem M+CuA (putative synapomorphy of Skleroptera with Coleopterida, uniquely present in these taxa) that distally divides into M and CuA (the point of separation of M from CuA is clearly indicated in Nel *et al.*, 2013: Fig. 1d); and stem of M+Cu well separated from R. The Coleopterida and Skleroptera also share the very long distal free part forewing CuP reaching distal eighth of forewing as putative synapomorphy (uniquely present in these taxa). Skleroptera, Coleoptera, Dermaptera, and some Dictyoptera have simple ScP, RP, and M. Thus these characters are not useful.

The Coleopterida and Skleroptera can be separated from the other insect clades as follows: in Archaeorthoptera and Acercaria, there is a fusion R+M+CuA, or M+CuA is basally appressed to R (Béthoux & Nel, 2002; Nel *et al.*, 2012), which is not the case in Coleopterida and Skleroptera. In Miomoptera (now in stem-Acercaria), the venation is of a completely different type, with a basal fusion R+M+CuA (Prokop *et al.*, 2017). In Dictyoptera, M(P) is not fused at all with CuA in a common stem, the same occurs with the fossil taxa currently in ‘Grylloblattodea’. Some important differences were shown in sclerotized forewings (tegmina or elytra) of Coleoptera and Dictyoptera (Kirejtshuk *et al.*, 2013; Nel *et al.*, 2014). In Phasmida and in Embioptera, M is also not fused with CuA at all (after our recent revision of the venations of Phasmida and Embioptera; Chintauan-Marquier *et al.*, submitted). *Stephanastus* is clearly not an Embioptera nor a stick insect. In Protelytroptera, CuA has no common stem with M (except in *Umenocoleus* Chen et T’an, 1973, a taxon probably close to Coleopterida, see below). The Dermaptera have shortened tegmina, with a very different venation, with no stem M+CuA and long anal veins (Zhang, 2002). In Paleoptera, CuA is not fused with M too (except in Odonata, but Skleroptera are clearly not Odonoptera). Hymenoptera have a completely different venation with a pterostigma and several large cells, among other characters. Neuropterida and Mecopterida have branches of ScP, M, RP, CuP, and no stem M+CuA. Nel *et al.* (2013) extensively argued on the differences between *Stephanastus* and the Glosselytrodea.

Besides, other common characters of Coleopterida and Skleroptera are not projecting coxae and short trochanters.

Beutel *et al.* (2018a) did not formulate their argumentation on the basis of all available data and criticized only some facts which, according to their own opinion, contradict their general concept. In particular, they assigned *Stephanastus* to polyneopterans because “weakly sclerotized tegmina are common in most groups of lower neopteran insects (monophyletic Polyneoptera ...), with the exception of Zoraptera, Embioptera and Isoptera” (p. 4). This character is not a synapomorphy of the Polyneoptera, thus their proposal of an attribution to this clade is not supported at all. They

do not risk to propose a precise subclade of the Polyneoptera. They illustrated their conclusion by references to figures in Carpenter (1992: 145, Fig. 3: *Apachelytron transversum* Carpenter & Kukalová, 1964 (Apachelytridae)) and reconstruction of “*Acosmelytron delicatum*” (Protelytroptera: Permelytridae) in Haas & Kukalová-Peck (2001: 471, Fig. 18). However, Beutel *et al.* (2018a) did not pay attention that the venation in the first taxon is completely different (even that M is separated from CuA) and that the second is reconstructed without proximal part of forewing where could be the characters for comparison (and without these characters such comparison is scarcely possible). Beutel *et al.* (2018b) summarized the same proposal “The wing venation [of *Stephanastus*] does not support a placement in Coleopterida, but rather suggests affinities with extinct polyneopteran lineages, such as †Protelytroptera ...” without further arguments. The holotype of *Stephanastus polinae* has no trace of exposed ovipositor and, therefore, it is presumably a male without cerci. Cerci are well present in all Polyneoptera, even if one-segmented in many Orthoptera (a clade to which *Stephanastus* does not belong, see above). *Stephanastus* has no visible cerci. The strong reduction or absence of cerci is a character proper to the Holometabola and extant Acercaria. The situation is unknown in Protelytroptera, a set of taxa supposed to be the ‘ancestor’ of the Dermaptera that have quite visible cerci (some fossil protelytropteran genera show segmented cerci: Carpenter 1992). Beutel *et al.* (2018a) ignored this difficulty when they supposed that *Stephanastus* is a Polyneoptera. Of course, it is always possible to say that *Stephanastus* had cerci and that they are not visible. But science is based on what is observed or tested, not on what could be present.

Beutel *et al.* (2018a) indicated that “The authors point out close affinities between †*Stephanastus* and †Umenocoleoidea s.str. (†*Umenocoleus* Chen & T’an, 1973; see Chen & T’an 1973; Vršanský 1999, 2003; Lee 2016; Bai *et al.* 2016). They consider the latter taxon as the closest relative of Coleoptera (within Coleopterida) based on its sclerotized forewings (Kirejtshuk & Nel 2013). This is in contrast to an interpretation of †*Ponopterix burkhardi* Nel *et al.*, 2014 as a roach-like insect (Nel *et al.* 2014), a species which shares several synapomorphies with †*Umenocoleus* (P. Vrsansky, pers. comm.). Leathery tegmina are characteristic for several families of †Protelytroptera s.l. (Vršanský 2003), and we consider this order as the most probable one to which †*Stephanastus* belongs.” Beutel *et al.* (2018b) repeated the same argumentation “A close affinity of †Umenocoleoidea with Coleoptera was also suggested by Kirejtshuk & Nel (2013), without presenting specific evidence”. These two assumptions contain several errors: first, the original attribution of *Ponopterix* is not simply based on the sclerotized tegmina, but on an extensive discussion concerning the venation, ignored by Beutel *et al.* (2018). Second, Nel *et al.* (2014) proposed a series of precise characters (including clear synapomorphies) to justify the difference between *Umenocoleus* and the Dictyoptera, again ignored by Beutel *et al.* (2018a, b). *Umenocoleus* according to the original descriptions (types of both species, *Umenocoleus nervosus* Zhang, 1997 and *U. sinuatus* Chen and T’an, 1973 are at the moment missing in the Chinese collections) differs from the true dictyopteran taxa that have been mixed with, it in the following crucial points: a long stem of Cu+M that is well separated from radius in basal part of wing, and RA simple. These characters are typical of the Coleopterida, after Kirejtshuk *et al.*

(2013). Beutel *et al.* (2018a, b) ignored this last paper in which the beetle venation is extensively discussed and re-interpreted. Beutel *et al.* (2018b) cited Bai *et al.* (2016) as a reference to support their assumption: “However, this group [*Umenocoleus*] of ‘roachoids’ belongs to Dictyoptera (Vršanský, 2003), and is apparently closely related to the recently described †Alienopteridae (Bai *et al.*, 2016), ...” But Bai *et al.* (2016) only indicated this sentence about the ‘Umenocoleidae’: “However, during their history of more than 300 Ma, more or less highly specialized groups (of Dictyoptera) have evolved several times, for example the Mesozoic †Umenocoleidae, a group strongly resembling beetles, with heavily sclerotized tegmina and a small pronotum ...” These arguments based on ‘resemblances’, are weak to support an attribution of *Umenocoleus* to the Dictyoptera. Lastly, Beutel *et al.* (2018b) cited Vršanský (2003), a paper in which the presence of a basal stem M+CuA is completely ignored for this taxon (a character absent in Dictyoptera), the proposed diagnosis of *Umenocoleus* being: “radius poorly branched, fused with simple M; Cu strongly curved, S-shaped; anal veins multiple.” This diagnosis shows that Vršanský correctly identified CuA but also that he erroneously supposed that there was a fusion of R with M which is not visible (see drawing reconstruction and photograph of *Umenocoleus* in Carpenter (1992: Fig. 89).

Remark

In addition to the original description, it can be tentatively supposed that *Stephanastus polinae* had only forewings but not hindwings which, in case of their presence, should be traced at least by some remains of main veins (taking into consideration that the venation of both forewings is rather clear). The presence of the abdomen supports the hypothesis that the hind wings were not removed during the decay and fossilization process. This species could have no hindwings at all or it could happen that the examined specimen lost its hindwing and keep its forewings (but it is extremely rare to find fossil neopteran insects with the forewings and the abdomen and not the hind wings). A certain level of lateral compression of the body of this species is supported not only by good expression of both forewings, but also by the position of the forewing bases and reduced anal region of its forewings in comparison with those in dorsoventrally depressed bodies of Coleoptera, Protelytroptera, and Dictyoptera (Kirejtshuk & Nel, 2013; Nel *et al.*, 2013). Body of *Stephanastus* could be somewhat similar to Glosselytroidea (Jurinida – placed by Ponomarenko in Neuropterida: Rasnitsyn & Quicke, 2001) according to the reconstructions of Ponomarenko in Rohdendorf & Rasnitsyn (1980: 91, figs. 44–45) and also to the specimen identified by Ponomarenko as “undescribed Jurinidae” (Rasnitsyn & Quicke, 2001: p. 197, Fig. 263, although the picture of the latter seems to be different from typical representatives of Glosselytroidea).

Conclusion

We still regard that it is impossible to explain the print of *Stephanastus polinae* in a way different from that when the order Skleropectera was proposed. Thus, this extinct form should interpreted as a member of Holometabola sharing apomorphies with the

Coleoptera but not as that of a Polyneoptera, as proposed by Beutel *et al.* (2018a, b). Lastly, we consider that *Umenocoleus* (and the Umenocoleidae restricted to this sole genus with two species known only after the original descriptions, see Nel *et al.* (2014), and needing a further re-testing of type specimens) is a group probably related to Coleopterida because it shares potential synapomorphies with this clade (characters uniquely present in Coleoptera), and because other authors failed to propose any synapomorphy that would support its attribution to the Dictyoptera or to the Protelytroptera. Of course, now only new researches based on new data, including new material, will allow to test the hypothesis of Skleroptera (and *Umenocoleus*) as representatives of the stem group of Coleopterida. It can be concluded that the available data make it possible to suppose that at least three groups of high taxonomic rank, which are here regarded as orders: Coleoptera, Strepsiptera, and Skleroptera, can be united into the superorder Coleopterida, and the latter of them is the oldest and still known only from the Carboniferous. Besides, the family Umenocoleidae recorded from the Albian (*Umenocoleus sinuatus*) and Aptian (*U. nervosus*) could preliminarily be a pretender to be linked with this superorder in case if a further study will confirm the synapomorphies with this superorder.

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