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New group of the Early Palaeozoic conodont-like fossils

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Abstract. The paper is devoted to the Upper Cambrian and Tremadocian organophosphatic microfossils which were hitherto treated as conodonts and assigned mainly to the genera *Coelocerodontus* and *Viirodus*. Individual elements of the fossils, similarly to the elements of conodonts, belonged originally to the multi-element apparatuses. Present studies, based mainly on the collections from Sweden, Poland (core sections), Estonia and Kazakhstan, show that despite the similarities of their individual elements to conodonts, they significantly differ from them in the inner structure, as well as in the construction of the apparatuses composed of them. Elements of their apparatuses are matched in shape to each other and certainly functioned in conjunction, while those belonging to the euconodont apparatuses are usually differentiated in shape and usually functioned in separation. All fossils of this group are provisionally named coelocerodonts in this paper. Their individual elements, as well as the apparatuses composed of them, are similar in construction to those of the genus *Phakelodus*, which is an ancestor of chaetognaths.

Key words: Cambrian, Conodonta, Chaetognatha, evolution, Ordovician, paraconodonts.

INTRODUCTION

Conodont-like microfossils occurring in the Cambrian–Ordovician transition beds are strongly diversified in structure. Excellent preservation of protoconodonts and paraconodonts in many localities was probably a result of their secondary phosphatization, which became very common in that period of time. As a result even the elements of originally organic composition, like the grasping spines of chaetognaths, are often well preserved (Szaniawski 1982, 2002). A structural study of these fossils is necessary to obtain a better knowledge and understanding of the early evolution of conodonts and chaetognaths.

In this paper the fossils collected from the uppermost Cambrian and early Tremadocian calcareous deposits of Sweden, Estonia, Poland (boring cores) and Kazakhstan (Malyj Karatau) are discussed. The most important fossils for these studies are the very abundant and well-preserved specimens from the Tremadocian of Öland Island (Fig. 1B–P), which have previously been described, briefly by Van Wamel (1974) and in detail by Andres (1988). Similar fossils from Malyj Karatau have been taxonomically described by Dubinina (2000) and shortly discussed by Szaniawski (2014). The present investigations are based on collections from the same localities and were conducted with a scanning electron microscope equipped with an energy-dispersive (EDS) detector for the chemical characterization of the specimens. The longitudinal and cross sections of the selected specimens were etched in 2% hydrochloric acid (Fig. 2). The investigated collection is housed in the Institute of Paleobiology of the Polish Academy of Sciences (institutional abbreviation ZPAL), Warszawa, Poland, with the collection number ZPAL C.23. The additional Arabic numerals indicate the number of the SEM stub and of the specimen on the stub.

RESULTS

Structural studies of very well-preserved Tremadocian conodonts from Öland Island show that some of the supposed conodonts, assigned usually to the genus *Coelocerodontus* Ethington, 1959 or *Stenodontus* Chen & Gong, 1986, and those of the genus *Viirodus* Dubinina, 2000, as well as those determined by Dubinina (2000) as ‘*Proacontiodus*’ An, 1982, differ significantly from all hitherto known euconodonts (= true conodonts) and paraconodonts. The differences concern not only the inner structure of their elements, but also the construction of the apparatuses composed of them. The elements consist of two layers. The outer one (Fig. 2B, C, E) is composed of calcium phosphate but, contrary to the crown of conodonts, it is very thin and not laminated. The layer covers the whole specimen, except the basal cavity. Longitudinal ridges occur on the surface of some elements (Fig. 1L, M). In some specimens the outer layer became partly separated from the whole element (Figs 1N, 2B). The EDS analyses show that the inner layer of the elements is thicker and much richer in organic matter than the outer one (Fig. 2C, E)

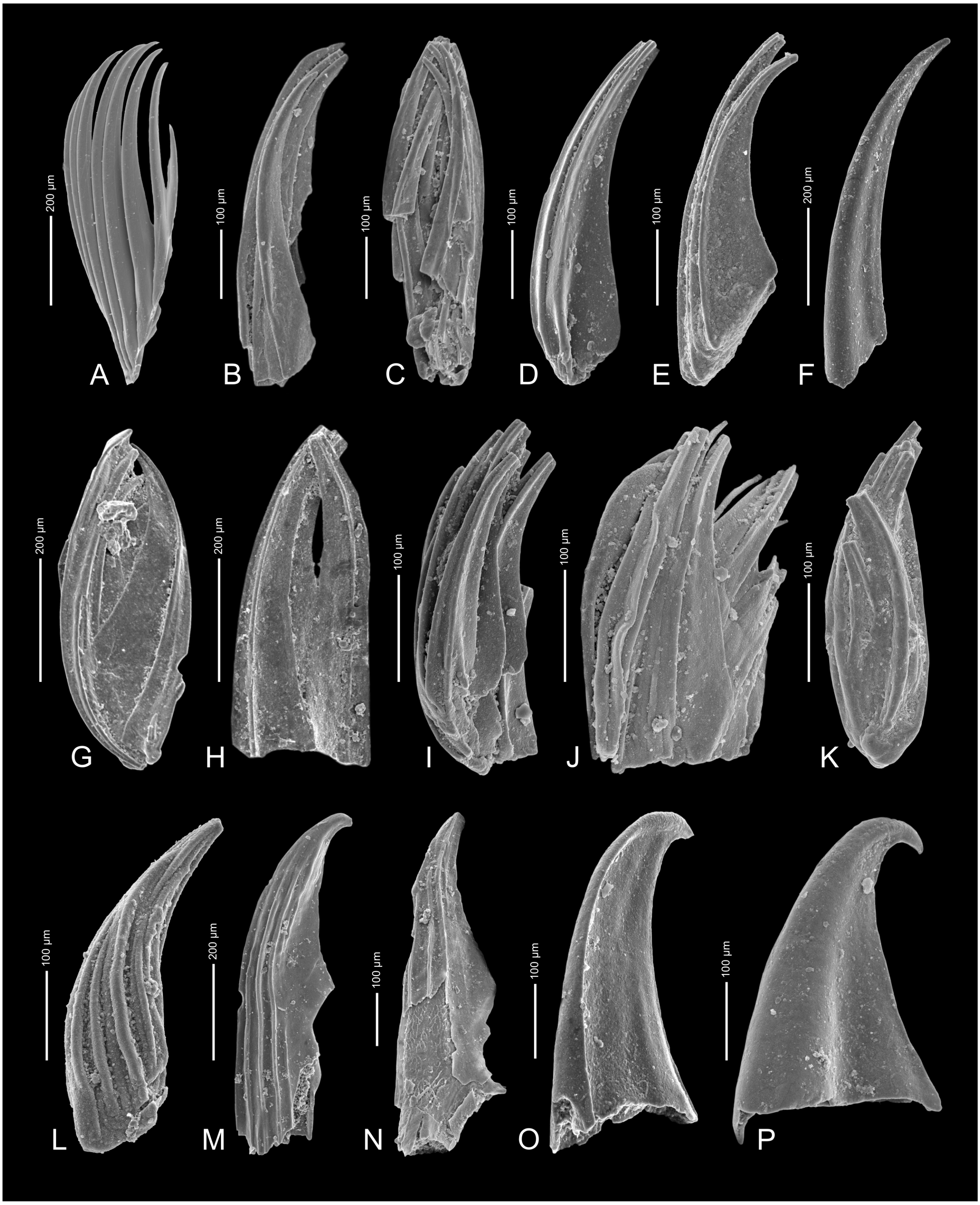

Fig. 1. A, recent *Sagitta* sp., grasping half apparatus in dorsal view; ZPAL CIV/1.1. **B, C**, *Phakelodus* sp., incomplete half apparatus in dorsal view, Tremadocian, Sweden, Äleklinta; ZPAL C23/1. **D–P**, elements and incomplete apparatuses of coelocerodonts (new term), Tremadocian, Sweden, Äleklinta; ZPAL C.23/2–16.

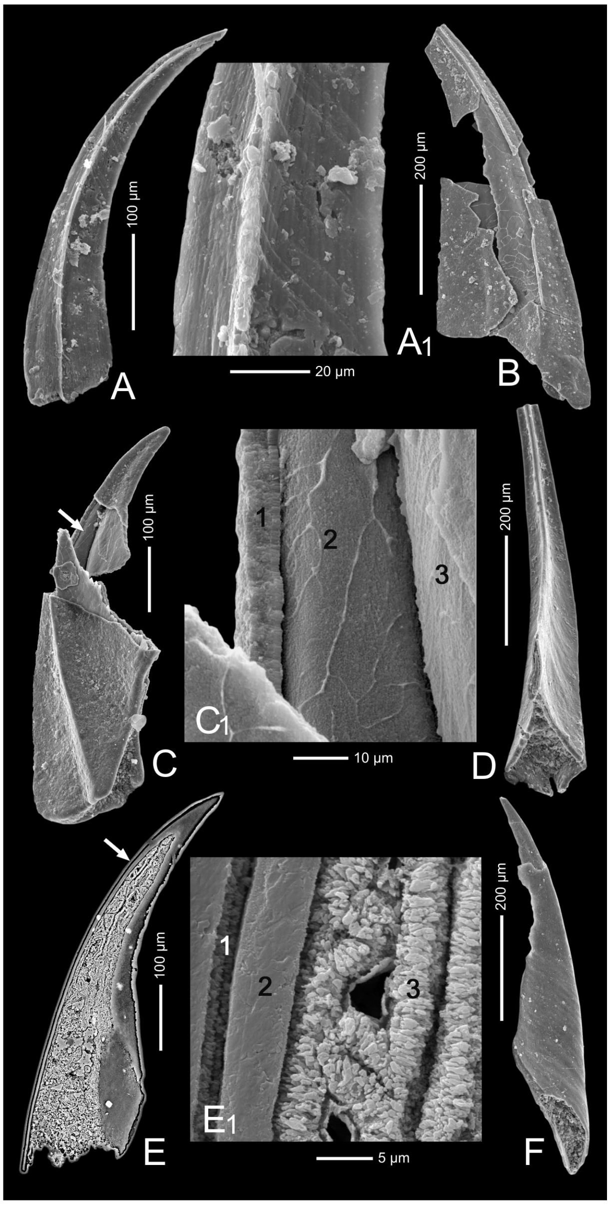

Fig. 2. **A**–**F**, inner structure of the elements of coelocerodonts; Tremadocian, Sweden, Äleklinta; ZPAL C23/17–23: **A**, specimen without the outer layer, A_1, higher magnification of the middle part showing diagonal striations; **B**, specimen partly crushed to show that the outer layer of some specimens can be easily separated; **C**, specimen specially fractured to show its inner structure, the arrow points to the magnified fragment; C_1, higher magnification; 1, fracture of the outer layer; 2, surface of the inner layer; 3, inner surface of the outer layer. **D**, **F**, specimens showing diagonal striations. **E**, specimen longitudinally sectioned and etched, the arrow points to the magnified fragment; E_1, higher magnification; 1, the outer layer; 2, the inner layer; 3, secondary filling of the specimen cavity.

and contains abundant levels of carbon. Attempts to etch the layer did not yield good results. All the elements possess a large cavity reaching almost the tip (Fig. 2E), which is usually filled with apatite and other material of secondary origin. The manner of growth of the elements is not well documented, but the diagonal striations visible in some specimens (Fig. 2A1, D, F) suggest that they grew similarly to the grasping spines of chaetognaths, by basal accretion of thin laminae (Szaniawski 2002).

Coelocerodonts differ from both euconodonts and paraconodonts (*sensu* Bengtson 1976) in the structure of their elements and the construction of the apparatuses composed of them. From the elements of euconodonts they differ mainly in lacking the thick, laminated calcium phoshate crown which grows by accretion of the new lamellae from the outside. They differ from them also in possessing a much greater cavity and lacking the 'basal body', which in euconodonts fills the cavity. The 'basal body' of euconodonts is composed of a mixture of organic matter and phosphate and, as the elements of coelocerodonts, grows in the basal direction. However, a detailed comparison of the manner of their growth has not yet been completed. They differ from paraconodont elements in possessing the outer calcium phosphate layer and a much deeper central cavity. Both types of elements grow in the basal direction but in a different manner. As mentioned above, the elements of coelocerodonts most probably grew in the manner characteristic of the grasping spines of chaetognaths, by the addition of a new fibrous lamina to the base (see Szaniawski 2002). Paraconodonts, however, grew mainly basally but added part of the new lamella also to the inner side of the element, making the element thicker and partly filling the cavity. Euconodonts and coelocerodonts both possessed apparatuses composed of elements of different shapes but the construction of these apparatuses is substantially different. Elements of the euconodont apparatuses are usually diversified in shape and not fused together, while the elements of coelocerodonts are matched in shape (Fig. 1D, G, I) and often fused at the base (Fig. 1K). Because of that they are often preserved as fused clusters. Moreover, elements of some of the coelocerodont apparatuses are very similar to each other (Fig. 1, D, E, H–J). In this respect they are very similar to the apparatuses of *Phakelodus* Miller, 1980. Additionaly, there are also transitional forms between them (Fig. 1–E). Moreover, some elements of the coelocerodont apparatuses are slightly deformed in the manner suggestive of their original flexibility (Fig. 1J). Such deformations are common among the elements and apparatuses of *Phakelodus* and are characteristic of fossils of the original organic composition. *Phakelodus* is treated as an ancestor of chaetognaths (Szaniawski 1982, 2002). This has recently been confirmed by the discovery of Cambrian chaetognath body fossils (Chen

& Huang 2002) with grasping spines preserved, which is suggestive of an affiliation between coelocerodonts and chaetognaths.

Apparatuses of paraconodonts composed of strongly differentiated elements are not known.

CONCLUSIONS

Early Palaeozoic microfossils of the genera *Coelocerodontus* Ethington, 1959 and *Viirodus* Dubinina, 2000, treated hitherto as conodonts, in fact strongly differ from both euconodonts and paraconodonts. They should therefore be treated as a separate group of fossils, provisionally named coelocerodonts in this paper. Structurally the fossils are most similar to the grasping apparatuses of *Phakelodus* which is an ancestor of chaetognaths. The conclusion is consistent, to some extent, with the view of Sweet (1988), who included several taxa, treated commonly as euconodonts, in the separate class Cavidonti, to which he assigned also the genus *Coelocerodontus*.

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