MIDDLE DEVONIAN JAWED POLYCHAETE FAUNA FROM THE TYPE EIFEL AREA, WESTERN GERMANY, AND ITS BIOGEOGRAPHICAL AND EVOLUTIONARY AFFINITIES

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Abstract: A rich assemblage of Middle Devonian (late Eifelian) polychaete jaws (scolecodonts) from the Blankenheimerdorf section in the type Eifel area, western Germany, is described. The top part of the section also reflects the onset of the global Kačák Event. The sediments of the section were deposited in a shallow to deep subtidal environment on the southern Avalonian margin. The habitat was obviously favourable for jaw-bearing polychaetes, which are represented by 18 species belonging to 9 genera. The assemblage is dominated by polychaetaspids, followed by mochtyellids, paulinitids and kielanoprionids. Notably, this study documents one of the oldest records of kielanoprionids, a polychaete family common since the Middle Devonian and closely related to the extant Hartmaniellidae. This may indicate that a prominent change in jawed polychaete evolution occurred during the Early–Middle Devonian transition. Moreover, we present new information on polychaete palaeobiogeography, which when compared with previously described Devonian scolecodonts shows that very similar polychaete faunas with many species in common were widespread in today’s Europe and North America.

Key words: polychaete jaws, scolecodonts, Eifel area, Eifelian, Middle Devonian, Eunicida.

Polychaete worms constitute an important component of modern marine invertebrate communities. Thanks to their strong and resistant jaws (scolecodonts) several groups of these otherwise soft-bodied creatures are well represented in the fossil record starting from the Ordovician (Kielen-Jaworowska 1966). Having long been neglected by palaeontologists due to their relatively low biostratigraphical value and complex multi-element-based taxonomy, the last few decades have seen an increase in the number of research papers based on large collections, providing new data on the taxonomy, evolution, palaeoecology, palaeobiogeography and diversification of the group (see Eriksson et al. 2013 and references therein). The vast majority of these recent studies have focused on Ordovician and Silurian faunas, particularly from Baltica and Laurentia, while the post-Silurian history of jaw-bearing polychaetes has remained largely unexplored. For the Devonian, our knowledge is still largely based on historical accounts of bedding plane material and single-element-based taxonomy (summary in Eriksson et al. 2011; Szaniawski and Drygant 2014).

During an integrated palaeontological and sedimentological study of the Middle Devonian Blankenheimerdorf section of the type Eifel area, western Germany (Königshof et al. 2015), abundant and relatively well-preserved scolecodonts were discovered. Altogether, the assembled collection turned out to be one of the largest Middle Devonian scolecodont collections available. This relatively diverse assemblage is well dated biostratigraphically, and well characterized with respect to palaeo-environmental setting. The aim of this study was to document and illustrate the scolecodont assemblage, discuss the taxonomic composition and palaeobiogeographical affinities and provide new insights into the evolution and diversification history of jaw-bearing polychaete worms during the Devonian Period.

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GEOLOGICAL SETTING

The study area is located in the Eifel region, western Germany, west of the river Rhine (Figs 1–2). Structurally this area is composed of several synclines, which are interpreted as a north–south trending axial depression of the Rheinisches Schiefergebirge. During the Early Devonian and early Middle Devonian (Eifelian), siliciclastic sedimentation prevailed in the area. Later, during the Givetian, shallow water platforms became widespread and subtropical carbonates were deposited over most of the region. The Blankenheimerdorf section lies within the Blankenheim syncline (Fig. 2), between the villages of Blankenheim and Blankenheimerdorf. It includes the Junkerberg and Freilingen formations, comprised of shallow-shelf mixed carbonate and siliciclastic facies, which accumulated on the southern margin of the former Avalonia microcontinent (Königshof et al. 2015 and references therein). The rocks underwent very low- to low-grade metamorphism (Helsen and Königshof 1994) with conodont alteration index (CAI) values of 1.5–2 (Königshof et al. 2015), and thus, the fossils are generally well preserved (for overview see Ernst et al. 2011).

Stratigraphically, the studied section covers the Tortodus kockelianus and Polygnathus ensensis conodont biozones (latest Eifelian age). Geochemical data, conodont distribution and microfacies analyses suggest that the top part of the section spans through the beginning of the Kačák Event Interval (for more information on the event, see House 1996). A thorough lithological description and biofacies analysis of the Blankenheimerdorf section is provided by Königshof et al. (2015).

MATERIAL AND METHOD

In total, 15 samples of 1–3 kg were collected in 2012 from the Blankenheimerdorf section for extracting conodonts (Fig. 3). The samples were dissolved using 15–20% formic acid in the University of Graz, and conodonts were picked after heavy liquid separation of the insoluble residues (see full details in Königshof et al. 2015). The residues were then examined in the Tallinn University of Technology, and the scolecodonts electrostatically hand-picked from dry residues under a stereomicroscope. Those specimens that needed cleaning were treated with

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**FIG. 1.** Geological map of the Rheinisches Schiefergebirge and Ardennes (slightly modified from Wehrmann et al. 2005). The rectangle demarcates the study area (Fig. 2). Colour online.
hydrogen peroxide (5%, 1–24 h of treatment), surfactant Rewoquat (20 min) or hydrofluoric acid (1 h).

The entire scolecodont collection contains c. 750 first and second maxillae, the elements that are of higher diagnostic value. Only a single partly fused jaw apparatus was recovered, but in many cases the isolated jaws were reconstructed into jaw apparatuses based on previous recorded similar taxa, morphological characteristics and co-occurrence data. Additionally, several hundreds of jaw fragments and minor jaws with lesser taxonomic value were recovered from the samples. The preservation of scolecodonts is relatively good (Figs 4–6), even though many specimens are fractured or fragmented, perhaps having partly occurred during sediment compaction. Some scolecodonts are coated by iron oxides that could also be the cause of and explanation for their brittleness and fragmentation.

In the richest samples (BL12-3, BL12-6, BL12-7 and BL12-20), the abundance of posterior maxillae reaches over 70/kg of rock (Fig. 3). These limestones, mainly wackestones to grainstones, dominated by crinoids and tube worms, were deposited in mid-ramp to deep-ramp settings (Königshof et al. 2015). The lowest abundance and highest fragmentation of scolecodonts were documented in sample BL12-34a that corresponds to a strongly bioturbated bioclastic wackestone. The microfaunas approaches points to an upper ramp position, with a moderate water depth just below a fair weather wave base (Königshof et al. 2015). By comparison, conodont average yields range from <10 up to 30 elements per kilogram, with a higher number of specimens occurring between samples BL 12-29c and BL 12-22 (Königshof et al. 2015). The scolecodont abundance data cannot be directly compared with that of other studies, as some of the light fraction may have become lost during conodont separation.

For imaging, three scanning electron microscopes were used: Hitachi S-3700N in the National Museum in Prague, Mira3 Tescan in the Czech Geological Survey and Zeiss EVO MA 15 in the Tallinn University of Technology. The descriptive terminology of polychaete jaw apparatuses and isolated jaws follows Kielan-Jaworowska (1966), and Jansonius and Craig (1971). The sample residues and all figured scolecodonts are housed at the Institute of Geology at Tallinn University of Technology under collection number GIT 724. Sample numbers are prefixed by BL12 to indicate the locality (Blankenheimendorf) and collection year (2012).

**PREVIOUS RECORD OF MIDDLE DEVONIAN SCOLECODONTS**

Despite the fact that the first report on Devonian scolecodonts had been published by the end of the nineteenth century (Hinde 1879), our knowledge on this group is still very limited. In total, there are about 40 papers dealing in detail with Devonian scolecodonts, and only 15 of them are focused on the Middle Devonian interval. A summary of the history of the research on Devonian scolecodonts was recently provided by Eriksson et al. (2011) and Szaniawski and Drygant (2014).

The limitation of data from historical publications arises from the distorted taxonomy. Two taxonomic approaches have been used for classifying scolecodonts: parataxonomy (the single-element-based system); and natural taxonomy, an apparatus-based concept (see discussion by Eriksson and Bergman 1998; Eriksson et al. 2000). In this study, we use the latter system, which was introduced by Lange (1947) based on Devonian material, and became widely accepted and adopted since the work by the ‘Polish school’, particularly Kozłowski (1956) and
FIG. 3. Schematic profile of the studied section with sample positions and taxa distribution (families and species). Note that the values of abundance of scolecodonts per kilogram of rock are only tentative, as some of the specimens might have been lost during the samples processing. The numbers refer to following species: 1, Oenonites spp.; 2, Mochtyella sp. 1; 3, Oenonites sp. 3; 4, Kettnerites aff. martinssonii; 5, Kielanoprion cf. elleri; 6, Mochtyella sp. 2; 7, Attraktoprion sp. 1; 8, Tetraprion sp.; 9, Kielanoprion sp. 1; 10, Skalenoprion sp. 1; 11, Oenonites aff. wyszogrodensis; 12, Xanioprion sp.; 13, Kettnerites aff. huberti; 14, Hindenites sp. 1; 15, Mochtyella sp. 3; 16, Oenonites sp. 1; 17, Oenonites sp. 2.
Kielan-Jaworskia (1966). However, a majority of the publications on Devonian scolecodonts are based on the single-element-based parataxonomical approach, which has generated hundreds of form taxa that are difficult to use, and comparisons with these taxa can be misleading. Most of the historical collections of Devonian scolecodonts are in need of revision and resampling of the type localities using modern extraction techniques and a taxonomical approach.

The first study on Middle Devonian scolecodonts was published by Hinde (1879), based on a collection from the Hamilton Group of Ontario. Subsequently, the same strata were studied by Clarke (1887), and a similar stratigraphic level was discussed by Stauffer (1939) from the Lake Erie district. In the 1930s, E. R. Eller, curator of the Carnegie Museum, started his extensive work on scolecodonts. His first paper on Middle Devonian scolecodonts described specimens from the Hamilton Group of the New York area (Eller 1934). Subsequently, Eller published reports on the Potter Farm Formation (Givetian) from Michigan (Eller 1938, 1955), Givetian Windom Member of the Moscow Formation, Hamilton Group of New York (Eller 1941), Eifelian Dundee limestone of Michigan (Eller 1961, 1963a) and Eifelian Delaware limestone from Ohio and Ontario (Eller 1964). In 1967, he published a short revision of Hinde’s collection from the Hamilton group. To date, the last detailed report from North America is that by Boyer (1975), who summarized the data from the Eifelian Columbus Formation of Delaware County, Ohio.

The regions outside of North America are considerably less well covered. Middle Devonian scolecodonts were included in publications by Taugourdeau, who described material from the Llandovery to lower Carboniferous of the Sahara (Taugourdeau 1968), and from the Givetian of Boulonnais, France (Taugourdeau 1971). Middle Devonian scolecodonts of western Siberia were studied by Männil and Zaslavskaya (1985). More recently, Suttner and Hints (2010) described a small and poorly preserved collection of imprecisely dated Devonian scolecodonts from the Tynaueraml, Graz Palaeozoic, Austria. A few reports have also come from China: Zhu et al. (2008) reported occurrences of Middle Devonian scolecodonts from the eastern Junggar Basin, Xinjiang (Kazakhstan Plate), and Ye (1994) studied late Silurian to Frasnian scolecodonts of the West Qinling Mountains, China.

The first and the only previous report on scolecodonts from the type Eifel area was published by Pichler (1971), who depicted three specimens, all assigned to the genus Arabellites Hinde, 1879. Only one specimen was determined to the species level, as Arabellites comis Eller, 1938. Pichler also mentioned other findings of Emsian to Givetian scolecodonts from the Eifel region, but without further information or illustrations.

RESULTS AND DISCUSSION

Characterization of the polychaete fauna

The studied polychaete fauna contains at least 18 species belonging to 9 genera, with up to 13 species found in one sample. The actual number of species represented in the collection may be slightly higher, as some jaws could not be confidently placed into any particular apparatus; thus, it remains unknown whether they represent individual taxa or unknown elements of species that are already counted (Figs 4AF, 5M–O). Taxonomically, the assemblage represents a single fauna with relatively little variation between individual samples. The fauna is dominated by polychaetaspids and mochtyellids, followed by kielanoprionids, paulinitids and atraktoprionids, and with sporadic occurrences of skalenoprionids, tetraprionids and xanioprionids (Fig. 3).

The collection undoubtedly contains new species; however, we have kept these under open nomenclature due to the limited number of specimens, poor preservation and/or lack of proper apparatus reconstructions. Moreover, the comparison of the studied fauna with previous records is largely based on published information rather than first-hand study of the original collections. Taking into account that the illustrations in historical publications are often artistically distorted or of inadequate quality, no final conclusions could be drawn on the species synonymy (see discussion on these issues by, e.g. Eriksson 2008).

Family MOCHTYELLIDAE Kielan-Jaworowska, 1966

Mochtyellids are present in all samples, representing 7–30% (average 20%) of the assemblage. The four species that are distinguished in this study are all tentatively assigned to the genus Mochtyella Kielan-Jaworowska, 1962.

Mochtyella sp. 1

Figure 4A–B

This is the most common mochtyellid species in the studied assemblage. This taxon is characterized by elongated first maxillae (M1); the jaws are more than three times longer than wide. Its basal and laeobasal ridges/plates are unknown, most likely broken off, and the right maxilla lacks the second ridge. Therefore, the species can only tentatively be assigned to Mochtyella. The anterior part of the apparatus remains unknown. Noteworthy is a polygonal pattern in the anterior of the inner faces observed in several specimens (Fig. 4A–B).
Very similar jaws have been found throughout the lower Palaeozoic (PT and OH, pers. obs.). Published examples of coeval species that could be conspecific with Mochtyella sp. 1 include the following: Stauropphericalites truncatus from the Givetian of Western New York (Eller 1941); Stauropcephalites concavisus and S. caniferus from the Frasnian of Boulonnais, France (Taugourdeau 1971); and Stauropcephalites sp. from the Frasnian of Canada (Jansonius and Craig 1971, 1974).

Mochtyella sp. 2
Figure 4C–E

This taxon is distinguished from Mochtyella sp. 1 by its relatively shorter and laterally more compressed first maxillae with fewer denticles (the jaws are approximately 2.5 times longer than wide). The second ridge is indistinct and undenticulated, but present in several specimens. The laeobasal ridge reaches approximately half of the jaw length. The basal ridge is not observed, but is likely similar to the laeobasal ridge.

Mochtyella sp. 2 is reminiscent of the Frasnian Mochtyella kielanae described from Poland by Szaniawski and Wrona (1973); however, it has a shorter laeobasal ridge and shorter secondary ridge. Similar jaws were described as Pistoprion sp. (Stauropcephalites sp.) by Jansonius and Craig (1974) from the Late Devonian of Canada.

Mochtyella sp. 3
Figure 4M

The collection contains several left maxillae of mchtyellid appearance possessing a short posteromediadly directed ramus-like extension on the outer face. Such morphology suggests the presence of a very long laeobasal plate. The right jaw is unknown, but it most likely bears similar characteristics.

We have not found similar specimens in the published literature.

Mochtyella sp. 4
Figure 4F

This is the least abundant species among mchtyellids. It looks very similar to the Orдовician and Silurian Mochtyella fragilis. Unfortunately, only left incomplete maxillae can be found in the samples, but there is obviously a long laeobasal ridge (extending more than a half of the jaw length), as in the type specimen of M. fragilis.

Comparison with other faunas will be possible when more complete specimens are recovered.

Family XANIOPRIONIDAE Kielan-Jaworowska, 1966

Xanioprion sp.
Figure 4X

Placognath jaws are often fragmented in the samples. Some of them are only tentatively assigned to xaniopri- onids and determined as Xanioprion sp. These jaws rep- resent approximately 4% of the assemblage. Only in one sample (BL12-5) do they reach a higher value (10%); however, this may be distorted by the low yield of scoleco- dents in this sample (Fig. 3). Nevertheless, well-pre- served xanioprioid jaws were described by Szaniawski and Wrona (1973) from the Late Devonian of Poland; therefore, their occurrence in the Middle Devonian would be expected.

Family TETRAPRIONIDAE Kielan-Jaworowska, 1966

In total, only 20 jaws from all samples have been assigned to the Tetraprionidae, the only family with a ctenognath- type jaw apparatus. Tetraprionids generally represent only

FIG. 4. Photomicrographs of selected sclerocodont specimens belonging to the following groups: mchtyellids (A–F, M), tetraprionids (G–L), polychaetaspids (N–W, Y–AE), xaniopri- onids (X), uncertain affinity (AF). Maxillae are in dorsal view except for C–E, I and W (position in figure descriptions). A–B, Mochtyella sp. 1; A, left MI, BL12-5, GIT 724-1; B, right MI, BL12-7, GIT 724-2. C–E, Mochtyella sp. 2; C, right MI in lateral view, BL12-5, GIT 724-3; D, left MI in lateral view, BL12-9c, GIT 724-4; E, left MI in lateral view, BL12-33, GIT 724-5. F, Mochtyella sp. 4, left MI, BL12-2, GIT 724-6. G–L, Tetrarpion sp.; G, fused left MI and lateral teeth, BL12-7, GIT 724-7; H, right maxilla, BL12-20, GIT 724-8; I, left MI, BL12-1, GIT 724-9; J, right MIIR, BL12-1, GIT 724-10; K, right maxilla, BL12-1, GIT 724-11; L, right maxilla in ventral view, BL12-7, GIT 724-12. M, Mochtyella sp. 3, left MI, BL12-20, GIT 724-13. N–P, Oenonites sp. 1; N, left MI, BL12-13, GIT 724-14; O, left MI, BL12-3, GIT 724-15, P, right MI, BL12-20, GIT 724-16. Q, Oenonites sp. 2, right MI, BL12-6, GIT 724-17. R–W, Oenonites sp. 3; R, left MI, BL12-6, GIT 724-18; S, right MI, BL12-7, GIT 724-19; T, left MI, BL12-14, GIT 724-20; U, right MI, BL12-33, GIT 724-21; V, right MI, BL12-6, GIT 724-22; W, right MI in ventral view, BL12-6, GIT 724-23. X, Xanioprion sp., left MI?, BL12-7, GIT 724-24. Y–Z, Oenonites aff. wyszogrodensis; Y, left MI, BL12-20, GIT 724-25; Z, right MI, BL12-2, GIT 724-26. AA–AE, polychaetaspid jaws, probably belonging to the genus Oenonites; AA, left MI, BL12-20, GIT 724-27; AB, left MI, BL12-7, GIT 724-28; AC, right MI, BL12-14, GIT 724-29; AD, basal plate, BL12-3, GIT 724-30; AE, reversed right MI, BL12-29a, GIT 724-31. AF, basal plate of unknown affinity, 12-29c, GIT 724-32. Scale bar represents 100 and 200 μm for Q, AD.
a few percentage of the assemblage. The samples BL12-29c and BL12-33 are exceptions, where this family accounts for c. 10% of specimens, but this may be skewed as a result of a low total abundance of scolecodonts.

**Tetraprion? sp.**

Figure 4G–L

The scarce material at hand does not allow us to fully reconstruct the architecture of the apparatus of this species. However, the apparatus seems to be symmetrical, consisting of several pairs of maxillae and numerous lateral teeth. Figure 4G shows a left (first?) maxilla preserved with several anterior teeth, but other jaws are not connected. The denticles of this species are relatively large, sharply pointed and bent posteriorly. The anterior teeth are secondarily denticulated, a feature which has not been previously observed among tetraprionids. Such teeth were previously depicted from other regions as detached jaws, for example by Taugourdeau (1967) from France under the designation *Paraglycerites* sp.

A similar form was described by Eller (1961) as *Oenonites canaliculatus* from the Eifelian of Michigan. To confirm whether these two species are conspecific, a restudy of the original collection would be needed. Moreover, the appearance of the maxillae of the Devonian taxon is very similar to some lower Palaeozoic tetraprionid jaws, particularly *Tetraprion* from the Wenlock of Poland (Szaniawski 1970) and *Tetraprion* sp. A from the Ordovician to Silurian of Baltoscandia (Hints 2000; Hints et al. 2006). Possibly they represent the same undescribed long-ranging genus.

**Family POLYCHAETASPIDAE** Kielan-Jaworowska, 1966

The family Polychaetaspidae represents the most abundant and diverse family in the studied samples (Fig. 3). A similar predominance of polychaetaspids is common in Ordovician and Silurian assemblages. The family is represented by at least four species of the genus *Oenonites* Hinde, 1879. Note that Szaniawski and Drygant (2014) considered *Oenonites* to be a *nomen dubium* that should be replaced by a younger synonym *Polychaetaspis*. In this study, we follow the concept of Eriksson (1997). The right jaws outnumber the left ones, hampering reconstruction of the jaw apparatuses as well as proper separation of different taxa. Such jaws are grouped into *Oenonites* spp. (Fig. 4AA–AE).

**Oenonites aff. wyszogrodensis**

Figure 4Y–Z

This morphological type of *Oenonites* is very common throughout the lower and middle Palaeozoic (Kielan-Jaworowska 1966; Eriksson 1997) and most likely includes a number of species that are difficult or impossible to distinguish based on isolated jaws. Typical for the first maxillae of this group is a posteriorly tapering slender outline, with missing or narrow inner wing, the greatest width occurring at approximately one-third of the jaw length and a subtriangular ramus.

Among coeval faunas, an example of the resembling species was described as *Lumbriconereites cooperi* from the Givetian Potter Farm Formation of Michigan (Eller 1938).

**Oenonites sp. 1**

Figure 4N–P

*Oenonites* sp. 1 has a patchy occurrence throughout the section. Both left and right MI are study, resembling jaws of the ‘*Polychaetaspis warkae*’ group, erected by Kielan-Jaworowska, which has a typically short bight (approximately one-quarter of the jaw length; cf. Kielan-Jaworowska 1966, p. 75). The bight of *Oenonites* sp. 1 represents approximately 0.25 of the jaw length. The first maxillae are approximately 2.5 times longer than wide,
their inner and outer margins go almost parallel before the jaw tapers at the posterior part, fangs are relatively prominent and bent posteriorly, and inner wings are indistinct. The right MI superficially resembles ramphoponid jaws, but the left MI is typical of polychaetaspids; a similar trend in morphology was described from the Ordovician by, for example, Eriksson and Frisk (2011, fig. 7k).

*Lumbriconereites compactilis* from the Eifelian Dundee limestone of Michigan (Eller 1961, pl. 1 fig. 21) resembles *Oenonites* sp. 1. Other specimens of *L. compactilis* depicted by Eller show a slightly different morphology; thus, a restudy of the original material is needed to solve the relationship of the two species.

**Oenonites** sp. 2
Figure 4Q

This species occurs only in the upper part of the studied section. Characteristic for this taxon is the rather big size (length around 1 mm) and the slender appearance of both left and right MI. The widest part of *Oenonites* sp. 2 is situated in the posterior second third of the jaw, and the bight of the right first maxilla (MIr) represents c. 0.4 of the jaw length.

*Oenonites* sp. 2 resembles some early Palaeozoic forms, for example *Oenonites eichwaldi* described by Eriksson (1997) from the Silurian of Gotland, Sweden.

**Oenonites** sp. 3
Figure 4R–W

*Oenonites* sp. 3 is the most abundant polychaetaspid species in the studied collection. It resembles slightly the peculiar Silurian species *Oenonites? honki* Eriksson, 2000. The features in common include a conspicuous club-shaped ramus in the right MI, and a long undenticulated portion of ridges in both MI (c. 0.2 of the dentary length). The length of MI ranges from 0.4 to 0.7 mm, and they are 2–2.5 times longer than wide and equipped with 11–15 denticles. The inner wing is very indistinct in the right MI and protrudes only slightly in the posterior two-quarters of the jaw in the left MI. In the anterior part, the inner and outer margins of MI become almost parallel, and the posterior end of the maxillae is sharply pointed.

No similar species have been recorded from the Devonian strata; therefore, this taxon may be distinct for the Eifel region.

Family PAULINITIDAE Lange, 1947

The family Paulinitidae is the fourth most common group in the collection, representing 5–20% of the assemblage, with two genera, *Kettnerites* and *Hindenites*. Szaniawski and Drygant (2014) questioned the validity of the genus *Kettnerites* mainly because its holotype is lost. According to Tonarová (2012, p. 41, 75–80, fig. 7A–C),...
the holotype is present in the collections of the National Museum in Prague under the number L42160; therefore, the genus is viewed as valid. Commonly, even fragments can be assigned to this family thanks to their characteristic appearance; however, for a generic and species-level determination, both the first and second maxillae are usually needed. Often only the second maxillae (MII) bear diagnostic characteristics (Bergman 1989). In the studied samples, three paulinitid species are distinguished, and several jaws have been identified only to the family level due to broken or insufficient material. For example, the specimen shown in Figure 5A bears characteristics of paulinitids, but the extremely small inner wing is unknown in this family. However, a similar type of inner wing is found in kielanoprionids.

**Kettnerites aff. martinssonii**

*Figure 5F–H*

*Kettnerites aff. martinssonii* is almost indistinguishable from the Silurian *K. martinssonii* described by Bergman (1989). Typical for this species is one precuspidal denticle on the right MII. The ramus of second maxillae of the Eifelian species is a little more pointed than that of the Silurian species. The outer and inner margins of MI are almost parallel, there is only a slight concave curvature in the anterior part of the inner margin, a spur is visible in the outer margin, and MI are equipped with 11–13 stout denticles. MI are generally more robust and less bent at the anterior part than in the Silurian *K. martinssonii*.

The first maxillae of *K. aff. martinssonii* look very similar to *Nereidavus concavibusus* described from the Givetian and Frasnian of Boulonnais (Taugourdeau 1971). Unfortunately, Taugourdeau did not assign diagnostic second maxillae to the latter species; therefore, it is not possible to synonymize the two species.

**Kettnerites aff. huberti**

*Figure 5I–L*

The right MII of *Kettnerites aff. huberti* has two precuspidal denticles. The first maxillae are more tapering in the anterior part than those of *Kettnerites aff. martinssonii*; and they are also more slender than the latter species. The number of denticles in the first maxillae is small (around 6), and the anterior part of dentary is undenticulated. However, the denticulation tends to be very variable in the genus *Kettnerites*; and thus not species-diagnostic. The inner wing of the MI is prominent, with a protruding anterior part.

*Kettnerites aff. huberti* is very similar to *K. huberti* from the Silurian of Gotland (Bergman 1989), but the ramus of MII of *K. aff. huberti* is less pointed and bent more posteriorly. A rather similar species was recently described as ‘*Kettnerites* huberti’ from the Lochkovian of Podolia (Szaniawski and Drygant 2014). Moreover, *Nereidavus exploratus* from the Eifelian Dundee limestone of Michigan (Eller 1963a) and *Nereidavus harbisonae* described by Eller (1941) from the Givetian of New York as well as by Taugourdeau (1971) from the Frasnian of Boulonnais may be conspecific with the species described herein.

**Hindenites sp. 1**

*Figure 5B–E*

Jaws of *Hindenites sp. 1* are very rare in the studied collection. All second maxillae are broken; nevertheless, they show the diagnostic narrow ramus. They are very similar to the Silurian specimens of the genus (Bergman 1989) except for the less prominent cusp in the left MII. Among the first maxillae, the left MI are better preserved. Typical for these jaws is their anteriorly tapering outline (with a prominent curvature in the upper half of the jaw) that is undenticulated or only crenulated. Three to four stout denticles are visible in the lower part of the inner margin of the left MI, and the denticulated inner margin is somewhat shorter than in the Silurian specimens. The inner wing is rather prominent, and the outer posterior margin bears a spur-like extension, forming a little ridge at the outer outline.

Very similar left and right MI were described and illustrated from the Permian–Triassic of Norway by Nakrem et al. (2001) who provisionally assigned these jaws to *Paulinites* sp. A and *Paulinites* sp. B, with a note that they both belong to the same but undescribed genus.

**Family KIELANOPRIONIDAE** Szaniawski, 1968

The family Kielanoprionidae represents approximately 15% of the studied assemblage. Two species of this family are distinguished in the studied assemblage, both assigned to the genus *Kielanopron* Szaniawski, 1968. Some scolecodonts reflecting kielanoprionid affinity could not be determined to the genus and species level due to an insufficient number of specimens (Fig. 5P–Q).

This family appears to be rather common in the Late Devonian (Eller 1963b; Taugourdeau 1968) and ranges at least to the Triassic (Szaniawski and Imajima 1996). Szaniawski and Imajima (1996) carried out a morphological analysis of extinct and extant hartmaniellids, reaching the conclusion that the Hartmaniellidae are most closely related to Kielanoprionidae, or that they had a common ancestor.

The specimens from the Eifel area represent one of the oldest records of kielanoprionids. The other Middle
Devonian occurrences of this family are from the Lake Erie district (Arabellites comis; Stauffer 1939), from the Eifelian Delaware limestone of Ontario (A. comis; Eller 1964) and from the Givetian of Western New York (A. comis; Eller 1941) and Michigan (Eller 1938). However, the mentioned historical papers did not give a proper description or documentation, nor an exact stratigraphical position according to the standards of today. Hitherto, there is no record of kielanoprionids from the Early Devonian or older strata, and thus, the family might have evolved during the Early–Middle Devonian transitional interval.

**Kielanoprion cf. elleri Szaniawski and Wrona, 1973**

Figure 5R–Z

The species reported herein is very similar to *Kielanoprion elleri*, except that the inner wings of both left and right MI are more prominent and more protruding. The number of denticles of MI is 10–11, which falls into the intraspecific variability according to Szaniawski and Wrona (1973). The second maxillae are identical with those of the type species. However, the appearance of the inner wing is variable even within the studied samples (compare Fig. 5R and Fig. 5X). Szaniawski (1968) had previously reported that the genus *Kielanoprion* generally shows a great morphological variability, which we have confirmed in this study. The stratigraphical range of *K. elleri* is extended from the Eifelian to the Frasnian.

Comparison of *Kielanoprion elleri* with a single-element-based, parataxonomical species was provided by Szaniawski and Wrona (1973, p. 248). They did not discuss the kielanoprionid *Arabellites comis* reported and depicted by Pichler (1971) from the Eifelian lower Junkerberg-Schichten (‘Lepidocentrus-Mergel’) of the Eifel Mountains that is regarded here to be conspecific with *Kielanoprion cf. elleri*.

**Kielanoprion sp. 1**

Figure 5AA–AE

This type of maxillae was depicted by Szaniawski and Wrona (1973, pl. 4, fig. 2) and assigned to *Kielanoprion elleri*. In our opinion, differences in morphology of these forms are too striking to be included within intraspecific variability. Both left and right MI are much more slender than in *K. elleri*, they are more than three times longer than wide, and the spur in the posterior of the outer face of the maxilla is much more prominent. Similarly, Taugourdeau (1968) had already introduced the concept of separation of the two different forms of kielanoprionids, even though his species designation was *Arabellites comis*.

The second maxillae of *Kielanoprion* sp. 1 were tentatively assigned to the species, and they are very similar to those of *K. elleri*. The right MII has two equally sized first denticles, followed by a small gap and row of denticles that increase in size towards the middle of the jaw. The left MII has a small pre cuspidal denticle followed by a cusp, and then a row of denticles that grow in size towards the middle of the jaw. Both MII are slender, and almost the whole length of inner margin is denticulated (with 10–13 denticles).

*Arabellites demissicus*, described by Eller (1963b) from the Famennian of Iowa, might be conspecific with *Kielanoprion* sp. 1. In general, the first maxillae of *Kielanoprion* sp. 1 resemble the corresponding jaws of the Late Devonian Elleri prion Kozur, 1970 and Palurites Kozur, 1967 of the family Hartmaniellidae (see discussion in Szaniawski and Imajima 1996); however, the posterior parts of the first maxillae of *Kielanoprion* sp. 1 are much more elongated.

**Family ATRAKTOPRIONIDAE Kiela-Jaworowska, 1966**

This family with a prionognath type of jaw apparatus represents <5% of the assemblage apparently with only one species present.

**Atraktoprion sp. 1**

Figure 6D–H

The first maxillae are elongated (approximately two times longer than wide), the dentary is straight and equipped with 7–8 sharply pointed denticles, and the hook is slender and represents half of the jaw length. The bight of the right MI extends c. one-third of the jaw length; indistinct wing-like extension is at the posterior outer margin. The inner wing of the left MI is wider than in the right MI.

The second maxillae (Fig. 6E) are very similar to other MII of this genus; they are triangular in shape with a prominent first denticle and bent ramus.

Several Devonian species are similar to *Atraktoprion sp. 1*: *Arabellites anatinus* and *Protarabellites hamiltonensis* from the Middle Devonian of Lake Erie district (Stauffer 1939); *Ildraites anatinus* and *Arabellites hamiltonensis* from Windom of Western New York (Givetian; Eller 1941). Zawidzka (1975) synonymized *Arabellites anatinus* and several other parataxonomical species with *Atraktoprion anatinus*; however, we do not agree with that decision. The Triassic specimens of Zawidzka have maxillae with a shape similar to the Devonian species, but they also differ in important characteristics; notably, the posterolateral wing-like extensions of the first maxillae of *Atraktoprion anatinus* are more prominent.
Family SKALENOPRIONIDAE Kielen-Jaworowska, 1966

This family with a prionognath type of apparatus represents up to 5% of the assemblage, and only one distinct species is recognized. A similar relative frequency was also observed in the Silurian strata of Gotland (Eriksson et al. 2004).

Skalenopri ol sp. 1

Figure 6A–C

Both left and right MI bear characteristics of the skalenopri onids. They have long and bent hooks, extending for about half of the jaw length, and the basal plate is fused with the right MI. Characteristics for Skalenopri ol sp. 1 are as follows: the straight posterior margin in both MI; the small size and low number of denticles (four distinct denticles); the left and right MI are almost mirror image of each other except for a fused basal plate in the right MI; and both MI have prominent posterolateral wings.

A similar species was described as Arablellites commend abl is from the Eifelian of Michigan (Eller 1961); however, it differs in having more denticles and a more prominent posterolateral wing. Eller (1964) described a skalenopri onid from the Middle Devonian of Ontario and Ohio as Drilonereites longicusculus. The hook of the latter species is longer than that of Skalenopri ol sp. 1. Skalenopri ol sp. A from the Lower Devonian of Podolia (Ukraine), described by Szaniawski and Drygant (2014), is also very similar to our Eifelian species, but Skalenopri ol sp. A has a more slender overall appearance and the hook is distinctively longer than in Skalenopri ol sp. 1.

Comparison with other jawed polychaete faunas

In general, the diversity of the fauna described herein is lower than in Ordovician or Silurian strata, where the number of species per sample is usually around 20, and the total number of species in a section can be nearly 60 (Eriksson et al. 2013). This can be either a result of methodological bias or the beginning of a diversity and abundance decrease in scolecodonts that has previously been observed towards younger Palaeozoic and Mesozoic strata. It seems that in the Mesozoic, the fossilization potential of polychaete jaws decreased due to a change in their composition (Szaniawski 1996).

The families dominating the studied assemblage are the same as in the Ordovician and Silurian, except for the presence of kielanopri onids that first appear in the Middle Devonian. At the genus level, the majority of genera persist from the older periods, such as Oenonites, Moch tyella, Ketnerites, Hindenites, Atraktopri ol and Skalenopri ol. On the other hand, a number of genera that are very common in the Or dovician and Silurian (such as Vistulella, Kozlowskipri ol or Pistoprion) have not been recorded in the studied section. Kozlowskipri ol and Pistoprion were recorded in the Emsian of the Prague Basin (PT, pers. obs.), and the latter has also been described from the Eifelian of Michigan (under designation Staur ocephalites cucullus; Eller 1961).

There are only a handful of papers dealing with Early Devonian jawed polychaetes. Three papers using natural taxonomy have been published, the first one by Lange (1947) who studied Emsian strata of the Paraná Basin, Brazil, which was later restudied by Eriksson et al. (2011), and the last one by Szaniawski and Drygant (2014) reporting a Lochkovian and Pragian collection from Podolia, Ukraine. The former two studies report a paulinitid assemblage from the cool-water Malvinokaffric Realm that is not comparable with any other regions. The latter study introduced a more diverse assemblage with close links to the Silurian faunas, especially at the family and genus levels. The studied collection herein has species in common with the Lower Devonian of Podolia, but only among paulinitids (see discussion above).

Previous assemblage-level studies on Middle Devonian scolecodonts are virtually non-existent; therefore, it is not possible to compare, for example, the quantitative distribution of the studied families. Nevertheless, based on descriptions and illustrations in published historical papers, the studied fauna seems to have several species in common with coeval faunas from North America (see discussion above and Eller 1938, 1941, 1961; Stauffer 1939). Similar results have also been reached for other fossil groups. For example, studies of the latest Eifelian brachiopods of the Central Appalachians (the Stony Hollow Member of the basal Hamilton Group in eastern New York and Pennsylvania) have shown that this member contains an Old World Realm fauna (Boucot and Blodgett 2001). Similarly, many bryozoan species were found in common between the Eifel area and Eastern American realm (Ernst and Schroeder 2007; Ernst et al. 2011).

Comparison of the assemblage from the Blankenheimerdorf section with Late Devonian scolecodonts from North America (Eller 1963b; Jansonius and Craig 1971, 1974), France (Taugourdeau 1971) and Poland (Szaniawski and Wróna 1973) reveal that there are several taxa in common among mochtyellids, paulinitids and kielanopri onids (discussion above). The high resemblance of Middle Devonian and Late Devonian faunas suggests that the period of evolutionary changes in the Early–Middle Devonian was followed by a rather stable interval until the end of the Devonian (or maybe longer), since some species are morphologically close to even Permian or early Mesozoic species (compare with Nakrem et al.
2001). Nevertheless, to confirm our findings, more studies that fully document jawed polychaete assemblages using apparatus-based taxonomy are needed, especially from the key origination and extinction intervals.

CONCLUSIONS

The scolecodont assemblage described herein represents one of the largest from the Middle Devonian. In general, the genus composition is quite similar to those of the better known Ordovician and Silurian assemblages (Eriksson et al. 2013). In comparison with older assemblages, taking into account only the relatively abundant families, ramphoprionids, kalloprionids, polychaeturids and symmep- troprionids are not present in the Eifelian assemblage. On the other hand, the family Kielanoprionidae does not appear until the Middle Devonian, and the studied assemblage is one of its oldest known records. This family ranges into the Triassic, when the Palaeozoic fauna is replaced by ‘modern’ polychaetes (Szaniawski 1996). Our data suggest that most Middle Devonian polychaete species of the Eifel area also occurred in other regions of Europe and North America, and were stratigraphically long ranging, extending into the Late Devonian.

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