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Bond, David P.G. (2006) The fate of the homoctenids (Tentaculitoidea) during the Frasnian-Famennian mass extinction (Late Devonian). Geobiology, 4 (3). pp. 167-177. ISSN: 1472-4669

https://doi.org/10.1111/j.1472-4669.2006.00078.x

Published paper
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THE FATE OF THE HOMOCTENIDS (TENTACULITOIDEA) DURING THE FRASNIAN-FAMENNIAN MASS EXTINCTION (LATE DEVONIAN)

"FRASNIAN-FAMENNIAN HOMOCTENIDS"

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Abstract: The homoctenids (Tentaculitoidea) are small, conical-shelled marine animals which are amongst the most abundant and widespread of all Late Devonian fossils. They were a principal casualty of the Frasnian-Famennian (F-F, Late Devonian) mass extinction, and thus provide an insight into the extinction dynamics. Despite their abundance during the Late Devonian, they have been largely neglected by extinction studies. A number of Frasnian-Famennian boundary sections have been studied, in Poland, Germany, France, and the United States. These sections have yielded homoctenids, which allow precise recognition of the timing of the mass extinction. It is clear that the homoctenids almost disappear from the fossil record during the latest Frasnian "Upper Kellwasser Event". The coincident extinction of this pelagic group, and the widespread development of intense marine anoxia within the water column, provides a causal link between anoxia and the F-F extinction. Most notable is the sudden demise of a group, which had been present in rock-forming densities, during this anoxic event. One new species, belonging to *Homoctenus* is described, but is not formally named here.

Key words: *Homoctenus*, homoctenids, tentaculitoids, Frasnian-Famennian, Devonian, extinction.

THE HOMOCTENIDS are a group of poorly understood, small, conical-shelled marine animals which were widespread and abundant in Late Devonian seas. Despite the fact that they are amongst the most abundant of all Late Devonian fossils, often reach rock-forming densities, they have been largely neglected in studies of the F-F extinction. Little is known of the animal that inhabited the shell, although recent work by Farsan (1994, 2005) has improved our knowledge of their morphology and ontogenetic development. Their facies distribution remains the best indicator of their life strategy, which was probably pelagic. This paper presents a review of the stratigraphic range of the homoctenids, together with new data from F-F boundary sections in Europe and North America, which has allowed the precise recognition of the timing of their extinction, in broadly separated locations (Fig. 1). Ultimately, the demise of the homoctenids represents the extinction of the entire class Tentaculitoidea.

Homoctenids reached their maximum diversity in the Late Devonian before essentially becoming extinct during the F-F crisis (Schindler, 1990; Hallam and Wignall, 1997; Bond *et al*., 2004). A few specimens have been reported from the earliest Famennian (e.g. Sherrard, 1975; Schindler, 1990; Over, 1997; Niko, 2000 (not strictly homoctenids, see discussion later)), but nevertheless, they were a principal casualty of the extinction and thus provide a good record of the extinction dynamics.

The F-F mass extinction is known as one of the “big 5” extinctions of the Phanerozoic (e.g. Raup and Sepkoski, 1982; Sepkoski, 1996), and several causal mechanisms have been proposed. These include habitat loss caused by widespread marine anoxia (e.g. Bond *et al.*, 2004), characterised by the classic “Kellwasser Horizons”. The Lower and Upper Kellwasser Horizons (LKH and UKH) are evidence of anoxic pulses which are principally recorded in European and North African submarine rise settings (e.g. Walliser *et al.*, 1988; Walliser 1996), but equivalent sediments were deposited under anoxic conditions in a variety of other settings. In the classic localities in Germany, these anoxic pulses occurred in the lower part of the Late *rhenana* conodont zone and topmost part of the *linguiformis* Zone respectively (Fig. 2). The LKH, although widespread (e.g. Schindler, 1993), does not appear to have been globally synchronous, for instance, a corresponding anoxic pulse begins earlier, in the Early *rhenana* Zone in France (La Serre), but later, at the end of the Late *rhenana* Zone in Poland (Feist and Schindler, 1994; Crick *et al.*, 2002; Bond *et al.*, 2004). In contrast, the UKH appears to have been a globally widespread, synchronous event, with anoxic or euxinic conditions developing in many settings during the latest part of the topmost Frasnian *linguiformis* Zone (for a review of depositional conditions in European F-F boundary sections, see Bond *et al.*, 2004). As with any mass extinction study, it is critical to constrain the timing of the extinction in order to evaluate causal mechanisms. As such, a detailed review of the stratigraphic range of homoctenids during the Devonian is presented here. This is supported by high resolution studies of F-F boundary sections in Europe and North America.

CLASSIFICATION AND PALAEOECOLOGY

The class Tentaculitoidea Lyashenko, 1957, (= Cricoconarida of Fisher, 1962) comprises the orders Tentaculitida Lyashenko, 1955, Homoctenida Bouček, 1964, and Dacryoconarida Fisher, 1962. Of these, the Homoctenida includes the families Homoctenidae Lyashenko, 1955, and following the revision of Alberti (1993), the Paranowakiidae Bouček, 1964. The

Homoctenidae are dominant in the Frasnian and hence there relevance to this study. They are geographically widespread and occur in many marine facies, being common in limestones but less so in sandstones. They have also been recorded in shales and siltstones and are known from shallow, intermediate and deep-water facies (Sherrard, 1975; Lűtke, 1985). However, homoctenids are most commonly observed in outer shelf and deeper water environments. Their abundance in Devonian fine-grained marine sediments deposited in outer shelf environments, including the anoxic black shales of the Russian Domanik Horizon (Lyashenko, 1957), suggests that the homoctenids were pelagic forms (Fisher, 1962; Ludvigsen, 1972; Lűtke, 1985; Truyols-Massoni, 1989; Tunnicliff, 1989; Hajłasz,1993; Gessa and Lecuyer, 1998).

STRATIGRAPHIC RANGE DURING THE DEVONIAN

Several homoctenid genera are known from the Middle to Late Devonian. Each species appears to be geographically widespread and has a short range, and thus are potentially valuable as zonal index fossils in sequences lacking in conodonts (Truyols-Massoni, 1989).

A number of species belonging to *Homoctenus* Lyashenko, 1955, are widespread in the Frasnian basins of Europe and North Africa, where it has been observed in Poland, Belgium, Germany, France, Spain, Czech Republic, Russia, Algeria, and Morocco (e.g. Zagora, 1964; Lardeux, 1969; Blumenstengel, 1975; Babin and Regnault, 1978; Freyer, 1977; Ruchholz, 1978; Sauerland, 1983; Truyols-Massoni, 1989). Most are dated between the *jamiae* and *linguiformis* conodont zones. The earliest recorded *Homoctenus* is observed in Emsian of Morocco (Jansen *et al.*, 2004). *Homoctenus* is also observed in upper Eifelian to upper Frasnian deep-water facies of the Russian platform (Lyashenko, 1967), including the black shales and limestones of the Domanik Horizon. Hajłasz (1993) recorded several homoctenids from Givetian borehole samples from Poland, including the species *Homoctenus hanusi* Bouček, 1964, *H. krestovnikovi* Lyashenko, 1957, *H. tokmovensis* Lyashenko, 1959, and *Polycylindrites tenuigradatus* Lyashenko, 1959.

Homoctenus is recorded in the middle Frasnian shallow water limestones of the Canning Basin (Sherrard, 1975), the only such recorded occurrence of the genus in such facies.

The genus *Homoctenus* was reported from the black shales of the topmost Frasnian Matagne Formation in southern Belgium (Casier, 2003), where they become extinct during the *linguiformis* Zone. Schindler (1990) reported rare specimens tentatively ascribed to *Homoctenus* from the basal Famennian beds at the Kellwasser type locality in the Harz Mountains, from Aeke Valley and from Steinbruch Schmidt, Germany.

Several species of *Homoctenus* are known from the Upper Devonian Daihua Formation of southern China, where they are common in grey limestones and black, laminated limestones (Li and Hamada, 1987). Associated conodonts in the Chinese sections include *Palmatolepis gracilis gracilis*, *P. delicatula*, *P. marginifera marginifera* and *P. minuta schleizia*. *P. gracilis gracilis* ranges from the *rhomboidea* to *praesulcata* Zones (Zhang *et al*., 2001), suggesting an *expansa* Zone (upper Famennian) distribution for *Homoctenus*, making them among the few survivors of the F-F event (Li and Hamada, 1987). Li (2000) also records tentaculitoids from the Daihua Formation, including the styliolinids *Striatostyliolina* and *Styliolina*, and four species of homoctenids belonging to *Homoctenus*. The homoctenid species, which have not been observed in other sections globally, include *H. luofensis* Li, 1995, *H. crassus* Li, 1995, *H. arctus* Li, 1995, and *H. opima* Li, 1995. These range from the Frasnian *jamiae* Zone, to above the earliest occurrence of the conodont *P. minuta*, suggesting a youngest age of at least the Middle *triangularis* Zone.

The genus *Polycylindrites* Lyashenko, 1955, is recorded from the Eifelian to upper Frasnian of the Russian platform where it is prolific in the bituminous Domanik Horizon (Lyashenko 1967). A further poorly known genus, *Heteroctenus* Lyashenko, 1955, is recorded from the Eifelian to upper Frasnian of Russia, and is suggested to extend to the basal Famennian (Lyashenko, 1967).

In the USA, the genus *Diploctenus* Lűtke, 1985, is found in the Lower Devonian (Pragian) Rabbit Hill Limestone of Eureka County, Nevada (Lűtke, 1985). This was assigned to the homoctenids on the basis of shape of the apex, and if truly a homoctenid, considerably extends their lower range.

HOMOCTENIDS IN STUDIED EUROPEAN SECTIONS

Most of the rocks encountered in this study are carbonates, and thus extraction of the calcium carbonate homoctenid shells was not possible. Accurate identification was only possible when a well-preserved specimen was found on a clean surface.

Coumiac Upper Quarry, Montagne Noire, France

This section records deposition on a carbonate slope / submarine rise. For detailed section information, and locality details, see Becker and House (1994), and Bond *et al*. (2004). *Homoctenus* is present throughout much of the Frasnian, often occurring in abundance, particularly in a homoctenid packstone that marks their last occurrence in the topmost Frasnian. This bed is considered to be equivalent to the German UKH (Becker and House, 1994). Schindler (1990) has identified subspecies of *H. tenuicinctus* Roemer, 1850, *H. ultimus* Zagora, 1964, and *H. ultimus pergracilis* Sauerland, 1983, ranging into the upper part of the *linguiformis* Zone, but was unable to differentiate between species in the topmost Frasnian bed. Schindler (1990) also records homoctenid fragments in nodules dated as Early *triangularis* Zone in a section some tens of metres distant to the main Coumiac section, although it is possible that these samples have been reworked.

La Serre Trench C, Montagne Noire, France

This section records basinal deposition and detailed section information and locality details are given by Becker and House (1994). As at Coumiac, *Homoctenus* is common in much of the Frasnian, and is again abundant in some beds, particularly in the Early to Late *rhenana* Zones (Fig. 3a). The species *Homoctenus tenuicinctus* ssp., *Homoctenus tenuicinctus tenuicinctus* Roemer, 1850, *Homoctenus tenuicinctus neglectus* Sauerland, 1983 and *Homoctenus ultimus* ssp., are all recorded during the Frasnian (Schindler, 1990) and persist until the topmost Frasnian, where they abruptly become extinct, contemporaneous with the main pulse of extinction at Coumiac.

Steinbruch Benner, Rheinisches Schiefergebirge, Germany

This section is a condensed pelagic limestone sequence which records deposition in a submarine rise setting. Detailed section and locality information is provided by Schindler (1990). Tentaculitoids are very common during the Frasnian, and a graphic log of this section is provided, which illustrates the presence of *Homoctenus* in the majority of the Frasnian beds (Fig. 4). In the base of the section (Early *rhenana* Zone) both styliolinids (which belong to the family Styliolinidae Grabau and Shimer, 1910, and the order Dacryoconarida) and homoctenids are present, sometimes in abundance. Unfortunately it has not been possible to identify the styliolinids because they are poorly preserved, but the homoctenids belong to *H. tenuicinctus* ssp. (Fig. 3b) and *H. ultimus* ssp. Styliolinids last occur during the Early *rhenana* Zone at Benner, in a bed below the LKH. Homoctenids are much more common, being present in almost every bed in the Frasnian. They are particularly abundant in the UKH, where they are the dominant fauna. However, in the upper part of the UKH they become less abundant, and are not observed above this bed. A single, unidentified specimen was observed in the basal Famennian bed. This is clearly not a homoctenid – it is a smooth, short cone that more closely resembles a styliolinid, although it is possible that it is a foraminifera (Earlandiacea?).

At nearby Steinbruch Schmidt, which was probably deposited on the same submarine rise, Schindler (1990) recorded a similar range distribution, with homoctenids very common during the Frasnian. *Homoctenus ultimus* ssp. is abundant in the middle part of the UKH before almost becoming extinct in the upper part. Very rare specimens of *Homoctenus* sp. are reported (but not illustrated) from the basal Famennian bed (Schindler, 1990), but they do not persist above this.

Kostomłoty, Poland

This section records slope deposition, and is described in detail by Racki *et al.* (2004). Tentaculitoids are abundant in early Frasnian limestones and shales but species diagnosis is difficult due to poor preservation. The fauna includes straight, ribbed forms with a pointed apex, which resemble homoctenids, and larger, smooth forms, which resemble more closely the styliolinids.

Kowala Quarry, Poland

This section records deep slope deposition, and is described in detail by Bond *et al*. (2004). The section is not condensed and hence homoctenids do not immediately appear to be as abundant as they are in the German and French sections. However, several species are present throughout the Frasnian, including *H. ultimus ultimus* Zagora, 1964 (Fig. 3c), *H. ultimus derkaouensis* Lardeux, 1969, *H. ultimus pergracilis*, *H. tenuicinctus tenuicinctus* (Fig. 3d), *H. tenuicinctus neglectus*, *Homoctenus deflexus*, and *Homoctenus* sp. A. (Fig. 3e). Their occurrences are shown on a graphic log of the Kowala section (Fig. 4).

Although rare species are unlikely to faithfully record true extinction events, it is clear that homoctenids are abundant in the Frasnian at Kowala, and several species are present in the upper part of the UKH equivalent. By concentrating on the most abundant taxa, it is possible to conclude that homoctenids became extinct at this level, shortly before the F-F boundary.

Płucki Trench, Poland

This section records deep basinal deposition, and is described in detail by Racki (1990). *Homoctenus* is present throughout most of the *linguiformis* Zone, being very common in the lower part of the UKH equivalent, but absent in the upper part, a level that coincides with the F-F boundary according to Dzik (2002).

HOMOCTENIDS IN STUDIED NORTH AMERICAN SECTIONS

Tentaculitoids are not common in the Frasnian sections studied in the United States and specific identification has not been possible, because they are usually only observed in thin-section, not on bedding plane chips. In Nevada and Utah, they have been observed in the Coyote Knolls and Tempiute Mountain sections. In New York State, they are known from the Beaver Meadow Creek section at Java Village.

Coyote Knolls, Utah

This section records deposition in a deep-water, intrashelf basin, and is described in detail by Sandberg *et al*. (1988, 1997) and Bond and Wignall (2005). Tentaculitoids are fairly common in the condensed biomicrites of the Early *rhenana* Zone Guilmette Formation, where they are associated with a diverse fauna of corals, brachiopods, bivalves, goniatites, ostracods and trilobites. In thin-section, they are seen to be thin-walled forms, with evenly spaced rings on the outer wall, which are repeated on the inner wall surface, and therefore belong to homoctenids. They closely resemble specimens of *Homoctenus* observed in thin section from other sections. The overlying Pilot Shale basinal / base of slope facies contains rare homoctenids, which range from the Late *rhenana* Zone up to the *linguiformis* Zone, where they become extinct in the lower part of the UKH equivalent.

Tempiute Mountain, Nevada

This section records deposition in a high-energy, upper slope setting, described by Morrow (2000). Fauna is generally sparse, although tentaculitoids are common in samples from the *punctata* to *jamiae* Zones. These are poorly preserved and accurate identification has not been possible (Fig. 3f). However, some are smooth-walled forms, which suggests they are styliolinids, whereas others have rings and resemble homoctenids. Indeterminate tentaculitoids are also present within the *linguiformis* Zone but none are observed above this level.

Java Village, New York State

This section records basinal deposition and is described by Over (1997). Tentaculitoids are present in cephalopod-bearing concretions from the lower part of the Hanover Shale Member, where they are associated with a conodont fauna characteristic of the lower part of Montagne Noire conodont Zone 13 (of Klapper, 1989), which correlates to the Late *rhenana* Zone. Tentaculitoids are also present in the topmost *linguiformis* Zone, within the 0·9 m thick black shale which corresponds to the UKH. These have been identified as *Homoctenus* (Kirchgasser in Over, 1997). It is highly likely that the Late *rhenana* Zone examples also belong to *Homoctenus*. Over (2002) notes that homoctenids range across the boundary, and are common in a 0·02 m thick grey shale, some 0·11 m above the boundary. This is their last recorded occurrence in any New York State boundary section. It is notable that the F-F boundary in this section has been defined by Over (1997) as the *common* (my italics) occurrence of the zonal index fossil, *Palmatolepis triangularis*, rather than the more usual *first* occurrence of this species. Furthermore, Over (1997) notes that this species first appears in “close association with the mass extinction... several centimetres below the boundary” (p. 167). Thus the F-F boundary may have been placed too high in this section: if it were taken as the first occurrence of *P. triangularis*, then the homoctenid extinction would be defined precisely at the F-F boundary. Nevertheless, it is possible that in New York State, as has been suggested for Germany (Schindler, 1990), a single species of *Homoctenus* persisted into the lowest Famennian before also becoming extinct. Elsewhere, in western New York State, Yochelson and Kirchgasser (1986) report late Frasnian occurrences of *Homoctenus* from the Angola Shale.

DISCUSSION

As a class, the tentaculitoids reached their maximum diversity in the Middle Devonian (Fisher, 1962), but, by the late Frasnian, the family Homoctenidae dominates. Almost all of the tentaculitoids present in the F-F boundary sections studied here are homoctenids, indeed only one genus, *Homoctenus* is widely represented. Each species has a short range but a wide geographical distribution. At any one time, they have a low diversity, but their species turnover is high.

Range termination in studied sections

The F-F mass extinction accounts for almost all late Frasnian tentaculitoids (Fig. 5). In Europe, the species *H. tenuicinctus tenuicinctus*, *H. tenuicinctus neglectus*, *H. ultimus ultimus*, *H. ultimus derkaouensis*, and *H. ultimus pergracilis* all persist up to the topmost *linguiformis* Zone, often in abundance. Almost all became extinct during deposition of the UKH or the equivalent beds, with only rare specimens belonging to *Homoctenus* reported by Schindler (1990) from the basalmost Famennian in Germany and France. Certainly no new species are observed in the Famennian.

In several sections in this study, in particular Benner (Fig. 4), Coumiac, La Serre, and Kowala (Fig. 4), *Homoctenus* is common or abundant in many of the Upper Frasnian beds, thus their absence in the broadly similar facies of the early Famennian, does indeed provide evidence of their extinction, and is not merely a taphonomic artefact. In terms of both diversity and abundance, the decline in homoctenids, and their near complete disappearance from the fossil record can be placed at a sharply defined level, within the UKH equivalent in the latest Frasnian. In North America, tentaculitoids are not so commonly observed, probably due to high sedimentation rates of the sections studied. However, where homoctenids have been identified, they also range up to the *linguiformis* Zone, before becoming extinct during the UKH equivalent (at Coyote Knolls). At Java Village, New York, *Homoctenus* (dependent on the definition of the F-F boundary in this section) ranges into the basal Famennian, where they too become extinct within sediments deposited under intensely anoxic conditions (Over, 2002).

While it may be true that the tentaculitoids were in decline by the Late Devonian from their maximum diversity in the Middle Devonian, with just styliolinids and homoctenids (dominated by just one genus, *Homoctenus*) being represented world-wide by the late Frasnian, they were still an exceptionally abundant group, often occurring in rock-forming densities, and they were therefore one of the principal casualties of the F-F mass extinction. Ultimately, the major phase of their extinction falls within the UKH in Germany, or its global equivalent. In the rare occurrences where a few specimens persist into the basal Famennian, they too become extinct within essentially the same anoxic event, where dysoxic / anoxic conditions prevailed across the boundary (e.g. Bond *et al.*, 2004).

Reported post-Frasnian occurrences

Niko (2000) reports a tentaculitoid (placed in the order Tentaculitida and family Gotlandellitidae) from the uppermost Carboniferous of Japan, and Weedon (1991) amends the class Tentaculitoidea to include the new order Microconchida, which comprises an unnamed family of helically coiled, vermiform "gastropods" (p. 227), ranging from the Middle Devonian to the Lower Triassic. Whether these are true tentaculitoids remains highly questionable. The specimens of Niko (2000) only superficially resemble tentaculitoids, being distinctly curved and flask-shaped, with a large rim at their aperture. If they are tentaculitoids, they must represent a unique Lazarus taxa. The vermiform "gastropods" of Weedon (1991) bear little resemblance to tentaculitoids, and are not widely considered to be true tentaculitoids.

More convincing reports of post-Frasnian tentaculitoids come from China. Li and Hamada (1987) reported homoctenids from the Late Famennian *expansa* Zone. Li (2000) described four species of *Homoctenus* which range at least into the Middle *triangularis* Zone. Although definitive Famennian conodont species are lacking in the earlier study, the latter certainly suggests that *Homoctenus* survived well past the basal Famennian in China. The species *H. krestovnikovi* and *H. tokmovensis* reported by Li and Hamada (1987) are common during the middle Frasnian, but are not known from the late Frasnian. It is therefore particularly odd that these species should disappear from the fossil record long before the F-F extinction, before returning as Lazarus taxa in the upper Famennian. It is certainly curious that a supposedly pelagic group of global distribution should suddenly become restricted to this single area, whereupon they ceased to exhibit their characteristically high turnover.

Schindler (1990) describes the F-F extinction at Steinbruch Schmidt in Germany as a step-wise event, beginning with the disappearance of the styliolinids within the Early *rhenana* Zone (a similar distribution is observed at Steinbruch Benner). The homoctenids in the Schmidt section suffer a great reduction in the upper part of the UKH (Schindler, 1990). Only very rare specimens range higher than the UKH, and the final step of the extinction occurs as the last homoctenids disappear in the basal Famennian bed. Thus, although Schindler (1990) considers the extinction to be step-wise, the vast majority of homoctenids become extinct at the same level within the UKH, in accordance with the data presented within this study.

In summary, the homoctenids were amongst the most abundant and widespread of all Late Devonian fossils, being particularly common in European basinal sections, and also known from North Africa, the United States, Russia, China, and Australia. They were largely unaffected by the anoxic event during the *rhenana* Zone (the LKH or its equivalent), which was not a globally synchronous event (Bond *et al.*, 2004). Several species persist in great abundance up to the F-F boundary, where they almost disappear from the fossil record (within the UKH or its equivalent). The very rare specimens reported to persist into the basal Famennian in France and Germany survive for only a short time, before they too disappear from the record. The younger records from China are intriguing and these sections require further study. The record of the styliolinids is less complete, and it was not possible to accurately constrain the timing of their extinction, although Li (2000) suggests that styliolinids range as high as the homoctenids.

Frasnian-Famennian extinction scenario

Numerous causal mechanisms for the F-F mass extinction have been proposed since McLaren's (1970) suggestion that bolide impact was responsible. The majority of these fit broadly into two categories, essentially an extraterrestrial versus an earth-bound cause. Anoxic facies are widespread during the latest Frasnian, and consequently anoxia features in many extinction models. Buggisch (1972) and House (1985) were among the early proponents of the anoxia kill mechanism, suggesting that the spread of stagnant, anoxic, shallow seas during the Frasnian caused extinction amongst benthic organisms. The Late Devonian was a time of widespread anoxic bottom waters, with clear evidence for a synchronous, globally widespread anoxic pulse in the latest Frasnian *linguiformis* Zone, manifest as the UKH in Germany (e.g. Joachimski and Buggisch, 1993; Walliser, 1996; Joachimski *et al.*, 2001). To understand any mass extinction it is critical to precisely locate the timing of the extinction for various fauna. This study demonstrates that the homoctenids, the last surviving tentaculitoids, which were abundant during the Frasnian, suffered a major decline in both abundance and diversity during the very latest *linguiformis* Zone, during the upper part of the UKH, or its equivalent. A few specimens in Germany and France struggle into the basal Famennian before disappearing from the record. Geochemical data (Bond *et al.*, 2004) indicates that the basal Famennian at these sections still records dysoxic / anoxic deposition, and thus it is considered here that these specimens died during the same "event". The major homoctenid losses were concurrent with an intensification of anoxic conditions in several settings, and with the spread of anoxia into shallow settings and into the upper water column, as evidenced by the development of syngenetic pyrite framboid populations (see Bond *et al*., 2004). The homoctenids are widely regarded as pelagic forms, and thus would not be expected to suffer from benthic anoxic conditions, as is evidenced from their abundance in many anoxic facies. The fact that their ultimate demise in the latest *linguiformis* Zone coincides with the development of upper water-column anoxia lends considerable support to the anoxic kill hypothesis, i.e. a scenario whereby the pelagic homoctenids would have become trapped by pervasive anoxic waters. A final point for future discussion: such a kill mechanism would be effective irrespective of any fluctuations in eustatic sea-level. Several authors have suggested that a regressive pulse (and probably an increase in marine oxygenation) is associated with the Upper Kellwasser Horizon and its global equivalents (and is therefore implicit in the extinction scenario, e.g. Sandberg *et al*., 1988; Sandberg *et al*., 1997) – on the contrary, the intensification and spread of marine anoxia during this interval was likely responsible for the extinction amongst pelagic groups such as the homoctenids.

ACKNOWLEDGMENTS

The author wishes to thank Paul Wignall (University of Leeds), and Grzegorz Racki (University of Silesia) for their invaluable support during this research. Dick Lindemann and Montserrat Truyols-Massoni provided helpful criticism of an earlier version of this manuscript. This work was supported by a NERC PhD Studentship, and a British Council research grant.

REFERENCES

ALBERTI GKB (1993) Dacryoconaride und homoctenide Tentaculiten des Unter und MittelDevons. *Courier Forschungsinstitut Senckenberg*, **158**, 1-229.

BABIN C, REGNAULT S (1978) Presence de Devonien superieur fossilifere dans la partie centrale du synclinorium median armoricain; consequences structurales et paleogeographiques. *Bulletin de la Societé Géologique de France*, **20**, 112-114.

BECKER RT, HOUSE MR (1994) Kellwasser events and goniatite successions in the Devonian of the Montagne Noire with comments on possible causations. *Courier Forschungsinstitut Senckenberg*, **169**, 45-77.

BLUMENSTENGEL H (1975) Mikropalaeontologische Untersuchungen in der Harzgeroeder und Blankenburger Zone. *Zeitschrift fuer Geologische Wissenschaften*, **3**, 327-331.

BOND DPG, WIGNALL PB (2005) Evidence for Late Devonian (Kellwasser) anoxic events in the Great Basin, western United States. In: *Understanding Late Devonian and Permian-Triassic Biotic and Climatic Events: Towards an Integrated Approach* (eds. Over DJ, Morrow JR, Wignall PB). Developments in Palaeontology and Stratigraphy **20**, 225-262.

BOND DPG, WIGNALL PB, RACKI G (2004) Extent and duration of marine anoxia during the Frasnian-Famennian (Late Devonian) mass extinction in Poland, Germany, Austria and France. *Geological Magazine*, **141**, 173-193.

BOUČEK B (1964) *The tentaculites of Bohemia; their morphology, taxonomy, ecology, phylogeny and biostratigraphy*. Czechoslovakian Academy of Sciences, Prague.

BUGGISCH W (1972) Zur Geologie und Geochemie der Kellwasserkalke und ihrer begleitenden Sedimente (Unteres Oberdevon). *Abhandlungen des Hessischen Landesamtes fuer Bodenforschung*, **62**, 1-67.

CASIER J-G (2003) Ostracods from the late Frasnian of the Neuville railway section (Dinant Synclinorium, Belgium); relation to the Kellwasser Event. *Bulletin de la Societé Géologique de France*, **174**, 149-157.

CRICK RE, ELLWOOD BB, FEIST R, EL HASSANI A, SCHINDLER E, DREESEN R, OVER DJ, GIRARD C (2002) Magnetostratigraphy susceptibility of the Frasnian/Famennian boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **181**, 67-90.

DZIK J (2002) Emergence and collapse of the Frasnian conodont and ammonoid communties in the Holy Cross Mountains. *Acta Palaeontologica Polonica*, **47**, 565-650.

FARSAN NM (1994) Tentaculiten: Ontogenese, Systematik, Phylogenese, Biostratonomie und Morphologie. *Abhandlungen der senckenbergischen naturforschenden Gesellschaft*, **547**, 1-128.

FARSAN NM (2005) Description of the early ontogenetic part of the Tentaculitids, with implications for classification. *Lethaia*, **38**, 255-270.

FEIST R, SCHINDLER E (1994) Trilobites during the Frasnian Kellwasser crisis in European Late Devonian cephalopod limestones. *Courier Forschungsinstitut Senckenberg*, **169**, 195-223.

FISHER DW (1962) Small conoidal shells of uncertain affinities. In: *Treatise on Invertebrate Paleontology*. *Part W*. *Miscellanea* (ed. Moore RC). Geological Society of America, New York, and University of Kansas Press, Lawrence, pp. W98-W116.

FREYER G (1977) Tentaculiten aus dem Oberdevon des Wildenfelser Zwischengebirges. *Freiberger Forschungshefte, Reihe C: Geowissenschaften, Mineralogie-Geochemie*, **326**, 25-31.

GESSA S, LECUYER C (1998) Evolutionary dynamics of Pragian Dacryoconarida (Lower Devonian, Tentaculitoidea); evidence from palaeontological data and delta (super 13)

C of marine carbonates from Czech Republic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **138**, 69-83.

GRABAU AW, SHIMER HW (1910) *North American Index Fossils; Invertebrates (Volume II)*. Seiler et Cie, New York.

HAJŁASZ B (1993) Tentaculites from the Givetian and Frasnian of the Holy Cross Mountains. *Acta Palaeontologica Polonica*, **37**, 385-394.

HALLAM A, WIGNALL PB (1997) *Mass Extinctions and Their Aftermath*. Oxford University Press, New York.

HOUSE MR (1985) Correlation of mid-Palaeozoic ammonoid evolutionary events with global sedimentary perturbations. *Nature*, **313** (5997), 17-22.

JANSEN U, BECKER G, PLODOWSKI G, SCHINDLER E, VOGEL O, WEDDIGE K (2004) Pragian and Emsian near Aouinet Torkoz (SW Dra Valley, Morocco). *Documents de l'Insitut Scientifique, Rabbat*, **19**, 64-68.

JOACHIMSKI MM, BUGGISCH W (1993) Anoxic events in the late Frasnian – causes of the Frasnian-Famennian faunal crisis? *Geology*, **21**, 675-678.

JOACHIMSKI MM, OSTERTAG-HENNING C, PANCOST RD, STRAUSS H, FREEMAN KH, LITTKE R, SINNING-DAMSTE JS, RACKI G (2001) Water column anoxia, enhanced productivity and concomitant changes in δ^{13}C and δ^{34}S across the Frasnian-Famennian boundary (Kowala – Holy Cross Mountains / Poland). *Chemical Geology*, **175**, 109-131.

KLAPPER G (1989) The Montagne Noire Frasnian (Upper Devonian) conodont succession. *Memoir of the Canadian Society of Petroleum Geologists*, **14**, 449-468.

LARDEUX H (1969) *Les Tentaculites d'Europe Occidentale et d'Afrique du Nord*. Cahiers de Paléontologie, Paris.

LI YX (1995) Famennian tentaculites from Luofu, Guangxi: survivors of F/F extinction event. *Journal of Guilin Institute of Technology*, **15**, 157-170. [In Chinese with English abstract].

LI YX (2000) Famennian Tentaculitids of China. *Journal of Paleontology*, **74**, 969-975.

LI YX, HAMADA T (1987) Occurrence of Tentaculites in the Upper Devonian Daihua Formation of the Dachang area, Guangxi, China. *Scientific Papers of the College of Arts and Sciences, The University of Tokyo*, **36**, 163-171.

LUDVIGSEN R (1972) Late Early Devonian Dacryoconarid Tentaculites, Northern Yukon Territory. *Canadian Journal of Earth Sciences*, **9**, 297-318.

LÜTKE F (1985) Devonian tentaculites from Nevada (USA). *Courier Forschungsinstitut Senckenberg*, **75**, 197-226.

LYASHENKO GP (1955) New data on the systematics of tentaculitoids, nowakiids, and styliolinids. *Bulletin of the Moscow Society for the Investigation of Nature, Geology Division*, **24**, 94-95. [In Russian].

LYASHENKO GP (1957) Systematics of the tentaculitoids, nowakiids, and styliolinids. *Ezhegodnik Vsesoyuznogo Paleontologicheskogo Obshchestva*, **16**, 82-99. [In Russian].

LYASHENKO GP (1959) *Devonian Conoconchia of the central and eastern parts of the Russian Platform*. The All-Russian Research Institute of Oil (VNIGNI), Moscow.

LYASHENKO GP (1967) Coniconchia (Tentaculitida, Nowakiida, Styliolinida) and their importance in Devonian biostratigraphy. In: *International symposium on the Devonian system 2* (ed. Oswald DH). Alberta Society of Petroleum Geologists, Calgary, pp. 897-903.

MCLAREN DJ (1970) Time, life, and boundaries. *Journal of Paleontology*, **44**, 801-815.

MORROW JR (2000) Shelf-to-basin lithofacies and conodont palaeoecology across Frasnian-Famennian (F-F mid-Late Devonian) boundary, central Great Basin (western U.S.A.). *Courier Forschungsinstitut Senckenberg*, **219**, 1-57.

NIKO S (2000) Youngest record of tentaculitoids; *Hidagaienites* new genus from near the Carboniferous-Permian boundary in central Japan. *Journal of Paleontology*, **74**, 381-385.

OVER DJ (1997) Conodont biostratigraphy of the Java Formation (Upper Devonian) and the Frasnian-Famennian boundary in western New York State. In: *Paleozoic Sequence Stratigraphy, Biostratigraphy, and Biogeography: Studies in Honor of J. Granville ("Jess") Johnson* (eds. Klapper G, Murphy MA, Talent JA). Geological Society of America Special Paper **321**, pp. 161-177.

OVER DJ (2002) The Frasnian/Famennian boundary in central and eastern United States. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **181**, 153-169.

RACKI G (1990) Frasnian-Famennian event in the Holy Cross Mts, Central Poland: Stratigraphic and ecologic aspects. *Lecture Notes in Earth Sciences*, **30**, 169-181.

RACKI G, PIECHOTA A, BOND DPG, WIGNALL PB (2004) Geochemical and ecological aspects of lower Frasnian pyrite-ammonoid level at Kostomłoty (Holy Cross Mountains, Poland). *Geological Quarterly*, **48**, 267-282.

RAUP DM, SEPKOSKI JJ (1982) Mass extinction in the marine fossil record. *Science*, **215**, 1501-1503.

ROEMER FA (1850) Beiträge zur Kenntnis des nordwestlichen Harzgebirges. *Palaeontographica, Abteilung A: Palaeozoologie-Stratigraphie*, **3**, 1-67.

RUCHHOLZ K (1978) Ueber Verbreitung und stratigraphische Bedeutung der Tentakuliten im Devon der DDR; II, Harz. *Zeitschrift fuer Geologische Wissenschaften*, **6**, 541-556.

SANDBERG CA, ZIEGLER W, DREESEN R, BUTLER JL (1988) Part 3: Late Frasnian extinction: conodont event stratigraphy, global changes, and possible causes. *Courier Forschungsinstitut Senckenberg*, **102**, 263-307.

SANDBERG CA, MORROW JR, WARME JE (1997) Late Devonian Alamo impact event, global Kellwasser events, and major eustatic events, eastern Great Basin, Nevada and Utah. *Brigham Young University Geology Studies*, **42**, 129-160.

SAUERLAND U (1983) Dacryoconariden und Homocteniden der Givet- und Adorf-Stufe aus dem Rheinischen Schiefergebirge (Tentaculitoidea, Devon). *Gőttinger Arbeiten zur Geologie und Paläontologie*, **25**, 1-86.

SCHINDLER E (1990) Die Kellwasser-Krise (hohe Frasne-Stufe, Ober Devon). *Gőttinger Arbeiten zur Geologie und Paläontologie*, **46**, 1-115.

SCOTESE CR, McKERROW WS (1990) Revised world maps and introduction. *Memoir of the Geological Society of London*, **12**, 1-21.

SEPKOSKI JJ (1996) Patterns of Phanerozoic extinction: a perspective from global data bases. In: *Global Events and Event Stratigraphy* (ed. Walliser OH). Springer-Verlag, Berlin, pp. 35-52.

SHERRARD K (1975) Devonian tentaculitids from North-west Australia. Proceedings *of the Royal Society of Victoria*, **87**, 179-186.

TRUYOLS-MASSONI M (1989) Devonian homoctenids of the Cantabrian zone (NW Spain); an attempt of biozonation. *Geobios*, **22**, 671-676.

TUNNICLIFF SP (1989) An early record of probable nowakiid tentaculitoids from Wales. *Palaeontology*, **32**, 685-688.

WALLISER OH (1996) Global events in the Devonian and Carboniferous. In: *Global Events and Event Stratigraphy* (ed. Walliser OH). Springer-Verlag, Berlin, pp. 225-250.

WALLISER OH, LOTTMANN J, SCHINDLER E (1988) Global events in the Devonian of the Kellerwald and Harz Mountains. *Courier Forschungsinstitut Senckenberg*, **102**, 190-193.

WEEDON MJ (1991) Microstructure and affinity of the enigmatic Devonian tubular fossil Trypanopora. *Lethaia*, **24**, 227-234.

YOCHELSON EL, KIRCHGASSER WT (1986) The youngest styliolines and nowakiids (Late Devonian) currently known from New York. *Journal of Paleontology*, **60**, 689-700.

ZAGORA K (1964) Tentaculiten aus dem thűringschen Devon. *Geologie* (Berlin), **13**, 1235-1273.

ZHANG R, WANG C, HU N, FENG S (2001) Biostratigraphy of Famennian in Hainan Island, South China. *Science in China (Series D)*, **44**, 1057-1064.

APPENDIX: DESCRIPTION OF SPECIES IN THIS STUDY

There follows a brief description of the homoctenids observed in this study. All material used in this study is deposited in the University of Leeds School of Earth and Environment palaeontological collection.

Homoctenus Lyashenko, 1955

Short (average length 3 mm), straight to gently curved, narrow cone, with a small apical angle. Shell has a large number of transverse rings, which are narrow and generally high in profile. Shell is thin, with the internal surface reproducing the features of the external surface. Longitudinal ornamentation absent or only weakly developed. Apical region may have two or three partitions. Apical region of the shell is initially cone shaped, and is often prolonged by a needle-like, hollow, tubular appendix, open at its point.

Homoctenus ultimus Zagora, 1964

The species *Homoctenus ultimus* comprises the subspecies *H. ultimus ultimus* Zagora, 1964, *H. ultimus derkaouaensis* Lardeux, 1969, and *H. ultimus pergracilis* Sauerland, 1983. *H. ultimus* may be differentiated from *H. tenuicinctus* by its greater apical angle, and higher density of transverse rings. *H. ultimus* should not be confused with *H. krestovnikovi*, which is similar in appearance but differs in that it has more rings in the median region. The three subspecies are described below.

Homoctenus ultimus ultimus Zagora, 1964

Shell straight obtaining maximum length of 4·5 mm and maximum diameter of 0.4 mm. Average length is 3 mm and average diameter is 0·3 mm. An apical spine is rarely observed, but may reach 0·2 mm in length. Shell is almost straight with apertural angle only slightly larger than apical angle. Ornamentation comprises 32 rings per millimetre length in median region, 30 per millimetre in apertural region. There are 6 rings in a length equal to the diameter in the middle region, and 8-12 in the apertural region of the shell. Apical angle is between 6-7 º.

Homoctenus ultimus derkaouaensis Lardeux, 1969

Shell straight, rarely with a gently curved apical spine. The shell obtains maximum length of 2·5 mm and maximum diameter of 0·35 mm. The apical region is rarely observed, but the apical bulb may reach 0·2 mm in length, and the apical spine may reach 0.24 mm length. Ornamentation comprises 28-35 rings per millimetre length in apical region, 24-25 per millimetre in apertural region. There are 8 rings in a length equal to the diameter in the median region, between 7 and 8 in the apertural region of the shell. Apical angle is 9-10 º.

Homoctenus ultimus pergracilis Sauerland, 1983

Short, straight shell, obtaining maximum length of 2·8 mm and maximum diameter of 0·3 mm. The apical region is rarely observed, but the apical bulb and spine may reach 0·4 mm length. Ornamentation comprises 40-48 well-defined rings per millimetre length in apical region, 22-30 per millimetre in apertural region. There are 8 rings in a length equal to the diameter in the median region, 10 in the apertural region of the shell. Apical angle is 5-7 º and does not increase significantly towards the aperture, as the shell is almost straight. Fine longitudinal striations may also be present.

Homoctenus tenuicinctus tenuicinctus Roemer, 1850

Narrow, long shell, with a maximum length of 6 mm, and maximum diameter 0·45 mm. The apical bulb and spine reach 0·8 mm in length. Ornamentation comprises 22-28 well-defined rings per millimetre length in apical region, 10 per millimetre in apertural region. There are 4-5 rings in a length equal to the diameter in the median region, 5 in the apertural region of the shell. Apical angle is 3-5 º. Fine longitudinal striations may also be present.

Homoctenus tenuicinctus neglectus Sauerland, 1983

Narrow shell, with a maximum length of 5 mm, and maximum diameter 0·42 mm. The apical bulb and spine reach 0·6 mm in length. Ornamentation comprises 36 well-defined rings per millimetre length in apical region, and 16-20 per millimetre in apertural region. There are 4 rings in a length equal to the diameter in the median region, 5 in the apertural region of the shell. Apical angle is 3-8 º. Fine longitudinal striations may also be present.

Homoctenus deflexus Lardeux, 1969

Short, conical shell, with a strongly curved apical region. Average length is 2·5 mm, but length can reach 3·6 mm. Maximum diameter is 0·5 mm. Ornamentation comprises transverse rings of uniform height, with 19-23 rings per mm in the apical region, and 14-20 per mm in the apertural region. The apical angle is 9-10 °. Faint longitudinal striations may be observed.

Homoctenus sp. A.

Insufficient material was recovered to designated a species name. This species is observed in the *jamiae* Zone of the Frasnian, in deposits at Kowala Quarry, Poland. *Homoctenus* sp. A. exhibits a long (0·4 mm), narrow, smooth apex, followed by a tripartite arrangement of rings. It is this arrangement of rings which allows a clear separation from *H. tenuicinctus neglectus*. It is at least 2 mm in length, although only the apical and median portions of the shell are preserved. The maximum width reaches only 0·2 mm. The apical angle is small, approximately 4°. In the apical region, there are approximately 36 rings per mm.

EXPLANATION OF FIGURES

FIGURE 1. Late Devonian palaeogeographic reconsruction (based on Scotese and McKerrow, 1990) showing location of study areas. NV = Nevada; UT = Utah; NY = New York State; F = France; G = Germany; and PL = Poland. Other F-F tentaculitoid localities are also shown (e.g. South China and North Africa).

FIGURE 2. The Late Devonian standard conodont zonation, showing the approximate timing of the Lower and Upper Kellwasser Horizons in classic German boundary sections, and the position of the Frasnian / Famennian mass extinction.

FIGURE 3. 3a) Homoctenids in thin-section from the Lower Kellwasser Horizon, La Serre. Original (probably calcite) shell material is visible at high magnification, which displays laminae. The lower shell contains a small, inverted cone within its juvenile chamber. This appears to be a fragment of another tentaculitoid which has been washed into the shell (cone in cone appearance). Note the diagnostic depressed, angulate rings on the inner shell wall, repeating the appearance of the outer surface; 3b) *Homoctenus tenuicinctus* ssp. from the Lower Kellwasser Horizon, Steinbruch Benner; 3c) *Homoctenus ultimus ultimus* from the *jamiae* Zone, Kowala Quarry. At the top of the figure is a homoctenid with a smooth juvenile portion. This would originally have had rings, but they have not been preserved; 3d) Adult stage fragment of *Homoctenus tenuicinctus tenuicinctus* from Early *rhenana* Zone, Kowala Quarry. Note the slightly irregular shape which is occasionally observed in this species in the late stages of growth (Sauerland, 1983); 3e) An unnamed species, *Homoctenus* sp. A from the *jamiae* Zone, Kowala Quarry. Note tripartite arrangement of rings, which diagnostically separates this specimen from the similar *Homoctenus tenuicinctus neglectus*; 3f) Tentaculitoid from the *punctata* Zone at Tempiute Mountain. This photograph demonstrates the poor preservation of these examples. This specimen appears smooth and has a characteristic bulb shaped end, typical of styliolinids. (Scale bars are provided for reference).

FIGURE 4. Stratigraphic logs of Steinbruch Benner section, Germany, and Kowala Quarry, Poland, showing the position of the Kellwasser Horizons (LKH and UKH in Germany and anoxic equivalents in Poland) and beds which yield species belonging to *Homoctenus*. Conodont zonation after Schindler (1990), and Racki (1990). ? = possible occurrence.

FIGURE 5. Stratigraphic range of tentaculitoids during the Frasnian and Famennian in sections in this study. “?” = Rare specimens of *Homoctenus* in Famennian of Germany and France (Schindler, 1990) and New York (Over, 1997).