

The fate of the homoctenids (Tentaculitoidea) during the Frasnian–Famennian mass extinction (Late Devonian)

DAVID BOND

School of Earth and Environment, University of Leeds, Leeds LS2 9JT, UK

ABSTRACT

The homoctenids (Tentaculitoidea) are small, conical-shelled marine animals that are among 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 USA. 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.

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Corresponding author: David Bond. Tel.: +44 113 3435242; fax: +44 113 3435259 e-mail: eardpgb@earth.leeds.ac.uk.

INTRODUCTION

The homoctenids are a group of poorly understood, small, conical-shelled marine animals that were widespread and abundant in Late Devonian seas. Despite the fact that they are among the most abundant of all Late Devonian fossils, often reach rock-forming densities, they have been largely neglected in studies of the Frasnian–Famennian (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 & 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)), 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 & 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), characterized by the classic 'Kellwasser Horizons'. The Lower and Upper Kellwasser Horizons (LKH and UKH) are evidence of anoxic pulses that 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 & 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

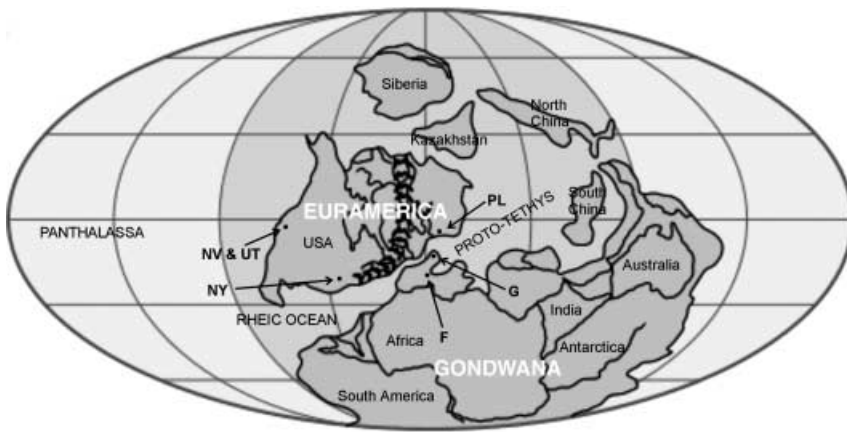


Fig. 1 Late Devonian palaeogeographical reconstruction (based on Scotese & McKerrow, 1990) showing location of study areas. NV = Nevada; UT = Utah; NY = New York State; F = France; G = Germany; and PL = Poland. Other Frasnian-Famennian tentaculitoid localities are also shown (e.g. South China and North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

Upper Devonian	Famennian	—	<i>praesulcata</i>	extinctions	
		—	<i>expansa</i>		
		—	<i>posterea</i>		
		—	<i>trachytera</i>		
		—	<i>marginifera</i>		
		—	<i>rhomboidea</i>		
	Frasnian	L	—		
		M	<i>crepida</i>		
		E	—		
		L	—		
		M	<i>triangularis</i>		
		E	—		
		—	<i>linguiformis</i> (formerly <i>Urn gigas</i>)		UKH
		L	<i>rhenana</i>		LKH
E	(formerly Lower and Upper <i>gigas</i>)				
—	<i>jamieae</i> (formerly <i>A. triangularis</i>)				
L	<i>hassi</i> (formerly <i>A. triangularis</i>)				
E	<i>hassi</i> (formerly Upper <i>asymmetricus</i>)				
—	<i>punctata</i> (formerly Middle <i>asymmetricus</i>)				

Fig. 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. E = Early, M = Middle, L = Late.

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 Bouèk (1964); and Dacryoconarida Fisher (1962). Of these, the Homoctenida includes the families Homoctenidae Lyashenko (1955); and following the revision of Alberti (1993), the Paranowakiidae Bouèk (1964). The Homoctenidae are dominant in the Frasnian and hence their 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; Lütke, 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; Lütke, 1985; Truyols-Massoni, 1989; Tunnicliff, 1989; Hajłasz, 1993; Gessa & 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 is 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; Freyer, 1977; Babin & Regnault, 1978; Ruchholz, 1978; Sauerland, 1983; Truyols-Massoni, 1989). Most are dated between the *jamieae* 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. Hajlasz (1993) recorded several homoctenids from Givetian borehole samples from Poland, including the species *Homoctenus hanusi* Bouček (1964); *Homoctenus krestovnikovi* Lyashenko (1957); *Homoctenus tokmovenis* 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 & Hamada, 1987). Associated conodonts in the Chinese sections include *Palmatolepis gracilis gracilis*, *Palmatolepis delicatula*, *Palmatolepis marginifera marginifera* and *Palmatolepis minuta schleizia*. *Palmatolepis 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 & 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* Lütke (1985) is found in the Lower Devonian (Pragian) Rabbit Hill Limestone of Eureka County, Nevada (Lütke, 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 & 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 & 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 & 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 that 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 & Shimer, 1910; 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

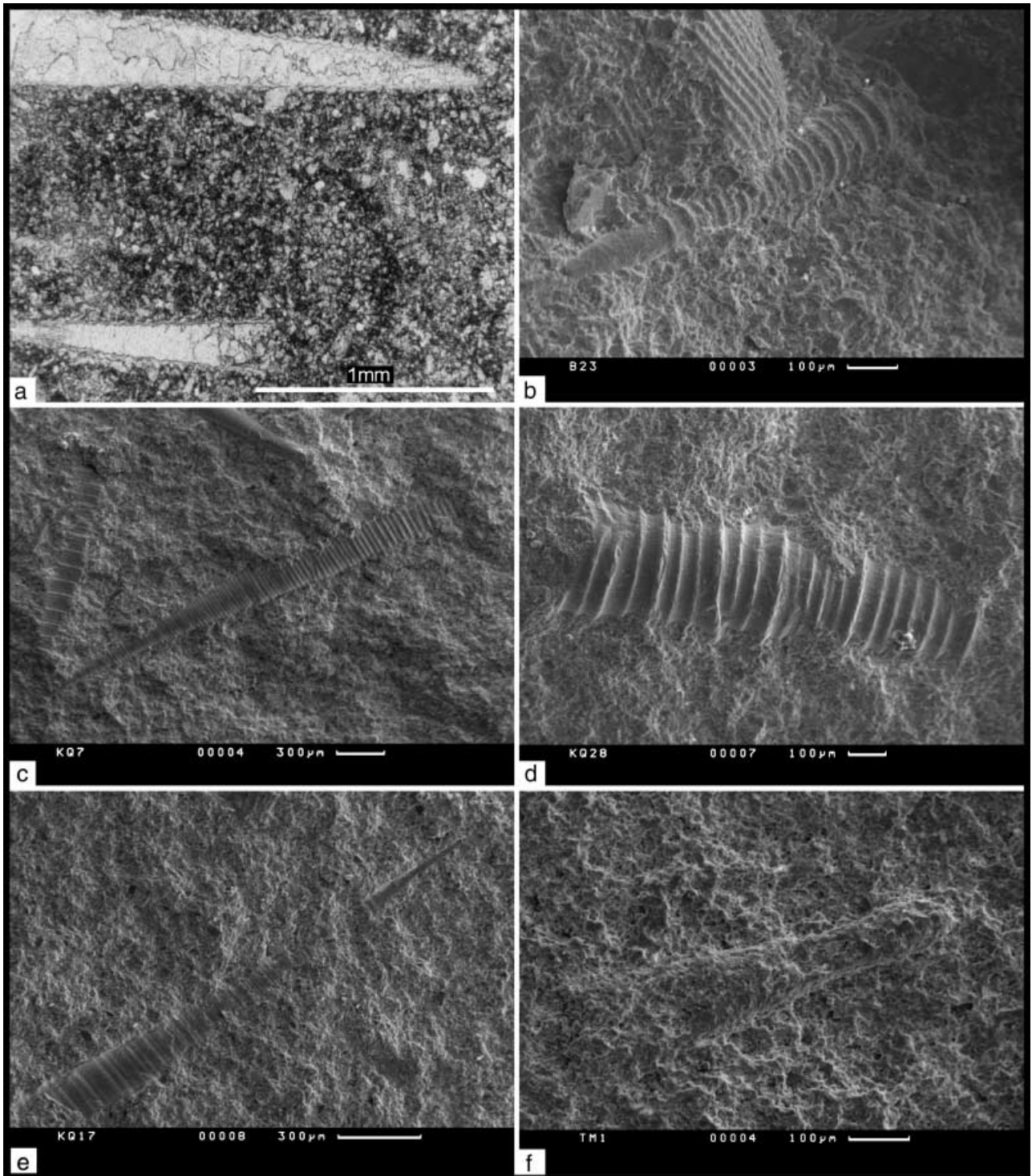


Fig. 3 (a) Homoctenids in thin section from the Lower Kellwasser Horizon, La Serre. Original (probably calcite) shell material is visible at high magnification, which displays laminae. The lower shell contains a small, inverted cone within its juvenile chamber. This appears to be a fragment of another 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; (b) *Homoctenus tenuicinctus* ssp. from the Lower Kellwasser Horizon, Steinbruch Benner; (c) *Homoctenus ultimus ultimus* from the *jamiæ* 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; (d) 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); (e) An unnamed species, *Homoctenus* sp. A from the *jamiæ* Zone, Kowala Quarry. Note tripartite arrangement of rings, which diagnostically separates this specimen from the similar *Homoctenus tenuicinctus neglectus*; (f) 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).

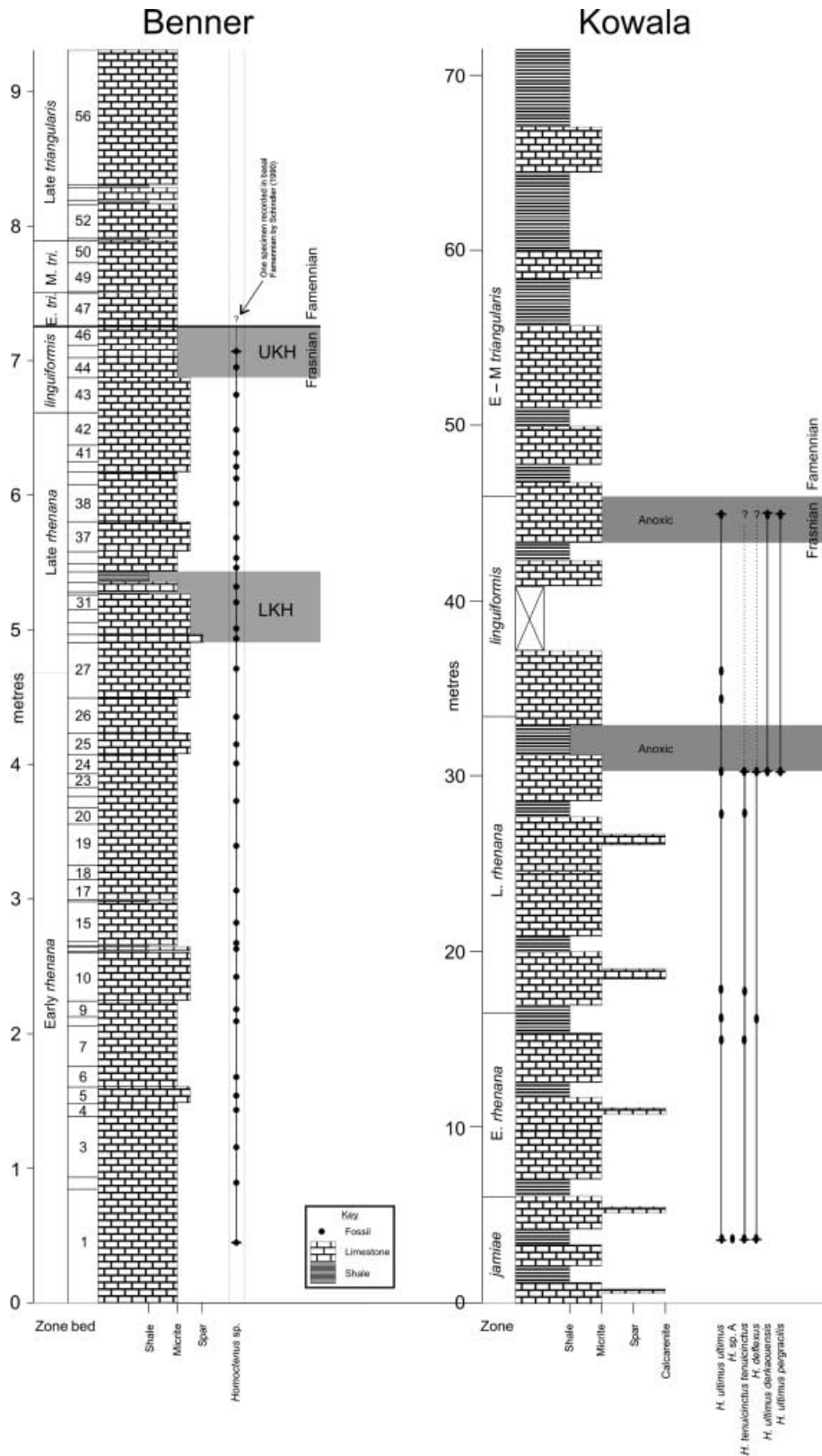


Fig. 4 Stratigraphic logs of Steinbruch Benner section, Germany, and Kowala Quarry, Poland, showing the position of the Kellwasser Horizons (LKH and UKH in Germany and anoxic equivalents in Poland) and beds which yield species belonging to *Homocotenus*. Conodont zonation after Schindler (1990), and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

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 (Earlandiaceae?).

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.

Plucki 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 USA 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 & 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 suggest that 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 that 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,

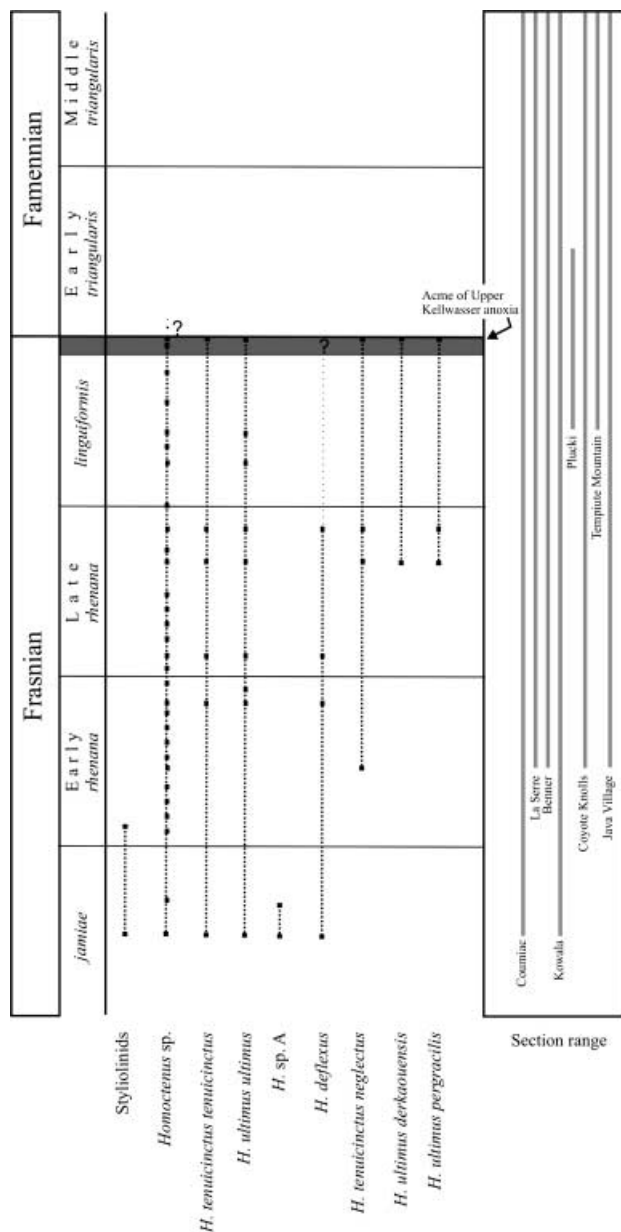


Fig. 5 Stratigraphic range of tentaculitoids during the Frasnian and Famennian in sections in this study. '?' = Rare specimens of *Homoctenus* in Famennian of Germany and France (Schindler, 1990) and New York (Over, 1997).

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 & 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 particular 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 taxon. 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 & Hamada (1987) reported homoctenids from the Late Famennian *expansa* Zone. Li (2000) described four species of *Homoctenus* that 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. tokmovenis* reported by Li & 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 stepwise, 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 among the most abundant and widespread of all Late Devonian fossils, being particularly common in European basinal sections, and also known from North Africa, the USA, 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 vs. 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 among 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 & 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) indicate 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 were likely responsible for the extinction among pelagic groups such as the homoctenids.

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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 six 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° and 7°.

***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 eight rings in a length equal to the diameter in the median region, between seven and eight in the apertural region of the shell. Apical angle is 9–10°.

***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 eight 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° 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 four to five rings in a length equal to the diameter in the median region, five in the apertural region of the shell. Apical angle is 3–5°. 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 four rings in a length equal to the diameter in the median region, five in the apertural region of the shell. Apical angle is 3–8°. 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 designate 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.