

Silurian oncocerid cephalopods from Gotland

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Silurian oncocerid cephalopods from Gotland

SVEN STRIDSBERG



Project Ecostratigraphy

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Two new genera, *Jeppssonoceras* and *Plemeroceras*, eight new species, *Trimeroceras bulbosum*, *Pentameroceras facula*, *Clathroceras plicatum*, *Jeppssonoceras concentratum*, *Plemeroceras cassis*, *Octameroceras sinuosum*, *O. pugil* and *O. unguifer*, and four old species of oncocerids are described from Gotland. Comparative studies are made on material from Czechoslovakia, Great Britain, Estonia and the United States. Immature and mature growth stages are discussed. Growth patterns in the apertural area support the interpretation that the number of sinuses does not necessarily reflect any specific genus, or species. Sexual dimorphism based on size and shape of shell is demonstrated in six species. Truncation seems to occur in three species. Floating conditions and swimming abilities are discussed as well as colour patterns. Comparisons are made with the extant *Nautilus* and *Spirula*. Malformation and bore holes in shell are described.

Sven Stridsberg, Geologiska Institutionen, Sölvegatan 13, S-223 62 Lund, Sweden; 22nd January, 1985.

Contents

Introduction	3	Family Trimeroceratidae Hyatt 1900	30
Acknowledgements	3	Genus <i>Trimeroceras</i> Hyatt 1884	30
Historical review	3	<i>Trimeroceras cylindricum</i> (Barrande 1865) n. comb. . .	30
Geology of the area	4	<i>Trimeroceras bulbosum</i> n. sp.	34
Localities	4	Genus <i>Pentameroceras</i> Hyatt 1884	37
Material and methods	8	<i>Pentameroceras mirum</i> (Barrande 1865)	37
Photography	9	<i>Pentameroceras facula</i> n. sp.	40
Shell orientation	9	Genus <i>Inversoceras</i> Hedström 1917	42
Measuring methods	10	<i>Inversoceras perversum</i> (Barrande 1865)	42
Deposition and preservation of shell	10	Genus <i>Clathroceras</i> Foerste 1926	45
Apertural growth	11	<i>Clathroceras plicatum</i> n. sp.	45
Dimorphism	12	Genus <i>Jeppssonoceras</i> n. gen.	48
Truncation	15	<i>Jeppssonoceras concentratum</i> n. sp.	48
Malformation, regeneration and parasitism	18	Genus <i>Plemeroceras</i> n. gen.	49
Epifauna	21	<i>Plemeroceras cassis</i> n. sp.	49
Colour pattern	23	Family Hemiphragmoceratidae Foerste 1926	51
Palaeoecology	24	Genus <i>Octameroceras</i> Hyatt 1900	51
Aperture	24	<i>Octameroceras sinuosum</i> n. sp.	53
Buoyancy	25	<i>Octameroceras pugil</i> n. sp.	56
Swimming	27	<i>Octameroceras rimosum</i> (Barrande 1865)	57
Classification	28	<i>Octameroceras unguifer</i> n. sp.	59
Taxonomic descriptions	30	Summary	61
Class Cephalopoda Cuvier 1797	30	Appendix: Locality list	62
Subclass Nautiloidea Agassiz 1847	30	References	63
Order Oncocerida Flower 1950	30		

Introduction

Apart from extensive publications by Barrande in the 19th century and later discussions by Hyatt, Foerste, Flower and Teichert, very little work has been carried out on Silurian brevicone cephalopods. A reason for this state of affairs is probably the rarity of brevicone fossils. The limited number of known specimens of brevicones has not given palaeontologists the opportunity to compare material from different places and thus many species are known only from one specimen. With the exception of some American species, most specimens discussed hitherto originate from the Barrandian collection in Prague, Czechoslovakia. Even within this material the number of known specimens of each species is generally small.

At the end of the 19th century, however, a great number of brevicone Silurian cephalopods were collected on the island of Gotland, Sweden. The material was stored at the Swedish Museum of Natural History (SMNH), in Stockholm, and has not been described until now. The great advantage of this collection is that most species are represented by a comparatively large number of specimens, thus giving the possibility of studying variations within a species and occasionally even the ontogeny.

The SMNH collection of Silurian brevicones is one of the largest known and includes the best preserved specimens, and therefore, apart from describing the Gotland fauna, I have been able to address questions of functional morphology and life habits. Thanks to the well preserved nature of the material, details not observed before have been identified and shed some light on the enigmatic aperture closure of nautiloids.

Acknowledgements. – When I decided to work with cephalopods in 1975, my plans were to study the Ordovician fauna of the Baltic Island of Öland. I was, however, persuaded by Sven Laufeld and Anders Martinsson to join the Silurian Project Ecostratigraphy and move to the next island in the Baltic, Gotland. For this piece of advice I am most thankful, especially after seeing the huge piles of broken unidentifiable orthocones on Öland. The work within Project Ecostratigraphy has been most inspiring and for this I would like to thank all my colleagues in the team.

The major part of my work has been carried out at the Department of Historical Geology and Palaeontology, University of Lund, and for all facilities put at my disposal I am very grateful to Gerhard Regnéll, Anita Löfgren and Kent Larsson. Gerhard Regnéll also assisted me by checking the latin names used for the new species.

For improvements and valuable comments on my manuscript I am most obliged to Jan Bergström, Kent Larsson, Harry Mutvei and Vojtech Turek. This goes for Lennart Jeppsson as well, whose time I have also used, and abused, for endless discussions on what I hope are mutual interests.

With few exceptions the described material was put at my disposal by Valdar Jaanusson at Naturhistoriska Riksmuséet, Stockholm, and by Lennart Jeppsson, whose Project Silicified Silurian Fossils

from Gotland (PSSFG) provided unique silicified material. For this I am very grateful. For stimulating guidance in the field in Bohemia and great help during my examinations of the Barrandian collections in Narodni Muzeum, Prague, I would like to express my thanks to Vojtech Turek. For help during visits to museums, sincere thanks also go to Adrian Rushton on the British Geological Survey, London, H. Owen at the British Museum of Natural History, London, Sven Laufeld and Anders Damberg at Sveriges Geologiska Undersökning, Uppsala, Hermann Jaeger at Museum für Naturkunde, Berlin, and Dr. Jauch at Wilhelma Aquarium in Stuttgart. Desmond H. Collins at the Royal Ontario Museum of Palaeontology provided material for which I am very thankful.

Grants from Statens Naturvetenskapliga Forskningsråd (NFR) through Project Ecostratigraphy and Kungliga Fysiografiska sällskapet paid my field-work and made it possible for me to visit collections in Uppsala, Stockholm, Prague, London and Berlin, as well as to study living *Nautilus* in Stuttgart.

The manuscript was linguistically read by David Sugden and Helen Sheppard. Typing was performed by Erna Hansson and Ingrid Lineke, and the drawings were made by Christin Andreasson and Inger Lander. To all these persons I give my sincere thanks.

Last, but not least, I would like to thank my wife Marie-Anne for good companionship during field-works and unlimited patience during my endless working sessions at home.

Historical review

Literature describing the Silurian cephalopod fauna of Gotland and surrounding areas dates back as far as the 18th century when German naturalists described fossil fragments found in erratic boulders in Germany. These descriptions were not very detailed and, apart from two minor publications by Klein (1731) and Breynius (1732), we had to wait until the end of the 18th century for the first specific publication concerning cephalopods from Gotland. This was by Modéer (1796) who described some orthocone cephalopods. He made no distinction between Foraminifera and Cephalopoda but there is no doubt that he discussed the latter, since he wrote about the position of the siphuncle.

Knowledge of the Gotland cephalopods increased at the beginning of the 19th century when Hisinger started publishing numerous descriptions. Lindström (1890) made a detailed list of all the articles and discussed Hisinger's efforts to establish six new species of the genus *Orthoceratites* and one new species of the genus *Nautilus*, namely *Nautilus complanatus* (Hisinger 1829). This name, however, was a junior homonym to *Nautilus complanatus* Sowerby 1820 and the fossil described by Hisinger was renamed by D'Orbigny as *Nautilus hisingeri*.

The next important work concerning the Silurian of Gotland was by Angelin (1880). He described five new species

and observed another three species of the genus *Orthoceras*. He also described a new species of the genus *Ophidoceras* but together these constituted only a very small part of the total cephalopod fauna. The purpose of Angelin's work, however, was to describe what was regarded as the total Silurian fauna all over southern Sweden.

Lindström (1890) concentrated his studies on the Ascoceratidae and the Lituitidae only and the result was an outstanding presentation of these two groups. As early as 1867, however, Lindström had published a catalogue of the known Gotland fossil species. In this catalogue there were 14 species of cephalopods, including *Inachus costatus* Hisinger. *Inachus costatus* was at that time believed to be a gastropod and therefore included in the list of gastropods. In the new list of fossils from Gotland by Lindström (1885) the number of cephalopod species had increased to 30. *Inachus costatus* had now been transferred to the genus *Trochoceras* as *T. (Inachus Hisinger) costatum* Hisinger and was consequently included in the list of cephalopods. Finally, in 1888 the last list including a total of 37 species was published (Lindström 1888).

We have every reason to assume that Lindström intended to continue to describe the cephalopod fauna of Gotland, following publication of the monograph on Ascoceratidae and Lituitidae and during the 1890s he and two of his staff, Florin and Liljevall (the latter well known for his high-quality illustration in publications by Lindström and others), collected a large material, including a great number of oncocerids. The Gotland cephalopod fauna would almost certainly have been better known today had not Gustaf Lindström suddenly died after a short illness in 1901 (Holm 1912).

Another Swedish contribution to the cephalopod literature from Gotland was produced by Hedström in 1917. He investigated the fauna of the genus *Phragmoceras* and described 32 new species (Hedström 1917). Hedström did not agree with Barrande's distinction between *Phragmoceras* and *Gomphoceras*, and out of Barrande's 33 species of *Phragmoceras*, Hedström only accepted 14. Hedström preferred to place most remaining species in the genus *Gomphoceras*. This classification, however, did not last and during the 1920s Foerste made great efforts to sort out the different genera, although he did not study the Gotland material (Foerste 1926, 1929 and 1930).

Many years before Hedström made his *Phragmoceras* studies, Holm at the Geological Survey of Sweden (SGU), had collected, among other fossils, oncocerid cephalopods on Gotland. Unfortunately Holm did not describe his localities very carefully and therefore we only know very roughly where he collected the fossils. It was obvious for Wiman (1927), who wrote the biography of Gerhard Holm, that future work on Holm's material would be problematic. In fairness it should be mentioned that Lindström's staff worked in the same way and that as a result all the remaining material is of uncertain geographic origin.

After the death of Lindström in 1901, Holm was selected to succeed him as professor at the Museum of Natural History in Stockholm and, when moving to the museum, Holm brought parts of his collections from SGU (Wiman 1927). Holm also studied the material collected by Lindström and his staff during Lindström's last years at the

museum and together these collections constitute the major part of the known Gotland oncocerid material.

During his time at the Museum of Natural History, Holm sorted out the cephalopod material and intended to publish some major cephalopod works, including an extensive publication dealing with the Baltic Silurian cephalopods. However, as the work he carried out to display the museum collections was overwhelming, Holm never got time to finish his cephalopod studies. Obviously he planned to continue his work on cephalopods after his retirement (Grönwall 1927), but unfortunately he did not live long enough to realize his plans. The only preserved text material consists of some labels together with the fossils and eleven excellent plates with photographs of various genera of cephalopods. As far as my investigations reached, no oncocerids were included on these plates.

The oncocerid material from the Museum of Natural History was put at my disposal in 1976 and constitutes the main part of the material described in this publication. Lindström partly named and sorted the material into what he believed were seventeen new species, but did not write any descriptions. To honour Lindström's efforts in oncocerid cephalopod studies, I have decided to use eight of his names when establishing eight new species based on the material.

A later contribution to the documentation of the Gotland cephalopods was made by Mutvei (1957). He described a new genus of a cyrtocone, *Lyeoceras*, with two new species *L. gotlandense* and *L. longistriatum*. The material of these species originates from the same localities in the Hemse Beds as some of the oncocerids described herein.

Geology of the area

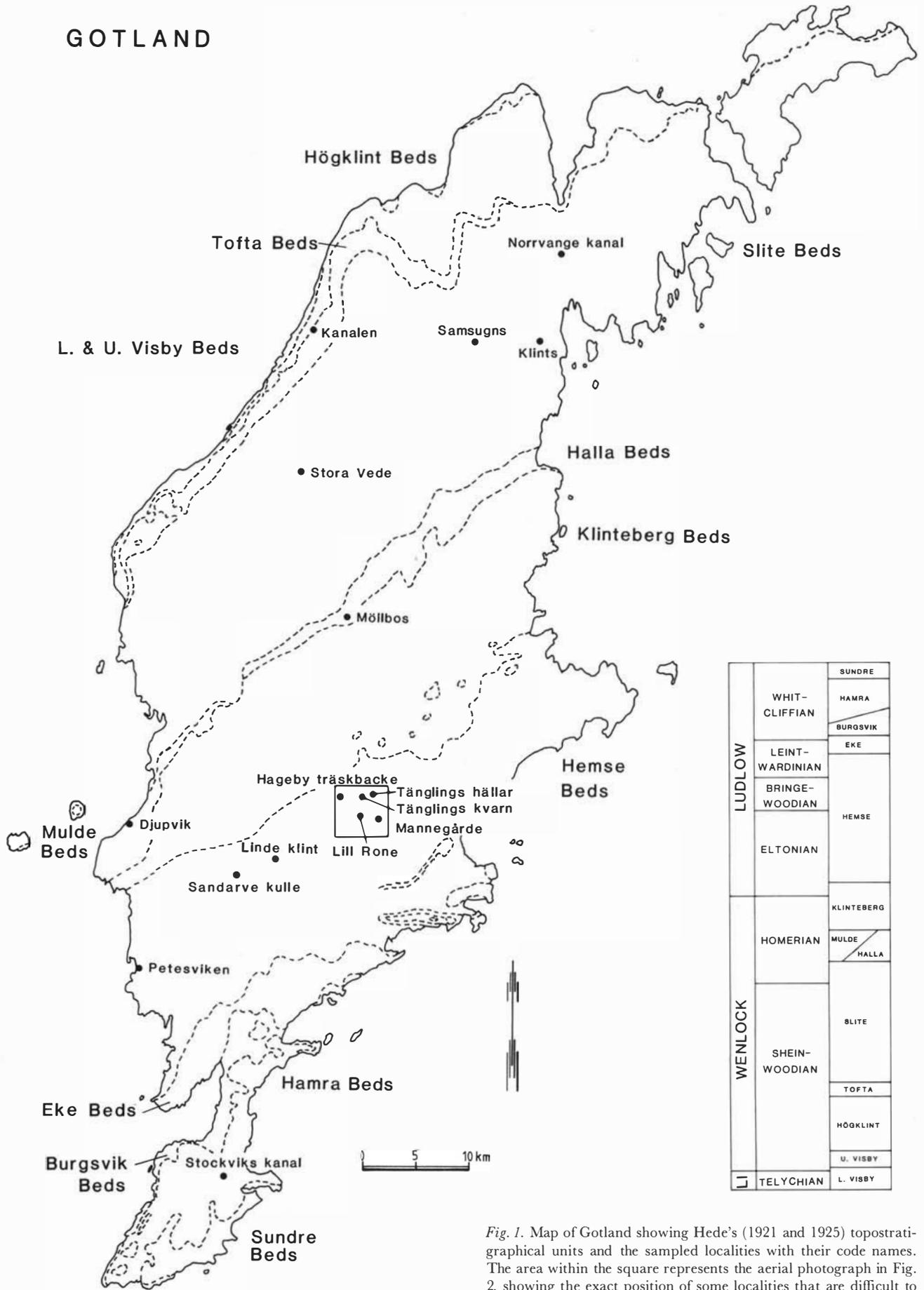
The Silurian of Gotland comprises a succession dominated by tropical limestones and marls, ranging in age from latest Llandoveryan in the northwestern part of the island to latest Ludlovian in the south. Hede (1921 and 1925a) established thirteen topostratigraphical units (Fig. 1). Reefs are extensive in the Högklint, Slite, Klinteberg, Hemse, Hamra and Sundre Beds.

The geology of Gotland has been described by various authors (e.g. Hede 1960, Martinsson 1967 and Manten 1971), and an excellent review was published by Laufeld (1974b).

The Gotland oncocerids discussed herein originate mainly from the Slite and Hemse Beds. About two thirds of the total number of specimens derive from the Hemse Beds in the Lye area (Fig. 2) and, with few exceptions, the rest of the material was collected from the Slite Beds at Samsugns. Furthermore, most species occur together at the more fossiliferous localities, and thus there is limited stratigraphical resolution (Table 1).

Localities

When mapping the Silurian of Gotland, Hede published a great number of faunal lists from all over the island (Hede



LUDLOW	WHIT-CLIFFIAN	SUNDRE
		HAMRA
		BURGSVIK
	LEINTWARDINIAN	EKE
BRINGE-WOODIAN	HEMSE	
ELTONIAN		
WENLOCK	HOMERIAN	KLINTEBERG
		MULDE
	SHEIN-WOODIAN	HALLA
		SLITE
	TOFTA	
	HÖGLINT	
	U. VISBY	
	L. VISBY	
	TELYCHIAN	

Fig. 1. Map of Gotland showing Hede's (1921 and 1925) topostratigraphical units and the sampled localities with their code names. The area within the square represents the aerial photograph in Fig. 2, showing the exact position of some localities that are difficult to find. Base map from Laufeld (1964a). Stratigraphical column based on Laufeld & Jeppsson (1976) and Jeppsson (1983). For description of localities, see Appendix.

Table 1. Stratigraphical distribution of Gotland oncocerids.

Localities		Species											
		<i>Trimeroceras cylindricum</i>	<i>Trimeroceras bulbosum</i>	<i>Pentameroceras mirum</i>	<i>Pentameroceras facula</i>	<i>Inversoceras p. perversum</i>	<i>Clathroceras plicatum</i>	<i>Jeppssonoceras concentratum</i>	<i>Plemeroceras cassis</i>	<i>Octameroceras sinuosum</i>	<i>Octameroceras pugil</i>	<i>Octameroceras rimosum</i>	<i>Octameroceras unguifer</i>
LUDLOW	Stockviks kanal (Hamra Beds)	X											
	Petesviken (Hemse Beds)			X									
	Linde Klint (Hemse Beds)			X		X							
	Sandarve kulle (Hemse Beds)	X	X						X				
	Tänglings hällar 1 (Hemse Beds)	X	X	X			X			X			
	Mannegårde 1 (Hemse Beds)	X	X				X	X	X	X	X	X	X
	Lill Rone 1 (Hemse Beds)					X			X	X		X	
	Hageby träskbacke (Hemse Beds)			X									
WENLOCK	Djupvik (Mulde Beds)		X										
	Möllbos 1 (Halla Beds)		X										
	Klints (Slite Beds)										X		
	Samsugns 1 (Slite Beds)		X	X							X		X
	Stora Vede 1 (Slite Beds)		X										
	Norrvange kanal (Slite Beds)			X	X								
	Kanalen (Högklint or Tofta Beds)				X								

1925b, 1927a, 1927b, 1928, 1929, 1933, 1936 and 1940). In these lists cephalopods are observed from 84 localities, although many include only *Orthoceras* sp. The beds of Gotland are fairly rich in cephalopods, but only a few are oncocerids.

The three major locality names, frequently occurring on the labels of the specimens are Lill Rone, Tänglings hällar and Mannegårde. As these names are fairly common in the area north-west of Lye (Fig. 2) this information is rather too inaccurate. Intensive field work did not solve the locating problems entirely, as only a limited number of oncocerid cephalopods were found. Neither was any distinctive outcrop situated close to any of the geographical localities so we do not know exactly where the fossils were collected.

Even if we do not know who the collector was, we can most certainly concentrate our investigations on a small group. Lindström himself did not collect the material. The

fieldwork for his investigation was, as stated above, performed by Florin and Liljevall, and these gentlemen are not known to have left any field diaries from this period.

Holm, at the Geological Survey of Sweden, also showed a great interest in Silurian cephalopods and during the 1890s he carried out fieldwork on Gotland. Fortunately Holm's field diaries are still available at SGU, Uppsala, and these books were found to give some help. There is no evidence that Holm collected any of the material dealt with in this paper, but the localities described by him agree with the labels from the Museum of Natural History, so there is reason to believe that these places are the sources of the material. Although Holm did not work at the museum at this time, it is documented that he brought some of his collection with him when he succeeded Lindström at the museum after the latter's death.



Fig. 2. Aerial photograph showing six of the sampled localities, all in the Hemse Beds. For position on Gotland, see Fig. 1. The white bar in the lower left corner represents 1 km. Reproduced with permission of Lantmäteriverket 1984-05-07.

Since this material is presumably still there (Wiman 1927), some of the cephalopods described here could derive from his collection.

In his field diary of August 1898, Holm described the locality Lill Rone (Holm's locality 286) and he also mentioned that Florin and Liljevall had used explosives in the exposure and collected a lot of samples for the Museum of Natural History. This indicates that Lill Rone was sampled before 1898, not by Holm but by Lindström's staff. Lill Rone is described by Holm as a small section, less than 1 m high, made for the railway and facing eastwards. He also mentioned a small outcrop a few meters east of the nowadays disused railway. This outcrop showed the typical reddish limestone

identical to the material around the SMNH specimens found at the locality Lill Rone. The southern of two existing outcrops visible today, which is less than 1 m deep and about 10 m long, is probably the same one as described by Holm and the lithology fits very well with his notes (Fig. 2). During fieldwork in 1983 a few specimens of oncocerids, including *Octameroceras sinuosum* and *Pentameroceras mirum* were found. Considering the rarity of this material, these finds strongly indicate that this is indeed the locality named Lill Rone.

In the fossil collections of SGU in Uppsala there are labels on cephalopods stating 'den röda kalken' and 'järnvägsskärningar väster om Lill Rone' ('the red limestone', 'Railway cuttings

west of Lill Rone'). These labels were written by Hedström who visited this locality in 1894 (Gerhard Regnéll, personal communication).

Tänglings hällar (Swedish 'häll' means exposed bedrock) is comprised of a wide outcrop along the road between Etelhem and Lye. Laufeld (1974a) has described the two localities Tänglings 1 and Tänglings 2 immediately east of the new road. These sections cannot be the source of the SMNH material as the road section does not show the typical reddish 'cephalopod limestone', as Holm named it, but consists of a white limestone.

Only about two hundred metres east of the above mentioned localities of Tänglings there are, however, a number of small quarries in the surface of the limestone. These quarries were made for local building purposes. In his field diaries from 1898, at locality 284, Holm describes the white, bedded limestone close to the road and a 'red or reddish limestone with concretions of red marl rich in cephalopods' only a small distance eastwards from the road. A new visit to the place was made in 1900 and at this time Holm intended to take photographs of the area, showing 'the small outcrops east of the road'. However, he wrote that this was not possible because of the lack of good bedrock surfaces, and this statement is equally valid today. The oncocerid material in the Museum of Natural History, labelled Tänglings hällar, probably derives from a number of these outcrops (Fig. 2).

The reddish limestone is also exposed in an old 'marble' quarry about 550 m west of the road at Tänglings hällar, some 500 m north of the farm Tänglings. As is the case with Tänglings hällar, the red limestone has green impliments, and a few cephalopods were found here during field work. These were mainly orthocones but included one *Ophioceras* and also one unidentifiable oncocerid. The locality, here named Tänglings kvarn 1, is not mentioned in Holm's field diaries or any other geological literature from Gotland.

The third major source of the oncocerids from Gotland is Mannegårde. Mannegårde is a common name in the area and refers to a farm built in an agricultural area with thick Holocene clay. No outcrops are located in the neighbourhood and inquiries concerning well drillings gave no positive information. Again, Holm's diaries are the only source of information. In 1898 Holm visited two road exposures (localities 287 and 288 in Holm 1898) about one kilometre north of the farm Mannegårde on the road between Lye and Etelhem. He described the red limestone as very similar to that of Lill Rone, concerning both the lithology and the fossil content. Unfortunately, the two exposures are no longer accessible as they are covered by the present road (Fig. 2). In the ditch east of the road at Mannegårde 1, however, slabs of reddish limestone rich in crinoids can be found. This is probably the remains of Holm's locality 287 and fits well with his description. Regrettably the limestone is not *in situ* and no cephalopods have been discovered.

Apart from the three major localities described above, oncocerids were only collected in any significant number at Samsugns 1, an old quarry in the Slite beds. This locality is described by Laufeld (1974a).

Finally Möllbos 1 in the Halla Beds must be mentioned, not because of a great number of oncocerid cephalopods, as there are less than a dozen, but for the excellently preserved,

silicified cephalopods and other groups (Stridsberg 1981a and Liljedahl 1983, 1984 and 1985).

For a detailed locality description, see Appendix.

Material and methods

Oncocerid cephalopods from Gotland are only occasionally mentioned in the literature. Apart from reports of *Gomphoceras* sp. by Lindström (1867, 1885 and 1888), Hedström (1910 and 1923), Hede (1925b and 1927a) and Manten (1971), no information on representatives from this fauna has been published. None of the specimens mentioned in these papers have been described and in most cases they were not even collected by the authors mentioned.

The material of Gustaf Lindström and Gerhard Holm studied here was probably collected during the 1890s. In view of the comparatively great number of specimens, roughly 330, it is astonishing to find that they originate mainly from only four localities. If one bears in mind that Hede in his lists of localities noted the presence of oncocerids at only two of his 84 localities with cephalopods, it seems clear that for some reason oncocerid shells are irregularly distributed. They are either very abundant or almost absent. This phenomenon has also been observed regarding the Phragmocerotidae of Gotland, another cephalopod family with constricted aperture, known from only a few localities. In the eastern part of the old quarry at Klinthagen (Jeppsson 1983, p. 142), south of Storugns, an enormously large number of phragmocerids could be observed until the area was recently buried under waste material from the Storugns quarry. More than two hundred specimens were collected by the author at Klinthagen. Today no large new finds of oncocerids have been made on Gotland, but only occasional single specimens.

When Lindström divided the oncocerid cephalopods collected on Gotland into 17 new species he did not know, because he had not studied the material collected by Barrande in Czechoslovakia, that four of the species from Gotland were already described and named by Barrande in 1865. This oversight is easily understood when comparing Barrande's material with the excellent, but sometimes idealized drawings in his illustrated works (Barrande 1865 and 1877). The restorations were sometimes too imaginative, and made it difficult for Lindström and other palaeontologists to recognize the already described species. Personally, I discovered this problem first after a visit to Narodni Muzeum in Prague, where I could compare the Gotland and Barrandian material. These comparative studies were very valuable as many details could only be observed when comparing the specimens directly.

Lindström was not the only one who had problems with the hand-drawn illustrations of Barrande's material. Foerste (1926) described a new species from such an illustration and, as noted earlier (Stridsberg 1981a, p. 274), Foerste missed some vital details concerning the aperture constriction.

It should be emphasized that the drawings made for Barrande are very realistic, but that any reproduction of the shape and form of fossils can, unfortunately, never be completely satisfactory for all aspects of studies. This is equally

valid for photographic illustrations as well, since the light setting can accentuate or reduce details on the specimen. In photographs, however, improvements of details like apertures are not so easily achieved.

When comparing the Gotland material with the Barrandian material, it is striking that the majority of the Gotland oncocerids are preserved with the shell while the Barrandian fossils are mainly internal moulds. Furthermore, the Gotland fossils are in general better preserved. This is to be expected due to the total lack of tectonic and folding movements on Gotland, while this is not the case in the Barrandian area.

The oncocerid collection from the Swedish Museum of Natural History was presumably in good condition when collected, and has also gone through extensive preparation. This has been performed with greatest care, but in a few rare cases there is reason to believe that the aperture shape has been slightly changed. Furthermore, Holm sliced a number of phragmocones to get access to details of the siphuncle, as he realized that the shape of the latter was vital for the taxonomy.

Apart from the SMNH collection and material obtained during my field work, a number of silicified specimens were provided by Project Silicified Silurian Fossils from Gotland (PSSFG), organized by Lennart Jeppsson, Lund (Laufeld & Jeppsson 1976 and Jeppsson 1983, see also Liljedahl 1983, 1984 and 1985). The silicified material is very well preserved, even if no specimen is complete, and gives access to details not studied before (Stridsberg 1981a). All silicified cephalopods treated in this publication originate from Möllbos 1 and are deposited in the type collection of Sveriges Geologiska Undersökning, the Geological Survey of Sweden (SGU).

Photography. – For photographic illustrations a macro-tele lens with a focal length of 100 mm and 24° opening angle was used on a 35 mm camera. The photographic distance was calculated so that only half the opening angle of the lens was used. The purpose of this lens used in combination with a long photographic distance was to achieve the correct proportions between the apertural area and the shell diameter by using a viewing angle of only about 10°. This would not be the case with a lens with shorter focal length and closer distance to the specimen, as only the apertural part of the half-spherical body chamber would be reproduced, thus giving the impression of a disproportionately large apertural area.

Apart from preserving good proportions, the long photographic distance gave a greater depth of field, valuable because of the bulky fossils. The advantage of this greater depth of field was that no contour retouch was needed on the photographs as the entire specimens were photographed in focus with a black background positioned well below the specimens to avoid dark reflections on the fossils.

Ammonium chloride was used for coating specimens and to bring out details of growth lines, malformation, apertural growth and other small details. Unfortunately the coating hid coloured growth lines lacking relief and thus specimens with such details were not coated.

In cases where the photographs have been retouched, this is stated in the caption.

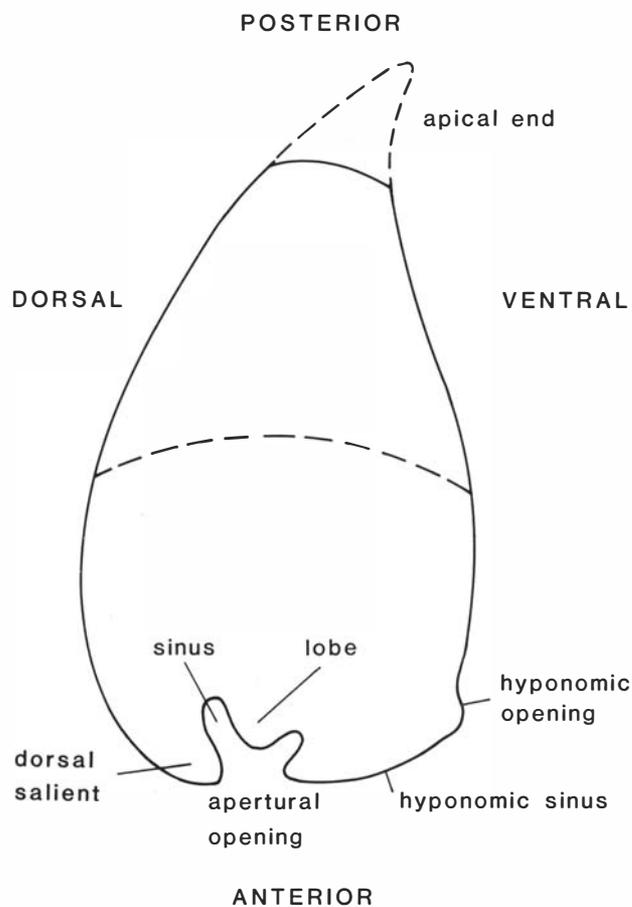


Fig. 3. Orientation of brevicone cephalopod shell and some of the morphological terms used in the descriptions.

Specimens cut dorso-ventrally along the long axis were painted with glycerine before being photographed to increase the contrast.

Shell orientation. – For almost 200 years the orientation of cephalopod shells has followed that of *Nautilus*. This means that the apertural end of the shell is regarded as the anterior and the apex as the posterior. The ventral side is equivalent to the side where the hyponome and the hyponomic sinus are situated and the dorsal side is consequently on the opposite side of the shell.

This conventional orientation is valid for *Nautilus* and also for straight orthoconic shells, if we accept the latter to be carried in a horizontal way, which nowadays is the generally accepted opinion (Flower 1957). There are, however, disagreeing views and Flower (1939), Mutvei (1964b), and some other palaeontologists have pointed out that the conventional orientation was perhaps not in harmony with the biologic situation.

In the case of the oncocerid shells dealt with in this paper the conventional orientation is misleading as the shells were carried with the aperture facing downwards. However, a change in terminology would unfortunately cause confusion when performing comparative literature studies. To avoid any misinterpretations I have decided to keep the conventional terminology (Fig. 3), although this will cause some

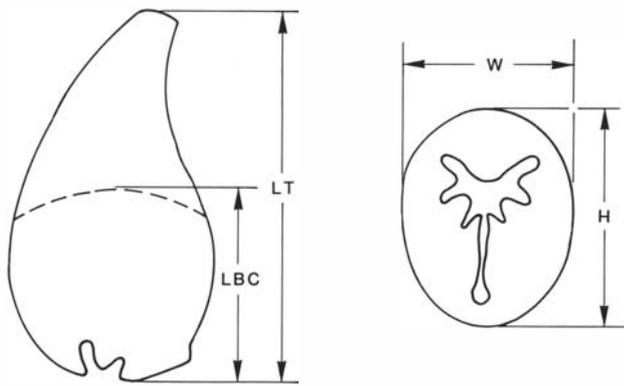


Fig. 4. Lateral and anterior views of brevicone cephalopod shell, showing measured distances. Abbreviations used for Tables 2–13: LT – total preserved length; LBC – length of the body chamber; W – width; H – height.

contradictions in the discussion regarding functional morphology.

Concerning the orientation of the illustrated specimens I have, however, placed the shells in what I believe is the living position. In my opinion cephalopods have been illustrated upside-down for too long and the reason for this is difficult to understand. Presumably the reason for illustrating brevicones upside-down is the old tradition of publishing orthocones with the apical end downwards. In some cases, especially among ammonites and particularly with *Nautilus*, artistic impression has decided what is up and what is down. Who would dream of illustrating an *Australopithecus* upside-down?

Measuring methods. – When measuring the specimens in this paper I have defined total length (LT) as the distance between the oldest preserved part of the shell and the aperture edge (Fig. 4). This distance will of course vary depending on the completeness of the preserved shell and therefore these figures cannot be used for statistical purposes as no specimens are found with all chambers preserved. The total length, however, gives an idea about the size of the fossils in the group.

The length of the body chamber (LBC) is defined as the greatest distance from the middle of the last septum to the edge of the aperture. This length can only be determined on isolated body chambers or in specimens cut along the long axis. Naturally it can be estimated on internal moulds where the suture is visible, but this has not been done as it does not give an accurate result.

The only parameters used for statistics within the oncocerids are the height and width (Fig. 4). These figures, H and W respectively, can be measured on most specimens, both with and without the shell preserved. As the width is compared with the height, there should be great variations if the fossils were deformed in the sediment. The body chamber was often filled with sediment during deposition, but this is not always the case with the chambers in the phragmocone. Still they are mostly well preserved.

As the only measurable parameters were the height and width, statistical analysis is naturally very limited. Nevertheless different species show a specific signature in a dia-

gram, indicating consistent variations in the shapes of the shells.

All figures in brackets in the Tables are to be regarded as approximate. They refer to measurements on material which is not well preserved.

In the text a distinction is made between aperture and apertural opening in the sense that aperture comprises apertural opening, hyponomic sinus and hyponomic opening. In some species with a broad aperture the different parts cannot be discerned, while in other species, the apertural opening is located far away from the hyponomic opening, with a very narrow hyponomic sinus as the only connection.

A vernier calliper was used for all measurements.

Deposition and preservation of shell

The material described and discussed herein derives from limestones except for a few specimens collected in marly beds. Most specimens originate from large concentrations of cephalopod shells. The explanation of these shell assemblages at various places on Gotland is most certainly to be found in postmortal drift with the help of currents. These thanatocoenoses can reach large dimensions and at Klinthagen 1 (Jeppsson 1983, p. 142), an old quarry in the Slite Beds, the limestone was largely made up of cephalopod shells, mainly phragmocerids, but unfortunately no oncocerids. An understanding of postmortal shell drift is essential when reconstructing thanatocoenoses, and experimental studies have been carried out by Reyment, who constructed models of cephalopod shells of different shapes and studied their floating behaviour under various conditions (Reyment 1958 and 1973).

On the whole, the oncocerid shells found on Gotland are very well preserved. In some cases even the colour pattern on the phragmocone is visible, as is discussed in the chapter 'Colour pattern'.

Although most shells are well preserved, all specimens lack the apical end. In a few cases the reason is truncation, as discussed later, but the great majority of the shells are broken just below the apical end. The apical end is the most delicate part of the shell and the absence of this part could be explained by problems in collecting and preparation of the specimens. However, when specimens still in the sediment were cut by a macro saw (Isomet), no apical end was found. Flower (1955, p. 860) pointed out that cephalopod shells as a rule are broken just apically of the septum surface since, because of the shell construction, this is the natural point of weakness.

An explanation for the loss of the apical end might be found in the postmortal drift of the shell. Thanatocoenoses indicate that the empty shells were transported fairly long distances and during this transport, presumably along the sea floor, the delicate apical end must have been broken off. Directly after the death of the animal, the decaying soft parts in combination with the gas-filled phragmocone are likely to have given the shell positive buoyancy, as is the case with *Spirula* (Schmidt 1922). Postmortal floating of the shell

might have been the general procedure according to Mutvei and Reyment (1973). After having lost the soft parts and becoming more or less water-filled by leakage or puncturing, the shell sank to the sea floor where the sea floor currents influenced the final deposition (Stridsberg 1984, p. 96). An unbroken shell, partly water-filled, will float with the apical end above the body chamber and thus the apical end would be at a safe distance from the sea floor. Furthermore, a vertically orientated almost floating shell with the apertural part orientated towards the bottom, would suffer damage to the apertural area instead when hitting objects on the sea floor. The great majority of the studied specimens, however, lack apertural injuries and even the most delicate lobes are preserved. As most of the specimens were found in greater or smaller thanatocoenoses, the protruding apical ends might have been knocked off when the shells were pressed together.

Almost all the shells discovered in the field were lying horizontally in the sediment and this indicates that most chambers were water-filled when deposited, since any greater amount of gas left in the chambers would leave the shell in a vertical position (Reyment 1968). Even if only a few brevicones were found in a vertical position, such a preservation is by no means unique among fossil cephalopods (Reyment 1970, p. 110).

If, however, the Gotland oncocerids were bottom dwellers with negative buoyancy, heavy enough not to rise because of decaying soft parts, there is a theoretically interesting solution to the problem of the missing apical end. This theory is also valid if the cephalopod died below a certain depth, as experiments have been made which show that, depending on shell type, cephalopod shells below a specific depth would sink as the compressed gas in the chambers could not maintain positive buoyancy under high water pressures (Raup 1973). The theory is that after the death of the animal, the shell was transported to deep waters by sea floor currents. If for any reason the siphuncular connection to the apical end was blocked, either by remains from the siphuncle or by a plug from the accretion of the shell, the pressure in the apical end would remain constant. Outside the shell, however, the water pressure would increase with increasing depth and finally the apical end would implode.

Regarding the Gotland oncocerids this hypothesis is not likely, as the water was far too shallow, according to many different indications, e.g. the fauna (Laufeld and Martinsson 1981).

Apertural growth

Among species belonging to Hemiphragmoceratidae Foerste 1926 and Trimeroceratidae Hyatt 1900, apertural closing starts very late in the ontogeny of the animal. The different configurations of the aperture depend entirely on the growth of the lobes accreted by the mantle. Consequently, any disturbance of the outer edge of the mantle would have produced variations which diverged from the normal pattern of apertural shape of the species.

Apertural closing started with a round, sometimes almost triangular, opening and from the surrounding apertural rim a number of lobes grew into the open apertural space

(Stridsberg 1981a, p. 273), a sequence easily traced through the investigated specimens of *Octameroceras sinuosum* (Fig. 38F) and *Pentameroceras mirum* (Fig. 31D). The number of lobes and their positions reflect the places of accretion of shell material and thus the position of the mantle. The empty space in the sinuses must consequently have corresponded to the position of the appendages, whatever they looked like, and the activities of these soft parts must, to some extent, have influenced the outermost edge of the mantle where the shell accretion took place. If the mantle was constantly blocked by the soft parts, minor irregularities in the growth were bound to result.

Apertural growth differed between genera of the Hemiphragmoceratidae and Trimeroceratidae. Genera belonging to the Trimeroceratidae, such as *Trimeroceras* and *Pentameroceras* have mostly two dorsal lobes, separated by a dorsal sinus but occasionally this sinus did not develop. Genera belonging to the Hemiphragmoceratidae, as for example *Octameroceras*, have a dorsal salient.

Within the species *Octameroceras pugil*, *O. sinuosum* and *O. unguifer*, a fairly wide variation in the number of sinuses in the apertural opening can be observed (Stridsberg 1981a, p. 274). The variation is found in the ventral part of the apertural opening, and presumably results from a greater or smaller hindrance of the mantle by the appendages of the cephalopod.

Macroconchs of *Octameroceras pugil* and *O. sinuosum* have usually not developed the ventralmost lobes (Figs. 38 and 40). Therefore, in most of these specimens the ventral sinus, or in other words the dorsal part of the hyponomic sinus, was wide enough to permit more comprehensive activities of the appendages. Instead of accretion of the two ventralmost lobes, dividing the wide ventral sinus into four sinuses, the mantle performed shell accretion along the peristome from the hyponomic sinus to the ventro-lateral sinuses (Figs. 38J and 40E).

Extra lobes may also occur on the ventralmost part of the apertural opening. These extra lobes are mostly smaller than the regular ones, but occasionally they are of the same size. The latter is mostly the case within *Octameroceras unguifer*, but extremely small lobes may also exist within this species, as is mentioned in the description of the species (Fig. 43K). Two specimens of *O. unguifer* have nine sinuses.

Regarding the position of the lobes, there is a tendency among some species of *Octameroceras* for the asymmetry between opposite lobes to increase towards the venter (Stridsberg 1981a, p. 274). The ventralmost lobes and sinuses exhibit a zigzag pattern.

Apart from dissimilarity concerning the number of sinuses and their position, the apertural construction can exhibit other variations between species. To strengthen the apertural area most species described here have developed reinforcements along the peristome. Only one, *Octameroceras unguifer*, lacks or has reduced reinforcements around the peristome. It should be mentioned, however, that even if *O. unguifer* has an aperture similar to that found in *O. pugil* and *O. sinuosum*, and the internal shapes of the apertures are similar, the external shape is different. The absence of apertural reinforcements in *O. unguifer* is evident in the respect that the shell has an external depression around the aperture, corresponding to the area where other species have

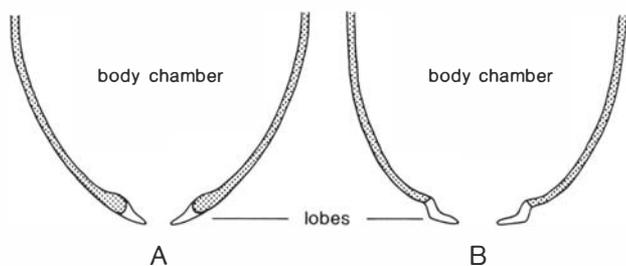


Fig. 5. Cross sections showing lateral lobes and apertural reinforcement in *Octameroceras sinuosum* (A) and the absence of similar reinforcement in *Octameroceras unguifer* (B).

their internal reinforcements. As a consequence of this depression the peristome at the bottom of the sinuses seems to form a restricted aperture, although this is not actually the case (Fig. 5). The depression around the aperture on *O. unguifer* also gives the false impression that the lobes of this species are more perpendicular to the long axis of the shell than those of other species of *Octameroceras*.

In *Trimeroceras* as well as *Pentameroceras* the closing of the apertural opening started with accretion of the ventro-lateral lobes (Fig. 6A–D), resulting in the beginning of the hyponomic sinus and a separated hyponomic opening. When these lobes had reached slightly less than half their final size, the beginning of the lateral lobes was indicated. In *Trimeroceras* these lateral lobes were mostly very small (Fig. 6C) and appeared very late in the ontogeny. The two dorsal lobes were the last ones to form. They are very distinctive in *Pentameroceras* and most species of *Trimeroceras*, but within *T. bulbosum* there seem to occur specimens completely devoid of dorsal lobes (Figs. 6D and 30).

In *Trimeroceras* as well as in *Pentameroceras* the hyponomic sinus is occasionally very wide towards the dorsal side. This widening is, however, different from that of *Octameroceras* as it is symmetric and shows no signs of developing lobes and sinuses. Thus the rich variation in the number of sinuses, typical for *Octameroceras*, has no counterpart in Trimeroceratidae.

Two species within the Trimeroceratidae have an apertural opening reminiscent of a simplified *Trimeroceras*. *Inversoceras perversum* and *Plemeroceras cassis* both have a dorsal position of the apertural opening and the anterior end of the shell is closed, apart from a slit-like hyponomic sinus ending

in a ventrally situated hyponomic opening. In addition to the closure of the anterior end of the shell, a pair of lateral lappets restricts the apertural opening. These two species are the only cephalopods in the investigated material with the apertural and hyponomic openings situated opposite each other. The reason for this is probably due to swimming conditions and will be discussed in the chapter 'Swimming'.

Dimorphism

Sexual dimorphism among brevicone cephalopods has been discussed by various authors. Ruedemann (1921, pp. 317–318) described three specimens of *Oncoceras pupaeforme* Ruedemann. Two of the specimens had contracted apertures and were identical in all aspects except for size. The third specimen had a wide-open aperture and was intermediate in size. Furthermore, the latter did not have more closely arranged septa just before the living chamber, and was therefore regarded as immature. Ruedemann considered the two specimens with contracted apertures to represent sexual dimorphism, and suggested that the big specimen was the female and the small specimen the male. Concerning the determination of sexes, Ruedemann referred to observations in recent cephalopods where, as a rule, the females are bigger than the males. As an example he mentioned *Argonauta* in which the female is as much as fifteen times as long as the male. The third specimen of *Oncoceras pupaeforme* with the intermediate size was interpreted as an immature female.

In a redescription of *Inversoceras perversum* (Barrande), Foerste (1926, p. 355) divided Barrandes *Phragmoceras perversum* into four species. Two of these species, *I. constrictum* and *I. barrandei* differed from *I. perversum* and *I. percurvatum* by being constricted at the base of the dorsal collar, and Foerste questioned whether or not these differences were sexual dimorphism rather than characters of specific value. These species were also discussed in the *Treatise* as a possible example of sexual dimorphism (Teichert 1964, K 49).

However, as is discussed in the taxonomic part herein, *Inversoceras constrictum* and *I. barrandei* were based on internal moulds and do not reflect any apertural constriction at all but rather internal reinforcements as illustrated in Fig. 33I. Thus there is no sexual dimorphism within *I. perversum* according to constriction of the dorsal collar.

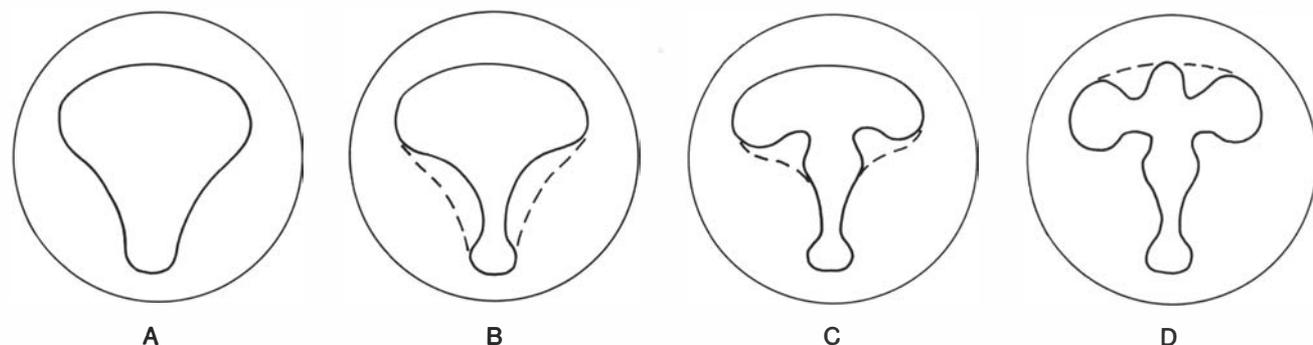


Fig. 6. Four different stages in the apertural growth of *Trimeroceras bulbosum*. The additional growth between the stages is marked with dotted lines in the drawings A–D. The growth stages in B, C and D can be compared with Fig. 30N, K and D respectively.

Foerste, however, as well as Barrande, never discussed size dimorphism among brevicones, but according to their descriptions they both accepted a fairly wide variation in the size of the specimens within a species.

In a paper describing Devonian brevicones Flower (1938, p. 7) discussed sexual dimorphism based on slender and gibbous forms. He stated that the variation is less obvious than that presented by Ruedemann and the reason might be that Ruedemann's specimens were flattened by compaction and thus deformed. Flower also discussed the problems of studying sexual dimorphism, when there were so few specimens available. He wrote that, even if Silurian brevicones occasionally were abundant, the great number of genera and species kept the number of specimens within a particular species very low.

Sexual dimorphism was also discussed by Teichert in his description of the Devonian *Wadeoceras australe* from Australia (Teichert 1940, pp. 59–63). He was short of specimens too and, apart from a fragmentary holotype, had only two almost complete specimens. These specimens were similar in most aspects and differed only in size and 'a greater length of the camerae' in the big specimen. Both were regarded as mature in view of the shortness of the last chamber. Furthermore, Teichert pointed out that the size differences were more pronounced than in the Devonian brevicones described by Flower and closely comparable to the differences found in Ruedemann's *Oncoceras pupaeforme*.

Ruedemann, Flower and Teichert were all of the opinion that variation in size within a species is to be interpreted as sexual dimorphism. Unfortunately all three had very limited material to investigate, and thus could not produce any conclusive evidence.

Apart from the papers by Ruedemann (1921), Flower (1938) and Teichert (1940), all dealing with brevicones, most papers concerning sexual dimorphism among cephalopods refer to ammonites. The ammonite genus *Kosmoceras* from the Middle Jurassic of England is discussed by Callomon (1963) and the important characteristics of probable sexual dimorphism were differences in overall size and variation in ornamentation and apertural form. The often very remarkable size variation in ammonites, as for example in *Kosmoceras*, is by no means so pronounced among the brevicone nautiloids. The amplitude of the size variation in the brevicones described above as well as in my material is rather similar to that of the extant *Nautilus*.

By tradition, size dimorphism has been synonymous with sexual dimorphism. This is probably true but it must be emphasized that size dimorphism does not occur in all species of brevicone cephalopods. *Trimeroceras bulbosum* n. sp. for example, has a wide variation in size but does not show two size groups. Intermediate mature forms between the biggest and smallest specimens occur and dimorphism is probably to be found more in the morphologic dimorphism of the apertural construction, rather than in size dimorphism (Fig. 7). *T. bulbosum* is discussed later in this chapter.

The Gotland material dealt with in this paper comprises 246 measured specimens. In addition 16 specimens from Barrande's collection in Prague have been measured and included in the graphs. The comparatively extensive material has made it possible to produce graphs, showing the size composition within the six species with more than fourteen

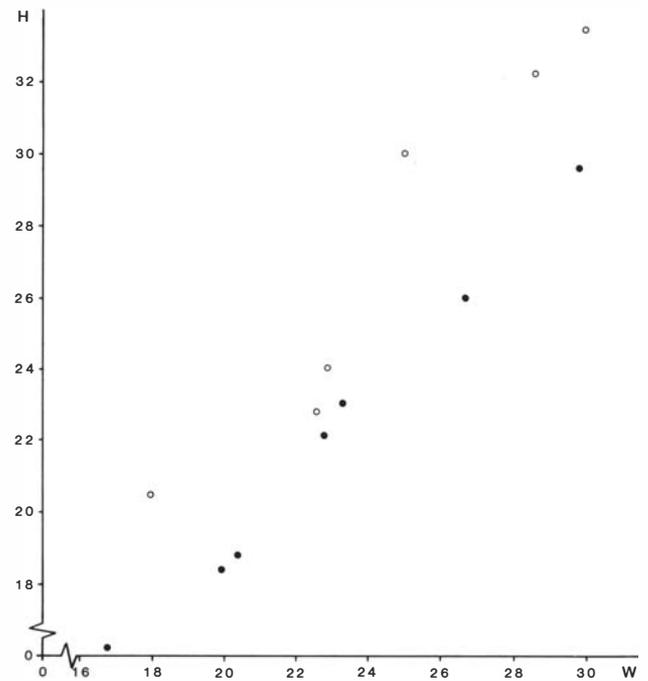


Fig. 7. Dimorphism within the species *Trimeroceras bulbosum*. The open circles indicate specimens with a convex dorsal side of the body chamber, while the black dots indicate specimens with a straight dorsal side of the body chamber. (Dimensions in mm.)

measurable specimens. In the graphs the proportions between height (H) and width (W) of the body chamber are used and all measurable specimens in each species are included.

To distinguish the dimorphism the terms macroconch and microconch will be used in the following. These two terms are used purely as descriptive terms, and should not be interpreted as synonymous with female and male respectively, as has been done regarding ammonites. As is concluded at the end of this chapter, I am rather of the opposite opinion.

Within the examined collection of *Octameroceras sinuosum* the 50 measurable specimens fall into two very distinct size groups, with 40 microconchs and 10 macroconchs respectively. The calculated average difference in volume between the two groups is more than twice as great as the volume variation within each group, thus indicating a clear dimorphism. As illustrated in Fig. 8 there is no overlap between the two groups. The size variation within the group of macroconchs is wide (Fig. 8), but the volume variation in this group is still much smaller than in the group of microconchs. The macroconchs are not only fewer in number, but mostly poorly preserved as well. This is also the case with other species of this size and is probably the result of the use of explosives in collecting as previously mentioned.

Apart from size dimorphism within *Octameroceras sinuosum* there is a morphologic difference between the micro- and macroconchs, the latter being more stout. Furthermore, as discussed in the description of *O. sinuosum* (see Figs. 38D, E, F and J), the macroconchs have fewer but proportionately much wider sinuses than the microconchs.

The 17 measurable specimens of *Octameroceras pugil* in the examined material are distributed in a way similar to that of

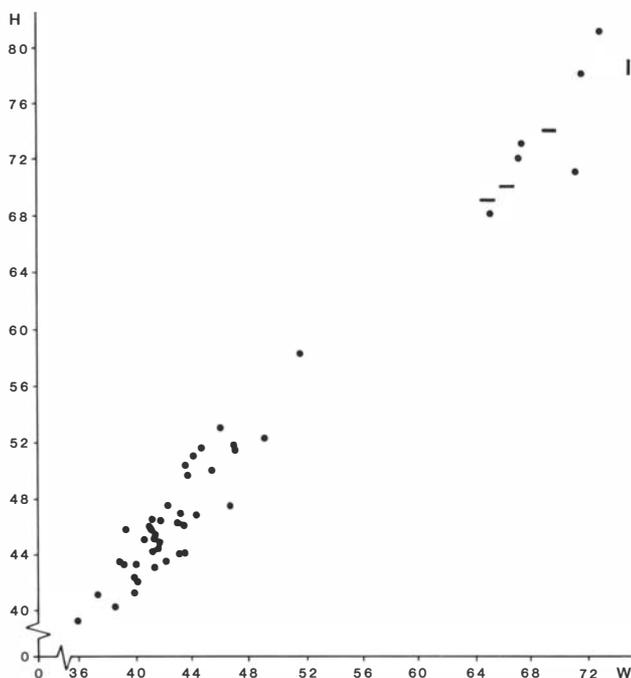


Fig. 8. Size dimorphism within the species *Octameroceras sinuosum*. The horizontal dashes indicate specimens with no measurable width (W) while the vertical dash indicates a specimen with no measurable height (H). (Dimensions in mm.)

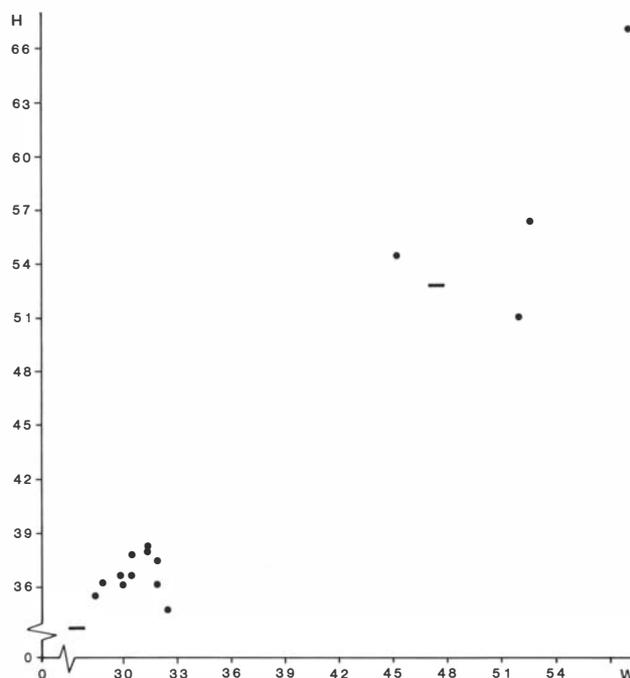


Fig. 9. Size dimorphism within the species *Octameroceras pugil*. The horizontal dashes indicate specimens with no measurable width (W). (Dimensions in mm.)

O. sinuosum as illustrated in Fig. 9. The average volume difference between the two size groups is somewhat bigger but as the number of specimens is much smaller there is not necessarily any significance in this difference. As is the case with *O. sinuosum*, there is no overlap between the two size groups. The difference in the number of sinuses and their size among the macroconchs of *O. sinuosum* is obvious as well within *O. pugil*. Variation of the apertural shape of *O. pugil* is also discussed in the description of the species.

The other two species of *Octameroceras* described in this publication, *Octameroceras rimosum* and *O. unguifer*, show neither obvious size dimorphism nor any other kind of dimorphism. Regarding *O. rimosum* it is true that the lectotype is smaller than the Gotland specimens and, furthermore, there is a distinctly bigger specimen of *Phragmoceras rimosum* (Barraude 1865, Pl. 48:1-3) in the Barrandian collection. It could be that the Gotland specimens represent only one sex. However, as discussed in the description of *O. rimosum*, I find the number of specimens (eight) too small to reach any conclusions about dimorphism.

Regarding *O. unguifer*, the material is very homogeneous in size but, since there are only ten specimens altogether, they could all represent one and the same sex. Therefore I prefer to leave it out of the discussion of dimorphism until more material has been collected.

The largest group in the examined material is *Pentameroceras mirum* with 86 specimens. Of these the 59 measurable specimens form two very pronounced groups with 17 microconchs and 42 macroconchs, respectively. Of the remaining 27 specimens, two are microconchs and the remaining 25 are macroconchs. As is the case with *Octameroceras sinuosum* and *O. pugil*, the average volume difference between the two groups is much greater than the volume variation within

each group. Furthermore, there is a very distinct gap between the two fairly closely spaced groups. As illustrated in Fig. 10 the three smallest microconchs within *Pentameroceras mirum* seem to be separated from the other microconchs. This is because these three specimens lack a shell. In the investigated material a lack of shell affects the graphs significantly only within *P. mirum* because of the diminutive size of this species.

The six specimens within the examined *Pentameroceras facula* appear to have a similar size dimorphism as *P. mirum*, but the very limited material prevents further conclusions being reached.

Within *Trimeroceras cylindricum* size dimorphism is evident in the Barrandian as well as in the Gotland material. As both collections are very small, six and nine measurable specimens respectively, a combination of the measurements, as illustrated in Fig. 11, strengthens the arguments for a distinct size dimorphism. Even if the number of specimens is small, there is no overlap between the two groups.

Dimorphism within the discussed brevicones is not always characterized by size dimorphism. *Clathroceras plicatum* exhibits a fairly weak size dimorphism, but is more distinctly divided into two morphological groups, one with slender shells and the other with stout shells. Bearing in mind the limited number of specimens, there is no overlap between the slender and stout specimens as seen in the size graph in Fig. 12. This indicates a combination of morphological as well as size dimorphism. Presumably the pronounced stoutness of the macroconch leads to a similar effect with regard to the difference in volume as occurred in the more pronounced size dimorphism in other taxa. In the latter cases the difference in stoutness is far less evident, although it does exist.

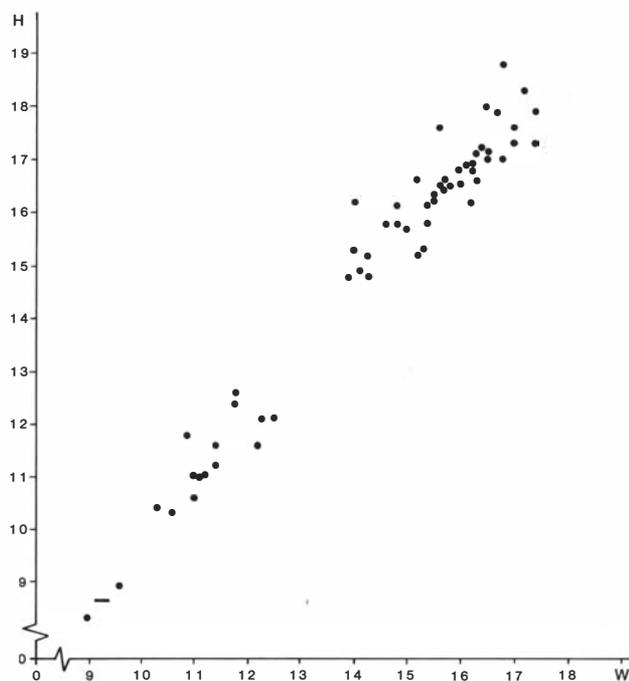


Fig. 10. Size dimorphism within the species *Pentameroceras mirum*. The horizontal dash indicates a specimen with no measurable width (W). The three specimens in the isolated group in the lower left corner lack the shell. (Dimensions in mm.)

Morphological dimorphism without size dimorphism is observed in the material of *Trimeroceras bulbosum*. As shown in the description of the species, the specimens form two morphological groups, one with a fairly straight dorsal side of the body chamber and the other with a more or less convex dorsal side. The graph in Fig. 7 illustrates how the two morphs differ widely in size. Because of the more stout or gibbous appearance of the group with a convex dorsal side, these specimens are found above the others in the graph. Apart from the overlap in size, these relatively stout specimens are similar in character to the stout macroconchs of *Clathroceras plicatum*.

Dimorphism, chiefly characterized by slender and stout shells, seems to occur within the material of *Plemeroceras cassis*, but as is also the case with *Jeppsonoceras concentratum*, the very limited number of specimens makes it inadvisable to draw firm conclusions.

The last investigated species, *Inversoceras perversum*, appears to show size dimorphism in the Barrandian as well as the Gotland material, but more specimens need to be examined before size dimorphism can be considered proven.

In conclusion, the variation in size dimorphism is very wide. In some cases, for example within *Octameroceras sinuosum*, a living chamber of the macroconchs is at least four to five times the volume of a microconch. In other species there is an overlap between the measured dimensions of the groups and therefore it is difficult to establish firm rules for determining the sex among brevicones. The three specimens of *Oncoceras pupaeforme* presented by Ruedemann (1921) could belong to one sex rather than two sexes as originally suggested.

Octameroceras sinuosum, *O. pugil*, *Trimeroceras cylindricum* and *Pentameroceras mirum* all have a group of macroconchs and a

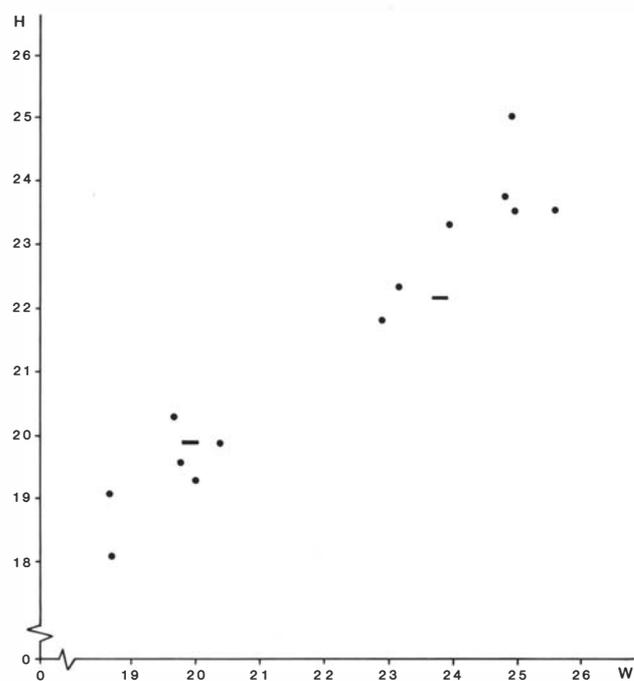


Fig. 11. Size dimorphism within the species *Trimeroceras cylindricum*. The horizontal dashes indicate specimens with no measurable width (W). (Dimensions in mm.)

similar tendency also occurs within *Trimeroceras bulbosum* and *Clathroceras plicatum* specimens. This finding raises the question of how the soft parts of these animals differed from those of the small and slender animals. A hypothesis might be that an organ, corresponding to the spadix and antispadix on *Nautilus*, required this extra space. If so the macroconchs would represent the males. However, much more evidence is needed before this hypothesis can be considered proven.

To sum up, dimorphism is evident among the discussed brevicones. This dimorphism is mainly reflected in the size of the shells and there are good reasons for suggesting that this is sexual dimorphism. As to which is female and which is male we are still uncertain. Personally I am of the opinion that the macroconchs represent the males. In such a case the oncocerids resemble the only existing nautiloid, *Nautilus*, rather than the less closely related modern cephalopods, where the females are bigger and stouter.

Truncation

Natural truncation of the apical part of the phragmocone among orthocones was described in 1868 and 1877 by Barrande. He studied a great number of *Orthoceras truncatum* Barrande, now *Sphooceras truncatum* (Flower 1962), and observed that the remaining anterior part of the phragmocone in this species consisted of four to eight chambers. Based on his observations Barrande speculated on repeated truncations during the life of the animal. A number of other examples of truncation within the family Orthoceratidae have since been described by various authors (Teichert 1964), but most well known for truncation is the order

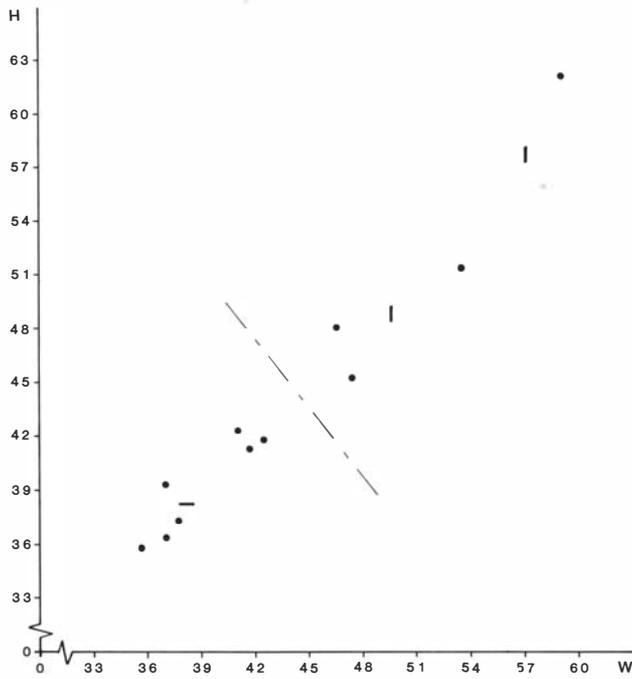


Fig. 12. Dimorphism within the species *Clathroceras plicatum*. The vertical dashes indicate specimens with no measurable height (H) while the horizontal dash indicates a specimen with no measurable width (W). Dimorphism within *C. plicatum* is characterized by stout macroconchs (to the upper right of the line) and slender microconchs. (Dimensions in mm.)

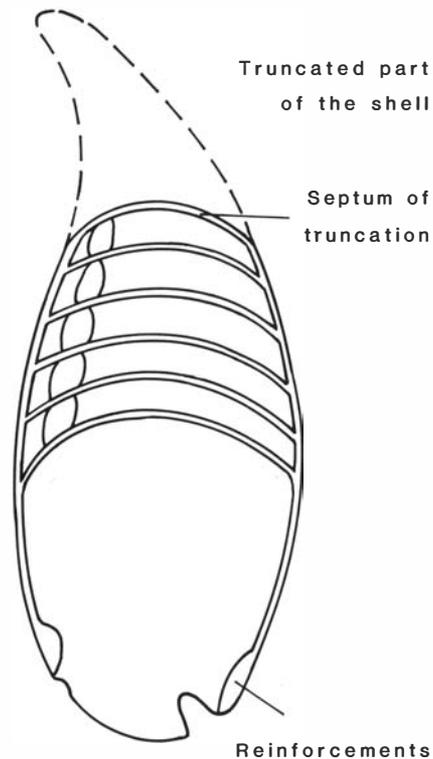


Fig. 13. *Trimeroceras bulbosum* with reconstructed truncated part of the phragmocone and the terminology used in this publication.

Ascozerida. Barrande discussed truncation within this order and about 40 years later exquisite material was presented by Lindström (1890) from Gotland. Lindström discussed functional aspects of shell morphology and the great advantage of his material was that it included both the truncated apical part of the phragmocone, or the deciduous portion, and the body chamber with the anterior end of the phragmocone, also called the mature portion of the conch. Further details of the well studied shell truncation among the Ascozerida were presented by Furnish & Glenister (1964).

The reason for truncation among Ascozerida is widely discussed. The generally accepted explanation is that truncation took place to reduce the hydrodynamic hindrance of a long shell and was thus an adaptation for swimming (Furnish & Glenister 1964, K 269).

Apart from Orthocerida and Ascozerida, Barrande (1865, Pl. 83:1–9 and 1867, p. 271) also described truncation within the species *Gomphoceras alphaeus* Barrande, in the order Oncozerida. This species might perhaps belong to *Trimeroceras* but as the shape and form of the siphuncle differ from that of typical *Trimeroceras* and as I have not examined the specimens, I prefer to leave this question open. What is interesting about *Gomphoceras alphaeus* is that the distance between successive septa decreases gradually towards the anterior in both described specimens. Furthermore, the siphuncle is notably narrower immediately anterior to the septum of truncation (Barrande 1865, Pl. 83:8–9). The distinctly increased thickness of the oldest preserved septum and the general appearance of the two specimens confirm Barrande's interpretation of truncation.

In the Gotland material, described herein, truncation is observed in the three species *Trimeroceras bulbosum*, *Trimeroceras cylindricum* and *Pentameroceras mirum*. In specimen RM Mo 152777 (Figs. 13 and 14A), a truncated specimen of *T. bulbosum*, the septum of truncation is more strongly curved than the other septa, and thus the adjacent chamber is slightly larger than the next. Specimen RM Mo 56281 (Fig. 14B) a non-truncated *T. bulbosum*, has been cut dorso-ventrally along the phragmocone. This specimen shows a change from more strongly curved septa in the apical part of the phragmocone to less curved septa in what might be the mature portion of the conch. Because of poor preservation of the outer wall the expected thinning of this wall in the chamber of truncation could not be studied. What might be the septum of truncation is one of the few preserved septa and this is as curved as the septum of truncation in specimen RM Mo 152777 (Fig. 14A).

The very smooth continuation of the septum of truncation to the dorsal shell surface in specimens RM Mo 152777 and RM Mo 56618 (Figs. 14A and 14C), accentuates the morphologic change in the shell construction at this septum. As mentioned in the description, the endogastric apical, or deciduous portion of the phragmocone turns exogastric in the mature portion of the shell. The septum of truncation is situated at the place of this change in curvature as seen in specimen RM Mo 56618, Fig. 14C. In this specimen, the septum of truncation is not the last preserved, but second last, as can be seen by the smooth continuation from this septum to the dorsal shell wall. Furthermore, as observed in Fig. 14C, the shell wall in the oldest preserved chamber is

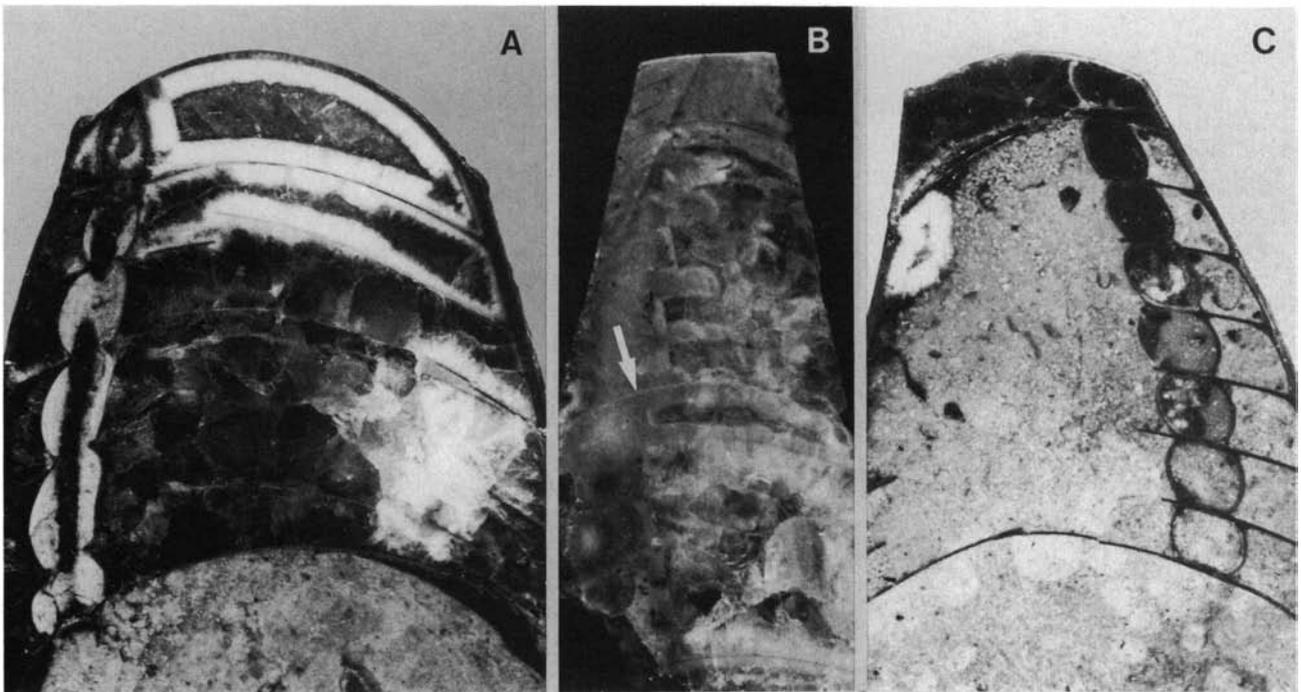


Fig. 14. Three specimens of *Trimeroceras bulbosum* with septum of truncation. □A. The septum of truncation in this truncated specimen is more strongly curved and is thicker than the other septa. In the chamber of truncation the siphuncle turns towards the ventral side, thus indicating an endogastric apical part, RM Mo 152777, $\times 3.7$, (see also Fig. 30G). □B. Untruncated specimen with a supposed septum of planned (?) truncation at the white arrow. Apical to this septum, the septa are more curved than those in the mature portion, RM Mo 56281, $\times 3.7$. □C. In this specimen the septum of truncation is the second oldest preserved, as can be observed on the thinner shell on the oldest septum and the shell wall around the oldest chamber. The septum of truncation is at least twice as thick as the other remaining septa, RM Mo 56618, $\times 3.7$, (see also Fig. 30I).

much thinner than the shell wall in the rest of the phragmocone. The reason for this decreasing thickness might either be internal resorption, or absence of the internal reinforcement occurring in the later chambers. Anyhow, the result is that the last chamber in the deciduous portion of the specimen RM Mo 56618 has a thinner wall than the remaining part of the phragmocone, and this strengthens the conclusion of truncation.

Truncation in *Trimeroceras cylindricum* is demonstrated by the regular length of the mature portion of the conch and the very strongly increased thickness of the septum of truncation. It has the same thickness as the shell wall. In cut specimens (Figs. 15A and 15B) the number of chambers is around 6 to 8 and uncut specimens have a similar shell length, indicating a similar number of chambers. On all shells a cicatrix of truncation is visible around the septum of truncation. These remains of the shell wall are very smooth. However, the possibility that this is a secondary post mortem effect cannot be excluded.

As is the case with *Trimeroceras bulbosum*, the septum of truncation in *Trimeroceras cylindricum* is more curved than the next septum in the mature portion of the conch. This change in curvature is demonstrated by specimen RM Mo 57423, Fig. 15A. The orientation of the septum of truncation indicates that the deciduous portion of the conch was exogastric as well as the mature part of the conch.

Truncation within the examined *Pentameroceras mirum* is found in stout specimens as discussed in the taxonomic description. The truncated specimens, identified by a very smooth cicatrix of truncation and a reinforced septum of

truncation, do not have equal lengths of the mature portion of the conch. This length depends on the tapering of the phragmocone and the most slender specimens seem not to be truncated at all. No specific groups of tapering can be discerned.

To compare the floating capacity of stout truncated specimens and slender non-truncated specimens of *P. mirum*, one of each category was measured. The truncated, short and wide specimen, RM Mo 56702 and the long and slender specimen RM Mo 56740 (Figs. 16A and 16B) have almost equally sized body chambers. Thus, to keep the same degree of buoyancy, they need the same lifting capacity, or in other words the same volume in their remaining phragmocones. Rough calculations show that the slender specimen has more than 90 % of the volume of the mature part of the phragmocone in the stout specimen. This difference can be explained by the slightly bigger body chamber on the latter. Furthermore, the missing apical end of the slender specimen was probably not truncated but lost post mortem. In addition to, in most cases, a bigger chamber anterior to the septum of truncation, this septum is also as thick as the shell wall in cut specimens of *Pentameroceras mirum*.

The reasons for and the mechanism behind shell truncation are, as mentioned above, widely discussed. In the case of Ascocerida and Orthocerida truncation seems to be repeated during ontogeny (Barrande 1877 and Furnish & Glenister 1964) and the benefit for these horizontally orientated animals was to keep the best possible hydrodynamic shape by shortening an over-long shell. Regarding the vertically orientated brevicones, the hydrodynamic aspects were

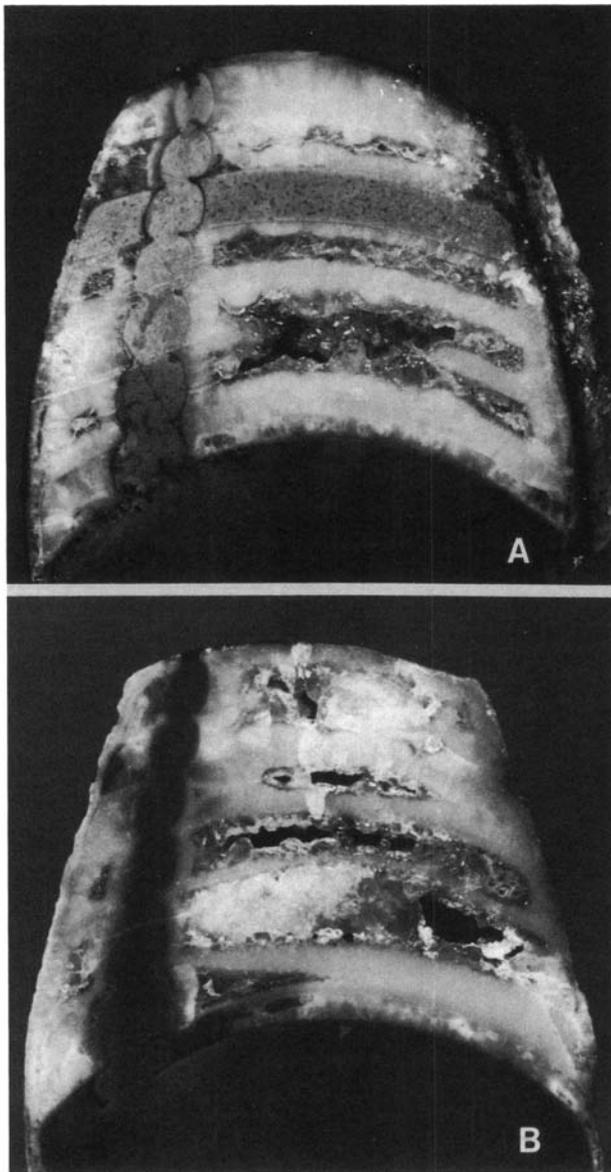


Fig. 15. Two specimens of *Trimeroceras cylindricum* with truncated apical ends. In both specimens the septum of truncation is distinctly thicker than the other septa. □A. In the siphuncular passage through the septum of truncation a calcareous plug can be seen, RM Mo 57423, $\times 3.8$, (see also Fig. 29G). □B. In this specimen the curvature of the septum of truncation is less than in A, while the thickness of the septum is increased, perhaps to compensate for the reduced strength of the less curved septum, RM Mo 56226, $\times 3.8$, (see also Fig. 29F).

probably of less importance than for the long slender orthocones. However, truncation reduced the water drag to some extent and this is further discussed in the chapter 'Swimming'.

As truncation within Oncocerida seems less beneficial than within Orthocerida and Ascocerida the question arises why it happened at all. As the function of the phragmocone is most certainly to give the animal floating capacity, buoyancy must necessarily become negative if a part of the phragmocone is truncated, since each chamber contributes to the lift of the body chamber. One way for the cephalopod to avoid sinking to the sea floor when truncating, is to produce a more or less instantaneous floating capacity, and

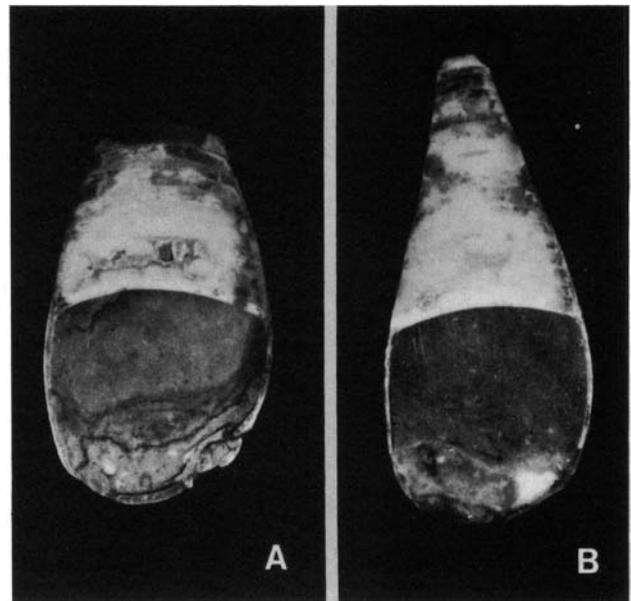


Fig. 16. Two specimens of *Pentameroceras mirum* with almost equal space in the body chambers and almost the same buoyancy. □A. Stout specimen with truncated apical end, RM Mo 56702, $\times 1.7$. □B. Slender untruncated specimen. The missing apical end is probably broken *post mortem* as there is no septum of truncation, RM Mo 56740, $\times 1.7$.

this is most easily achieved by emptying a newly constructed large chamber. This seems to be the case with, e.g., *Ascoceras manubrium* (Lindström 1890, Pl. 6:3) as large chambers occur regularly. If, however, the deciduous portion of the phragmocone had reached neutral buoyancy balance, before truncation by shell deposition or by secretion of liquid, the buoyancy of the cephalopod would not be affected. Such a method seems highly likely among the orthocones as these would otherwise lose their horizontal balance.

The described oncocerids do not have any large chambers for balance adjustment as the ascocerids do, and therefore it might be assumed that the truncated part had neutral buoyancy, otherwise the animal had to spend some time on the sea floor. If the animal was a bottom dweller a neutral buoyancy of the truncated part was not necessary, but on the other hand, there would be less reason for the small truncation that occurs.

Malformation, regeneration and parasitism

Malformation of the shell due to disturbance of the mantle has been observed on extant *Nautilus* as well as on many fossil cephalopods. Such abnormal growth can either originate from pathological growth disturbance or from injury of the mantle caused by predators. The mantle, however, has a remarkable healing power, and wounds and broken apertural rims are mostly repaired fairly soon (Teichert 1964).

Scars. – Scars and furrows in the shell are fairly common in fossil cephalopods as well as in living *Nautilus*. These disfi-



Fig. 17. Malgrowth lateral to the hyponomic sinus of a *Trimeroceras cylindricum* due to damage on the mantle, RM Mo 56512, $\times 6.5$, (see also Fig. 291).

gurements must have been caused either by simple shell breaking with or without injury to the mantle, or by growth disturbance of the mantle. Shell breaking and wounds on the mantle may have external causes such as the action of predators. Due to the growth pattern it can be established that such damage to the shell is not simply a post-mortal fracture.

In one specimen of *Trimeroceras cylindricum*, RM Mo 56512, a distinct disfigurement on the left side of the hyponomic opening can be observed (Fig. 17). It seems to be the result of damage to the mantle during secretion of the shell, which caused unusual growth. The mantle does not appear to have completely healed as the malformation continues all the way to the apertural rim.

Occasionally the apertural edge could be broken with no or very little harm to the mantle. This is demonstrated on a specimen of *Pentameroceras mirum*, RM Mo 154005, about 6 mm posterior to the left sinus. This scar, 2–3 mm wide (Fig. 18) was completely repaired and there are no traces at all in the repaired area of any growth disturbance. Anterior to the repaired area the shell growth continues with the normal appearance of the apertural rim.

In extant *Nautilus* scar repairs are very common; fairly big pieces of the edge can be broken off and the edge then healed (Fig. 19). Willey (1902) discussed shell damage in *Nautilus* and suggested the scars were made by fish, but according to Arnold (1980) the origin of scars on *Nautilus* is predation, parasitism or probably mating habits. Furthermore, Carlsson (1982) describes how *Nautilus* is very well capable of biting through the apertural rim of other *Nautilus*, as well as eating the soft tissues. Regarding the Gotland fossil material, however, the injuries cannot have been inflicted by another



Fig. 18. Malformation due to a fracture in the apertural edge during growth of a *Pentameroceras mirum*. The mantle, however, appears to have suffered no harm as normal shell growth was quite quickly re-established. Average thickness of growth lines is 50 μm . RM Mo 154005, $\times 12$, (see also Fig. 31C).

specimen of the species as we must assume that the probable jaw apparatus was situated inside the shell. The fossil scars might be an indication of the existence of predators on the cephalopods in the Silurian sea (Stridsberg 1981a, p. 275).

More spectacular shell damage was described by Kauffman & Kesling (1960) in their paper on an ammonite which was bitten at least 16 times by a mosasaur. A similar course of events was investigated by Mapes & Hansen (1984) who discussed an attack by a Pennsylvanian shark, probably a specimen of *Symmorium reniforme*, on a coiled nautiloid of an uncertain taxon. The visible result of this attack was a number of circular holes in the body chamber from the teeth of the shark.

Malformation. – A special kind of abnormal growth among brevicone cephalopods can be observed in Barrande's illustrations of *Gomphoceras vespa* (Barrande 1865, Pl. 77:1–4), later referred to the genus *Vespoceras* Flower (Flower & Teichert 1957), *Gomphoceras atrophum* (Barrande 1865, Pl. 79:18–20, 23) and *Gomphoceras aegrum* (Barrande 1865, Pl. 79:24) (Fig. 20). These species exhibit an abnormal swelling of the phragmocone immediately posterior to the last septum or, in *Gomphoceras vespa*, fairly close to the posterior end of the phragmocone. The sectioned specimen of the latter (Bar-

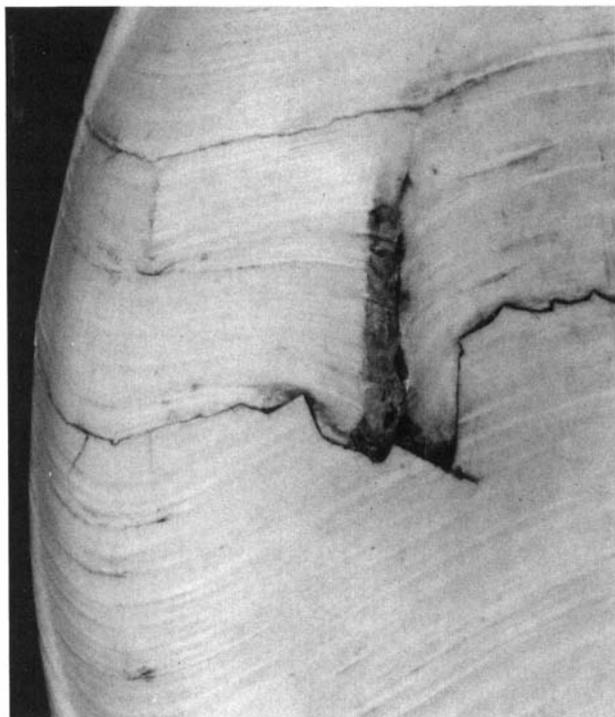


Fig. 19. Malformation on a *Nautilus pompilius* shell, probably due to the bite of a predator or another *Nautilus*. The bite also wounded the mantle as can be observed by the irregular shell growth after damage, authors private collection, $\times 2$.

rande 1865, Pl. 77:3) shows how irregularly the last septa are formed and a similar tendency can be observed in the sectioned specimen of *Gomphoceras atrophum* (Pl. 79:23). In the descriptions of the three species, Barrande did not discuss the unusual shape of the phragmocones. Obviously he accepted the malformation as being characteristic for the species.

Abnormal swelling is also found in one specimen in the collection of *Pentameroceras mirum* (RM Mo 154007) (Fig. 21). The swelling starts in the second last chamber and the widening of the shell because of this continues along the body chamber, resulting in a comparatively large volume.

Similar swellings are observed on extant *Nautilus pompilius* in captivity (Fig. 22) and Dr Jauch at the Wilhelma Aquar-

ium in Stuttgart, West Germany, has confirmed (personal communication, Nov. 1983) that specimens of *Nautilus pompilius* often become affected by this malgrowth when captured and placed in an aquarium. In one extreme case of a *Nautilus pompilius* in Wilhelma, the widening of the apertural rim did not stop and then return to normal growth, but formed instead a roughly 25 mm wide collar below the apertural opening. The final result of this malgrowth is not known as the specimen is still alive when this is written. Abnormal growth was also studied at the Artis-Aquarium in Amsterdam, Holland, by de Graaf (1981, p. 83) and here lateral as well as ventral malgrowth occurred.

The mechanism behind the above described malgrowth is not known and it may be misleading to compare the situation of modern *Nautilus* in captivity with Silurian brevicones showing the same symptom.

Bore holes. – Apart from biting predators, the Silurian cephalopod fauna of Gotland had to cope with drilling organisms as well. In two specimens of *Octameroceras unguifer*, RM Mo 56875 and RM Mo 57285, bore holes have been drilled into the body chambers (Fig. 23A and B). The diameter is 3.5 mm on both shells and the holes are circular. A similar bore hole is also observed on a specimen of *Pentameroceras mirum* RM Mo 56763, but in this case the diameter of the hole is only 1.4 mm (Fig. 23E).

Regarding the bore hole in specimen RM Mo 56875 (Fig. 23A), it appears to have been repaired by the cephalopod, as additional shell material can be observed on the sides of the hole inside the shell wall. Such excess accretion of shell material is also observed inside a 3.0 mm wide bore hole in the body chamber of an unidentifiable silicified, probably cyrtoconic cephalopod, SGU Type 4001. These repairs demonstrate active resistance against the drilling organism, and in the latter case the cephalopod seems to be the loser, since the repair itself is also penetrated (Fig. 23C and D).

The positions of the bore holes on the two specimens of *Octameroceras unguifer* and the single *Pentameroceras mirum* are more or less identical. All holes are drilled ventrolaterally about the mid body chamber, although not on the same side (Figs. 43H and 31R). Regarding the silicified cyrtocone, SGU Type 4001 (Fig. 23C and D), the position of the bore hole is ventrolateral as well. However, as the anterior part of the body chamber is missing, it cannot be confirmed wheth-

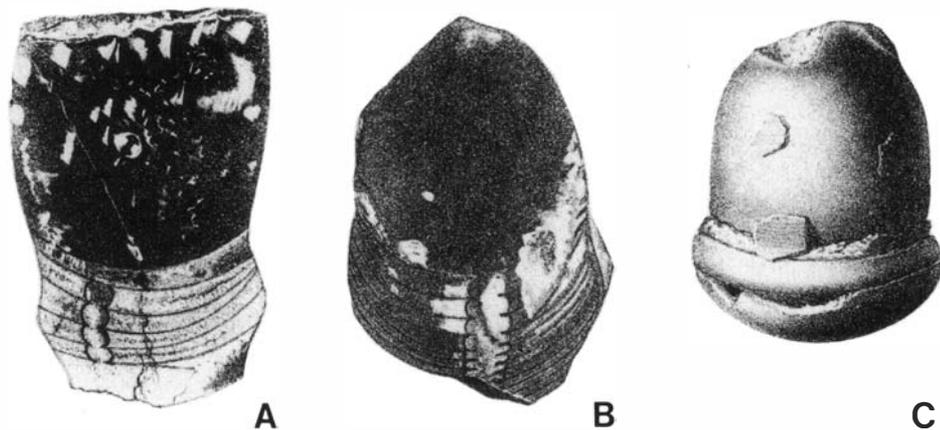


Fig. 20. Abnormal shell growth in three different species of brevicones as illustrated by Barrande (1865). □A. *Vespoceras vespa* (Barrande), $\times 1$. □B. *Gomphoceras atrophum* Barrande, $\times 1$. □C. *Gomphoceras aegrum* Barrande, $\times 1$. Reillustrated from Barrande 1865, Pl. 77:3, Pl. 79:23, and Pl. 79:24, respectively.

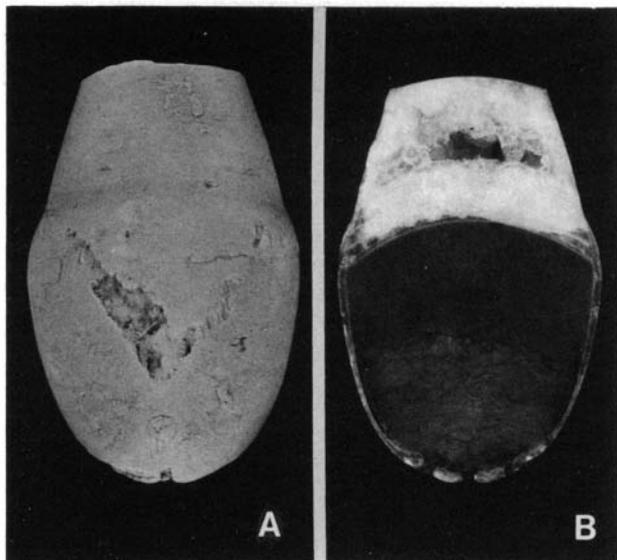


Fig. 21. Abnormal swelling in the last chambers of a *Pentameroceras mirum*. The widening of the shell continues in the body chamber, and thus increases its volume. □A. Ventral external view, RM Mo 154007, $\times 2$. □B. The same specimen as A, cut in the lateral plane.

er the position is also the mid body chamber, although it seems likely.

Whether this ventrolateral position of the bore holes indicates an optimal place for the drilling organism or is just a coincidence, is uncertain because of the limited material. Liljedahl (1985) has described bore holes in bivalves from the same locality as the cyrtoconic cephalopod (Möllbos 1), and these holes were all situated in the anterior part of the shells. If there is a favoured position of bore holes among Silurian cephalopods, it could be suggested that the drilling organisms were parasites rather than predators. An argument supporting parasitism is the fact that the cephalopod had time for some kind of resistance, as it tried to keep the enemy out by shell secretion inside the bore hole. The bore holes in the four described cephalopods are drilled in that part of the body chamber that would probably correspond to the mantle cavity, and this strengthens the idea of parasitism. Parasites would certainly appreciate the respiration water and the various kind of secretion from the cephalopod mantle cavity. In the specimen RM Mo 57285 of *Octameroceras unguifer* no repairs are visible inside the bore hole and this might indicate an almost instant killing or even drilling after the death of the cephalopod. If the driller was a parasite, the latter alternative would be improbable.

On the specimen RM Mo 56875 five circular spots with a diameter of 1.8–2.5 mm indicate other possible bore holes (Fig. 23A). It has, however, not been possible to demonstrate whether these holes penetrate the shell wall or not. These smaller holes are situated anterior-laterally on the shell.

One silicified specimen of *Pentameroceras mirum*, SGU Type 3997, with only a part of the body chamber around the hyponomic opening preserved, has a number of small bore holes. These are slightly less than 1 mm in diameter and at least one of them shows excess shell accretion on the inside (Fig. 23F).



Fig. 22. A juvenile living specimen of *Nautilus pompilius* with a swelling in the posterior end of the shell. This swelling is the result of a growth disturbance associated with the capturing in the Pacific Ocean and transportation to Stuttgart (BRD). The juvenile condition is deduced from the presence of camouflage on the ventral side of the shell. Wilhelma Aquarium, Stuttgart, German Federal Republic, approximately $\times 0.5$. (July 1984.)

In conclusion, two major types of drilling are observed in the Gotland cephalopod material, one with a diameter of about 2–3.5 mm and the other with less than 1 mm diameter. The origin of the drilling can only be speculative and gastropods are usually supposed to be responsible. Bromley (1981, p. 62), however, suggests that there is a possibility of shell drilling Palaeozoic cephalopods as well, and this mode of life would certainly suit the more or less locked-up oncocerids.

Epifauna

Epifauna on cephalopod shells can be associated with either the active life of the animal or with post-mortal shell deposition. Any addition of epifaunal weight must have caused buoyancy problems for a swimming cephalopod and it is worth mentioning that epifauna does not appear to trouble *Nautilus*. Stenzel (1964, p. K92) suggests that living *Nautilus* is free of encrusting organisms because it is an active and rapid swimmer. A few individuals, however, lacking an umbilical callus, are found with groups of small tubicolous annelids or small stalked cirripeds on each umbilicus (Stenzel 1964, p. K92). In one way or another *Nautilus* manages to keep the shell clean and perhaps this is partly achieved by washing parts of the shell with the help of the hyponome.

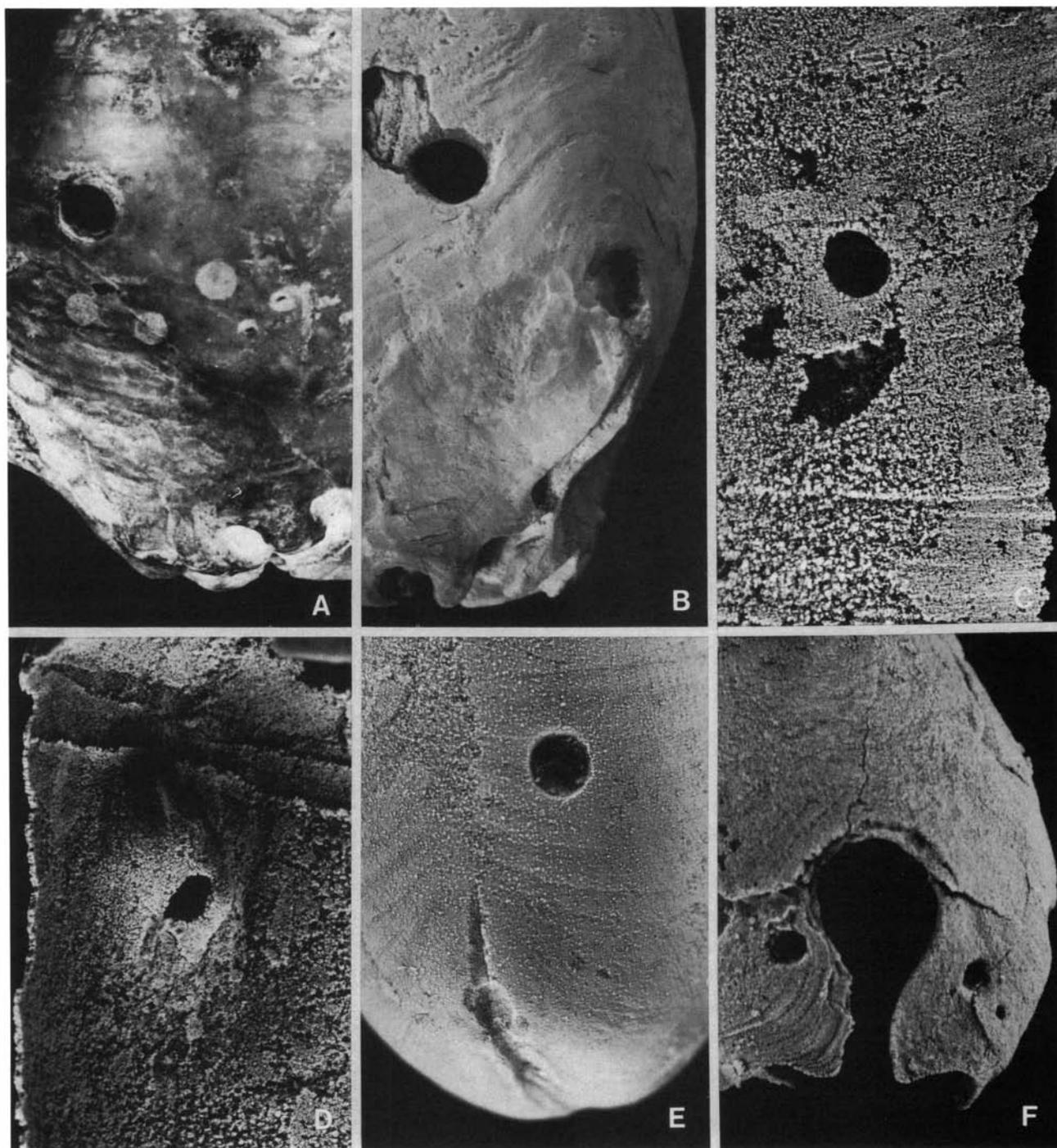


Fig. 23. Bore holes in the ventrolateral part of the body chamber of four brevicones (A, B, E and F) and one cyrtocone (C and D). □A. A penetrating hole, 3.4 mm in diameter, in an *Octameroceras unguifer* and five possible bore holes. The penetrating hole is sealed off on the inside by shell accretion of the animal, RM Mo 56875, $\times 3.2$, (see also Fig. 43H). □B. Penetrating bore hole, 3.4 mm in diameter, close to the hyponomic opening of an *Octameroceras unguifer*, RM Mo 57285, $\times 4.3$, (see also Fig. 43L). □C. Bore hole, 3 mm in diameter, in the phragmocone of a silicified cyrtocone, SGU Type 4001, $\times 4.5$. □D. The same bore hole as in C, but seen from the inside. Shell material was produced by the animal to stop the intruder, but this reinforcement was also penetrated. The remains of the two last septa can be observed above the bore hole, SGU Type 4001, $\times 3.6$. □E. Bore hole in a small *Pentameroceras mirum*. The diameter of the hole is 1.4 mm. Below the bore hole the hyponomic opening can be observed, RM Mo 56763, $\times 7$ (see also Fig. 31R and S). □F. Two, less than 1 mm wide, bore holes on each side of the hyponomic sinus of a silicified *Pentameroceras mirum*. An even smaller bore hole is situated below the right one, SGU Type 3997, $\times 5$.

During studies of living *Nautilus pompilius* in an aquarium, I have noticed that *Nautilus* kept some irritating shrimps away from the hood with help of sudden and well directed water jets. Perhaps this method was also useful against encrusting organisms. Heptonstall (1970, p. 321) proposed that the periostracum of the *Nautilus* shell has special properties

which deter organisms from becoming attached. Even if, for example, oysters require a clean surface for attachment, this must not be too clean according to Young (1960).

Epifauna, consisting of oysters, which had settled on the shell of an active ammonite is described by Seilacher (1960). The ammonite, a specimen of *Buchiceras bilobatum*, carried a

number of oysters, and some located on the ventral side of the shell were interpreted as evidence of encrustation during lifetime. This means that the ammonite had to compensate for the added weight of the oysters to keep buoyant. Similar epizoan growth is not known from other specimens of *Buchiceras bilobatum*, and Heptonstall (1970, p. 321) suggested that the individual was pathological.

None of the shells in the SMNH collection have any kind of epifauna, but as all specimens were carefully prepared at the beginning of this century, we have no knowledge at all about the original condition. In the material collected during the last decade, however, epifauna was found on eight silicified cephalopod shells from the locality Möllbos 1. Liljedahl (1985) describes epibionts on empty bivalve shells from the same locality. Two, or perhaps five, of the cephalopods were oncocerids and belong to the species *Trimeroceras bulbosum*, while the remaining three specimens were discosorids. The epifauna consists of bryozoans and tabulates (Fig. 24) and because of the position of these close to the aperture, it might be suggested that the encrustation took place after the death of the animal, as the position would otherwise have allowed the cephalopod to defend itself, either with water jets from the hyponome or with its appendages.

Colour pattern

Colour markings on fossil cephalopod shells have been illustrated in various papers (e.g. Barrande 1866, Barrande 1877, Angelin & Lindström 1880, Ruedemann 1921, Foerste 1930b, and Teichert 1964). The oldest known markings were found on two specimens of *Hedstroemoceras haelluddense*, Foerste 1930, an orthocone from the middle Ordovician of Öland, SE Sweden (Foerste 1930b, p. 125).

Ruedemann (1921, p. 315) described colour bands on orthoconic as well as cyrtoconic shells, and due to the distribution of the bands he interpreted the living position of the animal. He suggested that orthocones with colour bands on one side of the shell only, dragged the conch behind when crawling along the bottom. Consequently it was sufficient with colour markings on the upper side. The fact that cyrtoconic shells had colour bands around the entire shell, was according to Ruedemann, an indication that these animals also crawled along the sea floor, although carrying the shell fairly upright. Even if Ruedemann used the existence of colour bands as an indication of the living position, he did not discuss the biological function of the colour bands.

Colour markings on fossil cephalopods have more recently been compared with the camouflage pattern on *Nautilus* (Teichert 1964, p. K25, and Cowen *et al.* 1973), and the general idea about the fossil colour bands is that they served as camouflage.

Foerste, however, described a specimen of *Orthoceras dunbari* Foerste 1930 with colour markings on one side only, as in other species of *Orthoceras*, but on the ventral side (Foerste 1930b, p. 133). Normally specimens with colour markings on one side only, have them on the dorsal side, as is the case with the camouflage pattern on *Nautilus*. Foerste was of the opinion that the horizontal floating position of the conch was adopted only by a few of the smaller orthoconic cephalopods

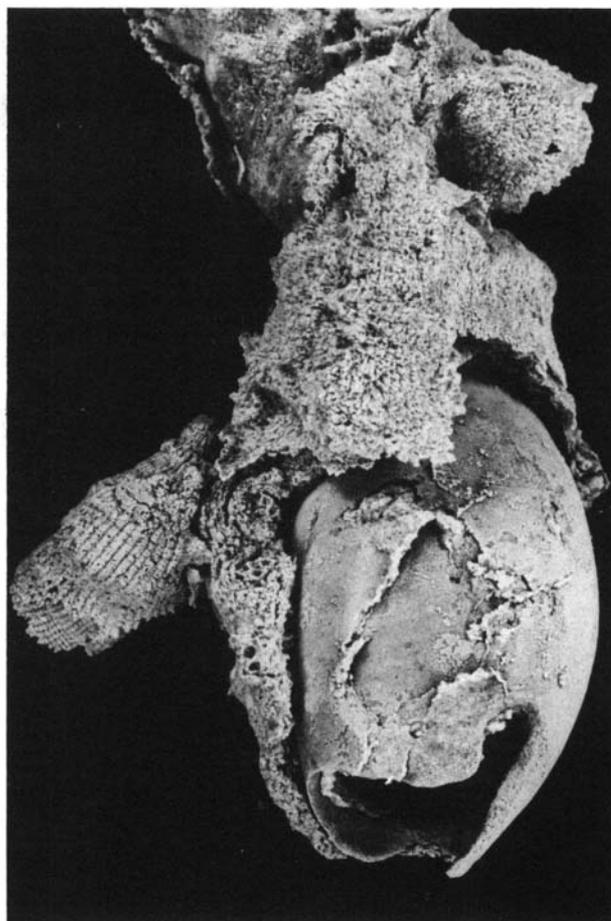


Fig. 24. A silicified specimen of *Trimeroceras bulbosum* with post-mortem epifauna, SGU Type 4000, $\times 2$; Möllbos 1 (see also Fig. 30 M and N).

and this interpretation he based on the observation that colour patterns on the ventral side of the conch were only known from a few species (Foerste 1930b, p. 140). The consequence of this assumption is that Foerste considered that colour pattern on the ventral, not dorsal, side indicated a horizontal position of the conch among the orthocones.

In total, Foerste (1930b, p. 119) discussed 41 species, all at that time known cephalopods with colour markings. From these, 25 species are of Silurian age and 18 of these originated from Bohemia in Czechoslovakia. These 18 species were brevicones and were all referred to the genus *Cyrtoceras* by Foerste.

From the Silurian of Gotland, Angelin & Lindström (1880, Pl. 10:1) described a specimen of *Orthoceras columnare* Marklin with a colour striated shell surface. These colour markings were, however, only discovered on a small fragment of a shell and no entire shell with colour markings was illustrated.

Some of the brevicones investigated in the present work, particularly representatives of *Octameroceras rimosum* and *O. sinuosum*, occasionally even *Pentameroceras mirum* and *Plemeroceras cassis*, have well defined colour patterns. These comprise colour bands around the shell, closely following the growth lines and probably reflecting an original colour pattern. In such a case the colouring substance must have influenced shell replacement during the recrystallization

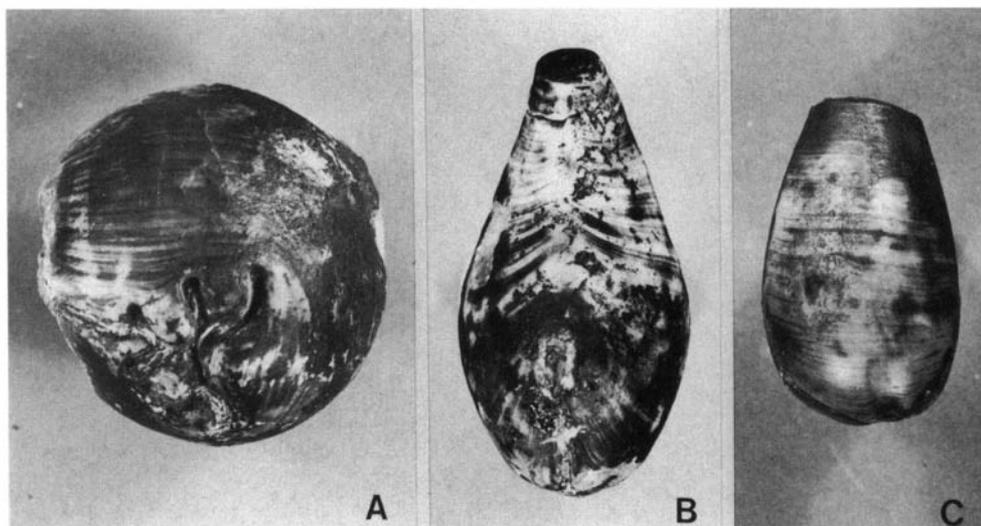


Fig. 25. Colour bands on three brevicones. □A. The apertural area of *Octameroceras sinuosum*, RM Mo 56802, $\times 1.2$, (see also Fig. 38F). □B. The ventral side of *Octameroceras rimosum*, RM Mo 56302, $\times 1.5$, (see also Fig. 42A–D). □C. Lateral view of *Pentameroceras mirum*, RM Mo 154005, $\times 1.5$, (see also Fig. 31A–D).

process. The colour bands are not located on the phragmocone only, but cover the body chamber and apertural area as well (Fig. 25A). This is not analogous with the camouflage situation of *Nautilus*, as the latter has no camouflage on the bottom side (Fig. 22).

On some specimens of *Octameroceras rimosum* (Fig. 25B) and *Pentameroceras mirum* (Fig. 25C), the colour bands very clearly follow the growth pattern on the ventral side, showing the successive growth stages of the hyponomic sinus. A similar type of colour band occurs on *Nautilus*, even if it is obvious that there is no close co-ordination between growth lines and colour bands on the latter. Comparative studies of camouflage patterns in *Nautilus* and some fossil cephalopods were carried out by Cowen *et al.* (1973) and, apart from detailed presentations of coloured camouflage patterns on *Nautilus* and some ammonites, Cowen *et al.* (1973, p. 209) discussed life orientation of a brevicone shell. They suggested that because of the cross banded camouflage, the shell must have floated horizontally, and not vertically as supposed by Teichert (1964, p. K24). Cowen *et al.* based their opinion on the fact that *Nautilus*, observed from above, has transverse colour bands and thus a superb camouflage. This might make sense to camouflage arguments, but unfortunately not in regard to buoyancy, which demands a vertical floating position. Furthermore, if the brevicone illustrated by Cowen *et al.* (1973, p. 209, Fig. 9) was floating horizontally, why did it in that case have camouflage on the ventral side of the shell? As discussed in their paper, adult *Nautilus* totally lacks ventral camouflage, so conclusively the *Nautilus* comparison cannot be fully used. Even if the camouflage of *Nautilus* is transverse on the top surface, the colour bands are horizontal when seen from the posterior. A brevicone such as *Octameroceras rimosum* for example, floating vertically, would have horizontal colour bands, and because of the pointed narrow upper end of the shell, these bands would almost form rings when seen from above.

Cott (1940) discussed the benefit of camouflage in certain situations and in which way a colour pattern helps to disturb a potential predator. Personally I believe that a predator on the brevicone cephalopods would be confused by the horizontal colour bands, if approaching from any side. *Nautilus*

has one lateral fan-shaped camouflage, one posterior with horizontal bands and one anterior dotted camouflage pattern (Fig. 22). Because of the rotation of the *Nautilus* shell during growth, *Nautilus* cannot have different patterns on different sides. On the whole, its camouflage is more or less a compromise. The camouflage from all the sides cannot be the most effective and, if the horizontal band type is the best one, the brevicones had reason to feel confident inside their cross-banded shells.

Palaeoecology

The restricted apertural opening and the general outline of the brevicone cephalopods have caused much speculation on the life habits of the animal. Jaekel (1902) suggested that cephalopods with almost closed apertures, such as *Gomphoceras*, *Phragmoceras*, *Tetrameroceras* and *Hexameroceras*, were embedded in the sediment with the aperture facing upwards. The tentacles would have stretched out to grasp food and the hyponome would have facilitated respiration. Jaekel, however, did not discuss the benefit of a gas-filled phragmocone in such a living position.

As previously mentioned, Ruedemann (1921, p. 317) discussed whether the brevicones were crawlers on the sea floor. Cowen *et al.* (1973, p. 209, Fig. 9), on the other hand, introduced the idea of horizontally floating brevicones, and including the nowadays generally accepted idea about vertically floating brevicones, with the aperture facing downwards (Dzik 1984, p. 50), we have all possible living positions suggested.

In the following the mode of life of brevicone cephalopods will be discussed, based on the conditions given by the only remaining part of the animal, the shell.

Aperture. – In cephalopods with a restricted aperture the apertural shape must reflect the shape and function of the soft parts. As indicated earlier the final apertural growth was affected by the position of these soft parts. If we assume that the Silurian oncocerids functioned in a similar way to mod-

ern cephalopods, including *Nautilus*, the sinuses ought to have served as openings for tentacles, and most certainly for a pair of eyes. Naturally it cannot be taken for granted that the oncocerids did have tentacles, but the narrow passages leave few other alternatives than very slender appendages. Furthermore, Flower (1955, p. 863) presented interesting photographs showing tentacular impressions of a Late Ordovician orthocone cephalopod.

The number of sinuses among the investigated oncocerids ranges from two to eight, and occasionally nine. However, it is most unlikely that this number corresponds to the number of tentacles, since such a wide variation would mean very different specializations within the group. Furthermore, as discussed earlier, there is a variation in the number of sinuses even within some species. It is more likely that different living habits gave rise to varying numbers of sinuses.

The question is in what way the apertural shape influenced the life habits of the cephalopod, or more correctly, what kind of activity that gave birth to the different apertural shapes. An aperture like that of *Octameroceras rimosum* can only allow a small number of tentacles to be used outside the aperture at the same time. Even if we assume that each tentacle was very slender there will be very little space for movement. From a practical point of view, such an aperture could only allow less than a dozen tentacles. Any extra tentacle would be an obstacle in the narrow sinuses. On the whole, the number of tentacles among the oncocerids was presumably fairly small and in no case as large as in the modern cousin *Nautilus*.

It is of interest to discuss the purpose of these tentacles. Beyond transportation duties, which will be discussed below, food-gathering must be the most important task. It must, however, be out of the question that the animal used the appendages to grab any bigger prey, because the sinuses, for example in *Octameroceras rimosum* and *O. unguifer*, would not permit it to pass into the body chamber, unless the tentacles could divide the food into smaller bits and pieces outside the aperture. Species like *Clathroceras plicatum* and *Jeppsonoceras concentratum*, however, have a considerably bigger apertural opening than the above mentioned species of *Octameroceras* which would permit bigger prey to pass through.

Mutvei (1964a) discussed the numerous retractor muscles, arranged uniformly around the body, and suggested later (Mutvei 1979) that this arrangement might have been somehow connected to a microphagous feeding habit.

In the discussion about restricted apertures, the benefits of these must be penetrated. A swimming cephalopod, scavenging or living on planktic organisms, would find security inside a restricted aperture when threatened. A similar mode of protection can be observed in recent *Spirula*, which retracts the soft parts inside the mantle cavity when disturbed (Schmidt 1922, p. 788 and Bruun 1943, p. 5). After retraction, the edge of the mantle almost entirely closes around the animal, leaving only a narrow slit. Protected like this, *Spirula* is safe from small predators, as the mantle wall is very strong. The hood of the extant *Nautilus* serves the same purpose.

A crawling, vertically positioned cephalopod, would probably find a narrow aperture quite uncomfortable as this

would restrict the movements of the tentacles when crawling around. Furthermore, a good method of protection against predators would be to lower the shell to the sea floor and for the animal to stay entirely inside. This would not require a restricted aperture. Even if a predator was able to turn the shell over, the cephalopod would not necessarily be unprotected if the aperture was open because the floating capacity of the phragmocone would restore the vertical floating position. If, however, the predator could keep the shell turned over, by force, an open aperture would be disastrous. The consequence is that a crawling oncocerid might perfectly well have needed a restricted aperture. If so, then restricted apertural shapes would not definitely indicate any specific mode of life, only an overall protective function (Stridsberg 1981a, p. 275).

Buoyancy. – The question of buoyancy and the orientation of the shell is of greatest importance in understanding the moving abilities and mode of life among the oncocerids.

In the discussion of buoyancy in fossil cephalopods, comparisons are often made with modern cephalopods such as *Nautilus* and *Spirula* (Mutvei 1964, Denton & Gilpin-Brown 1973 and Denton 1974). Apart from the buoyancy mechanism, *Spirula* (Denton *et al.* 1967) is of special interest in comparisons with oncocerid cephalopods as *Spirula* too floats vertically in water (Fig. 26). This floating position is attained when the centre of gravity is located directly below the centre of buoyancy, which has been demonstrated in *Nautilus* by Denton & Gilpin-Brown (1966, Pl. 1).

Calculation of the buoyancy is complicated as the difference in weight between floating and not floating is very small. If the organism was buoyant, the lifting capacity of the shell must have been equivalent to the weight of the shell and the soft parts in water. As the soft parts have only slightly higher density than the surrounding sea-water this weight is marginal. Denton & Gilpin-Brown (1966) have given the figure 1.068 g/cm³ as the density of the body tissues of *Nautilus* and 1.026 g/cm³ for sea-water density. When estimating the gas volume in the phragmocone and the total weight of the shell, there are so many uncertain factors that the errors in any calculations will be of a much greater magnitude than the weight of the soft parts. As the thickness of shell and septa are not the same after recrystallization (Reyment 1958, p. 146–147), weight and volume of the different septa cannot be measured with any accuracy. Furthermore, the weight and volume of the missing apical end can only be very roughly approximated and thus gives no help in the calculations. As a result, I do not believe that buoyancy questions can be solved by experiments with replicas or by mathematical calculations.

An argument for buoyancy is the existence of a phragmocone. Shells with more or less concealed chambers ought to be buoyant or nearly buoyant, as the added weight of each new septum would be disadvantageous for the animal if the added weight was not compensated for. There is, however, also the possibility that the function of the gas-filled chambers was to decrease the weight of the shell for a benthic organism.

Within the gastropod family Euomphalidae, the oldest part of the whorl could be sealed off by septa (Kerr 1931). In this case, however, the chambers did not have any lifting

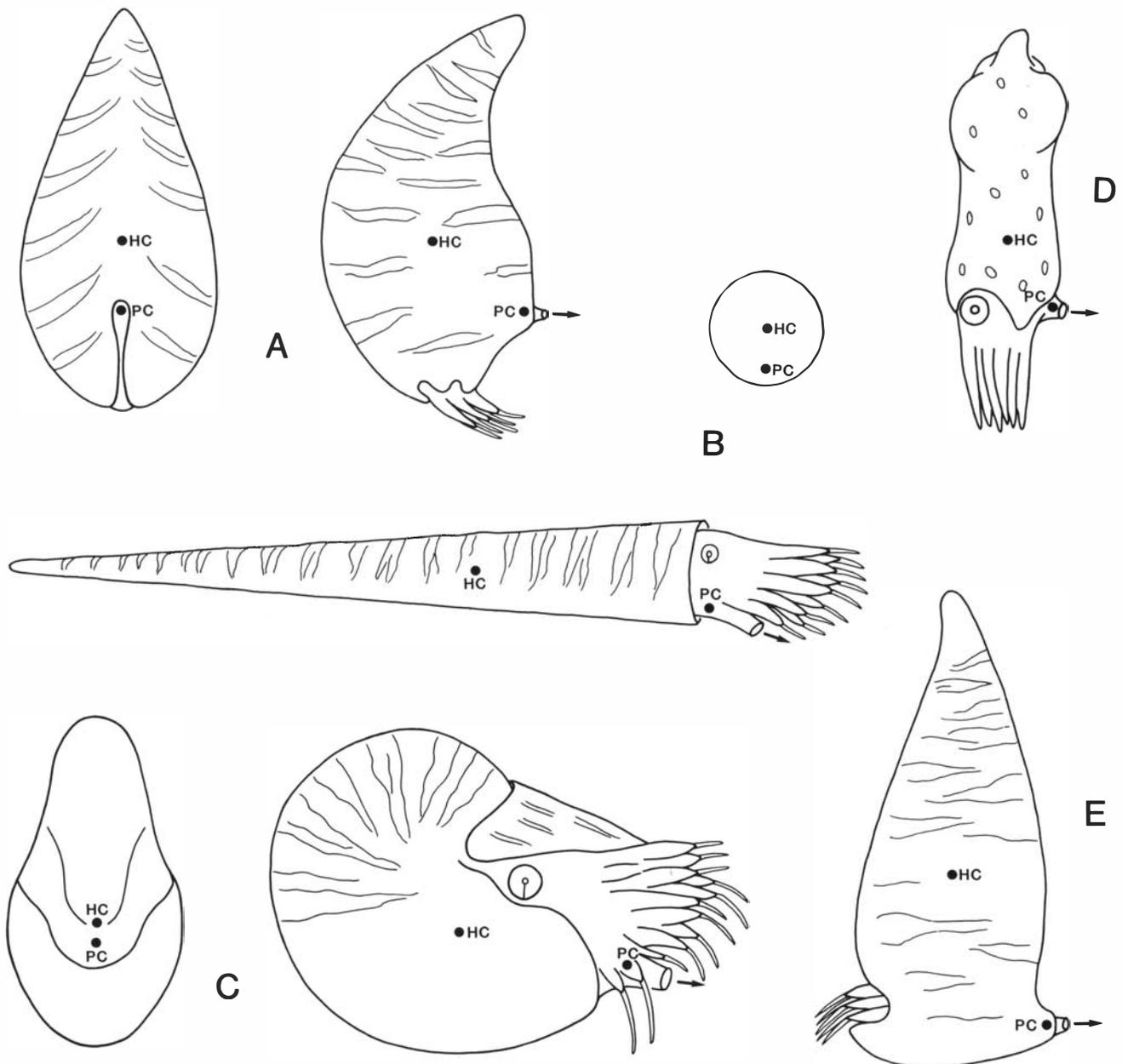


Fig. 26. Swimming conditions for various cephalopods. Effective swimming, accomplished by jet propulsion, is dependant on the position of the propulsive centre (PC) relative to the hydrodynamic centre (HC). □A. The propulsive centre of *Octameroceras rimosum* is situated below the hydrodynamic centre thus causing unstable locomotion. □B. With a diminutive dipping of the hyponome, an orthocone can adjust the position of the propulsive centre and place this almost on a level with the hydrodynamic centre. Due to the new hydrodynamic shape, caused by the lowered apical end, the hydrodynamic centre must be slightly above the propulsive centre to allow strictly horizontal locomotion. □C. *Nautilus* has an almost ideal position of the propulsive centre in relation to the hydrodynamic centre. The small divergence results in a minor oscillation. □D. The low position of the hyponome, and thus propulsive centre in *Spirula* is compensated for by the protrusion of the soft parts which help to lower the hydrodynamic centre when swimming. □E. The considerable distance between the hydrodynamic centre and propulsive centre in *Plemeroceras cassis* must have resulted in a very unstable propulsive locomotion.

capacity as they most certainly contained fluid. As the gastropods do not have any siphuncle, they cannot empty the closed chambers and thus cause a reduction in the shell weight. The siphuncle is a unique cephalopod feature and gives this group an exclusive opportunity to carry large shells. The shell, reminiscent of the ancestral monoplacophoran shell, must have served the purpose of either buoyancy or protection. The generally accepted idea is that the shell served both functions.

In the evolution of cephalopods, the shell initially served as a protective cover. The group did not primarily construct

the gas-filled phragmocone to obtain buoyancy. They had to evolve this ability to be able to carry their protective shell and to swim. Evolution has later shown how the shell has diminished within the group and even become completely reduced in order to favour fast swimming. The density of the soft parts does not require a gas-filled shell. It is only the protective duty that required Palaeozoic cephalopods to keep the shell. Modern cephalopods need no shell for protection, as the absence of this allows the animal to move very quickly. The oncocerids and phragmocerids with restricted apertures were probably those groups who developed a real-

ly safe shell, and the price for this was very restricted movement.

An important evolutionary step was taken when the first cephalopod left the sea floor and started to swim. The time at which this happened is unknown, but there are indications that at least orthocone cephalopods were swimming. The growth pattern with deposits in old chambers and siphuncle, shows that the organism struggled to keep the shell in a horizontal position (Flower 1957, p. 834). This would be unlikely if the animal was benthic, as a horizontal shell would in such a case be rather an obstacle. Concerning the Silurian oncocerids dealt with in this paper, no cameral deposits are known, but as mentioned above the apical end is always missing. If the oncocerids were to float in a horizontal attitude, the apical end had to be more or less solid to balance the great body chamber. However, the shape and position of the hyponomic sinus would not permit any effective jet propulsion if the shell was orientated horizontally, as the jet stream would leave the shell at right angles from the long axis (Fig. 26A). A horizontal shell orientation would only favour a nectic animal as the hyponomic sinus would otherwise be buried in the sediment. If the animal was a swimmer, the angle of the hyponome would be so ineffective that this interpretation must be regarded as most unlikely.

In conclusion, all information indicates that the oncocerids lived with the phragmocone above the body chamber. Therefore there would be no reason for the apical end to contain deposits, as is the case with the rest of the phragmocone.

Swimming. – As the Palaeozoic cephalopods are supposed to have lacked external soft parts, their swimming abilities must have been restricted to jet propulsion. Horizontally oriented orthocones were well adapted for jet propulsion, thanks to their slender shape, but even more bulky shells, like that of *Nautilus*, are fairly well suited for this kind of swimming.

One important factor regarding jet propulsion is the position of the hydrodynamic centre in relation to the hyponome (Fig. 26A). To allow the jet force to move the shell without turning it over in the pitching plane the hyponome must be close to or level with the hydrodynamic centre. In the case of orthocones this could be established by a slight dipping of the apical end, as the hyponome is situated slightly below the hydrodynamic centre (Fig. 26B). Regarding *Nautilus*, the hydrodynamic centre is situated fairly close to the hyponome (Fig. 26C) but during growth the horizontal balance of the shell changes, causing a more or less correct position of the hyponome. The result is the typical oscillation in the pitching plane, often seen in swimming *Nautilus* (Packard *et al.* 1980, p. 318).

However, among some Silurian oncocerids with strongly contracted apertures, the situation was completely different. The shells floated vertically with the hyponome far below the hydrodynamic centre. Because of this it is obvious that the oncocerids could not use jet propulsion to escape from enemies by a sudden rush. Instead jet propulsion could only be used for slow transportation purposes, as any sudden rush would cause a vigorous swing, followed by a return swing when the animal respired (Fig. 27). As we know nothing about soft parts and swimming abilities, we must

assume that, in case of danger, the animal withdrew all soft parts inside the shell and waited. Such behaviour is observed in living *Spirula*, as described in the chapter 'Aperture'. Even if oncocerid soft parts could assist in swimming, the shell would still have the same problem of oscillation as the aperture and protruding soft parts were situated far below the hydrodynamic centre.

Concerning modern cephalopods, these have totally different conditions as they lack the shell, and furthermore have the ability to move the hyponome to the level of the hydrodynamic centre and thus can control the balance.

A better comparison for the brevicone shells is *Spirula*. This genus has the soft parts hanging below the chambered part, giving a fairly similar hydrodynamic shape to the brevicones (Fig. 26D). As described by Schmidt (1922, p. 788), *Spirula* can make 'swift jerky movements' with the help of jet propulsion. When performing these movements, *Spirula* can either swim forwards or backwards by directing the hyponome in different directions. It is unlikely that the oncocerids had this manoeuvring ability with the hyponome, as the hyponomic opening restricted its movements considerably. Furthermore, the oncocerids were not equipped with small fins on the uppermost part of the body as is the case with *Spirula*, because of their lack of an external mantle.

Even if the position of the hydrodynamic centre of *Spirula* is similar to that of the oncocerids, it can be strongly influenced by position of the soft parts. *Spirula* swims with the arms hanging down and this lowers the hydrodynamic centre (Fig. 26D). It is unlikely that the oncocerids could extrude a comparatively large volume below the shell, because of the restricted volume of the body chamber, but on the other hand their hyponomic sinus is sometimes positioned a short distance above the lowermost part of the shell. Consequently, horizontal swimming by jet propulsion might very well have been similar to that in *Spirula*.

When comparing *Spirula* and oncocerids, it must be stressed that the hyponomic opening on some oncocerids restricts the manoeuvrability in such a way that jet propulsion seems unlikely. Modern cephalopods have a superb manoeuvrability thanks to the more or less total freedom to move their hyponome.

If the oncocerids were to perform the same refined movements as the modern cephalopods, their hyponome must have been extended and easily moved outside the shell. As the hyponomic opening in, for example, *Plemeroceras cassis* is elongated (Figs. 26E and 36J), the hyponome itself must have been of considerable length, in order not only to reach the outer end of the sinus, but also to be able to turn in all directions. Such a long hyponome must increase the resistance of the water passing through, especially as the hyponome must have been very slender in order to fit the hyponomic sinus. A long hyponome would be disadvantageous for the animal and it is hardly probable that an organism would create a construction making respiration more difficult. The prolonged hyponomic opening ought mainly to be related to respiration rather than a specialized mechanism for moving. However, a construction of the hyponome consisting of two lappets, as that of *Nautilus*, would allow the animal to respire through a fairly wide opening and to diminish the opening for simple navigation by jet propulsion.

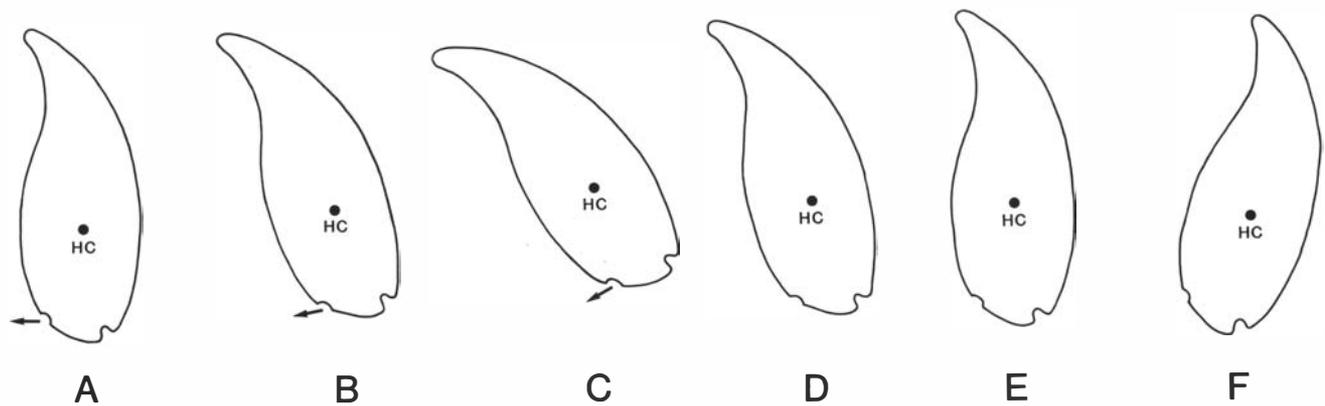


Fig. 27. The use of jet propulsion by *Trimeroceras bulbosum* with the hyponomic opening close to the anterior end of the shell would cause an oscillating swimming mode. In A–C the animal moves towards the right by jet propulsion. In D–F a return swing occurs when the animal respire.

A possible explanation of the high position of the hyponomic sinus within some oncocerids might be that the organism was a suspension feeder. If so, it must have been of great importance to keep the respiration water well above the suspension surface. Evidence which contradicts this theory is the fact that a few other oncocerids do have their hyponomic opening very close to the aperture. This would be of no advantage in a suspension feeder. Perhaps the position of the hyponomic opening reflects the volume of the extruding soft parts in that a high position indicates a large volume of extruding soft parts and thus a better hydrodynamic balance. On the other hand, if an oncocerid used jet propulsion to escape from a predator, extruding soft parts would reduce the speed. If the animal could retract the soft parts this would most certainly favour escape. To prevent the undesirable movements illustrated in Fig. 27, the hyponomic opening must shift upwards to establish a better hydrodynamic shape. Were the fastest oncocerids perhaps those with the hyponomic opening far away from the apertural opening?

Genera such as *Plemeroceras*, *Inversoceras* and others with the hyponomic opening situated on the lowermost part of the body chamber must have acquired a protruding soft-part volume bigger than the total body chamber for good swimming, and this preposterousness might indicate a comparatively poor swimming ability.

From a hydrodynamic point of view an endogastric shell is more suitable for swimming than an exogastric shell. The occurrence of exogastric shells, however, does not simplify the swimming interpretations, and within the illustrated genera or species endogastric as well as exogastric shells exist. The occurrence of exogastric shells is problematic, but at least it can be said that the exogastric shells were certainly not shaped for fast swimming.

An interesting interpretation of active swimming phases of an endogastric cyrtocone of the genus *Cyrtocycloceras* was made by Marek (1971, p. 125). Marek demonstrated how the shape of the vertically floating cyrtoconic shell, after being launched by jet propulsion, made an arc before returning to the sea floor a short distance away. This method of propulsion seems reasonable but is not applicable, however, to the species described here as all these species have the hyponomic sinus situated more or less ventrally.

Presumably the oncocerids were swimmers, but because

of the shell shape, this swimming was fairly slow and probably not sufficient for escaping predators, unless these were slow as well. Protection was accomplished by withdrawal into the shell. *Spirula* behaves in a similar way, even if the shell is replaced by a contracted, tough and slippery mantle (Bruun 1943, p. 5).

Miller and Furnish (1937, p. 57) noted that brevicones with greatly restricted apertures, such as *Hexameroceras*, did have a well developed hyponomic sinus, and therefore it might be concluded that these forms were not entirely floaters. Furthermore, they stated that the brevicones had probably lost their ability to swim effectively but that they had retained their hyponome merely as part of their respiratory apparatus. As a conclusion Miller and Furnish (1937, p. 57) assumed that the brevicones were presumably relatively inactive and feeble swimmers.

Because of their restricted swimming ability it must be assumed that the oncocerids did not inhabit very shallow waters in reef areas, as such an environment with strong currents and wave activity would cause the cephalopod distress. The animals probably spent their lives close to the sea floor, perhaps at various depths as the living *Nautilus* does.

Classification

When Sowerby (1839) introduced the genus *Gomphoceras* and named it 'from its club-like form', he based the genus on a shell which according to him 'was a link between the genera *Orthoceras* and *Phragmoceras*, differing from the latter only in being straight'. However, an inspection of the type collection has showed that *Orthoceras pyriforme* Sowerby, the species which caused Sowerby to establish the genus *Gomphoceras*, is not straight. Sowerby (1839, Pl. 8:19–20) published three drawings of what appears to be two specimens, his Pl. 8:19 showing a lateral and a ventral view and Fig. 20 showing a specimen cut along the long axis. As pointed out by McCoy (1851, p. 45), Sowerby's fig. 19 comprises two specimens, the upper being slightly curved and the lower being straight. Sowerby supposed the curvature to be the result of deformation due to pressure, and it was therefore neglected by him.

McCoy, and myself as well, do not agree with such an interpretation as the specimen is uncrushed, and in 1851 McCoy excluded the lower, straight specimen in Fig. 19 (Sowerby 1839, Pl. 8) and established another species based on it, *Poterioceras ellipticum*. McCoy later transferred his new species back to the old genus *Orthoceras* (Sedgwick & McCoy 1855, p. 321), and then Blake placed both *Orthoceras pyriforme* and *O. ellipticum* in the genus *Gomphoceras* (Blake 1882, p. 192). Both specimens are preserved in the Geological Society Collection, nowadays kept at the British Geological Survey Museum in London. *Gomphoceras pyriforme* has Geol. Soc. Coll. no. 6737 and *G. ellipticum* has Geol. Soc. Coll. no. 6738.

The very slight curvature of *Gomphoceras pyriforme* is easy to dismiss as a deformation if all studied shells belong to the genera *Orthoceras* or *Phragmoceras*, but when other brevicone cephalopods were discovered and described in the middle of the 19th Century, the slight curvature became important, as this shape is very common among these shells. This question is fundamental as, during the later half of the 19th Century, *Gomphoceras* became mixed up with the genus *Phragmoceras* and vice versa.

According to the prevailing opinion, specimens belonging to *Gomphoceras* should be brevicones with a straight shell while specimens belonging to *Phragmoceras* should have a curved shell with the siphuncle on the concave side, or in other words have an endogastric shell. Barrande (1867, p. 195) soon found out that these rules did not work in reality and three of his 33 species of *Phragmoceras* were exogastric. Furthermore, some of the species he put in the genus *Gomphoceras* were not straight.

This confusion, caused by the incorrect statement regarding the differences between *Gomphoceras* and *Phragmoceras*, led to many taxonomic misunderstandings. In 1860 Angelin was in contact with Barrande and reported two specimens of *Gomphoceras* found on Gotland. Although no illustrations were published, Barrande included them in *Phragmoceras perversum* (Barrande 1867, p. 249). Hedström, who worked with the *Phragmoceras* of Gotland excluded *P. perversum* from the genus *Phragmoceras* and established a new genus *Inversoceras* (Hedström 1917). The two specimens found by Angelin were, however, not described by Hedström. They have now been rediscovered in the SMNH collections and are described here.

Hyatt (1884), however, found the situation unsatisfactory and introduced another distinguishing characteristic by including 'all the straight and arcuate forms which have symmetrical T-shaped apertures' in the genus *Gomphoceras*. Hyatt's restriction to specimens with T-shaped apertures is interesting as Sowerby had not described such an aperture on his *Orthoceras pyriforme*. Hyatt also split up the genus *Gomphoceras* as interpreted by Barrande, and described the new genera *Trimeroceras*, type species *G. staurostoma* Barrande, and *Pentameroceras*, type species *G. mirum* Barrande. He also established *Septameroceras*, type species *G. inflatum* Billings. Hyatt also defined new genera from the genus *Phragmoceras* as defined by Barrande. These were *Tetrameroceras*, type species *P. bicinctum* Barrande and *Hexameroceras*, type species *P. panderi* Barrande.

Hyatt's taxonomy was based on the number and orientation of sinuses in the aperture. The difference in number of sinuses between similar genera had already been studied by

Barrande. He put together similar genera in groups called Trimerion, Tetramerion and Pentamerion (Barrande 1867). The application of some of Hyatt's new genera later turned out to be fairly confusing when new species with a configuration unknown to Hyatt were described, since the terms in Hyatt's definition were not always applicable.

The classification introduced by Hyatt (1884) has been widely adopted since. Newell (1888) described two new species of *Gomphoceras*, after the definition established by Hyatt, and he also described species of *Pentameroceras* and *Hexameroceras*.

A number of American species of *Gomphoceras* were described by Hall in 1879 and 1888, and in the main he followed the definition of Sowerby, including only straight specimens. Hyatt, however, was convinced that the generic characters he used were reliable, and in 1900 he (Hyatt 1900) introduced *Octameroceras* as having a brachial area with eight lateral sinuses.

During the second half of the 19th century, *Gomphoceras* was a genus with many species. Due to the introduction of Hyatt's new genera, *Gomphoceras* and even *Phragmoceras* lost a great number of species. Today *Gomphoceras* is strongly diminished and is, furthermore, in the *Treatise on Invertebrate Palaeontology* included in the genera dubia (Sweet 1964, K 318). Concerning *Phragmoceras*, Hedström discussed the problematic definition and produced a covering description of this genus (Hedström 1917, p. 6).

The final word on *Gomphoceras* must be given to Foerste: 'it is evident that the genus *Gomphoceras* cannot be regarded as well established until specimens of *Gomphoceras pyriforme* are found which definitely show the character of the dorsal expansion of their aperture' (Foerste 1929, p. 364).

Foerste accepted Hyatt's definitions of brevicone genera based on the number of sinuses and described numerous new species between 1921 and 1938. During these years he published 37 papers, most of them very substantial, dealing with nautiloid cephalopods.

During his work with the phragmocerids, Foerste reduced Hyatt's family Trimeroceratidae by removing all genera with an 'origin from an endogastric stock', or in other words those genera with only lateral sinuses and no dorsal sinus. These genera were transferred to the new family Hemiphragmoceratidae (Foerste 1926, p. 358) (see also p. 51 herein). Trimeroceratidae and Hemiphragmoceratidae are now included in the order Oncocerida (Flower in Flower & Kummel 1950, p. 611).

Although Hyatt's separation of *Hemi-*, *Tri-*, *Tetra-*, *Penta-*, *Hexa-*, *Septa-* and *Octameroceras* appeared to be a correct classification system, problems arose when more material was examined. Thus Foerste pointed out the preposterous situation, writing 'the American species usually referred to *Hexameroceras* belong to *Octameroceras*, in which all sinuses are lateral, rather than to typical *Hexameroceras*, in which two of the sinuses are directed posteriorly' (Foerste 1926, p. 359).

The type species of *Septameroceras* Hyatt, was the undescribed species *Gomphoceras inflatum* Billings, a nomen nudum. According to Foerste the only known specimen is rather a *Hexameroceras*, and as the species was neither illustrated nor described by Billings or Hyatt, Foerste described it as *Hexameroceras inflatum* (Foerste 1929, p. 381). Another seven-sinused specimen was described and illustrated by

Hall as *Gomphoceras septoris*, having six lateral sinuses in addition to a dorsal zygous one (Barrande 1867, p. 711). However, later investigations (Foerste 1926, p. 357) showed that this specimen had only six lateral sinuses and a broken dorsal lobe which had been incorrectly interpreted by Hall as a sinus.

In conclusion, there is no evidence for the existence of any specimen referable to '*Septameroceras*' as defined by Hyatt.

Regarding the genera within Hemiphragmoceratidae, the number of sinuses varies greatly even within the single species (Stridsberg 1981a and herein). The number of sinuses in *Octameroceras sinuosum*, for example, varies between four and eight, or even nine. A specimen of *O. sinuosum* with six sinuses shows no similarities with the type species of *Hexameroceras*, but is similar to other specimens of *Octameroceras sinuosum* with fewer or more sinuses (see also the chapter 'Apertural growth').

Of the generic names *Tri-*, *Tetra-*, *Penta-*, *Hexa-*, *Septa-* and *Octameroceras*, only four seem to be valid. *Trimeroceras* and *Pentameroceras* are distinct genera and can be well defined within the Trimeroceratidae. In the Hemiphragmoceratidae I have only included *Hexameroceras* and *Octameroceras* of the above remaining genera, since I am convinced the latter genus comprises the type species of *Tetra-* and *Septameroceras*, as is further discussed on p. 51.

The other genera in Hemiphragmoceratidae and Trimeroceratidae which were accepted in the *Treatise on Invertebrate Paleontology* (Sweet 1964) are not found on Gotland. However, two new genera within the Trimeroceratidae, *Jeppssonoceras* and *Plemeroceras* are described herein.

Taxonomic descriptions

Class Cephalopoda Cuvier 1797

Subclass Nautiloidea Agassiz 1847

Order Oncocerida Flower in Flower & Kummel 1950

(*nom. correct.* Sweet 1964, K282, *pro* Oncoceratida Flower in Flower & Kummel 1950).

Family Trimeroceratidae Hyatt 1900

Fig. 28

The family name Trimeroceratidae was introduced in 1900 by Hyatt when he discussed the ingrowth of the apertural sides among smooth brevicones, having different numbers of 'brachial sinuses'. In doing this Hyatt reduced the old family Gomphoceratidae and also moved the genus *Gomphoceras* to the family Phragmoceratidae.

In his new family, Trimeroceratidae, Hyatt included his established equilobate (not inequiolobate as stated by Hyatt 1884, p. 277) genera *Mandaloceras*, *Trimeroceras*, *Pentameroceras* and *Septameroceras* as well as his inequiolobate (not equilobate as stated by Hyatt 1884, p. 278) genera *Tetrameroceras* and *Hexameroceras*. As new genera he added *Hemiphragmocereras* and *Octameroceras*.

Mandaloceras was later transferred to the family Mandaloceratidae Flower in Flower & Teichert, within the order

Discosorida (Teichert 1964, p. K 340) and the inequiolobate genera were moved to a new family Hemiphragmoceratidae by Foerste (1926, p. 358), as he considered the absence of the dorsal sinus sufficient for establishing a new family. It is notable that Foerste only studied the apertural outline and did not consider the shape of the siphuncle. This is slender and empty in the Trimeroceratidae and completely different from the nummuloidal, actinosiphonate form in the Hemiphragmoceratidae. Already Hyatt (1884, p. 259) had realized that the siphuncle, or rather the septal necks, were of great taxonomic importance.

Genus *Trimeroceras* Hyatt 1884

Type species. – *Trimeroceras staurostoma* (Barrande 1865). (Original combination: *Gomphoceras staurostoma*.)

Emended diagnosis. – Circular or almost circular, nearly straight brevicone. Inflated body chamber with a contracted visored aperture, having hyponomic, one pair of lateral, and occasionally mid-dorsal sinus. Empty slender siphuncle.

Species. – *Trimeroceras staurostoma* (Barrande 1865), *T. cylindricum* (Barrande 1865) and *T. bulbosum* n. sp.

Trimeroceras cylindricum Barrande 1865)

n. comb.

Figs. 15, 17, 28, 29A–I

Synonymy. – □ *Gomphoceras cylindricum* Barr. – Barrande (1847). □ *Gomphoceras cylindricum* Barr. – Barrande (1865, Pl. 79: 1–5, 6–8, 9–10, 11–14, Pl. 104:5–9). □? *Gomphoceras cylindricum* Barr. – Barrande (1865, Pl. 79:15, 16, 17). □ *Gomphoceras cylindricum* Barr. – Barrande (1867:246, 309–310).

Lectotype. – Specimen illustrated by Barrande (1865, Pl. 79:11–14) L 9219 selected herein.

Type stratum. – e², Ludlow.

Type locality. – Dlauka-Hora, Czechoslovakia.

Material. – Six specimens from Bohemia; L 334, L 335, L 401, L 9219, L 9220 and L 35050 at Narodni Muzeum in Prague, Czechoslovakia. Eleven specimens from Gotland; RM Mo 56218, Mo 56219, Mo 56220, Mo 56221, Mo 56223, Mo 56226, Mo 56227, Mo 56228, Mo 56512, Mo 56990 and Mo 57423 at SMNH, Stockholm, Sweden. All specimens are mature.

Diagnosis. – A species of *Trimeroceras* with a circular or slightly depressed, cyrtconic, exogastric brevicone, in mature specimens with contracted aperture. Narrow T-shaped aperture consisting of one pair of lateral sinuses in a straight line and a hyponomic sinus, ending with a small hyponomic opening. Siphuncle situated fairly close to the wall.

Description. – Circular straight body chamber with slightly curved exogastric phragmocone. The orientation of the old-

est preserved septum indicates that the exogastric curvature was probably more dominant on the absent apical end of the phragmocone. The body chamber is slightly longer than wide and almost twice as long as the preserved phragmocone. All preserved phragmocones are similar in size and have almost the same number of chambers, implying that eventually the apical end was truncated. This is discussed in the chapter 'Truncation'.

A diminished last chamber can be observed in specimens cut dorsoventrally along the long axis, and this confirms the mature stage (cf. Stridsberg 1981:270–271). Distance between septa in the mature part is fairly constant with an average of 2 mm, except the last chamber which is only 1.3 mm thick.

On specimens with no shell preserved, muscle imprints can be observed along the last four or five chambers.

The apertural opening is extremely restricted by two ventrolateral lobes, leaving a very narrow T-shaped opening (Fig. 29D, E and I). The dorsal lobe has a small protuberance opposite the hyponomic sinus, making the two lateral sinuses equally wide (Fig. 29E). On cut specimens a reinforcement can be observed below this dorsal protuberance, and this is also the case around the hyponomic opening. The specimen in Pl. 79:11–14 (Barrande 1865), here selected as lectotype, shows very well the reinforcement along the inside of the apertural rim.

The hyponomic sinus is as narrow as the lateral sinuses and the hyponomic opening is only marked as a slight widening at the end of the sinus. One specimen, RM Mo 56512 (Fig. 29I), is bigger than the other Gotland specimens and has a more developed hyponomic opening, but unfortunately the specimen comprises only the anterior part of the body chamber.

The hyponomic opening is marked by a small protrusion on the shell, as is fairly common on oncocerid shells.

The nummuloidal siphuncle is situated 1.5–2 mm from the convex shell surface and follows the curvature of the shell (Fig. 29F–G).

Within the Gotland collection, as well as among the Barrandian specimens, the size variation is fairly wide. In both collections, however, two groups can be discerned which are of the same amplitude in both faunas. Sexual dimorphism seems obvious and is discussed in a separate chapter (Fig. 11).

Discussion. – Barrande's description (1865 and 1867) of *Gomphoceras cylindricum* was based on eight specimens. Of these the specimen in Pl. 79:11–14 (Barrande 1865) is here selected as lectotype. The specimen is fairly well preserved but does not show the siphuncle, as do none of the Barrandian specimens, except those in Pl. 79:15 and 16 (Barrande 1865). However, the specimen in Pl. 79:15 does not show any aperture and the specimen in Pl. 79:16 consists of the phragmocone only. The shape of this is very similar in several species, as is the type of siphuncle, so I find no conclusive evidence for including these two specimens in *T. cylindricum*.

Concerning the specimen in Pl. 79:17 I doubt it belongs to *T. cylindricum*, not because of its small size, but because of its shape and total appearance. As is the case with *Phragmoceras rimosum*, Pl. 48:4–5 (Barrande 1865), Barrande described the

Table 2. *Trimeroceras cylindricum* (Barrande), dimensions in mm. Illustrations marked with an asterisk are from Barrande (1865).

Specimen No	Illustration	LT	LBC	H	W
L 9219 (lectotype)	Pl. 79:11–14*	41		19.1	18.7
L 334	Pl. 79:1–5*	51		23.5	25.6
L 335	Pl. 79:6–8*	49		23.5	25.0
L 401	Pl. 104:5–9*	41		19.6	19.8
L 9220	Pl. 79:9–10*	48		19.9	20.4
RM Mo 56218	Fig. 29E			23.7	24.9
RM Mo 56219	Fig. 29A–D	39		21.8	22.9
RM Mo 56220		39		(22.1)	
RM Mo 56221		35	21.4	19.9	
RM Mo 56223		46		(25)	(25)
RM Mo 56226	Fig. 29F	35	21.8	20.3	19.7
RM Mo 56227		36		22.3	23.2
RM Mo 56228					
RM Mo 56512	Fig. 29I				
RM Mo 56990	Fig. 29H	41		23.3	24.0
RM Mo 57423	Fig. 29G	38	21.7	19.3	(20)

specimen in Pl. 79:17 as juvenile, probably because of its small size. This is, however, not the case, as can be inferred from the fully grown aperture. A definite *T. cylindricum* (L 35050) with the same size as the specimen in Pl. 79:17 was found in Barrande's collection in Prague, although he did not publish it.

The eleven specimens of *T. cylindricum* from Gotland are more or less complete. Of these, two are broken body chambers with the aperture preserved and two were cut dorsoventrally along the long axis. One of the former, RM Mo 56512, is notably bigger and has an extremely well preserved aperture with distinct growth lines and a repaired malformation, probably caused by a wounded mantle (Fig. 17). This deformation is discussed in a separate chapter.

Comparison. – Only one specimen of *Gomphoceras centrale* Barrande (Pl. 74:1–5, Barrande 1865) was dealt with in Barrande's description. This fossil shows a great resemblance to *T. cylindricum* regarding the apertural shape. The small dorsal inward bend visible in Pl. 74:2 is less outstanding on the specimen and has almost the same appearance as in the lectotype of *T. cylindricum*.

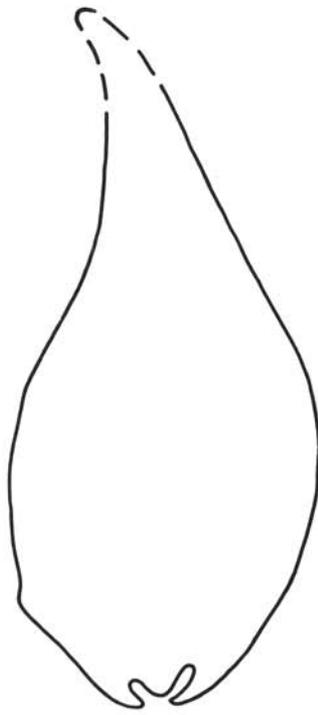
The body chamber in *G. centrale* is slightly shorter and wider than that of *T. cylindricum*. The major divergence, however, is the position of the siphuncle which is almost central in *G. centrale* while it is ventral in *T. cylindricum*. Furthermore, the siphuncle in *G. centrale* is very wide compared with *T. cylindricum*, but unfortunately no details can be observed unless the specimen is cut.

Occurrence. – Czechoslovakia: Hinter-Kopanina, Karlstein, Dlauha-Hora and Lochkov. e, Ludlow. Sweden, Gotland: Mannegårde 1, Tänglings hällar 1 and Sandarve kulle.

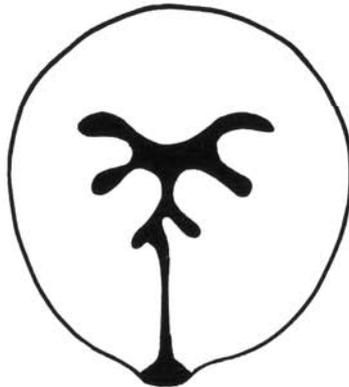
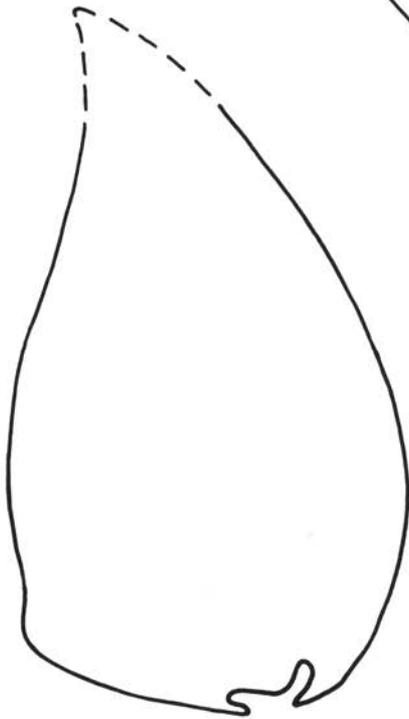
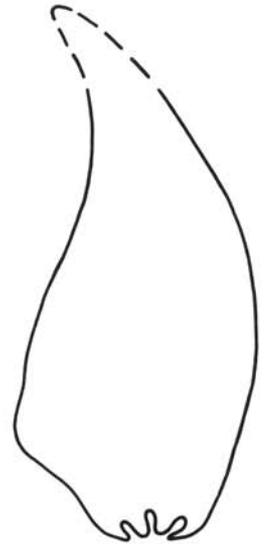
Fig. 28 (overleaf). Lateral and apertural views of all the known oncocerid species from Gotland, described herein. All specimens are drawn in natural size and represent the average size within each species. The apical end is reconstructed on those species lacking this part of the shell. In truncated species, a line represents the septum of truncation.



Octameroceras pugil



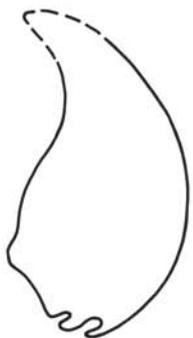
Octameroceras unguifer



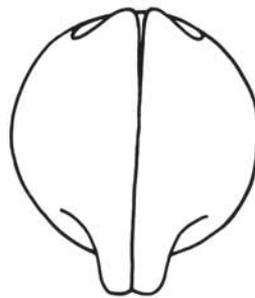
Octameroceras sinuosum



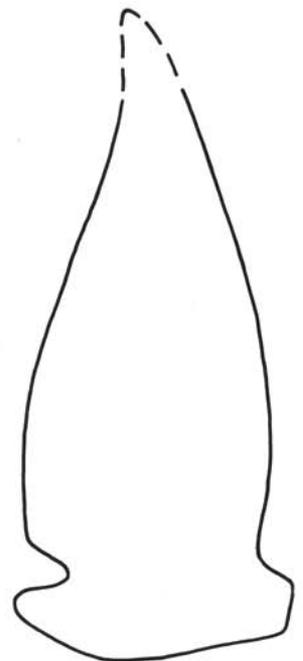
Inversoceras perversum perversum

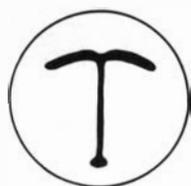


Octameroceras rimosum

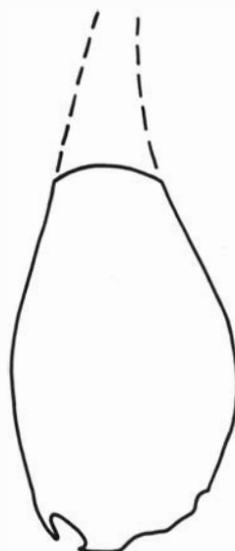


Plemeroceras cassis

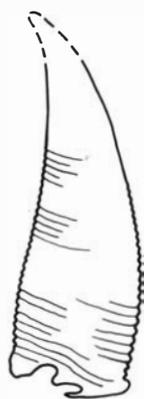




Trimeroceras
cylindricum



Trimeroceras
bulbosum



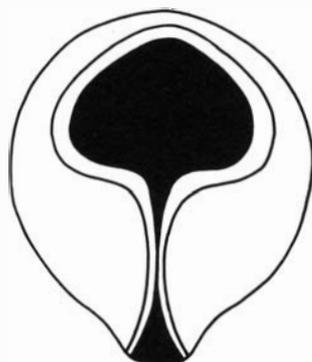
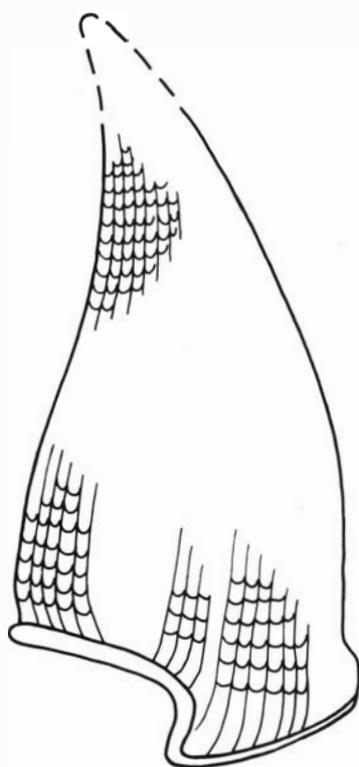
Pentameroceras
facula



Pentameroceras
mirum



Jeppssonoceras
concentratum



Clathroceras
plicatum

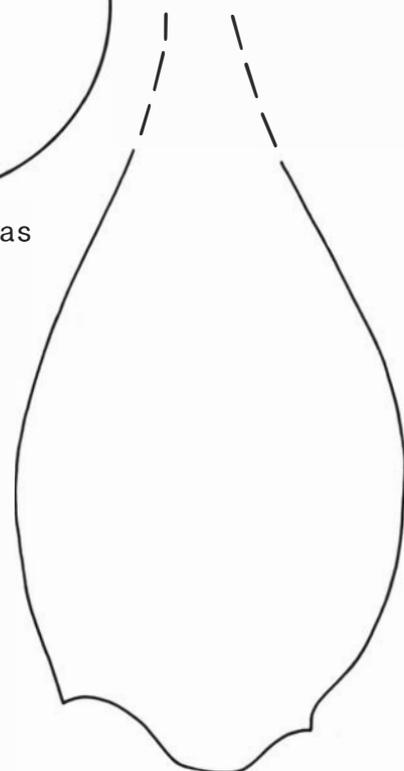




Fig. 29. *Trimeroceras cylindricum* (Barrande), $\times 1.5$. □A, B, C and D. Dorsal, lateral, ventral and apertural views of RM Mo 56219; Mannegårde 1. □E. Apertural view of RM Mo 56218; Mannegårde 1. □F. Specimen cut dorsoventrally along the long axis. The white arrows indicate the reinforcement posterior to the hyponomic opening, RM Mo 56226; Sandarve kulle (see also Fig. 15B). □G. Specimen with the phragmocone and posterior part of the body chamber cut dorsoventrally along the long axis, RM Mo 57423; Tänglings hällar 1 (see also Fig. 15A). □H. Lateral view of RM Mo 56990; Parish of Lye. □I. Apertural view of RM Mo 56512; Stockviks kanal (see also Fig. 17).

Hemse Beds. Bringewoodian or early Leintwardinian, Ludlow. Stockviks kanal. Hamra Beds, Whitcliffian, Ludlow.

Trimeroceras bulbosum n. sp.

Figs. 14, 24, 28, 30A–O

Synonymy. – □ *Gomphoceras* sp. – Neben & Krueger (1973, Pl. 104:3–4).

Derivation of name. – Latin *bulbosus*, bulb-shaped, referring to the bulbous outline of the shell.

Holotype. – RM Mo 56552.

Type stratum. – Slite Beds, unit g. Wenlock.

Type locality. – Samsugns 1, Gotland, Sweden.

Fig. 30. *Trimeroceras bulbosum* n. sp., $\times 1.2$. □A, B, C and D. Dorsal, lateral, ventral and apertural views of the holotype, RM Mo 56552; Samsugns 1 (see also Fig. 6D). □E and F. Apertural and ventral views of RM Mo 56501; Samsugns 1. □G. Cut specimen with truncated phragmocone. Note the reinforcement posterior to the sinuses, RM Mo 152777; Djupvik (see also Fig. 14A). □H. Cut specimen probably with truncated phragmocone, RM Mo 57164; Samsugns 1. □I. Cut specimen with partly truncated phragmocone. The septum of truncation is the second last preserved and is more curved than the last, RM Mo 56618; Djupvik, (see also Fig. 14C). □J. Cut specimen with fairly complete phragmocone. No identifiable septum of truncation, RM Mo 56348; Samsugns 1. □K. Oblique apertural part of silicified body chamber. Note the growth of the lateral lobes, SGU Type 1213; Möllbos 1 (see also Fig. 6C). □L. Inside of the ventral side of the body chamber of a silicified specimen. Note the reinforcement around the hyponomic opening, SGU Type 1213. □M. Ventral side of a silicified specimen. The white arrow indicates the beginning of two dorsal lobes, SGU Type 4000; Möllbos 1 (see also Fig. 24). □N. Apertural area of the same specimen as in M (see also Fig. 6B). □O. Apertural view showing the early growth of the dorsal lobes, RM Mo 56559; Djupvik.

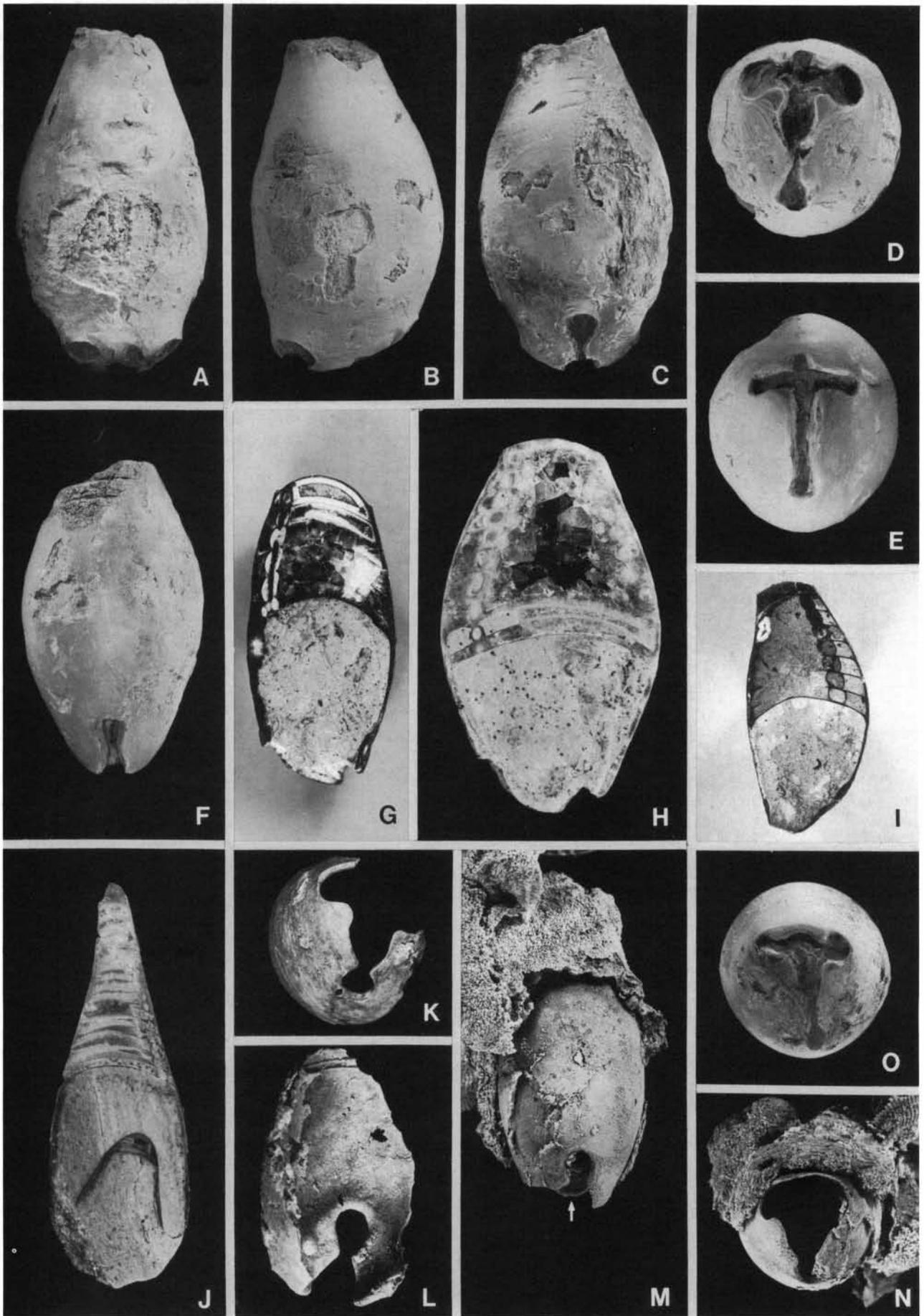


Table 3. *Trimeroceras bulbosum* n. sp., dimensions in mm. Regarding specimens marked with +, see the description. Specimens marked with an asterisk are also illustrated in Stridsberg 1981a, Figs. 1 and 4.

Specimen No	Illustration	LT	LBC	H	W
RM Mo 56552 (holotype)	Fig. 30A–D	52		29.6	29.8 +
RM Mo 56278		35	19.2	20.5	18.0
RM Mo 56279		28		16.2	
RM Mo 56280		58		(24)	22.9
RM Mo 56281	Fig. 14B	47	20.7		18.5
RM Mo 56282		35			
RM Mo 56348	Fig. 30J	62		22.8	22.6
RM Mo 56501	Fig. 30E–F	49		32.2	28.6
RM Mo 56559	Fig. 30O	51		26.7	26.0 +
RM Mo 56616		36		18.8	20.4 +
RM Mo 56617		28		16.2	16.8 +
RM Mo 56618	Fig. 30I	38	20.1	18.4	20.0 +
RM Mo 57078		47	(26)	(30)	(25)
RM Mo 57164	Fig. 30H	58	27.8	33.4	(30)
RM Mo 152777	Fig. 30G	46	(27)	22.1	22.8 +
SGU Type 1213*	Fig. 30K–L				+
SGU Type 1214*					+
SGU Type 3998					+
SGU Type 3999		40			
SGU Type 4000	Fig. 30M–N	50		(23)	23.3 (+)

Material. – Twenty specimens from Gotland; RM Mo 56278, Mo 56279, Mo 56280, Mo 56281, Mo 56282, Mo 56348, Mo 56501, Mo 56552, Mo 56559, Mo 56616, Mo 56617, Mo 56618, Mo 57078, Mo 57164 and Mo 152777 at SMNH, Stockholm and SGU Type 1213, 1214, 3998, 3999 and 4000 as SGU, Uppsala, Sweden. Most specimens are mature.

Diagnosis. – A species of *Trimeroceras* with a circular, almost straight, primary endogastric and, later in ontogeny, exogastric brevicone. In mature specimens there is a contracted and occasionally constricted aperture with two lateral lobes, almost as wide as half the diameter of the body chamber, which close the ventral half of the opening. Two dorsal and two ventrolateral lobes divide the apertural opening in an almost four-leaf clover pattern. Empty, almost nummuloidal, siphuncle.

Description. – Slender circular endogastric phragmocone which turns exogastric in the last quarter of its total length (Fig. 30G). The siphuncle, about 2.5 mm thick, is almost nummuloidal and lacks deposits in the investigated material. It is situated 1/6 of the shell diameter from the ventral shell surface and follows the curvature of this, except in the two last formed chambers where it lies perpendicular to the curved septa, resulting in a slightly dorsal direction of the siphuncle. The average distance between septa is 2.4 mm, except in the last chamber where the corresponding distance is about half this distance.

The body chamber has its greatest width at the last septum and the proportion between width and length is nearly 1:1 (Fig. 30G–I). Towards the aperture, the body chamber decreases steadily in width and the conic shape is obvious in length section. Along the peristome the shell is reinforced and on a silicified specimen, SGU Type 1213 (Fig. 30L and Stridsberg 1981a, Fig. 4), it can be observed how the reinforcement starts at the very bottom of the lateral

lobes, about 5 mm behind the peristome. In the silicified specimens, SGU Type 3999 and 4000 (Fig. 30M), this reinforcement can also be observed with an equal extension on the dorsal side of the body chamber, while towards the peristome it becomes thinner.

The apertural opening is primarily restricted by two lateral lobes with a width of about half the diameter of the shell. These lobes almost demarcate the ventro-anteriorly situated hyponomic opening. Secondly two dorsal and two ventrolateral lobes, 1.5–2.5 mm wide and up to 3 mm long, divide the apertural opening into four more or less circular areas, one central, two lateral and one almost ventral (Fig. 6). The latter, in fact the dorsal part of the hyponomic sinus, is diminished on many specimens and in extreme cases, e.g. on the specimen RM Mo 56501, it is absent (Fig. 30E).

In two of the specimens, RM Mo 56618 (Fig. 30I) and RM Mo 152777 (Fig. 30G), cut dorsoventrally along the long axis for studies of the internal structure, approximately the eighth septum from the body chamber has a remarkable curvature on the dorsal side. The angle between septum and outer wall is smaller than on other septa, and this results in a smooth continuation from septum to outer wall. Furthermore, this septum is notably thicker in both specimens, as well as in specimen RM Mo 56278. Two of these specimens seem to be truncated and the third in the process of truncation at this particular septum. In one specimen, RM Mo 57164 (Fig. 30H), an eventual truncation took place at the eleventh septum from the body chamber.

Apart from truncated specimens, most shells have a poorly preserved apical part. Three specimens, however, exhibit an almost complete, dorsally rather straight, phragmocone.

Discussion. – The investigated Gotland material varies considerably in size but *T. bulbosum* does not show the two well separated groups typical of most other dimorphic oncocerids from Gotland. The largest specimens are twice the size of the smallest ones, but many intermediate sizes are found (Fig. 7).

Apart from the variation in size, the specimens can be divided in two morphologic groups. One group (Fig. 30A–D, G, I, K–N and O), indicated with a + in Table 3, has a fairly straight dorsal side of the body chamber and an expansion of the hyponomic sinus immediately ventral to the ventrolateral lobes. The remaining specimens have a more convex dorsal side of the body chamber (Fig. 30E–F, H and J) and less developed dorsal and ventrolateral lobes, resulting in a smoother dorsal peristome and a wider hyponomic sinus. Within this group some specimens have a wide apertural opening, giving the impression of a possible immature stage. This is pronounced on one of the silicified specimens, SGU Type 3999, but in the same specimen the ventrolateral lobes are fully grown (Fig. 6C). This intermediate specimen indicates a connection between the two types of aperture. Furthermore, on one of the silicified specimens, SGU Type 4000 (Fig. 30M), a small inward bend on the dorsal peristome indicates the beginning of two dorsal lobes. The ventrolateral lobes are already developed and consequently this is an example of an immature specimen, belonging to the group with the expanded hyponomic sinus, even if the present appearance resembles the group with a wide apertural opening.

Neben & Krueger (1973, Pl 104:3–4) illustrated a specimen from an erratic boulder found in northern Germany or in the Netherlands, but originating from the Baltic area. They classified the specimen as *Gomphoceras* sp. but from the two photographs, a lateral and an apertural view, it is obviously a well preserved specimen of *Trimeroceras bulbosum*.

Comparison. – In his description of *Trimeroceras*, Hyatt (1884, p. 278) used *Gomphoceras staurostoma* Barrande (Barrande 1865, Pl. 73:1–5) as an example of a specimen with two lateral sinuses in addition to a median sinus. This species has a certain resemblance to *Trimeroceras bulbosum* but the latter lacks the straight and symmetric phragmocone and the more or less spherical form of the anterior end. Furthermore, the hyponomic sinus is drop-shaped in *T. bulbosum*, and circular in *T. staurostoma*. In conclusion, I believe that *T. bulbosum* and *T. staurostoma* are two distinct species.

In his description of *Eotrimeroceras*, Foerste (1929, p. 378) stated that there was a single typical species of *Trimeroceras* on Gotland. He continued 'there are also three species which might be described as species of *Mandaloceras* in which the aperture is T-shaped'. He went on to describe the apertural shape and compared it with *Eotrimeroceras*. Finally he considered whether the 'swellings in that part of the narrowly contracted division of the aperture which is nearest the dorsal expansion of the aperture' could be regarded as incipient lobes, suggesting how *Pentameroceras* might have originated.

There is no information about which Swedish material Foerste discussed but, according to his description, it must have been specimens of *T. bulbosum*, presumably the 'single typical species of *Trimeroceras*' was the specimen RM Mo 56501 (Fig. 30E–F).

Regarding the suggestion as to how *Pentameroceras* originated I cannot agree with Foerste, since the 'swellings', the ventro-lateral lobes on *T. bulbosum*, are established secondarily on the lateral lobes, not primarily as on *Pentameroceras*.

Dzik (1984, p. 63) discussed a species from the Halla Beds of Gotland, 'showing variability in aperture constriction from *Trimeroceras* to *Pentameroceras* shape'. However, he did not describe or illustrate the species, so the question is whether he referred to the same species as Foerste or not.

Occurrence. – Sweden, Gotland: Samsugns 1 and Stora Vede 1. Slite Beds, unit g, Wenlock. Möllbös 1. Halla Beds, unit b, Wenlock. Djupvik. Mulde Beds, lower part, Wenlock.

Pentameroceras Hyatt 1884

Type species. – *Pentameroceras mirum* (Barrande 1865). (Original combination: *Gomphoceras mirum* Barrande 1865.)

Emended diagnosis. – Circular or slightly compressed straight or exogastric phragmocone. Inflated body chamber with a contracted, visored aperture, having mid-dorsal, hyponomic and two pairs of lateral sinuses. Empty slender siphuncle. Smooth or transversely annulated external shell surface.

Species. – *Pentameroceras mirum* (Barrande 1865), *P. rarus* Parks 1915, *P. byronense* Foerste 1930, *P. cumingsi* Flower 1943, and *P. facula* n. sp.

Pentameroceras mirum (Barrande 1865)

Figs. 16, 18, 21, 23E–F, 25C, 28, 31A–S

Synonymy. – □ *Gomphoceras mirum* Barr. – Barrande (1865, Pl. 82:19, 20–25, Pl. 91:10–14). □? *Gomphoceras mirum* Barr. – Barrande (1865, Pl. 82:17, Pl. 91:7, 8–9). □ *Gomphoceras mirum* Barr. – Barrande (1867, pp. 319–320). □ *Gomphoceras mirum* Barr. – Barrande (1877, Pl. 478:12). □ *Pentameroceras mirum* (Barrande). – Hyatt (1884, p. 278). □ *Pentameroceras mirum* (Barrande). – Newell (1888, p. 483). □ *Pentameroceras mirum* (Barrande). – Foerste (1926, pp. 356–357, Pl. 50:6 A–C). □ *Pentameroceras mirum* (Barrande). – Foerste (1929, p. 379). □ *Pentameroceras mirum* (Barrande). – Foerste (1930, pp. 116, 117). □ *Pentameroceras mirum* (Barrande). – Flower (1943, p. 89). □ *Pentameroceras depressum* (Flower). – Flower (1943, p. 90). □ *Pentameroceras mirum* (Barrande). – Sweet (1964, pp. K 297, K 299).

Lectotype. – Specimen illustrated by Barrande (1865, Pl. 91:10–14), L 368, selected by Flower (1943, p. 90).

Type stratum. – Probably Kopanina F (lower part), Ludlow.

Type locality. – Hinter-Kopanina, Czechoslovakia.

Material. – Three specimens from Bohemia, L 368, L 9233 and L 9234 at Narodni Muzeum, Prague, Czechoslovakia. Eighty-three specimens from Gotland, RM Mo 56399, Mo 56400–56401, Mo 56420, Mo 56423–56424, Mo 56702, Mo 56704–56717, Mo 56721–56724, Mo 56727–56730, Mo 56740–56744, Mo 56751, Mo 56760, Mo 56762–56768, Mo 56774, Mo 56781–56782, Mo 56784, Mo 56813–56819, Mo 56970–56974, Mo 57127, Mo 57253, Mo 57424–57439 and Mo 154004–154008 at SMNH, Stockholm and SGU Type 3997 at SGU, Uppsala, Sweden. Most specimens are mature.

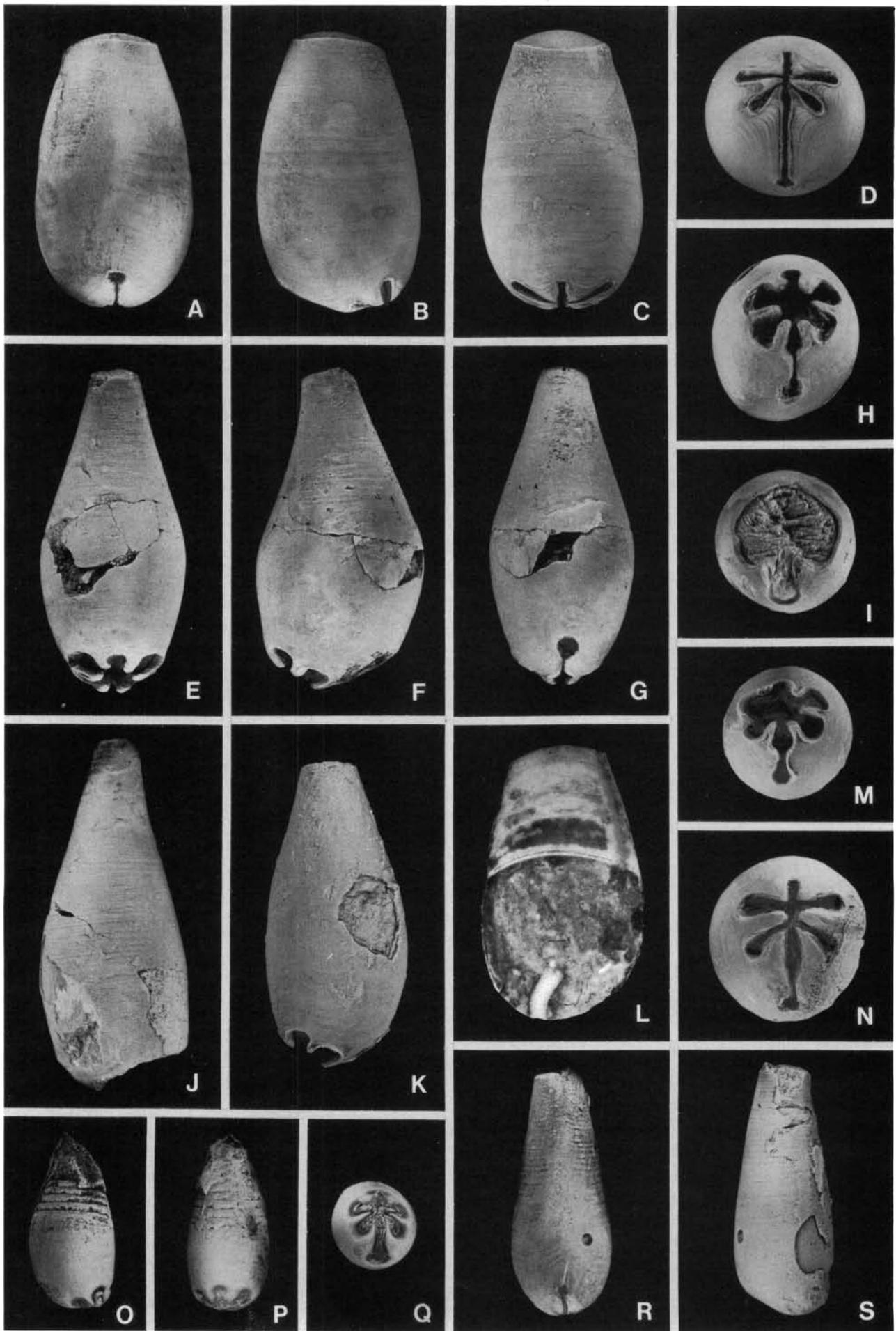
Diagnosis. – A species of *Pentameroceras* with a circular, or slightly compressed, exogastric brevicone. Mature specimens with contracted aperture, consisting of one dorsal, two lateral and two ventrolateral sinuses. Hyponomic sinus sometimes wide in its dorsal part while the rest is very narrow. Slender, empty siphuncle.

Description. – Circular or occasionally somewhat compressed, slightly exogastric phragmocone. The shape of the conch ranges from fairly stout to very slender. The former has a notably shorter phragmocone.

The slender, empty siphuncle, 1.5 mm wide as a maximum, is situated immediately inside the ventral shell wall, except in the last chambers, where it turns slightly dorsally. Average distance between septa is about 1.3 mm, except in the last chamber where the distance is about half this distance.

The anterior half of the body chamber is almost hemispherical and the proportion between height and length of body chamber is close to 1:1.

Mature specimens of *Pentameroceras mirum* have a characteristic apertural shape, consisting of two dorsal, two lateral and two ventral lobes, all very narrow. The length of the lobes is about 4–4.5 mm on macroconchs and about 2 mm



on microconchs. On immature specimens the apertural growth pattern can be observed. Primarily, the ventral lobes are formed in the immature, almost circular apertural opening. Secondly the lateral lobes start growing, later followed by the dorsal lobes (Fig. 31I). The growth pattern of the lobes is further discussed in the chapter 'Apertural growth'.

The dorsal, lateral and ventrolateral sinuses, as well as the hyponomic sinus, are usually very narrow slits (Fig. 31D). On some specimens, however, all sinuses, including the dorsal half of the hyponomic sinus, are very wide and almost circular (Figs. 31H and M). These specimens have the widest part of the sinuses close to the prior peristome.

On well preserved specimens of *Pentameroceras mirum* an external ridge can be observed along the edge of all sinuses, including the hyponomic sinus and the hyponomic opening (Fig. 31M). However, this is often worn away completely and only a close study can reveal the former existence of this external reinforcement, and then only in specimens that are reasonably well preserved.

The hyponomic opening is anteroventral and circular on all specimens, including those with narrow sinuses as well as those with wide and circular sinuses. The diameter of the hyponomic opening is 1–2 mm, depending on the size of the specimen (Figs. 31A and G).

In addition to the distinct size dimorphism, illustrated by Barrande (1865), there is a great variation in the conic shape of the phragmocone. Some specimens have a stout phragmocone with slight tapering while other specimens have a more pronounced tapering (Fig. 16A–B). Regarding the degree of tapering all successive stages are present. It is notable that in very stout specimens the phragmocone is broken into almost equal lengths, and the breakage is extraordinarily clean, giving an impression of truncation. Rough calculations indicate that the volume in the possibly truncated stout phragmocone is comparable to the volume of the almost complete, but slender phragmocone. Compared specimens have similarly sized body chambers. The consequence of a truncation is that specimens with stout phragmocones could maintain the same buoyancy by truncation as specimens with slender phragmocones.

Many of the Gotland specimens have very well preserved growth lines. On specimen RM Mo 154005 (Fig. 31A–D), very thin growth lines are measured and the average distance is 50 micrometres (Fig. 18). These growth lines demonstrate very well the growth of the lobes and the apertural

shape when the lobes started to develop. Comparisons with immature specimens confirm the identification of mature and immature specimens in the Gotland material.

Internal reinforcements on *Pentameroceras mirum* are found along the edge of all lobes except the dorsal ones. Here the reinforcement follows the former peristome before the development of the dorsal lobes.

Two specimens have a notably swollen last chamber, resulting in an extra wide beginning of the body chamber (Fig. 21) (see p. 20).

Discussion. – As previously mentioned, *Pentameroceras mirum* has a distinct size dimorphism. The Barrande material of *Gomphoceras mirum* consists of three large and three small specimens, of which I only accept one large and two small specimens within the species. One of these small specimens was chosen as lectotype by Flower (1943, p. 90). Flower also suggested that the specimen on Pl. 82:20–25 (Barrande 1865) was another species because 'the section is markedly depressed ...' (Flower 1943, p. 90), and proposed the name *Pentameroceras depressum* for this species. However, the divergence between the lectotype of *P. mirum* and Flower's *P. depressum* is due to the fact that the latter is an internal mould and has depressions in the place of the reinforcements. Furthermore, Flower tends to exclude the specimens on Pl. 82:17–20 from *P. mirum* or *P. depressum* because the specimens are too small. Unfortunately there must be a misunderstanding because the size of Flower's *P. depressum* is exactly the same. As a matter of fact, Figs. 20 and 21 on Barrande's Pl. 82 actually show the same specimen, but at two different magnifications as mentioned in the figure caption. Thus there is no need to establish the species *P. depressum*. The size variation within *P. mirum* is further discussed in the chapter 'Dimorphism' (Fig. 10).

The three specimens on Pl. 82:17, Pl. 91:7 and Pl. 91:8–9 (Barrande 1865) all have a very poorly preserved apertural area and therefore I prefer to classify them as possibly *Pentameroceras mirum*.

Newell (1888) described a collection of *Pentameroceras mirum* from Indiana, U.S.A., consisting of 'several casts of the living chamber with a number of closed chambers attached and without the shell'. He stated that the American specimens were similar to those collected in Bohemia but that the dorsal side of the specimens was not as flat, nor was the ventral side as round as Barrande's specimens on Pl. 82 (Barrande 1865). The specimens described by Newell were, instead intermediate between the specimens on Barrande's Pl. 82 and Pl. 91. Newell's statement is very interesting, as the American specimens thus correspond very well to the material from Gotland in the general shape of the shell, even if the Gotland material has a wide variation.

Foerste (1929, p. 379) gives the information that there were four species of *Pentameroceras* on Gotland. He did not give the source of this information but presumably it was based on the collection at the Museum of Natural History in Stockholm, i.e. the material described here. Lindström, who started to sort out this material at the end of the 19th century, put labels with his new, but never published names together with the specimens. These labels show that Lindström considered different growth stages of *Pentameroceras mirum* to be different species. Lindström's interpretation

Fig. 31. *Pentameroceras mirum* (Barrande), $\times 1.8$. □A, B, C and D. Ventral, lateral, dorsal and apertural views of RM Mo 154005; Mannegårde 1 (see also Fig. 18). □E, F, G and H. Dorsal, lateral, ventral and apertural views of RM Mo 56399; Norrvange kanal. □I and J. Apertural and lateral views of an immature specimen, RM Mo 56813; Samsugns 1. □K. Lateral view of RM Mo 57253; Samsugns 1. □L. Specimen cut dorsoventrally along the long axis, RM Mo 56705; Mannegårde 1. □M. Apertural area of the same specimen as in K. Note the ridge along the edge of all sinuses including the hyponomic opening. □N. Apertural view of RM Mo 56420; Samsugns 1. □O, P and Q. Lateral, dorsal and apertural views of a specimen with no shell preserved. Note the depressions around the sinuses, indicating the place of the reinforcement. Periphraet visible in O, RM Mo 56730; the area of Östergarn. □R and S. Ventral and lateral views of a specimen with a bore hole, RM Mo 56763; Mannegårde 1 (see also Fig. 23E).

Table 4. *Pentameroceras mirum* (Barrande), dimensions in mm. The first group comprises macroconchs and the second microconchs. Only the best preserved specimens are included. Illustrations marked with an asterisk are from Barrande (1865).

Specimen No	Illustration	LT	LBC	H	W
L 368 (lectotype)	Pl. 91:10–14*	31	(22)	18.8	16.8
RM Mo 56399	Fig. 31E–H	34		16.8	(16)
RM Mo 56400		29		16.2	(14)
RM Mo 56420	Fig. 31N			17.3	17.0
RM Mo 56712		29		16.4	15.5
RM Mo 56713		31		15.7	14.6
RM Mo 56714		32		14.8	14.4
RM Mo 154004		31		16.5	15.6
RM Mo 154005	Fig. 31A–D	29		17.0	16.5
RM Mo 154006		29		17.1	16.4
RM Mo 154007		26		17.1	16.3
RM Mo 154008		33		17.0	16.6
L 9234	Pl. 82:20–25	17		8.3	9.0
L 9233	Pl. 82:19*	20		8.6	
RM Mo 56728			12.3	12.5	11.8
RM Mo 56729			11.9	11.6	10.9
RM Mo 56730	Fig. 31O–Q	18		8.9	8.6
RM Mo 56751		21		10.4	10.2
RM Mo 56760		23		12.2	12.3
RM Mo 56761		29		11.1	11.4
RM Mo 56762		27		10.9	10.9
RM Mo 56763	Fig. 31R–S	26		10.3	10.5
RM Mo 56766		25		10.6	11.0
RM Mo 56781		28		11.5	11.3
RM Mo 56782				11.1	11.1
RM Mo 56784		20		11.7	12.1

was evidently accepted by Foerste (1929, p. 379), who suggested how *Septameroceras* might have originated from one of the Gotland 'species' of *Pentameroceras*.

Comparison. – *Pentameroceras rarum*, Parks 1915, is very similar to *P. mirum* apart from the reinforcement on the dorsal side of the body chamber. The reinforcement appears to be thicker and more widespread than that of *P. mirum*. The holotype of *P. rarum*, no. 324 S of the Royal Ontario Museum of Paleontology, consists only of a steinkern of the body chamber with outlines of the five sinuses as well as the hyponomic sinus. The dimensions of this body chamber are very close to those of the lectotype of *P. mirum*, but the lack of information on the shape of the missing phragmocone makes it impossible to decide the taxonomic value, if any, of the difference in the reinforcement.

Pentameroceras byronense, Foerste 1930, also has a holotype which consists of a steinkern of the body chamber. This species has a more conic body chamber towards the posterior end than *P. mirum*. Furthermore, the hyponomic sinus of *P. byronense* is much shorter and the apertural area is in general smaller.

Occurrence. – Czechoslovakia: Hinter-Kopanina, Lochkov. Kopanina F, Ludlow. Sweden, Gotland: Norrvange kanal. Slite Beds, Wenlock. Samsugns l. Slite Beds, unit g, Wenlock. Hageby träskbacke, Linde klint, Mannegårde l, Petesviken, Sandarve kulle, Tänglings hällar l. Hemse Beds, Ludlow. U.S.A., Indiana: Delphi. Guelph, Ludlow. Ohio: Guelph, Ludlow.

Pentameroceras facula n.sp.

Figs. 28, 32A–K

Derivation of name. – Latin *facula*, diminutive of *fax*, torch, referring to the torch-like outline.

Holotype. – RM Mo 56453.

Type stratum. – Hemse Beds, Ludlow.

Type locality. – Tänglings hällar l, Gotland, Sweden.

Material. – Six specimens from Gotland; RM Mo 56273, Mo 56453, Mo 56464, Mo 56783, Mo 56785 and Mo 154003 at SMNH, Stockholm, Sweden. Four specimens are mature and two specimens, Mo 56783 and Mo 56785, are immature.

Diagnosis. – A species of *Pentameroceras* with a circular exogastric slender brevicone, having transverse surficial annulations. In mature specimens with a contracted aperture, consisting of two pairs of lateral sinuses, one dorsal and one hyponomic sinus. Slender empty siphuncle, situated close to the ventral wall.

Description. – Straight or exogastric, circular phragmocone and almost straight body chamber. The shell surface consists of transverse annulations, very fine at the apical end with a width of less than 0.4 mm. The annulations, sometimes wrinkled, grow thicker towards the anterior end and have a width of about 1.5 mm at the mid body chamber. On the ventral side the typical V-shape in the annulations, due to the hyponomic sinus, can be observed all the way from the apical end (Fig. 32A). The average distance between septa in the long slender phragmocone is around 0.65 mm at the apical end and slightly more than 1 mm in the anterior part. The 1 mm thick empty siphuncle is situated close to the ventral wall.

The proportion between the length and width of body chamber is almost 2:1. Thus *Pentameroceras facula* is exceptional among the Gotland oncocerids, whose proportions usually are closer to 1:1.

Mature specimens of *P. facula* have an apertural shape consisting of two dorsal, two lateral and two ventrolateral lobes. The hyponomic sinus, situated between the ventrolateral lobes, is 1–2 mm wide and ends in the hyponomic opening which points anteroventrally and is 2–2.5 mm in diameter.

The development of the lobes can be observed on the two immature specimens. On specimen RM Mo 56783 the beginning of the ventrolateral lobes indicates an early stage of apertural closing (Fig. 32I), and there are still no signs of the lateral lobes. Unfortunately none of the six investigated specimens has a complete dorsal sinus preserved, but remains of one of the dorsal lobes on two specimens, RM Mo 56453 (Fig. 32H) and RM Mo 154003, confirm the existence of a dorsal sinus.

In addition to external reinforcement in the shape of transverse annulations, internal reinforcements appear around the hyponomic opening, hyponomic sinus and the lateral sinuses. Because of poor preservation of the specimens preserved as internal moulds, further details regarding the internal reinforcements cannot be observed.

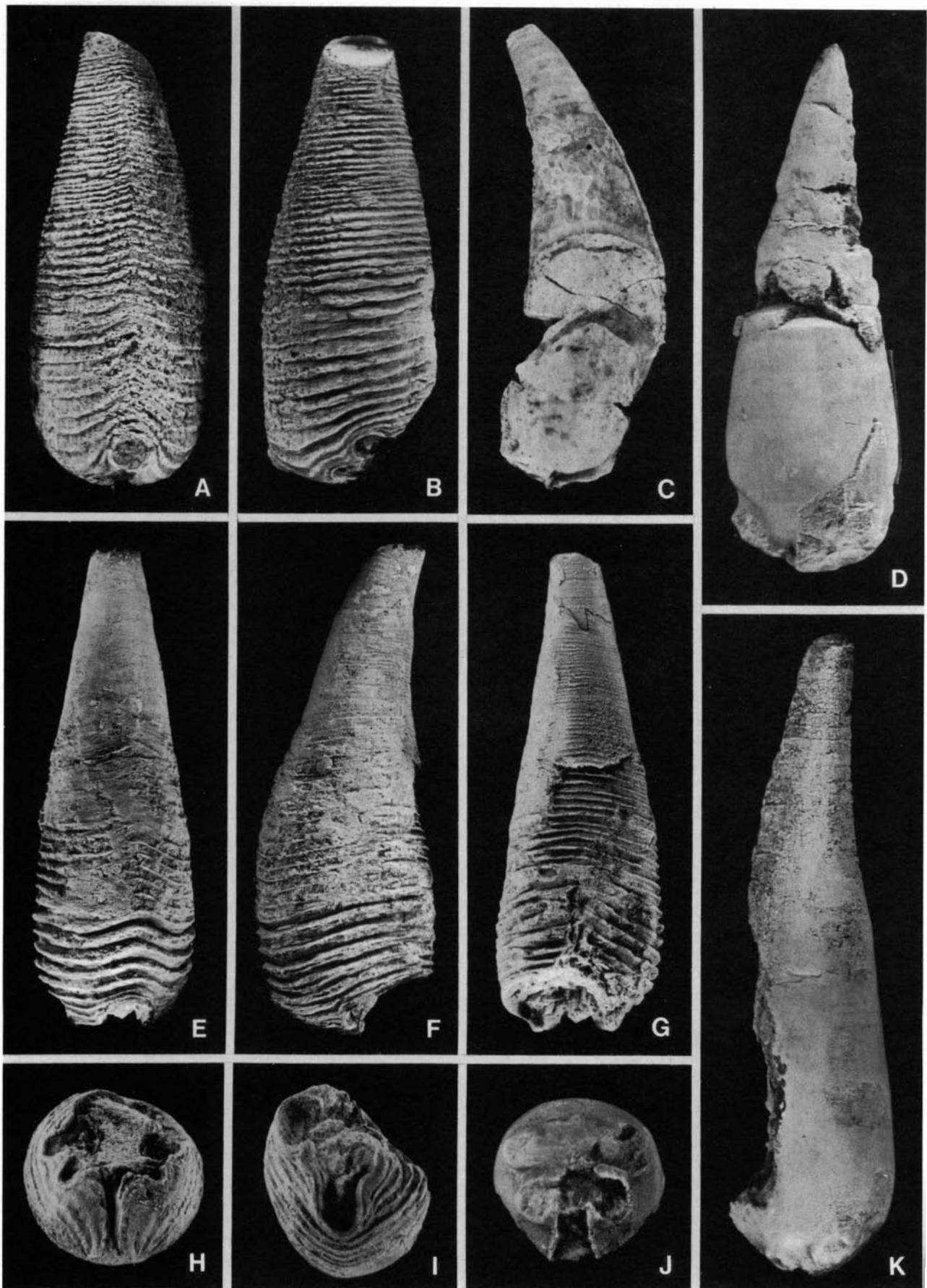


Fig. 32. *Pentameroceras facula* n. sp., $\times 2$. □A and B. Ventral and lateral views of the holotype, RM Mo 56453; Tänglings hällar 1. □C. Specimen cut dorsoventrally along the long axis, RM Mo 56785; Norrvange kanal. □D. Lateral view of a specimen with no shell preserved. Note the imprint of the reinforcement around the hyponomic opening on the left side of the body chamber, RM Mo 154003; Parish of Hörsne. □E, F and G. Ventral, lateral and dorsal views of RM Mo 56783; Norrvange kanal. □H. Apertural view of the holotype, RM Mo 56453; Tänglings hällar 1. □I. Apertural view of the same specimen as in E, F and G. □J and K. Apertural and lateral views of a specimen with no shell preserved, RM Mo 56273; Kanalen.

Table 5. *Pentameroceras facula* n. sp., dimensions in mm.

Specimen No	Illustration	LT	LBC	H	W
RM Mo 56453 (holotype)	Fig. 32A–C and H	(42)		16.4	16.4
RM Mo 56273	Fig. 32J–K	59	30.1		15.3
RM Mo 56464			(19)	(14)	13.8
RM Mo 56783	Fig. 32E–G and I	45		(16)	(15)
RM Mo 56785		43	23.1		
RM Mo 154003	Fig. 32D	49	23.0	15.5	14.4

Discussion. – The Gotland material consists of four specimens with the shell and the transverse annulations well preserved and two internal moulds. All specimens comprise a body chamber and most of the phragmocone. Two of the specimens with annulations are immature, and thus give valuable information concerning the early ontogenetic stages.

The typical size dimorphism among the Gotland oncocerids is not very pronounced within *Pentameroceras facula*. There is a size variation, especially between the holotype and the similarly mature specimen Mo 56464, but the total number of specimens is too small for any reliable statements.

Comparison. – Apart from the transverse annulation the general outline of *Pentameroceras facula* is rather similar to that of *P. mirum*. *P. facula*, however, has its apertural opening situated considerably more dorsally than *P. mirum* and has a considerably bigger body chamber. These facts in combination with the long, slender phragmocone of *P. facula*, a hindrance when swimming, might indicate a mode of life different from that of *P. mirum*. Regarding the possible truncation of the apical end of the phragmocone in *P. mirum*, there are no signs of a similar course of events in *P. facula*.

Although there are similarities between *P. mirum* and *P. facula*, such as the apertural configuration, siphuncle and the shape of the shell, *P. facula* possesses morphological qualities that indicate that they are probably not very closely related.

Occurrence. – Sweden, Gotland: Kanalen. Högkint or Tofta Beds, Wenlock. Norrvange kanal. Slite Beds, Wenlock. 'Parish of Hörsne'. Halla Beds, Wenlock. Tänglings hällar 1. Hemse Beds, Ludlow.

Genus *Inversoceras* Hedström 1917

Type species. – *Inversoceras perversum* (Barrande 1865). (Original combination: *Phragmoceras perversum*.)

Diagnosis. – See Sweet (1964, K 298).

Species. – *Inversoceras perversum* (Barrande 1865).

Inversoceras perversum (Barrande 1865)

Diagnosis. – A species of *Inversoceras* with slightly compressed, slender cyrtoconic exogastric brevicone, in mature specimens with contracted visored aperture, sloping adapically from the dorsal to the ventral side. Aperture opening re-

stricted by two anterior and one broad dorsal lappet, separated by lateral sinuses and a V-shaped emargination on each side. Hyponomic opening spout-like.

Discussion. – In a letter to Prof. Bronn in Heidelberg, Barrande (1854, p. 10–11) discussed the problems of separating *Gomphoceras* and *Phragmoceras*. He had found specimens typical of *Phragmoceras* except for having, as he described it, a dorsal siphuncle. Barrande suggested that this confusing species was transitional between the two genera but, nevertheless, he put it in the genus *Phragmoceras* and named it *P. perversum*. No specimen was illustrated in this publication, but in a later publication (Barrande 1865) 12 specimens were illustrated.

The specimen in Pl. 53:1–6 (Barrande 1865) is selected here as lectotype for *Inversoceras perversum* (Barrande 1854). The specimen is well preserved in most aspects. In the material described by Barrande two groups could be distinguished, based on the curvature of the shell, and Barrande therefore divided the species into two varieties, *Phragmoceras perversum* var. *falciformis* and *P. perversum* var. *subrecta*.

Foerste (1926, p. 355) considered that Barrande's specimens of *Phragmoceras perversum* represented four species and introduced three new names. However, Foerste did not pay any attention to the fact that two varieties of *P. perversum* had been named by Barrande. Therefore one of the well preserved specimens of *P. perversum* var. *falciformis* was given a new species name, *Inversoceras percurvatum* Foerste, and the other two new species *I. constrictum* Foerste and *I. barrandei* Foerste were based on two internal moulds of *P. perversum* var. *subrecta* and *P. perversum* var. *falciformis* respectively. The two species *I. perversum* and *I. constrictum* were characterized by an almost straight shell while *I. percurvatum* and *I. barrandei* were distinctly arcuate. *I. constrictum* and *I. barrandei* differed from *I. perversum* and *I. percurvatum* in the same respect, namely the 'constriction' of the base of the dorsal collar. This constriction, however, does not reflect the shell surface as supposed by Foerste, but is the internal mould of the reinforcement due to the apertural growth, as illustrated in Fig. 33I. The influence of reinforcements on internal moulds has previously been discussed (Stridsberg 1981a, p. 273).

Consequently the two names *Inversoceras constrictum* and *I. barrandei* are synonymous to *I. p. perversum* and *I. p. falciformis* respectively. *I. percurvatum* is another synonym for *I. p. falciformis*.

Foerste's action with *Inversoceras perversum* is also discussed on p. 12.

Inversoceras perversum perversum (Barrande 1865)

Figs. 28, 33A–I

Synonymy. – □ *Phragmoceras perversum* Barr. – Barrande (1854, p. 10–11). □ *Phragmoceras perversum* var. *subrecta* Barr. – Barrande (1865, Pl. 53:1–6, 7–12, 13–14, 24–27, 29–32, Pl. 100:10–13). □? *Phragmoceras perversum* var. *subrecta* Barr. – Barrande (1865, Pl. 53:33, Pl. 100:14–16, 17–19). □ *Phragmoceras perversum* Barr. – Barrande (1867, p. 241–243, 249). □ *Inversoceras perversum* (Barrande). – Hedström (1917, p. 6–

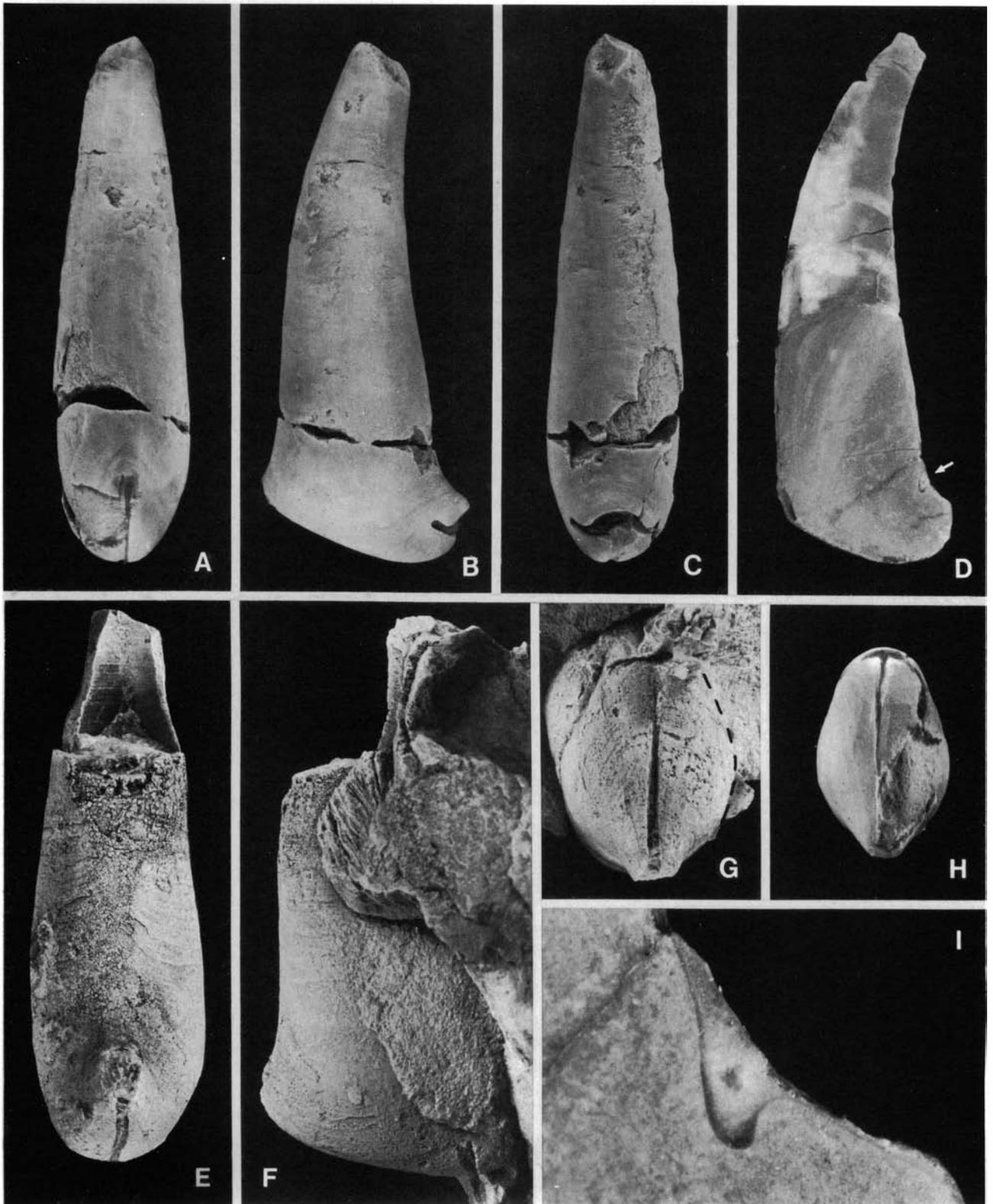


Fig. 33. *Inversoceras perversum perversum* (Barrande), $\times 2$ except I. □A, B and C. Ventral, lateral and dorsal views of RM Mo 56557; Linde klint. □D. Specimen cut dorsoventrally along the long axis. The siphuncle is partly visible on the left side of the phragmocone. The white arrow indicates the reinforcement posterior to the apertural opening, enlarged in I, RM Mo 56556; Linde klint. □E, F and G. Ventral, lateral and apertural views of a specimen still partly in the matrix. The upper half of E is retouched, RM Mo 156381; Lill Rone l. □H. Apertural view of the same specimen as in A, B and C. □I. The reinforcement indicated by the white arrow in D, $\times 15$.

Table 6. *Inversoceras perversum perversum* (Barrande), dimensions in mm. The dimensions of the Bohemian specimens are calculated from the drawings in Barrande (1865). These illustrations are made in natural size. Illustrations marked with an asterisk are from Barrande (1865).

Specimen No	Illustration	LT	LBC	H	W
L 279 (lectotype)	Pl. 53:1-6*	48		17	15
L 9118	Pl. 53:7-12*	52		16	15
L 280	Pl. 53:13-14*	45		17	15
L 282	Pl. 53:24-27*	(47)		15	12
L 283	Pl. 53:29-32*	56		(21)	19
L 391	Pl. 100:10-13*	45	(21)	15	14
RM Mo 56556	Fig. 33D and I	46		12.8	10.9
RM Mo 56557	Fig. 33A-C and H	46		13.7	11.4
RM Mo 156381	Fig. 33E-G			(19)	14.8

7). □ *Inversoceras perversum* (Barrande), *Inversoceras constrictum* Foerste. – Foerste (1926, p. 355–356, Pl. 35:4 A–D). □ *Inversoceras perversum* (Barrande). – Teichert (1964, p. K 49). □ *Inversoceras perversum* (Barrande). – Sweet (1964, p. K 297–K 299).

Lectotype. – Specimen illustrated by Barrande (1865, Pl. 53:1–6) L 279 selected herein.

Type stratum. – ? Kopanina F.

Type locality. – Kozorz, Czechoslovakia.

Material. – Six specimens from Bohemia; L 279, L 280, L 282, L 283, L 391, and L 9118 at Narodni Muzeum in Prague, Czechoslovakia. Three specimens from Gotland; RM Mo 56556, Mo 56557 and Mo 156381 at SMNH, Stockholm, Sweden. All specimens are mature.

Diagnosis. – A subspecies of *Inversoceras perversum* with a straight body chamber and slightly curved phragmocone. Anterior end oblique and almost flat in lateral view.

Description. – Slightly compressed slender exogastric phragmocone with decreasing curvature towards the anterior end. Slender siphuncle situated fairly close to the shell surface. Space between septa is 1–2 mm. The slightly compressed conic body chamber, occupying slightly less volume than the phragmocone, is almost straight and has its greatest diameter just adapically of the contracted part. The aperture is visored on the dorsal side of the shell and slopes adapically towards the ventral side and the hyponomic opening. The visored apertural opening is restricted by two lateral lobes which grew towards each other and closed the anterior opening during the terminal growth. Finally, two dorsal lappets were formed on the lateral lobes. The slit-like hyponomic sinus is extremely narrow (Fig. 33G–H), less than 1 mm all the way across the anterior end of the shell, and ends in the hyponomic opening situated in a spout-like protrusion. The hyponomic opening is about 1 mm wide and slightly higher.

The posterior side of the apertural opening is formed by a broad lappet which ends laterally with 2 mm long horizontal sinuses. On specimen RM Mo 56557 the fully mature aper-

ture has the shape of the upper half of a circle, 4 mm in diameter, with the lateral sinuses making an 8 mm long bottom line, connected in the middle with the hyponomic sinus (Fig. 33C and H).

Growth lines on the body chamber show that during ontogeny the peristome grew faster on the dorsal rather than the ventral side of the shell. Furthermore, deep V-shaped growth lines on the ventral side indicate that the hyponomic sinus was already developed in juvenile stages.

Discussion. – The selection of a lectotype for *Inversoceras perversum* makes the subspecific name *I. p. perversum* Barrande 1854 a senior synonym for *I. p. var. subrecta*, since the latter name is to be interpreted as of subspecific rank (International Code of Zoological Nomenclature, article 45 e, as emended in 1972).

Concerning the specimens presently referred to *I. p. var. falciformis*, it is possible that the two 'varieties' represent sexual dimorphism, but I have to leave this question open for the time being.

The three specimens illustrated by Barrande (1865) in Pl. 53:33, Pl. 100:14–16 and 17–19 are referred to *P. p. var. subrecta* by Barrande, but as the first two have only the phragmocone preserved and the third specimen has a distinctly different general outline, I prefer not to include them in the subspecies *Inversoceras perversum perversum*.

In 1860 Prof. Angelin at the Museum of Natural History, Stockholm, informed Barrande that two specimens of the genus *Gomphoceras* had been found on Gotland. According to Angelin's description of the aperture and siphuncle, Barrande assumed (1867, p. 249) that they belonged to his *Phragmoceras perversum*. It is most likely that the two Gotland specimens in Figs. 33A–C and 33D, described here, are the same as those mentioned by Angelin.

A third Gotland specimen (Fig. 33E–G) was collected in 1983 at Lill Rone and this was notably larger than the two previous ones found.

The Bohemian material too is divided into two groups on the basis of size. Unfortunately the limited material includes only one representative of the larger form (Barrande 1865, Pl. 53:29–32). The three Gotland specimens are more slender than those from Bohemia and it might be the case that the Gotland population was made up of smaller individuals than the Bohemian.

Size dimorphism is typical for most oncocerids from Gotland, and with regards to *Inversoceras*, Foerste suggested sexual dimorphism within this genus (1926, p. 356). As described above, this dimorphism was based, not on size variation, but on the two varieties of *Phragmoceras perversum* as established by Barrande.

Comparison. – *Inversoceras perversum* var. *falciformis* (Barrande 1865) is rather like *I. p. perversum* in regard to the size and general outline. The main differences are the curvature of the shell and the convex hyponomic sinus. Furthermore, the variety *falciformis* has a nummuloidal siphuncle compared with the more slender form in *I. p. perversum* (Barrande 1865).

Occurrence. – Czechoslovakia: Kozorz, Lochkov, Hinter-Kopanina and Butovitz. e¹ and e², Ludlow. Sweden, Gotland:

Linde klint and Lill Rone. Hemse Beds, Ludlow, Leintwardinian.

Genus *Clathroceras* Foerste 1926

Type species. – *Clathroceras sulcatum* (Barrande 1865). (Original combination: *Phragmoceras sulcatum*.)

Diagnosis. – See Sweet (1964, K 298).

Species. – *Clathroceras sulcatum* (Barrande 1865) and *C. plicatum* n.sp.

Clathroceras plicatum n.sp.

Figs. 28, 34A–J

Derivation of name. – Latin *plicatus*, plicate, referring to the parallel ridges on the shell surface.

Holotype. – RM Mo 152159.

Type stratum. – Hemse Beds, Ludlow.

Type locality. – Tänglings hällar, Gotland, Sweden.

Material. – Fourteen specimens from Gotland; RM Mo 56578, Mo 56585, Mo 56586, Mo 56587, Mo 56976, Mo 56977, Mo 57200, Mo 57201, Mo 57351, Mo 57362, Mo 56371, Mo 57379, Mo 57383 and Mo 152159 at SMNH, Stockholm, Sweden. All specimens are mature.

Diagnosis. – A species of *Clathroceras* with a circular, cyrtoconic, exogastric brevicone, in mature specimens with contracted transverse broad oval aperture. Pronounced peristome and a very narrow hyponomic sinus, ending with a circular hyponomic opening on a distinct ventral protrusion. Shell surface with longitudinal grooves and, perpendicular to these, distinct growth lines.

Description. – In cross section circular exogastric phragmocone with the nummuloidal siphuncle situated 1–1.5 mm from the convex ventral shell surface (Fig. 34J). The diameter of the siphuncle is about 1 mm at septal necks and almost double between septa. The distance between septa is 3 mm and appears to be constant in those preserved phragmocones which were cut.

Body chamber occupies approximately two thirds of the total estimated shell volume. The posterior part of the body chamber is circular in cross section while the hyponomic opening is located on an accentuated protrusion. The preserved length of this protrusion is about 5–6 mm and hosts a very restricted hyponomic opening, approximately 5 mm wide, pointing in a ventral and slightly anterior direction. The hyponomic sinus between the hyponomic opening and the aperture is almost closed and no open space can be observed in the investigated specimens.

The aperture is between oval and rhombic in configuration and occupies the dorsal half of the anterior end of the body chamber. Around the aperture is a roughly 2 mm thick

Table 7. *Clathroceras plicatum* n. sp., dimensions in mm.

Specimen No	Illustration	LT	LBC	H	W
RM Mo 152159	Fig. 34A–D	88	(55)	47.3	45.2
(holotype)					
RM Mo 56578				(62)	(59)
RM Mo 56585			61.3	51.3	53.4
RM Mo 56586		72	(56)		49.5
RM Mo 56587	Fig. 34F and J	60	40.8	35.8	35.7
RM Mo 56976	Fig. 34I	77		42.3	(41)
RM Mo 56977			(43)	38.1	
RM Mo 57200		95			(57)
RM Mo 57201		98		(48)	46.3
RM Mo 57351		72		41.8	42.4
RM Mo 57362			43.4	36.3	37.0
RM Mo 57371		85		39.3	(37)
RM Mo 57379	Fig. 34E and G	82	(49)	41.3	41.8
RM Mo 57383	Fig. 34H		(44)	37.2	37.7

rim on the outside of the shell (Fig. 34D). On internal moulds, reinforcements can be observed along the inner edge of the peristome.

The shell surface is covered by a series of longitudinal grooves and ridges about one millimetre apart, and these external grooves do not correspond with the longitudinal grooves visible on internal moulds of the body chamber. The latter represent muscle imprints while the former, almost double in number, presumably formed a kind of reinforcement or external deposits. Furthermore, the external grooves are not represented by a corresponding ridge on the internal side of the shell, as the inside appears to be comparatively smooth.

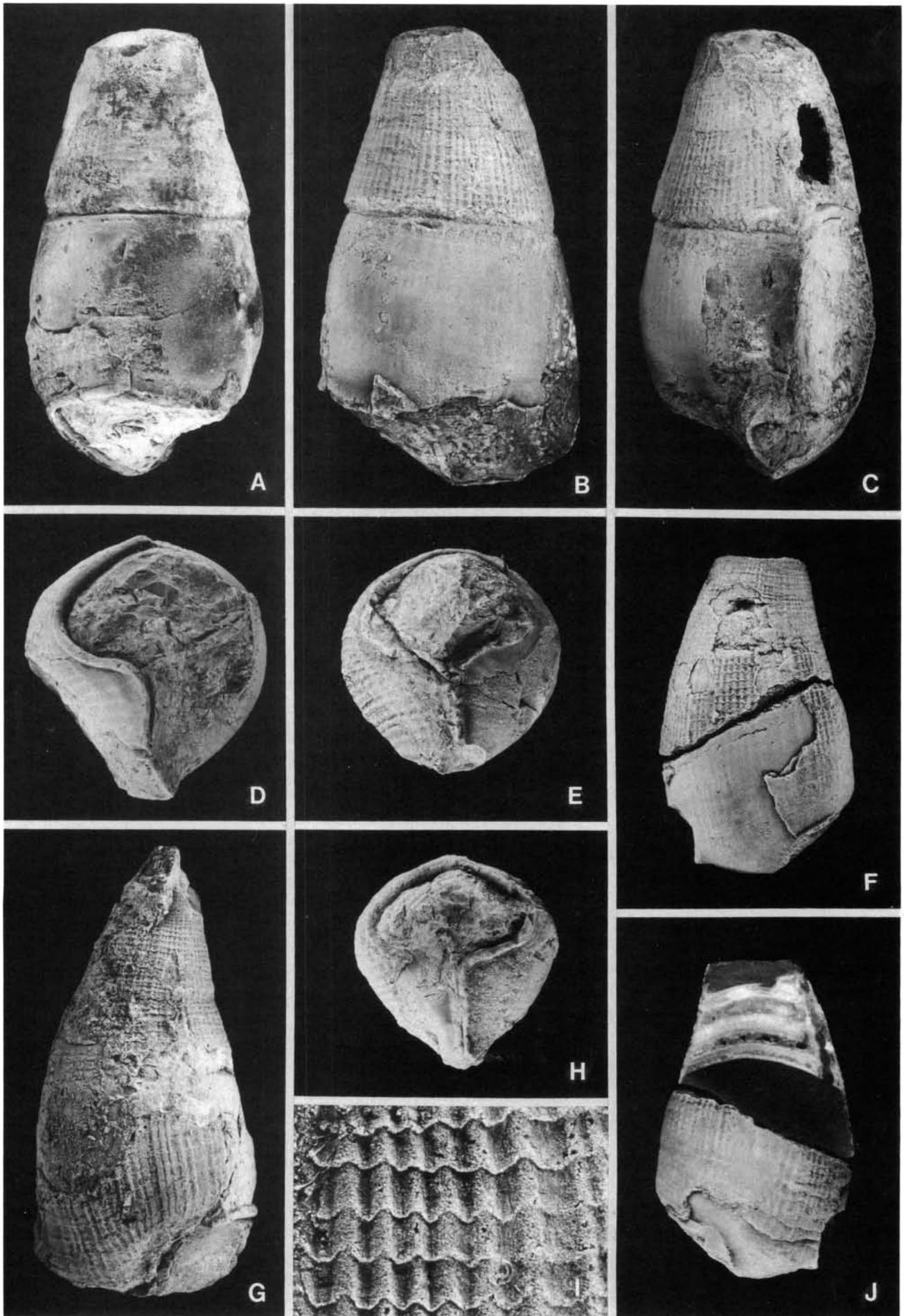
Perpendicular to the external grooves, undulating growth lines appear on both the phragmocone and the body chamber. Together the longitudinal grooves and the growth lines make a chequered pattern (Fig. 34I). The growth lines are closely parallel to the suture, except on the ventral side where a distinct V-shaped growth pattern occurs from the middle part of the phragmocone, indicating the development of the hyponomic sinus already in the juvenile stage. Furthermore, the growth lines are very pronounced with regular intervals of 1–2 mm.

Discussion. – No single specimen of the investigated *C. plicatum* has a complete aperture, although four specimens have a fairly well preserved main opening. The hyponomic opening is very poorly preserved on all specimens and the protrusion might have been longer than the measured 5–6 mm.

Within the studied specimens of *C. plicatum*, two groups can be distinguished according to the shape of the shell. One group, including the holotype RM Mo 152159 (Fig. 34A–D), has a sturdy phragmocone as well as body chamber, while the other group, including specimen RM Mo 57379 (Fig. 34E and G), is much more slender. Undoubtedly this is a case of sexual dimorphism (Fig. 12).

Comparison. – *Gomphoceras sulcatum* (Barrande 1847), later placed by Barrande in *Phragmoceras* (Barrande 1867, p. 239) and by Foerste (1926) transferred to his new genus *Clathroceras*, shows many similarities with *C. plicatum*.

The unusual combination of grooves and growth lines, giving this species a special look, was regarded by Barrande



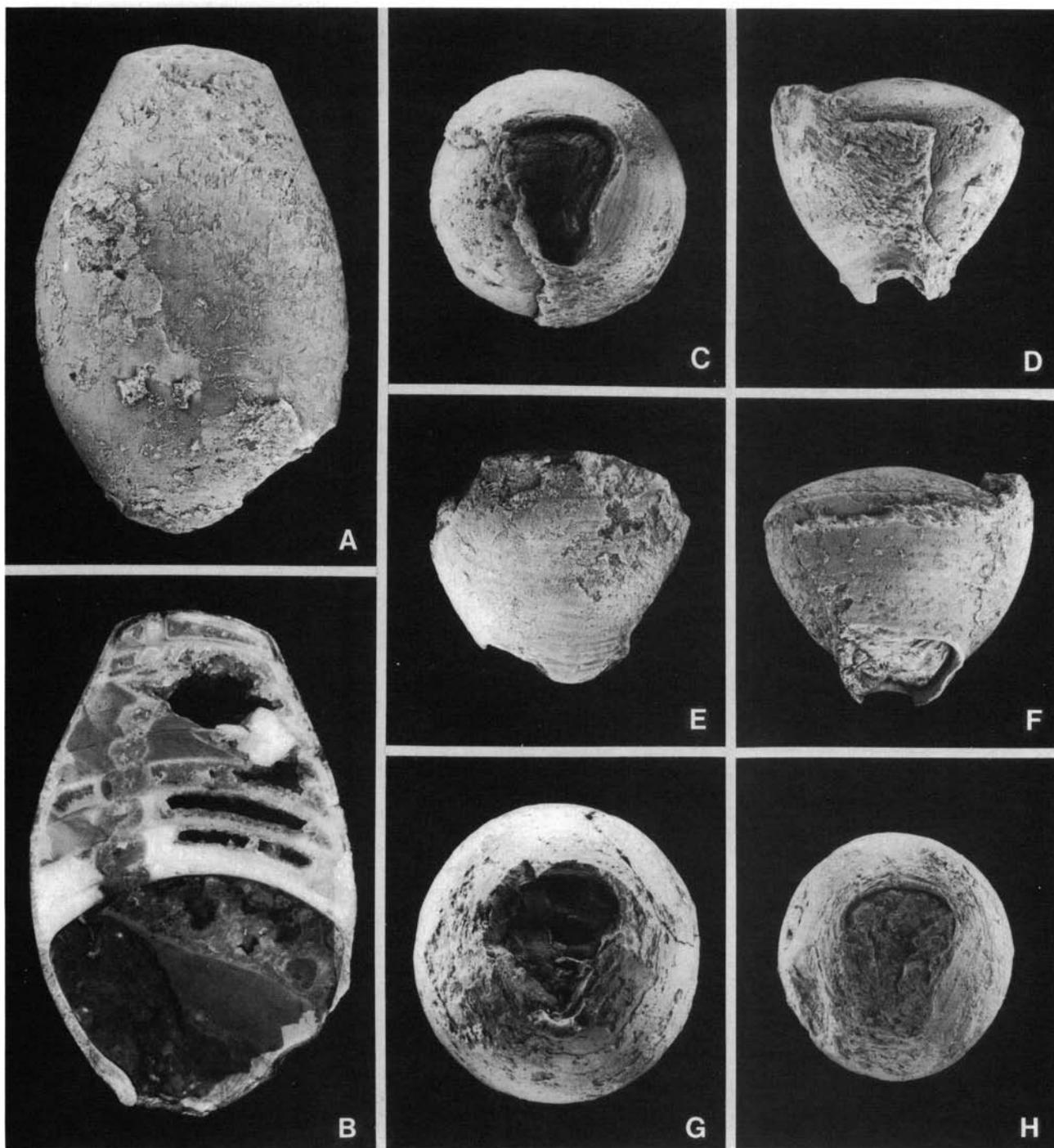


Fig. 35. *Jeppssonoceras concentratum* n. sp., $\times 1$. □A. Lateral view of RM Mo 56320; Mannegårde 1. □B. The same specimen as in A, cut dorso-ventrally along the long axis. □C, D, E and F. Apertural, ventral, lateral and dorsal views of the holotype, RM Mo 56319; Parish of Lye. □G. Apertural view of RM Mo 56324; Parish of Lye. □H. Apertural view of RM Mo 56326; Parish of Lye.

Fig. 34. *Clathroceras plicatum* n. sp., $\times 1$ except I. □A, B, C and D. Dorsal, lateral, ventral and apertural views of the holotype. Note the periphraet in B, RM Mo 152159; Tänglings hällar 1. □E. Apertural view of RM Mo 57379; Tänglings hällar 1. □F. Lateral view of specimen with the body chamber partly covered by the shell, RM Mo 56587; Tänglings hällar 1. □G. Lateral view of the same specimen as in E. □H. Apertural view of RM Mo 57383; Tänglings hällar 1. □I. Enlargement of the longitudinal grooves and perpendicular to these, the growth lines, RM Mo 56976, $\times 6$; Tänglings hällar 1. □J. Lateral view of the same specimen as in F but with the phragmocone and part of the body chamber cut dorso-ventrally along the long axis.

as unique among *Phragmoceras*. Apart from a more arcuate form of *C. sulcatum*, it is the aperture which shows the greatest divergence between the species. *C. sulcatum* has an oval main aperture and a wide hyponomic sinus, terminating in a comparatively large hyponomic opening. Furthermore, *C. sulcatum* has its aperture placed at the very anterior end of the phragmocone, while *C. plicatum* has the aperture placed more dorsally. *C. sulcatum* seems not to have the pronounced protrusion around the hyponomic opening characteristic for *C. plicatum*. The differences between *C. sulcatum* and *C. plicatum* are sufficient to treat them as distinct species.

Table 8. *Jeppssonoceras concentratum* n. sp., dimensions in mm.

Specimen No	Illustration	LT	LBC	H	W
RM Mo 56319 (holotype)	Fig. 35C–F		35.7	39.2	39.2
RM Mo 56320	Fig. 35A–B	79	36.8	48.5	47.5
RM Mo 56324	Fig. 35G	77		49.5	(49)
RM Mo 56325		76	42.8	(44)	(42)
RM Mo 56326	Fig. 35H	65		(40)	(39)

Occurrence. – Sweden, Gotland: Mannegårde 1 and Tänglings hållar 1. Hemse Beds, Ludlow, Bringewoodian or early Leintwardinian.

Genus *Jeppssonoceras* n.gen.

Derivation of name. – Named in honour of Lennart Jeppsson, Lund.

Type species. – *Jeppssonoceras concentratum* n.sp.

Diagnosis. – Circular, almost straight brevicone. Body chamber situated anterior to the greatest width of the shell in mature specimens. Contracted aperture with protruding lateral lappets. Empty spacious siphuncle.

Discussion. – When Barrande described the species *Gomphoceras microstoma* (Barrande 1865, Pls. 72 and 92), he illustrated five specimens. One of these specimens (Barrande 1865, Pl. 72:14–17) seems closely comparable to *J. concentratum*. A revision of *G. microstoma* may resolve the question whether these two species are to be regarded as congeneric.

Species. – *Jeppssonoceras concentratum* n.sp.

Jeppssonoceras concentratum n.sp.

Figs. 28, 35A–H

Derivation of name. – Latin *concentratus*, concentrated, referring to the constricted apertural opening.

Holotype. – RM Mo 56319.

Type stratum. – Hemse Beds, Ludlow.

Type locality. – Not known exactly as the label only states 'parish of Lye' but it is presumably Mannegårde 1, Gotland, Sweden.

Material. – Five specimens from Gotland; RM Mo 56319, Mo 56320, Mo 56324, Mo 56325 and Mo 56326 at SMNH, Stockholm, Sweden. All specimens are mature.

Diagnosis. – A species of *Jeppssonoceras* with a circular, cyrtoconic, slightly exogastric brevicone, in mature specimens with a protruding, contracted, almost triangular aperture. Hyponomic sinus with short lappets on the lateral sides. Siphuncle situated about 1/4 of the shell diameter from the wall.

Description. – Circular, almost straight shell. The orientation of the oldest preserved septum indicates that the phragmocone was slightly exogastric. Proportion of length and width of body chamber is 3:4. Body chamber almost rounded, triangular in side view and furnished with preserved muscle imprints.

The apertural rim protrudes a few mm and has two lateral lappets of about 5 mm in length on either side of the hyponomic sinus. The peristome has a small internal reinforcement and restricts the aperture to a concentrated opening of rounded triangular shape, including the hyponomic opening.

The last septum is strongly curved, almost 80 degrees of a circle, and demarcates a small chamber. The average distance between the older septa is 4–4.5 mm, and the 2.5–4 mm wide nummuloidal siphuncle is situated about 1/4 of the phragmocone diameter from the convex ventral shell surface and follows the curvature of the wall. No siphonate deposits have been observed in the empty, very spacious siphuncle. The average width of the connecting rings is about 7 mm.

The very limited material, only five specimens, does not allow any accurate studies of size variations but it can be established that there is no specific uniform size. The variation, however, is not particularly wide compared with that of other oncocerids from Gotland.

According to the fossil material and comparisons with other species of oncocerid cephalopods from the same locality, the shell of *J. concentratum* seems to have been extraordinarily thick, in the phragmocone as well as in the body chamber (Fig. 35B).

Discussion. – The material of *Jeppssonoceras concentratum* did not include any perfect specimen. The five specimens comprise four more or less complete specimens with very incomplete apertures, and one body chamber with a well preserved aperture. The latter specimen was chosen as holotype as the apertural configuration is considered to be more diagnostic than the general shape of the phragmocone (Fig. 35C–F). It must be emphasized, however, that total conformity occurs between the holotype, RM Mo 56319, and the paratype, RM Mo 56320 (Fig. 35A–B).

Apertural growth lines are clearly visible on the holotype, showing the terminal growth of the lappets (Fig. 35E).

The consequence of the thick shell of *J. concentratum* is that the shell is heavy, and to compensate for this weight, the phragmocone volume had to be large compared with the body chamber volume. This is in fact the case (Fig. 35B), as the body chamber is unusually small compared with the remaining, or reconstructed phragmocone.

J. concentratum seems to have been an animal with an unusually strong shell and good protection of the soft parts, thanks to the reinforced aperture.

Comparison. – *Jeppssonoceras concentratum* so far is reported only from Gotland, Sweden. From Bohemia, Czechoslovakia, Barrande (1865, Pl. 72:14–17) has described a specimen with great resemblance, *J. microstoma* (Barrande 1865), and as mentioned above I find this specimen closely related to *J. concentratum* and thus included in *Jeppssonoceras*. *J. concentratum* and *J. microstoma* have both the conic shape of the body chamber and the spout-like aperture with lateral lappets on

the hyponomic part of the aperture. As is the case with other oncocerid cephalopods from Gotland compared with identical or similar species from Bohemia, the Bohemian specimens are straighter. There is, however, a very small indication on the specimen in Pl. 72:14 (Barrande 1865) that the shell might be exogastric like that of *J. concentratum*, but the indications are so tentative that they cannot be used as an evidence for an exogastric shell.

Occurrence. – Sweden, Gotland: Mannegårde l. Hemse Beds, Ludlow, Bringewoodian or early Leintwardinian.

Genus *Plemeroceras* n.gen.

Derivation of name. – A play upon words in honour of Ple, a close friend of the author's from Gotland.

Type species. – *Plemeroceras cassis* n.sp.

Diagnosis. – Circular, almost straight brevicone. Aperture consisting of a dorsal, laterally visored opening and a hyponomic opening in a ventral protrusion. Slender empty siphuncle.

Species. – *Plemeroceras cassis* n.sp.

Plemeroceras cassis n.sp.

Figs. 28, 36A–M

Derivation of name. – Latin *cassis*, helmet, referring to the very restricted aperture.

Holotype. – RM Mo 56299.

Type stratum. – Hemse Beds, Ludlow.

Type locality. – Mannegårde 1, Gotland, Sweden.

Material. – Eleven specimens from Gotland; RM Mo 56286, Mo 56288, Mo 56290, Mo 56291, Mo 56293, Mo 56294, Mo 56295, Mo 56296, Mo 56297, Mo 56299 and Mo 57463 at SMNH, Stockholm, Sweden. All specimens are mature.

Diagnosis. – A species of *Plemeroceras* with a circular, exogastric brevicone, in mature specimens with a dorsally situated, laterally wide, compressed visored aperture. Hyponomic sinus very narrow, less than 1 mm wide, and hyponomic opening located in a long ventral protrusion at least 5 mm long. Aperture restricted by two anterior lappets, cutting off the aperture from the anterior end of the shell.

Description. – Circular straight body chamber and slightly curved, exogastric phragmocone. Greatest diameter of shell is found in the middle of the body chamber. The phragmocone is slender and has distinctly smaller volume than the body chamber. Most investigated specimens have a very fragmentary phragmocone, except the holotype and two other specimens, in which the exogastric curvature is observed.

Table 9. *Plemeroceras cassis* n. sp., dimensions in mm.

Specimen No	Illustration	LT	LBC	H	W
RM Mo 56299 (holotype)	Fig. 36A–D	69		29.5	29.8
RM Mo 56286		71			33.9
RM Mo 56288		60	(38)	33.2	(31)
RM Mo 56290	Fig. 36E and J–K		44.0	32.5	32.9
RM Mo 56291	Fig. 36G–I		40.1	31.4	31.0
RM Mo 56293		59		35.2	(36)
RM Mo 56294	Fig. 36L–M	56	(33)	28.6	
RM Mo 56295		54		32.7	31.2
RM Mo 56296	Fig. 36F	61		31.8	(31)
RM Mo 56297		47	(38)	31.4	32.7
RM Mo 57463			(41)	31.5	32.6

The average distance between septa in three specimens, cut dorsoventrally along the long axis, is 2.4–2.7 mm, except between the last three septa which are separated by about half this distance.

The siphuncle is located about 1 mm from the ventral wall, except in the last two chambers where the siphuncle is perpendicular to the curved septa, resulting in a slight dorsal direction of the tube. This arrangement is also observed among other oncocerids from Gotland. The septal necks in the last three chambers have a cyrto-choanitic shape and the slender empty siphuncle, 2–3 mm wide in the older parts of the phragmocone, expands here by about 50 percent.

The spacious body chamber has the hyponomic opening distinctly separated from the dorsally situated aperture. The hyponomic sinus is a narrow slit, less than 1 mm wide, and apart from this slit, the hyponomic opening about 5 mm wide is almost circular (Fig. 36K) and forms a tube at least 5–6 mm long, pointing almost perpendicular to the long axis of the shell (Fig. 36J). Internal moulds of the body chamber show that the hyponomic tube is directed slightly towards the posterior. The anterior end of the shell slopes adapically from the dorsal to the ventral side, and the dorsally located aperture is visored by the terminating dorsal growth of the lateral lobes, forming one lappet on each side of the hyponomic sinus. These lappets, approximately 8 mm long, close off the aperture from the anterior side of the body chamber. The compressed oval-rhombic aperture is 16–18 mm wide and about 6 mm high (Fig. 36G). The centre of the posterior end of the aperture has an inward bend, formed very late during growth, as is evident from the orientation of the dorsal growth lines, which are straight up to the inward bend.

Preserved growth lines show that the hyponomic opening was completed before the lappets were established. These lappets may have been formed at the same time as the reinforcements along the hyponomic sinus at the hyponomic end. The transition between the body chamber and the space in the hyponomic protrusion is very smooth on those specimens where the internal mould can be observed.

Discussion. – Most investigated specimens of *Plemeroceras cassis* are very poorly preserved. The aperture with its delicate lappets is rarely complete and only two specimens, RM Mo 56286 and RM Mo 56291 (Fig. 36I), show almost unbroken lappets. The majority, including the holotype (Fig. 36A–

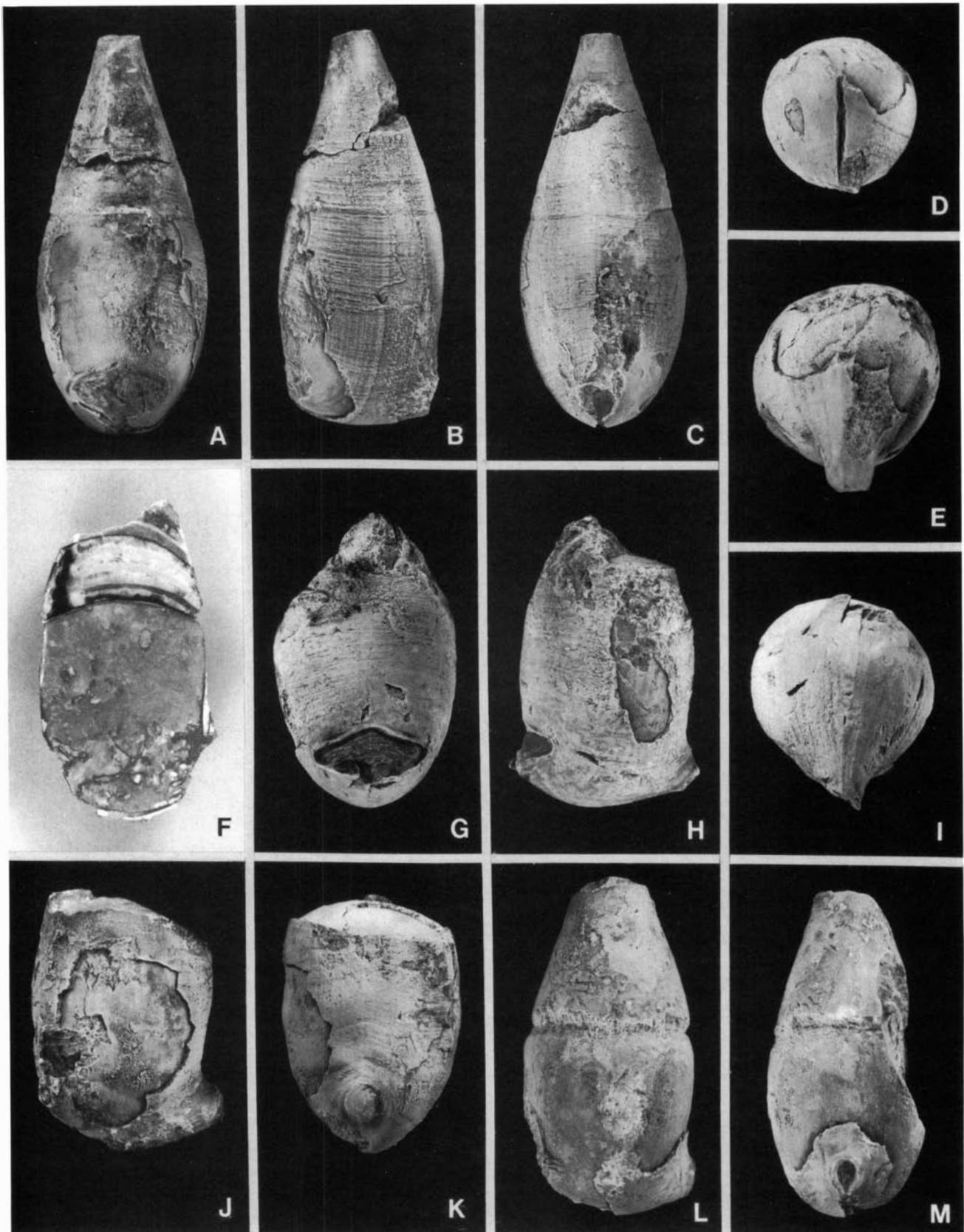


Fig. 36. *Plemeroceras cassis* n. sp., $\times 1$. □A, B, C and D. Dorsal, lateral, ventral and apertural views of the holotype, RM Mo 56299; Mannegårde 1. □E. Apertural view of a specimen with well preserved hyponomic protrusion, RM Mo 56290; Lill Rone 1. □F. Specimen cut dorsoventrally along the long axis, RM Mo 56296; Mannegårde 1. □G, H and I. Dorsal, lateral and apertural views of RM Mo 56291; Lill Rone 1. □J and K. Lateral and ventral views of the same specimen as in E. □L and M. Lateral and ventral views of a specimen with the shell preserved only around the hyponomic protrusion, RM Mo 56294; Sandarve kulle.

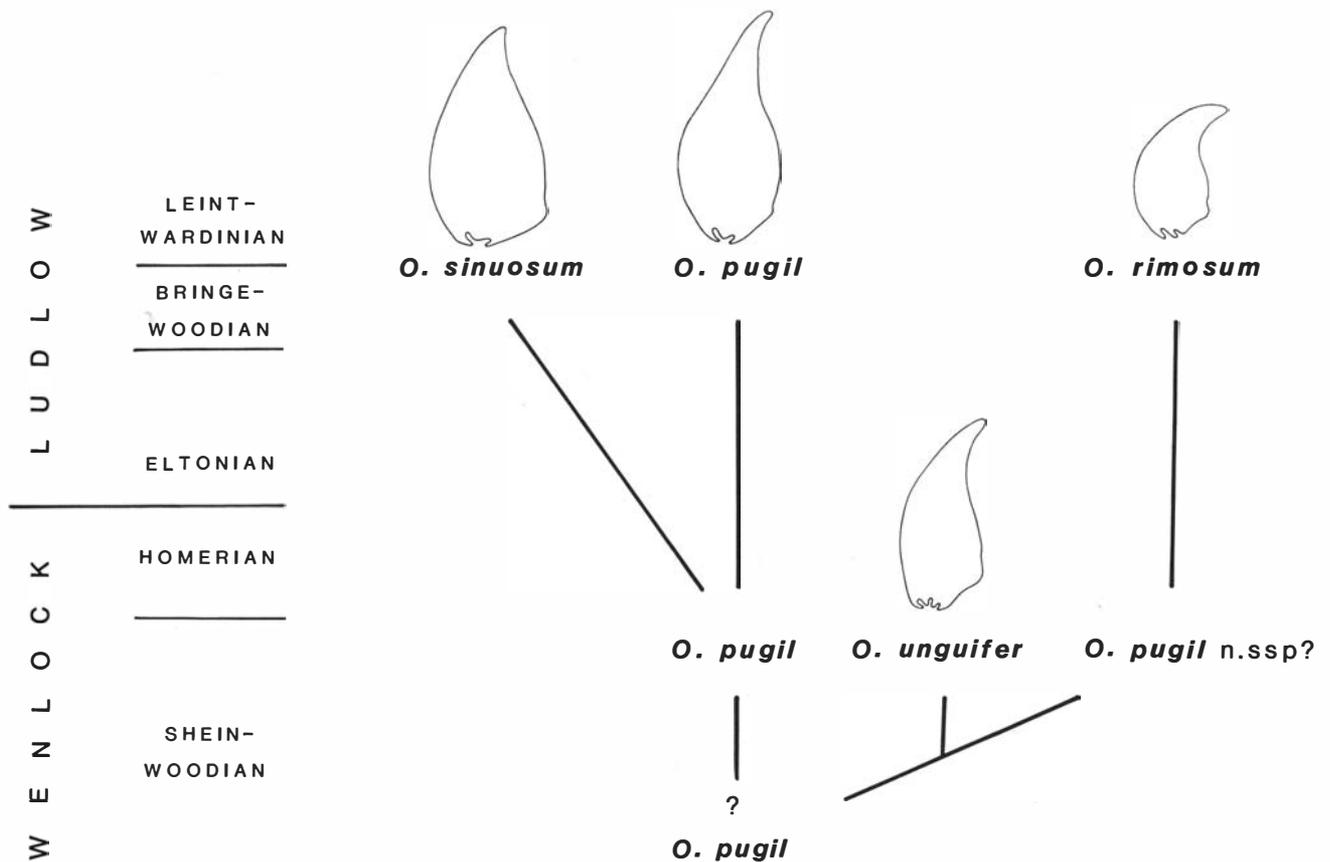


Fig. 37. Possible evolution within the genus *Octameroceras*, based on the investigated Gotland material.

D), have only fragmentary lappets and some specimens only faint traces of the aperture. The situation is similar with the hyponomic protrusion as this is only preserved in RM Mo 56290 (Fig. 36J and K) and is fragmentary on a few others. It cannot even be established that the whole protrusion is present in Mo 56290, as the outer end is partly broken.

The smooth transition between the body chamber and the protrusion was presumably to allow a good fit for the hyponome, which must have had a very restricted freedom of movement.

Within *Plemeroceras cassis* two groups can be distinguished, one with a slender shell and the other with stouter shells, possibly indicating sexual dimorphism. Unfortunately the material is too limited to allow any firm conclusions.

Occurrence. – Sweden, Gotland: Mannegårde 1, Sandarv kulle and Lill Rone 1. Hemse Beds, Ludlow, Bringewoodian or early Leintwardinian.

Family Hemiphragmoceratidae Foerste 1926

The family name Hemiphragmoceratidae was proposed by Foerste (1926, pp. 358–359) for phragmoceroids having an aperture with only lateral sinuses and no dorsal sinus. Genera included were *Hemiphragmoceras*, *Tetrameroceras*, *Conradoceras*, *Paraconradoceras*, *Hexameroceras*, *Pristeroceras* and *Octameroceras*. *Paraconradoceras* was later transferred to the oncocerid family Nothoceratidae Fisher, (Sweet 1964, p. K305) and *Pristeroceras* was transferred to the family Phragmoceratidae

Miller, in the order Discosorida (Teichert 1964, p. K338).

Regarding *Hexameroceras*, two of the lobes are dorsal and not lateral. Thus it is better to describe the family following Sweet (1964, p. K295), who noted among other characteristics the nummuloidal actinosiphonate siphuncle.

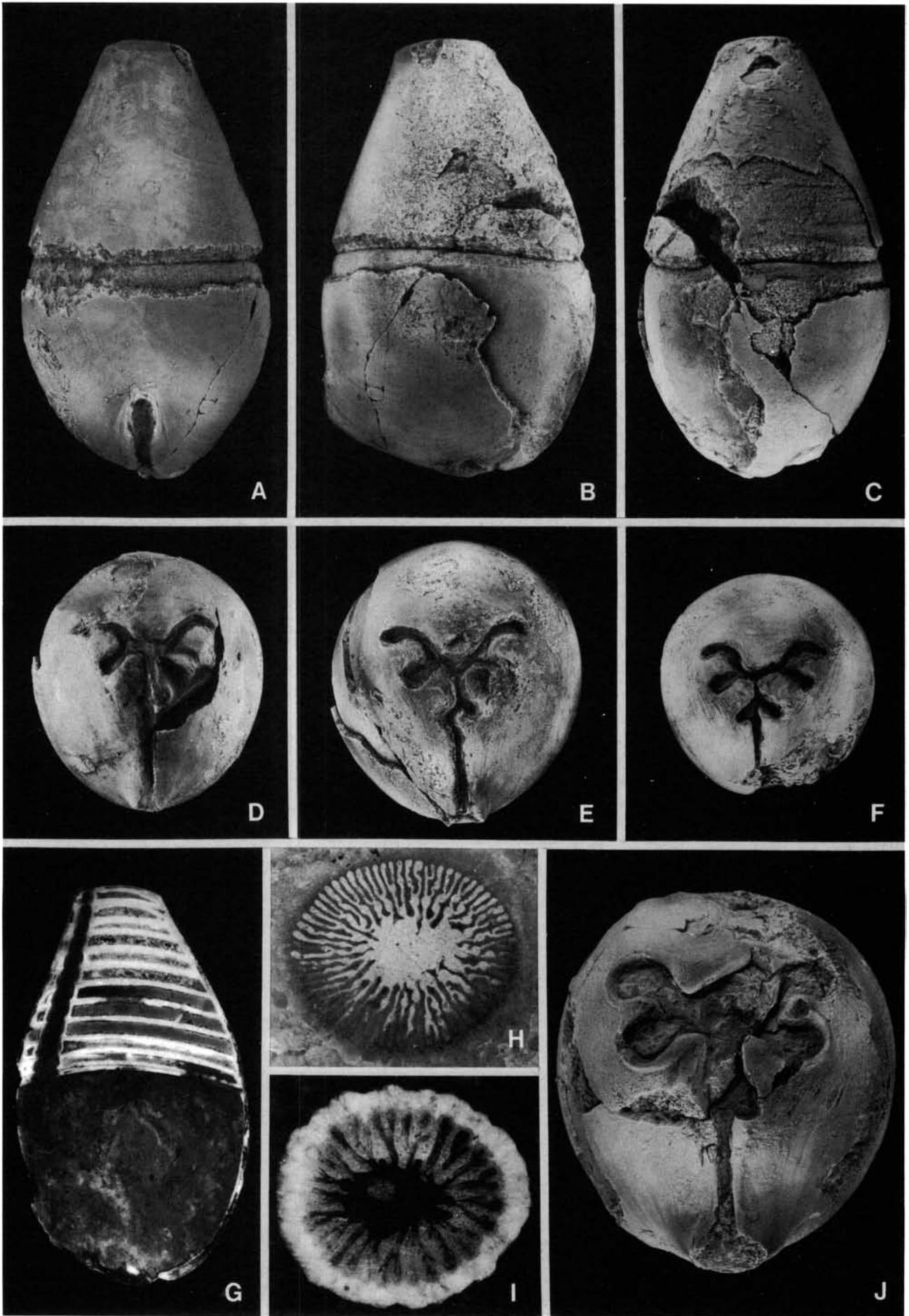
Genus *Octameroceras* Hyatt 1900

Type species. – *Octameroceras callistoma* (Barrande 1865). (Original combination: *Phragmoceras callistoma*. Lectotype for the type species is Barrande 1865, Pl. 47:1–6, selected by Foerste 1926, p. 363, see Teichert & Sweet 1962.)

Emended diagnosis. – Slightly compressed brevicone, in early ontogeny with endogastric phragmocone which in later ontogenetic stages turns straight or exogastric. Inflated body chamber with a contracted, visored aperture, having a triangular shape with a varying number of lateral and ventrolateral lobes. Actinosiphonate siphuncle. Hyponomic opening situated anteriorventrally, about half-way between main apertural opening and periphraet.

Discussion. – In his description of *Octameroceras*, Hyatt (1900, p. 531) considered this genus to include specimens having eight lateral sinuses. As is discussed in the chapter ‘Apertural growth’, the idea of establishing genera based on the number of sinuses is not applicable within the Hemiphragmoceratidae.

The similarities between the type species of *Octameroceras*



(only one specimen known) and the species *O. sinuosum*, *O. pugil* and *O. unguifer* are so evident that I put them in the same genus. *O. rimosum*, with only four sinuses, is suggested as being a descendent of *O. pugil* and is therefore also put in the genus *Octameroceras*. According to the I.C.Z.N. nomenclature rules, *Octameroceras* must be the name of this genus, although the name may be considered misleading.

Octameroceras is rather similar to *Hexameroceras* Hyatt 1884, but the latter genus can be distinguished by the lack of the typical broad dorsal salient in the aperture as well as the successively diminishing sinuses along the ventral part of the apertural opening.

Octamerella Teichert and Sweet 1962 has a similar apertural shape as the emended *Octameroceras*, but a totally different shape of the shell.

Species. – *Octameroceras callistoma* (Barrande 1865), *O. osiliense* (Jaekel 1902), *O. sinuosum* n.sp., *O. pugil* n.sp., *O. rimosum* (Barrande 1865) and *O. unguifer* n.sp.

It is likely that the following species also belong to the genus *Octameroceras*: *O. pollens* (Barrande 1865, Pl. 91:1–4 only), *O. cacabiformis* (Newell 1888, p. 481) and *Octamerella callistomoides* (Foerste 1926, p. 363–364).

Octameroceras sinuosum n.sp.

Figs. 25A, 28, 38A–J, 39A–B

Derivation of name. – Latin *sinuosus*, sinuous, referring to the winding sinuses.

Holotype. – RM Mo 56798.

Type stratum. – Hemse Beds, Ludlow.

Type locality. – Lill Rone 1, Gotland, Sweden.

Material. – Fifty-four specimens from Gotland; (microconchs): RM Mo 56787–56788, Mo 56790, Mo 56794, Mo 56796–56798, Mo 56800–56807, Mo 56809–56811, Mo 56975, Mo 57186–57188, Mo 57407, Mo 152123, Mo 152125, Mo 152129–152133, Mo 152135, Mo 152140, Mo 152161, Mo 152174–152177, Mo 152182, Mo 152184, Mo 152252, Mo 152254 and Mo 152258–152259, (macroconchs): Mo 56894–56897, Mo 56902, Mo 56904, Mo 152128, Mo 152137–152138, Mo 152165 and Mo 152180 at SMNH, Stockholm, Sweden. All specimens are mature.

Diagnosis. – A species of *Octameroceras* with a slightly compressed, primary endogastric, and later in its ontogeny

Table 10. *Octameroceras sinuosum* n. sp., dimensions in mm. The first group comprises microconchs and the second macroconchs. Only the best preserved specimens are included.

Specimen No	Illustration	LT	LBC	H	W
RM Mo 56798 (holotype)	Fig. 38A–D	84	(43)	51.7	47.1
RM Mo 56787		89	41.8	51.8	(47)
RM Mo 56788		77		51.0	44.1
RM Mo 56790			43.6	52.2	49.1
RM Mo 56796			40.0	(46)	43.4
RM Mo 56797			38.9	45.0	40.6
RM Mo 56802	Fig. 38F			42.0	40.1
RM Mo 56803		78	(43)	49.6	43.7
RM Mo 56804			40.3	45.8	39.4
RM Mo 56811	Fig. 38E			58.2	51.7
RM Mo 56975	Fig. 38G	73		43.0	41.4
RM Mo 57186		76		39.2	36.0
RM Mo 152130			39.1	45.8	41.2
RM Mo 152140		80		(50)	45.4
RM Mo 152161			42.9	46.4	41.8
RM Mo 152174		84		46.9	43.2
RM Mo 152175			39.8	44.2	41.3
RM Mo 152252		73	40.5	47.5	42.3
RM Mo 152258		70		45.1	41.5
RM Mo 56896	Fig. 39B	117		(71)	71.0
RM Mo 56897		127		(81)	72.7
RM Mo 56902		121		(74)	
RM Mo 56904				(78)	71.4
RM Mo 152165		114	(58)	(70)	
RM Mo 152180	Figs. 38J, 39A		63.7	73.0	66.6

slightly exogastric brevicone. In mature specimens there is a contracted aperture with a broad dorsal salient, two lateral and between two and four ventrolateral lobes. Narrow hyponomic sinus, occasionally wide in the dorsal part, ending in a 3–5 mm long protrusion, surrounding the drop-shaped ventrally directed hyponomic opening.

Description. – Slightly compressed phragmocone with a convex dorsal side. The ventral side is concave in the apical part and slightly exogastric in the remaining part. The average distance between septa is around 5 mm in the macroconchs and 3.0–3.5 mm in the microconchs, except in the last chamber where it is about half the distance in both groups. The actinosiphonate siphuncle (Fig. 38H–I) has orthochoanic necks and is situated at the same distance from the ventral wall as the siphuncle is wide (Fig. 38G). This distance, and corresponding width, can reach 11 mm in macroconchs while the average is around 5 mm in microconchs.

The proportion between height and length of the body chamber is about 5:4, and a well preserved periphraet can be observed on a number of the investigated specimens, extensively prepared (Figs. 38A–C and 39A). The number of muscle imprints is between 38 and 46 and the species is ventromyarian (the retractor muscles being situated on the ventral side of the body).

The apertural opening, which is more or less triangular in shape, is dominated by a 10–20 mm wide dorsal salient. In addition, the aperture is diminished by two lateral and two, three or even four ventrolateral lobes. In the group of macroconchs, two ventrolateral lobes are the most common, but all combinations occur among the microconchs (Fig. 38D–F and J).

Fig. 38. *Octameroceras sinuosum* n. sp., ×1 except H and I. □A, B, C and D. Ventral, lateral, dorsal and apertural views of the holotype, RM Mo 56798; Lill Rone 1. □E. Apertural view of RM Mo 56811; Mannegårde 1. □F. Apertural view of RM Mo 56802; Lill Rone 1 (see also Stridsberg 1981a, Fig. 6). □G. Specimen cut dorsoventrally along the long axis, RM Mo 56975; Tänglings hällar 1. □H. Section of the siphuncle in one of the last chambers in a macroconch, RM Mo 157981, ×4.3; Parish of Lye. □I. Section of the siphuncle in one of the last chambers in a microconch. Photographed by Gerhard Holm in the 1890s, probably RM Mo 152254, ×8; Lill Rone 1. □J. Apertural view of RM Mo 152180; Parish of Lye (see also Fig. 39A).

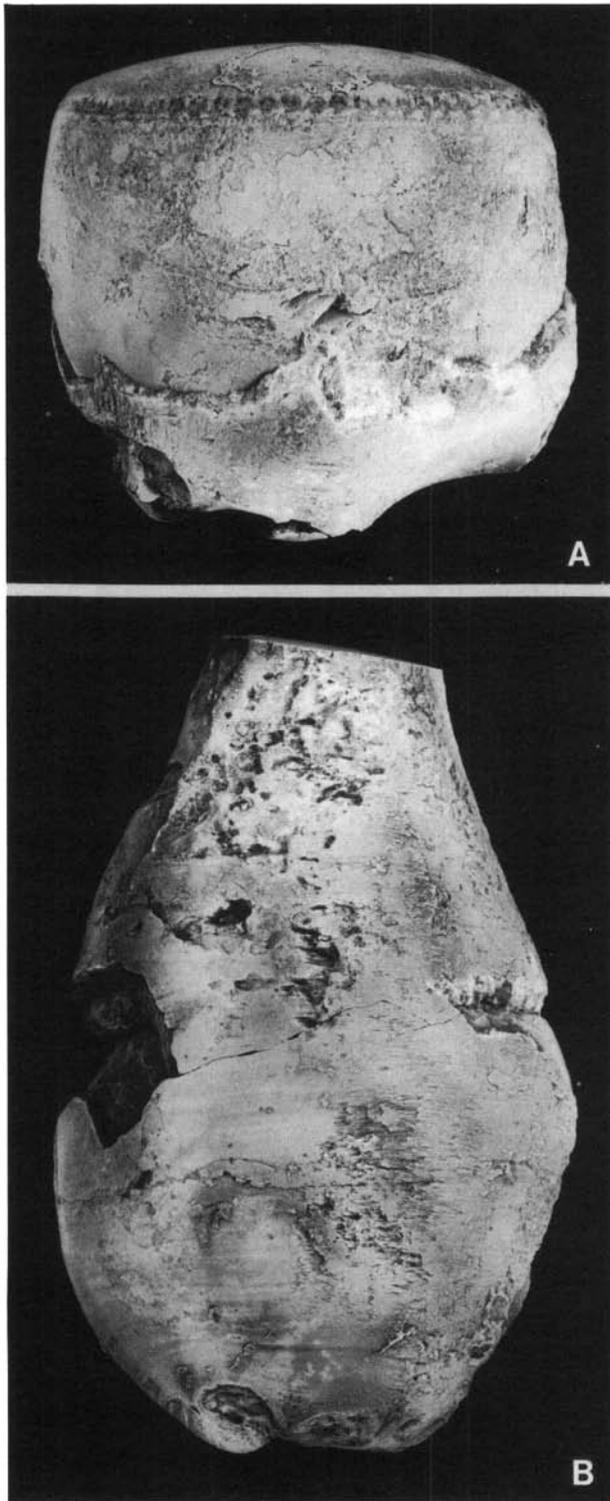


Fig. 39. *Octameroceras sinuosum* n. sp., $\times 1$. □A. Lateral view of the body chamber. Note the periphraet around the upper part of the specimen, RM Mo 152180; Parish of Lye (see also Fig. 38J). □B. Lateral view of RM Mo 56896; Mannegårde 1.

On big specimens with only two ventrolateral lobes, the hyponomic sinus is an extension of a ventral sinus formed between these lobes. Apart from disturbance from the ventralmost lobes, the hyponomic sinus is very narrow and ends in the hyponomic opening in a protrusion a few mm thick, situated about half-way between the aperture and the periphraet.

On specimens preserved as internal moulds strong reinforcements can be observed along the peristome. Reinforcements also occur along the hyponomic sinus and around the hyponomic opening.

On one of the macroconchs, RM Mo 152180, considerable external reinforcement along the lateral and ventrolateral lobes can be observed (Fig. 38J). The lateral and ventrolateral sinuses as well as the ventral sinus are about 8 mm wide and the central apertural opening is more than 20 mm wide. Furthermore, in lateral view the hyponomic sinus is concave and the hyponomic protrusion on this specimen, as well as on some other macroconchs, is broken, but has an external width of about 15 mm.

Octameroceras sinuosum is the oncocerid collected in greatest numbers on Gotland, although from only three localities and from the same stratigraphic unit. The material is very uniform regarding the shell shape but the apertural shape varies considerably. The number of sinuses range from as few as four to as many as eight or nine. Furthermore, all successive stages between have been observed (Stridsberg 1981a, p. 274, Fig. 7).

Typical for *O. sinuosum* is the lack of bilateral symmetry in the ventral part of the apertural opening. As is discussed in the chapter 'Apertural growth', the ventral sinuses are not situated opposite each other, and in all investigated specimens the left ventralmost sinus is situated more dorsally than the corresponding right one. Consequently, the dorsal part of the hyponomic sinus is undulating (Fig. 38E).

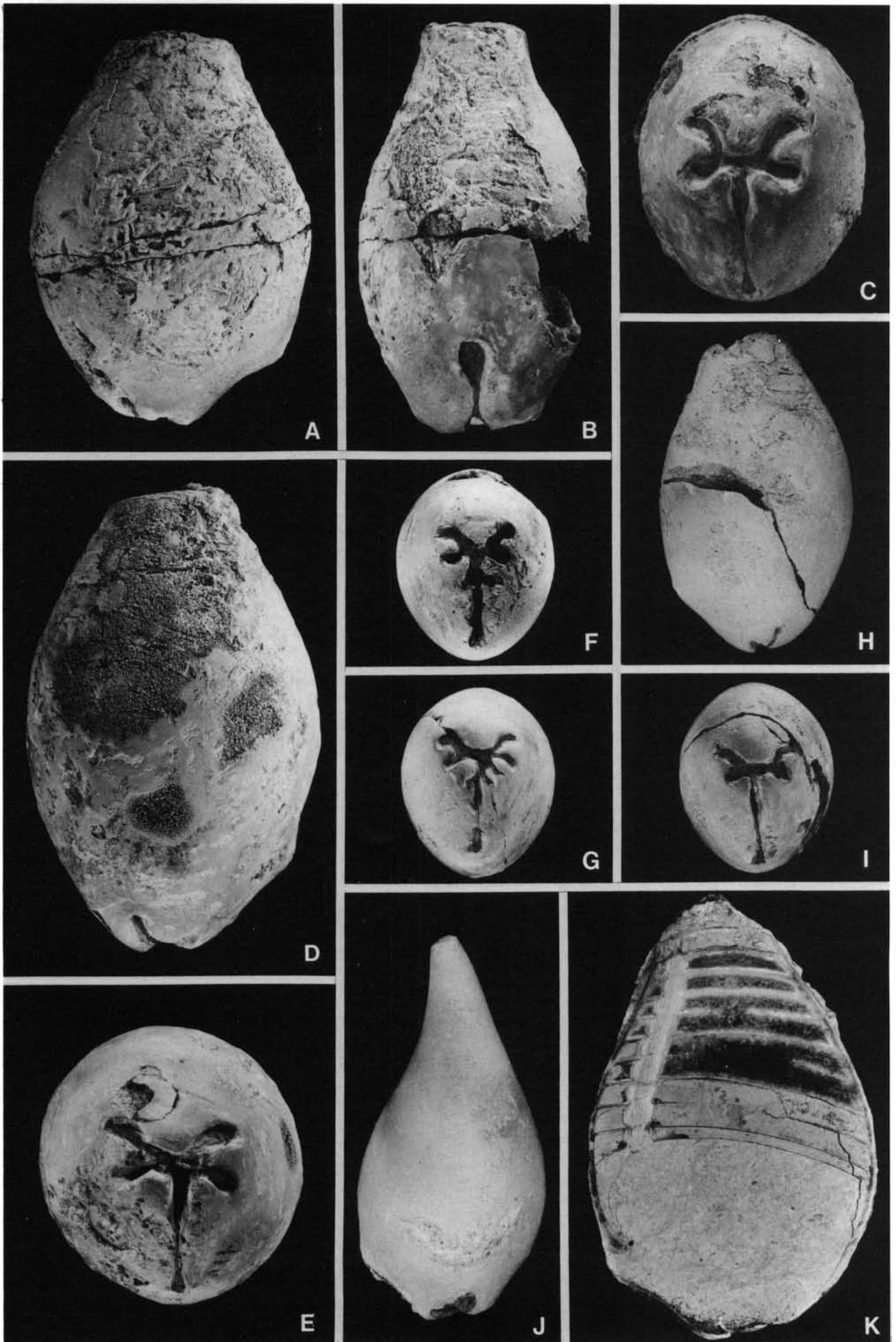
As is the case with *O. pugil*, *O. sinuosum* includes two distinct size groups (Fig. 8) and this dimorphism is discussed in the chapter 'Dimorphism'.

Comparison. – *Octameroceras sinuosum* is closely similar to both *O. pugil* and *O. unguifer*, in the shape of the shell as well as in the apertural configuration. This is discussed in the description of *O. pugil*.

The type species for *Octameroceras*, *O. callistoma* (Barrande 1865), has an apertural shape more or less identical to that of *O. sinuosum*. The shell, however, is broader and has another curvature, but the two species are almost certainly closely related. The situation is the same with the only specimen of *Octamerella*, *O. callistomoides* (Foerste 1926), but the extreme ventral position of the siphuncle and the almost straight and, in early ontogenetic stages, very narrow phragmocone make it less closely related to *O. sinuosum*.

Occurrence. – Sweden, Gotland: Lill Rone 1, Mannegårde 1 and Tänglings hällar 1. Hemse Beds, Ludlow, Bringewoodian or early Leintwardinian.

Fig. 40. *Octameroceras pugil* n. sp., $\times 1$. □A, B and C. Lateral, ventral and apertural views of the holotype, RM Mo 56627; Samsugns 1. □D and E. Lateral and apertural views of RM Mo 56643; Samsugns 1. □F. Apertural view of RM Mo 56469; Samsugns 1. □G. Apertural view of RM Mo 56483; Klints. □H and I. Lateral and apertural views of RM Mo 56653; Samsugns 1. □J. Lateral view of RM Mo 57282; Samsugns 1. □K. Specimen cut dorsoventrally along the long axis. Note the striations in the siphuncle (see also Fig. 38H and I), RM Mo 152172; Samsugns 1.



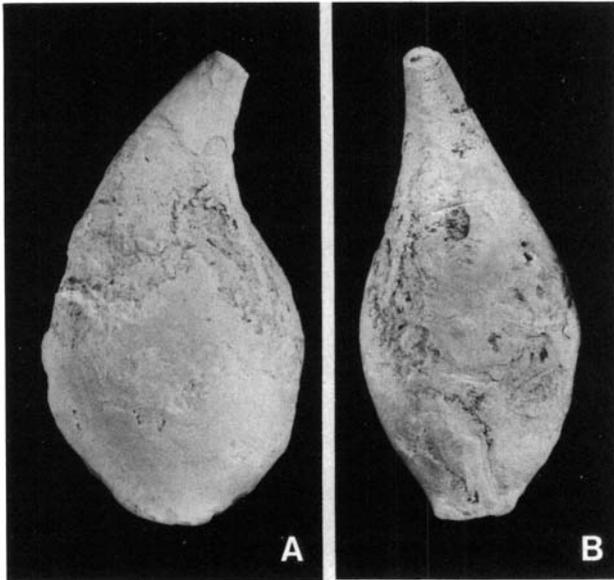


Fig. 41. *Octameroceras pugil* n. ssp., $\times 1.2$. □A and B. Lateral and ventral views of RM Mo 56484; Stora Vede 1.

Octameroceras pugil n.sp.

Figs. 28, 40A–K, 41A–B

Derivation of name. – Latin *pugil*, referring to the outline of a fist.

Holotype. – RM Mo 57283.

Type stratum. – Slite Beds, unit g. Wenlock.

Type locality. – Samsugns 1, Gotland, Sweden.

Material. – Twenty-one specimens from Gotland; RM Mo 56468, Mo 56469, Mo 56473–56478, Mo 56483, Mo 56488, Mo 56627, Mo 56643, Mo 56653, Mo 56655, Mo 56672, Mo 56683, Mo 57274, Mo 57282, Mo 57283, Mo 152171 and Mo 152172 at SMNH, Stockholm, Sweden. All specimens are mature.

Diagnosis. – A species of *Octameroceras* with a slightly compressed, primary endogastric, and later in its ontogeny exogastric brevicone. In mature specimens there is a contracted aperture, restricted by one broad dorsal salient, two lateral and two narrow ventrolateral lobes. Occasionally two small ventral lobes appear. Hyponomic sinus dorsally wide and narrow in its middle part, just before the drop-shaped hyponomic opening. Specimens with the two ventral lobes have two small additional sinuses instead of the wide dorsal part of the hyponomic sinus.

Description. – Slightly compressed shell with apically endogastric phragmocone. During the estimated last third of the growth of the phragmocone it turns exogastric (Fig. 40J–K). The average distance between septa is 4.3 mm in the macroconchs and 3.0 mm in the microconchs, except in the last chamber where the distance is approximately half the distance in both size groups. The actinosiphonate siphuncle has

Table 11. *Octameroceras pugil* n. sp., dimensions in mm.

Specimen No	Illustration	LT	LBC	H	W
RM Mo 56627 (holotype)	Fig. 40A–C	77		54.4	45.4
RM Mo 56468				37.7	30.6
RM Mo 56469	Fig. 40F	51		36.5	30.6
RM Mo 56473		59		39.8	
RM Mo 56474		64		(36)	
RM Mo 56475		55	25.2		(36)
RM Mo 56476				36.1	(29)
RM Mo 56477		57		35.5	28.6
RM Mo 56478		45		33.6	
RM Mo 56483	Fig. 40G			36.5	30.0
RM Mo 56488		63		34.7	33.6
RM Mo 56643	Fig. 40D–E	90		56.2	52.3
RM Mo 56653	Fig. 40H–I	60		38.1	31.5
RM Mo 56655		62	30.3	(36)	(32)
RM Mo 56672		68		36.0	30.1
RM Mo 56683		90	47.5	(51)	(52)
RM Mo 57274		97	(52)	60.7	
RM Mo 57282	Fig. 40J	74		37.4	(32)
RM Mo 57283		63		(38)	31.6
RM Mo 152171				(67)	(58)
RM Mo 152172	Fig. 40K	82	36.0	52.8	

orthochoanic septal necks and is situated at the same distance from the ventral shell wall as the siphuncle is wide. On the macroconchs this width, and corresponding distance, is 6 mm at the anterior end and diminishes towards the apical end.

The proportion between height and length of the body chamber is almost 5:4 and the peristome is slightly protruding. On most macroconchs the apertural opening is diminished by a wide dorsal lobe, more than 10 mm long, two lateral and two ventrolateral lobes about half the length of the dorsal one. The growth of these lobes results in two pairs of 3–4 mm wide lateral sinuses and one slightly narrower ventral sinus, the latter continuing smoothly into the slit-like hyponomic sinus (Fig. 40C and E).

Some of the group of microconchs have an aperture similar to that described above, but the majority have two minor ventral lobes in addition to the lateral and ventro-lateral lobes (Fig. 40F and G). These extra minor lobes make the ventral sinus occurring in the macroconchs significantly wider.

The hyponomic sinus, which has a concave outside in lateral view ends in a drop-shaped hyponomic opening, situated in a minor protrusion about half-way between the apertural opening and the last septum.

On cut specimens and well preserved apertures, *O. pugil* does not seem to have any notable apertural reinforcements, except around the posterior part of the hyponomic opening.

Discussion. – As mentioned above the investigated material of *Octameroceras pugil* can be divided in two groups, on the basis of either size or shape of the aperture. Two distinct size groups can be discerned, with macroconchs having almost twice the diameter of the microconchs (Fig. 9).

A separation into two groups based on the apertural shape does not coincide with the size groups. All macroconchs have four lateral sinuses and one ventral sinus, while the microconchs either have this type of aperture or the more

complex form with six lateral sinuses. As is discussed in the chapter 'Dimorphism', the sexual dimorphism within *O. pugil* is reflected in the size variation and not the apertural shape.

One specimen, RM Mo 56484 *O. pugil* n.ssp², has, apart from being somewhat smaller, a different shell shape (Fig. 41A–B). The curvature on the dorsal side is more pronounced and the diminishing thickness of the phragmocone towards the apical end is similar to that of *O. rimosum*.

Comparison. – The similarities between *O. pugil* and *O. pugil* n.ssp² were presumably derived from a mutual ancestor and there is reason to believe that the Ludlovian *O. rimosum* descended from the Wenlockian *O. pugil* n.ssp² because of their great similarities in shape and size. For further discussion, see the description of *O. rimosum*. See also *O. unguifer* and Fig. 37.

Octameroceras pugil and *O. sinuosum* show great similarities, both in the shape of the shell and in the number of lobes and sinuses in the apertural opening. Both species are divided into two size groups but on the whole, *O. pugil* is smaller than *O. sinuosum*. Furthermore, *O. pugil* is more inflated and therefore has a stronger curvature on the dorsal side and a more pronounced concave ventral side of the phragmocone. In lateral view, *O. pugil* has a more rounded anterior end of the shell and has the hyponomic sinus sloping 35–40 degrees dorsally from the small protrusion around the hyponomic opening. The hyponomic sinus of *O. sinuosum* slopes only about 10 degrees and the protrusion with the hyponomic opening is more pronounced than that of *O. pugil*.

On the whole, *O. pugil* and *O. sinuosum* are so similar that there is good reason to believe that they are closely related. *O. pugil* is found in the Wenlockian Slite Beds, except for one specimen from the Ludlovian Hemse Beds, where all the known *O. sinuosum* are found. It might be suggested that *O. sinuosum* is descended from *O. pugil*, but unfortunately there is no material known from the beds between Slite and Hemse Beds.

Another species closely related to *O. pugil* is *O. unguifer*, also known from the Slite Beds. *O. unguifer* is in general slightly smaller and has a protruding apertural area. In lateral view the dorsal side of the body chamber on *O. unguifer* is fairly straight and the hyponomic sinus exhibits a concave profile. The apertural shape is almost the same in the two species, except for the fact that while *O. pugil* mostly has between four and six sinuses, *O. unguifer* has between six and eight sinuses.

Occurrence. – Sweden, Gotland: Samsugns l. Slite Beds, unit g, Wenlock. Mannegårde l. Hemse beds, Ludlow, Bringewoodian or early Leintwardinian.

Octameroceras rimosum (Barrande 1865)

Figs. 25B, 28, 42A–I

Synonymy. – □ *Phragmoceras rimosum* Barr. – Barrande (1865, Pl. 98:5–7). □ ? *Phragmoceras rimosum* Barr. – Barrande (1865, Pl. 48:1–3, 6–7). □ non *Phragmoceras rimosum* Barr. – Barrande (1865, Pl. 48:4–5, Pl. 98:8–9). □ *Phragmoceras rimosum* Barr. – Barrande (1867:230–231).

Table 12. *Octameroceras rimosum* (Barrande), dimensions in mm. Illustrations marked with an asterisk are from Barrande (1865).

Specimen No	Illustration	LT	LBC	H	W
L 383 (lectotype)	Pl. 98:5–7*	39		(21)	16.4
RM Mo 56301	Fig. 42F	41		24.3	22.8
RM Mo 56302	Fig. 42A–D	40		22.8	21.1
RM Mo 56304	Fig. 42G–H				21.6
RM Mo 56309	Fig. 42E			26.8	24.3
RM Mo 56310	Fig. 42I	41		(26)	22.5
RM Mo 56312		37	19.1		(22.4)
RM Mo 56313			21.2	24.3	(23)

Lectotype. – Specimen illustrated by Barrande (1865, Pl. 98:5–7) L 383 selected herein.

Type stratum. – e², Ludlow.

Type locality. – Hinter-Kopanina, Czechoslovakia.

Material. – One specimen from Bohemia; L 383 at Narodni Muzeum, Prague, Czechoslovakia. Seven specimens from Gotland; RM Mo 56301, Mo 56302, Mo 56304, Mo 56309, Mo 56310, Mo 56312 and Mo 56313 at SMNH, Stockholm, Sweden. All specimens are mature.

Diagnosis. – A species of *Octameroceras* with a slightly compressed, cyrtoconic endogastric brevicone, in mature specimens with contracted aperture. Mid dorsal salient and four opposite located lobes, leaving a very narrow aperture with four lateral sinuses and a narrow hyponomic sinus. The latter is unusually long and ends with the hyponomic opening located about mid body chamber. Siphuncle situated fairly close to the wall.

Description. – Strongly curved phragmocone with constantly decreasing diameter towards the apical end. The body chamber occupies almost 2/3 of the entire shell volume and the length is about equal to that of the phragmocone (Fig. 42F).

The specimens RM Mo 56301 (Fig. 42F) and RM Mo 56312 were cut dorso-ventrally along the long axis to allow examination of the interior of the phragmocones. The appearance of a distinctly diminished last chamber in front of the body chamber indicates that the cephalopods had reached maturity (Stridsberg 1981).

The body chamber's access to the outside is restricted to a very narrow aperture. One dorsal, two lateral and two lateroventral lobes diminish the apertural opening to a system of less than 1 mm wide, curved sinuses (Fig. 42D, E and I). The hyponomic sinus is unusually long, compared with those of other oncocerid cephalopods, and ends with only a minor widening at the site of the hyponomic opening on a protrusion at about the middle of the ventral side of the body chamber (Fig. 42G). On most specimens the hyponomic protrusion is not preserved and all specimens lack the protoconch and most of the apical end. Along the apertural sinuses are strong reinforcements observed on specimens with the shell partly removed.

Colouration is clearly visible on some specimens and con-

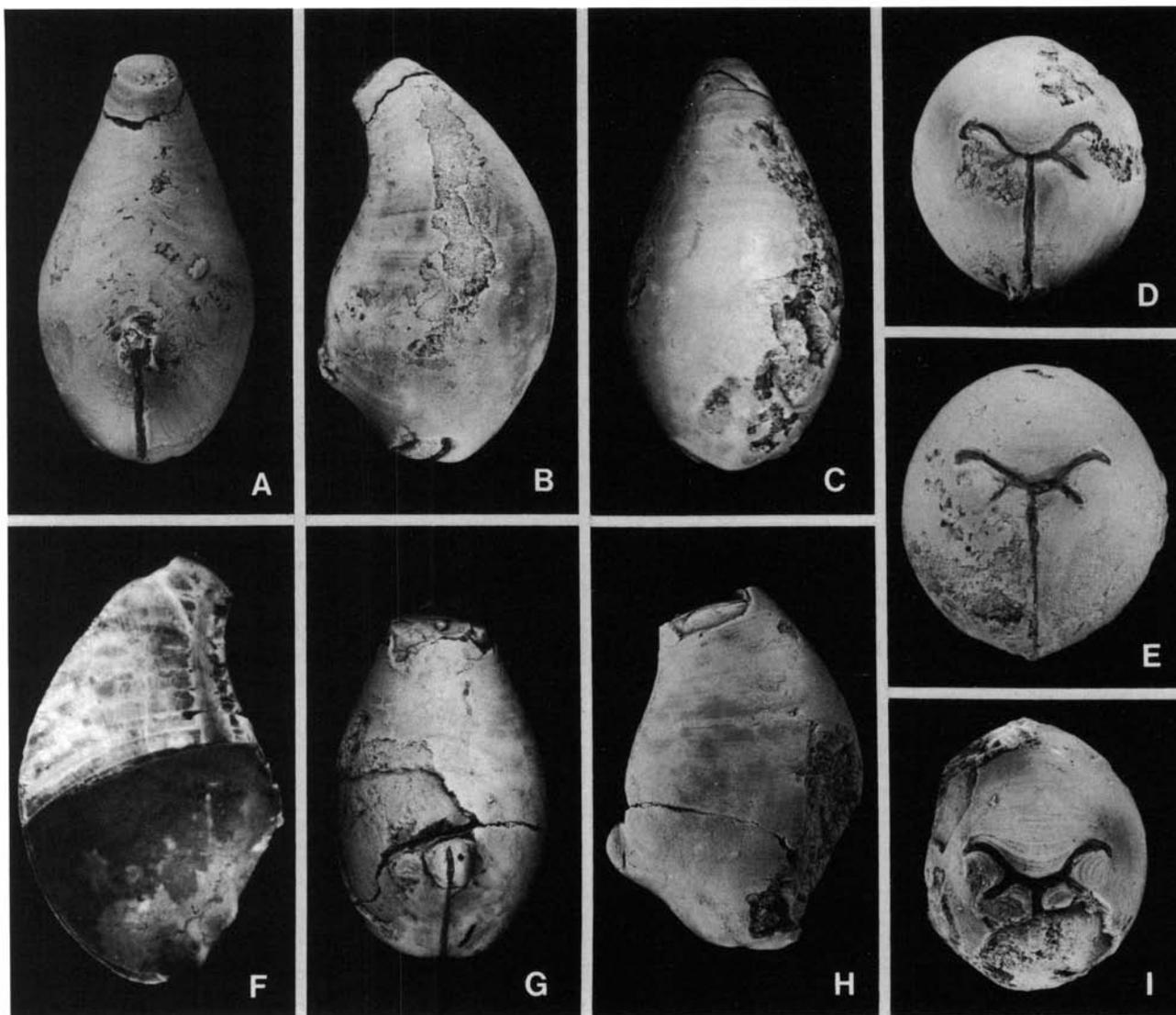


Fig. 42. *Octameroceras rimosum* (Barrande), $\times 1.5$. □A, B, C and D. Ventral, lateral, dorsal and apertural views of RM Mo 56302; Mannegårde 1. □E. Apertural view of RM Mo 56309; Mannegårde 1. □F. Specimen cut dorsoventrally along the long axis, RM Mo 56301; Mannegårde 1. □G and H. Ventral and lateral views of RM Mo 56304; Lill Rone 1. □I. Apertural view of RM Mo 56310; Mannegårde 1.

sists of transverse bands following the growth lines. Notable is the distinct V-shaped depression of the colour bands and accordant growth lines on the ventral side of the body chamber, ending around the hyponomic sinus (Fig. 25B).

The actinosiphonate siphuncle, situated 1.5 mm from the concave ventral shell surface in the last six chambers, is straight in this part. In the older chambers, the siphuncle follows the curvature of the shell and gets closer to the shell wall towards the apical end.

The distance between septa is fairly constant and has an average of 1.5 mm, except in the last chamber which is only 0.7 mm thick.

Discussion. – In his description of *Phragmoceras rimosum*, Barrande (1865 and 1867) referred to five specimens. The specimen in Pl. 98:5–7 (Barrande 1865) is one of the two best preserved and is here selected as the lectotype for *Octameroceras rimosum* (Barrande 1865). It should be pointed out, however, that the drawing in Pl. 98:5 (Barrande 1865) is slightly false with regard to the aperture, as the ventral pair

of sinuses merge into the dorsal pair of sinuses, rather than into the hyponomic sinus as is drawn in Fig. 5.

The specimen in Pl. 48:1–3 (Barrande 1865) is notably bigger and about twice the size of the lectotype and the Gotland specimens. General shape and form of aperture are, however, identical with the lectotype. The question arises if this is sexual dimorphism or not. Unfortunately only two specimens, this large one and the lectotype, have been found in Bohemia and all seven in the Gotland material are small. Therefore the specimen in Pl. 48:1–3 (Barrande 1865) can only tentatively be included within the species *O. rimosum*, until more material has been collected.

Concerning the specimen illustrated in Pl. 48:6–7 (Barrande 1865), I find it in such a poor state of preservation that it is hazardous to describe it as an *O. rimosum*. The illustrated aperture is very poorly visible on the specimen but some fragmentary traces indicate that it might be a similar aperture. I find the evidence too weak, however, to include this specimen in the species *O. rimosum*.

The two specimens in Pl. 48:4–5 and Pl. 98:8–9 (Barrande

1865) are poorly preserved with regard to the aperture, and the configuration of this is not clearly visible in either specimen. Without knowledge of the shape of the aperture and the position of the hyponomic sinus, these two specimens must be considered as most uncertain members of the species *O. rimosum*.

Barrande pointed out in the text to Pl. 48:4–5 (Barrande 1865) that this was a juvenile specimen. He did not explain, however, if his statement was based on the size of the shell or its straightness. Anyway, it is interesting to notice that Barrande seems to have accepted the idea that the aperture was already closed on juvenile specimens. The consequence of this must be that resorption took place during growth of the shell. With reference to the straight shell, it must be assumed that post-juvenile bending is not possible on a shell as this must mean total resorption of the shell. No resorption at all has been observed on any oncocerid shell. Furthermore, Barrande described the specimen in Pl. 48:6–7 (1865) as slightly older than the specimen on figs. 4–5 in the same plate, in spite of the fact that the curved shell is about the same size.

In conclusion I assume that the specimen in Pl. 48:4–5 does not belong to *O. rimosum*. Concerning the specimen in Pl. 98:8–9, the aperture appearance is not as convincing in the specimen as it is in the illustration. The reinforcement around the sinuses is only visible in this specimen and two of the specimens from Gotland, but overall the general outlook does not correspond too well with the lectotype. I prefer to leave the specimen in Pl. 98:8–9 out of the discussion on *O. rimosum*.

The Gotland material of *Octameroceras rimosum* is very homogenous and comprises six more or less complete specimens and one body chamber. The fossils are very well preserved with the recrystallized shell in an extremely good shape.

The phragmocone on the six Gotland specimens shows a distinct curvature with a convex dorsal side. This feature is not so dominant on the Barrandian lectotype and the question is how important this difference is. It should be mentioned, however, that the curvature on the dorsal side of the lectotype is not as straight as in the illustration in Pl. 98:6 (Barrande 1865).

Comparison. – *Octameroceras rimosum* seems to be closely related to *O. pugil* n.ssp?. This is discussed in the description of *O. pugil*. See also *O. unguifer*.

Occurrence. – Czechoslovakia: Hinter-Kopanina. c², Ludlow. Sweden, Gotland: Lill-Rone 1 and Mannegårde 1. Hemse Beds, Ludlow, Bringewoodian or early Leintwardinian.

Octameroceras unguifer n.sp.

Figs. 23A–B, 28, 43A–M

Derivation of name. – Latin *unguis*, unguis, referring to the unguiculated outline of the aperture.

Holotype. – RM Mo 56874.

Type stratum. – Slite Beds, unit g, Wenlock.

Table 13. *Octameroceras unguifer* n. sp., dimensions in mm.

Specimen No	Illustration	LT	LBC	H	W
RM Mo 56874 (holotype)	Fig. 43A–D	51		29.7	25.5
RM Mo 56853	Fig. 43F–G	62		28.1	25.9
RM Mo 56860		49	26.7	28.4	
RM Mo 56861		45	28.0	(29)	(25)
RM Mo 56862	Fig. 43J	46		(28)	
RM Mo 56863	Fig. 43K	44		28.8	24.7
RM Mo 56864		44		(28)	
RM Mo 56875	Fig. 43H–I	45		28.1	(22)
RM Mo 56881		50	26.3	29.6	
RM Mo 57285	Fig. 43E and L	49		28.5	25.2

Type locality. – Samsugns 1, Gotland, Sweden.

Material. – Ten specimens from Gotland; RM Mo 56853, Mo 56860, Mo 56861, Mo 56862, Mo 56863, Mo 56864, Mo 56874, Mo 56875, Mo 56881 and Mo 57285 at SMNH, Stockholm, Sweden. All specimens are mature.

Diagnosis. – A species of *Octameroceras* with a slightly compressed endogastric brevicone, in mature specimens with a contracted aperture, having a dorsal salient, two lateral, two ventrolateral and two diminished ventral lobes. Hyponomic sinus very narrow and terminating in the hyponomic opening, situated in an anterioventral protrusion.

Description. – Slightly compressed shell with a primary endogastric phragmocone. Approximately the last quarter of the phragmocone, as well as the body chamber, grew almost straight, even if the dorsal side as well as the ventral side of the body chamber, are convex.

Average distance between septa is about 3 mm, except in the last chamber where the distance is about half this amount (Fig. 43M). The actinosiphonate siphuncle, straight in the last chambers, follows the ventral shell wall at a distance of about 2 mm. The width of the siphuncle is a little more than 4 mm in the last chamber. The septal necks are orthochoanic.

The body chamber is fairly straight on its dorsal side, as is also the case with the ventral shell wall between the hyponomic opening and the periphraet. Proportion between height and length of the body chamber is about 1:1.

Octameroceras unguifer has an unusual apertural area as it protrudes a few millimeters (Fig. 43A–B). The result of this is that there is no smooth continuation of the outer shell wall on to the apertural lobes, but a fairly sharp angle. The apertural opening is diminished by one dorsal salient, two lateral, two ventrolateral and two ventral lobes. The length of the dorsal salient, as well as the lateral and ventrolateral lobes is about 5 mm. The ventral lobes, however, are mostly very short, only 1–2 mm, but occasionally they can reach the same size as the other lobes. On one specimen, Mo 56863, the left ventral lobe is 5 mm and ventral to this is an extra lobe, about 1 mm long. Unfortunately the ventral part of the opposite side of the aperture is damaged so it cannot be observed if there was an extra lobe as well (Fig. 43K).

Specimen RM Mo 57285 seems to have developed a minor lobe about 1 mm long between the right ventrolateral and

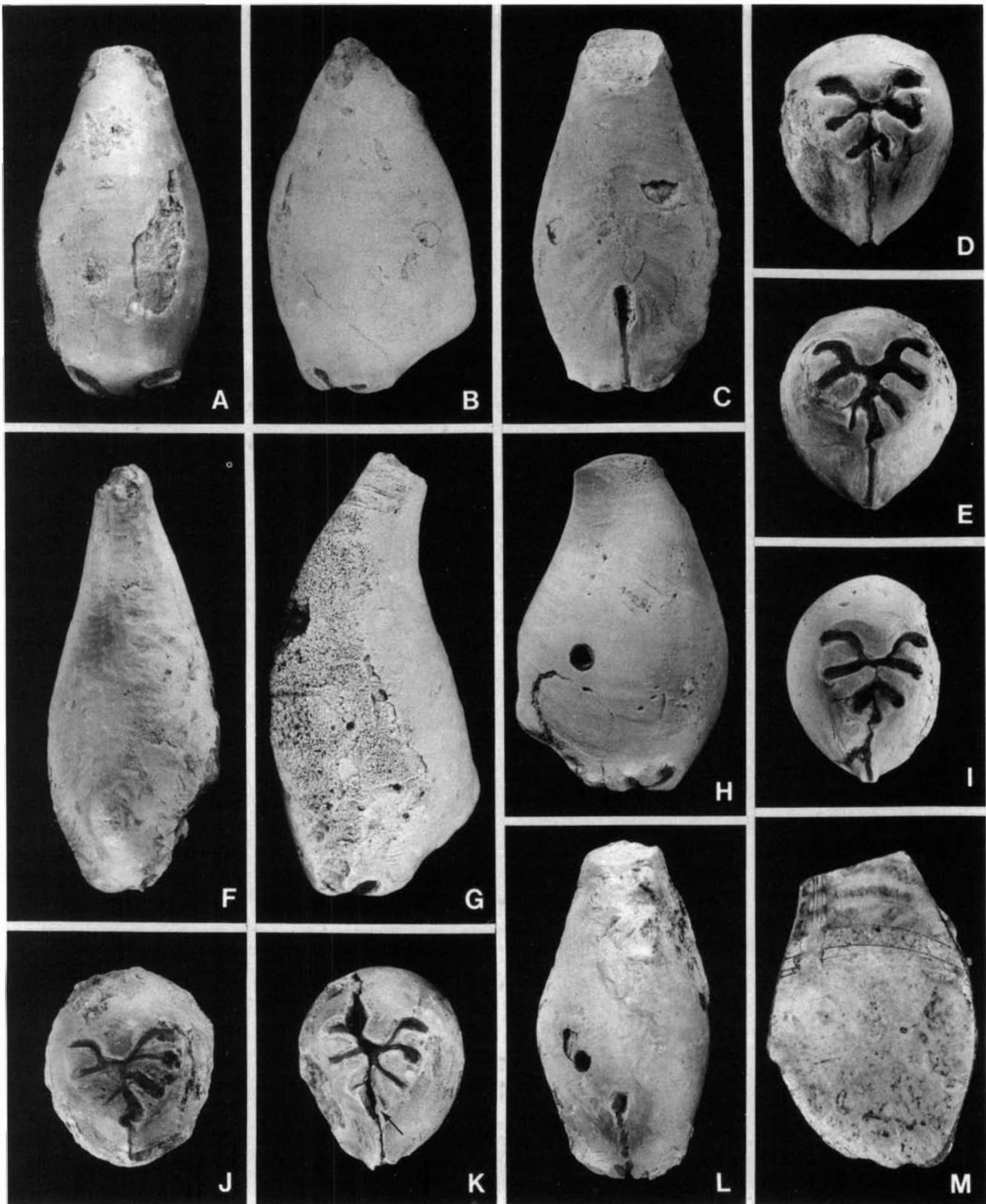


Fig. 43. *Octameroceras unguifer* n. sp., $\times 1.2$; Samsugns l. □A, B, C and D. Dorsal, lateral, ventral and apertural views of the holotype, RM Mo 56874. □E. Apertural view of RM Mo 57285. □F and G. Ventral and lateral views of RM Mo 56853. □H. Lateral view. Note the bore hole in the body chamber, RM Mo 56875 (see also Fig. 23A). □I. Apertural view of the same specimen as in H. □J. Apertural view of RM Mo 56862. □K. Apertural view. The black arrow indicates a small ventral lobe, RM Mo 56863. □L. Ventral view of the same specimen as in E. Note the bore hole close to the hyponomic opening (see also Fig. 23B). □M. Specimen cut dorsoventrally along the long axis, RM Mo 56861.

right ventral lobes. The latter is fairly small, only 3.5 mm long, and situated very close to this extra lobe. Furthermore, the right ventral lobe is even smaller than the opposite left ventral lobe which is 5 mm long (Fig. 43E). A further discussion about the development of extra lobes is found on p. 11.

In lateral view the very narrow hyponomic sinus is concave because of the hyponomic protrusion and the protruding apertural area (Fig. 43B). The drop-shaped 2 mm wide hyponomic opening, situated about half-way between the apertural opening and the periphraet, is located in the middle of the 2–3 mm long hyponomic protrusion.

As far as can be observed on the investigated material with the shell preserved, there seems to be no reinforcement along the peristome just before the beginning of the lobes.

Discussion. – Within *Octameroceras unguifer* no size dimorphism can be observed in the investigated material. Neither does any notable variation in the apertural shape exist, except the development of an extra lobe, or perhaps an extra pair of lobes, as described above. The only possible indication of dimorphism is the more slender shape of the phragmocone in specimen Mo 56875 (Fig. 43H–I). The difference is very small and can presumably be regarded as an individual variation. It should be pointed out, however, that the slenderness is reminiscent of the shape of the single specimen, here described as *O. pugil* n.ssp?, even if it is not so pronounced.

The consequence of the constriction posterior to the peristome due to the protruding apertural area, is that the continuation from the more or less constricted shell to the apertural lobes must be fairly sharp and the lobes are almost perpendicular to the shell wall. Furthermore, the peristome in the bottom of the sinuses tends to lean outwards. This partial constriction is extraordinary among the Gotland oncocerids.

Comparison. – *Octameroceras unguifer* appears to be closely related to *O. pugil* and distinguishing characteristics are discussed in the description of *O. pugil*. The apertural shape of *O. pugil* n.ssp? is very similar to that of *O. unguifer*. On the whole, however, the lateral and dorsal views as well as the remains of the damaged hyponomic protrusion of *O. pugil* n.ssp? correspond to *O. rimosum*. This supports the idea of a close relationship to *O. rimosum* rather than to *O. unguifer*, even if the latter is also related to *O. pugil* (Fig. 37).

From the Estonian island Oesel, about 170 km ENE of Gotland, Jaekel (1902) has illustrated and named a species *Hexameroceras osiliense*, which has an aperture very similar to that of *Octameroceras unguifer*. *O. osiliense*, however, does not have the protruding apertural area characteristic of *O. unguifer*. The holotype of *O. osiliense*, the only known specimen, consists of a mould and a cast and because of the poor state of preservation and absence of vital parts, its taxonomic relationship to *O. unguifer* cannot be determined. The specimen, MB.–C.749.1–2 is deposited in Museum für Naturkunde in Berlin (DDR).

Occurrence. – Sweden, Gotland: Samsugns l. Slite Beds, unit g. Wenlock.

Summary

In the Wenlockian and Ludlovian Beds on Gotland fairly rich faunas of oncocerid cephalopods have been collected. In these faunas four species, originally described from the Barrandian, were identified and eight new species described. The four earlier known species were *Trimeroceras cylindricum*, *Pentameroceras mirum*, *Inversoceras p. perversum* and *Octameroceras rimosum*. When describing the new species it turned out that two new genera were involved, here named *Jeppssonoceras* and *Plemeroceras*. The new species were *Trimeroceras bulbosum*, *Pentameroceras facula*, *Clathroceras plicatum*, *Jeppssonoceras concentratum*, *Plemeroceras cassis*, *Octameroceras sinuosum*, *O. pugil* and *O. unguifer*.

During the descriptive work an extensive revision within Trimeroceratidae and particularly within Hemiphragmoceratidae was necessary. Studies of the apertural growth in immature and mature specimens showed that the number of sinuses is not a reliable characteristic when describing new genera, or even species. Thus species earlier included in the genera *Tetrameroceras*, *Hexameroceras* (except the type species) and *Octameroceras* can be shown to belong to one and the same genus. The correct name of this genus turned out to be *Octameroceras*.

Comparative studies on material from Barrandian collections and that from Gotland showed that four species were in common. Comparisons with British material did not reveal any mutual species but one of the species found on Gotland and in Czechoslovakia, *Pentameroceras mirum*, was also known from the United States.

A tendency shown in the material is that species with a small shell and very restricted aperture are more widespread than species with a large shell and open aperture. Naturally the investigated material is far too limited to allow any conclusions but it can be demonstrated that this tendency is also observed among the Gotland localities. This might very well indicate different living habits between species with a large thick shell, such as *Jeppssonoceras concentratum*, and species with a small delicate shell, as for example *Pentameroceras mirum*. Perhaps the large ones were bottom dwellers and the small ones global drifters.

In six of the investigated species a distinct dimorphism was recorded. This dimorphism was either characterized by the size of the shell or in a few cases, by varying stoutness, or both. Dimorphism did probably occur in another three species, but here the number of specimens known was too small for any reliable conclusions. The volume difference between the macroconchs and the microconchs is by no means as large as within the ammonites. Contradictory to the interpretation of the dimorphism within these, it is here suggested that the oncocerid macroconch represented the male, as is the case with *Nautilus*, the only extant nautiloid genus.

Truncation of the apical end of the phragmocone can be demonstrated in three species. The benefit of truncation is unclear, but presumably hydrodynamic aspects are involved in the sense that a truncated shell is more adapted for good swimming. The mechanism behind truncation is not known but resorption of the shell inside the chamber, posterior to the septum of truncation, might be a possibility. In spite of the fact that none of the specimens in the remaining nine

species has the apical end preserved, truncation was not provable among any of these.

Apart from improving the swimming ability, truncation could, but did not have to, influence the buoyancy of the shell. In such a case, the effect must have been very limited as the very small loss of floating capacity, represented by the narrow apical end, could only have caused marginal changes.

Malformation of the shell in the apertural region, due to attack by predator or pathological reasons, can be observed in a few specimens. The oncocerids, however, had a remarkable healing power and in all cases the shells were repaired fairly soon. Even when the oncocerids were attacked by boring organisms, they were able to defend themselves. In some shells an additional shell secretion was found in the body chamber, immediately inside the bore hole. This defence was not always successful as the intruder occasionally penetrated the reinforcement. As almost all bore holes were drilled at a specific place on the body chamber, slightly posterior to the hyponomic opening, the possibility of parasitism is evident.

Colour pattern, consisting of horizontal striations on the shell, occurred on some oncocerids and this feature must be regarded as equivalent to the camouflage pattern on the extant *Nautilus*.

Palaeoecological studies of oncocerid cephalopods are complicated as the shells are transported *post mortem*. The apertural configuration, however, in combination with shell studies, indicates specific swimming abilities and buoyancy conditions. The apertural opening must reflect the activities of the soft parts and the narrow sinuses on the oncocerids can only have permitted very limited movement. Presumably their main purpose was that of food-gathering, as swimming was probably performed by the hyponome. The restricted aperture was certainly developed for mainly protective purposes. Because of the hindrance of a shell, the animal could not escape from predators, and therefore a closed shell was very useful. Regarding moving ability among the oncocerids this was totally dependant on whether the shell was buoyant or not. If locomotion was accomplished by jet propulsion, this demanded a floating shell.

Comparisons made with living *Nautilus* and *Spirula*, the latter being particularly suitable as it floats vertically as the oncocerids are supposed to have done, strengthen the hypothesis that swimming was performed by jet propulsion. This demands a specific location of the hydrodynamic centre and the hyponome. Different degrees of swimming ability depend on the shape of the shell and the location of the hyponomic sinus.

Appendix

Localities

Rikets nät grid system is used. Within brackets, UTM grid system.

DJUPVIK, 552–559 403–411 (CJ 274–282 548–554), ca. 4000–5200 m SW of Fröjel church. Topographical map sheet 6 I Visby SO. Geological map sheet Aa 164 Hemse.

An about 1 km long cliff section along the shore SW of the harbour of Djupvik. No details are known where the fossils labelled

Djupvik were found. Laufeld (1974) has a list of references on more precise localities in Djupvik. See also Jeppsson (1983).

Mulde Beds, lower part.

Oncocerids: *Trimeroceras bulbosum*.

HAGEBY TRÄSKBACKE, 5900 6015 (CJ 4735 5700), ca. 2100 m SW of Etelhem church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 164 Hemse.

No details are known where the fossils labelled Hageby träskbacke were found, but presumably it might be the fairly steep hill E of Hageby träsk.

Hemse Beds.

Oncocerids: *Pentameroceras mirum*.

KANALEN

The locality description on the label left with the specimen states only 'Kanalen, Lummelunda'. *Kanal* is the Swedish word for canal, and the canal at Lummelunda is about 3 km long. The eastern half of the canal is dug in Tofta Beds and the western part in Högklint Beds. However, south of the middle part of the canal is a farmhouse called Kanalen, and the locality might be close to this. Laufeld described a section in the canal, close to the house. This locality, Kambs 2 (Laufeld 1974), might be synonymous with 'Kanalen, Lummelunda'.

Högklint or *Tofta Beds*.

Oncocerids: *Pentameroceras facula*.

References: Hede 1940, p. 35, lines 3–5 from below; Laufeld 1974, Kambs 2.

KLINTS

The specimens from the Museum of Natural History labelled 'Klints, Othem' were probably collected at Klints backar south of Othem. This is an inland cliff and is described by Laufeld (1974a) as Spillings 1 and Spillings 2.

Slite Beds, unit g.

Oncocerids: *Octameroceras pugil*.

References: Martinsson 1962, p. 52; Hede 1928, p. 24 lines 3–8 from below (reference to the area in general); Laufeld 1974a, p. 124 and 125.

LILL RONE 1, 5705 6215 (CJ 4920 5495), ca. 2300 m NW of Lye church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 156 Ronehamn.

The southern of two small outcrops about 5 m E of the previous railway between Etelhem and Stånga, 450 m NW of the farm house of Lill Rone.

Hemse Beds, probably middle or upper part.

Oncocerids: *Inversoceras p. perversum*, *Plemeroceras cassis*, *Octameroceras sinuosum* and *O. rimosum*.

References: Holm 1898, locality 286 in Holms field diary, available at SGU, Uppsala.

LINDE KLINT, 535–540 542–553 (CJ 410–422 519–524), ca. 100–1200 m NW of Linde church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 164 Hemse.

Linde klint is a steep hill with a sloping south side. No details are known where the fossils labelled Linde klint, were found.

Hemse Beds, upper part.

Oncocerids: *Pentameroceras mirum* and *Inversoceras p. perversum*.

MANNEGÅRDE 1, 5675 6350 (CJ 5055 5495), ca. 1100 m NNW of Lye church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 156 Ronehamn.

No longer accessible road section 150 m SE of the house Manne-gårde, E of the road between Etelhem and Lye.

Hemse Beds, probably middle or upper part.

Oncocerids: *Trimeroceras cylindricum*, *Pentameroceras mirum*, *Clathroceras plicatum*, *Jeppssonoceras concentratum*, *Plemeroceras cassis*, *Octameroceras sinuosum*, *O. pugil* and *O. rimosum*.

References: Holm 1898, locality 287 in Holm's field diary, available at SGU, Uppsala.

MANNEGÅRDE 2, 5645 6380 (CJ 5065 5415), ca. 850 m NNW of Lye church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 156 Ronehamn.

No longer accessible road section 350 m SE of the house Mannegårde, E of the road between Etelhem and Lye.

Hemse Beds, probably middle or upper part.

References: Holm 1898, locality 288 in Holm's field diary, available at SGU, Uppsala.

MÖLLBOS 1, *Halla Beds*, unit b.

Oncocerids: *Trimeroceras bulbosum*.

References: Laufeld 1974a, b; Laufeld & Jeppsson 1976; Larsson 1979; Claesson 1979; Laufeld & Martinsson 1981; Stridsberg 1981a, b; Liljedahl 1981, 1983, 1984, 1985; Jeppsson 1983.

NORRVANGE KANAL, N of Lärbro church. Topographical map sheet 7 J Fårösund SO & NO. Geological map sheet Aa 171 Kappelshamn.

No details are known where the fossils labelled Norrvange kanal were found. The only canal in the neighbourhood of the farmhouse Norrvange, 1300 m NW of Lärbro church, is dug east of the road between Lärbro and Kappelshamn.

Slite Beds.

Oncocerids: *Pentameroceras mirum* and *P. facula*.

PETESVIKEN, *Hemse Beds*.

Oncocerids: *Pentameroceras mirum*.

References: Larsson 1979.

SAMSUGNS 1, *Slite Beds*, unit g.

Oncocerids: *Trimeroceras bulbosum*, *Pentameroceras mirum*, *Octameroceras pugil* and *O. unguifer*.

References: Lindström 1881, p. 9; Laufeld 1974a.

SANDARVE KULLE, 526–530 530–532 (CJ 3985–4005 5110–5155), ca. 1300 m N of Fardhem church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 164 Hemse.

Sandarve kulle is a steep hill, about 400 m long, with a number of exposures. No details are known where the fossils labelled Sandarve kulle were found.

Hemse Beds, probably upper part.

Oncocerids: *Trimeroceras cylindricum*, *Pentameroceras mirum* and *Plemeroceras cassis*.

STOCKVIKS KANAL, ca. 1–4 km N of Hamra church. Topographical map sheet 5 I Hoburgen SO & 5 J Hemse SV. Geological map sheet Aa 152 Burgsvik.

The label found with the specimen from the Museum of Natural History states only 'Stockviks kanal, near Hamra'. North of Hamra a network of canals have been dug and the fossil in question must have been found somewhere in this area.

Hamra Beds.

Oncocerids: *Trimeroceras cylindricum*.

STORA VEDE 1, *Slite Beds*, unit g.

Oncocerids: *Trimeroceras bulbosum*.

References: Laufeld 1974a.

TÄNGLINGS HÄLLAR 1, 587 631 (CJ 503 565), ca. 1700 m SE Etelhem church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 156 Ronehamn.

A number of small quarries and outcrops 200–300 m E of the road between Lye and Etelhem, about midway between Nyhagetorp and the SE part of the 'skjutbana' (shooting-range).

Hemse Beds, middle or upper part.

Oncocerids: *Trimeroceras cylindricum*, *Pentameroceras mirum*, *P. facula*, *Clathroceras plicatum* and *Octameroceras sinuosum*.

References: Holm 1898, locality 884 mistakenly written, should be 284; Holm 1900; field diaries available at SGU, Uppsala.

TÄNGLINGS KVARN 1, 5895 6220 (CJ 4945 5680), ca. 1100 m S of Etelhem church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 156 Ronehamn.

Old quarry in a hill in the SE corner of a small wood, 325 m W of the old wind mill.

Hemse Beds, probably middle or upper part.

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