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Telescoping in Orthoconic Nautiloids: An Indication of High or Low Energy Hydrodynamic Regime?

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„Teleskop”-Erhaltung bei orthoconen Nautiloideen: Hinweise auf hoch- oder niedrig-energetischen Lebensraum?

Zusammenfassung

Häufigkeit und taphonomische Erhaltung von teleskopartig ineinander geschobenen orthoconen Nautiloideen aus dem Silur der Karnischen Alpen wurden sowohl im Gelände, wie auch in Dünnschliffen untersucht, um festzustellen, ob diese Erscheinung auf ein hydrodynamisches System mit hoher oder niedriger Energie hinweist. Die Beobachtungen an diesem „Teleskop”-Phänomen ergaben, dass für die betreffenden stratigraphischen Abschnitte ein niedrig-energetisches Environment anzunehmen ist. „Teleskop”-Gehäuse bilden nur einen geringen Prozentsatz der gesamten erhaltenen Nautiloideen-Fauna.

Eine Überprüfung der Literatur zu diesem Thema zeigt, dass zwei Arten von „Teleskop”-Erhaltung erwähnt werden: die eine ist in Environments mit niedriger Energie zu beobachten, wo kleinere Orthocone einen Teil der Sedimentfüllung der Wohnkammer oder des Siphos bilden, ohne die Wirtsschale zu zerbrechen. Die andere tritt in Hochenergie-Environments auf, wo ein Gehäuse in ein anderes eindringt und dabei die Wirtsschale beschädigt. Die Gehäusemorphologie ist im letzteren Fall ein wesentlicher Faktor. „Teleskop”-Erhaltung scheint bei den orthoconen Nautiloideen ein relativ seltenes Phänomen zu sein.

Abstract

A study of the frequency of occurrence and taphonomic preservation of telescoped orthoconic nautiloid specimens both in the field and in thin section was carried out in order to determine whether the phenomenon is indicative of either high or low energy hydrodynamic regimes. The specimens studied are from the Silurian of the Carnic Alps (Austria) and a low energy environment is inferred from the observations of the telescoping phenomenon for the stratigraphic intervals investigated. Telescoped specimens form a small percentage of the overall nautiloid fauna preserved.

A literature review of this topic demonstrates that two types of telescoping may be recognised: one occurs in low energy environments where smaller orthocones form part of the sedimentary infill of the body chamber or siphuncle without breakage of the host shell; the second takes place in a high energy environment where one shell penetrates another damaging the host shell. Shell morphology is a major contributary factor in the latter case. Telescoping in orthoconic nautiloid shells appears to be a relatively rare phenomenon.

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1. Introduction

The phenomenom of telescoping in orthoconic nautiloids has been accepted as an indicator of a high energy depositional environment in the Silurian Cephalopod Limestone biofacies and of orthocerid nautiloid concentrations in general (FERRETTI, 1989; BOGOLEPOVA & HOLLAND, 1995; FERRETTI & KRIZ, 1995; FERRETTI et al., 1999; HISTON et al., 1999).

However, the actual mechanism of how it occurs is not clearly understood. Several studies of the "*Orthoceras* Limestone" and the Cephalopod Limestone biofacies in Silurian sequences have been done over the last decades (GNOLI et al. [1980] for SW Sardinia; HOLLAND et al. [1994] gave a general review of cephalopod concentrations globally in the Lower Palaeozoic; KRIZ [1998] and FERRETTI & KRIZ [1995] for the Prague Basin; BOGOLEPOVA & HOLLAND [1995] for Russia and Kazakhstan; BOGOLEPOVA [1998] for North Asia; FERRETTI et al. [1999], HISTON [1999], HISTON & SCHÖNLAUB [1999] for the Carnic Alps) but each case appears to present particular environmental conditions and consistent similarities which may be used to determine the reason for the development of this facies are difficult to ascertain. The phenomenom of telescoping, characteristic of these limestones, has been regarded by the above mentioned authors as indicative of an high energy environment. However, no detailed study has been done of the telescoping frequency in the nautiloid populations nor of the taphonomy of the nautiloids within these limestones in which the telescoping occurs in order to substantiate a high energy environment conclusion. Taphonomic studies of the post-mortem behaviour and deposition of nautiloid cephalopod shells (REYMENT, 1958; BOSTON & MAPES, 1991; HEWITT & WESTERMANN, 1996) deal with many aspects of their preservation; however, telescoped specimens were not considered in these studies.

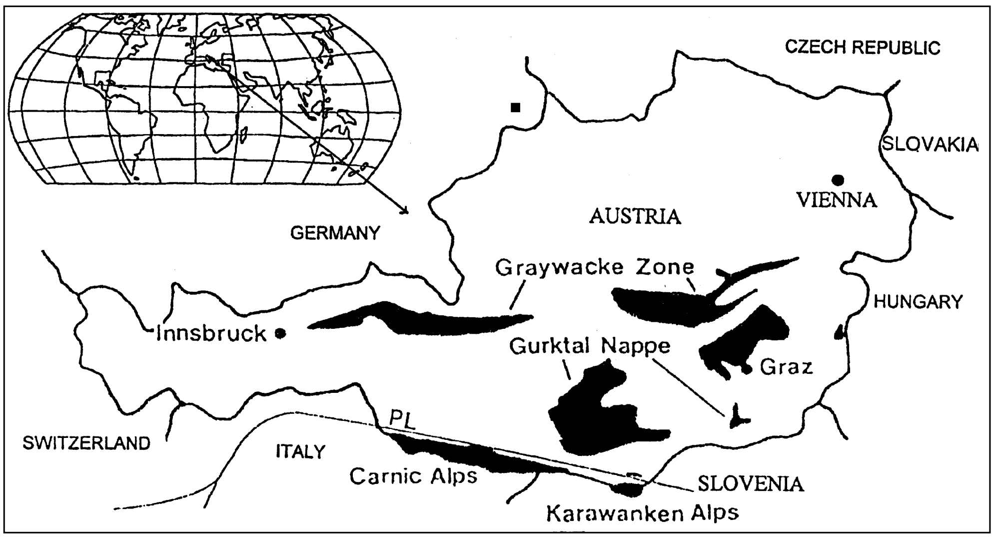
A study of the frequency of occurrence and taphonomic preservation of telescoped nautiloid specimens both in the field and in thin section was carried out in order to determine whether the phenomenon is indicative of either a high or low energy hydrodynamic regime. The majority of specimens studied are from the Silurian of the Carnic Alps, Austria (Text-Fig. 1). Examples are also noted from the Silurian of the Prague Basin and Morocco. A literature review of telescoping in orthoconic nautiloids is also included and the conclusions of those authors are discussed in relation to the new data presented here.

2. Previous Studies

HALL (1847, p. 207) in his descriptions of the many specimens, which he assigned to his new genus *Endoceras*, proposed the idea that smaller orthoconic nautiloids within the siphuncle of larger orthocones implied that the specimens in the siphuncle were the embryoes developing within the parent shell. The majority of these embryo specimens we now know are siphuncular deposits called endocones, but in some cases these were telescoped specimens (1847, pl. 18). HALL did not accept that small shells could accidentially be found within larger shell siphuncles and he argued that their constant orientation with the apex in the same direction as the parent shell thereby excluded this possibility.

BARRANDE (1874, 1877) discussed the inclusion of smaller orthocones within larger ones on two separate occasions in his text on the cephalopod fauna of Bohemia: one in connection with the genus *Endoceras* HALL, the other under the heading of "Fossilisation". He considered at length (1874, p. 773–782) the theory by HALL that the occurrence of small orthocones within the siphuncle of the "mother" outer orthocone was a form of reproduction in *Endoceras* and gave a detailed translation of HALL's documentation of this "feature". He outlined his arguments against this theory both with his own studies on the Prague Basin material and by citations from contemporary studies. He concluded that the explanation was simply that the young shells form part of the infilling matrix of the siphuncle and that this happened after decay of the animal where floating fragments of slender orthocones penetrated the siphonal cavity of a species with a larger siphon. He considered this event to be a rare occurrence.

In his chapter on "Fossilisation ou Remplissage inorganique de la coquille des Céphalopodes" (1877, p. 1246–1280) he treated the phenomenom of small orthocones within larger shells in great detail. He stated that penetration was of two types: one due to impact where it is seen that one shell has traversed the septa and shell of another; the other a non-violent introduction of smaller shells into an open cavity such as the body chamber or siphuncle of an orthocone together with other shell material within the sediment during immersion and burial. In the first case he noted that certain thin shelled species with numerous structurally weak septa appertained to the shells that were more commonly penetrated as they were more susceptible to breakage and frequently showed



Text-Fig. 1.
Location map of the Carnic Alps, Austria.
PL = Periadriatic Line.

broken septa and conch wall. BARRANDE envisioned that this occurred during impact while floating in great numbers in a restricted space or during immersion in the water as the shells were washed up on the shore. He gave examples (1866, pl. 217) from certain strata in the Prague Basin to support his theory but stated that he considered this phenomenon as being relatively rare considering the numerous shells contained within these particular layers.

In the second case (1866, pl. 216) he considered smaller slender shells or fragments of easily broken, thin shelled orthocones having penetrated the siphuncle or the body chamber of larger more resistant shells. He remarked that it maybe the lack of a body chamber lost during impact which allows material to be mechanically deposited within the siphuncle on the sea bottom. He also noted that chemical action of the seawater in some cases had dissolved completely or in part the septa and siphuncle of the shell during the long post-mortem floating period thus providing a cavity which could easily be infilled by sediment or other shell material. He concluded that the phenomenom of orthocones within orthocones occurred slowly during immersion and burial on the sea floor as sediment and other material, such as gastropods, may be seen in the chambers of some shells. Geopetal evidence showed that the orthocones were in a horizontal not vertical position when this took place. BARRANDE's detailed study, supported by well-illustrated specimens still stands as one of the best discussions of this topic and his conclusion that two distinct mechanisms were responsible for telescoped specimens has not been disproved by evidence from other areas where this phenomenon is known. He completed his study with a review of illustrations and references by earlier authors to these orthocones within orthocones and commented on their conclusions in light of his own ideas.

MILLER & YOUNGQUIST (1949) described a coquina of nautiloid cephalopods from the Maquoketa Shale (Ordovician), Iowa and concluded that wave action in shallow water accounted for telescoping in these specimens. They noted that as many as four specimens could be telescoped together with the orientation to each other sometimes being reversed and that the septa invariably have been fractured. Since the concentration of shells is dominated by one species which has a small siphuncle and thin septa, they presumed that this factor facilitated the telescoping effect. The conch wall was however, quite thick and therefore could withstand the stress of an impact and breakage of the septa. A high percentage of the specimens in this accumulation are telescoped together, and this fact, together with their random orientation to bedding, lead them to the conclusion that the wave action was very strong.

GNOLI et al. (1980) described the occurrence of telescoped specimens from the "*Orthoceras* limestones" of SW Sardinia and interpreted the environment as being predominantly tranquil and only occasionally affected by an oscillatory wave motion which caused the larger orthoconic shells to be penetrated by smaller ones. They illustrated two situations (1980, Text-Fig. 3); one with telescoped specimens in the body chamber, the other one with small orthocones in the siphuncle. No evidence of septal breakage by penetration was noted in the study. The shells themselves are also stated to be well preserved with apex and body chamber frequently intact. The shells are concentrated on preferred planes sometimes being oriented on the horizontal plane but also sometimes being randomly oriented.

FREY (1989) in his study of an Ordovician nautiloid assemblage from Ohio noted a few fragmentary specimens from thin packstone beds which were occasionally telescoped and attributed this to reworking by storm currents in an otherwise low energy shallow marine environment. Specimens within the assemblage were generally preserved with unbroken septa although it is not clear if this also applies to the telescoped specimens.

FERRETTI & KRIZ (1995) discussed the phenomenon of telescoping in relation to a study of the Silurian Cephalopod Limestone Biofacies in the Prague Basin. The environment for the Branik type cephalopod limestone, where they observed this phenomenon, is given as below normal wave base with little or no current activity with episodic higher energy deposition due to currents of the cephalopod bearing beds. The authors proposed that telescoping happened prior to deposition during the high energy event but they did not exclude the likelihood that telescoping may have occurred on the sea floor immediately after deposition due to turbulence just behind the host shell. They noted that transverse sections of the shells show that telescoping had happened when the outer bigger conchs were partly filled by sediment. They did not state if broken septa were observed in these specimens.

As may be seen from the above treatments of this phenomenon summarised here, the palaeoenvironmental interpretations vary from shallow low energy conditions occasionally affected by episodes of higher energy to high energy storm deposition events. In addition, different workers have come to remarkedly different opinions regarding the mechanism that produced the telescoping condition in orthoconic nautiloids.

3. Nautiloid Material Studied

3.1. Method and Material

Two approaches were used in order to obtain a detailed data set for telescoped specimens:

1) Observation directly in the field or hand specimen and
2) in thin section where the preservation of the outer and inner shells in relation to each other could be studied.

Frequency counts of particular features of orthoconic nautiloids such as telescoping, iron coating, fragmentation and their orientation to bedding have been taken at particular levels in the field using a one half meter square quadrat. Each orthoconic nautiloid specimen within that area was marked with a numbered dot so as to avoid recounting of specimens. The presence of a series of preserved characters were noted for each specimen: telescoped specimens and their position within the outer conch i.e. in the body chamber or phragmocone; nature of coating or infilling of the shell and presence of geopetals; fragmentation of the outer or inner shells; orientation of the shell to the bedding plane; orientation of the apexes of the shell on the bedding plane; presence of the body chamber and any other features thought relevant to the study. The telescoped specimens were further investigated for their orientation to bedding, section observed (longitudinal or transverse), presence of septa in the outer orthocone and presence of the body chamber.

Two sections from the Silurian of the Carnic Alps ranging in age from Wenlock to middle Ludlow where telescoped specimens occur were studied. The results from three cases are given in Text-Fig. 2 for

1) Cellon section: bed 13 (Wenlock).
2) Cellon section: bed 18 (Ludlow).
3) Rauchkofelbodentörl section: Wenlock.

The data is presented as a percentage of the total number of specimens occurring within the studied area with the specific data for telescoped specimens being illustrated separately.

Thin sections from the Silurian sequences of the Carnic Alps prepared for a taphonomic and microfacies study of these strata also revealed some telescoped orthoconic nautiloids. These telescoped specimens were not in great abundance in the thin sections because they were not taken specifically for the present study. But, these sections show interesting preservation of the outer and inner shells in relation to each other and in particular of the infilling of body chambers with sediment containing smaller orthoconic shells.

Additional general observations were made on other available material. An example includes polished slabs and hand specimens from Morocco. Frequency counts were not carried out on this material.

3.2. Stratigraphy of the Nautiloid Localities

3.2.1. Cellon Section

The Cellon section is located in a narrow avalanche gorge on the eastern flank of Mount Cellon near the Austrian/Italian border at an altitude of 1560 m and is well-known for its rich fossil occurrences (SCHÖNLAUB, 1997). The strata range in age from the Late Ordovician to the Early Devonian and are dated both by conodonts (WALLISER, 1964) and graptolites (JAEGER, 1975). Nautiloid cephalopods are abundant in the Silurian particularly in the Wenlock and Ludlow sequences. Two stratigraphic intervals within the mainly carbonate Kok Formation were considered for this study: Bed 13, dated as the *O. sagitta* conodont biozone (Middle Wenlock in age) and Bed 18, the *ploeckensis* conodont biozone (Early Ludlow in age). The ferruginous limestones are characteristically red/grey in colour with frequent stylolites and contain a rich fossil fauna which includes trilobites, bivalves, brachiopods, and gastropods. The condensed limestone sequence represents the Plöcken lithofacies, a shallow to moderately deep marine environmental setting which exhibits frequent changes in sealevel (SCHÖNLAUB & HISTON, 2000).

A taphonomic study of the nautiloid fauna from the Silurian sequences of this section has shown that small scale cyclic preservation of the fauna indicating changing energy levels could be identified through the degree of fragmentation of the shells and by considering telescoped specimens as an indicator of a higher energy regime (HISTON et al., 1999; HISTON & SCHÖNLAUB, 1999). This latter conclusion prompted the present study of the frequency of occurrence of telescoped specimens and their mode of preservation as to whether this may give some indications as to the mechanism behind this phenomenon, and thus, more reliable data related to the hydrodynamic regime within which these specimens are deposited.

3.2.2. Rauchkofelbodentörl section

The Rauchkofelbodentörl section is located on the southwestern slope of Mount Rauchkofel at an altitude of 2200 m and was described in detail by JAEGER & SCHÖNLAUB (1970). The Silurian sequence in this section is interpreted as a transitional shallow marine environmental facies between the Wolayer and Plöcken lithofacies. This sequence is particular in that a rich conodont, trilobite and graptolite fauna occur together which may be used for stratigraphic dating of the shale and limestone strata. The section ranges in age from Upper Llandovery to Upper Wenlock (Kok Formation) with ferruginous red limestones rich in nautiloid cephalopods occurring in the *O. sagitta* conodont biozone (Middle Wenlock). The present study was carried out on the limestone horizons at the base of this zone as the nautiloid preservation is apparently quite varied at this level and telescoped specimens quite abundant. A detailed taphonomic study of these strata has not been done at this section but it is important to the present study to have a data set from various environmental settings at a particular stratigraphic interval (i.e. *O. sagitta* conodont biozone) in order to compare results and examine the results for common factors.

4. Field Study

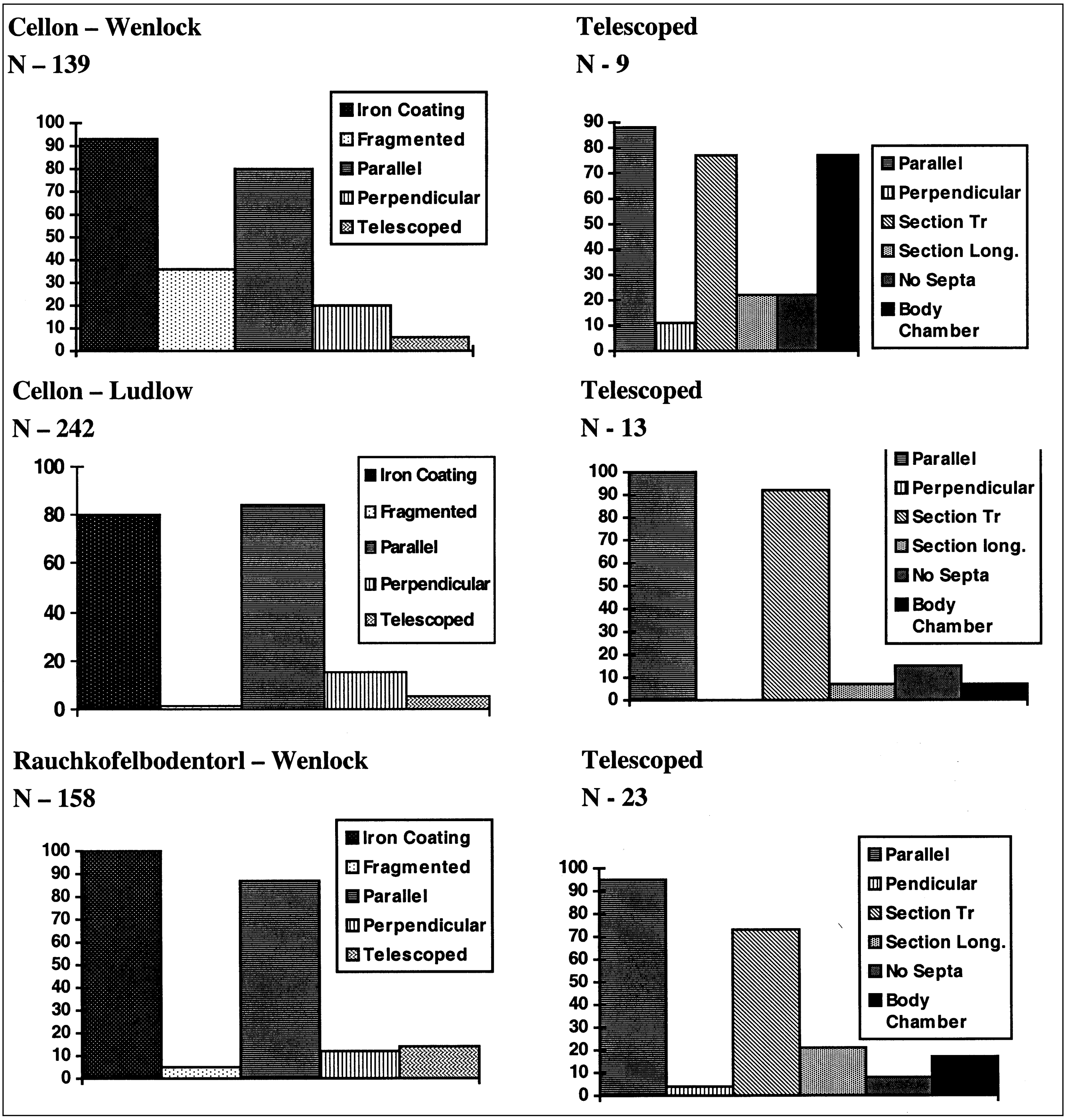
The results of the study of the frequency of occurrence of telescoped specimens from specific stratigraphic intervals from two sections in the Silurian of the Carnic Alps are presented as percentages of the total number of nautiloids counted within quadrats of 0.5 m^2. The telescoped specimens are then treated separately with the most particular features of their preservation, as outlined above in the section on Method and Material, being considered (Text-Fig. 2).

4.1. Cellon Section – Wenlock

The 0.5 m^2 quadrat was placed about 1 m above the base of bed 13 and a total of 139 nautiloids were counted within that area. As may be seen in Text-Fig. 2 the majority of the specimens (80 %) are oriented parallel to bedding with 20 % being perpendicular or oblique. No preference was seen for the position of the body chamber being upward or downward in the latter specimens. The nautiloids are almost all (93 %) preserved with an outer iron red coating which may be algal in origin (KREUTZER & SCHÖNLAUB, 1997; HISTON & SCHÖNLAUB, 1999). More than one third are fragmented, and where the inner chambers were exposed they are usually calcite filled. Geopetal structures were rarely observed. Nine specimens show telescoping which account for just 6 % of the total number (Text-Fig. 2). The latter are for the most part parallel to bedding and retain the body chamber. The majority were seen in transverse section, presumably of the body chamber which was invariably infilled with sediment and within which the telescoped specimens showed a variety of positions but never being dominantly central (Text-Fig. 3). One specimen was noted with the telescoped orthocones having a finer sediment infill than their host and geopetal structures not in position implying that they were probably reworked.

4.2. Cellon Section – Ludlow

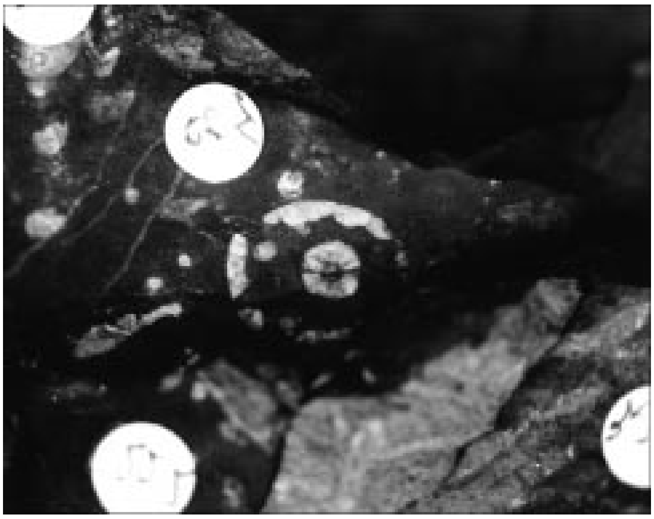
The 0.5 m^2 quadrat was placed about 0.35 m from the base of bed 18 and a total of 242 nautiloids were counted within that area (Text-Fig. 2). There is a marked increase in the number and variety of nautiloid specimens observed at this level than was previously noted in the Wenlock (see above). Most of the specimens are again preserved with an outer red coating and more than 80 % are parallel to bedding. Only 15 % are oriented obliquely or



Text-Fig. 2. ▲△▲
Results presented as percentages of the total number of nautiloids (N) counted within quadrats of 0.5 m^2 from three specific stratigraphic intervals from the Cellon (Wenlock and Ludlow) and Rauchkofelbodentörl (Wenlock) sections from the Carnic Alps.
Taphonomic features were noted such as iron coating of the nautiloid shells, percentage of fragmented shells, parallel or oblique/perpendicular orientation to bedding and percentage of shells showing telescoping. The telescoped specimens (N) are then treated separately on the right hand side of the diagram. Features noted, shown as percentages, are parallel or oblique/perpendicular orientation to bedding; section observed: Tr = transverse section; section long. = longitudinal section: No septa = absence of septa; Body chamber = presence of the body chamber.

Text-Fig. 3. ►▷►
Telescoped specimens in body chamber, transverse view.
The telescoped specimens show a variety of positions within the sedimentary infill of the body chamber but are never dominantly central.
Cellon section, bed 13, Wenlock (*O. sagitta* conodont biozone).
Diameter host shell = 3 cm.

Text-Fig. 4.
Nautiloid oriented obliquely to the bedding plane with body chamber oriented downwards with a preferred lateral direction indicating current activity.
Cellon section, bed 18, Ludlow (*Ploeckensis* conodont biozone).
Diameter shell = 1 cm.



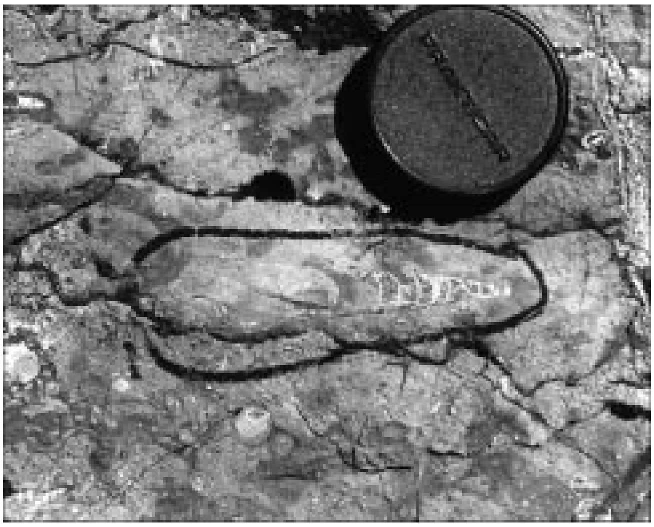
Text-Fig. 5.
Nautiloid with sediment in cameral chamber, transverse view showing central siphuncle.
This may indicate draft-infilling of the conch.
Cellon section, bed 18, Ludlow (*Ploeckensis* conodont biozone).
Diameter shell = 1.5 cm.

perpendicular to the bedding plane but these in general have the body chamber oriented downwards with a preferred lateral direction (Text-Fig. 4). The few observed with the body chamber oriented upwards show the opposing lateral direction indicating current action. In contrast to the Wenlock study area only 1 % are fragmented. Cameral chambers, when observed, are infilled with quartz or occasionally sediment (Text-Fig. 5) and the septa appear intact. Geopetal structures are rare and always parallel to bedding. Telescoped specimens are again rare accounting for only 5 % of the overall total and are oriented parallel to bedding. The majority of the telescoped specimens were observed in transverse section. The telescoped orthocones show no preference of orientation within the host shells which are in general infilled with sediment.

4.3. Rauchkofelbodentörl Section – Wenlock

The 0.5 m² quadrat was placed at the base of the Wenlock limestone sequence and a total of 158 nautiloids were counted within that area (Text-Fig. 2). The shells are mainly oriented parallel to bedding (87 %) with the remainder being either perpendicular or oblique. No prefered direction of orientation of the body chamber was noted (Text-Fig. 6). All show an outer red iron coating and only a small proportion are fragmented (5 %). Geopetal structures are usually parallel to bedding, but many specimens display a fine pink sedimentary infill which contrasts sharply with the surrounding reddish limestone strata, indicating that they were reworked (Text-Fig. 7). One specimen was noted with just the mold of the cameral chambers completely disarticulated implying dissolution of the shell material.

The number of telescoped specimens (14 %) is more than double that seen in the other two case studies and shows a marked contrast to the level sampled at Cellon for the same stratigraphic interval. These are generally



Text-Fig. 6.
Longitudinal section showing septa and sediment in chambers, body chamber oriented to left.
No preferred lateral orientation of conchs was observed implying little or no current action.
Rauchkofelbodentörl section, Wenlock (*O. sagitta* conodont biozone).
Diameter shell = 3 cm.

Text-Fig. 7.
Geopetal structure in transverse view, infilling sediment finer grained and differs in colour to the enclosing sediment implying that the shell has been reworked.
Rauchkofelbodentörl section, Wenlock (*O. sagitta* conodont biozone).
Diameter shell 1.5 cm.

Text-Fig. 8.
Telescoped nautiloid with opposite orientation to the host shell, implying a bimodal current.
Infilling sediment also differs from the enclosing sediment so the shell has been reworked.
Rauchkofelbodentörl section, Wenlock (*O. sagitta* conodont biozone).
Diameter host shell 2 cm.

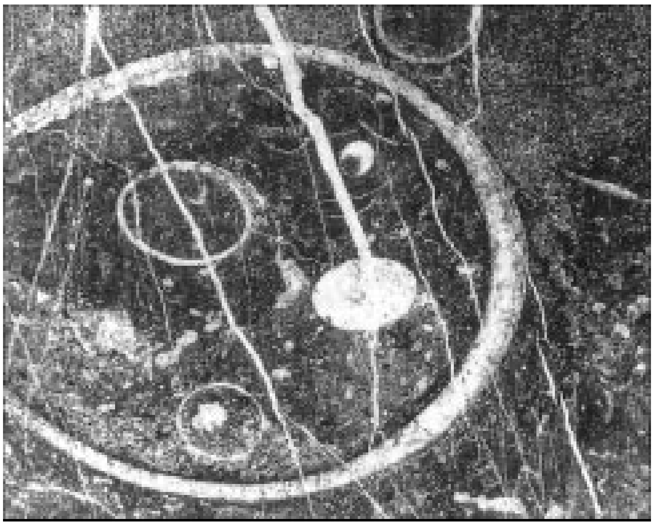
oriented parallel to bedding (95 %) and were seen in transverse section, presumably of the body chamber. The host shells in general appear to be sediment filled. In one longitudinally sectioned shell a small inner orthocone is oriented in the opposing direction to its host (Text-Fig. 8) and has a finer sedimentary infill of its chambers implying that it was reworked and that the current was bimodal. Preserved septa are seldom seen in longitudinal sections of telescoped specimens and in the rare case where they are present are often fragmented within the sedimentary infill of the conch.

The overall conclusions from the three case studies given above are that:

1) telescoping was not frequent and occurred mainly in specimens oriented parallel to bedding,
2) smaller orthoconic shells accumulated within the sedimentary infill of the body chambers of larger orthocones and do not have a preferred orientation within the latter,
3) these internal orthocones sometimes show evidence of having been reworked implying an increase in energy level of the hydrodynamic regime of the environmental setting,
4) previous dissolution or fragmentation of septa allows the sediment to infill the entire conch,
5) environmental setting plays an important role in the frequency of telescoping as may be noted in the results from the same stratigraphic interval from two different sections (Cellon Wenlock/Rauchkofelbodentörl Wenlock),
6) penetration of the septa of the host shell by the smaller telescoped orthocones was not observed in any of the specimens noted in the three study areas, and
7) the overall lack of fragmentation of the nautiloid fauna indicates a relatively low energy level in the environmental setting.

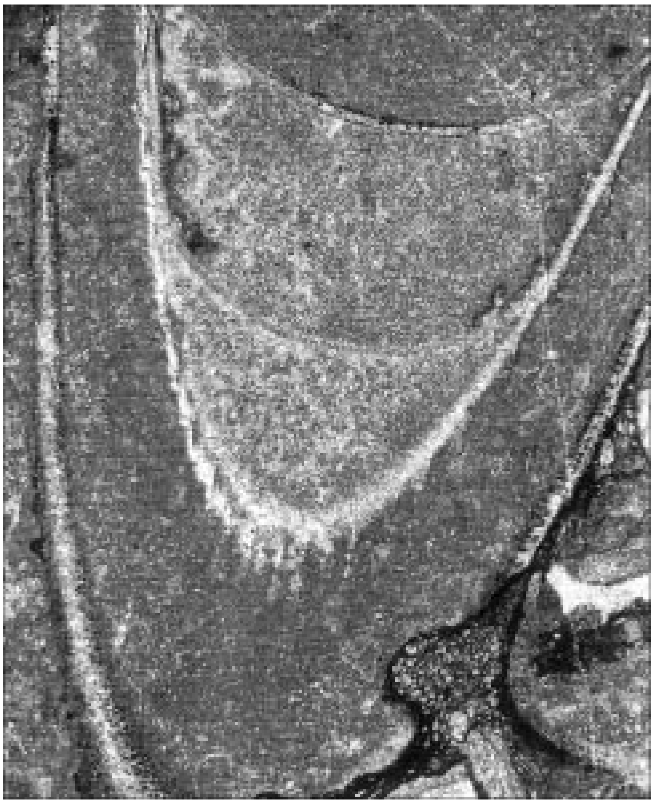
5. Thin Section Study

In thin section rare transverse sections of specimens have been observed with smaller orthocones telescoped within the body chamber of the larger specimen (Text-



Text-Fig. 9.
Thin section of body chamber infilled with small nautiloid shells that are parallel to the host shell and which show sections both of the body chamber and cameral chambers (spar-filled).
Cellon section, Ludlow; ×3.

Fig. 9). The smaller shells appear to form part of the sedimentary infill which also contains other elements of the accompanying fauna. The orthocones do not show a preferred position within the host shell. A specimen seen in longitudinal section encloses a smaller orthocone, whose septa are intact, within the phragmocone however, the larger outer orthocone shows pressure dissolution effects and its septa are no longer preserved (Text-Fig. 10). This may reflect long term exposure on the seafloor of the larger orthocone which with time becomes infilled with



Text-Fig. 10.
Thin section of telescoped nautiloid shells; note the host shell lacks septa and is infilled with sediment, implying that the outer shell has undergone dissolution and sedimentary infill.
Cellon section, Ludlow; ×20.

sediment and smaller elements of the fauna including smaller orthocones (see Text-Fig. 8). Evidence of breakage of septa due to high energy penetration of smaller orthocones into the host phragmocone has not been observed in the material studied here from the Carnic Alps.

6. Discussion

There are many questions remaining to be resolved about the telescoping phenomenon. Some of these are as follows:
1) the mechanism behind it;
2) whether it occurs on the seafloor or in the water column;
3) what the implications are for the prevailing current i.e. unidirectional or bimodal, and above all,
4) what conclusions may be made with regard to environmental setting.

The evidence presented above and by previous researchers will be analysed in an attempt to answer these questions. Many factors must be taken into consideration in a study of the phenomenon of telescoping. These include the following:
1) morphology of the nautiloid shell,
2) preservation of the shell – fragmentation,
3) dissolution,
4) geopetal structures,
5) evidence from the associated fauna, and,
6) sedimentology for the environmental setting where these telescoped shells occur.

The most important factor is the morphology of the nautiloid shell itself and how certain shell forms may be more susceptible to breakage or more easily act as a host into which other shells may be infiltrated. The form of the aperture and in particular the size of the body chamber are both crucial elements as the wider the opening and the longer the body chamber the greater the chance that smaller narrow shells can be swept inside when it is deposited on the seafloor. A longer and larger body chamber also has more weight, and therefore, after the death of the animal, would most probably sink to the seafloor rather than float to the surface. These kinds of body chamber are also less likely to be carried or substantially moved or transported by subsurface currents. This consideration argues against the possibility that telescoping observed in such specimens could have happened in the water column prior to the shell settling to the water-sediment interface. Massive body chambers probably acted as an anchoring device and pivot point when the shell was deposited on the seafloor. This would cause the phragmocone to be rotated into the prevailing current so that the open aperture would face into the current, and thus the body chamber could be infilled with sediment. In the case of a bimodal current the direction of the shell could change direction during the process of sediment infilling which may account for cases where telescoped shells have an opposing direction to their host (see Text-Fig. 8). FERRETTI & KRIZ (1995) suggested that turbulence behind the deposited host shell may be the reason that smaller shells become trapped within it. Based on internal sediment differences and tilted geopetal structures which differ from the host shell some telescoped specimens can be interpreted as having been reworked. This is probably the result of occasional higher energy events including storm episodes. However, the more typical situation is that both host and telescoped specimens display a similar orientation implying that the host shell became infilled slowly during the buildup of sediment on the seafloor and smaller orthoconic shells as well as other elements of the benthic fauna were included into the "open" space of the body chamber as infilling occurred. The prevailing current, unidirectional or bimodal, would eventually determine the orientation of host to telescoped shells.

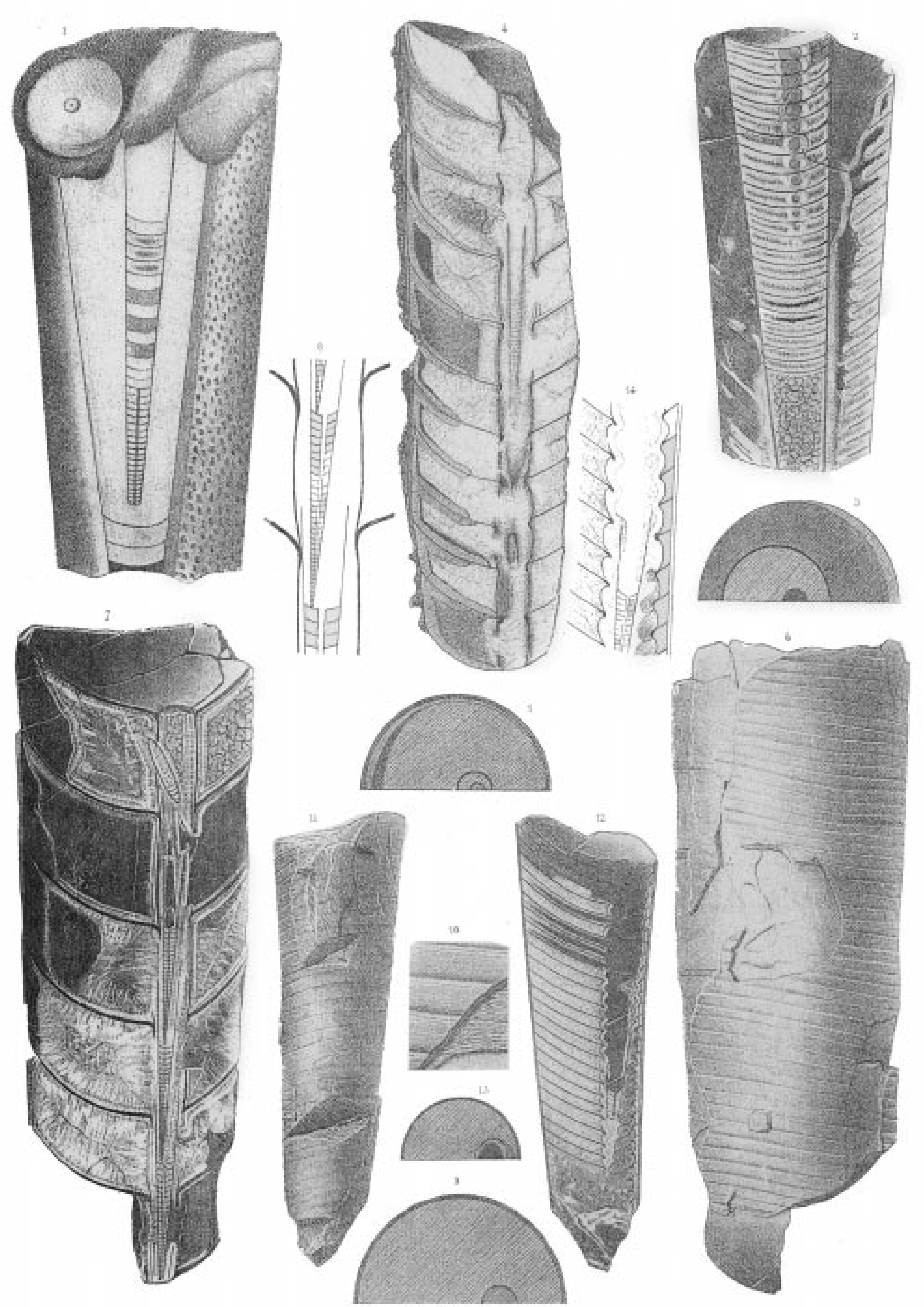
The width of the septal foramen and of the siphuncle determine if sediment may easily infiltrate the phragmocone of the shell and if the width is enough to allow also smaller shells to enter the siphuncle. Telescoped specimens (i.e. those found within another shell) are in general longicones with a small angle of expansion or juvenile specimens.

Several examples were illustrated by BARRANDE (Text-Fig. 11) where the smaller orthocones in some cases have also penetrated the most adoral part of the siphuncle and sometimes form a plug as sediment infilling the body chamber is restricted in its infiltration of the siphuncle by these obstructions. The smaller orthocones invariably display geopetal structures which seem to reflect the position of the larger enclosing orthocone on the seafloor. This may reflect a slow accumulation of the smaller orthocones within the larger more immobile host conch as deposition took place. GNOLI et al. (1980) also document a similar situation from Sardinia with infill of the body chamber and occasional specimens within the siphuncle.

Another striking example of a specimen consisting of only the body chamber and final cameral chamber from the Silurian of Morocco (Locality unknown) illustrates the same phenomenom (Text-Fig. 12) where the siphuncle has been plugged by several small orthocones (Text-Fig. 13). The small orthocones within the body chamber however, show geopetal structures in a perpendicular orientation to the host shell. To produce these orientations it must be assumed that the body chamber remained upright in the sediment as infilling occurred. Whether the body chamber was still attached to the phragmocone during infilling we cannot determine.

MAEDA & SEILACHER (1996) have illustrated many examples of sheltered preservation where concentrations of small ammonoid shells are found within the body chambers of larger shells. After deposition on the seafloor the body chambers of large orthocones may have been used for shelter by juvenile or small specimens. These specimens may have died within this habitat and as the host body chambers became infilled with sediment their shells remained in this position. Rare specimens sheltering in the body chamber may have been pulled or sucked back into the siphuncle due to pressure changes caused by remaining gas within the phragmocone (MAPES, pers.

Text-Fig. 11. ►▷►
Illustrations of telescoped nautiloid specimens in the body chamber and siphuncle of larger specimens with geopetal structures.
The specimen in the lower left hand corner is particularly striking as 5 specimens have infiltrated the siphuncle and one of those shows an opposing orientation to the others. Neither the host nor the telescoped specimens show evidence of breakage. Sediment is observed in one of the adoral chambers of the host shell which may imply draft-infilling. This may have caused slight changes in pressure due to which the small shells were pulled into the siphuncle.
Reproduced from BARRANDE (1866, Pl. 216).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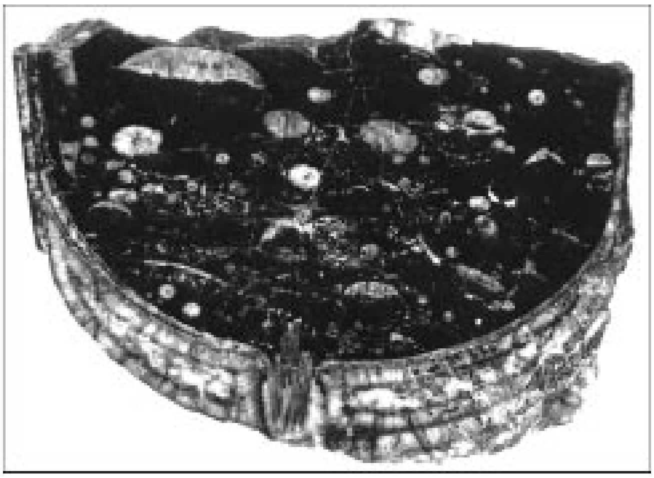

Text-Fig. 12.
A longitudinal section of a large nautiloid body chamber showing telescoped juvenile specimens trapped in the septal foramen.
Those in the body chamber have geopetal structures which show a perpendicular orientation to the host shell.
(Ristedt private collection, University of Bonn, Locality unknown – Morocco, Silurian); ×0.8.

comm.). The situation illustrated by the Moroccan specimen (Text-Figs. 12, 13) could also be explained in this way as the juvenile specimens forming a plug in the siphuncle of the larger orthocone may have been sheltering there as the larger shell lay in a horizontal position on the seafloor (MAPES, pers comm.). Reworking of the host body chamber, probably detached from the phragmocone, could have brought it into a vertical postion. The body chamber could then have been infilled with sediment and smaller orthoconic shells. These latter shells were deposited in a perpendicular orientation to the body chamber itself as is evidenced by the geopetal structures.

Text-Fig. 13.
Close up of Text.-Fig. 12 showing juvenile specimens trapped in the septal foramen forming a plug; ×6.

The thickness of the conch wall and septa of the host shell is also of importance as structurally weak septa and shells will break easily on impact and allow penetration by more robust specimens. Although considered unlikely a scenario may be envisaged where this could occur while these lighter shells were floating in the water in large numbers where space was limited and the chances of impact high, as in a nearshore high energy environmental setting. However, for this scenario to be feasible both a large concentration of nautiloids would be required and that the shells were still buoyant enough to remain floating in the water column after death. HOLLAND et al. (1994) put forward various reasons for the occurrence of large concentrations of Palaeozoic nautiloid shells, the most likely explanation being mass mortality such as is seen in the present day accumulations of the giant squid *Architeuthis monachus* on beaches along the coast of Newfoundland. The second point has been partly discussed above with regard to shell morphology and the body chamber, however, the buoyancy of the post-mortem shell due to gas remaining in the cameral chambers should also be taken into consideration. HEWITT & WESTERMANN (1996) concluded that post-mortem buoyancy of nautiloid shells was limited as most lived on or near the seabottom and would sink quite soon after death rather than float to the surface as the cameral chambers flooded. Therefore it is considered that nautiloid shells were deposited on the seafloor after death and that they would have floated only for short periods within the water column, if at all. A more probable scenario than the one described above for telescoped specimens showing breakage of septa is that impact and penetration of one shell by another occurred on the seafloor in a high energy setting as the shells deposited there were moved against one another. Structurally weaker shells would be more prone to damage and penetration in this case.

FLOWER (1957) commenting on the paper by MILLER & YOUNGQUIST (1949) on telescoping where breakage of septa was frequent, supported their theory that telescoping is facilitated by shells with weak septa. BARRANDE (1877) had also noted that due to the reduced thickness of the shell and of the septa penetration was more frequently seen in thin shelled species with many septa such as *Cyrthoceras* or *Oncoceras*. He illustrated many examples from the Prague Basin (1866, pl. 217) where breakage of septa had taken place but stated that he considered this phenomenon as being relatively rare considering the numerous shells contained within these particular layers.

Another puzzling feature are telescoped specimens which are perfectly symmetrical one within another with sometimes three or four specimens found in this way. Is this just a chance occurrence? These specimens seem to be quite rare in nautiloid accumulations and the mechanism behind this feature may only be imagined but MILLER & YOUNGQUIST (1949) noted several in their high energy accumulation of thin shelled species so morphology is obviously a determining factor.

The mode of preservation of the telescoped shells is a key factor in interpreting the mechanism behind this phenomenon as has been shown above. It is of great importance to observe whether breakage of the host shells has occurred before, during or after telescoping. Only this determination will allow a possible interpretation that in some cases they have been penetrated in a high energy environmental setting.

Other preservational features worth noting are the spar filled cameral chambers, which indicates rapid intact burial of the shell, whereas, the sediment fill of the cameral chambers where the septa have been broken implies that the shell remained exposed on the seafloor long enough for this to happen. If sediment is seen in only some of the chambers then it is possible that there was some external breakage or boring of the shell wall so that draft-infilling could take place (SEILACHER, 1971). This random filling of the chambers is evidence that the shell remained on the seafloor for some time before burial. This would allow the body chamber to be slowly infilled with sediment and smaller orthocones during normal sedimentation. Telescoping observed in shells that show evidence of rapid burial, spar filled cameral chambers, implies that this probably occurred soon after death and prior to burial.

Dissolution of the orthoconic shell during extended exposure on the seafloor may make penetration of the conch by other more recently deposited shells more likely, especially during high energy episodes in otherwise tranquil environments. Dissolution of the septa may also occur prior to dissolution of the conch wall thereby creating an extended “open” space of the body chamber into the phragmocone for accumulation of smaller shells within normal sedimentation (see Text-Fig. 10). This case may be distinguished from conchs where implosion of septa has occurred due to hydrostatic pressure (HEWITT & WESTERMANN, 1996) as fragments of the imploded septa are to be seen within the phragmocone.

The presence of geopetal structures within the host or telescoped shell and whether they are situated in the chambers, siphuncle or only the body chamber is indicative of the timing of sediment infilling during the post-depositional history of the shells. It is important to determine whether they correspond in orientation to one another or whether either the host or telescoped specimen have been reworked (see Text-Figs. 7, 8).

All of the features of telescoped specimens considered above, shell morphology, mode of preservation, dissolution effects and geopetal structures may help to resolve the mechanism behind the phenomenon and to determine whether telescoping took place on the seafloor after deposition of the host shell and/or which hydrodynamic regime was the determining factor.

The effect of the environmental setting in which this phenomenon takes place must also be considered. An important factor in this discussion is whether the nautiloid shell could float after death of the animal. And operating under the assumption that the shell could float whether telescoping could happen at the air/water interface. Salinity and temperature of the water will affect the buoyancy potential of the shell (REYMENT, 1958) as will its morphology as has been discussed previously. It is unlikely that thin-shelled nautiloids would float for any considerable length of time or distance (BOSTON & MAPES, 1991) considering their morphology and the palaeobiogeography of this group (CRICK, 1990, 1993).

If breakage of septa within the host shell, due to penetration by another shell, has occurred then it may be presumed that it took place within a high energy environment. However, if we find that no internal breakage has taken place and we are looking at a simple infilling of the larger host shell’s body chamber or siphuncle then a low energy environment is envisaged.

If the host shell is perfectly intact it may be presumed that it underwent limited transport after deposition. The direction of telescoped shells relative to the host shell i.e. a small telescoped shell with the apex in the opposing direction to the larger host shell may be the result of tidal currents i.e. a bimodal current (see Text-Fig. 8). Apart from this latter case it is not possible to determine if a unidirectional current or bimodal current was acting on the orthocones.

Evidence from the associated fauna and the sedimentology of the strata in which the phenomenon is observed is critical to understanding the complete scenario and for determination of the environmental setting. The majority of the documented cases of the telescoping phenomenon have been interpreted as occurring in shallow water environments therefore the effect of a bimodal current, regardless of energy level, is probably a contributory factor.

7. Palaeoenvironmental Implications

This study of the telescoping phenomenon in orthoconic nautiloid specimens was carried out in order to determine whether telescoped specimens are indicative of high or low energy hydrodynamic regimes. The effects of cephalopod morphology, taphonomic processes and depositional environments have all been taken into consideration. As may be concluded from the evidence described herein two different types of telescoping are present. One type is a simple sedimentary infill of the host shell, without breakage of the internal chambers, in a low energy hydrodynamic regime. In cases where dissolution of internal septa has taken place due to prolonged seafloor exposure sedimentary infill of the "open" space of the conch occurs. The second type is developed by breakage and penetration of one shell by another due to a high energy hydrodynamic regime and structurally weak orthoconic shells. Both types of telescoping are quite rare even when large numbers of orthocones are present.

The observations presented here of the frequency of occurrence and taphonomic preservation of telescoped nautiloid specimens in the Silurian sequences of the Carnic Alps reflect local hydrodynamic conditions, but it is important to note that environmental interpretations other than high energy are possible. The evidence given above certainly does not support this theory as the sole mechanism that produces telescoped orthocones. In all three case studies no breakage of septa was observed in telescoped shells. Therefore the second type of telescoping utilizing a high energy regime cannot be applied. An overall lack of fragmentation of the entire nautiloid fauna counted within the quadrats demonstrates that the environments at these stratigraphic levels were relatively tranquil. The orthocones showing telescoping are predominantly oriented parallel to bedding and sometimes show dissolution effects. The phenomenon occurs rarely within the fauna. Telescoped specimens appear to be restricted to shells with an open body chamber and are dominantly found to have penetrated only the body chamber of the host shell, not the phragmocone. They show no preferred orientation within the host shell.

Therefore it may be concluded that these smaller shells accumulated within the body chambers of the host shell during normal sedimentation on the seafloor. It is also possible that they used the body chamber as a sheltered habitat and later after death remained in this position to become part of the sedimentary infill of the body chamber. Some telescoped specimens showed evidence of reworking implying variability in the hydrodynamic regime of the environment, however, this situation is still within an overall low energy depositional environment.

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