

Nautiloid cephalopods – a review of their use and potential in biostratigraphy

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Abstract: In terms of their use as biostratigraphical tools, nautiloid cephalopods are the poor relations of ammonoids. Nevertheless, in certain situations, they may provide useful biostratigraphical data, particularly where other biostratigraphically valuable taxa are not present; or in certain situations demonstrate a resolution as great as, or greater than ammonoids, trilobites, graptolites or conodonts. Nautiloid cephalopods are of especial value in palaeobiogeographical studies, but their use for this purpose may be hampered by the poor understanding of the stratigraphical ranges of individual taxa. The biostratigraphical value of nautiloid cephalopods is demonstrated here through a number of case studies of Ordovician taxa, combined with a review of their biostratigraphical use in Palaeozoic and Mesozoic successions. These both demonstrate the potential of this group and indicate great scope for further research.

Keywords: Nautiloids, cephalopods, biostratigraphy, Palaeozoic, Mesozoic

Introduction

The widespread stratigraphical and geographical occurrence of nautiloid cephalopods, particularly, but not exclusively during the Lower Palaeozoic is documented in many substantial monographic works (e.g. HALL 1847 [Ordovician and Silurian]; BARRANDE 1865-1877 [Ordovician to Devonian]; BLAKE 1882 [Ordovician and Silurian]; FOORD 1897-1903 [Carboniferous]; FOERSTE 1932, 1933 [Ordovician]; FLOWER 1946 [Ordovician]; KUMMEL 1953 [Triassic]; MILLER & YOUNGQUIST 1949 [Permian]; STURGEON et al. 1997 [Carboniferous]; ZHURAVLEVA 1974 [Devonian]). Unlike ammonoids, which have been utilised as stratigraphical tools since the early nineteenth century (e.g. SMITH 1816; OPPEL 1865; BUCKMAN 1898; HOUSE 1978; CALLOMAN et al. 1989; KORN 1996; KLUG 2002; BECKER 2000; PAGE 2009), and despite the great variation in conch morphology that 'nautiloids' display, examples of their use in the development of biostratigraphical schemes are relatively scarce. There are several possible reasons for this:

1. Biostratigraphical markers: There are a range of other rapidly evolving and widely occurring taxa such as graptolites, ammonoids, conodonts and foraminifera that are of proven value, and may occur in great abundance, facilitating correlations using samples extracted from cores.

2. Similarity of morphology: Many of the groups comprising these cephalopods cannot be determined

taxonomically without investigation of the internal morphology of the phragmocone due to the similarities of the external features, thus entailing the preparation of polished or thin sections for study, requiring more effort, and possibly resulting in more equivocal data than might be gained from the preparation of (for example) a conodont sample.

3. Taphonomy: Amongst the many forms with orthoconic shells, there is great potential for post-mortem – pre-burial breakage and preferential removal of parts of the phragmocone to bring about the selective preservation of parts of the shell on which the diagnosis of a particular taxon may be based. Taphonomic studies of the post-mortem behaviour and deposition of nautiloid cephalopod shells (REYMENT 1958; BOSTON & MAPES 1991; HEWITT & WESTERMANN 1996; HISTON 2012a) deal with many aspects of their preservation. If there is more than one mode of preservation for a particular taxon, and particularly if these occur at different horizons, there is potential for mistakenly splitting that taxon and failing to recognise its full stratigraphical range. For example, *Polymeres demeterum* MURCHISON from the Floian of England and Wales occurs at several different horizons where the preserved remnants of conch represent either adoral, medial or apical portions, whilst their preservation may take the form of internal and external moulds, lacking original shell, or original shell may have been replaced by pyrite followed by further replacement with limonite. Without careful study of this material and an understanding of its taphonomy,

it would be easy to determine these as separate taxa and set up spurious ranges for them.

4. Fidelity of palaeogeographical distribution: An important factor in this discussion is whether the nautiloid shell could float after death of the animal as then the original palaeoenvironmental setting and any hypothesis related to facies and assemblages would be prone to error. This has led to the use of nautiloids as reliable biostratigraphic markers and precise indicators of palaeoenvironment being treated with doubt or completely dismissed in holostratigraphical studies. HEWITT & WESTERMANN (1996) concluded that post-mortem buoyancy of nautiloid shells was limited as most individuals lived on or near the seafloor and would sink 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 shortly after the death of the organism and would have remained buoyant for only a short period, if at all (KRÖGER et al. 2009; KLUG et al. 2010; HISTON 2012b).

As a probable consequence, examples of the direct application of nautiloid cephalopods as biostratigraphical tools are relatively few. However, this is principally due to the fact that nautiloid biostratigraphical zones/schemes have never been attempted, not as a result of failure in their application. More often, biostratigraphical studies of these cephalopods are markedly descriptive, and may largely represent an extension of a monographic study (e.g. FREY 1995; STURGEON et al. 1997; KRÖGER 2008a; EVANS 2005, 2011), or the provision of known ranges for a particular region/locale (e.g. WILSON 1961; CATALANI in SLOANE 1987). Rousseau FLOWER was probably one of the main exponents of the use of these cephalopods as biostratigraphical tools, and used his knowledge of their distribution, particularly in North America, to review the biostratigraphy of various successions of Lower, Middle and Upper Ordovician age and also as a tool to better understand the evolution of this group of cephalopods (see FLOWER 1976; 1985 for summaries). In one instance, FLOWER (1964) used his knowledge of the stratigraphical distribution of Canadian (= Lower Ordovician) cephalopods of North America to date some of the larger clasts present in the Levis Conglomerate of Quebec, demonstrating that the boulders originated from carbonates ranging (in modern terminology) from Skullrockian to Blackhillsian in age, and indicating a source or sources further shoreward on the Laurentian platform. In this case the general lack of other macrofossils made these cephalopods a key to the age determination of this material, and although today, age would probably be determined by conodont sampling, the value of these cephalopods in assisting age determination in situations where other macrofossils are

relatively rare, as in the Durness Group of Northwest Scotland (EVANS 2011) should not be underestimated.

The study of the distribution of nautiloid cephalopods for palaeobiogeography and as tools for palaeogeographical reconstruction was strongly proposed by CRICK in the 1980's and 1990's (CRICK 1980, 1988, 1990, 1993). He put forward valid arguments supported by a sound database of systematic works to support his hypotheses that these faunas are particularly sensitive to distance or water depth separating landmasses and to fluctuations in sea level. As CRICK pointed out faunas should be described using precise systematic criteria within a strictly controlled biostratigraphic framework in order to fully exploit their potential. When CRICK published his major contributions this was not always the case and many systematic studies were lacking a precise stratigraphic context even at series level, many taxa being referred to as "Upper Ordovician", "lower Silurian" etc. These seminal works by CRICK gave impetus to a broad array of studies over the last twenty years by other authors (e.g. CICHOWOLSKI, EVANS, FREY, HERWIG & POSENATO, HISTON, HOLLAND, KING, KLUG, KRÖGER, MAPES, and NIKO among others: see reference list for details) on these faunas from a variety of geographic locations ranging stratigraphically from the Ordovician to the Triassic that have shown without doubt that nautiloid cephalopods are indeed reliable palaeobiogeographical indicators. Nautiloid studies are now much more accurate in this respect when based on newly collected material, however, material being redescribed from historical collections is still a major problem and as CRICK suggested, is often only of use from a taxonomic point of view.

More recent studies of nautiloid cephalopods may recognise the difficulties that can arise when attempting to use these organisms as biostratigraphical tools and make use of new collections sampled within a well-constrained biostratigraphical framework. Studies of the Silurian cephalopods from Europe in particular (e.g. HISTON 2012a; HISTON et al. 2010; MANDA et al. 2009) make use of such a well-constrained biostratigraphical framework to accurately constrain the range of taxa occurring within the succession, and contributes, in combination with previous studies of other European faunas (see sections below for references) to their use in biostratigraphical correlation as well as a palaeobiogeographical tool within the framework of Northern Gondwana. Such an approach, which recognises that the stratigraphical distribution of these cephalopods should be assessed within a background of other biostratigraphical constraints are more likely to yield useful results in terms of developing their biostratigraphical value.

Examples from recent studies

There are a number of situations where the real or potential biostratigraphical value of these cephalopods may be of significance. Where other biostratigraphically critical fossil biota may be relatively rare, as is the situation along parts of the Laurentian margin during the Early Ordovician (above), areas of the North Gondwana margin where Silurian cephalopod limestones dominate, or in parts of the Early Jurassic successions of the North Somerset coast (United Kingdom) described further below. Where these cephalopods are particularly abundant, as in parts of the Ordovician successions of Scandinavia and South China, some groups, such as the lituitids (see below), underwent a rapid evolution, and may be distinguished as a sequence of distinct taxa that in some cases can be recognised on both palaeoplates, and may potentially be used as correlative tools. Studies by MANDA (2009) of the phragmocerids from the classic Silurian deposits of the Prague Basin also demonstrate this aspect. Use of Silurian nautiloid assemblages by GNOLI (1990) and MANDA & KRIZ (2006) highlight the potential for correlation. Significant, and/or relatively rapid evolutionary events during the history of these cephalopods may also have some degree of biostratigraphical value, and examples from the early history of the Orthoceratoidea and the Eothinoceratidae are described here. Finally, where the stratigraphical distribution of cephalopods are well constrained, whilst they may not provide the primary evidence on which to found a biostratigraphical scheme, may provide a significant contribution to more comprehensive, holostratigraphical schemes.

The examples provided below have a strong Ordovician and lower Palaeozoic bias, reflecting the research interests of the authors. As such, they provide an indication of the potential for the use of nautiloid cephalopods as biostratigraphical tools, and indicate, together with the Mesozoic examples that these cephalopods can be used in a biostratigraphical context.

Ordovician

1. Orthoceratoidea. Research carried out during the past decade has pushed back the origins of the Class Orthoceratoidea well into the late Tremadocian (KRÖGER 2008; KRÖGER & EVANS 2011) whilst indicating that diversification of these cephalopods was already taking place in the Tremadocian (KRÖGER & EVANS 2011) and increased in the early Floian (EVANS 2005, 2011) as demonstrated by the extended ranges of several Laurentian taxa (EVANS 2011, and Fig. 1 herein).

The proposed revision of the position of the Stairian-Tulean boundary to approximately coincide with

the Tremadoc-Floian boundary based on the stratigraphical and palaeogeographical distribution of pelagic trilobites (ADRAIN 2011) indicates that the delay between the appearance of the Orthoceratoidea in high latitude sites on the west Gondwana margin and at low latitudes (NW Scotland, Newfoundland, SW United States) is significantly less than previously thought. Such a rapid dispersion (if that is what we are observing) of this group of cephalopods would appear to be in accord with a move to a more pelagic habitat (KRÖGER et al. 2009) and would suggest that the adaptations noted by KRÖGER (2005); particularly the appearance of a small subspherical protoconch that may have facilitated the rapid dispersal of large numbers of offspring, took place very early in the history of the group and is likely to be present in all the taxa referred to in Fig. 1, despite the lack of any evidence of this morphology in most of these taxa as a consequence of the rarity of preservation of the apical portion of the phragmocone.

At present, with the exception of *Slemmestadoceras attavus* (BROEGGER), the earliest known members of the Orthoceratoidea are represented by taxa possessing marginal siphuncles. These may be assigned to *Bactroceras* HOLM, or closely related genera, all of which so far have shown no evidence of the presence of cameral deposits, and only *Thoraloceras bactroceratoides* KRÖGER & EVANS possesses endosiphuncular deposits that may be interpreted as a conical lining that is thicker at the septal necks than along the rest of the siphonal segment. Given that this taxon is known only from very fragmentary material and it is not known whether cameral deposits might have been present, some doubt will remain regarding its assignment to the Troedsonellidae (Dissidocerida).

Uncertainty regarding an appropriate assignment for *Thoraloceras*, together with the presence of *Bactroceras* in the same assemblage, combined with a possible *Cochlioceras* that is marginally younger means that it is not possible to resolve the relationships between these taxa without additional data. A cladistic analysis (KRÖGER 2008b) generated over one hundred similarly parsimonious trees, although it should be noted that characters including the presence/absence and nature of endosiphuncular and cameral deposits were not included in the analysis. Comparison of the two trees figured by KRÖGER (2008b, fig. 3) illustrates the problem. Nevertheless, if this group of taxa achieved their wide distribution through (at least in part) the innovation of the small spherical protoconch, then this could provide the character that unites the Orthoceratoidea. This implies that the late Tremadocian and the Floian was a period of rapid radiation for the Orthoceratoidea, much of the documentation of which remains to be discovered.

		Avalonia	Montagne Noire	Morocco	Perunica	Andean Basin	Baltica	Southern China	Laurentia	Australia	North China	
Lower Ordovician	Tremadocian	1a				Sal. cf. sericium						
		1b	?									
		1c										
		1d										
		2a	Saloceras sp. — Sal? sp. —	Bathmoceras sp. — Sal. chinianense — Sal. murvielense — Sal. pradense —	B. australe — B. taichoutense —	B. complexum —	Sal. spp. — Eothinoceras renatae — Margaritoceras margaritae — M. diploide — M. sp. —	B. linnaerstoni —		E. americanum —	Sal? contrarium — E. maitlandi —	Protothinoceras — Conothinoceras — Mesothinoceras — Tangshanoceras —
		2c	Saloceras sericium —									
	Middle Ordovician	Dapingian	3a									
			3b									
		Darrivilian	4a	Sarcodosoceras promus — Bathmoceras llanvirniense —								
			4b									
	4c											

Fig. 2: Worldwide stratigraphical distribution of members of the Eothinoceratidae and Bathmoceratidae during the Early and Middle Ordovician.

fig. 3). Nevertheless, the fauna of the Liangchiashan Formation clearly records what may have been a short-lived proliferation of genera that could have arisen from *Eothinoceras* and probably gave rise to the Cyrtocerinidae through *Tangshanoceras* CHEN (CHEN & TEICHERT 1987). The appearance of *Eothinoceras* at distant locations during the latest Tremadoc and early Floian is difficult to explain unless it is accounted for by a longer history of the genus or a capacity for rapid dispersal. *Eothinoceras renatae* CECIONI & FLOWER from the Floian of Bolivia, and *E. marchaense* BALASHOV from the Floian of Siberia provide further evidence of this wide, if sporadic, distribution of this genus during the Floian.

The occurrence of *Eothinoceras* and *Saloceras? contrarium* (TEICHERT & GLENISTER) in the Canning Basin of Western Australia, combined with the occurrence of *Bathmoceras australe* (TEICHERT) from the late Floian-early Dapinginian Horn Valley Siltstone (COOPER 1981, fig. 5), as well as further occurrences of the latter species and *B. taichoutense* KRÖGER & LEFEBVRE, from horizons regarded as of early to mid-Floian age in Morocco (KRÖGER & LEFEBVRE 2012) make for difficulty in identifying the ancestor of *Bathmoceras*. Nevertheless, when all records are considered, with the exception of South

America, *Bathmoceras* is present in western Gondwana from the mid-Floian to the Darrivilian and is also present in the Southern China and the Baltic during the Dapinginian and Darrivilian.

Margaritoceras CECIONI & FLOWER from the Floian of Bolivia and *Sarcodosoceras* EVANS from the Darrivilian of the Welsh Basin are similar, although the latter differs in its lower rate of conch expansion, narrower siphuncle, and compressed ovoid cross-section (EVANS 2005). Although they are likely to be closely related, *Margaritoceras* is at present known only from the Central Andean Basin of Bolivia and northwest Argentina, where *M. diploide* is now known to be present in the mid Floian possibly late Floian (CICHOWOLSKI unpublished data) whilst a further species of *Margaritoceras* is known from the late Floian (CICHOWOLSKI unpublished data). Additional, undescribed taxa are known from the mid-Floian of the Central Andean Basin (CICHOWOLSKI unpublished data). As it stands, the evidence from South America suggests that the Eothinoceratidae underwent a radiation at least during the Floian that appears to be restricted to South America, although taxa such as *Sarcodosoceras* may suggest that some of these lineages later extended into Avalonia.

		Balto-scandian Stages	Swedish Formations	Trilobite zonation	Lituitid zonation	Graptolite zonation	Conodont zonation	
Darrivilian	4c	Uhakuan (part)	Furudal Limestone	<i>Illaenus crassicaudata</i>	<i>Ancistroceras undulatum</i>	<i>Hustedograptus teretiussulcatus</i>	<i>Pygodus anserinus</i>	
		Lasnamägian	Folkeslunda Limestone	<i>Illaenus schroeteri</i>	<i>Lituites perfectus</i>	<i>Didymograptus murchisoni</i>	<i>Pseudoamplexograptus distichus</i>	<i>Pygodus serra</i>
			Seby Limestone		<i>Lituites lituus</i>			
			Skärlov Limestone		<i>Trilacnoceras discors</i>			
		Aserian	Skärlov Limestone	<i>Illaenus planifrons/ Illaenus platyurus</i>	<i>'Lituites' toernquisti</i>	<i>Pterograptus elegans</i>	<i>Eoplacognathus suecicus</i>	
			Segerstad Limestone		<i>Angelinoceras latum</i>			
	4b	Kundan	Holen Limestone	<i>Megistaspis gigas</i>	<i>Holmiceras praecurrens</i>	<i>Didymograptus bifidus</i>	<i>Nicholsongraptus fasciculata</i>	<i>Eoplacognathus pseudoplanus</i>
				<i>Megistaspis obtusicauda</i>			<i>Holmograptus lentus</i>	<i>Yangtzeplacognathus crassus</i>
				<i>Asaphus raniceps</i>			<i>Undulograptus austrodentatus</i>	<i>Lenodus variabilis</i>
	4a			<i>Asaphus expansus</i>				

Fig. 3: Stratigraphical distribution of lituitid species in Baltica during the Darrivilian, demonstrating the high resolution provided by these taxa in comparison with trilobites, graptolites and conodonts.

The Eothinoceratidae and Bathmoceratidae were widely distributed around Gondwana during the Early and Middle Ordovician, and where the range of a species is known, may resolve to a stage or even a timeslice (Fig. 2). As some inshore assemblages of high latitude Gondwana (e.g. parts of the early Floian, Bolahaul Member of the Ogof Hên Formation of Wales) may be dominated by molluscs, whilst graptolites and trilobites are relatively rare (e.g. FANG & COPE 2004), these cephalopods may have the potential to constrain ages in some cases.

3. Lituitida. Lituitid nautiloids are common and distinctive components of Middle Ordovician cephalopod faunas in the 'Orthoceratite Limestone' facies of Baltoscandia (especially Sweden) and coeval carbonate sequences, such as the Dawan Formation in China. They are virtually cosmopolitan in occurrence, and are known from the USA and Newfoundland (FLOWER 1975), Wales (EVANS 2005, in prep.), China (e.g.

YU 1930; LAI 1982; LAI 1986; QI 1980), Korea (YUN 1999, 2002), Estonia (BALASHOV 1953), Norway (SWEET 1958), Sweden (ANGELIN & LINDSTRÖM 1880; HOLM 1891; KING 1999) and the 'Diluvium-Geschiebe' of northern Poland (DZIK 1984) and Germany (BOLL 1857; NOETLING 1884; REMELÉ 1880, 1881). A substantial number of lituitid genera have been described since the 19th century (e.g. HYATT 1894; TEICHERT et al. 1964) and the taxa are firmly established within cephalopod literature.

The Swedish lituitid fauna extends mainly from the early Kundan to Uhakuan stages. This general succession of taxa closely corresponds with lituitid faunas described elsewhere, especially China (CHEN & LIU 1976). In the Swedish 'Orthoceratite Limestone' sequence, biostratigraphical data from the latest Volkhovian and earliest Kundan stages of Öland and Östergötland indicate that the weakly cyrtoconic Sinoceratidae occur below the coiled Lituitidae. The former are represented by

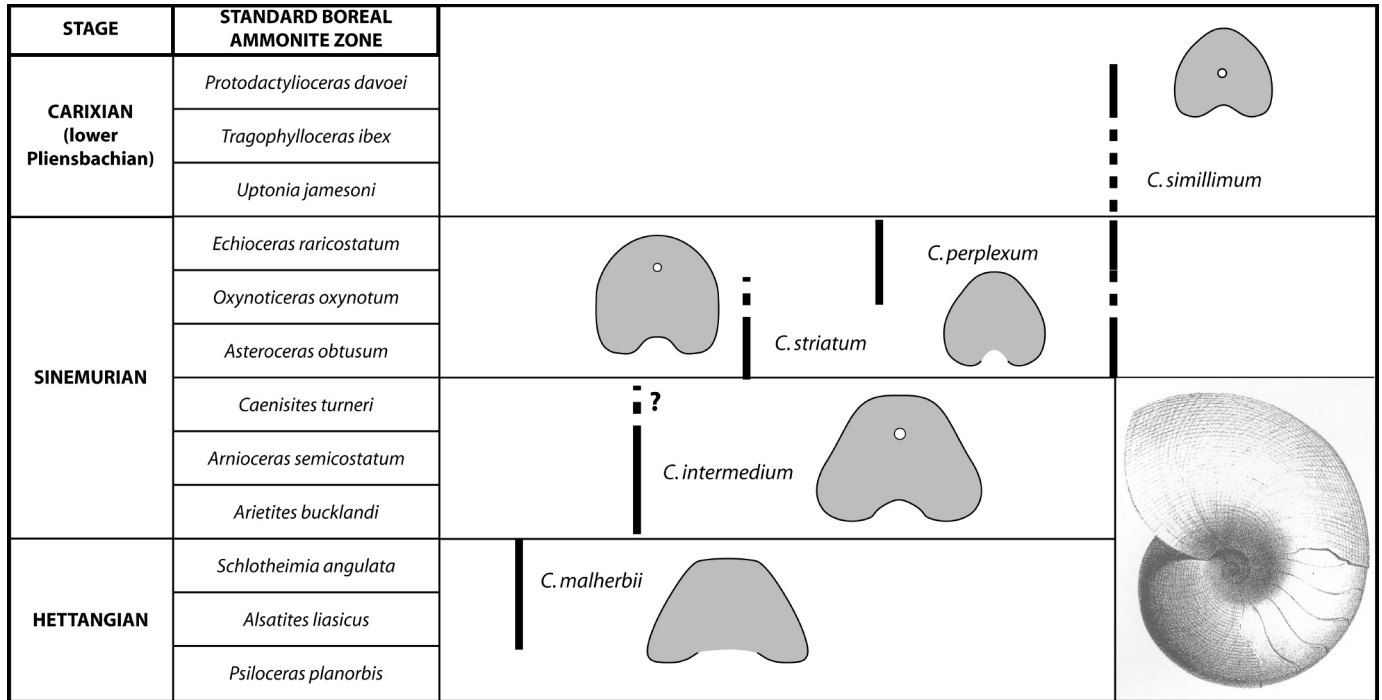


Fig. 4: Occurrence ranges of *Cenoceras* species in the Early Jurassic of southern England, compared with the standard ammonite zonation. Inset: *Cenoceras intermedium* (SOWERBY, 1816), reproduced from D'ORBIGNY (1843: pl. 27, fig. 1).

Rhynchorthoceras and related genera that extend up into the Aserian and Lasnamägian stages. The earliest Lituitidae occur in the mid Kundan and are represented by forms such as *Holmiceras praecurrens* (HOLM, 1891). *Ancistroceras*, with its very rapidly expanding conch is recorded from the late Kundan of Kinnekulle, Västergötland, and extends through the Aserian and Lasnamägian, but is more typical of and numerous in the late Lasnamägian and Uhakuan stages. *Angelinoceras latum* (ANGELIN & LINDSTRÖM, 1880) is recorded only from the lower part of the Segerstad Limestone (Aserian) and the maximum development and diversity of Lituitidae is attained within the Lasnamägian-aged Seby and Folkeslunda limestones where various species of *Lituites*, *Trilacmoceras* and *Cyclolituites* are of common occurrence.

Apart from the possession of complex sutures, lituitids possess all the attributes typically associated with ammonoids (especially ammonites) which make them such valuable and reliable biozonal indicators and capable of biostratigraphic correlation with a high degree of resolution. Namely, lituitids possess distinctive, easily recognisable conchs whose form and ornament enables taxa to be readily distinguished; they evolved rapidly and have a wide geographical occurrence; and although they are more commonly found in shallow water, platform carbonate sequences, they also occur in mudstone facies, such as those of the Llanfawr Mudstone Formation of central Wales (EVANS in prep).

Within Sweden, the use of some lituitid taxa as stratigraphical indicators has long been recognised (e.g. JAANUSSON & MUTVEI 1953; JAANUSSON 1963) and their common occurrence in some beds has given rise to former names such as 'Ancistroceras Limestone' (now termed Furudal Limestone). Closer examination of the Darriwilian lituitid faunas (KING 1990, unpublished and in prep.) demonstrates that these lituitids have considerable potential as zonal fossils, and achieve a resolution at least as good as, and for the Aserian and Lasnamägian portion of the succession, potentially finer than that currently recognised using established trilobite, graptolite or conodont zonal schemes (Fig. 3).

Silurian-Devonian

In recent years concentrated efforts have been made to improve the knowledge of the distribution and taxonomy of Silurian nautiloid cephalopod faunas and many existing collections have been revised using up to date taxonomic criteria as well as collection of new material from horizons with precise biostratigraphic data. Consequently systematic studies of Silurian nautiloid cephalopods from a variety of geographical settings and the observed temporal and spatial data from these faunas may now be considered a reliable tool for palaeobiogeographical reconstruction. In Europe the main work on Silurian faunas has been done in the British Isles (EVANS 1994; EVANS & HOLLAND 1995; HOLLAND 1998, 1999, 2000a-c, 2002, 2003, 2004, 2007, 2010; HOL-

LAND & STRIDSBERG 2004), Sweden (STRIDSBERG 1985), Prague Basin (DZIK 1984; GNOLI 1997; KOLEBABA 1975, 1977, 1999, 2002; MANDA 1996, 2008; MANDA & KŘÍŽ 2006, 2007; MANDA & TUREK 2009a,b; MAREK 1971; MAREK & TUREK 1986; STRIDSBERG & TUREK 1997; TUREK 1975, 2008), South West Sardinia (GNOLI 1990; GNOLI & SERPAGLI 1977, 1991; GNOLI & SERVENTI 2006, 2009 and references therein; SERPAGLI & GNOLI 1977), Spain (BOGOLEPOVA 1998a), France (RISTEDT 1968; SERVENTI & FEIST 2009) the Carnic Alps of Austria and Italy (BOGOLEPOVA 1998b; GNOLI & HISTON 1998; GNOLI & SERVENTI 2008; GNOLI et al. 2000; HISTON 1997, 1998, 1999a, b, 2002, 2012a, b; RISTEDT 1968, 1969, 1971; SERVENTI & GNOLI 2000; SERVENTI et al. 2006, 2010) and the Graz Palaeozoic of Austria (HISTON et al. 2010). Tentative correlations are now possible between Avalonia (British faunas), some areas positioned along the Northern Gondwana Margin (Carnic Alps, Sardinia, France and Spain) and Bohemia and Baltica, although problems do still exist in recognition of faunas at both generic and specific level due to poor preservation and lack of precise taxonomic diagnoses.

Detailed study of Silurian-Devonian nautiloid faunas from Morocco by (KRÖGER 2008) presented together with precise stratigraphic and lithofacies data for the collection localities has highlighted further exchange of faunas between Peri-Gondwana Terranes. Studies of particular taxa and nautiloid biodiversity, again within precise stratigraphic biozones and detailed facies studies, in the Silurian of the Prague Basin in relation to palaeobiogeographical distribution and oceanic states of the North Gondwana area and Perunica by MANDA et al. (2009, 2010) and others (see list above) are important contributions to these fields and confirms that nautiloid cephalopods are indeed reliable indicators for this interval. Studies of faunas at both a local and regional scale within single biozones are still preferable for building a consistent database for future reference.

Certain taxa show potential as biostratigraphical indicators for the Silurian-Devonian interval as has been shown by various studies (see list above): *Orthocycloceras*, *Hemicosmorhoceras*, *Plagiostomoceras*, *Pseudocycloceras*, *Columenoceras*, *Parakionoceras*, *Kionoceras*, *Dawsonoceras*, *Sphaerorthoceras*, *Temperoceras* as well as representatives of the Phragmocerids, Oncocerids and Tarphycerids such as *Ophioceras*. Nautiloid cephalopod assemblages were broadly defined by GNOLI & SERPAGLI (1991) and by MANDA & KŘÍŽ (2006) using a suite of taxa which dominated in certain Silurian series: *Pseudocycloceras transiens-Columenoceras grande* (Wenlock–early Ludlow), *Merocycloceras declive-Cryptocycloceras deludens* (early Ludlow), *Kopaninoceras thyrus-Orthocycloceras fluminese* (late Ludlow–Pridoli/Early Devonian, *Pseudocycloceras duponti-*

Sphooceras truncatum (Wenlock), *Pseudocycloceras duponti-Kionoceras doricum* (early Ludlow) and *Pseudocycloceras nereidum-Sphooceras truncatum* (Ludlow). Taxa such as *Deiroceras* and *Jovellania* have been seen to dominate in certain intervals of the Devonian in Morocco (KRÖGER 2008) and may prove useful for recognition of marker beds deposited within sequences.

There have been numerous studies of the well-known Silurian-Devonian in age ‘Orthoceras limestones’ or Cephalopod Limestone Biofacies both with regard to their depositional cycles and biotic content. The Carnic Alps of Austria is a key locality along the Northern Gondwana margin regarding Silurian biostratigraphical correlation where the Silurian Cephalopod Limestone Biofacies is well preserved. The Cellon section has been utilized as a geographic reference district (RD) for both conodont correlation studies (KLEFFNER 1989, 1995) and for evaluation of global eustatic changes (JOHNSON 2010) for the North Gondwana area. Recognition of environmental and water depth changes based on the fossil assemblages (mostly trilobites, brachiopods and bivalves) from the Silurian depositional sequences developed there (BRETT et al. 2009) places a tight control on small scale bioevents within well-defined conodont (WALLISER 1964), graptolite (JAEGER 1975) and chitinozoan (PRIEWALDER 1997) biozones. Particular emphasis has been placed in these studies on establishing the response of marine faunas to oscillations in sea-level and to the oceanic variations (chemistry, temperature, currents) recorded (WENZEL 1997; KŘÍŽ 1998, KŘÍŽ et al. 2003) during this time interval on a local scale for comparison with data from other North Gondwana terranes such as Sardinia and Bohemia and on a global scale with some sectors of Avalonia (the British Isles) and Laurentia (North America).

Correlation of the nautiloid faunal assemblages from the cephalopod limestone biofacies levels and their taphonomic signatures within the contexts outlined above with evidence for pronounced redox changes, surface currents, regression/transgression sequences within precise intervals from the Carnic Alps (Austria) successions may identify common controlling factors in the palaeogeographic distribution and migrational routes of these faunas (HISTON 2012b). Current studies, in line with those of MANDA (2009), MANDA & FRYDA (2010) and others, attempt to identify controlling factors on a local scale for nautiloid distribution within precise time slices that may then be recognized in other areas where these faunas occur along the North Gondwana Margin (HISTON 2012a). This is an on-going study done in parallel with revision of historical collections (GNOLI & HISTON 1998; HISTON 1999; GNOLI et al. 2000), systematic collection and description within precise biozones

(HISTON 2002; HISTON et al. 2010) and taphonomic studies (HISTON 1999, 2002, 2012a and references therein;). This holostatigraphical approach may provide further evidence for the reconstruction of reliable nautiloid assemblages or identification of precise marker taxa.

Carboniferous

The monographic works by HYATT, MILLER and others in the USA, SHIMANSKY in Russia, FOORD and TURNER in the British Isles, and DE KONINCK from Belgium constituted the foundations for the study on Carboniferous nautiloid cephalopods (see papers listed under references). In recent years some taxonomic revision of these nautiloids has been carried out (see studies listed by HISTON, MAPES, NIKO, STURGEON and others), but the use of rapidly evolving goniatite lineages to establish a biostratigraphy, particularly for the Upper Carboniferous is predominant and consideration of the stratigraphical potential of nautiloid cephalopods has been neglected. However, several taxa are worthy of mention and are known to be abundant at certain intervals in a diverse range of palaeogeographical settings. Large specimens of *Rayonoceras* are known to be markers within Lower Carboniferous strata of Europe and the USA where they are common in the Brigantian /Mississippian. The annulated *Cycloceras* and taxa of the Oncocerida such as *Potrioceras* and *Welleroceras* are common in the Lower Carboniferous. Several Pseudorthocerataceae taxa are restricted to the Carboniferous such as *Mitorthoceras*. The distinctively ornamented *Brachycycloceras* is a common element in the Upper Carboniferous. A variety of coiled nautiloid taxa such as *Vestinautilus*, *Trigonoceras*, *Aphelaeceras*, *Epistroboceras*, *Maccoceras*, *Asymptoceras*, *Acanthonautilus* and *Bistrialites* are typical of the Lower Carboniferous of the British Isles, Belgium, Asia and the USA. More precise biostratigraphical data may be obtained through further study of the ranges of these taxa at species level. However, to date, such a zonal scheme has not been developed.

Permian

The papers by MILLER et al. (1942, 1949) of the Permian nautiloids of the USA still stand as reference works for taxonomy of the group. However, there are few studies in relation to the development of the biostratigraphical potential of nautiloid cephalopods for this interval. An investigation of the Late Permian nautiloid faunas of the Bellerophon Formation from the Dolomites of Northern Italy (POSENATO & PRINOTH 2004, 2007; POSENATO 2010) indicates that certain nautiloid taxa representing species of *Tainoceras*, *Tirolonautilus*, *Liroceras* and *Foordiceras* may indeed be used as markers for precise levels within the succession whilst

some species may be assigned lineages and may be compared with assemblages described by TEICHERT & KUMMEL (1973) from the Late Permian of northwest Iran.

Triassic

Despite the relative paucity of works on Triassic nautiloid cephalopods, there is strong evidence of their potential value to some aspects of Triassic biostratigraphy. KUMMEL (1953) reviewed many Triassic nautiloid genera, indicating their stratigraphical ranges and a potential for their biostratigraphical use. This potential has been realised through the development of a detailed zonal scheme using nautiloids (SOBOLEV 1994) for the Boreal Triassic of Siberia. Such a scheme clearly demonstrates the value of the organisms as biostratigraphical tools.

Jurassic and Cretaceous

After the disappearance of seven families and approximately thirty genera during the Late Triassic extinctions (KUMMEL 1964, fig. 294), only the Nautilidae, represented by the single genus *Cenoceras* is conventionally regarded as having survived into the Jurassic where it underwent a radiation that led to all subsequent nautiloid genera including *Nautilus*. Analysis of the distribution of Middle Jurassic nautilids in western France by BRANGER (2004) indicates that the ranges of some taxa may be no more than one or two ammonite zones, indicating a potential utility as biostratigraphical tools. The same appears to be true for Lower Jurassic nautilids.

Historically the name *Cenoceras* has been broadly applied to a diverse range of Late Triassic to early Middle Jurassic nautilids that constitute a “plastic evolving complex” (KUMMEL 1956, p. 361). It is now recognised that this masks a number of distinct lineages within a rapidly evolving nexus of Lower Jurassic nautilid faunas (TINTANT 1984, 1987; RULLEAU 2008). Previous workers (HYATT 1894; SPATH 1927) recognised a number of different morphotypes within the ‘*Cenoceras* complex’ and provided names for several forms (including *Digonoceras*, *Ophionutilus* and *Sphaeronautilus*). The taxonomic status of these taxa requires revision.

More recently, TINTANT (1984) described three subgenera within *Cenoceras*: *Cenoceras* (in a restricted sense) for forms with relatively stout, involute conchs possessing a spiral ornament on the ventral and lateral surfaces of the whorls; *Hemicenoceras* for compressed forms possessing spiral ornament that is mainly confined to the ventral area, and *Metacenoceras* for forms with a flattened venter and an ornament consisting only of weak transverse growth lines. The earliest *Metacenoceras* occur in the early Sinemurian (Shales-with-Beef

Member, Charmouth Mudstone Formation near Lyme Regis, Dorset, UK [KING unpublished data]); *Hemicenoceras* is typically first encountered in the Carixian, where it is represented by *H. arare* (DUMORTIER, 1869) and *H. egregium* (PIA, 1914). In this paper, *Cenoceras* is used in the restricted sense employed by TINTANT.

The Hettangian to Carixian sequence of *Cenoceras malherbii* (TERQUEM, 1855) – *C. intermedium* (SOWERBY, 1816) – *C. striatum* (SOWERBY, 1817) – *C. pertextum* (DUMORTIER, 1867) – *C. simillimum* (FOORD & CRICK, 1890) was recognised in French successions by TINTANT (1984). In the United Kingdom, the same sequence of taxa is present (in part) in the Lower Jurassic of South Wales, and on the North Somerset and Dorset coasts (Fig. 4). Within this lineage there is a tendency for conchs to become more involute (from 20% in Hettangian forms to <10% in Carixian taxa); for the siphuncle to migrate from a ventrocentral to central position; for the whorl section to become more rounded and arched, and less quadrate; and for suture lines to become more sinuous, culminating with *C. jourdani* (DUMORTIER, 1874) in the Toarcian (KING 2011).

Late Hettangian and early Sinemurian strata on the Somerset coast (particularly within the *angulata* and *bucklandi* zones) include several monotonous beds of dark grey to black shales and bituminous mudstones which are virtually devoid of ammonites. These units contain fossil nautilids that are embedded in the substrate at orientations that range from horizontal to vertical, and provided hard attachment surfaces for a range of organisms of which oysters and crinoids are the most abundant.

Wherever ammonites are present in the Lower Jurassic, by comparison, nautilids make relatively poor biostratigraphical indicators. However, when ammonites are absent, cenoceratid nautilids can be used for biostratigraphical purposes and provide a resolution of at least stage or even substage level. Unlike Middle Jurassic nautilids (BRANGER 2004), there are, at present, no known Lower Jurassic cenoceratid taxa that are characteristic indicators of an individual ammonite zone, although further research may change this picture.

Cretaceous nautilids from southern South America are relatively scarce and of low diversity. Most belong to one or two genera: *Cymatoceras* HYATT, and *Eutrephoceras* HYATT. Both genera possess a strongly involute, inflated and globose conch with an orthochoanitic, sub-central siphuncle, as well as simple sutures. Both genera are cosmopolitan in distribution, but at species level, cosmopolitan distributions are almost nonexistent (CICHOWLSKI 2003) which may reflect the nektobenthic habit of these animals, as well as the lack of a plankton-

ic larval stage. Furthermore, the skeletal morphology of nautilids in general, and of these genera in particular, is markedly homogeneous with respect to the characters used to diagnose different species.

All these considerations suggest that attempts to use Cretaceous nautilids for biostratigraphical purposes are likely to be disappointing. This is compounded when the long stratigraphical ranges of some of the species are taken into consideration. *Cymatoceras perstriatum* (STEUER) is a typical example of such a species. *C. perstriatum* (STEUER) occurs in strata of Tithonian-Hauterivian age in the Neuquén Basin (CICHOWLSKI 2003); the late Tithonian-early Berriasian of the Chilean Aconcagua platform (CORVALÁN 1959; BIRÓ-BAGÓCZKY 1964), and the late Valanginian-early Albian of the Chañarcillo Basin (northern Chile: HOFSTETTER et al. 1957; SEGERSTROM 1960). The whorl cross-section, the sutural pattern, and overall shape of the conch all exhibit a marked ontogenetic and intraspecific variability (CICHOWLSKI 2003). Such a range of variation implies that an extra effort may be required in order to positively identify individual members of this particular taxon.

However, there are some nautilid species possessing easily recognisable morphologies that present low variability within and between individuals. When such taxa have a relatively short stratigraphical range, and other biostratigraphic markers are lacking, they may provide valuable information with regard to the age of the strata in which they are found. One such example may be provided by *Eutrephoceras dorbygnianum* (FORBES in DARWIN, 1846), known from the Antarctic Peninsula, Quiriquina Island in Chile, the Austral Basin of southern Argentina, and possibly from Angola (STEINMAN 1895; SPATH 1953; HOWARTH 1965; STINNESBECK 1986; CICHOWLSKI et al. 2005; NIELSEN & SALAZAR 2011). This species is characterized by an almost straight suture, combined with a small, acute, umbilical saddle, and a semilunate whorl cross-section (CICHOWLSKI et al. 2005). Based on its occurrence, this species ranges through the Campanian and Maastrichtian, becoming particularly abundant during the Maastrichtian. Thus, like the Lower Jurassic *Cenoceras*, the stratigraphical range of some Late Cretaceous nautilids may resolve to one or two stages.

Concluding remarks

This survey of the use and potential use of nautiloid cephalopods in biostratigraphy is inevitably, incomplete. Nevertheless, examples provided by the liutitids (above) and the Triassic nautiloids of Siberia (SOBOLEV 1994) demonstrate that when diversification rates are high, these organisms may be used to define biostrati-

graphical schemes to resolutions that are at least equivalent to those generated through the use of other groups of organisms. In situations where other groups of organisms are rare or not present, nautiloid cephalopods may provide an alternative basis for a biostratigraphical scheme. Finally, and perhaps more significantly, nautiloid cephalopods are powerful palaeobiogeographical tools, especially, but not exclusively during the Ordovician and Silurian. In order to refine their value as palaeobiogeographical tools, it will be necessary also to further refine their biostratigraphy. This is a task that will continue through the study of well-documented collections as well as newly collected material that may help resolve questions related to older collections, and bring to light new material from poorly known areas.

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