High-level classification of the nautiloid cephalopods: a proposal for the revision of the *Treatise Part K*

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Abstract

High-level classification of the nautiloid cephalopods has been largely neglected since the publication of the Russian and American treatises in the early 1960s. Although there is broad general agreement amongst specialists regarding the status of nautiloid orders, there is no real consensus or consistent approach regarding higher ranks and an array of superorders utilising various morphological features has been proposed. With work now commencing on the revision of the *Treatise Part K*, there is an urgent need for a methodical and standardised approach to the high-level classification of the nautiloids. The scheme proposed here utilizes the form of muscle attachment scars as a diagnostic feature at subclass level; other features (including siphuncular structures and cameral deposits) are employed at ordinal level. We recognise five subclasses of nautiloid cephalopods (Plectronoceratia, Multiceratia, Tarphyceratia nov., Orthoceratia, Nautilia) and 18 orders including the Order Rioceratida nov. which contains the new family Bactroceratidae. This scheme has the advantage of relative simplicity (it avoids the use of superorders) and presents a balanced approach which reflects the considerable morphological diversity and phylogenetic longevity of the nautiloids in comparison with the ammonoid and coleoid cephalopods. To avoid potential confusion arising in the higher levels of nautiloid classification employed in the revision of the *Treatise Part K*, we propose herein to replace the suffix '-oidea' at subclass level with the suffix '-ia'. Apart from removing ambiguity and clarifying the nomenclature, this approach also brings greater consistency and affinity with modern zoological classification schemes used for cephalopods. The original *Treatise Part K* adopted an 'abbreviated' form of name for nautiloid orders using the ending '-cerida' rather than '-ceratida' (e.g., Order Actinocerida rather than Actinoceratida). For the revision of *Treatise Part K*, we propose using the 'full' version of the ordinal names. This approach re-employs several order names in their original form, e.g., Ellesmeroceratida, Oncoceratida, and Tarphyceratida. For reasons of consistency, we also apply the same to ordinal names created since the original *Treatise Part K*; therefore, Order Bisonocerida becomes Bisonoceratida.

Keywords Classification · Plectronoceratia · Multiceratia · Tarphyceratia · Nautilia · Orthoceratia · *Treatise*

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Introduction

More than 50 years have elapsed, since the original Russian *Osnovy paleontologii Volume V Mollusca–Cephalopoda I* and American *Treatise on Invertebrate Paleontology Part K* (*Mollusca 3*) covering the nautiloid cephalopods were published (Ruzhentsev et al. 1962; Teichert et al. 1964). During that time, knowledge of nautiloid phylogeny, morphology, and systematics has developed considerably with several new superorders and orders erected, and very many new genera described. Since publication of *Treatise Part K*, a variety of schemes have been proposed for the high-level classification of the nautiloid cephalopods. Different workers have placed varied

emphasis and taxonomic weight on a range of morphological features and their value in classification; in some instances, the interpretation or even existence of some of the features used is debatable, and often, these classification schemes are not compatible with each other.

Work on the long-awaited revision of the *Treatise Part K* is now commencing and there is a pressing need for a modern, high-level classification of the nautiloid cephalopods. We believe that such a scheme should achieve 'reasonable consensus' amongst palaeontologists and be aligned with the generally well-established classifications of the ammonoid and coleoid cephalopods (covered in *Treatise Parts L* and *M,* respectively). It also needs to adequately reflect the considerable morphological diversity and phylogenetic longevity of the nautiloids in comparison with other main groups of cephalopods.

We propose here a revised classification of nautiloid cephalopods which is based on the overall morphology and position of the muscle attachment scars as a high-level (subclass) feature. This is employed in combination with other characters including structure and form of the ectosiphuncle, endosiphuncular, and cameral deposits (which are used at ordinal level). This revised classification proposes five subclasses: Plectronoceratia (Late Cambrian), Multiceratia (Late Cambrian to early Carboniferous, possibly Permian), Tarphyceratia nov. (early Ordovician to late Silurian), Orthoceratia (earliest Ordovician to late Triassic), and Nautilia (early Devonian to present day).

History of classification

The origin of the modern classification of nautiloid cephalopods can be traced back to Flower and Kummel (1950) which in turn influenced both the Russian *Osnovy* (Ruzhentsev et al. 1962) and American *Treatise Part K* (Teichert et al. 1964). Thorough reviews of the history of nautiloid systematics since that time have been provided by Wade (1988) and Shevyrev (2006).

Since 2006, nomenclatural additions to the high-level classification of the nautiloid cephalopods have been provided mainly by Mutvei (2013, 2015, 2017) who has proposed four new superorders: the Multiceratoidea, Nautilosiphonata, Calciosiphonata and Mixosiphonata. Mutvei erected the last three superorders mainly on the basis of the detailed structure of the siphuncle wall, specifically the connecting ring.

For purposes of comparison, the high-level taxonomic schemes employed by Flower and Kummel (1950), *Osnovy* and the original *Treatise Part K* are summarised in Table 1.

Evidence from muscle scars

Muscle attachments circumscribe the conch wall in a narrow band at the apical end of the body chamber. They form an annular elevation that is only very occasionally visible as a shallow groove on the surface of the internal mould of the body chamber. This band may be widened in places, reflecting the insertions of particular muscle pairs. In *Nautilus*, a pair of large muscles associated with the retraction of the head are inserted into the lateral surfaces of the body chamber. The variety of attachment patterns that occur amongst fossil ectocochliate cephalopods means that homologies with *Nautilus* are uncertain and the likely function of the muscles associated with different attachment patterns remains speculative and is a topic deserving much attention.

Muscle attachment scars have been recognised since the nineteenth century (Foord and Crick 1889), but their potential taxonomic value was first mooted when Mutvei (1957) recognised a correlation between ventromyarian muscle attachment scars and exogastrically curved conchs, and between dorsomyarian muscle attachments and endogastrically curved conchs. Later, Mutvei (1964a) proposed three groups based on muscle attachment patterns (Fig. 1g): the Oncoceratomorphi (oncomyaryan), Nautilomorphi (ventromyarian and pleuromyarian) and Orthoceratomorphi (dorsomyarian)—and regarded these as of the same taxonomic rank as ammonites and belemnites. By contrast, Sweet (1959) argued that the ventromyarian and dorsomyarian conditions were the consequence of repeated adaptive convergence. Muscle attachment patterns have been discussed by several workers (e.g., Flower 1964b; Teichert 1964; Dzik 1984) and their opinions regarding the taxonomic value of these structures have varied. Much of the uncertainty regarding their significance arises from the rarity of their preservation, but they have also been considered suspect because of the patchy knowledge of their distribution and inconsistent patterns within particular taxonomic groups. Records of muscle attachment scars remain relatively scarce, but recent documentation of these structures (e.g., Turek 1975; Mutvei 2002a, b, 2013; Mutvei and Stumbur 1971; Kröger and Mutvei 2005; Kröger et al. 2005; Kröger 2007) across a broad range of orders facilitates a firmer assessment of their taxonomic value (Table 2). While the number of documented remains of muscle attachments scars remain small, when each record is taken as being representative of a family as a whole, where known, the nature of the muscle attachment scars is seemingly consistent across orders (Table 3).

Inconsistencies in distribution patterns have often been used as evidence that invalidates the taxonomic significance of muscle attachment scars rather than an indication

Table 1 Comparison of the higher level classification schemes of nautiloid cephalopods used by Flower and Kummel (1950) and the Russian and American treatises

Flower and Kummel (1950)		Ruzhentsev et al. (1962) (*Osnovy*)		Teichert et al. (1964) (*Treatise Part K*)	
Subclass	Order	Superorder	Order/suborder	Subclass	Order/superfamily
Nautiloidea	Not recognised	Nautiloidea	Order Volborthellida	Doubtful nautiloid	Order Volborthellida
	Order Ellesmeroceratida		Order Ellesmeroceratida	Nautiloidea	Order Ellesmerocerida
	Order Bassleroceratida				
	Order Tarphyceratida		Order Tarphyceratida		Order Tarphycerida
	Order Barrandeoceratida		Suborder Tarphyceratina		Order Barrandeocerida
			Suborder Barrandeoceratina		
	Order Michelinoceratida		Order Orthoceratida		Order Orthocerida
					Superfamily Orthocerataceae
					Superfamily Pseudorthocerataceae
	Order Ascoceratida		Order Ascoceratida		Order Ascocerida
	Order Discosorida		Order Discosorida		Order Discosorida
	Order Oncoceratida		Order Oncoceratida		Order Oncocerida
	Orders Nautilida, Centroceratida, Rutoceratida and Solenochilida		Order Nautilida		Order Nautilida
			Suborder Rutoceratina		Superfamily Trigonocerataceae
			Suborder Tainoceratina		Superfamily Tainocerataceae
			Suborder Centroceratina		Superfamily Aipocerataceae
			Suborder Liroceratina		Superfamily Clydonicerataceae
			Suborder Nautilina		Superfamily Nautilaceae
	Order Actinoceratida	Actinoceratoidea	Order Actinoceratida	Actinoceratoidea	Order Actinocerida
	Order Endoceratida	Endoceratoidea	Order Endoceratida	Endoceratoidea	Order Endocerida
			Suborder Proterocameroceratina		
			Suborder Endoceratina		
	Not recognised		Order Intejoceratida		Order Intejocerida
	Not recognised	Bactritoidea	Order Bactritida	Bactritoidea	Order Bactritida

that there might be problems with the particular taxonomic scheme in use—such cases are discussed further below. We are well aware, however, that muscle attachment patterns might also have originated through convergence and this needs to be investigated through independent tests.

Sweet (1959) argued that the lituitids, placed in the Tarphyceratida, but possessing dorsomyarian rather than ventromyarian muscle attachment scars, was an example of adaptive convergence arising from the straightening of the conch. The lituitids were placed in the Tarphyceratida (Balashov 1962a; Furnish and Glenister 1964b), but were

regarded as derived from an orthoceratid lineage (Dzik 1984; King 1999). Dzik (1984) argued for such an assignment on the grounds of the stratigraphical order of appearance of genera comprising his Suborder Lituitina. However, there is other strong evidence for such a relationship, including the nature of the protoconch (Kröger 2006), the presence of cameral deposits, and the structure of the connecting ring (Mutvei 2002a, b). All these characters are congruent with an orthocerid ancestry, as are the dorsomyarian muscle attachments.
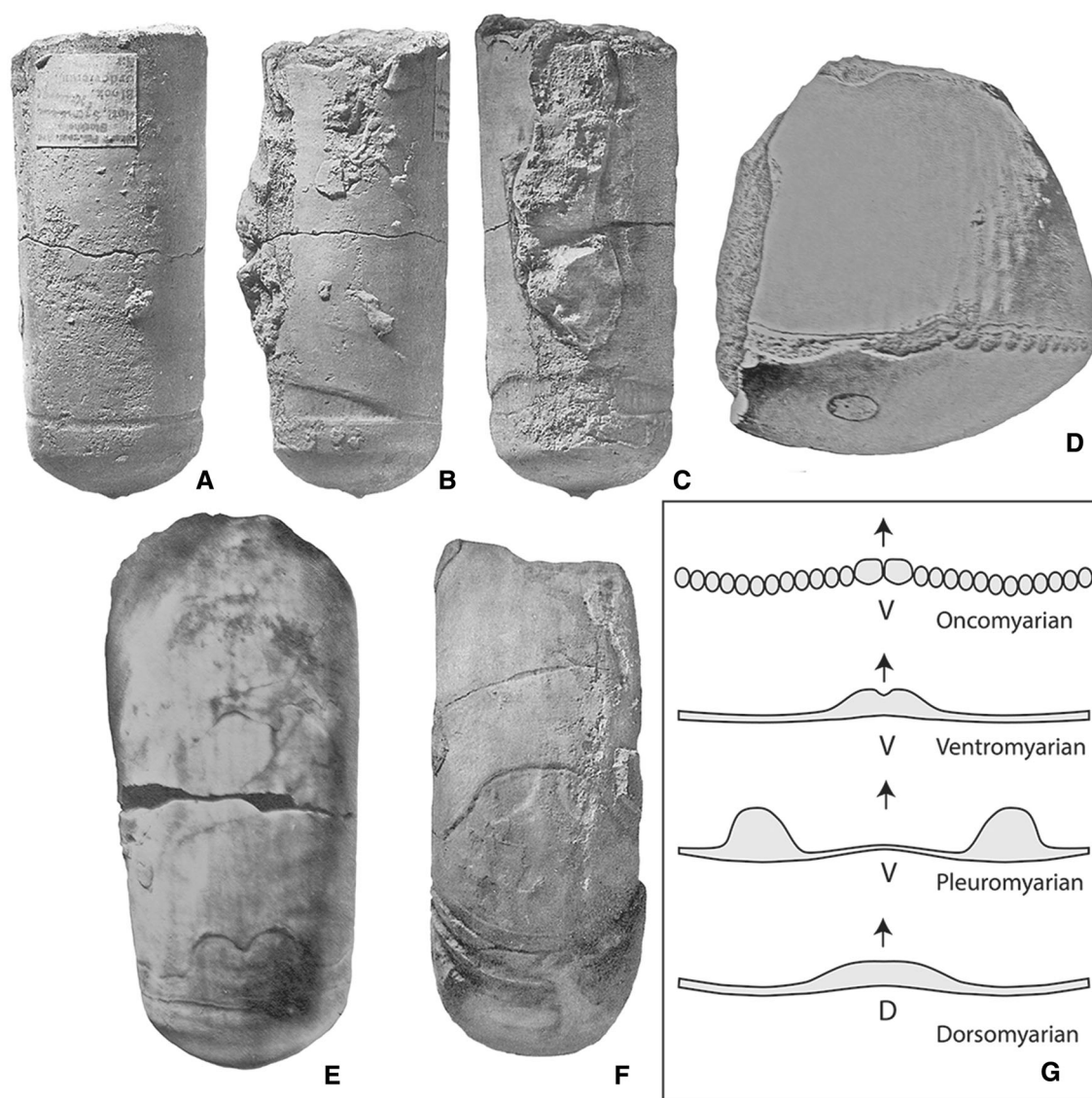
Fig. 1 Examples of nautiloid muscle scars. Muscle attachment scars preserved on the internal moulds of body chambers. **a–c** Ventral, lateral (dorsum on left), and dorsal views of the dorsomyarian muscle attachment scars of *Orthoceras regulare* (Schlotheim, 1820), × 0.57; **d** internal mould of the body chamber of the oncocerid *Diestoceras* sp. showing multiple pairs of muscle attachment scars circumscribing the base of the body chamber, with a pair of enlarged scars over the venter; **e** *Uranoceras* (?) *longitudinale* (Angelin, 1880), bilobed ventromyarian scar at base of body chamber, × 0.8; **f** Body chamber of *Estoniceras perforatum* Schröder, 1888 with large ventral muscle attachment area × 1.0; **g** Line diagrams showing the four main types of muscle attachment scars seen on nautiloid cephalopods. Arrows indicate direction of aperture, *V* venter, *D* dorsum. **a–c, e, f** After Mutvei (1957, pl. 2, figs. 5, 6; pl. 6, fig. 1 and pl. 4, fig. 2), respectively. **d** After Sweet (1959, pl. 42, fig. 6)

The Ellesmeroceratida, as documented by Flower (1964a) and Furnish and Glenister (1964a), has been steadily reduced in scope, with many of the constituent families having been transferred to other orders. Of those that remain, with the possible exception of the Basslero-ceratidae, where the nature of the attachment scars is currently unknown, all possess oncomyarian attachments. Some members of the Ellesmeroceratida such as the Cyclostomiceratidae possess an enlarged pair of scars over the venter (Mutvei and Stumbur 1971; King 1998; Kröger and Mutvei 2005) and this may form the basis for their future removal from the Ellesmeroceratida. Such differentiation appears to be lacking in the ellesmeroceratid *Paradakeoceras* (Kröger 2007) and a specimen attributed to *Ellesmeroceras* (Kröger 2007), while specimens of *Balkoceras*, *Palaeoceras,* and possibly *Plectronoceras* illustrated by Flower (1964a) show the tracks of oncomyarian muscle scars on the phragmocones, indicating that the Plectronoceratida are also oncomyarian.

Table 2 Current knowledge of numbers of families where muscle attachment scars have been reported distributed across orders

Subclass	Order/suborder	No. of families per subclass	No. of families per (sub)order	No. of families where attachment pattern is known	Attachment pattern (O, V, P, D)	% of families per subclass where attachment pattern is known	% of families per order where attachment pattern is known
Plectronoceratia	Plectronoceratida	4	2	2	O	50	100
	Yanheceratida		1	0	?		0
	Protactinoceratida		1	0	?		0
Multiceratia	Ellesmeroceratida	48	7	3	O	35	43
	Cyrtocerinida		3	1	O		33
	Bisonoceratida		11	1	O		9
	Oncoceratida		17	9	O		53
	Discosorida		10	3	O		30
Tarphyceratia nov.	Tarphyceratida	12	10	6	V, Pl	67	60
	Ascoceratida		2	2	V		100
Nautilia	Nautilida	24	24	8	Pl	33	33
Orthoceratia	Rioceratida	45	2	1	D	22	50
	Dissidoceratida		9	1	D		11
	Dissidoceratina		7	1	D		14
	Troedssonellina		2	0	?		0
	Orthoceratida		9	4	D		44
	Pseudorthoceratida		3	0	?		0
	Actinoceratida		8	1	D		13
	Astroviida		8	2	D		38
	Lituitina		2	2	D		100
	Pallioceratina		6	0	?		17
	Endoceratida		6	1	D		17

Numbers of families are derived from the *Treatise Part K* 1964 and a range of subsequent publications. The numbers are inevitably subjective and dependent on opinions regarding the validity of particular family groupings. For sources of data regarding records of muscle attachment scars, see Online Appendix 1

O oncomyarian, *V* ventromyarian, *Pl* pleuromyarian, *D* dorsomyarian

Mutvei (1957) documented dorsomyarian attachments in the then ellemeroceratid *Baltoceras burchardi*, leading Teichert (1964) to speculate that the dorsomyarian condition might be primitive for cephalopods. By transferring the Baltoceratidae to the Dissidoceratida, the Ellesmeroceratida and their likely ancestors, the Plectronoceratida, consist of taxa that possess oncomyarian muscle attachments either with or without a differentiated ventral pair of scars.

Dzik (1984) argued that the muscle attachments of *Trocholites contractus* and *T. orbis* (Tarphyceratida) with their retractor scars located laterally or subdorsally, demonstrated that the diagnostic value of muscle attachment scars was not as great as claimed by Mutvei (1964a). This case should be viewed in the context of the range of locations of the retractor scars muscle in the Tarphyceratida as a whole. Muscle attachments known from the Estonioceratidae and other members of the Trocholitidae (*Discoceras*) (Kröger and Mutvei 2005; Mutvei 1957, 2013) show well-developed retractor scars over the venter. Members of the Uranoceratidae, as illustrated by *Uranoceras* (Mutvei 1957, pl. 7) and *Siljanoceras* (Kröger 2013, pl. fig. 34) exhibit large and markedly bifid ventral attachments, while in the leichritrochoceratid, *Kosovoceras* (Turek 1975, fig. 4), they are widely separated on the ventrolateral or lateral surfaces.

The development of a pair of large ventral retractors in the tarphyceratids and the reduction or loss of the muscle attachments circumscribing the base of the body chamber may have facilitated the freedom of the retractor muscles to migrate to ventrolateral, lateral, or even sub-dorsal positions within the body chamber in response to changes in the morphology of the body chamber or overall conch. Regardless of this flexibility in the position and shape of the retractor attachment, all belong to the Tarphyceratida and thus lie in a single lineage.

Classifications of the Nautilida have been proposed in which the order either originated as independent lineages

Table 3 Character matrix table summarizing distribution of morphological features against proposed classification used in the revised *Treatise Part K*

Subclass	Order/suborder	Muscle attachment scars				Connecting rings		CD	Endosiphuncular deposits							Embryonic conch									
		O	V	P	D	N	C		D	En	R	P	A	Ar	Ec	Ci	Ca R	Ca P	Cr	Hs	Sp	S	L	ES	EL
Plectronoceratia	Plectronoceratida	Y					Y?		Y							?	?	?	?	?	?	?	?	?	?
	Yanheceratida	?							Y							?	?	?	?	?	?	?	?	?	?
	Protactinoceratida	?					Y?		Y							?	?	?	?	?	?	?	?	?	?
Multiceratia	Ellesmeroceratida	Y				Y			Y							?	?	?	?	?	?	?	?	?	?
	Cyrtocerinida	Y				Y			Y							?	?	?	?	?	?	?	?	?	?
	Bisonoceratida	Y				Y			Y	Y						?	?	?	?	?	?	–	Y	?	Y
	Oncoceratida	Y				Y			Y							Y	?	?	Y	?	?	Y	Y	?	Y
	Discosorida	Y				Y			Y	Y		Y				Y	Y	?	Y	?	?	?	Y	?	?
Tarphyceratia nov.	Tarphyceratida		Y	Y		Y										?	Y	?	Y	?	?	Y	Y	?	Y
	Ascoceratida		Y			Y										?	?	?	?	?	?	?	?	?	?
Nautilia	Nautilida			Y		Y										Y	Y	?	Y	?	?	?	Y	?	Y
Orthoceratia	Rioceratida nov.				Y	?	?		Y							?	?	?	?	?	?	?	?	?	?
	Dissidoceratida				Y		Y	Y	Y	Y	Y	Y	Y			?	?	?	?	Y	?	Y	?	?	?
	Dissidoceratina				Y			Y	Y		Y	Y		Y		?	?	?	?	?	?	?	?	?	?
	Troedssonellina						Y	Y	Y	Y	Y	Y	Y			?	?	?	?	?	?	?	?	?	
	Orthoceratida				Y		Y	Y					Y			Y	?	?	Y	Y	Y	Y	?	?	
	Pseudorthoceratida				?			Y				Y	Y			Y	Y	Y				Y	?	Y	Y
	Actinoceratida				Y		Y	Y						Y		?	Y					?	Y	?	?
	Astroviida				Y		Y	Y						Ec Y		?	?	?	?	Y	Y	?	?	?	?
	Lituitina				Y		Y	Y						Y		?	?	?	?	Y	Y	Y	?	?	?
	Pallioceratina				?			Y								?	?	?	?	?	?	?	?	?	?
	Endoceratida				Y	Y			Y	Y					Y	?	?	?	?	?	?	Y	?	Y	?

Muscle attachment scars: *O* oncomyarian, *V* ventromyarian, *P* pleuromyarian, *D* dorsomyarian. Connecting ring = Connecting ring type: *N*= nautilosiphonate, *C* calciosiphonate. *CD* cameral deposits. Endosiphuncular deposits: *D* diaphragms, *En* endocones, *R* rods, *P* parietal, *A* annuli, *Ar* radially divided annuli, *Ec* ectosiphonal deposits. Embryonic conch: *Ci* cicatrix (present/absent), *Ca R* cap-shaped rounded, *Ca P* cap-shaped pointed, *Cr* curved, *Hs* hemispherical, *Sp* spherical, *S* small protoconch, *L* large protoconch, *ES* embryonic conch small, *EL* embryonic conch large, *Y* definite presence

from the Rutoceratidae (Shimanskiy 1957, 1967) or from the Rutoceratidae and other unspecified oncocerids (Kummel 1964). Both of these models require that pleuromyarian muscle attachments arose from oncomyarian ancestors at least twice, and as many as four times if all the Palaeozoic nautilid superfamilies contain pleuromyarian taxa. The Rutoceratidae were assigned to the Oncoceratida (Manda and Turek 2009, 2011; Manda 2001; Turek 2007). An alternative derivation of the Nautilida from Devonian members of the Lechritrochoceratidae (Dzik and Korn 1992) only requires minor changes to the shapes of the retractor attachments and minor shifts in their location. The ultimate origin for the Nautilida as proposed by Dzik and Korn (1992) was in the orthocerid *Stereospryroceras champlainense* (Flower 1955), followed by a series of steps via *Centrocyrtoceras* (Barrandeoceratidae) and *Uranoceras* (Uranoceratidae). This is difficult to conceive of, since other orthocerids are dorsomyarian and possess proportionately longer body chambers (and in the case of *S. champlainense*, well-developed cameral and endosiphuncular deposits). It seems simpler to derive the various families that were placed in the Barrandeoceratida from the Tarphyceratida, which, with a shell already coiled combined with ventromyarian muscle attachments, have more in common with each other than either do with the Orthoceratida. Using molecular clock data, Kröger et al. (2011) derived an earliest Devonian date for the divergence of *Nautilus* from coleoids. Where such dates to be correct, the only possible origin for the Nautilida lies within the Orthoceratida. The alternative could be that there are serious problems with these methods. This seems possible, given the margins of error for some of the dates generated. Indeed, the date obtained by Warnke et al. (2011) at 453 ± 60 Ma could even reflect the Early Ordovician diversification of the Cephalopoda, in which case derivation from the Tarphyceratida remains possible.

In his review of ascoceratids from the Boda Limestone of Sweden, Kröger (2013) considered it more probable that the ancestors of the Ascoceratida lay within mid Ordovician Barrandeoceratidae or Aspidoceratidae (assigned by Kröger to the Order Barrandoceratida, placed here with the Tarphyceratida) than lying within the Orthoceratida. We concur that morphological evidence, including the presence of ventromyarian muscle scars (in the genera *Billingsites* and *Probillingsites*; Flower 1963; Sweet 1959; see Online Appendix 1) supports a closer relationship between the Tarphyceratida ('Barrandeoceratida') and Ascoceratida than with the Orthoceratida (which are dorsomyarian).

The Brachycycloceratidae, placed in the Orthoceratida by Sweet (1964), are anomalous both in the general form of the phragmocone and body chamber and in the possession of pleuromyarian muscle attachment scars. It may be

argued that the family provides an example, where dorsomyarian attachments separated and migrated to the lateral surfaces of the body chamber, but the similarity of *Brachycycloceras* to the neptunoceratid *Texanoceras* (Niko and Mapes 2011) suggests that they may be closely related. The Neptunoceratidae were assigned to the Nautilida by Shimansky (1967), but their endogastric curvature, as interpreted by Niko and Mapes (2011) on the basis of the transverse section of *Texanoceras*, would make them extremely anomalous members of that order. However, as indicated by the presence of a dorsal furrow (Niko and Mapes 2011, fig. 1.8) and a conchal furrow (Niko and Mapes 2011, fig. 1.9), *Texanoceras* is exogastric with a sub-ventral siphuncle. Thus, *Brachycycloceras* and *Texanoceras* may be better assigned to the Nautilida (which are pleuromyarian), and with their relatively breviconic conchs, may be affiliated with the Scyphoceratidae.

Sweet (1959) argued that ammonites, if derived from orthoceratids, must have achieved a degree of stability in relation to the positioning of muscle attachments, since they are dorsomyarian, but exogastrically coiled, and hetermorph ammonites retained dorsomyarian attachments. Paired or bilobed dorsomyarian attachments are common to orthoceratids and ammonites, but the patterns of attachment in the latter are more complex and involve unpaired dorsal and ventral scars, as well as paired lateral scars in addition to the dorsomyarian attachments (Kennedy et al. 2002; Mironencko 2015; Doguzhaeva and Mapes 2015). Since the Ammonoidea originated from the Orthoceratida (Klug et al. 2015), it would appear that the shape of the body chamber, at least in terms of its curvature, had no influence on the position of attachment of the muscles, suggesting that this pattern was inherited from orthoceratid ancestors.

Evidence from other characters

Connecting ring structure

In terms of overall shape, the connecting ring, as with the septal necks, may exhibit a range of morphologies (shape and thickness) that have been used in the diagnoses of taxa from ordinal to species level. Descriptions of the fine structure of the connecting ring were largely limited to polished or thin sections where layering and other discrete structures within the connecting ring distinguished by colour and/or texture, could be recognised (see for example Flower and Teichert 1957, fig. 7; Flower 1964b, p. 31). While some of these features might represent original structures, in most individuals, such fabrics were obliterated during diagenesis.

Mutvei (2002a, b) distinguished between two types of connecting ring based on their fabric. The first possessed an outer spherulitic–prismatic layer and an inner calcified-perforate layer (calciosiphonate). The second, of the *Nautilus*-type (nautilosiphonate), consisted of an outer spherulitic–prismatic layer and an inner organic fibrous layer that is particularly susceptible to diagenetic effects and is not preserved in fossils. The inner calcified-perforate layer described in ammonites by Mutvei and Dunca (2007) was interpreted as diagenetic in origin by Kulicki et al. (2007). This finding may raise doubts as to the reality of the presence of this fabric described from the connecting rings of other cephalopods. Mutvei (2016) re-described the connecting rings of a number of taxa including the actinocerid *Adamsoceras holmi*. Regardless of the reality of pores and cavities in this outer part of the connecting ring in *A. holmi*, the presence of a laminar fabric within the outer layer suggests that the construction of the connecting ring is distinctly different from that of *Nautilus*. Moreover, while these structures have been reported from phosphatised preservations and could be regarded as suspect on the basis of the observations of Kulicki et al. (2007), similar structures have been reported in non-phosphatised material including the narthecoceratid *Donacoceras* (Mutvei 1998), *Eushantungoceras, Huroniella,* and *Rayonnoceras* (Mutvei 1996). However, images purporting to show calciosiphonate connecting rings in members of the Uranoceratidae (Mutvei and Dunca 2011) and the Plectronoceratida (Mutvei et al. 2007) are difficult to interpret and unconvincing.

Cameral deposits

Despite doubts voiced with regard to whether cameral deposits were formed in vivo, post-mortally, or through a bacterially mediated process (e.g., Mutvei 2018), the fact that cameral deposits possess characteristic and repeatable forms while exhibiting morphological changes from camera to camera in an ontogenetic series indicates that they were an integral part of the organism (Kröger et al. 2005; Pohle and Klug 2018). The occurrence of cameral deposits appears to be restricted to members of the Orthoceratia.

Cameral deposits also were reported from the Discosorida (Flower and Teichert 1957, p. 28). However, with the exception of the Ruedemannoceratidae, these deposits can be better interpreted as the tracks of oncomyarian muscle attachment scars along the length of the phragmocone. Cameral deposits reported from *Ruedemannoceras* Flower, 1940 (Flower and Teichert 1957, pl. 2, fig. 1; pl. 5, fig. 7) were described as being developed on the ventral side of the phragmocone and as episeptal deposits that extended onto the dorsal side apically and then over the dorsal wall onto the hyposeptal surfaces of the camerae. The assignment of *Ruedemannoceras* and *Madiganella* Teichert & Glenister, 1952, to the Discosorida was questioned by Dzik (1984) who suggested that they were instead related to the Orthoceratida. Given the heavily recrystallized state of this material, further study is required to establish the nature of the purported cameral deposits in these taxa.

Endosiphuncular deposits

The importance of endosiphuncular deposits in the study of the systematics of nautiloid cephalopods is clearly reflected in the names that have been applied to various groups at higher levels within the systematic hierarchy (e.g., Endoceratoidea Teichert 1933; Actinocerida Teichert 1933; Stereoplasmoceratidae Kobayashi 1934; *Rhabdiferoceras* Flower 1964a).

Some endosiphuncular deposits, including the annulosiphonate deposits of actinoceratids and the endocones of endoceratids, were considered to have been precipitated from within the siphonal tissue (Teichert 1933; Flower 1955, 1964b). Here, we follow Mutvei (1964b) and Evans and King (2012) in regarding all such structures as having been secreted by the siphonal epithelium. Endosiphuncular deposits represent a diverse range of structures that were deposited onto the septal necks and connecting rings. The microstructure of endosiphuncular deposits is poorly known, as they appear to have been particularly susceptible to diagenesis (Fischer and Teichert 1969, p. 13). A greater knowledge of the microstructure of the various types of endosiphuncular deposits is key to an enhanced understanding of their development, function, and potential taxonomic value at a high level. This must await the discovery of better-preserved material, or else an understanding of their diagenesis, such that it becomes possible to interpolate the original fabrics.

Where endosiphuncular microstructures appear to be relatively well-preserved, as in the dissidoceratid *Donacoceras* Foerste, 1925 (investigated by Mutvei 1998), they consist of radially arranged calcareous lamellae constructed from crystallites that splay out from a central plane in a 'feather-like' fashion; these compete with growth from adjacent lamellae and progressively infill the lumen of the siphuncle. These structures originated as discrete units distributed radially around the inner surfaces of the septal necks and the connecting rings and grew forwards with the growth of the organism (Mutvei 1998, fig. 3). Whatever the microstructure of endosiphuncular deposits is found to be in other taxa, in *Donacoceras,* the microstructure is quite distinct from that of the septal necks and connecting rings and, therefore, served a different function.

The microstructures and morphologies of the connecting ring reflect an overall strategy for the efficient transfer of fluid from the camerae, primarily through increasing the relative surface area of the connecting ring (Kröger 2003). The primary function of the endosiphuncular deposits was to decouple the siphuncle from the camerae. This reduced both the metabolic cost of removing fluid returning to the camerae and the cost of maintaining a coupling to camerae, where their function was no longer providing a significant contribution to the hydrostatic functioning of the organism as a whole (Evans 1992; Kröger 2003). Where the relative diameter of the siphuncle was large, as in the Endoceratida, Bisonoceratida, and Actinoceratida, endosiphuncular deposits may have had a further hydrostatic function as ballast while also influencing the poise of the organism (Flower 1957; Westermann 1977; Crick 1988).

The simplest forms of endosiphuncular deposits are diaphragms. These consist of partitions of unknown composition, but presumably originally comprised aragonite or calcite in an organic matrix. Diaphragms either occur at regular intervals within the lumen of the siphuncle or may be crowded together; they may be planar, convex or concave in shape. Although the spaces between adjacent diaphragms were previously considered to contain organically deposited aragonite that constituted part of the overall structure (Chen and Teichert 1983), these spaces were later demonstrated to have been empty during life (Evans 1992; Mutvei et al. 2007). Primary endosiphuncular diaphragms (i.e., diaphragms that have no association with any other endosiphuncular deposits) occur across a range of orders (see Table 3). Their distribution, which includes the Plectronoceratia and Multiceratia, indicates that this character is plesiomorphic and of little use for defining taxa at any but a very high level (Dzik and Kiselev 1995). Secondary diaphragms occur in combination with other endosiphuncular deposits including endocones, parietal and annulosiphonate deposits, and endosiphuncular rods. They appear to partition off voids left unfilled by other deposits and may reflect the staged resorption of the siphonal strand from the apical end of the siphuncle. Given the probable function of secondary diaphragms combined with their distribution across the Multiceratia and Orthoceratia, they may be of little use for defining taxa.

The term endocone has been applied to endosiphuncular deposits possessing a conical shape with the tip directed toward the apical end of the conch. Evans and King (2012) reported endocones from several orders belonging to the Multiceratia (Discosorida, Bisonoceratida) and Orthoceratia (Endoceratida, Dissidoceratida). Discosorid endocones are distinct in that they are formed from parietal deposits that originate on the septal necks and connecting rings and extend apically over older parietal deposits to fuse and form a conical structure (Flower and Teichert 1957). This feature demonstrates that parietal deposits are not restricted to the Orthoceratia, although further research may demonstrate contrasting microstructures in parietal deposits of the Discosorida and the Orthoceratia.

The endocones found in members of the Bisonoceratida and Endoceratida are likely to have originated through the increasing concavity of primary diaphragms, combined with such reduction in the intervals between diaphragms that they effectively became a stack of conical lamellae (Evans and King 2012, fig. 2). In the Bisonoceratida, the development of conchiolin crests in the form of lamellae projecting from the walls into the lumen of the siphuncle provided an additional substrate for the endocones to develop on, and where multiple (and sometimes branched) conchiolin crests were present, complex structures involving infula, inverted endocones and multiple and discrete stacks of endocones were generated. In contrast, the Endoceratida lack conchiolin crests and their endocones remained simple in form.

It is within the Orthoceratia that the morphology of the annulosiphonate deposits plays an important current and historical role in elucidating the relationships of the component taxa. A detailed discussion of the nature and distribution of annulosiphonate deposits across the Orthoceratia is beyond the current scope of this paper, but a single example will suffice to demonstrate the importance of elucidating the structure of the deposits in efforts to resolve taxonomic problems within this subclass.

Hook and Flower (1977, fig. 1) proposed an origin of the Troedssonellidae from the 'Rod-bearing Baltoceratidae' and for the Michelinoceratidae (= Geisonoceratidae) from the 'vacuosiphonate Baltoceratidae'. The evidence for this was based on material from the late Early Ordovician Blackhillsian Stage of North America, and suggested a polyphyletic origin for the Orthoceratida as then understood by Hook and Flower. Material from the Early Ordovician Moridunian Stage of England and Wales (Evans 2005), which is older than that from North America, includes representatives of the Troedssonellidae and Polymeridae. The mode of preservation of the endosiphuncular deposits in these forms enables study in three dimensions, with finer structures being preserved in limonite. These demonstrate that in the Polymeridae, a marginal siphuncle with endosiphuncular rod and annulosiphonate and endocone-like deposits were present. A similar combination of structures is present in the troedssonellid *Moridunoceras* Evans, 2005, which possesses a sub-central siphuncle. Furthermore, in troedssonellids such as *Buttsoceras* Ulrich & Foerste, 1933, where endosiphuncular deposits are well developed, annulosiphonate deposits are also present at the septal necks (Flower 1962, pl. 11, figs. 8, 9; Hook and Flower 1977, pl. 11, fig. 11). Such evidence suggests a high degree of flexibility in the

morphology of the endosiphuncular deposits amongst early members of the Orthoceratia. This further indicates that an understanding of the distribution and development of endosiphuncular deposits is essential to the understanding of the origins and diversification of this subclass.

Early development of the conch

Since the publication of the original *Treatise*, knowledge of the protoconch and the early developmental stages of the conch in fossil nautiloids have increased substantially (Ristedt 1968; Kröger 2006; Kröger and Mapes 2004, 2007; Manda 2008; Turek 2007, 2010), but still remains relatively sparse given the overall size of the group. Associating the fragmentary remains of the embryonic stages of these organisms with later growth stages can also be a substantial obstacle to assessing their taxonomic value.

The cicatrix forms a distinct zone at the apex of the embryonic portion of the conch. It is generally cap-shaped with a prominent medial depression. In *Nautilus,* the cicatrix is composed of an outer conchiolin, and inner spherulitic–prismatic layer, later underlain by the proseptum (Tanabe and Uchiyama 1997). The outer edge of the cicatrix may be marked by a weak constriction beyond which the conch wall consists of an outer conchiolin layer, an outer prismatic layer, a middle nacreous layer, and inner prismatic layer (Tanabe and Uchiyama 1997, fig. 8).

Although the taxonomic distribution of cephalopods possessing a cicatrix is incompletely known, its presence appears to correlate with the cap-shaped morphology of the protoconch. These forms define the Palcephalopoda, while those taxa lacking a cicatrix and possessing a small hemispherical protoconch have been assigned to the Neocephalopoda (Engeser 1996). In these latter forms, the shell of the protoconch and early portion of the phragmocone is composed only of prismatic layers (Doguzhaeva et al. 1999).

Kröger (2006) demonstrated that the Orthoceratida contained both palcephalopods and neocephalopods, arguing that the order was polyphyletic, and transferred those forms possessing a cicatrix to the Pseudorthoceratida. The Orthoceratia, however, contains both palcephalopods and neocephalopods, and may be regarded as polyphyletic with respect to the nature of the protoconch. Here, the subclass is regarded as united by the possession of a dorsomyarian muscle attachment pattern—the autapomorphy that may define the subclass.

Regardless of the presence or absence of the cicatrix, the size of the protoconch as well as the size of the prehatching embryo may vary substantially. Small embryonic conchs are generally produced by taxa that invest reproductive resources in the production of large numbers of small eggs combined with the rapid growth to maturity (r strategists). Other taxa may invest in small numbers of slow developing large-yolked eggs, facilitating the development of embryonic conchs that are substantially larger at hatching (k strategists) and perhaps better able to avoid predation (Manda and Frýda 2010). R strategies, particularly where floating egg masses and planktotrophic embryonic conchs are utilised, may favour the survival of offspring where anaerobic, dysaerobic or toxic seafloor and bottom waters would have a lethal impact on the population (Mapes and Nützel 2009). By the same token, such a strategy may also favour the dispersion of offspring over long distances, increasing the probability of establishing new populations, but at the same time making them sensitive to extinction from impacts such as climate change (Laptikhovsky et al. 2013; see also Tajika and Wani 2011; Tajika et al. 2018). By comparison, k strategies may be suited to more stable environments.

Although the concept of k/r selection has been superseded by models based on life history adaptions, for many fossil groups, where relatively little can be deduced of life history and autecology, this concept (recognising that it represents a continuous spectrum) remains useful. Laptikhovsky et al. (2013) found that ectocochliate cephalopod egg size was negatively correlated with temperature and that there was a general trend towards smaller egg sizes over time, while the size of the embryonic shell in some Orthoceratia appears to have increased over time (Laptikhovsky et al. 2018).

The proposal that the Pseudorthoceratida are the sister group of the Actinoceratida (Kröger and Mapes 2007, fig. 2) would imply that there was a substantial reduction in the size of the embryonic shell in Carboniferous pseudorthoceratids, where the diameter of the initial camerae does not exceed 2 mm and may be as little as 0.5 mm (Kröger and Mapes 2004) compared with that of their actinoceratid ancestors (approximately 8 mm in diameter in *Actinoceras tennuifilum* (Hall, 1843) [Flower 1940]). This was reversed in the Carbactinoceratidae (placed in the Pseudorthocerida by Kröger and Mapes (2007), where the conch diameter at the first septum reached 15 mm and 13 mm, respectively, in *Rayonnoceras solidiforme* Croneis and *Carbactinoceras torleyi* Schindewolf (Kröger and Mapes 2007, fig. 7b).

Amongst early members of the Tarphyceratida, the diameter of the initial portion of the conch measured on 16 taxa illustrated by Ulrich et al. (1942) range from 2 to 10 mm (mean 4.4 mm, median 4 mm). In the Silurian tarphyceratid *Ophioceras simplex,* the diameter of the initial portion of the conch ranges from 1.2 to 2.6 mm ($N = 94$) (Turek and Manda 2016). This diameter appears to have a similar range in Silurian species of *Discoceras* (Manda and Turek 2018) and suggests a decrease in the

size of the protoconch in at least some tarphyceratid lineages.

Since the size and shape of the initial portion of the conch may vary within lineages and may be especially sensitive to selective pressures that result in adaptions to particular life strategies, this character may be at its most useful in elucidating lineages at the familial level and below.

Proposed classification

Whichever classification scheme is eventually employed in the revised *Treatise Part K*, there are several key nomenclatural issues to consider.

Within both the Russian *Osnovy* (Ruzhentsev et al. 1962) and American *Treatise* (Teichert et al. 1964), and since their publication, higher ranking names used in nautiloid systematics have often utilised an '-oidea' suffix (e.g., subclasses Nautiloidea, Endoceratoidea, Actinoceratoidea in Teichert et al. 1964: superorders Plectronoceratoidea, Nautilatoidea in Wade 1988; superorder Astrovioidea in Zhuravleva and Doguzhaeva 2004; superorder Multiceratoidea in Mutvei 2013). The main exceptions to this have been Starobogatov (1983) and Mutvei (2015, 2017), the latter using the detailed structure of the siphuncle wall (septal necks and connecting rings) to define his new superorders Calciosiphonata, Nautilosiphonata, and Mixosiphonata.

The decision by ICZN (1999, Article 29.2) to use the suffix '-oidea' at superfamily level potentially creates some difficulties for the high-level systematic classification of nautiloid cephalopods and nomenclature. This becomes apparent in cases involving the former superfamiles Nautilaceae de Blainville 1825 and Orthocerataceae M'Coy 1844 (both were employed in the Russian *Osnovy* and the American *Treatise*) which subsequently become re-named as superfamilies Nautiloidea de Blainville 1825 and Orthoceratoidea M'Coy 1844, respectively. The term 'Nautiloidea' has been variously employed throughout the long history of classification of the nautiloid cephalopods and the 'Subclass Orthoceratoidea' has been used by many authors (e.g., Teichert 1967; Zhuravleva 1994; Wade 1988; Evans 2005; Kröger 2008; Kröger and Evans 2011; Aubrechtová 2015).

Consequently, to avoid any potential confusion arising in the higher levels of nautiloid classification employed in the revision of the *Treatise Part K*, we propose herein to replace the suffix '-oidea' at subclass level with the suffix '-ia'. Apart from removing any ambiguity and clarifying the nomenclature, this approach also has the merit of bringing greater consistency and affinity with modern zoological classification schemes used for cephalopods (e.g., Ponder and Lindberg 2019, in press). Therefore, as

examples, in our proposed approach, the former Subclass Orthoceratoidea becomes Orthoceratia, and the Nautiloidea becomes the Nautilia; in addition, the former superorder Multiceratoidea (Mutvei 2013) is amended and elevated in rank to Subclass Multiceratia (our proposed classification does not utilise the rank of superorder). The subclass names we propose employing are listed in Table 4. We strongly support the view that terms such as 'nautiloid' or 'nautiloids' should continue to be used in a general and informal sense.

In the original *Treatise Part K*, Teichert et al. (1964) adopted an 'abbreviated' form of name for nautiloid orders preferring to use the ending '-cerida' rather than '-ceratida' (e.g., Oncocerida, Endocerida, and Actinocerida are employed rather than Oncoceratida, Endoceratida, and Actinoceratida). The reasons for this approach were explained essentially as facilitating the distinction between orders and families if the names are used informally (Teichert 1969, 1988). This contrasts with the form of nomenclature used in *Osnovy* (Ruzhentsev et al. 1962) which employed the 'full' version of the ordinal names, e.g., Ellesmeroceratida, Tarphyceratida, Actinoceratida, and Endoceratida. Furthermore, ammonite workers readily use the 'full' version of ordinal or subordinal names (such as Lytoceratida, Lytoceratina, and Phylloceratina, not Lytocerida, Lytocerina, or Phyllocerina) when referring to lytoceratid and phylloceratid ammonoids, respectively, without any apparent risk of causing confusion (e.g., Wright et al. 1996).

Therefore, we are not convinced of the merits of using 'abbreviated' names for nautiloid orders and do not see any need to make a special case for nautiloids in comparison with the format of classification widely used for other cephalopods. For the revision of *Treatise Part K*, we propose using the 'full' version of the ordinal names as listed in Table 4. This approach also has the merits of employing several of the order names in the form they were originally erected, e.g., Ellesmeroceratida, Oncoceratida, and Tarphyceratida as proposed by Flower (in Flower and Kummel 1950). For reasons of consistency, we also apply the same format to any ordinal names created since the original *Treatise Part K*; therefore, Order Yanhecerida becomes Order Yanheceratida (Chen and Qi in Chen et al. 1979) and Order Bisonocerida becomes Order Bisonoceratida (Evans and King 2012).

A phylogenetic model

There have been several attempts to use cladistic techniques to tease out the relationships amongst ectocochliate cephalopods (= 'nautiloids') (Evans and King 1990;

Table 4 Proposed high-level classification of nautiloid cephalopods to be used in the revision of the *Treatise Part K*

Subclass Plectronoceratia *nom. correct.* Wade, 1988[a]

  Order Plectronoceratida Flower, 1964a

  Order Yanheceratida Chen and Qi in Chen, Tsou, Chen and Qi, 1979

  Order Protactinoceratida Chen and Qi in Chen, Tsou, Chen and Qi, 1979

Subclass Multiceratia *nom. correct.* Mutvei, 2013[b]

  Order Ellesmeroceratida Flower in Flower and Kummel, 1950

  Order Cyrtocerinida Flower, 1964a

  Order Bisonoceratida Evans and King, 2012[m]

  Order Oncoceratida Flower in Flower and Kummel, 1950

  Order Discosorida Flower in Flower and Kummel, 1950

Subclass Tarphyceratia nov.[c]

  Order Tarphyceratida Flower in Flower and Kummel, 1950[d]

  Order Ascoceratida Kuhn, 1949[e]

Subclass Nautilia *nom. correct.* Wade, 1988

  Order Nautilida Agassiz, 1847[f]

Subclass Orthoceratia *nom. correct.* Teichert, 1967[g]

  Order Rioceratida nov.[h]

  Order Dissidoceratida Zhuravleva, 1964[i]

    Suborder Dissidoceratina Zhuravleva, 1964

    Suborder Troedssonellina Kobayashi, 1935

  Order Orthoceratida Kuhn, 1940

  Order Pseudorthoceratida Flower and Caster, 1935[j]

  Order Actinoceratida Teichert, 1933

  Order Astroviida Zhuravleva and Doguzhaeva, 2004[k]

    Suborder Lituitina Starobogatov, 1983[l]

    Suborder Pallioceratina Marek, 1998[k]

  Order Endoceratida Teichert, 1933[m]

[a] The Subclass Plectronoceratia contains the earliest cephalopods (Late Cambrian age) which exhibit oncomyarian muscle scars (Flower 1964a). Usually small, narrow to rapidly expanding cyrtocones or slender longicones; always narrowly camerate, often with siphonal diaphragms. We follow Chen and Teichert (1983) and subsequent workers in recognising the orders Plectronoceratida, Yanheceratida and Protactinoceratida, but note that many of the constituent genera are based on longitudinal sections of shell portions only; further research will likely result in taxa being synonymised. We regard present evidence of any relationship between the Yanheceratida and Endoceratida to be unconvincing—the 'endoconic deposits' associated with apical diaphragms in the Yanheceratida may be diagenetic in origin

[b] Originally defined as a superorder by Mutvei (2013), the Multiceratoidea is considered here to merit subclass status (Subclass Multiceratia) and is emended to contain the oncomyarian orders Ellesmeroceratida, Cyrtocerinida, Bisonoceratida, Oncoceratida and Discosorida. Constituent orders are typically distinguished by the form of modified siphonal structures or siphonal deposits (e.g., thick connecting rings in the Ellesmeroceratida, extraordinarily thickened connecting rings in the Cyrtocerinida, complex endocones in the Bisonoceratida, endosiphuncular linings and bullettes in the Discosorida, actinosiphonate deposits in some Oncoceratida) or the presence of modified, often constricted, apertures (present in both the exogastric Oncoceratida and predominantly endogastric Discosorida). Many early genera in all orders possess siphonal diaphragms. The Multiceratia is derived from the Plectronoceratia via the Ellesmeroceratida during the late Cambrian and range into the early Carboniferous (e.g., Poterioceratidae)

[c] The Subclass Tarphyceratia nov. is proposed here for exogastrically coiled, ventromyarian taxa, becoming weakly pleuromyarian in some younger forms. Lower and Middle Ordovician tarphyceratid faunas are relatively well known and are widely regarded as a 'natural group' (Schröder 1882; Ulrich et al. 1942; Flower and Kummel 1950; Flower 1976; Dzik 1984; Kröger and Landing 2008, 2009; King 2014). There is no convincing evidence to suggest that tarphyconic coiling (with ventromyarian muscle scars) arose independently in more than one lineage— other coiled shell morphologies (including gyrocones, torticones, cyrtocones and ascoceroid) occur in derived forms. We, therefore, regard the ventromyarian condition as an autapomorphy for the Subclass Tarphyceratia nov. and its descendants, akin to the development of the dorsomyarian condition that defines the Subclass Orthoceratia. The Subclass Tarphyceratia nov. is considered here to contain the orders Tarphyceratida (Furnish and Glenister 1964b; King 2014) and Ascoceratida (Holland 1999; Aubrechtová and Meidla 2016). See also [d] and [e] below

Table 4 (continued)

[d]The Tarphyceratida are the earliest representatives of the Subclass Tarphyceratia nov. and contain the first 'coiled' nautiloids. Derivation of the tarphyceratids from the Family Bassleroceratidae, Order Ellesmeroceratida, is undisputed (Flower 1976; Dzik 1984; Kröger and Landing 2008). We follow Flower (1984) in regarding the former Order Barrandeoceratida as polyphyletic; taxa previously placed in this order are now mainly (but not entirely) re-assigned within an expanded Order Tarphyceratida. The youngest tarphyceratids occur in the Middle Devonian

[e]The Ascoceratida are ventromyarian (e.g., Flower 1941, 1952; Sweet 1959; Evans 1988). Kröger (2013) has presented a case for their origin from the Uranoceratidae (formerly assigned by Kröger to the Order Barrandeoceratida). The deciduous nature of the ascoceratid conch is not a feature unique to this order; similar ontogenetic truncation of the shell is recorded in other unrelated nautiloids such as the Sphooceratidae (Turek and Manda 2012) and the oncoceratid family Trimeroceratidae (Stridsberg 1985). The deciduous nature of the conch in the Brachycycloceratidae (Furnish et al. 1962) is less certain (e.g., Niko 2010, Niko and Mapes 2011) and this family may be better assigned to the Nautilida

[f]The Subclass Nautilia ranges from the Early Devonian (possibly late Silurian) to the present day where it is represented by the extant genera *Nautilus* and *Allonautilus*. The subordinal and superfamilial classification within the mainly pleuromyarian Order Nautilida has a very complex history and requires further analysis. Significantly different systematic schemes and approaches were adopted in the Russian and American treatises (Ruzhentsev et al. 1962; Teichert et al. 1964). Retention of a Suborder Nautilina is considered likely in the future revision of *Treatise Part K*, although the status of other previously recognised suborders such as the Rutoceratina is less clear. Some Devonian genera formerly assigned to the Rutoceratidae (and other nautilid families) may be better placed elsewhere, including the Order Oncoceratida

[g]The Subclass Orthoceratia represents one of the largest and most important nautiloid subclasses which gave rise independently to the ammonoids, bactritoids and coleoids. The subclass is regarded here to include all dorsomyarian nautiloids, the majority of which are orthoconic or weakly cyrtoconic longicones and—apart from the Rioceratida nov. and Endoceratida—mostly possess various combinations of siphonal deposits (including annuli, parietal linings, siphonal rods) and cameral deposits. The Endoceratida possess simple endocones but lack cameral deposits. The Orthoceratia ranges from Early Ordovician (Tremadocian) to Late Triassic (possibly Early Cretaceous, Doguzhaeva 1995)

[h]The Rioceratida nov. is proposed here to accommodate dorsomyarian orthoceratoids that lack cameral deposits and possess a ventral siphuncle which is vacuosiphonate. The new order contains two families: the Rioceratidae (Kröger and Evans 2011) and the Bactroceratidae nov. Further details are provided in the definition of new systematic names section of this paper

[i]We follow Zhuravleva (1994) regarding the overall classification and composition of the Dissidoceratida, with modifications and additions as published by Evans (2005). The order contains the dissidoceratids (with intrasiphonal deposits concentrated ventrally) and troedssonellids (with intrasiphonal deposits forming long, thin endocones or 'parietal linings' extending throughout the whole circumference of the siphonal wall); we propose these differences merit recognition at subordinal rank. The poorly known intejoceratids and bajkaloceratids (Balashov 1960, 1962b; Zhuravleva 1978) are likely dissidoceratids or possibly actinoceratids; possession of extensive cameral deposits and siphonal lamellae precludes any possible relationship between the intejoceratids and endoceratids (Flower 1976)

[j]The relationship of the pseudorthoceratids to other orthoceratids and actinoceratids remains uncertain in places. Several Ordovician taxa previously regarded as pseudorthoceratids in the original *Treatise Part K* are now considered to be better assigned to the Order Orthoceratida, possibly related to the Geisonoceratidae. Kröger and Mapes (2007) provide an important review and cladistical analysis of selected taxa and we follow them in distinguishing the Pseudorthoceratida as a separate order from the Orthoceratida and Actinoceratida

[k]Zhuravleva and Doguzhaeva (2004) defined the Superorder Astrovioidea (containing the orders Lituitida Starobogatov 1983 and Pallioceratida Marek 1998) as orthoconic or lituiticonic orthoceratoids in which the connecting ring is ruptured or destroyed during life and cameral deposits (in places apparently continuous with siphonal linings) are formed. The evidence for this and the validity of the Pallioceratida has been questioned (e.g., Turek and Manda 2012). Pending further research, we provisionally recognise these highly specialised forms as a single order Astroviida comprising the suborders Lituitina and Pallioceratina. However, should future evidence demonstrate that the astroviids or pallioceratids are polyphyletic and an invalid group, then we would propose recognising a distinct Order Lituitida (which is widely regarded to represent a natural group of related nautiloids) with taxa formerly assigned to the Suborder Pallioceratina being re-assigned elsewhere

[l]Starobogatov (1983) proposed a fundamental restructuring of cephalopod classification based on shell position, form of the mantle, structure of arms and specialisation of the apical portion of the inner sac (summarised by Shevyrev 2006). Within his Subclass 'Actinocerationes', Starobogatov recognised an 'Order Lituitiformes' but omitted the ancestral family Sinoceratidae; he also retained a relationship between lituitids and tarphyceratids (within his Superorder 'Tarphyceratiformii'). Although Starobogatov's classification has not been adopted by any other workers, his brief definition of the 'Lituitiformes' is clear and unambiguous. Therefore, Starobogatov's authorship of the Suborder Lituitina (or Order Lituitida—see above) has priority over the Suborder Lituitina proposed by Dzik (1984), although Dzik's work is much closer to current views regarding definition of the lituitid nautiloids and their orthoceratid origins

[m]We follow Evans and King (2012) in recognising that as traditionally described, the endoceratids were polyphyletic. This necessitated a significant revision which proposed the splitting of the former 'Order Endocerida' (as described in the original *Treatise Part K*) into two orders: the Bisonoceratida (oncomyarian forms, often rapidly expanding cyrtocones or brevicones—or secondarily orthocones—which possess complex endocones with infula, multiple endosiphotubes, conchiolin crests and complex 'endosiphoblade' patterns); and the Endoceratida (restricted to dorsomyarian orthoconic or weakly cyrtoconic longicones with simple endocones which lack infula or conchiolin crests)
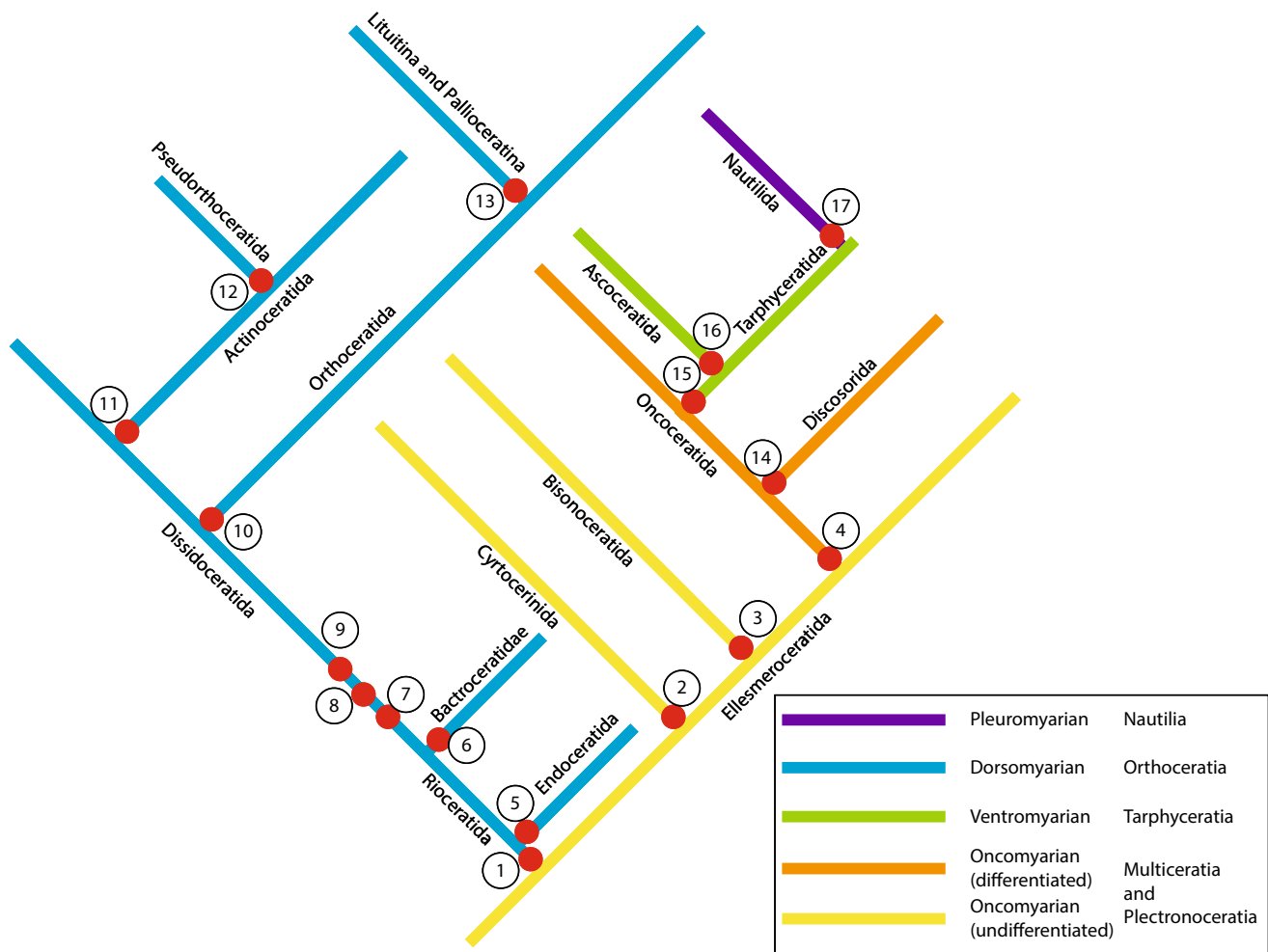
Fig. 2 Provisional scheme for the phylogenetic relationships amongst nautiloid cephalopods utilising muscle attachment scar patterns as a high-level criterion. 1. Dorsomyarian muscle attachment scars. 2. Thickening of connecting rings. 3. Endosiphuncular deposits (endocones) templated on conchiolin crests. 4. Differentiation of ventral pair (or pairs) of oncoceratid attachment scars. 5. Densely spaced conical endosiphuncular diaphragms form endocones. 6. Loss of cicatrix and development of small hemispherical protoconch. 7. Calciosiphonate connecting ring. 8. Appearance of annulosiphonate, parietal and 'rod-like' endosiphuncular deposits. 9. Appearance of cameral deposits. 10. Loss of cicatrix and development of small hemispherical protoconch. 11. Radial division of annulosiphonate endosiphuncular deposits. 12. Reduction in number of radial divisions of annulosiphonate deposits. 13. Development of ectosiphuncular deposits. 14. Thickening of connecting rings and development of bullettes. 15. Reduction of muscle attachment scars to pair or pairs of ventrally placed scars. 16. Truncation of conch and development of sinusoidal septa. 17. Migration of major muscle attachment scars to lateral or dorso-lateral positions

Kröger 2006; Kröger and Mapes 2007). These are hampered by the relatively small number of characters available for use, and by the commonly fragmentary preservation, which makes the assessment of the ontogenetic changes that may occur during development particularly hard to assess and include in such analyses. The scheme set out here (Fig. 2) is not the subject or product of any statistical processing, but a provisional analysis using characters discussed above.

Proposed structure for revised *Treatise Part K*

Table 5 provides a summary of the proposed contents and layout of the three parts (volumes K1, K2, and K3) likely to comprise the revised *Treatise Part K*. The overview and introduction to the Class Cephalopoda and nautiloid cephalopods in Part K1 and coverage of the Subclass Orthoceratia in Part K3 seem logical; at this stage, we retain flexibility over whether Part K1 would also contain the Order Nautilida or cover the Cambrian cephalopods comprising the orders Plectronoceratida, Yanheceratida,

Table 5 Summary outline of proposed contents and coverage across *Treatise Part K* (revised), volumes K1–K3

K (Mollusca 3 Revised)[1] Volume 1: CEPHALOPODA General Features 'NAUTILOIDS' Nautilia	K (Mollusca 3 Revised)[2] Volume 2: 'NAUTILOIDS' (PALCEPHALOPODA) Plectronoceratia, Multiceratia, Tarphyceratia	K (Mollusca 3 Revised)[3] Volume 3: 'NAUTILOIDS' (PALCEPHALOPODA, NEOCEPHALOPODA) Orthoceratia
CLASS CEPHALOPODA	SUBCLASS PLECTRONOCERATIA	SUBCLASS ORTHOCERATIA
Introduction	Order PLECTRONOCERATIDA	Order RIOCERATIDA
General features and biology	Order YANHECERATIDA	Order DISSIDOCERATIDA
Morphology	Order PROTACTINOCERATIDA	Suborder Dissidoceratina
Major divisions and classification	SUBCLASS MULTICERATIA	Suborder Troedssonellina
Origin and References	Order ELLESMEROCERATIDA	Order ORTHOCERATIDA
'NAUTILOID' CEPHALOPODS	Order CYRTOCERINIDA	Order PSEUDORTHOCERATIDA
Introduction	Order BISONOCERATIDA	Order ACTINOCERATIDA
Morphology of hard parts	Order ONCOCERATIDA	Order ASTROVIIDA
Living *Nautilus* and *Allonautilus*	Order DISCOSORIDA	Suborder Lituitina
Classification and stratigraphic distribution	SUBCLASS TARPHYCERATIA	Suborder Pallioceratina
Glossary	Order TARPHYCERATIDA	Order ENDOCERATIDA
SUBCLASS NAUTILIA	Order ASCOCERATIDA	Incertae sedis—Aptychopsids etc.
Order NAUTILIDA	References	References
References	Index	Index
Index		

Protactinoceratida, and Ellesmeroceratida (in part). The former approach would conveniently place the pleuromyarian Nautilida (including the extant genera *Nautilus* and *Allonautilus*) within the same volume as the morphological description of living cephalopods; the latter approach would follow more of a chronological coverage of nautiloid orders within Parts K1 and K2, similar to that adopted in the revision of *Treatise Part L* covering the ammonoid cephalopods.

Conclusions

We propose a high-level classification of the nautiloid cephalopods for the revision of the *Treatise Part K* which utilizes the form of muscle attachment scars as a diagnostic feature at subclass level (Table 4). Such patterns, when used in combination with other characters (presence/absence of cameral deposits, form of endosiphuncular deposits, nature of juvenile growth stages, composition and morphology of the connecting rings), provide a firm basis for divisions at ordinal level and below.

Despite criticism of their taxonomic value by some workers, muscle attachment scar patterns appear to reflect high-level taxonomic divisions within the ectocochliate cephalopods. Discrepancies in the taxonomic distribution of muscle attachment scars are considered likely to reflect inadequacies in previous taxonomic schemes, since the rearrangement of discrepant groups based on muscle attachment patterns as a criterion also leads to greater congruence between other characters. However, where there are contradictions or uncertainties, other characters have to be examined to rule out homoplasies.

Our proposed scheme recognises five subclasses on the following basis:

1. Subclass Plectronoceratia—late Cambrian nautiloids which are narrowly camerate and possess 'simple siphuncles' which lack any deposits, but typically exhibit siphonal diaphragms in the apical portion of the siphuncle. Where known, the muscle-scar type is oncomyarian.

2. Subclass Multiceratia—late Cambrian to Early Carboniferous nautiloids which are all oncomyarian. Constituent orders are typically distinguished by the form of modified siphonal structures or siphonal deposits (e.g., thick connecting rings in the Ellesmeroceratida; extraordinarily thickened connecting rings in the Cyrtocerinida, complex endocones in the Bisonoceratida, endosiphuncular linings and bullettes in the Discosorida, actinosiphonate deposits in some Oncoceratida) or the presence of modified, often constricted, apertures (present in both the exogastric Oncoceratida and predominantly endogastric

Discosorida). Many early genera in all orders possess siphonal diaphragms.

3. Subclass Tarphyceratia nov.—early Ordovician to middle Devonian nautiloids which are predominantly ventromyarian, becoming weakly pleuromyarian in some forms. Contains the earliest 'coiled' nautiloids but shell form ranges from loosely coiled tarphyceracones, serpenticones, and gyrocones (occasionally torticones) with varying degrees of adoral divergence (Order Tarphyceratida) to simple, slender cyrtocones which adorally become inflated, breviconic and at maturity develop modified sigmoidal sutures (Order Ascoceratida). Connecting rings generally thickened; cameral and siphonal deposits absent.

4. Subclass Nautilia—early Devonian (possibly late Silurian) to present day nautiloids which are mainly pleuromyarian. The single-order Nautilida contains mostly nautilicone forms which lack any internal deposits.

5. Orthoceratia—early Ordovician to-late Triassic (possibly Early Cretaceous) nautiloids. One of the largest and most important nautiloid subclasses which gave rise independently to the ammonoid (including bactritid) and coleoid cephalopods. Includes all dorsomyarian forms, the majority of which are orthoconic or weakly cyrtoconic longicones and—apart from the Rioceratida nov. and Endoceratida—mostly possess various combinations of siphonal deposits (including annuli, parietal linings, and siphonal rods) and cameral deposits. The Endoceratida possess simple endocones but lack any cameral deposits.

We propose the Order Rioceratida nov. for dorsomyarian orthoceratians which are unique in exhibiting marginal vacuosiphonate siphuncles and lack cameral deposits. This order contains the families Rioceratidae (Kröger and Evans 2011) and Bactroceratidae nov., the latter being proposed here for the single genus *Bactroceras*.

The proposed layout and contents of the revised *Treatise Part K* (which we believe is likely to comprise 3 volumes) is summarised in Table 5.

Definitions of new systematic names

Subclass Tarphyceratia nov.

Diagnosis Exogastric, predominantly ventromyarian forms, becoming weakly pleuromyarian in some taxa. Shell form variable, ranging from loosely coiled tarphyceracones, serpenticones and gyrocones (occasionally torticones) with varying degrees of adoral divergence (Order Tarphyceratida) to simple, slender cyrtocones which adorally become

inflated, breviconic and at maturity develop modified sigmoidal sutures (Order Ascoceratida). Septal necks typically short, connecting rings thickened; cameral and siphonal deposits absent.

Constituent orders Tarphyceratida Flower in Flower and Kummel (1950) (including the former Barrandeoceratida Flower in Flower and Kummel, 1950), Ascoceratida (Kuhn 1949).

Remarks Contains the earliest 'coiled' nautiloids which are derived from the weakly cyrtoconic Bassleroceratidae (Order Ellesmeroceratida) during the Early Ordovician (Tremadocian) by an increase in shell coiling (e.g., Flower 1976; Dzik 1984).

Range Early Ordovician (Tremadocian) to mid Devonian.

Order Rioceratida nov.

Diagnosis Dorsomyarian, slender orthoconic to weakly cyrtoconic conchs with a vacuosiphonate, ventral siphuncle. Siphuncle wall orthochoanitic to hemichoanitic, septal necks thin to only moderately thickened. Cameral deposits absent. Where known (Bactroceratidae nov.) the apical portion of the shell comprises a small, hemispherical protoconch, cicatrix absent.

Constituent families Rioceratidae (Kröger and Evans, 2011); Bactroceratidae nov.

Remarks Earliest representatives of the dorsomyarian Subclass Orthoceratia. Distinguished from all other orthoceratians by combination of their vacuosiphonate marginal siphuncle and lack of any cameral deposits.

Range Early Ordovician (Tremadocian)—Late Ordovician (Katian).

Family Bactroceratidae nov.

Diagnosis Dorsomyarian, slender orthoconic to weakly cyrtoconic shell; ornamentation usually faint, transverse growth lines or low striae. Siphuncle marginal, narrow and vacuosiphonate, Septal necks orthochoanitic to hemichoanitic, connecting rings thin and homogeneous, slightly expanding into chambers. Cameral deposits absent. Embryonic shell moderately large, subspherical and with constriction; cicatrix absent.

Constituent genera: *Bactroceras* Holm, 1898

Remarks The Bactroceratidae is erected for the stenosiphonate genus *Bactroceras* which has been described in detail by Aubrechtová (2015). In contrast, the Rioceratidae (Kröger and Evans 2011) which is confined to the early Ordovician (Tremadocian to early Floian), is more diverse and contains genera with relatively broad siphuncles

including *Rioceras*, *Felinoceras*, *Microbaltoceras* and *Pachendoceras*.

Range Lower Ordovician (Tremadocian) to Upper Ordovician (Katian).

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