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Taxonomic review of early Darriwilian estonioceratids (Tarphycerida, Nautiloidea) from Sweden, Estonia, and the 'Diluvium-Geschiebe' of northern Germany and Poland

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Abstract: Estonioceratid nautiloids are a common and attractive component of mid-Ordovician (early Darriwilian) cephalopod faunas in Baltoscandia. Their distinctive conchs are typically loosely coiled, and vary from forms which possess an apically coiled portion with divergent final whorl, to open gyrocones and even torticones. This paper briefly reviews the taxonomy of several mainly Swedish and Estonian estonioceratid genera which were formerly poorly known at the time of the publication of the Tarphycerida section of the 'Nautiloid Treatise Part K' (FURNISH & GLENISTER 1964) or have been described since.

Keywords: Systematics, Estonioceratidae, Kundan, Aserian

Introduction

Fossil tarphycerid nautiloids are widespread and commonly encountered within the Mid Ordovician 'Orthoceratite Limestone' facies of Baltoscandia, especially Sweden and Estonia, and coeval glacial erratic boulders ('Diluvium-Geschiebe') of northern Germany and Poland. The majority of forms that occur within the Kundan and Aserian Stages (early Darriwilian) belong to the family Estonioceratidae. Their loosely coiled gyroconic shells are very distinctive and in Sweden these nautiloids are referred to as 'böjda Cephalopoda' meaning literally 'bent Cephalopoda'.

In common with other groups of cephalopods, the preservation of tarphycerids within the 'Orthoceratite Limestone' facies is generally very good. Although many of the sequences are highly condensed, the fine-grained limestones often enable detail of external shell ornament to be discerned and many conchs are relatively uncrushed facilitating examination of whorl cross-sections and early apical stages. Occasionally limestone beds are phosphatised, which permits extremely fine detail of the siphuncle wall and structure of connecting rings to be observed (MUTVEI & DUNCA, 2011).

This paper briefly reviews the status and taxonomy of estonioceratid nautiloids from the early Darriwilian Stage of Baltoscandia. The taxa covered include *Estonioceras* HYATT *in* ZITTEL, 1900 along with five previously little known or obscure genera, namely *Falcilituites* REMELÉ, 1886, *Tragoceras* REMELÉ, 1890, *Eichwaldoceras* BALASHOV, 1955, *Bentoceras* STUMBUR, 1962 and *Aserioceras* STUMBUR, 1962. The torticonic genus *Pakrioceras* was extensively described by STUMBUR & MUTVEI, 1983, and is only briefly summarised here for reasons of completeness.

Revision of a number of these genera is long overdue. Within the Tarphycerida section of the 'Nautiloid Treatise Part K' (FURNISH & GLENISTER, 1964, pp. K357-K359) *Falcilituites* was regarded as synonymous with *Estonioceras*; *Eichwaldoceras* was "Poorly known. Apparently like *Tragoceras*" and *Tragoceras* was considered "similar to *Aphetoceras* and possibly synonymous". Although *Bentoceras* and *Aserioceras* were erected before publication of the Treatise Part K, they were omitted from the volume. The re-examination of type material along with study of additional specimens from Sweden and Estonia now enables the status of all these genera to be re-assessed, and provisional lists of their constituent species to be presented here. A more thorough revision of the Baltoscandian estonioceratids, including assessment of the range of intraspecific variation and the description of new taxa, is currently in preparation by the author.

Stratigraphy

Within Baltoscandia, the estonioceratid nautiloids are mainly found within limestones assigned to the ear-

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Table 1: Biostratigraphical correlation of the Baltoscandian Stages/Substages with trilobite, graptolite and conodont zonation schemes.

		Baltoscandian Stages / Substages		Trilobite zonation	Graptolite zonation	Conodont Zonation
DARRIWILIAN	4c	UHAKUAN		*Illaenus crassicaudata*	*Hustedograptus teretiusculatus*	*Pygodus anserinus*
		LASNAMÄGIAN		*Illaenus schroeteri*	*Pseudoamplexograptus distichus*	*Pygodus serra*
		ASERIAN		*Illaenus planifrons / Illaenus platyurus*	*Pterograptus elegans*	*Eoplacognathus suecicus*
	4b	KUNDAN	Aluojan	*Megistaspis gigas Megistaspis obtusicauda*	*Nicholsongraptus fasciculata*	*Eoplacognathus pseudoplanus*
	4a		Valastean	*Asaphus raniceps*	*Holmograptus lentus*	*Yangtzeplacognathus crassus*
			Hunderumian	*Asaphus expanses*	*Undulograptus austrodentatus*	*Lenodus variabilis*

GENUS ➡ ▼ CHARACTER	*Estonioceras* Noetling, 1883	*Falcilituites* Remelé, 1886	*Tragoceras* Remelé, 1890	*Eichwaldoceras* Balashov, 1955	*Aserioceras* Stumbur, 1962	*Bentoceras* Stumbur, 1962	*Pakrioceras* Stumbur & Mutvei, 1983
Shell form	Stout, moderately expanding. Early whorls in contact, final whorl divergent	Slender, early whorls in contact, final whorl divergent	Very slender. Final whorl divergent, early whorls unknown but likely in contact	Moderately expanding, gyroconic. Final whorl divergent, inner whorl(s) unknown	Moderately expanding, likely gyrononic. Final whorl divergent, inner whorl(s) unknown	Slender, gyroconic, no whorls in contact. Final whorl divergent.	Moderately expanding, loose torticonic spiral
Whorl section	Early whorls depressed to fusiform, final whorl slightly depressed to circular	Slightly depressed to weakly compressed	Compressed	Circular	Weakly compressed	Subcircular to weakly compressed	Subcircular to weakly depressed
Siphuncle position	Subventral	Subventral - subcentral	Ventral	Ventral	Ventral	Subcentral to subventral	Ventral
Ornament	Indistinct, fine growth lines	Distinct raised growth lines and lirae	Moderately coarse, faint irregular lirae and growth lines	Coarse lirae	Coarse lirae	Smooth, with feeble growth lines	Distinct narrow annuli with growth lines
Sutures	Transverse	Transverse or with very shallow lateral saddle	Curved with distinct lateral saddle	Transverse	Broad shallow lateral and dorsal saddles	Transverse	Transverse laterally with shallow ventral lobe
Stage (Substage) occurrence	Kundan	Kundan	Kundan (Aluojan)	Kundan (Hunderumian – Valastean)	Aserian	Kundan	Aserian and possibly early Lasnamägian

Table 2: Character matrix table and stratigraphic occurrence of Baltoscandian estonioceratid genera.

ly Darriwilian Kundan or Aserian stages. The correlation of these stages (and their substages) with standard international graptolite and conodont zonation schemes is provided in Table 1. The Kundan and Aserian stages (represented in Sweden by the Holen Limestone and Segerstad Limestone formations respectively) equate approximately to the *Didymograptus 'bifidus'* (*Undulograptus austrodentatus* to *Nicholsongraptus fasiculata*) and lower *Didymograptus murchisoni* (*Pterograptus elegans*) graptolite zones; and the upper part of the *Lenodus variabilis* to near top of the *Eoplacognathus suecicus* conodont zones. Megistaspid, asaphid and illaenid trilobites are also useful locally within the condensed Swedish and Estonian 'Orthoceratite Limestone' sequences to facilitate correlation.

Taxonomy

In this section and figure captions, the following abbreviations are used when referring to material or museum collections:

GIT – Institute of Geology, University of Tallinn, Estonia

RM – Museum of Natural History, (Naturhistoriska Riksmuseet), Stockholm, Sweden

MNH – Museum of Natural History, London, UK

MfN – Museum für Naturkunde, Berlin, Germany

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Order Tarphycerida
FLOWER *in* FLOWER & KUMMEL, 1950

Family Estonioceratidae HYATT in ZITTEL, 1900

Diagnosis: Smooth or ribbed gyroconic to loosely coiled, rarely torticonic tarphyceracones, typically with divergent last whorl. Whorl section depressed to compressed, dorsal impression absent or only weakly developed. Siphuncle ventral to subventral. Septal necks orthochoanitic, connecting rings thick. Growth lines and raised lirae form conspicuous broad, shallow to deep hyponomic sinus (adapted from FURNISH & GLENISTER 1964: K357).

Discussion: Following FURNISH & GLENISTER (1964), the Estonioceratidae is retained here as a separate family and distinguished from the similar Tarphyceratidae (HYATT, 1894) on the general basis of conch form (more tarphyceraconic in the Tarphyceratidae) and for tarphyceratids to possess an impressed area in the dorsal region of the whorl, related to tightness of coiling. The Trocholitidae SCHRÖDER, 1891 differs from both the Tarphyceratidae and Estonioceratidae in possessing a dorsal siphuncle.

Estonioceratid faunas in Sweden, Estonia and Russia, and from coeval glacial erratic boulders in northern Germany and Poland have much in common. All taxa possess similar siphuncular features (orthochoanitic septal necks and thickened connecting rings) and distinction at generic and specific levels tends to reply upon overall conch form and expansion rate, whorl section, position of the siphuncle, shape of the suture and type of external shell ornament (KING 1999: 150). A summary of the main morphological features that distinguish each of the Baltoscandian estonioceratid genera and their stratigraphical occurrence is provided in Table 2.

Constituent genera: *Estonioceras* NOETLING, 1883; *Aethoceras* TEICHERT & GLENISTER, 1954; *Alaskoceras* MILLER & KUMMEL, 1945; *Aphetoceras* HYATT, 1894; *Aserioceras* STUMBUR, 1962; *Bentoceras* STUMBUR, 1962; *Clytoceras* ULRICH, FOERSTE, MILLER & FURNISH, 1942; *Eichwaldoceras* BALASHOV, 1955; *Falcilituites* REMELÉ, 1886; *Pakrioceras* STUMBUR & MUTVEI, 1982; *Pycnoceras* HYATT, 1894; *Shumardoceras* ULRICH & FOERSTE, 1936 and *Tragoceras* REMELÉ, 1890.

Occurrence: The Estonioceratidae, as defined above, occurs within the Floian to Darriwilian stages and has an extremely widespread distribution extending from Canada, Newfoundland, Alaska and North America through Baltoscandia (especially Sweden and Estonia) to Russia, Northwest China and Australia. The family is also recorded from glacial erratic boulders ('Diluvium-Geschiebe' derived from Baltoscandia) in northern Germany and Poland.

Genus *Estonioceras* NOETLING, 1883 (Fig. 1A–D)

Remeleceras HYATT, 1894

Type species: *Lituites lamellosus* HISINGER, 1837 [by original designation; NOETLING 1883: 275]

Diagnosis: Moderately expanding, relatively stout conch, early whorls in contact, with depressed or fusiform section and typically with umbilical perforation; last whorl divergent, slightly depressed to circular in section. Conch narrowly to widely camerate, sutures straight, transverse. Siphuncle subventral, septal necks short, orthochoanitic; connecting rings very thick and layered. External ornament indistinct, consisting of fine growth lines which form an inconspicuous, very broad ventral sinus.

Discussion: *Estonioceras* is a common tarphycerid in the Kundan Stage of Baltoscandia; its conch form and expansion rate readily distinguish it from other estonioceratid genera. The differences with *Falcilituites* are noted under that genus below.

HYATT (1894: 525) erected *Remeleceras* for forms closely allied to *Estonioceras* but differing in possessing a depressed, elliptical whorl section with deeper dorsal impressions and an "extraordinary form of annular muscle". Examination by the present author of material belonging to the type species of *Remeleceras*, *Estonioceras impressum* (HYATT, 1894, also figured by MUTVEI 1957: pl. 2) failed to provide sufficient evidence for distinguishing the two genera. Some species of *Estonioceras*, notably *E. perforatum* SCHRÖDER, 1891, also exhibit a very shallow, weak but conspicuous impressed area. The other characteristic features mentioned in the description of *Remeleceras* are also considered here to fall within the morphological range exhibited by *Estonioceras*.

Numerous Baltic cephalopod species have been assigned to *Estonioceras*. Many of these were described during the 19th century (e.g. HISINGER 1831, 1837; QUENSTEDT 1846; REMELÉ 1880, 1886, 1890; SCHRÖDER 1891) and were based primarily on the form of coiling. The diagnostic value of that criterion is regarded warily here, especially in view of the coiling variation exhibited by *Bentoceras proteus* (HOLM, 1891) and the variation in size of the apical coiled portion in *Falcilituites decheni* (REMELÉ, 1880) / *Falcilituites subcostatum* (ANGELIN *in* ANGELIN & LINDSTRÖM, 1880). Consequently features such as expansion rate, whorl section and whorl width:whorl height ratios are considered as more reliable indicators on which to base taxonomic study. Ongoing research tends to corroborate many, although not all, the species of *Estonioceras* erected by earlier workers and it is considered likely that 'approximately half-a-dozen' species are genuinely distinct. Whilst recognising the amount of intraspecific variation in some species of *Estonioceras*, the

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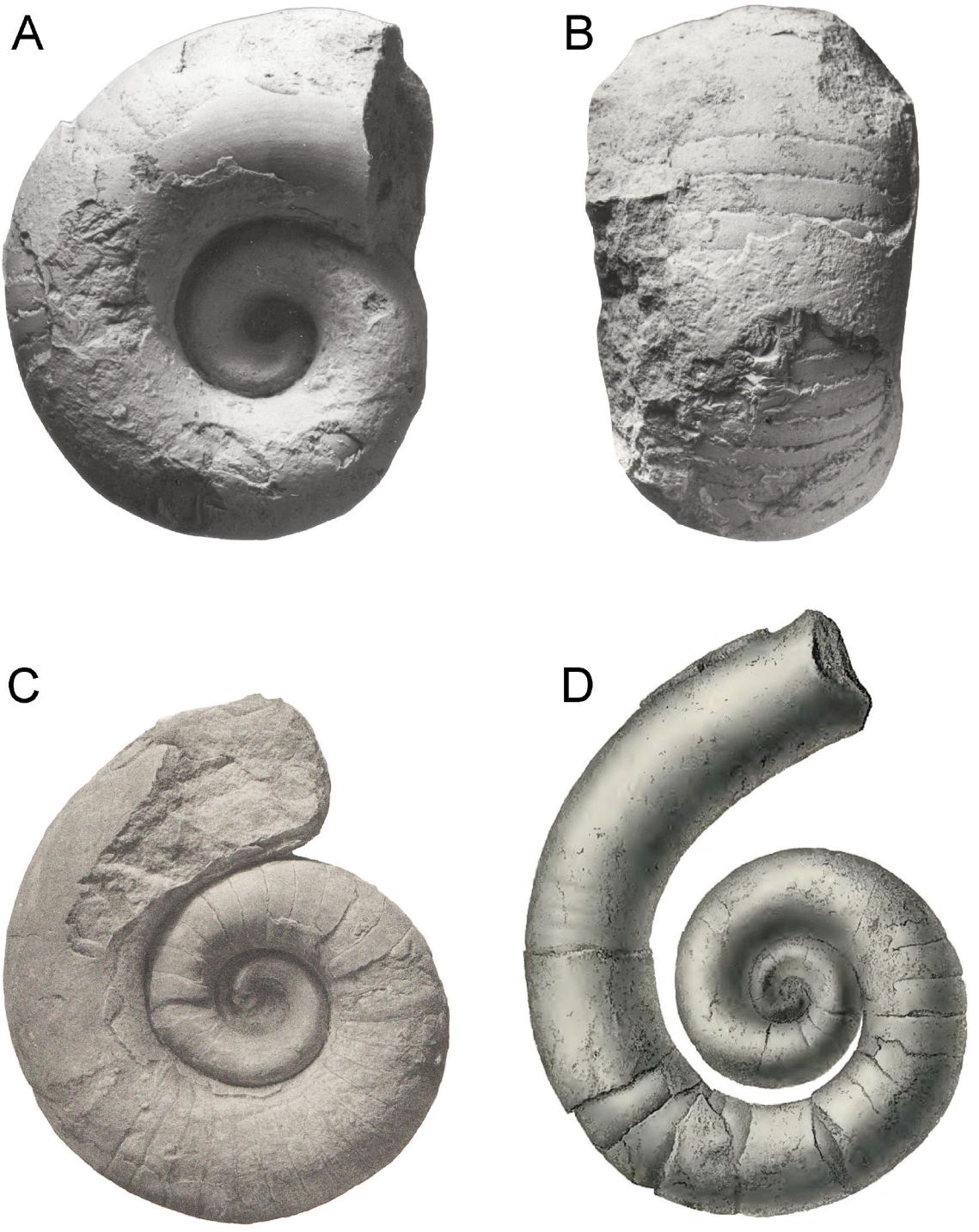

Fig. 1: (**A-B**) *Estonioceras lamellosum* (HISINGER, 1837), RM Mo152356, early Kundan stage, Dalarna, Sweden; lateral and ventral views, diameter 70 mm [original of ANGELIN & LINDSTRÖM 1880: pl. 10, fig. 4]. (**C**) *Estonioceras imperfectum* (QUENSTEDT, 1846), RM Mo149982, late Kundan Stage, Tallin, Estonia; lateral view, diameter 90 mm [original of MUTVEI 1957: pl. 3, fig. 4]. (**D**) *Estonioceras ariense* (SCHMIDT, 1858), late Kundan Stage, Kunda, Estonia; lateral view, maximum diameter 209 mm [Holotype, original of SCHRÖDER (1891: pl. 2, figs 5a-e) and BALASHOV (1953: pl. 1, fig. 1)].

claim expressed by DZIK (1984: 39) that "there is only a single described species of *Estonioceras* in the Baltic area" seems to be an over-simplification of the position.

Constituent species: The following list is provisional and represents 'research in progress' by the present author:

Estonioceras lamellosum (HISINGER, 1837)

Estonioceras convolvans (HISINGER, 1831). [*Estonioceras heros* (REMELÉ, 1880) and *Estonioceras kundense* BALASHOV, 1953 are probably synonymous with *E. convolvans* (HISINGER, 1831)]

Estonioceras imperfectum (QUENSTEDT, 1846)

Estonioceras ariense (SCHMIDT, 1858)

Estonioceras muellaueri (DEWITZ, 1880) [Status uncertain]

Estonioceras peforatum SCHRÖDER, 1891

Estonioceras impressum (HYATT, 1894) [Type of *Remeleceras*]

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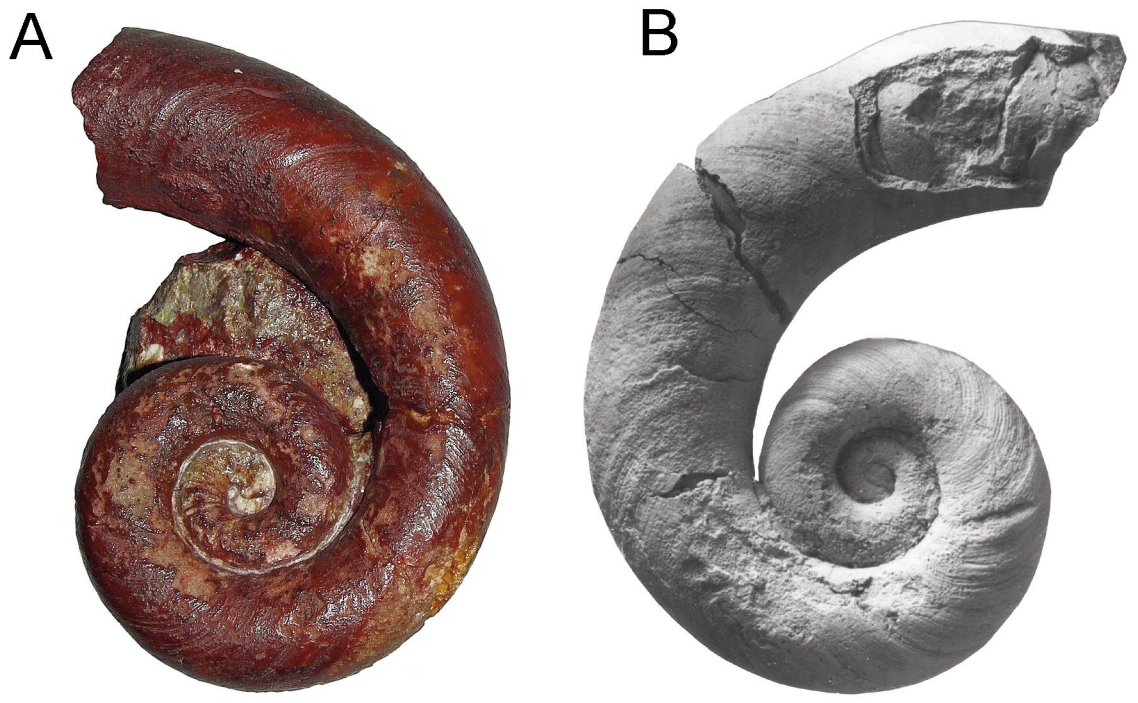

Fig. 2: (**A**) *Falcilituites decheni* (REMELÉ, 1880), Kundan Stage, glacial erratic boulder, northern Germany; lateral view, maximum diameter 66 mm [Holotype, original of REMELÉ (1880: pl. 2, figs 1a-c) and NEBEN & KRUEGER (1971: pl. 18, figs 2-3)]. (**B**) *Falcilituites subcostatum* (ANGELIN *in* ANGELIN & LINDSTRÖM, 1880), RM Mo150566, late Kundan Stage, Alsarbyn, Dalarna, Sweden; lateral view, maximum diameter 80 mm [Syntype, original of ANGELIN & LINDSTRÖM (1880: pl. 11, figs 5-8)].

Occurrence: *Estonioceras* is common and widespread in the Kundan Stage of Sweden, and is recorded from Öland, Dalarna, Östergötland and Västergötland. The genus is also known from the Kundan Stage of Estonia (Tallinn, Kunda, Aseri, Paldicki), Russia (St Petersburg district) and coeval erratic boulders in northern Germany. CHANG (1964) recorded the genus from the middle Ordovician of Qilianshan, Northwest China, but records of *Estonioceras* sp. from the Emanuel Limestone of Western Australia (TEICHERT & GLENISTER 1954) may be based on a species of *Aethoceras*.

Genus *Falcilituites* REMELÉ, 1886 (Fig. 2A, B)

Type species: *Lituites Decheni* REMELÉ, 1880 [by original designation; REMELÉ 1886: 467]

Diagnosis: Slowly expanding, relatively slender conch with early loosely coiled inner whorls, often with small umbilical perforation; last whorl becoming divergent. Whorl section slightly depressed to weakly compressed or subquadrate. Conch narrowly camerate, sutures straight to weakly sinuous with broad ventral saddle. Siphuncle subventral to subcentral, septal necks short, orthochoanitic; connecting rings thick and layered. External ornament of distinct raised growth lines and lirae which form a conspicuous, deep ventral sinus.

Discussion: *Falcilituites* was placed in synonymy with *Estonioceras* by FURNISH & GLENISTER (1964: K357) although FLOWER (1976: 544) listed the genera separately. Despite both taxa possessing shells with an apical coiled portion and divergent last whorl, beyond this any external similarity ceases and comparison of the type species readily confirms they are distinct; *Estonioceras* is a much stouter and often larger shell than *Falcilituites*, typically with a greater expansion rate and a fusiform section to the inner whorls. In contrast, the shell form of *Falcilituites* is much more slender than *Estonioceras*, the whorls are slightly depressed to compressed in section and the external ornament is much more distinct and regular.

Ongoing research on Swedish specimens of *Falcilituites* indicates that the apical coiled portion may vary from 1.5 to 2 whorls being in contact before the final whorl becomes divergent. Consequently the diameter of the coiled portion may also vary slightly within a species. Therefore more reliable morphological features of the shell (such as expansion rate, whorl section, detailed form of the ornament and sutures) are currently being used by the author to elucidate the taxonomy of new species of *Falcilituites* present in the Kundan Stage of Sweden.

Constituent species: *Falcilituites decheni* (REMELÉ, 1880) and *Falcilituites subcostatum* (ANGELIN *in* ANGELIN & LINDSTRÖM, 1880) are currently assigned to the genus, although these species are similar and further study may demonstrate they are conspecific.

Occurrence: From the Kundan Stage (Valastean and Aluojan Substages) of Sweden (Öland, Dalarna, Västergötland), Estonia (Tallinn, Kunda, Aseri, Iru), Russia (St Petersburg district) and coeval erratic boulders in Poland (Mochty) and northern Germany.

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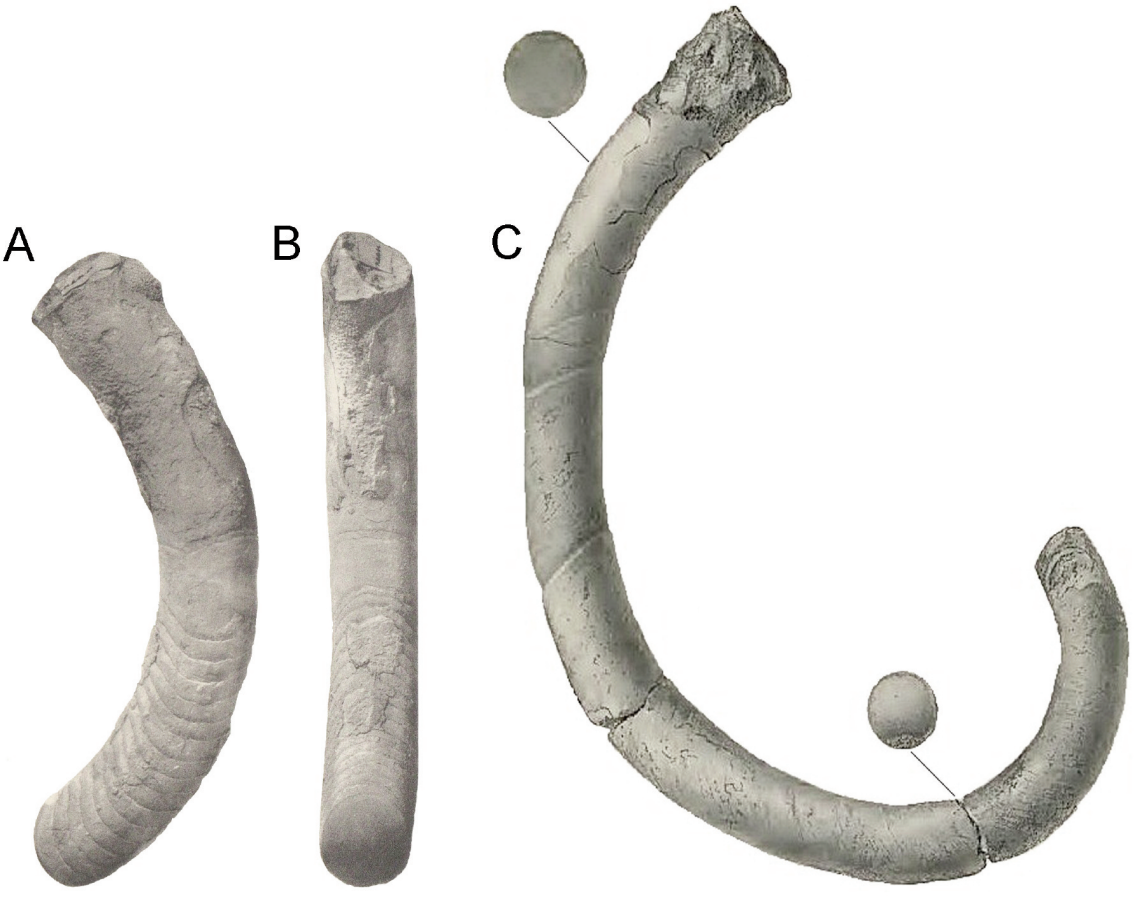

Fig. 3: *Tragoceras falcatum* (SCHLOTHEIM, 1820), late Kundan Stage, Tallin, Estonia. (**A-B**) RM Mo149984, lateral and dorsal views, length 114 mm [original of MUTVEI (1957: pl. 5, figs 4-6)]. (**C**) Lateral view, length 218 mm [original illustration of SCHRÖDER (1891: pl. VI, figs 1a-c)].

Genus *Tragoceras* REMELÉ, 1890 (Fig. 3A–C)

Planctoceras SCHRÖDER, 1891

Type species: *Orthoceratites falcatus* SCHLOTHEIM, 1820 [by monotypy; REMELÉ 1890: 35]

Diagnosis: Slender, very slowly expanding gyroconic conch with laterally compressed section, and outer divergent whorl; inner whorls unknown but probably in contact. External ornament of moderately coarse, irregular, relatively faint growth lines and lirae which form a broad, ventral sinus. Sutures sinuous with wide lateral lobes and corresponding ventral saddle. Siphuncle narrow, situated near ventral margin; septal necks orthochoanitic, connecting rings thickened.

Discussion: SCHRÖDER (1891: 41) rejected *Tragoceras* REMELÉ, 1890 as a valid genus and proposed *Planctoceras* in its place on the grounds of similarity of name with *Tragoceros* or *Tragocerus* which had previously been used for a Pleistocene antelope. However under ICZN rules, *Tragoceras* was available and is a valid taxon. FURNISH & GLENISTER (1964: K359) maintained *Tragoceras* REMELÉ, 1890 with *Planctoceras* SCHRÖDER, 1891 regarded as an objective junior synonym. That course is followed here.

The inner whorls of *Tragoceras* are unknown, but on the basis of coiling geometry are likely to be similar to *Falcilituites* REMELÉ, 1886; DZIK (1984: 38, fig. 8) provides a very plausible reconstruction of the complete shell. Study of Swedish material indicates that *Tragoceras* and *Falcilituites* are closely related: A new species of *Falcilituites* from northern Öland exhibits undulatory sutures of a style normally associated with *Tragoceras falcatum* (SCHLOTHEIM, 1820), and a specimen of *Tragoceras falcatum* (from Fjäcka, Dalarna) has a laterally compressed whorl section which when traced apicad becomes more circular in section, approaching the condition found in *Falcilituites decheni* REMELÉ, 1880. However, both genera are retained here on the basis that in all known specimens *Tragoceras* consistently exhibits a very slowly expanding, slender conch with near- ventral siphuncle and the shell ornament is coarser and more irregular than in *Falcilituites*. However, discovery and study of more complete specimens showing variation with shell size and maturity may necessitate a rethink of this position.

DZIK (1984: 37) suggested that *Aserioceras purtsensis* STUMBUR, 1962 may represent the youngest record of *Tragoceras*. However, the different expansion rates, posi-

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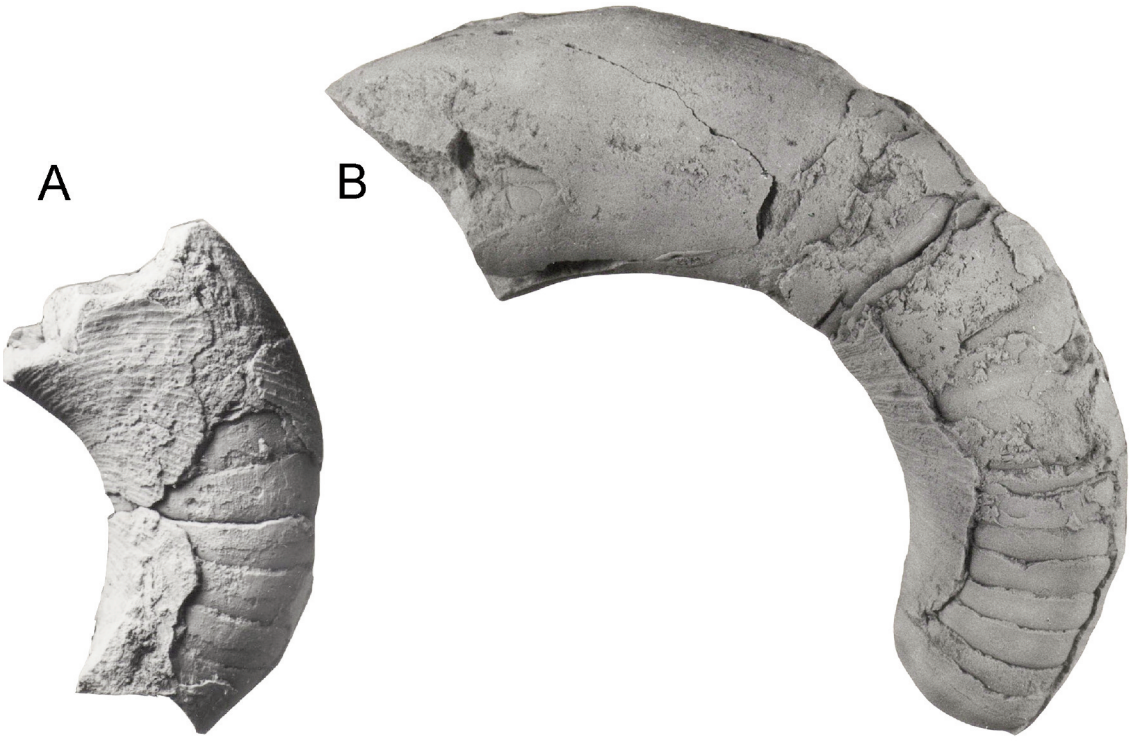

Fig. 4: (**A**) *Eichwaldoceras crispulum* (ANGELIN *in* ANGELIN & LINDSTRÖM, 1880), RM Mo15047, early Kundan Stage, Gerse, Dalarna, Sweden; lateral view, length 53mm [Holotype, original of ANGELIN & LINDSTRÖM (1880: pl. 16, figs 6, 12)]. (**B**) *Eichwaldoceras volchovense* BALASHOV, 1955, RM Mo158400, early Kundan Stage, Hälludden, Öland, Sweden; lateral view, maximum length 184 mm.

tion of siphuncle and types of ornament readily distinguish the two taxa, and makes this relationship unlikely.

Constituent species: Two species have previously been assigned to *Tragoceras*, *T. falcatum* (SCHLOTHEIM, 1820) and *T. arciforme* BALASHOV, 1953. However, there are taxonomic problems in recognising the latter species (which BALASHOV [1953] may have mistakenly based on true *T. falcatum*), and consequently the genus may be regarded as monotypic.

Occurrence: From the Late Kundan Stage (Aluojan Substage) of Estonia (Tallinn, Kunda, Aseri, Iru), Russia (St Petersburg district), Sweden (Fjäcka, Dalarna) and coeval 'Diluvium-Geschiebe' in Poland (Mochty) and northern Germany.

Genus *Eichwaldoceras* BALASHOV, 1955 (Fig. 4A, B)

Type species: *Eichwaldoceras volchovense* BALASHOV, 1955 [by original designation; BALASHOV 1955: 45]

Diagnosis: Conch gyroconic with moderate expansion rate adorally, inner whorls not known; whorl section circular. External ornament of distinct, coarse growth lirae which form a broad, shallow ventral sinus; sutures straight. Siphuncle narrow, situated at the ventral margin; septal necks orthochoanitic, connecting rings very thick.

Discussion: BALASHOV (1955) based *Eichwaldoceras* on four incomplete but well preserved specimens from the Kundan Stage of Estonia and the Saint Petersburg (Leningrad) area. FURNISH & GLENISTER (1964: K359) regarded the genus as poorly known, but revision here using Swedish material confirms *Eichwaldoceras* is a valid taxon which can be readily distinguished from all other estonioceratids in its combination of conch form, circular section, ventral siphuncle and coarse ornament (comments regarding the similar genus *Aserioceras* STUMBUR, 1962 are dealt with under that taxon below).

The apical parts of *Eichwaldoceras* remain unknown, although evidence from the coiling geometry of Swedish specimens indicates that the conch may have been gyroconic with a relatively large protoconch, and comprise approximately two volutions. Reconstructions based on specimens of *E. volchovense* in the RM suggest that complete conchs could easily have reached 20-25cm in diameter.

Constituent species: Two species are currently recognised within the genus: *E. volchovense* BALASHOV, 1955 and *E. crispulum* ANGELIN *in* ANGELIN & LINDSTRÖM, 1880.

Occurrence: Early Kundan Stage (Hunderumian-Valastean Substages) of Russia (St Petersburg district), Estonia (Kunda) and Sweden (Öland, Östergötland and Dalarna). The genus has not yet been recorded from the 'Diluvium-Geschiebe'.

Genus *Bentoceras* STUMBUR, 1962 (Fig. 5A–C)

Type species: *Bentoceras rubeli* STUMBUR, 1962 [by original designation; STUMBUR 1962: 141]

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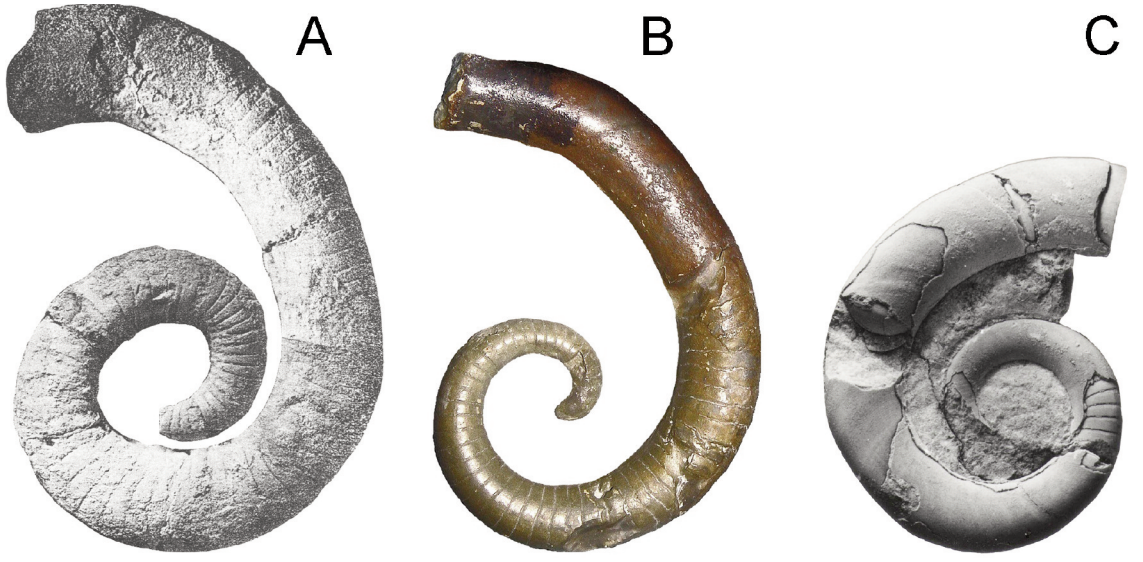

Fig. 5: (**A**) *Bentoceras rubeli* STUMBUR, 1962, GIT C1341, late Kundan Stage, Hiimäe, northern Estonia; lateral view, maximum diameter 96 mm [Holotype, original of STUMBUR (1962: pl. 1, fig. 1)]. (**B**) *Bentoceras proteus* (HOLM, 1898), Kundan Stage, glacial erratic boulder, northern Germany; lateral view, maximum diameter 62 mm [original of NEBEN & KRUEGER (1971: pl. 18, fig. 6), assigned in error to *Tragoceras falcatum* (SCHLOTHEIM, 1820)]. (**C**) *Bentoceras proteus* (HOLM, 1898), RM Mo158393, early Kundan Stage, Hälludden, Öland, Sweden; lateral view, maximum diameter 66 mm.

Diagnosis: Conch gyroconic and slender, consisting of two to two and a quarter whorls which are not in contact; the last volution becomes divergent at maturity. Whorl section subcircular to weakly depressed, expansion rate low. Body-chamber relatively short, approximately one quarter of a whorl long. External ornament of indistinct, feeble growth lines which trace out a broad ventral sinus; sutures transverse to very slightly sinuous. Siphuncle subventral; septal necks orthochoanitic, connecting rings thick.

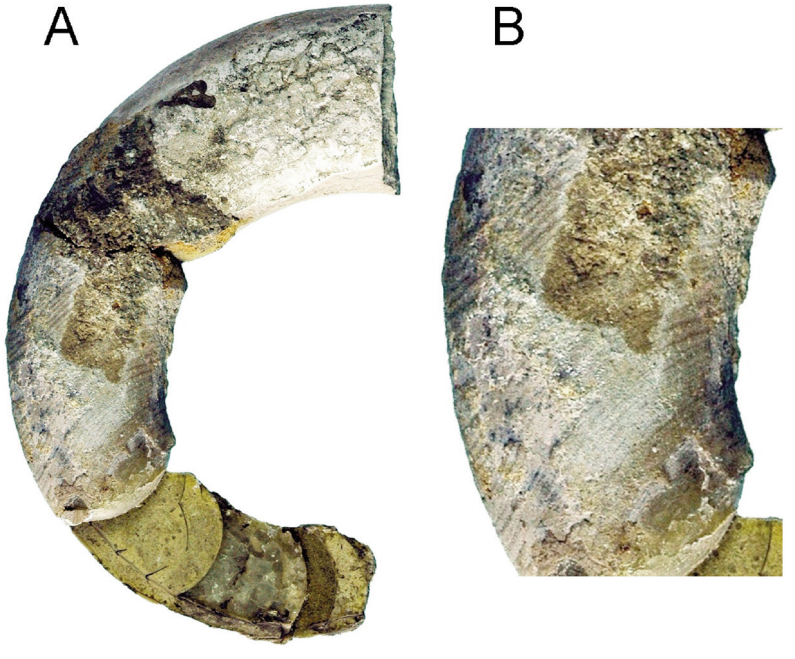

Fig. 6: (**A**) *Aserioceras purtsensis* STUMBUR, 1962, GIT C1331, Aserian Stage, Lüganuse, northern Estonia; lateral view, maximum diameter 85 mm [Holotype, original of STUMBUR (1962: pl. 1, fig. 2)]. (**B**) Same, detail of ornament.

Discussion: The distinctive gyroconic conch form with weak external ornament readily identifies *Bentoceras* from all other tarphycerids; *Eichwaldoceras* and *Aserioceras* are typically larger, more rapidly-expanding shells with strong lirate ornament; *Tragoceras* has marked undulatory sutures, a ventral siphuncle and coarser external ornament. DZIK (1984: 37, fig. 12) linked *Aphetoceras* HYATT, 1894 (from the Floian of North America, Newfoundland and Western Australia) with *Bentoceras* and indicated the former may have been ancestral to the Kundan forms. *Aphetoceras* (based on the type species *A. americanum* HYATT, 1894) is distinguished here from *Bentoceras* by its larger conch consisting of three or more whorls, weak ribbing, more laterally compressed section and smaller protoconch.

Bentoceras proteus (HOLM, 1898) shows considerable variation in the degree of coiling, varying from an open, circular gyrocone to forms with a more tightly coiled conch (see Figs 5B, C). The volutions may not lie exactly in one plane and the conch is very slightly torticonic. HOLM (1898: 363) regarded the more tightly coiled form as sufficiently distinct to merit the variety name *demissa*. However, examination of more than 20 specimens in collections held at the RM, SGU and MNH indicates that a whole range of variously coiled 'morphological intermediates' occur.

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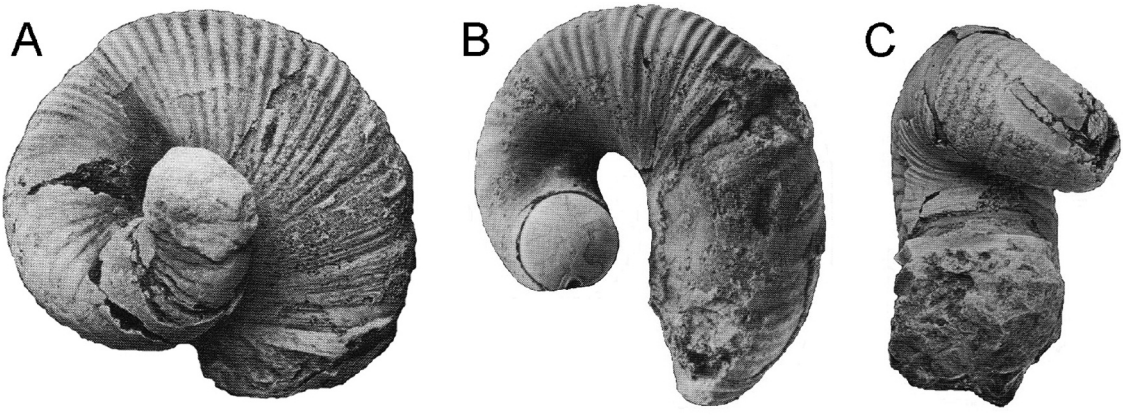

Fig. 7: *Pakrioceras holmi* STUMBUR & MUTVEI, 1983, Aserian Stage, Estonia. (**A**) RM Mo5690, lateral view, maximum diameter 42 mm. (**B**) GIT C1710, lateral view, maximum diameter 43 mm. (**C**) RM Mo5689, ventral view, maximum length 49 mm [GIT C1710, RM Mo5690 and RM Mo5689 are Holotype and two Paratypes respectively, originals of STUMBUR & MUTVEI (1983: figs 1D, G and B respectively)].

Constituent species: *Bentoceras proteus* (HOLM, 1898), *B. rubeli* STUMBUR, 1962 and *B.* sp. STUMBUR, 1962 are currently assigned to the genus.

Occurrence: *Bentoceras proteus* is known from the early Kundan Stage (Hunderumian-Valastean substages) of northern Öland and Kinnekulle, Västergötland. NEBEN & KRUEGER (1971: pl. 18, fig. 6) figured a specimen of *B. proteus* (mistakenly identified under *Tragoceras falcatum* (SCHLOTHEIM, 1820)) from an erratic boulder of early Kundan age from northern Germany. STUMBUR (1962) recorded the slightly younger *B. rubeli* and *B.* sp. from the late Kundan Stage (Aluojan Substage) of northern Estonia (Hiimäe, Ida-Viru County).

Genus *Aserioceras* STUMBUR, 1962 (Fig. 6A, B)

Type species: *Aserioceras purtsensis* STUMBUR, 1962 [by original designation; STUMBUR 1962: 143]

Diagnosis: Shell likely gyroconic with moderate expansion rate, but inner whorls unknown. Conch section compressed, slightly flattened laterally. Siphuncle narrow, positioned near the ventral margin, siphuncle wall orthochoanitic, connecting rings slightly thickened. Sutures with broad, shallow lateral and dorsal saddles, camerae relatively deep. Shell ornament consists of relatively coarse lirae which run obliquely across the lateral areas and trace out a broad ventral sinus.

Discussion: STUMBUR (1962) originally assigned *Aserioceras* to the Barrandeoceratidae, although its gyroconic form and slightly thickened connecting rings supports placement within the Estonioceratidae. *Aserioceras purtsensis* is the only species definitely assigned to the genus, although STUMBUR (1962: 143) also briefly refers to two other fragments from the Lasnamägian Stage of Estonia which may belong to a different species. *Aserioceras* is similar to *Eichwaldoceras*, and the two taxa are likely related. A distinction is maintained here on differences in conch section (circular in *Eichwaldoceras*, compressed in *Aserioceras*), and stratigraphical occurrence (Kundan Stage for *Eichwaldoceras*, Aserian stage for *Aserioceras*). However, further material may prove these genera to be synonymous.

Constituent species: *Aserioceras purtsensis* STUMBUR, 1962 is the only species currently assigned to the genus.

Occurrence: Aserian Stage at Lüganuse, northern Estonia (STUMBUR 1962).

Genus *Pakrioceras* STUMBUR & MUTVEI, 1983 (Fig. 7A–C)

Type species: *Pakrioceras holmi* STUMBUR & MUTVEI, 1983 [by original designation; STUMBUR & MUTVEI 1983: 43]

Diagnosis: Medium-sized shell, comprising approximately two whorls which coil dextrally in a loose torticonic spiral. Shell diameter increasing moderately except in the body chamber where it remains constant. Conch section subcircular to weakly depressed. Siphuncle narrow, in contact with the ventral margin of the shell. Septal necks orthochoanitic, connecting rings considerably thickened. Sutures straight laterally, forming an adorad-pointing lobe across the venter. The shell ornament consists of distinct narrow annuli with growth lines (adapted from STUMBUR & MUTVEI 1983).

Discussion: *Pakrioceras* is readily distinguished from all other estonioceratids by its combination of torticonic form and conch ornament. The poorly known Floian (Upper Canadian) genus *Aethoceras* TEICHERT & GLENISTER, 1954 from Western Australia, is also a loosely-coiled dextral torticone with slightly depressed section, but it differs from *Pakrioceras* in possessing a submarginal siphuncle, and an ornament of ribs which attenuate as delicate flanges.

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Constituent species: The only species currently assigned to the genus is *Pakrioceras holmi* STUMBUR & MUTVEI, 1983.

Occurrence: Aserian Stage of northern Estonia (Väike Pakri Island and Viimsi, near Tallinn). STUMBUR & MUTVEI (1983: 47) also mention a fragmentary specimen which may belong to *Pakrioceras* from the Vikarby or Seby Limestone (late Aserian or early Lasnamägian age) at Nedre Gärdsjö, Dalecarlia (Dalarna), Sweden.

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