MORPHOGENESIS AND PHYLOGENETIC RELATIONSHIPS OF CLITAMBONITIDINES, ORDOVICIAN BRACHIOPODS

OLEV VINN

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

The present thesis is based on the following original papers which are referred to by their Roman numerals:

I   Vinn, O. and Rubel, M. 2000. The spondylium and related structures in the clitambonitidine brachiopods. Journal of Paleontology 74 (3), pp. 439–443.

II   Vinn, O. and Spjeldnæs, N. 2000. Clitambonitidine Brachiopods from the Middle and Upper Ordovician of the Oslo Region, Norway. Norsk Geologisk Tidsskrift, 80, pp. 275–288.

III   Popov, L., Vinn, O., Nikitina, O. (in press). Brachiopods of the redefined family Tritoechiidae from the Ordovician of Kazakhstan and South Urals. Geobios.

IV   Vinn, O. (in press). The occurrence of new subspecies of the clitambonitidine brachiopod *Estlandia catellatus* (Öpik) in the Middle Ordovician of Osmussaar Island, Estonia. TA Toimetised, Geoloogia.

ABSTRACT

Clitambonitidine brachiopods have been studied since the 19th century. They constitute a peculiar group of brachiopods, often endemic to the Baltic, and limited to the Ordovician. According to the latest classification in the Treatise, clitambonitidines embrace 32 valid genera and one new *Korinevskia* gen.n. The study of juvenile shells of clitambonitidines resulted in the discovery of growth patterns of their ventral muscle attachment structure (spondylium). Spondylium evolved not by convergence of dental plates as previously believed, but is derived from free spondylium, which lack the supporting median septum characteristic for protorthids. Spondylium bearing (without dental plates) clitambonitidines dorsal articulation structures resembles also those of Middle Cambrian arctohedrids (portorthid brachiopods). The Clitambonitidina is not monophyletic: Clitambonitoidea and Polytoechoidea are derived distantly related ancestors.

INTRODUCTION

Clitambonitidines form a distinctive group of brachiopods limited to rocks of Ordovician age. Although widely distributed in the shallow seas of the time, clitambonitidines are particularly associated with the Baltic fauna of Estonia and western Russia (Ingria), which are key areas for the study of these brachiopods (Rubel and Wright 2000).

The globally widespread clitambonitid brachiopods have been recognised for a long time, first described in the Baltic in the 19th century. Conceptions of the taxonomic content and evolutionary ideas of this group have changed throughout more than a hundred years of research. Thus, Baltic clitambonitids were described as endemic brachiopods to this region. However, claims have been made that similar Ordovician brachiopods are related to Baltic clitambonitids. Several stocks have been included and excluded from the clitambonitids, so there has been no generally accepted concept of what constitutes a clitambonitid. In his basic monograph "Über Klitamboniten," Öpik (1934) established the systematics and basic concept of clitambonitid morphology. According to the Öpik's vision, the clitambonitidines in addition to the Baltic representatives, Estlandiidae, Kullervoidea, Clitambonitiidae *sensu* Öpik (1934) also include the following non-Baltic, somewhat different Polytoechiidae, Finkelnburgiidae and Skenidiidae. Interestingly, the presence of a raised spondylium triplex-like ventral muscle field in *Polytoechia* led Öpik to include this genus in the family Estlandiidae (see Öpik 1934, p. 76).

The next wholesale revision of the clitambonitidines was by Williams (1965), in which three types of spondylium were introduced, and groups with some orthid features (finkelnburgiids and skenidioids) were excluded.

Recently, Wright and Rubel (1996) revised the morphology of clitambonitids to reflect the relationships between themselves as well as with other early ·barchiopods. However, in a subsequent classification, Rubel and Wright (2000), proposed only two clades, Polytoechioidea and Clitambonitoidea, the latter with two families, Clitambonitidae and Gonambonitidae, leaving open the use of other structures as well as their phylogenetic analysis with recent tools.

The task of this research was to describe clitambonitidine morphological diversity by encompassing all morphological features in all genera, and to study the critical yet poorly understood ontogeny of the shell using available and new collections, especially those of the earliest representatives, in order to clarify phylogenetic relationships between the clitambonitidines themselves and their possible ancestors.

The revision of the morphological structures was based on rich and exceptionally well-preserved collections of Baltic clitambonitoids and related brachiopods which allowed re-evaluation of the understanding of some structures (spondylium, delthyrial covers, shell material, cardinalia, vascular marks) including their ontogeny on direct observations of neanic specimens, serial

sectioning and SEM microscopy. The main collections on the Clitambonitoidea studied include those of the Baltic and Ingermanland Ordovician housed in the geological museum of The University of Tartu, Geological Institute of Tallinn Technical University, State University of Petersburg, The Natural Museum of London, and The Museum of Natural History in Stockholm. The following were described from new collections: Middle Ordovician clitambonitoids from Norway (Vinn and Spjeldnaes 2000 — PAPER II), Ordovician polytoechioids from Kazakhstan and the southern Urals (Popov *et al.* in press — PAPER III), as well as one Middle Ordovician species from Estonia (Vinn in press — PAPER IV).

CHAPTER 1. THE GENERA AND DISTRIBUTION

Williams (1965) recorded 31 generic names that had been ascribed to clitambonitidines, of which 23 were considered to be valid. According to the data set of Rex Doescher, recently modified by Thomas Dutro and Maurice Grolier, Smithsonian Institution, Washington D. C., 43 generic names are currently ascribed to the Clitambonitidina. Of these the genus *Eosotrematorthis* Wang (1955, p. 336, type species *E. sinensis*) was transferred to the suborder Orthidina soon after its description (see Williams, 1965). Similarly, the genus *Djindella* Menakova (1991, p. 26, type species *D. plana*) with its bifurcated cardinal process and pseudopunctate shell substance is associated more appropriately with strophomenid brachiopods. The systematic position of the genus *Anomalorthis* Ulrich and Cooper (1936, p. 622, type species *A. utahensis*) may be the most controversial, and its relationship with other clitambonitidines, especially genera *Progonambonites* and *Oslogonites* (see Williams 1965, p. H355), has not been confirmed by analysis of overall similarity and phylogenetic relationships. According to its orthid cardinalia, exceptionally fine radial costellation and fibrous shell substance with atypical pseudopunctae, the affinities of this genus are more likely to lie with the orthidines rather than the clitambonitidines (see Cooper 1956, p. 391; Wright and Rubel 1996).

There are four objective and four subjective synonyms among the remaining 40 generic names. The generic rank and content of species of the genus *Hemipronites* Pander, 1830 have been changed from that of Schuchert and Cooper (1932) to the concepts of Öpik (1934) and Williams (1965). The well-preserved deltidial covers in some specimens of the genus *Progonambonites* Öpik 1934 suggests it is congeneric with the genus *Gonambonites* Pander 1830 (Rubel and Wright 2000).

Thirty-two traditional and one new clitambonitidine genera with the following stratigraphic and geographical distributions ensue from the papers noted above and added during this study (PAPERS I to IV) (see: figures 1, 2):

Acanthotoechia Williams and Curry, 1985: Upper Arenig; Ireland.

Admixtella Rozman, 1978: Lower Caradoc; Tien Shan Mountains.

Anchigonites Öpik, 1939: Arenig-?Lower Llanvirn; Norway, Estonia, western Russia, China.

Antigonambonites Öpik, 1934: Lower Arenig-Lower Llanvirn; Norway, Estonia, western Russia, Poland, Newfoundland (Canada), China.

Apomatella Schuchert and Cooper, 1931: Arenig-Lower Llanvirn; Norway, Estonia, western Russia.

Asymphylotoechia Ross, 1970: Upper Llanvirn; Nevada (USA).

Atelelasma Cooper, 1956: Llandeilo-Lower Caradoc; Virginia, Tennessee, Oklahoma, Alabama, Wisconsin, ?New York, ?Vermont (USA), Wales, Siberia, Mongolia.

Atelelasmoidea Zeng, 1987: Arenig; central and south-western China.
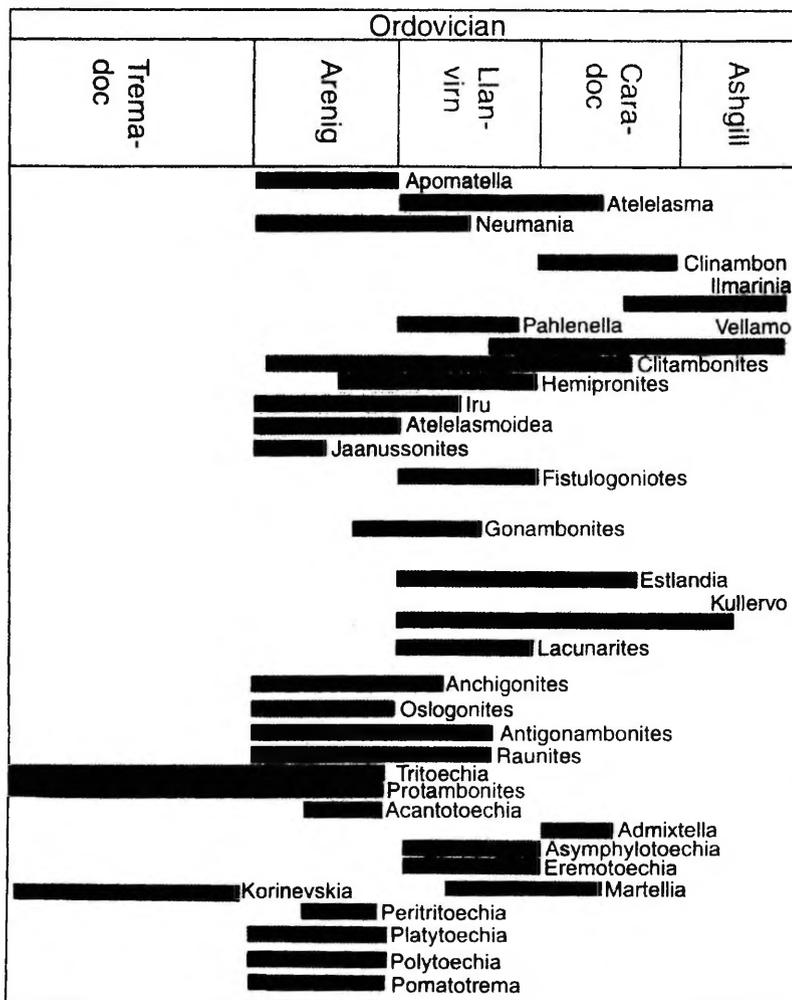
Figure 1. Stratigraphic distribution of clitambonitidines genera (*sensu* Rubel and Wright 2000), including *Korinevskia* gen.n (Popov *et al.* in press — PAPER III).

Clitambonites Pander, 1830: Arenig-Lower Caradoc; Estonia, Russia, Norway, Sweden, China.

Clinambon Schuchert and Cooper, 1932: Caradoc; Estonia, western Russia.

Estlandia Schuchert and Cooper, 1931: ?Lower Llanvirn-Middle Caradoc; Estonia, western Russia.

Eremotoecia Cooper, 1956: Llanvirn-Llandeilo; Tennessee, Alabama (USA), Scotland, Kazakhstan, Argentina, south-western China.
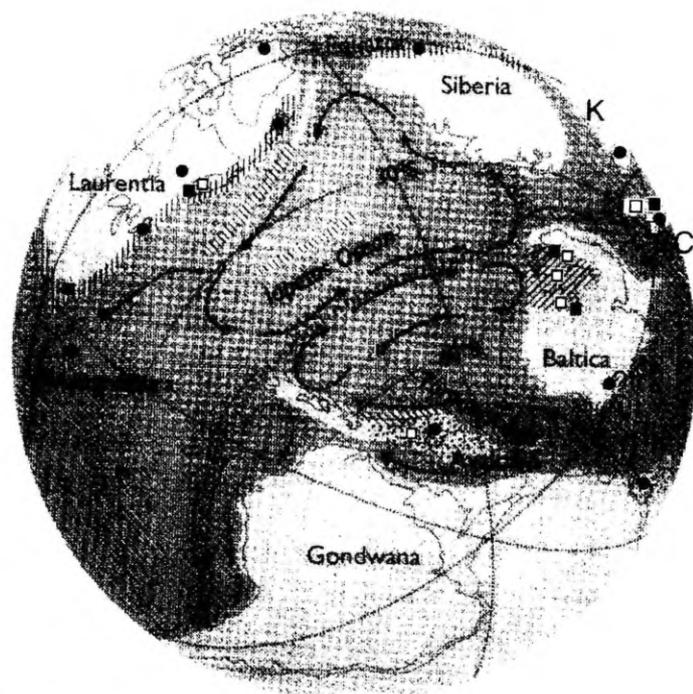
Figure 2. Arenig biogeographic distribution of clitambonitidines families (sensu Rubel and Wright 2000): Clitambonitidae (black squares), Gonambonitidae (blank squares) Polytoechiidae (black circles). Abbreviations: SC — South China, K — Kazakhstan The palaeogeographic map and ocean circulation is based on Christiansen and Stouge (1999).

Fistulogonites Neumann, 1971: Llanvirn; Newfoundland (Canada), China.

Gonambonites Pander, 1830 (=*Progonambonites* Öpik, 1934): Upper Arenig Lower Llanvirn; Estonia, western Russia, China.

Hemipronites Pander, 1830 (=*Ladogiella* Öpik, 1934): Upper Arenig-Llanvirn. Estonia, western Russia, Norway.

Ilmarinia Öpik, 1934: Upper Caradoc-Upper Ashgill; Estonia, Norway, Russia, Sweden.

Iru Öpik, 1934: Arenig-Lower Llanvirn; Estonia, western Russia, Sweden.

Jaanussonites Neuman, 1976: Upper Arenig; eastern North America (New-foundland, Maine).

Korinevskia gen.n. Popov *et al.*: Tremadoc; South Urals, Russia.

Kullervo Öpik, 1932: Upper Llanvirn-Middle Ashgill; Eurasia, North America.

Lacunarites Öpik, 1934: Llanvirn; Estonia, western Russia.

Martellia Wirth, 1936: Upper Arenig-Llanvirn; central and south-western China, Argentina.

Neumania Harper, 1981: Lower Arenig-Lower Llanvirn; Newfoundland, Wales, Norway, Estonia, western Russia.

Oslogonites Öpik, 1939: Arenig-Lower Llanvirn; Norway, Estonia.

Pahlenella Schuchert and Cooper, 1931: Lower Llanvirn; western Russia, Estonia.

Peritritoechia Xu, Rong, and Liu, 1974: Upper Llanvirn-Lower Caradoc; south-western China.

Platytoechia Neuman, 1964: Upper Arenig; Maine (USA).

Polytoechia Hall and Clarke, 1892: Arenig; Alabama, Arkansas, Oklahoma, Texas, Vermont (USA), Greenland, Manchuria (China).

Pomatotrema Ulrich and Cooper, 1932: Arenig; Oklahoma, Vermont (USA), Alberta, Quebec (Canada), Greenland, Ireland, China, Korea.

Protambonites Havliček, 1972: Tremadoc-Arenig; Bohemia, Spain, China, Urals.

Raunites Öpik, 1939: Arenig-Lower Llanvirn; Estonia, western Russia.

Tritoechia Ulrich and Cooper, 1936: Tremadoc-Arenig; North America, South America, Australia, Ireland, England, Wales, China, Siberia, Kazakhstan.

Vellamo Öpik, 1930: Llandeilo-Upper Ashgill; Eurasia, North America, North Africa, Tasmania.

CHAPTER 2. MORPHOLOGY

The vital functions of any brachiopod are (1) to be able to open its valves to feed, and (2) to maintain a position on sea floor, initially achieved by attachment to the substrate via the pedicle.

It is reasonable that structures associated with these functions are likely to be more important in morphological diversification (Wright and Rubel 1996). In clitambonitidines these structures are the delthyrial cover, deltidium, pseudodeltidium, chilidial plates, chilidium original position of pedicle opening, muscle attachment structures, e.g., spondylium, pseudospondylium (Figure 3). These structures have been used as diagnostics in the classifications by Öpik (1934), Williams (1965), and Rubel and Wright (2000).
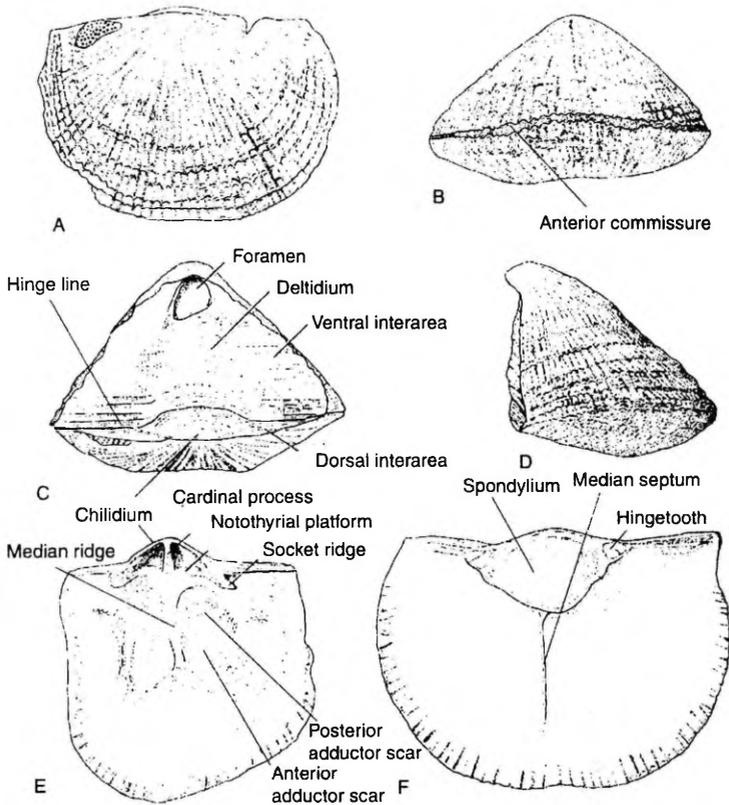

Figure 3. Basic clitambonitidine morphology, based on specimens of *Vellamo oanduensis* Öpik; a–d dorsal, anterior, posterior, lateral views of conjoined valves; e, dorsal valve interior with quadripartite adductor scars and some vascular markings preserved; f, ventral valve interior (adapted from Wright and Rubel, 1996)

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Anterior adductor scar tracks. Tracks of attachment of anterior pair of adductor muscles. The adductor muscles contract to close the shell (Figure 3).

Chilidium. Crescentic convex plate covering apex of notothyrium (Williams *et al.* 1997). A chilidium is characteristic of clitambonitidines. *Clitambonites* has a large, high, semicircular chilidium with flattened lateral margins, well demarcated from the dorsal interarea. The deltidium of *Clitambonites* has its shell layers undercut away from the umbo and towards the hinge line as would be expected. The lamellose arrangement of its deltidium is stacked in the same direction as that of the chilidium. The same type of stacking on the chilidia is present, though not so pronounced, in forms like *Clinambon* and *Ilmarinia*. Other clitambonitidines, such as *Antigonambonites* and *Estlandia*, posses smaller, less pronounced and more triangular chilidia on which the growth lines are undercut on the side of the hinge line. In these cases the growing edges would have been external, i.e., unconcealed within the conch by the deltidium, and lined internally by the outer epithelium in the usual manner (Wright and Rubel 1996) (Figure 3).

Chilidial plates. Pair of posterior plate-like extensions of notothyrial walls, forming lateral boundaries of cardinal process (Williams *et al.* 1997). In addition to the two arrangements of the chilidia, the notothyrium in other clitambonitidines is either flanked by chilidial plates, as in *Tritoechia*, or, as with *Oslogonites*, lacks calcareous plates within an open notothyrium. The various forms of the structure have accordingly been used as a basis for differentiating stocks (Wright and Rubel 1996).

Cardinal process. Blade or variably shaped boss of secondary shell situated medially in posterior end of dorsal valve and serving for separation or attachment of paired diductor muscles (Williams *et al.* 1997). The cardinal process is a simple, generally narrow, and prominent ridge in the centre of the notothyrial platform that extends towards, and may fuse with, the inner surface of chilidium. The cardinal process is not always present, but its absence as a generic character is unreliable (Wright and Rubel 1996) (Figure 3).

Commissure. Line of junction between edges or margins of valves (Williams *et al.* 1997) (Figure 3).

Delthyrium. Median triangular or subtriangular aperture bisecting ventral cardinal area, serving as pedicle opening in some genera (Williams *et al.* 1997).

Deltidium. Cover of delthyrium formed by conjunct deltidial plates; line of junction of visible plates (Williams *et al.* 1997). The term 'symphytium' is used to describe when the deltidial plates are fused, and there is no median junction line (Williams and Rowell 1965, p. H88), although this is fundamentally the same structure (Wright and Rubel 1996). In some clitambonitidines, such as the Atelelasmatinae and Anomalorthinae (excluded from clitambonitidines; Rubel

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and Wright 2000), the delthyrium is open or with only selvages of shell along the lateral margins. Williams (1965, p. H346) interpreted this state as indicating that the pseudodeltidium probably failed to develop 'during the differentiation of the young shell'. Nevertheless, this growth pattern is typical of a deltidium, not of a pseudodeltidium, which always defines the front of a pedicle foramen (Wright and Rubel 1996). According to the Treatise, the delthyrial cover in clitambonitidines is always deltidium (Rubel and Wright 1997), although the delthyrial cover in polytoechioids has recently been identified as pseudo-deltidium (Popov *et al.* in press — PAPER III) (Figure 3).

Deltidial plates. Two plates growing medially from margins of the delthyrium, partly or completely closing it (Williams *et al.* 1997). Occurs in all juvenile clitambonitoids, which have covered delthyrium in adult growth stages.

Interarea. Posterior sector of shell with growing edge at hinge line; also more commonly used for any plane or curved surface lying between beak and posterior margin of valve and bisected by delthyrium or notothyrium (Williams *et al.* 1997) (Figure 3).

Foramen. Sub-circular to circular perforation of shell through which the pedicle passes (Williams *et al.* 1997). Is supra-apical in polytoechioids and delthyrial in clitambonitoids (Popov *et al.* in press — PAPER III; Figure 3)

Median septum. Secondary shell junction between spondylium bottom and valves floor. Median septum occurs in all mature clitambonitoids, but lacking in juveniles (Vinn and Rubel 2000 — PAPER I; Figure 3)

Notothyrium. Median sub-triangular opening, bisecting dorsal cardinal area (Williams *et al.* 1997).

Notothyrial platform. Umbonal thickening of floor of dorsal valve between ·inner socket ridges (Williams *et al.* 1997). Notothyrial platform in a standard clitambonitidine is well-developed, but in *Polytoechia* and associated species the platform is only weakly developed (Wright and Rubel 1996) (Figure 3).

Posterior adductor scar tracks. Tracks of the attachment of the posterior pair of adductor muscles (Figure 3).

Pseudopuncta. Conical deflection of the secondary shell, pointing inwardly and anteriorly as to appear on the internal surface of the valve as a tubercle (Williams *et al.* 1997).

Pseudospondylium. Cup-shaped chamber accommodating ventral muscle field and comprising undercut callus of secondary shell contained between discrete dental plates (Williams *et al.* 1997). The term pseudospondylium is applied here only for structures that simulate a spondylium triplex, e.g., the structures in *Poly-toechia*, *Antigonambonites* and *Raunites* (Vinn and Rubel 2000 — PAPER I).

Spondylium. Trough-shaped or spoon-like apparatus composed of dental plates in various stages of coalescence (Williams *et al.* 1997). This definition is not for clitambonitidines spondylium and protorthids spondylium in terms of phylogenesis. These structures in clitambonitidines and protorthids are not derived from the ancestral discrete dental plates. In merely morphological terms, by the position and shape, it is correct to so designate all the structures that support ventrally teeth dental plates regardless of the basic differences in their origin. In my opinion the dental plates (in evolutionary terms) are unrelated to spondylium both phylogenetically and functionally (Vinn and Rubel 2000 — PAPER I) (Figure 3).

Sondylium simplex. Spondylium supported by variably developed simple ventral median septum (Williams *et al.* 1997). Originated in clitambonitidines from the free (unsupported) spondylium in early growth stages (Vinn and Rubel 2000 — PAPER I)

Spodylium triplex. Spondylium supported by median septum and two lateral septa (Williams *et al.* 1997). Originated in clitambonitidines from spondylium simplex in early growth stages (Vinn and Rubel 2000 — PAPER I).

Socket ridges. Linear elevations of secondary shell extending laterally from cardinal process and bounding the anteromedian margin of dental sockets (Williams *et al.* 1997). The clitambonitidenes socket ridges extend lateroanteriorly from within the limits of the notothytrium from the underside of the chilidium and forming a ridge lying along the lateral extensions of the notothyrial platform, defining the sockets medially and commonly culminating in a small ventrally projecting process (Wright and Rubel 1996). The shape and orientation of socket ridges varies greatly within genera, but is quite constant for each species (Figure 3)

Spines. Hollow cylindrical projections from external shell surface (Williams *et al.* 1997). The well-developed spines occur in some species of *Estlandia* (Wright and Rubel 1996; Vinn in press — PAPER IV) and *Acanthotoechia* (Wright and Rubel 1996).

Hemisyrinx. Conical chamber extending medially along floor of clitambonitoid spondylium and delineated posteriorly by a pair of discrete ridges (Williams *et al.* 1997). The structure is unknown in any other brachiopod other than *Kullervo*.

Hingeteeth. Two principal articulating processes situated anterolateral margins of delthyrium and articulating with dental sockets in dorsal valve (Williams *et al.* 1997). The teeth of clitambonitidines are deltidiont (Jaanusson 1971, p. 35; pl. 1, fig. 5) (Figure 3)

Hinge line. Straight posterior margin of shell, parallel with hinge axis; previously used as synonym for the cardinal margin (Williams *et al.* 1997) (Figure 3).

Subspondylial lateral septa. Pair of secondary shell ridges below the spondylium bottom in some gonambonitids. Subspondylial lateral septa are lacking in juveniles (Vinn and Rubel 2000 — PAPER I)

CHAPTER 3. PHYLOGENY AND CLASSIFICATION

3.1. The suprageneric classification of clitambonitidines applied in Treatise (Rubel and Wright 2000)

The classification presented below summarises previous hierarchies, based all on certain characteristics selected to subdivide the clitambonitidines and related brachiopods into suprageneric taxa according to their alleged phylogenetical relationships.

Class STROPHOMENATA Williams & others, 1996
Order BILLINGSELLIDA Schuchert, 1893
Suborder CLITAMBONITIDINA Öpik, 1934.

Superfamily CLITAMBONITOIDEA Winchell and Schuchert, 1893. Dental plates form spondylium; shell substance impunctate or pseudopunctate.

Family CLITAMBONITIDAE Winchell and Schuchert, 1893. Dental plates join into spondylium simplex; dorsal adductor scars quadrate; shell substance impunctate. Assigned genera: *Clitambonites* (= *Pronites*), *Apomatella*, *Atelelasma*, *Clinambon*, *Fistulogonites*, *Hemipronites* (= *Ladogiella*), *Ilmarinia*, *Iru*, *Lacunarites*, *Neumania*, *Pahlenella*, *Vellamo*.

Family GONAMBONITIDAE Schuchert and Cooper, 1931. Spondylium supported by lateral plates; dorsal adductor scars mostly radiating; shell substance pseudopunctate. Assigned genera: *Gonambonites* (= *Progonambonites*), *Anchigonites*, *Antigonambonites*, *Atelelasmoidea*, *Estlandia*, *Jaanussonites*, *Kullervo*, *Oslogonites*, *Raunites*.

Superfamily POLYTOECHIOIDEA Öpik, 1934. Dental plates reach the valve floor to form pseudospondylium; shell substance impunctate. Assigned genera: *Polytoechia*, *Acanthotoechia*, *Admixtella*, *Asymphylotoechia*, *Eremotoechia*, *Martellia*, *Peritritoechia*, *Platytoechia*, *Pomatotrema*, *Protambonites*, *Tritoechia*.

3.2. Newly proposed phylogenetical classification of clitambonitidines (Popov *et al.* in press — PAPER III)

Unlike most previous attempts based on subjective evaluation of phylogenetic importance of characteristics, the new phylogenetical classification is based on cladistical analyses of characteristics, revised in some cases and representing the morphological diversity of clitambonitidines and related brachiopods in order to their evolution.

To test the phylogenetic relationships of clitambonitidine genera, two cladistical analyses were performed using the PAUP 4.0 program for MS Windows (Swofford 1999). All characteristics used were taken initially unordered and with the equal weight, enabling polarity to be determined exclusively by the outgroup method.

First, the superfamily Polytoechioidea was tested (Popov *et al.* in press — PAPER III). A heuristic search using global swapping with the MULPARS option performed in this analysis resulted in six shortest trees, each 122 steps long, with a consistency index of 0.615, homoplasy index of 0.385 and re-scaled consistency index of 0.417. A 50% majority rule tree derived from six equally parsimonious shortest trees is presented on Figure 4 (Table 1, 2).
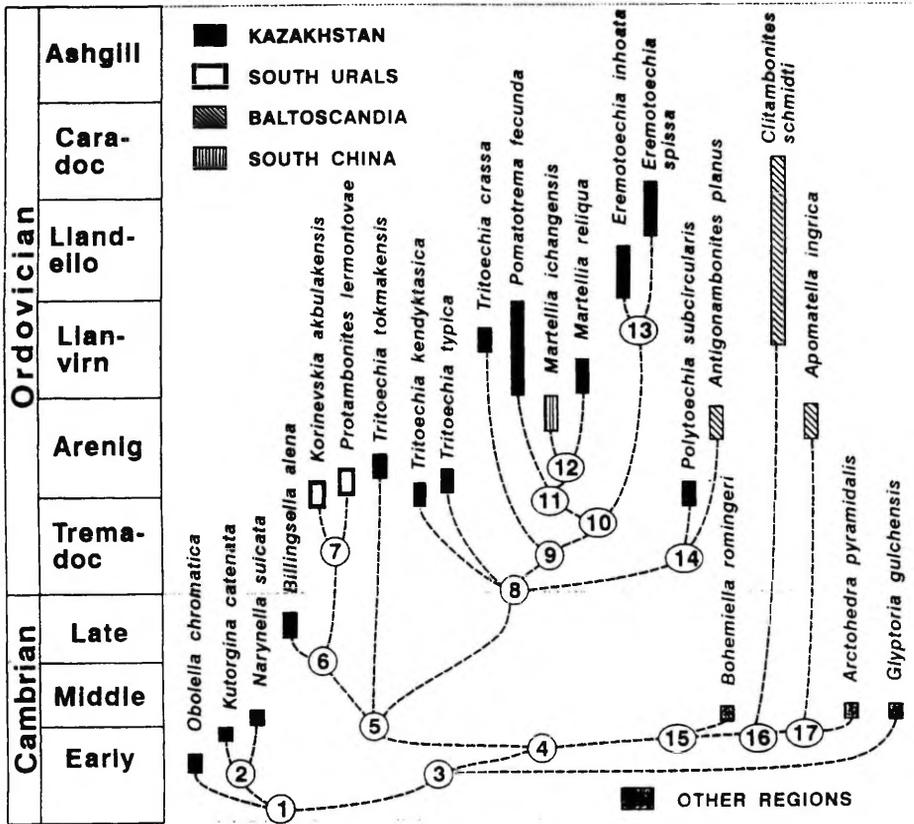

Figure 4. Stratigraphic ranges and inferred phylogenetic relationships of nine Kazakh tritoechiide species (shown in black) and selected taxa of early rhynchonelliformean brachiopods and clitambonitides based on 50% majority rule consensus of six trees (Table 1, 2).

Table 1. Characters and character states in phylogenetic analysis.

1. out — outline: transversely semi-elliptical (0), elongate sub-rectangular to sub-quadrate (1), transverse sub-rectangular (2), sub-hexagonal (3), sub-circular (4).
2. prl — profile (sagittal): planoiconvex (0), dorsibiconvex (1), ventribiconvex (2), subequally biconvex (3), convexoplane (4).
3. acm — anterior commissure: rectimarginate (0), sulcate (1), gently uniplicate (2), strongly uniplicate (2).
4. pmw " maximum shell width, width: anterior to hinge line (0), at hinge line (1).
5. psd — pseudodeltidium: absent (0), present (1).
6. del — deltidium: absent (0), present (1).
7. pvv — pedicle opening: posterior cleft`(0), suproapical (1), formed by fusion of deltidial plates (2).
8. vsl — ventral median sulcus: absent (0), weakly defined (1), well developed (2).
9. dmf — dorsal median fold: absent (0), weakly defined (1), well developed (2), umbonal (3).
10. dsu — dorsal median sulcus: absent (0), present (1), fading anteriorly (2).
11. ufo — suproapical foramen: no pseudodeltidium (0), open (1), sealed (2).
12. nop — notothyrium: absent (0), widely divergent (1), narrowly divergent (2).
13. chi — chilidium: absent (0), separated plates (1), complete (2).
14. dia — dorsal pseudointerarea: absent (0), rudimentary (1), well developed (2).
15. orr — radial ornament: absent (0), finely multicostellate (1), multicostellate (2), parvicostellate (3), ramicostellate (4) costate (5), capillae (6).
16. adt — adticules: absent (0), present (1).
17. vii — ventral interarea, inclination: strongly apsacline to orthocline (1), apsacline (2), procline to catacline (3).
18. vip — ventral interarea, profile: curved (0), planar (1).
19. fbd — furrows along the lateral sides of pseudodeltidium: absent (0), present (1).
20. plf — sockets: absent (0), present, partly composed of primary shell (1), present, formed by secondary shell (2).
21. dtt — deltidiodont teeth: absent (0), present (1).
22. scb — socket ridges/brachiophores: absent (0), brachiophore knobs (1), socket ridges (2), brachiophores (3).
23. vmf — spondylial structures: absent (0), free (1), supported by median septum (2).
24. dpl — dental plates: absent (0), present (1).
25. vdl — ventral diductor scar, length: not applicable (0), shorter then adductors (1), about equal length (2), longer then adductors (3).
26. psp — pseudospondylium: absent (0), present (1), no discrete dental plates (2).
27. vmr — median ridge anterior to the muscle field: absent (0), present (1).
28. vur — median ridge in the umbonal area: absent (0), present (1).
29. vmc — ventral mantle canals: pinnate (0), saccate (1).
30. npl — notothyrial platform: absent (0), present, low (1), well developed, strongly inclined posteriorly (2), high, hanging anteriorly (3).
31. cpr — cardinal process: absent (0), rudimentary (1), simple, ridge-like (2).
32. daf — dorsal adductor field: obscure (0), impressed on valve floor (1), impressed on callus of secondary shell (2).
33. asc — adductor scars: median and posterolateral pairs (0), radially arranged (1), quadripartite (2).
34. dms — dorsal median ridge: absent (0), present as a low ridge (1), septum (2).
35. ssp — side septa: absent (0), present (1).
36. aad — anterior adductors: larger then posterior pair (0), about equal size (1), smaller (2).

Table 2. Character state matrix for analysis of taxa, as discussed in the text.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
	out	pri	acm	pmw	psd	dei	pvv	vsl	dmf	dsu	ufo	nop	chi	dia	orr	adt	vii	vip
Obolella chromatica	4	2	0	1	0	0	0	1	0	0	0	0	0	0	6	0	0	1
Bohemiella romingeri	3	2	0	1	0	0	0	0	0	2	0	2	0	2	4	0	2	0
Kutorgina catenata	3	2	0	1	1	0	1	0	0	0	1	1	0	1	0	0	1	1
Narynella sulcata	3	2	0	1	1	0	1	0	0	1	1	1	0	2	3	0	1	1
Glyptoria gulchensis	3	3	2	1	0	0	0	0	2	2	0	2	0	2	5	0	1	1
Arctohedra pyramidalis	0	2	1	0	0	0	0	0	0	0	0	2	0	2	5	0	2	1
Billingsella seletensis	1	4	0	0	1	0	1	0	0	0	2	2	1	2	3	0	0	1
Korinevskia akbukakensis	1	4	0	1	1	0	1	0	0	0	2	2	2	2	4	0	0	1
Protamb. lermontovae	1	4	0	1	1	0	1	0	0	0	2	2	2	2	4	0	0	1
Trytoechia typica	2	3	0	1	1	0	1	0	0	2	1	2	1	2	2	1	1	1
T. tokmakensis	2	2	0	0	1	0	1	0	0	0	1	2	1	2	3	0	1	1
T. crassa	2	2	1	1	1	0	1	0	0	1	1	2	2	2	3	0	1	1
T. Kurdayca	2	2	1	1	1	0	1	0	0	1	1	2	1	2	2	?	2	1
Pomatotrema fecunda	1	0	0	1	1	0	1	1	1	0	1	2	2	2	3	1	1	1
Martellia ichangensis	3	2	2	1	1	0	1	1	1	0	1	2	2	2	1	?	1	1
M. reliqua	3	2	2	1	1	0	1	1	1	0	1	2	2	2	1	?	1	1
Eremotoechia spissa	2	1	3	1	1	0	1	2	2	0	1	2	2	2	2	0	1	1
E. inhoata	2	1	2	1	1	0	1	2	2	0	1	2	2	2	2	0	1	1
Apomatella ingrica	2	2	0	0	0	0	0	0	0	1	0	2	0	2	4	0	2	1
Clitambonites schmidti	2	2	0	1	0	1	2	0	0	3	0	2	2	2	4	1	1	1

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
	tbd	plf	dtt	scb	vmf	dpl	vdl	psp	vmr	vur	vmc	npl	cpr	daf	asc	dmr	ssp	aad
Obolella chromatica	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0
Bohemiella romingeri	0	2	1	3	0	1	2	0	0	0	1	1	1	1	1	1	0	?
Kutorgina cingulata	1	0	0	0	0	0	?	0	0	0	?	1	0	0	1	0	0	?
Narynella sulcata	1	1	0	0	0	0	2	0	0	0	0	1	0	1	1	0	0	0
Glyptoria gulchensis	0	2	1	1	1	0	2	2	0	0	0	3	0	0	?	0	0	?
Arctohedra pyramidalis	0	2	1	3	1	0	2	2	0	0	1	1	1	1	2	1	0	2
Billingsella seletensis	0	2	1	2	0	1	3	0	0	1	1	1	2	1	1	1	0	0
Korinevskia akbukakensis	0	2	1	2	0	1	3	0	0	1	1	2	2	1	1	2	0	0
Protamb. lermontovae	0	2	1	2	0	1	3	0	1	1	0	2	2	1	1	1	0	0
Trytoechia typica	0	2	1	2	0	1	2	0	1	0	0	2	2	1	1	1	0	1
T. tokmakensis	0	2	1	2	0	1	3	0	0	0	1	1	2	1	1	1	0	2
T. crassa	0	2	1	2	0	1	1	0	1	0	1	2	2	1	1	1	0	1
T. Kurdayca	0	2	1	2	0	1	2	0	1	0	0	1	2	1	1	1	0	2
Pomatotrema fecunda	0	2	1	2	0	1	1	1	1	0	1	2	2	2	1	2	1	1
Martellia ichangensis	0	2	1	2	0	1	1	1	1	0	1	3	2	2	1	2	1	1
M. reliqua	0	2	1	2	0	1	1	1	1	0	1	3	2	2	1	2	1	1
Eremotoechia spissa	0	2	1	2	0	1	?	0	?	0	?	1	2	2	1	1	1	1
E. inhoata	0	2	1	2	0	1	?	0	?	0	?	1	2	?	1	1	1	?
Apomatella ingrica	0	2	1	2	2	0	?	2	2	0	1	1	2	1	2	1	0	0
Clitambonites schmidti	0	2	1	2	2	0	3	2	2	1	1	1	2	1	2	1	0	0

All six cladograms show billingsellids and tritoechiids as a single and very consistent monophiletic clade (Fig. 4, node 6) that excludes clitambonitoideans. The latter group is represented in the analysis by two taxa (*Apomatella ingrica*, family Atelelasmatidae and *Clitambonites schmidti*, family Clitambonitidae), which form another clade together with a derived protorthoidean *Arctochedra pyramidalis* (Fig. 4, node 16). In five cladograms this clade appears as a sister group of another clade uniting orthides, represented in the analysis by *Bohemialla romingeri*, billingsellids and tritoechiids. In a single cladogram, orthides emerged as a sister group of clitambonitoideans and derived protorthoideans.

The true clitambonitidines represent an ingroup within Protorthida. It is also interesting to note, that the most primitive protorthides similar to *Glyptoria*, which had acquired true teeth, but still lacked a fully formed deltidiodont articulation, appeared in the analysis as a sister group of all other brachiopods with deltidiodont articulation (Fig. 4, node 3).

As well as the acquisition of the dental plates recognised in the analysis as one of synapomorphies uniting orthides, billingsellids and tritoechiides in the same clade, the absence of dental plates in *Billingsella* is attributed to their secondary loss. However, there is still a possibility that lack of dental plates in Billingsellidae is a primary feature and their appearance in the orthides and tritoechiides represents homoplasy, which remained unrecognised. Therefore the presence of dental plates is regarded here as the main distinctive feature of Tritoechiidae, which distinguishes this family from Billingsellidae, in spite of the possible paraphyletic nature of the group. The paraphyletic nature of *Tritoechia* is another outcome of this analysis. This is not surprising, because some significant differences in shell morphology are evident from the study of Kazakh species.

Tritoechiid species from the southern Kazakh terranes belong to a single clade (Fig. 4, node 9) and their divergence pattern matches well with the chronological sequence of their appearances. In contrast, Uralian *Korinevskia akbulakensis* and *Protambonites lermontovae* are placed distantly and demonstrate more similarities to *Billingsella* (Fig. 4, node 7). The possible explanation of the observed pattern is that these two species are among the oldest tritoechiids originating from a different location at the southern margin of the Baltic plate, which faced West Gondwana in the early Ordovician (Christiansen and Stouge 1999).

Second, the superfamily Clitambonitoidea was tested including all its 21 genera, plus two representatives of Polytoechioidea (*Tritoechia, Protambonites*) and seven outgroup genera representing the different higher taxa of Cambro-Ordovician articulate brachiopods (*Obolella, Narynella, Kutorgiana, Bohemiella, Billingsella, Glyptoria, Arctohedra*). Thirty characteristics were used to analyse this set of genera (see Table 3, 4). The heuristic search was undertaken by the stepwise addition of taxa. *Obolella* was chosen as outgroup because it is expected to be one of the closest groups to the classes of Strophomenata and Rhynchonellata (Williams *et al.* 1996). The analyses resulted in 97 trees. On the 50% strict consensus tree, the clitambonitoids genera excluding *Antigonambonites* and *Raunites* but including *Arctohedra* form a sister group to the pro-

torthid *Glyptoria*. The paraphyletic clade of this protortid and clitambonitoids (including *Arctohedra*) is a sister group to a paraphyletic clade of representatives of polytoechioids, early orthoids as well as *Antigonambonites* and *Raunites*.

Table 3. List of coded characters used in cladistical analysis (Figure 5) of clitambonitoid genera with the possible outgroup genera of Cambro-Ordovician brachiopods. The number after the character indicates weight assigned to the character in the scale weighted analyses.

1. Outline (250): subcircular (1); subhexagonal (2); subquadrate (3); transversely semielliptical (4).
2. Shell (125): resupinate (1); concavoconvex (2); planoconvex (3); ventribiconvex (4); biconvex (5); dorsibiconvex (6); convexoplane (7); convexoconcave (8).
3. Anterior commissure (333): sulcate (1); rectimarginate (2); uniplicate (3).
4. Costella (333): absent (1); costellate (2); capillae (3).
5. Imbricative sculpture (500): absent (1); present (2).
6. Concentric ornamentation — fila (333): absent (1); present (2); prominent (3).
7. Ventral interarea profile (500): flat (1); curved (2).
8. Ventral interarea attitude (333): procline (1); cataline (2); apsacline (3).
9. Dorsal interarea (333): absent (1); rudimentary (2); well developed (3).
10. Deltidiont teeth (500): absent (1); present (2).
11. Sockets (333): absent (1); present, partly composed of primary shell (2); present, formed by secondary shell (3).
12. Socket ridges/brachiophores (333): absent (1); brachiophore knobs (2); present (3).
13. Pedicle opening (500): suproapical (1); posterior cleft (2).
14. Deltidium (333): absent (1); lateral plates (2); present (3).
15. Pseudodeltidium(500): absent (1); present (2).
16. Spondylium (500): present (1); absent (2).
17. Subspondylian lateral septa (333): present (1); absent (2); no spondylium (3).
18. Ventral subspondylial median septum (333): absent (1); present (2); no spondylium (3).
19. Sharp crest separating spondylium (333): absent (1); present (2); no spondylium (3).
20. Dental plates (500): present or rudimentary (1); absent (2).
21. Pseudospondylium (333): present (1); absent (2); no discrete dental plates (3).
22. Ventral adductor scars (250): not applicable (1); shorter than diductor scars (2); about eqaul length (3); longer than diductors (4).
23. Notothyrium (250): covered by chilidium (1); flanked by chilidial plates (2); open (3); absent (4).
24. Cardinal process (333): well developed (1); weakly develped (2); absent (3).
25. Notothyrial platform (333): absent (1); weakly developed (2); well developed (3).
26. Adductor field (333): radiate (1); quadripartite (2); median and posterolateral pair (3).
27. Dorsal median ridge (500): absent (1); present (2).
28. Dorsal adductor field (333): obscure (1); impressed on valve floor (2); impressed on calus of secondar (3).
29. Anterior dorsal adductor scars (333): larger than posterior pair (1); about equal size (2); smaller (3).
30. Shell substance (500): pseudopunctate (1); impunctate (2).

Table 4. Character-state matrix used in PAUP analyses (Fig. 2–4) of character as listed in Table 1. Missing data coded as?

'Anchigonites'	42221213323323111121234123123131
'Apomatella'	44121212323323221122123322322212
'Atelelasma'	33122212323323221122123411322122
'Atelelasmoidea'	44221212323323211122123333322112
'Clinambon'	34321211323323231122223311322212
'Clitambonites'	34122223323323231122123411322212
'Lacunarites'	42121323323323231122123331231217?1
'Estlandia'	36121213323323231112123411312231
'Fistulogonites'	44121223323323231112123333312127?1
'Gonambonites'	36121223323323231112123421312231
'Hemipronites'	14222123323323231122123411322112
'Ilmarinia'	14321121323323231122223411322212
'Iru'	18322221323323221122123421322172
'Jaanussonites'	33?2121332332323111121233123312312121
'Kullervo'	44121322323323231112123412312211
'Neumania'	34122122323323221122123422322212
'Oslogonites'	43221213323323211112123333312131
'Pahlenella'	42121123323323231122123311322312
'Vellamo'	33222223323323231122123411322222
'Antigonambonites'	31121213323311223331411312231
'Protambonites'	47221113323311233312332212172
'Raunites'	41221213323311223331131312331
'Tritoechia'	34221113323311223331232121212232
'Obolella'	14231213111121123332314313121
'Bohemiella'	242211233323321123331233221?2?2
'Kutorgina'	24211?1321111122333237332111?2
'Narynella'	24221?13312?11223332333332111212
'Glyptoria'	253?1?133232211121123333327?1132
'Arctohedra'	44121213323321112112333232322132
'Billingsella'	37221213323311223332222121212212

The subsequent analyses using the scale-weighted characteristics (Table 3, 4) resulted in 24 equally parsimonious trees with a length of 42226 steps (consistency index = 0.449, retention index = 0.717 and homoplasy index = 0.551). On the 50% strict consensus tree (Figure 5), the phylogenetic relationships of genera in the ingroup of clitambonitoids and *Arctohedra* are generally resolved. On the consensus tree, the ingroups of gonambonitids and of clitambonitids form a sister group for *Arctohedra* and *Atelelasmoidea*. The ingroup of gonambonitids, clitambonitids, *Atelelasmoidea* and *Arctohedra* begins with basal polychotomy. Thus, their phylogenetic relationships are unresolved on the consensus tree (Figure 5).
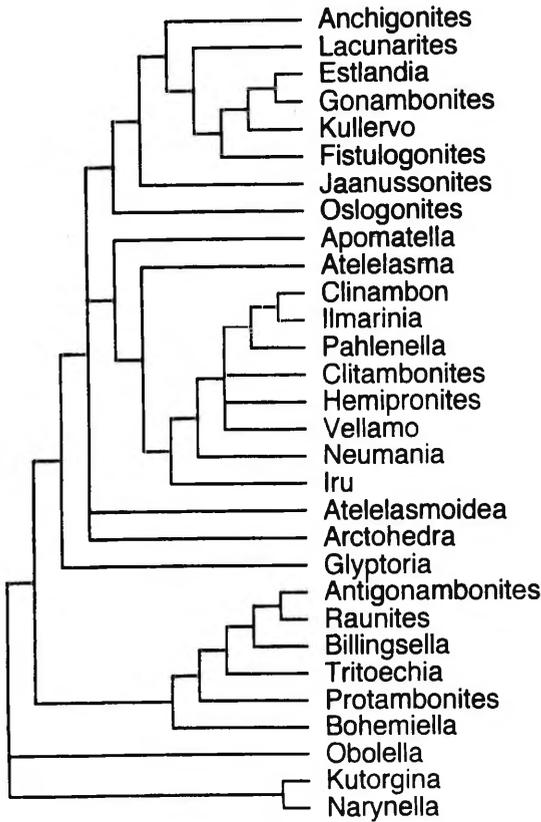
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Figure 5. Strict consensus of 24 trees of analyses performed with scale weighted characteristics (Table 3, 4). Outgroup chosen <u>Obolella</u>.

The main difference between superfamilies Clitambonitoidea and Gonamboni-toidea lies in presence or absence of pseudopunctation, the type of dorsal muscle field, and the presence of subspondylial lateral septa. However, the lateral subspondylial septa do not occur in all gonambonitoidean genera and appear in ontogeny after the formation of the spondylium simplex (Vinn and Rubel 2000 — PAPER I).

The arcthohedrids and clitambonitoids are possibly most closely related to the Order Protorthida, but their different advanced morphology of cardinalia links them also to the Order Orthida. Thus the position of Suborder Clitamboni-tidina within Rhynchonellata remains unresolved without more comprehensive phylogenetic analyses including all higher taxa of the Rhynchonelliformea.

The relationship between polytoechioids and billingselloids remains nebulous, because their fibrous shell structure links them with orthids rather than billingselloids. However, the overall morphological similarity of polytoechioids with billingselloids suggests a monophyletic clade. The fibrous shell structure in

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the polytoechioids is presumably an apomorphic feature and should be considered so, until the shell structure of all polytoechioids, especially the early representatives of the stock become better known. Thus, it is reasonable to include the polytoechioids within the billingselloids clade.

These phylogenetical relationships suggest a classification as follows:

Class Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov 1996
    Order Protorthida Schuchert and Cooper 1931
      Suborder Clitambonitidina Öpik 1934

Diagnosis (emended). Concavoconvex to convexoconcave strophic, deltidiont shells with overwhelmingly costellate ribbing and smooth or filose to imbricate concentric ornament; ventral valve predominantly with long procline to apsacline ventral interarea and arched deltidium, enclosing apical pedicle foramen; simple teeth, slightly lateral of delthyrial edges, uniting with free spondylium in juveniles, which commonly develops into form of spondylium simplex or triplex in adults; cardinal process normally simple ridge fused with strong chilidium, set on strong transverse notothyrial platform bearing widely divergent socket ridges; dorsal adductor field quadripartite to radiate; mantel canal system pinnate, rarely saccate; secondary shell fibrous, impunctate or pseudopunctate.

Superfamily Clitambonitoidea Winchell & Schuchert 1893

Diagnosis (emended). Ventral muscle field in form of spondylium simplex or triplex, shell substance impunctate or pseudopunctate.

Family Arctohedridae Williams & Harper 2000
see Williams & Harper 2000, p. 710
Family Clitambonitidae Winchell & Schuchert 1893

Diagnosis (emended). Well-developed deltidium (or rare deltidial plates) or opened delthyrium; ventral muscle field in form of spondylium simplex; dorsal adductor scars quadrate; shell substance impunctate.

    Genera assigned: *Apomatella*; *Atelelasma*; *Atelelasmoidea*; *Clinambon*; *Clitambonites* (= *Pronites*); *Hemipronites* (= *Ladogiella*); *Ilmarinia*; *Iru* Öpik; *Neumania*; *Pahlenella*; *Vellamo*.

Family Gonambonitidae Schuchert & Cooper 1931

Diagnosis (emended). Ventral muscle field commonly in form of spondylium triplex, rarely spondylium simplex; dorsal adductor scars radiating; shell substance pseudopunctate.

    Genera assigned: *Anchigonites*; *Estlandia*; *Fistulogonites*; *Gonambonites* (= *Progonambonites*); *Jaanussonites*; *Kullervo*; *Lacunarites*.

Class Strophomenata Williams, Carlson, Brunton, Holmer & Popov 1996
  Order Billingsellida Schuchert, 1893
    Suborder Billingsellidina Schuchert, 1893
      Superfamily Billingselloidea Walcott & Schuchert, 1908
      Family Tritoechiidae Ulrich & Cooper, 1936

Diagnosis (emended): Shell dorsibiconvex to ventribiconvex, impunctate, radial ornament costellate, concentric lamellae variably developed; ventral interarea apsacline to cataline with pseudodeltidium and minute supra-apical foramen; notothyrium covered by chilidial plates or chilidium; ventral interior with will developed dental plates; ventral muscle field confined mainly to the bottom of delthyrial cavity, with adductor scar completely separating diductor scars; dorsal interior with widely diverging socket plates, broad, highly raised, high, posteriorly inclined notothyrial platform and simple ridge-like cardinal process; dorsal adductor scars radially arranged; ventral mantle canals saccate or pinnate, dorsal mantle canals pinnate.

  Genera assigned: *Tritoechia*; *Admixtella*; *Eremotoechia*; *Martellia*; *Peritritoechia*; *Platytoechia*; *Pomatortrema*; *Protambonites*; *Acanthotoechia*; *Asymphylotoechia*; *Korinevskia* gen.n.

Family Polytoechiidae Öpik 1934
  Genera assigned: *Polytoechia*; ?*Antigonambonites*; ?*Raunites*.

Discussion. The Polytoechia has been linked to Antigonambonites and Raunites in two cladistical analyses using different data sets (Popov *et al.* in press — PAPER III). However, they possibly have different shell substance, at least the presence of pseudopuncta is unknown in Polytoechia. In addition, their pseudospondyliums, their most important apomorphy in cladistical analyses, have a slightly different outline, making the solution in part of these genera even more suspicious. Thus, it is reasonable they remain united, their morphological evidence provides insufficient grounds for diagnosis of the taxon.

CHAPTER 4. PALAEOBIOGEOGRAPHY AND PALAEOECOLOGY

The most remarkable characteristic in the paleobiogeographical and stratigraphical records of two superfamilies of clitambonitidines (Rubel and Wright 2000; Popov *et al.* in press — PAPER III), polytoechioids and clitambonitoids, respectively, is their different distribution patterns (Figure 1, 2).

These differences are explained by the polyphyly of clitambonitidines as supposed above (Vinn and Rubel 2000 — PAPER I).

The earliest known polytoechioid genera *Tritoechia*, *Protambonites* and *Korinevskia* gen.n. are known from the Tremadoc and were widespread in Gondwana, China, Bohemia and the southern Urals (Wright and Rubel 2000, Popov *et al.* in press — PAPER III). The first representatives of clitambonitoids are known from the early Arenig of Baltica; only the early genus *Atelelasmoidea* has no record in Baltica. Thus, the diversification of clitambonitoids in Baltica took place rapidly during the Arenig.

The palaeoecology of clitambonitidines is not well established, but two major groups are recognised (Vinn and Spjeldnaes 2000 — PAPER II), the first, having pandemic distribution, were able to live in various habitats, and the second, which was highly adapted to life on the carbonate platform with no potential to colonise districts with unfavourable environments beyond Baltica. The characteristic endemic genera are early Ordovician *Apomatella*, *Iru*, *Lacunarites*, or the late Ordovician *Ilmarinia* and *Clinambon*, all known only from the Baltica and of Baltic origin. Genera such as the early Middle Ordovician *Neumania* or late Middle to Late Ordovician genus *Kullervo* are generally pandemic and their origins were most likely outside of Baltica, possibly in the dynamic environments of micro-continents or island arcs (Vinn and Spjeldnaes 2000 — PAPER II).

CHAPTER 5. CONCLUSIONS

(1) The spondylium in clitambonitoids evolved not by the convergence of dental plates, rather derived from protorthid-like free spondylium without median septum.

(2) The polytoechiids are characterised by the presence of pseudodeltidium and supra-apical foramen.

(3) The Clitambonitidina is not monophyletic: Clitambonitoidea and Polytoechoidea are distantly related ancestors.

(4) Endemic Baltic genera such as Ilmarinia and Clinambon had a low migration potential due to possible high adaptations to specific environments related to the carbonate platform of Baltica. The pandemic genera as Neumania or Kullervo had origins outside the Baltica and had higher migration potential.

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REFERENCES

CHRISTIANSEN, J. L. & STOUGE, S. 1999. Oceanic circulation as an element in palaeogeographical reconstructions: the Arenig (early Ordovician) as an example. *Terra Nova*, 11, pp. 73–78.

COOPER, G. A. 1956. Chazyan and related Brachiopods. *Smithonian Miscellaneous Collections*, 127, pp. 1–1245, pls. 1–269.

COOPER, G. A. 1976, Lower Cambrian brachiopods from the Rift Valley (Israel and Jordan). *Journal of Paleontology*, 50, 269–289.

DALLWITZ, M. J., PAYNE & ZURCHER, E. J. 1993. 'User's Guide to the DELTA System: a General System for Processing Taxonomic Descriptions.' 4th edition. http://biodiversity.uno.edu/delta/

HALL, J., & CLARK, J. M. 1892, An Introduction to the Study of the Genera of Paleozoic Brachiopoda. *New York Geological Survey*, 8. Pt. 1:i–xvi, 1–367, pl. 1–20.

HARPER, A. T. D. 1981. The stratigraphy and faunas of the Upper Ordovician High Mains Formation of the Girvan district. *Scottish Journal of Geology*, 17, pp. 247–255.

HAVLIČEK, V. & JOSOPAIT, V. 1972. Articulate Brachiopods from the Iberian Chains, Northeast Spain (Middle Cambrian-Upper Cambrian-Tremadoc). *Neues Jahrbuch für Paleontologie und Geologie*, 140, (3): 328–353.

HAVLIČEK, V. 1977, Brachiopods of the Order of Orthida in Czehoslovakia. *Rozpravy Ústredniho Ústavu geologického*, 44, 1–328.

JAANUSSON, V. 1971. Evolution of the brachiopod hinge. 33–46. *In* Dutro, J. T. Jr (ed.). Paleozoic perspectives: a paleontological tribute to G. Arthur Cooper. Smithonian Contribution to Paleobiology, 3, 390 pp.

KOZLOWSKY, R. 1929. Les brachipodes gothlandiens de la Podolie polonaise. Paleontologia Polonica 1, 1–254.

MENAKOVA, G. N. 1991. Brakhiopody, p. 80–100. *In* M. R. Dzhalilov (ed.). Atlas iskopaemoi fauny i flory Tadzhikistana. Ordovik. Silur. Devon. Donish, Dushanbe, Tajikistan (in Russian).

NEUMAN, R. 1964. Fossils in Ordovician tuffs, Northeastern Maine. *Bulletin U. S. Geological Survey*, Washington, 1181-E, pp. 1–38, pls. 1–7.

NEUMAN, R. 1971. An early middle Ordovician brachiopod assembladge from Maine, New Brunswick, and northern Newfoundland. In J. T. Dutro Jr., ed., Paleozoic Perspectives: Paleontological Tribute to G. Arthur Cooper. Smithonian Contributions to Paleobiology 3: 113–124, 2 pl.

NEUMAN, R. 1976. Early Ordovician (late Arenig) brachiopods from Virgin Arm, New World Island, Newfoundland. Geological Survey of Canada Bulletin 261: 11–61.

ÖPIK, A. 1930. Brachiopoda Protremata der estländischen ordovizischen Kukruse-Stufe. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis)*, A 17.1., pp. 1–261.

ÖPIK, A. 1932. Über die Plectellinen. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis)*, A23, pp. 1–84.

ÖPIK, A. 1934, Über Klitamboniten. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis)*, A26, pp. 1–239.

ÖPIK, A. 1939. Brachiopoden und Ostracoden aus dem Expansusschiefer Norwegens. *Norsk Geologisk Tidsskrift*, Bd. 19, pp. 117–142.

PANDER, C. H. 1830. Beiträge zur Geognosie des Russischen Reiches. Karl Kray, St. Petersburg, 165 pp., 31 pls.

POPOV, L. E. 1992. The Cambrian radiation of brachiopods. *In* Signor (ed.) Origin and Early Evolution of the Metazoa. (New York: Plenum Press), pp. 399–423.

POPOV, L. E., HOLMER, L. M. & BASSETT, M. G. 1996. Radiation of the earliest calcareous brachiopods. *In* D. Copper and J. Jin (Eds.) Brachiopods. Proceedings of the Third International Brachipod Congress, Sudbury/Ontario, Canada. (Rotterdam: Balkema Press), pp. 209–213.

POPOV, L. E., VINN, O. & NIKITINA, O. I. (in press). Brachiopods of the family Tritoechiidae from the Ordovician of Kazakhstan. *Geobios*.

ROSS, R. J. Jr. 1970. Ordovician brachiopods, trilobites and stratigraphy in eastern and central Nevada. United States Geological Survey Professional Paper 639: 1–103, pl. 1–19.

ROZMAN, Kh. S. 1978. Brakhiopody obikalonskikh sloev [Brachiopods of Obikalon Beds.] *Akademia Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Trudy*, 97, 5–101. [In Russian].

RUBEL, M & WRIGHT, A. D. 2000. Clitambonitidina. *In*: R. L. KAESLER (ed.) Treatise on Invertebrate Paleontology, (Pt. H, Brachiopoda 3) (Kansas: Geological Society of America and University of Kansas Press, Lawrence), pp. 692–708.

SCHUCHERT, C. & COOPER, G. A. 1931. Synopsis of the brachiopod genera of the suborders Orthoidea and Pentameroidea, with notes on the Telotremata. American Journal of Sciences. Serie 5, Volume 22, pp. 241–251.

SCHUCHERT, C. & COOPER, G. A. 1932. Brachiopod Genera of the Suborders Orthoidea and Pentameroidea. Memoirs of the Peabody Museum of Natural History, Volume 4, Part 1, pp. 26–29.

SWOFFORD, D. L. 1999. Pylogenetic analysis using parsimony. Version 4b4a for PC. Computer program. Illinois Natural History Survey, Champaign, Illinois.

ULRICH, E. O. & COOPER, G. A. 1932. *Pomatotrema*. *In* SCHUCHERT, C. & COOPER, G. A eds.) Brachiopod Genera of the Suborders Orthoidea and Pentameroidea. Memoirs of the Peabody Museum of Natural History, Volume 4, Part 1, pp. 26–29

ULRICH, E. O. & COOPER, G. A. 1936. New genera and species of Ozarkian and Canadian brachiopoda. *Geological Society of America Special Paper*, 13, 323 p.

VINN, O. & RUBEL, M. 2000. The spodylium and related structures in the clitambonitidine brachiopods. *Journal of Paleontology*, 74, 439–443.

VINN, O. & SPJELDNÆS, N. 2000. Clitambonitidine Brachiopods from the Middle and Upper Ordovician of the Oslo Region, Norway. Norsk Geologisk Tidsskrift, 80, pp. 275–288.

WANG, Yu. 1955. New genera of brachiopods. *Scientia Sinica (Bejing)*, 4, (2), 327–357.

WILLIAMS, A. 1968. Evolution of the shell structure of articulate brachiopods. *Special Papers in Palaeontology*, 2, 1–55

WILLIAMS, A. 1970. Origin of laminar-shelled articulate brachiopods. *Lethaia*, 3, 329–342.

WILLIAMS, A. & CURRY, G. B. 1985. Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo. *Bulletin of the British Museum (Natural History)*, Geology Series, 38, pp. 183–269.

WILLIAMS, A. & ROWELL, A. J. 1965. Morphology. *In* R. MOORE (ed.) Treatise on Invertebrate Paleontology, (Pt. H, Brachiopoda 1) (Lawrence: Geological Society of America and University of Kansas Press), pp. H57–H138.

WILLIAMS, A., CARLSON, S. J., BRUNTON, C. H. C., HOLMER, L. E. & PO-POV, L. E. 1996. A supra-ordinal classification of the Brachiopoda. Philosophical Transactions of the Royal Society of London (series B) 351, pp. 1171–1193

WILLIAMS, A., BRUNTON, C. H. C., & MACKINNON, D. I., 1997. Morphology. *In*: R. L. KAESLER (ed.) Treatise on Invertebrate Paleontology, (Pt. H, Brachiopoda 1) (Kansas: Geological Society of America and University of Kansas Press, Lawrence), pp. 388–392.

WIRTH, E. 1936. Über *"Clitambonites" Giraldii* Martelli und *Yangtzella Poloi* Martelli aus dem Ordoviz Chinas. *Paläontologische Zeitschrift*, 18, 292–303.

WRIGHT, A. D., 1996 (a). Some morphological problems of brachiopod taxonomy. *GFF*, 118, Jubilee Issue, A62–63.

WRIGHT, A. D. 1996 (b). Taxonomic importance of the body-mantle relationships in the brachiopoda. *In* D. COPPER & J. JIN (Eds.) Brachiopods. Proceedings of the Third International Brachipod Congress, Sudbury/Ontario, Canada. (Rotterdam: Balkema Press), pp. 299–304.

WRIGHT, A. D. & RUBEL, M. 1996. A review of the morphological features affecting the classification of the clitambonitidine brachiopods. *Palaeontology*, 39, 53–75.

XU Han-kui, RONG Jia-Yu & LIU Di-yong. 1974. Brachiopoda (Ordovician). In A Handbook of the Stratigraphy and Palaeontology in Southwest China. Sciences Press. Peking. p. 144–154.

ZENG Qing-luan. 1977. Phylum Brachiopoda. In Hubei Institute of Geological Sciences and others, eds., Palaeontological Atlas of Central-South Region, Early Palaeozoic section. Beijing. p. 27–69, pl. 10–23.

SUMMARY IN ESTONIAN

Ordoviitsiumi klitambonitiidsete
käsijalgsete morfogenees ja fülogeneetlised seosed

Klitambonitiidsed brahhiopoodid on olnud juba 19. sajandist peale paleontoloogide tähelepanu objektiks. Nad kujutavad endast omapärast, suuresti Baltika paleokontinendile endeemilist käsijalgsete rühma, mis eksisteeris erandituilt Ordoviitsiumi ajastul. Klitambonitiidide karbi kasvu ja varajases arengustaadiumis olevate eksemplaride uurimisega õnnestus selgitada nende kõhtmise lihaste kinnituse ehk spondüüliumi arengulugu. Selgus, et nimetatud struktuur ei tekkinud mitte dentaalplaatide liitumise tulemusena nagu arvati varem, vaid on arenenud protortiididele iseloomulikust ilma toetava septita ehk vabast spondüüliumist. Spondüüliumiga (dentaalplaatideta) klitambonitiidide (Clitambonitoidea) selgmine lukustusmehhanism on samuti samane protortiidsete käsijalgsete hulka kuuluvate Kesk-Kambriumi vanusega arktohedriidi vastava struktuuriga. Kladistiline analüüs näitab klitambonitoidide põlvnemist protortiididest, mitte aga billingselliididest, nagu arvati varem. Seevastu dentaalplaatidega klitambonitiidid (Polytoechioidea) on oma morfoloogialt (pseudodeltiidiumi esinemine, supraapikaalne foraamen) tõepoolest lähedased bilingselliididega. Kaks ebatüüpilise ehitusega klitambonitoidide perekonda *Antigonambonites* ja *Raunites* on varases arengustaadiumis identsed polütehhioididega.

PUBLICATIONS

I

THE SPONDYLIUM AND RELATED STRUCTURES IN THE CLITAMBONITIDINE BRACHIOPODS

OLEV VINN AND MADIS RUBEL

Institute of Geology, University of Tartu, Vanemuise 46, Tartu 50090, Estonia
<vinn@ut.ee>, <rubel@ut.ee>

ABSTRACT—Development of the ventral muscle field has been studied in 12 genera of clitambonitidine brachiopods: *Eremotoechia, Clitambonites, Vellamo, Pahlenella, Lacunarites, Oslogonites, Gonambonites, Estlandia, Anchigonites, Kullervo, Antigonambonites,* and *Raunites.* The last two have a pseudospondylium instead of spondylium, which links them to polytoechiids. The spondylium of the studied genera is not derived from convergent dental plates, but develops from the free plate in the early phase of morphogenesis. The early growth stages of spondylium triplex and simplex are identical. The hypothetical ancestor of clitambonitidines with spondylium was presumably a protorthid-like brachiopod probably of the mid-Cambrian age. On the contrary, polytoechiids, as well as *Antigonambonites* and *Raunites,* may have been derived from a late Cambrian billingsellid with dental plates. The polyphyly of clitambonitidines follows from development of their ventral muscle field.

INTRODUCTION

THE RAISED ventral muscle field, called the spondylium, is common among some Palaeozoic brachiopods, e.g., the clitambonitids and the pentamerids among others. The origin of the spondylium was possibly independent in different evolutionary lineages. Following Kozlowski's (1929) terminology and interpretations, Öpik (1934) suggested that the spondylium of the clitambonitidines evolved from an ancestor with discrete dental plates. Convergence of these plates leads to formation of the spondylium supported by a median septum (spondylium simplex) or median and lateral septae (spondylium triplex).

Williams and Rowell (1965) distinguished two main types of raised ventral muscle fields in clitambonitidines, either between subparallel or convergent dental plates, and named these the polytoechiid pseudospondylium and clitambonitid-gonambonitid spondylium, respectively.

In general, the spondylium is defined by Williams et al. (1997, p. 388) as a structure formed by "convergent dental plates that united with each other in such a way as to elevate the entire ventral muscle field above the floor of the ventral valve." The purpose of this contribution is to show that the spondylium of clitambonitids and gonambonitids is formed independently of dental plates, and that except for two genera these plates do not take part in fashioning their spondylium.

MATERIAL AND METHODS

The growth patterns of the spondylium were studied in 11 clitambonitid and gonambonitid genera from the Ordovician of Estonia and the St. Petersburg Region, Russia, and one polytoechiid genus from the Ordovician of South Kazakhstan (Table 1). The adult specimens were cross-sectioned and, in two cases, *Clitambonites* and *Antigonambonites,* along the symmetrical plane of shell, taking serial plastic peels at intervals of 0.5 to 1.5 mm, according to the dimensions of specimens. The photos of the serial sections were produced directly from the peels. The juvenile shells were studied using a scanning electron microscope (SEM) at the SEM laboratory of the Institute of Geology, at the University of Oslo. The sectioned specimens, peels, and SEM samples are deposited in the collection TUG 1019 of the Geological Museum of the University of Tartu, Estonia.

THE SPONDYLIUM

Öpik (1934) assumed that the ventral valve of the juvenile *Clitambonites* must have had discrete dental plates that flanked median septum, merging during subsequent growth into a single structure, the clitambonitid spondylium or spondylium simplex.

However, the real juvenile ventral valves of *Apomatella ingrica* and *Oslogonites* sp. as well as ontogenetic changes studied by sectioning ventral valves of 11 genera suggest a different mode of spondylium formation in the clitambonitid, kullervoid, and most gonambonitid genera. The last have a spondylium fashioned by anteromedian growth of apical plate, which makes possible the attachment of adductors and diductors.

The smallest juvenile ventral valves of *Apomatella ingrica* have an extremely simple, nearly dorsally directed and uplifted concave thickening with a concave anterior margin in the delthyrial cavity (Fig. 1.1, 1.2, 1.4, 1.6, 1.10). It is difficult to determine whether the thickening extending from the teeth and following the ventral muscle field, slightly elevated, is connected to the dental plates. During growth the thickening turns more ventrally and grows farther as a plate at a constant angle to the interarea, forming an apical plate free of septal support. Popov (1992, p. 417) referred to an analogous structure in the protorthids as a free plate. The median septum develops under such a spondylium in later growth stages and is well defined in the adult specimens.

Rare juvenile specimens of *Oslogonites* sp. show a similar scenario for the formation of the spondylium in early ontogeny. The early spondylium of juvenile *Oslogonites* (Fig. 1.5, 1.7, 1.11) has a concave anterior edge and no dental plates, as does the juvenile *Apomatella.* The median septum of *Oslogonites* develops earlier than the lateral septa under its spondylium. The juvenile stages of the sectioned clitambonitids *Clitambonites, Vellamo, Clinambon, Pahlenella,* and *Lacunarites* show no evidence of either discrete dental plates or converging dental plates (Fig. 1.18). The early growth stages of their spondylia are assumed to be similar to those in juvenile specimens of *Apomatella ingrica,* described above.

A spondylium of *Clitambonites schmidti* figured by Öpik (1934, pl. 3, fig. 1) appears to be markedly different from the spondylia of the other species of the genus. The spondylium however, can be considered an extreme case, with its base fused with the valve floor and its sides resembling discrete dental plates.

A spondylium with a weak median septum but concave anterior edge, like in some juvenile *Apomatella,* is observable in immature specimens of *Clitambonies schmidti* (Öpik 1934, fig. 33). With some exceptions e.g., *Clitambonites schmidti* and *Hemipronites,* the concave anterior edge of the spondylia in the early stages of ontogeny then develops, into a tongue like anterior margin in the adult stages of *Clitambonites, Vellamo, Clinambon, Ilmarinia, Atelelasma,* and *Pahlenella.*

II

TABLE *1*—The list of specimen used for serial sectioning or SEM studies. According to the classification by Williams and Rowell (1965): Clit., *Clitambonitidae*; Gon., *Gonambonitidae*; Kull., *Kullervoidae*; Polyt., *Polytoechidae*.

Species, family	Museum numbers of specimen	British series	Locality
Apomatella ingrica Pahlen (juvenile), Clit.	TUG 10119/1–1019/2	Arenig	Lava River, Ingerland, Russia
Pahlenella sp., Clit.	TUG 1019/6	Llanvirn	North Estonia
Clitambonites adcendens Pander, Clit.	TUG 1019/7	Caradoc	Kiviôli, north-east Estonia
Vellamo aenigma Ôpik, Clit.	TUG 1019/16	Caradoc	North Estonia
Oslogonites sp. (juvenile), Gon.	TUG 1019/3–1019/4	Arenig	Lava River, Ingerland, Russia
Oslogonites sp.	TUG 1919/11	Llanvirn	Harku, North Estonia
Antigonambonites planus Pander, Gon.	TUG 1019/9	Arenig	Lynna River, Ingerland, Russia
Raunites janishewsky Lesnikowa, Gon.	TUG 1919/8	Arenig	Lynna River, Ingerland, Russia
Gonambonites sp., Gon.	TUG 1019/13	Llanvirn	North Estonia
Estlandia sp., Gon.	TUG 1019/5	Llanvirn	North Estonia
Lacunarites sp., Gon.	TUG 1019/14	Llanvirn	Lynna River, Ingerland, Russia
Anchigonites sp., Gon.	TUG 1019/12	Llanvirn	Lynna River, Ingerland, Russia
Kullervo sp., Ôpik, Kull.	TUG 1019/15	Caradoc	Kiviôli, north-east Estonia
Eremotoechia sp., Polyt.	TUG 1019/10	Caradoc	South Betpak-Dala, Kazakhstan

The spondylium of the gonambonitids *Oslogonites*, *Kullervo*, *Gonambonites*, *Estlandia*, *Anchigonites*, *Antigonambonites*, *Lacunarites*, and *Raunites* has been sectioned to study its formation, including development of lateral septa, the diagnostic component of spondylium triplex. All these genera, except for *Antigonambonites* and *Raunites*, form their early spondylium as described above, i.e., without structures that can be associated with dental plates (Figs. 1.12, 1.13, 1.16, 1.20, 2.1, 3.1, 3.2). It is noteworthy that the lateral septa of such spondylia appear after this early stage but with a weak medium septum. The lateral septa appeared just below the teeth in the manner of dental plates (Figs. 2.2, 2.3, 2.5, 3.4, 3.5). They grow slightly medially towards the valve floor until fusing with vascular ridges of the valve floor as with *Anchigonites* (Fig. 2.4) and *Estlandia* (Fig. 1.15) or, alternatively, remaining rudimentary throughout ontogeny as with *Kullervo* (Fig. 2.8). For the latter the low lateral septa reach the valve floor only in the umbonal region (Ôpik, 1934). The rudimentary lateral septa of *Oslogonites* do not reach the valve floor anywhere. In *Gonambonites* (Fig. 2.6) the lateral septae are not always developed, but occur sporadically in some species.

The longitudinally-sectioned ventral valves of *Clitambonites adscendens* show stepwise growth of spondylium. Each growth lamella seems to be added only anteriorly (Fig. 1.3). The lack of any other secretion on the anterior half of the spondylium floor shows unambiguously that most of this space (spondylium) was occupied by the body (coelomic) cavity. Exceptionally, the deltidium as well as its continuation on the base of the spondylium around the pedicle (including Ôpik's *pulvillus*) constitute an area of additional secretion.

THE PSEUDOSPONDYLIUM

The ventral valve of *Antigonambonites* and *Raunites* differs from the other gonambonitids and clitambonitids described above. The dental plates in *Antigonambonites* and *Raunites* are developed from their earliest growth stage while their ventral muscle fields between dental plates were elevated later during ontogeny as a pseudospondylium (Figs. 1.8, 1.9, 1.12, 1.16, 1.20, 3.4, 3.6–3.8). The earliest growth stages of latter genera strongly resemble those of polytoechiids such as *Eremotoechia* or *Tritoechia* with respect to their ventral muscle fields (see Figs. 1.8, 1.19, 1.13, 3.4–3.6).

Thus, in medium-sized specimens of *Antigonambonites planus* and *Raunites* sp., the ventral muscle field between the dental plates is lifted up from the valve floor only marginally, having a sessile adductor field or even wider area (Figs. 1.9, 1.16, 3.7, 3.8). Only in some (gerontic) specimens of these genera (*Antigonambonites* and *Raunites*) is their ventral muscle field entirely lifted up as a discrete plate (Fig. 1.12, 1.20), supported medially by a septumlike thickening.

The presence of discrete dental plates and partly or entirely raised ventral muscle fields in *Antigonambonites* and *Raunites* can be unambiguously identified as a polytoechiid pseudospondylium sensu Williams and Rowell (1965), or simply as a pseudospondylium.

FUNCTIONAL AND EVOLUTIONARY IMPLICATIONS

The juvenile stages of the *Apomatella ingrica* described above give some indication of the ancestor of clitambonitidines as well as a possible solution for the task of retaining an effective operating muscle system in case of strongly convex ventral shells. Such an ancestor had to have considerably high and catacline ventral interarea flanked by keellike teeth (Fig. 1.14) but without any supporting structures that could be considered dental plates (Fig. 4). However, the muscles had to lengthen with the heightening of interarea during the growth of such shell. When muscles reached a crucial length, one solution to grow shell further in the same way could have seen to keep the efficient distance by
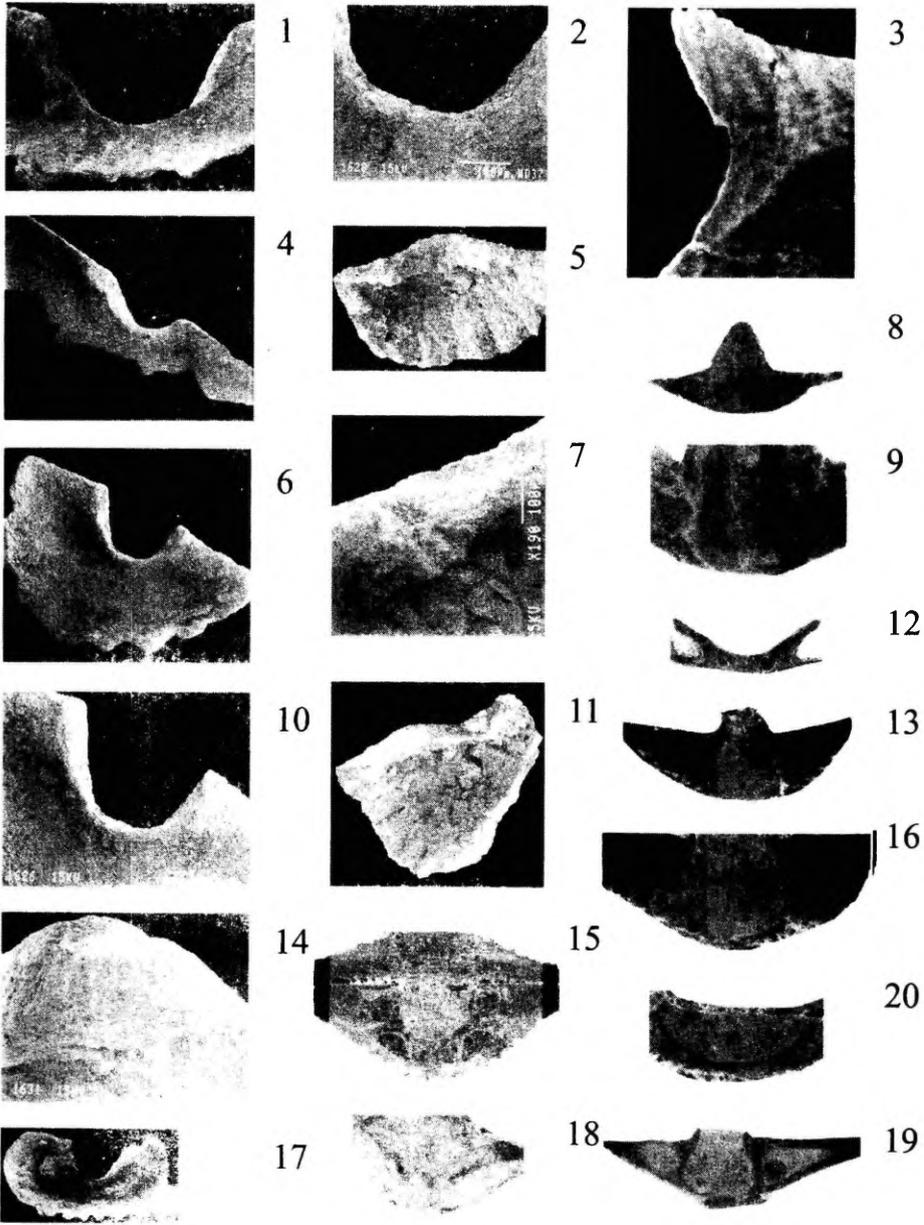
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FIGURE 2—*1–2, Oslogonites* sp., TUG 1019/11; *1*, cross-section through the spondylium simplex growth stage in umbonal region of the valve, note the lack of lateral septae, ×13; *2*, cross-section through the spondylium triplex at the mid-length, note the rudimentary lateral septae under the teeth, ×8. *3–4, Anchigonites* sp., TUG 1019/12; *3*, cross-section through the spondylium triplex at mid-length, ×13; *4*, cross-section through the anterior region of spondylium triplex, ×11. *5, Olsogonites* sp., cross-section through the anterior region of spondylium triplex, TUG 1019/11, ×10. *6, Gonambonites* sp., cross-section through the anterior region of spondylium simplex, TUG 1019/13, ×4. *7, Lacunarites* sp., cross-section through the anterior region of spondylium simplex, TUG 1019/14, ×8. *8, Kullervo* sp., cross-section through the spondylium simplex at the mid-length TUG 1019/15, ×6.

lifting up the sites of muscle attachments. In other words, the origin of spondylium appears to be an adaptation associated with shells having a high cataclne ventral interarea.

Indeed some Mid-Cambrian protorthids possess a free plate or free spondylium and no dental plates, which evidently did not develop until the Late Cambrian (Cooper, 1976; Havlíček, 1977; Wright, 1996). Thus, one could compare the protorthid delthyrial plate with the early stages of the clitambonitid spondylium described above. Then the origin of free spondylium extends back to the Mid-Cambrian, i.e., well before dental plates began to evolve in billingsellids.

The expected ancestral morphology of polytoechiids together with *Raunites* and *Antigonambonites* strongly resemble that of billingsellids. There is an aberrant member, *Arctohedra*, among the Mid-Cambrian protorthids, which has "advanced" cardinalia and ventral free plate. The presence of an anteriorly-widened median furrow on the free plate of *A. austrina* has been interpreted as the preserved muscle track, evidence that the plate functioned as a muscle platform (Brock, 1998, p. 615). Due to the "advanced" nature of cardinalia of the genus, Popov (in Popov et al., 1996) has recently suggested that *Arctohedra* might not be a true protorthid but a core taxon of a separate family. The similar outline of the free plate in *Arctohedra* and juvenile *Apomatella* (see Fig 1.17 and 1.5, 1.6), but also the "advanced" nature of cardinalia in the former genus indicate that *Arctohedra* could well be the core taxon for one part of clitambonitidines.

The billingsellids have been considered probable ancestors for clitambonitidines. This is possible, but only for polytoechiids, *Antigonambonites* and *Raunites* i.e., for clitambonitidines with the dental plates. The origin of dental plates in the polytoechiids

as well as in *Antigonambonites* and *Raunites* can be considered an adaptation to the more or less flat shell, with long and apsacline ventral interarea to strengthen the articulation mechanism via supporting teeth. Such shells, are weakly convex enable the muscles to be effective throughout life. The origin of raised muscle fields between dental plates on the pseudospondylium is presumably the result of the same growth mechanism and functions as those of a true spondylium, i.e., to ensure an effective length for columnar adductors-diductors during growth of the shell.

The main differences between the spondylium and pseudospondylium lie in the presence or absence of discrete dental plates in the ancestor, rather than in the growth mechanism generating the lifted ventral muscle platform. Thus the only reasonable way to have true spondylia is to derive it from an ancestor with dental plates where the apsacline ventral valve of the ancestor transformed into a cataclne form, simultaneously losing its dental plates.

In gonambonitids the lateral septae of the spondylium triplex reaching the valve floor, as with Estlandia and Anchigonites, may have had a strengthening function for the wide and flat spondylium. However, the lateral septa, separating the vascula genitalia from the vascula media, may well have evolved due to developments in the vascular system of the ventral mantle (Williams et al., 1997). The growth mechanism of lateral septa is supposed here to be similar to that of dental plates.

CONCLUSIONS

1) *Raunites* and *Antigonambonites* have a pseudospondylium

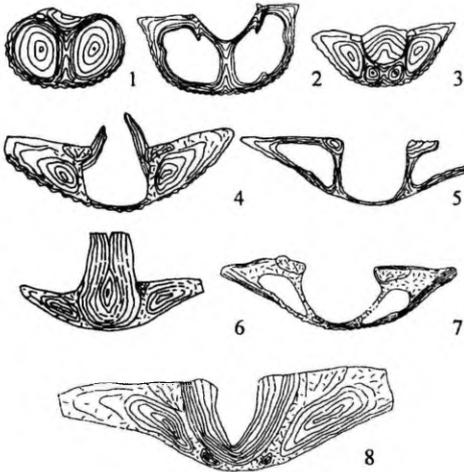2) In the earliest growth stages, the spondylium triplex and simplex pass through an identical free plate states.
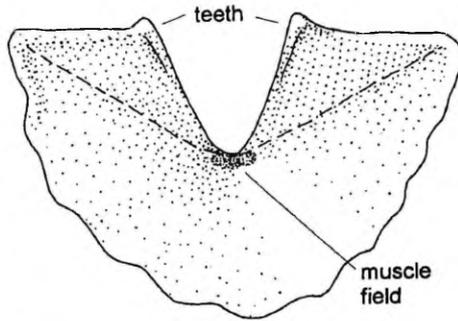
FIGURE 4—Stylized view of the ventral interior of the hypothetical precursor of clitambonitidines with spondylium and the other brachiopods with the ventral free plate.

FIGURE 3—Morphogenesis of the spondylium triplex (*1–3*), pseudospondylium (*4, 6–8*), and structure of ventral muscle field confined to the valve floor (*5*). *1*, Spondylium simplex, *Oslogonites* sp. (TUG 1019/11); cross-section taken at 0.5 mm from beak of ventral valve; at 15×. *2*, Immature spondylium triplex in *Oslogonites* sp. (TUG 1019/11); cross-section taken at 0.5 mm from beak of ventral valve; at 12×. *3*, Mature spondylium triplex in *Anchigonites* sp. (TUG 1019/12); cross-section taken at 2.5 mm from beak of ventral valve; at 10×. *4*, Ventral muscle field confined to the valve floor in juvenile *Antigonambonites planus* (TUG 1019/9); cross-section taken at 0.5 mm from beak of ventral valve; at 20×. *5*, Ventral muscle field confined to the valve floor in adult *Eremotoechia* sp. (TUG 1019/10); cross-section taken at 5.0 mm from beak of ventral valve; at 10×. *6*, Ventral muscle field confined to the valve floor in juvenile *Raunites janishewsky* (TUG 1019/8); cross-section taken at 0.5 mm from beak of ventral valve; at 18×. *7*, Pseudospondylium in adult *Antigonambonites planus* (TUG 1019/9); cross-section taken at 8.0 mm from beak of ventral valve; at 8.5×. *8*, Pseudospondylium in adult *Raunites janishewsky* (TUG 1019/8); cross-section taken at 9.0 mm from beak of ventral valve; at 10.0×.

REFERENCES

BROCK, G. A. 1998. Middle Cambrian articulate brachiopods from the southern New England Fold Belt, north eastern N. S. W., Australia. Journal of Paleontology, 72:604–619.

COOPER, G. A. 1976. Lower Cambrian brachiopods from the Rift Valley (Israel and Jordan). Journal of Paleontology 50:269–289.

HAVLÍČEK, V. 1977. Brachiopods of the Order of Orthida in Czechoslovakia. Rozpravy Ústředního Ústavu geologického, 44:1–328.

KOZLOWSKI, R. 1929. Les brachiopodes gothlandiens de la Podolie polonaise. Palaeontologia Polonica, 1:1–254.

ÖPIK, A. 1934. Über Klitamboniten. Acta et Commentationes Universitatis Tartuensis (Dorpatensis), A26, 239 p.

POPOV, L, YU. 1992. The Cambrian radiation of brachiopods, p. 399–423. *In* P. W. Signor (ed.), Origin and Early Evolution of the Metazoa. Plenum Press, New York.

——, L. M. HOLMER, AND M. G. BASSETT. 1996. Radiation of the earliest calcareous brachiopods, p. 209–213. *In* P. Copper and J. Jin (eds.), Brachiopods: Proceedings of the Third International Brachipod Congress, Sudbury/Ontario, Canada. Balkema Press, Rotterdam.

WILLIAMS, A., AND A. J. ROWELL. 1965. Morphology, p. H57–H138. *In* R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Part H, Brachiopoda 1. Geological Society of America and University of Kansas Press, Lawrence.

——, C. H. C. BRUNTON, AND D. I. MACKINNON. 1997. Morphology, p. 388–392. *In* R. L. Kaesler (ed.), Treatise on Invertebrate Paleontology, Part H, Brachiopoda 1. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

WRIGHT, A. D. 1996. Some morphological problems of brachiopod taxonomy. Geologiska Föreningen Förhandlingar 118 Jubilee Issue, A62–63.

——, AND M. RUBEL. 1996. A review of the morphological features affecting the classification of the clitambonitidine brachiopods. Palaeontology, 39:53–75.

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3) The growth patterns of the clitambonitid spondylium with lateral septa (spondylium triplex) and pseudospondylium in mature growth stages are supposed to be identical in terms of secretion activity of the mantle. Thus, the only difference between the lateral septa in the gonambonitids and the dental plates of polytoechiids is not in morphology, but simply in the different time of activation of the morphogenetic mechanisms in ontogeny, responsible for development of these structures.

4) Clitambonitid spondylia evolved in highly convex shells are adaptations to the shape of shell in order to optimise the length of the diductor and aductor muscles.

5) Dental plates evolved in weakly convex shells with the apsacline ventral valve as an adaptation to shell shape in order to strengthen the articulation mechanism.

II

Clitambonitoid Brachiopods from the Middle and Upper Ordovician of the Oslo Region, Norway

OLEV VINN & NILS SPJELDNÆS

Nine species of clitambonitoid brachiopods have been described from the Middle and Upper Ordovician of the Oslo Region, Norway. They include, *Hemipronites*? sp., *Clitambonites schmidti, Clinambon anomalus, Ilmarinia dimorpha, Vellamo oandoensis, Kullervo hibernica, Kullervo* aff. *parva, Kullervo* aff. *punctata* and *Kullervo* cf. *lacunata*. The palaeobiogeography and palaeoecology of the Upper Ordovician clitambonitoid brachiopods are discussed. The species found in the northern and western parts of the Oslo Region are mostly related to those of the Baltic carbonate platform, despite surprisingly large differences in lithology. The foreland basin (the Oslo-Scania confacies belt of Jaanusson & Bergström, 1980) has a different fauna, dominated by pandemic species of *Kullervo*. This genus is supposed to have developed in parallel in Avalonia (pandemic species and the North American species) and Baltica (all endemic species to Baltica), from an early kullervo of either Baltic or Avalonian origin. The rapid spread of the genus in the North Atlantic area is linked – in time – to the large bentonite in the Middle Caradocian.

Olev Vinn, Institute of Geology, University of Tartu, Vanemuise 46, 50090 Tartu, Estonia (e-mail: vinn@ut.ee); Nils Spjeldnæs, Department of Geology, University of Oslo, P.O. Box 1047, Blindern, N-0316 Oslo, Norway (e-mail: nils.spjeldnas@geologi.uio.no)

Introduction

The Lower Ordovician clitambonitoids of the Oslo Region (Fig. 1) are well known and have been described, among others, by Öpik (1939); much less studied are those of the Upper Ordovician. However, one of the authors (N. Spj.) has studied them sporadically as a continuation of the "*Chasmops*" project (cf. Størmer 1953, pp. 38–41). Because of the small number of specimens and the lack of comparative material, progress was slow until establishment of the present cooperative venture.

The few references to clitambonitoids from the Upper Ordovician of the Oslo Region include: "*Clitambonites* cf. *schmidti*" of Størmer (1953, p. 64), from what is now the Arnestad Formation at Slependen in Asker and which is a specimen of *Kullervo*. Opalinski & Harland (1981) mentioned (based on information from Spjeldnæs) *Vellamo* sp. (*V. oandoensis*) from the Mjøsa Formation. Spjeldnæs (1982, p. 156) mentioned *Kullervo* from Furuberget in the Hamar–Nes District (Mjøsa), and the migrations of *Kullervo* were discussed by Spjeldnaes (1978, pp. 142, 145; and 1984, p. 223). Finally, Owen et al. (1990, p. 22) noted *Kullervo* cf. *lacunata* Öpik – determined by D. A. T. Harper – from the Arnestad Formation in the Oslo–Asker District (Fig. 2).

As is usual in the Oslo Region Ordovician, much of the material is preserved as moulds, but the photographic figures are based mostly on latex replicas, in order to facilitate comparisons with the better preserved Estonian and American material.

In the present paper, the focus is on the taxonomy and ecology of Norwegian Upper Ordovician clitambonitoids, as well as on their palaeobiogeography and stratigraphical distribution within the Baltica and beyond. The term Middle Ordovician is used here for the interval from the base of *Tripodus laevis* conodont Biozone to the top of *Nemagraptus gracilis* graptolite Biozone, or in terms of Baltic stages from Volkhovian to upper Uhakuan (Webby 1998).

Systematic descriptions

Repositories. – All the specimens used in this study belong to the Palaeontological Museum, University of Oslo (PMO).

Abbreviations appearing in the text are as follows: L = maximum length, W = maximum width. All measures are in mm.

Suborder Clitambonitidina Öpik, 1934

Superfamily Gonambonitoidea Winchell et Schuchert, 1895

Family Kullervoidae Öpik, 1934

Genus *Kullervo* Öpik, 1932

Remarks on occurrence

One of the most perplexing observations in this study is the high number of sympatric species of *Kullervo* (in Fangberget 2, in Arnestadtangen 2, in Bratterud 3, and in even Billingstad 4). According to the current species criteria for *Kullervo*, there are distinct categories in the

ORDOVICIAN
OUTCROPS
OF THE OSLO REGION
AND
ADJACENT DISTRICTS

50 km

PRECAMBRIAN
OUTSIDE
OSLO REGION

ORDOVICIAN
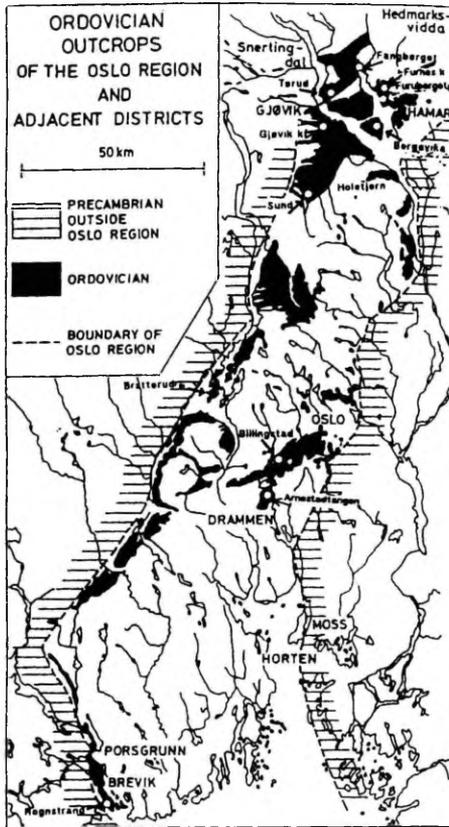
BOUNDARY OF
OSLO REGION

Fig. 1. Locality map of the Oslo Region showing the main localities of Middle and Upper Ordovician clitambonitoids.

material present. This can be explained in two ways: either there may have been ecological niches, not recorded in the sediments, and not seen in the rest of the genera of brachiopods, with separate *Kullervo* species, or the presently used species concept of *Kullervo* is not really valid, and the species are much more variable than previously supposed.

Further studies on the variability in larger – as yet unavailable – populations of *Kullervo* are needed to resolve this problem.

Kullervo hibernica Harper, 1952

Figs. 4, A–P, 5J–M, X; 6A–G.

1952 *Kullervo hibernica* n.sp. – Harper, pp. 100–101, pl. 6,

figs. 6,7. 1980 *Kullervo* sp. – Hiller, p. 171, fig. 239. 1994 *Kullervo* aff. *hibernica* – Parkes, p. 154, pl. 9, figs. 6, 9.

Material. – One shell (PMO 162.085, L = 9.0, W = 16.0;), four dorsal valves (PMO 162.079, L = 13.0, W = 17.0; PMO 162.068, L = 11.5, W = 15.0), eight ventral valves (PMO 162.080, L = 17.0, W = 20.0; PMO 162.081, L = 14.0, W = 14.0; PMO 162.088, L = 17.0, W = 19.0; PMO 162.089, L = 0.??? W = 16.0; PMO 162.091, L = 14.0, W = 16.0), two moulds of the ventral exteriors, one ventral interior (PMO 162.087), five dorsal interiors (PMO 162.069; PMO 162.090, L = 14.0, W = 11.5) and probably one mould of the ventral interior.

Locality and horizon. – Ventral valves from the Arnestad Formation (Caradoc) at Bratterud in Ringerike. Dorsal interior and exterior from the Arnestad Formation at Billingstad and Arnestadtangen in Asker, from the Furuberget Formation at Fangberget Nord in Ringsaker, and from the same formation at Furuberget in the Hamar–Nes District, and from Sund, at Einavann in the southernmost part of the Toten District, in beds with *Scopelochasmops conicopthalmus*, probably corresponding in age to the upper part of the Arnestad Formation, and possibly also partly to the, Furuberget Formation (Caradoc, Upper Ordovician).

Description. – Shell subpentagonal, mature specimens 60–90% as long as wide with the maximum width at midlength, immature specimens usually as long as wide with the maximum width at the hingeline, but also not remarkably less wide at mid-length of the shell. Anterior commissure gently sulcate, anterior margin straight or gently rounded. Cardinal extremities obtuse to acute, sides posterolaterally straight or slightly concave.

Radial ribs bifurcating, in maximum with two branchings, on average five ribs per 5 mm along the anterior margin in the adult specimens. Number of primary ribs 7–9 in ventral valve and 6–9 in dorsal valve. Lateral sectors without or with the weakly developed radial ribs clearly subordinate to the concentric ornament.

The whole shell is covered with fine, on average 0.2 mm wide, evenly spaced concentric ridges. In the dorsal valve the concentric ridges become gradually more closely spaced in the postero-anterior direction. Frequency of the ridges per 5 mm of valve length, measured medianly anterior to the 5 mm growth stage, is 7–10 in ventral valves and 14–25 in the dorsal valves.

Ventral valve strongly convex, with flat to curved surface in the lateral profile, one specimen (PMO 162.080) is unevenly convex, subcarinate, the low median fold originating about mid-length in the same slightly more than 1/3 as wide as shells width.

Ventral interarea of long, triangular to subtriangular, flat to gently concave, apsacline, about 70% as long as wide. Delthyrium about 30–45% as wide as hingeline and about 50–90% as wide as long. Deltidium long, almost flat to moderately convex, projecting 0.6–1.4 mm away from the
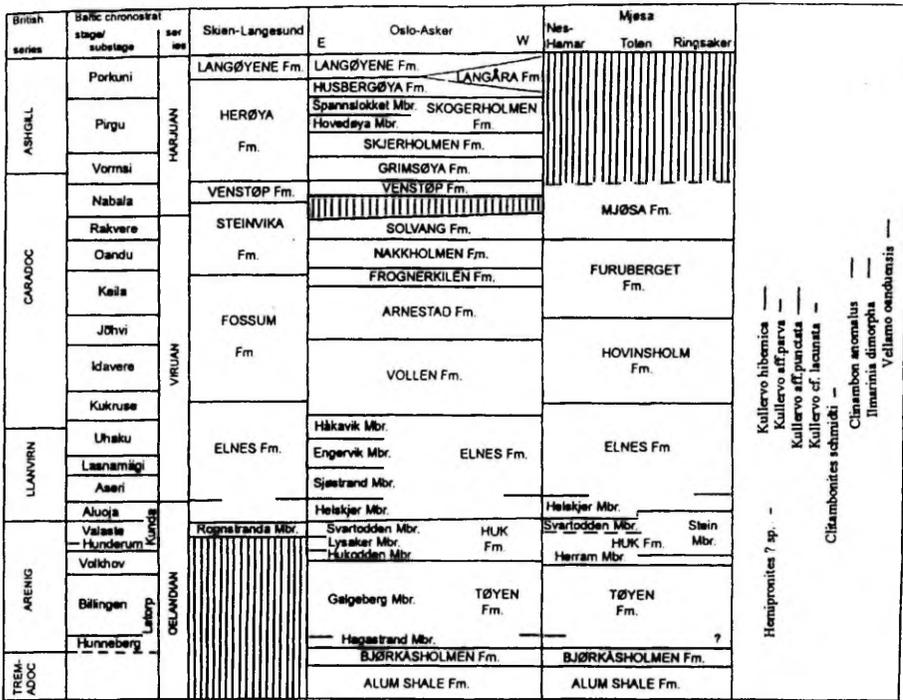
British series	Baltic chronostrat stage/substage	ser ies	Skien-Langesund	Oslo-Asker (E ... W)	Nes-Hamar / Mjøsa (Toten, Ringsaker)
ASHGILL	Porkuni	HARJUAN	LANGØYENE Fm.	LANGØYENE Fm. / HUSBERGØYA Fm. / LANGÅRA Fm.	
	Pirgu		HERØYA Fm.	Spannslokket Mbr. / Hovedøya Mbr. SKOGERHOLMEN Fm. / SKJERHOLMEN Fm.	
	Vormsi			GRIMSØYA Fm.	
CARADOC	Nabala	VIRUAN	VENSTØP Fm.	VENSTØP Fm.	MJØSA Fm.
	Rakvere		STEINVIKA Fm.	SOLVANG Fm.	
	Oandu			NAKKHOLMEN Fm.	FURUBERGET Fm.
	Keila			FROGNERKILEN Fm.	
	Jõhvi		FOSSUM Fm	ARNESTAD Fm.	
	Idavere			VOLLEN Fm.	HOVINSHOLM Fm.
	Kukruse				
LLANVIRN	Uhaku		ELNES Fm.	Håkavik Mbr.	ELNES Fm
	Lasnamägi			Engervik Mbr. ELNES Fm.	
	Aseri			Sjøstrand Mbr.	
	Aluoja	KUNDA	Rognstranda Mbr.	Helskjer Mbr.	Helskjer Mbr.
ARENIG	Valaste–Hunderum			Svartodden Mbr. HUK Fm. / Lysaker Mbr. / Hukodden Mbr.	Svartodden Mbr. / HUK Fm. Stein Mbr. / Herram Mbr.
	Volkhov	OELANDIAN			
	Billingen			Galgeberg Mbr. TØYEN Fm.	TØYEN Fm.
	Hunneberg			Hagastrand Mbr.	?
TREM-ADOC				BJØRKÅSHOLMEN Fm.	BJØRKÅSHOLMEN Fm.
				ALUM SHALE Fm.	ALUM SHALE Fm.

Biostratigraphical distribution of clitambonitoids (right-hand columns): Hemipronites ? sp.; Kullervo hibernica; Kullervo aff. parva; Kullervo aff. punctata; Kullervo cf. lacunata; Clitambonites schmidti; Clinambon anomalus; Ilmarnia dimorpha; Vellamo oanduensis.

Fig. 2. Stratigraphical units (Owen et al. 1990; Webby 1998) and biostratigraphical distribution of clitambonitoids in the Middle and Upper Ordovician of the Oslo Region.

surface of the interarea. Foramen moderate to large, rounded, functional, subapical, with diameter of 1.0–2.0 mm, in smaller specimen just in the middle of deltidium, about 2.0 mm from the apex in two complete valves (PMO 162.080; 162.081) (Fig. 3C).

Dorsal valve considerably flatly convex, with the moderate to wide shallow sulcus originating in the umbonal part of valve, on average half as wide as valve, bounded by gently convex flanks with flattening over lateral extremities. Dorsal sulcus about one-third as wide as the valve width anteriorly. Dorsal interarea short relative to valve length, nearly cataline to slightly anacline, notothyrium 3/4 covered by gently convex chilidium, projecting 1.1 mm away from surface of interarea (PMO 162.068).

Ventral interior with the spondylium triplex with hemisyrinx (Fig. 3B). The lateral septa of spondylium extending valve floor in the umbonal part of the valve.

Cardinal process prominent. Socket walls divergent about two times as wide as long, merging anteromedianly with the notothyrial platform, continuing laterally from the sockets in the form of narrow, low, posteriorly incurved

ridges which surround sockets latero-anteriorly, extending nearly cardinal extremities. Median ridge emerging from notothyrial platform, posteriorly slightly lower than platform, highest and widest at mid-length of valve. About at the mid-length of the valve the median ridge tapers into a thin, low median septum, reaching anteriorly two-thirds valve length. Dorsal adductor field subpetaloid, impressed on shell floor, extending to about two-thirds valve length. Anterior adductor scars tongue-shaped, slender, longer, but seem to be slightly smaller than posterior ones, with the strongly raised anteriors. The posterior adductor scars subtriangular, between anterior scars and socket walls.

Discussion. – The Norwegian specimens described can be identified with *K. hibernica* on the basis of its holotype, the dorsal valve, with nearly identical interior. The type species is described from the Knockerk House Sandstone Member of Lower Caradoc Knockerk Formation at Grangegeeth, Ireland (Harper 1952; Romano 1980).

The Norwegian material is better preserved than the type one. However, the incomplete nature of the holotype does not enable comparison of all characters, especially in
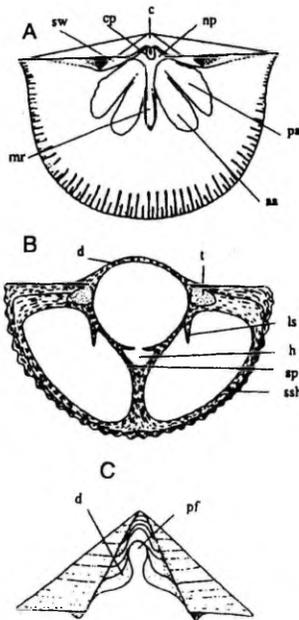
Fig. 3. A. Generalized illustration of the dorsal valve of the kullervos showing typical morphological features to the *Kullervo hibernica*. **aa** – anterior adductor scars, **c** – chilidium, **cp** – cardinal process, **mr** – middle ridge, **np** – notothyrial platform, **pa** – posterior adductor scars, **sr** – subperipheral rim, **sw** – socket ridge. B. Section through spondylium triplex of the pedicle valve of *Kullervo* aff. *punctata*, **d** – deltidium, **h** – hemisyrinx, **ls** – lateral septum, **sp** – spondylium, **ssh** – secondary shell, **t** – tooth. C. Stylized reconstruction of the pedicle foramen of immature *Kullervo hibernica*, illustrating the possible forming of subapical foramen, **d** – deltidium, **pf** – pedicle foramen.

the part of cardinalia and the ventral valve. The only difference is in the length of the thin median septum, which is longer in the holotype (NMING: F14034; Parkes 1994, p. 154, pl. 9, fig. 18), but it could also be result of the mode of preservation. The rest of the specimens described by Parks (1994, p. 154, pl. 9) as *K.* aff. *hibernica* have not been included in the synonymy list here, mostly because the characters typical for the species were not sufficiently recognizable on the photographs.

The incomplete specimen described by Hiller (1980, p. 171, fig. 239) from the upper part of the Dolhir Formation (middle Ashgill) of the Glyn Ceiriog District, north Wales, is assigned to species because of the ornamentation and outline, being typical for *K. hibernica*. *Kullervo* aff. *parva* Figs. 4Q–Y

Material. – Two ventral valves (PMO 162.074, L = 12.5, W = 11.0; PMO 162.077) and one dorsal valve (PMO 162.078, L = 11.0, W = 14.5). One mould of the dorsal

interior (PMO 162.075), and a mould of the ventral interior (PMO 162.076).

Locality and horizon. – Billingstad, Asker; Arnestad Formation, just below big (Kinnekulle) bentonite, (Upper Ordovician).

Description. – Shell ventribiconvex, clearly subpentagonal in outline, on average 90% as wide as long, with the maximum width along the hingeline. Anterior margin straight, commissure sulcate. Cardinal extremities acute. Sides usually nearly straight, becoming gently concave posteriorly.

Radial ribs bifurcating, 11 ribs per 5 mm along anterior margin in the ventral valve and 13 in dorsal valve. Number of primary ribs in umbonal area 6–7. The ribs are lacking or less developed on cardinal extremities.

Concentric ridges cover whole shell, 4–15 per 5 mm of valve length, measured medianly anterior to 5 mm growth stage, in two ventral valves.

Ventral valve strongly convex in lateral profile, convex and medianly flat in transverse profile, with faint sulcus originating umbonally. Ventral interarea long triangular, moderately to strongly apsacline, concave in lateral profile, about half as wide as long. Delthyrium about 40% as wide as the hingeline and about 75% as wide as long. Deltidium convex, projecting 1.2 mm away from surface of interarea. Foramen small, functional in two specimens studied; apical when entirely open (PMO 162.077), or slightly subapical (PMO 162.074) when partially filled by secondary shell, with the diameter of 1.0 mm.

Dorsal valve strongly convex in both profiles with sulcus originating umbonally. Dorsal interarea long (about 2.5 mm), moderately anacline, flat. Chilidium gently convex, with W shaped distal edge.

Ventral interior with spondylium triplex. Subspondylial lateral septa rudimentary, reaching the valve floor in umbonal part.

Cardinal process thin, plate-like, continuous with the chilidium. Socket walls divergent, about three times as wide as long, extending slightly further than half valve width, proceeding antero-laterally from the sockets in form of a narrow posteriorly incurved ridges, reaching nearly the four-fifths valve width. Socket walls merge anteromedianly with the notothyrial platform. Median ridge weakly developed, slender, long, posteriorly half as wide as socket walls, continuous with the notothyrial platform, but clearly lower, extending to the margin of the adductor field. Notothyrial platform triangular. Dorsal adductor field subpetaloid, impressed on floor of the shell, extending to about three-fourths valve length. The anterior adductor scars gently divergent, less divergent than posterior pair. Anterior pair of the adductor scars slightly greater, steeper, clearly longer, and more strongly expressed than posterior pair, with the gently raised anteriors.

Discussion. – *K. parva* was originally described by Cooper (1956) from the Effna and Edinburgh formations in
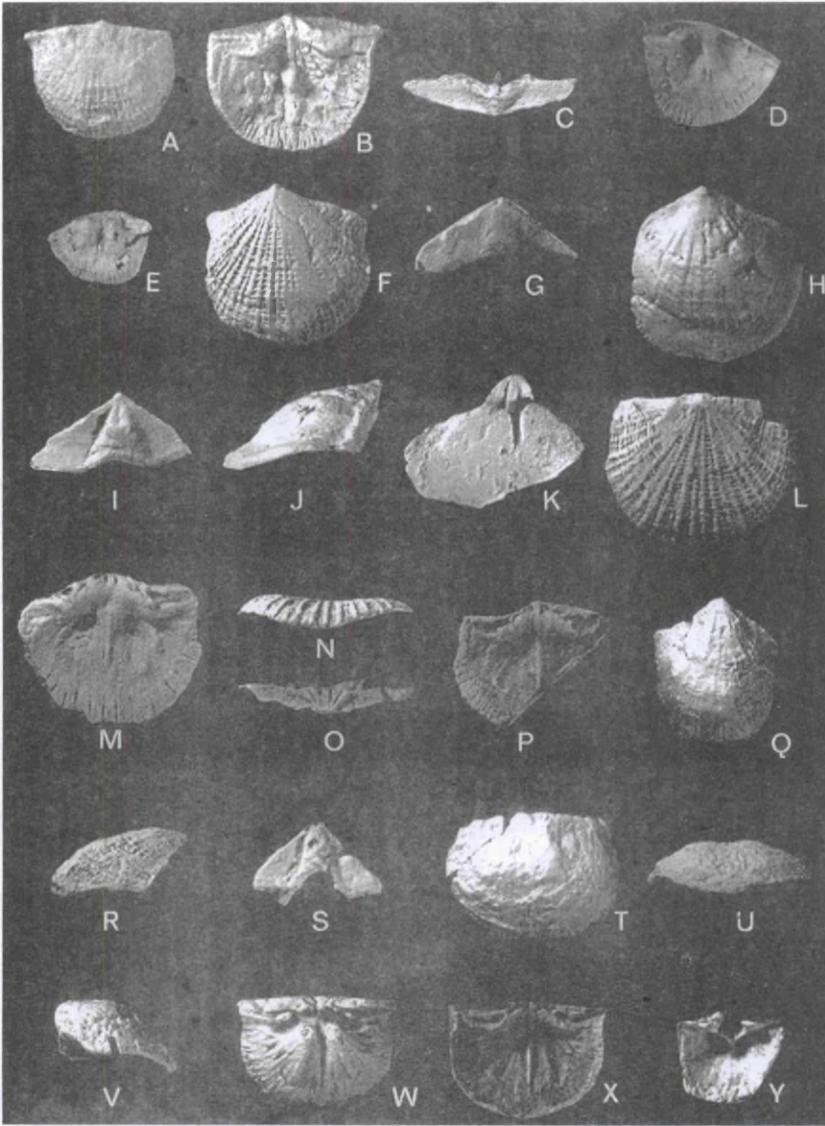
Fig. 4. A–C. *Kullervo hibernica* Harper, 1952, PMO 162.068. Dorsal valve, Billingstad, Arnestad Formation, ×2. D. *Kullervo hibernica* Harper, 1952, PMO 162.069. Dorsal interior, latex cast, ×2.0. E. *Kullervo hibernica* Harper, 1952, PMO 162.069. Impression of the dorsal interior, Billingstad, Arnestad Formation, ×1.5. F–G. *Kullervo hibernica* Harper, 1952, PMO 162.081, ventral valve, Arnestadtangen, Arnestad Formation, ×2.4. H–J. *Kullervo hibernica* Harper, 1952, PMO 162.080, ventral valve, Bratterud, Arnestad Formation, ×2. K. *Kullervo hibernica* Harper, 1952, PMO 162.087, impression of the ventral interior, Bratterud, Arnestad Formation, ×2. L–O. *Kullervo hibernica* Harper, 1952, PMO 162.079, dorsal valve, Bratterud, Arnestad Formation, ×2.2. P. *Kullervo hibernica* Harper, 1952, PMO 162.080, latex cast from the impression of the dorsal interior, Arnestadtangen, Arnestad Formation, ×2.2. Q–S. *Kullervo* aff. *parva*, PMO 162.074, ventral valve, Billingstad, Arnestad Formation, ×2.4. T–V. *Kullervo* aff. *parva*, PMO 162. 077, dorsal valve, Billingstad, Arnestad Formation, ×2.4. W. *Kullervo* aff. *parva*, PMO 162.075, impression of the dorsal interior, Billingstad, Arnestad Formation, ×2.4. X. *Kullervo* aff. *parva*, PMO 162.075, latex cast, ×2.4. Y. *Kullervo* aff. *parva*, PMO 162.076, latex cast from the impression of the ventral interior, Billingstad, Arnestad Formation, ×2.4.
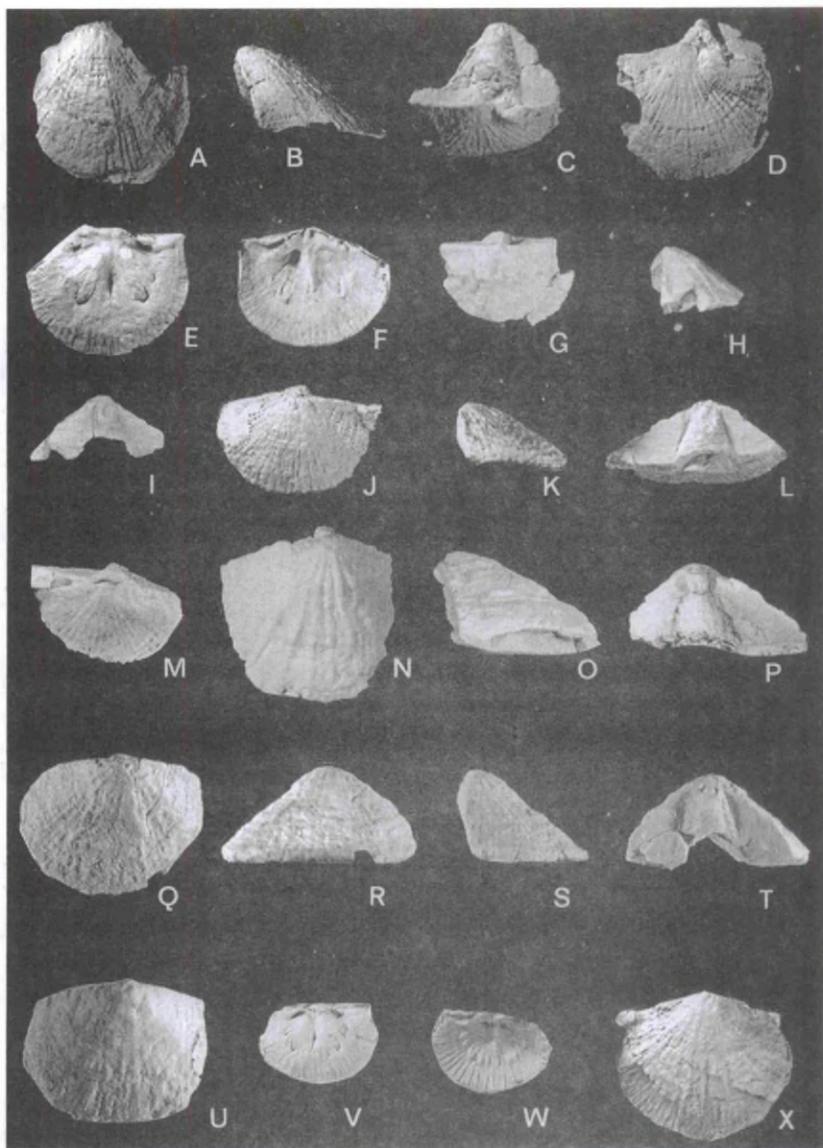
Fig. 5. A–D. *Kullervo* aff. *punctata,* PMO 162.070, ventral, lateral, posterior and dorsal view, Bratterud, Arnestad Formation, ×2. E. *Kullervo* aff. *punctata,* PMO 162.072, impression of the ventral interior, Bratterud, Arnestad Formation, ×2.2. F. *Kullervo* aff. *punctata,* PMO 162.072, latex cast, ×2.2. G–I. *Kullervo* aff. *lacunata,* PMO 162.083, ventral valve, Bratterud, Arnestad Formation, ×2.0. J–M. *Kullervo hibernica* Harper, 1952, PMO 162.085, ventral, lateral, posterior and dorsal view, Billingstad, Arnestad Formation, ×2.0. N–P. *Kullervo* aff. *lacunata,* PMO 162.086, ventral valve, Billingstad, Arnestad Formation, ×3.0. Q–T. *Kullervo* aff. *punctata,* PMO 162.065, ventral valve, Billingstad, Arnestad Formation, ×3.0. U. *Kullervo* aff. *punctata,* PMO 162.066, ventral valve, Billingstad, Arnestad Formation, ×3.0. V. *Kullervo* aff. *punctata,* PMO 162.067, impression of the dorsal interior, Billingstad, Arnestad Formation, ×2.0. W. *Kullervo* aff. *punctata,* PMO 162.067, latex cast, ×2.0. X. *Kullervo hibernica* Harper, 1952, PMO 162.088, ventral valve, Bratterud, Arnestad Formation, ×2.0.
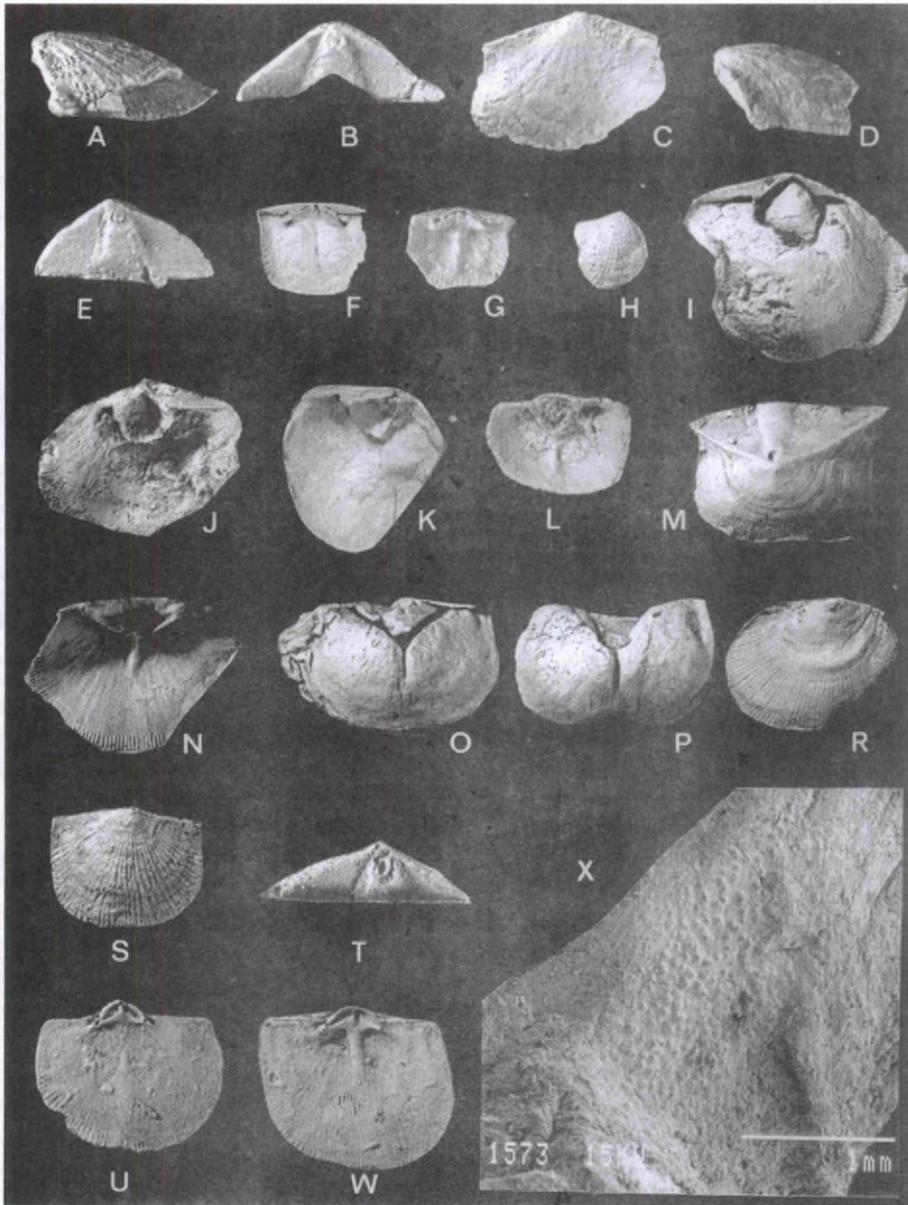
Virginia, corresponding to the lower part of the *tvaerensis* conodont Biozone and middle part of the same Biozone, respectively (see Bergström 1990, fig. 17), USA. The anterior margin of these specimens is medially invaginated, but not rounded as in the Norwegian specimen. Cooper (1956, p. 528) describes the pseudodeltidium as 'appearing as a vestige stage of that plate at the apex', which is nothing but the mere remains of the seal of the pedicle foramen, while the deltidium itself is broken off (see Cooper 1956, pl. 80, B, figs. 7–8).

The Norwegian specimens described here are affiliated with *K. parva* mostly because of the presence of similar sulcus in the dorsal valve, anteriorly drawn into short tongue, and ponderous cardinalia, and strong convexity of the dorsal valve.

K. aff. *parva* resembles *K. hibernica*, but the latter is easily distinguished from the former by its relatively wider shell, less concave sides, almost flat dorsal valve, more regular and less closely spaced ornamentation, short dorsal interarea with shorter umbonal chilidium, less deep dorsal sulcus, and by the strongly subapical foramen in the middle of a less convex deltidium. The subapical foramen described in one ventral valve (PMO 162.074) of *K.* aff. *parva* is a result of the sealing of the foramen, which has not grown entirely full in that case (Fig. 4S).

Kullervo aff. *punctata*

Figs. 5A–F, Q–T, V, W.

Material. – Two shells (PMO 162.070, L = 16.0, W = 15.0; PMO 162.072, L = 12.0, W = 15.0); nine ventral (PMO 162.065, L = 11.0, W = 16.0; PMO 162.066, L = 11.1, W = 14.5; PMO 162.105) and two dorsal valves of good to satisfactory preservation; eight moulds of the dorsal interiors (PMO 162.073, PMO 162.067).

Locality and horizon. – Bratterud, Arnestad Formation, just above big bentonite; Billingstad, Asker, Arnestad Formation, just below big bentonite; and from the Furuberget Formation (in the *Coelosphaeridium sphaer-*

icum beds) at Fangberget (Ringsaker District) and Furuberget (Hamar–Nes District).

Description. – Shell fairly ventribiconvex, subquadrate in outline, some specimens clearly asymmetrical (PMO 162.065), 70–80% as long as wide with the maximum width along the hingeline to the mid-length. Anterior margin straight to rounded, in commissural plane rectimarginate. Cardinal extremities obtuse to gently acute. Sides broadly convex, gently concave postero-laterally.

Radial ribs weakly to well developed, bifurcating, with maximum of three branches, resulted in 8–9 ribs per 5 mm along the anterior margin. Number of primary ribs 8 up to 12.

The whole shell is covered with the concentric ridges. Frequency of the ridges per 5 mm of valve length, measured medially anterior to 5 mm growth stage, is 10–16 in ventral valves and 14 in a dorsal valve.

Ventral valve pyramidal with slightly concave to gently convex shell surface in lateral profile. Ventral interarea high, triangular, nearly cataclinate to moderately apsacline, usually slightly concave in lateral profile becoming umbonally more apsacline, on average 50–80% as long as wide. Delthyrium about one-third as wide as the hingeline and about 65–80% as wide as long. Deltidium nearly flat to convex, projecting 0.9–1.8 mm away from the surface of interarea. Foramen small, always in the umbonal quarter of the deltidium, entirely apical or, in one specimen about 1.1 mm from apex (PMO 162.073), often sealed, on average with diameter of 1.5–1.7 mm.

Dorsal surface gently convex in lateral and transverse profiles. Dorsal interarea moderately anacline, flat, chilidium convex.

Ventral interior with a spondylium triplex with hemisyrinx. Subspondylial lateral septa rudimentary, slender and low, reaching nearly to the anterior edge of the spondylium.

Cardinal process thin, plate-like, continuous with the chilidium. Socket walls divergent, about three times as wide as long, extending about half valve width, merge anteromedially with the notothyrial platform. Median ridge well developed, wide, continuous with the notothy-

Fig. 6. A–B. *Kullervo hibernica* Harper, 1952, PMO 162.088, ventral valve, lateral and posterior view, Bratterud, Arnestad Formation, ×2.0. C–E. *Kullervo hibernica* Harper, 1952, PMO 162.089, ventral valve, ventral, lateral and posterior view, Bratterud, Arnestad Formation, ×2.0. F. *Kullervo hibernica* Harper, 1952, PMO 162.090, impression of the dorsal interior, Arnestad, Arnestad Formation, ×2.0. G. *Kullervo hibernica* Harper, 1952, PMO 162.090, latex cast of the impression of the dorsal interior, ×2.0. H. *Hemipronites* ? sp. PMO 162.092, latex cast of the impression of the ventral interior, Road section at Nydal-Furnes Church, Helskjer Member, Elnes Formation, ×1.5. I. *Clitambonites schmidti* Pahlen, 1877, PMO 162.093, impression of the ventral interior, from loose block, Rongstrand, probabaly *Coelosphaeridium-Mastropora* beds, Fossum Formation, ×1.2. J. *Clitambonites schmidti* Pahlen, 1877, PMO 162.093, latex cast, Fossum Formation, ×1.2. K. *Vellamo oandoensis?* Öpik, 1934, PMO 162.095, latex cast of the impression of the ventral interior, Bergevika, unit IV of the Mjøsa Limestone, ×1.5. L. *Vellamo oandoensis?* Öpik, 1934, PMO 162.096, latex cast of the impression of the ventral interior, Holetjern quarry SE part, lower part of the Mjøsa Limestone, ×1.5. M. *Clinambon anomalus* Schlotheim, 1822, PMO 162.097, latex cast of the impression of the ventral exterior, Gjøvik Kalkfabrikk, *Coelosphaeridium sphaericum* beds, Furuberget Formation, ×1.3. N. *Clinambon anomalus* Sclotheim, 1822, PMO 162.098, latex cast of the impression of the ventral interior, Tørud, *Coelosphaeridium sphaericum* beds, Furuberget Formation, ×1.3. O. *Ilmarinia dimorpha* Öpik, 1934, PMO 162.100, impression of the ventral interior, Fangberget, *Coelosphaeridium sphaericum* beds, Furuberget Formation, ×1.2. P. *Ilmarinia dimorpha* Öpik, 1934, PMO 162.099, impression of the ventral interior, Tørud, *Coelosphaeridium sphaericum* beds, Furuberget Formation, ×1.2. R. *Vellamo oandoensis* ? Öpik, 1934, PMO 162.104, latex cast of the impression of the ventral interior, Bergevika North, unit V of the Mjøsa Limestone, ×1.5. S. *Vellamo oandoensis* Öpik, 1934, PMO 162.101, latex cast of the impression of the ventral exterior, ventral view, Bergevika North, unit V of the Mjøsa Limestone, ×1.3. T. *Vellamo oandoensis* Öpik, 1934, PMO 162.101, latex cast of the impression of the ventral exterior, posterior view, Bergevika North, unit V of the Mjøsa Limestone, ×1.3. U. *Vellamo oandoensis* ? Öpik, 1934, PMO 162.103, latex cast of the impression of the ventral interior, Bergevika North, unit V of the Mjøsa Limestone, ×1.8. W. *Vellamo oandoensis* Öpik, 1934, PMO 162.102, latex cast of the impression of the ventral interior, Bergevika North, unit V of the Mjøsa Limestone, ×1.8. *Kullervo* aff. *punctata*, PMO 162.106, SEM photo of the edge of spondylium, pseudopunctae and lateral septum, Billingstad, Arnestad Formation, ×29.

ial platform, but slightly lower, extending almost to margin of adductor field (see Fig. 5E). Notothyrial platform triangular. Adductor field subpetaloid, impressed on floor of the shell, extending to about valve mid-length or slightly anterior. The adductor scars gently divergent, slender, elongated, drop-shaped. Anterior pair of adductor scars larger than posterior pair, and twice as wide, strongly raised anteriorly. In one immature specimen (PMO 162.067) the anterior and posterior adductor scars of nearly equal size. It has also some fine, short, ray-like, radially arranged mantle canal tracks between the anterior adductor scars on both sides of the median ridge (Fig. 5, V, W). Weakly to well-developed marginal grooves, subparallel to valve margin.

Discussion. – The American type material from the Pratt Ferry Formation belong to the conodont Biozone of *Pygodus anserinus*. The described Norwegian specimens are affiliated to *K. punctata* on the basis of the ornamentation typical for this species, and almost straight cardinal extremities (cf. Cooper 1956). However, the Norwegian specimens have very variable exteriors, which differ from those of *K. punctata*, and rectimarginate anterior commissure instead of the emarginated one in the type material.

K. aff. *punctata* is similar to *K.* aff. *parva* (see above) with its relatively fine and equally developed pitted ornamentation. It differs from *K.* aff. *parva* in its rectimarginate anterior and lack of sulci in both valves, slightly coarser radial and concentric ornament, less convex lateral profile of both valves. The described species also has shorter and less acute cardinal extremities compared to *K.* aff. *parva*. However, *K.* aff. *punctata* has an unexpectedly similar dorsal interior to that of *K. panderi*, with nearly identical shape of the adductor scars. Such an arrangement of the adductor muscle field was, up to now, known only in the stratigraphically older, Estonian *K. panderi*

Remarks. – One ventral valve (PMO 162.084), included in the species, differs from the rest of the specimens in its subcircular outline, more convex lateral profile of the ventral valve, wider delthyrium and bigger foramen. It also has rounded cardinal extremities and clearly unequal strength of radial ornamentation.

Kullervo cf. *lacunata*

Figs. 5G–I, N–P.

Material. – Two ventral valves (PMO 162.083; PMO 162.086, L = 8.0, W = 10.5, measurements taken at 8 mm growth stage) and one latex cast of the ventral exterior (original not preserved).

Locality and horizon. – Bratterud, Arnestad Formation, just above the big (Kinnekulle) bentonite; Arnestadtangen, Asker, Arnestad Formation; Billingstad, Asker; Arnestad Formation, just below big bentonite, Upper Ordovician.

Description. – Ventral valve subpentagonal in outline, about 60–80% as long as wide with the maximum width at hingeline. Anterior margin in younger growth stages straight, anterior commissure rectimarginate. Cardinal extremities gently acute to acute, sides posteriorly slightly concave.

Radial ribs strong, sparse, less developed in lateral regions, absent on cardinal extremities, bifurcating, branching twice, 4 costellae per 5 mm at 5 mm growth stage, measured medianly lateral. Number of primary ribs in umbonal area is 9.

Weak concentric ridges postero-laterally unequally developed, more continuous on the cardinal extremities and umbonally, nearly indistinguishable antero-medianly. Number of ridges per 5 mm of valve length, measured laterally anterior to the 5 mm growth stage, about 10.

Ventral valve pyramidal, with evenly flat surface and gently convex umbo in the lateral profile. Ventral interarea triangular, flat, apsacline, 90% as long as wide. Delthyrium about one-third as wide as the hingeline and about 90% as wide as long. Deltidium convex, projecting 1.2–1.7 mm away from the surface of interarea. Foramen moderate to large size, apical, with the diameter of 1.8–2.5 mm, surrounded by a small 1.0 mm high lip.

Discussion. – The specimen described by Alikhova (1969, p. 80, pl. V, fig. 2) from the Idaverean Stage of Valdai, Russia as *K. panderi* has ornament and outline that strongly resembles that of *K.* cf. *lacunata* from the Arnestad Formation of Oslo Region, but the latter could still be easily distinguished from the former by the presence of the elevated lip around the foramen. The described species resembles also the type material of *K. panderi* Öpik (1930, p. 234, pl. 19, fig. 228 pl. 21, fig. 260; Öpik 1934; pl. 35, figs. 1–5, pl. 37, fig. 2, text-figs. 37, 38, 39, 52) in having coarse, sparse radial ornamentation and the concentric ornamentation strongly developed and predominant only in the lateral regions.

The described species has also a relatively high ventral area and entirely apical foramen similar to that of *K. panderi*, but it could easily be distinguished from the latter by the less acute cardinal extremities, and the less impressed concentric ornamentation in the ventral lateral regions. It differs also by its smaller pedicle foramen and more irregular shape and slightly unequal strength of radial ribs. Orientation of the ventral interarea in *K. panderi* is catacline (Öpik 1934, p.169, text-fig. 39), rather than apsacline as in *K.* cf. *lacunata*.

Moderately acute cardinal extremities as in *K. aluverensis* Öpik (1934, pp. 172–173, pl. 38, fig. 1–1b, text-fig. 39, 53) and its general outline like *K.* cf. *lacunata*, but the latter has no subapical foramen in the middle of the deltidium, rather, an entirely apical pedicle foramen and also slightly thinner costellae than in *K. aluverensis*.

In outline, *K.* cf. *lacunata* also resembles *K. hibernica*, but it has an entirely different ornamentation on the ventral valve and less acute cardinal extremities.

Owen et al. (1990, p. 22) mentioned *Kullervo* cf.

lacunata Öpik – determined by D|A|T. Harper – from the Arnestad Formation in the Oslo–Asker District. The described *K*. cf. *lacunata* resembles indeed *K. lacunata* Öpik (see Öpik 1934) in its extremely acute cardinal extremities. Therefore, the species identified by Harper as *K*. cf. *lacunata* is most likely conspecific with the material described here as *K*. cf. *lacunata*.

Family Clitambonitidae Winchell & Schuchert, 1895

Genus *Hemipronites* Pander, 1830

Hemipronites? sp.

Fig. 6H.

Material. – One mould of the ventral exterior (PMO 162.092).

Locality and horizon. – Road section at Nydal–Furnes Church (cf. Nikolaisen 1963, fig. 3) in the Helskjer Member of the Elnes Formation, early Llanvirn, as defined by Owen et al. (1990, p. 18). According to Owen et al. (1990, p. 18) the age is indicated as being late Kundan, in Baltic terms, Middle Ordovician.

Description. – Ventral valve transversely subquadrate in outline, slightly convex in lateral profile, with the maximum width at hingeline, and maximum height at about one-quarter of the valve length. Cardinal extremities slightly acute, anterior commissure with the shallow sulcus, and slightly emarginate anterior margin. Radial ribs bifurcating, on average 15 ribs per 5 mm along the anterior margin ventral valve. Ribs very fine, equally developed and evenly spaced. Concentric growth lamellae form a well-expressed imbricate sculpture.

Discussion. – The preservation state of the only Norwegian specimen available does not enable us to identify the genus without some doubt. However, the described specimen has been affiliated with *Hemipronites* (see Öpik 1934, pp. 96–98, pl. 42, figs. 1, 2; pl. 43, figs. 1a–b; text-figs. 12, 13.) because of its outline, imbricate sculpture and closely spaced fine radial ribs, all typical for the genus.

Genus *Clitambonites* Pander, 1830

Clitambonites schmidti Pahlen, 1877

Figs. 6I–J.

1877 *Orthisina schmidti* n.sp. – Pahlen, p. 23, pl. 2, figs. 5,6,7–9. 1930 *Clitambonites schmidti* (Pahlen) – Öpik, pp. 210–212, pl. 18, figs. 211–217; 19, fig. 218; pl. 21, fig. 250. 1934 *Clitambonites schmidti* (Pahlen) – Öpik, pp. 83–89, pl. 3, figs. 1, 2; pls. 5–7; pl. 8, figs. 1, 2; pl. 10, fig. 1; text-figs, 8, 26, 33.

Material. – One mould of the ventral interior (PMO 162.093, L = >25, W = 35.0).

Locality and horizon. – One specimen (PMO 162.093) found in a loose block fallen from the top of the cliff at Rognstrand, Langesund–Skien District, probably from the *Coelosphaeridium* – *Mastopora* beds, Fossum Formation, Upper Ordovician.

Description. – Ventral valve transversely semielliptical in outline, convex in the lateral profile, with the maximum width about at mid-length of the valve. Cardinal extremities obtuse, the anterior margin rounded, commissure rectimarginate. Costellae of equal size, evenly spaced. Concentric growth lamellae, preserved on anterior of the specimen (PMO 162.093), forming a well-developed imbricate sculpture.

Ventral interarea short relative to length, flat and apsacline. Delthyrium as wide as long, less than half covered by convex deltidium. Foramen is not clearly observable in any specimen studied, possibly very small, sealed and entirely apical.

Ventral interior with wide, shallow spondylium, gently elevated anteriorly, supported medianly by short wide septum.

Discussion. – The described Norwegian specimens are assigned to the species *Clitambonites schmidti* on the basis of their ventral interior, ornament, deltidium and especially, the shape of spondylium, all typical for this species. In Estonia, this species has been found from the Aserian (C_{1a}) to Jöhvian Stages (D_1) (Öpik 1934).

Genus *Clinambon* Schuchert and Cooper, 1932

Clinambon anomalus Schlotheim, 1822

Figs. 6M, N.

1822 *Anomites anomala* n.sp. – Schlotheim, p. 65, pl. 14, figs. 2a–c. 1934 *Clinambon anomalus* (Schlotheim) – Öpik, pp. 118–124, pl. 1, figs. 3, 4; pl. 14, figs. 8, 8a–b; pl. 15; pl. 16, figs. 1,2,3; pl. 17, figs. 1, 1a–e; pl. 20, fig. 1; pl. 38, fig. 4; text-fig. 32.

Material. – One mould of the ventral exterior (PMO 162.097, L = 22.0, W = 30.0) and three moulds of the ventral interior (PMO 162.098).

Locality and horizon. – Found in the *Coelosphaeridium sphaericum* beds, Furuberget Formation, Upper Ordovician, in the localities Fangberget and Tørud in the Ringsaker District, and in a low road section S. of the old quarry at Gjøvik Kalkfabrikk, in the Toten District.

Description. – Ventral valve subquadrate in outline, with the maximum length at the hingeline, cardinal extremities

acute, anterior margin straight and commissure gently uniplicate. Costellae of equal size, fine, evenly spaced.

Ventral interarea of medium length, flat, strongly procline. Delthyrium narrow, covered with the gently convex deltidium, pedicle foramen small, apical, oval, about with the diameter of 3 mm.

Ventral interior with the spondylium elevated anteriorly, supported medianly by septum half as long as valve. Adductor scars separated from diductors by invaginated sides of spondylium.

Discussion. – The described Norwegian specimens are assigned to *Clinambon anomalus* Schlotheim because of their species-characteristic profile, ornamentation and the ventral interior, and especially the shape of the spondylium. In Estonia, the species occurs in the interval from Jöhvi (D_1) to Oandu stage (D_3) (Öpik 1934).

Genus *Ilmarinia* Öpik, 1934

Ilmarinia dimorpha Öpik, 1934 Figs. 6O, P.

1934 *Ilmarinia dimorpha* n.sp. – Öpik, pp. 127–128, pl. 18, 40; text-fig. 26.

Material. – One mould of the ventral exterior and three moulds of the ventral interior (PMO 162.099, L = 22.0, W = 34.0; PMO 162.100, L = 26.0, W = 37.0).

Locality and horizon. – The two localities are in the *Coelosphaeridium sphaericum* beds, Furuberget Formation, Upper Ordovician, at Tørud and Fangberget in the Ringsaker District.

Description. – Ventral valve subquadrate in outline, strongly sulcate, with maximum length at the one-third length of valve, cardinal extremities obtuse, the anterior margin emarginate, commissure uniplicate. Ventral interarea of medium length, strongly procline. Delthyrium wide, slightly wider than long, about 60% as wide as the hingeline, covered by gently convex deltidium, foramen large, apical, suboval, about half as long as deltidium.

Ventral interior with the short spondylium, elevated anteriorly, supported medianly by septum. Sides of the spondylium slightly invaginated.

Discussion. – The described Norwegian specimens are assigned to the species *Ilmarinia dimorpha* (Öpik 1934, pp. 127–128, pl. XVIII, XL; text-fig. 26) because of their ventral sulcus, profile and the shape of spondylium, all typical for the species. The species was originally described by Öpik (1934) from the Oanduan Stage in Estonia.

Genus *Vellamo* Öpik, 1930

Vellamo oandoensis Öpik, 1934

Figs. 6K, L, R–U, W.

1934 *Vellamo oandoensis* n.sp. – Öpik, pp. 113–114, pl. 12, figs. 11a–14; pl. 30, figs. 1, 3; text-fig. 29.

Material. – Two moulds of the ventral exteriors (PMO 162.101, L = 19.0, W = 22.0; PMO 162.104), one ventral interior (PMO 162.094, L = 25.0, W = 25.0) and three moulds of the dorsal interiors (PMO 162.102, L = 18.0, W = 20.0; PMO 162.103, L = 17.0, W = 21.0). Probably two ventral interiors (PMO 162.095, L = 14.0, W = 19.0; PMO 162.096).

Locality and horizon. – Most of the material from the shore section at Bergevika N, in bed V, one in bed IV of Spjeldnæs 1982, Mjøsa Limestone. The rest of the material is from the same beds in the road section also of Bergevika N. (cf. Spjeldnæs 1982, fig. 3), Mjøsa Formation, Upper Ordovician. Two problematic ventral interiors from the lower part of the Mjøsa Formation in the quarry at Holetjern SE, in the Toten District.

Description. – Shell transversely semielliptical in outline. Anterior margin straight, in one specimen rounded. Cardinal extremities orthogonal to obtuse. Sides straight. Anterior commissure slightly sulcate.

Radial ornament bifurcating resulting in average seven ribs per 5 mm along the anterior margin ventral valve.

Ventral interarea short, flat and gently apscaline. Delthyrium narrow, slightly more than one-fourth as wide as the hingeline, covered entirely by convex deltidium. Foramen large, subapical, about two-thirds as long as the deltidium.

Dorsal valve subquadrate to semiovate, interarea anacline. Notothyrium covered by semicircular, convex chilidium. Dorsal interior with the plate-like cardinal process. Notothyrial platform nearly flush with dorsal interarea. Adductor field weakly impressed on floor of valve. Anterior pair of adductor scars almost equal size with posterior pair, median ridge weakly developed, extending to margin of adductor field, in one specimen confined to the umbonal region.

Discussion. – The described specimens have an outline and dorsal interior typical for the *V. oandoensis*. The Norwegian form also resembles *V. diversa* from America in its outline, but could be distinguished by its clearly less impressed dorsal adductor field and thinner dorsal valve (personal consultations with Mrs. Oive Tinn from Tartu). *V. oandoensis* was originally described by A. Öpik (1934) from the Oanduan Stage in Estonia, which is of approximately the same age as unit V of the Mjøsa Limestone in the Oslo Region (Spjeldnæs 1982). The other ventral moulds (PMO 162.104) (Fig. 6R) found in the same beds have finer radial ribs, 11 per 5 mm along the anterior, rounded anterior margin and strongly asymmetrical shell, different from that of *Vellamo oandoensis*. Two ventral interiors (PMO 162.095; 192.096) (Fig. 6K, L) *included here to Vellamo may also belong to V. oandoensis.*

Paleobiogeography

There are many interesting palaeobiogeographic points regarding the clitambonitoids from the Upper Ordovician of the Oslo Region. The first concerns the distribution of the genus *Kullervo*, and the second the presence of typical East Baltic clitambonitoids in Norway.

In the central part of the Oslo Region (Oslo–Asker–Ringerike) the Atlantic Province assemblage occurs in beds around, and especially just above, the Kinnekulle Bentonite (of Bergström et al. 1995).

The great majority of the specimens of *Kullervo* are from above the level of bentonite, but, since the bentonite itself is missing (being washed out, or squeezed out tectonically) in the two localities where most of the specimens are found – Bratterud and the tunnel-roof at Billingstad – it cannot be excluded that the first occurrence of *Kullervo* in the Oslo Region is even below the bentonite. All the four species *K. hibernica, K.* aff. *parva, K.* aff. *punctata* and *K.* cf. *lacunata* have a range within the Arnestad and Furuberget formations of the Caradoc Series of Oslo Region.

This invasion of new genera, with a Baltic/American stamp in the Oslo Region was termed the Kukruse wave by Spjeldnæs (1978), based on the then current miscorrelation of the Norwegian beds with Estonian ones. Now the beds in question (upper part of the Arnestad Formation) correspond to Keila (from the upper part of the *D. multidens* Biozone to the lowest part of the *D. clingani* Biozone; see Männil, 1990) and perhaps latest Jöhvian stages (middle part of the *Diplograptus multidens* Biozone; see Männil & Meidla, 1994) of the Estonian chronostratigraphic scale (Fig. 2).

The genus *Kullervo* Öpik was originally described from Estonia, where it is part of the Middle Ordovician radiation of the clitambonitoids in this region (Öpik 1934, 1939). However, the earliest known occurrence of the genus is *Kullervo* sp. from Wales, a form resembling *K. complectens*, from the Middle part of Ffairfach Group in Llandeilo of Upper Llanvirn age (Lockley & Williams 1981), broadly equating with the uppermost *artus* to a level near the top of the *murchisoni* graptolite Biozones (Williams et al. 1972). That age is noteworthy, because it could indicate the time of migration of the first kullervoid from Baltica to Avalonia.

On the other hand, the first *Kullervo* in Estonia (*Glyptograptus teretiusculus* Biozone; see Männil & Meidla, 1994, chart 1) occurs shortly after the first occurrence of the genus in Wales and was probably derived independently from the last common ancestor of both the endemic Baltic species and pandemic Avalonian/American ones. Moreover, the oldest Estonian species, *K. lacunata*, has neither sulcus nor strongly pitted ornamentation, different from that of *K.* sp. from Wales. The oldest known records of gonambonitids are all from Baltica, there is nothing known about the gonambonitids from Avalonia predating the *K.* sp. and suitable for an ancestor of *Kullervo*, and so suggesting a Baltic species to be the descendants of an earlier Avalonian migrant.

In England, Wales and Ireland the genus has a range at least from the Llanvirn (Lockley & Williams 1981) to the Ashgill (Wright 1964, Hiller 1980). The Irish species *K. hibernica* was originally described from the Upper tuffs and shales in Grangegeeth of Caradoc age (Harper 1952). The occurrence of *K.* aff. *panderi*, the species resembles of *K.* aff. *punctata*, in the Derfel Limestone of N. Wales (Whittington & Williams 1955) is remarkable, especially because it occurs along with other brachiopods of the American assemblage mentioned below (such as *Palaeostrophomena* and *Sowerbyella*).

The Derfel Limestone is recently recognized as being Harnagian in age (see Zalasiewicz 1992, pp. 379–389). Because of the similarity in fauna, the Derfel Limestone may be correlated with the upper part of the Arnestad Formation in the Oslo Region, of supposed *peltifer* age, just above the rhyolitic Kinnekulle Bentonite.

In Estonia, several species have been found, in typical carbonate platform sediments, with low net sedimentation rates. The oldest known species of the genus in Estonia is *K. lacunata* from the Raasikuan Substage of Uhakuan Stage (C_1c) (Röömusoks 1970). This level is close to the base of *Pygodus anserinus* Biozone (Männil & Meidla 1994). The ranges of the temporally next two species *K. panderi* and *K. intacta* are restricted to the lower part of the Kukruse Stage (C_{II}) (Röömusoks 1970). The stage is defined in the North Atlantic conodont succession as ranging from the upper part of the *Pygodus anserinus* Biozone to the lower part of *Prioniodus gerdae* subzone of the *Amorphognathus tvaerensis* Biozone, and in the graptolite succession it roughly corresponds to the interval of the *Nematograptus gracilis* Biozone (Männil 1986; Männil & Meidla 1994). *K. aluverensis* from the upper part of the Idaverean Stage (C_{III}) (Röömusoks 1970) corresponds to the interval represented by the lowermost part of the *Diplograptus multidens* Biozone (Männil & Meidla 1994), and is the youngest known occurrence of the *Kullervo* in Estonia, except for the possible occurrence of *K. complectens* in the Pirgu Stage (Öpik 1934). The stage corresponds to the upper part of the *Pleurograptus linearis* Biozone (Männil & Meidla 1994).

The three American species – *Kullervo parva, K. sulcata* and *K. punctata* were originally described (Cooper 1956) from formations which have been dated slightly older than Estonian stages named above (the corresponding Pratt Ferry, which was correlated with the Boutetout, Effna and Arline Formations by Cooper) and belong to the conodont Biozone of *Pygodus anserinus*. More recently, Bergström (1990) equated the lowest part of the Effna Formation with the lower part of the *tvaerensis* conodont Biozone and included the Boutetort and Edinburgh formations in the middle of that Biozone. The Pratt Ferry Formation was placed at a level low in the *anserinus* Biozone.

The Caradoc species *K. parva, K. ornata* and *K. sulcata*, as well as the Ashgill *K. pyramidata* in America may have been derived from an earlier migrant from Avalonia, but they may also be of Avalonian origin.

Kullervo is found in the Atlantic Province of Jaanusson

& Bergström (1980) of North America, and occurs there along with a number of brachiopod genera of possible Baltic origin, such as *Palaeostrophomena, Christiania, Sowerbyella, Diambonia* and *Bilobia* as well as genera of less specific, possibly American origin, such as *Ptychoglyptus, Anisopleurella* and *Cyphomena* (Jaanusson & Bergström 1980).

This assemblage is unknown in the Mid-Continent part of North America, but recurs (without reports of *Kullervo*) in the westernmost part of North America, where it [s]long] to terrains or platelets added to North America after the Ordovician (Potter et al. 1980).

The picture that emerges from *Kullervo* is that they may have had two diversification centres; one in Avalonia and the other in Baltica, where they evolved in parallel from a common early kullervoid ancestor. That early kullervo or the last common ancestor for both the endemic species of Baltica and the Avalonian/American ones may have been migrated from Baltica to Avalonia or evolved there already by the Early Llanvirn. During the Late Llanvirn, the *Kullervo*(*K.* sp and/or its descendants; see Lockley & Williams 1981) probably migrated from Avalonia to North America, and finally settled again in Baltica (Oslo Region; *K. hibernica*, and probably also *Kullervo* aff. *punctata* and *Kullervo* aff. *parva*) in the time of the big bentonites. The distinct "Baltic" species *K. complectens* shares the similar outline and ventral muscle field with *K. complectens albida* (Caradoc/Ashgill, Avalonia) and the *K. pyramidata* (Ashgill, North America, see Cooper & Kindle 1936) and its occurrence in the Ashgill of Baltoscandia (see above) may indicate that it was a migrant from American/Avalonian.

However, it cannot be excluded that the migration was in the opposite direction, from Baltica to Avalonia in late Llanvirn. Thus, some Baltic *Kullervo* may be found in Avalonia. On the other hand, by the time in question the endemic Baltic species were probably already highly adapted to the specific habitat on the Baltic carbonate platform, so they should have had low migration potential.

The paleobiogeography and ecology of the other clitambonitoids found in the Oslo Region is different from that of the almost cosmopolitan *Kullervo*. *Clinambon, Ilmarina* and partly *Clitambonites* are otherwise endemics to the Baltic carbonate platform. *Vellamo* has a world-wide distribution, but also mostly in carbonate platforms. In the Oslo Region they are found in the northern and western districts of the region, which are well known for their Baltic fauna (Holtedahl 1909; Størmer 1953).

The precise correlation of the beds in these districts (Mjøsa, Skien–Langesund and Hadeland) is not well developed, and the presence of Baltic species and genera is generally taken as an indication of the same age as in Estonia (it was a mistake with *Kullervo* in the Oslo–Asker and Ringerike Districts, and caused some doubt regarding correlation also in the other districts).

With few graptolites, and without a well-established conodont stratigraphy in these districts, it is difficult to use both the clitambonitoids and other conventional fossils

such as trilobites and brachiopods, because we do not know if they are part of the faunal area of the Baltic Platform, or if they have a distribution and migration pattern similar to that seen in *Kullervo*.

The main reason for this doubt is that in the Oslo Region the genera in question (*Clinambon, Clitambonites, Ilmarina* and *Vellamo*) occur in sediments strikingly different from those in Estonia and Sweden. In the carbonate platform areas, their enclosing carbonate, partly with a slight clay content, shows a low net sedimentation rate. In Norway, the same genera occur in rapidly sedimented silt-clay-carbonate rocks which not only look different, but also indicate strikingly different bottom conditions as well as sedimentation rates.

On the other hand, *Clitambonites, Ilmarinia, Clinambon* and *Vellamo* from the silt-clay carbonate rocks of the Oslo Region are not found in the shales where the *Kullervo* occurs, and vice versa. These two different assemblages are presumed to reflect neither different ages nor geographical distances, but the different ecology of *Kullervo* as compared with the rest of Middle and Upper Ordovician clitambonitoids in Baltica. However, the differences in water depth and especially in the bottom conditions between the shale facies of foreland basin and the silt-clay-carbonate rock facies of the slope of the carbonate platform may have played a big part in the separation of clitambonitoids in the Oslo Region.

Since modern benthic invertebrates are generally very sensitive to changes in substrate and sedimentation rate, it is difficult to refer the Norwegian material to Estonian species without some doubt. In Estonia, *Clinambon anomalus* occurs in both the clay-marls and limestones, indicating low rather than high sensitivity of the species there in this respect. However, the subspecies in the Oslo Region could be different from those described by Öpik in Estonia (see Öpik 1934).

The present samples are too small to resolve this problem on the species level, and can therefore only help to ascertain the presence of the genera, and the palaeobiogeographic relationships the Baltic Carbonate Platform and the Oslo Region.

References

Alikhova, T. N. 1969: *Stratigrafiia i brakhiopody sredneordovikskikh otlozhenii Moskovskoi sineklenzy. (Middle Ordovician Stratigraphy and Brachiopoda of the Moscovian Syneclise)* "Nedra", 1–91, pls 1–10.

Bergström, S. M. 1990: Biostratigraphic and biogeographic significance of Middle and Upper Ordovician conodonts in the Girvan Succession, South-West Scotland. *Courier Forschungsinstitut Senckenberg 113*, 1–43.

Bergström, S. M., Huff, W. R., Kolata, D. R. & Bauert, H. 1995: Nomenclature,

stratigraphy, chemical fingerprinting, and areal distribution of some Middle Ordovician K-bentonites in Baltica. *GFF (Geologiska Föreningens i Stockholm Förhandlingar) 117*, 1–56.

Cooper, G. A. 1956: Chazyan and related brachiopods. *Smithsonian Miscellaneous Collections 127*, 1–1245, pls. 1–269.

Cooper, G. A. & Kindle, C. H. 1936: New brachiopods and Trilobites from the Upper Ordovician of Percé, Quebec 2. *American Journal of Science 20*, 265–288, pls. 1–3.

Harper, J. C. 1952: The Ordovician Rocks between Collon (Co. Louth) and Grangegeeth (Co. Meath). *Scientific Proceedings of royal Dublin Society 26*, 85–112, pls. 5–7.

Hiller, N. 1980: Ashgill Brachiopoda from the Glyn Ceiriog District, North Wales. *Bulletin of the British Museum (Natural History), Geology Series 34 (3)*, 110–216.

Holtedahl, O. 1909: Studien über die Etage 4 des norwegischen Silursystems beim Mjøsen. *Videnskab-selskabets Skrifter, Matematisk-Naturvidenskabelige Klasse I, 1906, no. 7*, 1–76.

Jaanusson, V. & Bergström, S. M. 1980: Middle Ordovician Faunal Spatial Differentiation in Baltoscandia and the Appalachians. *Alcheringa 4*, 89–110.

Lockley, M. G. & Williams, A. 1981: Lower Ordovician Brachiopoda from mid and southwest Wales. *Bulletin of the British Museum (Natural History), Geology Series 35*, 54–55.

Männil, R. 1986: Stratigrafiya kukersitonosnykh otlozheniy $C_I b$-C_{III}. *In* Puura, V. (ed.): Stroeniye slantenosnoy tolshchi Pribaltiskogo basseyna goryuchikh slantsev-kukersitov. (Stratigraphy of the kukersitic rocks of $C_I b$-C_{III}. *In* Puura, V. (ed.): Structure of the Kukersite Oil Shale Sequence in the East Baltic Basin). Tallinn, Valgus, 12–24.

Männil, R. 1990: The Ordovician of Estonia. *In* Kaljo, D. & Nestor, H. (eds.). Field meeting Estonia 1990. An Excursion Guidebook. Tallinn, 11–20.

Männil, R. & Meidla, T. 1994: The Ordovician system of the east European platform (Estonia, Latvia, Lithuania, Byelorussia, Parts of Russia, the Ukraine and Mouldova). *In* Webby, B. D. et al. (eds.). The Ordovician system of the east European platform and Tuva (southeastern Russia). *IUGS Publication No. 28*, 1–41.

Nikolaisen, F. 1963: The Middle Ordovician of the Oslo Region, Norway, 14. The trilobite family Telefinidae. *Norsk Geologisk Tidsskrift 43*, 345–399.

Owen, A. W., Bruton, D. L., Bockelie, J. F. & Bockelie, T. G. 1990: The Ordovician succession of the Oslo Region, Norway. *Norges geologiske undersøkelse, Special Publications 4*, 1–54.

Opalinski, P. R. & Harland, T. L. 1981: The Middle Ordovician of the Oslo Region, Norway. XXIX, Stratigraphy of the Mjøsa Limestone Formation in the Toten and Nes-Hamar areas. *Norsk Geologisk Tidsskrift 61*, 59–78.

Öpik, A. 1930: Brachiopoda Protremata der estländischen ordovizischen Kukruse-Stufe. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis) A XVII 1*, 1–161, pls. 1–22.

Öpik, A. 1932: Über die Plectellinen. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis) A XXIII 3*, 1–85.

Öpik, A. 1934: Über Klitamboniten. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis) A XXXVI 5*, 1–239, pls. 1–4.

Öpik, A. 1939: Brachiopoden und Ostrakoden aus dem Expansusschiefer Norwegens. *Norsk Geologisk Tidsskrift 19*, 117–142, pls. 1–6.

Pahlen von der, A. 1877: Monographie der baltisch-silurischen Arten der Brachiopoden gattung Orthisina. *Memoirs de l'Academie de St.-Petersburg ser 7, 24 (8)*, i–iv + 1–52.

Pander, C. H. 1830: *Beiträge zur Geognosie des Russisches Reiches.* Karl Kray, St Petersburg, 165 pp., 31 pls.

Parkes, M. A. 1994: The Brachiopods of the Duncannon Group (Middle-Upper Ordovician) of southeast Ireland. *Bulletin of the British Museum (Natural History) Geology Series 50*, 105–174, pls 1–16.

Potter, A. W., Gilbert, W. G., Ormitson, A. R. & Blodgett, R. B. 1980: Middle Ordovician brachiopods from Alaska and northern California and their paleogeographic implications. Abstracts with Programs. *Geological Society of America 12, 3*, 147.

Romano, M. 1980: The stratigraphy of the Ordovician rocks between Slane (County Meath) and Collon (County Louth), eastern Ireland. *Journal of Earth Science, Royal Dublin Society 3*, 53–79.

Römusoks, A. 1970: Stratigrafia viruskoy i kharjuskoy seriy (ordovik) Severnoy Estonii. *[Stratigraphy of the Viruan Series (Middle Ordovician) in Northern Estonia].* Tallinn, Valgus, 1–346.

Schlotheim von, E. F. 1822: *Nachträgen zur Petrefactenkunde. Erklärung der Kupfertafeln.* Becker, Gotha, 114 pp, 37 pls.

Schuchert, C. & Cooper, G. A. 1932: Brachiopod genera of the suborders Orthoidea and Pentameroidea. *Memoirs of the Peabody Museum of Natural History 4*, 1–270.

Spjeldnæs, N. 1978: Faunal provinces and Proto-Atlantis. *In* Bowes, D. R. & Leake, B. E. Crustal evolution in northwestern Britain and adjacent regions. *Geological Journal, Special Issue 10*, 139–150.

Spjeldnæs, N. 1981: Lower Palaeozoic Palaeoclimatology. *In* Holland, C. H. (ed.): *Lower Palaeozoic of the Middle East, Eastern and Southern Africa, and Antarctica*, 199–256. John Wiley & Sons, Chichester.

Spjeldnæs, N. 1982: The Ordovician of the districts around Mjøsa. *In* Bruton, D. L. & Williams, S. H. (eds.): Field Excursion Guide. 4th International symposium on the Ordovician System. *Palaeontological Contributions from the University of Oslo 279*, 148–163.

Størmer, L. 1953: The Middle Ordovician of the Oslo Region, Norway. *Norsk Geologisk Tidsskrift 31*, 37–141.

Webby, B. D. 1998: Steps toward a global standard for Ordovician stratigraphy. *Newsletter of Stratigraphy 36 (1)*, 1–33.

Williams, A., Strachan, I., Bassett, D. A., Dean, W. T., Ingham, J. K., Wright, A. D. & Whittington, H. B. 1972: A correlation of Ordovician rocks in the British Isles. *Geological Society London, Special Report 3*, 74.

Whittington, H. B. & Williams, A. 1955: The fauna of the Derfel limestone of the Arenig District, North Wales. *Royal Society of London, Philosophical Transactions, Ser. B*, 238, 397–430, pls. 3.

Winchell, N. H. & Schuchert, C. 1895: The Lower Silurian Brachiopoda of Minnesota. *In The Geology of Minnesota 3*, 333–474, pls. 29–34. Minneapolis.

Wright, A. D. 1964: The fauna of the Portrane Limestone, II. *Bulletin of the British Museum (Natural History), Geology Series 9*, 157–256, pls 1–11.

Zalasiewicz, J. 1992: Graptolite dating of the Ordovician vulcanicity in the Arenig Area, North Wales. *Geological Journal 27*, 379–389.

III

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Brachiopods of the redefined family Tritoechiidae from
the Ordovician of Kazakhstan and South Urals. Geobios.

BRACHIOPODS OF THE REDEFINED FAMILY TRITOECHIIDAE FROM THE ORDOVICIAN OF KAZAKHSTAN AND SOUTH URALS

LEONID E. POPOV, OLEV VINN, & OLGA I. NIKITINA

ABSTRACT. The Tritoechiidae are redefined following study of nine species of the genera *Tritoechia, Eremotoechia, Martellia Pomatotrema, Protambonites* and *Korinevskia* nov. gen. in Kazakhstanian brachiopod faunas from the upper Tremadoc to lower Caradoc. Six species are new: — *Tritoechia crassa, T. tokmakensis, Eremotoechia inchoata, E. spissa, Martellia reliqua* and *Pomatotrema fecunda.* In key characters of shell morphology the Tritoechiidae demonstrate close affinity with billingsellids and are therefore reassigned to the superfamily Billingselloidea.

KEY WORDS: brachiopoda, tritoechiidae, morphology, ordovician, kazakhstan, south urals.

INTRODUCTION

Some rhynchonelliformean brachiopods considered by us in limit of a revised family Tritoechiidae form a distinctive but poorly known component of the early and mid Ordovician (Tremadoc to early Caradoc) brachiopod faunas of Kazakhstan (Nikitin 1972; Popov 1976; Nikitina & Timofeeva 1991) as well as South Urals. However, only *Tritoechia kendyktassica* from the Lower Ordovician Agalatas Formation of the Kendyktas Range (Rukavishnikova, 1961) and *Tritoechia* (=*Protambonites*) *lermontovae* from the Lower Ordovician of the South Urals (Andreeva, 1960) are the only known species of them described and illustrated until recently.

Six tritoechiid genera (*Eremotoechia, Korinevskia* nov. gen., *Martellia, Pomatotrema, Protambonites* and *Tritoechia*) and nine species are identified in Kazakhstanian and south Uralian brachiopod assemblages in the present study. In south-central Kazakhstan their geographical occurrences are within the southern segments of the Stepniak-Betpakdala-North Tien-Shan (Kendyktas Range) and Ermentau-Chu-Ili (Chu-Ili Range, area south-west of the Alakul Lake and south Betpakdala) tectonofacies belts of Nikitin *et al.* (1991) in the south-central Kazakhstan and in the South Urals within the so-called 'Sakmara Belt' (Vagranov *et al.* 1973; Korynevskiy 1989). Currently available palaeobiogeographical and geological data suggest that these Kazakhstanian tectonofacies belts are confined mainly to two separate crustal terranes located during the Ordovician somewhere

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between equatorial East Gondwana and Baltica (Popov *et al.* 1997). In the South Urals tritoechiids co-occur with lingulate brachiopods characteristic of the *Leptembolon-Thysanotos* Assemblage and available data suggest, that these brachiopods inhabited the rifted southern margin of Baltica (Popov & Holmer 1994).
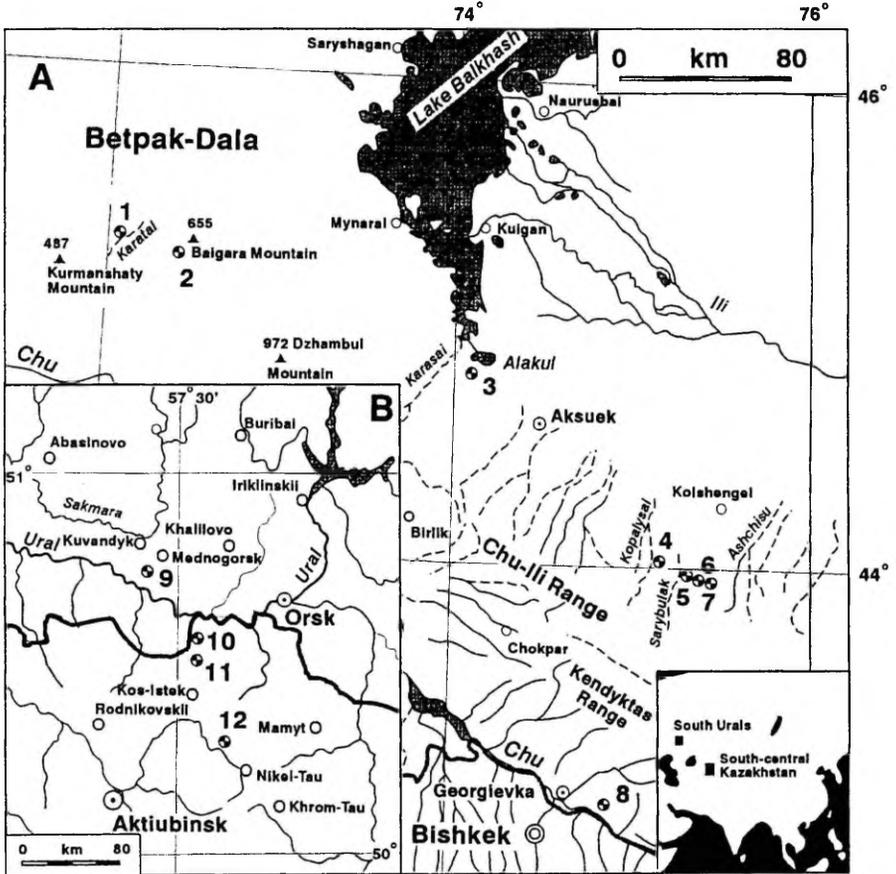
Figure 1. Sketch maps showing position of tritoechiid collecting sites in south Kazakhstan (A) and South Urals (B): 1, Karatal river; 2, area about 7 km south-west of Baigara Mountain; 3, area about 4 km south west of Alakul Lake; 4, east side of Kopalysai river; 5, Kujandysai section; 6, Kurzhaksai section; 7, Sarybulak section; 8, Agalatas river valley 14 km east of Georgievka; 9, Tyrmantau Range east of the Novodmitrievka village; 10, east side of Alimbet river about 2,5–3 km south of Alimbet farm; 11, upper reaches of Akbulaksai river; 12, west side of Koagash river.

LOCALITIES AND STRATIGRAPHY

SOUTHERN KENDYKTAS RANGE

The best Tremadoc and early Arenig sections in the Kendyktas Range is exposed along both sides of the Agalatas River about 14 km east of the town of Georgievka (Figs 1, 2). Ordovician geology and stratigraphy of this area was described by Keller & Rukavishnikova (1961) and later by Popov & Holmer (1994).

The uppermost Cambrian and lower Ordovician deposits of the Kendyktas Range are subdivided into three major lithostratigraphical units: (1) the Kendyktas Formation of dark grey and greenish grey sandstones, siltstones and argillites, 350 m thick and containing the lingulate brachiopods *Broeggeria salteri* (HALL), *Elliptoglossa lingulae* (WESTEREGÅRD), *Eurytreta* cf. *sabrinae* (CALLAWAY) and trilobites; (2) the Agalatas Formation comprising mostly limestones up to 400 m thick with *Lingulella? antiquissima* (JEREMEJEW) in the basal unit of cross bedded sandstone, conodonts of the *Drepanoistodus proteus* Biozone, and a diverse assemblage of lingulate microbrachiopods and trilobites in a black limestone unit in the uppermost part; and (3) the mainly siliciclastic Kurday Formation more then 470 m thick.

Tritoechia kendyktasica RUKAVISHNIKOVA is one of the most common brachiopod species in the uppermost Agalatas Formation and the lower Kurday Formation. It occurs at numerous localities exposed in the middle reaches of the Agalatas River on both sides of the valley (Fig. 2). Specimens for the present
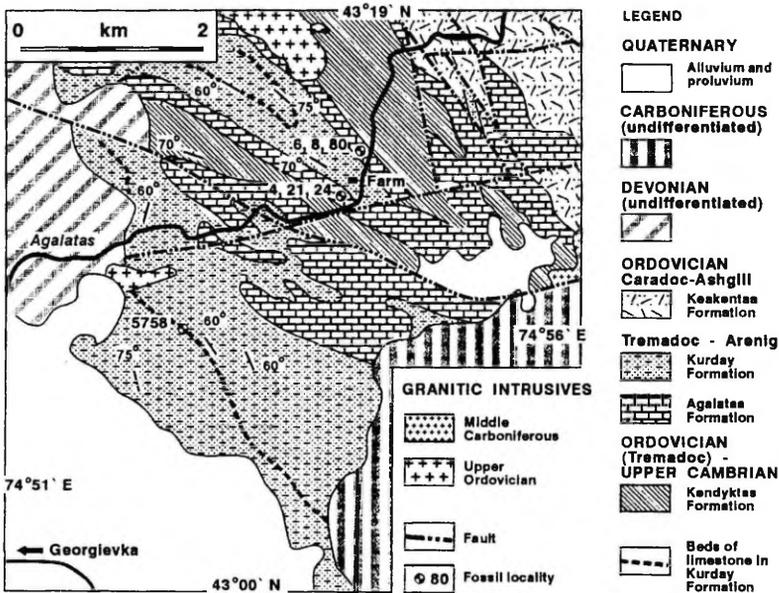

Figure 2. Generalised geological map of Agalatas river valley in southern Kendyktas Range (after B. A. Salin, unpublished) showing position of fossil localities with tritoechiids.

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study were sampled from localities 6, 4, 8, 21, 24, 80, 82 of Rukavishnikova (locality numbers of South Kazakhstan Geological Survey, 1947).

Tritoechia tokmakensis nov. sp. occurs only in three samples 5758, 7384 and 7386 of B. A. Salin (locality numbers of South Kazakhstan Geological Survey, 1958) from the sandstone unit of the Kurday Formation exposed south of the Agalatas River valley (Fig. 1, 2).

CHU-ILI RANGE

All known occurrences of the described brachiopods in the Chu-Ili Range are confined to the Uzunbulak Formation (Llanvirn) exposed between the rivers Kopalysai and Astchisu (Figs 1, 3). An outline of the geology and Ordovician stratigraphy of the region is given by Nikitin (1972), Melnikova (1986) and Nikitina & Timofeeva (1991).

Tritoechia crassa nov. sp. was sampled from two localities exposed west of the Uzunbulak river valley (Fig. 1, 3). This brachiopod occurs in a grey siltstone unit with some beds of calcarenite totalling 35–65 m thick (Unit 6 of Nikitina & Timofeeva 1991: 41, fig. 1b) in association with the brachiopods *Orthidium* sp., *Taphrodonta* nov. sp. and *Leptellina* cf. *seletensis* NIKITIN & POPOV.

Pomatotrema fecunda nov. sp. and *Martellia reliqua* nov. sp. are relatively abundant in a total 10–15 m thick unit of nodular algal limestone with thin layers of argillite and siltstone (Unit 3 of Nikitina & Timofeeva 1991; fig. 1a, c; samples 156, 158, 303, 304, F-129) exposed between the rivers Kujandysai and Kstausai. The associated fossils include calcareous sponges, the brachiopods *Paralenorthis rgaitensis* (NIKITINA), *Yangtzella* sp., *Aporthophyla kasachstanica* RUKAVISHNI-KOVA, *Christiania hastata* RUKAVISHNIKOVA, and the trilobites *Anamitella granulata* (WEBER).

Pomatotrema fecunda nov. sp. was also sampled from thin (0.3–0.8 m) beds of calcarenite in the upper part of the Uzunbulak Formation (Unit 9, sample F-111 of Nikitina & Timofeeva, 1991: 42, fig. 1c) in the association with the brachiopods *Orthidium* sp., *Paralenorthis rgaitensis* (NIKITINA), *Toquimia* sp., and *Christiania hastata* RUKAVISHNIKOVA.
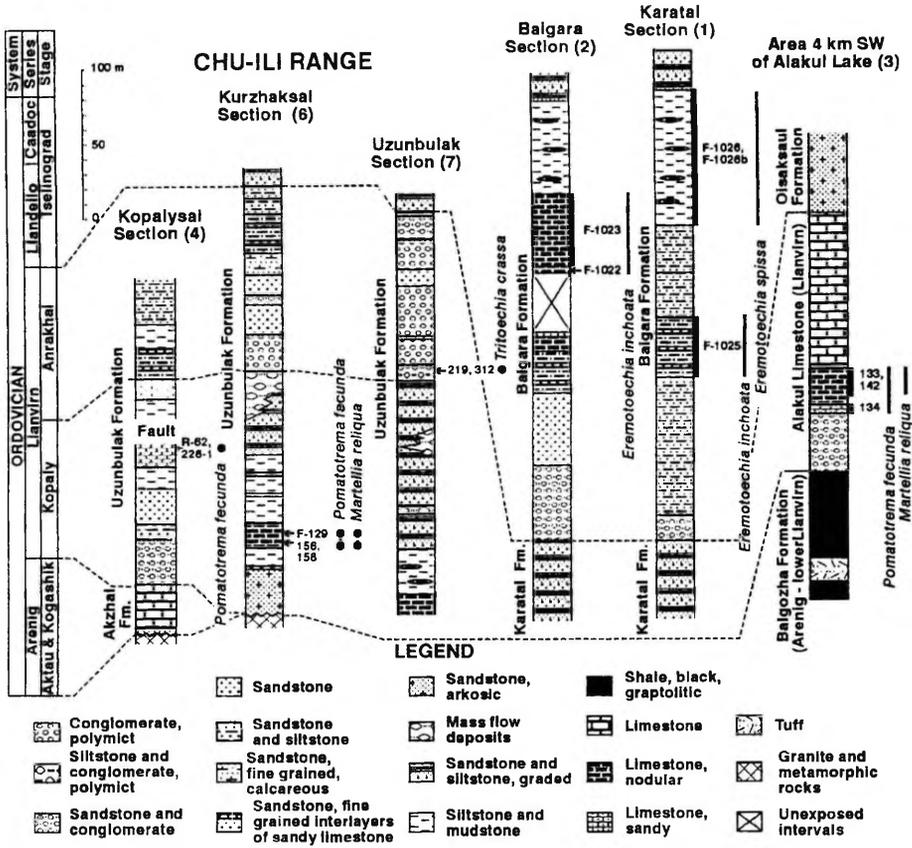
Figure 3. Generalised stratigraphical columns of the Arenig to lower Caradoc deposits in the south Betpak-Dala desert, south Chu-Ili Range and area south-west of Alakul Lake showing stratigraphical position of the samples with tritoechiids. Numbers of the localities are the same as on Fig. 1A.

AREA ABOUT 4 KM SOUTH-WEST OF LAKE ALAKUL

A succession of Arenig and Llanvirn volcanic and sedimentary rocks is exposed within the quadrangle covering 44°45'–44°50'N and 74°00'–74°07'30"E (Figs 1, 3). The geology and stratigraphy of the area was outlined briefly by Melnikova (1986: 9, fig. 3). *Pomatotrema fecunda* nov. sp. and *Martellia reliqua* nov. sp. occur here in the lower part of the unnamed limestone formation which is 135 m thick. Silicified brachiopods were sampled here from a bed of nodular, stromatolitic limestone (samples 133, 134 of O. I. Nikitina). The associated fauna includes

stromatoporoids, the brachiopods *Archaeorthis* sp.; *Tuvinia* sp.; *Trematorthis* sp.; *Aportophyla kasahstanica* RUKAVISHNIKOVA; and *Leptella* sp., the trilobites *Annamitella granulata* (WEBER); *Bumastoides betpakensis* WEBER, *Illaenus* sp.; the ostracodes *Coeloenellina inconstans* MELNIKOVA, and *Alakolites superbus* MELNIKOVA. This assemblage suggests an early Llanvirn age and correlation with the Kopalyan Stage.

SOUTH BETPAK-DALA

The youngest known described brachiopods in Kazakhstan are two species of *Eremotoechia*, which occur in the lower Baigara Formation exposed in the southern Betpak-Dala desert between the Karatal River and the Baigara Mountain (Fig. 1, 3). The Ordovician geology and stratigraphy of this area was outlined by Palets (1965) and Nazarov & Popov (1980). The Baigara Formation sits unconformably on the Karatal Formation comprising graded sandstones and siltstones with some tuff beds and including graptolites characteristic of the Kopalyan and Anrakhaian stages (Llanvirn), overlain in turn by Anderken Formation (lower to middle Caradoc) made up of polymict conglomerates, sandstones and siltstones with the brachiopods *Ectenoglossa sorbulakensis* POPOV, *Phragmorthis conciliata* POPOV, and *Sowerbyella rukavishnikovae* POPOV, among others.

Eremotoechia inchoata is relatively abundant in the lower part of the Baigara Formation, in the section exposed about 7 km south-west of Baigara Mountain (Figs 1, 3). This species occurs in the beds of nodular limestone, about 65 m thick (units 8 and 9 after Nazarov & Popov 1980, p. 11), together with the brachiopods *Paralenorthis numerosa* (NIKITIN & POPOV); *Grammoplecia* sp.; *Shlyginia* cf. *declivis* NIKITIN & POPOV, *Ishimia ishimensis* NIKITIN, *Strophomena rukavishnikovae* NIKITINA, etc. (samples F-1022, F-1023). The upper part of the Baigara Formation in this section consists of graded sandstones and siltstones total up to 630 m thick, containing the rare graptolites *Climacograptus* sp., *Dicellograptus* sp. and *Leptograptus* sp. (Palets 1965).

Both *Eremotoechia inchoata* and *E. spissa* occur in another section exposed about 20 km north-west of Baigara Mountain, and about 1 km west of the Karatal river. The lower part of the Ordovician here comprises the following sequence in ascending order from the base:

1. Conglomerate, polymict, about 17 m thick.
2. Alternating green and brownish red sandstones and siltstones with lenses of polymict conglomerate, about 95 m thick.
3. Siltstones and fine grained sandstones, greyish green and brownish green with several beds and lenses of nodular argillaceous limestones, total 103 m thick. *Eremotoechia inchoata* occurs in this unit in an association of brachiopods *Paralenorthis numerosa*, *Ishimia ishimensis*, *Shlyginia* cf. *declivis*, etc. (sample F-1025).

4. Alternating fine-grained sandstones and siltstones with lenses and nodules of argillaceous limestones, total 90 m. *Eremotoechia spissa* occurs in sandstone (sample F-1026) and limestone lenses (sample F-1026b), together with brachiopods *Trematis* aff. *parva* COOPER, *Pseudocrania karatalensis* POPOV, *Paralenorthis numerosa*, *Grammoplecia globosa* (NIKITIN & POPOV), *Kajnaria derupta* NIKITIN & POPOV, and *Bimuria* sp.
5. Sandstones and siltstones, graded, up to 1000 m thick. The lower ~50 m of this unit contains the brachiopods *Paralenorthis numerosa*, *Bimuria* sp., *Sowerbyella verecunda* NIKITIN & POPOV (sample F-1026a).

SOUTH URALS

In the South Urals two described below species *Protambonites lermontovae* (ANDREEVA) and *Korinevskia akbulakensis* (ANDREEVA) were sampled in four sections from the predominately clastic Kidryas, Alimbet and Akbulaksay formations, which are mostly stratigraphic equivalent of the Hunnebergian Stage (uppermost Tremadoc and lowermost Arenig) of Baltoscandia (Popov & Holmer 1994). Details of the Ordovician geology, lithostratigraphy and characteristic faunal are given by Korinevskiy (1989) and Popov & Holmer (1994).In the South Urals two tritoechiid species *Protambonites lermontovae* (ANDREEVA) *Korinevskia akbulakensis* (LESSNIKOVA in ANDREEVA) were sampled in four sections from the predominately clastic Kidryas, Alimbet and Akbulaksay formations, which mainly represent stratigraphic equivalent of the Hunneberg Stage (uppermost Tremadoc and lowermost Arenig) of Baltoscandia (Popov & Holmer 1994). A detailed outline of Ordovician geology, lithostratigraphy and characteristic faunal assemblages of these localities was provided by Korinevskiy (1989) and Popov & Holmer (1994).

In the Tyrmantau Range, east of Novodmitrievka village (Fig. 1) *Protambonites lermontovae* was sampled from the isolated locality B-786-6 (Korinevskiy 1989; Popov & Holmer 1994: 11, fig. 10), referred to the upper part of the Kidryas Formation. The associated brachiopods include *Altorthis kinderlensis* ANDREEVA and *Medessia uralica* ANDREEVA.

In the Tyrmantau Range east of the Novodmitrievka village (Fig. 1) *Protambonites lermontovae* was sampled from the isolated locality B-786-6 (Korinevskiy 1989; Popov & Holmer 1994, p. 11, fig. 10) referred presumably to the upper part of the Kidryas Formation. The associated brachiopod assemblage includes *Altorthis kinderlensis* ANDREEVA and *Medessia uralica* ANDREEVA. In the section exposed on the east side of the Alimbet River about 2.5–3 km south of Alimbet farm (Fig. 1), *Protambonites lermontovae* occurs together with *Altorthis kinderlensis* in the middle part of the Akbulaksai Formation (Korinevsky 1989; Popov & Holmer 1994: 16, figs 15–16, Unit 4, sample 778-2).

In the section exposed on the east side of the Alimbet River about 2,5–3 km south of the Alimbet farm (Fig. 1) *Protambonites lermontovae* occurs together

with *Altorthis kinderlensis* in the middle part of Akbulaksai Formation (Korinevsky 1989; Popov & Holmer 1994, p. 16, fig. 15–16, Unit 4, sample 778-2).

In the upper reaches of the Akbulaksai River, the same species occur in a number of samples from the Akbulaksai Formation (Korinevskiy 1989; Popov & Holmer 1994: 16, fig. 17–18). In the lower part of this formation (samples B-607-9, B-607-15), *Korinevskia akbulakensis* occurs in association with the lingulide *Hyperobolus andreevae* (POPOV & HOLMER) and the acrotretides *Eurytreta chabakovi* (LERMONTOVA) and *Acrotreta korinevskii* (HOLMER & POPOV), while *P. lermontovae* occurs in the upper part of this formation (samples B-607-1, B-607-7, B-607-8) together with *Altorthis kinderlensis*, *Medessia uralica* ANDREEVA and *Alimblella armata* ANDREEVA.

In the upper reaches of the Akbulaksai River tritoechiide brachiopods occur in a number of samples from the Akbulaksai Formation (Korinevskiy 1989; Popov & Holmer 1994, p. 16, fig. 17–18). The lower part of this formation (samples B-607-9, B-607-15) *Korinevskia akbulakensis* was found in association with the lingulide *Hyperobolus andreevae* (POPOV & HOLMER) and acrotretides *Eurytreta chabakovi* (LERMONTOVA) and *Acrotreta korinevskii* (HOLMER & POPOV), whereas *Protambonites lermontovae* occurs in the upper part of this formation (samples B-607-1, B-607-7, B-607-8) together with *Altorthis kinderlensis*, *Medessia uralica* and *Alimblella armata* Andreeva.

Protambonites lermontovae is also characteristic of the upper part of the Akbulaksai Formation exposed on the west side of the Koagash river (Popov & Holmer 1994: 20, fig. 21, Unit 5, samples B-786, G-196-1, B-786) where it occurs together with *Thysanotos siluricus* (EICHWALD) and *Leptembolon lingulaeformis* (MICKWITZ).

Protambonites lermontovae is also characteristic of the upper Akbulaksay Formation exposed on the west side of the Koagash river (Popov & Holmer 1994, p. 20, fig. 21, Unit 5, samples B-786, G-196-1). The co-occurrence of *Protambonites lermontovae* together with *Thysanotos siluricus* (Eichwald) and *Leptembolon lingulaeformis* (MICKWITZ) in this section (sample B-786) is remarkable.
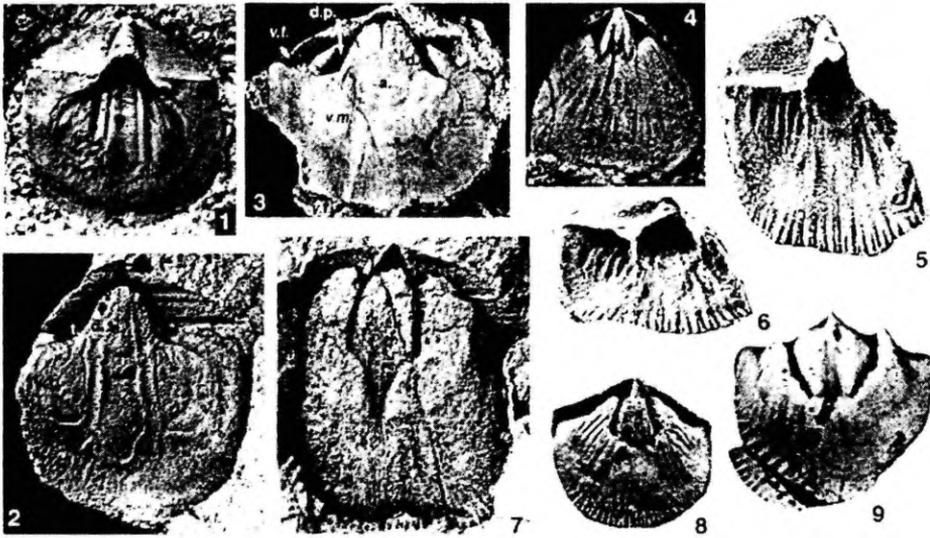
Figure 4. Ventral valve interiors of selected billingsellid and tritoechiid species. **1,** *Billingsella* sp.; Upper Cambrian, Kujandy Formation, east side of Olenty River north-western slope of Aksak-Kujandy mountain, north-central Kazakhstan; CNIGR 1/12604, ventral valve interior, × 2. **2,** *Billingsella* sp.; Upper Cambrian, Kujandy Formation, sample 7837, Satpak, north-central Kazakhstan; ventral internal mould showing strong teeth lacking dental plates (t.), broad, triangular adductor track (a.) much longer then narrow diductor scars (d.), saccate mantle canals with subparallel *vascula media* (*v.m.*) and *vascula terminalia* (*v.t.*) developed along the posterior margin × 2. **3.** *Korinevskia akbulakensis* (Andreeva); Lower Ordovician, Akbulaksai Formation, sample B607-9, Akbulaksai, South Urals; NMW98.67G10, ventral internal mould showing well developed dental plates (d.p.), saccate mantle canals and large ventral muscle field, × 2. **4,** *Tritoechia crassa* nov. sp.; Ordovician, Llanvirn, Uzunbulak Formation, sample 219, Kurzhaksai section, Chu-Ili Range; USNM 485066, ventral internal mould, showing small ventral muscle field with strongly impressed diductors slightly longer than strongly raised adductor muscle scar and pinnate mantle canals, × 2. **5–7,** *Protambonites lermontovae* (Andreeva); Lower Ordovician, Akbulaksai Formation, Akbulaksai, South Urals; **5–6,** sample B607-1, NMW98.67G.2, ventral valve, latex cast of interior, oblique anterior view of interior, × 2; **7,** sample B786, Koagash river, NMW98.67G.3, ventral internal mould, × 2. **8,** *Tritoechia tokmakensis* nov. sp., Ordovician, Arenig, Kurday Formation, sample 5758, left side of Agalatas River, Kendyktas Range; NMW 98.64G.11, holotype, ventral internal mould, × 2. **9.** *Martellia reliqua* nov. sp., Ordovician, Llanvirn, Uzunbulak Formation, sample 158, Kurzhaksai section, Chu-Ili Range, NMW 98.28G.2, ventral view of internal mould showing pseudospondylium and narrow adductor track, × 2.7.

KEY FEATURES OF SHELL MORPHOLOGY KEY FEATURES OF SHELL MORPHOLOGY

The latest analysis and interpretation of shell morphology of the Suborder Clitambonitidina, to which *Tritoechia* and related genera have been assigned until now, is based mostly on Baltoscandian taxa (Wright & Rubel 1996). Their study reinterpreted the nature and importance of some critical features including delthyrial covers, characters of muscle scars and mantle canal configurations, but mostly in the clitambonitids and gonambonitoids. The family Tritoechiidae was established by Ulrich and Cooper (1936), but was synonymised subsequently with the family Polytoechiidae (Williams 1965; Rubel and Wright 2000). However, *Polytoechia*, the type genus of this family, has a complex ventral muscle platform between separated dental plates, and is elevated anteriorly on a median septum (Williams *et al.* 2000: 391). A similar muscle platform is also characteristic of *Antigonambonites* and *Raunites*, as demonstrated recently by Vinn & Rubel (2000). The ventral platform in these three genera is different from a typical pseudospondylium because it is raised anteriorly and supported throughout by the median septum; however, it is not homologous with the spondylium triplex of Gonambonitidae as in *Oslogonites* and *Estlandia* because it is formed between separated dental plates and does not represent a true spondylium (Vinn & Rubel 2000).

In all other genera within the Polytoechioidea (e.g., *Tritoechia, Eremotoechia, Martellia, Pomatotrema* and *Protambonites*), as defined by Rubel & Wright (2000), the ventral muscle field is confined mainly to the bottom of the delthyrial cavity between long, divergent to subparallel dental plates (Figs 4.5–4.9; 7), and they lack a true spondylium in contrast to Clitambonitoidea, or a muscle platform raised anteriorly on the median septum characteristic of *Polytoechia*. The highly raised ventral muscle field of *Martellia* was interpreted erroneously as a sessile spondylium by Wirth (1936). Wirth (1937) again reported the presence of a *spondylium simplex* in juvenile *Martellia*, but as seen in transverse sections, the median ridge does not provide support to the raised ventral muscle field in this genus (Figs 7.1–7.4); instead the muscle field is situated directly on the thickened valve area known as a pseudospondylium (*sensu* Williams *et al.* 2000).

There is a constant difference between Polytoechioidea and Clitambonitoidea in detailed morphology of the deltidiodont teeth. Teeth in the majority of Polytoechioidea are commonly large, transverse, subparallel to the hinge line, anteriorly directed and only slightly inclined to the commissural plane (Figs 4.6, 5.5, 6.1), as in *Billingsella* (Fig. 4.1). This patternusually correlates with the presence of a strongly apsacline ventral interarea. A subpyramidal ventral valve with procline interarea and oblique teeth, like as *Tritoechia billingsi* NEUMAN or *Tritoechia. crassa* sp. nov., is very rare and appears late in the phylogeny of the group. By contrast, teeth of Clitambonitoidea are oblique, curved dorsally and bluntly triangular in outline (Wright & Rubel 1996; pl. 2, figs 2–4; pl. 4, figs 6–8), and subpyramidal ventral valves with procline to catacline interareas are quite

characteristic and appear in the earliest known representatives of the superfamily (Rubel & Popov 1994).

Wright & Rubel (1996) provide a detailed discussion of the development of the foramen and delthyrial covers in a number of genera of the Clitambonitoidea. It is remarkable that the earliest and apparently most primitive genera of this superfamily (e.g. *Apamotella* and *Neumania*) lack integral delthyrial covers (Rubel & Popov 1994), whereas derived taxa (e.g., *Clitambonites, Ilmarinia* and *Vellamo*) possess a true deltidium formed by fusion of the deltidial plates beneath the pedicle opening. As a difference, a complete delthyrial cover of Tritoechiidae aod Polytoechiidae is present already in the earliest genera (e.g. *Tritoechia* and *Protambonites*) formed by a single, convex plate perforated at the beak by a minute supra-apical foramen, which may be sealed in some genera (Figs 4.3–4.4; Pl. 3, figs 16, 24). The observed pattern suggests clearly that the delthyrial covers in tritoechiid genera are not significantly different from those of billingselloideans (Fig. 4.1–4.2), and can be classified therefore as a pseudodeltidia.

Aditicules and hollow ribs are among the most characteristic features of surface ornament in the Clitambonitidae (Wright & Rubel 1996). We have not observed these in Kazakhstanian species of *Eremotoechia* and *Tritoechia*, but they are definitely present in *Pomatotrema*, which is characterised by very fine and closely spaced concentric lamellae (Pl. 3, fig. 15, 17). Aditicules and hollow ribs are also known in *Tritoechia typica* (Ulrich & Cooper 1938, pl. 33, fig. 26).

The dorsal adductor muscle scars in Tritoechiidae are arranged radially (Fig. 5; Pl. 2, fig. 7). This disposition is notably different from genera of the Clitambonitidae as redefined by Rubel & Wright (2000), which are characterised by a quadripartite dorsal muscle field (Rubel & Popov 1994, pl. 1, fig. 3; Wright & Rubel 1996: 64). Radially arranged dorsal adductor scars are also characteristic of the families Billingsellidae (Williams *et al.* 1996) and Gonambonitidae (Rubel 1963; Rubel & Wright 2000).

Öpik (1934) described pinnate mantle canals in both valves as one of the most distinctive features of the Clitambonitidina. Wright & Rubel (1996, text-fig. 3-4) demonstrated that saccate mantle canals occur in early Ordovician genera of the family Atelellasmatidae (e.g., *Apomatella* and *Neumania*), and also characterise some taxa of the family Clitambonitidae (e.g., *Ladogiella*). In the family Tritoechiidae as considered below, both pinnate and saccate mantle canal patterns occur in the ventral valve. In particular, pinnate ventral mantle canals are characteristic of *Protambonites* (Havliček & Josopait 1972) and the Kazakhstanian species *Tritoechia crassa* (Fig. 4.4). The presence of pinnate mantle canals in the ventral valve of *Martellia* was reported by Wirth (1936), but it has not been confirmed in the present study of the Kazakhstanian *Martellia reliqua* and the Chinese *Martellia ichangensis*. The ventral mantle canals in both taxa are invariably saccate. A saccate condition is also characteristic of *Tritoechia kendyktasica* (Fig. 6.1) and *Tritoechia tokmakensis*. Both tritoechiids and billingsellids possess *vascula terminalia* extending across the ventral interarea (Fig. 4.1, 4.3, 6.1).
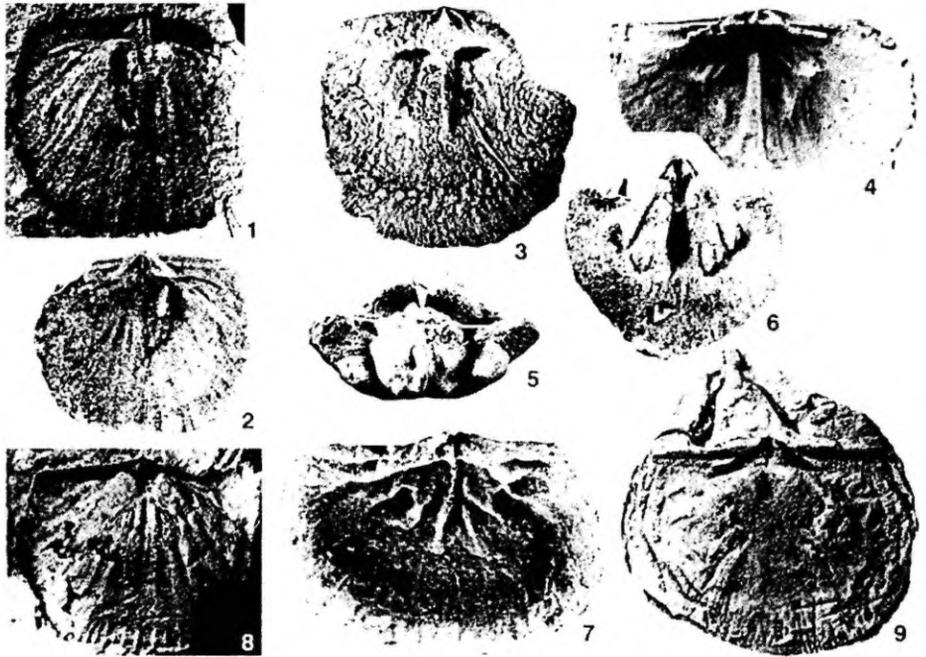
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Figure 5. Dorsal valve interiors of selected billingsellid and tritoechiid species. **1–2, 8,** *Protambonites lermontovae* (Andreeva); Lower Ordovician, Akbulaksai Formation, sample B607-1, Akbulaksai, South Urals, NMW98.67G1, dorsal valve, internal mould, × 2, latex cast of interior, × 1.7; **8,** sample B786, Koagash river, NMW98.67G.4, dorsal internal mould, × 2. **3, 7,** *Pomatotrema fecunda* nov. sp.; Ordovician, Llanvirn, **3,** Alakul Limestone, sample 133, area 4 km SW of Alakul Lake; NMW 98.28G.6, dorsal valve interior showing radially arranged adductor scars situated on a callus of secondary shell, high median septum and high notothyrial platform steeply inclined posteriorly, × 3; **7,** Uzunbulak Formation, sample F-111, Kujandysai section, Chu-Ili Range, NMW 98.28G.7, latex cast of dorsal interior of juvenile specimen, × 7.5. **4,** *Tritoechia crassa* nov. sp.; Ordovician, Llanvirn, Uzunbulak Formation, sample 219, Kurzhaksai section, Chu-Ili Range; USNM 485068, latex cast of dorsal interior, × 4. **5–6,** *Martellia reliqua* nov. sp.; Ordovician, Llanvirn, Uzunbulak Formation, sample 158, Kurzhaksai section, Chu-Ili Range, NMW 98.28G.2, posterior and dorsal views of internal mould showing dip umbonal cavities in dorsal valve separated by high median septum and strongly impressed adductor scars, × 3.3. **9,** *Tritoechia kendyktasica* Rukavishnikova; Lower Ordovician, Agalatas Formation, sample 24, right side of Agalatas River, Kendyktas Range; NMW 98.64G.6, dorsal view of internal mould, showing relatively low notothyrial platform and weekly developed median ridge, × 4.

Shell structure remains poorly known in Polytoechioidea. A difference from billingsellids is that secondary shell is fibrous in *Eremotoechia* (Williams 1968), but is unknown in other tritoehciides. *Antigonambointes*, which is regarded here as

a member of the Polytoechiidae, is also characterised by a pseudopunctate shell with a fibrous secondary layer. Shell structure is potentially important for evaluation of the phylogenetic relationships of early rhynchonelliformeans, but this character is difficult to use at present because of inadequate knowledge of most of the Cambrian stocks including kutorginides, protorthides and early orthides.

SYSTEMATIC PALAEONTOLOGY

Specimens studied are deposited in the Geological Museum, Institute of Geological Sciences of Kazakhstan, Almaty (IGNA); Central Scientific-Research and Geological Exploration Museum, St Petersburg (CNIGR); National Museum of Wales, Cardiff (NMW); United States National Museum, Washington (USNM).

Abbreviations and statistics in the tables of measurements and text are as follows: Lv, Ld = sagittal ventral and dorsal valve length; W = maximum width; Iw = width of interarea; IHv, IHd = height of ventral and dorsal interarea; T = thickness of shell; Tv = height of ventral valve; Td = height of dorsal valve; MVl, MVw = length and width of ventral muscle field; MDl, MDw = length and width of dorsal muscle field; Sl = length of dorsal median ridge; X = mean; S = standard deviation from the mean; OR = observed range; MAX = maximum value; MIN = minimum value.

Order BILLINGSELLIDA Schuchert, 1893
Superfamily POLYTOECHIOIDEA Öpik, 1934

Discussion. In the recently proposed classification of the Palaeozoic rhynchonelliformean Polytoechioidea, they are regarded as a separate superfamily within the suborder Clitambonitidina of the order Billingsellida (Rubel & Wright 2000). Currently available data on the early ontogeny of the clitambonitoidean shell demonstrate, that there are no discrete dental plates in clitambonitoideans, and that spondylial structures both in clitambonitids and gonambonitids developed from a free spondylium, which strongly resembles a free muscle platform, or spondylium in the ventral valve of the Cambrian protorthides (Vinn & Rubel 2000). Similar structures are not at all characteristic of either Billingselloidea, which lack dental plates and any kind of spondylium, nor Polytoechioidea, which have well developed separate dental plates. This suggests that the present concept of Clitambonitidina is heterogeneous. As outlined above, Polytoechioidea demonstrate a number of distinct similarities to billingsellides, and this stock is retained here therefore within the order Billingsellida, whereas Clitambonitoidea in a strict sense are placed rather distantly from both groups and their affinities to the protorthides and early orthides should be re-evaluated.

Family TRITOECHIIDAE ULRICH & COOPER, 1936

Diagnosis (emended). Shell dorsibiconvex to ventribiconvex, impunctate, radial ornament costellate, concentric lamellae variably developed; ventral interarea apsacline to cataclyne with pseudodeltidium and minute supra-apical foramen; notothyrium covered by chilidial plates or chilidium; ventral interior with well developed dental plates; ventral muscle field confined mainly to base of delthyrial cavity, with adductor scar completely separating diductor scars; dorsal interior with widely divergent socket ridges, broad, highly raised, a high, posteriorly inclined notothyrial platform and simple ridge-like cardinal process; dorsal adductor scars radially arranged; ventral mantle canals saccate or pinnate, dorsal mantle canals pinnate.

Genera assigned. *Tritoechia* ULRICH & COOPER, 1936; *Acanthotoechia* WILLIAMS & CURRY, 1985; *Admixtella* ROZMAN, 1978; *Asymphylotoechia* ROSS, 1970; *Eremotoechia* COOPER, 1956; *Martellia* WIRTH, 1936; *Peritritoechia* XU, RONG & LIU, 1974; *Platytoechia* NEUMAN, 1964; *Pomatotrema* ULRICH & COOPER, 1932; *Protambonites* HAVLÍČEK, 1972.

Discussion. Tritoechiidae differs from Polytoechiidae mainly in the characters of the ventral muscle field. In the latter family this musculature is situated on the muscle platform a raised high anteriorly on a median septum, whereas in Tritoechiidae it rests on the floor of the delthyrial cavity or is situated on a solid pseudospondylium. As was mentioned by Williams *et al.* (2000) the ventral muscle platform of *Polytoechia* is situated between separated dental plates and represents a highly modified pseudospondylium. Therefore its affinity to the *spondylium triplex* of Gonambonitidae is superficial. Vinn & Rubel (2000) provide evidence that ventral muscle platforms similar to *Polytoechia* are characteristic also of *Antigonambonites* and *Raunites*. These two genera also possess a pseudodeltidium and should therefore be reassigned to the family Polytoechiidae.

Genus *Tritoechia* ULRICH & COOPER, 1936

Type species. *Deltatreta typica* ULRICH & COOPER, 1932 from the Lower Ordovician, Arbuckle Limestone of Oklahoma, USA.

Remarks. The present concept of *Tritoechia* is in need of revision. The genus includes species with both parvicostellate and multicostellate radial ornaments. Aditicules characteristic of the type species may be completely absent in others, and ventral mantle canals are saccate in *Tritoechia kenyctasica*, whereas they are clearly pinnate in *Tritoechia typica*. The type species is also characterised by a relatively large, suboval, supra-apical foramen crossing the growth lines, whereas in the majority of other species it is preserved as a minute circular opening within the apex. Separated chilidial plates, sometime joined apically are characteristic of

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most *Tritoechia*, but some late Arenig and Llanvirn species, e.g. *Tritoechia billingsi* NEUMAN, 1968 as well as described below *Tritoechia crassa* nov. sp. possess a complete chilidium. *Tritoechia efimovae* ORADOVSKAJA, 1968, from the upper Arenig, Elgenchak Formation of north-east Siberia, is unique in having a uniplicate anterior commissure, distinct ventral sulcus and dorsal median fold. It may represent a separate new genus transitional between *Tritoechia* and *Eremotoechia*.

Tritoechia crassa nov. sp.

Pl. 1, figs 14–26, Figs 4.4, 5.4

Etymology. From Latin *crassus*, thick, stout.

Holotype. USNM 485064, conjoined valves, Ordovician, Llanvirn (Anrakhaian Stage), Uzunbulak Formation,

Material. 63 mostly exfoliated complete shells, dorsal and ventral external and internal moulds.

Diagnosis. Shell strongly ventribiconvex, about 80% as long as wide with sulcate anterior commissure; ventral interarea high, steeply apsacline to catacline; dorsal sulcus shallow, originating at the umbo; chilidium well developed; radial ornament parvicostellate with 4–6 ribs per 3 mm along anterior margin; ventral muscle field slightly elongated, raised anteriorly; fine ventral median ridge meets anterior termination of adductor scars.

Description. Shell highly ventribiconvex, subquadrate in outline, with slightly obtuse cardinal extremities. Maximum width near midlength, slightly greater than both hinge width and length. Anterior commissure weakly sulcate. Ventral valve pyramidal, with maximum height at the umbo, about 79% (OR=66–96%, N=5) as long as wide and 56% (OR=50–66%, N=5) as high as long. Ventral interarea high, plane, steeply apsacline to catacline, with radial striae parallel to sides of delthyrium, about 87% (OR=77–94%, N=4) as wide as maximum valve width. Delthyrium covered by convex, apically perforated pseudodeltidium. Dorsal valve moderately convex, about 74% (OR=61–83%, N=3) as long as wide and 27% (OR=18–32%, N=3) as high as long, gently convex in lateral profile, with maximum height somewhat posterior to the mid-valve. Dorsal interarea low, planar, anacline, with notothyrium completely covered by a convex chilidium. Sulcus originating at the umbonal area, deepening towards the anterior margin.
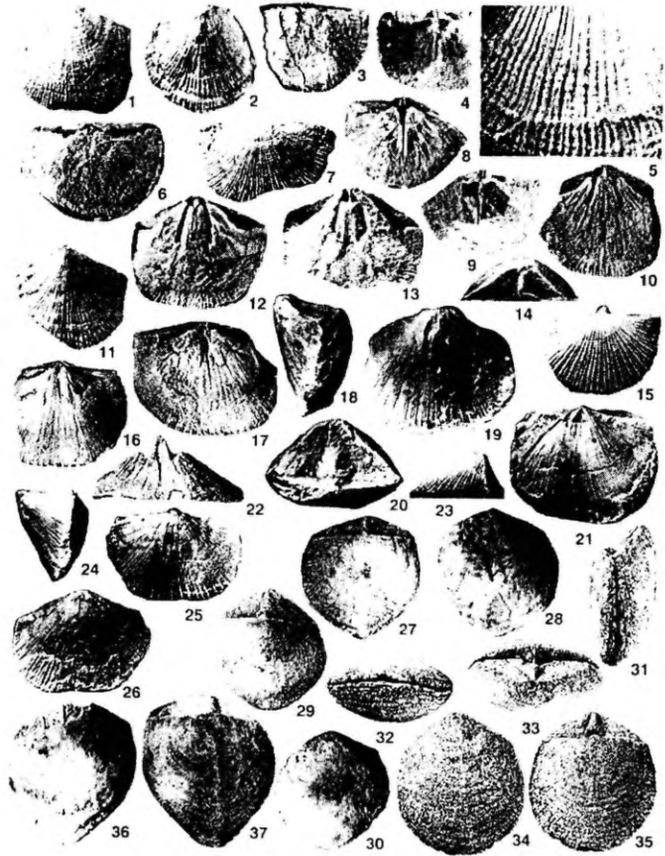
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PLATE 1

Figs 1–13. *Tritoechia tokmakensis* nov. sp., Ordovician, Arenig, Kurday Formation, sample 5758, left side of Agalatas River, Kendyktas Range; **1, 5**, NMW 98.64G.11, ventral exterior, latex cast, × 2, radial ornament, external mould, × 5; **2**, NMW 98.64G.12, ventral exterior, latex cast, 2; **3–4**, NMW 98.64G.14, dorsal interval mould and latex cast, × 2; **6**, NMW 98.64G.15, dorsal internal mould, × 2; **7**, NMW 98.64G.16, dorsal valve exterior, latex cast, 2; **8–9**, NMW 98.64G.17, dorsal interval mould and latex cast, × 2; **10**, NMW 98.64G.18, ventral internal mould; **11**, NMW 98.64G.19, ventral exterior, latex cast, × 2; **12**, NMW 98.64G.13, ventral internal mould; **13**, NMW 98.64G.20, ventral internal mould, × 2.

    Figs 14–26. *Tritoechia crassa* nov. sp., Ordovician, Llanvirn, Uzunbulak Formation, sample 219, Kurzhaksai section, Chu-Ili Range; **14–15, 23**, USNM 485069, latex cast of ventral valve, posterior, ventral and lateral views, × 2; **16**, USNM 485063, dorsal internal mould, × 2; **17**, CNIGR 3/12604, dorsal internal mould, × 2; **18–21**, USNM 494065, exfoliated conjoined valves, holotype, lateral, ventral, posterior and dorsal views, × 2; **22**, CNIGR 4/12604, ventral internal mould, × 3; **24–26,** USNM 494064, exfoliated conjoined valves lateral, dorsal and ventral views, × 2.

    Figs 27–37. *Martellia reliqua* nov. sp., Ordovician, Llanvirn; **27–30, 36–37**, Uzunbulak Formation, Chu-Ili Range; **31–35**, Alakul Limestone, sample 133, area 4 km SW of Alakul Lake; **27–28**, NMW 98.28G1, conjoined valves ventral and dorsal views, sample, 156, × 2,5; **29–30,** collection of I. F. Nikitin, conjoined valves, dorsal and ventral views, × 2,3; **31–35**, NMW 98.28G.2, conjoined valves of aberrant specimen, lateral, anterior, posterior, ventral and dorsal views, × 2; **36–37, —** NMW 98.28G.3, holotype, conjoined valves ventral and dorsal views, sample, 158, × 2,5.

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Radial ornament unequally and finely parvicostellate. Most of the costellae are added by intercalation, a few by branching; they vary in number from 6 to 8 per 3 mm through the mid part of the shell and decrease to 4–6 near the anterolateral margins of full grown specimens more then 10 mm long. Concentric ornament of fine, closely spaced, elevated fila cross the costellae.

Ventral interior with short, wide teeth, supported by short dental plates merging on the shell floor with raised lateral margins of muscle field. Muscle field slightly elongate, subtriangular. Narrow, drop-shaped diductor scars are set below the narrow adductor track, anteriorly rounded, extending beyond but not enclosing adductor scars. Ventral median ridge short and narrow, joined to anterior termination of adductor scars, fading at mid-length of the valve. Mantle canals probably pinnate, weakly impressed, limited to a pair of straight divergent *vascula media* and four thin, radially disposed imprints of *vascula genitalia* on posterolateral quarter of shell floor.

Dorsal interior with an elevated, posterior-sloping, triangular notothyrial platform defined laterally by chilidial bases. Cardinal process simple, increasing in height and thickness across platform length. Socket ridges long, widely divergent, bounding wide, narrow, triangular sockets. Adductor field large, radial, bisected by the median ridge that extends from the beneath platform to mid-length of the valve; posterior pair of adductor scars on thickened shell large, elongate, extending to about mid-length of deeply impressed anterior pair. Faint, radial ridges on posterolateral part of shell floor are probably remnants of *vascula genitalia*.

Measurements. See Table 1.

Remarks. *Tritoechia crassa* is similar to *Tritoechia billingsi* NEUMAN (1968: 38; pl. 1–3, figs 2a–i) from the Shin Brook Formation of New Brunswick, Canada both having strongly ventribiconvex shell with high ventral interarea, parvicostellate radial ornament, complete chilidium, and short dental plates, but the former differs from the latter in its dorsal sulcus and sulcate anterior commissure. *Tritoechia occidentalis* ULRICH & COOPER (1938: 164; pl. 31, figs 18, 22–26) from the Sarbach Formation of Alberta, Canada and from the Dawan Formation of South China (Zeng 1977) possesses also a high, strongly apsacline to near procline ventral interarea and fine parvicostellate radial ornament, but the Kazakhstanian species differs from it in its higher, subpyramidal ventral valve, well developed dorsal sulcus, and complete chilidium.

There is a number of species of the genus with variably developed dorsal sulcus (e.g. *Tritoechia dice* (WALCOTT) (Ulrich & Cooper 1938: 163; pl. 31, figs 14–17, 19–21) from the Look Hill Formation of Vermont and *Tritoechia sinuata* ULRICH & COOPER (1938: 167; pl. 32, fig. 8) from the upper Pogonip Formation of Nevada), but *Tritiechia crassa* differs from them in having a steep, cataline in large specimens ventral interarea and a complete chilidium.

Table 1. Measurements of six specimens of *Tritoechia crassa* sp. nov.

USNM no.	Lv	Ld	W	IW	IHv	IHd	Tv	Td
485070	15.5	16.4	19.8	15.3	8.2	1.2	8.5	3.0
494564	8.5	7.8	12.8	11.0	4.6	–	5.6	2.5
494565	10.5	10.2	12.8	12.0	5.0	0.8	5.2	3.2
485067	13.5	–	14	–	–	–	8.0	–
485069	7	–	10	9	1.5	0.5	3.5	–

Occurrence. Ordovician, Llanvirn, Anrakhaian, Uzunbulak Formation, samples 209, 219, of Kurzhaksai valley; sample 312 of Uzunbulak river; all from Chu-Ili Range, south-central Kazakhstan.

Tritoechia kendyktasica RUKAVISHNIKOVA, 1961

Pl. 3, figs 1–13; Fig. 5.9

1961 — *Tritoechia kendyktasica* Rukavishnikova: 36; pl. 1, figs 4–17.

Holotype. IGNA 2468/2, ventral internal mould, Ordovician, upper Tremadoc — lower Arenig, Aktauan and Kogashikian, Agalatas Formation, west side of Agalatas river, Kendyktas Range, South Kazakhstan.

Material. 12 complete shells and 11 shell fragments.

Diagnosis. Shell transverse, suboval in outline; anterior commissure rectimarginate to weakly sulcate; ventral valve strongly and evenly convex in lateral profile with strongly apsacline, interarea; dorsal valve evenly convex with very shallow sulcus fading anteriorly; radial ornament unequally multicostellate, lacking hollow ribs, with 15–17 costellae per 5 mm at 5 mm from the umbo; ventral muscle field strongly impressed, diductor scars slightly longer then adductor scar; short and broad median ridge present anterior to ventral muscle field; ventral mantle canals saccate with straight, divergent *vascula media* and pouch-like vas*cula genitalia*; dorsal interior with radially arranged adductor scars, anterior pair of which slightly larger than posterior one, bisected by low, short median ridge; dorsal mantle canals pinnate.

Measurements. See Table 4.

Remarks. Rukavishnikova (1961) gave a detailed description and discussion on affinities of this species. It somewhat resembles *Tritoechia delicatula* ULRICH & COOPER (1936: 625; 1938: 162, pl. 31, figs 1–13) from the Arbuckle Limestone of Oklahoma and *Tritoechia typica* ULRICH (Schuchert & Cooper, 1932: 206, figs 10, 15, 19, 30) from the Arbuckle Limestone of Oklahoma in characters of shell

exterior, but differs from both in its smaller size, shorter ventral area and lack of hollow ribs.

T. kendyktasica is also comparable with *Tritoechia lewisi* BROWN (Laurie 1980: 18, fig. 6D–L) from the early Ordovician Florentine Valley Formation of Tasmania in its size, ventribiconvex shell and characters radial ornament, but can be distinguished in having a strongly apsacline ventral interarea, highly raised anteriorly ventral muscle field, strongly and evenly convex transverse ventral profile and in the presence of a short median ridge anterior to the ventral muscle field.

Occurrence. Ordovician, lower Arenig, Agalatas Formation, localities 6, 4, 8, 21, 24, 80, 82 of T. B. Rukavishnikova, Agalatas River, Kendyktas Range, south Kazakhstan.

Table 4. Basic statistics of 12 shells of *Tritoechia kendyktasica* RUKAVISHNIKOVA.

	Lv	Ld	W	T	Iw	Tv	Td
N	12	12	12	12	12	12	12
X	10.2	8.9	11.5	5.5	8.5	3.3	1.7
S	1.81	1.46	2.26	1.17	1.95	0.93	0.47
MIN	6.6	6	7.1	3.4	5	1.9	0.8
MAX	12.4	10.4	14.5	7.1	12	4.7	2.3

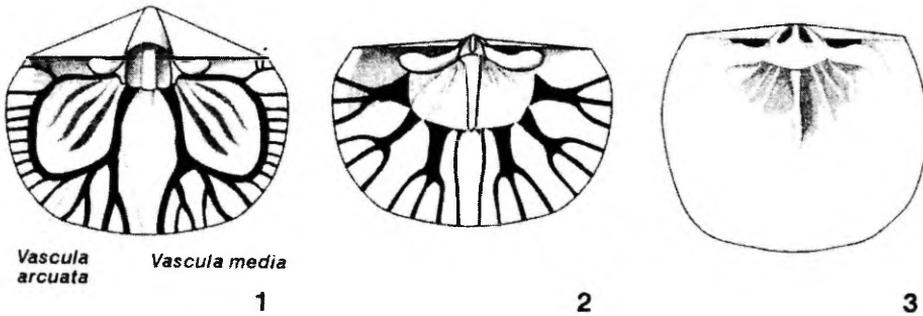|	Lv/W	Ld/W	T/Lv	Tv/Lv	Td/ld	Iw/W
N	12	12	12	12	12	12
X	90%	78%	53%	32%	19%	74%
S	5.8	6.9	4.9	6.4	3.5	6.9
MIN	81%	67%	46%	23%	13%	63%
MAX	97%	90%	63%	43%	23%	83%

Figure 6. 1–2, Schematic drawings of ventral and dorsal mantle canals in *Tritoechia kendyktasica*. 3, Schematic drawing of dorsal valve interior of *Pomatotrema fecunda*.

Tritoechia tokmakensis nov. sp.

Pl. 1, figs 1–13; Fig. 4.8

Etymology. After the town of Tokmak near the type locality.

Holotype. NMW 98.64G.11, ventral internal mould, Ordovician, lower Arenig, Rakhmetian, Kurday Formation, sample 5758, Agalatas River, Kendyktas Range.

Material. One complete shell, about 100 dorsal and ventral valves, 18 ventral and 11 dorsal internal moulds.

Diagnosis. Shell ventribiconvex, slightly transverse, subpentagonal in outline; anterior commissure rectimarginate; lateral profile of ventral valve almost straight anterior to the umbo, with maximum height near the beak; dorsal valve moderately and evenly convex; radial ornament parvicostellate with 4–5 costellae per 5 mm along the anterior margin of mature specimens; ventral muscle field large, elongated, extending anteriorly up to 33% of sagittal valve length; median ridge anterior to the ventral muscle field and dorsal median sulcus absent.

Description. Shell ventribiconvex, transverse, subpentagonal, about 90% as long as wide with maximum width at the hinge line. Anterior commissure rectimarginate. Cardinal extremities near right angled. Radial ornament slightly unequally parvicostellate with up to three generations of costellae and with 4–5 ribs in 5 mm along the anterior margin of full-grown specimens.

Ventral valve gently convex with maximum height in the umbonal area, about 90% as long as wide. Beak pointed, slightly acuminate. Ventral interarea high, triangular, plane and strongly apsacline, with a narrow triangular delthyrium completely covered by the convex pseudodeltidium. Foramen small, apical, about 1.5–2 mm in diameter. Dorsal valve non-sulcate moderately and evenly convex, about 75% as long as wide, with planar, anacline interarea. Notothyrium with a pair of chilidial plates joined near the apex.

Ventral interior with small teeth and high, slightly divergent dental plates with long ridge-like anterior extensions flanking the muscle field. Muscle field narrow, elongate subtriangular, about 82% as wide as long, and extending anteriorly up to 33% of sagittal valve length. Adductor track narrow, subtriangular, slightly shorter than weakly impressed diductor scars. Ventral mantle canals saccate with slightly divergent *vascula media* and pouch-like *vascula genitalia*. Dorsal interior with a simple, blade-like cardinal process situated on a high, narrow notothyrial platform strongly inclined posteriorly. Socket ridges low, widely divergent and curved distally towards the hinge line. Sockets deep, semiconical. Median ridge short and low, angular in cross-section, originating at the anterior margin of the notothyrial platform, fading in the anterior half of the adductor field. Adductor scars radially arranged, with larger posterior pair. Dorsal mantle canals pinnate, usually weakly

impressed with slightly divergent *vascula media* and bifurcating *vascula myaria*. *Vascula genitalia* vague, divergent.

Measurements. See Tables 2–3.

Remarks. This species is somewhat similar to *Tritoechia alata* XU & LIU (Xu *et al.* 1974: 148; pl. 65, figs 1–4) from the Meitan Formation of south-west China in general shell shape and characters of radial ornamentation, but differs in its strongly elongated, subtriangular ventral muscle field flanked by long, only slightly divergent dental plates and in the absence of a ventral median ridge. It is also similar to *Tritoechia florentinensis* LAURIE (1980: 21, fig. 6D–L) from the Lower Ordovician Florentine Valley Formation of Tasmania in general shape, transverse ventral profile, and characters of the ventral muscle field, but can be distinguished easily by the complete absence of a dorsal sulcus and coarser radial ornament.

T. tokmakensis differs from *Tritoechia kendyktasica* RUKAVISHNIKOVA (see above) in having a somewhat larger, dorsibiconvex shell, a lateral ventral profile with maximum height near the umbo, a strongly elongate ventral muscle field flanked laterally by long, ridge-like expansions of the dental plates, and in the absence of dorsal sulcus and ventral median ridge.

Occurrence. Ordovician, lower Arenig, Kurday Formation, samples 5758, 7384 and 7386, right side of Agalatas River, Kendyktas Range.

Table 2. Basic statistics of six ventral valves of *Tritoechia tokmakensis* nov. sp.

	Lv	W	VMl	VMw	Lv/W	VMl/Lv	VMl/VMw
N	6	3	6	6	3	6	6
X	15.2	16.2	4.4	3.6	90%	29%	82%
S	1.43	1.31	0.29	0.69	7.1	2.4	14.1
MIN	13.8	15.0	3.9	2.4	82%	25%	62%
MAX	17.9	17.6	4.7	4.4	96%	32%	102%

Table 3. Basic statistics of seven dorsal valves of *Tritoechia tokmakensis* nov. sp.

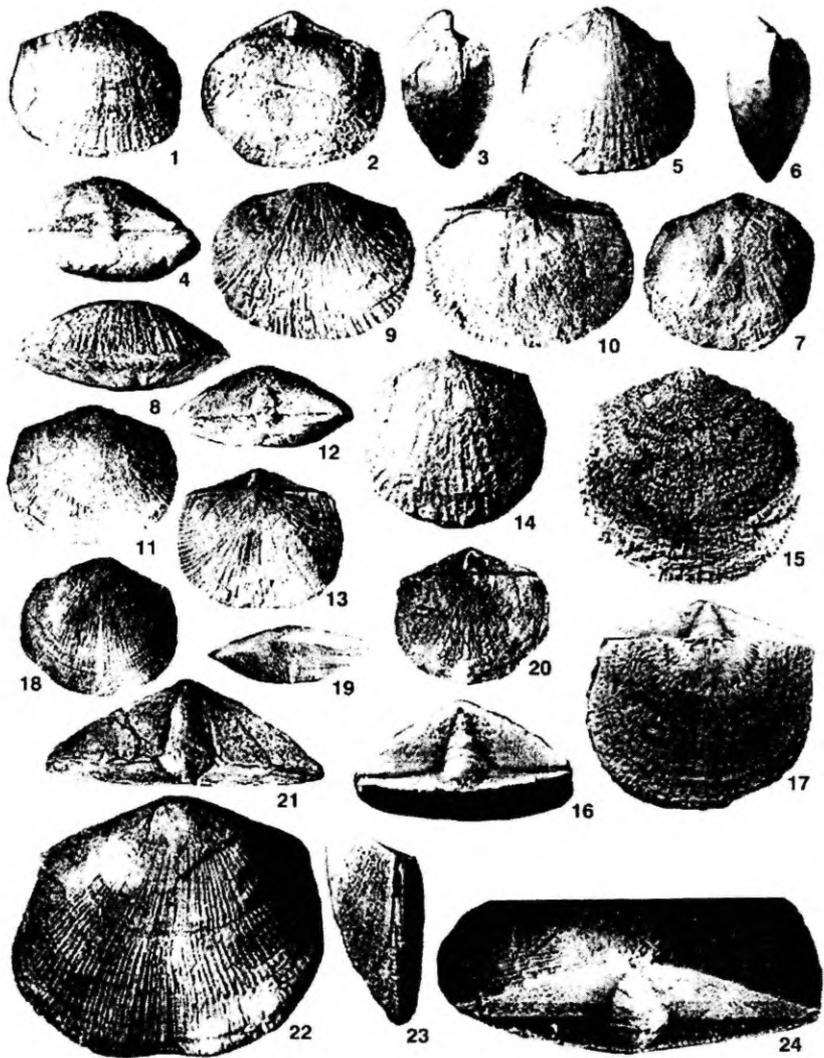|	Ld	W	DMl	DMw	Sl	Ld/L	DMl/L	Sl/L
N	7	6	6	6	6	6	6	6
X	11.8	15.8	3.0	6.0	2.5	75%	24%	19%
S	2.37	3.67	0.47	0.70	0.34	12.2	2.3	2.7
MIN	6.8	10.8	2.5	5.4	2.1	63%	21%	17%
MAX	14.5	20.4	3.9	7.2	3	95%	27%	25%

PLATE 2

Figs 1–7. *Eremotoechia spissa* nov. sp., Ordovician, Llandeilo — lower Caradoc, Baigara Formation, right side of river Karatal, south Betpak-Dala; **1–2**, sample F-1026b, NMW 98.28G.29, conjoined valves, dorsal and lateral views; **3–6**, sample F-1026b, NMW 98.28G.30, holotype, conjoined valves, ventral, lateral, dorsal and anterior views, sample F-1026B; **7**, NMW 98.28G.31, dorsal internal mould, sample F-1026; all × 3.

　　Figs 8–21. *Eremotoechia inchoata* nov. sp., Ordovician, Llandeilo — lower Caradoc, Baigara Formation, sample F-1023, about 7 km SW of Baigara mountain, south Betpak-Dala; **8–11**, NMW 98.28G.33, conjoined valves, lateral, dorsal, posterior and ventral views; **12–14**, NMW 98.28G.34, conjoined valves, ventral, dorsal and lateral views; **15–17**, NMW 98.28G.35, holotype, conjoined valves, dorsal, ventral and posterior views; **18–21**, NMW 98.28G.36, conjoined valves, lateral, dorsal, ventral and posterior views; all × 3.

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Genus *Eremotoechia* COOPER, 1956

Type species. *Eremotoechia cloudi* COOPER, 1956 from the Ordovician, Llandeilo-lower Caradoc, Arline Formation, Tennessee, USA

Diagnosis. See Cooper (1956: 513).

Species assigned. *Eremotoechia cloudi* COOPER 1956; Llandeilo-lower Caradoc, Arline Formation, Tennessee, USA. *Eremotoechia alabamensis* COOPER, 1956; Llandeilo-lower Caradoc, Little Oak Formation, Alabama, USA. *Eremotoechia inchoata* nov. sp.; Llandeilo-lower Caradoc, Baigara Formation, south Betpak-Dala, Kazakhstan. *Eremotoechia silicica* COOPER, 1956; Llandeilo-lower Caradoc, Arline Formation, Tennessee; Pratt Ferry Formation, Alabama, USA. *Eremotoechia spissa* nov. sp.; Llandeilo-lower Caradoc, Baigara Formation, south Betpak-Dala, Kazakhstan. *Eremotoechia yasachnaensis* ORADOVSKAYA, 1968; Llanvirn, Elgenchak Formation, north-east Siberia. *Eremotoechia ychangensis* ZENG (Zeng *et al.* 1983); middle Arenig – lower Llanvirn, Dawan Formation, South China. *Eremotoechia* sp. (Williams 1972); Llanvirn, Mweelrea Grits, western Ireland.

Eremotoechia inchoata nov. sp.

Pl. 2, figs 8–21

Etymology. From Latin *inchoatus*, imperfect, incomplete.

Holotype. NMW 98.28G.35, complete shell (L=19.4, W=24.6, T=7.8), Ordovician, Llandeilo — lower Caradoc, Tselinogradian, Baigara Formation, sample F-1023, area about 7 km south-west of Baigara Mountain, south Betpak-Dala.

Material. 52 complete shells.

Diagnosis. Shell strongly dorsibiconvex, transversely subrectangular in outline, with obtuse to rounded cardinal extremities and slightly uniplicate anterior commissure; ventral valve with lateral profile slightly concave anteriorly from the beak, with maximum height in the umbonal area; shallow ventral sulcus originates posterior to mid-length; dorsal valve with low median fold in anterior half; chilidium present; radial ornament ramicostellate with 5–10 costellae per 3 mm along anterior margin.

Description. Shell strongly dorsibiconvex, transversely subrectangular, on average 78% as long as wide, with maximum width at the mid-length and about 45% as thick as long. Cardinal extremities obtuse to slightly rounded. Anterior commissure weakly uniplicate. Ventral valve gently convex.

Its lateral profile, slightly concave anteriorly from the raised umbonal area in large specimens, with maximum height slightly anterior to the apex. Ventral interarea planar, slightly apsacline, with narrow strongly convex pseudodeltidium. Shallow ventral sulcus originates slightly posterior to the mid-valve in the adult specimens. Dorsal valve moderately convex, with maximum height at mid way between the apex and mid-valve. Umbonal area swollen. Dorsal interarea low, planar, strongly anacline to orthocline. Chilidium complete. Indistinct dorsal median fold originates anterior to the mid-valve. Radial ornament inequally ramicostellate with costellae of three generations on average 7 per 3 mm with the observed range from 5 to 10 along the anterior margin of adult specimens. Concentric ornament consists of fine, evenly spaced fila.

The interior of both valves has been studied in cross sections. Ventral interior with strong teeth and high, long, slightly divergent dental plates. Muscle field confined to the bottom of the delthyrial cavity with weakly impressed diductor and adductor scars. Dorsal interior with high, strongly curved socket ridges and deep sockets. Notothyrial platform high and narrow, inclined strongly posteriorly. Cardinal process simple, high, boss-like.

Measurements. See Table 5.

Remarks. Externally, *E. inchoata* is comparable with *E. cloudi* COOPER (1956: 514; pl. 77, figs 10–27) from the Arline Formation of Tennessee, but can be distinguished in having coarser radial ornament and a nearly straight to gently concave transverse profile of the ventral valve anterior to the umbo. The Kazakhstanian species differs from *E. silicica* COOPER (1956: 515; pl. 50, fig. 7; pl. 99, figs 47–52; pl. 186, figs 20–25) from the Pratt Ferry Formation of Alabama in its lateral profile of the ventral valve including maximum height at the umbonal area, coarser radial ornament, and more convex dorsal valve with maximum height posterior to the mid-valve. *E. inchoata* differs from *E. alabamensis* COOPER (1956: 514; pl. 78, figs 1–9) from the Little Oak Formation of Alabama and *E. yasachnaensis* ORADOVSKAYA (1973: 160; pl. 26, figs 1–12) from the Elgenchak Formation of north-east Siberia in having a strongly dorsibiconvex shell, coarser radial ornament, and a distinctly uniplicate anterior commissure.

Table 5. Basic statistics of 30 shells of *Eremotoechia inhoata* sp. nov.

	L	W	T	L/W	T/L
N	30	30	30	30	30
X	16.8	21.9	7.4	78%	45%
S	3.64	4.97	1.94	15.8	11.4
Min	9.9	15.1	4.4	53%	29%
Max	26.9	32.7	11.8	122%	74%

Occurrence. Ordovician, Llandeilo — lower Caradoc, Baigara Formation, south Betpak-Dala; samples F-1022, F-1023, area 7 km south-west of Baigara Mountain; sample F-1025, east side of Karatal River.

Eremotoechia spissa nov. sp.

Pl. 2, figs 1–7; Fig. 7.5–7

Etymology. From Latin *spissus*, cut, split.

Holotype. NMW 98.28G.30, complete shell (L=15.4, W=19.2, T=12.2), Middle Ordovician, Llandeilo — lower Caradoc, Baigara Formation, west side of Karatal river, south Betpak-Dala, sample 1026b.

Material. 32 complete shells and one dorsal internal mould.

Diagnosis. Shell dorsibiconvex, with uniplicate anterior commissure and a well defined ventral sulcus and dorsal median fold originating anterior to mid-valve; radial ornament unequally ramicostellate with 4–6 costellae per 3 mm along anterior margin.

Description. Shell strongly dorsibiconvex, transversely suboval in outline, about 87% as long as wide and 60% as thick as long, with rounded cardinal extremities. Anterior commissure uniplicate. Ventral valve moderately and evenly convex with maximum height slightly posterior to mid-valve. Ventral interarea apsacline with narrow, convex pseudodeltidium. Sulcus originates about 4–6 mm from the beak, broad and deep, evenly concave in transverse section anterior to the mid-valve. Dorsal valve moderately to strongly convex with maximum height at the mid-length. Dorsal interarea anacline. Chilidial plates fused near the apex of the notothyrium. An indistinct dorsal median fold originates anterior to the mid-length in adult specimens. Radial ornament unequally ramicostellate, with costellae of two or three generation, about 4–6 costellae per 3 mm along the anterior margin, with 11–16 costellae in the fold and sulcus, and 12–19 costellae on the flanks of both valves in mature specimens.

Ventral interior with strong teeth and long, thin, slightly divergent dental plates. Muscle field not elevated, confined entirely to the bottom of the delthyrial cavity. Dorsal interior with a narrow notothyrial platform inclined posteriorly and a simple, high, strongly thickened cardinal process. Socket ridges thin, widely divergent and strongly incurved towards the posterior margin. Median ridge weakly developed or absent. Adductor muscle scars arranged radially, raised strongly anteriorly, with posterior and anterior pairs of about equal sizes separated by strong side septa.

Measurements. See Table 6.

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Remarks. *E. spissa* differs from *Eremotoechia inchoata* (see above) in having a strongly dorsibiconvex shell about 60% as thick as long (Tables 5, 6) and lateral profile of both valves with maximum height near mid-valve, whereas in the later species maximum height of the ventral valve is usually placed in the umbonal area. Both species are characterised by a uniplicate anterior commissure and a ventral sulcus in the anterior half of the shell, but in *E. spissa* sulcus is usually somewhat deeper and well defined laterally. Specimens of *E. inchoata* are often distorted, but their shell is more transverse in outline (Tables 5, 6) and has a finer radial ornament than *E. spissa*.

Exterior of both valves of *E. spissa* is similar to *E. alabamensis* COOPER (1956: 514; pl. 78, figs 1–9) from the Little Oak Formation of Alabama, but Kazakhstanian species differs from the latter as well as from all other known species of this genus in having much coarser and irregular radial ornament and a strongly uniplicate anterior commissure with a well defined dorsal median fold and ventral sulcus.

Occurrence. Ordovician, Llandeilo — lower Caradoc, Baigara Formation, samples F-1026, F-1026b, west side of Karatal River, south Betpak-Dala, south-central Kazakhstan.

Table 6. Basic statistics of 35 shells of *Eremotoechia spissa* sp. nov.

	L	W	T	L/W	T/L
N	35	35	35	35	35
X	17.9	20.6	10.5	87%	60%
S	3.36	3.23	2.28	12.4	12.9
Min	10.3	13.6	6.5	66%	32%
Max	25.5	27.4	16.1	109%	86%

Genus *Martellia* WIRTH, 1936

Type species. *Orthisina giraldii* MARTELLI, 1901.

Diagnosis. Shell ventribiconvex, rounded to subhexagonal in outline with an acute anterior margin and weakly uniplicate anterior commissure; ventral sulcus and dorsal median fold variably developed; ventral interarea apsacline with pseudo-deltidium perforated apically by minute foramen; chilidium complete; radial ornament multicostellate; aditicules sporadically developed; subperipheral rims well defined in both valves; ventral interior with slightly divergent dental plates and pseudospondylium; ventral median ridge anterior the muscle field variably developed; ventral mantle canals saccate; dorsal interior with ridge-like cardinal process on wide, triangular notothyrial platform hanging anteriorly, supported by strong median septum; socket ridges low, widely divergent; two pairs of radially

disposed adductor muscle scars strongly impressed, situated on a callosity elevated above the valve floor; separated by two pairs of fine transmuscle ridges.

Species assigned. *Orthisina giraldii* MARTELLI, 1901; Ordovician, upper Arenig, Dawan Formation, South China. *Martellia ichangensis* WANG, 1956 (=*Martellia fenxiangensis* ZENG 1977); Lower Ordovician, upper Arenig, Hubei, South China (the later species came from the same localities as *Martellia ichangensis* in Yichang area, western Hubei, it is synonymised here with *M. ichangensis* in accordance with personal communication of Dr. Rong Jia-yu (1997), because it has no clear differences in the shell morphology and can be placed well within the limits of morphological variations observed in *Martellia ichangensis*). *Pomatotrema mesocosta* BENEDETTO, 1987; Llanvirn, San Juan Formation, Jachal District, San Juan Province, Argentina. *Pomatotrema talacostensis* BENEDETTO, 1987; Llanvirn, San Juan Formation, Los Banos, Talacosta, Argentina.

Species excluded. *Martellia orbicularis* ZENG, 1977 (= *Martellia transversa* FANG *in* Zeng); upper Arenig, Dawan Formation, South China. This species is characterised by an evenly rounded anterior commissure and very poorly defied to completely absent dorsal median fold and ventral sulcus. It can be assigned questionably to *Pomatotrema,* but differs in having a complete chilidium. *Martellia orbicularis* differ from *Martellia transversa* only in shell outline, which is a variable feature in Tritoechiidae. Moreover, they are from the same area and unit.

Remarks. The type species of *Martellia* is in need of revision, together with related species. The proposed synonymy with *Polytoechia* (Williams 1965) is not supported in this study, because *Martellia* has a pseudospondylium and not a *spondylium triplex* as in the former genus. *Martellia* somewhat resembles *Pomatotrema* and *Tritoechia,* but can be distinguished from them in its slightly uniplicate anterior commissure and very finely multicostellate radial ornament. The subhexagonal shell outline with an acute anterior margin, and a high notothyrial platform overhanging anteriorly and supported by a median septum are also characteristic of the genus and have no analogies in other genera of the Tritoechiidae.

Pomatotrema mesocosta BENEDETTO and *Pomatotrema talacostensis* BENEDETTO are assigned here to *Martellia,* because they both have a weakly uniplicate anterior commissure with a small, ventral tongue-like projection of the anterior margin and a dorsal valve interior characteristic of the latter genus.

Martellia reliqua nov. sp.

Pl.1, figs 27–37; Figs 4.9, 5.5–6, 7.1–4

Etymology. From Latin *reliquus*, relic, alluding to the latest occurrence of the genus in Kazakhstan.

Holotype. NMW 98.28G.3, conjoined valves, Middle Ordovician, lower Llanvim, Uzunbulak Formation, sample 158; Kurzhaksai section, Chu-Ili Range, South Kazakhstan.

Material. 38 complete shells, four ventral and one dorsal internal moulds.

Description. Shell ventribiconvex, slightly transverse, subhexagonal to suboval in outline, about 116% (OR=113–121%, N=3) as long as wide with maximum width along or close to the hinge line, and 49% (OR=46–51%, N=3) as thick as long. Cardinal extremities near right angled. Anterior commissure gently uniplicate with a characteristic tongue-like median projection. Ventral valve moderately convex with maximum height in the umbonal area. Ventral interarea high, triangular, plane, apsacline with a narrow, triangular, strongly convex pseudodeltidium perforated apically by a minute, circular foramen about 0.4–0.5 mm in diameter. A shallow ventral sulcus originates at about one quarter valve length from the umbo, terminating anteriorly in a variably developed, slightly acute tongue. Dorsal valve gently convex, maximum height anterior to mid-valve and about 97% (OR=94–103%, N=3) as long as wide. An inconspicuous median fold originates anterior to the umbo. Dorsal interarea plane, anacline with a notothyrium completely covered by a large, triangular chilidium. Radial ornament multicostellate with 9–12 rounded costellae per 3 mm in the median sector of the anterior margin of adult specimens. Ribs usually slightly thickened along the numerous fine, crowded concentric growth lamellae.

Ventral interior with strong teeth and long, divergent dental plates. Ventral muscle field confined mainly to the bottom of the delthyrial cavity, strongly raised anteriorly in the form of a pseudospondylium. Adductor track narrow, distinctly elongated with subparallel lateral margins, slightly raised anteriorly. Diductor scars large, strongly impressed, subtriangular in outline, slightly elevated anterolaterally and extending anterior to the adductor scar. Dorsal interior with a high notothyrial platform overhanging anteriorly and supported by a high median septum. Cardinal process simple, ridge-like, thickened anteriorly. Socket ridges wide, strongly divergent, almost subparallel to the posterior margin. Adductor scars form two radially arranged pairs of about equal size, strongly impressed in a thickened callus of secondary shell and bisected by two pairs of strong transmuscle ridges.
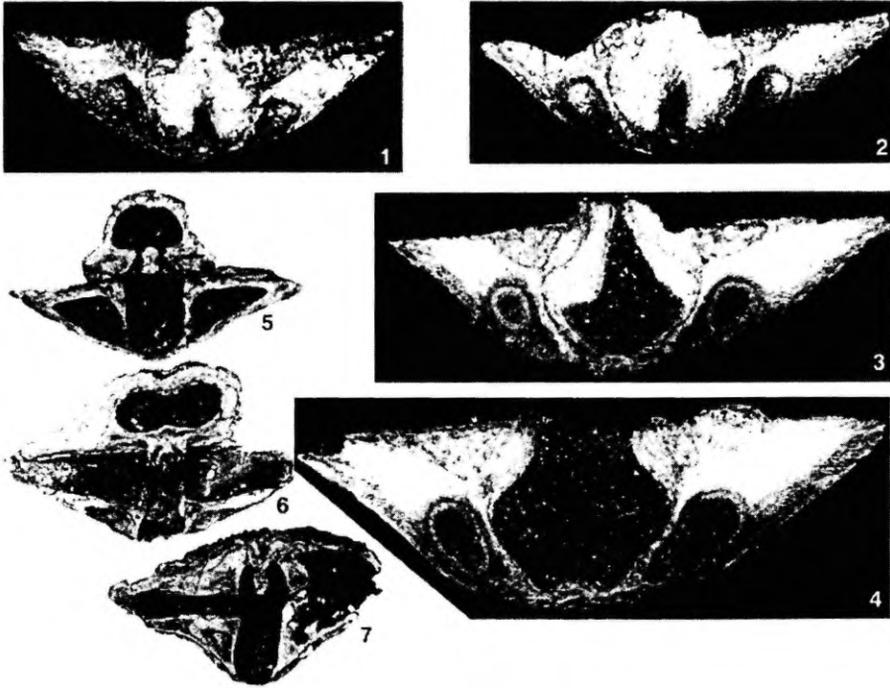
Figure 7. Photographs of transverse sections of selected tritoechiid shales from Kazakhstan. 1–4, *Martellia reliqua* nov. sp., Ordovician, Llanvirn, Uzunbulak Formation, sample 158, Kurzhakssai section, Chu-Ili Range; NMW 98.28G.16, ventral valve, serial sections in 1.2, 1.5, 2.3 and 3.,0 mm from the umbo; all × 11. **5–7**, *Eremotoechia spissa* nov. sp., Ordovician, Llandeilo — lower Caradoc, Baigara Formation, sample F-1026b, right side of river Karatal, south Betpak-Dala; **5,** NMW 98.28G.32, conjoined valves, serial section in 3.1 mm from ventral umbo, × 4; **6–7,** NMW 98.28G.33, conjoined valves, serial sections in 3.1 and 3.8 mm from ventral umbo, × 4.

Measurements. See Table 7.

Remarks. Externally the Kazakhstanian specimens are closely similar to *Martellia ichangensis* WANG, 1956 from the upper Arenig of Hubei, South China, but differ in having a somewhat larger average size and finer radial ornament, and in the absence of a ventral median ridge anterior to muscle field and strong transmuscle ridges crossing the dorsal adductor scars. The notothyrial platform of *M. reliqua* is remarkably high by comparison with the Chinese species and is underlain by two deep umbonal cavities divided by high median septum.

Occurrence. Ordovician, Llanvirn, Kopaly Regional Stage, lower Uzunbulak Formation, South Kazakhstan, Chu-Ili Range, Kurzhaksai, samples 156, 158, F-129, Kujandysai, samples 304, 313; area 4 km south-west of Lake Alakol, samples 133, 142.

Table 7. Measurements of 4 specimens of *Martellia reliqua* nov. sp.

	Lv	W	T	Ld	Iw	Td	Tv
NMW98.28G.1	17	13.1	–	11.5	–	1	–
NMW98.28G.2NMW98.28G.2	17.9	15.8	8.7	14.8	13.8	2.7	6.0
NMW98.28G.3NMW98.28G.3	19.4	17	8.9	16.3	14.2	3.5	5.4
NMW98.28G.4	13.8	11.4	7.1	11.7	9.6	2.1	4.3

Genus *Pomatotrema* ULRICH and COOPER *in* SCHUCHERT et COOPER, 1932

Type species. *Pomatotrema murale* Ulrich and Cooper, 1932, lower Ordovician, Arbuckle Limestone, Oklahoma, USA.

Diagnosis. See Ulrich and Cooper (1938: 170).

Pomatotrema fecunda nov. sp.

Plate 3, figs. 15–23; Pl. 4, figs 8–10; Figs 5.3, 5.7, 7.3.

Ethymology. After Latin *fecundus*, fruitful.

Holotype. USNM485064, conjoined valves; Ordovician, Llanvirn, area 4 km south-west of Lake Alakol, sample 133.

Material. More then 100 complete shells, dorsal and ventral valves.

Diagnosis. Shell slightly elongate, with anterior margin gently rounded, recti-marginate or very gently uniplicate; ventral interarea apsacline with minute apical foramen; dorsal interarea anacline with complete, strongly convex chilidium; radial ornament finely and unequally parvicostellate with 7–8 ribs per 3 mm along the anterior margin; dorsal interior with high notothyrial platform slightly over-hanging anteriorly and strong median ridge extending anteriorly to mid-valve.

Description. Shell planoconvex to ventribiconvex, transversely subrectangular in outline, about 85% as long as wide with maximum width slightly posterior to mid-length and 44% as thick as long. Cardinal extremities near right angled to slightly obtuse. Anterior commissure broadly rounded, very gently uniplicate to recti-marginate. Ventral interarea high, triangular, plane, apsacline with a narrow, triangular, strongly convex pseudodeltidium perforated apically by a minute circular foramen. A shallow sulcus originates at mid-length in some shells, but may be completely absent. Dorsal valve very gently convex to almost flat, about 70% as long as wide. Dorsal interarea low, anacline, with a complete, convex chilidium. Radial ornament finely and slightly unequally parvicostellate with

PLATE 3

Figs 1–13. *Tritoechia kendyktasica* Rukavishnikova, Lower Ordovician, Agalatas Formation, sample 24, right side of Agalatas River, Kendyktas Range; **1–4**, NMW 98.64G.1, conjoined valves, ventral, dorsal, lateral and posterior views, × 3; **5–7**, NMW 98.64G.2, conjoined valves, ventral, lateral and dorsal views, × 3; **8–10**, NMW 98.64G.3, conjoined valves, anterior, ventral and dorsal views, × 3; **11–13**, NMW 98.64G.4, conjoined valves, ventral, posterior and dorsal views, × 3; **14**, NMW 98.64G.5, ventral valve, × 4.

Figs 15–23. *Pomatotrema fecunda* nov. sp., Ordovician, Llanvirn, Alakul Limestone, sample 133, area 4 km SW of Alakul Lake; **15–17**, USNM 485070, conjoined valves, ventral, posterior and dorsal views, × 3; **18–20**, NMW 98.28G.8, conjoined valves, ventral, posterior and dorsal views, × 2; **21–23**, NMW 98.28G.9, conjoined valves, posterior, ventral and lateral views, × 3.

Fig. 24. *Martellia ichangensis* Wang, Ordovician, Dawan Formation, Huanghuachang, north Yichang, China; ventral interarea and supra-apical foramen (Coll. N. Spjeldnaes).

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accentuated costellae of three generations. The number of ribs is 7–8 per 3 mm along the anterior margin in mature specimens. Very fine aditicules are present sporadically along the margins of fine, closely spaced crowded growth lamellae.

Ventral interior with strong teeth supported by long, subparallel dental plates. Muscle field strongly raised anteriorly in the form of a pseudospondylium. Adductor scars elongate, suboval, divided medially by a strong myophragm, shorter than strongly impressed diductor scars. A short median ridge originates anterior to the ventral muscle field. Dorsal interior with a high notothyrial platform; cardinal process simple, ridge-like, strongly thickened anteriorly. Socket ridges low, widely divergent. Adductor muscle scars radially arranged, strongly impressed in the callus of secondary shell, raised slightly above the valve floor. Median septum crosses the whole adductor field and is about half as long as the valve. Low subperipheral rim present in the both valves.

Measurements. See Table 8.

Table 8. Basic statistics of 9 specimens of *Pomatotrema fecunda* nov. sp.

	Lv	W	T	Ld	Iw	Lv/W	Ld/W	T/Lv	Iw/W
N	9	9	9	9	9	9	9	9	9
X	19.0	22.5	8.2	15.7	18.1	85%	70%	44%	81%
S	2.26	3.41	0.92	1.79	4.34	5.2	4.4	4.9	17.2
MIN	15.8	17.9	7	12.6	9.2	76%	62%	35%	37%
MAX	21.4	28.1	9.3	18.2	24.4	93%	77%	49%	92%

Remarks. The new species is similar to *Martellia orbicularis* ZENG (1977: 47; pl. 15, figs 10–12) from the Dawan Formation of South China in general outline of the ventribiconvex shell, gently rounded anterior margin and vestigial dorsal fold and ventral sulcus. The Kazakhstanian species can be distinguished from the Chinese one by its shorter dorsal median ridge and adductor field, which does not extend anterior to mid-valve, and by its very fine unequally parvicostellate radial ornament. Both *Pomatotrema fecunda* nov. sp. and *Martellia orbicularis* are assigned here provisionally to *Pomatotrema* because they have a flat or only gently convex dorsal lateral profile, long subparallel dental plates, and lack a of well defined median fold and sulcus at all growth stages; however, they differ from the numerous North American species of *Pomatotrema* described by Ulrich and Cooper (1938) in having a highly raised notothyrial platform, a strong and long dorsal median ridge, and well developed chilidium instead of chilidial plates.

Occurrence. Ordovician, Llanvirn, Uzunbulak Formation, Kujandysai, sample 115; Kurzhaksai, samples F-129, F-129a, 156, 158; Kopalysai, samples R-62, 228-1; area 4 km south-west of Lake Alakol, samples 133, 134 and 142.

Genus *Protambonites* HAVLÍČEK *in* HAVLÍČEK & JOSOPAIT, 1972

Type species. *Tritoechia kolihai* HAVLÍČEK, 1949; Ordovician, upper Tremadoc — lower Arenig, Trenice Formation, Bohemia.

Diagnosis. See Havlíček & Josopait (1972: 348).

Species assigned. *Tritoechia kolihai* HAVLÍČEK, 1949; Ordovician, Trenice Formation, Bohemia. *Orthis soror* BARRANDE, 1879; Ordovician, Trenice Formation, Bohemia. *Tritoechia lermontovae* ANDREEVA, 1960; Ordovician, Kidryas, Akbulaksai and Alimbet formations, South Urals.

Protambonites lermontovae (ANDREEVA, 1960)

Plate 4, fig. 7; Figs 4.5–7, 5.1–2, 5.8

1960 *Tritoechia lermontovae* ANDREEVA, p. 291, pl. 72, figs 6–13

Material. 33 ventral and five dorsal valves.

Diagnosis. Shell convexiplane, subpentagonal, about as long as wide; radial ornament ramicostellate with 4–6 ribs per 3 mm along the anterior margin; ventral interior with large, elongate muscle field extending to the mid-valve and flanked laterally by long, subparallel dental plates; low median ridge occasionally present in front of the ventral muscle field.

Description. Shell convexiplane, rounded subpentagonal in outline, on average 96% as long as wide with maximum width at the hinge line; ventral interarea high triangular, plane, near orthocline to slightly apsacline with broad, convex pseudodeltidium perforated apically by a minute circular foramen sealed by deposits of secondary shell in full grown specimens. Dorsal valve rounded subrectangular in outline, on average 81% as long as wide, moderately and evenly convex in transverse profile with low, planar, anacline interarea. Radial ornament slightly unequally ramicostellate with 4–6 costellae per 3 mm near the anterior margin of adult specimens. Costellae rounded in cross section.

Ventral interior with strong teeth supported by long, subparallel dental plates Ventral muscle field strongly elongated, slightly raised and extending anteriorly to mid-valve. Adductor scars slightly longer than diductor scars. Posterior part of the bottom of the delthyrial cavity bisected by a very fine median ridge. A low median ridge is occasionally developed also in front of the ventral muscle field. Ventral mantle canal system pinnate. Dorsal interior with simple ridge-like cardinal process on high notothyrial platform. Socket ridges low, subparallel to the hinge line. Dorsal adductor scars radially arranged, divided medially by a low median ridge extending anteriorly to mid-valve. Dorsal mantle canals pinnate.

Measurements. See Tables 9–10.

Remarks. *Protambonites lermontovae* differs from *Protambonites kolihai* (HAVLI-ČEK) and *Protambonites soror* (BARRANDE) revised by (HAVLIČEK 1977) in having a less transverse shell outline with length about equal to maximum width, coarse and closely spaced costellae, elongate ventral muscle field extending anteriorly to mid-valve, and in presence of a low median ridge anterior to the ventral muscle field as well as absence of an umbonal dorsal sulcus. It also differs from the latter species in its larger size and shell outline with maximum width at the hinge line.

Tritoechia lacunata NASSEDKINA (1977: 16, pl. 3, figs 1–4, 7, 9) from the Lower Ordovician, Chaushka Formation of northern Mugodzhary, South Urals is known only from strongly deformed and distorted specimens. It may be conspecific with *Protambonites lermontovae*, which was reported from the same locality.

In the original description of *Protambonites lermontovae* it was published by Andreeva (1960) under the authorship of Lessnikova (in coll.) without other specific references. As well as the source of the name from the labial in the collection does not constitute a published work within the meaning of the ICZN Andreeva is regarded here as the author of this species.

Occurrence. Lower Ordovician, uppermost Tremadoc – lower Arenig, Kidryas Formation, samples B-786-6, Tyrmantau Range east of the Novodmitrievka village; Akbulaksai Formation, sample 778-2, Alimbet farm; samples B-607-1, B-607-7, B-607-8, Akbulaksai; samples B-768, G-196-1, Koagash river; all from South Urals. **Occurrence** ? Lower Ordovician, Kidryas Formation, samples B-786-6, Tyrmantau Range east of the Novodmitrievka village; Akbulaksai Formation, sample 778-2, Alimbet farm; samples B-607-1, B-607-7, B-607-8, Akbulaksai; samples B-768, G-196-1, Koagash river; all from South Urals.

Table 9. Basic statistics of 16 ventral valves of *Protambonites lermontovae* (ANDREEVA).

	L	W	Ml	Mw	L/W	Ml/L	Ml/Mw
N	16	16	11	11	16	11	11
X	21.0	22.0	11.4	6.8	96%	54%	168%
S	3.45	3.41	2.19	1.14	8.8	7.4	24.8
MIN	14.5	16.8	8.5	5	82%	42%	129%
MAX	25.6	29.5	14	8.5	114%	66%	206%

Table 10. Basic statistics of 6 dorsal valves of *Protambonites lermontovae* (ANDREEVA).

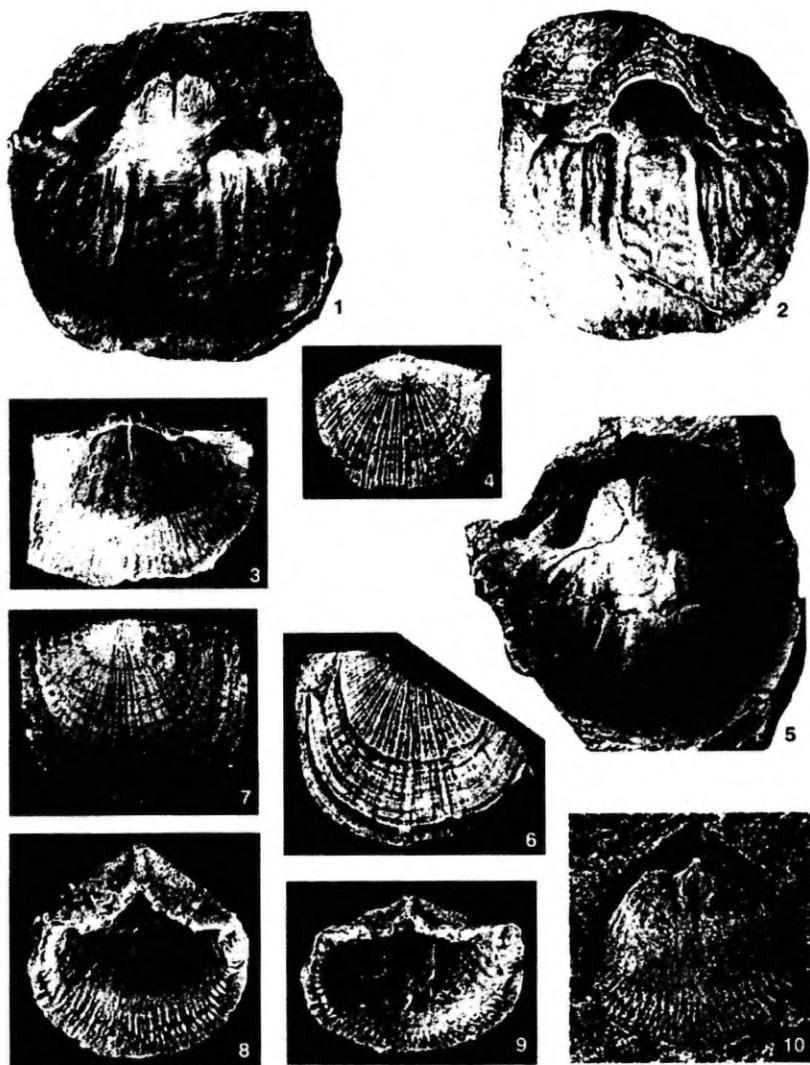|	L	W	L/W
N	6	6	6
X	16.0	19.25	81%
S	7.56	8.13	8.4
MIN	5.6	7.9	71%
MAX	22.8	26.9	95%

PLATE 4

Figs 1–6. *Korinevskia akbulakensis* (Andreeva), Lower Ordovician, Akbulaksai Formation, sample B607-9, Akbulaksai, South Urals; **1–2,** NMW98.67G.11, ventral valve, internal mould, exterior, × 2; **3,** NMW98.67G.13, dorsal valve, latex cast of interior, × 2; **4,** CNIGR 3/12604, latex cast of exterior of juvenile specimen, × 2; **5,** NMW98.67G.12, ventral valve, internal mould, × 2; **6,** NMW98.67G.14, incomplete ventral valve, latex cast of exterior, × 2.

Fig. 7. *Protambonites lermontovae* (Andreeva), Lower Ordovician, Akbulaksai Formation, sample B607-1, Akbulaksai, South Urals; CNIGR 4/12604, latex cast of dorsal exterior, × 2.

Figs 8–10. *Pomatotrema fecunda* nov. sp., Ordovician, Llanvirn, Uzunbulak Formation, sample F-111, Kujandysai section, Chu-Ili Range, NMW 98.28G.10, ventral valve, latex cast of interior, oblique anterior view of interior, internal mould, × 3.

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Genus *Korinevskia* nov. gen.

Etymology. After V. Korinevskiy, Uralian geologist from Miass.

Type and only species. *Billingsella akbulakensis* ANDREEVA, 1960 from the Lower Ordovician, Akbulaksai Formation of South Urals.

Diagnosis. Shell convexiplane, with rectimarginate posterior commissure, finely ramicostellate; ventral interarea high, triangular, almost orthocline, with well developed convex pseudodeltidium; dorsal interarea with broad, strip-like chilidium; ventral interior with short, divergent dental plates obscured in adult specimens by secondary shell beneath the interarea; ventral muscle field with adductor scars extending well beyond the delthyrial cavity and much shorter and narrower diductor scars ending near the anterior ends of the dental plates; umbonally bisected by a fine ridge; ventral mantle canals saccate with subparallel *vascula media*; dorsal interior with simple ridge-like cardinal process on a wide notothyrial platform and low socket ridges subparallel to the hinge line; dorsal adductor scars arranged radially, bisected by low median ridge; dorsal mantle canals pinnate.

Measurements. See Table 11.

Remarks. *Korinevskia* is most similar to *Protambonites* in having a convexiplane shell with a high, near orthocline ventral interarea, a low median ridge developed in the posterior part of the base of the delthyrial cavity, an unequally ramicostellate radial ornament as well as in general aspects of the internal morphology of the ventral valve. The main differences *Korinevskia* are: (1) saccate mantle canals with *vascula arcuata* reaching the outer sides of the dental plates and *vascula terminalia* directed towards the hinge line; (2) short, divergent dental plates obscured by secondary shell in the gerontic specimens; (3) a large ventral adductor scar extending well beyond the narrow triangular diductor scars located in the lateral sides of the base of the delthyrial cavity; and (4) a complete, strip-like chilidium.

Table 11. Basic statistics of 14 complete shells of *Korinevskia akbulakensis* (AND-REEVA).

	Lv	Ld	W	T	Iw	Lv/W	Ld/W	T/Lv
N	14	14	14	14	13	14	14	14
X	25.5	21.0	25.7	7.4	25.4	100%	83%	29%
S	2.01	1.45	2.64	1.29	2.18	9.0	12.2	3.6
MIN	22	18.8	18	5.4	21.5	88%	69%	24%
MAX	29.2	24.7	29.1	9.7	29.1	122%	119%	34%

The shape of the ventral muscle field with characteristic arrangement of the muscle scars as large and long adductor track, saccate ventral mantle canals with *vascula*

terminalia along the hinge line, a simple, ridge-like cardinal process and radially disposed dorsal adductor scars are similarities to *Billingsella*, but *Korinevskia* is distinguished easily, because it has well developed dental plates which are absent in typical representatives of *Billingsella*.

Korinevskia akbulakensis (ANDREEVA, 1960)

Plate 4, figs 1–6; Fig. 4.3.

1960 *Billingsella akbulakensis* Andreeva, p. 291, pl. 72, figs 2–5

Material. 30 complete shells, seven ventral and eight dorsal valves.

Diagnosis. As for genus.

Description. Shell planoconvex, subquadrate with maximum width slightly anterior to the hinge line, about 14% as thick a long. Anterior commissure rectimarginate, anterior margin broadly rounded. Ventral valve usually almost flat in transverse profile. Ventral interarea high, triangular, plane, strongly apsacline to almost orthocline, up to one third as high as sagittal valve length. Pseudodeltidium broad, convex, completely closing delthyrium, with minute, sealed supra-apical foramen. Dorsal valve evenly convex in lateral profile, about 83% as long as wide with a low, plane, anacline interarea. Chilidium well developed. Radial ornament ramicostellate with 8–12 ribs per 3 mm along the anterior margin of adult specimens. Concentric ornament of fine, evenly spaced fila and numerous thin growth lamellae in the anterior half of the valves.

Ventral interior with strong teeth supported by short, divergent dental plates, which in gerontic specimens are obscured by deposition of secondary shell filling the space between the inner sides of the interarea and the valve floor. Ventral muscle field large, extending anteriorly to the centre of the valve in gerontic specimens. Ventral adductor scars form a broad subtriangular track raised slightly anteriorly and flanked laterally by weakly impressed, short, narrow subtriangular diductor scars ending slightly beyond the dental plates. Umbonal area completely sealed and bearing a short median ridge. Mantle canals saccate with strongly impressed, subparallel *vascula media*. Dorsal interior with a high, broad, sub-triangular notothyrial platform inclined strongly posteriorly. Cardinal process simple, ridge-like. Adductor scars weakly impressed, radially arranged with a larger anterior pair. Median septum very high near its junction with notothyrial platform, fading rapidly in the anterior half of the adductor muscle field.

Remarks. This species was referred originally to *Billingsella*. Andreeva (1960) reported that it lacks dental plates, but the specimens from the type locality invariably possess dental plates, which can be obscured in gerontic specimens by deposition of secondary shell between the inner sides of the interarea and the valve

floor, but they are clearly visible in most internal moulds (Pl. 4, figs 1, 2, 5). Short dental plates are also present in one of the specimens illustrated by Andreeva (1960, pl. 72, fig. 2). Denticulation along the posterior margin of the ventral valve mentioned by Andreeva is actually strongly impressed *vascula terminalia* along the inner side of the ventral interarea (Pl. 4, figs 1, 5).

Occurrence. Lower Ordovician, uppermost Tremadoc – lower Arenig, lower Akbulaksai Formation, samples B-607-9, B-607-15; Akbulaksai section, South Urals.

PHYLOGENETIC ANALYSIS

OUTGROUP SELECTION AND METHODS

Major patterns of early radiation of Rhynchonelliformean brachiopods during the Early and early Mid Cambrian are still far from clear, and discrimination of plesiomorphic and apomorphic features remains somewhat difficult (Popov 1992; Williams *et al.* 1996). Thus we have used a wide selection of Cambrian species representing five major Cambrian rhynchonelliformean orders to polarize diagnostic characters of tritoechiids, viz. Obolellida, Kutorginida, Protorthida, Orthida and Billingsellida. They are: *Obolella chromatica* BILLINGS, from the Atdabanian of North America and Siberia, which is the oldest known rhynchonelliformean brachiopod; *Kutorgina catenata* KONEVA from the Botomian of the Alai Range, Kyrgyzstan and *Narynella silcata* (ROWELL & CARUSO, 1985) from the Middle Cambrian of Utah, both typifying kutorginides; two species of protorthides, *Arctohedra pyramidalis* AKSARINA, 1975 and *Glyptoria gulchensis* POPOV & TIKHONOV, 1993, from the Middle Cambrian of South Tien-Shan, Kyrgyzstan; *Bohemiella romingeri* (BARRANDE, 1848), from the Middle Cambrian of Bohemia, representing an early orthide; and the billingsellide *Billingsella aliena* NIKITIN, 1956, from the Upper Cambrian of north-central Kazakhstan. Also since Tritoechiidae have been referred usually to the suborder Clitambonitidina (Rubel & Wright 2000), two clitambonitoidean taxa, *Apomatella ingrica* (PAHLEN, 1877) and *Clitambonites schmidti* (PAHLEN, 1877) were used as reference taxa. Family Polytoechiidae is represented by *Polytoechia subcircularis* COOPER, 1952 from the Lower Ordovician of Oklahoma and *Antigonambonitus planus* (PANDER, 1830) from the Lower Ordovician of Baltoscandia.

The core of tritoechiid taxa is represented by nine Kazakhstanian species in the genera *Tritoechia*, *Eremotoechia*, *Korinevskia* nov. gen., *Martellia*, *Pomatotrema* and *Protambonites*, as described in this paper, plus *Martellia ichangensis* WANG (see pl. 3, fig. 24) from the Arenig of South China. A data matrix derived from 42 unordered and unweighted taxonomically significant characters with 134 character states, identified in ten species of tritoechiids two species of polytoechiids and ten species of the five early rhynchonelliformean orders (Table 12; Appendices 1–2)

was analysed cladistically using the Phylogenetic Analysis Using Parsimony (PAUP) programme; written and distributed by Swofford (1993).

RESULTS

A heuristic search using global swapping with the MULPARS resulted in the generation of three shortest trees, each 159 steps long, with a consistency index of 0.585, homoplasy index of 0.415, and a rescaled consistency index of 0.381. A strict consensus tree derived from three equally parsimonious shortest trees is shown as Fig. 8.

All three cladograms show billingsellids and tritoechiids as a single, consistent monophyletic clade (Fig. 8, node 5), which does not include clitambonitoideans. The latter group is represented in the analysis by two taxa (*Apomatella ingrica*, family Atelelasmatidae and *Clitambonites schmidti*, family Clitambonitidae), which form another clade together with a derived protorthoidean *Arctochedra pyramidalis* (Fig. 8, node 15) and early orthides represented in the analysis by *Bohemiella romingeri*.

The origin and phylogenetic relationships of true clitambonitidines are beyond the scope of this paper, but they may represent an ingroup within Protorthida or a sister group of Orthida. It is also interesting to note that the most primitive protorthides, similar to *Glyptoria*, which had acquired true teeth but still lack fully formed deltidiodont articulation, appear in the analysis as a sister group to all other brachiopods with deltidiodont articulation (Fig. 8, node 3).

Notwithstanding with the results of the present analysis (Fig. 8) a lack of dental plates in Billingsellidae is regarded here as a primary feature, and their appearance in the orthides and tritoechiides represents homoplasy, which remains unrecognized. In the Cambrian Billingsellidae true dental plates are absent invariably and this feature historically comes before their appearance in the Ordovician polytoechioideans. Therefore the presence of dental plates is regarded here as the main distinctive feature of Tritoechiidae and Politoechioidea, which distinguishes them from Billingselloidea, despite the possible paraphyletic nature of the group. The paraphyletic origin of some species presently assigned to *Tritoechia* is another outcome of the present analysis. This is not surprising, because some significant differences in shell morphology are evident from the study of Kazakhstanian species.

Tritoechiid species from southern Kazakhstanian terranes with the exception of *Tritoechia tokmakensis* belong to a single clade (Fig. 8, node 8) and the pattern of their divergence matches very well with the chronological sequence of their appearances. By contrast, the Uralian *Korinevskia akbulakensis* and *Protambonites lermontovae* are placed somewhat distantly and demonstrate more similarities to *Billingsella* (Fig. 8, node 7). A possible explanation of the observed pattern is that these two species are among the oldest tritoechiids and come from a different

geographical setting, located at the southern margin of the Baltica plate, which faced West Gondwana in the early Ordovician (Torsvik 1998).
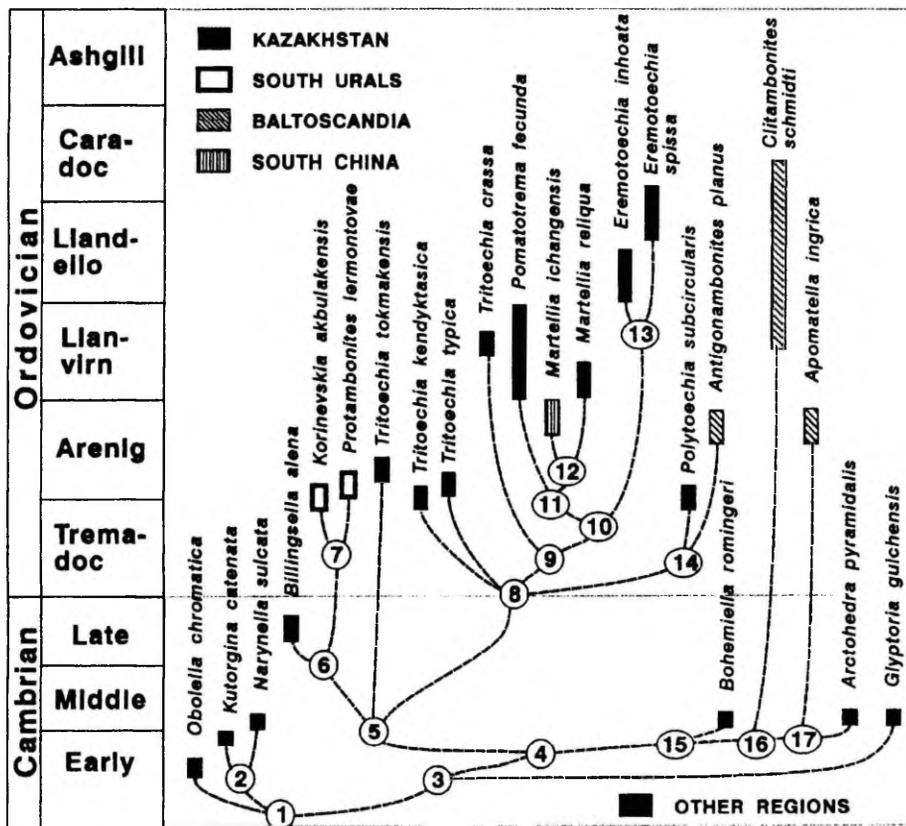

Figure 8. Stratigraphic ranges and inferred phylogenetic relationships of nine Kazakhstanian tritoechiid species (shown in black) and selected taxa of early rhynchonelliformean brachiopods and clitambonitides based on 50% majority rule consensus of six trees. Numbered nodes are supported by the character states listed in the Appendix.

AFFINITIES OF THE FAMILY TRITOECHIIDAE

Available data on shell morphology together with the phylogenetic analysis presented suggest a close affinity between Tritoechiidae and Billingsellidae. Both groups are characterised by the presence of a well developed pseudodeltidium with an apical foramen and chilidial plates or chilidium, which probably represent homologous structures; sockets bordered anteriorly by low socket ridges, which are subparallel to the hinge line; and radially arranged dorsal adductor scars. The ventral muscle field of Tritoechiidae and Billingsellidae is situated in some cases on a raised muscle platform, but there is no trace of a true spondylium. If one

assume a direct phylogenetic relationship between Tritoechiidae and Billingsellidae, as proposed by Havliček (1977: 25), the acquisition of dental plates may represent the only important novelty in the tritoechiid shell, but this feature is not recognised as synapomorphic in the cladistic analysis. Otherwise all tritoechiid genera display strong conservatism, and the basic features of their shell morphology including characters of the muscle fields, mantle canal system, general shell shape and ornament persist with only slight changes until their extinction in the early Caradoc. Both saccate and pinnate mantle canals are present in the Tritoechiidae, but polarity of this feature is difficult to resolve because both types of mantle canals were present already in the earliest Cambrian rhynchonelliformean stocks. Thus saccate and pinnate mantle canals in both groups could represent plesiomorphic features, which cannot be used to establish close phylogenetic relationships between the Tritoechiidae and other Clitambonitidina.

By contrast, the earliest Clitambonitidina (e.g., *Neumania* and *Apomatella*) have a well defined spondylium, quadripartite dorsal adductor field, and lack delthyrial covers (Wright & Rubel 1996), which evolved only in derived clitambonitidines (e.g., *Clitambonites*) not earlier than in the Llanvirn. Wright and Rubel (1996) interpreted these as true deltidium. The basic characters of the earliest, most primitive clitambonitidines suggest that their billingsellide ancestry seems to be unlikely. The derived Protorthoidea (e.g. *Arctohedra*), which had already developed a free spondylium, deltidiodont articulation, and quadripartite dorsal adductor scars, may represent the stock closest to clitambonitidines among the Cambrian brachiopods, but their affinities require more comprehensive study.

Polytoechiids represented in the analysis by *Polytoechia* and *Antigonambonites* appear in the analysis as a sister group of derived tritoechiides (Fig. 8, node 14). It is likely that they had evolved from the tritoechiid stem group sometime in the latest Cambrian – early Tremadoc.

Nevertheless, there are enough evidences to exclude the families Tritoechiidae and Polytoechiidae from the suborder Clitambonitidina, but they can be retained in Billingsellida as a separate superfamily.

It is also relevant to note that, during the early and mid Ordovician, the Tritoechiidae and Clitambonitidina were clearly separated biogeographically. The earliest known Clitambonitidina are from the Baltica Plate (Rubel & Popov 1994), from the early Arenig *Oepikodus evae* Biozone. Clitambonitidines achieved a relatively wide geographical distribution only from the Llanvirn, when they appear as insignificant component of brachiopod assemblages characteristic of the Laurentian and Siberian plates, but their diversity outside the Baltic plate remains very low (Williams 1973).

One of the earliest and most diverse tritoechiid brachiopod faunas is known from the early Ordovician of Laurentia (Ulrich & Cooper 1938). Here they replaced the late Cambrian rhynchonelliformean brachiopod assemblages, which are characterised by the abundance of billingsellids (Bell 1941). During the late Tremadoc—Arenig, Tritoechiidae were also spread widely across Gondwana and adjacent microplates and island arcs (e.g., Morocco, Bohemia, east Australia, south

China, south Kazakhstanian terranes). Their only occurrence on the Baltic plate is confined to its Uralian margin (Andreeva 1960) and they are completely unknown from the Baltoscandia. This difference in the geographic distribution is traceable until the early Caradoc, when the family Tritoechiidae became extinct.

Acknowledgements

REFERENCES

AKSARINA, N. A. 1975. Brakhiopody. [Brachiopods.] *In* REPINA, L. N., JASKOVICH, B. V., AKSARINA, N. A., PETRUNINA, Z. E., PONIKLENKO, I. A., RUBANOV, D. A., BOLGOVA, G. V., GOLIKOV, A. N., KHAJRULINA, T. I., & OSOKHOVA, M. M. Stratigrafiya i fauna nizhnego paleozoya severnykh predgoriy Turkestanskogo i Alayskogo khrebtov. *Trudy Instituta geologii i geofiziki, Akademija Nauk SSSR, Sibirskoje otdelemije,* **278**: 91–100. [In Russian].

ANDREEVA, O.N. 1960 — Novye vidy ordovikskikh brakhiopod Urala i Mugodzhar. [New species of Ordovician brachiopods of the Urals and Mugodzhary]. *In* B. P. MARKOWSKII (ed.): *Novye vidy drevnikh rastenii i bespozvonochnykh SSSR.* **1**: 286–298. Moscow. [In Russian].

BARRANDE, J., 1848 — Ueber die Brachiopoden der silurischen Schichten von Böhmen. *Haidingers Naturwissenschaftliche Abhandlungen,* **2**: 155–256.

BARRANDE, J., 1879 — Système Silurien du centre de la Bohême. Ière partie. *Recherches paléontologiques, v. 5. Classe des Mollusques. Ordre des Brachiopodes,* Prague & Paris: 1–226.

BELL, W. A. 1941 — Cambrian Brachiopoda from Montana. *Journal of Paleontology,* **15**: 193–255.

BENEDETTO, J. L. 1987 — Braquiopodos clitambonitaceos de la formacion San Juan (Ordovicico temprano), Precordillera Argentina. *Ameghiniana,* **24**: 95–108.

BROWN, J. A. 1948 — Lower Ordovician Brachiopoda from the Junee District, Tasmania. *Journal of Paleontology,* **22**: 35–39.

COOPER, G. A. 1952 — New and unusual species of brachiopods from the Arbuckle Group in Oklahoma. *Smithsonian Miscellaneous Collections,* **117**: 1–35.

COOPER, G. A. 1956 — Chazyan and related brachiopods. *Smithsonian Miscellaneous Collections,* **127**: 1–1245.

HAVLÍČEK, V. 1949 — Orthoidea a Clitambonoidea z Ceskeho Tremadoku. [Orthoidea and Clitambonoidea of the Bohemian Tremadoc]. *Statniho Geologickeho Ústavu Ceskoslovenske Republiky, Sbornik*, **16**: 93–144.

HAVLÍČEK, V. & JOSOPAIT, V. 1972 — Articulate Brachiopods from the Iberian Chains, Northeast Spain (Middle Cambrian-Upper Cambrian-Tremadoc). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **140(3)**: 328–353.

HAVLÍČEK, V. 1977 — Brachiopods of the order Orthida in Czechoslovakia. *Rozpravy Ústredniho Ústavu geologickeho*, **33**: 1–327.

KELLER, B. M. & RUKAVISHNIKOVA, T. B. 1961 — Tremadokskiye i smezhnyye s nimi otlozheniya khrebta Kendyktas [Tremadoc and related deposits of the Kendyktas Range]. *Trudy Geologicheskogo instituta Akademii Nauk SSSR*, **18**: 22–29 [In Russian].

KORINEVSKIY, V. V. 1989 — Opornye rasresy nizhnego ordovika Juzhnogo Urala (terrigennye fatsii) [Key sections of the Lower Ordovician of the South Urals (clastic facies)]. *Uralskoje otdelenie Akademii Nauk SSSR*, 1–67 [In Russian].

LAURIE, J. R. 1980 — Early Ordovician orthide brachiopods from southern Tasmania. *Alcheringa*, **4**: 11–23.

MARTELLI, A. 1901 — Fossili del Siluriano inferioredello Schensi. *Bollettino della Societa geologica italiana*, **20**: 305–307.

MELNIKOVA, L. M. 1986 — Ordovikskiye ostrakody Kazakhstana [Ordovician ostracodes of Kazakhstan]. *Trudy Paleontologicheskogo instituta*, **218**: 1–103 [In Russian].

NASEDKINA, V. A. 1977 — Ob ordovikskikh brakhiopodakh v basseine r. Chaushki v severnykh Mugodzharakh [On the Ordovician brachiopods from the Chaushka river basin in northern Mugodzhary]. *In* SAPELNIKOV, V. P. & CHUVASHOV, B. I. (eds), Materialy po paleontologii srednego paleozoya Urala i Sibiri. *Trudy Instituta geologii i geokhimii, Akademiya Nauk SSSR, Uralskiy Nauchnyi tsentr*, **126**: 11–23 [In Russian].

NAZAROV, B. B. & POPOV, L. E. 1980 — Stratigrafiya i fauna ordovikskikh kremnisto-karbonatnykh otlozhenii Kazakhstana [Stratigraphy and fauna of Ordovician siliceous-carbonate deposits of Kazakhstan]. *Trudy Geologicheskogo instituta Akademii Nauk SSSR*, **331**: 1–190 [In Russian].

NEUMAN, R.B. 1968 — Paleogeographic implications of Ordovician shelly fossils in the Magog Belt of the Northern Appalachians. *In:* ZEN E.-AN *ET AL.* (eds), *Studies of Appalachian Geology: Northern and Maritime*, N.Y., John Wiley & Sons: 35–48.

NIKITIN, I. F. 1972 — *Ordovik Kazakhstana, Chast 1, stratigraphiya [Ordovician of Kasakhstan, Part 1, stratigraphy]*. Nauka, Alma-Ata, 242 p. [In Russian].

NIKITIN, I. F, FRID, N. M. & ZVONTSOV, V. S. 1991 — Paleogeography and main features of volcanicity in the Ordovician of Kazakhstan and North Tien-Shan, *Geological Survey of Canada, Paper* **90-9**: 259–270.

NIKITINA, O. I. & TIMOFEEVA, L. S. 1991 — Novye dannye po stratotipam kopalinskogo i anrakhaiskogo gorizontov srednego ordovika. [New data on the stratotypes of the Kopaly and Anrakhai horizons of the Middle Ordovician]. *In* SHLYGIN, A. E (ed.), *Geologija i poleznyyje iskopayemyye yuga Kazakhstana*, Gylym, Alma-Ata: 37–46. [In Russian].

ÖPIK, A. 1934 — Über Klitamboniten. *Acta et Commentationes Universitatis Tartuensis (Dorpatensis)*, **A26**: 1–239.

ORADOVSKAYA, M. M. 1968 — Brakhiopody Omulevskikh i Elgenchakskikh gor [Brachiopods of the Omulevka and Elgenchak mountains]. *In* NIKOLAEV, A. A. (ed.). *Polevoi atlas ordovikskoi fauny Severo-Vostoka SSSR*, Magadan: 30–53. [In Russian].

ORADOVSKAJA, M. M. 1973 – Brakhiopody [Brakhiopody]. *In* Keller, B. M. (ed.). Biostratigraphiya nizhnei chasti ordovika Severo-Vostoka SSSR I biogeografiya kontsa rannego ordovika. *Trudy Geologicheskogo Instituta Akademii Nauk SSSR*, **213**: 141–209. [In Russian].

PAHLEN, A.VON 1877 — Monographie der Baltisch-Silurischen Arten der Brachiopoden-Gattung Orthisina. *Mémoires de l'Academie Imperiale des Sciences de St. Petersbourg, Ser.7*, **24**: 1–52.

PALETS, L. M. 1965 — Stratigrafiya otlozhenii ordovika severo-zapadnogo okonchaniya Chu-Iliiskikh gor (raion loga Karatal) [Stratigraphy of the Ordovician deposits in the north-western Chu-Ili Range (area of Karatal valley)]. *Materialy po geologii i poleznym iskopaemym Yuzhnogo Kazakhstana*, **3(28)**: 16–22 [In Russian].

PANDER, C. H. 1830 — *Beiträge zur Geognosie des Russischen Reiches*. K. Kray, St. Petersburg: 1–165.

POPOV, L. E. 1976 — Zonalnye kompleksy sredneordovikskikh brakhiopod Kazakhstana. [Zonal assemblages of Middle Ordovician brachiopods in Kazakhstan.] *Akademiia Nauk SSSR, Doklady*, **226**: 911–914. [In Russian].

POPOV, L. E. 1992 — The Cambrian radiation of brachiopods. *In* LIPPS, J. H. & SIGNOR, P. W. (eds). *Origin and early evolution of Metazoa*. Pergamon, New York: 399–423.

POPOV, L. E. & HOLMER, L. 1994 — Cambrian-Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. *Fossils and Strata*, **35**: 1–156.

POPOV, L. E., HOLMER, L. E. & GORJANSKY, V. J. 1997 — Late Ordovician and Early Silurian trimerellide brachiopods from Kazakhstan. *Journal of Paleontology,* **71**: 584–598.

POPOV, L. E. & TIKHONOV, YU. A. 1993 — Novyye nakhodki okremnennykh rakovin srednekembriiskikh brakhiopod v Yuzhnom Kyrgyzstane [New findings of silicified Middle Cambrian brachiopod shells in South Kyrgyzstan]. *In* MAMBETOV, A. M. (ed.). *Novyye dannyye po biostratigrafii dokembriya i paleozoya Kyrgyzstana*. Ilim, Bishkek: 33–40. [In Russian].

ROSS, A. 1970. Ordovician brachiopods, trilobites and stratigraphy in eastern and central Nevada. *United States Geological Survey, Professional Paper*, **639**: 1–103.

ROZMAN, KH. S. 1978 — Brakhiopody obikalonskikh sloev [Brachiopods of the Obikalon beds]. *Akademiia Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Trudy*, **397**: 75–101. [In Russian].

RUBEL, M. 1963 — O gonambonitakh (Clitambonitacea, Brachiopoda) nizhnego ordovika Pribaltiki [On the gonambonitids (Clitambonitacea, Brachiopoda (from the Lower Ordovician of the East Baltic]. *Eesti NSV Teaduste Akadeemia Geoloogia Instituudi, Uurimused*, **13**: 91–108 [In Russian].

RUBEL, M. & POPOV, L. E. 1994 — Brachiopods of the subfamily Atelelasmatinae (Clitambonitacea) from the Arenig, Ordovician of the Baltic Klint area. *Eesti NSV Teaduste Akadeemia Toimetised, Geoloogia*, **43 (4)**: 192–202.

RUBEL, M. & WRIGHT, A. D. 2000 — Clitambonitidina: 692–708. In WILLIAMS A., *et al. Treatise on Invertebrate Paleontology, Part H (Brachiopoda), Part H, Brachiopoda (revised)*, **3**. Boulder and Lawrence, Geological Society of America & University of Kansas: 424–919.

RUKAVISHNIKOVA, T. B. 1961 — Brakhiopody nizhnego ordovika khrebta Kedyktas [Brachiopods of the Lower Ordovician of the Kendyktas Range]. *Trudy Geologicheskogo Instituta Akademii Nauk SSSR*, **18**: 29–54 [In Russian].

SCHUCHERT, C. 1893 — *A classification of the Brachiopoda:* American Geologist, v. 11, no. 3: 141–167.

SCHUCHERT, C. & COOPER, G. A. 1932 — Brachiopod genera of the suborders Orthoidea and Pentameroidea. *Memoirs of the Peabody Museum of Natural History*, **4**: 1–270.

SWOFFORD, D. L. 1993. *Pylogenetic analysis using parsimony. Version 3.1.1. Computer program.* Illinois Natural History Survey, Champaign, Illinois.

TORSVIK, T. H., 1998. — Palaeozoic palaeogeography: A north Atlantic viewpoint. *GFF*, **120**: 109–118.

ULRICH, E. O. & COOPER, G. A. 1936 — New genera and species of Ozarkian and Canadian brachiopods. *Journal of Paleontology*, **10**: 616–631.

ULRICH, E. O. & COOPER, G. A. 1938 — Ozarkian and Canadian Brachiopoda. *Geological Society of America, Special Paper*, **13**, 323 p.

VAGRANOV, V. G., ANCYGIN, N. YA., NASSEDKINA, V. A., MILICINA, V. S., & SHURYGINA, M. V. 1973 — *Stratigrafiya i fauna ordovika Srednego Urala [Stratigraphy and faunas of the Ordovician of Central Urals]*. Moskow, Nedra, 228 p. [In Russian].

WALCOTT, C. D. 1905 — Cambrian Brachiopoda with descriptions of new genera and species. *United States National Museum, Proceedings*, **28**: 227–337.

WANG YU, 1956 — New species of brachiopods. *Scientia Sinica*, **5(1)**: 157–176.

WILLIAMS, A. 1965 — Orthida: 299–359. *In* MOORE, R. C. (ed.). *Treatise on Invertebrate Paleontology. Part H: Brachiopoda.* University of Kansas Press, xxxii+927 p.

WILLIAMS, A. 1972 — An Ordovician Whiterock fauna in Western Ireland. *Royal Irish Academy, Proceedings (B)*, **72**: 209–219.

WILLIAMS, A. 1973 — Distribution of brachiopod assemblages in relation to Ordovician paleogeography. *Special Papers in Palaeontology* **12**: 241–269.

WILLIAMS, A, BRUNTON, C. H. C. & MACKINNON, D. I. 2000 – Morphology: 321–422. In WILLIAMS A., *et al. Treatise on Invertebrate Paleontology, Part H (Brachiopoda), Part H, Brachiopoda (revised)*, **1**. Boulder and Lawrence, Geological Society of America & University of Kansas: 1–539.

WILLIAMS, A, CARLSON, S.J., BRUNTON, C.H.C., HOLMER, L.E. & POPOV, L.E. 1996 — A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions: Biological Sciences*, 355: 1171–1193.

WILLIAMS, A. & CURRY, G. B. 1985 — Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo, *Ireland. British Museum (Natural History), Bulletin, Geology*, **38**: 183–269.

WIRTH, E. 1936 — Über *"Clitambonites" Giraldii* Martelli und *Yangtzella Poloi* Martelli aus dem Ordoviz Chinas. *Paläontologische Zeitschrift*, **18**: 292–303.

WIRTH, E. 1937 — Beiträge zur Kenntnis des Paläozoicums in der Umradung des Roten Beckens von Szechuan, Südwest-China. *Neues Jahrbuch für Mineralogie, Geologie und paläontologie, Abt. B*, **77**: 77–111.

WRIGHT, A. D. 1994 — Mantle canals on brachiopod interareas and their significance in brachiopod classification. *Lethaia*, **27**, 223–226.

WRIGHT, A. D. & RUBEL, M. 1996 — A review of the morphological features affecting the classification of Clitambonitidine brachiopods. *Palaeontology*, 39: 53–75.

ZENG QING-LUAN 1977 – Brachiopoda: 31–69. *In* Paleontological atlas of South-Central China, early Papaeozoic part (ed..), **1**. Peking: 1–470 [In Chinese].

ZENG QING-LUAN, NI SHI-ZHAO, XU GUANG-HONG, ZHOU, T., WANG XIAO-FENG, LI ZHI-HONG, LAI, C., & XIANG, L. 1983 — Subdivision and correlation of the Ordovician in

the eastern Yangtze Gorges, China. *Bulletin of the Yichang Institute of Geology and Mineral Resources*, **6**: 1–68 [In Chinese].

XU HAN-KUI, RONG JIA-YU AND LIU DI-YONG, 1974 — Ordovician brachiopods: 144–145. *In* Handbook of Stratigraphy and palaeontology of southwest China (ed.). Science Press: 1–454 [In Chinese].

APPENDIX 1

Characters and character states in phylogenetic analysis.

1. out — shell outline: subcircular (0), transversely suboval to semioval (1), isometric to slightly elongated with posteriorly erected ventral umbo (2), subhexagonal (3).
2. prl — profile (sagittal): planoconvex (0), dorsibiconvex (1), ventribiconvex (2), subequally biconvex (3), convexiplane (4).
3. vvp – profile (ventral valve): evenly convex (0); flattened or weakly concave with maximum height at the umbo (1); convex with maximum height at the umbo (2); convex with maximum height between the umbo and mid-valve (3); convex with maximum height at mid-valve (4); subpyramidal (5).
4. dvp — profile (dorsal valve): evenly convex (0); flat (1); weakly convex with maximum height at the umbo (2); convex with maximum height between the umbo and mid-valve (3); convex with maximum height at mid-valve (4).
5. acm — anterior commissure: rectimarginate (0), sulcate (1), gently uniplicate (2), strongly uniplicate (3).
6. pmw — maximum shell width: at hinge line (0), anterior to hinge line (1).
7. psd — pseudodeltidium: absent (0), present (1).
8. del — deltidium: absent (0), present (1).
9. pvv — pedicle opening: posterior cleft (0), supra-apical (1), formed by fusion of deltidial plates (2).
10. vsl — ventral median sulcus: absent (0), weakly defined (1), well developed (2).
11. dmf — dorsal median fold: absent (0), weakly defined (1), well developed (2).
12. dsu — dorsal median sulcus: absent (0), present (1), fading anteriorly (2) .
13. ufo – supra-apical foramen: no pseudodeltidium (0), open (1), sealed (2).
14. nop — notothyrium: absent (0), widely divergent (1), narrowly divergent (2).
15. chi — chilidium: absent (0), separated plates (1), complete (2).
16. dia — dorsal interarea: absent (0), rudimentary (1), well developed (2).
17. orr — radial ornament: absent (0), finely multicostellate (1), multicostellate (2), parvicostellate (3), ramicostellate (4) costate (5), capillae (6).
18. adt — aditicules: absent (0), present (1).
19. vii — ventral interarea, inclination: strongly apsacline to orthocline (0), apsacline (1), procline to catacline (2).
20. vip — ventral interarea, profile: curved (0), planar (1).
21. fbd — furrows along the lateral sides of pseudodeltidium: absent (0), present (1).
22. plf — sockets: absent (0), present, partly composed of primary shell (1), present, formed by secondary shell (2).
23. dtt — deltidiodont teeth: absent (0), present (1).
24. tes — deltidiodont teeth (shape): not applicable (0), blindly triangular, oblique, curved dorsally (1); large, transverse, anteriorly directed (2); transverse strongly inclined to comissural plane (3).
25. scb — socket ridges/brachiophores: absent (0), brachiophore knobs (1), socket ridges (2), brachiophores (3).
26. vmf — spondylial structures: absent (0), free (1), supported by median septum (2).
27. fsp — free spondylium (ontogeny): absent (0), present in juveniles (1), present in juveniles and adults (2).
28. dpl — dental plates: absent (0), present (1).

29. vdl — ventral diductor scar, length: not applicable (0), longer than adductors (1), about equal length (2), shorter then adductors (3).
30. psp — pseudospondylium: absent (0), present (1), raised anteriorly on the median septum (2), no discrete dental plates (3).
31. vmr — median ridge/septum anterior to the muscle field: absent (0), median ridge (1), septum supporting anteriorly the muscle platform (2), septum supporting spondylium (3).
32. vur — median ridge in the umbonal area: absent (0), present (1).
33. vmc — ventral mantle canals: pinnate (0), saccate (1), baculate (2).
34. npl — notothyrial platform: absent (0), present, low (1), well developed, solid, strongly inclined posteriorly (2), high, hanging anteriorly (3).
35. cpr — cardinal process: absent (0), rudimentary (1), simple, ridge-like (2).
36. daf — dorsal adductor field: obscure (0), impressed on valve floor (1), impressed on callus of secondary shell (2).
37. asc — adductor scars: median and posterolateral pairs (0), radially arranged (1), quadripartite (2).
38. dms — dorsal median ridge: absent (0), present as a low ridge (1), septum (2).
39. ssp — side septa: absent (0), present (1).
40. aad — anterior adductor scars: larger then posterior pair (0), about equal size (1), smaller (2).
41. sst – secondary shell: with laminar, foliated (0); fibrous (1); laminar, cross-bladed (2).
42. ppt – pseudopunctation: absent (0), present (1).

APPENDIX 2

List of synapomorphies supporting the numbered nodes in Figure 8. Characters and character states marked as in Appendix 1.

Node 3. Narrow triangular notothyrial opening (14:2); ramicostellate radial ornament (17:4); sockets underlined by secondary shell (22:2); deltidiodont teeth (23:1) blindly triangular, curved dorsally (24:1); brachiophore knobs (25:1); no discrete dental plates (26:2).
Glyptoria gulchensis. Subequally biconvex shell (2:3); uniplicate anterior commissure (5:2); ventral median sulcus well developed (10:2); dorsal median fold well developed (11:2); costate radial ornament (17:5); free spondylium in juveniles and adults (26:1; 27:2); no dental plates (30:3); high notothyrial platform hanging anteriorly (34:3); weakly impressed dorsal adductor muscle field (36:0).
Node 4. Socket ridges (25:2); dental plates (28:1); saccate ventral mantle canals (33:1); simple, ridge-like cardinal process (35:2); low dorsal median ridge (38:1).
Node 5 (Order Billingsellida). Convex ventral valve with maximum height at the umbo (3:2); acquisition of pseudodeltidium, (7:1); supra-apical foramen (9:1) remaining open in adults (13:1); two separated chilidial plates (15:1); teeth large, transverse, anteriorly directed (24:2); notothyrial platform strongly inclined posteriorly (34:2).
Tritoechia tokmakensis. Maximum shell width at hinge line (6:0); parvicostellate radial ornament (17:3).
Node 6. Isometrical to slightly elongated shell outline with posteriorly erected ventral umbo (1:2); convexiplane shell (2:4); supra-apical foramen sealed in adults (13:2); ventral

interarea strongly apsacline to orthocline (19:0); ventral diductor scars shorter then adductor track (29:3); median ridge in umbonal area of ventral muscle field (32:1); laminar, cross-bladed secondary shell layer (41:2).

Billingsella alena. Maximum shell width at hinge line (4:0); dental plates absent (28:0); low notothyrial platform (34:1)

Node 7. Complete chilidium (15:2); ramicostellate radial ornament (17:4); flattened ventral valve with maximum height at the umbo (3:2).

Korinevskia akbulakensis. Dorsal median septum instead of ridge (38:2).

Protambonites lermontovae. Median ridge anterior to ventral muscle field (31:1); pinnate ventral mantle canals (33:0).

Node 8. Ventral valve convex with maximum height near mid-length (3:4); ventral median ridge anterior to the muscle field (31:1); ventral mantle canals pinnate (33:0).

Tritoechia typica. Dorsal sulcus fading anteriorly (13:2); aditicules present (18:1).

Tritoechia kendyktasica. Sulcate anterior commissure (5:1); dorsal sulcus (12:1); Apsacline ventral interarea (17:2); low notothyrial platform (30:1).

Node 9. Dorsal valve convex with maximum height between the umbo and mid-length (4:3); Anterior commissure sulcate (5:1); complete chilidium (15:2); parvicostellate radial ornament (17:3); ventral adductor scar shorter then diductor scars (29:1); saccate ventral mantle canals (33:1).

Tritoechia crassa. Ventral valve subpyramidal (3:5); dorsal median sulcus present (12:1); ventral interarea procline to catacline (19:2).

Node 10.

Node 11. Weakly convex dorsal valve with maximum height at the umbo (4:2); anterior commissure gently uniplicate (5:2); ventral median sulcus weakly defined (10:1); dorsal median fold weakly defined (11:1); dorsal adductor field impressed on callus of secondary shell (36:2); side septa present (39:1).

Pomatotrema fecunda. Planoconvex shell (2:0); ventral valve convex with maximum height at the umbo (3:2); rectimarginate anterior commissure (5:0).

Node 12. Subhexagonal shell outline (1:3); finally multicostellate radiual ornament (17:1); high notothyrial platform hanging anteriorly (34:3).

Martellia ichangensis. No apomorphic characters recognised.

Martellia reliqua. Median ridge anterior to ventral muscle field absent (31:0).

Node 13. Dorsibiconvex shell (3:1); ventral sulcus well developed (10:2); dorsal median fold well developed (11:2); multicostellate radial ornament (17:2); low notothyrial platform (34:1).

Eremotoechia inhoata. No apomorphic characters recognised.

Eremotoechia spissa. Dorsal valve strongly convex with maximum height at mid-valve (4:4); anterior commissure strongly uniplicate (5:3).

Node 14 (Polytoechiidae). Dorsibiconvex shell (2:2); Ventral adductor track longer then diductor scars (29:3); pseudospondylium raised anteriorly on the median septum (30:3; 31:3); pseudopinctation present (42;1).

Antigonambonites planus. Resupinate shell (2:5); ventral valve flattened to slightly concave with raised umbo (3:1); maximum width at hinge line (6:0); sealed suproapical foramen (13:2); side septa present (39:1).

Polytoechia subcircularis. Ventral interarea curved (20:0); dorsal adductor field obscure (36:0).

Node 15. Dorsal median sulcus fading anteriorly (12:2); apsacline ventral interarea (19:1); flat dorsal valve (4:1).

Bohemiella romingeri. Planoconvex shell (0); curved ventral interarea (20:0); brachiophores (25:3); rudimentary cardinal process (35:1); anterior adductor scars smaller then posterior ones (40:2).

Node 16 (Clitambonitoidea + *Arctohedra*). Multicostellate radial ornament (17:2); spondylium supported by septum (26:2; 31:1); no pseudospondylium (30:0); quadripartite dorsal adductor field (37:2); free spondylium present in juveniles (27:1).

Node 17. Subpyramidal ventral valve (3:5); anterior commissure sulcate (5:1); maximum shell width along the hinge line (6:1); dorsal median sulcus (12:1).

Arctohedra pyramidalis. Acquisition of brachiophores (25:3); free spondylium in juveniles and adults (26:1; 27:2); ventral median ridge absent (31:0); rudimentary cardinal process (35:1); dorsal adductor scars with smaller anterior pair (36:2).

Apomatella ingrica. Weakly convex dorsal valve with maximum height near the umbo (4:2).

Clitambonites schmidti. Deltidium (8:1); pedicle foramen formed by fusion of deltidial plates (9:2); complete chilidium (15:2); aditicules (18:1); ventral interarea apsacline (19:1); ventral adductor track longer then diductor scars (25:3).

IV

THE OCCURRENCE OF NEW SUBSPECIES OF THE CLITAMBONITIDINE BRACHIOPOD *ESTLANDIA CATELLATUS* (ÖPIK) IN THE MIDDLE ORDOVICIAN OF OSMUSSAAR ISLAND, ESTONIA

Olev VINN

Institute of Geology, University of Tartu,
Vanemuise 46, 51014 Tartu, Estonia; vinn@ut.ee

Abstract. New subspecies *Estlandia catellatus odini* have been described in the Uhaku Stage of Osmussaar Island in Estonia. The unusual co-occurrence of three species of the same genus (*E. marginata*, *E. pyron pyron*, *E. catellatus odini* subsp.n.) in one bed may have been resulted from their partial post mortem concentration from different habitats.

Key words: Brachiopoda, Gonambonitidae, *Estlandia catellatus odini* subsp.n., Ordovician, Llanvirn, Estonia

INTRODUCTION

Öpik (1934) established the species *Progonambonites* ? *catellatus* on single ventral valve from Duboviki of Russia dating it as Kunda age. Recently numerous specimens of this species were collected from the Uhaku Stage in Osmussaar Island (Fig. 1). Two fossiliferous planes (1.20 and 3.80m above the lower boundary of Lasnamägi Stage have been previously recorded within the Väo Formation in the uppermost part of the Osmussaar cliff (Suuroja et al. 1999). The new material comes mostly from the upper fossiliferous bed (Fig. 2), exposed at the northern coast of the island near the lighthouse. The upper fossiliferous plane, 5–10 cm thick, contains various trilobites, gastropods, bivalves and brachiopods in large number. Three species of the genus *Estlandia*: *E. pyron pyron* (Eichwald) (ten specimens; Pl. I, figs. 17, 18), *E. marginata* (Pahlen) (three specimens; Pl. I, figs. 19, 20, Fig. 4, A) and a new subspecies of *E. catellatus odini* (see below), as well as the clitambonitids *Clitambonites schmidti* (Pahlen), *C. squamatus* (Pahlen), *Vellamo simplex* (Öpik) have been identified from there.

One could note somewhat smaller size of the shells of *Estlandia pyron pyron* from Osmussaar if compared with those from the stratigraphically younger Kukruse Stage (Öpik, 1930, pl. XX, figs. 243–247, pl. XXII, fig. 278, text-fig. 26). But as there are no other differences in morphology of these specimens they are considered con-subspecific.

Fig. 1. Location of the Osmussaar, Estonia, and Duboviki sections, Russia. Dotted line — Baltic-Ladoga Klint.
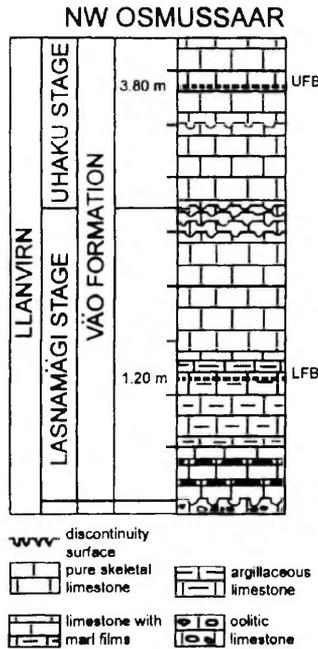

Fig. 2. Osmussaar section near the lighthouse at the northern coast. UFB — upper fossiliferous bed. LFB — lower fossiliferous bed. Stratigraphy follows here Suuroja *et al.* 1999.

The co-occurrence of three species of *Estlandia* in Osmussaar rise the question of their distinctivity there. However, besides the morphological evidents it sould be noted that the most of clitambonitidines valves are disarticulated (96% of 28 valves studied). They, as well as other groups of fossils are presumably not burried in situ, and such peculiar taphocoenoses may have resulted of concentration of shells from a different habitats by hydrodynamic activity.
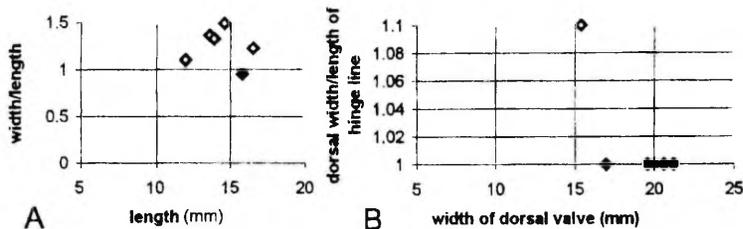
2

Fig. 3. A. Ratio of length and width of the ventral valves. Solid square — *E. catellatus catellatus* (Öpik), Blank squares — *E. catellatus odini* subsp.n.; B. Ratio of width of dorsal vallve and length of hinge line. Solid squares — *E. catellatus odini* subsp.n., Blank square — *E. catellatus catellatus* (Öpik)

The presence of *Estlandia catellatus odini* subsp.n. in limestones as high as the lowermost Uhaku Stage is surprising in wiev of Öpik's original record *E. catellatus catellatus* from the Kunda Stage of Duboviki, Russia, i.e. three stages below. But, as Duboviki quarry is situated on the exposure of Aseri, Lasnamägi and Uhaku stages (Männil 1963), then the younger age for the *E. catellatus catellatus* seems to be more realistic than the Kundan one assumed by Öpik (1934).

In Estonia the occurrence of the *E. catellatus odini* subsp.n. is quite restricted, to the Island of Osmussaar.

SYSTEMATIC DESCRIPTIONS

Repositories. All specimens are housed in the collections of the Museum of Geology, University of Tartu and have been assigned TUG numbers.

Abbreviations appearing in the text are as follows: L = maximum length, W = maximum width. All measures are in mm.

<div align="center">

Suborder CLITAMBONITIDINA ÖPIK, 1934
Superfamily CLITAMBONITOIDEA WINCHELL & SCHUCHERT, 1893
Family GONAMBONITIDAE SCHUCHERT & COOPER, 1931
Genus *Estlandia* Schuchert & Cooper, 1931

Plate I, Fig. 4

</div>

Type species. *Estlandia marginata* (Pahlen, 1877)
Species assigned. *E. pyron pyron* Eichwald, 1840, *E. pyron silicificata* Öpik, 1934, *E. seidlitzi* Rubel, 1963, *E. catellatus catellatus* Öpik, 1934, *E. catellatus odini* subsp.n.

<div align="center">3</div>
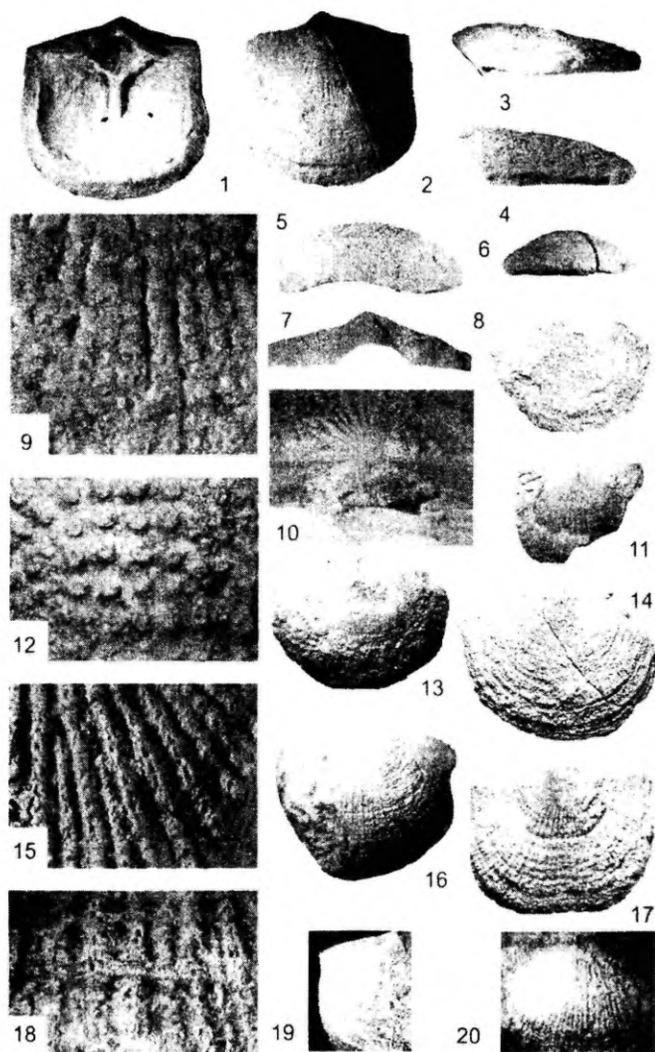
Explanation of Plate I

Figs. 1–3. *Estlandia catellatus catellatus* (Öpik), TUG1068-6 Holotype, Uhaku Stage ?, Duboviki quarry, Russia; 1, ventral valve interior, × 2.4; 2, ventral valve exterior, × 2.2; 3, ventral valve, lateral view, × 2.4; **Fig. 4–5.** *Estlandia catellatus odini* subsp.n., Uhaku Stage, Osmussaar Island, NW Estonia; 4, TUG1073-1 Holotype, ventral valve, lateral view, × 2.2; 5, TUG1073-4, dorsal valve, lateral view, × 2.2; **Fig. 6.** *E. catellatus catellatus* (Öpik), TUG1068-6 Holotype, Aseri Stage ?, Duboviki quarry, Russia, ventral valve anterior view, x1.7; **Figs. 7–8.** *E. catellatus odini* subsp.n., Uhaku Stage, Osmussaar Island, NW Estonia; 7, TUG1073-7, ventral interarea and deltidium, x2.5; 8,

4

TUG1073-3, ventral valve exterior, x2.2; **Fig. 9.** *Estlandia catellatus catellatus* (Öpik), TUG1068-6 Holotype, Aseri Stage ?, Duboviki quarry, Russia, spines on the ventral valve, × 10; **Figs. 10–14.** *E. catellatus odini* subsp.n., Uhaku Stage, Osmussaar Island, NW Estonia; 10, TUG72-210, umbonal view of the dorsal valve, × 7.5; 11, TUG1073-5, mould of dorsal valves interior, × 2.0; 12, Holotype, TUG1073-1, spines on ventral valve, × 12; 13, TUG46-125, dorsal valve exterior, × 1.8; 14, TUG1073-1, Holotype, TUG1073-1, ventral valve exterior, × 2.0; **Fig. 15.** *E. marginata* (Pahlen), TUG1073-20, Kiviõli, Kukruse Stage, NE Estonia, spines on the dorsal valve, × 7.0; **Fig. 16.** *E. catellatus odini* subsp.n., TUG1073-4, dorsal valve exterior, × 2.2; **Figs. 17–18**, *E. pyron pyron* (Eichwald), TUG72-208, Uhaku Stage, Osmussaar Island, NW Estonia; 17, ventral valve exterior, × 1.8; 18, poorly developed rare spines on the ventral valve, × 8.0; **Figs. 19–20**. *E. marginata* (Pahlen), TUG72-209, Uhaku Stage, Osmussaar Island, NW Estonia; 19, ventral valve exterior, × 1.2; 20, dorsal valve exterior, × 1.2.
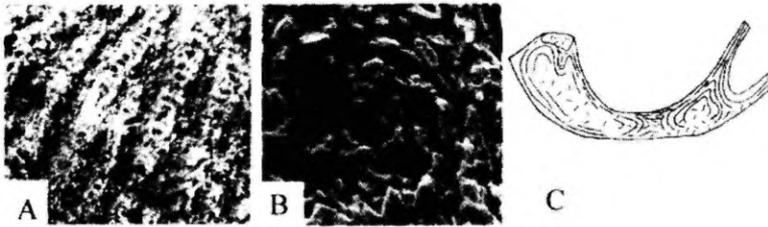

Fig. 4. Fig. A. *E. marginata* (Pahlen) TUG72-209, Uhaku Stage, Osmussaar Island, NW Estonia, spines on the dorsal valve, × 7.0; Figs. 2–3. *E. catellatus odini* subsp.n., TUG1073-3, Uhaku Stage, Osmussaar Island, NW Estonia; B, fibrous secondary layer with a pseudopuncta, x3000; C, subperpendcular cross section of the ventral valve, showing different growth stadiums of spondylium triplex (see Vinn & Rubel 2000, p. 443, fig. 3), immature (left half of figure) and adult stadium (right half of figure) respectively, × 10.

Estlandia catellatus odini subsp.n.
Plate I, figs. 4, 5, 7, 8, 10–14, 16, fig. 4 B, C

Holotype. Ventral valve TUG1073-1, Uhaku Stage, Osmussaar Island, Estonia.
Material and Dimensions. One shell (TUG1073-5, L=12.0; T=5.2; W=13.2), seven ventral valves (TUG1073-1, L=16.5, W=20.2; TUG1073-2, L=13.6, W=18.5; TUG1073-3; TUG1073-10, L=13.9, W=18.4; TUG1073-7, L=-, W=16.3; TUG1073-8; TUG1073-9, L=14.6, W=21.7) one ventral interior (TUG1073-6, L=-, W=21.4), five dorsal valves (TUG72-210, L=-, W=20.6; TUG1073-4, L=17.4, W=19.6; TUG46-125, L=16.0, W=20.0; TUG46-122, L=13.5, W=17.0; TUG46-121, L=16.0, W=21.1), one dorsal interior (TUG1073-11).

Locality and Distribution. Island of Osmussaar, NW Estonia, cliff on the northern coast near the lighthouse, Väo Formation, lower part of the Uhaku Stage, Middle Ordovician.

Description. Shell biconvex, semielliptical in outline, 67–76% as wide as long, with the maximum width at the hingeline, maximum height at the hingeline. Anterior commisssure rectimarginate, anterior margin slightly convex. Cardinal extremities obtuse to fairly acute, posterolateral sides straight.

Radial ornamentation finely multicostellate. Concentric fila forming evenly spaced, individual short tubulous spines of regular shape, well developed all over the shell, with almost always perpendicular apices to the surface. The round-shaped spines are 0.1 mm to 0.4 mm wide, increasing slightly in size towards the anterior commissure. The spines may be elongated in anterior region of shell.

Ventral valve moderately convex, nearly flat in lateral profile, with the maximum height at the hingeline. Ventral interarea of moderate length, apsacline and flat. Delthyrium covered by deltidium. Foramen very minute, sealed and situated in the topmost part of deltidium.

Ventral interior with the spondylium triplex, the well developed subspondylial lateral septa reaching the valve floor (Fig. 4, C). Median septum prominent extending up to midhalf of the valve length. Ventral subperipheral rim prominent.

Dorsal valve convex, strongly curved in lateral profile, with the maximum height at the mid-length of valve. Dorsal interarea flat, apsacline, 1.7–2.0 mm long, about two times shorter than ventral interarea. Notothyrium completely covered by well developed chilidium.

Adductor scars developed as fair tracks on the valve floor, not elevated anteriorly.

Dorsal anterior adductor scars slender and slightly longer than the posterior pair but the posterior pair is clearly wider. Adductor field about as long as the median ridge. Median ridge short and low, reaching about 1/3 length of valve umbo.

Cardinal process simple, ridge-like, fused with the chilidium. Subperipheral rim prominent.

Shell substance fibrous and pseudopunctate (Fig. 4, B).

Discussion. The *E. catellatus* has been placed here in the genus *Estlandia* because of its typical to that genus ornamentation, culminating often in the presence of spines. The species has also a well developed complete chilidium, median septa in both valves (see Alikhova 1953, p. 98; Rubel 1963, p. 106) and delthyrium covered by deltidium, all characteristic for the genus. The nominal subspecies *E. catellatus catellatus* (Pl. I, figs. 1–3, 6, 9; see also Öpik 1934, p. 141–142, pl. XXIV, fig. 4, 5; text-fig. 6F) has shell length larger than width (105% as wide as long, L=15.8, W=15.0 in holotype TUG1068-3), and

maximum width at the 1/3 length from the anterior, unlike the specimens of *E. catellatus odini* subsp. n., which have much wider shells (67–76% as wide as long), and maximum width of shell always at the hingeline (Fig. 3 A, B). The *E. catellatus* resembles most of all *E. marginata* (Pahlen) in its outline (see Öpik 1930, pl. XIX, figs. 229–236, fig. 248, pl. XX, figs. 236–239, text-figs. 24, 25): both have transverse outline, rectimarginate anterior commissure and equal size of shell. The former differs from the latter in its finer and smoother radial ornamentation, but also in its well developed and clearly finer spines (0.1– 0.4mm in *E. catellatus* versus 0.4–1.0mm in *E. marginata*), which are evenly spread all over the surface of shell and have more regular shape. *E. marginata* (Pahlen) has the coarser and less developed spines which occur only in the middle and anterior regions of the both valves. The spines in *E. marginata* are usually joined, side by side along the costellae (Pl. I, Fig. 15, Fig. 4, A), different to those in *E. catellatus* which are almost always individual.

One could distinguish three successive types of spines in *Estlandia*. This developmental line begins with *E. seidlitzi* (Rubel 1963, p. 104, pl. III, figs. 2, 5, 6) and *E. pyron pyron* (Eichwald) which have few and weakly developed spines (Pl. I, Fig. 18), if at all, the intermediate *E. marginata* (Pahlen) has has more or less well developed spines which are mostly joined along distal part of the costella (Pl. I, Fig. 15, Fig. 4, A); and, finally, *E. catellatus* (Öpik) has well developed and individul spines all over the shell (Pl. I, figs. 9, 12).

E. catellatus (Öpik) has less acute cardinal extremities than *E. marginata* (Pahlen), the latter has a faint sulcus on dorsal valve what completely fails in the first species. The *E. catellatus* (Öpik) has a radial ornamentation resembling that of *E. pyron* (Eichwald) (Öpik 1930, pl. XX, figs. 243–247, pl. XXII, fig. 278, text-fig. 26), but *E. catellatus* (Öpik) differs from *E. pyron* (Eichwald) by the lack of dorsal sulcus, and smaller size of spines and their more regular shape, greater number and presence in umbonal region of shell. The *E. pyron* (Eichwald) has clearly uniplicate anterior commissure, while the commissure in *E. catellatus* (Öpik) is rectimarginate

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REFERENCES

Alikhova, T. 1953. Rukovodyashchaya fauna brakhiopod ordovikskikh otlozheniy severo-zapadnoy chasti russkoy platformy. Gosudarstvennoe izdatelstvo geologicheskoy literatury, Moskva, p. 98–105. (in Russian)

Männil, R. 1963. On the correlation of the Ordovician strata of Estonia and Leningrad Region. ENSV TA Geol. Inst. Uurimused, **13**, p. 11–12. (in Russian, with English summary)

Öpik, A. 1927. Die Inseln Odensholm und Rogö. Ein Beitrag zur Geologie von NW-Estland. *Acta Comment. Univ. Tartuensis*, **12**, pp. 1–69.

Öpik, A. 1930. Brachiopoda Protremata der Estländischen Kukruse-Stufe. *Acta Comment. Univ. Tartuensis*, **17**, pp. 1–240.

Öpik, A. 1934. Über Klitamboniten. *Acta Comment. Univ. Tartuensis*, **26**, pp. 132–142.

Rubel, M. 1963. On Baltic Lower Ordovician Gonambonitids (Clitambonitacea, Brach.). ENSV TA Geol. Inst. uurimused **13**, p. 91–107. (in Russian, with English summary).

Schuchert, C. and Cooper, G. A. 1931. Synopsis of the Brachiopod genera of the suborder Orthoidea. *Am. Journal of Sci.*, **22.**

Schuchert, C. and Cooper, G. A. 1932. Brachiopod Genera of the Suborders Orthoidea and Pentameroidea. *Mem. of the Peabody Mus. Nat. Hist.*, **4**, Part 1, 115.

Suuroja, K., Saadre, T., Kask, J. 1999. Geology of Osmussaar Island. *Estonia Maritima* **4**, 39–63.

Vinn, O. and Rubel, M. 2000. The spondylium and related structures in the clitambonitidine brachiopods. *Journal of Paleontology*, **74**, 439–444.

KESKORDOVIITSIUMI KLITAMBONITIIDSE KÄSIJALGSE *ESTLANDIA CATELLATUS* (ÖPIK) UUS ALAMLIIK OSMUSSAARELT

Olev VINN

Osmussaarelt pärineva materjali põhjal on *Progonambonites? catellatus* (Öpik) loetud perekonda *Estlandia* kuuluvaks. Esmakordselt on kirjeldatud antud liigi dorsaalkaant ja uus alamliik *E. catellatus odini*. Uhaku vanune Osmussaare materjali olemasolu lubab kahelda Venemaalt Dubovikist pärineva holotüübi Kunda vanuses, tõenäoliselt pärineb holotüüp siiski noorematest kihtidest. Perekonna *Estlandia* kolme erineva liigi koosesinemine Osmussaarel ühes kihis on seletatav osaliselt eri biotoopidest kokkukantud materjaliga.

CURRICULUM VITAE

OLEV VINN

Date and
place of birth: 26.01.1971, Tallinn
Nationality: Estonian
Address: Raja 7a–8, Tallinn
Phone: +372 67 26 549
Fax: +372 64 64 201
E-mail: *olev.vinn.001@mail.ee*

Education

Graduated in geology 1993, University of Tartu, Institute of Geology
MSc. in geology in 1995, University of Tartu, Institute of Geology

Research interests

Evolution and ecology of palaeozoic brachiopods, phylogenetic classification
and palaeobiogeography.

CURRICULUM VITAE

OLEV VINN

Sünniaeg
ja koht: 26.01.1971, Tallinn
Rahvus: eestlane
Aadress: Raja 7a–8, Tallinn
Tel.:   (0) 67 26 549
Faks: (0) 64 64 201
E-post: *olev.vinn.001@mail.ee*

Haridus

Tartu Ülikool, diplom geoloogia erialal 1993
Tartu Ülikool, MSc. geoloogia erialal 1995

Peamised uurimisteemad

Paleozoiliste käsijalgsete evolutsioon ja ökoloogia, fülogeneetiline süstemaatika ja paleobiogeograafia.

DISSERTATIONES GEOLOGICAE
UNIVERSITATIS TARTUENSIS

1. Пээп Мянник. Конодонты в верхнеордовикских и нижнесилурийских отложениях Эстонии. Тарту, 1992. 355 с.

2. Elvi Tavast. Fennoskandia kilbi lõunanõlva ja sellega piirnevate alade aluspõhja reljeef. Tartu, 1992. 357 lk.

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