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Understanding linguloid brachiopods: *Obolus* and *Ungula* as examples

Leonid E. POPOV[1] and
Lars E. HOLMER[2]

Abstract: EMIG (2002) re-examined the taxonomy of the genus *Obolus* EICHWALD from the Middle Cambrian - earliest Ordovician of the East Baltic region as part of a proposal for a wholesale revision of the principles of linguloid systematics. He contended that previous taxonomic studies on *Obolus* and related forms were carried out erroneously using characters that have no taxonomic value. EMIG´s proposed revision is based mainly on the limited morphological diversity between fossil and Recent taxa within a single linguloid Family, the Lingulidae. However, the present study demonstrates the taxonomic validity of the diagnostic characters used for classification within the mostly extinct families of the Superfamily Linguloidea, for they exhibit far more variation in morphology. This study also shows that EMIG has provided no satisfactory basis for his radical changes and revisions to the existing widely accepted taxonomy of the Cambrian to earliest Ordovician Obolidae of the East Baltic. *Obolus* EICHWALD and *Ungula* PANDER are shown to constitute distinctive and discrete genera comprising the species *Obolus apollinis* EICHWALD, *O. ruchini* KHAZANOVITCH et POPOV, *O. transversus* (PANDER), *Ungula ingrica* (EICHWALD), *U. inornata* (MICKWITZ), and *U. convexa* PANDER.

Key Words: Taxonomy; *Obolus*; *Ungula*; Brachiopoda; Cambrian; Ordovician; East Baltic

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Résumé : *Comprendre les brachiopodes linguloides :* Obulus *et* Ungula *comme exemples.-* EMIG (2002) a revu la taxonomie du genre *Obolus* EICHWALD du Cambrien moyen - Ordovician basal des régions baltes orientales dans le cadre d'un projet de révision de l'ensemble des critères de la systématique des linguloides. Il a suggéré que les études taxonomiques antérieures sur *Obolus* et les formes apparentées sont fondées à tort sur des caractères dépourvus de toute valeur taxonomique. La révision proposées par EMIG s'appuie principalement sur les faibles variations morphologiques observées entre taxons fossiles et récents au sein d'une seule famille de linguloide, les Lingulidae. Notre article s'attache à démontrer la validité taxonomique des critères diagnostiques utilisés dans la classification au sein des familles, pour la plupart éteintes, de la Superfamille des Linguloidea, car ils présentent une bien plus grande diversité morphologique. Cette étude montre aussi que EMIG n'a pas proposé une base satisfaisante pour étayer les changements et révisions radicaux qu'il souhaite apporter à la taxonomie, en vigueur et largement acceptée, des Obolidae des séries du Cambrien à l'Ordovician basal des régions baltes orientales. *Obolus* EICHWALD et *Ungula* PANDER sont considérés comme des genres distincts comprenant les espèces *Obolus apollinis* EICHWALD, *O. ruchini* KHAZANOVITCH et POPOV, *O. transversus* (PANDER), *Ungula ingrica* (EICHWALD), *U. inornata* (MICKWITZ) et *U. convexa* PANDER.

Mots-Clefs : Taxinomie ; *Obolus* ; *Ungula* ; Brachiopoda ; Cambrien ; Ordovician ; Baltique orientale

Резюме: Л.Е. Попов, Л.Е. Холмер. ВОПРОСЫ СИСТЕМАТИКИ БЕЗЗАМКОВЫХ БРАХИОПД НА ПРИМЕРЕ РОДОВ *Obolus* И *Ungula*.- Эмиг (2002) недавно пересмотрел таксономию рода *Obolus* EICHWALD из среднего кембрия - раннего ордовика Восточной Прибалтики, как часть предполагаемой широкой ревизии основ систематики лингулид. Он настаивает на том что предыдущие исследования *Obolus* и близких к нему родов, опубликованные в работах Горянского, Попова, Пуура и Холмера, были по преимуществу основаны на анализе признаков лишенных таксономического значения. Критика Эмига основывается главным образом на его представлениях о морфологическом разнообразии в пределах единственного ныне существующего семейства однако, настоящее исследование демонстрирует значительно большее разнообразие таксономически значимых морфологических признаков строения раковины у древних, палеозойских лингулид, объединяемых в составе надсемейства которое в значительной степени выходит за рамки, известные среди мезо-кайназойских представителей этой группы. Нет также оснований для радикальных изменений существующей таксономии кембрийских и раннеордовикских оболид из Восточной Прибалтики. *Obolus* EICHWALD и *Ungula* PANDER представляют отличные и хорошо морфологически диагносцируемые роды семейства Obolidae. Они включают следующие разновидности: *Obolus apollinis* EICHWALD, *O. ruchini* KHAZANOVITCH et POPOV, *O. transversus* (PANDER), *Ungula ingrica* (EICHWALD), *U. inornata* (MICKWITZ) и *U. convexa* PANDER.

Ключевые слова: Таксономия, *Obolus*, *Ungula*, Брахиоподы, Кембрий, Ордовик, Прибалтика

[1] *Department of Geology, National Museum of Wales, Cathays Park, Cardiff CF10 3NP, Wales (U.K.)*
Leonid.Popov@nmgw.ac.uk
[2] *Institute of Earth Sciences, Palaeobiology, Uppsala University, SE-752 36 Uppsala (Sweden)*
Lars.Holmer@pal.uu.se
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Introduction

The linguloid brachiopod *Obolus* has been the subject of numerous controversies since it was first established by EICHWALD in 1829 (see summaries by MICKWITZ, 1896; GORJANSKY, 1969; POPOV *et alii*, 1989). Recently, EMIG (2002) used *Obolus* as an example in a proposal for revising linguloid taxonomy, by limiting the "valid" (*sensu* EMIG, 2002) taxonomic characters to a very restricted number of features (see also EMIG, 1982; 1983), declaring that previous studies of *Obolus* and related forms (*e.g.* GORJANSKY, 1969; POPOV *et alii*, 1989; HOLMER and POPOV, 2000; PUURA, 1996) are based mainly on characters that have "*no taxonomic value*" (*sensu* EMIG, 2002). The proposal by EMIG (2002) is based almost entirely on his experience with fossil and Recent members of a single linguloid Family, the Lingulidae (*e.g.* EMIG, 1982; 1983; BIERNAT and EMIG, 1993). Here we argue that the limited morphological diversity of the taxa found within this family is not a useful basis for working out the taxonomy of the 10 other extinct families now recognized within the very variable and diverse Superfamily Linguloidea (HOLMER and POPOV, 2000).

The present is obviously the key to the past, but we should not let the present *restrict* our understanding of the past; the fact is that there has been a drastic loss of diversity within many groups such as the Recent linguloid brachiopods. Furthermore, some of the most important new contributions to the understanding of the taxonomy and phylogeny of the Superfamily Linguloidea and related Lingulate taxa come from detailed studies of the shell structure and micro-ornamentation (Recent and fossil), which are proving to be *the most* valid characters for taxonomic purposes (*e.g.* CUSACK *et alii*, 1999; HOLMER, 1989, 2001; WILLIAMS, 2003; WILLIAMS and CUSACK, 1999; WILLIAMS *et alii*, 1994, 1997, 2000).

EMIG (2002) does not take into account these new developments in the understanding of the ultrastructure of the Lingulate shell and its phylogenetic importance. When dealing with fossil taxa it is also essential to understand something of the geological setting in which the taxa are found, and in particular the stratigraphic context must be considered. EMIG (2002) does not so the geological associations of *Obolus* and *Ungula* are summarised below.

Obolus and *Ungula* in the East Baltic - a brief review

The type species of *Obolus*, *O. apollinis* EICHWALD, is from a well known locality on the Luga River near the town of Kingisepp (formerly Jamburg, St. Petersburg or "Leningrad" District, Russia), where it occurs in several exposures of the so-called "*Obolus* sands" in the lower Tosna Formation (uppermost Upper Cambrian: *Cordylodus proavus* - lower *C. lindstromi* conodont biozones). Fortunately, the type material of *Obolus apollinis* EICHWALD, as well as that of another obolid species described by EICHWALD (1829) as *Obolus* (= *Ungula*) *ingrica*, is preserved in the Department of Historical Geology of St. Petersburg State University (contrary to the statement by EMIG, 2002, p. 8), and POPOV and KHAZANOVITCH (*in* POPOV *et alii,* 1989) selected lectotypes for both species. MICKWITZ (1896) monographed the brachiopods from the "*Obolus* sands" and erroneously synonymised these two species without checking the type material; this practice was also adopted by most subsequent researchers (*e.g.* WALCOTT, 1912; BULMAN, 1939; ROWELL, 1965, *etc.*) until GORJANSKY (1969) demonstrated the validity of *Obolus apollinis* and *Ungula ingrica* as discrete entities.

The monographic study of the brachiopods from the "*Obolus* sands" by POPOV and KHAZANOVITCH (*in* POPOV *et alii,* 1989) was based on a total of more than 10,000 specimens (from more than 100 localities including core material) with carefully measured biometric data that further demonstrated that *Obolus apollinis* and *Ungula ingrica* are disparate in both space and time. At the few localities where *Obolus apollinis* and *Ungula ingrica* occur together, the valves of the former species show clear signs of re-deposition (POPOV *et alii*, 1989).

POPOV and KHAZANOVITCH (*in* POPOV *et alii,* 1989) resolved the long-standing problems connected with several species of *Ungula* described by PANDER (1830) from the southern outskirts of St Petersburg. The original PANDER collection was lost possibly at the end of the nineteenth century (for details see JAANUSSON and BASSETT, 1993). However, precise information on the geology of the type area (provided by PANDER) made it possible to determine that the type locality of these species is on the Izhora River (near the abandoned village of Samsonovka). It is clear that PANDER's species are distinct and valid (see GORJANSKY, 1969; POPOV *et alii,* 1989, for details). Of these, *Obolus transversus* (PANDER, 1830), occurs in the Rebrovo Member of the Sablinka Formation (uppermost Middle Cambrian, Fig. 2), whereas *Ungula convexa* PANDER, 1830, is from the upper member of the Ladoga Formation (Upper Cambrian), where it occurs in association with moderately diverse acritarch and conodont assemblages that date the beds as being within the interval of the *Leptoplastus* and lower *Parabolina spinulosa* Biozones of the Scandinavian trilobite standard (MARTINSSON, 1974).

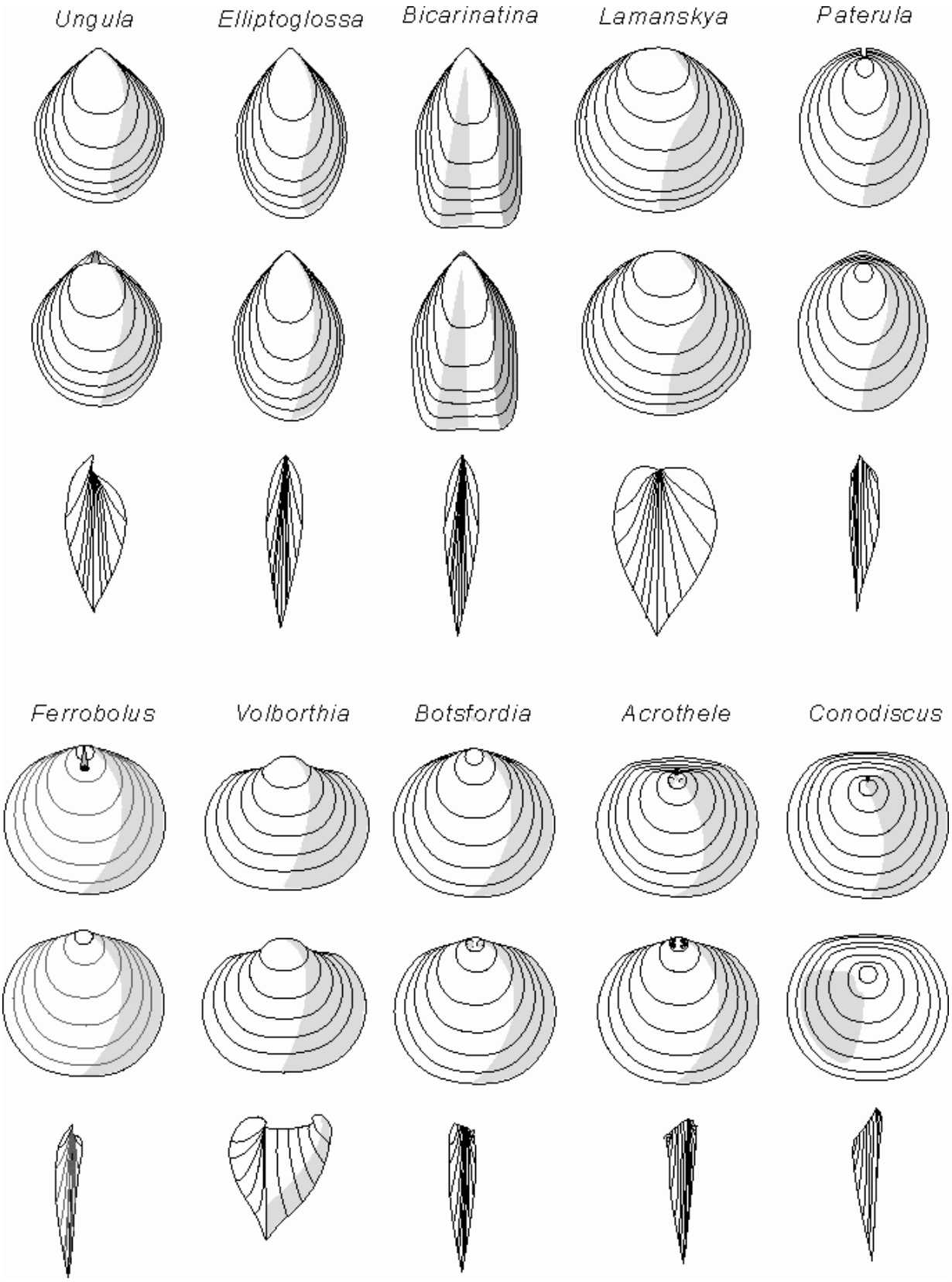


Figure 1: Examples of variations in shell outline and relative valve convexity in selected Palaeozoic lingulide genera.

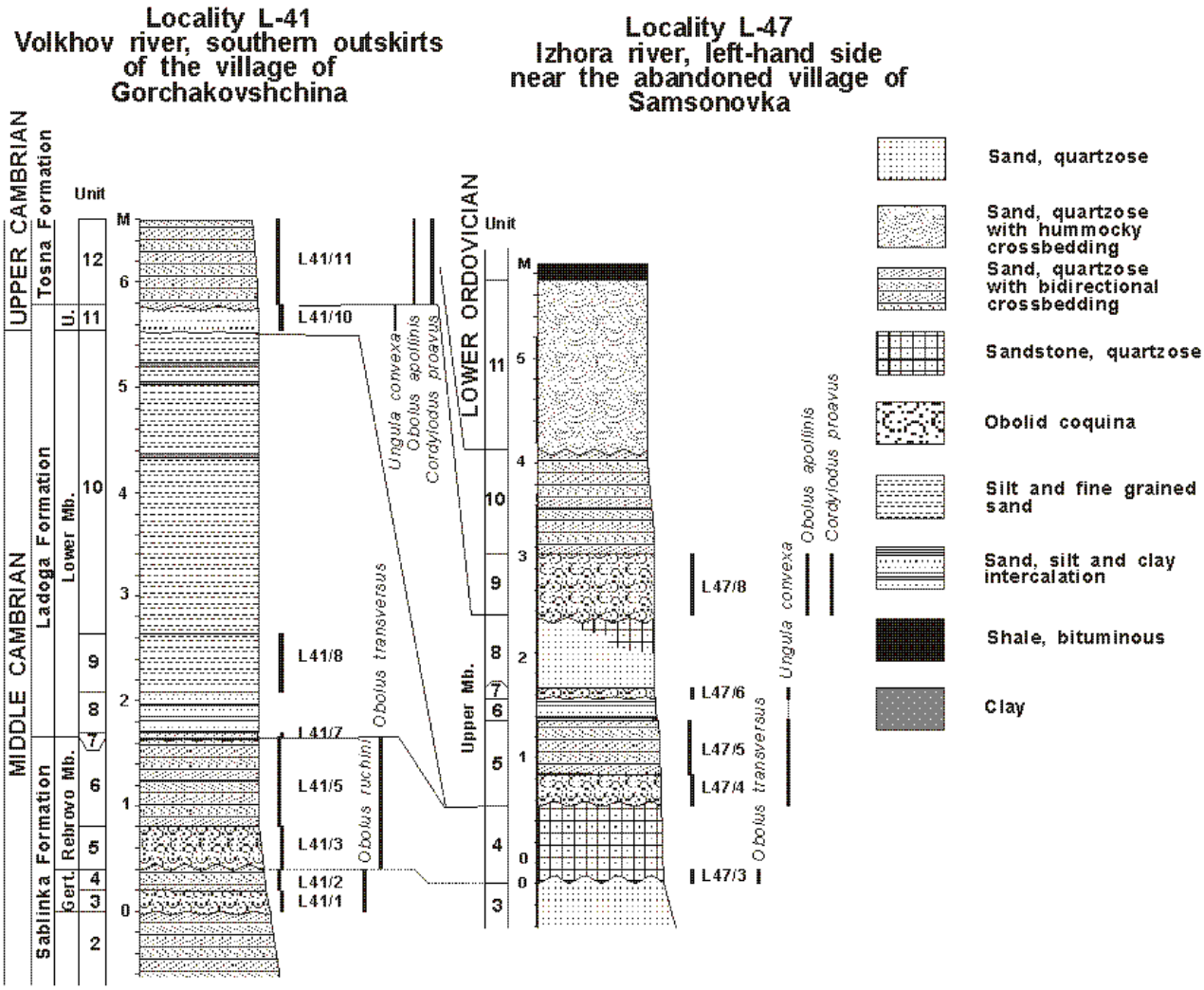


Figure 2: Columnar sections through the Cambrian-Ordovician boundary beds in the East Baltic at the Volkhov and Izhora rivers (see POPOV *et alii,* 1989, for details) showing of distribution of discussed relevant species.

Ungula convexa is the type of *Ungula* PANDER, 1830, which as demonstrated by POPOV and KHAZANOVITCH (*in* POPOV *et alii,* 1989) is different from *Obolus* (see further below).

Species of *Obolus* are generally associated with the *Skolithos* ichnofacies and show a preference for well-aerated shallow marine environments, possibly, with low primary biological productivity. Its relatively thin shells were not resistant to transportation and re-deposition and it is likely that coquinas with the best preserved shells from the Kingisepp quarry, Luga, Lava and Suma rivers were deposited in beach ridges above average sea-level during strong storm events (ARTYUSHKOV *et alii*, 2000).

Unlike *Obolus*, the species of *Ungula* do not co-occur with *Skolithos* ichnofacies, and the shells of *Ungula* are invariably enriched in sulfides and are secondarily phosphatized, which may suggest fossilization in a dysaerobic environment. The host rock often contains thin layers of black bituminous argillite. All these factors suggest that *Ungula* was adapted to life in shallow waters, characterized by high primary biological productivity, strong daily fluctuations in the content of oxygen, and possibly, periodical eutrophication. The phosphatized shells of *Ungula* were resistant to re-deposition and they constitute a significant part of the deposits that have been mined commercially in North Estonia (POPOV *et alii*, 1989).

Obolus and *Ungula* are currently regarded as endemic Baltoscandian taxa, each represented by three successive species (Kaljo *et alii*, 1986; POPOV *et alii*, 1989). *Obolus* is represented by two successive Middle Cambrian species, *Obolus ruchini* KHAZANOVITCH et POPOV, 1984 and *Obolus transversus* (PANDER, 1830) (Fig. 2). No species of *Obolus* occur in the lower and medial portions of the Upper Cambrian, but *Obolus apollinis* EICHWALD then appears in the *Cordylodus proavus* Biozone and ranges into the lower Tremadoc *Cordylodus angulatus* Biozone. In contrast, *Ungula* is confined entirely to the Upper Cambrian where it is represented by *Ungula inornata* (MICKWITZ, 1896), *Ungula convexa* (PANDER, 1830) and *Ungula ingrica* (EICHWALD, 1829). The stratigraphical ranges of

the most important of these species are illustrated by two sections in the St Petersburg region (Fig. 2; see POPOV *et alii*, 1989 for a full account of the brachiopod biostratigraphy). A more detailed summary in English of the lithostratigraphy of the Middle Cambrian to Lower Ordovician deposits and associated faunas in the East Baltic is given by KALJO *et alii* (1986).

Morphological diversity of Palaeozoic Linguloidea *versus* Mesozoic-Cenozoic Lingulidae

According to EMIG (2002, p. 2) "*the main taxonomic criteria used to discriminate between linguloid taxa were established and figured by EMIG (1982, 1983) and BIERNAT and EMIG (1993)*". He also noted (p. 3) that "*external features as shape, size and dimension ratios of the valves have been demonstrated to have no taxonomic value*" although at the same time making an exception for *Lingula adamsi* with its distinctive subrectangular shell outline. It is important to note that these statements are based only Recent and Mesozoic-Cenozoic Lingulidae, which do not represent the total morphological diversity of the group (shell shapes, ornament, shell structure, characters of pseudointerareas, *etc.*; Fig. 1). The post-Palaeozoic members of the Lingulidae, with their infaunal mode of life in near-shore environments represent only a small fraction of the diversity of shell morphologies and life styles observed in linguloids that lived in Palaeozoic times (BASSETT *et alii,* 1999; HOLMER and POPOV, 2000). It is not necessary to discuss all aspects of variation in linguloid shell morphologies in this paper, as it is treated in full in the latest edition of the *Treatise on Invertebrate Paleontology* (WILLIAMS, 1997; HOLMER and POPOV, 2000); however, the wide range of general shell shapes illustrated on Figure 1 is a good illustration of the diversity exhibited by Palaeozoic linguloids. It is clear that in many instances, outline, relative length, convexity and proportions of the valves in various linguloid stocks can be used as diagnostic characters. For instance, the strongly dorsibiconvex shell of *Volborthia* (Fig. 1) is a good example; it can be identified easily even without knowing details of the micro-ornament or internal morphology (HOLMER and POPOV, 1995). The dorsibiconvex shell in the genera referred to the Elkaniidae and the Eoobolidae make this feature useful in definition of these families, whereas the families Lingulasmatidae, Pseudolingulidae and Lingulidae with their specific infaunal mode of life are characterised by exclusively equibiconvex and almost equivalved, elongated shells. By contrast, the Family Obolidae demonstrates the greatest variability in shell shapes and outlines from one genus to another. For example, there is a distinct tendency towards miniaturisation of the shell in some linguloid lineages (*e.g.* Elliptoglossinae and Paterulidae), which would appear to have a most unusual mode of life as far from that of Recent Lingulidae as could be possible. The most extreme example is in *Paterula*. Shells of this genus range from the Ordovician to the Devonian, invariably demonstrating a very limited variation in the shape of the shell and in its size, which almost never exceeds three millimetres in width. *Paterula* is often found in sediments enriched in sponge spicules, and the discovery of Silurian sponges with *Paterula* shells clustering along their oscular margins (LENZ, 1993, fig. 2; brachiopods identified erroneously as *Craniops*) suggests that the observed association is not a coincidence.

The umbonal areas and pseudointerareas of Palaeozoic linguloids show a diversity in features, that are either poorly developed or absent in Mesozoic-Cenozoic Lingulidae and consequently are absent in the list of 'Main Taxonomic Characters' presented by EMIG (2002). Some linguloids (*e.g. Lingulellotreta*) have a pedicle foramen on the ventral pseudointerarea, whereas in others (*e.g. Elliptoglossa* and the Dysoristidae) the pedicle groove is completely absent (HOLMER and POPOV, 2000, figs. 25.1e, 34, 36.2d).

Thus most of the characters proposed by EMIG (2002) are useful within the Family Lingulidae, but are not applicable directly to other linguloid families, or for the Order Lingulida as whole.

Obolus - "*New diagnosis*" (all quotes below from EMIG, 2002, Table 1)

As noted by EMIG (2002, p.6), the diagnosis of any particular taxon cannot be based on features that demonstrably lack taxonomic value; EMIG´s proposed "New diagnosis", is re-examined below, and for comparison, we also discuss the "Previous diagnosis" (HOLMER and POPOV, 2000).

"*Bi-symmetrical muscle arrangement*".- The arrangement of muscle scars is obviously a taxonomically valuable feature; however, the symmetrical arrangement of the muscle scars in both valves of Obolidae cannot be a diagnostic character of *Obolus* (EMIG, 2002, p. 3), because it is actually a plesiomorphic character, at least for all members of the Class Lingulata. In contrast, the asymmetrical musculature of the Lingulidae is an important apomorphic character of the Family Lingulidae, as pointed out by HOLMER and POPOV (2000, p. 36).

"*Ventral valve:*"

"*Triangular umbonal region*".- In reality this is a very general feature, which characterises nearly 90 per cent of the Obolidae as well as all the Eoobolidae and the Lingulellotretidae, and can be demonstrated as a perfect example of a non-diagnostic character, lacking taxonomic value.

"*Pseudointerarea reduced, slightly concave, with elevated flexure lines*".- This could be a useful feature for identification of *Obolus*. However, the ventral pseudointerarea of *Obolus* is certainly not reduced, and can be said to be of average size (Fig. 3F). The Family Obolidae includes genera with very high pseudointerareas, *e.g. Rebrovia* and *Lingulepis* (HOLMER and POPOV, 2000, fig. 20.2) and taxa with rudimentary ventral pseudointerareas, *e.g. Apatobolus*, *Ralfia* and *Elliptoglossa* (HOLMER and POPOV, 2000, figs. 14.3, 19.1, 25.1).

"*Lateral umbonal plates overhanging the internal side*".- This is a new term, but in our view the so-called *umbonal plates* are nothing more than the tracks of the anterior migration of the muscles forming the anterior-lateral muscle fields (Fig. 3F), and are of little use taxonomically, unless distinct muscle platforms can be recognised (Fig. 4D).

"*Posterior adductor muscle paired, separated by short median septum*".- Available data suggest (HOLMER and POPOV, 2000) that the ventral umbonal muscles were paired in all early Palaeozoic obolides. Therefore this plesiomorphic feature has little value in the discrimination of genera within the Obolidae.

"*Dorsal valve:*"

"*Rounded umbonal region with reduced concave, pseudointerarea with flexure lines*".- A rounded umbonal region is present in many Palaeozoic linguloids and is again of little use as a taxonomic character. Moreover, the dorsal pseudointerarea of *Obolus* does not have any flexure lines. The so-called flexure lines illustrated and discussed by EMIG (2002, figs. 1, 3) are in fact not flexure lines but simply the outer boundaries of the median groove.

"*Lateral umbonal plates overhanging the internal side*".- See comments above.

"*Posterior adductor muscle unpaired*".- The expression of the umbonal scar in *Obolus* is variable in appearance due to taphonomic processes, and although the dorsal umbonal scar in some specimens may appear to be unpaired, other specimens have imprints of a paired dorsal umbonal muscle.

"*Previous diagnosis*" (all quotes below from HOLMER and POPOV, 2000, p. 40)

"*Shell circular to rounded triangular, dorsibiconvex to subequally biconvex*".- It can be demonstrated (Fig. 1) that shell shape and convexity are useful diagnostic features in recognizing genera such as *Obolus*, which is quite different from a number of genera with strongly elongated shells (*e.g. Aksarinaia, Anomaloglossa, Leontiella, Leptembolon, Lindinella, Lingulepis, Lingulella, Chakassilingula, Oepikites, Rebrovia, Palaeoglossa, Schmidtites, Spinilingula*). Moreover, some obolid genera are nearly equivalved and others like *Schmidtites* are ventribiconvex.

"*Ventral propareas with deep, narrow pedicle groove*" (Figs. 3F, 6D).- This character is important in distinguishing *Obolus* from other genera within the Obolinae; *e.g.* in *Anomaloglossa* the pedicle groove is widely triangular (see HOLMER and POPOV, 2000, p. 40-54, for numerous other examples).

"*Dorsal pseudointerarea lacking flexure lines*".- See above (Fig. 4A-C).

"*Visceral areas of both valves weakly thickened, extending to mid-valve; dorsal median ridge vestigial or absent*".- The relative thickness of the visceral area is an important character in, *e.g.* discriminating the genus from taxa with raised muscle platforms in one or both valves (*e.g. Dicellomus, Fordinia*, and *Ungula*). The relative length of the visceral area has also been demonstrated to be an important character by BIERNAT and EMIG (1993), since it is obviously related directly to the size of the lophophoral cavity. In a similar way, the presence or absence of a dorsal median ridge is an obvious important taxonomic character (*e.g. Leontiella* HOLMER and POPOV, 2000, fig. 16.2a).

"*Vascula lateralia of both valves submarginal, arcuate*" (Figs. 3F, 4A-C).- The shape of the mantle canals within the Obolidae is clearly of taxonomic importance, and some genera have straight proximal ventral *vascula lateralia*, which can be divergent or subparallel (*e.g. Palaeobolus* and *Dicellomus*).

In addition to the earlier diagnosis by HOLMER and POPOV (2000), current studies (work currently in progress) reveal that the first formed shell in *Obolus* (Fig. 5A-D) is finely pitted.

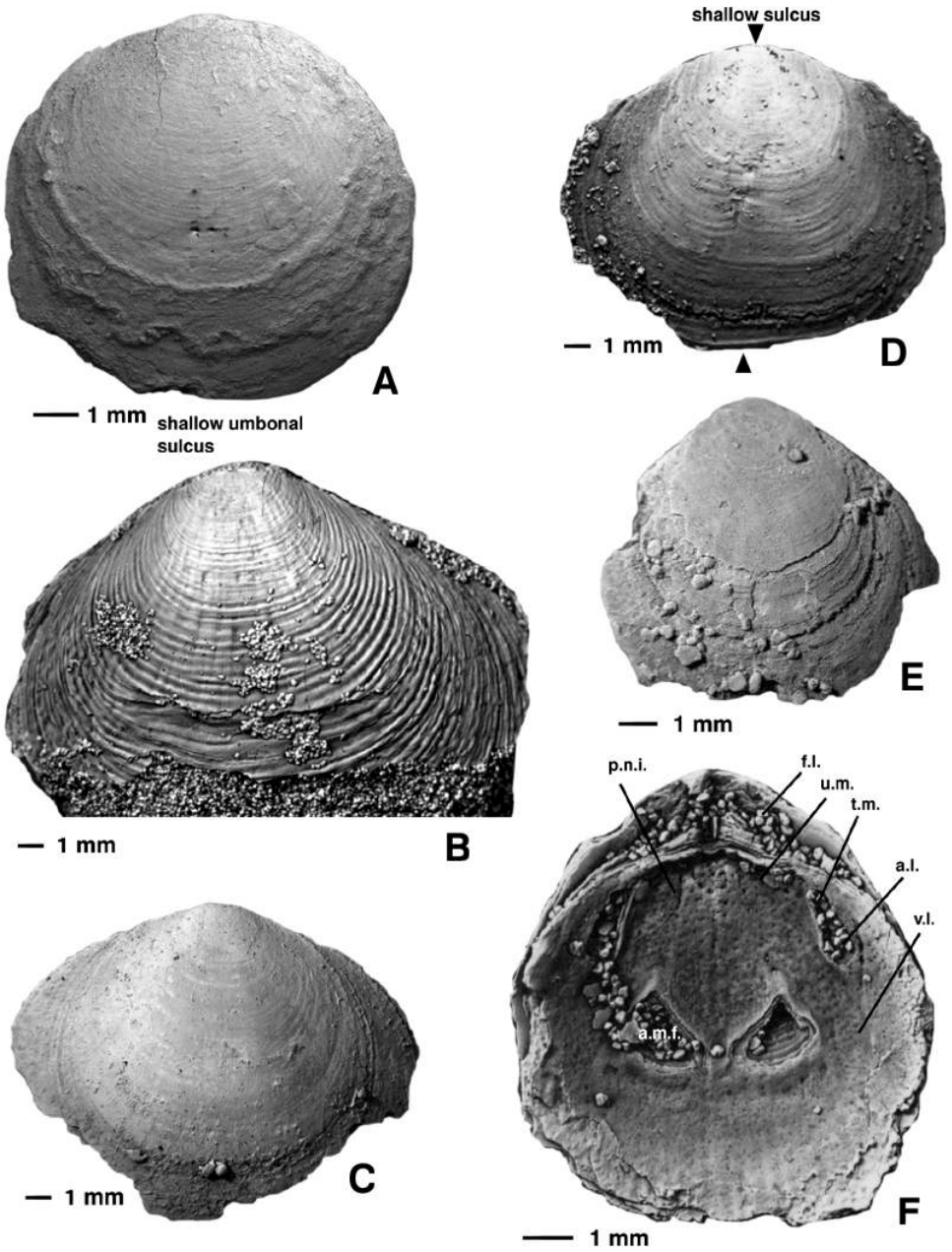


Figure 3: **A-E**, variations in the external shape of the dorsal valve and ornament in species of *Obolus* and *Ungula*. **A**, *Ungula convexa* (PANDER, 1830), NMW 2001.39G.4; Upper Cambrian, Ladoga Formation, locality B-2, Unit C_2 (POPOV *et alii*, 1989, fig. 3), on the right (facing downstream) bank of the Izhora River near the abandoned village of Samsonovka, St Petersburg District; note smooth shell with few growth rings and lack of median sulcus. **B**, *Ungula inornata* (MICKWITZ, 1896), CNIGR 160/12348; Upper Cambrian, upper Ulgase Formation, Sample E60/3 (POPOV *et alii*, 1989, fig. 10), outskirts of the village of Kallavere, North Estonia; note weak umbonal sulcus. **C**, *Obolus transversus* (PANDER, 1830), NMW 2001.39G.51; Middle Cambrian, Sablinka Formation, Rebrovo Member, Sample L-41/3 (POPOV *et alii*, 1989, fig. 2), right-hand side of Volkhov River in southern outskirts of the village of Gorchakovshchina, St Petersburg District; note lack of median sulcus. **D**, *Obolus ruchini* KHAZANOVITCH et POPOV, 1984; CNIGR 16/12348; Middle Cambrian, Sablinka Formation, Gertovo Member, Sample L6/1 (POPOV *et alii*, 1989, fig. 3), right bank of the Sarya River about 700 m downstream from the northern outskirts of the village of Voibokalo; note the very shallow median sulcus, which can be traced in nearly all dorsal valves of *Obolus* from Gertovo Member. **E**, *Obolus apollinis* EICHWALD, 1829; NMW 2001.39G.119; Upper Cambrian, Suurjogi Member, sample 1653/25 (POPOV *et alii*, 1989, fig. 1), borehole no. 1653 south east of Rakvere, North Estonia; note lack of sulcus. **F**, View of ventral valve interior of *Obolus apollinis* EICHWALD, 1829; CNIGR 2/12348; Upper Cambrian, lower Tosna Formation, sample L1/3 (POPOV *et alii*, 1989, fig. 3), right-hand side of lava River in southern outskirts of the village of Gorodishche; note well developed ventral pseudointerarea with narrow pedicle groove and deep flexure lines (f.l.), pair of weak diverging furrows of pedicle nerve impression (p.n.i.) flanked by paired impression of umbonal muscle scar (u.m.), posterolateral muscle fields bearing attachment scars of transmedian (t.m.) and anterior lateral (a.l.) muscles; paired anterior muscle fields formed by combined attachment scars of central, middle lateral and anterior lateral muscles (a.m.f.) and weakly impressed marginal *vascula lateralia* (v.l.); depressions under the muscle scars clearly formed as a result of post-mortem degradation of the organic shell matter and subsequent collapse of phosphatic layers.

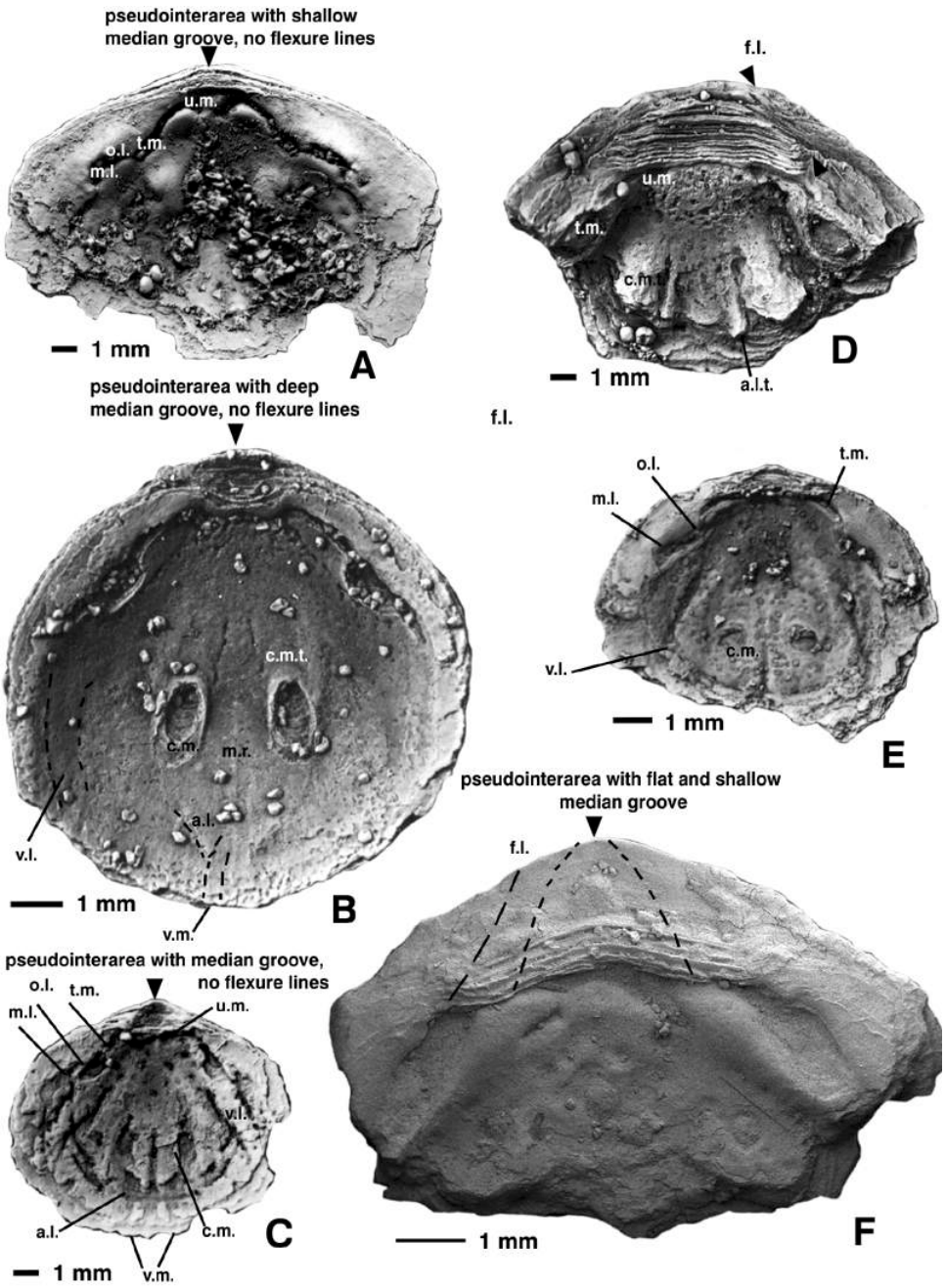


Figure 4: Main features of dorsal valve interior of *Obolus* and *Ungula*. **A**, *Obolus transversus* (PANDER, 1830), CNIGR 22/12348; Middle Cambrian, Sablinka Formation, Rebrovo Member, Sample L-41/3 (POPOV *et alii*, 1989, fig. 2), right-hand side of Volkhov River in southern outskirts of the village of Gorchakovshchina, St Petersburg District; note that mature specimen has low dorsal pseudointerarea occupied mainly weakly defined pedicle groove and lacks flexure lines, with paired umbonal muscle scars (u. m.) divided by short median ridge and posterolateral muscle fields slightly raised above the valve floor with attachment scars of transmedian (t.m.), oblique lateral (o.l.) and middle lateral (m.l.) muscles. **B**, *Obolus apollinis* EICHWALD, 1829; IGT, B1706; Upper Cambrian, lower Tosna Formation, sample L1/3 (POPOV *et alii*, 1989, fig. 3), right-hand side of lava River in southern outskirts of the village of Gorodishche, St Petersburg District; note narrow dorsal pseudointerarea, mainly occupied by median groove, very weak median ridge (m.r.) in anterior half of the visceral area, central muscle scars (c.m.) on the end of distinct tracks (c.m.t.) slightly raised above valve floor, but not forming platforms, anterior lateral muscle scars (a.l.) near the margins of the visceral area, proximal ends of weakly impressed, subparallel vascula media (v.m.) and submarginal, arcuate *vascula lateralia* (v.l.). **C**, *Obolus ruchini* KHAZANOVITCH et POPOV, 1984; CNIGR 13/12348; Middle Cambrian, Sablinka Formation, Gertovo Member, Sample L6/1 (POPOV *et alii*, 1989, fig. 3), right-hand side of Sarya River about 700 m downstream from the northern outskirts of the village of Voibokalo, St Petersburg District; note muscle scars and impressions of mantle canals. **D-F**, *Ungula convexa* PANDER, 1830, Upper Cambrian, Ladoga Formation; **D**, CNIGR 126/12348, sample L9/31b (POPOV *et alii*, 1989, fig. 4), Naziya River, left-hand side near the abandoned village of Novaya, St Petersburg District; mature specimen (*cf.* fig. 4A-B) with high pseudointerarea bearing broad flattened median groove separated from flexure lines (f.l.) on propareas, paired umbonal muscle scars and transmedian muscle scars on raised platforms; distinct, raised tracks of central (c.m.t.) and anterior lateral muscles (a.l.t.) in the median part of the shell represent a distinctive pattern markedly different from *Obolus*; **E**, CNIGR 129/12348; sample L47/4 (POPOV *et alii*, 1989, fig. 5), Izhora River, left-hand side, about 800 m upstream of the locality B2; juvenile specimens with raised muscle tracks and platforms not yet formed, but with well impressed muscle scars and

mantle canals; **F**, NMW 2001.39G.7; locality B-2, Unit C_2 (POPOV *et alii*, 1989, fig. 3), right hand side of Izhora River near the abandoned village of Samsonovka, St Petersburg District; showing distinction between margins of median groove and position of flexure lines on dorsal pseudointerarea.

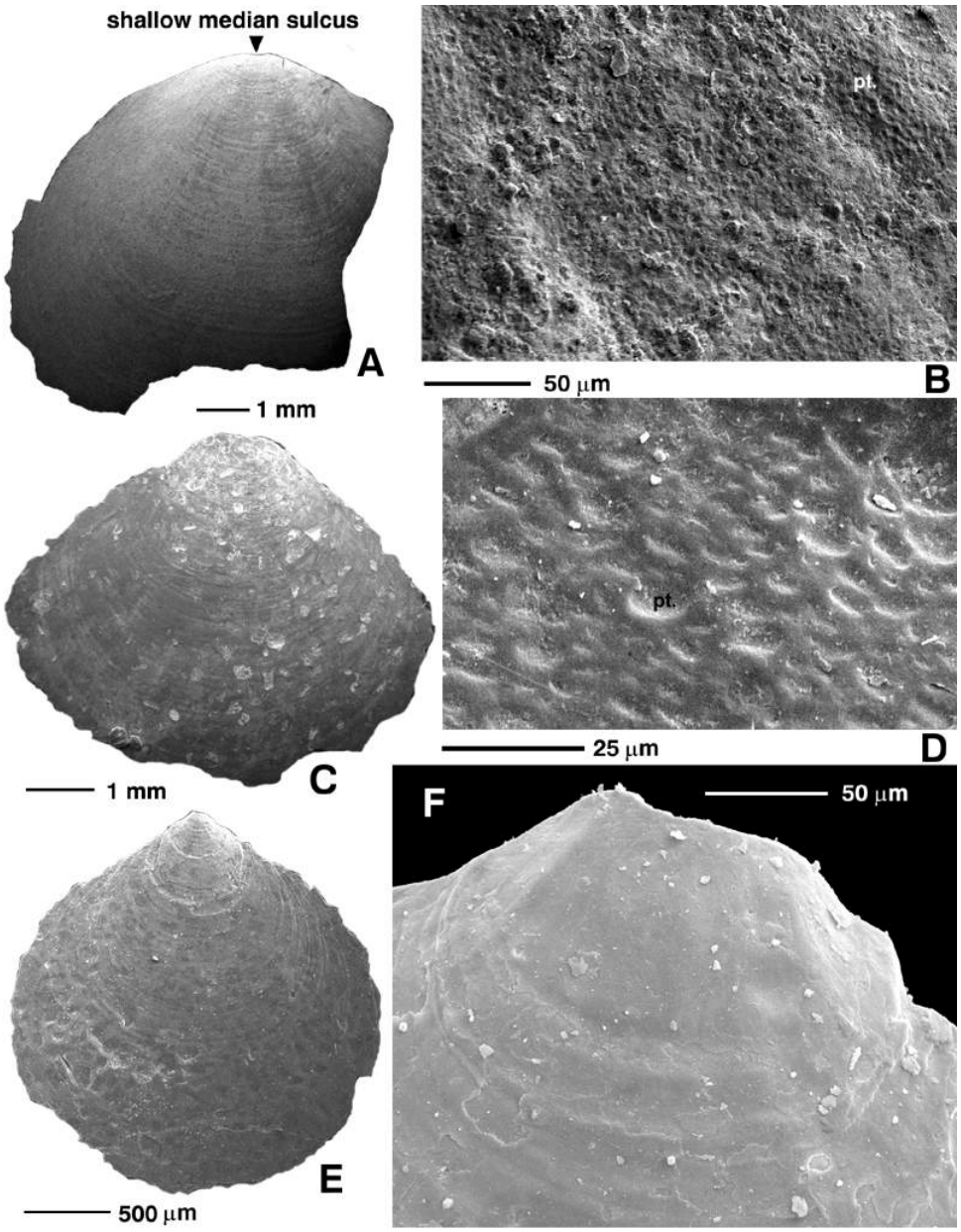


Figure 5: **A-B**, *Obolus ruchini* KHAZANOVITCH et POPOV, 1984; NMW 2001.102, dorsal valve; Middle Cambrian, Sablinka Formation, Gertovo Member, Sample L-40/5 (POPOV *et alii*, 1989, fig. 2), right-hand side of Volkhov River in southern outskirts of the village of Gorchakovshchina, St Petersburg District; note that the slightly exfoliated surface of the dorsal valve still preserves remnants of a finely pitted juvenile ("larval") shell, about 1.5 mm cross. **C-D**, *Obolus apollinis* EICHWALD, 1829; NMW 2001,39G.114, ventral valve; Upper Cambrian, lower Tosna Formation, *Cordylodus proavus* conodont biozone, sample 782/3, quarry on right-hand side of Tosna River downstream from the Sablino caves, St Petersburg District; note well preserved semi-cylindroid and hemispherical pits (pt.) on the juvenile ("larval") shell (D). **E-F**, *Ungula* sp.; NMW 2001.39G.109, ventral valve; Middle-Upper Cambrian, lower Ladoga Formation, sample L17/9 (POPOV *et alii*, 1989, fig. 2), Syas River, right-hand side, 200 m upstream of the village of Rebrovo, St Petersburg District; note well preserved smooth juvenile ("larval") shell.

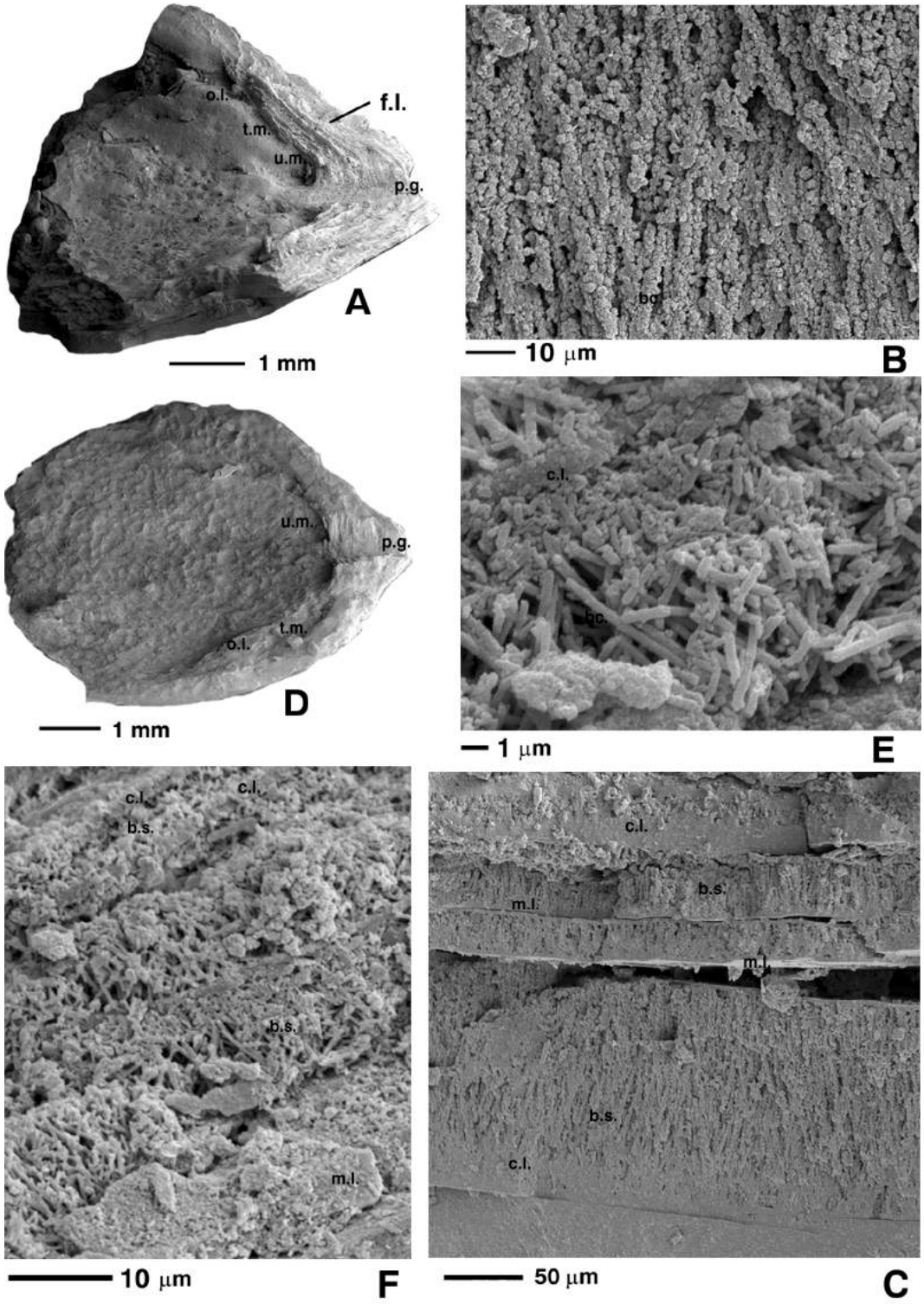


Figure 6: SEM microphotographs of fractured shells of *Ungula* and *Obolus* showing basic differences in microstructure under posterolateral muscle fields of the ventral valve (all abbreviations, are the same as on Figs. 3-5, unless otherwise stated). **A-C**, *Ungula convexa* (PANDER, 1830), NMW 2001.39G.5, ventral valve; Upper Cambrian, Ladoga Formation, locality B-2, Unit C_2 (POPOV *et alii*, 1989, fig. 3), right hand side of Izhora River near the abandoned village of Samsonovka, St Petersburg District; A oblique lateral view showing pedicle grove (p.g.) flexure lines and muscle scars; **B**, symmetrical baculate set showing compactly placed baculi usually exceeding 1 μm in diameter; C, general view through the broken shell showing alternating baculate sets (b.s.), thick compact laminae (c.l.) and membranous laminae (m.l.). **D-F**, *Obolus apollinis* EICHWALD, 1829, NMW 2001.39G.109, ventral valve; Upper Cambrian, Tosna Formation, *Cordylodus proavus* conodont biozone, sample L47/8 (POPOV *et alii,* 1989, fig. 5), Izhora River, left-hand side, about 800 m upstream of the locality B2; **D**, oblique lateral view showing pedicle grove, flexure lines and muscle scars; **E**, general view of baculate set showing relation with compact lamina; **F**, general view of the shell fracture showing alternating symmetrical baculate sets with loosely spaced inclined baculi and thin compact laminae; note that sizes of major structural elements (*e.g.* size of baculi and compact laminae) in the *Obolus* shell are about one order of magnitude smaller than in *Ungula*.

Defining species of *Obolus* and *Ungula*

The species *Obolus apollinis* EICHWALD; *Obolus ruchini* KHAZANOVITCH et POPOV and *Ungula transversa* PANDER were synonymised by EMIG (2002). However, his paper contains neither illustrations nor any detailed discussion stating the reasons for the revision. *Ungula convexa* PANDER was also synonymised with *Obolus apollinis* by the same author, but again without illustrations or detailed discussion. The reasons for retaining these species discrete are summarized below.

- *Obolus ruchini* KHAZANOVITCH et POPOV (from the Gertovo Member of the Sablinka Formation, Middle Cambrian) (Figs. 3D, 4C, 5A-B).-- The diagnostic features of this species include a shallow dorsal median sulcus (Figs. 3D, 5A), fading anteriorly, which is present in 90 to 100 percent of specimens in every sample from the Tosna, Sarya, and Volkhov rivers that was studied (observation based on 291 dorsal valves; for data on the number of specimens and localities see POPOV *et alii*, 1989, p. 101). A distinctive dorsal median sulcus is a very rare feature in lingulides. In Cambrian obolids from Baltoscandia a very fine umbonal sulcus is present only on the shells of *Ungula inornata* (MICKWITZ, 1896) (Fig. 3B); however, this species is unique in having a strong concentric ornament, well developed muscle platforms and heart-shaped depression in the ventral valve as well as in the presence of flexure lines on the dorsal propareas. A dorsal median sulcus is completely absent in all other species of *Obolus* (Fig. 3A, C, E).
- *Obolus transversus* (PANDER) (Rebrovo Member of the Sablinka Formation, Middle Cambrian) (Figs. 3C, 4A).-- This species lacks any trace of a dorsal median sulcus (Fig. 3C). It also differs from *Obolus apollinis* in having a shorter ventral visceral area with its anterior boundary situated well behind the mid-valve length, whereas in *O. apollinis* it extends to about mid-valve (POPOV *et alii,* 1989, Pl. 1, figs. 7, 11; HOLMER and POPOV, 2000, fig. 13.1b). *O. transversus* is also characterized by having a distinctive transverse outline in mature specimens (with 4 or more growth lamellae), and this type of outline is not present in any other Cambrian Obolidae from the East Baltic. It can be assumed that the last mentioned difference is of about the same taxonomic importance as the subquadrangular outline of *Lingula adamsi* as referred to by EMIG (2002). The dorsal central muscle scars of *O. transversus* lack the distinct relief present in the shells of *Obolus apollinis* (POPOV *et alii,* 1989, pl. 1, figs. 8-10; HOLMER and POPOV, 2000, fig. 13.1d). These consistent differences allow the two species to be distinguished even in the field; they are also separated by a stratigraphic gap (referred to above; Fig. 2) corresponding to about 3 to 5 MA.
- *Ungula convexa* PANDER (upper member of the Ladoga Formation, Upper Cambrian) (Figs. 3A, 4D-F, 6A-C).-- EMIG (2002) did not provide illustrations or relevant discussion of the morphology of this species, and thus it is difficult to understand why he regarded *U. convexa* as a junior synonym of *Obolus apollinis*. *U. convexa* can be distinguished easily from the East Baltic species of *Obolus* not only in the presence of dorsal flexure lines, but also in that it differs in having a much thicker shell, which may also be reflected in differences in the shell structures of *Obolus* and *Ungula* as discussed and illustrated by CUSACK *et alii* (1999). In particular *Ungula* (Fig. 4) is characterised by having coarse (more than 1 µm in diameter) pincoidal bacula, whereas in *Obolus* they are fine and prismatic (CUSACK *et alii,* 1999). *U. convexa* also has raised muscle platforms in the ventral valve and a heart-shaped depression. The shell surface of *Ungula* is entirely smooth including the first formed shell (Fig. 5E-F).

Discussion and conclusions

In summary, EMIG (2002) has provided no satisfactory basis for his radical revisions to the existing taxonomy of the Cambrian to earliest Ordovician Obolidae of the East Baltic. *Ungula* (with *U. convexa* as type species) represent a separate taxon, which can be distinguished readily from *Obolus* and other obolid genera. Thus there is no reason to change the type species of the genus as proposed by EMIG (2002, p. 5).

It is also important to point out that notwithstanding EMIG´s (2002, p. 8) comments, the type material of the taxa described by POPOV *et alii* (1989) is accessible in the CNIGR Museum (Sredniy Pr. 74, 199106 St Petersburg, Russia), where all the specimens are catalogued and properly curated. Moreover, the most important Middle to Upper Cambrian obolid brachiopod localities in the vicinity of St Petersburg, including the type localities of most of the discussed species, are also easily accessible for re-study, and any proposed revision of the taxonomy of the fauna of the "*Obolus* sands" obviously needs to include a careful re-study of both the type material and the type sections, something which is entirely lacking from the brief study by EMIG (2002).

We agree wholeheartedly that "systematics and taxonomy must propose new ideas and test hypotheses", but these should build upon, and extend previous studies, and in our view the study by EMIG (2002) does not represent "a first step in better understanding in linguloid taxonomy".

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