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Reply to L.E. POPOV and L.E. HOLMER (CG2003_A06_LEP-LEH): Obolid taxonomy

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Mots-Clefs : Critères taxinomiques ; Linguloidea ; Lingulidae ; Brachiopoda

Introduction

Since early in the 19th Century the taxonomy of fossil obolids has been the subject of numerous controversies (Table 1), so the development of new criteria for their proper differentiation is mandatory. Based on the extant species of the family Lingulidae (EMIG, 1982, 1983) and later applied to fossil taxa (BIERNAT and EMIG, 1993), new morpho-anatomical characters were established and their variability analysed. As a consequence, several shell structures commonly used to discriminate between genera and species of both extant and fossil taxa were determined to have no phylogenetic status.

In taxonomy attempts to define a species using a lot of these phylogenetically valueless characters on a huge number of specimens are futile. The aim must be to determine those elements that have a valid taxonomic significance: "la taxonomie est un outil, pas une fin en soi", or in other words "Systematics as a tool to identify a taxon is but a technical consequence" (EMIG, 2002). There can be no palaeontological approach to taxonomy; and stratigraphical range can be neither a character in nor a part of the description of a taxon used for stratigraphical purposes. The rules of the International Code of Zoological Nomenclature (1999) must be followed in any diagnosis.

The proposal to adapt the taxonomic tools valid for the living and fossil representatives of the family Lingulidae to the family Obolidae (EMIG, 2002) was a consequence of difficulties encountered in identifying specimens collected in the Baltic "*Obolus* sands": consequently the lingulide tools were adapted for use in the discrimination of four Cambrian obolid genera: *Obolus*, "*Ungula*", *Schmidtites* and *Oepikites*. Criteria used in previous diagnoses were emended. From the many outcrops studied in

Estonia in 1998-1999, several thousand specimens of various obolid species were examined and the obolid collections in the University of Tartu (Estonia) were studied.

In EMIG's (2002) study the genus *Obolus* was used as an example, not only because it is the most complex structurally among the above cited genera but also because it includes the largest number of species referred to this genus (Table 1), as does *Lingula* in its family. Each is the type-genus of its family. The genus *Lingula* was recognized first in Cenozoic strata, but in the last few years representatives have been described from the Palaeozoic and Mesozoic, sometimes based only on small fragments of a valve (EMIG, 2003). Linguloid systematics is in real need of updating (EMIG, 2000). But it is understandable that although such a need exists it is not widely accepted. Rarely do new ideas and hypotheses corroborate one's own standpoint as obviously as they do in this instance. Consequently, the following paragraphs clarify the most important areas of controversy with HOLMER and POPOV (2000) and POPOV and HOLMER (2003) regarding obolid taxonomy.

External features

First of all, it is important that the reader have all the pertinent information, not just a sketchy outline based on a minimum of observations. The judgements in my earlier publications in this venue about shell characters of no taxonomic value were based on the study of several living and fossil populations, in various ecological environments.

EMIG (1982) - p. 348: "L'analyse de la variabilité des dimensions de la coquilles a montré qu'aucun rapport ne peut être utilisé en taxonomie, tant pour la coquille que pour le protegulum."

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This applies also to the species of *Obolus* and "*Ungula*" (paper in preparation) (see Table 2).

EMIG (1983) - p. 477: (...) "*la forme générale présente une relative constance, ce qui permet de l'utiliser comme caractère complémentaire, sans lui accorder une valeur spécifique*".

This comment concerns also the description of *Lingula adamsi* in EMIG (1982). Nevertheless, POPOV and HOLMER (2003) state "*making an exception for Lingula adamsi*". The authors overlooked "*comme caractère complémentaire*". The cited sentence may also apply to an obolid species if its shell shows particularities.

BIERNAT and EMIG (1993) - p. 1: "*It is well known that such features (shell characteristics) may vary even between different populations of the same species, in response to environmental conditions.*"

This applies to all brachiopods, living or fossil, and to many other zoological groups. Such variations in eurytope species are sometimes overlooked in fossil communities.

p. 9: (...) "*the external characteristics of the shell are not sufficient either to identify or to describe a species. Variations of such features must be taken into account and cannot be used*

to separate genera from species".

Many fossil species have been named only on the basis of such differences in shell variations: this explains the large number of named *Lingula* species. This sentence applies equally to *Obolus* and "*Ungula*" (paper in preparation) (see Table 2). According to the diagnosis of *Obolus*: "*shell circular to rounded triangular, dorsibiconvex to subequally biconvex*" (no data given on height in Table 2) and of "*Ungula*": "*shell dorsibiconvex, subcircular to suboval*" (HOLMER and POPOV, 2000). Data in Table 2 indicate how weak the dorsibiconvex tendency in "*Ungula*" is: it seems unrealistic to argue that the convexity of the shell or its absence, a character fundamental to any diagnosis, is but a "diagnostic feature" as POPOV and HOLMER (2003) aver.

And in EMIG (2002) - p. 3: "*External features, such as the shape, size, and dimensional ratios of the valves, have been demonstrated to have no taxonomic value (EMIG, 1982, 1983; BIERNAT and EMIG, 1993). Consequently, they cannot be used to define either genus or species but may be given as an addition to the diagnosis. Only exceptionally is shell form diagnostic of a species, for example the quadrangular shape of the shell of *Lingula adamsi* when compared to those of the other species of *Lingula* (EMIG, 1982).*"

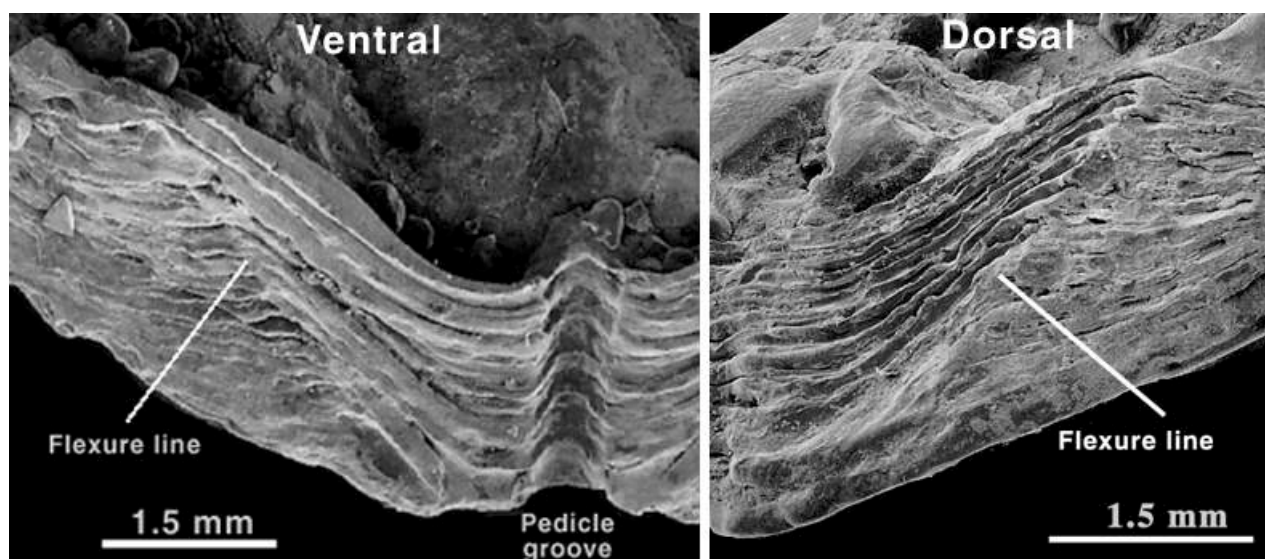


Figure 1: *Obolus apollinis*: Internal umbonal region of the ventral valve (left) and of the dorsal valve (right) with well-marked flexure lines.

This statement is based on data found in every paper concerning linguloids. In analyses of fossil taxa, confusion sometimes exists between specimen descriptions and species diagnoses. A diagnosis should include all the taxonomic (phylogenetic) characters that are pertinent to the identification of a specimen and the variability of these characters, if any, should be discussed. Thus, a diagnosis should not make reference to characters of another species, or to another genus; for example: *species A* has a shorter ventral visceral area than *species B*.

POPOV and HOLMER (2003) confuse the diagnosis of a species and the description of the specimens assigned to a species. Non-taxonomic characters should be discussed in a description that is not a part of its diagnosis. By the way, these authors commonly replace the term taxonomic character by diagnostic character - an unusual practise in systematics.

Status of "*Ungula*"

I agree with POPOV and HOLMER (2003) that *Obolus apollinis* and "*Ungula ingrica*" constitute

discrete species, although even they were sometimes confused (Table 1), thus corroborating the existence of a weakness in their taxonomy. Nevertheless, the type species *U. convexa* of the genus *Ungula* PANDER does not belong to this genus (EMIG, 2002) but to *Obolus*. According to Art. 67 of the ICZN (1999), "Type species *Ungula convexa* PANDER, 1830, is now regarded as a synonym of *Obolus apollinis* EICHWALD, 1829". Consequently, following Art. 65 (misidentification or altered concept), the case of *Ungula* is to be referred to the Commission for a ruling. However, when based on *Ungula ingrca* (EICHWALD, 1829) "*Ungula*" has well-defined taxonomic characters according to

criteria proposed by EMIG (2002).

As stated in EMIG (2002), most of the specimens studied were identified originally by L.E. POPOV. Consequently, some remarks of POPOV and HOLMER (2003) seem strange: "The species *Obolus apollinis* EICHWALD, *Obolus rukhini* KHAZANOVICH and 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".

<i>Obolus apollinis</i>
1829 <i>Obolus apollinis</i> n. sp.: EICHWALD, p. 274.
1830 <i>Ungula convexa</i> n. sp.: PANDER, p. 59.
1830 <i>Ungula plana</i> n. sp.: PANDER, p. 59.
1830 <i>Ungula triangularis</i> n. sp.: PANDER, p. 59.
1840 <i>Obolus apollinis</i> : EICHWALD, p. 194 [in part].
1845 <i>Obolus apollinis</i> : DE VERNEUIL <i>in</i> MURCHISON <i>et alii</i> , p. 290 [in part].
1848 <i>Aulonotreta polita</i> n. sp.: KORTUGA, p. 278.
1853 <i>Obolus apollinis</i> : DAVIDSON, p. 135.
1860 <i>Obolus apollinis</i> : EICHWALD, p. 925 [in part].
1861 <i>Obolus apollinis</i> : EICHWALD, p. 264 [in part].
1892 <i>Obolus apollinis</i> : HALL & CLARKE, p. 80 [in part].
1896 not <i>Obolus apollinis</i> var. <i>ingricus</i> n. var.: MICKWITZ, p. 137.
1896 not <i>Obolus apollinis</i> var. <i>maximus</i> n. var.: MICKWITZ, p. 140.
1896 not <i>Obolus apollinis</i> var. <i>quenstedti</i> : MICKWITZ, p. 143.
1898 not <i>Obolus apollinis</i> : WALCOTT, Pl. 26: 3-6.
1902 not <i>Obolus apollinis</i> var. <i>quenstedti</i> : MATTHEW, p. 93.
1905 not <i>Obolus apollinis</i> : WIMAN, p. 62.
1906 not <i>Obolus apollinis</i> : MOBERG & SEGERBERG, p. 65.
1912 not <i>Obolus apollinis ingricus</i> : WALCOTT, p. 384.
1912 not <i>Obolus apollinis maximus</i> : WALCOTT, p. 384.
1912 not <i>Obolus apollinis quenstedti</i> : WALCOTT, p. 384.
1964 not <i>Obolus apollinis</i> : BIERNAT, p. 73.
1965 not <i>Obolus apollinis</i> : ROWELL, p. H263.
1969 <i>Obolus (Obolus) apollinis</i> : GORYANSKIJ, p. 20, Pl. 1: 1-9.
1986 <i>Obolus apollinis</i> : KALJO <i>et alii</i> , Pl. 1: 4-7.
1989 <i>Obolus apollinis</i> : POPOV & KHAZANOVITCH (<i>in</i> POPOV <i>et alii</i>), p. 98.
1989 <i>Ungula convexa</i> : POPOV & KHAZANOVITCH (<i>in</i> POPOV <i>et alii</i>), p. 177.
1993 <i>Ungula convexa</i> : LASHKOV <i>et alii</i> , p. 101.

" <i>Ungula</i> " <i>ingrica</i>
1829 <i>Obolus ingricus</i> n. sp.: EICHWALD, p. 274.
1860 <i>Obolus ingricus</i> : EICHWALD, p. 926.
1861 <i>Obolus ingricus</i> : EICHWALD, p. 264.
1892 <i>Obolus quenstedti</i> n. sp.: MICKWITZ, p. 74 [in part].
1896 <i>Obolus apollinis</i> : MICKWITZ, p. 133 [in part].
1896 <i>Obolus apollinis</i> var. <i>ingricus</i> : MICKWITZ, p. 137.
1896 <i>Obolus apollinis</i> var. <i>maximus</i> : MICKWITZ, p. 140.
1896 <i>Obolus apollinis</i> var. <i>quenstedti</i> : MICKWITZ p. 143.
1896 <i>Obolus triangularis</i> n. sp.: MICKWITZ, p. 145.
1896 <i>Obolus triangularis</i> n. sp. var. <i>inornatus</i> n. var.: MICKWITZ p. 148.
1896 <i>Obolus panderi</i> n. sp.: MICKWITZ, p. 149.
1898 <i>Obolus apollinis</i> : WALCOTT, p. 385.
1902 <i>Obolus apollinis</i> var. <i>quenstedti</i> : MATTHEW, p. 93.
1905 <i>Obolus apollinis</i> : WIMAN, p. 62.
1906 <i>Obolus apollinis</i> : MOBERG & SEGERBERG, p. 65.
1906 <i>Obolus triangularis</i> : MOBERG & SEGERBERG, p. 65.
1912 <i>Obolus apollinis</i> : WALCOTT, p. 381.
1912 <i>Obolus apollinis ingricus</i> : WALCOTT, p. 384.
1912 <i>Obolus apollinis maximus</i> : WALCOTT, p. 384.
1912 <i>Obolus apollinis quenstedti</i> : WALCOTT, p. 384.
1912 <i>Obolus triangularis</i> : WALCOTT, p. 419.
?1964 <i>Obolus apollinis</i> : BIERNAT, p. 73.
1965 <i>Obolus apollinis</i> : ROWELL, p. H263.
1969 <i>Obolus (Obolus) ingricus</i> : GORYANSKIJ, p. 22.
1969 <i>Obolus (Obolus) apollinis</i> : GORYANSKIJ, p. 20, Pl. 1: 10-11.
1969 <i>Obolus (Obolus) triangularis</i> : GORYANSKIJ, p. 24.
1989 <i>Ungula ingrca</i> : POPOV & KHAZANOVITZ (<i>in</i> POPOV <i>et alii</i>), p. 119.
1989 <i>Ungula inornata</i> : POPOV & KHAZANOVITCH (<i>in</i> POPOV <i>et alii</i>), p. 121.
1989 <i>Ungula</i> sp. 1: POPOV & KHAZANOVITCH (<i>in</i> POPOV <i>et alii</i>), p. 122.
1993 <i>Ungula ingrca</i> : PUURA & HOLMER, p. 217.
1993 <i>Ungula inornata</i> : PUURA & HOLMER, p. 219.

Table 1: The list (not exhaustive) of specimens which can be referred to *Obolus apollinis* and "*Ungula*" *ingrica*. It attests the difficulties in establishing a valid taxonomy in these genera based on the determination of reliable characters and their degrees of variability.

These three "species" were placed in synonymy because they share identical taxonomic characters. *Ungula transversa* was redescribed as *Obolus transversus* (PANDER) by KHAZANOVICH *et alii* (1984) and POPOV *et alii* (1989). Furthermore, letters exchanged with the curator of CNIGR Museum, St Petersburg, indicated that the Museum had neither the specimens nor their catalogue numbers (see Recommendation 72F of the ICZN, 1999).

Valve characters

The new diagnoses of *Obolus* and *O. apollinis* are emendations of those in the previous papers, as stated in the captions in EMIG (2002). Characters without taxonomic value were deleted and some with taxonomic significance were added (EMIG, 2002). The main innovation is that figures now constitute a part of the diagnosis. Several characters need explanation.

"*Bi-symmetrical muscle arrangement*". - This feature should be used as a suprageneric one and is thus in concordance with statement of HOLMER and POPOV (2000) and POPOV and HOLMER (2003): "*a plesiomorphic character at least for*

all members of the Class Lingulata" (...) "*an important apomorphic character of the family Lingulidae*". But HOLMER and POPOV (2000) did not use this fundamental character in any diagnosis, nor as a possible criterion to split the class Lingulata. The same remark applies also to the posterior adductor muscles.

"*Lateral umbonal plates overhanging the internal side*". - The so-called umbonal plates overhang the internal side of the valve and have no relationship with the muscles scars, which are several millimetres below these plates (EMIG, 2002: Fig. 1, 2, and description in the text). They are a great taxonomic novelty that at the least distinguishes *Obolus apollinis*. If these plates are broken the specimens may be confused with "*Ungula ingrlica*", when the new characters proposed here are not applied. POPOV and HOLMER (2003) did not observed these plates correctly for they wrote: "*they are nothing more than the tracks of the anterior migration of the muscles forming the anterior-lateral muscle fields and are of little use taxonomically, unless distinct muscle platforms can be recognised*".

LENGTH			WIDTH			W/L			N.I.	HEIGHT			H/L			N.I.
MIN	MEAN	MAX	MIN	MEAN	MAX	MIN	MEAN	MAX		MIN	MEAN	MAX	MIN	MEAN	MAX	
"UNGULA" INGRICA VENTRAL VALVE																
5.5	16.3	28.7	5.3	17.7	31.5	0.85	0.99	1.17	39	1.9	3.5	5.4	0.10	0.18	0.26	34
"UNGULA" INGRICA DORSAL VALVE																
4.8	16.2	26.8	4.9	16.9	27.3	0.91	1.01	1.17	47	1.9	3.6	5.5	0.14	0.19	0.25	27

LENGTH			WIDTH			W/L			N.I.
MIN	MEAN	MAX	MIN	MEAN	MAX	MIN	MEAN	MAX	
OBULUS APOLLINIS									
	7.9			7.8			0.93		8
OBULUS APOLLINIS (RUKHINI)									
	4.6			4.3			0.93		10
OBULUS APOLLINIS (CONVEXA) VENTRAL VALVE									
3.5	6.4	28.7	3.5	6.6	8.8	0.94	1.02	1.10	4
OBULUS APOLLINIS (CONVEXA) DORSAL VALVE									
4.1	6.9	8.5	3.8	7.5	9.6	0.93	1.06	1.19	3

Table 2: Valve dimensions (in mm) and ratios of "*Ungula ingrlica*" (personal data and MICKWITZ, 1896) and those of *Obolus apollinis* (KHAZANOVITCH *et alii*, 1984; POPOV *et alii*, 1989). Between brackets the previous species name.

"Rounded umbonal region with reduced concave, pseudointerarea with flexure lines". – Although ventral and dorsal flexure lines look similar in *Obolus* and also in "*Ungula*", POPOV and HOLMER (2003) state that in the ventral valve such lines exist, but that in the dorsal valve, "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". Figure 1 demonstrates clearly the occurrence of flexure lines in the dorsal valve; a median concavity is present in both valves.

About the pseudointerarea: the definition given in the glossary by WILLIAMS and BRUNTON (1997) applies: "somewhat flattened, posterior sector of the shell of some inarticulated brachiopods secreted by the posterior sector of the mantle not fused with that of the opposite valve". On the other hand, the term propareas is not used because of a lack of precision in reference to the dorsal valve. The definition of the propareas by the above cited authors is: "pair of subtriangular halves of pseudointerarea divided medially by various structures (e.g. homeodeltidium, intertrough, and pedicle groove)". Both definitions apply only to some inarticulated brachiopods.

"Posterior adductor muscle unpaired in the dorsal valve". – This muscle is clearly unpaired in all the *Obolus* specimens studied; but it is paired in the hundreds of specimens of "*Ungula* *ingrica*" examined in Estonia. This character is important in differentiating the two genera and has phylogenetic implications. However, POPOV and HOLMER (2003) write: "although the dorsal umbonal scar in some specimens may appear to be unpaired, other specimens have imprints of a paired dorsal umbonal muscle".

"Visceral areas of both valves". – The thickness of the generally heart-shaped visceral area in *Obolus* and "*Ungula*" is highly variable: from an almost complete absence of thickening to a fairly complete filling of the visceral space. This thickening is clearly a taphonomic phenomenon and is an example of a post mortem effect that, at least in the two genera cited, has been mistakenly considered to have taxonomic significance. Taphonomic changes and calcification during life common on the internal side of linguloid valves have sometimes been used as taxonomic criteria, even in extant species.

Open discussion

I appreciate POPOV and HOLMER's (2003) positive contributions. But rather than responding in kind to the concluding sentence of these authors' critique: "EMIG (2002) has provided no satisfactory basis for his radical revisions to the existing" (...) "widely accepted

taxonomy of the Cambrian to earliest Ordovician Obolidae of the East Baltic", I suggest as a first step that we study together the 10,000 specimens in order to further the establishment of a more comprehensive taxonomy of the Family Obolidae.

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