Rivista Italiana di Paleontologia e Stratigrafia	volume 121	no. 3	pp. 267-283	November 2015

REVISION OF THE FAMILY HEBETOECHIIDAE HAVLÍČEK, 1960, AND PROPOSAL OF THREE NEW RHYNCHONELLID (BRACHIOPOD) FAMILIES

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Received: March 07, 2015; accepted: June 16, 2015

Key words: Brachiopods, rhynchonellids, Hebetoechiidae, Lanceomyoniidae fam. n., Ktenopotamorhynchidae fam. n., Eucharitinidae fam. n., *Ktenopotamorhynchus* gen. n.

Abstract. The heterogeneous contents of various rhynchonellid families indicate that their definition is either loose or insufficient, and opens the door to diverse and sometimes contradictory interpretations. The family Hebetoechiidae Havlíček, 1960 is one of them. Its diagnosis is revised. Some genera included in it at one time or another are assigned to the following new families: Lanceomyoniidae, Ktenopotamorhynchidae, and Eucharitinidae. A new genus, *Ktenopotamorhynchus*, with type species *K. borealiformis* (Siemiradzki, 1906a) is proposed, and the genus *Lanceomyonia* Havlíček, 1960 is revised.

Introduction

The late Silurian species *Lanceomyonia tarda* (Barrande, 1847), type species of the genus *Lanceomyonia* Havlíček, 1960, and the early Lochkovian species *L. borealiformis* (Siemiradzki, 1906a) have been abundantly and well-illustrated in recent literature (Plodowski 1973; Erlanger 1994; Balinski 2012). Transverse serial sections made from representatives of these long standing species show characters that have been so far overlooked or underestimated, such as presence or absence of dental plates, of cardinal process, and of connectivum covering septalium.

Examination of the external and internal characters of these two species leads to a revision of the genus *Lanceomyonia* Havlíček, 1960, the revaluation of its contents, and its assignment to another family than the family Hebetoechiidae Havlíček, 1960 to which it has usually been attributed, e.g. Savage (2002: 1104-5). Such changes have an impact on related taxa. They bring up the necessity of revising the family Hebetoechiidae, and of establishing three new families and a new genus.

It is stressed in the present paper that the following features are significant for the definition of genera and families: the presence or absence of a cardinal process, and its structure; the presence or absence of a connectivum covering the septalium; and the presence or absence of dental plates.

Institutional abbreviations: IRScNBa, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; SBNM-ČF, Sammlungen des Barrandiums des National-Museum, Prague, Czech Republic.

Revision of the family Hebetoechiidae Havlíček, 1960

General remarks

The family Hebetoechiidae was established by Havlíček (1960: 243); only the type genus, *Hebetoechia* Havlíček, 1959, and the genus *Lanceomyonia* Havlíček, 1960 were then included in the new family. The only internal features he brought out for characterizing the family were the septalium either uncovered ("frei") or filled out with a callus from which differently shaped cardinal processes take shape ("durch kallöse Substanz ausgefüllt, woraus sich verschiedenartig geformte Schlossfortsätze bilden"). As far as the only genus described in the publication – *Lanceomyonia* – is concerned, the two Bohemian species included in it, the Budnanian (late Silurian) type species *L. tarda* (Barrande, 1847), and the Lochkovian species *L. confinis* (Barrande, 1879), are characterized by an uncovered septalium not narrowing in its upper part ("oben nicht verengt"), the absence of a cardinal process, the presence of strong dental plates, and a significantly narrow ventral muscle field.

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HAVLÍČEK (1960)	HAVLÍČEK (1961)	SCHMIDT (1965)	SAVAGE (1996, 2002, 2007)
family HEBETOECHIIDAE Havlíček, 1960	family HEBETOECHIIDAE	family UNCINULIDAE Rzhonsnitskaya, 1956 subfamily HEBETOECHIINAE	family HEBETOECHIIDAE subfamily HEBETOECHIINAE
Hebetoechia Havlíček, 1959	*Hebetoechia*	*Hebetoechia*	*Hebetoechia*
Lanceomyonia Havlíček, 1960	*Lanceomyonia*	*Lanceomyonia*	*Lanceomyonia*
	Eucharitina Schmidt, 1955	→ family EATONIIDAE Schmidt, 1965	→ family UNCINULIDAE
	Glossinulus Schmidt, 1942	→ subfamily UNCINULINAE	→ family GLOSSINOTOECHIIDAE Havlíček, 1992
	Obturamentella Amsden, 1958 not described	? *Obturamentella*	→ family OBTURAMENTELLIDAE Savage, 1996
	Plethorhyncha Hall & Clarke, 1893	→ subfamily UNCINULINAE	→ family UNCINULIDAE
	Sphaerirhynchia Cooper & Muir-Wood, 1951 not described	*Sphaerirhynchia*	→ subfamily SPHAERIRHYNCHIINAE Savage, 1996 *
		? *Cassidirostrum* McLaren, 1961	→ subfamily BECKMANIINAE Savage, 1996 *
		Estonirhynchia Schmidt, 1954	→ subfamily SPHAERIRHYNCHIINAE *
		? *Pectorhyncha* McLearn, 1918	→ family OBTURAMENTELLIDAE
		Tadschikia Nikiforova, 1937	→ subfamily SPHAERIRHYNCHIINAE *
			Gerrhynx Baranov, 1991
			Lapradella Baranov, 1989
			Mongolorhynx Erlanger, 1992
			Voskopitoechia Havlíček, 1992
			Cerveratoechia García-Alcalde, 1998 **
			Lebanzuella García-Alcalde, 1999 **

Tab. 1 - Successive modifications in the content of the family Hebetoechiidae Havlíček, 1960.

→ assigned to different family or subfamily

* subfamily of the family Hebetoechiidae

** added in Savage (2007)

Havlíček (1960: 241) added that the family, as well as four other families of the new superfamily "Camarotoechiacea" (sic), i.e. Camarotoechiidae Schuchert, 1929, Septalariidae fam. n., Rhynchotrematidae Cooper, 1956, and Uncinulidae Rzhonsnitskaya, 1956, was characterized by the presence of a septalium in the dorsal valve, supported by a median septum or a median ridge ("durch das Vorhandensein des Septaliums in der Armklappe, das durch ein Mittelseptum oder Mittelwulst gestützt wird").

Havlíček (1961: 110-118) gave a full description of the family and of five of the seven genera assigned to it, *Lanceomyonia* and *Hebetoechia* among them. He described three species of the genus *Lanceomyonia*: the two species mentioned in 1960, and a third one, *L. borealiformis* (Siemiradzki, 1906a, b) from Podolia (now southwestern Ukraine), also present in Bohemia according to him and, contrary to Kozłowski (1929), considered distinct from *L. tarda*. Kozłowski and some authors following his lead included *L. borealiformis* into the synonymy of *L. tarda*. Successive modifications in the content of the family Hebetoechiidae are indicated in Tab. 1.

The three serial transverse serial sections from *L. tarda*, and the three transverse serial sections from *L. confinis* by Havlíček (1961: 115, 117), although lacking precision, show the detached dental plates and the absence of a cardinal process. So do the transverse serial sections from the Podolian species from the Borshchov horizon (Lower to lower Middle Lochkovian), *L. borealiformis*, by Kozłowski [1929: textfigs 43B, 51, erroneously called *Camarotoechia* (*Wilsonia*) *tarda*], and by subsequent authors (see comments on Kozłowski's sections below).

In the original description of the family Hebetoechiidae by Havlíček (1960; 1961) no word is written on the presence or absence of dental plates, but in the descriptions of the various genera assigned by him to the family, the dental plates are declared absent (obscured by callus?) or, when present, described as stout, distinct, high, thin, short or almost not existing. Thus, according to Havlíček, the family Hebetoechiidae encompasses genera without a cardinal process (Havlíček 1960: 241 for the family, 243 for the genus *Lanceomyonia*; Havlíček 1961: 111 for the family), and with a cardinal process (Havlíček 1960: 241 for the family; Havlíček 1961: 111 for the family). This cardinal process can be differently shaped (Havlíček 1960: 241 for the family): bilobate and characteristically crowned by fillets ("trägt einen charakteristischen Leistenbesatz") (Havlíček 1961: 118 for the genus *Hebetoechia*), bilobate, very seldom unilobate (Havlíček 1961: 121, textfig. 44, for *H. hebe*; Havlíček 1983: textfig. 5), bilobate with the two lobes separated by a thin groove (Havlíček 1961: 122-123, textfig. 45 for *H. ornatrix* Havlíček, 1961).

This alternative character has been maintained since in the various diagnoses or definitions of either the family Hebetoechiidae or the subfamily Hebetoechiinae in which the genera *Hebetoechia* and *Lanceomyonia* are always associated, e.g. "forming incipient cardinal process in some genera" by Schmidt in Schmidt

& McLaren (1965: *H*566 in the subfamily Hebetoechiinae *sensu* Schmidt), and "usually absent or incipient in early genera" and "cardinal process usually developed" by Savage (1996: 253; 2002: 1104), respectively. The only exception is Erlanger (1994: 86), who included, without reservation, a bilobate cardinal process in the definition of the genus *Hebetoechia* and the subfamily Hebetoechiinae.

To the genera *Hebetoechia* and *Lanceomyonia* Havlíček (1961: 111) added five others: *Eucharitina* Schmidt, 1955, *Glossinulus* Schmidt, 1942, *Obturamentella* Amsden, 1958, *Plethorhyncha* Hall & Clarke, 1893, and *Sphaerirhynchia* Cooper & Muir-Wood, 1951. Apart of the type genus, none of the other six genera belong to the family, which, consequently, could be qualified a catch-all name. This is obvious for the large middle Pragian genus *Plethorhyncha*. It is also obvious for the Pragian genus *Eucharitina* with its characteristic cardinal process, longitudinally oval to cordiform outline, very short dental plates, medium to large size, a moderate number of wide median costae, and narrower, numerous lateral costae; for the late Emsian genus *Glossinulus* with its characteristic cardinal process, cordiform outline, very short dental plates, small size, and fine costation; for the Lochkovian genus *Obturamentella* with its characteristic cardinal process, characteristic high tongue, absence of distinct dental plates, small size, and few costae; and for the Wenlockian genus *Sphaerirhynchia* with its spherical shape, absence of a cardinal process, medium size, and numerous costae. None of these genera has a connectivum covering the septalium. They were already excluded, with the exception of *Sphaerirhynchia*, from the subfamily Hebetoechiinae or the family Hebetoechiidae in the two editions of the Brachiopod Treatise: Schmidt in Schmidt & McLaren (1965: *H*563, *H*565, *H*566, *H*571, *H*572 for *Eucharitina*, *Glossinulus*, and *Plethorhyncha*), and Savage (1996: textfig. 4; 2002: 1092, 1095, 1117, 1126 for *Eucharitina*, *Glossinulus*, *Obturamentella*, and *Plethorhyncha*).

Schmidt in Schmidt & McLaren (1965: *H*566-*H*567) attributed eight genera, three of them questionably (?*Cassidirostrum, Estonirhynchia, Hebetoechia*, *Lanceomyonia*, ?*Obturamentella*, ?*Pectorhyncha*, *Sphaerirhynchia*, and *Tadschikia*), to the subfamily Hebetoechiinae, which, together with the subfamilies Hadrorhynchiinae McLaren in Schmidt & McLaren, 1965, Hypothyridininae Rzhonsnitskaya, 1956, and Uncinulinae Rzhonsnitskaya, 1956, composed the family Uncinulidae. The three other genera included by Havlíček (1961) in the family Hebetoechiidae were transferred by Schmidt in Schmidt & McLaren, 1965 to the family Eatoniidae Schmidt in Schmidt & McLaren, 1965 (*Eucharitina*), and the subfamily Uncinulinae (*Glossinulus* and *Plethorhyncha*); four genera, two questionably, all of them established in 1961 and earlier (?*Cassidirostrum* McLaren, 1961, *Estonirhynchia* Schmidt, 1954, ?*Pectorhyncha* McLearn, 1918, and *Tadschikia* Nikiforova, 1937), were added to the subfamily Hebetoechiinae.

Savage (1996: 253, fig. 4; 2002: 1104) followed suit, but included the subfamily Hebetoechiinae in the family Hebetoechiidae, superfamily Uncinuloidea Rzhonsnitskaya, 1956. Savage (1996: 252-253, figs 4, 5; 2002: 1092-1131) attributed to Uncinuloidea eight families: Eatoniidae, Glossinotoechiidae Havlíček, 1992, Hadrorhynchiidae, Hebetoechiidae, Hypothyridinidae, Innaechiidae Baranov, 1980, Obturamentellidae Savage, 1996, and Uncinulidae. He included in the family Hebetoechiidae six subfamilies: five in 1996 (Hebetoechiinae Havlíček, 1960, Sphaerirhynchiinae Savage, 1996, Glossinulininae Savage, 1996, Betterbergiinae Savage, 1996, and Beckmanniinae Savage, 1996), and one more in 2002 (Amsdenellinae Savage, 2002). The two only genera originally assigned by Havlíček (1960) to the family Hebetoechiidae, *Hebetoechia* and *Lanceomyonia*, were attributed to the subfamily Hebetoechiinae by Savage (1996). Savage also included in this subfamily four genera established around the nineties: *Gerrhynx* Baranov, 1991, *Lapradella* Baranov, 1989, *Mongolorhynx* Erlanger, 1992, and *Voskopitoechia* Havlíček, 1992. The other genera included by Havlíček (1961) in the family Hebetoechiidae, and by Schmidt in Schmidt & McLaren, 1965 in the subfamily Hebetoechiinae were placed by Savage in the various families and subfamilies mentioned above: *Eucharitina* and *Plethorhyncha* (Uncinulidae), *Glossinulus* (Glossinotoechiidae), *Obturamentella* and *Pectorhyncha* (Obturamentellidae), *Estonirhynchia*, *Sphaerirhynchia*, and *Tadschikia* (Sphaerirhynchiinae), and *Cassidirostrum* (Beckmanniinae). Later Savage (2007: 2707) added two genera to the subfamily Hebetoechiinae: *Cerveratoechia* García-Alcalde, 1998 and *Lebanzuella* García-Alcalde, 1999. None of these genera recently assigned to the family Hebetoechiidae seems to belong to it; only some of the reasons for exclusion (size, presence or absence of dental plates, cardinal process and connectivum covering septalium, shape of cardinal process) are indicated in parentheses: *Lapradella* Baranov, 1989 (type species *L. definita* Baranov, 1989, late Lochkovian; in need of further investigation, presence of connectivum and cardinal process are questionable); *Gerrhynx* Baranov, 1991 (type species *G. vescus* Baranov, 1991, late Pragian; in need of further investigation, because there is a conflict between small narrow cardinal process filling up the septalium and the eventual presence of connectivum, minute size, costae); *Mongolorhynx* Erlanger, 1992 (type species *M. drosdovae* Erlanger, 1992, late Emsian-Eifelian; small, multilobed cardinal process, connectivum, costae); *Voskopitoechia* Havlíček, 1992 (type species *V. orbona* Havlíček, 1992, Pragian; minute, costae, small

bilobed cardinal process, absence of septalium, hinge plates conjunct); *Cerveratoechia* García-Alcalde, 1998 [type species *C. cantabrica* (Binnekamp, 1965), Lochkovian-early Pragian; outline, costation, connectivum, no cardinal process]; *Lebanzuella* García-Alcalde, 1999 [type species *L. lebanza* (Binnekamp, 1965); early and middle Pragian; costae, narrow and solid cardinal process possessing strong ridges].

Revision of *Hebetoechia hebe* (Barrande, 1847), type species of the genus *Hebetoechia*

Havlíček (1961: 14, 119-121) gave the first and only full description of *Hebetoechia hebe* (Barrande, 1847), the type species of the genus *Hebetoechia*, from the Kopanina (Ludlow), Přídolí (uppermost Silurian), and Lochkov (lowermost Devonian) limestones. Havlíček (in Havlíček & Štorch 1990: 149; Havlíček 1992: 102-103, tab. 1, p. 57) suggested the following modified stratigraphic range: uppermost Silurian (Přídolí, uppermost part) – lowermost Devonian (Lochkovian, Kotýs Limestone and Radotín Limestone, lower part). Westbroek (1967) added some precisions to the description of the species. *Hebetoechia hebe* possesses a cardinal process, which, according to Havlíček (1959: 79; 1961: 121), is bilobate or, very seldom, unilobate. Havlíček (1983: fig. 5) and Havlíček in Havlíček & Štorch [1990: fig. 54 (= fig. 5 in Havlíček 1983), fig. 55] published transverse serial sections from two specimens of the species in order to compensate for the four unsatisfactory ones he sketched in 1961 (figs 44a-d). His sections of 1961 were reproduced by Schmidt in Schmidt & McLaren (1965: fig. 439: 1e-h) and, together with those of 1983, by Savage (2002: fig. 747: 1f-m).

As it is, adjustments need to be made to the description of the septalium, cardinal process, *paries geniculatus*, shape, and size of the shell of *H. hebe*, and, consequently to the definition of the genus *Hebetoechia*.

The open septalium is of moderate size as mentioned by Westbroek (1967: 75, enclosures I, II), cup- to drop-shaped with almost equal width and depth; it is not deep as stated by Havlíček (1992: 102).

According to Havlíček (1961: 118, 119, 121, fig. 44a; 1983, fig. 5) and Havlíček in Havlíček & Štorch (1990: figs 54, 55), the cardinal process of *H. hebe* and of the genus *Hebetoechia* is either bilobate or unilobate (very rarely) with its top covered with radial furrows and ridges ("radial gefurcht" in the description of *H. hebe*; with "charakteristischen Leisten" in the description of the genus *Hebetoechia*). Figure 44a (Havlíček 1961) shows a cardinal process partly covered with some vague furrows and ridges, but none is visible on fig. 5 (Havlíček 1983) and figs 54, 55 (Havlíček in Havlíček & Štorch 1990). The top is slightly undulating, and incised by a tiny median furrow, the "mehr oder minder tiefes Grübchen" mentioned by Havlíček (1961: 119) in his description of the genus *Hebetoechia*. This furrow and the full bilobation of the cardinal process it leads to are shown in some serial transverse sections (Havlíček 1983; Havlíček in Havlíček & Štorch 1990).

The presence of a *paries geniculatus* in *H. hebe*, in the genus *Hebetoechia* and in the family Hebetoechiidae is commonly mentioned in the literature since Havlíček (1960: 241; 1961: 118, 119, 120 as "abgestutzte Stirn- und Seitenwände"). As far as *H. hebe* is concerned, Havlíček conceded that these "abgestutzte Wände" were low ("nur niedrig") and not sharply separated from the rest of the shell. Westbroek (1967: 54) also described the *paries geniculatus* as very low and the geniculation as "nearly simultaneous along the entire commissure". As a matter of fact, *H. hebe* does not possess a true *paries geniculatus*. The term *paries geniculatus* is used here in the strictest sense of the word, i.e. as defined by Westbroek (1967: 7, 41): "*vertical* shell wall formed as a result of *geniculation*" (italics PS). Some confusion arises from the fact that Westbroek considered the *paries geniculatus* equivalent to the "abgestutzte Vorder- und Seitenwände" of Schmidt (1937) ("abgestutzt" means only "truncate"), and used the term he initiated in a rather loose way as just mentioned.

Hebetoechia hebe is presented in the literature, notably by Havlíček (1960: 241; 1961:118, 119, 121) as a high, medium sized ("mittelgross"), and semiglobular ("fast kugelförmig") species, although it is small and neither high nor globular (see Fig. $1A_{1-4}$ for estimation of size and globulosity).

Squamae and *glottae* are not developed in *H. hebe*, and costae start close to the beaks as it can be observed on the figures of the species given by Havlíček in Havlíček & Štorch, (1990: pl. 46: 18a-c, 19a-c, 20a, b), and as already stated by Westbroek (1967: 54, 74, enclosures I, II).

These precisions and modifications, added to Havlíček's 1961 detailed description of *H. hebe*, lead to the following conclusions: (i) various forms have been erroneously assigned to that species, e.g. those from Canada, *H.* cf. *H. hebe* from the Upper Silurian of northern Yukon Territory by Lenz (1970: 481, 482, 489, pl. 86: 1-10, textfigs 3, 4), *H.* cf. *H. hebe* from the Lower Lochkovian of the District of Mackenzie by Perry (1984: 75-76, pl. 25: 61-67, textfig. 7); (ii) the absence of a cardinal process or the presence of a connectivum covering the septalium eliminate from the genus *Hebetoechia* the species without a cardinal process, e.g. *H. sphaerulea* Havlíček, 1983 (Ludlow, lower Kopanina Formation, Bohemia), and those with a covered septalium, e.g. *H. woschmidti* Plodowski, 1973 (Upper Silurian, upper *Ozarkodina remscheidensis eosteinhornensis* Zone, Central Carnic Alps, Austria); (iii)

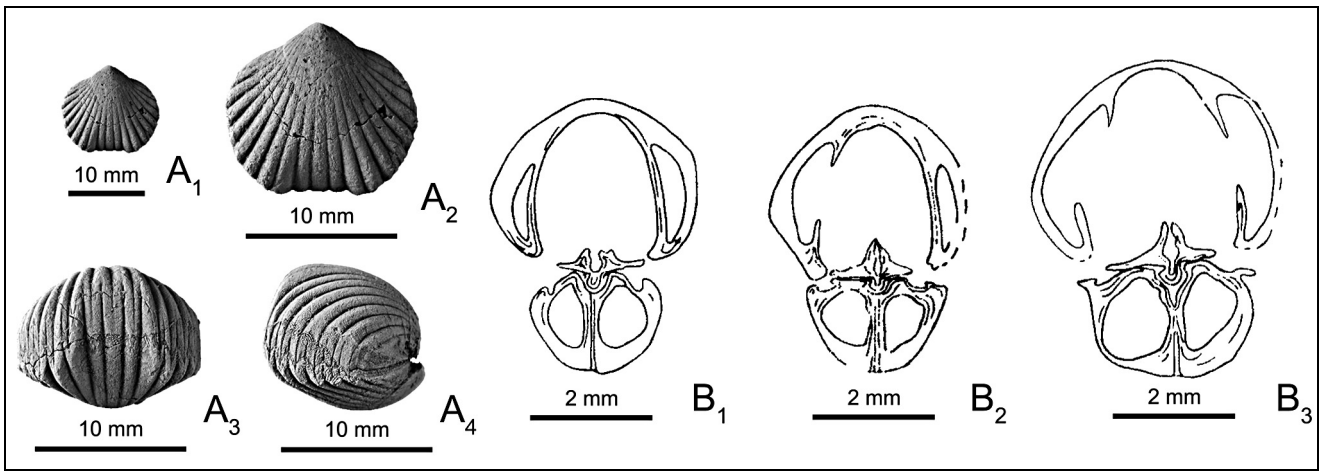

Fig. 1 - External and internal characters of *Hebetoechia hebe* (Barrande, 1847).
A) IRScNBa 12923, topotype; Czech Republic, Bohemia, Dlouhá hora; Upper Silurian, Přídolí Limestone; ventral (A_1, A_2), anterior (A_3) and lateral (A_4) views.
B) From Erlanger (1994); Czech Republic, Bohemia; Upper Silurian, Přídolí Limestone; serial transverse sections: Erlanger (1994: fig. 31, section 6) (B_1), Erlanger (1994: fig. 31, section 7) (B_2), Erlanger (1994: fig. 31, section 8) (B_3).

the inclusion at one time or another of some genera, notably the genus *Lanceomyonia* discussed below, in the family Hebetoechiidae or in the subfamily Hebetoechiinae has to be reconsidered.

To sum up, the family Hebetoechiidae is restricted at this point to its type genus *Hebetoechia*, which, in turn, is restricted to its type species.

Figure $1A_{1-4}$ are photographs of a specimen of *H. hebe*. Photographs of more specimens may be found in Havlíček (1961: pl. 17: 8-14); the best ones are by Havlíček in Havlíček & Štorch (1990: pl. 46: 18a-c, 19a-c, 20a, b). Demonstrative transverse serial sections from three topotypes were produced by Havlíček in Havlíček & Štorch (1990: figs 54, 55), and by Erlanger (1994: fig. 31, pl. 15: 1, 2); three of Erlanger's sections are reproduced on Fig. $1B_{1-3}$.

Revised diagnosis of the family Hebetoechiidae

The family Hebetoechiidae was introduced by Havlíček (1960: 241) as follows (translated from German):

"The family contains genera that present high shells and well developed truncated walls in ephebic individuals, and marginal spines. It is characterized by the presence of a septalium supported by a septum or by a cushion. The septalium is either free or filled up with callus in various ways that build up cardinal processes of various shapes. In particular genera the septalium undergoes various modifications". A more elaborate diagnosis given by Havlíček (1961: 110-111) is not considered here, because genera that do not belong to the family have been added to the two genera included in the family one year before, and because species that do not belong to it are incorporated in the genus *Hebetoechia*.

The revised diagnosis of the family is as follows:

Shell of small size, dorsibiconvex, thickest posterior to front margin. Outline rounded. Apical angle wide. Commissure moderately serrate. No true *paries geniculatus*. No *squamae* and *glottae*. Sulcus and fold start in the anterior part of the umbonal regions. Sulcus very shallow, moderately wide at front (53 to 64%, mostly 53 to 59%, the shell width in *Hebetoechia hebe*). Fold very low. Tongue high with rectangular outline. Costae simple (a division of a median costa is very rare), broad, separated by fine furrows; number of costae moderate (3 to 6, usually 4, 5, median costae, and 8 to 12 lateral costae in *H. hebe*); costae angular to angular with rounded top; costae start close to the beaks, but median costae are commonly not pronounced in the umbonal regions. Short marginal spine-like projections of costae with accommodating grooves. Dental plates, septum, and hinge plate thick. Dental plates and septum short. Septalium without connectivum, cup-shaped, of moderate size in section. Crura long, slender, raduliform, closely set, spear head-shaped in section proximately, oval to rounded distally. Cardinal process moderately developed, stocky, bilobate. Ventral muscle field slightly impressed, narrow, elongate.

Revision of the genus *Lanceomyonia* Havlíček, 1960

Original description of the genus *Lanceomyonia*

Havlíček (1960: 249) included the following internal characters in the diagnosis of the genus *Lanceomyonia*: strong and distinct dental plates; significantly narrow ventral muscle field enclosed by a ridge (hence the

name of the genus); open septalium not narrowing in its upper part; and absence of a cardinal process. Havlíček (1961) illustrated these characters when he described the type species, *L. tarda*, from the Upper Silurian (Přídolí Formation) of Bohemia. The narrow ventral muscle field is vaguely brought out (Havlíček 1961: pl. 14: 3) [Remark: the ventral muscle scars have been better represented by Havlíček in Havlíček & Štorch (1990: pl. 44: 8, 9)]. The other internal characters are illustrated by three transverse serial sections (Havlíček 1961: fig. 42) that have been reproduced by Schmidt in Schmidt & McLaren (1965: fig. 439: 3c-e), and by Savage (2002: fig. 748: 1e-g).

Additions to the knowledge of the genus *Lanceomyonia*

Plodowski (1973: 65, 66, 67, 69) made new observations on the internal structure ("Innenbau") of the type species of the genus *Lanceomyonia* in order to "complement Havlíček's (1961) excellent description" of the genus. Transverse serial sections made by Plodowski (1973: fig. 1) from a topotype (Dvorce locality) of *L. tarda* show the septalium covered by a connectivum, thus allowing to state that the presence of a connectivum has to be included in a revised diagnosis of the genus *Lanceomyonia*. Plodowski (1973: 66, 68) has been less affirmative in completing Havlíček's diagnosis of the genus by adding that the outer hinge plates could be bound together by a connectivum ("die äusseren Schlossplatten können durch ein Konnektivum miteinander verbunden sein"). He also suggested that another double possibility, an either free septalium or filled with secondary shell material spreading to the outer hinge plates, should be included in that diagnosis.

Presence of a connectivum is also observable in representatives of the genus *Lanceomyonia* other than the type species, e.g. in a specimen of *L. tardiplicata tardiplicata* Plodowski, 1973 from the late Silurian (upper *Ozarkodina remscheidensis eosteinhornensis* Zone, Central Carnic Alps, Austria) (Plodowski 1973: fig. 8), and in a specimen of *Lanceomyonia*? sp. from the upper Přídolí of Liévin (Artois, "Département du Pas-de-Calais", northern France) (Brice 1986: fig. 23C).

This is in opposition to the absence of a connectivum in the genus *Lanceomyonia* advocated by Havlíček (1960: 241, 243; 1961: 112, 116, fig. 42; 1992: 102), by Schmidt in Schmidt & McLaren (1965: *H*566, *H*567), and by Savage (2002: 1104, 1105), only to mention the two editions of the Treatise on Invertebrate Paleontology, Part H, Brachiopods. It is thus evident that the absence of a connectivum must be excluded from the diagnosis of the genus *Lanceomyonia*, of which it has hitherto been considered as a major distinctive element. This and the absence of a cardinal process, let alone other characters included in the diagnosis of the family Lanceomyoniidae fam. n. (see below), imply the rejection of the genus *Lanceomyonia* from the family Hebetoechiidae, and the modification of the diagnosis of that genus.

Discussion

Another evidence is that most species and subspecies assigned at one time or another to the genus *Lanceomyonia* – some thirty species and subspecies plus a similar number of forms in open nomenclature – ranging from the Ludlow to the late Emsian (mostly from the Přídolí to the Pragian), do not belong to it. It applies to all early Devonian species and subspecies included in the genus, and in first place to *L. borealiformis* as it is explained below. It applies in particular to Chinese species from the early Lochkovian of the Luqu-Tewo area (West Qinling Mountains, northwestern Sichuan and southeastern Gansu Provinces), notably those proposed by Tong (1982: 331-333): *L. convexoplanata* Tong, 1982, *L. longa* Tong, 1982, *L. modesta* Tong, 1982, *L. putonggouensis* Tong, 1982 plus two forms erroneously identified as *L. tarda* and *L. borealiformis*. Septalium in these species, contrary to *L. tarda*, the type species of the genus *Lanceomyonia*, is not covered by a connectivum; other characters (size, outline, costation, etc.) make them also distinct from these two species.

Plodowski (1973: 66) already indicated that neither *Lanceomyonia borealiformis* (Havlíček 1961: 112-114, pl. 13: 6, 7) and *L. confinis* (Havlíček 1961: 116-118, pl. 13: 4, 5) from the Lochkovian of Bohemia, nor *L. borealiformis* (Drot 1964: 116-119, pl. 13: 2a-c, 3a-c, 5a-c, 7a-c) and *L. borealiformis occidentalis* Drot, 1964 (Drot 1964: 119-123, pl. 13: 4, 6a-c) from the Gedinnian (and questionably Lower Siegenian) of Morocco (southern Anti-Atlas) belonged to the genus *Lanceomyonia*. (Remark: *occidentalis* elevated to the species rank since Becker et al. 2004: 5, 9). However, the present author does not believe that these species and subspecies could, even provisionally, be attributed to the latest Silurian genus *Oxypleurorhynchia* as suggested by Plodowski; Drot and L'Hotellier (1976: 265) already dismissed this possibility.

Tong (1982), who established the genus *Cratorhynchella* Tong, 1982 with type species *C. convexa* Tong, 1982 (1982: 333-334, 337), mentions only two differences between the genera *Lanceomyonia* and *Cratorhynchella*: the sulcus and costae appear in the anterior half of the shell in the former, and the septalium is not covered by a connectivum. *Cratorhynchella convexa* was described from the Lower Putonggou Formation (thickness: 175 m) of early Lochkovian age at Ruoergai, Zoige district (West Qinling Mountains, northwestern Sichuan Province). According to Cao (1987: 62, 63), the Lower Putonggou Formation encompasses a lower

Rhynchospirina-Spirigerina Assemblage zone and an upper *Lanceomyonia-Machaeraria* Assemblage zone. Rong et al. (1987: 6, 87-88, fig. 18) indicated in the same locality that the *Protathyris-Lanceomyonia* Fauna characterized the Lower Putonggou Formation.

Wang et al. (1987: 16, 17, 46, textfig. 13) proposed a new community, the Gedinnian *Protathyris-Lanceomyonia* Community, and adopted the subdivision of the Putonggou Formation by Qin & Gan (1976) into a Lower, Middle, and Upper Member at Xia Wunagou, Diebu County (West Qinling Mountains in southeastern Gansu). They suggested a late Gedinnian age for its Middle Member, in which the genus *Lanceomyonia* is among "the most abundant, dominant genera", because it occurred above the *Icriodus woschmidti*-bearing Lower Member, and below the *Spirigerina* fauna-bearing Upper Member.

Now that it has been demonstrated that *Lanceomyonia tarda* possesses a connectivum, this difference between *Cratorhynchella* and *Lanceomyonia* suggested by Tong (1982) cannot be considered. As far as the costae of *L. tarda* are concerned, they do not start in the anterior half of the shell as it is usually admitted, but in front of the umbonal regions. In short, *Cratorhynchella* differs from *Lanceomyonia* in size, outline, costation and eventually in some internal characters like the "nearly V-shaped" septalium mentioned by Tong. The three serial transverse sections made by Tong (1982: fig. 7) from a specimen of *C. convexa* are not good enough for allowing the observation of various elements of the inner structure of the shell. Better sections from specimens of two species assigned to the genus, *C. digna* Rong et al., 1987 (Rong et al. 1987: 11, 57-58, pl. 96: 5a-d, 6a-d) and *C. coverta* Rong et al., 1987 (Rong et al. 1987: 57, 58-60, pl. 96: 3a-d), show clearly a covered septalium. These species were described from the same beds (Lower Putonggou Formation) as the type species, but cropping out in southeastern Gansu Province at 50 to 70 km from the Zoige district. Nevertheless, because these two species differ externally and markedly from each other and from the type species of the genus *Cratorhynchella*, their assignment to that genus is questionable.

In short, *Cratorhynchella*, defined by its type species, is a genus that can be easily separated from the genus *Lanceomyonia* as revised in the present paper. Although a covered septalium enters the diagnosis of the genus *Cratorhynchella*, Savage (2002: 1105) declared it mistakenly a synonym of the genus *Lanceomyonia* (as understood before its present revision), defined, among other characters, by an "open septalium". Incidentally, Savage does not mention the absence of a cardinal process in the genus *Lanceomyonia*, although, according to him (Savage 2002: 1104), members of the subfamily Hebetoechiinae possess a "calluslike cardinal process usually developed".

It is of interest and importance to note that, according to Tong (1982: fig. 2), *Cratorhynchella convexa* is found in association with various species assigned to the genus *Lanceomyonia*: two identified as *L. tarda* and *L. borealiformis*, and three new ones, *L. convexoplanata*, *L. longa*, and *L. modesta*; a fourth new species, *L. putonggouensis* comes from beds exposed in the nearby locality of Diebu (Ganzu Province), correlated with those cropping out at Ruoergai. Rong et al. (1987: fig. 5, 3) considered these species, with the exception of *L. putonggouensis* and the addition of *L. gannanensis* Fu in Zhang et al., 1983, as synonymous with *L. modesta*, and questionably assigned *Phoenecitoechia margarita* Fu in Zhang et al., 1983 to the genus *Lanceomyonia*. All these species have a covered septalium and are of small size. None of them belongs to the genus *Lanceomyonia* (before and after its present revision).

Oxypleurorhynchia Plodowski, 1973 (Plodowski 1973: 85-86) with type species *O. acutiplicata* Plodowski, 1973 from the latest Silurian (uppermost *Ozarkodina remscheidensis eosteinhornensis* Zone, Central Carnic Alps, Austria) possesses also a covered septalium. Plodowski clearly underlined the differences between *Oxypleurorhynchia* and *Lanceomyonia*, but the assignment of the genus *Oxypleurorhynchia* to the subfamily Hebetoechiinae must be disregarded. *Hebetoechia*, the type genus of the family Hebetoechiidae, and *Oxypleurorhynchia* are similar in having rounded outline, wide apical angle, absence of *paries geniculatus*, sulcus and fold starting in the anterior part of the umbonal regions, maximum thickness slightly posterior to front margin, simple costae, thick and short dental plates, thick septum, cup-shaped septalium, strong outer hinge plates, slender, raduliform and closely set crura. But *Oxypleurorhynchia* differs from *Hebetoechia* by larger size, deeply serrated commissure, well marked sulcus and fold, deeper sulcus, higher fold, smaller number of angular and wide median and lateral costae separated by wide furrows and starting at some distance from the beaks, absence of marginal spine-like projections of costae and accommodating grooves, presence of a connectivum, absence of a cardinal process, strongly impressed ventral and dorsal muscle fields, and a bilobed ventral muscle field bordered by a rim. *Oxypleurorhynchia,* placed by Savage (1996: textfig. 3: 2002: 1062) in the subfamily Trigonirhynchiinae Schmidt, 1965, does not belong to the family Trigonirhynchiidae Schmidt, 1965 and can easily be separated from it by its rounded outline, medium size, few high strong wide and angular costae starting at some distance from the beaks, well-marked sulcus and fold, thick outer hinge plates and strongly impressed ventral muscle field.

In short, in the present author's opinion the genus *Lanceomyonia* should not be included into the family Hebetoechiidae, and *L. borealiformis* into the genus *Lanceomyonia*, but into *Ktenopotamorhynchus* gen. n. described below.

Lanceomyonia borealiformis deserves special attention. It is the most commonly mentioned and misidentified species of the genus *Lanceomyonia*, and it has often been mistaken for *L. tarda*, the type species of the genus.

Original definition of the species *Lanceomyonia borealiformis*

Lanceomyonia borealiformis was described for the first time by Siemiradzki (1906a: 171-172, pl. 7: 3a-d, 4, 5; see also 1906b: 258-259, pl. 7: 3a-d, 4, 5) under the name *Rhynchonella borealiformis* Szajnocha. Drot (1964: 116) called it *Lanceomyonia borealiformis* (Szajnocha in Siemiradzki, 1906a), and Erlanger (1994: 95) *Rhynchonella borealiformis* (Szajnocha in Siemiradzki, 1906a). In his latest papers, Havlíček (1999a: 77; 1999b: 304) called it *Lanceomyonia borealiformis* (Szajnocha), although he had named it *L. borealiformis* (Siemiradzki, 1906) in his previous publications.

Rhynchonella borealiformis was cited among the most common forms found in the Borszczów beds (Szajnocha 1889: 194, table, 196) attributed to the lower part of the Upper Ludlow beds and named for the small town in the southern part of Podolia (now southwestern Ukraine). According to Siemiradzki (1906b: 173), Szajnocha also wrote "eine kurze Notiz" in which the species is mentioned; there is no doubt that Szajnocha's name is a *nomen nudum*. Borszczów is the Polish spelling of the name of the town, and was accordingly used by Kozłowski (1929). In the present paper, Borshchov, the English transliteration of the Russian spelling of the name of the town and of the stratigraphic unit based on it, is adopted, because it is in most common use in the abundant literature of the region. [Remark: the spelling of stratigraphic units in the Podolian sequence has changed through time following adoption from German, Polish and Russian languages. Recently, Ukrainian names were introduced for regional subdivisions of the Lochkovian: Borshchiv (for Borshchov) beds (formation, stage, horizon), Khudykivtsi (for Tajna) beds (formation, member), Mytkiv (for Mitkov) beds (formation), Chortkiv (for Chortkov) beds (formation, stage, horizon); also, the Bogdanovka beds (upper part of the Borshchov horizon) were incorporated into the Chortkiv horizon (see Racki et al. 2012 and Balinski 2012)].

Designation of a lectotype of *Lanceomyonia borealiformis*

It is surprising that no lectotype has been designated so far for a species abundantly cited and discussed in the literature. On account of the questionable presence of *L. borealiformis*, and thus of the genus, in the Bogdanovka beds and Chortkov horizon, Nikiforova et al. (1985: 38) preferred to defer the designation of a lectotype pending further studies. Siemiradzki illustrated what he called "normal type" or "gewöhnliche Form" (Siemiradzki 1906a, b: pl. VII: 3a-d), and two "varieties" (Siemiradzki 1906a, b: pl. VII: 4, 5); the lithographs are poor and do not constitute a faithful representation of the species. Still, it is among them that a lectotype has to be chosen. The specimen figured by Siemiradzki (1906a, b: pl. VII: 3a-d) is here formally designated the lectotype of the species. Siemiradzki's figures were duplicated by Erlanger (1994: pl. 7: 6a, b, v, g, 7, 8).

Fortunately, an abundant illustration of the Podolian species has been given by Kozłowski (1929: pl. 7: 1, 1a-d, 2-12, 13-22, 13a-22a, 23-26) under the incorrect identification *Camarotoechia* (*Wilsonia*) *tarda*; figures 1, 1a-d, according to Kozłowski, represent a "typical specimen".

Differences between *Lanceomyonia borealiformis* and *L. tarda*

The Bohemian species *Lanceomyonia tarda* (Barrande, 1847) differs from the Podolian species *L. borealiformis*. Kozłowski's (1929: 161, 164) opinion that the two species are synonyms, because their external and internal characters show a complete concordance ("concordance complete"), does not meet with general acceptance, although some authors followed Kozłowski's lead. It is not impossible that Kozłowski's opinion was influenced by the late Ludlow age – an age approaching the one of the Bohemian species *tarda* – he gave to the Podolian species; this age maintained itself in the literature a long time after him.

Havlíček (1961: 113) was the first to point out at differences between the two abundant species of similar (medium) size: in the Podolian species, the sulcus is narrower and always clearly pronounced ("eingetieft"), costae are stronger and higher, the number of costae in the sulcus is lower (2 to 3; 4 to 6 in *tarda*), the number of lateral costae is higher than the number of costae in the sulcus (this number is lower in *tarda*), the ventral muscle field is wider with the narrow adductor scars surrounded anteriorly by the diductor scars. Another important external difference not mentioned by Havlíček is that the costae of *borealiformis* start close to the beaks, what is never the case for the median costae of *tarda*, but exceptional for its lateral costae. Havlíček, who apparently had no Podolian specimen at his disposal for sectioning, did not mention the presence of a cardinal process in *borealiformis*.

Plodowski (1973: 69) described the internal characters of *borealiformis* and demonstrated that they were

different from those of *tarda*, e.g. length and shape of the dental plates that are not free, but obscured by apical callus, wider ventral muscle field, high septum, absence of a connectivum, and long crura, rounded to oval in section and sharply recurved ventrally at their distal ends.

Plodowski (1973: 68-69 as *Lanceomyonia tarda* and *L.*? *borealiformis*) did not stress the point that the presence of a cardinal process in *borealiformis* was one element that made it different from *tarda*. He preferred to speak of a "septalium that is largely filled out with secondary material" for *L.*? *borealiformis*, and a "septalium that is generally open, but may be also be partially filled out with secondary shell material" for *L. tarda*.

It means that the presence or absence of this major internal feature has been overlooked or underestimated. Serial transverse sections made by Kozłowski (1929: figs 43B, 51) from a specimen of *borealiformis*, erroneously identified as *Camarotoechia* (*Wilsonia*) *tarda*, duplicated by Nikiforova (1937: fig. 15), do not show a cardinal process, although the "narrow gutter of the septalium, sometimes closed anteriorly by the bringing together of its borders" ("étroite gouttière du septalium, fermée parfois vers l'avant par le rapprochement de ses bords") mentioned by him on page 162 and clearly seen on his figure 51, allow to suspect that a cardinal process was indeed present. [Remark: Kozłowski's serial transverse sections show dental plates that are not (completely) embedded in the callus, but he explained (Kozłowski 1929: 161) that the dental plates were very short, and often almost completely welded into the wall of the shell].

Erlanger (1994: fig. 30), who studied the specimens of the type series of *borealiformis* housed in the State Natural History Museum of the National Academy of Sciences of Ukraine in Lviv (originally Muzeum Dzieduszyckich), made good serial transverse sections from a topotype of the Siemiradzki collection at her disposal. These sections show clearly a cardinal process that she considered (Erlanger, 1994: 99, 107) one of the four differences between *borealiformis* and *tarda.*

Range and distribution of *Lanceomyonia borealiformis*

Lanceomyonia borealiformis is understood as the Podolian species present in the three subdivisions of the Lower and Middle (lower part) Lochkovian Borshchov beds (= Borshchkov horizon, Borshchovian stage) composed from base to top of the Tajna, Mitkov, and Bogdanovka beds. The species has sometimes been mentioned in the lower part of the overlying Middle (upper part) Lochkovian Chortkov beds (= Chortkov horizon, Chortkov Formation, Chortkovian stage), e.g. by Nikiforova (1937: 9, table, as *Lanceomyonia tarda*), Havlíček (1961: 114), Tyazheva in Tyazheva et al. (1976: 22), and Breivel', I. A. and Breivel', M. G. in Breivel', M. G. et al. (1977: 80). These mentions have to be accepted with reservation, because, according to Kozłowski (1929: 165), the species is rare in the Chortkovian stage in which it presents "some modifications", may be a variety or a mutation, of the "type species".

Lanceomyonia borealiformis has been ably described by Kozłowski (1929: 161-165, fig. 45, pl. 7: 1, 1a-d, 2-12, 13-22, 13a-22a, 23-26), unfortunately under the erroneous name *Camarotoechia* (*Wilsonia*) *tarda*; Plodowski (1973: 68, 69, figs 2, 3) added a more detailed description of the internal characters, illustrated by accurate serial transverse sections.

Lanceomyonia borealiformis is present in Ukraine and probably in Belarus. Otherwise, the species has been commonly and mistakenly identified in Ludlow, Lochkovian, and Pragian (chiefly Lower Lochkovian) deposits of the following countries and regions of Europe, Africa, and Asia. In Western Europe, it was identified in Austria (Carnic Alps), Bohemia, Estonia (borings), France (Armorican Massif), Poland (borings), Spain (Guadaramma; Iberian Chains) and Sweden (Gotland); in Russia, in the Altai-Sayan Mountains, Arctic region (Taymyr), Eastern Siberia (North-East), Russian Platform, Ural Mountains and Western Siberia (Kuznetsk Basin, Salair Mountains); in North Africa, in Algeria (Ougarta Mountains, western Sahara), Mauritania (Zemmour) and Morocco (Anti-Atlas, Tindouf Basin); in Central Asia, in Tadzhikistan, Tyan'-Shan Mountains, Turkestan and Uzbekistan (Fergana valley); in China, in Inner Mongolia and West Qinling Mountains (northwestern Sichuan; southeastern Gansu Provinces). (Remark: some of the countries are mentioned in the text.)

Figure $2A_{1-3}$ shows a specimen of *Lanceomyonia tarda* from Bohemia. Photographs of more specimens may be found in Havlíček (1961: pl. 14: 1-7); the best ones are in Havlíček in Havlíček & Štorch (1990: pl. 44: 8, 9, 10a-c, 11a-d). Good serial transverse sections from one topotype were produced by Plodowski (1973: fig. 1); three of them are here reproduced on Fig. $2B_{1-3}$.

Figure $3A_{1-3}$ shows a specimen of *Ktenopotamorhynchus borealiformis* from Podolia. Photographs of more specimens may be found in Kozłowski [1929: pl. 7: 1, 1a-d, 2-12, 13-22, 13a-22a, 23-26, as *Camarotoechia* (*Wilsonia*) *tarda*], and in Balinski (2012: fig. 12: F1-F5, G1-G5, H1-H5). Good serial transverse sections from topotypes were produced by Plodowski (1973: textfigs 2, 3), and by Erlanger (1994: fig. 30, pl. 16: 1-3); three of Erlanger's sections are here reproduced on Fig. $3B_{1-3}$. Kozłowski [1929: figs 43B, 51, as *C.* (*Wilsonia*) *tarda*] has also drawn serial transverse sections from two topotypes. His figure 51, duplicated by Nikiforova (1937: fig. 15 as *Wilsonia tarda*), shows dental plates detached from the wall of the shell, contrary to

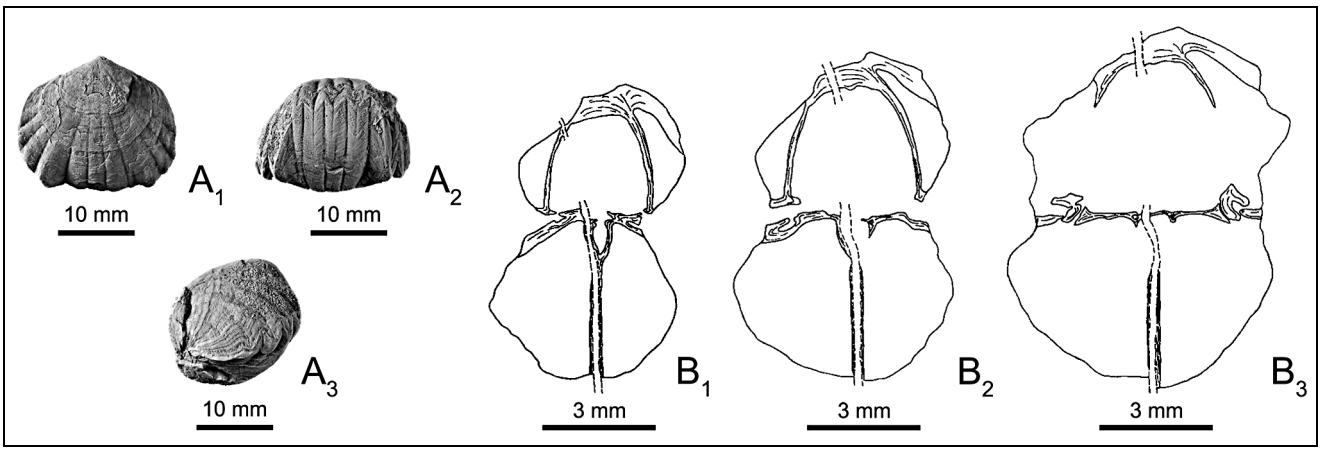

Fig. 2 - External and internal characters of *Lanceomyonia tarda* (Barrande, 1847).
A) IRScNBa 12924, topotype; Czech Republic, Bohemia, Zadní Kopanina, Upper Silurian, Přídolí Limestone; ventral (A_1), anterior (A_2) and lateral (A_3) views.
B) From Plodowski (1973); topotype; Czech Republic, Bohemia, Dvorce, Upper Silurian, Přídolí Limestone; serial transverse sections: Plodowski (1973, fig. 1, section 1.15) (B_1), Plodowski (1973, fig. 1, section 1.45) (B_2), Plodowski (1973, fig. 1, section 1.95) (B_3).

what can be seen on Plodowski's sections. Kozłowski himself noted (1929: 161-162) that the "dental plates are often almost welded into the lateral walls"; his figure 43B shows the relation between the septalium, septum and hinge plate.

Assignment of *Lanceomyonia borealiformis* to a new genus

Taking all differences into account, Plodowski (1973: 68, 69) questioned the assignment of *borealiformis* to the genus *Lanceomyonia* in describing the species under the name *L.*? *borealiformis*, and suggested that "generic consequences" should even be drawn from such differences. The present author agrees with such a suggestion, and proposes to consider *L. borealiformis* as the type species of *Ktenopotamorhynchus* gen. n. described below. Erlanger (1994: 107) considered as "evident" that *borealiformis* belonged to a new genus, but did not describe it.

Some of the differences between the genera *Lanceomyonia* and *Ktenopotamorhynchus* gen. n. being related to major components of the inner structure, a new family with type genus *Ktenopotamorhynchus* gen. n. is proposed and described below.

Revised diagnosis of the genus *Lanceomyonia*

The following elements have to be introduced in a revised diagnosis of the genus *Lanceomyonia*: sulcus, fold and costae starting in front of the umbonal regions (lateral costae occasionally starting close to the beaks); absence of a *paries geniculatus*; well developed *lunulae*; presence of a connectivum; undivided hinge plate; absence of a cardinal process; well impressed ventral muscle field.

These features, as well as other characteristics of the genus, are included in the diagnosis of Lanceomyoniidae fam. nov.

Proposal of new taxa

Lanceomyoniidae fam. n.

(*italics* indicate differences from the Ktenopotamorhynchidae fam. n.)

Diagnosis: Shell of medium size, strongly dorsibiconvex, thickest posterior to anterior margin. *Outline subcircular to subpentagonal.* Hinge line very short. Commissure moderately, but clearly serrate. Apical angle variable. Well defined sulcus, fold, and tongue; very shallow sulcus and very low fold, *developed anteriorly to the umbonal regions*; *sulcus wide at front*. Tongue high with trapezoidal to subrectangular outline. *Paries geniculatus* absent (dorsal flanks sloping abruptly, tending to become vertical near the commissure). Well developed ventral and dorsal *lunulae*. Absence of *squamae* and *glottae*. Length and thickness close to each other. Costae low, broad, angular with rounded top to rounded, *start anteriorly to the umbonal regions that are smooth*; occasionally a divided or an intercalated or an adventitious or a narrower median costa present; number of median and *lateral* costae low. Parietal costae absent. Long marginal spine-like projections of costae with accommodating grooves. *Dental plates distinct, short, thin and ventrally convergent. Septum high, thin, lamellar.* Septalium deep, *narrow, amphora-shaped, covered with a connectivum. Hinge plate thin, undivided.* Well marked crural bases. Crura *short*, closely set, raduliform, *slightly curved ventrally at their distal ends. Cardinal process absent. Ventral muscle field narrow, elongate, well impressed.*

Ktenopotamorhynchidae fam. n.

Type genus: *Ktenopotamorhynchus* gen. n.

Diagnosis: Shell of medium size, strongly dorsibiconvex, thickest posterior to front. Outline longitudinally suboval to circular. Hinge line very narrow. Commissure moderately, but clearly serrate. Apical angle variable. Well defined sulcus, fold, and tongue; very shallow sul-

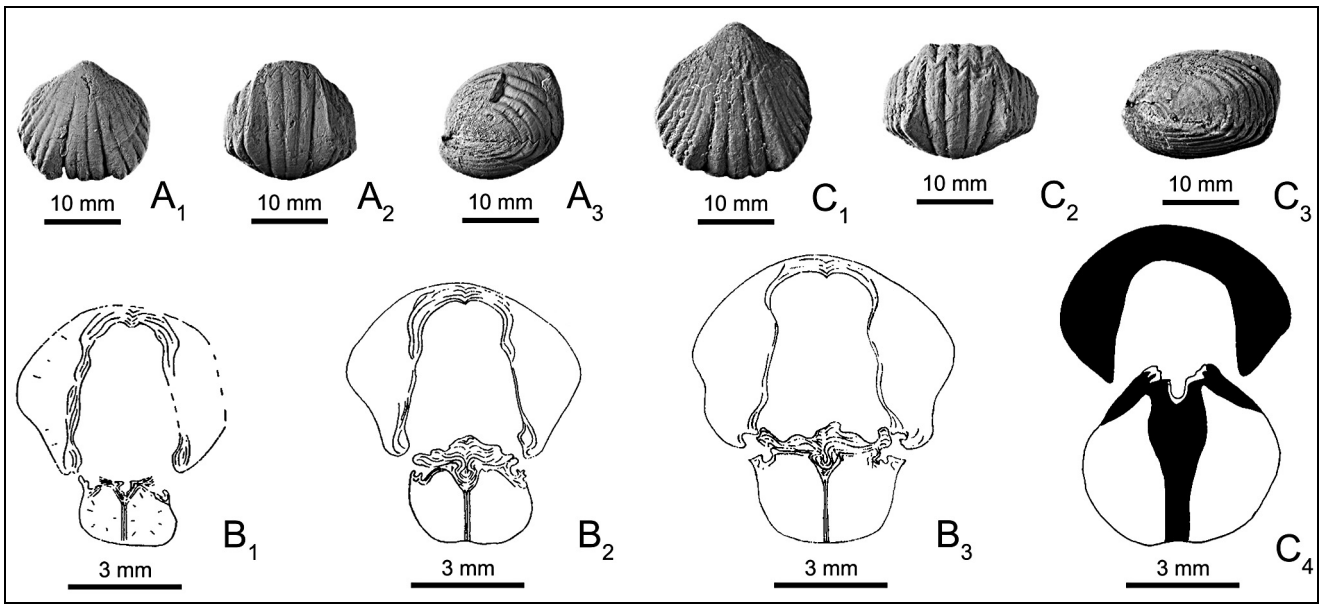

Fig. 3 - External and internal characters of the species attributed to *Ktenopotamorhynchus* gen. n. A-B. *Ktenopotamorhynchus borealiformis* (Siemiradzki, 1906a, b).
A) IRScNBa 12925, topotype; Ukraine, Volhynia, area of Ternopol', Lanovtsy; Lower Devonian, Lochkovian, Borshchov horizon; ventral (A_1), anterior (A_2) and lateral (A_3) views.
B) From Erlanger (1994) (as *Lanceomyonia borealiformis*); Ukraine, Podolia, left bank of the Dniester River, above the road between the villages Ust'e and Mitkovo; Lower Devonian, Lochkovian, Borshchov horizon; serial transverse sections: Erlanger (1994: fig. 30, section 6) (B_1), Erlanger (1994: fig. 30, section 7) (B_2), Erlanger (1994: fig. 30, section 8) (B_3).
C) *Ktenopotamorhynchus alter* (Barrande, 1879), IRScNBa 12927, topotype; Czech Republic, Bohemia, Svatý Jan, Lower Devonian, Lochkovian, Kotýs Limestone; ventral (C_1), anterior (C_2) and lateral (C_3) views of the plaster cast, transverse section 1.8 mm forward of the ventral umbo (C_4).

cus and very low fold start on the umbones. Tongue high with trapezoidal to rectangular outline. Length and width subequal. Costae low, broad, rounded, starting close to the beaks, occasionally a divided costa, or an intercalated costa, or an adventitious costa, or a narrower median costa present; median costae wider than lateral costae; number of median costae low; number of lateral costae moderately high. Parietal costae absent. Long marginal spine-like projections of costae with accommodating grooves. Dental plates absent (or obscured by callus?). Septum thick, lens-shaped in transverse section in its apical part. Septalium wide, relatively deep, uncovered (no connectivum). Hinge plate thick, divided. Well marked crural bases. Crura long, closely set, round to oval in section, strongly curved ventrally at their distal ends. Cardinal process made out of a thin veneer covering the walls of the septalium and the outer hinge plates. Ventral muscle field wide, oval, deeply impressed posteriorly.

Ktenopotamorhynchus gen. n.

Type species: *Rhynchonella borealiformis* Siemiradzki, 1906a

Etymology: Κτείς, κτενός (Greek, masculine) = comb; ποταμός, ού (Greek, masculine) = river; τὸ ρύγχος, (Greek, neuter) = beak. The name draws attention to the numerous collecting localities of the type species along a stretch of the Dniester River and some of its tributaries that are disposed in a comb-like pattern in southwestern Ukraine.

Diagnosis: Shell of medium size, strongly dorsibiconvex. Outline longitudinally suboval to circular. Costae low, rounded, starting close to the beaks; median costae few; lateral costae finer and more numerous. Dental plates absent (or obscured by callus?). Septalium uncovered. Hinge plate divided. Cardinal process with undulated top, covering septalium and outer hinge plates.

Species assigned to the genus: Besides the type species, another species assigned to the genus *Plethorhyncha* Hall & Clarke, 1893 by Havlíček (1961: 129-130), *P. altera* (Barrande, 1879), that has all the external characters of the new genus (but generally slightly larger) belongs to it. Photographs of four specimens of this rare species from the Kotýs Limestone (Lochkovian) of Bohemia have been given by Havlíček (1961: pl. XV, figs 4-7). Figure $3C_{1-3}$ shows the only specimen of the species at the author's disposal. Transverse serial sections were made from this specimen, but its matrix did not allow pursuing the grinding beyond the eleventh section represented on Fig. $3C_4$. This section, like the six sections given by Havlíček (1961: fig. 50), shows the absence of dental plates, and a cardinal process consisting of a thin veneer spread over the hinge plate.

Transverse serial sections made by Plodowski (1973: figs 2, 3) from two topotypes of *Lanceomyonia*? *borealiformis* show a similar (fig. 3) and a slightly thicker (fig. 2) cardinal process, but those made by Erlanger (1994; see Fig. $3B_{1-3}$) from another topotype of *L. borealiformis* indicate that the cardinal process may also be thick and variable.

Internal and external characters of the two Lochkovian species, *Ktenopotamorhynchus borealiformis* from Podolia and *K. alter* from Bohemia, are similar, but the latter is larger and possesses a simpler cardinal process. It is therefore suggested that *K. alter* could be a geographic counterpart of *K. borealiformis*.

Type locality, type horizon: The species has been found in abundance in the Borshchov horizon (= lower of the three horizons recognized in the Lower and Middle Lochkovian Tiver superhorizon) in many localities along the Dnieper and its tributaries in Podolia (southwestern Ukraine). Filipkowce is the first locality mentioned by Siemiradzki (1906a: 172; 1906b: 259) in a long list of localities.

Description. Shell of medium size, strongly dorsibiconvex, developing occasionally a *paries geniculatus*. Outline longitudinally suboval to circular. No *squamae* and *glottae* developed. Hinge line very short. Ventral beak slightly incurved, applied on the dorsal umbo. Commissure moderately, but clearly, serrate; anterior commissure (= crest of tongue) located generally lower than the maximum shell thickness. Very shallow sulcus and very low fold, well-marked, starting in the umbonal regions. Bottom of sulcus slightly convex. Tongue high, clearly delimited, with trapezoidal to rectangular outline; top of fold flat. Apical angle variable, usually 110° to 120°. Maximum width located around mid-length or anterior to it. Maximum thickness located posterior, sometimes considerably, to anterior margin; from this point the valve slopes very gently towards the front. Costae well marked, low, rounded, starting near the beaks; median costae sometimes wider (1½ to 2½ times, exceptionally more) than lateral costae; occasionally a divided or intercalated or adventitious median costa; occasionally also a median costa, narrower than the others; number of median and lateral costae: 3 to 5, and 8 to 13 (including those on the *lunulae*), respectively; parietal costae absent; median furrows fine. Long marginal spine-like projections of costae with accommodating grooves in the ventral median and dorsal lateral costae. Dental plates not present (or obscured by callus?). Septum thick, lens-shaped posteriorly, may reach half-length of valve. Septalium narrow, relatively deep, uncovered (no connectivum). Hinge plate divided, moderately thick to thick. Crural bases well marked. Crura long, round to oval in section, closely set, strongly curved ventrally at their distal ends. Cardinal process more or less thick with undulated top, filling in the septalium and covering the outer hinge plates, and even the dental sockets. Ventral muscle field wide, deeply impressed posteriorly, with a median myophragm.

Discussion. *Ktenopotamorhynchus* gen. n. and the genus *Lanceomyonia* have many external characters in common, e.g. medium size, strongly dorsibiconvex shape, narrow hinge line, occasional presence of a *paries geniculatus*, absence of *squamae* and *glottae*, slightly incurved ventral beak applied on the dorsal umbo, moderately but clearly serrated commissure, very shallow sulcus, very low fold, high trapezoidal to rectangular tongue, maximum thickness posterior to front margin, length and width subequal, low costae with occasionally a divided costa, or an intercalated costa, or an adventitious costa, or a median costa narrower than the others, long marginal spine-like projections of costae with accommodating median grooves, absence of parietal costae, deep septalium, well marked crural bases, closely set crura.

External and internal differences between the two genera are also numerous. Attention on some of them has already been drawn by Havlíček (1961: 113) and Plodowski (1973: 68) in their comparisons between *L. tarda* and *borealiformis*. *Ktenopotamorhynchus* gen. n. differs from *Lanceomyonia* by a longitudinally suboval to circular outline (subcircular to subpentagonal in *Lanceomyonia*), sulcus and fold starting on the umbones, narrower sulcus at front, generally smaller apical angle, narrower costae starting near the beaks, generally lower number of rounded (flat-rounded in *Lanceomyonia*) median costae being wider than the lateral costae, higher number of lateral costae, dental plates absent (or obscured by callus?), septum thick, lens-shaped posteriorly, septalium wide, cupula-shaped and uncovered (no connectivum), thick divided hinge plate, long crura, rounded to oval in section, strongly incurved ventrally at their distal ends, presence of a cardinal process, wide, oval and deeply impressed ventral muscle field.

The genera *Bortegitoechia* Erlanger, 1994, with type species *B. tsogtella* Erlanger, 1994 from the Lochkovian of Tsogt-Obo (Borteg Massif, eastern Gobi Desert, Mongolia) and *Ktenopotamorhynchus* gen. n. have many characters in common, e.g. size, dorsibiconvex lateral profile, anterior commissure uniplicate (= crest of tongue) located lower than the maximum shell thickness, very shallow sulcus and very low fold, maximum thickness located posterior to front margin, costae flat-rounded, separated by fine furrows, starting at or very close to the beaks, one-two divided or intercalated median costae occasionally present, dental plates absent or welded into the wall of the shell, strongly curved crura.

Bortegitoechia differs from *Ktenopotamorhynchus* gen. n. by an elliptical to rounded-pentagonal outline, wider sulcus, lower and wider tongue, generally higher number of median costae (5 to 7 in *tsogtella*; 3 to 5 in *borealiformis*), generally lower number of lateral costae (7 to 9 in *tsogtella*; 8 to 13 in *borealiformis*), wider apical angle, absence of marginal spine-like projections of costae, covered septalium, bilobate cardinal process. *Bortegitoechia*, placed by Savage (1996, textfig. 3; 2002: 1056) in the subfamily Trigonirhynchiinae Schmidt, 1965, in the present author's opinion does not belong to the family Trigonirhynchiidae Schmidt, 1965, and can be easily separated from it by round-pentagonal outline, medium size, wide, flat-rounded costae separated by fine furrows, occurrence of divided and intercalated median costae, dental plates welded into the wall of the shell, U-shaped septalium and by presence of a wide bilobed cardinal process.

The genus *Hebetoechia* can easily be separated from *Ktenopotamorhynchus* gen. n. by its smaller size, generally higher number of median costae starting close to the beaks, well developed cardinal process characteristically split into two parts, presence of dental plates, and wider delthyrial cavities.

Eucharitinidae fam. n.

Type genus: *Eucharitina* Schmidt, 1955

Diagnosis: Shell of medium to large size, strongly dorsibiconvex, convexoconcave. Outline longitudinally oval to cordiform. No true *paries geniculatus*; steep dorsal and flattened ventral flanks (slightly convex posteriorly, flat to slightly concave anteriorly), separated from the well-developed *lunulae* by a smooth ridge (sometimes even absent) and a sharp edge, respectively. Sulcus wide, shallow, starting imperceptibly at a short distance from beak and excavating a major part of the valve at front. Fold low. Tongue high, square to longitudinally or transversely rectangular. Maximum thickness at front. Costae low, simple, rounded to angular with rounded top, starting from beaks, but almost obliterated in the umbonal regions; number of median costae low to moderate [5 to 7 for *Eucharitina eucharis*; 2 to 7 for *E. oehlerti* (Bayle, 1878)]; number of lateral costae moderate (6 to 9 for *E. eucharis*); spine-like projections of costae edges. Shell thick posteriorly. Dental plates short, reduced or rudimentary. Ventral muscle field large, deeply impressed, oval, bounded by a marked rim. Septalium short, narrow, deep, V-shaped. Septum high. Hinge plate divided. Cardinal process overlapping the hinge plate, marked by two to four spine-like projections at its top. Crura long, slender, closely set.

Discussion. Schmidt (1955: 121), when she established the genus *Eucharitina*, had only a decorticated ("beschaltes") specimen of the Bohemian type species, *E. eucharis* (Barrande, 1847), from the Pragian (Koněprusy Limestone) at her disposal. Consequently, she relied on Barrande's description and figures. Schmidt did not assign the genus to a family. Thereafter the genus was included in three different families: in Uncinulidae by Rzhonsnitskaya (1956: 125, and subsequent publications), together, questionably, with the genus *Plethorhyncha*, and by Savage (1996: fig. 4; 2002: 1092, 1095), together with *Plethorhyncha*; in Hebetoechiidae by Havlíček (1961: 111, 132, and subsequent publications), together with *Plethorhyncha*, Drot (1964: 27, 123), and Brice in Brice et al. (2000: fig. 1); and in Eatoniidae Schmidt, 1965 by Schmidt in Schmidt & McLaren (1965: *H*571-572), Hamada (1971: 68), and Zhang et al. (1983: 319).

These various conceptions can be paralleled with the inconsistency of the definition of these families. [Remark: Westbroek (1967: 63) has already pointed out that the systematic position of *Eucharitina eucharis* was uncertain].

On account of the heterogeneous contents of the families Eatoniidae and Hebetoechiidae, comparison with the new family will have to be a comparison between type genera (*Eucharitina*, *Eatonia*, and *Hebetoechia*).

Although the families Eucharitinidae and Uncinulidae have few characters in common, they are compared, because the genus *Eucharitina* has been included in the family Uncinulidae soon after it was established and later by some authors.

The families Eatoniidae and Eucharitinidae fam. n. have some characters in common, e.g. strongly dorsibiconvex and convexoconcave shell, absence of a *paries geniculatus*, maximum thickness at front, simple costae, rounded to angular with rounded top, similar number of lateral costae, divided hinge plate, presence of a cardinal process.

Eatoniidae differ from Eucharitinidae fam. nov. by many features: generally smaller size, transversely oval to subcircular outline (longitudinally oval to cordate in *Eucharitina*), absence of *lunulae*, sharp sticking out commissure, narrower and deeper sulcus, higher fold, relatively higher trapezoidal to ogival tongue, slightly higher costae not obliterated in the umbonal regions, more constant number of median costae [3 to 4 for the type species *Eatonia medialis* (Vanuxem, 1842)], dental plates cemented to wall or slightly detached, larger ventral muscle field, lower septum, very large cardinal process with top marked by two slot-like depressions, short crura with flattened tips.

The families Hebetoechiidae and Eucharitinidae fam. n. have the following characters in common: strongly dorsibiconvex shell, absence of a true *paries geniculatus*, commissure not sticking out, shallow sulcus and low fold, costae simple, rounded to angular with rounded top, almost obliterated in the umbonal regions, moderate number of lateral costae, small septalium, divided hinge plate.

Hebetoechiidae differ from Eucharitinidae fam. n. by considerably smaller size, non convexoconcave shell, rounded outline, absence of *lunulae*, narrow sulcus, lower and always trapezoidal tongue, maximum thickness generally located posterior to anterior margin, lower costae, more constant number of median costae (3 to 6 for the type species, *Hebetoechia hebe*), well developed dental plates, small, narrow and slightly impressed ventral muscle field, simple, stocky, bilobed cardinal process.

The families Uncinulidae and Eucharitinidae fam. n. have few characters in common, e.g. a dorsibiconvex shell, deeply impressed ventral muscle field, small septalium, divided hinge plate.

Uncinulidae differ from Eucharitinidae fam. n. by many characters: completely different shape (shell globular and not convexoconcave), usually smaller size, well developed *paries geniculatus*, subcircular to transversely or longitudinally suboval outline, higher convex ventral valve, weaker *lunulae*, slightly convex to vertical front, narrow and extremely shallow sulcus, extremely low fold (sometimes almost wanting), maximum thickness posterior to front, tongue without relief, almost blending with the *paries geniculatus* and never transversely rectangular, crest of tongue located considerably lower than the highest point of shell, costae lower, rounded, not obliterated in the umbonal regions, with edges modified into long and slender spine-like projections, parietal costae present, substantially higher number of cost-

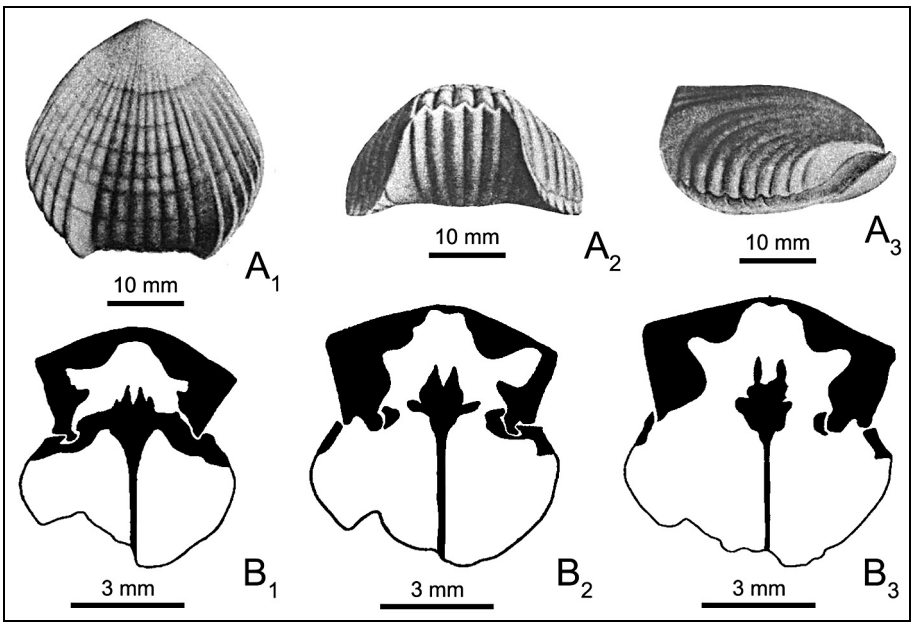

Fig. 4 - External and internal characters of *Eucharitina eucharis* (Barrande, 1847).
A) Holotype, SBNM-ČF-281; Czech Republic, Bohemia, Koněprusy; Lower Devonian, Pragian, Koněprusy Limestone; from Schmidt in Schmidt & McLaren (1965, fig. 447: 6a, c, d); ventral (A_1), anterior (A_2) and lateral (A_3) views.
B) IRScNBa 12926, topotype; Czech Republic, Bohemia, Koněprusy; Lower Devonian, Pragian, Koněprusy Limestone; transverse serial sections: 2.6 mm (B_1), 3.3 mm (B_2) and 3.8 mm (B_3) forward of the ventral umbo.

ae with some divisions and intercalations, shell thicker in the umbonal regions, dental plates residual or absent, very different l/w, t/w, and t/l values on account of width, length and thickness being subequal, stronger septum, stout crural bases and crura, and broad, stocky cardinal process covered by many lamellae at its top.

Figure 4A_{1-3} shows the holotype of *Eucharitina eucharis* from Bohemia. Photographs of more specimens may be found in Havlíček (1961: pl. 18: 1-6). Serial transverse sections have been published by Havlíček (1961: figs 51a-e, 52); Havlíček's figure 51 was duplicated by Schmidt in Schmidt & McLaren (1965: H573, fig. 447: 6e-i), and by Savage (2002: 1094, textfig. 740: 1e-i). Fig. 4B_{1-3} shows three sections made from a topotype.

Conclusions

The need of establishing new families and subfamilies for better organizing or/and consolidating the classification of various groups of fossil brachiopods, notably of the order Rhynchonellida Kuhn, 1949 examined in this paper, has become progressively evident. It has been exemplified by Baranov (1977: 79-80; 1980: 78; 1982: 41-42, 44, 47; 1991: 38; 1996: 107), who proposed eight new families and subfamilies, and especially by Savage (1996: 249, 251-257; 2002: 1041-1199, 1230-1235), who, as responsible for the Palaeozoic rhynchonellid brachiopods of the revised edition of the Treatise on Invertebrate Paleontology, Part H, Brachiopods, introduced thirty new families and subfamilies. The present author himself established fifteen families, including the three new families here described, within the last eighteen years.

If the long-established and recently introduced families and subfamilies give more consistency and reliability to the order, the number of genera attributed to them is commonly unduly inflated to the point that they have to be limited to their type genera.

This is partly due to the restriction of generic diagnoses to a small number of characters, some of them alternative. This insufficiency and lack of clarity open the door to more than one interpretation, and explain the inflation of the number of species in some genera. The erroneous assignment of various species to a given genus dilutes its identity and modifies its understanding, not to mention the arbitrary range and correlation it becomes subject to. It explains also the common transfer(s) of some genera from one family or subfamily to another family or subfamily that gives rise to suspicion and disbelief affecting the whole classification.

It is generally accepted that a diagnosis should be short. This is not justified, because the complexity of nature goes beyond what human eyes and memories are ready to easily accept.

Sartenaer (1987: 145) has explicitly expressed what he kept advocating for a long time, i.e. that attention should be focused on all characters of a genus: "when a new genus is described, its definition is made out of a set of internal and external characters, none of which, considered separately, can be, at the outset, considered as generic... it is therefore difficult and dangerous to decree that some characters are "relatively minor" or "inconsequential", while others are "important" or "real", while still others are "omitted".

Note of the editorial committee

Very sadly Paul Sartenaer passed away on July, 2015, after having completed the revision of this manu-

script. Paul was a famous palaeontologist, who devoted all his long life to the study of Palaeozoic brachiopods at the Royal Belgian Institute of Natural Sciences. His very serious and detailed research made substantial improvements to the knowledge of Palaeozoic brachiopods, of Rhynchonellida in particular. His contribution to geology and palaeontology will be valuable even for future generations of paleontologists.

Acknowledgements. The author is grateful for the opportunity he had to examine collections crucial for writing the paper: Havlíček collection at the National Museum (Národní Muzeum) and Central Geological Survey (Ústředni Ústav Geologický), Prague, and at the Rokycany Museum, Rokycany; Kozowski collection at the Museum of the Earth (Muzeum Ziemi), Warsaw; Plodowski collection at Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main; Baranov collection at the Institute of Diamond and Precious Metals Geology, Yakutsk Research Center, Russian Academy of Sciences, Siberian Division, Yakutsk, Sakha Republic (Yakutia); and Binnekamp collection at the National Museum of Natural History (Naturalis), Leiden.

Permission to study large collections in their care, granted by the following colleagues, is deeply appreciated: Dr Sarah Long (British Museum of Natural History, London), Dr Olga A. Erlanger (Palaeontological Institute, Russian Academy of Sciences, Moscow), Dr Ulrich Jansen (Senckenberg Forschungsinstitut und Naturuseum, Frankfurt am Main), Dr Cor F. Winkler-Prins (Naturalis, Leiden), and Dr N. M. Kadlets (TSNIGRI-Museum, Sankt-Petersburg).

Specimens of most species from Bohemia, Ukraine, Yakutia, Mongolia, and the Central Carnic Alps were presented to the author by the late Dr Vladimir Havlíček, Drs P. D. Tsegel'nyuk, Valeriy V. Baranov, Olga A. Erlanger, and Gerhard Plodowski, respectively. These colleagues and friends also allowed plaster casts to be made from primary types of various species. This paper could not have been written without their generous and invaluable help.

The author is particularly thankful to Dr. Fernando Alvarez (Departamento de Geología, Universidad de Oviedo) and Dr. Ulrich Jansen for critically reviewing the manuscript and providing helpful comments.

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