REVISION OF THE RHYNCHONELLID BRACHIOPOD GENUS RIPIDIORHYNCHUS SARTENAER

Paul SARTENAER

(1 plate, 5 figures, 2 tables)

Department of Palaeontology, Section of Invertebrate Fossils Belgian Royal Institute of Natural Sciences, Vautier street, 29, B-1000 Brussels, Belgium

ABSTRACT. Many species, subspecies and forms assigned to *Ripidiorhynchus* SARTENAER 1966 do not belong to it and give it an overextended published stratigraphic range of Givetian to Lower Carboniferous. Eight new genera are proposed: *Kedridorhynchus* [type species *K. cedarensis* (STAINBROOK 1942); late Givetian], *Poleomesorhynchus* [type species *P. gregeri* (BRANSON 1923); early Frasnian], *Hypselororhynchus* [type species *H. farsani* (BRICE 1977); middle-late Frasnian], *Porthmorhynchus* [type species *P. ferquensis* (GOSSELET 1887); middle-late Frasnian], *Paropamisorhynchus* [type species *P. kotalensis* (BRICE 1971); late Frasnian], *Saxulirostrum* [type species *S. saxatile* (HALL 1867); late Frasnian], *Piridiorhynchus* [type species *P. confinium* n. sp.; earliest Famennian], *Orophomesorhynchus* [type species *O. huotinus* (de VERNEUIL 1845); early Famennian]. Following revision of *Ripidiorhynchus* a new zone is introduced at the base of the Famennian based on *Piridiorhynchus confinium* in the southeastern and eastern parts of Dinant Basin. Some attention is also devoted to the alleged overlapping of the Frasnian/Famennian boundary by *Ripidiorhynchus*.

KEYWORDS: rhynchonellids, Ripidiorhynchus, Givetian, Frasnian, Famennian, world, systematics, stratigraphy.

RESUME. Ripidiorhynchus SARTENAER 1966 fait l'objet d'une révision rendue nécessaire par l'attribution au genre de nombreuses espèces, sous-espèces et formes n'y appartenant pas et qui lui confèrent une extension stratigraphique considérable (Givetien au Carbonifère Inférieur). En conséquence huit nouveaux genres sont fondés: Kedridorhynchus [espèce-type K. cedarensis (STAINBROOK 1942); Givetien supérieur], Poleomesorhynchus [espèce-type P. gregeri (BRANSON 1923); Frasnien inférieur], Hypselororhynchus [espèce-type H. farsani (BRICE 1977); Frasnien moyen-supérieur], Porthmorhynchus [espèce-type P. ferquensis (GOSSELET 1887); Frasnien moyen-supérieur], Paropamisorhynchus [espèce-type P. kotalensis (BRICE 1971); Frasnien supérieur], Saxulirostrum [espèce-type S. saxatile (HALL 1867); Frasnien supérieur], Piridiorhynchus [espèce-type P. confinium n. sp.; base du Famennien], Orophomesorhynchus [espèce-type O. huotinus (de VERNEUIL 1845); Famennien inférieur]. Un autre résultat du réexamen de Ripidiorhynchus est l'introduction d'une zone nouvelle basée sur Piridiorhynchus confinium à la base du Famennien dans les parties sud-orientale et orientale du Bassin de Dinant. Accessoirement quelques considérations sont émises à propos du prétendu chevauchement de la limite Frasnien/Famennien par le genre Ripidiorhynchus.

MOTS-CLES: rhynchonellides, Ripidiorhynchus, Givetien, Frasnien, Famennien, monde, systématique, stratigraphie.

1. Introduction

When establishing the genus *Ripidiorhynchus* SARTENAER 1966, the author assigned eleven species to it: six early Frasnian species from the Main Devonian Field [*R. aldoga* (NALIVKIN 1941), *R. biferus* (VENYUKOV 1886, *non* PHILLIPS 1841), *R. livonicus* (von BUCH 1834) the type species, *R. pskovensis* (NALIVKIN 1941), *R. strugi* (NALIVKIN 1941), and *R. tschudovi* (NALIVKIN 1941)]; three early Famennian species from the Central Devonian Field [*R. cernosemicus* (NALIVKIN 1934), *R. huotinus* (de VERNEUIL 1845),

and *R. zadonicus* (NALIVKIN 1934)]; one late Frasnian or early Famennian (most probably late Frasnian) species from the Alborz Mountains, Iran [*R. elburzensis* (GAETANI 1965)]; and one middle-upper Frasnian species from the Boulonnais, France [*R. ferquensis* (GOSSELET 1887)]. Two additional early Famennian species from the Central Devonian Field [*R.? brodicus* (NALIVKIN 1934)] and *R.? griasicus* (NALIVKIN 1934)] were considered as possible members of the genus, but because of the lack of material no firm decision was taken. The specific validity of the Russian species was not examined.

SARTENAER (1985, p.319, pp.321-324) gave the available stratigraphic information on the species of the genus known at that time but without considering their validity.

35 species, many erroneously, and about 25 other forms, in open nomenclature, are assigned to the genus from some 45 regions of the world. The high species content of Ripidiorhynchus, as well as its widespread geographical distribution, seems to indicate that the genus is reliable. The reverse is true for various reasons. Firstly, the general acceptance seems to be chiefly connected with exaggerated emphasis laid on two important external characters: the fan-shaped tongue (hence the name of the genus), and the presence of parietal costae. Secondly, the considerable stratigraphic range of the genus is surprising and therefore questionable. SARTENAER (1966, p.1, p.2, p.12) attributed an early Frasnian to early Famennian age to Ripidiorhynchus - even extended now to Givetian to Early Carboniferous in the literature -, but there rae allegedly no critical differences between the early Frasnian and early Famennian species of the genus. Failing to find a satisfactory explanation, he expressed reservations about such an extensive stratigraphic range; these reservations were repeated in 1985 (p.322, p.324). Finally, study of Ripidiorhynchus has reached recognition of the fourth stage (the breaking up) of the four stages SARTENAER (1986, pp.145-150) recognized in the evolution of the study of rhynchonellids.

In short, the 35 year old genus *Ripidiorhynchus* is in need of revision, because it has become unsatisfactory both systematically and stratigraphically, and this is the purpose of this paper, in which some species formerly assigned to *Ripidiorhynchus* are now placed in separate genera.

2. Piridiorhynchus n. gen.

SARTENAER (1970, p.350, p.353) indicated that what he identified as *Ripidiorhynchus* sp. was probably a new subgenus of *Ripidiorhynchus*. This form is designated as the type species of *Piridiorhynchus* n. gen.

Derivatio nominis: The name is formed by inversion of the first two syllables of *Ripidiorhynchus*.

Type species: Piridiorhynchus confinium n. gen., n. sp.

Species attributed to the genus: Besides the type species, another species from South Timan, *Ptychomaletoechia izhmaensis* YUDINA 1999 from the early Famennian of South Timan, is attributed; this species was described by YUDINA (1999, pp.16-17, figs.1-3).

Diagnosis: Medium-sized. Slightly transversely sub-elliptical. Well marked sulcus and fold, beginning at some distance from the beaks. Sulcus moderately deep. Fold moderately high. Tongue well defined, sub-trapezoidal. Top of tongue generally located lower than top of shell. Top of shell located in the anterior third of shell. Costae simple, moderate in number, beginning at the beaks. One parietal costa usually present on one or on both flanks of sulcus and fold. Short dental plates. Lamellar septum. Divided hinge plate. Short and shallow septalium. Crura rounded in their proximal part.

Description: Medium-sized. Uniplicate. Dorsibiconvex, brachial valve being much deeper than pedicle valve. Slightly transversely sub-elliptical. Sulcus and fold beginning at some distance from the beaks. Frontal and lateral commissures sharp and clearly indented by the cos-

1	Median costae	e		Parietal costae			Lateral costae			
number of costae	number of specimens	%	number of costae	number of specimens	%	number of costae	number of specimens	%		
3/2	4	14,3	0	4	18,2	4/5	1	3,4		
4/3	18	64,3	0-1/0-1 or	5	22,7	5/6	3	10,4		
5/4	5	17,8	1-0/1-0			6/7	8	27,6		
6/5	1	3,6	1-1/1-1	12	54,5	7/8	6	20,7		
			2-2/2-2	1	4,6	8/9	5	17,3		
						9/10	4	13,8		
						10/11	1	3,4		
						11/12	1	3,4		
-11 n s	28	100	Tradition	22	100	Series Dillere	29	100		

Table 1 - Piridiorhynchus confinium n. gen., n. sp. Number of median and lateral costae.

tae. Postero-lateral margins concave near commissure. Cardinal line short.

Flanks of pedicle valve very slightly convex. Ventral umbonal region without relief. Sulcus moderately deep, widening rapidly, wide at front, and clearly separated from flanks. Bottom of sulcus flat to slightly convex. Tongue high, sub-trapezoidal, and well defined. Upper part of tongue elongated anteriorly, tending to become vertical near the commissure. Top of tongue generally located lower than top of shell. Beak small, slightly incurved, not overhanging the hinge line. Interarea clearly separated from flanks. Length of interarea close to half the width of shell. Strong deltidial plates have been observed in serial transverse sections.

Brachial valve high. Dorsal umbonal region either vertical or slightly extended beyond the ventral umbonal region in the highest specimens. Flanks sloping sharply towards the lateral commissures. Fold moderately high. Top of valve generally located posterior to the frontal commissure.

Costae moderate in number, simple, regular, clearly marked. Median costae low to moderately high, moderately wide to wide, and angular with rounded top. Lateral costae often narrower and lower than median costae; exceptionally, this difference is observed on one flank only. Costae start at the beaks. Parietal costae commonly present.

Width is the greatest dimension. Maximum width of shell occurs at a point located somewhat anterior to mid-length. Maximum depth of pedicle valve located one guarter to one third anterior to the ventral beak. Maximum depth of brachial valve, and thus maximum thickness of shell, located in the anterior third of shell; from this point the valve slopes gently toward the front. Wide apical angle. Dental plates short, moderately thick. Umbonal cavities moderately wide. Teeth short, stout. Septum lamellar, slender to moderately thick, persisting for about one-third length of valve. Hinge plate divided, short. Outer hinge plates slightly convex. Septalium short, shallow to moderately deep, U- or V-shaped. Dental sockets wide. Crura diverging only slightly and progressively anteriorly. In serial transverse sections, crura are rounded in their proximal part, and progressively crescent- and Phrygian capshaped. Crura are ventrally curved at their distal end.

Comparisons: Piridiorhynchus and Ripidiorhynchus have many characters in common; a similar outline (strongly dorsibiconvex; transversely sub-elliptical); sulcus and fold well marked, and beginning at some distance from the beaks; sulcus widening and deepening rapidly towards the front; tongue high, sub-trapezoidal; top of shell located generally posterior to the frontal commissure; costae simple, regular, well marked, and starting at the beaks; strong deltidial plates; short dental plates, teeth, and septalium.

However *Piridiorhynchus* is distinct from *Ripidiorhynchus* in a larger size; pedicle valve not as

deeply excavated by the sulcus; fold and top of tongue never acuminate; smaller number of parietal costae (one in *Piridiorhynchus*, one to 4 in *Ripidiorhynchus*), and lateral (4 to 12, generally 6 to 10, in *Piridiorhynchus*, 5 to 16 in *Ripidiorhynchus*); costae wider; different proportions (t/l: 0.80 to 1.20, t/w: 0.67 to 0.88 for *Ripidiorhynchus*; t/l: 0.70 to 1.02, t/w: 0.58 to 0.80 for *Piridiorhynchus*); apical angle wider; dental plates stronger and shorter; septum not thickened in its posterior part; septalium shorter and not as deep with depth similar to width; connectivum absent; different shape of crura (rounded in their proximal part and progressively crescent- and Phrygian cap-shaped in *Piridiorhynchus*; crescent-shaped proximally and walking-stick-shaped distally in *Ripidiorhynchus*).

In spite of some resemblance, *Ptychomaletoechia* SARTENAER 1961 differs from *Piridiorhynchus* in many characters; the smaller size; top of brachial valve, and thus of shell, generally at front; tongue sub-rectangular with its upper part generally more or less recurved posteriorly; narrower sulcus at front (49 to 65 percent, most values between 49 to 57 percent of width of shell for *Ptychomaletoechia*; 62 to 71 percent for *Piridiorhynchus*); different proportions, more particularly similar values of thickness and length (t/l: 0.93 to 1.13, t/w: 0.74 to 0.90, l/w: 0.74 to 0.85 for *Ptychomaletoechia*; t/l: 0.70 to 1.02, t/w: 0.58 to 0.80, l/w: 0.76 to 0.89 for *Piridiorhynchus*); presence of a connectivum; different shape of crura (rounded proximally in *Ptychomaletoechia*)

Stratigraphic range and geographical distribution

Information on the Belgian species, *Piridiorhynchus confinium* is given below. *P. izhmaensis* is found, according to YUDINA (1999, pp.15-16 as *Ptychomaletoechia izhmaensis*; 2000, Abstract, as *P. izhmaensis*), in the lower part of the Izhma Formation on the right bank of the Izhma river near its junction with the Ukhta river, South Timan. An early Famennian age (*Palmatolepis triangularis* Zone) is assigned to the species.

3. Piridiorhynchus confinium n. gen., n. sp. (Plate 1, Figures 1-36; Text-figure 1)

? 1936 Terebratula subreniformis SCHNUR, J., 1851 - MAILLIEUX, p.24, pl.1, fig.3;

p.p.? 1970 *Ripidiorhynchus* sp. - SARTENAER, p.350, p.353, p.354, pl.1, pl.2;

1972 Ripidiorhynchus - BOUCKAERT et al., p.87;

? 1973 Ripidiorhynchus sp. - SARTENAER, p.5;

? 1974a les spécimens décrits et le spécimen figuré par E.MAILLIEUX sous *Terebratula subreniformis* sont des formes juvéniles d'une espèce du genre *Ripidiorhynchus* - SARTENAER, p.14;

? 1974b Ripidiorhynchus - SARTENAER, p.4; p.p.? 1977 Ripidiorhynchus - SARTENAER, p.74;

? 1983 Ripidiorhynchus - SARTENAER, fig.1, p.3; ? 1983 Ripidiorhynchus - SARTENAER in VANGUESTAINE et al., p.132, fig.3, p.133;

1984 Ripidiorhynchus sp. - SARTENAER in MARTIN, p.10, fig.11, p.41, p.44, p.45;

? 1988 Ripidiorhynchus - SARTENAER in BULTYNCK, fig.A 2/4, p.23;

1988a *Ripidiorhynchus* sp. - SARTENAER *in* SANDBERG *et al.*, p.68;

1988a Ripidiorhynchus - SARTENAER in SANDBERG et al., fig.A 8/1, p.69;

1988b Ripidiorhynchus - SARTENAER in SANDBERG et al., p.278;

? 1992 Ripidiorhynchus - SARTENAER in CASIER, p.111, table 1.

Derivatio nominis: *Confinium*, *ii* (Latin, substantive) = limit. The name, standing in apposition, draws attention to the position of the species in relation to the Frasnian/Famennian boundary.

Types

Holotype, IRScNB a11447 (Pl.1, Figs.1-5), paratypes A, IRScNB a11448, B, IRScNB a11449 (Pl.1, Figs.11-15), C, IRScNB a11450 (Pl.1, Figs.21-25), D, IRScNB a11451 (Pl.1, Figs.16-20), F, IRScNB a11453, J, IRScNB a11457 (Pl.1, Figs.31-33 and Text-fig.1). Northeastern flank of roadcut NW of the village of Sinsin along the road (N4) from Marche to Namur at the crossing with road N929 (Aye 1/20,000 topographic sheet), southeastern border of Dinant Basin, locality Aye 57. 25 to 55 cm below Bed 15 (see COEN, 1974, p.6), base of the Early *Palmatolepis triangularis* Zone (lowermost Famennian). Collector: P. SARTENAER, 1962.

Paratype E, IRScNB a11452 (Pl.1, Figs.6-10). Railroad cut S of the village of Hogne between km 107/9 and Km 108/4 along the railroad from Namur to Arlon (Aye 1/20,000 topographic sheet), southeastern border of Dinant Basin, locality Aye 24159. Between km 108/079 and km 108/085 on the northeastern flank of the railroad cut in the southern limb of a syncline, lowermost Famennian. Collector: P. SARTENAER, 1958.

Paratype G, IRScNB a11454 (Pl.1, Figs.26-30). Northeastern flank of roadcut half-distance between km 15 and km 16 along the road (N40) from Dinant to Neufchâteau (Houyet 1/20,000 topographic sheet), southeastern border of Dinant Basin, locality Houyet 25135. Between 30 and 40 cm below the base of the *Pampoecilorhynchus praenux* Zone, base of the Early *Palmatolepis triangularis* Zone (lowermost Famennian). Collector: P. SARTENAER, 1960.

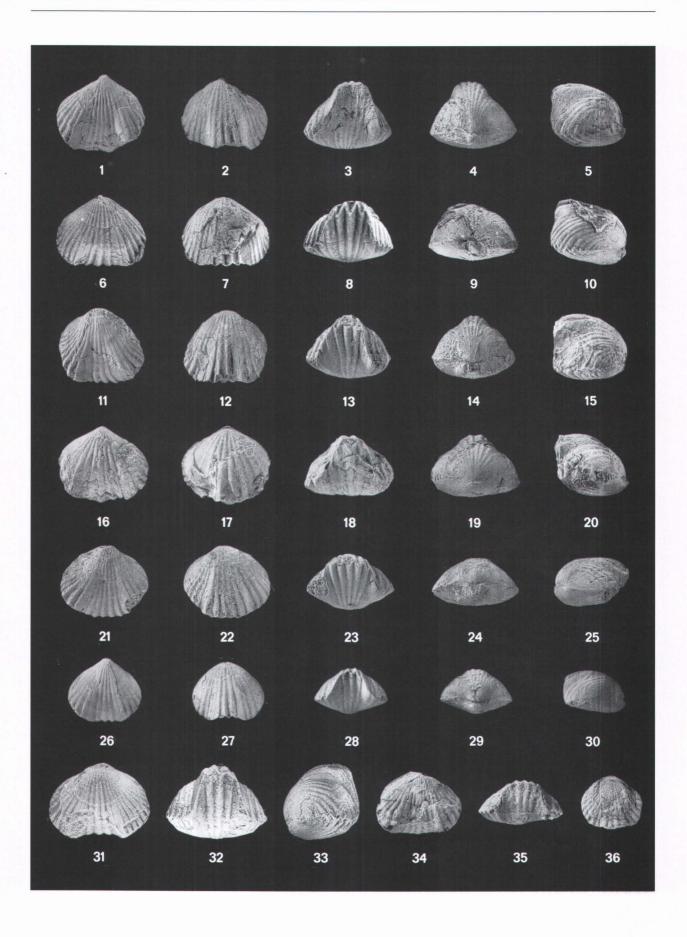
Paratypes H, IRScNB a11455 (Pl.1, Figs.34, 35), I, IRScNB a11456 (Pl.1, Fig.36). Railroad cut between the railroad station of Senzeilles and the northwestern wall of the tunnel of Senzeilles along the railroad from Charleroi to Vireux (Senzeilles 1/20,000 topographic sheet), Philippeville Massif, locality Senzeilles 6839b. This railroad cut, known in the literature under the name "tranchée de Senzeilles", does not now exist; it has been filled in to allow road construction. Uppermost part of the Matagne Formation, latest Frasnian. Collector: P.SARTENAER, 1967 and 1971.

Locus typicus: Northeastern flank of roadcut NW of the village of Sinsin along the road (N4) from Marche to Namur at the crossing with road N929 (Aye 1/20,000 topographic sheet), southeastern border of Dinant Basin, locality Aye 57.

Explanation of Plate 1

Piridiorhynchus confinium n. gen., n. sp. (all figures are natural size)

- Figs. 1-5. Holotype, IRScNB a11447. Ventral, dorsal, frontal, apical, and lateral views. Costal formula: 5/4; 1-1/1-1; 6/7.
- Figs. 6-10. Paratype E, IRScNB a11452. Ventral, dorsal, frontal, apical, and lateral views. Costal formula: 4/3; 2-?/2-2; ? and 11/12.
- Figs. 11-15. Paratype B, IRScNB a11449. Ventral, dorsal, frontal, apical, and lateral views. Costal formula: 4/3; 1-1/1-1; 7/8 and 9/10.
- Figs. 16-20. Paratype D, IRScNB a11451. Ventral, dorsal, frontal, apical, and lateral views. Costal formula: 4/3; 1-1/1-1; 8/9 and ?
- Figs. 21-25. Paratype C, IRScNB a11450. Ventral, dorsal, frontal, apical, and lateral views. Costal formula: 6/5; 0; 6/7 and 9/10.
- Figs. 26-30. Paratype G, IRScNB a11454. Ventral, dorsal, frontal, apical, and lateral views. Costal formula: 4/3; 1-1/1-1; 4/5.
- Figs. 31-33. Paratype J, IRScNB a11457. Ventral, frontal, and lateral views. Costal formula: 4/3; 1-1/1-1; 9/10 and 8/9. The specimen was photographed before grinding (see Text-fig.1).
- Figs. 34-35. Paratype H, IRScNB a11455. Ventral and frontal views. Costal formula: 5/4; ?-?/1-1; 6/7 and ?
- Fig. 36. Paratype I, IRScNB a11456. Dorsal view. Costal formula: 4/3; 0; 6/7.



196 PAUL SARTENAER

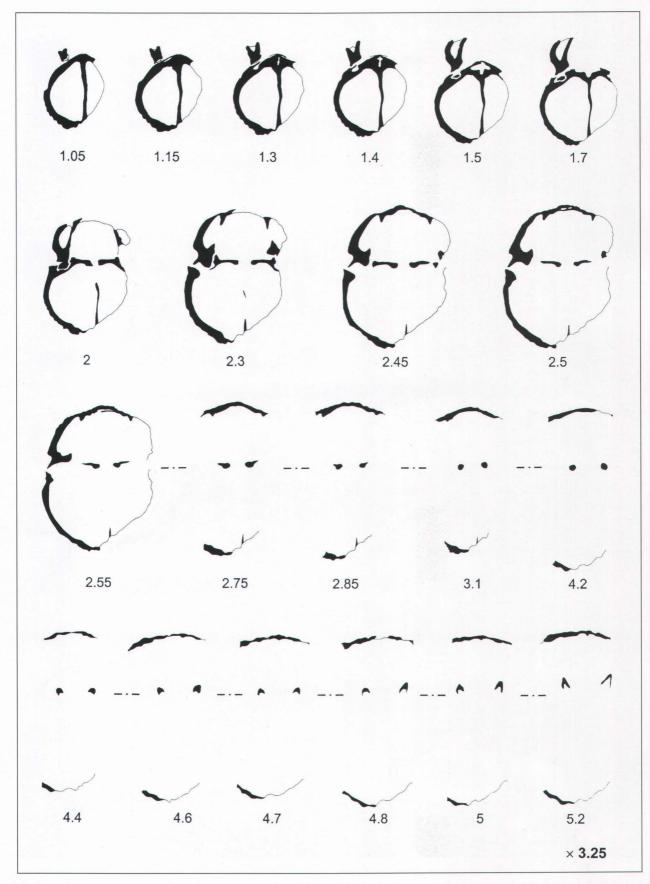


Figure 1 - *Piridiorhynchus confinium* n. gen., n. sp. Camera lucida drawings of serial transverse sections; figures are distances in mm forward of the ventral umbo. Paratype J, IRScNB a11457. Measurements: length = 22.1 mm; width = 28 mm; thickness = 21.2 mm. See also Pl.1, Figs.31-33.

	Paratype A	Paratype B	Paratype C	Paratype D	Holotype	Paratype E	Paratype F	Paratype G
in mm	a11448	a11449	a11450	a11451	A11447	a11452	a11453	a11454
1	22,2	(21)	20,3	19,4	19	18,9	16,7	16,6
W	27	23,7	24,6	25,1	24,4	23,7	22	20,4
lpv unrolled	34,5	(33)	27,5	(32)	32	30	29	24
t	19,2	17,6	14,3	18,5	19,4	16,6	17,3	12,3
tpv	7,1	6,5	6,1	4,9	5,9	5,5	5,5	4,2
tbv	12,1	11,1	8,2	13,6	13,5	11,1	11,8	8,1
1/w	0,82	(0.89)	0,83	0,77	0,78	0,80	0,76	0,81
t/w	0,71	0,74	0,58	0,74	0,80	0,70	0,79	0,60
t/1	0,86	(0.84)	0,70	0,95	1,02	0,88	1,03	0,74
apical angle	114°	?	122°	121°	116°	(116°)	121°	113°

Table 2 - *Piridiorhynchus confinium* n. gen., n. sp. Measurements (in mm) based on eight specimens; figures in parentheses are reasonable estimates on damaged specimens. Abbreviations used: l = length; w = width; t = thickness; pv = pedicle valve; bv = brachial valve.

Stratum typicum: 25 to 55 cm below Bed 15 (see COEN, 1974, p.6), base of the Early *Palmatolepis triangularis* Zone (lowermost Famennian).

Material: 113 specimens collected by the author in 1958 (8 sp., loc. Aye 24159, Aye 1/20,000 topographic sheet), 1960 (40 sp., loc. Houyet 25135, Houyet 1/20,000 topographic sheet), 1962 (24 sp., loc. Aye 57, Aye 1/20,000 topographic sheet), 1967 and 1971 (8 sp., loc. Senzeilles 6839b, Senzeilles 1/20,000 topographic sheet), 1968 (30 sp., loc. Houyet 25137, Houyet 1/20,000 topographic sheet), and 1973 (3 sp., loc. Esneux PS-73-10, Esneux 1/20,000 topographic sheet). Ten specimens are in good state of preservation, six satisfactory; 98 specimens are squashed or fragmental or both.

Description: This refers only to specific characters in need of further elaboration.

Sulcus beginning at 20 to 32 percent of shell length, most of the values varying between 23 and 29 percent, or from 18 to 27 percent of the unrolled valve length, most of the values varying between 18 and 23 percent. The sulcus reaches its greatest width (62 to 71 parcent of the shell width) at the junction of the frontal and lateral commissures.

The general costal formula, which is a grouping of at least 75 percent of the specimens in median, parietal, and lateral categories, is: 4 to 5/3 to 4; 0-1/0-1 (or 1-0/1-0) to 1-1/1-1; 6 to 9/7 to 10. In some specimens the number of costae can be different on both flanks (see Explanation of Plate). In five out of ten specimens parietal costae do not reach the commissure, while in the remaining five specimens the commissure is only slightly indented by them. An intercalated lateral costa was observed in one specimen. Width of median costae varies between 2 and 3 mm at the front.

Measurements of eight specimens, of which six have been photographed, are given on table 2. Columns 1 to 6 refer to adult specimens, columns 7 and 8 to ephebic specimens. Maximum width occurs at a point between 52 and 67 percent (most of the values varying between 52 and 61 percent) of the shell length anterior to ventral beak. Top of pedicle valve located posteriorly at a variable point between 25 and 33 percent of the shell length anterior to beak. Top of brachial valve, and thus of the shell, located at a point varying between 67 and 87 percent of the shell length anterior to the ventral beak. From this point the valve slopes gently toward the front, where the top of the tongue is 14 to 26 percent lower than the point of maximum shell thickness. In very few specimens the top of the brachial valve is located anteriorly. Length of ventral interarea varying between 45 and 60 percent of the shell width. Apical angle varying between 113° and 126°. Serial transverse sections of one specimen (paratype J, IRScNB a11457) are shown in text-figure 1; this specimen was photographed (Pl.1, Figs.31-33) before grinding.

Discussion of synonymy: *p.p.* (= *pro parte*) and ? relate to the questionable presence of the species in the uppermost Frasnian rocks of "Matagne" aspect (see 3.10).

Comparisons: It is probable that *Piridiorhynchus* confinium was sometimes mistaken for *Pampoecilorhynchus praenux* (SARTENAER 1958) in the literature. The two species are similar in some characters; comparable size and proportions; well marked sulcus and fold starting at some distance from the beaks; simple costae starting at the beaks; most of the internal characters (e.g. divided hinge plate, moderately wide umbonal cavities, presence of a septum). However, *P. praenux* can easily be separated from *Piridiorhynchus confinium* by the variable contour in ventral and dorsal

views, but generally mostly triangular in the posterior part of the shell, and sub-rounded in the anterior part (contour slightly transversely sub-elliptical Piridiorhynchus); lateral and frontal commissures fused in the flanks of the shell; frontal commissure generally between half and three quarters shell thickness (higher in Piridiorhynchus); sulcus slightly less deep; tongue bent at almost a right angle in front (tongue is elongated in Piridiorhynchus); upper part of tongue either almost vertical or recurved posteriorly (only tending to become vertical near the frontal commissure in *Piridiorhynchus*); borders of tongue tending to be parallel; small deltidial plates: different general costal formula [4/3; 0; 5 to 7/6 to 8 for Pampoecilorhynchus praenux (the almost complete absence of parietal costae is remarkable), 4 to 5/3 to 4; 0-1/0-1 (or 1-0/1-0) to 1-1/1-1; 6 to 9/7 to 10 for Piridiorhynchus confinium]; stronger costae [higher, wider, more angular (with less rounded top)]; median costae similar to the lateral costae; lateral costae bordering the sulcus sticking out at front; apical angle often smaller; thicker septum and hinge plate; crural bases not sticking out above the outer hinge plates; crura crescentshaped proximally (they are rounded proximally in Piridiorhynchus).

Stratigraphic range and geographical distribution

Piridiorhynchus confinium was found in the following localities of the southeastern and eastern borders of Dinant Basin:

Northeastern flank of roadcut NW of the village of Sinsin along the road (N4) from Marche to Namur at the crossing with road N929 (Aye 1/20,000 topographic sheet), southeastern border of Dinant Basin, locality Aye 57 [see SARTENAER (1968, pl.V), COEN (1973, fig.5, p.249; 1974, p.6), VANGUESTAINE et al. (1983, fig.2, p.125, fig.9, p.150), SANDBERG et al. (1988a, fig.A 8/1, p.69; 1988b, fig.10, p.283), STREEL & VANGUESTAINE (1988, fig.2; 1989, fig.3, p.113), CASIER & DEVLEESCHOUWER (1995, fig.2, p.53)]. 25 to 55 cm below Bed 15 (see COEN, 1974, p.6). COEN (1973, fig.5, p.249) considered Bed 13 as the base of the Early Palmatolepis triangularis Zone (lowermost Famennian). As a result of subsequent collecting and examination of conodonts by COEN (1974, p.4, p.6) and by DREESEN (unpublished), the base of the zone was lowered from Bed 13 to Bed 15, and then to an unnumbered bed designated here as Bed 15 bis. Bed 15 bis is located between Bed 15 and Bed 12, and corresponds to the bed called key Bed 13 by SANDBERG et al. (1988b, fig.10, p.283); Northeastern flank of roadcut halfway between 15 and 16 km along the road (N40) from Dinant to Neufchâteau (Houyet 1/20,000 topographic sheet), southeastern border of Dinant Basin, locality Houyet 25135 [see SARTENAER (1970, p.354, pl.1)]. Between 30 and 40 cm below the base of the Pampoecilorhynchus praenux Zone (lowermost rhynchonellid zone of the Famennian).

SARTENAER (1970, p.350, p.353, p.354, pl.1) considered the base of the *P. praenux* Zone as the base of the Famennian, and left in the uppermost Frasnian the beds containing *Ripidiorhynchus* sp. [although he indicated (p.350, p.353) that this form could belong to a new subgenus of *Ripidiorhynchus*], named *Piridiorhynchus confinium* in the present paper. It seems likely that the beds containing this species should be transferred to the lowermost Famennian;

Northeastern flank of roadcut between km 17 and km 18 along the road (N40) from Dinant to Neufchâteau (Houyet 1/20,000 topographic sheet), southeastern border of Dinant Basin, locality Houyet 25137a [see SARTENAER (1970, p.354, pl.2)]. Bed at 4.75 m below the base of the Pampoecilorhynchus praenux Zone (lowermost Famennian). SARTENAER (1970, p.350, p.353, p.354, pl.2) put in the uppermost Frasnian the bed containing Ripidiorhynchus sp. [although he indicated (p.350, p.353) that this form could belong to a new subgenus of Ripidiorhynchus], named Piridiorhynchus confinium in the present paper. It seems likely that the bed containing this species should be transfered to the Famennian; Railroad cut S of the village of Hogne between km 107/9 and km 108/4 along the railroad from Namur to Arlon (Aye 1/20,000 topographic sheet), southeastern border of Dinant Basin, locality Aye 24159. Between km 108/079 and km 108/085 on the northeastern flank of the railroad cut in the southern limb of a syncline, lowermost Famennian:

Railroad cut N of the station of Hony along the railroad from Liege to Jemelle (Esneux 1/20,000 topographic sheet), eastern border of Dinant Basin, locality Esneux PS-73-10 [see BOUCKAERT & THOREZ (1966, p.260), BOUCKAERT et al. (1972, p.91), BOUCKAERT (1974, pp.10-11), BECKER, G. et al. (1974, fig.2, p.12), VANGUESTAINE et al. (1983, fig.2, p.125, fig.5, p.139, fig.7, p.142, fig.9, p.150), SANDBERG et al. (1988b, fig.8, p.280, fig.9, p.282), STREEL & VANGUESTAINE (1988, fig.1; 1989, fig.2, p.112), CLAEYS et al. (1996, fig.2, p.493)]. Bed 48b in the base of the Early Palmatolepis triangularis Zone (lowermost Famennian). According to SANDBERG et al. (1988b, fig.8, p.280) the Early P. triangularis Zone begins slightly below Bed 48b.

In short, on the southeastern and eastern borders of Dinant Basin, a regional *Piridiorhynchus confinium* Zone is developed in 0.3 m of rocks of "Barvaux" aspect at the very base of the Famennian.

Although still in need of confirmation, the presence of *P. confinium* in the uppermost Frasnian rocks of "Matagne" aspect at one locality in the Philippeville Massif cannot be excluded. This locality is known under the name "tranchée de Senzeilles" [railroad cut between the railroad station of Senzeilles and the northwestern wall of the tunnel of Senzeilles along the railroad from Charleroi to Vireux (Senzeilles 1/20,000 topographic sheet), local-

ity Senzeilles 6839b] [see SARTENAER (1960, pls.I-III; 1983, fig.1, p.3)]. The railroad cut does not now exist; it was filled in in order to allow road construction. Outside of seven specimens collected by the author, of which the best two ones are photographed (Pl.1, Figs. 34-36), one other specimen from the same rocks (Schistes de Matagne) was described and figured by MAILLIEUX (1936, p.24, pl.I, fig.3 as Terebratula subreniformis SCHNUR, J., 1851). These occurrences and others were mentioned in the literature as Ripidiorhynchus sp. or Ripidiorhynchus by SARTENAER (1970, p.350, p.353; 1973, p.5; 1974a, p.14; 1974b, p.4; 1977, p.74; 1983, fig.1, p.3; in VANGUESTAINE et al., 1983, p.132; in BULTYNCK, 1988, fig.A 2/4, p.23; in CASIER, 1992, tab.1, p.111). SARTENAER (1970, p.350, p.353) indicated that these forms could belong to a new subgenus of Ripidiorhynchus. The poor preservation of the material, consisting of squashed specimens, does not allow a definite assignment to Piridiorhynchus confinium although the external characters of the largest and best preserved specimen (Pl.1, Figs. 34,35) suggest it. On account of the disappearance of the "tranchée de Senzeilles", it may prove necessary to grind down this specimen to investigate its internal characters; efforts to collect a better specimen in the protected site ("coupe témoin") of the Frasnian/Famennian boundary beds at this historical locality have failed so far. If serial transverse sections should show a covered septalium, these latest Frasnian specimens could belong to the same genus as the late Frasnian species known in the literature as Ripidiorhynchus kotalensis (see below). In that case, paratypes H and I would have to be excluded from the type series of Piridiorhynchus confinium.

Another problem to consider is the eventual overlapping of the *P. confinium* and *Pampoecilorhynchus praenux* Zones. Although such an overlap cannot be dismissed, the author failed to observe it. SANDBERG *et al.* (1988a, fig.A 8/1, p.69) indicated an overlap of *Ripidiorhynchus* (read *Piridiorhynchus confinium*) and *Pampoecilmorhynchus nux praenux* (read *P. praenux*), but material to substantiate it is not available. SANDBERG *et al.* (1988b, p.278) states that the author believes that the two genera do not overlap.

4. Kedridorhynchus n. gen.

Derivatio nominis: *Kedris*, *idos* (Greek, feminine) = fruit of cedar; *rhynchos*, *ous* (Greek, neuter) = beak. The name draws attention to the name of the lithostratigraphic unit from which the type species comes.

Type and only species: Camarotoechia cedarensis STAINBROOK 1942.

Kedridorhynchus cedarensis is a common late Givetian species from NE and CE Iowa. It is found in the upper-

most part of the Rapid Member of the Little Cedar Formation and in the lowermost part of the Coralville Formation of the Cedar Valley Group.

A description of the species, figures of two paratypes, and four serial transverse sections of a third paratype were given by STAINBROOK (1942, pp.611-612, pl.88, figs.10-15, figs.2a-d, p.607); the holotype comes from Littleton, Buchanan County.

Diagnosis: Shell small, generally wider than long. Dorsibiconvex, brachial valve being considerably deeper than pedicle valve. Subtriangular in ventral and dorsal views. Commissure sharp, clearly indented by the costae. Sulcus and fold starting very near the beaks. Sulcus moderately wide to wide, shallow. Bottom of sulcus flat. Tongue trapezoidal, low to moderately high. Ventral beak suberect to erect, projecting. Ventral interarea high. Fold low. Top of fold flat to slightly convex. Top of shell at front or slightly posterior to it. Costae well marked, moderate in number, simple, regular, angular with rounded top, starting at the beaks. One parietal costa occasionally present on one or on both flanks of sulcus and fold. Apical angle small. Dental plates and septum stout. Septum may reach half-length of shell. Hinge plate reduced and divided. Septalium deep and U-shaped. Dental sockets deep.

Comparisons: Many characters make *Ripidiorhynchus* distinct from *Kedridorhynchus*; its larger size; different outline (sub-elliptical for *Ripidiorhynchus*, subtriangular for *Kedridorhynchus*); deeper sulcus; higher fold; general presence and greater number of parietal costae; more lateral costae; wider apical angle; more delicate internal structures; covered septalium; and longer hinge plate.

5. Hypselororhynchus n. gen.

Derivatio nominis: *Hypselos*, *e*, *on* (Greek, adjective) = high; *oros*, *ous* (Greek, neuter) = mountain; *rhynchos*, *ous* (Greek, neuter) = beak. The name draws attention to the Hindu-Kush range from the western extremity of which the type species comes.

Type and only species: *Ripidiorhynchus farsani* BRICE 1977.

Hypselororhynchus farsani is a middle-upper Frasnian species from Robat-e-Paï, West Afghanistan.

A description of the species, figures of the holotype and four paratypes, and serial transverse sections in two pararatypes were given by BRICE (*in* BRICE & FARSAN, 1977, p.225, p.226, pp.227-228, pl.XIII, figs.1a,b, 2-4, 5a,b, figs.1A,B, p.229).

Diagnosis: Shell small, wider than long. Dorsibiconvex, brachial valve being considerably deeper than pedicle

valve. Sub-elliptical in ventral and dorsal views. Commissure sharp, clearly indented by the costae. Sulcus and fold starting at some distance (sometimes at a great distance) from beaks. Sulcus moderately wide (56 to 62 percent of shell width), moderately deep. Bottom of sulcus flat. Tongue trapezoidal, moderately high to high. Ventral beak slightly to strongly incurved, projecting. Ventral interarea high. Fold moderately high. Top of fold slightly convex. Top of shell at front or very near to it. Costae well marked, simple, regular, angular with rounded top, starting at the beaks. Median costae in moderate number (3 to 5). Lateral costae numerous (8 to 11). One or two parietal costae present on both flanks of sulcus and fold. Apical angle small to moderately wide. Internal structures thick. Dental plates and septum short. Reduced umbonal cavities. Undivided hinge plate. Deep and V-shaped septalium covered by a moderately strong connectivum. Deep dental sockets.

Comparisons: Many characters make *Ripidiorhynchus* distinct from *Hypselororhynchus*; the larger size; deeper sulcus; higher fold; pedicle valve more excavated by the sulcus; tongue fan-shaped; generally wider apical angle; larger number of lateral costae; different costal formula of parietal costae (2-2/2-2 to 3-3/3-3 for *Ripidiorhynchus*, 1-1/1-1 to 2-2/2-2 for *Hypselororhynchus*); delicate internal structures; larger umbonal cavities.

6. Porthmorhynchus n. gen.

Derivatio nominis: *Porthmos*, *ou* (Greek, masculine) = straits; *rhynchos*, *ous* (Greek, neuter) = beak. The name draws attention to the Pas-de-Calais (the Straits of Dover), which is at the same time the name of the straits between France and the British Isles and of the department where the Boulonnais is located and where the type species is found.

Type species: Rhynchonella ferquensis GOSSELET 1887

Porthmorhynchus ferquensis is a common middle-upper Frasnian species from the Ferques area, Boulonnais. The species was described and abundantly illustrated by GOSSELET (1887, p.194, p.195, pp.199-202, p.203, p.207, pl.I, figs.1a-d, 2d, 3a-d, 4d, 5a-d, 6a-d, 7a,c, 8a-d), and BRICE (*in* BRICE & MEATS, 1972, pp.223-226, pl.XXXVI, figs.13a-c, 14a,b, fig.1C, p.218) made additional observations on the species, described its internal characters with the help of serial transverse sections, and figured two specimens, one of them being lectotype.

Species attributed to the genus: Besides the type species, *Ptychomaletoechia elburzensis* GAETANI 1965 from the central Alborz Mountains (North Iran) is assigned to the genus; this late Frasnian species is com-

mon in one outcrop (Zaigun Valley). A description of the species, figures of the holotype and four paratypes, all from the Zaigun Valley, and serial transverse sections of paratypes were given by GAETANI (1965, p.686, p.689, p.691, fig.2, p.692, p.693, p.700, p.702, p.703, p.705, fig.4, p.709, pp.710-715, p.725, pl.68, figs.4a-e, 5a-e, 6a-e, 7a-e, pl.69, figs.1a-e).

Diagnosis: Small to medium-sized, wider (sometimes considerably) than long. Dorsibiconvex, brachial valve being much deeper than pedicle valve. Sub-elliptical in ventral and dorsal views. Commissure sharp, clearly indented by the costae. Sulcus and fold well marked, starting near the beaks. Sulcus moderately wide (54 to 68 percent of the shell width), moderately deep to deep. Bottom of sulcus flat to slightly convex. Tongue trapezoidal, high, elongated, tending sometimes to become vertical toward the frontal commissure. Ventral beak erect, projecting. Fold moderately high to high. Top of fold slightly convex. Costae well marked, simple, regular, angular with rounded top, starting at the beaks. Few median costae (2 to 5). Number of lateral costae ranging from 4 to 11. Parietal costae only sometimes present; when present there is only one, and not necessarily on both flanks of sulcus and fold. Top of shell usually posterior to front, rarely at front. Apical angle wide. Internal structures moderately thick. Dental plates subparallel. Septum short. Undivided hinge plate. Septalium moderately deep, cupule- or amphora-shaped, and covered by a connectivum. Crura crescent-shaped proximally, walking-stick-shaped distally.

Comparisons: Many characters make Ripidiorhynchus distinct from Porthmorhynchus; the slightly larger size in most specimens; different outline (although sub-elliptical in both genera, the major axis of the ellipse is smaller in Ripidiorhynchus on account of different proportions Porthmorhynchus is generally wider); deeper sulcus; higher fold; sulcus and fold starting at a greater distance from the beaks; pedicle valve more excavated by the sulcus; tongue often higher; top of tongue often strongly convex and sometimes acuminate; top of shell located closer to the front; smaller apical angle; different pattern of parietal costae (always present in Ripidiorhynchus with general formula 2-2/2-2 to 3-3/3-3 while only sometimes present in Porthmorhynchus, and in those cases there is only one costa, and not necessarily on both flanks of sulcus and fold); maximum number of lateral costae often higher. There are only slight differences between the internal structures of both genera; Ripidiorhynchus has more delicate internal structures, longer dental plates, a longer septum, and a deeper septalium.

Some external features of the genera *Villirhynchia* CHERKESOVA 1999 and *Porthmorhynchus* are similar in size, outline, well marked sulcus and fold starting near the beaks; well marked, simple and regular costae start-

ing at the beaks; few median costae and the wide apical angle. *Villirhynchia* differs in the smaller number of lateral costae; the absence of parietal costae; slightly curved dental plates; a long septum; a divided hinge plate and the absence of a connectivum. It must be borne in mind that the genus *Villirhynchia* is only known from its type species, *V. villiamensis* CHERKESOVA 1999, from the middle Frasnian (*Ancyrognathus triangularis* Zone) of NW Novaya Zemlya (SE coast of William Island), which in turn is represented only by three specimens (two photographed and a fragmental specimen).

7. Paropamisorhynchus n. gen.

Derivatio nominis: *Paropamisos* = ancient Greek name given to the western part of the Hindu-Kush range. The name draws attention to the area from which the type species comes.

Type and only species: *Ripidiorhynchus* (?) *kotalensis* BRICE 1971.

BRICE (*in* BRICE & LANG, 1968, p.120) provisionally identified as "*R*." n. sp. a specimen collected in an outcrop of the Iraq valley (Bamian Basin, eastern Central Afghanistan), and included it in an upper Frasnian-lower Famennian brachiopod fauna from various outcrops in the valley.

When the name R. (?) kotalensis was given to this new species by BRICE (1971, pp.38-41, 43, p.75, tab.1, p.78, p.79, p.80, p.315, p.318, p.319, tab.5, p.328, pl.II, figs.1a-e, 2a-e, 3a-c, 4a-e, 5a-e, fig.11, p.42, fig.12, p.44), the holotype and all the paratypes, with the exception of the specimen from the Iraq valley, were chosen from two outcrops from the Ghuk area (western Central Afghanistan). BRICE stressed that the age of the species was far from being definitely established. The "(middle?) Frasnian to lower Famennian" (p.38, p.39) or the "possible" middle Frasnian to lowermost Famennian (tab.1, p.78) age was mitigated by the following statements (p.43): "At Ghuk's outcrop 10 [five paratypes come from this outcrop], the species was found in the Cyphoterorhynchus koraghensis zone, which, in Iran, could indicate a middle or upper Frasnian age (SARTENAER P., 1966), but most of the specimens come from the Ghuk outcrop [the holotype and 31 paratypes come from this outcrop], which essentially yielded species belonging to the lower Famennian. However, it is possible that the upper Frasnian is also present in this outcrop. It is impossible for me to state definitely if R. (?) kotalensis is only a Frasnian species or if it still holds on at the base of the Famennian".

BRICE had some reservations about the generic assignment of the species. This is indicated by the question mark replacing the previous brackets and by the follow-

ing statements (p.41) "the Afghan species is slightly on the fringe of the Russian species of the genus gathered together by P. SARTENAER [1966] in the genus *Ripidiorhynchus*" on account of a "whole set of characteristics". Although abandoned in subsequent publications (in GOLSHANI et al., 1972, p.2104; in BRICE & MEATS, 1972, p.216, p.221, p.223; 1977, p.271; in BRICE et al., 1999, p.25) BRICE's reservations were quite justified.

According to subsequent publications a late Frasnian age is favoured.

Diagnosis: Medium- to large-sized. Uniplicate. Sub-elliptical in ventral and dorsal views. Dorsibiconvex, brachial valve being much deeper than pedicle valve. Commissure sharp and clearly indented by the costae. Very well marked sulcus and fold, beginning a short distance from the beaks. Sulcus moderately deep to deep, wide at front. Tongue trapezoidal, moderately high to high. Ventral beak slightly incurved. Ventral interarea clearly separated from flanks. Fold moderately high to high. Top of shell posterior to front. Costae simple, regular, clearly marked (particularly the median dorsal costae), and starting at the beaks. Few median costae (about half the number of lateral costae). One parietal costa usually present on one or on both flanks of sulcus and fold. Internal structures (dental plates, septum, hinge plate, crural bases, and connectivum) stout. Umbonal cavities almost non-existent or moderately wide. Crura subtriangular proximally, Phrygian cap-shaped distally.

Comparisons: Many characters, some of them already mentioned by BRICE (1971, pp.41,43), make *Ripidiorhynchus* distinct from *Paropamisorhynchus*; the smaller size; sulcus and fold beginning slightly further away from the beaks; top of tongue often strongly convex or even acuminate; finer costae; general presence and larger number of parietal costae; number of lateral costae not rarely larger; top of shell located closer to the front, and exceptionally at the front; more delicate internal structures; absence of apical thickening; deeper septalium; thinner connectivum; crura crescent-shaped proximally, walking-stick-shaped distally.

Paropamisorhynchus and Piridiorhynchus can scarcely be separated by means of external characters. The following minor features, considered as a whole, help to separate the two genera. In Paropamisorhynchus the width is slightly larger; sulcus and fold start slightly nearer to the beaks; sulcus is generally narrower; costae, more particularly the median ones, are higher; number of lateral costae commonly larger, and similar on both flanks. On the other hand internal differences are important. Paropamisorhynchus has a connectivum, stout dental plates, septum, hinge plate and connectivum; dental plates clearly converging anteriorly; umbonal cavities almost non-existent to moderately wide.

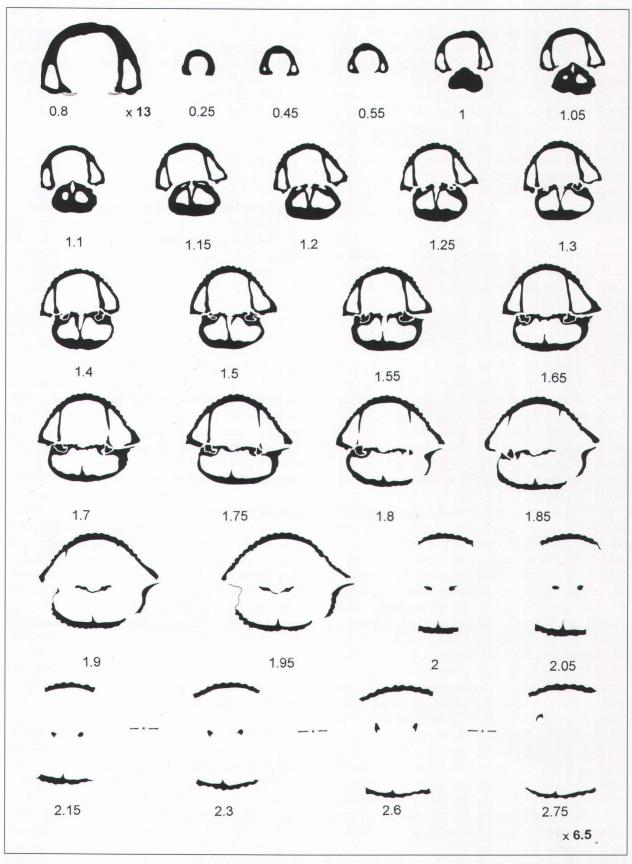


Figure 2 - *Saxulirostrum saxatile* (HALL 1867). Camera lucida drawings of serial transverse sections; figures are distances in mm forward of the ventral umbo (section 0.8 is enlarged x13 in order to show the deltidial plates). Topotype, IRScNB a11652. Rockford, Floyd County, NC Iowa. Cerro Gordo Member of the Lime Creek Formation, late Frasnian. Collector: P. SARTENAER, 1972. Measurements: length = 10.1 mm; width = 11.8 mm; thickness = 8 mm.

8. Saxulirostrum n. gen.

Derivatio nominis: Saxulum, i (Latin, neuter) = small rock; rostrum, i (Latin, neuter) = beak. The name draws attention to the type species.

Type and only species: Rhynchonella (Stenocisma) contracta var. saxatilis HALL 1867. Saxulirostrum saxatile (HALL 1867) is a rare late Frasnian (Cerro Gordo Member of the Lime Creek Formation) species from north-central Iowa. HALL (1867, pp.417-418) did not describe the species, because the material from Rockford at his disposal was not large enough for allowing such a description; he was content with comparing the variety with two New York species (R. contracta and R. eximia). Lectotype. It is evident that more than one genus was figured by HALL (1867, pl.54A, figs.44-51); the "characteristic specimen" of figures 44 to 48 is designated as the lectotype of the species.

Diagnosis: Shell small, only slightly wider (10 to 20 percent) than long. Dorsibiconvex, brachial valve being considerably deeper than pedicle valve; pedicle valve is very low, its flanks are flat, and, as a result, umbonal region shows strong relief. Slightly transversely sub-elliptical in ventral and dorsal views. Commissure very sharp, clearly indented by the costae. Sulcus and fold starting at some distance from beaks. Sulcus wide, deep. Tongue high, trapezoidal. Ventral beak suberect to erect, projecting. Ventral interarea high, clearly separated from flanks. Fold high. Top of shell at front or slightly posterior to it. Few median (3 to 4) and lateral (5 to 6) costae. Costae well marked, simple, regular, angular with rounded top, starting at the beaks. One parietal costa usually present on both flanks of sulcus and fold. Apical angle moderately wide. Deltitial plates slender. Internal structures slender (Text-fig.2). Dental plates subparallel and short. Umbonal cavities large. Delthyrial cavity wide. Teeth stout and short. Septum short. Septalium deep, amphorashaped. Hinge plate undivided; outer plates convex. Connectivum thin. Dental sockets deep. Crura subrounded proximally, crescent-shaped distally.

Comparisons: Ripidiorhynchus and Saxulirostrum exhibit similar features; a well-marked sulcus and fold starting at some distance from the beaks; a deep sulcus; a high fold; a high tongue; a sharp commissure clearly indented by the costae; simple, regular, and well marked costae starting at the beaks; subparallel and short dental plates; short septum; large delthyrial and umbonal cavities; a undivided hinge plate; the presence of a slender connectivum.

Some characters make *Saxulirostrum* distinct from *Ripidiorhynchus*; the smaller size; flatter ventral flanks; a usually wider sulcus; a usually smaller apical angle; different proportions, notably length larger in relation to width; a different general costal formula (less parietal

and lateral costae); a deeper septalium; crura subrounded proximally, crescent-shaped distally (they are crescent-shaped proximally and walking-stick-shaped distally in *Ripidiorhynchus*).

9. Orophomesorhynchus n. gen.

Derivatio nominis: *Orophos*, *ou* (Greek, masculine) = platform, roof; *mesos*, *e*, *on* (Greek, adjective) = central; *rhynchos*, *ous* (Greek, neuter) = beak. The name draws attention to the central part of the Russian Platform, from where the type species comes.

Type species: Terebratula Huotina de VERNEUIL 1845. This species was described and parsimoniously illustrated by de VERNEUIL (in MURCHISON, KEYSERLING & de VERNEUIL 1845, pp.81-82, pl.X, figs.4a,b). More figures were given by NALIVKIN (in MARKOVSKIY & NALIVKIN, 1934, pp.22-23, pl.II, figs.4a-d, 5a-d, 6a-d) and LYASHENKO (1959, p.22, p.92, p.202, pp.205-206, p.215, p.216, table 4, p.228, pl.76, figs.1a,b,v,g, 2a,b,v,g), who also described the species. This species from the early Famennian Zadonsk beds (horizon) (Middle and Late Palmatolepis triangularis, and P. crepida Zones) of the Central Devonian Field "occurs sporadically and is not very abundant" according to NALIVKIN, and is common according to LYASHENKO.

On account of priority the species was chosen as the type species in preference to *Camarotoechia zadonica* NALIVKIN 1934 which occurrs in abundance in the same beds, and is also assigned to the new genus. The following statements by NALIVKIN (*in* MARKOVSKIY & NALIVKIN, 1934, p.23) indicate that further studies could lead to the two species being conspecific: "it [*C. Huotina*] represents a variety of *C. zadonica*", "the two forms occur together", "transitions connect the two forms".

C. zadonica was briefly described and abundantly illustrated by NALIVKIN (in MARKOVSKIY & NALIVKIN, 1934, p.23, pl.III, figs.1a-d, 2a-d, 3a-d, 4a-d, 5a-d, 6a-d, 7a-d, 8a-d; 1947, p.12, p.87, pl.XIX, figs.7a-c). Among the various subsequent descriptions found in the Russian literature, the most complete one was given by LYASHENKO (1959, p.12, p.22, p.91, p.92, p.93, p.202, p.205, p.206, p.213, table 4, p.228, pl.76, figs.3a,b,v,g,d, 4, 5a,b,v,g, pl.79, figs.1a, 2a, 3a, 4v, 5b). The species is considered as a guide fossil of the Zadonsk beds by NALIVKIN (1947).

Species attributed to the genus: Only the two species mentioned above are assigned to the new genus.

Two other species, Camarotoechia brodica NALIVKIN 1934 and C. griasica NALIVKIN 1934 from the early Famennian Elets beds (horizon) (Palmatolepis rhomboidea Zone and lower part of the Early P. marginifera Zone) show some external similarity to

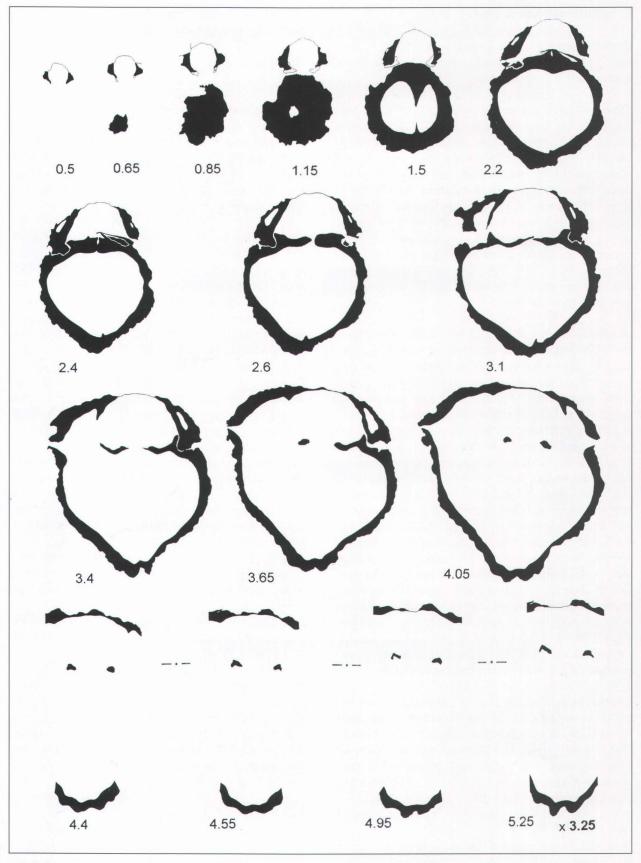


Figure 3 - *Orophomesorhynchus huotinus* (de VERNEUIL 1845). Camera lucida drawings of serial transverse sections; figures are distances in mm forward of the ventral umbo. Topotype, IRScNB a11653. Town of Zadonsk, left bank of the Don river, Central Devonian Field. Zadonsk beds, early Famennian. Collectors: B. MARKOVSKIY & D.V. NALIVKIN, around 1930 ($n \approx 4572$). Measurements: length = 15.6 mm; width = 21.2 mm; thickness = 17.9 mm.

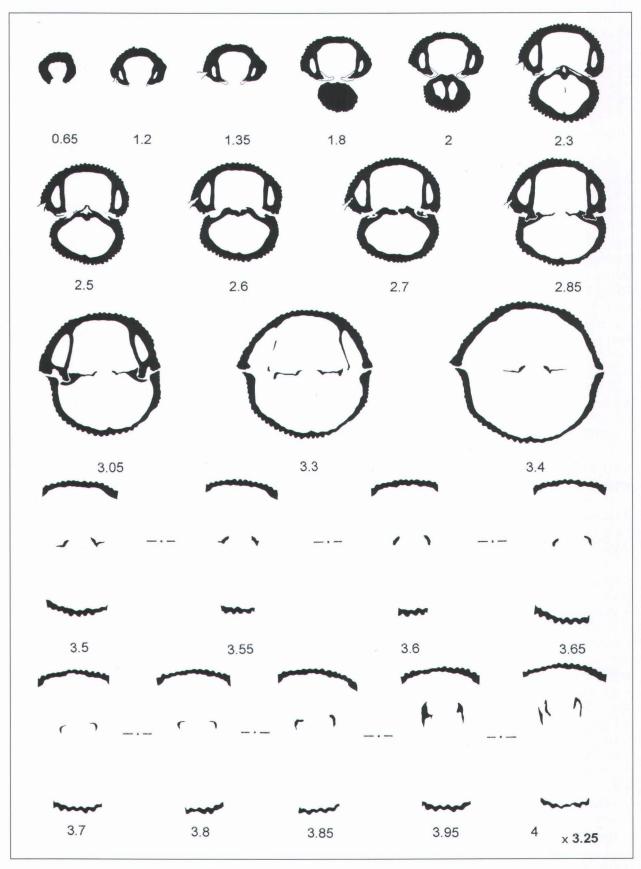


Figure 4 - *Orophomesorhynchus zadonicus* (NALIVKIN 1934). Camera lucida drawings of serial transverse sections; figures are distances in mm forward of the ventral umbo. Topotype, IRScNB a11654. Village of Koshary, left bank of the Don river, Central Devonian Field. Zadonsk beds, early Famennian. Collectors: B. MARKOVSKIY & D.V. NALIVKIN, around 1930 (n∞4572). Measurements: length = 13.9 mm; width = 17.3 mm; thickness = 13.8 mm.

Orophomesorhynchus huotinus and O. zadonicus, but differ from them in smaller size, less transverse outline, smaller thickness, lower tongue, and a generally smaller number of costae. SARTENAER (1966, p.2, p.3; 1985, p.322) mentioned that these two species were different from other species then erroneously assigned to the genus Ripidiorhynchus. Large collections, with precise information on the position of the species within the Elets beds and on the associated rhynchonellids, should show if these differences are fundamental or only specific. Above all the internal characters, which have not been studied so far, need to be investigated.

In the brief original description by NALIVKIN (*in* MARKOVSKIY & NALIVKIN, 1934, p.24, pl.III, figs.9a-d, 10a-d, 11a-d, 12a-d, 13a-d, 14a-d) *Camarotoechia brodica* is declared relatively rare, but in the best subsequent description by LYASHENKO (1959, p.12, p.22, p.94, p.95, p.210, p.212, p.213, table 4, p.228, pl.81, figs.4a,b,v,g,d, 5a,b,v,g,d) it is considered not only as common, but also as an important guide fossil for the Elets horizon.

The brief original description of *C. griasica* by NALIVKIN (*in* MARKOVSKIY & NALIVKIN, 1934, pp.23-24, pl.IV, figs.7a-d, 8a-d, 9a-d, 10a-d, 11a-d, 12a-d, 13a-d; 1947, p.13, pp.87-88, pl.XIX, figs.8a-c) was complemented by a subsequent description by LYASHENKO (1959, p.12, p.22, p.94, p.95, p.210, pp.212-213, p.217, table 4, p.228, pl.81, figs.6a,b,v,g,d, 7a,b,v,g,d). NALIVKIN (1947) considered this common species as a guide fossil for the Elets beds.

Diagnosis: Medium-sized. Dorsibiconvex, brachial valve being considerably deeper than pedicle valve. Sub-pentagonal to sub-elliptical in ventral and dorsal views. Commissure sharp, clearly indented by the costae. Sulcus and fold starting at some distance from the beaks. Sulcus deep, moderately wide to wide. Tongue high, trapezoidal with rounded top. Top of tongue either vertical or slightly recurved posteriorly. Ventral beak erect, projecting. Ventral interarea high, clearly separated from flanks. Fold high with convex top. Costae well marked, simple, regular, and starting at the beaks. Few angular and wide median costae (3 to 5). Lateral costae numerous (11 to 18), narrow, and angular with rounded top. Two to three parietal costae on both flanks of sulcus and fold. Maximum thickness posterior (slightly or at a greater distance) to front. Dental plates short and moderately thick. Delthyrial cavity wide. Umbonal cavities narrow to moderately wide. Teeth stout and short. No septum and thus no septalium (the median ridge observed on text-figures 3, 4 can be interpreted as a vestigial septum or a strong myophragm). Outer hinge plates thick posteriorly and thinning considerably anteriorly, almost meeting or slightly overlapping, but they never join. Crural bases crescent-shaped and sticking out above the outer hinge plates in serial transverse sections. Crura bean-shaped proximally, becoming crescent-shaped distally.

Comparisons: There are no clear and constant differences in the external characters of *Ripidiorhynchus* and *Orophomesorhynchus*. Species of the new genus are generally larger, and so are their deltidial plates. Other possible differences can only be assessed with large collections, which are not at the author's disposal. On the other hand, internal features allow an easy separation. The presence of a true septum, a septalium, and a connectivum in the genus. *Ripidiorhynchus* allows to separate it from *Orophomesorhynchus*.

10. Poleomesorhynchus n.gen.

Derivatio nominis: *Polis*, *eos* (Greek, feminine) = state; *mesos*, *e*, *on* (Greek, adjective) = central; *rhynchos*, *ous* (Greek, neuter) = beak. The name draws attention to the State of Missouri in the central part of the United States of America, from where the type species comes.

Type and only species: Camarotoechia gregeri BRANSON 1923.

Poleomesorhynchus gregeri is a rare early Frasnian (Snyder Creek Shale) species from Calloway County in central Missouri. The species was described and three specimens were figured by BRANSON [1923, p.41, p.91, pl.24, figs.5-9. Contrary to the explanation of his figures, three specimens (figs.5 and 8, fig.6, figs.7 and 9), and not two, are figured; figures are also enlarged (about 1.1)].

Diagnosis: Small- to medium-sized. Variable contour in ventral and dorsal views: sub-triangular to sub-elliptical. Dorsibiconvex, brachial valve being considerably deeper than pedicle valve. Commissure sharp, clearly indented by the costae. Sulcus and fold starting at some distance from the beaks. Sulcus moderately wide and moderately deep. Bottom of sulcus flat. Tongue moderately high, trapezoidal, elongated anteriorly. Ventral beak suberect to erect, projecting. Ventral interarea high, clearly separated from flanks. Fold moderately high. Top of fold convex. Costae well marked, moderate in number (median costae: 3 to 5; lateral costae: 6 to 8), simple, regular, angular with rounded top, and starting at the beaks. One parietal costa present generally on one flank, and rarely on both flanks of the sulcus and fold. Apical angle moderately wide. Top of shell posterior (slightly or, more often, at a greater distance) to front. Dental plates subparallel, moderately thick (Text-fig.5). Delthyrial cavity large. Umbonal cavities moderately large. Teeth short and stout. Septum thick and long. Septalium deep, Vshaped, short, and covered by a thin connectivum. Undivided hinge plate. Outer hinge plates thick and slightly concave. Crural bases strong. Crura short, crescentshaped proximally, oval-shaped distally.

Comparisons: Many characters make *Ripidiorhynchus* distinct from *Poleomesorhynchus*; the greater thickness;

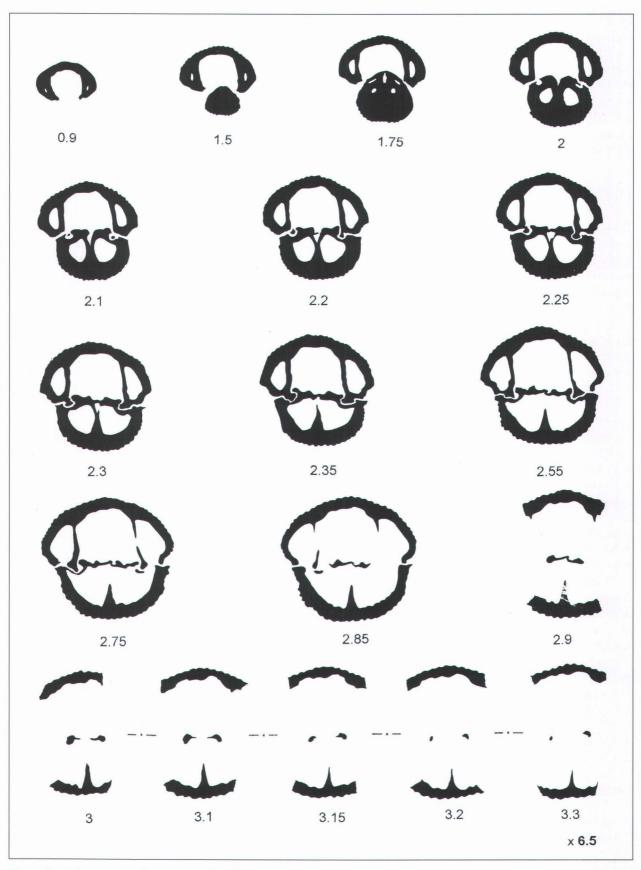


Figure 5 - *Poleomesorhynchus gregeri* (BRANSON 1923). Camera lucida drawings of serial transverse sections; figures are distances in mm forward of the ventral umbo. Topotype, IRScNB a11655. Cow Creek, Callaway County, central Missouri. Snyder Creek Shale, early Frasnian. Collector: P. SARTENAER, 1981. Measurements: length = 11.8 mm; width = 13.8 mm; thickness = 7.8 mm.

more constant contour in ventral and dorsal views and thus more variable proportions; lower pedicle valve, more excavated by the sulcus; deeper and wider sulcus; higher fold and tongue; different general costal formula (higher number of lateral costae; parietal costae always present with general formula 2-2/2-2 to 3-3/3-3); more delicate internal structures; crura walking-stick-shaped distally; large umbonal cavities; and the connectivum restricted to the anterior part of the septalium.

11. General systematic remarks

The present paper does not question the validity of the genus Ripidiorhynchus, which remains a well-defined genus characterized by the early Frasnian species R. livonicus (type species), R. pskovensis (junior synonym of R. livonicus; see SARTENAER, 1996, 1997), R. strugi, R. tschudovi, and R. belliloci BRICE & MEATS 1972. It is reasonable to recognize the subfamily Ripidiorhynchinae SAVAGE 1996, but with Ripidiorhynchus as sole representative and the subfamily elevated to family rank. Contrary to SAVAGE (1996, fig.3, p.256) the author is not inclined to include in the (sub)family Cyphoterorhynchus SARTENAER 1964, Hemiplethorhynchus von PEETZ 1898, and Pseudosinotectirostrum YUDINA 1991 (Sinotectirostrum SARTENAER 1961 is assigned to the subfamily Trigonirhynchiinae SCHMIDT 1965); the two former genera have a stout connectivum, the latter has none. The author considers the presence or the absence of a connectivum, as well as its character (thickness, fitting), as important distinctive features, while SAVAGE (1996, p.252) states that a septalium "with/without cover plate anteriorly" is one of the diagnostic features of the (sub)family.

The main purpose of this paper is to demonstrate that a large group of species, assigned to *Ripidiorhynchus* at one time or another, belong to known or new genera, some of them established here when the material and/or knowledge at hand was satisfactory. For some species, even if the lack of material precludes positive conclusions, the external features alone are characteristic enough for allowing the author (1985, pp.321-324) to eliminate them from *Ripidiorhynchus*. These include *R. daugaviensis* SOROKIN 1978 (*nomen nudum*; early Frasnian, Main Devonian Field), *R. newmexicoensis* COOPER & DUTRO 1982 (late Frasnian and middle Famennian, SC New Mexico), *R. orbicularis* (HALL 1860) (Chemung, SW New York), and *R. robustus* (LIEPIN_ 1958) (late Famennian, Central Devonian Field).

It is highly probable that other species, such as *R. barroisi* (RIGAUX 1908) (early Frasnian and, possibly, late Givetian, Boulonnais), *R. biferus* VENYUKOV 1886, *non* PHILLIPS 1841) (early Frasnian, Main Devonian Field), and *R. mutabilis* BARANOV 1996 (early Frasnian, North East, Russia) should belong to the genus *Comiotoechia*

LYASHENKO 1973; this is almost certain for *R. barroisi*. Unfortunately, sizable collections of the type species of *Comiotoechia*, *C. galinae* (LYASHENKO 1958), and of the two other Russian species are not available. *Comiotoechia* is a valid genus, and not a junior synonym of *Ripidiorhynchus* as suggested by BARANOV (1996, p.68); it is notably smaller, and has more costae.

What about the assignment of the new genera to higher taxonomic categories? It has been the author's view for a long time that many more genera need to be established before a solid classification can be envisaged and substituted for a provisional arrangement. The importance and persistence of some characters, the significance of some others such as the presence or absence of a dorsal septum, the various aspects of some features such as the cardinal process and connectivum can only be clarified with the help of a sufficient number of genera to make such observations plausible.

It would be simple, but wrong, to put in the same (sub)family as Ripidiorhynchus the new genera based on species previously assigned to that genus. It would be simple, but not advisable, to establish new monogeneric families. Therefore, the author provisionally includes the new genera, with reservations, within the family Trigonirhynchiidae SCHMIDT 1965. The reservations are related to the inclusion of alternative possibilities in the short diagnoses of the family: "small to medium-sized", "Rhynchonellacea von dreieckigem bis rundlichem Umriss" (Rhynchonellacea with triangular to rounded outline), "gut entwickeltes Septalium, das bei einigen Gattungen offen, bei anderen mehr oder weniger bedeckt ist" ("well-formed septalium that may be open or wholly or partly covered by plate uniting outer hinge plates") [according to the original diagnoses of SCHMIDT (1965, p.2) and SCHMIDT & McLAREN (1965, p.H559)]; "costae often extending from beaks, but commonly umbones smooth", "delthyrium open, or with disjunct-conjunct plates", "anterior commissure often dentate, sometimes spinose", "septalium with or without cover plate" [according to the diagnosis of SAVAGE (1996, p.252)].

12. Does the genus Ripidiorhynchus cross the Frasnian/Famennian boundary?

DUTRO (1986, fig.7, p.460, p.461, p.462) stated that in New Mexico the genus *Ripidiorhynchus*, and twelve other brachiopod genera, "occurs both below and above the Frasnian-Famennian boundary", the "most likely position" of this boundary being the base of the Middle *Palmatolepis triangularis* Zone. He wrote more precisely that *Ripidiorhynchus newmexicoensis* COOPER & DUTRO 1982, and five other brachiopod species, "crosses the boundary" in a restricted area near Rhodes Canyon in the San Andrés Mountains of south-central New Mexico. According to COOPER & DUTRO (1982, p.5, fig.7, pp.12-13, fig.8, pp.16-17, p.20, p.22, p.26, p.71,

pl.15, figs.1-20, pl.41, figs.34-40, p.129, p.131, p.132, p.136, p.137, p.140, p.145), R. newmexicoensis is a "longranging form" found in the latest Frasnian Contadero and in the middle Famennian Rhodes Canyon Formations and they noted that only an approximate age could be given to the Contadero Formation on the basis of conodonts, but "although no precise upper limit can be placed on the age of the Contadero...it is probably entirely Frasnian", the Frasnian/Famennian boundary being placed at the base of the Middle Palmatolepis triangularis Zone. The evidence for Ripidiorhynchus newmexicoensis crossing the Frasnian/Famennian boundary [no matter if an old definition (Middle P. triangularis Zone) or the one in use nowadays (Early *P. triangularis* Zone) is accepted], is not convincing as it stands for the following reasons: the species was found in the Rhodes Canyon Formation only at one locality (509u); the exact position of the species within the Contadero Formation is unknown or vaguely known, although this information is basic if the formation is proven to be not only Frasnian in age, but latest Frasnian-earliest Famennian; DUTRO (1986, p.462) acknowledges an "estimated 1 MY time gap between the Contadero and Thoroughgood assemblages", the Thoroughgood Formation being the formation underlying the Rhodes Canyon Formation. Furthermore, SORAUF (1984, 1988) modified the definition of these lithostratigraphic units as well as their age assignment. Finally, SARTENAER (1985, p.323) rejected Ripidiorhynchus newmexicoensis from the genus Ripidiorhynchus.

FARSAN (1986a., fig. 3, p. 191, p. 195; 1986b, p. 113, p.114, p.121, fig.4, p.124, p.125) advocated that Ripidiorhynchus, as well as Cyrtospirifer and Productella, "crossed the Frasnian-Famennian boundary unchanged", "survived into the early Famennian", and "persisted into Famennian" in three Afghan localities: Robat-e-Paï (West Afghanistan), Ghuk area (western Central Afghanistan), and Iraq valley (eastern Central Afghanistan). FARSAN (1986a, fig.4, pp.192-193; 1986b, fig.2, p.118, pp.121, 123, fig.3, p.122, fig.5) mentioned: R. sp. in the uppermost Frasnian, and R. kotalenis in the lowermost Famennian in Robat-e-Paï; R. (?) kotalensis both from the upper Frasnian and lower Famennian in the Ghuk area, according to BRICE (1971, pp.38-39, p.43, p.319); R. (?) kotalensis and R. elburzensis from the upper Frasnian in the Iraq valley, according to BRICE [in BRICE & LANG, 1968, p.120 as R sp (identified as R. elburzensis in 1971) and "R." n. sp. (identified as R. (?) kotalensis in 1971); 1971, p.39, p.43, p.315] [no species of Ripidiorhynchus is explicitly mentioned in the lower Famennian by FARSAN, but BRICE (in BRICE & LANG, 1968, p.121) "attributes the outcrops of Iraq in the Bamian basin to the upper Frasnian and lower Famennian", although she wrote that "the assemblage of brachiopods species [including R. sp. and "R."n. sp.] indicates a typically upper Devonian age with predominance of forms generally recorded from the upper Frasnian". The exact position of these taxa in rock units of considerable thicknesses (50 m and more) and taxonomic definition or redefinition of the taxa are needed before we can accept with some confidence that the genus *Ripidiorhynchus* does indeed cross the Frasnian/Famennian boundary in West and Central Afghanistan. As far as *R*. (?) *kotalensis* is concerned, its systematic position is discussed above.

We cannot exclude the possibility that the species *Piridiorhynchus confinium*, described above and previously named *Ripidiorhynchus* sp., could be present both in the lowermost Famennian and in the upper Frasnian. So far the species has been found with certainty only in rocks of "Barvaux" aspect and of lowermost Famennian age. A few squashed specimens collected in rocks of "Matagne" aspect and of upper Frasnian age are tentatively assigned to the species; however they may prove to belong to another genus after investigation of their internal characters [see discussion of *R*. (?) *kotalensis* above].

13. Acknowledgements

The author is grateful to D.V. NALIVKIN, Member of the Academy of Sciences (USSR), who kindly presented him in January, 1964 with specimens of *Camarotoechia huotina* and *C. zadonica*. He also wishes to express his thanks to A.J. BOUCOT (Oregon State University, Corvallis), L.R.M. COCKS (The Natural History Museum, London), and G. PLODOWSKI (Forschungsinstitut Senckenberg, Frankfurt am Main) for critically reading the manuscript, and for their helpful comments.

14. References

BARANOV, V.V., 1996. Otryad Rhynchonellida. *In*: Alekseeva, R.E., Atlas devonskikh brakhiopod Severo-Vostoka Rossii. *Trudy Paleontologicheskogo Instituta, Rossiyskaya Akademiya Nauk*, 266: 55-112.

BECKER, G., BLESS, M.J.M., STREEL, M. & THOREZ, J., 1974. Palynology and ostracode distribution in the Upper Devonian and basal Dinantian of Belgium and their dependence on sedimentary facies. *Mededelingen van de Rijks Geologische Dienst*, 25 (2), 91 pp.

BOUCKAERT, J., COEN, M., COEN-AUBERT, M. & DUSAR, M., 1974. Hony. Guidebook Excursion I. *In*: Bouckaert, J. & Streel, M. (eds), *International Symposium on Belgian micropaleontological limits from Emsian to Visean*. Geological Survey of Belgium, Brussels.

BOUCKAERT, J. & THOREZ, J., 1966. Contribution à l'étude du Dévonien supérieur dans la région d'Esneux. *Bulletin de la Société belge de Géologie*, 74: 258-264.

- BOUCKAERT, J., MOURAVIEFF, A., STREEL, M., THOREZ, J. & ZIEGLER, W., 1972. The Frasnian-Famennian boundary in Belgium. *Geologica et Palaeontologica*, 6, 87-92.
- BRANSON, E.B., 1923. The Devonian of Missouri. Missouri Bureau of Geology and Mines, Second Series, 17 (1922): 1-129, 276-279.
- BRICE, D., 1971. Étude paléontologique et stratigraphique du Dévonien de l'Afghanistan. Contribution à la connaissance des Brachiopodes et des Polypiers Rugueux. *Notes et Mémoires sur le Moyen-Orient*, 11 (1970), 364 pp.
- BRICE, D., 1977. Biostratigraphie du Dévonien d'Afghanistan. *In*: Livre à la mémoire de Albert F. de Lapparent (1905-1975) consacré aux recherches géologiques dans les chaînes de l'Asie du Sud-Ouest. *Mémoires hors série de la Société géologique de France*, 8: 267-276.
- BRICE, D. & LANG, J., 1968. Sur un nouveau gisement du Dévonien supérieur à Iraq (Bamian, Afghanistan). Compte rendu sommaire des séances de la Société géologique de France, 4: 120-121.
- BRICE, D. & MEATS, P., 1972. Le genre *Ripidiorhynchus* SARTENAER 1966 (Rhynchonellida Brachiopodes) dans le Dévonien de Ferques (Boulonnais France). *Annales de la Société géologique du Nord*, 91 (1971) (4): 215-228.
- BRICE, D. & FARSAN, M., 1977. Brachiopods from the upper Devonian of Robat-e-Paï (Afghanistan). Discovery of genera *Ladogia* Nalivkin, 1941 and *Eoparaphorhynchus* Sartenaer, 1961 (Rhynchonellida). *Annales de la Société géologique du Nord*, 96 (1976) (3): 225-232.
- BRICE, D., MISTIAEN, B. & ROHART, J.-C., 1999. New data on distribution of brachiopods, rugose corals and stromatoporoids in the Upper Devonian of central and eastern Iran. Paleobiogeographic implications. *In*: Contributions to: "North Gondwanan Mid-Palaeozoic Bioevent/Biogeography Patterns in Relation to Crustal Dynamics", I.G.C.P. 421, Isfahan, December 1998. *Annales de la Société géologique du Nord*, 7 (1): 21-32.
- BULTYNCK, P., 1988. Stop A2 Senzeilles, new Frasnian/Famennian reference section. *In*: Ziegler, W. (ed), 1st International Senckenberg Conference and 5th European Conodont Symposium (ECOS V), Contributions I. *Courier Forschungsinstitut Senckenberg*, 102 (1), 18-29.
- CASIER, J.- G., 1992. Description et étude des Ostracodes de deux tranchées traversant la limite historique Frasnien-Famennien dans la localité-type.

- Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 62, 109-119.
- CASIER, J.- G. & DEVLEESCHOUWER, X., 1995. Arguments (Ostracodes) pour une régression culminant à proximité de la limite Frasnien-Famennien, à Sinsin. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 65, 51-68.
- CLAEYS, P., KYTE, F.T., HERBOSCH, A. & CASIER, J.- G., 1996. Geochemistry of the Frasnian-Famennian boundary in Belgium: mass extinction, anoxic oceans and microtektite layer, but not much iridium? *Special Papers of the Geological Society of America*, 307, 491-504.
- COEN, M., 1973. Faciès, conodontes et stratigraphie du Frasnien de l'Est de la Belgique pour servir à une révision de l'étage. *Annales de la Société géologique de Belgique*, 95 (2, 1972), 239-253.
- COEN, M., 1974. Sinsin. *In*: Bouckaert, J. & Streel, M. (eds), *Guidebook of Excursion I. International Symposium on Belgian micropaleontological limits from Emsian to Visean. September 1st to 10th 1974* (Guides: Bouckaert, J., Coen, M. (Leader), Coen-Aubert, M. & Dusar, M.): 4,6. Geological Survey of Belgium, Brussels.
- COOPER, G.A. & DUTRO, J.T., Jr., 1982. Devonian brachiopods of New Mexico. *Bulletins of American Paleontology*, 82 & 83 (315), 215 pp.
- DUTRO, J.T., Jr., 1986. The Late Devonian extinction event as recorded by articulate brachiopod ranges in the United States of America. *In*: Racheboeuf, P.R. & Emig, C. (eds), Les Brachiopodes fossiles et actuels, Actes du 1er Congrès International sur les Brachiopodes, Brest 1985. *Biostratigraphie du Paléozoïque*, 4, 455-464.
- FARSAN, N.M., 1986a. Frasnian mass extinction a single catastrophic event or cumulative? (Faunistic investigations at the Frasnian-Famennian boundary in south-central Asia). *In*: Walliser, O.H. (ed), Global bio-events. A critical approach. Proceedings of the first international meeting of the IGCP Project 216: "Global biological events in earth history". *Lecture Notes in Earth Sciences*, 8, 189-197.
- FARSAN, N.M., 1986b. Faunenwandel or Faunenkrise? Faunistische Untersuchung der Grenze Frasnium/ Famennium im mittleren Südasien. *Newsletter on Stratigraphy*, 16 (3), 113-131.
- GAETANI, M., 1965. The geology of the Upper Djadjerud and Lar valleys (North Iran). II. Palaeontology. Brachiopods and molluscs from Geirud Formation, Member A (Upper Devonian and Tournaisian). *Rivista Italiana di Paleontologia e Stratigrafia*, 71 (3), 679-771.

GOLSHANI, F., JANVIER, P., BRICE, D., CORSIN, P. & de LAPPARENT, A.F., 1972. Découverte d'une faune de Poissons et de restes de Végétaux dans le Dévonien supérieur de Bidu, en Iran central. *Comptes rendus hebdomadaires des séances de l' Académie des Sciences*, D, 275 (19): 2103-2106.

GOSSELET, J., 1887. Note sur quelques rhynchonelles du terrain dévonique supérieur. *Annales de la Société géologique du Nord*, 14 (1886-1887), 188-221.

HALL, J., 1860. Contributions to palaeontology 1858 and 1859. Annual Report of the Regents of the University of the State of New York, 13, 55-125.

HALL, J., 1867. Natural History of New York. Part VI: Palaeontology. Volume IV, Part I containing descriptions and figures of the fossil brachiopods of the upper Helderberg, Hamilton, Portage and Chemung groups. Geological Survey of the State of New York, Albany, 428 pp.

LIEPIN_, P., 1958. O faune brakhiopod dankovolebedyanskikh sloev Tsentral'nogo Devonskogo Polya. *Izvestiya Akademii Nauk Latviiskoi SSR*, 1 (126), 143-154.

LYASHENKO, A.I., 1958. Brakhiopody nizhnefranskikh otlozheniy tsentral'noy chasti Russkoy Platformy. *Trudy Vsesoyuznogo Nauchno-Issledovatelskogo Geologorazvedochnogo Neftyanogo Instituta* (VNIGNI), 9, 105-156, 394-415.

LYASHENKO, A.I., 1959. Atlas brakhiopod i stratigrafiya devonskikh otlozheniy tsentral'nykh oblastey Russkoy platformy. *Vsesoyuzny nauchno-issledovatel'skiy geologorazvedochny neftyanoy institut (VNIGNI)*, 451pp. Gostoptekhizdat, Moskva.

LYASHENKO, A.I., 1973. Brakhiopody i stratigrafiya nizhnefranskikh otlozheniy yuzhnogo Timana i Volgo-Uralskoy neftegazonosnoy provintsii. *Trudy Vsesoyuznogo Nauchno-Issledovatelskogo Geologorazvedochnogo Neftyanogo Instituta* (VNIGNI), 134, 279 pp.

MAILLIEUX, E., 1936. La faune des schistes de Matagne (Frasnien supérieur). *Mémoires du Musée royal d'Histoire naturelle de Belgique*, 77, 75 pp.

MARKOVSKIY, B. & NALIVKIN, D., 1934. Zadonskie i eletskie sloi. *Trudy Glavnogo Geol.- Hidro.-Geodezicheskogo Upravleniya*, N.K.T.P., 313.

MARTIN, F., 1984. Acritarches du Frasnien Supérieur et du Famennien Inférieur du bord méridional du Bassin de Dinant (Ardenne belge). *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, *Sciences de la Terre*, 55 (7), 57 pp.

MURCHISON, R.I., de VERNEUIL, E. & de KEYSERLING, A., 1845. Géologie de la Russie d'Europe et des Montagnes de l'Oural, 2, 544 pp.

NALIVKIN, D.V., 1941. Brakhiopody Glavnogo Devonskogo Polya. *In: Fauna Glavnogo Devonskogo Polya*. Paleontologicheskiy Institut, Akademiya Nauk SSSR, 139-195.

NALIVKIN, D.V., 1947. Klass *Brachiopoda*. Brakhiopody. *In*: NALIVKIN, D.V. (Red.), Atlas rukovodyashchikh form iskopaemykh faun SSSR, tom III, Devonskaya Sistema. Moskva, Leningrad, pp.63-134.

PHILLIPS, J., 1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon and West Somerset, text (231pp.) and plates (60). Longman, Green, Brown & Longmans. London.

RIGAUX, E., 1908. Le Dévonien de Ferques et ses Brachiopodes, 33pp. Boulogne-sur-Mer.

SANDBERG, C.A., ZIEGLER, W. & DREESEN, R., 1988a. Stop A8 Sinsin road section = pp.68-69 *in* Field Trip A Ardennes (Belgium), and Eifel Hills (Federal Republic of Germany), 22.-24.July. *In*: Ziegler, W. (ed), 1st International Senckenberg Conference and 5th European Conodont Symposium (ECOS V), Contributions I. *Courier Forschungsinstitut Senckenberg*, 102 (1), 9-155.

SANDBERG, C.A., ZIEGLER, W., DREESEN, R. & BUTLER, J.L., 1988b. Late Frasnian mass extinction: conodont event stratigraphy, global changes, and possible causes. *In*: Ziegler, W. (ed), 1st International Senckenberg Conference and 5th European Conodont Symposium (ECOS V), Contributions I. *Courier Forschungsinstitut Senckenberg*, 102 (3), 263-307.

SARTENAER, P., 1958. De l'importance stratigraphique des Rhynchonelles famenniennes situées sous la zone à Camarotoechia omaliusi GOSSELET, J., 1877). Troisième Note: le groupe de la Camarotoechia nux. Bulletin de l'Institut royal des Sciences naturelles de Belgique, 34 (23).

SARTENAER, P., 1960. Visage 1960 de la "tranchée de Senzeilles" (partie famennienne). *Bulletin de la Société belge de Géologie*, 68 (3 et dernier), 430-442.

SARTENAER, P., 1961. Late Upper Devonian (Famennian) rhynchonelloid brachiopods. *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 37 (24), 10pp.

SARTENAER, P., 1964. Rhynchonelloidea de Shogran et Kuragh (Chitral). Italian expeditions to the Karakorum (K2) and Hindu Kush. Leader: A. Desio. Scientific Reports. Pt.IV: Paleontology-Zoology-Botany, 1, 51-62.

- SARTENAER, P., 1966. Ripidiorhynchus, nouveau genre de Brachiopode Rhynchonellide du Frasnien. *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, 42 (30).
- SARTENAER, P., 1968. De l'importance stratigraphique des Rhynchonelles famenniennes situées sous la Zone à Ptychomaletoechia omaliusi (GOSSELET, J., 1877). Sixième Note: Pampoecilorhynchus n. gen. Bulletin de l'Institut royal des Sciences naturelles de Belgique, 44 (43).
- SARTENAER, P., 1970. Le contact Frasnien-Famennien dans la région de Houyet Han-sur-Lesse. *Annales de la Société géologique de Belgique*, 92 (1969, 3 et dernier), 345-357.
- SARTENAER, P., 1973. Réflexions à propos de la limite entre les étages frasnien et famennien fixée depuis près d'un siècle dans la "tranchée de Senzeilles". *Bulletin de l'Institut royal des Sciences naturelles de Belgique*, *Sciences de la Terre*, 49 (4).
- SARTENAER, P., 1974a. Que sont les Schistes de Matagne? Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 50 (4).
- SARTENAER, P., 1974b. La Zone à Caryorhynchus tumidus, zone nouvelle de la partie supérieure du Frasnien. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 50 (6).
- SARTENAER, P., 1977. Un nouveau genre de Rhynchonellidé de la fin du Frasnien. *In*: Colloque Paléozoïque Europe Occidentale (2ème partie). *Annales de la Société Géologique du Nord*, 97 (1), 67-76.
- SARTENAER, P., 1983. Proposal for an international decision on the Frasnian/Famennian boundary (Middle *Palmatolepis triangularis* Zone). SDS meeting 1983, Montagne Noire, 14 pp.
- SARTENAER, P., 1985. *In*: ZIEGLER, W. & WERNER, R. (eds), Devonian Series Boundaries Results of worldwide Studies. The stratigraphic significance of rhynchonellid genera at the Frasnian-Famennian Boundary. *Courier Forschungsinstitut Senckenberg*, 75, 319-329.
- SARTENAER, P., 1986. L'accroissement du nombre de genres Rhynchonellides dévoniens traduit-il une nécessité ou une option? *Bulletin de l'Institut royal des de Belgique*, *Sciences de la Terre*, 56, 145-150.
- SARTENAER, P., 1996. Are all rhynchonellid species of the Main Devonian Field assigned to the genus *Ripidiorhynchus* SARTENAER, P., 1966 valid? The Third

- Baltic Stratigraphical Conference, Tallinn, October 8-10, 1996. *Abstracts*, 57-58.
- SARTENAER, P., 1997. Are all rhynchonellid species of the Main Devonian Field assigned to the genus *Ripidiorhynchus* SARTENAER, P., 1966 valid? *Eesti Teaduste Akadeemia Toimetised. Geoloogia*, 46 (3), 146-149.
- SAVAGE, N.M., 1996. Classification of Paleozoic rhynchonellid brachiopods. *In*: Copper, P. & Jin, J. (eds), Brachiopods, Proceedings of the Third International Brachiopod Congress, Sudbury, Ontario, Canada, 2-5 September 1995, 249-260.
- SCHMIDT, H., 1965. Neue Befunde an paläozoischen Rhynchonellacea (Brachiopoda). *Senckenbergiana lethaea*, 46 (1), 1-25.
- SCHMIDT, H. & McLAREN, D.J., 1965. Paleozoic Rhynchonellacea. *In*: Moore, R.C. (ed), Brachiopoda, Part H of Treatise on Invertebrate Paleontology, H552-H597. The Geological Society of America.
- SORAUF, J.E., 1984. Devonian stratigraphy of the San Andres Mountains, Doña Ana, Sierra, and Socorro Counties, New Mexico. *Circulars of the New Mexico Bureau of Mines & Mineral Resources*, 189, 32 pp.
- SORAUF, J.E., 1988. Rugose corals from the Frasnian (Upper Devonian) Sly Gap and Contadero Formations of the San Andres Mountains, south-central New Mexico. *Memoirs of the New Mexico Bureau of Mines & Mineral Resources*, 44: 153-183.
- SOROKIN, V.S., 1978. Kompleksy zamkovykh brakhiopod franskogo yarusa Glavnogo Devonskogo Polya. *In*: BRANGULIS, A.P. (ed), Otsherki Geologii Latvii, Vsesoyuzny nauchno-issledovatelskiy Institut Morskoy Geologii i Geofiziki Ministerstva Geologii SSSR, 49-63. "Zinatne", Riga.
- STAINBROOK, M.A., 1942. Brachiopoda of the Cedar Valley beds of Iowa Inarticulata, Rhynchonellacea and Rostrospiracea. *Journal of Paleontology*, 16 (5): 604-619.
- STREEL, M. & VANGUESTAINE, M., 1988. Palynomorph distribution in the "extinction layer" near the Frasnian/Famennian boundary in the shelf facies in Belgium. Document submitted to the International Subcommission on Devonian Stratigraphy, meeting in Rennes, August 2000.
- STREEL, M. & VANGUESTAINE, M., 1989. Palynomorph distribution in a siliciclastic layer near the Frasnian/Famennian boundary at two shelf facies localities in Belgium. *Bulletin de la Société belge de Géologie*,

98 (Festschrift Eva PAPROTH), 109-114.

VANGUESTAINE, M., DECLAIRFAYT, T., ROUHART, A. & SMEESTERS, A., 1983. Zonation par Acritarches du Frasnien Supérieur - Famennien Inférieur dans les Bassins de Dinant, Namur, Herve et Campine (Dévonien Supérieur de Belgique). *Annales de la Société géologique de Belgique*, 106 (1), 121-171.

VENYUKOV, P.N., 1886. Fauna devonskoi sistemy severozapadnoi tsentral'noi Rossii. Geologicheskiy Kabinet S.-Peterburgskago Universiteta, 308 pp.

von BUCH, L., 1834. Über Terebrateln, mit einem Versuch, sie zu classificiren und zu beschreiben. Abhandlungen der königlichen Akademie der Wissenschaften zu Berlin.

von PEETZ, H., 1898. Hemiplethorhynchus, novy podrod roda Camarotoechia Hall. *Trudy Imperatorskago S.*-

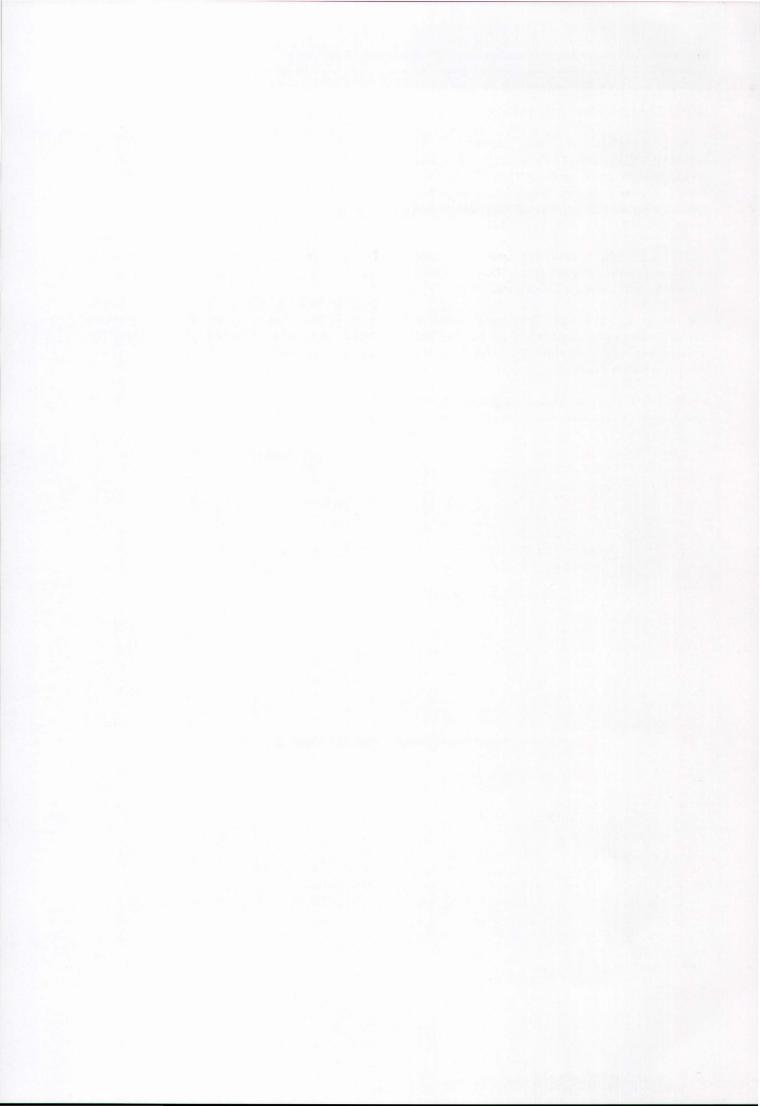
Peterburgskago Obshchestva Estestvoispytateley, 29 (1, 5), 178-181, 185-187.

YUDINA, Yu. A., 1991. Vnutrimakushechnye struktury novogo famenskogo roda rinkhonellid (brakhiopody). *Paleontologicheskii Zhurnal*, 1, 44-50.

YUDINA, Yu. A., 1999. Novy vid Ptychomaletoechia (Brachiopoda, Rhynchonellida) iz famenskikh otlozheniy Yuzhnogo Timana. *Paleontologicheskiy Zhurnal*, 2, 15-17.

YUDINA, Yu. A., 2000. Brachiopods of Palmatolepis triangularis Zone (Lower Famennian). The Millennium Brachiopod Congress, 10th-14th July, The Natural History Museum, London. Abstracts.

Manuscript received on 12.1.2001 and accepted for publication on 5.4.2001



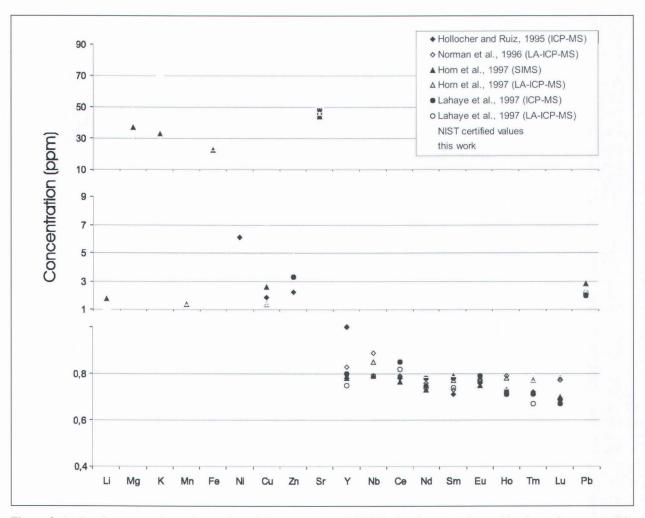


Figure 3. Analysed concentrations of a number of elements in the NIST614-glass in comparison with other values reported in literature. The analytical techniques used are between brackets. Bars represent 1 standard deviation.

3.3. Fluid inclusion analysis

3.3.1. Sample material

Quartz samples from a pegmatite in Minas Geraes (Brasil), containing large inclusions (50-100 µm), were used in the fluid inclusion study. All inclusions are present along secondary (pseudosecondary?) trails. Primary inclusions in growth zones or isolated in the crystals have not been identified. During cryogenic experiments, all of the inclusions show a similar melting behaviour, but a different melting temperature. The temperature of first melting ranges between -63.1 and -50.8°C. Three populations can be distinguished based on the final melting temperature of ice (Tm.; Fig. 4). Population I and II display a tight grouping, with Tm, -values ranging from -25.9 to -23.7°C and from -20.4 to -18.6°C, respectively. Population III shows a larger spread. Tm_{ice} varies between -15.2 and -6.0°C. These final melting temperatures of ice correspond to salinities ranging between 23.3 and 22.3 eq. wt% CaCl for population I, 20.8 and 19.8 eq. wt% CaCl, for population II and 17.9 and 10.2 eq. wt% CaCl, for population III (according to Oakes et al., 1990). In contrast to the common practice of addressing salinities as eq. wt% NaCl, we prefer to report all salinities as eq. wt% CaCl₂ in order to maintain a consistency among the data since Tm_{ice}-values < -21.2 °C cannot be expressed as eq. wt% NaCl. From each of the different populations, several inclusions were selected for LA-ICP-MS analysis.

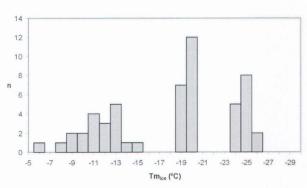


Figure 4. Tm_{ice} values of the fluid inclusions in the quartz samples investigated.

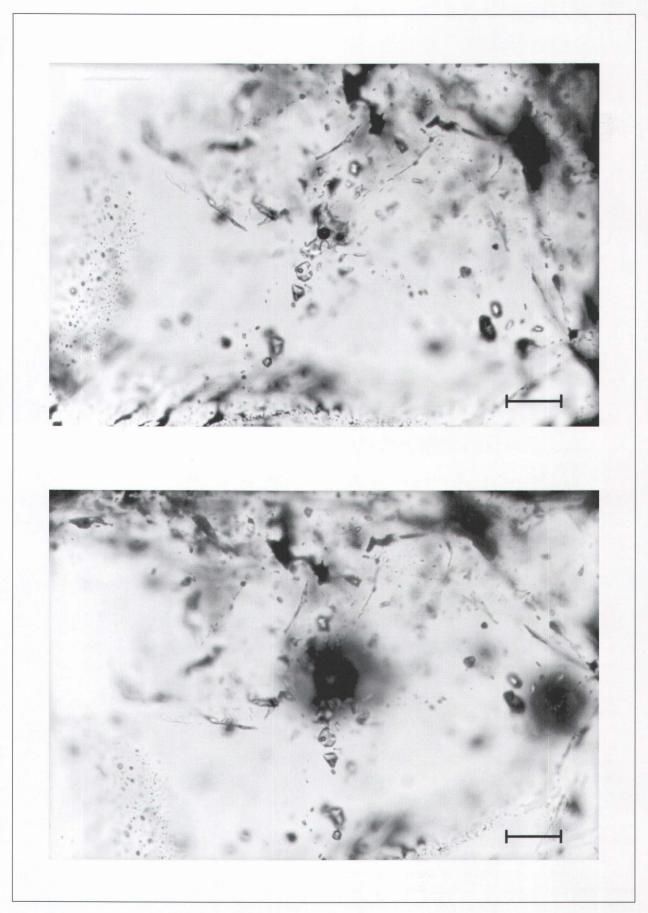


Figure 5. Photographs of a typical fluid inclusion in the quartz samples before and after ablation. Scale bar is $100 \, \mu m$.