

Anatomical distinctions of the Mesozoic lingulide brachiopods

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The long held view that *Lingula* represents an extremely bradytelic lineage is questioned. Examination of Mesozoic lingulides has shown that they significantly differ from their Recent relatives *Lingula* and *Glottidia* in having longer lophophoral cavities, shorter ventral canals, better developed posterior adductor muscles, and less acute umbones. Morphological characters of the shell interior are needed to identify members of the Lingulidae, not solely external shell characteristics. The apparent evolutionary tendency towards a reduction of the volume of the lophophoral cavity contradicts the traditional view that the 'living fossil' *Lingula* has survived without significant morphological change since the Paleozoic. Actually the today living lingulide genera probably arose in the early Cenozoic. A new inarticulate brachiopod genus, *Lingularia* is introduced, with three new species, Middle Triassic *L. siberica*, Middle Jurassic *L. similis*, and Cretaceous *L. smirnovae*.

Key words: lingulides, Brachiopoda, shell morphology, taxonomy, evolution, Paleozoic–Recent.

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Introduction

In the fossil brachiopods general shell characteristics, usually the only preserved, do not provide the necessary information to discriminate either genus and species. In result, too many fossil lingulide species have been defined simply on the basis of the shell proportions and erroneously ascribed to *Lingula* only because of their elongate shell outline. It is well known now that such features may vary even between different populations of the same species, in response to environmental conditions. In the

living lingulide species a number of specific morphological characters have been selected by Emig (1982, 1983) to define species. Those characters (in particular the shell interior) have been used for the first time in the present study on Mesozoic lingulides ranging in age from the Triassic to Cretaceous. Numerous and exceptionally well-preserved specimens of Jurassic lingulides from Spitsbergen (collection of the Polish paleontological expedition held in 1979) have been compared with small collections of related species from the Triassic of Siberia (Dagys 1965), and from the Cretaceous of Kazakhstan (received from T. Smirnova, Moscow). They show morphological differences of sufficient magnitude to separate in a new lingulide genus *Lingularia*, which was already suggested by Rowell (1970).

The collection of the studied lingulides is deposited in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland (abbreviation is ZPAL followed by specimen number).

Comparison of the Mesozoic *Lingularia* with the living lingulide genera *Lingula* and *Glottidia*

The genus *Lingularia*, with the present three identified species, *L. similis* n. sp., *L. siberica* n. sp., *L. smirnovae* n. sp., appears closely related to the genus *Lingula* (seven extant species). To distinguish both genera on the basis of the external shape and size of the shell is impossible which is why so many previous authors attributed Paleozoic and Mesozoic lingulide specimens to *Lingula*.

A comparison of the shell ratios (Tab. 1) between the living genera *Lingula* and *Glottidia* and the Mesozoic *Lingularia* shows that *Lingularia* species are close to the broadest *Lingula* species, *L. adamsi* Dall 1873 and *L. tumidula* Reeve 1841. Other *Lingula* species, i.e. *L. anatina* Lamarck 1801, *L. reevei* Davidson 1880, *L. rostrum* (Shaw 1798) overlap with *Lingularia* species only in the W/L ratio range but not with the mean W/L ratio. There is no overlap between *Glottidia* species and either *Lingula* and

Tab. 1. Range of the width to length (W/L), height to length (H/L), and height to width (H/W) ratios in shells of *Glottidia*, *Lingula* and *Lingularia*. The W/L mean indicates the range of the W/L mean of the species. In *Lingularia*, the H/L and H/W ratios based on 5 specimens of *L. similis* and 2 of *L. smirnovae*. Data on *Lingula adamsi* from Emig & Hammond (1981).

Genera	n	W/L		n	H/L		H/W	
		range	mean		range	mean	range	mean
<i>Glottidia</i>	35	0.32-0.44	0.33-0.40	35	0.09-0.11	0.09	0.15-0.24	0.20
<i>Lingula</i>	135	0.44-0.53	0.43-0.48	95	0.06-0.12	0.10	0.14-0.25	0.20
except <i>L. adamsi</i>	31	0.54-0.70	0.63	19	0.11-0.18	0.13	0.16-0.26	0.20
and <i>L. tumidula</i>	7	0.58-0.69	0.63					
<i>Lingularia</i>	82	0.45-0.75	0.51-0.65	17	0.12-0.23	0.16	0.20-0.44	0.32

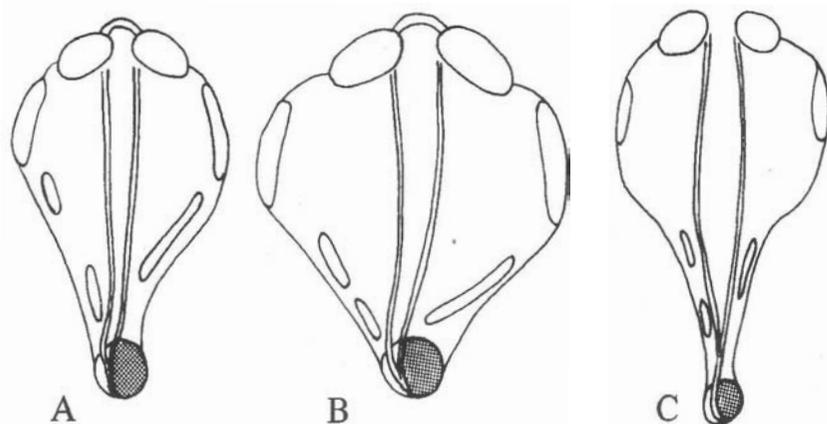


Fig. 1. Disposition of the pair of narrow V shaped ridges or lines on the ventral side of the soft body, and their relation to the muscle arrangement and perimial line. Stippled ornament indicates the muscle scar of the posterior adductor, as observed on the ventral valve interior. □A. *Lingula anatina* Lamarck 1801. □B. *L. adamsi* Dall 1873. ○C. *Glottidia albida* (Hinds 1844).

Lingularia species. From the data in Tab. 1, one can conclude that *Lingularia* species have a broader and a more convex shell than *Linguh* species. However, *Linguhria smirnovae* seems to have the lowest H/L and H/W ratios, close to those of *Lingula* species.

The shell of *Lingularia*, which is similar to *Lingula* in its elongate oval outline, does not have a straight anterior margin and external diverging 'ridges' from the posterior part of the shell to the anterior margin corners, particularly when compared with *Lingula tumidula* and *L. adamsi*. In the latter species, the rectangular-shaped shell is not simply biconvex, but the ventral valve is higher than the dorsal one (Emig 1982). In *Lingula*, the posterior margin and beak are generally more acute than in *Lingularia*, whilst the pedicle groove is flat and less deep than in *Lingularia*.

A pair of V-shaped grooves is also present on the internal side of the ventral valve in *Lingula* and *Glottidia* (Fig. 1). As in *Lingularia*, the grooves extend from the anterior adductors (Fig. 4). These grooves do not join at the midline of the shell under the posterior adductor in *Lingula* but on the right side of this muscle. They may curve inwards when surrounding a muscle (Fig. 1). In both living genera, these narrow grooves appear in general as only one broad or several small lines, visible on the dry shell. From histological investigation on living specimens, these grooves or lines are impressions of the pedicle nerves, as suggested previously by Broglio-Loriga (1968) and Hölmer (1991) in fossil material, and their traces can be related to the degree of internal thickening of the ventral valve. Such V-shaped grooves are also figured in *Lingula antarctica* from the Eocene of Seymour Island (Antarctica) by Wiedman *et al.* (1988) and in '*Glottidia* *rostrata*' from the Cretaceous of the Alexander Island (Antarctica) by Thomson & Owen (1979).

Tab. 2. Variation of the relative length of the lophophoral cavity and relative extent of the anterior mantle canals in *Glottidia*, *Lingula* and *Lingularia* (as well as in *Langella*, and *Pseudolingula*, taken from Holmer 1991), given as percentage of the whole valve length. The length of the lophophoral cavity is the distance between the distal limit of the muscle scars (i.e. anterior adductors on the ventral valve and anterior obliques on the dorsal valve) and the anterior margin of the valve. Extent of the mantle canal tip is expressed by a ratio of the distance between the tip of the canals and the anterior margin of the valve to the whole valve length.

Genera	nV/nD	Lophophoral cavity (Lc)				Mantle canal tip (Mct)				Mct-Lc	
		Ventral %		Dorsal %		Ventral %		Dorsal %		V%	D%
		range	mean	range	mean	range	mean	range	mean	mean	
<i>Glottidia</i>	35/35	33-43	38	19-33	26	9-15	13	12-15	14	25	12
<i>Lingula</i>	44/44	35-46	41	24-35	31	17-22*	20	17-23*	20	21	11
<i>Lingularia</i>	13/17	37-57	46	27-36	33	24-37	32	20-23	21	14	12
<i>Langella</i>	4/2	45-55	51	44-52							
<i>Pseudolingula</i>		49-64	52	25-51	39						

*) except for *Lingula adamsi* which is respectively 12 and 13.

A fairly narrow dorso-central ridge at the level of the anterior oblique muscles is present also in *Lingula* species, but not in *Glottidia*. The fact that the ventral canals in *Lingularia* are shorter than the dorsal canals (as measured by the distance between the distal limit of the mantle canal to the anterior margin of the valve) led us to compare the measurements with those obtained in living lingulide species (Tab. 2; Fig. 2). In addition, we have also measured and compared the length of the lophophoral cavity (part of the mantle cavity occupied by the lophophore), i.e. distance between the distal limit of the anterior adductor muscle scars (ventral valve) and of the anterior oblique scars (dorsal valve) to the anterior margin of the valve (Tab. 2). The attachment position of the lophophore to the body wall is determined by these muscles. Our data (Tab. 2; Fig. 2) show that only *Lingubria* has 'asymmetrical' canals while the lophophoral cavity decreases in length and volume from *Lingularia* to *Lingula* and then to *Glottidia* because the anterior muscles on dorsal and ventral side have moved distally and the width and height of the shell decrease. The length of the dorsal canals remains similar in all three genera (Fig. 2) whilst the length of the ventral canals increases, and their tips end more distally from *Lingubria* to *Lingula* to *Glottidia*. This progression is related to the muscle migration in the two latter genera in which the dorsal and ventral tips are at the same level. *Glottidia* has a specific characteristic, i.e. sack-like extensions of the mantle, which probably function in respiration and in uptake of dissolved organic matter (Emig 1983).

The general muscle disposition, or at least that of muscle scars, appears close in all the three genera, and similar in *Lingularia* and *Lingula* (Figs 1, 4), but there are specific arrangements in each species. Our terminology

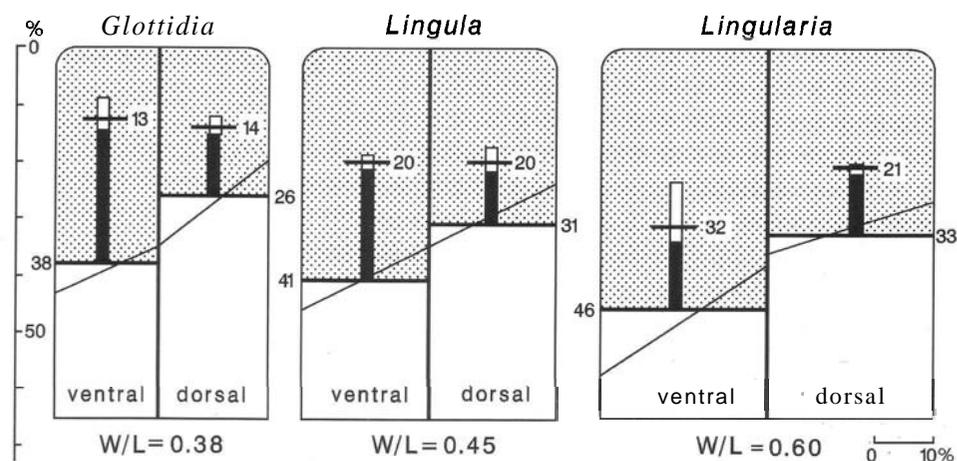


Fig. 2. Diagram of the extensions of the lophophoral cavity (stippled ornament indicates mean space) and of the mantle canals based on average shell dimensions in *Glottidia*, *Lingula* and *Lingularia* (see text and Tab. 2 for explanation).

for body muscles is that of Emig (1982). In *Glottidia*, the muscle arrangement is related directly to the internal septa, a generic character (Emig 1983). *Lingularia* differs in the shape of the posterior adductor muscle, which is heart-like whilst it is rounded in both living genera. It is probable that the posterior adductor is of paired origin: the heart-like shape can be considered as a remnant of this origin, whilst only the left adductor, or left part of the former shape, remains in *Lingula* and *Glottidia*, as emphasised by the right-side migration of the pair V-shaped grooves in the ventral valve (Fig. 1) and the presence of a single left muscle scar in both latter genera. Two posterior scars occur in *Lingularia* on each side of the junction of those grooves (Fig. 4). The perimal line, which is the line of attachment of the body wall to the valves, that surrounds the body muscles, is well-marked in all the three genera.

In summary, *Lingularia* differs from *Lingula* in having asymmetrical mantle canal extensions, in the morphology of the umbonal regions, the shape of the posterior adductor muscle scar, and the disposition of the pair of narrow subparallel, V-shaped, grooves. The similarities between both genera imply that *Lingularia* also had a spirolophous lophophore and a comparable ecological behaviour to the living lingulides.

Comparison of *Lingularia* with fossil lingulide genera

Shells of *Barroisella* Hall & Clarke 1892 and *Langella* Mendes 1961 also have a pair of ventral V-shaped grooves, but they differ from *Lingularia* in the presence of a more or less extended dorsal middle ridge. In *Barroisella*, this ridge is described in the original paper by Hall & Clarke (1892: p. 63)

as: 'a low and thickened median septum, bifurcating in the middle of the valve, the angle being occupied by an intercalated ridge, which extends for twice the length of the branches of the septum'. The triangular umbo is formed by propareas divided by a broad pedicle groove in continuation with the internal valve surface in *Barroisella* but not in continuation in the described *Lingularia* species. From the original description by Bittner (1899) and the redescription by Dagys (1965), *Lingula borealis* seems to belong to the genus *Barroisella*, as does *L. occidentaustralis* described by Archbold (1981) and the specimens referred to *L. sp. cf. L. borealis* by Rowell (1970) from the Triassic of West Pakistan. Consequently, *Barroisella* now has a longer stratigraphic range from the Late Devonian to Triassic at least. The W/L ratio range varies from 0.50–0.52 (Dagys 1965) to 0.53–0.60 (Archbold 1981), H/L is 0.09–0.12, and H/W is 0.17–0.22). The W/L ratio range in *Langella imbituwensis* (Oliviera 1930) from the Permian-Carboniferous of Brazil varies from 0.55 to 0.69 (mean 0.61 for 7 specimens; data from Oliviera 1930; Lange 1952; Mendes 1961), and the lophophoral cavity, estimated on 5 and 2 specimens respectively from the figures of Lange (1952) and Mendes (1961), seems more extended than in *Lingularia* (Tab. 2), as well as in *Pseudolingula quadrata* from the Late Ordovician of Sweden and Estonia according to data of Holmer (1991). As shell ratios are similar in *Lingularia*, *Langella* and *Barroisella*, they cannot be used to separate genera and species. Genus *Semilingula*, introduced by Popov (*in* Egorov & Popov 1990) from the Lower Permian of Siberian Platform and Novaya Zemlya, shows similarities with *Lingularia* in, i.e. 'asymmetrical' mantle canals, unpaired posterior adductor scars, V-shaped ventral grooves. There are, however, differences in muscle size and arrangement, straight lateral margins of the perimimal line, degree of extension of a broad dorsal median ridge, in morphology of the umbonal region with very reduced pseudointerareas and particularly in the presence of diverging vascula media on the dorsal side. This latter character does not occur in the family Lingulidae, the genera of which share, like *Lingularia*, only a pair of main mantle canals in each valve of the shell. Consequently, genus *Semilingula* cannot be included in Lingulidae as proposed Popov (*in* Egorov & Popov 1990).

A pair of diverging grooves on the ventral valve, like those observed in *Lingularia*, *Lingula*, *Glottidia*, *Barroisella*, *Langella* occurs also in other genera, such as in the Ordovician obolids *Fezzanoglossa* and *Wadiglossa* (Havliček & Massa 1973; Havliček & Röhlich 1987), Ordovician *Ectenoglossa* and *Pseudolingula* (Holmer 1991), Cambrian to Ordovician *Experilingula* and *Mirilingula* (Koneva & Popov 1983), in Silurian *Lingula*(?) *lounhensis* (Mansuy 1912) and *Lingula*(?) *lewisii* (Holmer 1991), in Ordovician *Paterula* (Percival 1978), and in Permian *Semilingula* (Egorov & Popov 1990). In several Palaeozoic lingulides, the mantle canals appear to be shorter on one side than on the other one, e.g. the ventral being shorter in *Lingula lewisii*, the dorsal in *Pseudolingula* and *Ectenoglossa* (from figures of

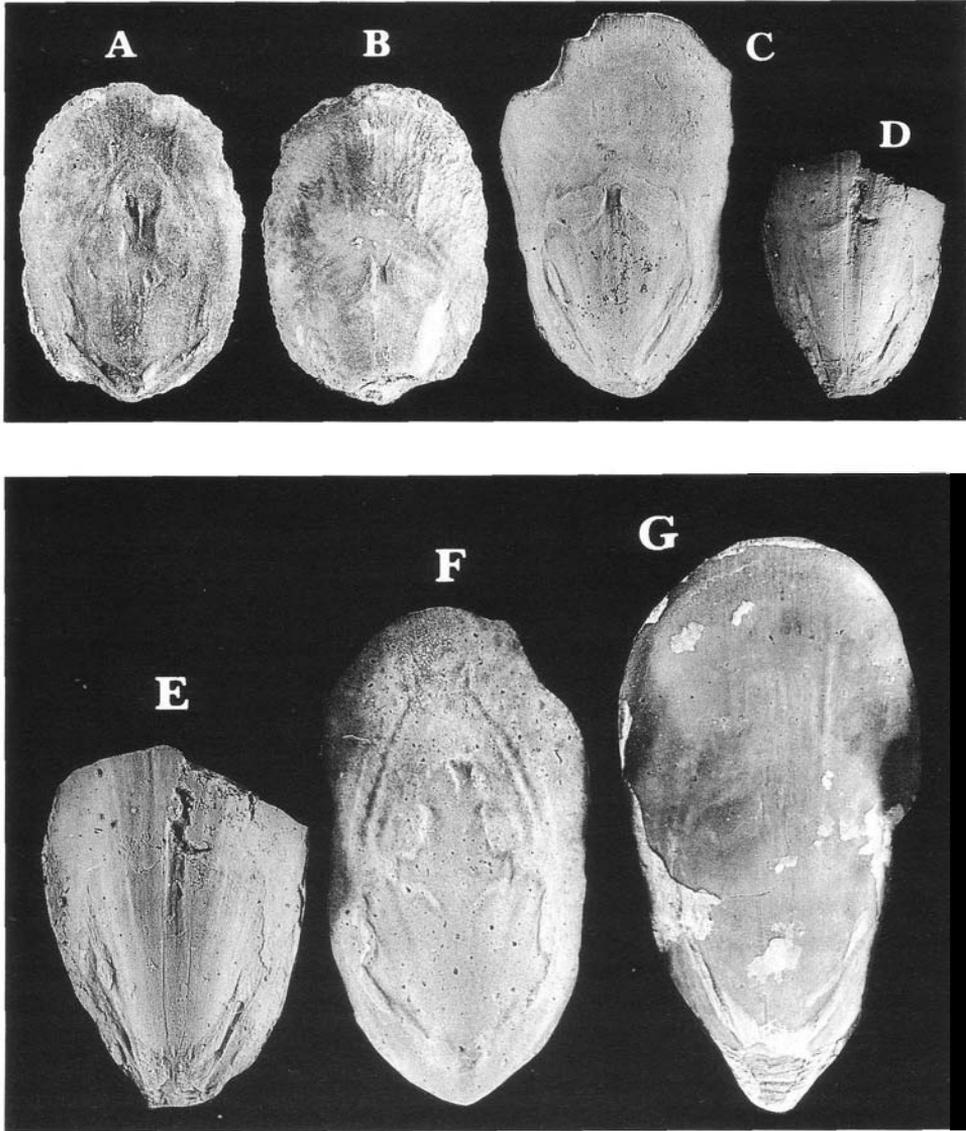


Fig. 3. Internal moulds of *Lingularia similis* gen. et sp. n. valves from phosphorite nodules of the Toarcian/Aalenian Brentskardhaugen beds, Wimanfjellet, Spitsbergen. □A, B. Holotype ZPAL Bp.XXIV/385, dorsal and ventral sides, x 2. □C. Paratype ZPAL Bp.XXIV/416, ventral side showing muscle scars, perimial line, and V-shaped grooves, x 3. OD, E. Paratype ZPAL Bp.XXIV/246, V-shaped grooves on the ventral side, x 2 and 3, respectively. OF. Paratype ZPAL Bp.XXIV/432, dorsal side showing mantle canals, muscles scars and perimial line, x 3. □G. Paratype ZPAL Bp.XXIV/418, ventral side with muscle scars, perimial line, V-shaped grooves, and umbonal region, x 3.

Holmer 1991). In *Semilingula taimyrensis* according to Egorov & Popov (1990) the ventral mantle canal is shorter.

Discussion on species related to *Lingularia*

Several fossil species previously referred to *Lingula* possibly belong to *Lingularia* although a re-examination of specimens in order to study the internal morphology of shell is necessary to support this statement, which is based on the original descriptions and figures of others. Our review here is therefore not exhaustive.

According to the description and figures of Graham (1970) of material from the Carboniferous of Scotland, *Lingula mytilloides* Sowerby 1812 (including *L. (?) elliptica* Phillips 1836 and *L. parallela* Phillips 1836) and *L. straeleni* Demanet 1934 (probably also a synonym of *L. mytilloides*), show the characteristics of the genus *Lingularia* and appear close to *Lingularia similis* sp. n. or *L. siberica* sp. n. in external and internal shell features but they differ by their convex-rounded dorsal mantle canals (Graham 1970: Pls 14:9, 15:4, Fig. 9). Graham (1970) pointed out that the shell of smaller specimens of *L. mytilloides* is generally more convex than in larger ones, that we also observed in our specimens of *Lingularia similis*. The shell dimensions of *L. mytilloides* from data of Graham (1970) and Bloxman & Thomas (1969), who report on several hundreds of specimens from the Carboniferous of South Wales, are: W/L range 0.54–0.76, H/L range 0.9–0.18 (0.15–0.32 in *L. straeleni*). The two other '*Lingula*' species described by Graham (1970), *L. lumsdeni* Graham (W/L range 0.48–0.56) and *L. squamiformis* Phillips 1836 (W/L range 0.50–0.72), can also be referred to *Lingularia*.

The specimens described as *Lingula tenuissima* by Broglio-Loriga (1968) from the Early Triassic of the Dolomites, Italy (W/L — 0.58–0.75; mean 0.63) have strong similarities with *Lingularia*. The material seems to be well-preserved with internal morphology that is described only briefly and poorly figured.

Lingula aoraki, described by Campbell (1987) from the Triassic of New Zealand, which is close to *L. olenekensis* Dagys 1965, probably belongs to *Lingularia*, but the W/L ratio (0.33–0.54, mean 0.42 on 12 specimens) is nearer to that of living forms, while the ratio of the ventral lophophoral cavity to shell length 43 per cent, is similar to *Lingularia* (Tabs 1, 2).

From the short original description of *Lingula polaris* Lundgren 1883, and of *L. arctica* Wittenburg 1910 from the Triassic of Spitzbergen it is impossible to decide on their generic identity, as is the case for *Lingula polaris* described by Bohm (1903) from the Triassic of the Bear Island; but because they are from closely adjacent localities and from the same stratigraphic horizon, it is possible to suggest that these two species belong to *Lingularia similis*.

The *Lingula* sp. described by Bottcher (1982) from the Cretaceous of Nubia, Egypt, has the posterior adductor scar similar to that in *Lingularia* but the general shape and form of the shell and the lophophoral cavity are closer to the living *Lingula*. By contrast, *Lingula sturti* described by Morton

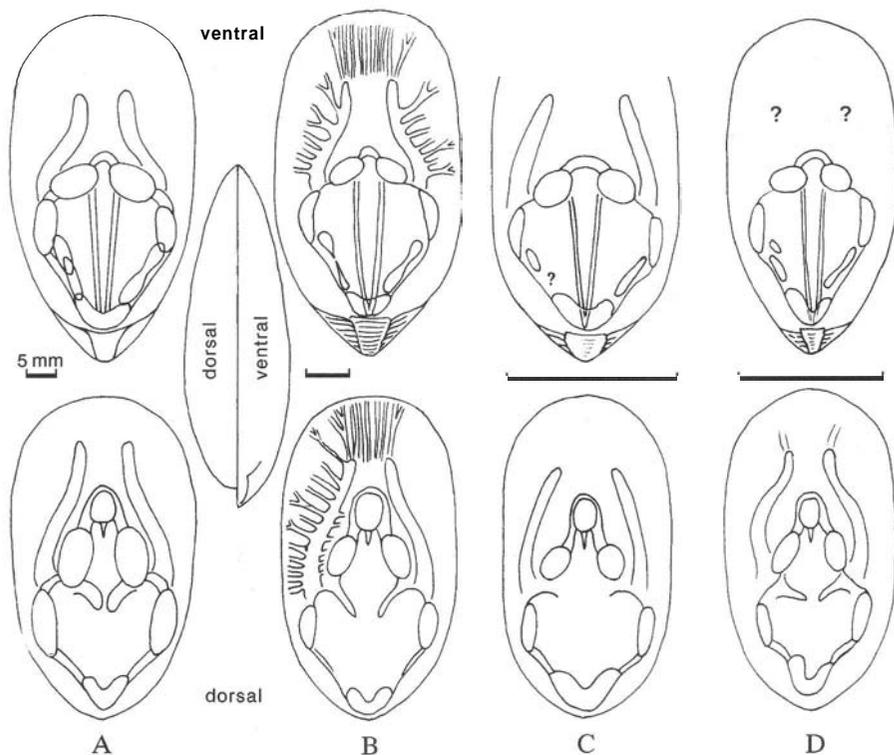


Fig. 4. Arrangement of the musculature within the perimial line and disposition of the two main anterior mantle canals in *Lingularia* species. □A, B. Middle Jurassic *L. similis* sp. n., outline of muscle scar range observed in the population and their arrangement in a specimen; transverse outline of the shell inserted in between. □C. Middle Triassic *L. siberica* sp. n., with outline range of muscle scars. OD. Middle Cretaceous *L. smirnovae* sp. n., umbonal region represented in the ventral valve (see text for explanation).

(1982) from the Cretaceous of SW Australia appears to be a *Lingularia* species.

Taxonomic and evolutionary implications

For fossil specimens with oval-elongate shells that are sometimes defined wrongly as being of *Lingula* shape or type, the external characteristics of the shell are not sufficient either to identify or describe a species. Variations in such features must be taken into account and cannot be used to separate genera or species. The height of fossil valves has to be used with care because of possible compaction during the fossilization processes.

Many fossil species have been separated only on the basis of differences in such shell variations, which explains the large number of named *Lingula* species and the difficulty of now referring specimens to a genus and species. For example, as stated above, *Lingularia*, *Barroisella*, and

Langella cannot be separated on the basis of their external shell characters (see also Fig. 6). A recent analysis by the junior author (unpublished results) of shell dimensions in five populations of *Lingula anatina* from New Caledonia demonstrates that environmental conditions can have a direct influence on the shell growth and shape of a population as in many brachiopods (Wright 1972).

To describe or determine a fossil species, internal shell and morphological characters must be available and used as in living forms. Nevertheless, calcification of internal areas of the valves, which can be highly variable between populations, must not be confused with taxonomic characters, such as grooves or ridges, which are of high taxonomic value. Consequently, good knowledge of living forms is required before interpreting important aspects of morphology. The narrow ventral V-shaped grooves can appear in fossil specimens as ridges, probably because of particular conditions of fossilization.

Comparison of the studied characters between *Lingularia* and living genera leads to some evolutionary considerations. Trends include a shortening of the lophophoral cavity; an increase in the length of the ventral mantle canals, from an 'asymmetrical' positioning of the termination of the canal tips up to termination at the same distal level (Fig. 2; Tab. 2); a decrease in the width and the height of the shell (Fig. 2; Tab. 1); a reduction of the posterior adductor muscle to the left area and a correlative change in the posterior disposition of the pedicle nerves (Figs 1, 4); a flattening of the pedicle groove and a trend towards a more acute umbonal region of the valves. From these apparent evolutionary trends and in line with Bassett's (1979, 1986) opinion and comments on Silurian lingulide genera, one can argue that no Paleozoic or Mesozoic (at least Lower Mesozoic) species of Lingulidae belongs to the extant genera *Lingula* or *Glottidia*. One of the main evolutionary tendencies appears to be a reduction of the volume of the lophophoral cavity when comparing Palaeozoic *Pseudolingula* and *Lungella* with Mesozoic *Lingularia* and then with living *Lingula* and *Glottidia* (see Tab. 2). These trends do not therefore support the traditional and commonly held view of Recent living lingulides as 'living fossils' that have survived and have undergone little significant morphological change since the Palaeozoic.

Descriptions of the new taxa

Class Inarticulata Huxley 1869

Order Lingulida Waagen 1885

Family Lingulidae Menke 1828

Genus *Lingularia* gen. n.

Type species: *Lingularia similis* gen. et sp. n.

Etymology: The name refers to the close relationship with the genus *Lingula*.

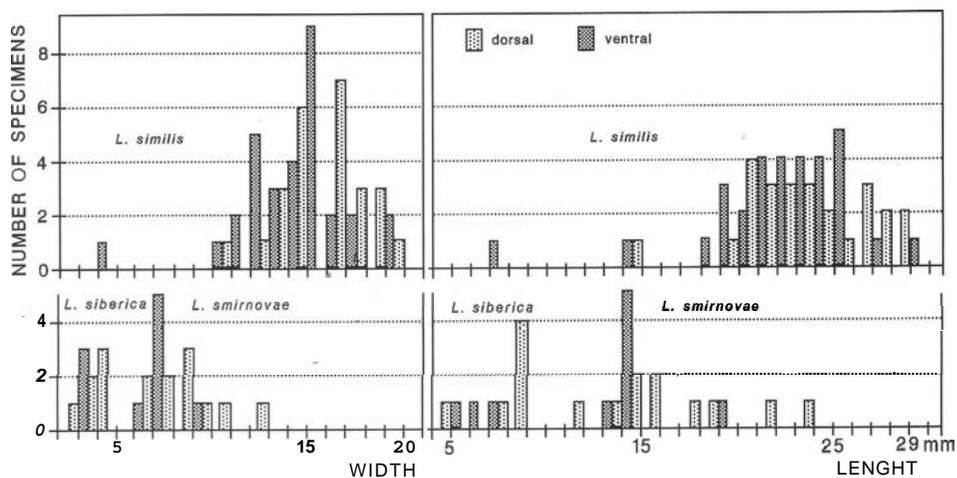


Fig. 5. Frequency distribution of the valve length and width measured in *Lingularia similis* sp. n. from the Middle Jurassic of Spitsbergen, *L. siberica* sp. n. from the Middle Triassic of Siberia, and *L. smirnovae* sp. n. from the Middle Cretaceous of Kazakhstan (see text).

Diagnosis.—Shell elongate oval in outline, lateral margins subparallel, anterior margin broadly rounded. Valves weakly to strongly convex. Dorsal valve with posterior margin rounded, narrow median beak sometimes present, narrow central ridge (internal side) extending over about 1 millimetre posterior to anterior oblique muscle scars. Ventral valve (internal side) with triangular umbo formed by small to large propleas, continuous with posterolateral margins and separated by deep pedicle groove; pair of narrow subparallel, V-shaped, grooves extending from the anterior adductor pair to posterior adductor where grooves join. Posterior adductor scar heart-like in outline. Main ventral canals shorter than dorsal canals.

Species included: *Lingularia siberica* sp. n. from the Middle Triassic of northern Siberia, *Lingularia similis* sp. n. from the Jurassic of Spitsbergen, *Lingularia smirnovae* sp. n. from the Cretaceous (Albian-Santonian) of western Kazakhstan. Tentatively referred species are *Lingulamylloides*, *L. straeleni*, *L. lumsdeni*, *L. squamiformis*, *L. aoraki*; see discussion above.

Occurrence.—Carboniferous of Scotland, south Wales, Triassic of the Bear Island and Spitsbergen, northern Spain, northern Siberia, western Pakistan, ?Japan, Wyoming, Italy, New-Zealand, Jurassic of Spitsbergen, and Cretaceous of western Kazakhstan, Egypt, and SW Australia.

Lingularia similis sp. n.

Figs 3-6.

Lingula borealis sp. n.; Bittner 1899, p. 25, Pl. 1-2:3a-b, 4, 5.

Lingula borealis Bittner 1899; Newell & Kummel 1942, p. 953, Pl. 2: Figs 1-4.

Lingula sp. ind.; Birkenmajer & Pugaczewska 1975, p. 54-55, Pl. 2: 7, 8.

?*Lingula aff. arctica* Wittenburg 1910; Dagys 1965, p. 15, Pl. 1: 14, 15.

Lingula cf. *beani* Phillips 1829; Bäckström & Nagy 1985, p. 50, Pl. 1: 1.

Holotype: ZPAL Bp.XXIV/385: Fig. 3A, B.

Type locality: Wimanfjellet (between Janusfjellet and Botneheia), Sassenfjorden area, Central Spitsbergen.

Type horizon: Brentskardhaugen bed (phosphorite nodules), Jurassic, Toarcian/Aalenian (Wierzbowski et al. 1981).

Etymology: 'Similis' relates to its similar appearance to *Lingula*.

Diagnosis.— Umbonal region rounded with median beak weak on dorsal valve, pointed on ventral valve; large propareas separated by a deep pedicle groove, not continuous with internal valve face. Body muscles characterized by internal median oblique narrowing at the third anterior; internal anterior oblique with drop-like shape, located near anterior oblique; and internal posterior oblique, weakly marked and tear-drop-like shaped, extending near to posterior adductor. Mantle canals with strong S-like curves on both sides.

Description.— Shell. Elongate oval in outline, lateral margins subparallel; anterior margin generally rounded (Fig. 3); shell surface bears only sub-concentric ribbing variable in prominence and spacing, but more marked near margins. Both valves moderately convex, convexity of shell generally decreasing with size increase; maximum height at the level of anterior adductor scars on ventral valve and between the anterior and posterior adductors on dorsal valve (Fig. 4). Maximum width at mid-length of shell. Shell thickened in both valves between anterior adductors.

Ventral valve and body area. Length: 7.9–29.2 mm, mean 22.3 mm; width: 4.5–19.0 mm, mean 13.9 mm; width/length ratio: 0.49–0.75 mean 0.62 (n=31 specimens) (Tab. 1; Figs 5, 6). A pair of narrow, subparallel grooves, arises a short distance posterior to the anterior adductors to unite and terminate at the level of the posterior adductor (Figs 3D, E, G, 4). The umbonal region is pointed, continuous with the posterolateral margins; large propareas are separated by a deep striated pedicle groove which is not continuous with the valve interior (Figs 3G, 4). The mantle canals are strongly incurved like the dorsal canals (Figs 3A, F, 4). The distance between the tip of the mantle canals and the anterior margin of the valve represents about 27 to 37 % (mean 32 %; n=7) of the whole valve length and the lophophoral cavity is about 37 to 52 % (mean 45 %; n=7) (Tab. 2; Fig. 2). The perimial line is well-marked (Figs 3D, E, 4); the internal median oblique muscle scar narrows in its anterior third; the internal anterior oblique muscle has a tear-drop-like shape, located near the anterior oblique scare; and the internal posterior oblique muscle, weakly marked and similarly tear-drop shaped, extends to near the posterior adductor (Figs. 3, 4). The scar of the heart-like shaped posterior adductor commonly covers the junction of the pair of grooves (Figs 3, 4).

Dorsal valve and body area. Length: 15.6–28.8 mm, mean 23.3 mm; width: 10.0–19.0 mm, mean 15.2 mm; width/length ratio: 0.58–0.72, mean 0.65 (n=25) (Tab. 1; Figs 5, 6). A central narrow ridge extends over generally 1–2 millimetres posteriorly from the anterior oblique muscle scars. The umbonal region is rounded, with a weak median beak (Figs 3F, 4). The distance between the tip of the mantle canals and the anterior

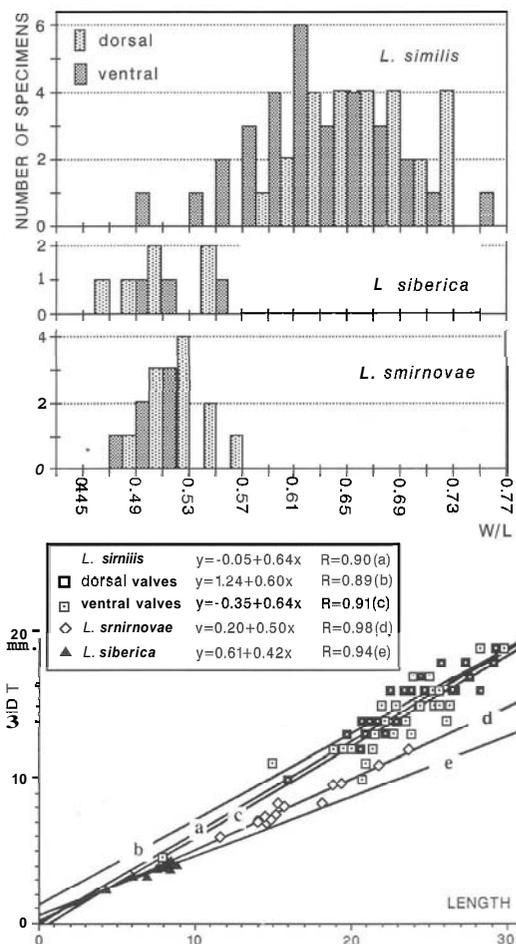


Fig. 6. Frequency distribution of the width to length ratios (W/L) and regression plots for *Lingularia similis* sp. n. from the Middle Jurassic of Spitsbergen, *L. siberica* sp. n. from the Middle Triassic of Siberia, and *L. smirnovae* sp. n. from the Middle Cretaceous of Kazakhstan (see text).

margin of the valve is about 20 to 23% (mean 21%; n=9) of the total valve length and the lophophoral cavity is about 27 to 36% (mean 33%; n=9) (Tab. 2; Fig. 2). The perimial line is well-marked.

The shape of the mantle canals in *Lingularia similis* is close to that of the canals in *Lingula reevei* and the muscle disposition ventrally is similar to that of *L. parva*, or *L. tumidula* (see Emig 1982).

Remarks.— Because the original description of *Lingula borealis* by Bittner (1899) does not provide with information on all the used taxonomic features for a detailed comparison with our specimens, this species is considered as synonym of *Lingularia similis*. The figures of *Lingula borealis* published by Newell & Kummel (1942) from the Early Triassic of Wyoming show many characteristics of *Lingularia similis*, i.e. S-like curved mantle canals, a pair of ventral grooves, a small narrow dorsal ridge, and of the muscle disposition; the W/L ratio measured on their figures varies from 0.54–0.69 (mean 0.60), the comparative extension of the tip of the mantle canals and the lophophoral cavity is respectively 23 and 29% dorsally and

27 and 41% ventrally. From the authors' description, the shell of 'full-sized individuals (about 1 cm long) commonly taper slightly toward the rear end of the shell' (Newell & Kummel 1942: p. 953); but they also write that there is a 'considerable variation in size and some variation in form'. The umbonal region is rounded on the dorsal valve and shows a weak beak on the ventral valve.

Lingula cuneata drawn by Hall & Clarke (1892: Figs 11, 12, Pl. 1) also shows some similarity to *Lingularia similis*. Conspecific with *L. similis* seems to be *Lingula* cf. *beani* briefly described by Backstrom & Nagy (1965) from the early Bajocian of Spitsbergen. The external and internal morphology of the only ventral valve figured by these authors (Backstrom & Nagy 1965: p. 30, Pl. 1: 1) appears to be close to that of *Lingularia similis*.

Photographs of internal moulds of '*Lingula*' *krausei* from the Cretaceous, sent by L. Holmer, illustrate a great deal of similarity between this latter species and *Lingubria similis*, particularly in the disposition of mantle canals and of the ventral muscles.

Material.— More than two hundred specimens from the type-locality, usually as well preserved external and internal moulds of dorsal and ventral valves with imprints of internal structures, i.e. muscle scars, mantle canals. Complete shells or moulds comprising both valves are few.

Occurrence.— Early Triassic of western Pakistan (Rowell 1970), northern Siberia, Primorye (Dagys 1965); Wyoming (Newell & Kummel 1942; Dagys 1965), ?Japan (Nakazawa 1958). Jurassic of Spitsbergen (Toarcian/Aalenian: Wierzbowski *et al.* 1981; Bajocian: Backstrom & Nagy 1985).

Lingularia siberica sp. n.

Figs 4–7A, B.

Lingula polaris Lundgren, 1883; Dagys 1965, p. 11.

?*Lingula polariformis* ex. aff. *polaris*; Wurm 1911, p. 121.

?*Lingula olenekensis* sp. n.; Dagys 1965, p. 14.

Holotype: ZPAL Bp.XXIV/3: Fig. 7A, B.

Type locality: Olenek River, northern Siberia (see Dagys 1965, p. 12).

Type horizon: Middle Triassic, Anisian.

Etymology: 'Siberica' because the specimens referred previously to *L. polaris* have been collected in the northern part of Siberia.

Diagnosis.— Numerous fine radial striae and commonly concentric microlines between thicker growth lines generally visible on the shell. Umbonal region rounded on dorsal valve, pointed on ventral valve; small propeareas separated by a deep and wide striated pedicle groove, not continuous with the internal valve face. Body muscles characterized by internal anterior oblique located near anterior oblique; internal posterior oblique not observed. Mantle canals almost straight, convergent on both sides.

Description.— Shell. Elongate oval in outline, lateral margins subparallel; anterior margin rounded; numerous fine radial striae are normally visible; both valves moderately to strongly convex; maximum height occurs between the mid-length and the posterior third; maximum width near the

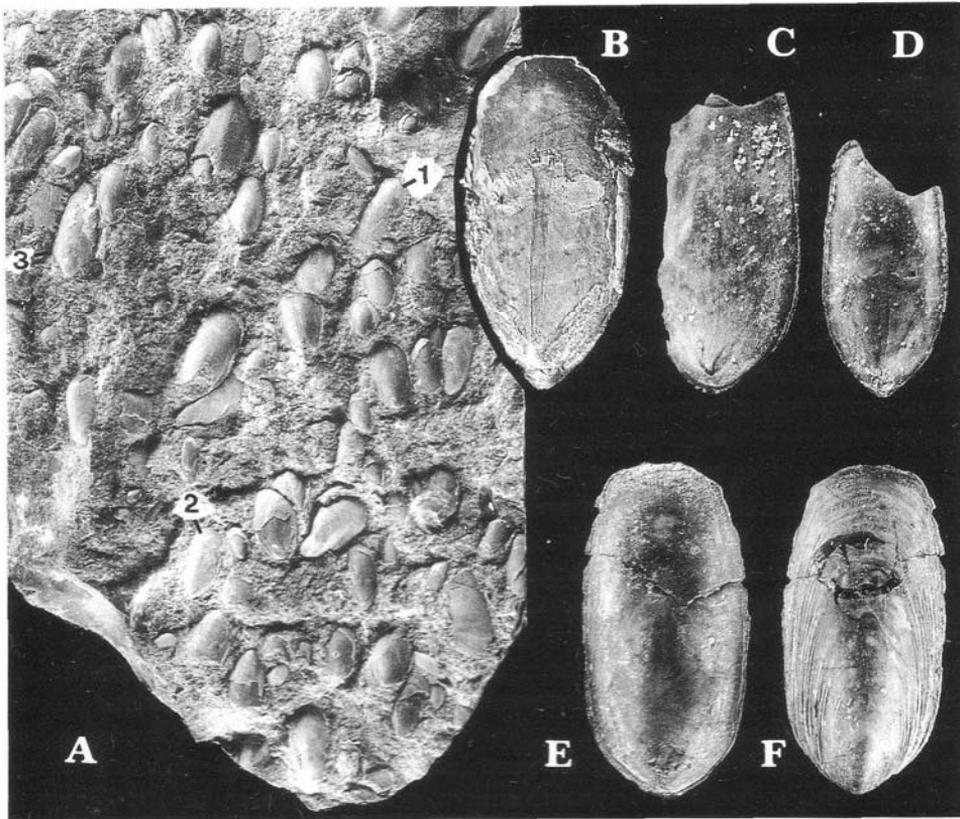


Fig. 7. □A, B. *Lingulariasiberica* sp. n., a slab (A) with the studied specimens from the Anisian of the Olenek River, northern Siberia (holotype indicated with arrow 2), x 1,5, and the ventral side (internal mould) of the holotype ZPAL Bp. XXIV/3, showing mantle canals, muscle scars, and V-shaped grooves (B), x 4. □C-F. *Lingularia smirnovae* sp. n. from the Albian of Mangyshlak, Kazakhstan; all figures x 3. C. Internal side of the dorsal paratype valve ZPAL Bp. XXIV/15. D. Internal side of the ventral paratype valve ZPAL Bp. XXIV/16, showing muscle scars, perimial line, and V-shaped grooves. E-F. External and internal side of the dorsal holotype valve ZPAL Bp. XXIV/14.

mid-length of the valves (Figs 4, 7A, B). Between the anterior adductors the shell is generally thickened slightly in both valves.

Ventral valve and body area. Length: 5.9–7.6mm, mean 6.8mm; width: 3.3–3.9mm, mean 3.5 mm; width/length ratio: 0.49–0.56, mean 0.52 (n=3) (Tab. 1; Figs 5, 6). The valve interior bears a pair of narrow subparallel grooves, which arise in front of the anterior adductors to unite and end at the level of the posterior adductor (Figs 7B, 4). The umbonal region is pointed; small propleas are separated by a deep and wide pedicle groove which is not continuous with the valve interior. Mantle canals almost straight, oblique on both sides, ventral canals are a little shorter than the dorsal ones (Fig. 4). The distance between the tip of the mantle canals and the anterior margin of the valve is about 24 to 30 % of

the whole valve length and the lophophoral cavity is about 41 to 50 % (mean 46 %; $n=6$) of the valve length (Tab. 2; Fig. 2). The perimial line is well-marked; the internal anterior oblique muscle is located near the anterior oblique, the internal posterior oblique could not be observed (Figs 7B, 4). The posterior adductor scar is large.

Dorsal valve and body area. Length: 4.3–8.5 mm, mean 7.5 mm; width: 2.3–4.4 mm, mean 3.7 mm; width/length ratio: 0.45–0.53, mean 0.50 ($n=6$) (Tab. 1; Figs 5, 6). A central narrow ridge extends about 1 millimetre posterior to the anterior oblique muscle scars. The umbonal region is rounded. The perimial line is well-marked; the posterior adductor muscle is well-developed. The distance between the tip of the mantle canals and the anterior margin of the valve is about 20 to 22 % of the whole valve length, and the ratio for the lophophoral cavity 29 to 35 % (mean 33 %; $n=4$) (Tab. 2; Fig. 2).

The shape of the mantle canals in *Lingularia siberica* is close to that of the canals in *Lingula parva* and the muscle disposition is similar to that of *L. tumidula* (see Emig, 1982).

Material.— More than 70 specimens ranging in length from about 5 mm to 26 mm, including more or less complete ventral and dorsal valves with internal imprints.

Occurrence.— Triassic of northern Siberia, Lena and Olenek Rivers (Anisian, Ladinian: Dagys, 1965); Spain, Aragon (Wurm 1911) with $W/L=0.47$ and $vLC=42\%$.

Lingularia smirnovae sp. n.

Figs 4–6, 7C–F, 8.

Holotype: ZPAL Bp.XXIV/14, Fig. 7E, F.

Type locality: Mangyshlak Peninsula, exposure 162, bed 10, southern part of the West Karatau anticline, Kazakhstan.

Type horizon: Albian phosphatic nodules (T. Smirnova, personal communication).

Etymology: The species is dedicated to Tatiana Smirnova (Department of Paleobiology, State University of Moscow) who kindly provided us with her large collection.

Diagnosis.— Umbonal region rounded with weak median beak on dorsal valve, pointed on ventral valve; small propareas separated by deep and narrow pedicle groove, not continuous with internal valve face. Body muscles characterized by small internal anterior oblique located near anterior oblique and above internal posterior oblique, posterior adductor more developed on right part of ventral side and on left of dorsal. Dorsal mantle canals strongly S-like curved (not observed on ventral side).

Description.— Shell. Elongate oval in outline, lateral margins subparallel; anterior margin generally rounded; shell surface bears only subconcentric ribbing variable in prominence and spacing. Both valves are weakly convex; maximum height at the level of the anterior adductor muscles. Maximum width at the mid-length of the shell (Fig. 7C–F).

Ventral valve and body area. Length: 13.7–19.1 mm, mean 15.1 mm; width: 6.9–9.6 mm, mean 7.6 mm; width/length ratio: 0.48–0.52, mean 0.50 ($n=6$) (Tab. 1; Figs 5, 6). A pair of narrow subparallel grooves, arises

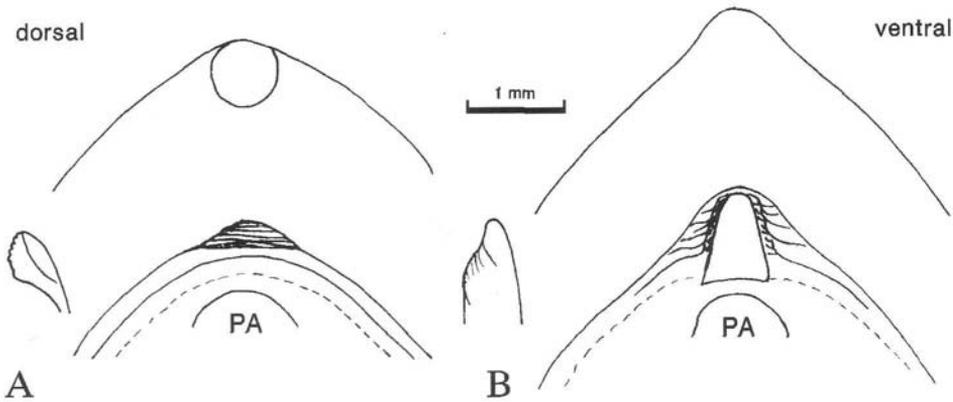


Fig. 8. Umbonal region of the dorsal (A) and ventral (B) valves of Middle Cretaceous *Lingularia smirnovae* sp. n., external and internal views, and profile (PA: posterior adductor muscle).

a short distance posterior of the anterior adductors and they unite and terminate at the level of the posterior adductor (Figs 7D, 4). The umbonal region is pointed (Figs 7D, 8); small propleas are separated by a narrow deep striated pedicle groove; striated groove which is not continuous to the valve interior. The umbonal region is rather close to that of *Lingula reevei* but the beak is more rounded and the pedicle groove deeper than in this latter species (Fig. 7C-F; see Emig 1982). The mantle canals could not be observed on the ventral side. No measurements are available for the distance of the mantle canal tips nor the lophophoral cavity because the ventral valve are incomplete in our available material. The perimial line is well-marked (Fig. 2); the internal median oblique muscle narrows slightly in its middle area; the internal anterior oblique is small, located near the anterior oblique and above the internal posterior oblique. The heart-like shaped posterior adductor is asymmetrically developed, i. e. more on the right part of the ventral side and on the left of the dorsal side.

Dorsal valve and body area. Length: 11.4–23.3 mm, mean 16.4 mm; width: 6.1–12.0 mm, mean 8.4 mm; width/length ratio: 0.47–0.55, mean 0.51 (n=11) (Tab. 1; Figs 4, 5). A narrow central ridge extends about 1–2 millimetres posterior to the anterior oblique muscle scars. The umbonal region is rounded with a weak median beak, similar to that in *Lingula reevei* (Figs 7C, E, F, 8; see Emig 1982). The mantle canals are strongly incurved (Fig. 4). The distance between the tip of the mantle canals and the anterior margin of the valve is about 22% of the whole valve length and the lophophoral cavity extends to about 33–36% (n=4) (Tab. 2; Fig. 2). The perimial line is well-marked; the posterior adductor is more developed on the left of the dorsal side.

The shape of the mantle canals in *Lingularia smirnovae* is quite different from that observed in *Lingula*; the muscle disposition is similar to that of *L. parva* except on the ventral side of both internal anterior oblique and

internal posterior oblique muscles which show no similar arrangement in any other species of *Lingularia* or *Lingula* (see Emig 1982).

Material.— About 60 specimens of separate valves, ventral and dorsal, several with well preserved internal characters, but few complete specimens.

Occurrence.— (T. Smirnova unpublished) Cretaceous of West Kazakhstan, Mangyshlak Peninsula. Albian of the southern part of the western Karatau anticline: Keimal village (SW of Ak-Kirke), upper part of the Kelengi Valley, SW slope of Kaimat dag (NE from Tagalake), southern wing of the Beka-Bashkuduskaja anticline, Uts-Kuju Valley, NW slope of Karashor Valley, southern Mangyshlak (Besokti section), east Mangyshlak (S of Kolodes Beskonti). Cenomanian-Turonian of the western Karatau (10 km from Dzhangeldi), Karashora Village, N margin of Karashor, N margin of Kum-Sebhen (40 km W from Kazakhe Village), 7 km from Seneka Village.

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Résumé

La traditionnelle opinion que *Lingula* représente une lingule très ancienne est remise en question. L'étude de lingules mésozoïques démontre que celles-ci diffèrent significativement des genres actuels *Lingula* et *Glottidia* par une cavité lophophorale plus volumineuse, des canaux ventraux du manteau plus courts, un développement plus important du muscle adducteur postérieur, les régions umbonales. Les caractères morphologiques internes s'avèrent indispensables pour pouvoir identifier les genres et espèces des Lingulidae, les caractères externes de la coquille étant insuffisants. La tendance évolutive d'une réduction de la cavité lophophorale s'oppose à l'opinion traditionnellement véhiculée que le genre fossile-vivant *Lingula* a survécu sans modification morphologique significative depuis le début du Paléozoïque: en fait, l'origine des lingules actuelles date probablement du début du Cénozoïque. Un nouveau genre de brachiopode inarticulé, *Lingularia*, est décrit avec trois nouvelles espèces, *L. sibirica* (Trias Moyen), *L. similis* (Jurassique Moyen) et *L. smimovae* (Crétacé).

Streszczenie

Badania dobrze zachowanych okazów mezozoicznych lingul wskazały, że te różnią się zasadniczo od współczesnych rodzajów *Lingula* i *Glottidia* objętością jamy lofoforalnej, długością kanałów wentralnego płaszczka, wykształceniem nieparzystego mięśnia tylnego adduktora oraz, dodatkowo, morfologią części dziobowych muszli. Zaznaczająca się tendencja ewolucyjna w kierunku redukcji objętości jamy lofoforalnej przeczy ogólnie przyjętemu pogładowi, że *Lingula* to „żyjąca skamieniałość”, która przeżyła, od wczesnego paleozoiku do dzisiaj, prawie bez zmian morfologicznych.

W pracy wyodrębniono nowy rodzaj *Lingularia* z 3-ma nowymi gatunkami: *L. sibirica* (trias), *L. similis* (jura), *L. smimovae* (kreda).