

Proof that *Lingula* (Brachiopoda) is not a living-fossil, and emended diagnoses of the Family Lingulidae

Christian C. EMIG¹

Abstract: *Lingula* is often considered a "living-fossil" based on its supposed lengthy morphological conservatism owing to its absence of evolution, and its remarkable survival for more than 550 M.Y. This conclusion is based on the typical apparently unchanged "linguliform" shape of the shell. However the taxa of the family Lingulidae show morphological evolutionary changes despite the fact that the group appears panchronic among the Recent Brachiopoda. Consequently, traditional opinion that *Lingula* is a "living-fossil" should be rejected. Diagnoses of the Family Lingulidae and of its three genera are herewith emended.

Key Words: living-fossil; *Lingula*; Lingulidae; Brachiopoda; taxonomy

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Résumé : *Preuves que Lingula (Brachiopoda) n'est pas un fossile vivant, avec de nouvelles diagnoses pour les taxons de la Famille des Lingulidae.*- *Lingula* est souvent considérée comme un fossile-vivant, voire le plus ancien actuellement connu, à cause de son long conservatisme morphologique basé sur une supposée absence d'évolution, ainsi qu'en raison de sa remarquable survie depuis plus de 550 MA. Cette assertion est basée sur une forme inchangée de la coquille, dite "linguliforme". Cependant, les taxons de la famille des Lingulidae montrent des changements évolutifs de la morphologie et de l'anatomie interne bien que ce groupe puisse être considéré comme panchronique au sein des Brachiopoda actuels. Il est démontré que l'opinion traditionnellement véhiculée selon laquelle les *Lingula* seraient des fossiles vivants doit être rejetée. En conséquence, de nouvelles diagnoses sont proposées pour la famille des Lingulidae et pour les trois genres pouvant s'y rapporter avec certitude.

Mots-Clefs : Fossile vivant ; *Lingula* ; Lingulidae ; Brachiopoda ; taxinomie

Introduction

Among the Brachiopoda *Lingula*, belonging to the Family Lingulidae, is often considered one of the most ancient "living-fossils". This assertion is based on the supposed morphological conservatism of the genus, its lack of morphological change, *i.e.* the absence of change in shell shape and structure and of evolution, and its remarkable survival for more than 550 M.Y. All of this because over the years many Palaeozoic species have been referred to *Lingula*.

Arising in the Early Cambrian, the Superfamily Linguloidea (Brachiopoda, Lingulata) expanded rapidly from the Medial Cambrian to the beginning of the Ordovician (BABIN *et alii*, 1992; EMIG, 1984a). After Devonian times only the Family Lingulidae subsists and it seems to be represented from the Carboniferous to the Cretaceous only by *Lingularia*, and since the Tertiary, or possibly from the Late Cretaceous, by the two extant genera *Lingula* and *Glottidia*.

Thus, it is reasonable to inquire into the validity of the traditional opinion that *Lingula*

represents a lineage of "living-fossils" that originated during the Cambrian, as well as the idea that *Lingula* has survived without significant morphological changes since the Early Palaeozoic.

Arguments

The living-fossil argument rests on a single piece of evidence; the typical shape of the shell - namely "linguliform" (from the common shape in *Lingula*; Fig. 1, Table 1) - with smooth external faces marked only by growth lines (EMIG, 1983a). This form is generally the only "character" remaining in fossil lingulides that has led many authors to refer specimens *ipso facto* to *Lingula*, regardless of the age of the outcrop, from the Earliest Cambrian to the present. Nevertheless, the "linguliform" shell indicates only an endobiont life in burrows (EMIG, 1982a, 1997a). This mode of existence is very common in the life history of many Palaeozoic genera and families of the Order Lingulida whereas *Lingula sensu stricto* appeared only at the beginning of the Tertiary or perhaps in the Late Cretaceous.

¹ CNRS UMR 6540, Centre d'Océanologie, Rue de la Batterie-des-Lions, 13007 Marseille (France)
e-mail: Christian.Emig@com.univ-mrs.fr

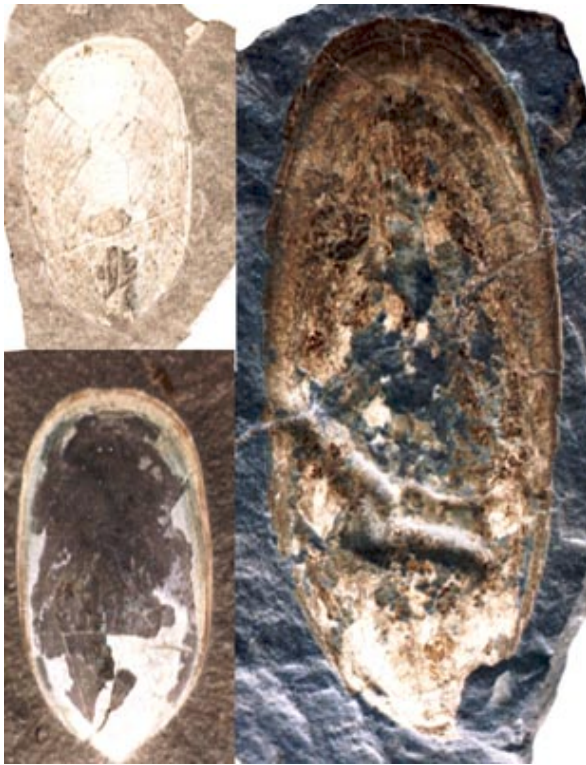


Figure 1: Linguloid specimens from the Ordovician (collection NMNH, Smithsonian Institution, Washington DC, USA) often described as *Lingula* species.

The persistence of this linguliform shell has been and is still interpreted by many palaeontologists as indicating morphological stability through the whole of the Phanerozoic record, although both the shell and its content have evolved since the Palaeozoic along with the phylogenetical characters of the Lingulida (BIERNAT and EMIG, 1993; EMIG, 2002).

If some important Lingulida anatomical features such as the lophophore (ZHANG *et alii*, 2003) arose before the Cambrian and remained in the *Lingulata*, others with taxonomic value have evolved since then among the Family Lingulidae: e.g. the reduction of the pseudointerareas with only vestigial propareas, an asymmetrical disposition of the body muscles, convergent main mantle canals (*vascula lateralia*) to become subparallel anteriorly, the absence of the median secondary mantle canals (*vascula media*), a single posterior adductor muscle on both ventral and dorsal side (Fig. 2, 3). All these characters are a part of the diagnosis of the Family Lingulidae (Table 1).

Lingularia, *Lingula* and *Glottidia* belong unquestionably to this family. Furthermore a number of evolutionary changes listed below took place in these three genera respectively (Fig. 2, 3; Table 1):

- a shortening of the lophophoral cavity: this main evolutionary tendency leads to a reduction of the volume of the lophophoral

- cavity and is related to shell dimensions;
- a decrease in the width and the height of the shell;
- an increase in the length of the ventral mantle canals, from an "asymmetrical" positioning of the termination of the canal tips up to a termination at the same distal level;
- a reduction of the posterior adductor muscle to the left area and a correlative change in the posterior disposition of the pedicle nerves;
- a flattening of the pedicle groove and a trend to a more acutely angled umbonal region of the valves.

These evolutionary changes do not support the view of Recent lingulides as "living-fossils" that have survived and undergone little significant morphological change since the Palaeozoic. On the contrary, no Palaeozoic or Mesozoic species is assignable to *Lingula sensu stricto*.

The current taxonomy revision of the Brachiopoda calls into question other families, not just the lingulides (BIERNAT and EMIG, 1993; EMIG, 2002). Until very recently soft parts were rarely considered to have taxonomic value, even in extant taxa where their anatomy is evident. This neglect occurred because skeletal characteristics were considered to be of primary importance by palaeontologists who found that using these "biological constraints" would make it impossible to describe or to redefine many fossil species. Because morpho-anatomical characters are not always available or are difficult to recognize, it seems best to avoid new descriptions (EMIG, 2002). Furthermore when making a cladistic analysis many systematists forget that all the phylogenetical characters have to be tested and that these criteria must also be applied in descriptions of taxa. Following the traditional path increases confusion among the taxa, and *Lingula* as well as *Obolus* are among the most prominent examples, for they have endured for nearly two centuries.

In the identification of genera and species of Linguloid taxa soft-bodied characters or their scars and impressions are required because external shell characters have no suprageneric taxonomical value. The diagnoses of the family Lingulidae, and of its three genera that can be recognized with certainty, have been emended on Table 1 based on the recent original descriptions (see EMIG, 2002). Diagnoses made recently by HOLMER and POPOV (2000) do not correspond to the original descriptions; these authors did not use many of the taxonomic characters established previously by EMIG (1982b, 1983b) to describe the extant lingulide species, and applied by BIERNAT and EMIG (1993) to the fossil genus *Lingularia* and its species, and to *Obolus* by EMIG (2002).

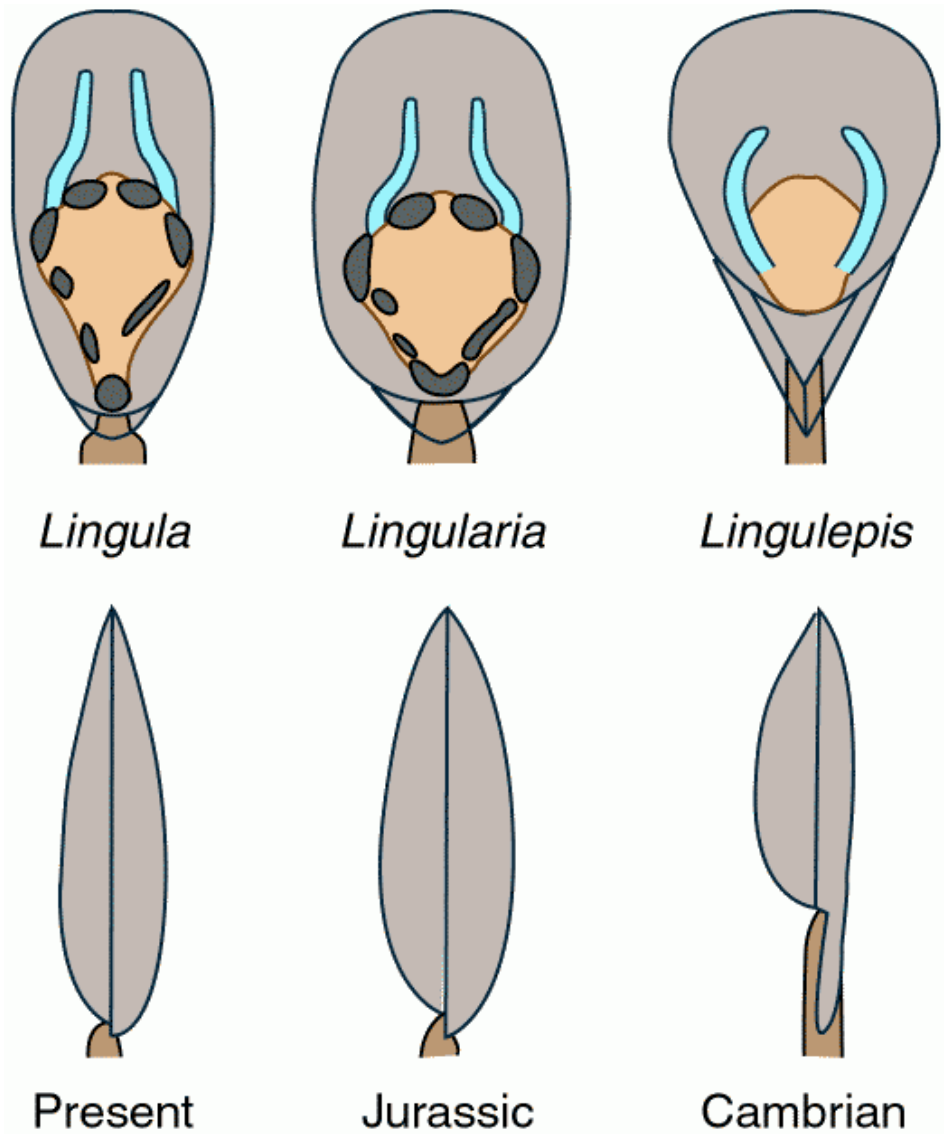


Figure 2: Shell outline and internal view of ventral valve (along with the body muscles involved in valve movements and the main mantle canals) and a lateral view of the shell (after EMIG, 1977a; BIERNAT and EMIG, 1993; JIN *et alii*, 1993).

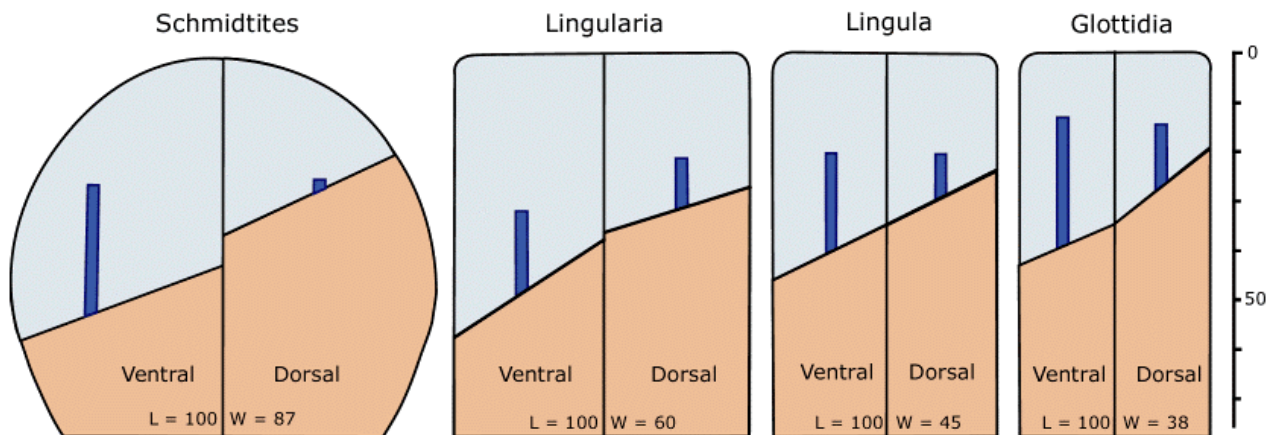


Figure 3: Diagram of the extensions (minimum-maximum) of the lophophoral cavity and of the mean extension of the mantle canals based on average shell dimensions in *Glottidia*, *Lingula* and *Lingularia* (see also BIERNAT and EMIG, 1993) and for comparison in the obolid *Schmidtites celatus* from the Upper Cambrian of Estonia (see EMIG, 2002).

Primitive characteristics of the living Lingulidae

As a group the living lingulides approach closely a steady state (EMIG, 1984b, 1989) in view to the following characteristics:

- slow growth;
- adult size and age more weighty as well as a longer life span compared to those populations of other species present in the ecosystem (as defined by ARNAUD and EMIG, 1987);
- recruitment potential reduced, slightly higher than the replacement of the population;
- K demography;
- ability to integrate and to preserve low energy contributions;
- long continuity in the geological time-span (several tens of millions of years for several species).

Most of the species of the Superfamily Linguloidea share an infaunal way of life as a plesiomorphic state in contrast to the epifaunal one of all other brachiopod taxa.

From this set of characteristics *Lingula* is obviously the most primitive representative among the Brachiopoda (about 420 species) From the ancestral infaunal behaviour it has retained the following features (Fig. 1, 4, 5, 6, 7):

- the general form of the shell;
- an arrangement of musculature more evolved than in other Linguloid taxa;
- a disposition in pseudosiphons of the setae of the anterior mantle margin (two inhalant and one exhalant pseudosiphons);
- a pedicle (anchorage and retraction of the animal into its burrow);
- metabolic adaptations as responses to osmotic stresses, low oxygen consumption,...

Despite a low specific diversity (respectively 7 and 5 species), the two extant genera show a broad geographical distribution on the continental shelf in many temperate and intertropical biocoenoses: *Lingula* in Asia, in Oceania, and in Africa; *Glottidia* on the American continent (EMIG, 1997b).

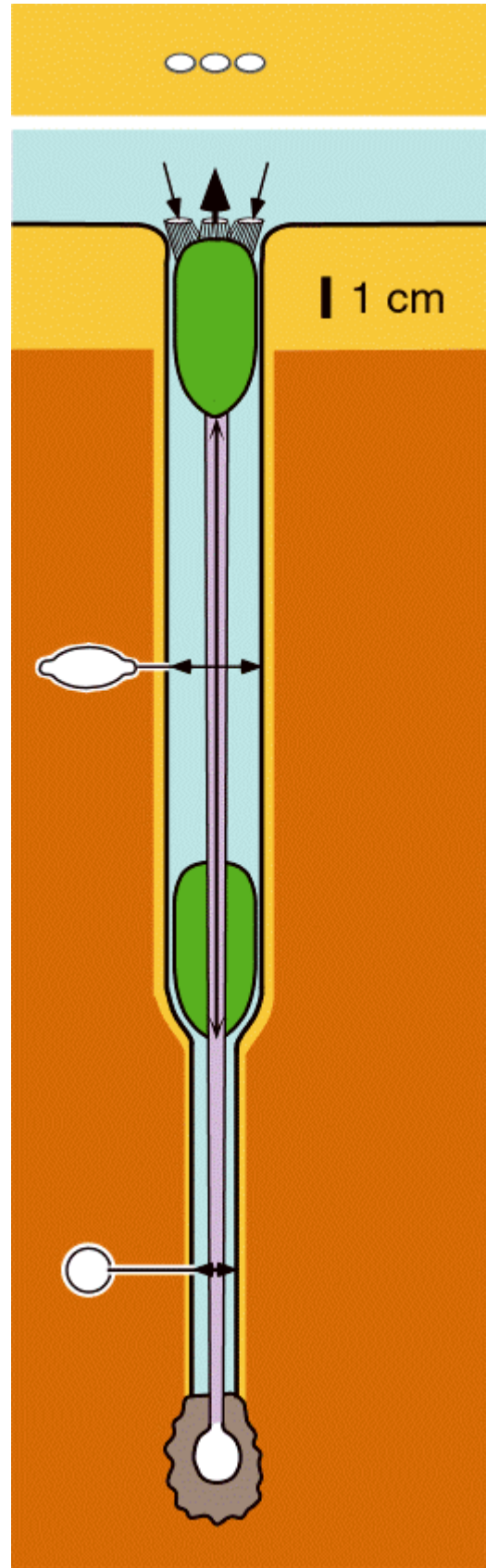


Figure 4: Diagram of a burrow of a lingulide (after EMIG, 1982a) with the animal in life position (= feeding one) and after retraction into its burrow.

Conclusions

Although the Recent Lingulidae constitute a panchronic group, the evaluation of the bradytelic evolution of a rather poorly preserved group with a low potential for fossilisation is under development based on the recent descriptions of anatomical structures in the fossil taxa (BIERNAT and EMIG, 1993; JIN *et alii*, 1993; KOWALEWSKI and FLESSA, 1996; EMIG, 2002; ZHANG *et alii*, 2003). Albeit they have kept surficial aspects derived from ancestral life, species of *Lingula* show significant evolutionary differences and can no longer be considered as "living-fossils"! Consequently, the traditional opinions regarding *Lingula* must be rejected because the diagnoses of the Lingulidae given here are based on recent morphological findings and evolutionary novelties.

In conclusion, the notion of "living-fossils" is very probably erroneous. In fact such a concept appears more journalistic than scientific, for it is based for the most part on a unique characteristic maintained over time, like the lingulide shape and the coelocanth fin and scale pattern. In any event only a species can be referred to as a living-fossil – supra-specific taxa are excluded automatically.

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Table 1: Systematic part: Emended diagnoses directly derived from the original descriptions and diagnoses, to replace the diagnoses of HOLMER and POPOV (2000).

Subphylum **Linguliformea** WILLIAMS, CARLSON & BRUNTON, 1996
 Class **Lingulata** GORYANSKY & POPOV, 1985
 Order **Lingulida** WAAGEN, 1885
 Superfamily **Linguloidea** MENKE, 1828

Family Lingulidae MENKE, 1828

Diagnosis:

Shell elongate oval to subrectangular, gently and subequally biconvex, subequivalved; lateral margins generally subparallel.

Ventral valve with wide triangular pedicle groove and lateral vestigial propleas.

Dorsal valve with posterior margin rounded, with a more or less developed median beak; anterior adductor and anterior oblique muscle scars closely spaced.

Asymmetrical muscle system with internal oblique muscles; unpaired posterior adductor muscle; pedicle nerve curving around posterior adductor muscle.

Mantle canal system bifurcate; *vascula lateralia* of both valves converging anteriorly to become subparallel; *vascula media* absent.

Long flexible pedicle; lophophore spirolophous, with apices of spires directed medially.

?Upper Devonian, Carboniferous-present

Only three genera have been retained in this family, because according to HOLMER and POPOV (2000) the other genera are *Apsilingula*, *Barroisella*, *Langella* and *Semilingula*, which remain only provisionally within this family.

Genus *Lingularia* BIERNAT & EMIG, 1993 ¹

Diagnosis:

Shell elongate oval in outline, lateral margins subparallel, anterior margin broadly rounded. Valves weakly to strongly convex.

Ventral valve with triangular umbo formed by vestigial to small internal propareas, continuous with posterolateral margins and separated by deep pedicle groove; pair of narrow subparallel, V-shaped, grooves extends internally from the anterior adductor pair to posterior adductor where grooves join.

Dorsal valve with posterior margin rounded, narrow median beak sometimes present, and a narrow internal central ridge extending over about 1 millimetre posterior to anterior oblique muscle scars.

Posterior adductor scar heart-like in outline. Main ventral canals (*vascula lateralia*) shorter than dorsal canals.

Carboniferous-Cretaceous

¹ Complete description in BIERNAT and EMIG (1993)



Figure 5: *Lingularia siberica* (from the Triassic of Northern Siberia) - shell length about 0.7 cm.

Genus *Lingula* BRUGUIÈRE, 1797 ²

Diagnosis:

Shell elongate oval or subrectangular in outline, lateral margins subparallel, anterior margin broadly rounded to straight.

Ventral valve with wide triangular pedicle groove and lateral vestigial propareas. Ventral visceral area extending to midvalve, with impression of pedicle nerve curving around unpaired posterior adductor muscle scar.

Dorsal valve with dorsal anterior adductor and anterior oblique muscle scars closely spaced, bisected by weak median septum; posterior margin rounded, with a median beak. Dorsal visceral area extending somewhat anterior to midvalve.

Main ventral and dorsal canals (*vascula lateralia*) ending at the same level.

?Cretaceous, Tertiary - present

² Complete description in EMIG (1982b)



Figure 6: *Lingula anatina* (from Sumatra) - shell length about 4.5 cm.

Genus *Glottidia* DALL, 1870³

Diagnosis:

Shell strongly elongate in outline, lateral margins subparallel to parallel, anterior margin broadly straight. Mantle canal system with papillae.

Ventral valve with a wide pedicle groove and lateral vestigial propareas; two divergent septa, serving as places of attachment for oblique muscles and support of body wall; pedicle nerve curving around unpaired posterior adductor muscle. Ventral visceral area extending anterior to midvalve.

Dorsal valve with median septum extending from posterior adductor muscle to internal oblique muscles; posterior margin rounded, with a median beak. Dorsal visceral area extending anterior to midvalve.

Main ventral and dorsal canals (*vascula lateralia*) ending at the same level.

?Cretaceous, Tertiary - present

³ Complete description in EMIG (1983b)



Figure 7: *Glottidia palmeri* (from the Gulf of California, Mexico) - shell length about 4.5 cm.