The lingulid brachiopod *Lingularia* from lowermost Cretaceous hydrocarbon seep bodies, Sassenfjorden area, central Spitsbergen, Svalbard

Lars Erik Holmer & Hans Arne Nakrem

Holmer, L.E. & Nakrem, H.A. The lingulid brachiopod *Lingularia* from lowermost Cretaceous hydrocarbon seep bodies, Sassenfjorden area, central Spitsbergen, Svalbard. *Norwegian Journal of Geology,* Vol 92, pp. 167-174. Trondheim 2012, ISSN 029-196X.

A series of Upper Jurassic to Lower Cretaceous samples of hydrocarbon seep bodies from central Spitsbergen (Svalbard) were treated with acetic acid to retrieve insoluble micro and macrofossils. The Lower Cretaceous samples yielded abundant lingulid material of *Lingularia similis*? Biernat & Emig 1993, represented by well preserved, but invariably fragmented shells. They provide the first critical ultrastructural information for this important extinct member of the extant Lingulidae.

Lars E. Holmer, Department of Earth Sciences, Palaeobiology, Uppsala University, Villavägen 16, SE-752 36 Uppsala, Sweden. E-mail: Lars.Holmer@pal.uu.se. Hans Arne Nakrem, Natural History Museum (Geology), University of Oslo, P.O. Box 1172 Blindern, NO-0318 Oslo, Norway. E-mail: h.a.nakrem@nhm.uio.no

Introduction

While excavating marine reptiles from Upper Jurassic black shales of the Slottsmøya Member, Agardhfjellet Formation, 15 carbonate bodies interpreted as fossil hydrocarbon seeps (Hammer et al. 2011) were encountered during fieldwork (2006-2009) in the Knorringfjellet-Janusfjellet area, Sassenfjorden, central Spitsbergen (Fig. 1). The age of the carbonate bodies varies from Late Volgian to Late Ryazanian (Wierzbowski et al. 2011). Lingulid brachiopods have so far only been found in the youngest bodies. Biernat & Emig (1993) provided the first detailed and well-illustrated study of the Jurassic type species *Lingularia similis* from the Toarcian/Aalenian of central Spitsbergen; all previous records of Mesozoic Lingulidae from Spitsbergen were discussed and synonymized with this species by Biernat & Emig (1993). However, Biernat & Emig (1993) based their study mainly on internal moulds of *Lingularia similis*, on which the main anatomical/morphological characters (musculature, mantle canals etc.) are well preserved. The new Early Cretaceous material of *Lingularia similis*? is the youngest published record from Svalbard and unlike all previous records, represented by well preserved, but invariably fragmented shells that were isolated from the matrix by etching with weak acetic acid. As pointed out by Biernat & Emig (1993) and Holmer & Bengtson (2009), most previously described Mesozoic Lingulidae are too poorly known to allow close taxonomic discrimination and the new material from Svalbard provides new critical ultrastructural information for an important extinct member of the extant Lingulidae.

Material and methods

Altogether 15 carbonate seep bodies were found during fieldwork in the Knorringfjellet-Janusfjellet area, Sassenfjorden, Spitsbergen. Five bodies ranging in age from Late Volgian through Late Ryazanian were selected for acetic acid treatment. Limestone blocks ranging in size between 2 and 5 kilo were dissolved in weak (10%) acetic acid and wet sieved. Fractions larger than 90 µm were dried and picked. The lingulid shells were generally picked from fractions larger than 500 µm. Agglutinated foraminiferans were picked from the smaller fractions. Only the youngest samples of Ryazanian age contained lingulid brachiopods. This was expected because thin-section studies (Fig. 2) of all seep bodies had revealed lingulids only in the younger ones (seeps 2007-01 and 2007-03).

Geological setting

The Slottsmøya Member of the Agardhfjellet Formation consists of dark-grey shales with local occurrences of black paper shales containing red to yellowish siderite concretions, cold seep carbonate bodies and siderite and dolomite interbeds. Sedimentological and micropaleontological data support a model with deposition of siliciclastic sediments under restricted to open marine shelf conditions, alternating oxic to hypoxic, and water depths between 100 and 300

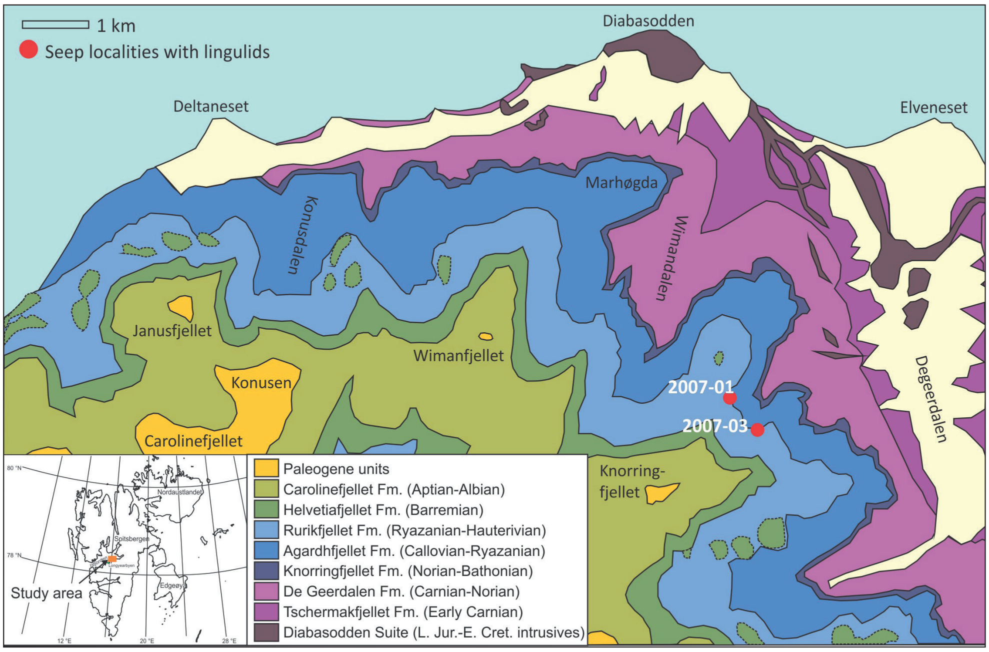


Figure 1. Geological map of the area (modified from Dallmann et al. 2001) with inset map of Svalbard indicating the study area.

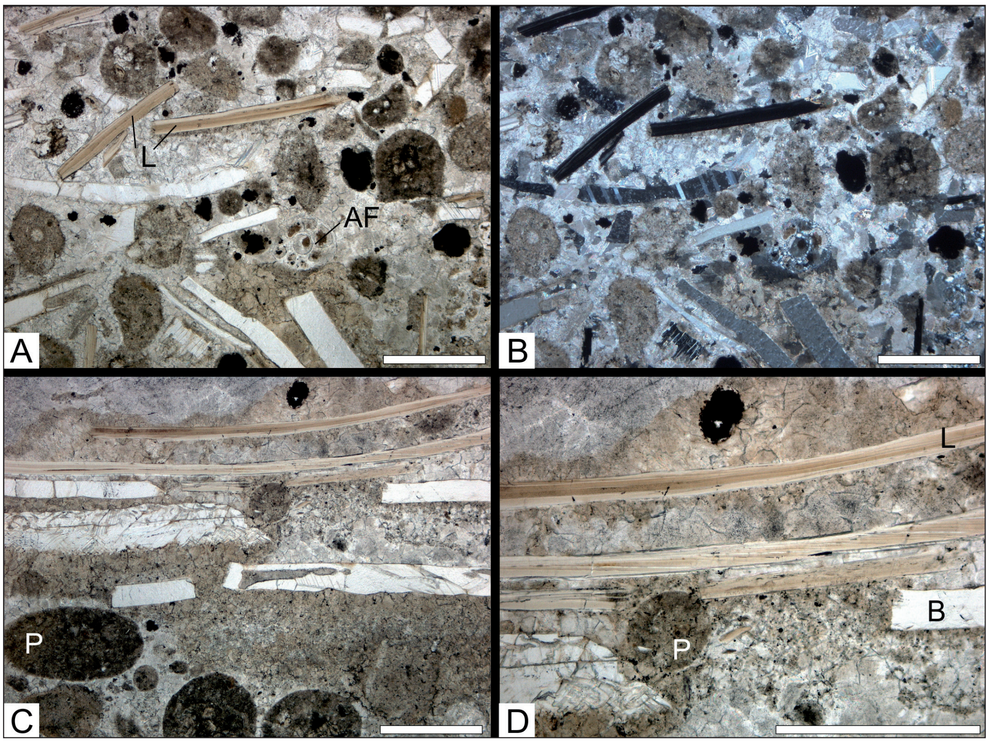


Figure 2. Thin-sections showing lingulid coquina and associated microfacies components.
A: Agglutinated foraminiferan (AF) and lingulid shells (L) (normal transmitted light);
B: As A, but cross-polarised transmitted light;
C: Lingulid shells and peloids (P);
D: Lingulid shells (L), peloids (P) and recrystallised bivalve shell (B).
All from thin-section PMO 170.975.

Scale=0.5 mm.

m (Dypvik et al. 1991, 2002; Nagy et al. 2009; Smelror et al. 2009: p.106). Microfacies analysis of the seep bodies indicates, however, that they may have formed under shallower conditions (Hryniewicz et al., 2012).

The Slottsmøya Member is dated as Early Volgian to Late Ryazanian (Nagy & Basov 1998; Mørk et al. 1999; Wierzbowski et al. 2011) based on ammonites, agglutinated foraminifera and palynology.

The largest seep carbonate body (2007-01) is c. 5 m in diameter, but has been fractured by frost wedging, and thus some of the lateral extent may be due to downslope-transported loose blocks. The other seep carbonate bodies are smaller, less than 2 m in diameter, and many also have downslope fields of scattered small carbonate blocks.

The seep environment macrofossils include benthic elements such as sponges, bivalves, gastropods, scaphopods, brachiopods, echinoderms and tube worms, and allochthonous elements from the water column (ammonites, belemnites and pieces of wood). Microfossils include foraminifera, ostracods, dinocysts, spores and pollen.

Agglutinated foraminifera in the seep bodies include among others the genera *Ammobaculites, Bulbobaculites, Cribrostomoides* and *Recurvoides* (Hjálmarsdóttir et al., 2012). These morphotaxa have a shallow infaunal life strategy (Nagy et al. 2009) probably similar to the lingulids burrowing in the locally soft mud in the seep environment.

Associated macrofossil benthic faunal elements include bivalves (at least 13 species, among them shallow to deeper infaunal taxa like lucinid(s), solemyid(s), *Nucinella, Thyasira*, arcticid(s), *Goniomya*), gastropods, non-lingulid brachiopods and semi-infaunal vestimentiferan tube worms (Hammer et al. 2011).

No lingulid brachiopods have been observed in the surrounding black shales despite careful searching and preparation.

Systematic paleontology

The specimens described here are deposited in the Palaeontological Collections of the Natural History Museum, University of Oslo.

Class LINGULATA Gorjansky & Popov, 1985
Order LINGULIDA Waagen, 1885
Family LINGULIDAE Menke, 1828

Genus LINGULARIA Biernat & Emig, 1993

Type species. – By original designation: *Lingularia similis* Biernat & Emig, 1993 from the Middle Jurassic of Spitsbergen.

Diagnosis. – See Biernat & Emig (1993, p. 11) and Holmer & Popov (2000, p. 36).

Species included. – See list by Biernat & Emig (1993, p. 11) and Holmer & Bengtson (2009, p. 257); in addition to *Lingularia*? *notialis* Holmer & Bengtson, 2009, from the upper Turonian of the Sergipe Basin, Brazil; as well as the Middle Triassic *Lingularia* cf. *smirnovae* Biernat & Emig, from Spain (Marquez-Aliaga et al. 1999).

Remarks. –The main anatomical differences between *Lingularia* and the extant *Lingula* and *Glottidia* include a larger, longer, lophophoral cavity, shorter ventral *vascula lateralia*, and a larger, more strongly developed and paired umbonal muscle that is bisected by V-shaped grooves, representing the impression of the pedicle nerves (Biernat & Emig 1993). In describing the musculature of *Lingularia*, Biernat & Emig (1993) employed the terminology of Emig (1982), whereas that of Bulman (1939) and Williams & Rowell (1965) is used in the present work.

Lingularia similis? Biernat & Emig, 1993.
Figs. 3-5
Diagnosis. – See Biernat & Emig (1993, p. 14).

Material. – A total of 12 ventral and 14 dorsal fragmentary valves.
Description. – Shell elongate oval in outline, lateral margins subparallel; anterior margins not preserved (Figs. 3A, 4A). Both valves moderately convex, with maximum width at around the mid-length of the shell. Ornamentation consists of very low, evenly spaced finer growth lines (Fig. 3I); some shells with more infrequent, more widely spaced and pronounced growth lines (Fig. 5A).

Ventral pseudointerarea wide, occupying more than half of the maximum valve width, divided by widely triangular and deep pedicle groove occupying one third of the total width of pseudointerarea, and extending as strongly raised and thickened platform anterior of the pseudointerarea (Fig. 3B-F). Ventral propareas small but strongly thickened, outlined by strongly raised annulated rim that is sometimes undercut in larger valves and overhanging the pedicle groove (Fig. 3B-G). Ventral anterior margin of propareas lined by thickened and strongly raised crescent-shaped area (Fig. 3B-F). Median sector of ventral valve interior with narrow subparallel, V-shaped, deep grooves (impressions of pedicle nerve) bisecting the visceral cavity, and bisecting possibly paired, triangular to heart-shaped, umbonal muscle scar (Fig. 3B-F). Ventral transmedian and anterior lateral muscle scars poorly defined. Combined scars of outside and central muscle scars and middle lateral scars in ventral valve well defined (Fig. 3B-F).

Dorsal pseudointerarea poorly defined, almost catacline, very short and narrow, occupying less than one fifth of the maximum valve width, with crescent-shaped thickened rim (Fig. 4B-E). Dorsal visceral area strongly thickened with deeply impressed muscle scars, but lacking median ridge. Dorsal umbonal muscle scars possibly paired, with asymmetrically placed larger, suboval scar to the right and smaller left scar (Fig. 4B-E). Dorsal scars of combined outside and middle lateral and transmedian muscles long and narrow, somewhat crescent-shaped (Fig. 4B-E). Dorsal scars of central muscle well defined at the posterior part of short anterior tongue, but anterior lateral scars poorly impressed (Fig. 4B-E). Problematic large central half-moon-shaped depression in the centre of the visceral area, directly posterior of deeply impressed dorsal gastroparietal band (Fig. 4B).

Mantle canals of both valves poorly visible, but proximal parts of dorsal *vascula lateralia* preserved (Fig. 4B-E).

Comparisons. – The new isolated Cretaceous material from the Ryazanian of central Spitsbergen is clearly close to the older Jurassic type species of *Lingularia similis* Biernat & Emig, 1993, based mainly on internal moulds from the the Toarcian/Aalenian of central

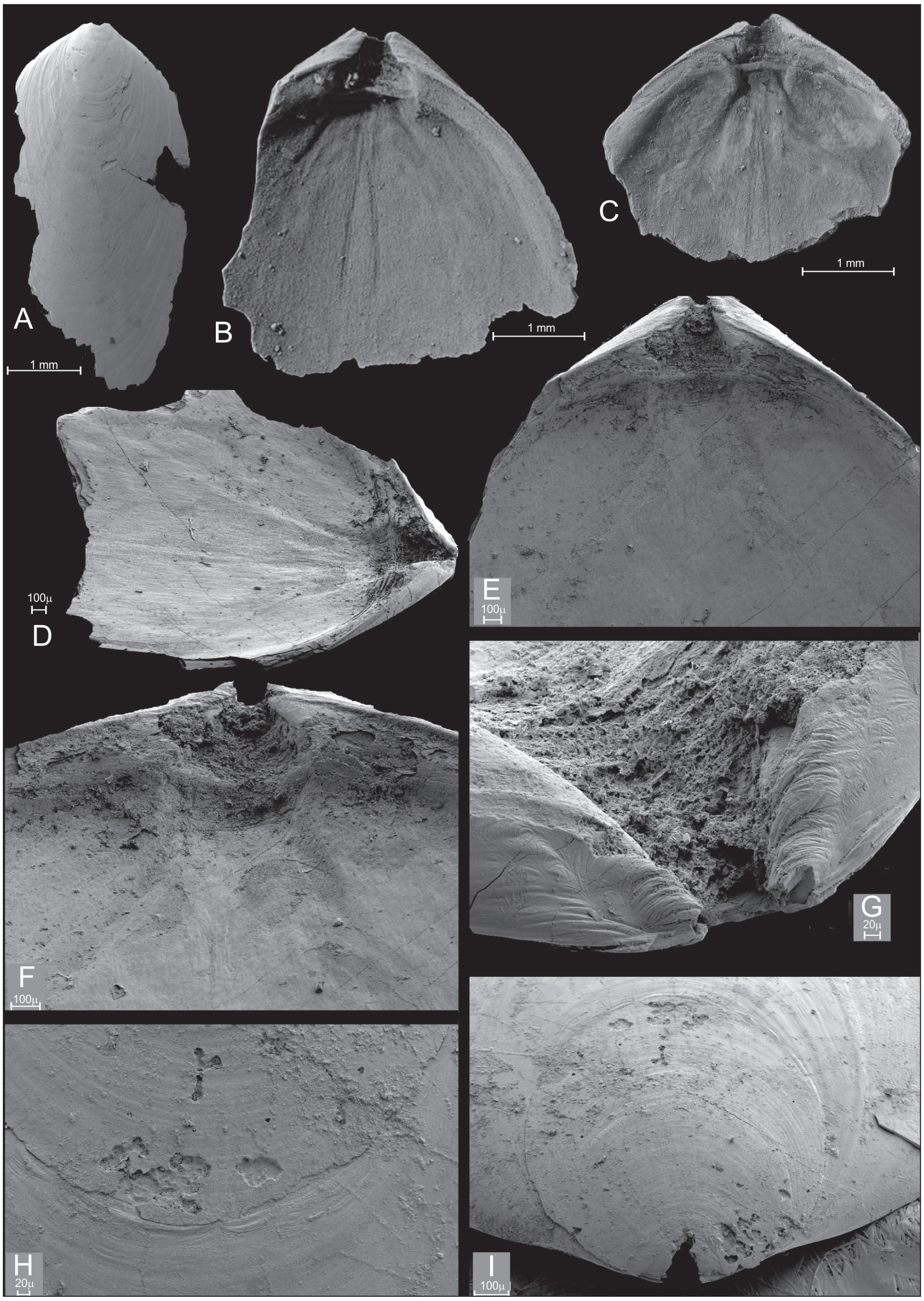
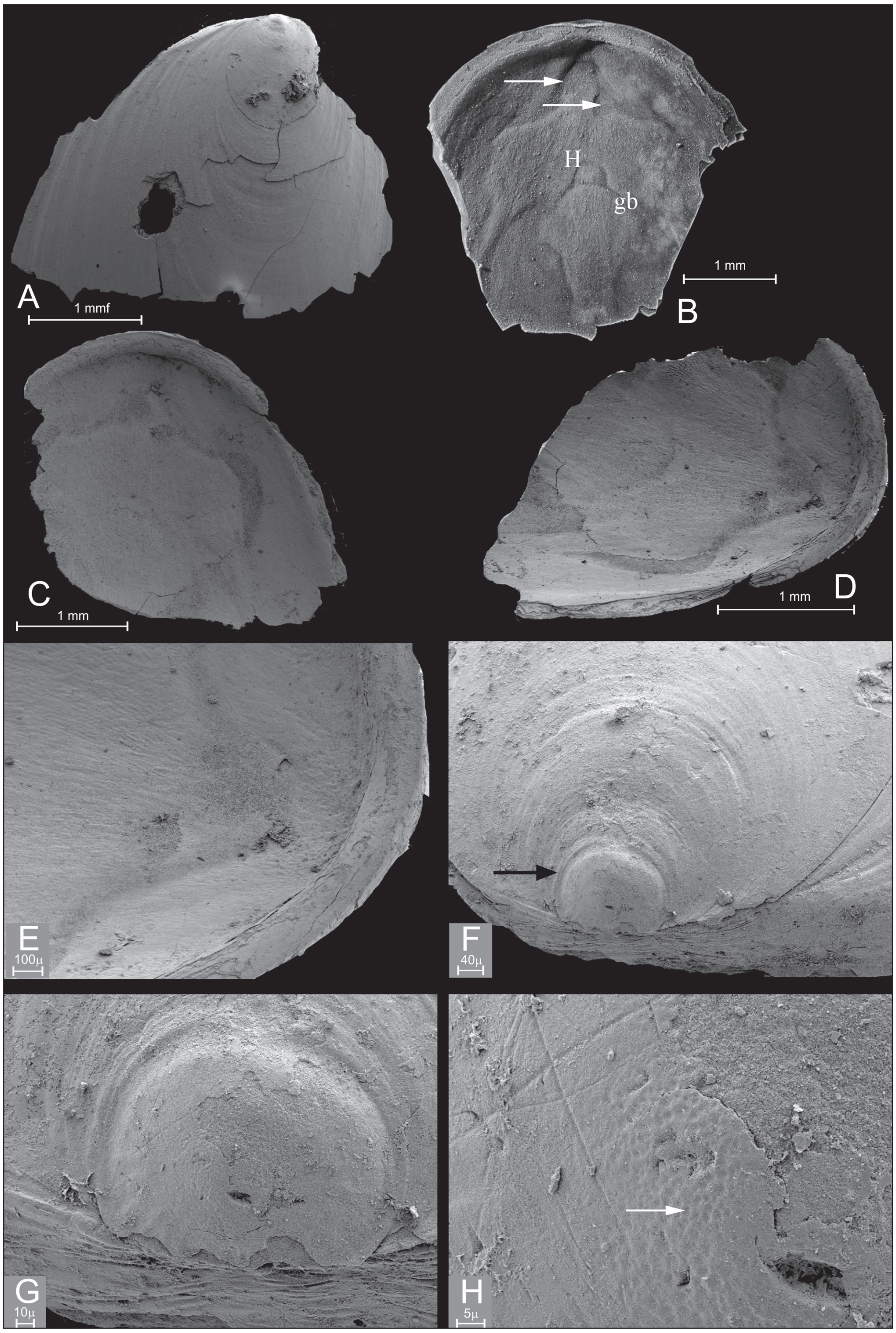


Figure 3. Lingularia similis? *Biernat & Emig, 1993; Early Cretaceous (Late Ryazanian), SEEP-2007-01, Knorringfjellet, central Spitsbergen, ventral valve;*
A. Exterior, PMO 221.371. B. Interior, PMO 221.372. C. Interior, PMO 221.373. D. Oblique lateral view of interior, PMO 221.374. E. Detail of pseudointerarea, PMO 221.375. F. Oblique anterior view of pseudointerarea of E. G. Oblique posterior view of pseudointerarea of E. H. Detail of edge of larval shell, PMO 221.376. I. Oblique posterior view of larval shell of H.

Spitsbergen; both taxa are similar in outline, shape, ornamentation and morphology of the ventral pseudointerarea, as well as in the general interior characters. However, a detailed taxonomic comparison with the type species is difficult due to the difference in preservation, and the lack of complete information on mantle canals, musculature, size of the lophophoral cavity and other characters in the new Cretaceous material. Moreover, the material of the type species lacks detailed information on, e.g., the dorsal pseudointerarea and the fine structure of the ventral propareas and posterior margins (Biernat & Emig 1993). The Cretaceous material differs from the Jurassic type species in being less biconvex and apparently having a somewhat smaller ventral pseudointerarea; moreover, the single dorsal/ventral umbonal muscle scars in the Jurassic type species are close to symmetrical, whilst those of the Cretaceous form appear to be paired and strongly asymmetrical. Other aspects of the preserved muscle scars are more comparable between the two taxa, but the Cretaceous form differs in having thinner, crescent-shaped transmedian scars, and poorly defined anterior lateral scars. The dorsal gastroparietal bands are deeply impressed in both taxa, but the problematic half-moon-shaped depression in the centre of the dorsal visceral area is not known from the type species. In view of this the assignation of the new

Figure 4: Lingularia similis? *Biernat & Emig, 1993; Early Cretaceous (Late Ryazanian), SEEP-2007-01, Knorringfjellet, central Spitsbergen, dorsal valve; A. Exterior, PMO 221.377. B. Interior, paired umbonal scar marked by arrows, H – half-moon shaped impression, gb – gastroparietal band, PMO 221.378. C. Interior, PMO 221.379. D. Oblique lateral view of C. E. Oblique lateral view of pseudointerarea of D. F. Oblique posterior view of embryonic and larval shell of A, edge of embryonic shell marked by arrow. G. Oblique posterior of embryonic shell of F. H. Detail of edge of embryonic shell of G, surface pits marked by arrow.*



Cretaceous form to the type species is tentative, pending further better material of both forms. In the asymmetric shape of the umbonal scars, the Cretaceous form is also comparable to the Cretaceous Brazilian *Lingularia*? *notialis* Holmer & Bengtson, 2009, but the asymmetry in the Brazilian species is much more pronounced. The distribution of this character was discussed in more detail by Holmer & Bengtson (2009), and it is interesting to note that a divided umbonal scar is already present in members of the Palaeozoic Pseudolingulidae (Holmer 1991). Double ventral umbonal scars have also been described in a Cretaceous "*Lingula*" sp, from Nubia, Egypt, but the dorsal umbonal scar in this form is single and heart-shaped and both appear to be symmetrical (Böttcher 1982, fig. 10). As pointed out by Biernat & Emig (1993) and Holmer & Bengtson (2009), most described Mesozoic Lingulidae are too poorly known to allow close taxonomic discrimination.

Ontogeny

The larval shell of both valves of the Cretaceous *Lingularia similis*? is well defined and delineated by a strongly developed rim, marking a major interruption in growth that is about 0.75 – 0.85 mm wide and 0.95 – 1.00 mm

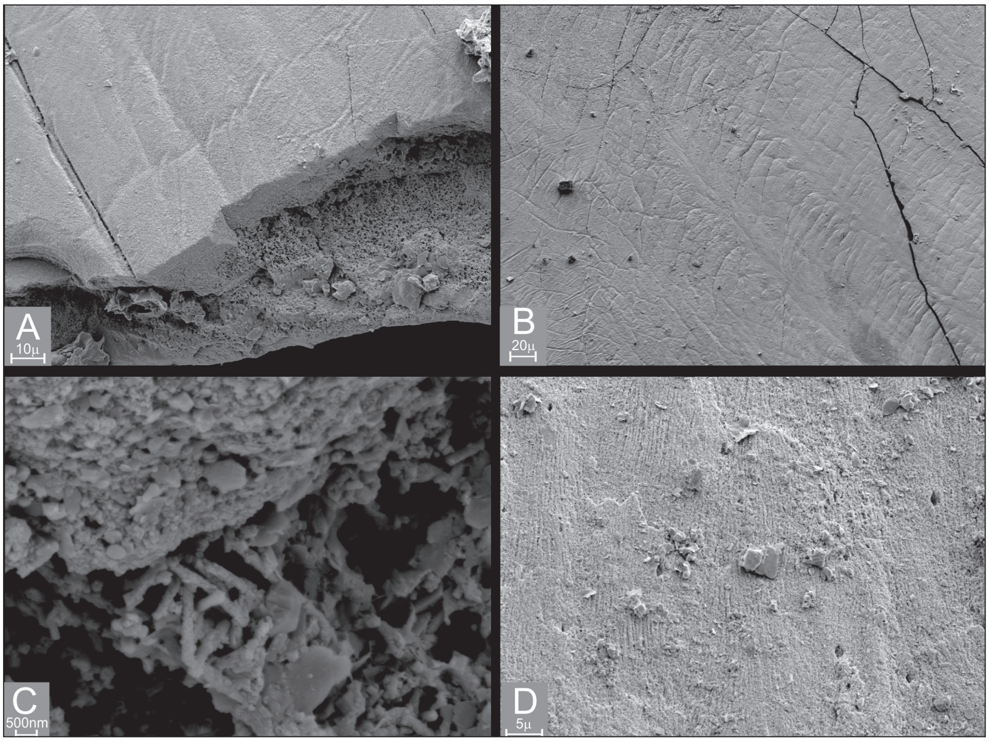


Figure 5: Lingularia similis? *Biernat & Emig, 1993; Early Cretaceous (Late Ryazanian), SEEP-2007-01, Knorringfjellet, central Spitsbergen, dorsal valve; A. Detail of contact between primary and secondary shell, PMO 221.371. B. Detail of ornamentation of A. C. Detail of baculate secondary shell of A. D. Detail of fibrous interior surface, PMO 221.379.*

long (Figs. 3H-I, 4, 4F). The edge of the larval shell of both valves is further accentuated by numerous smaller and larger nick-points, defining drapes, about 50-200 μm across (Fig. 3H-I). The ventral umbo is invariably fragmented and there is no embryonic shell preserved (Fig. 3H-I). In contrast, the dorsal embryonic shell is extremely well preserved in numerous shells, forming a cup-shaped subcircular shell, about 180 μm wide and 150 μm long, but the posterior margin is invariably fragmented, and seemingly has been broken where it overhangs the dorsal pseudointerarea (Fig. 4F-H). The central area is strongly raised (around some 10-20 μm high), and is surrounded by a narrow depressed rim, around 10-15 μm wide, which is provided with a single anterior indentation (Fig. 4F-H). The posterior margins of most of the embryonic shells are provided with a distinctive radial pattern with up to twelve thin ribs, around 5-8 μm wide and 50 μm long (Fig. 4F-H). Some of the embryonic shells also preserve a distinctive pitted micro-ornamentation, with densely spaced, rounded pits, up to about 2 μm across, covering most of the shell surface (Fig. 4H).

Shell structure and micro-ornamentation. – The shell structure of the Cretaceous *Lingularia similis*? is well preserved on broken and exfoliated shells. The primary shell is comparatively well defined, up to 10-20 μm thick, and is made up entirely of homogenous, closely packed, micro-granular apatite grains, generally less than 300 nm across (Fig. 5A). The outer surface of the primary shell lacks finer structures at the highest magnification, but invariably has a pattern with regular fine radial folds 10-20 μm across, superposed on the regular fine growth lines (generally about 4-15 μm across), and sometimes also bears more irregular folding (Fig. 5B). The secondary layer follows directly beneath the primary layer; it is entirely composed of stacked, impersistent baculate laminae, each having an outer and inner lamella (also termed compact lamina), around 1 μm thick (Fig. 5C). The central part of each baculate lamina is entirely filled with a criss-crossing pattern of thin rods (also termed bacula) of apatite, each around 300 nm in diameter; the space between individual rods is most commonly empty, but in some sections the interspaces are filled with micro-granular apatite (Fig. 5C).

The interior surface of the visceral area of both valves has a characteristic fibrous surface pattern, composed of closely spaced, long anastomosing apatite, less than 1 μm across; the interior surface of the visceral area of both valves is provided with widely spaced shallow pits, up to 8 μm across (Fig. 5D).

Discussion

Shell structure, micro-ornamentation and ontogeny. – The studies by Cusack & Williams (1996), Cusack et al. (1999), Williams & Cusack (1999), Williams et al. (2000) and Holmer & Bengtson (2009) proved that studies of shell structure and micro-ornamentation should accompany any systematic studies of the extant and extinct members of the Family Lingulidae. Most importantly, these studies indicate that at least within the Lingulidae the presence of a baculate or virgose shell structure defines taxa belonging to the two major lineages – the *Glottidia*-, and *Lingula*-like forms respectively – which may have retained their independence since the Late Palaeozoic (see also Holmer 2001). However, these assertions are presently difficult to evaluate due to the lack of information from most Lingulidae, and e.g. Pettersson Stolk et al. (2010) recorded a possible virgose shell structure from an exceptionally preserved Middle Cambrian member of the Obolidae. All well known species of *Lingularia* including the new Cretaceous material indicate that members of this genus invariably have a baculate shell structure that is almost identical between taxa (Cusack et al. 1999; Williams et al. 2000; Holmer & Bengtson 2009). Detailed information about the interior and exterior characters as well as information on the micro-ornamentation are also critical and as shown by Holmer & Bengtson (2009) the fossil specimens of *Lingularia* commonly preserve fine details of surface ornamentation including early ontogenetic stages that may be important for close taxonomic discrimination. In particular, the shape and morphology of the embryonic shell of *Lingularia* seemingly can be distinguished from Recent Lingulidae, by being approximately three times smaller than the modern ones. Embryonic shells that are almost identical in size and morphology to those described from *Lingularia* in this study have been described from problematic Devonian lingulids (Balinski 2001) and the even more enigmatic Early Palaeozoic forms (Tapanila & Holmer 2006). Balinski (2001) suggested convincingly that the radial patterns on the embryonic shells are related to setae (see also Williams & Holmer 1992), and this interpretation is here also adopted for the identical structures as preserved on the Cretaceous embryonic shells. Balinski (2001) also noted that the separate dorsal and ventral embryonic shells in the Devonian forms indicate that, unlike extant *Lingula*, the embryonic shells were secreted by separate mantle lobes; this can also convincingly be inferred for the Cretaceous forms described here. The pitted nature of the embryonic shells of Cretaceous *Lingularia* may indicate that the embryonic periostracum was provided with some kind of vesicular structures as known from both extinct and extant discinoids as well as Palaeozoic linguliforms (e.g., Holmer 1989; Williams & Holmer 1992; Williams et al. 1998; Balinski & Holmer 1999). As noted by Holmer & Bengtson (2009), the internal fibrous pattern can be directly compared with the possibly collagenous fibres described by Curry & Williams (1983, fig 7c) from extant *Lingula*.

Acknowledgements – Fieldwork at Svalbard (2007–2010) was financed by the Norwegian Research Council, Norwegian Petroleum Directorate, Spitsbergen Travel, ExxonMobil, Fugro, Statoil, OMV, Powercontrols and Hydro, and by grants nos. EC0425-09 and EC0435-09 from the National Geographic Society. The authors are also grateful to all the volunteers and students that have contributed weeks of fieldwork for free on the project. Special thanks to Øyvind Hammer and Krzysztof Hryniewicz for discussions on the geology and the stratigraphy of the Jurassic of Spitsbergen, and to journal referees Uwe Balthasar and Leonid Popov for their valuable comments that improved the manuscript. Lars Holmer´s research is supported by the Swedish Research Council (VR) and the Swedish Polar Research Secretariat.

References

Balinski A. & Holmer L.E. 1999: The Late Devonian trematid lingulate brachiopod *Schizobolus* from Poland. *Acta Palaeontologica Polonica 44*, 335–346.

Balinski, A. 2001: Embryonic shells of Devonian linguloid brachiopods. *The Systematics Association Special Volume 63*, 91–101.

Biernat, G. & Emig, C.C. 1993: Anatomical distinctions of the Mesozoic brachiopods. *Acta Palaeontologica Polonica 38*, 1-20.

Böttcher, R. 1982: Die Abu Dallas-Formation (*Lingula* shale) (Apt?) der Nubischen Gruppe Südwest-Ägyptens. *Berliner Geowissenschaftlische Abhandlungen (A) 39*, 1-145.

Bulman, O.M.B. 1939: Muscle systems of some inarticulate brachiopods. *Geological Magazine 76*, 434-444.

Curry, G.B. & Williams, A. 1983: Epithelial moulds on the shells of the early Palaeozic brachiopod Lingulella. *Lethaia 16*, 11-118.

Cusack, M. & Williams, A. 1996: Chemico-structural degradation of Carboniferous lingulid shells. *Philosophical Transactions of the Royal Society of London Series B 351*, 33-49.

Cusack, M., Williams, A. & Buckman, J. O. 1999: Chemico-structural evolution of the shell of linguloid brachiopods. *Palaeontology 42*, 799-840.

Dallmann, W.K., Major, H., Haremo, P., Andresen, A., Kjarnet, T. and Nottvedt, A. 2001: Geological map of Svalbard 1:100,000, sheet C9G Adventdalen. With explanatory text. *Norsk Polarinstitutt Temakart 31/32*, 4-55.

Dypvik, H., Håkansson, E. & Heinberg, C. 2002: Jurassic and Cretaceous palaeogeography and stratigraphic comparison in the North Greenland – Svalbard region. *Polar Research 21*, 91 - 108.

Dypvik, H., Nagy, J., Eikeland, T.A., Backer-Owe, K., Andresen, A., Haremo, P., Bjærke, T., Johansen, H. & Elverhøi, A. 1991: The Janusfjellet Subgroup (Bathonian to Hauterivian) on central Spitsbergen: a revised lithostratigraphy. *Polar Research 9*, 21-43.

Emig, C.C. 1982: Taxonomie du genre *Lingula* (Brachiopodes, Inarticulés). *Bulletin du Muséum National d´Histoire naturelle de Paris 4*, 337-367.

Gorjanski, V.Y. & Popov, L.E. 1985: The morphology, systematic position, and origin of inarticulate brachiopods with carbonate shells. *Paleontological Journal 19*, 1–11.

Hammer, Ø., Nakrem, H.A., Little. C.T.S., Hryniewicz, K., Sandy, M.R., Druckenmiller, P., Knutsen, E.M., Hurum, J.H. & Høyberget, M. 2011: Hydrocarbon seeps from close to the Jurassic–Cretaceous boundary, Svalbard. *Palaeogeography, Palaeoclimatology, Palaeoecology 306*, 15-26.

Hjálmarsdóttir, H.R., Nakrem, H.A. & Nagy, J. 2012: Foraminifera from Late Jurassic – Early Cretaceous hydrocarbon seep carbonates, central Spitsbergen, Svalbard – preliminary results. *Norwegian Journal of Geology 92*, 157-165.

Holmer, L.E. 1989: Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna, Sweden. *Fossils and Strata 26,* 1-172.

Holmer, L.E. 1991: The systematic position of Pseudolingula Mickwitz and related lingulacean brachiopods. *In* MacKinnon, D.I., Lee, D.E. & Campbell, J.D. (eds.): B*rachiopods through time*. Proceedings of the 2nd International Brachiopod Congress, 15-21. Rotterdam, Balkema.

Holmer, L.E. 2001: Phylogeny and classification: Linguliformea and Craniiformea. *The Paleontological Society Papers 7*, 11-26.

Holmer, L.E. & Bengtson, P. 2009: The first occurrence of a lingulid brachiopod from the Cretaceous of Sergipe, Brazil, with a restudy of "Lingula" bagualensis Wilckens, 1905 from southern Patagonia. *Paläontologisches Zeitschrift 83*, 255-266.

Holmer, L.E. & Popov, L.E. 2000: Lingulida. *In* Kaesler, R.L. (ed.): *Treatise on Invertebrate Paleontology, Part H Brachiopoda, revised, 2*, 32-95. Lawrence, Kansas and Boulder, Colorado, Geological Society of America.

Hryniewicz, H., Hammer, Ø., Nakrem, H.A. & Little, C.S.T. 2012: of Microfacies of the Volgian-Ryazanian (Jurassic-Cretaceous) hydrocarbon seep carbonates from Sassenfjorden, central Spitsbergen, Svalbard. Norwegian *Journal of Geology 92*, 113-131.

Marquez-Aliaga, A., Emig, C.C. & Brito, J.M. 1999: Triassic lingulide brachiopods from the Iberian Range (Spain). *Geobios 32*, 815-821.

Menke, C.T. 1828: *Synopsis methodica Molluscorum generum omnium et specierum earum, quae in Museo Menkeano Adservantur*. 91 pp. Pyrmonti.

Mørk, A., Dallmann, W.K., Dypvik, H., Johannessen, E.P., Larssen, G.B., Nagy, J., Nøttvedt, A., Olaussen, S., Pčelina, T.M. & Worsley D. 1999: Mesozoic lithostratigraphy. *In:* Dallmann, W.K. (Ed.): *Lithostratigraphic lexicon of Svalbard. Upper Palaeozoic to Quaternary bedrock. Review and recommendations for nomenclature use.* 127-214. Tromsø, Norsk Polarinstitutt.

Nagy, J. & Basov, V.A. 1998: Revised foraminiferal taxa and biostratigraphy of Bathonian to Ryazanian deposits in Spitsbergen. *Micropaleontology 44*, 217 – 255.

Nagy, J., Reolid, M. & Rodríguez-Tovar, F.J. 2009: Foraminiferal morphogroups in dysoxic shelf deposits from the Jurassic of Spitsbergen. *Polar Research 28*, 214–221.

Pettersson Stolk, S., Holmer, L.E. & Caron, J-B. 2010: First record of the brachiopod Lingulella waptaensis with pedicle from the Middle Cambrian Burgess Shale. *Acta Zoologica 91*, 150-162.

Smelror, M., Petrov, O.P., Larssen, G.B. & Werner, S.C. (Eds.) 2009: *Geological History of the Barents Sea – Atlas*. 135 pp. Trondheim, Norwegian Geological Survey.

Tapanila, L. & Holmer, L.E. 2006: Endosymbiosis in Ordovician-Silurian corals and stromatoporoids: A new lingulid and its trace from eastern Canada. *Journal of Paleontology 80*, 750-759.

Waagen, W. 1885: Productus limestone fossils: Salt Range fossils, Pt. 4(2), Brachiopoda. Memoirs of the Geological Survey of India, *Palaeontologia Indica, Series 13(4)*, 729–770.

Wierzbowski, A., Hryniewicz, K., Hammer, Ø., Nakrem, H.A. & Little, C.T.S. 2011: Ammonites from hydrocarbon seep carbonate bodies from the uppermost Jurassic–lowermost Cretaceous of Spitsbergen, Svalbard, and their biostratigraphic importance. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 262*, 267–288.

Williams, A. & Cusack, M. 1999: Evolution of a Rhytmic Lamination in the Organophosphatic Shells of Brachiopods. *Journal of Structural Biology 126*, 227-240.

Williams, A. & Holmer, L.E. 1992: Ornamentation and shell structure of acrotretoid brachiopods. *Palaeontology 35*, 657-692.

Williams, A. & Rowell, A.J. 1965: Morphology. *In* Moore, R.C. (ed.): *Treatise on Invertebrate Paleontology, Part H, Brachiopoda*, H57 H138. Lawrence, Geological Society of America and University of Kansas,.

Williams, A., Cohen, B.L., Cusack, M. & Long, S. 2000: Provenance of Atlantic lingulid brachiopods. *Palaeontology 43*, 999-1018.

Williams, A., Cusack, M. & Buckman, J.O. 1998: Chemico-structural phylogeny of the discinoids brachiopod shell. *Philosophical Transactions of the Royal Society of London B 353*, 2005-2038.