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## Brachiopods from Late Jurassic—Early Cretaceous hydrocarbon seep deposits, central Spitsbergen, Svalbard

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### Abstract

Late Jurassic–Early Cretaceous (Late Volgian–latest Ryazanian) rhynchonellate brachiopods are described from eight out of 15 hydrocarbon seep deposits in the Slottsmøya Member of the Agardhfjellet Formation in the Janusfjellet to Knorringfjellet area, central Spitsbergen, Svalbard. The fauna comprises rhynchonellides, terebratulides (terebratuloids and loboidothyridoids) and a terebratellidine. The rhynchonellides include: *Pseudomonticlarella varia* Smirnova; *Ptilorhynchia mclachlani* **sp. nov.**; and *Ptilorhynchia obscuricostata* Dagys. The terebratulides belong to the terebratuloids: *Cyrtothyris?* sp.; *Cyrtothyris* aff. *cyrta* (Walker); *Praelongithyris?* aff. *borealis* Owen; and the loboidothyridoids: *Rouillieria* cf. *michalkowii* (Fahrenkohl); *Rouillieria* aff. *ovoides* (Sowerby); *Rouillieria* aff. *rasile* Smirnova; *Uralella?* cf. *jani-maniensis* Makridin; *Uralella?* sp.; *Pinaxiothyris campestris?* Dagys; *Placothyris kegei?* Harper *et al.*; and *Seductorithyris septemtrionalis* **gen. et sp. nov.** The terebratellidine *Zittelina?* sp. is also present. Age determinations for all but one of the brachiopod-bearing seeps are based on associated ammonites. Five of the seep carbonates have yielded *Lingularia similis?*, and it is the only brachiopod species recorded from two of the seeps. Other benthic invertebrate taxa occurring in the seeps include bivalves, gastropods, echinoderms, sponges, and serpulid and non-serpulid worm tubes. The brachiopod fauna has a strong Boreal palaeobiogeographic signature. Collectively, the Spitsbergen seep rhynchonellate brachiopods exhibit high species richness and low abundance (<100 specimens from 8 seeps). This contrasts markedly with other Palaeozoic–Mesozoic brachiopod-dominated seep limestones where brachiopods are of low diversity (typically monospecific) with a super-abundance of individuals. The shallow water environmental setting for the Spitsbergen seeps supported a diverse shelf fauna, compared to enigmatic Palaeozoic–Mesozoic brachiopod-dominated seeps.

**Key words:** Brachiopoda, Rhynchonellida, Terebratulida, hydrocarbon seeps, Jurassic, Cretaceous, Spitsbergen, Svalbard, new genus, new species

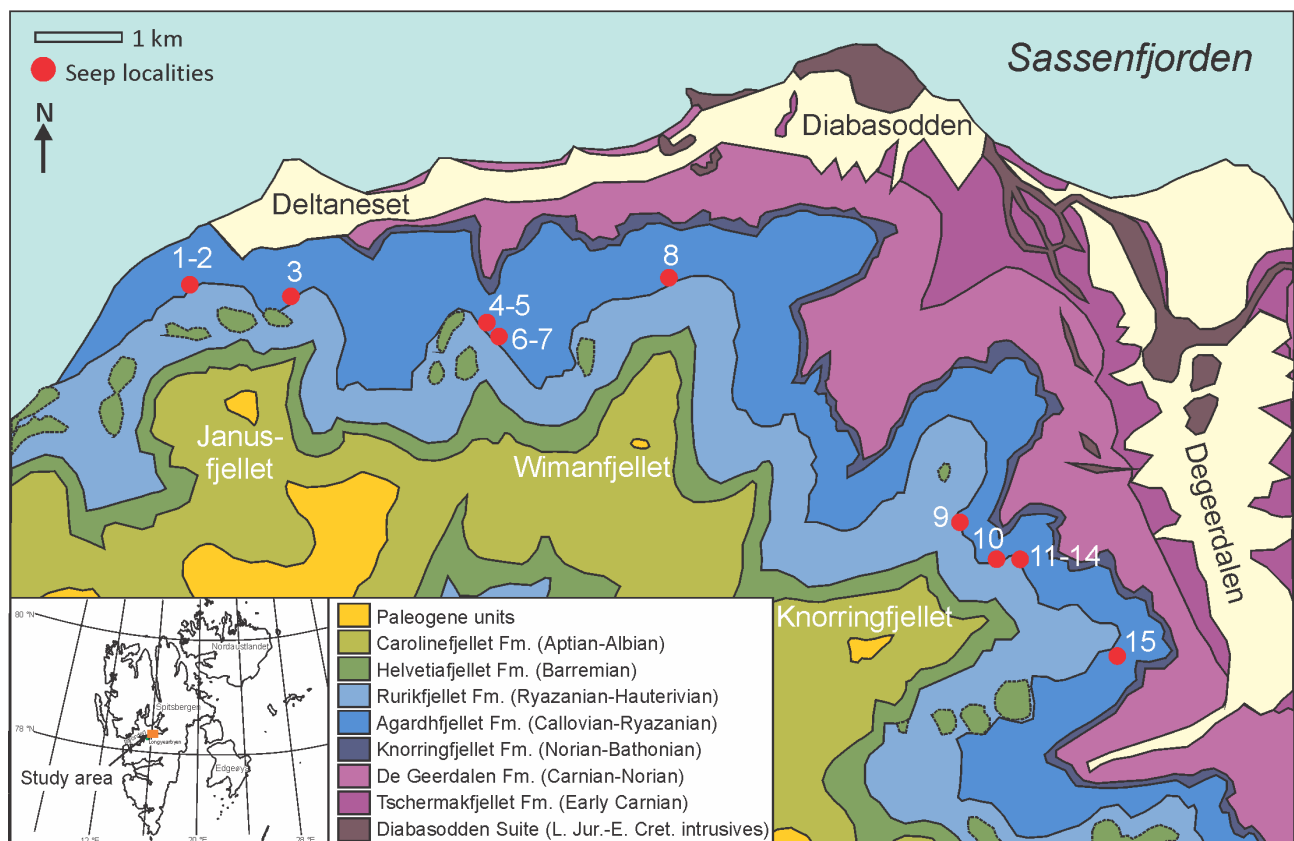
### Introduction

Fifteen carbonate bodies interpreted as fossil hydrocarbon seeps (Hammer *et al.* 2011) were identified during fieldwork (2006–2010) in the Janusfjellet to Knorringfjellet area, Sassenfjorden, central Spitsbergen (Fig. 1). The seeps are hosted by the Slottsmøya Member, which is composed mainly of grey to black organic-rich shales with lesser silty beds and carbonate concretions, and was deposited on the middle-to outer shelf (Nagy *et al.* 1988; Dypvik *et al.* 1991; Collignon & Hammer 2012). The strata (Fig. 2) are part of the post-Devonian cover sequence of the Main Spitsbergen Basin (Harland 1997, fig. 3.9).

Based on ammonite biostratigraphy, the seep carbonates range in age from Late Volgian to latest Ryazanian, spanning approximately a nine million year interval (Wierzbowski *et al.* 2011). The Volgian and Ryazanian are informal Boreal stages established due to strong provincialism of ammonite faunas around the Jurassic–Cretaceous

boundary (e.g. Harland & Kelly in Harland 1997; Abbink *et al.* 2001; Rogov & Zakharov 2009). They equate roughly to the Tithonian and Berriasian standard stages (e.g. Zakharov & Rogov 2008). The Tithonian–Berriasian and hence the Jurassic–Cretaceous boundary is positioned within the Upper Volgian Taimyrensis zone, so the Lower to lowermost Upper Volgian equates to the Tithonian and the uppermost Volgian and Ryazanian equates with the Berriasian (Houša *et al.* 2007). This means that all of the Volgian seeps from Spitsbergen are Tithonian and all Ryazanian seeps are Berriasian in age.

Collecting from the Sassenfjorden area seeps was not standardized and seeps 1, 2, 3, 8 and 9 were extensively sampled during multiple field seasons, whereas remaining deposits were bulk sampled on a single occasion only. The highest diversity recorded among the brachiopod fauna (at order, genus and species level) is from seep 9 (Table 1; Hammer *et al.* 2011, table 2). The highly weathered nature of the seep deposits makes it difficult to accurately reconstruct the shape and structure of the original carbonate masses, but they are all less than four metres in width and thickness.



**FIGURE 1.** Geological map of the Late Jurassic–Early Cretaceous hydrocarbon seep carbonate localities, Spitsbergen (modified from Dallmann *et al.* 2001), with inset map of Svalbard indicating the study area.

### The brachiopod fauna

Eight of the 15 Sassenfjorden area seeps contain rhynchonellate brachiopods. Each species considered herein is typically represented by 1 to 15 specimens. There are at least 12 taxa present among the 80 specimens (Table 1) represented by complete, damaged, or fragmentary material. In over 50% of the specimens the beak of the ventral valve is damaged or missing. This is unfortunate as it means that the nature (and presence/absence) of some important taxonomic characters, such as the shape of the umbo, beak ridges, pedicle foramen, deltidial plates/symphytium, and interarea, cannot be ascertained for these specimens. A smaller number of specimens have damaged anterior and/or lateral commissures.

The rhynchonellate brachiopod fauna comprises rhynchonellides, terebratulides (terebratuloids and loboidothyridoids) and terebratellidines. The rhynchonellide brachiopods are represented by forms referred to

*Pseudomonticlarella varia* Smirnova, *Ptilorhynchia mclachlani* **sp. nov.** and *Ptilorhynchia obscuricostata* Dagys. Specimens referred to ‘*Lacunosella*’ (in Hammer *et al.* 2011, following Owen 1976) are now referred to *Ptilorhynchia* as a result of having made serial sections that reveal internal structures. Two terebratulide taxa were originally identified in this fauna: ‘*Praelongithyris*’ and ‘*Cyrtothyris*’ (Hammer *et al.* 2011). Again, serial sections have now been taken of some terebratulide specimens and assignments emended, with forms referred to the terebratuloids *Cyrtothyris?* sp., *Cyrtothyris* aff. *cyrta* (Walker), *Praelongithyris?* aff. *borealis* (Owen) and the loboidothyridoids: *Rouillieria* cf. *michalkowii* (Fahrenkohl); *Rouillieria* aff. *ovoides* (Sowerby); *Rouillieria* aff. *rasile* Smirnova; *Uralella?* cf. *janimaniensis* Makridin; *Uralella?* sp.; *Pinaxiothyris campestris?* Dagys; *Placothyris kegeli?* Harper *et al.*; and *Seductorithyris septemtrionalis* **gen. et sp. nov.** A terebratellidine has been referred to *Zittelina?* sp.

The inarticulate brachiopod *Lingularia similis?* Biernat & Emig was described by Holmer & Nakrem (2012) from seeps 9 and 12, and is also observed in thin sections from seeps 1, 5 and 15 (Hammer *et al.* 2011). It is the most abundant brachiopod taxon from the Spitsbergen seeps (Table 1). *Lingularia* has been observed at two seeps that lack other brachiopod taxa (seeps 5 and 15); whereas at seeps 1, 9 and 12 other species are present (Table 1; cf. Hammer *et al.* 2011, table 2). Prior to the overview by Hammer *et al.* (2011) only inarticulated Mesozoic brachiopods had been figured and described from Svalbard. These Triassic and Jurassic species were originally referred to *Lingula* and subsequently to *Lingularia* by Biernat & Emig (1993). In addition a Jurassic species, *Discinisca spitsbergensis* Biernat (1995), was described from the Toarcian/Aalenian, Brentskardhaugen Bed of Spitsbergen. It is likely that *Lingularia* is also represented in the nearby Barents Sea borehole (from undifferentiated Berriasian–Valanginian, Århus *et al.* 1990).

| Ma  | Age (Ogg & Hinnov 2012) |               | Boreal zonation | Lithostratigraphy (Mørk et al. 1999) |                   |                      | Revised age (Wierzbowski et al. 2011) |
|-----|-------------------------|---------------|-----------------|--------------------------------------|-------------------|----------------------|---------------------------------------|
|     |                         |               |                 |                                      |                   |                      |                                       |
| 130 | Cretaceous              | Early (pars.) | Hauterivian     | Adventdalen Group                    | Rurikfjellet Fm.  | Ullaberget Mbr.      | ?                                     |
|     |                         |               | Valanginian     |                                      |                   | Wimanfjellet Mbr.    |                                       |
|     |                         |               | Berriasian      |                                      |                   | Myklegardfjellet Bed |                                       |
| 140 | Jurassic                | Late          | Tithonian       | Adventdalen Group                    | Agardhfjellet Fm. | Myklegardfjellet Bed | Slottsmøya Member                     |
|     |                         |               | Kimmeridgian    |                                      |                   | Slottsmøya Mbr.      |                                       |
|     |                         |               | Oxfordian       |                                      |                   | Oppdalsåta Mbr.      |                                       |
|     |                         | Middle        | Callovian       |                                      |                   | Lardyfjellet Mbr.    | Kapp Toscana Group (pars.)            |
|     |                         |               | Bathonian       |                                      |                   | Oppdalen Mbr.        |                                       |
|     |                         |               |                 |                                      |                   |                      |                                       |
|     |                         |               |                 |                                      |                   |                      |                                       |

**FIGURE 2.** Lithostratigraphic subdivision and age relationships of the Middle Jurassic to Early Cretaceous succession of central Spitsbergen. The black hemispherical symbols indicate the relative position and range of the hydrocarbon seep carbonate bodies discussed in this paper.

## Previous studies

Important monographs dealing with contemporaneous brachiopods from Boreal faunas are those by Makridin (1964), who described Jurassic brachiopods from the Russian Platform, and Dagys (1968), on the Jurassic and Early Cretaceous brachiopods of northern Siberia. Subsequent contributions on Early Cretaceous brachiopods of the Russian Platform include those by Smirnova (1975, 1978, 1987; Smirnova & Ushatinskaya 2001). Smirnova has also described Early Cretaceous brachiopods from Kamchatka (Smirnova 1994; Smirnova & Pergament 1969), the Anadyr’ River Basin (Smirnova & Terekhova 1972) and the Primor’ye (Smirnova & Konovalov 1986). Palaeobiogeographical reviews of Early Cretaceous brachiopod faunas were given by Middlemiss (1973, 1979)

and Owen (1973), primarily from Europe, while Smirnova (1984, 1997) also considered broader palaeobiogeographic distributions. Ager provided numerous discussions of Jurassic and Mesozoic brachiopod palaeobiogeography (e.g. 1967, 1971a, 1973; Ager & Sun, 1989). Other works giving an overview of aspects of Mesozoic brachiopod palaeobiogeography include, for example, Sandy (1991), Manceñido & Dagys (1992, in which some Siberian species from Dagys (1968) are discussed and refigured) and Manceñido (2002). The Early Cretaceous brachiopods of East Greenland (Muir-Wood 1953; Owen 1976) are of a slightly younger age (Valanginian–Albian(?); Harper *et al.* 2005) than those from Spitsbergen (Volgian–Ryazanian).

The brachiopod fauna from Svalbard described herein was initially identified in a preliminary survey of the invertebrate fauna from the seep carbonates (Hammer *et al.* 2011) prior to detailed ammonite age-assignments being available for the majority of the seeps (Wierzbowski *et al.* 2011).

### Palaeobiogeographic considerations

The brachiopod seep fauna from Spitsbergen reveals strong Boreal affinities, including the genera *Pseudomonticlarella* Smirnova, *Ptilorhynchia* Crickmay, *Rouillieria* Makridin, and *Uralella* Makridin that have been described from the Russian Platform (Makridin 1964; Smirnova 1987); all of these, except *Pseudomonticlarella*, are also known from northern Siberia (Dagys 1968). *Rouillieria* and *Uralella* have also been recorded from northern Europe (e.g. Ager 1971b; Middlemiss 1976). The forms referred to *Cyrtothyris* and *Praelongithyris* in the Spitsbergen seep fauna are representative of taxa more broadly distributed throughout lower latitudes, having both been recorded from northern Europe (Middlemiss 1959, 1976, 1979) and South Africa (Owen 1980; northern Zululand); however the assignments to these genera in Spitsbergen are tentative. As it is only known from Spitsbergen the new genus, *Seductorithyris*, does not add any palaeobiogeographic links and can be considered an endemic element to the fauna. *Ptilorhynchia* is a component of Boreal faunas, but also appears to have had a broad latitudinal distribution and has even been considered bipolar or cosmopolitan (Thomson & Owen 1979; Århus *et al.* 1990; Sandy 1991) and more recently as circum-Pacific (Manceñido 2002; MacFarlan *et al.* 2011). *Ptilorhynchia mclachlani* **sp. nov.** also implies a component of endemism at the species level, but is part of an evolving plexus of closely-related *Ptilorhynchia* species and does not necessarily imply strong endemism.

Smirnova (1975) commented that among the terebratulides, the Loboidothyridoidea (with long flanges on the brachidium and complex loop ontogeny) are widely distributed in the Boreal and Tethyan Realms in the Late Jurassic; Makridin (1964) also noted that the terebratulides with a short simple-loop (Terebratuloidea) occupied a subordinate position in Boreal faunas. The Loboidothyridoidea were considered to become extinct in Tethys in the Tithonian (Smirnova 1975) and subsequently the Terebratuloidea are exclusively present in the Tethyan Lower Cretaceous. Early Cretaceous Boreal terebratulides were somewhat delayed in their development compared to Tethyan faunas (Smirnova 1975). This presumably applies to the Terebratuloidea as the Loboidothyridoidea are well-represented in Late Jurassic–Early Cretaceous faunas with Boreal affinities (Makridin 1964; Dagys 1968); in addition, subsequent work has not identified any terebratuloids in the Lower Cretaceous of the Russian Platform (Smirnova 1975, 1987). The composition of the Volgian (Ager 1971b; Smirnova, 1997) and Neocomian (Owen 1965; Smirnova 1997) brachiopod faunas of the Russian Platform and Western Europe (specifically eastern England and northern Germany) point to marine connections between these two areas. In addition, brachiopod faunal components indicate marine connections between the Russian Platform and the Arctic basin of Siberia in the Valanginian (Smirnova 1997).

The presence of loboidothyridoids in Spitsbergen supports the Boreal association of this Superfamily (e.g., Makridin 1964; Smirnova 1975), specifically for *Rouillieria* and *Seductorithyris*. Of the forms referred herein to the terebratuloid genera *Cyrtothyris* and *Praelongithyris* these assignments are tentative as investigations of internal structures (i.e., the brachidium) have not been carried out. Owen's (1976) investigation of likely congeneric forms from shallow water sediments of East Greenland has also not confirmed these as terebratuloids, as it is not possible to determine the length of the brachidial flanges in Owen's serial sections (1976, figs. 6, 7). Of the East Greenland taxa recorded from deeper water sediments with Tethyan affinities (Harper *et al.* 2005), terebratuloids (including *Pygope*, *Nucleata*, *Moutonithyris*) are present and are consistent with Smirnova's (1975) observations regarding low-latitude faunas. Having said that, the brachidium of only one of the terebratulide taxa from the Lower Cretaceous of East Greenland discussed in Harper *et al.* (2005), *Placothyris*, has been investigated



(fig. 3 in Harper *et al.* 2005; exterior of sectioned specimen figured herein, Fig. 13.9–13.12). *Placothyris* is now considered a loboidothyridoid (Lee *et al.* 2006). So palaeobiogeographic patterns are likely to be more complicated than previously considered.

## Palaeoecology

In addition to brachiopods from the Sassenfjorden area the hydrocarbon seeps contain a high diversity of bivalves (17 species, Hryniewicz *et al.* 2014), gastropods (~10 species; unpublished data) and serpulids (four species; Vinn *et al.* in press). This makes the Spitsbergen seep faunas very different from many of the Palaeozoic–Mesozoic seep deposits that contain shell beds or lenses dominated by monospecific accumulations of brachiopods (e.g. Campbell & Bottjer 1995; Sandy 1995, 2010; Sandy *et al.* 2012; Peckmann *et al.* 2007, 2011, 2013; Kiel & Peckmann 2008). Clearly the overall taxonomic diversity of the Spitsbergen seep communities is much greater and the brachiopod species richness is higher too (Table 1; Hammer *et al.* 2011, table 2; cf. Sandy 2010, table 9.1). In contrast to these Palaeozoic–Mesozoic brachiopod-dominated seeps the Spitsbergen seep brachiopods are not abundant and are represented by dispersed specimens.

The occurrence of brachiopods in the Spitsbergen seep deposits and not in the surrounding shales can be explained by the early cementation of sediment (Hammer *et al.* 2011; Hryniewicz *et al.* 2012) providing suitable hardgrounds for brachiopod pedicle attachment (Campbell 2006; Sandy 2010), as would other shells. These substrates lead to the development of oases (or refuges) on the otherwise clay-dominated substrate of the encompassing Barents Shelf, which would have been further fuelled by the enhanced food availability in the seep environment compared to the surrounding substrate (Hammer *et al.* 2011). The shelf setting of the Spitsbergen seep deposits contrasts with the Palaeozoic–Mesozoic brachiopod-dominated seep deposits which occur in marine basins in regions of compressive tectonics (e.g. Peckmann *et al.* 2011, 2013), or basin slope-environments (Sandy *et al.* 2012). The apparent paucity of invertebrate diversity in brachiopod-dominated seep carbonates contrasts with the higher taxonomic diversity in the Spitsbergen seep deposits, presumably as a result of the shallower shelf water-depths of the latter.

The occurrence of *Lingularia* in the Slotsmøya Member is the first record of an inarticulated brachiopod from hydrocarbon seeps (Hammer *et al.* 2011). Lingulids are common in very shallow water Valanginian sediments on East Greenland and are believed to be shallow water indicators (Scott 1970; Plaziat *et al.* 1978; Fürsich 1984; Emig 1986).

## Methods

Serial sections were taken of a few specimens to investigate internal structures. The technique used was that described by Sandy (1989). Infilling sparry calcite and silicification makes it difficult to trace internal structures such as the descending branches of the brachidium in the terebratulides and anterior projecting crura in the rhynchonellides. However, in some cases the level of detail recorded on acetate peels was of a high quality, and results obtained have aided genus-level assignments of the material. The carbonate matrix infill precluded attempts at micro computed tomography of specimens to investigate their internal structures.

In particular, there were problems in obtaining good quality acetate peels at times, such as one of the specimens of *Ptilorhynchia mclachlani* **sp. nov.** (Fig. 5A). After grinding to prepare for taking an acetate peel, the specimen was etched with a dilute mixture of hydrochloric acid for a few seconds. However, brachiopod shell was rapidly removed during the etching process and this resulted in problems with air bubbles in the acetate peels. To counteract this problem after each grinding of the specimen, no etching with acid was carried out. The results were much better in that the air bubbles were much reduced in quantity and size, and subsequent peels then showed details that had previously been obscured by air bubbles, such as the outline of the dorsal valve and associated internal structures. The grinding wheel marks that remained as a result of not etching the specimen did not prove to be problematic in interpreting the internal structures preserved on the acetate peels. The second specimen of *Ptilorhynchia mclachlani* **sp. nov.** that was sectioned (Fig. 5B) was mostly infilled with micrite and this proved fortuitous as this matrix provides very good quality acetate peels. Use of carbonate staining techniques during the preparation of serial sections was not attempted during this study (as described by Manceñido & Walley 1989).

**TABLE 1.** Distribution of Jurassic – Cretaceous (Volgian – Ryazanian) brachiopods from seep carbonates 1, 3, 5, 7–10, 12, 13, and 15 in the Slottsmøya Member of the Agardhfjellet Formation from the Knorringfjellet–Janusfjellet area, Sassenfjorden, Svalbard archipelago (Figs. 1, 2). Key: x = present, ? = uncertain identification; E = Early, L = Late, M.-L. = (Mid – Late) Late; Ryaz = Ryazanian; Volg = Volgian.

| Seep number                                  | 1            | 3       | 5         | 7                     | 8       | 9                  | 10                 | 12                 | 13      | 15           |
|--|--------------|---------|-----------|-----------------------|---------|--------------------|--------------------|--------------------|---------|--------------|
| LINGULIDA                                    |              |         |           |                       |         |                    |                    |                    |         |              |
| <i>Lingularia similis?</i>                   | x            |         | x         |                       |         | x                  |                    | x                  |         | x            |
| RHYNCHONELLIDA                               |              |         |           |                       |         |                    |                    |                    |         |              |
| <i>Pseudomonticlairella varia</i>            |              |         |           | x                     |         |                    | ?                  |                    | x       |              |
| <i>Ptilorhynchia mclachlani</i>              |              |         |           |                       |         | x                  |                    |                    |         |              |
| <i>Ptilorhynchia obscuricostata</i>          |              | x       |           |                       |         | x                  |                    | x                  |         |              |
| TEREBRATULIDA                                |              |         |           |                       |         |                    |                    |                    |         |              |
| TEREBRATULOIDEA                              |              |         |           |                       |         |                    |                    |                    |         |              |
| <i>Cyrtothyris?</i> sp.                      |              | x       |           |                       | x       |                    |                    |                    |         |              |
| <i>Cyrtothyris</i> aff. <i>cyrta</i>         |              |         |           |                       |         | x                  |                    |                    |         |              |
| <i>Praelongithyris?</i> aff. <i>borealis</i> | x            |         |           |                       |         | x                  |                    | x                  |         |              |
| LOBOIDOTHYRIDOIDEA                           |              |         |           |                       |         |                    |                    |                    |         |              |
| <i>Rouillieria?</i> cf. <i>michalkowii</i>   |              |         |           |                       | x       |                    |                    |                    | x       |              |
| <i>Rouillieria</i> aff. <i>ovoides</i>       |              |         |           |                       | x       |                    |                    |                    | x       |              |
| <i>Rouillieria</i> aff. <i>rasile</i>        |              |         |           |                       | x       |                    |                    |                    |         |              |
| <i>Uralella?</i> cf. <i>janimaniensis</i>    |              | x       |           |                       |         |                    |                    |                    |         |              |
| <i>Uralella?</i> sp.                         |              | x       |           |                       |         |                    |                    |                    |         |              |
| <i>Seductarthyris septemtrionalis</i>        |              |         |           |                       |         | x                  |                    |                    |         |              |
| <i>Pinaxiothyris campestris?</i>             |              |         |           |                       |         | x                  |                    |                    |         |              |
| <i>Placothyris kegeli?</i>                   |              | x       |           |                       |         |                    |                    |                    |         |              |
| TEREBRATELLIDINA                             |              |         |           |                       |         |                    |                    |                    |         |              |
| <i>Zittelina?</i> sp.                        |              |         |           |                       |         | x                  |                    |                    |         |              |
| Ammonite determined ages                     |              |         |           |                       |         |                    |                    |                    |         |              |
| Brachiopod derived ages                      |              |         |           |                       |         |                    |                    |                    |         |              |
|  | L. Ryazanian | Volgian | Ryazanian | L. Volg./<br>E. Ryaz. | Volgian | M.-L.<br>Ryazanian | M.-L.<br>Ryazanian | M.-L.<br>Ryazanian | Volgian | L. Ryazanian |
| Seep number                                  | 1            | 3       | 5         | 7                     | 8       | 9                  | 10                 | 12                 | 13      | 15           |

## Systematics

Specimens designated with a PMO number are housed in the Palaeontological Collections of the Natural History Museum, University of Oslo, Norway. ? after the specimen number = questionable assignment of specimen to taxon. Other abbreviations used: MGUH = Geological Museum, University of Copenhagen, Denmark; USGS = United States Geological Survey, Mesozoic Collections housed at the Federal Center, Denver, Colorado. Annotations on synonymy lists and taxon names follow Matthews (1973).

### Phylum Brachiopoda Duméril, 1806

#### Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer & Popov, 1996

#### Class Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov, 1996

#### Order Rhynchonellida Kuhn, 1949

#### Superfamily Norelloidea Ager, 1959

#### Family Norellidae Ager, 1959

#### Subfamily Praemonticlarellinae Manceñido & Owen, 2002

#### Genus *Pseudomonticlarella* Smirnova, 1987

**Type species.** *Pseudomonticlarella varia* Smirnova, 1987

**Diagnosis.** Small, equibiconvex, striate, somewhat ligate; outline variable from rounded-triangular to rounded or pyriform; maximum width at midvalve; 3 to 5 lateral folds or plicae; anterior commissure with lateral folds resembling *Monticlarella*; ventral sulcus broadly arcuate with trapezoidal linguiform extension; ventral umbo long with pointed and slightly incurved beak; foramen small, hypothyrid. Hinge teeth long, deeply inserted; dental plates subparallel to weakly ventrally divergent; strong socket ridges; elongated hinge plates supported by strong, low septum. From Manceñido *et al.* 2002, p. 1314.

**Discussion.** This diagnosis is for the genus established by monotypy. Therefore, it is also the diagnosis for the type species, *Pseudomonticlarella varia* Smirnova. It does not require emendation in the light of the new Spitsbergen material.

**Occurrence.** Upper Volgian–Lower (?Upper) Ryazanian.

#### *Pseudomonticlarella varia* Smirnova, 1987

(Figs. 3.1–3.12, 4)

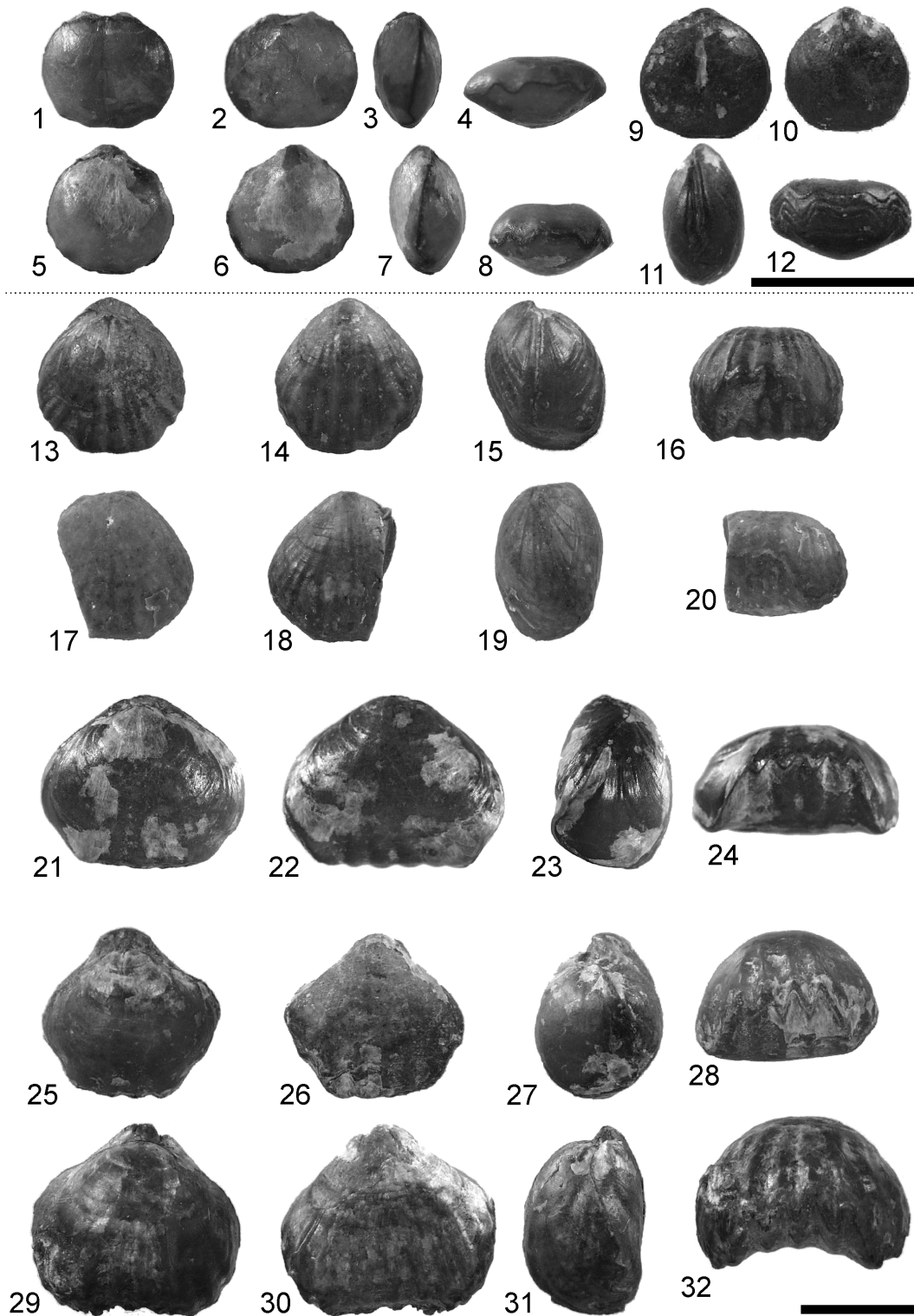
1987 *Pseudomonticlarella varia* new species—Smirnova, p. 33, pl. 4, figs. 1, 2, 5–7, text-fig. 1.

2002 *Pseudomonticlarella varia* Smirnova—Manceñido *et al.*, p. 1314, fig. 891.3a–3p.

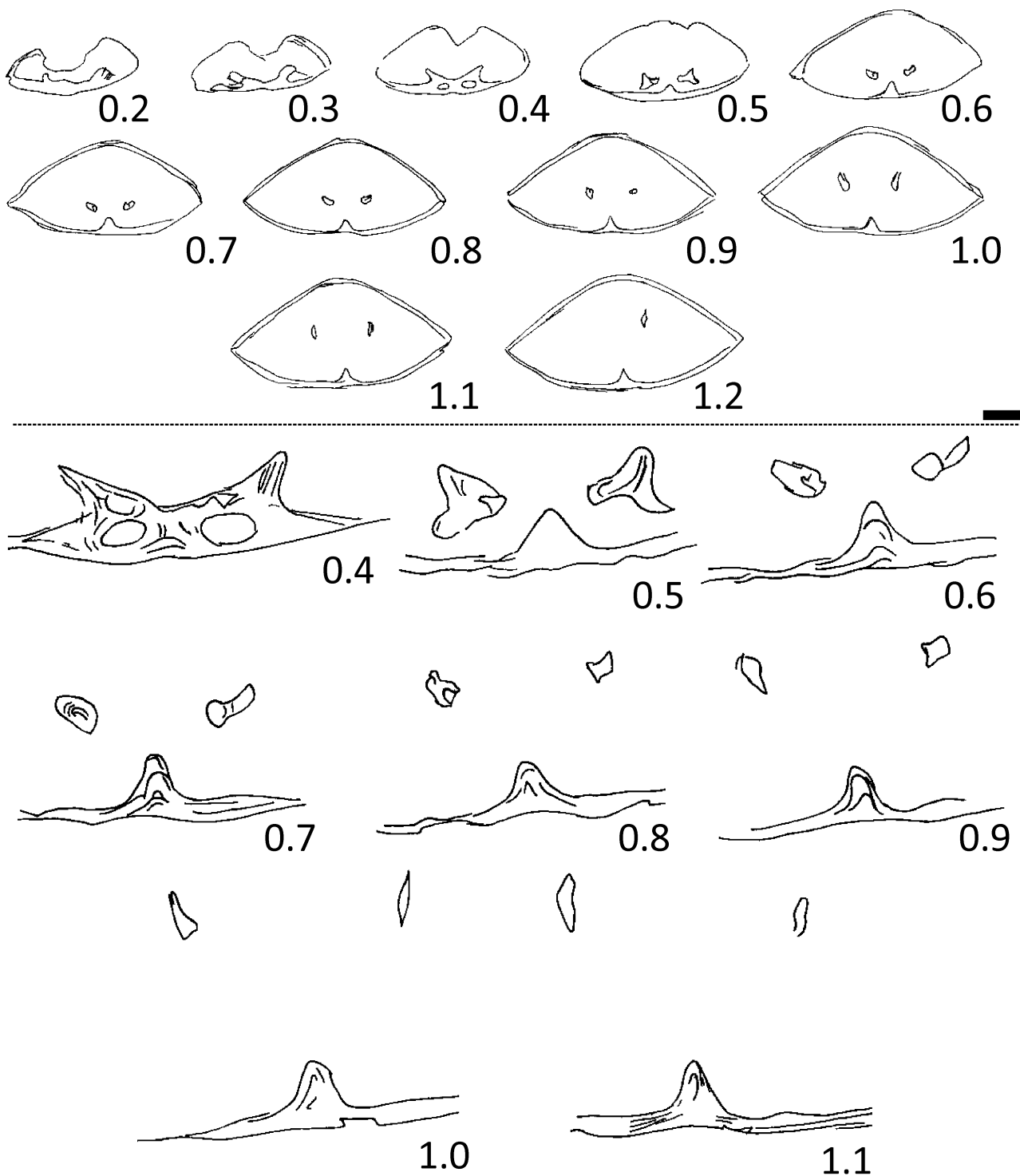
**Material and occurrence.** Seep 7 (PMO 227.419), seep 13 (PMO 227.416–418), seep 10 [damaged specimen, anterior commissure not present, PMO 224.923?].

**Description.** Small (less than 1 cm in length, width, and thickness), smooth rhynchonellide that shows traces of capillate ornament in places. However, the decortication of specimens makes it difficult to verify the ornament of the shell exterior. The anterior commissure is bisulcate with weakly developed sulcii at the commissure; central sulcus shallower than lateral sulcii.

The following internal characters may be visible from external examination, either through translucent shell or because of decortication: dental lamellae in the ventral umbo; a median septum extending at least half the length of



**FIGURE 3.** 1–12. *Pseudomonticlarella varia* Smirnova. 1–4. PMO 227.416, seep 13, dorsal, ventral, lateral, and anterior views. Specimen serially sectioned (Figure 4). 5–8. PMO 227.419, seep 7, dorsal, ventral, lateral, and anterior views. 9–12. PMO 227.418, seep 13, dorsal, ventral, lateral, and anterior views. 13–16. *Ptilorhynchia mclachlani* **sp. nov.** 13–16. PMO 224.876, seep 9, dorsal, ventral, lateral, and anterior views. 17–20. PMO 224.879, seep 9, dorsal, ventral, lateral, and anterior views. Specimen serially sectioned (Figure 5B). 21–24. PMO 227.431, seep 9, dorsal, ventral, lateral, and anterior views. Specimen serially sectioned (Figure 5A). 25–28. PMO 224.871, seep 9, dorsal, ventral, lateral, and anterior views. 29–32. Holotype, PMO 224.882, seep 9, dorsal, ventral, lateral, and anterior views. Dotted line delimits photographs at the same magnification. Scale bars = 1 cm.



**FIGURE 4.** Transverse serial sections of *Pseudomonticlarella varia* Smirnova, seep 13, PMO 227.416. Sections 0.4–1.1 mm given at higher magnification below dotted black line. Serial sections prepared perpendicular to maximum length of the specimen, numbering of sections starts at 0.0 mm the initial section through the specimen. Dimensions of sectioned specimen: L 7.0+; W 8.1; T 4.1 mm (+ = dimension damaged/specimen broken in that direction). Scale bars = 1 mm.

the dorsal valve. Internal characters were also determined from serial sections (Fig. 4): a small septalium-like structure is present due to the concave ventral surface of the hinge plates (Fig. 4, sections 0.3–0.4 mm); crura develop on the inner margins of the hinge plates (sections 0.5–0.7); crura arch ventrally (sections 0.7–1.1). Dental lamellae were not seen in the serial sections (ventral valve umbo of the sectioned specimen was damaged, Fig. 3.1–3.4), but observed from the external examination of specimens.

**Discussion.** The general outline and profile of the specimens from Spitsbergen are similar to those of specimens figured by Smirnova (1987, pl. 4, figs. 1–2) from the Russian Platform, in particular that in pl. 4, fig. 1. This specimen appears to be smooth, developing costae at the anterior margin. The Russian Platform specimens reach maximum lengths close to 6 mm (Smirnova 1987, p. 42) so are smaller than the Spitsbergen material that reach 8 mm in length.

Smirnova provided serial sections of two specimens of *Pseudomonticlarella varia* (1987, fig. 1a–b). Both series of sections show a septalium and crura that arch ventrally anteriorly. These are features that are shared with the Spitsbergen specimen (Fig. 4). The internal structures (from the initial section through the brachiopod) were traced for 4.12 mm in specimen No. 139/584 (Smirnova 1987, fig. 1a) and for 1.45 mm in specimen No. 139/590 (fig. 1b). In the Spitsbergen specimen the internal structures were traced to section 1.2 mm (i.e., 1.2 mm from the initial section through the specimen).

It was thought originally that these diminutive specimens could be juveniles of the form referred herein to *Ptilorhynchia mclachlani* sp. nov. However, posteriorly the ventral valve of *Pseudomonticlarella varia* lacks any developing or incipient costae, which are often present posteriorly on specimens of *Ptilorhynchia mclachlani*. Also, posteriorly, the dorsal valve of *Pseudomonticlarella varia* is weakly sulcate (possibly enhanced by some decortication). This sulcate condition does not appear to characterize specimens of *Ptilorhynchia mclachlani*. In addition, *Ptilorhynchia mclachlani* and *Pseudomonticlarella varia* are not co-occurring. Obviously they should co-occur if they are conspecific (although this could reflect a collecting failure). The specimens of *Pseudomonticlarella varia* all occur with similar maximum dimensions and there are currently no other intermediate-sized forms between these and larger-sized species such as *Ptilorhynchia mclachlani*.

**Stratigraphic and geographic distribution.** Upper Volgian–Lower (?Upper) Ryazanian of Spitsbergen and originally described from the Upper Volgian of the Russian Platform (Smirnova 1987).

## Superfamily Rhynchonelloidea d’Orbigny, 1847

### Family Rhynchonellidae d’Orbigny, 1847

#### Subfamily Piarorhynchiinae Shi & Grant, 1993

#### Genus *Ptilorhynchia* Crickmay, 1933

**Type species.** *Ptilorhynchia plumasensis* Crickmay, 1933

#### *Ptilorhynchia mclachlani* sp. nov.

Figs. 3.13–3.32, 5

2011 v. partim ‘*Lacunosella*’ sp.—Hammer *et al.*, p. 21, table 2, fig. 7R.

2011 v. partim ‘*Monticlarella*’ sp.—Hammer *et al.*, p. 21, table 2.

**Material and occurrence.** Holotype: PMO 224.882; paratypes: PMO 227.431, PMO 227.432, PMO 224.871–873, PMO 224.875, PMO 224.883, PMO 217.199, PMO 224.914 (crushed). Juvenile specimens: PMO 224.876–879, PMO 227.433. All specimens from seep 9.

**Type locality.** Knorringfjellet, central Spitsbergen, N78° 18’ 49.9” E16° 10’ 58.9”.

**Etymology.** For the late Mr. Archie McLachlan, Department of Geology, Queen Mary College, University of London (see Middlemiss 1997, p. 169).

**Dimensions of the holotype.** PMO 224.882—Length 17.1 mm, width 18.9 mm, thickness 11.6 mm.

**Diagnosis.** Subtriangular in outline, generally evenly biconvex in profile. Valve surface smooth except for ornament of costae which may be traceable over most of the length of the valves but are most strongly developed at the anterior commissure. Number of costae on valves variable, with typically 3–4 costae in the sulcus of the dorsal valve and 4–5 on the corresponding fold of the ventral valve. Dental lamellae present in ventral valve. Well-developed septalium in dorsal valve, outer hinge plates horizontal from which inner socket ridges are deflected.

Crura develop at top of Y-shape of septalium, where inner and outer hinge plates meet. Anteriorly crura arch ventrally.

**Discussion.** The beak of the ventral valve is frequently damaged/incomplete in the specimens. As a result, the dental lamellae are usually clearly visible in the umbo of the ventral valve. Juvenile specimens have costae developed over both valves, some larger specimens have costae developed primarily in the sulcus of the ventral valve and at the anterior margin.

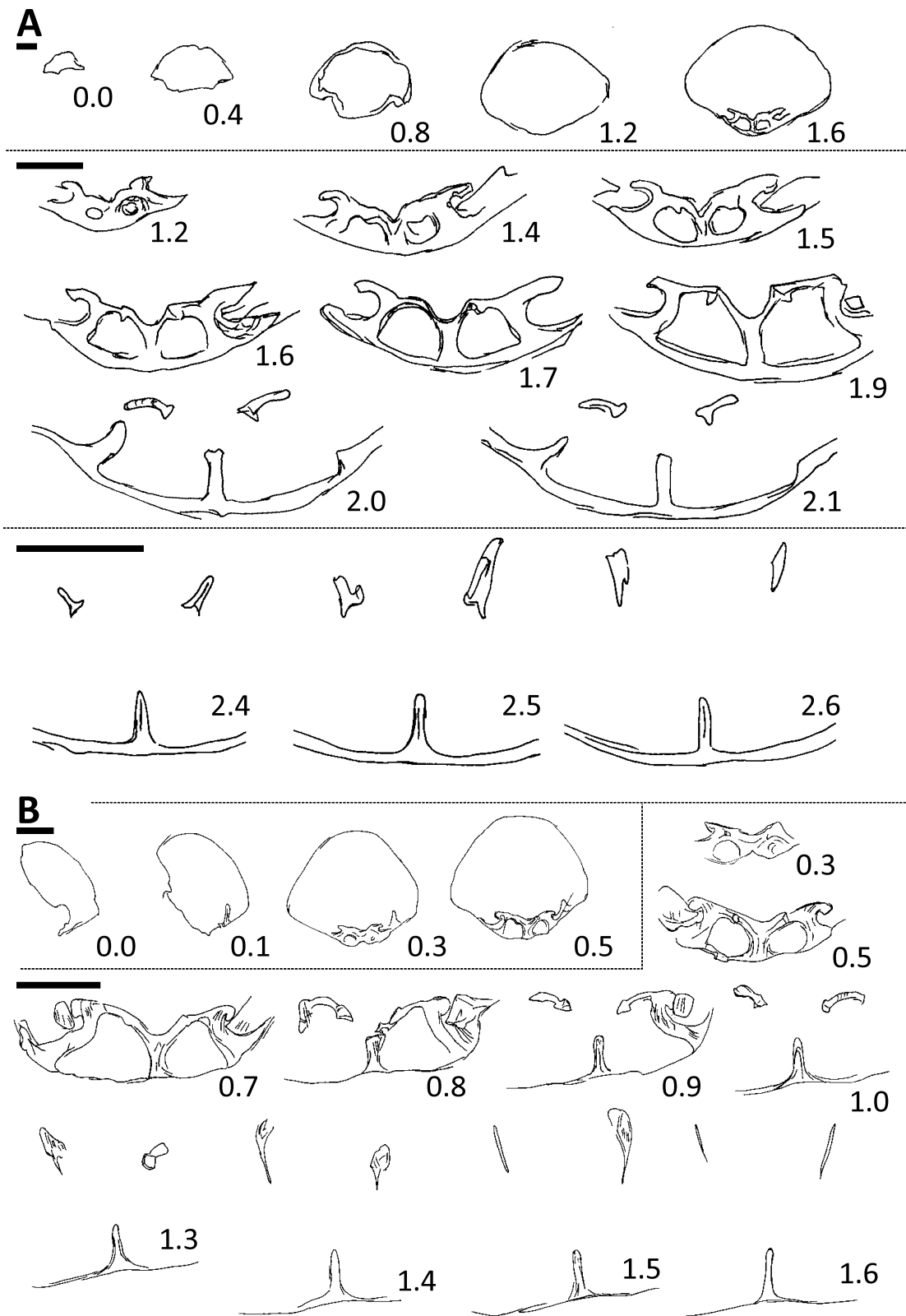
The material from Spitsbergen shows variability in outline and number of costae. The costae are traceable over most of the length of the valves. Owen (1972) described a variable species that he referred to *Ptilorhynchia jeletzkyi* from the latest Jurassic of British Columbia which is very similar to the material from Spitsbergen.

Owen (1972, p. 2) comments on *Ptilorhynchia jeletzkyi* “The shell surface is smooth, exhibiting no sign of striae, but often developing strong marginal plicae which originate midway between the umbones and anterior commissure. These plicae number from one to four . . .”. However, these strong plicae are not obvious in figured specimens (Owen 1972, pl. 1, figs. 1–4) or a specimen referred herein to *Ptilorhynchia jeletzkyi* from the Upper Jurassic (Kimmeridgian–Tithonian?) of Alaska (Fig. 6.5–6.8). This specimen is slightly damaged at the anterior commissure and the lateral margin, but does show the generally smooth shell ornament and the development of marginal costae (3 costae on the dorsal fold, 2 in the ventral sulcus). The number of costae in the sulcus (at the anterior commissure) in *Ptilorhynchia jeletzkyi* ranges from one to 4 or 5 (Owen 1972, fig. 4, pl. 1, figs. 1c, 2–4). *Ptilorhynchia jeletzkyi* is reported from the *Buchia fisheriana* and *B. piochii* zones (i.e., Upper Tithonian, in part equivalent to the Upper Volgian).

In *Ptilorhynchia mclachlani*, the specimens may show well-marked costae which may extend across most of the length of the specimen (e.g. Fig. 3.29). This costate shell ornament is not typical of *Ptilorhynchia*, which tends to show costation developed at the shell margin (e.g. species figured by Dagys 1968; Owen 1972; Owen & Manceñido 2002; and *P. jeletzkyi* herein, Fig. 6.5–6.8, and a specimen identified as *P. aff. plumasensis* from the Middle Jurassic of Alaska, Fig. 6.1–6.4 close to the type species from the Middle Jurassic Hinchman Formation (Callovian) of California (Crickmay 1933; see also Owen 1972). MacFarlan *et al.* (2011) claim the type horizon for *P. plumasensis* to be the Upper Jurassic Knoxville Formation, but their reason for this revised assignment was not given). Most of the specimens from Spitsbergen display four costae on the dorsal fold and three costae in the ventral sulcus. Due to the distinctive nature of the costation it is considered desirable to refer the Spitsbergen material to a new species rather than to the morphologically similar *P. jeletzkyi*.

The weakly costate *Ptilorhynchia mclachlani* resembles some species referred to *Ptilorhynchia* by Dagys (1968). Of these, the Spitsbergen specimens are closest to *P. lenaensis* in the nature of the costation of the anterior commissure but the overall size of the latter is smaller, and the number of costae on the fold and sulcus fewer than in the Spitsbergen specimens. Matching closely in outline and costation is *P. anadyrensis* Dagys (1968, pl. 4, figs. 3, 4) although the nature of the costation appears more angular at the anterior commissure when compared to *Ptilorhynchia mclachlani*. The specimens of these species figured by Dagys appear to all be decorticated. The age assignment of *P. lenaensis* is Valanginian (Dagys 1968) so it is slightly younger in age than the Spitsbergen specimens while *P. anadyrensis* was given as of uncertain age, referred questionably to the Bathonian–Callovian (Dagys 1968, table 1, p. 145). A single rhynchonellide specimen (internal cast of a ventral valve, approximately 8 mm x 8 mm) from undifferentiated Berriasian–Valanginian of the Barents Sea (Århus *et al.* 1990) identified as *Ptilorhynchia* sp., was tentatively referred to this genus. MacFarlan *et al.* (2011) described *Ptilorhynchia pugnaciformis* from the Lower Cretaceous of the Misool Archipelago, eastern Indonesia. Like other species of *Ptilorhynchia* already discussed, the number of costae for this species is considered to be variable (between 3–6 per valve; MacFarlan *et al.*, table 1). The posterior profile of the dorsal valve in *P. pugnaciformis* is not as rounded as it is in *P. mclachlani* or *P. jeletzkyi*; in *pugnaciformis* the profile may be cynocephalous and therefore resembling, at least in profile, *Homoeorhynchia* Buckman.

Small multicostate specimens are considered juveniles of *Ptilorhynchia mclachlani*. These specimens had been tentatively referred to *Monticlarella* by Sandy in Hammer *et al.* (2011); they have a similar outline to *Monticlarella triloboides* (Quenstedt) in Childs (1969, pl. I, figs. 5–7). However, the nature of the costation is consistent with *Ptilorhynchia mclachlani* and the broad uniplicate fold develops more strongly as the brachiopod approaches maturity, with a concomitant deflection of the lateral commissure (Fig. 3.21–3.24, 3.29–3.32 cf. for juveniles, Fig. 3.13–3.20, 3.25–3.28). Dental lamellae and a median septum can be readily discerned in the majority of the smaller specimens; characters that if present in *Monticlarella* are typically poorly developed (e.g. Owen 1968;



**FIGURE 5.** A and B, transverse serial sections from two specimens of *Ptilorhynchia mclachlani* sp. nov., seep 9. A) Specimen PMO 227.431, sections above third dotted line. Dotted lines delimit groups of sections drawn at the same magnification. Dimensions of specimen: L 15.3+; W 18.3; T 9.8 mm. Serial sections prepared perpendicular to maximum length of specimen; numbering of sections starts at 0.0 mm, the initial section through the specimen. B) Specimen PMO 224.879, sections below third dotted line. Dimensions of sectioned specimen: L 12.9; W 12.8+ ; T 9.0 mm. Serial sections prepared perpendicular to length of dorsal valve; numbering of sections starts at 0.0 mm, the initial section through the specimen. Scale bars = 1 mm.



Manceñido *et al.* 2002, p. 1316). (From the palaeobiographic point of view, *Monticlarella* has not been recorded from Boreal faunas of the Russian Platform or Siberia, whereas several species have been referred to *Ptilorhynchia* from these regions.) Serial sections were taken of one of the smaller-sized specimens of *Ptilorhynchia mclachlani* to clarify the relationships among the material (Fig. 5B). The serial sections show remnants of a dental lamella on the right side of the specimen (Fig. 5B, section 0.1), a well-developed septalium (0.3–0.7) and crura that arch ventrally towards the anterior of the brachiopod (1.0–1.6). The crura develop as discrete structures at the junction between the outer hinge plates and the inner hinge plates of the septalial structure (0.5–1.0). These serial sections are very similar in overall aspect to those taken from the larger specimen (Fig. 5A) and both are considered *Ptilorhynchia mclachlani*.

In comparing the serial sections of *Ptilorhynchia mclachlani* (Fig. 5) with *Ptilorhynchia jeletzkyi* (Owen 1972, fig. 1) there are similarities in the development of the septalium and the crura on the inner margins of the hinge plates, and the crura then arch ventrally anteriorly. The larger Spitsbergen specimen (Fig. 5A) did not capture the dental lamellae of the ventral valve, and this is also true when comparing the serial sections of species referred to *Ptilorhynchia* by Dagys (1968). The presence of well-developed dental lamellae in the ventral valves of the Canadian (Owen 1972), Siberian (Dagys 1968) and Indonesian (MacFarlan *et al.* 2011) material is a difference from the Spitsbergen material. The ventral umbo of the larger specimen selected for serial sectioning (Fig. 3.21–3.24) was damaged, with the outline of dental lamellae visible, and their traces can also be determined in the duplicate cast taken of this specimen. In addition, dental lamellae are clearly visible in the damaged ventral umbones of other specimens. Traces of dental lamellae were not seen in the serial sections and acetate peels (for specimen in Fig. 5A). This specimen was decorticated and the calcite shell of the dental lamellae apparently lost through decortication or weathering in the umbonal region of the ventral valve. Most of the external shell of the specimen was absent too. Of the serial sections of species described by Dagys, *P. lenaensis* Dagys (1968, fig. 43) and *P. anadyrensis* Dagys (1968, fig. 39) appear closest to those of *Ptilorhynchia mclachlani* (Fig. 5) based on the development of the septalium, hinge plates, and derivation of the crura from the inner margins of the hinge plates. It should be noted that plates 2 and 5 in Dagys 1968 were printed in the wrong order. The taxonomic descriptions and caption for plate 5 refers to *P. glabra*, *P. lenaensis* and *P. obscuricostata*. However, these species are figured on plate 2.

Serial sections of the Spitsbergen material (Fig. 5) lack the falciform crura characteristic of the genus *Lacunosella* recorded from Greenland (Owen 1976, fig. 3).

**Stratigraphic and geographic distribution.** Upper Ryazanian of Spitsbergen.

### ***Ptilorhynchia obscuricostata* Dagys, 1968**

Fig. 6.9–6.17

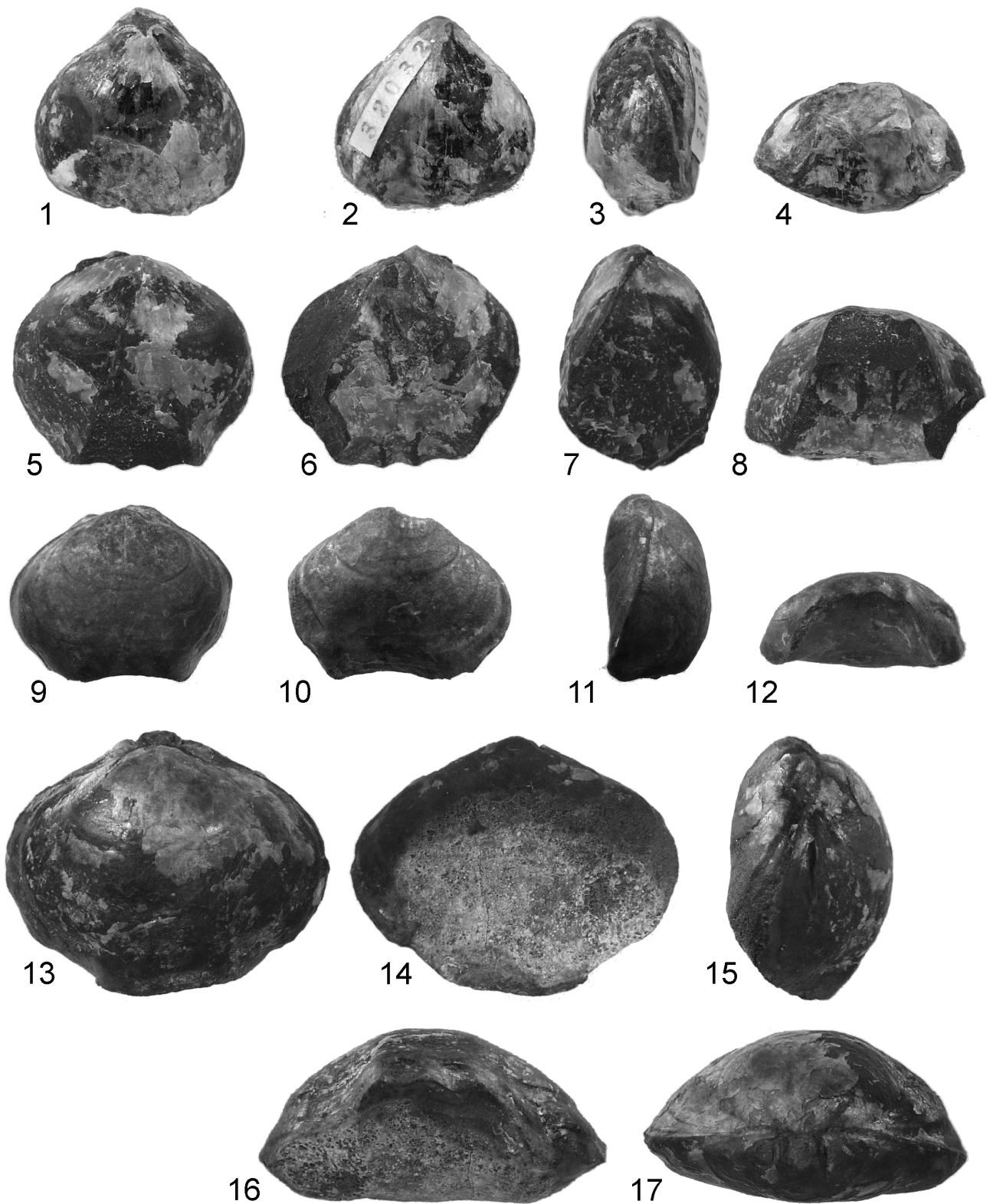
1968 *Ptilorhynchia obscuricostata* new species—Dagys, p. 63, pl. 5, fig. 6, 7, text-fig. 42.

2011 v. partim ‘*Lacunosella*’ sp.—Hammer *et al.*, p. 21, table 2.

**Material and occurrence.** Seep 3 (PMO 224.915), seep 9 (PMO 224.881, PMO 224.880), seep 12 (PMO 224.884).

**Description.** Wide triangular outline. Biconvex profile. Broad flat-topped uniplication of the anterior commissure. Smooth shelled with weak or incipient costae developed at the anterior margin, primarily in the fold/sulcus of the anterior commissure. A few growth lines are present. Median septum and dental lamellae are visible. Other internal structures have not been investigated.

**Discussion.** The generally smooth and uniplicate form with the development of costae only towards the margin of the valves was one reason why this material was tentatively referred to ‘*Lacunosella*’ (Hammer *et al.* 2011), due to its resemblance to *L. groenlandica* Owen (1976; and in Harper *et al.* 2005). However, the smooth shell, presence of costae at the valve margins, and broad uniplication of the anterior commissure are also characteristic of *Ptilorhynchia obscuricostata* (Dagys 1968). Even in the absence of serial sections of the present material, some useful observations can be made. The Spitsbergen specimens do not appear to show the massive shell-thickening of the ventral umbo that Owen observed in serial sections of *L. groenlandica* (Owen 1976, fig. 3). The presence of distinct dental lamellae in the umbo of the ventral valve is consistent with *Ptilorhynchia*, but of course not diagnostic of this genus as they are present in many rhynchonellide genera. In *L. groenlandica* Owen dental



**FIGURE 6.** 1–4. *Ptilorhynchia* aff. *plumasensis* Crickmay, USGS Mesozoic Locality 32032 (=80Ace119), Karluk Quadrangle, Alaska, Shelikof Formation, Callovian, Middle Jurassic, dorsal, ventral, lateral, and anterior views. 5–8. *Ptilorhynchia jeletzkyi* Owen, USGS Mesozoic locality 14496, co-occurs with *Buchia mosquensis* (von Buch), probably Naknek series, Kimmeridgian–Tithonian(?), Upper Jurassic, McCarthy Quadrangle, Alaska. Collector, Fred H. Moffit, 1928. Dorsal, ventral, lateral, and anterior views. 9–12. *Ptilorhynchia obscuricostata* Dagys. 9–12. PMO 224.880, seep 9, dorsal, ventral, lateral, and anterior views. 13–17. PMO 224.881, seep 9, dorsal, ventral, lateral, anterior and posterior views. Scale bar = 1 cm.

lamellae are massively overgrown (Owen 1976, fig. 3). A median septum is present in the dorsal valve of the Spitsbergen material whereas *Lacunosella* lacks a median septum (e.g. Owen 1976, fig. 3; Manceñido & Owen 2002, p. 1208).

**Stratigraphic and geographic distribution.** Upper Volgian–uppermost Ryazanian, Spitsbergen and Lower Volgian of northern Siberia (Dagys 1968).

## Order Terebratulida Waagen, 1883

### Suborder Terebratulidina Waagen, 1883

### Superfamily Terebratuloidea Gray, 1840

### Family Sellithyrididae Muir-Wood, 1965

### Subfamily Rectithyridinae Muir-Wood, 1965

### Genus *Cyrtothyris* Middlemiss, 1959

**Type species.** *Terebratula depressa* var. *cyrta* Walker, 1868

### *Cyrtothyris?* sp.

Fig. 7.5–7.8

1976 ? v. “*Cyrtothyris*” *maynci* new species—Owen, p. 13, pl. 2, fig. 1a–c, pl. 3, fig. 4a–c, text-fig. 7.

2011 v. partim ‘*Cyrtothyris*’ sp.—Hammer *et al.*, p. 20, table 2.

**Material and occurrence.** Seep 3 (PMO 224.870, PMO 224.904?, PMO 224.919?), seep 8 (PMO 227.428?).

**Description.** Rounded, circular, to gently elongate outline, equibiconvex lateral profile, rectimarginate anterior commissure.

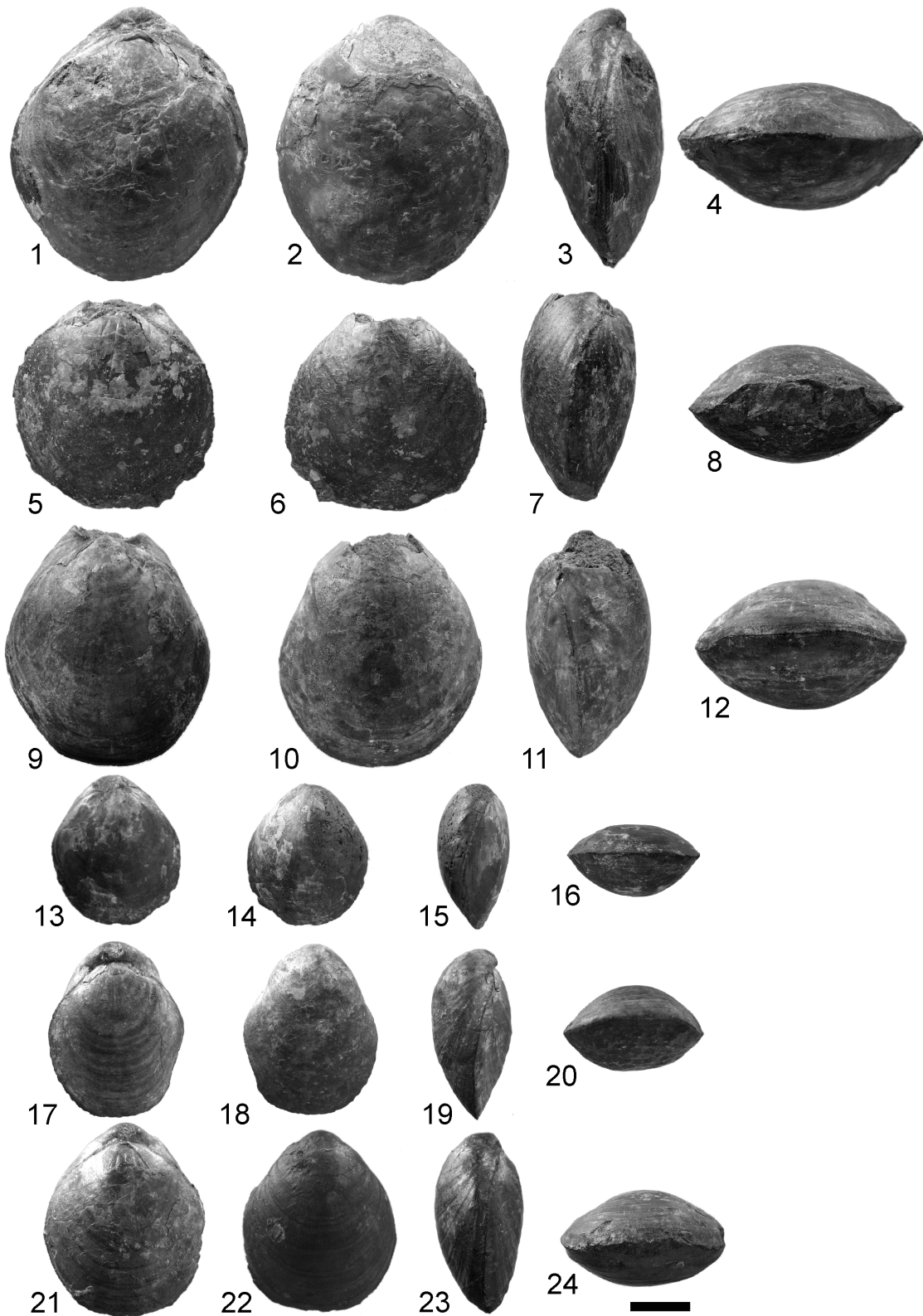
**Discussion.** The material from Spitsbergen reaches larger maximum dimensions than “*Cyrtothyris*” *maynci* described from Greenland (Owen 1976). Broken ventral umbones hamper identification (e.g. Fig. 7.5–7.8) and referral to *Cyrtothyris* must be considered tentative. Owen commented that the Greenland form has an incipient uniplicate anterior commissure. The Spitsbergen specimens show a rectimarginate anterior commissure to possibly weakly uniplicate (Fig. 7.8, anterior commissure damaged). The Greenland material is from the Falskebugt Member (Harper *et al.* 2005) of Valanginian age whereas the Spitsbergen specimens are from the Upper Volgian. *Cyrtothyris* has not been recorded from the Upper Jurassic and these specimens may represent a new form.

Some of the Spitsbergen brachiopods are morphologically close to *Cyrtothyris* and *Rouillieria*. Species referred to these two genera may be morphologically very similar and details of the ventral umbo and profile can be important in distinguishing between them (as discussed by Middlemiss 1976). Several specimens from seep 9 are now considered to be *Seductorithyris septemtrionalis*; these have an erect beak and lack the produced ventral beak of *Cyrtothyris*, and are typically less inflated in profile than the latter. However, one specimen from seep 9 (Fig. 7.1–7.4; PMO 224.895) with a suberect ventral umbo and incipiently uniplicate anterior commissure, is referred to *Cyrtothyris* aff. *cyrta* (Walker). Middlemiss (1976) considers that this species has a rectimarginate to uniplicate anterior commissure.

**Stratigraphic and geographic distribution.** Upper Volgian of Spitsbergen.

### Genus *Praelongithyris* Middlemiss 1959

**Type species.** *Terebratula praelonga* J. de C. Sowerby in Fitton, 1836



**FIGURE 7.** 1–4. *Cyrtothyris* aff. *cyrta* (Walker). PMO 224.895, seep 9, dorsal, ventral, lateral, and anterior views. 5–8. *Cyrtothyris*? sp. PMO 224.870, seep 3, dorsal, ventral, lateral, and anterior views. 9–20. *Praelongithyris*? aff. *borealis* Owen. 9–12. PMO 224.907, seep 1, dorsal, ventral, lateral, and anterior views. 13–16. PMO 224.898, seep 9, dorsal, ventral, lateral, and anterior views. Resembles juvenile *Cyrtothyris*. 17–20. PMO 224.886, seep 1, dorsal, ventral, lateral, and anterior views. Form resembling *Moutonithyris moutoniana* (d’Orbigny). 21–24. *Rouillieria* cf. *michalkowii* (Fahrenkohl). PMO 224.901, seep 9, dorsal, ventral, lateral, and anterior views. Scale bar = 1 cm.

## ***Praelongithyris?* aff. *borealis* Owen, 1976**

Fig. 7.9–7.20

1976 v. aff. “*Praelongithyris*” *borealis* new species—Owen, p. 11, pl. 2, fig. 2, text-fig. 6.

2011 v. ‘*Praelongithyris*’ sp.—Hammer *et al.*, p. 20, table 2.

**Material and occurrence.** Seep 1 (PMO 224.886?, PMO 224.912, PMO 224.907, PMO 224.908?), seep 9 (PMO 227.424–425, PMO 224.888–890, PMO 224.898), seep 12 (PMO 224.887?, PMO 224.935–936).

**Description.** Elongate rounded to sub-pentagonal outline with dorsal valve longer than wide, evenly biconvex profile with dorsal valve flatter, euseptoidum present, elongate adductor muscle scars. Rounded beak ridges. Lateral commissure gently arched, anterior commissure rectimarginate to incipiently or broadly uniplicate.

**Discussion.** The elongate outline and biconvex profile are comparable to “*Praelongithyris*” *borealis* Owen. As with *Cyrtothyris* discussed above, the Spitsbergen specimens reach larger dimensions than the material from Greenland. A uniplicate specimen with an elongate-oval outline (Fig. 7.17–7.20) resembles *Moutonithyris moutoniana* (d’Orbigny). A juvenile specimen (Fig. 7.13–7.16) is similar in outline to *Cyrtothyris cyrta* (Middlemiss 1976, pl. 7, fig. 5) although the profile of the latter has a less inflated dorsal valve; however, the generalized rounded outline is typical for juveniles of many terebratulide species.

*Praelongithyris?* aff. *borealis* is similar in outline to *Taimyrothyris kropotkini* (Moisseiev) figured by Dagys (1968, pl. 23, fig. 3). The material recorded by Dagys reaches larger maximum dimensions than the largest Spitsbergen specimen, being L 48; W 34; T 29 mm (Dagys 1968, p. 128) and is more inflated in profile. It is difficult to be certain as to the affinities of the Spitsbergen material without the aid of details of internal structures. However the Spitsbergen specimens, where decorticated, show no trace of crural plates (that would be expected) adjoining the floor of the dorsal valve, typical of the Boreiothyrididae (as in *Taimyrothyris*, Dagys 1968, fig. 76) and it is concluded that the material is not referable to *Taimyrothyris*. Dagys recorded *Taimyrothyris kropotkini* from the Lower Volgian and questionably from the Callovian–Oxfordian. Owen (1976) recorded “*Praelongithyris*” *borealis* from the Valanginian of Falskebugt, Wollaston Forland, East Greenland. The Spitsbergen material comes from the Upper Ryazanian.

**Stratigraphic and geographic distribution.** Upper Ryazanian of Spitsbergen.

## **Superfamily Loboidothyridoidea Makridin, 1964**

### **Family Lissajousithyrididae Cooper, 1983**

#### **Subfamily Lissajousithyridinae Cooper, 1983**

#### **Genus *Rouillieria* Makridin, 1960**

**Type species.** *Terebratula michalkowii* Fahrenkohl, 1856

#### ***Rouillieria* cf. *michalkowii* (Fahrenkohl)**

Figs. 7.21–7.24, 8.1–8.8, 9

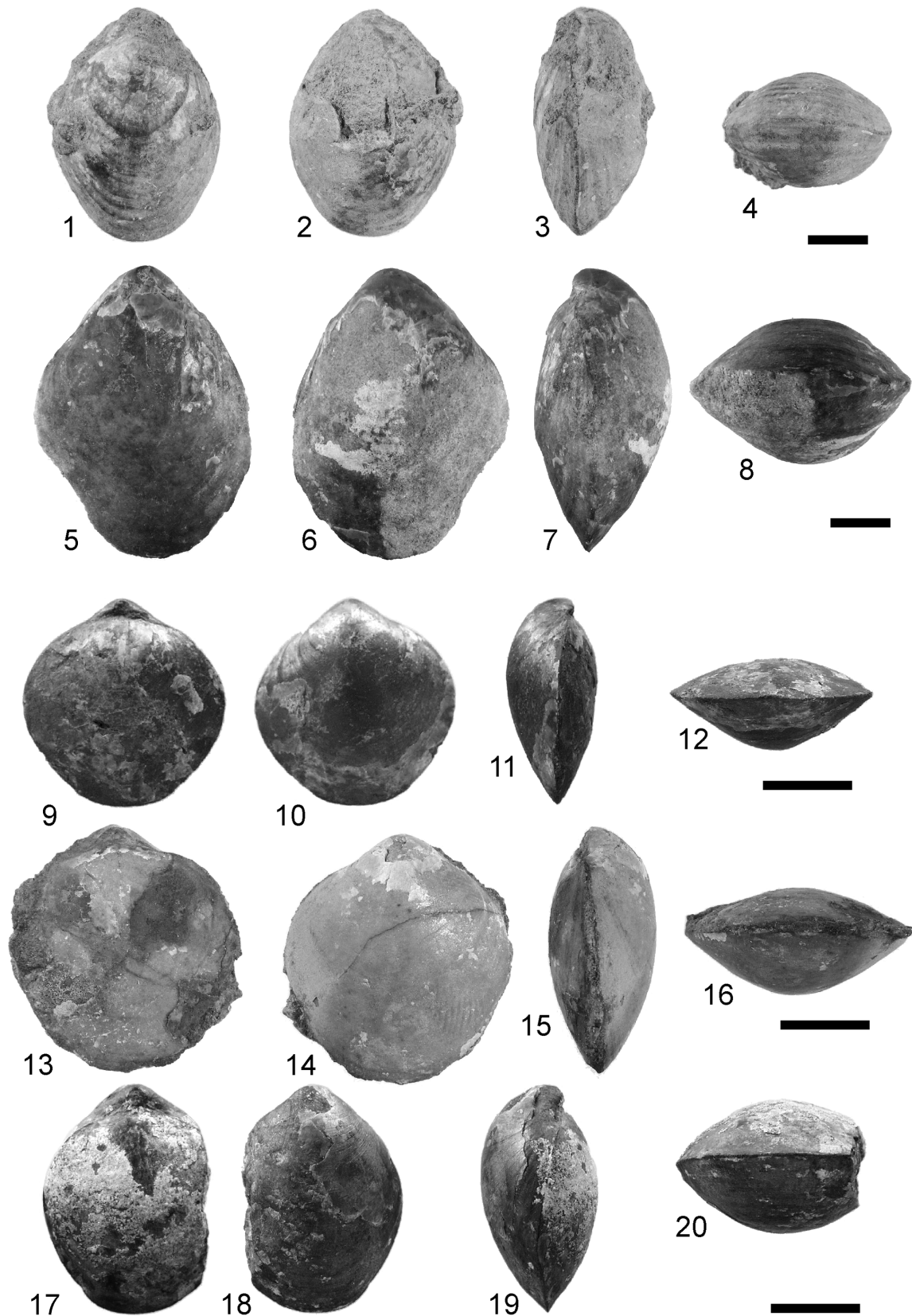
1964 cf. *Rouillieria michalkowii* (Fahrenkohl)—Makridin, p. 249, text-figs. 83, 84, pl. XVI, figs. 7, 8, pl. XVII, figs. 1–3.

2011 v. partim ‘*Praelongithyris*’ sp.—Hammer *et al.*, p. 20, table 2.

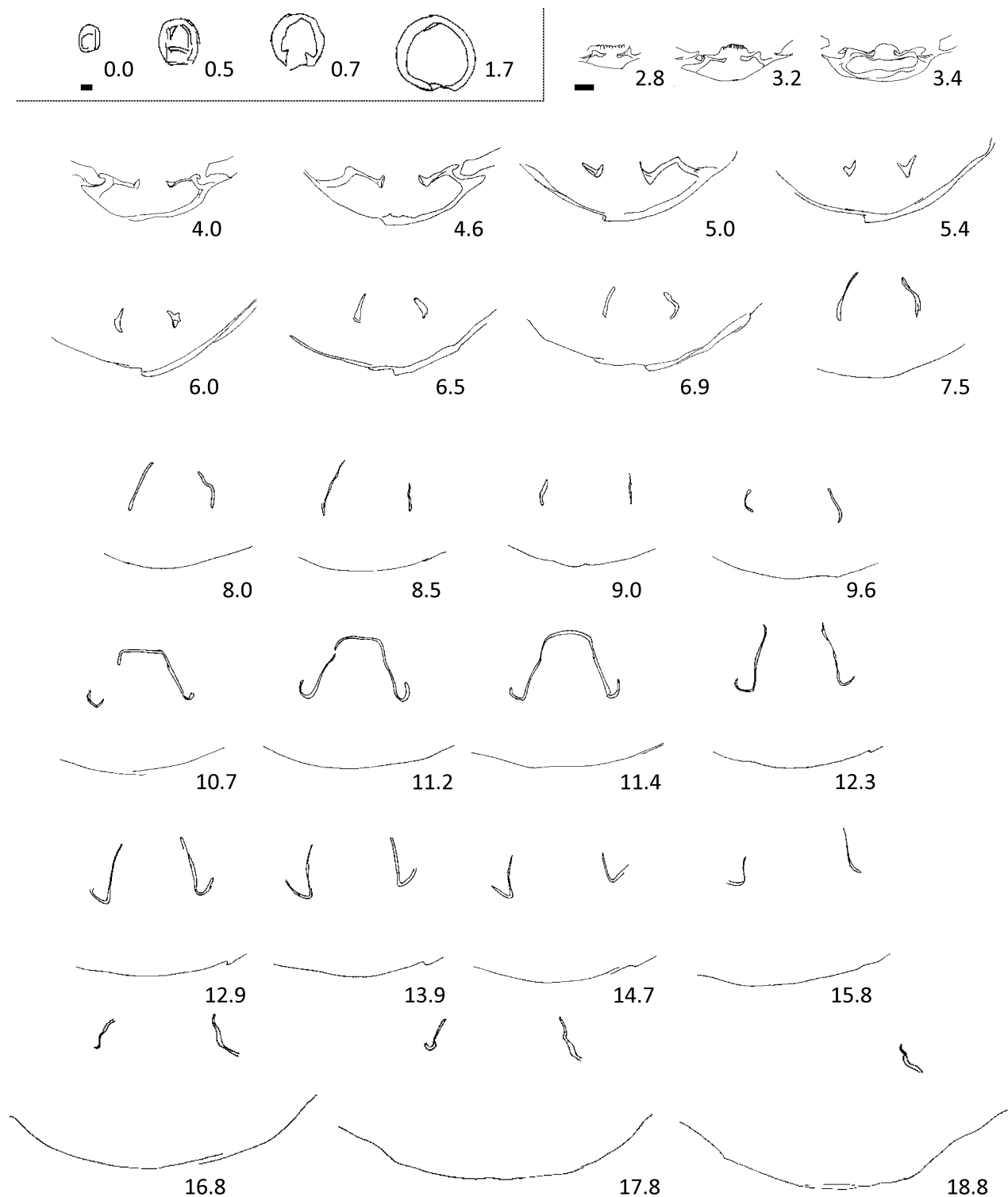
**Material and occurrence.** Seep 8 (PMO 227.420, PMO 224.925?, PMO 224.927, PMO 224.930?), seep 13 (PMO 227.421–423, PMO 224.901–902, PMO 224.905).

**Description.** Elongate-oval to subtriangular to subpentagonal outline, evenly biconvex profile. Lateral commissure straight to gently ventrally arched. Broad, weak uniplication of the anterior commissure.

Serial sections were prepared from one specimen (Fig. 9) which show traces of a pedicle collar (Fig. 9; sections 0.5, 0.7), cardinal process (sections 2.8–3.4), and flat and broad hinge plates with ventrally directed crural



**FIGURE 8.** 1–8. *Rouillieria cf. michalkowii* (Fahrenkohl). 1–4. PMO 227.422, seep 13, dorsal, ventral, lateral, and anterior views. 5–8. PMO 227.420, seep 8, dorsal, ventral, lateral, and anterior views. Specimen serially sectioned (Figure 9). 9–16. *Rouillieria aff. ovoides* (Sowerby). 9–12. PMO 224.926, seep 8, dorsal, ventral, lateral, and anterior views. 13–16. PMO 227.426, seep 13, dorsal, ventral, lateral, and anterior views. 17–20. *Rouillieria cf. rasile* Smirnova, PMO 224.929, seep 8, dorsal, ventral, lateral, and anterior views. Scale bars = 1 cm for each specimen.



**FIGURE 9.** Transverse serial sections of *Rouillieria* cf. *michalkowii* (Fahrenkohl), seep 8, PMO 227.420. Serial sections prepared perpendicular to maximum length of the specimen, numbering of sections starts at 0.0 mm the initial section through the specimen. Dotted line delimits sections drawn at the same magnification. Dimensions of sectioned specimen: L 35.1; W 26.5; T 16.9mm. Scale bar = 1 mm.

bases (sections 3.2–5.0). The crura develop anteriorly at an acute angle from the hinge plates in a “v”-shaped configuration (sections 5.0–5.4). Crural processes are high-arched (sections 7.5–8.5). The transverse band is flat topped.

**Discussion.** The material is referred to the lobidothyridoid genus *Rouillieria* Makridin. However, it has not

been possible to determine the length of the flanges of the brachidium with certainty. The flanges of the brachidium were tentatively traced anteriorly to section 18.8 (Fig. 9). Sparry calcite infilling of the brachiopod made tracing the flanges difficult and it is unclear if this represents the maximum length of the loop. The serial sections do not show the exceedingly long anterior flanges on the brachidium seen in Makridin (1964, fig. 83). The sectioned Spitsbergen specimen (Figs. 8.5–8.8, 9) is approximately half the length of the largest representatives figured by Makridin and this may account for the possibly shorter flanges. Some species referred to *Rouillieria* (Makridin 1964) do not appear to attain such large proportions as the type species.

Middlemiss (1976, text-figs. 27, 29) provided serial sections of species referred to *Rouillieria* from the Claxby Ironstone Formation (Valanginian–Hauterivian), Nettleton, Lincolnshire, England—*R. tilbyensis* (Davidson) and *R. walkeri* (Davidson). These serial sections show similarities to the Spitsbergen specimen (Fig. 9) in the presence of a cardinal process, relatively flat to flat hinge plates, ventrally projecting crural bases, high arching crural processes, and a high-arched transverse band. The strongly concave juvenile hinge plates considered significant by Middlemiss (1976) have not been observed in the Spitsbergen sections.

The Spitsbergen material is similar in outline to the elongate, tear-drop shaped loboidothyridoids *Atelithyris crestensis* Smirnova, *Boreiothyris pelecypodaeformis* (Moisseiev), *Moisseevia sokolovi* Makridin and *Spasskothyris rjasanensis* Smirnova. *Atelithyris crestensis* from the Lower Hauterivian of the Russian Platform (Smirnova 1975) tends to have a more oval outline compared to the other species and has a deflected uniplicate anterior commissure. The development of the hinge plates and crural bases is similar to *Rouillieria* (in Makridin 1964) but lacks the long anterior flanges of the brachidium seen in *Rouillieria*. However, it would appear that *Atelithyris* could be derived from *Rouillieria*. Compared with the other taxa discussed here, *Spasskothyris rjasanensis* is more elongate in outline and has a broad uniplicate anterior commissure. The internal morphology is distinct, and it is distinguished “from all Jurassic and Early Cretaceous genera of long-flanged terebratulids by the development of inner hinge plates . . .” (Smirnova 1975, p. 346). However, these inner hinge plates appear to be strongly keeled crural bases, at least initially. The development of these inner hinge plates in *Spasskothyris* is quite different from that in the Boreiothyrididae, such as in *Boreiothyris*, where the hinge plates meet in the medial plane of the dorsal valve (see serial sections in Dagys 1968). The internal structures of *Moisseevia sokolovi* Makridin are unknown but judging from external morphology it appears very close to the genus *Rouillieria*.

**Stratigraphic and geographic distribution.** Upper Volgian of Spitsbergen.

### ***Rouillieria* aff. *ovoides* (Sowerby, 1815)**

Fig. 8.9–8.16

1971b aff. *Rouillieria ovoides* (J. Sowerby)—Ager, p. 394, pl. 14, pl. 15, fig. A.

**Material and occurrence.** Seep 8 (PMO 224.924, PMO 224.926, PMO 224.931–932), seep 13 (PMO 224.906, PMO 227.426).

**Description.** Quadrate outline, equally biconvex profile, rectimarginate anterior commissure.

**Discussion.** The material is homoeomorphic with other material described herein from Spitsbergen, *Uralella?* cf. *janimaniensis* Makridin and *Seductorithyris septemtrionalis* **gen. et sp. nov.** From *Uralella?* cf. *janimaniensis* it may be distinguished by its smaller size, more rounded hinge line and lesser inflated profile, especially with respect to the dorsal valve. *Seductorithyris septemtrionalis* has a rounder hinge line, rounder outline, and narrower apical angle of the ventral beak when compared to *Rouillieria* aff. *ovoides*; the latter has a more quadrate outline.

The Spitsbergen material does not show a posterior shallow sulcation or groove in the dorsal valve. This does appear to be a variable feature (Ager 1971b; Middlemiss 1976). A rounded keel to the posterior of the ventral valve is considered characteristic (Ager 1971b; Middlemiss 1976).

Ager (1971b, p. 395) considered some variability in external morphology acceptable within *Rouillieria ovoides* but questioned the validity of the total number of species referred to *Rouillieria* by Makridin (i.e., he wondered if there might be fewer, more variable species). The *R. ovoides* material described by Ager (1971b) was collected from Spilsby Sandstone Formation glacial erratics in Norfolk, England. Kelly (in Kelly & Rawson 1983) noted that glacial erratics of grey glauconitic Spilsby Sandstone (Kelly’s “Lithology 2” of four erratic lithotypes) contained the ammonite *Paracraspedites oppressus* Casey, bivalves, and ‘nests’ [preserved biocoenoses?/clumps



*sensu* Kidwell *et al.* 1986] of *R. ovoides*. These erratics are considered to come from the upper Middle Volgian part of the succession (Kelly in Kelly & Rawson, 1983).

Middlemiss (1976) discussed the differences between species of *Rouillieria* from the Claxby Ironstone Formation, Lincolnshire, England. *Rouillieria walkeri* (Davidson) typically has a sulcate anterior commissure and *R. tilbyensis* (Davidson) is typically uniplicate, whereas the Spitsbergen material is rectimarginate, more like *R. ovoides*. There are other subtle morphological differences between *R. ovoides* and *R. tilbyensis* (Middlemiss 1976, pp. 69–70) and the latter can also be confused with *Cyrtothyris cyrta*.

Smirnova (1975, 1997) referred Sowerby's *Rouillieria ovoides* (in Ager 1971b) to *Okathyris*, described from the Russian Platform (Smirnova 1975). However, she did not give in detail the reasons for this assignation. The hinge plates of *Rouillieria ovoides* figured by Ager (1971b, fig. 1) are narrow compared with *R. michalkowii* (Makridin 1964, fig. 83). Ager did show that the flanges of the brachidium for *R. ovoides* from England extended at least 17.8 mm beyond the crest of the transverse band (located 20.4 mm from the posterior of the sectioned specimen), indicating long loop flanges. These flanges are proportionately more comparable in length with those recorded for *Rouillieria* (Makridin 1964, fig. 83) whereas the loop flanges for *Okathyris* are shorter (Smirnova 1975, figs. 1, 3). In serial sections of *Okathyris chevkinensis* Smirnova (1975, fig. 1) and *O. sokolovi* Smirnova (1975, fig. 3) the loop flanges anterior of the transverse band are approximately 6–7 mm in length. The brachidial flanges for *Rouillieria cf. michalkowii* (Fig. 9 herein) are also shorter than those for the genus in Makridin (1964) and have already been discussed under that species.

**Stratigraphic and geographic distribution.** Upper Volgian of Spitsbergen.

### ***Rouillieria aff. rasile* Smirnova, 1975**

Fig. 8.17–8.20

1975 aff. *Rouillieria rasile* new species—Smirnova, p. 350, pl. X, fig. 3.

**Material and occurrence.** Seep 8 (PMO 224.929).

**Discussion.** One damaged specimen that has a similar outline to the specimen figured by Smirnova (1975). The Spitsbergen specimen has a slightly more shouldered appearance at the hinge line compared to Smirnova's figured specimen. The long, very wide ventrally concave hinge plates and apparently relatively small crural bases (Smirnova 1975, fig. 8) do point to this species as having internal structures that are atypical of *Rouillieria*. However, in the diagnosis for *Rouillieria* Lee *et al.* (2006, p. 2098) state “outer hinge plates broad”. The diagnosis for the genus also refers to crural bases that form lateral umbonal cavities reaching the valve floor (e.g. serial sections of *R. michalkowii* in Makridin (1964, fig. 83)). However, these lateral umbonal cavities presumably develop due to secondary shell overgrowth and therefore depend on the growth stage of the sectioned specimen. It is probable that these cavities are more likely to develop in maturing or gerontic individuals (or they may even become infilled with secondary shell material in the latter).

Smirnova described *Rouillieria rasile* from Chevkino Village, Ryazan Province, Russia and it was recorded from the “Berriasian, Ryazan horizon” (Smirnova 1975, p. 351).

**Stratigraphic and geographic distribution.** Upper Volgian of Spitsbergen.

### **Genus *Urallella* Makridin in Licharew, Makridin & Rzhonsnitskaya, 1960**

**Type species.** *Terebratula strogonofi* d'Orbigny, 1845

### ***Urallella? cf. janimaniensis* Makridin, 1964**

Fig. 10.1–10.8

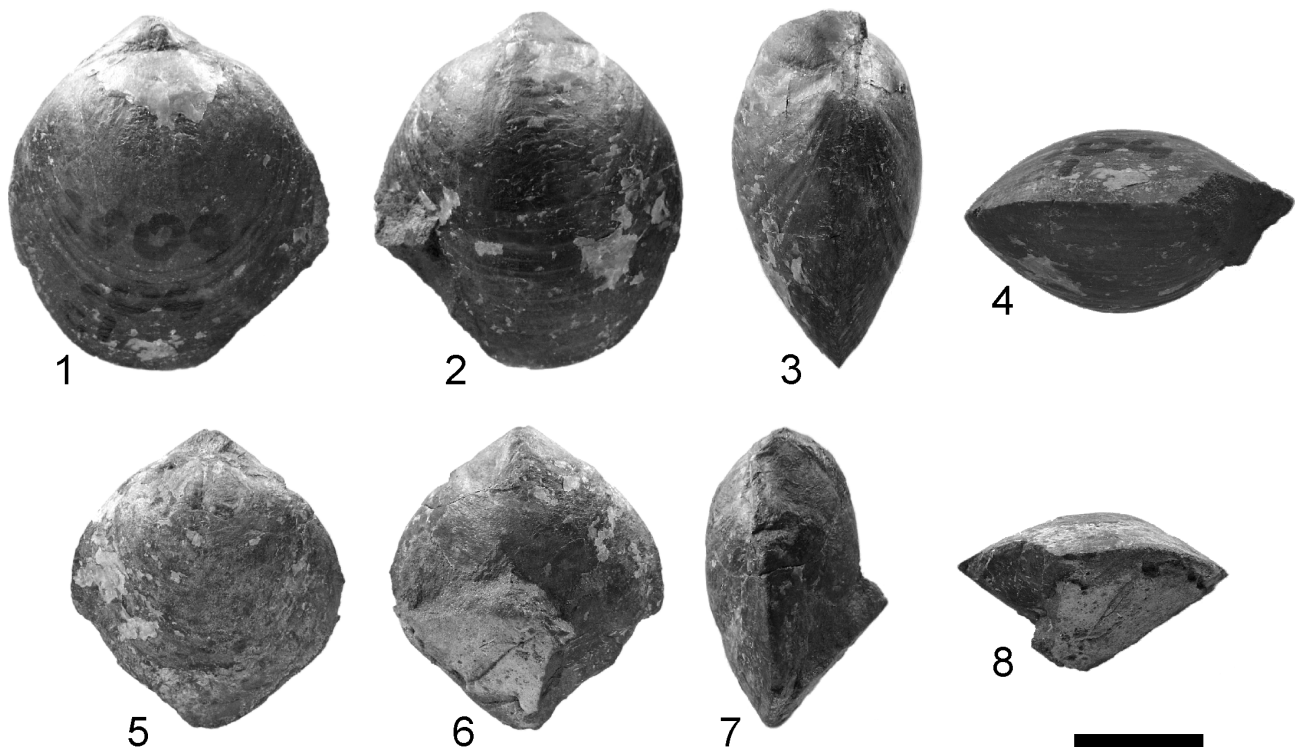
1964 cf. *Urallella jani-maniensis* new species—Makridin, p. 258, text-figs. 87, 88, pl. XIX, fig. 2, pl. XX, fig. 1.

**Material and occurrence.** Seep 3 (PMO 224.916?, PMO 224.921, PMO 224.928, PMO 224.938–939?, PMO 224.941, PMO 224.944).

**Discussion.** Specimens have a rounded quadrate outline and inflated profile that is suggestive of *Uralella* Makridin. The outline of the specimens compare to that of *U. janimaniensis* Makridin and *U. strogonofi* (d'Orbigny) in Makridin (1964, given as *strogonowii*, p. 254 and in text and plate captions; *strogonovii* in table 3). The rounder hinge line of the latter may help to differentiate these two forms. The outline is also reminiscent of specimens referred to *Rouillieria* aff. *ovoides* herein. Makridin (1964) recorded *Uralella janimaniensis* from the Upper Volgian. *Uralella strogonofi* was recorded from the Lower Volgian (Dagys 1968).

A single incomplete specimen that has a highly inflated profile is suggestive of *Uralella*. This specimen is tentatively referred to *Uralella* sp., specimen number PMO 224.943, from seep 3, Upper Volgian.

**Stratigraphic and geographic distribution.** Upper Volgian of Spitsbergen.



**FIGURE 10.** 1–8. *Uralella?* cf. *janimaniensis* Makridin. 1–4. PMO 224.944, seep 3, dorsal, ventral, lateral, and anterior views. 5–8. PMO 224.938, seep 3, dorsal, ventral, lateral, and anterior views. Scale bar = 1 cm.

#### Family Loboidothyrididae Makridin, 1964

##### Subfamily Loboidothyridinae Makridin, 1964

##### Genus *Seductorithyris* gen. nov.

**Diagnosis.** Round outline, with the dorsal valve almost circular. Profile equi- to gently ventribiconvex. Smooth shell with growth lines. Erect beak. Ventral valve umbo keeled. Lateral commissure straight, anterior commissure rectimarginate. Internal structures: cardinal process present, flat/horizontal and wide hinge plates deflect dorsally, crural bases develop on inner margin of hinge plates, clubbed and weakly deflected dorsally. Transverse band curved, low-arched, and approximately at mid-point of brachidium, anterior flanges long.

**Etymology.** For the deceptive way that homoeomorphy among brachiopods may mask their affinities (deceiver—latin *seductor*).

**Occurrence.** Uppermost Ryazanian of Spitsbergen.

**Type species.** *Seductorithyris septemtrionalis* sp. nov.

***Seductorithyris septemtrionalis* sp. nov.**

Figs. 11.1–11.16, 12

2011 v. partim '*Cyrtothyris*' sp.—Hammer *et al.*, p. 20, table 2, fig. 7.S.

**Material and occurrence.** Holotype: PMO 224.896; paratypes: PMO 217.198, PMO 224.892–893, PMO 224.911, PMO 224.913, PMO 227.427?, PMO 227.430. All from seep 9.

**Type locality.** Knorringfjellet, central Spitsbergen, N78° 18' 49.9" E16° 10' 58.9".

**Diagnosis.** As for the genus.

**Etymology.** For the northern high-latitudes that Spitsbergen occupies (*septem triōnēs* [also septentrional]: the seven stars of the constellation of *Ursa Major* [the Great Bear, or the Plough]—a constellation visible in the northern hemisphere throughout the year and a useful aid to finding North; also “of the north” or “north wind”).

**Dimensions of the holotype.** PMO 224.896—Length 33.7 mm, width 29.8 mm, thickness 16.1 mm.

**Description.** Length slightly greater than width, rounded outline, with the dorsal valve almost circular. Biconvex profile with the dorsal valve tending to be flatter, but not necessarily. Smooth shell with growth lines. Erect beak. Ventral valve umbo has a broad round keel. Lateral commissure straight, anterior commissure rectimarginate.

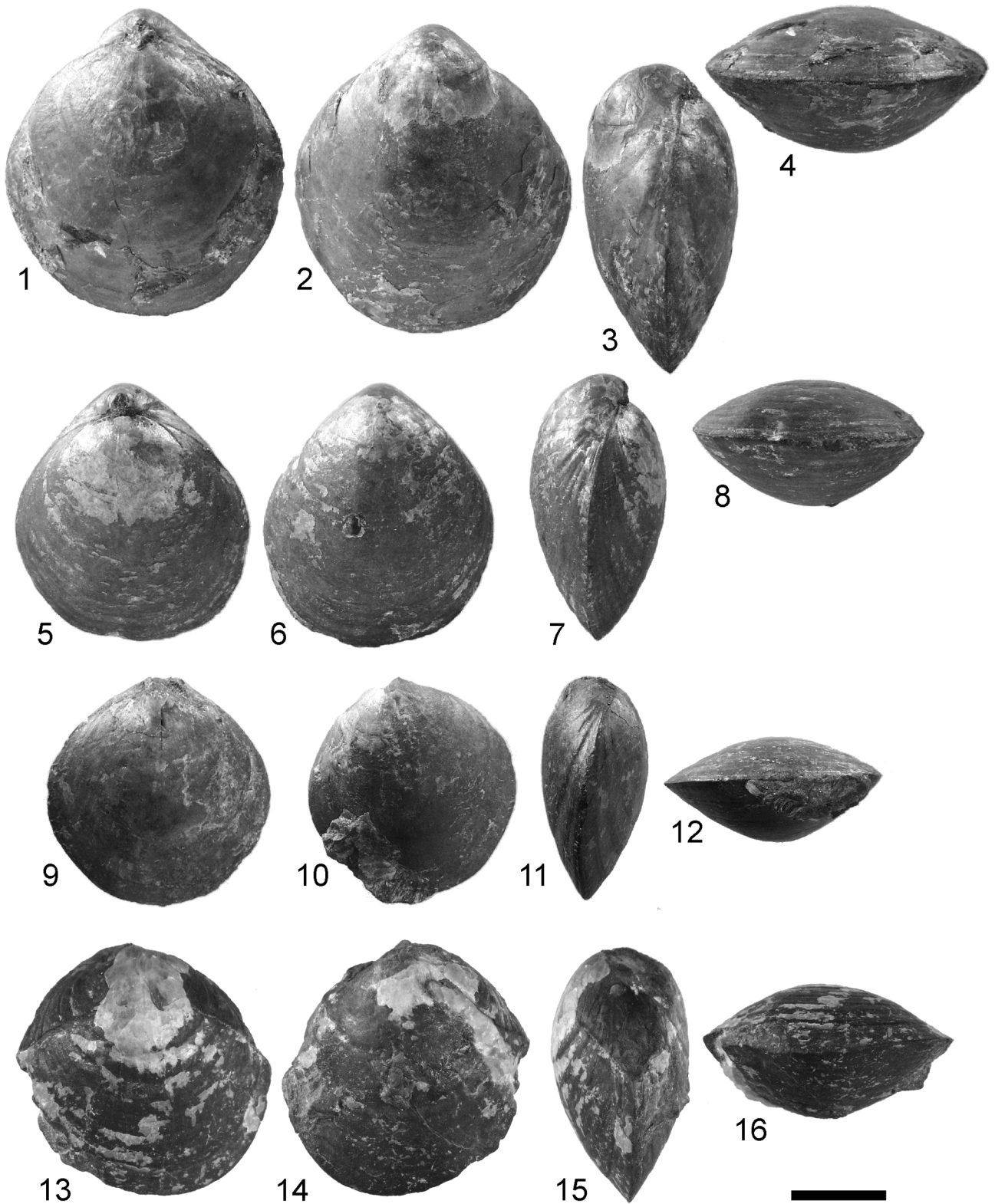
Cardinal process developed (Fig. 12, sections 0.7–1.2 mm), flat, horizontal and wide hinge plates deflected dorsally (sections 1.2–2.3), crural bases develop on inner margin of hinge plates (sections 1.6–2.3) and have a clubbed appearance initially (section 1.8). Crura are initially weakly deflected dorsally (sections 2.3–2.7). Transverse band is curved and low-arched (section 6.6, this is approximately at the mid-length of the brachidium, based on the distance the loop was traced), anterior flanges of the brachidium extend significantly beyond the transverse band (at least 5.8 mm). Loop traced to at least 11.4 mm from initial section through brachiopod (ventral umbo of sectioned specimen is damaged).

**Discussion.** The beak of the ventral valve is erect in *Seductorithyris septemtrionalis* whereas in “*Cyrtothyris*” *maynci* from East Greenland the beak is slightly produced, suberect, and with a massive umbo dominated by a large circular foramen (Owen 1976). The outline of the Spitsbergen material is comparable to that of rounded terebratulide species discussed by Middlemiss (1976) from the Claxby Ironstone Formation of Lincolnshire, England, such as *Rouillieria tilbyensis* (Davidson) and *Cyrtothyris cyrta* (Walker). Both of these species show rounded and elongated morphotypes and appear however to have a more massive pedicle foramen and may develop a uniplicate anterior commissure, which helps to distinguish them from *Seductorithyris septemtrionalis*. The rounded outline of *Seductorithyris septemtrionalis* is similar to that of *Pinaxiothyris campestris* (Dagys 1968, pl. 10, figs. 1–3), although the latter appears to have a slight elongation to its outline, reaching a greater size. One specimen from Spitsbergen is tentatively referred to *Pinaxiothyris campestris* Dagys (Fig. 13.1–13.4). It is similar in outline to an elongate specimen figured by Dagys (1968, pl. 10, fig. 4). The development of the cardinal process, flat hinge plates, crura, crural processes, and transverse band show similarities between the internal characters of *Seductorithyris septemtrionalis* (Fig. 12) and *Pinaxiothyris* (Dagys, 1968, fig. 52). The latter has hinge plates that are not as wide and the crural bases do not show the slight dorsal deflection seen in *Seductorithyris*.

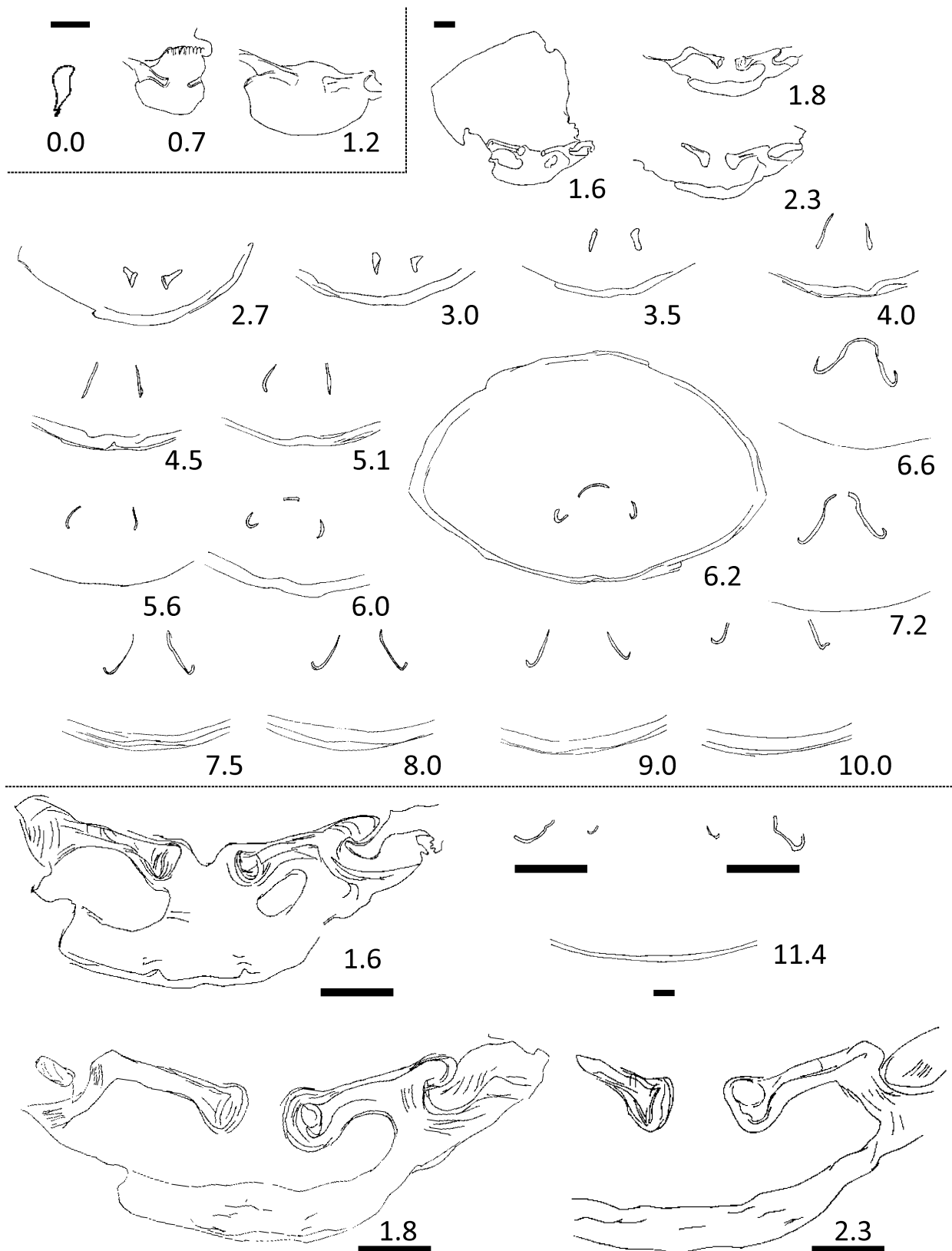
Another genus considered during classification of this species was *Moutonithyris*, characterized by distinctive horizontal hinge plates and crural bases derived from the inner margins of the hinge plates. However, the crescent-shaped attached crura seen in *Moutonithyris* (e.g. Middlemiss 1976; Nekvasilova 1980) are different from the club-shaped crural bases of *Seductorithyris*. In addition, *Moutonithyris* has a lower-arched transverse band compared to that of *Seductorithyris*, and does not appear to share the long flanges of the brachidium seen in the latter.

The nature of the horizontal hinge-plates with the rounded crural bases could be described as clubbed (after Cox & Middlemiss 1978) due to secondary overgrowth (Fig. 12, section 1.8). The crura project weakly dorsally and do not conform to those of any described Mesozoic terebratulide. The hinge-plates are short in length (sections 0.7–2.7) and the loop develops rapidly to the crural processes (section 4.0) before reaching the transverse band at 6.6 mm. The loop flanges were traced for another 5.8 mm to 11.4 mm.

The sectioned specimen might represent a juvenile specimen because of its size and hence also in its loop development. The ontogenetic development of the brachidium can hardly be said to be well understood among terebratulide brachiopods, and even less so perhaps the relationship between the hinge plates and the crural bases. However, these elements of the cardinalia appear stable in juvenile brachiopods judging from serial sections of



**FIGURE 11.** *Seductorithyris septemtrionalis* **gen. et sp. nov.** 1–4. Holotype, PMO 224.896, seep 9, dorsal, ventral, lateral, and anterior views. 5–8. PMO 224.911, seep 9, dorsal, ventral, lateral, and anterior views. 9–12. PMO 224.913, seep 9, dorsal, ventral, lateral, and anterior views. 13–16. PMO 227.430, seep 9, dorsal, ventral, lateral, and anterior views. Specimen serially sectioned (Figure 12). Scale bar = 1 cm.



**FIGURE 12.** Transverse serial sections of *Seductorithyris septemtrionalis* **gen. and sp. nov.**, seep 9, PMO 227.430. Serial sections prepared perpendicular to maximum length of the specimen, numbering of sections starts at 0.0 mm the initial section through the specimen. Dotted lines delimit groups of sections drawn at the same magnification. For section 11.4 mm enlargement of brachidial flanges shown adjacent to lower magnification drawing. Dimensions of sectioned specimen: L 25.3+; W 25.1+; T 13.9 mm. Scale bars = 1 mm.

growth-series of brachiopods (e.g. Dagens 1972; Smirnova 1973 (for rhynchonellides), 1984, 2008; see also Lee *et al.* 2001 and Tort & Laurin 2001). In *Seductorithyris* the crural bases develop as rounded to cuneate processes that project weakly dorsally, or at least do not project ventrally while attached to the hinge plates, thereby making a unique configuration that suggests a new brachiopod genus that is certainly distinct from its contemporaries. This configuration of the clubbed crura is quite different from the pendant or keeled crural bases typical of representatives of the terebratuloid *Gibbithyris* or the loboidothyridoid *Placothyris*. A specimen from seep 3 (Fig. 13.5–13.8; Upper Volgian) is comparable to *Placothyris kegeli* from Wollaston Forland, East Greenland (Fig. 13.9–13.12; Valanginian, infilling matrix is a red micrite).

**Stratigraphic and geographic distribution.** Uppermost Ryazanian of Spitsbergen.

## Suborder Terebratellidina Muir-Wood, 1955

### Superfamily Kingenoidea Elliott, 1948

#### Family Kingenidae Elliott, 1948

#### Subfamily Kingeninae Elliott, 1948

#### Genus *Zittelina* Rollier, 1919

**Type species.** *Terebratula orbis* Quenstedt, 1858

#### *Zittelina?* sp.

Fig. 13.13–13.20

1976 ?v. “*Zittelina*” sp.—Owen, p. 16, pl. 3, fig. 1.

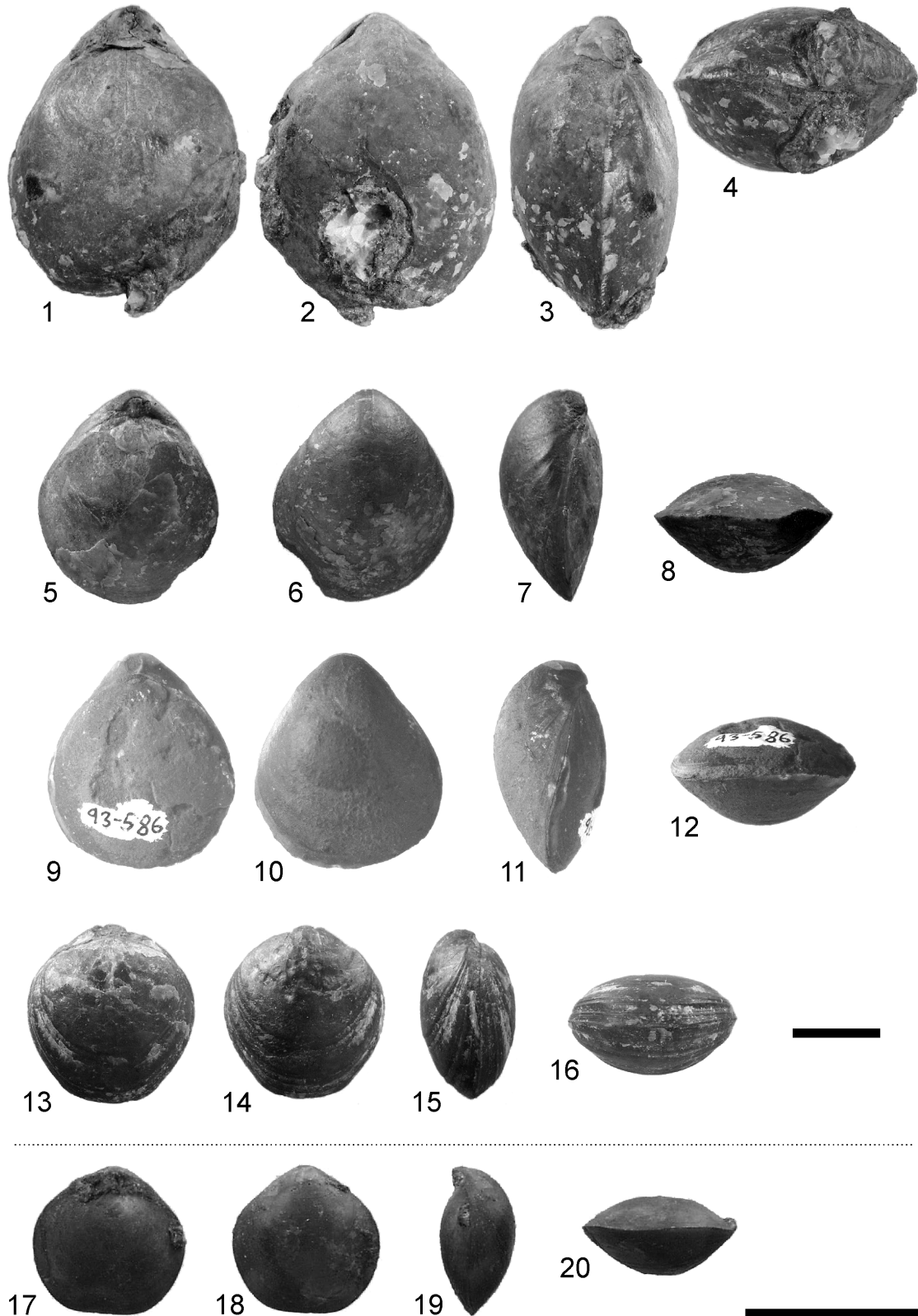
2011 v. ‘*Zittelina*’ sp.—Hammer *et al.*, p. 20, table 2, fig. 7T.

**Material and occurrence.** Seep 9 (PMO 217.200, PMO 224.869, PMO 224.885).

**Description.** Round and weakly subpentagonal outline, somewhat ventribiconvex profile, and rectimarginate, to possibly incipiently sulcate anterior commissure. Dental lamellae are present in the ventral valve umbo and a median septum is present in the dorsal valve indicating a long-looped terebratellidine. Decorticated specimens (Fig. 13.13–13.16 and Hammer *et al.* 2011, fig. 7T) show the presence of dental lamellae and a median septum. A smaller specimen is a possible juvenile (Fig. 13.17–13.20).

**Discussion.** Owen (1976, pl. 3, fig. 1) figured a specimen from the Valanginian of Wollaston Forland, East Greenland that has a pentagonal outline, inflated biconvex profile, and ventrally deflected anterior commissure but with no obvious concomitant sulcation developed on the dorsal valve. The specimen from Spitsbergen has a round outline, rectimarginate anterior commissure, and biconvex profile but with a lesser degree of inflation compared to the Greenland specimen. The relationship between the Greenland and Spitsbergen material is difficult to assess at present as only one specimen was identified from Greenland and only two mature specimens are known from Spitsbergen. The differences in outline, profile and commissure make it unlikely that the forms from Greenland and Spitsbergen are conspecific. Given the predominantly Boreal aspect of the fauna from Spitsbergen it may be that this form is allied to *Rugitela* Muir-Wood (considered to be the senior synonym of *Russiella* Makridin (Baker 2006)). The specimens lack the sulcate dorsal valve and sulcus of the anterior commissure seen in *Rugitela hippopus* (Roemer) that has been recorded from East Greenland (Harper *et al.* 2005). ?*Rugitela* sp. (Owen 1976) was put in synonymy with *Rugitela hippopus* (Harper *et al.* 2005) but this seems rather unlikely as the latter is elongate-quadrate in outline and weakly sulcate.

The Early Cretaceous age of this material suggests that an affinity to *Zittelina* rather than *Kingena* Davidson is more likely. However, both genera are very similar in external morphology (discussed by Owen 1970). The granular shell ornament considered characteristic of *Kingena* has not been observed, although well-developed endopunctuation has. The incipient(?) sulcation of the anterior commissure (Fig. 13.16, 13.20) might suggest an



**FIGURE 13.** 1–4. *Pinaxiothyris campestris*? Dagens, PMO 227.429, seep 9, dorsal, ventral, lateral, and anterior views. 5–8. *Placothyris kegeli*? Harper *et al.*, PMO 224.922, seep 3, dorsal, ventral, lateral, and anterior views. 9–12. *Placothyris kegeli* Harper *et al.*, MGUH 27501, Brorson Halvø, Wollaston Forland, North–East Greenland; Albrechts Bugt Member, Lower Valanginian. Specimen serially sectioned by Sandy in Harper *et al.* (2005, fig. 3). 13–20. *Zittelina*? sp. 13–16. PMO 224.869, seep 9, dorsal, ventral, lateral, and anterior views. 17–20. PMO 224.885, seep 9, dorsal, ventral, lateral, and anterior views. Scale bars = 1 cm.

affinity to *Zittelina* in contrast to faint uniplication that could suggest *Kingena* (based on generic diagnoses given by MacKinnon *et al.* 2006; although a rectimarginate anterior commissure is common to both genera). Species referred to *Dzirulina* Nutsudidze (considered a senior subjective synonym of *Belothyris* Smirnova by Sandy *et al.* 1995) typically have a more elongate outline than for *Zittelina* and *Kingena* (discussed by Owen 1970).

**Stratigraphic and geographic distribution.** Uppermost Ryazanian of Spitsbergen.

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