The brachiopod faunas from the Fezouata Shale (Lower Ordovician; Tremadocian-Floian) of the Zagora area, Anti-Atlas, Morocco: evidence for a biodiversity hub in Gondwana

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Abstract.

Since the early 2000s, the discovery of fossils and their collection from the Fezouata Shale has accelerated; this has enabled us to understand the faunas more thoroughly. The brachiopod fauna has not been investigated for the past 50 years, and we present here the results of our recent studies. The material represents about 350 samples, in which 30 species were identified, assigned to 23 genera. Among these, one new genus (*Tinzoulinorthis*) and four new species (*Wosekella maghribi, Rafanoglossa inversa, Orbithele tazagurta, Lacunites punctum*) are erected; one taxon is recognised at family level. The fauna described from the upper Tremadocian horizons is more diverse than those in the Floian. The former is characterised by a high γ-diversity, although at the horizon level the α-diversity is low to medium. This fauna is typical of high-energy, shallow-water, unstable environmental conditions preventing long-lived communities to develop climax communities and indicating that the succession of opportunists were regularly smothered in-situ and killed by storm deposits. Multivariate analyses of the faunas indicate that the Tremadocian fauna, characterised by many endemic taxa, shows closer affinities with faunas from peri-Gondwanan terranes, in particular Bohemia. The Tremadocian Fezouata fauna is very rich in taxon first occurrences, which coupled with high γ-diversity, suggest it may have been a diversity hub. On the other hand, the Floian Fezouata fauna shows stronger connections with Bohemia and the Montagne Noire albeit also links with the South Urals and Baltica reflecting the changing Early Ordovician palaeogeography.

Keywords: biodiversity hub, Brachiopoda, Early Ordovician, Morocco, palaeobiogeography, taxonomy.

The Fezouata Biota as recognized today was discovered by Mohamed Ben Moula, a fossil collector and dealer from Taichoute, about 120 km NE of Zagora, during prospecting in late 1999 or early 2000 (Lefebvre et al. 2016a). Initially a single specimen of *Tremaglaspis* (aglaspidid arthropod) was recovered and remained the only exceptionally-preserved fossil known for a couple of years, until more material of the same calibre was collected. From 2003 and over the next decade, successive fieldwork campaigns were organised [notably the RALI and VALORIZ projects that enabled the elaboration of a stratigraphic framework (Lefebvre et al. 2016a), implemented in the present work], combining the joint efforts of Moroccan and international teams of palaeontologists and the Ben Moula's unique knowledge of the area, unearthing a vast amount of exceptionally preserved faunas (including echinoderms, demosponges, marrellomorph arthropods, halkieriid-like molluscs…), but the site is renowned for the exquisite preservation of soft-bodied animals. The Fezouata Shale, as established by Martin et al. (2016a), is the sole Early Ordovician Burgess Shale-type Lagerstätte to yield a rich and diverse assemblage of marine organisms (Potin et al. 2023). The various assemblages are documented in the volume edited by Lefebvre et al. (2016b) and in publications by Kröger & Lefebvre (2012), Valent & Corbacho (2015), Van Roy et al. (2015), Lefebvre et al. (2019), Saleh et al. (2020a) and Hunter & Ortega-Hernández

(2021). The present work aims to fill the gap in the knowledge of the Tremadocian and Floian brachiopod assemblages from the Fezouata Shale. A comprehensive account of the history of the discovery of the Fezouata Biota is available in Lefebvre et al. (2016a).

Prior to this work, the Lower Ordovician brachiopod fauna has only been documented by Havlíček (1971) and Mergl (1981), whose combined publications described a handful of taxa. *Saccogonum saccatum* Havlíček was collected from the upper Cambrian or lowest part of the Fezouata Shale (lowest Tremadocian), but Havlíček (1971) could not be more precise. *Plectorthis simplex* Havlíček was collected from the Lower Fezouata Shale, whereas *Ranorthis fasciata* Havlíček was collected from the Lower and Upper Fezouata Shale. *Tarfaya marocana* Havlíček*, Paurorthis tadristensis* Havlíček and *Angusticardina* sp. were documented from the Upper Fezouata Shale. This fauna was collected from various localities scattered in the east and north-east of Zagora, in the Tafilalt area, and in the Zagora region to the south-west of the Anti-Atlas Mountains, near the city of Tarfaya (Fig. 1). Mergl (1981) documented *Orbithele vana* Mergl from the lower Floian of Foum Zguid, 100 km west of Zagora, and Mergl (1988) described *Incorthis marocana* Mergl from the Floian of the Safi region. Destombes et al. (1985, p. 190) noted that in the Lower Fezouata Shale, the upper part yielded “the most varied species distributed over numerous strata”.

The fauna described and figured here was collected from the Zagora Region, centred in an area north of Beni Zoli, and within a 35 km radius around Beni Zoli (Fig. 2).

Geological setting.

During the Early Ordovician (Tremadocian-Floian), the Anti-Atlas Mountains were located on the northern margin of Gondwana, at high latitudes, near the South Pole (about 75°S, see Scotese 2023, p. 96, fig. 3a). Around the Cambrian-Ordovician boundary, Avalonia started to rift northward from Gondwana, opening the Rheic Ocean (Cocks & Torsvik 2005). The epicontinental sea created by the newly rifted and subsiding margin of Gondwana was the setting for the deposition of the Fezouata Shale (Nowak et al. 2016). In the Zagora area (central Anti-Atlas), the Lower Ordovician (Tremadocian-Floian) deposits of the Fezouata Shale rest unconformably on the Cambrian sandstones of the Tabanite Group (Lefebvre et al. 2016c). The Fezouata Shale is composed of a thick (over 850 m) monotonous succession of silty and micaceous argillites (Martin et al. 2016a). The boundary between the Lower Fezouata (Tremadocian) and the Upper Fezouata (Floian) Shale is marked, in the eastern Anti-Atlas, by a ferruginous horizon transitioning laterally into a glauconitic horizon (Havlíček 1971), which marks the apex of the long-term transgression that started at the beginning of the Ordovician (Meyers & Peters 2011) and highlights a maximum flooding surface (Havlíček 1971, Destombes et al. 1985, Martin et al 2016a). The Fezouata Shale was interpreted as being deposited in a cold water, storm-wave dominated sedimentary environment (Martin et al. 2016b) modulated by the action of tides, on a relatively shallow shelf gently deepening to the north-west (Vaucher et al. 2016, 2017; Saleh et al. 2020b).

The Fezouata Shale is remarkable for the co-occurrence of exceptionally preserved faunas of Cambrian Burgess Shale-type and typical members of Ordovician faunas. The distribution of these horizons with exceptional preservation is not random (Saleh et al. 2021), and can be found in two discrete stratigraphic intervals (Lefebvre et al. 2016a, 2018). The lower interval is about 70 m-thick in the *Sagenograptus murrayi* graptolite biozone (upper Tremadocian, Tr3), whereas the upper interval is about 50 m-thick occurring between the upper part of the *C. protobalticus* and *B. jacksoni* graptolite biozones (middle Floian, Fl2). The age of these horizons was based on data from acritarchs, conodonts and graptolites published by Gutiérrez-Marco & Martin (2016), Lehnert et al. (2016), Nowak et al. (2016) and Lefebvre et al. (2018).

The rapid deposition of thick amounts of sediment was demonstrated to be a key factor that initiated the exceptional preservation in the Fezouata Shale: these conditions currently occur in the most distal storm-influenced zone (distal lower shoreface) (Vaucher et al. 2017). The depositional environment of the Fezouata Shale is that of a shallow marine environment dominated by storms, with exceptionally preserved animals living below the storm-wave base. (Saleh et al. 2021).

Material and methods.

The samples studied here were borrowed from the Yale Peabody Museum (New Haven, USA) and comprise about 78 lots (prefix YPM IP), and from the Cadi Ayyad University in Marrakesh (Morocco), on loan at the Université Claude Bernard 1, Lyon (France). The latter comprise about 250 lots (prefix AA). A small collection (17 lots) from the Université Claude Bernard-Lyon1 was also studied (prefix UCBL-FSL). Additional material was collected during the 2018 fieldwork organised by the Université Claude Bernard-Lyon 1 and is deposited there.

The specimens selected to illustrate the taxonomic descriptions were coated with ammonium chloride sublimate and photographed using a Nikon D3200 camera attached to a Wild M420 microscope or to a Nikkor-P lens 1:4 (f=105 mm) mounted on a Nikon PB-4 Macro Bellows, using standard lighting technique. When needed, contrast and brightness were optimized using image manipulation software.

Scanning Electron Microscopy images were obtained as described by Candela et al. (2014, p. 88) as follows: "Backscattered micrographs were recorded with a 4-quadrant fluorescence backscatter electron detector (BSC) of a CamScan 2500 scanning electron microscope (SEM), working in controlled pressure mode with fully open lower aperture (Envac, 40 Pa). The micrographs were recorded at the analytical working distance of 15 mm with an accelerating voltage of 20 kV working with a 5 spot size. Surface topography was enhanced by selectively switching off some of the quadrants of the BSC detector". Images were taken by Dr. Lore Troalen (National Museum of Scotland).

List of localities.

The localities from the Marrakesh Collection listed below are the result of discoveries in the Zagora area made by local fossil collector Mohamed Ben Moula and successive fieldwork campaigns from early 2003 to early 2017 (Lefebvre et al. 2016c; Saleh et al. 2018). These field studies have resulted in the production of a synthetic, composite stratigraphic column, used in the present paper, that enables the precise stratigraphic position of the material collected from these localities.

The localities from the Yale Peabody Museum listed below were investigated by Mohamed Ben Moula. Localities names and coordinates are as given on the Yale Peabody Museum database (available online at https://collections.peabody.yale.edu/search/).

There may be discrepancies in the spelling of some of the localities due to the fact that these were recorded verbally.

The brachiopod fauna.

The total sample studied is composed of 389 identified individuals; more specimens were studied but these were not counted as they were unidentifiable due to poor preservation. The fauna is very diverse with 30 taxa identified, including a new genus, four new species erected and one taxon described at the family level. The brachiopod fauna is more diverse in the upper Tremadocian horizons than in the Floian horizons, but this might be due to the extensive collecting during the past 20 years concentrating on this interval, as researchers were focussing on the discovery of horizons with exceptional preservation. The Tremadocian horizons show a high γ-diversity with at least 15 taxa represented, but at the locality level, α-diversity varies from fairly diverse (e.g. Z-F51c) to relatively poorer (e.g. Z-F3, Z-F4). The high density of individuals is commonly observed at some horizons [Fig. 3; horizon Z-F2(3g)]. In the Lower Fezouata Shale (upper Tremadocian), unstable environmental conditions prevailed in shallow-water settings, which prevented the establishment of long-ranging communities of shallow infaunal, epibenthic or sessile taxa onto the sea bottom (Saleh et al. 2018). These particularly unstable, high-energy environmental conditions might elucidate the spatial (horizontally and vertically) and taxonomic diversity of the interval. The succession of short-lived (horizon level), low-diversity and high-disparity assemblages indicates that these opportunistic communities of epifaunal and shallow infaunal taxa were regularly smothered in-situ and killed by distal storm deposits (Saleh et al. 2018).

The brachiopod assemblages were plotted on the synthetic log of the Fezouata Shale (Figure 4), compiled from three successive fieldwork campaigns undertaken between 2012 and 2014 within the scope of the RALI project (2011-2015) and the Franco-Moroccan collaboration VALORIZ project (2013-2014). Only the field collections from Marrakesh and Lyon were plotted onto the synthetic log, because these only were collected within the stratigraphic framework. The collection from the Yale Peabody Museum cannot be plotted onto this log with confidence, at the horizon level, because the material was not obtained using the same methodology.

In the upper Tremadocian, the genera *Orbithele* and *Celdobolus* are the dominant taxa, collected almost continuously throughout the *Sagenograptus murrayi* Biozone: these two taxa almost always occur together in the same horizon (Fig. 4). The succession of assemblages shows a diverse and disparate composition of alternating linguliformean and rhynchonelliformean taxa with more rarely rhynchonelliformeans occurring together with linguliformeans. Nonetheless, some taxa recur through the upper Tremadocian interval, implying a recurrent replacement of communities. The linguliformean genera include *Wosekella*, *Orbithele*, *Celdobolus,* and *Rafanoglossa* [e.g. Z-F51c, Z-F50a, Z-F2(1a)], a combination showing affinities with the Bohemian Floian *Elkania-Acrotreta* Community. The presence of the thick-shelled taxon *Celdobolus* indicates shallower and coarser sediments, whereas the presence of taxa such as *Rafanoglossa* and *Wosekella* indicate deeper, muddy substrates (Mergl 2002). This alternates with and assemblage composed of *Celdobolus, Orbithele* with sometimes large *Thysanotos*. This association shows affinities with the Bohemian Tremadocian *Leptembolon* Community interpreted as shallow-water marine and with a low diversity

(Havlíček 1982a; Mergl 1996), however, locally, this is different and shows high diversity (Mergl 2002).

The assemblages include taxa with varied shell sizes and shapes, as well as linguliformean ornamentation ranging from almost smooth to spinose. This reflects a broad range of life strategies and habitats indicating a varied range of adaptations in the Early Ordovician (Mergl 2002). The linguliformean brachiopods can be divided into three ecological strategies: endobenthic (e.g. *Rafanoglossa* and *Lingulella*), semi-endobenthic (e.g. *Wosekella*) and epibenthic (e.g. *Orbithele* and *Celdobolus*).

Palaeobiodiversity and palaeobiogeographical relationship of the fauna

The Tremadocian is a key interval in geological history, marking the transition between the Cambrian and Paleozoic evolutionary faunas (e.g., Saleh et al. 2022). The new Fezouata data are compared with those from 25 other Tremadocian localities. The data are heterogenous. A number of sites have high diversities, largely accounted for by a large proportion of phosphatic brachiopods extracted from carbonate horizons by acid etching. These faunas also display the interface between the Cambrian evolutionary faunas, dominated by non-articulate brachiopods with those in the Paleozoic evolutionary fauna with a strong presence of rhynchonelliforms. Moreover the faunas are derived from a wide range of environmental setting and sedimentary facies, some in carbonates and others in siliciclastics. These different signals are difficult to isolate thus the multivariate analyses have included all the available data.

The relationships of the Fezouata Tremadocian fauna with coeval faunas from Gondwana, Laurentia, Avalonia and Siberia are represented in the Nonmetric Multidimensional Scaling analysis – NMDS – (Fig. 5), using the Raup-Crick similarity index, and a network analysis (Fig. 6). The lack of data from a number of key areas together with heterogeneities within the data currently obscure many of the true relationships between localities. Nevertheless some patterns emerge.

Previous studies on selected phyla described from the Fezouata Shale as a whole (Tremadocian–Floian) have established closer links to coeval faunas from the Montagne Noire, France (e.g. Ebbestad 2016 for Gastropoda, Tergomya and Paragastropoda; Polechová 2016 for bivalves; Martin et al. 2016a for trilobites; and Lefebvre et al. 2016c for echinoderms). The brachiopod fauna from the Montagne Noire area in southern France was described by Havlíček (1980), Babin et al. (1982) and revised by Vizcaïno et al. (2001). The Tremadocian St-Chinian Formation brachiopod fauna is relatively rare and of low diversity with only two taxa (one of which is common to the Fezouata Tremadocian assemblage). Whereas the Floian Landeyran Formation assemblage is more diverse with an abundant fauna, comprising 12 taxa, five of which are common to the Fezouata Floian assemblage. The weak connection between the Tremadocian Fezouata and Montagne Noire faunas is confirmed by their adjacent positions in the NMDS and network analysis (Figs 5, 6). On the other hand, Havlíček (1971) remarked the similarity of the Ordovician brachiopod faunas with those from Bohemia, which he attributed to similar geological settings, although he only collected rhynchonelliform taxa, missing the diverse linguliform fauna, and therefore had an incomplete view of the assemblages. The Montagne Noire and Bohemia lie at the same latitude on the NMDS figure (Fig. 5) and are adjacent in the network analysis (Fig. 6).

Nevertheless, the main connection of the Tremadocian fauna of Fezouata is with Bohemia, emphasised by the primary connections observed on the network analysis (Fig. 6). The Tremadocian Fezouata fauna is characterised by many endemic brachiopod taxa (10; see Fig. 6), many of which also represent the earliest occurrence of the taxon (e.g., *Wosekella, Glossella, Nocturnellia, Rafanoglossa, Incorthis* and the new genus *Tinzoulinorthis*). Moreover, the Tremadocian Fezouata fauna is characterised by some taxa that are either previously unknown outside of Bohemia (*Paldiskites, Wosekella*) or represent the oldest occurrence in Morocco (*Euorthisina*). This richness in early occurrences as well as the relatively high γ-diversity of the Fezouata fauna indicates that it may be regarded as a biodiversity hub (alongside Poland, Sweden and Bohemia; Fig. 6), from which taxa emerged and spread their geographical ranges.

In the Floian, several groups of linguliform brachiopods originating at high-latitude and temperate-latitude Gondwana, dispersed from these sites to sub-equatorial and low latitudes (Popov et al. 2013). High-latitude Gondwana was also characterised by rhynchonelliform brachiopods such as *Paurorthis, Prantlina* and '*Ranorthis*' (Gondwanan forms are now reassigned to the new genus *Tinzoulinorthis*) (Harper et al. 2013).
The Floian Fezouata brachiopod fauna is compared with data from 31 other localities, some of which are very diverse, highlighting the increase in brachiopod diversity, compared to the Tremadocian, across peri-Laurentian and Baltica sites. These Floian faunas also make the move away from their Cambrian origins to diversify from Tremadocian stocks particularly in peri-Gondwana areas. The Floian was characterised by the rise of the plectambonitoid brachiopods, originating in peri-equatorial latitude in the late Tremadocian (Altay-Sayan; Harper et al. 2004). Several occurrences of plectambonitoids are reported here but these occur mainly around Laurentia and peri-Laurentian terranes, spreading to the more temperate Baltica, Avalonia and peri-Gondwana (Montagne Noire).

The relationships of the Fezouata Floian fauna with coeval faunas from Laurentia, peri-Laurentia, Avalonia, peri-Gondwana (temperate to circum-polar latitudes) and peri-equatorial Gondwana, Baltica and South Urals are shown in the Nonmetric Multidimensional Scaling analysis (Fig. 7), using the Raup-Crick similarity index, and a network analysis (Fig. 8). The data appear more coherent than in the Tremadocian, and two broad groups can be distinguished from the NMDS plot (Fig. 7). The low-latitude brachiopod fauna, characterised by Laurentian, peri-Laurentian and peri-equatorial Gondwanan faunas, is here also recognised and groups faunas from Avalonia. Peri-Gondwana faunas (Fezouata, Montagne Noire, Bohemia and Iran) are linked together and are closely connected with faunas from Baltica and South Urals (Fig. 7). Identical patterns are shown in the network analysis output (Fig. 8), but this output clearly shows the strong relationship between Floian Fezouata, characterised by a smaller number of endemic taxa, and Bohemia (Klabava Formation; characterised by the large amount of endemic or singleton taxa [21]) and the Montagne Noire (Landeyran

Formation). The strong connection is marked by the common occurrence of some linguliform taxa (such as *Celdobolus, Orbithele, Paldiskites* and *Rafanoglossa*) with Bohemia, and some rhynchonelliform taxa (such as *Paralenorthis* and *Tinzoulinorthis*) with the Montagne Noire. *Rafanoglossa* and *Tinzoulinorthis* are common to all three. Figure 8 also reflects the rise in diversity of the brachiopod faunas in general, with more connections established between the nodes than previously in the Tremadocian (Fig. 6), illustrating too the changing palaeogeography.

Systematic Palaeontology

Subphylum Linguliformea Williams *et al.*, 1996
Class Lingulata Gorjansky & Popov, 1985
Order Lingulida Waagen, 1885
Superfamily Linguloidea Menke, 1828
Family Pseudolingulidae Holmer, 1991

Genus *Sedlecilingula* Mergl, 1997

Type species. Sedlecilingula sulcata Mergl, 1997 from the Klabava Formation, Floian–Dapingian, Ordovician, Bohemia, Czech Republic.

***Sedlecilingula* sp.**

Figure 9A–C

Material and horizon. Four ventral and one dorsal valves from localities 42, 50, 57 and 62.

Description. Ventral valve convex, subpentagonal, slightly longer than wide, 105% as long as wide; emargination 38% as wide as valve width; long pseudointerarea, possibly orthocline, extending for 23% of valve length, bisected by long pedicle groove extending anteriorly for 32% of valve length. Dorsal valve convex, subpentagonal, 112% as long as wide, 14.5% as deep as long; emargination 32% as wide as valve width; short pseudointerarea, orthocline, extending for 4% of valve length. Ornamentation with well-marked growth lamellae and faintly impressed fine filae.

Remarks. Few morphological details can only be observed on the poorly preserved specimens. One specimen (YPM IP 531534; Fig. 9A) shows a faint impression of the ventral pseudointerarea with a faintly intersecting pedicle groove very similar to the features on *Sedlecilingula* as shown by Mergl (1997, fig. 4A, I). The pentagonal outline of the valve, the anterior emargination and the ornamentation are also similar features to those present in *Sedlecilingula*. Unfortunately, no internal features are well preserved,

Family Obolidae King, 1846

Subfamily Obolinae King, 1846

Genus *Lingulella* Salter, 1866

Type species. Lingula davisii M'Coy, 1851 from the Ffestiniog Flags Formation, Merioneth Series, Furongian, Cambrian, North Wales.

***Lingulella lata*? Koliha, 1924**

Figure 9D–H

Material and horizon. 20 ventral valves, from localities 6, 8, 12, 44, 46 and 49.

Description. Valve elongate, oval, 80% as wide as long, convex in both profiles; anterior commissure rectimarginate; pseudointerarea anacline, extending anteriorly for about 15% of valve length; flexure lines faintly preserved; pedicle groove triangular, narrow and elongate. Interior features poorly preserved; pedicle nerve impressed, extending anteriorly for 25% of valve length. Microornamentation consisting of fine radial pitting organised radially, numbering 10 per 100µm.

Remarks. The identification of these specimens is difficult. It is similar to *Lingulella* and possesses the same microornamentation as that of *Wosekella*. The large ventral pseudointerarea, flexure lines and relatively narrow pedicle groove suggest possible identification as *Lingulella lata* from the Olešná Member (Floian) of The Klabava Formation in the Lower Ordovician of Bohemia (see Mergl 1997, 2002).

Genus *Paldiskites* Havlíček, 1982b

Type species. *Lingula sulcata* Barrande, 1879 from the Klabava Formation, Floian–Dapingian, Ordovician, Bohemia, Czech Republic.

***Paldiskites* aff. *sulcatus* (Barrande, 1879)**

Figure 9I–J

Material and horizon. The internal and external moulds of a dorsal valve, UCBL-FSL 713629, from locality TA-F1, Taichoute, 30°58'51"N, 05°16'52"W, *?Baltograptus* jacksoni zone, middle Floian.

Description. Dorsal valve spatulate, longer than wide, about 116% as long as wide, with maximum width at approximately 60% of valve length; pseudointerarea short, extending for 7% of valve length, orthocline, with gently concave median depression and linear undivided propareas; internal features not well defined. Ornament consisting of densely preserved concentric growth lines better developed in the posterior half and lateral flanks of the valve, intersected by discontinuous radial plications, more strongly developed antero-medially.

Remarks. With only a single valve available, comparisons with other species are not statistically significant, but nevertheless useful. The present specimen is different from *Paldiskites peracutus* Mergl, 2002 from the Darriwilian in Bohemia in its larger size, and stronger ornament (both concentric and radial) nevertheless the outline, shape and position of maximum width are similar. The present specimen is probably a different species from *P. sulcatus* (Barrande, 1879) from Bohemia (upper Floian to Dapingian) based on differences in outline: the Moroccan specimen is spatulate, whereas *sulcatus* is more circular; therefore, the maximum width in *sulcatus* is at mid valve length. The concentric ornament is similar to that of *sulcatus* and in the Moroccan specimen, both samples develop marked ornament on the posterolateral parts of the shell. The radial plications are more pronounced and more plications (up to 4-5, see Mergl 2002, plate 6, figs 16, 17) are developed at the anterior commissure in *sulcatus*, whereas two are present at the anterior commissure in the Moroccan specimen. The plications are also better developed at an earlier stage of growth in *sulcatus* than in the Moroccan specimens.

Paldiskites has also been tentatively recorded from the upper Darriwilian Furudal Limestones in Dalarna, Sweden (*Paldiskites*? sp. nov. a; see Holmer, 1989, pp. 74-76) and also from the middle Darriwilian Hope Shales in the Shelve District, Shropshire, England [*Obolus subditivus* Williams, 1974, assigned to *Paldiskites*? by Holmer (1989)]. However, these records have not been validated. The present occurrence represents the oldest record of the genus and its first occurrence outside Bohemia.

Genus *Wosekella* Mergl, 2002

Type species. *Lingula debilis* Barrande, 1879 from the Šárka Formation, Darriwilian, Ordovician, Bohemia, Czech Republic.

Remarks. *Wosekella* has only been described from the Lower Ordovician of Bohemia. Three species were identified by Mergl (2002): *W. debilis* (Barrande, 1879) from the Šárka Formation, lower Darriwilian; *W. senilis* Mergl, 2002 from the Dobrotivá Formation, upper Darriwilian – lower Sandbian; and *W. filiola* Mergl, 2002 from the Klabava Formation, Floian – Dapingian. The present specimens represent the first and the oldest (Tremadocian) occurrence of the genus outside Bohemia.

Wosekella maghribi **sp. nov.**

Figure 9K–O

LSID. https://zoobank.org/xxxxxxxxxxx

Holotype. A ventral valve, AA-TGR1c-oi-155, from horizon Z-F51c, locality 24.

Paratype. A dorsal valve, AA-TGR1c-oi-102, from horizon Z-F51c, locality 24.

Material and horizon. Twelve ventral, seven dorsal and one broken valves from localities 14, 22 and 24.

Derivation of name. Arabic word for ‘from Morocco’.

Diagnosis. Species characterised by fine pitting; ornament of radial plications developed laterally; long pseudointerarea; long, narrow pedicle groove; long, thin median septum.

Description. Shell elongate oval to spatulate. Ornament consisting of radial plications variably developed, better preserved on the valve flanks; concentric fila superimposed on the radial ornament; fine radial pitting organised in rows numbering about 6 per 100µm.

Ventral pseudointerarea flat, long, with growth lines; pedicle groove narrowly triangular, widening slightly anteriorly; visceral area unclear.

Dorsal pseudointerarea long, undivided, clearly defined anteriorly and laterally; median septum extending for about 40 % of valve length; visceral area unclear.

Remarks. These specimens are described as *Wosekella* based on the low and large pseudointerareas, the presence of low radial plications laterally on the exterior of valves. However, the presence of a fine dorsal median septum in the Moroccan specimens is not present in Bohemian species of *Wosekella*. The Moroccan specimens are morphologically different from the species described by Mergl (2002) from the Lower Ordovician of Bohemia, but they are closest to *W. debilis* (Barrande), especially in the similar external radial ornament and shape and size of the pseudointerareas. The major differences lie in the presence of finely micropitted ornament, and absence of a subcarinate profile in the ventral valves of the Moroccan specimens.

Wosekella filiola **Mergl, 2002**

Figure 10A–F

Material and horizon. Five ventral, three dorsal and three undetermined valves from localities 15, 39, 41 and 60.

Description. Ventral valve oval; pseudointerarea orthocline with strongly impressed growth lines; flexure lines faint, developed toward the outer margin of the

pseudointerarea; pedicle groove wide and short. External ornamentation consisting of a fine, dense concentric ornament intersected by radial fila.
No dorsal internal features are preserved.

Remarks. These specimens differ from the new species of *Wosekella* in the absence of fine pitting, the presence of radial fila on the entire shell surface, and the broader and shorter pedicle groove. Nevertheless, based on the similar radial ornament, pedicle groove and pseudointerarea, these specimens are regarded here as identical to *Wosekella filiola* Mergl, 2002 from the lower part of the Klabava Formation (lower Floian) in Bohemia.

Subfamily Glossellinae Cooper, 1956

Genus *Glossella* Cooper, 1956

Type species. *Glossella papillosa* Cooper, 1956 from the Pratt Ferry Beds, Darriwilian, Ordovician, Alabama, USA.

***Glossella* sp.**

Figure 10G–H

Material and horizon. A dorsal valve exterior and interior (part and counterpart) from locality 44.

Description. Valve spatulate in outline, longer than wide, 70% as wide as long; anterior commissure rectimarginate; sides gently curved but broadly subparallel; maximum convexity at umbo, lateral and anterior sides flatter. Ornament preserved posteriorly and laterally only, consisting of concentric rows of pustules 40 µm in diameter; wave-length of rows 50µm. Internal features obscure.

Remarks. A single specimen was collected nonetheless it resembles in outline and profile the specimen described and illustrated by Cooper (1956, p. 229; pl. 3G) from the Sandbian Botetourt Formation in Virginia, USA. The generic identification is proposed mainly on the basis of the characteristic pustulose ornament. *Glossella* is known form the Floian to Katian in peri-Iapetus terranes (geographic range from Holmer & Popov 2000). For example, it is present in the Scoto-Appalachian province of SE Laurentia, from the Darriwilian to lower Katian (Scotland; Williams 1962) to the upper Katian (Pomeroy, Northern Ireland; Mitchell 1977). New occurrences have been published since that monograph was published, extending the geographical distribution of the genus. A new species was described by Lavié & Benedetto (2016) from the San Juan Formation (Darriwilian) of the Precordillera basin (Cuyania), Argentina, while Lavié & Benedetto (2019) documented an occurrence under open nomenclature from Suri Formation (Floian) of the Famatina Range, Argentina. Occurrences were also described by Maslova (2012) from the Sandbian and Katian of the Siberian platform. Another Panthalassic occurrence was described by Hansen & Holmer (2011) from the Dapingian and Darriwilian of Spitsbergen, which was located close to NE Laurentia in the Early Ordovician. Zhen et al. (2015) described an occurrence at the extreme northern part of the Gondwana continent, in modern day Queensland (Australia) recording the northernmost occurrence of the genus (then in the northern hemisphere).

Genus *Rafanoglossa* Havlíček, 1980

Type species. *Lingula impar* Barrande, 1879 from the Dobrotivá Formation, Darriwilian, Ordovician, Bohemia, Czech Republic.

Rafanoglossa inversa **sp. nov.**

Figure 10I–J, 11A–C

LSID. https://zoobank.org/xxxxxxxxxxx

Holotype. A dorsal valve YPM IP 525707 from Ezegzaou, locality 46.

Paratype. Paratype, ventral valve, YPM IP 521282, from a quarry between Ezegzaou and Bou Glf, locality 48.

Etymology. Median septum with a reversed orientation from other species: tapering anteriorly rather than posteriorly.

Material and horizon. Four ventral and four dorsal valves from localities 2, 20, 41, 46, 48, 53, 56, 58 and 59.

Diagnosis. Species characterised by spatulate valves, well-developed ventral pseudointerarea, dorsal median septum tapering anteriorly; finely pitted ornament.

Description. Shell biconvex, longer than wide; lateral sides slightly curved to almost parallel; anterior commissure convex (shell dacryate) becoming truncated (shell spatulate) in larger specimens; ornament consisting of dense concentric fila, often intersected by fine radial ornament, fine pitting observed in some specimens. Ventral valve with orthocline, striated pseudointerarea extending anteriorly for 15% of valve length at pedicle groove, with anterior margin curved latero-anteriorly; no flexure lines; pedicle groove narrow and triangular. Dorsal valve characterised by median septum extending anterior to half valve length; median septum broad and shallow, maximum width about 6% of valve width, tapering anteriorly.

Remarks. The specimens from Morocco present a mix of features diagnostic of *R. impar* (Barrande, 1879) from the Dobrotivá Formation (Darriwilian) and *R. platyglossa*

Havlíček, 1982b from the Klabava Formation (Floian). They have a well-developed ventral pseudointerarea and dense growth lines (*R. impar*) and valves with a truncated anterior commissure (*R. platyglossa*). The Moroccan specimens are also characterised by a dorsal valve with the median septum tapering anteriorly rather than posteriorly as in *platyglossa* and *impar*. *Rafanoglossa trimera* (Barrande, 1879) from the Dobrotivá Formation (Katian) was described by Havlíček (1982b) from material collected from siliceous nodules, but Mergl (2002) reassigned the species and tentatively referred it to the genus *Pseudolingula* Mickwitz, 1909.

Rafanoglossa sp. has also been recorded from the Floian of the Montagne Noire (France) in the La Maurerie, Setso, Foulon and Landeyran formations. However, Havlíček (1980) noted that the French specimens may be related to the Bohemian species *platyglossa* (in press at the time but published two years later), but “owing to deformation of the French valves”, “an exact comparison is not possible”. It is clear from the chronology of publication that Havlíček had intended to publish his 1982b paper earlier than the actual publication date reported; the manuscript was received by the journal in October 1979. Few months after submitting this paper, he described the material from France, which was published by a small local periodical and was printed faster. It is unusual to see that the new genus *Rafanoglossa* was defined on the basis of Bohemian specimens and in an article about the French specimens, and illustrated by those specimens described in open nomenclature. Havlíček (1980) noted that the new genus *Rafanoglossa* is “discussed in detail in the paper devoted to the Lower Ordovician inarticulate brachiopods of Bohemia.”

Havlíček (1980) documented briefly the French specimens as characterised by a well-developed ventral pseudointerarea and pedicle groove, and a dense concentric ornament consisting of concentric microrugellae. Other species of *Rafanoglossa* possess the same type of ornament, and therefore this character is not diagnostic at the species level. *Rafanoglossa platyglossa* possesses a small ventral pseudointerarea and a narrower pedicle groove, which differentiate this species from the French material. The specimens from Morocco have a longer ventral pseudointerarea extending anteriorly for a similar proportion to that of the French specimens. Moreover, they also possess a well-developed pedicle groove. The French and Moroccan material may therefore be related and they both differ from *R. platyglossa*. More dorsal valves detailing in particular internal features are necessary to confirm or otherwise the similarity between the two samples.

Subfamily Glossellinae Cooper, 1956

Genus *Spondyglossella* Havlíček, 1980

Type species. *Spondyglossella spondylifera* Havlíček, 1980 from Saint-Chinian Formation, horizon f, Floian, Ordovician, Montagne Noire, north of Félines-Minervois, Hérault, France.

***Spondyglossella*? sp.**

Figure 11D–E

Material and horizon. Eight ventral, three dorsal and eight undetermined valves from locality 6.

Description. The sample collected comprises 19 disarticulated valves including eight ventral valves (on average one and a half as long as wide), three dorsal valves (slightly longer than wide) and eight undetermined valves. No internal features are observed due to the variable preservation of the material. The specimens are characterised externally by fine concentric fila (wave length about 50 µm) intersected anteriorly and antero-laterally by radial fila (wave length about 45 µm). The specimens are characterised by a flat limbus surrounding the edges of the valves. The identification is based on the presence of the limbus.

Remarks. The genus *Spondyglossella* was previously known from the upper Tremadocian and Floian of the Montagne Noire, France (Havlíček, 1980; Babin et al. 1982) only. Other occurrences from the latest Tremadocian–earliest Floian of Bohemia (Mergl 2002) and the Dapingian – Darriwilian of south Kazakhstan (Nikitina et al. 2006) have been described. The upper Tremadocian occurrence from Morocco indicates a peri-Gondwanan origin for the genus. The genus is part of the deep environment *Elkania*-Acrotreta Community described by Mergl (2002) from the Floian Klabava Formation in Bohemia, and also of a deep-water (BA 5-6) brachiopod assemblage in the Darriwilian Uzunbulak Formation in south Kazakhstan (Nikitina et al. 2006; Popov & Cocks 2021). Although there is a reasonable number of specimens collected, their preservation prevents any meaningful comparison with the type species (from France and Bohemia) or with the samples available from south Kazakhstan.

Obolidae indet.

Figure 11J

Material and horizon. A dorsal valve exterior and its internal counterpart from locality 36.

Description. Dorsal valve small, subcircular, convex, longer than wide, 80% as wide as long, 15% as deep as long. Interior characterised by the impressions of the central muscle scars extending anteriorly for 45% of valve length, and the anterior lateral muscle scars extending anteriorly for 62% of valve length.

Remarks. This identification remains tentative based on a single specimen; however, the valve profile and outline as well as the muscle scars strongly indicate the genus *Obolus*. Nevertheless, more material is required to confirm this identification.

Family Zhanatellidae Koneva, 1986

Genus *Thysanotos* Mickwitz, 1896

Type species. Obolus siluricus Eichwald, 1840 from the Leetse Formation, Floian, Ordovician, Estonia.

***Thysanotos* cf. *siluricus* (Eichwald, 1840)**

Figure 11F–I, K–L

Material and horizon. One ventral, four dorsal and a conjoined valve from localities 12, 16 and 30.

Description. Shell equally biconvex, subcircular with obtuse apex; large specimens, ranging between 20-25mm in length and width; maximum width at about mid valve length. Ornament consisting of irregularly spaced concentric growth lines; 5 concentric rugae per mm; finer wrinkles on growth lines (wave-length: 40µm); spines variably preserved, numbering 6-7 per mm near commissure. Internal features not well preserved: one branch of *vascula lateralia* is preserved in the ventral valve of the conjoined specimen; impression of ventral muscle field preserved in one valve, extending for 37% of valve length.

Remarks. The specimens collected from Morocco are larger than *Thysanotos primus* (Koliha, 1924) from the upper Tremadocian (upper Třenice to lower Mílina formations) of Bohemia (almost twice the length and width), but they are comparable in size with *Thysanotos siluricus* (Eichwald, 1840) from the upper Tremadocian (lower Leetse Beds) in Estonia (see Popov & Holmer 1994). *Thysanotos siluricus* from the middle Tremadocian to Floian (Alimbet, Akbulaksai and Kidryas formations) in South Urals are larger reaching up to 40 mm in length. Specimens of *T. siluricus* from the upper

Tremadocian in the Miedzygorz Sandstone Formation of the Holy Cross Mountains, Poland are on average about 10% smaller and those from the upper Tremadocian (Mílina Formation) of Bohemia are about 15% larger than the Moroccan specimens. Only external features are compared as internal features are poorly preserved in the Moroccan specimens. Marginal spines are more densely developed in the present specimens, with 6-7 per mm than in *T. siluricus* which possesses 5 spines per mm. There are no differences between the specimen collected from the upper Tremadocian and those collected from the upper Floian.

Superfamily Acrotheloidea Walcott & Schuchert in Walcott, 1908

Family Acrothelidae Walcott & Schuchert in Walcott, 1908

Subfamily Acrothelinae Walcott & Schuchert in Walcott, 1908

Genus *Orbithele* Sdzuy, 1955

Type species. Discina contraria Barrande, 1868 from the Leimitz Shales, Tremadocian, Ordovician, Bavaria, Germany.

Remarks. Popov & Holmer (1994) discussed the genus and comprehensively illustrated the species *O. ceratopygarum* (Brøgger, 1882). They also listed the species they regarded as valid, placing in synonymy many of the species described by Mergl (1981) from the upper Tremadocian to lower Floian of Bohemia with those erected by Barrande (1879). We include, in the remarks below, the species described by Mergl (1981) and reiterated by Mergl (2002), as these are sufficiently distinct both morphologically and stratigraphically.

***Orbithele tazagurta* sp. nov.**

Figure 12A–E

LSID. https://zoobank.org/xxxxxxxxxxx

Holotype. YPM IP 518823, a dorsal valve from the hillside at Ezegzaou 1, locality 45.

Paratypes. YPM IP 522001, a dorsal valve; YPM IP 522682, a ventral valve (part and counterpart) from Bou Glef, localities 37 and 56.

Etymology. Derived from the Berber name for Zagora, Tazagurt, located 20 km south of the type locality.

Material and horizon. 19 ventral and 18 dorsal valves measured; specimens from localities 2, 3, 11, 12, 19, 22, 24, 37, 39, 41, 45, 47, 48, 56, 59-61, and 63.

Diagnosis. Species characterised by ornament of wavy concentric lines, short narrow sulcus anterior to ventral apex, flat ventral posterior margin, and curving peripheral margin on dorsal valve.

Description. Shell ventribiconvex, subcircular in outline, sometimes wider than long. Ventral valve conical in profile with slightly concave slopes; posterior margin flat; apex positioned from mid valve to a third of valve length from posterior margin; pedicle foramen at a quarter to a third of mid valve length from posterior margin, filled anteriorly by a listrium; narrow sulcus developed anteriorly from apex fading when valve becomes concave. Dorsal valve gently convex to flat, with umbo at or near posterior margin. Ornament of fine concentric wavy lines, regularly spaced, numbering 9-11 per mm; short spines developed at the circumference ranging from 11 to 13 per mm; spines often preserved at the 3 mm growth stage (on average, when preserved) numbering 13 to 14 per mm. Radial fila developed from umbo up to 0.6 mm anteriorly and laterally (ventral valve, and up to 1.1-1.5 mm from umbo anteriorly and laterally (dorsal valve).

Dorsal interior with pseudointerarea orthocline to slightly anacline, intersected by a broad and triangular median groove; muscle scars faintly preserved; transmedian, and outside and middle lateral muscle scars indistinct, inserted close to a faintly developed median ridge; central muscle scars at midvalve length, developed along anterior end of median ridge; anterior lateral muscle scar developed anterior to median ridge about two-third of valve length.

Remarks. Mergl (1981) described *O. vana* from the lower Floian of Morocco, in Foum Zgouid, located about 100 km west of Zagora. *Orbithele vana* was distinguished from *discontinua* in its denser spine ornament. Although the specimens from the upper Tremadocian possess a similar density of short spines at the anterior margin (here 11-13 per mm), they are different from *vana* in the presence of fila, denser concentric wavy ornament, flat posterior margin in ventral valve, ventral valve slope concave, the presence of a short, narrow sulcus anterior to ventral apex, and dorsal valves with evenly curving peripheral margin.

The upper Tremadocian specimens are similar in size to *O. discontinua* and *O. vana*; the widest valve reaches 7.3 mm, but the bulk of the collection is not wider than 6 mm. The present specimens are characterised by a concentric ornament of regular wavy lines similar to the ornament in *discontinua*, however, it is not as dense (about half as dense than in *discontinua*) and by the presence of spines sometimes preserved on larger valves posterior to the 4 mm growth line.

***Orbithele* sp. 1**

Figure 12F, I

Material and horizon. One ventral valve (UCBL-FSL 711 960) from locality 33.

Description. A single large ventral valve subcircular in outline, 85% as long as wide and subconical, 17% as high as long; apex at 33% of valve length from posterior margin; brephic shell subcircular, 1.5 mm long and 1.57 mm wide. Pseudointerarea vestigial, faintly marked; ventral foramen posterior to apex, anterior margin located at 25% of valve length from posterior margin, filled anteriorly by a listrium. Ornament not observed, but posterior to foramen four coarse rugae are preserved, wave-length about 4 mm.

Remarks. The Floian specimen is characterised by its large size, and therefore different from *Orbithele vana* Mergl, 1981, and also different from *O. tazagurta* sp. nov. from the upper Tremadocian Fezouata Shales. The size of the Floian specimen is comparable with *O. secedens* (Barrande, 1879) from the upper Tremadocian (Třenice Formation) of Bohemia, which is the largest species in Bohemia reaching up to 14 mm in width (Mergl, 2002). The posterior margin of the Moroccan specimen is characterised by a coarsening of ornamentation similar to *O. secedens*, *O. maior* Mergl, 1981 and *O. rimosa* Mergl, 1981, the latter two species being collected from the upper Tremadocian (Mílina Formation) and the upper part of the Klabava Formation (Dapingian). Insufficient material prevents any meaningful comparisons.

***Orbithele* sp. 2**

Figure 12G

Material and horizon. A dorsal valve (with possible ventral counterpart) from locality 54.

Description. Dorsal valve large, 10.6 mm wide, flat, subcircular, 85% as long as wide. Ornament of concentric rugellae, numbering 10-11 per mm at the 5 mm growth stage. Interior with anterior lateral muscle scars extending anteriorly for 56% of valve length.

Remarks. This specimen is similar to *Orbithele* sp. 1, characterised by its large size for the genus, but *Orbithele* sp. 1 is twice the size of the present specimen. These two samples cannot be included within a single species with any confidence. *Orbithele* sp. 2 is more similar in size to *Orbithele rimosa* Mergl, 1981 of the upper part of the Klabava Formation (Dapingian) in the Czech Republic, but possess a very different ornament. More material is required to confirm with confidence its identity.

Order Acrotretida Kuhn, 1949

Superfamily Acrotretoidea Schuchert, 1893

Family Acrotretidae Schuchert, 1893

Genus *Eurytreta* Rowell, 1966

Type species. *Acrotreta curvata* Walcott, 1902 from the Pogonip Limestone, Tremadocian, Ordovician, Eureka district, Nevada, USA.

Eurytreta sp.

Figure 12H, J

Material and horizon. Two dorsal valves from locality 52.

Description. Dorsal valve subcircular, slightly wider than long; both profiles gently convex. Pseudointerarea short, anacline, less than 10% as long as valve; median groove triangular; anterior commissure sulcate; valve periphery bordered by a low brim, 20% as long as valve; brim bisected by the anterior end of the median septum and shallow sulcus.

Interior with low median septum, uniformly high along its length, extending for 77% of valve length, extending to the brim; cardinal muscle scars oval, oblique, extending anteriorly for 33% of valve length and laterally for 50% of valve width; anterocentral muscle scars oval flanking the median septum 16% as long as valve length, extending anteriorly for 65% of valve length.

Remarks. The genus *Eurytreta* originated in the Upper Cambrian of Kazakhstan, USA, England and Mexico and according to the Treatise (Holmer & Popov 2000) has remained until its extinction in the Sandbian a peri-Iapetus taxon, present in Laurentia, Avalonia, Siberia and Baltica. Streng et al. (2011) questioned the upper Cambrian species, *discors* and *sublata* from Kazakhstan and the USA as included in the genus *Eurytreta*. Three species were not included from the genus: *stapeleyensis* (upper Dapingian, Shropshire, England), *intermedia* (Darriwilian, NE Poland) and *minor* (Tremadocian, Poland; upper Tremadocian, Sweden; middle Tremadocian, Kazakhstan). Nevertheless, new data is now published that widens the geographical spread of the genus. In the Lower Ordovician, species have been recorded from the Tremadocian of the Eastern Alborz (Iran) (Ghobadi Pour et al. 2011), Utah (USA) (Holmer et al. 2001, 2005), Nova Scotia (Canada) (Landing & Fortey 2011), NW Argentina (Mergl et al. 2015; Lavié & Benedetto 2023), Kazakhstan (Popov & Holmer 1994; Holmer et al. 2001, Popov et al. 2001), South Urals (Popov & Holmer 1994), USA (Holmer et al. 2001), Sweden (Popov & Holmer 1994; Streng et al. 2022), Mexico (Streng et al. 2011), and Wales and England (Sutton et al. 2000); from the Floian of Spitsbergen (Hansen & Holmer 2011), South Urals (Popov et al. 2001), Kazakhstan (Popov & Holmer 1994), and England (Sutton et al. 2000).
Eurytreta ahmadii Ghobadi Pour et al., 2011 from the middle Tremadocian of Iran, has similar dorsal median septum (although it is elevated anteriorly) than the Moroccan specimens, extending for three-quarters of the valve length, but do not possess a brim. *E. harringtoni* Mergl & Herrera, 2015 in Mergl et al. 2015 from the lower Pupusa Formation (lower Tremadocian), NW Argentina, possesses the same median septum and brim characteristics. Similarly, *Eurytreta sabrinae* (Callaway, 1877) [and its junior

synonym, *E. bisecta* (Matthew, 1901); see Sutton et al. 2000] from the Shineton Shales Formation, Shropshire, England and the middle Tremadocian of South Wales (Owens et al. 1982; Sutton et al. 2000) is similar to the Moroccan specimens in the shape and size of the dorsal median septum, and the size of the distinct brim. Unfortunately, the lack of material cannot help refining the comparisons further. Until more material is available, the Moroccan specimens are left on open nomenclature.

Order Siphonotretida Kuhn, 1949

Superfamily Siphonotretoidea Kutorga, 1848

Family Siphonotretidae Kutorga, 1848

Genus *Celdobolus* Havlíček, 1982b

Type species. Obolus complexus Barrande, 1879 from the Klabava Formation, Floian–Dapingian, Ordovician, Bohemia, Czech Republic.

***Celdobolus mirandus* (Barrande, 1879)**

Figure 12K–L, 13A–H

Material and horizon. 48 ventral, 40 dorsal and 19 indeterminate valves, from localities 2-5, 21-25, 37, 39, 41, 49, 52 and 56. 28% and 26% of the total number of specimens were collected from localities 2 and 24, respectively.

Description. Shell subcircular to slightly elongated, biconvex; concentric growth lines marked by the absence of spines; fine spines on juvenile shells; maximum width at around mid-valve length. Concentric growth lines preserved on occasion; spines or impression of spines usually preserved on small valves; pustules representing the bases of spines preserved in larger valves; spines/pustules distributed evenly on valves; spine/pustule density independent from valve size and variable, measured anterior to mid valve length, numbering 7 to 11 in an area 0.25 mm x 0.25 mm in size; diameter of spines/pustules ranging between 20 and 40 µm (mode 25 µm); spines often preserved at valve margins (posteriorly, laterally and anteriorly) extending for over 15–31% of valve length at anterior commissure.

Ventral pseudointerarea apsacline, extending for 6.7–10% of valve length. Visceral area rhomboidal; pedicle nerve seldom preserved as pair of subparallel branches, extending for 36–49% of valve length. Central muscle scar subparallel, developed on low pads and extending anteriorly for 45% of valve length. *Vascula lateralia* arcuate.

Dorsal pseudointerarea large, orthocline, extending for 7.5–11.4% of valve length, characterised by strong, coarse lateral striae. Median septum shallow, but raised medianly, developed posteriorly to the posterior end of the central muscle scars and extending anteriorly for 52–81% of valve length. Central muscle scars divergent, inserted on weakly to highly elevated pads, oval in outline, extending anteriorly for 41–54.5% of valve length. *Vascula lateralia* arcuate, developed concentrically with the lateral margins of the valve; secondary branches developed anteriorly to the commissure.

Remarks. Celdobolus complexus (Barrande, 1879) from the Dapingian (upper part of the Klabava Formation) of Bohemia differs from the Floian species *C. mirandus* in the presence of coarse tubercules in the zone between the *vascula lateralia* and the anterior and lateral margins of both valves, and lacking any trace of the pedicle tube indicating that it atrophied in early stages of growth (Havlíček 1982b). Moreover, *C. complexus* is also characterised by a consistently denser spine arrangement, and a longer dorsal median septum. Externally, the Moroccan specimens are similar to *C. mirandus* in pustule density. Internally, there are no other features to differentiate between *complexus, mirandus* and the Moroccan specimens. The absence of the coarse pustules in the anterior and lateral belt of valve interiors in the Moroccan specimens indicate a similarity with *mirandus*. The Moroccan specimens are smaller than the Bohemian specimens, but this does not constitute a diagnostic character to establish a new species. The Moroccan specimens are regarded as conspecific with *mirandus.*

Class Paterinata Williams et al., 1996

Order Paterinida Rowell, 1965

Superfamily Paterinoidea Schuchert, 1893

Family Paterinidae Schuchert, 1893

Genus *Lacunites* Gorjansky, 1969

Type species. Lacunites balaschovae Gorjanski, 1969 from the Vasilkovo Member, Leetse Formation, Floian (*Oepikodus evae* Biozone), Ordovician, Ingria.

Lacunites punctum **sp. nov.**

Figure 13I–L

LSID. https://zoobank.org/xxxxxxxxxxx

Holotype and only available specimen. YPM IP 523944, external and internal moulds of a dorsal valve from Bou Glf, 783 m, locality 40.

Diagnosis. Shell transverse semi-oval; no rugae; sharp increase in pit diameter at half valve length; pits merging anteriorly to form a zig-zag pattern; narrow rim surrounding pits.

Material and horizon. One valve, part and counterpart from locality 40.

Etymology. With reference to the small pits observed in the external ornament.

Description. Dorsal valve transverse, less than two-third as long as wide, resupinate (convex then concave), characterised by a geniculate anterior and lateral margin. Ornament consisting of pits of increasing sizes arranged in radii in a staggered manner giving the impression of a divaricate distribution of the pits; pits varying in shape from circular in the posterior half of the valve to transverse oval (long axis normal to radius) towards the anterior margin, often fusing with the antero-lateral pit to form a zig-zag pattern; size of pits increases sharply anterior to half valve length; narrow rims surrounding pits; band with no or poorly preserved/developed pits from 2.4 to 3.2 mm from posterior margin on the dorsal valve.

Remarks. Due to the paucity of the Moroccan material and its preservation, comparisons with other species are based on exterior features. The Moroccan specimen is similar in outline to *Lacunites balaschovae* Gorjansky, 1969 from the Leetse Formation in Ingria, but the rim between the pits is narrower in the Moroccan specimen than in the type species *L. balaschovae*. The rim is also narrower than in *L. ivantsovi* Holmer et al., 2017 from the Volkhov Formation (lower Darriwilian) in Ingria, north-western Russia and *L. jaroslavi* Mergl & Kraft, 2016 from the Klabava Formation (Floian-Dapingian) in Bohemia. The rim is as narrow in *L. walcotti* (Růžička, 1927) from the Třenice Formation (lower Tremadocian) in Bohemia but the pits are smaller and less circular in the Moroccan species. Pit density is higher in the Moroccan specimen with about 13 in 2 mm radially from the posterior margin, whereas in the other species (*balaschovae, ivantsovi, jaroslavi* and *walcotti*) counts range from 7 to 8 in 2 mm radially.

Class Rhynchonellata Williams et al. 1996

Order Orthida Schuchert & Cooper, 1932

Suborder Orthidina Schuchert & Cooper, 1932

Superfamily Orthoidea Woodward, 1852

Family Orthidae Woodward, 1852

Genus *Paralenorthis* Havlíček & Branisa, 1980

Type species. Paralenorthis immitatrix Havlíček & Branisa, 1980 from Darriwilian rocks, Ordovician, near San Lucas, Bolivia.

***Paralenorthis*? sp.**

Figure 14A–C

Material and horizon. Four ventral and one dorsal valves from locality 31.

Description. Specimens small, ranging from 2.5 to 3.0 mm long; shells ventri-biconvex, semi-oval, with maximum width at posterior quarter of valve. Ornament consisting of angular, sharp costae, numbering 4 per mm at 2 mm growth stage; interspace between costae as wide as costae.

Remarks. There are relatively few members of the Orthidae in the Lower Ordovician. The specimens are poorly preserved, and only external moulds were collected. The coarse-ribbed orthid is tentatively assigned to the cosmopolitan genus *Paralenorthis*. It is similar in ornament and shape to those of *P. immitatrix* Havlíček & Branisa, 1980, the type species of the genus, from the Lower Ordovician of Bolivia (Havlíček & Branisa, 1980) and Peru (Gutiérrez-Marco & Villas 2007). It is suboval with coarse costae but capillae, a diagnostic feature of the genus, have not been identified. *Paralenorthis* is widespread occurring in peri-Gondwanan regions such as Avalonia (Cocks & Popov, 2019) and Ganderia (Harper & Bates, 2023) together with the Alborz Mountains (Popov et al., 2009). *Paralenorthis*? sp. is retained to identify the taxon pending discovery of more material.

Family Nanorthidae Havlíček, 1977

Genus *Nothorthis* Ulrich & Cooper, 1938

Type species. Nothorthis delicatula Ulrich & Cooper, 1938 from the Tremadocian of Quebec, Canada.

***Nothorthis* sp.**

Figure 14D–G

Material and horizon. Four ventral and one dorsal valve from localities 17, 28, and 51.

Description. Shell transversely semioval, ventri-biconvex; anterior commissure unisulcate; cardinal angles round and obtuse. Ventral valve with orthocline interarea extending for 15% of valve length; delthyrium open. Dorsal valve with interarea short and anacline; notothyrium open. Ornament consisting of fine ramicostellae, numbering 7-8 per 2 mm at the 5 mm growth stage.

Ventral valve interior with short, triangular and undifferentiated muscle scar, extending for 25% of valve length; muscle scar raised on low callus; teeth supported by receding dental plates.

Dorsal valve interior with low notothyrial platform extending anteriorly into a broad median ridge; cardinal process rudimentary, simple; brachiophores short, blade-like not extending anterior to notothyrial platform; adductor scar quadripartite with a pair of round antero-median scars and a pair of round postero-lateral scars extending anteriorly for half valve length.

Remarks. The Moroccan specimens are similar to the type species *N. delicatula* Ulrich & Cooper from the Lower Ordovician of Québec, Canada in the shell outline and profile and interiorly with a raised ventral muscle field, a low notothyrial platform and short brachiophores. The lack of sufficient material prevents meaningful comparisons with other species. In the Ordovician, the genus *Nothorthis* was a cosmopolitan taxon with occurrences in Laurentia (Floian to Sandbian), Baltica (Dapingian), Gondwana (upper Tremadocian), South China (Floian to Darriwilian), Kazakhstan (Floian) and Siberia (Floian to Darriwilian).

Family Tarfayidae Popov et al., 2009

Remarks. The family Tarfayidae was established for the genera *Tarfaya* and *Xianorthis* by Popov et al. (2009). They noted that *Tarfaya* was impunctate although otherwise similar to the punctate heterorthids and platyorthids. Within the orthidines the genus is probably most similar to the Plaesiomyidae and probably gave rise to a separate lineage of endopunctate brachiopods (Benedetto & Munoz, 2017).

Genus *Tarfaya* Havlíček, 1971

Type species. Tarfaya marocana Havlíček, 1971 from the Fezouata Shale, Floian, Ordovician, Anti-Atlas, Morocco.

***Tarfaya marocana* Havlíček, 1971**

Figure 16D–G, I–J

Material and horizon. 21 ventral and 26 dorsal valves from localities 34 and 51.

Description. Ventri-biconvex shell, subcircular in outline; cardinal angles round and obtuse; anterior commissure unisulcate; sulcus originating at umbo. Ventral valve with carina; interarea apsacline, gently concave; delthyrium open, triangular. Dorsal valve with interarea long, flat, triangular, anacline, extending anteriorly for 10% of valve length; notothyrium open, triangular. Ornamentation consisting of costellae branching by intercalation, numbering 4 per mm medianly at 5 mm growth stage; space between costellae wider than costellae.

Ventral interior with short, stout dental plates, extending anteriorly for 15% of valve length, flanking approximately the posterior half of the muscle scars; muscle scar non differentiated, extending anteriorly for 33% of valve length; small callus bounding muscle scar anteriorly.

Dorsal interior with brachiophores blade-like, widely divergent; cardinal process simple, blade-like, developed on elevated notothyrial platform; cardinal process higher anteriorly than posteriorly; notothyrial platform not undercut; dental sockets deep; median septum narrow, blade-like, developed anteriorly from notothyrial platform and seem to prolong anteriorly the cardinal process; cardinal canals preserved as tubular casts along the cardinal angles; median septum extending anteriorly for mid valve length; quadripartite adductor muscle scars, comprising a pair of deep postero-lateral scars inserted just anterior to the notothyrial platform, and a pair of shallow antero-medial scars flanking the median septum; adductors scars extending anteriorly up to almost mid valve length.

Remarks. The genus is characterised by the preservation of the internal expression of the distal extremities of costellae, along the commissure, from one cardinal angle to the other. The younger genus *Tissintia* Havlíček (1970) from Bolivia, Morocco and Wales presents a similar feature.

The specimens described by Havlíček (1971) were collected at Jbel el-Khannfra (locality 983; *locus typicus*), south of the Zini Mountain Range, Tarfaya Province from the lower Floian part of the Fezouata Shale. The present sample was collected some 600 km north-east of the type specimens, from the middle and upper Floian at Bou Chrebeb, 30 km NNE of Zagora and at Taakil, 50 km NNW of Zagora, respectively. There are no morphological differences between the two samples, which are regarded as conspecific.

Tarfaya **sp.**

Figure 16H, K–L, O

Material and horizon. Four ventral and three dorsal valves from locality 17.

Description. Ventri-biconvex shell, subcircular in outline; cardinal angles round and obtuse; anterior commissure unisulcate; sulcus originating at umbo. Ventral valve with carina; interarea apsacline, gently concave, extending anteriorly for 10% of valve length; delthyrium open, triangular. Dorsal valve with interarea short, flat, triangular, anacline, extending anteriorly for 7% of valve length; notothyrium open, triangular.

Ornamentation consisting of costellae branching by intercalation, numbering 4 per mm medianly at 5 mm growth stage; space between costellae wider than costellae.

Ventral interior with short, stout dental plates, extending anteriorly for 15% of valve length, flanking approximately the posterior half of the muscle scars; scars triangular, not differentiated, extending anteriorly for less than 25% of valve length; small callus bounding muscle scar anteriorly.

Dorsal interior with short, blade-like, divergent brachiophores; cardinal process short, simple, blade-like, developed on elevated notothyrial platform; notothyrial platform not undercut; dental sockets deep; median septum broad, more like a ridge, developed anteriorly from notothyrial platform, and extending anteriorly for mid valve length; adductor muscle scars non differentiated developed just anterior to the notothyrial platform and flanking the median septum; adductors scars extending anteriorly for 45% of valve length.

Remarks. The specimens from the sample collected on the hill north of Ouaoufrout show few differences from the sample collected from the Floian localities, identified as *Tarfaya marocana*. Although having similar ornamentation, the Tremadocian specimens are smaller, but also have shorter ventral muscle scars, shorter dorsal interarea, smaller cardinal process, shorter notothyrium platform with respect to the valve dimensions. The sample from the Tremadocian may represent a new species of *Tarfaya* on the basis of the differences noted above, but it is not clear whether these differences are only due to the smaller size (possibly juvenile) of the specimens. Therefore, the specimens are left under open nomenclature; more material is required to potentially identify a new species.

Superfamily Plectorthoidea Schuchert & LeVene, 1929

Family Plectorthidae Schuchert & LeVene, 1929

Genus *Plectorthis* Hall & Clarke, 1892

Type species. Orthis plicatella Hall, 1847 from the Trenton Group, Sandbian to early Katian, Ordovician, New York State, USA.

***Plectorthis*? cf. *simplex* Havlíček, 1971**

Figure 14H–L

Material and horizon. Three ventral and two dorsal valves, 10 undifferentiated valves from localities 17 and 33.

Description. Shell subcircular in outline about 85% as long as wide, and biconvex in profile. Ornament consisting of coarse ribs, round in section, as wide as interspace, numbering 2 per mm at 5mm growth stage; wave-length 0.7 to 0.9 mm; about 26 costae in total.

Ventral valve with short, curved, apsacline interarea extending for about 12% of valve length; dental plates thin subparallel to gently divergent anteriorly, extending for 25% of valve length, bounding laterally undifferentiated muscle scar; muscle scar triangular, elongate, delimited anteriorly by small callus.

Dorsal valve interior not preserved.

Remarks. Plectorthis simplex Havlíček is a well-established species, from the lower part of the Fezouata Formation (Tremadocian). It was described by Havlíček (1971) from a locality south-west of Jbel Tijakhet (Destombes locality 1540), south of Tafilalt region, about 160 km ENE of Zagora. The present specimens were collected about 25 km NW of Zagora. The material described here is considered conspecific with Havlíček's species. The Plectorthidae are relatively rare at this level and the material lacks some key characteristics of the genus, for example the cardinalia are not known, and on the shell surfaces the double rows of aditicules and capillae appear absent. These latter features are not always apparent, and some species lack these; their preservation is commonly dependent on the grain size of the matrix. The general shape and macro-ornament suggest *Plectorthis* but the assignment to that genus is tentative. The species is thus described as *Plectorthis*? cf. *simplex* pending the recovery of more informative material.

Genus *Nanorthis* Ulrich & Cooper, 1936

Type species. Orthis hamburgensis Walcott, 1884 from the Manitou Limestone, Tremadocian, Ordovician, Colorado, USA.

Remarks. Williams & Harper (2000) placed *Nanorthis* within the family Nanorthidae Havlíček, 1977. In the last volume of the revised Treatise, Harper (2007) reviewed the taxa in this family and re-assigned *Nanorthis* to the superfamily Plectorthoidea and the family Plectorthidae, placing the Nanorthidae with the Archaeorthidae. Benedetto (2007) offered a revision of the family Nanorthidae, in which he included *Nanorthis*, but kept Nanorthidae in the superfamily Plectorthoidea. Ghobadipour *et al.* (2011) followed Benedetto's (2007) comments and recommendations. In this paper, we follow Harper (2007) and keep *Nanorthis* within the family Plectorthidae.

***Nanorthis* sp.**

Figure 14M–S

Material and horizon. Seventeen ventral and 15 dorsal valves from localities 1, 5, 7, 8, 17, 24, 25, 27, 29, 51, 55 and 56.

Description. Shell ventri-biconvex in profile (both valves shallowly convex), subcircular in outline; maximum width at mid valve length; anterior commissure sulcate; hinge line straight; cardinal angles obtuse. Ventral interarea apsacline, convex and short, extending for 8% of valve length. Dorsal interarea anacline, short, extending for 10% of valve length; notothyrium open. Ornament ramicostellate, with costellae separated by deep and wide interspaces; costae high and angular, flanked by angular costellae, more slender and lower in height.

Ventral interior characterised by a triangular, elongated, undifferentiated muscle scar, elevated on shell thickening; muscle scar extending anteriorly for 35% of valve length; dental plates low, fused to valve floor; short, stout teeth; crural fossettes small, no fulcral plates.

Dorsal interior characterised by an elevated notothyrial platform with cardinal process as a faint, thin ridge; brachiophores blade-like, extending for 17% of valve length; dental sockets small, cup-like; notothyrial platform merging anteriorly with broad, rounded median ridge; quadripartite adductor scars, extending anteriorly for over half of valve length, consisting of a pair of suboval postero-lateral scars just anterior of the platform, and a pair of elongate antero-median scar, flanking the median ridge.

Remarks. The Moroccan material is assigned to *Nanorthis*. The specimens differ from the genus *Gondwanorthis* Benedetto & Muñoz, 2017. That genus was introduced to differentiate species of *Nanorthis* described from NW Argentina from the other species of *Nanorthis*, based on differences in ornament, morphology of the cardinalia, ventral muscle scars and dorsal adductor scars, in particular the bilobed anterior pair. Benedetto & Muñoz (2017) also included the Iranian species *bastamensis*, described by Ghobadi Pour *et al*. (2011), within *Gondwanorthis*. The Moroccan species possess brachiophores converging onto the valve floor, a very low median ridge, and unilobed anterior adductor scars (as in type specimens *Nanorthis hamburgensis* (Walcott, 1884) from the Tremadocian of western USA), which are diagnostic of *Nanorthis*. *Nanorthis hamburgensis* differs from the Moroccan species in having a shorter ventral muscle scar, in adductor scars extending anteriorly for slightly longer and a denser ramicostellate ornamentation.

Barrande (1868) described *Nanorthis bavarica* from the Lower Ordovician of Hof in Bavaria (Germany), based on two poorly preserved specimens. The illustration of one of these shows a deformed ventral valve, therefore the description of the species is based on this valve representing an exterior. No comparisons can be drawn. Havlíček (1949; reillustrated in 1977) described *Nanorthis rara* from the Třenice Formation (Tremadocian) in Bohemia, however, the Moroccan specimens show a more ramose ramicostellate ornamentation. Laurie (1980) described a new species from the Florentine Valley Formation (Lower Ordovician) of southern Tasmania, but *N. carinata* is characterised by a transverse outline. The Moroccan sample includes too few specimens to enable a new species to be erected. However, the material collected clearly indicates that it may represent a new species. In the meantime, these specimens are best left in open nomenclature. *Nanorthis* is regarded as a cosmopolitan genus. It has, however, never been recorded from the Moroccan regions of marginal Gondwana.

Family Euorthisinidae Havlíček, 1977

Genus *Euorthisina* Havlíček, 1950

Type species. Orthisina moesta Barrande, 1879 from the Šárka Formation, Darriwilian, Ordovician, Bohemia, Czech Republic.

***Euorthisina* sp. 1**

Figure 15A–D

Material and horizon. One ventral and one dorsal valve from localities 47 and 59.

Description. Shell subcircular in outline, convex in profile with maximum convexity at posterior end of ventral and dorsal valves. Dorsal valve with broad, shallow sulcus. Ornament consisting of fine costellae, numbering 5 per mm measured 3 mm from posterior margin; costellae numbering in total 38-40 at three-quarters of valve length measured from the posterior end; ornament bifurcating in posterior half of the valve; wave length of costellae 0.3 mm measured medianly at anterior margin; 5 costellae are developed in the sulcus.

Ventral interior with arcuate, subparallel dental plates, extending anteriorly for less than 25% of valve length; muscle field elongate, constricted laterally by dental plates and anteriorly by small callosity; muscle field extending for 25% of valve length.

Dorsal interior characterised by short septalium extending anteriorly for 5-6% of valve length, supported by slender median septum extending anteriorly for 10% of valve length.

***Euorthisina* sp. 2**

Figure 15E–J

Material and horizon. Two ventral and one dorsal valves from localities 31 and 33.

Description. Shell transversely oval in outline, convex in profile with maximum convexity at posterior end of both ventral and dorsal valves, the anterior and lateral sides are shallower; maximum width at mid valve length; cardinal angle obtuse and round. Ornament ramicostellate, with coarse costellae, round in section, bifurcating at different stages of growth, but anteriorly from mid valve, numbering 3 per mm, measured 3 mm from posterior margin; costellae numbering in total 28-30 at three-quarters of valve length measured from the posterior end; ornament asymmetrical on both left and right sides of valves; wavelength of costellae 0.8 mm medianly at anterior margin; fine concentric filae intersecting the radial ornament.

Ventral valve with interarea apsacline, short, curved extending anteriorly for 12% of valve length; delthyrium wide, open, 10% as wide as valve width. Dorsal valve with interarea short, orthocline or gently anacline, extending for 5% of valve length, notothyrium open.

Ventral interior with sickle-shaped, arcuate dental plates extending anteriorly for almost 40% of valve length, supporting simple teeth; dental plates normal to valve floor; muscle scar delimited laterally by dental plates; muscle scar lanceolate, extending for 25% of valve length, with thin pair of diductor scars flanking elongate adductor scar; adductor scar bounded anteriorly by small callosity and divided by very thin longitudinal furrow.

Dorsal interior with fused converging crural plates to form a narrow and short septalium, extending for 5-8% of valve length, and supported by a slender, short median septum extending anteriorly for 20% of valve length; adductor scar not preserved.

Remarks. The genera *Euorthisina* and *Notorthisina* are very similar, but according to Villas *et al.* (2009), can only be differentiated with confidence by the arrangement of their dental plates. Radial ornamentation is very variable across the two genera, therefore this feature cannot be regarded as a character to differentiate the genera. The septalium, which is supported by a thin septum in *Euorthisina* and by a median ridge in *Notorthisina* is similarly not a valid diagnostic character to differentiate the genera, according to Villas *et al.* (2009). The specimens described here belong to the genus *Euorthisina* based on the subparallel dental plates.

The genus *Euorthisina* has been described from the South China palaeoplate, peri-Gondwanan terrane (Bohemia, Bolivia, Peru, NW Argentina and Morocco but from the Darriwilian Tachilla Formation) and Eastern Avalonia (Shropshire, England). Although the material collected is scarce, the Tremadocian and Floian specimens can be separated on account of the finer and denser ornament, shorter dental plates and shorter dorsal median septum in the Tremadocian specimens.

In Morocco, Havlíček (1971) recorded *Euorthisina minor* Havlíček, 1950 in the Tachilla Formation (Darriwilian) from the area of Sarho and Tafilalt. Both samples described here from the Fezouata Shale are clearly different from the younger Moroccan species and the conspecific sample from the Šárka Shale (Darriwilian) in Bohemia and the Mytton Flags Formation (middle to upper Floian) in Shropshire, England. The specimens from the Fezouata Shale (Tremadocian and Floian) do not have an ornamentation of high, strong narrow ribs, and possess a finer, denser ornament than those of *E. minor*.

Euorthisina sp. 2 possesses similar rounded radial ornament that divides only exceptionally than *E. moesta* and *E. moesta sarkaensis*, both from the Šárka Shale in Bohemia, but the interiors of both valves in the present Moroccan sample are different. The dental plates and septalium extend for longer relative to the respective valve length in the Moroccan sample. Havlíček & Branisa (1980) have described two species from the Obispo Shale (Dapingian) in Bolivia, namely *E. kobayashii* and *E. orthiformis* (the latter also described by Gutiérrez-Marco & Villas (2007) from the lower part of San Jose Formation (upper Floian) in Peru). These are different from both samples from the Fezouata Shale mainly on account of a coarser ornament and internally, both the dental plates and the septalium do not extend as far anteriorly with respect to the valve length.

Benedetto (1998, 2007) described two samples; *E.* sp. from the lower Floian Acoite Formation and *E.*? *nazarenensis* from the upper Tremadocian Santa Rosita Formation, respectively, in north-western Argentina. These differ from the Tremadocian and Floian Moroccan species on the basis that they do not possess hollow costellae. The specimens described from the Acoite Formation look similar to *Euorthisina* sp. 2, but in the latter the dorsal valves are not sulcate. Moreover, no ventral valves are described from north-western Argentina. Three species, *E. multicostata* Xu, Rong & Liu, 1974*, E. parva* Xu & Liu, 1984 and *E. paucicostata* Xu & Liu, 1984, have been described from the Yingpan Formation (uppermost Floian-Dapingian) in south-western China. *Euorthisina parva* is unlike the Moroccan species in their external ornament which is characterised by few, strong costae (about 15). *Euorthisina paucicostata* is characterised by angular costae with sharper ridges than in *E. multicostata*. *Euorthisina* sp. 2 possesses similar ornament to *E. multicostata* with rounded ramicostellae that often bifurcate at the anterior third of the valve, near the commissure. However, internally, the dental plates do not extend anteriorly for as long in the Chinese species than in *E.* sp.2, although the dorsal median septum extends for as long in both species. Muscle scars are also well defined in the Moroccan species with clear differentiation between the adductor scar and the diductor scars, whereas the muscle scars in the Chinese species are weak and undifferentiated.

Family Giraldiellidae Williams & Harper, 2000

Genus *Kvania* Havlíček, 1994

Type species. Nothorthis kvanica Mergl, 1984 from the Mílina Formation, Tremadocian, Ordovician, Bohemia, Czech Republic.

***Kvania* sp.**

Figure 15K–L

Material and horizon. One dorsal valve from locality 1.

Description. Dorsal valve subcircular, about 75% as long as wide, with maximum width at mid valve length; valve convex with maximum convexity in posterior fifth of valve length; cardinal angles obtuse and rounded; broad shallow sulcus 45% as wide as valve at anterior commissure; ornamentation fascicostellate with up to three orders of costellae; costellae round in profile, numbering 3 per mm medially at the anterior commissure; interspace between costellae of the same amplitude as costellae; costellae fanning out laterally, anterior to 45% of valve length.
Interior characterised by cardinalia elevated on broad U-shaped, short notothyrial platform, extending anteriorly for 5% of valve length, supported by broad median ridge, shallowing and broadening anteriorly; cardinal process absent; brachiophores indistinct, possibly broad. Adductor scars oval but undifferentiated and faintly impressed, extending for about 30% of valve length, flanking the broad median ridge.

Remarks. The type species for the genus erected by Havlíček (1994), *Nothorthis kvanica* from the Mílina Formation (upper Tremadocian) in Central Bohemia, 50 km south-west of Prague, has been thoroughly described and discussed by Mergl (1984). Subsequently, *Kvania* has been recorded by Villas in Sdzuy *et al.* (2001) from the Vogtendorf Formation (upper Tremadocian) of Bavaria, Germany (as *K. kvanica* (Mergl, 1984) but reidentified as *K. mergli* by Benedetto, 2007), and several species were erected by Benedetto (2007) from the uppermost Cambrian (although with caveats as it is a morphologically transitional form; see p. 277) and the Lower Ordovician of Argentina. These are *Kvania*? *primigenia* from the Lampazar Formation (uppermost Cambrian) in the Puna region, *K. lariensis* from the lower part of the Vicuñas Formation (uppermost Cambrian?-lowermost Ordovician) in the Puna region, *K. azulpampensis azulpampensis* from the uppermost Casayok Formation and lowermost Azul Pampa Formation (lower

Tremadocian) in the Jujuy Province, and *K. azulpampensis dichotoma* from the Cardonal Formation (lower Tremadocian) in the Jujuy Province.

The present specimen is morphologically closest to *K. mergli* from the upper Tremadocian of Bavaria than to any other species. However, it differs in its ornament (fascicostellae are round rather than high and angular as in *mergli*), and the position and size of the notothyrium platform (more posterior and shorter in the Moroccan specimen). The Moroccan specimen may be a new species but is left on open nomenclature as the paucity of the material prevents establishing a new taxon with confidence.

Family Ranorthidae Havlíček, 1949

Genus *Tinzoulinorthis* gen. nov.

LSID. https://zoobank.org/xxxxxxxxxxx

Type species. By original designation; *Tinzoulinorthis fasciata* (Havlíček, 1971) from the Floian at Jbel el-Khannfra (locality 983; *locus typicus*), south of Zini Mountain Range, Tarfaya Province Morocco.

Derivation of name. After the nearby palm grove of Tinzouline, located about 30 km NW of Zagora.

Diagnosis. Genus with ventral valve semicircular and dorsal valve transversely oval in outline; delthyrium and notothyrium open; ventral valve with muscle scar raised on callosity; dorsal valve sulcate with broad median ridge.

Discussion. This genus is included in the family Ranorthidae, based on the ramicostellate ornament, short ventral interarea, triangular muscle field, and divergent brachiophores lacking supporting plates. The genus is comparable to *Ranorthis* Öpik, 1939 but differs in many important features: see Remarks below for additional detail.

Tinzoulinorthis fasciata **(Havlíček, 1971)**

Figure 15M–S

Material and horizon. Sixteen ventral and 17 dorsal valves from localities 9, 20, 24, 26, 34, and 51.

Description. Shell strongly ventri-biconvex; ventral valve semicircular about 80% as long as wide and over 20% as deep as long; delthyrium open; dorsal valve transversely oval about 70% as long as wide, strongly sulcate, gently convex; sulcus almost 40% as wide as maximum valve width; notothyrium open. Ornament ramicostellate, with 25-30 costellae in total; 4 costellae in dorsal sulcus, arising by branching from the costellae bounding the sulcus, parallel to the medial axis of the valve; 5 costellae on ventral fold; median rib strong and slightly more angular in ventral valve, flanked by a pair of two second order ribs; costellae numbering 4 per mm at anterior margin.

Ventral interior with short, convex interarea, apsacline; muscle field triangular, extending anteriorly for about 25% of valve length, with narrow adductor scar flanked by a pair of diductor scars; *vascula media* strongly divergent, developed anteriorly to the muscle scar.

Dorsal interior with very short interarea, anacline; cardinal process small, blade-like, on stout notothyrial platform; brachiophores stout, short, triangular in section, and widely divergent; dental sockets cup-like, broadly triangular; median ridge broad and developed as the internal counterpart of the sulcus; adductor scars oval, consisting of a pair of thin postero-lateral and a pair of thin antero-medial scars extending anteriorly not further than 40% of valve length.

Remarks. Havlíček (1971) described the new species *Ranorthis fasciata* collected from the Fezouata Shale, at Jbel el-Khannfra (locality 983; *locus typicus*), south of Zini Mountain Range, Tarfaya Province from the lower Floian and also at Bou-Dhir, north of Zagora (locality 1157) from the lower part of the *Sagenograptus murrayi* zone (upper Tremadocian). Unfortunately, dorsal valve interiors were not illustrated; nevertheless, a description of the characters was provided. Complementary material is fully illustrated here. There is no morphological difference between Havlíček's (1971) material and the newly collected material described here.

The type species *Ranorthis norvegica* Öpik, 1939 from the Darriwilian Expansus Shale (now Lysaker Member of the Huk Formation, see Owen et al. 1990), is characterised by a strongly carinate ventral valve ("glockenförmig" – bell-shaped – of Öpik's (1939, p. 120) diagnosis), a deep dorsal valve sulcus and a long, strong dorsal median septum. The ventral valve is triangular in outline due to its strong carinate profile. Species of *Ranorthis*, from Baltica, were collected from the Floian and Dapingian, and species from Argentina and Iran were collected from the Floian (Benedetto 2002) and the Tremadocian (Popov et al 2009), respectively. The species from Bohemia (Tremadocian and Floian; Havlíček 1977), Bavaria (Tremadocian; Sdzuy et al. 2001) and the Montagne Noire, France (Floian; Babin et al. 1982) that are assigned to *Ranorthis*, like the specimens from the Fezouata Shale in Morocco (Havlíček 1971), they are not carinate but possess a deep dorsal sulcus (except for the Bavarian species). Moreover, the ventral valve is semicircular in outline. The dorsal interiors are not characterised by a long and strong median septum, but rather by a broad median ridge mirroring the sulcus. Based on these similar characteristics, the species from Bohemia, Bavaria, the Montagne Noire and Morocco are better included within the same new taxon *Tinzoulinorthis*.

Moreover, there are strong similarities with *Ranorthis parvula* (Lamansky, 1905) revised by Rubel, 1961 from the Floian of Estonia. The Estonian species is not carinate like typical *Ranorthis* species, but like *Tinzoulinorthis* possesses a subcircular ventral valve and a broad dorsal median ridge mirroring the sulcus. Therefore, we provisionally include *R. parvula* in *Tinzoulinorthis* pending further study.

***Tinzoulinorthis*? sp.**

Figure 16A–C

Material and horizon. Two ventral valves exteriors and interiors (p+cp) from locality 63.

Description. Valves small, convex, subcircular, about 80-85% as long as wide, and less than 15% as deep as long; maximum convexity in posterior half of valve; anterior commissure rectimarginate. Ornamentation consisting of high and round fascicostellae, numbering 4 per mm at anterior commissure.
Interior with short, triangular muscle scar, extending for 15% of valve length, impressed on callus; dental plates subparallel.

Remarks. Identification is tentative here because of the paucity of the material and poorer preservation. The two ventral valves are tentatively assigned to the new genus *Tinzoulinorthis* on the basis of the ornamentation, the muscle scars supported by a callus and the shape of the dental plates.

Suborder Dalmanellidina Moore, 1952

Superfamily Dalmanelloidea Schuchert, 1913

Family Angusticardiniidae Schuchert & Cooper, 1931

Genus *Angusticardinia* Schuchert & Cooper, 1931

Type species. Porambonites recta Pander, 1830 from the Floian, Ordovician of Russia.

***Angusticardinia* sp.**

Figure 16M–N

Material and horizon. One ventral valve (part and counterpart) from locality 11.

Description. Valve small, oval in outline, convex in profile, 73% as long as wide. Sulcus originating near umbo, 25% as wide as valve width. Ornament consisting of 3 narrow costae per mm at commissure, wider intercostae, costae wave-length 400 µm. Internal impression of ventral muscle field, extending anteriorly for 25% of valve length.

Remarks. The generic identification of this specimen was made based on the rhynchonelloid valve shape and external ornament. It is very similar to *Angusticardinia recta* from Ingria (see Schuchert & Cooper 1931) and *A.? parva* from the Kolyma area, eastern Russia (Keller 1973) on the basis of the ornamentation and valve shape. The internal impression of the muscle scar is putative. More information will be taken from a wider collection when available. *Angusticardinia* is known from the Lower Ordovician of Ingria and Kolyma, Russia and of the Tallinn area, Estonia. Poorly preserved shell referred to *Angusticardinia* are also known from putative Tremadocian rocks in East Bohemia (Havlíček 1949).

Havlíček (1971, p. 66) described a single valve in the upper Fezouata Shale (Floian) from Tadrist (locality 1766 of Destombes), situated about 50 km north of Zagora, he identified as *Angusticardinia* sp., based on the ornamentation. The specimen collected by Havlíček (1971) and the present valve do not seem conspecific, based on the few morphological features available.

Family Heterorthidae Schuchert & Cooper, 1931

Genus *Incorthis* Havlíček & Branisa, 1980

Type species. Incorthis boliviana Havlíček & Branisa, 1980 from Darriwilian rocks, Ordovician, near San Lucas, Bolivia.

***Incorthis* sp.**

Figure 15T–V

Material and horizon. Four ventral and four dorsal valves; other valves undeterminable, from locality 11.

Description. Shell ventri-biconvex, with both ventral and dorsal valves gently convex; shell subcircular in outline; anterior commissure unisulcate; cardinal extremities obtuse; hinge line straight; maximum width anterior to mid valve length. Ventral valve with delthyrium open and interarea steeply apsacline. Ornamentation parvicostellate; costellae rounded, numbering 8-9 per 2mm at the 5 mm growth stage; fine concentric striations in interspaces.

Remarks. Unfortunately, no internal moulds were collected which would have allowed a more accurate comparison with other species of *Incorthis*. The identification is based on external features, especially the strophomenoid-like ornamentation intersected by fine concentric striations in interspaces (see Havlíček & Branisa 1980), the shape of the shell and the steeply apsacline interarea. Mergl (1988) described *Incorthis marocana* from the Floian of north-western Morocco but these are different from the studied specimens in their coarser ornament. Havlíček & Branisa (1980) described *Incorthis boliviana* from the Obispo Shale in southern central Bolivia, but these differ from the Moroccan specimens by a finer ornamentation. *Incorthis* sp. was described by

Benedetto (1994) from the Suri Formation (upper Floian) in Argentina, and its ornamentation is similar to that observed in the Moroccan specimens.

Superfamily Enteletoidea Waagen, 1884

Family Draboviidae Havlíček, 1950

Subfamily Draboviinae Havlíček, 1950

Genus *Nocturnellia* Havlíček, 1950

Type species. Orthis nocturna Barrande, 1879 from the Klabava Formation, Floian, Ordovician, Bohemia, Czech Republic.

***Nocturnellia* sp.**

Figure 16P–S

Material and horizon. One ventral and two dorsal valves from localities 1, 11, 44 and 58.

Description. Shell semioval, gently biconvex; shallow sulcus. Ornament parvicostellate by intercalation; costellae round, of irregular strength, numbering 4-5 per mm at the 2 mm growth stage.

Ventral interior with small muscle field, extending anteriorly for 20% of valve length, with a straight anterior margin; internal features are obscured by poor preservation.

Dorsal interior with thin, subparallel brachiophore supporting plates, slightly convex internally, delimiting muscle field; muscle field consisting of two pairs of elongately oval adductor scars, restricted to the posterior half of the valve and divided by a short median ridge extending anteriorly for 40% of valve length; two small hemispherical bulges present on slightly raised platform.

Remarks. Comparison with other taxa is difficult due to the paucity of the material. Nevertheless, observed internal features such as subparallel brachiophore supporting plates, a ventral triangular muscle field with a straight anterior margin and a wide, shallow dorsal sulcus, comparison with the genus *Nocturnellia* Havlíček, 1950 from the upper part of the Klabava Formation (upper Floian-Dapingian) in Bohemia. Havlíček (1977) described a new species *Nocturnellia bachori*, from the same level as *Nocturnellia nocturna* (Barrande, 1879). These were separated on the basis of size and ornamentation (*bachori* is smaller and possesses coarser ornamentation), and the anterior margin of the ventral muscle field is anteriorly curved in *bachori*, although these are likely synonyms. Therefore, the present specimens are closer to *nocturna*, but more material is needed to compare with confidence the two samples.

Conclusion.

This study describes 30 species representing 23 genera of Early Ordovician (upper Tremadocian to Floian) brachiopods from the well-known Fezouata Shale in the Zagora region, Morocco. Two distinct assemblages were recognized: an upper Tremadocian and a Floian. The upper Tremadocian fauna is characterized by high γ-diversity and low to medium α-diversity, coupled with diverse and disparate assemblages of alternating linguliformean and rhynchonelliformean taxa; it is more diverse than the Floian assemblage. In the late Tremadocian, the unstable and high-energy environmental conditions accounted for variations in these successive, short-lived, poorly diverse assemblages. These are interpreted as opportunistic communities regularly smothered in situ and killed by distal deposits. The high γ-diversity of the upper Tremadocian fauna is associated with an abundance of first occurrences and endemic taxa, suggesting the Fezouata assemblage may have been a hub for diversity. The Floian fauna, on the other hand, shows strong affinities with Bohemia and the Montagne Noire, but with also links to faunas in Baltica and the South Urals, in sympathy with changing Early Ordovician palaeogeography.

Acknowledgments. The authors are very grateful to all the colleagues who have provided help for this paper. We are particularly grateful to Susan Butts and Jessica Utrup (Yale Peabody Museum, New Haven, USA) for facilitating the visit of YC and DATH to the collections in their care, and for providing the loan of the material studied here. We are equally grateful to Bertrand Lefebvre and Emmanuel Robert (Université Claude Bernard 1, Lyon, France) for enabling access (for YC and DATH) to the Lyon collection during various research visits and for the loan of the material studied here, and to Khadija El Hariri (Université Cadi Ayyad, Marrakesh, Morocco) for providing access to the Marrakesh collection. Romain Vaucher, Emmanuel Martin and Farid Saleh, as well as the late Bernard Pittet are gratefully acknowledged for their help with plotting localities onto the composite log. YC would like to thank Renbin Zhan (NIGP (CAS)) for kindly providing translations of Chinese articles, and to Ross Anderson (NMS Library) for procuring essential scientific references. We are very grateful to Leonid Popov and an anonymous referee for comments and suggestions that greatly improved the manuscript. We are also grateful to Lesley Cherns for editing the manuscript. DATH acknowledges funding from the Leverhulme Trust (UK). YC thanks Bertrand Lefebvre for the invitation to participate to fieldwork in Morocco and acknowledges funds to travel to Morocco.

Author contributions. Conceptualization Y Candela (YC), DAT Harper (DATH); **Formal Analysis** DATH; **Investigation** DATH, YC; **Project Administration** YC, DATH, M Mergl (MM); **Visualization** YC; **Writing – Original Draft Preparation** YC, DATH, MM; **Writing – Review & Editing** YC, DATH, MM.

Data Archiving Statement. The published work and the nomenclatural acts it contains have been registered in ZooBank: https://zoobank.org/xxxxxxxxx. The data used in the network analysis and Nonmetric Multidimensional Scaling analysis are available in the Dryad Digital Repository:
https://doi.org/10.5061/dryad.h70rxwds9

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Table. List of the localities investigated. For the Marrakesh collection, the localities are listed chronologically then by horizon number. For the Yale Peabody Museum collection, the localities are listed chronologically then by alphabetical order.

Figure 1. General map of Morocco (A), locating the Ordovician outcrops distributed along the Anti-Atlas (B), as well as the field area (black box around Zagora) shown in more detail on Figure 2. Redrawn after Destombes et al. (1985) and Lefebvre et al. (2016c). The Taichoute locality [TA-F1] is located on this map, but is located out of the frame of Figure 2.

Figure 2. Map of the study area showing the localities investigated (A) – detail of localities in text – with enlargement of the area north of Beni Zoli (B), where fieldwork had concentrated. Enlarged area shown with a black box in A. Base map by Google Map using the terrain filter: Map data ©2023 Google, https://maps.app.goo.gl/8kcLhffZpWCKbZkN6.

Figure 3. Two slabs showing *Celdobolus mirandus* on sample AA-FETg-oi-1 (A) and *Lingulella lata*? on sample AA-FETg-oi-2 (B), both in horizon Z-F2(3g) showing monotaxic high density of material. Scale bars: 5 mm.

Figure 4. Composite, synthetic log of the Lower Ordovician Fezouata Shale succession, plotting (A) the Tremadocian brachiopod fauna and (B) the Floian brachiopod fauna. The log was based on fieldwork undertaken mainly by the late Bernard Pittet, and with the help of Emmanuel Martin and Romain Vaucher. Redrawn from Lefebvre et al. (2018) and including taxonomic updates by Maletz et al. (2017). First column = Formation; Second column = Age; Third column = Graptolite biozones.

Figure 5. Non-metric multidimensional scaling (NMDS) plot of the Tremadocian brachiopod fauna from the Fezouata Shale with coeval brachiopod assemblages from

Laurentia, Baltica, Siberia, Avalonia and Gondwana, using the software package PAST (Hammer et al., 2001), with the Raup-Crick similarity coefficient.

Figure 6. Graphical output of network analysis using GEPHI (Bastian et al. 2009) of the Tremadocian brachiopod fauna from the Fezouata Shale with coeval brachiopod assemblages from Laurentia, Baltica, Siberia, Avalonia and Gondwana. The diameter of circles reflects the relative diversity of the faunas. Endemic taxa in purple.

Figure 7. Non-metric multidimensional scaling (NMDS) plot of the Floian brachiopod fauna from the Fezouata Shale with coeval brachiopod assemblages from Laurentia, Baltica, Avalonia and Gondwana, using the software package PAST (Hammer et al., 2001), with the Raup-Crick similarity coefficient. *Abbreviations: eSvalb : East Svalbard (Laurentia), Greenl : Greenland (Laurentia), Miss : Mississippi (Laurentia), Nev : Nevada (Laurentia), Nwfdland : Newfoundland (1 = Avalonia; 2 = Laurentia), Skye = Scotland (Laurentia), Tenn : Tennessee (Laurentia), Tex : Texas (Laurentia).*

Figure 8. Graphical output of network analysis using GEPHI (Bastian et al. 2009) of the Floian brachiopod fauna from the Fezouata Shale with coeval brachiopod assemblages from Laurentia, Baltica, Avalonia and Gondwana. The diameter of circles reflects the relative diversity of the faunas. Endemic taxa in purple. Same abbreviations as in Figure 7.

Figure 9. A–C. *Sedlecilingula* sp. A, a ventral valve interior, YPM IP 531534 from Tigzigzaouine, 799-800m. B, a ventral interior, YPM IP 521429 from Ezegzaou Hill, 837 m. C, dorsal valve interior, YPM IP 531688 from Bou Glf, 800 m. D–H. *Lingulella lata?* Koliha, 1924*.* D, a dorsal valve interior, YPM IP 525461 from Ezegzaou, 839 m. E–F, a ventral valve interior and its counterpart, YPM IP 523767 from Bou Zorgan. G–H, ventral and dorsal valve interiors and counterparts, YPM IP 531801, from Tigzigzaouine, 793 m. I–J. *Paldiskites* aff. *sulcatus* (Barrande, 1879). A dorsal valve exterior and interior

counterpart, UCBL-FSL 713629, from locality TA-F1, Taichoute, *?Baltograptus jacksoni* zone. K–O. *Wosekella maghribi* sp. nov. K, Holotype, a ventral valve interior, AA_TGR1c_OI_155. L, Paratype, a dorsal valve interior, AA_TGR1c_OI_102. M–O, backscattered SEM micrographs showing valve surface of AA_TGR1c_OI_155. Both specimens from Tamegroute, "Trou de Pierre", horizon Z-F51c, *Sagenograptus murrayi* zone. Scale bars represent: 5 mm (A–C); 2 mm (D, G–H, K–L); 1 mm (E–F, I–J); 200 µm (M); 50 µm (N); 20 µm (O).

Figure 10. A–F. *Wosekella filiola* Mergl, 2002. A, a ventral valve exterior, AA_OTIk_OI_1, coupe along the west bank of Oued Tarhia N'Imrhaldene, Z-F11k. B, F, a ventral valve interior and detail of pseudointerarea with pedicle groove, YPM IP 522712 from Bou Glf. C, D, a dorsal valve interior and detail, YPM IP 532417 from Bou Glf, 792 m. E, a dorsal and ventral valve interior, YPM IP 519367 from quarry/pit at site Ezegzaou 2, 2.9 km E of road, 12.9 km NNE on road NNE of Route N9 along the Draa Valley, approximately 25 km NW (by road) of Zagora, 862 m. G, H. *Glossella* sp. An exfoliated dorsal valve interior and detail of the external pustulose ornament, YPM IP 524709, from Bou Zorgan. I–J. *Rafanoglossa inversa sp*. nov. I–J, Holotype, a dorsal valve exterior and interior, YPM IP 525707 from Azizaoi = Ezegzaou. Scale bars represent: 2 mm (A, E, G, I–J); 1 mm (B–C, F, H); 100 µm (D).

Figure 11. A–C. *Rafanoglossa inversa sp*. nov. A, a dorsal valve interior, YPM IP 532261 from Bou Glf, 792 m. B–C, a ventral valve interior and detail of pseudointerarea with pedicle groove, YPM IP 521282 from a large (~20 m wide) quarry between Ezegzaou and Bou Glf, 809 m. D–E. *Spondyglossella*? sp. D, a ventral valve, AA-BZL-OI-54. E, a dorsal valve, AA_BZL_OI_107. Both specimens from Beni Zoli (4,9 km E of village), Zagora province; horizon Z-F3, *Sagenograptus murrayi* zone. F–I, K–L. *Thysanotos* cf. *siluricus* (Eichwald, 1840). F–H, a dorsal valve (G) and detail or ornament (F, H), AA-TISc-oi-28 from the southernmost south end of the west bank of Oued Tarhia N'Imrhaldene section, horizon Z-F12c, *Sagenograptus murrayi* zone. I, detail of microornament on

valve exterior, AA-TNA3-oi-4. K, a ventral valve interior, UCBL-FSL 713 630. Specimens on (I) and (K) from Touna, horizon Z-F15(3), *Sagenograptus murrayi* zone. L, a dorsal valve exterior, UCBL-FSL 713 632 from Bou Zargouan, horizon Z-F7, *Sagenograptus murrayi* zone. J. Obolidae gen. et sp. indet. A dorsal valve interior, YPM IP 530545 from Asif n'Moutn, near Beni Zoli, 775 m. Scale bars represent: 10 mm (K); 5 mm (G, L); 1 mm (A–B, D–E, H–I); 500 µm (C, F, J).

Figure 12. A–E. *Orbithele tazagurta* sp. nov. A, Holotype, a dorsal valve interior, YPM IP 518823 from exact quarry unknown, hillside at Ezegzaou 1. B–C, ventral and dorsal valve with counterparts of specimens AA-TGR0a-oi-89 and AA-TGR0a-oi-13, Tamegroute, horizon Z-F50a. D–E a ventral valve interior and counterpart, YPM IP 522682 from Bou Glf. F, I. *Orbithele* sp. 1. A ventral valve interior and detail of the pseudointerarea, FSL 711 960 from Toumiat, horizon Z-F26, *Cymatograptus? protobalticus* zone, lower Floian. G. *Orbithele* sp. 2. A dorsal valve interior, YPM IP 518152 from one of the quarries at Bou Glf, an area of excavation approx. 20 km N of Zagora; Upper Fezouata Formation, Floian. H, J. *Eurytreta* sp. Two dorsal valve interiors (H) and latex cast (J) of the valve at the bottom of image (H), YPM IP 518794 from Bou Glf 786 m. K–L. *Celdobolus mirandus* (Barrande, 1879). K, detail of dorsal pseudointerarea, YPM IP 521910 from Bou Glf. L, a ventral valve exterior showing extension of marginal spines, AA-TGR1c-oi-167, from Tamegroute, “trou de Pierre”, horizon Z-F51c, *Sagenograptus murrayi* Zone, upper Tremadocian. Scale bars represent: 5 mm (F); 2 mm (G, I); 1 mm (A–E, L); 500 µm (H, J–K).

Figure 13. A–H. *Celdobolus mirandus* (Barrande, 1879). A, a slab with concentration of disarticulated valves; with ventral valves(B, C) and dorsal valves(D, E, H) on specimen AA-FETg-oi-1, from the east side of Jbel Tizagzaouine section, level g, horizon Z-F2(3g), *Sagenograptus murrayi* Zone, upper Tremadocian. F, a dorsal valve exterior showing development of spines, AA-TGR2a-oi-2, Tamegroute, horizon Z-F52a, *Sagenograptus murrayi* Zone, upper Tremadocian. G, two ventral valve exteriors showing development

of spines, AA-JTZb-oi-14, southernmost part of Jbel Tizagzaouine (level a), horizon Z-F2(1a), *Sagenograptus murrayi* Zone, upper Tremadocian. I–L. *Lacunites punctum* sp. nov. Holotype, part and counterpart, YPM IP 523944 from Bou Glef. I, L, part, internal mould of dorsal valve and latex cast. J–K, counterpart, external mould of dorsal valve and latex cast. Scale bars represent: 10 mm (A); 2 mm (B, H–L); 1 mm (C–G).

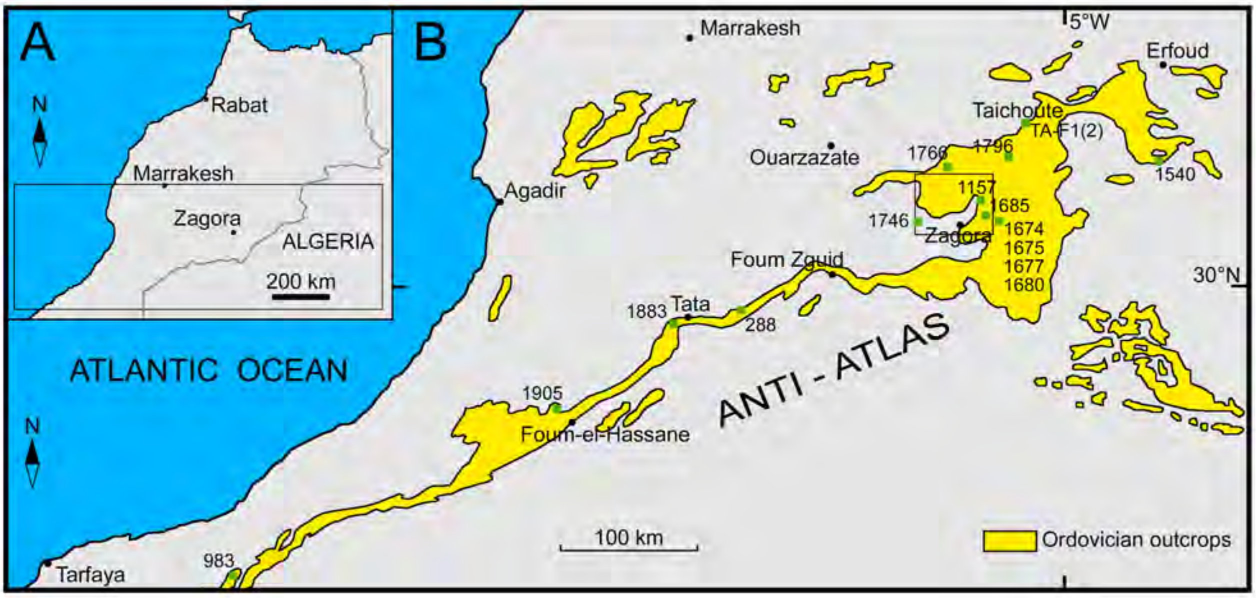
Figure 14. A–C. *Paralenorthis*? sp. A–B, group of several disarticulated valves. C, dorsal valve; all on specimen ML 20-269394, from Bou Chrebeb, horizon Z-F25a, *Baltograptus jacksoni* zone, middle Floian. D–G. *Nothorthis* sp. D–E, a ventral valve exterior and interior, AA-TGR3b-oi-2, Tamegroute, horizon Z-F53b, *Sagenograptus murrayi* zone, upper Tremadocian. F–G, a dorsal valve interior and latex cast, AA-CNOl-oi-7, hill north of Ouaoufraout, horizon Z-F13l, *Hunnegraptus copiosus* zone, upper Tremadocian. H–L. *Plectorthis*? cf. *simplex* Havlíček, 1971. H–I, a ventral valve exterior and latex cast. J–K, a ventral valve interior and latex cast, AA-CNOc-oi-25. L, a dorsal valve exterior, AA-CNOc-oi-10. All specimens from Hill north of Ouaoufraout, horizon Z-F13c, *Hunnegraptus copiosus* zone, upper Tremadocian. M–S. *Nanorthis* sp. M, a dorsal valve exterior on YPM IP 524231. N–O, a dorsal valve interior and latex cast on YPM IP 524231. P–S, a ventral valve exterior and latex cast, and the ventral interior counterpart and latex cast, AA-FETi-oi-2 from section of the eastern slope of Jbel Tizagzaouine (niveau i), Z-F2(3i), *Sagenograptus murrayi* Zone, upper Tremadocian. Scale bars represent: 2.5 mm (F–G); 2 mm (D–E, H–S); 1 mm (A–C).

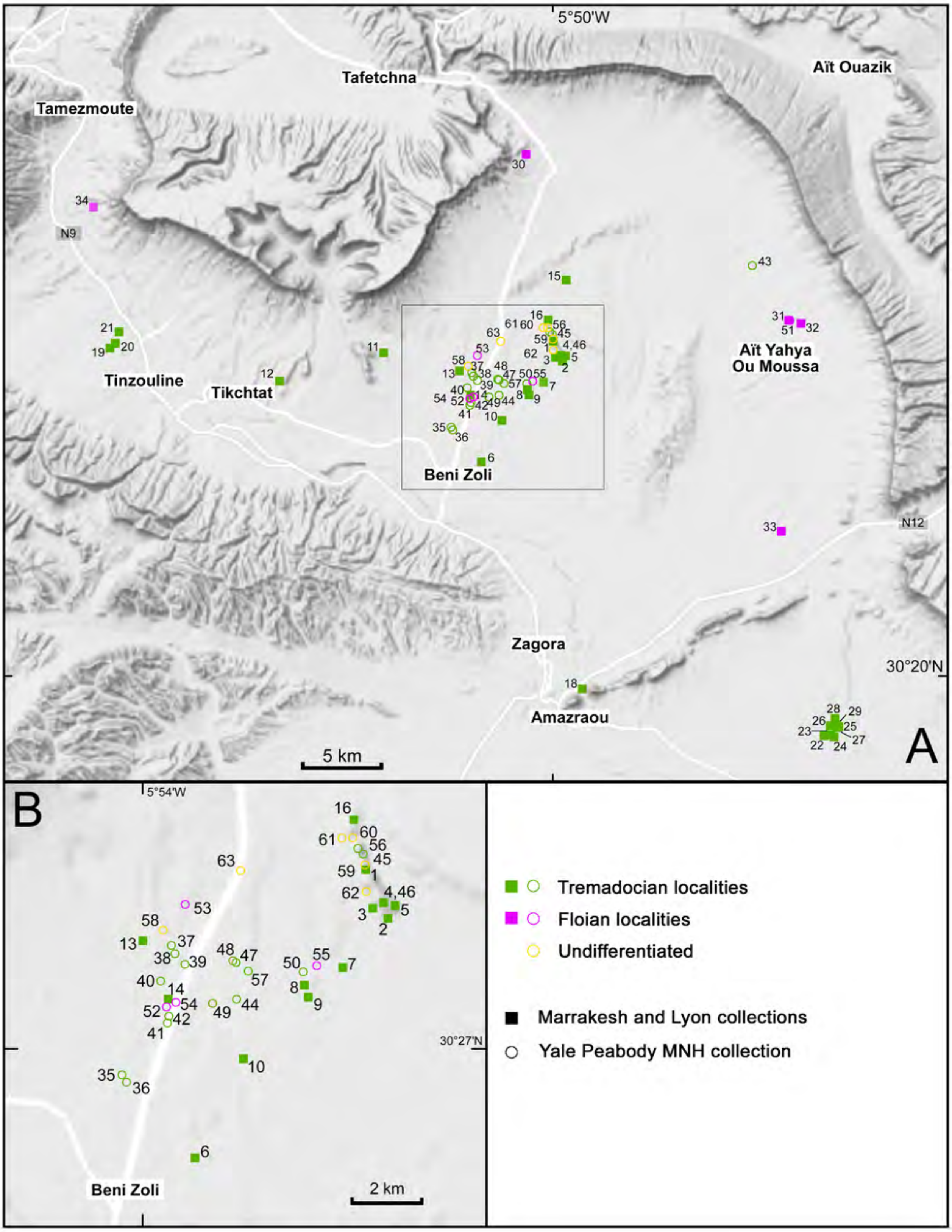
Figure 15. A–D. *Euorthisina* sp. 1. A, a ventral valve interior, YPM IP 521632, from a large quarry (~20 m wide) quarry between Ezegzaou and Bou Glf. B–D, a dorsal valve exterior, interior counterpart and detail of posterior margin, YPM IP 525779 from Azizaoi = Ezegzaou. E–J. *Euorthisina* sp. 2. E, I–J, a dorsal valve exterior, its interior counterpart and latex cast, YPM IP 520554 from Toujimot. F, a ventral valve interior, FSL 711653 from Toumiat, horizon Z-F26, *Cymatograptus? protobalticus* zone, lower Floian. G–H, a

ventral valve interior and latex cast, AA-BCBa-oi-7 from Bou Chrebeb, horizon Z-F25a, *Baltograptus? jacksoni* zone, middle Floian. K–L. *Kvania* sp. a dorsal valve interior and latex cast, AA-JTZ0c-oi-15 from Jbel Tizagzaouine pass section, level c, horizon Z-F2(0c), *Sagenograptus murrayi* Zone, upper Tremadocian. M–S. *Tinzoulinorthis fasciata* (Havlíček, 1971). M, a ventral valve exterior, AA-TIN1c-oi-5. N, a dorsal valve exterior, AA-TIN1c-oi-1. O, a ventral valve interior, AA-TIN1c-oi-1. P, a ventral valve interior, AA-TIN1c-oi-3. Q–R, a dorsal valve interior and latex cast, AA-TIN1c-oi-5. S, a dorsal valve interior, AA-TIN1c-oi-3. Specimens from Tinzouline, oued west of El Kasba, position c, horizon Z-F42c, *Sagenograptus murrayi* Zone, upper Tremadocian. T–V. *Incorthis* sp. T, a ventral valve exterior. U, a dorsal valve exterior. V, a slab with several specimens of ventral and dorsal valves.All from the same slab, AA-OFTa-oi-13 from Ouaoufraout, lower level, horizon Z-F6a, *Sagenograptus murrayi* Zone, upper Tremadocian. Scale bars represent: 5 mm (V); 2 mm (E–L, T–U); 1 mm (A–C, M, O–S); 500 µm (N); 250 µm (D).

Figure 16. A–C. *Tinzoulinorthis*? sp. A, a ventral valve interior, YPM IP 520766. B, C, a ventral valve exterior and internal counterpart, YPM IP 519526. Both specimens from Tamagroute. D–G, I–J. *Tarfaya marocana* Havlíček, 1971. D, a ventral valve exterior (partly exfoliated revealing the interior), YPM IP 519194. E, dorsal valve exterior, YPM IP 519010; specimens on (D) and (E) from Bou Chrebeb. F, a ventral valve interior, AA-TKL3-oi-4. G, a dorsal valve interior, AA-TKL9-oi-1. I–J, a dorsal valve interior and latex cast, AA-TKL9-oi-1; specimens on (F–G, I–J) from Taakil, Z-F46(3), between ‘*Azygograptus* interval’ and *?Baltograptus minutus* zones, upper Floian. H, K–L, O. *Tarfaya* sp. H, K, a ventral valve exterior and interior counterpart, AA-CNOr-oi-6. L, a dorsal valve interior, AA-CNOm-oi-6. O, a dorsal valve exterior, AA-CNOq-oi-1. All specimens form Hill north of Ouaoufraout, horizons Z-F13r, q, m, *Hunnegraptus copiosus* zone, upper Tremadocian. M–N. *Angusticardinia* sp. A ventral valve mould and latex cast, AA-OFTa-oi-78, Ouaoufraout, horizon Z-F6, zone with *Sagenograptus murrayi* Zone, upper Tremadocian. P–S. *Nocturnellia* sp. P–Q, a dorsal valve interior and latex cast, AA-OFTa-oi-49, Ouaoufraout, lower level, horizon Z-F6a; R–S, Ventral valve exterior

(cast and mould), AA-JTZ-oi-159 + 84, Jbel Tizagzaouine pass section, level c, horizon Z-F2(0c); both specimens from zone with *Sagenograptus murrayi* Zone, upper Tremadocian. Scale bars represent: 5 mm (E); 2 mm (D, F–L, O, R–S); 1 mm (A–C, M–N, P–Q).


A
N
Rabat
Marrakesh
Zagora
ALGERIA
200 km
ATLANTIC OCEAN
N
Tarfaya
983
B
Marrakesh
5°W
Erfoud
Taichoute
TA-F1(2)
1766
1796
Ouarzazate
1540
Agadir
1157
1685
1746
Zagora
1674
1675
1677
1680
Foum Zguid
30°N
1883
Tata
288
ANTI - ATLAS
1905
Foum-el-Hassane
100 km
Ordovician outcrops


5°50'W
Tafetchna
Aït Ouazik
Tamezmoute
30
34
N9
43
15
16
61 60
56
45
63
53
59
4,46
62
5
3
2
58
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13
38
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47
50 55
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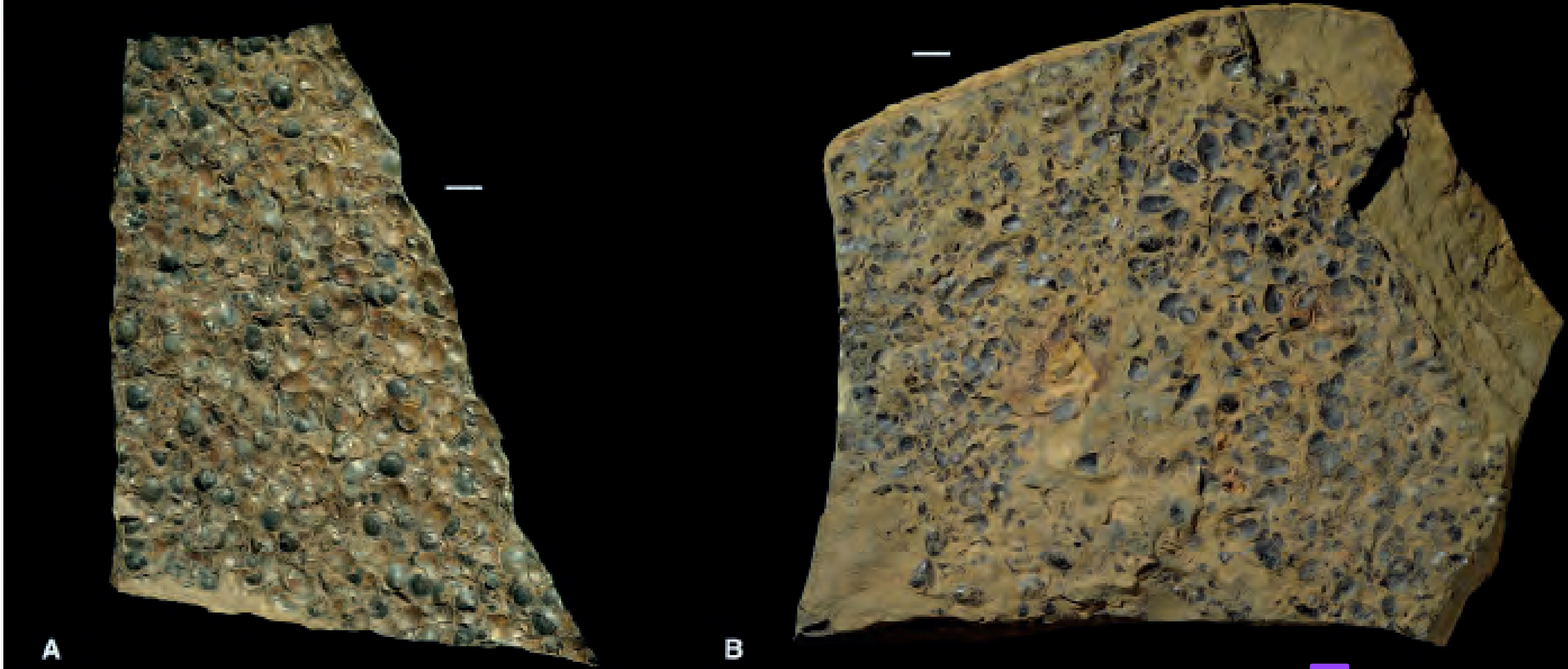
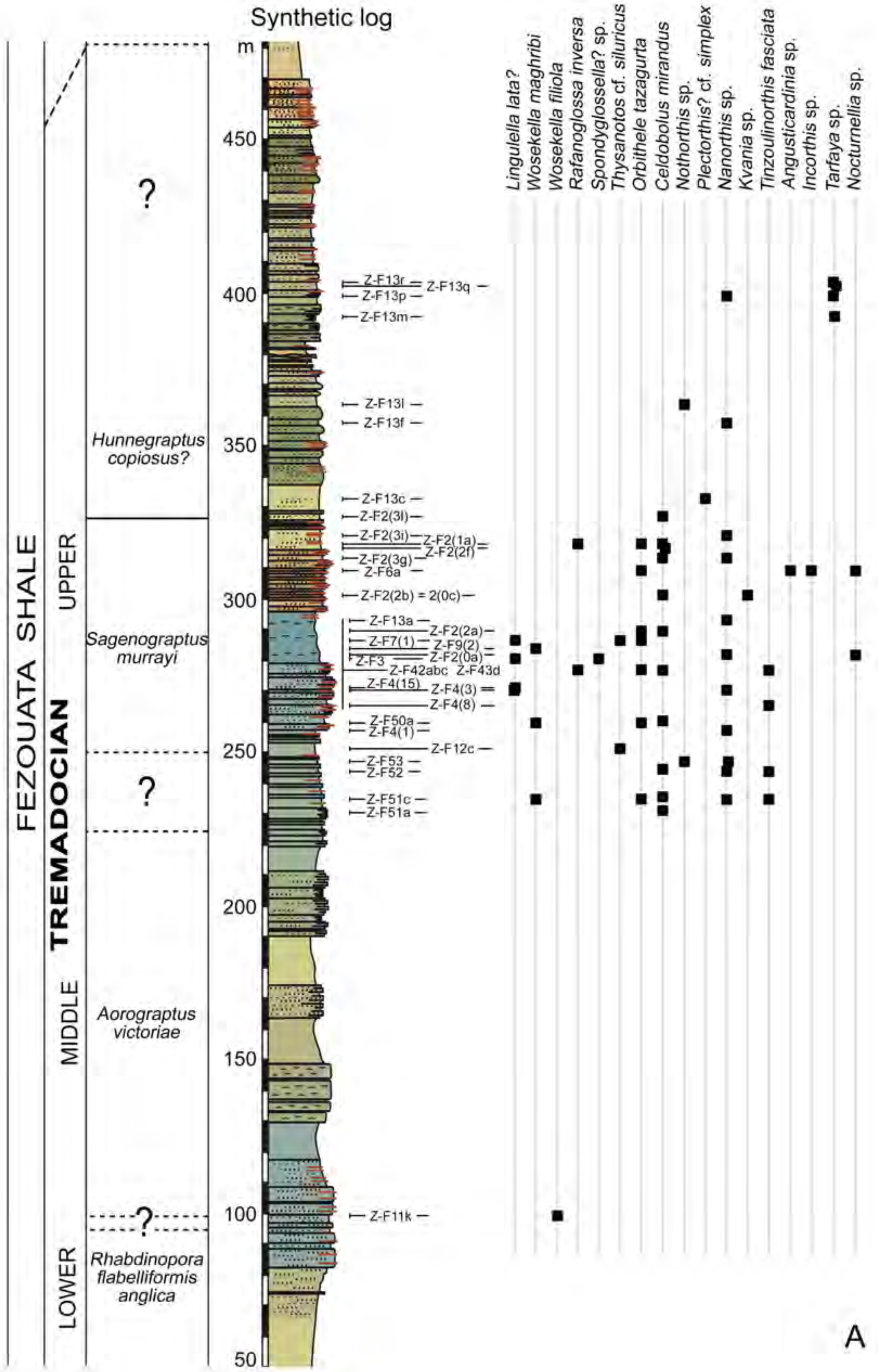
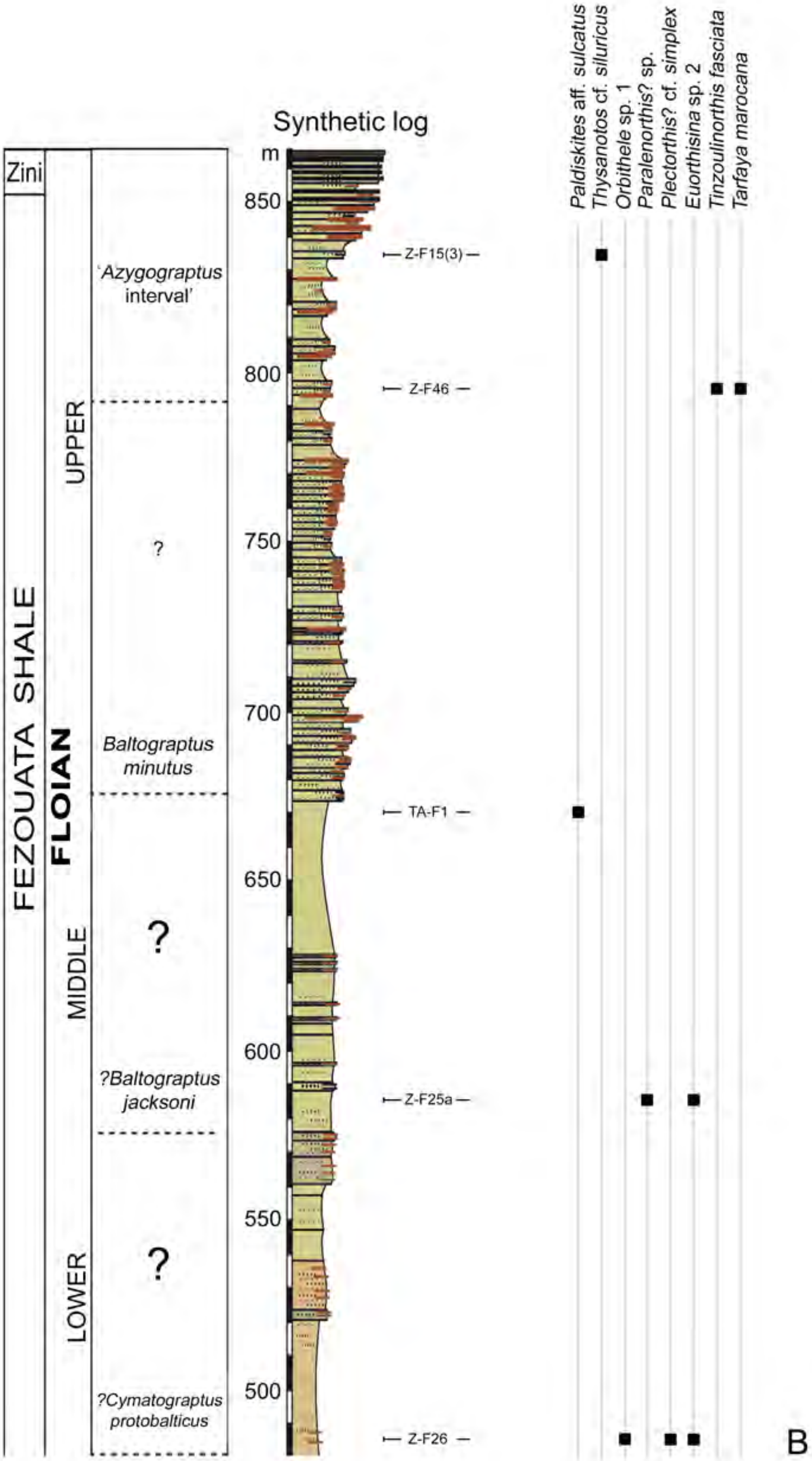
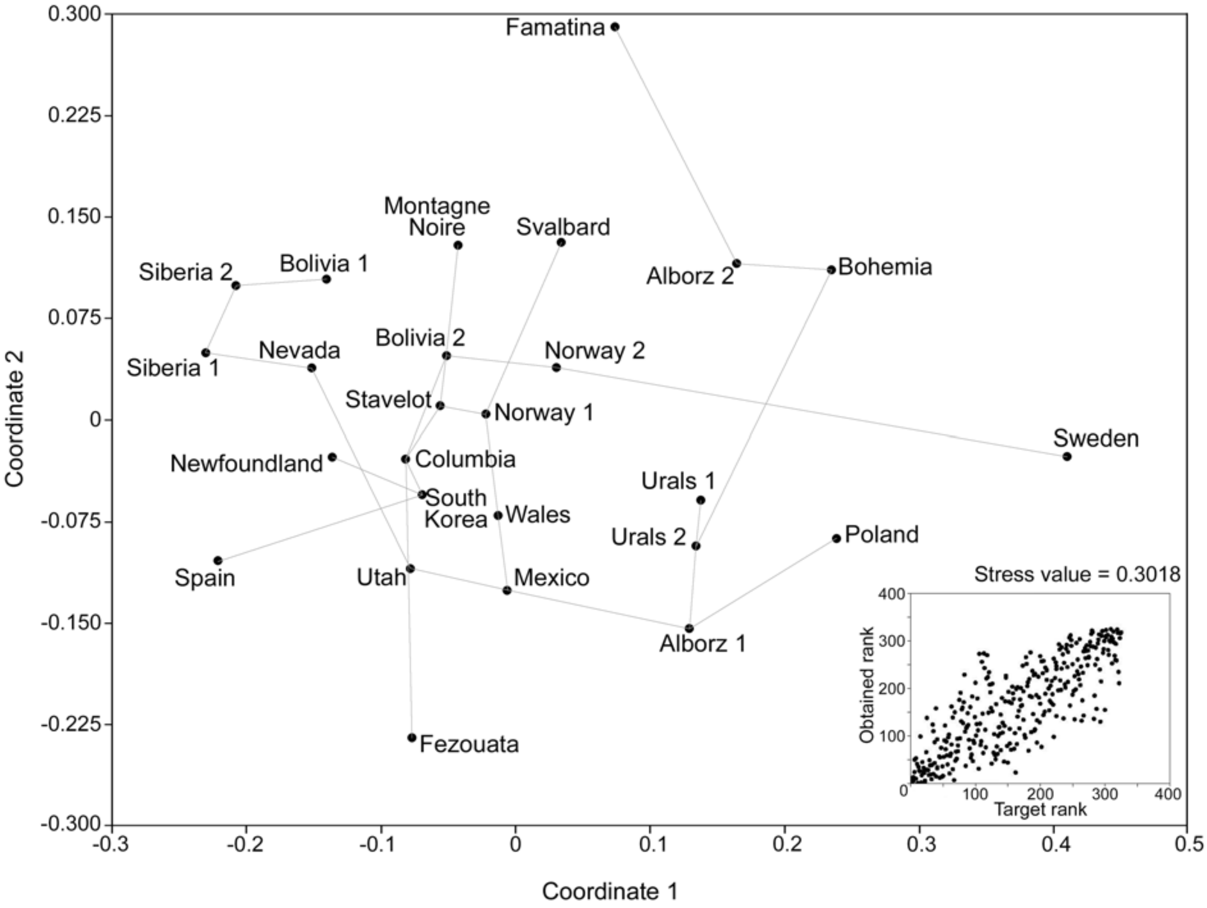
39
57
40
8
54
52
14
49 44
9
42
41
10
35
36
6
Beni Zoli
11
12
21
19
20
Tinzouline
Tikchtat
31
51
32
Aït Yahya Ou Moussa
33
N12
Zagora
18
Amazraou
30°20'N
28
29
26
25
23
22
24
27
5 km
A
B
5°54'W
1
30°27'N
2 km
Tremadocian localities
Floian localities
Undifferentiated
Marrakesh and Lyon collections
Yale Peabody MNH collection


A
B


Synthetic log
FEZOUATA SHALE
TREMADOCIAN
LOWER
MIDDLE
UPPER
Rhabdinopora flabelliformis anglica
?
Aorograptus victoriae
?
Sagenograptus murrayi
Hunnegraptus copiosus?
?
m
50
100
150
200
250
300
350
400
450
Z-F11k
Z-F51a
Z-F51c
Z-F52
Z-F53
Z-F12c
Z-F4(1)
Z-F50a
Z-F4(8)
Z-F4(3)
Z-F4(15)
Z-F42abc
Z-F43d
Z-F3
Z-F2(0a)
Z-F9(2)
Z-F7(1)
Z-F2(2a)
Z-F13a
Z-F2(2b) = 2(0c)
Z-F6a
Z-F2(3g)
Z-F2(2f)
Z-F2(1a)
Z-F2(3i)
Z-F2(3l)
Z-F13c
Z-F13f
Z-F13l
Z-F13m
Z-F13p
Z-F13r
Z-F13q
Lingulella lata?
Wosekella maghribi
Wosekella filiola
Rafanoglossa inversa
Spondyglossella? sp.
Thysanotos cf. siluricus
Orbithele tazagurta
Celdobolus mirandus
Nothorthis sp.
Plectorthis? cf. simplex
Nanorthis sp.
Kvania sp.
Tinzoulinorthis fasciata
Angusticardinia sp.
Incorthis sp.
Tarfaya sp.
Nocturnellia sp.
A


Synthetic log
m
850
800
750
700
650
600
550
500
Zini
FEZOUATA SHALE
FLOIAN
LOWER
MIDDLE
UPPER
'Azygograptus interval'
?
Baltograptus minutus
?
?Baltograptus jacksoni
?
?Cymatograptus protobalticus
Z-F15(3)
Z-F46
TA-F1
Z-F25a
Z-F26
Paldiskites aff. sulcatus
Thysanotos cf. siluricus
Orbithele sp. 1
Paralenorthis? sp.
Plectorthis? cf. simplex
Euorthisina sp. 2
Tinzoulinorthis fasciata
Tarfaya marocana
B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Svalbard
Siberia 2
Bolivia 1
Alborz 2
Bohemia
Bolivia 2
Norway 2
Siberia 1
Nevada
Stavelot
Norway 1
Sweden
Newfoundland
Columbia
Urals 1
South Korea
Wales
Urals 2
Poland
Spain
Utah
Mexico
Alborz 1
Fezouata
Stress value = 0.3018
Obtained rank
Target rank
0
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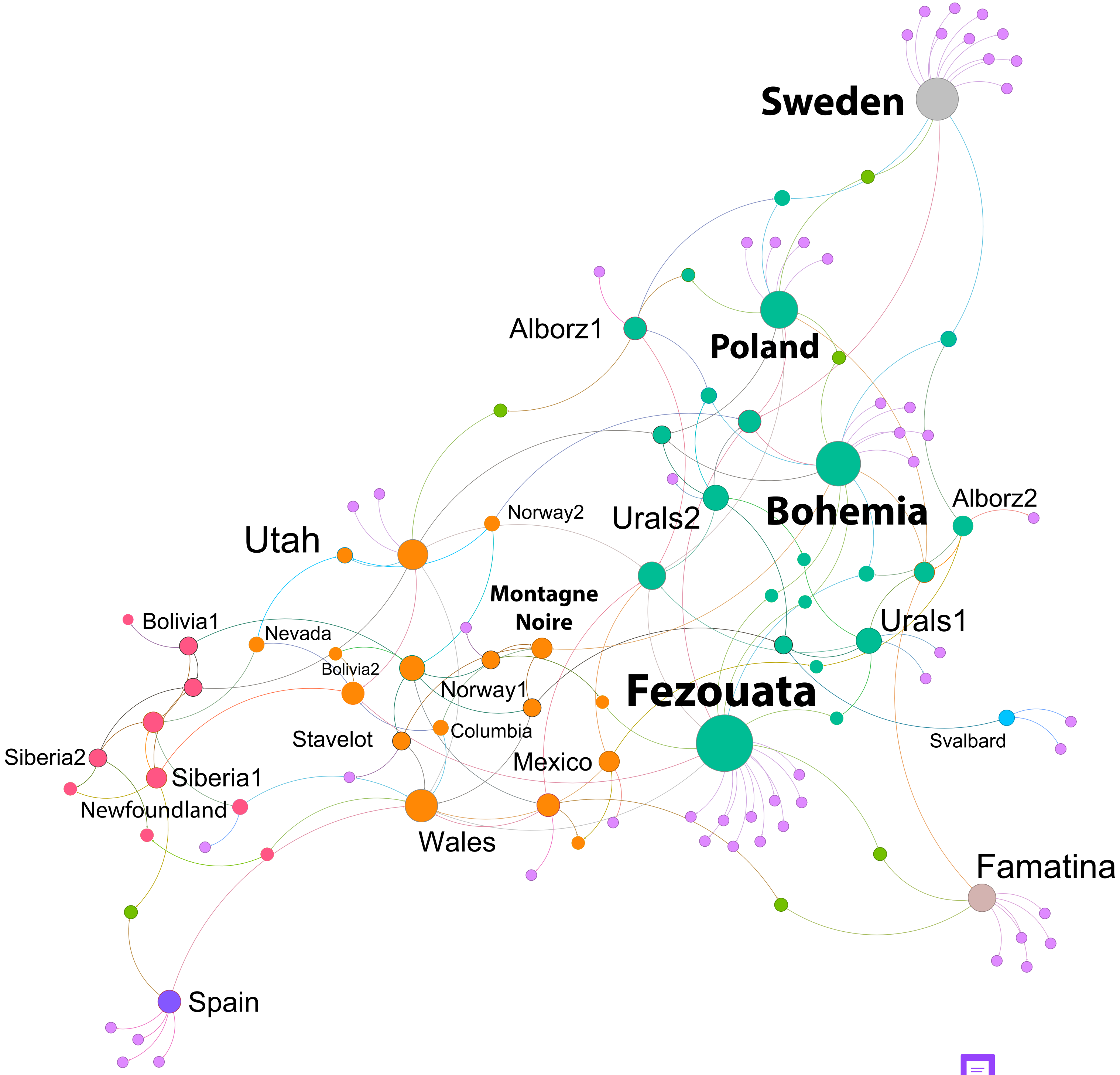
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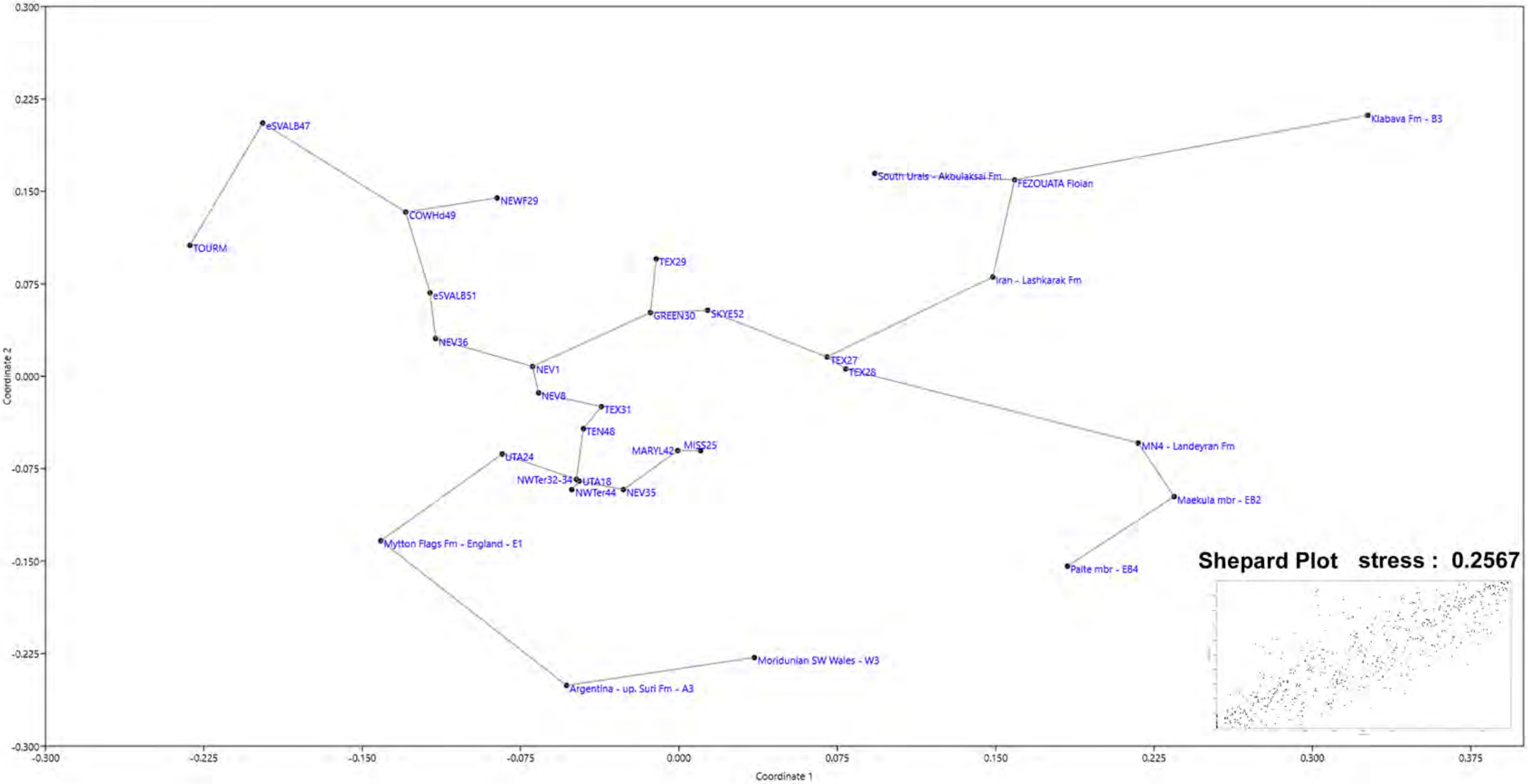
Svalbard
Newfoundland
Wales
Famatina
Spain



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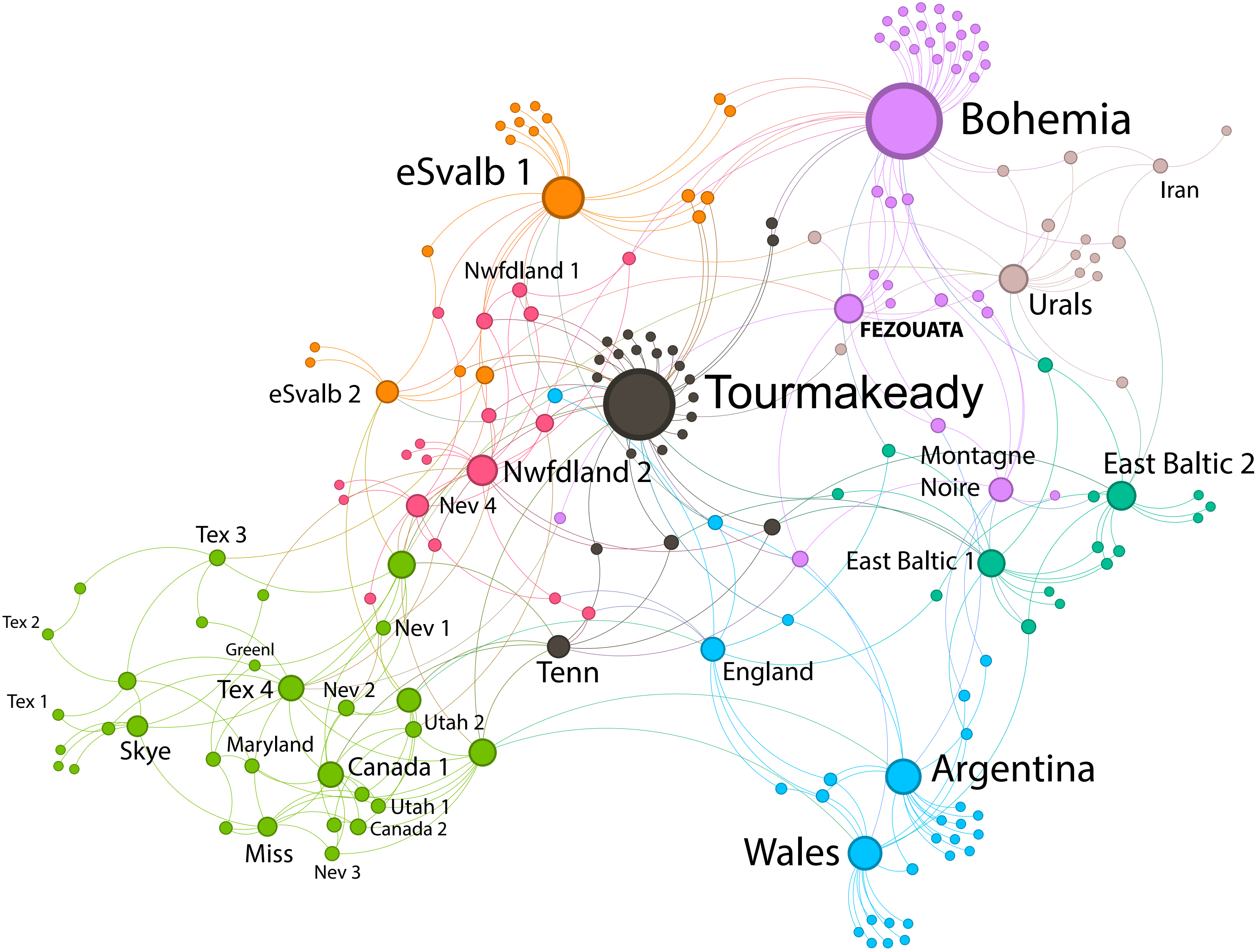
NEWF29
eSVALB51
NEV36
NEV1
NEV8
TEX31
TEN46
TEX29
GREEN30
SKYE52
TEX27
TEX28
MARYL42
MISS25
UTA24
NWTer32-34
UTA18
NWTer44
NEV35
Mytton Flags Fm - England - E1
Argentina - up. Suri Fm - A3
Moridunian SW Wales - W3
South Urals - Akbulaksai Fm
FEZOUATA Floian
Klabava Fm - B3
Iran - Lashkarak Fm
MN4 - Landeyran Fm
Maekula mbr - EB2
Palte mbr - EB4
Shepard Plot stress : 0.2567


Bohemia
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Iran
Nwfdland 1
Urals
FEZOUATA
eSvalb 2
Tourmakeady
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Nwfdland 2
Nev 4
Tex 3
East Baltic 1
Tex 2
Nev 1
Greenl
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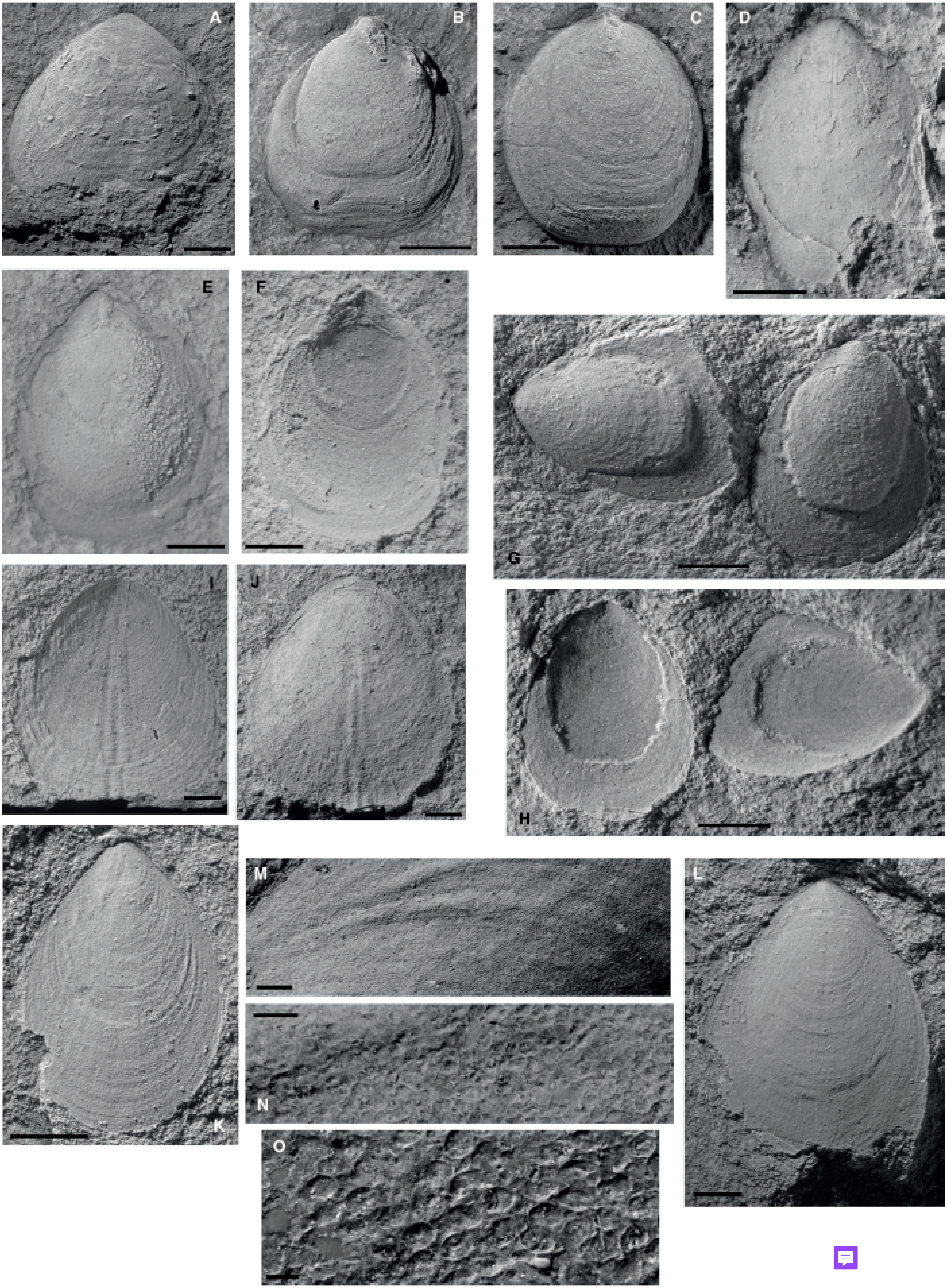
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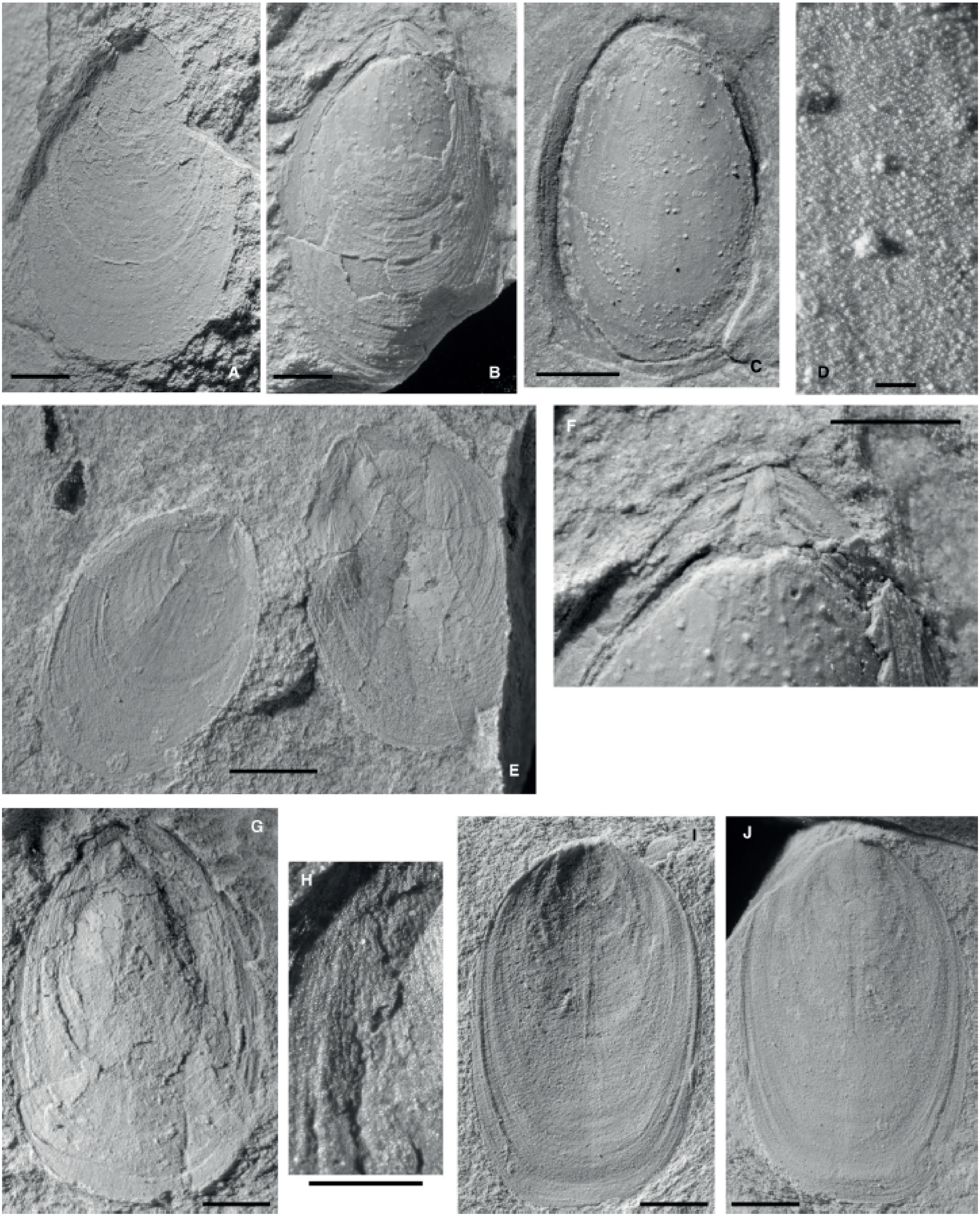
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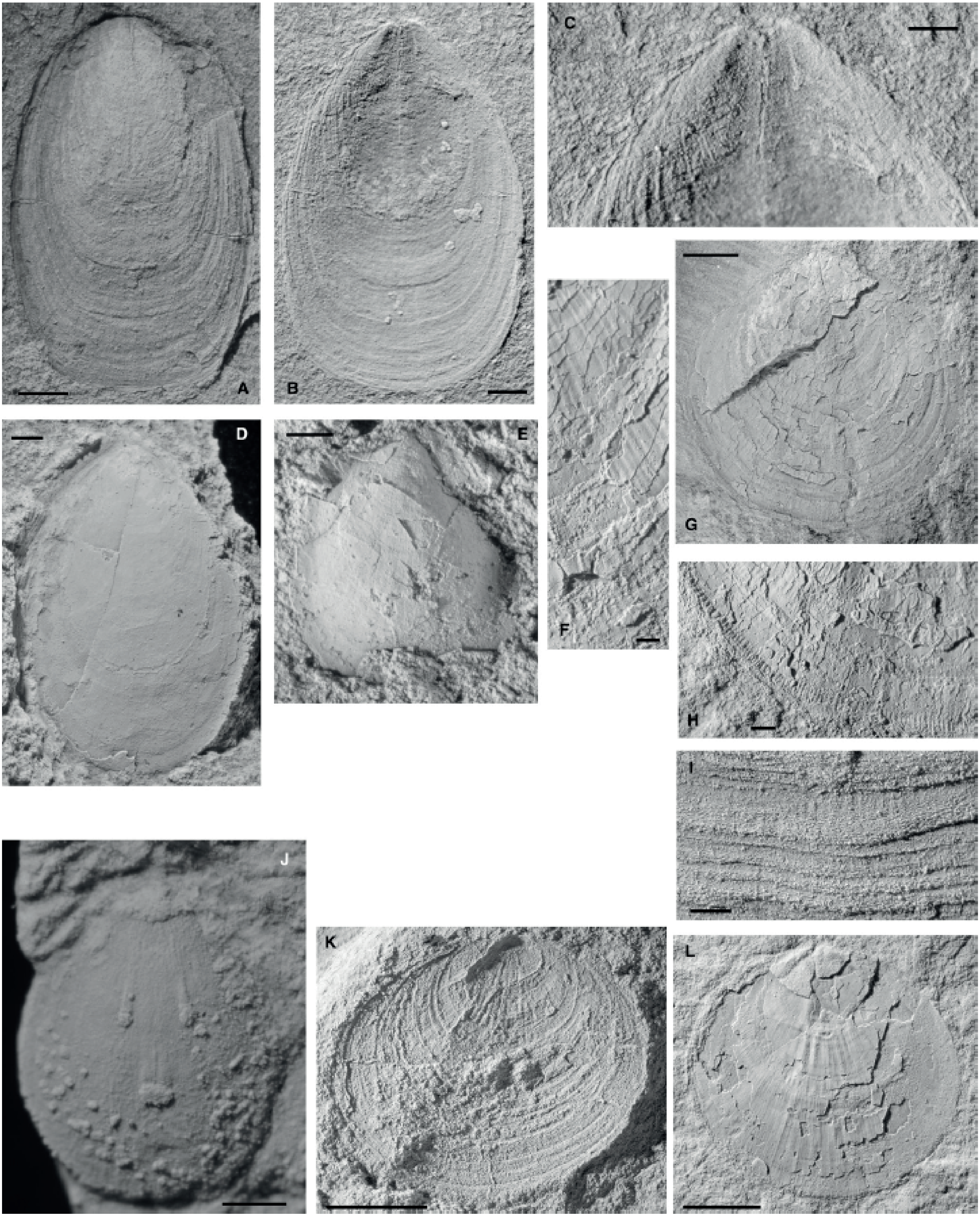
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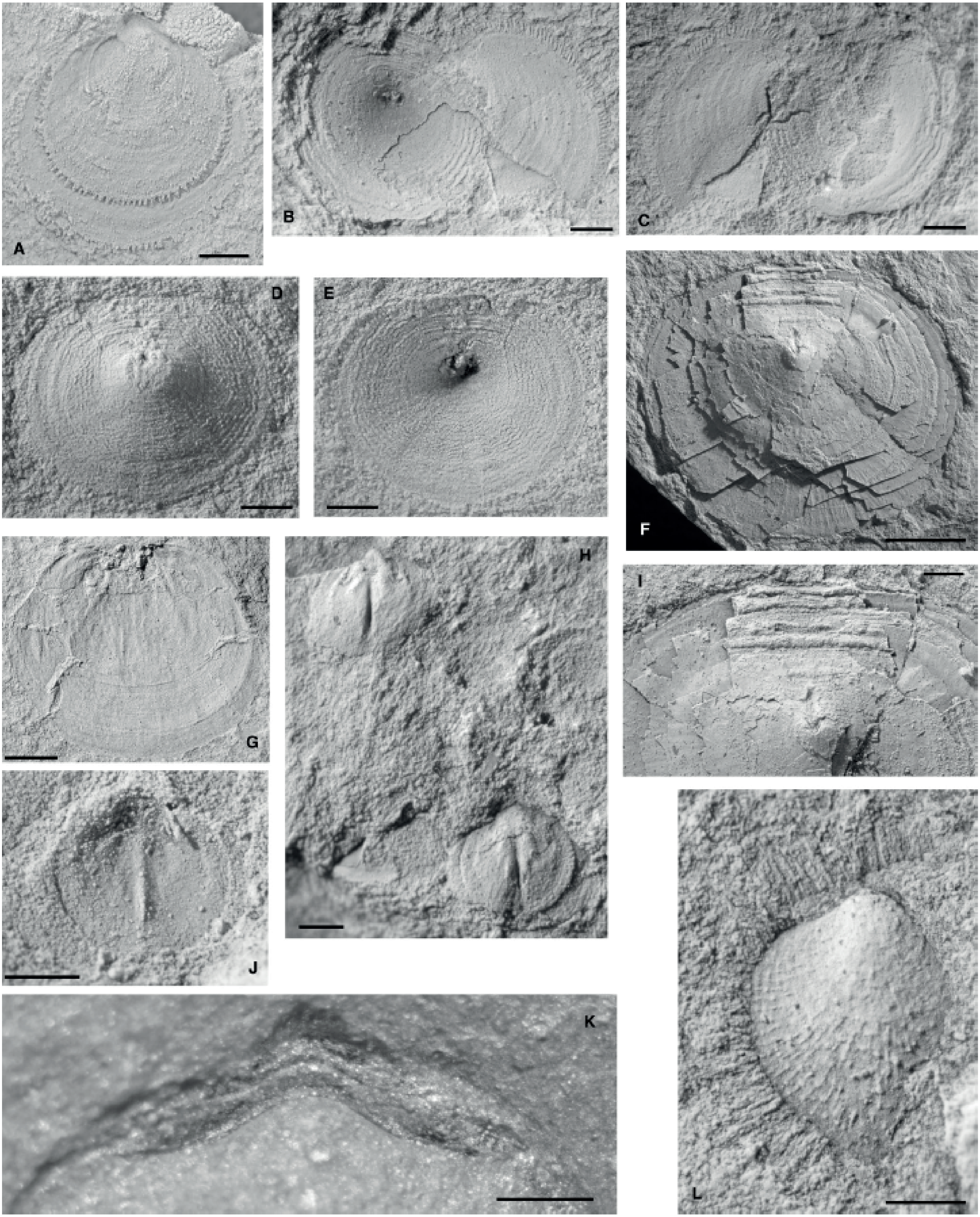
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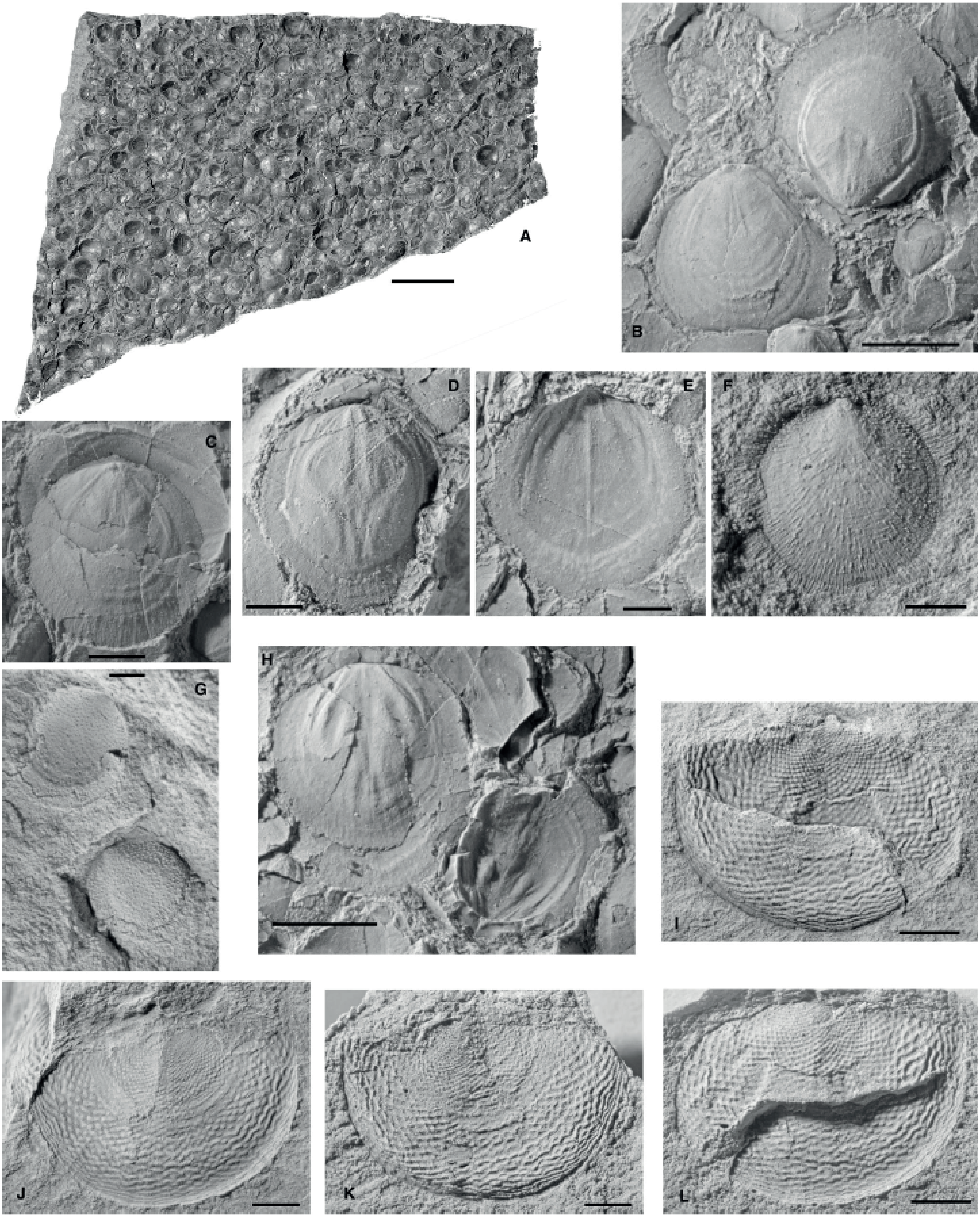
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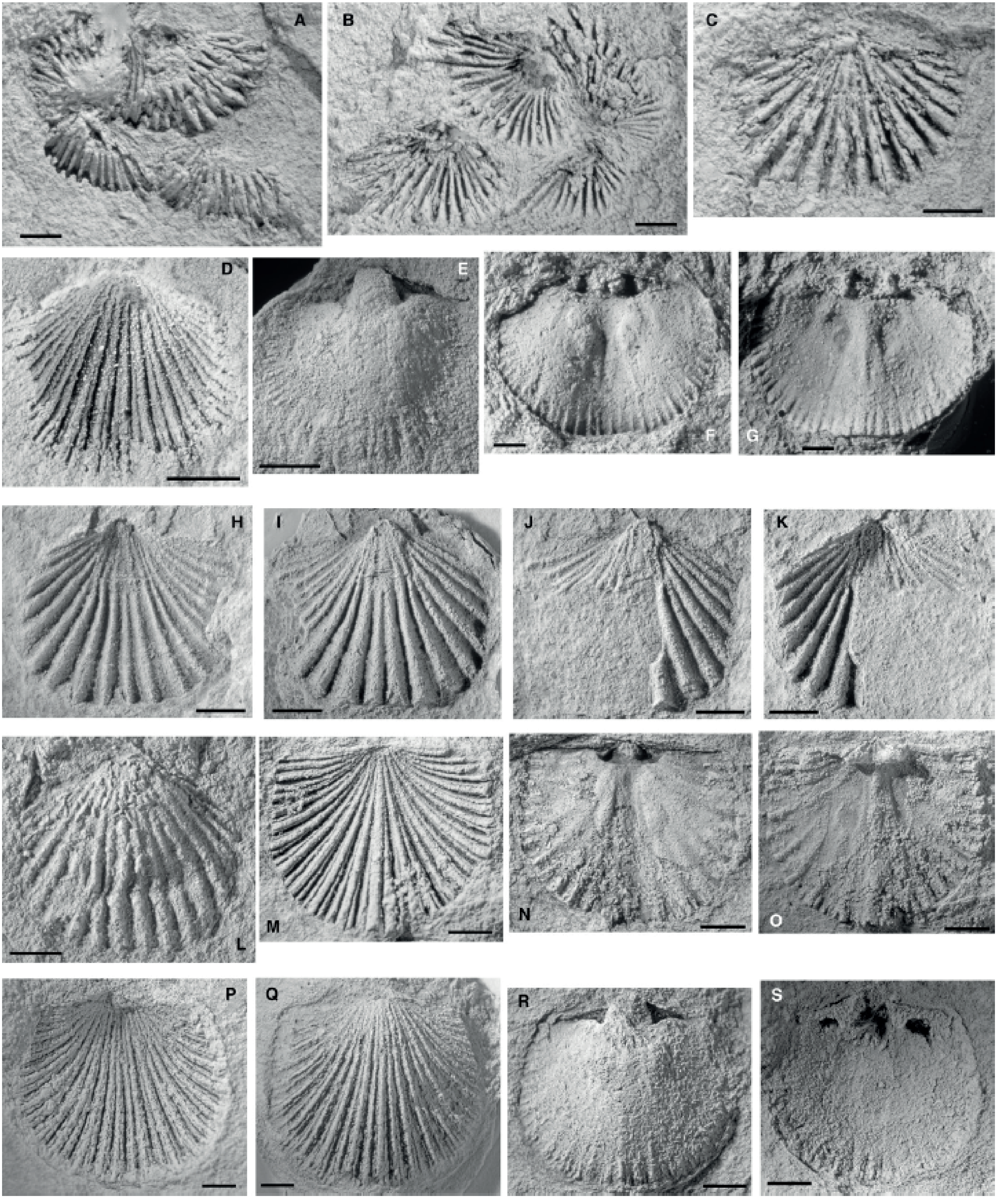
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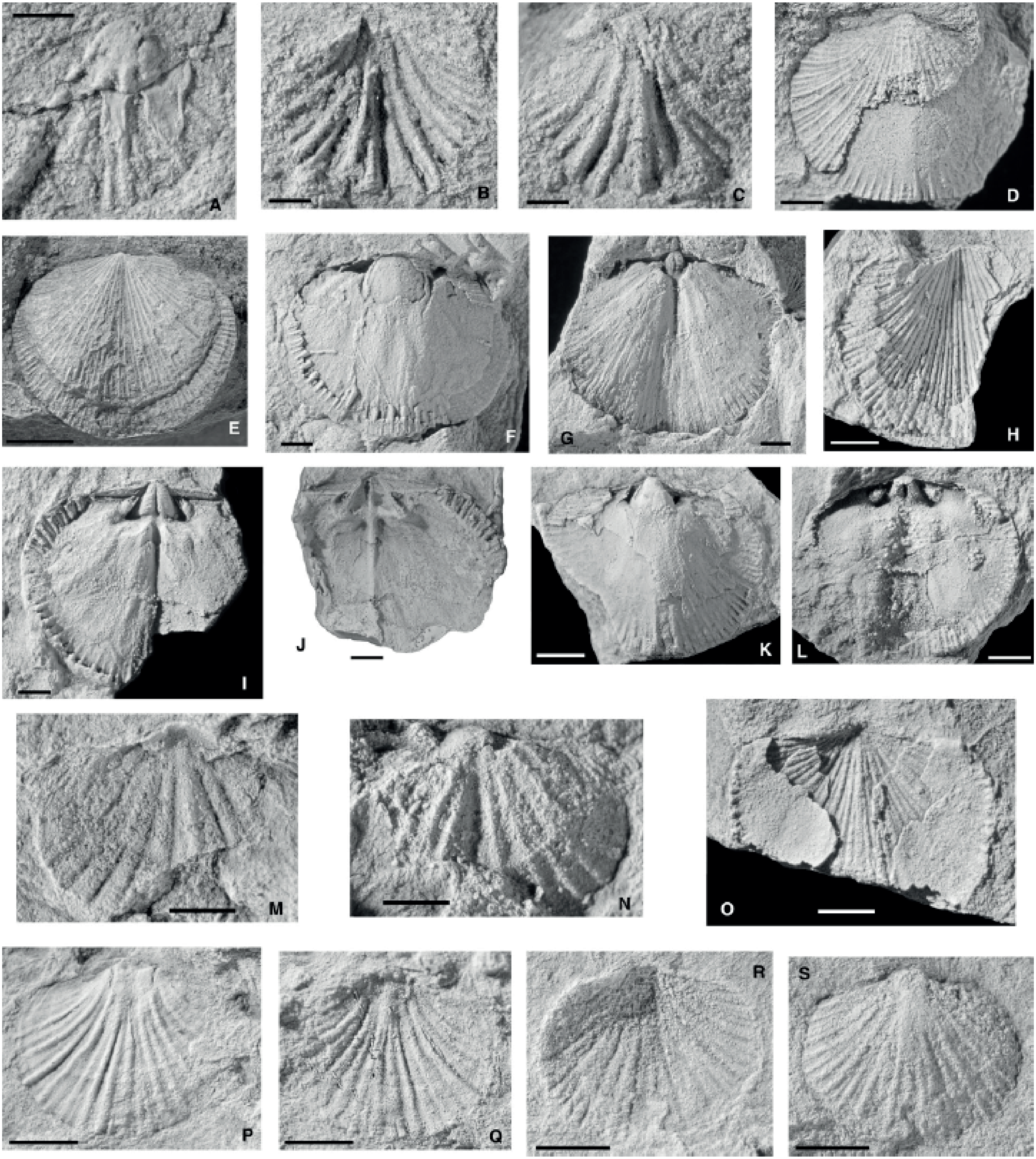
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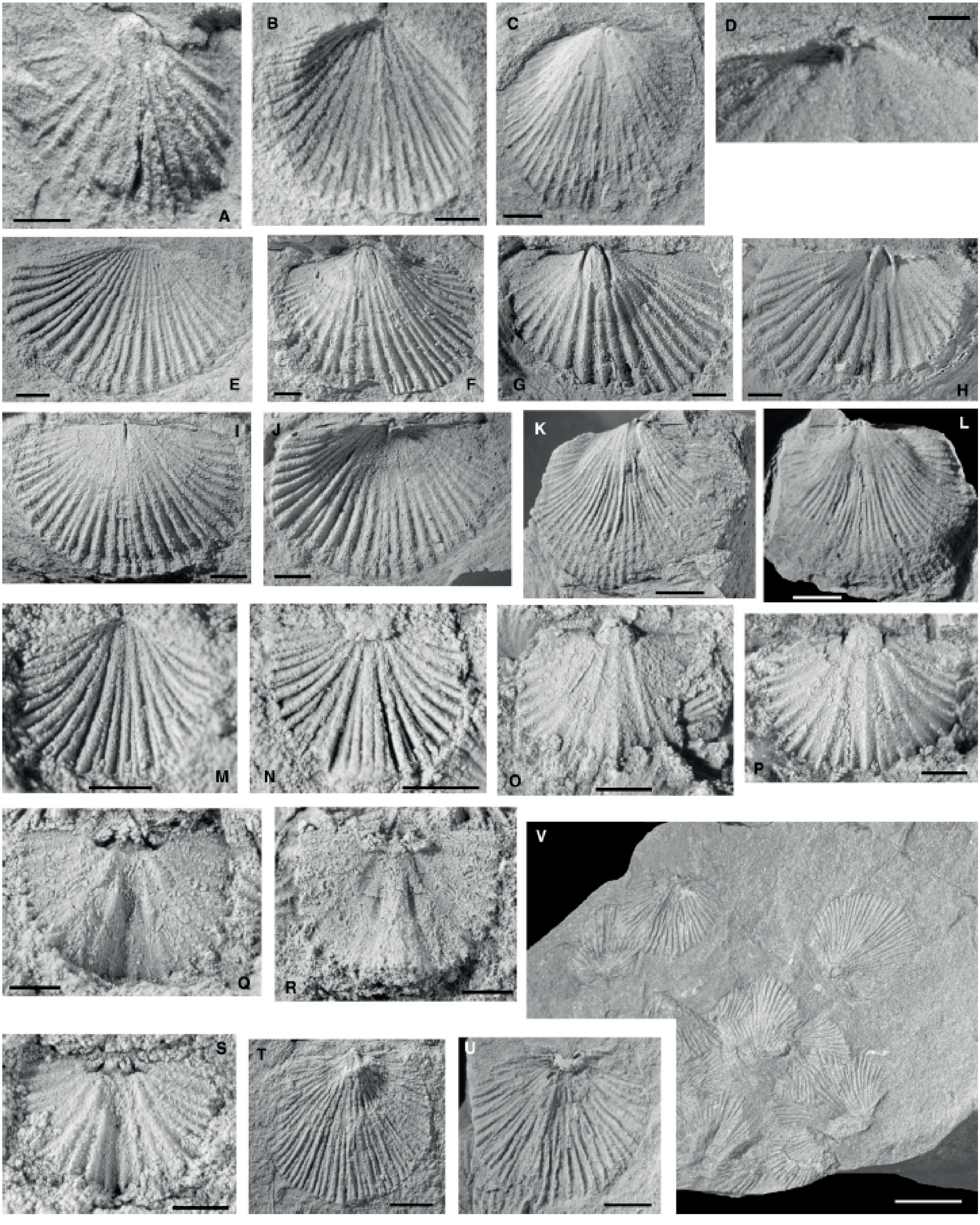
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	Horizon	Location	Coordinates	Note
Marrakesh Collection				
Tremadocian Stage				
1	Z-F2(0a) Z-F2(0c)	Jbel Tizagzaouine	30°31'42"N, 05°49'58"W	Section of the pass, specimens from individual horizons (level a, level c)
2	Z-F2(1a)	Jbel Tizagzaouine	30°31'00"N, 05°49'37"W	Southern end of the section, level a
3	Z-F2(2a)	Jbel Tizagzaouine	30°31'04"N, 05°49'50"W	Western slope, level a
	Z-F2(2b)		30°31'06"N, 05°49'49"W	Western slope, level b
4	Z-F2(2f)	Jbel Tizagzaouine	30°31'11"N, 05°49'42"W	Western slope, level f
5	Z-F2(3g) Z-F2(3i) Z-F2(3l)	Section on eastern slope of Jbel Tizagzaouine	30°31'10"N, 05°49'25"W	Specimens from individual horizons (level g, level I, level l
6	Z-F3	Beni Zoli (4.9 km E of the village)	30°27'28"N, 05°52'50"W	
7	Z-F4(1)	Bou Izargane	30°30'15"N, 05°50'16"W	
8	Z-F4(3)	Bou Izargane	30°29'59"N, 05°51'00"W	
	Z-F4(4) = BS1		30°30'00"N, 05°50'59"W	
	Z-F4(15)		30°30'00"N, 05°50'58"W	
	Z-F4(35)		30°30'01"N, 05°50'58"W	
9	Z-F4(8)	Bou Izargane	30°29'50"N, 05°50'52"W	
10	Z-F5	Oued Beni Zoli	30°28'54"N, 05°52'03"W	
11	Z-F6a	Ouaoufraout (lower level)	30°31'15"N, 05°56'44"W	
12	Z-F7	Bou Zargouan	30°30'18"N, 06°00'51"W	

13	Z-F9(1)	Bou Glef	30°30'39"N, 05°53'40"W	
14	Z-F9(2)	Bou Glef	30°29'47"N, 05°53'16"W	“Trou de Fleur”
15	Z-F11k	Section along the western bank of Oued Tarhia N’Imrhaldene	30°33'44"N, 05°49'32"W	
16	Z-F12c Z-F12g	Southernmost end of the section on the western bank of Oued Tarhia N’Imrhaldene	30°32'25"N, 05°50'08"W	Specimens from individual horizons (level c, level g)
17	Z-F13a Z-F13c Z-F13f-h Z-F13j Z-F13l-m Z-F13p Z-F13r-s	Hill north of Ouaoufraout	31°31'55"N, 05°56'21"W	Specimens from individual horizons (level a, level c, level f, level h, level j, level l, level m, level p, level r, level s
18	Z-F30a	Jbel Zagora	30°19'42"N, 05°48'45"W	Section in the pass, eastern slope, level a
	Z-F30 p		30°19'42"N, 05°48'45"W	Section in the pass, eastern slope, level p
19	Z-F42a	Tinzouline	30°31'28"N, 06°07'43"W	Oued west of El Kasba, point (a)
20	Z-F42b	Tinzouline	30°31'37"N, 06°07'30"W	Oued west of El Kasba, point (b)
	Z-F42c		30°31'38"N, 06°07'27"W	Oued west of El Kasba, point (c)
21	Z-F43 Z-F43d Z-F43f	Tinzouline	30°32'04"N, 06°07'21"W	Hill NW of El Kasba; specimens from individual horizons
22	Z-F50a	Tamegroute	30°18'04"N, 05°39'11"W	
23	Z-F51a	Tamegroute	30°18'06"N, 05°38'48"W	
24	Z-F51c	Tamegroute	30°18'01"N, 05°38'46"W	“Trou de Pierre”
25	Z-F52a Z-F52b	Tamegroute	30°18'23"N, 05°38'48"W	
26	Z-F52c Z-F52d	Tamegroute	30°18'22"N, 05°38'49"W	

27	Z-F53a	Tamegroute	30°18'20"N, 05°38'40"W	
28	Z-F53b	Tamegroute	30°18'38"N, 05°38'40"W	
29	Z-F53c	Tamegroute	30°18'24"N, 05°38'41"W	
Floian Stage				
30	Z-F15(3) Z-F15(4)	Touna	30°38'11"N, 05°50'57"W	Specimens from individual horizons (level 3, level 4)
31	Z-F25a	Bou Chrebeb	30°32'26"N, 05°40'19"W	
32	Z-F25b	Bou Chrebeb	30°32'14"N, 05°40'13"W	
33	Z-F26	Toumiat	30°25'06"N, 05°40'53"W	
34	Z-F46(1) Z-F46(3-5) Z-F46(7-11)	Taakil	30°36'17"N, 6°08'18"W	Specimens from individual horizons (level 1, level 3-5, level 7-11
Yale Peabody Museum Collection				
Tremadocian Stage				
35	-	Asif n'Moutn, near Bni Zoli [= Beni Zouli, Beni Zoli]	30°28'40"N, 5°53'59"W	789 m
36	-	Asif n'Moutn, near Bni Zoli [= Beni Zouli, Beni Zoli]	30°28'36"N, 5°53'56"W	775 m
37	-	Bou Glf	30°30'25"N, 5°53'10"W	
38	-	Bou Glf	30°30'30"N, 5°53'11"W	
39	-	Bou Glf	30°30'17"N, 5°52'59"W	
40	-	Bou Glf	30°30'02"N, 5°53'21"W	783 m
41	-	Bou Glf	30°29'34"N, 5°53'13"W	792 m
42	-	Bou Glf	30°29'34"N, 5°53'15"W	800 m
43	-	Bou Krba	30°34'12"N, 5°42'03"W	881 m
44	-	Bou Zorgan (Zagora area)	30°29'45"N, 5°52'04"W	
45	-	Exact quarry unknown, hillside at Ezegzaou 1	30°31'50"N, 5°49'59"W	

46	-	Ezegzaou	30°31'47"N, 5°49'23"W	839 m
47	-	Large (~20 m wide) quarry between Ezegzaou and Bou Glf	30°30'08"N, 5°51'57"W	798-809 m
48	-	Large (~20 m wide) quarry between Ezegzaou and Bou Glf	30°30'08"N, 5°51'57"W	798-809 m
49	-	Tigzigzaouine	30°29'50"N, 5°52'27"W	793 m
50	-	Tigzigzaouine	30°30'00"N, 5°50'59"W	West side of quarry, 799-800 m
Floian Stage				
51	-	Bou Chrebeb	30°32'25"N, 5°40'21"W	880 m
52	-	Bou Glf 1	30°29'41"N, 5°53'13"W	786 m
53	-	Bou Glf 2, 1km to W of road, 11.2 km NNE of Route N9 along Draa Valley, approximately 25 km north of the town of Zagora	30°31'10"N, 5°52'56"W	803 m
54	-	One of the quarries at Bou Glf, an area of excavation approx. 20 km N of Zagora	30°29'39"N, 5°53'12"W	
55	-	Expansive plain between Oued Bni Zoli and Ezegzaou (Bou Zeroual?)	30°30'04"N, 5°50'44"W	806 m
Undifferentiated (lower / upper Fezouata Fm.)				
56	-	Bou Glf	30°31'57"N, 5°50'02"W	
57	-	Errachidia; 1.6 km E of road, 8.9 km NNE on road NNE of Route N9 along the Draa Valley, approximately 25 km NW (by road) of Zagora	30°30'09"N, 5°51'53"W	
58	-	Errachidia; Bou Glf	30°30'50"N, 5°53'21"W	820 m
59	-	Azizaoi = Ezegzaou	30°31'47"N, 5°49'57"W	
60	-	Quarry/pit at site Ezegzaou 2, 2.9 km E of road, 12.9 km NNE on road NNE of Route N9 along the Draa Valley, approximately 25 km NW (by road) of Zagora	30°32'13"N, 5°50'09"W	866 m
61	-	Quarry/pit at site Ezegzaou 2, 2.9 km E of road, 12.9 km NNE on road NNE of Route N9 along	30°32'08"N, 5°50'15"W	846 m

		the Draa Valley, approximately 25 km NW (by road) of Zagora		
62	-	Ezegzaou Hill	30°31'12"N, 5°49'49"W	837 m
63	-	Tamagroute	30°31'26"N, 5°52'09"W	

Citation on deposit: Candela, Y., Harper, D. A. T., & Mergl, M. (2024). The brachiopod faunas from the Fezouata Shale (Lower Ordovician; Tremadocian–Floian) of the Zagora area, Anti-Atlas, Morocco: evidence for a biodiversity hub in Gondwana. Papers in Palaeontology, 10(5), Article e1592. https://doi.org/10.1002/spp2.1592