



# Marine benthic invertebrates from the Upper Jurassic of northern Ethiopia and their biogeographic affinities

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## ARTICLE INFO

### Article history:

Received 16 April 2010

Received in revised form 5 October 2010

Accepted 21 October 2010

Available online 30 October 2010

### Keywords:

Ethiopia

Jurassic

Bivalves

Brachiopods

Corals

Biogeography

## ABSTRACT

We present the first modern description of corals, brachiopods and bivalves from the Antalo Limestone in the Mekele Outlier of northern Ethiopia. This fauna is largely of Oxfordian age and lived in shallow subtidal environments and in small patch reefs. In combining our new data with fossil occurrence data from the Paleobiology Database, we conducted multidimensional scaling analyses to assess biogeographic patterns and the delineation of the Ethiopian Province for the Callovian to Kimmeridgian stages. Results suggest that an Ethiopian Province is indeed evident for our focal groups, but this is more confined than traditionally assumed. The so defined Ethiopian Province includes Tunisia, the Levant, Arabia and much of East Africa, but excludes Tanzania and India. The special status of India and Tanzania is perhaps due to latitudinal gradients in faunal composition.

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## 1. Introduction

Marine invertebrate fossils are poorly known from the Ethiopian Jurassic. Apart from older accounts, mostly from the Blue Nile and Dire Dawa regions (Blanford, 1870; Douvillé, 1886; Merla and Minucci, 1938; Wells, 1943; Arkell, 1956; Jaboli, 1959; Zuffardi-Comerci, 1959; Ficcarelli, 1968; Jordan, 1971), fossils are usually just mentioned in a geological context and neither described in detail nor figured. This represents a major shortcoming, not only because Ethiopia contains large outcrops of marine Jurassic sedimentary rocks, but also because it is eponymous of the Jurassic Ethiopian Province (Neumayr, 1885; Uhlig, 1911; Arkell, 1956; Hallam, 1971).

In the so-called Mekele Outlier of northern Ethiopia (Tigray Province) (Fig. 1), previous studies have focused on sedimentology, stratigraphy, and geochemistry (Beyth, 1972; Bosellini et al., 1995, 1997; Martire et al., 1998; Worash and Valera, 2002), whereas paleontology is poorly known. Here we present the first modern detailed description of three major benthic invertebrate groups from the Upper Jurassic of northern Ethiopia: scleractinian corals, rhynchonelliform brachiopods, and bivalves. These groups represent the majority of macrofossils in the limestone succession of

the Mekele Outlier. Besides a documentation of the faunas, we revisit the Ethiopian Province by evaluating biogeographic affinities of the benthic faunas.

## 2. Geological setting and stratigraphy

The Mekele Outlier in Ethiopia's Tigray Province (Fig. 1) represents a succession of late Paleozoic and Mesozoic sedimentary rocks, which overlies unconformably Precambrian basement. The Mesozoic succession is unconformably overlain by Cenozoic flood basalts, which protected the Mesozoic rocks from erosion (Bosellini et al., 1997). The nearly circular outlier covers approximately 8000 km<sup>2</sup> and is bordered by tectonic lineaments to the north, east and south. Most prominent is the great escarpment of the Ethiopian rift in the east.

The general stratigraphy of the sedimentary succession is simple and was developed by Blanford as early as in 1870. Siliciclastic sediments of Paleozoic age form the base of the sedimentary succession (Bussert and Schrank, 2007). Continental siliciclastic rocks, known as the Adigrat Sandstone, also form the base of the Mesozoic strata. The Adigrat Sandstone grades via marine calcareous sandstones into the Antalo Limestone, which is overlain conformably by the Agula "Shale", or unconformably by the Amba Aradam Formation (Bosellini et al., 1995, 1997; Martire et al., 1998). The chronostratigraphic assignments of these units are

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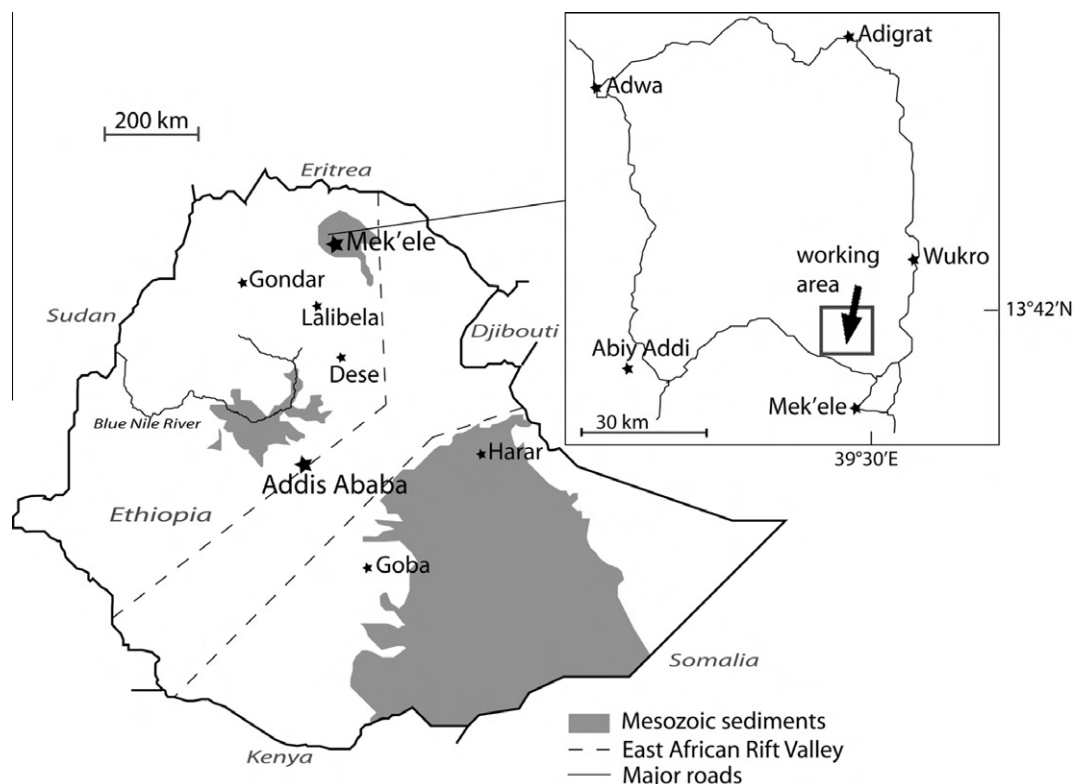


Fig. 1. Location map. The study area is situated in the Tigray Province of northern Ethiopia and is part of the Mekele Outlier.

not entirely resolved. The Adigrat Sandstone has now been interpreted to range from the Upper Triassic to the upper Middle or lower Upper Jurassic (Bosellini et al., 1997). The Antalo Limestone (AL) was originally assigned to the Middle or Upper Jurassic (Blanford, 1870; Merla and Minucci, 1938; Arkell, 1956), but it is now obvious, based on ammonites and foraminifers, that it is limited to middle Oxfordian to lower Kimmeridgian (Martire et al., 1998, 2000), at least in its type area around Mekele (also spelled Mek'ele or Mekelle). Because the first Kimmeridgian ammonites are reported in AL Member 3, we assign an Oxfordian age to the older two members (AL 1–2) and a Kimmeridgian age to AL 3–4. Together with the underlying Adigrat Sandstone and the overlying Agula Shales, the Antalo Limestone comprises the Antalo Supersequence (Bosellini et al., 1997), which is exposed over vast areas in East Africa and Yemen (Bosellini et al., 2001). As its base is time-transgressive ranging from the Pliensbachian to the Oxfordian, the formation name Antalo Limestone should probably be restricted to the area around Mekele, where its type locality is located.

The lower Antalo Limestone around Mekele was deposited in an inner to middle ramp setting with common discontinuity surfaces that record rapid sea-level fluctuations (Martire et al., 2000). The ramp setting does not suggest that an extensive barrier reef system was developed to the east as hypothesized by Beyth (1972).

### 3. Materials and methods

Field work was conducted by a group of five geologists in the area north of Mekele in April 2007. The intention of field work was to check for the presence of coral reefs and compare them with those of the European Tethys. Detailed mapping was supplemented by measuring sections and quantitative sampling. Field work focused on the area around the Geyedamo River and covered

an area of approximately 15 km<sup>2</sup> from 13°36'N to 13°39'N and from 39°25'E to 39°27'30"E (Fig. 2). Fossils were collected from outcrop and bulk samples were taken wherever possible, but samples from scree supplemented our collections. Counts of reef-building organisms were conducted in line transects taking notes in 5 cm intervals.

We followed Bosellini et al. (1997) in separating four informal members within the Antalo Formation. Fossils were largely gathered from the two basal members (AL1 and AL2). Sixty thin sections were prepared for microfacies analyses and coral identifications. Macrofossils were prepared mechanically and coated with ammoniumchloride for photography.

All fossils are stored in the Museum für Naturkunde. Occurrence data of identified fossil material in the Mekele Outlier have been entered in the Paleobiology Database (PaleoDB, <http://paleodb.org>) where they are openly accessible (collection numbers: 93029, 93031, 93032, 93206, 93853–93869, 93871, 94311–94322, 94324, 94326, 94330, 94332, 94335–94339, 94455, 94788). These collections were used, together with previously published material available in the Paleobiology Database, to assess biogeographic relationships of the Ethiopian fauna.

Biogeographic analyses were conducted on corals, brachiopods, and bivalves for the time interval Jurassic 5, which includes the Callovian, Oxfordian and Kimmeridgian stages. Based on the downloaded data (as of 23 September, 2010), we calculated Bray–Curtis dissimilarities of aggregated occurrence data. The resulting dissimilarity matrix is equivalent to proportional dissimilarities. We chose to use this quantitative metric rather than simple presence/absence measures because it is less sensitive for different sample sizes and carries more information. Although biogeographic analyses often emphasize marker taxa, we focus here on full fauna comparisons, because incomplete sampling may prevent detection of marker taxa and because the choice of biogeographic marker taxa is usually subjective (e.g., Heinze, 1996).

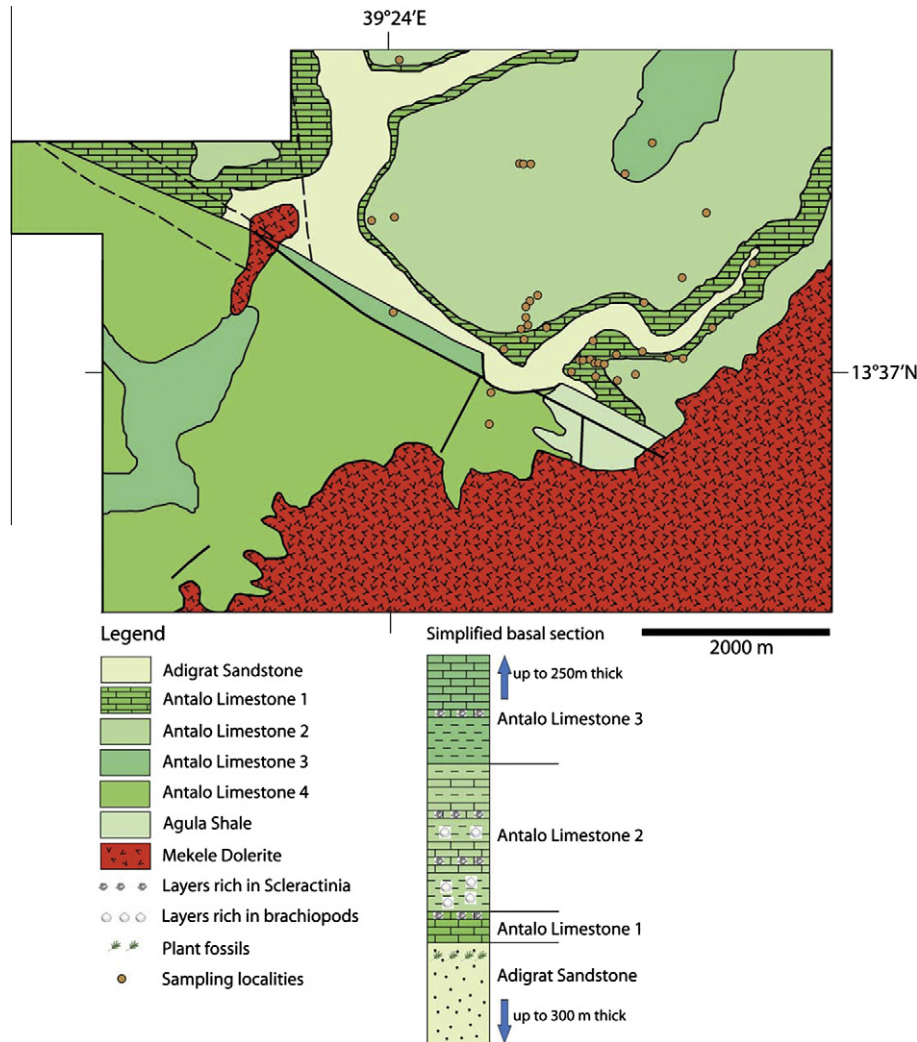


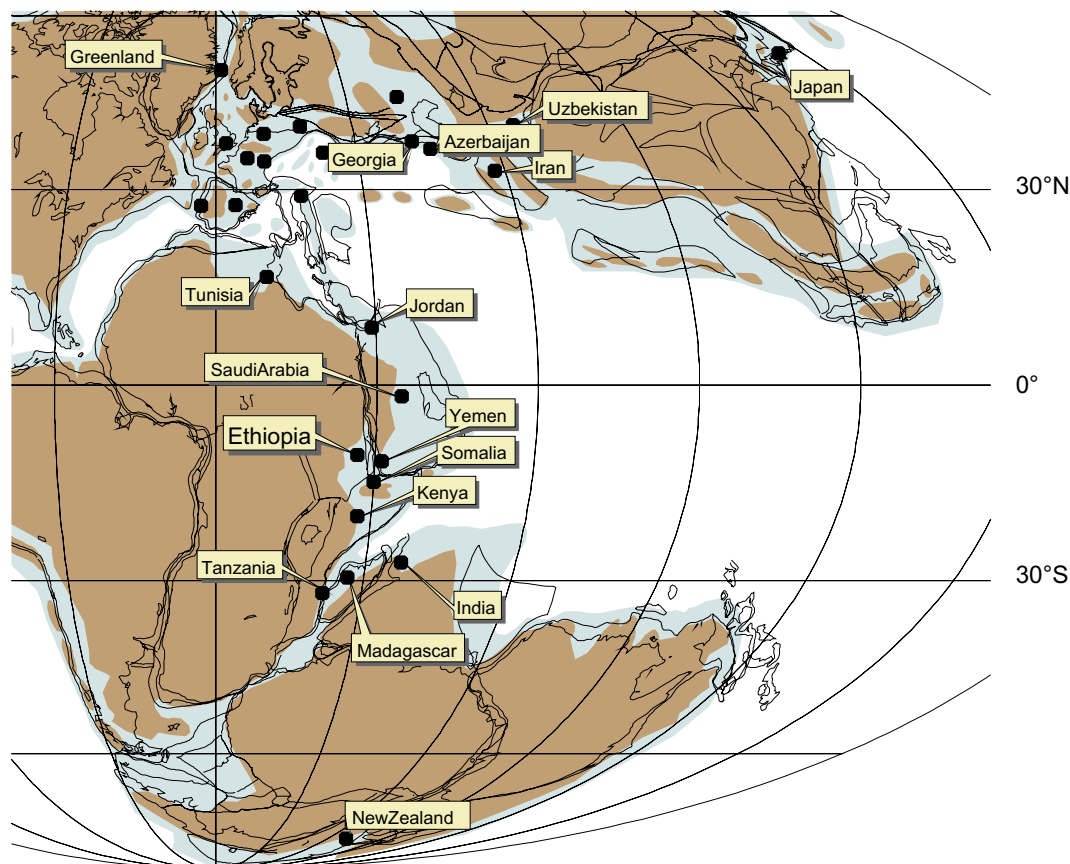
Fig. 2. Geological map of the study area and location of sampling localities mentioned in the text. The Antalo Limestone ranges from Oxfordian to Kimmeridgian in age.

All analyses were done at the genus level. Global species-level analyses are currently not feasible due to taxonomic problems. For bivalves we limited our analyses to genera identified to the species level and applied offline taxonomic corrections (Kiessling et al., 2007) prior to analyses. For corals and brachiopods we used all genera. The wastebasket genus “*Terebratulina*” was omitted from the dataset if no reliable genus assignment was possible.

We aggregated data by countries and paleogeographic grids. We focus on countries because the exact paleogeographic position of some plates is still disputed in the Jurassic. For example, the plate tectonic reconstruction of Scotese (pers. comm. 2001), which underlies the automated rotations of collections in the PaleoDB, differs from other reconstructions (e.g., Golonka, 2002; Scotese, 2004) by plotting parts of Azerbaijan, Iran and Georgia close to the Arabian plate, whereas these are otherwise shown as part of the Northern Tethys margin (Fig. 3). Although Bray–Curtis dissimilarity is little affected by different sample sizes, results become unreliable when samples are too small. Accordingly, we have set thresholds for the number of occurrences reported from a taxon and area to be included in the analyses. For our analyses on groups by country these thresholds were: 50 for corals, 40 for brachiopods and 90 for bivalves. A combined analysis of all three groups was run with a threshold of 120 occurrences per country.

We refrain from reporting cluster analyses because (1) cluster analysis always detects hierarchical structure, even if there is none

and (2) results vary profoundly among agglomeration methods. Instead we use multidimensional scaling (MDS) to investigate biogeographic relationships. MDS is an ordination technique that takes a matrix of dissimilarities and returns a set of points that are plotted such that the distances between points are approximately equal to the dissimilarities. The number of axes is chosen prior to the analysis and the data are fitted to those dimensions. The distance matrix of all variables (proportions of each taxon in each area) is transformed to a best-fit two-dimensional plot such that the distances between the points are approximately equal to the dissimilarities. MDS differs from other ordination techniques (such as principal component analysis) in that it is designed for projecting quantitative distance metrics between multiple variables on a two (or three) dimensional plot rather than seeking eigenvectors to explain as much of the overall variance as possible. As it is the distance on a plot rather than the alignment of points along an axis that matters in MDS, an MDS solution can be rotated or inverted as desired. We chose metric MDS, which is also known as principal coordinate analysis (Gower, 1966). We also performed non-metric MDS, which gave the same basic results albeit with a larger overall scatter. Although non-metric MDS makes fewer assumptions on the nature of the data, we focus on metric MDS because it always finds a globally optimum solution, whereas non-metric iteratively seeks a best solution, which may just represent a local optimum. In addition metric MDS is intuitive



**Fig. 3.** Plate tectonic reconstruction of the early Late Jurassic (Golonka, 2002). Countries from which sufficient data were available in the PaleoDB for biogeographic analyses are marked by black boxes approximately at mean paleo-coordinates of occurrences. Countries outside of Europe are labeled. Brown color = land, light blue = shelf, white background = deep ocean. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for biogeography in that taxon-quantitative differences are mapped as if they represented spatial distances among areas. Great circle distance among sampling areas were computed to compare spatial and taxon-quantitative distances. All analyses were done in the R programming environment ([www.r-project.org](http://www.r-project.org)).

#### 4. Facies and fauna

##### 4.1. General account

Marine faunas are first evident in the calcareous sandstones of the transition beds between the Adigrat Sandstone and the Antalo Limestone. The foraminifers *Nautiloculina ootolithica* and *Kurnubia palastiniensis* in these transition beds suggest a late Callovian/early Oxfordian age. Wackestones and packstones dominate the sequence of the Antalo Limestone. The cliff-forming AL1 represents a shallowing-upward sequence of wackestones and packstones. AL1 is rich in stromatoporoids and corals. Non-reefal thickets occur repeatedly and are usually dominated by stromatoporoids. Growth density is moderate in these thickets, varying in coverage between 15% and 48% in five line transects (average 33%). Small patch reefs and laterally extensive biostromes are present but no larger reefs were observed. Coral patch reefs are usually dominated by few species of corals, such as *Actinastrea crassoramosa*. These are maximally 1.5 m thick and 3 m wide. Growth density is high, with less than 14% of matrix. Laterally extensive (up to 100 m) biostromes occur at the top of AL1 and are dominated by stromatoporoids constituting up to 72% of the volume. Corals comprise a maximum of 30% of framebuilders in these biostromes. Pure stromatoporoid

biostromes were observed near May Magden (outside the map) at the top of AL3.

Rhynchonelliform brachiopods are very common and excellently preserved, especially in marly beds at the base of AL2. Rhynchonellid brachiopods dominate in abundance over terebratulid brachiopods. Of eleven sites, from where more than 10 specimens of brachiopods were collected, the proportion of rhynchonellids ranges from 33% to 100% (mean = 66%).

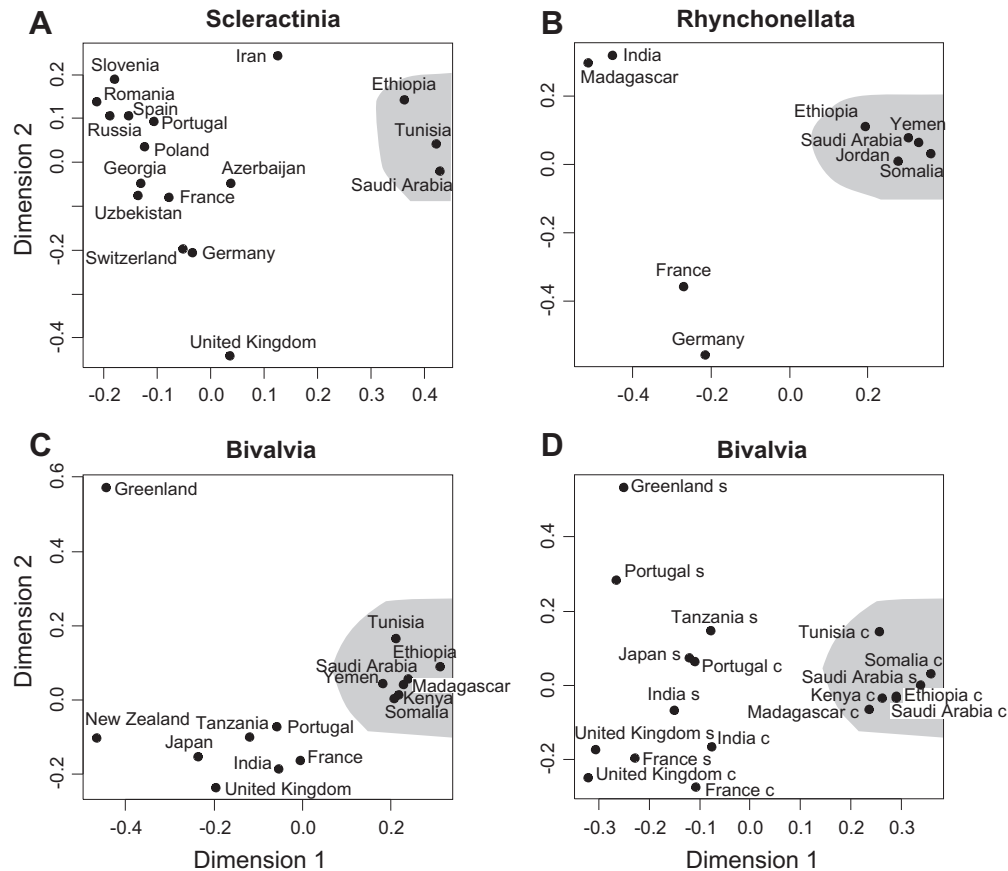
Brachiopods are usually associated with bivalves and gastropods. In limestones the latter are usually rarer than brachiopods, but bivalves are common in marls and dominant in shales, especially the Agula Shale. Bivalves are moderately diverse, with both epifaunal and infaunal taxa well represented. Among gastropods only *Nerinea* sp. could be identified with certainty.

Echinoids are common but usually small. We identified two species, both found in Antalo Member 1, as *Hemicidarites abyssinica* Blanford and *Pygurus jurensis* Marcou, respectively. Large nautilids (cf. *Paracenoceras*) are common in the limestone-marlstone succession on top of AL1.

##### 4.2. Faunal peculiarities

The most striking aspect of the coral fauna is the absence of *Thecosmilia* and *Montlivaltia*, which were very common in Europe during the Late Jurassic. Several species reported previously from the Upper Jurassic of Saudi-Arabia (El-Asa'ad, 1991) and Iran (Pandey and Fürsich, 2003) are present in our working area. Besides *Actinastrea*, *Lochmaeosmilia trapeziformis* is a conspicuous component of the coral fauna but only occurs in AL1.





**Fig. 4.** Metric multidimensional scaling of proportional distances of aggregated fossil occurrences by country in the Callovian to Kimmeridgian stages. Due to the problematic position of India and Tanzania, the traditional Ethiopian Faunal Province is not well discerned, but a core Ethiopian Province (grey-shaded) is evident for (a) corals, (b) brachiopods and (c and d) bivalves. Different substrate conditions do not seem to be responsible for this pattern as these cluster closely together within countries as depicted for bivalves in (d). Letters after country names refer to carbonate substrates (c) including marls and siliciclastic substrates (s) indicating sandstones, siltstones and mudstones as primary lithology. See text for discussion.

The great abundance and good preservation of brachiopods is striking. The most conspicuous taxon is *Somalirhynchia* of which more than 100 specimens were collected. Interestingly, the geologically youngest occurrences of several brachiopod genera were observed in the working area. Genera such as *Amydroptychus* and *Cymatorhynchia* were previously only known from the Middle Jurassic.

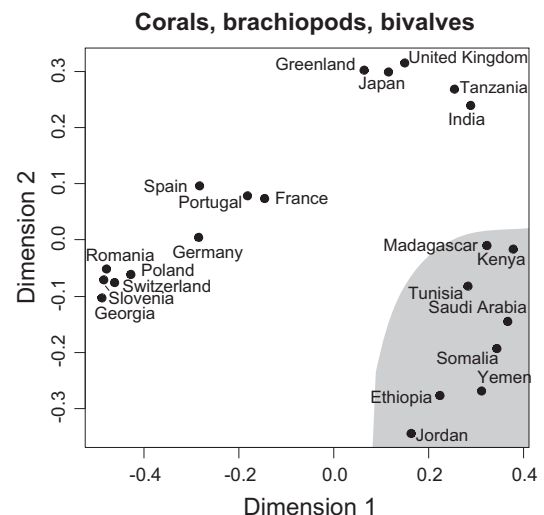
Among bivalves, two observations are noteworthy. First, epifaunal cementing bivalves, in particular *Actinostreon*, are abundant. This is attributed to the many hardgrounds in the Antalo Limestone, which were interpreted as flooding events in the carbonate ramp setting (Martire et al., 2000). Second, the large and conspicuous infaunal bivalve *Pholadomya* (*Bucardiomya*) *somaliensis* is locally common. This species also occurs in Saudi Arabia, Somalia and Yemen.

## 5. Biogeography

Multidimensional scaling produced the results depicted in Fig. 4. There is a tendency of countries that were geographically close to Ethiopia in the Jurassic 5 interval to cluster together in the diagrams. Overall, the correlation coefficient between the great circle distance in kilometers and the dissimilarity in taxon-quantitative composition is 0.53 for corals, 0.63 for brachiopods and 0.54 for bivalves. It is thus no surprise that regions that were close to Ethiopia in Late Jurassic, also tend to be close in MDS plots. That the correlations are significant in all cases lends credit to our data

and methods and that they are imperfect allows the detection of biogeographic pattern in the first place.

For corals, Tunisia and Saudi Arabia plot close to Ethiopia (Fig. 4a). This cluster is separated from countries that were situated along the northern Tethyan shelf. Iran (Lut Block) plots in an



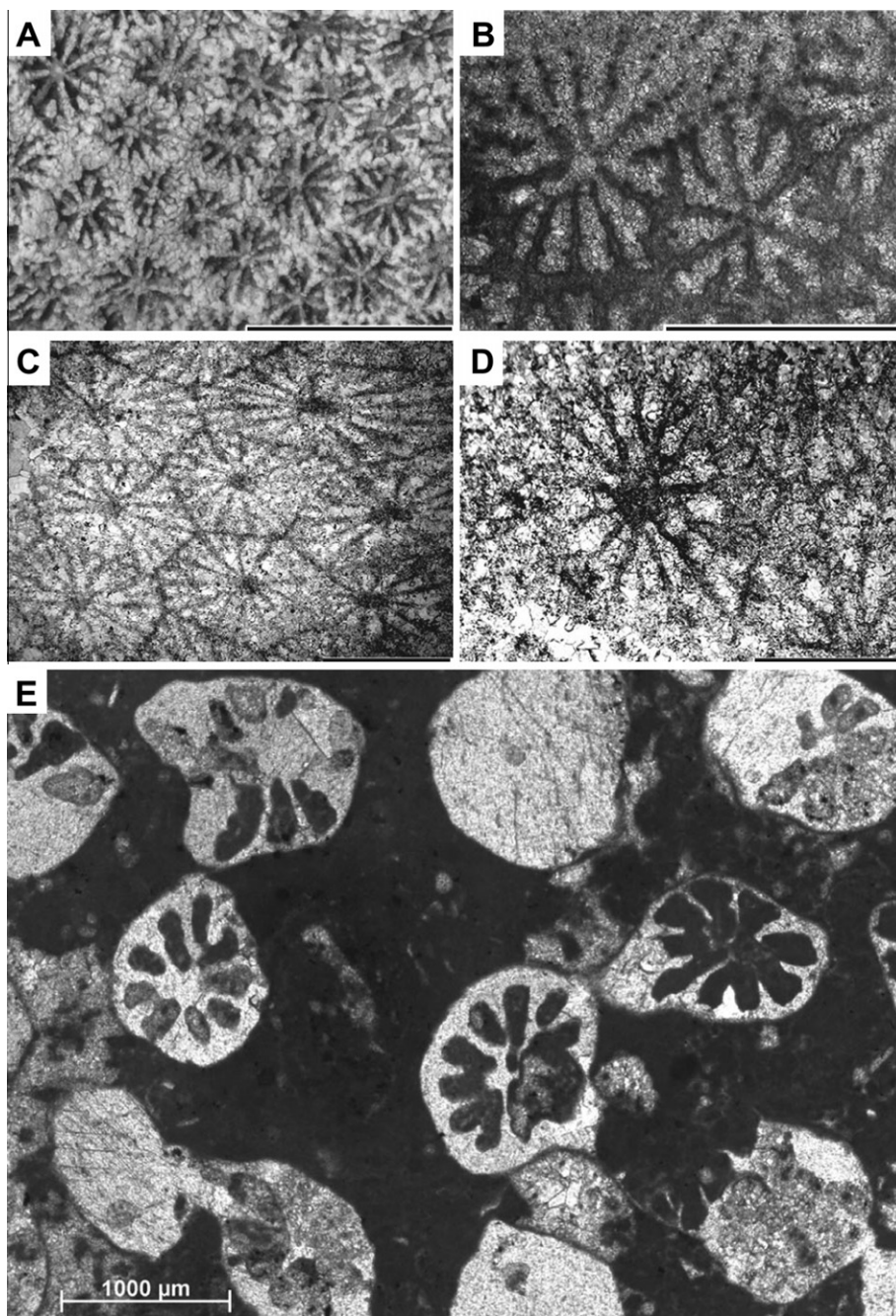
**Fig. 5.** Multidimensional scaling of corals, brachiopods and bivalves combined.

intermediate position. From this pattern we can infer an Ethiopian Province that was separated from a Northern Tethyan Province containing nearly all other countries and ranging from Portugal in the west to Uzbekistan in the east. Only Iran and Britain cannot be assigned to one of these provinces.

Rhynchonellate brachiopods show a quite distinct pattern (Fig. 4b). The traditional Ethiopian Province for Middle and Late Jurassic brachiopods (Muir-Wood, 1935) is well depicted. However, India and Madagascar plot as far from Ethiopia as France and Germany and thus cannot be included in an Ethiopian Province. In the absence of sufficient data from other countries, we

might infer three provinces from this map: Ethiopian, Southwestern Tethys and European.

Bivalves show the most complex pattern. There is a distinct clustering of points around Ethiopia (Fig. 4c) supporting an Ethiopian Province from Tunisia in the north to Madagascar in the south (Fig. 3). However, India and Tanzania that are usually assigned to the Ethiopian Bivalve Province (Heinze, 1996; Liu et al., 1998) cannot be included because they plot closer to countries such as Portugal and France than they plot to any country in the traditional Ethiopian Province. Most data from India stem from siliciclastic sediments and data from Tanzania exclusively so. This raises the



**Fig. 6.** Actinostreaid and stylinid corals from the Antalo Limestone north of Mekele. (A and B): *Actinostrea crassoramosa* (Michelin). (A) Surface of a ramose colony showing cerioid integration and distinct calices. Scale bar = 5 mm (col. 94319, MB.K.7837). (B) Thin-section micrograph of a few corallites showing absence of columella and a few dissepiments. Scale bar = 2.5 mm (94330, MB.K.7838). (C and D) Transverse thin sections of *Coenastrea arabica* El Assad (94326, MB.K.7858). Note ring of dissepiments in (D). Scale bar = 4 mm and 2 mm, respectively. (E) *Lochmaeosmilia trapeziformis* (Gregory). Transverse thin section showing corallites initially connected by a tube and later showing apophyses (93868, MB.K.7859).

possibility that depositional environment exerted a control on differences in faunal composition. A simple test is provided in Fig. 4d, where occurrences were grouped by substrate and country before doing the MDS analysis. The results suggest that facies was not a main driver of the biogeographic pattern. The Indian occurrences from both carbonate and siliciclastic depositional environments plot closer to European countries than to countries of the Ethiopian Province. Although most occurrences in the Ethiopian Province are from carbonate sediments, the clastic portions from Saudi Arabia are well included within it. The most distant countries to Ethiopia are New Zealand and Greenland. These are considered representatives of different faunal realms, the Austral and Boreal Realm, respectively (Liu et al., 1998).

An analysis of the combined dataset suggests three distinct clusters that might represent faunal provinces (Fig. 5). An Ethiopian Province is evident ranging from Tunisia in the north to Madagascar in the south. A European Province comprises all countries of continental Europe. The interpretation of the third cluster is less straightforward because it includes countries from paleogeographically distant areas such as Greenland, Japan and India. An obvious, unifying feature is a relatively high paleolatitude of all those countries with are at the northern and southern margins of our analyzed data (Fig. 3).

In summary, an Ethiopian Province consisting of Ethiopia, Somalia, Jordan, Yemen, Kenya, Madagascar, Saudi Arabia, and Tunisia is evident. India and Tanzania, however, cannot be assigned to the Ethiopian Province, perhaps due to paleolatitude playing an important role in governing faunal composition.

## 6. Taxonomy

Synonymy lists, descriptions and discussions are kept as brief as possible. Supplementary information may be found online in the PaleoDB (<http://paleodb.org>) and in cited references. Original sample names were replaced with PaleoDB collection numbers in the figure captions to allow tracing the geological and paleontological context of each record.

### 6.1. Corals

Coral material is stored in the Museum für Naturkunde in Berlin; inventory numbers MB.K.7837–MB.K.7888. Abbreviations in measurements mean: d, diameter of corallites; c–c, nearest distance between corallite centers; Ns, number of septa; Nc, number of costae; Dt, density of trabeculae at the distal margin of septa; Wp, width of peritheca; Ws, maximum width of a series; Lc, maximum length of colline; St, maximum thickness of stereozone; Pd, Pennular density.

Class Anthozoa Ehrenberg

Subclass Zoantharia Blainville

Order Scleractinia Bourne

Suborder Astrocoeniina Vaughan and Wells

Family Actinastraeidae Alloiteau

Genus *Actinastrea* d'Orbigny

Type species: *Astrea geminata* Goldfuss

*Actinastrea crassoramosa* (Michelin) (Fig. 6A and B)

1843 *Astrea crassoramosa* sp. nov. – Michelin: 109, pl. 25, Fig. 2.

1885 *Astrocoenia crassoramosa* (Michelin) – Koby: 295, pl. 87, Figs. 2 and 3.

1955 *Actinastrea crassoramosa* (Michelin) – Geyer: 320, pl. 1, Figs. 1–3.

2003 *Enallocoenia crassoramosa* (Michelin) – Pandey and Fürsich: 13, pl. 2, Fig. 7.

Material: 60 larger fragments of colonies (47 from AL1, 13 from AL2).

Dimensions:  $d = 1.3\text{--}3.1\text{ mm}$ ;  $c\text{--}c = 2.1\text{--}2.9\text{ mm}$ ;  $Ns = 12\text{--}23$ ;  $Dt = 4$  in  $0.5\text{ mm}$ .

Remarks: The Antalo specimens match the characteristic Upper Jurassic species *Actinastrea crassoramosa*, which has been variously assigned to *Actinastrea* or *Enallocoenia*. *Enallocoenia* d'Orbigny differs from *Actinastrea* by non-anastomosing septa and dominantly parathecal walls, which are anastomosing and dominantly septothecal in *Actinastrea*. The septothecal walls of the Antalo specimens are indicative of *Actinastrea*.

Genus *Coenastrea* Etallon

Type species: *Coenastrea martis* Etallon

Remarks: Stanley and Beauvais (1990) revalidated the genus which was once grouped with unidentified genera by Wells (1956). The diagnostic characters were reported as cerioid corals like *Isastrea* but with columella. *Actinastrea* is also a cerioid coral with columella. Without information on microstructures it is impossible to separate the two genera. Although not a generic character, corallite diameters are larger in *Coenastrea* than in *Actinastrea* and the number of septa coincides with the lowest value recorded for *Isastrea*. Until the type-material is reinvestigated or some well preserved specimens with preserved microstructure are studied, we follow Stanley and Beauvais (1990) in retaining the genus *Coenastrea*.

*Coenastrea arabica* El-Asa'ad. (Fig. 6C and D)

1991 *Coenastrea arabica* sp. nov. – El-Asa'ad: 274, pl. 5, Figs. 1a–e.

Material: One specimen from AL2.

Dimensions:  $d = 2.2\text{--}2.9\text{ mm}$  (plocoid) or  $4.3\text{--}5.5\text{ mm}$  (cerioid);  $c\text{--}c = 2.7\text{--}3.0\text{ mm}$  (plocoid) or  $3.5\text{--}4.7$  (cerioid);  $Wp = 0\text{--}1.7\text{ mm}$ ;  $Ns = 12\text{--}27$ .

Description: Corallum colonial, cerioid with polygonal outline, partially plocoid with circular outline. Budding intracalicular. Septa compact, moderately thick, occasionally anastomosing near the columella, lateral surface covered with very fine spinules. Septa arranged in three cycles. Septa of first and second cycle join in the center and form a thick pseudocolumella. Endothecal dissepiments subtabular to vesicular, occasionally forming a ring in the middle of corallites, which produces a plocoid appearance. Wall septoparathecal.

Remarks: The morphological characters and dimensions match the Oxfordian species *Coenastrea arabica* from Saudi Arabia. The American species, *Coenastrea hyatti* (Wells) possesses smaller corallite diameters (1–2 mm), non-anastomosing septa, and an isolated columella.

Suborder Stylinina Alloiteau

Family Stylinidae d'Orbigny

Genus *Lochmaeosmilia* Wells

Type species: *Stylosmilia trapeziformis* Gregory

*Lochmaeosmilia trapeziformis* (Gregory) (Fig. 6E)

1900 *Stylosmilia trapeziformis* sp. nov. – Gregory: 47, pl. 11, Figs. 5–14.

1958 *Lochmaeosmilia trapeziformis* (Gregory) – Alloiteau: 68, pl. 16, Fig. 10; pl. 22, Fig. 1, pl. 30, Fig. 2.

1993 *Lochmaeosmilia trapeziformis* (Gregory) – Pandey and Fürsich: 12, pl. 1, Figs. 4, 9, text-fig. 9.

(continued on next page)



Material: 16 larger fragments of colonies from AL1.

Dimensions:  $d = 1.0\text{--}1.2\text{ mm}$ ;  $c\text{--}c = 0.9\text{--}1.3\text{ mm}$ ;

Ns = 8–14.

Description: Corallum moderately large, phaceloid, budding intratentacular. Small corallites initially connected by a tube, which later shows apophyses. Septa thin, compact, mostly arranged in two cycles; those of first cycle fused and forming a columella. Inner margin of septa occasionally swells out or shows auriculae. Wall septothecal. Columella feeble to distinct.

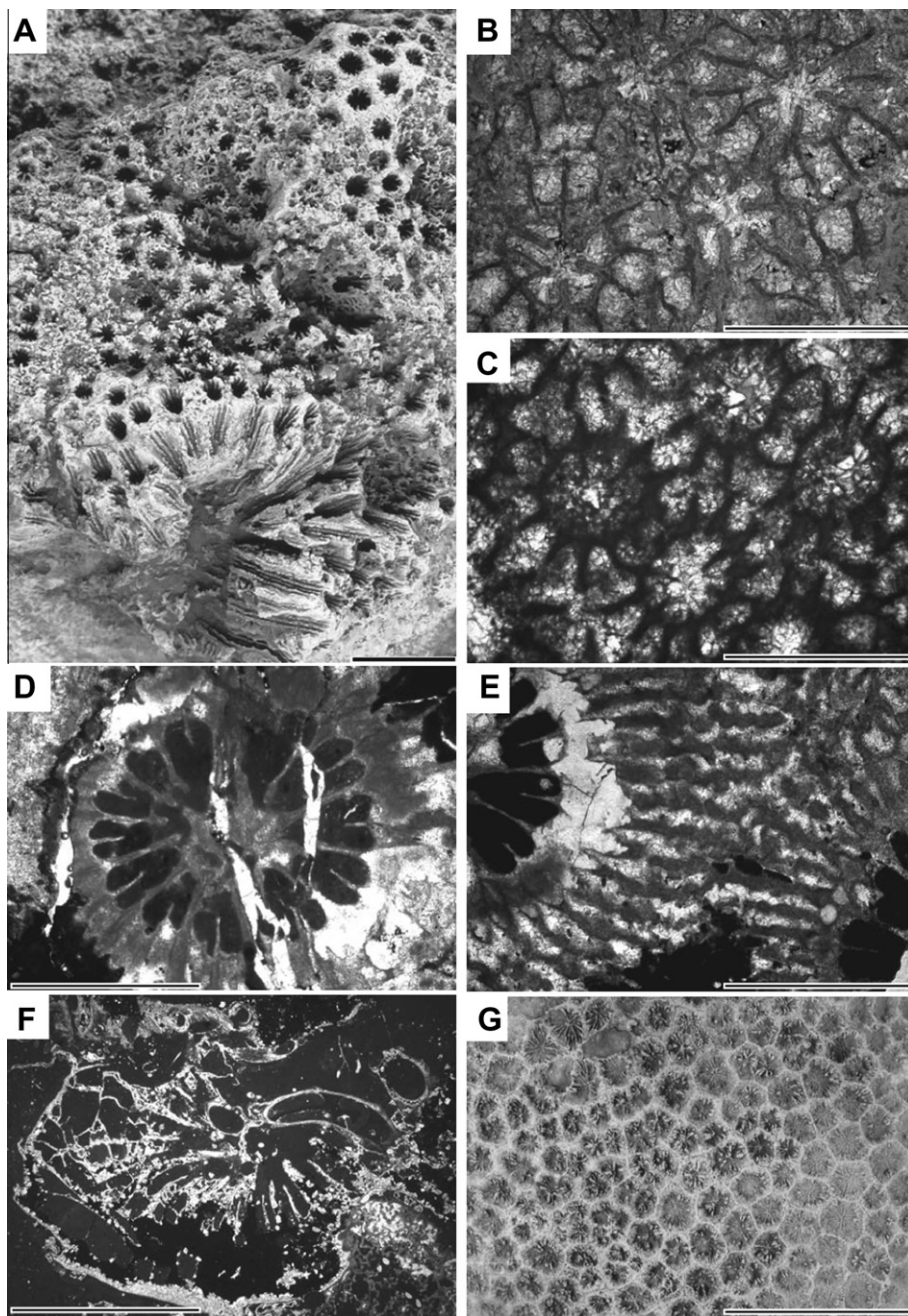
Remarks: The specimens are poorly preserved but the morphological features available agree well with *Lochmaeosmilia trapeziformis* (Gregory). The endothecal vesicular dissepiments are rarely seen in transverse thin section.

Genus *Cryptocoenia* d'Orbigny

Type species. *Astrea alveolata* Goldfuss

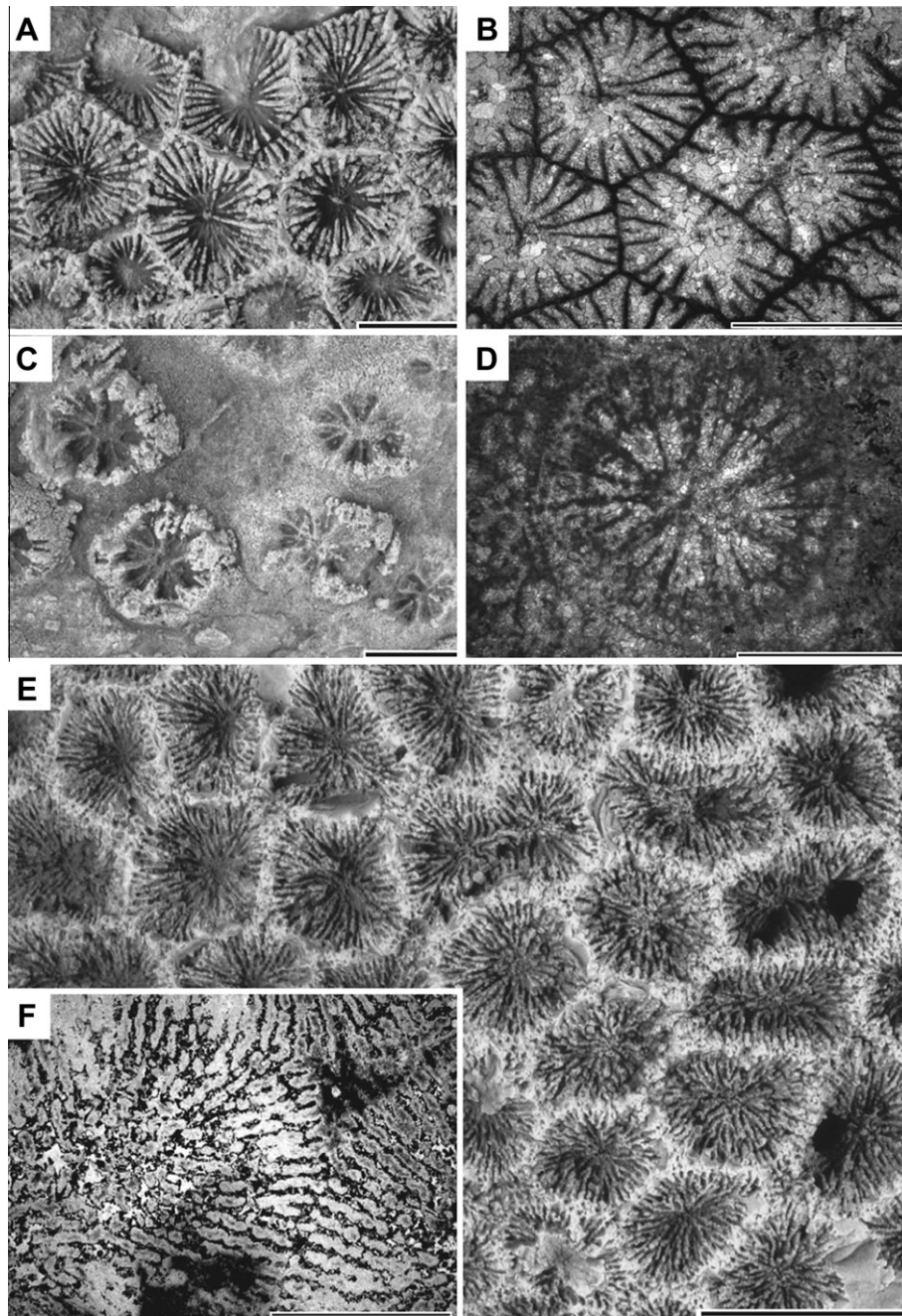
*Cryptocoenia slovenica* (Turnšek). (Fig. 7A–C)

1972 *Pseudocoenia slovenica* sp. nov. – Turnšek: 83, pl. 4, Figs. 1–2; pl. 5, Figs. 1–4.



**Fig. 7.** Stylinid, placocoeniid, cladophyllid, and isastreid corals from the Antalo Limestone north of Mekele. (A–C) *Cryptocoenia slovenica* (Turnšek). (A) Part of upper surface (94336, MB.K.7865). Scale bar = 10 mm. (B and C) Transverse thin sections showing two hexamerally arranged costo-septal cycles, mostly non-anastomosing septa, and absence of columella (94326, MB.K.7866 and 94330, MB.K.7867, respectively). Scale bar = 4 mm. (D and E) Transverse thin sections of *Columnocoenia gemmans* (de Fromentel) (94322, MB.K.7873). (D) Single corallite. Scale bar = 4 mm. (E) Two adjoining corallites with costae confluent with those of adjoining corallites. Note the rhomb-shaped outline of the trabeculae of the septa. Scale bar = 2 mm. (F) *Cladophyllia excelsa* (Koby) (94314, MB.K.7875). Scale bar = 8 mm. (G) *Isastrea bernensis* Etallon; part of upper surface (94330, MB.K.7877). Scale bar = 20 mm.





**Fig. 8.** Isastroid, rhipidogyrid, and latomeandrid corals from the Antalo Limestone north of Mekele. (A and B) *Isastrea bernensis* Etallon. (A) Part of upper surface showing tetragonal to hexagonal calices (94330, MB.K.7877). Scale bar = 5 mm. (B) Transverse thin section showing incipient budding (94324, MB.K.7878). Scale bar = 4 mm. (C and D) *Ironella arabica* El-Asa'ad (94324, MB.K.7881). (C) Part of upper surface. Scale bar = 5 mm. (D) Thin-section micrograph of a single corallite. Scale bar = 4 mm. (E and F) *Latiastrea greppini* (Koby). (E) Upper surface of large colony showing prevalence of monocentric corallites (94324, MB.K.7883). Scale bar = 10 mm. (F) Thin-section micrograph. Scale bar = 4 mm.

2003 *Pseudocoenia slovenica* Turnšek – Pandey and Fürsich:  
27, pl. 5, Fig. 5; pl. 6, Figs. 1–6.

Material. 11 specimens (7 from AL1, 4 from AL2).

Dimensions:  $d = 1.8\text{--}2.7$  mm;  $c\text{--}c = 2.0\text{--}5.4$  mm;

$Wp = 0.6\text{--}2.5$ ;  $Ns = 12$ .

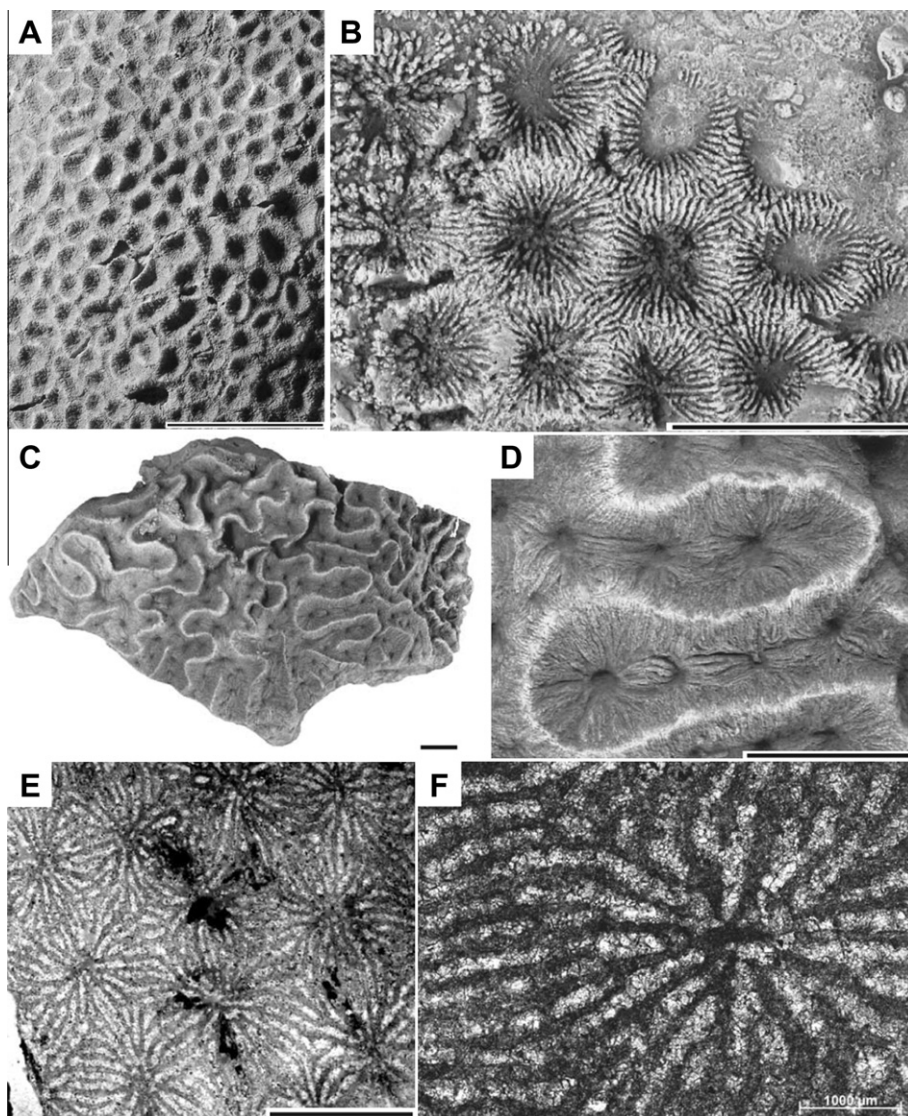
Description: Corallum moderately large, plocoid. Calices small, deep, circular in outline, separated by coenosteum.

Coenosteum consisting of costae and tabular and vesicular dissepiments. Costosepta bicuneiform, rarely anastomosing, compact, moderately thick, hexamerally arranged in two

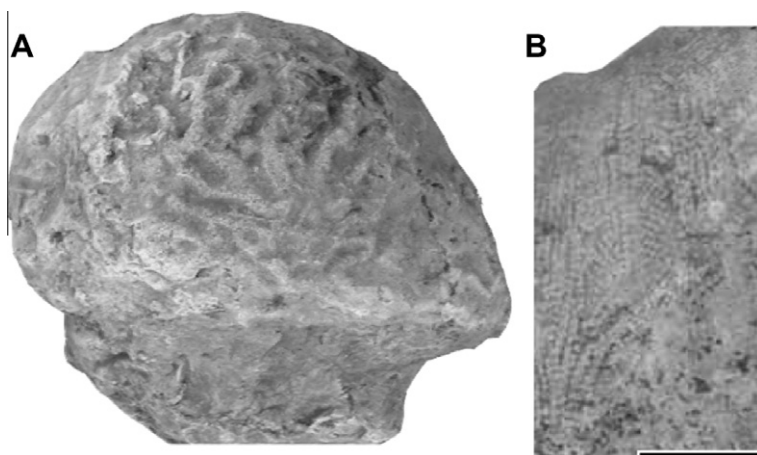
cycles. Lateral surfaces of septa ornamented with fine granules. Wall septoparathecal. Columella absent.

Remarks: The microstructure is poorly preserved, but calcification centers appear to be confined to the axial plane of the costosepta. The morphological features match the Upper Oxfordian–Lower Kimmeridgian species *C. slovenica* (Turnšek). *Cryptocoenia hexaphyllia* d'Orbigny is distinguished by its slightly larger corallites and twice as many costae. See Pandey et al. (2009) for a discussion of the generic placement.

(continued on next page)



**Fig. 9.** Latomeandrid, microsolenid, and kobyastreaeid corals from the Antalo Limestone north of Mekele. (A and B) *Ovalastrea michelini* (Milne-Edwards & Haime). (A) Surface of a large colony (94319, MB.K.7887). Scale bar = 3 cm. (B) Part of upper surface of another specimen (94326, MB.K.7888). Scale bar = 10 mm. (C and D) Upper surface of *Collignonastraea* cf. *grossouvrei* Beauvais (93857, MB.K.7889). Scale bar = 10 mm. (E and F) Transverse thin section of *Kobyastraea lomontiana* (Etallon) (94321, MB.K.7890). Scale bar = 5 mm and 1 mm, respectively.



**Fig. 10.** *Comoseris meandrinoides* (Michelin) (94314, MB.K.7891). (A) Complete colony, 6.5 cm wide. (B) Longitudinal side view. Scale bar = 5 mm.

Family Cladophylliidae Morycowa and Roniewicz

Genus *Cladophyllia* Milne-Edwards and Haime

Type species. *Lithodendron dichotomum* Goldfuss

*Cladophyllia excelsa* (Koby) (Fig. 7F)

1888 *Schizosmilia excelsa* sp. nov. – Koby: 435, pl. 114, Fig. 3a–d.

2003 *Cladophyllia excelsa* (Koby) – Pandey and Fürsich: 31, pl. 4, Fig. 3.

Material. One specimen from AL3.

Dimensions:  $d = 11.7\text{--}15.5$  mm (smallest outlier measures 4.7 mm);  $Ns = 19\text{--}40$ ;  $Ds = 3\text{--}4$  per 2 mm.

Description: Colonial, phaceloid, occasionally fused with walls of adjacent corallites, corallites circular to subcircular in outline. Septa compact, anastomosing, lateral surfaces covered with spinules. Septa arranged in at least three cycles. Septa of first cycle long and thick, joining in center with columella. Septa of higher cycles thin and shorter. Endothecal dissepiments common. Columella irregular in outline.

Remarks: The large diameter of corallites in the present specimen matches that of specimens from Iran (Pandey and Fürsich, 2003). All other known species of *Cladophyllia* have considerably smaller corallites.

Suborder Faviina Vaughan and Wells

Family Placocoeniidae Alloiteau

Genus *Columnocoenia* Alloiteau

Type species. *Columnocoenia lamberti* Alloiteau

*Columnocoenia gemmans* (de Fromentel) (Fig. 7D and E)

1861 *Stylina gemmans* sp. nov. – de Fromentel: 186.

1964 *Columnocoenia gemmans* de Fromentel – Beauvais: 175 pl. 11, Fig. 3.

Material: Two specimens from AL1.

Dimensions:  $d = 7.3\text{--}8.1$  mm;  $c\text{--}c = 7.0\text{--}8.1$  mm;  $Ns = 6 + 6 + 12 + 2$ ;  $Nc = 48$ ;  $Wp = 1.2\text{--}3.1$  mm.

Description: Corallum colonial, plocoid. Costosepta compact, bipinnate, moderately thick, arranged in four cycles of hexameral systems. Septa of first two cycles long bearing swollen, lamellar, pali-like structure at inner edge. Septa of third cycle short. Septa of fourth cycle incomplete and rudimentary. Wall septothecal. Coenosteum consists of twice as many costae as septa. Costae confluent with those of adjoining corallites. Common endothecal and exothecal dissepiments. Columella elongated, modified by septa of first cycle.

Remarks: *C. gemmans* can be distinguished from similar species by its thick perithecium.

Family Isastreidae Alloiteau

Genus *Isastrea* Milne-Edwards and Haime

Type species *Astrea helianthoides* Goldfuss

*Isastrea bernensis* Etallon. (Figs. 7G, 8A and B)

1864 *Isastrea bernensis* sp. nov. – Etallon: 392, pl. 55, Fig. 12.

1990 *Isastrea bernensis* Etallon – Errenst: 193, pl. 11, Fig. 1a–c.

Material: 42 specimens (20 from AL1, 22 from AL2).

Dimensions:  $d = 3.3\text{--}8.2$  mm;  $c\text{--}c = 2.0\text{--}6.2$  mm;  $Ns = 24\text{--}40$ ;  $Ds = 5\text{--}6$  per 2 mm.

Description: Corallum colonial, large, massive cerioid, formed by bisepal, intratentacular budding. Corallites hexagonal, pentagonal and tetragonal in outline. Calices distinct, moderately deep, mostly monocentric, rarely dicentric. Septa compact, thick, covered with granules and spinules. Septa arranged in at least four cycles, anastomosing at the inner edge. Septa of first and second cycles nearly reaching the center, occasionally forming a pseudocolumella. Distal edges of septa with sharp denticles corresponding to

trabeculae. Septa non-confluent with those of adjacent corallites. Vesicular dissepiments common near the wall. Wall septothecal.

Remarks: This species is distinguished from similar species of *Isastrea* by its indistinct columnar area and corallite dimensions.

Suborder Rhipidogyrina Roniewicz

Family Rhipidogyridae Koby

Genus *Ironella* Krasnov and Starostina

Type species. *Ironella giseldonensis* Krasnov and Starostina

*Ironella arabica* El-Asa'ad (Fig. 8C and D)

1991 *Ironella arabica* sp. nov. – El-Asa'ad: 284, pl. 5, Fig. 2a–c.

Material: 12 specimens from AL1.

Dimensions:  $d = 5.2\text{--}10.4$  mm;  $c\text{--}c = 5.9\text{--}11.2$  mm;  $Ns = 12\text{--}50$ ;  $Wp = 0\text{--}2.9$  mm.

Description: Corallum colonial, massive plocoid. Corallites distinct, calices circular to suboval in outline, shallow. Septa compact, arranged in four cycles. Septa of first cycle long, thick, reaching up to center, occasionally anastomosing near the center, producing a pseudocolumella. Endothecal vesicular dissepiments common near the wall. Columella rudimentary. Wall septothecal. Costae short, confined to wall. Exothecal vesicular dissepiments common. Septal microstructure consisting of several small-sized centers of calcification arranged in two to three rows in each primary septum.

Remarks: The present specimens match with *I. arabica*, which is currently only known from the Oxfordian of Saudi Arabia. *Ironella rutimeyeri* (Koby) is similar but differs in having smaller corallite diameters.

Suborder Microsolenina Morycowa and Roniewicz

Family Latomeandridae Alloiteau

Genus *Latiastrea* Beauvais

Type species: *Latiastrea foulassensis* Beauvais

*Latiastrea greppini* (Koby) (Fig. 8E and F)

1885 *Latimaeandra greppini* sp. nov. – Koby: 239, pl. 68, Fig. 3.

1991 *Latiastrea greppini* Koby – El As'sad: 278, pl. 2, Fig. 1a–d.

Material: Five specimens (two from AL1, three from AL2).

Dimensions:  $d = 6.9\text{--}12.5$  mm;  $c\text{--}c = 5.0\text{--}11.6$  mm;  $Ns = 56\text{--}70$ ;  $Ds = 6\text{--}7$  per 2 mm.

Description: Corallum colonial, cerioid. Corallites distinct, hexagonal in outline, moderately deep, mostly monocentric, occasionally dicentric. Septa thin, pennular, subcompact, anastomosing, arranged in at least five cycles. Septa of first and second cycles equal, reaching columella; septa of third to fifth cycles equally thick but shorter. Pores irregularly distributed. Menianae mostly continuous, bearing fine denticles. Synapticulae present. Wall septoparathecal. Columella papillose to spongy.

Remarks: This species differs from other species of *Latiastrea* by its corallite diameters, the scarcity of polycentric series, and septal densities.

Genus *Ovalastrea* d'Orbigny

Type species: *Astrea caryophylloides* Goldfuss

*Ovalastrea michelini* (Milne-Edwards and Haime) (Fig. 9A and B)

1851 *Parastrea? michelini* sp. nov. – Milne-Edwards and Haime: 116

1884 *Favia michelini* (Michelin) – Koby: 206, pl. 71, Figs. 1–5

1993 *Ovalastrea michelini* Milne-Edwards & Haime – Bertling: 100: 153, pl. 5, Fig. 1 (see for more synonymy)

Material: Three specimens (including one complete colony) from AL2.

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Dimensions:  $d = 5.5\text{--}6.8$  mm;  $c\text{--}c = 5.6\text{--}6.4$  mm;  $Ns = 46\text{--}51$ ;  $Ds = 6\text{--}7$  per 2 mm.

Remarks: The morphological characters such as plocoid colony, circular to suboval outlines of the calices, pennular subcompact septa and papillose to spongy columella match with *Ovalastrea* d'Orbigny. However, due to densely packed corallites and internal recrystallization the exothecal elements are not known. The dense packing of corallites, the cerio-plocoid nature of the colony, and diameter of corallites match *O. michelini* (Milne-Edwards and Haime). *O. proeminens* (Koby) has similar dimensions but a thicker coenosteum.

Genus *Collignonastraea* Alloiteau

Type species: *Comoseris jumarense* var. *radiata* Gregory  
*Collignonastraea* cf. *grossouvrei* Beauvais. (Fig. 9C and D)  
cf. 1972 *Collignonastraea grossouvrei* sp. nov. – Beauvais: 48, pl. E, fig. 3.

Material: One specimen from AL2.

Dimensions:  $d = 3.8\text{--}11.8$  mm;  $c\text{--}c = 3.9\text{--}7.2$  mm;

$Ws = 3.8\text{--}8.5$  mm;  $Lc \leq 50$ ;  $Ns \approx 75$ ;  $Ds = 9\text{--}10$  per 2 mm.

Description: Corallum colonial, flat, meandroid, formed by intracalicular linear budding. Valleys sinuous, wide, with mostly one, rarely two series of calice centers. Valleys divide into two towards the periphery. Septa subcompact; distal margin with fine, acute to obtuse denticles. Septa confluent within valley (thamnasterioid aspect). Collines prominent, tectiform to tholiform. Stereozone developed (up to 1.4 mm thick). Septa thin and numerous, mostly non-anastomosing, pennular.

Remarks: The morphological characters and dimensions, particularly septal density and trabecular density match *Collignonastraea grossouvrei* Beauvais (1972), but due to lack of information on microstructure, the present specimen has been identified with qualification.

Family Microsolenidae Koby

Genus *Comoseris* d'Orbigny

Type species: *Pavonia meandrinoides* Michelin

*Comoseris meandrinoides* (Michelin) (Fig. 10)

1843 *Pavonia meandrinoides* sp. nov. – Michelin: 100, pl. 22, Fig. 3.

1964 *Comoseris meandrinoides* (Michelin) – Beauvais: 236 (with synonymy).

2007 *Comoseris meandrinoides* (Michelin) – Pandey et al.: 47, pl. 13, Figs. 2a–b.

Material: One complete colony from AL3.

Dimensions:  $d = 1.9\text{--}2.3$  mm;  $Lc > 50$ ;  $Ws = 4.3$  mm;  $Ds = 7\text{--}8$  per 2 mm.

Description: Corallum compound, massive, globular, meandroid with moderately large attachment area. Upper surface convex. Budding intracalicular. Calices arranged as series demarcated by tholiform collines. Stereozone thick. Valleys sinuous, long, moderately deep. Costosepta thin, pennular, fenestrate, confluent and parallel, crossing the collines at right angles. Menianae continuous.

Remarks: Although the nature of the columella is not known, morphological features such as the meandroid colony and pennular and fenestrate septa are indicative of *Comoseris*. The septal density and width of series match *C. meandrinoides* (Michelin).

Suborder Fungiina Verrill

Family Kobyastraeidae Roniewicz

Genus *Kobyastrea* Roniewicz

Type species: *Thamnastraea lomontiana* Etallon  
*Kobyastrea lomontiana* (Etallon) (Fig. 9E and F)

1864 *Thamnastraea lomontiana* sp. nov. – Etallon: 399, pl. 56, Fig. 14.

1970 *Kobyastrea lomontiana* (Etallon) – Roniewicz: 140, pl. 1, Figs. 1 and 2; pl. 2, Fig. 1; pl. 3, Fig. 4.

1991 *Kobyastrea lomontiana* (Etallon) – El As'sad: 282, pl. 4, Fig. 1a–c.

Material: One specimen from AL1.

Dimensions:  $d = 3.3\text{--}7.1$  mm;  $c\text{--}c = 3.2\text{--}5.6$  mm;  $Ns = 20\text{--}30$ .

Description: Corallum colonial, lamellar, thamnasterioid.

Calices shallow. Columella styliiform. Septa anastomosing, granulated.

Remarks: The corallites are much larger than in the similar genus *Thamnasteria*. Dimensions fit *K. lomontiana* (Etallon).

## 6.2. Brachiopods

The brachiopod material is stored in the Museum für Naturkunde in Berlin; inventory numbers MB.B.3355–MB.B.3410. We were able to identify only one species with certainty: *Somalirhynchia africana* Weir. All the other specimens were identified to the genus level and are only briefly described. In addition to the taxa discussed below we also found the genera *Colpotoria* and *Septaliphoria*.

Class Rhynchonellata Williams et al.

Order Rhynchonellida Kuhn

Family Tetrarhynchiidae Ager

Genus *Somalirhynchia* Weir

Type species: *Somalirhynchia africana* Weir

*Somalirhynchia africana* Weir (Fig. 11A–E)

\*1925 *Somalirhynchia africana* sp. nov. – Weir: 80, pl. 12, Figs. 20–30.

v. 1935 *Somalirhynchia africana* – Muir-Wood: 94, text-figs 7–8, pl. 10, Fig. 7-a.

v. 2001 *Somalirhynchia africana* – Feldman et al.: 641, text-figs 3, pl. 1, Figs. 7–15.

Material: More than 100 individuals, mostly from AL2.

Remarks: Our specimens fit the description of *Somalirhynchia africana* by Feldman et al. (2001), so that we can assign them with certainty to this species. Specimens vary profoundly in size, reaching up to 4.2 cm in width.

Genus *Cymatorhynchia* Buckman

Type species: *Rhynchonella cymatophorina* Buckman

*Cymatorhynchia* sp. (Fig. 11F–J)

Material: 16 individuals from AL2.

Description: Large cymatorhynchiid specimens, with on average 8 costae on a low fold, transverse rather than subpentagonal in outline, dorsi-biconvex in longitudinal section. Anterior commissure widely uniplicate. Uniplication moderately developed, fold conspicuous but gently elevated, sulcus originates in the anterior third of ventral valve. Costae on complete valve numbering 20–28, angular in cross-section.

Remarks: Our specimens are externally similar to the specimens of *Cymatorhynchia quadriplicata* (Zieten) figured in Shi and Grant (1993). However, without knowing the internal morphology, we prefer to use open nomenclature. Our specimens represent the youngest occurrences of *Cymatorhynchia*, which has been only reported from the Middle Jurassic until now.

Genus *Daghanirhynchia* Muir-Wood

Type species: *Daghanirhynchia daghaniensis* Muir-Wood  
*Daghanirhynchia* sp. (Fig. 11P–T)

Material: 54 individuals (3 from AL1, 51 from AL2).

Description: Large *Daghanirhynchia* specimens with 8–10 subangular, coarse and narrow costae on ventral flank and conspicuous fold and sulcus. Shells dorsi-biconvex with maximum width at about mid-length of shell. Profound sulcus starting in the posterior third of valve ending in a prominent sulcus tongue. Fold clearly elevated.

Remarks: *Daghanirhynchia* consists of several species, most of them are identified by internal morphology. Externally our material resembles mostly *D. macfadyeni* Muir-Wood.

Genus *Amydroptychus* Cooper

Type species: *Amydroptychus formosus* Cooper  
 cf. *Amydroptychus* sp. (Fig. 11K–O)

Material: 10 individuals from base of AL2.

Description: Specimens are wider than long, subtriangular in outline, and gently dorsi-biconvex to equi-biconvex in longitudinal section. Fold and sulcus inconspicuous, dorsal fold mostly not recognizable (Fig. 8N), with faint uniplication. Costae angular to rounded in few cases with small furrows intercalated at the ventral umbo. Dorsal median septum short (Fig. 11L and O).

Remarks: Our material is somewhat wider and less globose than *A. formosus* (Cooper, 1989), the type species of this genus, which has been reported from the Bajocian of Israel and Saudi Arabia. However, *A. formosus* resembles our specimens in overall outline and curvature as well as in the structure of costae. Regarding the differences in geographical and stratigraphical occurrences between *A. formosus* and our specimens, it is very likely that this fauna contains a new species of *Amydroptychus*.

## Order Terebratulida Waagen

## Suborder Terebratulidina Waagen

## Family Lissajousithyrididae Cooper

Genus *Monsardithyris* Alm  ras

Type species: *Terebratula ventricosa* Hartmann

*Monsardithyris* sp. (Fig. 12A–E)

Material: 20 individuals from AL2.

Description: Shells subcircular in outline or elongated. Surface smooth. Anterior margin gently rectimarginate to uniplicate but sulcus and fold not recognizable on shell surface. Growth lines gently visible at anterior margin. Beak short with large foramen.

Remarks: Our specimens are rather small in comparison to other *Monsardithyris* taxa. This may explain the faint development of sulcus and fold, which are more clearly developed in larger forms. Therefore, we interpret our material as young adult forms.

## Family Loboidothyrididae Makridin

Genus *Cererithyris* Buckman

Type species: *Terebratula intermedia* J. Sowerby

*Cererithyris* sp. (Fig. 12F–J)

Material: 106 individuals (1 from AL1, 105 from AL2).

Description: Shells elongate and quite globular, equi-biconvex in longitudinal section. Beak low with large foramen. Anterior margin sulcinate. Sulcus very weak with broad but low median costa which starts shortly anterior of hinge line. Fold in the anterior half with clearly developed but low median furrow that is rounded in cross-section.

Remarks: Taxa of *Cererithyris* are characterized by a strong intraspecific variability. At this stage of research it is impossible to identify our material to species level.

## 6.3. Bivalves

The classification of higher taxa follows the taxonomic listing of extant bivalve families of Bieler and Mikkelsen (2006). In the synonymy lists we focus on the most important references with an emphasis on figured specimens from East Africa. The material is stored in the Museum f  r Naturkunde in Berlin; inventory numbers MB.M.8117–MB.M.8178. In addition to the described material we found *Camptonectes* (*Camptonectes*) sp. and *Falcimylus* cf. *jurensis* (Roemer).

## Class Bivalvia Linnaeus

## Subclass Pteriomorpha Beurlen

## Order Mytiloida F  russac

## Family Mytilidae Rafinesque

Genus *Arcomytilus* Agassiz

Type species: *Mytilus pectinatus* J. Sowerby

*Arcomytilus laitmairensis* (de Loriol) (Fig. 13A and B)

1883 *Mytilus laitmairensis* sp. nov. – de Loriol and Scharolt: 57, pl. 8, Figs. 6–12.

1930 *Mytilus subpectinatus* d'Orb. – Basse: 138, pl. 5, Fig. 10.

1931 *Mytilus laitmairensis* de Loriol – Diaz-Romero: 29, pl. 2, Figs. 11–12.

1935 *Mytilus* (*Arcomytilus*) *laitmairensis* de Loriol – Cox: 164, pl. 15, Figs. 13–14 (see for synonymy list).

1939 *Mytilus* (*Arcomytilus*) *cossmanni* Roll. – Stefanini: 215, pl. 23, Fig. 22.

1940 *Brachidontes* (*Arcomytilus*) *laitmairensis* (de Loriol) – Cox: 81, pl. 5, Figs. 15–17.

1959 *Mytilus* (*Arcomytilus*) *laitmairensis* de Loriol – Jaboli: 44, pl. 5, Fig. 10.

1965 *Brachidontes* (*Arcomytilus*) *laitmairensis* (de Loriol) – Cox: 41, pl. 4, Fig. 3.

1965 *Brachidontes* (*Arcomytilus*) *laitmairensis* (de Loriol) – Freneix: 97, pl. 5, Fig. 14.

1971 *Mytilus* (*Arcomytilus*) *laitmairensis* de Loriol – Jordan: 152, pl. 20, Figs. 8a and b.

1995 *Arcomytilus laitmairensis* (de Loriol 1883) – Jaitly et al.: 201, pl. 21, Figs. 1–3.

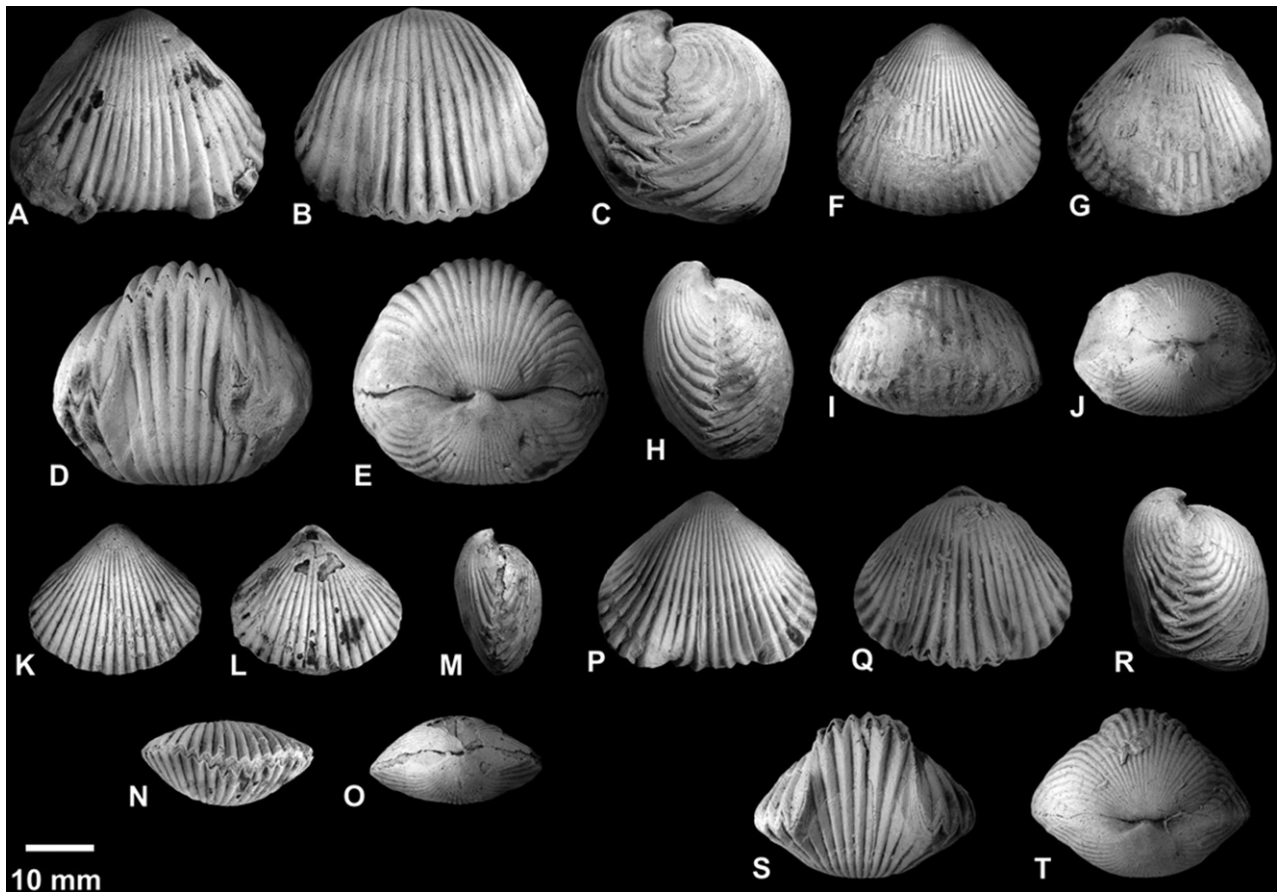
1998 *Arcomytilus laitmairensis* (de Loriol 1883) – Holzapfel: 96, pl. 3, Fig. 12.

1999 *Arcomytilus laitmairensis* (de Loriol 1883) – Ahmad: 24, pl. 2, Figs. 7–8.

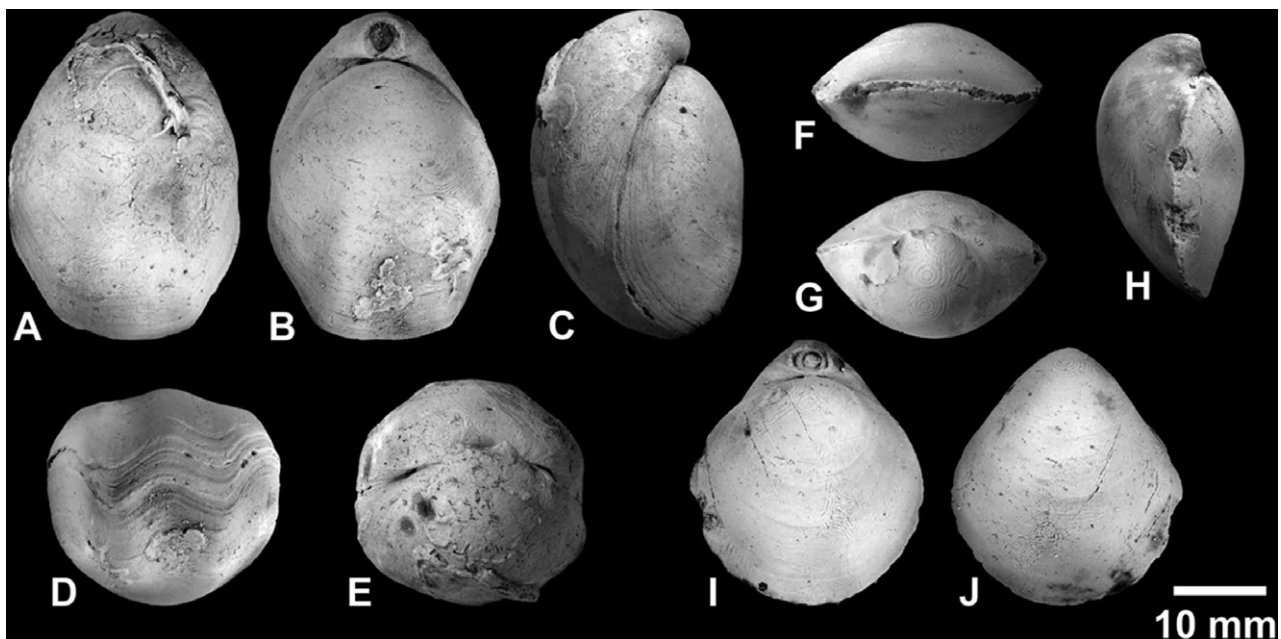
Material: 3 left valves, 1 right valve and 4 articulated specimens (AL1 and AL2).

Remarks: This widespread species of *Arcomytilus* is characterized by a recurved shell with an evenly convex postero-dorsal and ventral margin and the absence of a distinct umbonal ridge. The shell surface is ornamented with radial, divaricating ribs, which sometimes bifurcate and undulate. The ornament is missing on the region ventrally of the beaks, but in several specimens fine riblets are present just below the beaks. In this respect, the ornament is reminiscent of that of *Musculus*. This feature also has been observed in some specimens of *Arcomytilus morrissi* (Sharpe) from the Kimmeridgian of Portugal (F  rsich and Werner, 1988).

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**Fig. 11.** Rhynchonellid brachiopods from the Antalo Limestone of Ethiopia. (A–E) *Somalirhynchia africana* Weir, 1925 (93858, MB.B.3355). Ventral (A), dorsal (B), lateral (C), anterior (D), and posterior (E) views. (F–J) *Cymatorhynchia* sp. (93858, MB.B.3356). Ventral (F), dorsal (G), lateral (H), anterior (I), and posterior (J) views. (K–O) cf. *Amydroptychus* sp. (93858, MB.B.3357). Ventral (K), dorsal (L), lateral (M), anterior (N), and posterior (O) views. (P–T) *Daghanirhynchia* sp. (93860, MB.B.3358). Ventral (P), dorsal (Q), lateral (R), anterior (S), and posterior (T) views.



**Fig. 12.** Terebratulid brachiopods from the Antalo Limestone north of Mekele. (A–E) *Monsardithyris* sp. (93856, MB.B.3360). Ventral (A), dorsal (B), lateral (C), anterior (D), and posterior (E) views. (F–J) *Cererithyris* sp. (93856, MB.B.3361) Posterior (F), anterior (G), dorsal (H), ventral (I), and lateral (J) views.



Genus *Modiolus* LamarckType species: *Mytilus modiolus* Linnaeus*Modiolus* (*Modiolus*) *imbricatus* J. Sowerby. (Fig. 13C)1818 *Modiola imbricata* sp. nov. – J. Sowerby: 21, pl. 112, Figs. 1 and 3.1870 *Modiola imbricaria*, Sow. var. – Blandford: 201, Fig. 2.1930 *Modiola subangustissima* Dacqué – Basse: 138, pl. 5, Figs. 11a and b.1935 *Mytilus* (*Modiolus*) *imbricatus* (J. Sowerby) – Cox: 162, pl. 16, Figs. 3–5 (see for synonymy list).1939 *Mytilus* (*Modiola*) *imbricatus* Sow. – Stefanini: 213, pl. 23, Figs. 18–20.1959 *Mytilus* (*Modiolus*) *imbricatus* (Sowerby) – Jaboli: 40, pl. 5, Fig. 7.1959 *Mytilus* (*Modiolus*) *gortanii* sp. nov. – Jaboli: 42, pl. 6, Fig. 1.1965 *Modiolus imbricatus* (J. Sowerby) – Cox: 36, pl. 3, Figs. 5 and 6.1995 *Modiolus* (*Modiolus*) *imbricatus* J. Sowerby – Jaitly et al.: 203, pl. 22, Figs. 4–10 (see for synonymy list).1998 *Modiolus* (*Modiolus*) *imbricatus* J. Sowerby – Holzapfel: 97, pl. 3, Figs. 18–19 (see for synonymy list).

Material: 3 double-valved specimens (2 from AL1, 1 from AL2).

Remarks: We consider *M. gortanii* Jaboli to be a large specimen of *M. imbricatus*.Genus *Musculus* RödingType species: *Mytilus discors* Linnaeus*Musculus* (*Musculus*) *somaliensis* (Cox) (Fig. 13D)1886 *Modiola aspera* Sow. – Douvillé: 228, pl. 12, Fig. 11.1925 *Modiola autissiodorensis* Cott. – Stefanini: 170, pl. 28, Fig. 7.1935 *Mytilus* (*Musculus*) *somaliensis* sp. nov. – Cox: 164, pl. 16, Figs. 1 and 2.1939 *Mytilus* (*Musculus*) *somaliensis* Cox – Stefanini: 215, pl. 23, Fig. 21.1959 *Mytilus* (*Musculus*) *somaliensis* Cox – Jaboli: 44, pl. 5, Figs. 8 and 9.1965 *Musculus somaliensis* Cox – Freneix: 98, pl. 5, Figs. 15 and 16.1968 *Musculus somaliensis* (Cox, 1935) – Ficarelli: 32, pl. 3, Fig. 6.1971 *Mytilus* (*Musculus*) *somaliensis* Cox – Jordan: 148, pl. 19, Fig. 3a and b.1998 *Musculus* (*Musculus*) *somaliensis* (Cox, 1935) – Holzapfel: 97, pl. 3, Figs. 13 and 14.

Material: 2 articulated specimens from AL1 and AL2.

Remarks: *Musculus somaliensis* has a modioliform shape with a straight to weakly convex dorsal margin. A rounded carina runs from the umbo to the postero-ventral corner of the shell, forming an angle of ca. 45° with the dorsal margin, ventrally followed by a shallow sulcus. The antero-ventral part of the shell is inflated and has a convex antero-ventral margin. In these morphological features it differs from the similarly ribbed *Arcomytilus laitmairensis* (see above) which is mytiliform in outline and exhibits an evenly rounded postero-dorsal margin. Its carina is more strongly curved and in its distal part forms an angle of ca. 60–70° with the dorsal margin. A sulcus is absent, the antero-ventral part is low and limited by a concave antero-ventral margin.

## Order Pterioidea Newell

## Family Pinnidae Leach

Genus *Stegoconcha* BöhmType species: *Pinna granulata* J. Sowerby*Stegoconcha gmuelleri* (Krenkel) (Fig. 13E)1910 *Pinna G. Mülleri* sp. nov. – Krenkel: 203, pl. 21, Fig. 5.1933 *Stegoconcha solida* J. Böhm var. *tendagurensis* n. var. – Dietrich: 61, pl. 9, Figs. 138–139.1965 *Stegoconcha gmuelleri* (Krenkel) – Cox: 47, pl. 5, Fig. 8.1995 *Stegoconcha gmuelleri* (Krenkel, 1910) – Jaitly et al.: 176, pl. 9, Fig. 1; pl. 10, Fig. 1.

Material: 2 articulated specimens from AL2.

Remarks: With its distinct, arched umbonal ridge and its wavy rounded radial ribs on the area postero-dorsally of it, the Ethiopian specimens agree well with those figured from eastern Africa and India.

## Family Ostreidae Rafinesque

Genus *Liostrea* DouvilléType species: *Ostrea sublamellosa* Dunker*Liostrea* sp. (Fig. 13F)

Material: 2 specimens from AL1 and AL2.

Remarks: Due to the absence of radial ribs, chomata and spirally incoiled umbones, this oyster can be referred to the genus *Liostrea*.

## Family Palaeolophidae Malchus

Genus *Actinostreon* BayleType species: *Ostrea solitaria* J. de C. Sowerby*Actinostreon solitarium* (J. de C. Sowerby) (Fig. 13G)1824 *Ostrea solitaria* sp. nov. – J. de C. Sowerby: 105, pl. 468, Fig. 11933 *Lopha solitaria* (J. Sowerby) – Arkell: 185, pl. 22, Fig. 4; pl. 23, Figs. 5–71935 *Lopha solitaria* (J. de C. Sowerby) – Cox: 171, pl. 17, Figs. 9–121939 *Lopha solitaria* (Sow.) – Stefanini: 197, pl. 22, Figs. 6–71959 *Lopha solitaria* (Sowerby) – Jaboli: 36, pl. 5, Fig. 11965 *Lopha solitaria* (J. de C. Sowerby) – Cox: 69, pl. 9, Fig. 41971 *Lopha solitaria* (J. de C. Sowerby) – Jordan: 152, pl. 20, Figs. 4–51998 *Actinostreon solitarium* (J. de C. Sowerby) – Holzapfel: 106, pl. 6, Figs. 15–17 (see for synonymy list)

Material: 75 specimens, 10 from AL1 and 65 from AL2.

Remarks: This is the most abundant bivalve species in the sampled sections. Based on the more rounded outline and lower number of radial ribs of *A. solitarium* as compared to the more elongate *A. gregareum* (J. Sowerby) which also carries more numerous and dichotomous ribs (see Arkell, 1933), the studied material is assigned to the former.

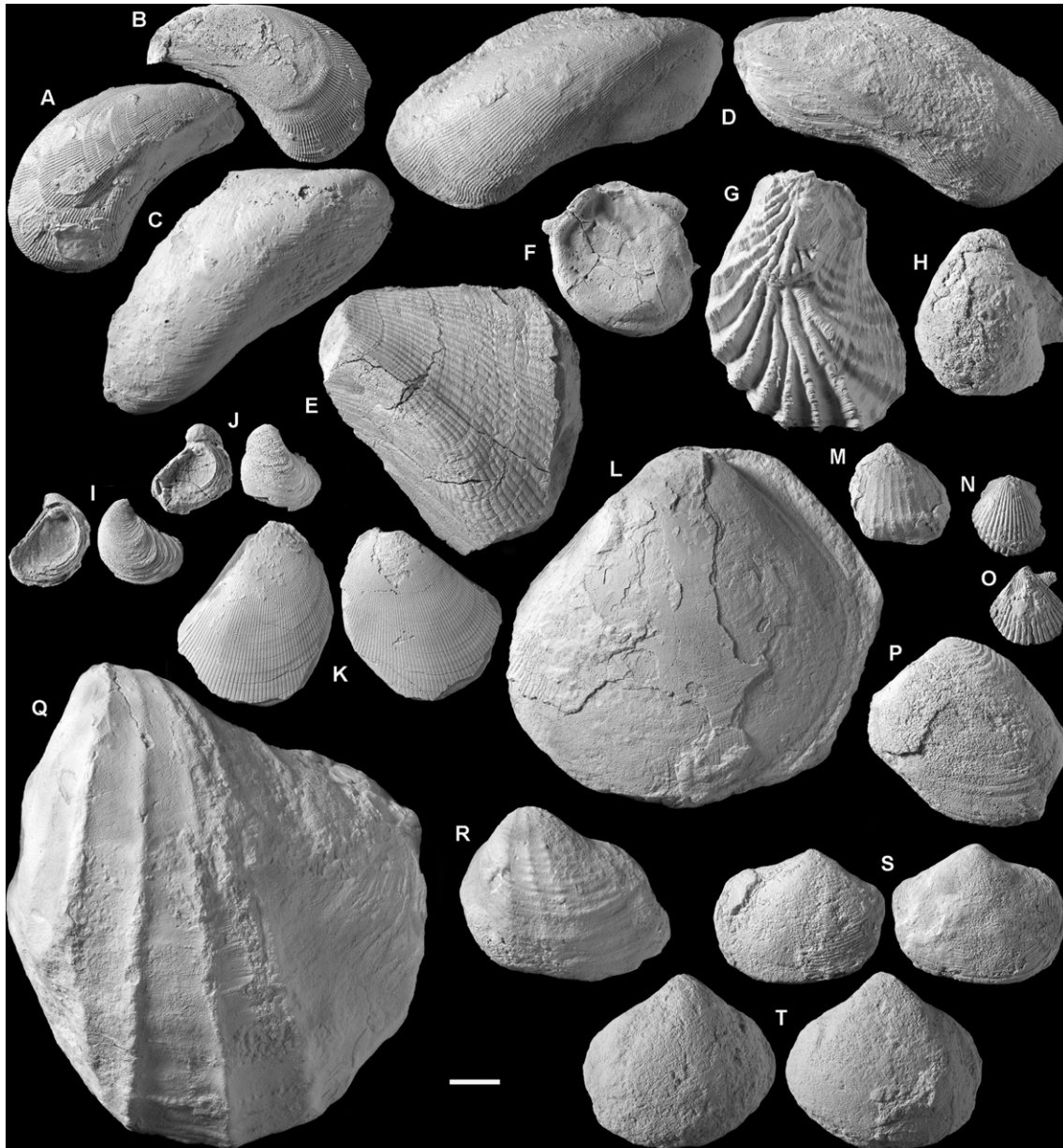
## Family Gryphaeidae Vyalov

Genus *Gryphaea* LamarckType species: *Gryphaea arcuata* LamarckSubgenus *Bilobissa* StenzelType species: *Gryphaea bilobata* J. de C. Sowerby*Gryphaea?* (*Bilobissa?*) *balli* (Stefanini) (Fig. 13H)1925 *Liogryphaea balli* sp. nov. – Stefanini: 164, pl. 29, Fig. 2.1935 *Gryphaea balli* (Stefanini) – Cox: 173, pl. 18, Figs. 1–7 (see for synonymy list).

Material: 1 left valve from AL1.

Remarks. Based on the presence of a well detached posterior flange the species is tentatively assigned to *Gryphaea* (*Bilobissa*). While our specimen does not show radial ribs on the left valve, the material examined by Cox (1935) sometimes exhibits a few ill-defined radial folds on the

(continued on next page)



**Fig. 13.** Jurassic bivalves from the Antalo Limestone north of Mekele, Ethiopia. (A and B) *Arcomytilus laitmairiensis* (de Lorient), (A) right valve view of articulated specimen (93871, MB.M.8117), (B) left valve view (94788, MB.M.8118.1); (C) *Modiolus (Modiolus) imbricatus* J. Sowerby, right valve view of articulated specimen (93861, MB.M.8119); (D) *Musculus (Musculus) somaliensis* (Cox), right valve (left) and left valve view (right) of articulated specimen (93858, MB.M.8120); (E) *Stegoconcha gmuelleri* (Krenkel), left valve view of articulated specimen (93858, MB.M.8121.1); (F) *Liostrea* sp., interior view of right valve (93869, MB.M.8122); (G) *Actinostreon solitarium* (J. de C. Sowerby), left valve view of articulated specimen (94788, MB.M.8123.1); (H) *Gryphaea? (Bilobissa?) balli* (Stefanini), left valve view (93868, MB.M.8124); (I–J) *Nanogyra nana* (J. Sowerby), (I) right valve (left) and left valve view (right) of articulated specimen (93860, MB.M.8125.1), (J) right valve (left) and left valve view (right) of articulated specimen (93860, MB.M.8125.2); (K) *Plagiostoma harronis* (Dacqué), left valve (left) and right valve view (right) of articulated specimen (93031, MB.M.8126); (L) *Plagiostoma sublaeviusculum* (Krumbeck), left valve view (93866, MB.M.8127); (M) *Eopecten velatus* (Goldfuss), left valve view (93871, MB.M.8128); (N–O) *Spondylopecten (Spondylopecten) palinurus* (d'Orbigny), (N) right valve view (93868, MB.M.8129), (O) right valve view (93864, MB.M.8130); (P) *Seebachia ("Eoseebachia") sowerbyana* (Holdhaus), left valve view (93860, MB.M.8131); (Q) *Pholadomya (Bucardiomya) somaliensis* Cox, left valve view of articulated specimen (93866, MB.M.8132.1); (R) *Pholadomya (Bucardiomya) lirata* (J. Sowerby), left valve view of articulated specimen (93029, MB.M.8133); (S) *"Lucina" cf. cecchii* Jaboli, right valve (left) and left valve view (right) of articulated specimen (93861, MB.M.8134); (T) *Integricardium (Integricardium) cf. bannesianum* (Contejean), right valve (left) and left valve view (right) of articulated specimen (93029, MB.M.8135.1). Scale bar = 10 mm.

umbo of the left valve, a feature that is reminiscent of the genus *Africogryphaea*.

#### Genus *Nanogyra* Beurlen

Type species: *Gryphaea nana* J. Sowerby

*Nanogyra nana* (J. Sowerby) (Fig. 13I and J)

1822 *Gryphaea nana* sp. nov. – J. Sowerby: 114, pl. 383, Fig. 3.

1886 *Exogyra imbricata* Krauss – Douvillé: 230, pl. 12, Figs. 8–9.

1925 *Exogyra fourtaui* sp. nov. – Stefanini: 168, pl. 39, Fig. 3 (non Fig. 4).

1929 *Exogyra fourtaui* Stefanini – Weir: 20, pl. i, Figs. 6–8, 10 (non Fig. 9).

1931 *Exogyra vinassai* sp. nov. – Diaz-Romero: 35, pl. 2, Figs. 17–20; pl. 3, Figs. 1 and 2.

1931 *Exogyra fourtaui* Stef. – Diaz-Romero: 38, pl. 3, Figs. 6–8 (non Figs. 9 and 10).  
 1935 *Exogyra fourtaui* Stefanini – Cox: 174, pl. 17, Fig. 14a and b (see for synonymy list).  
 1935 *Exogyra nana* (J. Sowerby) – Cox: 175, pl. 17, Fig. 16a and b (see for synonymy list).  
 1959 *Exogyra nana* (Sowerby) – Jaboli: 38, pl. 5, Fig. 5.  
 1965 *Exogyra nana* (J. Sowerby) – Cox: 73, pl. 11, Figs. 5–6 (see for synonymy list).  
 1968 *Exogyra fourtaui* Stefanini, 1925 – Ficarelli: 35, pl. 2, Figs. 5–9.  
 1968 *Exogyra fourtaui* Stefanini f. *sinuata* n. – Ficarelli: 35, pl. 2, Figs. 10, 10a and b.  
 1971 *Exogyra fourtaui* Stefanini 1925 – Jordan: 152, pl. 20, Figs. 6 and 7.  
 1995 *Nanogyra nana* (J. Sowerby 1822) – Jaitly et al.: 189, pl. 16, Figs. 13–15; pl. 17, Figs. 1 and 2.  
 1998 *Nanogyra nana* (J. Sowerby 1822) – Holzapfel: 108, pl. 6, Figs. 6 and 7.  
 Material: 2 articulated specimens from AL2.  
 Remarks: *Nanogyra fourtaui* from the Ethiopian Province (see synonymy list) is characterized by a narrow umbonal region and a lunate outline. This shape is due to a tiny attachment area. Because this morphotype is also found in large populations of *N. nana* from Europe and India with highly variable size of the attachment area (e.g. Jaitly et al., 1995), we consider *N. fourtaui* as a junior synonym of *N. nana*.

#### Order Limoida Waller

##### Family Limidae d'Orbigny

##### Genus *Plagiostoma* J. Sowerby

Type species: *Plagiostoma giganteum* J. Sowerby

*Plagiostoma harronis* (Dacqué) (Fig. 13K)

1905 *Lima harronis* sp. nov. – Dacqué: 133, pl. 15, Figs. 13 and 14.

1935 *Lima* (*Plagiostoma*) *harronis* Dacqué – Cox: 179, pl. 19, Figs. 2 and 3 (see for synonymy list).

1959 *Lima* (*Plagiostoma*) *bianchii* sp. nov. – Jaboli: 30, pl. 4, Figs. 6 and 7.

? 1968 *Lima* (*Plagiostoma*) sp. aff. *harronis* Dacqué, 1905 – Ficarelli: 34, pl. 4, Fig. 1. Material: 3 left valves, 5 right valves and 2 articulated specimens (4 specimens from AL1, 6 from AL2).

Remarks: Jaboli (1959) erected the new species *P. bianchii* because it is larger than the type specimen of *P. harronis* and exhibits the radial sculpture also in the umbonal region. Because size per se is not a useful character to discriminate species, and intensity of ribbing in the umbonal region varies with the state of preservation, we include *bianchii* in the synonymy of *harronis* herein.

*Plagiostoma sublaeviusculum* (Krumbeck) (Fig. 13L)

1905 *Lima sublaeviuscula* sp. nov. – Krumbeck: 99, pl. 3, Fig. 3a and b.

1965 *Lima* (*Plagiostoma*) *sublaeviuscula* Krumbeck – Cox: 62, pl. 8, Figs. 5 and 6.

Material: 1 left valve, 1 right valve and 1 articulated specimen, all from AL2.

Remarks: The Ethiopian specimens agree well in shape with *P. sublaeviusculum* from the Upper Jurassic of Lebanon and Kenya (see synonymy list). They exhibit the characteristic ornament of low, irregularly spaced radial ribs which are confined to the anterior, posterior, and ventral parts of the

shell surface, whereas the central part of the shell is smooth.

#### Order Pectinoida Adams and Adams

##### Family Pectinidae Rafinesque

##### Genus *Eopecten* Douvillé

Type species: *Hinnites tuberculatus* Goldfuss

*Eopecten velatus* (Goldfuss) (Fig. 13M)

1833 *Pecten velatus* sp. nov. – Goldfuss: 45, pl. 90, Fig. 2.

1886 *Pleuronectites aubryi* sp. nov. – Douvillé: 228, pl. 12, Fig. 3.

1933 *Velata inaequistriata* (Voltz) – Dietrich: 67, pl. 8, Fig. 129.

1939 *Velata aubryi* (Douv.) – Stefanini: 186, pl. 20, Figs. 10 and 11; pl. 21, Fig. 1.

1939 *Velata* sp. n. indet. – Stefanini: 189, pl. 21, Fig. 2a–d.

1965 *Eopecten aubryi* (Douvillé) – Cox: 52, pl. 6, Figs. 3 and 4.

1965 *Eopecten thurmanni* (Brauns) – Cox: 53, pl. 6, Fig. 8.

1965 *Eopecten* aff. *albus* (Quenstedt) – Cox: 54, pl. 6, Fig. 7.

1984 *Eopecten velatus* (Goldfuss) – Johnson: 150, pl. 5, Figs. 4, 5, 7, 8 (see for synonymy list).

1995 *Eopecten velatus* (Goldfuss) – Jaitly et al.: 196, pl. 19, Figs. 5, 9–11; pl. 20, Fig. 1 (see for synonymy list).

1998 *Eopecten velatus* (Goldfuss) – Holzapfel: 101, pl. 4, Figs. 19–21.

1999 *Eopecten velatus* (Goldfuss) – Ahmad: 24, pl. 5, Figs. 1 and 2.

Material: 1 left valve from AL1.

Remarks: Although only a single small left valve was available, it can be assigned to *E. velatus* because of its diagnostic differentiation of the ornament into costae and striae (see Johnson, 1984)

##### Genus *Spondylopecten* Roeder

Type species: *Pecten* cf. *erinaceus* Buvignier

*Spondylopecten* (*Spondylopecten*) *palinurus* (d'Orbigny). (Fig. 13N and O)

1850 *Pecten palinurus* sp. nov. – d'Orbigny: 342.

1984 *Spondylopecten* (*Spondylopecten*) *palinurus* (d'Orbigny) – Johnson: 92, pl. 3, Figs. 8–14 (see for synonymy list).

1995 *Spondylopecten* (*Spondylopecten*) *palinurus* (d'Orbigny) – Jaitly et al.: 194, pl. 18, Figs. 16–18.

1998 *Spondylopecten* (*Spondylopecten*) *palinurus* (d'Orbigny) – Holzapfel: 100, pl. 4, Figs. 11–15.

Material: 2 right valves from AL1.

Remarks: Johnson (1984) distinguished *S. palinurus* from all other species of *S. (Spondylopecten)* by the low number of radial plicae (26 or less). The two specimens from Ethiopia have 22 plicae respectively and therefore fall within this range. The rows of spines of the figured specimen are only preserved in the anteriormost ribs due to abrasion.

#### Subclass Heterodonta Neumayr

##### Order Carditoida Dall

##### Family Astartidae d'Orbigny

##### Genus *Seebachia* Holub and Neumayr

Type species: *Astarte bronni* Krauss, 1850

Subgenus “*Eoseebachia*” Fürsich, Heinze and Jaitly, 2000

Remarks: The subgenus is here given in quotation marks because it awaits formal designation of a type species.

*Seebachia* (“*Eoseebachia*”) *sowerbyana* (Holdhaus) (Fig. 13P)

1913 *Astarte sowerbyana* sp. nov. – Holdhaus: 443, pl. 94, Figs. 12, 13, 15; pl. 100, Fig. 1.

1913 *Astarte scytalis* sp. nov. – Holdhaus: 444, pl. 100, Figs. 2 and 3.

1929 *Astarte scytalis* Holdhaus – Weir: 5, pl. 3, Fig. 20.

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1930 *Astarte stefanini* sp. nov. – Basse: 110, pl. 5, Fig. 9a–c.  
 1933 *Astarte krenkeli* sp. nov. – Dietrich: 40, pl. 4, Figs. 62, 64, 66.  
 1935 *Astarte scythalis* Holdhaus – Cox: 180, pl. 19, Figs. 4–5.  
 1959 *Astarte scythalis* Holdhaus – Jaboli: 49, pl. 6, Fig. 6.  
 1965 *Astarte sowerbyana* Holdhaus – Cox: 88, pl. 13, Fig. 6a and b.  
 1966 *Astarte krenkeli* Dietrich – Henriques da Silva: 63, pl. 2, Fig. 1; pl. 4, fig. 1.  
 2000 *Seebachia* (*Eoseebachia*) *sowerbyana* (Holdhaus, 1913) – Fürsich et al.: 92, pl. 6, Fig. 24; pl. 7, Figs. 1–5; pl. 8, Fig. 1; pl. 10, Fig. 5.  
 Material: 2 left valves from AL2.  
 Remarks: Internal features are not observed in the available material, but overall shape and style of ribbing closely correspond to *S. sowerbyana* as discussed and figured recently by Fürsich et al. (2000).

#### Order Anomalodesmata Dall

#### Family Pholadomyidae King

#### Genus *Pholadomya* G.B. Sowerby

Type species: *Pholadomya candida* G.B. Sowerby

#### Subgenus *Bucardiomya* Rollier

Type species: *Pholadomya bucardium* Agassiz

*Pholadomya* (*Bucardiomya*) *somaliensis* Cox. (Fig. 13Q)

1935 *Pholadomya somaliensis* sp. nov. – Cox: 192, pl. 21, Figs. 1 and 2.

1968 *Pholadomya somaliensis* Cox, 1935 – Ficarelli: 42, pl. 3, Fig. 7.

Material: 7 double-valved specimens (one from AL1, 6 from AL2).

Remarks: Cox (1935) separated *Pholadomya somaliensis* from the Upper Jurassic of Somalia from the very similar *P. protei* by its style of ribbing, consisting of five tuberculated main ribs, the prominent second rib from the anterior end forming a conspicuous keel. These features are also constantly evident in the available specimens from Ethiopia.

*Pholadomya* (*Bucardiomya*) *lirata* (J. Sowerby) (Fig. 13R)

1818 *Cardita* ? *lirata* sp. nov. – J. Sowerby: 220, pl. 197, Fig. 3.

1935 *Pholadomya lirata* (J. Sowerby) – Cox: 190, pl. 21, Figs. 8 and 9 (see for synonymy list).

1959 *Pholadomya protei* (Brongniart) – Jaboli: 67, pl. 9, Figs. 1–3.

1965 *Pholadomya lirata* (J. Sowerby) – Cox: 126, pl. 20, Fig. 8 (see for synonymy list).

1968 *Pholadomya* cf. *protei* (Brongniart, 1821) – Ficarelli: 42, pl. 3, Figs. 8 and 8a.

1996 *Pholadomya* (*Bucardiomya*) *lirata* (Sowerby, 1818) – Pandey et al.: 55, pl. 2, Figs. 8–11; pl. 3, Figs. 1–4 (see for synonymy list).

1998 *Pholadomya* (*Bucardiomya*) *lirata* (J. Sowerby, 1818) – Holzapfel: 121, pl. 10, Figs. 17 and 18.

Material: 1 double-valved specimen from AL2.

Remarks: The specimen assigned to *Pholadomya lirata* deviates from *P. somaliensis* described above by being more elongate and by more pronounced commarginal crenulations.

#### Order Veneroida Adams and Adams

#### Family Lucinidae Fleming

#### Genus *Lucina* Bruguière

Type species: *Venus jamaicensis* Spengler

"*Lucina*" cf. *cecchii* Jaboli (Fig. 13S)

cf. 1959 *Lucina cecchii* sp. nov. – Jaboli: 54, pl. 7, Fig. 2.

cf. 1959 *Lucina* sp. I ind. – Jaboli: 55, pl. 7, Fig. 3.

Material: 4 double-valved specimens from AL2.

Remarks: The type specimen (Jaboli, 1959: pl. 7, Fig. 2) differs by having more anteriorly placed umbones. The studied specimens are therefore referred to this species with reservation. The generic identity must remain open because internal shell features are unknown.

#### Family Cardiidae Lamarck

#### Genus *Integricardium* Rollier

Type species: *Cardium dupinianum* d'Orbigny

*Integricardium* (*Integricardium*) cf. *bannesianum* (Contejean) (Fig. 13T)

cf. 1860 *Cardium bannesianum* sp. nov. – Contejean: 276, pl. 15, Figs. 1–5.

cf. 1959 *Cardium bannesianum* Contejean

– Jaboli: 59, pl. 7, Fig. 9.

cf. 2000 *Integricardium* (*Integricardium*) *bannesianum* (Contejean) – Fürsich et al.: pl. 12, Figs. 14–18.

Material: 4 left valves, 1 right valve and 3 double-valved specimens (7 specimens from AL1, one from AL2).

Remarks: The otherwise not distinguishable species

*Integricardium bannesianum* and *I. (I.) propebannesianum* (Dietrich) can possibly be separated by the presence of a shallow pallial sinus in *I. propebannesianum* (see discussion in Cox, 1965 and Fürsich et al., 2000). The pallial line is not preserved in our material and therefore we assign the Ethiopian specimens to *bannesianum* with qualification.

## 7. Discussion and conclusions

Our new paleontological data from the Mekele Outlier of northern Ethiopia allow us to critically evaluate the significance of an Ethiopian Province in the late Jurassic. The Jurassic Ethiopian Province was originally defined for ammonites (Uhlig, 1911; Arkell, 1956) and belemnites (Stevens, 1963) but has also been noted for bivalves (Hallam, 1977; Liu et al., 1998) and brachiopods (Ager and Sun, 1988; Feldman et al., 2001), whereas little is known about coral provinciality in the Jurassic. The distinctive character and spatial extent of the Ethiopian province has been discussed repeatedly, even for ammonites (Hillebrandt et al., 1992; Enay and Cariou, 1997).

Our analyses, based on newly recorded corals, brachiopods and bivalves and occurrence data from the PaleoDB, confirm that a distinct African province was indeed evident in Callovian–Kimmeridgian times incorporating a vast region from Tunisia in the north to Madagascar in the south. Ethiopia, situated approximately in the center of this province, deserves being eponymous of this province. The spatial extent of the Ethiopian Province was perhaps smaller than usually assumed, at least for brachiopods and bivalves. India and Tanzania should probably not be included in the Ethiopian Province. These countries exhibit similar faunal associations but plot far from other countries of the Ethiopian Province.

We suspect that oceanographic clines, linked to latitudinal temperature gradients are responsible for the distinct character of India and Tanzania, which were situated at approximately 30°S in the Late Jurassic (Fig. 3). Interestingly, a distinct South Gondwana Province was suggested based on ostracods to comprise Tanzania, India and Madagascar (Mette, 2004) and Enay and Cariou (1997) assigned the ammonites from Kachchh (India) to a subaustral fauna. Brachiopod data agree well with a separate province in the southwestern Tethys (Fig. 4b), but problematic in this scenario is

the proximity of Madagascar to Ethiopia and its distance to both Tanzania and India in the MDS plot for bivalves (Fig. 4c–d). We cannot rule out that taxonomic biases are involved here. For example, virtually all data from Madagascar stem from a single, older reference (Besairie and Collignon, 1972), whereas modern taxonomy and a variety of sources underlie the data from India and Tanzania. Accepting the bivalve pattern as realistic would suggest that bivalves but not brachiopods had a roughly “bipolar” distribution (Crame, 1986, 1993), whereby the Ethiopian Province represented a central barrier between European and Indo-Tanzanian bivalve faunas.

Liu et al. (1998) have noted that the northern boundary of the Ethiopian Bivalve Province is poorly defined with a large overlap with what they called the Mediterranean Bivalve Province. In contrast, patterns of corals and brachiopods indicate a fairly sharp boundary between the Ethiopian and European Provinces running just north of Jordan and Tunisia.

Some marginal differences among taxonomic groups aside, it is interesting to note that groups with different life styles and reproductive and larval modes show broadly similar geographic distribution patterns. That the extent of the Ethiopian Province is almost identical for corals, brachiopods and bivalves suggests that physical drivers such as ocean currents or plate tectonics might have been more important than biological drivers such as dispersability in shaping Jurassic biogeographic patterns.

The confusion upon defining faunal realms and provinces (Westermann, 2000) may in part stem from the subjective consideration and weighting of taxa (genera and species) and from the different emphasis on endemic taxa. We have already learned from a quantitative analysis of faunal similarities through time (Miller et al., 2009) that narratives on ancient (and perhaps also recent) biogeography may be misleading. Our study underlines this conclusion in demonstrating that quantitative approaches may differ considerably from traditional views.

## Acknowledgments

This study was supported by the VolkswagenStiftung. We thank Eva Mohrmann and Falko Reichel for assistance in the field, Franz Fürsich and Uta Merkel for entering many of the Jurassic occurrence data into the Paleobiology Database, Robert Bussert for an introduction to the geology of the area, and David Lebenie for logistic support. Insightful reviews of Franz Fürsich and Anthony Hallam are greatly acknowledged. This is Paleobiology Database publication #126.

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