Echinoids and pectinid bivalves from the Early Miocene Mishan Formation of Iran

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ABSTRACT:

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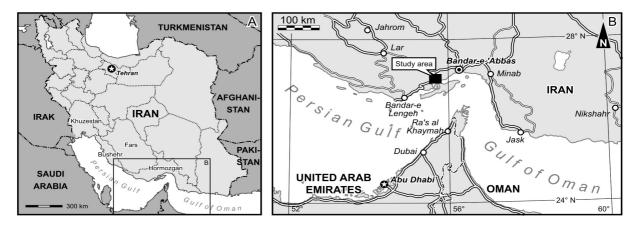
Shallow marine echinoids and pectinid bivalves from the Early Miocene Guri Member of the Mishan Formation cropping out at the Gery Sheikh section north of Bandar Pohl in the area of the Hormuz Strait, Iran, are reported. The echinoid fauna indicates a Burdigalian age for the Guri Member. This is supported by new calcareous nannoplankton data from this unit, which suggest an age from Aquitanian to middle Burdigalian (NN1–NN3). From a palaeobiogeographic point of view the fauna of the Guri Member is related to the faunas from central Saudi Arabia, southeast Pakistan and northwest India. The absence of Western Tethyan elements supports earlier data suggesting that a faunal separation between Proto-Mediterranean and Proto-Indian Ocean faunas was well developed before the Terminal Tethyan Event. The echinoids *Fibularia damensis* Kier, 1972 and *Anisaster arabica* Kier, 1972 are new records for Iran, having been known before solely from Saudi Arabia. *Brissus daviesi* Jain, 2002 is transferred to *Rhynobrissus* based on the characters of its fascioles, petalodium and plas tron; this constituting the first fossil record of the genus.

Key words: Echinoidea; Pteriomorphia; Persian Gulf; Burdigalian; Guri Member; Systematics new records; New combinations.

INTRODUCTION

The Middle East is a key area for unravelling the history of the closure of the connection between the Indian Ocean and the Proto-Mediterranean Sea. This closure – the Terminal Tethyan Event (Adams *et al.* 1983) in the late early Burdigalian (Reuter *et al.* 2009) – is one of the largest palaeogeographic changes in the younger Earth History and is comparable to the closure

of the Isthmus of Panama or the opening of the Drake Passage. All of these events had profound effects on the oceanographic conditions of the world oceans, including marine and associated atmospheric circulation, sea-surface temperatures and last, but not least biotic evolution, both in the marine and terrestrial realms (Harzhauser *et al.* 2007). Numerous molecular and phylogeographic studies (e.g. Lessios *et al.* 2001) use these events for calibration of molecular clock models



Text-fig. 1. Location of the studied section in south Iran. Inset (B) shows the detailed position of the study area. Iranian provinces mentioned in the text are indicated in A

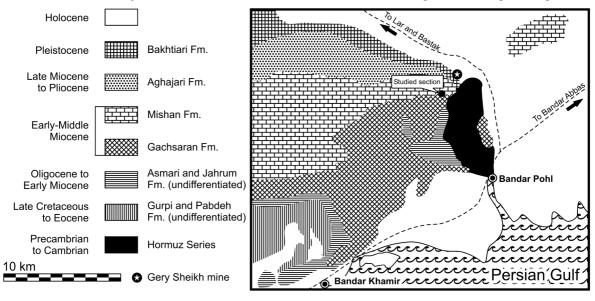
and precise dating of these events is thus of utmost importance.

Due to the huge efforts made by the petroleum industry the general lithostratigraphic framework of the Middle East Late Mesozoic and Cenozoic deposits is well understood. On a smaller scale, however, many questions remain, including especially the precise dating of individual lithostratigraphic units, which in many cases is poorly constrained. Thus well-dated Neogene faunal assemblages are comparatively rare in the Middle East. Here we report on the fauna of the Guri Limestone in the basal part of the Mishan Formation, exposed at the Gery Sheikh mine, north of Bandar Pohl, Hormozgan Province, southern Iran. The section studied is located 77 km west of Bandar Abbas on the eastern flank of the Khamir salt dome (Text-fig. 1). It can be accessed via the road from Bandar Pohl north towards Lar and Bastak. The Gery Sheikh mine lies 12 km north from the junction to Bandar Abbas

(Text-fig. 2). The section was measured c. 2 km west of the road at N $27^{\circ}6'6.48''$, E $55^{\circ}44'12.12''$ (base of section).

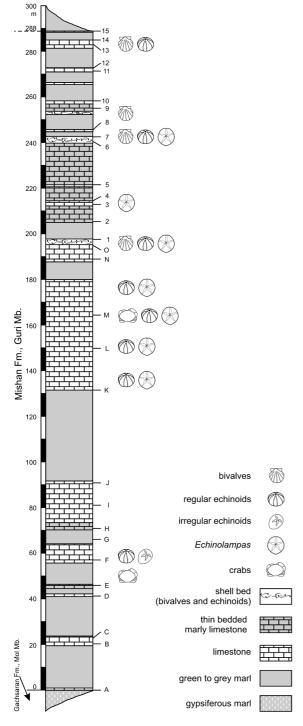
GEOLOGICAL SETTING

The study area is a part of the southeastern end of the folded Zagros Zone which consists of a simple anticline-syncline system. The Hurmoz Series is the oldest exposed unit in the Zagros Mountains and is composed of rhyolites, basalts, carbonates and evaporites. According to Stöcklin and Setudehnia (1991) and Aghanabati (2004), this series is of Late Precambrian to Middle Cambrian age. The vertical movements of salt domes originating from the Hurmoz Series have changed the geological situation of the southeastern Zagros Mountains and led to local exposure of older units covered in other parts of the Zagros Range. In the



Text-fig. 2. Geological map of the study area

study area the Hormuz Series is overlain by the Asmari and Jahrum formations. These, in turn, are covered by the Gachsaran Formation and the overlying Mishan Formation. The Mishan Formation has an important role in local geomorphology as it forms the sides of anticlines and appears in the plains as low marly foothills.



Text-fig. 3. Stratigraphic column of Guri Member (Mishan Formation) in the Gery Sheikh section

The Pliocene Aghajari marls and sandstones overlie marls at the top of the Mishan Formation. The youngest strata in the study area are represented by the conglomerates of the Bakhtiati Formation (Text-fig. 2).

Our research focuses on the faunal content of the Mishan Formation introduced by James and Wynd (1965). Its type section was measured in the Gachsaran oilfield. The Mishan Formation represents the middle part of the Fars Group. It crops out widely in coastal Iran (Fars, Bushehr, Khuzestan and Hormozgan provinces) and consists of a thinner lower member (Guri Limestone or Guri Member, "worm beds") composed of fossiliferous limestone and marl, and a thicker, unnamed upper member consisting mainly of marl. The total thickness of the Mishan Formation reaches 710 metres at the type section, that of the basal Guri Member 61 m. The type section of the Guri Member has been measured in Tange Guri, near the city of Lar, south of the Fars province, where it is 112.8 m thick. The Guri Member crops out over most of the area of the Mishan Formation but is most prominent in the study area and the region of Bandar Khamir, where the total thickness of the Mishan Formation reaches 1200 m, the lower 288 m being represented by the Guri Member (Text-fig. 3).

The Mishan Formation overlies the Gachsaran Formation and underlies the Aghajari Formation. The boundary between the Mishan and Aghajari formations is conformable and gradual. The boundary between the Guri Member and the Mol Member of the Gachsaran Formation is conformable and sharp. The base of the Guri Member is marked by the first *Operculina* limestone bed overlying the gypsiferous marls of the Mol Member and its upper limit is taken at the top of the last fossiliferous thin bedded limestone.

This part of the Mishan Formation is highly fossiliferous and contains numerous fossil invertebrates, including corals, bivalves, echinoids, foraminifera, corallinacean algae, and crustaceans. Due to diagenetic dissolution the shells of the aragonitic molluscs are dissolved, leaving only moulds and steinkerns, the preservation of which is usually very poor in the Guri Member.

The Guri Member has been characterized by previous researchers as composed mostly of limestone (Stöcklin and Setudehnia 1991; Motiei 1993). In the Gery Sheikh section, however, the lower 56.5 m are composed mainly of marls with intercalations of limestones. The middle part is composed of 103.2 m of rough rock-wall forming white to brownish weathered limestone and marly limestone with marl intervals. The upper part is an alternation of marl and limestone (46.7 m) and terminates with thin bedded limestone. Reefal facies described by previous authors (Stöcklin and Setudehnia 1991; Motiei 1993) from the Guri Member were not observed in the Gery Sheikh section. Instead, three prominent shell beds composed mainly of bivalves and echinoids are present (Text-fig. 3).

Abbreviations

FO – first occurrence; LO – last occurrence; LOD – last occurrence date; NHM – Natural History Museum, London, UK; NHMW – Naturhistorisches Museum Wien, Vienna, Austria; TH – test height; TL – test length; TW – test width.

In synonymy lists: * - first description; p - partly; nec - it is not the synonym

BIOSTRATIGRAPHY

Previous work

Adams *et al.* (1983, fig. 2) indicate that the Mishan Formation is diachronous, being of Middle to Late Miocene age in northern Iran, but Early to Middle Miocene in southern Iran. According to their table, the Guri Member, which occurs exclusively in southern Iran, was deposited during the Langhian at Qeshm Island, where it overlies the Gachsaran Formation. A little farther to the north, at the Kuh-e-Baz section, deposition of the Guri Member started earlier, during the Burdigalian, and the member rests there on deposits of the Razak Formation. Higher levels of the Mishan Formation are said to contain *Orbulina* and are therefore no older than Middle Miocene (Adams *et al.* 1983, p. 281), albeit convincing documentation of these records is lacking.

On the basis of its micro- and macrofauna the Mishan Formation has been assigned an Early to Middle Miocene age by Stöcklin and Setudehnai (1991). The Guri Member was assigned by the same authors to the Early Miocene to early Middle Miocene, whereas Kalantari (1992) accepted an Early Miocene age only. Goff *et al.* (1994, fig. 2) attributed the Guri Member of the Khuzestan province to the calcareous nannoplankton Zone NN5 without presenting any data; moreover, they erroneously included parts of the Early Miocene age for the Guri Limestone, but in their lithostratigraphic chart (Alsharhan and Nairn 1995, fig. 2) indicated a Middle to Late Miocene age.

A similar age assignment was also reported by Jones and Racey (1994, fig. 16.6), who gave the age range of the Mishan Formation as NN4 to NN10 (i.e.

late Early Miocene to early Late Miocene) for coastal Iran. They indicated that both the base and top of the Mishan Formation were diachronous (citing an unpublished report by Wynd 1965). According to them (p. 284–285), the Mishan Formation locally (at the Kuh-e-Baz section) contains the larger benthic foraminifera *Flosculinella bontangensis* (Rutten, 1912) and *Pseudotaberina malbarica* (Carter, 1853), indicating a latest Early to earliest Middle Miocene age (Lower Tf of Adams 1970)

Pseudotaberina malabarica was regarded as a Middle Miocene marker species and has been recorded from the Letter Stages Tf1 and Tf2 (Burdigalian to Serravalian; Jauri and Khare 1990; Renema 2007, 2008). New data from the South Indian Quilon Formation at Padappakkara (formerly of uncertain Early to Middle Miocene age) indicates that this species occurs in the Burdigalian already [planktonic foraminiferal Zone N5/M2 (Berggren *et al.* 1995), calcareous nannoplankton Zone NN3] based on micropalaeontological evidence (Reuter *et al.* 2011).

New calcareous nannoplankton data

Samples for calcareous nannoplankton were taken from fossiliferous matrix attached to echinoid specimens throughout the Gery Sheikh section. Most of these, however, contain no identifiable nannofossils (e.g. samples 3-4, 14 and G). In contrast, smear slides from samples 7, 8 and 11 contained abundant, well preserved nannoplankton (mainly Cyclicargolithus floridanus; LOD 13.33 Ma, lower NN6). Stratigraphically important species recovered are: Reticulofenestra pseudoumbilicus (5-7 µm; FO in NN1/NN2) and numerous, poorly preserved sphenoliths (Sphenolithus cf. multispinatus, S. cf. capricornutus, S. conicus, S. cf. delphix). S. multispinatus is known from NN3 to NN4, S. delphix and S. capricornutus from NN1, S. conicus ranges up to NN3. Helicosphaerids are missing, except for Helicosphaera euphratis (Sample 7, LO in NN5).

The assemblage provides a rather crude age estimate as marker species employed in the standard zonation are, unfortunately, absent from the samples. Overlapping species ranges indicate calcareous nannoplankton zones NN1 to NN3, i.e. an Aquitanian to middle Burdigalian age for sample 11.

New macrofaunal data

Echinoids and bivalves are extremely abundant in some beds of the Guri Member exposed at the Gery Sheikh section. As mentioned above, however, aragonitic forms are preserved only as worn steinkerns.

 Sample 8 (from the matrix of NHMW 2010/0251/0022) <i>Cyclicargolithus floridanus</i> (Roth & Hay, 1967) Bukry, 1971 f <i>Reticulofenestra haqii</i> Backman, 1978 r <i>Reticulofenestra minuta</i> Roth, 1970 c <i>Reticulofenestra pseudoumbilicus</i> (Gartner, 1967) Gartner, 1969 r <i>Sphenolithus</i> cf. <i>abies</i> Deflandre 1953 r <i>Sphenolithus moriformis</i> (Brönnimann & Stradner, 1960) Bramlette & Wilcoxon, 1967 r <i>Sphenolithus</i> cf. <i>capricornutus</i> Bukry & Percival, 1971 r <i>Watznaueria barnesae</i> (Black, 1959) Perch-Nielsen, 1968 r* Sample 7 (from the matrix of NHMW 2010/0250/0005) <i>Cyclicargolithus floridanus</i> (Roth & Hay, 1967) Bukry, 1971 r <i>Helicosphaera euphratis</i> Haq, 1966 r <i>Reticulofenestra haqii</i> Backman, 1978 r <i>Sphenolithus moriformis</i> (Brönnimann & Stradner, 1960) Bramlette & Wilcoxon, 1967 r Sample 11 (from the matrix of NHMW 2010/0253/0004) <i>Coccolithus pelagicus</i> (Wallich, 1871) Schiller, 1930 r <i>Cyclicargolithus floridanus</i> (Roth & Hay, 1967) Bukry, 1971 c <i>Reticulofenestra aglida</i> (Geitzenauer, 1972) Backman, 1978 r <i>Reticulofenestra haqii</i> Backman, 1978 r <i>Reticulofenestra gelida</i> (Geitzenauer, 1972) Backman, 1978 r <i>Reticulofenestra haqii</i> Backman, 1978 r 	
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Table 1. Calcareous nannoplankton assemblages; abbreviations behind taxa indicate abundance in the studied assemblage (c=common >50%; f=few 10-50%; r=rare <10%)

These are of limited taxonomic significance, being attributable only to genus or family level in most cases. We therefore limited our research to the well preserved pectinid bivalve and echinoid faunas (described in detail below). From a biostratigraphic point of view, *Talochlamys articulata*, the single pectinid bivalve taxon recovered from the section, is of limited significance, as its range is currently poorly constrained. This widespread species (Eastern Africa to Pakistan, Sumatra and Java), however, has a distinct acme in the Early Miocene, supporting the idea that the Guri Member is of Early rather than Middle Miocene age.

The echinoids documented from the Guri Member are much less widely spread and less long-lived. *Fibularia damensis* and *Brissus latidunensis* are known exclusively from the Burdigalian of the Persian Gulf region and from Saudi Arabia (Dam Formation). *Echinolampas jacquementi* and *Schizaster granti* are also known from the Gaj Formation in Pakistan and northwest India. The age of the latter formation is Aquitanian to Burdigalian according to Iqbal and Shah (1980), whereas Mohan and Chatterji (1956) considered a Burdigalian age only based on foraminiferal evidence. The echinoid fauna thus indicates a Burdigalian age for the Gery Sheikh section.

Conclusions

These new calcareous nannoplankton data from the uppermost part of the Guri Member exposed at the Gery

Sheikh section (sample 11, 271 m above the base of the section) are in conflict with some previous biostratigraphic data. The data suggest that this part of the section is not younger than middle Burdigalian (NN3) and not older than Aquitanian (NN1). The echinoid fauna described below supports the new nannoplankton data and indicates a Burdigalian age for the Guri Member.

The data presented by previous authors come from different sections of the Mishan Formation and the Guri Member. This could be interpreted as evidence that these units are indeed diachronous as suggested by Adams *et al.* (1983, fig. 2) and that the Guri Member indeed extends into the earliest Middle Miocene elsewhere.

From a palaeobiogeographic point of view, the echinoids of the Guri Limestone are related to the faunas from central Saudi Arabia, southeast Pakistan and northwest India, belonging to an Early Miocene faunal province first identified by Kier (1972, p. 13, 15). New records of Saudi Arabian forms in southern Iran documented here (Fibularia damensis, Anisaster arabica) support this pattern. The single pectinid species recovered from the Guri Member is more widespread, being known from Eastern Africa to the western Indo-Malayan Archipelago (Burma). None of the species recorded herein occurs farther west than central Saudi Arabia, supporting the arguments presented by Harzhauser et al. (2002, 2007, 2009) that the separation between Proto-Mediterranean and Proto-Indian Ocean faunas was well developed before the final closure.

SYSTEMATIC PALAEONTOLOGY

(classification of Echinoidea following Kroh and Smith, 2010)

Phylum Echinodermata Bruguière, 1791 Class Echinoidea Leske, 1778 Subclass Euechinoidea Bronn, 1860 Carinacea Kroh and Smith, 2010 Echinacea Claus, 1876 Order Camarodonta Jackson, 1912 Infraorder Temnopleuridea Kroh and Smith, 2010 Family Temnopleuridae A. Agassiz, 1872 Genus *Temnopleurus* L. Agassiz, 1841

TYPE SPECIES: *Cidaris toreumatica* Leske, 1778, p. 155, by original designation. Recent; Indo-West Pacific.

Temnopleurus latidunensis Clegg, 1933 (Text-figs 4–5)

- * 1933. *Temnopleurus latidunensis*, sp. nov., Clegg, p. 18-19, pl. 2, figs 5a–c.
- ? 1933. Temnopleurus sp. aff. toreumaticus, Ag., Clegg, p. 12–13, pl. 2, figs 6a–c.

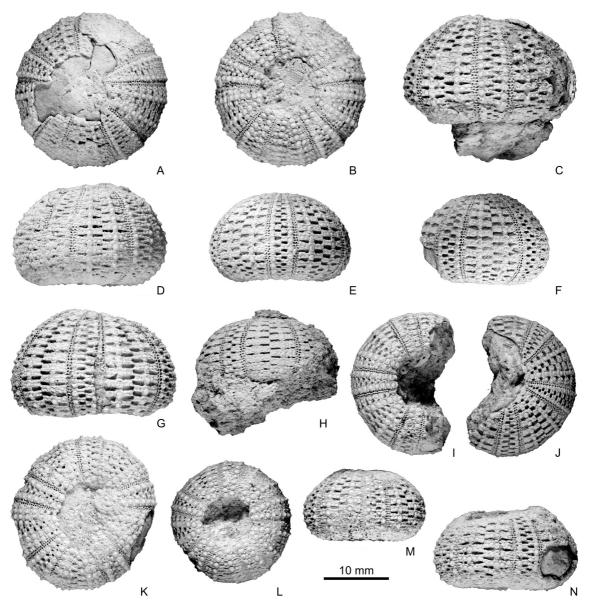
MATERIAL: 2 specimens (NHMW 2010/0250/0004, and 2010/02350/0005) from sample 7, 2 specimens from sample 8 (NHMW 2010/0251/0021, 2010/0251/0022), 1 specimen from sample 11 (NHMW 2010/0253/0004), and 38 specimens (2010/0254/0003 to 0040) from sample 14 of the Gery Sheikh section, north of Bandar Pohl, southern Iran.

DESCRIPTION: Moderately large regular eucchinoid with corona diameter ranging from 10.5 to 29.5 mm in the studied material. Test fragments indicate that specimens with diameters larger than 35 mm were present. Outline circular, in profile corona domed with high, rounded ambitus situated slightly below half test height. Test height variable, ranging from 45 to 66 % test diameter. Apical disc small, caduceous, not preserved in any of the specimens.

Ambulacra consisting of trigeminate plates of the echinoid compound type. Poriferous zones straight, with densely crowded P1 to P2 type pore pairs (classification of Smith 1979). Each ambulacral plate bears a single, relatively small primary tubercle and numerous, densely crowed secondary and miliary tubercles. Interambulacra about one and a half times as wide as ambulacra at ambitus. Each plate bears a single, central, crenulate imperforate primary tubercle. The areoles of adjacent primary tubercles touch each other and form straight vertical rows. Multiple enlarged secondary tubercles arranged in horizontal rows present. In specimens of c. 20 to 25 mm diameter two such tubercles are usually present on each side of the primary tubercle. Test ornamentation consists of large wedgeshaped to triangular pits. The pits are steep walled, well defined, relatively deep and arranged in a highly regular pattern. In the ambulacra they are located at the triple suture junctions along the perradial suture. In the interambulacra they are arranged along horizontal sutures, on either side of the primary tubercle.

Peristome diameter about 35 to 42 % of test diameter, with shallow buccal notches. Girdle consisting of auricles connected by a relatively high wall in the interambulacra. Lantern and spines not preserved.

VARIATION: The material is remarkable homogeneous and shows little intraspecific variation, apart from relative test height, a feature known to be affected by minor environmental differences also in extant echinacean echinoids (Ernst 1973). Additionally, the



Text-fig. 4. *Temnopleurus latidunensis* Clegg, 1933; A–B, D – aboral (A), oral (B) and lateral (D) view of NHMW 2010/0254/0005; C – lateral view of NHMW 2010/0254/0006; E–F, I–J – lateral (E, F), oral (I) and aboral (J) view of NHMW 2010/0254/0024; G – lateral view of NHMW 2010/0254/0033; H – lateral view of NHMW 2010/0254/0026 (note echinoid-type compounding of ambulacra); K, N – oral (K) and lateral (N) view of NHMW 2010/0254/0037; L–M – oral (L) and lateral (M) view of NHMW 2010/0254/0013

exact shape and size of the sutural depressions varies slightly, being comparatively smaller and of rounded rectangular shape in smaller specimens, but tending to be more triangular and wedge-shaped in larger ones. We interpret this as an effect of allometric growth due to the fact that the same variation can be observed from apex to ambitus in large specimens.

REMARKS: In contrast to Clegg (1933, p. 18–19), we did not observe any subdivision of the adradial sutural pits, nor were we able to confirm his observations on

photographs of the holotype. Clegg himself, however, was unsure about the nature and presence of this subdivision and this probably was an artefact of the poor preservation of the holotype. As far as we can tell, our material is identical to Clegg's in all other respects.

Temnopleurus persica Clegg, 1933 from the Daliki, northeast Bushehr, Iran, differs among other features in its strikingly different sutural pits, which are less wide, slit-like and not subdivided by the vertical row of primary tubercles. Additionally, *T. persica* has three large subequal tubercles on each plate ambitally rather than a well defined central primary tubercle flanked by enlarged secondary tubercles.

Temnopleurus aff. *toreumaticus* Agassiz described by Clegg (1933, p. 12–13) from Rahdar (W of Shiraz, Iran), is closely similar to the smaller *Temnopleurus* specimens recovered from the Gery Sheikh section and is here interpreted as *T. latidunensis*.

Temnopleurus cf. *reynaudi* Agassiz described by Clegg (1933, p. 19–20) from Henjam (Qeshm Island, Iran) most likely came from the Pliocene Aghajari Formation and seems to be a subadult *T. toreumaticus*. [Remark: *T. reynaudi* L. Agassiz and Desor, 1846 is a junior synonym of the extant *T. toreumaticus* (Leske, 1778) see Kroh and Mooi 2010].

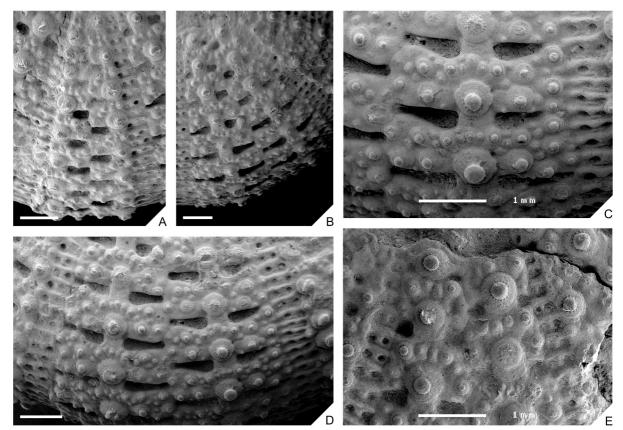
T. latidunensis is very similar to the extant *T. toreumaticus*, but differs in its very conspicuous, larger and differently shaped, sharply delimited sutural pits, presence of a clearly defined primary tubercle (3 subequal tubercles ambitally in *T. toreumaticus*) and less offset pore pairs (almost vertically aligned in *T. latidunensis* vs. arranged in weak arcs in *T. toreumaticus*).

T. latidunensis is the oldest confirmed representative of the genus *Temnopleurus* known to date. It shows striking similarities to the Eocene temnopleurid *Opechinus costatus* d'Archiac and Haime, 1853, but differs from that taxon in its crenulate tubercles (noncrenulate in *Opechinus*) and in not having subdivided sutural pits.

T. iranicus Douglas, 1928 from the "Upper Fars" of southern Iran is probably better referred to the genus *Opechinus* based on the presence of divided sutural pits, a feature in which this species differs from the Gery Sheikh material.

OCCURRENCE: *T. latidunensis* was originally described from a place called "Latidun" (Clegg 1933) which is not found on modern maps but, according to the coordinates provided (N 27° 10', E 55° 49'), is only about 10 km to the NE of Gary Sheikh. A much younger record from the Pliocene Aghajari Formation of Qeshm Island and the adjoining mainland (James and Wynd 1965, p. 2242) might be based on a misidentification of the Pliocene to extant species *T. toreumaticus*. No other occurrences are known.

Irregularia Latreille, 1825 Microstomata Smith, 1984



Text-fig. 5. Temnopleurus latidunensis Clegg, 1933, SEM images of NHMW 2010/0250/0005; A – aboral ambulacrum; B – aboral interambulacrum; C – ambital interambulacrum; E – adapical interambulacrum. Scale bars equal 1 mm

Neognathostomata Smith, 1981 Order Echinolampadoida Kroh and Smith, 2010 Family Echinolampadidae Gray, 1851a Genus *Echinolampas* Gray, 1825

TYPE SPECIES: *Echinanthus ovatus* Leske, 1778, p. 127; by subsequent designation of Pomel, 1883, p. 62. Extant, Indo-Pacific.

Echinolampas jacquemonti d'Archiac and Haime, 1853 (Text-fig. 6)

- * 1853. *Echinolampas jacquemonti*, nov. spec., d'Archiac and Haime, p. 211–212, pl. 14, figs 5a, b.
 - 1885. Echinolampas Jacquemonti, d'Archiac and Haime; Duncan and Sladen, p. 332–337, pl. 53, figs 1–14.
 - 1928. *Echinolampas jacquemonti* d'Archiac and Haime; Douglas, p. 12–13, pl. 8, figs 2, 2a–b.
- non 1999. *Echinolampas jacquemonti*, d'Archiac and Haime; Srivastava and Singh, p. 33-34, pl. 9, figs 7-9

MATERIAL: 45 specimens (NHMW 2010/0252/0001 to 045) from sample 3–4, 3 specimens (NHMW 2010/0250/0001 to 0003) from sample 7, 20 specimens from sample 8 (NHMW 2010/0251/0001 to 0020), 3 specimens from sample 11 (NHMW 2010/0253/0001 to 0003), and 1 specimen (2010/0254/0002) from sample 14 of the Gery Sheikh section, north of Bandar Pohl, southern Iran.

HOLOTYPE: NHM E78558, Lower Miocene, "Chaîne d'Hala", Mountain range of Hala, N Hyderabad, Sindh, Pakistan.

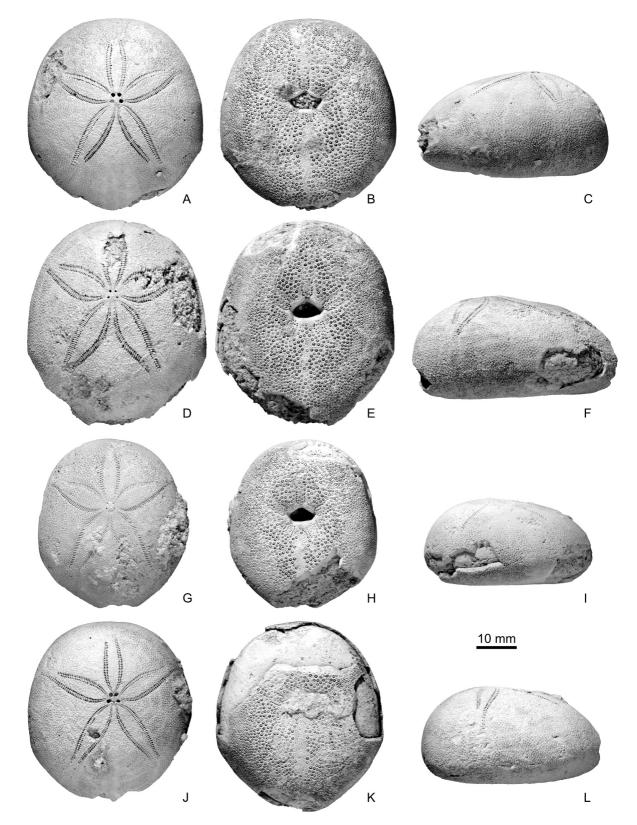
MEASUREMENTS: see Table 2.

DESCRIPTION: Test of moderate size, ranging from c. 30 mm to c. 60 mm test length in the studied material, with specimens in the size class between 45 and 55 mm being most common. The outline of the test is longitudinally elongated oval, with a rounded anterior and pointed posterior end. The maximum width lies posteriorly, coinciding with the distal ends of the posterior paired petals at about 70 to 75 % test length from the anterior margin. There is a distinct and characteristic kink in the outline at or slightly behind the maximum width. In profile the test is ovate, with tumid anterior and tapering posterior ends. The maximum height coincides with the apical disc and lies about 36 % from the anterior margin (range: 32 to 40 %). The apical disc is monobasal with 4 gonopores.

Adapically the ambulacra are petaloid. The petals are composed of densely crowded conjugated anisopores arranged in slightly sunken poriferous zones. The petals are comparatively small, the anterior paired petals extending usually about between 70 and 75 % of the corresponding test radius (posterior paired petals: 55–65 %). The poriferous zones of the frontal petal are of almost equal length, column IIIa surpassing IIIb only by 2 to 3 pore pairs. In the paired petals, the pore zones are more

specimen no.	TL	ΤW	ΗT	Ant-Apic	Ant-Ps	PsD	APP_L	APP_L_CR	PPP_L	PPP_L_CR
2010/0252/0001	56,7	49	24,5	18,2	21	6,7	21,5	28	23,9	37,4
2010/0252/0005	56,7	49	26,3	20,2	21,9		20,4	28,1	22,1	38,9
2010/0252/0018	47,2	43,9	25,4	16,9	18,3	7,6	18,9	24,9	19,3	33,3
2010/0252/0026	60,2	51,9	25,4	22,8	23,4					
2010/0252/0036	41	34,6	20,8	16,1	15,6	5,9	12	20,3	12,8	27,9
2010/0250/0001	47,6	41,6	23,9	15,7			16,5	23,6		
2010/0251/0003	52	45,7	25,5	19,4	21,4	6,4	20,1	26,6	21,2	34,5
2010/0251/0006	45	40,9	23,7	16,4	18,3	5,6	20	26	19,4	30,7
2010/0251/0019	42	36,5	20,2	16,2	16,5	5,7	14,6	20,9		
2010/0251/0020	42,5	37,2	21,8	16,9	17	5,7	17,2	22,2	18,5	28,3

Table 2. Echinolampas jacquemonti d'Archiac and Haime, 1853, measurement series for studied specimens. TL – test length, TW – test width, TH – test height, Ant-Apic – distance between apical disc and anterior margin, Ant-Ps – distance between peristome and anterior margin, PsD – horizontal peristome diameter, APP_L – length of anterior paired petals (APP), APP_L_CR – corresponding test radius of APP, PPP_L – length of posterior paired petals (PPP), PPP_L_CR – corresponding test radius of PPP



Text-fig. 6. Echinolampas jacquemonti d'Archiac and Haime, 1853; A–C – aboral (A), oral (B) and right lateral (C) view of NHMW 2010/0252/0018; D–F – aboral (D), oral (E) and left lateral (F) view of NHMW 2010/0251/0003; G–I – aboral (G), oral (H) and left lateral (I) view of NHMW 2010/0251/0020; J, L – aboral (J) and left lateral (L) view of NHMW 2010/0251/0006; K – oral view of NHMW 2010/0250/0001

uneven, with poriferous zones IIa and VIb being up to 8 pore pairs longer and zones Ib and Va being 2 to 5 pore pairs longer. There are neither trailing podia (Mooi 1989), nor occluded plates at the distal ends of the petals. At the widest point of the petals there are usually 5 to 8 tubercles across the interporiferous zones. Adorally the ambulacra form short but distinct phyllodes with dense outer pore series and 3 to 6 widely space pores in the two inner series. There are short double rows of 5 to 8 sunken; biserial offset sphaeridial pits running along the midline of the phyllodes close to the peristome.

The interambulacra are virtually flush with the ambulacra and covered by a homogeneous, dense tuberculation aborally. Distances between adjacent tubercles are usually in the order of the diameter of the areoles. At the ambitus the tuberculation becomes very dense, with areoles separated only by narrow ridges. Towards the peristome tubercles become gradually more widespread again and increase in size till they reach about twice the size of the aboral and ambital tubercles. Oral and lateral ambital tubercles have asymmetric areoles, being slightly enlarged on the posterior side of the tubercle (facilitating a directional power stroke of the spines). In the midline of oral interambulacrum 5 there is a conspicuous naked zone of variable extent halfway between the peristome and the periproct.

The peristome lies anterior of the centre of the slightly concave oral side, about 37 to 41 % of test length from the anterior margin. It is distinctly pentagonal, with weakly inflated bourrelets and has a mean width of 13.5 % of test length. The periproct lies inframarginally on the very posterior end of the test, visible (in part) also in posterior view. It is transversely oval and slightly wider than the peristome, but is poorly preserved in most of the specimens examined.

VARIATION: Exact test profile, test height and size of the petalodium do vary considerably in the material studied. Likewise does the extent and shape of the naked zone in adoral interambulacrum 5 and the size of the gonopores, which are rather large in some specimens. This might be an effect of sexual dimorphism (compare Kier 1967, 1969), which, however, is so far unknown in echinolampadids.

REMARKS: The material studied clearly belongs to the characteristic Early Miocene *E. jacquemonti*. The Guri Limestone specimens, however, differ from the specimens from the type region in a distinct naked zone along the midline of adoral interambulacrum 5. As outlined above, however, this appears to be a highly variable feature; in some specimens it is quite prominent (specimen 2010/0251/0020), in others it is almost absent

(specimen 2010/0251/0003), like in the type material. We thus do not think that this feature warrants establishing a new species for the Guri Limestone material.

E. spheroidalis d'Archiac in d'Archiac and Haime, 1853 from the Early Miocene of Pakistan differs from *E. jacquemonti* in its more marginal periproct and more unequal poriferous zones in the posterior petals, but is otherwise closely similar. Re-examination of material from the type area is needed to establish if separation of the two species is justified. Another similar species from the Early Miocene of Kachchh, *E. indica* Duncan and Sladen, 1883 differs from *E. jacquemonti* in its more rounded outline (without distinct kink) and strongly unequal poriferous zones in the posterior petals. Additionally a naked zone appears never to be developed in that species.

OCCURRENCE: Common at numerous outcrops of the Gaj Formation in Sindh, southeast Pakistan (Aquitanian–Burdigalian according to Iqbal and Shah 1980, whereas Mohan and Chatterji 1956 inferred a Burdigalian age based on foraminifera).

> Order Clypeasteroida L. Agassiz, 1835 Suborder Clypeasterina L. Agassiz, 1835 Infraorder Laganiformes Desor, 1847 Family Fibulariidae Gray, 1855 Genus *Fibularia* Lamarck, 1816

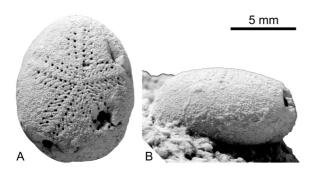
TYPE SPECIES: *Fibularia ovulum* Lamarck, 1816, p. 17, by ICZN ruling, 1950, 4, p. 519. Recent, Indo-Pacific.

Fibularia damensis Kier, 1972 (Text-fig. 7)

- * 1972. *Fibularia damensis* Kier, new species, Kier, p. 90– 91, pl. 59, figs 2–10, pl. 60, fig. 1.
 - 1976. *Fibularia damensis* Kier; Roman, p. 25–26, pl. 4, figs 17–19.

MATERIAL: 1 specimen (NHMW 2010/0248/0001) from sample G of the Gery Sheikh Section, N Bandar Pohl, southern Iran.

DESCRIPTION: Corona small (TL: 10.4 mm, TW: 8.3 mm, TH: 5.5 mm), with oval, antero-posteriorly elongated outline. In profile high with thick, tumid ambitus and slightly aboral and oral sides. Ambitus thick and curved. The apical disc is located centrally on the aboral side and is tetrabasal with four gonopores and a curved furrow in which the hydropores are situated.



Text-fig. 7. *Fibularia damensis* Kier, 1972, NHMW 2010/0248/0001; A – aboral view; B – left lateral view

Aborally the ambulacra are petaloid, with 8–9 pore pair's in each ambulacral column in the petals (simple, conjugate isopores, with narrow connecting groove). Accessory pores poorly visible, but apparently numerous and arranged in short lines and irregular groups, preferentially along horizontal plate boundaries. The petals are flush with the interambulacra and extend almost to the ambitus. Outer pore zones converging distally, inner pore zones straight. Close to the apical disc the interambulacra appear very narrow in between the petals and barely discernible. The perradial pores of the petals actually pierce the interambulacral plates, thus evoking the impression of extremely narrow interambulacra. Although plate sutures are poorly visible, the interambulacra appear to be biserial throughout, except possibly for a single uniserial plate bordering adapically.

REMARKS: The single specimen recovered from the Guri Limestone is closest to Fibularia damensis Kier. 1972 from the Dam Formation of Saudi Arabia. It is difficult to separate this species from the closely similar Fibularia dubarensis Kier, 1957 from the Miocene of Somalia, especially so when single specimens rather than populations are concerned. The low test height and large petalodium, however, favour attribution to F. damensis. Fibularia voeltzkowi (Tornquist, 1905) (= F. gracilis Tornquist, 1905, = F. woodi (Currie, 1930) according to Stephenson 1968, p. 136-137) from the Lower Miocene of Kenya and Madagascar is also similar to the present specimen (compare e.g. Currie 1930: pl. 16, figs 1a - 1b), but differs in the distinct uniserial plate arrangement in the adapical interambulacra, with as many as 4 single plates in a row (Stephenson 1968, fig. 1).

OCCURRENCE: Also known from the Burdigalian (Adams *et al.* 1983) Dam Formation of Saudi Arabia and Qatar (Kier 1972; Roman 1976).

Atelostomata von Zittel, 1879 Order Spatangoida L. Agassiz, 1840a Suborder Paleopneustina [possibly paraphyletic] Family Schizasteridae Lambert, 1905 Genus *Schizaster* L. Agassiz, 1835

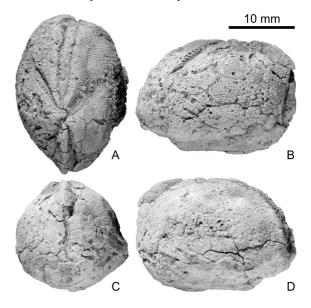
TYPE SPECIES: *Schizaster studeri* L. Agassiz, 1836, p. 185, by ICZN ruling, 1948. Late Eocene (Priabonian), southern Europe.

Schizaster granti Duncan and Sladen, 1883 (Text-fig. 8)

- * 1883. *Schizaster* Granti, Duncan and Sladen; Duncan and Sladen, p. 70–72, 88–89, pl. 6, figs 8–12.
 - 2002. Schizaster granti Duncan and Sladen; Jain, p. 127, pl. 5, figs 24–26.

MATERIAL: 1 specimen (NHMW 2010/0254/0001) from sample 14 of the Gery Sheikh Section, north of Bandar Pohl, southern Iran.

DESCRIPTION: Test of small size (TL: 23.4 mm, TW: -, TH: ~16 mm, specimen laterally distorted), with oval to slightly cordiform outline and shallow frontal notch. In profile test high, with rounded anterior and vertically truncated posterior end. Maximum height lies slightly posterior of centre, coinciding with the crests of the adapical interambulacra around the apical disc. The paired ambulacra are



Text-fig. 8. Schizaster granti Duncan and Sladen, 1883, NHMW 2010/0254/0001; A – aboral view; B – left lateral view; C – posterior view; D – right lateral view

petaloid, whereas the ambulacrum III is nonpetaloid, forming a deeply sunken groove aborally. The posterior petals are short and closing distally. The anterior paired petals are about twice as long, extending more than two thirds the corresponding test radius and have straight posterior and bowed anterior poriferous zones. In the anterior pore zones the size of the pore pairs increases more slowly than in the posterior zone. In the anterior zone the largest pores are located about halfway down the petal resulting in a characteristic, backwards bowed, banana-like shape of the anterior petals. The interambulacra form sharp crests in between the petals aborally. Orally interambulacrum 5 forms a large, raised plastron. The labral plate is short, stout, mushroom-shaped and does not extend beyond the first plates of the adjacent ambulacra. The peristome lies close to the anterior border at the end of a shallow groove. Its posterior margin is strongly raised, forming a distinct lip. The periproct lies high on the vertical posterior face and is overhung by a small hood. The peripetalous fasciole is moderately wide and strongly indented in interambulacra 1, 4 and 5. In interambulacra 2 and 3 it runs from the tip of the petals perpendicularly towards the frontal groove. On the crests developed in interambulacra columns 2b and 3a it makes a 90° turn and follows the ridge towards the anterior margin. Sediment infill in the frontal groove obscures the part of the fasciole that crosses the groove. A latero-anal fasciole is present. Its fasciole band is only about half as wide as that of the peripetalous fasciole.

REMARKS: Despite the fact that only a single, moderately preserved specimen is available, the specific determination is quite straightforward. The bowed, banana-shaped anterior petals in combination with a high, non-wedge shaped profile and the 90° turn of the peripetalous fasciole in interambulacra 2 and 3 are characteristic of Schizaster granti Duncan and Sladen, 1883. Very few other species of Schizaster are known from the area. Schizaster beluchistanensis d'Archiac and Haime, 1853 from the Eocene of northwest India differs in its wedge-shaped profile, sigmoidal anterior paired petals and smaller petalodium. Schizaster newboldi d'Archiac and Haime, 1853 from the ?Miocene of southeast Pakistan differs in its wide frontal notch, anteriorly flexed anterior paired petals and its angular, almost hexagonal outline.

OCCURRENCE: Common species in the Early Miocene Gaj Formation of Kachchh and Kathiawar, northeast India (Duncan and Sladen 1883; Jain 2002) and southeast Pakistan (Duncan and Sladen 1885).

Family Prenasteridae Lambert, 1905 Genus Anisaster Pomel, 1886

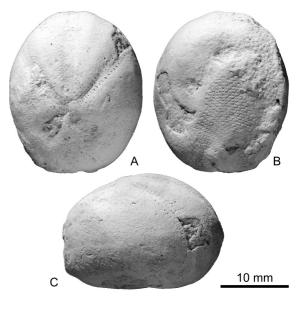
TYPE SPECIES: *Agassizia gibberulus* Cotteau, 1847, p. 20, by original designation. Eocene, southern Europe and North Africa.

Anisaster arabica Kier, 1972 (Text-fig. 9)

* 1972 Agassizia (Anisaster) arabica Kier, new species, Kier, p. 96–97, pl. 65, figs 3–8, pl. 66, figs 1–3.

MATERIAL: 1 specimen (NHMW 2010/0252/0046) from sample 3-4 of the Gery Sheikh section, north of Bandar Pohl, southern Iran.

DESCRIPTION: Test of small size (TL: 24.3 mm, TW: 20.3 mm, TH: 17.8 mm), with oval, antero-posteriorly elongated outline. In profile test high, globular with thick tumid anterior margin and vertically truncated posterior end. Maximum height slightly posterior of centre (c. 52 % TL from anterior margin), coinciding with apical disc. Apical disc ethmolytic with 4 gonopores. Anterior ambulacrum (III) nonpetaloid, slightly sunken and bearing widely spaced oblique to vertically oriented partitioned isopores. At the ambitus it is almost flush with the adjoining interambulacra, forming a faint frontal notch only. Anterior paired petals long, almost extending to the ambitus and slightly sunken. From their midlength on they bow posteriorly. Anterior porif-



Text-fig. 9. Anisaster arabica Kier, 1972, NHMW 2010/0252/0046; A – aboral view; B – oral view; C – right lateral view

erous zones with minute pore pairs aborally, gradually increasing in size distally until they reach about the same size as those of the posterior poriferous zone in the distal half of the petals. 24 pore pairs present in the posterior poriferous zone of ambulacrum II. Posterior petals lobate, slightly sunken and short, extending only about 25 % of TL.

The interambulacra are only weakly inflated adapically in between the petals. They are covered by fine, uniform tuberculation interspersed with fine granules, except on the plastron where large densely packed tubercles are found. Plastron large and wide, with short but broad labrum that does not extend beyond the first adjacent ambulacral plates. Peristome relatively small and situated anteriorly, about 20 % TL from the anterior margin. Periproct high on the posterior face, but poorly exposed in the investigated specimen. Apparently oval, transversely elongated.Narrow peripetalous and lateroanal fascioles present. Peripetalous fasciole only very slightly indented in interambulacrum 5, whereas it is deeply indented in the lateral interambulacra (1+4), running up almost three thirds along the anterior paired petals towards the apical disc before curving backwards to the tips of the posterior petals. Anteriorly, the fasciole band passes well below the tips of the anterior petals and crosses ambulacrum III slightly below the ambitus (visible in oral view). The latero-anal fasciole branches off at the height of the tips of the anterior petals and runs more or less straight posteriorly along the ambitus. It forms a deep V beneath the periproct.

REMARKS: The single specimen available clearly belongs to the genus Anisaster, based on its globular shape, weakly sunken petals and fasciole development. It differs from Agassizia which has only rudimentary pores in the anterior poriferous zones of the anterior petals. The specimen is very similar to those described as Agassizia (Anisaster) arabica by Kier (1972) from a locality of uncertain, possibly Late Eocene to Oligocene age and appears to be conspecific with them. The only differences are the slightly longer anterior petals, with slightly more pores, but this difference might be simply attributed to the c. 20% larger size of the Iranian specimen. Later authors (e.g. Smith 2010 "The Echinoid Directory", accessed 9. July 2010) have attributed A. arabica to the Burdigalian Dam Formation. Few other Anisaster species are known. The one closest to the Iranian species apart from A. arabica is A. gibberulus Cotteau, 1847 from the Eocene of southern Europe and northern Africa. That species, however, differs from the Gery Sheikh specimen in its longer and less diverging posterior petals. The contemporaneous and closely related forms Agassizia persica Clegg, 1933 and Ag. powersi Kier, 1972 are

true representatives of *Agassizia* lacking enlarged pores in the anterior poriferous zone of the anterior petals, which, furthermore are forwards flexed rather than backwards as in *A. arabica* and can thus not be easily confused with that form.

OCCURRENCE: Also known from Wadi Sirhan, northwest Saudi Arabia (Kier 1972).

Suborder Brissidina Stockley *et al.*, 2005 Family Brissidae Gray, 1855 Genus *Brissus* Gray, 1825

TYPE SPECIES: *Spatangus brissus unicolor* Leske, 1778, p. 248, by ICZN ruling, 1948. Late Miocene to Recent, Mediterranean Sea, Atlantic coast of Europe and Caribbean Sea.

Brissus latidunensis Clegg, 1933 (Text-fig. 10)

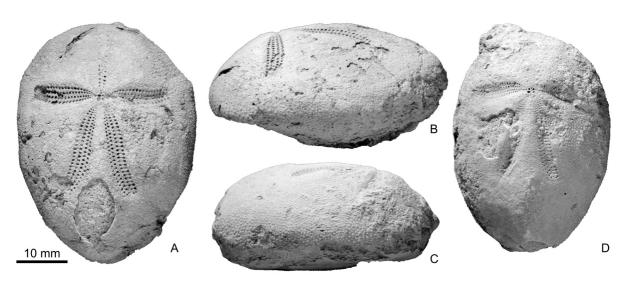
- * 1933. *Brissus latidunensis,* sp. nov.; Clegg, p. 30–33, pl. 3, figs 7a–c.
 - 1972. Brissus latidunensis Clegg; Kier, p. 101-102, pl. 62, figs 5-7, pl. 63, figs 1-4.

MATERIAL: 2 specimens (NHMW 2010/0252/0047 and 0048) from sample 3–4 of the Gery Sheikh section, north of Bandar Pohl, southern Iran.

MEASUREMENTS (in mm):

	TL	TW	TH
NHMW 2010/0252/0047	44.1	31.6	21.7
NHMW 2010/0252/0048	48.0	36.1	25.7

DESCRIPTION: Test moderately large, with oval, antero-posteriorly elongated outline without frontal notch. In profile test curved gradually from the highest point (halfway in between the apical disc and the posterior end) towards the frontal margin. Posterior end vertically truncated. The apical disc is ethmolytic with 4 gonopores and lies anteriorly, about 27 % TL from the anterior margin. Ambulacrum III nonpetaloid, not sunken, with minute pores. Anterior petals long (27-31 % TL), narrow and distinctly sunken. They diverge at c. 180-195° and have slightly anteriorly flexed tips. The posterior petals are likewise long (35-40 % TL), narrow and sunken, diverge at an acute angle of c. 30° and have laterally flexed tips. Interambulacrum 5 forms a prominent rounded keen aborally. The peristome lies anteriorly, close to the margin and is kidney-shaped. The periproct lies on the ver-



Text-fig. 10. Brissus latidunensis Clegg, 1933; A–B – aboral (A) and left lateral view of NHMW 2010/0252/0048; C–D – right lateral (C) and aboral view (D) of NHMW 2010/0252/0047

tical posterior face, which is poorly preserved in all available specimens. Peripetalous fasciole moderately indented in interambulacrum 5, but deeply indented in the lateral interambulacra (1+4), running up to midlength of the anterior petals before curving backwards. Anteriorly, the fasciole band passes ambulacrum III just above the ambitus. It zigzags distinctly in interambulacra 2 and 3. The subanal fasciole is partly obscured but appears to be shield-shaped.

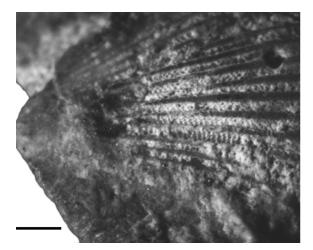
REMARKS: The two specimens available are very similar to the type material of B. latidunensis described by Clegg (1933) from contemporaneous beds and there can be little doubt about their specific identity. B. latidunensis is close to extant B. unicolor (compare discussion in Kier 1972, p. 101-102), but their relationship remains unresolved. The only other Brissus species known from the Early Miocene of the region is B. daviesi Jain, 2002 from the Early Miocene Gaj Formation of Kathiawar, northwest India. It is strikingly different from B. latidunensis. Based on its oval, nonindented peripetalous fasciole, lanceolate subequal petals, pointed posterior end and narrow plastron, this species is here transferred to the genus Rhynobrissus (compare Mortensen 1951, p. 486-488), which is the first fossil record of that genus. Brissus sp. reported from the Early Miocene Gaj Formation of southeast Pakistan by Duncan and Sladen (1885, p. 354-356, pl. 55, fig. 9) is known from poorly preserved specimens only. Based on the description by Duncan and Sladen, however, this too seems to represent Rhynobrissus rather than Brissus and cannot be confused with B. latidunensis.

OCCURRENCE: Also known from the "Lower Fars series" 100 feet above the gypsum bed (= Lower Mishan Formation) of Latidun, Iran (Clegg 1933) and the Burdigalian Dam Formation of central Saudi Arabia (Kier 1972).

Phylum Mollusca Class Bivalvia LINNE, 1758 Subclass Pteriomorphia Beurlen, 1944 [emend. WALLER, 1978] Order Ostreoida FÉRUSSAC, 1822 [emend. WALLER, 1978] Suborder Pectinina WALLER, 1978 Superfamily Pectinacea WILKES, 1810 [emend. WALLER, 1978] Family Pectinidae Wilkes, 1810 [emend. WALLER, 1978] Subfamily Chlamydinae von TEPPNER, 1922 Tribe Chlamydini von TEPPNER, 1922 [emend. WALLER, 1978] Genus *Talochlamys* Iredale, 1929

TYPE SPECIES: *Chlamys famigerator* Iredale (*=Pecten pulleineanus* Tate) from the Holocene of southern and eastern Australia – original designation by Iredale (1929).

Talochlamys articulata (J. DE C. SOWERBY, 1840) (Text-figs 11, 12.1–13)



Text-fig. 11. *Talochlamys articulata* (J. de C. Sowerby, 1840), detail of the proximal disc portion demonstrating the presence of extremely fine scale shagreen microsculpture in rib interspaces of the right valve measured for Table 1. The scale bar marks 1 mm distance

- * 1853. *Pecten Bouei* d'Arch.; d'Archiac and Haime, p. 269– 270, pl. 24, fig. 1.
- *,p 1853. *Pecten Hopkinsi* d'Arch.; d'Archiac and Haime, p. 271, pl. 24, fig. 4. [non fig. 3 = *P. labadei*].
- *,p 1886. *Pecten Halaensis* n.n., Frauscher, p. 98. [excl. Eocene specimens and figs]
 - * 1901. *Pecten kokenianus* spec. nov., Noetling, p. 117–121, pl. 4, figs 2–6.
 - 1916. Pecten (Chlamys) senatorius Gmel.; Martin, p. 263.
 - 1928. *Pecten (Chlamys) articulatus* J. de C. Sowerby; Vredenburg, p. 434.
 - 1928. Chlamys Senatoria (Gmelin.); Douglas, p. 2–4, pl. 8, figs 3–5.
- p? 1936. *Chlamys senatoria* (Gmelin); Cox, p. 54–55, pl. 5, fig. 18, pl. 6, fig. 9. [presumably only Fars Group occurrence].
 - 1950. Chlamys senatoria (Gmelin) 1791; Eames, p. 145.
- p? 1956. *Chlamys senatoria* (Gmelin), 1791; Eames and Cox, p. 14. [presumably only Fars Group occurrence].

This synonymy list includes only occurrences where a shagreen microsculpture has been documented by illustration or by description [except *Pecten halaensis* which represents a replacement name for *P. hopkinsi*].

HOLOTYPE: a left valve (J. de C. Sowerby 1840, pl. 5, fig. 15) housed at the Natural History Museum, Department of Palaeontology, London, UK (Cox 1927). The type locality is a bank of the Runn of Kutch (probably the southern one), a large ephemeral salt marsh in western India bearing Miocene deposits that probably correlate with the Gaj Formation of the adjoining Sindh province of Pakistan to the west (Vredenburg 1928).

MATERIAL: 7 articulated specimens, 2 right valves and 1 fragment collected between samples 8 and 9 (NHMW 2010/0257/0001 to 0010. One left valve in sample 14 (NHMW 2010/0254/0041).

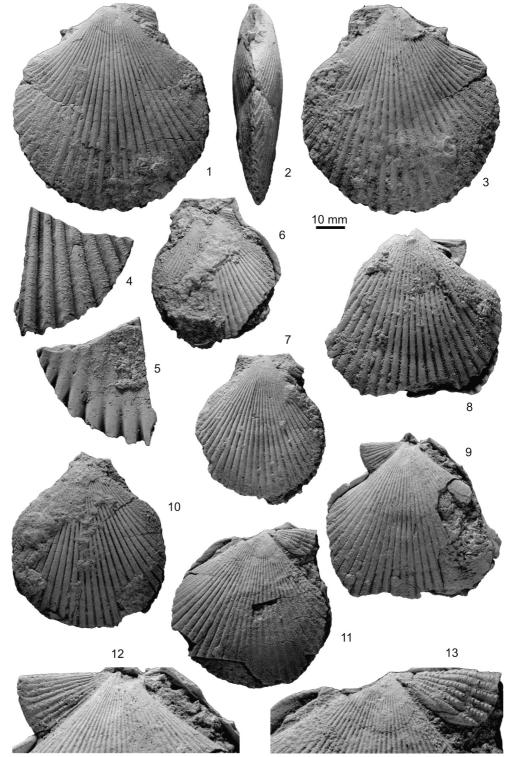
MEASUREMENTS: see Table 3.

DESCRIPTION: The shell is rather large, moderately thick walled, aequipectinoid shaped, rounded in outline, somewhat higher than long, with obtuse umbonal angle of about 105° in mature individuals, low to moderately biconvex with about 26 prominent ribs fixed early in ontogeny and moderately sized, and with anteriorly inclined ears bearing scaly riblets. The mature individuals in the studied material attain a maximum disc height of 76 mm, whereas the usual height ranges between 50 and 70 mm.

Disc outline is roughly equilateral to slightly inequilateral due to postero-ventral elongation, with umbonal angle less obtuse in smaller individuals and stronger obtuse in adult specimens. That is reflected in the shape of the dorsal margins becoming progressively concave during ontogeny. Beak does not project over the hinge line. Convexity is low to moderate with a mean of about

Specimen no.	valve	HD (mm)	LD/HD (%)	HDa/HD (%)	HDp/HD (%)	LDa/LD (%)	(%) AH/bah	C/HD (%)	HMC/HD (%)	α D (°)	NRd	NRv	LE/LD (%)	LEa/ LE (%)
NHMW 2009z0115/0003 NHMW 2009z0115/0007 NHMW 2009z0115/0002 NHMW 2009z0115/0008	L R R L	72.3 49.8 74.8 31.3	94.5 89.2 96.3 93.0	48.4 56.2 56.1 48.6	51.2 56.2 56.1 50.8	48.3 47.3 44.7 45.0	0 0 0	12.4 11.4 14.3 21.1	36.0 36.7 44.9 43.5	107.0 98.0 105.0 91.0	24 26 27 23	26 28 27 25	55.6* 58.0* 40.0* 61.0	50.3* 55.1* 50.3* 56.2

Table 3. *Talochlamys articulata* (Sowerby, 1840), measurement series for studied specimens. The sections of measurement definitions are after Waller (1969). Abbreviations are as follows: HD – Disc height, LD – Disc length, HDa – Anterior partial disc height, HDp – Posterior partial disc height, LDa – Anterior partial disc length, HDd – Disc projection over umbo, C – Convexity (distance to shell axis), HMC – Point of maximum shell convexity distance to dorsal disc margins, αD – Umbonal angle (tangential angle of dorsal disc margins), NRv Ventral ribs number, LE – Ears length, LEa – Anterior ear length, HEa – Anterior ear height, HEp – Posterior ear height, LEp – Posterior ear length, * – based on reconstructed section



Text-fig. 12. *Talochlamys articulata* (J. de C. Sowerby, 1840), specimens collected between sampled beds 8 and 9 of the studied section: 1–3. – Articulated specimen in left (1), anterior (2) and posterior (3) view. 4–5 – Fragment showing details of ventral disc sculpture in exterior (4) and interior (5) view. 6–7 – Articulated specimen with preserved shagreen microsculpture at proximal disc exterior (not visible) in left (6) and right (7) view (see also text-fig. 11 for a detail of its right proximal disc). 9, 13 – Articulated specimen with well preserved anterior left ear in left view. 10–11, 13 – Articulated specimen with well preserved anterior ear in left (10) and right (11, 13) views. The scale bar defines 10 mm distance for all illustrations except for figure 4 and 5 (20 mm) and 12 and 13 showing magnified proximal portions of specimens illustrated in figures 9 and 11. All specimens are coated with ammonium chloride

13 % of disc height. Point of maximum convexity is placed in the dorsal disc portion at second quarter of height. Disc flanks are flattened to slightly concave posteriorly and anteriorly with low sigmoid transitions to ear planes in cross section. Disc gapes are absent. Disc sculpture comprises 23 to 27 primary ribs fixed early in ontogeny. At lateral margins one or two additional ribs can subsequently develop. Ribs are prominent, moderately convex, and slightly top-flattened in cross section with narrower, concave interspaces. Several riblets are introduced in interspaces in posterior and anterior disc exterior, sometimes developing the prominence of the primary rib. Riblets at the flanks are rare in the studied material, instead projecting scales commonly occur in the corresponding rib flank position. Shagreen microsculpture is developed in rib interspaces at least proximally although it can extend distally as well. Disc interior shows plicae that are largely shallow except for the very distal margin where they suddenly broaden and deepen. Although internal rib tops flatten marginally getting quadrangular in cross section no carinae seems to develop.

Ears are moderate in size, with height that does not reach 25 % of disc height and length attaining about 55 % of disc length. Their dorsal margins are straight; the lateral margins dip posteriorly by about 60°. Whereas the byssal notch is rather deep, the byssal sinus is moderately deep. Ear surface comprises up to 5 more or less prominent scaly riblets best developed at the right anterior ear. Whereas the posterior dorsal margins are rather smooth, the right anterior one bears scaly riblets as well. Byssal fasciole is broad. Hinge shows short but prominent resiliar tooth pair and equally prominent, strongly elongated dorsal tooth pair starting somewhat distally from the origin of growth.

VARIATION: The single specimen from sample 14 (Table 3) is distinctly smaller than any specimen of the other sample investigated and we interpret it as young adult individual. The specimen is more convex, has a lower number of primary and secondary ribs and larger ears, but its sculpture and outline agree well with the specimens described above.

DISCUSSION: Douglas (1928) was the first author to report the occurrence of *T. articulata* (as *Chlamys senatoria*) in the Fars Group. *C. senatoria*, however, is a younger synonym of *Mimachlamys sanguinea* (Linnaeus, 1758) (Dijkstra 1999) and lacks shagreen microsculpture. In the Mishan Formation material, in contrast, this microsculpture is well developed (Textfig. 11 and Douglas 1928). Its presence indicates that the Mishan material is not related to *Mimachlamys*. According to Waller (1991, 1993, 2006), shagreen microsculpture represents a synapomorphic character for unrelated genera of the Chlamydini. The apparent similarity with *Mimachlamys sanguinea* must thus be disregarded at present and interpreted as representing a product of homeomorphic evolution in consequence of adaptation to a similar habitat type.

Modern *Talochlamys* representatives show shagreen microsculpture at least early in ontogeny. Some Middle Miocene specimens from Australia regarded by Beu and Darragh (2001) as belonging to *Talochlamys* show apparent similarity with our material. *Talochlamys keiloriana* shows primary ribs starting at the central disc portion early in ontogeny and a large number of prominent ribs. We follow these authors and place our species into *Talochlamys*, albeit this genus is usually characterized by intercalations of secondary ribs within the rib interspaces at the disc exterior. In our material, as well as in the Australian specimens, such intercalations became apparently restricted to the very marginal posterior and anterior disc areas, producing the erroneous impression that all ribs start within the proximal disc portion.

From the numerous nominal species names available for this species, *Pecten articulatus* J. de C. Sowerby represents the most senior, valid designation. Vredenburg (1928) was the first to point out the presence of a shagreen microsculpture in that species, enabling differentiation from the otherwise quite similar *Pecten somrowensis* J. de C. Sowerby.

DISTRIBUTION: Miocene of western Proto-Indo-Pacific with apparent acme in the Lower Miocene.

Specimens with shagreen microsculpture have been observed and described from the Lower and Middle Miocene Fars Formation in southwest Iran (Douglas 1928; Cox 1936; Eames and Cox 1956), the Lower Miocene Gaj Formation, including the species type locality, in west India and southeast Pakistan (Vredenburg 1928), and from the Lower Miocene of Burma (Noetling 1901).

Morphologically similar specimens without positive evidence for a shagreen microsculpture were documented from the Lower Miocene of Tanzania (Cox 1927; Eames and Cox 1956), Madagascar (Collignon and Cottreau 1927), Kenya (Cox 1930), Mozambique (Cox 1939), South Africa (King 1953), Pakistan (d'Archiac and Haime 1853; Vredenburg 1928) and India (Sowerby 1840; Vredenburg 1928).

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