UPPER TRIASSIC BRACHIOPODS AND LAMELLIBRANCHS FROM THE OMAN PENINSULA, ARABIA

by R. G. S. HUDSON and R. P. S. JEFFERIES

ABSTRACT. Norian brachiopods (4 species) and lamellibranchs (25 species, 2 subspecies) from the Asaf and Sumna Formations (Elphinstone Beds) of the Jebel Hagab area, Oman, Arabia, are critically identified, new morphological features being described. The fauna shows considerable resemblance to those of the same age from Spiti, Central Himalayas, and Indonesia, notably Miosed. Brachiopods described include *Hapalodiscina arabica* gen. et sp. nov., and *Miosed kentidactyla* sp. nov. New species and subspecies of lamellibranchs are *Maldanum onoceni*, *Indopincta ann salariens*, *I. elongato* (Krumbrock) *superior*, *Palaeospondyla supercondylus* (Krumbrock) *kels*, and *Thouaia proviris*. Structural colour-binding in *Indopicta* is discussed.

THE Ruus al Jibal, the mountain range of the Oman Peninsula, is formed from a lower series of limestones and dolomites (Upper Permian to Middle Trias, 1,487 metres thick), a middle series of limestones, marls, and some sandstone (Upper Trias, 431 metres thick) and an upper series of limestone (Jurassic to Lower Cretaceous, 1,475 metres thick). The main exposure of the Upper Trias, the fauna of part of which is described in this paper, is on the east side of the peninsula where it outcrops on the western flank of the coastal anticline. It is also exposed in the northern part of the peninsula where it outcrops in the core of the Shumma Anticline on the sides of both the Elphinstone Inlet (Khor ash Shumma) and the Malcolm Inlet (Ghabbat al Ghazira). To the south on the western side of the peninsula and to the east of Ras al Khaima it outcrops on the flanks of the Hagab Monocline. There, on the southern flank, it is well exposed and accessible in Wadi Milaha and at the entrance to Wadi Bih, and it was there that the Upper Trias succession was measured and the fossils described in this paper collected.

Triassic fossils from Oman were first collected by Blanford (1872) from the Elphinstone Inlet and variously named by Soltyska and Diener (1906) as of Triassic and Lower Cretaceous age. In 1924 and 1925 G. M. Lees and Washington Gray collected from the Upper Trias of the Elphinstone Inlet and from the mountain front of the Jebel Hagab area, about 5 miles east of Ras al Khaima. These fossils were named by Lees (1928) and considered to be of Upper Triassic age, probably Norian. The 500 feet of brown limestones, shales, and sandstones from which they were collected he named the Elphinstone Beds. In the spring of 1951 R. G. S. Hudson, R. V. Browne, and Z. R. Beydoun, geologists of the Iraq Petroleum Company, measured and sampled the Elphinstone Beds of Wadi Milaha. The fossils described in this paper were then collected by R. G. S. Hudson.

From their colleagues, both in the field and in the laboratory, and from L. R. Cox of the British Museum (Natural History), the authors have received every help. To them and to the Directors and Chief Geologist of the Iraq Petroleum Company, who permitted the publication of this paper, the authors record their thanks. The fossils described in this paper have been presented to the Department of Palaeontology, British Museum (Natural History), and are referred to in this paper by their registration numbers, those of the brachiopods being preceded by the letters BB and those of the lamellibranchs by LL. Numbers preceded by the letter L are of specimens collected by G. M. Lees (1928).

FAUNAL STRATIGRAPHY

The general succession (Permain to Lower Cretaceous) of the Ruus al Jibil was outlined by Hudson, McGugan, and Morton (1954), its upper part (Musandum Limestone; Rhaetian to Aptian) being subsequently described by Hudson and Chatton (1959) and its lower part (Permian to Upper Trias) by Hudson (1960). In this last paper the Elphinstone Beds were redefined as a group to include the following:

<table>
<thead>
<tr>
<th>Formation</th>
<th>Score (m)</th>
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<tbody>
<tr>
<td>Shuba Limestone and Sandstone; Upper Trias</td>
<td>64</td>
</tr>
<tr>
<td>Sakhr Limestone; Upper Trias</td>
<td>23</td>
</tr>
<tr>
<td>Sumra Limestone and Marl; Norian</td>
<td>56</td>
</tr>
<tr>
<td>Asfal Limestone, Marl, and Sandstone; Norian</td>
<td>108</td>
</tr>
<tr>
<td>Milaha Limestone; Upper Trias (Carnian–Norian)</td>
<td>180</td>
</tr>
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The fossils described in this paper are from the Asfal and Sumra Formations only, mostly from the Sumra. All fossils from Oman discussed in this paper are from the Wadi Milaha, Jebel Hagab area, unless otherwise designated.

Asfal Beds. In the lowest 42 metres of these beds there is as much sandstone as limestone and marly shale, both usually sandy: the remainder of the formation consists of limestone and shale, very much interbedded, some of the limestones being massive and fine-grained or even calcite-mudstones. There are occasional beds of shell debris and, more rarely, entire fossils. A common fossil is *Spiriferina abieti* Oppel occurring more particularly in 4 metres of sandy marls and marly limestones, 42 metres from the base of the formation. Another common brachiopod, *Misolita*, usually *M. lentiscula* sp. nov., occurs in a nodular limestone 1.5 metres thick and 90 metres from the base. Ellongate megalodontids, probably *Dicerocardium*, are abundant in the upper part of the formation notably in a feature-forming limestone, 2 metres thick and 73 metres from the base. Occasionally there are assemblages of small lamellibranchs comparable to those occurring in the Sumra Formation. Otherwise the only fossils are hydrozoans, mainly stomatoporoids, occurring in the more massive fine-grained limestones. Such a fauna occurs in the *Loxonepore* Limestone, 3 metres thick, which forms a marked feature and is taken as the top bed of the formation.

Sumra Beds. These are mainly thin-bedded, brown-weathering, shelly limestones, and reddish-purple, yellow or brown marly shales, closely interbedded. In the 15 metres at the top of the group, shales are more common than the limestones. There are also occasional massive fine-grained limestones. The fauna is essentially one of small lamellibranchs with occasional corals. The lower part (27 metres) is marked by an abundance of *Lopha balfourii* and is distinguished as the *Lopha* Beds: the upper part (29 metres) has an abundance of *Modiolus* and *Myophoria* and is distinguished as the *Modiolus* Beds. Corals, mainly *Thecosomia* and *Thamnasteria*, occur at various levels, notably in the uppermost 15 metres of shales with limestones.

The brachiopod-lamellibranch fauna of the Sumra Beds is listed below (the number following the name is the number of specimens determined; * or ** indicates forms found respectively only in the *Modiolus* Beds or the *Exogyra* Beds). Numerous fossil fragments, mostly *Lopha*, were broken away.

**Brachiopoda:** *Hapalorhynchia arctica* sp. nov., 10*; *Misolitae noctilignii* (Bittner), 1*.

**Lamellibranchia:** *Nucula (?Nuculopsis) milosensis* Jaworski, 1*; *Modiolus javorskii* Wanner and
THE AGE AND GEOGRAPHICAL AFFINITIES OF THE SUMRA AND ASFAL FORMATIONS

Most of the forms from Oman discussed in this paper occur in Tethyan Upper Triassic of other areas (Table 1). They range from Hungary and Lombardy in the west to the Misis Archipelago in the east, a distance of some 9,000 miles. Affinities, however, are much stronger with the Indo-Pacific region than with Europe. In the Himalayas, Sumra and Asfal forms are found from the Juvrites Beds to the Lower Kioto or Megalodon Limestone of Spiti (Diener 1908a, 1912), from the Proclydonautillus griesbachi Beds to the Sagenites Beds in Painkhandu (Bittner 1899; Diener 1912), and as isolated occurrences at Vih (Kashmir), Dapsang (Tibet), and Attock (West Pakistan). The Juvrites Beds and equivalent Proclydonautillus griesbachi and Hauzites Beds are dated as Norian by their ammonites (Diener 1912, p. 94) and the Monotis Beds are also proved Norian by the presence of Monotis saltans Brinn. There is, unfortunately, no satisfactory evidence for the age of the Quartzite Series or the overlying lower parts of the Kioto Limestone and it is at least possible that some of these horizons are Rhaetian. Subject to this qualification, however, comparison with the Himalayas suggests that the Sumra and Asfal Formations are of Norian age. The same comparison suggests that a Carnian age for the Asfal and Sumra can be excluded. The Carnian of the Himalayas, which immediately underlies the Juvrites and Proclydonautillus griesbachi Beds, is well dated by ammonites (Diener 1912, p. 97) and contains many brachiopods and lamellibranchs, but, so far as is known, is entirely without Elphinstone elements.

In Indonesia, Sumra and Asfal forms mainly occur in the Nucula Marl and Athyris Limestone of Misol and the Fogi Beds of Buru. The Nucula Marl and Fogi Beds are dated as Norian by ammonites related to Hallstatt Limestone forms (Krumbeck 1913, p. 117; Jaworski 1915, p. 156) and also by elements related to those of the Himalayan Norian. Comparison with Indonesia, therefore, like the Himalayas, suggests a Norian age for the Sumra and Asfal Formations.

Sumra and Asfal forms also occur in the Naiband Calciferous Sandstone of Persia, considered by Douglas (1929) to be Norian partly because the overlying Hauz-i-Khan Limestone contains European Rhaetian brachiopods.

Thus by comparison with Indonesia, Persia, Spiti, and Painkhandu, the Sumra and Asfal Formations are Norian, and this conclusion is not contradicted by the other occurrences shown in Table 1. The only possible reason for doubting this conclusion is the scarcity of well-described Rhaetian Indo-Pacific lamellibranch and brachiopod faunas. A Rhaetian lamellibranch fauna has, however, been fully described from the Napeng Beds of Burma (Healey 1908), and in it there are no Elphinstone forms.

Geographically the Sumra and Asfal Formations belong to the Indo-Pacific Province.
with Indopeten, Misola and Spiriferina abichi, and, as Lees pointed out (1928, p. 596), a near absence of European species. The claim by Douglas (1929, p. 631) that Arabia and Persia in Norian times were connected with Indonesia not via the Himalayas but by newly opened seaways through Gondwanaland is probably not justified on faunal grounds. It is true that some forms are recorded in the Middle East and Indonesia but not in the Himalayas (as Nucula miagolensis, Modiota jaworskii, the Lopha flanfordi-parasite group, Plagiochisma subalveolense, Palaeocardiella bursae, P. trapezoidalis, and Protocardia rhaeticana), but this may well be due to facies variation and the fact that Indonesian Norian faunas have been more extensively described than the Himalayan. The genus Indopeten, the distribution of which was thought by Douglas to support his views (1929, p. 631), does occur in the Himalayas as well as in Persia, Oman, and Indonesia (see later).

**BRACHIOPODA**

by R. P. S. JEFFERIES

*Family Rhynchonellidae* Gray 1848

*Genus Hagabirhynchia* nov.

_Type species Hagabirhynchia ar命ia* sp. nov.

**Diagnosis.** Small multicostate rhynchonellids, inversely sulcate when very small. Deltidial plates conjunct. Cardinal process present, no septarium, hinge-plate divided, even at umbo, crura rudilifer, ending in broad, thin, vertically disposed plates. Weak median septum in brachial valve. In pedicle valve, strong dental plates, teeth non-dentilicate, no pedicle collar.

**Comparisons.** Of the Liassic genera discussed by Ager (1956, 1958) *Prionorhynchia, Cirpa*, and *Rudibranchia* are similar enough to *Hagabirhynchia* to merit further comparison. *Prionorhynchia* Buckman resembles *Hagabirhynchia* in the numerous ribs, the weak median septum in the brachial valve, the absence of a septarium, and the form of the crura. It differs from *Hagabirhynchia* in not being inversely sulcate when young, in having the hinge-plate entire for a short distance posteriorly, in having disjunct deltidial plates, and in being larger. *Cirpa de Gregorio*, though larger, resembles *Hagabirhynchia* externally but differs (Ager 1958) in having the hinge-plate entire at the posterior margin and in having curious double deltidial plates. *Rudibranchia* Buckman differs from *Hagabirhynchia* in having a septarium, and often a pedicle collar, and in lacking the plate-like crura. It is interesting that of these three genera *Prionorhynchia* and *Cirpa* are mainly Tethyan in distribution (Ager 1956, p. 47).

Among Moiseev’s (1936) genera of rhynchonellids, *Robinsonella* is externally almost identical to *Hagabirhynchia* but differs internally in having the hinge-plate entire for a considerable distance posteriorly, and in the form of the crura.

On external characters alone *Hagabirhynchia* would include some if not all of the small, multicostate rhynchonellids of *liassic* *Habitus*, placed in the *Rhynchonella subrimosa* and *R. fessicostata* group by Bittner (1890, p. 313). The internal structure of *R. subrimosa*, as far as known (Zugmayer 1882, p. 37, pl. 14, fig. 12), is also like that of *Hagabirhynchia*. 
Hagabirhynchia arabica gen. et sp. nov.

Plate 1, figs. 18–21; text-fig. 1

Holotype. BB20248 (Pl. 1, figs. 18–21). Paratypes. BB20249 (text-fig. 1), BB20512–19. Modiolus Beds, Sumra Formation.

Description. Length (BB20248, holotype) 10 mm., breadth 11 mm., thickness 6 mm. Apical angle about 95°. Anterior commissure with normal arched sulcus in adult but with weak inverted sulcus (noretiform stage) when very young and rectimarginate at 3–5 mm. from the brachial umbo. Ribs present even at the umbones, often forking once or twice during ontogeny, particularly near the median line. In adult about seventeen ribs in the brachial valve, one less in the pedicle valve, three to four ribs present on floor of sulcus in pedicle valve (four in holotype), one more on central fold in brachial valve. Beak suberect; beak ridges strong. Deltidial plates conjunct; foramen circular, hypothyrid.

Internal structure as for genus (see text-fig. 1). Muscle scars unknown.

Comparison. *H. arabica* is either identical to, or an external homeomorph of, *Rhynchonella bambanagenesis* Bittner (1899, p. 44, pl. 8, fig. 4, p. 56, pl. 9, fig. 18; Diener, 1908a, p. 128, pl. 23, fig. 8) from the Himalayan Norian. One particular point of resemblance is the distinct inverted sulcus in the very early growth-stages as shown by the specimen of *R. bambanagenesis* figured by Diener (1908a, pl. 23, fig. 8). However, the internal structure of the Oman specimens justifies a new genus and since it would be unwise to make *R. bambanagenesis* the genotype of this genus because its internal
structure is unknown and its identity with the Oman material therefore uncertain, the Oman specimens are here allocated to a new species.

*H. arabica* externally resembles *Rhynchonella levantina* Bittner (1891, p. 107, pl. 1, figs. 1–3) except that this latter species has a more acute apical angle. Externally it is also very similar to *Robinsonella masdabanensis* Moiseev (1936) but this species differs internally (see under genus above).

*H. arabica* occurs in the Sumra Formation of Oman where it is fairly common. It has been considered to be possibly identical with *Rhynchonella bamburanensis* Bittner which occurs in the Coral Limestone, *Monotis* Beds and Quartzite Series of Spiti, and the *Spiriferina griesbachii* Beds of Painkhandha, all of which formations are Norian in age.

**Family SPIRIFERINIDAE Davidson 1884**

**Genus SPIRIFERINA d’Orbigny 1847**

*Spiriferina abichii* Oppel

Plate 1, figs. 13–17, 22, 23; text-fig. 2

*Spiriferina abichii* Oppel 1865, p. 298, pl. 88, figs. 6a, b.
*Spirifer abichii* Davidson 1866 (Jan. or Feb.), p. 41, pl. 2, fig. 4.
*Spirifer abichii* Davidson 1866 (Jan. or Feb.), p. 41, pl. 2, fig. 5.
*Spirifer abichii* Davidson 1866 (Sept. or later), p. 28, pl. 3, figs. 1, 2.
*Spirifer aliformis* Stoliczka 1866 (Sept. or later), p. 28, pl. 3, fig. 3.
*Spiriferina Griesbachii* Bittner 1899, p. 51, pl. 9, figs. 1–13; Diener 1908a, p. 121, pl. 22, figs. 7–13.

**Material.** BB20490 (Pl. 1, figs. 13–17), BB20491 (Pl. 1, fig. 23), BB20492–500, BB20501 (Pl. 1, fig. 22), and BB20502–7. All from *Spiriferina* Bed, Asaf Formation.

**Description.** Outline varying from slightly broader than long without cardinal extremities (Pl. 1, figs. 13–17, cf. *Spiriferina vihiana*), through forms with produced cardinal extremities (Pl. 1, fig. 23), to strongly transverse (Pl. 1, fig. 22, cf. *S. kashmeriensis*). Delthyrium with narrow deltidial plates meeting only at the umbo. Brachial valve with low area and notothyrium. Sulcus of pedicle valve strong, with single, angular, median rib, corresponding to strong fold in brachial valve which is divided by single median furrow. Lateral slopes with about ten rather angular ribs separated from area of both valves by narrow ribless zone. Number of ribs increases in ontogeny by appearance of ribs at anterior edge of ribless zone.

Pedicle valve with strong median septum touching deltidial plates where these are in contact at umbo. Dental lamellae strong, reaching to floor of pedicle valve, roughly parallel to median septum. Anterior margins of dental lamellae and median septum concave, the septum extending farther anteriorly than the lamellae. Cardinal process bifid, supported on hinge-plate which is clearly separated from floor of brachial valve and supported by weak, thin septum. Spiralia of about fourteen whorls, connected by simple U-shaped jugum.

**Dimensions (in mm.)**

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<th>Length</th>
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<th>Thickness</th>
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<tr>
<td>BB20490 (without produced cardinal extremities)</td>
<td>14-7</td>
<td>20-3</td>
<td>15-2</td>
</tr>
<tr>
<td>BB20503 (with produced extremities)</td>
<td>17-3</td>
<td>23-6</td>
<td>12-2</td>
</tr>
<tr>
<td>BB20501 (transverse form)</td>
<td>19-4</td>
<td>23-35</td>
<td>14-8</td>
</tr>
</tbody>
</table>
TEXT-PL. 2. Serial sections of *Spirocerina abichti* Oppel, × 1.5. *Spirocerina* Bed, Aftal Formation. Where the external shell has been dissolved, a thin line represents the contact between the external matrix and the infilling. Numbers are distances in mm. from the apex of the pedicle valve.
Remarks. The nomenclature of this species is extremely confused but the name *Spiriferina griesbachi* Bittner, by which it is usually known, is certainly invalid.

Bittner himself remarked (1899, p. 52) that his species *S. griesbachi* was probably identical with *Spirifer tibeticus* and *S. altivaus* Stoliczka 1866: the probability of their identity was strengthened by von Krafft (1900, p. 223) who showed that Stoliczka's specimens were probably from the Coral Limestone (— *Spiriferina griesbachi* Bed) of Spiti. Bittner also noticed the resemblance between *Spiriferina griesbachi* and *S. vihiana* Davidson 1866, which, though supposedly Carboniferous at the time of description, came from an area (Vih in Kashmir) where Upper Triassic rocks were later found (Middlemiss 1909). *Spirifer kaishmeriensis* Davidson 1866, though much more transverse than *S. vihiana*, is nevertheless probably conspecific. This view is based firstly on the fact that Davidson's figured specimens (here respectively designated holotypes) of *S. kaishmeriensis* and *S. vihiana* occur on the same block, B62126, together with other fragments of *Spiriferina* and secondly on the existence of a transition between normal and transverse forms, noticed by Dierer in *Spiriferina griesbachi* (1908a, pl. 22, figs. 7–12) and now confirmed from the Oman material.

Davidson's names (*vihiana* and *kaishmeriensis*) have priority over Stoliczka's names (*altivaus* and *tibeticus*) since they were published in the first part of Vol. 22, *Quart. J. Geol. Soc. London*, which appeared before 16 February 1866 (Council Report, *Q.J.G.S.* vol. 22, p. 1), Stoliczka's work being published in Memoir 3 of the Geological Survey of India with Oldham's covering letter to the volume dated September 1866.

However, the valid foundation by Oppel (1865) of *Spiriferina abichi* seems to have escaped the notice of Bittner. Oppel based his description on a single pedicle valve whose age was unknown; its identity to *tibeticus, altivaus, vihiana, kaishmeriensis*, and *griesbachi* is scarcely in doubt, however, since, besides the apparent identity of form and ribbing, there is also similarity of age, the village of Tingti where *S. abichi* was found being now known to be situated in the marine Triassic outcrop of Spiti.

The internal structure of *S. abichi* from Oman is almost exactly like that of the type species of the genus, *S. walcotti* (Sowerby). The latter, however, because of the low convexity of the brachial valve, has a very much smaller space between the floor of the valve and the hinge-plate, and the median septum of the brachial valve, which is weak in *S. abichi*, is sometimes absent in *S. walcotti*. These differences are not of generic value and *S. abichi* is therefore confirmed as a *Spiriferina* (s.s.).

Three other Triassic spiriferinds closely resemble *S. abichi*, particularly in the presence of a rib in the median sulcus. These are *S. moscat* Bittner (1892, p. 80) from the Upper Trias of Anatolia, *S. lipolti* Bittner (1890, p. 139) from the Ludovician and Carnian of the Alps, and *S. subgriesbachi* Krumbeck 1924 from the Upper Trias of Timor. Of these *S. subgriesbachi* differs from *S. abichi* in being smaller, having coarser growth-lines and fewer but coarser ribs. Its internal structure is unknown but Krumbeck, as the name implies, closely related it to *S. abichi*. *S. lipolti* resembles *S. abichi* externally but has no dental lamellae and so cannot be closely related. *S. moscat*, on the other hand, has strong dental lamellae and must be close to *S. abichi*, particularly to the more transverse variants. It differs from these latter, however, in its more rounded lateral extremities and in having fewer (about five) more rounded ribs on the lateral slopes.

The Oman specimens of *S. abichi* are smaller than typical specimens from the gries-
bachii Bed of the Himalayas, but the Indian populations of the species vary in size (Diener 1908a, p. 121).

*S. abichi* thus occurs in the Asfal and Sumra Beds of Oman, the Triassic of the Vih laughs, Kashmir, the *S. griebachii* Beds of Painkhand, and the Coral Limestone, *Momois* Beds, and Quartzite series of Spiti.

Family **Athyridae** Davidson 1884

Genus **Misola** von Seidlitz 1893

*Misola noetlingii* (Bittner)

Plate 1, figs. 5–8

*Spirigeras? Noetlingii* Bittner 1899, p. 68, pl. 11, figs. 2, 3; Diener 1908a, p. 135, pl. 24, figs. 1, 2; Merla 1933, p. 111, pl. 5, fig. 4.

*Misola noetlingii* (Bittner), Seidlitz 1913, p. 191.


The Oman specimens agree very well externally with those figured by Bittner and Diener though the umbones cannot be compared since they have been damaged in the Oman specimens. Apart from the fact that spirulae are definitely present the complicated internal structures described by Seidlitz (1913) in *M. misolica* from the *Athyris* Limestone of Misol could not be proved in the Oman material. *M. noetlingii* is thus referred to its genus mainly on external features.

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**EXPLANATION OF PLATE 1**

All figured specimens are from the Elphinstone Beds, Upper Trias, of Wadi Milaha, Jebel Hagab area, near Ras al Khaima, Trucial Oman, Arabia. All, except those of figs. 1–4, were coated with ammonium chloride before photography.

Figs. 1, 2, 3, *Indoplecton elegans* aestor subsp. nov. *Momois* Beds, Sumra Formation. 1, Right valve, LL314, 1:5, holotype; 2, Left valve, LL315, 1:5, paratype, showing *Indoplecton* structure and the introduction of a radial genulation just anterior to the posterior row of tubercles. 3, LL321, 1:10. Showing *Indoplecton* structure in part of shell where the eulithic layer has mostly been removed but persists in the zigzag thickenings.

Fig. 4. **Pseudolinea* exxamamica* (Bittner). LL375, 1:10. Right valve showing secondary ribs in the troughs between slightly abraded radial folds, and raised growth lines considerably stronger than the radial striae. *Momois* Beds, Sumra Formation.


Fig. 22. *Spiriferina abichi* Oppel, transverse form, cf. *S. kaswanensis* (Davidson), BB20501, 1:5. *Spiriferina* Bed, Asfal Formation.

M. noetlingii is more tumid, narrower, and more strongly sulcate than M. lenticulata sp. nov., M. maniensis (Diener), or M. maniensiformis (Diener), and its ribs are coarser than even the coarsest ribbed specimens of M. misolica Seidlitz. The Misolia which Krumbeek (1913, p. 30) compared with M. noetlingii has more ribs which fork more often and is less tumid and less deeply sulcate. M. noetlingii lacks the characteristic asymmetry of M. asymmetrica Wanner, Knipscheer, and Schenk (1952, p. 72) which is also present in the various species of Misolia described by Kutassy (1934). M. noetlingii is longer and more tumid than M. pinaeae Krumbeek (1923, p. 327) and lacks the crenulations on the ribs of M. aspera Krumbeek (1924). Spirigera tricupit Bittner 1892 is like M. noetlingii in general shape but has no ribs in the sulcus. The specimen which Merla (1933, p. 111) identified as M. noetlingii is not typical since it has three ribs instead of two in the median sulcus.

Apart from Oman, M. noetlingii is thus only known from the Megalodon Limestone of Spiti.

**Misolia lenticulata sp. nov.**

Plate 1, figs. 9-12

*Holotype.* BB20243 (Pl. 1, figs. 9-12). *Paratypes.* BB20244-7, BB20251-48. All from Misolai Bed, Asfal Formation.

Description. Shell terebratuliform, both valves of low but about equal convexity. Dimensions (BB20243, holotype): length 28 mm., breadth 26 mm., thickness 12 mm. Sulcus of pedicle valve shallow; linguiform process not prominent. Median fold of brachial valve weak. Two ribs in sulcus of pedicle valve correspond to two furrows separating three ribs on median ridge. Lateral slopes with five or six ribs on each valve on each side, the number of ribs increasing in ontogeny by addition of ribs near the umbo. On material seen the ribs do not branch. Concentric growth-lines weak. Beak erect to sub-erect without beak ridges. Pedicle opening large, permesothyrid. Strong subparallel dental lamellae and distinct hinge-plate present: fragments of spiralia also observed. Other features not ascertainable in specimens examined.

Remarks. This species is less tumid than M. noetlingii Bittner. Probably the most closely related species is M. maniensiformis Diener (1906a, p. 126). The latter, which was based on one specimen from the Quartzite Series of Spiti, is similar to M. lenticulata in having two ribs in the sulcus and in its low convexity. It differs by being more strongly sulcate and perhaps by having fewer ribs on the lateral slopes (three instead of about five). M. aspera Krumbeek 1924 resembles M. lenticulata in its low tumidity but has more numerous ribs which branch fairly often; it also has coarse growth-lines. More numerous, more often branching ribs also distinguish M. pinaeae Krumbeek 1923 and M. cf. noetlingii Krumbeek 1913 from M. lenticulata. M. asymmetrica Wanner, Knipscheer, and Schenk 1952 and species such as M. loczyi described by Kutassy (1934) are distinctly asymmetrical in rib-arrangement. It may be of phylogenetic significance that Arabian and Indian species of *Misolia* (M. noetlingii, M. maniensis, M. maniensiformis, M. lenticulata) have fewer, simpler ribs than Indonesian species.

LAMELLIBRANCHIA

by R. G. S. HUDSON and R. P. S. JEFFERIES

Family NUCULIDAE d’Orbigny 1846

Genus NUCULA Lamarck 1799

Subgenus NUCULOPSIS Girty 1911

?Nuculopsis misolenis (Jaworski)

Plate 2, figs. 15, 19, 20

Nacula sp. nov. Krumbeck 1913, p. 53, pl. 3, figs. 18a, b.

Nacula misolenis Jaworski 1915, p. 106, pl. 44, figs. 7–13; Warner and Knipscheer 1951, p. 58, pl. 5, fig. 5.


HUDDSON AND JEFFERIES: UPPER TRIASSIC BRACHIOPODS

Material. LL120, internal cast with tooth lamellae preserved (Pl. 2, figs. 15, 19, 20). Modiolus Beds, Sunnma Formation.

This specimen agrees very well in shape with Type B of Nucula misolenis Jaworski (1915, pl. 44, fig. 13, not fig. 12). However, it is much smaller than most of the specimens of this species figured by Jaworski and also smaller than that figured by Wanner and Knipscheer (1951, pl. 5, fig. 5). It is, therefore, probably juvenile, which would explain why it lacks the internal ribs recorded by Wanner and Knipscheer and also, since the number of teeth in a taxodont increases with the age of the shell (Bernard 1896), why the anterior tooth-row has thirteen teeth instead of about twenty.

In his synonymy of N. misolenis, Jaworski quoted N. fritschi Boettger 1880. Though there is fairly good agreement between N. misolenis and the specimen figured by Boettger (1880, pl. 1, figs. 19, 20), later figures of N. fritschi (Krumbeck 1914, pl. 16, figs. 16a–d, 17) show a strong keel. There is also a strong external resemblance between N. misolenis and N. strigillata Goldfuss from the Ladinian of the Alps (see, for example, Bittner, 1895, pl. 17, figs. 1–17). The latter species, however, has a keel running forward from the umbo and its anterior dorsal sides are less steeply inclined to the median plane and are clearly visible in lateral view. Wanner and Knipscheer stated that the hinge of N. misolenis was not like that of N. strigillata since, in the former, the chondrophore slanted forward from the umbo and the anterior tooth row slightly overlapped the posterior, features which were both noticed by Quenstedt (1930) in the Jurassic species N. hamneri DeFrance.

The resemblance to N. hamneri suggests the allocation of N. misolenis to Paleonucula Quenstedt 1930, of which N. hamneri is the type. According to Schenck (1934, p. 36), however, Paleonucula is probably only a subgenus of Nuculopsis Girty 1911 to which, therefore, the present species is tentatively ascribed.

N. misolenis is the name-fossil of the Nucula Marl of the Misol Archipelago and is also known from the Fogi Beds of the west Buru and possibly from the Upper Triassic of Yunnan.

Family MYTILIDAE Fleming

Genus MODIOLUS Linnæus 1759

Modiolus jaworskii Wanner and Knipscheer

Text-fig. 4a

Modiolus spec. indet. Jaworski 1915, p. 105, pl. 45, fig. 4.

Modiolus jaworskii Wanner and Knipscheer 1951, p. 57, pl. 5, figs. 2–4.

Material. LL126, LL127, LL139–45 (LL140, text-fig. 4a), Lopha Beds, Sunnma Formation. LL128–38, Modiolus Beds, Sunnma Formation.

The Oman specimens agree very well with published figures of M. jaworskii from Indonesia though it is true that the shading in Jaworski’s figure (1915, pl. 45, fig. 4) seems to indicate that the sulcus connecting the umbo with the middle of the ventral margin is deeper than in the Oman material. But the sulcus does not show in the growthlines of the same figure and Jaworski says that the ventral margin is ‘ganz geradlining, vielleicht ganz schwach konkav eingebuchtet’. This would exactly describe the ventral margin of an Oman specimen. Some specimens of M. jaworskii figured by Wanner and
Knipscheer show strong concentric sulci. These, however, do not appear to be present in all Indonesian specimens and are occasionally found in specimens from Oman. Consequently they do not justify specific separation.

*M. javorskii* grows to a greater size than *M. omanensis* while young specimens can be distinguished from the latter by having a weaker suture, straighter ventral margin, longer hinge margin, and greater obliquity. From most other Triassic *Modiolus*, *M. javorskii* can be separated by its great height in relation to its length. *M. dubius* Healey (1908, p. 55, pl. 8, fig. 11) is very small but probably close to *M. javorskii*, as also is Bittner's *Myoconcha* sp. (1899, pl. 7, fig. 21). *Modiola* sp. (Krumbeek 1913, p. 49, pl. 3, figs. 9-10) is longer and slimmer than *M. javorskii* and has a much more concave ventral margin and deeper suture.

*M. javorskii* is recorded from the *Nucula* Marl of the Misol Archipelago.

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**Text-fig. 4c.** *Modiolus javorskii* Warner and Knipscheer, left valve, LL140, ×2-5. 4b and c, *Modiolus speciosus* Merla, left valve, LL146, ×1-5. c, Dorsal view looking down commissural plane of left valve. Both from *Lophia* Beds.

Specimens of text-figs. 4-12 except 10) are from Samra Formation, Wadi Milaha, Oman. All, except text-fig. 7, were coated with ammonium chloride before photography.

*Modiolus speciosus* Merla

**Text-figs. 4b, 4c**

*M. spatulata* sp. ind. Diener 1908a, p. 139, pl. 24, fig. 6.

*Modiola speciosa* Merla 1933, p. 117, pl. 6, fig. 17.

**Material.** LL146 (text-figs. 7b, 7c), LL147-8, *Lophia* and *Modiola* Beds, Samra Formation.

Merla rightly compared his new species with *M. paronai* Bittner (1895, p. 48, pl. 5, fig. 19) from the Carnian of Lombardy and with *M. frugi* Healey (1908, p. 54, pl. 8, figs. 8-10) from the Burmese Rhaetian. *M. speciosus*, however, differs from *M. paronai* and most other described Triassic *Modiolus* in its strong carina. It differs from *M. frugi* in having no sharp angle between the hinge-line and posterior margin.

*M. spatulata* sp. ind. (Diener 1908a) is clearly a specimen of *Modiolus speciosus*. In con-
sidering its generic position it is noteworthy that Diener compared his specimen with Modiolus minutus (Goldfuss) from the German Muschelkalk.

The type specimens of M. speciosus Merla came from the Upper Norian of Depsang, Tibet, and the specimen figured by Diener (1908a) from the Megatodus Limestone of Spiti.

Modiolus omanensis sp. nov.

Text-fig. 5a–c

Holotype, LL154 (text-figs. 5b, c). Paratype, LL150–3, LL200 (text-fig. 5a). Other specimens, LL155–99, LL201–303, LL305, all from Modiolus Beds, Sumra Formation.

Description. Dimensions (LL186): Length 18 mm., height 14 mm., width 8 mm. Outline rounded trigonal or oblong with height only slightly less than length. Hinge-line somewhat convex, grading into anterior and posterior margins. Slightly convex posterior margin grades into slightly concave ventral margin with which it makes an angle of about 10° (in oblong forms) or 20° (in trigonal forms). A weak sulcus runs from the umbo to the slight concavity of the ventral margin. Umbones projecting above hinge, subterminal, somewhat prosogyrous, without an umbonal septum. Shell thin, brownish as preserved, ornamented with weak concentric growth-lines and revealing characteristic radial mytilid structure when slightly weathered.

Comparison. The forms which Healey described (1908) from the Rhaetian of Burma as Modiolus spp. 1, 2, 3, and 4 are almost certainly conspecific and closely resemble M. omanensis. The latter, however, has a less pronounced antero-ventral angle. M. omanensis is also superficially like Datta oscellaris Healey (1908) but lacks the well-developed posterior wing and the very strange hinge-structure of that species. M. fragi Healey (1908) from the Burmese Rhaetian, and M. salzstettensis Hohenstein (1913) from the Trechtkalk of the Black Forest are small, rather trigonal forms like M. omanensis but their umbones are more nearly terminal. M. southerness Vaughan (1904) from the Rhaetian of South Wales is more orbicular in outline than M. omanensis and its height still more nearly equal to its length. Krumbeck's Modiola sp. (1914, p. 49, pl. 3, figs. 9, 10) from the Fogli Beds of west Buru is more elongate than M. omanensis but similar in general outline. Diener, however (1923, p. 202), thought this species was a Myoconcha, a matter which could only be decided by examining its shell structure.
Family pteridae Meek
Genus cassianella Beyrich 1861
Cassianella cf. subeuglypha Krumbeck

Comparisons
Cassianella subeuglypha Krumbeck 1913, p. 141, pl. 1, fgs. 16a-d.
Cassianella cf. subeuglypha Krumbeck. Jaworski 1915, p. 94, pl. 43, fgs. 18, 19.

Material. LL149a, a single left valve with ventral parts missing. Mediolus Beds, Summa Formation. L52751, coll. Lees, poor internal cast of left valve. Five miles east of Ras al Khaima, Oman.

The Oman specimens are very like C. subeuglypha as figured by Krumbeck (1913, pl. 1, fgs. 16a-d). His figured specimen, however, seems to have a concave anterior car and more deeply concave sulci between the radial keels or ribs; it is also somewhat less oblique than the Oman specimens. These differences suggest that the Oman form is possibly a new species.

Other species differ from the Oman specimens as follows: C. kattalotica Krumbeck from the Norian of Sumatra (Krumbeck, 1914, p. 226, fgs. 2-4) has a greater length/height ratio and a posterior keel only weakly developed. C. verbeeki Krumbeck 1914 lacks the anterior keel but has a general resemblance in shape. C. cf. subeuglypha Jaworski (1915, p. 96, pl. 43, fgs. 18-19) differs by having a better developed central keel; otherwise it is very close indeed. C. nov. sp. aff. subeuglypha Krumbeck (1924, p. 248, pl. 186, fgs. 16a-b) differs in the shape of the anterior car and by its strong radial ornament.

C. subeuglypha Krumbeck and C. cf. subeuglypha Jaworski come respectively from the Athyris Limestone of Jilu (Misol Archipelago) and from the Nacuta Marl of Misol.

ExPLANATION OF PLATE 2

All figured specimens are from the Elphinite Beds, Upper Trias of Wadi Milaha, Jebel Habab area, near Ras al Khaima, Trucial Oman, Arabia. All were coated with ammonium chloride before photography. Figs. 1-14, 16-18, 21, 23-26, ×1. Figs. 15, 19, 20, 22, ×2.

Figs. 1-4, 8, 9. Halopesten elegansi superior subsp. nov. 1-3, LL321; 4, 8, LL310; 9, LL313. Mediolus Beds, Summa Formation. 1, 4. Left valve; 2, 8, 9. posterior view; 3, right valve. Figs. 1-4 are abraded specimens which, in consequence, resemble 'Pecten' marginicostatus Diener.

Figs. 5-7. Halopesten amasiformis sp. nov., holotype, LL309. 5, Right valve; 6, posterior view; 7, left valve. Diacoracidium Limestone, Asfal Formation.


Figs. 13, 17. Megalodon [(marginicostatus) Kuitassy, LL427e. 13. Dorsal view; 17, right valve. Elphinite Beds (exact horizon not known).

Figs. 15, 19, 20. Nacuta modestes Jaworski, LL120. 15. Left valve; 19, dorsal view; 20, posterior view. Mediolus Beds, Summa Formation.

Figs. 18, 23, 24. Acropesten verraticostus (Bittner), LL306. 18. Dorsal view; 23, left valve; 24, right valve. Lophya Beds, Summa Formation.

Fig. 22. Megalodon rostriformis Krumbeck, LL429, left valve. Mediolus Beds, Summa Formation.

Fig. 25. Pterocoracidium dieneri, LL462, left valve. Mediolus Beds, Summa Formation.

Fig. 26. Myophoria verbeeki mensutii Reed, LL422, left valve. Lophya Beds, Summa Formation.
Family PECTINIDAE Fleming
Genus AEQUIPECTEN Fischer 1886
AEQUIPECTEN SERRATICOCA (Bittner)

Plate 2, figs. 18, 23, 24; text-fig. 3a.

LIMA SERRATICOCA Bittner 1889, p. 50, pl. 8, figs. 12, 13; p. 51, pl. 10, fig. 26.

LIMA cf. SERRATICOCA Bittner. Diener 1908a, pp. 99, 132, pl. 17, fig. 6.

Indopecten sp. Cox 1935, p. 3, pl. 1, figs. 1a, b.


Morphology. Right valve more convex than left. Left valve with eight radial folds, the anterior and posterior pairs being much weaker than those between. All folds, except the most anterior and the most posterior, distinctly angular in section and separated by furrows of same shape and amplitude. Crest of each fold carries a row of tubercles. Whole surface ornamented by close-set, fine, concentric growth-lines, every fourth or fifth growth-line being raised and the free edge characteristically crimped (text-fig. 3a). These crimped growth-lines do not show on a weathered specimen since the crimping affects only the free edge of a raised growth-line and the base is not involved. Shell consists of an outer, transparent, thin, dark-brown layer and an inner, opaque, thick, light-brown layer, the former being thickest over the tubercles. No trace of Indopecten structure (see later). Ornament of right valve like that of left but nine radial folds instead of eight. This is due to additional coarse median fold. One valve (right) much thicker-shelled than the other and provided with strong radial ribs before and behind each radial fold. Internal radial ribs on the thinner valve lie opposite those on the thicker and are less well developed. Ears not seen. Divided from flank in both valves by slightly concave areas perpendicular to the commissure.

Comparison. In specimen LL306 the two most anterior ribs are farther apart than in the first figured specimen of Lima serraticoa (Bittner 1889, pl. 8, fig. 12): otherwise there is very good agreement. The Oman specimen also resembles the other specimen figured by Bittner (1889, pl. 8, fig. 13): this, however, is an internal cast so that comparison is difficult. The Oman specimens are less like the specimen figured by Bittner on pl. 10, fig. 26: this has non-tuberculate ribs and comes from a higher horizon than the other two specimens. Indopecten sp. from the Triassic of the Attock district (Cox 1935) is probably A. serraticoa. Since it did not show Indopecten structure it was thought to be a right valve.

Generic allocation. Bittner (1889) and Diener (1908a) allocated 'serraticoa' to Lima: this is clearly incorrect since Lima is never inequivalent. Subsequently Krumbeek (1924, p. 343) placed it near his new species Pecten (Aequipecten) sub-serraticoa. The latter has rather sparse Indopecten structure on the left valve and for this reason Krumbeek placed it in the 'verhekt' group. Consequently, when this group was made the basis for the new genus Indopecten, both serraticoa and sub-serraticoa Bittner were allocated to that genus (Douglas 1929, p. 633). It seems very likely that the present species is indeed related to Indopecten sub-serraticoa Krumbeek for there is a strong resemblance in the ribbing and the internal ribs are also Indopecten-like. There is, however, no true Indopecten structure though the outer brown layer is especially thick over the tubercles of the
left valve which suggests that these tuberules looked like dark spots when the animal was alive, that is, it had a colour pattern produced in fundamentally the same way as in *Indopecten*. Since *serraticosta* is neither a *Lima* nor an *Indopecten* and since it has an inequivalve shell and because of the nature of its ribbing it is here placed in *Aequipecten*.

*Distribution.* Known from the 'Tropies Beds' (= Harkories and Procyonanthus griesbachi Beds) and possibly from the 'Spiriferina griesbachi' Beds and Sagenites Beds of Painkunda, the Javaries and Monotis Beds and Quartzite Series of Spiti, and from beds referred to Triassic in the Attock district.

**Genus Indopecten** Douglas 1929

*Structural colour-banding.* The genus *Indopecten* Douglas (type species: *Pecten elignetti* Krumbek 1913) is based on Krumbek's 'verbeeki' group (1924, p. 343). It includes a number of Upper Triassic Indo-Pacific Pectens which have the left valve somewhat less convex than the right and in which both valves carry five or more weak or strong radial folds and have internal ribs arranged in pairs near the ventral border: the shell structure is also characteristic for both valves consist of an outer translucent dark-brown layer covering an inner opaque light-brown layer, and in the left valve zigzag thickenings of the outer layer lie into the outer surface of the inner layer show from outside as a pattern of dark-brown lines within the shell. This structure of zigzag brown lines is in the paper referred to as *Indopecten* structure (Pl. I, figs. 3, 4).


Krumbeck (1913, p. 39) hesitantly suggested that *Indopecten* structure served to strengthen the left valve. It seems more likely to have been an expression of colour-banding. This would explain its restriction to the left valve since Pectens always swim or lie with the left valve uppermost so that this valve is usually more brightly coloured than the right. Structures superficially comparable to *Indopecten* structure also occur in recent molluscs, such as the gastropod *Notitia communis* from the Philippines. If this interpretation is correct the presence of *Indopecten* confirms that the Sumra Formation was deposited in photic conditions.

*Indopecten* structure is by no means confined to *Indopecten*: it also occurs in the following Triassic species of *Entolium*: *Pecten discites* Schlotheim 1820, *P. illusus* Hauer 1857, *P. azzarolae* Stoppani 1861, *P. schlösseri* Wörthmann 1889, *P. cf. subdenissus* Bittner 1895, *P. (Syncyclonema) quotidianus* Healey 1908, and *P. (Entolium) decoratifloris* Krumbek 1924. It does not seem to be known whether *Indopecten* structure is restricted to the left valve in these forms. They are most likely closely related to each other and probably to *Indopecten*, and Jaworski (1915, p. 147) included them in his
clignetii group together with Indopecten. It should be noted that Bittner (1895, p. 165) described Indopecten structure as color-banding in Eutolium cf. subdenticulatum (Muenster).

Fischer (1925) described three color varieties of Pleuropecten laevigatus (Schlotheim) from the Muschelkalk near Toulon. One of these varieties, P. laevigatus derogatus (Fischer), shows what is essentially Indopecten structure on the left valve only. Presumably this variety is not phylogenetically connected either with Indopecten or with the species of Eutolium listed above: its Indopecten structure must be an independent development.

The distribution of Indopecten. Douglas (1929, p. 631) based far-reaching palaeo-geographical conclusions on the distribution of many forms supposedly absent from the Himalayas but present in Indonesia and the Middle East. Among such forms he wrongly included Indopecten which had already been found in Spiti (Diener 1935a) and recorded as Pecten aff. moniliferus (= I. clignetii) and as Pecten sp. ind. aff. massalogni Stoppani (= I. amusiformis sp. nov.). Pecten (Variumssium) margaricostatus is also probably an Indopecten, possibly I. clignetii.

Arkell (1956, p. 401) has already refuted Douglas's views on the basis of the Indopecten sp. recorded by Cox (1935, p. 3, pl. 1, fig. 1) from the Attock district of the Himalayas. As pointed out above, however, Cox's specimen is probably Aequipecten serraticostus (Bittner) and hence cannot be used as evidence against the views of Douglas.

Indopecten amusiformis sp. nov.

Plate 2, figs. 5-7

Pecten sp. ind. aff. Massalogni Stoppani. Diener 1935a, p. 131, pl. 23, fig. 10.

Holotype, IL.300 (Pl. 2, figs. 5-7). Dicroeocardium Limestone, Asfal Formation.

Description. Shell thin-shelled, right valve slightly more convex than left. Length 32 mm., height 36 mm., thickness 11 mm. Umbones median, projecting slightly above hinge-line; apical angle about 100°. Outline of flank of shell (apart from ears) an almost regular pentagon, but angles rounded (except umbo).

Left valve with six weak folds separated by five weak furrows. Near the umbo these folds are stronger than farther away and somewhat angular. The two median folds coincide with rounded obtuse angles in ventral margin. Three median folds near umbo have weak secondary ribs which quickly die out ventrally. Indopecten structure present over whole valve. Ears separated from flank by elongate, concave areas, roughly perpendicular to commissural plane. Anterior margin of anterior ear arcuate with distinct byssal sinus. Posterior margin of posterior ear probably sinuous. Near ventral margin internal ribs present before and behind second to fifth radial folds. Internal ribs anterior and posterior to this possibly present but not seen.

Right valve with five radial folds, very weak except near umbo. Folds separated by four furrows that are distinctly angular in section near umbo but much weaker ventrally. Internal ribs present near ventral margin in pairs before and behind each furrow with the addition of a single rib before the anterior radial fold. Ears separated from flank by sharp flexure. Anterior margin of anterior ear with distinct byssal notch. Posterior margin of posterior ear sinuous.
Remarks. The holotype of *I. amusiformis* clearly belongs to the same species as the specimen from the *Monaxis* beds of Spiti described by Diener (1908a) as *Pecten* sp. ind. aff. *Massalongi*. This specimen, contrary to Diener’s opinion, is a left valve for his figure shows excellent *Indopecten* structure. *I. amusiformis* is not very similar to *P. massalongi* Stoppani in which the internal ribs are much more numerous.

The new species differs from *I. elgnettii asperior* (subsp. nov.) and *I. elgnetti eignetii* (Krumbein) in being more nearly equivaclid, in having weaker secondary ribs, a thinner shell, and no crenulations on the radial folds of either valve. It differs from *I. krumbecki* (Jaworski) in having much weaker radial folds and from *I. verbeekii* (Boettger), *I. microglyptus* (Boettger), and *I. misolaensis* (Jaworski) in lacking crenulations on both valves.

*I. glabra* Douglas (not Krumbein 1913) is a much bigger species, very inequivaclad and with strong secondary ribs. *Entalith* cf. *subdivissum* Muenst. (Diener 1908a, p. 138, pl. 24, fig. 12) at first sight closely resembles the present species but shows no sign of radial folds or *Indopecten* structure. Of the species just mentioned the one closest to *I. amusiformis* is probably *I. microglyptus* (Boettger).

*Indopecten elgnettiii asperior* subsp. nov.

Plate 1, figs. 1–3; Plate 2, figs. 1–4, 8, 9.

?Pecten (Varianmussium) marmariticostatus Diener 1908a, pp. 97, 131, pl. 18, figs. 1–3.


*Pecten (Aequipecten) elgnetti* Krumbein (pars) 1913, p. 41; Krumbein (pars) 1923, p. 345. Pl. 193, fig. 9.

Chlamys (Aequipecten) elgnetti G. Boehm eneod. Krumbein, Lees 1926, p. 636, pl. 44, fig. 3.

Holotype, LL314, right valve (Pl. 1, fig. 1). Paratype, LL315, both valves (Pl. 1, fig. 2). Other specimens: LL310 (Pl. 2, fig. 9), LL311, 312, LL312 (Pl. 2, figs. 4, 8), LL316–20, LL321 (Pl. 1, fig. 3; Pl. 2, figs. 1–3). LL322–4, LL330–37, LL339–21 from *Moudus* Beds; LL318, LL332–4 from *Lopha* Beds. All from *Summa* Formation.

Description. Shell thick-shelled, inequivaclad; both valves convex but right more convex than left. Shell nearly equilateral but umbones slightly anterior. Umbones not prominent, apical angle about 90°. Left valve with six narrow radial folds separated by five broad furrows. Anterior and posterior folds much weaker than the others. The three median furrows each carry two radial secondary ribs. No secondary ribs in the anterior furrow. The posterior furrow bears two secondary ribs near the umbo of which the more posterior is much the stronger and changes ventrally into a sharp radial incanxulation. All six folds carry a single row of crenulations which tend to die out ventrally but persist longer on the median four folds than on the anterior or posterior folds. The secondary ribs and the posterior incanxulation also often die out ventrally. The left valve has *Indopecten* structure. Before and behind the four median folds the brown lines are curved divaricate. Between these two areas the lines are zigzag with the bisectors of the angles of the zigzag radiating from the umbo.

Right valve with five primary radial folds separated by four radial furrows narrower than the folds. The anterior and posterior folds are much weaker than the others. Each fold carries rows of tuberces; there are one to two rows on the anterior and posterior folds and usually three on the others, and the tuberces are concentrically paired or tripled on each fold. Furrows without secondary ribs.

In both valves concentric growth-lines are convex distally in the furrows, convex
proximally over the primary folds. Inside both valves, except near the umbo, there are radial internal ribs. In the left valve, one internal rib lies beneath the posterior radial fold, and internal ribs lie just before and behind the second to fourth radial folds. There is no internal rib beneath the anterior radial fold. In the right valve there is an internal rib opposite every internal rib of the left valve. Ears like portion of cylinder with horizontal axis (compare those of *Pecten maximus* (L.)). Ears of left valve concave, separated from flank by areas roughly perpendicular to plane of commissure; ears of right valve convex, separated from flank by sharp flexures. Left anterior ear with arcuate anterior margin; right anterior ear with strong byssal notch. Posterior border of posterior ear sinuous.

**Remarks**. *I. clignetii asperior* differs from *I. clignetii clignetii* (Krumbeek 1913, p. 36, pl. 2, figs. 1–8, pl. 4, fig. 29) by having three rows of tubercles on the third rib of the right valve (and sometimes on second and fourth ribs also) instead of only two. This difference, however, does not demand full specific separation since the form with three rows of tubercles is known in Indonesia (Krumbeek 1913, p. 41; 1923, pl. 193, fig. 9) within the *I. clignetii clignetii*plexus. The Oman form is therefore considered to be a geographical variant of the Indonesian species. The name *asperior* (= rougher) indicates that the tubercles are more abundant than in *I. clignetii clignetii*.

The form which Diener (1908a) figured and described as *Pecten aff. monilifera* is clearly specifically identical with *I. clignetii*. Which subspecies it belongs to, however, cannot be decided until the right valve is known. It is also possible that *Pecten margariticostratus* Diener 1908a is based on abraded specimens of *I. clignetii*. Certainly abraded specimens of *I. clignetii asperior* (Pl. 2, figs. 1–4) from Oman have a strong resemblance to one of the figures of *P. margariticostratus* (Diener 1908a, pl. 18, fig. 1). If *P. margariticostratus* is identical with *I. clignetii* the latter is a junior synonym. The matter, however, can only be decided by examination of the type specimens of the former. Pending such examination it is better to retain the specific name *clignetii*. *I. seinaensis* (Krumbeek 1923, p. 344, pl. 193, figs. 10–12) differs from *I. clignetii asperior* by having more than five tuberculate folds on the right valve, by having up to five rows of tubercles on the median fold of the right valve, and by the absence of distal weakening in the ornament.

*I. clignetii asperior* probably spent most of its life with the commissure about level with the sea-bed and the right valve buried. The radial folds of the right valve would help to hold the shell in place; a suggested explanation for why they are so much stronger than those of the left valve.

**Distribution**. *I. clignetii asperior* is known from the Fugi Beds and *Athyris* Limestone of the Misol Archipelago. *I. margariticostratus* (Diener) and *Pecten aff. monilifera*, which may be identical with *I. clignetii asperior*, are known from the Jura river Beds, *Monotis* Beds, and Quartzite Series of Spiti.

**DIMYIDAE Dull**

**Genus Dimyodon Munier-Chalmas 1886**

*Dimyodon cf. subrichtofeni* Krumbeek

**Compare**

*Dimyodon subrichtofeni* Krumbeek 1924, p. 347, pl. 193, fig. 1; Reed 1927, p. 221.

*Dimyopsis* sp. Lees 1928, p. 637.
Material. LL325, LL326 (attached to Spirographis abich (Dav.) x, 3. BR20491, BR20502, BR20503 from Spirographis Limestone, Asial Formation. LL327 (attached to shell fragment), Lophia Bed, Summa Formation. LL427b attached to Megalodon hongricum; exact horizon in Elphinstone Beds not known. LL344, thirteen specimens attached to holotype of Myosphera gigantea; Lees (= M. vebeek/ nassifii Reed).

The genus Dimyodus (Bittner 1895, p. 219), in which Lees placed his specimens of this species, differs from Dimyodus in having no teeth. This distinction, however, is very difficult in practice since the umbo region of these forms is thin and has usually been damaged. Thus of the seventeen specimens examined in the present investigation only two show the two small diverging teeth of the right valve characteristic of Dimyodus: the differences between these specimens and the others are certainly preservational and have no taxonomic value whatever.

None of the specimens seen are well enough preserved to prove that they belong to Dimyodon subricihofani Krumbeek rather than to D. richihofani Bittner (1895, p. 217). They have been compared with the former species only because an Indonesian relationship seems more likely than a European one. The specimens described as Dimyopus cf. intestistrata Emmrich from the Fogi Beds and Athyris Limestone of the Misol Archipelago (Krumbeek 1913, p. 44) and as Dimyodon richtofeni Bittner from the Nicula Marl of Misol (Jaworski 1913, p. 103) are probably specifically identical with the Ottoman specimens. The left valve of D. subricihofani has not previously been described. It is thin, moderately convex, and with faint radial striae. Some of the specimens of 'Myosphera gigantea' show both valves in apposition.

The type of D. subricihofani is from the Carnian of Timor. Comparable forms are known from the Norian of the Misol Archipelago and the Upper Triassic of Yunnan.

Family OSTRIDAE Fleming
Genus LOPHA Bolten 1798
Lophia blanfordi (Lees)

Text-figs. 3b, 8d, e

Eugyra Stoliczka in Blanford 1872, p. 76.
Eugyra sp. ind. aff. conica Diener 1908b, p. 159, pl. 36, fig. 4 (not Chama conica J. Sowerby 1813).

Ostracod (Eugyra) Blanfordi Lees 1928, pl. 634, pl. 44, figs. 2a-b.
Alectryonis parasitica Saurin 1941, p. 7, pl. 1, fig. 38, pl. 2, figs. 2-5 (not Krumbeek 1913).
Probably Aelectryonis aff. mooris caprile Saurin 1941, p. 7, pl. 1, figs. 39-41, pl. 2, fig. 1 (not Kilipstein 1845).


Morphology. Internal features seen in specimen LL363. Anterior external ligament trace reduced or absent. Internal ligament trace not a distinct groove but marked by series of growth-lines slightly convex distally. Adductor scar just ventral to umbo. No pseudo-taxodont dentition, no internal marginal crenulations; left valve not thicker shelled than right. External folds only reflected internally near the shell margins.

Remarks. The present species has the strong radial ribs and serrated commissure of Lophia (= Alectryonis) and the involute umbones of Eugyra. In fact it could almost
Hudson and Jefferies: Upper Triassic Brachiopods

equally well be placed in either genus. It is here referred to *Lopha* because the nature of the ribbing is somewhat easier to see than the nature of the umbo. Krumbein would probably have approved this ascription since he called the most nearly related form *Alectryonita parasitica* (1913, p. 47, pl. 3, figs. 4–8).

*L. blanfordi* differs from *A. parasitica* Krumbein in having somewhat stronger ribs which begin at the attachment area instead of more distally. The weaker ribbing of *A. parasitica* is probably not due to the nature of the attachment since the attachment area varies greatly in size in the published figures (Krumbein, 1913, pl. 3, figs. 4–8) and the ribbing is not affected. *Ostrea (Alectryonita) cf. parasitica* Krumbein (1923, p. 206, pl. 13, figs. 2–4) is still more like *L. blanfordi* but the ribs seem wider and do not always start at the attachment area. The form which Saurin (1941, p. 7) called *A. parasitica* is more like *L. blanfordi* since it is ribbed over the whole free surface. It also seems likely that *A. aff. montiscapritis* of Saurin is of the same species as his *A. parasitica* and should also be united with *L. blanfordi*. Saurin described the form of his specimens as not *courbe* without describing the curvature of the umbones which in true *montiscapritis* are non-involute (Bittner 1912, pl. 6, fig. 17). In his synonymy of *L. blanfordi* Lees (1928, p. 634) rather doubtfully quoted *A. cf. haldingeriana* of Healey (1908, p. 37, pl. 5, figs. 18–19). This seems to have been a mistake, however, for Healey stated of her specimens that though the umbo was twisted in certain examples, in most it remained straight (p. 37). The umbo is also straight in the form identified by Fleming (1953, p. 276) as *L. cf. haldingeriana* (Emmrich) from the Rhaetian of New Zealand. Krumbein (1913, p. 48) mentioned the occurrence of oysters with involute umbones in the Rhaetian of Hungary. These forms must be closely related to *L. parasitica* and *L. blanfordi*.

*L. blanfordi* is recorded from the Elphinstone Beds of the Elphinstone Inlet and of the area 5 miles east of Ras al Khaima, and from the Upper Triassic of Huai Hunh, south Amman.

**Family Limidae**

**Genus Pseudolimnea** Douglas and Arkell 1932

*Pseudolimnea? cumaunica* (Bittner)

Plate 1, fig. 4; text-figs. 3o, 6o, 8

Lima camaunica Bittner 1899, p. 59, pl. 10, fig. 25, 1908a. "Lima camaunica" Bittner, p. 137, pl. 24, figs. 10, 11.

Lima subcamaunica Lees 1928, p. 636; not Jaworski 1915, p. 96, pl. 43, figs. 20, 21; not Limn (Rudolphi) subcamaunica Krumbein 1913, p. 34, pl. 1, figs. 19, 20.

Material. LL368, LL369 (text-fig. 6o, 8), LL370-4, LL375 (pl. 1, fig. 1), LL377-98. Medjahan Beds, Sumna Formation. LL401-3, Sumna Formation (exact horizon not known). LL406 Spiniferina Bed, Asfal Formation.

Morphology. Flank with about fifteen strong primary ribs having flat sides and rounded apices. Anterior flank ribs sometimes strongly crenulate distally. Primary flank ribs separated by furrows which are rounded and equal to the ribs in width near umbo (up to a shell length of about 10 mm.) but wider than the ribs and flat-bottomed away from umbo. The rounded parts of the furrows near the umbo carry a distinct secondary rib. Surface covered with numerous regularly spaced growth-lines which are weak on lunule.
and escutcheon but strong and raised on the flank, not only in the furrows but also over the main ribs when the specimen has not been abraded. The raised growth-lines are interrupted by the secondary ribs and crossed by numerous radial striae weaker than the growth-lines. The growth-lines are convex away from the umbo over the flank ribs and in general convex towards the umbo in the furrows. Where they touch the secondary ribs, however, they form an obtuse angle pointing away from the umbo. This obtuse angle is also present in the parts of the shell farther from the umbo where secondary ribs have disappeared.

Radial ribs usually absent on lunule and escutcheon except on the parts nearest the flank. Ears subequal. Hinge-line with distinct triangular internal ligament-trace and about two small pseudo-taxodont teeth on each side near the cardinal extremities (see text-fig. 3b).

**Remarks.** *Lima cumanica* Bittner is referred to *Pseudolinea* Douglas and Arkell 1932 because of its small size and the presence of strong flat-sided ribs and secondary ribs. There is some disagreement about the hinge of *Pseudolinea*. Arkell (1932, text-figs. 20, 21) figured two *Pseudolinea* hinges, both of them edentulous, but Cox (1944) has pointed out that pseudo-taxodont teeth do sometimes occur in the genus. The nature of the hinge, therefore, does not exclude *L. cumanica* from *Pseudolinea*.

The Oman specimens tentatively referred to *P. cumanica* agree with Bittner's and Diener's figures of this species in size, outline, number of flank ribs, the presence of secondary ribs (see Diener 1908a, pl. 24, fig. 8), and, with a few exceptions, the general lack of radial ribs on most of the lunule and escutcheon (Bittner 1899, p. 59). The horizon is also similar since the species is known in the Himalayas from the *Megalodon* Limestone and the *Spiriferina griesbachii* Bed. The Oman material, however, has very prominent growth-lines, whereas Bittner described the growth-lines of his specimens as scarcely perceptible. He had, however, only two valves and these may have been abraded. For this reason it seems better tentatively to identify the Oman material with Bittner's species than to create a new one.

Lee's identified the shells in his collection as *Lima subcumanica* Krumbein. The latter is certainly closely related to *L. cumanica* and has been much better described (Krumbein 1913, pl. 34; Jaworski 1915, p. 96). It differs from the Oman specimens by being more oblique (the angle between the hinge-line and the greatest diameter being about 55° instead of 65°), by normally having abundant radial ribs on lunule and escutcheon, and by having the fine radial lines as strong as the growth-lines instead of being much weaker (Krumbein 1913, pl. 1, fig. 19b; Jaworski 1915, pl. 43, fig. 21a). With the possible exception of the last, all these features also distinguish *L. subcumanica* from the Himalayan *L. cumanica*.

A number of other *Pseudolinea* from the Himalayas deserve mention. *Lima sp.* (Bittner 1899, p. 50, pl. 7, fig. 20) from the *Halobia comata* Beds is more orbicular in
outline than *L. cumaunica*. *Limna* sp. (Bittner 1899, p. 50, pl. 8, fig. 11) is rather close to *L. cumaunica* but too badly preserved for detailed comparison: *Limna* sp. ind. aff. *cumaunica* (Dienzer 1908a, p. 132, pl. 23, fig. 14) may possibly be identical with *L. cumaunica*.

Five of the specimens of *P. cumaunica* from Oman are double-valved. Two of these, LL395 and LL397, give the impression, from the way they are crushed, that they were buried with the commissure roughly vertical. This suggests that in life *P. cumaunica* adopted the same position as modern *Limna* with the antero-dorsal margin resting on the sea-bed. This is the more likely in view of the somewhat excavated lunule of the species which would make a very firm base. A similar mode of preservation with the animal resting on the lunule also occurs in *L. lineata* Schlotheim from the German Wellenkalk. The other double-valved specimens, which from their mode of crushing were probably buried with commissure horizontal, were probably rolled over by current action after death.

*P. cumaunica* is known from the *Spiriferina grisbachi* Beds of the Painkhanda and the Megafodon Limestone of Spiti. The closely related *P. subcumaunica* is from the Fogi Beds of Buru and the *Nucula* Marl of Misol.

**Text-fig. 7. Plagioistoma nudum** (Parona). LL404, 0.9, from Lophia Beds. *a* Left valve showing concentric colour bands; *b* outline of anterior view; *c* right valve showing radial and concentric colour bands (*a* and *c* coated with oil).

**Genus Plagioistoma** Sowerby 1814

*Plagioistoma nudum* (Parona)

Text-figs. 7a-e

*Limna (Plagioistoma) nudum* Parona 1889, p. 83, pl. 4, fig. 5; Wöhrmann 1893, p. 652.

*Limna (Plagioistoma) mysica* Bittner 1891, p. 109, pl. 2, fig. 1.

**Material.** LL404 (text-fg. 7a-e), Lophia Beds, Sumna Formation.

**Remarks.** The surface of the unweathered shell is completely smooth except for growth-lines. These are fine over most of the shell but coarse in the lunule and on the anterior ear. Weathering reveals a fine radial shell-structure. The one specimen collected shows clear concentric colour-bands over the whole shell, and radial colour-bands on the anterior dorsal part of the right valve. This colour banding, like that of *Indopecten*,
strongly suggests that the Sunna Formation was laid down in the photic zone of the sea (see above).

In outline, size, and total lack of radial ornament, the Oman specimen agrees very well with the type specimen (Parona 1889) which came from the Carnian of Lombardy. The internal cast which Reed (1927, p. 229, pl. 18, fig. 31) recorded as Lima (Plagiostoma) cf. vacca shows rather strong concentric folds and hence is probably not very close to the true L. vaca, L. (P.) myatica Bittner from the Upper Trias of Balia in Anatolia does not seem to differ essentially from P. vaca, L. (P.) sp. (Krumbeek 1913, p. 33, pl. 1, fig. 17) is probably closely related to the Oman specimen but shows weak radial ornament.

Plagiostoma subvalonians Krumbeek


Remarks. Though badly preserved, the Oman specimens agree with the type specimens (Krumbeek 1923, pl. 12, figs. 17–19) in every ascertainable particular. Krumbeek’s figured specimens vary considerably in height/length ratio and the Oman specimens correspond to the taller form (Krumbeek 1923, pl. 12, fig. 17a). Krumbeek was wrong to describe the internal cast of this species as smooth: in his figures and on the larger Oman specimen (L.3751) the internal cast clearly reflects the external radial ribs. The ribs of the present species are broader and less numerous than those of P. praecursor (Quenstedt) or P. valoniense (Debrance) which are probably its closest relatives.

The types of P. subvalonians are from the Norian Kanike Beds of Cerin.

Family MYOPOHORIDAE

Genus COSTATORIA Waagen 1907

Costatoria omanica (Diener)

Text-figs. 5c, 8a–e

Myophoria aff. chenosus Laube. Stoliczka in Blanford 1872, p. 76.
Myophroria omanica Diener 1906, p. 156, pl. 24, figs. 1–3; Lee 1928, p. 685.
Material. LL405–6, Lopha Beds, Sunna Formation. LL407 (juv.). LL408–21 (LL410, text-figs. 8a–e), Modiolus Beds, Sunna Formation.

Morphology. Shell equivale, umbones slightly prosogyrous. Ornament the same in both valves. On flank are about eight radial ribs (not counting marginal carina), narrower than the intercostal furrows and strongly crenulate, the crenulations being elongated concentrically. Siphonal area radially concave, divided at about two-thirds of its height above the base by radial groove, and separated from escutcheon by crenulate external carina. Limul somewhat sunken, smooth except for growth-lines. Hinge of left valve (text-fig. 3c) seen in one juvenile specimen (LL407). 2a strong, not bifid, ventral border convex; 4a fairly strong, narrow, as long as 2a, with fine striae perpendicular to commissure on posterior face; 4b weak, marginal. Socket for 3a (of right valve) much deeper than socket for 3b, The whole supported on a cardinal plate.

Remarks. The hinge of this species is undoubtedly Myophoriiid rather than Trigoniid
and the species must be referred to *Costatoria* (Waagen 1907) because of its strong radial ribs. Striae may have been present on other parts of the hinges besides the posterior face of 4a. Three European Carnian species closely resemble *C. omanica* externally. *Myophoria inaequicostata* Klipstein (see Bitner 1895, p. 94, figs. 1–14) has the flank ribs in two groups, the anterior ones being closer together than the posterior. *M. chenopodi* Laube is still more like *C. omanica* but is longer relative to its height. *M. whaleyciae* Buch has weaker and sparser ribs.

![Image of brachiopods](image)


The types of *Costatoria omanica* are from the Elphinstone Beds of the Elphinstone Inlet. The species was also recorded by Lees (1928) from 5 miles east of Ras al Khaima.

*Costatoria? vestitaformis* (Krumbeek)

**Text-figs. 3r, 9a–e.**

*Myophoria vestitaformis* Krumbeek 1923, p. 210 (nom. nov. for: *M. vestita subvestita* Jaworski 1915, p. 112, pl. 44, figs. 20, 21a, b, c; not *M. vestita Krumbeek 1913*).

**Material.** LL-023, LL-244 (small left valve, text-figs. 3r, d). LL-245 (large damaged right valve, text-figs. 9a–c), *Lopha* Beds, *Sumra* Formation. LL-246 (small right valve), *Modiolus* Beds, *Sumra* Formation.
Morphology. Shell probably slightly inequivalve with left valve more convex than right (see Jaworski 1915, pl. 44, figs. 21b, c). Ornament the same on both valves. Seven to nine prominent angular radial ribs on flank between lunule and marginal carina. These flank-ribs are steep-sided with weak, radially elongate crenulations. Anterior flank-ribs crossed by weak oblique ribs which form elongate crenulations at the intersections. Lunule smooth. Hinge of right valve with two elongate narrow subequal cardinals (3a and 3b), the anterior face of the posterior cardinal (3b) being coarsely grooved. Striations or grooves may be present also in other parts of the hinge but could not be proved on the specimen examined (LL.426).

Remarks. Myophoria vestitaeforsis Krumbeck (1923, p. 210) was a new name for the form which Jaworski (1915) called Myophoria vestita subvestita (not Myophoria sub-

vestita Krumbeck 1913). Krumbeck summarized the differences from M. subvestita as follows: M. vestita subvestita Jaworski obviously differs from M. subvestita by being slightly inequivalve (the left valve is higher and thicker than the right), by the characteristic wing-like extension of the upper part of the area, by the absence of an areal rib, and by being less convex. The most important of these distinctions is the areal extension of the area. The slightly inequivalve nature of M. vestitaeforsis, which Krumbeck insisted on, is clear from Jaworski’s figures (1915, figs. 21b, 21c) though it disagrees with his description (1915, p. 112). The principal reasons for identifying the Oman material with M. vestitaeforsis are the anterior ornament (oblique ribs surrounding a smooth lunule), the general outline, and the areal extension of the area. The identification is not certain, however, since the hinge is unknown in Indonesia, and double-valved forms, which would show whether the shell was inequivalve, are not known from Oman.

The hinge of the Oman material is definitely Myophoridi for, though the teeth are in places coarsely grooved, the anterior right cardinal (3a) is too narrow for a Trigoniid. The hinge is very like that of M. subvestita Krumbeck (1913, pl. 4, fig. 1a). In view of the hinge and the strong, unequally spaced, radial ribs, M. subvestita, M. vestitaeforsis, and probably M. vestitaeforsis should be placed in Costatoria Waagen 1907. M. seramensis Krumbeck 1923 is like M. vestitaeforsis in anterior ornament and general
outline (though without the alate area). Its hinge, however, is Trigonid with 3a wide and triangular. The species should therefore be placed in Myophoria Cox 1952.

Apart from Oman, Costatoria vestitaformis (Krumbeek) is known to the authors only from the Naeola Marl of Misol.

**Genus MYOPHORIA Bronn 1835**

Myophoria verbeeki (Boettiger) mansuyi Reed

Plate 2, fig. 26

Myophoria subvestita Krumbeek Mansuyi Reed 1927, p. 215, pl. 18, figs. 12-14.

Myophoria verbeeki (Boettiger) curta Reed 1927, p. 216, pl. 18, figs. 15-17.

Myophoria cf. napengensis Healey. Reed 1927, p. 217, pl. 18, fig. 26 (not Myophoria napengensis Healey 1908).

Myophoria gigantea Lees 1928, p. 635, pl. 44, figs. 1a, b.

Myophoria verbeeki (Boettiger). Douglas 1929, p. 636; Robinson 1937.

Material, L.51449 (holotype of Myophoria gigantea Lees 1928, p. 635, pl. 44, figs. 1a, b) from Elphinstone Beds, 5 miles east of Ras al Khaima. LL422 (pl. 2, fig. 26) from Lophia Beds, Sumra Formation.

**Morphology.** Ornament of both valves the same. The flank bears six strong, regularly spaced, radial ribs with concentrically elongate crenulations. Lunule anterior to anterior flank rib is flat, smooth except for weak growth-lines, and perpendicular to commissural plane.

**Remarks.** In 1927 Reed described a number of *Myophoria* from a single bed and locality in Yunnan and referred them to *M. subvestita* Krumbeek Mansuyi Reed, *M. verbeeki* (Boettiger) *curta* Reed, and *M. cf. napengensis* Healey. In the opinion of the authors, all the specimens figured belong to the same form and the question arises as to their valid name. With one exception (pl. 18, fig. 17) all the figures are of internal casts. The exception, which Reed called *M. verbeeki curta*, has the same ornament as *M. verbeeki* (Boettiger) from Sumatra (see Krumbeek 1914, p. 249, pl. 17, figs. 8-11) in that it has a non-crenulate marginal keel and wide-spaced, crenulate flank ribs but differs from it in having the posterior margin vertical instead of sloping. It can therefore be justifiably considered a subspecies of *M. verbeeki* (Boettiger). Reed's reason for allocating his subspecies *mansuyi* to *M. subvestita* Krumbeek was the smoothness of its ribs—a feature of the internal cast and of no diagnostic value: otherwise it is much closer to *M. verbeeki* than to *M. subvestita*. *M. subvestita mansuyi* (1927, p. 215) has page priority over *M. verbeeki curta* (1927, p. 216). The various forms are therefore renamed *M. verbeeki mansuyi* Reed.

As its author recognized (1928, p. 635), *M. gigantea* Lees is very like *M. verbeeki* (Boettiger) but differs in outline since the posterior margin is vertical instead of sloping, a feature characteristic of the *Myophoria* recorded by Reed (1927) from Yunnan and renamed above. There seems no reason therefore why *M. gigantea* should be separated from *M. verbeeki mansuyi*. Lees (1928, p. 635) stated that *M. gigantea* was larger than *M. verbeeki* but there is little difference in size between his only specimen and Krumbeek's largest figured specimen (1914, pl. 17, fig. 10). Examination of the holotype shows that *M. gigantea* is not, as suggested by Lees (1928, p. 635), slightly inequivalve, the structure which suggests this being due to slight crushing.
The unfigured records of *M. vebeeki* in Douglas 1929 and Robinson 1937 should be accepted with reserve. Since they occur in Persia and Armenia the specimens referred to may be *M. vebeeki maysayi* rather than *M. vebeeki vebeeki* which is only known in Indonesia.

The hinges of the present subspecies and of *M. vebeeki vebeeki* are not known, and may be Trigonid or Myophorid. If Trigonid the species would belong to *Mino- trigonia* Kobayashi and Kayama 1938; if Myophorid to *Costatoria* Waagen 1907. Pending more evidence it seems best to leave it in *Myophoria* s.l.

*M. vebeeki maysayi* is thus known from the Upper Triassic of Yunnan and probably from the Norian of Armenia and Persia. *M. vebeeki vebeeki* is known from the Norian-Chulung Beds of Sumatra.

**Family Carditidae**

**Genus Palaeocardita Conrad 1867**

*Palaeocardita buruca* (Krumbeek)

*Text-figs. 8f-h*

*Venericardita buruca* Boehm 1906, *m. n. r. p. 400.

*Cardita buruca* Krumbeek 1913, p. 60, pl. 4, figs. 6–13.

*Palaeocardita globiformis* Boettger, Javorski 1915, p. 115, pl. 45, figs. 1, 2 (not *Cardita globiformis* Boettger 1880).

*Palaeocardita buruca* Krumbeek 1924, p. 248, pl. 19, figs. 28, 29; Douglas 1929, p. 637.

Material. L.I.450, L.I.451 (text-figs. 8f-h). The former from the Lophas Beds, the latter from the Mediolus Beds, Sumatra Formation.

Javorski (1915, p. 115) seems to have been wrong to unite *P. globiformis* Boettger with *P. buruca* Krumbeek, for the latter is less quadrata, less elongate, and has less anterior umbones. Furthermore, nothing is yet known about the lunule or the hinge of *P. globiformis* (see Krumbeek 1924, p. 249) and the asymmetric lunule of *P. buruca* is the most striking feature of the species. The Oman specimens agree exactly in appearance with *P. buruca* as figured by Krumbeek from Buru (1913) and Timor (1924) and the number of ribs (about 25) is within the range (20–30) that Krumbeek (1924, p. 249) quoted for typical Buru specimens of *P. buruca*. It seems doubtful if *P. buruca* var. *mariosensis* Krumbeek (≡ *P. globiformis* Boettger of Javorski 1915) and *P. buruca* var. *serenaensis* Krumbeek 1923 are really distinct from typical *P. buruca*.

The conmixis of *P. globiformis* Boettger var. *healeyi* Reed from Yunnan seems to pass through the lunule instead of to the left of it (Reed 1927, pl. 18, fig. 6a); this variety is, therefore, probably not very close to *P. buruca*. *P. maysayi* Reed 1927 differs from *P. buruca* in having the crenulations on the ribs restricted to the part of the shell away from the umbo and also seems to have a symmetrical lunule.

*P. quadrata* Trechmann (1917) from the New Zealand Carnian is more quadrata and has more anterior umbones than *P. buruca*, and *Cardita singularis* Healey from the Burmese Rhætian is much more quadrata, more elongate, and probably much narrower.

*P. buruca* occurs in the Fog Beds of west Buru, the *Nicula* Marl of Misol, and possibly in the Upper Triassic of Armenia and the Norian of Nalband, Persia.
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**Palaeocardiita trapezoidalis trapezoidalis** (Krumbeek)

Test-fig. 10a

**Cardita** Krumbeek 1913, p. 147, pl. 4, figs. 15a, b, c.
**Cardita** Krumbeek nov. var. Jaworski 1915, p. 117, pl. 45, fig. 5.


**Material.** LL149b, a single left valve (text-fig. 10a), *Modiolus* Beds, Sumna Formation. LS2742, Lees coll., Elphinstone Inlet, Oman, and LL369b from *Modiolus* Beds are *P. trapezoidalis* subsp. indet.

**Morphology.** Umbones slightly opisthogyrous. Outline trapezoidal, expanding posteriorly. Escutcheon slightly concave, meeting the commissural plane at right angles, invisible in lateral view; lunule deeply sunken. Primary crenulate radiating ribs, nine on siphonal area, ten on flank, separated by furrows each bearing, on the siphonal area and the posterior flank, a fine secondary rib. Lunule and escutcheon probably ornamented by fine radiating ribs.

*P. trapezoidalis* trapezoidalis is recorded from the Fogi Beds of west Buru, the *Nucula* Marl and *Athyris* Limestone of Misil, and, possibly, the Upper Triassic of Yunnan.

**Palaeocardiita trapezoidalis leesi** subsp. nov.

Test-fig. 10b

**Cardita** cf. *singularis* Healey. Lees 1928, p. 637 (not *Cardita* *singularis* Healey 1908).

**Material.** LS2744 (text-fig. 10b), two well exposed left valves and a number of badly exposed valves. Lees coll., Elphinstone Beds, Elphinstone Inlet.

**Comparison.** Similar to *P. trapezoidalis* trapezoidalis except in the following features:

(a) More elongate. Dimensions (respectively LS2744a and b): length, 13 mm., 10 mm.; height, 8 mm., 8 mm.; width 1-4 mm. (one valve).
(b) Escutcheon less steeply inclined to commissural plane and hence clearly visible in lateral view.
(c) Less convex.
(d) With fewer ribs on the siphonal area (7 instead of 9) and more on the flank (13-15 instead of 10). There are six radial ribs on the escutcheon.

**Remarks.** Krumbeek seems to have made a mistake in describing the umbones of *P. trapezoidalis* as prosogyrous (1913, p. 147). They are clearly opisthogyrous in Jaworski's figure of the species (1915, pl. 45, fig. 56), Reed describes them as *retrorse* (1927, p. 224),
and Krumbeck’s anterior and posterior views (1913, pl. 4, figs. 5b and c) give the impression of opisthogyrous umbones. Lees compared his material with Cardita singularis Healey: in the opinion of the authors it agrees better with P. trapezoidalis since the umbones are opisthogyrous and the shape is trapezoidal with the greatest depth near the posterior end.

A series of good specimens of P. trapezoidalis from Oman would probably show that the subspecies leesti grades into the typical form: numerous bad specimens from Wadi Milaha and the Elphinstone Inlet cannot be placed in one or the other. It is just possible that the lower convexity and laterally visible escucheon of leesti are really due to crushing though the specimens seem to be true shells rather than casts and do not seem distorted.

**Family ANTHRACOSIDAE Amalitzky**

**Genus ANODONTOPHORA Cossmann 1897**

*Anodontophora griesbachii* Bittner

Text-figs. 3r, 11a–c

*Anodontophora Griesbachii* Bittner 1899, p. 60, pl. 8, figs. 14–16; Diener 1908a, p. 130, pl. 23, fig. 9; Krumbeck 1913, p. 55, pl. 3, figs. 21–23; Javorský 1915, p. 109, figs. 22–24; Patie 1926, p. 163, pl. 10, fig. 36.

*Anodontophora (Ancylidophora) cf. Griesbachii* Bittner, Mansuy 1908, p. 70, pl. 18, figs. 22, 23.

*Material.* LL463–LL484 (LL473, text-fig. 11r; LL475, text-fig. 11d; LL476, text-figs. 11a–c). All from Sunna Formation (mainly *Modiolus* Beds).

Comparison. Species of Anodontophora are variable and thus difficult to separate. A. griesbachi, for instance, varies in shape from almost trigonal to oblong (Krumbein 1912, p. 56). The normal form also lacks a keel and has a convex posterior margin yet some Oman specimens are slightly carinate with almost straight backward-sloping posterior margin. A. griesbachi is like A. fassaensis (Wissmann) except that the latter has opisthogyrous instead of prosogyrous umbones (Bender, 1921, p. 55).

Distribution. A. griesbachi is known from the Fogi Beds of west Buru, the Athyris Limestone and Nucula Marl of the Misol Archipelago, from the Tropites Beds (= Proclado-
nautilus griesbachi Beds and Haterites Beds), the Spiriferina griesbachi Beds and Sogenites Beds of Painkhandha, and in the Monois Beds and possibly the Juvativas Beds, and Quartzite Series of Spiti. It is also known from the Triassic of Tonkin. It may possibly occur in Europe as well since Bender (1921) stated that similar forms to A. fassaensis reached the Rhætian in the Alps.

Anodontophora cf. leitica (Quenstedt)

Text-figs. 12a-c

Material. LL121, LL122 (text-figs. 12a-c). Modiolus Beds, Sunra Formation.

Umbones prosogyrous; no lunule, no escutcheon. No ornament except for variable concentric growth-lines. Apart from being thicker and having a straighter ventral margin this form resembles Anodontophora leitica from the Lettenkohle.

Family MEGALODONTIDAE Zittel

Genus MEGALODON Sowerby 1827

Megalodon hungaricum Kutassy

Plate 2, figs. 13, 17

Comparate

Megalodos hungaricus Kutassy 1933, p. 17, pl. 2, figs. 4a-c; Terrannini 1958, p. 164, pl. 6, fig. 11.

Material. LL4276 (pl. 2, figs. 13, 17). Sunra Formation (exact horizon not known).

Morphology. Shell inequivalve with right valve two-thirds thickness of left. Umbones involute, prosogyrous. Left umbo more involute and prominent than right umbo. Lunule small, elongate, excavated. Siphonal area large, elongate, perpendicular to commissural plane and hence invisible in lateral view, about twice as wide on left valve as on right, separated from flanks in each valve by a very strong sharp keel; a very weak radial groove just anterior to keel in each valve. Ligament opisthodetic, supported by nymphs lodged in elongate ligament area about one-quarter the length of siphonial area. Escutcheon absent. Ornament of weak concentric growth-lines.

Remarks. M. hungaricum Kutassy was based on two internal casts, whereas the Oman specimen has the shell still preserved. This difference in preservation, together with the
fact that the hinge is unknown, prevents a definite identification. Ascertainable features, however, agree very well. These include the strongly inequivalent nature, the very sharply defined siphonal area, and the absence of an escutcheon. The groove corresponding to the posterior adductor ridge in the left valve of the casts figured by Kutassy is probably represented in the Oman specimen by the shallow groove just in front of the siphonal area.

_M. complanatum_ Gümbel, _M. laczkoi_ Hoernes, and _M. bovekhi_ Hoernes are less inequivalent than _M. hungaricum_ and have the siphonal area less well defined. _M. castilianum_ is less inequivalent. _M. ladakhense_ Bittner is very similar to _M. hungaricum_, but much less inequivalent.

_M. hungaricum_ is recorded from the Norian Hauptdolomit of Hungary, and from the Norian of Songavazzo in Lombardy.

?Megalodon rostratiforme Krumbeek

_Plate 2, fig. 22_

?_Megalodon rostratiforme_ Krumbeek 1913, p. 64, pl. 4, figs. 17a–c, 18–21, 22a, b.

_Material._ LL428, slab with numerous internal casts. LL429, slab with small weathered single valves (Pl. 2, fig. 22). Both from _Modiolus_ Beds, Sunna Formation.

_Morphology._ Umbones prosogyrous. A rather strong keel, convex dorsally, runs from umbo to postero-ventral angle. Another rather strong keel from umbo to postero-dorsal angle defines the elongate narrow excavated escutcheon. A rather weak keel running forward from the umbo defines a deep lunule. Posterior muscle scar shows on some internal casts as a slightly raised rounded tetragonal area near the posterior end of the siphonal area.

_Remarks._ The Oman specimens agree almost exactly with those figured by Krumbeek and some of them show clearly the alate siphonal area that Krumbeek emphasized. The species varies greatly in height/length ratio but, like Krumbeek, we can see no reason to subdivide it on this basis. An extensive discussion of the affinities of this species is given by Krumbeek. _M. misterense_ (Wanner and Knipscheer 1951, p. 59, pl. 5, figs. 6–9) is small like the present species but has only a weak siphonal keel and has the right valve somewhat more convex than the left.

The type of _?Megalodon rostratiforme_ is from the Fogi Beds of west Buru.

Family PLEUROMYIDAE Zittel

Genus PLEUROMYA Agassiz 1842

_Pleuromya hinaica_ Diener

_Plate 2, fig. 25_

_Pleuromya hinaica_ Diener 1908a, p. 132, pl. 23, fig. 15.

_Material._ LL454–LL462: LL454–8, LL462 (Pl. 2, fig. 25) well preserved; LL459–61 ill preserved. All from _Modiolus_ Beds, Sunna Formation.

_Description._ Umbones slightly prosogyrous. Dorsal part of posterior margin with fairly strong gape. Anterior gape possibly absent, at most only slight. Outline and height/length ratio very variable. Usually with a weak keel running vertically downwards
fromumbo and with slight sulcus behind the keel. Lunule cordate, defined by a sharp line on surface of shell. Escutcheon elongate, defined by a weak keel running backwards from umbo. Hinge margin (as deduced from internal cast) strongly thickened just before and behind the umbo of both valves. Just before and beneath the umbo is a flat triangular extension of the margin of the right valve. This overlaps a weaker extension of the margin of the left valve just beneath and behind the umbo. The posterior thickenings of the hinge margins of both valves probably correspond to ligament-nymphs.

<table>
<thead>
<tr>
<th>Dimensions (in mm.)</th>
<th>Length</th>
<th>Height</th>
<th>Thickness</th>
</tr>
</thead>
<tbody>
<tr>
<td>LL455</td>
<td>38</td>
<td>27</td>
<td>17</td>
</tr>
<tr>
<td>LL456</td>
<td>28</td>
<td>22</td>
<td>14</td>
</tr>
<tr>
<td>LL457</td>
<td>28</td>
<td>19</td>
<td>15</td>
</tr>
<tr>
<td>LL458</td>
<td>33</td>
<td>20</td>
<td>14</td>
</tr>
</tbody>
</table>

Remarks: The hinge of the Oman specimens, in so far as it can be studied, agrees best with Pleuromya as Douvillé (1907) described it. It might possibly indicate Panopea but we have found no sign of the enlarged, arched, left ligament nymph of that genus, which, moreover, usually has a much bigger posterior gape than the Oman specimens.

P. himatica Diener was founded on a single specimen and no others have since been described. Consequently nothing is known of the range of variation in this species. However, it was probably as variable as other species of Pleuromya. For this reason we identify the Oman specimens with it though none exactly agrees in shape with the type specimen. This also has a weak keel running almost vertically down from the umbo followed by a weak sinus, a feature which also occurs in many of the Oman specimens. A similar keel and sinus occur in the German Muschelkalk species P. musculoides (Schlotheim) figured by Bender (1921, p. 79, pl. 2, figs. 1–5, pl. 2, fig. 1). This species resembles P. himatica in shape and the two may perhaps be identical. This cannot be decided, however, without examining good material of both.

There are four published figures of the New Zealand Ladinian species P. mariana (Wilckens). Three of these figures (Marwick 1953, pl. 6, fig. 5; Wilckens 1927, pl. 8, figs. 12a, b, as Pleuromya? sp.) show the same specimen, which is like P. himatica and might at first be thought identical. The fourth published figure (Wilckens, 1927, pl. 8, fig. 6, as Nucula mariana) has, however, a much sharper umbo than P. himatica. The two species are therefore not the same though it is possible their ranges of variation overlap considerably.

P. suetica Rolle (1857, pl. 1, figs. 2–3), with which Diener compared the present species, is variable in shape but has more prominent, less anterior umbones than P. himatica. The same is true of the umbones of P. cf. suetica (Goettel 1917, pl. 9, fig. 8). P. salcattinana Krumbeck (1913, p. 71, pl. 5, figs. 11a, b) may be related to P. himatica but has a much sharper vertical sulcus.

P. himatica occurs in the Monotis Beds of Spiti.

Family CARDIIDAE Fleming
Genus PROTOCARDIA Beyrich 1842

Protocardia rhaeica (Merian)
Plate 2, figs. 12, 16, 21
Curvium rhaeticae Merian in Escher v. d. Linth 1853, p. 19, pl. 4, figs. 40, 41.


Protocoria proteus Krumbeck 1913, p. 69, pl. 5, figs. 2–10; ?Douglas 1929, p. 628.

Protocoria rhaetica (Merian). Javorskì 1915, p. 122, pl. 94, figs. 15, 16.

For other references to this species see Diener (1923, p. 224) and Kutassy (1931, p. 412).

Material. LI430 (Pl. 2, figs. 12, 16, 21), LI431–3. All internal casts from Molnius Beds, Sumna Formation. LS2748, Lees coll. (ish of limestone with several ill preserved specimens). Eilatolmstone Inlet, Oman.


Comparison. We agree with Javorskì (1915, p. 123) who could see no essential difference between P. proteus Krumbeck 1913 and P. rhaetica (Merian). Both are highly variable in outline and in the prominence and position of the umbo and both have in common the absence or extreme weakness of the keel. P. proteus was said (Krumbeck 1913, p. 71) to have taller, more anterior, and more prosogyrus umbones than the type specimens of P. rhaetica figured by Merian. This is true, but so have many English examples of P. rhaetica. The prominence of the umbones in P. proteus is probably partly due to the fact that the species was based on internal casts, most of them large. The smaller complete shells which Krumbeck (1913, p. 67) called P. aff. contusa Healey are probably well preserved juveniles of the P. proteus population. P. contusa Healey 1908 is more quadrate than most English P. rhaetica, though some of the latter are identical in form with P. contusa (Healey 1908); this, however, does not prove, as Healey asserts, that P. contusa occurs in England.

According to Krumbeck (1923, p. 216) P. subrhaetica is likewise more uniform in outline than P. rhaetica. Though close, the two species are not identical.

P. rhaetica is a widespread species in the Rhaetic of Europe. In Asia it is known from the Nicula Marl of Misol, the Fogi Beds of west Buru (as P. aff. contusa and P. proteus), and from the Naibund Calefereous Sandstone of Persia (as P. aff. contusa and P. proteus).

Family PANOPAEIDAE Zittel

Genus HOMONYMA Agassiz 1842

?HOMONYMA SUBARIANA Krumbeck

Plate 2, figs. 10, 11, 14


?HOMONYMA SP. ind. Diener 1908a, p. 133.

HOMONYMA SUBARIANA Krumbeck 1913, p. 72, pl. 5, figs. 12–14; ?Douglas 1929, p. 637.

Material. LI452 (Pl. 2, figs. 10, 11, 14), LI453. Lopho Beds, Sumna Formation.

Morphology. Shell equilvalve, gaping posteriorly. Umbones rather prominent, prosgyrous. Weak keels run from the umbo to the postero- and antero-ventral angles. Ornament of coarse, rounded, concentric folds which increase in amplitude ventrally. Near the umbo the primary folds are accompanied by secondary concentric folds.
Krumbeck (1913) describes radial rows of granules near the umbo but these are not visible in the Oman specimens.

**Remarks.** The generic allocation of this species is uncertain since nothing is known of its hinge. The best preserved of the above specimens does not seem to gape anteriorly which, if original, would not only exclude it from *H. sublariana* which is definitely stated by Krumbeck to gape anteriorly but also from *Homomyza*. The apparent absence of an anterior gape, however, may be due to crushing. It is noteworthy that some of the forms recorded from the German Muschelkalk as *H. alberti* Voltz also have no obvious anterior gape (Bender 1921, pl. 1, fig. 1b). *H. lariana* (Stoppani) differs from *H. sublariana* in not having anterior and posterior keels; it therefore does not have the characteristic cylindrical flank of *H. sublariana*.

*H. sublariana* is recorded from the Fogi Beds of west Buru, the Calcareous Sandstone of Naibband, and, probably, from the Juravites and Monotis Beds of Spiti.

**Text-Figs. 12a–e.** *Anodontophora cf. letonia* (Quenstedt), LL122, ×2.5, *Mediolus* Beds. *a.* Anterior view; *b.* dorsal view; *c.* right valve. 12d–f. *Thracia prosavitia* sp. nov., holotype, LL123, ×2.5, *Mediolus* Beds. *d.* Dorsal view; *e.* left view; *f.* right valve.

**Family THRACIDAE Dall**

**Genus THRACIA Leach 1824**

*Thracia prosavitia* sp. nov.

Text-figs. 12d–f

**Material.** LL123 (text-figs. 12d–f), LL124–5. From the *Mediolus* Beds, Sumera Formation.
Description. Shell thin-shelled, rather strongly inequivalve, right valve being more convex than left. Probably closed. Ornament of weak growth-lines. Umbones slightly posterior (beak distance — six-tenths), slightly opisthogyrous. Escutcheon clearly defined and siphonal area delimited by weak carina. Posterior part of shell somewhat rostrate, posterior margin straight and vertical. Ventral margin divided into two almost straight portions by obtuse angle directly beneath umbo. Length (LL123) c. 22 mm.; height 14 mm., thickness c. 10 mm.

Comparison. Few Thracia are known from the Trias. T. applenata Krumbeck (1913, p. 74) is much larger and more elongate than T. pravitai, and T. priscia Healey (1908, p. 61) from the Napeng Beds of Burma, has rather coarse concentric ribs.

T. proavita is similar in outline to the form described by Philippi (1898, p. 177, pl. 7, fig. 9) as T. mactroides (Schlotheim) from the Trigonodudolomit. This German form, however, has the left valve more convex than the right. There is, incidentally, little resemblance between T. proavita and Myzocites mactroides Schlotheim, which Bender (1921, p. 95) placed in Pleuroxynia, or T. mactroides (Schlotheim) as figured by von Seeueich (1861, p. 636, pl. 15, figs. 5a, b, c).

Among Jurassic species of Thracia perhaps that most like T. proavita is T. lana (Agassiz 1845, p. 267, pl. 36, figs. 1–15, as Corinaya) from the oldie inferieur of Switzerland. This species, however, lacks the blunt angle dividing the ventral margin of T. proavita, and is also less inequivalve.

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HUDSON AND JEFFERIES: UPPER TRIASSIC BRACHIOPODS


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