EARLY JURASSIC BRACHIOPODS FROM GIBRALTAR, AND THEIR TETHYAN AFFINITIES

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ABSTRACT. A spiriferinid *Liospiriferina rostrata*, two rhynchonellids *Gibbirhynchia correcta* and *Pontaltorhynchia schopeni* gen. nov., a terebratulid *Merophricus mediterranea*, and a zeilleriid *Calpella aretusa* gen. nov., constitute the first invertebrate fauna to be described systematically from the 'Gibraltar Limestone'. This formation, a 600 m thick cyclic sequence of well-cemented peritidal dolomitic limestones, has also yielded stromatolitic and oncoidal algae, a stromatoporoid, and locally common but generically indeterminate gastropods and bivalves. The brachiopods are of early Lias (Sinemurian) age, based on comparisons with faunas largely from Morocco and Sicily, and those described from the upper Sinemurian of the Central Apennines, Italy. The Sinemurian age verified for a significant part of the Rock of Gibraltar, an isolated and partly overturned klippe, allows its correlation with other tectonically displaced carbonates in the Betic-Rif arc which borders the western extremity of the Mediterranean Sea. Elements of a similar brachiopod fauna ranging from Italy through Gibraltar to Morocco are associated with thick Liassic platform carbonates which characterized the southern continental margin of the Tethys until its widespread collapse, generally in the mid–late Liassic.

GIBRALTAR is a peninsula, 1·6 km in natural maximum width, 5·2 km long, and some 6 km^2 in land area, which juts south from Spain at the western entrance to the Mediterranean Sea (Text-fig. 1). The peninsula is dominated by the Rock, a 600 m thick sequence of limestones and dolomites, the North Face of which rises precipitously to over 400 m above the northern isthmus, and which continues laterally for 2·5 km as a sharply ridged crest before descending to the two successive plateaux which truncate it to the south.

The carbonates of Gibraltar form an isolated outcrop, flanked by Quaternary screes and sands and surrounded by the sea except for the low-lying isthmus of Quaternary sands which joins the peninsula northwards to mainland Spain, a region essentially of Tertiary flysch sandstones. The closest comparable carbonates occur at Los Pastores, on the southern edge of Algeciras, 9 km to the west across the Bay of Gibraltar; near Manilva, inland from Estepona, 30 km to the north of La Linea; and at Gebel Musa in Morocco, 24 km south across the Strait of Gibraltar. Their relationships are controversial, since stratigraphical ages are imprecise, and overall the principal structural-stratigraphical units of this western Mediterranean region have been subject to considerable displacement, by major strike-slip faulting and/or thrusting due to nappe emplacement associated with African–European continent–continent collision during the late Cenozoic (Rose and Rosenbaum 1994*a*). Structurally, Gibraltar lies at the boundary of the external and internal zones (Iberian and Alboran domains) long distinguished in the Betic region of south-east Spain, and gives its name to the Gibraltar Arc which unites the Betics southwards with the Rif mountains of Morocco.

A Jurassic age for the Gibraltar carbonates has long been established on the basis of fossil identifications recorded by Smith (1846: terebratulid brachiopod casts), Ansted (1859: an ammonite and some terebratulid brachiopods), Roemer (1864: brachiopods and a gastropod), Hochstetter (1866: casts of brachiopods and molluscs), Ramsay and Geikie (1878: a rhynchonellid brachiopod), Choffat (1892: a large gastropod plus terebratulid and rhynchonellid brachiopods), Dubar and Le Maître (1935: terebratulid and spiriferid brachiopods, a spongiomorphid, and gastropods), and Dubar (1942: brachiopods); this age was duly accepted by Reed (1949). Bailey (1952) listed

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identifications by H. M. Muir-Wood of six brachiopod species/subspecies based on the 26 specimens collected and mentioned by Smith (1846), with the inference that these indicated an Early Jurassic age (equivalent to the Lower Lias of north-west Europe). He also listed identifications by L. F. Spath of ammonites collected in 1943 by A. L. Greig from shales at the base of the North Face and east coast of the Rock. These specimens were small, immature or badly preserved, but the fauna was recognized as Domerian (Mid Lias) in age, and therefore provided evidence that the stratigraphical sequence in the main ridge of the Rock had been inverted. Arkell (1956) followed Bailey (1952) in ascribing the Gibraltar succession largely to the Lower Jurassic (Lias). However, on a more recent Spanish map (Fontboté 1970) it is depicted as Middle–Upper Jurassic.

The total Jurassic invertebrate fauna recorded from Gibraltar is sparse, with component taxa hitherto either imprecisely or only tentatively identified. Only two species identifications have been based on rigorous systematic description and discussion: a brachiopod, *Zeilleria* cf. *tenuiplicata* Dubar (*in* Dubar 1942), and the spongiomorphid *Stromatomorpha liasica* Le Maître (*in* Dubar and Le Maître 1935). Few specimens have yet been illustrated. A comprehensive description and review is therefore given here to clarify age assignments of lithostratigraphical units recently distinguished and mapped on the Rock (Rose and Rosenbaum 1990, 1991*a*, 1991*b*; Rosenbaum and Rose 1991).

GEOLOGY OF GIBRALTAR

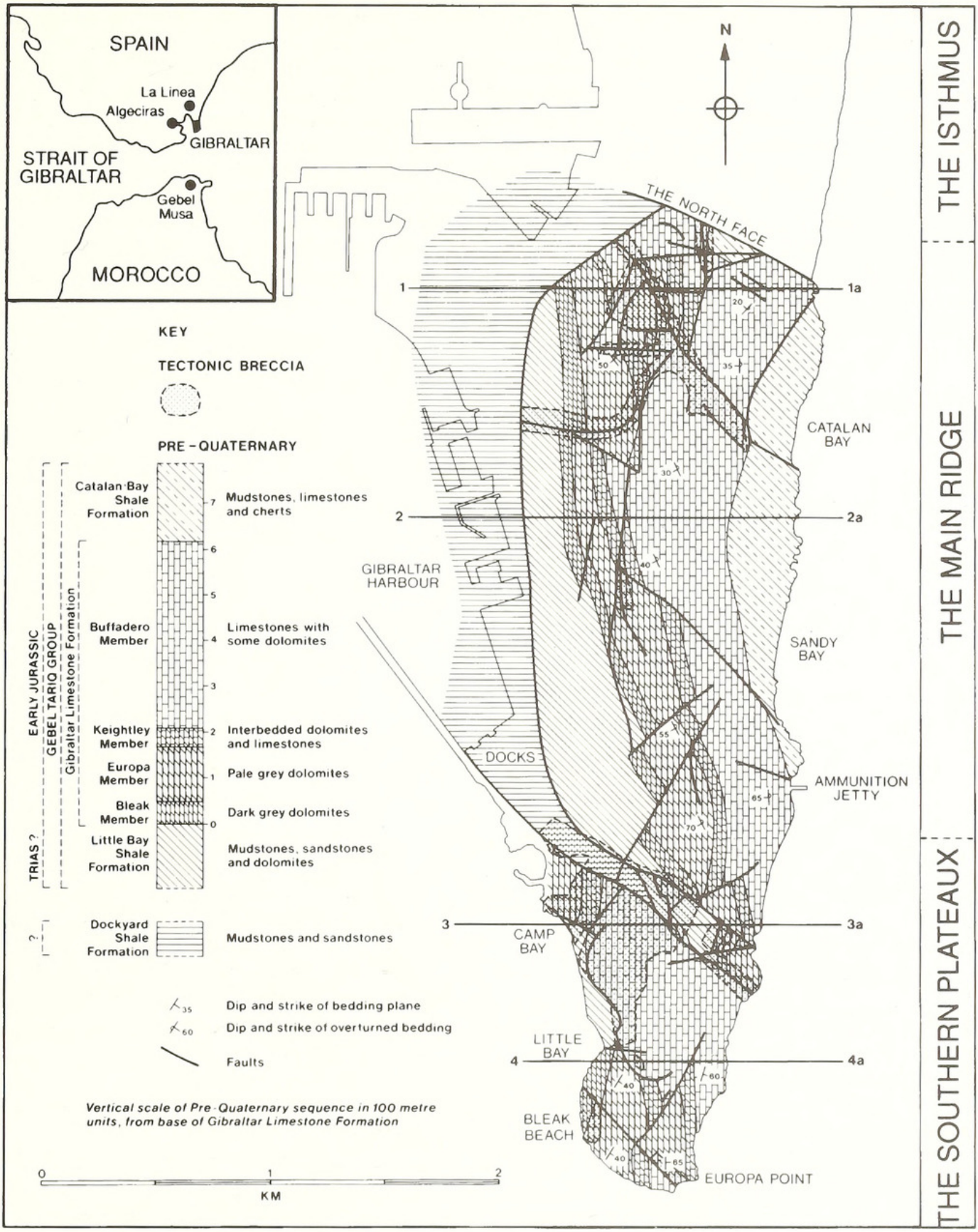
Structurally, the Rock of Gibraltar is divisible into two components separated by a north-west–south-east fault, the 'Great Main Fault' of Ramsay and Geikie (1878), which extends south-east from the Gibraltar docks as a 200 m wide zone of fractured bedrock. North of this fault, in the main ridge area of the Rock, the sequence is overturned and dips at moderate to high angles to the west. South of the fault, in the southern plateaux, the sequence is the 'right way up' and dips at moderate to high angles to the east. Correlation between the two components is based on lithology rather than biostratigraphy, but similarities in cyclic peritidal depositional conditions and subsequent dolomitization of the thick carbonate sequences which dominate both components are sufficiently close to indicate their broad equivalence. In consequence, it is possible to recognize a composite tripartite division of the Gibraltar bedrock succession as currently exposed.

Little Bay Shale Formation

Up to 15 m of red and green fissile mudstones with thin beds of fine sandstone and pebble conglomerate, together with thicker beds of dark grey dolomite, crop out at the base of cliffs in Little Bay on the west coast of the southern plateaux. No age-diagnostic fossils have been described from these rocks, but the beds dip steeply eastwards beneath uninverted Gibraltar Limestone so must represent the oldest exposed bedrock. Red and green fissile mudstones with thin chert bands can be traced as sheared exposures at the base of faulted limestone/dolomite cliffs northwards into Camp Bay. Farther north, vertical 'shales' of similar appearance were mapped by Ramsay and Geikie (1878) along the coast west of the main ridge of the Rock, but have largely been removed or obscured by construction works, so are known now from patchy exposures, boreholes for foundation works, or old records. The Dockyard Shales shown on Text-figure 1 have been designated (Rose and Rosenbaum 1990) on the basis of photographs made during construction of the dockyards at the beginning of the 20th century. They are known to have had an eastward dip contrasting with the steep westward dip of the carbonates close by in the main ridge of the Rock, but their relationship to the Little Bay Shales is unproven.

Gibraltar Limestone Formation

Most of the Rock is formed by a 600 m thick succession of massively bedded carbonates, passing gradationally from dark grey bituminous dolomites at the base through pale grey-white dolomites, then a distinctively well-bedded unit of dolomites and limestones, to a very thick, relatively



TEXT-FIG. 1. Map of bedrock (pre-Quaternary) geology of Gibraltar, indicating localities mentioned in the text (from Rose and Rosenbaum 1990: see original publication for cross sections drawn along lines indicated on this figure).

homogeneous sequence of light or medium grey fine-grained limestones, dolomitic at the base. Fenestral and peloidal mudstones and wackestones, stromatolitic algal laminites, and carbonate conglomerate lenses with scoured bases occur in shallowing and fining upward cycles of 1–3 m thickness (J. L. Wood, *in* Rose and Rosenbaum 1994*b*). These are common features of tropical or sub-tropical tidal flats traversed by migrating channels. Fossils recorded from Gibraltar in the last century, as noted above, are inferred to have been collected largely from this formation. The sparse recorded fauna is partly a reflection of the difficulty of extracting specimens: the rock is strong and crystalline, very similar in general appearance to the Carboniferous Limestone of England and Wales. Where they do occur, fossils are almost invariably seen only in cross section. Moreover, since much of the lower (and most accessible) part of the sequence is formed by algal limestones and intraformational conglomerates of peritidal origin, its depositional conditions were largely unfavourable for the proliferation or preservation of shelly marine invertebrates.

Catalan Bay Shale Formation

Medium-bedded grey cherty limestones alternating with thinner beds of reddish-grey fissile mudstones are exposed beneath inverted Gibraltar Limestone near Catalan Bay; the south end of Sandy Bay; some 500 m farther south; and at Ammunition Jetty, all on the east coast. They are exposed also at the base of the North Face of the Rock. Quarries at Catalan Bay and the North Face yielded the ammonites to which Spath (*in* Bailey 1952) gave a Domerian (Mid Lias) age.

Early descriptions of Gibraltar (notably Ramsay and Geikie 1878) recognized only a single 'shale' formation, along the west coast, supposedly overlying the 'limestone'. By 1943 quarrying had exposed 'shales' also at the base of the North Face, and along the eastern coast. On the basis of similar mudstone lithology, red/green colour and association with cherts, Bailey (1952) also correlated all the 'shales' on Gibraltar as part of a single formation, but on tentative biostratigraphical evidence from the northern and eastern outcrops he inferred that the 'shales' underlie rather than overlie the 'limestone'. However, since the western shales differ from the northern/eastern shales in aspects of their lithology, and their age equivalence is unproven, they were described and mapped as separate formations by Rose and Rosenbaum (1990, 1991*a*, 1991*b*) and Rosenbaum and Rose (1991). The ammonites on which the Domerian (= late Pliensbachian) age of the Catalan Bay Shales is based (*Rhacophyllites stella* (J. de C. Sowerby), *Rhacophyllites* sp., *Lytoceras* aff. *andax* (Meneghini), *Harpoceras* sp., and *Phylloceras* aff. *calais* (Meneghini) from Catalan Bay quarry; and *Lytoceras* sp. from the North Face) cannot now be traced in the collections of the British Geological Survey, The Natural History Museum in London, the Gibraltar Museum, or elsewhere (despite advertisement in *The Geological Curator* and extensive search) so are presumed lost.

Brachiopods are the only age-diagnostic fossils currently available. For specimens described below, NHM = Department of Palaeontology, The Natural History Museum, London; ONCP = Office National de Gestion des Collections Paléontologiques, Centre des Sciences de la Terre, Université Claude Bernard, Lyon 1, Villeurbanne, France.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA Duméril, 1806
Class ARTICULATA Huxley, 1869
Superfamily SPIRIFERINACEA Davidson, 1884
Family SPIRIFERINIDAE Davidson, 1884

Genus LIOSPIRIFERINA Rouselle, 1977

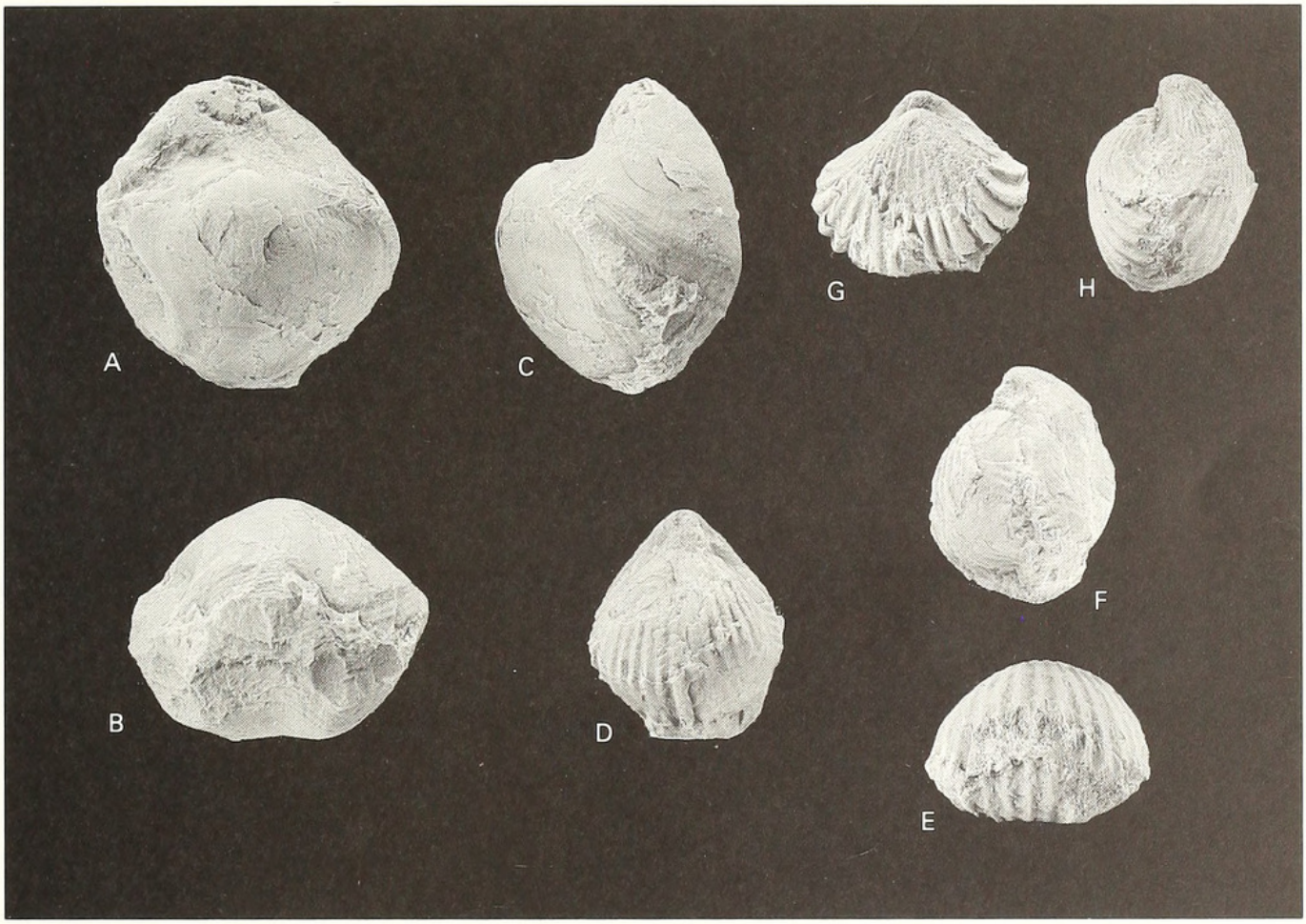
Type species. Terebratulites rostratus Schlotheim, 1822, p. 260, pl. 16, fig. 4a–c, from the Lias of Balingen, Württemberg, Germany.

Liospiriferina rostrata (Schlotheim, 1822)

Text-figure 2A–C

1822 *Terebratulites rostratus* Schlotheim, p. 260, pl. 16, fig. 4a–c.
1832 *Delthyris rostrata* Schlotheim; Zieten, p. 50, pl. 35, fig. 1.
1871 *Spirifer rostratus* Schlotheim; Quenstedt, pl. 54, fig. 96.
1886 *Spiriferina rostrata* Schlotheim; Di Stefano, p. 35, pl. 1, figs 1–8.
1886 *Spriferina haasi* Di Stefano, p. 39, pl. 1, figs 9–10.
1977 *Liospiriferina rostrata* (Schlotheim); Rouselle, p. 164, pl. 1, figs 5a–c, 8a–c.

Material. A single damaged ONCP specimen, EM20311, 35·0 mm long, 32·2 mm wide and 27·3 mm thick.



TEXT-FIG. 2. A–C, *Liospiriferina rostrata* (Schlotheim, 1822); EM20311; dorsal (A), anterior (B) and lateral (C) views, showing rounded beak ridges, wide interarea and inflation of the dorsal umbo. D–F, *Gibbirhynchia correcta* (Di Stefano, 1886); EM20312; dorsal (D), anterior (E) and lateral (F) views. G–H, *Pontaltorhynchia schopeni* (Di Stefano, 1886); EM20313; dorsal (G) and lateral (H) views. ONCP specimens, inferred in the text to be from the Gibraltar Limestone at the north-east of the Rock; Lower Lias, Sinemurian; × 1·5.

Description. Medium-sized, smooth spiriferinid. Ventral valve with massive umbo and sub-erect beak truncated by a large foramen; beak ridges rounded and smooth; lateral flanks of the valve steep with faint concentric growth lines. Anterior margin uniplicate, exposing a broad, shallow ventral sulcus which narrows posteriorly. Delthyrium triangular, bounded by extensive flat interareas. Dorsal valve posteriorly inflated, with less steep flanks than the ventral valve. A low dorsal fold extends anteriorly, complementing the shallow ventral sulcus at the anterior margin.

Remarks. The specimen described here was identified by E. de Verneuil as *Spirifer tumidus* (Roemer 1864; Hochstetter 1866), but without illustration or description. Ansted (1859) and Dubar and Le Maître (1935) recorded spiriferids from Gibraltar, but without more precise identification.

Rouselle (1977, p. 164) described the genus *Liospiriferina* to accommodate specimens from Mid Liassic localities in Morocco and north-east Spain. *Terebratulites rostratus* Schlotheim, originally described from the Lias of Germany, was designated type species. Examples of morphotypes identified as conspecific were listed (p. 165) and examples figured (pl. 1, figs 5–9). Of these, two specimens (figs 5, 8) are considered here to be typical of the specimen figured by Schlotheim (1822, pl. 16, fig. 4a–c) and to compare favourably with the Gibraltar specimen illustrated by our Text-figure 2A–C.

Di Stefano (1886) described several spiriferinid species from the Lias of Sicily and the central Apennines, some of which were costate but many were smooth-shelled. Of these, *Spiriferina haasi* Di Stefano, 1886, although slightly larger, is proportionately similar to the specimen figured here from Gibraltar (Text-fig. 2A–C). Di Stefano gave a series of dimensions of four specimens collected from the Calcare grigio of Gullo near St. Antonio, Taormina, Sicily. Their mean length is calculated as 39·5 mm, width 39·0 mm and thickness 31·5 mm. The morphological features match the Gibraltar specimen closely and we have no difficulty in assigning Di Stefano's *Spiriferina haasi* also to *Liospiriferina rostrata* (Schlotheim).

Several other species of smooth shelled Spiriferinidae have been described from the Lower Lias of the central Apennines by Canavari (1884) and Di Stefano (1886), both of whom recorded *Spiriferina rostrata* (Schlotheim). A specimen which approaches those assigned to *Spiriferina haasi* Di Stefano in general morphological aspects was described as *S. rostrata* var. *striata* Schlotheim, by Canavari (1884, p. 77, pl. 9, fig. 2a–d), but this can be distinguished from *Liospiriferina rostrata* (Schlotheim) in having a more arcuate incurved beak, less inflated dorsal umbo and an ornament of faint striae covering the surface of both valves.

NHM specimens BB13837–13842, identified as *Spiriferina serinensis* (Gemmellaro, 1874) and said to have been collected from the Toarcian of Ait Daoud Ou Azzi, Morocco by the late R. V. Melville in 1952, can be compared to similar specimens BB20291–20292 collected from the *davoei* Zone '*Leptaena*' Bed of the foreshore on the east side of Taormina Bay, Sicily by Dr M. K. Howarth in 1957. They differ from the specimen from Gibraltar, figured here, in their smaller dimensions, deeper ventral sulcus, shorter umbo and less inflated dorsal valve. There are no closer similarities with spiriferinid species listed by Dubar (1932) amongst Liassic brachiopod faunas of Morocco.

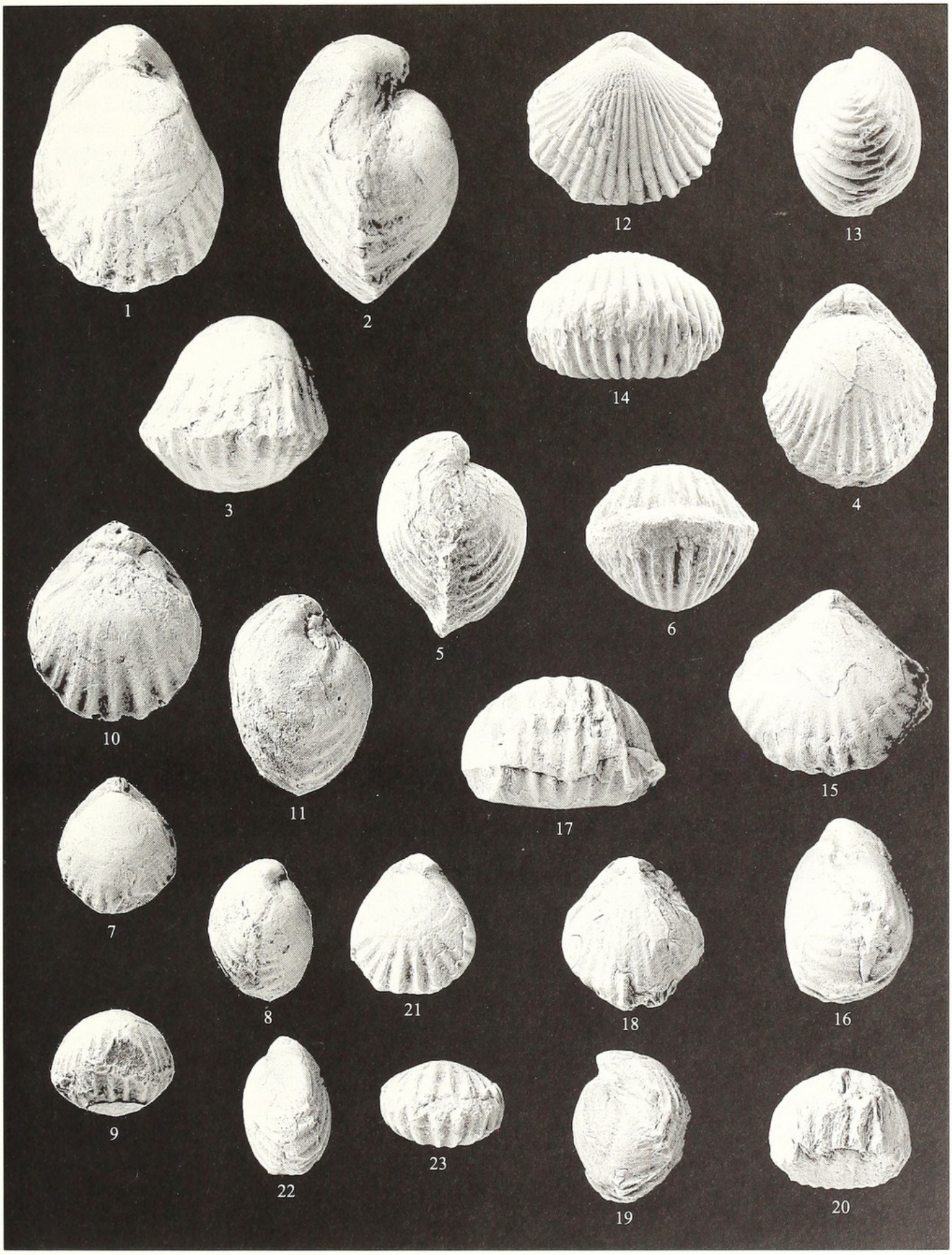
EXPLANATION OF PLATE 1

Figs 1–11. *Merophricus mediterranea* (Canavari, 1884). 1–3, NHM B85440; Gibraltar (inferred in the text to be from the Gibraltar Limestone; Lower Lias, Sinemurian); × 1·5. 4–6, NHM B19524; showing the typical elongate-oval outline and equibiconvexity of the valves; Catalan Bay, Gibraltar, presumed Sinemurian; × 1·5. 7–9, NHM B85434; showing marginal plicae and almost smooth dorsal valve; same locality and horizon as figs 1–3; × 1. 10–11, NHM BB13872; Lower Lias, Ait-Oufella, High Atlas Mountains, Morocco; for comparison with specimens from Gibraltar; × 1·5.

Figs 12–17. *Pontaltorhynchia schopeni* (Di Stefano, 1886), gen. nov. 12–14, NHM B14969; Lower Lias, upper Sinemurian; Pontalto, central Apennines, Italy; showing rounded costae and typical broad oval anterior. 15–17, NHM B85427; Gibraltar, details as for figs 1–3; × 1·5.

Figs 18–20. *Gibbirhynchia correcta* (Di Stefano, 1886); NHM B85428; Gibraltar, details as for figs 1–3. The subquadrate outline and costation are typical of the genus and are comparable to the specimens figured by Di Stefano (1886); × 1·5.

Figs 21–23. *Calpella aretusa* (Di Stefano, 1886) gen. nov. NHM B85421; Gibraltar, details as for figs 1–3; showing somewhat less acutely biconvex valves but maintaining the same general outline as the specimen figured by Di Stefano (1886, pl. 2, fig. 54a–d); × 1·5.



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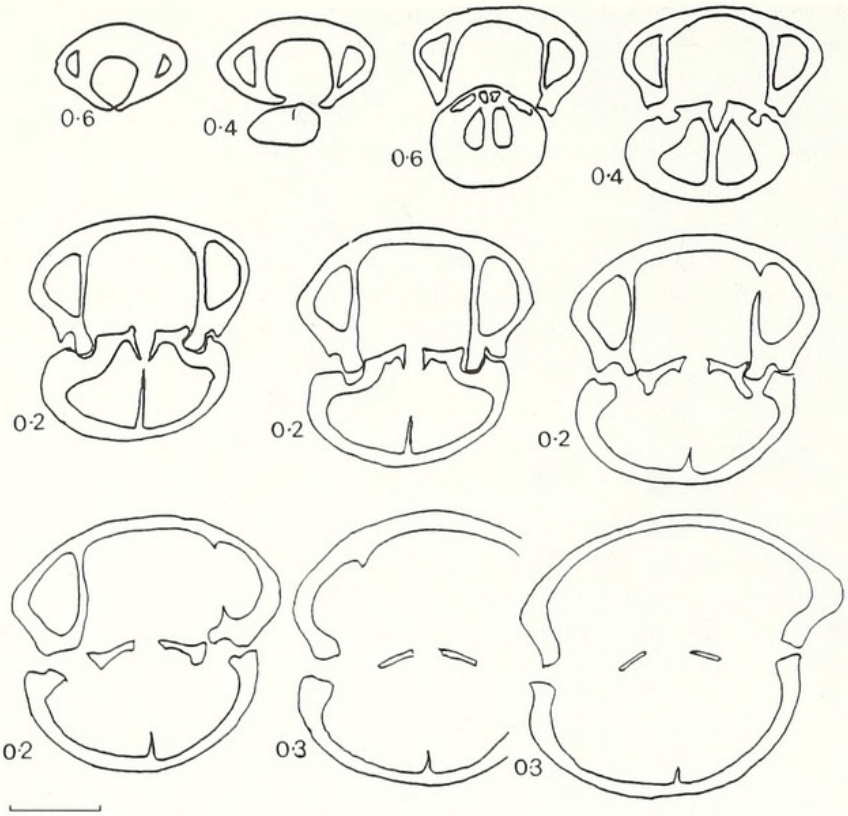


TEXT-FIG. 3. Ten transverse serial sections through the umbo of a specimen of *Pontaltorhynchia schopeni* (Di Stefano, 1886) gen. nov. showing the deep septalium, strong median dorsal septum and the ventrally deflected hinge plates. The numerals denote the distance in millimetres between each section. NHM BB20290; Lower Lias, *jamesoni* Zone, Cape Taormina, Sicily. Scale bar represents 5 mm.

Superfamily RHYNCHONELLACEA Gray, 1848
Family RHYNCHONELLIDAE Gray, 1848
Subfamily TETRARHYNCHIINAE Ager, 1965

Genus GIBBIRHYNCHIA Buckman, 1918

Type species. Gibbirhynchia gibbosa Buckman, 1918, p. 43, pl. 13, fig. 7, from the Middle Lias of South Petherton, Somerset.

Gibbirhynchia correcta (Di Stefano, 1886)

Plate 1, figures 18–20; Text-figure 2D–F

1886 *Rhynchonella correcta* Di Stefano, p. 65, pl. 2, figs 39–41.
1892 *Rhynchonella correcta* Di Stefano; Choffat, p. x.
1952 *Rhynchonella correcta* Di Stefano; Muir-Wood, *in* Bailey, p. 164.

Material. Four NHM specimens from Gibraltar: B 85428 figured here (Pl. 1, figs 18–20), with shell approximately 16·3 mm long, 15·1 mm wide and 12·9 mm deep; B 85423, 16·5 mm long, 17·8 mm wide, 12·1 mm deep; B 85425, 16·4 mm long, 16·8 mm wide and 11·9 mm deep; and B85424 (embedded in matrix). A single ONCP Gibraltar specimen, EM20312, figured here as Text-figure 2D–F: 16·5 mm long, 14·1 mm wide and 13·3 mm deep.

Diagnosis. Small, biconvex, semisphaeoridal, uniplicate rhynchonellid. Umbo short, beak slightly incurved, deltidial plates poorly exposed. Dorsal fold almost imperceptible; ventral valve with shallow sulcus and extensive linguiform extension.

Description. Dorsal valve more acutely convex than the ventral valve, with a slight umbonal inflation and poorly developed fold which appears to develop just anterior to mid valve, ventral sulcus beginning to broaden at about the same distance from the umbo. Shell ornament consists of approximately 15 strong, fairly well incised angular costae on each valve, four of which occupy the ventral sulcus and extend to meet four or five on the dorsal valve. In general outline the species tends towards a sub-quadrate morphology, being slightly broader than long and having a shallow trapezoidal linguiform extension.

Internal structure. The highly crystalline nature of the matrix has made examination of the internal structures impossible and the generic assignment of this species should be regarded as provisional.

Remarks. The external morphology of this species is typical of the genus described by S. S. Buckman (1918, p. 43, pl. 13, fig. 7) as *Gibbirhynchia*, the type species of which, *G. gibbosa*, was emended by Ager (1954, p. 36). Although the type species occurs in the Middle Lias, the genus is known to range from the Lower Lias, *jamesoni* Zone, where it is represented by *G. curviceps* (Quenstedt, 1871) in Britain and Germany. The species described here as *Gibbirhynchia correcta* (Di Stefano) bears a strong resemblance to *G. curviceps* in both size and in general outline. It differs from Quenstedt's species, however, in its less acute sub-quadrate general outline, slightly produced umbo, longer or more extensive linguiform extension, and has fewer costae and a less well developed dorsal fold. The same distinguishing features separate it from Middle Liassic species, such as *G. northamptonensis* (Davidson, 1878), *G. thorncombiensis* (Buckman, 1922) and *G. tiltonensis* Ager, 1962 which appear to be confined to northern European facies (Ager 1962).

Genus PONTALTORHYNCHIA gen. nov.

Derivation of name. From Pontalto, central Apennines, Italy; NHM specimens from this locality are better preserved than those from Sicily or Gibraltar.

Type species. Rhynchonella schopeni Di Stefano, 1886, p. 68, pl. 2, figs 45–46, from the Sinemurian of Sicily.

Diagnosis. Transversely oval, multicostate, equibiconvex rhynchonellid. Umbo massive, beak short, sub-erect. Beak ridges rounded, indistinct, bordering a short interarea. Deltidial plates not exposed. Dorsal fold poorly developed, ventral sulcus shallow, trapezoidal linguiform extension moderate.

Remarks. Bearing a superficial resemblance to species of *Tetrarhynchia*, *Quadratirhynchia* and *Pseudogibbirhynchia*, it can be distinguished from these genera in its shorter beak, rounded beak ridges and less angular or more rounded costae which are not so deeply incised. The internal characters as seen in the transverse serial sections are also distinct; described here for the type species.

Pontaltorhynchia schopeni (Di Stefano, 1886)

Plate 1, figures 12–17; Text-figures 2G–H, 3

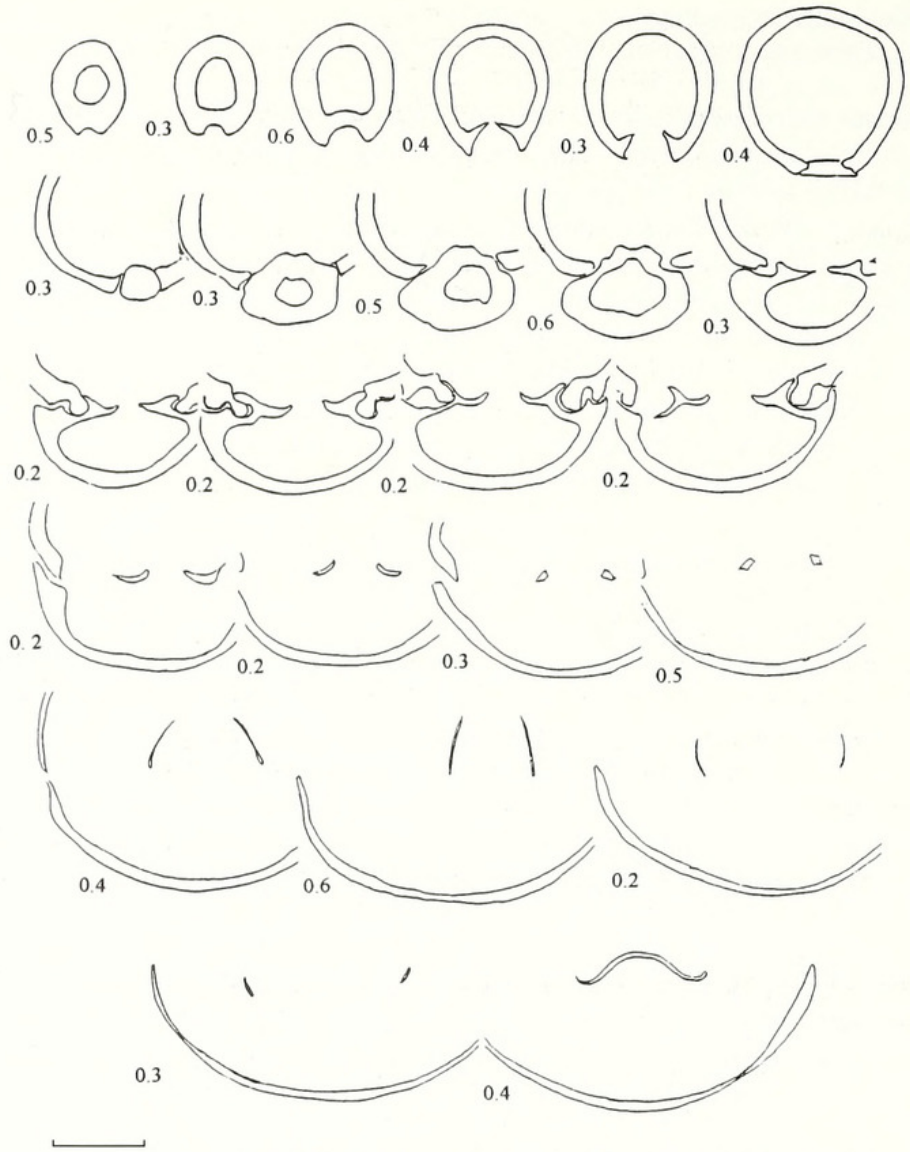
1886 *Rhynchonella schopeni* Di Stefano, p. 68, pl. 2, figs 45a–c, 46a–c.
1952 *Rhynchonella schopeni* Di Stefano; Muir-Wood, *in* Bailey, p. 164.

Material. NHM specimens B85419, 85426–85427, 85439 from Gibraltar; B14969–14970 from Pontalto, Italy; and BB20288–20290 from Cape Taormina, Sicily; plus a single ONCP specimen, EM20313, from Gibraltar.

Diagnosis. As for genus.

Description. Medium-sized rhynchonellid, transversely oval in general outline. Lateral profile elongate-oval, anterior commissure broadly uniplicate with shallow linguiform extension. Mean dimensions approximately 19·1 mm long, 21·0 mm wide and 14·9 mm deep. Shell ornament of 25–28 strong, sub-angular to rounded costae originating from the umbo on each valve, with six to eight in the ventral sulcus and a corresponding number on the almost imperceptible dorsal fold. Short triangular planareas bounded by poorly defined beak ridges form the low apex of the shell.

Internal structure. Description of the internal structures of this species is based on transverse serial sections through the umbo of a specimen collected from the Lower Lias, *jamesoni* Zone on the foreshore east of Cape Taormina, Sicily, by Dr M. K. Howarth (Text-fig. 3). It has been compared and agrees favourably with the figure given by Di Stefano (1886, pl. 2, figs 45–46) for *Rhynchonella schopeni* from the Calcare grigio, Gullo near St Antonio, Cape Taormina. The current location of this type material is unknown.



TEXT-FIG. 4. Twenty-four transverse serial sections through the umbo of a specimen of *Merophricus mediterranea* (Canavari, 1884) showing the pedicle collar, flat cardinal process, short ventrally concave hinge plates and low arcuate transverse band of the brachial loop; NHM BB13873; Lower Lias of Ait-Oufella, High Atlas Mountains, Morocco. Scale bar represents 5 mm.

No pedicle collar is developed within the ventral umbo. Sub-parallel dental plates develop early and support deeply inserted sub-quadrate hinge teeth. A strong high dorsal septum supports a deep septalium which diminishes rapidly. Moderately long hinge plates are ventrally deflected, their ventral surfaces becoming slightly convex. The hinge plates get thinner anteriorly developing into elongate crural bases. It was not possible to observe further internal structures beyond the tenth section due to the crystalline nature of the infilling matrix.

Remarks. Ager (1954, p. 30), in a description of the genus *Gibbirhynchia*, drew attention to what he considered to be the close relationship between that genus and the genera *Tetrarhynchia*, *Quadratirhynchia* and *Grandirhynchia* which range within the British Lias. Although external morphological aspects suggest a possible relationship, the internal characters of the specimen sectioned and described here as *Pontaltorhynchia schopeni* (Di Stefano) have little in common with other Liassic species. Serial sections of the type species of *Tetrarhynchia* figured by Ager (1956, p. 7, fig. 7) show an absence of a pedicle collar, a short septalium, moderately short hinge plates and elongate crural bases and thus could have been derived from the same original stock. *Quadratirhynchia* and *Grandirhynchia* share none of these internal characters with *Pontaltorhynchia*.

Superfamily TEREBRATULACEA Gray, 1840
Family TEREBRATULIDAE Gray, 1840
Subfamily PLECTOCONCHINAE Dagis, 1974

Genus MEROPHRICUS Cooper, 1983

Type species. Merophricus dubarii Cooper, 1983, p. 113, pl. 54, figs 14–15 (= *Terebratula* cf. *semiarata* Dubar, 1942, p. 63, pl. 3, fig. 26a–e), from the Lias of the High Atlas Mountains, Morocco.

Merophricus mediterranea (Canavari, 1884)

Plate 1, figures 1–11; Text-figure 4

1880 *Terebratula fimbrioides* E. Deslongchamps; Canavari, p. 13, pl. 2, figs 1–2.
1881 *Terebratula fimbrioides* E. Deslongchamps; Canavari, p. 182, pl. 9, fig. 10a–d.
1884 *Terebratula mediterranea* Canavari, p. 85.
1935 *Terebratula mediterranea* Canavari; Dubar and Le Maître, p. 9.
1942 *Terebratula mediterranea* Canavari; Dubar, p. 56, pl. 3, fig. 12a–d.
1952 *Terebratula mediterranea* Canavari; Muir-Wood, *in* Bailey, p. 164.
1952 *Terebratula mediterranea* var. *elongata* Dubar; Muir-Wood, *in* Bailey, p. 164.
1952 *Terebratula mediterranea* var. *pectita* Dubar; Muir-Wood, *in* Bailey, p. 164.

Material. NHM specimens B85420, 85422, 85430–85438, 85440–85441 (Smith/Silvertop collection), B10409, 19524 (Goldie/Evans collection), and BB11504–11505 (Alexander collection) from Gibraltar; and BB13868–13875 from the Upper Sinemurian of Ait-Oufella, Morocco.

Diagnosis. Medium to large, biconvex, polyplicate terebratulid with suberect beak and distinct beak ridges.

Description. Shell elongate-oval in general outline, acutely biconvex with the dorsal valve slightly deeper than the ventral valve. Triangular conjunct deltidium obscured by a slightly incurved beak which is truncated by a large circular foramen. Lateral commissures straight or rectimarginate: anterior commissure varies from rectimarginate to slightly uniplicate. Broad anterior uniplication of the shell margins subject to polyplications which vary from coarse to moderately fine pseudocostation, originating from a point just anterior to the midvalve area.

Internal structures. We have been unable to gain access to type material from the Lower Lias of the central Apennines: none could be located in the Canavari collection at the Department of Earth Sciences of the University of Pisa, Italy (L. Ragaini, pers. comm. 1996). Comparison has therefore been made between NHM specimen BB13873, taken from a series collected from Morocco by the late R. V. Melville, the illustrations of Canavari (1881, pl. 9, fig. 10a–d), and also those of Dubar (1942, pl. 3, fig. 12a–d).

A series of transverse serial sections made through the umbo of the Moroccan specimen is illustrated here as Text-figure 4. The series shows a pedicle collar present, within the first 2 mm of the umbo. The conjunct deltidial plates are visible in transverse section and a flat, poorly developed cardinal process is evident in the dorsal umbo. Short triangular, concave, dorsally deflected hinge plates give rise to transversally sub-quadrate descending branches of the brachial loop which quickly develop long, inwardly curving processes which diminish anteriorly and finish in a broad but low arcuate traverse band.

Remarks. Canavari (1880, p. 13) described a terebratulid from the Lower Lias of the central Apennines, assigning it to a species described by Eudes Deslongchamps (1855, 1862–85) as *Terebratula fimbrioides* from the Jurassic of Sarthe, Normandy. The specimens figured by Canavari (1880, pl. 2, figs 1–2) under the name *T. fimbrioides*, whilst resembling the specimens figured by Deslongchamps in having marginal plicae more strongly developed on the anterior part of the shell, do not agree in general outline, convexity or umbonal features. The specimens figured by Deslongchamps tend towards less acute biconvexity and a somewhat more pentangulate general outline.

Canavari (1881, p. 6, pl. 9) again described and figured a specimen as *Terebratula fimbrioides* Deslongchamps, but this time he figured a different specimen (fig. 10) from the Lower Lias of the central Apennines which was more acutely biconvex, with a faint uniplication of the anterior margin and with strong or well developed marginal plicae. In a further description of brachiopod species from the same area Canavari (1884, p. 85) described, without illustration, a specimen under the new taxon *Terebratula mediterranea* and assigned his two specimens previously described under the name *Terebratula fimbrioides* E. Deslongchamps to the synonymy. Selection of a lectotype for the species is deferred whilst search for the specimens currently missing from the Canavari brachiopod collection at Pisa continues.

Dubar (1942), in a description of Lower Liassic polyplicate Zeilleriidae and Terebratulidae from the Atlas Mountains and nearby regions, described and figured a specimen of a plicate terebratulid as *Terebratula mediterranea* Canavari (Dubar 1942, p. 42, pl. 3, fig. 12a–d). This specimen compares favourably with the specimen figured by Canavari (1881, pl. 9, fig. 10a–d) and also has many features recognized in Gibraltar specimens of polyplicate terebratulids.

Among the many varieties of *Terebratula mediterranea* erected by Dubar (1942) is one which he described as *Terebratula mediterranea* var. *pectita* from Ait-Oufella, near Itzer (pl. 4, fig. 1a–c). A NHM specimen (B85440) comparable to this variant, collected from Gibraltar, is figured here (Pl. 1, figs 1–3). It is a large specimen, 29·5 mm long, 20·5 mm wide and 19·7 mm deep. Dimensions of other Gibraltar specimens are: B85434, 23·0 mm long, 20·2 mm wide, 17·8 mm deep; B85435, 20·3 mm long, 18·8 mm wide, 14·1 mm deep; B85437, 19·8 mm long, 18·7 mm wide, 17·1 mm deep; B85438, 18·0 mm long, 16·2 mm wide and 14·2 mm deep.

The species is here assigned to the genus *Merophricus*, hitherto known only from the type and the two closely similar originally assigned species *M. semiarata* (Dubar, 1942) and *M. moreti* (Dubar, 1942), on the basis of external morphology together with characteristic cardinalia and broad transverse band of the brachial loop. The brachial loop differs from those known in all other post-Palaeozoic terebratulacean genera (Cooper 1983).

Superfamily ZEILLERIACEA Allan, 1940
Family ZEILLERIIDAE Allan, 1940

Genus CALPELLA gen. nov.

Derivation of name. From Calpe, the classical name for Gibraltar.

Type species. *Zeilleria aretusa* Di Stefano, 1886, p. 93, pl. 2, fig. 54, from the Lower Lias of St. Antonio, Taormina, Sicily.

Diagnosis. Small polyplicate, sub-pentagonal zeilleriid.

Remarks. Since its original description by Di Stefano, authors have consistently accepted the type species of *Calpella* as a zeilleriid. However, the genus can be distinguished from other Zeilleriidae by its shell ornament of strong plicae which, in some species, tend to be more highly developed marginally. Unlike *Zeilleria sensu stricto* it has a short interarea which is slightly concave and has marked beak ridges which are not persistent, nor are there any lateral depressions, as in *Antiptychina*, or anterior sulcation of either valve.

Calpella aretusa (Di Stefano, 1886)

Plate 1, figures 21–23

1886 *Zeilleria aretusa* Di Stefano, p. 93, pl. 2, fig. 54a–d.
1935 *Zeilleria arethusa* [*sic*] Di Stefano; Dubar and Le Maître, p. 9.

1942 *Zeilleria* cf. *tenuiplicata* Dubar, p. 45, pl. 1, figs 23a–c, 24a–d.
1952 *Zeilleria* aff. *tenuiplicata* Dubar; Muir-Wood, *in* Bailey, p. 164.

Material. NHM specimens B85420–85421 from Gibraltar.

Diagnosis. As for genus.

Description. The best preserved of these small zeilleriids is 15 mm long, 13·3 mm wide and 9·2 mm deep, subtriangular in general outline, polyplicate with 10–12 well-developed plicae originating from the midvalve area and radiating anteriorly. Lateral margins are straight and the anterior margin rectimarginate, profile oval. The umbo is short and the beak suberect. Permesothyrid beak ridges border a short, slightly concave triangular interarea. The foramen is comparatively large.

Internal structures. These have not been determined by serial sections because of the crystalline nature of the matrix. They are thought to be typically zeilleriid in form since a marked median septum can be seen through the dorsal valve extending from the umbo to a point just over half the length of the shell.

Remarks. In general outline, plication and size, the specimen described and figured here (Pl. 1, figs 21–23) has very much in common with the specimen figured by Di Stefano (1886, pl. 2, fig. 54a–d). It differs from that specimen, however, in its less acute biconvexity. It can be compared to a specimen figured by Dubar (1942, pl. 1, fig. 24a–d) from the Lower Lias of Tisdadine near Timhadit, Morocco which he included in the description of a series of polyplicate Zeilleriidae. This is very close to the specimen figured by Di Stefano (1886) as *Zeilleria aretusa* and shows the same degree of biconvexity of the valves and a very similar general outline. A further specimen figured by Di Stefano (1886) as *Zeilleria aretusa* shows the same degree of biconvexity of the valves and a very similar general outline. A specimen figured by Dubar as *Zeilleria* cf. *tenuiplicata* in the same publication (Dubar 1942), although more elongate and acutely biconvex than the specimen figured here (Pl. 1, figs 21–23) nevertheless bears a strong resemblance to that specimen and is therefore included in the synonymy. It is probable that another specimen figured by Dubar (1942, pl. 1, fig. 23a–b) also belongs to the species *Calpella aretusa* (Di Stefano) but this is represented by a larger, flatter and broader example.

DISCUSSION

The systematic account is based upon the 26 specimens discussed by H. M. Muir-Wood (*in* Bailey 1952) and eight additional specimens. All but four (B19525, 85417–85418, 85442) have been identified to species level, with revised generic assignments.

Despite their revised nomenclature, the brachiopod taxa are consistent with an early Lias (Lotheringian = late Sinemurian) age, as recognized previously for Gibraltar brachiopods by Dubar and Le Maître (1935), Dubar (1942), and Muir-Wood (*in* Bailey 1952). According to their labels, the Natural History Museum specimens are those obtained by Colonel Charles Silvertop and James Smith, identified and discussed although not formally described by Muir-Wood; three further specimens (one presented by J. W. Goldie prior to 1899, two by F. Evans in 1903) previously wrongly identified as *Hemiptychina* and of Carboniferous age (Reed 1949); and two specimens presented by Captain G. B. Alexander, effectively in 1948. Three specimens loaned by the Office National de Gestion des Collections Paléontologiques at the Université Claude Bernard: Lyon 1 were those originally obtained by D. T. Ansted from the Austrian Consul-General on Gibraltar, sent to E. de Verneuil for identification, and subsequently donated to the École des Mines in Paris.

The exact provenance of the Silvertop/Smith specimens is not known: there is nothing other than 'Gibraltar' on the labels which accompany them and Smith (1846) in his reference to brachiopods gave no locality data. The matrix associated with the specimens is a crystalline carbonate, typical both of the Gibraltar Limestone Formation and of beds within the lower part of the Catalan Bay Shale Formation. No brachiopods have been collected from either formation in recent years. However, Ansted (1859) and Hochstetter (1866) referred to brachiopods collected by Mr Frembly (the Austrian Consul-General) during four years of military quarrying on the north-east side of the

Rock, Ramsay and Geikie (1878) recorded that their 'only good specimens' (of brachiopods) all came from a quarry on the North Face, and Dubar (*in* Dubar and Le Maître 1935) also seems to have obtained brachiopods from the North Face. Since the Catalan Bay Shales were not exposed either at the North Face or in Catalan Bay along the east coast until much later and after more extensive military quarrying (Rose and Rosenbaum 1991*b*, pp. 79, 167), it is almost certain that it was the Gibraltar Limestone Formation which yielded all these brachiopods, and that in consequence at least part of it can be dated as Sinemurian. The Goldie/Evans specimens are more precisely sourced, to Catalan Bay Quarry. Although this quarry is now the type locality for the Catalan Bay Shales, the Shales were not exposed until the quarry was extended in 1943 to provide fill for the expansion of the airfield. At the time the brachiopods were collected (prior to 1903), only the Gibraltar Limestone and Quaternary screes derived from it in the cliffs above were accessible. The near vertical cliffs tower to a height of some 300 m above the quarry floor, exposing a faulted succession in which all four members of the Gibraltar Limestone Formation are represented. The horizon yielding the brachiopods has not yet been identified. The Alexander specimens are recorded as from the 'searchlight scree, above Arow Street, 300 feet above the base of the limestone'.

The dolomitic lower members of the Gibraltar Limestone Formation reveal few fossils other than oncolitic or stromatolitic algae. However, molluscs are increasingly abundant higher in the succession. Disarticulated bivalves are locally common at horizons within both the Keightley and Buffadero members (Rose and Rosenbaum 1991, figs 6.10, 6.13c), and gastropods (Rose and Rosenbaum 1991, fig. 6.13) are locally common within the Buffadero Member. Coral and echinodern fragments are also known from this horizon. Unfortunately, the rock is very well cemented and the fossils are seen only in cross section, so cannot be identified precisely, or easily extracted. A large gastropod variously identified as *Eulima hedingtonensis* Sowerby or as *Pseudomelania* (by Choffat 1892), originally in the James Smith collection at the Geological Society of London, seems not to have survived the transfer of most of the Society's collection to The Natural History Museum, London (Dr N. J. Morris, pers. comm. 1994). Dubar and Le Maître (1935) referred to beds of *Chemnitzia* at the North Face, possibly the same taxon. The Gibraltar Museum contains the internal mould of a large pleurotomariid gastropod, labelled as from Little Bay, but its matrix is not that of the Gibraltar Limestone. However, since the specimen cannot be more precisely identified and therefore dated (N. J. Morris, pers. comm.), it is of little significance. Smaller, thick-shelled cerithiid gastropods are commonly seen in cross section in the higher beds of the Limestone, where their increasing abundance coincides with a decrease in abundance of the algal laminites and presumably a change to less restricted marine environments. *Stromatomorpha liasica* Le Maître, described by Dubar and Le Maître (1935) as a spongiomorphid but conforming to the currently accepted definition (Wood 1987) of stromatoporoid sponges, is known only from the type specimens, collected from the North Face. A fossil, 'apparently a nautilus', was observed in a building stone by Duckworth (1911, p. 355), but the identification was tentative, and the source of the stone uncertain. The building has now been demolished and the specimen lost. Thus as yet the brachiopods provide the only means of dating.

That the Gibraltar Limestone Formation of the main ridge area of the Rock has been overturned can be demonstrated convincingly both from algal growth directions and from statistical analysis of geopetal infills of the numerous gastropod shells. The Catalan Bay Shale Formation which crops out beneath the overturned Gibraltar Limestone Formation at the base of the North Face and along parts of the east coast of the Rock should therefore have a younger date. Although the ammonites to which L. F. Spath (*in* Bailey 1952) ascribed a Mid Lias (Domerian, late Pliensbachian) age have now been lost, M. K. Howarth (*in* Rose and Rosenbaum 1990) has confirmed that in his identifications and discussion of these ammonites, Spath was almost certainly correct in his age assignment.

Of the supposedly closest comparable carbonate outcrops, that at Los Pastores, 9 km westwards across the Bay of Gibraltar, is now largely quarried away, tectonically complex, and of broader but imprecise Triassic–Jurassic date (Valenzuela Tello 1993). A thick, well-exposed sequence of shallow-

water carbonates associated with cherty 'shales' occurs immediately north-east of Manilva, Spain, some 30 km to the north of Gibraltar, and has been mapped as of Liassic age (Fontboté 1970). Approximately 24 km southwards across the Strait of Gibraltar, Gebel Musa (which in classical times was twinned with Gibraltar under the name 'Pillars of Hercules') has also been described as a klippe dominantly of Early Jurassic carbonates (Durand-Delga and Villiaumey 1963). However, so far as we are aware, none of these localities has yielded a described brachiopod fauna.

The closest faunal comparisons currently possible are with the Liassic faunas of the High Atlas in Morocco (Dubar 1932, 1942), and of Taormina in eastern Sicily (Di Stefano 1886). Of the five species described here from Gibraltar, three (*Gibbirhynchia correcta*, *Pontaltorhynchia schopeni*, *Calpella aretusa*) were first described from Sicily (Di Stefano 1886), one (*Merophricus mediterranea*) from the central Apennines (Canavari 1884), and the fifth (*Liospiriferina rostrata*) as a Sicilian species here merged in synonymy. The new genus *Pontaltorhynchia* is defined herein on the basis of material not only from Gibraltar but also Sicily and the central Apennines. Faunal affinities between Gibraltar and the Lower Lias of Italy are therefore very clear.

Additionally, three of the species have been described from Morocco (as '*Terebratula*' *mediterranea* and '*Zeilleria*' *aretusa*, and *Liospiriferina rostrata*), extending their apparent geographical range over 2000 km westwards. '*T.*' *mediterranea* is here newly ascribed to the genus *Merophricus*, according to Cooper (1983, p. 114) a genus endemic to Morocco and with a distinctive morphology: a brachial 'loop unlike any genus described' in his massive, authoritative account of the post-Palaeozoic Terebratulacea (204 genera). '*Z.*' *aretusa* is here made the type of the new genus *Calpella*. Both *Merophricus* and *Calpella* thus appear to be widespread in, but also endemic to, the Lower Lias of the western Mediterranean.

Dubar and Le Maître (1935, p. 9) correlated Gibraltar brachiopods (from low on the North Face) with those from the Sinemurian of Morocco, but failed to recognize that the sequence in the North Face was inverted. Consequently, their relative ages and correlations assigned to the beds bearing *Chemnitzia* and *Stromatomorpha* must be in error.

An Early Jurassic age for much of the Gibraltar Limestone Formation is, however, consistent with that of the thick Bahamian-type platform carbonates widely developed along the southern continental margin of the Alpine-Mediterranean Tethys. Bernoulli and Jenkyns (1974) reviewed evidence for thick sequences of Liassic shallow-water carbonates in the Subbetic region of Spain, in the northern Rif and High Atlas regions of Morocco, in Tunisia, and in Sicily and several regions of mainland Italy. As in Gibraltar these sequences terminate with a sharp change to more pelagic sedimentation in the mid–late Lias, a change that Bernoulli and Jenkyns correlated with widespread block faulting, probably related to the onset of rifting in the oceanic Tethys.

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