

A CARIBBEAN RUDIST BIVALVE IN OMAN: ISLAND-HOPPING ACROSS THE PACIFIC IN THE LATE CRETACEOUS

by P. W. SKELTON and V. P. WRIGHT

ABSTRACT. The hippuritid rudist bivalve *Torreites* is described from the Maastrichtian of Oman and the United Arab Emirates. Together with the single fragment from the region on which *T. milovanovici* Grubić, 1979 was based, the specimens are placed in a newly recognized geographical subspecies of *T. sanchezi* (Douvillé, 1927), a species previously considered endemic to the Caribbean Province. The Arabian *T. s. milovanovici* Grubić differs from its Caribbean parent, *T. s. sanchezi* (Douvillé) (incorporating all previously recognized *T. sanchezi*, as well as *T. coxi* Grubić, 1979) only in the angle (α) between the *arête cardinale* and the ventralmost pillar: α is 12°–75° in the former and 50°–126° in the latter.

The loss of the normal hippuritid pore and canal system in *Torreites* is confirmed and shown to have been associated with exposure of the mantle margins, which may have contained symbiotic algae, as in the living *Tridacna*.

Homeomorphy and plate tectonic drifting are rejected as explanations for the apparent disjunct endemism of *Torreites*. Rather, larval dispersal along a corridor of shallow staging posts is favoured. A Mediterranean Tethys/Atlantic route is considered unlikely, because of barriers. There is good evidence, in contrast, for such staging posts across the Pacific and eastern Tethys in Campanian–Maastrichtian times.

ALTHOUGH the distinctive Late Cretaceous rudist bivalve *Torreites* has generally been considered endemic to the Caribbean Province (Kauffman 1973), a single worn fragment of a right valve from Sheikdom Sharjah, in the United Arab Emirates (UAE), was assigned to the genus by Grubić, in 1979. Such a strikingly disjunct distribution for a sessile benthic inhabitant of shallow equatorial seas demands a palaeobiogeographical explanation. Yet this and other purported cases of apparent disjunct endemism between the eastern Tethyan and Caribbean regions (e.g. Chubb 1956; Elliott 1981) have attracted surprisingly little comment in the literature. Possibly there has been a tacit (though uninformed) assumption that such distantly separated forms are more likely to have been mere homeomorphs than true congeners, or that the currently known localities are but preservational relics of an originally cosmopolitan range.

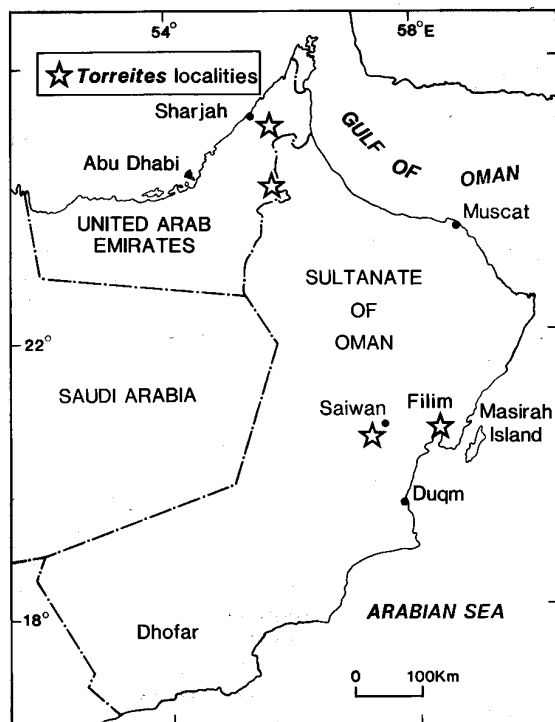
During geological reconnaissance work in Oman (by V.P.W. in 1983) and in the UAE (by P.W.S. in 1984), we found several further, well-preserved specimens of *Torreites*. The purpose of this paper is to establish recognition of the genus in the region beyond any doubt, on the basis of a suite of characters, the replication of which by homeomorphy would have been exceedingly unlikely. The quality of our material also prompts a systematic re-evaluation of the new species of the genus erected for the Middle Eastern form by Grubić, and allows the reconstruction of some previously unrecognized aspects of the original soft part anatomy and life habits of the animal.

Grubić (1979) inferred that the disjunct distribution of the genus implied closer proximity of Oman to the Caribbean in Late Cretaceous times. However, recent Deep Sea Drilling Project work in the Pacific (Schlanger *et al.* 1981) has shown that, in the Late Cretaceous, shallow-water benthos with Caribbean affinities extended far across the Pacific, exploiting shallow-water 'stepping stones' formed by numerous volcanic seamounts and islands. We argue here that the disjunct distribution of *Torreites* was more probably the product of larval dispersal via such staging posts than of the drifting apart of Oman and the Caribbean implied by the hypothesis of Grubić.

GEOLOGICAL SETTING

The main suite of specimens described here was collected from the foot of a small escarpment of Cretaceous strata east of the main Tertiary escarpment, some 30 km south-south-west of the Saiwan airfield, in eastern central Oman, at latitude $20^{\circ} 39' \text{ N.}$ and longitude $57^{\circ} 31' \text{ E.}$ (text-fig. 1). The area is remote, with no previous published account of its Mesozoic geology, although a generalized geological map of the region is given by Gorin *et al.* (1982). The scarcity of landmarks and settlements makes it impossible to provide more precise locality details. The rudists were loose specimens from the talus at the foot of the escarpment. They are associated with a yellow-weathering bioclastic calcarenite. The Upper Cretaceous of the area comprises a basal clastic member overlain by a limestone member, which yields the rudists. Both members fall within the Aruma Group of Glennie (1977), of Santonian–Maastrichtian age. It is unclear as to whether the rudist-bearing limestone is high in the Fiqa Formation (a predominantly marly formation of Santonian–Maastrichtian age) or if it corresponds to the Simsim Formation (Late Maastrichtian, according to Harris *et al.* 1984, though work in progress on this formation in the UAE by P.W.S. with S. C. Nolan, indicates, rather, an early to medial Maastrichtian age). The age of the *Torreites*-bearing units, however, must be considered tentative because of the lack of earlier work in the area. One further specimen was collected in Oman, at Filim in northern Masirah Bay (lat. $20^{\circ} 36' \text{ N.}$ and long. $58^{\circ} 12' \text{ E.}$) (text-fig. 1).

The specimens from the United Arab Emirates were found at two localities (text-fig. 1). A small hillock, Qarn Murrah, projecting through the desert sands some 8 km west of Jebel Faiyah, in eastern Sharjah (lat. $25^{\circ} 07' \text{ N.}$ and long. $55^{\circ} 46' \text{ E.}$), has several specimens in life position, in a sequence of reddish bioclastic packstones to grainstones. To the south the basal chert conglomerate exposed around the core of an anticline at Jebel Huwayyah, some 10 km north-east of Buraimi/Al Ayn (lat. $24^{\circ} 16' \text{ N.}$ and long. $55^{\circ} 48' \text{ E.}$), yielded a single worn right valve. In both cases, a



TEXT-FIG. 1. Localities in Oman and the United Arab Emirates where the specimens of *Torreites* described in this paper have been collected and/or observed.

Maastrichtian age is indicated, by the accompanying large foraminifera, *Orbitoides media* (d'Archiac) and *Omphalocyclus macroporus* Lamarck, as well as by the hippuritid rudist *Pironaea praeslavonica* Milovanović, Sladić and Grubić, at Qarn Murrah, and by the large foraminifer, *Loftusia* sp. in conformably overlying beds at Jebel Huwayyah. Work in progress by P.W.S., with S. C. Nolan, suggests that both occurrences may indeed be confined to the Lower Maastrichtian.

Grubić (1979, p. 85) stated that his specimen came from 'Guru Mileih, Sheikdom Sharjah', and he assigned it a Maastrichtian age from its association with *Orbitoides media* and *Omphalocyclus macroporus*. The lithology of the matrix on this specimen is very similar to that observed at Qarn Murrah, however, and the specimen may indeed come from there (enquiries about the names of small hills in deserts often provokes confusing responses).

SYSTEMATIC PALAEONTOLOGY

Superfamily HIPPURITACEA Gray, 1848

Family HIPPURITIDAE Gray, 1848

Genus TORREITES Palmer, 1933

Type Species. Hippurites (Vaccinites) Sanchezi Douvillé, 1927.

Emended diagnosis. Medium to large-sized hippuritid, with a conical right valve (RV), and an operculiform left valve (LV) with a ventrally biased apex. The outer shell layer of the LV is externally smooth and devoid of pores and canals. It is also much thinner than that of the RV, the internal margin of which is thus exposed. Apically blind radial canals penetrate the inner shell layer of the LV. The RV exterior is radially ribbed, with three solid radial infoldings (text-fig. 2) comprising a dorsal 'arête cardinale' (P₀) and two posterior pillars (P₁ and P₂). The former has a rounded inner tip and extends much further inwards than either of the subequal pillars. The three infoldings tend to be uniformly thick, though the *arête cardinale* may taper inwards. Their crests project through sinuses indented from the LV margin. They are positioned around an angle of arc of between 12 and 126°. The two teeth and posterior myophore of the LV are strongly projecting, and are arrayed at between 25 and 50° across the inner end of the *arête cardinale*.

Remarks. The original description of the type species (Douvillé 1927) drew attention to the unusually elongate *arête cardinale* and to the even thicknesses of the pillars. Palmer's (1933) original diagnosis for the genus noted most of the other key features: the imperforate outer layer of the LV; the radiating canals in the inner shell layer of the LV; and the sinuses in the LV for the RV infoldings. Rutten (1936) demonstrated that the canals in the inner shell layer of the LV open directly over the body cavity (in contrast to those in the outer shell layer of the LV in other hippuritids: see Skelton, 1976). He, MacGillavry (1937), Jung (1970), and Van Dommelen (1971) provided many quantitative data, including a higher range of values (75–120°) for the angle of arc formed by the RV infoldings in *T. sanchezi* than that observed (45–70°) in a smaller species, *T. tschoppi* MacGillavry. Grubić (1979) erected three new species, two based on previously described Caribbean specimens (*T. coxi*, based on specimen G.14066 of Jung, 1970, and *T. chubbi*, based on that described by Chubb, 1971) and the third, *T. milovanovici*, on the single RV fragment from Sharjah. This latter was distinguished by the very low angle of arc between P₀ and P₂—only 'about 10°'. Our specimens from Oman and the UAE share the latter feature, but are otherwise so similar to *T. sanchezi* that we would judge them merely to represent a subspecific variant of that species (see the synonymy below).

Stratigraphical ranges. In the Caribbean region the genus *Torreites* ranges from the Santonian or lowest Campanian to the Lower Maastrichtian. *T. sanchezi* is characteristically found in the 'Barrettia Beds', in Cuba, Puerto Rico, and Jamaica, with either or both of *Barrettia monilifera* Woodward and *B. gigas* Chubb (Van Dommelen, 1971, p. 34; though N. F. Sohl, pers. comm. of August 1983, refers more specifically to a consistent co-occurrence with the latter species). MacGillavry and his co-workers (summarized in MacGillavry 1937) favoured a Maastrichtian age for the *Barrettia* Beds, based largely on orbitoid foraminifera in those of the Cuban Habana Formation. In contrast, Hawkins (1924), working on Jamaican echinoids, and Muellerried

(1936), extrapolating from ammonite-bearing sequences in Chiapas, Mexico, postulated a Turonian age. Subsequent work has refuted the conclusions of Hawkins and Muellerried (N. F. Sohl, pers. comm.), and largely vindicated those of MacGillavry and his co-workers. *B. monilifera* is now judged to be of Late Campanian, and *B. gigas*, of latest Campanian/earliest Maastrichtian age (Sohl and Kollmann 1985, fig. 19). De la Torre *et al.* (1978) referred the *Barrettia* fauna of Cuba to the upper part of the Lower Maastrichtian. So the inferred range of *T. sanchezi* in the Caribbean is best bracketed within the Upper Campanian to Lower Maastrichtian interval.

The specimen described by Chubb (1971) as '*T. cf. sanchezi*' (= *T. chubbii* Grubić, 1979), however, comes from the Peter's Hill Limestone of Jamaica, now considered of latest Santonian to earliest Campanian age (N. F. Sohl, pers. comm.).

T. tschoppi was considered 'probably Upper Campanian' by MacGillavry (1937, p. 20), though Van Dommelen (1971, text-fig. 18) extended its range into the Santonian, albeit with uncertainty. It is certainly older than *T. sanchezi* (Van Dommelen, 1971; N. F. Sohl, pers. comm.).

The specimens from the UAE are all considered Maastrichtian, while those from Oman can probably be assigned to that stage, too, though with less certainty (see p. 506).

Characters of systematic value. Text-fig. 2 shows the characters measured and the abbreviations used for them in the description of specimens that follows.

The five main characters of systematic value are:

1. the overall size of the shell (L, D₁ and D₂);
2. the angle of arc between the *arête cardinale* and the ventralmost pillar (α);
3. the lengths (l) and widths (w) of the *arête cardinale* (P₀) and pillars (P₁ and P₂);
4. the angle made by the myocardial array with the inner tip of the *arête cardinale* (β);
5. the character of the RV outer shell layer (its thickness, rib-width, and depth of intervening grooves between ribs).

The symbols used alongside the synonymy list are as explained in Matthews (1973).

Torreites sanchezi (Douvillé)

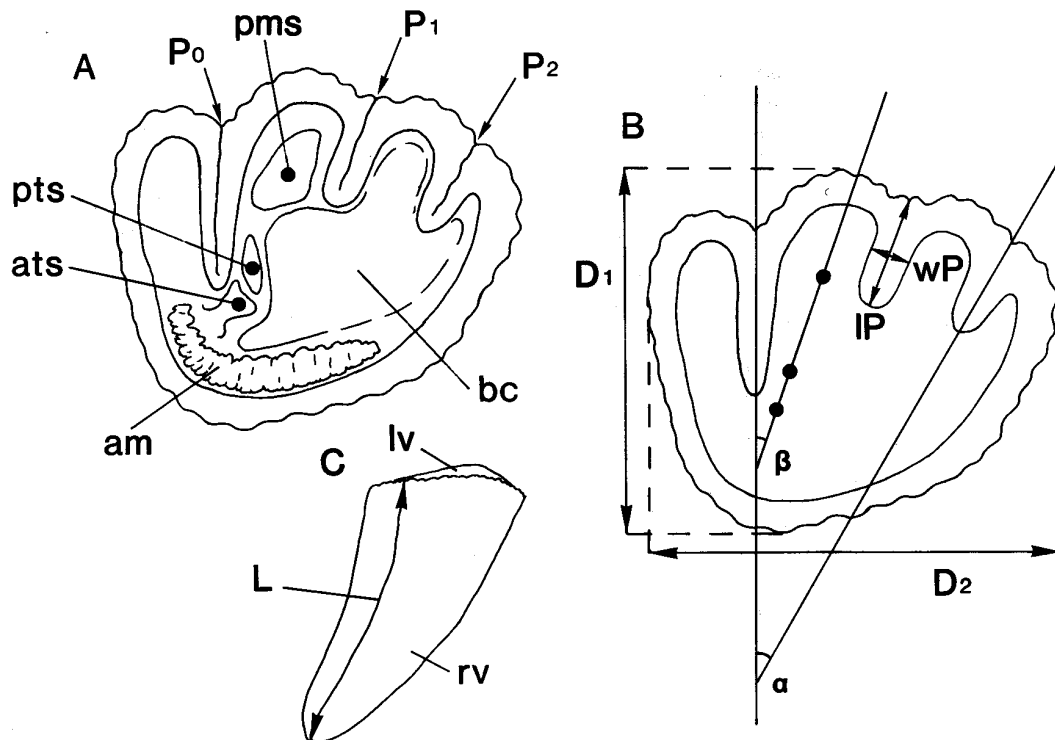
Plate 61, figs. 1–5; Plate 62, figs. 1–4

- *1927 *Hippurites* (*Vaccinites*) *Sanchezi* Douvillé, p. 54, pl. 4, fig. 1.
- 1933 *Torreites sanchezi* Douvillé; Palmer, p. 100, pl. 7, figs. 1 and 2; pl. 8, figs. 1 and 2.
- 1936 *Torreites sanchezi* (Douvillé); Rutten, p. 135, text-fig. 4g.
- 1937 *Torreites sanchezi* (Douvillé); Vermunt, p. 269 (description only).
- 1937 *Torreites sanchezi* (Douvillé); MacGillavry, p. 128, pl. 5, fig. 4e–h.
- 1970 *Torreites sanchezi* (H. Douvillé); Jung, p. 5, pls. 1–3, text-figs. 1 and 2.
- 1971 *Torreites sanchezi* (Douvillé); Van Dommelen, p. 34, table 5.
- v. 1979 *Torreites milovanovici* Grubić, p. 84, pls. 1 and 2; text-fig. 4.
- . 1979 *Torreites coxi* Grubić, p. 86, text-figs. 5 and 6 [text-fig. 5 = *T. sanchezi* (H. Douvillé); Jung, 1970, pl. 3].

Emended diagnosis. Large species of *Torreites*: D may exceed 100 mm and L, 200 mm. Ventral flank of RV flattened, even embayed, and separated from somewhat flattened anterior part by a blunt carina. Outer shell layer of RV very thick (5–10 mm), and marked externally by deeply indented radial grooves separated by broad rounded ribs usually over 5 mm wide. These indentations correspond to salient ridges on the inner margin of the valve, and are present along the three infoldings of the RV wall, as well as around its periphery. The outer shell layer of the LV is only about 1 mm thick, and its marginal growth laminations are recurved over at least the peripheral parts of the valve's outer surface. The *arête cardinale* and pillars are spaced around an arc (α) of 12–126°. *Arête cardinale* much longer than the subequal pillars (of which P₁ tends to be the longer).

Holotype. *Hippurites* (*Vaccinites*) *Sanchezi* Douvillé, 1927, p. 54, pl. 4, fig. 1.

Material studied. Five full-sized specimens were collected by V.P.W. some 30 km south-south-west of the Saiwan airfield, eastern central Oman, in 1983 (see p. 506), and have been deposited in the British Museum (Natural History) (nos. BMNH LL 28000–28004). One further specimen (P.W.S. Collection, no. 84/x.1) was collected by V.P.W. from Filim (north Masirah Bay), in 1983. All are well preserved, though with some patchy



TEXT-FIG. 2. Diagrams showing the morphology and measured characters of *Torreites sanchezi*. A, RV interior. Abbreviations are: am, anterior adductor muscle scar; ats, anterior tooth socket; bc, body cavity; P₀ *arête cardinale*; P₁ and P₂, the two pillars (infoldings of the RV outer shell layer); pms, socket for the LV posterior myophore; pts, posterior tooth socket. B, as in A, showing measured characters. Abbreviations are: α, angle of arc described by lines drawn through the middles of P₀ and P₂; β, angle of arc described by lines drawn through P₀ and the myocardial array (using the black dots centred on the sockets shown in A); D₁, commissural diameter parallel to P₀; D₂, commissural diameter normal to P₀; IP, pillar length; wP, pillar width. C, outline of both valves. Abbreviations are: L, RV length, measured along the external trace of P₀; lv, left valve; rv, right valve.

silicification of the outer (calcitic) shell layer, and with the inner shell layers (originally aragonitic) now replaced by calcite spar. Four of the specimens have all or part of both valves preserved, while the remaining two (BMNH LL 28003 and 28004) are RVs only, though the latter also has a fragment of another, juvenile RV attached to its flank. A slightly worn RV was recovered by P.W.S., in 1984, from the basal chert pebble and shell rubble conglomerate underlying the Simsim Formation at Jebel Huwayyah, near Al Ayn, UAE (see p. 506) (P.W.S. Collection, no. 84/32.1). Other specimens, in life position, were studied in the field (but not collected) by P.W.S., in 1984, at Qarn Murrah, Sharjah (see p. 506).

Description. Measurements of the specimens are shown in Table 1, and plots of their overall dimensions, and of changes in shape of the *arête cardinale* and pillars, as well as in their arrangement (α), with respect to commissural diameter (D₁), are shown in text-figs. 3, 4, and 5, respectively.

The RVs in BMNH LL 28000–28004 are of gently curved elongate conical form, reaching over 230 mm in length in LL 28001. The other two specimens have RVs of more obtusely conical form. The LVs are operculiform and only very gently convex towards the strongly ventrally biased apex. The commissure is of rounded trigonal form, with the anterior and ventral margins slightly flattened, and the posterodorsal margin, with the infoldings, somewhat bulging (Pl. 61, fig. 1; text-fig. 6E–G).

TABLE 1. Measurements on specimens of *Torreites sanchezi milovanovici* Grubić from the Maastrichtian of Oman and the United Arab Emirates, described in this paper. Specimen numbers beginning with LL are housed in the British Museum (Natural History), and those with P.W.S., in the collection of the senior author. Locality data are given in the text (p. 506), and the abbreviations for the measurements explained in text-fig. 2.

Specimen	Shell size (mm)			Hinge Angle (°)	Pillar Angle (°)	Pillar dimensions (mm)					
	L	D ₁	D ₂	β	α	1P ₀	1P ₁	1P ₂	wP ₀	wP ₁	wP ₂
(a) LL 28000	190	103	89	—	39	32	29	26	8	10	9
(b) LL 28001	234	96	110	—	31	46	40	34	6	13	10
		80	91	—	37	31	21	25	6	10	9
		> 48	56	—	49	18	13	14	7	6	6
		35	42	—	70	11	> 9	> 7	5	5	6
(c) LL 28002	226	104	113	—	28	36	29	42	14	11	7
(d) LL 28003	164	93	89	—	42	36	29	23	8	10	10
(e) LL 28004	> 127	100	98	25	15	45	36	33	10	12	11
		70	78	—	31	27	19	19	8	10	8
		44	57	—	61	15	12	11	8	7	7
(f) LL 28004 (small RV)	—	> 48	> 52	—	50	16	> 11	> 10	5	7	7
(g) P.W.S. 84/x.1	160	108	113	—	40	45	33	23	8	~10	~10
(h) P.W.S. 84/32.1	> 42	116	> 93	—	20	> 50	> 35	20	16	12	9
		38	45	—	75	22	20	16	6	6	5

The pale brown, calcitic outer shell layer of the RV is more than 5 mm thick in all the adult specimens, with a highly distinctive ornament (Pl. 61, fig. 4): broad ribs, 5–8 mm wide, with coarse growth rugae, are separated by deeply indented grooves. The latter are expressed on the inner valve margin as salient spurs (Pl. 62, fig. 3). The spurs continue along the infolded shell wall of the *arête cardinale* and pillars, giving them the distinctively branched medial structure, when seen in section (Pl. 61, figs. 2 and 3), noted by Grubić (1979).

The calcitic outer layer of the LV is only about 1 mm thick, and, apart from faint growth undulations, is smooth (Pl. 62, fig. 1); no vestiges of any pores or canals are seen in it. Sections across the margins of this outer shell layer (Pl. 62, fig. 4; text-fig. 7) show the growth lines to be recurved on to at least the periphery of its upper surface. The subdued character of its growth undulations contrast markedly with the coarse rugae of the RV.

The discrepancy in thickness between the outer shell layers of the two valves means that most of the inner margin of the RV extends out beyond the rim of the LV (Pl. 62, figs. 1 and 3).

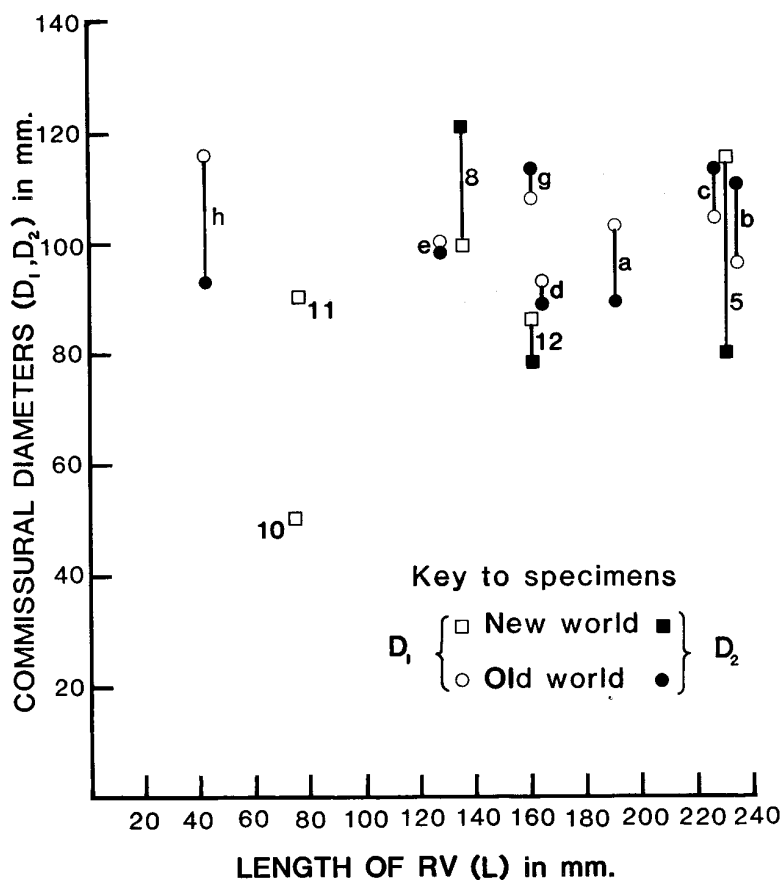
Although the inner shell layers, which would originally have been aragonitic (Skelton, 1976), are now replaced by calcite spar, evidence for the blind canals that penetrate the LV inner shell can be seen in one of the specimens (Pl. 61, fig. 5).

EXPLANATION OF PLATE 61

Figs. 1–5. *Torreites sanchezi milovanovici* Grubić, 1979. 1–3, BMNH LL 28004, unnamed limestone member in Aruma Group (probably Maastrichtian), 30 km south-south-west of the Saiwan airfield (lat. 20° 39' N. and long. 57° 31' E.), eastern central Oman. 1, RV interior (see text-fig. 2 for explanation); 2, 3, sections across successively younger ontogenetic stages of the RV, which is attached to the RV of another juvenile individual (*lower right*), all $\times 1$. 4, BMNH LL 28002, locality and age details as in 1–3; ventral flank of RV, $\times 0.5$. 5, P.W.S. 84/x.1, unnamed limestone member of Aruma Group (probably Maastrichtian), Filim, northern Masirah Bay (lat. 20° 36' N. and long. 58° 12' E.), Oman; detail of broken section across posteroventral part of LV, showing the (dark) thin calcitic outer shell layer above, and the canaliferous recrystallized inner layer (originally aragonite), below, forming a descending prominence, $\times 3$.



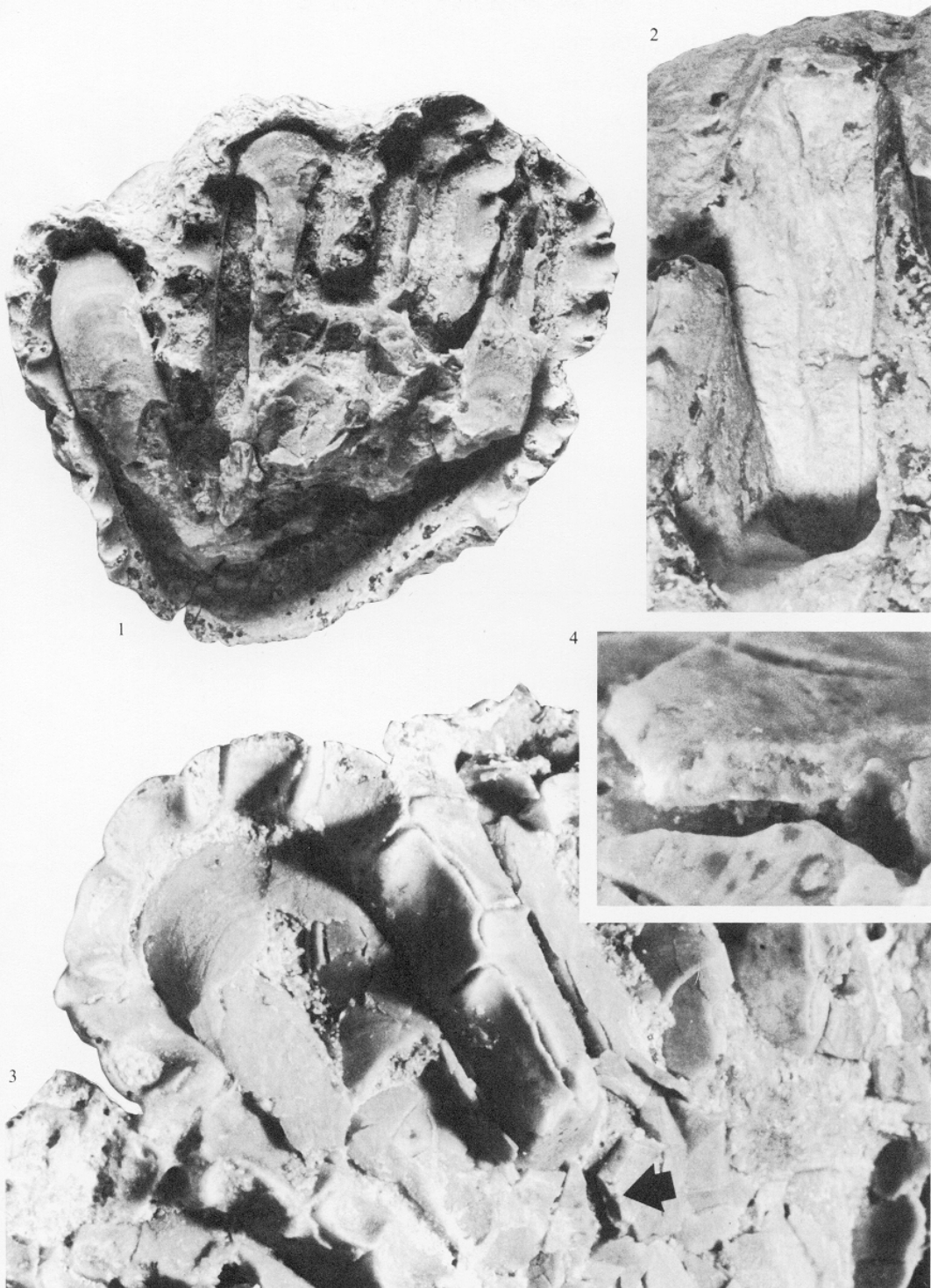
SKELTON and WRIGHT, *Torreites*



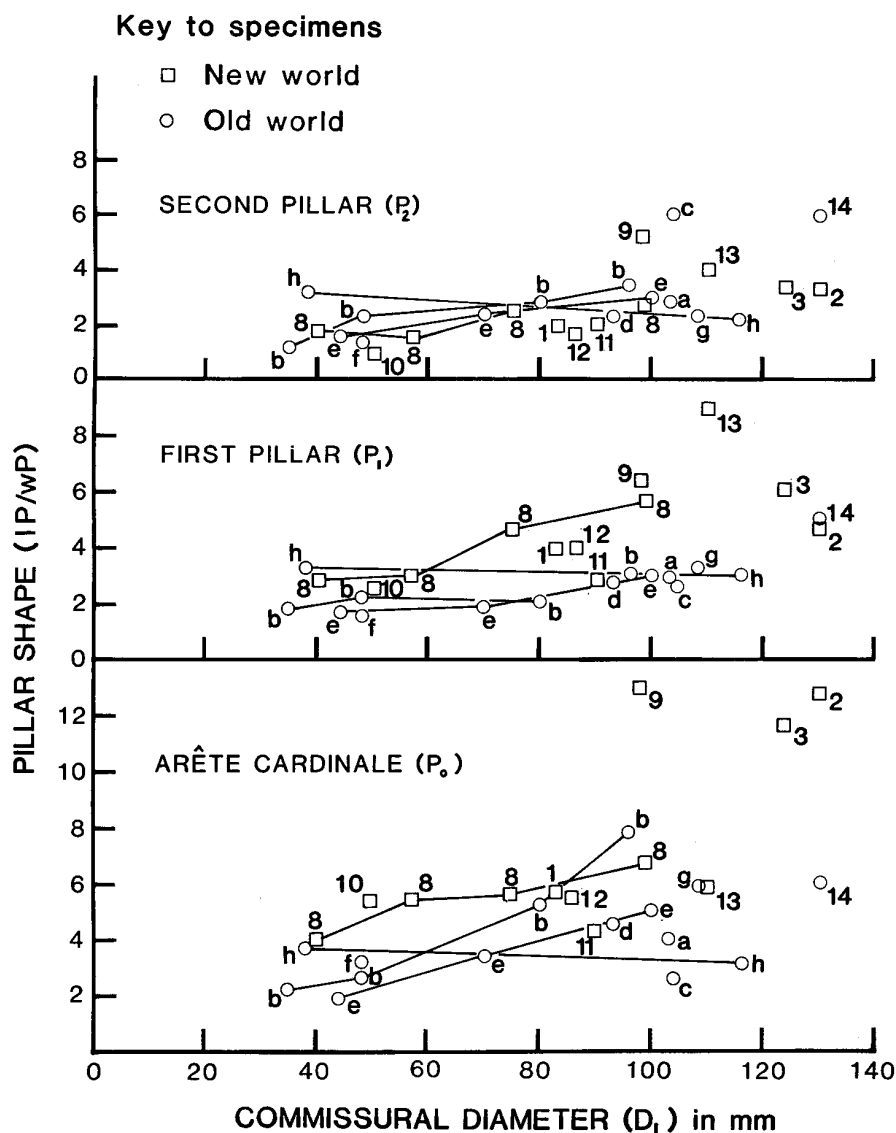
TEXT-FIG. 3. Graph of D_1 and D_2 against L for the specimens of *Torreites sanchezi* listed in Tables 1 and 2. The measurements are explained in text-fig. 2.

EXPLANATION OF PLATE 62

Figs. 1–4. *Torreites sanchezi milovanovici* Grubić, 1979. 1, BMNH LL 28002, unnamed limestone member in Aruma Group (probably Maastrichtian), 30 km south-south-west of the Saiwan airfield (lat. 20° 39' N. and long. 57° 31' E.), eastern central Oman; bivalved specimen, viewed from the LV side, showing the (incomplete) operculiform LV fitting in the RV, the inner margins of which are thus exposed around the LV periphery, $\times 0.75$. 2, BMNH LL 28001, locality and age details as in 1; detail showing blade-like posterior myophore of LV (centre), seen in section from dorsal side, projecting down between the *arête cardinale* (P_0 , right) and P_1 (left) of the RV, $\times 1.25$. 3, 4, BMNH LL 28003, locality and age details as in 1. 3, posterodorsal region of bivalved shell, viewed from the LV side, showing the somewhat crushed operculiform LV, with subdued external growth undulations, as well as the exposed RV inner margin, with salient ridges, running around the LV periphery and projecting up through sinuses in the latter, above the *arête cardinale* (P_0 , left) and pillars (P_1 and P_2), $\times 2.5$; 4, close-up of broken section across a chip of the LV margin, indicated by an arrow in 3, showing the recurved growth lines in the outer shell layer (see text-fig. 7 for explanation), $\times 10$.



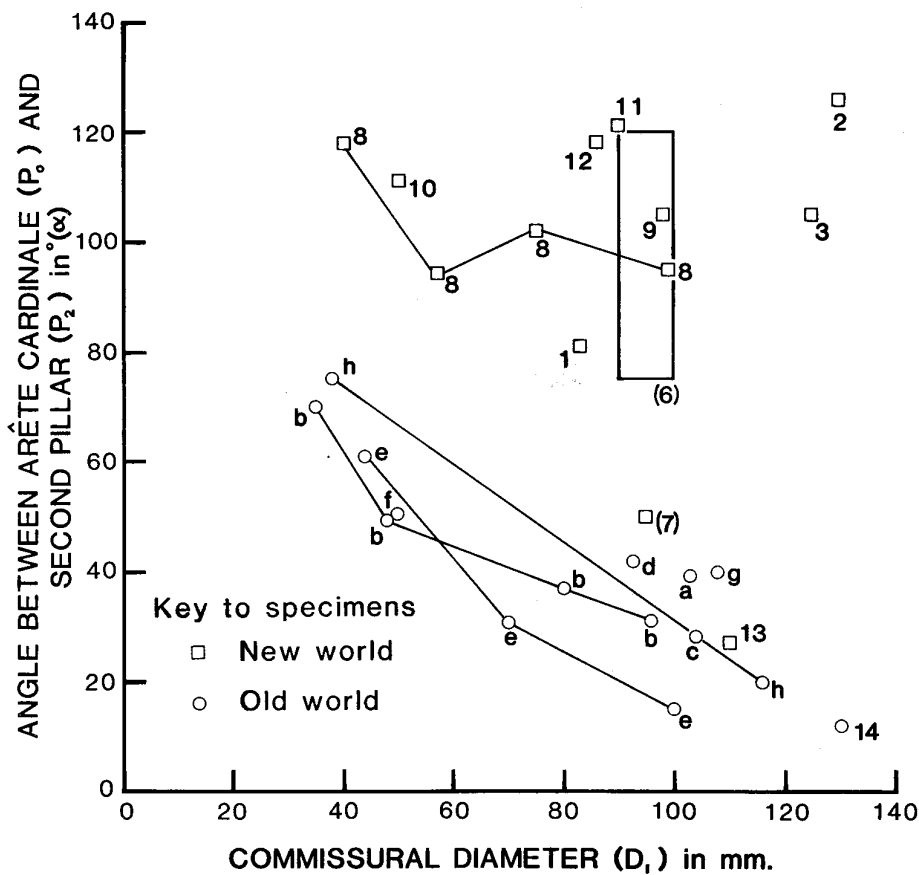
SKELTON and WRIGHT, *Torreites*



TEXT-FIG. 4. Graphs of $1P/wP$ against D_1 for P_0 , P_1 , and P_2 of the specimens of *Torreites sanchezi* listed in Tables 1 and 2. The measurements are explained in text-fig. 2.

Three deep radial grooves on the posterodorsal flank of the RV correspond with the infolded *arête cardinale* and pillars. The crests of these project through wide sinuses embayed from the margin of the LV (Pl. 62, fig. 1).

The elongate *arête cardinale* and the shorter, subequal pillars are wide and finger-like in section. P_1 is usually, but not invariably longer than P_2 (see Table 1). In some specimens the *arête cardinale* tapers inwards slightly, so becoming narrower than the pillars (Pl. 62, fig. 1). The strikingly low values of α are achieved ontogenetically: sections across the RV show the angle to reach 75° in the juvenile shell (Pl. 61, figs. 1-3; text-figs. 5 and 6E-G).



TEXT-FIG. 5. Graph of α against D_1 for the specimens of *Torreites sanchezi* listed in Tables 1 and 2. The measurements are explained in text-fig. 2.

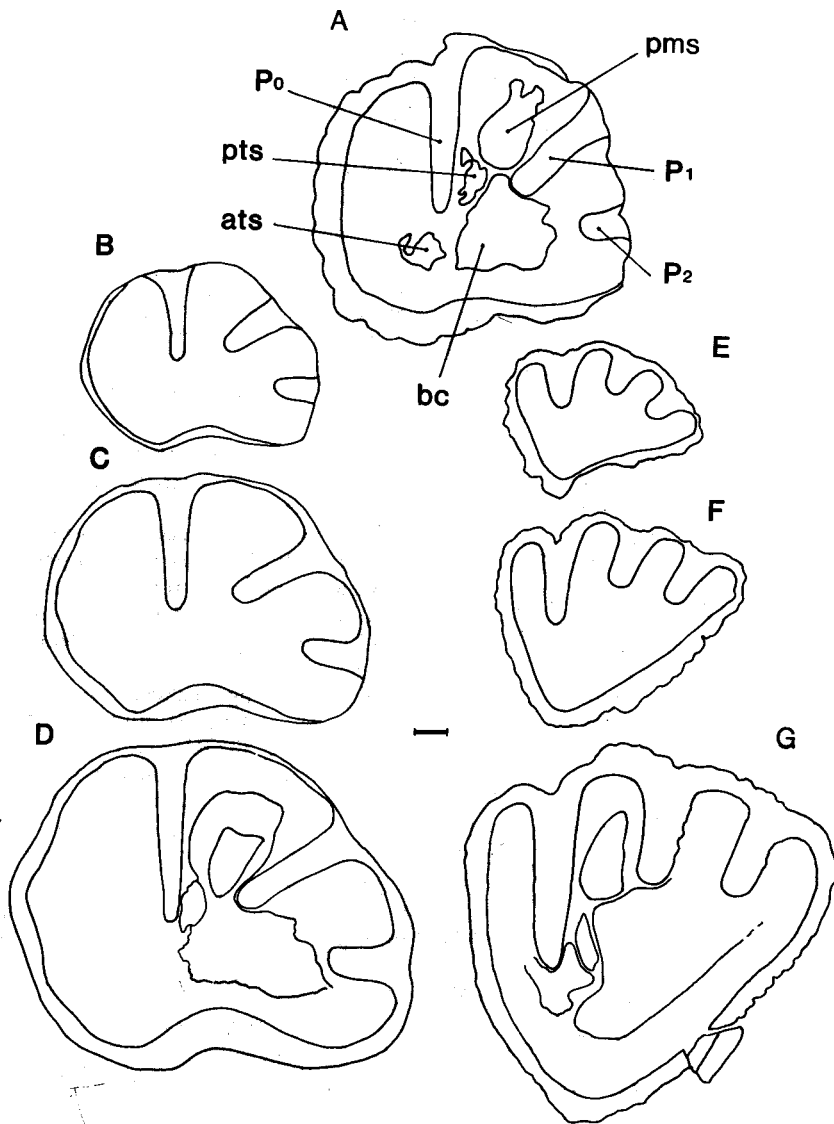
The dentition (Pl. 61, fig. 1), shows β to be about 25° . The narrow sockets for the LV teeth are separated by a pinched, wall-like RV tooth lying posteriorly to the inner tip of the *arête cardinale*. The latter has a rounded inner termination indicating complete absence of a ligament. The tooth-like posterior adductor myophore of the LV is situated dorsally behind the teeth, projecting down between P_1 and the *arête cardinale* (Pl. 62, fig. 2), where it is received in the RV by a large socket (Pl. 61, fig. 1; text-fig. 2A). The anterior adductor myophore of the LV forms an arcuate ledge extending some way around the anterior and ventral margins, where it faces on to a broad inclined shelf in the RV, supporting a distinctively reticulate muscle scar (Pl. 61, fig. 1; text-fig. 2A).

The body cavity is very shallow, and its volume further reduced by the large, downwardly projecting myocardial elements of the LV. Much of the apical 'limb' of the RV is filled by tabulae, though these are largely obscured by recrystallization.

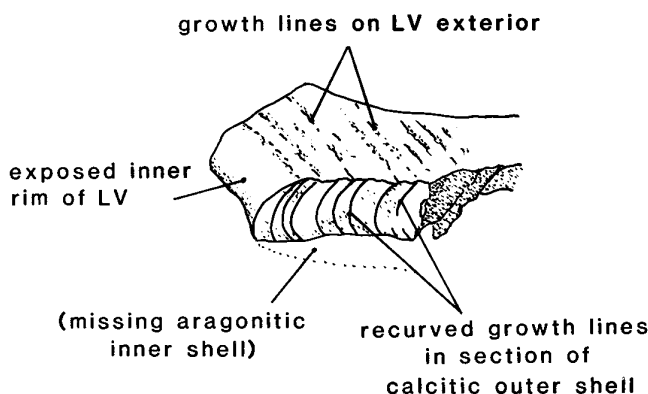
Palaeoecology. Though found close together, specimens BMNH LL 28000-28004 were recovered as loose blocks, and so their original life position remains uncertain. Evidence for attachment of one individual to another is shown by specimens LL 28001 and LL 28004 (Pl. 61, fig. 3). Otherwise they represent solitary individuals. The elongated and curved horn shape of specimens LL 28000, LL 28001, and LL 28002 suggests a reclining, boat-like habit, with the convex flank of the RV shallowly embedded in the sediment and the commissure raised up, away from it (text-fig. 8). The evidence of associated borings and epibionts lends some

TABLE 2. Measurements on specimens of *Torreites sanchezi sanchezi* (Douvillé) (1–12) from the Upper Campanian to Lower Maastrichtian of the Caribbean, '*T. cf. sanchezi*' (13) from the topmost Santonian to basal Campanian of Jamaica, and *T. s. milovanovici* Grubić (14) from the Maastrichtian of Sharjah (UAE), taken from the literature. The original species designations and references thereto (where locality details may be found) are recorded for each specimen cited. The abbreviations for the measurements are explained in text-fig. 2.

Specimen	Shell size (mm)			Hinge Angle (°)	Pillar Angle (°)	Pillar dimensions (mm)					
	L	D ₁	D ₂	β	α	1P ₀	1P ₁	1P ₂	wP ₀	wP ₁	wP ₂
<i>T. sanchezi</i>											
1. Douvillé (1927) (holotype)	—	83	>83	34	81	40	>32	>14	7	8	7
2. Palmer (1933), pl. 7, fig. 2	—	130	>120	—	126	90	20	52	7	11	6
3. Palmer (1933), pl. 8, fig. 2	—	124	120	50	105	70	49	27	6	8	8
4. Rutten (1936) (description)	—	—	—	20–30	—	—	—	—	—	—	—
5. Vermunt (1937), (description)	230	115	80	—	—	—	—	—	—	—	—
6. MacGillavry (1937)	—	'90–100'		—	'75–120'		—	—	—	—	—
7. MacGillavry (1937), exceptional specimen	—	—	—	—	50	—	—	—	—	—	—
8. Jung (1970), G.14065 on pl. 2	135	99	122	—	95	54	40	25	8	7	9
		75	98		102	39	33	>20	7	7	8
		>57	>72		94	27	>21	>13	5	7	7
		>40	>43		118	>16	>11	>9	4	4	5
9. Jung (1970), G.14066 on pl. 3	—	98	104	34	105	65	45	26	5	7	5
10. Van Dommelen (1971), J.3702a (table 5)	74	(50)		—	111	27	15	5	5	6	5
11. Van Dommelen (1971), J.3702b (table 5)	76	(90)		49	121	>30	26	14	7	9	7
12. Van Dommelen (1971), J.3676 (table 5)	>160	86	78	32	118	33	24	14	6	6	8
' <i>T. cf. sanchezi</i> '											
13. Chubb (1971)	—	>110	—	—	27	65	45	28	11	5	7
' <i>T. milovanovici</i> '											
14. Grubić (1979)	—	>130	100	—	12	>60	50	60	10	11	10



TEXT-FIG. 6. Drawings of sections across the RVs of *Torreites sanchezi* showing the ontogenetic divergence in pillar arrangement between the Caribbean (A-D) and the Arabian (E-G) subspecies. The drawings show the outlines of the outer shell layer, as well as some of the internal features in A, D, and G, and are all the same scale (scale bar = 1 cm). A is from the holotype (Douvillé 1927, pl. 4, fig. 1). Abbreviations are as in text-fig. 2A. B-D are from a specimen (G.14065) illustrated by Jung (1970, pl. 2, fig. 1*b*, *c*, and *d* respectively). E-G are from specimen BMNH LL 28004, illustrated here in Plate 61, figs. 3-1 respectively.



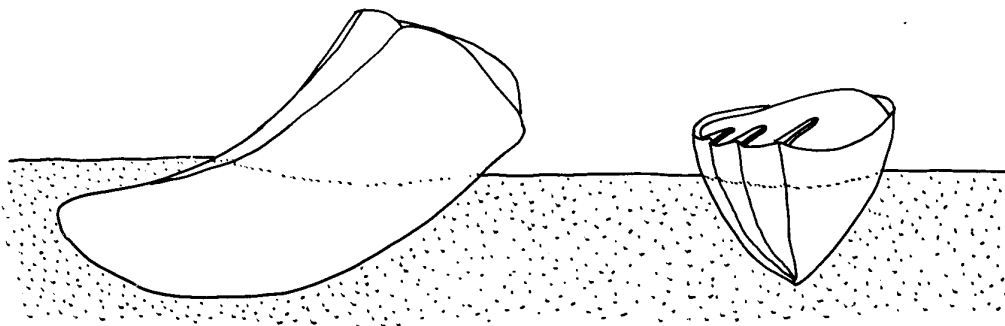
TEXT-FIG. 7. Explanatory drawing of the marginal fragment of LV outer shell layer of *Torreites sanchezi* (specimen BMNH LL 28003), shown in Plate 62, fig. 4. A radial section across the valve rim, adjacent to the inner tip of P_1 , is shown facing the observer.

support. In LL 28001 there is a slight preponderance of borings on the concave dorsal flank of the RV, where the fragment of another individual is also attached: the convex ventral flank would here seem likely to have been lowermost, and such a position is further substantiated by the orientation of some fine geopetal sediment inside the shell. LL 28002 is of similar shape, but has borings and rare encrusters scattered around all its flanks: possibly it suffered post-mortem displacement. However, it clearly shows xenomorphic overgrowth on to another rudist fragment high up on its convex ventral flank, again hinting at this surface having lain against the seafloor in life. In LL 28000 the anterodorsal face is convex and the posteroventral face is concave. A slight preponderance of borings on the latter face, as well as a couple of compactional indentations on to that surface hint at it having been uppermost.

LL 28003 and LL 28004 have more or less straight RVs, with borings scattered around all their flanks. These would seem to have lived in an essentially upright position (text-fig. 8). Burial in such a position is indicated in specimen LL 28003 by compaction along the central axis of the RV.

The matrix associated with these specimens is a pale yellow (weathered), medium-grained bioclastic packstone with subangular to subrounded bioclasts: it is presumably of shallow marine origin, as suggested by the grain-supported texture and rounding of the bioclasts.

Specimens PWS 84/x.1 and PWS 84/32.1 have obtusely conical RVs, and are likely to have been shallowly embedded, barrel-like elevators (text-fig. 8). Specimens of similar form were observed *in situ* at Qarn Murrah, Sharjah, with such an upright habit (text-fig. 9). Again, these are associated with medium-grained to fine-grained biomicrite packstones of presumed shallow marine origin.



TEXT-FIG. 8. Diagram showing the two kinds of life position apparently exhibited by *Torreites sanchezi milovanovici*—a reclining, boat-like habit (left) and an upright habit (right). Note that elevation of the commissure from the substratum (dotted ornament) is achieved in both cases. The difference between them probably only reflects variability in the orientations established during larval settlement and early growth.

TEXT-FIG. 9. Two RVs of *Torreites sanchezi milovanovici* shown in section in upright life position (cf. text-fig. 8, right), on the upper surface of a bedding plane of Maastrichtian limestone (Simsima Formation) at Qarn Murrah, Sharjah (UAE) (see text-fig. 1 and p. 506 for locality details). The lens cap is 5.5 cm across.



Discussion. The possibility of our specimens merely being Old World homeomorphs of *Torreites* can be immediately rejected: they share with the New World forms too many constructionally independent, specialized features for coincidental convergence to be plausible. The features in question comprise: (1) the smooth upper surface of the left valve; (2) the apically blind canals in the LV inner shell; (3) the unusual relative sizes and shapes of the RV pillars and *arête cardinale*, and their exposure through broad sinuses in the LV; and (4) the distinctive radially indented ornament of the RV outer shell.

Plots of the overall dimensions (text-fig. 3), and of the shapes (text-fig. 4), and relative positions of the pillars and the *arête cardinale* (text-fig. 5) of our specimens, drawn from Table 1, form compact, well-defined clusters; they clearly all belong to one species population. The fragmentary RV holotype of '*T. milovanovici* Grubić' represents a slightly larger individual than any of ours (see Table 2, specimen 14), but all its measured features plot comfortably as extrapolations from the cluster of data points for our specimens. In fact the obliquity of the section across the valve figured by Grubić (1979, pl. 1) is slightly misleading in making the pillars look more extended than they are. Our measurements are taken directly from the specimen itself, with allowances being made for this 'cut effect'.

All the Old World specimens, then, may satisfactorily be grouped in a single species. It is the relation of this to the New World species that is more problematical.

Prior to Grubić (1979) only two species of *Torreites* had been recognized, the type species *T. sanchezi* (Douvillé) and *T. tschoppi* MacGillavry. The latter is typically much smaller than the Old World form (rarely > 40 mm in commissural diameter), with simple costulate ribs about 1–2 mm wide, and is found in dense clusters of individuals, rather than in ones or twos (MacGillavry 1937, p. 129). Besides, it also appears to be older than the Old World specimens (see p. 506). It is thus clearly distinct from the Old World species. However, it approaches the latter in having a relatively low α , of about 45–70°, according to MacGillavry (1937).

Measurements reported for, or taken directly from the published figures of all described specimens referred to *T. sanchezi* are shown in Table 2, and are also plotted on text-figs. 3–5. Grubić (1979) erected two new species from among these, *T. coxi* and *T. chubbi*. The former was founded on two

specimens, the holotype being one of those described by Jung (1970) (specimen 9, Table 2). It has the same size, ornament, and basic pillar arrangements as in the other *T. sanchezi*, but was considered to differ in possessing a relatively longer and thinner *arête cardinale*, and pillars with slightly bulging inner tips. With such small samples available, these subtle distinctions do not carry conviction. The holotype simply lies at the edge of a rather broad cluster of points for *arête cardinale* shape in the New World *T. sanchezi* (text-fig. 4). Moreover, the swelling of the pillar tips shown in Jung's Plate 3 is only very slight. The species cannot be upheld and we here suppress it as a junior subjective synonym of *T. sanchezi*.

T. chubbi is based on a single poorly preserved specimen described as *T. cf. sanchezi* by Chubb (1971) (specimen 13, Table 2). Again, its independent status is dubious, though the specimen is intriguing in possessing a relatively low value of α (27° , rather than the 40° reported by Grubić). It is also older than the other specimens considered here (probably latest Santonian to earliest Campanian; see p. 506). Further material is needed to clarify its position, particularly in relation to the coeval *T. tschoppi*.

The final comparison left to be made, then, is with *T. sanchezi* itself. Plots of the shapes and relative positions of the pillars and *arête cardinale* (text-figs. 4 and 5) for all the specimens included here in the New World *T. sanchezi* (specimens 1–12 in Table 2) form coherent, if somewhat broadly spread clusters of data points, supporting their inclusion within one species population. Their commissural diameters (text-fig. 3) also plot together reasonably well, with the exception of the small specimen 10 on Table 2; the variation in shell length can readily be attributed to ecophenotypic variation in relation to life position (text-fig. 8).

The Old World specimens share with the New World *T. sanchezi* the same adult size range (text-fig. 3) as well as precisely the same distinctive external ornament: the broad radial ribs of the Old World specimens have widths varying from about 5 to 8 mm, exactly as in those of the New World specimens (e.g. Jung 1970, pl. 1, figs. 2 and 3). The one value of β from the Old World specimens (from BMNH LL 28004) is at the lower end of the range exhibited by those from the New World (compare Tables 1 and 2). Pillar form in the two populations (text-fig. 4) is closely similar in smaller (younger) individuals, though in the largest individuals P_1 tends to become relatively longer and more slender in the New World specimens. A similar trend in the *arête cardinale* (P_0) is even more pronounced. There is thus some slight ontogenetic divergence between the two populations from a more or less similar juvenile condition. This divergence may be linked constructionally with the rather more marked separation of the two populations on the basis of α values (text-fig. 5): those in the Old World specimens are notably smaller than those of the others. Again, there appears to have been ontogenetic divergence, involving reduction in α throughout growth in the Old World forms, but with little change in the New World forms. Yet the existence of some specimens among the New World population with low values of α (e.g. specimen 7 on Table 2, cited by MacGillavry 1937, p. 129) gives support for close linkage between the two populations.

Although these few differences between the adults of the Old and New World populations are sufficient to render each distinctly recognizable, it is the close similarity of the two populations in all other respects that is the more striking. Given the small samples involved and our relative ignorance of many aspects of rudist functional morphology, it is really a matter of subjective judgement as to whether the Old World population should still be recognized as a distinct species ('*T. milovanovici*'), or whether it should be treated, as we propose here, as a geographical subspecies of *T. sanchezi*, which we label *T. s. milovanovici* Grubić, 1979, in contrast with the New World stock of *T. s. sanchezi* (Douvillé, 1927), in which we include all the New World records of *T. sanchezi* recognized here. We favour this latter option because of the existence of exceptional specimens in the New World with α values close to those of specimens from the Old World. These suggest that the one significant diagnostic feature of the Old World population may already have existed within the range of morphological variability of the New World population.

The paradox of the extraordinarily wide geographical separation of the two subspecies will be considered in a later section (p. 522).

PALAEOBIOLOGY AND EVOLUTIONARY RELATIONSHIPS OF *TORREITES*

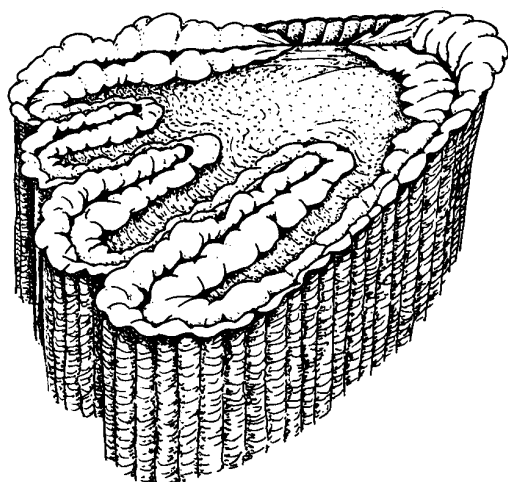
Torreites is rare in the Caribbean Province; Grubić (1979, p. 94) noted that the then published record of the genus was founded on only about twenty specimens (which have nevertheless fuelled at least nine systematic papers alone!). Our material, as well as expanding the recorded total of specimens by at least a third, is also significant for its good state of preservation. Placement of the genus in the Hippuritidae can be confirmed, while the reason for its aberrant lack of pores in the LV can now be explained from investigation of the growth lines in that valve.

Though generally considered a hippuritid because of its pillars (Douvillé, 1927), *Torreites* differs from all other hippuritids in its lack of pores. Van Dommelen (1971, p. 65) commented: 'In reality, however, all we know about the VS [= LV] of *Torreites* is, that the outer shell layer is imperforate in the parts between L, S and E [= P₀, P₁ and P₂]. But what about the slit-like openings over these infoldings of the available eroded specimens? Have they been covered or not covered, and if covered, was this cover a reticulum or something different?' MacGillavry (1937, p. 128) too, queried whether or not the pillars really had been exposed through open sinuses in the LV. It is unambiguously clear from our specimens (e.g. Pl. 61, fig. 5 and Pl. 62, figs. 1, 3, 4) both that, no roof of any kind existed over the crests of the *arête cardinale* and the pillars, and that the LV outer shell layer is indeed imperforate. Is *Torreites* thus a hippuritid that has lost its pores, or one descended from a primitive form that never had them, or not a hippuritid at all? The latter option is the least likely. Not only does *Torreites* possess the pillars so characteristic of the family, albeit of unusual form, it also has a typically hippuritid myocardial apparatus with its markedly tooth-like posterior myophore in the LV, received in a socket in the RV. Its overall shell form, with an elongate-conical RV and operculiform LV, is also typical of, though not exclusive to the family.

If *Torreites* is accepted as a hippuritid, the lack of pores is unlikely to be a primitive trait. Pores are already well established in the earliest hippuritids, which predate the oldest *Torreites* by about two stages. *Torreites* is further characterized by such specializations as the extreme elongation of the *arête cardinale*, despite loss of the ligament itself, and the blind canals in the LV interior.

Two features in our specimens together suggest that the lack of pores is secondary: (1) the thinness of the outer shell layer in the LV relative to that in the RV, with the margin of the latter projecting well beyond that of the former (Pl. 62, fig. 3); and (2) the recurvature of the growth lines in the outer shell layer of the LV on to its outer surface (Pl. 62, fig. 4; text-fig. 7), indicating that mantle tissue reached out on to at least the peripheral parts of the outer surface of the valve. Mantle tissue would thus have been freely exposed both around the inner margin of the RV and around the periphery, if not more, of the outer surface of the LV. In normal hippuritids, no mantle tissue was directly exposed in this manner. Rather, extensions of it lined the pore and canal system in the LV outer shell layer, where its cilia are interpreted as having driven water currents, drawn from above the shell, over the covered inner rim of the RV, enabling the entrapment there of food particles, without the need of valve gaping (Skelton 1976). The free exposure of mantle tissue in *Torreites* would have made redundant the canal and pore system of its ancestors. Its atrophy would then have been hastened by the lowering and retreat of the LV outer shell layer to allow maximum exposure of the RV inner rim. A reconstruction of *Torreites* in life, with its corona of exposed mantle tissue is shown in text-fig. 10.

What was the adaptive significance of this exposure of mantle tissue? One possibility is that the externalization of food entrapment (Skelton 1976) was taken a stage further than in the ancestral hippuritids, with direct trapping of food particles on the exposed mantle projections, as has been proposed for radiolitids (Skelton 1979a). But such a trivial modification of function seems an unsatisfactory explanation for so considerable a morphological change; it is hard to conceive of any obvious benefit to feeding efficiency that might have been won thereby, and the increased exposure would seem in any case to have carried an increased risk of physical or biological damage to the mantle rims. One significant effect of the exposure, however, would have been the emergence of mantle tissue from the darkened confines of the ancestral pore/canal and covered rim system, into the light. This immediately calls to mind the possibility of symbiotic zooxanthellae, by analogy



TEXT-FIG. 10. Reconstruction of the appearance in life of *Torreites sanchezi milovanovici*. The upper part of the shell is shown, with thick extensions of mantle margin projecting out between the valve rims, in the manner of the living Giant Clam, *Tridacna*. It may be surmised that, as in the latter, these mantle extensions were vividly and variably coloured.

with the Giant Clam, *Tridacna*. The possibility of algal symbiosis in rudists has frequently been raised in the literature (e.g. Kühn 1937; Philip 1972; Coates 1973; Kauffman and Sohl 1974; Vogel 1975; and Skelton 1979a) and has recently been ably reviewed by Cowen (1983). The consensus of most of these works is that such symbiosis was widespread in the group—a conclusion supported by Cowen himself. Skelton (1979a), in contrast, argued that positive evidence for possession of zooxanthellate tissue, in the form of clear adaptation of the shell to allow maximum exposure of mantle tissue to the light, is only seen in certain broad-rimmed radiolitid genera. Their symbiosis is considered to have arisen as a secondary adaptation of the enlarged mantle margins associated originally with food particle entrapment. The layout of the pore and canal system in normal hippuritids, in particular, was well suited for supplying the RV mantle rim with feeding currents, and is most satisfactorily explained thus. Cowen nevertheless felt that the tissue within the canal and pore system could have been exposed to light through the shelly cover over the radiating canals. Yet in some hippuritids this cover is actually quite thick (often over 3 mm), and, moreover, the canals show no tendency to flatten out in such a way as to maximize exposure to light. Many hippuritids seem, in any case, to have lived in somewhat turbid, poorly lit waters (Skelton 1979b). It thus remains unlikely that any of the normal hippuritids, at least, possessed zooxanthellae. With *Torreites*, however, we may have an exception; its clear morphological adaptation for free exposure of mantle tissue suggests a hippuritid 'redesigned' as a photophile. The scarce palaeoecological information on *Torreites*—implying a basically upward growth form and occupation of shallow, clear waters—is consistent with the algal symbiosis hypothesis.

SIGNIFICANCE OF THE PRESENCE OF *T. SANCHEZI* IN OMAN AND THE UAE

Torreites is not alone among Campanian–Maastrichtian shallow marine benthos in showing disjunct endemism between the Caribbean Province of Kauffman (1973) and various sites in the eastern part of the Tethyan Realm, ranging from the Middle East to the East Indies. Chubb (1956), recognized such a distribution in the radiolitid rudist genus, *Thyrastylon*, remarking (p. 39): 'It is indeed interesting that in the same epoch, the Maastrichtian [*sic*], a form closely resembling *T. coryi* [a Caribbean species] was living in Persian seas, so that the geographic range of *Thyrastylon* extended from Guatemala to Persia, a distance of nearly 10,000 miles.' Kollmann and Sohl (1980) stated that the itieriid gastropod, *Vernedia friesi* Kollmann and Sohl, from the Upper Cenomanian or Lower Turonian of Colima Province, Mexico, had a closer affinity with a southern Indian form, *V.*

globoides (Stoliczka), from the Campanian to Maastrichtian Arrialeor Group of the Trichinopoly District, than with the European and Transcaucasian species of the genus. Another gastropod, *Actaeonella borneensis* Nuttall and Leong, is known both from an uncertain Cenomanian to Campanian level in Borneo and from Campanian to Maastrichtian strata in Mexico and Cuba (Sohl and Kollmann 1985). The codiacean alga *Ovulites* occurs in the Upper Cretaceous of the Caribbean and in northern Iraq, Afghanistan, and Tibet, though not from the Mediterranean Tethys (Elliott 1981). These are but a few examples that complement the clear-cut case of *Torreites* to establish this form of disjunct endemism as a palaeobiogeographical problem in need of a solution.

There are three possible explanations for such a highly disjunct distribution of shallow-water benthic taxa: (1) false synonymy of coeval homeomorphs; (2) plate tectonic drifting apart of formerly united shallow-water provinces; and (3) temporary range extension between the two regions brought about by the development of a continuous intervening chain of shallow-water 'staging posts' for planktonic larval dispersal.

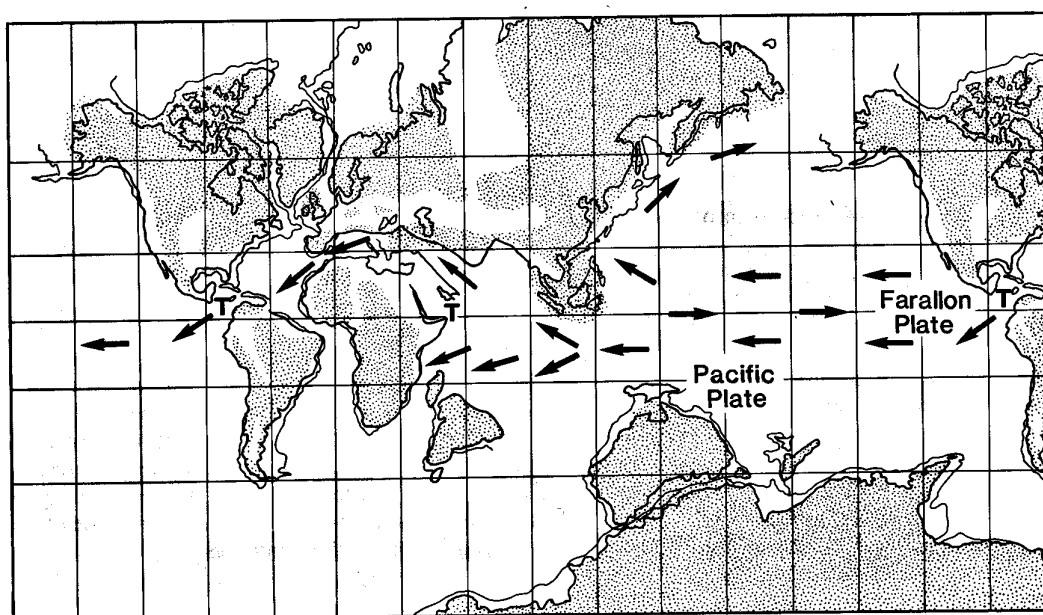
The first option, of coeval evolution of not one, but several pairs of homeomorphs in the two regions, over the same limited time interval, is in itself improbable, and becomes yet more so with every new example of the disjunct distribution that is added to the list. The importance of *Torreites* is that its several constructionally independent diagnostic features allow us expressly to reject homeomorphy as a reasonable hypothesis in its case; any argument for homeomorphy in the other examples cited must now be relegated to special pleading for particular examples.

The second explanation, based on drifting apart of the two regions was evidently that favoured by Grubić (1979, p. 94), who concluded: 'The presence of a specific Caribbean Upper Cretaceous rudist from in the eastern Mediterranean can by no means be interpreted other than by assuming that both Americas, Antilles and the Mediterranean were much closer in the Upper Cretaceous.' Such an explanation would be reasonable if there were matching geotectonic evidence. However, there is none for Oman having been anywhere near the Caribbean in Late Cretaceous times. The strata containing *Torreites* in Oman and the UAE represent the first marine autochthonous deposits upon the Semail Nappe, itself already obducted on to the Arabian foreland (see Glennie 1977 and Murris 1980 for details). So the area in question was then, as it is today, firmly part of the Arabian continent. Likewise, the Caribbean sites with *Torreites* (Cuba, Jamaica, and Puerto Rico) were unambiguously associated with the central American region in the Late Cretaceous (Mattson and Lewis 1980).

We are then left with the third possibility, of planktonic larval dispersal along a chain of staging posts. In the absence of recorded fossils of rudist prodissococonchs, the character of rudist larvae can only be surmised from circumstantial evidence. The geologically almost simultaneous appearance in the Late Turonian of the primitive hippuritid species, *Hippurites resectus* Defrance in Europe and North Africa (Douville 1890–1897, 1910) and of the almost certainly synonymous '*H. mexicanus* Barcena' in Mexico (Muellerried 1930), for example, favours a readily dispersed planktonic larval stage (incidentally, this is against the notion of a larval brood pouch speculated upon by Skelton (1976)). So it is not unreasonable to suppose that such a larval stage existed in *Torreites*.

The two possible oceanic routes for dispersal between the Old and New World sites of *Torreites* are: (1) via the Mediterranean Tethys and Atlantic; and (2) across the Pacific and eastern Tethys (text-fig. 11).

The Mediterranean/Atlantic route is considered unlikely for two reasons. First, the bivalve endemism data of Kauffman (1973) suggest that the 'north Indian Ocean sub-province' (incorporating Oman and the UAE) and neighbouring 'eastern Mediterranean sub-province' became significantly distinct from the 'western Mediterranean sub-province' in Campanian–Maastrichtian times, implying the presence between them of barriers to dispersal. In a recent study of Campanian/Maastrichtian rudist distributions in the Mediterranean region, Philip (1985) similarly establishes a clear distinction between an 'Aquitano-Pyrenean palaeobiogeographic unit' and an 'eastern and central Mediterranean' one, with continental barriers lying between them. A few central Mediterranean forms are preserved in southern Spain, however, presumably derived via a North African



TEXT-FIG. 11. Inferred Campanian-Maastrichtian palaeogeography of the World, showing oceanic surface currents (arrows). The Americas are duplicated at each end of the map to allow direct comparison between the Mediterranean Tethys/Atlantic and Pacific marine connections between the two sites from which *Torreites* has been recovered (indicated by T). It is argued in the text that a chain of shallow staging posts, spread across the Pacific and eastern Tethys, was the most likely means by which the range of *Torreites* was extended, by larval dispersal, from the Caribbean, across to the Arabian region. Continental positions derived from Smith and Briden (1977), land (dotted ornament) and sea (white) distributions from Zeigler *et al.* (1983), and ocean currents from various sources cited in the text.

route (Philip 1983). In any case, there are no records, as yet, either of *Torreites* or *Thyrastylon*—both very distinctive fossils—anywhere in the Mediterranean region.

The second objection to the Mediterranean/Atlantic route is the increasingly impassable width of the Atlantic in Campanian-Maastrichtian times, as reflected in the rising generic dissimilarity between its two sides with respect to bivalves (Kauffman 1973) and, in particular, to rudists (Coates 1973).

The alternative explanation is that *Torreites*, *Thyrastylon*, and the other disjunct endemics discussed earlier were somehow able to cross the Late Cretaceous Pacific Ocean. In which direction might such dispersal have taken place? Many authors have argued for a circum-global East to West equatorial current during the Cretaceous, passing through Tethys, and across the Pacific Ocean (text-fig. 11; Luyendyk *et al.* 1972; Gordon 1973; Berggren and Hollister 1974, 1977; and Lloyd 1982). The Tethyan Realm was thus extended for several thousand kilometres into the eastern Pacific (Gordon 1973) and many Pacific seamounts have now been found to have been capped by rudist-bearing atolls in Aptian to Cenomanian times (recently reviewed, with references therein, by Winterer and Metzler 1984 and Konishi 1985). From mid-Aptian times onwards, the opening Atlantic promoted the growth of endemism in the Caribbean, with respect to the rest of Tethys (Coates 1973; Skelton 1982), to provincial levels by Late Santonian times (Kauffman 1973). This suggests that the Late Cretaceous *Torreites* is most likely to have originated in the Caribbean, and then dispersed westwards towards eastern Tethys (text-fig. 11). Such a model is consistent with MacGillivray's (1937) identification of the older Caribbean species *T. tschoppi* as an ancestral form.

Evidence for staging posts that would have facilitated the trans-Pacific dispersal of *Torreites* and other forms is now well documented from DSDP work. Beckmann (1976), for example, has described redeposited Campanian–Maastrichtian shallow-water foraminifera from the Line Islands seamount chain. Two of the genera, *Asterorbis* and *Sulcoperculina*, had previously only been recorded from the Caribbean and surrounding areas. A third, typical Caribbean form, *Pseudorbitoides israelskyi* Vaughan and Cole, was also known from eastern Tethyan sites (details in Dille 1973). Other findings, reviewed by Schlanger *et al.* (1981), have extended the evidence for such staging posts as far across the ocean as the Nauru Basin (Marshall Islands). These records indicate that the Pacific Plate was studded with islands and/or seamounts which served as stepping stones for some Caribbean shallow-water benthos in Campanian–Maastrichtian times. Evidence that the Farallon Plate, which at that time separated the Pacific Plate from the Americas by some 6000 km, was similarly endowed was also provided by Schlanger *et al.* (1981). This survives in the form of ophiolite complexes with exotic limestones, plastered on to the western flanks of the Americas during subduction of the plate.

There is thus direct evidence for former staging posts, carrying a Caribbean-derived shallow marine benthic fauna of Campanian–Maastrichtian age, for over half the distance between the Caribbean and Oman. Documentation of suitable staging posts along the remaining (eastern Tethyan) part of the route is very much more difficult, because the available evidence is now caught up in the various Tethyan suture zones running from the East Indies to the Middle East (Audley-Charles *et al.*, 1980). It seems, however, that some shallow or even emergent physiographical prominences, such as island arcs and small continental blocks may then still have lain in the oceanic gap between India and Eurasia, although most of these had already been accreted on to Eurasia by mid-Cretaceous times (Tapponnier *et al.* 1981). Moreover, Maastrichtian orbitoid and rudist-bearing facies are known from the southern edge of the Lhasa Block, in Tibet (Herm *et al.* 1985 and pers. comm.), which was by then accreted on to the southern flank of Eurasia.

From the evidence given above, it is therefore not unreasonable to postulate that *Torreites* spread from the Caribbean to Oman, exploiting a continuous chain of shallow-water staging posts that stretched across the Pacific and eastern Tethys during Campanian–Maastrichtian times.

As a test for this hypothesis, we predict that *Torreites*, or other forms with the same disjunct distribution, such as *Thyrastylon*, will eventually be recovered either from DSDP material from the Pacific, or from shallow-water Tethyan carbonates of Campanian–Maastrichtian age caught up in Himalayan and other eastern Tethyan suture zones. Conversely, the discovery of such faunal elements in the western Mediterranean (e.g. north-western Africa or southern Spain) would militate against our hypothesis.

Two palaeobiogeographical corollaries to this model are worth noting. First, the repeated population-sampling effect that would have accompanied the successive westward dispersals of spat from staging post to staging post ought, surely, to have resulted in a pronounced ‘founder’ effect in the population that eventually became established in Oman and the UAE (see Mayr 1970, for explanation of the founder principle). It is thus remarkable that the only significant modal deviation of the Old World population from the Caribbean population is in the ontogenetic reduction of α (p. 520), which, in our view, only merits distinction at the subspecific level.

Our model for the historical biogeography of *Torreites* and its ‘fellow travellers’ also bears on the current debate about the relative roles of vicariance and dispersal in explanations for the geographical distributions of taxa (concisely reviewed by Forey 1981). In identifying the Caribbean as the centre of origin for *Torreites*, and treating its appearance in eastern Tethys as a result of dispersal along staging posts between the two areas, we have clearly adopted a ‘dispersalist’ explanation for the disjunct distribution of the genus. In our view the appearance of the staging posts caused the decline of the Pacific Ocean as a barrier to dispersal of Caribbean shallow-water benthos during the Campanian–Maastrichtian. The Pacific, then, became a ‘filter’ for biogeographical range expansion (Simpson 1962) at that time, because selected taxa appear to have made the full crossing. Forey’s (1981) characterization of such accounts as emphasizing processes supposed from *ad hoc* considerations to have brought about distributional patterns, and as lacking in any general principles

of pattern analysis—an advantage reserved for vicariance studies—is a misleading criticism, suggesting, as it does, that the accounts are difficult, if not impossible, to test. The hypothesis of the appearance of a trans-Pacific filter for the westward dispersal of Caribbean shallow marine benthos in the Late Cretaceous, could readily be tested by an analysis of fossil distributions. If our model is correct, then among the taxa showing apparent disjunct endemism on either side of the Pacific there should be an overwhelming preponderance of stratigraphically older records, for each of the taxa considered, on the Caribbean side. The test should be workable, because the purported sequence of events was spread over a 'geological' time scale of millions of years, and so ought to have left a realistically detectable imprint on the fossil record. In the case of *Torreites*, for example, there is a generous stratigraphical spread between (1) the first record of *Torreites* in the Santonian or earliest Campanian, (2) the establishment of the full chain of staging posts in the Campanian–Maastrichtian, and (3) the first record of *Torreites* in the Old World (Early Maastrichtian). It should be noted, however, that what is being discussed here is a biogeographical range expansion provoked by changes in the geological context for dispersal. The process of larval dispersal itself is admittedly beyond geological analysis, because such events on the 'ecological' time scale would be, to all intents and purposes, geologically instantaneous.

Since we are dealing with the effect on the distribution of taxa of the disappearance of a former barrier (the Pacific Ocean prior to the completion of the chain of staging posts), we could not, indeed, employ any vicariance method of analysis, simply because these are all irrelevant to such a phenomenon. As Forey (1981) makes clear, the aim of vicariance analysis is to unravel the history of progressive fragmentation of an already widespread ancestral biota. Were we investigating, say, the partitioning of the Tethyan Realm in the Late Cretaceous as a result of the *appearance* of barriers, then some form of vicariance analysis might be both appropriate and effective. Our point, then, is that barriers come and go on a geological time scale, and so the two methods of analysis both have roles to play in palaeobiogeography: vicariance analysis where developing barriers fragmented an ancestral biota; and 'dispersal' analysis where the demise of barriers has allowed range extensions to take place. Both methods, we believe, can yield hypotheses about historical biogeography that can be further tested from fossil distributions.

SUMMARY OF CONCLUSIONS

Systematics. The hippuritid rudist bivalve species, *T. sanchezi* (Douvillé, 1927), is here considered to comprise two geographical subspecies. The nominotypical subspecies, *T. s. sanchezi* (Douvillé) is known from the Upper Campanian to Lower Maastrichtian of the Caribbean Province of Kauffman (1973), and is considered, by subjective synonymy, to include *T. coxi* Grubić, 1979, as well as the other unquestionable records of *T. sanchezi* in the faunal province. An Arabian subspecies, *T. s. milovanovici* Grubić, 1979, is recognized from new specimens collected by ourselves from the Maastrichtian of eastern central Oman and the United Arab Emirates together with the single specimen from Sharjah Emirate, which constitutes the holotype for the former '*T. milovanovici* Grubić'. The only essential morphological difference between the two subspecies is in the angle (α) between the *arête cardinale* and the ventralmost pillar in adult shells: that in *T. s. sanchezi* ranges from 50 to 126°, while, in *T. s. milovanovici*, this angle is from 12 to 75°.

Palaeobiology. The extension of the inner margin of the RV beyond that of the LV and the recurvature of the shell growth laminations in the LV on to its smooth upper surface, in *Torreites*, indicates that marginal mantle tissue was freely exposed in life (text-fig. 10). It is considered likely that the mantle tissue, thus exposed, contained symbiotic zooxanthellae, as in the living Giant Clam, *Tridacna*. The externalization of the mantle tissue accounts for the atrophy of the (redundant) canal and pore system in the LV, diagnostic of other hippuritids. The upward growth tendency, and preference for shallow, well-lit marine settings, of *Torreites*, as indicated by sedimentological data, are consistent with the zooxanthellate hypothesis.

Palaeobiogeography. Three possible explanations for the apparent disjunct endemism of *Torreites* (along with certain other shallow marine benthic taxa) in the Caribbean and in Oman and the UAE are considered: (1) homeomorphy is rejected due to the negligible probability of several distinctive and constructionally independent diagnostic features arising in two coeval populations; (2) the plate tectonic drifting apart of originally neighbouring areas (as favoured by Grubić 1979) is rejected since all the available geotectonic evidence is against any possibility of the two regions having been conjoined in the Late Cretaceous; and (3) an episode of range extension between the regions, brought about by larval drift along a continuous but temporary chain of staging posts between them, is favoured by us. Of the two possible routes thus implicated, we prefer the trans-Pacific option to that via the Mediterranean Tethys and across the Atlantic. First, palaeobiogeographical data from the Mediterranean suggest that significant barriers to dispersal existed there by Campanian/Maastrichtian times (Kauffman 1973; Philip 1985). Secondly, the Atlantic is also known to have become a major barrier by this time (Kauffman 1973). In contrast, the equatorial Pacific Ocean floor is known to have been studded with shallow seamounts and islands, stocked by shallow marine benthos derived from the Caribbean, at this time (Schlanger *et al.* 1981). These, combined with the shores and/or other shallow marine promontories of eastern Tethys could have served as staging posts for the trans-Pacific dispersal of *Torreites* and the other taxa sharing its strikingly disjunct distribution.

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