The Late Eocene – Recent *Bradleya johnsoni* Benson lineage (Crustacea, Ostracoda) in the Central Equatorial Pacific

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ABSTRACT – Three stratigraphically successive species of *Bradleya* Hornibrook, 1952 from abyssal sediments of the central equatorial Pacific (Leg 85, Deep Sea Drilling Project) form an unbranching evolutionary sequence designated as the *B. johnsoni* Benson lineage. These taxa are *B.* sp. 1 (Lower Oligocene), *B. johnsoni* (Upper Oligocene – Middle Miocene) and *B. thomasi* n. sp. (Upper Miocene – Recent). A shared synapomorphic character, the posterior bridge complex, establishes the kinship of these species. Their stratigraphic ranges and a traceable series of changes in the organisation and mass of the reticulum are consistent with the hypothesis of direct ancestor/descendant relationships between them. *Bradleya johnsoni* is distinguished from *B.* sp. 1 by the appearance of new primary muri in the posteroventral region and by a general increase in reticular mass. In *B. thomasi*, the overall reticular pattern is maintained but it becomes more delicate and less rectilinear. Each species of this lineage shows similar variation in the posteroventral reticulum.

INTRODUCTION

Most of the approximately 35 described species of the trachyleberidid ostracode *Bradleya* Hornibrook, 1952 are strongly reticulate. Secondarily smooth carapaces have evolved in a few species through celation or mural loss (Benson, 1972, 1982; Whatley *et al.*, 1984). The exoskeletal framework of *Bradleya* includes primary features, such as the bridge complex and ventro-lateral and dorsal carinae (see Benson, 1972, fig. 9) and a latticework of raised muri. The pattern of the reticular grid and the relative prominence of its components have been emphasised by taxonomists in the differentiation of species – level taxa. Each fossa in the reticular grid is the surface expression of a secretory cell in the underlying, carapace-forming epidermis (Okada, 1981, 1982). This one-to-one relationship allows the paleontologist to monitor evolution on the histological level by tracing the number and alignment of fossae over time (e.g. Benson, 1972, 1977a, 1982, 1983).

An undescribed species from the Paleocene of Chatham Island, New Zealand is the oldest taxon which can be assigned with confidence to *Bradleya* (Benson, 1972, pl. 1, fig. 9). Of shallow-water origin, it possesses a small, subquadrate carapace and a massively calcified reticulum. Similar morphologic attributes are also found in a diverse group of Cenozoic shelf species endemic to Australasian waters (see Benson, 1972, 1982; Whatley *et al.*, 1984).

Bathyal species first occur in the Early Eocene of the s.w. Pacific (Whatley, 1983, 1985; Whatley *et al.*, 1984). Migration into the abyssal realm occurred between 40 and 38 Ma as but one component of a major downslope colonisation of the sea-floor by shallow-water ostracode groups (Benson, Chapman and Deck, 1984, 1985). This event most likely took place in the s.w. Pacific, the site of the origin and initial radiation of *Bradleya* (Whatley, 1983, 1985). Once established on the sea-bed, the trans-Pacific dispersal of *Bradleya* was accomplished rapidly. The oldest known form outside the Indopacific is *B. "dictyon"* of van den Bold (1986) recovered from Upper Eocene sediments of bathyal origin (planktonic foraminiferal zones P16–P17), Chapopote Fm., Tampico Embayment, Mexico. The existence of this population on the eastern rim of the Pacific implies that bradleyids were also present in the study area at this time. Unfortunately, ostracodes are absent from sediments of equivalent age in the Leg 85 cores. By Oligocene time, bathyal and abyssal species of *Bradleya* were widely distributed in the World Ocean (Benson, 1977b; Benson and Peypouquet, 1983; Steineck *et al.*, 1984, 1988; Ducasse and Peupouquet, 1986). Such forms are typically blind, cosmopolitan in distribution and larger and more delicately ornamented than their shallow-water counterparts.

This report summarises the morphology and stratigraphic distribution of *Bradleya* in Oligocene to Recent abyssal sediments of the central equatorial Pacific. It is based on the analysis of more than 500 samples from the core inventory of Leg 85 of the Deep Sea Drilling Project (see Fig. 1; Mayer, Theyer, *et al.*, 1985). Three temporally successive and non-overlapping species have been recognised and placed into an evolutionary
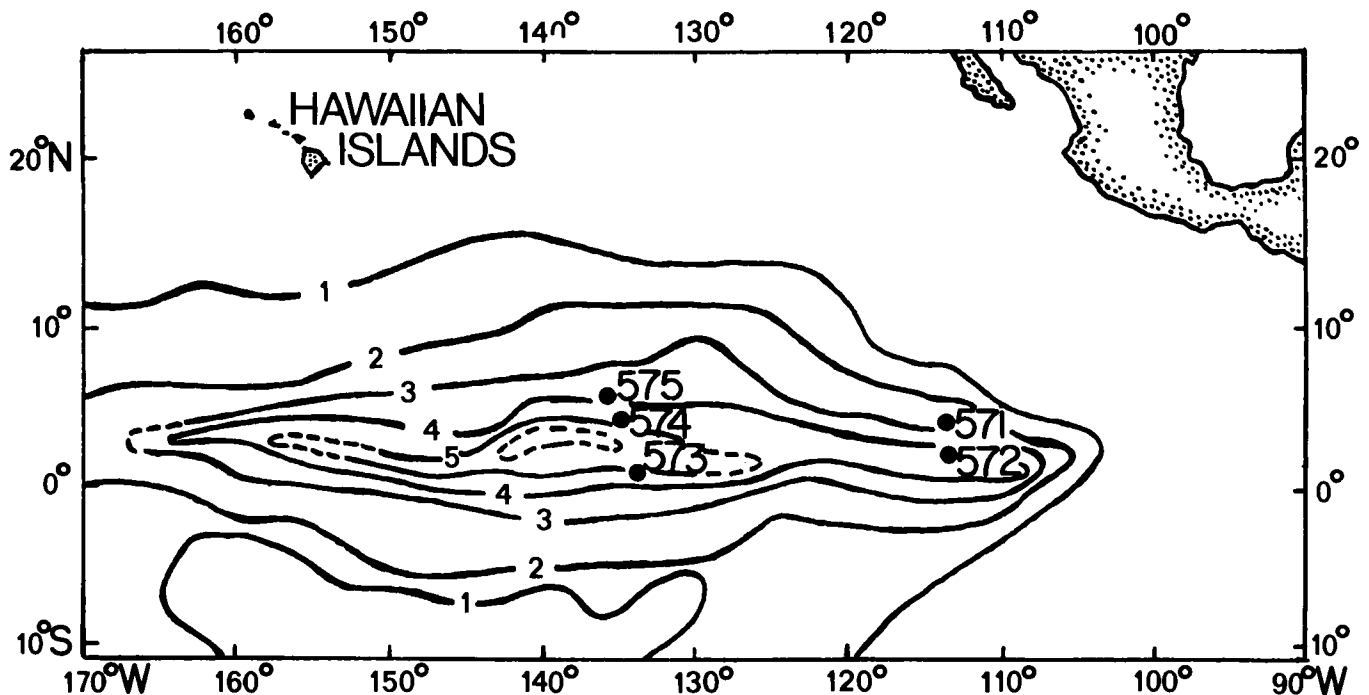
Fig. 1. Location map, sites 571 through 575, Leg 85, DSDP. Depth contours in km. Location and present depth of sites as follows: 575, 5°51'N, 135°02.16'W, 4536 m; 574, 4°12.52'N, 133°18.57'W, 4555 m; 573, 0°29.92'N, 133 18.57'W, 4039 m; 572, 1°26.09'N, 113°50.52'W, 3839 m. Site 571 not sampled for ostracodes. From Fig. 1 of Theyer, Mayer & Thomas (1985).

sequence here designed as the *Bradleya johnsoni* Benson lineage. A review of previously published work and re-examination of specimens from Jamaica and Barbados revealed that these taxa occur in the Atlantic and Caribbean provinces. Access between these regions and the Pacific was provided by a deep oceanic corridor in the region of the present day Isthmus of Panama which remained an important pathway for microfaunal interchange until the Upper Miocene (Keller & Barron, 1983).

THE *BRADLEYA JOHNSONI* BENSON LINEAGE: OVERVIEW

In the post-Eocene sediments of the central equatorial Pacific, three species of *Bradleya* replace each other over time, namely *B.* sp. 1 (Lower Oligocene), *B. johnsoni* (Upper Oligocene Middle Miocene) and *B. thomasi* n.sp. (Upper Miocene – Recent) (Fig. 2). These taxa possess a unique morphologic feature, the posterior bridge complex (PBC-Fig. 3) which is not found in other known species of *Bradleya*. We interpret this character as a synapomorphic (derived, homologous) trait establishing the kinship of these species. An explicit hypothesis of the ancestor/descendant relationships of these taxa is based on: 1) their stratigraphic succession without overlap; and 2) a traceable series of changes manifest in the organisation and mass of the reticulum (Fig. 4). Thus, chronistic and phenetic data from the Pacific suggest that the sequential appearance of *B.* sp. 1, *B. johnsoni* and *B. thomasi* is the product of anagenetic speciation within a clade designated the *B. johnsoni* lineage.

This lineage is distinguished by the following morphologic characters: 1) the PBC centred over the muscle-scar node; 2) two horizontal muri connecting the PBC to the ocular ridge; and 3) the basic arrangement of muri and fossae in the posteroventral quadrant. This arrangement consists of an arcuate column of 4 (*B.* sp. 1) or 8 (*B. johnsoni*, *B. thomasi*) fossae between muri 1 and 2 (see Fig. 4), bordered posteriorly by two groups of fossae, a dorsal triplet (EE' E" of Fig. 4) and a box-like ventral cluster of four (FGHI of Fig. 4). The evolution of *B. johnsoni* was marked by longitudinal cell division in the region between muri 1 and 2 to form the couplets A' A, B' B etc. (compare Fig. 4 a, b with 4 c, d) and by a general increase in the mass of the reticulum. In contrast, the emergence of *B. thomasi* did not entail discrete changes in the reticular matrix. Instead, within a basic reticular pattern duplicating that of *B. johnsoni*, the sculptural relief diminished and the grid of intersecting muri became less rectilinear.

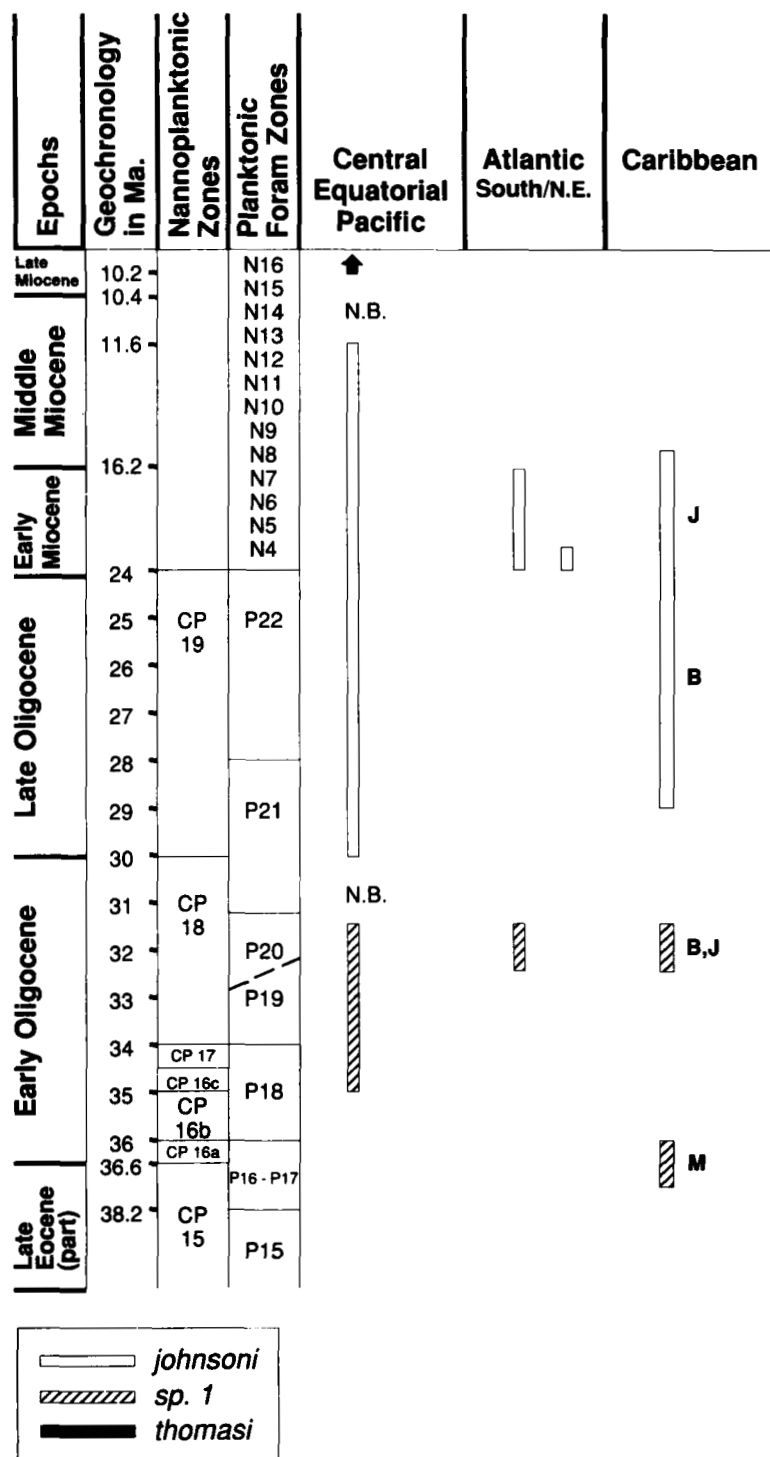Within the fundamentally conservative and predictable posteroventral reticular matrix typifying each

Fig. 2. Known biostratigraphic and geographic occurrences of species in the *Bradleya johnsoni* Benson lineage. Note change in chronometric scale at Oligocene-Miocene boundary. Zonal assignments for equatorial Pacific (Leg 85) taken from Saito (1985) and Barron *et al*, (1985). Nannoplankton zones of Okada & Bukry (1980) correlated to planktonic foraminiferal zones according to Miller *et al.* (1985) & Berggren *et al.* (1985). Geochronology after Berggren *et al.* (1985); see Haq, Hardenbol & Vail (1987) for an alternate geochronologic calibration. N.B. = no bradleyids. South Atlantic data from Benson (1977b) and Benson & Peypouquet (1983). Caribbean records: B, Oceanic Fm., Barbados (Steineck *et al.*, 1984); J, Montpelier Fm., Jamaica (Steineck, 1981); M, Chapapote Fm., Tampico Embayment, Mexico (van den Bold, 1986).

species of the *B. johnsoni* lineage, we have observed minor intraspecific variation. This variation, represented by the rotation of fossae peripheral to the triplet EE′ E″, will be described in a succeeding section.

Present data place the earliest known occurrences of *B. johnsoni* and *B. thomasi* in the central Pacific. Consequently, these species are considered to have arisen there and shortly thereafter, to have dispersed to other regions. However, Fig. 2 shows that the stratigraphic record of *Bradleya* in the central equatorial Pacific contains gaps which preclude the *in situ* indentification of the *B.* sp. 1 – *B. johnsoni* and *B. johnsoni* – *B. thomasi* speciation events. Therefore, the possibility that *B. thomasi* and *B. johnsoni* evolved elsewhere and subsequently emigrated to the central Pacific cannot be completely ruled out.

The origin and early development of the *Bradleya johnsoni* lineage cannot be established at the present time. The oldest taxon referred to this clade is the undescribed form reported by van den Bold (1986) from Upper Eocene sediments of the Tampico Formation, Mexico (see Plate I, fig. 4). We consider these specimens as a stratigraphically early variant of *B.* sp. 1 from the Pacific but they may prove to represent a distinct species. Nevertheless, the PBC and arrangement of fossa in the posteroventral quadrant indicate a close relationship to the *johnsoni* clade. Comparative studies are needed to clarify the phylogenetic affinities between these taxa and Eocene forms described from the s.w. Pacific by Whatley *et al.* (1984). It is perhaps significant that constituent species of the *B. dictyon*

(see Whatley *et al.*, 1984) lineage are characterised by orthogonal muri of equal height in the posterior reticulum. If this shared morphocharacter proves to be synapomorphic, then both groups can be considered sister-taxa derived from a common but as yet undiscovered ancestor in the early Paleogene.

BRADLEYA SP.1

In the central equatorial Pacific, *Bradleya* sp. 1 ranges from zones CP16C/P18 to C18/P20 in the biostratigraphy of Barron *et al.* (1985) and Saito (1985) (Fig. 2). This interval is equivalent to the time span of 34.8 to 31.5 Ma according to the geochronometric scale of Berggren *et al.* (1985, fig. 5). Outside the Pacific, *B.* sp. 1 occurs in the Upper Eocene of Mexico (van de Bold, 1986; see Plate I, Fig. 4) and in the Lower Oligocene of Barbados (Steineck *et al.*, 1984; see Plate I, Fig. 5), Jamaica (Steineck, 1981, p. 355) and the south Atlantic (Benson, 1977b, plate 1, Fig. 4). The Mexican occurrence, represented by three specimens from the type locality of the Chapapote Fm., Tampico Embayment may represent the earliest occurrence of *Bradleya* in the Caribbean region. Abyssal ostracode faunas of Late Middle Eocene age from the Oceanic Fm., Barbados do not contain this genus (Steineck *et al.*, 1984).

BRADLEYA JOHNSONI BENSON

In the central equatorial Pacific, this species ranges from CP19A/P21 to NI2 (Fig. 2). Interpolation from biostratigraphic and sedimentation-rate data constrains
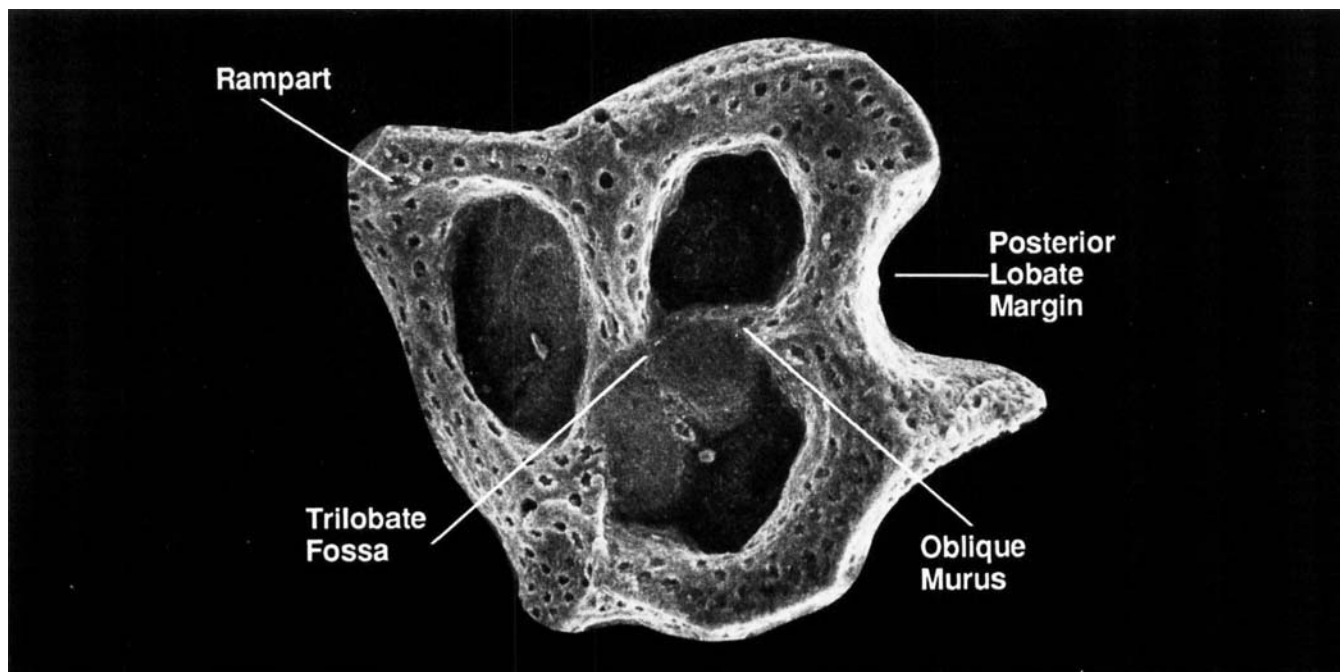

Fig. 3. Posterior bridge complex in *Bradleya johnsoni* Benson, Closeup of adult female left valve, sample CC-1, zone P22, Oceanic Fm., Barbados. See Pl. 2, fig. 1. 600x.

its origin to the interval from 31.5 to 30.4 Ma. Absence of bradleyids in Leg 85 samples correlated with zones N13 to N15 precludes accurate determination of its true extinction level.

The morphology of *B. johnsoni* is stable over its extended stratigraphic and geographic ranges. Several morphologic innovations – new macroreticular elements in the posteroventral quadrant, increased thickness and height of muri, secondary reticulation in the anterior and anteroventral regions, massively calcified rampart of the PBC – readily distinguishes this form from *B.* sp.1.

Pacific assemblages of *B. johnsoni* show considerable variation in reticular mass. End-members of this apparently gradational morphocline are illustrated in Plate 1, fig. 10 (delicate) and Plate 2, fig. 4 (massive). Similar variation in south Atlantic populations can be inferred from a comparison of the holotype from the Rio Grande Rise (Benson & Peypouquet, 1983, pl. 3,

fig. 8) with a second figure specimen (Benson, 1972, pl. 8, fig. 7) recovered from the central portion of the South Atlantic. The geographic and stratigraphic significance and causation of this variation not yet clear.

BRADLEYA THOMASI N. SP.

This species occurs from zone N16 to the Recent in the central equatorial Pacific. Morphologic divergence between *Bradleya thomasi* n. sp. and its ancestor becomes more pronounced with time. Although early specimens of *B. thomasi* (e.g. N16, N17) can be readily differentiated from late examples of *B. johnsoni*, some characteristics of the latter recur in the former but in a reduced or incomplete state. An analogous case of interspecific evolution in an Eocene lineage of the related genus *Echinocythereis* Puri, 1954, has been described by Reyment (1985, p. 187). He speculated that weak directional selection was responsible for the gradual divergence from the ancestral form, an ex-
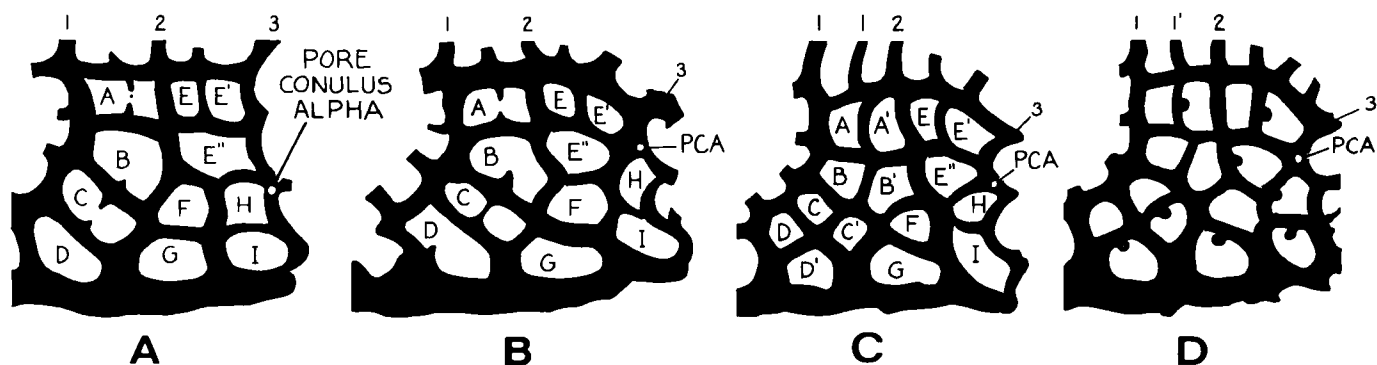

Fig. 4. Reticular patterns of the posterovental quadrant, adult left valves of *Bradleya* sp. 1 and *B., johnsoni* Benson. *Homologous fossae* designated by letters; *homologous muri* identified by numbers. A, B = *Bradleya* sp. 1: note the undivided row of fossae (ABCD) between muri 1 and 2. C, D = *Bradleya johnsoni*: note subdivision of fossae between muri 1 and 2 to form couplets AA', BB' etc. and murus 1'. In D, fossal coding omitted to show location of solar pore conuli. Basal (B) morph = A, C; Laterial (L) morph = B, D. Magnification of drawings 145x. A, Pl. 1, fig. 2. B, Pl. 1, fig. 1. C, Pl. 2, fig. 8. D, Pl. 2, fig. 1. PCA = pore conulus alpha.
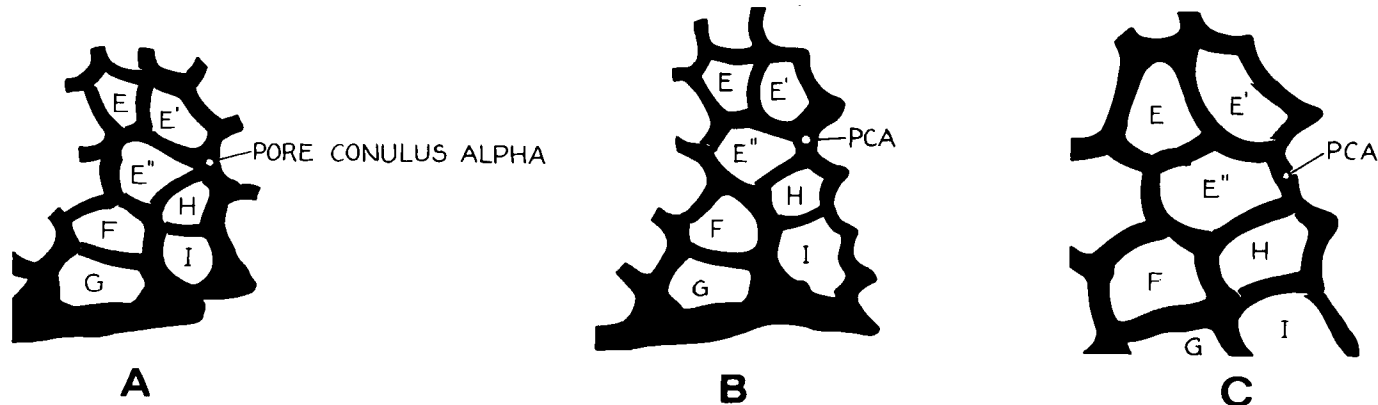

Fig. 5. Reticular patterns of the posteroventral quadrant, adult left valves of *Bradleya johnsoni* Benson and *B. thomasi* n. sp. Fossal coding as in fig. 4. Intermediate morphs = A, B; Basal morph = C. A, *B. johnsoni*, site 573B, core 9, section 1, zone N10 (Middle Miocene), 145x. B, *B. johnsoni*, pl. 2, fig. 4, 145x. C, *B. thomasi*, pl. 3, fig. 7, 260x.

planation that might also apply to *B. thomasi*.

Both the evolution of *B. thomasi* and a decrease in the diversity of the ostracode fauna occupying the central equatorial Pacific took place in synchrony with the growing dominance of frigid, corrosive waters in the abyssal circulation of this region (Steineck *et al.*, 1988; for paleoceanographic background see Theyer, Mayer & Thomas, 1985; Thomas, 1985; Mayer, Shipley & Winterer, 1986). However, present-day occurrences in the World Ocean (e.g. Cronin, 1983) suggest that *B. thomasi* has subsequently developed broader environmental tolerances. The delicate, low reticulum of *B. thomasi* may be an adaptation to central Pacific bottom-waters which during the Late Miocene were becoming progressively depleted in dissolved calcium carbonate.

DISCUSSION

Several investigators have concluded that reticular patterns in advanced cytheraceans are stable in, and diagnostic of species (Benson, 1972; 1977a; 1982; 1983; Liebau, 1975, 1977; Al-Furraih, 1977; Okada, 1981, 1982). In accord with these findings, species of the *Bradleya johnsoni* lineage display remarkably consistent arrangements of muri and fossae. This regularity is clearly demonstrated in the posteroventral reticulum; Figs. 4 and 5 depict silhouettes of the surface sculpture in this region, on which homologous elements are identified by an alphanumeric code. However, close inspection of these diagrams reveals, that within the basic design, there exists in each species similar variation in the relative positions of fossae adjacent to E″.

In qualitative terms, the intraspecific variation can be modelled as a gradational morphocline in which fossae E and H "migrate" in an arc relative to E″. The series of morphotypes so produced terminates at two configurations termed the B (Basal) – morph and the L (lateral) – morph. In the B-morph (Figs. 4a, c, Fc; Plate 1, fig. 3; Plate 3, fig. 6), H is located beneath the posteroventral border of E″, and the ridge separating F and H and the ventral ridge of E″ intersect at a Y-shaped junction. In the L-morph (Fig. 4b, d; Plate 2, fig. 11), H is positioned laterally along the posterior edge of E″, and its apex is in contact with the ridge forming the base of EE′. In the intermediate morph, H occupies a partly lateral and partly basal location with respect to E″ (Fig. 5a, b).

From another perspective, the intraspecific variation present in species of the *Bradleya johnsoni* lineage can be described in relation to a prominent mural pore here designated as pore conulus alpha. Because the number and location of pore conuli are commonly thought to be the most constant heritable feature on the ostracode carapace, they provide useful reference points for plotting variation in the position of fossae (e.g. Benson, 1977a, 1982, 1983).

Pore conulus alpha has been observed to occur in the following positions: 1) at the posteroventral corner of E″ (Figs. 4a, c; 5a, b); 2) at the posteroventral corner of E′ (Fig. 4b, d); and 3) on the vertical murus forming the posterior boundary of E″ (Fig. 5c). Within the morphotypes defined previously, there is no consistent placement of fossae relative to the position of pore conulus alpha. This observation suggests that the fossae under discussion (E′, E″ and H) not only change their relative positions but that they also "pivot" on the carapace surface relative to pore conulus alpha.

With the limited data provided by the Leg 85 samples, we have demonstrated the temporal coexistence of different variants and the presence of similar

PLATES

Abbreviations: ALV, adult left valve; ARV, adult right valve; M, male; F, female. Specimens from Leg 85 samples unless otherwise noted. HVH = Henry V. Howe Collection, Louisiana State University Museum. USNM = United States National Museum of Natural History, Washington, D.C.
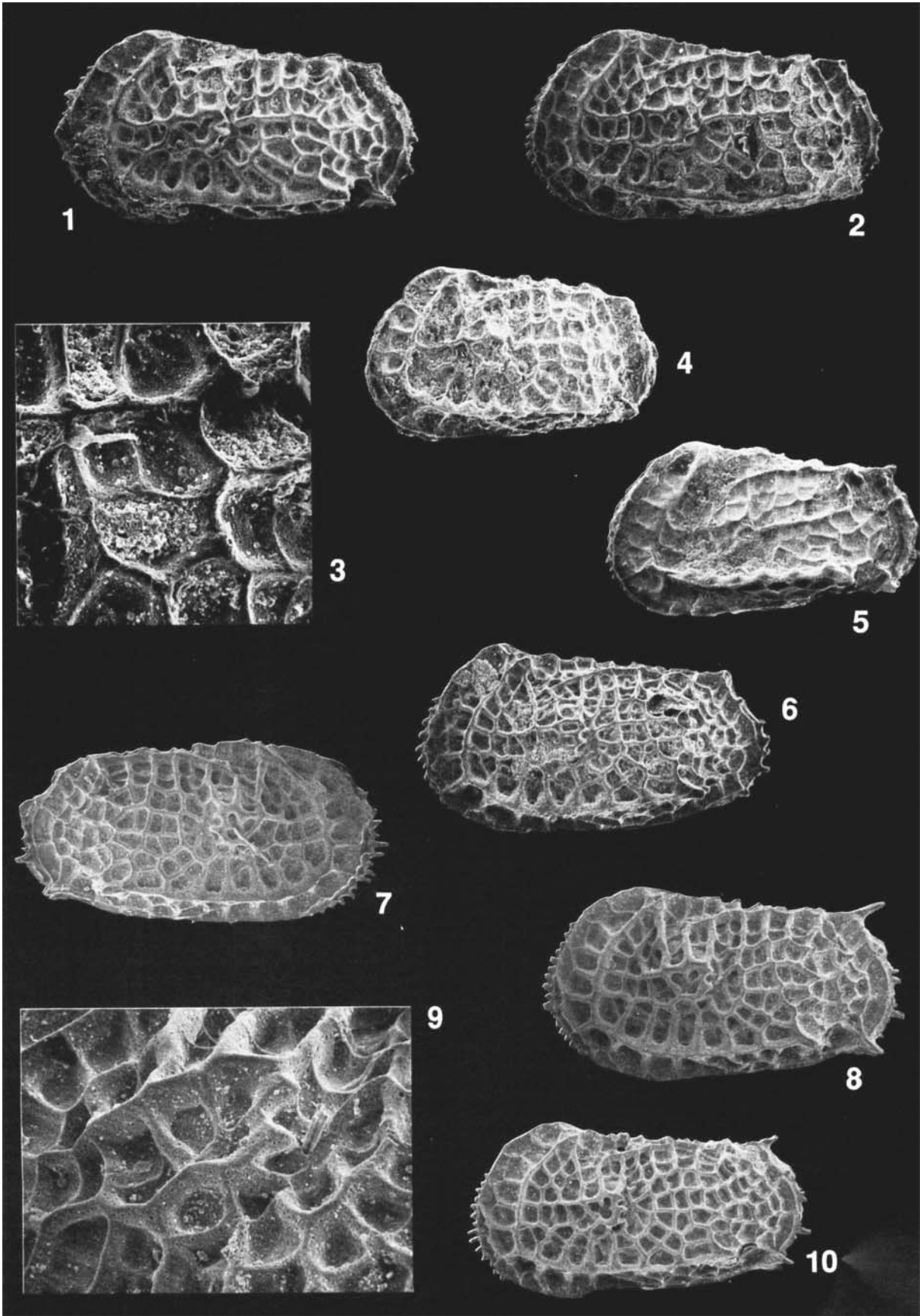
Plate 1

1–5. *Bradleya* sp. 1.
1. ALV-F, site 573B, core 35, section 5, zone P19, 103x.
2. ALV-F, site 574C, core 29, section 2, zone P19, 98x.
3. Closeup of fossal group EE′E″, B-morph, same specimen as 2, 420x.
4. ALV-F, Type locality of the Chapapote Fm., Tampico Embayment, Mexico, Zone P16–P17, 97x, HVH 10816.
5. Left lateral view of carapace of penultimate instar, sample 17, Windy Ridge, Oceanic Formation, Barbados, zone P20, 85x.

6–10. *Bradleya johnsoni* Benson
6. ALV-F, site 573B, core 26CC, zone P21, 101x.
7. ARV-F, site 575A, core 17, section 2, zone N5, 88x.
8. ALV-F, site 573B, core 10, section 2, zone N9, 86x.
9. Oblique closeup of PBC, same specimen as 8, 310x. Note heavily calcified rampart, and deep, steep-walled fossae. Angle of tilt 35°.
10. ALV-M, site 572D, core 30, section 1, zone N9, 80x.

variants in successive species of the *B. johnsoni* lineage. Nevertheless, it would be rash to draw far-reaching conclusions at the present time about the causative mechanisms underlying this variation. Clearly, further quantitative analysis of larger and geographically widespread assemblages is needed to establish the stratigraphic and geographic distribution of this variation and to investigate its correlation with genetic, developmental or ecologic factors.

SYSTEMATIC DESCRIPTIONS
Class Ostracoda Latrielle, 1806
Order Podocopida Muller, 1894
Suborder Podocopina Sars, 1806?
Superfamily Cytheracea Baird, 1850
Family Trachyleberididae Sylvester-Bradley, 1948
Genus *Bradleya* Hornibrook, 1952
Type species *Cythere arata* Brady, 1880
Bradleya thomasi sp. nov.
(Pl. 3, figs. 1–11)

1972 *Bradleya dictyon* (Brady): Benson: 126, pl. 9.
1983 *Bradleya dictyon* (Brady): Cronin: 109, pl. 3, fig. D.
1988 *Bradleya dictyon* (Brady): Steineck *et al.*: 598, pl. 2, figs. 2–4.

Derivation of name. Dr. Ellen Thomas, Wesleyan University, in recognition of her exemplary studies of Cenozoic deep-sea foraminiferal faunas.

Material. 45 carapaces and valves. Type specimens are deposited in the collections of the United States National Museum. ALV = adult left valve. ARV = adult right valve.

Table 1.

USNM Specimen Number	Sample	Biostratigraphic Level	Dimensions in mm. L.	H.
ALV Holotype 419482	572C 6/2	N20 (Pliocene)	1.28	.68
ALV Paratype 419483	572C 16/2	N17 (Upper Miocene)	1.28	.75
ALV Paratype 419484	572D 2/1	N17 (Upper Miocene)	1.25	.75
ALV Paratype 419485	572A 17/3	N17 (Upper Miocene)	1.30	.72
ARV Paratype 419486	572A 17/3	N17 (Upper Miocene)	1.30	.67

Distribution. Upper Miocene (N16) to Quaternary, sites 572, 573 and 574, Leg 85 DSDP-IPOD, central equatorial Pacific; paleodepth 3–4 km. Recent of Mozambique Channel (Benson, 1972) and Florida–Hatteras Slope (Cronin, 1983).
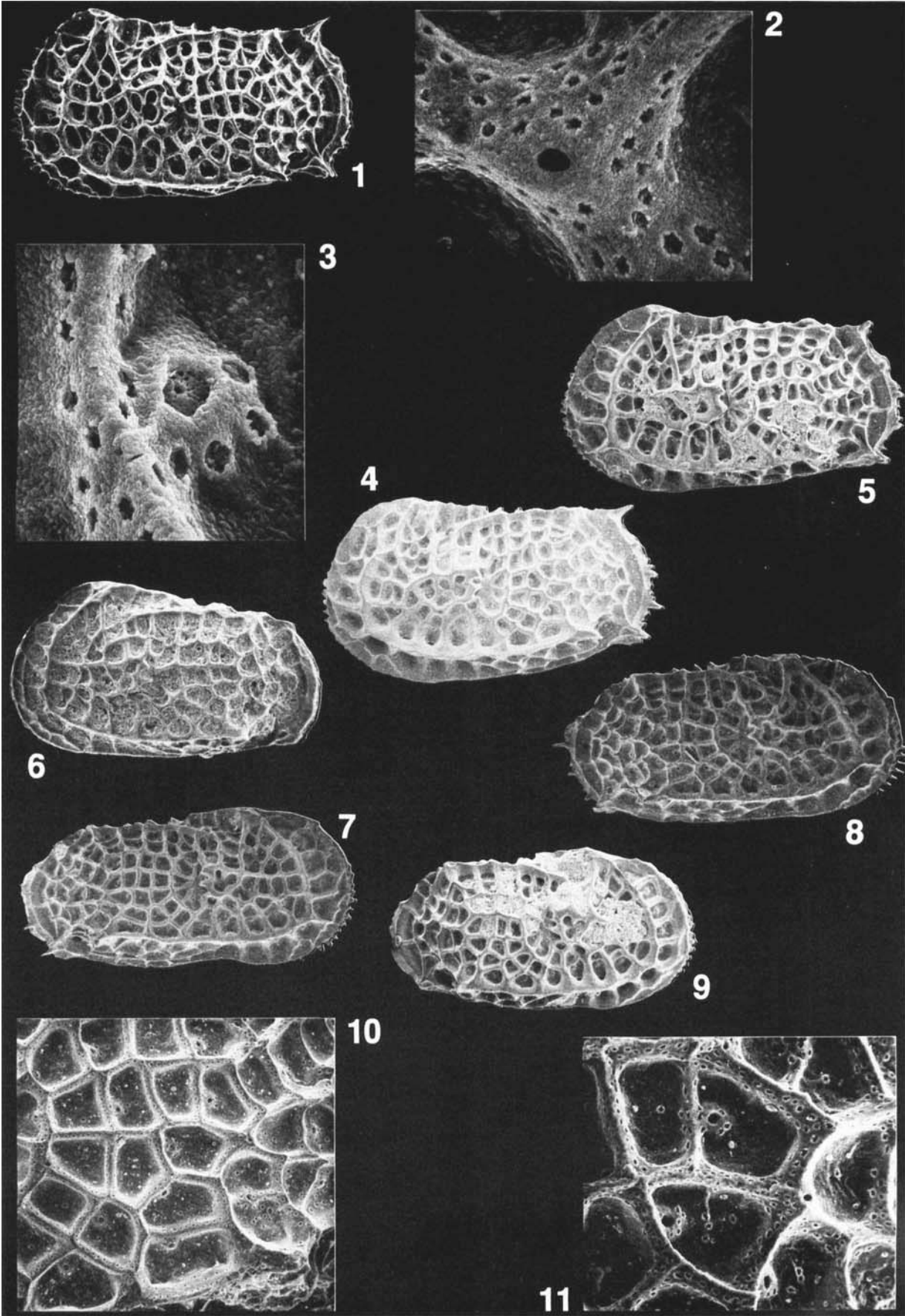
Description. Carapace large, robust; elongate-oval in shape with a broadly rounded anterior margin with 12–15 short denticles and a truncate posterior margin with prominent spines in dorsal and ventral corners. Dorsal margin straight except for anterior projection. Greatest width at central margin. Ventral margin gently concave in lateral view, broad and flat. Valve surface reticulate containing thin, sharp-edged muri enclosing shallow, flat to weakly concave sola. Muri and sola densely foveolate; foveolae stellate in outline. A single row of foveolae is present on the lateral surfaces of muri. Horizontal and vertical muri equally emphasised. Posterior reticulum composed of a honeycomb arrangement of polygonal cells. Posteromedian ridge subdued and disrupted.

Ponticulate ventrolateral carina prominent and flaring, continuing anteriorly into a subdued ocular ridge. Bridge present; PBC prominent, typical in form with low rampart. Internal space of mural loop closed dorsally by weak horizontal partitions but tending to be open in ventral portion. Sensillum pores of two types:

Plate 2

1–11. *Bradleya johnsoni* Benson.
1. ALF-F, sample CC-1, Codrington College, Oceanic Formation, Barbados, zone P22, 92x.
2. Closeup of conjunctive pore conulus, mid-ventral region, same specimen as 1, 1590x. Note multiple rows of stellate foveolae on lateral surfaces of muri.
3. Closeup of murus and celate, foveolate, sieve-type sensillum pore on solum, mid-dorsal region, same specimen as 1, 2190x.
4. ALV-F, 572D, core 33, section 5, zone N10, 86x.
5. ALV-F, 573B, core 7, section 1, zone N12, 81x.
6. LV-M(?), penultimate instar, sample M29, Montpelier Formation, Jamaica, zone N8, 98x.
7. ARV-M, site 573B, core 9, section 1, zone N10, 80x.
8. ARV-F, site 572, core 30, section 1, zone N9, 90x.
9. ARV-F, DSDP Leg 81, site 553, core 8, section 2 (northeast Atlantic), zone N4, 95x.
10. Closeup of posteroventral reticulum, same specimen as Pl. 1, fig. 10, 280x. L-morph.
11. Closeup of fossal group EE'E", same specimen as 1, 530x. L-morph.

medium-sized conjunctive or intramural pores situated in low conuli; large sieve-pores located in sola, projecting from surface on high, celate, foveolate tubercles. Anterior inner lamellae broad, without a vestibule; 12–15 normal pore canals, concentrated in ventral third. Hinge holoamphidont, massively calcified with faintly crenulate median element. Eye tubercle absent. Dimorphic; presumed males longer and less concave ventrally than females. Muscle scars include three vertically aligned, reniform adductor scars and two similarly shaped frontal scars. Posteroventral reticulum polymorphic.

Remarks. The PBC and the arrangement of posteroventral reticular elements differentiate *B. thomasi* from *B. dictyon* (Brady). The bridge of *B. dictyon* is subdivided internally by horizontal and vertical partitions; its posterior termination consists of a straight or gently curved ridge of variable height which supports a single horizontal murus projecting into the lumen of the mural loop (Benson, 1972, fig. 13b; Whatley *et al.*, 1984, p. 287, pl. 1, figs. 1–3). In *B. dictyon*, the posteroventral reticulum is most often complex and non-rectilinear (Ducasse & Peypouquet, 1979, pl. 3, fig. 9; Whatley *et al.*, 1984, pl. 1, figs. 2, 3). However, Benson (1972, fig. 13b) figured a specimen from the Recent of the eastern Pacific with three rows of verticially aligned fossae. This pattern, although reminiscent of *B. thomasi*, nevertheless, lacks the characteristic triplet of fossae enumerated as EE'E (see Plate 3, fig. 4; Fig. 5c) of that species.

Bradleya lordhowensis Whatley, Downing, Kesler & Harlow from the upper Neogene of the Lord Howe Rise resembles *B. thomasi* in size, outline and in the low, delicate reticulum. In the former taxon, the bridge is absent or suppressed in contrast to its prominent development in the latter. These forms also differ in the number of fossae in the region posterior to the mural loop and immediately below the posteromedian ridge.

In *B. thomasi*, four quadrangular fossae form a box-like cluster (Pl. 3, fig. 5). This is replaced in *B. lordhowensis* by a roughly triangular group of three fossae whose basal element is circular in outline (Whatley *et al.*, 1984, pl. 2, figs. 10, 12).

Bradleya johnsoni Benson is more heavily calcified and has higher, excavate, distally rounded muri with multiple rows of lateral foveolae. In addition, in this species, the PBC is enclosed by an elevated, flat-topped rampart which contrasts with the more subdued and rounded rampart of *B. thomasi*. Most specimens of *B. thomasi* can be distinguished from *B. johnsoni* by the absence of a prominent posteromedian ridge and the diminished contrast between primary and secondary muri.

Bradleya johnsoni Benson
(Pl. 1, figs. 6–10, Pl. 2, figs. 1–11)

1972 *Bradleya dictyon* (Brady): Benson: 124, pl. 8, fig. 7.
1983 *Bradleya johnsoni* Benson in Benson & Peypouquet: 811, pl. 3, fig. 8.
1984 *Bradleya dictyon* (Brady): Steineck *et al.*: 1468, fig. 6 h–k.
1988 *Bradleya johnsoni* Benson: Steineck *et al.*: 604, pl. 2, fig. 1.
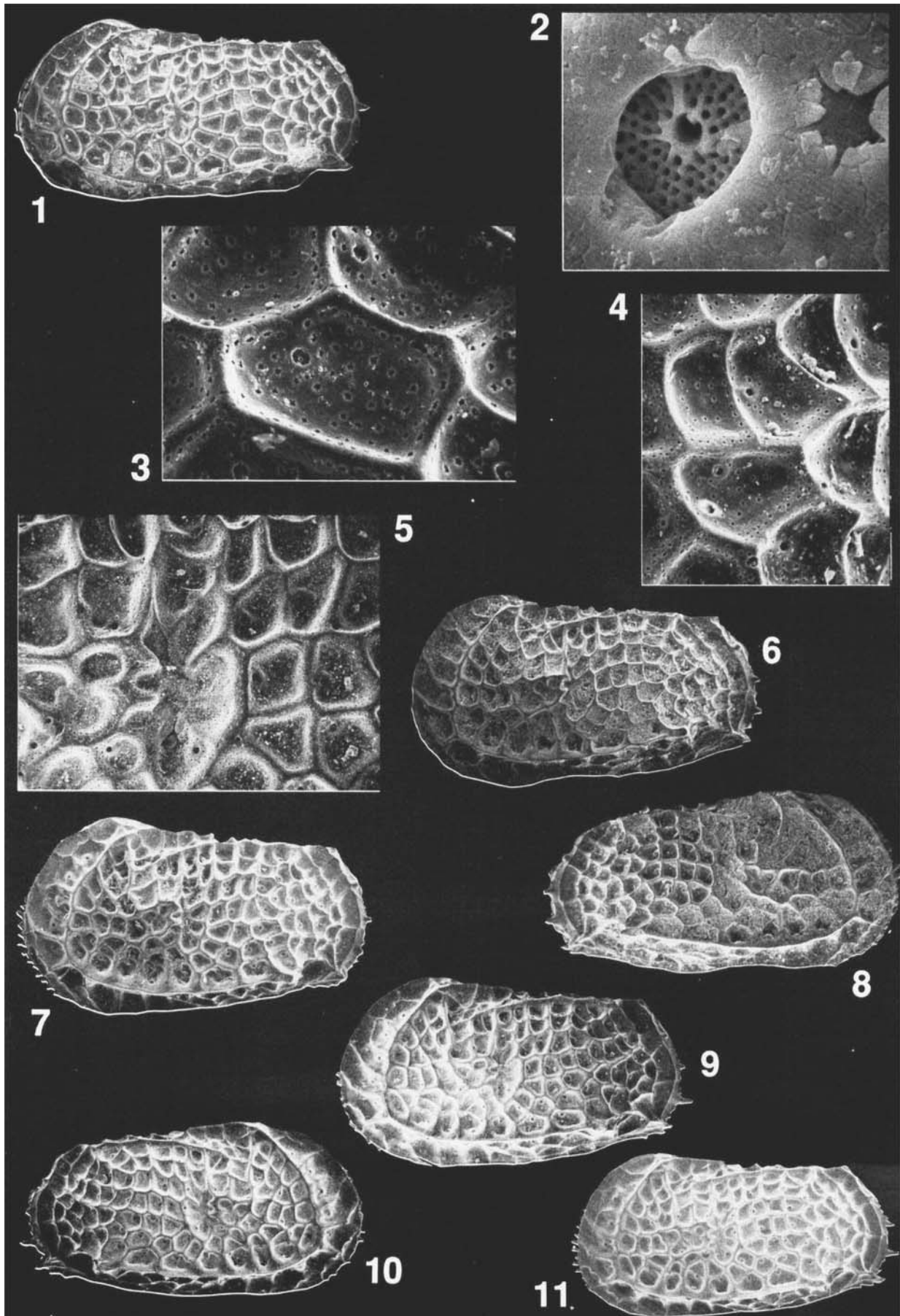
Material. Twenty-six adult values and carapaces.
Distribution. Central equatorial Pacific: P21–N12, paleodepth 3 km. Oceanic formation, Barbados: P21–P22, paleodepth 2–3 km (see Saunders *et al.*, 1984; Wood, Miller & Lohmann, 1985). South Atlantic : Lower Miocene, mid to lower bathyal (Benson & Peypouquet, 1983). Montpelier Formation, Jamaica: N4–12, lower bathyal (Steineck, 1981). Northeast Atlantic (Leg 81, site 553, D.S.D.P.) N4, bathyal (J.P. Peypouquet, personal communication, 1987).

Plate 3

1–11. *Bradleya thomasi* n. sp.

1. Holotype, USNM 419482, ALV-F, site 572C, core 6, section 2, zone N20, 88x.
2. Closeup of solar, sieve-type sensillum pore and stellate foveolae, same specimen as 1, 6100x.
3. Closeup of fossa in posterodorsal reticulum, same specimen as 1, 682x. Note polygonal outline, thin muri with single row of foveolae on lateral surfaces and shallow, densely foveolate solum.
4. Closeup of fossal group EE'E″, ALV-F, site 572C, core 5, section 3, zone N20, 430x. B-morph.
5. Closeup of central reticulum, ALV-F, site 572A, core 2, section 1, zone N22, 190x. Note PBC, open ventral segment of mural loop and box-like cluster of four fossae posterior to mural loop and beneath posteromedian ridge.
6. Paratype, USNM 419485, ALV-F, site 572A, core 17, section 3, zone N17, 90x.
7. Paratype, USNM 419483, ALV-F, site 572C, core 16, section 2, zone N17, 92x.
8. Paratype, USNM 419486, ARV-F, site 572A, core 17, section 3, zone N17, 88x.
9. ALV-F, site 572A, core 1, section 3, zone N23, 75x.
10. ARV-F, site 572A, core 1, section 3, zone N23, 75x.
11. ALV-M(?). site 572A, core 2, section 1, zone N22, 80x.

Description. Elongate, subrectangular species with a dense, orthogonal reticulum. Sculptural elements often massive in character. Raised, linear posteromedian ridge present. PBC with great relief; internal triangular fossae surrounded by an elevated, flat-topped rampart. Muri high, excavate with bluntly rounded to gently angled tops. Foveolae present on distal and lateral (multiple rows) surfaces. Concave sola set in deep, steep-walled fossa. Subdued secondary muri, contrasting with primary reticulation, present in anterior and anteroventral regions.

Remarks. This widespread Oligo-Miocene species ranges from zones P21 to N21 in the Leg 85 collections. It can be distinguished from *B.* sp. 1 by the addition of primary reticular elements in the posteroventral quadrant and by the general massiveness of the reticulum. The muri are always of great relief and steep-walled but vary in thickness from broad, blunt-top elements (Benson & Peypouquet, 1983, pl. 3, fig. 8; plate 2, fig. 5), to more narrow struts with angled distal surfaces (Benson, 1972, pl. 8, fig. 7; pl. 1, fig. 1, 11). The PBC is always enclosed by a conspicuous, elevated rampart.

Bradleya sp. 1
(Pl. 1, figs. 1–5)

1977b *Bradleya dictyon* (Brady): Benson: 764, pl. 1, fig. 4.

Diagnosis. Blind, elongate form distinguished from other species of *Bradleya* by the combination of the open, simple reticulum in the posteroventral quadrant, undivided vertical row of fossae between muri 1 and 2 (see Fig. 4a, b), fully developed PBC, bold muri with rounded distal surfaces, prominent posteromedian ridge, robust ocular ridge and clearly defined horizontal muri connecting the PBC to the anterior margin.

Material. Three adult left valves.

Distribution. Zones P18–P20 sites 572, 573, Leg 85, DSDP (abyssal). Zone P20, Oceanic Formation, Barbados (abyssal). Zones P16–P17m Chapapote Fm., Tampico Embayment, Mexico (Bathyal). Zone P20, south Atlantic (Bathyal).

Remarks. Left in open nomenclature because of the limited number of specimens available in the Leg 85 samples. *Bradleya "dictyon"* of van den Bold (1986) is smaller and more quadrate than Pacific examples (see Pl. I, fig. 4) but the bridge structure and robustness and pattern of the reticulum suggests placement here. Plate I, fig. 5 illustrates a corroded and compressed specimen from the Lower Oligocene of Barbados. This carapace appears to be an instar of *B.* sp. 1.

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