A NEW GENUS OF JURASSIC BIVALVE MOLLUSC ANCESTRAL TO *GLOBOCARDIUM*

by C. P. PALMER

ABSTRACT. A new genus of bivalve mollusc *Cryptocardia* is described and assigned to the subfamily Protocardiinae. Four new species are described from the Domerian, Bajocian, and Bathonian stages of Europe, and from the Callovian stage of Africa. This Jurassic genus, characterized by the presence of posterior internal radial ridges and no external radial ornament, is ancestral to the Cretaceous genus *Globocardium*. A tendency, throughout the Mesozoic, to suppress the internal ridges and to increase the size of shell and coarseness, both of external ornament and internal hinge structure, is established as an evolutionary trend for the two genera. There is no material from the Upper Jurassic or the Caenozoic. A homeomorphous Cretaceous species of *Protocardia* is described, which departed from the usual subtrigonal outline of Mesozoic *Protocardia* and converged towards that of *Globocardium*.

STUDY of bivalves from the French Jurassic, in the British Museum (Natural History), revealed a number of heterodont bivalves that were difficult to place in any existing genus. The difficulty was caused by a unique feature seen on the internal surface of the posterior part of the shell. Beneath the thin semi-transparent shell were two lines, one in each valve, running from the posterior side of the beak, passing about 5 mm anterior to the posterior adductor muscle scar, and terminating at the postero-ventral margin (Pl. 18, fig. 1*a*, *c*). The lines were caused by the presence of three ridges, one in the left and two in the right valve, which left corresponding grooves on the surface of internal moulds. At the postero-ventral edge of the shell the end of the single left-hand ridge fitted between the ends of the paired right-hand ridges (Pl. 18, fig. 4*c*).

Sixteen specimens from the Bajocian and Bathonian of England and France clearly demonstrated that: (*a*) the posterior internal ridges were constantly present—two in the right valve and one in the left; (*b*) the fossils were referable to no previously described species or genus; (*c*) the Bathonian forms were morphologically distinct from those of the Bajocian. The sample contained only three specimens with the shell intact and the rest, being internal moulds, showed no hinge. Of the three intact shells only one could be separated and the hinge teeth developed. The distant anterior and posterior laterals and single tubercular cardinal proved the cardiid affinity of the shells and indicated that they were related to the subfamily Protocardiinae (Pl. 18, fig. 2*c*).

A search for possible ancestors in the Lower Jurassic produced only one internal mould from the Middle Lias, Marlstone Rock Bed, of Ilminster, Somerset. This, though lacking the posterior internal grooves of the Middle Jurassic forms, was clearly related to them. No other *Cryptocardia* have been seen from the European Jurassic, but grooves on some internal moulds collected by N. J. Morris from the Callovian of Tanzania show that these are related to the European forms. They are generally similar to Bathonian specimens from Ranville, France, but the grooves on the inner moulds are not so sharply incised and square-sectioned as in the French forms, being more rounded and shallower, and tending to fade toward the umbonal

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region. This obsolescence of the internal ridges heralds the more advanced condition found in the related Cretaceous genus *Globocardium*, in which the internal ridges are almost obliterated by secondary thickening of the shell so that only a shallow groove is produced on the inner mould for a short distance from the ventral edge of the shell. This is illustrated by Hayami (1956, pl. 16, figs. 3, 5, 6), and also on several British *Globocardium sphaeroidium* (Forbes) in which a shallow groove is seen for about one-quarter of the height of the shell, while a faint and fading track continues to the umbo. In contrast to the Jurassic forms, *Globocardium* bears a continuous external trace of the position of the internal ridges as a distinct flexure in the growth lines as they pass over them. This is sharply marked at the beak but fades to a broad flexure in the coarse concentric ornament toward the ventral edges (Pl. 20, fig. 5).

No examples of *Cryptocardia* higher than the Callovian in the Jurassic have been discovered, but a search for Cretaceous forms revealed that the Aptian *Protocardia rothpletzi*, described by Krenkel from Tendaguru, Tanzania (Dietrich 1933, p. 51, pl. vi, figs. 89–91) was probably related either to the Jurassic forms or to the Cretaceous *Globocardium*. This was confirmed when a topotype was freed of matrix to reveal a typical protocardiid dentition and also the rounded knobs on the inner postero-ventral edge of the shell formed by the ends of the internal ridges (Pl. 20, figs. 1, 2). Thus the small Jurassic internally ridged *Cryptocardia* was ancestral to Hayami's *Globocardium*, type species *Cardium sphaeroideum* Forbes 1845, and the Tanzanian Cretaceous *Protocardia rothpletzi* was related to the British *Globocardium sphaeroideum*. This is confirmed by comparing Dietrich's figures of *Protocardia rothpletzi* with Woods's (1908, pl. 31, fig. 2), figures which show the presence of rugged concentric ornament only and, on the posterior surface, a broad track marking the position of the internal ridges. The large size and coarse concentric ornament of the Cretaceous *Globocardium* contrasts strongly with the smaller and more delicately ornamented Jurassic forms; so they are not congeneric. Hence it is proposed that *Globocardium* Hayami 1956 be restricted to the larger, more coarsely ornamented Cretaceous forms; and that *Cryptocardia* be used for the smaller and more finely ornamented Jurassic forms.

EXPLANATION OF PLATE 18

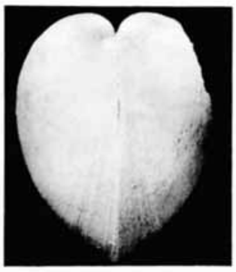
Fig. 1*a–c*. *Cryptocardia bajocensis* sp. nov. Holotype, B.M. 66193; Bajocian of St. Vigor near Bayeux (Calvados), France; purchased M. Tesson. 1*a*, lateral view of right valve; 1*b*, anterior view; 1*c*, posterior view with umbones tilted away to show external marks of internal ridges. × 1.

Fig. 2*a–c*. *Cryptocardia ranvillensis* sp. nov. Holotype, B.M. 66203; Bathonian of Ranville (Calvados), France; purchased M. Tesson. 1*a*, left side of inner mould, with some shell adhering, showing single posterior groove; 1*b*, right side of inner mould showing paired posterior grooves; 1*c*, internal view of right valve showing cardinal tooth and anterior lateral posterior lateral; broken away. Figs. *a–b* × 1½, fig. *c* × 4.

Fig. 3*a–c*. *Cryptocardia bajocensis*. Paratype, B.M. 66197; same locality as Fig. 1. 3*a*, left side of inner mould with single posterior groove; 3*b*, right side of mould with some shell adhering and paired posterior grooves; 3*c*, anterior view. × 2.

Fig. 4*a–c*. *Cryptocardia ranvillensis*. Paratype, B.M. 66243; Bathonian of Ranville (Calvados), France; O. Ward collection. 4*a*, right side of inner mould with paired posterior grooves; 4*b*, left side with single groove; 4*c*, posterior view with umbones tilted away to show posterior grooves at postero-ventral edge. × 1½.


1a


1b


1c


2a


2b


2c


3a


3b


3c


4a


4b


4c

PALMER, *Cryptocardia*

SYSTEMATIC PALAEONTOLOGY

Family CARDIIDAE Lamarck 1809
Subfamily PROTOCARDIIDAE Keen 1951
Genus CRYPTOCARDIA nov.

Type species: *Cryptocardia bajocensis* sp. nov.

Diagnosis. Small protocardiids with globose outline and fine concentric ornament only. Posterior internal radial ridges usually present: two in right valve, one in left valve. Margins of valves smooth.

Description. Small to medium sized for the family, height 26–37 mm; subquadrate to regularly ovate, umbones central or just anterior to the midline and beaks slightly prosogyrous. Valves without marginal denticulations, shell smooth apart from fine concentric growth lines, about 5–8 lines to 1 mm near the ventral edge. Internal posterior radial ridges, two in the right valve and one in the left. Upper Domerian to Callovian.

The position of *Cryptocardia* within the Protocardiinae should be next to *Globocardium* Hayami 1956 and near both to *Tendagurium* Dietrich 1933 and *Integricardium* Rollier 1912. *Tendagurium* is Jurassic in age, has a more trigonal outline and is altogether longer; the Cretaceous *Integricardium* has less projected umbones. Both lack the posterior internal ridges of *Cryptocardia* and *Globocardium*.

The chief differences between *Cryptocardia* and *Globocardium* are:

Cryptocardia	*Globocardium*
Shell small, up to 40 mm in height	Large, up to 100 mm in height
Shell thin, fine concentric ornament	Shell thick, coarse concentric ornament
Hinge with delicate teeth	Hinge with coarse tubercular teeth
Clear track of square-sectioned internal ridges on internal mould, only faint trace on external surface of shell.	Internal ridges almost obliterated by secondary thickening of the shell, distinct track on external surface of shell caused by flexure in growth lines over the internal ridges.

The Bernard system of hinge notation, with modifications by subsequent authors, is used throughout this text.

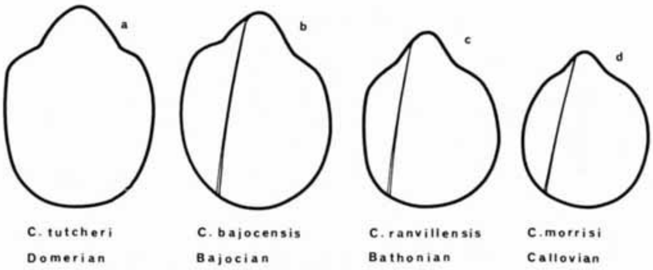
Cryptocardia(?) *tutcheri* sp. nov.

Plate 19, fig. 4*a*–*b*

Material. Holotype, an internal mould from the 'Middle Lias of Ilminster, Somerset', collected by J. W. Tutcher, B.M. 77330. The matrix clearly indicates that it is from the Marlstone, Spinatum Zone, probably from Moolham Farm.

Diagnosis. *Cryptocardia*-like shell lacking posterior internal ridges, umbones broader, valves more equilateral and quadrate in outline than other described species.

Description. Dimensions of holotype: length 2·6 cm, height 3·2 cm, inflation 2·5 cm. This sole specimen is placed with some hesitation in *Cryptocardia* since it lacks the internal ridges in the shell but in all other respects is clearly related to and possibly ancestral to the other species. It resembles *C. ranvillensis* in the less convex posterior outline, and *C. bajocensis* in its more broadly based umbones. The pallial line is entire and terminates at one end in a pyriform anterior adductor and, at the other, in a depressed region bounded by a bluntly rounded step (raised in the shell) which continues, past the elongate posterior adductor, up



TEXT-FIG. 1. Comparative outlines of the right valves of four Jurassic species of *Cryptocardia*: *a*, *C. tutcheri*, Domerian of Ilminster, Somerset; *b*, *C. bajocensis*, Bajocian of St. Vigor (Calvados), France; *c*, *C. ranvillensis*, Bathonian of Ranville (Calvados), France; *d*, *C. morrisi*, Callovian of Tanzania, East Africa. In figs. *b–d* the position of the paired, posterior, internal ridges are indicated by two converging lines. Scale approximately $\times \frac{1}{2}$.

to the beak (Pl. 19, fig. 4*b*). On the mould this step presents the appearance of an incipient internal ridge but the step is also present in the holotype of *C. ranvillensis* and posterior to the internal ridges.

Cryptocardia bajocensis sp. nov.

Plate 18, figs. 1*a–c*, 3*a–c*

Material. Holotype, B.M. 66193, from the Bajocian of St. Vigor near Bayeux (Calvados), France, purchased M. Tesson 1857. Paratypes: B.M. 66243, same locality and horizon; six specimens collected by the author from a temporary road section in the Upper Inferior Oolite, Parkinsoni Zone, at Harford Bridge, 1 mile ESE of Naunton, Oxfordshire, B.M. LL. 31290–31295, also B.M. LL. 31251–31253.

Diagnosis. Ovate *Cryptocardia* with sharp internal ridges, valves less equilateral, and umbones smaller than *C. tutcheri*, umbones longer and ornament finer than in *C. ranuillensis*.

Description. Dimensions of holotype: length 3 cm, height 4·7 cm, inflation 2·8 cm. Smooth, ovate, slightly prosogyrous; beaks on the midline and rising 0·5 cm above the hinge line in the holotype; dorsal margin projected posteriorly, rather like *Inoceramus*; anterior, ventral, and posterior margins in a continuous ovoid curve with the greatest curvature at the antero-ventral edge but flattening along the dorsal margin—the hinge margin. Shell wholly lacking in radial ornament but covered with fine concentric growth lines which average five per 1 mm at the ventral edge; occasional growth halts produce a slight undulation in the otherwise perfectly curved and heart-shaped outline when viewed from the anterior. Internal surface of shell with two square sectioned ridges in the right valve and one in the left; these extend from the beak to the ventral margin, the single left-hand ridge fitting between the two right-hand ridges at the postero-ventral margin where they meet. As they pass over the radial ridge the growth lines are deflected slightly in a dorsal direction and a corresponding flexure is seen in the otherwise entire pallial line where it crosses the internal ridge.

The anterior muscle scars, faintly seen on the internal moulds, are subovate, while the posterior adductor scars are elongate and set in a heart-shaped depression, bounded by a slight step, in the siphonal region. Margins without crenulations. Hinge not seen.

Remarks. The belief that this species might be identical with d'Orbigny's *Cardium cryptum* (prod. no. 334, p. 279, 'species subovate, very inflated, remarkable for the striations on the interior, always very prominent on the mould') was dispelled by M. Boule's figure (1909: 88) of a mould with less prominent umbones and radial striations over the whole surface of the mould. Boule also observed that the radial striations are spiny and *C. cryptum* is probably an undescribed genus.

Cryptocardia ranvillensis sp. nov.

Plate 18, figs. 2*a–c*, 4*a–c*; Plate 19, figs. 1*a–c*, 2*a–c*, 3

Material. Holotype, B.M. 66203, from the Bathonian of Ranville (Calvados), France. Paratypes: B.M. 66243, 66183, from the same locality; and two internal moulds B.M. L.77973, 77974, collected by D. T. Donovan from the Fullers Earth of Kelston, near Keynsham, Somerset.

Diagnosis. Ovate *Cryptocardia* with sharp internal ridges, smaller umbones, and coarser growth lines than *C. bajocensis*.

Description. Dimensions of holotype: length 2·1 cm, height 2·7 cm, inflation 2 cm. Similar in all respects to *C. bajocensis* but differing in being smaller, slightly shorter, and less inflated; umbones slightly narrower and with the posterior margin less convex. The posterior adductor scars are slightly more impressed and are bounded by a more conspicuous step. The growth lines, about five per mm at the ventral edge, are regular and more sharply incised than in *C. bajocensis* since each growth increment terminates in a raised lip. The valves of the holotype were disarticulated and sheared, and a development of the right hinge revealed a typical cardiid hinge with a single peg-like cardinal 3b and a socket anterior to it for the reception of the cardinal 2 in the left. Anterior laterals were present, 1·4 cm apart, as small, short lamellae, curved in the anterior and parallel in the posterior. Left hinge unknown.

Remarks. One of the two Keynsham specimens has a fragment of badly eroded shell adhering to it. This shows the same incised growth lines as in the holotype.

Cryptocardia morrisi sp. nov.

Plate 19, figs. 5–9

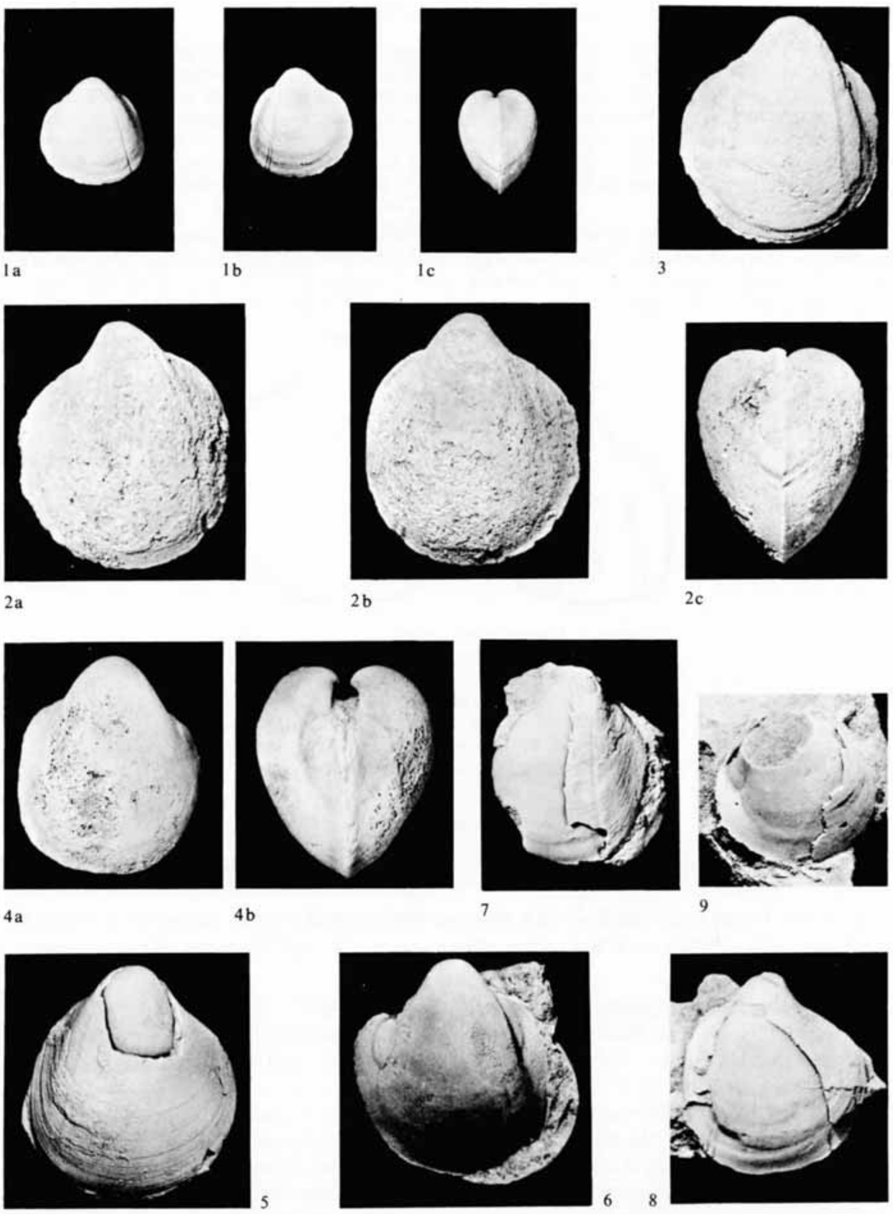
Material. Holotype, B.M. LL. 31285, right valve. Paratypes: B.M. LL. 31286–31289, from the Callovian of Tanzania.

Diagnosis. Ovate *Cryptocardia* with rounded posterior internal ridges, and with smaller umbones and a more convex posterior outline than other species of *Cryptocardia*.

EXPLANATION OF PLATE 19

Figs. 1–3. *Cryptocardia ranvillensis.* Fig. 1. B.M. 66183; Bathonian of Ranville (Calvados), France; purchased M. Tesson. 1*a*, left side with single posterior groove; 1*b*, right side of mould with paired posterior grooves; 1*c*, posterior view, tilted away to show grooves at postero-ventral edge. ×1½. Fig. 2. B.M. L. 77973; Bathonian, Fullers Earth, at Kelston Pound Hill, near Keynsham, Somerset; collected D. T. Donovan. 2*a*, left side of eroded inner mould with single groove; 2*b*, right side with terminal ends of posterior grooves at postero-ventral edge; 2*c*, posterior view with umbones tilted away to show grooves at postero-ventral edge. ×1½. Fig. 3. B.M. L. 77974; same locality and horizon as Fig. 2. Left side of inner mould showing pallial line and slight flexure where the posterior groove crosses it. ×1½. Fig. 4. *Cryptocardia*(?) *tutcheri* sp. nov. Holotype, B.M. L. 77330; Domerian, Spinatum Zone, of Ilminster (probably Moolham's farm), Somerset; collected J. W. Tutcher. 4*a*, right side of eroded inner mould; 4*b*, posterior view showing impressed (raised on shell) posterior adductor scars. ×1.

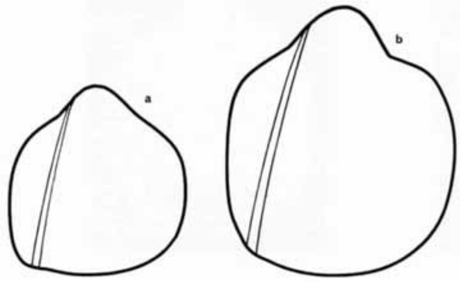
Figs. 5–9. *Cryptocardia morrisi* sp. nov. Fig. 5. Holotype, B.M. LL. 31285; Middle Callovian, Manyuli stream section, Mendawa–Mahokondo anticline, Kiswere area, Tanzania. External view of right valve with trace of posterior internal ridges visible at surface of shell. ×1½. Fig. 6. Paratype, B.M. LL. 31286. Left side of inner mould showing faint and shallow posterior groove and distinct anterior adductor scar. ×1½. Fig. 7. B.M. LL. 31287. Left side of inner mould with some shell still adhering and posterior ridge visible at shell surface. ×1½. Fig. 8. B.M. LL. 31288. Right side of inner mould with shell adhering and paired, shallow posterior grooves near postero-ventral edge. ×1½. Fig. 9. B.M. LL. 31289; Longi stream section, Mendawa–Mahokondo anticline, Kiswere area, Tanzania. Left side of inner mould with shell adhering and showing distinct anterior adductor scar. ×1½.



PALMER, *Cryptocardia*

Description. Dimensions of holotype: length 2·1 cm, height 2·5 cm, inflation 0·9 cm, single valve only. Smooth, ornate, slightly prosogyrous; beaks on the midline. Umbone elevated, bluntly rounded forming a right angle with slightly concave anterior and posterio-dorsal margins which merge into the nearly semicircular outline of the ventral margin, giving the shell a distinctly 'tear-drop' appearance. The posterior margin is straighter than the anterior which projects in a round curve. The surface of the shell is covered with fine concentric growth lines, about eight per mm at 2·2 mm height. Hinge could not be developed; however a cast taken from one of the moulds showed the hinge to be virtually identical with that of *C. ranvillensis*.

Remarks. This species closely resembles *C. ranvillensis*, differing in its reduced height/length ratio, its more closely spaced ribs (which are around 8 to 1 mm compared with 5 to 1 mm at a height of 2·2 cm in *C. ranvillensis*), and its more projected and rounded anterior margin. At one horizon in the Callovian of Tanzania it is common, since several valves are present in pieces of rock no more than 4 cm. long.



TEXT-FIG. 2. Comparative outlines of the right valves of two Cretaceous species of *Globocardium*: *a*, *G. rothpletzi* from the Aptian of Tanzania; *b*, *G. sphaeroidium* from the Aptian of the Isle of Wight, Hampshire. The broad track on the exterior of the shell marking the position of the two internal ridges is indicated by two diverging lines. Scale approximately $\times \frac{1}{2}$.

Genus GLOBOCARDIUM Hayami 1956

Type species. Cardium sphaeroideum Forbes 1845, Aptian and Albian of Western Europe and Aptian of Japan.

Diagnosis. Large protocardiid with globose outline and coarse concentric ornament and track of posterior internal ridges which, except for the terminal ends, are internally obsolescent.

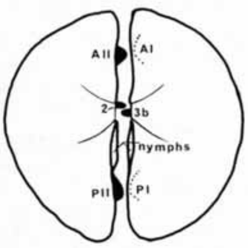
Description. 'Strongly inflated *Protocardia* having globose shell, widely spaced concentric costae on the disc and a nearly smooth posterior area without any conspicuous radial ribs; posterior carina weak or absent; ventral margin smooth internal; hinge similar to that of *Protocardia*' (Hayami 1956, p. 116). His diagnosis requires the addition of three internal degenerate ridges in the posterior of the shell, two in the right valve and one in the left. The external concentric ornament is modified over the internal ridges forming a continuous swollen track from the umbone to the ventral edge. The internal margin ventral margin though lacking denticulations contains the interdigitating ends of the internal ridges and forms a pronounced sinus in the ventral commissure.

G. imbricataria was recognized as a *Globocardium* by Hayami (1956, p. 116). *G. dupinianum* (d'Orbigny 1844, pl. 242, figs. 1–3) lacks radial ornament but also (on the drawing) any trace of an external track to mark the position of the internal ridges. The hinge of d'Orbigny's fig. 3 is comparable with that of *G. sphaeroideum* although the tooth 3a is more strongly developed in the French examples.

Globocardium sphaeroideum (Forbes 1845)

Plate 20, figs. 3–5

Cardium sphaeroideum E. Forbes 1845: p. 243, pl. 2, fig. 8.
Protocardia sphaeroidea (Forbes) Woods 1908: p. 195, pl. 31, figs. 2, 3.
Cardium neckerianum Pictet & Roux 1852: p. 424, pl. 30, fig. 3.
Protocardia (*Globocardium*) *sphaeroidea* (Forbes) Hayami 1956: p. 117, pl. 16, figs. 1–6, with synonymy.



TEXT-FIG. 3. Dorsal view of *G. sphaeroidium*, viewed down the plane of the commissure, to show the articulation of the hinge teeth. The beaks are 'cut-away' to expose the position of the cardinal teeth. Solid black teeth are those projecting beyond the plane of the commissure. Dotted lines represent position of lateral teeth within the plane of the commissure. The solid black laterals AII and PII articulate above, that is dorsal to, the dotted laterals AI and AII. The obsolescent cardinals 3a and 4b are omitted for clarity.

Material. Eighteen specimens from the Aptian, Lower Greensand Perna Bed of Atherfield, Isle of Wight; Casey (1961, p. 497, Table 1) placed the Perna Bed in the Fissicostatus Zone of the Lower Aptian. Also one internal and one external mould from the Upper Greensand of Haldon, Devon, and three external moulds from the Upper Greensand of Wiltshire.

Description. 'Shell inflated, rather oblong and angulated posteriorly. The surface is marked by deep and regular transverse sulcations, which are cut off from the somewhat truncated side by a deep longitudinal furrow. The sulcations on a specimen of the above dimensions are about eighty in number. The shell is thick especially at the margins. The beak is very prominent. The cast is smooth' (Forbes 1845, p. 243). The 'deep longitudinal furrow' is the track of the internal ridges which is partly eliminated internally by shell thickening except for a short distance from the shell margin where the terminal ends of the ridges produce three prominent rounded projections. Woods's figured specimen (1908, pl. 31, figs. 2, 3) is a well-preserved articulated two-valved shell which shows an S-shaped sinus in the ventral commissure where the internal ridges terminate (Pl. 20, fig. 5).

Remarks. This species, though related to *Cryptocardia*, is larger than the Jurassic forms. The average height is 8 cm and ranges up to 10 cm. The concentric ribs, here much coarser than *Cryptocardia*, continue on to the siphonal area without radial ornament, other than the track produced by the internal ridges. Left hinge of: a strong tuberculate anterior lateral AII; a strong cardinal 2 and a weak 4b; and an elongated posterior lateral PII apparently continuous with the ligamental nymph. Right hinge of: a deeply sunk, broad, anterior lateral AI (socket for the tuberculate AII of the left valve); a weak cardinal 3a and a strong tuberculate 3b; and a posterior lateral PI, less deeply sunk than the anterior (forming a socket for PII in the left valve). This hinge is the same as *G. rothpletzi* apart from its greater size, and differs from the *Cryptocardia* only in the more robust form of the anterior lateral AII, to judge by the relative size and depth of the anterior lateral AI in *C. ranvillensis* (Pl. 18, fig. 2*c*).

Following Woods (1908, p. 195), *Cardium neckerianum* of Pictet and Roux 1852 is placed in synonymy with this species (see also Hayami 1956, p. 116). Their pl. 30, fig. 3 shows a right valve, whose outline falls within the variation of specimens from the Lower Greensand of the Isle of Wight. However, there is no trace on their fig. 3 of any external track to mark the position of the internal ridge. Forms indistinguishable from *G. sphaeroideum* are found in the Upper Albian Upper Greensand at Devizes, Wiltshire, and at Shaftesbury in Dorset. In the Upper Greensand of the Haldon Hills, Devon, slightly larger specimens occur, all showing the characteristic outline of *G. sphaeroideum*, the same density of ribbing, and the broad external track marking the position of the internal ridges. There are no records of *Globocardium* from the Gault Clay between the Upper and Lower Greensand, indicating the preference of *G. sphaeroideum* for coarser sediment and higher-energy environments.

Globocardium rothpletzi (Krenkel 1910)

Plate 20, figs. 1–2

Protocardia rothpletzi Krenkel 1910: p. 216, pl. 21, fig. 1.
Cardium (*Tendagurium*) *rothpletzi* (Krenkel) Dietrich 1933: p. 51, pl. 6, figs. 89–91.

Material. One right value, B.M. LL. 31255, collected by N. J. Morris from the Lower Aptian, Trigonia Schwarzi Beds of Tanzania, and one left value collected by J. Parkinson, B.M. L. 51837.

Description. Similar in all respects to *G. sphaeroideum* but differing in the finer ornament which at 5·5 cm height shows seven concentric undulations per centimetre compared with only five in *G. sphaeroideum* at the equivalent height. The siphonal area is smoother and the outline slightly more quadrate than the English form, and the maximum height does not appear to exceed 6 cm.

Remarks. Dietrich placed *P. rothpletzi* in *Tendagurium*, type species *Cardium* (*Tendagurium*) *propebanneianum* Dietrich 1933 (p. 50, pl. 6, figs. 92, 93). His fig. 92 is a right valve with a straight hinge line, long laterals, and small cardinals. His fig. 93 is of an internal mould with prominently raised muscle platforms, a sharply angled carina bounding the siphonal area, and a pallial line with a moderately deep sinus in it. The internal mould of a left valve shows no trace of a groove representing internal ridges. By these characters *Tendagurium* differs from *Globocardium* and justifies the removal of *P. rothpletzi* from *Tendagurium* and placing it in *Globocardium*. This view was also expressed by Hayami (1956, p. 117) but for slightly different reasons. The left hinge (Pl. 20, fig. 1) has two unequal cardinals, a strong 2 and a weak 4b, a stout, conical anterior lateral AII, and an elongated, smaller posterior lateral PII. The right hinge (Pl. 20, fig. 2) has two cardinals, a strong 3b, and a weak 3a fused to the lunular margin; two laterals the anterior of which AI forms a broad, deep socket for the reception of the short conical anterior lateral tooth of the left valve; the posterior lateral PI forms a much narrower socket for the posterior lateral in the left valve. The hinge of this species is the same as *Cryptocardia ranvillensis* and *Globocardium sphaeroideum*.

EXPLANATION OF PLATE 20

Figs. 1, 2. *Globocardium rothpletzi* (Krenkel). Fig. 1. B.M. L. 51834; Lower Aptian, north of Mbemkuru River, Niongala, Tendaguru, Tanzania. Internal view of hinge of left valve cleared of matrix and terminal knob (arrow) at postero-ventral edge. ×1. Fig. 2. B.M. LL. 31255; Lower Aptian, Trigonia Schwarzi Beds at stream SE. of Nossa Stream, N. of Mbemkuru River (W. 39°, 14′, 40″; S. 09°, 35′), Tanzania. Internal view of right valve showing hinge cleared of matrix and paired terminal knobs (arrow) at postero-ventral edge. ×1.

Figs. 3–5. *Globocardium sphaeroideum* (Forbes). Lower Aptian, Perna Bed, Culver Cliff, Sandown, Isle of Wight. Fig. 3. B.M. LL. 8466. Internal view of left valve with matrix cleared showing hinge and single terminal knob (arrow) at postero-ventral edge. ×$\frac{2}{3}$. Fig. 4. B.M. 48626. Internal view of right valve showing hinge cleared of matrix and paired knobs (arrow) at postero-ventral edge. ×$\frac{2}{3}$. Fig. 5. B.M. L. 8247; Beckles collection. Ventral view of the original of Woods 1908, pl. 31, fig. 2, showing external track and terminal knobs at postero-ventral commissure. ×$\frac{2}{3}$.

Fig. 6. *Protocardia vicaryi* sp. nov. Holotype, B.M. L. 17041; Uppermost Upper Albian (or lowest Cenomanian), Haldon Hills, Devon; W. Vicary collection. External view of right valve, the original of Woods 1908, pl. 31, fig. 4, slightly reduced.

1

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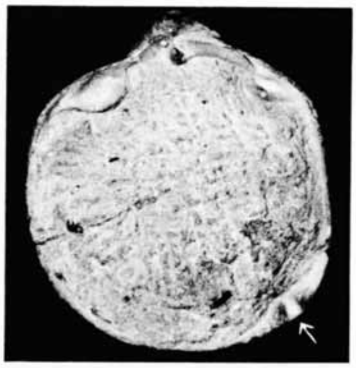

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PALMER, *Cryptocardia*

Genus PROTOCARDIA von Beyrich 1845

Type species. Cardium hillanum J. Sowerby 1813.

In dealing with the Cretaceous species of *Globocardium* it became apparent that an undescribed protocardiid, previously figured by Woods but not named, had been placed by Hayami in synonymy with *G. sphaeroideum*. Since this deceptive homeomorph needed to be removed from *Globocardium* and placed in *Protocardia*, it seemed appropriate to describe and name it here.

Protocardia vicaryi sp. nov.

Plate 20, fig. 6

Diagnosis. Protocardia with height: length ratio about 130%, greater than all other species of *Protocardia*.

Material. Holotype, B.M. L. 17041, from the Upper Cretaceous, probably Upper Albian, Haldon Hills, Devon; the original of Woods's (1908), pl. 31, fig. 4. Paratype, B.M. LL. 31296, same locality. Both specimens collected by W. Vicary.

Description. Dimensions of holotype: length 4·7 cm, height 6·2 cm, inflation 3·4 cm. Shell smooth, ovate, slightly prosogyrous; beaks in front of the midline and rising about 5 mm above the somewhat narrow hinge line. The anterior and ventral margins form a continuous and regular curve as far as the postero-ventral edge where it changes direction in a bluntly rounded curve and continues to the hinge line in a vertical, slightly concave, line. The valves are more noticeably inequilateral than species of *Cryptocardia* and *Globocardium*, and are covered with fine concentric growth lines and occasional growth halts. Faint radial striations are visible on the siphonal area where a slight fold makes a bluntly rounded ridge on the internal surface of the shell. The last deceptively suggests that it is a species of *Globocardium* but the external radial ornament, crenulate margin, and markedly inequilateral aspect shows that it is not. The hinge of the holotype, though partly obscured by matrix, is apparently similar to that of *Globocardium* and *Protocardia*, but other internal features are unknown.

Remarks. This Upper Greensand protocardiid bears a superficial resemblance to *G. sphaeroideum*, but differs in that it has narrower umbones, the outline is more oblique, it displays faint radial ornament on the siphonal area, it lacks internal ridges, it has a nearly smooth shell with only fine growth lines, and the siphonal area is sharply concave and undulatory. The nearest described species to *P. vicaryi* is *P. guerangeri* (d'Orbigny 1844, p. 35, pl. 249, figs. 3, 4) from the Cretaceous of France, but it differs in its more prosogyrous beaks, smaller umbones, more rounded umbonal ridge, and its generally larger size. Most species of *Protocardia* have height: length ratios which are usually around 100%. However *P. vicaryi* and *P. guerangeri* have ratios closer to 130% and are noticeably taller than the majority of *Protocardia*. Hayami (1956, p. 116) included *P. vicaryi* in his genus *Globocardium*, a position which cannot be upheld here since: (*a*) there is neither a trace of the internal ridges nor track on the external ornament; (*b*) there is faint external radial ornament on the siphonal area of the paratype and also a trace of it on the holotype; (*c*) the margin is finely crenulated. The siphonal area is demarcated by a bluntly rounded umbonal ridge which passes into a sharp concave fold producing a thickened ridge visible on the internal surface of the shell of the holotype. The paratype reveals that this ridge lies posterior to the adductor scar and is therefore not comparable with the internal ridges of *Cryptocardia* and *Globocardium*, in which the ridges lie anterior to the posterior adductor scar. The age of the type locality is either highest Upper Albian or basal Cenomanian—the matter is not yet settled by Cretaceous stratigraphers.

DISCUSSION AND CONCLUSIONS

Function of the internal ridges. No satisfactory explanation can be offered for these puzzling features. The simple hypothesis, that the terminal ends of the internal ridges provided a shear-resistant mechanism, may be refuted by the following: (*a*) shear stress is greatest when a bivalve is actively burrowing, for then the valves are necessarily open and the ends of the internal ridges cannot then interlock; (*b*) conversely when the bivalve is not actively burrowing the ends of the internal ridges interlock but shear stress is no longer present. To postulate that this feature is a response to predation is unhelpful unless a predator employing a shear action on bivalves can be identified—starfishes do not qualify for this role.

Palaeoecology. The Domerian and Bajocian species of *Cryptocardia* occur in oolitic limestone, the Callovian in fine sandstone, while the Cretaceous species of *Globocardium* occur in coarse gritty sandstone. All are associated with an abundant benthic fauna dominated by mollusca. The increase in coarseness of sediment, together with the presence of an abundant associated benthos, is taken as evidence that these two genera favoured a high-energy environment which increased during their evolution. The massive lateral teeth in *Globocardium*, and their prominence in *Cryptocardia*, indicate that these were active burrowers in coarse sediments. It further points to a probable connection between the increasing oxygen consumption and demands of the progressively more active bivalves and the greater availability of oxygen in the higher energy facies.

Evolution. The development during Mesozoic times of the two genera *Cryptocardia* and *Globocardium* may be summarized as follows: (*a*) increase in size and massiveness of shell, particularly above the Jurassic/Cretaceous boundary; (*b*) a coarsening of hinge characters and external ornament with increase of size—particularly in *Globocardium*; (*c*) suppression of the square-sectioned internal ridges by an increase of secondary thickening of the internal part of the shell; (*d*) a gradual transference of the internal ridges from that of an internal feature of the shell in *Cryptocardia* to that of an external track, formed by a flexure in the growth lines, in *Globocardium*.

The known range of *Cryptocardia* is from the uppermost Domerian to the Callovian stage of the Jurassic. No examples from the Oxfordian, Kimmeridgian, and Portlandian stages of the Jurassic, and the Neocomian stage of the Cretaceous, have come to the writer's attention. Since *Cryptocardia* was probably ancestral to *Globocardium* it follows that intermediate forms existed during Oxfordian to Neocomian times. These, being stratigraphically intermediate between the Callovian *C. morrisi* and the Aptian *G. rothpletzi*, would have shell characters intermediate between these two forms. No examples of *Globocardium* younger than Upper Albian (or Lower Cenomanian) are known to the writer, and a search for possible descendants in the Caenozoic proved fruitless. Any descendants probably continued the trend towards suppression of the internal ridges, and a steady increase in shell size, coupled with a coarsening of the concentric ornament and of the hinge characters.

It is probable that the Jurassic *Cryptocardia* was ancestral to the Cretaceous *Globocardium*. *Cryptocardia* first appeared as an offshoot of the *Protocardia* group in uppermost Domerian times. By the Bajocian it had lost all trace of external radial ornament and had developed unique posterior internal ridges—two in the right and one in the left valve. During Callovian times the internal ridges became less pronounced and this obsolescence, together with an increase in over-all shell size, led to the Cretaceous *Globocardium*. This evolutionary series of protocardiids tended to occupy increasingly higher energy condition through their history. During mid-Cretaceous times a *Protocardia vicaryi*, with faint posterior radial ornament, departed from the usual subtrigonal outline of Mesozoic protocardiids and converged towards the elongated and globose shape of the *Cryptocardia/Globocardium* group.

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