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THE PELECYPOD FAMILY CARDIIDAE: A TAXONOMIC SUMMARY

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I. ABSTRACT

The family Cardiidae is here considered to comprise six subfamilies: Cardiinae, Trachycardiinae, Fraginae, Hemidonacinae, Protocardiinae, and Laevicardiinae. The Eurasian brackish-water groups are regarded as a separate family, the Lymnocardiidae. Of 109 nominal taxa assigned to the family, 77 are accepted as useful at the generic or subgeneric levels, and one other is listed but considered of doubtful utility. The family began to emerge during late Triassic time and has radiated widely. In present-day seas cardiids are most abundant on sandy bottoms and in shallow water, although they may occur offshore in depths to 300 meters.

Morphologic differences between the generic units in each of the subfamilies are summarized in dichotomous keys. Insofar as possible illustrations are of the type species for each unit, and figures of shell interiors and hinges are of left valves.

A tabular summary of classification is designed to show distribution of each unit in time and space. Phylogeny of the family can be only sketchily suggested as yet, because of gaps in the fossil record. Strongest relationship seems to be to the superfamily Carditacea.

Some notes on a recent review of the family by Prof. Édouard Fischer-Piette are included in an appendix. A second appendix discusses placement of two new generic units that were published by Robert Scott while this paper was in the editorial office.

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II. INTRODUCTION

In 1935, as a beginner in the study of mollusks, I made a simple observation that led to a lifetime interest in cardiids. Noticing that specimens of "*Cardium corbis*" (as I was then calling it) had prosogyrate beaks, I asked Professor Hubert Schenck, a Stanford University paleontologist, whether this was significant. Missing no chance to stimulate research, he countered by suggesting I try to find out. As any systematist can guess, the answers I found only led to more questions. Before I was through I had started to index all the names of species allocated to *Cardium*. My file now comprises several thousand cards. Like most other Linnean genera, *Cardium* had already begun to be subdivided, and the cluster of generic taxa accorded family status, as the Cardiidae. Before long I felt constrained to propose yet another generic category (Keen, 1936a) for the "*Cardium corbis*" of authors and its close relatives, *i.e.*, *Clinocardium*. This proposal had to be supported by a paper listing other named units in the family (Keen, 1937). Then I began work on a monograph I thought should wrap up my research nicely; yet somehow it would not fall into satisfactory form. The generic key planned as its central feature proved, when tested, to be unworkable. In one sense, the intended synopsis has lain dormant these forty years. In another it has not, for sections have appeared in print (Keen, 1950; 1951; 1954; Keen *in* Moore *et al.*, 1969); and I have had time to test my insights on relationships by extensive study of specimens and literature.

The figures I had prepared to illustrate the groupings I saw as subfamilies still are usable. Perhaps now, with longer experience, I may be able to modify the planned key into more satisfactory form. Indeed, it is time I should elaborate on my conclusions, for competing classifications have recently begun to surface (Kafanov, 1975; Fischer-Piette, 1977; Kafanov & Popov, 1977), and even while this paper was under editorial review two new taxa have been proposed (Scott, 1978), which can be only partially taken into account herein.

Not only was I guided in arriving at a classification of the Cardiidae by Professor Schenck but also by the counsel of other active systematists of that time. In a letter dated Sept. 26, 1936, commenting on a preliminary draft of my intended work, Dr. Wendell Woodring of the U. S. Geological Survey gave some advice that I do not forget: "Workers who spend much time on one family or one genus are likely to get an exaggerated idea of the number of major categories that can be recognized. My treatment of the Turridae [*i.e.*, his paper in 1928 on the Bowden Miocene gastropods of Jamaica] is a fine, or rather, a terrible example. . . I am in favor of narrowly defined categories, but I am not in favor of an indiscriminate boosting of categories to higher ranks."

Dr. Don L. Frizzell was then a graduate student at Stanford University. His counsel is epitomized in a statement on Veneracea (Frizzell, 1936), the group on which he wrote his doctoral thesis. He pointed out that a phylogeny or hypothetical line of succession must not be based upon a single character, such as the hinge, for this ignores the principle of summation of characters; scrutiny of orthogenetic or convergent trends as well as of the ontogenetic development of representative species must be prerequisite to any trustworthy scheme of classification.

Another mentor of that period was Professor Gordon Ferris of the Biology Department of Stanford. I read and re-read his essay on classification (Ferris, 1928) — a philosophy encapsulated in one sentence that he italicized: ". . *the essence of classification is grouping*." As he said, the tendency should be "to conserve groups rather than to separate them, unless that separation be the separation of *groups*." This is a wholesome about-face from the common practice of saying, "Here is a specimen (or species, or genus, or whatever) that is different; therefore I propose to regard it as a new . . ." Instead, one should say, "Here is a specimen (or species, etc.) that shares a number of traits with these others; therefore I will group them together." Obviously, one must note differences (it is axiomatic that no two living things are exactly alike), but the emphasis should be on relationships and the number of traits in common. Grouping into larger constellations will be on balance, and one is saved having to decide which traits or measurable characters are more important than others.

The classification of Cardiidae took place, naturally, more by dismemberment than by grouping. Although there had been several reviews, such as those of Römer (1868-69), Fischer (1887), and Dall (1901), the first person to begin to try to draw groups together within the family seems to be Stewart (1930), who recognized three subfamilies, Cardiinae, Trachycardiinae, and Fraginae, the latter two of which he proposed as new. I added Laevicardiinae (Keen, 1936b) and Protocardiinae (Keen, 1951). Other nominal categories have been proposed since — Cerastodermatinae Nordsieck, 1969; Hemidonacinae Iredale and McMichael, 1962, as recognized by Boss, 1971; and Clinocardiinae Kafanov, 1975.

The thorny problem of the brackish-water Cardiacea I am deliberately shunting aside. Stoliczka in 1870 had split them off as a subfamily, Lymnocardiinae. During medial Tertiary time a Tethyan-Mediterranean molluscan fauna became isolated in southeastern Europe, in the Euxine Basin area. As the water freshened, marine invertebrates were obliged either to adapt or to die out. The cardiids adapted. Whether the several cardiid stocks then extant — *Cerastoderma*, *Laevicardium*, *Parvicardium*, *Nemocardium*, and *Cardium* s. s. — were able to hybridize or whether the stress released potentialities for immense variation within a single strain among them is a question that no one seems to have attacked. Unfortunately, most of the literature on them is in Russian or other Slavic languages and difficult of access. My studies having been primarily on the marine cardiids, I have not attempted to untangle the web of relationship between these dissociated groups. The brackish-water forms have proliferated through late Tertiary time and still are represented by a number of distinctive species, of which some have long siphons and a pallial sinus, some have thin or almost transparent shells, and some have heavy shells with aberrant hinges. Biochemical studies of the soft parts as well as careful anatomical comparisons with the normal marine stocks would be a fruitful line of study for anyone who is equipped to make such analyses. Meanwhile, it seems preferable to draw an arbitrary dividing line between the main-line and the derived forms. I have, therefore, assigned all of the brackish-water nominal taxa to Lymnocardiidae as a separate family, which I have summarized at more length in the *Treatise on Invertebrate Paleontology* (Keen *in* Moore *et al.*, 1969).

Three papers that are titled as revisions of the Cardiidae have appeared in recent years. The one by Fischer-Piette (1977) gives no rationale for the groupings it effects. No subfamily categories are cited; genera are divided into subgenera and "sections," in a sequence different from that of any other author. Because there is no explanation for these innovations, I see little point in attempting item-by-item commentary, although I have added as an appendix to this paper a summary of the new species Fischer-Piette describes, with notes on the allocations that I would make of these and the species for which he gives figures of type specimens. He seems to put more weight on priority of generic names than on morphological characters of the shells themselves. At least this is the only explanation I can find for the use of *Corculum* Röding, 1798, as the generic name for the West American species assigned to *Clinocardium* Keen, 1936, in modern literature; however, his substitution of *Keenocardium* Kafanov, 1975, as the subgeneric taxon for them instead of *Clinocardium*, under *Corculum*, leaves one puzzled.

The classifications by Kafanov (1975) and Kafanov and Popov (1977) do have an undergirding of descriptive text in Russian. My reluctance to accept especially the Kafanov and Popov classification stems from its having been based upon elaboration of a single character, microstructure of the shell. Although shell structure may well be useful as one of the criteria for grouping, using it exclusively ignores the basic principle of summation of characters. Kafanov and Popov would divide Cardiidae into six subfamilies: Cardiinae, with five tribes and 19 generic taxa; Clinocardiinae, with three tribes and seven genera; Fraginae, with three tribes and 22 genera; Hemidonacinae, one genus; Protocardiinae, for which they mention seven genera that occur in the Tertiary and omit 17 that are mostly of Mesozoic distribution; and Lymnocardiinae, with nine tribes and 71 genera. Although some of their reallocations have plausibility, I cannot accept the use of a single criterion, such as microstructure, without more exhaustive study of ontogenetic series, of chronogenetic successions, of locus effects (*i.e.*, what part of the shell is sectioned), of habitat effects, and so on. No matter how basic the structural character, one cannot ignore the soft parts, the hinge elements, shell contour, ribbing patterns, surface sculpture, and other variables. Shell microstructure may, in fact, prove to be iterative or progressive, as gill structure has already proved to be in bivalve classification. Newell (*in* Moore *et al.*, 1969, p. N-209) has observed that original shell microstructure rarely is preserved in the earlier bivalve fossils and may even be destroyed in fossils that are geologically rather young; also that there are differences within groups in stability of structure — some may be environmentally modified, others not.

A workable classification, of course, must be based upon morphological characteristics. The implicit assumption is that groups with many observable traits in common are more or less closely related, differentiated through isolation and genetic drift. Observed distribution in time and space should not be a factor to influence judgments on morphology. However, if, after the classification is established, one finds a geographic or geologic coherence in the groups, it is useful confirmatory evidence that a true relationship exists and that distribution reflects past dispersal pathways. A classification that does not examine both the morphologic bases and the distribution risks being superficial.

In general, I have been satisfied that distributional patterns did support my subdivisions of cardiid groups. While preparing the index cards, I was also making tentative allocations of the nominal species. When these were summarized, I found that distributions were homogeneous, with few exceptions, as indicated in Section 3 of this paper.

III. ACKNOWLEDGMENTS

Several of those to whom I am indebted for help during the forty years that this paper has been generating no longer are living — notably Professor Hubert G. Schenck, Stanford University; Dr. Don L. Frizzell (then a Stanford student); and David Vernon, a local amateur. Others, such as Dr. Wendell Woodring of the U. S. Geological Survey and Dr. Hollis Hedberg, probably have forgotten that at one time they had been asked for advice and had given useful suggestions. I owe much also to the many correspondents who replied to letters of inquiry and loaned or gave material. A German paleontologist, for example — Dr. W. O. Dietrich — not having an extra reprint that I needed, sent me his proof sheets and original photographs, from which I now have been able to reconstruct a hinge hitherto unillustrated. A number of competent artists have lent their skill to making the line drawings, especially E. H. Quayle in the 1930s, Jeanne Janish in the 1940s, and Perfecto Mari in more recent years. Philip Palmer has helped me on reallocation of some Mesozoic units. Ellen J. Moore of the U. S. Geological Survey and Dr. Robert Robertson of the Academy of Natural Sciences, Philadelphia, have supplied needed reference material. To Dr. Eugene Coan I owe thanks not only for critical reading of the manuscript but also for his encouragement toward my completion of this long-unfinished report, and Sandra Gardner has read some parts of the text. To all these people goes my deep appreciation for their help.

I acknowledge, with thanks, permission from the editors of the *Treatise on Invertebrate Paleontology* to reprint illustrations published as a part of my revision of Cardiacea in that work.

IV. FORMAT

The plan of the present work is as follows: Section 1 is an alphabetical listing of all the marine cardiid generic-level taxa that I have been able to discover in the literature, with notes on original references (except for those few that are invalid because of primary homonymy); the name of the type species; manner of designation; and synonyms. An asterisk is used to avoid the repetition of the words "type species" (in the style of the *Treatise on Invertebrate Paleontology*). The standard symbols for manner of type designation are explained under "Abbreviations," in the final pages of this paper. Names accepted as valid and usable are written in capitals; synonyms and nomenclaturally invalid names are in italics. The number at the end of each entry refers to the placement of the unit in the formal classification of Section 3. Synonyms are indicated by square brackets, the enclosed number being that of the unit under which they are presumed to fall.

Section 2 comprises keys to the generic units within each of the subfamilies recognized. A single key to all the genera proved to be unworkable because no one character can be found that without exception will subdivide the major groupings; instead, grouping must be arrived at on the basis of summation of characters. To use the keys one makes judgments of the general relationships of the shell in hand either by scanning the introductory paragraphs for each of the separate keys or by use of Table 1, an analytical summary of the principal characters of the cardiid shell. This table attempts to show the incidence of each trait, whether common to the entire subfamily or present only in a few of the generic units. The plates are grouped, insofar as practicable, according to subfamily, which may also help in narrowing choices. For the novice who does not already have a working idea of relationships of the shells being keyed, the multiple keys are, I admit, an obstacle to quick determinations. A process of trial and error — trying first the table, then, if no clear choice emerges, one key after another, checking with the given figures to assess plausibility — will build up gradually the skill needed to start immediately into the proper key. For experience there is no ready substitute.

Could one have only a single view of a cardiid shell, the best choice would be the interior of he left valve, for the right hinge is complicated by some degree of fusion of the cardinal teeth. The left valve interior shows not only the construction of the hinge but reveals much about the shape of the shell, the strength of the ribs, and their relative distribution. This view is the one selected for the line drawings that I had prepared especially for this work. Figures of exteriors also are included here, mostly copied from literature. In the keys, numbers in square brackets following the names of the keyed generic units refer to the placement in the classification of Section 3.

The formal classification of the Cardiidae resulting from my studies of the family comprises Section 3. Here each nominal taxon that is considered useful is numbered in sequence. Distribution in time and space is summarized, and reference is made to the illustrations. The figures are, with minor exceptions, those of the type species. Only when no good figures of the hinge of the type species could be obtained were substitutions made — hinges of presumably representative species. A few good figures of typical sculpture also are representative rather than type species, but in every case these are clearly indicated as not type species.

Lastly, Section 4 is an outline of the phylogeny of Cardiidae as I have been able to construe it from my studies of the literature and of material in several large museum collections.

Section 1: Generic units of the Cardiidae

Taxon number, in section 3

ACANTHOCARDIA Gray, 1851. List of specimens . . British Mus., Pt. VII, p. 23. **Cardium aculeatum* Linné, 1758; SD, Stoliczka, 1870, p. 207. Syn.: *Archicardium; Eucardium; Orbis; Sphaerocardium* 4

Acanthocardium Römer, 1868 (?1865). Syst. Conch. Cab., ed. 2, vol. 10, pt. 2, Cardiacea, p. 17. **Cardium aculeatum* Linné, 1758; SD, Tryon, 1869, p. 60 ....[4]

ACROSTERIGMA Dall, 1900. Trans. Wagner Free Inst. Sci., vol. 3, pt. 5, p. 1073. **Cardium dalli* Heilprin, 1887; OD 27

Africofragum Eames, 1957. Bull. British Mus. (Nat. Hist.), Geol., vol. 3, no. 2, p. 61. **Fragum (A.) newtoni* Eames, 1957; OD. = *Schedocardia*..................................[8]

AFROCARDIUM Tomlin, 1931. Ann. Natal Gov. Mus., vol. 6, pt. 3, p. 449. **Fragum (A.) shepstonense* Tomlin, 1931; OD............36

AGNOCARDIA Stewart, 1930. Spec. Publ. Acad. Nat. Sci. Phila., vol. 3, p. 37, 264. **Cardium claibornense* Aldrich, 1911; OD. . .5

AMERICARDIA Stewart, 1930. *Ibid.*, p. 37, 267. **Cardium medium* Linné, 1758; OD........39

Amphicardium Von Martens, 1880, *in* Möbius, Beiträge zur Meeresfauna Mauritius, p. 324. **Cardium lyratum* Sowerby, 1841; SD, Keen, 1937, p. 5. = *Lyrocardium*. ....[61]

Aphrodite Lea, 1834 (*non* Hübner, 1816). = *Serripes*.................................[76]

APIOCARDIA Olsson, 1961. Panama-Pacific Pelecypoda, p. 252. **Cardium obovale* Sowerby, 1833; OD. 40

Archicardium Sandberger, 1863. Conchylien des Mainzer Tertiärbeckens, p. 317. **Cardium aculeatum* Linné, 1758; SD, Keen, 1937, p. 5. = *Acanthocardia*. ....[4]

ARCTOPRATULUM Keen, 1954. Bulls. Amer. Paleont., vol. 35, no. 153, p. 317. **Nemocardium (A.) griphus* Keen, 1954; OD..........54

Awadia Abbass, 1962. United Arab Repub. Min. Industry, Geol. Survey, Geol. Mus., Pal. Ser., Monog. 1, p. 128. **Nemocardium (A.) magharense* Abbass, 1962 (as *magharensis*); OD. = *Nemocardium*. ....[53]

BREVICARDIUM Stephenson, 1941. Univ. Texas Publ. no. 4101, p. 203. **B. fragile* Stephenson, 1941; OD....................43

BUCARDIUM Gray, 1853. Ann. Mag. Nat. Hist., (ser. 2) vol. 11, p. 40. **Cardium ringens* "Chemn.," i.e., Bruguière, 1789; SD, Von Vest, 1875, p. 323. Syn.: *Ringicardium*......2

Cardea Whitfield, 1885. U. S. Geol. Surv. Monog. 9, p. 134, note. **Cardium dumosum* Conrad, 1870; M. = *Criocardium*................[10]

Cardiarius Duméril, 1806. Zool. Analytique, p. 333. **Cardium edule* Linné, 1758; SM, Froriep, 1806, p. 83. = *Cerastoderma*. ....[70]

Cardissa Megerle von Mühlfeldt, 1811 Ges. Nat. Fr. Berlin, Mag., Vol. 5, p. 52. **C. alba* Meg. V. Mühlfeldt, 1811 = *Cardium cardissa* Linné, 1758; M. = *Corculum*. ....[34]

CARDIUM Linné, 1758. Systema Naturae, p. 678. **C. costatum* Linné, 1758; SD, Children, 1823, p. 315. Syn.: *Cordium; Tropidocardium*. 1

Cerastes Poli, 1795 (*non* Laurenti, 1768). = *Cerastoderma*. ....[70]

CERASTODERMA Poli,1795. Test. utriusque Sicil., vol. 2, p. 252, 258. **Cardium edule* Linné, 1758; SD Von Martens, 1870, p. 586. Syn.: *Cerastes; Cardiarius; Edulicardium*. 70

CILIATOCARDIUM Kafanov, 1974. Zool. Zh. Akad. Nauk, SSSR, vol. 53, no. 10, p. 1469. **Cardium ciliatum* Fabricius, 1780; OD. ...72

CLINOCARDIUM Keen, 1936. Trans. San Diego Soc. Nat. Hist., vol. 8, no. 17, p. 119. **Cardium nuttallii* Conrad, 1837; OD. ?Syn.: *Keenocardium*. 71

CONILOCARDIUM H. Vokes, 1977. Tulane Stud. Geol. Paleont., vol. 13, no. 4, p. 157. **Cardium cestum* Dall, 1900; OD. 23

Cor Mörch, 1852. Catal. conchyl. Yoldi, p. 36. [Not validly proposed — cited only in synonymy.] = *Corculum*......................[34]

CORCULUM Röding, 1798. Museum Boltenianum, p. 188. **Cardium cardissa* Linné, 1758; SD Von Martens, 1870, p. 586. Syn.: *Cardissa; Cor; Cordissa; Hemicardia*. 34

Cordissa Gistel, 1848. Naturges. Thier., p. xiv. [Emendation] = *Corculum*. ....[34]

Cordium Gistel, 1848. *Ibid.*, p. xiv. [Emendation] = *Cardium*..............................[1]

CRIOCARDIUM Conrad, 1870. Amer. Jour. Conch., vol. 6, p. 75. **Cardium (C.) dumosum* Conrad, 1870; SD Stoliczka, 1871, p. 486. Syn.: *Cardea; Criocarpium*, spelling error.......10

CRYPTOCARDIA Palmer, 1974. Palaeontology, vol. 17, no. 1, p. 168. **C. bajocensis* Palmer, 1974; OD.............................44

CTENOCARDIA H. & A. Adams, 1857. Genera Rec. Moll., vol. 2, p. 459. **Cardium hystrix* Reeve, 1844 (*non* Lightfoot, 1786) = *Fragum symbolicum* Iredale, 1929; SD, Dall, 1900...35

DALLOCARDIA Stewart, 1930. Spec. Publ. Acad. Nat. Sci. Phila., no. 3, p. 37, 264. **Cardium quadragenarium* Conrad, 1837; OD...24

Decussicardium Fischer-Piette, 1977. Mem. Mus. Natl. d'Hist. Nat., (n.s.) Ser. A, Zool., vol. 101, p. 94. [*Nomen nudum;* no type species designated; no generic diagnosis or discussion].

DINOCARDIUM Dall, 1900. Trans. Wagner Free Inst. Sci., vol. 3, pt. 5, p. 1074. *"*Cardium magnum* Born, 1778" (*non* Linné, 1758) = *C. robustum* [Lightfoot], 1786; OD. Syn.: *Exocardium*. 67

DISCORS Deshayes, 1858. Anim. s. vert. Bassin Paris, vol. 1, p. 553, 569. **Cardium discors* Lamarck, 1805 (*non* Montagu, 1803) = *C. parisiense* Orbigny, 1850; T. Syn.: *Hemidiscors*. 55

DIVARICARDIUM Dollfus & Dautzenberg, 1886. Feuille Jeunes Natural., 16me Ann., no. 188, p. 95. **Cardium discrepans* Basterot, 1825; SD, Cossmann, 1886, p. 175..........56

DOCHMOCARDIA Scott, 1978. Jour. Paleont., vol. 52, no. 4, p. 894. **Cardium pauperculum* Meek, 1871; OD. [*See* Appendix II]

Donacicardium Von Vest, 1875. Jahrb. mal. Ges., vol. 2, p. 322; OD. Syn.: *Donaciocardium*, emend. = *Hemidonax*. ....[41]

Edulicardium Monterosato, 1923. R. Comitato Talass. Ital., Mem. 107, p. 4. **Cardium edule* Linné, 1758; M. = *Cerastoderma*. ....[70]

ETHMOCARDIUM White, 1880. Proc. U. S. Natl. Mus., vol. 2, p. 291. **Cardium speciosum* Meek & Hayden, 1857 (*non* Adams & Reeve, 1850) = *C. whitei* Dall, 1900; OD. 11

Eucardium Fischer, 1887. Man. Conchyl., p. 1037. **Cardium aculeatum* Linné, 1758; SD, Stewart, 1930. = *Acanthocardia*. ....[4]

EUROPICARDIUM Popov, 1977. Trans. Paleont. Inst. SSSR, vol. 153, p. 44 [*Nom. nud.*, Popov, 1974]. **Cardium multicostatum* Brocchi, 1814; OD............................6

Exocardium Olsson, 1964. Neogene moll. Northwestern Ecuador, p. 55. **Cardium ecuadoriale* Olsson, 1932 (as *ecuadorialis*); OD. = *Dinocardium*............................[67]

FRAGUM Röding, 1798. Museum Boltenianum, p. 189. **F. flavum* Röding, 1798 = *Cardium fragum* Linné, 1758; T. Syn.: *Hemicardium; "Hemicardia* Spengler" of authors. 32

FRIGIDOCARDIUM Habe, 1951. Genera Japanese Shells: Pelecypoda, no. 2, p. 152. **Cardium eos* Kuroda, 1929; OD. Syn.: *Erigidocardium*, spelling error. 57

FULVIA Gray, 1853. Ann. Mag. Nat. Hist., (ser. 2) vol. 11, p. 40. **F. aperta* [Bruguière] = *Cardium apertum* Bruguière, 1789; M. 68

FUSCOCARDIUM Oyama, 1973. Palaeont. Soc. Japan, Spec. Pap., no. 17, p. 100. **Cardium braunsi* Tokunaga, 1906; OD.............73

GLOBOCARDIUM Hayami, 1965. Mem. Fac. Sci. Kyushu Univ., ser. D, Geol., vol. 17, no. 2, p. 116. **Cardium sphaeroideum* Forbes, 1845; OD. 45

GRANOCARDIUM Gabb, 1869. Geol. Survey Calif., Paleont., vol. 2, p. 266. **Cardium carolinum* Orbigny, 1844; SD, Stewart, 1930, p. 264. 9

HABECARDIUM Glibert & Van de Poel, 1970. Mém. Inst. Roy. Soc. Natl. Hist. Belgique, (ser. 2) fasc. 84, p. 34. **Cardium tenuisulcatum* Nyst, 1836; OD. 58

Hassbergia Krumbeck, 1939. Sitzber. phys.-mediz. Soz. Erlangen, vol. 71, p. 46. [Invalidly proposed; no type designation.] = *Protocardia*. . . . .[42]

HEDECARDIUM Marwick, 1944. Trans. Roy. Soc. New Zealand, vol. 74, pt. 3, p. 260. **Cardium waitakiense* Suter, 1907; OD. . . .20

Hemicardia Fleming, 1818. Encycl. Brit., Suppl. vols. 4-6, p. 304.**Cardium cardissa* Linné, 1758; M. [Earlier usage of *Hemicardia* by Spengler, 1799 was not at a generic but at a group level, as an informal term; the "*Hemicardia* Spengler" of authors is here considered a synonym of *Fragum*.] = *Corculum*. . . . .[34]

Hemicardium Schweigger, 1820. Handb. Naturg., p. 707. **Cardium cardissa* Linné, 1758; M. = *Corculum*. . . . .[34]

Hemidiscors Rovereto, 1898. Atti Soc. Ligustica, vol. 9, p. 181. **Cardium rugiferum* Rovereto, 1898; OD. = *Discors*. . . . .[55]

HEMIDONAX Mörch, 1870. Malak. Bl., vol. 17, p. 121. **Donax pictus* Tryon, 1870, = *Cardium donaciforme* Bruguière, 1792 [cited by Boss, 1971, as of Schroeter, 1786; a non-binomial work, *fide* Sherborn, *Index Anim*., vol. 1, 1902]; M. Syn.: *Donacicardium*. 41

INCACARDIUM Olsson, 1944. Bulls. Amer. Paleont., vol. 28, no. 111, p. 211. **Cardium (I.) mellisum* Olsson, 1944; OD. 12

INTEGRICARDIUM Rollier, 1912. Mém. Soc. Pal. Suisse [=Abh. Schweiz Pal. Ges.], vol. 38, p. 127. **Cardium dupinianum* Orbigny, 1844; OD. 50

JURASSICARDIUM Cossmann, 1906. Compt.-Rend. Assoc. Franç. Avanc. Sci., vol. 34, p. 294. **Cardium (J.) axonense* Cossmann, 1906; M. [sole species eligible for designation; SD Keen, 1937]. 52

Kathocardia Tucker & Wilson, 1932. Bulls. Amer. Paleont., vol. 18, no. 65, p. 44. **Cardium (K.) aclinense* Tucker & Wilson, 1932 (as *aclinensis*); OD. = *Trachycardium*. . . . . . .[22]

KEENAEA Habe, 1951. Genera Japanese Shells: Pelecypoda, no. 2, p. 152. **Cardium samarangae* Makiyama, 1934; OD. 59

?KEENOCARDIUM Kafanov, 1974. Zool. Zh. Akad. Nauk, SSSR, vol. 53, no. 10, p. 1468. **Cardium californiense* Deshayes, 1839; OD. [Of doubtful utility; probably = *Clinocardium, s.s.*, although named as a subgenus.]. . . . .[74]

[KOROBKOVIELLA] Merklin, 1974. Trans. Palaeont. Inst., vol. 145, p. 97. **Cerastoderma (K.) kiktenkoi* Merklin, 1974; OD. [Reallocated to Lymnocardiinae by Popov, 1977, p. 77].

LAEVICARDIUM Swainson, 1840. Treatise Malac., p. 373. **Cardium oblongum* "Chemn.," i.e., Gmelin, 1791; SD, Stoliczka, 1871, p. xviii. Syn.: *Levicardium; Liocardium; Loevicardium*, emendations. 66

LEPTOCARDIA Meek, 1876. U. S. Geol. Surv. Terr., vol. 9, p. 172. **Cardium subquadratum* Evans & Shumard, 1857; SD, Dall, 1901, p. 385. 46

LOPHOCARDIUM Fischer, 1887. Man. Conchl., p. 1038. **Cardium cumingii* Broderip, 1833; M. 60

LOXOCARDIUM Cossmann, 1886. Ann. Soc. Roy. Malac. Belgique, vol. 21, p. 172. **Cardium formosum* Deshayes, 1858; SD, Crosse, 1887, p. 332. 13

LUNULICARDIA Gray, 1853. Ann. Mag. Nat. Hist., (ser. 2) vol. 11, p. 41. **L. retusa*, i.e., *Cardium retusum* Linné, 1767; M. Syn.: *Opisocardium*. 33

LYROCARDIUM Meek, 1876. U. S. Geol. Surv. Terr., vol. 9, p. 173. **Cardium lyratum* Sowerby, 1841; SD, Dall, 1900, p. 1076. Syn.: *Amphicardium*. 61

MAORICARDIUM Marwick, 1944. Trans. Roy. Soc. New Zealand, vol. 74, pt. 3, p. 263. **Cardium spatiosum* Hutton, 1873; OD. 16

MEXICARDIA Stewart, 1930. Spec. Publ. Acad. Nat. Sci. Phila., no. 3, p. 37, 263. **Cardium procerum* Sowerby, 1833; OD. 25

MICROCARDIUM Thiele, 1934. Handb. Syst. Weichtierk., pt. 3, p. 878. **Cardium peramabile* Dall, 1881 (as *peramabilis*); SD, Keen, 1937, p. 15. 62

MICROFRAGUM Habe, 1951. Genera Japanese Shells: Pelecypoda, no. 2, p. 148. **Cardium festivum* Deshayes, 1854; OD. 37

NEMOCARDIUM Meek, 1876. U. S. Geol. Surv. Rept., vol. 9, p. 167. **Cardium semiasperum* Deshayes, 1858; SD, Sacco, 1899, p. 56. Syn.: *Awadia*. 53

ONESTIA McLearn, 1933. Trans. Roy. Soc. Canada, (ser. 3) vol. 27, pt. 4, p. 152. **Laevicardium onestae* McLearn, 1931; OD. 51

Opisocardium Bayle, 1879. Jour. Conchyl., vol. 27, p. 35. **Cardium retusum* Linné, 1767; OD. = *Lunulicardia*. . . . .[33]

Orbis Blainville, 1825 (*non* Müller, 1767). = *Acanthocardia*. . . . .[4]

ORTHOCARDIUM Tremlett, 1950. Proc. Malac. Soc. London, vol. 28, p. 128. **Cardium porulosum* Solander, 1766; OD. 3

OVICARDIUM Marwick, 1944. Trans. Roy. Soc. New Zealand, vol. 74, pt. 3, p. 268. **Trachycardium (O.) rossi* Marwick, 1944; OD. 28

PACHYCARDIUM Conrad, 1869. Amer. Jour. Conch., vol. 5, p. 96. **Cardium spillmani* Conrad, 1858; SD, Dall, 1900, p. 1076. 47

PAPILLICARDIUM Sacco, 1899. I Molluschi terr. terz. Liguria, pt. 27, p. 44. **Cardium papillosum* Poli, 1795; OD. 17

PAPYRIDEA Swainson, 1840. Treat. Malac., p. 374. **Cardium soleniforme* Bruguière, 1789; SD, Gray, 1847, p. 185 30

PARVICARDIUM Monterosato, 1884. Nomencl. gen. e spec. medit., p. 19. **Cardium parvum* Philippi, 1844 (*non* Da Costa, 1778) = *C. exiguum commutata* Bucquoy, Dautzenberg, & Dollfus, 1892; SD, Crosse, 1885, p. 140 14

Pascoella Cox, 1949. Bull. Inst. Geol. Peru, no. 12, p. 33. **P. peruviana* Cox, 1949; OD. = *Septocardia*. . . . .[18]

Pectunculus Mörch, 1853 (*non* Da Costa, 1778). = *Vepricardium*. . . . .[19]

PERUCARDIA Olsson, 1944. Bulls. Amer. Paleont., vol. 28, no. 111, p. 209. **Cardium (P.) brueggeni* Olsson, 1944; OD. 21

PHLOGOCARDIA Stewart, 1930. Spec. Publ. Acad. Nat. Sci. Phila., no. 3, p. 38, 263. **Cardium belcheri* Broderip & Sowerby, 1829; OD. 26

PLAGIOCARDIUM Cossmann, 1886. Ann. Soc. Roy. Malac. Belgique, vol. 21, p. 168. **Cardium granulosum* Lamarck, 1805; SD, Crosse, 1887, p. 332. 15

PLANICARDIUM Olsson, 1967. Some Tertiary mollusks . . Caribbean, p. 11. **Cardium virginianum* Conrad, 1839; OD. 75

PLEURIOCARDIA Scott, 1978. Jour. Paleont., vol. 52, no. 4, p. 893. **Cardium kansasense* Meek, 1871; OD. [*See* Appendix II]

PRATULUM Iredale, 1924. Proc. Linn. Soc. N. S. Wales, vol. 49, p. 182. **Cardium thetidis* Hedley, 1902; OD. 63

PROFULVIA Kafanov, 1976. Paleontol. Zh., SSSR, no. 4, p. 111. **Papyridea harrimani* Dall, 1904; OD. 69

PROTOCARDIA Von Beyrich, 1845. Zeit. f. Malak., vol. 2, p. 17. **Cardium hillanum* J. de C. Sowerby, 1813; SD, Herrmannsen, 1847, p. 336. Syn.: *Protocardium*, invalid emendation; *Hassbergia*. 42

REGOZARA Iredale, 1936. Rec. Australian Mus., vol. 19, no. 5, p. 275. **R. olivifer* Iredale, 1936; OD. 29

Ringicardium Fischer, 1887. Man. Conchyl., p. 1037. **Cardium ringens* "Chemn.," i.e., Bruguière, 1789; M. = *Bucardium*. . . . . . .[2]

RUDICARDIUM Coen, 1915. Ann. Mus. Civico Storia Nat. Genova, vol. 46, p. 299. **Cardium tuberculatum* Linné, 1758; SD, Keen, 1937, p. 17. 7

SCHEDOCARDIA Stewart, 1930. Spec. Publ. Acad. Nat. Sci. Phila., no. 3, p. 38, 255. **Cardium hatchetigbeense* Aldrich, 1886; OD. Syn.: *Africofragum*. 8

SEPTOCARDIA Hall & Whitfield, 1877. Rept. U. S. Geol. Surv. Explor. Exped. 40th Parallel, vol. 4, p. 294. **S. typica* Hall & Whitfield, 1877; OD. Syn.: *Pascoella*. 18

SERRIPES Gould, 1841. Invert. of Massachusetts, p. 93. **Cardium groenlandicum* Bruguière, 1789; M. Syn.: *Aphrodite; Yagudinella* 76

Sphaerocardium Coen, 1933. Mus. Com. Talass. Ital., Mem. no. 192. p. 132. **Cardium paucicostatum* Sowerby, 1841 (*non* Deshayes, 1838); SD, Keen, 1937. Syn.: *Sphoerocardium*, spelling error. = *Acanthocardia*. . . . .[4]

TENDAGURIUM Dietrich, 1933. Palaeontographica, Suppl. 7, Reihe 2, Teil 2, Lief. 1, p. 50. **Cardium (T.) propebanneianum* Dietrich, 1933; SD, Salisbury, 1934, p. 103. 48

TRACHYCARDIUM Mörch, 1853. Catal. conchyl. Yoldi, p. 34. **Cardium isocardia* Linné, 1758; SD, Von Martens, 1870, p. 586. Syn.: *Kathocardia*. 22

TRIFARICARDIUM Habe, 1951. Genera Japanese Shells: Pelecypoda, no. 2, p. 152. **T. nomurai* Habe, Sept., 1951, *ex* Kuroda & Habe MS, June, 1951 .64

TRIGONIOCARDIA Dall, 1900. Trans. Wagner Free Inst. Sci., vol. 3, pt. 5, p. 1075. **Cardium graniferum* Broderip & Sowerby, 1829; OD. 38

Tropidocardium Römer, 1868 (?1865). Syst. Conch. Cab., ed. 2, vol. 10, pt. 2, Cardiacea, p. 13. **Cardium costatum* Linné, 1758; SD Tryon, 1869, p. 60. Syn.: *Tropicardium*, emend.; = *Cardium, s.s.* . . . .[1]

[Tulongocardium] "Chen, J.Chen, & Zhang," *in* Wen Shi-xuan *et al.*, 1976. Rept. Sci. Exped. Mount Jolmo Lungma Region Palaeont., Fasc. 3, p. 31. **Cardium (T.) pluriradiatum* "Chen, Chen, & Zhang" in Wen Shi-xuan *et al.*, 1976; OD. [Probably not cardiid; ?= *Tutcheria* Cox, in Astartacea.]

VARICARDIUM Marwick, 1944. Trans. Roy. Soc. New Zealand, vol. 74, pt. 3, p. 266. **Cardium patulum* Hutton, 1873; OD. 65

VASTICARDIUM Iredale, 1927. Rec. Australian Mus., vol. 16, p. 75. *"*Cochlea nebulosa* Martyn," =*Cardium elongatum* Bruguière, 1789; OD. 31

VEPRICARDIUM Iredale, 1929. Australian Zool., vol. 5, p. 338. **V. pulchricostatum* Iredale, 1929; OD. Syn.: *"Pectunculus"*. 19

Yagudinella Kafanov, 1975. [Investigations of Mollusks, 5th Meeting], Zool. Inst., Akad. Nauk, SSSR, p. 147. **Cardium notabile* Sowerby III, 1915; OD. =*Serripes*. 76

YOKOYAMAINA Hayami, 1958. Japanese Jour. Geol. Geogr., vol. 29, p. 24. **Cyrena elliptica* Yokoyama, 1904 (*non* Dunker, 1843), =*Y. hayamii* Keen & Casey *in* Moore, *et al.*, 1969; OD. [Originally allocated to the Arcticidae by Hayami; reassigned, with new evidence, to Cardiidae by Hayami, 1972 (Geol. & Paleont. of Southeast Asia, vol. 10, p. 204, pl. 38, figs. 10-11)]. 49

Section 2: Keys to the generic units within Subfamilies

FAMILY CARDIIDAE

Diagnosis of family:

Shells: Equivalve, usually tumid, with well developed radial sculpture; posterior slope normally set off from central and anterior slopes by an umbonal ridge or angle or by a change in ribbing pattern; ligament parivincular, external, mostly short; hinge with two conical cardinal teeth, of unequal size in left valve, somewhat fused in right, arrangement of cardinal teeth in many cruciform (*i.e.*, interlocking in the form of a cross); lateral teeth distant from cardinals, normally one anterior and one posterior in left valve, two anterior and one posterior in right valve (wanting in some groups); adductor muscle scars subequal; pallial line entire in most.

Soft parts: Foot elongate, geniculate (sickle-shaped) in all but one group (see Plate 3, figure 1); siphons short, not markedly extensile or retractile, not having any elaborate siphonal retractor muscle connections; adductor muscles subequal; mantle gape extensive, from the area of the incurrent aperture to the anterior adductor muscle; pallial eyes and pedal-byssal groove present in most; gills plicate, the axis generally dorso-ventrally skewed, with both inner and outer demibranchs.

Distribution: worldwide, greatest abundance in the tropics; also occurring in cold-temperate seas, mainly in shallow water on sandy shores, in sand or sandy mud, shallowly burrowing; some groups offshore in depths to 300 m.

SUBFAMILY CARDIINAE

Shells tumid to inflated, outline mostly equilateral or nearly so; ribs well developed, symmetrical, characteristically sculptured along the rib midline by a spinose or nodose thread or by a groove; posterior margin usually notched by rib ends; interspaces between ribs often with concentric striae; hinge long, hinge teeth nearly in a straight line (*i.e.*, a line joining lateral teeth would bisect the cardinals or be bent less than 25°); cardinal teeth subequal in size, tending to be twisted in left valve or even to lie horizontally one above the other.

Key to generic units

[Taxon number, in section 3]

1. With a large posterior gape . . . . CARDIUM s.s. [1]
   Posterior gape small, or posterior end tightly closed 2
2. Posterior ribs prolonged (digitate), interlocked . . . . .BUCARDIUM [2]
   Posterior ribs notching margin but not digitate 3
3. Ribs of two sizes: *i.e.*, intercalary riblets present 4
   Ribs without any intercalary riblets between main ribs 5
4. Intercalaries two to three in number . . . . GRANOCARDIUM [9]
   With only one, usually spinous, intercalary CRIOCARDIUM (in part) [10]
5. Valve interior pitted in the inter-rib spaces . . . . .ETHMOCARDIUM [11]
   Interior not pitted 6
6. A deep cavity below hinge for lodgment of the anterior adductor muscle . . . . SEPTOCARDIA [18]
   No deep cavity below anterior part of hinge 7
7. Outline somewhat inequilateral, *i.e.*, trapezoidal or oblique-elliptical 8
   Outline nearly equilateral 13
8. Shells small, adults mostly less than 15 mm long 9
   Shells medium-sized to large, more than 15 mm long 10
9. Hinge weak, cardinal teeth minute; ribs with spines or prickles . .PARVICARDIUM [14]
   Hinge with well-developed cardinal teeth; ribs with rounded beads . . . . PAPILLICARDIUM [17]
10. Trapezoidal; sculpture of spines or nodes .11
    Ovate; sculpture of regular beads 12
11. Rib sculpture well developed, often with spines . . . . .ACANTHOCARDIA [4]
    Rib sculpture irregular, of low scales or absent anteriorly . . . . .SCHEDOCARDIA [8]
12. Shells medium-sized; cardinal teeth about midway between laterals . . . . PLAGIOCARDIUM [15]
    Shells mostly large-sized; anterior section of hinge shorter than posterior . . . . MAORICARDIUM [16]
13. Ribs ornamented with well-spaced A-shaped, non-imbricate scales or nodes . . . . AGNOCARDIA [5]
    Ribs not with A-shaped nodes 14
14. Hinge relatively short (about ½ length of shell) 15

Hinge relatively long (more than ½ length of shell) 17

15. Posterior area set off by a sinuous ventral margin .... INCACARDIUM [12]

Posterior area not set off ventrally by a sinuosity 16

16. Ribs numerous (usually more than 60) EUROPICARDIUM [6]

Ribs less numerous (about 35 to 55) LOXOCARDIUM [13]

17. Ribs with rounded nodes along central furrow 18

Ribs either with spines or nearly smooth .. 19

18. Interspaces between ribs narrow .... PERUCARDIA [21]

Interspaces as wide as ribs .... RUDICARDIUM [7]

19. Sculpture of ribs spinose 20

Ribs nearly smooth except for a faint central groove 21

20. Hinge plate meeting posterior and anterior margins at a right angle .... ORTHOCARDIUM [3]

Hinge plate rounding into posterior and anterior margins ..... VEPRICARDIUM [19]

Table 1. Salient characters of cardiid subfamilies

++: Present in all generic taxa (genera or subgenera)
x: Present in many or most generic taxa
o: Present in only a few taxa

	Cardiinae	Fraginae, Hemidonacinae	Trachycardiinae	Protocardiinae	Laevicardiinae
POSTERIOR MARGIN					
Notched	x	x	++	x	
Wavy	o	o			++
Smooth (may be crenulate within)				o	x
POSTERIOR SLOPE					
More strongly ribbed than rest of shell				x	
Less strongly ribbed than rest of shell		o		o	++
Equally strong ribbed	x	x	++	o	o
Smooth				o	x
OUTLINE					
Quadrate			x	x	
Elliptical-ovate	x	o	x	x	x
Trigonal	o	x		o	
Trapezoidal	x	o		x	x
RIB SURFACES					
Smooth or unsculptured	x	o	o	x	o
With raised cross-threads		x	x	x	x
Nodose	x				
Spinose	x	x	x	x	
RIB INTERSPACES					
Smooth, with growth lines only	x	o	x	x	x
With raised to ladder-like cross-striae	x	x		o	
Spinose	o		o		
HINGE					
Short, ½ or less shell length	o	x	++	o	
Long, more than ½ length	x			x	
Straight, deflection mostly less than 25°	++		x	x	
Angulate to arched, deflection more than 25°		++	x	x	++
Relatively wide, teeth strong and solid		x	x	x	
Relatively narrow, teeth thin to blade-like	x				x

21. Shell medium-sized to large; interspaces between ribs wide .HEDECARDIUM [20]
    Shell relatively small, interspaces narrow to linear ......CRIOCARDIUM (in part) [10]

SUBFAMILY TRACHYCARDIINAE

Mostly asymmetrical or inequilateral shells; ribs asymmetrical in cross section, well developed throughout shell; spines or other sculpture on ribs usually stronger on posterior edges of ribs; posterior margin notched or even digitate; hinge relatively short, usually less than one-half length of shell, the hinge plate wide in most, cardinal teeth unequal, posterior cardinal in left valve slender.

Key to Generic Units

1. Shell with a posterior gape PAPYRIDEA [30]
   Posterior margins of shell in contact or separated by no more than a chink 2
2. Height and length nearly equal; sculpture, especially along posterior sides of ribs, thorn-like. ....DALLOCARDIA [24]
   Height greater than length; sculpture various but not of thorn-like spines on posterior edges of ribs 3
3. Rib ornamentation of beads and imbricate or overlapping hollow scales .... TRACHYCARDIUM [22]
   Rib ornamentation not of hollow scales 4
4. Ribs triangular in cross section............5
   Ribs rounded to rectangular in cross section 6
5. Shell heavy for its size ...MEXICARDIA [25]
   Shell not markedly heavy for its size .... CONILOCARDIUM [23]
6. Rib ornamentation of knobbed frills along sides, especially on central slope .... PHLOGOCARDIA [26]
   Rib ornamentation not of knobbed frills 7
7. Hinge plate with an oblique groove behind posterior cardinal tooth .... OVICARDIUM [28]
   Hinge plate flat behind posterior cardinal tooth 8
8. Hinge sharply bent to an angle greater than 60°; ribs nearly smooth .... ACROSTERIGMA [27]
   Hinge angle not more than 60°; ribs with wrinkles or scales, especially along eaves.................................9
9. Ribs relatively numerous (more than 30) ..... VASTICARDIUM [31]
   Ribs usually fewer than 30 . .REGOZARA [29]

SUBFAMILY FRAGINAE

Shell inequilateral in outline; umbonal ridge strong in most; posterior margin meeting ventral margin at a 90° angle or less; ribs equally emphasized throughout, intercostal spaces with concentric striations, an intritacalx (chalky surface layer) present in most well-preserved specimens; posterior margin usually notched; hinge relatively short, angulate (*i.e.*, anterior and posterior sections meeting at a sharp angle). Soft parts as in most groups of the family, with geniculate foot.

SUBFAMILY HEMIDONACINAE

Shell inequilateral, much as in Fraginae, but anterior end relatively longer; ribs smooth-surfaced, lacking any intritacalx, intercostal spaces without concentric striations; lateral teeth of hinge elongate. Animal with bilaterally compressed, not geniculate, foot; no pallial eyes or pedal-byssal groove; axis of ctenidia not dorsoventrally skewed. With only one genus, *Hemidonax*.

Combined Key to Generic Units of Fraginae and Hemidonacinae

1. Ribs sculptured with tubular spines 2
   Ribs variously sculptured but not with tubular spines 3
2. Umbonal ridge weak; outline elliptical to ovate ....AFROCARDIUM [36]
   Umbonal ridge clearly evident; outline trapezoidal to quadrate ...CTENOCARDIA [35]
3. With a deep lunule distorting the hinge ...... LUNULICARDIA [33]
   With no lunule; hinge not markedly distorted 4
4. Shell compressed laterally; posterior slope nearly flat; height more than twice length CORCULUM [34]
   Not laterally compressed; height and length approximately equal....................5
5. Anterior lateral teeth crowded against cardinals 6
   Cardinal teeth nearly equidistant between laterals 7
6. Ribs with beaded sculpture along crests ..... TRIGONIOCARDIA [38]
   Ribs smooth or nearly so . .APIOCARDIA [40]
7. Adult shells small, less than 15 mm in height MICROFRAGUM [37]
   Adult shells more than 15 mm in height 8
8. Elongate-trigonal, length greater than height; intercostal spaces not striate .... HEMIDONAX [41]
   Length not greater than height; interspaces concentrically striate 9
9. Hinge oblique, not parallel to ventral margin FRAGUM [32]
   Hinge roughly parallel to ventral margin..... AMERICARDIA [39]

SUBFAMILY PROTOCARDIINAE

Shell rounded-quadrate in outline, nearly equilateral; radial ribs present in most; posterior slope usually more strongly ribbed than remainder of shell, ribs often spinose; ribs of central and anterior slopes, when present, fine and numerous; hinge line long, nearly straight to somewhat arched; cardinal teeth, especially anterior cardinals, well developed; anterior laterals strong (rarely wanting).

Key to generic units

1. Shell smooth, lacking either radial or concentric ribs externally (weak radial threads or internal ridges may occur in some) 2
   Shell with clear-cut external sculpture on at least one slope 6
2. Outline elliptical; shell lacking any umbonal ridge . . . . INTEGRICARDIUM [50]
   Outline ovate-quadrate; with an umbonal ridge setting off posterior area 3
3. With one or two internal ribs at junction of central slope and posterior area (not always leaving a trace on surface of shell) . . . . CRYPTOCARDIA [44]
   No internal ribs bounding posterior area (a low ridge is not considered to be a rib) . . .4
4. Ligament short, in a deep groove; pallial line entire . . . . ONESTIA [51]
   Ligament moderate to long; pallial line with a small sinus 5
5. Umbones broad, elevated, nearly central . . . TENDAGURIUM [48]
   Umbones narrow, low, anterior to midline . . . . YOKOYAMAINA [49]
6. Radial ribs present only at umbonal angle LEPTOCARDIA [46]
   Radial ribs not confined to umbonal angle area 7
7. With well-defined, regular concentric ribs on at least the anterior slope 8
   Concentric ribbing weak to wanting or irregular (some oblique sculpture may be present) 12
8. With faint radial ribs on central and anterior slopes, forming cancellate sculpture at intersections . . . . . . BREVICARDIUM [43]
   Radial sculpture of anterior and central slopes too weak to cause cancellations . . .9
9. Concentric sculpture somewhat irregular, on anterior and ventral marginal areas only . . . . VARICARDIUM [65]
   Concentric sculpture regular, covering anterior and central slopes 10
10. Height nearly twice length (*i.e.*, shell ovate) PACHYCARDIUM [47]
    Height equal to length (*i.e.*, shell circular or quadrate) 11
11. With a weak internal ridge setting off posterior slope, crenulating margin as one or two large knobs . . GLOBOCARDIUM [45]
    With no internal ridge and no large knob on ventral margin at junction of central and posterior areas . . . . . PROTOCARDIA [42]
12. With secondary sculpture oblique to growth lines on one or more slopes 13
    Secondary sculpture, when present, congruent with growth lines 15
13. Secondary sculpture on anterior and posterior slopes . . . . DIVARICARDIUM [56]
    Secondary sculpture on central and anterior slopes 14
14. Shell inequilateral, outline oblique; secondary sculpture unevenly spaced and sinuous . . . . DISCORS [55]
    Shell equilateral, quadrate; secondary sculpture even spaced . . . LYROCARDIUM [61]
15. Anterior lateral teeth wanting . . . . LOPHOCARDIUM [60]
    Anterior lateral teeth present 16
16. Posterior margin meeting dorsal at a right angle . . . . JURASSICARDIUM [52]
    Posterior margin meeting dorsal in a wide arc 17
17. Marginal crenulations coarser on posterior margin than elsewhere 18
    Marginal crenulations about the same throughout 22
18. Radial ribs on central and anterior slopes fine to smooth-surfaced 19
    Radial ribs on central or anterior slopes beaded 20
19. Ribs of posterior slope with beads or spines NEMOCARDIUM [53]
    Ribs of posterior slope smooth-surfaced . . . . HABECARDIUM [58]
20. With beading on anterior slope only . . . . TRIFARICARDIUM [64]

PLATE 1

Illustrated terminology

Figures

1. Terms applied to shell interior
2-5. Types of sculpture
6. Terms applied to shell exterior
7. Method of measuring hinge angle

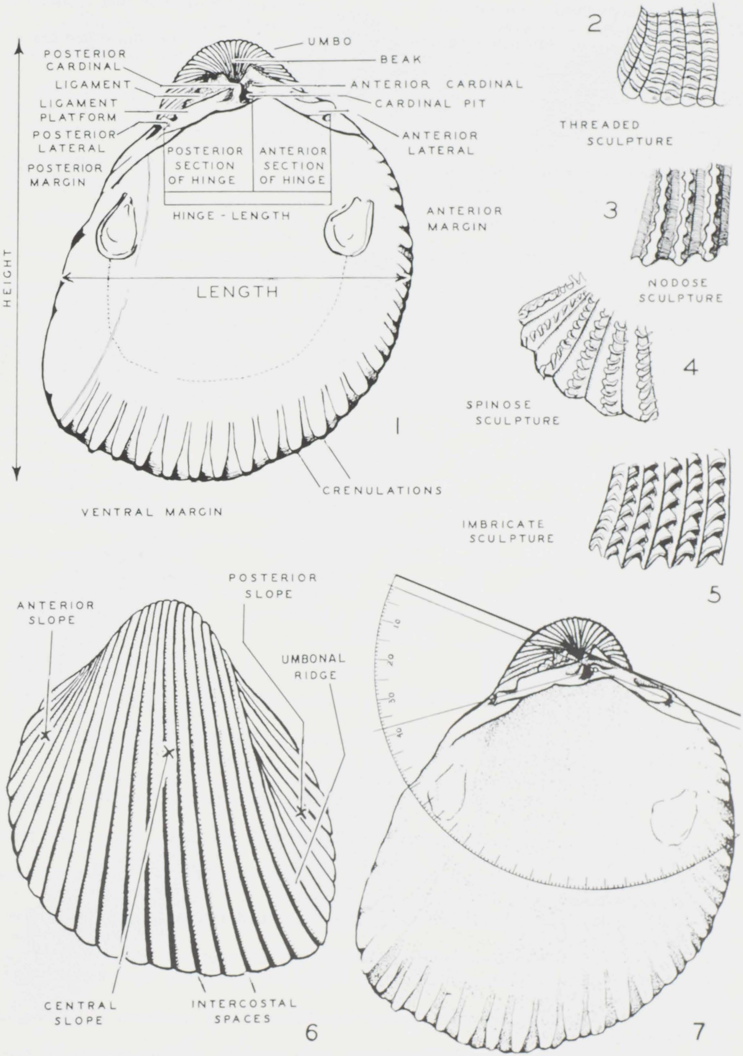
UMBO
BEAK
POSTERIOR CARDINAL
LIGAMENT
LIGAMENT PLATFORM
POSTERIOR LATERAL
POSTERIOR MARGIN
ANTERIOR CARDINAL
CARDINAL PIT
ANTERIOR LATERAL
POSTERIOR SECTION OF HINGE
ANTERIOR SECTION OF HINGE
HINGE - LENGTH
ANTERIOR MARGIN
HEIGHT
LENGTH
1
CRENULATIONS
VENTRAL MARGIN
2
THREADED SCULPTURE
3
NODOSE SCULPTURE
4
SPINOSE SCULPTURE
IMBRICATE SCULPTURE
5
ANTERIOR SLOPE
POSTERIOR SLOPE
UMBONAL RIDGE
CENTRAL SLOPE
INTERCOSTAL SPACES
6
10
20
30
40
7

PLATE 1

Beading not confined to anterior slope . . .21

21. Beaded ribs fine, all the same size . . . . MICROCARDIUM [62]

    Beading somewhat coarse, alternate ribs larger . . . . FRIGIDOCARDIUM [57]

22. With secondary concentric laminae throughout . . . . PRATULUM

    Secondary concentric laminae on posterior slope only 23

23. Outline quadrate, hinge relatively long . . . . . KEENAEA [59]

    Outline trigonal, hinge relatively short . . . . . . ARCTOPRATULUM [54]

SUBFAMILY LAEVICARDIINAE

Shell outline elliptical-oblique; posterior slope smoother or less heavily ribbed than remainder of shell; posterior margin entire or slightly wavy but not notched at rib-ends (a few crenulations may be present within); ribs mostly weak or lightly incised; hinge line long, arched; anterior lateral tooth long, often bladelike.

Key to generic units

1. Radial ribs present on anterior and posterior slopes but obsolete on the central part . . . . SERRIPES [76]

   Radial ribs present on at least central slope 2

2. Outer surface of shell mostly smooth or finely striate (radial ribs may be present internally in middle layer of shell, reflected as fine marginal crenulations) 3

   Outer surface with well developed ribs on anterior and central slopes, weaker or absent on posterior .4

3. Marginal crenulations, if present, faint; all shells thin and fragile . . . . FULVIA [68]

   Marginal crenulations well developed; some shells thin, others sturdy . . . . LAEVICARDIUM [66]

4. Beaks prosogyrate, the initial part or tip lying above anterior cardinal teeth 5

   Beaks orthogyrate, tip above midpoint between the two cardinal teeth 9

5. Ribs triangular in section, often with a periostracal fringe along crest . . . . CILIATOCARDIUM [72]

   Ribs rounded to squarish in section; periostracum, if present, not fringed 6

6. Intercostal spaces, especially on central slope, as broad as ribs 7

   Intercostal spaces narrower than ribs 8

7. Ribs smooth, their tops flattened . . . . PLANICARDIUM [75]

   Ribs granulated, with slightly rounded tops FUSCOCARDIUM [73]

8. Ribs sculptured with coarse cross-threads CLINOCARDIUM [71]

   Ribs sculptured with fine cross-threads . . . . . ?KEENOCARDIUM [74]

9. Height greater than length . . . . DINOCARDIUM [67]

   Height equal to or less than length 10

10. Anterior part of hinge with a heavy inner buttress . . . . [KOROBKOVIELLA]

PLATE 2

Subfamily Cardiinae, interiors of left valves

Figures

1. *Loxocardium formosum* (Deshayes). *Ex* Deshayes, 1858. Eoc., France (× 2)
2. *Cardium costatum* Linné. SU specimen. Rec., W. Afr. (× 0.5)
3. *Cardium (Bucardium) ringens* Linné. SU specimen. Rec., W. Afr. (× 1.5)
4. *Vepricardium (Vepricardium) pulchricostatum* Iredale. SU specimen. Rec., Moreton Bay, Australia (× 0.75)
5. *Granocardium (Criocardium) dumosum* (Conrad). SU coll., from plaster cast of topotype. Cret., New Jersey (× 1.5)
6. *Granocardium (Granocardium) proboscideum* (J. Sowerby, 1817). Not the type species. After Woods, 1908. Cret., England (× 1)
7. *Parvicardium commutatum* (Bucquoy, Dautzenberg, & Dollfus). SU specimen. Rec., Palermo, Sicily (× 5)
8. *Plagiocardium (Papillicardium) papillosum* (Poli). SU specimen. Rec., France (× 4)
9. *Granocardium (Ethmocardium) whitei* (Dall). SU specimen, topotype. U. Cret., Montana (× 5)
10. *Plagiocardium (Plagiocardium) granulosum* (Lamarck). SU specimen. U. Eocene, La Guepelle, France (× 2)
11. *Acanthocardia (Schedocardia) hatchetigbeensis* (Aldrich). After original figure. Eoc., Mississippi (× 1)
12. *Acanthocardia (A.) aculeata* (Linné). SU specimen. Rec., France (× 1)

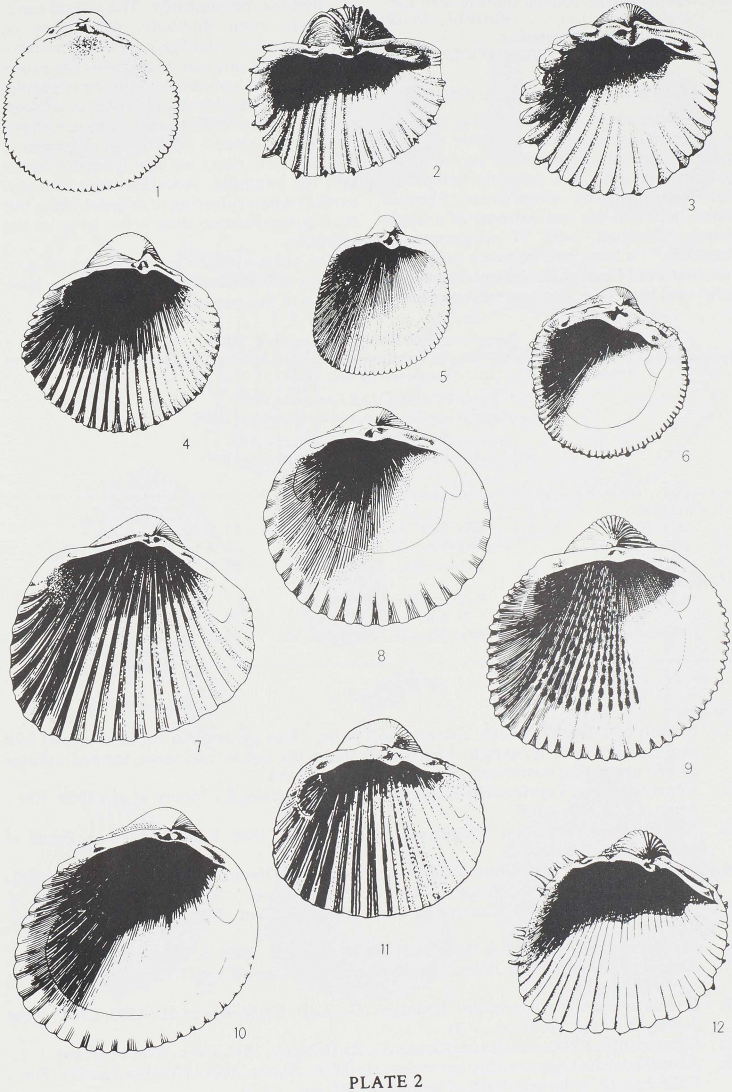

PLATE 2

Anterior part of hinge not buttressed 11
11. Posterior margin slightly or moderately gaping ....PROFULVIA [69]
Posterior margin not gaping .... CERASTODERMA [70]

Section 3. Classification here Adopted

Grouping of recognizably distinct units into larger constellations is a matter of judgment. There are, fortunately, no rules that govern ranking. The patterns arrived at here represent the compromises I would make between the one extreme of a single genus, *Cardium*, with 77 subgenera or "sections" (a term now obsolete under the *International Code of Zoological Nomenclature*) and the other extreme of recognizing as full genera all units that can be distinguished morphologically. The actual ranking may even fluctuate, depending on purpose: a few broad groups would be justified in a semi-popular work, whereas in one addressed to specialists, who need finely-drawn divisions for stratigraphic or ecological interpretations, much more emphasis should be placed on subtle differences. Perhaps one need not always write out in full, for example, *Acanthocardia (Schedocardia)* when referring to *Schedocardia;* but such subordination does serve to point out affinities.

The abbreviations in the column on geographic distribution are explained in a later section of this paper.

Superfamily CARDIACEA Lamarck, 1809
[proposed as a vernacular term, "famille cardiacées"; spelling latinized by Goldfuss, 1820; ranking corrected by Gill, 1871]

Family CARDIIDAE Lamarck, 1809
[vernacular spelling latinized by Broderip, 1839]

Subfamily CARDIINAE Lamarck, 1809
[first ranked as a subfamily by Stoliczka, 1871]

Taxon	Distribution	Illustrations
1. *Cardium*		
(Cardium)	Mio.-Rec., W. Afr.-Medit.	Pl. 2, fig. 2; Pl. 4, fig. 2
2. *(Bucardium)*	Mio.-Rec., W. Afr.-Medit.	Pl. 2, fig. 3; Pl. 4, fig. 4
3. *(Orthocardium)*	Paleoc.-Eoc., Eu.	Pl. 4, fig. 1
4. *Acanthocardia*		
(Acanthocardia)	U.Oligo.-Rec., Eu.-Medit.-N.Am.	Pl. 2, fig. 12; Pl. 4, fig. 5
5. *(Agnocardia)*	Eoc.-Mio., N.Am.-S.Am.-Eu.	Pl. 3, fig. 9

PLATE 3

Figures
1. Sketch of a living cardiid, showing soft parts. Note genticulate (sickle-shaped) foot projecting anteriorly, at right, long mantle that is slit, below, and short, fringed siphons at left, projecting posteriorly. *Ex* H.&A. Adams, 1858.
2. ***Vepricardium (Vepricardium) pulchricostatum*** Iredale. *Ex* Moore *et al.*, 1969. Rec., Australia (R ext. × 0.6)
3. ***Loxocardium formosum*** (Deshayes). *Ex* Deshayes, 1858. Eoc., France (a, detail of sculpture; b, L ext. × 2)
4. ***Vepricardium (Perucardia) brueggeni*** (Olsson). *Ex* Olsson, 1944. U. Cret., Peru (a, L ext.; b, L, section of the hinge; c, detail of sculpture; a-b, × 0.5)
5. ***Incacardium mellisum*** (Olsson). *Ex* Olsson, 1944. U. Cret., Peru (a, R ext.; b, R int.; × 1.5)
6. ***Septocardia typica*** (Hall & Whitfield). *Ex* Moore *et al.*, 1969. a, R int.; b, L int. (Trias., Alaska); c, R ext. (Trias., Peru), holotype of *S. peruviana* (Cox) (?=*S. typica*). (a,b, × 2; c, × 1.5)
7. ***Granocardium (Criocardium) dumosum*** (Conrad). *Ex* Moore *et al.*, 1969. Cret., New Jersey (a, R ext.; b, R int.; × 1)
8. ***Granocardium (G.) carolinum*** (Orbigny). *Ex* Orbigny, 1844. Cret., France (L ext. × 1)
9. ***Acanthocardia (Agnocardia) sorrentoensis*** (M. A. Hanna, 1927). Not type species. Eoc., California (a, enlarged detail of sculpture; b, L ext. × 1.5)

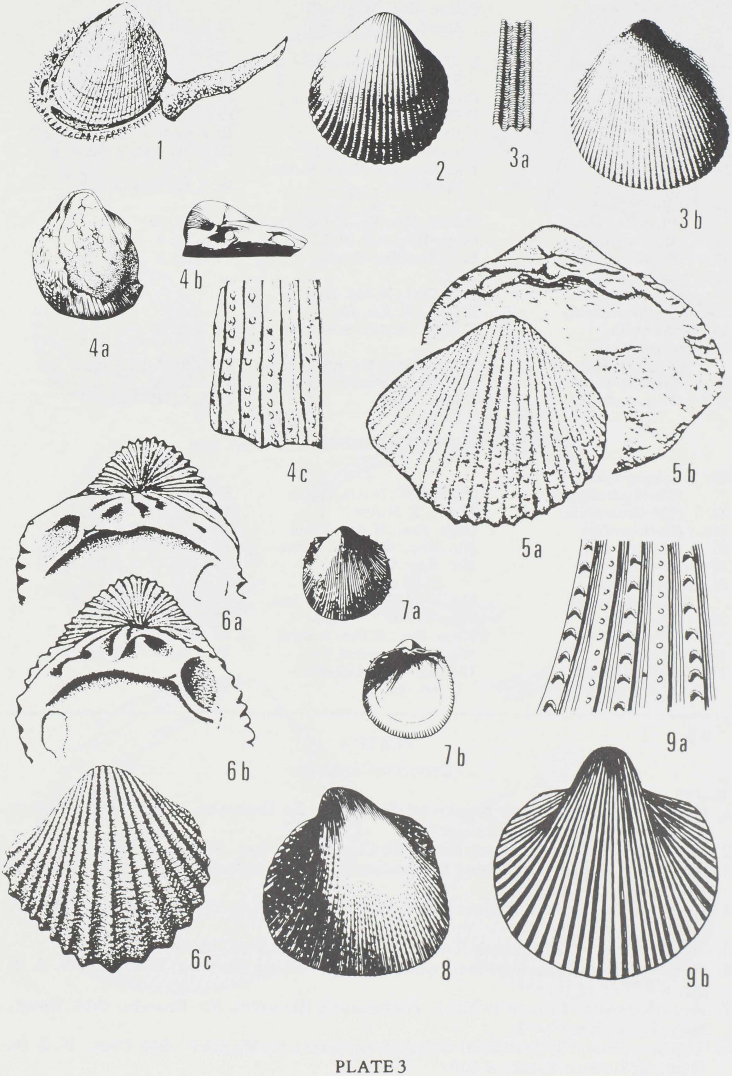

PLATE 3

6. *(Europicardium)*	Eoc.-Plio.-?Rec., Eu.	Pl. 4, fig. 7
7. *(Rudicardium)*	Mio.-Rec., Medit.	Pl. 4, fig. 3
8. *(Schedocardia)*	Paleoc.-Eoc., W.Afr.-SE Asia-S.Am.	Pl. 2, fig. 11
9. *Granocardium* *(Granocardium)*	L.-U.Cret., Eu.-Asia-Afr.-S.Pac.-N.-S.Am.	Pl. 2, fig. 6; Pl. 3, fig. 8
10. *(Criocardium)*	Cret., N.Am.-Eu.-W.Asia	Pl. 2, fig. 5; Pl. 3, fig. 7
11. *(Ethmocardium)*	U.Cret., N.Am.-S.Pac.	Pl.2, fig. 9
12. *Incacardium*	U.Cret., Peru	Pl. 3, fig. 5
13. *Loxocardium*	Eoc.-Mio., Eu.-?N.Am.	Pl. 2, fig. 1; Pl. 3, fig. 3
14. *Parvicardium*	Eoc.-Rec., Eu.-N.Atl.-E.Afr.-?W.N.Am.	Pl. 2, fig. 7
15. *Plagiocardium* *(Plagiocardium)*	Paleoc.-Mio.,Eu.-E. Ind.	Pl. 2, fig. 10
16. *(Maoricardium)*	Oligo.-Rec., Afr.-N.Z.	Pl. 4, fig. 6
17. *(Papillicardium)*	Eoc.-Rec.,Eu.-W.Asia	Pl. 2, fig. 8
?17a. *Pleuriocardia* *(Pleuriocardia)*	L.-U.Cret., N.Am.-Eu.	
?17b. *(Dochmocardia)*	U.Cret., N. Am.-Eu.	
18. *Septocardia*	U.Trias., N.Am.-S.Am.-Eu.	Pl. 3, fig. 6
19. *Vepricardium* *(Vepricardium)*	Paleoc.-Rec., Eu.-Afr.-Austral.	Pl. 2, fig. 4; Pl. 3, fig. 2
20. *(Hedecardium)*	Eoc.-Mio.,S.Pac.-S.Asia	Pl. 4, fig. 8
21. *(Perucardia)*	U.Cret., Peru	Pl. 3, fig. 4

Subfamily TRACHYCARDIINAE Stewart, 1930

22. *Trachycardium* *(Trachycardium)*	Oligo.-Rec., N.Am.-S.Am.	Pl. 5, fig. 1; Pl. 8, fig. 5
23. *(Conilocardium)*	Mio., S.E. N.Am.	Pl. 6, fig. 7; Pl. 8, fig. 4
24. *(Dallocardia)*	Oligo.-Rec., N.Am.-S.Am.	Pl. 5, fig. 4; Pl. 8, fig. 3
25. *(Mexicardia)*	Mio.-Rec., W.C.Am.-S.Am.	Pl. 5, fig. 5; Pl. 8, fig. 2
26. *(Phlogocardia)*	Mio.-Rec., C. Am.	Pl. 5, fig. 3; Pl. 8, fig. 1
27. *Acrosterigma* *(Acrosterigma)*	Mio.-Plio., S.E. USA-W.Ind.	Pl. 5, fig. 6; Pl. 6, fig. 8
28. *(Ovicardium)*	Plio., S. Pac.	Pl. 6, fig. 12
29. *(Regozara)*	Neog.-Rec., E.Ind.-Austral.	Pl. 8, fig. 8
30. *Papyridea*	Mio.-Rec., tropical Am.	Pl. 5, fig. 7; Pl. 6, fig. 11
31. *Vasticardium*	U. Oligo.-Rec., IndoPac.-C.Am.-Eu.	Pl. 5, fig. 2

PLATE 4

Cenozoic Cardiinae

Figures

1. *Cardium (Orthocardium) porulosum* (Solander). *Ex* Deshayes, 1824-37. Eoc., France (a, R ext.; b, L hinge; c, R hinge; × 1)
2. *Cardium (Cardium) costatum* Linné. *Ex* Chenu, 1862. Rec., W. Afr. (R ext. × 0.5)
3. *Acanthocardia (Rudicardium) tuberculata* (Linné). *Ex* Chenu, 1862. Rec., Medit. (L ext. × 1)
4. *Cardium (Bucardium) ringens* Linné. Moore *et al.*, 1969, *ex* Chenu, 1862. Rec., W. Afr. (× 0.5)
5. *Acanthocardia (A.) aculeata* (Linné). *Ex* Chenu, 1862. Rec., Medit. (L ext. × 1)
6. *Plagiocardium (Maoricardium) spatiosum* (Hutton). *Ex* Marwick, 1944. Plio., N. Z. (L int. × 0.7)
7. *Acanthocardia (Europicardium) multicostata* (Brocchi). *Ex* Brocchi, 1814. Neog., Italy (L int.; R ext.; × 1)
8. *Vepricardium (Hedecardium) waitakiense* (Suter). *Ex* Marwick, 1944. Oligo., N. Z. (a, R int.; b, L int.; c, L ext.; × 0.8)

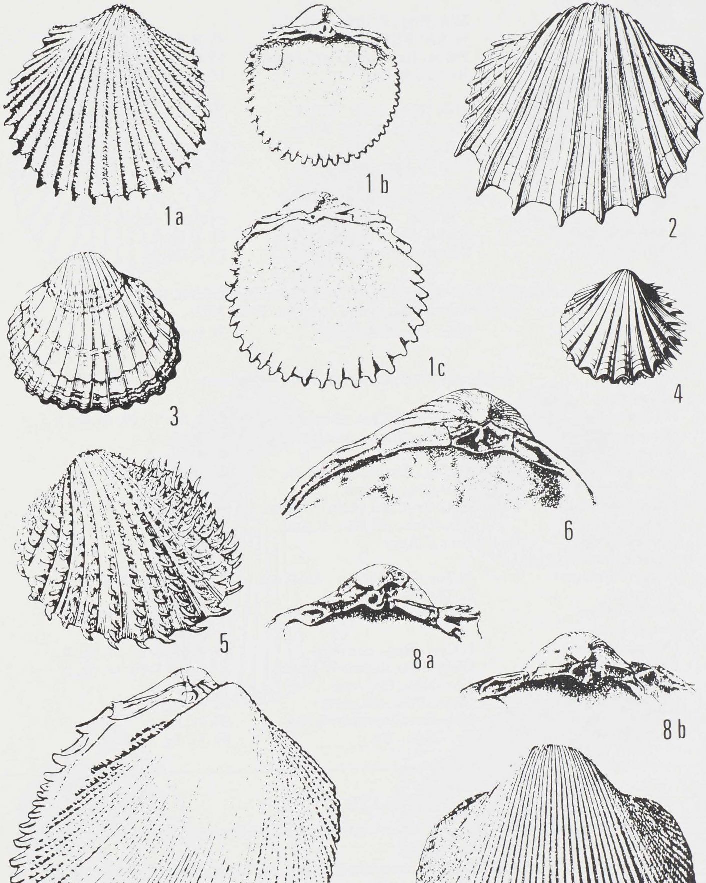

PLATE 4

Subfamily FRAGINAE Stewart, 1930

32. *Fragum*		
(Fragum)	Mio.-Rec., E.Ind.-Austral.-W.Afr.-SE USA	Pl. 6, fig. 5; Pl. 7, fig. 5
33. *(Lunulicardia)*	Pleist.-Rec., IndoPac.-Japan	Pl. 6, fig. 3; Pl. 7, fig. 6
34. *Corculum*	Rec., E.Indies	Pl. 6, fig. 6; Pl. 7, fig. 2
35. *Ctenocardia*		
(Ctenocardia)	Mio.-Rec., E.Afr.-E.Ind.	Pl. 6, fig. 4; Pl. 7, fig. 1
36. *(Afrocardium)*	Pleist.-Rec.,S.Afr.-E.Ind.-Austral.	Pl. 7, fig. 3
37. *(Microfragum)*	Rec., E.Ind.-Japan	Pl. 6, fig. 2
38. *Trigoniocardia*		
(Trigoniocardia)	Oligo.-Rec., tropical Am.-W.Afr.	Pl. 6, fig. 10; Pl. 7, fig. 4
39. *(Americardia)*	L.Mio.-Rec., N.Am.-S.Am.	Pl. 7, fig. 7
40. *(Apiocardia)*	Plio.-Rec., tropical Am.	Pl. 6, fig. 9

Subfamily HEMIDONACINAE Iredale and McMichael, 1962
(as Hemidonacidae; rank reduced, Boss, 1971)

41. *Hemidonax*	Rec., E.Indies	Pl. 6, fig. 1

Subfamily PROTOCARDIINAE Keen, 1951

42. *Protocardia*		
(Protocardia)	U.Trias.-U.Cret.,cosmop.	Pl. 9, fig. 11; Pl. 10, fig. 2
43. *(Brevicardium)*	U.Cret., N.Am.-Asia-Eu.	Pl. 10, fig. 3
44. *(Cryptocardia)*	M.-U.Jur., Eu.	Pl. 10, fig. 4
45. *(Globocardium)*	L.Cret., Eu.-E.Afr.-Japan	Pl. 10, figs. 7, 8
46. *(Leptocardia)*	L.-U.Cret., N.Am.	Pl. 9, fig. 7
47. *(Pachycardium)*	L.-U.Cret.,Eu.-Asia,N.-S.Am.	Pl. 9, fig. 5
48. *(Tendagurium)*	Jur.-Cret., Afr.-Eu.-E.Asia	Pl. 9, fig. 8
49. *(Yokoyamaina)*	Jur., E.Asia	Pl. 10, fig. 6
50. *Integricardium*		
(Integricardium)	M.Jur.-U.Cret.,Eu., Asia, Afr.	Pl. 9, fig. 10; Pl. 10, fig. 5
51. *(Onestia)*	L.-U.Cret., Canada	Pl. 9, fig. 9
52. *Jurassicardium*	Jur., Eu.(France), ?S.Am.	Pl. 9, fig. 12; Pl. 10, fig. 1
53. *Nemocardium*		
(Nemocardium)	L.Cret.-Rec., cosmop.	Pl. 9, fig. 3; Pl. 11, fig. 6
54. *(Arctopratulum)*	Oligo.-Mio.,Japan-W.N.Am.	Pl. 8, fig. 7; Pl. 11, fig. 5
55. *(Discors)*	Eoc.-Mio., Eu.-Asia	Pl. 9, fig. 13
56. *(Divaricardium)*	Oligo.-Plio., Eu.-Asia	Pl. 11, fig. 4
57. *(Frigidocardium)*	Mio.-Rec.,Japan-IndoPac	Pl. 11, fig. 2
58. *(Habecardium)*	Eo.-Oligo., Eu.	Pl. 11, fig. 10

PLATE 5

Interior views, left valves, subfamily Trachycardiinae

Figures

1. *Trachycardium (Trachycardium) isocardia* (Linné). SU specimen. Rec., Florida (× 1)
2. *Vasticardium elongatum* (Bruguière). SU specimen. Rec., Luzon I., Philippines (× 0.5)
3. *Trachycardium (Phlogocardia) belcheri* (Broderip & Sowerby). SU specimen. Rec., Gulf of California (× 1.5)
4. *Trachycardium (Dallocardia) quadragenarium* (Conrad). SU specimen. Rec., San Pedro, California (× 0.25)
5. *Trachycardium (Mexicardia) procerum* (Sowerby). SU specimen. Rec., Nicaragua (× 0.7)
6. *Acrosterigma (Acrosterigma) dalli* (Heilprin). SU specimen. Caloosahatchee Pliocene, Florida (× 0.5)
7. *Papyridea soleniformis* (Bruguière). SU specimen. Rec., John's Pass, Florida (× 1.4)

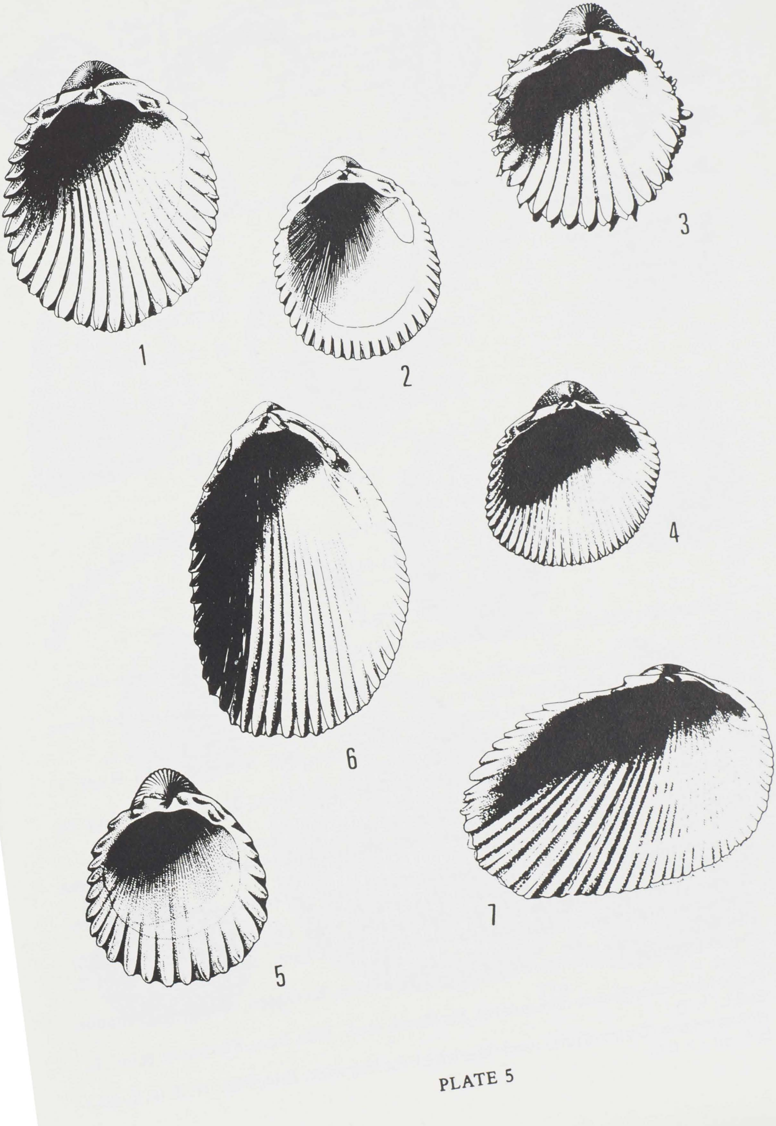

PLATE 5

59.	*(Keenaea)*	Oligo.-Rec.,Japan,W.N.Am.	Pl. 11, fig. 1
60.	*(Lophocardium)*	Mio.-Rec., C.Am.-S.Am.	Pl. 9, fig. 1
61.	*(Lyrocardium)*	Mio.-Rec., IndoPac.	Pl. 9, fig. 6; Pl. 11, fig. 7
62.	*(Microcardium)*	Mio.-Rec., C.Am.	Pl. 9, fig. 4
63.	*(Pratulum)*	L.Cret.-Rec.,Eu.-S.Pac.	Pl. 9, fig. 2; Pl. 11, fig. 9
64.	*(Trifaricardium)*	Pleist.-Rec., Japan	Pl. 11, fig. 3
65.	*(Varicardium)*	Mio., N.Z.	Pl. 11, fig. 8
?65a.	*Pleuriocardia*		
	(Pleuriocardia)	L.-U.Cret., N.Am.-Eu.	
?65b.	*(Dochmocardia)*	U.Cret., N. Am.-Eu.	
		Subfamily LAEVICARDIINAE Keen, 1936	
66.	*Laevicardium*		
	(Laevicardium)	Eoc.-Rec.,E.-W.Atl., IndoPac-E.Pac.	Pl. 12, fig. 4; Pl. 13, fig. 2
67.	*(Dinocardium)*	Eo.-Rec., N.Am.-S.Am.	Pl. 12. fig. 6
68.	*(Fulvia)*	Pleist.-Rec.,IndoPac-Japan	Pl. 12, fig. 1
69.	*(Profulvia)*	Oligo.-Plio., NW Pac.-Alaska	Pl. 13, fig. 6
70.	*Cerastoderma*		
	(Cerastoderma)	U.Oligo.-Rec., Eu.-N.Atl.	Pl. 12, fig. 2; Pl. 13, fig. 1
	[*(Korobkoviella)*	U.Oligo., USSR; transferred to Lymnocardiidae, subfamily Lymnocardiinae by Kafanov & Popov, 1977]	
71.	*Clinocardium*		
	(Clinocardium)	M.Oligo.-Rec., N.Pac.	Pl. 8, fig. 6; Pl. 12, fig. 3; Pl. 13, fig. 5
72.	*(Ciliatocardium)*	L.Oligo.-Rec., NW Pac.-N.Atl.	Pl. 13, fig. 7
73.	*(Fuscocardium)*	Pleist., Japan	Pl. 13, fig. 8
74.	?*(Keenocardium)*	M.Oligo.-Rec., N.Pac.	Pl. 8, fig. 9
75.	*(Planicardium)*	Mio., N.W.Atl.	Pl. 13, fig. 4
76.	*Serripes*	Mio.-Rec., N.Atl.-N.Pac.-Japan	Pl. 12, fig. 5; Pl. 13, fig. 3

PLATE 6

Subfamilies Trachycardiinae, Fraginae and Hemidonacinae, mainly exterior views

Figures

1. *Hemidonax donaciformis* (Bruguière). Rec., E. Ind. (a, L ext.; b, R int., *ex* Tryon, 1870; c, L ext., *ex* Chenu, 1862; × 1)
2. *Ctenocardia (Microfragum) festiva* (Deshayes). *Ex* Prashad, 1932. (L ext. × 1)
3. *Fragum (Lunulicardia) retusum* (Linné). *Ex* Chenu, 1862. Rec., E. Ind. (a, R ext.; b, anterior view, both valves. a, × 0.5; b, × 1)
4. *Ctenocardia (Ctenocardia) symbolica* (Iredale). *Ex* Chenu, 1862. Rec., E. Ind. (a, posterior view, both valves; b, R ext.; × 1)
5. *Fragum (Fragum) fragum* (Linné). *Ex* Moore *et al.*, 1969. Rec., E. Ind. (R ext. × 1)
6. *Corculum cardissa* (Linné). *Ex* Chenu, 1862. Rec., E. Ind. (Anterior view, both valves × 1)
7. Diagrammatic section of *Trachycardium (Conilocardium) cestum* (Dall), to show profile of radial ribbing. *Ex* Vokes, 1977. Mio., Florida (× 2)
8. *Acrosterigma (A.) dalli* (Heilprin). *Ex* Moore *et al.*, 1969. Plio., Florida (L ext. × 0.25)
9. *Trigoniocardia (Apiocardia) obovalis* (Sowerby). *Ex* Olsson, 1961. Rec., N. Peru (L ext. × 2)
10. *Trigoniocardia (T.) granifera* (Broderip & Sowerby). *Ex* Olsson, 1961. Rec., Ecuador (L ext. × 2)
11. *Papyridea soleniformis* (Bruguière). *Ex* Moore *et al.*, 1969. Rec., Florida (a, R int.; b, L ext.; × 1)
12. *Acrosterigma (Ovicardium) rossi* (Marwick). *Ex* Marwick, 1944. Plio., N. Z. (a, L ext.; b, L int.; × 0.6)

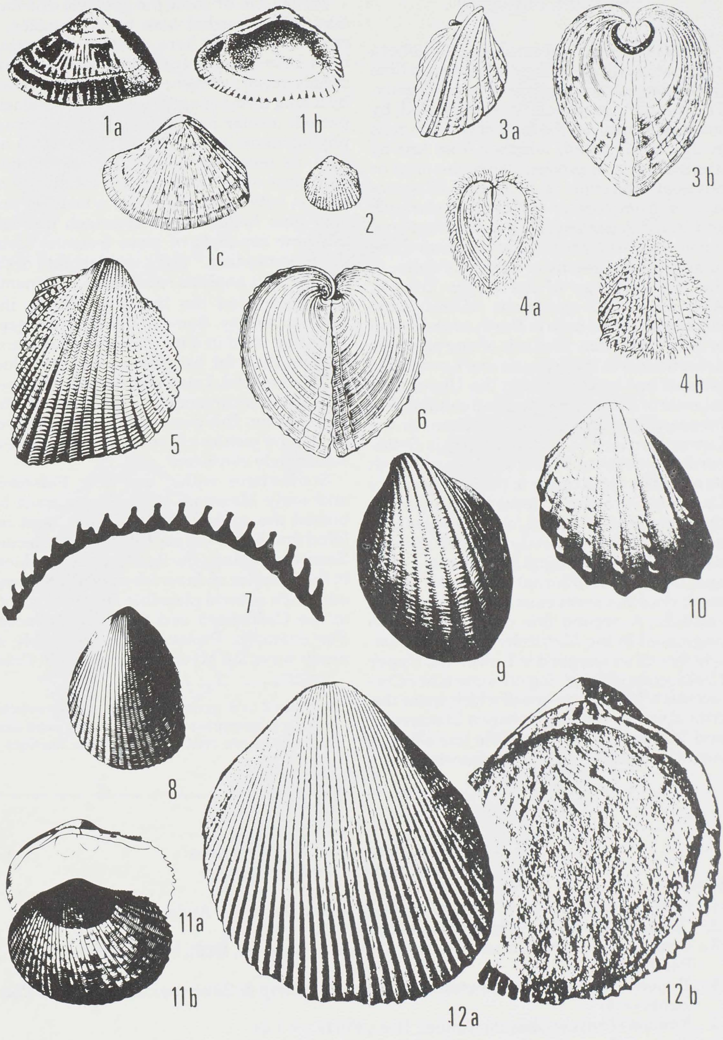

PLATE 6

Section 4: Phylogeny

One could hope that arranging the genera in the order of when they appeared in time would sketch the outline of a phylogeny. The matter, however, is complicated by several factors, not the least of which is gaps in the fossil record, whether from loss by weathering and erosion, from chemical or physical alteration of sediments (diagenesis), or from lack of sufficient exploration and study. A particularly good illustration is the line of *Cardium* s. s. The earliest record of any cardiid seems to be *Septocardia*, in the Norian Stage of the Upper Triassic. Well preserved specimens of this taxon have been found both in North America and in South America. Records of any plausible descendants in the Jurassic and Lower Cretaceous are lacking, but in the Upper Cretaceous of Peru there is a good candidate in *Incacardium* as a successor. Then, in the Lower Tertiary of Europe, there is *Orthocardium* that may fit into this line, although its affinities seem closer to the later Tertiary *Cardium-Bucardium* descendants than to the presumed ancestral forms. Beyond the general cardiid pattern of radial ribbing, deployment of cardinal and lateral teeth, and features of internal scars, this entire stock does not seem closely related to other cardiids. A second line of Cardiinae also originated in the Mesozoic: *Granocardium*, which was widespread in Lower and Upper Cretaceous time, giving off some other Cretaceous offshoots, no one of which spans the critical time-boundary between Cretaceous and Paleocene. However, the line allied to *Acanthocardia* is a plausible descendant.

Tables 2 to 6* show the geologic distribution of the cardiid taxa by subfamilies. I make no attempt here to draw connecting lines between generic units. These charts simply report presence or absence (shown by a long dash) of each unit at each geologic period, insofar as my records go. To draw phylogenetic lines, one would need to be able to reconcile geographic distribution with past opportunities for interchange of faunas between continents, a task we are only now beginning to approach through the new concepts of plate tectonics, seafloor spreading, and continental drift. Rather, this analysis records my judgments as I examined the literature during the years of survey. Some of the apparent gaps might be filled in if a canvass were made of locality lists, for by concentrating on illustrated material, I may well have overlooked reported occurrences, especially in the Pleistocene. But even with uncertainties in detail, the picture of the family as a whole is satisfyingly consistent.

Somewhere within the later Paleozoic and early Mesozoic Heterodonta must lie buried the roots of the Cardiidae and related families of the superfamily Cardiacea. Searching among the figures of heterodonts in the *Treatise on Invertebrate Paleontology*, one finds several plausible ancestral stocks in the Carditacea and the Crassatellacea. For example, Protocardiinae resemble in many ways the Myophoricardiidae in Cras-

*In tables 2 to 6, generic names are abbreviated in order to compress the tables to one-page size. Full names are readily available in Sections 1 and 3.

PLATE 7

Subfamily Fraginae, interior of left valves
All from specimens in the SU collection

Figures

1. *Ctenocardia (Ctenocardia)* cf. *C. symbolica* (Iredale). Rec., Andaman Is. (× 3)
2. *Corculum cardissa* (Linné). Rec., Philippine Is. (× 1)
3. *Ctenocardia (Afrocardium) exocha* (Melvill & Standen, 1906). Not type species. Rec., Persian Gulf (× 5)
4. *Trigoniocardia (Trigoniocardia) granifera* (Broderip & Sowerby). Rec., Gulf of California (× 4)
5. *Fragum (Fragum) fragum* (Linné). Rec., Fiji Is. (× 1.4)
6. *Fragum (Lunulicardia) retusum* (Linné). Rec., Hong Kong (× 1)
7. *Trigoniocardia (Americardia) media* (Linné). Rec., Florida (× 1.5)

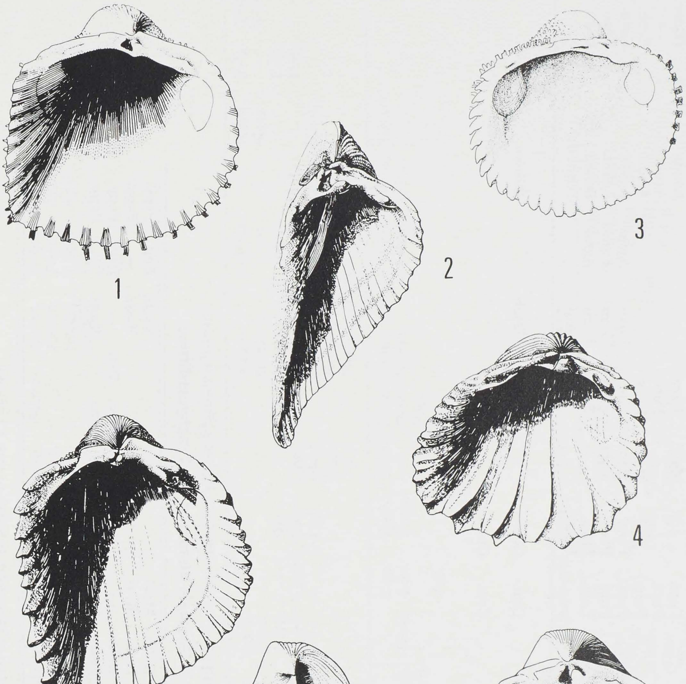

PLATE 7

Table 2. Geologic history of the Cardiinae

Recent	Card.	Buc.	Vepr.		Papi.		Maor.	Parv.			Acant.	Rudi.	?Euro.
Pleistocene	Card.	—	—		Papi.		—	Parv.			Acant.		—
Pliocene	Card.	—	Vepr.		Papi.		Maor.	Parv.			Acant.		Euro.
Miocene	Card.	Buc.	Vepr.	Hede.	Papi.	Plag.	Maor.	Parv.	Loxo.	Agno.	Acant.		Euro.
Oligocene	Orth.		Vepr.	Hede.	Papi.	Plag.	Maor.	Parv.	Loxo.	Agno.	Acant.		Euro.
Eocene	Orth.		Vepr.	Hede.	Papi.	Plag.		Parv.	Loxo.	Agno.	Sched.		Euro.
Paleocene	Orth.		?Vepr.			Plag.			Loxo.		?Sched.		
Upper Cretaceous	Inca.		Peru.		Crio.	Grano.		?Pleu.	?Doch.		Ethmo.		
Lower Cretaceous	—				Crio.	Grano.		?Pleu.					
Upper Jurassic	—												
Middle Jurassic	—												
Lower Jurassic	—												
Upper Triassic	Septo.												

Table 3. Geologic history of the Trachycardiinae

Recent	Trach.	Dallo.	Mexi.		Phlog.			Vasti.	Reg.	Papy.
Pleistocene	Trach.	Dallo.	Mexi.		—			Vasti.	—	Papy.
Pliocene	Trach.	Dallo.	—		—	Acro.	Ovi.	—	Reg.	Papy.
Miocene	Trach.	Dallo.	Mexi.	Conil.	Phlog.	Acro.		Vasti.		Papy.
Oligocene	Trach.	Dallo.						Vasti.		
Eocene										
Paleocene										

Table 4. Geologic history of the Fraginae

Recent	Lunul.	Frag.	Corc.	Afro.	Cteno.	Micro.	Ameri.	Trigo.	Apio.
Pleistocene		Frag.		Afro.	Cteno.		Ameri	Trigo.	Apio.
Pliocene		Frag.			Cteno.		Ameri.	Trigo.	Apio.
Miocene		Frag.			Cteno.		Ameri.	Trigo.	
Oligocene								Trigo.	
Eocene								Trigo.	
Paleocene									

Table 5. Geologic history of the Protocardiinae

Recent					Mic.	Lyro.	Loph.				Nemo.		Prat.		Keen.	Frig.	Trif.
Pleist.					—	Lyro.	—				Nemo.		—		Keen.	—	Trif.
Pliocene					—	Lyro.	—	Div.			Nemo.		Prat.		—	Frig.	
Miocene					Mic.	Lyro.	Loph.	Div.	Disc.	Var.	Nemo.		Prat.	Arct.	—	Frig.	
Oligocene								Div.	Disc.		Nemo.	Habe.	Prat.	Arct.	Keen.		
Eocene									Disc.		Nemo.	Habe.	Prat.				
Paleocene											Nemo.	?Hab.	Prat.				
Upper Cret.	Ones.	Int.		?Ten.			Lep.	Pach.	Brev.	Prot.	Nemo.		Prat.	?Pleu.	?Doch.		
Low. Cret.	Ones.	Int.		Tend.	Cryp.	Glob.	Lep.	Pach.		Prot.	Nemo.		Prat.	?Pleu.			
Upper Jur.		Int.		Tend.	Cryp.					Prot.							
Mid. Jura.		Int.	Yok.	Tend.			Jur.			Prot.							
Low. Jura.										Prot.							
U. Triassic										Prot.							

Table 6. Geologic history of the Laevicardiinae

Recent	Laevi.	Dino.	Ful.		Ceras.	Clino.			Ciliat.	Serr.
Pleistocene	Laevi.	—	Ful.		Ceras.	Clino.	Fusco.		Ciliat.	Serr.
Pliocene	Laevi.	—		Prof.	Ceras.	Clino.			Ciliat.	Serr.
Miocene	Laevi.	Dino.		Prof.	Ceras.	Clino.		Plani.	Ciliat.	Serr.
Oligocene	Laevi.	Dino.		Prof.	Ceras.	Clino.			Ciliat.	
Eocene	Laevi.	?Dino.								
Paleocene										

satellacea, and the anterior muscle scar buttress of the upper Triassic *Septocardia* is foreshadowed by such groups of Carditacea as the Permophoridae during the Carboniferous. In spite of the strong resemblance of *Septocardia* to members of the cardiid line, Kafanov and Popov (1977) do not accept it as cardiid but jettison it by proposing a new family, "Septocardiidae Kafanov and Starobogatov *in* Kafanov and Popov," which they allocate to Tridacnacea, a Tertiary superfamily that has no firm record in the Mesozoic. May it not be, instead, that *Septocardia* is a link to the Carditacea through the genus *Palaeocardita* Conrad, 1867, which ranges throughout the Triassic? The genus *Septocardia* Hall and Whitfield, 1877, until recent years had been placed in Carditacea (see, for example, Vokes, 1967, p. 257). However, the reviser of Carditacea for the *Treatise on Invertebrate Paleontology*, André Chavan, rejected *Septocardia* from his list. His suggestion that the unit might belong in Cardiacea led me to examine it and accept the reallocation. If Chavan (*in* Moore *et al.*, 1969, p. N554) is correct in his interpretation of *Palaeocardita*, then many of the species now assigned to that unit by authors actually are *Septocardia*, and this genus was widely distributed in the Upper Triassic not only in the Americas but also in Europe. Specimens of *Septocardia* that I have seen from Alaska and Nevada exhibit a considerable variation in outline from quadrate to ovate, inequilateral to equilateral. The hinge has a distinctive anterior muscle scar buttress that is not shown at all in Chavan's figure nor mentioned by him in his diagnosis of *Palaeocardita*.

As I see it, the family may seem to be polyphyletic because the divergence from early ancestral stocks took place so far back in time that all the links have been obliterated. Thus, the subfamily Cardiinae seems to have two main branches — the *Septocardia-Cardium* line and the *Granocardium-Acanthocardia* line; the subfamily Protocardiinae, traceable almost as far back as *Septocardia*, shows resemblance only in the exaggerated size of the lateral hinge teeth but has a very different sculpture pattern. Two taxa within the Protocardiinae — *Nemocardium* and *Pratulum* — bridged that critical horizon between Cretaceous and Paleocene (called by some authors "the time of the great dying").

A New Zealand taxon, *Varicardium*, provides a good example of what appears to be iterative (*i.e.*, repetitive) evolution. Paleontologists of a century ago who were examining cardiids were content to say that *Protocardia, sensu stricto*, died out at the end of the Cretaceous everywhere except in New Zealand, for some species there had the *Protocardia* pattern of concentric sculpture anteriorly and radial sculpture posteriorly. However, with more knowledge of distribution and with a more critical evaluation of morphology, we now see that *Varicardium* is an offshoot of the *Nemocardium*

PLATE 8

Figures

1. *Trachycardium (Phlogocardia) belcheri* (Broderip & Sowerby). *Ex* Olsson, 1961. Rec., Ecuador (L ext. × 1)
2. *Trachycardium (Mexicardia) procerum* (Sowerby). SU specimen. Rec., Panama (R ext. × 0.5)
3. *Trachycardium (Dallocardia) senticosum* (Sowerby). With typical sculpture but not type species. *Ex* Olsson, 1961. Rec., Ecuador (R ext. × 0.8)
4. *Trachycardium (Conilocardium) cestum* (Dall). *Ex* Vokes, 1977. Mio., Florida (a, R ext.; b, L int.; × 1)
5. *Trachycardium (Trachycardium) consors* (Sowerby). *Ex* Olsson, 1961. Rec., Panama Typical sculpture but not type species. (L ext. × 0.8)
6. *Clinocardium (Clinocardium) nuttallii* (Conrad). SU specimen. Rec., Oregon (L ext. × 0.7)
7. *Nemocardium (Arctopratulum) griphus* Keen. Holotype, SU coll. Mio., Washington (R ext. × 1)
8. *Acrosterigma (Regozara) olivifer* (Iredale). Holotype, courtesy Australian Museum. Rec., Australia (L int. × 1)
9. *Clinocardium (?Keenocardium) californiense* (Deshayes). *Ex* Deshayes, 1841. Rec., N.W. Pac. (R ext. × 1)

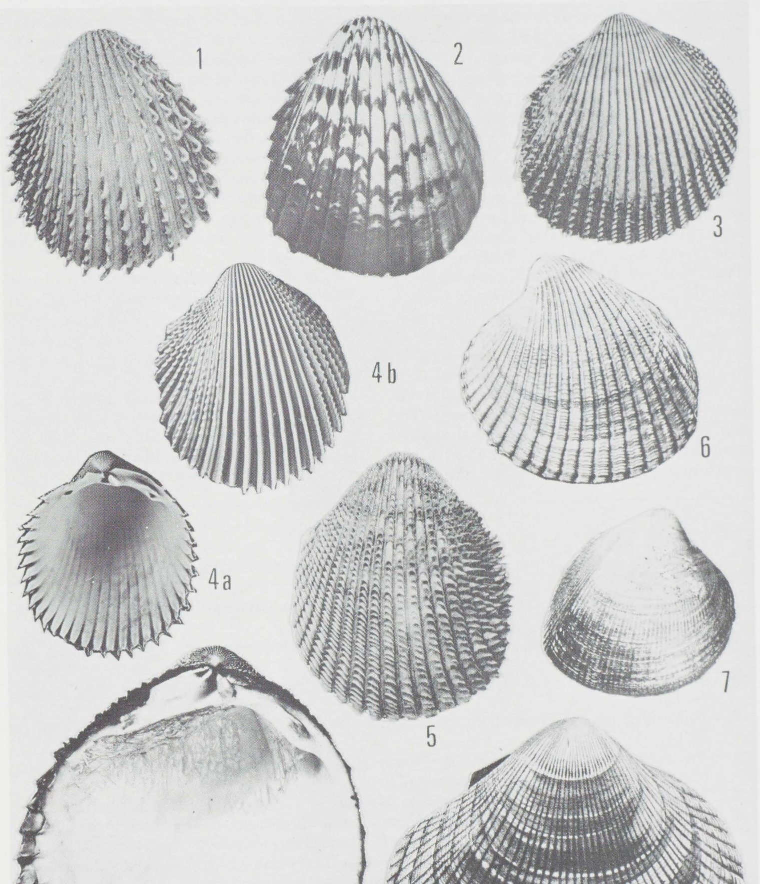

PLATE 8

line, branching off in the Miocene. The concentric folds of the anterior slope are irregular and superficial, not like the fine and regular costae of true *Protocardia*.

The relationships of the subfamily Hemidonacinae are unclear, for as yet it lacks a fossil record. Wilson and Stephenson (1977, p. 10) even defer acceptance of it in the family until more anatomical work is done. Derivation of the other three subfamilies from the two main Mesozoic stocks are fairly clear: Trachycardiinae and Fraginae branching off from the Cardiinae and Laevicardiinae from the Protocardiinae. The *Trachycardium* line is in general a New World counterpart of the Old World *Europicardium* stock. Fraginae show relationship to the *Acanthocardia* line in the sculpture of intercostal spaces and also, as Popov (1977) has shown, in the microstructure. The Laevicardiinae seem by definition to be diametrically opposite to Protocardiinae in the sculpture of the posterior slope, although in general outline and in the arched hinge there are affinities. One taxon in the Tertiary, *Habecardium*, bridges the gap between the two, for the juvenile shells have typical *Pratulum* ribbing, whereas the adults develop sculpture more like that of *Nemocardium*, except that the ribs of the posterior slope are not only without spines but may in part disappear, especially along the dorsal marin of the slope. Thus the shell comes to resemble *Laevicardium* so much that Glibert and Van de Poel, who named *Habecardium*, made it a subgenus of *Laevicardium* rather than of *Nemocardium*, where other workers had placed the several species.

This, then, is a shadowy sketch of possible relationships of groups within Cardiidae. Until horizons are studied that now represent gaps, we can only speculate about the pathways of dispersal and the morphological adaptations of these mollusks. Newell (*in* Moore *et al.*, 1969, p. N213) summarized the whole matter very tersely: "Phylogenetic relationships are best deduced from the geologic history of the class, and this is poorly known."

PLATE 9

Subfamily Protocardiinae: interior view of left valves

Figures

1. *Nemocardium (Lophocardium) cumingii* (Broderip). CAS specimen. Rec., Colombia (× 2)
2. *Nemocardium (Pratulum) thetidis* (Hedley). SU specimen. Rec., Victoria, Australia (× 2.3)
3. *Nemocardium (N.) semiasperum* (Deshayes). SU specimen. Ypresian Eocene, France (× 1.5)
4. *Nemocardium (Microcardium) peramabile* (Dall). SU specimen. Rec., Gulf of Mexico (× 5)
5. *Protocardia (Pachycardium) spillmani* (Conrad). SU, plaster cast of topotype, courtesy USNM. U. Cret., Mississippi (× 0.5)
6. *Nemocardium (Lyrocardium) lyratum* (Sowerby). SU specimen. Rec., Japan (× 1)
7. *Protocardia (Leptocardia) subquadrata* (Evans & Shumard). SU specimen; hinge reconstructed from cast of other valve. U. Cret., Pierre shale, South Dakota (× 5)
8. *Protocardia (Tendagurium) propebanneiana* (Dietrich). U. Jur., E. Afr. Composite tracing from original figures, with hinge reconstructed from cast of other valve. (× 0.5)
9. *Integricardium (Onestia) onestae* (McLearn). From a plaster cast of holotype, SU coll. Cret., Alberta, Canada (× 1.4)
10. *Integricardium (I.) dupinianum* (Orbigny). Reconstructed hinge, from original figure of other valve. Cret., France (× 0.5)
11. *Protocardia (P.) hillana* (Sowerby). After Woods, 1908. L. Cret., England (× 1.2)
12. *Jurassicardium axonense* (Cossmann). From a syntype in the Cossmann coll., Sorbonne. Bathonian Jur., France (× 3.5)
13. *Nemocardium (Discors) parisiense* (Orbigny). SU specimen. Auversian Eoc., France (× 3)

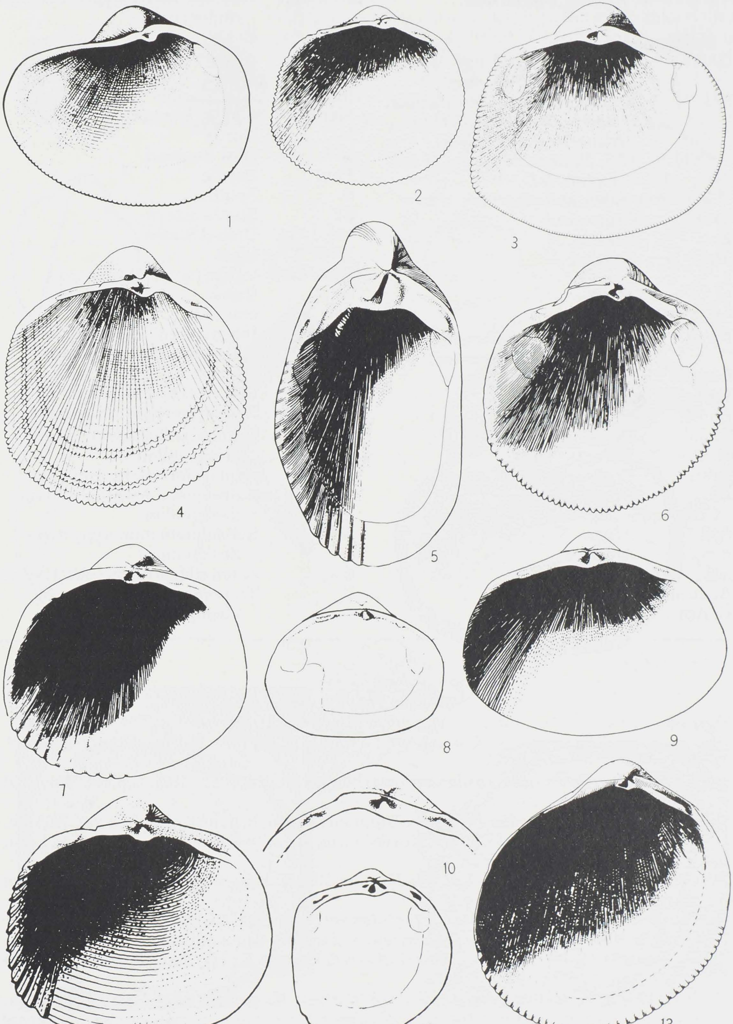

PLATE 9

V. ABBREVIATIONS

Institutions

CAS	California Academy of Sciences, San Francisco
SU	Stanford University (collection now housed at California Academy of Sciences)
USNM	U.S. National Museum, Washington, D.C.

Geologic periods and other time terms

Cret.	Cretaceous
Eoc.	Eocene
Jur.	Jurassic
L.	Lower
M.	Middle
Mio.	Miocene
Neog.	Neogene (*i.e.*, Miocene/Pliocene, undifferentiated)
Oligo.	Oligocene
Paleoc.	Paleocene
Pleist.	Pleistocene
Plio.	Pliocene
R.,Rec.	Recent
Trias.	Triassic
U.	Upper

Geographic localities

Afr.	Africa
Am.	America
Atl.	Atlantic
Austral.	Australia
C. Am.	Central America
cosmop.	cosmopolitan (*i.e.*, present in all major seas)
E.	East
Eu.	Europe
Ind.	Indies
IndoPac.	Indo-Pacific
Medit.	Mediterranean
N.	North
N.Z.	New Zealand
Pac.	Pacific
S.	South
SE	Southeastern
US, USA	United States
W.	West

Systematic terms; morphologic terms

ex	from
ext.	exterior
ICZN	International Commission on Zoological Nomenclature
int.	interior
L	left (referring to left valve)
M	Monotypy (type designation)
OD	Original designation (type designation)
R	right (referring to right valve)
SD	Subsequent designation (type designation)
SM	Subsequent monotypy (type designation)
s. s.	*sensu stricto* (in the strict sense)
T	Tautonymy (designation by absolute tautonymy)

PLATE 10

Mesozoic Protocardiinae

Figures

1. *Jurassicardium axonense* (Cossmann). *Ex* Moore *et al.*, 1969. M. Jur., France (R ext. × 2)
2. *Protocardia (Protocardia) hillana* (Sowerby). *Ex* Moore, *et al.*, 1969. L. Cret., England (L ext. × 0.5)
3. *Protocardia (Brevicardium) fragilis* (Stephenson). 3a, b, d, after Stephenson, 1955; 3c, after Stephenson, 1941. U. Cret., Mississippi (a, R ext. × 5; b,d, L int., ext. × 6; c, L int. × 3)
4. *Cryptocardia bajocensis* Palmer. *Ex* Palmer, 1974. Outline showing position of internal ridges. Jur., France (× 0.5)
5. *Integricardium (Integricardium) dupinianum* (Orbigny). *Ex* Moore *et al.*, 1969, after Orbigny, 1844. Cret., France (a, R hinge; b, dorsal view of both valves; × 0.6)
6. *Protocardia (Yokoyamaina) hayamii* (Keen & Casey). *Ex* Hayami, 1972. Jur., E. Asia (× 1)
7. *Protocardia (Globocardium) sphaeroidea* (Forbes). *Ex* Palmer, 1974. Cret., England (a, outline, showing position of the internal ridge × 0.3; b, L int., arrow pointing to internal knob; c, ventral view, both valves, posterior area at right × 0.7)
8. *Protocardia (Globocardium) rothpletzi* Krenkel, 1910. After Dietrich, 1933. U. Jur., E. Afr. Figured by Dietrich as *Cardium (Tendagurium)*; transferred to *P. (Globocardium)* by Palmer, 1974. (L int. × 0.5)

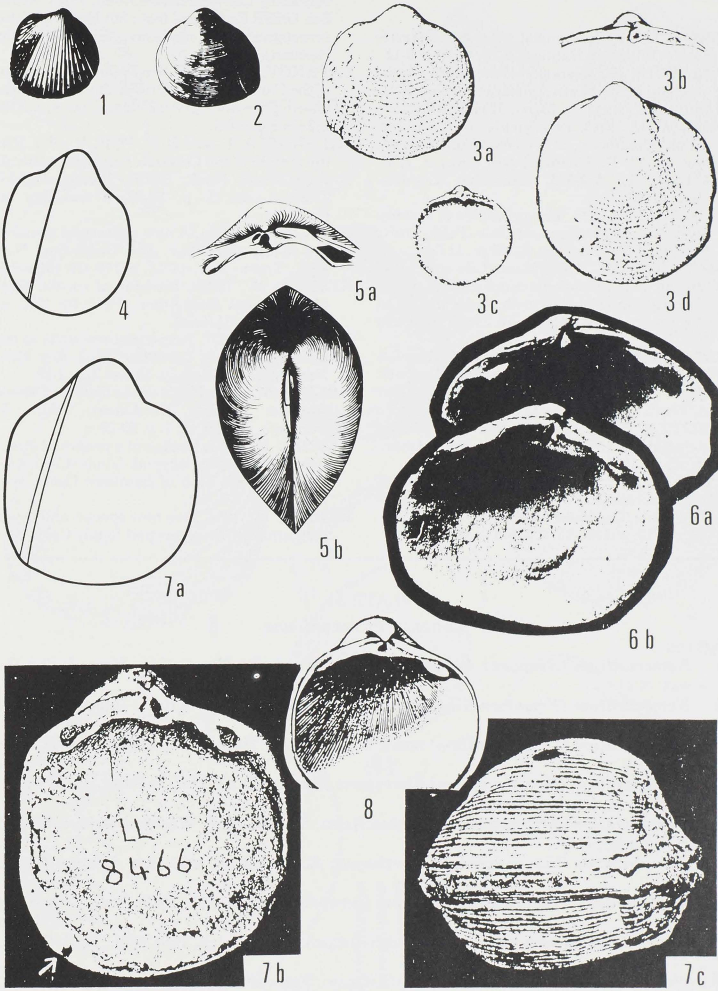

PLATE 10

VI. LITERATURE CITED

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PLATE 11

Cenozoic Protocardiinae

Figures

1. *Nemocardium (Keenaea) samarangae* (Makiyama). *Ex* Habe, 1951. Rec., Japan (L ext. × 1)
2. *Nemocardium (Frigidocardium) eos* (Kuroda). *Ex* Habe, 1951. Rec., Japan (L ext. × 1)
3. *Nemocardium (Trifaricardium) nomurai* (Habe). *Ex* Habe, 1951. Rec., Japan (L ext. × 1.5)
4. *Nemocardium (Divaricardium) discrepans* (Basterot). *Ex* Dall *in* Zittel, 1913. Mio., France (a, L int.; b, L ext.; × 1)
5. *Nemocardium (Arctopratulum) griphus* Keen. SU coll. Mio., Washington (a, L hinge; b, R hinge; × 1)
6. *Nemocardium (N.) semiasperum* (Deshayes). *Ex* Deshayes, 1858. Eoc., France (L ext. × 1)
7. *Nemocardium (Lyrocardium) lyratum* (Sowerby). *Ex* Chenu, 1862. Rec., E. Ind. (L ext. × 1)
8. *Nemocardium (Varicardium) patulum* (Hutton). *Ex* Marwick, 1944. Mio., N. Z. (R ext. × 0.7)
9. *Nemocardium (Pratulum) pulchellum* (Gray). Typical sculpure but not type species. *Ex* Marwick, 1944. Rec., N. Z. (R ext. × 2)
10. *Nemocardium (Habecardium) tenuisulcatum* (Nyst). Juvenile form: a, R int., b, R ext., c, detail of sculpture; *Ex* Deshayes, 1858, Oligo., France (× 1) Adult form, often identified as *N. cingulatum* (Goldfuss, 1837): d, L int., e, L ext., *ex* Von Koenen, 1893, Oligo., Germany (× 1)

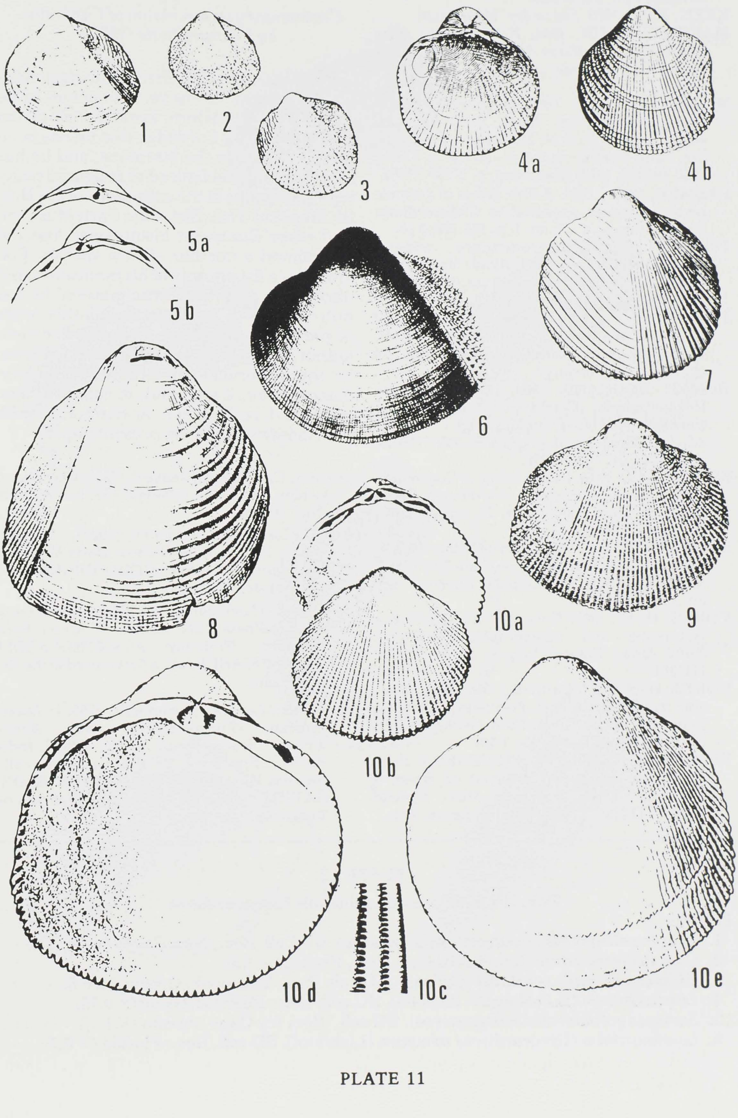

PLATE 11

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VII. APPENDIX I

Commentary on a revision of Cardiidae by Fischer-Piette (1977)

Prof. Édouard Fischer-Piette has compiled the most extensive synonymies to be found in any modern work, on all of the species of living Cardiidae that he has been able to detect in the literature, and he has searched out and figured or refigured many type specimens in the collections of the British Museum (Nat. Hist.), the Paris Museum, and other European institutions. Also, he has named a number of new species. Following is a list not only of his innovations but also of the significant type material he has put on record. Each entry has this order of parts: specific name; original allocation; author; date; [allocation by Fischer-Piette, in square brackets]; locality; repository; commentary, if any; and, in capital letters, suggested reallocation to harmonize with the classification of the present paper.

aequale, *Cardium*, Deshayes, 1855; *[Corculum];* locality unknown; holotype, British Museum (Nat. Hist.).

auri, *[Corculum (Trigoniocardia)]*, Fischer-Piette, 1977. Gulf of Guinea; Paris Museum. An extension of range of TRIGONIOCARDIA to the eastern Atlantic.

couvrili, *[Laevicardium (Trachycardium)]*, Fischer-Piette, 1977. Gabon, W. Africa; Paris Museum. Probably ACANTHOCARDIA (EUROPICARDIUM), a first record in the Recent fauna.

elongatum, *Cardium*, Bruguière, 1789; [=*Laevicardium (Trachycardium)* sect. *Acrosterigma) leucostomum* (Born, 1780)]. Indo-Pacific. Specimen in the Lamarck coll., Geneva Museum. VASTICARDIUM ELONGATUM, type of *Vasticardium*, as shown by Vokes (1977, p. 160).

PLATE 12

Interiors of left valves, subfamily Laevicardiinae

Figures
1. *Laevicardium (Fulvia) apertum* (Bruguière). SU Coll. Rec., New Caledonia (× 1.5)
2. *Cerastoderma edule* (Linné). SU Coll. Rec., France (× 1.5)
3. *Clinocardium (C.) nuttallii* (Conrad). SU coll. Rec., Tillamook, Oregon (× 0.6)
4. *Laevicardium (L.) oblongum* (Gmelin). SU coll. Rec., Palermo, Sicily (× 0.75)
5. *Serripes groenlandicus* (Bruguière). SU coll. Rec. Icy Cape, Alaska (× 1)
6. *Laevicardium (Dinocardium) robustum* [Lightfoot]. SU coll. Rec., Florida (× 0.7)

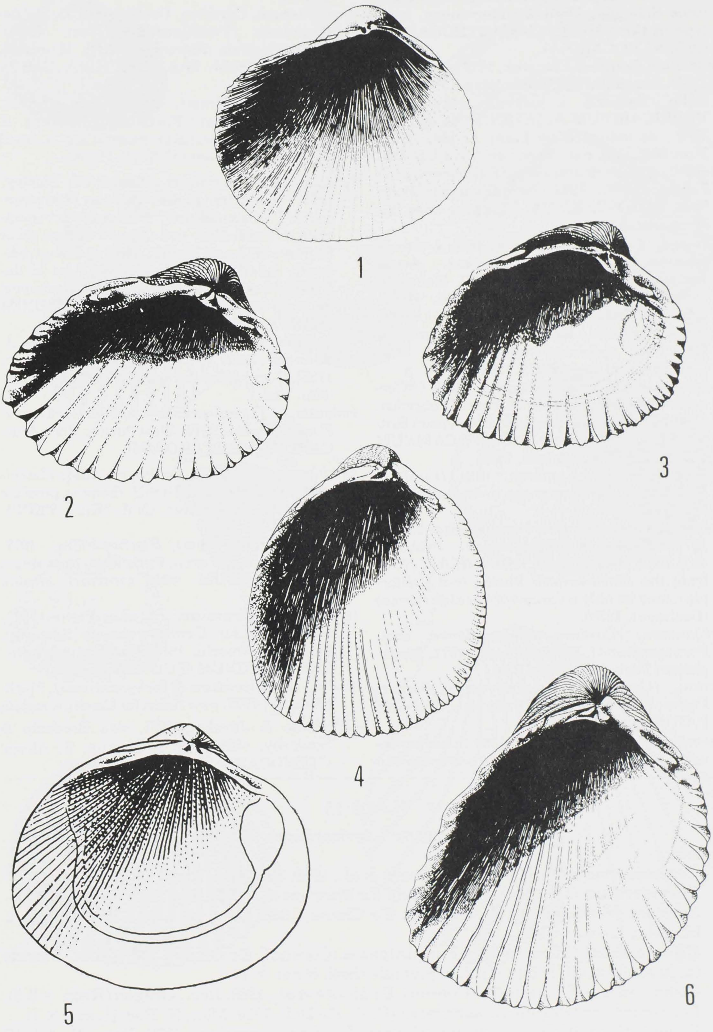

PLATE 12

erinaceum, Cardium, Lamarck, 1819; [=*Cardium (Cerastoderma,* sect. *Acanthocardia) spinosum* Solander, 1786]. Mediterranean; holotype in Paris Museum. ACANTHOCARDIA (ACANTHOCARDIA).

fimbriatum, Cardium, Lamarck, 1819 (*non* Linné, 1758). Locality unknown; holotype, Paris Museum. Probably a juvenile specimen of VEPRICARDIUM ASIATICUM (Bruguière, 1789), as indicated by Lamy in 1941 (Bull. Mus. Nat. Hist. nat., Paris, ser. 2, v. 13, p. 459).

gaillardi, [Laevicardium (Trachycardium)] Fischer-Piette, 1977. New Zealand; Paris Mus. VASTICARDIUM. Locality may be open to question.

gratiosum, Cardium, Deshayes, 1855. [=*Laevicardium (Trachycardium,* sect. *Acrosterigma) enode* (Sowerby, 1834)]. Moluccas; syntype in British Museum (Nat. Hist.). ACROSTERIGMA (REGOZARA).

hiulcum, Cardium, Reeve, 1845; *[Papyridea].* Red Sea; specimen figured, Paris Mus. CTENOCARDIA (AFROCARDIUM).

hudsoniense, Cardium, Deshayes, 1855. [=*Corculum (Keenocardium) ciliatum* (Fabricius, 1780)]. Hudson Bay; possible holotype in British Mus. (Nat. Hist.). =PARVICARDIUM PINNULATUM (Conrad, 1831).

indicum, Cardium, Lamarck, 1819; *[Cardium (Cardium)].* Mediterranean area; Paris Mus., holotype.

interrogatorium, [Laevicardium], Fischer-Piette, 1977. California, Paris Mus. Probably =CLINOCARDIUM UCHIDAI (Habe, 1955), from the northwestern Pacific (not California); may be only a variant of *C. californiense* (Deshayes, 1839).

iranjanense, [Cardium (Cerastoderma, sect. *Parvicardium)],* Fischer-Piette, 1977. Madagascar; Paris Mus. FRAGUM.

lavrani, [Cardium (Cerastoderma)], Fischer-Piette, 1977. East Africa; Paris Mus. Probably PARVICARDIUM.

leucostomum, Cardium, Born, 1780; *[Laevicardium (Trachycardium,* sect. *Acrosterigma)].* Jamaica; holotype, Vienna Mus. VASTICARDIUM.

mauritianum, Cardium, Deshayes, 1855; [=*Laevicardium (Trachycardium,* sect. *Acrosterigma) enode* (Sowerby, 1834)]. Mauritius; syntype, British Mus. (Nat. Hist.). VASTICARDIUM.

nemo, [Laevicardium], Fischer-Piette, 1977. Locality unknown; Paris Mus., holotype. A fragmentary specimen resembling a fossil *Clinocardium* from the North Pacific.

"*philippinense, Cardium,* (Deshayes) Shirley, 1912" of Fischer-Piette, 1977, as *[Laevicardium (Trachycardium)].* Philippine Is.; specimen in Paris Mus. coll. *Nomen nudum* as of Shirley, 1912, and Tomlin, 1934; specimen evidently labelled by reference to a lot in the British Mus. coll. that carried only Deshayes' manuscript name. =VASTICARDIUM ORBITA (Sowerby, 1833).

productum, Cardium, Deshayes, 1855 (*non* J. Sowerby, 1832); [=*Corculum cardissa* (Linné, 1758]. Torres Straits; syntype in British Mus. (Nat. Hist.).

rudentis, [Laevicardium (Vepricardium)], Fischer-Piette, 1977. West Africa; Paris Mus. CARDIUM (BUCARDIUM).

serrulatum, Cardium, Deshayes, 1855; *[Laevicardium (Trachycardium)].* Guinea; possible holotype, British Mus. (Nat. Hist.). VEPRICARDIUM.

soyeri, [Laevicardium], Fischer-Piette, 1977. ?Mediterranean area; Paris Mus. Probably a VASTICARDIUM with incorrect locality data.

tertium, [Laevicardium], Fischer-Piette, 1977, new name for *Cardium fragile* Sowerby, 1834, *non* Brocchi, 1814. Locality unknown. LAEVICARDIUM (FULVIA).

thielei, [Laevicardium (Trachycardium)], Fischer-Piette, 1977, new name for *Cardium radula* Thiele & Jaeckel, 1931, *non* Broderip & Sowerby, 1829. Dar es Salaam, E. Africa. CTENOCARDIA (AFROCARDIUM).

PLATE 13

Cenozoic Laevicardiinae

Figures

1. *Cerastoderma edule* (Linné). *Ex* Moore *et al.*, 1969. Rec., Eu. (L ext. × 1)
2. *Laevicardium (L.) oblongum* (Gmelin). *Ex* Moore *et al.*, 1969. Rec., Eu. (R ext. × 0.5)
3. *Serripes groenlandicus* (Bruguière). *Ex* Chenu, 1862. Rec., N. Atl. (a, R hinge; b, L hinge; c, L ext.; × 1)
4. *Clinocardium (Planicardium) virginianum* (Conrad). *Ex* Olsson, 1967. Mio., Florida (a, juvenile shell, R int. × 1.2; b, juvenile shell, R ext. × 1)
5. *Clinocardium (C.) nuttallii* (Conrad). *Ex* Moore *et al.*, 1969. Rec., Oregon (R ext. × 0.5)
6. *Laevicardium (Profulvia) harrimani* (Dall). *Ex* Dall, 1910. Mio., N. Pac. (L ext. × 1)
7. *Clinocardium (Ciliatocardium) ciliatum* (Fabricius). *Ex* Sars, 1878. Rec., N. Atl. (R ext. × 1.5)
8. *Clinocardium (Fuscocardium) braunsi* (Tokunaga). *Ex* Oyama, 1973. Pleist., Japan (a, juvenile, L ext. × 1; b, adult, L int. × 1; c, adult, L ext. × 1)

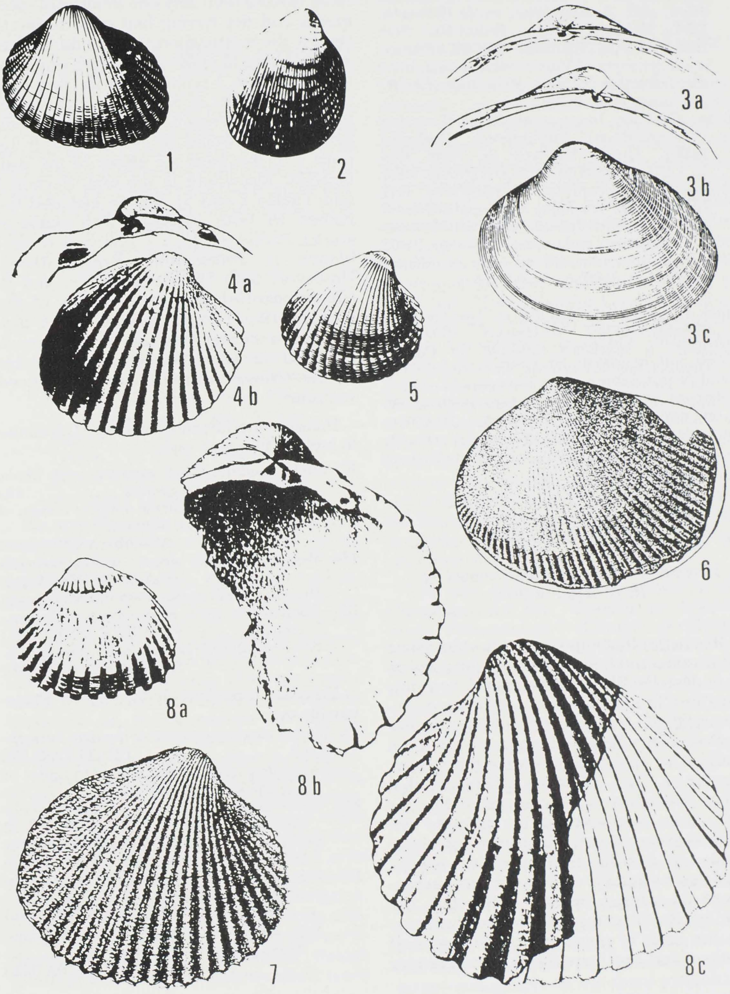

PLATE 13

tumidum, *Cardium*, Deshayes, 1855 (*non* Kloeden, 1834). [=*Laevicardium (Trachycardium*, sect. *Acrosterigma) enode* (Sowerby, 1834)]. Moluccas; syntype, British Mus. (Nat. Hist.). ACROSTERIGMA (REGOZARA) sp.; not a synonym of *Vasticardium enode*, but it may fall within the range of variation of *A. (R.) gratiosum*, cited above.

vulva, *Cardium*, Jousseaume, 1898; [=*Corculum (Keenocardium) californiense* (Deshayes, 1839)]. Japan; holotype in Paris Mus. =CLINOCARDIUM BUELOWI (Rolle, 1896).

williami, *[Microcardium]* Fischer-Piette, 1977. Unnecessary new name for a supposed homonym: *Protocardia panamensis* Dall, 1908, versus *Cardium panamense* Sowerby, 1833, species that now fall not only in different genera but in different subfamilies.

Note: Fischer-Piette identifies as "*Laevicardium (Trachycardium) senticosum* (Sowerby, 1833)" a specimen collected by DuPetit Thouars, labelled as from "Monterey, California." He cites it on p. 54 and figures it on pl. 4, fig. 3 and pl. 5, fig. 1. It is instead TRACHYCARDIUM (DALLOCARDIA) QUADRAGENARIUM (Conrad, 1837) and is probably from southern California, near Santa Barbara or Los Angeles.

VIII. APPENDIX II

Placement of two new taxa named by R. W. Scott in 1978

In a paper that appeared only a short time after mine had been submitted for publication, Robert W. Scott proposed two new taxa in Cardiidae. He was, of course, unaware that I had in preparation a further review of the family. Even belatedly, I am glad to be able to incorporate them here, insofar as I can. I find it a satisfaction that these have been given formal status, for both taxa were among the hitherto unnamed groups that my literature search revealed as possibly distinctive. However, I find that he and I are not in complete agreement on where the taxa fall within the family. He allocates them to the Cardiinae on the basis of rib sculpture. The general outline and the heavy and arched hinges seem to me to point toward the Protocardiinae. Having seen only one small lot of specimens and not having had opportunity to review the matter thoroughly, I do not feel justified here in making a positive reassignment. Rather, I have added the two new names in the list of Section 1 but have deferred a final decision. Below are the modifications that would be required to fit the units into the keys for either of the subfamilies. Elsewhere in the text (Section 3 and Tables 2 and 5), I have included the names in both settings, with question marks. *Pleuriocardia* s. s. has some resemblance to *Protocardia (Brevicardium)*. However, both *Pleuriocardia* s.s. and *P. (Dochmocardia)* may be offshoots of the *Nemocardium (Pratulum)* line, which also originated during the Lower Cretaceous. Dr. Scott considers the two taxa to be closer to the *Granocardium* line, with reduced sculpture.

Possible modification of key to Cardiinae to include two new taxa:

12. Shells medium-sized; cardinal teeth about midway between laterals 12a
    Shells mostly large-sized; anterior section of hinge shorter than posterior .... MAORICARDIUM [16]

12a. Beading on rib crests well developed PLAGIOCARDIUM [15]
    Beading on rib crests weak to wanting . 12b

12b. Shell nearly erect; beaks only slightly prosogyrate .... PLEURIOCARDIA [17a]
    Shell prosocline; beaks clearly prosogyrate DOCHMOCARDIA [17b]

Possible modification to Key to Protocardiinae:

22. With secondary concentric laminae throughout .... PRATULUM [63]
    Concentric laminae wanting or irregular or on posterior slope only 22a

22a. Secondary concentric laminae on posterior slope 23
    Secondary concentric laminae wanting or irregular 22b

22b. Ribs fine; shell nearly erect; beaks only slightly prosogyrate .... PLEURIOCARDIA [65a]
    Ribs relatively coarse; shell prosocline; beaks clearly prosogyrate .... DOCHMOCARDIA [65b]