

Phylogeny of the Cardiidae (Mollusca, Bivalvia): Protocardiinae, Laevicardiinae, Lahilliinae, Tulongocardiinae subfam. n. and Pleuriocardiinae subfam. n.

JAY A. SCHNEIDER

Accepted 7 June 1995

Schneider, J.A. 1995. Phylogeny of the Cardiidae (Mollusca, Bivalvia): Protocardiinae, Laevicardiinae, Lahilliinae, Tulongocardiinae subfam. n. and Pleuriocardiinae subfam. n.—*Zool. Scr.* 24: 321–346.

In a preliminary cladistic analysis of the bivalve family Cardiidae (Schneider 1992), members of the subfamilies Protocardiinae, Lahilliinae, and Laevicardiinae, plus the genus *Nemocardium*, were found to be the least derived taxa of cardiids. A cladistic analysis is undertaken of the genera and subgenera of these cardiid taxa, plus several Mesozoic taxa which have never been assigned to any subfamily. The Late Triassic *Tulongocardium*, which is placed in Tulongocardiinae subfam. n., is the sister taxon to all other cardiids. Protocardiinae is restricted to the genus *Protocardia*. Most other Mesozoic taxa which have been placed in the Protocardiinae are found to be members of the Lahilliinae. *Nemocardium* is placed in the Laevicardiinae. *Incacardium*, *Pleuriocardia*, and *Doehmocardia* form a monophyletic group, Pleuriocardiinae subfam. n. Pleuriocardiinae, Laevicardiinae, and the remaining members of the Cardiidae (herein informally termed “eucardiids”) form a monophyletic group.

Jay A. Schneider, Smithsonian Tropical Research Institute, Box 2072, Balboa, Republic of Panama. Present address: Department of Geology, Youngstown State University, Youngstown, OH 44555-3612, U.S.A. Tel.: 216-742-1755; Fax: 216-742-1754

Introduction

Bivalves of the family Cardiidae (cockles and giant clams) originated in the Late Triassic and have a present-day diversity of nearly 200 species (Rosewater 1965; Fischer-Piette 1977). Cardiids have been the subject of considerable taxonomic work by both paleontologists and malacologists, and numerous subfamilies, genera, and subgenera have been erected. However, few studies of the phylogenetic relationships amongst these taxa within the Cardiidae have been undertaken.

The only published phylogenies for cardiids are those of Kafanov & Popov (1977) and Schneider (1992). They based their phylogeny on two key character complexes: shell microstructure and morphology of the stomach. Kafanov and Popov addressed only the group's Cenozoic evolution, and considered neither the origin of the Cardiidae nor its Mesozoic history. Schneider (1992) proposed a preliminary phylogenetic hypothesis for the Cardiidae based on a cladistic analysis of 54 characters of 36 taxa (Fig. 1). In that analysis, at least one member from each of the subfamilies recognized by Kafanov & Popov (1977) and Keen (1951, 1969, 1980) was included, as well as additional taxa of uncertain affinities. *Palaeocardita*, usually placed in the Carditidae (Cox 1949; Chavan 1969a), was found to be the least derived cardiid. The next two taxa on the preliminary cladogram were *Septo-*

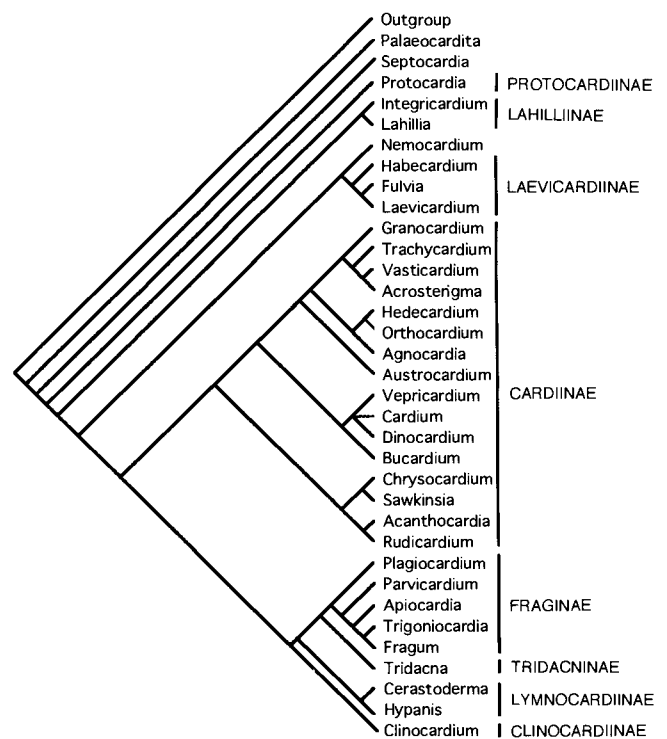


Fig. 1. Phylogenetic relationships within the family Cardiidae. From Schneider (1992).

cardia and *Protocardia*. Almost all members of the cardiid subfamily Protocardiinae have been placed in the genera *Protocardia*, *Integricardium*, and *Nemocardium* (Keen 1951, 1969, 1980). In the preliminary analysis, *Integricardium* was found to be the sister taxon to *Lahillia*. Marwick (1944) and Keen (1969) had placed *Lahillia* in its own cardioid family Lahilliidae. *Nemocardium* was found to be the sister taxon to the Laevicardiinae. Therefore, the Protocardiinae as generally understood is a paraphyletic group (i.e. contains some, but not all, the descendants of a most recent common ancestor).

There are several Mesozoic taxa whose subfamilial affinities are uncertain. There has been no previous attempt to place the Late Triassic taxa *Tulongocardium* and *Vietnamicardium* in any subfamily. Scott (1978) erected *Pleuriocardia* (*Pleuriocardia*) and *Pleuriocardia* (*Dochmocardia*) for some Cretaceous species, placing them in Cardiinae. However, Keen (1980) thought that *Pleuriocardia* and *Dochmocardia* belonged in Protocardiinae. Keen (1951, 1969, 1980) classified the Upper Cretaceous *Incardium* as a subgenus of the Cenozoic cardiine *Acanthocardia*, but this taxonomy contradicts her 1980 description of cardiid phylogeny.

The purpose of the present study is to propose a detailed phylogenetic hypothesis for the primitive cardiids. This paper will discuss:

- (1) appropriate outgroup(s) for the Cardiidae;
- (2) the status, content, and interrelationships of the subfamilies Protocardiinae, Lahilliinae, and Laevicardiinae, and the genus *Nemocardium*; and (3) the phylogenetic relationships of the problematic Mesozoic taxa *Tulongocardium*, *Vietnamicardium*, *Pleuriocardia*, *Dochmocardia*, and *Incardium*.

Material and methods

Selection of ingroup taxa

All genera and subgenera of Protocardiinae and Laevicardiinae accepted by either Keen (1951, 1969, 1980) or Kafanov & Popov (1977) are represented in the analysis (see Appendix I). The cardiine, *Granocardium*, is included to represent the clade comprising the subfamilies Cardiinae, Clinocardiinae, Lymnocardiinae, Fraginae, and Tridacninae. These five subfamilies will be informally referred to as "eucardiids". Fossils of *Granocardium* are known from the Aptian (late Early Cretaceous; Keen 1969, 1980) and are the oldest eucardiid fossils.

Keen (1951, 1969, 1980) classified the Upper Cretaceous *Incardium* as a subgenus of the Cenozoic cardiine *Acanthocardia*. However, Keen (1980) considered *Incardium* as intermediary between the Norian (middle Late Triassic) *Septocardia* and the Cardiinae, whereas she derived *Acanthocardia* from *Granocardium*. The problematic taxa *Pleuriocardia* and *Dochmocardia* are also included (see Introduction).

Chen, Chen & Zhang in Lan and Chen (1976) erected *Tulongocardium* (type species *Cardium* [*T.*] *pluriradiatum* Chen, Chen & Zhang in Lan & Chen 1976) as a subgenus of *Cardium*, and assigned nine Late Triassic species to this new taxon. Vu-Khuc (1977), apparently unaware of *Tulongocardium*, erected the genus *Vietnamicardium* [type species *V. vietnamicum* (Vu-Khuc in Vu-Khuc *et al.* 1965)]. All four of the species that Vu-Khuc placed in *Vietnamicardium* had been put in *Tulongocardium* by Chen, Chen and Zhang. Keen (1980) did not accept *Tulongocardium* as a cardiid, and placed it in the Astartidae; she was apparently unaware of *Vietnamicardium*. The only well-preserved material of *Tulongocardium* is that of *Cardium nequam* Healey, 1908, and this species was chosen to represent *Tulongocardium* in the present analysis. With the exception of *Cardium cloacinum* Quenstedt, 1858 [which Chen, Chen & Zhang in Lan & Chen (1976) had put in *Tulongocardium*, but Cox (1948) assigned to the astartid genus *Tucheria*], all other species assigned to *Tulongocardium* and *Vietnamicardium* are clearly

cardiids. However, these species could not be coded for the three hinge characters (14–16). The other characters would be coded identically to the scheme for *C. nequam*. Since there are no autapomorphies (characters unique to a taxon) to distinguish *Vietnamicardium*, it is synonymized with *Tulongocardium*.

Noda (1988) erected *Tobarum* [type species *Frigidocardium* (*Tobarum*) *tobaruense* Noda, 1988; Pliocene, Japan] as a monotypic subgenus of *Frigidocardium*, which Habe (1951) erected as a genus. *Frigidocardium* has also been treated as a subgenus of *Nemocardium* by Keen (1969, 1980), and synonymized with *Pratulium* by Popov (1977) or with *Microcardium* by Wilson & Stevenson (1977). *F. tobaruense* would have the identical cladistic coding as *Microcardium* (Table 1). Since *Tobarum* has no autapomorphies to distinguish it from *Microcardium*, I consider *F. tobaruense* to be a species of *Microcardium* (as does J.-M. Poutiers, pers. comm., 1991), and it is not considered separately in this analysis.

Tendagurium was introduced by Dietrich (1933) as a subgenus of *Cardium*, and included two Mesozoic species. Generic names published after 1930 must be accompanied by the fixation of a type species [International Code of Zoological Nomenclature, 3rd edition (Ride *et al.* 1985), article 13(b)]. However, Dietrich (1933) neglected to designate a type species. Salisbury (1934) rectified this situation [thus satisfying ICZN article 13(b)] by designating *Cardium propebanneaimum* Dietrich, 1933, as the type species. Salisbury's (1934) designation satisfies ICZN article 13(a)ii because it references Dietrich's (1933) description of *Tendagurium*. Therefore, the name *Tendagurium* is valid, and the taxon is considered to have been erected by Salisbury (1934). Subsequent authors, apparently unaware of Salisbury's (1934) type designation, accepted Dietrich as the author of *Tendagurium* (Keen 1937, 1969; Amano *et al.* 1958; Vokes 1968, 1980). Keen (1937) and Amano *et al.* (1958) unnecessarily designated a type species for *Tendagurium*. Hayami (1958) considered the name *Tendagurium* unavailable. Keen (1980) is the only reference to Salisbury's (1934) original type species designation.

Guo (1988) proposed *Grypocardia* as a Rhaetian (latest Triassic) monotypic subgenus of *Protocardia*. All specimens are internal molds, and I cannot confirm their identity as cardiids. Therefore, *Grypocardia* is not included in this analysis.

Cossmann (1906) erected *Jurassicardium* as a monotypic subgenus of *Cardium*, and felt it was most closely allied to *Protocardia* and *Nemocardium*. Keen (1951, 1969, 1980) classified *Jurassicardium* as a genus in Protocardiinae. The only well-preserved material of *Jurassicardium* is the type material of the type species, *J. axonense* Cossmann, 1906. Unfortunately, the whereabouts of the type material is unknown, and *Jurassicardium* is not included in this analysis. *Jurassicardium* is not monotypic, as erroneously stated in Schneider (1992); two other species have been described under this genus [see Cossmann (1916) and Yamani and Schairer (1975)].

Zinsmeister (1984) considered *Lahilleona* to be a junior synonym of *Lahillia*. *Lahilleona* is not represented in the analysis.

Most of the taxa considered in the present analysis are illustrated by Keen (1969, 1980). Alexander Kafanov is currently working on a species-level monograph of Cenozoic and Recent cardiids (A.I. Kafanov, pers. comm., 1994).

Selection of outgroup

Some authors (Cox 1949; Keen 1969, 1980; Newton 1986; Schneider 1992) have derived the Cardiidae from a member of the Carditoidea, postulating an evolutionary scenario of the Permo-Triassic carditid *Palaeocardita* originating from some Late Palaeozoic permorphid carditidoid (such as the Permian *Gujocardita*), with *Septocardia* [Norian (middle Late Triassic)] being subsequently derived from *Palaeocardita*. Keen (1969, 1980) placed *Septocardia* in the subfamily Cardiinae, although no other cardiines appear until the Aptian (late Early Cretaceous). However, Morris (1978) and Morris *et al.* (1991) have argued that the Permophoridae are not carditoids, but anomalodesmatans convergent on veneroids. Although I previously considered (Schneider 1992) *Palaeocardita* and *Septocardia* to be cardiids, I presently think that there is significant doubt about their phylogenetic relationships. They are considered as members of neither the ingroup nor the outgroup in the present analysis.

In the preliminary phylogenetic analysis of the entire family Cardiidae (Schneider 1992), a hypothetical ancestor, based on character states from the Recent carditids *Cyclocardia ventricosa* (Gould, 1841) and *Cardita variegata* Bruguière, 1792, was used as the outgroup. The use of carditids as the outgroup to cardiids was based on the postulated evolutionary sequence of Paleozoic carditids—*Palaeocardita*—*Septocardia*—Cardiidae. If the Paleozoic carditids and *Palaeocardita* (and, presumably, other members of the Devonian to Early Jurassic subfamily Palaeocardiinae) are anomalodesmatans, then, according to Chavan (1969a), the only remaining pre-Cretaceous carditids are the

Triassic–Jurassic *Tutcheria* and the Jurassic *Pseudopsis*. Cox (1946) erected both *Tutcheria* and *Pseudopsis*, placing them in Astartidae on the basis of their hinges and external sculpture. Cox emphasized that the presence of radial ribs on *Tutcheria* and *Pseudopsis* does not automatically make them carditids, for some astartids have external radial ribs, and all astartids have internal radial ribs (Chavan 1952, 1969b). Given the excellent fossil record of molluscs (Raup 1979; Allmon 1988; Valentine 1989), it seems that the Carditidae, with no true representatives before the Cretaceous and no shared derived characters to unite them with the Cardiidae, are not an appropriate outgroup for the Cardiidae, which originated in the Late Triassic.

Waller (1988, 1990), in discussing the phylogeny of heterodont bivalves, considered the Lucinoidea as the sister group to all other heterodonts, the latter being rooted in the Crassatelloidea, which contains the Astartidae (Boyd & Newell 1968; Yonge 1969). Stanley (1968) argued that the siphonate eulamellibranch bivalves were derived from an astartid. Therefore, it was decided to seek outgroup information among members of the Astartidae.

Astartid shell evolution has been very conservative; early Devonian astartids differ little from modern forms (Morris 1978). Species of the genus *Astarte* are among the most primitive living eulamellibranchs (Stanley 1968). *Astarte* is also one of the oldest living genera of bivalves, having appeared in the Hettangian [earliest Jurassic; Sepkoski, unpublished compendium of marine invertebrate stratigraphic ranges; see Sepkoski (1986, 1989); Raup & Boyajian (1988); and Jablonski (1994) for a detailed description of Sepkoski's compendium], and is only slightly younger than the entire family Cardiidae, which originated in the Norian (middle Late Triassic). Therefore, *Astarte* is used as an outgroup for the Cardiidae, with character state data taken from three Recent species of *Astarte*: *Astarte castanea* Say, 1822, *A. sulcata* (Da Costa, 1778), and *A. undata* Gould, 1841. Conchological states were encoded from my examinations of the shells, and anatomical states were coded from Saleuddin's (1965, 1967) descriptions of these species.

It has been recommended that cladistic analyses be run with more than one outgroup (Maddison *et al.* 1984). However, this presumes a certain amount of previous knowledge of phylogeny which I do not think is presently available. For this particular analysis, I feel it is best to be cautious and use only that one group—with character analysis of three different species—which can confidently be considered as an appropriate outgroup.

Seilacher (1984) contended that bivalves have undergone too much convergent and parallel evolution to be studied cladistically. Successful studies of various bivalve groups have been conducted by cladistic analysis (Waller 1978, 1993; Miyazaki & Mickevich 1982; Bieler & Mikkelsen 1992; Huelsenbeck 1994). Numerous cladistic studies of various taxa have shown that cladistic analysis, when undertaken in concert with rigorous character analysis, is not hampered by what a priori has been perceived as convergent evolution, but actually has the ability to discern theretofore unknown or under-appreciated cases of convergence and parallelism (Crane 1985; Doyle & Donoghue 1986; Fortey & Cooper 1986; Gauthier *et al.* 1988; Brooks 1989; Patterson & Rosen 1989; Sluys 1989; Fortey 1990; Smith & Wright 1990; Begle 1991; Marshall & Schultze 1992; Novacek 1992; Carlson 1993; Simms & Sevastopulo 1993; Lanyon 1994; Kambhampati 1995). Cladistic analysis does not assume that convergence and parallelism are rare (Farris 1983). It is through cladistic analysis that we are able to discern convergence and parallelism from homology. Arguments against the use of cladistics for one reason or another have been put forth regarding many taxa, not just bivalves (Sneath & Sokal 1973; Gingerich 1979; Lazarus & Prothero 1984; Campbell & Barwick 1990). It should also be noted that Seilacher's (1984) paper appeared before the widespread use of user-friendly cladistic computer programs with numerous options with which the systematist may tailor the cladistic analysis to the data at hand [such as Farris (1988), Swofford (1991, 1993) and Maddison & Maddison (1992)], and examine alternative tree topologies and character state reconstructions.

Abbreviations of repositories

AM: Australian Museum. Sydney, Australia.
 AMNH: American Museum of Natural History, New York, New York, USA
 ANSP: Academy of Natural Sciences of Philadelphia. Philadelphia, Pennsylvania, USA.
 DSIRGS: New Zealand Department of Scientific and Industrial Research, Geology and Geophysics. Lower Hutt, New Zealand.
 FMNH: Field Museum of Natural History. Chicago, Illinois, USA:
 FMNH: Recent molluscan collection
 FMNH P: Paleontological collection
 FMNH UC: University of Chicago collection, now incorporated into the paleontological collections of the FMNH
 GSC: Geological Survey of Canada. Ottawa, Ontario, Canada.

LACMNH: Los Angeles County Museum of Natural History. Los Angeles, California, USA.
 MCZ: Museum of Comparative Zoology, Harvard University. Cambridge, Massachusetts, USA.
 MM: University of Tokyo Geological Institute. Tokyo, Japan.
 MNHN: Muséum National d'Histoire Naturelle. Paris, France.
 NHM: The Natural History Museum. London, United Kingdom.
 PRI: Paleontological Research Institution. Ithaca, New York, USA.
 SBMNH: Santa Barbara Museum of Natural History. Santa Barbara, California, USA.
 UNC: University of North Carolina—Chapel Hill, Department of Geology. Chapel Hill, North Carolina, USA.
 USNM: United States National Museum. Washington, D.C., USA.
 USNM JHU: Johns Hopkins University collection, now incorporated into the collections of the USNM.
 UWBM: Thomas Burke Memorial Washington State Museum. Seattle, Washington, USA.
 YPM: Yale Peabody Museum. New Haven, Connecticut, USA.

Material examined

Each of the ingroup taxa is represented in the present analysis by a single species, usually the type. Therefore, this analysis should be taken as a phylogeny for these species only. Character states presented may not be constant throughout all species of a given genus or subgenus. Except as where noted, all character states were encoded from examination of specimens. All Recent taxa were investigated anatomically, as well as conchologically, except for *Trifarcardium*, for which there is no anatomical material available. Material examined is shell material, unless otherwise indicated. Species examined are the type species of the genus or subgenus, unless otherwise indicated. The number of specimens in each lot is indicated by the number in parentheses.

Astarte [type species *A. scotica* (Maton and Rickett, 1807)]. *Astarte castanea* (Say, 1822): AMNH 198665 (32); FMNH 9005 (1), 13775 (1), 13860 (2), 50593 (3), 54723 (2), 182910 (2), 182939 (1), 184597 (2).
A. sulcata (Da Costa, 1778): AMNH 199767 (10); FMNH 2609 (2), 16355 (1), 149997 (2), 169261 (2).
A. undata (Gould, 1841): AMNH 199082 (8); FMNH 2608 (3), 30271 (2), 50594 (3), 148389 (1), 149899 (15), 184828 (3), 185692 (6); USNM 711294 (76). Anatomical data from Saleuddin (1965, 1967).
Tulogocardium (type species *T. pluriradiatum* Chen, Chen & Zhang in Lan & Chen, 1976). *Tulogocardium nequam* (Haley, 1908): data from Healey (1908).
Protocardia (*Protocardia*) *hillana* (Sowerby, 1813): ANSP 36497 (4); MCZ 10386 (6), 101697 (1); NHM L3370 (2), L17030 (4), 24140 (1).
Protocardia (*Leptocardia*) *subquadrata* (Evans & Shumard, 1857): USNM 278 (2, hypotypes); AMNH 9401 (2), 9402 (2); ANSP 37108 (9); FMNH P3504 (1); YPM IP.006889 (100).
Protocardia (*Pachycardium*) [type species *P. spillmani* (Conrad, 1858)]. *Protocardia* (*Pachycardium*) *stantoni* (Wade, 1926): USNM 32794 (1, syntype), USNM 315519 (1, syntype), 315520 (1, syntype), USNM 482408 (1); AMNH 2496 (2).
Protocardia (*Tamilicardia*) *pulchella* Chiplonkar & Tapaswi, 1976. Data from Chiplonkar & Tapaswi (1976).
Integricardium dupinianum (Orbigny, 1844). Data from Orbigny (1844).
Onestia onestae (McLearn, 1931): GSC 6345 (1, holotype), 8003 (1, hypotype), 8004 (1, hypotype).
Cryptocardia bajocensis Palmer, 1974: NHM 66193 (1, holotype), 66243 (1, paratype), 66197 (1, paratype).
Globocardia sphaeroideum (Forbes, 1845): NHM LL.8466 (1), 48626 (1), L.8247 (1); FMNH UC33133 (1).
Yokoyamaina hayamii Keen & Casey in Moore *et al.* 1969: MM 2866 (1, paratype), 2867 (1, paratype).
Tendagurium propebanneianum (Dietrich, 1933). Data from Dietrich (1933).
Lahillia [type species *Lahillia angulata* (Philippi, 1887)]. *Lahillia wilckensi* Zinsmeister, 1984: USNM 365500 (1, holotype), 365496 (1, paratype), 365497 (1, paratype), 365498 (1, paratype), 365499 (1, paratype).
Granocardium [type species *Granocardium carolinum* (Orbigny, 1844)]. *Granocardium kuemmelii* (Weller, 1907): USNM 21126 (1, holotype), AMNH 45042 (1), 45043 (1), 45044 (1), 45045 (1), 45046 (1), 45047 (1), 45048 (1); ANSP 36475 (5); YPM IP.025574 (1). The AMNH and ANSP and material was misidentified as *Granocardium dumosum* in Schneider (1992).
Pleuriocardia (*Pleuriocardia*) *kansasense* (Meek, 1871): USNM 7905 (1, lectotype). Additional data from Scott (1970, 1978).
Pleuriocardia (*Dochmocardia*) [type species *Pleuriocardia* (*Dochmocardia*) *paupercula* (Meek, 1871)]. *Pleuriocardia* (*Dochmocardia*) *eufaulense* (Conrad, 1860): ANSP 19597 (1, holotype), ANSP 36491 (7); USNM 20847 (1), AMNH 45040 (1), 45041 (1); FMNH 18647 (2).

- Pleuriocardia (Incardium) mellisa* Olsson 1944: PRI 4830 (1, holotype), 4831 (1, paratype).
Nemocardium (Nemocardium) bechei (Reeve, 1847): ANSP 252661 (4). Anatomical: USNM 747190 (1).
Nemocardium (Varicardium) patulum (Hutton, 1873): DSIRGS 11794 (2).
Nemocardium (Lyrocardium) lyratum (Sowerby, 1841): ANSP 216424 (4); USNM 344806. Anatomical: USNM 746647 (1).
Nemocardium (Lophocardium) cumingii (Broderip, 1833): ANSP 216379 (4), 394333 (2); FMNH 278007 (1), 278008 (1). Anatomical: FMNH 278007 (2); MCZ 147452 (1).
Nemocardium (Pratulium) thetidis (Hedley, 1902): ANSP 226837 (15). Anatomical: AM 170001 (2).
Nemocardium (Brevicardium) fragile Stephenson, 1941: USNM 76644 (1, holotype), 20701 (1, paratype), 128151 (1), 128152 (1); ANSP 36494 (5).
Nemocardium (Arctopratalium) griphus Keen, 1954: USNM 561859 (1, paratype).
Nemocardium (Divaricardium) discrepans (Basterot, 1825): MNHN B23982 (6).
Nemocardium (Keenaea) (type species *Nemocardium (Keenaea) samarangae* [Makiyama, 1934]). Material examined. *Nemocardium (Keenaea) centifilosum* (Carpenter, 1864): USNM 162620 (1, holotype), USNM 331633 (68), 323892 (2). Shell and anatomy: SBMNH 35526 (11); LACMNH 54–78.1 (35); FMNH 278004 (2), 278005 (2), 278006 (2).
Nemocardium (Microcardium) peramibilis (Dall, 1881): ANSP 176654 (6); USNM 323892 (24). Anatomical: USNM 801861 (9).
Nemocardium (Frigidocardium) [type species *Nemocardium (Frigidocardium) eos* (Kuroda, 1929)]. *Nemocardium (Frigidocardium) exasperatum* (Sowerby, 1838): USNM 297106 (4), 21168 (2). Shell and anatomy: USNM 746892 (3), 747006 (3), 747646 (3).
Nemocardium (Trifaricardium) nomurai Habe 1951: USNM 204363 (2); FMNH 278009 (2); ANSP 343543 (2).
Habecardium tenuisulcatum (Nyst, 1836): AMNH 20259 (3); ANSP 10267 (8); USNM JHU 76 (4); UWBM 3169 (1); YPM 35380 (1), 35381 (1), 35382 (1).
Fulvia aperta (Bruguière, 1789): USNM 658817 (4). Shell and anatomy: USNM 655038 (10).
Laevicardium [type species *Laevicardium oblongum* (Gmelin, 1791)]. *Laevicardium laevigatum* (Linne, 1758): AMNH 210132 (5); ANSP 61034 (1), 83809 (5), 326257 (4); UNC 5891 (1), 8316 (3), 14228 (2), PRI 3716E (2); USNM 503002 (2). Anatomical: ANSP A1022 (8); USNM 734711 (1), 801059 (1), 801845 (1), 804198 (1), 804301 (1), 836963 (1).
Discors parisiense (Orbigny, 1850): ANSP 7680 (3), 7681 (3); USNM 325921 (2), 482841 (2).

Abbreviations used in figures

<i>aa</i>	anterior adductor
<i>ac</i>	anterior cardinal
<i>ah</i>	apparent height
<i>al</i>	anterior length
<i>as</i>	anterior slope
<i>cs</i>	cross-striae
<i>dv</i>	divaricate sculpture
<i>h</i>	height
<i>hn</i>	hinge
<i>id</i>	inner demibranch
<i>ip</i>	inner labial palp
<i>l</i>	length
<i>lr</i>	lateral ridge
<i>ml</i>	midline (line connecting midpoints of adductors)
<i>og</i>	oral groove
<i>op</i>	outer labial palp
<i>pc</i>	posterior cardinal
<i>pf</i>	periostracal frill
<i>pl</i>	posterior length
<i>ps</i>	posterior slope
<i>rr</i>	radial ribs
<i>s</i>	spine
<i>u</i>	umbo
<i>v</i>	varicate sculpture
<i>vr</i>	ventral ridge

Characters and character states

A cladistic analysis of 33 taxa with 16 characters comprising 53 character states was performed using PAUP 3.1.1

(Swofford 1993). The heuristic branch-swapping routine with random addition and tree-bisection–reconnection options was used. The accelerated transformation option (ACCTRAN) was used, and steps were not added to taxa with polymorphisms. Missing data are coded by a question mark “?” [see Swofford (1993) for explanations of these options]. Fourteen of the 16 characters are unordered. Two characters, ribbing pattern (8) and shell shape (9), are ordered on the basis of ontogeny and outgroup analysis. The states of these ordered characters are assembled into character state trees which are fed into the analysis with the USERTYPE command (see Swofford 1993). All extinct taxa are coded missing (?) for anatomical and periostracal characters. The data matrix is presented in Table I.

Anatomical characters

1. Connection between inner labial palp and inner demibranch (Fig. 2). In most cardiids, the anterior end of the inner demibranch fuses to the oral groove between the inner and outer labial palps. However, in *Laevicardium* and *Fulvia*, the inner labial palp is connected to the bottom of the inner demibranch. States: (0) inner demibranch fuses to oral groove between the inner and outer labial palps, (1) inner labial palp attaches to bottom of inner demibranch.

2. Lateral ridges on foot (Fig. 3). States: (0) absent, (1) present, moderate, (2) present, strong.

3. Ventral ridge on foot (Fig. 3). In the present data set, this character is coded exactly as character 2. It is considered an independent character because several eucar-

Table I. Data matrix for cladistic analysis. Taxa in rows, characters in columns. *Pleuriocardia* and *Dochmocardia polymorphic* (states 1 and 3) for character 7, indicated by “X”. “?” signifies missing data

Outgroup	0000	0000	0000	0000
Tulongocardium	????	??11	1000	?101
Protocardia	????	??12	1000	?101
Leptocardia	????	??12	1000	?101
Pachycardium	????	??12	1000	?101
Tamilicardia	????	??12	1000	????
Integricardium	????	??23	200?	?101
Yokoyamaina	????	??23	300?	????
Tendagurium	????	??23	300?	?101
Cryptocardia	????	??23	401?	?101
Globocardium	????	??23	401?	?101
Onestia	????	??23	200?	?101
Lahillia	????	??23	200?	?101
Brevicardium	????	??34	1000	?202
Nemocardium	0110	1034	4000	0202
Varicardium	????	??34	4000	0202
Lyrocardium	0110	1014	4000	?202
Lophocardium	0110	1114	4000	?302
Pratulium	0110	1035	1000	0202
Arctopratalium	????	??35	1000	0202
Divaricardium	????	??35	1000	?202
Microcardium	0110	1035	4101	0202
Frigidocardium	0110	1035	4001	0202
Trifaricardium	????	?035	4101	0202
Keenaea	0110	1135	1000	?202
Habecardium	????	??16	5000	?202
Discors	????	??27	5000	?202
Fulvia	1221	2017	5000	?202
Laevicardium	1221	2027	5000	?202
Pleuriocardia	????	??X1	6002	1412
Dochmocardia	????	??X1	6002	1412
Incardium	????	??11	6002	1412
Granocardium	????	?01	4000	0202

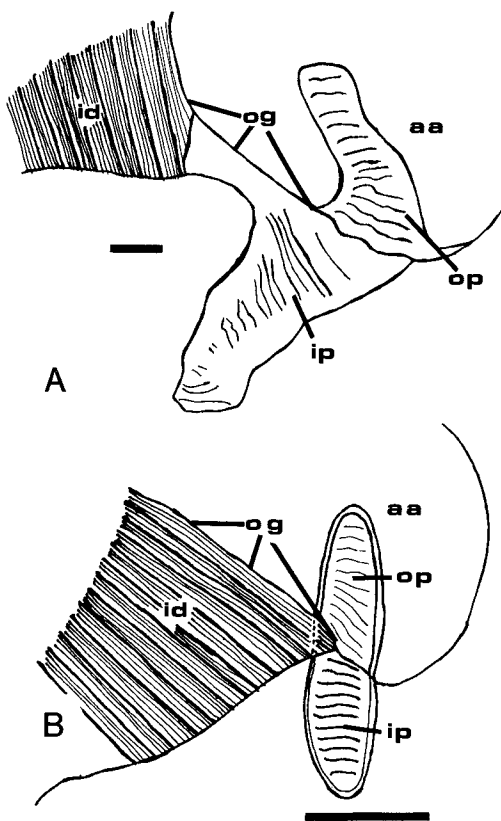


Fig. 2. Right lateral view of inner demibranch-labial palp connections. Both inner and outer labial palps shown with ridged surface exposed.—A. *Laevicardium laevigatum* (ANSP A1022). Top of inner labial palp connected to bottom of inner demibranch (state 1). Scale bar equals 1 mm.—B. *Nemocardium (Frigidocardium) exasperatum* (USNM 746892). Inner demibranch inserts into oral groove between inner and outer labial palps (state 0). Scale bar equals 2 mm.

diids (*Vepricardium*, *Papillicardium*, *Yagudinella*, *Serripes*, *Microfragum*) display discordant states for the two characters (Schneider 1993). States: (0) absent, (1) present, moderate, (2) present, strong.

4. Position of right caecum on stomach floor. States: (0) right side of stomach floor, (1) middle of stomach floor.

5. Eyes. Eyes occur on the distal tip of some of the siphonal tentacles of cardiids. These eyes consist of a multicellular lens, a retina composed of a single layer of cells, and an enclosing sheath. A nerve runs in the tissue of the tentacle, and sends a branch off to the eye. The nerve is inverse, in that it passes between the lens and retina before going to the sensory cells. *Laevicardium* and *Fulvia* possess more complex eyes, which have a globular apparatus, a closed cavity, pigmented subepithelial cells, crystalline cells, a vitreous body, and a tapetum next to an ocular globe. Eyes are lacking in the outgroup, *Astarte*. Data from Kishinouye (1894), Nagel (1897), Zugmayer (1904), Weber (1908), Pelseneer (1911), Roche (1925), Braun (1954) and personal observation. States: (0) absent, (1) simple, (2) complex.

Periostracal character

6. Periostracal frill (Fig. 4). In *Nemocardium (Lophocardium)* and *Nemocardium (Keenaea) centifilosum*, the periostracum forms a tuft or flange at the junction between the posterior and central portion of the shell, where

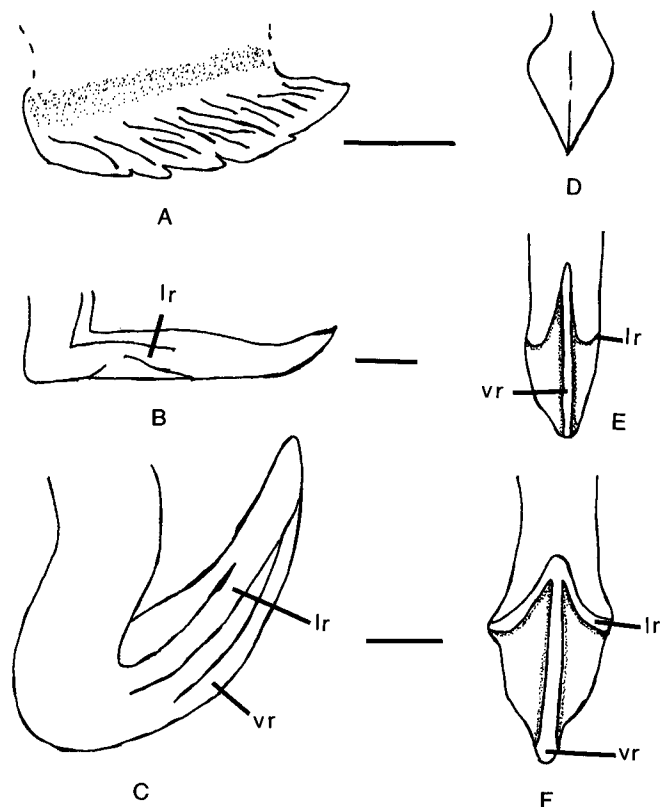


Fig. 3. Feet.—A–C. Right lateral views of feet.—D–F. Anterior views of feet.—A, D. *Astarte sulcata* (from Saleuddin, 1965). States 2:0; 3:0. Scale bar equals 6 mm.—B, E. *Nemocardium (Frigidocardium) exasperatum* (USNM 746892). States 2:1; 3:1. Scale bar equals 2 mm.—C, F. *Laevicardium laevigatum* (ANSP A1022). States 2:2; 3:2. Scale bar equals 5 mm.

there is a change in the ribbing pattern. Wilson & Stevenson (1977) report that a frill exists on *N. (N.) bechei*, but I have never detected a frill on any specimen of this species. This frill is absent in the type species of *Keenaea*, *N. (K.) samarangae*. States: (0) absent, (1) present.

Shell characters

7. Posterior margin (Fig. 5). Posterior margins in cardiids can be digitate, crenulate, or smooth. To determine margin type, a line parallel to the line connecting the midpoints of the adductor muscles is drawn from the distal end of a posterior rib (or rib interspace) towards the anterior end of the shell. If the line traverses empty space before it crosses the shell margin, it is considered digitate. If the line encounters only shell on its anterior traverse, then the margin is considered crenulate. If neither the ribs nor the interspaces extend beyond the shell margin, then the posterior margin is considered smooth. *Astarte* has internal radial ribs whose distal ends are manifested along the internal margin only; this state is not considered homologous with any other state. States: (0) inner margin crenulate, exterior margin smooth, (1) crenulate, (2) smooth, (3) digitate.

8. Ribbing pattern. A character state tree can be constructed for this character based on ontogeny combined with outgroup analysis. The outgroup condition is found in *Astarte*, in which there are internal radial ribs, and the external sculpture is of concentric growth lines (state 0; Figs 6A and 7A). Some cardiids have a sculpture

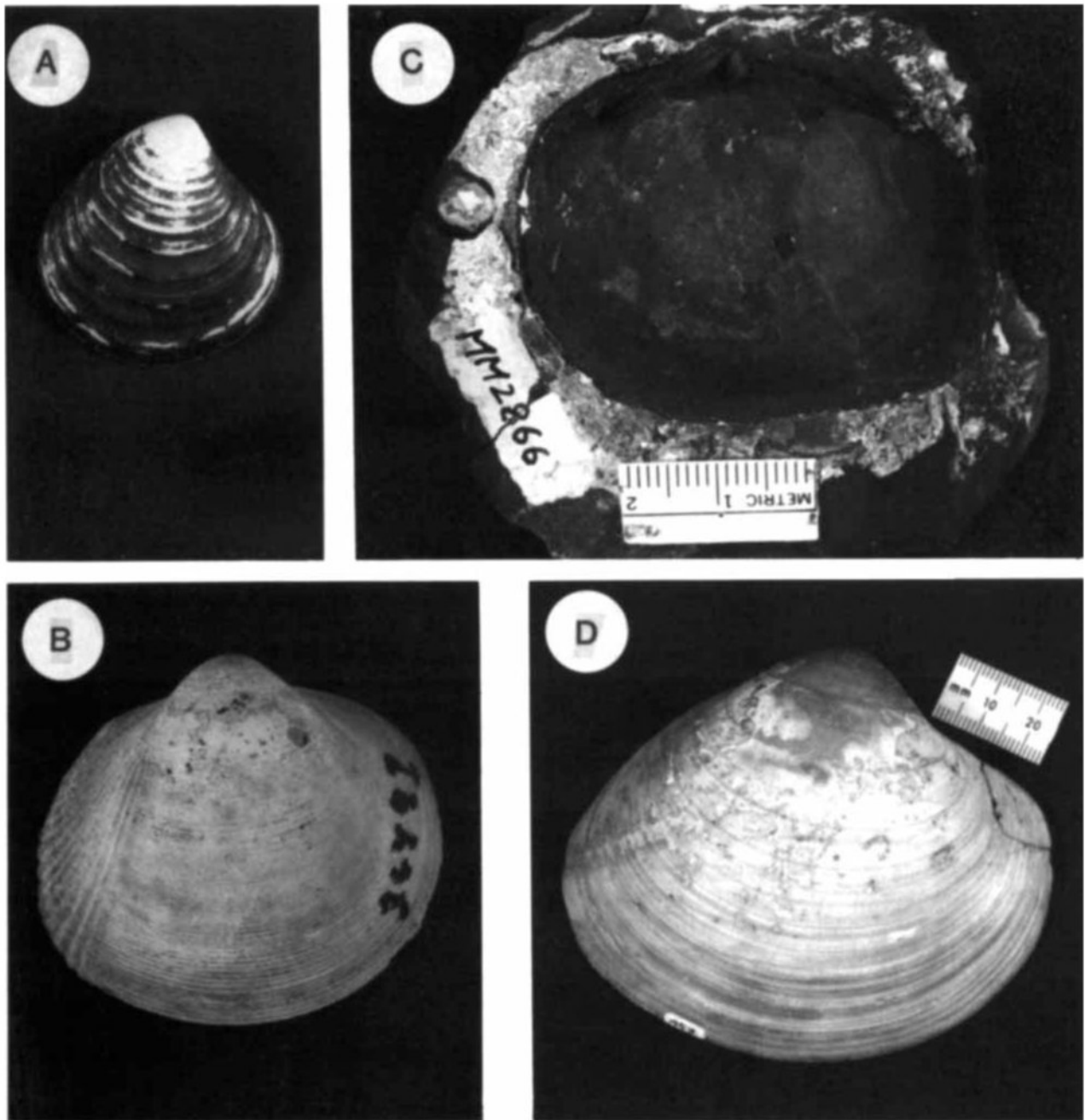


Fig. 7. Right valves.—A. *Astarte castanea* (FMNH 13860), $\times 2$.—B. *Protocardia* (*Protocardia*) *hillana* (ANSP 36497), $\times 1.8$.—C. *Yokoyamina hayamii* (MM 2866), internal mold of right valve, scale indicated in figure.—D. *Lahillia wilckensi* (USNM 365500), scale indicated in figure.

Cladistic analysis

Data sets with many more taxa than characters, like the one analyzed here, have the potential to be so incongruous that a personal or Macintosh-type computer cannot complete a cladistic analysis because of insufficient memory. The relatively small number of potential synapomorphies (shared derived characters) invites the possibility that hundreds, if not thousands, of most parsimonious trees will be produced by the program. McKittrick's (1991) cladistic analysis of avian hindlimb musculature had 103 taxa and 68 characters. She terminated the PAUP 3.0q (Swofford 1991) analysis at 6000 trees due to memory constraints. McKittrick also analyzed the data set with Hennig86 (Farris 1988) which self-terminated at 884 trees because the memory capacity of the program had been reached. However, some of the incongruity in

McKittrick's analysis may have been caused by her limiting her coding scheme to 10 states per character, even when she recognized that more states existed. PAUP 3.0 can accommodate well over 50 states per character [integers 0 through 9, letters a through z, and nearly every other symbol that the keyboard can generate, not just 0 through 9 as McKittrick (1991, p. 51) states]. Another incongruous data set is that of Erséus (1992), who used PAUP 3.0 to analyze the phylogeny of phalloidriline oligochaete annelids. The data set comprised 103 taxa and 36 characters. The computer ran out of memory after saving 4638 equally parsimonious trees. No attempt was made to investigate a broad spectrum of tree topologies by producing sets of initial trees using random addition and replication. Maddison (1991) recognized that the set of most-parsimonious trees for a cladistic data matrix may include several distinct classes of trees. Using the method-

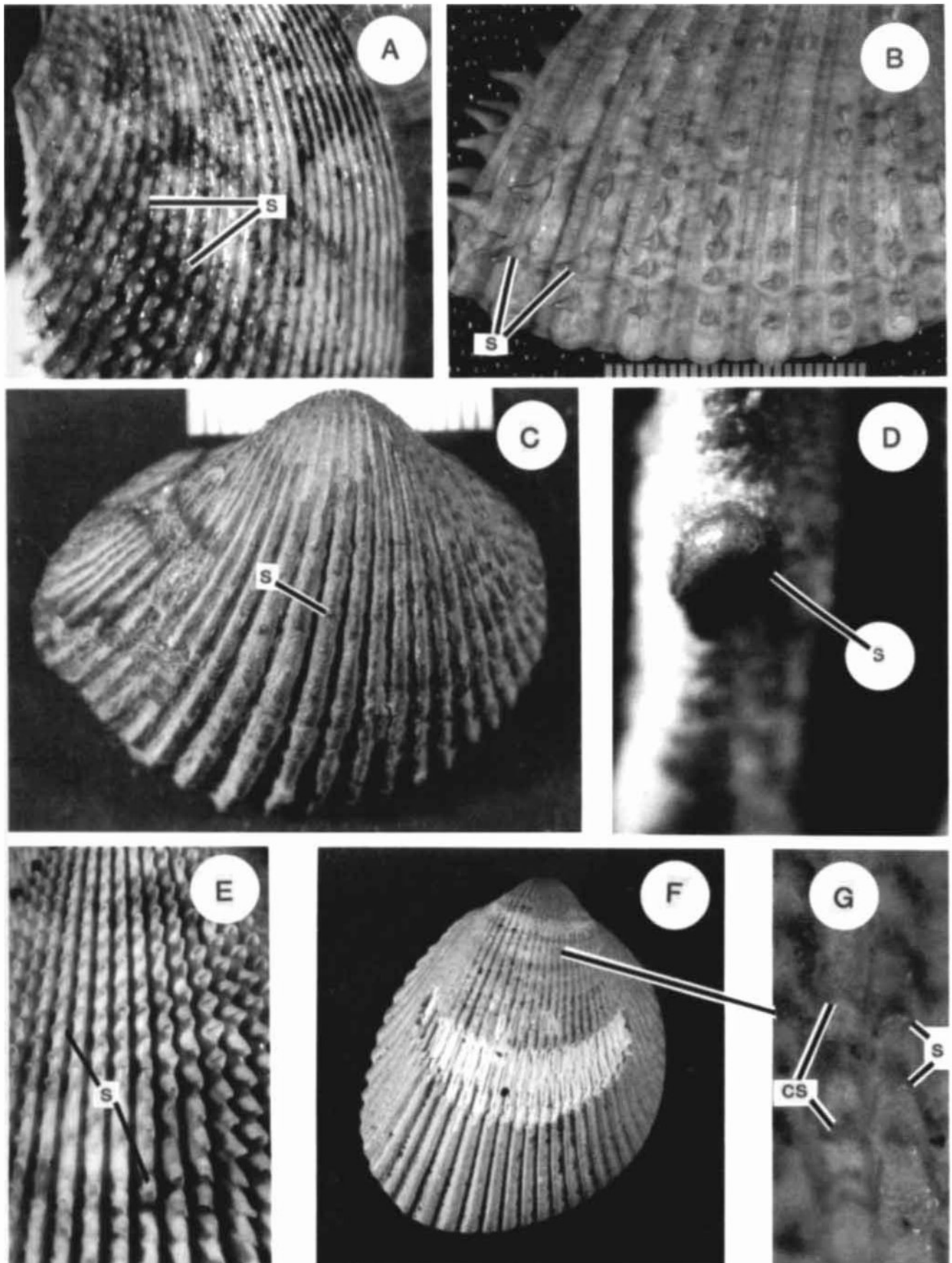


Fig. 8. Spines.—A. Posterior slope of right valve of *Nemocardium* (*Nemocardium*) *bechei* (ANSP 252661), $\times 2.6$.—B. Central and posterior slopes of right valve of *Acanthocardia aculeata* (USNM 304723), $\times 2.5$.—C–D. *Pleuriocardia* (*Incacardium*) *mellisa*, (PRI 4830).—C. Right valve, $\times 3.5$.—D. Close-up of individual spine, $\times 15.4$.—E. Central slope of *Trachycardium isocardia* (ANSP 54003), $\times 1.6$.—F–G. *Pleuriocardia* (*Dochmocardia*) *eufaulense* (ANSP 36491).—F. Right valve, $\times 2.75$.—G. Detail of surface ornament, to show spines and cross-striae, $\times 10$.

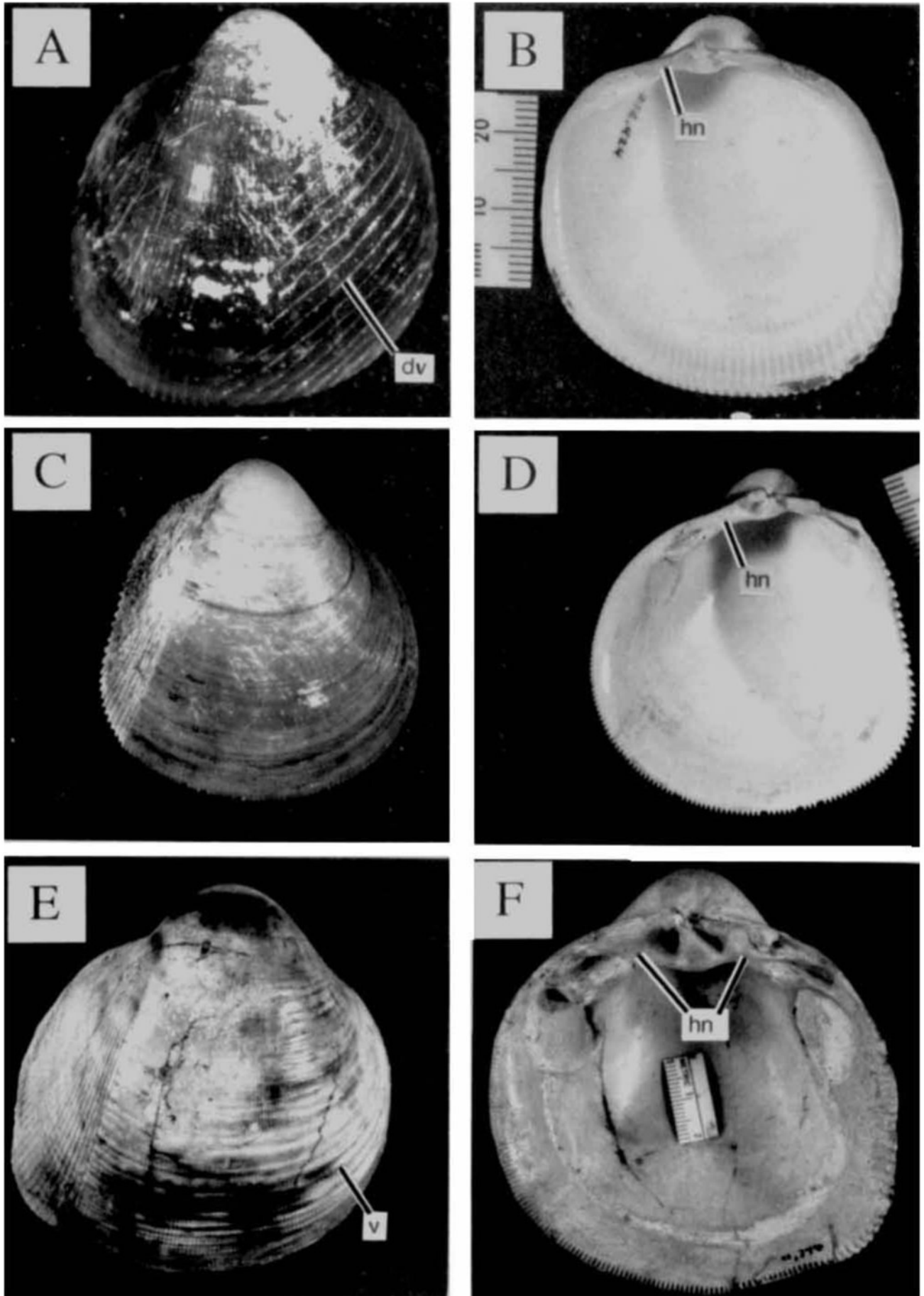


Fig. 9.—A–B. *Nemocardium (Lyrocardium) lyratum* (ANSP 216424).—A. Right valve external, $\times 1.5$.—B. Right valve internal, $\times 1.45$.—C–D. *Nemocardium (Nemocardium) bechei* (ANSP 252661).—C. Right valve internal, $\times 1.2$.—D. Right valve external, $\times 1.2$.—E–F. *Nemocardium (Varicardium) patulum* (DSIRGS 11794).—E. Right valve external, $\times 0.72$.—F. Right valve internal, $\times 0.8$.

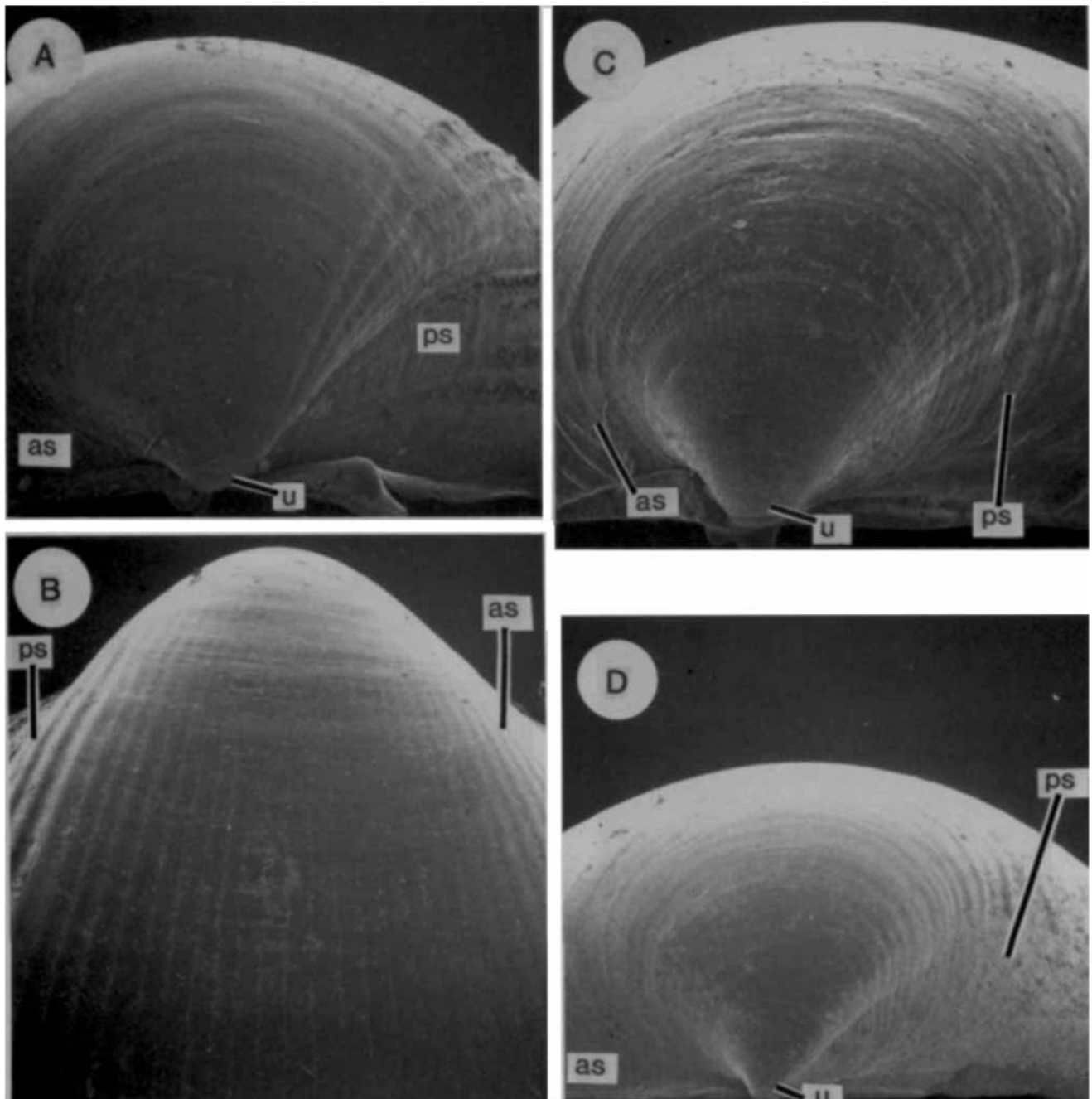
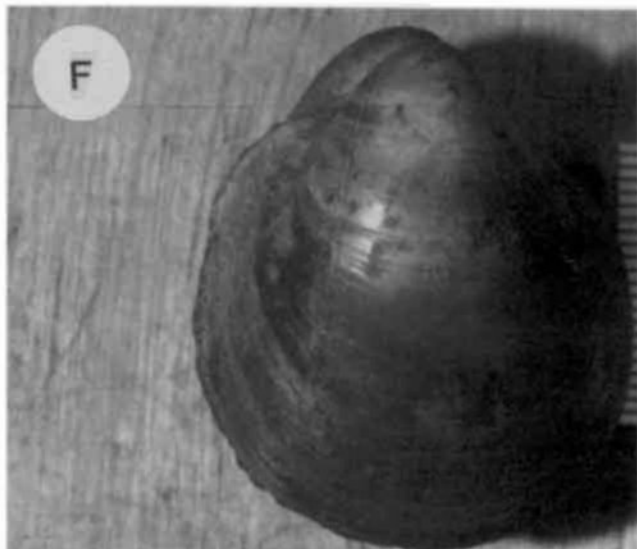
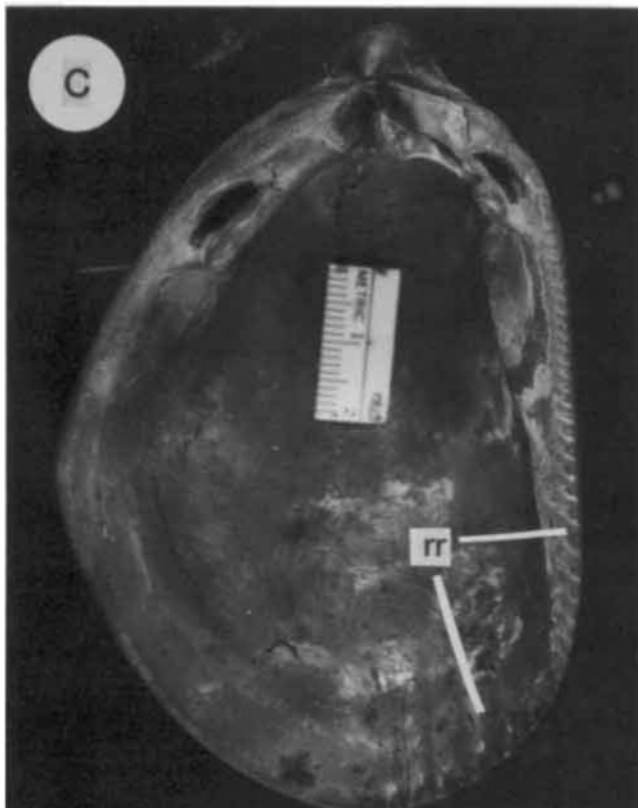
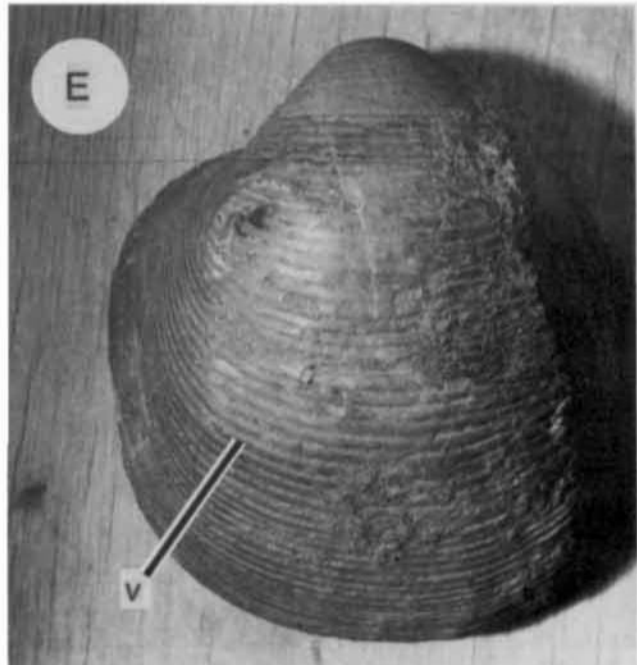
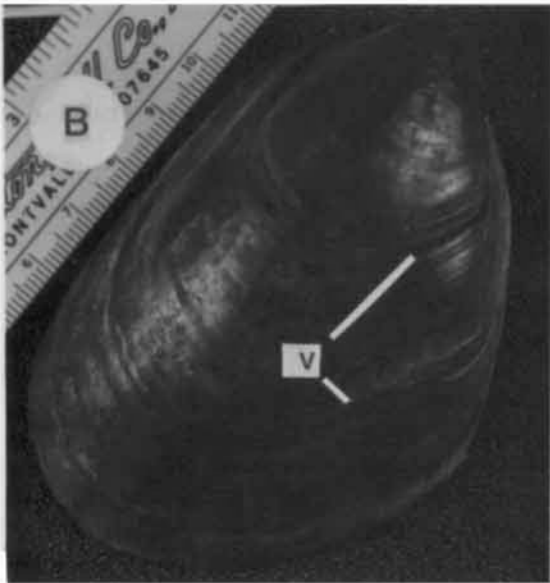
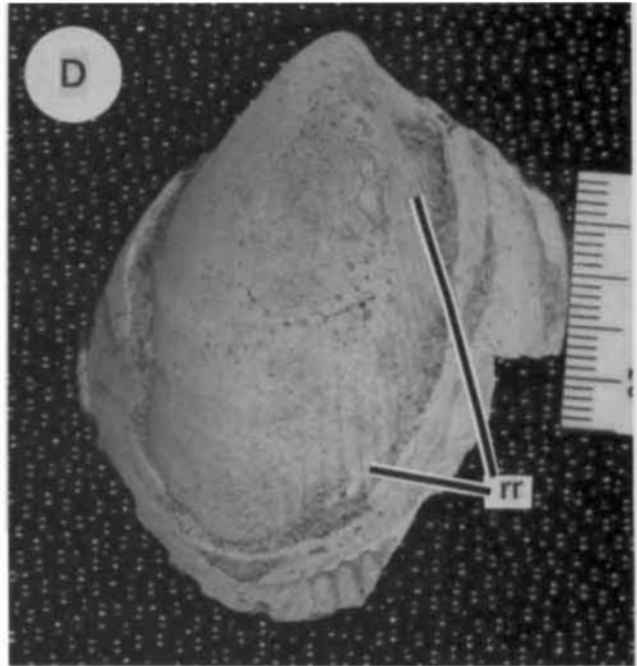
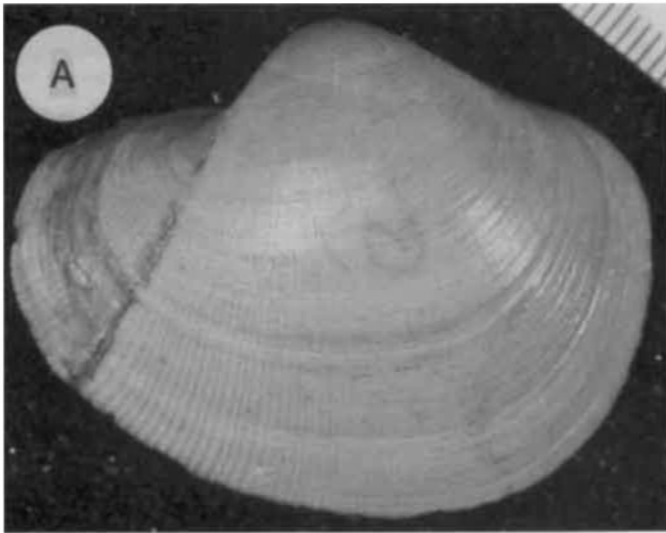


Fig. 10. Early ontogeny of ribbing in laevicardiines, all right valves, $\times 20$.—A–B. *Fulvia aperta* (USNM 658817).—A. Dorsal view.—B. Lateral view.—C. *Discors parisiensis* (USNM 325921), dorsal view.—D. *Laevicardium laevigatum* (USNM 503002), dorsal view.

ology of Erséus (1992), in which a cladistic analysis that is terminated due to memory constraints is run only once, invites the possibility that only a non-random subset (in which not all distinct classes of trees are equitably represented) of all the most-parsimonious trees may be found. Maddison defined the term *island* as “a collection of trees, all less than a specified length, each tree connected to every other tree in the island through a series of trees, and each one differing from the next by a single rearrangement of branches.” Islands are easily found by tree-searching programs, and multiple islands can be discovered by conducting numerous searches, with each search beginning with a different tree (Maddison 1991). Therefore, to find a representative subset of all the most-parsimonious trees, I had PAUP 3.1.1 perform 10 replications with a random addition of taxa, with no more than

two trees saved for each replication. These sets of initial trees ($n = 12, 14, 16, 18, \text{ or } 20$) were used as seeds to search for up to 2000 most parsimonious trees. This procedure was repeated 100 times. PAUP was unable to find any trees shorter than 47 steps. One hundred trees—one tree from each of the 100 sets of 2000 trees—were chosen at random to be used as seeds to find as many most parsimonious trees as possible. The memory limit of the computer in use, a Macintosh Quadra 700 with 8 Mb of RAM, was reached after finding 5300 trees of length 47 steps. These 5300 trees had a consistency index = 0.809 (see Kluge & Farris 1969), homoplasy index (also known as homoplasy excess ratio) = 0.234 (see Archie 1989), and a retention index = 0.923 (see Farris 1989). The computer was unable to find a shorter tree after swapping on each one of the 5300 trees. A 75% majority-rule consensus tree



of these 5300 trees (Fig. 18) is presented to summarize the results of the analysis. Given the number of most-parsimonious trees, a strict consensus tree may collapse into an unresolved bush in the presence of only one or two taxa whose position on the tree is unstable, even if the other taxa are consistently related in all cladograms (Adams 1986; Smith 1994). The usual cut-off point for majority-rule consensus trees is 50% (Smith 1994; see Eernisse *et al.* 1992, for an example), but it was decided to present a more rigorous 75% majority-rule consensus tree. Synapomorphies for each node are presented in Table II, and a suggested taxonomy for these cardiids is presented in Table III

The enormous number of most parsimonious trees produced is the only reason that the majority-rule consensus tree is chosen to summarize the results. Barrett *et al.* (1991) have pointed out the dangers of using consensus trees, but offer no alternatives in cases such as the present one when numerous most parsimonious trees are produced.

To study character evolution and alternative phylogenetic hypotheses, the phylogenetic results produced by PAUP were analyzed with MacClade Version 3 (Maddison & Maddison 1992).

Results and discussion

Phylogenetic analysis

The *Cardiidae* is united by three anatomical- and two hinge characters: presence of lateral and ventral ridges on the foot (the cardiid geniculate foot, see Adams & Adams 1858; Dall 1901; Keen 1980) (2:1; 3:1), simple inverse eyes (5:1), and shape of the cardinal teeth in the right valve (14:1 and 16:1).

Tulongocardium is the sister group to the rest of the *Cardiidae*, and is placed in *Tulongocardiinae* subfam. n. (see Appendix II). It appears in the Norian (middle Late Triassic; Vu-Khuc 1977), and is the least-derived cardiid. *Tulongocardium* includes the oldest representatives of the family.

At node (2) (Fig. 18) is a six-way polytomy, with five of the six branches comprising *Lahillia* and the Mesozoic members of the subfamily *Protocardiinae*. This node is united by one synapomorphy, a ribbing pattern of radial ribs on the posterior and concentric ribs on the anterior and central portions of the shell (8:2). *Leptocardia*, *Pachycardium*, and *Tamilicardia* have generally been classified as subgenera of *Protocardia* (Keen 1969, 1980; Chiplonkar & Tapaswi 1976). Except for the missing data (?) for the hinge (characters 14–16) of *Tamilicardia*, which are unknown, these four taxa are coded identically. *Protocardia*, *Leptocardia*, *Pachycardium*, and *Tamilicardia* are distinguished by autapomorphies. However, there are no synapomorphies to unite any of these four taxa with one another. The fifth clade (united at node 3) is

united by a smooth posterior margin (7:2) and lack of external ribbing (8:3). *Lahillia* had been placed in its own subfamily, *Lahilliinae* (Finlay & Marwick 1937), which was subsequently raised to a family level (Marwick 1944; see Keen 1969). McLearn (1933) erected *Onestia* as a subgenus of *Integricardium* and later raised it to a generic level (McLearn 1945). Day (1978) proposed that *Integricardium* was ancestral to *Onestia*, which was in turn ancestral to *Lahillia*, and transferred *Onestia* to *Lahilliidae*. As with the *Protocardia*-group, these three taxa (*Onestia*, *Integricardium*, and *Lahillia*) are coded identically but are distinguished by autapomorphies. *Yokoyamaina* and *Tendagurium* share an elliptical shell shape (9:3). *Cryptocardia* and *Globocardium* share a quadrate-short shell shape (9:4) and the presence of an internal ridge (11:1). Palmer (1974) noted that these two taxa shared these two characters and therefore considered the Middle Jurassic *Cryptocardia* ancestral to the Early Cretaceous *Globocardium*, and that this clade was closely related to *Tendagurium* and *Integricardium*.

The results suggest that the subfamily *Protocardiinae* should be dismantled. The inclusion of *Nemocardium* within the *Protocardiinae* makes the latter a polyphyletic group [in the following discussion, “*Nemocardium*” will refer to the entire genus *sensu* Keen, and *N.* (*Nemocardium*) will refer to the subgenus, represented by *N.* (*N.*) *bechei* (Reeve, 1847) in the cladistic analysis]. It is clear, therefore, that *Nemocardium* should be removed from the *Protocardiinae*. The resemblance between *Nemocardium* and *Protocardia* is based upon a symplesiomorphy (a shared primitive character), namely the presence of strong radial ribs occurring only on the posterior slope of the shell. On the basis of its ribbing pattern, Meek (1876) considered *Nemocardium* transitional between *Protocardia* and “*Cardium*” (roughly equivalent to what has herein been termed “*eucardiids*”). Even if the definition of the *Protocardiinae* is limited to the wholly Mesozoic *Protocardia*, *sensu* Keen (with *Brevicardium* reassigned to *Nemocardium*, and *Yokoyamaina*, *Tendagurium*, *Cryptocardia*, and *Globocardium* transferred to *Lahilliinae*), a paraphyletic group still remains on the majority-rule consensus tree. However, as stated previously, a majority-rule consensus tree must be understood only as a summarization of numerous most parsimonious trees. Analysis of the results on MacClade demonstrates that construction of a monophyletic group of *Protocardia*, *Leptocardia*, *Pachycardium*, and *Tamilicardia* yields a tree of length 47 steps (Fig. 19A), the same length as the trees found in the PAUP analysis. Since a monophyletic group comprising *Protocardia*, *Leptocardia*, *Pachycardium*, and *Tamilicardia* is as parsimonious as the relationship in which these taxa are each separate branches as part of a six-way polytomy, it is unwarranted to overturn prevailing taxonomy. These four taxa are retained as subgenera in the genus *Protocardia*, the sole genus in *Protocardiinae*. Furthermore, it was found with MacClade that trees in which the *Protocardiinae* and *Lahilli-*

Fig. 11.—A. *Nemocardium* (*Lophocardium*) *cumingii* (ANSP 216379) right valve, $\times 2$.—B.—D. *Protocardia* (*Pachycardium*) *stantoni*.—B. External view of right valve (USNM 315520) to show varicate sculpture, $\times 0.85$.—C. Internal view of same specimen, to show manifestation of radial ribs on internal posterior margin, scale indicated in figure.—D. Exfoliated left valve (USNM 482408) showing internal radial ribs on posterior slope, $\times 1.35$.—E. *Globocardium* *sphaeroideum* (NHM LL8466) left valve, $\times 0.85$.—F. *Cryptocardia* *bajocensis* (NHM 666193) right valve, $\times 1.3$.

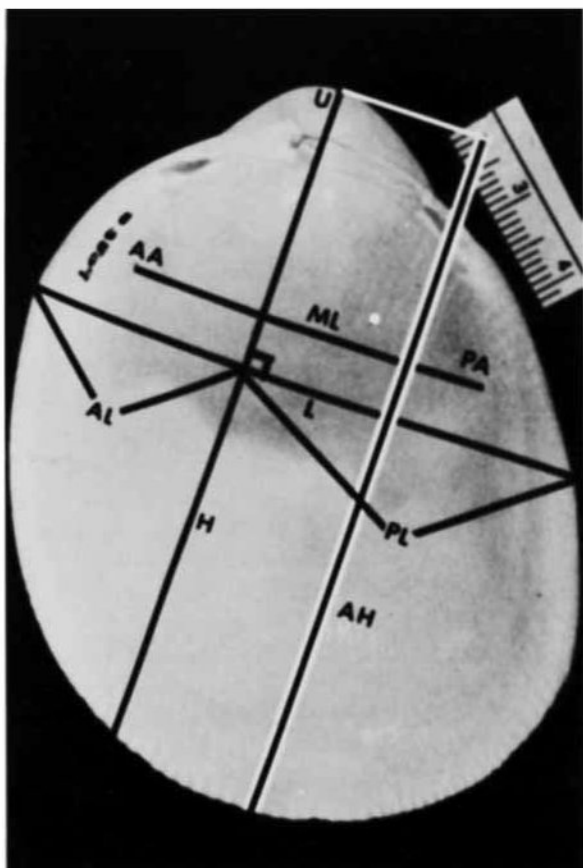


Fig. 12. Diagram of the internal view of a right valve of *Laevicardium laevigatum* (ANSP 83809), showing various measurements necessary to determine shell shape. Anterior length (AL) + posterior length (PL) = length (L). Height (H) is line from top of umbo to ventral shell margin, perpendicular to length. Apparent height (AH) is distance from umbo (U) to ventralmost shell point, parallel to height (may be the same line). Scale indicated on figure.

nae are sister taxa (Fig. 19B) are the same length (47 steps) as the most parsimonious trees found by PAUP. Therefore, Lahilliinae may be the sister taxon to Protocardiinae.

The predominantly Cenozoic eucardiids, represented by *Granocardium*, are the sister group to a clade comprised of *Pleuriocardia*, *Pleuriocardia (Dochmocardia)*, and *Incacardium*. Scott (1978) erected *Pleuriocardia (Pleuriocardia)* and *P. (Dochmocardia)*, and placed them in Cardiinae on the basis of their ribbing pattern of entirely radial ribs. Keen (1980) placed them in Protocardiinae on the basis of shell shape and their "heavy and arched hinges." With *Incacardium*, these taxa share five derived characters, and are placed in Pleuriocardiinae subfam. n. (see Appendix II). Olsson (1944) erected the Late Cretaceous *Incacardium* as a monotypic subgenus of *Cardium* (there is one other species, yet to be described), and suggested that it was related to *Trachycardium* on the basis of its triangular spines. Keen (1969, 1980) classified *Incacardium* as the only Mesozoic subgenus of the cardiine *Acanthocardia*. However, according to Keen (1980; see Fig. 20), besides the Protocardiinae, there are two main lineages of cardiids in the Mesozoic. *Incacardium* is the most primitive member of a group containing *Orthocardium*, *Cardium*, and *Bucardium*. *Acanthocardia*—the genus under which Keen (1969, 1980) classifies *Incacardium*—is said to be descended from *Granocar-*

dium. This is an internal contradiction. *Incacardium*'s spines are symmetrical, and emanate from the tops of the ribs (Figs 8C, D), as do the microscopic spines of *Pleuriocardia* (Fig. 8G). *Trachycardium*'s spines are asymmetrical and emanate from the posterior of the ribs (Fig. 8E). No form of *Acanthocardia* has symmetrical, triangular, concave-down spines (Fig. 8B). [Microstructural study of the spines of *Incacardium*—which would involve destructive analysis—has not been undertaken because the only specimens of this genus are the two cotypes of the type species, *Cardium (Incacardium) mellisum* Olsson, 1944, and the single specimen of the undescribed species.] *Incacardium* also shares with *Pleuriocardia* the shape of the right anterior cardinals (14:4) and the low angle of the right posterior cardinal socket (15:1; Figs 17A, B). *Trachycardium*'s cardinal teeth (Fig. 17D) are like those of *Granocardium* (Fig. 17C), and *Acanthocardia*'s cardinal teeth are quite different from those of any Mesozoic cardiid (Fig. 17E). *Incacardium* is considered a subgenus of *Pleuriocardia*.

Eucardiids and pleuriocardiines form the sister group to a clade which comprises the subfamily Laevicardiinae and *Nemocardium*. *Habecardium* has been recognized as transitional from *Nemocardium* to the Laevicardiinae (Glibert & van de Poel 1970; Keen 1980; Schneider 1992) because of its ontogenetic change in ribbing pattern from that of *Nemocardium* as a juvenile to that of *Fulvia* as an adult. Other members of Laevicardiinae *sensu* Keen (1951, 1969, 1980) have been placed in the subfamilies Clinocardiinae, Lymnocardiinae, and Cardiinae (Kafanov & Popov 1977; Kafanov 1980; Voskuil & Onverwagt 1989; Schneider 1992).

Habecardium + *Fulvia* + *Discors* + *Laevicardium* is the best-supported clade. Five of the seven synapomorphies are anatomical characters. Keen (1951, 1969, 1980) classified *Discors* as a subgenus of *Nemocardium*; Popov (1977) and Kafanov & Popov (1977) raised *Discors* to a genus of protocardiine allied to *Nemocardium*. However, *Discors* has the laevicardiine ribbing pattern (8:7) and shell shape (9:5), as well as a smooth posterior margin (7:2), to unite it with *Laevicardium*. The idea that *Discors* is allied to *Laevicardium* rather than *Nemocardium* is hardly new, as Cossmann (1919, 1921), Cossmann & Pissarro (1906) and Dey (1961) considered *Discors* a subgenus of *Laevicardium*, as does J.-M. Poutiers (pers. comm. 1991). The association of *Discors* with *Nemocardium* occurred because some workers considered the divaricate sculpture on *Discors* to be homologous to the divaricate sculpture on either or both of the *Nemocardium* subgenera *Divaricardium* and *Lyrocardium*. Divaricate and varicate sculpture on cardiids will be discussed below.

Nemocardium is not a monophyletic group. *Discors* is the sister taxon to *Laevicardium*; *Lophocardium* and *Lyrocardium* form a four-way polytomy with (1) the Laevicardiinae and (2) the remaining subgenera of *Nemocardium* (node 14), a clade united by one character, a digitate posterior margin (7:3). Neither *N. (Nemocardium)* nor *Varicardium* has any shared characters to unite them with any other taxon within this clade; except for missing data for *Varicardium*, these two taxa are coded identically and uniting them as sister groups adds no steps

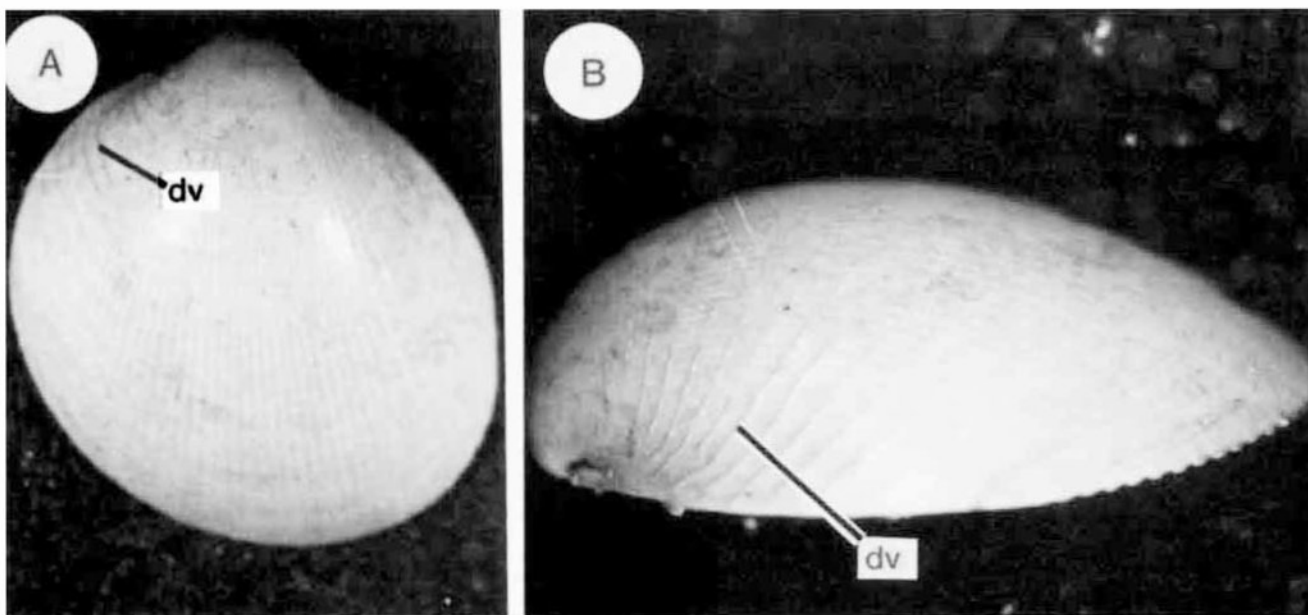


Fig. 13. Divaricate sculpture of *Discors parisiensis*.—A. External view of left valve (ANSP 7680), $\times 10$.—B. Anterior view of same specimen, $\times 17.75$.

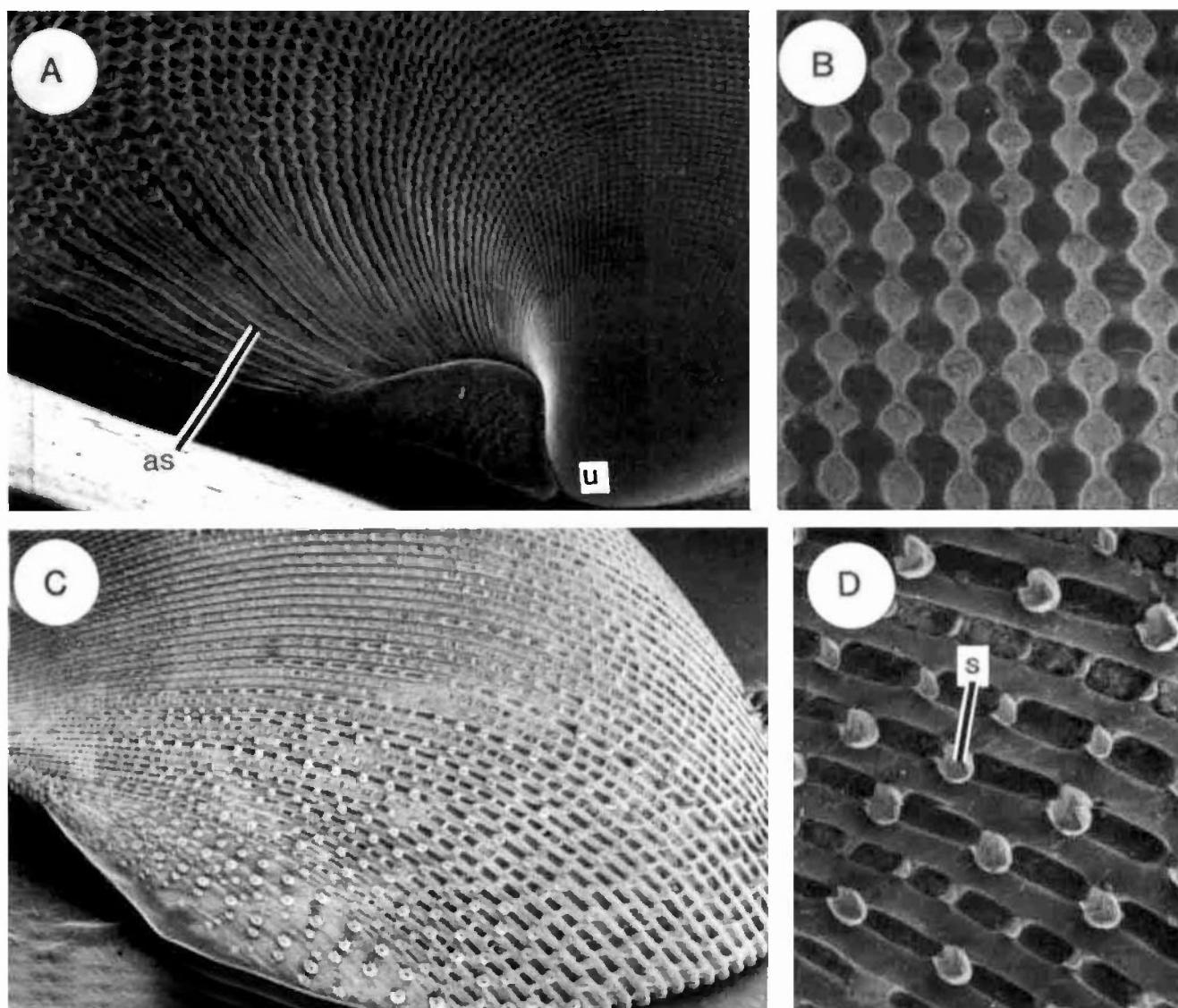


Fig. 14. Surface ornament of right valve of *Nemocardium (Microcardium) peramibilis* (ANSP 176654).—A. Dorsal view of anterior slope, $\times 17.2$. Note absence of radial ribs, and presence of concentric sculpture confluent with concentric sculpture on central slope.—B. Detail of central slope, $\times 41.2$.—C. Posterior slope, $\times 10.7$. Note presence of spines and ladder-like cross-striac.—D. Detail of posterior slope, showing spines, $\times 50.5$.

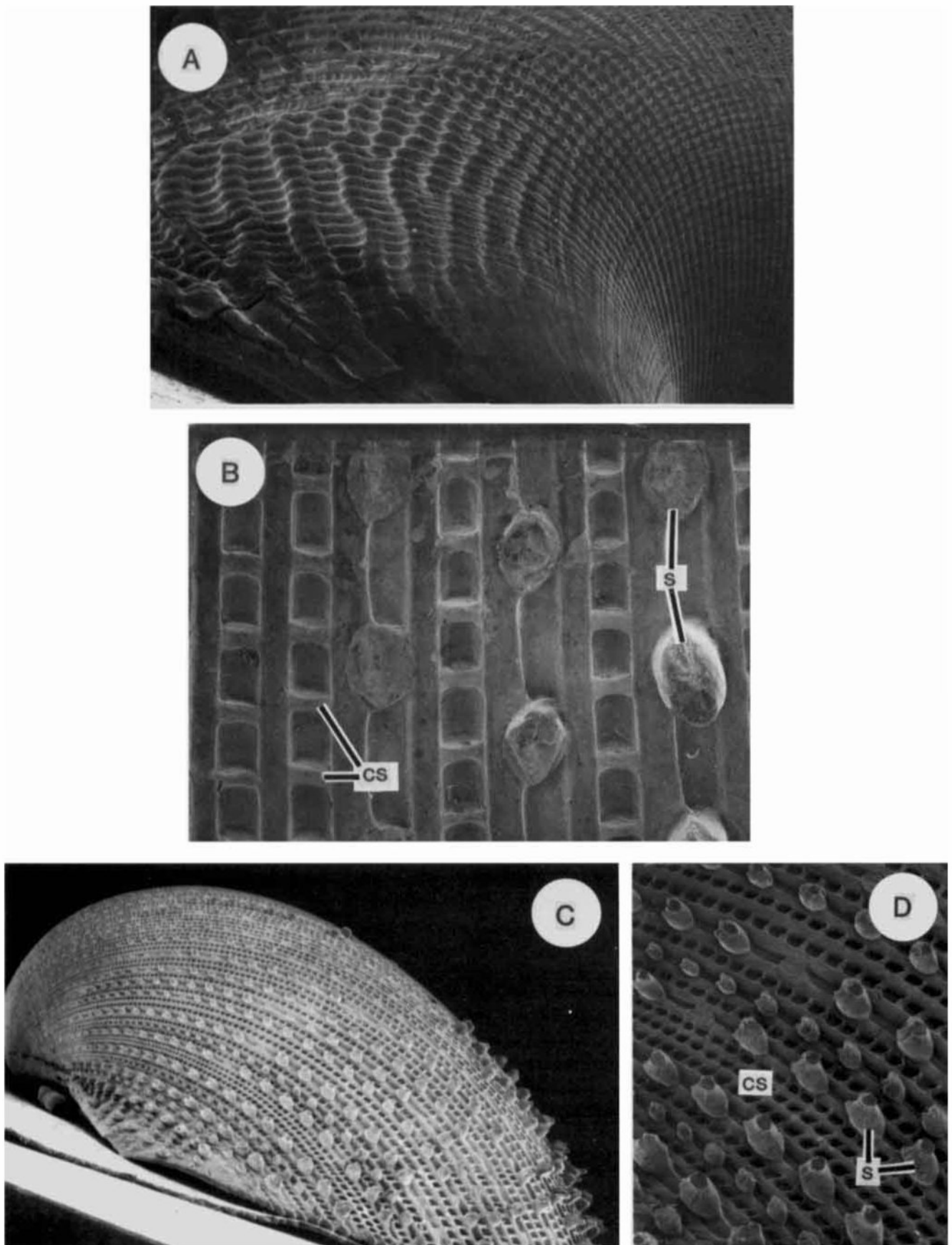


Fig. 15. Surface ornament of right valve of *Nemocardium (Trifarcidium) nomurai* (FMNH 278009).—A. Dorsal view of anterior slope, $\times 17$. Note weakness and irregularity of radial ribs (compare with C and D) and strength of irregular concentric sculpture.—B. Detail of central slope, to show ladder-like cross-striae and spines, $\times 52.5$.—C. Posterior slope, $\times 7.9$.—D. Detail of posterior slope, to show ladder-like cross-striae and spines, $\times 22$.

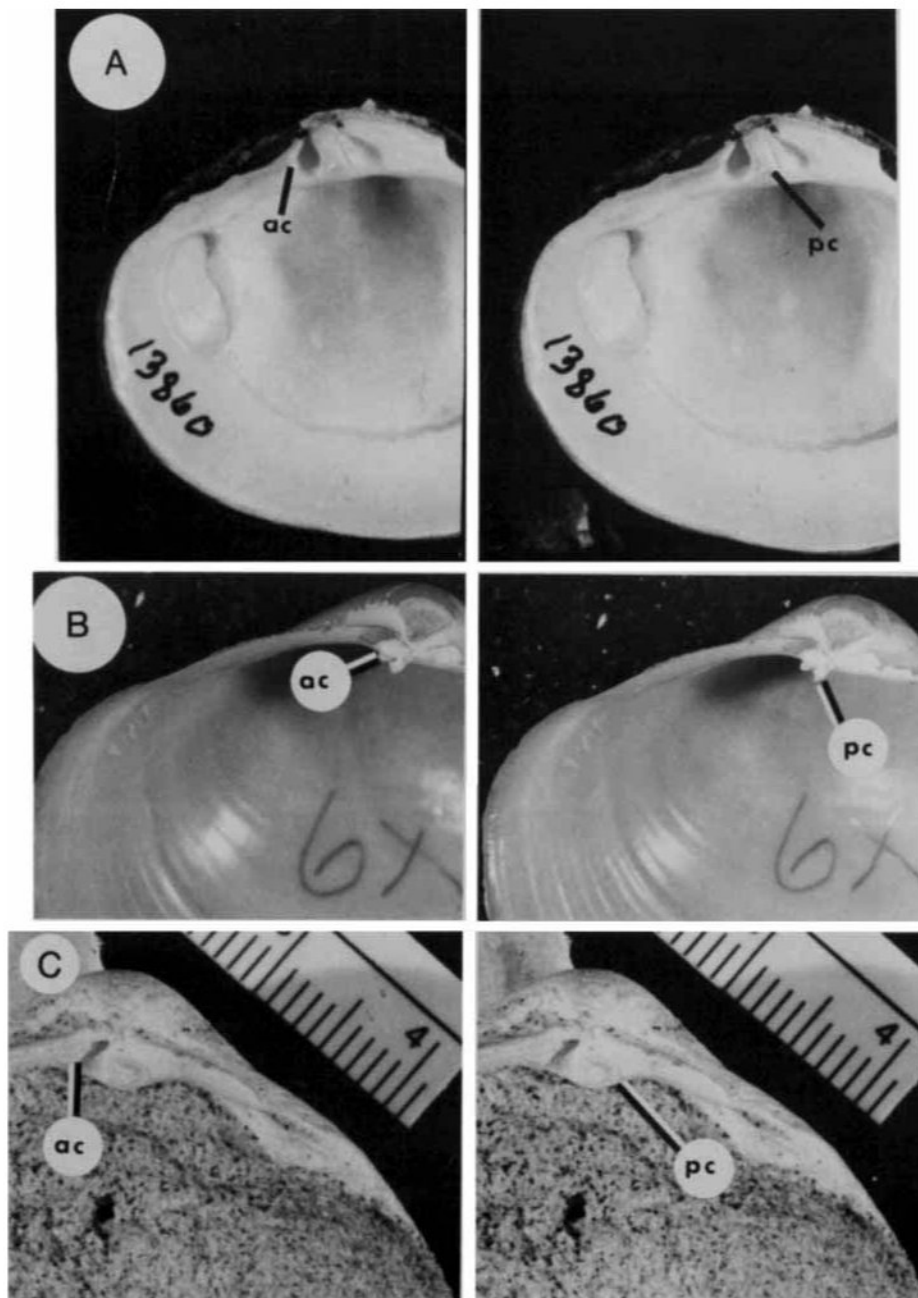


Fig. 16. Right cardinal teeth.—A. *Astarte castanea* (FMNH 13860), stereophotograph, $\times 3$. Anterior cardinal shape 0, posterior cardinal shape 0.—B. *Nemocardium* (*Lophocardium*) *cumingii* (ANSP 216379), stereophotograph, $\times 5.4$. Anterior cardinal shape 3, posterior cardinal shape 2.—C. *Protocardia* (*Protocardia*) *hillana* (MCZ 101697), $\times 2.2$. Anterior cardinal shape 1, posterior cardinal shape 1.

to the most parsimonious trees (Fig. 19C). *Microcardium*, *Trifaricardium*, and *Frigidocardium* are united by ribbing pattern (8:5) and the presence of ladder-like cross-striae (12:1). *Brevicardium*, *Pratulium*, *Arctopratulium*, *Keenaea*, and *Divaricardium* are united by quadrate-long shell-shape (9:1) and the same type of ribbing pattern (8:5) that unites *Microcardium*, *Trifaricardium*, and *Frigidocardium*. All the taxa in the Laevicardiinae + *Nemocardium* clade are Cenozoic [*N.* (*Nemocardium*) and *Pratulium* originate in the Mesozoic but are extant], except for the Campanian to Maastrichtian *Brevicardium*, which Keen (1951, 1969, 1980) classified as a subgenus of *Protocardia*.

Keen's (1951, 1969, 1980) acceptance of numerous subgenera within the genus *Nemocardium* has been questioned by Wilson & Stevenson (1977), Popov (1977) and Kafanov & Popov (1977), who recognized that many of

the subgenera were erected on the basis of details of the external shell ornamentation, and therefore synonymized many of them. However, these same authors raised several of the taxa they considered valid to generic status. Other authors (Habe 1951; Poutiers 1992) also consider many of the taxa, that Keen (1951, 1969, 1980) considered subgenera of *Nemocardium*, as having generic status, including *Frigidocardium* and *Trifaricardium*, which Popov (1977) synonymized with *Pratulium*. In this analysis, *Nemocardium* is classified as in Keen (1951, 1969, 1980), as one genus with numerous subgenera.

For the most part, the results of the cladistic analysis are consistent with stratigraphic data (Table III and Fig. 21). The best estimate of the phylogeny of a taxon comes from combining the results of a character-based cladistic analysis with biostratigraphic data [Smith 1994; see Jackson & Cheetham (1994) for an excellent example]. Sev-

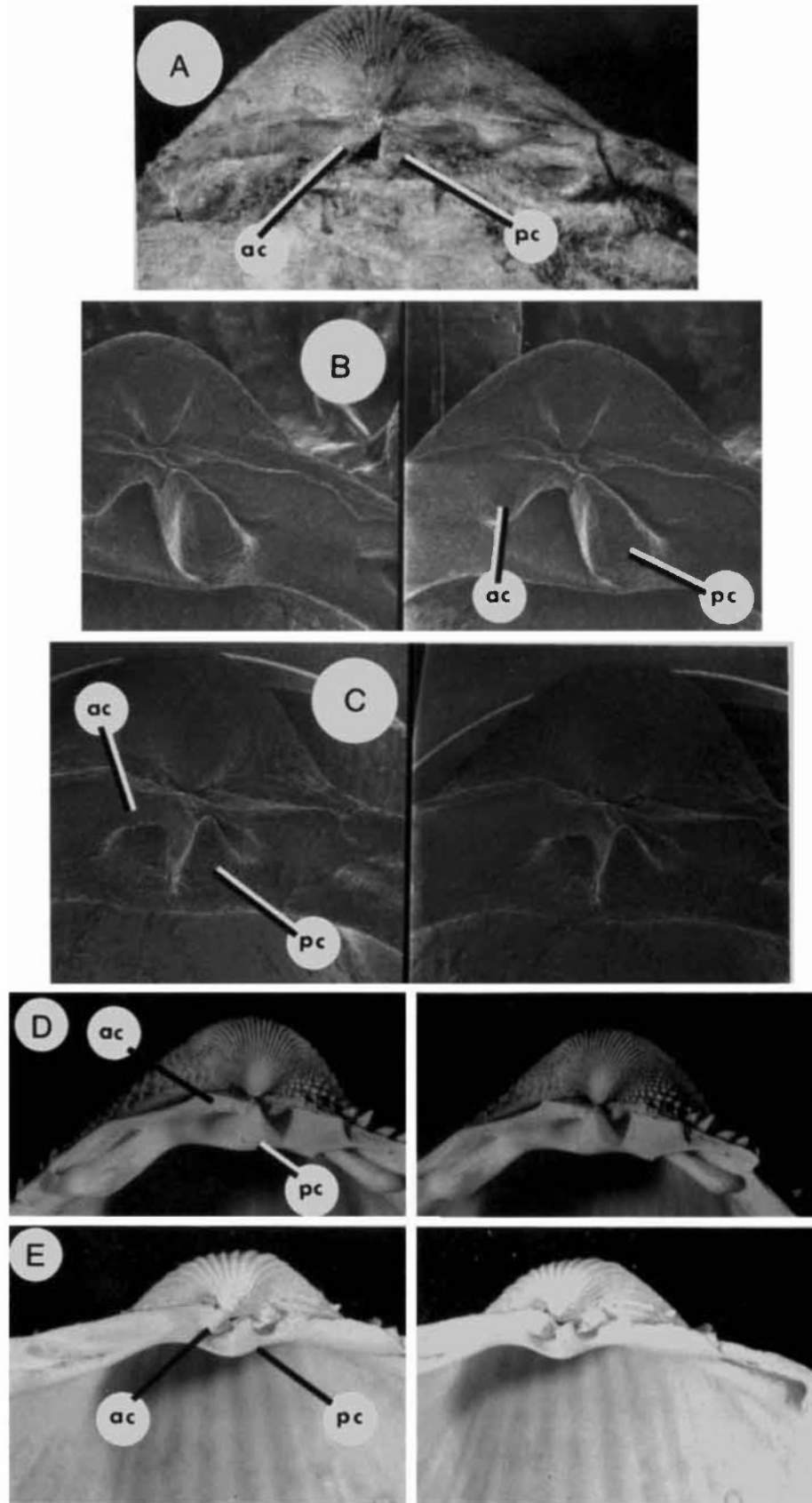


Fig. 17. Right cardinal teeth.—A. *Pleuriocardia (Incacardium) mellisa* (PRI 4830), $\times 3.75$. Anterior cardinal shape 4, posterior cardinal shape 2.—B. *Granocardium kuemmeli* (AMNH 45047), stereophotograph, $\times 4.4$. Anterior cardinal shape 2, posterior cardinal shape 2.—C. *Pleuriocardia (Dochmocardia) eufaulense* (ANSP 36491), stereophotograph, $\times 7.4$. Anterior cardinal shape 4, posterior cardinal shape 2.—D. *Trachycardium isocardia* (ANSP 54003), stereophotograph, $\times 2.1$. Compare shape of cardinal teeth to that of *G. kuemmeli*.—E. *Acanthocardia aculeata* (UNC 15376), stereophotograph, $\times 1.7$.

Table II. Synapomorphies for interior nodes of 75% majority-rule cladogram (Fig. 18)

Node	Synapomorphies (character:state)
1	2:1, 3:1, 5:1, 14:1, 16:1
2	8:2
3	7:2, 8:3
4	9:2
5	9:3
6	9:4, 11:1
7	9:4, 14:2, 16:2
8	8:1
9	9:6, 12:2, 13:1, 14:4, 15:1
10	8:4
11	1:1, 2:2, 3:2, 4:1, 5:2, 8:6, 9:5
12	8:7
13	7:2
14	7:3
15	8:5, 9:1
16	8:5, 12:1
17	10:1

Table III. Suggested taxonomy of the subfamilies *Tulongocardiinae* subfam. n., *Protocardiinae*, *Pleuriocardiinae* subfam. n., and *Laevicardiinae*, based on results of present phylogenetic analysis. Stratigraphic ranges from Sepkoski (unpubl.), except where indicated. Abbreviations of stratigraphic units from Harland et al. (1990)

Subfamily <i>Tulongocardiinae</i> subfam. n.	
<i>Tulongocardium</i> (= <i>Vietnamicardium</i>)	Nor-Rht (Vu-Khuc 1977)
Subfamily <i>Protocardiinae</i>	
<i>Protocardia</i> (<i>Protocardia</i>) (<i>Leptocardia</i>) (<i>Pachycardium</i>) (<i>Tamilcardia</i>)	Rht-Maa Neo-Maa Neo-Maa Sen (Chiplonkar & Tapaswi 1976)
Subfamily <i>Lahilliinae</i>	
<i>Lahillia</i> (= <i>Lahilleona</i>) <i>Cryptocardia</i> <i>Globocardium</i> <i>Integricardium</i>	Sen-Mio (Keen 1969) Baj-Clv Apt-Alb Het-Tha [Marincovich (1993); Schneider & Marincovich, unpubl.]
<i>Onestia</i>	Alb-Tha (Schneider & Marincovich, unpubl.)
<i>Tendagurium</i>	Dog-Cen (Cox 1935; Riccardi 1977)
<i>Yokoyamaina</i>	Het
Subfamily <i>Pleuriocardiinae</i> subfam. n.	
<i>Pleuriocardia</i> (<i>Pleuriocardia</i>) (<i>Dochmocardia</i>) (<i>Incacardium</i>)	Alb-Maa Apt-Maa Sen
Subfamily <i>Laevicardiinae</i>	
<i>Laevicardium</i>	Eoc-Hol (Cooke 1926; Keen 1969, 1980)
<i>Discors</i>	Ypr-Srv
<i>Fulvia</i>	Rup-Hol
<i>Habecardium</i>	Eoc-Oli (Keen 1980)
<i>Nemocardium</i> (<i>Nemocardium</i>) (<i>Arctoprattulum</i>) (<i>Brevicardium</i>) (<i>Divaricardium</i>) (<i>Frigidocardium</i>) (<i>Keenaea</i>) (<i>Lophocardium</i>) (<i>Lyrocardium</i>) (<i>Microcardium</i>) (= <i>Tobarum</i>) (<i>Prattulum</i>) (<i>Trifaricardium</i>) (<i>Varicardium</i>)	Apt-Hol (Keen 1950) Oli-Srv Cmp-Maa Oli-Pli Mio-Hol (Poutiers 1992) Rup-Hol Srv-Hol Mio-Hol (Keen 1980) Mio-Hol Brm-Hol (Keen 1950, 1980) Mio-Hol (Poutiers 1992) Lut-Srv (Maxwell 1992)
Cardiidae incertae cedis:	
<i>Jurassicardium</i>	Lia-Tth [Cossmann (1906, 1916); Yamani & Schairer (1975)]

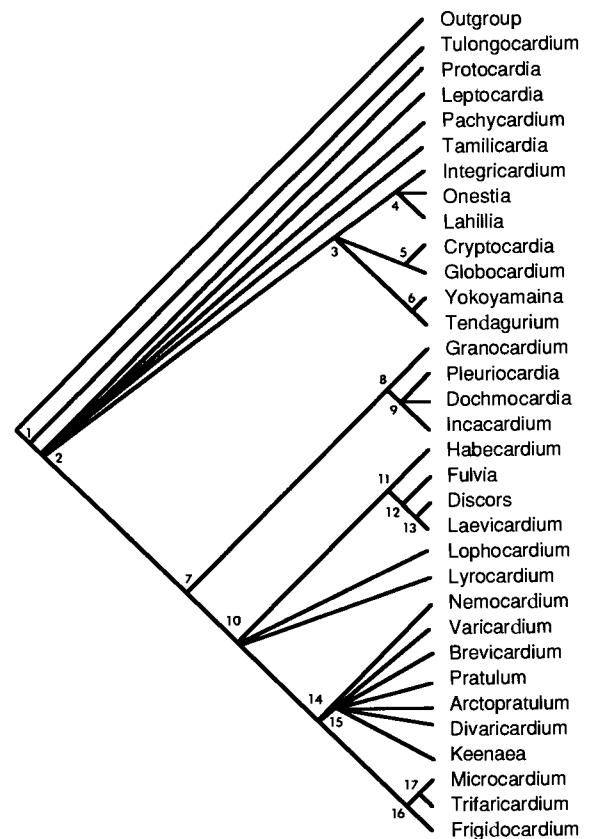


Fig. 18. 75% majority-rule consensus tree of 5300 most parsimonious trees for the present phylogenetic analysis. Node 8 supported by 84% of trees; node 14 supported by 94% of trees; node 16 supported by 87% of trees; node 17 supported by 85% of trees. All other nodes supported by 100% of trees. Synapomorphies supporting each node indicated in Table II.

eral issues must be kept in mind regarding the way the taxa are represented in the analysis and application of stratigraphic ranges to those taxa: (1) each genus and subgenus is represented by a single species, which has been present for only a portion of each taxon's true stratigraphic range; (2) most, if not all of these (sub)genera are paraphyletic, and the stratigraphic ranges that have been assigned to them (Keen 1969, 1980; Popov 1977; Sepkoski, unpublished compendium; Schneider, herein) are therefore not the stratigraphic ranges of monophyletic taxa [I use the term "monophyletic" in the sense of Hennig (1966): a monophyletic taxon includes all, not just some, of the descendants of a most recent common ancestor. This usage of the term "monophyletic" is therefore equivalent to the term "holophyletic" of Ashlock (1971), which has never gained wide acceptance and which I consider to be an archaism. Paraphyletic taxa are not monophyletic because paraphyletic taxa include only some, but not all, of the descendants of a most recent common ancestor]; (3) the species or specimens that have been used by the above authors for the stratigraphic ranges may not actually belong to the taxa that each author has assigned them, because of either paraphyly or misidentification.

With the foregoing caveats understood, there are some minor problems reconciling the fossil record of the *Laevicardiinae*/*Nemocardium*-group with the results of the purely character-based phylogeny. *Lophocardium* and *Lyrocardium* have long been considered allied to

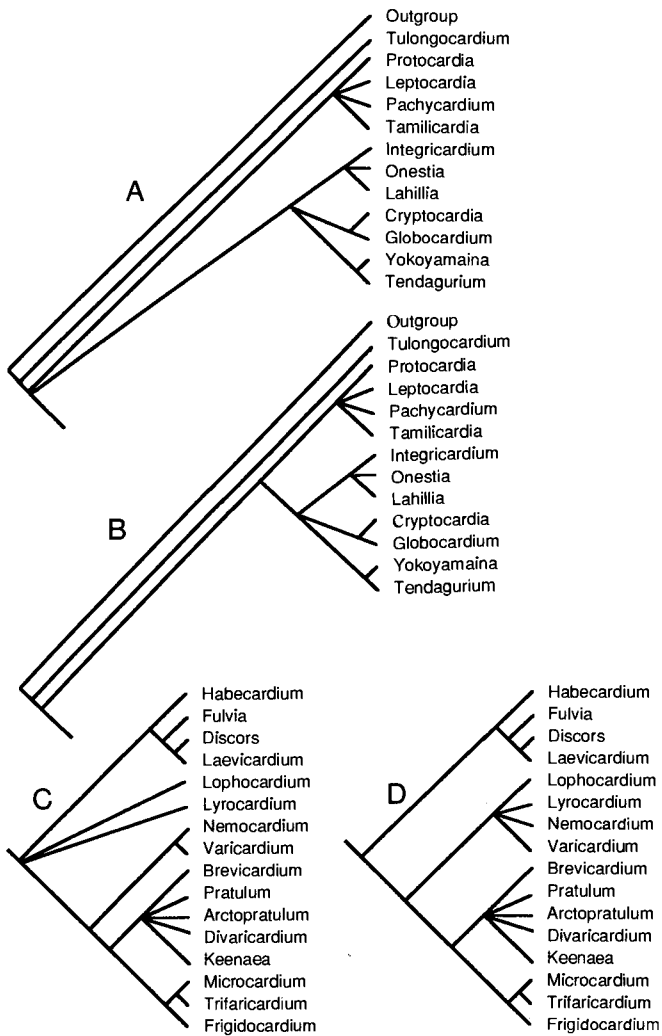


Fig. 19. Alternate phylogenetic reconstructions.—A. *Protocardia*, *Leptocardia*, *Pachycardia*, and *Tamilicardia* as a monophyletic group.—B. Protocardiinae and Lahilliinae as sister taxa.—C. *Nemocardium* (*Nemocardium*) and *N. (Varicardium)* as sister taxa.—D. *N. (Nemocardium)*, *N. (Varicardium)*, *N. (Lophocardium)*, and *N. (Lyrocardium)* as a monophyletic group.

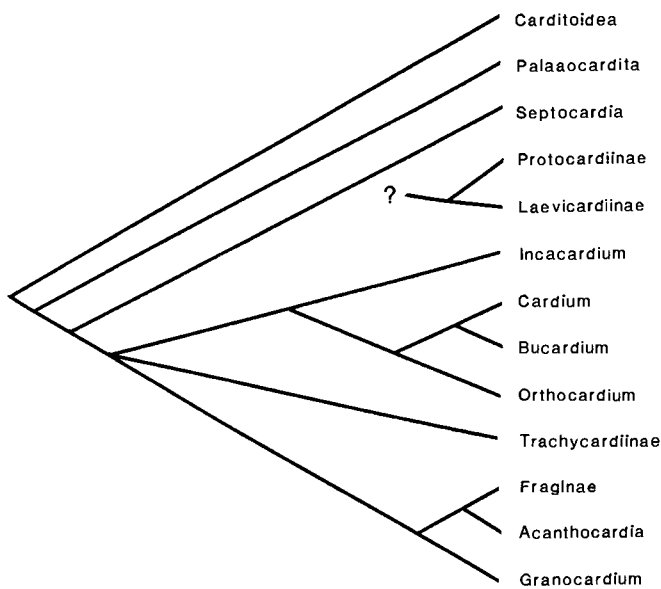


Fig. 20. Phylogenetic relationships within the Carditidae according to Keen (1980). Diagram from Schneider (1992). Note positions of *Incacardium*, *Acanthocardia*, and *Granocardium* and compare with Keen's (1980) taxonomy in Appendix I.

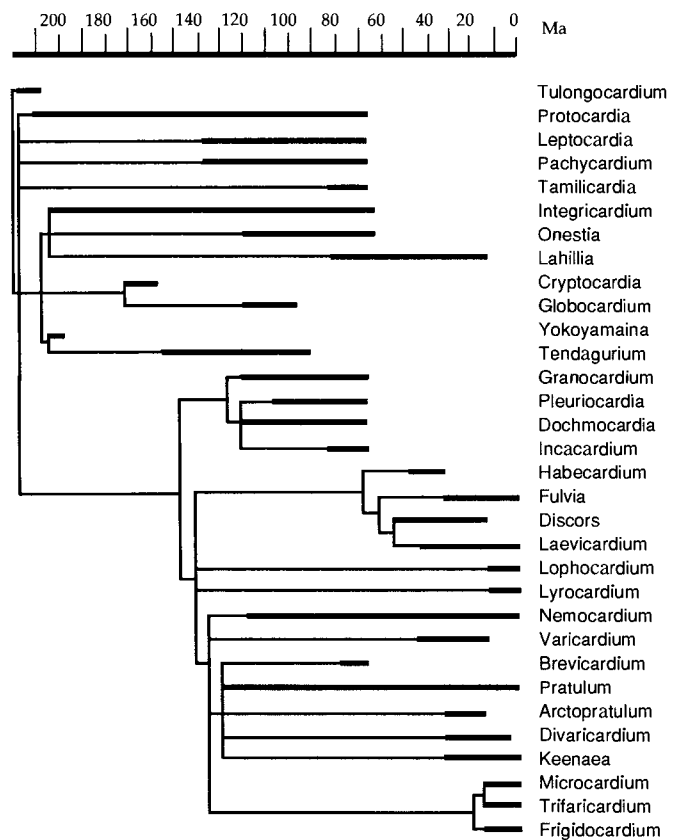


Fig. 21. Phylogenetic relationships of Tulongocardiinae subfam. n., Protocardiinae, Lahilliinae, Laevicardiinae, and Pleuriocardiinae subfam. n. plotted against geologic time, in millions of years (Ma). Narrow lines indicate phylogenetic relationships. Heavy lines indicate known fossil record (range-through method used).

Nemocardium (Keen 1951, 1969, 1980; Popov 1977). On the consensus tree, *Lophocardium* and *Lyrocardium* are two separate taxa in a four-way polytomy with *Nemocardium* and Laevicardiinae. *Pratulium* and *N. (Nemocardium)* are known from the Barremian and Aptian (Early Cretaceous), respectively (Keen 1950), whereas *Lophocardium* and *Lyrocardium* first occur in the Miocene [Keen 1980; there are questionable specimens of *Lophocardium* from the late Eocene (Clark & Durham 1946)]. The oldest laevicardiine fossils are from the Eocene (Cooke 1926; Keen 1969, 1980). Thus, there is a situation in which one taxon in the polytomy originates in the Early Cretaceous (*Nemocardium*), one in the Eocene (Laevicardiinae), and two in the Miocene (*Lophocardium* and *Lyrocardium*). The character uniting *Nemocardium* (node 14) is a digitate posterior margin (7:3). *Lophocardium* and *Lyrocardium* have crenulated posterior margins (7:1). Except for the posterior margin and its absence of spines (13:?), *Lyrocardium* is coded identically to *Nemocardium*. *Lyrocardium*'s crenulated posterior margin is related to two autapomorphies: reduction of rib strength and development of divaricate shell sculpture. In both internal and external shell form, *Lyrocardium* and *N. (Nemocardium)* look remarkably alike (Figs 9A, B, D, E).

Lophocardium (Fig. 11A) has a highly modified shell related to its deep-burrowing habit. Like many deep-burrowing suspension feeders, many of its shell characters are reduced or lost (Stanley 1970). The shell is thin, unornamented, and elongate, and the hinge teeth are

small (Figs 11A, 16B). *Lophocardium* is the only non-lymnocardiine cardiid that is entirely lacking in lateral teeth (Fischer 1887; Dall 1889; Smith 1945; Keen 1969, 1980). The radial ribs are markedly weak. Deep-burrowers have evolved from shallow-burrowers repeatedly in many different bivalve clades (Kauffman 1969; Stanley 1970). *Lophocardium* is more likely to have been derived from *N.* (*Nemocardium*) or some closely related form, than to be one of the least derived taxa of *Nemocardium*—and hence originating in the Early Cretaceous—but absent from the fossil record until the Eocene, or more probably the Miocene. It is equally unlikely that *Lyrocardium* originated in the Early Cretaceous, but is unknown in the fossil record until the Miocene. Postulating a clade comprising *N.* (*Nemocardium*), *Varicardium*, *Lyrocardium*, and *Lophocardium* adds only one step to the most parsimonious trees (Fig. 19D).

The evolution of crenulated posterior margins of *Lyrocardium* and *Lophocardium* is a case of convergence that was not detected as such by examining the set of shortest (most parsimonious) trees found by PAUP 3.1.1. This would appear to give credence to Seilacher's (1984) contention regarding the inability of cladistics to reconstruct bivalve phylogeny because of convergence. However, with programs such as PAUP and MacClade, systematists are free to examine alternative tree topologies and character state reconstructions in light of data from the fossil record and functional morphology.

Laevicardiinae is the sister taxon to *Nemocardium*, but the oldest fossil laevicardiines are Eocene in age (Cooke 1926; Keen 1969, 1980). It is possible that, instead of a sister-group relationship, Laevicardiinae was derived from some form of *Nemocardium*, and therefore its true phylogenetic relationship lies within *Nemocardium*, not as its sister taxon. A more detailed, species-level phylogenetic analysis of the Laevicardiinae/*Nemocardium* clade is necessary to resolve this issue. For this reason, I decline to name a new subfamily for *Nemocardium*, even though it is in a sister-group relation to Laevicardiinae. Instead, *Nemocardium* is incorporated into Laevicardiinae.

Savazzi (1985, p. 294) explicitly adopted Keen's (1980) cardiid taxonomy, placing *Nemocardium* as a genus of Protocardiinae. However, Savazzi (pp. 316–317) used the term "Nemocardiinae" for *Nemocardium sensu* Keen (1969, 1980). Therefore, there is clear evidence that Savazzi's use of the word "Nemocardiinae" is a *lapsus calami*. "Nemocardiinae" is not considered to have been proposed, either validly or invalidly.

The preferred cladogram, based on the results of the cladistic analysis (Figs 18 and 19), and stratigraphic data (Table III), is presented in Figure 22.

Surface sculpture. Variccate and divaricate sculpture are each found in three different cardiid taxa. Variccate sculpture occurs as concentric ridges in a superficial shell layer that serves to thicken the shell. The superficial nature of this shell layer can best be seen in *Pachycardium* (Figs 11B–D). The partially exfoliated shell (Fig. 11D) reveals that the posterior radial ribs do persist internally. However, the variccate sculpture is only barely developed in

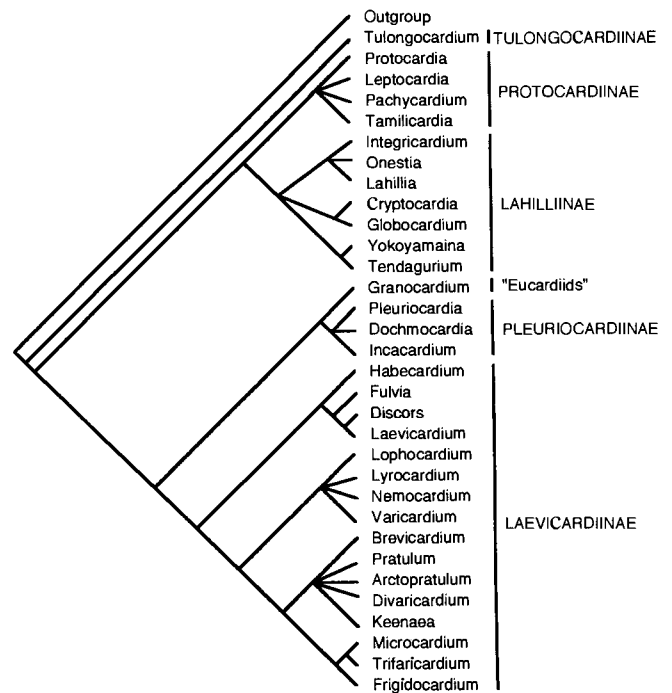
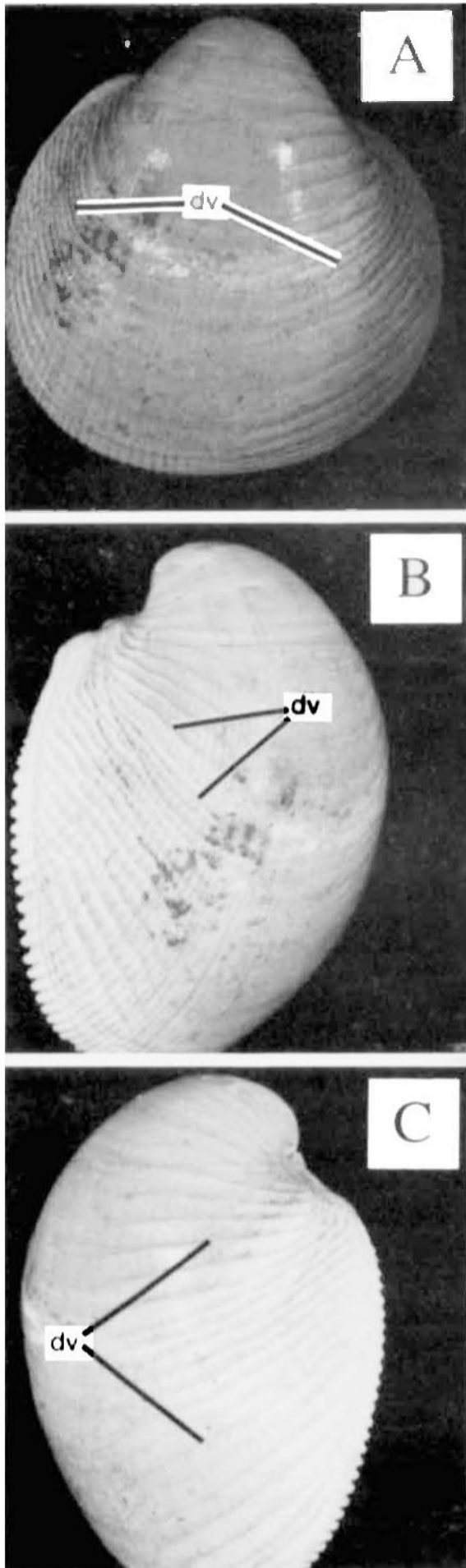


Fig. 22. Preferred hypothesis of phylogenetic relationships of Tulongocardiinae subfam. n., Protocardiinae, Lahilliinae, "eucardiids", Pleuriocardiinae subfam. n. and Laevicardiinae, based on parsimony analysis, stratigraphic data, and functional morphology.

this taxon. The shell of *Globocardium* is very thick and has secondary concentric sculpture on its anterior and central portions (Fig. 11E). Given that its sister taxon is the smooth-shelled Middle Jurassic *Cryptocardia* (Fig. 11F), the late Early Cretaceous *Globocardium* presumably lost its primary concentric ribs (the ones that would be homologous to the concentric ribs on *Protocardia*), and only later developed new concentric sculpture on its additional shell layer. The third form with variccate sculpture is *Varicardium*. *Varicardium*'s morphology is very close to that of *Nemocardium* (*Nemocardium*) (Figs 9A, C, D, F), except that it also has a thickened, globose shell, and the radial ribs on the anterior and central slopes are weaker. The hinge of *Varicardium* is more robust than that of *N.* (*Nemocardium*). Irregular concentric sculpture occurs on the anterior and central slopes. *Pachycardium*, *Globocardium*, and *Varicardium* have always been considered separate taxa, and their variccate sculpture has never caused any taxonomic confusion. The same cannot be said for divaricate sculpture.

Divaricate sculpture is secondary sculpture that is at a high angle to concentric ribbing or growth lines. Seilacher (1972) and Savazzi (1985) call this type of sculpture growth-unconformable. Savazzi (1985) found that the divaricate sculpture of *Lyrocardium* results from the secondary deposition of calcareous material on top of a previously secreted shell region. The secondarily deposited material is separated from the underlying shell by a thin organic, red-colored layer, similar in appearance to the periostracum. In *Lyrocardium* and *Discors*, the divaricate sculpture is limited to the anterior portion of the shell. On *Lyrocardium*, the sculpture is evenly spaced (Fig. 9B), whereas on *Discors*, the sculpture is irregular and sinuous (Fig. 13). *Divaricardium* (Fig. 23) has divaricate sculpture on both anterior and posterior slopes. On



the anterior slope of *Divaricardium*, the divaricate sculpture is at a much lower angle to the growth lines than on *Lyrocardium*. *Divaricardium*'s anterior sculpture is similar to that of *Discors*, but stronger. As with taxa with varicate sculpture, divaricate sculpture occurs on taxa with weak primary ribbing (although not as weak as those with varicate sculpture). *Discors*, like other laevicardiines, has weak radial ribs. *Lyrocardium* has fewer and weaker radial ribs than *Nemocardium* (*Nemocardium*) (Wilson & Stevenson 1977); *Lyrocardium* is also missing spines (13:?).

Many authors have assumed that the divaricate sculptures on *Discors*, *Lyrocardium*, and *Divaricardium* are homologous and have synonymized two or all three of these taxa (for example: Cossmann 1886; Cossmann & Peyrot 1911; Glibert & van de Poel 1970; Fischer-Piette 1977; Kafanov & Popov 1977; Popov 1977). However, since all three forms of divaricate sculpture are distinctive, I decline to consider any two of the states as homologous. All three states of divaricate sculpture are thus considered autapomorphies. Therefore, divaricate sculpture was not considered a character in the cladistic analysis. The results (Figs 18 and 22) indicate that divaricate sculpture originated three separate times. Neither varicate nor divaricate sculpture is known among the eucardiids.

Limitations of phylogenetic analysis. The lack of characters in the present data set, and hence the lack of potential synapomorphies, is responsible for the production of thousands of most parsimonious trees, and therefore the low degree of resolution in the majority-rule consensus tree. In fact, the paucity of characters used in the traditional classifications of the Protocardiinae (*sensu* Keen) has been noted by many authors, thus giving rise to several drastically different taxonomies of this group of cardiids. Furthermore, this problem has been compounded by (1) the use of superficial, analogous characters for purposes of taxonomy and phylogeny reconstruction, and (2) the presence of only five useful anatomical characters for this group. These five characters are useful only for defining the Cardiidae (node 1) and uniting *Habecardium*, *Fulvia*, *Laevicardium* and *Discors* (node 11). There are no anatomical synapomorphies within *Nemocardium sensu* Keen.

Additional work is necessary to resolve the phylogenetic relationships (1) of *Protocardia*, *Leptocardia*, *Pachycardium*, and *Tamilicardia*, and (2) within the Laevicardiinae. To gain greater phylogenetic resolution, these analyses need to be undertaken at the species level. Use of additional taxa would hopefully increase the number of characters for phylogenetic analysis. Incorporation of species-level stratigraphic data could prove useful in determining the timing of splitting of lineages. However, use of all the substantiated species of these taxa would probably result in an unwieldy number of taxa for a single analysis. A time-stratified analysis (Wagner 1990) of the

Fig. 23. *Nemocardium* (*Divaricardium*) *discrepans* (MNHN B23982) right valve. Note divaricate sculpture on all slopes.—A. Lateral view, $\times 2.2$.—B. Posterior slope, $\times 2.2$.—C. Anterior slope, $\times 1.9$.

aforementioned taxa would both incorporate stratigraphic data and reduce the number of taxa in a single analysis. Further data from the Recent species of Laevicardiinae, such as histological and molecular data, should prove to add additional characters to the data set.

Conclusions

Cardiids originated during the Norian (Late Triassic), and the most primitive representatives of this group are placed in the genus *Tulongocardium* (= *Vietnamicardium*) in the Tulongocardiinae subfam. n. The subfamily Protocardiinae is restricted to the genus *Protocardia*, which contains the nominal subgenus plus the subgenera *Pachycardium*, *Leptocardia*, and *Tamilicardia*. Other forms once classified as Protocardiinae are found to be members of the subfamily Lahilliinae. *Nemocardium* is transferred to Laevicardiinae. A monophyletic group exists that includes Pleuriocardiinae subfam. n., the Laevicardiinae, and all other cardiids (eucardiids). The eucardiids are the sister group to pleuriocardiines, which contains the genus *Pleuriocardia* with its three subgenera: *Pleuriocardia* (*Pleuriocardia*), *P.* (*Dochmocardia*), and *P.* (*Incardium*). Eucardiids and the pleuriocardiines together form the sister group to laevicardiines, which includes two monophyletic groups: (1) the remnants of Keen's subfamily Laevicardiinae—*Laevicardium*, *Fulvia*, *Habecardium* and *Discors*—the last of which had long been considered to be more closely related to *Nemocardium*, and (2) *Nemocardium sensu* Keen, with 12 subgenera.

The sister-group relationships of Protocardiinae and Lahilliinae, both to each other and to the rest of the Cardiidae, remain unresolved. The lack of resolution results from a paucity of characters to unite taxa into monophyletic groups.

For the most part, the character-based phylogenetic analysis is consistent with stratigraphic data. A species-level phylogenetic analysis of these cardiids is necessary to elucidate further the details of the evolutionary history of primitive cardiid bivalves.

Acknowledgements

This project was made possible with support from the Jessup Fund of the Academy of Natural Sciences of Philadelphia. I would like to thank the malacology and paleontology staff members of the ANSP for their assistance, support, ideas, and permission to borrow specimens: G. Rosenberg, G. Davis, E. Benamy, A. Bogan, K. Emberton, E. Spamer, R. Robertson, and A.E. Schuyler. Many other individuals and institutions have allowed me to examine collections or borrow specimens: T.R. Waller, W. Blow, R. Hershler, R. Houbriek, M.G. Harasewych, S. Greenhouse, R.N. Germon, J. Thompson (USNM); N. Eldredge, N. Landman, A.A. Lwin, R. Chamberlain (AMNH); I. Hayami, T. Oji (University of Tokyo); N. Morris, R. Cleavelly, P. Jeffery, P. D. Taylor (NHM); R. Bieler, J. Slapcinski, M. Baker, M. Nitecki, S. Lidgard, G. Buckley (FMNH); W.D. Allmon, P. Hoover (PRI); Y. Gayraud, S. Freneix, J.-P. Fischer (MNHN); W. Ponder, I. Loch (AM); C. C. Coney, J. McLean (LACMNH); T. E. Bolton (GSC); A. Beu, I. W. Keyes (DSIRGS); F. Collier, K. Boss (MCZ); R. Eng (UWBM); R. White (YPM); R. P. A. Voskuil; and S. Hobbs. Most of the work on *Nemocardium* (*Keenaia*) *centifilosum* as done at the Marine Bivalve Workshop in July, 1991, at Moss Landing Marine Laboratory, organized by P. H. Scott and J. Nybakken. Computer facilities have been provided by S. Kidwell, D. Jablonski, N. Knowlton, P. Sereno, L.

Weigt, A. G. Coates, W. Wheeler, the Department of Invertebrates of the AMNH, R. Beiersdorfer and Youngstown State University. SEM facilities were provided by the FMNH and USNM. The following agencies have provided financial support for my research: The Jessup Fund of the Academy of Natural Sciences of Philadelphia, Western Society of Malacologists, National Capital Shell Club, Lerner-Gray Foundation of the American Museum of Natural History, The Geological Society of America, Sigma Xi, Hinds Fund of the University of Chicago, Gurley Fund of the University of Chicago, Conchologists of America, The Paleontological Society, Santa Barbara Shell Club, and the Amoco Corporation. During my graduate study at the University of Chicago, I was supported by a grant from the National Science Foundation (EAR-90-05744) to D. Jablonski. D. Jablonski, R. Bieler, M. LaBarbera, J. J. Sepkoski Jr., P. Sereno and three anonymous referees reviewed the manuscript, and R. Bieler helped solve a pair of difficult taxonomic problems. I would like to thank P. W. Wagner III, D. Miller, K. Roy, A. J. Cain and J. B. C. Jackson for their advice and criticism.

References

- Ackerly, S. C. 1992a. Morphogenetic regulation in the shells of bivalves and brachiopods: evidence from the geometry of the spiral.—*Lethaia* 25: 249–256.
- Ackerly, S. C. 1992b. The structure of ontogenetic variation in the shell of *Pecten*.—*Palaeontology* 35: 847–867.
- Adams, E. N. 1986. N-trees as nestings: complexity, similarity, and consensus.—*J. Classif.* 3: 299–317.
- Adams, H. & Adams, A. 1858. *The genera of Recent Mollusca; arranged according to their organization, Vol. 1*. John van Voorst, London.
- Allmon, W. D. 1988. Paleontological completeness of the record of Lower Tertiary mollusks, U.S. Gulf and Atlantic coastal plains: implications for phylogenetic studies.—*Hist. Biol.* 3: 141–158.
- Amano, M., Ogata, S. & Nire, N. 1958. On the *Tendagurium* from the lower bed of the Goshonoura Group in Shishi-jima, Kagoshima Prefecture, Kyushu, Japan.—*Kumamoto J. Sci., ser. B, sect. 1, Geology* 3: 17–20.
- Archie, J. W. 1989. Homoplasy excess ratios: New indices for measuring levels in phylogenetic systematics and a critique of the consistency index.—*Syst. Zool.* 38: 253–269.
- Ashlock, P. D. 1971. Monophyly and associated terms.—*Syst. Zool.* 20: 63–69.
- Barrett, M., Donoghue, M. J. & Sober, E. 1991. Against consensus.—*Syst. Zool.* 40: 486–493.
- Begle, D.P. 1991. Relationships of the osmeroid fishes and the use of reductive characters in phylogenetic analysis.—*Syst. Zool.* 40: 33–53.
- Bieler, R. & Mikkelsen, P. M. 1992. Preliminary phylogenetic analysis of the bivalve family Galeommatidae.—*Am. malac. Bull.* 9: 157–164.
- Boyd, D. W. & Newell, N. D. 1968. Hinge grades in the evolution of crassatellacean bivalves as revealed by Permian genera.—*Am. Mus. Novit.* 2328: 1–52.
- Braun, R. 1954. Zum Lichtsinn augenloser Muscheln.—*Zool. Jb.* 65: 194–208.
- Brooks, D. R. 1989. The phylogeny of the Cercomeria (Platyhelminthes: Rhabdocoela) and general evolutionary principles.—*J. Parasitol.* 75: 606–616.
- Campbell, K. S. W. & Barwick, R. E. 1990. Paleozoic dipnoan phylogeny: functional complexes and evolution without parsimony.—*Paleobiology* 16: 143–169.
- Carlson, S. J. 1993. Phylogeny and evolution in 'pentameride' brachiopods.—*Palaeontology* 36: 807–837.
- Chavan, A. 1952. Distinction et classement des Astartidés.—*Cah. Géol.* 15: 123–127.
- Chavan, A. 1969a. Superfamily Carditacea Fleming, 1820. In *Treatise on invertebrate paleontology, Part N, Vol. 2, Mollusca 6, Bivalvia* (ed. R. C. Moore): 543–561. The Geological Society of America, and the University of Kansas Press, Lawrence, Kansas.
- Chavan, A. 1969b. Superfamily Crassatellacea Ferussac, 1822. In *Treatise on invertebrate paleontology, Part N, Vol. 2, Mollusca 6, Bivalvia* (ed. R. C. Moore): 562–582. The Geological Society of America, and the University of Kansas Press, Lawrence, Kansas.
- Checa, A. 1991. Sectorial expansion and shell morphogenesis in mollusks.—*Lethaia* 24: 97–114.
- Chiplonkar, G. W. & Tapaswi, P. M. 1976. On some veneroids and pholadomyoids from the Upper Cretaceous of Trichinopoly District, south India.—*Biovigyanam* 2: 151–160.
- Clark, B. L. & Durham, J. W. 1946. Eocene faunas from the Department of Bolivar, Colombia.—*Mem. geol. Soc. Am.* 16: 1–87.

- Clench, W. J. & Smith, L. C. 1944. The Family Cardiidae in the western Atlantic.—*Johnsonia* 13: 1–32.
- Cooke, W. 1926. New Eocene mollusks from Jackson, Miss.—*J. Wash. Acad. Sci.* 16: 132–138.
- Cossmann, M. 1886. Catalogue des coquilles fossiles de l'Éocène des environs de Paris.—*Annl. Soc. r. malacol. Belg.* 21: 17–186
- Cossmann, M. 1906. Description de quelques pélecypodes Jurassiques de France.—*Compt.-Rend. Assoc. franç. Avanc. Sci.* 34: 284–297.
- Cossmann, M. 1916. Étude complémentaire sur le Charmouthien de la Vendée.—*Bull. Soc. géol. Normandie* 36: 113–174.
- Cossmann, M. 1919. Monographie illustrée des mollusques oligocènes des environs de Rennes.—*J. Conch.* 64: 133–9.
- Cossmann, M. 1921. Synopsis illustré des mollusques de l'Éocène et de l'Oligocène en Aquitaine.—*Mem. Soc. géol. France Paléont.* 55: 5–112.
- Cossmann, M. & Peyrot, A. 1911. Conchologie néogénique de l'Aquitaine.—*Act. Soc. linn. Bordeaux* 65: 51–333.
- Cossmann, M. & Pissarro, G. 1906. *Iconographie complète des coquilles fossiles de l'Éocène des environs de Paris. Tome Ier.—Pélecypodes. Fasc. II.* Pls. XVIII–XLV. M. Pissarro, Paris.
- Cox, L. R. 1935. Jurassic Gastropoda and Lamellibranchia. In *The Mesozoic palaeontology of British Somaliland. Part II of the geology and palaeontology of British Somaliland* (ed. W. A. Macfadyen): 148–197. Government of the Somaliland Protectorate, London.
- Cox, L. R. 1946. *Tucheria* and *Pseudopsis*, new lamellibranch genera from the Lias.—*Proc. malac. Soc. Lond.* 27: 34–48.
- Cox, L. R. 1948. On the occurrence of the genus *Tucheria* in the Upper Trias and Rhaetic.—*Proc. malac. Soc. Lond.* 27: 247–248.
- Cox, L. R. 1949. Moluscos del Triasico Superior del Peru.—*Instituto Geol. Peru Bol.* 12: 1–48.
- Crane, P. R. 1985. Phylogenetic relationships in seed plants.—*Cladistics* 1: 329–348.
- Dall, W. H. 1889. Preliminary reports on the collection of Mollusca and Brachiopoda obtained in 1887–'88.—*Proc. U.S. natn. Mus.* 12: 219–362.
- Dall, W. H. 1901. Synopsis of the family Cardiidae and of the North American species.—*Proc. U.S. natn. Mus.* 23: 381–392.
- Day, R. W. 1978. *Onestia* McLearn, an unusual cardiacean pelecypod from the Lower Cretaceous of Australia and Canada.—*Bull. Bur. Miner. Resour. Geol. Geophys. Aust.* 192: 37–44.
- Dey, A. K. 1961. The Miocene Mollusca from Quilon, Kerala (India).—*Mem. geol. Surv. India Palaeont. indica, new ser.* 36: 1–116.
- Dietrich, W. O. 1933. Zur Stratigraphie und Paläontologie der Tendaguruschichten.—*Palaeontographica, Supplement VII. II. Reihe Teil II, Lieferung I:* 1–86.
- Doyle, J. A. & Donoghue, M. J. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach.—*Bot. Rev.* 52: 321–431.
- Eernisse, D. J., Albert, J. S. & Anderson, F. E. 1992. Annelida and Arthropoda are not sister taxa: a phylogenetic analysis of spiralian metazoan morphology.—*Syst. Biol.* 41: 305–330.
- Erséus, C. 1992. A generic revision of the Phalloidrilinae (Oligochaeta, Tubificidae).—*Zool. Scr.* 21: 5–48.
- Farris, J. S. 1983. The logical basis of phylogenetic analysis.—*Advances in cladistics* 2: 7–36.
- Farris, J. S. 1988. *Hennig86, version 1.5.* Computer program distributed by J. S. Farris, Port Jefferson Station, New York.
- Farris, J. S. 1989. The retention index and the rescaled consistency index.—*Cladistics* 5: 417–419.
- Finlay H. J. & Marwick, J. 1937. The Wangoloan and associated molluscan faunas of Kaitangata-Green Island subdivision.—*N.Z. Dept. Sci. industr. Res. geol. Surv. Branch Palaeont. Bull.* 15: 1–140.
- Fischer, P. 1887. *Manuel de conchyliologie et de paléontologie conchyliologique.* Librairie F. Savy, Paris.
- Fischer-Piette, É. 1977. Révision des Cardiidae (mollusques lamellibranches).—*Mém. Mus. natn. Hist. nat., Paris, nouv. sér., sér. A., Zoologie* 101: 1–212.
- Fortey, R. A. 1990. Trilobite evolution and systematics.—*Short Courses Paleont.* 3: 44–65.
- Fortey, R. A. & Cooper, R. A. 1986. A phylogenetic classification of the graptoloids.—*Palaeontology* 31: 165–222.
- Gauthier, J., Kluge, A. G. & Rowe, T. 1988. Amniote phylogeny and the importance of fossils.—*Cladistics* 4: 105–209.
- Gillet, S. 1924. Études sur les lamellibranches néocomiens.—*ém. Soc. géol. France, nouv. sér. I:* 1–224.
- Gingerich, P. D. 1979. Paleontology, phylogeny, and classification: an example from the mammalian fossil record.—*Syst. Zool.* 28: 451–464.
- Glibert, M. & van de Poel, L. 1970. Les Bivalvia fossiles du Cénozoïque étranger des collections de l'Institut Royal des Sciences Naturelles de Belgique. VI (fin). Oligodontina (2), Asartodontina et Septibranchida.—*Mém. Inst. r. Sci. nat. Belg., deuxième sér. Fasc.* 84: 1–160.
- Guo, F. 1988. New Genera of Fossil Bivalves from Yunnan.—*Yunnan Geol.* 7: 112–144.
- Habe, T. 1951. *Genera of Japanese shells. Pelecypoda no. 2:* 97–186.
- Harland, W. B., Armstrong, R. L., Cox, A. V., Craig, L. E., Smith, A. G. & Smith, D. G. 1990. *A geologic time scale 1989.* Cambridge University Press, New York.
- Hayami, I. 1958. A review of the so-called Liassic "Cyrenoids" in Japan (Studies on the Liassic Pelecypods in Japan. 7).—*Japan. J. Geol. Geogr.* 29: 1–27.
- Hayami, I. 1965. Lower Cretaceous marine pelecypods of Japan. Part II.—*Mem. Fac. Sci. Kyushu Univ., ser. D. Geology* 17: 73–150.
- Hayami, I. 1972. Lower Jurassic Bivalvia from the Environs of Saigon.—*Geol. Paleont. Southeast Asia* 10: 179–230.
- Healey, M. 1908. The Fauna of the Napcng Beds or the Rhaetic Beds of Upper Burma.—*Mem. geol. Surv. India Palaeont. indica, new ser., Vol. II,* 4: 1–88.
- Hennig, W. 1966. *Phylogenetic systematics.* University of Illinois Press, Urbana.
- Huelsenbeck, J. P. 1994. Comparing the stratigraphic record to estimates of phylogeny.—*Paleobiol.* 20: 470–483.
- Jablonski, D. 1994. Extinctions in the fossil record.—*Phil. Trans. r. Soc. Lond.* 344B: 11–17.
- Jackson, J. B. C. & Cheetham, A. H. 1994. Phylogeny reconstruction and the tempo of speciation in cheilostome Bryozoa.—*Paleobiol.* 20: 407–423.
- Johnston, M. R., Tabachnick, R. E. & Bookstein, F. L. 1991. Landmark-based morphometrics of spiral accretionary growth.—*Paleobiol.* 17: 19–36.
- Kafanov, A. I. 1975. K sisteme podsycmycystva Laevicardiinae Kcen, 1936 (Bivalvia, Cardiidae). In *Mollyuski, ikh sistema, evolyutsia i pol'v prirode:* 145–147. Nauka, Moscow.
- Kafanov, A. I. 1976. K sistematcheskomu položzeniyu dal'nevostochnykh Papyridea (Bivalvia, Cardiidae).—*Paleont. Zh.* 1976: 110–112.
- Kafanov, A. I. 1980. Systematics of the subfamily Clinocardiinae Kafanov, 1975 (Bivalvia, Cardiidae).—*Malacologia* 19: 297–328.
- Kafanov, A. I. & Popov, S. V. 1977. K sisteme kaynozoysskikh kardioidey (Bivalvia).—*Paleont. Zh.* 1977: 55–64.
- Kambhampati, S. 1995. A phylogeny of cockroaches and related insects based on DNA sequence of mitochondrial rihosomal RNA genes.—*Proc. Natl. Acad. Sci. USA* 92: 2017–2020.
- Kauffman, E. G. 1969. Form, function, and evolution. In *Treatise on invertebrate paleontology, Part N, Vol. 2, Mollusca 6, Bivalvia* (ed. R. C. Moore): 129–205. The Geological Society of America, and the University of Kansas Press, Lawrence, Kansas.
- Keen, A. M. 1937. Nomenclatural units of the pelecypod family Cardiidae.—*Bull. Mus. r. Hist. nat. Belg.* 13: 1–22.
- Keen, A. M. 1950. Notes on the history of *Nemocardium* (family Cardiidae).—*J. Conch.* 90: 23–29.
- Keen, A. M. 1951. Outline of a proposed classification of the pelecypod family Cardiidae.—*Minut. conch. Club Sth. Calif.* 111: 6–8.
- Keen, A. M. 1969. Superfamily Cardiacea Lamarck, 1809. In *Treatise on invertebrate paleontology, Part N, Vol. 2, Mollusca 6, Bivalvia* (ed. R. C. Moore): 583–594. The Geological Society of America and the University of Kansas Press, Lawrence, Kansas.
- Keen, A. M. 1980. The pelecypod family Cardiidae: a taxonomic summary.—*Tulane Stud. Geol. Paleont.* 16: 1–40.
- Kira, T. 1962. *Shells of the Western Pacific in color, Vol. 1.* Hoikusha Publishing Company, Osaka.
- Kishinouye, K. 1894. Note on the eyes of *Cardium muticum* Reeve.—*J. Coll. Sci. imp. Univ. Tokyo* 6: 279–285.
- Kluge, A. G. & Farris, J. S. 1969. Quantitative phyletics and the evolution of anurans.—*Syst. Zool.* 18: 1–32.
- Lan, X. & Chen, C.-Z., eds. 1976. *Fossil Lamellibranchia from the Mount Johnno Lungma Region. A report of scientific expedition in the Mount Johnno Lungma Region (1966–1968), Paleontology, Fasc. III.* Science Press, Beijing (in Chinese)
- Lanyon, S. M. 1994. Polyphyly of the blackbird genus *Agelaius* and the importance of assumptions of monophyly in comparative studies.—*Evolution* 48: 679–693.
- Lazarus, D. B. & Prothero, D. R. 1984. The role of stratigraphic and morphologic data in phylogeny.—*J. Paleont.* 58: 163–172.
- Løvtrup, S. & Løvtrup, M. 1988. The morphogenesis of molluscan shells: a mathematical account using biological parameters.—*J. Morph.* 197: 53–62.
- McKittrick, M. C. 1991. Phylogenetic analysis of avian hindlimb musculature.—*Misc. Publs Mus. Zool. Univ. Mich.* 179: 1–85.
- McLearn, R. H. 1933. Pelecypods of the Lower Cretaceous Clearwater Formation, northern Alberta.—*Trans. r. Soc. Can. sect. 4, ser. 3,* 27: 139–156.

- McLearn, R. H. 1945. Revision of the Lower Cretaceous of the western interior of Canada (2nd edition).—*Pap. geol. Surv. Can.* 44-17: 1-14.
- Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees.—*Syst. Zool.* 40: 315-328.
- Maddison, W. P., Donoghue, M. J. & Maddison, D. R. 1984. Outgroup analysis and parsimony.—*Syst. Zool.* 33: 83-103.
- Maddison, W. P. & Maddison, D. R. 1992. *MacClade version 3. Analysis of phylogeny and character evolution*. Sinauer Associates, Sunderland, Massachusetts.
- Marincovich, L. Jr 1993. Danian mollusks from the Prince Creek Formation, northern Alaska, and implications for Arctic Ocean paleogeography.—*Paleont. Soc. Mem.* 35: 1-35.
- Marshall, C. R. & Schultze, H. -P. 1992. Relative importance of molecular, neontological, and paleontological data in understanding the biology of the invertebrate invasion of land.—*J. Molec. Evol.* 35: 93-101.
- Marwick, J. 1944. New Zealand fossil and Recent Cardiidae (Mollusca).—*Tr. roy. Soc. N. Z., pt. III* 74: 255-272.
- Maxwell, P. A. 1992. Eocene Mollusca from the vicinity of McCulloch's Bridge, Waihao River, South Canterbury, New Zealand: Paleogeology and systematics.—*N. Z. geol. Surv. Paleont. Bull.* 65: 1-280.
- Meek, F. B. 1876. A report on the invertebrate Cretaceous and Tertiary fossils.—*Rep. U.S. geol. Surv. Terr.* 9: LIV + 629 pp.
- Miyazaki, J. M. & Mickevich, M. F. 1982. Evolution of *Chesapecten* (Mollusca: Bivalvia, Miocene-Pliocene) and the biogenetic law.—*Evol. Biol.* 15: 369-409.
- Morris, N. J. 1978. The infaunal descendents of the Cycloconchidae: an outline of the evolutionary history and taxonomy of the Heteroconchia, superfamilies Cycloconchacea to Chamacea.—*Phil. Trans. r. Soc.* 284B: 259-275.
- Morris, N. J., Dickins, J. M. & Astafieva-Urbaitis, K. 1991. Upper Palaeozoic anomalodesmatan Bivalvia.—*Bull. Br. Mus. nat. Hist., Geology* 47: 51-100.
- Nagel, W. 1897. Über rathselhafte Organe an den Siphonpapillen von *Cardium oblongum*.—*Zool. Anz.* 20: 406-409.
- Newton, C. R. 1986. Late Triassic bivalves of the Martin Bridge Formation, Hell's Canyon, Oregon: taphonomy, paleoecology, paleozoogeography.—*Prof. Pap. U.S. geol. Surv.* 1435: 7-22.
- Noda, H. 1988. Molluscan fossils from the Ryukyu Islands, southwest Japan. Part 2. Gastropoda and Pelecypoda from the Shinzato Formation in the middle part of Okinawa-jima.—*Sci. Rep. Inst. Geosci. Univ. Tsukuba sect. B*, 9: 29-85.
- Novacek, M. J. 1992. Fossils, topologies, missing data, and the higher level phylogeny of eutherian mammals.—*Syst. Biol.* 41: 58-73.
- Olsson, A. A. 1944. Contributions to the paleontology of northern Peru. Part VII. The Cretaceous of the Paita Region.—*Bull. Am. Paleont.* 28: 163-304.
- Orbigny, A. d' 1844. *Paléontologie Française. Description zoologique et géologique de tous les animaux mollusques et rayonnés fossiles de France*. Arthur Bertrand, Paris.
- Palmer, C. P. 1974. A new genus of Jurassic bivalve mollusc ancestral to *Globocardium*.—*Palaeontology* 17: 165-178.
- Patterson, C. & Rosen, D. E. 1989. The Paracanthopterygii revisited: order and disorder.—*Sci. Ser. Nat. Hist. Mus. Los Ang. Co.* 32: 5-36.
- Pelseneer, P. 1911. Les lamellibranches de l'expédition du Siboga. Partie anatomique.—*Siboga Expeditie* 53a: 1-125.
- Popov, S. V. 1977. Mikrostruktura rakoviny i sistematika kardiid.—*Trudy paleont. Inst.* 153: 1-124.
- Poutiers, J.-M. 1992. The Australasian Protocardiinae revisited (Bivalvia: Cardiidae).—*Am. malac. Bull.* 9: 139-144.
- Raup, D. M. 1966. Geometric analysis of shell coiling: general problems.—*J. Paleont.* 41: 1178-1190.
- Raup, D. M. 1979. Biases in the fossil record of species and genera.—*Bull. Carnegie Mus. nat. Hist.* 13: 85-91.
- Raup, D. M. & Boyajian, G. E. 1988. Patterns of generic extinction in the fossil record.—*Paleobiol.* 14: 109-125.
- Riccardi, A. C. 1977. Berriasian invertebrate fauna from the Springhill Formation of Southern Patagonia.—*Neues Jb. Geol. Paläont. Abh.* 155: 216-252.
- Ride, W. D. L., Sabrosky, C. W., Bernardi, G. & Melville, R. V., eds. 1985. *International Code of Zoological Nomenclature. Third Edition*. International Trust for Zoological Nomenclature in association with the British Museum (Natural History) London, and the University of California Press.
- Roche, W. L. 1925. Note on the microscopic anatomy of the tentacular sense organ of *Cardium edule*.—*J. roy. microscop. Soc.* 1925: 154-158.
- Rosewater, J. 1965. The family Tridacnidae in the Indo-Pacific.—*Indo-Pac. Moll.* 1: 347-396.
- Saleuddin, A. S. M. 1965. The mode of life and functional anatomy of *Astarte* spp. (Eulamellibranchia).—*Proc. malac. Soc. Lond.* 36: 229-257.
- Saleuddin, A. S. M. 1967. Notes on the functional anatomy of three North American species of *Astarte*, *A. undata* Gould, *A. castanea* Say and *A. esquimalti* Baird.—*Proc. malac. Soc. Lond.* 37: 381-384.
- Salisbury, A. E. 1934. Mollusca. *The Zoological Record* 70, part VIII. The Zoological Society, London.
- Savazzi, E. 1985. Adaptive themes in cardiid bivalves.—*Neues Jb. Geol. Paläont. Abh.* 170: 291-321.
- Schneider, J. A. 1992. Preliminary cladistic analysis of the bivalve family Cardiidae.—*Am. malac. Bull.* 9: 145-155.
- Schneider, J. A. 1993. *Evolutionary patterns of cardiid bivalves*. Unpublished Ph.D. dissertation, University of Chicago.
- Schneider, J. A. 1994. On the anatomy of the alimentary tracts of the bivalves *Nemocardium (Keenaea) centifolium* (Carpenter, 1864) and *Clinocardium nuttallii* (Conrad, 1837) (Cardiidae).—*Veliger* 37: 36-42.
- Scott, R. 1970. Paleogeology and paleontology of the Lower Cretaceous Kiowa Formation, Kansas.—*Paleont. Contr. Univ. Kans. Art.* 52: 1-94.
- Scott, R. 1978. Paleobiology of Comanchean (Cretaceous) cardiids (Cardiinae), North America.—*J. Paleont.* 52: 881-903.
- Seilacher, A. 1972. Divergent patterns in pelecypod shells.—*thais* 5: 325-343.
- Seilacher, A. 1984. Constructional morphology of bivalves: evolutionary pathways in primary versus secondary soft-bottom dwellers.—*Palaeontology* 27: 207-234.
- Sepkoski, J. J. Jr. 1986. Phanerozoic overview of mass extinction. In *Patterns and processes in the history of life* (eds D. M. Raup & D. Jablonski): 277-295. Springer, Berlin.
- Sepkoski, J. J. Jr. 1989. Periodicity in extinction and the problem of catastrophism in the history of life.—*J. geol. Soc. Lond.* 146: 7-19.
- Simms, M. J. & Sevastopulo, G. D. 1993. The origin of articulate crinoids.—*Palaeontology* 36: 91-109.
- Sluys, R. 1989. Rampant parallelism: an appraisal of the use of nonuniversal derived character states in phylogenetic reconstruction.—*Syst. Zool.* 38: 350-370.
- Smith, A. B. 1994. *Systematics and the fossil record*. Blackwell Scientific Publications, Boston.
- Smith, A. B. & Wright, C. W. 1990. British Cretaceous echinoids. Part 2, Echinothurioida, Diadematoidea and Stirodonta (1, Calycina).—*Paleontogr. Soc. Monogr.* 143: 101-198.
- Smith, L. C. 1945. Notes on the family Cardiidae.—*Occ. Pap. Mollusks Harv.* 4: 29-32.
- Sneath, P. H. A. & Sokal, R. R. 1973. *Numerical taxonomy*. W. H. Freeman and Co., San Francisco.
- Stanley, S. M. 1968. Post-Paleozoic adaptive radiation of infaunal bivalve molluscs—a consequence of mantle fusion and siphon formation.—*J. Paleont.* 42: 214-229.
- Stanley, S. M. 1970. Relation of shell form to life habits in the Bivalvia (Mollusca).—*Mem. geol. Soc. Am.* 125: 1-296.
- Stewart, R. B. 1930. Gabb's California Cretaceous and Tertiary type lamellibranchs.—*Spec. Publ. Acad. nat. Sci. Philad.* 3: 1-314.
- Swofford, D. L. 1991. *PAUP: Phylogenetic Analysis Using Parsimony, version 3.0q*. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
- Swofford, D. L. 1993. *PAUP: Phylogenetic Analysis Using Parsimony, version 3.1.1*. Computer program distributed by D. L. Swofford, Smithsonian Institution.
- Valentine, J. W. 1989. How good was the fossil record? Clues from the Californian Pleistocene.—*Paleobiol.* 15: 83-94.
- Vokes, H. 1968. Genera of the Bivalvia: a systematic and bibliographic catalogue.—*Bull. Am. Paleont.* 51: 1-394.
- Vokes, H. 1980. *Genera of the Bivalvia: a systematic and bibliographic catalogue (revised and updated)*. Paleontological Research Institution, Ithaca, New York.
- Voskuil, R. P. A. & Onverwagt, J. P. H. 1989. Inventarisatie van de Recent European and west African Cardiidae (Mollusca, Bivalvia).—*Gloria Maris* 28: 49-96.
- Vu-Khuc, D. 1977. Reviziya nektorykh rodov dvustvorchatykh molyluskov iz verkhnetriasovykh otlozheniy Sevrnogo V'yctnama.—*Dokl. Akad. Nauk SSSR* 232: 676-679.
- Vu-Khuc, D., Dags, A. S., Kiparisova, L. D., Nguyen, N. B., Bao, T. C. & Srebrodolskaia, I. N. 1965. *Hoa thach chi dao dia tang Trias mien Viet-nam*. Direction Générale de Géologie, Hanoi.
- Wagner, P. W. III. 1990. Phylogenetic analysis of the Lophosphiridae (Gastropoda: Pleurotomariina): implications for diversity studies.—*Geol. Soc. Am. Abstr. Progr.* 22: :221.
- Waller, T. R. 1978. Morphology, morphoclines and a new classification of the Pteriomorpha (Mollusca: Bivalvia).—*Phil. Trans. r. Soc. Lond.* 284B: 345-365.
- Waller, T. R. 1988. A phylogeny of the Bivalvia: progress and problems. *Program and Abstracts, Fifty-fourth Annual Meeting, American Malacological Union*, p. 19.
- Waller, T. R. 1990. The evolution of ligament systems in the Bivalvia. In

- The Bivalvia—Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986* (ed. B. Morton): 49–71. Hong Kong University Press, Hong Kong.
- Waller, T. R. 1993. The evolution of “*Chlamys*” (Mollusca: Bivalvia: Pectinidae) in the tropical western Atlantic and eastern Pacific.—*Am. malac. Bull.* 10: 195–249.
- Weber, F. L. 1908. Über sinnesorgane des Genus *Cardium*.—*Arb. Zool. Inst. Univ. Wien* 17: 187–220.
- Wilson, B. R. & Stevenson, S. E. 1977. Cardiidae of Western Australia.—*Western Aust. Mus. Spec. Publ.* 9: 1–114.
- Yamani, S.-A. & Schairer, G. 1975. Bivalvia aus dem Dolomit von Grossmehring bei Ingolstadt (Untertithon, Südliche Frankenalb, Bayern).—*Mitt. bayer. Staats. paläont. hist. Geol.* 15: :19–27.
- Yonge, C. M. 1969. Functional morphology and evolution within the Carditacea (Bivalvia).—*Proc. Malac. Soc. Lond.* 38: 493–527.
- Zinsmeister, W. J. 1984. Late Eocene bivalves (Mollusca) from the La Meseta Formation, collected during the 1974–1975 joint Argentine–American expedition to Seymour Island, Antarctic Peninsula.—*J. Paleont.* 58: 1497–1527.
- Zinsmeister, W. J. & Macellari C. E. 1988. Bivalvia (Mollusca) from Seymour Island, Antarctic Peninsula.—*Mem. geol. Soc. Am.* 169: 253–284.
- Zugmayer, E. 1904. Über Sinnesorgane an den Tentakeln des Genus *Cardium*.—*Z. wiss. Zool.* 1904: 478–508.

Appendix I

Previous classifications of subfamilies Protocardiinae and Laevicardiinae. Kafanov and Popov (1977), Kafanov (1980) and Schneider (1992, 1993) found *Dinocardium* to belong to subfamily Cardiinae. Kafanov (1975, 1976, 1980), Kafanov and Popov (1977) and Schneider (1992, 1993) placed *Cerastoderma* in the subfamily Lymnocardiinae and *Clinocardium*, *Profulvia*, and *Serripes* in the subfamily Clinocardiinae.

Popov (1977) and Kafanov &

Popov (1977)	Keen (1980)
Subfamily Protocardiinae	Subfamily Protocardiinae
<i>Protocardia</i>	<i>Protocardia</i>
(<i>Protocardia</i>)	(<i>Protocardia</i>)
(<i>Brevicardium</i>)	(<i>Brevicardium</i>)
(<i>Cryptocardia</i>)	(<i>Cryptocardia</i>)
(<i>Globocardium</i>)	(<i>Globocardium</i>)
(<i>Leptocardia</i>)	(<i>Leptocardia</i>)
(<i>Pachycardium</i>)	(<i>Pachycardium</i>)
(<i>Tendagurium</i>)	(<i>Tendagurium</i>)
	(<i>Yokoyamaina</i>)
<i>Integricardium</i>	<i>Integricardium</i>
(<i>Integricardium</i>)	(<i>Integricardium</i>)
(<i>Onestia</i>)	(<i>Onestia</i>)
<i>Jurassicardium</i>	<i>Jurassicardium</i>
<i>Nemocardium</i>	<i>Nemocardium</i>
(<i>Nemocardium</i>)	(<i>Nemocardium</i>)
(= <i>Divaricardium</i>)	(<i>Arctopratalum</i>)
(<i>Varicardium</i>)	(<i>Discors</i>)
(<i>Habecardium</i>)	(<i>Divaricardium</i>)
	(<i>Frigidocardium</i>)
<i>Pratulum</i>	(<i>Habecardium</i>)
(= <i>Arctopratalum</i> ,	(<i>Keenaea</i>)
<i>Frigidocardium</i> ,	(<i>Lophocardium</i>)
<i>Keenaea</i> ,	(<i>Lyrocardium</i>)
<i>Microcardium</i> , and	(<i>Microcardium</i>)
<i>Trifaricardium</i>)	(<i>Pratulum</i>)
<i>Lophocardium</i>	(<i>Trifaricardium</i>)
<i>Discors</i>	(<i>Varicardium</i>)
(= <i>Lyrocardium</i>)	
Subfamily Laevicardiinae	Subfamily Laevicardiinae
<i>Laevicardium</i>	<i>Laevicardium</i>
(<i>Laevicardium</i>)	
<i>Fulvia</i>	(<i>Dinocardium</i>)
	(<i>Fulvia</i>)
	(<i>Profulvia</i>)
	<i>Cerastoderma</i>
	<i>Clinocardium</i>
	<i>Serripes</i>

Appendix II

Description of new taxa. Subfamily Tulongocardiinae subfam. n.
Type genus: *Tulongocardium* Chen, Chen & Zhang in Lan & Chen, 1976 (= *Vietnamocardium* Vu-Khuc, 1977, subjective).
Description: Cardiidae with shell sculpture of radial ribs on entirety of shell, shell quadrate, longer than high, posterior margin crenulate. Spines absent. Hinge as in *Protocardia*, but right anterior cardinal smaller (absent in some specimens).
Content: *Tulongocardium* Chen, Chen & Zhang in Lan & Chen, 1976.
Range: Norian of Indonesia; Norian and Rhaetian of Peoples' Republic of China (Yunnan Province), northern Vietnam and Burma.

Subfamily Pleuriocardiinae subfam. n.
Type genus: *Pleuriocardia* Scott, 1978.
Description: Cardiidae with sculpture of radial ribs on entirety of shell, cross-striae in rib interspaces. Unlike most cardiids, the right cardinal teeth are of almost equal size: anterior right cardinal tooth large, wide, blunt, arching over anterior cardinal socket. Posterior right cardinal tooth shaped as in *Nemocardium* and *Granocardium*, but rotated counterclockwise so that the tooth and the right posterior cardinal socket are at less than a 35° angle from the horizontal. Spines of concave-down triangles emanating from top of ribs (may be microscopic).
Content: *Pleuriocardia* Scott, 1978, includes: *P. (Pleuriocardia)*, *P. (Dochmocardia)* Scott, 1978, and *P. (Incacardium)* Olsson, 1944.
Range: Albian to Maastrichtian, United States, Mexico, Jamaica, Peru, France, England, Algeria, Libya, Egypt.