

The evolution of "*Chlamys*" (Mollusca: Bivalvia: Pectinidae) in the tropical western Atlantic and eastern Pacific

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Abstract: The phylogenetic relationships and paleontological history of six species of "*Chlamys*" living in the Caribbean were analyzed for the purpose of determining how each originated and is related to geminate species elsewhere in the world ocean. Particular emphasis is on origins and dispersal relative to the closure of seaways connecting the tropical western Atlantic and eastern Pacific. The resulting systematic revision demonstrates that these species are not a monophyletic assemblage, nor are they a single genus, nor are any of them members of the genus *Chlamys* in a strict sense.

The Caribbean species "*Chlamys*" *multisquamata* is placed in a new genus *Laevichlamys*, which originated in the western Indo-Pacific and dispersed westward to the eastern Atlantic, thence to the western Atlantic. Arrival in the Caribbean region occurred after the mid-Pliocene seaway closure, and *L. multisquamata* has no geminate species in the eastern Pacific. True *Hinnites*, represented at present by the relic species *H. corallinus* from west Africa and by Mio-Pliocene *H. crispus* of the Mediterranean, is shown to be derived from a stem species in *Laevichlamys*.

Four of the Caribbean species, *Chlamys sentis*, *C. ornata*, *C. mildredae*, and *C. imbricata*, comprise a new monophyletic genus *Caribachlamys* characterized by a unique lecithotrophic-type larval shell. This group also originated in post-closure time, probably in the late Pliocene, and is restricted to the tropical western Atlantic. *Caribachlamys* is placed in a new tribe *Crassadomini* with the more plesiomorphic genus *Crassadoma*. The definition of the latter is expanded to include not only its type species, *C. gigantea* of the eastern Pacific, but also *C. multistriata* and *C. pusio* of the eastern Atlantic. The phylogenetic histories of these species are discussed and it is shown that the cemented habit of *C. gigantea* and *C. pusio* arose independently and at different times.

Lastly, "*Chlamys*" *benedicti* of the Caribbean is made the type species of a new genus *Spathochlamys*, which has a long history in the tropical western Atlantic but originated from ancestors in the eastern Atlantic. Entry of members of the genus into the eastern Pacific occurred via Central American seaways probably in the late Miocene, giving rise to *S. vestalis* (= *S. lowei*), which has now dispersed as far as the Galapagos Islands with some morphological divergence.

The results suggest that: (1) eurytopy bestows resistance to both extinction and speciation; (2) long distance dispersal facilitates allopatric speciation but so also does lecithotrophy in reef habitats; (3) evolution within some scallop clades has been very rapid; and (4) gene flow between Bermuda and the Antilles was interrupted during the late Pleistocene. Finally, marine evolutionary events in the Neogene of the tropical Americas are related only incidentally to seaway closure; many of the differences that separate modern Caribbean and tropical eastern Pacific faunas arose both well before and well after closure.

In addition to the introduction of two new tribes, three new genera, and one new fossil species, lectotypes are designated for certain species named by Linnaeus (1758), Gmelin (1791), Poli (1795), Lamarck (1819), and Reeve (1853).

It has long been known that the modern Caribbean marine fauna was formerly part of a larger Tertiary biogeographic province that extended into the tropical eastern Pacific through connecting seaways in Central America and northern South America (Woodring, 1966). It has been assumed that the final closure of these seaways set off a divergence between the Atlantic and Pacific parts of a once continuous fauna. The Panamic fauna is said to have remained relatively unchanged, whereas the Caribbean fauna declined in diversity and species richness. These assumptions have been based mainly on data stemming from taxic censuses, particularly of gastropods at the level of genus and subgenus (Woodring, 1966; Petuch, 1982b; Jones and Hesson, 1985; Vermeij and Petuch, 1986; Vermeij, 1993; Allmon *et al.*, 1993).

New approaches, however, are yielding new infor-

mation on both the timing and the effects of seaway closure. Studies of the physical stratigraphy and biostratigraphy of the Isthmus point to a final closure date of about 3.5 million years ago, in the middle Pliocene (Coates *et al.*, 1992, and references therein). Allmon *et al.* (1993) compiled species-level data on gastropods and found that the modern warm western Atlantic gastropod fauna is not less diverse than the eastern Pacific one but has undergone considerably more taxonomic turnover since closure. Budd *et al.* (1992), in a study of reef coral species, also found that taxonomic turnover, not diversity decline, was the major event in the post-closure Caribbean. Caribbean extinctions increased after closure, but so also did originations. Furthermore, these and other recent studies (Jackson *et al.*, 1993; Knowlton *et al.*, 1993; Vermeij, 1993) indicate that many of the differences that now exist between the faunas

on the two sides of the Isthmus did not originate exactly at the time of final closure. Jackson and Jung (1992), using species-level data, found that strong contrasts between the mollusk faunas of the western Atlantic and eastern Pacific were already present 2 Ma before final closure and that extinction in the Caribbean did not become massive until 1.8 to 1.5 Ma after final closure. Collins (1992) found that the main restructuring of the benthic foraminiferal faunas of the upper continental slope to inner continental shelf of the Caribbean occurred in the latest Miocene well before seaways closed. Cheetham and Jackson (1992) concluded from a phylogenetic study of some cheilostome bryozoans that cladogenesis reached a peak in the Late Miocene "well before final closure of the Panamanian portal, but after formation of the sill that disrupted oceanic circulation patterns throughout the region." Knowlton *et al.* (1993), in a study of the biochemical and reproductive divergence of trans-isthmian pairs of snapping shrimp, found "that isolation was staggered rather than simultaneous."

It is apparent from these recent studies that species-level analyses provide new insight to the dynamics of evolutionary change in the tropical American marine faunas before and after seaway closure. Aside from a few species-level studies, however, these efforts still depend mainly on taxonomic census data, albeit at a finer level than that in previous studies.

The objective of the present paper is to examine the general question of how the Caribbean marine fauna was assembled before and after seaway closure by means of a species-level examination of phylogeny in a subset of

Caribbean mollusks. Specifically, for each species considered, it will be asked where, when, and from what it originated. Are the stem groups for Caribbean species in the Caribbean or elsewhere? Is there a center of origin for Caribbean species, and how are origins distributed through time? Lastly, is there evidence for geographic subspeciation within the tropical western Atlantic? If so, what is the polarity of morphological differences among subspecies and how might this polarity be explained?

The bivalve family Pectinidae has been selected for three reasons: (1) my research concentrates on this group, and the results of earlier phylogenetic studies (Waller, 1991) can be readily applied to a new problem; (2) pectinid shells, owing to their largely calcitic composition, are commonly preserved where wholly aragonitic mollusk shells are not; (3) although Neogene pectinids appear to have low survivorship and greater extinction rates than other molluscan groups (Stanley, 1986a), they also appear to be capable of more rapid evolution and are thus ideally suited for an examination of events of the past few million years. A subset of Pectinidae consisting of species traditionally placed in the genus *Chlamys* has been selected because of their generally similar byssate life habits and alleged congeneric status. The species analyzed are the six Caribbean species of "*Chlamys*" and their close relatives elsewhere in the world ocean (Table 1). It will be shown that these species, far from being congeneric, in fact represent four extant genera distributed among three tribes. This has necessitated a taxonomic revision which has been

Table 1. Extant American "*Chlamys*" and related species of the eastern Atlantic analyzed in the present study.

Original name	Genus in this study	Tribe	Provenance	Stratigraphic range
<i>Pecten multisquamatus</i> Dunker, 1864	<i>Laevichlamys</i> new genus	Chlamyidini	W. Atlantic & Caribbean	Pleist.-Recent
<i>Lima gigantea</i> Gray, 1825	<i>Crassadoma</i>	Crassadomini new tribe	E. Pacific	Lower? Mio.-Recent
<i>Ostrea multistriata</i> Poli, 1795	<i>Crassadoma</i>	Crassadomini	E. Atlantic & SW Indian O.	Lower Mio.-Recent
<i>O. pusio</i> Linnaeus, 1758	<i>Crassadoma</i>	Crassadomini	E. Atlantic	Pleist.-Recent
<i>P. sentis</i> Reeve, 1853	<i>Caribachlamys</i> new genus	Crassadomini	W. Atlantic & Caribbean	Plio.-Recent
<i>P. ornatus</i> Lamarck, 1819	<i>Caribachlamys</i>	Crassadomini	W. Atlantic & Caribbean	Lower? Pleist.-Recent
<i>P. (Chlamys) imbricatus mildredae</i> Bayer, 1941	<i>Caribachlamys</i>	Crassadomini	W. Atlantic (SE Florida)	Upper Plio.-Recent
<i>O. imbricata</i> Graelin, 1791	<i>Caribachlamys</i>	Crassadomini	W. Atlantic & Caribbean	Lower? Pleist.-Recent
<i>Chlamys benedicti</i> Verrill and Bush, 1897	<i>Spathochlamys</i> new genus	Mimachlamyidini new tribe	W. Atlantic & Caribbean	Upper? Plio.-Recent
<i>P. (Chlamys) lowei</i> Hertlein, 1935 [= <i>Pecten vestalis</i> Reeve, 1853]	<i>Spathochlamys</i>	Mimachlamyidini	E. Pacific	Upper Mio.-Recent

extended to two eastern Atlantic species in order to establish the morphological integrity of a new tribe and to assist in the demonstration that cementation, present in one American species, is a highly polyphyletic phenomenon among pectinids.

Table 2 is a practical morphological key to the identification of the four genera listed in Table 1 plus four that are relevant to understanding phylogeny and biogeography in the tropical American regions.

MATERIALS AND METHODS

This study is based mainly on the extensive Recent and fossil shell collections of the Departments of Invertebrate Zoology and Paleobiology of the United States National Museum of Natural History, supplemented by specimens from the collection of John Waldrop and Druid Wilson, Lake Wales, Florida, the Florida Museum of Natural History Museum, Gainesville, and the Paleontological Research Institution, Ithaca, New York. Additional information stems from earlier examinations of Recent and fossil specimens housed in major natural history museums in the United States, western Europe, and Great Britain. Some new information on West Coast species was obtained after the initial version of the manuscript was reviewed. These late additions resulted from an opportunity to study collections at the United States Geological Survey office in Menlo Park, California, the Museum of Paleontology of the University of California (Berkeley), and the Los Angeles

County Museum of Natural History. Morphological terms are explained in Waller (1991) and measurement definitions are given in Waller and Marinovich (1992). In accord with these earlier studies, the terms "commarginal" and "antimarginal" refer to sculptural features that are approximately parallel or perpendicular to the shell margin, respectively. In contrast, the term "radial" refers to features that radiate from the beak, meaning that these features may be nearly parallel to the margin at the disk flanks but nearly perpendicular in the midventral region.

All specimens in the Smithsonian collections have been examined with a light microscope (Wild M-5) using reflected or transmitted light, the latter particularly useful in the examination of microsculpture in thin-shelled early growth stages. Prodissoconch morphology was studied at x50 with the light microscope, with verification of inferred prodissoconch configuration provided by examination of selected specimens with a scanning electron microscope (SEM). SEM specimens were sputter-coated with gold in a vacuum chamber and examined at accelerating voltages of 10kv.

Abbreviations

- AHF: Catalogue of the Alan Hancock Foundation Collection, now housed at LACM.
 AM: Zoological Museum, Amsterdam.
 ANSP: Academy of Natural Sciences of Philadelphia.
 AOL: length of anterior outer ligament.
 BMNH: The Natural History Museum, London.

Table 2. Key to some genera of "*Chlamys*" referred to in the text (asterisk (*) marks those genera that are extinct or absent in the tropical American region).

1. Simple non-branching radial ribs introduced early and persisting throughout ontogeny	2
Complex pattern of rib introduction, with introductions occurring through most of ontogeny	3
2. Rib interspaces with a single medial riblet, at least in early ontogeny	4
Rib interspaces lacking medial riblets and crossed by antimarginal, oblique, or herringbone striae; internal rib carinae limited to juvenile stage or absent	<i>Mimachlamys</i> *
3. Ribbing coarse and scaly; commarginal lirae commonly present in interspaces at least in early ontogeny; posterior margins of posterior auricles concave	6
Ribbing fine, with repeated introductions of new ribs by medial intercalation on both valves, filling interspaces; commarginal lirae absent; posterior margins of posterior auricles convex	<i>Laevichlamys</i>
4. Scales atop ribs concave toward dorsum; commarginals present in rib interspaces at least in early ontogeny; ribs carinate on internal shell surface near margin	5
Scales atop ribs convex toward dorsum; commarginals in rib interspaces obscure or absent; ribs without internal carinae	<i>Dimarzipecten</i> *
5. Rib interspaces in early ontogeny crossed by more or less straight commarginal lirae	<i>Spathochlamys</i>
Rib interspaces in early ontogeny having wavy or looped commarginal lirae of the <i>Aequipectininae</i> type	Genus A*
6. Prodissoconch with short PI stage and long PII stage	7
Prodissoconch with PI stage large and PII stage limited to a narrow fringe	<i>Caribachlamys</i>
7. Antimarginal striae but not commarginal lirae dominant at start of ribbed stage; shagreen microsculpture sometimes present on parts of valves	<i>Chlamys</i> *
Commarginal lirae present in rib interspaces at start of ribbed stage at least on left valve; shagreen microsculpture absent	<i>Crassadoma</i>

BRM: Institut royal des Sciences naturelles de Belgique, Brussels.

CAS: California Academy of Sciences, San Francisco.

DMNH: Delaware Museum of Natural History, Wilmington, Delaware.

GNH: Museum d'Histoire naturelle de Geneve, Switzerland.

Ht.: height, the maximum dorsoventral dimension perpendicular to the hingeline.

HUB: Zoologisches Museum, Museum für Naturkunde der Humboldt Universität, Berlin.

kv: 1,000 volts.

LACM: Los Angeles County Museum of Natural History, Los Angeles, California.

LM: Rijksmuseum van Natuurlijke Historie, Leiden.

Ma: millions of years, the standard abbreviation in the *Système International d'Unités* of the General Conference on Weights and Measures (Harland *et al.*, 1982).

MNH: Muséum national d'Histoire naturelle, Paris.

NMB: Naturhistorisches Museum Basel, Basel, Switzerland.

POL: length of posterior outer ligament.

PRI: Paleontological Research Institution, Ithaca, New York.

R/V: Research vessel.

SEM: scanning electron microscope or micrograph.

TU: Locality register of H.E. and E.H. Vokes, Tulane University, New Orleans.

TUI: Dipartimento di Scienze della Terra, Università degli Studi di Torino, Torino, Italy.

UCBL: Centre des Sciences de la Terre, Université Claude Bernard Lyon I, Villeurbanne, France.

UCD: Department of Geology, University of California, Davis.

UCMP: Museum of Paleontology, University of California, Berkeley.

UF: Florida Museum of Natural History, University of Florida, Gainesville.

USFC: United States Fish Commission.

USGS: Register of Cenozoic localities of the U.S. Geological Survey.

USGS(MP): Branch of Paleontology and Stratigraphy, U.S. Geological Survey, Menlo Park, California.

USNM: Department of Invertebrate Zoology (Mollusks), National Museum of Natural History, Smithsonian Institution, Washington, D.C.

USNM(P): Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

YPM: Peabody Museum, Yale University, New Haven,

Connecticut.

ZMC: Zoological Museum, University of Copenhagen, Copenhagen.

SYSTEMATICS

Family Pectinidae Wilkes, 1810 [emend. Waller, 1978]

Diagnosis.— Pectinacea having a ctenolium at least in early ontogeny.

Discussion.— Authorship of the family name is usually attributed to Rafinesque (1815). The earlier use of the name by Wilkes (1810, as "Pectinoidae") was brought to my attention by Eugene Coan (pers. comm., 1991).

The arrangement of the enormous number of living and fossil taxa of Pectinidae into a coherent phylogenetic arrangement above the species level is still far from

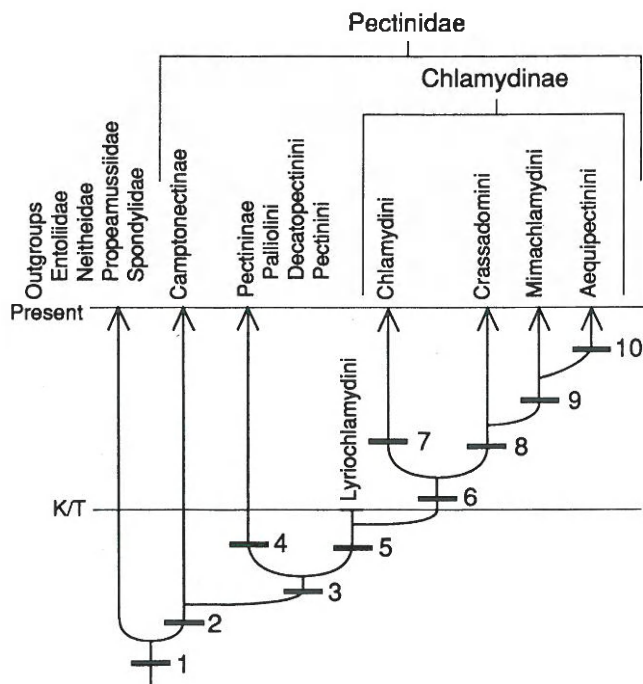


Fig. 1. A phylogeny of major groups of Pectinidae. Lineages ending in arrows are extant; the one ending at a cross-bar is extinct. K/T refers to the Cretaceous-Tertiary boundary. Numbered blocks refer to apomorphies: (1) resilium with non-fibrous core; (2) ctenolium; (3) radial plicae and straightened anterodorsal margin; (4) modified hinge teeth with dorsal and/or intermediate teeth dominant; (5) two-element hinge dentition with resilial teeth emphasized; (6) withdrawal of crossed-lamellar aragonite to inside pallial line; (7) shagreen microsculpture; (8) modified antimarginal striae in early ontogeny; (9) pitted left beak, simple ribs, and internal rib carinae; (10) resilial teeth extended and tending to parallel hinge (see text for further explanation).

being completed. Waller (1991, fig. 8) presented an hypothesis of the relationships of major groups and discussed what little can presently be said about the synapomorphies present at each node in a phylogenetic diagram. The phylogenetic events with which the present study is concerned are at finer levels (Fig. 1). In this figure, pairs of clades that comprise sister groups are shown by a U-shaped branching pattern; paraclades, which cannot yet be characterized on the basis of unique apomorphies, are shown as continuations of stem lineages. The tribe Chlamydini, for example, is a clade that is the sister group of a clade consisting of the tribes Crassadomini (new tribe), Mimachlamydini (new tribe), and Aequipectinini. The tribes Crassadomini and Mimachlamydini are each paraclades in the light of present knowledge. The tribe Crassadomini is the continuation of the stem group for the tribes Mimachlamydini and Aequipectinini; the tribe Mimachlamydini is a continuation of the stem group for the tribe Aequipectinini, the latter being a true clade in that its members share unique derived features.

The family Pectinidae (Node 2 in Fig. 1) is rooted in a single but universal apomorphy, a ctenolium along the ventral edge of the byssal notch of the right valve (Waller, 1984). The subfamily Camptonectinae is viewed as the paraphyletic stem group from which all other Pectinidae were derived and is at present characterized by plesiomorphic features. Specifically, the subfamily is sculpturally simple, without strong radial ribbing, microsculpture dominated by a simple pattern of broadly sweeping antimarginal striae ("*Camptonectes striae*"), and an anterodorsal disk margin that is concave in lateral view. (See Waller (1991) for a more detailed discussion.)

The subfamilies Chlamydiae and Pectininae are joined at Node 3 (Fig. 1) by the advent of coarse ribbing and the straightening of the anterodorsal disk margin. As discussed by Waller (1991), these subfamilies (each referred to in that paper as a series of groups) were already in place well before the end of the Mesozoic era, where they are respectively exemplified by the genera *Lyrioclamys* Sobetski, 1977, and *Microclamys* Sobetski, 1977. Although the subfamily names Chlamydiae and Pectininae used in the present study are based on the generic names *Chlamys* and *Pecten*, each associated with a well-known shell shape, these shapes are in no way characteristic of an entire subfamily. The chlamydoid form is probably plesiomorphic, but the pectinoid form (as in *Pecten*, *sensu stricto*) and other forms such as those associated with the genera *Amusium* and *Aequipecten* have evolved repeatedly and independently in both subfamilies. At present these subfamilies are based mainly on extensive linkages between extinct lineages (Waller, unpub. data) and are difficult to define or diagnose on the basis of universal synapo-

morphies. In general, however, there is an approximate difference in the style of hinge development, with the Chlamydiae (Node 5) emphasizing resillial teeth and the Pectininae (Node 4) emphasizing dorsal and intermediate teeth (Waller, 1991, fig. 6). Also in an approximate way, the Chlamydiae display greater microsculptural complexity than do the Pectininae.

Enumeration of apomorphies within the Chlamydiae (i.e. above Node 5, Fig. 1) becomes more straightforward and is taken up in the following discussion of tribes present in the Caribbean and adjacent regions.

Subfamily Chlamydiae von Tepper, 1922

Discussion.— Based on comparison with taxa in Mesozoic outgroups such as the Camptonectinae and *Lyrioclamys* in the Chlamydiae, it seems likely that primitive characters in the Chlamydiae include commarginal lirae in interspaces, a small posterior auricle with a concave posterior margin, and microsculpture consisting of antimarginal striae arrayed in a broad sweeping "*Camptonectes*" pattern that is continuous across radial ribbing. This pattern of antimarginal striae begins early in ontogeny at the edge of the prodissoconch on the left valve and at the edge of the prismatic stage on the right valve. The primitive radial ribbing pattern is complex in the sense that rib introduction by both branching and intercalation is present in the same individual and commonly on the same valve. The ribs themselves, however, are simple corrugations, without carinate edges on the shell interior (Waller, 1991, fig. 5).

An important change occurred in shell microstructure between Cretaceous *Lyrioclamys* and the modern Chlamydiae beginning in the late Cretaceous and early Paleocene (Waller, 1991; Waller and Marinovich, 1992; Fig. 1, Node 6). This involved the withdrawal of the area of deposition of crossed lamellar aragonite on the shell interior to a position bounded distally approximately by the pallial line, in contrast to Cretaceous and earlier *Lyrioclamys*, in which aragonite deposition extended nearly to the shell margins and comprised most or all of the hinge structures.

The subfamily Chlamydiae can be subdivided into four extant tribes related as shown in figure 1. The apomorphies for each branching point are as follows:

Node 7 (Chlamydini). The character that forms the basis for the tribe Chlamydini is shagreen microsculpture, a screenlike pattern formed by the offset contacts of frilled commarginal lamellae (Fig. 2; see also Waller, 1972, 1991, and Hayami and Okamoto, 1986). Although this structure is not universally present in all extant members of this tribe, the succession of morphologies among extant and fossil species suggests that it was present initially in the basal lineages contained in the clade. In contrast, no

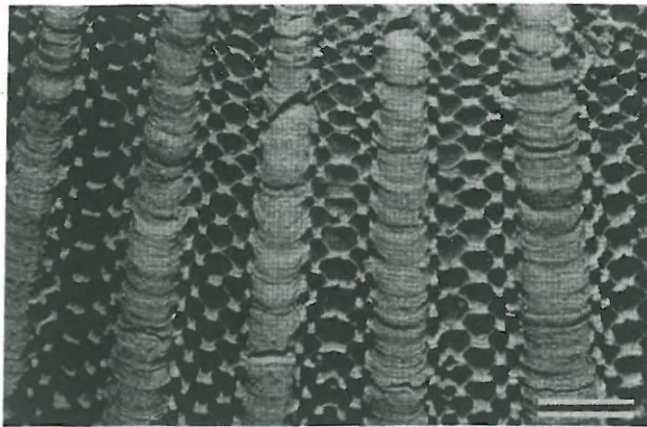


Fig. 2. Shagreen microsculpture in center of left valve of *Chlamys islandica*, USNM 764635, Recent, off Godhavn, Greenland (ht. of valve = 20 mm, scale bar = 1.0 mm).

unequivocal shagreen microsculpture is known among extant or fossil members of the tribes Crassadomini (new tribe), Mimachlamymini (new tribe), and Aequipectinini, which collectively comprise the sister group of the Chlamymini. Where commarginal lirae are present in the Chlamymini, they begin after the start of radial ribbing. This allows the plesiomorphic sweeping pattern of antimarginal striae to be prominent in very early ontogeny, before the beginning of the radial stage on the left valve and continuing at least through the early part of that stage. The more derived lineages in the Chlamymini, which will be discussed in greater detail below (under *Laevichlamys*, new genus), lose both commarginal lirae and shagreen microsculpture altogether and develop numerous intercalated costae in the interspaces of major ribs, tending to fill the interspaces completely (Fig. 4). As will be shown below, true *Hinnites* and the genus *Pedum* Lamarck, 1799, are both within this tribe. The subfamily names Hinnitinae Habe, 1977, and Peduminae Habe, 1977 (*sic*, emended to Pedinae) are therefore reduced in rank and made junior synonyms of Chlamymini.

Node 8 (Crassadomini + Mimachlamymini + Aequipectinini). The only synapomorphy that unites these groups is the loss of the plesiomorphic sweeping pattern of antimarginal striae in the early radial stage. Instead, commarginal lirae tend to dominate microsculpture at least between the proximal ends of the simple radial ribs (Figs. 5, 7). The microsculpture of the left-valve pre-radial region in the Crassadomini is variable, ranging from interrupted antimarginal striae (Fig. 7g) to a pitted or nearly smooth condition (Fig. 5d). There is a trend toward simplification of ribbing patterns. Medial intercalations, present on both valves in many Chlamymini and in Mesozoic *Lyrio-chlamys*, become rare on right valves except for a few examples of

secondary origin of precisely medial intercalary costae (e.g. in *Spathochlamys*, new genus, described below).

The plesiomorphic state of ribbing cross-sections at Node 8 (Fig. 1) remains as simple corrugations, without internal carinae on mature shells. The hinge also remains in its plesiomorphic state as in the Chlamymini, consisting of a simple two-element structure, with the dorsal teeth and resilial teeth being of about equal strength in most taxa.

Node 9 (Mimachlamymini + Aequipectinini). Three apomorphies unite the tribes Mimachlamymini and Aequipectinini: (1) Left-valve beaks display a densely pitted microsculpture (Waller, 1991, figs. 4b, 9c,d), although as previously stated this feature was already making its appearance in some Crassadomini; (2) the ribbing pattern becomes further simplified, with the ribs that are introduced in early ontogeny commonly being the only ribs or at least remaining as the major ribs throughout ontogeny (Figs. 10, 11); (3) the edges of the ribs on inner surface of the shell become carinate (Figs. 10h, m). These carinae are variably expressed in populations of extant *Mimachlamys varia* but consistently developed in many other extant and extinct members of this clade. The hinge of the Mimachlamymini retains its basic plesiomorphic two-element structure, as in the Chlamymini and Crassadomini, although some extinct *Mimachlamys* show some thickening and incipient bifidity of the resilial teeth of the right valve. Shell shape remains *Chlamys*-like in the Mimachlamymini, as does the shape of

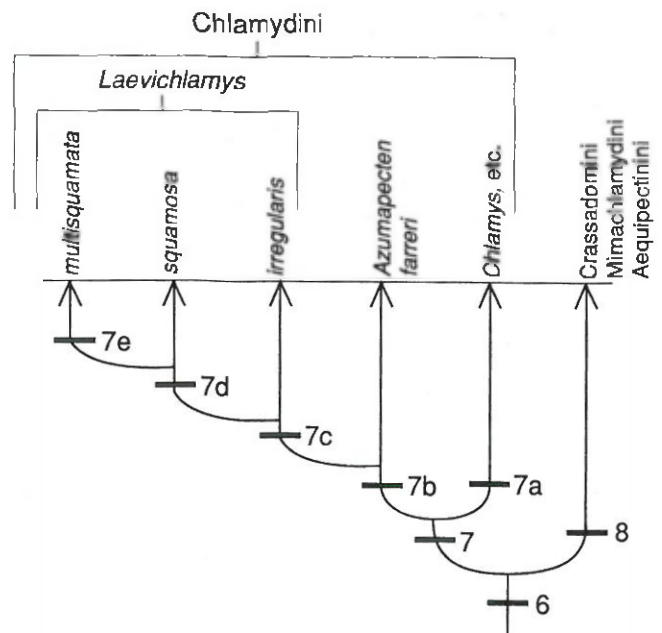


Fig. 3. A phylogeny showing derivation of the new genus *Laevichlamys* within the tribe Chlamymini (numbered blocks refer to apomorphies; those numbered 6, 7, and 8 are as shown in figure 1; see text for explanation).

the posterior auricle, which generally retains a concave posterior margin.

At Node 10 (Fig. 1), the tribe Aequipectinini is marked by the onset of a hinge structure dominated by resilial teeth, which enlarge and extend anteriorly and posteriorly, nearly paralleling the dorsal teeth (Waller, 1991, pl. 5, fig. 14). There are attendant changes in valve symmetry, shape becoming more equilateral and the anterior and posterior auricles more equal in size. Lastly, there is a sculptural change in the early commarginal lirae, which display a ventrally concave looped trend on the rib flanks, at least in the early ontogeny of many taxa.

This basic framework of four extant tribes in the Chlamydiae was already in place by the Eocene epoch, 36 million years ago (Waller, 1991). The main evolutionary radiation of these tribes, however, did not become extensive until the beginning of the Miocene, when the proto-Mediterranean was still open at its eastern end to the Indian Ocean and the Caribbean was still open to the eastern Pacific. The search for ancestors of extant Caribbean species in these tribes therefore should not be limited to the western Atlantic and eastern Pacific.

Tribe Chlamydiae von Teppner, 1922

Diagnosis.— Chlamydiae retaining in early ontogeny a microsculptural pattern of continuous antimarginal striae that sweep across early radial ribbing; shagreen microsculpture present at least in early lineages.

Discussion.— Six extant species in the Caribbean and adjacent western Atlantic waters have traditionally been placed in the genus *Chlamys*, *sensu stricto*, because of their asymmetric auricles (the anterior one the longer) and deep byssal notch floored by an ontogenetically persistent ctenolium: *Chlamys benedicti* Verrill and Bush, 1897, *C. imbricata* (Gmelin, 1791), *C. mildredae* (Bayer, 1941), *C. multisquamata* (Dunker, 1886), *C. ornata* (Lamarck, 1819), and *C. sentis* (Reeve, 1853). In the present study, these species are found to represent three tribes in the Chlamydiae (Table 1), and none can be assigned to *Chlamys* unless that name is used so broadly as to encompass almost the entire subfamily.

The sole extant member of the tribe Chlamydiae in the tropical and subtropical western Atlantic is "*Chlamys*" *multisquamata*. This species, with its flattened form, flaring disk, and fine sculpture (Figs. 4a-i, l, m), stands apart from the other Caribbean species and is strikingly similar to "*Chlamys*" *squamata* (Gmelin, 1791) of the western Indo-Pacific (Figs. 4j, k, n). The resemblance extends beyond

the flattened streamlined form of these species. There are also strong similarities in ribbing pattern, early microsculpture, color pattern, and the strong dorsal projection of the dorsal margin of the right anterior auricle. Resemblance even extends to the common presence of a tiny dense pattern of curved intersecting white pigment lines that appears on the beaks before the end of the prismatic stage of the right valve. This same pigmentation pattern occurs in several Indo-West Pacific chlamydoid species but is especially common in "*Chlamys*" *squamata* and its close relatives. To appreciate whether these similarities are shared derived characters, and, if so, how a western Atlantic species can be related to a western Indo-Pacific species with no apparent intermediate geographic links in either the eastern Pacific or the eastern Atlantic, requires an overview of the tribe Chlamydiae as here defined.

Figure 3 diagrams a phylogenetic pathway through an array of species in the tribe Chlamydiae that show important differences in microsculpture and ribbing patterns. It is important at this point to review the plesiomorphic conditions that were present (Node 6) before the origin of the Chlamydiae, because these conditions help to polarize the derived states that provide crucial phylogenetic information. The plesiomorphic character states at Node 6 are as follows:

- 1) Shell shape acline or prosocline, not markedly opisthocline or opisthogyrate, with a deep byssal notch.
- 2) Dorsal auricular margins not sharply folded and not projecting dorsally very far beyond the outer ligaments.
- 3) Ontogenetic transgression of an inner layer of foliated calcite ventrally from the dorsal region across the umbonal region absent; aragonite (most commonly crossed-lamellar except in muscle attachment scars) present throughout the region inside the pallial line.
- 4) Posterior auricles small but with their posterior margins concave in shape, with the overall trend of the margin forming nearly a right angle with the hinge line.
- 5) Antimarginal striae in a broad sweeping pattern with trends not significantly interrupted by radial ribbing, at least in the early ontogeny of the radial stage.
- 6) Left-valve beak sculpture exhibiting the same antimarginal pattern as in the early radial stage; beak secondarily smooth in some taxa, but seldom coarsely pitted.
- 7) Commarginal lirae present in interspaces during at least part of ontogeny.
- 8) Several modes of rib introduction present on same shell, including branching, rib-flank intercalation, sub-medial intercalation, and medial intercalation on a single valve.
- 9) Ribs in the form of simple radial folds, without

thickening of edges on the shell interior, i.e., without internal rib carinae.

The base of the Chlamydini (Node 7, Figs. 1, 3) is marked by the advent of shagreen microsculpture (Fig. 2). The primitive expression of this is probably as small patches in rib interspaces on the disk and auricles. Extensive shagreen over virtually the entire shell seems to be a derived condition that has been reached independently in different species lineages, most notably in the *Semipallium* group (see Waller, 1991, fig. 10).

The lineage marked "*Chlamys*, etc." on Figure 3, Node 7a, marks a polytomous assemblage of groups some of which appeared early in the radiation of the tribe. Among these are genera such as *Chlamys*, *Zygochlamys*, *Talochlamys*, *Semipallium*, and even the *Patinopecten* group, each characterized by a set of autapomorphies. *Chlamys*, *sensu stricto*, contains species exemplified by (1) the type species of the genus, *Chlamys islandica* (Müller, 1776), living in the northeastern and northwestern Atlantic, (2) a group of closely related northern Pacific species including *C. albida* (Arnold, 1906, [ex Dall MS]), *C. behringiana* (Middendorf, 1849), *C. rubida* (Hinds, 1845), and *C. hastata* (Sowerby, 1842), and (3) the eastern Atlantic cemented species "*Hinnites*" *ercolanianus* (Cocconi, 1873). These taxa are all united by a byssal notch that is shallower than the plesiomorphic state, by a foliated-calcite transgression, and by an early irregularity in the antimarginal microsculpture before the advent of the first shagreen microsculpture. The expression of shagreen microsculpture is highly variable among and within species of *Chlamys*, *s.s.*, and even within population samples. In the eastern Pacific, for example, there is some evidence of a southward disappearance of shagreen microsculpture in the sequence *C. albida*, *C. hastata hastata*, *C. hastata hericea*, a sequence that also displays increasingly derived macrosculptural patterns.

Chlamys, as here restricted, appears to have originated in the Pacific and entered the eastern Pacific and northern Atlantic via northern routes (Waller, 1991). *Chlamys islandica* itself penetrated as far south as the Mediterranean during cold pulses of the Pleistocene (Roger, 1939: p. 170). "*Hinnites*" *ercolanianus* (Cocconi, 1873), of which *Hinnites absconditus* P. Fischer in Locard, 1883, is a junior synonym (Adam, 1960), presently lives in the eastern South Atlantic off the Cape Verde Islands and along the Atlantic coast of Africa from the Gulf of Guinea (4° 44'N) to northern Angola (8° 30'S) at depths in the 100 to 200 m range (Adam, 1960; Waller, unpub. data). The living members of this species, however, are but a relict of a much more widespread occurrence in the Pliocene of the Mediterranean (Raffi, 1971) and the Miocene of Belgium (Glibert, 1945, referring to the Anversian or Serravalian

stages). The ancestor of this species, which is considered to be "*H.*" *brussoni* (de Serres, 1829) from the Burdigalian of southern France (Roger, 1939: p. 175), has shagreen microsculpture.

In spite of the long history of *Chlamys*, *s. s.*, no member of this genus is known to be living in the present-day tropical American regions that are the subject of the present study. As will be shown below, taxa from these regions that have been referred to *Chlamys* in fact belong to other genera with very different histories.

Three derived features are important at Node 7b (Fig. 3): (1) the advent of a somewhat opisthocline and opisthogyrate shell form; (2) a straightening (loss of concavity) of the posterior margins of the posterior auricles, these margins becoming straight or even convex; and (3) an increase in the frequency of rib introduction by intercalation. Shagreen microsculpture is retained at this node, as is also the plesiomorphic absence of a foliated calcite transgression on the shell interior. This stage of phylogenetic development is characterized by the genus *Azumapecten* Habe, 1977, of which *A. farreri* (Jones and Preston, 1904) is the type species. The shell shape and deep byssal notch suggest that this level represents an increased adaptation to byssate life, a conclusion that is corroborated by increasingly common shell irregularity in response to growth in confined spaces. Geographically, this stage of development among extant species seems to be limited to the western Indo-Pacific.

At Node 7c (Fig. 3), the following derived features appear: (1) increase in rib introduction by intercalation to the point that rib interspaces are eliminated in late ontogeny; (2) the ontogenetically late appearance of the first radial ribs, allowing a zone of prominent coarse antimarginal striae to develop in the pre-radial stage of the left valve; (3) disappearance of shagreen microsculpture from at least the center of the disk and usually from the entire shell; (4) trend of posterior margins of posterior auricles forming an oblique angle with the hinge line, the margins themselves being most commonly nearly straight or only slightly concave or convex. Also at this stage is a common presence of a minute net of white pigment lines in very early ontogeny, still within the prismatic stage of the right valve. This stage and the following one characterized by rib crowding and the ontogenetic disappearance of interspaces encompass species placed in *Laevichlamys*, new genus. The stage at Node 7c is best represented by species such as *L. irregularis* (G.B. Sowerby II, 1842) and *L. wilhelminae* (Bavay, 1904) (see illustrations in Waller, 1972b, where these species were referred to as *Chlamys irregularis* and *C. marshallensis* Waller, 1972, the latter name being a junior synonym of Bavay's name).

Node 7d (Fig. 3) is marked by (1) decreased shell

convexity, (2) dorsal projection of the dorsal margins of the right-valve auricles, particularly that of the right anterior auricle, and (3) marked obliquity and common convexity of the posterior auricular margins. This stage is exemplified by *Laevichlamys squamosa* (Figs. 4j, k, n).

Finally, Node 7e is marked by the advent of sharp recurvature of the right anterior auricle's dorsal margin and a recurvature of the dorsal margin of the right posterior auricle to produce a slight trough along this margin (Fig. 4c, arrow). The convex curvature of the posterior margin of the posterior auricles and the trend of this margin to produce a very oblique angle with the hinge (Fig. 4g) are both more extreme than in *L. squamosa* (Fig. 4k). These features represent the most derived states of characters already present at Node 7b, and this stage is represented by a single extant species, *L. multisquamata* of the western Atlantic.

The morphological trends from *Azumapecten* to advanced *Laevichlamys* are not exclusively exemplified by these genera, because there are other generic names that have been introduced on the basis of "degree of difference" considerations. The monotypic Indo-west Pacific genus *Pedum* Lamarck, 1799, for example, exhibits a bizarre shell form because it lives embedded and entrapped in massive hard corals such as *Porites* (Yonge, 1967; Waller, 1972; Kleemann, 1990). The early growth stage of this taxon, however, has closely packed intercalated ribs, a projecting right anterior dorsal margin, and oblique posterior auricles that suggest derivation from above Node 7d (Fig. 3), probably from *Laevichlamys squamosa* or a similar species. *Coralichlamys* Iredale, 1939, a less bizarre, irregularly shaped, secondarily commarginally lamellate genus that lives embedded in coral in the Indo-Pacific, may also be monotypic. Its morphology suggests derivation from above Node 7b (Fig. 3). The Indo-Pacific genus *Scaeoichlamys* Iredale, 1929, represented by two extant species, *S. livida* (Lamarck, 1819) and *S. tegula* (Wood, 1828), is characterized by a strongly opisthogyrate form, flattened right valve, and hypertrophied scales on major ribs. Its auricular shapes and presence of shagreen both indicate that it is above Node 7b.

Based on the geographic distribution of living and fossil species, the early evolutionary radiation of the Chlamydini above Node 7b (Fig. 3) was apparently mainly within the tropical to warm-temperate western Pacific and Indian oceans, because no primitive *Laevichlamys* are known from the eastern Pacific, the western Atlantic, or the eastern Atlantic. This Indo-Pacific evolutionary radiation of *Laevichlamys* seems to have been well underway by the Late Miocene, but the extent of the radiation by that time is difficult to judge because of the very meager Miocene fossil record on low, reef-dominated tropical Indo-Pacific islands. If the radiation of advanced *Laevichlamys* (Nodes

7c and 7d, Fig. 3) occurred no earlier than Late Miocene, then its dispersal from the Indian Ocean to the Caribbean by way of the proto-Mediterranean would not have been possible, because the eastern portals of the Mediterranean were effectively closed by the end of the early Miocene (late Burdigalian; Adams *et al.*, 1983, 1990; Piccoli *et al.*, 1986; Por, 1989). Alternatively, entry into the Atlantic may have been by way of chance dispersal from the Indian Ocean around the southern tip of Africa. In either case, one would expect some evidence of the presence of advanced *Laevichlamys*, either living or fossil, in the eastern Atlantic.

The search for evidence of dispersal of *Laevichlamys* between the Indian Ocean and the Atlantic has led to one of the most surprising findings of the present study. A probable descendant from *Laevichlamys* turns out to be an extant cemented species of the eastern Atlantic, *Hinnites corallinus* (G.B. Sowerby I, 1827), which in turn may prove to be the same as the presumably extinct type species of the genus *Hinnites*, *H. crispus* (Brocchi, 1814), known mainly from the Mediterranean Pliocene. The evidence that has led to this interpretation is as follows:

1) Specimens reported by Kensley (1985) from Namibia were determined by me (pers. comm. to Kensley, 1985) to represent two species of "*Hinnites*". One of these, found in Cape Province, South Africa, is the familiar "*Hinnites*" *ercolanianus* (Cocconi, 1873), previously known from the Angolan coast (see Adam, 1960). As mentioned above, "*H.*" *ercolanianus* is derived from a shagreen-bearing ancestor and is probably referable to *Chlamys*, *sensu stricto*. In the same personal communication quoted by Kensley, I suggested that the second species from Namibia is possibly new. It was distinguished from the former on the basis of the macro- and microsculpture of the early *Chlamys* stage. As shown in Figures 4o to 4r, this Namibian *Hinnites* has a pattern of rib introduction like that present in *Laevichlamys*, where rib interspaces are filled by the repeated medial intercalation of new radial costae. Furthermore, a close relationship to *L. squamosa* is indicated by auricular shapes, the dorsal margin of the right anterior auricle extending prominently above the hinge line and the posterior margin of the posterior auricle exhibiting a convex outline tending to form an oblique angle with the hinge. Lastly, some specimens of the Namibian species show the minute net of white pigment lines that is common in species above Node 7b in Figure 3. Although Kensley (1985) thought that the specimens of this Namibian species were fossil, the immature shells show little sign of wear and have adhering ligamental material.

2) Cosel and Gofas (1984), in a paper that I received after the aforementioned identification for Kensley (1985) was completed, described a new cemented pectinid species, *Hinnites spectabilis* Cosel and Gofas, 1984, which

they reported as living along the southern part of the coast of Angola. Their description and illustrations leave no doubt that this is the same as the Namibian species.

3) Cosel (pers. comm., August, 1992) examined the type specimen of *Hinnites corallinus* G.B. Sowerby I, 1827, originally said to come from East Africa, and determined that it is the same as the species that he and Gofas (1984) had described as new. The East African locality is apparently in error.

4) The macro- and microsculpture of the *Chlamys* stage of *Hinnites corallinus* is remarkably similar to that of the type species of *Hinnites*. The latter is *H. crispus* (Brocchi, 1814), a fossil originally described from the Pliocene of Italy. The fossil species tends to be larger in size and thicker shelled than the living one, but there are broad similarities in form as well as in sculptural detail (see Roger, 1939). It is possible that these differences are ecophenotypic and that these species may be synonymous, in which case the living east African specimens are but a relic of a previously more broadly distributed species.

5) If it is true that *Hinnites crispus* is derived from an ancestral species in the new genus *Laevichlamys*, then the fossil record of *H. crispus* tends to support the idea that *Laevichlamys* did not enter the Atlantic by westward dispersal across the proto-Mediterranean. This is because the oldest specimens of *H. crispus* are known not from the Mediterranean but from the Atlantic side of France (Helvetian of the Aquitaine Basin and Loire Valley; Roger, 1939). Although the species has been reported from the late Miocene (Tortonian) of Austria, Hungary, and Bulgaria (Cuenca, 1980: 62; Raffi: 1971:124), it did not become widely distributed in the Mediterranean until the Pliocene, at which time it also extended as far as the British Isles (Roger, 1939: 174). Roger (1939: 174) thought that the species persisted into the late Pleistocene (Sicilian) in the western Mediterranean based on specimens from the Alpes-Maritimes region of France. Unfortunately, there is no Miocene or Pliocene fossil record of *H. crispus* (or *H. corallinus*) in southern Africa, nor is there any fossil record of a preceding free-living *Laevichlamys* in the eastern Atlantic.

6) The fossil record of the Caribbean species, *Laevichlamys multisquamata*, discussed below, is no older than Pleistocene.

A reasonable interpretation of this evidence is that a species of advanced *Laevichlamys* had entered the eastern Atlantic from the Indian Ocean by late Miocene time via a route around southern Africa. A derivative of this species adopted a cemented mode of life, evolved into true *Hinnites*, dispersed into the Mediterranean through its western portal after the end of the Miocene, and nearly became extinct during the late Pliocene and early Pleistocene cli-

matic cooling that profoundly affected the early Pliocene fauna of the Mediterranean (Raffi *et al.*, 1985). If the extant *Hinnites corallinus* is indeed synonymous with *H. crispus*, then the species survives today in refugia along the west African coast. It seems likely that another propagule of *Laevichlamys* dispersed to the tropical Western Atlantic and evolved, during the Pleistocene, into *Laevichlamys multisquamata*. This species has no geminate sister species in the eastern Pacific because it originated in the tropical western Atlantic region after the closure of connecting seaways.

Laevichlamys, new genus

Etymology.— The name *Laevichlamys* is derived from the Latin word *levis* (or *laevis*), meaning smooth, with reference to macrosculpture of low relief, and the genus name *Chlamys*.

Diagnosis.— Non-cemented Chlamydini with shagreen microsculpture secondarily absent at least on central sector of disk and commonly on entire shell; radial ribs initially low, tending to originate in ontogeny well after end of prismatic stage, and preceded by zone of uninterrupted anti-marginal striae; rib introduction mainly by repeated intercalation medially in interspaces of preceding ribs on both valves, nearly or entirely filling interspaces between ribs; regular commarginal lirae absent.

Type species.— *Pecten multisquamatus* Dunker, 1864, living, tropical western Atlantic.

Other species.— In addition to the type species, extant species included in the new genus are as follows: *Pecten irregularis* G.B. Sowerby II, 1842; *P. lemniscatus* Reeve, 1853; *P. limatulus* Reeve, 1853; *P. mollitus* Reeve, 1853; *P. ruschenbergeri* Tryon, 1869; *Ostrea squamosa* Gmelin, 1791; and *Chlamys wilhelminae* Bavay, 1904. All of these live in the Indo-Pacific region.

There is still much to learn about the fossil record of this genus, but two extinct species are included thus far: *Pecten (Chlamys) lauensis* Ladd in Ladd and Hoffmeister, 1945, Fiji, late Miocene or Pliocene; *P. shirahamaensis* Nomura and Niino, 1932, Japan, Early Pliocene (Masuda, 1962, p. 185).

Geographic range.— Western Indo-Pacific and western Atlantic.

Stratigraphic range.— Upper Miocene to present.

Discussion.— As argued in the preceding section dealing

with the tribe Chlamydini, the new genus *Laevichlamys* probably has a tropical Indo-Pacific origin, and morphologically advanced species entered the eastern Atlantic in the late Miocene probably via a southern African route of dispersal. The former presence of the genus in the Mediterranean and eastern Atlantic is indicated by the presence in these areas of *Hinnites*, which likely evolved from a species of *Laevichlamys*.

Laevichlamys is paraphyletic in that specialized, derived genera such as *Hinnites* DeFrance, 1821, and *Pedum* Lamarck, 1799, are excluded (see preceding discussion of the tribe Chlamydini). The alternative to achieve a holophyletic status would be to broaden the concept of the genus to include all of these, but the name based on priority would then become *Pedum*, a taxon well-known for its highly unusual form and specialized living habit embedded in massive corals. This would clearly raise havoc with the morphological concepts that have long been attached to particular names.

***Laevichlamys multisquamata* (Dunker, 1864)**
(Figures 4a-i, l, m)

Pecten multisquamatus Dunker, 1864: 100, Recent, Havana Bay, Cuba.

Pecten multisquamatus Dunker, 1864. Dunker, 1865: 67, pl. 23, figs. 1-3.

Pecten effluens Dall, 1886: 219, Recent, off Havana, 127 fathoms [232 m].

Chlamys effluens (Dall, 1886). Verrill, 1897: 59.

Chlamys multisquamata (Dunker, 1864). Waller, 1973: 41, figs. 9-11.

Types.— The specimen illustrated by Dunker (1865), a pair of matching valves, is of the same dimensions given in his original description in 1864 and would be the logical choice for a lectotype. It is not known, however, whether this specimen still exists. I did not find it among Dunker's material in the collections of the Humboldt University Museum of Berlin, raising the possibility that it may still be in Cuba, perhaps in the collection of J. Gundlach, from whom Dunker received his specimens. According to Dr. José Espinosa of the Instituto de Oceanología of Cuba (pers. comm., 1993), however, no specimens of *Pecten multisquamatus* are present in that collection. A second, smaller pair of matching valves from Cuba that bears one of Dunker's manuscript names is housed with some of Dunker's collection in the Humboldt University Museum in Berlin. This specimen, a pair of matching valves collected by Felipe Poey from Cuba, is selected herein as the lectotype of *P. multisquamatus*. Its dimensions are height, 43.1 mm, length 39.5 mm, convexity of articulated valves 8.0

mm, length of anterior outer ligament 10.8 mm, and length of posterior outer ligament 5.0 mm.

Dall (1886) provided no illustration with his original description of *Pecten effluens* but referred to the largest valve as having a height of 26.0 mm and a width of 22.0 mm. In the type collection of the National Museum of Natural History, the lot marked "types" (USNM 62236) contains a left valve and a smaller, non-matching right valve. The left valve, although conforming to Dall's description, is only half the size that he stated. Three years later Dall (1889, pl. 42, fig. 9) illustrated a *Pecten effluens* which he said had a height of 26 mm. This specimen, a left valve, corresponds exactly in shape and ribbing pattern to the left valve in USNM 62236 that is only half the size. It is assumed that Dall misstated the measurements from an enlarged drawing provided by an artist, and the left valve (ht. = 13.2 mm) in USNM 62236 is herein selected as the lectotype of *P. effluens* (Fig. 4h).

Type locality.— Havana Bay, Cuba.

Diagnosis.— *Laevichlamys* of low convexity and streamlined, flaring form, the umbonal angle exceeding 90° for specimens greater than 20 mm in height; dorsal margin of right anterior auricle sharply folded and dorsal margin of right posterior auricle with slight trough; posterior margins of posterior auricles convex, producing distinctly oblique angle with hinge; ribbing retaining low relief throughout ontogeny, with all ribs and riblets having low, tiny, closely spaced scales.

Morphological variation.— *Laevichlamys multisquamata* attains a moderate size, the largest specimens having a shell height of about 70 mm. The amplitude of the first-order radial plicae can vary considerably (compare Figs. 4b and 4f). The surfaces of some specimens are nearly flat, with only the fine costae present or with the first-order radial plicae limited to early ontogeny. The yellowish tinge on the umbones illustrated by Dunker (1865) and referred to by Dall (1886) is common but not present on all specimens.

Comparison.— The morphology of *Laevichlamys multisquamata* is unique among chlamydoid scallops in the western Atlantic and eastern Pacific. The early, *Chlamys* stage of *Hinnites corallinus* of the eastern Atlantic off west Africa (see preceding discussion of the tribe Chlamydini) is similar but differs in having more prominent and persistent first-order radial plicae and in having less numerous secondary intercalated radials. Among Indo-Pacific *Laevichlamys*, the species that is closest in morphology is *L. squamosa* (Waller, 1972, pl. 3, figs. 38-41, and Figs. 4j, k, n herein). The latter differs from *L. multisquamata* in

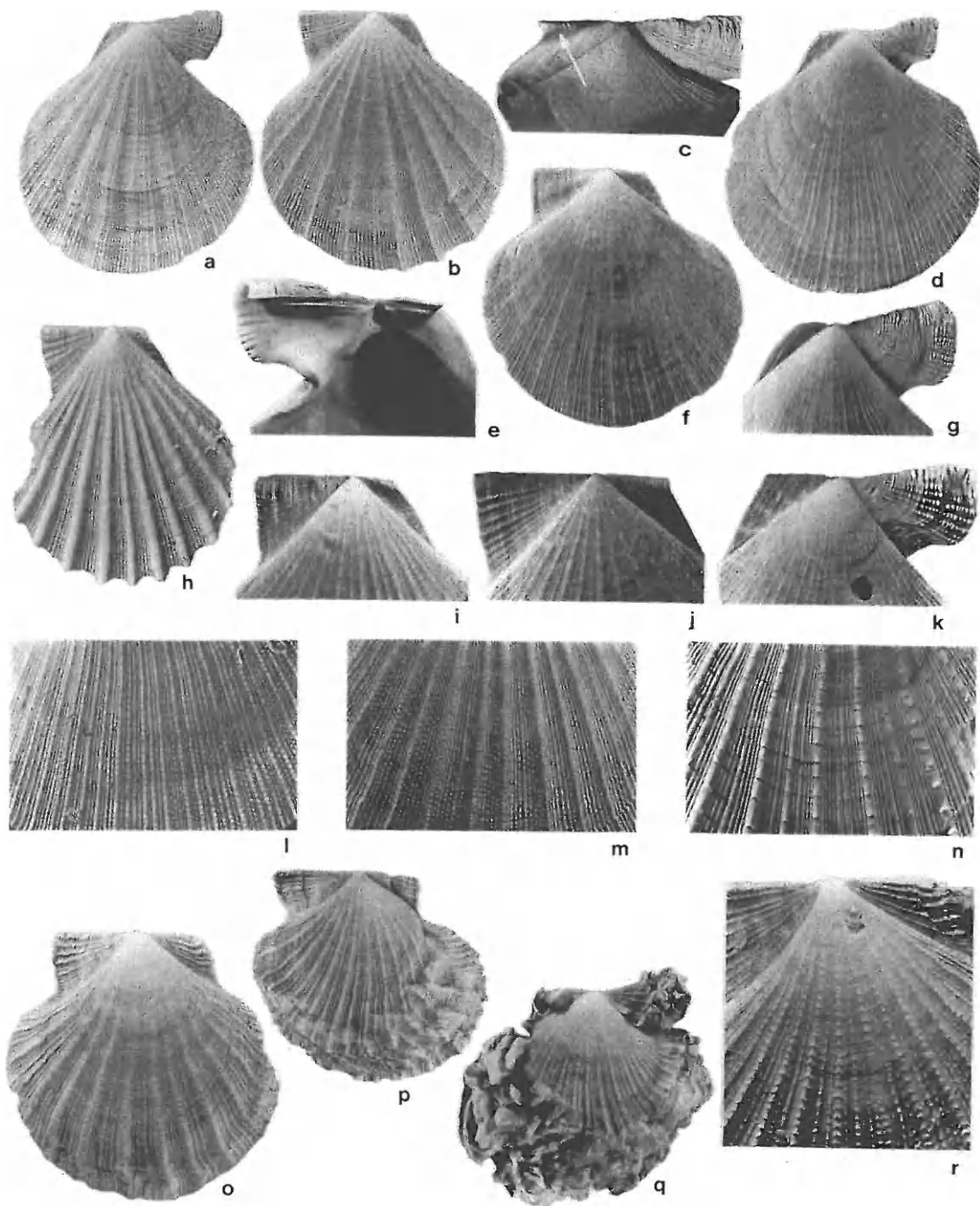


Fig. 4. *Laevichlamys* (a-m) and *Hinnites* (n-q). **a, b.** *L. multisquamata*, USNM 764750, Guadeloupe, West Indies, matching right and left valves, height 26.1 mm. **c, e.** *L. multisquamata*, USNM 846201, off Boynton Beach, Florida, dorsolateral view of right dorsal margin showing trough (arrow) on posterior auricle and interior view of right hinge, hinge length 7.2 mm. **d, f.** *L. multisquamata*, USNM 710926, south coast at St. Luce, Martinique, West Indies, matching right and left valves, height 47.9 mm. **g, i, l.** *L. multisquamata*, USNM 764749, La Chorrera, Havana, Cuba, right dorsal exterior, hinge length 23.2 mm., non-matching left dorsal exterior, hinge length 14.2 mm., and details of sculpture on same right and left valves, horizontal field widths both 26 mm. **h.** *L. multisquamata*, USNM 62236, probably Dall's illustrated specimen of *Pecten effluens*, off Havana, Cuba, left valve, height 13.3 mm. **j, k, n.** *L. squamosa*, USNM 846209, Manana Id., Fiji, dorsal exteriors of matching left and right valves, hinge length 20.3 mm., and detail of sculpture on left valve, horizontal field width 25 mm. **o-r.** *H. corallinus*, USNM 782400, Bosluisbaai, Namibia, left valve exterior, height 24.4 mm; another left valve, height 38.0 mm; right valve matching preceding; and detail of exterior of preceding left valve, horizontal field width 12.5 mm.

having a narrower umbonal angle (less than 90°) and hence a less flaring aspect, a tendency for scales to be present only on the higher order radial ribs, and in having a less sharply refolded dorsal margin on the right anterior auricle.

Living habits.— *Laevichlamys multisquamata* lives on tropical or subtropical coral reef fronts, between coral or dead shells or in crevices, at depths generally greater than 30 m to well over 100 m; dead shells have been dredged from depths greater than 200 m (Waller, 1973: 47; Abbott, 1974: 443; Suty, 1986: 102).

Geographic range.— Throughout the Antilles from Barbados northward to southeastern Florida, the Bahamas, and Bermuda (Waller, 1973: 47) and southward to Brazil. The Brazilian record, not previously reported, is based on a right valve found by me in the Paris Museum Collection, where it had been incorrectly identified as *Chlamys ornata*. It is from Calypso Station 45, 11° 22.5'S, 37° 10' W, from a depth of 31 m. A second specimen from Brazil, but without locality details, is present in the BMNH collection. A label indicates that it had been identified by Bavay as "*squamosus* var." In the southern Caribbean, the species extends westward to Panamá (based on a living specimen dredged by the R/V Pilsbry of the University of Miami at a depth of 51 m at 9° 24.8'N, 78° 12.7'W (R/V *John Elliott Pillsbury* Sta. P-417). The species is thus far known from the Gulf of Mexico only from the deep Flower Garden Reef off the Texas coast (Boone, 1978).

Stratigraphic range.— Lower Pleistocene to Recent.

Laevichlamys multisquamata has not previously been reported from the fossil record. In the present study, specimens of this species were found in unidentified collections from the Pleistocene reef deposits of Barbados (BMNH), from undated beds in northern Cuba that are probably no older than Pleistocene in age (PRI), and from the Moín Formation of Costa Rica (USNM). Also, D. G. Robinson (pers. comm., August, 1992) reported finding this species in the topmost beds of the Moín Formation of Costa Rica between plates of the coral, *Agaricia* Lamarck, 1801. The Moín Formation, considered in the past to be early to middle Pleistocene in age (Akers, 1972: 44; Robinson, 1990, 1992), has more recently been considered to include upper Pliocene sediments, although the uppermost part of the formation is still dated as early Pleistocene (Coates *et al.* 1992).

Discussion.— As outlined in the previous discussion of evolution within the tribe Chlamydini, it seems very likely that the ancestor of *Laevichlamys multisquamata* was a species present in the eastern Atlantic during the Late

Miocene and Pliocene. Although *L. multisquamata* at present has a broad distribution in the Caribbean region and has been collected from the Caribbean coast of Panamá, no geminate or sister species are known from the eastern Pacific. This would suggest that the origin or at least the dispersal of the species to the western Atlantic has occurred since the closure of seaways by the rise of the Isthmus of Panamá, i.e. since the middle Pliocene. This is corroborated by the negative evidence of the fossil record; thus far no fossils of this species or probable ancestors have been found in rocks that are known to be older than Pleistocene.

Material examined.— Recent material: USNM: 16 lots containing 33 specimens, from southeastern Florida, Bermuda, Cuba, Puerto Rico, the Bahamas, Jamaica, Martinique, Barbados, and Panamá. DMNH: 2 lots containing 2 specimens, from the Bahamas and Jamaica. BMNH: 2 lots containing 2 specimens, from Guadeloupe and Brazil. MNHN: 2 lots containing 6 specimens, from Guadeloupe and Brazil. HUB: 1 lot containing 1 specimen, from Cuba.

Fossil material: BMNH: several specimens, Pleistocene Coral Rock at Bathsheba and Highgate, Barbados. PRI 1257k: a single articulated shell from the D.K. Palmer Collection, Locality 898P: Road cut on Carretera Central, just west of Nena Machado Hospital ["= Bermúdez 5"], Matanzas Province, Cuba. [Locality published in Palmer, 1948.] USNM: USNM(P) 474809, a fragmented left valve, USGS 18693, "colline en démolition," Limón, Costa Rica.

Tribe Crassadomini Waller, new tribe

Diagnosis.— Chlamydinae with shell shape and two-element hinge of *Chlamys*, but without continuous antimarginal striae before beginning of radial ribs; prominent commarginal lirae present in rib interspaces in early ontogeny of left valve or both valves. Left beak microsculpture with discontinuous antimarginal striae, pitted, or secondarily smooth. Rib introductions occurring over much of ontogeny, leading to variously clustered and ordered ribbing patterns; internal rib carinae absent in mature shells, rarely present but weakly developed in juvenile shells.

Discussion.— The pre-radial stage of the left valve in the Crassadomini lacks the plesiomorphic continuously striate condition found in the Chlamydini. In the Crassadomini, commarginal lirae are more prominent than antimarginal striae at the start of the radial stage (Figs. 5, 6), whereas in the Chlamydini, antimarginal striae are more prominent than the commarginals at the same growth stage. No shagreen microsculpture has been detected in any member of the Crassadomini, whereas this feature is present in at least

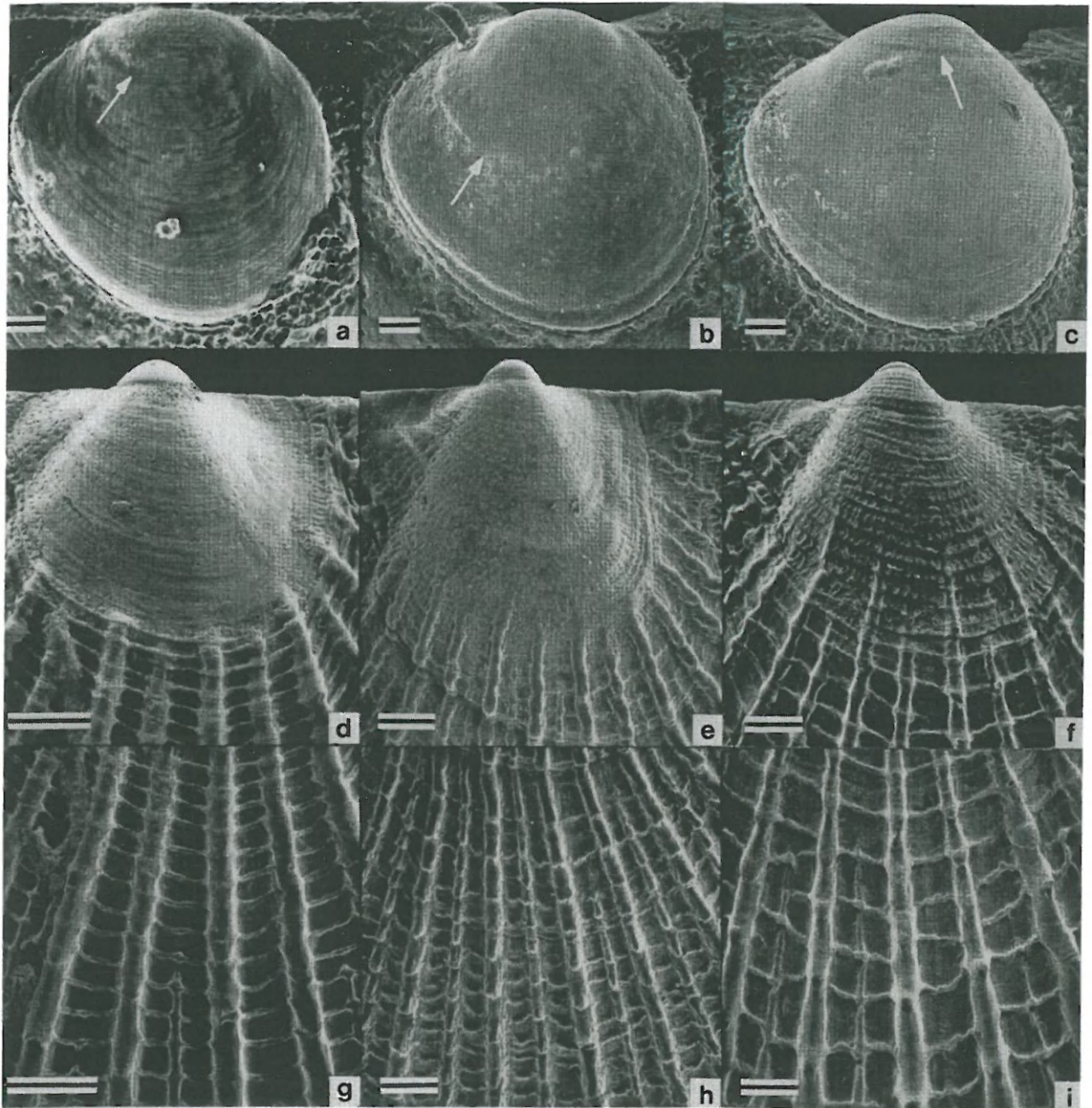


Fig. 5. Scanning electron micrographs of prodissoconchs (a-c), pre-radial stage microsculpture (d-f), and early radial stage sculpture (g-i) of left valves of species of *Crassodoma*. **a, d, g.** *C. multistriata*, USNM 764329, San Pedro Bay, Sao Vicente, Cape Verde Ids. **b, e, h.** *C. pusio*, USNM 196540, Shetland Ids., Scotland. **c, f, i.** USNM 764941, off Long Point, Santa Catalina Id., California. Arrows point to approximate position of PI/P11 boundary. Projecting object on anterodorsal side of b is not part of prodissoconch. Scale bars: a-c = 25 μ m, d-i = 200 μ m.

the early lineages in the Chlamydingi.

The style of rib introduction in the Crassadomini is plesiomorphic, with introduction on the right valve being primarily by branching and that on the left valve by intercalation (Figs. 5, 6). This differs from the *Azumapekten-Laevichlamys* clade in the Chlamydingi, where intercalation is important on the right valve as well as on the left (Fig. 4). Both the Mimachlamydingi and Aequipectinini have simple

ribbing patterns in which the primary ribs remain dominant over secondary ribs throughout ontogeny; the edges of these primary ribs have prominent carinae on the inner shell surface (Waller, 1991, fig. 5b; Figs. 10h, m, herein). In contrast, rib introductions in the Crassadomini are spread unevenly during ontogeny to produce variously ordered or clustered rib patterns; these ribs in adults lack internal carinae. Both the Mimachlamydingi and Aequipectinini have a

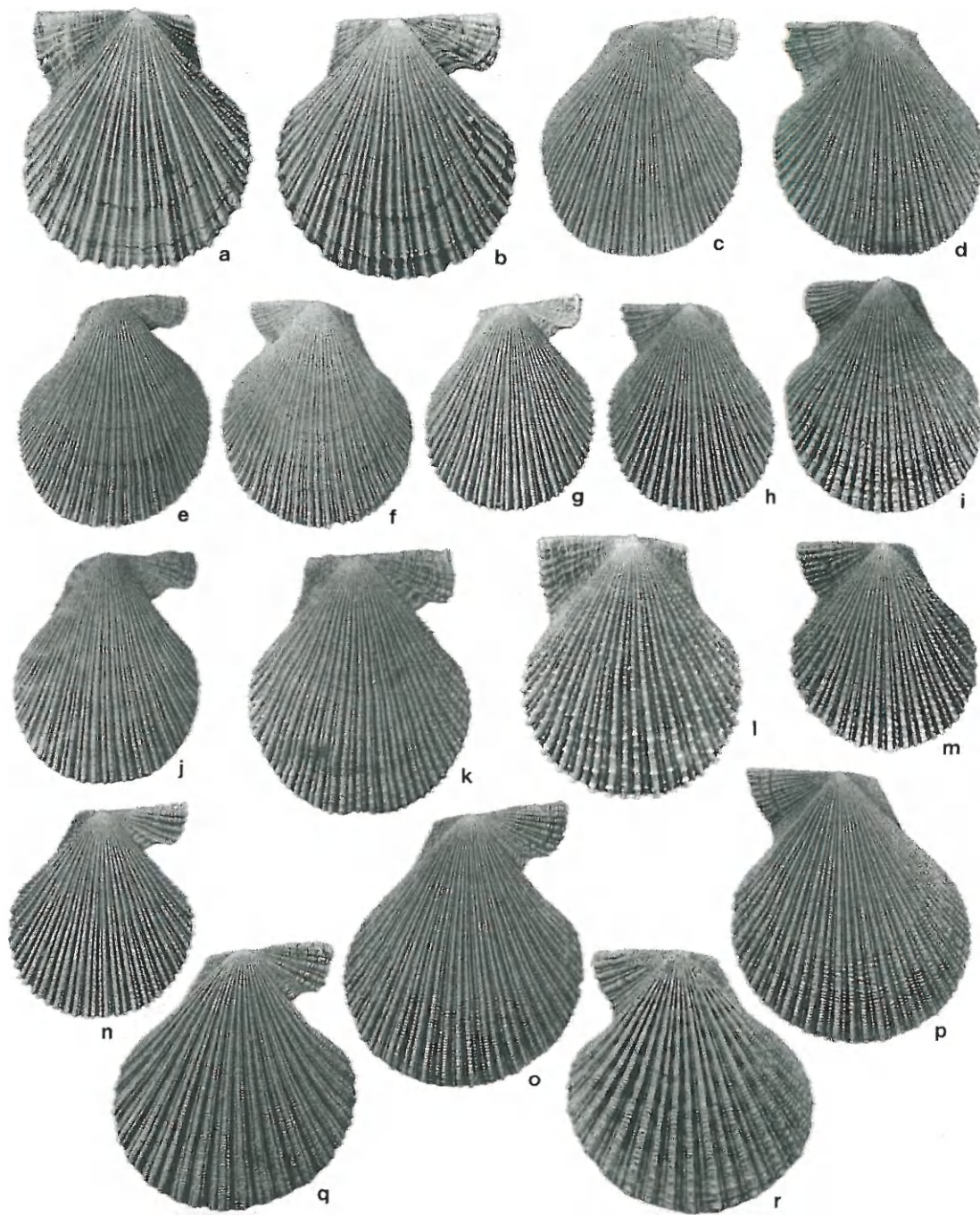


Fig. 6. *Crassadoma* (a-l) and *Caribachlamys* (n-r). a, b. *Crassadoma gigantea*, USNM 764946, channel reef, Egmont, British Columbia, Canada, matching left and right valves before cementation, height 16.0 mm. c, d. *C. multistriata*, USNM 196495, Naples, Italy, matching right and left valves, height 30.0 mm. e, f. Lectotype of *Pecten unctus* Reeve (= *C. multistriata*), BMNH 1981247/1, locality unknown, matching right and left valves, height 32.5 mm. g, h. Lectotype of *P. effulgens* Reeve (= *C. multistriata*), BMNH 1993039/1, locality unknown, matching right and left valves, height 18.8 mm. i. Lectotype of *P. textilis* Reeve (= *C. multistriata*), BMNH 1993040/1, locality unknown, single left valve, height 24.9 mm. j. paralectotype of *P. textilis* Reeve (= *C. multistriata*), BMNH 1993040/2, locality unknown, single right valve, height 24.4 mm. k, l. *C. pusio*, USNM 196511, Langland Bay, Wales, matching right and left valves before cementation, height 13.7 mm. m, n. *Caribachlamys sentis*, BMNH 1993041/1, lectotype, locality unknown, matching left and right valves, height 15.9 mm. o, p. *C. sentis*, USNM 599341, Venetian Causeway, Miami, Florida, matching right and left valves, height 32.9 mm. q, r. *C. ornata*, USNM 764717, Plantation Key, Florida, matching right and left valves, height 32.5 mm.

more distinctly pitted microsculpture on the left beak in the pre-radial stage compared to the pattern in the *Crassadomini*, where there is a complex interplay of discontinuous antimarginal striae, pits, and commarginal lines (Figs. 5, 6).

The new tribe *Crassadomini* contains only two genera: *Crassadoma* Bernard, 1986, and *Caribachlamys*, new genus.

Crassadoma Bernard, 1986

Original diagnosis.— "Juvenile a typical *Chlamys*, equivale, biconvex. Right valve ornamented with bifurcating weakly imbricated riblets. Anterior auricle long, with imbricated radial sculpture. Byssal notch deep, ctenolium with six teeth. Posterior auricle small, wide. Left valve with 10 to 15 spinose ribs, separated by three small weakly imbricate riblets. Free or byssiferous. Adult cemented to substrate by right valve. Shell ponderously thickened, irregular, auricles and byssal notch obsolete. Right valve idiomorphic flat or deeply cupped, ornamented with concentric lamellae or with radial rows of imbricated scales. Left valve flattened, with radial rows of imbricated ribs. Hinge line distorted, displaced resulting in large cardinal area." (Bernard, 1986: 72).

Emended diagnosis.— Byssate or cemented *Crassadomini* with normal prodissoconch (small PI stage and large PII); antimarginal striae absent or weakly developed between commarginal lirae in rib interspaces in early ontogeny; medial intercalation of secondary riblets in rib interspaces recurrent throughout ontogeny of left valve.

Type species.— *Lima gigantea* Gray, 1825, by original designation (Bernard, 1986).

Other species.— *Ostrea pusio* Linnaeus, 1758, extant, eastern Atlantic; *O. multistriata* Poli, 1795, extant, eastern Atlantic; *Chlamys harmeri* Regteren Altena, 1937, Pliocene, Europe.

Geographic range.— Eastern Pacific and eastern Atlantic.

Stratigraphic range.— Early? Miocene, Middle Miocene to present. (See following section on the type species, *Crassadoma gigantea*.)

Discussion.— Bernard (1986) included only one species in his new genus, the extant "*Hinnites*" *giganteus* of the eastern Pacific, and asserted that shell attachment to the substrate in this species evolved independently of the same habit among other extant cementing species (see above dis-

ussion of tribe *Chlamydini*). He also contended that *Crassadoma* is an obligatory cementer, whereas *Hinnites* is only a facultative one, its right valve merely appressed against the substrate, not cemented. Unfortunately, Bernard (1986: 71) misstated the type species of *Hinnites* to be *Hinnites distortus* (DaCosta, 1778) (= *H. pusio*) and gave no information on *H. crispus*, the correct type species. Bernard's (1986) diagnosis of *Crassadoma*, quoted above, is merely a description of the type species and does not serve to differentiate this from other genera that may or may not assume a cemented life habit. Harper (1991: 193) found that although some specimens of "*Hinnites*" *pusio* may be uncemented and merely wedged into the substrate by their irregular growth, the cemented forms are cemented in the same manner as *Crassadoma* and other "*Hinnites*".

In the present study, the concept of *Crassadoma* is expanded to encompass both non-cemented and cemented *Crassadomini* that have a plesiomorphic normal prodissoconch (small PI and large PII stage, Fig. 5). This prodissoconch morphology distinguishes *Crassadoma* from the tribal new genus *Caribachlamys*, all species of which share a derived state of the prodissoconch (large PI and small PII stage, Fig. 7). The two genera also differ in the development of antimarginal striae between the commarginals. In *Crassadoma* these striae are obscure or absent (Fig. 5); in *Caribachlamys* they are strong (Figs. 7i, j) and in the more derived species cause the commarginal lirae to assume irregular trends (Fig. 7l). Cemented species of *Crassadoma* are well separated on the basis of the macro- and microsculpture of the *Chlamys* stage from other "*Hinnites*", most of which fall within the tribe *Chlamydini* (see preceding discussion of the tribe *Chlamydini*).

Evidence from the fossil record suggests that cementation in the *Crassadomini* has evolved independently and at different times in *Crassadoma gigantea* of the eastern Pacific and in *C. pusio* of the eastern Atlantic (see following sections on species). Like all cemented *Chlamydinae*, these species display changes in morphology resulting from cementation and growth in a confined space, including ventral migration of the ligament system and increased distance between the pallial line and the shell margin (Yonge, 1951; Waller, 1972, 1991; Harper, 1991). Like many species adapted to cooler waters, whether cemented or not, these cemented species have a prominent transgression of foliated calcite ventrally across the originally aragonitic region of the umbonal interior. These are features that occur in each independent origin of "*Hinnites*", including the two examples of cemented species in the *Chlamydini* described above. A foliated-calcite transgression has also evolved in many species in other clades both within and outside of the subfamily *Chlamydinae* (Waller, 1991; Waller and Marincovich, 1992).

Crassadoma gigantea (Gray, 1825)

(Figs. 5c, f, i, 6a, b)

Lima gigantea Gray, 1825: 139. No locality specified.*Hinnita giganteus* Gray, 1826: 103.*Pecten* (*Chlamys*) *multirugosus* Gale, 1928: 92. New name for *Hinnita gigantea* Gray.

Refer to Grau (1959: 134) and to Roth and Coan (1978) for details of synonymy and nomenclature.

Types.— The holotype of *Lima gigantea* Gray, 1825, which Grau (1959: 136) said is in the British Museum (Natural History), was not examined.**Type locality.**— "Juan de Fuca Strait (between Vancouver Island, British Columbia, Canada, and the state of Washington, U.S.A.)" (Grau, 1959: 136).**Diagnosis.**— Cemented *Crassadoma*; left valve with scaly radial ribs of at least three orders, with total number of ribs of all orders exceeding 100 at distal margin in mid-ontogeny; rib number commonly decreasing in late ontogeny due to disappearance of lower order riblets; first and second order ribs of left valve remaining distinctly higher in relief than intervening lower order riblets in mid-ontogeny; right valve with fasciculated radial ribs in early ontogeny and at least two orders of ribs in mid-ontogeny; interior of shell vivid purple in color on auricles and hinge plate, foliated calcite transgression extensive, completely covering area inside of pallial line except for muscle scars.**Morphological variation.**— During the *Chlamys* stage of ontogeny of "*Hinnites*", before cementation to the substratum by the right valve, shell attachment is by means of a byssus, with the right valve having a deep byssal notch, well-developed ctenolium (Waller, 1984), and uniform shell curvature. At the end of this stage the mantle of the right valve loses its structural integrity and begins to conform to the substratum surface. Regular sculpture disappears where cementation occurs, but sculptural patterns return whenever the mantle lifts away from the substratum. In *Crassadoma gigantea*, the shell height of the *Chlamys* stage (Figs. 6a, b) varies from about 15 to 30 mm even within population samples (e.g. USNM 764937, Newport Beach, California). Although no geographic trends in maximum size were noted among specimens examined, Hertlein (1972: 212) indicated that size increases northward. The largest specimen that I observed is from Alaska (USNM 678351, Prince of Wales Island, ht. = 24 cm), but Hertlein (1972, p. 212) mentions a "huge specimen" of 23 cm shell height from Santa Cruz Island, California. Shell thickness and the degree of ventral migration of the ligament system are both

strongly correlated with size. Extreme ventrad ligament migration produces large ligament areas and a resilium that is much higher than long.

Comparison.— *Crassadoma gigantea* differs from its cemented congener of the eastern Atlantic, *C. pusio* (see below), in being of much greater maximum size and in having more prominently fasciculated ribs on its right valve and more distinctly ordered ribs on its left (compare Figs. 6a, b with Figs. 6k, l). The vivid purple color present on the hinge plate of *C. gigantea*, particularly on the left valve, is absent or faint in *C. pusio*. Although it is generally assumed that *C. gigantea* is thicker shelled than is *C. pusio*, it is doubtful that there is any significant difference when size is taken into account. Both *C. gigantea* and *C. pusio* have extensive development of foliated calcite inside the pallial line, and in both species the crossed lamellar aragonite that is present in this region in early ontogeny is covered over by foliated calcite earlier on the left valve interior than on the right, a common phenomenon among pectinids. *C. gigantea* is more derived than *C. pusio* in the sense that the foliated calcite transgression begins earlier in ontogeny, appearing on the umbonal interior of right valves as small as 11 mm in shell height and on left valves as small as 7 mm. In *C. pusio* it has been observed in right valves no smaller than 17 mm and on left valves no smaller than 13 mm. In *C. multistriata* the plesiomorphic condition persists; there is no foliated calcite transgression over the umbonal interiors at any stage of ontogeny.Adegoké (1969: 103) described a new species of "*Hinnites*", *Hinnites benedicti* Adegoké, 1969, from the Late Miocene Santa Margarita Formation of California. Although this species was found in the same beds as *H. multirugosus crassiplicatus* (Gale, 1928) [= *Crassadoma gigantea*], Adegoké regarded it as distinct because of its larger *Chlamys* stage and more even ribbing. My own examination of Adegoké's types at UCMP confirmed this distinctness but did not confirm that "*Hinnites*" *benedicti* has a cementing habit. The maximum size of the *Chlamys* stage (34 mm) given by Adegoké is exceeded by the height of the holotype (46.8 mm) and two of the paratypes, none of which show any evidence of cementation. The holotype, a right valve, would be expected to show an abrupt sculptural change and xenomorphic growth if cemented. Instead, the degree of shell irregularity is comparable to that of extant *Laevichlamys irregularis* of the Indo-Pacific, a species with a byssate, nestling living habit. The style of ribbing of *H. benedicti* and the apparent lack of commarginal lirae suggest that it is not a *Crassadoma*, but its generic assignment awaits examination of better preserved material. Most likely it is a *Chlamys*, s.s. on the basis of its style of ribbing introduction.

Living habits.— From just below low tide level to 80m (Hertlein, 1972: 212; Grau, 1959: 137; Bernard, 1983: 25); attached to rocks, coarse gravel, and other hard objects. Specimens in northern waters tend to live closer to shore and at shallower depths than those in southern waters (Hertlein, 1972: 212).

Geographic range.— Aleutian Islands, Alaska, to Bahía Magdalena, Baja California, Mexico; offshore in Santa Barbara Islands, California, Guadalupe Island, Mexico (Grau, 1959: 137), and Islas de Revillagigedo, Mexico (reported herein, CAS 60266).

Stratigraphic range.— Early Miocene?, Middle Miocene to present.

The presence of *Crassadoma gigantea* in the Middle Miocene through Pleistocene of California is apparently well established (Moore, 1984: 66). Lower Miocene records, however, are few in number and could require reexamination. The only Lower Miocene record listed by Moore (1984: 66) is from the Painted Rock Member of the Vaqueros Formation. Arnold (1906: 94) also listed a single occurrence, "associated with *Turritella hoffmanni*" in rocks that he referred to as Lower Miocene. Smith (1991a: 35), in reviewing the changing concepts of the age of the "Vaqueros Stage", pointed out that some records in faunal lists need redetermination and further collecting to determine stratigraphic position. The earliest reliable records in California appear to be from the "Margaritan Stage", which Smith (1991a, figs. 12, 14) shows as ranging from planktic foraminiferal zone N12 into lower N16 (Langhian into lower Tortonian stages of Europe) and as correlating with the Shoal River and Yellow River Formations of Florida.

Discussion.— Previous workers (e.g. Grant and Gale, 1931: 161; Waller, 1991: 23) have assumed that *Crassadoma gigantea* evolved from a member of the *Chlamys* group, e.g. *Chlamys hastata*, within the eastern Pacific. For reasons given above, however, this is unlikely. *C. hastata* and its congeners in the eastern and northern Pacific have features that place them squarely within the tribe Chlamydini as herein defined, whereas *C. gigantea* has a microsculptural pattern shared with the other species placed here in the tribe Crassadomini. Specifically, in the early ontogeny of *C. gigantea* the plesiomorphic pattern of continuous sweeping antimarginal striae is absent and commarginal lirae are prominent in rib interspaces (Fig. 5f).

Crassadoma gigantea has a ribbing pattern that is more derived in comparison to the patterns of its eastern Atlantic congeners, and its large size and purple hinge also are derived in comparison to the eastern Atlantic species and to outgroup Chlamydinae. Given the absence of

Crassadoma in the Indo-west Pacific, it is highly likely that *C. gigantea* evolved from species that were present in the Atlantic. There remains the problem, however, of where the fossils are which should corroborate this ancestry. If it is true that *C. gigantea* was already present in the eastern Pacific by the middle Miocene, it is likely that an ancestor was present in the western Atlantic and that it dispersed through seaways to the Pacific at this time or earlier. If the ancestral species was eurytopic with a preference for warm temperate but not strictly tropical temperatures, it is possible that it avoided the shallow water habitats that predominate in the early Miocene stratigraphic sections thus far known in the Caribbean. The absence of these fossils thus could be the result of a facies sampling bias in the region in which they are most likely to be found. The most likely interval of the middle Miocene for speciation to have occurred may have been during the time of initial emergence of the Isthmus of Panamá. This uplift cut off the flow of intermediate water between the Atlantic and Pacific and intensified the southward flow of the cool California Current along the Mexican coast, creating a thermal barrier to the west-to-east dispersal of shallow water taxa (Duque-Caro, 1990).

Material examined.— Recent material: USNM: 90 lots containing about 150 specimens, from Baja California, Mexico, to Alaska.

Fossil material: USNM: about a dozen lots containing fewer than 20 specimens, Miocene (Santa Margarita Formation) to Pleistocene, from Baja California, Mexico, and California.

Crassadoma multistriata (Poli, 1795)

(Figs. 5a,d,g; 6c-j)

Ostrea multistriata Poli, 1795: 164, pl. 28, fig. 14, living, Sicily.

Pecten tinctus Reeve, 1853, species 106, pl. 26, fig. 106, living, locality unknown.

Pecten effulgens Reeve, 1853, species 156, pl. 33, fig. 156, living, locality unknown.

Pecten textilis Reeve, 1853, species 174, pl. 35, fig. 174, living, locality unknown.

Pecten multistriatus (Poli), Bucquoy *et al.*, 1887: 104. Gives extensive synonymy.

Chlamys multistriata (Poli), Roger, 1939: 165. Gives extensive synonymy.

Types.— Poli's (1795) work on the living bivalves of Sicily was based largely on his own extensive shell collection (Dance, 1966: 95; Kohn, 1988: 39), which apparently has not been preserved. Previous authors who have discussed

the taxonomy of this well-known species in detail, e.g. Bucquoy *et al.* (1887: 104), Sacco (1897: 6), and Roger (1939: 165), have not mentioned type specimens, possibly because Poli provided an illustration the identity of which has never been questioned. Following the International Code of Zoological Nomenclature [Art. 74(b)] and the example of Kohn (1988: 39), the specimen represented by the figure in Poli (1795, Pl. 28, Fig. 14) is herein selected as the lectotype.

The types of the three species of Reeve (1853) listed in the synonymy were examined at The Natural History Museum, London. All are represented by syntype series. In the interest of nomenclatural stability, lectotype designations are as follows:

Pecten tinctus Reeve, syntypes, two complete shells and a single right valve. The specimen of height 32.5 mm, length 27.5 mm, and convexity of the complete shell 13.0 mm, BMNH 1981247/1 is herein selected as the lectotype (Figs. 6e,f), because it is apparently the specimen that Reeve figured. The paralectotypes are BMNH 1981247/2-3.

Pecten effulgens Reeve, syntypes, two complete shells. The darker of the two, BMNH 1993039/1, height 18.8 mm, length 15.0 mm, is represented in Reeve's figure 156 and is herein selected as the lectotype (Figs. 6g,h). This taxon was recently incorrectly placed in the synonymy of *P. cruentatus* Reeve, 1853, by Rombouts (1991: 27). Reeve's *P. cruentatus* is a *Mimachlamys* that is closely related to and possibly a junior synonym of the Indo-Pacific *Mimachlamys senatoria* (Gmelin, 1791).

Pecten textilis Reeve, syntypes, a single right valve (Fig. 6j) and single left valve (Fig. 6i). The left valve, BMNH 1993040/1, height 24.9 mm, length 20.2 mm, is represented in Reeve's fig. 174 and is selected herein as the lectotype.

Type locality.— Sicily.

Diagnosis.— Byssate, non-cemented *Crassadoma* of small size (less than 40 mm in height); ribs introduced continuously throughout ontogeny without distinct clustering or ordering; 70 to 80 continuously scaly ribs and riblets present at distal margin of mature shells; inner surface of shell inside pallial line lacking foliated calcite throughout ontogeny.

Morphological variation.— The only significant geographic variation in *Crassadoma multistriata* occurs along the Atlantic and Indian Ocean coasts of southern Africa, where specimens tend to have narrower umbonal angles (as narrow as 80°) and correspondingly higher height to length ratios (as high as 1.34). Some authors have considered these narrow forms to be a distinct species, *Chlamys tinctoria*

(Reeve, 1853) (Figs. 6e,f). The two forms, however, overlap in shell narrowness and are identical in details of ribbing and microsculpture.

Some authors have thought that *Crassadoma multistriata* becomes cemented in the northern part of its range along the Atlantic coast of France and have therefore treated this species and *C. pusio* as synonyms (see following discussion). On the basis of the evidence on hand, however, I have not been able to substantiate intergradation of these taxa. Bucquoy *et al.* (1887: 104) noted the presence of both regular and distorted forms in single samples from Brest, France, but illustrated a regular specimen that was still within the size range of the pre-cementation stage of *C. pusio*. Shell distortion in the absence of cementation is not a diagnostic feature, because it occurs in many independent lineages of byssate, nestling chlamydoid pectinids. In *C. multistriata*, distortion is common among many specimens in the Atlantic, including specimens at both the northern and southern limits of its geographic range. Pre-cemented *C. pusio*, however, can generally be distinguished from *C. multistriata* in the same size range using criteria summarized below.

Comparison.— *Crassadoma multistriata* (Figs. 6a-j) closely resembles its western Atlantic counterpart, *Caribachlamys sentis* (Figs. 6m-p), in shell shape, color, and the lack of a foliated-calcite transgression on the inner shell surface in the umbonal region. The former, however, has a normal prodissoconch (Fig. 5a), whereas that of the latter has a prodissoconch dominated by the PI stage (Figs. 7a,g). The umbonal region of the disk of *C. multistriata* is more inflated and less flattened than that of *C. sentis*, and the byssal fasciole of *C. multistriata* generally has a deeply incised groove whereas that of *C. sentis* does not.

Crassadoma multistriata differs from *C. pusio* (Figs. 6k,l) in lacking cementation and foliated-calcite umbonal transgressions throughout ontogeny. In *C. pusio* cementation and attendant changes in morphology begin at shell heights between about 12 and 25 mm. The pre-cementation growth stage of *C. pusio* closely resembles shells of *C. multistriata* of similar size. Even at this early stage, however, the two species can be distinguished by two features. First, in *C. multistriata*, there is no transgression of foliated calcite from the hinge region ventralward across the region inside the pallial line at any stage of growth. In *C. pusio*, foliated calcite generally begins to form on the inner shell surface at the dorsal edge of the umbonal region at a shell height of about 17 mm in right valves and about 13 mm in left valves, generally before cementation begins. In mature shells over most of the geographic range of *C. pusio*, this foliated calcite may extend ventrally at least to the level of the top of the adductor scar. Secondly, the beak

of the left valve of *C. multistriata* has only weak microsculpture, particularly near the distal margin of the preradial stage (Fig. 5d); microsculpture at this same stage is stronger in *C. pusio*, consisting of distinct, generally discontinuous antimarginal striae and pits (Fig. 5e).

Crassadoma multistriata also resembles *C. harmeri* (Regteren Altena, 1937) of the Plio-Pleistocene of western Europe and Great Britain. The fossil species differs in reaching a larger size (commonly exceeding a height of 70 mm), in having a minor foliated-calcite transgression on the inner shell surface in the umbonal region of each valve, and in having a distinct anterior-posterior trending ridge on the inner surface of its right anterior auricle.

Living habits.— *Crassadoma multistriata* lives byssally attached to hard objects on the substrate at shallow shelf depths from below low tide level to at least 100 m in normal marine environments. Dead shells, particularly of juveniles, have been dredged from depths as great as 700 m. The species is apparently eurythermal and possibly has been ecologically generalized throughout much of its history. Blondel and Demarcq (1990: 250), in a study of the Early and Middle Miocene (late Burdigalian to early Langhian) fossil record of northern Tunisia, refer to the species as eurytopic.

Geographic range.— *Crassadoma multistriata* has an enormous latitudinal range, occurring from the Brittany coast of France southward into the Mediterranean and thence southward along the African coast to southernmost South Africa (Nicklès, 1955). The species occurs throughout the Mediterranean as well as in the Madeira, Canary, and Cape Verde Islands. It is also present in the central South Atlantic at St. Helena (USNM 124060 and 764331). Along the southern and southeastern coasts of Africa, *C. multistriata* is abundantly represented in USNM collections from False Bay, South Africa, to southern Mozambique (USNM 764201 and 764219) in the Indian Ocean.

Stratigraphic range.— Lower Miocene to present.

Sacco (1897: 9) showed the stratigraphic range of "*Chlamys*" *multistriata* as extending as far down as the Tortonian (Upper Miocene) and that of its lineage antecedent, "*Chlamys*" *tauroperstriata* Sacco, 1897, *sensu stricto*, as extending as far down as the lowermost Miocene (Aquitanian). Cox (1927: 42-43) thought that "*Chlamys*" *pusio* (which he used as a senior synonym of *Chlamys multistriata*) was "well established in Lower Miocene times" and was present in the Miocene of Persia. Roger (1937: 167) noted that "*Chlamys*" *multistriata* is common in the Lower Miocene (Burdigalian) in the Mediterranean region from the Rhône Valley to the Vienna Basin. It is generally

thought that the species has a Mediterranean origin (Lauriat-Rage, 1981: 43). The stratigraphic history of the species in the eastern Atlantic outside of the Mediterranean, however, is not precisely known.

Discussion.— The discrimination and nomenclature of *Ostrea multistriata* Poli, 1795, and *O. pusio* Linnaeus, 1758, have long been contentious issues in pectinid taxonomy. Many authors, e.g. Jeffreys (1863: 52), Bucquoy *et al.* (1887: 107-108), Dautzenberg and Fischer (1925), and Roger (1939: 166), have considered the two species to be intergradational, with cementation absent throughout the ontogeny of Mediterranean specimens but variably present or absent in the later ontogeny of specimens living in the Atlantic. If intergradation in fact exists, then clearly the two names should be synonymized, and one would normally expect the name with priority, *O. pusio*, to apply to both. Many authors (Bucquoy *et al.*, 1887: 104; Sacco, 1897: 7; Roger, 1939: 165), however, have pointed out that the Linnaean name is poorly founded, not only because of the generalized brief description given by Linnaeus, but also because the species is not represented by a clearly isolated specimen in the Linnaean Collection. These authors have therefore discarded the name *O. pusio* and have elected to use Poli's name *multistriata* instead, applying the name *Chlamys multistriata* to both byssate and cemented forms. In so doing, these authors have ignored the priority of *Pecten distortus* Da Costa, 1778, as well as the possible validation of Linnaeus's name by Pennant (1777), who provided an excellent illustration. Da Costa's name has been used extensively by British malacologists for the cementing form, which is the only form known to be present in British waters.

If the only criterion for distinguishing *Crassadoma multistriata* from *C. pusio* is the presence of cementation in the advanced growth stages of the latter, then cementation itself cannot be used to settle the problem of intergradation, because its presence becomes a circular argument for the discrimination of the two species. On the basis of the two characters discussed in the preceding comparison (the extent of the foliated-calcite transgression on the inner shell surface and the degree of coarseness of left beak sculpture), I was unable to find evidence of intergradation in the extensive eastern Atlantic Jeffreys Collection (USNM). The position taken in the present study, therefore, is that the cementing and non-cementing forms of *Crassadoma* in the eastern Atlantic are distinct species which, for reasons of priority, must retain the names *C. pusio* and *C. multistriata*, respectively. The issue of the type specimen of *C. pusio* is treated in the following section.

Material examined.— Recent material: USNM: 73 lots

containing about 300 specimens, mainly Mediterranean (Spain, France, Italy, Yugoslavia, Turkey, Tunisia, Algeria) but also eastern Atlantic off Africa (Cape Verde Islands, Guinea-Bissau, Senegal, Angola, Namibia), Indian Ocean (off southern Mozambique), and central Atlantic (St. Helena). In addition to the type specimens discussed above, numerous non-type lots were examined at museums in Great Britain and Europe, particularly at BMNH, BRM, AM, LM, and ZMC.

Fossil material: Numerous specimens at BMNH, BRM, UCBL, and TUI.

***Crassadoma pusio* (Linnaeus, 1758)**

(Figs. 5b,e,h, 6k,l)

Ostrea pusio Linnaeus, 1758: 698, no. 169, living, in "O. australiore."

Pecten pusio (Linnaeus). Pennant, 1777, pl. 61, fig. 65, living, Great Britain.

Pecten distortus Da Costa, 1778: 148, pl. 10, figs. 3, 6, living, England and Scotland (Orkneys).

Ostrea sinuosa Gmelin, 1791: 3319, living, in British seas.

Pecten spinosus Brown, 1827, pl. 33, fig. 8, living, Northumberland coast, England [name and figure only]; Brown, 1844: 73 [description, with 1827 figure repeated].

Pecten crotilus Reeve, 1853, species 150, pl. 33, fig. 150, living, locality unknown.

Type specimens.—In the Linnaean Collection at the Linnaean Society, London, the pair of matching valves of a distorted and cemented "*Chlamys*" present in the tray bearing Collection Sequence No. 179, with height 37 mm and length 35 mm, is herein designated the lectotype of *Ostrea pusio* Linnaeus, 1758. The background and basis for this designation are given in the following discussion.

The type or types of *Pecten distortus* Da Costa, 1778, have not been examined nor has their depository been determined. Dance (1966: 283) reported that some Da Costa types are in The Natural History Museum, London, and some are in the Glasgow University Museum. Ms. Kathie Way, Collections Manager at BMNH (Invertebrates I), reported that no type material for *P. distortus* has been found there (pers. comm., 1993).

The type series of *Pecten crotilus* Reeve, 1853, BMNH 1993042, consists of four specimens mounted on a board in the Cuming Collection in The Natural History Museum (London). I examined these and determined that they are young *Crassadoma pusio*.

Type locality.— Herein specified as northeastern Atlantic.

Diagnosis.— Cemented *Crassadoma* of moderate size (uncommonly greater than 60 mm in height); ribs introduced continuously throughout ontogeny without distinct clustering or ordering; 60 to 80 ribs and riblets present at distal margin of mature shells; inner surface of valves with small foliated-calcite transgression in umbonal region, seldom extending past level of dorsal edge of adductor in mature shells.

Morphological variation.— The height of right valves at the time of their cementation to the substratum varies from about 12 to 25 mm. There is no evidence in the collections examined for geographic changes in the height at first cementation or in the frequency of cementation within samples. In general, all individuals within populations of *Crassadoma pusio* seem to become cemented after a certain stage of ontogeny is reached. Harper (1991: 192), however, found that some individuals remain uncemented and merely become lodged into the substratum by means of their irregular growth form. The presence of small foliated-calcite transgressions in the umbonal region of both valves is fairly consistent, again without observed geographic trends. Some exceptional specimens (USNM 543396) collected from floating mines and buoys off the Atlantic coast of Morocco, however, lack foliated calcite in the umbonal region even at a shell height of 36 mm, well past the stage of initial cementation. A foliated-calcite transgression is present, however, in a specimen from deeper water off Morocco (USNM 196510, 132-234 m) and in a specimen from 90 m off Ivory Coast (USNM 764327). All of these specimens have coarse microsculpture in the pre-radial stage of the left valve like that of more typical *C. pusio*.

Comparison.— The pre-cemented growth stage of the shell of *Crassadoma pusio* closely resembles the shell of *C. multistriata* of a similar size. Refer to the preceding section on *C. multistriata* for comparative details. *C. pusio* differs from other cementing "*Hinnites*" of the eastern Atlantic in being of smaller maximum size and having less extensive foliated calcite inside the pallial line. Both *Hinnites corallinus* and *Chlamys ercolaniana* (see above) lack the prominent commarginal lirae that are present between ribs in the early ontogeny of *C. pusio*. The early *Chlamys* stage of *H. corallinus* differs from those of the other two cementing species in having ribs that begin late, following an extensive pre-radial area having antimarginal striae in a uniform sweeping pattern. The *Chlamys* stage of *Chlamys ercolaniana* differs from that of *C. pusio* in having a distinctive microsculpture in rib interspaces. This consists of antimarginal striae of highly irregular trends, probably a vestige of the shagreen microsculpture present in the ancestry of this species. Contrary to a statement by Harper (1991: 190), *C.*

pusio lacks shagreen microsculpture. The microsculptural pattern that she interpreted to be shagreen (her fig. 4.4) is a typical plesiomorphic pattern of antimarginal striae.

Living habits.— The early growth stage of *Crassadoma pusio* is byssate on hard objects, particularly rocks or shells, later becoming cemented by the edges of the right valve to the same substratum. Depth records for specimens collected alive range from just below low tide level to about 100 m. Jeffreys (1863: 52) reported that the species lives in depths from 5 to 85 fm (9 to 155 m), with only young specimens found near or in the tidal zone.

Geographic range.— Common throughout the British Isles from the Orkney Islands to Cornwall and extending across the North Atlantic as far westward as southwestern Iceland (Madsen, 1949: 30); present along European coasts from northern Norway (69° 22.5'N, Soot-Ryen, 1951) southward to Spain and Portugal; uncommon on African coast from Morocco to Ivory Coast; present in Azores; apparently rare in the westernmost Mediterranean.

Stratigraphic range.— Pleistocene? to present.

The common tendency for authors to combine cemented and non-cemented *Crassadoma* in a single species referred to as either *Chlamys pusio* or *C. multistriata* makes it difficult to tabulate stratigraphic occurrences from the literature when the presence of cementation is not specified (e.g. Sacco, 1897; Roger, 1939; Eames and Cox, 1956). Roger (1939: 167) noted that fossils with the form of *C. distorta*, presumably meaning cemented forms, are quite rare in the fossil record of the Mediterranean but occur in the Pliocene of France. Apparently the only cemented pectinid in the Pliocene Coralline Crag of Great Britain is the gigantic form that Wood (1861: 19) referred to as *Hinnites cortesyi* De France, 1821. Roger (1939) considered the latter to be a junior synonym of *H. crispus*. Indeed, Wood's superb illustration leaves little doubt that this is a true *Hinnites* and not a *Crassadoma* (see above). Fossils that Wood (1861: 33) determined to be "*Pecten pusio*, Pennant" are also present in the Coralline Crag as well as the younger Red Crag. These shells, as noted by Wood (1861: 34), are not cemented and retain their shell regularity to large size (greater than 50 mm). Specimens of these that I examined can be identified with *Crassadoma harmeri* (Regteren Altena, 1937), which Glibert and Van de Poel (1965: 34) consider to be a subspecies of "*Mimachlamys*" *multistriata* (Poli). If these fossil *Crassadoma* are ancestors of true *C. pusio*, it is possible that the modern cemented form that is so common in British waters originated within the Pleistocene and possibly very late in the Pleistocene. Harper (1991: 197), who studied the phenome-

non of cementation among many bivalve clades, also concluded that cementation in this species has a post-Pliocene origin.

Discussion.— Malacologists have long acknowledged that the original description of *Ostrea pusio* by Linnaeus is too generalized to be useful and that the lot in the Linnaean Collection bearing this name contains shells belonging to more than one species. In the first detailed study of the Linnaean Collection after Linnaeus's death, Hanley (1855) reported that the marked receptacle bearing the name *O. pusio* in the collection "has unfortunately been converted into a general depository for all the loose valves of the smaller *Pectens*..." He acknowledged, however, that the box contained shells belonging to "the *pusio* of the British writers and the *albolineatus* of Sowerby's [1842] Monograph," as well as a "white valve of the young *Islandicus*." He conjured that Linnaeus's ill-fitting description may have been of a composite consisting of the valves of different species. He concluded, however, that the species then known to British writers as "*P. sinuosus* (= *pusio*) ... (of which there are many loose specimens in the cabinet) accords the best with the definition..."

This conclusion did little to resolve the problem of a type for *Ostrea pusio*, and in subsequent years Linnaeus's name, as well as the names *Pecten distortus* Da Costa, 1778, and *O. sinuosa* Gmelin, 1791, have all been used for the cemented pectinid of the northeastern Atlantic. Cox (1927: 43), adamantly defending the use of Linnaeus's name but applying it to both the cemented form of the Atlantic and the byssate form of the Mediterranean, said that he would propose "a definite specimen from the Linnaean Collection and figure it as the lectotype of the species." However, I can find no record that he ever did so. Dodge (1952: 178), in a later study of the Linnaean Collection, added nothing new to the findings of Hanley (1855). He urged retention of Linnaeus's name, however, because of its extensive use, particularly by writers in the last half of the nineteenth century. Glibert and Van de Poel (1965: 33) followed Dodge's advice, but noted further that even if *O. pusio* of Linnaeus be regarded as an unacceptable name, *P. pusio* Pennant, 1777, which applies to the British cemented species, is available and has priority over *O. multistriata* Poli, 1795 (and also over *P. distortus* Da Costa, 1778, and *O. sinuosa* Gmelin, 1791). Wallin (1991: 154), who reported on the contents of the Queen Ulrica Collection (which contains material that may have been examined by Linnaeus prior to the publication of his tenth-edition names in 1758) found specimens of *O. pusio* to be present. My own examination of the Linnaean Collection at the Linnaean Society in London in 1977 found that the tray labeled in Linnaeus's hand as *O. pusio* contains four speci-

mens: a pair of matching valves of cemented *Crassadoma pusio*, height 37 mm, length 35 mm, with approximately 40 radial ribs (secondary ribs not counted); a pair of matching valves of *Mimachlamys albolineata* (G.B. Sowerby II, 1842); a single left valve of *M. albolineata*; and a single juvenile right valve of *Chlamys islandica* (Müller, 1776).

Dance (1967: 8) urged that caution is necessary when designating types from the Linnaean Collection because of the checkered history of the specimens in the collection, which now includes non-Linnaean material. In the case of *Ostrea pusio*, however, it seems likely that specimens of this common species of the northeastern Atlantic were available to Linnaeus, as indicated by their presence in both the Linnaean and Queen Ulrica Collections. In view of the long history of usage of the name, the above designation of a lectotype from the Linnaean Collection seems to be justified.

Material examined.— Recent material: USNM: 55 lots containing about 250 specimens, mainly from Great Britain but including material from Sweden, France, the Azores, Morocco, and the Ivory Coast. In addition, numerous specimens were examined in the collections abroad, mainly at BMNH, BRM, MNHN, AM, LM, and ZMC.

Fossil material: No unequivocal cemented *Crassadoma pusio* were found among material examined at museums abroad, underscoring the apparent late origin of this cemented species. At the time of my European studies, however, the ontogenetic criteria for differentiating *C. pusio* and *C. multistriata* had not yet been discovered.

Caribachlamys Waller, new genus

Etymology.— The name *Caribachlamys* combines a prefix signifying Caribbean with the genus name *Chlamys*.

Diagnosis.— Byssate, non-cemented Crassadomini with lecithotrophic-type prodissoconch (large PI stage, short or absent PII stage); strong antimarginal striae present between commarginal lirae in rib interspaces in early ontogeny.

Type species.— *Pecten sentis* Reeve, 1853.

Other species.— *Pecten ornatus* Lamarck, 1819; *Caribachlamys paucirama* Waller, new sp.; *Pecten (Chlamys) imbricatus mildredae* Bayer, 1941; *Ostrea imbricata* Gmelin, 1791.

Geographic range.— Caribbean Sea and adjacent waters of the warm-temperate to tropical western Atlantic from

North Carolina to Brazil and Bermuda.

Stratigraphic range.— Upper Pliocene to Recent.

Discussion.— The new genus *Caribachlamys* is based on the discovery that four extant species of the Caribbean and adjacent waters share a unique prodissoconch morphology (Figs. 7a-f) and a unique pattern of commarginal and antimarginal microsculpture in rib interspaces (Figs. 7g-l). The phylogenetic relationships of these extant species and one new extinct species are shown in Figure 8. *Caribachlamys ornata* (Node B, Fig. 8) resembles *C. sentis* very closely in ribbing pattern but differs in developing smooth-crested scaleless ribs that are I-beam shaped in cross-section. In the Bahamas the two species nearly intergrade in that specimens identified herein with *C. ornata* develop I-beam shaped ribs only in very early ontogeny and otherwise resemble *C. sentis* (see following section on *C. ornata*). *C. paucirama*, *C. mildredae*, and *C. imbricata* have ribs that have a plesiomorphic rounded cross-sectional shape (not I-beam shaped) like that in the likely stem species, *C. sentis*, meaning that it is unlikely that *C. ornata* can have given rise to any other species in the genus. *C. paucirama*, *C. mildredae*, and *C. imbricata* are united (Node C, Fig. 8) by decrease in prominence of the early commarginal lirae in rib interspaces and by the onset of substantial irregularity in the trends of these lirae. At Node D, *C. paucirama* develops an autapomorphy: rib introductions beyond a shell height of 20 mm are few in number or absent altogether, leading to a pattern of ribs of fairly uniform height and spacing at the distal margin. *Caribachlamys mildredae* and *C. imbricata* (Node E) share fasciculation of ribs, increase in scale spacing on major ribs, a tendency toward cusping of scales, and marked flattening of the left disk. Finally, *C. imbricata* (Node F) has evolved a unique ribbing pattern consisting of 9 or 10 major plicae with a tendency for secondary ribs to be eliminated. The scales on the ribs of this species commonly form closed knobs, the left disk is markedly flattened, and the maximum observed irregularity and inconsistency in direction of the early commarginals is reached.

Caribachlamys sentis (Reeve, 1853)

(Figs. 6m-p, 7a, d, g, j)

Pecten sentis Reeve, 1853, species 129, pl. 29, fig. 129, living, locality unknown.

Chlamys sentis Reeve, Abbott, 1954: 363, pl. 34a.

Types.— Among Reeve's types in The Natural History Museum, London, are two pairs of matching valves in a single box labeled "*sentis* Reeve." Upon examining these specimens, I found that the larger specimen, which is a deep orange in color, corresponds in dimensions to Reeve's

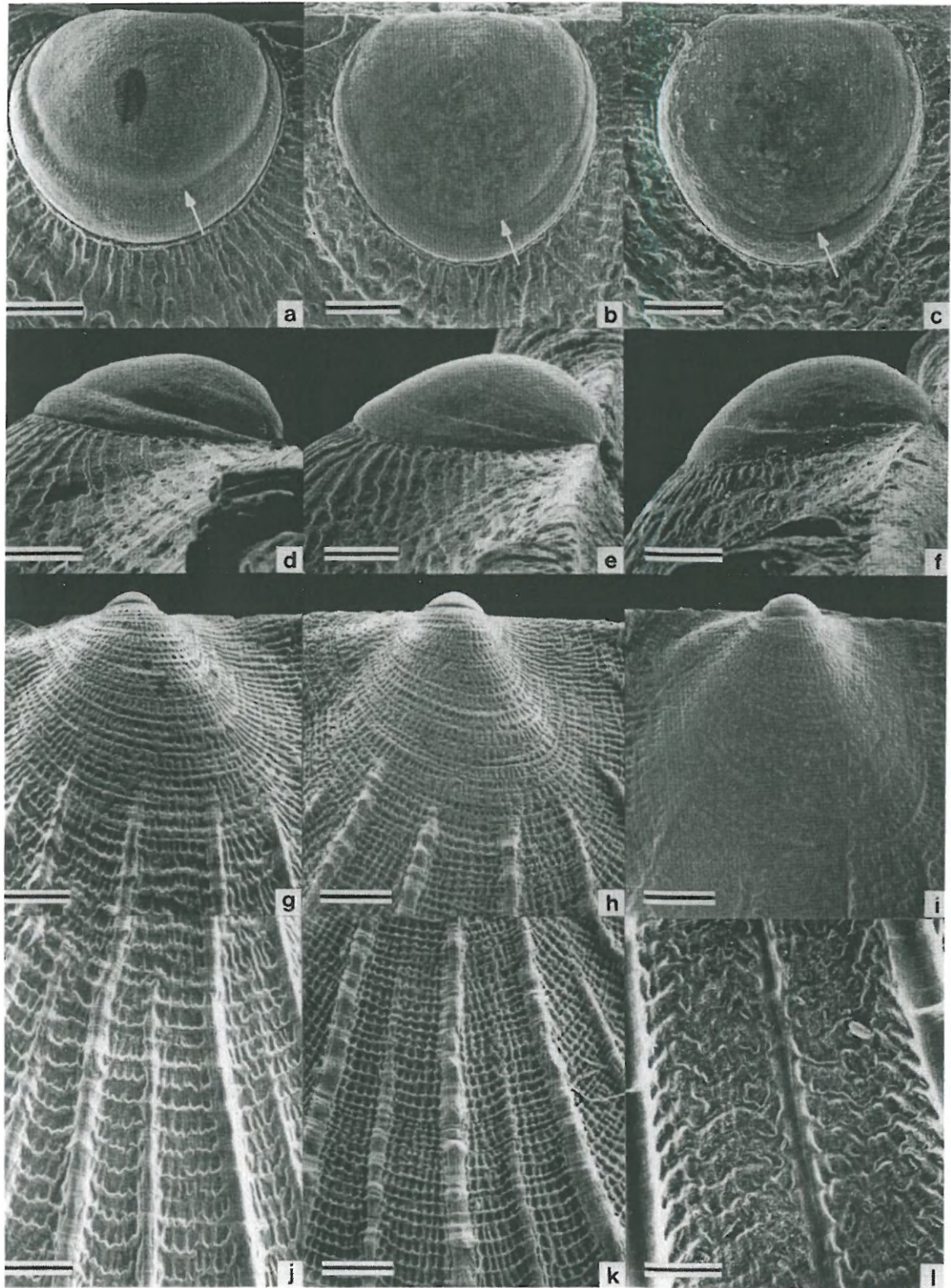


Fig. 7. Scanning electron micrographs of prodissoconchs in planar view (a-c), prodissoconchs in posterior view (d-f), pre-radial microsculpture (g-i), and early radial stage sculpture (j-l) of left valves of *Caribachlamys*. a, d, g, j. *C. sentis*, USNM 764706, Molasses Reef, Monroe Co., Florida. b, e, h, k. *C. ornata*, USNM 766643, Carrie Bow Cay, Belize. c, f, i, l. *C. imbricata*, USNM 457668, Bahia Honda, Cuba. Arrows point to approximate position of PI/PII boundary. Scale bars: a-f = 50 µm, g-l = 200 µm.

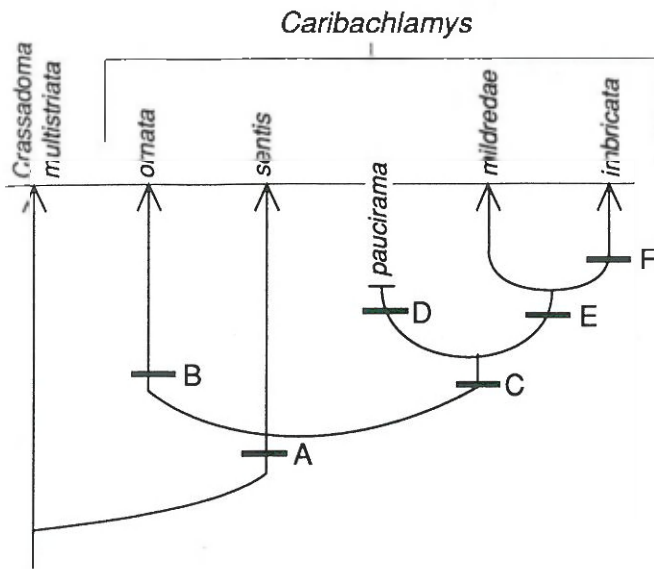


Fig. 8. A phylogeny of species in the new genus *Caribachlamys* in the Plio-Pleistocene of the tropical western Atlantic. Lineages ending in arrows are extant; the one ending at a terminal cross-bar is extinct. Lettered blocks refer to apomorphies: (A) larval shell with large PI and small PII stage; (B) I-beam shaped ribs with smooth crests; (C) subdued commarginal lirae of irregular trend in early ontogeny; (D) rib introductions limited to early ontogeny, later ribs evenly spaced without significant clustering; (E) fasciculation of ribs, increased scale spacing with tendency toward cusping, and flattening of left valve; (F) reduction of ribs to 9 or 10 major plicae with tendency to eliminate secondary ribs, scales commonly forming closed knobs, and left valve markedly flattened.

fig. 125. The smaller specimen, although nearly of the same color, is not the same species but rather is a specimen of *Spathochlamys benedicti* (Verrill and Bush, 1897) (see following section). The larger specimen, BMNH (ht., 15.9 mm; L, 14.3 mm; length of anterior outer ligament, 2.9 mm; length of posterior outer ligament, 0.9 mm) is herein selected as the lectotype (Figs. 6m, n).

Type locality.—Reeve had no locality data for the species that he described. The type locality is herein specified as the western North Atlantic off southeastern Florida.

Diagnosis.—*Caribachlamys* with valves about equal in convexity; ribs closely spaced, fine, continuously scaly, rounded, and of many different heights, introduced continuously throughout ontogeny, with more than 70 ribs and riblets at distal margin of mature individuals; major ribs with straight or slightly undercut sides but not I-beam shaped in cross section; scales fine, closely spaced, erect, distally concave, and open; commarginal lirae well developed in rib interspaces in early ontogeny and fairly uniform in trend across rib interspaces; antimarginal striae prominent between commarginals but variably present on rib

crests.

Morphological variation.—*Caribachlamys sentis* is of small size, seldom exceeding a height of 40 mm; no geographic trends in maximum size were observed. The ribs tend to be continuously scaly beginning at their origins at the beginning of the radial stage of growth; there is in general no abrupt change in ontogeny from a non-scaly to a scaly condition. Exceptions occur in the western Caribbean along the coast of Panamá (USNM 743733, Payardi Island, and USNM 743360, San Blas Archipelago). The ribs of the left valves of some of the specimens in these samples lack scales in early ontogeny up to a shell height of from 4.5 to 6.5 mm and then change fairly abruptly to a scaly phase. Unlike the non-scaly phase of ribs in *C. ornata*, however, these ribs have a rounded crest and are not I-beam shaped in cross section.

The shell color and color pattern of *Caribachlamys sentis* are variable. Most commonly, shells are orange or purple with maroon mottling in early ontogeny. In some cases an orange phase may change abruptly along a commarginal growth line to a purple phase, but the reverse has not been observed. Rarely the color may be nearly uniform white or yellow, usually with an early orange-mottled phase.

Comparison.—*Caribachlamys sentis* closely resembles *C. ornata* in ribbing density and pattern. The ribs differ, however, in cross-sectional shape, at least in early ontogeny. In *C. sentis* the rib shape is high and rounded, with the rib crests not flattened, whereas in *C. ornata* the ribs at least in early growth have an I-beam cross-section, with the crests flattened and non-scaly and the rib sides strongly undercut. Specimens from the northern Bahamas identified herein as *C. sentis* are very close to being transitional between the two species in rib shape in early ontogeny. Unworn shells of *C. ornata* have dense antimarginal striae present on the flattened rib crests, whereas in *C. sentis* such rib-crest striae are not so strongly developed. *Caribachlamys sentis* tends to have more uniform coloration than does *C. ornata* and generally does not develop the strongly contrasting color pattern that is common in most *C. ornata*, where dark maroon spots or bars form on a stark white background. *Caribachlamys sentis* and *C. ornata* also tend to differ in living habits. Where the two occur in the same area, *C. sentis* is generally found at more protected sites on reefs, whereas *C. ornata* lives in the more turbulent areas of the reef front.

Caribachlamys sentis also closely resembles *Crassadoma multistriata* (eastern and central Atlantic and southwestern Indian Ocean) in ribbing pattern, color, and color pattern. In *C. multistriata*, however, the prodisso-

conch is of the normal plesiomorphic type, with a PII stage that is relatively large compared to PI (Fig. 5a); in *C. sentis* the prodissoconch is almost entirely composed of the PI stage, the PII stage being only a narrow fringe or absent (Figs. 7a, d). *C. sentis* also differs from *C. multistriata* in having a somewhat less inflated shell and in generally lacking a distinct groove along the center of the outer surface of its byssal fasciole. Aside from the difference in prodissoconch morphology, young individuals of the two species can be distinguished on the basis of microsculpture. In *C. sentis* the spaces between commarginal lirae of the early commarginal stage are occupied by well-developed antimarginal striae; in *C. multistriata*, antimarginal striae between commarginals are either very poorly developed or absent.

Living habits.— Byssally attached beneath coral heads and between rocks and coral rubble on reef crests in shallow backreef areas, on near-shore rock jetties, and in deeper fore-reef rubble zones; depth range from just below low tide level to about 30 m. Deeper offshore specimens are dead shells only, known to occur as deep as 52 m. Diaz *et al.* (1991), reporting on the molluscan fauna of the Santa Marta area of Colombia, found *Caribachlamys sentis* living in three types of habitats: (1) at a depth of 22 to 27 m at base of the reef front on a bottom of "conglomerates of coral rubble partly bound together by sponges; dead coral heads and scattered debris patches may also be present." (2) at a depth of about 8 to 15m, with the bottom described as "upper reef-slope with large coral heads forming caves and an intricate system of cryptic microhabitats. Species of sea fans, sea whips, and sea plumes are also common." (3) at depths less than 10 m, with the bottom described as "rocky boulders and pebble partly covered by filamentous algae, crusting zoanthids, and fire corals. This zone is present in calm environments in shallow water."

Geographic range.— From Jupiter Inlet, southeastern Florida, southward through the Florida Keys; uncommon in northern, western, and southern Gulf of Mexico [records from Flower Garden Reef, Texas, and off Tamaulipas, Mexico (USNM 764714)]; western Caribbean (Nicaragua, Panamá, Colombia); western Atlantic off Brazil as far south as the state of Santa Catarina (29°S). The presence of the species in southern Brazil is based on Rios (1985: 222); I have not examined these specimens.

Stratigraphic range.— Lower? Pliocene to present.

Discussion.— The only fossil *Caribachlamys sentis* found thus far is a single right valve (USNM(P) 474635) collected by the late S. E. Hoerle from the north side of the

Caloosahatchee River, 3.4 km (2.1 miles) west of Ortona Locks, Glades County, Florida. Unfortunately the precise stratigraphic position of this specimen is unknown, because the stratigraphic section at this site likely includes the Caloosahatchee, Bermont, and Ft. Thompson Formations. All that can be said is that it is likely that the specimen is Pleistocene in age.

I have not yet observed unequivocal pre-Pleistocene fossils of *Caribachlamys sentis*, and my estimate of a Pliocene origin is based upon two indirect lines of evidence. First, the oldest fossil member of the tribe Crassadomini in the western Atlantic thus far identified is possibly the specimen figured by Woodring (1925, pl. 7, fig. 10) as "*Chlamys (Chlamys) sp.*" from the Bowden Formation (Bowden shell beds) at Bowden, Jamaica. This specimen, USNM(P) 352779, is an abraded juvenile right valve only 4.4 mm in height. Its pattern of rib introduction, by rib-flank intercalation, is remarkably like that at a similar growth stage of *C. sentis* (cf. USNM 764710). The microsculpture of the specimen does not appear to be preserved except for traces of antimarginal striae on the anterior and posterior edges of the disk and disk flanks and some obscure traces of commarginal lirae. The prodissoconch of the specimen is not preserved, but the impression of it remains on the underlying shell material. This impression has a length of 163 μm , exactly the length that one would expect for the prodissoconch of a *Caribachlamys*. The prodissoconchs in species of *Crassadoma* are, so far as known, of a larger size (about 200 μm). On this basis the specimen is placed tentatively in *Caribachlamys*, and it may well be an early representative of *C. sentis*. The Bowden beds are now considered to be early Pliocene in age (see below, under *Spathochlamys vaginula*).

Secondly, the next oldest fossil *Caribachlamys* thus far discovered occur in the "Pinecrest beds" and Caloosahatchee Formation of Florida of late Pliocene and early Pleistocene age (see below). These specimens, however, are identified with either *Caribachlamys paucirama*, new species, or *C. mildredae*, both of which have morphological features that are more derived than are the corresponding features of *C. sentis* (see preceding discussion of the genus *Caribachlamys* and Fig. 8). This suggests that *C. sentis* itself must have been present before the time of deposition of these beds.

Woodring (1982: 590) identified "*Chlamys sentis* (Reeve)?" from the Emperador Member of the La Boca Formation, Lower Miocene, of Panamá, but neither his illustrated specimen (USNM(P) 647216) nor the other two specimens to which he referred are members of this species. Rather they appear to belong to the genus *Dimarzipecten* Ward, 1992, which is discussed below under *Spathochlamys*, new genus.

Recently Garrafiolo and Távora (1989) included *Chlamys sentis* in a list of species from the Pirabas Formation, early Miocene, Brazil. This identification is doubtful, however, because they include *Chlamys japericensis* Ferreira, 1960, originally described from the Pirabas Formation, as a junior synonym of *C. sentis*. A specimen of *C. japericensis* sent to the USNM by Dr. Ferreira has shagreen microsculpture and is not a *Caribachlamys*.

Material examined.—Recent material: USNM: 61 lots containing about 300 specimens, from southern Florida, the Florida Keys, Mexico, Nicaragua, Panamá, and Colombia. MNHN: 4 lots containing 4 specimens, from off Brazil (8° 22.5' S, 12° 56.0' W, and the Abrolhos Archipelago). CAS: 2 lots containing 5 specimens, from Bahía Limón, Panamá and Baía de Todos os Santos, Bahia, Brazil.

Fossil material: USNM: USNM(P) 474635, 1 RV, probably Pleistocene, from the Caloosahatchee River area of south Florida (see preceding discussion).

Caribachlamys ornata (Lamarck, 1819)

(Figs. 6q,r; 7b,e,h,k; 9a,b)

Pecten ornatus Lamarck, 1819: 176, from southern Atlantic Ocean.

Chlamys ornata (Lamarck), Verrill and Bush, 1897: 59.

Types.— Specimens of *Pecten ornatus* in the Lamarck Collection in Geneva are in two lots. One of these, GNH 1088/75, which contains a single pair of matching valves of length 28.2 mm, is selected herein as the lectotype, because the specimen conforms to Lamarck's measurement and is the specimen illustrated by Chenu (1845, pl. 35, figs. 3 and 3a). The second lot, GNH 1088/73, contains five pairs of matching valves some of which clearly belong to species other than *P. ornatus*.

Type locality.— Lamarck's reference to the locality of this species as "l'Océan atlantique austral" is overly generalized. *Caribachlamys ornata* extends south of the Equator for only a short distance to islands offshore from Brazil. The type locality is herein emended to the Antillean region of the western Atlantic,

Diagnosis.— *Caribachlamys* with valves about equal in convexity or with left valve slightly less convex than right but not markedly flattened; closely spaced, fine ribs with early non-scaly phase followed by scaly phase; ribs introduced continuously throughout ontogeny, with more than 70 ribs at distal margin of disk on mature shells; ribs of right valve commonly in clusters of three, those of non-scaly phase of left valve high and I-beam shaped in cross

section, with deeply undercut rib flanks; scales fine, closely spaced, erect, distally concave, and open; commarginal lirae well developed in rib interspaces in early ontogeny and fairly uniform in trend and spacing across rib interspaces; antimarginal striae prominent between commarginal lirae and well developed on rib crests.

Morphological variation.— *Caribachlamys ornata*, like its congeners, is of small size, seldom exceeding a height of 40 mm; no geographic trends in maximum size were observed. The degree to which the ribs of *C. ornata* are non-scaly, smooth crested, and I-beam shaped is highly variable both within and among population samples. Furthermore, these features are less well developed on the right valve than on the left valve. Among 30 measured valves from Florida and the Bahamas, the non-scaly phase of ribs in the central sector of the disk was found to disappear at shell heights ranging from 7 to 10 mm on the right valve and from 9 mm to 25 mm on the left valve. There is much less variation in shell color and color pattern than in ribbing. Most *C. ornata* have dark red, maroon, or purple maculations on a light-colored, generally white, background. Distinct orange coloration in this background is relatively rare, occurring in the collections examined from eastern Puerto Rico through the Virgin Islands to Dominica. Specimens from the northern Bahamas, represented by a good suite of specimens in the Delaware Museum of Natural History, are lightly pigmented, and the extent of the I-beam phase of their ribbing is highly variable.

Comparison.— *Caribachlamys ornata* resembles *C. sentis* in both the ribbing-introduction pattern and the microsculpture of the early commarginal stage. *C. ornata* differs, however, from *C. sentis* and all other *Caribachlamys* in having a distinct non-scaly I-beam-shaped ribbing phase in early ontogeny, persisting on the left valve at least to a shell height of 9 mm (refer to preceding section on *C. sentis*).

Living habits.— *Caribachlamys ornata* lives byssally attached beneath rocks and coral heads in shallow water on the more turbulent parts of coral reefs, on hard, rocky bottoms, or in channels with strong currents. The only documented depth records for live specimens are all shallower than 20m. Dead shells, apparently dislodged from reef fronts, have been dredged from as deep as 165 to 180 m (USNM 501824, off Lazaretto, Barbados).

Geographic range.— *Caribachlamys ornata* occurs throughout the Antilles and in the northern Bahamas, southeastern Florida, and the Florida Keys. I have not been able to substantiate its presence in Bermuda, an occurrence which Abbott (1974, p. 443) also questioned. In the south-

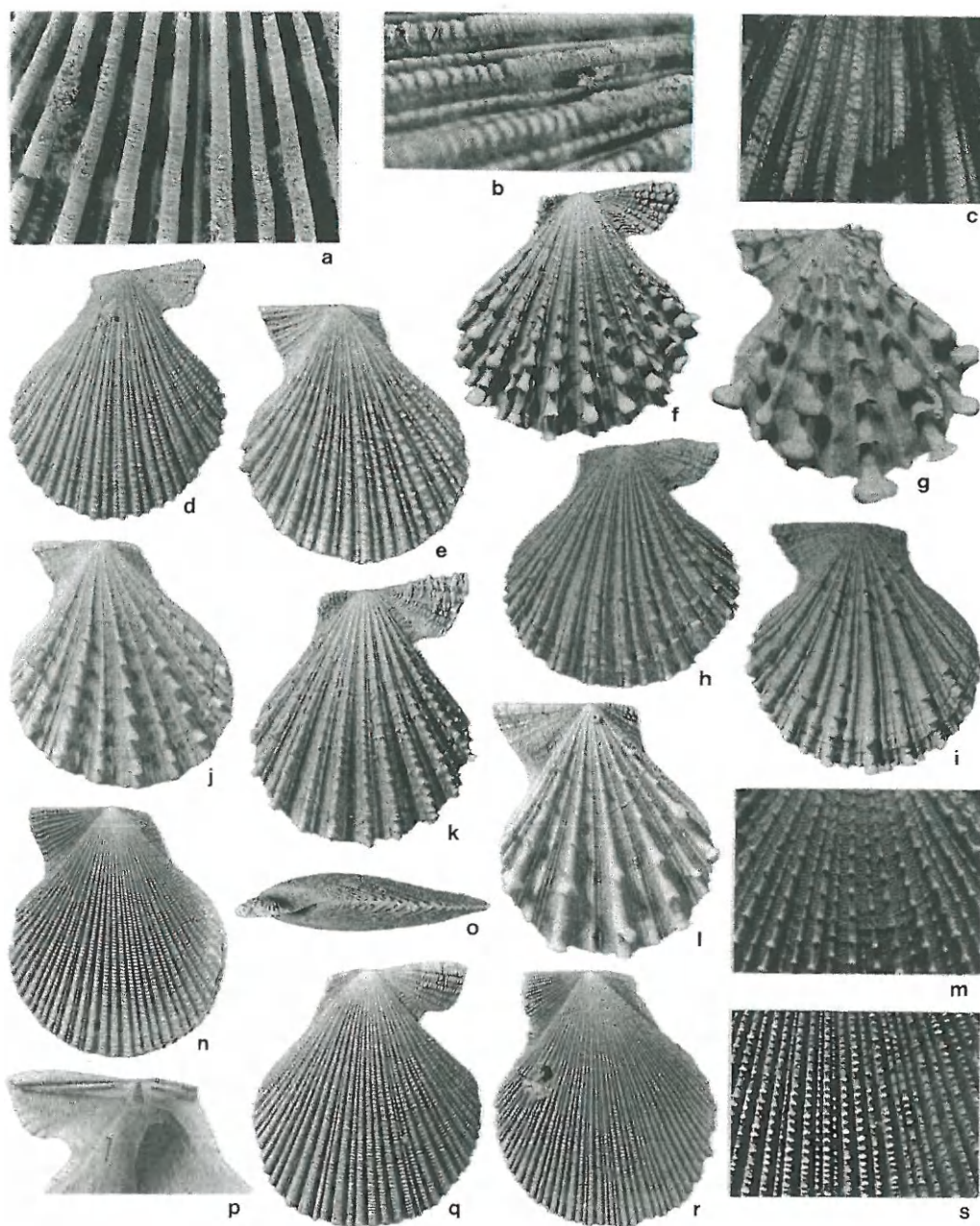


Fig. 9. *Caribachlamys*. a, b. *C. ornata*, USNM 683533, The Baths, Gorda Id., Virgin Ids., West Indies, left valve, planar and oblique views of I-beam shaped ribs, horizontal widths of fields 10 mm and 9 mm. c. *C. mildredae*, USNM 764745, Long Reef, Florida, juvenile right valve showing irregular com-marginal and antimarginal microsculpture in rib interspaces, transmitted light, horizontal field width 4 mm. d, e. *C. mildredae*, USNM 598977, holotype, Long Key Reef, Dry Tortugas, Florida, matching right and left valves, height 37.0 mm. f, g. *C. imbricata*, USNM 764733, Florida morph, La Chorrera, Havana, Cuba, non-matching right and left valves, heights 29.1 and 25.2 mm. h, i. *C. imbricata*, Bermuda morph, USNM 764735, near Bermuda Biological Station, St. Georges, Bermuda, matching right and left valves, height 39.8 mm. j. *C. imbricata*, Bermuda morph, USNM 743734, suction dredge spoil from near edge of coral reef, Payardi Id., Minas Bay, Panamá, single left valve, height 30.6 mm. k, l. *C. imbricata*, Bermuda morph, USNM 760081, Pico Feo Id., Gulf of San Blas, Panamá, matching right and left valves, height 18.3 mm. m, o. *C. paucirama*, UF 24894, Caloosahatchee Fm.?, spoil in Cochran Shell Pit, Hendry Co., Florida, detail of sculpture of left valve, horizontal field width 4.6 mm, and anterior view of articulated shell, shell height 36.5 mm. n. *C. paucirama*, USNM(P) 474637, holotype, Caloosahatchee Fm.?, spoil at rock pit east of Ft. Denaud, Hendry Co., Florida, single left valve, height 29.6 mm. p, q. *C. paucirama*, UF 24479, Caloosahatchee Fm.?, spoil in Cochran Shell Pit, Hendry Co., Florida, right valve, interior of hinge and exterior, hinge length 15.5 mm, valve height 30.3 mm. r, s. *C. paucirama*, USNM(P) 474638, "Pinecrest Beds," northeast of Naples and southwest of Immokalee, Collier Co., Florida, left valve, height 30.7 mm, horizontal field width of detail, 14 mm.

ern and western Caribbean, the species occurs on or near reefs adjacent to islands off Venezuela, Belize, and Quintana Roo, Mexico. In the Gulf of Mexico (other than along the Florida Keys), the species is apparently either very rare or absent. The USNM collections have one poorly documented lot from Veracruz, Mexico (USNM 57655). Rios (1985: 222) reported the presence of this species in the Brazilian islands of Fernando de Noronha and Atol das Rocas.

Stratigraphic range.— Lower? Pleistocene to present.

The oldest fossil occurrences of *Caribachlamys ornata* thus far known are specimens reported by Trechmann (1933: 33) from both high (300 m) and low levels of the Coral Rock of Barbados. Two specimens collected by Trechmann and deposited in The Natural History Museum, London (Palaeontology Section) were examined by me in 1979. Although both clearly belong to *C. ornata*, nothing further can be said about their relationship to modern forms without reexamining the specimens. It was noted at the time that one of the specimens, a left valve from "below the Garrison, west side of Barbados," still retains a remnant of a typical *C. ornata* color pattern. Trechmann (1933) argued that the Coral Rock of Barbados, now tilted and variously displaced by tectonic sliding, may be of fairly uniform age, mainly early Pleistocene. More recent studies (Mesolella, 1967; Ladd *et al.*, 1990) have emphasized that Barbados emerged throughout the Pleistocene.

Specimens of *Caribachlamys ornata* of Pleistocene age have also been collected on San Salvador Island, Bahamas, from a fossil coral reef northwest of the center of Cockburn Town [USNM(P) 474636]. This reef is Sangamonian in age, based on ^{234}U - ^{230}Th dates that range from 130.75 ± 1.5 ky to 119.2 ± 1.5 ky (Curran and White, 1989).

Dall (1898) reported that this species occurs in the Pleistocene of the Florida Keys and the Antilles.

Discussion.—There remains some doubt as to whether *Caribachlamys ornata* is distinct from *C. sentis* at the species level or whether the two are merely subspecies. Along the southeastern Florida coast and in the Florida Keys, where both forms occur, there is little doubt that they are well separated morphologically. In the Bahamas, however, particularly at Abaco Island, specimens identified herein as *C. ornata* have only a very short early growth stage with I-beam shaped, non-scaly ribs, and after this phase even shell color can become uniform and similar to that of *C. sentis*. The specimen of Lamarck chosen here as the lectotype in fact is close to these specimens in having a short I-beam phase and an abrupt shift to a more uniform color pattern. A possible interpretation is suggested by the fact that *C. ornata* appears to have a very recent origin in

the later Pleistocene. It could well be that the species is still in the process of change and that selection pressures have operated more strongly in reef-front situations in the Lesser Antilles and Florida than on the carbonate banks and patch reefs of the Bahamas.

Material examined.— Recent material: USNM: 93 lots containing about 250 specimens, from the Florida Keys, the Bahamas, Cuba, Grand Cayman, Jamaica, Haiti, the Dominican Republic, Puerto Rico, the Virgin Islands, Saint-Martin, Antigua, Dominica, St. Lucia, Barbados, Tobago, Aruba, Mexico (Quintana Roo), and Belize. DMNH: many specimens from the Bahamas. AM: several lots, from Saint-Martin, St. Eustatius, Barbados, Bonaire, and Curacao.

Fossil material: USNM: USNM(P) 474636, 7 specimens plus fragments from a fossil coral reef northwest of Cockburn Town, San Salvador Island, Bahamas, Pleistocene (Sangamonian, see preceding section on stratigraphic range). BMNH: 2 specimens from the Pleistocene Coral Rock "below the Garrison", west side of Barbados, collected by Trechmann (1933).

Caribachlamys paucirama Waller, new species

(Figs. 9m-s)

Etymology.— From the Latin, *paucus*, meaning few, combined with *ramus*, meaning branch, with reference to the relatively few rib introductions in the late ontogeny of the shell.

Types.— Holotype: USNM(P) 474637, 1 left valve (Fig. 9n), from rock pit at east edge of Ft. Denaud, Hendry County, Florida, probably from the Caloosahatchee Formation of early Pleistocene age. Ht. = 29.6 mm, L. = 25.7 mm, umbonal angle = 92° , AOL = 9.4 mm, POL = 4.3 mm.

Paratypes: USNM(P) 474638 (Figs. 9r,s), 1 left valve, USGS 26543 (TU 1175) from spoil banks along canals south of Florida Highway 858, 3.2 km (2 miles) east of junction with Florida Highway 846 (SE $1/4$, section 24, T48S, R27E), northeast of Naples and southwest of Immokalee, Collier Co., Florida. Pinecrest Beds. Collected by S. E. and R. E. Hoerle.

USNM(P) 474639, 1 juvenile right valve and 2 fragments, rock pit 5.6 km (3.5 miles) west of LaBelle, off Florida Highway 78 on north side of Caloosahatchee River, Glades County, Florida. Caloosahatchee Formation.

USNM(P) 474640, 1 right valve, 3 left valves, and 1 fragment, Cochran Shell Pit, NE $1/4$ sec. 23, T43S, R28E, Hendry County, Florida. Collected from spoil, Caloosahatchee Formation.

UF 24479, 1 right valve (Figs. 9p,q) and 2 left valves, same data as preceding.

UF 24894 (Figs. 9m,o), 1 pair of valves, 3 right valves, and 5 left valves, same data as preceding.

UF 24986, 1 left valve, same data as preceding.

UF 41906, 1 right valve, same data as preceding.

UF 55665, 3 right valves and 2 left valves, same data as preceding.

UF 9492, 3 left valves, Caloosahatchee River, Florida, precise locality not specified, presumed to be from the Caloosahatchee Formation.

Diagnosis.— *Caribachlamys* with valves about equally convex; well-spaced, fine, continuously scaly, rounded ribs equal to or narrower than interspaces, with new rib introductions uncommon after mid-ontogeny (shell height of about 15 mm); about 40 to 50 ribs and riblets at margin of mature individuals (shell height of about 30 mm); scales fine, closely spaced, distally concave, and open; commarginal lirae absent; microsculpture in rib interspaces consisting of antimarginal striae of irregular trend in early ontogeny, regularly diverging antimarginal striae in later ontogeny; crests of ribs without antimarginal striae.

Description of holotype.— Exterior: Left valve with height somewhat greater than length ($Ht/L = 1.15$) and anterior auricle much larger than posterior one ($AOL/POL = 2.19$); anterior auricle pointed, with deep byssal sinus; posterior auricle oblique, forming an angle with hingeline of about 120° ; posterior margin of posterior auricle nearly straight, slightly convex, or slightly concave. Prodissoconch not preserved; radial ribs originating at shell height of 1 mm, initially 10 in number, increasing to 27 at shell height of 5 mm, 37 at 10 mm, and 42 at distal margin at shell height of 30 mm. Ribs high and rounded in cross-section, bearing erect, distally concave, open, closely spaced scales throughout ontogeny; ribs remaining narrower than or equal to interspaces in width. Rib introduction initially mainly by intercalation submedially in interspaces of earlier ribs; microsculpture of pre-radial stage of beak pitted or with short discontinuous antimarginal striae; microsculpture in rib interspaces consisting of striae of irregular, mainly antimarginal, trends; commarginal lirae obscure or absent in early ontogeny.

Interior: Hinge dentition of two-element type as in *Chlamys*; umbonal region aragonitic, without foliated-calcite transgression; adductor and pedal retractor muscle scars not preserved; ribs expressed internally near margin as simple corrugations without internal carinae.

Morphological variation.— The oldest specimen, USNM(P) 474638, from the Pinecrest Beds (Figs. 9r,s), dif-

fers from most of the other specimens, all from the Caloosahatchee Formation, in having a slightly greater number of ribs at shell heights of 10 mm and 20 mm, and it exceeds most but not all of the Caloosahatchee specimens in number of ribs present at the distal margin of its disk.

Comparison.— *Caribachlamys paucirama* resembles *C. sentis* in overall aspect but differs in having most of its rib introductions limited to early ontogeny, thereby producing by late ontogeny a far more regular ribbing pattern and a lower total number of ribs at maturity. By the time a shell height of 20 mm is reached, *C. paucirama* rarely has as many as 50 ribs, whereas *C. sentis* has between 50 and 60. Specimens of *C. sentis* that are 30 mm in height or greater have at least 60 radial ribs present along the margins of their disks; in contrast *C. paucirama* generally has fewer than 50. In microsculpture the two species differ in their first 10 mm of growth. Distinct commarginal lirae of fairly regular trend are present in *C. sentis*, whereas *C. paucirama* has irregular antimarginal striae.

Caribachlamys paucirama also resembles *C. mildredae*. The microsculpture pattern of the two species in early ontogeny is very similar but ribbing patterns differ. *C. mildredae* generally has fewer than 30 ribs at a shell height of 10 mm, whereas *C. paucirama* generally has more than 30. The ribs of *C. mildredae* are distinctly clustered on the right valve and distinctly ordered on the left; those of *C. paucirama* tend to be more uniform in spacing and height. Lastly, the scales on the ribs of *C. mildredae*, particularly those on its left valve, are more widely spaced than are the scales of *C. paucirama*, with the scales of some specimens of *C. mildredae* approaching the closed knobby condition that is common in *C. imbricata*.

Paleoecology.— *Caribachlamys paucirama* appears to be most abundant in the Caloosahatchee Formation at sites where there are abundant scleractinian corals. Presumably the living habit and habitat of the new species were similar to, if not the same as, that of extant reef-dwelling members of the genus.

Geographic range.— Thus far known only from southern Florida.

Stratigraphic range.— Middle and Upper Pliocene (Pinecrest Beds) and Lower Pleistocene (Caloosahatchee Formation).

The age of the Pinecrest Beds has been somewhat controversial, depending on how the boundaries for this formation are drawn. The Middle to Late Pliocene age is based on studies by Akers (1974), Waldrop and Wilson (1990: 220), and Jones *et al.* (1991).

Discussion.— *Caribachlamys paucirama* is quite clearly a member of the same clade that contains *C. mildredae* and *C. imbricata*, the shared derived characters being the reduction of early commarginal lirae in rib interspaces, the irregularity of early antimarginal microsculpture, and the reduction in rib number (see preceding section on genus *Caribachlamys* and Figure 8). In its lack of distinct rib clustering, the new species is the most primitive known member of this clade. Although there is only a single specimen of the new species available from the Pinecrest beds, the ribbing pattern of this specimen suggests that between Pinecrest and Caloosahatchee time, rib introductions decreased and rib spacing became more regular. This is just the opposite of a trend that produced *C. mildredae* and *C. imbricata*, in which the ribs are strongly clustered and ordered, with a common trend toward distant spacing of scales on major ribs and toward cusping of scales. This trend in addition to the peculiar microsculpture of *C. paucirama*, with highly irregular antimarginal striae and a lack of commarginal lirae, suggests that the new species is a sister group of a clade that contains both *C. mildredae* and *C. imbricata* (Fig. 8).

Material examined.— USNM: the 10 specimens and fragments listed above as types. UF: the 22 specimens listed above as paratypes.

Caribachlamys mildredae (Bayer, 1941)
(Figs. 9c-e)

Pecten (*Chlamys*) *imbricatus mildredae* Bayer, 1941: 46, pl. 3, figs. 16, 17.

Pecten (*Chlamys*) *mildredae* Bayer, Bayer, 1943: 110, pl. 12, fig. 7.

Chlamys mildredae (F. M. Bayer), Abbott, 1954: 363, pl. 34, fig. c.

Holotype.—USNM 598977, a pair of matching valves. ht. = 37 mm, from Long Key Reef, Dry Tortugas, depth not specified. Bayer (1941) did not give the locality of the holotype in his original description. In a later note (Bayer, 1942) he specified Biscayne Bay as the type locality on the grounds that the greatest number of shells came from the Miami area.

Diagnosis.— *Caribachlamys* with left valve less convex than right and somewhat flattened; fine, continuously scaly, rounded ribs introduced continuously but sparingly throughout ontogeny, with fewer than 50 ribs and riblets at distal margin of disks of mature individuals; ribs distinctly clustered on right valve and with at least three distinct

orders of rib height on left; scales large, widely spaced, commonly strongly inclined distally with tendency to form closed knobs; early commarginal lirae obscure, scarcely higher in relief than intervening antimarginal striae and of irregular trend and spacing; antimarginal striae absent from crests of major ribs.

Morphological variation.— The distinctive and fairly constant feature of *Caribachlamys mildredae* is its ribbing pattern. On the left valve this is commonly expressed as four orders of rib height (Fig. 9e). Ribs of the first order, the highest in amplitude and generally five in number, tend to be more lightly pigmented than the other ribs, which appear to alternate in height between ribs of the next higher order. On the right valve, the ribs tend to be clustered in groups of from two to four (Fig. 9d). As in other species of *Caribachlamys* and *Crassadoma*, the predominant mode of rib introduction is by rib-flank intercalation on the right valve and by either rib-flank or sub-medial intercalation in rib interspaces on the left. Because rib introductions occur throughout ontogeny, the ribs at the margin are of many different sizes. The estimate in the diagnosis that fewer than 50 ribs are produced in mature individuals is based on the largest individuals examined, which have heights between 30 and 40 mm. The major ribs of some individuals have undercut flanks, but because the crests are rounded rather than flattened, the ribs can hardly be called I-beam shaped in cross section. The left valves of all of the specimens examined have a zone in early ontogeny in which the scales atop the major ribs are very widely spaced (spacing between 1.5 and 2 mm). Most specimens have distally open scales, the closed knobby condition being rare.

Coloration of the shell is highly variable, with orange or purple maculations forming in the spaces between major ribs in early ontogeny, the color pattern becoming more uniform later. Some individuals have valve interiors that are yellow, but this is not a constant feature.

Comparison.— *Caribachlamys mildredae* differs from both *C. sentis* and *C. ornata* in having fewer ribs which, on the left valve, are more distinctly ordered. The major ribs of the left valve of some *C. mildredae* have undercut sides but differ from the I-beam shaped ribs of *C. ornata* in lacking flattened, non-scaly, antimarginally striate crests. *C. mildredae* more closely resembles *C. imbricata* in color, including the yellow internal hue, but differs in having four orders of rib height on its left valve and from 40 to nearly 50 ribs and riblets at the distal margin of mature individuals. *C. imbricata*, in contrast, has only three orders of rib height, and its major ribs bear fewer and much larger scales than do those of *C. mildredae*. For a comparison with *C. paucirama*, see the preceding section.

Living habits.— *Caribachlamys mildredae* lives in shallow water (1-20 m) on coral reefs and in crevices on rock jetties, its living habit thus overlapping that of *C. sentis*.

Geographic range.— Thus far *Caribachlamys mildredae* is known with certainty only from southeastern Florida (West Palm Beach southward through Florida Keys to Dry Tortugas). Reports of its presence in Bermuda (Abbott, 1974: 443) are possibly the result of misidentification of what is herein referred to as the Bermuda morph of *C. imbricata* (see below).

Stratigraphic range.— Middle Pliocene? to present.

No unequivocally identified specimens of *Caribachlamys mildredae* are known from the fossil record. There is, however, a small (15.5 mm) left valve from the Pinecrest Beds of Florida that could be an early representative of this species (USNM(P) 474641). It is from the same locality (USGS 26543) that yielded the single Pinecrest specimen of *C. paucirama* in Collier County (see above). This specimen has a greater number of ribs at a shell height of 10 mm than do specimens of extant *C. mildredae* and also a greater number of ribs at its disk margin than would be expected in *C. mildredae* of comparable size. The specimen differs from co-occurring *C. paucirama*, however, in having its ribs distinctly ordered, the largest ribs lacking scales in early ontogeny and later having scales that are much more widely spaced than those on intervening riblets. The microsculpture of the specimen is consistent with that of either *C. paucirama* or *C. mildredae*.

Discussion.— In his original description of *Pecten (Chlamys) imbricatus mildredae*, Bayer (1941: 46) gave as his basis for linking the new taxon to *P. imbricatus* "the similar scheme of ribbing; the enlarged, sometimes cupped scales; the yellow and purple interior; and the large size of individuals." He did not, however, describe any intergradation between the two taxa, nor did he mention any ecological or geographic separation, both of which would be expected if the two taxa are indeed subspecies. Bayer (1943: 110) later elevated his new "variety" to species rank, while still maintaining that *P. imbricatus* is its closest relative.

Abbott (1974: 443) mentioned that *Chlamys mildredae* "may be a hybrid between *sentis* and *ornata*" but gave no reason why hybridization should not be between *Caribachlamys sentis* and *C. imbricata*, the latter being the species to which Bayer thought *C. mildredae* to be most closely related. At any rate, the hybridization hypothesis seems to have little merit. *C. mildredae* shows no more variation than do associated species; there is no indication of a "hybrid swarm" such as is known to occur commonly

in hybridizing situations. It seems more likely, particularly in view of the new species *C. paucirama* described above, that *C. mildredae* is a relict species and that its morphology represents an early stage in the evolution of the *C. imbricata* lineage. This could also explain its present-day rareness and its limited geographic distribution.

Material examined.— Recent material: USNM: 11 lots containing 11 specimens; ANSP: 3 lots containing 3 specimens, from southeastern Florida and Florida Keys.

Fossil material: USNM(P) 474641, 1 Right valve, USGS 26543 (TU 1175) from spoil banks along canals south of Florida Highway 858, and 3.2 km [2 miles] east of junction with Florida Highway 846 (SE¹/₄, section 24, T48S, R27E), northeast of Naples and southwest of Immokalee, Collier Co., Florida. Pinecrest Beds. Collected by S. E. and R. E. Hoerle.

Caribachlamys imbricata (Gmelin, 1791)

(Figs. 7c,f,i,l; 9f-j)

Ostrea imbricata Gmelin, 1791: 3318, living, "in mari rubro" [erroneous].

Pecten imbricatus (Gmelin), Lamarck, 1819: 171.

Chlamys imbricata (Gmelin), Abbott, 1954: 364, pl. 34f.

Type specimens.— The specimen represented by the figure that Gmelin cited, which is in Chemnitz (1784), vol. 7, pl. 69, fig. G, is designated as the lectotype of *Ostrea imbricata* Gmelin. Many of the specimens illustrated by Chemnitz were from the Spengler Collection housed at the Zoological Museum of Copenhagen (Keen, 1966). It is possible that the illustrated specimen of *O. imbricata* could be in that collection. I examined specimens labeled as *Pecten imbricatus* by Lamarck in Paris and Geneva; they all conform to existing concepts of the western Atlantic taxon.

Type locality.— Corrected herein to the Antillean region, western Atlantic.

Diagnosis.— *Caribachlamys* with left valve less convex than right and distinctly flattened; major ribs few in number, commonly 10 on right valve and nine on left, with five ribs on left valve tending to be more prominent and with higher scales than others; secondary riblets variably developed, of much lower height than major ribs; major ribs somewhat trigonal in cross section on right valve, rounded on left; scales on major ribs large, widely spaced, distally concave, commonly forming closed knobs; early commarginal lirae obscured by stronger antimarginal striae and of highly irregular trend; antimarginal striae absent from crests of major ribs.

Morphological variation.— *Caribachlamys imbricata* displays substantial geographic variation, but on the basis of the collections examined this variation appears to be geographically clustered rather than clinal. For purposes of discussion, two intergradational extremes of variation are referred to herein as the Florida morph and the Bermuda morph. Parallel differences between the two are as follows:

Florida morph (Figs. 9f, g): (1) In the early ontogeny of the right valve of the Florida morph, secondary costae that are close to or on the flanks of the primary ribs appear by a shell height of 5 mm. By a height of 10 mm, these secondary costae either disappear or are represented by the expanded, rounded rib flanks of the primary ribs; (2) The posterior auricle of the right valve has unevenly distributed costae, the dorsal one or two closer together and much stronger than the others; (3) On the left valve, third-order riblets are usually absent at least in early ontogeny (up to a shell height of 10 mm) and commonly absent throughout ontogeny; (4) On the left valve, there is usually only one riblet present on the anterior side of the anteriormost primary rib in early ontogeny, increasing to two in later growth. These anteriormost riblets lack scales; (5) On the left valve, radial riblets are unevenly distributed on both auricles, the dorsalmost riblets commonly much stronger than the others.

Bermuda morph (Figs. 9h-l): (1) On the right valve, secondary riblets are distinct and well separated from the primary ones at a shell height of 5mm. At a shell height of 10mm, these secondary costae are still distinct from the major ribs, the major ribs being without expanded flanks; (2) The posterior auricle of the right valve has fairly evenly distributed riblets of even amplitude; (3) On the left valve, third-order riblets are commonly present by a shell height of 10 mm and may be numerous by this stage of ontogeny; (4) On the left valve, there are usually two distinct and fairly strong riblets present on the anterior side of the anteriormost primary rib, commonly increasing to three in later growth. One of these anterior riblets may bear cusped scales; (5) On the left valve, radial riblets are numerous on both auricles, with only slight or no increase in amplitude toward the dorsal margin.

Caribachlamys imbricata is generally lightly pigmented, the darkest parts being the dark reddish or purple maculations that occur in earlier ontogeny between the primary ribs. Solidly colored shells, such as are common for *C. sentis*, are relatively rare. They have been observed, however, among specimens of the Bermuda morph from the Caribbean coast of Panamá. The valve interiors of both morphs are commonly yellow, sometimes brilliantly so.

Comparison.— *Caribachlamys imbricata* can be distinguished from its congeners by its broad, high-amplitude

major ribs. Unlike congeneric species, the scales on these major ribs remain widely spaced throughout ontogeny and commonly form closed knobs.

Living habits.— *Caribachlamys imbricata* lives byssally attached in crevices, beneath coarse rubble and coral heads, and between coral branches on reefs and in both back-reef and fore-reef areas. Depth records for live-collected specimens in museum collections are all shallow, ranging from low subtidal to 20m.

Geographic range.— *Caribachlamys imbricata* appears to have a tropical distribution. It occurs in Bermuda, along the North American mainland only from Miami southward through the Florida Keys, in the Bahamas, and through the Antilles to Curacao and Aruba along the Venezuelan coast. It appears to be absent from the northern Gulf of Mexico, and the only record from the southern Gulf is from Alacran Reef on the north side of the Yucatan Peninsula. Few records are as yet available from the Caribbean coast of Central America with the exception of Belize (offshore cays) and Panamá, which are the best sampled areas. The species is not known from the Atlantic coasts of South America.

All specimens of *Caribachlamys imbricata* from Bermuda examined by me are members of the Bermuda morph, but this morph is also present in Jamaica, Panamá, Colombia, Venezuela, and possibly within samples that also contain the Florida morph in the Bahamas.

Stratigraphic range.— Lower? Pleistocene to present.

The oldest fossils of *Caribachlamys imbricata* thus far found are specimens in the Trechmann collection (BMNH) from the Pleistocene Coral Rock of Barbados at "Cane Garden" and "Highgate". These did not appear in the lists published by Trechmann; the species determinations are based on my examination of the specimens in 1979. As reviewed above in the section on *C. ornata*, Trechmann (1933) considered the Coral Rock to be mainly of early Pleistocene age.

I also found fossil *Caribachlamys imbricata* (USNM(P) 474642) in limestone blocks on Windley Key in the Florida Keys. These blocks presumably came from the Windley Key quarry, which exposes the Key Largo Limestone of late Pleistocene age (Multer, 1969; Stanley, 1966). According to Multer (1969: 109), this limestone represents a back-reef environment and is only about 100,000 years old. Although the specimens are fragmentary, they have ribbing characteristics that suggest that they belong to the Bermuda morph.

The only other known occurrences of fossil *Caribachlamys imbricata*, from Cuba, Haiti, and the

Dominican Republic, also appear to be Pleistocene in age (see below under material examined).

Discussion.— The two extremes of morphology described above as the Florida morph and the Bermuda morph are of considerable interest in that the former is clearly more derived than the latter when they are compared to outgroup taxa within *Caribachlamys*, particularly *C. mildredae*. Among the fossil specimens examined, those from the Windley Key Limestone of Florida (USNM(P) 474642) have ribbing characteristics that suggest that they belong to the Bermuda morph, and this also applies to the specimens from Haiti (USNM(P) 481997 and 481998). The sole Cuban specimen on hand, however, belongs to the Florida morph.

A likely explanation for the extant Bermuda populations, which belong exclusively to the Bermuda morph so far as known, is that they represent dispersal to Bermuda early in the evolution of the species at some time during the Pleistocene. Apparently modern oceanographic conditions do not permit continued dispersal of this species to Bermuda, and most members of populations elsewhere have assumed a more derived condition than those in Bermuda. The presence of Bermuda morphs among some extant populations outside of Bermuda suggests that the Bermuda populations should not be referred to as a geographic subspecies.

Material examined.— Recent material: USNM: 60 lots containing about 150 specimens, from southeastern Florida, Florida Keys, Bermuda, Bahamas, Mexico (Alacran Reef), Jamaica, Cuba, Puerto Rico, Virgin Islands, Anguilla, Barbuda, Curacao, Aruba, Belize, Panamá, Colombia, and Venezuela; MNHN: several specimens from Guadeloupe and 2 specimens in the Lamarck Collection without locality; GNH: 3 specimens in the Lamarck Collection, without locality; AM: specimens from Bonaire, Curacao, and Aruba; UCD, collection of Geerat J. Vermeij: a complete shell of the Bermuda morph from a depth of 5 m in a cave near Runaway Bay, north coast of Jamaica.

Fossil material: USNM: USNM(P) 474642, 7 valves or fragments, Windley Key, Florida, Key Largo Limestone, Upper Pleistocene; USNM(P) 481977 and 481978, 2 LV and 1 RV fragment, USGS 9764, on coast 100 m west of old fort on west side of entrance to Port-de-Paix harbor, Département du Nord Ouest, Haiti, "Bed 2 of section, Pleistocene, collected by W. P. Woodring, 1921; USNM(P) 481998, 1 LV, same locality as preceding; USNM(P) 474810, 1 RV, USGS 7943, Naval Station, Guantánamo Bay, Cuba, 6 to 18 m (20 to 60 ft) above sea level, Pleistocene, collected by P. Bartsch, 1917. BMNH: Barbados, Coral Rock, Pleistocene (see "Stratigraphic

Range" for details). FIELD SPECIMENS: Fossils in place in the lowest (and youngest) Pleistocene reef terrace along the south coast of the Dominican Republic east of Boca Chica. (These were too brittle and fragile to remove from the rock.)

Tribe *Mimachlamydini*, New Tribe

Diagnosis.— Chlamydiae with pitted microsculpture in pre-radial stage of left valve, the pits commonly extending into early radial stage; ribbing pattern simple, with the first ribs introduced in ontogeny tending to remain as major ribs and commonly the only ribs throughout ontogeny; ribs on shell interior usually with carinate edges; commarginal lirae in rib interspaces absent, obscure, or limited to early ontogeny; microsculpture between ribs commonly in a divaricating or herringbone pattern.

Discussion.— The new tribe *Mimachlamydini* is represented by the extant genera *Mimachlamys* Iredale, 1929, of the eastern Atlantic and Indo-Pacific and *Spathochlamys*, new genus, of the western Atlantic and eastern Pacific. It also includes the extinct genus *Dimarzipecten* Ward, 1992, of the tropical western Atlantic. The tribe forms a bridge between the tribes *Crassadomini* and *Aequipectinini* and is a sister group of the *Aequipectinini* in that both share the common presence of a coarsely pitted left beak before the start of the radial stage and a simple ribbing pattern in which the first ribs introduced tend to remain the major ribs and commonly the only ribs throughout the remainder of ontogeny. In both the *Mimachlamydini* and *Aequipectinini* these ribs develop carinate edges on the shell interior. In the *Mimachlamydini*, however, internal rib carinae are absent in the late ontogeny of the more primitive members of the tribe, whereas in the *Aequipectinini* these carinae are universally present throughout ontogeny.

Mimachlamydini differ from *Aequipectinini* in having a plesiomorphic chlamydid two-element hinge with the resilial teeth not elongated toward the free edges of the auricles. In the *Aequipectinini* the resilial teeth become larger in size than the dorsal teeth and tend to dominate the hinge structure. Lastly, the *Aequipectinini* develop characteristic wavy and looped commarginal lirae not present in the *Mimachlamydini*.

The greatest number of extant species in the *Mimachlamydini* occurs in the western Indo-Pacific region. The genus *Mimachlamys* in particular contains at least a dozen species but with scores of species-group names available due to the prolific overnaming that characterized typological systematics of earlier days. Among these species are the well known *M. senatoria* (Gmelin, 1791) complex, the colorful *M. nobilis* (Reeve, 1852) of Japanese waters, and

the giant *M. townsendi* (G. B. Sowerby III, 1895) of the Red Sea, the last being one of the largest of extant pectinids. In the eastern Atlantic and Mediterranean, the tribe is represented at present only by *M. varia* (Linnaeus, 1758). Phylogenetic relationships of some of these species were recently reviewed by Waller (1991: 31). The tribe is absent in the eastern central Pacific including the Hawaiian Islands, but a pair of extant geminate species assigned herein to *Spathochlamys*, new genus, is present in the tropical American region, one member of the pair in the eastern Pacific, the other in the western Atlantic.

The tribe Mimachlamyidini has an extensive fossil record in the Tertiary of Europe beginning in the Paleocene (Waller, 1991: 32) but is poorly represented in the American Tertiary. The new genus *Spathochlamys* is apparently the only member of the group that dispersed through seaway connections from the tropical Atlantic into the eastern Pacific.

Spathochlamys, new genus

Etymology.— Based on the Greek "spathe," meaning spade, in reference to concave-up scales, combined with the genus name *Chlamys*, which in turn is based on the Greek word "chlamys," meaning "mantle".

Diagnosis.— Mimachlamyidini with rounded or broadly trigonal ribs separated by interspaces each containing a single very narrow riblet; crests of major ribs bearing narrow erect scales that are concave on their upper (dorsal) sides; edges of ribs on inner surfaces of valves strongly carinate; microsculpture in early rib interspaces obscure or dominated by commarginal lirae which cross interspaces without strong curvature.

Type species.— *Pecten benedicti* Verrill and Bush in Verrill, 1897, extant, western Atlantic.

Other Species.— *Pecten vestalis* Reeve, 1853 [= *Pecten (Chlamys) lowei* Hertlein, 1935], extant, eastern Pacific, and *P. vaginulus* Dall, 1898, fossil, Miocene-Pliocene, Caribbean region and southeastern United States.

Geographic range.— Western Atlantic from at least Massachusetts to Brazil and throughout the Gulf of Mexico and Caribbean; eastern Pacific and Gulf of California from southern California to Ecuador and westward to the Galápagos Islands.

Stratigraphic range.— Upper Miocene to present.

Discussion.— The new genus differs in a number of quali-

tative features from *Mimachlamys*. Both the extant and fossil species of *Spathochlamys* have much more strongly developed carinate edges on the ribs on the inner shell surface than do species of *Mimachlamys*, where these carinae are sometimes minimally developed or restricted to early growth stages (as in *M. varia*, an extant species of the eastern Atlantic). Concave-up scales, which form atop at least some of the ribs in *Spathochlamys*, are unknown among extant species of *Mimachlamys*, where scales are concave-down (i.e. concave side facing toward the ventral margin). Some extinct European middle and upper Tertiary Mimachlamyidini, e.g., *M. angelonii* (De Stefani and Pantanelli, 1878), have concave-up scales but lack medial riblets, and other aspects of their morphology suggest that they have a phyletic history that is independent of that of *Spathochlamys*.

There is a strong resemblance in ribbing pattern between *Spathochlamys* and *Dimarzipecten* Ward, 1992, a genus recently introduced to accommodate what its author believed to be a single species, *Pecten crocus* Cooke, 1919, that was originally described from the early Miocene (or late Oligocene) of Anguilla. Ward (1992) stressed that *Dimarzipecten* has a narrow stratigraphic range (restricted to lower Miocene and possibly upper Oligocene) and a broad geographic range extending from the Antilles to the Belgrade, Edisto, and Tampa Formations and correlative stratigraphic units of the Carolinas, Georgia, and Florida. However, I have identified a second apparently undescribed species of *Dimarzipecten* in the Chipola Formation of Florida (USNM(P) 474643 and 474644, from Farley Creek, NE $\frac{1}{4}$ sec. 21, T1N, R9W, Calhoun Co.). This extends the stratigraphic range of the genus into the upper lower Miocene (Burdigalian in age; see Akers, 1972: 10).

Like *Spathochlamys*, *Dimarzipecten* has a *Chlamys*-like shape, ribs that become trigonal in cross-section at least in late ontogeny, narrow scales atop the ribs, and a fairly regular ribbing pattern with a single medial riblet in each interspace. *Dimarzipecten*, however, differs from *Spathochlamys* in lacking internal rib carinae and in having convex-up rather than concave-up scales on the rib crests. Furthermore, *Dimarzipecten* has a plesiomorphic microsculptural pattern of coarse antimarginal striae in the rib interspaces. The configuration of these striae is like that present in many modern *Mimachlamys*, including a herringbone-like configuration in rib interspaces in the center of the disk in early ontogeny. In *Spathochlamys*, antimarginal striae are absent or obsolete in early ontogeny except on and near the disk flanks, and commarginal lirae are present in the rib interspaces.

A third genus, possibly new and referred to herein as Genus A pending further research, is characterized by *Pecten sansebastianus* Maury, 1920, of which *P. (Chlamys)*

portoricensis Hubbard, 1920, is a junior synonym. This species occurs in the San Sebastian Shale and lower Lares Limestone of Puerto Rico (Maury, 1920; Hubbard, 1920), formations that are considered middle to late Oligocene in age (Maurrasse, 1990, fold-out correlation chart, Column 20). Genus A has a high, narrow shape like that of *Dimarzipecten*, and as in members of that genus, a small medial riblet appears in most rib interspaces in late ontogeny. Like *Spathochlamys*, Genus A has minute concave-up scales on its rib crests and the ribs have strongly carinate edges on the inner surfaces of the valves. Genus A differs from both *Dimarzipecten* and *Spathochlamys* in having a distinctive *Aequipecten*-like microsculpture in rib interspaces in early ontogeny. This pattern consists of wavy commarginal lirae that are strongly looped in a dorsal direction on the rib flanks and in a ventral direction in the rib interspaces; the looped lirae on the rib flanks may become cusped, as in some *Aequipecten* and in most *Cryptopecten*. Like *Dimarzipecten* and *Spathochlamys*, Genus A lacks a foliated-calcite transgression on the inner surface of its umbonal region, but this is a plesiomorphic state that cannot serve as an indicator of close relationship. Tentatively, Genus A is considered a member of the tribe Aequipectinini based on its microsculptural pattern.

If *Spathochlamys* originated from a species of *Dimarzipecten*, then it seems likely that this origin was within the middle Miocene. The latest *Dimarzipecten* thus far uncovered is the Chipola (Burdigalian) species referred to above, and the earliest undoubted *Spathochlamys* are the specimens of *S. vaginula*, late Miocene and early Pliocene, referred to below. Although fossil specimens of *Spathochlamys* are rare, those that have been brought together for this study suggest that *S. vaginula* of the Miocene and early Pliocene gave rise to both of the extant species but at different times. *S. vestalis* of the eastern Pacific probably originated in the late Miocene; *S. benedicti* of the western Atlantic probably originated in the late Pliocene.

***Spathochlamys benedicti* (Verrill and Bush, 1897)**

(Figs. 10a-k)

Pecten mundus Reeve, 1853, species 151, pl. 33, fig. 151, locality unknown, *non Pecten mundus* M' Coy, 1844, p. 97, Carboniferous of Ireland.

Chlamys benedicti Verrill and Bush, *In*: Verrill, 1897: 74-75, "off Marthas Vineyard, in 1356 fath., dead; West Indies, in 25 to 72 fath., living."

Chlamys benedicti Verrill and Bush, Verrill and Bush, 1898, 20(1139): 834-835, pl. 84, figs. 1-2.

Chlamys verrilli Dollfus, 1898: 180, new name for *Chlamys benedicti* Verrill and Bush, 1897, *non*

Pecten benedictus Lamarck, 1819. [invalid new name.]

Pecten (Chlamys) mundus Reeve, Bavay, 1902: 404-406, pl. 8, figs. 8, 9. "European" [erroneous].

Pecten (Chlamys) nymphe Bavay, 1906: 246-247, pl. 7, figs. 3, 4. "Caribæum mare?"

Pecten mundus Reeve, Bavay, 1913: 26, "Bahia" [Brazil].

Chlamys (Chlamys) benedicti Verrill and Bush, Weisbord, 1964: 139-142, pl. 14, figs. 8-11, Playa Grande Formation (Catia Member), "Pliocene" [now dated as Pleistocene], Distrito Federal, Venezuela.

Chlamys (Chlamys) munda Reeve, Fischer-Piette and Testud, 1967: 184-185, Brazil.

Types.— Johnson (1989: 23) designated as lectotype of *Chlamys benedicti* Verrill and Bush a specimen from the Yale Peabody collection (YPM 8833) on the grounds that the "figured holotype" that was supposed to be in the USNM could not be located. The lectotype, a single right valve illustrated by Johnson (1989, pl. 8, fig. 4), is from R/V *Albatross* Stations 2369-2374, 29° 11' 15"N, 85° 29' 32"W, south of Panama City, Florida, 25-27 fm (= 46-49m). In fact, Verrill and Bush (1897) did not specify a holotype in their original description, which referred to specimens from two localities. When they republished the same description a year later, they presented a drawing of one of their specimens, an articulated shell, USNM 202999, from United States Fish Commission [R/V *Albatross*] Stations 2369 to 2374, 25 to 27 fm, Gulf of Mexico between the Mississippi Delta and Cedar Keys, Florida. This is clearly the same set of stations from which the lectotype designated by Johnson (1989) came. Although Johnson's lectotype stands, the specimen illustrated in 1898 (USNM 202999) has now been located in the USNM collections.

The holotype of *Pecten mundus* Reeve, 1853, is a pair of matching valves, the left broken, in The Natural History Museum, London (BMNH 1950.11.14.48). The right valve is refigured herein (Figs. 10a,b).

The holotype of *Pecten (Chlamys) nymphe* Bavay, 1906, is the specimen illustrated herein (Figures 10c and 10d). The specimen, which is in Paris (MNHN), is the one that Bavay illustrated and apparently was the only specimen that was available to him at the time that he wrote his description.

Type locality.— Gulf of Mexico, 29° 11' 15"N, 85° 29' 32"W, south of Panama City, Florida, 25-27 fm (= 46-49m).

There is a potential source of confusion regarding the type locality of *Spathochlamys benedicti*. In their original description Verrill and Bush (1897: 75) referred to two

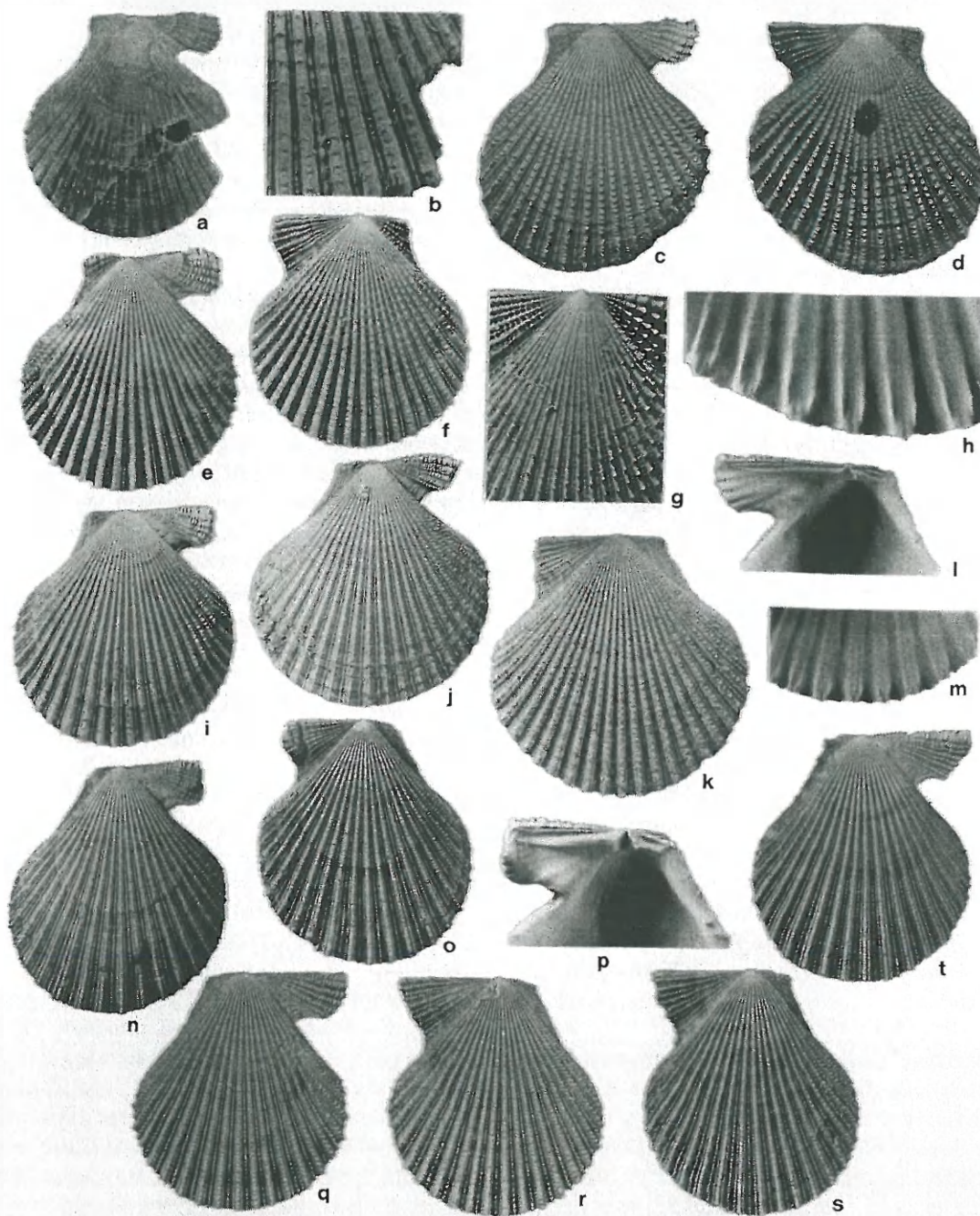


Fig 10. *Spathochlamys*. **a, b.** Holotype of *Pecten mundus* Reeve (= *S. benedicti*), BMNH 1950.11.14.48, locality unknown, right valve uncoated, height 13.3 mm, and detail of surface, horizontal field width 4 mm. **c, d.** Holotype of *P. nympha* Bayay (= *S. benedicti*), Caribbean?, Paris Museum, matching right and left valves, height 15.6 mm. **e-g.** *S. benedicti*, USNM 523035, Gulf of Mexico off Carabelle, Florida, matching right and left valves, height 17.0 mm., and detail of left exterior, horizontal field width 5.7 mm. **h.** *S. benedicti*, USNM 764660, Gulf of Mexico off Campeche, Mexico, internal rib carinae of left valve, horizontal field width 9 mm. **i.** *S. benedicti*, USNM(P) 474645, James City Fm., right bank of Neuse River, 3.2 km below James City, Craven Co., North Carolina, right valve, height 21.9 mm. **j.** *S. benedicti*, USNM(P) 474656, Pleistocene?, Minnitimmi Creek, Bocas Island, Panamá right valve, height 17.9 mm. **k.** *S. benedicti*, USNM(P) 474655, Pleistocene?, Bocas Island, Panamá, left valve, height 19.2 mm. **l, m, q, r.** *S. vestalis*, mainland morph, USNM 774188, Gulf of California off Angel de la Guardia Id., Mexico, matching right and left valves: right hinge of length 10.0 mm; internal rib carinae, horizontal field width 9.3 mm; right and left exteriors, valve height 17.8 mm. **n-p.** *S. vestalis* tectotype, BMNH 1992115. "West Indies" [erroneous], matching right and left valves, valve height 22.0 mm, and right hinge of length 9.3 mm. **s, t.** *S. vestalis*, mainland morph, USNM 774191, off North Isle, Pinas Bay, Panamá, matching left and right valves, height 14.9 mm.

localities, one "off Martha's Vineyard, in 1356 fath., dead," the other "West Indies, in 25-72 fath., living" [italics added]. Specimens from the first locality are present in the Smithsonian collection, catalogued as USNM 52542, USFC Station 2571, with the locality data from that station corresponding to that given in the original description. The lot consists of two right valves, the larger of which is exactly 6mm in height and lemon yellow in color; it is clearly the "largest specimen" referred to by Verrill and Bush in their original description.

In the following year, Verrill and Bush (1898: 834-835, pl. 84, figs. 1, 2) repeated their original description, but this time they provided a drawing of a pair of matching juvenile valves (USNM 202999). Because the description is identical to the first one, it can be inferred that the two localities to which they refer in the second description are also the same as in the first. The deeper station, USFC Sta. 2571, is certainly the same, but the second, from which the illustrated specimen came, presents a problem. In the 1898 description the second locality is given as "stations 2369 to 2374, in 25 to 27 fm [italics added]," and this time no mention was made of the West Indies. The station-book entries for USFC Stations 2369 through 2374 verify the depth range of 25 to 27 fm and give the locality as the Gulf of Mexico between the Mississippi Delta and Cedar Keys, Florida, 1885.

Because there is no material in the Smithsonian collections of *Chlamys benedicti* from the West Indies bearing either the depth range of 25-72 fm as originally published or 25 to 27 fm as published a year later, it is inferred that the references to "West Indies" and "72 fathoms" in the original description were errors and that the specimen later illustrated by Verrill and Bush (1898) from the Gulf of Mexico is one that was before them when they wrote the original description.

Diagnosis.— *Spathochlamys* with length of anterior outer ligament less than twice length of posterior outer ligament; major ribs commonly scaly throughout ontogeny; rib-flank costae poorly developed, not becoming scaly until late ontogeny; posterior auricles erect, with posterior auricular margins forming an angle with hinge line of 90° or less.

Morphological variation.— No apparent geographic trends in size, shell shape, or sculpture were detected across the broad geographic range of this species. The largest specimen examined has a shell height of only 23 mm, and most specimens are in the range of 10 to 15 mm.

Comparison.— *Spathochlamys benedicti* closely resembles its eastern Pacific geminate species, *S. vestalis*. Mature shells of the former have relatively larger posterior

auricles, the AOL/POL ratio being less than two, whereas in *S. vestalis* this ratio is greater than two. The posterior auricles of *S. benedicti* have an erect appearance, tending to form a right or acute angle with the hinge, whereas those of *S. vestalis* are uniformly obtuse. Lastly, the rib-flank costae of *S. benedicti* are generally not well developed and seldom bear prominent scales; in *S. vestalis* these same costae tend to develop early in ontogeny and form scales that rival those of the major ribs in height.

Spathochlamys benedicti resembles the extinct western Atlantic *S. vaginula* (Dall, 1898) in shape of disk and auricles but differs in having consistently scaly and trigonal ribs throughout ontogeny, even in the central sector of the disk. In *S. vaginula* the ribs lack scales in early ontogeny in the central part of the disk and are commonly rounded rather than trigonal in cross section. Lastly, *S. vaginula* from the Neogene of the Florida Peninsula attains a much larger size (commonly 30 to 35 mm in shell height).

Living Habits.— The species lives in tropical to temperate waters across a broad range of depths, from about 2 to 800 m, but generally seems to be most common on the middle shelf at depths ranging from about 40 to 90 m (Waller, 1973: 47). The deep byssal notch, prominent active ctenuellium, adhering byssal threads on mature dried shells, and data taken at the time of collection all indicate that *S. benedicti* is probably byssally attached throughout life. Individuals attach to a great variety of substrates, including coral debris, sponges, and algal mats (Waller, 1973, and unpub. data). Reed and Mikkelsen (1987) referred to *Chlamys benedicti* as being a common member of the community associated with the scleractinian coral *Oculina varicosa* Lesueur, 1830, off eastern Florida.

Geographic Range.— Although dead specimens have been collected as far north as Latitude 40° 9' N, southeast of George's Bank (the locality referred to by Verrill and Bush in their original description), the distribution of this species is primarily from off Cape Hatteras southward throughout the Gulf of Mexico and Caribbean and as far south as Brazil. Rios (1985: 222) reported the species (as *Chlamys munda*) in Brazil from Amapá to Espírito Santo and in the Abrolhos and Trindade Islands. The species is also present in Bermuda (Waller, 1973).

Stratigraphic Range.— Upper? Pliocene to present.

Fossils of *Spathochlamys benedicti* are reported herein for the first time from the James City Formation of North Carolina (Fig. 10i). There is now substantial agreement that the age of this formation is early Pleistocene (Cronin *et al.*, 1984: 40; Ward and Blackwelder, 1987: 114; Miller III, 1989; Cronin, 1990). Weisbord (1964) reported

the species from the Playa Grande Formation (Catia Member) of Venezuela. The age of the Playa Grande Formation is generally considered to be early Pleistocene (Bermúdez, 1980: 303), not early Pliocene as originally stated by Weisbord (1964), but the stratigraphic relationships of formations in the Cabo Blanco area of Venezuela are still controversial (e.g. see, for example, Gibson-Smith, 1976: 4). The fossil occurrences in Costa Rica are from beds now placed in the Moín Formation, which most workers have considered to be Pleistocene in age (e.g. Akers, 1972: 42; Cassell and Sen Gupta, 1989: 147; Robinson, 1990; Lyons, 1991: 159). Coates *et al.* (1992: 821), however, date what are apparently the same beds as late Pliocene-early Pleistocene. The Panamanian fossils (Figs. 10j,k) are all from Bocas del Toro area from beds that contain a fauna that is clearly younger than that of the Miocene Gatun Formation and is assumed herein to be of late Pliocene or early Pleistocene age. Coates *et al.* (1992: 819) have recently described a stratigraphic sequence in this general area that extends in age from the late Miocene through the Pliocene, but they do not specifically mention what is present on Bocas Island and Nancy Cay, the sites that yielded *S. benedicti*. The oldest known representative of *S. benedicti* could be a specimen [USNM(P) 474649] from the Quebradillas Limestone of Puerto Rico. This limestone apparently forms the upper part of the Camuy Formation and may be early Pliocene in age but younger than the Gurabo Formation of the Dominican Republic and the Bowden shell beds of Jamaica (Bermúdez and Sieglie, 1970).

Discussion.— The holotype of *Pecten mundus* Reeve, BMNH 1950.11.14.48, was examined. It is a pair of matching valves, both broken, the right valve (Fig. 10a) having a restored height of 12.7 mm. Reeve's species is clearly a senior synonym of *Chlamys benedicti* but is a junior primary homonym of *P. mundus* M'Coy, 1844, a fossil from the Carboniferous of Ireland.

Dollfus (1898: 180) introduced the new name *Chlamys verrilli* to replace *Chlamys benedicti* Verrill and Bush on the erroneous assumption that Verrill and Bush's name is a junior homonym of *Pecten benedictus* Lamarck, 1819. The endings of the two names, however, differ in case, not in gender, and this is sufficient to prevent homonymy.

Bavay (1902) applied the name *Pecten (Chlamys) mundus* Reeve to two small shells in a collection said to come from Corsica and concluded that the species is "European and even French" [translation]. Although the specimen that he illustrated appears to be what is here called *Spathochlamys benedicti*, there is no reason to believe that the locality data are correct. My own studies of

European pectinid collections have not turned up any authentic records of the species in the eastern Atlantic. In a later publication, Bavay (1913: 26) identified shells from Salvador (Bahia), Brazil, as *P. mundus* Reeve, concluding that the species is present on both sides of the Atlantic. In support of this contention, he reported that *P. commutatus* Monterosato, a well-known Mediterranean species, also occurs in Bahia, Brazil. It seems more likely, however, that his "*P. commutatus*" was in fact *Argopecten noronhensis* (Smith, 1885), a species which is known only from the western Atlantic and which may co-occur with *S. benedicti* (Waller, 1973).

Bavay (1906) described *Pecten (Chlamys) nymphe* on the basis of a shell in the Paris museum collection. Because the shell was found glued to a board that also held a specimen of *P. antillarum* Récluz, 1853, a well-known Caribbean species, Bavay assumed that his new species also came from that region. The holotype, a pair of matching valves marked by Bavay as the figured type, is refigured herein (Figs. 10c, d). It is clearly a junior synonym of *Spathochlamys benedicti*.

Weisbord (1964: 139), in his report of fossil *Chlamys benedicti* from the Pleistocene Playa Grande Formation of north central Venezuela, referred (p. 141) to "the type" of *C. benedicti* and to "illustrations of the type" but gave no references. He was apparently assuming that the specimen illustrated by Verrill and Bush (1898) is the holotype, although it was never specified as such.

Fischer-Piette and Testud (1967) applied the name *Chlamys munda* Reeve to specimens from Brazil, apparently drawing support from Bavay's (1913) previous report of its occurrence there. Apparently neither Fischer-Piette and Testud (1967) nor Bavay (1902, 1913) were aware that the name *C. benedicti* was already in use for this same species in the western Atlantic.

Material examined.— Recent material: USNM: about 500 lots, from throughout the geographic range of the species; BMNH: syntypes of Reeve (1853) listed in above synonymy; BRM: 7 lots, from Antilles and South America; LM: 18 lots, mainly from off Guyana; MNHN: 7 lots, from South America.

Fossil material: USNM:

North Carolina

USNM(P) 474645, 1 RV, USGS D273, "Croatan Sand", right bank of Neuse River, 3.2 km [2 miles] below James City, Craven County. Collected by MacNeil and Malde, 1954.

USNM(P) 474646 and 474647, 2 RV, James City Formation, about 0.4 km [$\frac{1}{4}$ mile] upstream from Johnson Point and at Johnson Point, right bank of Neuse River,

Craven County. Collected by T. R. Waller, 1963.

Mississippi

USNM(P) 474648, 10 RV, 12 LV, USGS 24729, shell bed between Clay Units I and II (Morgan *et al.*, 1968, p. 151,152), on Mudlump 90, a mudlump island to the west of the entrance to the South Pass of the Mississippi River delta. Collected by T. R. Waller, 1969.

Puerto Rico

USNM(P) 474649, 1 RV, USGS 19814, Quebradillas Limestone, from sink on Ramey Air Force Base, 1 km west and 3.3 km south of edges of quadrangle, Aquadilla Quadrangle. Collected by C. W. Cooke and A. D. Watt, 1955.

Costa Rica

USNM(P) 474650, 1 LV, USGS 5884b, section exposed in railroad cut, from third fossiliferous zone above level of rails, Moín Hill. Collected by D. MacDonald, 1911.

USNM(P) 474651, 1 LV, USGS 18693, "colline en démolition," Limón. Collected by Pittier, 1898 or 1899.

USNM(P) 474652, 1 RV, 1 LV, USGS 21035, hillside cut and spoils dump at new site of buildings of Colegio de Limón in northeastern outskirts of Puerto Limón. Collected by E. Malavassi, A. A. Olsson, and W. P. Woodring, 1958.

USNM(P) 474653, 2 RV, USGS 21036, scraped hillside slope in Barrio Cementario distinct in southern outskirts of Puerto Limón, east of cemetery. Collected by E. Malavassi, A. A. Olsson, and W. P. Woodring, 1958.

Panamá

USNM(P) 474654, 1 LV, USGS 8306, Bocas Island. Collected by A. A. Olsson, 1917.

USNM(P) 474655 (Fig. 10k), USGS 8307, 1 LV, Bocas group, Bocas Island. Collected by A. A. Olsson.

USNM(P) 474656 (Fig. 10j), USGS 8309, 3 RV, 1 LV, Minnitimmi Creek, Bocas Island. Collected by A. A. Olsson.

USNM(P) 474657, 11 RV, 7 LV, USGS 8349, Bocas group, Conch Point member, Bocas Island. Collected by A. A. Olsson and Sears, 1919.

USNM(P) 474658, 2 RV, USGS 8494, "*Spondylus* group" [apparently with reference to a group of strata], Nancy Cay. Collected by A. A. Olsson, 1919.

Spathochlamys vestalis (Reeve, 1853)

(Figs. 10 l-r; 11 a,b)

Pecten vestalis Reeve, 1853, species 154, pl. 33, fig. 154, "West Indies" [erroneous].

Pecten (Chlamys) lowei Hertlein, 1935: 308-311, pl. 19, figs. 1, 2, 7, 8. "Gulf of California; Galápagos Islands. ?Catalina Island, California."

Types.— The syntypes of *Pecten vestalis* Reeve comprise three specimens: a pair of matching valves and two smaller specimens, one a right valve and the other a non-matching left valve. The first, BMNH 1992115 (Figs. 10n,p), ht. = 22.0 mm, L = 19.3 mm, is the specimen figured by Reeve (1853, pl. 33, species 154) and is selected herein as the lectotype.

The holotype of *Pecten (Chlamys) lowei* Hertlein is a pair of matching valves, California Academy of Sciences, no. 6878, from Carmen Island, Gulf of California, depth 37 m (20 fm) (Hertlein, 1935: 308, pl. 19, figs. 1,2,7,8).

Type locality.— Eastern Pacific off Baja California, Mexico.

Diagnosis.— *Spathochlamys* with length of anterior outer ligament greater than twice length of posterior outer ligament; rib-flank costae beginning on right valve at shell height of less than 12 mm; rib crests with scales ranging from very high in relief to low and sometimes absent on ribs in center of disk; free margin of posterior auricle slightly concave or straight, forming an angle with dorsal margin exceeding 110°.

Morphological variation.— *Spathochlamys vestalis*, like *S. benedicti*, is small in size, seldom attaining a shell height greater than 23 mm. Unlike its western Atlantic counterpart, *S. vestalis* displays some geographic variation in morphology, particularly between mainland populations and those of the Galápagos Islands. These end-points of variation are referred to below as the "mainland morph" and the "Galápagos morph."

The mainland morph (Figs. 10 l-t), which includes the lectotype (Figs. 10n-p), is typified by populations from Santa Catalina Island, California, southward along Baja California, Mexico, throughout the Gulf of California, and along the Mexican coast. These morphs are characterized by the abundant well-developed scales both on the crests of the major ribs and on the secondary rib-flank and medial costae. They also have a conspicuous commarginally lirated stage in early ontogeny. In this early stage, the commarginal lirae are prominent in the rib interspaces and are of higher relief than the proximal ends of the medial costae, which are interrupted by the lirae. The extent of the lirated stage is variable, extending to shell heights from 6 to 10 mm on the right valve and slightly less on the left valve. The number of major ribs is generally 20 or 21, but there may be as few as 17 or as many as 23.

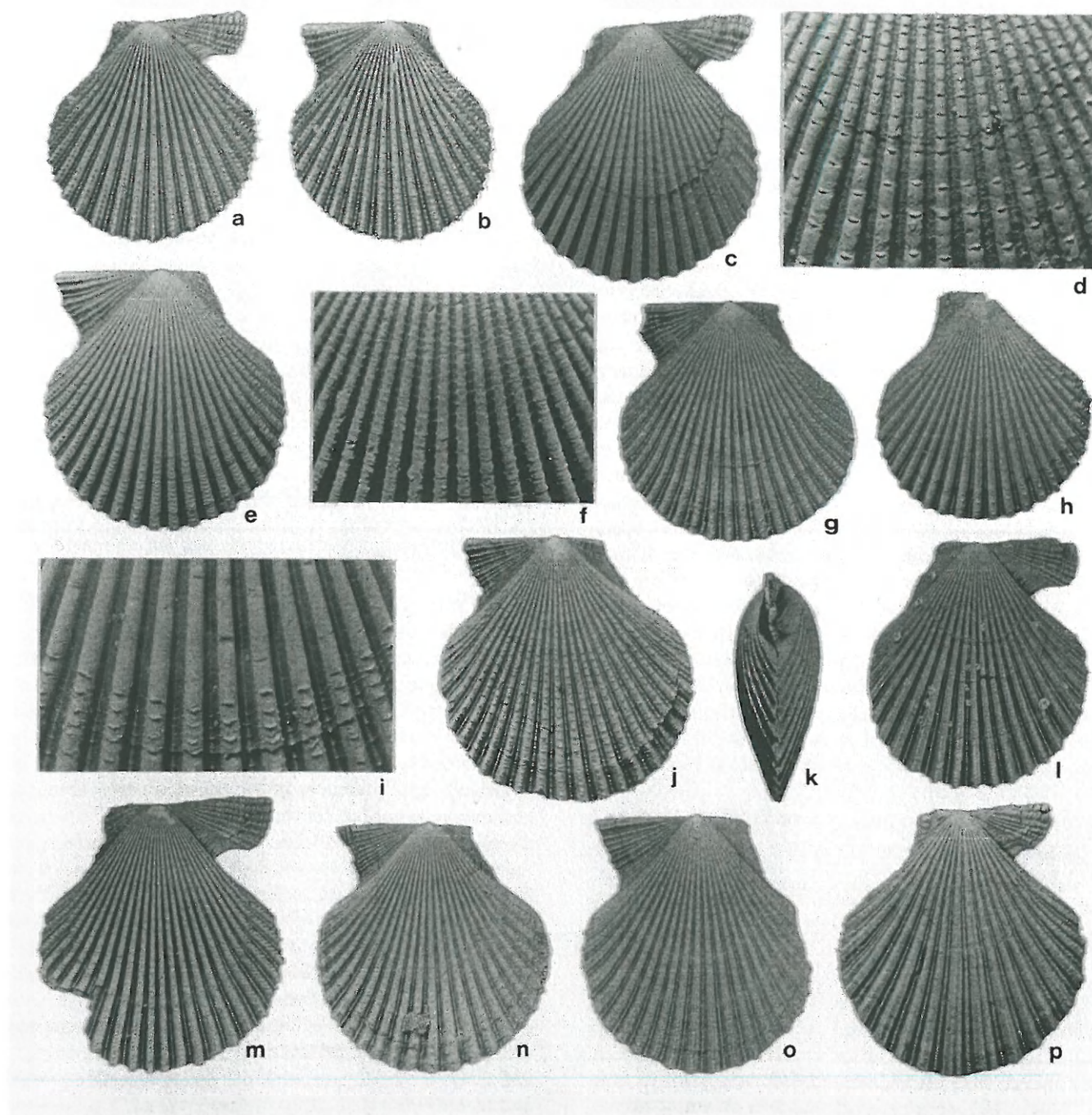


Fig. 11. *Spathochlamys*. **a, b.** *S. vestalis*, Galapagos morph, USNM 774206, Tagus Cove, Albemarle Id., Galápagos Ids., Ecuador, matching right and left valves, height 12.2 mm. **c-f.** *S. vaginula*, lectotype (right valve) and paralectotype (non-matching left valve), USNM(P) 135786, USGS Loc. 2580, Lower Pliocene, Bowden Beds, Bowden, Jamaica: right valve, height 14.4 mm; ribbing of right valve, horizontal field width 5.5 mm; left valve, height 14.5 mm; ribbing of left valve, horizontal field width 7 mm. **g-i.** *S. vaginula*, USNM(P) 474659, Upper Miocene or Lower Pliocene, Gurabo Fm., Río Yaque del Norte, Dominican Republic: left valve, height 13.8 mm; non-matching right valve missing anterior ear, height 12.8 mm; detail of ribbing on left valve at start of scaly phase, horizontal field width 6 mm. **j.** *S. vaginula*, USNM(P) 474660, Upper Miocene or Lower Pliocene, Gurabo Fm., Río Gurabo, Dominican Republic, left valve, height 14.8 mm. **k-o.** *S. vaginula*, Tamiami Fm. *sensu* Waldrop and Wilson (1991) [= "Bed 11"], APAC Pit, near Sarasota, Sarasota Co., Florida: **k**) USNM(P) 474661, anterior view, height 30.2 mm; **l**) USNM(P) 474662, right valve, height 33.1 mm; **m**) USNM(P) 474663, right valve, height 22.8 mm; **n**) USNM(P) 474664, left valve, height 33.9 mm; **o.** USNM(P) 474665, left valve, height 29.1 mm. **p.** *S. vaginula*, USNM(P) 474666, Upper Miocene or Lower Pliocene, near base of Jackson Bluff Fm., Jackson Bluff, Leon Co., Florida, right valve, height 22.2 mm.

On the basis of the few specimens available for study, mainland morphs from off Panamá (Fig. 10s, t) and Colombia and some of those from off Isla Clarión, Islas de Revillagigedo, Mexico, differ from the typical mainland morphs in having smaller scales and smoother rib interspaces in early ontogeny. They tend to lack conspicuous commarginal lirae in the interspaces of the right valve before the start of medial costae, while their left valves retain a commarginally lirated early growth stage. The absence of commarginal lirae is not due to wear, because fine antimarginal microsculpture is still present in the interspaces.

The Galápagos morph (Figs. 11a,b) differs in having a broader umbonal angle (95 to 100°, in contrast to that of the mainland morph, which has an umbonal angle ranging from 85 to 96°). The Galápagos morph is also somewhat more inflated even though it is smaller in size. The most distinctive feature of the Galápagos morph, however, is the diminutive scales present on the rib crests. The rib crests are somewhat flattened while still retaining a narrow central keel bearing the scales. With few exceptions, specimens from the Galápagos Islands are of this morphology. This morph also occurs, however, off Isla Gorgona, Colombia (LACM: AHF 221-34), and off La Plata Island, Ecuador (LACM: AHF 213-34). Both of these islands are near the shelf edge.

These morphs are not separated by a distinct morphological gap. Transitional specimens occur, although rarely, in the Galápagos Islands and also along the Ecuador coast.

Comparison.— *Spathochlamys vestalis* differs from both *S. benedicti* and *S. vaginula* in having a more asymmetric hinge line, with the anterior outer ligament much longer than the posterior one. The AOL/POL ratio in specimens greater than 12 mm in shell height is generally above 2.05 in *S. vestalis* and is commonly in the range of 2.2 to 2.7. In *S. benedicti* the AOL/POL ratio is generally less than 2.0 and commonly in the range of 1.8 to 1.9. The posterior auricles of *S. vestalis* compared to *S. benedicti* are not only smaller relative to the anterior auricles, but they also are more oblique with a straighter, more inclined posterior margin. This difference in posterior auricular obliquity increases with ontogeny. The secondary rib-flank costae, one on each side of each major rib in the central region of the disk, generally appear earlier in *S. vestalis* than in the other species although there is considerable overlap in time of appearance with that in *S. benedicti*. The medial costae on the right valve of *S. vestalis* generally begin later in ontogeny than in *S. benedicti*. In *S. vestalis* these costae seldom originate before a shell height of 3 mm is reached; in *S. benedicti* the origination point is generally at shell heights

ranging from 1.5 to 2.5 mm.

Hertlein (1935: 309) compared his new species, *Pecten (Chlamys) lowei* (= *P. vestalis*), to several fossil species. These fossil taxa, however, are not closely related, and most are now known to belong to the tribe Aequipectinini. This is also true for *Chlamys corteziana* Durham, 1950 (see also Moore, 1984: B22), which Durham (1950, p. 64) thought resembled *C. lowei*. *C. onzola* Olsson, 1964, thought by Olsson (1964: 35) to be "probably closest to *C. lowei* (Hertlein)", is also not closely related. I examined the holotype of Olsson's species and found that it is more closely related to the extant eastern Pacific *C. incantata* Hertlein, 1972, of the Galápagos Islands. Hertlein (1972) thought that this Galápagos species "bears a general similarity to that of illustrations of *P. (Chlamys) nymphe* Bavay", a species that is now known to be a junior synonym of *Spathochlamys benedicti* (see above). Sculptural details of both *C. onzola* and *C. incantata*, however, indicate that these species both belong in *Veprichlamys* Iredale, 1929, an Indo-Pacific genus that can be placed in the tribe Chlamydini on the basis of its pre-radial microsculpture and lack of internal rib carinae.

Living habits.— The total depth range of live *Spathochlamys vestalis*, based on specimen data in the USNM collection, is from 9 to 183 m, with most specimens having been dredged between 40 and 90 m. Grau (1959) and Bernard (1983) listed depths as shallow as one and two meters, but such shallow occurrences do not appear to be common for living specimens. There do not appear to be any significant differences in the depth preferences of the two morphs described above nor among different parts of the geographic range of the species. Bernard (1983) gave the sea-bottom temperature range of the species as 10 to 29°C. Data on substrate preference and living position are few. Grau (1959: 93) concluded that the species occurs on "rocky, sandy or muddy bottoms, associated with algae, kelp, bryozoa, coral, coralline and sponge." The only specimens in the USNM collections with the bottom type indicated as mud were collected as dead valves. Some specimens show nearly total cover by thin encrusting sponge, and the persistent byssal notch suggests persistent byssal attachment.

Geographic range.— From Santa Catalina Island, California (USNM 774180) southward to Isla La Plata, Ecuador (1° 16' S. Lat.; USNM 774194), in Gulf of California as far north as Bahía San Felipe (USNM 774189), and in the Galápagos Islands (Grau, 1959: 92).

Stratigraphic range.— Upper? Miocene to Recent.

The Upper Miocene limit is based on the occur-

rence of this species in the Imperial Formation of southern California (Powell, 1986, 1988), discussed below.

Discussion.—Reeve gave the locality for this species as "West Indies", but the morphology of the syntypes (Figs. 10n-p) clearly indicates that they belong to the eastern Pacific species *Pecten (Chlamys) lowei* Hertlein, 1935, which thus becomes a junior synonym of *P. vestalis* Reeve, 1853. The features of Reeve's syntypes that are characteristic of the eastern Pacific species are as follows:

(1) The ratio of the length of anterior outer ligament to length of posterior outer ligament (AOL/POL) is 2.56 in the lectotype and 2.41 and 2.46 in the paralectotypes. These ratios are higher than any found in the western Atlantic species (AOL/POL = 1.76 to 2.03 where height is greater than 12 mm, n=6) but are within the normal range of variation of the eastern Pacific species (2.04-2.88 where height is greater than 12 mm, n=9).

(2) The rib-flank costae of the right valves of the syntypes of *Pecten vestalis* begin at heights of 7.5 and 10 mm. This is earlier than the beginning of comparable costae in the western Atlantic species but is consistent with the ontogeny of these costae in the eastern Pacific species.

(3) The numbers of major ribs on the right valves of the syntypes of *Pecten vestalis* are 21 (lectotype) and 19 (both paralectotypes), lower than the number of major ribs present on right valves of the western Atlantic species (22-24).

Provenance data in nineteenth century works such as Reeve's *Conchologia Iconica* are notoriously inaccurate, and I have uncovered other locality inconsistencies in Reeve's work. That shells from the Pacific side of North America were available to Reeve is indicated by the fact that he described two other pectinids from this region, *Pecten arthriticus* [now *Nodipecten arthriticus*; see Smith, 1991a: 88] and *P. leucophaeus* [= *Argopecten circularis* (Sowerby); Waller, unpub. data]. Both of these species were listed by Reeve as from unknown localities. Vokes (1991) has commented on similar errors.

The only known reports of *Spathochlamys vestalis* from the fossil record are those of Powell (1986, 1988 reported as *Chlamys lowei*) from the Imperial Formation of southern California. As detailed above, fossil taxa considered closely related to "*Chlamys lowei*" by Hertlein (1935, 1972) and Olsson (1964) are neither ancestral nor congeneric. Moore (1984) listed no records of *S. lowei* in her compendium of Tertiary Pectinidae of California and Baja California, and my own search of the extensive Pacific Coast collections of the USNM did not turn up any specimens. The possibility that this species will eventually be found in strata as old as Pliocene is based on its inferred

derivation from an Atlantic ancestor while seaways were still open.

I examined the collection from the Imperial Formation on loan from UCMP to C.L. Powell II at USGS(MP). Two specimens of *Spathochlamys vestalis* were found, both from UCMP Locality A-1415, a part of the section that Powell places in the lower part of the upper member of the formation and interprets as possibly representing a storm deposit formed at inner-shelf depths (Powell, 1993, pers. comm; also see Powell, 1985). One of these specimens is a small incomplete left valve (ht., 9.4 mm) on which rib-flank costae have not yet developed. Medial costae appear to begin late (at about 4.5 mm). These ontogenetic features are consistent with those in *S. vestalis*. The second specimen is a badly crushed and incomplete valve missing its dorsal region. Its original height was probably about 12 mm. Scaly rib-flank costae are present and appear to have formed at a reconstructed shell height of about 7 mm, also consistent with this feature in *S. vestalis*.

The age of the Imperial Formation has been a matter of some debate, but it apparently includes sediments of both Miocene and Pliocene age (Powell, 1985, 1986, 1988; Smith, 1991b). The deposits in the northern Salton Trough area of Riverside County, California, that yielded the specimens of *S. vestalis* appear to be no younger than late Miocene. This age constraint is based on a radiometric (K/Ar) date of about six million years obtained from a basalt flow in overlying beds (Powell, 1986, 1988; Smith, 1991b; based on data in Matti *et al.*, 1985).

Material examined.—Recent material: USNM: Pacific Ocean off southern California and Mexico, 7 lots, 22 specimens; Gulf of California, 17 lots, 33 specimens; Panamá, 4 lots, 9 specimens; Colombia, 1 specimen; Ecuador, 1 specimen; Galápagos Islands, 16 lots, about 40 specimens. LACM: Gulf of California, 11 lots, about 50 specimens; Mexico: 7 lots, 10 specimens; Panama: 2 lots, 3 specimens; Colombia: 2 lots, 2 specimens; Ecuador mainland: 3 lots, 4 specimens; Galápagos Islands: 22 lots, 72 specimens.

Fossil material: UCMP Loc. A-1415(RAB 168A): "About the center of the north boundary of NE¹/₄ of NW¹/₄ of section 36, T2S, R3E, [Desert Hot Springs 7.5' Quadrangle, Riverside County, California]. About 1m (50 ft.) south of the divide, in the stream bed of the head of the north directed branch [which separates from the main canyon about 1370 m (4500 ft) from its mouth] of the second canyon east of the Whitewater River. Pebble-bearing siltstone. Collected by R. Bramkamp. (=Burro Bend Member)." (Powell, 1986, Appendix 2.) Two valves, both incomplete.

Spathochlamys vaginula (Dall, 1898)

(Figs. 11c-p)

Pecten (Chlamys) ornatus Lamarck? var. *vaginulus* Dall, 1898: 715-716, "Oligocene", Bowden, Jamaica.

Pecten vaginulus Dall, Maury, 1917: 186, pl. 34, fig. 7. Tertiary, Samba Hills, Dominican Republic

Chlamys (Chlamys) vaginulus (Dall), Woodring, 1925:65-66, pl. 8, figs. 1, 2, "Miocene", Bowden, Jamaica.

Types.— Dall (1898: 715-716) mentioned having "seven small valves" of his new variety from the Bowden Beds of Jamaica but provided no illustration, no measurements, and no type designation. This type series was subsequently referred to by Schuchert et al. (1905: 490) as "cotypes" and was catalogued as USNM(P) 135786. The entry for this number in the catalogue, however, mentions only six valves. The discrepancy is apparently due to the recognition, after Dall's 1898 publication, that one of the seven valves does not belong to the same species. (In fact it is an *Argopecten*, not a *Spathochlamys*.) Woodring (1925, pl. 8, figs. 1, 2) provided the first illustrations of members of the type series, a right valve and a non-matching left valve, but continued to refer to these as cotypes. The right valve illustrated by Woodring (1925, pl. 8, fig. 1) is herein selected as the lectotype and refigured (Figs. 11c-f). The type locality is USGS 2580 (see following section on materials examined)

Diagnosis.— *Spathochlamys* with length of anterior outer ligament commonly greater than twice length of posterior outer ligament, especially where shell height exceeds 20 mm; early ribs commonly rounded rather than trigonal in cross section, with scales variably developed or absent; rib-flank costae not appearing until late in ontogeny, generally at shell heights exceeding 12 mm; medial costae variably developed, commonly weak in early ontogeny of left valve; ontogenetic persistence of commarginal lirae in rib interspaces variable, commonly persisting throughout ontogeny, with height of lirae greater than that of medial costae in early ontogeny; posterior margins of posterior auricles slightly concave to nearly straight, forming oblique angle with dorsal margin.

Morphological variation.— In addition to the six valves of the type series from the Bowden Shell Beds of Jamaica, there are about 30 additional valves and fragments from the type locality (USGS 2580) in the USNM collections. The range of variation of these specimens seems to encompass the morphology of specimens from the Gurabo Formation of the Dominican Republic. In general these Bowden and Gurabo specimens have robust simple ribs that tend to be

rounded in cross section in early ontogeny, becoming trigonal later. Rib-flank costae are present only on the largest specimens and commonly do not begin to form in ontogeny until a shell height of about 15 mm is reached. The Bowden and Gurabo specimens share rib counts within the range of 21 to 25. Trigonal ribs are common among the specimens from the Dominican Republic but rare among the specimens from Bowden, Jamaica. The Bowden specimens in general have more prominent commarginal lirae in rib interspaces and medial costae that begin later in ontogeny than in the Dominican Republic.

Specimens of *Spathochlamys* from the Tamiami Formation in a pit near Sarasota, Florida (see below), also appear to be within the range of variation of *S. vaginula*. The Tamiami specimens (Figs. 11k-o) differ from those of the Bowden Shell Beds of Jamaica and the Gurabo Formation of the Dominican Republic mainly in being of much greater size, with shell heights ranging from 18 to 34 mm (mean = 27 mm) compared to the maximum shell height of 17 mm for the other samples. Like the Bowden specimens, however, those from the Tamiami Formation have ontogenetically persistent commarginal lirae in rib interspaces, robust rounded major ribs, and late-appearing medial costae.

A single right valve 22 mm in height [USNM(P) 474666, Fig. 11p] was collected by the author from near the base of the Jackson Bluff Formation of Florida (see following discussion of stratigraphy). It resembles the specimens from the Bowden, Gurabo, and Tamiami Formations in having poorly developed scales on the crests of ribs in the center of its disk and in lacking clearly delimited rib-flank costae. The Jackson Bluff specimen differs, however, in having fewer ribs (only 18 at the valve margin compared to 21 to 25 in the other samples). Furthermore, the ribs of the Jackson Bluff specimen are distinctly trigonal in cross-section, and a few of the central ribs bifurcate. The latter feature has been observed to occur in extant species in response to injury or simply as extremes of variation in otherwise simple-ribbed populations.

Comparison.— *Spathochlamys vaginula* differs from both of the extant species, *S. benedicti* and *S. vestalis*, primarily in having less scaly rib crests on the central part of the disk at least in early ontogeny and in having less trigonal ribs at an early growth stage. Many but not all specimens of *S. vaginula* have ontogenetically persistent commarginal lirae in rib interspaces, whereas in the extant species these are limited to early ontogeny.

Weisbord (1964: 142) included both "*Chlamys vaginula* Dall" and "*Pecten (Chlamys) portoricensis*" in his comparisons for *Spathochlamys benedicti*. As discussed above in the description of *Spathochlamys*, *P. portoricensis*

sis differs from all *Spathochlamys* species in having an *Aequipecten*-like microsculpture in early ontogeny and is not considered to be congeneric.

Paleoecology.— The molluscan fauna of the Bowden Formation of Jamaica has been interpreted as representing a paleoecological mixture that includes deep-water elements (Woodring, 1928: 37-38). Specimens of *Spathochlamys vaginula* from the Dominican Republic appear to be restricted to facies representing deposition in deeper waters. Saunders *et al.* (1986: 16) noted that depth of deposition increased rapidly in the part of the Gurabo Formation that yielded NMB 15941 and 15835 (see below), with water depths eventually exceeding 200 m. A specimen from about this same level (TU Loc. 1210) is covered by a cemented *Dimya* sp., a genus that is most commonly found at present on the outer continental shelf and slope (H. E. Vokes, 1979: 37). One of the Río Yaque samples, TU 1227A, occurred in a lens interpreted to be a turbidity-flow lens, again suggesting deep water. Scleractinian corals collected at this same locality suggested to Cairns and Wells (1987: 25) a depth of deposition greater than 200 m. The single valve of *S. vaginula* from the Jackson Bluff Formation of Florida (see below) is from the part of this formation determined by DuBar and Taylor (1962: 356) to represent maximum marine transgression and maximum water depth, which they inferred may have been up to 20 fm (37 m) deep. The *S. vaginula*-bearing bed in the pit near Sarasota (Unit 11 of Petuch, 1982a) was interpreted by Petuch (1982a: 19) as representing "a quiet, deeper water lagoonal habitat with depths of around 10 m," but the remains of whales, sharks, and brachiopods suggest to this author that a deeper water environment may have been present. That was also the opinion of E. H. Vokes (1988: 2, footnote), who suggested that the Tamiami deposits in the Sarasota area represent "a more offshore facies" than the overlying Pinecrest Beds.

Geographic range.— North Carolina, Florida, Jamaica, and the Dominican Republic.

Stratigraphic range.— uppermost Miocene (planktic foraminiferal zone N17) through lower Pliocene (upper planktic zone N19/N20).

The definition and age of the Tamiami Formation of south Florida have been matters of considerable confusion, the history of which was most recently summarized by Lyons (1991: 137). In a paper that was written while Lyons's study was in press, Waldrop and Wilson (1990) have further clarified part of this history and have provided some biostratigraphic constraints on the age of the formation in the Sarasota area. They restrict the term Tamiami Formation to beds unconformably underlying the

"Pinecrest Beds" in the APAC (or MacAsphalt) Pit at Sarasota. (The latter formational name is preoccupied, and Waldrop and Wilson renamed these beds the Fruitville Formation.) They also report (p. 202) that at some localities near Sarasota the Tamiami Formation interfingers with beds of the upper Bone Valley Formation and that the vertebrate fossils overlying the Tamiami Formation at these sites are of late Hemphillian age. Tedford *et al.* (1987: 183), on the basis of K/Ar and fission-track dates, gave 4.5 to 6 Ma as the age of the late Hemphillian interval (cited incorrectly as 4.5 to 5.0 Ma in Waldrop and Wilson, 1990: 202). This interval thus spans the Miocene-Pliocene boundary, which most workers now agree is at approximately 5 ma (5.2 ma in Haq *et al.*, 1987: 1158). This would suggest that the specimens of *Spathochlamys vaginula* from the Tamiami Formation in the Sarasota area are of either latest Miocene or earliest Pliocene age. The overlying Pinecrest Beds (Fruitville Formation of Waldrop and Wilson, 1990) are apparently middle to late Pliocene in age (Akers, 1972; Waldrop and Wilson, 1990; Jones *et al.*, 1991).

The specimens of *Spathochlamys vaginula* from the Gurabo Formation of the Dominican Republic are probably of approximately the same age as those from the Tamiami Formation at Sarasota, Florida. In the extensive collections from along the Río Gurabo in the Dominican Republic made by Peter Jung and colleagues of the Natural History Museum of Basel, Switzerland, this species occurs in only two samples, NMB 15941 and 15835. These are closely spaced stratigraphically, NMB 15835 occurring only about 2 m above NMB 15941. As stated by Saunders *et al.* (1986: 17), NMB 15941 lies about 5 m below the Miocene-Pliocene boundary if that boundary is demarcated by the first occurrence of the planktic foraminifer *Globorotalia margaritae* Bolli and Bermúdez, 1965. They also note that NMB 15941 represents the approximate stratigraphic position of the nannofossil NN11-NN12 zonal boundary, generally taken to be just below the Miocene-Pliocene boundary. This NN11-NN12 zonal boundary occurs within the upper part of planktic foraminiferal zone N17 (Bybell and Poore, 1991, fig. 2). The only other Río Gurabo specimens known to me are from two localities, USGS 8548 and TU 1210, both of which are apparently close to but somewhat higher than the site of the NMB samples (Saunders *et al.*, 1986, text-figs. 4, 5). Other specimens from the Dominican Republic are from sections along the Río Yaque del Norte, collected by both the U. S. Geological Survey (USGS 8726) and by H. E. and E. H. Vokes of Tulane University (TU 1227A).

The Bowden Formation of Jamaica is now generally considered to be within the *Globorotalia margaritae* zone and hence of early Pliocene age (Bolli and Bermúdez, 1965, pp 125, 146; Bolli and Premoli Silva (1973: 479, fig.

2; Jung, 1989: 11). The presence of *G. margaritae* in the Bowden suggests that this formation may be younger than that part of the Gurabo Formation that yielded *Spathochlamys*, which is below the *G. margaritae* zone. In the Dominican Republic the *G. margaritae* zone begins just above the nannofossil NN11/NN12 boundary (upper zone N17) and extends to the NN15/NN16 boundary (Saunders *et al.*, 1986, table 3), this upper limit being near the top of planktic foraminiferal zone N19 (Bybell and Poore, 1991, fig. 2). Both Woodring (1928: 37-38), on the basis of molluscan faunas, and Bold (1971: 327), on the basis of ostracode faunas, considered the Bowden shell beds to be stratigraphically correlative with the Gurabo Formation.

The single, possibly aberrant, valve of *Spathochlamys vaginula* collected from near the base of the Jackson Bluff Formation in western Florida is possibly about the same age as the Gurabo specimens. The lower Jackson Bluff Formation (the *Ecphora* faunizone) was dated as early Pliocene (middle of Zone N18 to within Zone N19) at its type area at Alum Bluff on the basis of planktic foraminifera, among which is *Globorotalia margaritae* (Akers, 1972: 15 and 20). At Jackson Bluff, from a locality near where the *Spathochlamys* reported here was obtained, Akers (1972: 20) obtained planktic foraminifera that indicated an age ranging from the upper part of Zone N18 to the upper part of Zone N19, but his samples did not include *G. margaritae*. Because the precise location of the foraminiferal samples relative to the base of the Jackson Bluff formation was not specified, it is possible that the *Spathochlamys* collected by me from less than a meter above the base of the formation is near the maximum allowable age (N18) determined by Akers (1972: 15). Zone N18 is just above the Miocene-Pliocene boundary,

Discussion.— *Spathochlamys vaginula* is the closest of the three species of *Spathochlamys* to the probable outgroup genus, *Mimachlamys*, in having the greatest extent of left-valve rib development without scales, the least trigonal rib cross-sections in early ontogeny, the ontogenetically latest appearing medial costae in the rib interspaces, and the most ontogenetically persistent commarginal lirae. The derived features of the eastern Pacific species, *S. vestalis*, relative to the states of characters present in *S. vaginula* include the following: (1) increase in obliquity of the posterior auricle, (2) reduction in the relative size of the posterior ear, and (3) earlier ontogenetic origin of costae on the flanks of the primary ribs, these rib-flank costae becoming more scaly. In *S. benedicti*, two of these characters show opposite trends relative to their condition in *S. vaginula*: (1) The posterior auricle becomes less oblique, its posterior margin forming a 90° or acute angle with the hinge; (2) the posterior auricle increases in relative size. The Galapagos specimens of *S.*

vestalis appear to be more derived than their mainland counterparts in having a more inflated form, with the rib crests secondarily flattened except for a very low, narrow crest from which very narrow scales develop.

These morphological differences and stratigraphic occurrences imply that *Spathochlamys vaginula* gave rise to both of the extant species but at different times. Speciation seems to have occurred before final seaway closure in the eastern Pacific (based on the occurrence of *S. vestalis* in the Imperial Formation) but after seaway closure in the western Atlantic (based on the earliest known *S. benedicti*).

Material examined.—

Jamaica

USGS 2580. Bowden, Jamaica. Fine sandy stratum in wagon road cut at foot of a hill that is 300 ft high. Collected by J. B. Henderson and C. T. Simpson, 1894. Bowden Shell Beds. Pliocene. 6 valves including the lectotype, catalogued as USNM(P) 135786, and about 30 uncatalogued valves and fragments.

Dominican Republic

NMB 15835. Río Gurabo near highway bridge, Dominican Republic. Gurabo Formation. From macrofossil sample collected by P. Jung, 1978. See Saunders *et al.* (1986, text-fig. 4) for plot of location and stratigraphic position. 4 valves.

NMB 15941. Río Gurabo about 0.6km downstream from highway bridge. Hard massive silt with diverse fauna scattered and in pockets. Gurabo Formation. From microfossil sample collected by J. B. Saunders, 1978. See Saunders *et al.* (1986, text-fig. 4) for plot of location and stratigraphic position. 3 valves.

USNM(P) 474811. USGS 8548. Right bank of Río Gurabo, 500 ft [152 m] below lower ford at Gurabo Adentro Bluff A, Distrito de Monte Cristi, Dominican Republic. Collected by T. W. Vaughan and C. E. Cooke, 1919. 1 valve in several pieces.

USNM(P) 47812. USGS 8726. La Canela, south side of Río Yaque del Norte, 15 km west of Santiago, Dominican Republic. Formation not specified but probably the Gurabo Formation. Collected by T. W. Vaughan, C. W. Cooke, and others, 1919. 1 valve.

USNM(P) 474659 and 474667. TU-1227A. Turbidity-flow lens (about 30 inches [76 cm] long and 6 inches [15 cm] thick) about 2 feet [61 cm] above base of outcrop at point approximately 75 feet [23 m] downstream from highway bridge, Río Yaque del Norte, Dominican Republic. Gurabo Formation. Collected by E. H. and H. E. Vokes. 10 valves (Figs. 11g-i).

USNM(P) 474660. TU-1210. Río Gurabo, east

bank, first bluff downstream from bridge on Los Quemados-Sabaneta road (equivalent to USGS 8544, Maury's Zone B), Dominican Republic. Gurabo Formation. [See Saunders *et al.* (1986, text-fig. 5) for plot of locality.] 1 valve (Fig. 11j).

Florida

USNM(P) 474661-474665 and 474813, Mac-asphalt Co. shell borrow pit complex (currently the APAC Pit) on the eastern outskirts of Sarasota, 0.3 km west of Interstate Highway I-75, sec. 12, T36S, R18E, Bee Ridge Quadrangle, Sarasota County, Florida. Collection from a drainage ditch and pit floor of the pit that was first opened in December, 1988. Tamiami Formation (*sensu* Waldrop and Wilson, 1990). Collected in July, 1989, and February, 1991 by John Waldrop, Druid Wilson, and Earlene Mitchell. 5 figured specimens (Figs. 11k-o) and 41 not figured.

USNM(P) 474666. Marl pit atop Jackson Bluff on left bank of Ochlockonee River a short distance downstream from Lake Talquin Dam, Leon County, Florida. Upper bed of *Ecphora* faunizone 3.5 to 5 feet [0.9-1.5 m] above base of Jackson Bluff Formation. 1 valve (Fig. 11p).

SUMMARY AND CONCLUSIONS

The six species of "*Chlamys*" presently living in the tropical and subtropical western Atlantic (Table 1) are not a monophyletic assemblage, nor are they a single genus, nor are any of them members of the genus *Chlamys* in a strict sense. The only features held in common by these species are their byssate living habit and its attendant form, where the byssal notch is deep, the active ctenolium persistent, and the auricles asymmetric, with the anterior one the larger. The fact that each species is a member of the Caribbean fauna is a coincidence stemming from a variety of circumstances involving very different phylogenetic histories and different times of arrival of ancestral lineages in the western Atlantic.

The different phylogenetic and biogeographic histories of these species are reflected in the fact that their closest extant relatives may be in the western Indo-Pacific, the eastern Atlantic, the western Atlantic, or the eastern Pacific. The morphological study of closely related living and fossil species, coupled with outgroup comparisons based on a continuing study of the Pectinidae on a worldwide basis, has made it possible to construct phylogenies. These phylogenies, coupled with data on present and past distributions, lead to the following conclusions:

1) All six of the extant tropical western Atlantic "*Chlamys*" species have ancestors to the east, in the eastern

Atlantic, the Mediterranean, or the western Indo-Pacific. There is no morphological or paleontological basis for supposing that any originated in the eastern Pacific and then dispersed eastward to the western Atlantic.

2) All of the tropical western Atlantic "*Chlamys*" species are constrained by middle latitudes, meaning that it is highly unlikely that they could have dispersed from the western Atlantic to the eastern Pacific by polar routes.

3) The extant tropical American "*Chlamys*" species, as well as the extant eastern Pacific "*Hinnites*", are distributed among four genera, *Laevichlamys*, *Crassadoma*, *Caribachlamys*, and *Spathochlamys*, each of which has a different history of entry into or origin within the Caribbean region. The timing of these origins or arrivals relative to the final closure of the seaways connecting the Caribbean and the eastern Pacific is the primary factor that determines whether geminate species are present in the eastern Pacific. These genus-level histories, which are illustrated diagrammatically in Figures 12-14, are as follows:

Laevichlamys originated in the western Indo-Pacific in the Miocene and dispersed either through the Mediterranean or, more likely, around southern Africa into the eastern Atlantic and thence to the tropical western Atlantic (Fig. 12). The fossil record suggests that its arrival in the tropical western Atlantic and the origin of the Caribbean species *Laevichlamys multisquamata* occurred in post-closure time, i.e. in the late Pliocene or Pleistocene. This is corroborated by the absence of both extant and fossil *Laevichlamys* in the eastern Pacific.

Crassadoma, the type species of which is a cemented form living in the eastern Pacific, has a long and continuous history in the eastern Atlantic, particularly in the Mediterranean (Fig. 13). This history stems from at least the early Miocene, when the Mediterranean was still open at its eastern end to the Indian Ocean. Dispersal to the western Atlantic by members of *Crassadoma* apparently occurred twice (Fig. 13). The first was in the early or middle Miocene, based on evidence that extant *Crassadoma gigantea* of the eastern Pacific is a sister species of *C. multistriata* of the eastern Atlantic. The second entry into the western Atlantic occurred much later, probably in post-closure time, giving rise within the Caribbean to the new genus *Caribachlamys*. The key morphological feature of *Caribachlamys* is its lecithotrophic-type larval shell, possibly an adaptation to sequester larvae in reef habitats that were under stress during the rapid sea-level changes of the Pleistocene. Speciation within *Caribachlamys* has occurred rapidly within the Pleistocene to produce four extant species (*C. sentis*, *C. ornata*, *C. mildredae*, and *C. imbricata*) and one extinct Plio-Pleistocene species (*C. paucirama*, new species).

The new genus *Spathochlamys* is represented in

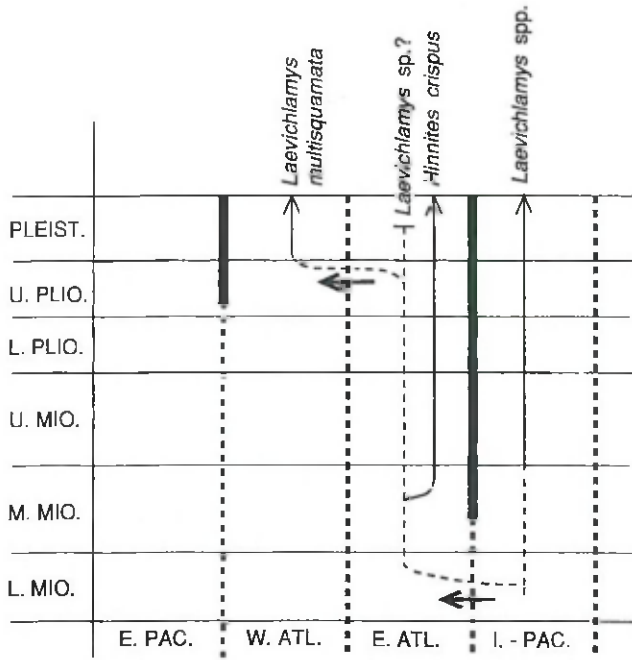


Fig. 12. The evolution of *Laevichlamys* among world oceans. Solid vertical lines = physical barriers to dispersal; dashed vertical lines = seaways (Tethyan, south African, or central American) or distance barriers; dashed lineage lines = missing data from the fossil record. Arrows indicate dispersal directions based on the polarities of morphological changes and on stratigraphic records.

the present-day Caribbean by *S. benedicti*, which is the most populous and widespread of all of the extant tropical western Atlantic "Chlamys" species. It is also the most eurytopic, living on a variety of bottoms across a span of depths centered on the middle shelf. The genus originated in the tropical western Atlantic in pre-closure time from ancestors in the new tribe Mimachlamyidini, which has its most extensive history in the eastern Atlantic and western Indo-Pacific (Fig. 14). The known fossil record of *Spathochlamys* in the western Atlantic is sparse but continuous from the late Miocene, and the succession of morphologies suggests that its entry into the eastern Pacific was in the late Miocene, possibly during a general transgression that permitted deeper water taxa to disperse across seaways that were at other times too shallow. The geminate sister species of *S. benedicti* in the eastern Pacific, *S. vestalis* [= *S. lowei*], at present also has a broad distribution in similar habitats and has dispersed as far westward as the Galápagos Islands with minor morphological divergence from mainland populations.

It is logical to assume that eurytopsy bestows resistance to extinction and that stenotopy, coupled with small population size, invites extinction (Stanley, 1986b). The eurytopic species *Spathochlamys benedicti* seems to epitomize

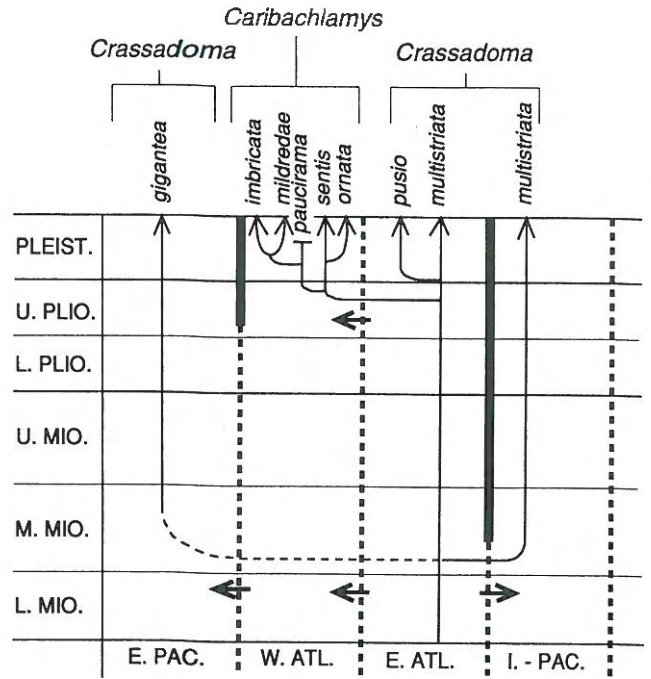


Fig. 13. The evolution of *Crassadoma* and *Caribachlamys* among world oceans (symbols are as in figure 5). *Crassadoma multistriata* is presently distributed around southern Africa into the southwestern Indian Ocean.

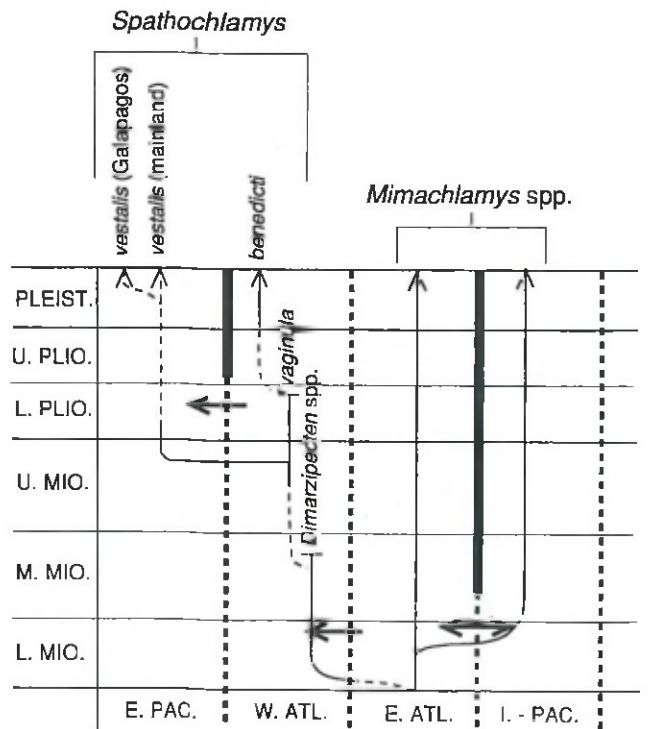


Fig. 14. The evolution of *Spathochlamys* from *Dimarzipecten* and *Mimachlamys* among world oceans (symbols are as in figure 5).

mize this kind of resistance. It is of interest to note, however, that the lineage of *S. benedicti* has also been resistant to speciation within the western Atlantic in post-closure time. Extant *S. benedicti* is probably a lineage descendant of *S. vaginula*, a species that lived in the tropical western Atlantic during the late Miocene and early Pliocene. The only demonstrable speciation of this lineage is that associated with its dispersal through seaway bottlenecks into the eastern Pacific. Once these seaways were closed, the presumably small founder populations that were isolated in the eastern Pacific were subject either to greater selection pressure or to genetic drift, causing them to diverge from the western Atlantic stem group. The same process is possibly in progress today, forcing divergence of the Galápagos populations of *S. vestalis* that are separated by a deep-water barrier from their mainland counterparts.

Most of the clade originations outlined in the above systematic revision suggest that long-distance dispersal facilitates allopatric speciation. The exception is the endemic Caribbean genus *Caribachlamys*, the most speciose of the three western Atlantic genera. The five species (one extinct) in this genus have apparently all originated since the beginning of the Pliocene within a time span of less than five million years, and one of the species has apparently originated during the Pleistocene. Although the founding populations of this clade may have arrived in the western Atlantic by long distance dispersal from the east, the synapomorphy that unites the species of the genus, and which presumably contributed to its rapid speciation, is a derived prodissoconch morphology (large PI stage and short PII stage) that suggests lecithotrophy and limited dispersal ability.

The key to understanding why a decrease in dispersal ability is associated with rapid speciation in *Caribachlamys* could lie in the common habitat preferences of these species. All are associated with reef-delimited habitats, either reef fronts, reef platforms, or back-reef areas. At present such habitats are not contiguous and are spatially limited; presumably they were even more fragmented during the extensive sea-level fluctuations of the Pleistocene. Reef-adapted byssate pectinid bivalves may have evolved diminished planktic dispersal ability under selective pressure to keep their young in place and to maximize the reproductive potential of local populations. By the same token, if only a very short dispersal phase is present, the possibilities for allopatric speciation are increased by chance transport of these larvae over even relatively short distances. Because all of these species are ctenidial feeders on suspended food particles and do not appear to be gregarious, there is little possibility for direct competition for food. Once reproductive isolation has occurred, daughter species can be reintroduced by chance dispersal into the

habitats of their founders. Indeed, the present overlapping geographic ranges of the four extant and to some degree successive species is testimony that this has occurred.

The only strong indication of geographic infraspecific variation within the Caribbean species analyzed here occurs in *Caribachlamys imbricata* from Bermuda. Both outgroup comparison and the fossil record suggest, however, that the Bermuda populations are primitive rather than derived compared to populations from throughout the Antilles and in southeastern Florida. The Bermuda populations are therefore relictual and evidence from the fossil record suggests that gene flow to Bermuda has become restricted beginning in the late Pleistocene.

There has long been a tendency for researchers to view the final closure of the Isthmus of Panamá as an instantaneous event that triggered divergence, speciation, and extinction of once continuous populations of species remaining on the two sides. It is becoming increasingly apparent, however, that the shoaling of seaways was gradual and that divergences occurred both well before and well after closure.

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