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A new genus and four new species of Chamidae (Mollusca, Bivalvia) from the Indo-West Pacific with reference to transposed shells

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Abstract. — Four new species of *Chama*, *Eopseuma* and *Carditochama* n. gen. (Bivalvia, Heterodonta) are described based on material from tropical Indo-West Pacific offshore waters. The dentition of the adult shells of *Eopseuma* species is corbiculoid-type and that of *Carditochama* species is lucinoid-type. Both genera exhibit a paedomorphic condition of the hinge, namely a radial arrangement of cardinals. *Eopseuma palaeodontica* n. sp. has both "normal" and "inverse" forms. The dentition and size of the early dissoconch suggest that *E. palaeodontica* is foundamentally an "inverse" species. The similarity of the hinge arrangement of "normal" and "inverse" forms in infraspecies or infrageneric taxa is not a result of convergence of different phylogenetic groups that share similar habitats, but is a result of transposition of the shell and hinge. A full developmental study is necessary to discuss the intergeneric similarity. Although "inverse" forms of Chamidae usually show transposition of both the shells and hinge, the "inverse" form of *Carditochama mindoroensis* n. gen. and n. sp. exhibits transposed shells with "normal" dentition. Therefore, transposition of hinge and shell can occur independently.

Key-words. — Cementation, transposition, Recent, Cenozoic, classification, Chamidae.

Description de quatre nouvelles espèces de *Chama*, *Eopseuma* et *Carditochama* n. gen. (Bivalvia, Heterodonta) des eaux tropicales profondes de l'Indo-Ouest-Pacifique

Résumé. — La dentition des valves adultes des espèces de *Eopseuma* est du type corbiculoïde et la dentition de *Carditochama* est du type lucinoïde. La dentition des *Eopseuma* et *Carditochama* possède un stade paedomorph. *Eopseuma palaeodontica* n. sp. présente des configurations normales et des configurations inverses. La similitude d'organisation de la charnière des configurations normales ou inverses au niveau infraspécifique ou infragénérique ne résulte pas d'une convergence de différents groupes phylétiques qui partagent le même habitat, mais de la transposition des valves et des charnières. Une étude complète du développement est nécessaire pour discuter de la similitude au niveau du groupe des genres. Bien que les formes inverses de Chamidae présentent en général une inversion à la fois des valves et de la charnière, *Carditochama mindoroensis* n. gen. et n. sp. a des valves inversées avec une charnière normale. La transposition de la charnière et des valves peut donc se produire de façon indépendante.

Mots-clés. — Fixation, caractères inversés, Actuel, Tertiaire, classification, Chamidae.

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INTRODUCTION

A transposed hinge is one of the few discontinuous shell character variables found in the Bivalvia. In common with sinistral coiling in gastropods, the frequency of occurrence is strongly associated with specific phylogenetic groups (PELSENEER 1920; MATSUKUMA in press). Among

recent bivalves, the superfamily Chamoidea has been recognized as a group frequently associated with transposition. In contrast to sinistral coiling, which is associated with anatomical asymmetry, hinge and shell transposition are not linked with anatomical organization (ODHNER 1919). There are no data available on the genetic control of transposition in individuals, but some phylogenetic associations, including the restriction of the phenomenon to specific taxa, suggest that it may be genetically controlled.

A transposed hinge is defined as one that exhibits in the right valve the hinge elements normally occurring in the left valve, and *vice versa* (POPENOE & FINDLAY 1933). A transposed shell is defined as one that exhibits in the right valve the shell elements normally occurring in the left valve, and *vice versa*. In a broad sense, a transposed shell includes a transposed hinge, but in this paper I use the term transposed shell for a transposition in external shell form, convexity and ornamentation. YONGE (1967) pointed out that a transposed hinge (inversion as cited by YONGE) is of pallial origin alone. The viscero-pedal mass is not affected. A transposed shell, as it is secreted by the mantle, may be assumed to be the result of transposition of the mantle function. A study of the transposed hinge and shell may elucidate an evolutionary transition within certain bivalve groups, especially the Chamoidea.

Chamid bivalves most frequently attach themselves to the substratum by the left valve ("normal" forms) or less frequently by the right valve ("inverse" forms). The attached and free valves develop different hinge structures, shell shapes and ornamentation. The hinge of the pediveliger stage is close to that of Carditoidea, and only at permanent settlement and cementing does the peculiar chamoid dentition develop. Studies of the nepionic hinge and its transition may be of considerable value in tracing the phylogeny of the Chamoidea. A drawback with the Chamoidea as a study group is the considerable degree of ecophenotypic variation and the resulting confusion in taxonomy at the species level. This is portrayed by the few revisions available. BERNARD (1976) reviewed the eastern Pacific species. However, since LAMY (1928), there has been no comprehensive taxonomic review of living species of the Indo-West Pacific. More recently, some investigators studied the chamids of the Red Sea (DELSAERDT 1986; OLIVER 1992) and Australia (LAMPRELL & WHITEHEAD 1992; HEALY *et al.* 1993). DELSAERDT (1986) provided many photographs of type material and much useful information, but many species are still poorly understood. Only a few investigators have published anatomical data (GRIESER 1913; ODHNER 1919; YONGE 1967; ALLEN 1976), or on the development of Chamidae (LABARBERA & CHANLEY 1971; ALLEN 1976; SCARPA & WADA 1994).

In this paper, I describe one new genus and four new species of Chamidae collected by offshore dredging in the Indo-West Pacific. The dentition of the Chamidae, shell transposition, and the similarity of dentition in "normal" and "inverse" forms are discussed.

ABBREVIATIONS AND TERMINOLOGY

Institutional abbreviations:

AMS	Australian Museum, Sydney, Australia;
BM(NH)	The Natural History Museum, London, England;
MNHN	Muséum national d'Histoire naturelle, Paris, France;
NM	Natal Museum, Pietermaritzburg, South Africa;
NSMT	National Science Museum, Tokyo, Japan;
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.

Abbreviations of figures:

a	anus;
aa	anterior adductor;
aac	catch muscle of anterior adductor;
aaq	quick muscle of anterior adductor;
dc	early dissoconch;
f	foot;
gf	genital folliculi;
go	genital opening;
ida	ascending lamellae of inner demibranch;
idd	descending lamellae of inner demibranch;
lpi	inner labial palp;
lpo	outer labial palp;
m	mouth;
oda	ascending lamellae of outer demibranch;
pa	posterior adductor;
pac	catch muscle of posterior adductor;
paq	quick muscle of posterior adductor;
pc	prodissoconch;
po	pedal opening;
se	exhalant siphon;
sf	siphonal fold;
si	inhalant siphon;
vg	visceral ganglion;
vm	visceral mass;
ya	young adult shell (= late dissoconch).

The terminology for describing juvenile and early adult shells is defined as follows and given in Fig. 1A and Table 1.

Prodissoconch

D-shaped, semi-globular shell of a veliger, secreted by the shell gland, without ornamentation (Prodissoconch I), or by the mantle edge, with growth striae (Prodissoconch II).

Nepionic shell

"Juvenile" shell of authors. Shell of the earliest post-larval stage, consisting of early dissoconch.

Early dissoconch

Dissoconch is a post-larval shell secreted by the mantle edge. In the Chamidae, there are two distinct phases in the dissoconch, namely the early dissoconch and the late dissoconch. The early dissoconch, "dissoconch" of YONGE (1967), is a shell of the umboned veliger (CARRIKER 1961) and pediveliger stage. Larvae in the pediveliger stage have both a foot and a velum, and crawl about freely and weakly attach to the substratum by a byssal thread (this is the plantigrade stage of CARRIKER 1961). They have a nearly free-living mode of life. The shell is equivalve and ornamented with growth lines, regular commarginal lamellae, fine radial striae, minute punctations, and so on.

Late dissoconch

Mantle-secreted shell of the postlarval stage after cementing, which is irregular in form and has the adult ornamental pattern. The young adult shell (YONGE 1967) is the late dissoconch just after abrupt postneanic change in shell character.

Measurements of nepionic and adult shells are defined in Fig. 1B-D.

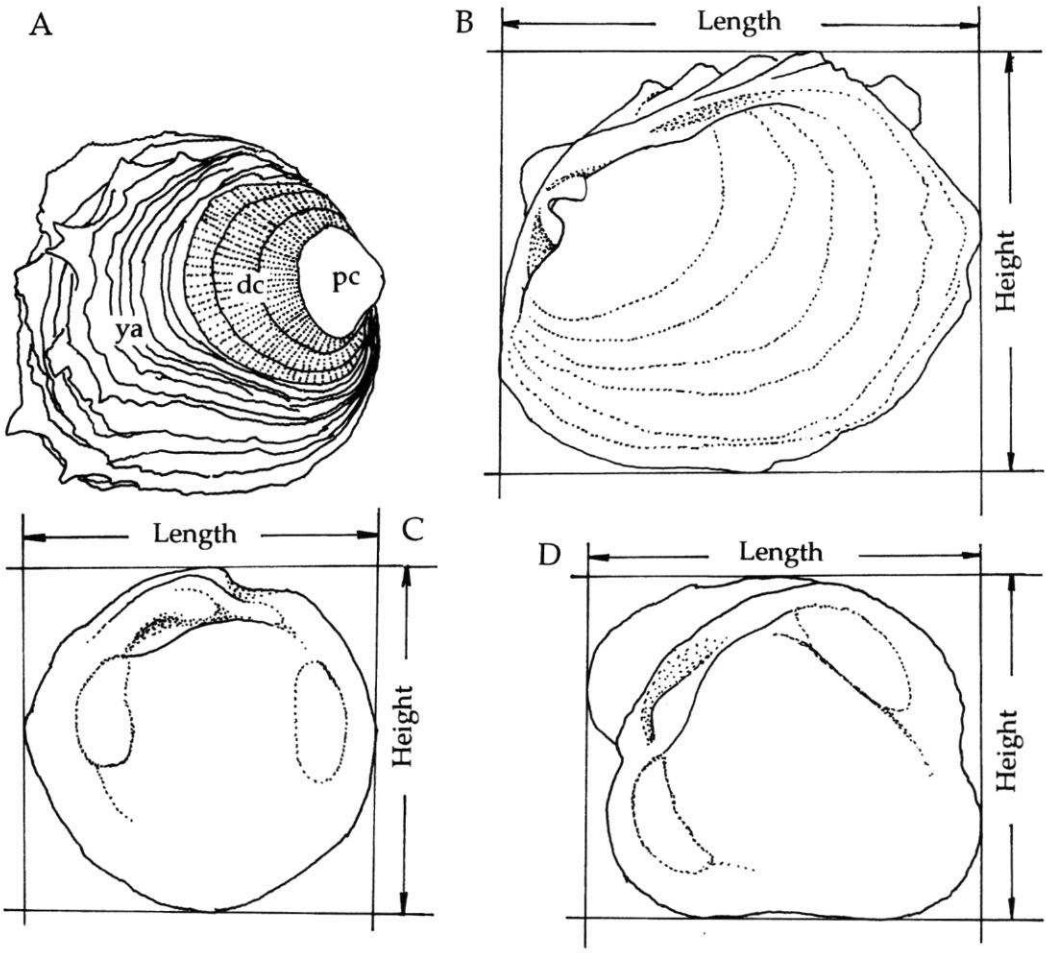


FIG. 1. — Terminology of juvenile shell and measurements. A: prodissoconch, early dissoconch and young adult shell of Chamidae. B: measurements of juvenile shells of *Eopseuma* and *Carditochama*. C: measurements of orbicular, oval, or irregular shape species, *i.e. Chama oomedusae*, *Eopseuma palaeodontica* and *Carditochama mindoroensis*. D: measurements of trapezoidal species, *i.e. Eopseuma phyllotrapezium*.

TAXONOMY

Family CHAMIDAE de Blainville, 1825

DIAGNOSIS

Shell thick, irregularly rounded, strongly inequilateral, inequivalve, with spirally coiled prosogyrous umbos; consisting of outer aragonitic crossed-lamellar layer, middle aragonitic myostracal layer, and inner aragonitic complex crossed-lamellar layer, occasionally with an outermost

calcitic prismatic layer (TAYLOR & KENNEDY 1969; KENNEDY *et al.* 1970). Hinge plate thick; adult dentition "pachyodont"-type, attached valve with a broad anterior cardinal, a long, narrow posterior cardinal, and a posterior lateral; free valve with a long, narrow cardinal, a wide ventral socket, and a posterior lateral; dentition of juvenile shell of left valve attached species ("normal" forms) heterodont-type (lucinoid-type), with two cardinals more or less parallel to hinge plate, a posterior lateral, and occasionally with an anterior lateral in each valve; dentition of juvenile shells of right valve attached species ("inverse" forms) heterodont-type (corbiculoid-type), with two diverging cardinals and a posterior lateral in the right valve, and a strong and two weak cardinals and posterior laterals in the left valve. Outer surface with well-developed sculpture of lamellae, spines, and folds. Shell margins completely closed, internally crenulated or smooth. Ligament parivincular, opisthodetic, in deep groove along hinge line. Pediveliger crawling freely (Table 1), and initially attached to substratum by a frequently broken byssal thread (LABARBERA & CHANLEY 1971; SCARPA & WADA 1994), *i.e.* a byssal plantigrade stage of CARRIKER (1961); then cemented to hard substrata by the left or right valve, at least during an early stage of ontogeny. Nearly isomyarian; anterior and posterior adductor scars dorso-ventrally elongated. Pallial line entire, nonsinuate. Mantle with a ventral fusion of inner mantle fold, pedal opening, and two siphonal apertures. Siphons short, with tentacles. Gills eulamellibranchiate (RIDEWOOD 1903), with outer and inner demibranchs, highly plicate; gill ciliation pattern type C of ATKINS (1937). Labial palps small, type 2 of STASEK (1963). Stomach types IV and V of PURCHON (1958, 1960), or intermediate between them (ALLEN 1976), type IIIa of DINAMANI (1967).

TABLE 1. — Terminology of shell and mode of life of early stages in Chamidae.

Shell terminology		Mode of life		Shell secreting organ
Prodissoconch I & II	Veliger shell	Planktonic (straight-hinged veliger)		Shell gland Mantle edge
SPATFALL				
Early dissoconch	Nepionic shell	Free-living	Swimming, crawling & byssal attachment (plantigrade stage; pediveliger; umboned veliger)	Mantle edge
ABRUPT POSTNEANIC CHANGE IN SHELL CHARACTER				
Late dissoconch	Early adult shell Adult shell	Cementing (juvenile plantigrade stage) Cementing, occasionally secondary free-living		Mantle edge Mantle edge

REMARKS

A nomenclatural review of genera and subgenera of the Chamidae was made by NICOL (1952a). A key to the genera of recent species is given in Table 2.

TABLE 2. — Genera of the Recent Chamidae.

	Attached valve	Nepionic shell		Adult shell
		Size (mm)	Dentition	Dentition
Chama	Left (right)	less than 1.2	3a, 3b, LPI/ 2, 4b, LPII ("normal" form)	(1), 3a + 3b, (5b) LPI/ 2, 4b, (6b) LPII ("normal" form)
Pseudochama	Right (left)	1.0-2.5	1, 3b, LPIII/ (2a), 2, (4b), LPII ("inverse" form)	1 + 3b, (5b), LPIII/ 2a, 4b, (6b), LPII ("inverse" form)
Eopseuma	Right (left)	1.6-2.5	—	1, 3b, (5b), LPIII/ 2a, (2b), 4b, LPII, LPIV ("inverse" form)
Amphichama	Left (right)	less than 1	—	3a + 3b, 5b, LPI/ (2), 4b, 6b, LPII ("normal" form)
Arcinella	Right	2.5	1, 3b, LPIII/ (2a), 2b, (4b), LPII	1 + 3b, 5b, LPIII/ (2a), 4b, (6b), LPII
Carditochama	Left or right	1.2-1.8	—	LAI, LAIII, (3a), 3b, LPIII/ LAII, 2, 4b, LPII

	Ornamentation	
	Nepionic shells	Adult shells
Chama	Commarginal lamellae, fine radial striae, punctations	Commarginal lamellae, spines
Pseudochama	Commarginal lamellae, punctations	Commarginal lamellae, spines
Eopseuma	Commarginal lamellae	Commarginal lamellae, spines; escutcheon defined
Amphichama	Commarginal lamellae	Commarginal lamellae, nodules
Arcinella	Commarginal lamellae	Radial rows of spines, nodules; lunule well defined
Carditochama	Commarginal lamellae	Commarginal lamellae, flat spines; lunule well defined

Genus **CHAMA** Linné, 1758

TYPE SPECIES. — *Chama lazarus* Linné, 1758, Syst. Nat., ed. 10: 691; tropical Pacific Ocean, subsequently designated by CHILDREN 1823: 28.

DISTRIBUTION. — Cretaceous to Recent. Cosmopolitan. Tropical to temperate waters, intertidal zone to 500 m.

DIAGNOSIS

Shells usually attached by the left valve, entirely aragonitic, with outer crossed-lamellar layer, middle myostracal layer, and inner complex crossed-lamellar layer. Nepionic shell small, less than 1.2 mm long, prodissoconch without ornament, early dissoconch having minute sculpture of closely spaced radiating striae, punctations and somewhat more distant commarginal riblets. Hinge of nepionic shell and adult "pachyodont"-type; hinge formulae of nepionic shell: 3a, 3b, LPI in the right valve and 2, 4b, LPII in the left; each tooth somewhat parallel to the hinge plate. Adult free right valve: single long, narrow cardinal (3a) + 3b, a wide ventral socket below the cardinal, parallel to hinge plate, denticles (5b) below nymph, and a posterior lateral (LPI); adult attached left valve: a broad anterior cardinal (2) parallel to the hinge plate, a dorsal socket, a weak, long, narrow, posterior cardinal (4b), and a posterior lateral (LPII).

REMARKS

Chama species are usually attached by the left valve, but occasionally by the right valve in the "inverse" form of the same species.

Chama oomedusae n. sp.
(Fig. 2F ; Figs 10-15)

TYPE MATERIAL. — Holotype, a live-collected specimen, R/V "*Alis*", SMIB 5, st. DW90, 22°19.1'S, 168°41.6'E, Loyalty Ridge, New Caledonia, 340 m (MNHN).

Paratypes: New Caledonia — R/V "*Vauban*", SMIB 3: st. DW8, 24°45'S, 168°08'E, 233 m (paratype: 1, a live-collected specimen, MNHN); st. DW10, 24°42'S, 168°07'E, 235 m (paratypes 2 and 3, two live-collected specimens, MNHN). R/V "*Alis*", SMIB 4: st. DW40, 24°46'S, 168°09'E, 240-260 m (paratype 4, a live-collected specimen, MNHN); st. DW41, 24°44'S, 168°09'E, 230-235 m (paratype 5, a live-collected specimen, MNHN); st. DW43, 24°47'S, 168°09'E, 235-245 m (paratype 6, a live-collected specimen, MNHN); st. DW44, 24°46'S, 168°08'E, 270-300 m (paratype 7, a live-collected specimen, paratype 10, a right valve, NM; paratype 8, a live-collected specimen, paratype 9, a right valve, AMS); st. DW47, 24°46'S, 168°08'E, 250-280 m (paratype 11, a live-collected specimen, MNHN); st. DW48, 24°46'S, 168°09'E, 240-245 m (paratype 12, a live-collected specimen, USNM); st. DW56, 23°21'S, 168°05'E, 230-260 m (paratype 13, a live-collected specimen, paratype 15, one right valve, NSMT; paratype 14, a live-collected specimen, MNHN). R/V "*Alis*", SMIB: 6: st. DW130, 19°04.9'S, 163°21.0'E, 225-230 m (paratype 17, a live-collected specimen, MNHN). R/V "*Coriolis*", CHALCAL 2: st. DW69, 24°44'S, 168°08'E, 260 m (paratype 18, a left valve, MNHN); st. DW70, 24°46'S, 168°09'E, 232 m (paratype 19, a right valve, USNM); st. DW71, 24°42'S, 168°10'E, 230 m (paratype 20, a right valve, MNHN). R/V "*Vauban*": st. 23, 24°50'S, 167°16'E, 480-505 m (paratype 21, a live-collected specimen, MNHN). R/V "*Vauban*", MUSORSTOM 4: st. DW162, 18°35'S, 163°10'E, 535 m (paratype 28, a left valve, MNHN). R/V "*Alis*", BATHUS 4: st. CP937, 19°03'S, 163°28'E, 257-261 m (paratypes 29-30, two live-collected specimens, MNHN).

Loyalty Ridge — R/V "*Alis*", SMIB 5: st. DW85, 22°20'S, 168°42.9'E, 260 m (paratype 16, a live-collected specimen, MNHN).

New Hebrides Arc — R/V "*Alis*", VOLSMAR, Gemini seamounts: st. DW48, 21°00.1'S, 171°03.3'E, 200 m (paratype 27, one right valve, MNHN). R/V "*Alis*", VOLSMAR: st. DW9, 22°22.7'S, 171°41.8'E, 275-300 m (paratypes 22-24, one left valve and two right valves, MNHN); st. DW17, 22°23.2'S, 171°41.7'E, 260-300 m (paratypes 25-26, two right valves, MNHN).

TYPE LOCALITY. — Loyalty Ridge, New Caledonia.

DISTRIBUTION. — Recent. New Caledonia and New Hebrides Arc, live specimens collected at depths of 225 to 505 m. A poorly preserved left valve from the Philippines (Fig. 15; R/V "*Jean-Charcot*", ESTASE 2, st. CP5, 04°59'N, 125°41'E, approximately 1190 m, MNHN) and a right valve from New Hebrides Arc (R/V "*Alis*", VOLSMAR, st. DW5, 22°26'S, 171°46'E, 620-700 m, MNHN) may also represent this species.

HABITAT. — *Chama oomedusae* n. sp. is one of the most common molluscs on shelly-gravel bottoms on the continental slope of New Caledonia to New Hebrides Arc.

ETYMOLOGY. — Named from a combination of the Greek noun *oon* and *Medousa* (Medusa's egg), to draw attention to the remarkable globose shells with scattered spines.

DESCRIPTION

Shell small, to 33 mm long, oval, with both valves globosely inflated. All 31 specimens examined attached by the left valve; attachment area small, with elevated attachment lamellae at the anterior umbonal region. Outer colour creamy-white to light brown. Free right valve postero-ventrally elongated, flatter, smaller than the attached valve, ornamented with very fine commarginal lamellae with short spines at the umbonal region and radial riblets with irregularly erect semi-cylindrical spines towards shell margin. The attached left valve deep, ornamented with fine concentric lamellae at the umbonal region and low, crowded, radial riblets towards the margin, occasionally with somewhat strong, irregularly spaced, radial rows of erect spines. Inner colour white to pale brown. Shell margin finely crenulated. Nepionic shell small, approximately 0.7 mm long, well inflated; early dissoconch ornamented with commarginal lamellae and fine radial striae, dentition unknown. Dentition of adult shell: a large socket with a postero-dorsal tooth and a weak posterior lateral (LPI) in the right valve; a strong tooth with a dorsal socket and a weak posterior lateral (LPII) in the left valve.

Gills, especially outer demibranch, large, occupying nearly the entire shell cavity. Visceral mass small, situated below hinge plate. Foot flat, long, narrow; posterior end of foot weakly angulate (Fig. 2F). Pedal opening small, from antero-ventral part of anterior adductor to just behind of the adductor, approximately a fifth of lower ventral margin. Siphonal opening large, nearly half of pallial line. No siphonal fold. Anus slightly protruding into postero-ventral cavity at lower part of posterior adductor.

COMPARISONS

Chama oomedusae is similar to the globose Panamic *Chama corallina* Olsson, 1971, which occurs from Sonora, Pacific coast of Mexico, to Punta Escondido, Gulf of Panama, at depths of 18 to 95 m (BERNARD 1976). The outer colour of *C. oomedusae* is white to light brown, whereas that of *C. corallina* is pinkish, brown, or coral red (OLSSON 1971; BERNARD 1976). *Chama corallina* has closely spaced, frilled, commarginal lamellae around the umbones, producing small crowded radial wrinkles and occasionally with a few radial rows of small, sharp spines towards the ventral margin. *Chama oomedusae* differs from C. *corallina* in having small spines producing very fine commarginal rows over the umbonal region and finer, more crowded radial riblets towards the margin of the free valve. It inhabits deeper water than the Panamic species.

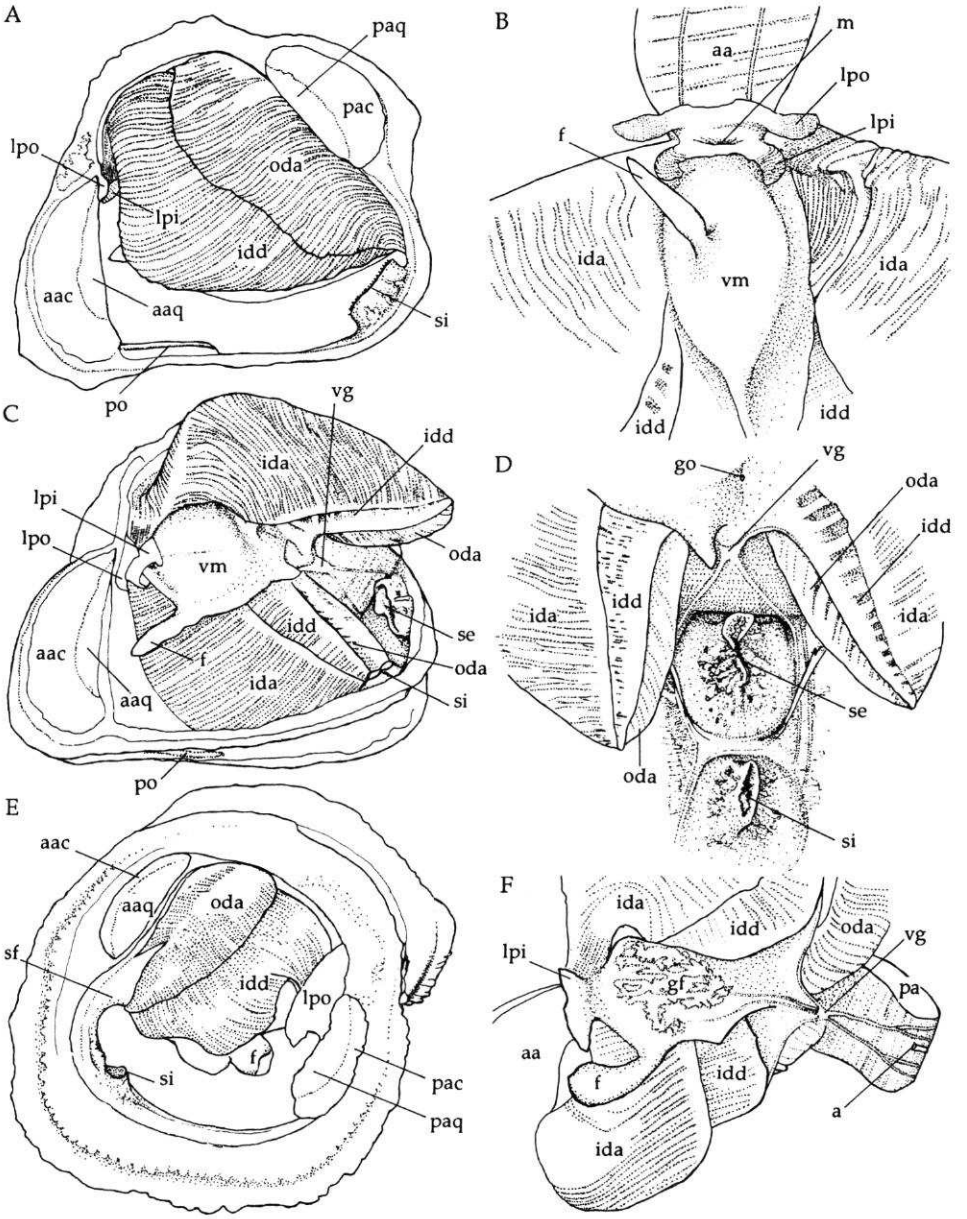


FIG. 2. — External morphology of chamid soft parts. A-D: *Eopseuma phyllotrapezium*, n. sp., paratype 1. A: left side view without mantle. B: ventral view showing mouth area. C: left side view; left demibranchs turned over. D: siphonal area. E: *Chama crenulata* Lamarck, 1819, from Guinea. Postero-ventral extremity of demibranchs connected with siphonal fold (sf), which completely covers exhalant siphon. F: *Chama oomedusae*, n. sp., paratype 29, left side view, left demibranchs turned over.

TABLE 3. — Measurements (mm) of type material of *Chama oomedusae*. *: Convexity of conjoined specimen. ( ): measurement approximate. R: right valve. L: left valve.

	Valve	Length	Height	Height/ Length	Convexity	Convexity/Length
Holotype	Right + Left	L 27.7	L 30.0	1.083	22.6*	0.816*
Paratype 1	Right + Left	L(21.0)	L(23.8)	(1.133)	16.4*	(0.781*)
Paratype 2	Right + Left	L(32.5)	L(35.4)	(1.089)	27.7*	(0.852*)
Paratype 3	Right + Left	R(21.2)	L(31.9)	(1.505)	27.0*	(1.274*)
Paratype 4	Right + Left	L(23.7)	L(26.8)	(1.131)	20.5*	(0.865*)
Paratype 5	Right + Left	L(20.3)	L(23.6)	(1.163)	20.0*	(0.985*)
Paratype 6	Right + Left	L(22.6)	L(25.4)	(1.124)	18.9*	(0.836*)
Paratype 7	Right + Left	L 18.1	L 21.8	1.204	13.7*	0.757*
Paratype 8	Right + Left	L(16.6)	L(18.5)	(1.114)	14.2*	(0.855*)
Paratype 9	Right	18.1	18.8	1.039	7.7	0.425
Paratype 10	Right	13.7	14.5	1.058	5.6	0.409
Paratype 11	Right + Left	R 18.1	R 18.8	1.039	R 8.3	0.459
		L 18.4	L 25.3	1.375	L 11.7	0.636
Paratype 12	Right + Left	L(27.4)	L(31.8)	(1.161)	23.4*	(0.854*)
Paratype 13	Right + Left	L 28.1	L(29.6)	1.053	20.3*	0.722*
Paratype 14	Right + Left	L(24.2)	L(26.6)	(1.099)	21.9*	(0.905*)
Paratype 15	Right	16.4	16.0	0.976	5.8	0.354
Paratype 16	Right + Left	L 22.0	L 27.4	1.245	13.6*	0.618*
Paratype 17	Right + Left	—	—	—	—	—
Paratype 18	Left	22.9	(24.8)	(1.083)	12.1	0.528
Paratype 19	Right	14.1	14.8	1.050	5.2	0.369
Paratype 20	Right	21.1	22.3	1.057	6.9	0.327
Paratype 21	Right + Left	L(27.1)	L(30.1)	(1.111)	24.5*	(0.904*)
Paratype 22	Right	23.3	23.8	1.021	(12.4)	(0.532)
Paratype 23	Right	20.0	20.5	1.025	7.6	0.380
Paratype 24	Left	19.4	21.7	1.119	10.0	0.515
Paratype 25	Right	21.6	22.1	1.023	9.5	0.440
Paratype 26	Right	20.2	20.0	0.990	6.6	0.327
Paratype 27	Right	14.0	14.1	1.007	5.3	0.379
Paratype 28	Left	22.3	25.1	1.126	12.9	0.578
Paratype 29	Right + Left	R 20.2	R 21.9	1.084	22.4*	1.109*
Paratype 30	Right + Left	R 24.7	R 24.4	0.988	27.3*	1.105*

	Valve	Mean	s.d.	N	
Height/Length	Right	1.027	0.031	13	
	Left	1.172	0.111	7	
Convexity/Length	Right	0.387	0.046	10	
	Left	0.564	0.055	4	

Genus **EOPSEUMA** Odhner, 1919

TYPE SPECIES. — *Pseudochama pusilla* Odhner, 1919, Handl. Kungl. Svenska Vetenskakad., **59** (3): 25; from Makassar Strait, Indonesia, original designation.

DIAGNOSIS

Shell attached by the right valve, occasionally by the left valve. Dentition corbiculoid-type; adult attached valve with strong anterior cardinal consisting of two closely spaced teeth (1 &

3b), a long, narrow posterior cardinal (5b), and a posterior lateral with a ventral socket (LPIII); free valve with a wide socket corresponding to the strong cardinal of the attached valve, several denticles (= anterior cardinal, 2a) at antero-dorsal margin of the socket, a strong posterior cardinal (4b) just behind the socket, a central cardinal (2b), oblique to the hinge plate, at midpoint of the socket, and posterior laterals (LPII & LPIV) at both sides of a small socket. Nepionic shell large, to 2.5 mm long; early dissoconch smooth except for several commarginal lamellae. Adult hinge notation of the "normal" form: [2a], [2b], [4b], [LPII] & [LPIV] in the right valve; [1], [3b], [5b] & [LPIII] in the left valve. Square brackets denote that the tooth is a mirror image of that in the opposite valve.

REMARKS

In the adult shells of *Eopseuma,* the separation of the strong cardinal in the attached valve and the radial arrangement of cardinals suggest the genus is primitive in comparison to *Pseudochama* (*s. str.*) and *Chama* (ODHNER 1919, 1955).

As a developmental study of the *Eopseuma* hinge has not yet been done, I tentatively adopt the hinge notation of ODHNER (1919). The posterior lateral in the right valve of *E. pusilla* has both ventral and dorsal sockets, so ODHNER's LPI should be read LPIII.

Eopseuma phyllotrapezium n. sp.
(Fig. 2A-D; Fig. 3A, B ; Figs 17-19)

TYPE MATERIAL. — Holotype, a live-collected specimen, R/V "*Coriolis*", CORAIL 2, st. DW63, 19°15'S, 158°48'E, Chesterfield Plateau, New Caledonia, 71 m (MNHN).

Paratypes: New Caledonia — R/V "*Vauban*", MUSORSTOM 4: st. DW187, 19°08'S, 163°29'E, 65-120 m (paratypes 9 & 10, a live-collected gerontic specimen and a conjoined empty gerontic specimen, MNHN); st. DW231, 22°34'S, 167°10'E, 75 m (paratype 1, a live-collected specimen, NSMT; paratype 2, a live-collected specimen, MNHN); LAGON, st. 382, 22°30.4'S, 167°14.1'E, Grand Récif Sud, 57 m (paratype 6, a live-collected specimen, AMS; paratype 7, a live-collected specimen, MNHN); st. 737, 22°08'S, 166°59'E, Secteur de Yaté, 49-50 m (paratype 11, a live-collected specimen, MNHN).

Chesterfield Islands — R/V "*Coriolis*", CORAIL 2: st. DW77, 19°12'S, 158°36'E, 60 m (paratypes 3 & 4, a live-collected specimen and a left valve, MNHN); st. DW56, 19°18'S, 158°47'E, 66 m (paratype 5, a left valve, MNHN); R/V "*Coriolis*", CHALCAL 1, st. DC50, 21°04.4'S, 158°40.7'E, 70 m (paratype 8, a left valve, MNHN).

TYPE LOCALITY. — Chesterfield Plateau, New Caledonia.

DISTRIBUTION. — New Caledonia and Chesterfield Islands, Coral Sea, live specimens from depths of 60 to 120 m.

HABITAT. — Adult *Eopseuma phyllotrapezium* are attached to shell fragments and pebbles by a small area. Some of them seem to be adopting a secondary free-living mode of life.

ETYMOLOGY. — The name is derived from a combination of the Greek nouns *fullon* and *trapezion* (trapezoidal shell with foliation), referring to the remarkable shell form and surface ornamentation.

DESCRIPTION

Shell to 60 mm long, trapezoidal, with a wide sulcus from the umbo to mid-ventral border, very thick and solid, strongly inequilateral, inequivalve, not exhibiting the marked degree of bilateral asymmetry normal for the Chamidae. The 12 specimens examined were all attached by

the right valve. Attached area small. Umbos high, prosogyrous. Antero-ventral corner narrow. Wide, round ridges running from umbo to the antero-ventral corner and to the postero-ventral corner. Wide escutcheon bordered by deep groove from umbo to the postero-ventral corner. Right, attached valve larger and deeper than the left, free valve, ornamented with fine radial wrinkles and foliae on the anterior slope of the posterior ridge at mid-ventral region. Left, free valve with fine radial wrinkles and distantly spaced, strong foliae on the anterior slope of the anterior ridge, on the postero-ventral side of posterior ridge, and in the escutcheon. Wrinkles frequently irregular in direction, especially in the escutcheon, distantly spaced, perpendicular to postero-dorsal margin. Nepionic shell, 2.4 mm long and 1.9 mm high, shining, smooth, except for seven, regularly spaced, commarginal lamellae. Ligament parivincular, opisthodetic, sunk into a deep groove. Inner ventral margin finely crenulated. Inside pale orange; occasionally tinged with purple postero-dorsally. Anterior adductor scar in the left valve oval-elongate, smaller than posterior adductor scar. In the right valve, both adductor scars oval, nearly equal in size. Pallial line entire. Dentition of adult shell: right valve with three cardinals, a small anterior and a large middle cardinals (1, 3b) below the umbo, a long, narrow, posterior cardinal (5b) near the nymph, a posterior lateral (LPIII) with a dorsal and ventral sockets; left valve with two nearly parallel cardinals, the anterior cardinal (2) below the umbo and the posterior cardinal (4b) near the nymph, and posterior laterals (LPII and LPIV) on both sides of the socket. Dentition of nepionic shell unknown.

Visceral mass moderately small, attaining nearly half of shell height. Foot long, narrow; anterior end of the foot pointing toward lower part of anterior adductor; posterior end of foot thin, pointed. Gills very large; lower end of outer and inner demibranchs free from posterior adductor; upper extremity of inner demibranch inserted between small outer and inner labial palps. Pedal opening at antero-ventral margin of anterior adductor to behind the adductor, nearly a quarter of the length of pallial line, with long, narrow folds interiorly on both sides of the slit. Inhalant and exhalant siphons small but wide, papillate, with irregular radial rows of white granules; tip of inhalant siphon minutely serrate; exhalant siphon exposed, no siphonal fold. Antero-posterior (mouth-anus) axis nearly parallel to ventral margin.

COMPARISONS

Eopseuma phyllotrapezium is similar to *Chama lobata* Broderip, 1835 (Fig. 16) from China and Philippines. Both species commonly share somewhat trapezoidal shells with a distinct escutcheon and foliated lamellae. *Eopseuma phyllotrapezium* attached by the right valve differs from *C. lobata*, which is a left valve attached species, in having somewhat bilaterally symmetrical shells. The outer surface of the attached right valve of *E. phyllotrapezium* is ornamented with finer, sometimes intermittent, radial wrinkles or nodules, whereas *C. lobata* has bilaterally distinctly asymmetrical shells, the left, attached valve of which is deeper than the right free valve and is ornamented with stronger radial riblets. The outer surface of the free left valve of *E. phyllotrapezium* is ornamented with three radial rows of foliations with fine wrinkles between them, whereas the outer surface of the free right valve of *C. lobata* is ornamented with strong, foliated commarginal lamellae. The undersides of the foliations of *C. lobata* are supported by regularly spaced radial riblets, and the interstices of the riblets under the lamellae are roundly concave.

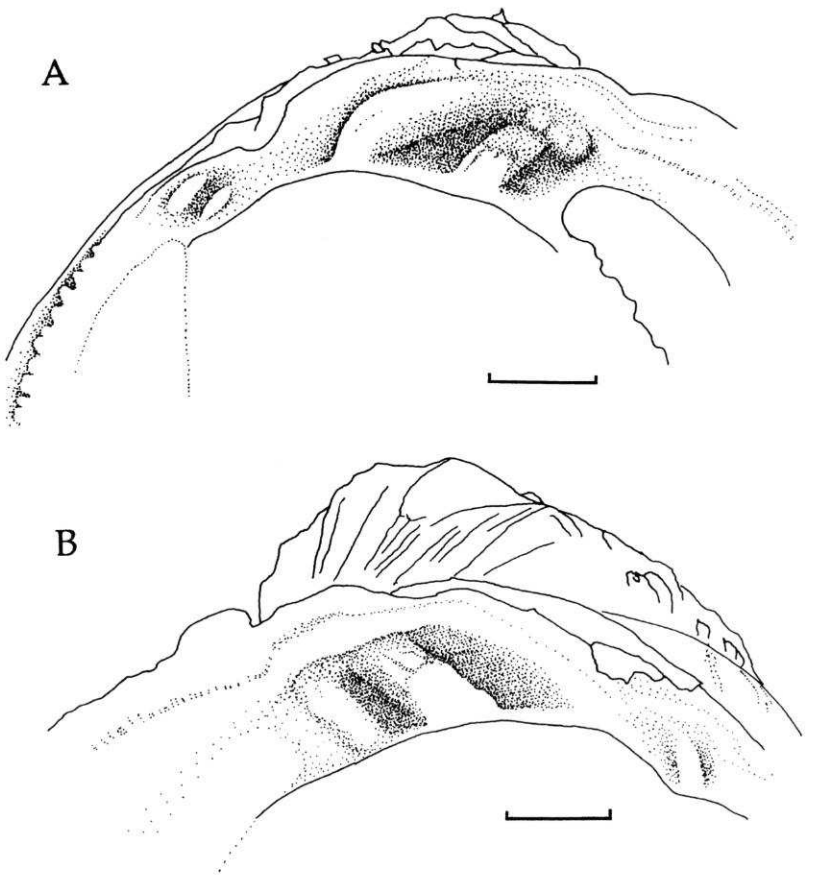


FIG. 3. — Dentition of *Eopseuma phyllotrapezium*, paratype 6, "inverse" form (MNHN). A: left valve. B: right valve. Scale: 3 mm.

In *E. phyllotrapezium*, the lamellae of the attached right valve are foliated on the anterior slope of the posterior ridge. Those of the left valve are foliated on the anterior ridge, posterior ridge and the escutcheon. In *C. lobata*, the lamellae of the free right valve are foliated in the middle and posterior parts of the shell, and those of the left valve are foliated in the anterior part.

Chama pulchella Reeve, 1846, from North-east Australia (Figs 24-25) and Chesterfield Islands, also looks similar to *E. phyllotrapezium*, because both species have subtrapezoidal shells with distantly spaced foliated lamellae. *Chama pulchella* is said to attach to the substratum by the left or right valve indifferently (REEVE 1846; LAMPRELL & WHITEHEAD 1992; HEALY *et al.* 1993). One of the syntypes in BM(NH) illustrated by REEVE (1846, pl. 3, Fig. 10b) differs from the other (REEVE 1846, pl. 3, Fig. 10a) in having an oval shell with somewhat crowded foliated

TABLE 4. — Measurements (mm, without lamellae) of type material of *Eopseuma phyllotrapezium*. *: convexity of conjoined specimen. ( ): measurement approximately.

	Valve	Length	Height	Height/ Length	Convexity	Convexity/ Length	Nepionic shell (LxH)
Holotype	Right	35.0	30.4	0.869	15.5	0.443	—
	Left	31.8	27.8	0.874	13.8	0.434	2.06 × 1.75
Paratype 1	Right	41.4	36.7	0.886	19.4	0.469	—
	Left	39.1	30.8	0.788	15.2	0.389	2.38 × 1.88
Paratype 2	Right	35.5	34.3	0.966	28.0	(0.394)	—
	Left	31.6	28.6	—	—	—	—
Paratype 3	Right	38.7	34.8	0.899	18.3	0.473	—
	Left	33.0	31.9	0.967	16.1	0.488	—
Paratype 4	Left	—	(16.5)	—	8.7	—	2.25 × 1.75
Paratype 5	Left	33.6	30.2	0.899	(15.1)	(0.449)	—
Paratype 6	Right	27.5	26.0	0.945	12.9	0.469	—
	Left	26.8	23.0	0.858	13.0	0.485	2.10 × 1.80
Paratype 7	Right	23.9	21.0	0.879	12.6	0.527	—
	Left	23.7	19.8	0.835	7.3	0.308	2.22 × 1.71
Paratype 8	Left	28.5	24.9	0.874	11.4	0.400	—
Paratype 9	Right	58.6	54.3	0.927	(34)	(0.580)	—
	Left	52.4	44.8	0.855	24.5	0.468	—
Paratype 10	Right	55.6	49.3	0.887	—	—	—
	Left	53.1	43.5	0.819	(21)	(0.395)	—
Paratype 11	Right	15.6	15.8	1.013	8.0	0.513	—
	Left	5.2	14.2	0.934	5.3	0.349	1.57 × 1.31

	Valve	Mean	s.d.	N	
Height/Length	Right	0.919	0.048	9	
	Left	0.873	0.051	11	
Convexity/Length	Right	0.482	0.031	6	
	Left	0.415	0.066	8	
Nepionic shell	—	2.10 × 1.70	0.28; 0.20	6	

lamellae without radial riblets and distinctly crenulated inner margin. Therefore, I follow ODHNER's opinion that *C. pulchella* Reeve, 1846 includes two distinct species, *i.e. C. pulchella* for REEVE (1846, pl. 3, Fig. 10a) and *Pseudochama similis* Odhner, 1917, for REEVE (1846, pl. 3, Fig. 10b). The outer surface of the free valve of *C. pulchella* has somewhat widely spaced commarginal lamellae with regular radial striations (REEVE 1846; LAMPRELL & WHITEHEAD 1992). *Eopseuma phyllotrapezium* lacks the regular radial striations on the lamellae. The type specimens of *C. pulchella* and *P. similis* show that the attached valves of both species have one broad anterior cardinal, whereas *E. phyllotrapezium* has two closely set cardinals below the umbo, which are similar to those of *E. pusilla* Odhner, 1919, from Makassar Strait, Indonesia.

Eopseuma phyllotrapezium differs from *E. pusilla* in having widely spaced foliated lamellae and irregular wrinkles between the lamellae. The outer surface of *E. pusilla* is ornamented with radial rows of fine, vaulted spines (ODHNER 1919, 1955).

Eopseuma palaeodontica n. sp.
(Figs 4A-D, 5A-C ; Figs 20-23)

TYPE MATERIAL. — Holotype, a live-collected specimen attached by the right valve, Farquhar Group, Seychelles (USNM 718951).

Paratypes: La Réunion — MD/32, st. DC86, 20°59'S, 55°15'E, 75-90 m (paratype 1, a live-collected specimen attached by the left valve, MNHN; paratype 2, a free left valve, MNHN); st. DC85, 21°00'S, 55°15'E, 58-70 m (paratypes 3-5, three free right valves, MNHN).

Seychelles — Farquhar Group, a live-collected free left valve (paratype 6, USNM 887512).

TYPE LOCALITY. — Farquhar Group, Seychelles.

DISTRIBUTION. — Seychelles and La Réunion, at depths of 58-90 m.

ETYMOLOGY. — The name is derived from a combination of the Greek adjectives *palaios* (old) and *odontikos* (related to tooth), referring to the remarkable dentition that exhibits a paedomorphic condition.

DESCRIPTION

Shell small, length to 26 mm, higher than long, with a wide escutcheon. Of the seven specimens examined, four attached by the left valve and three by the right. Free valve flat, with a distinct posterior sulcus from the umbo to the postero-ventral margin, ornamented with widely spaced radially striated commarginal lamellae. Outer colour light brown, occasionally with brown radial rays, inner colour creamy white with purplish brown blotches, light brown towards margin. Adult free valve with a broad cardinal below umbo, posterior lateral, and a dorsal socket. Attached valve deep, ornamented with widely spaced erect commarginal lamellae. Outer colour creamy

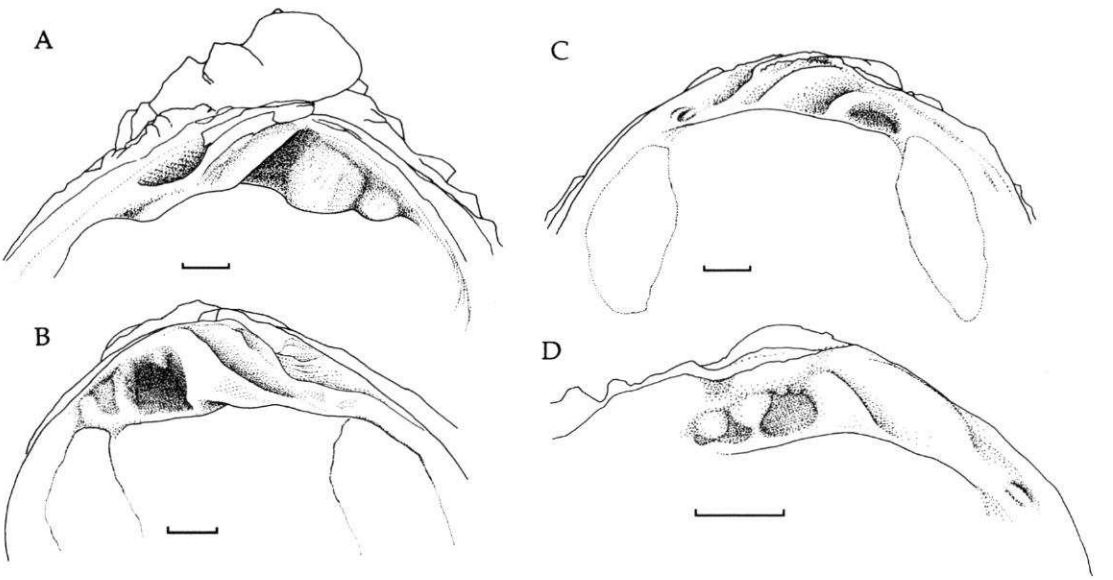


FIG. 4. — Dentition of *Eopseuma palaeodontica*. A, B: paratype 1, "normal" form (MNHN). C: *Eopseuma palaeodontica*, paratype 2, "inverse" form (MNHN). D: paratype 5, " normal" form (MNHN). Scale: 1 mm.

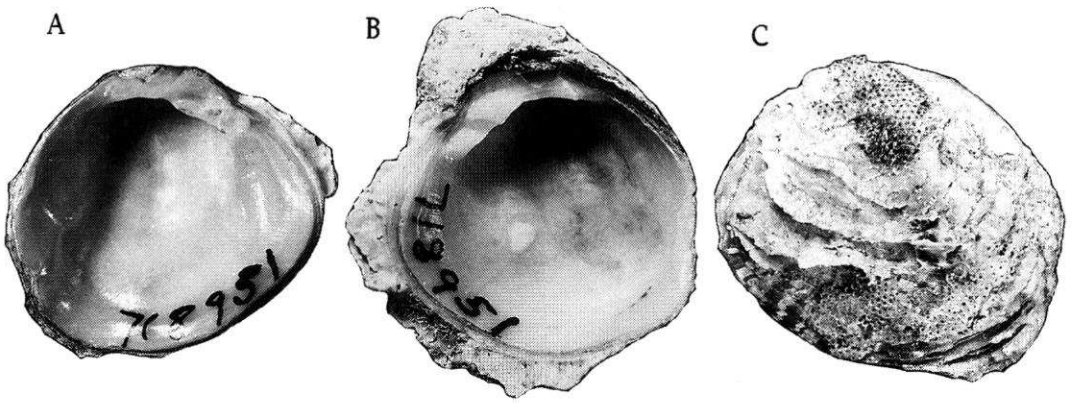


FIG. 5. — *Eopseuma palaeodontica* n. sp. A, B: holotype, "inverse" form, USNM718951. A: left valve, shell length 22.5 mm. B: right valve, shell length 25.6 mm. C: paratype 6, "inverse" form, USNM887512 (ex USNM718951). Left valve, shell length 25.0 mm.

white to light brown; inner colour creamy white, purplish brown posteriorly, light brown towards margin. Adult attached valve with two closely set subumbonal cardinals with a broad posterior socket; posterior lateral with a ventral socket. Nepionic shell large, attaining 2.4 mm long; early dissoconch with five commarginal lamellae; interstices of lamellae shining, smooth except for fine growth striae. Nepionic shell dentition unknown. Inner margin smooth.

TABLE 5. — Measurements (mm) of type of *Eopseuma palaeodontica*.
*: "inverse" form. **: measurement including lamellae.

	Valve	Length	Height	Height/ Length	Convexity	Convexity/ Length	Nepionic shell (L×H)
Holotype*	Right	25.6**	30.7**	1.199	—	—	—
	Left	22.5	21.2	0.942	8.2	0.364	—
Paratype 1	Right	11.3	14.8	1.310	4.0	0.354	—
	Left	12.3	19.1	1.553	7.8	0.634	2.43 × 1.88
Paratype 2*	Left	12.0	13.2	1.100	5.2**	0.433**	2.00 × 1.62
Paratype 3	Right	10.4	13.7	1.317	2.8	0.269	—
Paratype 4	Right	9.7	11.7	1.206	3.7	0.381	—
Paratype 5	Right	7.5	8.2	1.093	3.3**	0.440**	2.06 × 1.66
Paratype 6*	Left	25.0	24.6	0.984	7.7	0.308	—

	Valve	Mean	s.d.	N	
Height/Length	Left	1.225	0.092	5	
		1.145	0.280	4	
Convexity/Length	Right	0.361	0.071	4	
	Left	0.435	0.142	4	
Nepionic shell	—	2.16 × 1.72	0.23; 0.14	3	

COMPARISONS

Eopseuma pusilla (Odhner, 1919), the type species of *Eopseuma*, *E. phyllotrapezium* and *E. palaeodontica* share the same characteristic hinge. *Eopseuma palaeodontica* differs from *E. pusilla* in having higher shells with widely spaced commarginal lamellae and in lacking inner marginal crenulations. The outer surface of *E. pusilla* is ornamented with radial rows of vaulted scales.

Eopseuma palaeodontica differs from *E. phyllotrapezium* in having dorso-ventrally elongated shells with a smooth inner margin and in lacking wrinkles between the foliations.

CARDITOCHAMA n. gen.

TYPE SPECIES. — *Carditochama mindoroensis* n. sp., Mindoro Strait, Philippines, by original designation.

ETYMOLOGY. — Named from a combination of genera *Cardita* and *Chama* referring to a *Chama* with a *Cardita*-like appearance.

DIAGNOSIS

Shell with a small lunule and a very small escutcheon, attached by the right or left valve. Outer surface of free valve ornamented with commarginal lamellae producing broad, flat spines towards the shell margin. Outer surface of attached valve ornamented with distantly spaced commarginal lamellae. Not only nepionic shells, but also adult shells, having lucinoid-type dentition, with anterior and posterior laterals and diverging cardinals. Right valve with anterior laterals (LAI & LAIII), a weak and a strong cardinals (3a & 3b), and a posterior lateral (LPIII) with a ventral socket. Left valve with an anterior lateral (LAII), two diverging cardinals (2 & 4b), a posterior lateral (LPII), and a dorsal socket. Dentition characteristic of the right or left valve, not of the attached or free valve. Inner margin crenulated. Outer shell layer crossed-lamellar structure.

REMARKS

Carditochama is an intermediate form of chamid and carditid. The lucinoid-type dentition suggests that the genus should be placed in the Carditidae, but the cementing mode of life with strongly inequilateral shells shows that it is closer to the Chamidae rather than the Carditidae.

The genus *Carditochama* is monospecific.

Carditochama mindoroensis n. sp.
(Figs 6A-F, 7A-C)

TYPE MATERIAL. — Holotype, a live-collected specimen, attached by the left valve, R/V "*Coriolis*", MUSORSTOM 3, st. DR117, 12°31'N, 120°39'E, Mindoro Strait, Philippines, 92-97 m (MNHN).

Paratypes: Philippines — A young adult free left valve collected with the holotype (paratype 1, MNHN); Albatross St. 5268, 13°42'N, 120°57.25'E, off Matocot Point, West Luzon, 311 m (paratype 2, one free left valve, USNM 295890); Albatross St. 5357, 8°06'N, 117°17.17'E, NE off Balabac, Balabac Is, West Luzon, 124 m (paratypes 3-7, three free right valves and two free left valves, USNM 297587).

Borneo — Albatross St. 5584, 4°17.67′N, 118°57.7′E, North-west of Si Ami Island, Sibuko Bay, 526 m (paratype 8, a left valve, USNM 299704).

TYPE LOCALITY. — Mindoro Strait, Philippines.

DISTRIBUTION. — Recent. Mindoro Strait, Philippines and North-east Borneo, at depths of 92 to 526 m.

ETYMOLOGY. — The name is derived from the type locality Mindoro Strait, Philippines.

DESCRIPTION

Shell small, up to 10 mm long, with small lunule and very small escutcheon, attached by the right or left valve indifferently, higher than long, inequilateral, inequivalve. Beaks small, prosogyrate. Free valve, irregularly waved, flatter than attached valve; the outer surface ornamented with commarginal lamellae, with regularly spaced, nearly horizontal, broad spines; the spines on a lamella sometimes linked to each other and producing a small pore between each spine; commarginal lamellae and radial rows of spines showing a reticulate appearance. Outer colour light brown; inner colour dirty white, marginally tinged with light brown. Attached valve ornamented with distantly spaced reflexed commarginal lamellae with minute nodules on the upper surface and regularly spaced, obscure radial riblets. Outer colour dirty white; inner colour dirty white, marginally tinged with light brown. Inner margin strongly crenulated. Nepionic shell

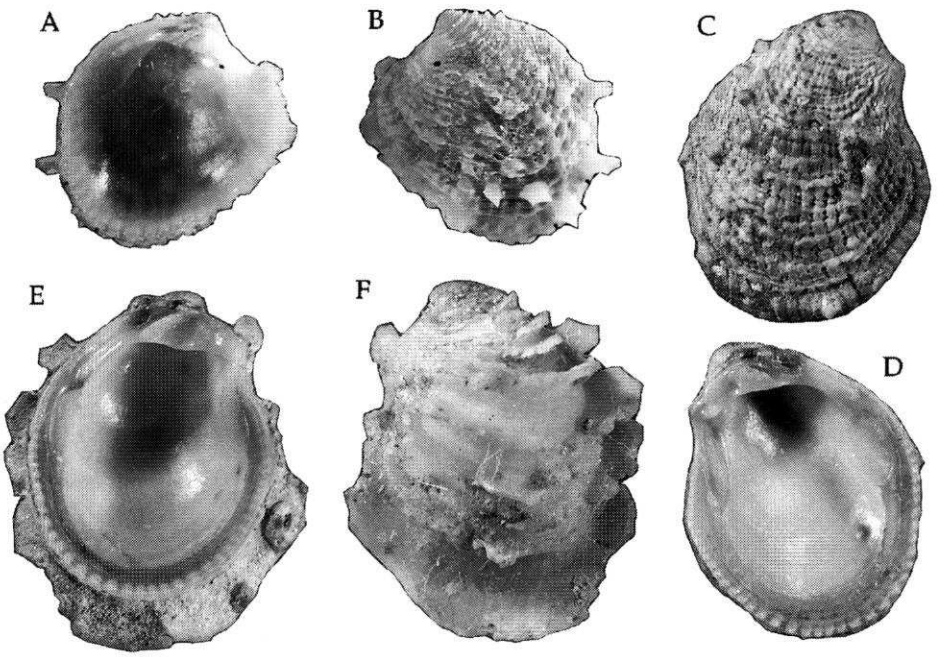


FIG. 6. — *Carditochama mindoroensis*, n. gen. and n. sp. A, B: paratype, MNHN. Left valve, "inverse" form. Shell length 4.1 mm. C, D: holotype, right valve, "normal" form, MNHN. Shell length 7.2 mm. E, F: holotype, left valve, "normal" form, MNHN. Shell length 8.4 mm.

quadrate, large, up to 1.8 mm long, with numerous commarginal lamellae. Left valve of young adult and adult shells, either attached valve or free, with a short rounded anterior lateral (LAII) with a ventral socket, two strong diverging cardinals (2 & 4b), a long inner posterior lateral (LPII), and a weak outer posterior lateral (LPIV) on both sides of a socket. Right valve of adult shell with a short but distinct inner anterior lateral (LAI) and a weak outer anterior lateral on both sides of a socket, a weak anterior cardinal (3a), a big triangular posterior cardinal (3b), a long posterior lateral(LPIII) with a long shallow ventral socket (Fig. 6D).

COMPARISONS

Carditochama mindoroensis is somewhat similar to *Chama carditaeformis* Reeve, 1847, because both have a *Cardita*-like shell form; however, the new species clearly differs from the latter in having a shell with commarginal lamellae producing broad, flat spines, radiating cardinals in the left valve, and anterior laterals in adult shells. *Chama carditaeformis* may be a junior synonym of *C. pacifica* Broderip, 1835 (DELSAERDT 1986).

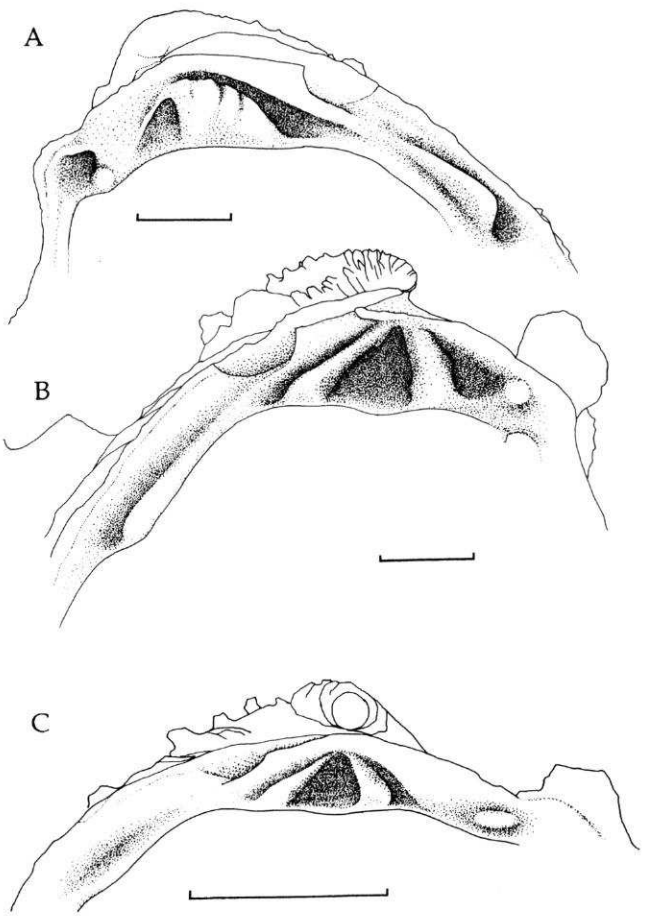


FIG. 7. — Dentition of *Carditochama mindoroensis*. A, B: holotype, "normal" form (MNHN). C: paratype 1, "inverse" form, left valve (MNHN). Scale: 1 mm.

TABLE 6. — Measurements (mm) of type material of *Carditochama mindoroensis*. *: attached valve. **: measurements including lamellae.

	Valve	Length	Height	Height/ Length	Convexity	Convexity/ Length	Nepionic shell (L×H)
Holotype	Right	7.2	8.8	1.22	2.8	0.39	1.77 × 1.26
	Left*	8.4**	10.0**	1.19	5.0**	0.60**	–
Paratype 1	Left	4.1	3.7	0.90	1.5	0.37	1.23 × 1.05
Paratype 2	Left	2.6	3.5	1.35	1.1	0.42	–
Paratype 3	Right	9.5	10.0	1.05	3.3	0.35	–
Paratype 4	Right	6.9	7.8	1.13	3.0	0.43	–
Paratype 5	Right	6.1	6.5	1.07	2.6	0.43	–
Paratype 6	Left	10.3	10.3	1.00	–	–	–
Paratype 7	Left	7.4	7.5	1.01	2.8	0.38	–
Paratype 8	Left	4.2	4.7	1.17	1.8	0.43	–
		Mean		s.d.	N		
Nepionic shell		1.50 × 1.16		0.382; 0.148	2		

DISCUSSION

SIMILARITY OF HINGE IN "NORMAL" AND "INVERSE" FORMS

It is well known that adult attached valves of *Chama* and *Pseudochama*, irrespective of right or left valve, have a similar hinge structure, convexity and ornamentation (MUNIER-CHALMAS 1882). The hinge structure of their free valves is also similar. There are two interpretations of the similarity, a transposition hypothesis and a convergence hypothesis. Although many authors (*e.g.* ANTHONY 1905; SYKES 1905; PELSENEER 1911, 1920; LAMY 1928; DAVIES 1935; DECHASEAUX 1952; YONGE 1967; COX 1969; KENNEDY *et al.* 1970; HEALY *et al.* 1993) consider that the dentition of shells attached by the right valve ("inverse" forms) shows transposition from that of shells attached by the left valve ("normal" forms), some investigators have denied that transposition has occurred in the Chamidae (ODHNER 1919; BERNARD 1976). ODHNER (1919) considered that "inverse" forms develop from a different type and thus are not at all "inverse", and he consequently placed "normal" forms and "inverse" forms into two different genera, namely *Chama* and *Pseudochama* respectively. The same author suggested that similarity of arrangement of hinge elements is the result of growth characteristics. BERNARD (1976) noted that nepionic shell dentition is identical in arrangement in *Chama* cf. *pellucida* Broderip, 1835 and *Pseudochama corrugata* (Broderip, 1835), so he concluded that no dental transposition occurs.

NEVESSKAYA *et al.* (1971) considered the Chamidae (*s. l.*) to consist of two different groups and proposed the family Arcinellidae for all species referred to *Arcinella* Schumacher, 1817, *Pseudochama* Odhner, 1917, *Eopseuma* Odhner, 1919, and *Amphichama* Habe, 1961, to separate them from the Chamidae, including *Chama* Linné, 1758. They said the Arcinellidae have stomach type IV of PURCHON (1958) without caeca and the Chamidae (*s. str.*) have stomach type V with right and left caeca, and placed the Arcinellidae in the order Hippuritoida and the Chamidae in the order Veneroida. According to PURCHON (1958, 1987), *Chama lazarus* L., 1758, type species of *Chama*, *C.* cf. *brassica* Reeve, 1847 and *C. gryphoides* L., 1758, which are all "normal"

forms, have a stomach of type V, whereas *C. multisquamosa* Reeve, 1846, which is also a "normal" form, has a stomach of type IV. ALLEN (1976) noted that the stomach of *C. gryphoides* has a morphology intermediate to those of *C. lazarus* and *C. multisquamosa*, so he concluded the division of the bivalve stomach into types IV and V is not valid, at least in the case of the Chamidae. ODHNER (1919) noted *Pseudochama*, *Eopseuma* and *Arcinella* lack a lateral caecal appendage of the stomach. No *Pseudochama*, *Arcinella*, and *Amphichama* species have been examined by PURCHON (1958) and ALLEN (1976) for stomach types specifically. NEVESSKAYA *et al.* (1971) had doubts about the generic assignment of *C. multisquamosa* by REEVE (1846) and PURCHON (1958), and placed the species in the Arcinellidae without providing any evidence.

The family Arcinellidae is not accepted by most investigators, because both "normal" and "inverse" forms may occur within a species. KENNEDY *et al.* (1970) doubted the validity of *Pseudochama* Odhner, 1917, because some species that are usually attached by one valve sometimes show attachment by the other. The outermost calcitic prismatic layer present in *Chama pellucida* Broderip, 1835, *Pseudochama exogyra* (Conrad, 1837) (TAYLOR & KENNEDY 1969; KENNEDY *et al.* 1970), *C. arcana* Bernard, 1976 (BERNARD 1976) and *P. granti* Strong, 1934 (HAMADA *et al.* 1995) suggests a close relationship between these four eastern Pacific species. The "inverse" forms found along with "normal" forms and the "normal" forms found in along with "inverse" forms have been recorded by many authors (*e.g.* REEVE 1846; NICOL 1952b; HABE 1958; YONGE 1967; KURODA *et al.* 1971; LAMPRELL & WHITEHEAD 1992; OLIVER 1992; HEALY *et al.* 1993; VON COSEL 1995). Although these records should be critically re-examined, it is certain that several species, including *Eopseuma palaeodontica* n. sp. (Figs 4C-F), *Amphichama argentata* (Kuroda & Habe in HABE 1958), and *A. scutulina* (Poutiers, 1981), have both "normal" and "inverse" forms within a species.

Recent *Eopseuma* species, including *E. pusilla* (Odhner, 1919) and *E. phyllotrapezium* n. sp., are "inverse" forms, whereas in *E. palaeodontica* there are both "normal" and "inverse" form in nearly the same frequency. Therefore, *Eopseuma* has "inverse" form species and indifferently attached species in the same genus.

KENNEDY *et al.* (1970) noted that the dentition of the French Eocene species *Chama calcarata* Lamarck, 1806, shows a more or less primitive condition. The hinges of the following Cenozoic species are also similar to that of *Eopseuma*: *Chama custugensis* Doncieux, 1903 (Eo-

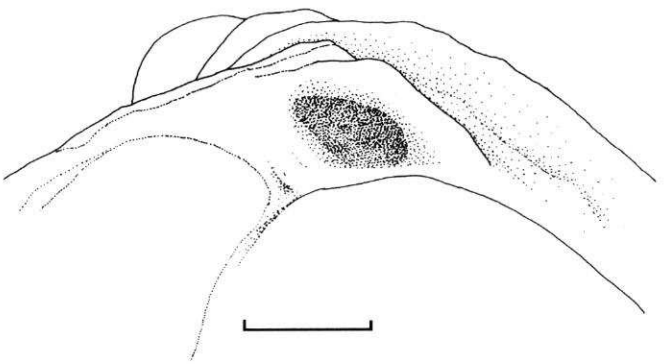


FIG. 8. — Dentition of *Chama custugensis*, "normal" form, right valve, the Eocene of Coustouge, France, Dept. Paleont. coll. No 15660 (MNHN). Scale: 5 mm.

cene); *Chama granulosa* D'Archiac, 1850 (Eocene); and *Chama laminosa* Millet, 1854 (Miocene to Pliocene). *Chama custugensis* from the middle Lutetian (Lower Eocene) of Coustouge, South-east France (LAUZIET 1970), is attached by the left valve, and the free trapezoidal right valve has widely spaced commarginal lamellae and a strong cardinal oblique to the hinge plate (Fig. 8). *Chama granulosa* from the Bartonian (Upper Eocene) of Côte des Basques, Biarritz, South-west France (BOUSSAC 1911), was examined. Of 12 specimens, all were attached by the left valve.

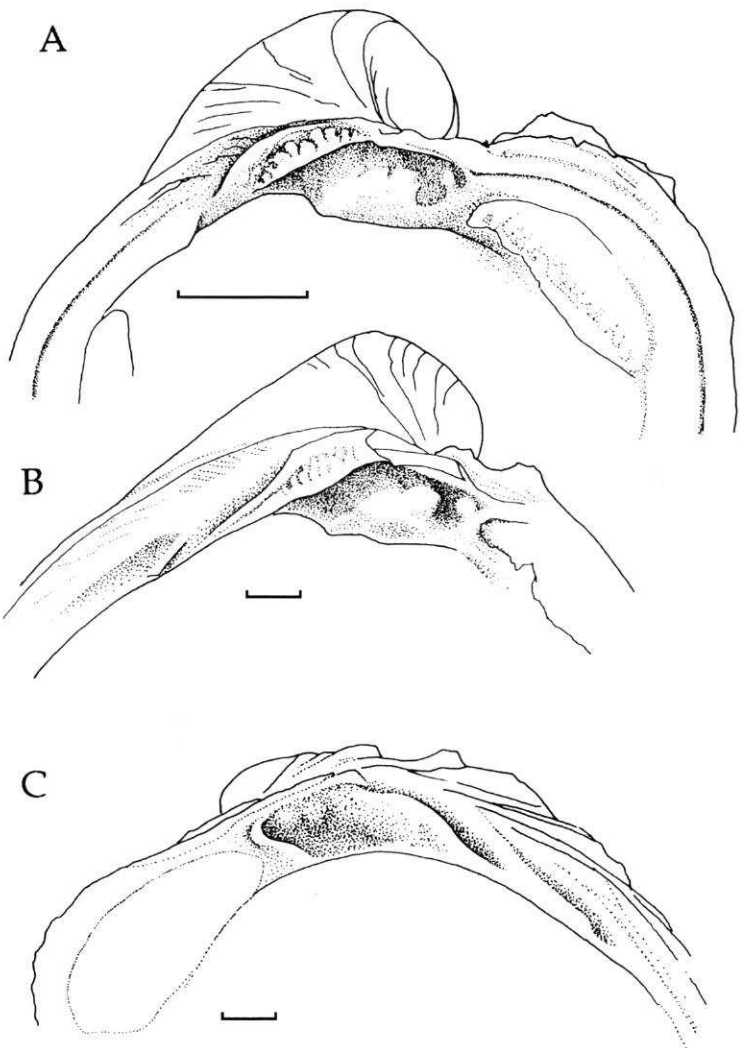
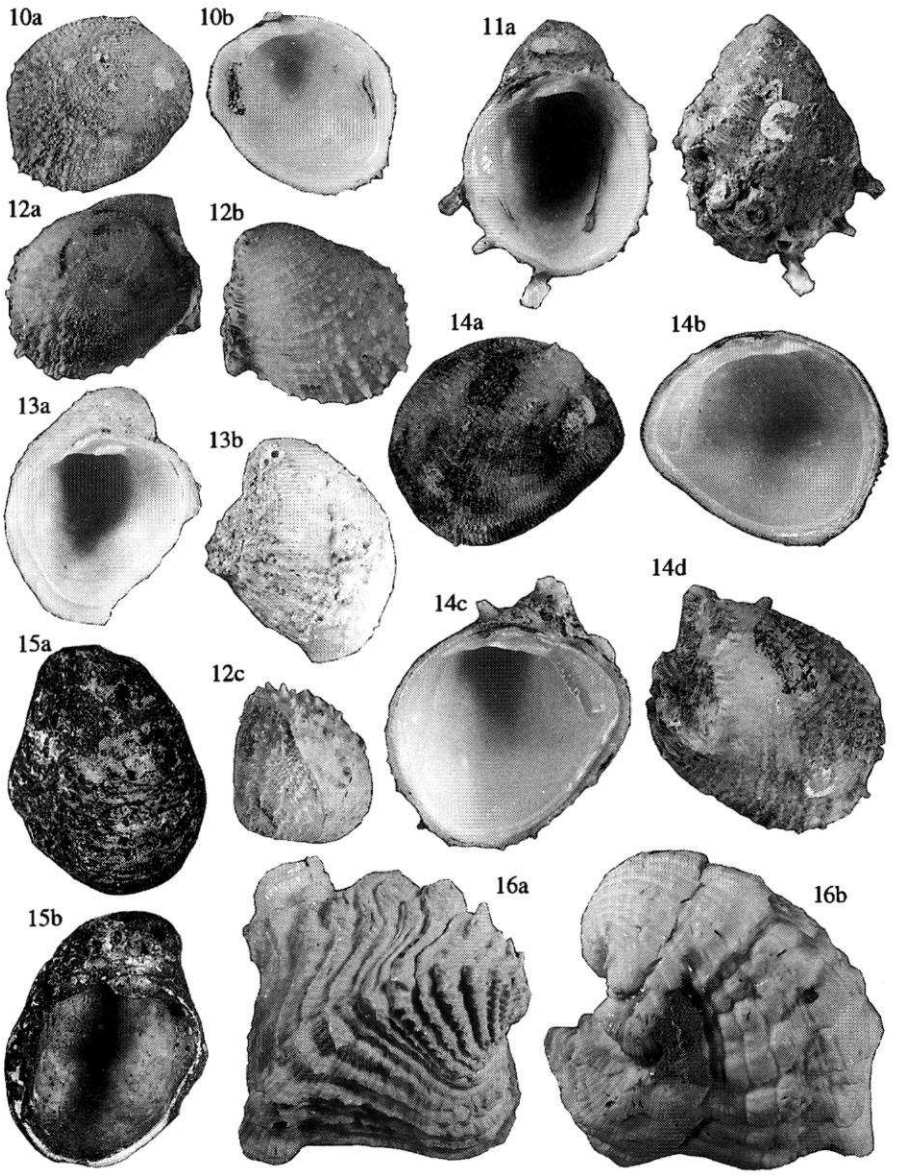


FIG. 9. — Dentition of *Chama granulosa*, "normal" forms, the Eocene of Biarritz, France, Dept. Paleont. reg. No 16517 (MNHN). A, B: left valves. C: right valve. Scale: 1 mm.



FIGS 10-16. — 10, *Chama oomedusae* n. sp., paratype 20, MNHN. Right valve, shell length 21.1 mm; 11, *Chama oomedusae* n. sp., paratype 16, MNHN. Left valve, shell length 22.0 mm; 12a-c, *Chama oomedusae* n. sp., paratype 1, MNHN. 12a: conjoined specimen. Shell length of right valve approx. 20.5 mm. 12b: left valve, shell length approx. 21 mm. 12c: posterior view. Convexity of both valves 16.4 mm; 13, *Chama oomedusae* n. sp., paratype 18, MNHN. Left valve, shell length 22.9 mm; 14a-d, *Chama oomedusae* n. sp., holotype, MNHN. 14a-b: right valve, shell length 27.3 mm. 14c-d: left valve, shell length 27.7 mm; 15, *Chama* cf. *oomedusae* n. sp., from Philippines, MNHN. Left valve, shell length 23.0 mm; 16a-b, *Chama lobata* Broderip, 1835. A syntype, BM(NH). Nevis Island, Leeward Islands, West Indies. 16a: right valve, shell length 36.8 mm. 16b: left valve, shell length 45.2 mm.

This species has a small anterior cardinal, a strong central cardinal oblique to the hinge plate, a series of granules in front of the nymph, and a posterior lateral with a ventral socket in the left valve, and a small anterior and a large posterior cardinals, a deep socket between the cardinals, and a posterior lateral with a dorsal socket in the right valve (Figs 9A-C). *Chama laminosa* from the Redonian (Upper Miocene to Lower Pliocene) of Angers, western France (LAURIAT-RAGE 1981), is attached by the left or right valve. The free valve has a cardinal within a wide socket and attached valve with the anterior strong tooth consisting of two cardinals. All these French Cenozoic species seem to be "normal" forms and their dentition is somewhat similar to that of *Eopseuma palaeodontica*.

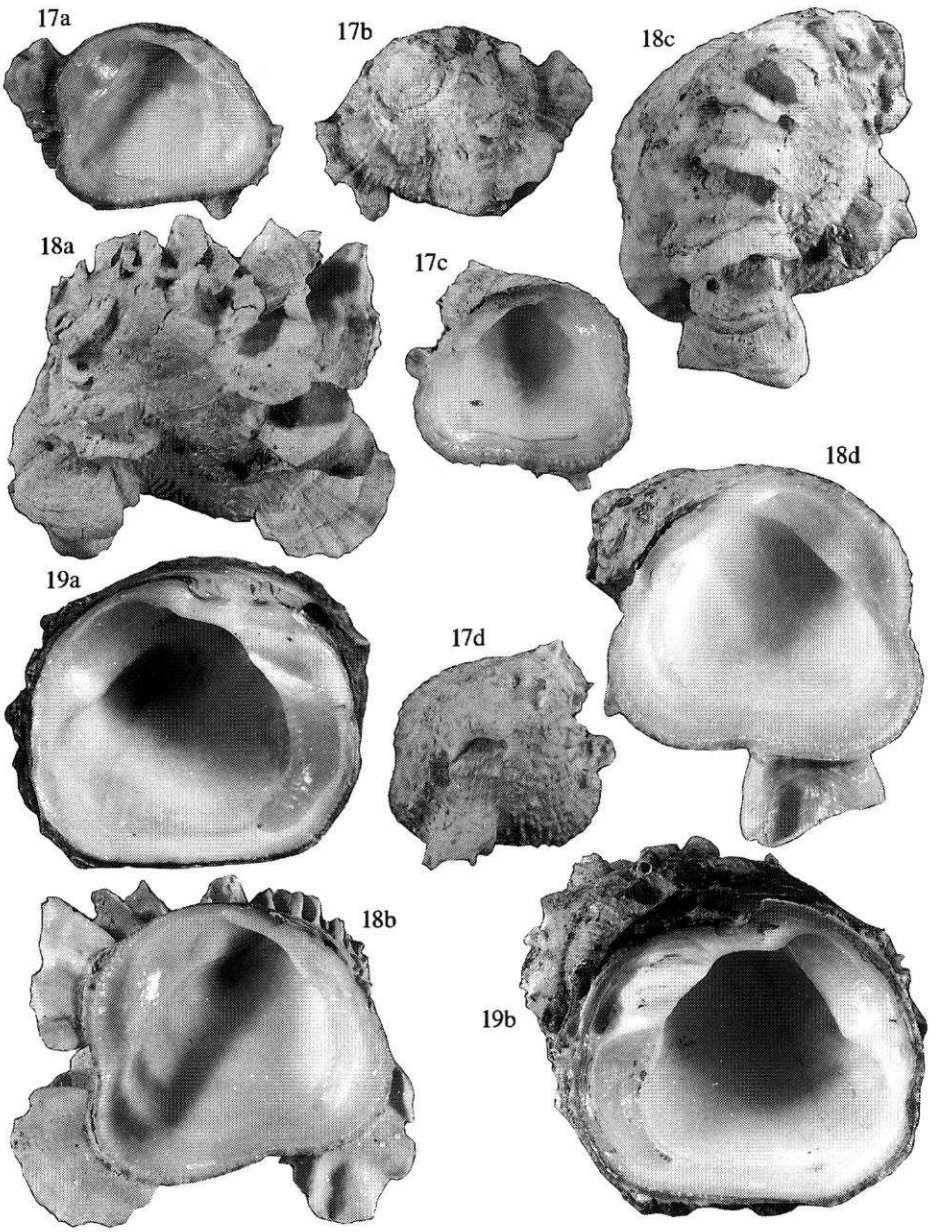
I conclude that the similarity of hinge arrangement in both forms in the same species, or in the same genus, is not a result of convergence of different phylogenetic groups that share similar habitats, but a result of transposed hinge. For discussion of the similarity between "normal" and "inverse" forms above genus level, a developmental study of both forms is necessary.

Many authors apply *Pseudochama* Odhner, 1917 to "inverse" forms, without discussion of anatomy and nepionic shell characters, including size, dentition, and ornamentations. *Pseudochama* should be applied to species that have the following characteristics: animal without lateral caecal appendage of the stomach, nephridia with the pericardial tubes not covered on their median side by the distal sacs; shell usually attached by the right valve; nepionic shell sculptured just as in *Arcinella* Schumacher, 1817, with rather distantly spaced commarginal lamellae, and no or very fine punctations or only traces of radiating riblets; the size of early dissoconch more considerable, length up to 1.0-2.5 mm; hinge formula of nepionic shell: 1, 3b, LPI in the right valve and (2a), 2b, (4b), LPII in the left; hinge formula of adult shell: 1 + 3b, 5b, LPIII in the right valve and (2a), 4b, LPII in the left (Table 2).

NEPIONIC AND ADULT SHELL DENTITION

The hinge notation of the Chamidae is in a confused state, because the adult dentition is very different from the nepionic heterodont phase. Nepionic shells of the following "inverse" form species have two distinct diverging cardinals (1 & 3b) in the right attached valve and one strong (2b) and two weak cardinals (2a & 4b) in the left free valve: *Arcinella arcinella* (Linné, 1767) (ODHNER 1919; FERREIRA & XAVIER 1981), *A. collinsi* Nicol, 1952 (NICOL 1952b), *Pseudochama ferruginea* (Reeve, 1846) (ODHNER 1919), and *P. gryphina* (Lamarck, 1819) (ODHNER 1919). DALL (1903) recorded a juvenile shell dentition with diverging cardinals and anterior and posterior laterals. Although he identified his material with *Chama pellucida* Broderip, 1835, ODHNER (1919) considered it to be a *Pseudochama* species, and BERNARD (1976) suspected the species was not a chamid, but a venerid. Judging from the hinge arrangement, I think it is probably an *Arcinella* or a *Pseudochama* species. The adult shell has a large anterior (1 + 3b) and a weak posterior (5b) cardinals in the right valve and a weak anterior (2a) and a strong posterior (4b) in the left valve.

The nepionic shell dentition of the following *Chama* species, "normal" forms, is reported by previous authors: *Chama* sp. (Anthony, 1905), *C. reflexa* Reeve, 1846 [= *C. japonica* Lamarck, 1819] (ODHNER 1919: pl. 2, Figs 13-14). It differs from that of *Arcinella* and *Pseudochama*. The nepionic shells of *Chama* species have two cardinals in each valve, namely 3a and 3b in the right valve and 2 and 4b in the left valve (ANTHONY 1905; ODHNER 1919), which are some-



FIGS 17-19. — 17a-d, *Eopseuma phyllotrapezium* n. sp., paratype 7, MNHN. 17a-b: left valve, shell length 23.7 mm. 17c-d: right valve, shell length 23.9 mm; 18a-d, *Eopseuma phyllotrapezium* n. sp., holotype, MNHN. 18a-b: left valve, shell length 31.8 mm. 18c-d: right valve, shell length 35.0 mm; 19a-b, *Eopseuma phyllotrapezium* n. sp., paratype 9, MNHN. 19a: left valve, shell length 52.4 mm. 19b: right valve, shell length 58.6 mm.

what parallel to the hinge plate and rather easily identifiable with the adult dentition. The adult shell has a moderately strong anterior (3a + 3b) and a weak posterior (5b) in the right valve and a strong anterior (2) and a weak posterior (4b) cardinals in the left valve.

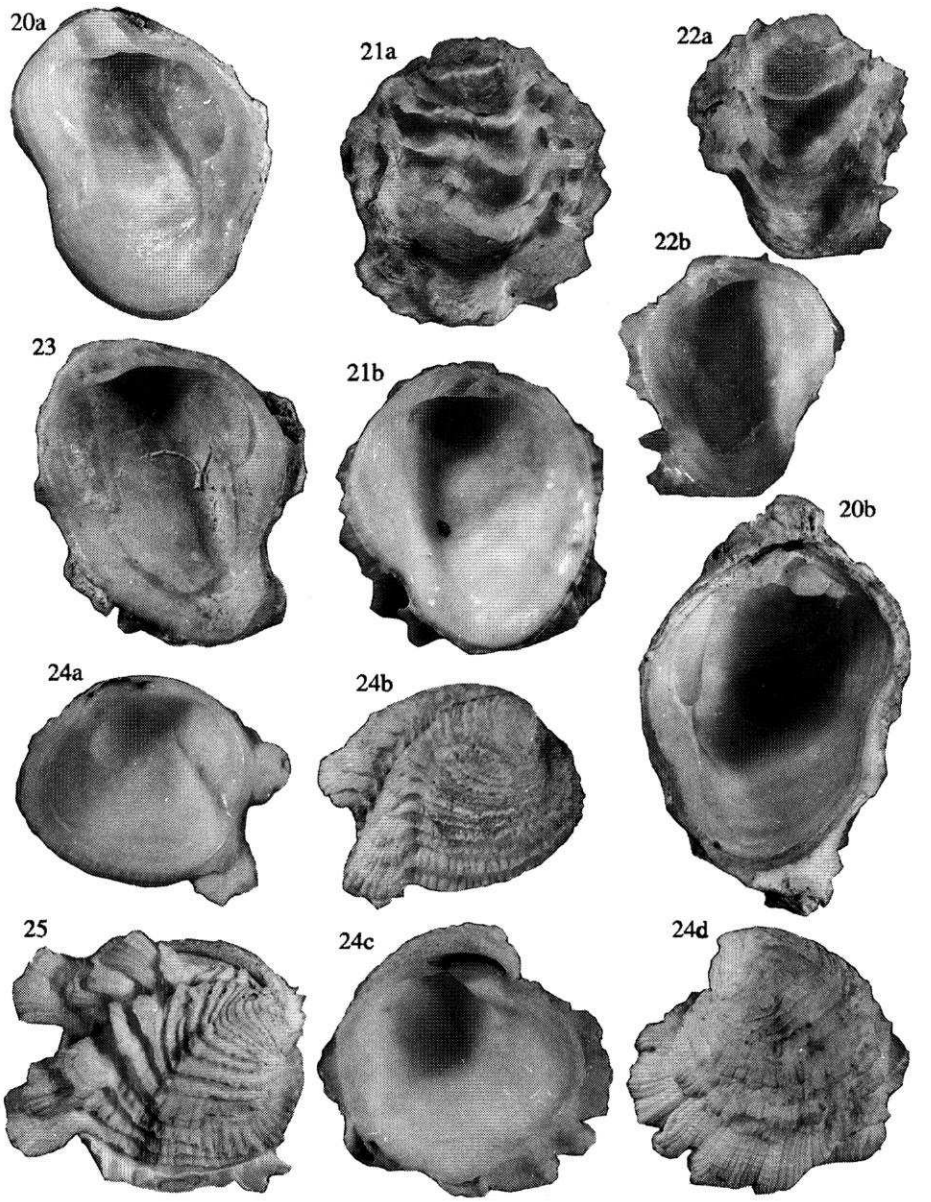
ANTHONY (1905: Fig. 41) figured semi-fossil juvenile shells of *Chama* sp. prior to cementation collected from Gulf of Tadjurah, Red Sea, which have two cardinals (1 & 3) and a posterior lateral (LPI) in the right valve and a strong cardinal (2) and a posterior lateral (LPII) in the left valve. The hinge teeth arrangement is "pachyodont"-type. The young adult shell has an early dissoconch with several commarginal lamellae and fine radial striae between the lamellae. The radial striae of early dissoconch are shared by *Chama gryphoides, C. asperella* Lamarck, 1819, and *C. pacifica* Broderip, 1835 (= *C. japonica* Lamarck, 1819). The dentition of *Chama* sp. of ANTHONY (1905) and *C. japonica* illustrated by ODHNER (1919) is identical with that of *C. gryphoides*. Although BERNARD (1976) noted that juvenile dentition is identical in arrangement in *Chama* cf. *pellucida* Broderip, 1835, and *Pseudochama corrugata* (Broderip, 1835), no early dissoconch representing heterodont phase with diverging cardinals has been observed in *Chama* (*s. str.*) species.

The dentition of *Carditochama mindoroensis* 3a and 3b in the right valve and 2 and 4b in the left valve, differs from other members of the Chamidae, in that the hinges of adult shells still exhibit the anterior and posterior laterals and a radial arrangement of the cardinals, a heterodont phase with diverging cardinals that may reflect an earlier stage of the development of the family. The dentition of adult *C. mindoroensis* is of the lucinoid-type of BERNARD (1895) and is similar to the Cretaceous (Albian) species *Cardita tenuicostata* (J. de C. Sowerby, 1836) illustrated by KENNEDY *et al.* (1970, pl. 75, Fig. 1). The dentition is also similar to that of nepionic shells of *Arcinella* and *Pseudochama* species, but is completely a mirror image of them. The characteristics of *Carditochama* dentition do not persist in most other adult shells of the Chamidae hitherto known, except for *Eopseuma* species, the adult shells of which exhibit a remnant of a radial arrangement of the cardinals. The hinge character of these two genera, especially *Carditochama*, may represent a plesiomorphic condition in chamid evolution.

TRANSPOSED HINGE

MATSUKUMA (in press) separates the hinge condition of the heterodont bivalves into four types: phenotype I – normal anterior lateral(s) & cardinals and normal posterior lateral(s), phenotype II – normal anterior lateral(s) & cardinals and transposed posterior lateral(s), phenotype III – transposed anterior lateral(s) & cardinals and normal posterior lateral(s), and phenotype IV – transposed anterior lateral(s) & cardinals and transposed posterior lateral(s).

If the "inverse" form is a fundamental condition of *Eopseuma*, a hinge notation of the right valve is 1, 3b, 5b, LPIII, and that of the left valve is 2a, 2b, 4b, (LPII) and LPIV (ODHNER 1919). *Eopseuma palaeodontica* shows both "normal" form and "inverse" form of dentition. The paratype 1 (Fig. 20) and paratypes 3-5 (Figs 4D, 22-23) are "normal" forms, whereas the holotype (Fig. 5A-B), paratype 2 (Fig. 21), and paratype 6 (Fig. 5C) show "inverse" form. Paratype 1 has widely spaced foliated lamellae, a large shining early dissoconch and *Eopseuma pusilla*-like dentition. These characteristics are identical with those of "normal" forms. The hinge formula of "inverse" form (paratype 1) is (2a), 2b, (4b), (LPII), LPIV. The hinge formula of the right



FIGS 20-25. — 20a-b, *Eopseuma palaeodontica* n. sp., paratype 1, "normal" form, MNHN. 20a: right valve, shell length 11.3 mm. 20b: left valve, shell length 12.3 mm; 21, *Eopseuma palaeodontica* n. sp., paratype 2, "inverse" form, MNHN. Left valve, shell length 12.0 mm; 22, *Eopseuma palaeodontica* n. sp., paratype 4, "normal" form, MNHN. Right valve, shell length 9.7 mm; 23, *Eopseuma palaeodontica* n. sp., paratype 5, "normal" form, MNHN. Right valve, shell length 7.5 mm; 24a-d, *Chama pulchella* Reeve, 1846, one of syntypes, BM(NH). 24a-b: right valve, shell length, except lamellae, 26.9 mm. 24c-d: left valve, shell length, except lamellae, 27.7 mm; 25, *Chama pulchella* Reeve, figured syntypes, BM(NH). Right valve, shell length, except lamellae, 25.6 mm.

valve of "normal" form is [2a], [2b], [4b], [LPII] and [(LPIV)] and that of the left valve is [1], [3b], [5b] and [LPIII]. Parentheses denote that the tooth is weak and indistinct, and square brackets indicate that the tooth is a mirror image of opposite valve. The dentition of "normal" form of *E. palaeodontica* has all hinge transposed and is phenotype IV of MATSUKUMA (in press).

TRANSPOSED SHELL

The left valve of the holotype of *C. mindoroensis* is an attached valve, which is obviously deeper than the free right valve. The outer surface of the left valve of holotype is ornamented with widely separated, erect commarginal lamellae, some of them being attaching lamellae with smooth interspaces. The paratype 1 is a young adult, free, left valve, and its outer surface is ornamented with commarginal lamellae with flat spines, which are sometimes linked to each other and produce a small pore between each spine. These two left valves have the same dentition (LAII, 2, 4b, LPII) and different ornamentation, *i.e.* the attached valve sculpture or free valve sculpture. There is no doubt that these two shells belong to *Carditochama mindoroensis*, because both the free valve of holotype (the right valve) and the paratype 1 (the left valve) have the same characteristic nepionic shells and the same ornamentation of the adult free valve (Figs 6B, C). This is an obvious example of a transposed shell without a transposed hinge. MATSUKUMA & SCOTT (in press) reported a specimen of *Chama pulchella* Reeve, 1843 with a transposed shell without a transposed hinge. This evidence shows that a transposition of shell and hinge can occur independently.

Eopseuma palaeodontica also presents "normal" and "inverse" forms in the same species. This species has shells with transposition of both hinge and shell.

SYNTHESIS

As a result of these studies I recognize six genera for recent species (Table 2) for which I provide the following key:

I. Attachment:
- A. Majority attached by the left valve ("normal" forms) V
- B. Majority attached by the right valve ("inverse" forms) IV
- C. Frequencies of "normal" and "inverse" forms nearly equal V
- D. Tendency of attached valve unknown II

II. Adult dentition:
- A. Heterodont-type with anterior lateral ..... *Carditochama*
- B. Heterodont-type without anterior lateral ..... *Eopseuma*
- C. "Pachyodont"-type III

III. Early dissoconch:
- A. More than 1 mm; dentition heterodont-type with diverging cardinals IV
- B. Less than 1.2 mm; dentition "pachyodont"-type like adult shells V
- C. Size and dentition unknown IV

IV. Anterior cardinal of adult attached valve:
  A. Divided VI
  B. Undivided ..... *Pseudochama*
V. Attached valve:
  A. Ornamented with commarginal lamellae and nodules; outer layer of free valve with pearl-like shining ..... *Amphichama*
  B. Ornamented with commarginal lamellae and spines ..... *Chama*
VI. Adult shell:
  A. With a distinct lunule, nodules, and radial rows of strong spine ..... *Arcinella*
  B. Without a distinct lunule, nodules, and radial rows of strong spine ..... *Eopseuma*

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