

THE GIANT WHITE CLAM FROM THE GALAPAGOS RIFT, *CALYPTOGENA MAGNIFICA* SPECIES NOVUM

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ABSTRACT

During DSRV/ALVIN cruises to the Galapagos Rift and the East Pacific Rise in 1977 and 1979, dense populations of large white clams were found associated with the thermal vents. On the basis of shell characters, M. Keen identified them as a species of *Calyptogena*, family Vesicomidae. These clams exceed 260 mm in length and are the largest known living members of this family, though some fossil vesicomids are comparable in size. Morphologically they closely resemble *C. pacifica* and *C. kilmeri*, the only species of *Calyptogena* which have been studied anatomically. Specimens ranging from 34.5 to 263 mm in length obtained during the 1977 and 1979 cruises are here described as a new species, *C. magnifica*, most closely related to *C. elongata* from off the coast of southern California, a species described by Dall on the basis of shells only.

In Appendix 1, C. Berg and R. D. Turner describe living specimens, noting the pink-purple iridescences of the mantle, the yellow-brown, wrinkled periostracum, the short siphons which do not extend beyond the valves, and the large iridescent-pink protrusible foot. The red blood pigment, a haemoglobin, gives the visceral mass a red appearance. The gills in large specimens are mottled red-brown with purple lines on the ventral margin while in small specimens they are a uniformly pinkish cream.

In Appendix 2, K. Boss provides an annotated checklist of ten fossil and seven living species of *Calyptogena*. One species is from the eastern Atlantic, off Africa; two are from the western Caribbean and 14 from the eastern and northern Pacific and Peru to Japan.

INTRODUCTION

Lonsdale (1977) reported unusually dense macrobenthic communities, including large white clams, associated with thermal anomalies along the deep-sea spreading centers of the Galapagos Rift. Samples from these peculiar ecosystems were obtained during DSRV/ALVIN Cruise 90 (Corliss et al., 1979) and during a biological investigation (ALVIN Cruise 102, legs 8 and 9) in January-February 1979 (Grassle et al., 1979) and Cruise 103, leg 5, in November-December 1979. The unusual habitat and organisms have received considerable attention in the public media, including an illustrated popular account by Corliss & Ballard (1977) and Ballard & Grassle (1979).

The big white clams, which provided the nickname "Clambake" for one of the hot vents, caused great excitement among oceanographers and marine biologists. They were referred to the genus *Calyptogena* by

Keen (1977a, b). The large size (all specimens from the 1977 cruise were about 200 mm in length) and unusual habitat of these clams led us to believe that they represented a new species closely related to *C. modioliforma* (Boss), a species from the Caribbean based on a unique specimen, and *C. elongata* Dall from off southern California known only from three specimens all less than 50 mm in length.

When DSRV/ALVIN revisited the Galapagos Rift in 1979, several smaller specimens were collected which produced a growth series ranging from 34.5 mm in length (which is smaller than the type-specimen of *C. elongata*) to 240 mm in length. Though the type-locality of *C. elongata* is some hundreds of miles north of the northernmost specimens collected by ALVIN, these widely separated populations show relatively minor morphological differences in the shells except the size of the valves and the ligament.¹ The discovery of new populations of *Calyptogena* as

¹Turekian, Cochran & Nozaki (1979) have calculated the age of the shells of this species to be between 6.5 and 830 years old.

exploration of the East Pacific Rise progressed northward (Fig. 13), and the variability shown by many species in this genus has led us to consider the 'hot vent' clams as a new species most closely related to *C. elongata*. This is a tentative assignment for, though we are secure in our assignment on the basis of the shells, the anatomy of the soft parts of *C. elongata* and other species of *Calyptogena* is essential before we can positively determine the relationship of these species.

SYSTEMATICS AND DESCRIPTIONS

Family Vesicomysidae Dall & Simpson 1901

Description. Shell of adults from less than 10 to over 200 mm in length, ovate to elongate in outline, inequilateral and equivalve, usually without gape; shell substance aragonitic with homogeneous inner and outer layers without tubulations or cross-lamellations; periostracum present, usually well developed; umbos prosogyrous, sometimes partially enrolled; lunule and escutcheon variable, present or absent. Ligament external, opisthodontic, and parivincular. Dentition with variably formed, more or less subumbonal cardinal teeth diverging or subundulate beneath the beaks. Adductor muscle scars subequal and with pedal retractor scars at their dorsal inner margin. Pallial line sometimes broadened, usually entire and sometimes with variously formed posterior 'pallial sinus.' Pedal gape extending from anterior adductor muscle to fusion of mantle folds to form the short posterior siphons. Foot strong, with byssal gland.

Remarks. The family Vesicomysidae was instituted by Dall & Simpson (1901) and later used by Dall (1908). Keen (1969) corrected the spelling to Vesicomysidae but dated it from Dall (1908). Thiele (1934) apparently, and possibly correctly, did not recognize the family Vesicomysidae. He placed *Calyptogena* Dall, 1891 in the Carditidae and *Vesicomys* in Kelliellidae Fischer, 1887 (*nomen correctum* Dall, 1900 *pro* Kellyellidae Fischer, 1887, see Keen, 1969). However, according to Boss (1969b), *Callocardia atlantica* Smith, 1885, the type-species of *Vesicomys* Dall, 1886 may prove to belong in the genus *Kelliella* and, if so, the family name Kelliellidae will take precedence. Alteration of familial and super-familial classification is out of place in the present context, but evidence is accumulating to show that the more primitive heterodont veneroids have been excessively divided at the higher phyletic ranks (Yonge, 1969). Fur-

ther, the difficulty in assigning many taxa currently included in the Vesicomysidae is reflected by their earlier placement in such families as the Arcticidae (= Cyprinidae), Carditidae, Kelliellidae and Veneridae.

The systematics of the family Vesicomysidae is beset with difficulties because there is at present no satisfactory diagnosis which would exclude the constituent taxa from all other heterodonts based on shared derived character states. Among the reasons for this difficulty are the rarity of samples, their considerable variability, the lack of anatomical data, and the ill-defined boundaries of the numerous families of heterodont bivalves with which vesicomysids have been associated.

Most species listed by Lamy (1920), Odhner (1960) and Boss (1969a) are represented by few specimens or by mere fragments. Large ontogenetic series are usually lacking; many species are known from single localities, usually at considerable depths. Vesicomysids, particularly *Calyptogena*, are highly variable (Kanno, 1971). The unreliability of certain conchological features is shown by two obviously conspecific specimens of an undescribed vesicomysid taken in the same dredge haul in the North Atlantic. They are the same size, texture, color, sculpture and shape, but one possesses, and the other lacks, a fully formed, impressed lunule, a feature sometimes used to distinguish genera.

Genus *Calyptogena* Dall, 1891

Calyptogena Dall, 1891: 189 (type-species, by monotypy, *Calyptogena pacifica* Dall, 1891).

?*Pleurophopsis* van Winkle, 1919: 23 (type-species, by monotypy, *Pleurophopsis unioides* van Winkle, 1919).

?*Pleurophopsis* van Winkle. Cossmann, 1920: 29, error for *Pleurophopsis*, van Winkle, 1919.

?*Pleurophoropsis* Cossmann, 1920: 29, *nomen vanum* for *Pleurophopsis* van Winkle, 1919.

Phreagena Woodring, 1938: 50 (type-species, by original designation, *Phreagena lasia* Woodring, 1938).

Ectenagena Woodring, 1938: 51 (type-species, by original designation, *Calyptogena elongata* Dall, 1916).

Akebiconcha Kuroda, 1943: 14 (type-species, by monotypy, *Akebiconcha kawamurai* Kuroda, 1943).

?*Hubertschenckia* Takeda, 1953: 85 (type-species, by original designation, *Tapes ezoensis* Yokoyama, 1890).

Description. Shell white, usually chalky, heavy, and more or less elongate, length being about 1.5 to 2 or more times the height. Sculpture usually of irregular growth lines, most apparent peripherally. Beaks anterior to middle, generally in anterior third or quarter. Ligament external, opisthodontic, rather strong and resting on variously developed nymphal callosities. Generally without lunule; escutcheon weak or absent to relatively strong. Pallial line broad and generally with shallow posterior indentation or 'pallial sinus.' Valves often constricted mesially, forming gena or cheeks. Periostracum usually dehiscent, dull, variously developed. Dentition irregularly developed, consisting principally of subumbonal cardinal elements without well developed distal lateral dentition. In left valve, subumbonal cardinal tooth more or less curved, \supset -shaped, with central socket between the two dental elements, which may be referred to as the anterior ramus (or anterior dorsal cardinal tooth) and posterior ventral ramus (or posterior ventral cardinal tooth). Posterior subumbonal cardinal tooth or irregular keel or ridge radiating posteriorly from beneath umbo, just ventral to the beginning of the nymphal callosity, ligament and posterior dorsal margin. Right valve, with subumbonal cardinal teeth, consisting of variously developed \supset -shaped elements, which may be separated distally into two dental elements (Fig. 10, Cb; Boss, 1968: figs. 16–17) and of a more or less curved ventral tooth, with an irregular \supset -shaped socket which separates these dental elements. Additionally, posteriorly radiating nymphal callosity subtending the ligament on posterior dorsal margin may appear as subobsolete, ridge-like dental element.

Animal with pedal gape extending from anterior adductor muscle to fusion of mantle folds beneath siphons. Foot strong, variously pointed and with poorly developed byssal gland and groove; apparently non-byssate in adult. Mantle edge thickened, broad anteriorly, and forming an embayment or "pallial sinus" posteriorly in vicinity of short, separate, incurrent and excurrent siphons. Ctenidia homorhabdoid without distinguishable food groove, at least in *C. magnifica*; inner and outer demibranchs present; extensive dorsal extension of ascending lamella of outer demibranch present. Labial palps reduced, obsolete and lip-like. Stomach with style-sac not differentiated from midgut.

Remarks. The genus *Calyptogen*a and *C. pacifica* Dall were instituted by Dall (1891) in the family Carditidae. He maintained this

placement (1895a: 541; 1903a: 70; 1903b: 1410) and was followed by other authors, notably Lamy (1922: 349), Grant & Gale (1931: 278) and Thiele (1935: 838). *Calyptogen*a, however, is not confamilial with the Carditidae because, though the shells are aragonitic, the outer and inner layers in *Calyptogen*a are homogeneous while in the Carditidae they are cross-lamellar and have a dense system of tubulations (Oberling & Boss, 1970; Taylor, Kennedy & Hall, 1973). Additionally, carditids usually have strong radial sculpture and crenulate valve margins, are byssate in the adult stage, lack a formed incurrent siphon, have the ventricle beneath the rectum, and have a tendency to brood the young (Boss, 1968; Yonge, 1969). Dall's placement of *Calyptogen*a *pacifica* in the Carditidae may have been based on the superficial resemblance of its hinge with that of *Cardita affinis* Sowerby from the Pacific coast of Mexico (Boss, 1968).

Woodring (1938) indicated the vesicomyid affinities of *Calyptogen*a based on hinge structures and established the genera *Ectenagen*a (type-species, *C. elongata* Dall, 1916) and *Phreagen*a (type-species, *P. lasia* Woodring, 1938). He subsequently indicated that *Phreagen*a was a synonym of *Calyptogen*a (Winterer & Durham, 1962; Boss, 1968; Woodring, personal communication). The type-species of *Ectenagen*a is closely related to *C. pacifica*. Okutani (1966b) suggested that *Calyptogen*a and *Akebiconcha* (type-species, *A. kawamurai* Kuroda), a Japanese genus thought to belong to the Cyprinidae (= Arctidae, see Boss 1969b), were confamilial.

The homology of the hinge elements of the arctids and vesicomyids is difficult to determine because well-differentiated lateral teeth are not found in *Calyptogen*a and there is great infraspecific variation of all dental elements (Fig. 10; Boss, 1968: figs. 16–17 and 19–20). *Akebiconcha* and *Calyptogen*a cannot be separated on the basis of valve shape and dentition (Boss, 1968).

There are also many anatomical differences between *Calyptogen*a and the single living species of *Arctica* (Saleuddin, 1964; Zaitsepin & Filatova, 1961). *Arctica islandica* has a laterally compressed, hatchet-shaped foot, the gut is long and elaborately coiled, and the labial palps are distinct and large. In contrast, *Calyptogen*a and other known vesicomyids have greatly reduced labial palps, a short gut and a pointed conical foot.

The tenuous inclusion of *Pleurophopsis*

and its synonyms in the synonymy of *Calypptogena* is based on the exceptionally large specimens of an unnamed species of *Pleurophopsis* from supposed Oligocene deposits in Colombia (USNM 11253, "No. 33, from a point ¼ mile north of junction of Arroyo-Piedras Palmar and Palmar-Molinero road on the Palmar-Molinero road. Plane table station 245 of Link and White"). The coordinates of sta. 245 are 10°40'N; 75°03'W, a point several miles south of Barranquilla, Colombia. These specimens exceed 200 mm in length and, externally, appear very close to *Calypptogena* but the hinge structure is unknown. Species associated with *Pleurophopsis* in Oligocene deposits of Peru include *Solemya* and *Vesicomya*, further evidence of a relationship between *Calypptogena* and *Pleurophopsis* (Olsson, 1931). The type-species of *Pleurophopsis* from Trinidad, originally thought to be Oligocene but probably Pliocene (Woodring, personal communication), is similar to *Calypptogena* in outline and has two cardinal teeth in each valve (Woodring, 1938).

Hubertschenckia Takeda, based on an Oligocene fossil, is tentatively considered a synonym of *Calypptogena* because Keen (1969) and Habe (1977) included it in the Vesicomyidae and Kanno (1971) infers that it is closely related to *Calypptogena*.

Although Habe (1977) placed the genus *Adulomya* Kuroda, 1931 in the Vesicomyidae and though some species that were once referred to it (e.g. *Adulomya chitanii* Kanehara, 1937) are species of *Calypptogena* (see Kanno, 1971: 80–82, text-figs. 10–12, and pl. 7, figs. 5, 6a–b, and pl. 17, fig. 12), we have not considered it a synonym of *Calypptogena* because the type-species of *Adulomya*, *A. uchimuraensis* Kuroda, is supposedly edentulous and is not a vesicomyid (Kanno & Ogawa, 1964: 285). According to Cox (1969), *Adulomya* belongs in the Solemyidae.

Most species of *Calypptogena*, both living and fossil are found in the Pacific Ocean, occurring from Japan to the Gulf of Alaska and south to off South America. In the Atlantic they are known from the Caribbean and off the coast of Africa. They occur from the Oligocene to the Recent and in depths ranging from about 100 m to over 2600 m. (Ap-

pendix 2 lists the species currently referable to the genus *Calypptogena*.)

Subgenus *Ectenagena* Woodring, 1938

Ectenagena Woodring, 1938: 51 (type-species, by original designation, *Calypptogena elongata* Dall, 1916).

Description. Shell similar to *Calypptogena*, s.s., sometimes exceeding 200 mm in length. Escutcheon generally not demarcated nor well developed. Dental configuration as in *Calypptogena* except teeth more or less blunt and comparatively shorter; hinge plate comparatively less extensive and thinner. Right valve lacking anterior dorsal cardinal element, probably resulting from reduction of dorsal ramus of \supset -shaped subumbonal cardinal tooth (Fig. 10, Eb and Fb). Ctenidia with strong interlamellar septa.

Remarks. Boss (1968) used *Ectenagena* as a genus but, considering the intraspecific variation of *Calypptogena*, s.s. and the paucity of distinguishing traits, we follow Keen (1969) in considering it a subgenus of *Calypptogena*.

As we are placing the white clam from the Galapagos Rift in the subgenus *Ectenagena* we include here a description of *C. elongata*, the type-species of the subgenus.

Calypptogena (Ectenagena) elongata Dall, 1916

Figs. 10E, 11, 12A–C

Calypptogena elongata Dall, 1916: 408 (Albatross Sta. 4432, off Point Loma, California, in 275 fathoms [8 mi. S. of Brockway Point, Santa Rosa Id., Channel Ids.];² holotype, USNM 110774); 1921: 32, pl. 3, fig. 3; Oldroyd, 1924: 116, pl. 22, fig. 6; Grant & Gale, 1931: 279; Oinomikado & Kanehara, 1938: 73; Otatume, 1942: 198; Okutani, 1957: 28; Okutani, 1962: 23; Bernard, 1974: 18, *non C. elongata* Ozaki, 1958.

Ectenagena elongata (Dall). Woodring, 1938: 51, fig. 2c; Boss, 1968: 739, 744, figs. 25, 28; Bernard, 1974: 19.

Calypptogena (Ectenagena) elongata (Dall). Keen, 1969: N664, fig. E138, 8a, b.

Range. Known only from the type-locality—Albatross Sta. 4432, 8 miles S. of Brockway

²The three specimens are catalogued separately. In the original description Dall gave the locality for the holotype (USNM 110774) as Albatross Station 4432, off Point Loma, California in 275 fathoms and the specimen is so labeled in the USNM. A paratype (USNM 205888) is labeled as from the same station but the depth is given as 183 fathoms. The third specimen, a paratype (USNM 209309), also from Albatross Station 4432 is labeled as off Santa Rosa, Santa Barbara Island, California in 270–280 fathoms. Recourse to the Dredging and Hydrographic Records for 1904 and 1905 (published 1906) give the station data as indicated under *Range*.

Point, Santa Rosa Island, Channel Islands in 272–270 fathoms [500 m].

Specimens examined. Holotype and two paratypes (only known specimens).

Description. Shell white, elongate, elliptical, equivalved but inequilateral, periostracum yellow-brown, largest known specimen 44 mm in length, 17.5 mm in height and 10 mm in width. Umbos low, small, pointed and located on anterior $\frac{1}{4}$ of valves. Anterior margin of valves rounded, anterior dorsal margin $\frac{1}{4}$ total dorsal margin and sloping from the umbos at an angle of about 20° . Ventral margin long, nearly straight. Posterior margin rounded, posterior dorsal margin $\frac{3}{4}$ total dorsal margin sloping from umbos at an angle of about 10° . Valves smooth, sculptured only with rather conspicuous incremental growth lines. Escutcheon and lunule absent. Ligament moderate in size (based on area of attachment, the ligament proper was missing in the type specimens) extending about $\frac{1}{2}$ posterior dorsal margin. Periostracum thin and uniform over entire valve.

Interior of valve porcelaneous white, muscle scars and pallial line impressed. Anterior adductor scar rounded anteriorly, nearly straight posteriorly, well impressed. Anterior pedal retractor triangular in outline, impressed and located near the dorsal, posterior margin of the anterior adductor muscle. Posterior adductor sub-elliptical, lightly impressed, co-extensive with the posterior pedal retractor anteriorly. Pallial muscle scar only lightly impressed.

Measurements (mm).

length	height	width	
44	17.5	10.0	USNM 110774: holotype
38.8	16.2	09.3	USNM 205888: paratype
38.7	16.2		USNM 209309: paratype

Remarks. *Calypdogena elongata* is known only from the shells of the three small specimens which constitute the type-series and which may be the young of a much larger species. Though most species in the Vesicomidae are small, those in the genus *Calypdogena* such as *C. pacifica* Dall, *C. modioli-forma* (Boss) and *C. ponderosa* Boss are larger. Specimens of these species may reach 100 mm or more in length.

Dall (1916) related *C. elongata* to *C. pacifica*, and Boss (1968) stated that *C. modioli-forma* was most closely related to, and was

the Atlantic homolog of *C. elongata* from which it differed in being larger and higher. *Calypdogena elongata* is probably most closely related to *C. magnifica*, differing in having a more uniform persistent periostracum, more anteriorly placed umbos, a smaller ligament, in lacking the "shelf" beneath the ligament so prominent in *C. magnifica* and in having a similar but more delicate hinge area. See also *Remarks* under *C. magnifica*. Unfortunately, until the soft anatomy of *C. elongata*, and for that matter other species of *Calypdogena*, is known, it is impossible to state definitely the relationship of these species.

Calypdogena (Ectenagena) magnifica,
Boss & Turner, species novum
Figs. 1–9, 10F–G, 11, 12D–F, 13

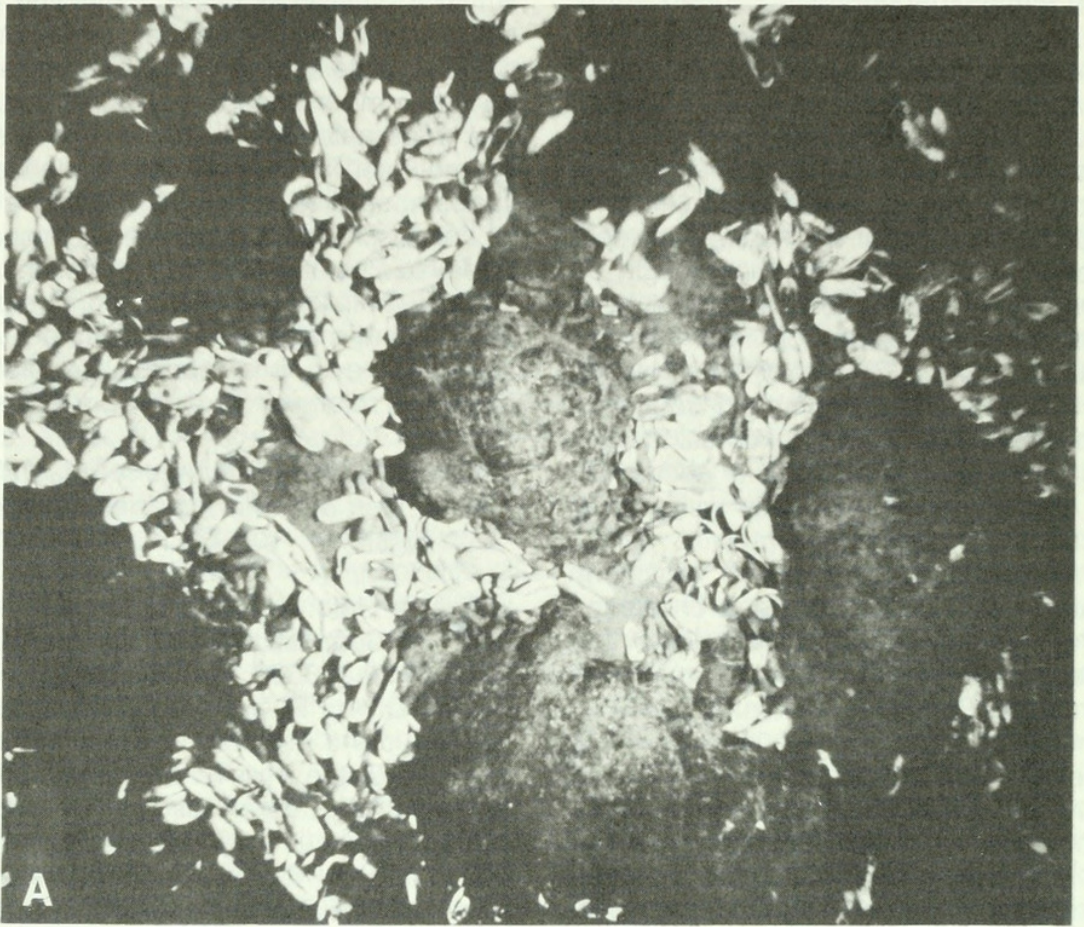
Types. Holotype, Mollusk Department, Museum of Comparative Zoology, Harvard University, no. 288500, from Galapagos Rift vent ALVIN Dive 717. Paratypes have been deposited in the Museum of Comparative Zoology (MCZ), the Division of Mollusks, National Museum of Natural History (United States National Museum, USNM), the Department of Malacology of the Academy of Natural Sciences of Philadelphia (ANSP), The Department of Invertebrate Zoology, Los Angeles County Museum (LACM), Mollusca Section of the British Museum (Natural History) (BMNH), Muséum National d'Histoire Naturelle, Paris (MNHN) and the Invertebrate Collection of the Scripps Institution of Oceanography (SIO) and are all from ALVIN dives as follows: 727 (MCZ; USNM); 879 (MCZ); 887 (MCZ); 888 (MCZ); 892 (MCZ); 895 (MCZ); 896 (MCZ); 981 (SIO); 983 (MCZ); 984 (MCZ; ANSP; BMNH; LACM; MNHN; SIO; USNM); 986 (MCZ); 991 (MCZ).

Type-locality. The holotype is from ALVIN Dive 717 at $0^\circ 47.9'N$; $86^\circ 08.5'W$ in 2495 m. Paratypes are from other vents on the Galapagos Rift taken on ALVIN dives listed under *Specimens examined* and from ALVIN Dive 981 on the East Pacific Rise vent at $20^\circ 50'N$; $109^\circ 06'W$ in 2600 m off Mexico.

Range. This species is apparently confined to the area of the thermal vents along the Galapagos Rift and the East Pacific Rise from $21^\circ N$ south to $0^\circ 47'N$ in depths ranging from 2445 to 2680 m.

*Species examined.*³ Mexico: ALVIN

³Specimens identified from pictures only show that *C. magnifica* was also seen on ALVIN Dive 909, $20^\circ 51.9'N$; $109^\circ 4.4'W$ in 2645 m; ALVIN Dive 915, $20^\circ 51'N$; $109^\circ 04.9'W$ in 2655 m; ALVIN Dive 917, $20^\circ 49.9'N$; $109^\circ 04.8'W$ in 2655 m (all about 200 miles off Punta Mita, Mexico) as well as ALVIN Dive 733 (see Fig. 1A) from $0^\circ 47.3'N$; $86^\circ 07.8'W$ in 2496 m.



Dive 981, 20°50'N; 109°06'W in 2600 m (about 20 miles W of Punta Mita, Mexico) (1 entire specimen); Galapagos Islands (all on the Galapagos Rift, about 200 miles NE of San Cristobal Island): ALVIN Dive 727, 0°47.4'N; 86°08.9'W, in 2680 m (2 specimens); ALVIN Dive 879, 0°48.18'N; 86°04.11'W, in 2495 m (1 specimen); ALVIN Dive 887, 0°48.5'N; 86°09.1'W in 2488 m (2 specimens); ALVIN Dive 888, 0°47.07'N; 86°08.5'W, in 2478 m (1 specimen); ALVIN Dive 892, 0°48.3'N; 86°13.8'W, in 2454 m (4 specimens); ALVIN Dive 895, 0°47.9'N; 86°09.3'W, in 2480 m (1 specimen); ALVIN Dive 896, 0°48.23'N; 86°13.6'W, in 2445 m (1 specimen); ALVIN Dive 983, 0°48.24'N; 86°13.47'W in 2450 m (2 specimens); ALVIN Dive 984, 0°48.24'N; 86°13.47'W in 2450 m (30 specimens); ALVIN Dive 986, 0°47.89'N; 86°9.21'W in 2492 m (2 specimens); ALVIN Dive 991, 0°47.89'N; 86°9.21'W in 2492 m (3 specimens).

Description. Shell white, thick, brittle, chalky in texture, slightly gaping, equivalve, elongate, and subelliptical; present specimens reaching 240 mm⁴ in length, 110 mm in height and 60 mm in width (Figs. 2–4). Valves inequilateral; umbos low, abraded in adult, and located on anterior third of valve. Anterior margin of valves rounded, ventral margin long, variable, ranging from nearly straight to rather strongly concave medially; posterior margin broadly rounded, posterior dorsal margin about $\frac{2}{3}$ total dorsal margin, descending from umbo at angle of about 12°; anterior dorsal margin about $\frac{1}{3}$ length and descending at angle of about 26° from umbo (Fig. 11). Valves nearly smooth, sculptured with irregular growth ridges interspersed with fine irregular growth increments (Fig. 3A). Escutcheon and lunule not developed. Ligament massive, extending length of posterior dorsal margin, opisthodontic and parivincular with strong periostracal layer, thick calcareous outer layer and thin inner layer. Periostracum dark brown, coextensive with ligament dorsally,

forming thick “ruffled” band along anterior margin in many specimens, extending posteriorly to about midway along the ventral margin, but reduced to traces on posterior margin and along growth ridges (Fig. 4C–E).

Interior of valves porcelaneous white, muscle scars and pallial line impressed. Anterior adductor scar rounded anteriorly, irregular posteriorly and deeply impressed. Anterior pedal retractor deeply impressed, elongate, irregular in outline and located slightly dorsal and posterior to anterior adductor scar (Fig. 3B, C). Posterior adductor scar irregularly subelliptical, rounded posteriorly and coextensive with small rounded posterior pedal retractor anteriorly. Ventral pallial muscle scar broad anteriorly, becoming narrower over midportion of valve (disc) and broadening again posteriorly where its breadth and slight indentation suggest a “pallial sinus.” Fine, closely spaced scars extending dorsally at right angle from ventral pallial line indicating variable mantle attachments (Fig. 3B). Series of small scars just ventral to hinge line marking dorsal mantle attachments. Distinct, but difficult to discern, scars in umbonal cavity on inner medial surface of cardinal plate marking insertion of ctenidial retractor or elevator muscle (Figs. 5 [no. 11], 8C).

Ligament. (Figs. 2A, 3B, C, 4A, B, 12D–F). Large strong, external opisthodontic; extending from umbo posteriorly to posterior pedal retractor muscles, subtended by elongate nymphal callosities and underlain by highly differentiated fused mantle isthmus. Periostracal layer elastic, horny, differentiated into thin, blackish outer portion and horn-colored inner portion, and becoming yellowish posteriorly. Outer layer thick, calcareous (somewhat disintegrated anteriorly in specimen dissected) with closely-spaced dorso-ventral cleavage planes. Inner layer thin, immediately ventral to outer calcareous layer and formed by mantle isthmus. For a discussion of the structure of the bivalve ligament see Yonge (1978a).

⁴A specimen we have not seen was reported by Keen (1977b) to be 250 mm in length; another collected in 1979 by Mr. G. Ellis, an ALVIN Pilot, was 263.5 mm long.

FIG. 1. A) Expired hot vent at the site referred to by Corliss & Ballard (1977) as Clambake II (0°47.3'N; 86°07.8'W; 2496 m). ALVIN Dive 733, with large numbers of dead *Calyptogena magnifica* Boss & Turner. B) Habitat shot of an active hot vent (referred to as Clambake I) showing a few living *Calyptogena magnifica* nestled among large numbers of mussels and with a few large galatheid crabs running around and over them (0°47.4'N; 86°08.9'W; 2680 m), ALVIN Dive 727. (Photographs courtesy R. Ballard, Woods Hole Oceanographic Institution.)

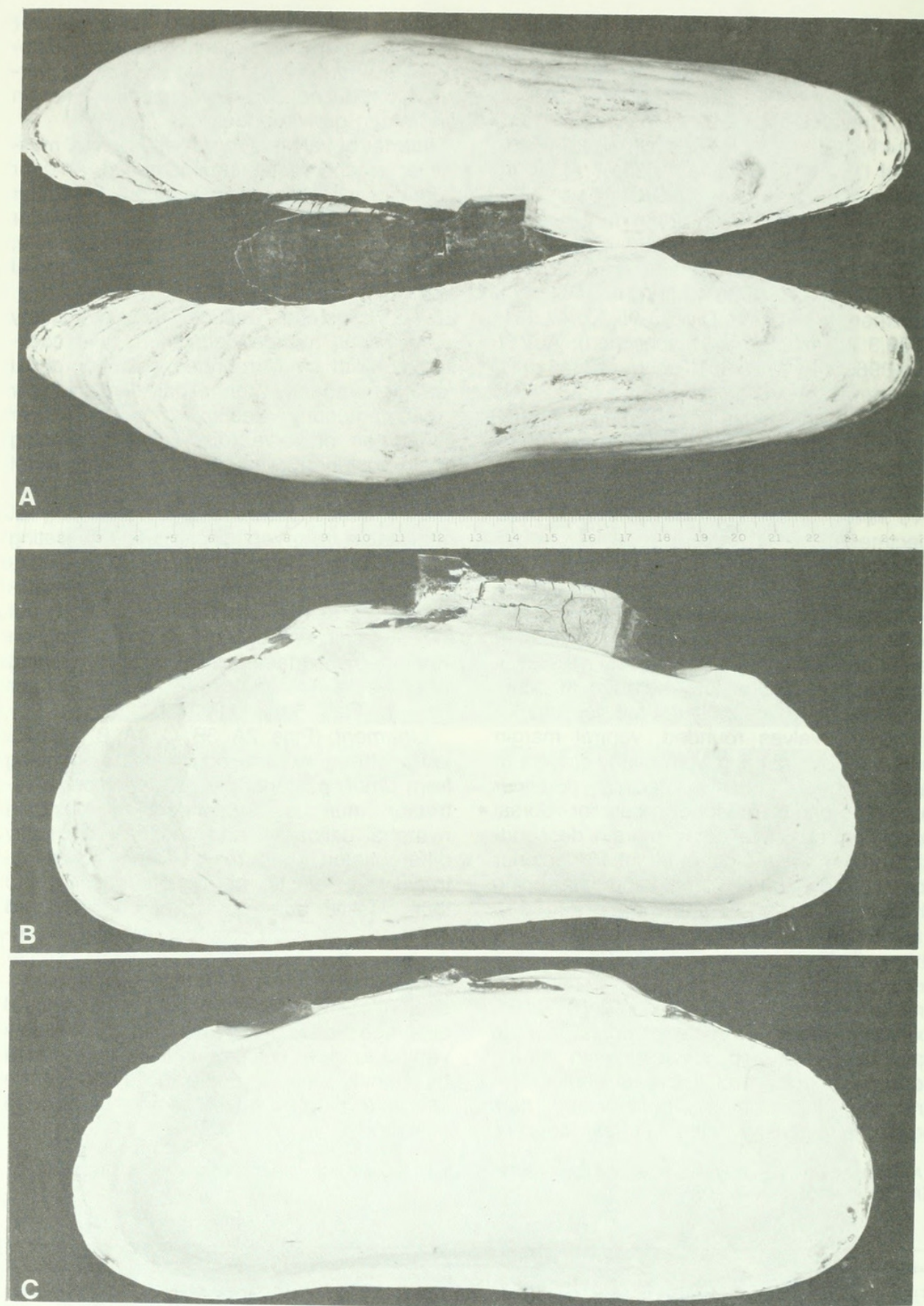


FIG. 2. *Calyptogena magnifica* Boss & Turner. A) Dorsal view of apposed valves. B) Inner view of right valve. C) Inner view of left valve. (Scale is in mm.) Specimens from Clambake I, 0°47.4'N; 86°08.9'W at 2680 m, taken on ALVIN Dive 727. Specimens at Woods Hole Oceanographic Institution. (All pictures by Woods Hole Oceanographic Institution Photographic Laboratory.)

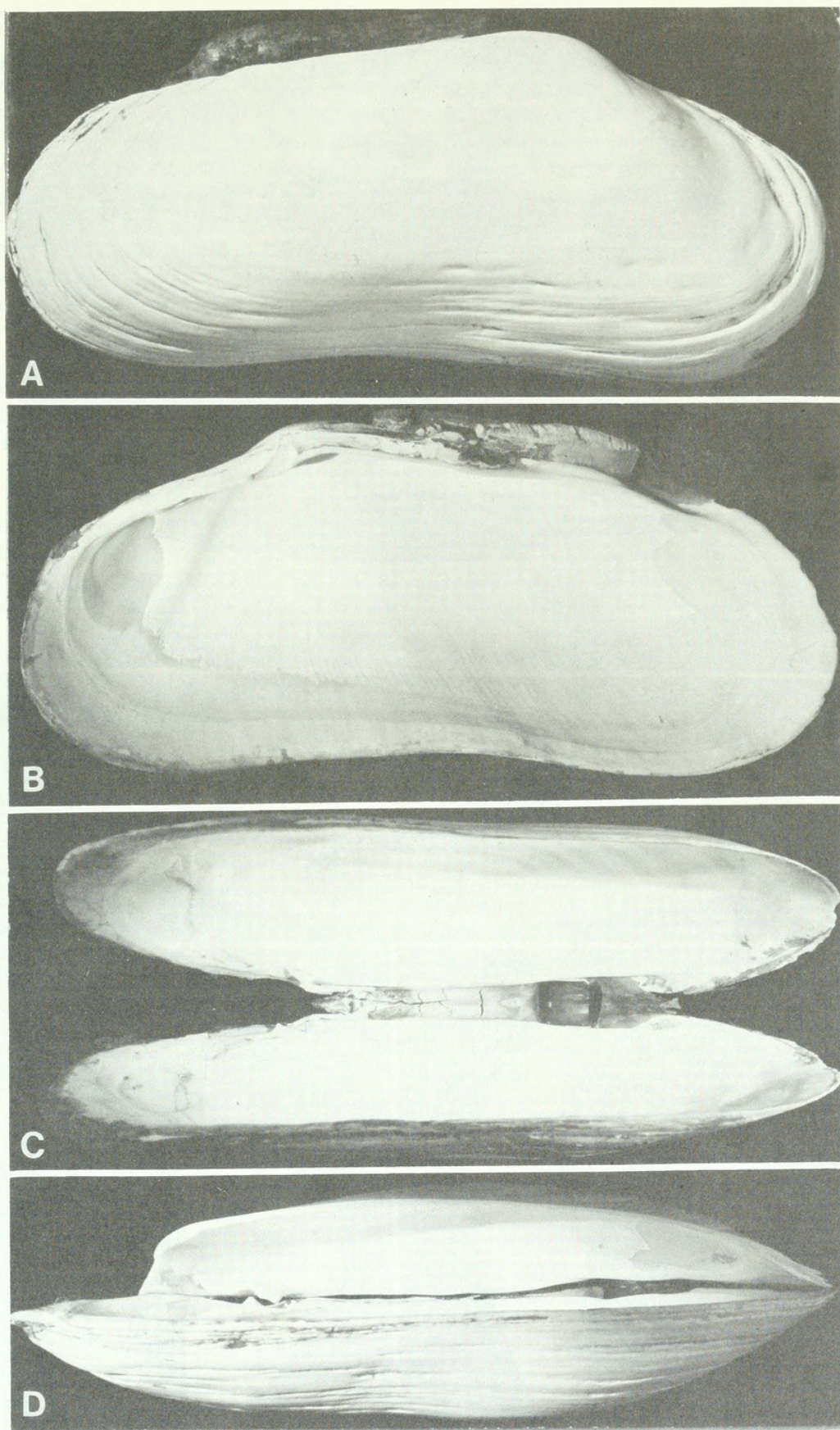
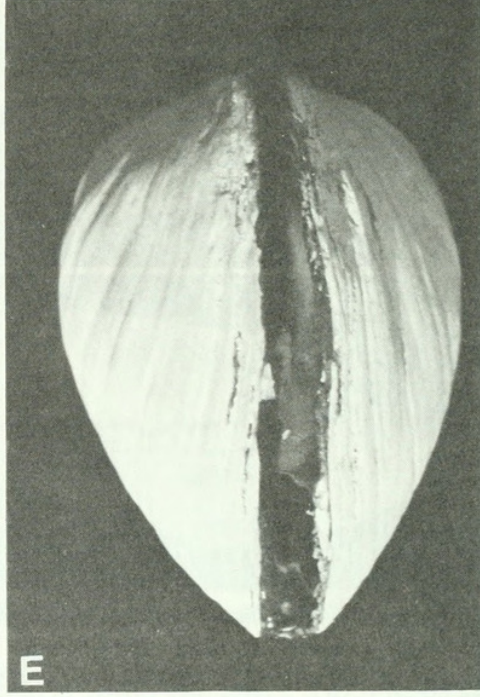
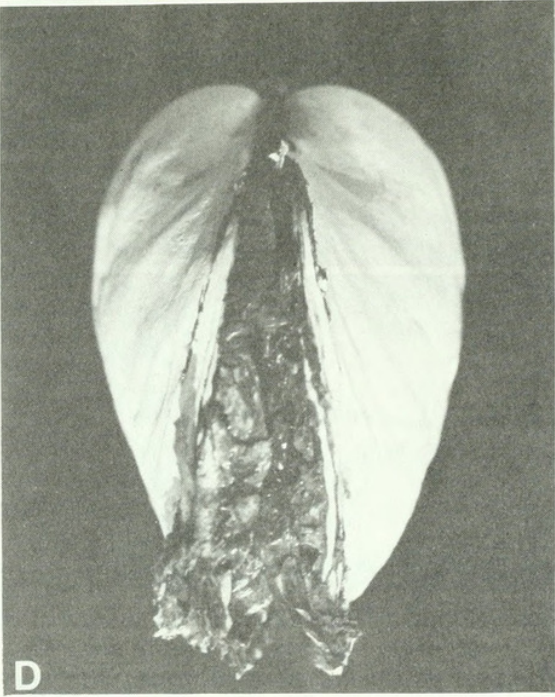
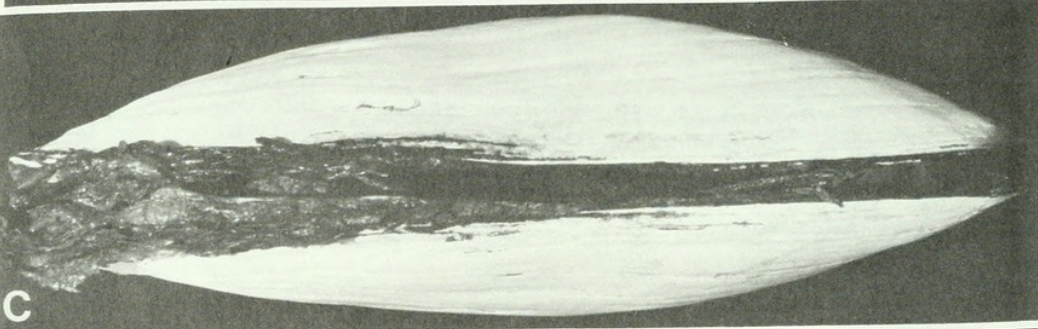
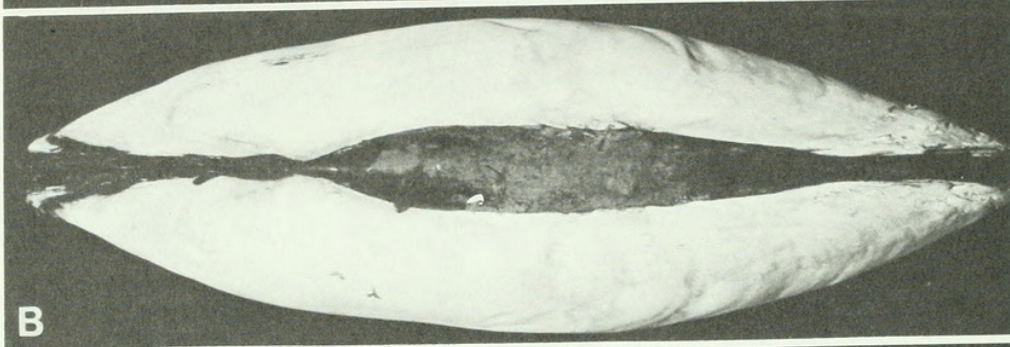
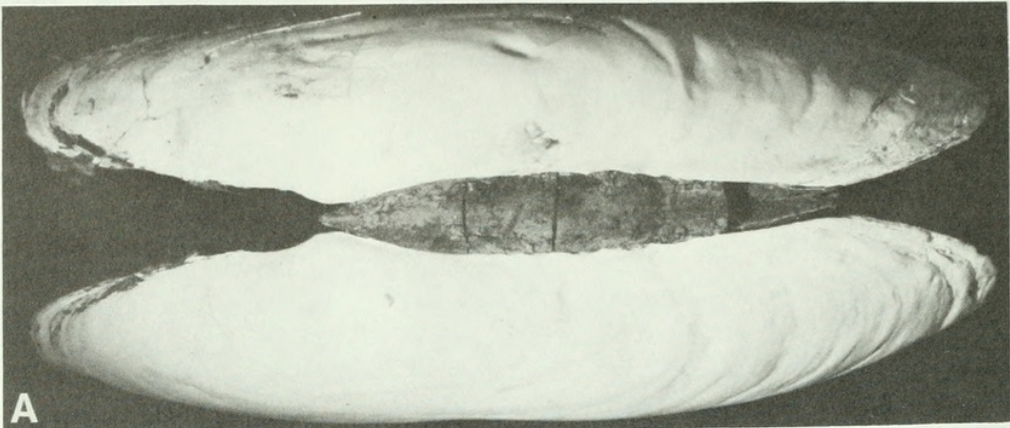


FIG. 3. *Calyptogena magnifica* Boss & Turner. A) Outer view of right valve. B) Inner view of right valve showing external ligament, muscle scars, hinge. C) Inner view of apposed valves to show ligament and hinge when valves are gaping. C) Inner view of apposed valves with the left valve broken showing position of hinge and ligament when valves are closed, and anterior pedal retractor muscle scars. Specimen in A, B and D is 240 mm in length (paratype MCZ 288499) from ALVIN Dive 727. Specimen in C is 190 mm in length (holotype MCZ 288500) from ALVIN Dive 717. (Photographs by A. Coleman, Photographic Laboratory, Museum of Comparative Zoology.)



Hinge teeth (Figs. 10F–G, 12E–F). Dentition irregular and somewhat worn in larger specimens. Hinge plate concomitantly thickened but rather small for large shelled individuals. Left valve with \supset -shaped subumbonal cardinal tooth consisting of weak, more or less straight, ridge-like, upcurled dorsal anterior ramus or tooth radiating from umbo, ventral ramus or tooth with two blunt points; excavated \supset -shaped socket between; weak ridge-like keel or posterodorsal cardinal tooth radiating posteriorly from umbo toward nymphal callosity. Right valve with diverging subumbonal cardinal dentition and lacking an anterior dorsal cardinal element which probably represents a reduction of the \supset -shaped umbonal cardinal tooth in *Calyptogena*, s.s. Posterior cardinal tooth blunt to shelf-like and ventral cardinal element more or less sharply keeled, upcurled, and ridge-like; elements separated by \supset -shaped socket. Somewhat excavated between teeth and anterior dorsal margin.

Measurements (mm).

length	height at umbo	width	ALVIN Dive	
240	110	60	727	Paratype
208.7	87.1		887	Paratype
196.5	86.1		888	Paratype
196.1	88.5		887	Paratype
190	79.4		717	Holotype
188.5	88.4		895	Paratype
180.0	78.2	53.3	879	Paratype
179.5	76.8	45.9	727	Paratype
130.6	57.2	36.8	896	Paratype
82.5	36.5	22.0	892	Paratype
56.7	25.5		984	Paratype
54.8	24.8		984	Paratype
54.2	23.7		984	Paratype
34.5	16.8		984	Paratype

Animal. Description of morphology of soft parts based on two preserved specimens available for study; the details of internal anatomy based on single specimen (for notes on living specimens see Appendix 1).

Mantle and siphons. Mantle lobes bilaterally symmetrical, with unusual thickenings both anteriorly and posteriorly (Fig. 5, nos. 2, 36,

54 & 55) firmly attached to shell ventrally by broad pallial muscles and dorsally by series of small muscles just ventral to mantle isthmus. Mantle cavity open ventrally from anterior adductor muscle posteriorly to base of incurrent siphon. Mantle with outer fold producing calcareous shell layers; periostracal glands on inner surface of outer fold giving rise to extensive, thick periostracum, particularly at anterior end (Fig. 4C, D), and middle fold with short papillae (Fig. 5, no. 3; Fig. 6A).

Inner mantle folds fused anteriorly over anterior adductor muscle to mantle isthmus; posterior fusions of inner lobe forming incurrent and excurrent siphons (Figs. 6E, 7C) and extending over dorsal surface of posterior adductor muscle to mantle isthmus.

Pallial muscles particularly extensive ventral to anterior adductor muscle and in region of siphons (Fig. 5, nos. 36, 55). Anterior thickened region of mantle heavily vascularized and glandular.

Siphons separate (Fig. 5, nos. 32, 34; Figs. 6E, 7C); incurrent siphon narrow, elliptical, and with numerous (about 40) short papillae on its inner margin; excurrent siphon rounded and lacking papillae. Rather large, rounded "papilla" ventral to incurrent siphon.

Muscles and foot. Anterior and posterior adductor muscles (Fig. 5, nos. 4 & 29) sheathed with heavy connective tissue, and composed of antero-ventral "catch" portion and larger mostly postero-dorsal "quick" portion; fibers form discrete bundles (Fig. 6C, D).

Anterior pedal retractor muscles (Fig. 5, no. 6) arising in postero-dorsal portion of foot and extending anteriorly through visceral mass to insert on valves beneath hinge plate just posterior and dorsal to anterior adductor muscle. Posterior pedal retractor muscles (Fig. 5, no. 26) arising in antero-dorsal portion of foot and inserting on valves adjacent to dorsal anterior portion of posterior adductor muscle.

Foot large and composed of two distinct portions, graded dorsally into wall of visceral mass and composed of several discrete layers of longitudinal and oblique muscles.

FIG. 4. *Calyptogena magnifica* Boss & Turner. Holotype MCZ 288500 from ALVIN Dive 717 (see also Fig. 3C). A) Dorsal view of gaping valves, after removal of body. B) Dorsal view of closed valves to show ligament and dorsal extension of the periostracum. C) Ventral view of apposed valves to show width of the specimen and the development of the periostracum along the ventral margin. D) Anterior view of apposed valves to show slight anterior gape and the development of the ruffled periostracal layers along the anterior margin. E) Posterior view of apposed valves to show width of specimen and lack of periostracum. (Photograph A by A. Coleman, Photographic Laboratory, Museum of Comparative Zoology; B–E, by R. D. Turner.)

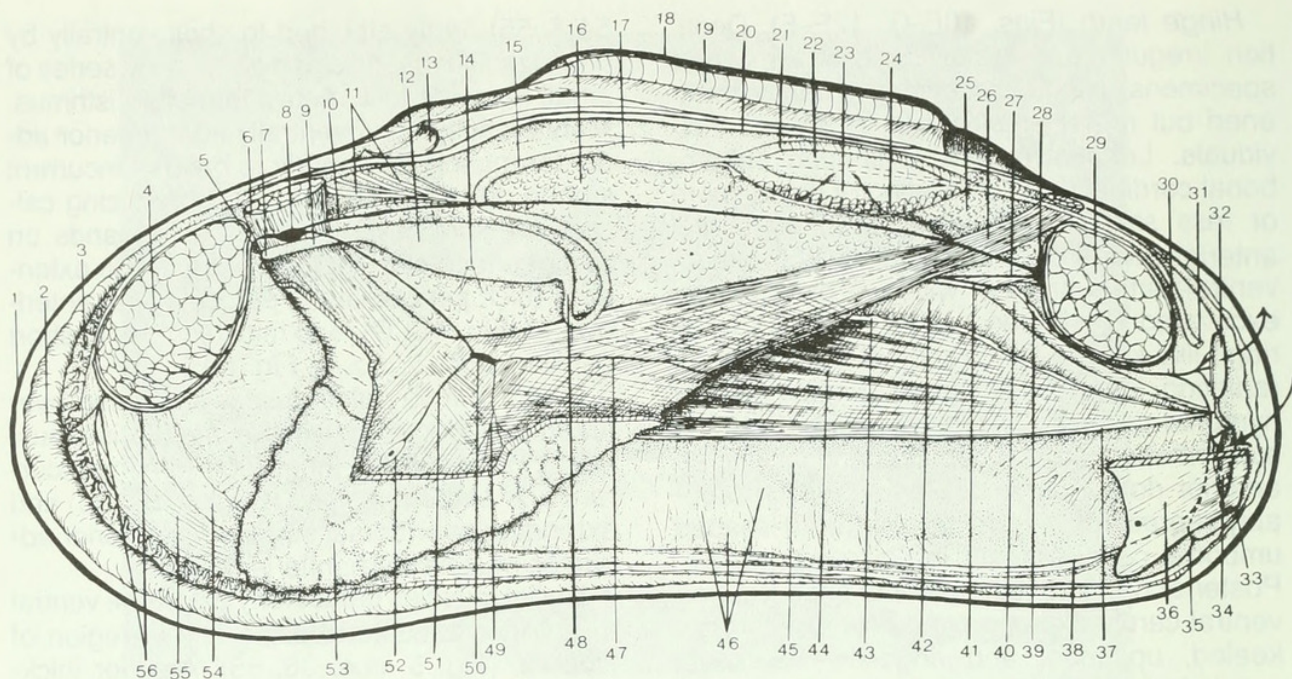


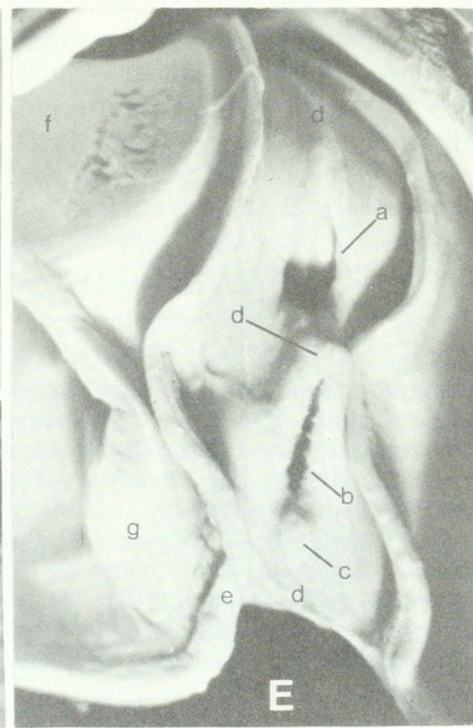
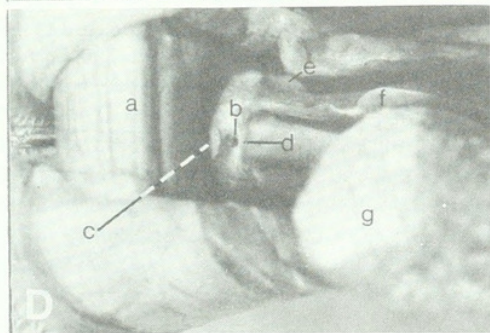
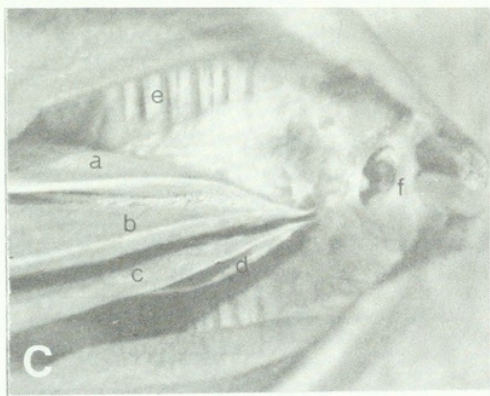
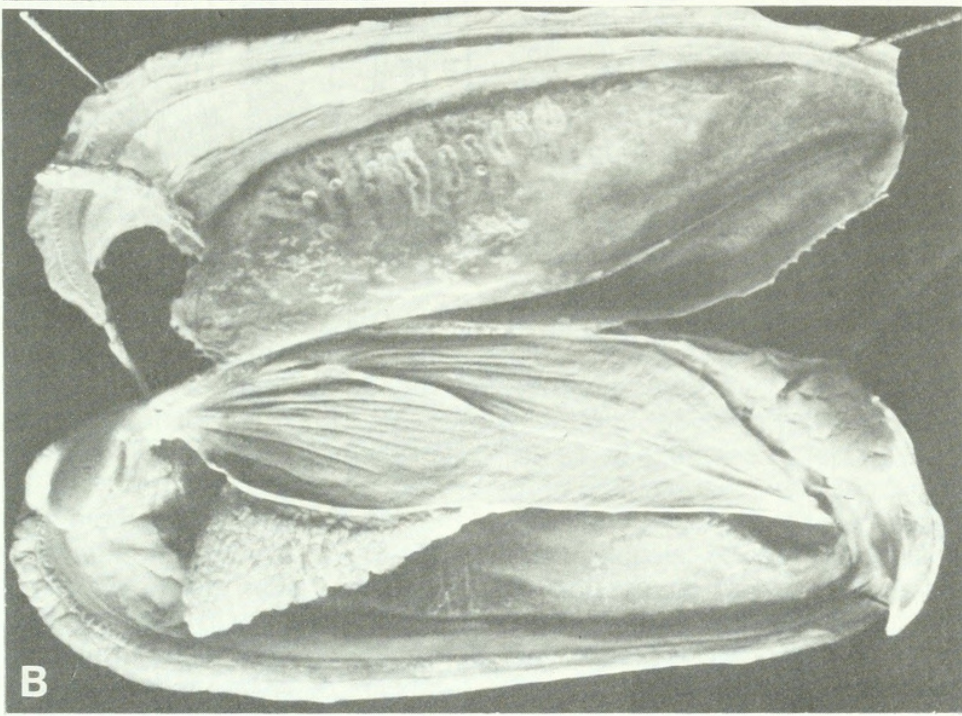
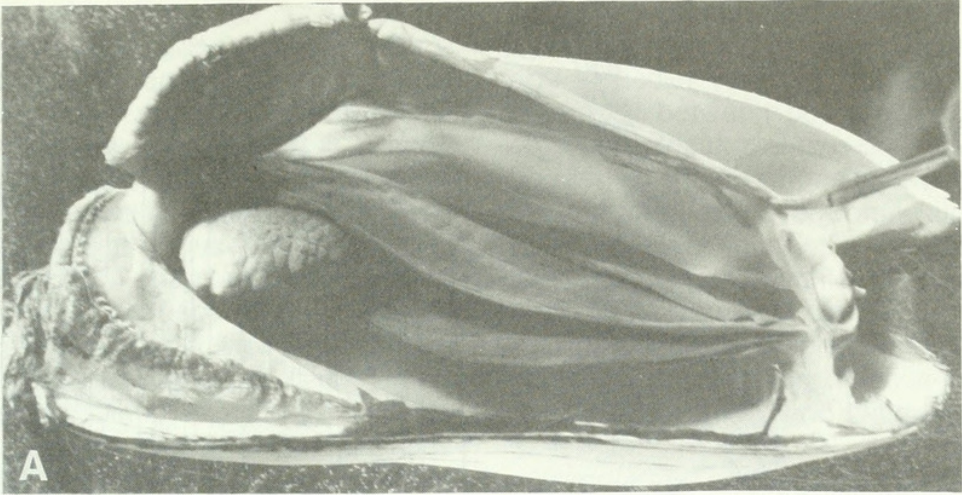
FIG. 5. Semidiagrammatic sketch of the anatomy of *Calyptogena magnifica* Boss & Turner. The valve, mantle, ctenidium and outer layers of body wall on the left side have been removed and a section of the foot cut away. 1. shell; 2. thickened outer edge of mantle; 3. band of sensory papillae; 4. anterior adductor muscle; 5. labial palp (upper); 6. anterior pedal retractor; 7. mouth; 8. cerebral ganglion; 9. esophagus; 10. cerebro-visceral connective; 11. ctenidial retractor or elevator muscle; 12. stomach; 13. hinge tooth; 14. opening of duct of digestive gland into stomach; 15. intestine; 16. digestive gland; 17. broadened section of intestine with typhlosole; 18. periostracal layer of ligament; 19. outer layer of ligament; 20. mantle; 21. pericardium; 22. ventricle; 23. auricle; 24. pericardial gland; 25. kidney; 26. posterior pedal retractor muscle; 27. branchial nerve; 28. visceral ganglion; 29. posterior adductor; 30. pallial nerve; 31. anus; 32. excurrent siphon; 33. fusion of inner mantle lobe to form incurrent siphon; 34. incurrent siphon lobes; 35. outer circumpallial nerve; 36. section of muscular portion of posterior mantle which forms the "pallial sinus"; 37. smooth margin of ctenidium; 38. inner circumpallial nerve; 39. torn edge of ctenidial attachment; 40. descending lamella of outer demibranch of right ctenidium; 41. ctenidial vein; 42. descending lamella of inner demibranch of right ctenidium; 43. torn edge of ctenidial attachment; 44. ascending lamella of inner demibranch of right ctenidium; 45. thickened spongy glandular area of mantle; 46. "ducts" in mantle; 47. posterior pedal nerve; 48. mid-gut; 49. ventral pedal nerve; 50. pedal ganglion; 51. statocyst nerve; 52. statocyst; 53. papillose foot; 54. circumpallial "vessel"; 55. thickened anterior mantle; 56. anterior pallial nerve.

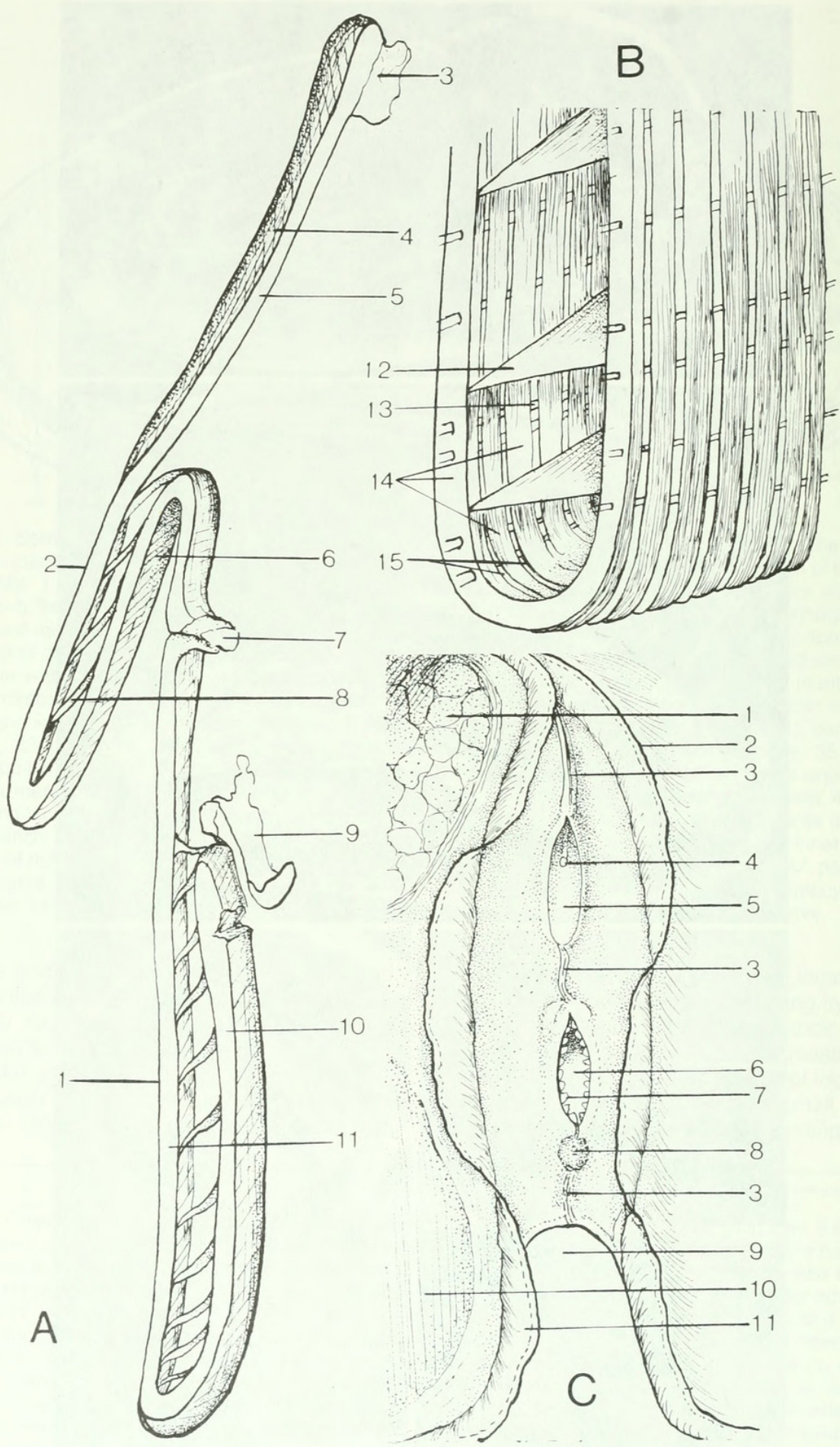
Ventral portion of foot pointing anteriorly and sub-conical in shape (triangular in side view), strongly rugose and papillate in preserved specimens. Histologically, outer layer highly glandular and inner portion forming complex of crossing muscle fibers. Byssal groove discernible along mid-ventral line of rugose por-

tion of foot; small, byssal gland located at junction with heel; specimens lacking byssus.

Ctenidia. Large, thick, homorhabdic, non-plicate, covering entire visceral mass from pericardial cavity to ventral portion of foot, and composed of large inner, and small outer demibranchs, both with descending and

FIG. 6. *Calyptogena magnifica* Boss & Turner (compare these halftones with the drawings in Figs. 5 and 7). A) Opened specimen still partially attached to the valves showing the thickened mantle margin, the papillae, periostracal groove and periostracum. B) Specimen removed from shell, with the left mantle lobe turned back, and with left ctenidium still in place. C) Ventral view showing relation of ctenidia to posterior adductor muscle: a, outer demibranch and b, inner demibranch of left ctenidium; c) inner demibranch and d, outer demibranch of right ctenidium; e, posterior adductor muscle showing discrete muscle bundles; f, opening to excurrent siphon. D) Ventral view of anterior end showing: a) anterior adductor muscle; b, mouth; c, dorsal lip; d, ventral lip; e, outer demibranch of left ctenidium; f) inner demibranch of left ctenidium; g, foot. E) Posterior view showing: a, excurrent siphon; b, incurrent siphon; c, sensory knob; d, fused inner mantle lobe; e, outer mantle lobe; f, posterior adductor muscle; g, muscular portion of posterior mantle. (Photographs by R. D. Turner.)





ascending lamellae (Figs. 7a, B, 8A, B). In preserved specimens, gills contracted dorso-ventrally, producing antero-posterior ridges and a "herring-bone" appearance to filaments and their chitinous rods (Fig. 8A). Paired demibranchs weakly fused to each other posteriorly and weakly attached to the siphonal septum distally, thus separating small epibranchial or anal chamber from large infrabranchial chamber. Ascending lamellae of outer demibranchs fused to visceral mass anteriorly and to mantle posteriorly; strong interlamellar septa uniting lamellae; filaments fused by numerous interfilamentar junctions (Figs. 7A, B, 8B). Ventral margin of both demibranchs appearing smooth and showing no evidence of food groove (Fig. 8A) in preserved specimens.

Digestive system. Mouth small, rounded, located just posterior to the anterior adductor muscle. Labial palps greatly reduced, and consisting of small non-plicate ridges (Fig. 6D), representing vestiges of inner palpal lamellae. Dorsal (= anterior) palpal ridge, co-extensive with the ctenidium, fusing with distal edge of ascending lamella of outer demibranch; ventral (= posterior) palpal ridge fusing with inner demibranch.

Mouth opening into short, thin-walled esophagus (Fig. 5, no. 9) leading to thin-walled elongate stomach about four times diameter of esophagus (Fig. 5, no. 12). Large, paired digestive diverticula with numerous secondary dichotomising ducts opening into latero-ventral anterior third of stomach via large short ducts. Short combined midgut-style sac (though no style detected) extending from stomach postero-ventrally to thin-walled intestine which recurves sharply dorso-anteriorly paralleling midgut to about midway over stomach where it turns postero-dorsally as flattened ribbon-like structure and passes through visceral mass to pericardial cavity; posterior half of this section of intestine with thickened walls and ventral typhlosole (Fig. 5,

no. 17). Rectum thin-walled in pericardial cavity, surrounded by extensive anterior aorta and muscular ventricle, passing through kidneys and between posterior pedal retractor muscles. Rectum ribbon-like posteriorly, imbedded in sheath of posterior adductor muscle and extending over dorsal surface of posterior adductor muscle to terminate at papillate anus in epibranchial chamber near the opening of excurrent siphon.

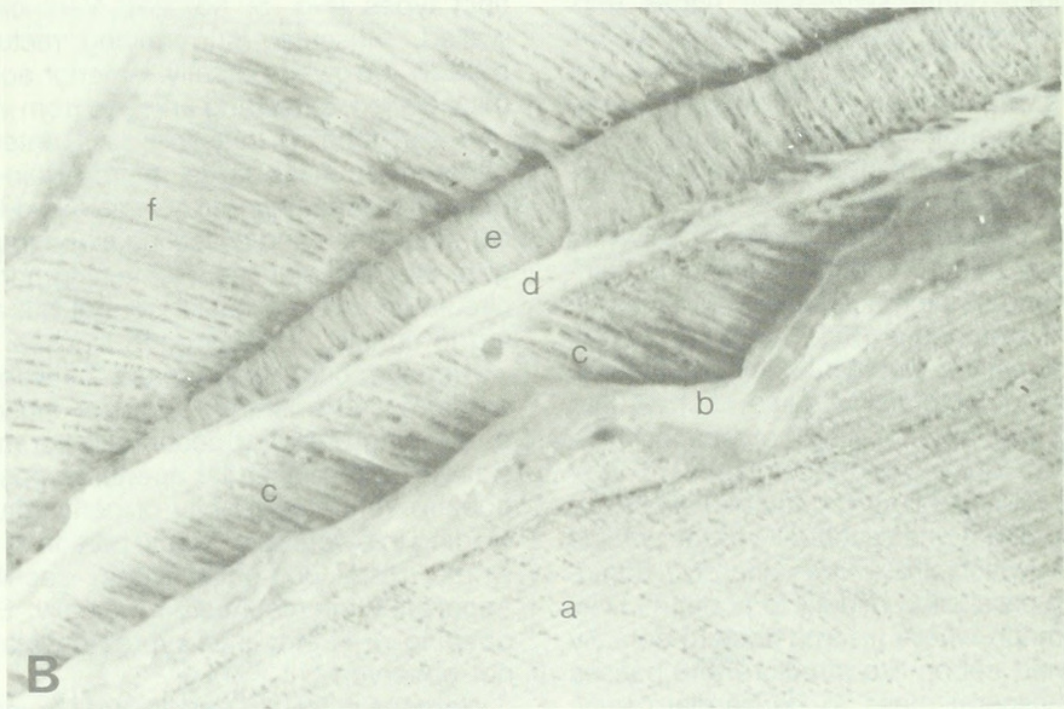
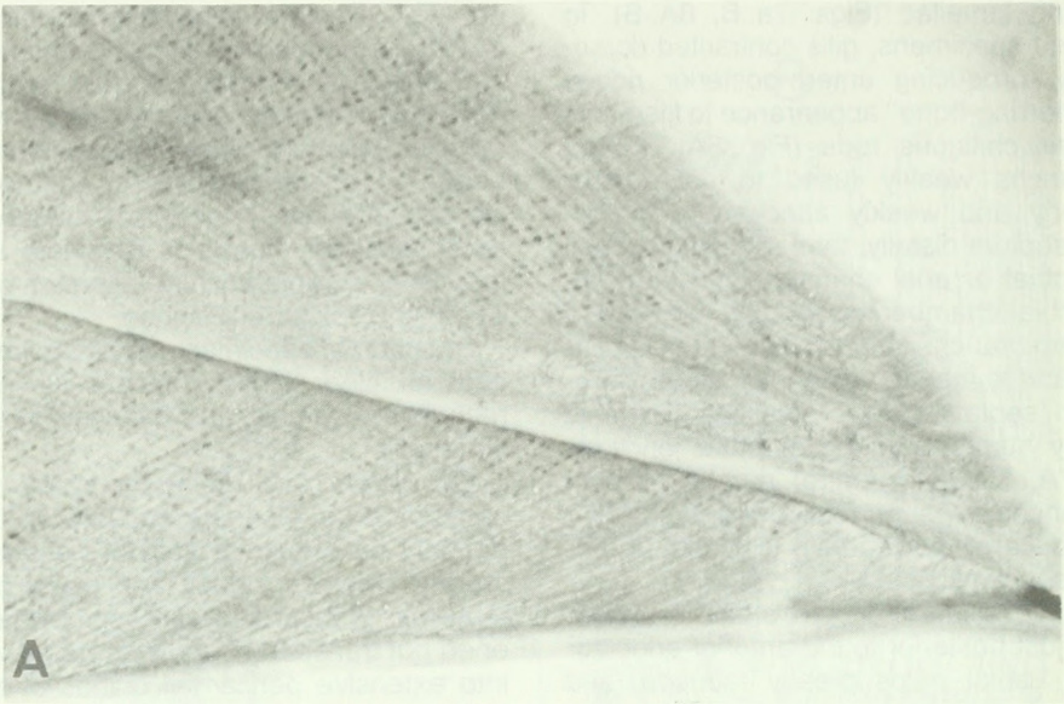
Stomach of specimen examined empty, except for clear whitish mucous-like material; rectum also empty and flattened throughout its length.

Circulatory and excretory systems. Pericardium large, elongate and located postero-dorsally on surface of visceral mass and posteriorly between kidney and pedal retractor muscles. Pericardial walls somewhat thickened but transparent and elaborated ventrally into extensive pericardial glands of two distinct types (Fig. 5, no. 24). Ventricle thick-walled, muscular, surrounding rectum and broadly furrowed dorsally. Anterior aorta also thick walled, extending anteriorly from ventricle and surrounding intestine as it enters pericardium. Auricles large, paired, thin-walled, triangular, opening into ventricle mid-laterally via small ostia and collecting blood from elongate ctenidial sinuses. Remaining portions of circulatory system not discerned but appearing to consist of many open sinuses.

Kidneys occupying space between pericardium and posterior adductor muscle and enveloping posterior pedal retractor muscles. Paired reno-pericardial apertures opening at postero-ventral extremity of pericardium and leading into ventral proximal portion of kidney. Dorsal distal portion of kidney sac-like and apparently interconnected medially. External opening of kidney into suprabranchial cavity not observed.

Nervous system. Ganglia and nerves easily discerned (Figs. 5, 9). Cerebral ganglia (Fig. 5, no. 8) situated beneath anteroventral sur-

FIG. 7. *Calyptogena magnifica* Boss & Turner. A) Diagrammatic sketch of section through ctenidium. 1. inner demibranch; 2. outer demibranch; 3. attachment membrane of outer demibranch; 4. outer surface of ascending lamella of outer demibranch; 5. cut edge of demibranch; 6. outer surface of descending lamella of outer demibranch; 7. attachment area and blood vessel; 8. interlamella septum; 9. attachment membrane of inner demibranch; 10. ascending lamella of inner demibranch; 11. descending lamella of inner demibranch (see also Fig. 8A, B). B) Diagrammatic enlarged section of demibranch. 12. interlamellar septum; 13). interfilamental space; 14. filaments; 15. interfilamental junctions. C) Diagrammatic sketch of posterior siphonal area (see also Fig. 6E). 1. posterior adductor muscle; 2. right outer mantle lobe; 3. fusion of inner mantle lobes; 4. anus; 5. excurrent siphon; 6. incurrent siphon; 7. papillae around incurrent siphon; 8. "sensory knob" or "button"; 9. open mantle cavity; 10. muscular portion of mantle attachment; 11. left outer mantle lobe.



face of anterior pedal retractor muscle and directly above mouth, closely juxtaposed and connected by very short supraesophageal commissure. Pallial nerves arising from anterior portion of cerebral ganglia and giving off branches to anterior adductor muscle. Neither buccal ganglia nor labial palp nerves observed. Cerebro-visceral connectives arising from posterior lateral regions of cerebral ganglia and coursing posteriorly along sides of visceral mass to connect with visceral ganglia anterolaterally. Pleural ganglionic thickenings present on the cerebro-visceral connectives near the junction of esophagus with stomach. Cerebro-pedal connectives arising from anterior lateral region of cerebral ganglia and passing posteroventrally into foot and enter dorsal surface of partially fused, but distinctly bilobate pedal ganglion. Branches innervating intrinsic foot muscles and deep portions of anterior pedal retractor muscle arising from connectives. Fused pedal ganglia giving rise to three pairs of nerves: 1) ventral pedal nerves dividing into medial and lateral rami serving distal papillose portions of foot; 2) posterior pedal nerves bifurcating into medial and lateral branches and innervating posterior intrinsic muscle, deep portions of posterior pedal retractor muscle and byssal gland; and 3) long anterior nerves terminating in hollow bulb-like statocyst with refractive granular statolith. Paired visceral ganglia, partially fused, and located on anterior surface of posterior adductor muscle. Branchial nerves arching anteriorly from lateral portion of visceral ganglia and recurving to innervate axes of ctenidia. Visceral ganglia giving rise posteriorly to large pallial nerves with numerous branches to posterior adductor muscle and dorsal mantle. Pallial nerve ventrally bifurcating to form outer and inner circumpallial nerves, sending numerous discrete branches to excurrent and incurrent siphons and associated sensory structures as well as extending along ventral mantle margin. Two small protuberances on ventral surface of posterior adductor muscle and closely associated with visceral ganglia probably represent abdominal sense organs.

Remarks. As a member of a family of typically burrowing infaunal bivalves, *Calypatogena magnifica* is an unusual species not only for its size but for its remarkable ability to exploit a unique epifaunal niche, nestled in crevices and among mussels surrounding the abyssal hot vents.

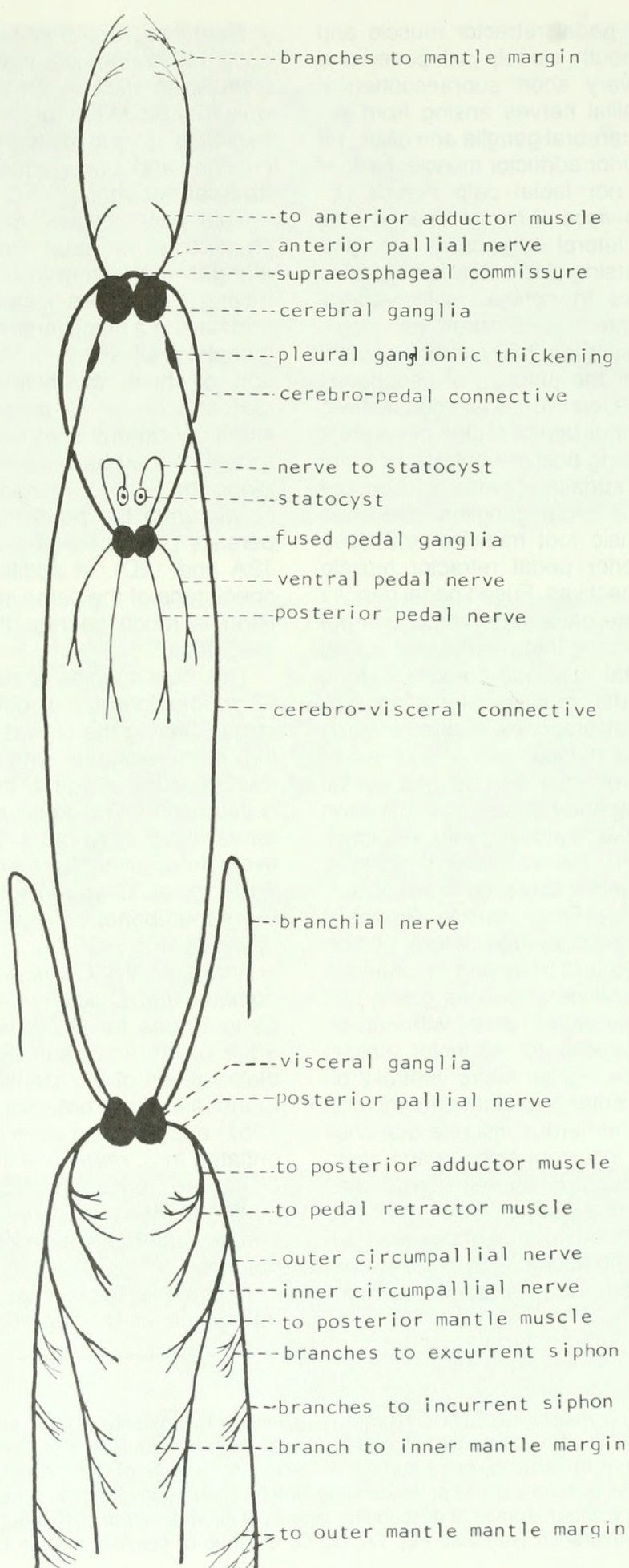
This new species, on the basis of shell characters, is most closely related to *C. elongata* but differs in attaining greater size, having the umbos located more posteriorly and having a much larger ligament and longer nymphal callosity (see Fig. 12 for a comparison of these characters). In addition, the periostracum of *C. magnifica*, even in very small specimens does not remain on the disc though it may be present as a large "ruffle" along the anterior margin (see Fig. 4C–D). In *C. elongata* the periostracum is thinner and persists over the entire valve (compare Fig. 12A and 12D). In addition when comparing specimens of the same size the cardinal dentition is much coarser though similar in *C. magnifica*.

This new species is also closely related to *C. modioliforma*, but differs in being much larger, having the umbos more posterior, being more elongate and having the periostracum on the margin of the valves more highly developed. The dentition of *C. modioliforma* tends to be more blunt, thickened, and relatively more extensive than in *C. magnifica*. In addition, as *C. magnifica* increases in size, the subumbonal cardinal tooth tends to curl upwards (Fig. 10F–G).

Anatomically, *C. magnifica* resembles *C. pacifica* and *C. kilmeri*—the only species of *Calypatogena* for which we have any knowledge of the soft parts (Bernard, 1974). The elaborations of the mantle folds, comparable to those in other heterodont bivalves (Yonge, 1957) appear to be even more strongly differentiated in *C. magnifica* than in *C. pacifica* or *C. kilmeri*. Sensory papillae along the anterior mantle folds and an extensive periostracal border anteriorly are characteristic of *C. magnifica* (Figs. 4C, D, 5, 6A, B).

The mantle thickenings in the anterior ventral region of *C. magnifica* are more highly

FIG. 8. *Calypatogena magnifica* Boss & Turner. A) Closeup of posterior end of external surface of left ctenidium to show smooth ventral margins and texture of demibranchs (see also Figs. 6 and 7). B) Dorsal view of left ctenidium to show: a, outer surface of ascending lamella of outer demibranch; b, connecting membrane to mantle; c, inner surface of descending lamella of outer demibranch; d, ctenidial axis with blood vessel and muscle; e, inner surface of descending lamella of inner demibranch; f, inner surface of ascending lamella of inner demibranch (see also Fig. 7A, B). C) Closeup of ctenidial muscle (see also Fig. 5).



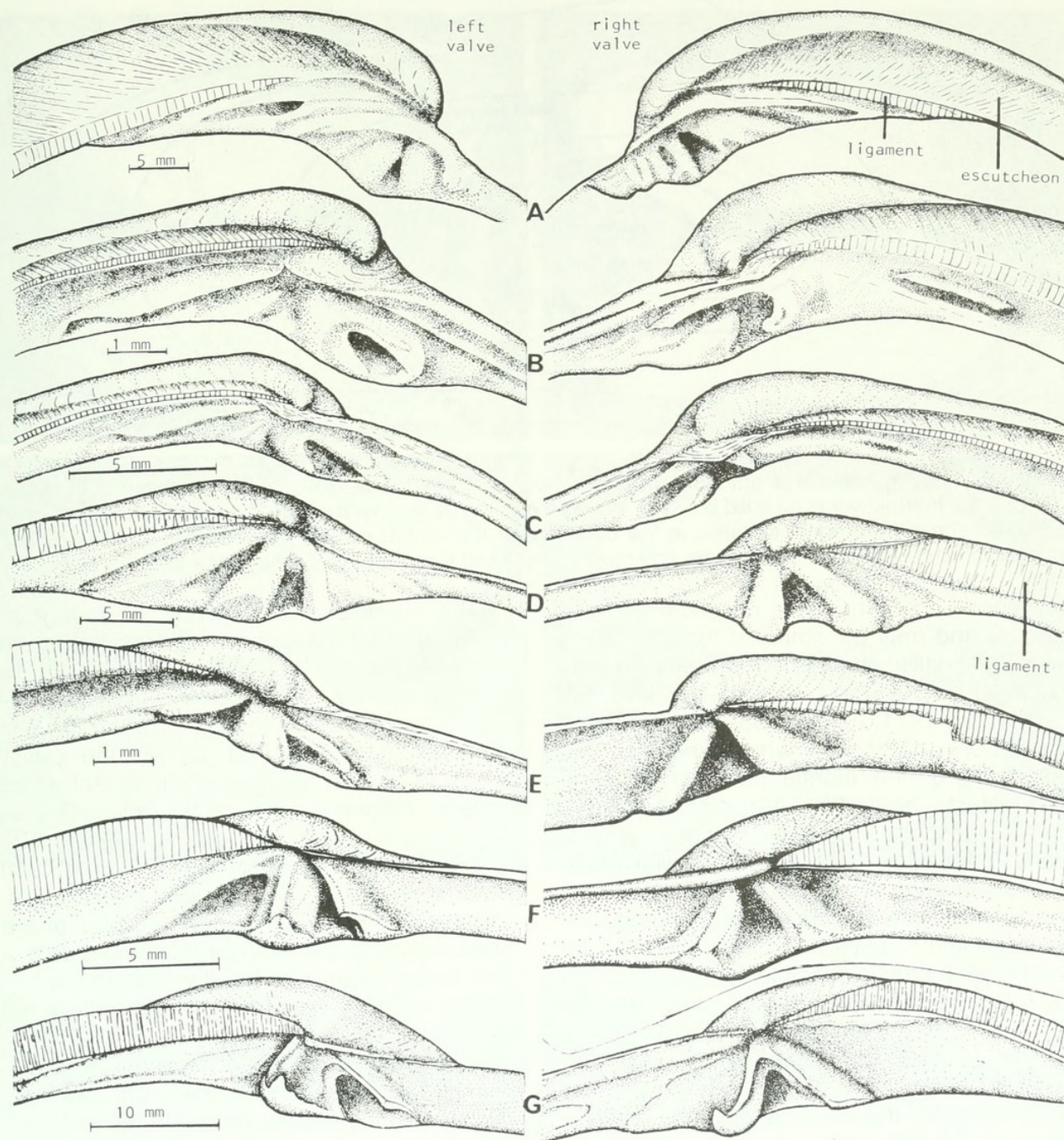


FIG. 10. The hinge and ligament of *Calyptogena*. A–C) Species in *Calyptogena*, s.s. Note small ligament and the presence of an escutcheon. D–G) Species in the subgenus *Ectenagena*. Note the presence of a large ligament and the lack of an escutcheon. A a, b) *C. (Calyptogena) ponderosa* Boss. Holotype, Oregon I, sta. 1426, 29°07'N; 87°54'W, about 77 mi. S of Mobile Bay, Gulf of Mexico, in 1097 m. B a, b) *C. (Calyptogena) pacifica* Dall. Syntype, Albatross sta. 3077, Clarence Strait, Dixon Entrance, Alaska, 55°46'N; 132°24'W, in 580 m. Young specimen 30.5 mm long. C a, b) *Ibid.* Adult specimen 47.5 mm long. D a, b) *C. (Ectenagena) modioliforma* Boss. Holotype, Pillsbury sta. 394, 9°28.6'N; 76°26.3'W; Golfo del Darien, 66 mi. NNE of Punta Caribana, Colombia, in 421–641 m. E a, b) *C. (Ectenagena) elongata* Dall. Holotype, off Point Loma, California, in 486 m. Specimen 44 mm long. F a, b) *C. (Ectenagena) magna* Boss & Turner, Galapagos Rift, ALVIN dive 892. Specimen 82.5 mm long. G a, b) *C. (Ectenagena) magna* Boss & Turner, Galapagos Rift, ALVIN dive 896. Specimen 130.6 mm long.

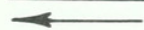


FIG. 9. Diagrammatic sketch of the nervous system of *Calyptogena magna* Boss & Turner from the dorsal aspect. (See Fig. 5 for the lateral view of the essential elements of the nervous system.)

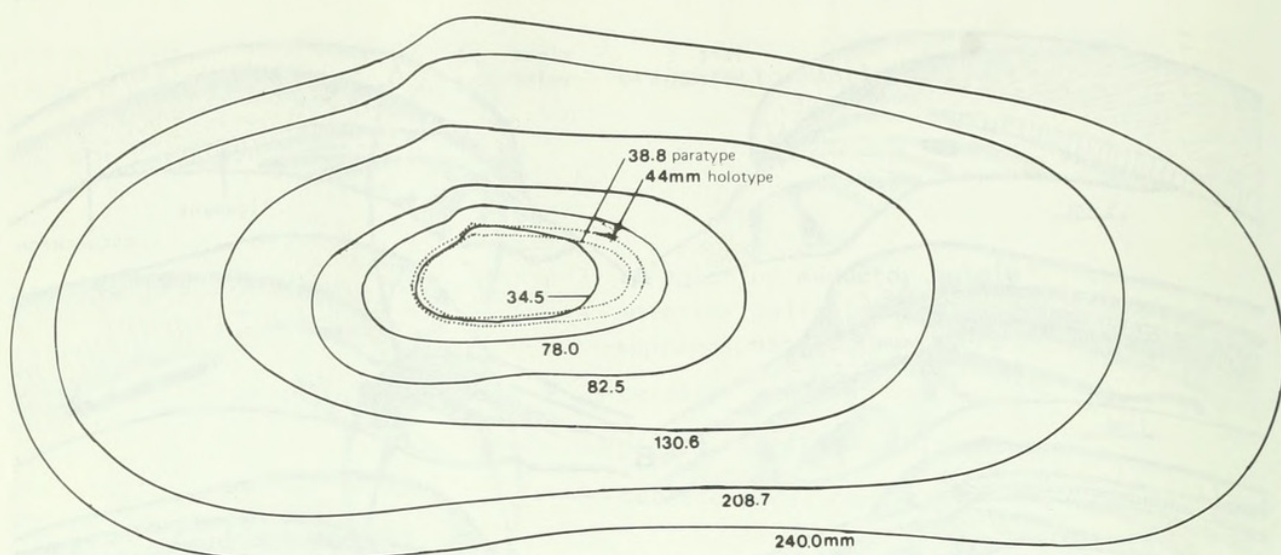


FIG. 11. Inset outlines of a graded series of valves of *C. magnifica* Boss & Turner obtained from the Galapagos thermal vents (in solid lines) as well as the holotype and paratype of *C. elongata* Dall (in dashed lines) to show the gradual increase in the curvature of the ventral margin with increase in size and the proportional difference in shell length and height position of the umbos in *C. magnifica* and *C. elongata*.

developed than in either *C. pacifica* or *C. kilmeri*, and may be similar in function to the so-called 'pallial gills' or 'Mantelkiemen' of the Lucinacea (Duvernoy, 1853; Semper, 1880; Pelseneer, 1911; Allen, 1958) or to the pallial glands of carditaceans, which function in the cleansing of the mantle cavity (Pelseneer, 1911; Harry, 1966; Allen, 1968; Yonge, 1969). In *Calyptogena*, however, neither special transverse folds nor definitive pallial blood vessels leading directly to the auricles, as in the lucinids, are apparent though some kind of secondary respiratory function may be surmised. It seems possible that this region in *C. magnifica* even though it is not between the outer and middle mantle folds (Figs. 4C, D, 6A), is developed for the massive production of periostracum, which may protect the anterior end of the valves against the environment of the hot vents or assist, perhaps, in maintenance of position. The region might also be similar in function to the anterior mantle thickenings or pallial mucous glands found in the Saxicavacea (Yonge, 1971).

Bernard (1974: 13) described as hypertrophied the posterior portion of the thickened mantle musculature of *C. pacifica*. The impression on the valves of this extensive posterior development is variable and has been called, by numerous authorities, the 'pallial sinus.' The siphons of vesicomyids are not greatly extendable and the radiating fan-like siphonal retractor muscles which form the pallial sinus in so many families of bivalves (Pelseneer, 1891; Boss & Kenk, 1964) are not present.

The so-called 'pallial sinus' is a dubious character for taxonomic discrimination in *Calyptogena* or other vesicomyids, but in a group with few differentiating features, this character may have to be employed. As can be seen from Figs. 2B, C, 3B, the 'pallial sinus' is only a reflection of the extent, in an anterior-posterior axis, of the thickening or hypertrophy of the edge of the mantle. The 'pallial sinus' of *C. magnifica* is 14% of total shell length while in *C. pacifica* it is 22%. Unfortunately, when the internal surface of the shell is glossy, the configuration and extent of the 'pallial sinus' is difficult to determine.

The sensory papillae of the mantle edge are protrusible posteriorly in the siphonal region and anteriorly in the vicinity of the maximum periostracal development. The fused inner lobe of the mantle ventral to the incurrent siphon forms an extrusible velum in *C. pacifica* and *C. kilmeri* (Bernard, 1974). The same appears to be true for *C. magnifica*. The "sensory knob" beneath the incurrent siphon (Figs. 6E, 7C) is similar to the "sensory button" in *Thyasira* (Allen, 1958: 435, fig. 10b).

In *Calyptogena*, as with many bivalves (Yonge, 1962), the byssus may be functional only during settlement and in the young stages. The foot, capable of protrusion beyond the valves, probably functions in locomotion and positioning. In contrast to the rather smooth pedal integument found in *C. pacifica* and *C. kilmeri* (Bernard, 1974), the foot of *C. magnifica* is highly rugose, roughened, or subpapillose with the distal portion containing glandular structures. Since most species of

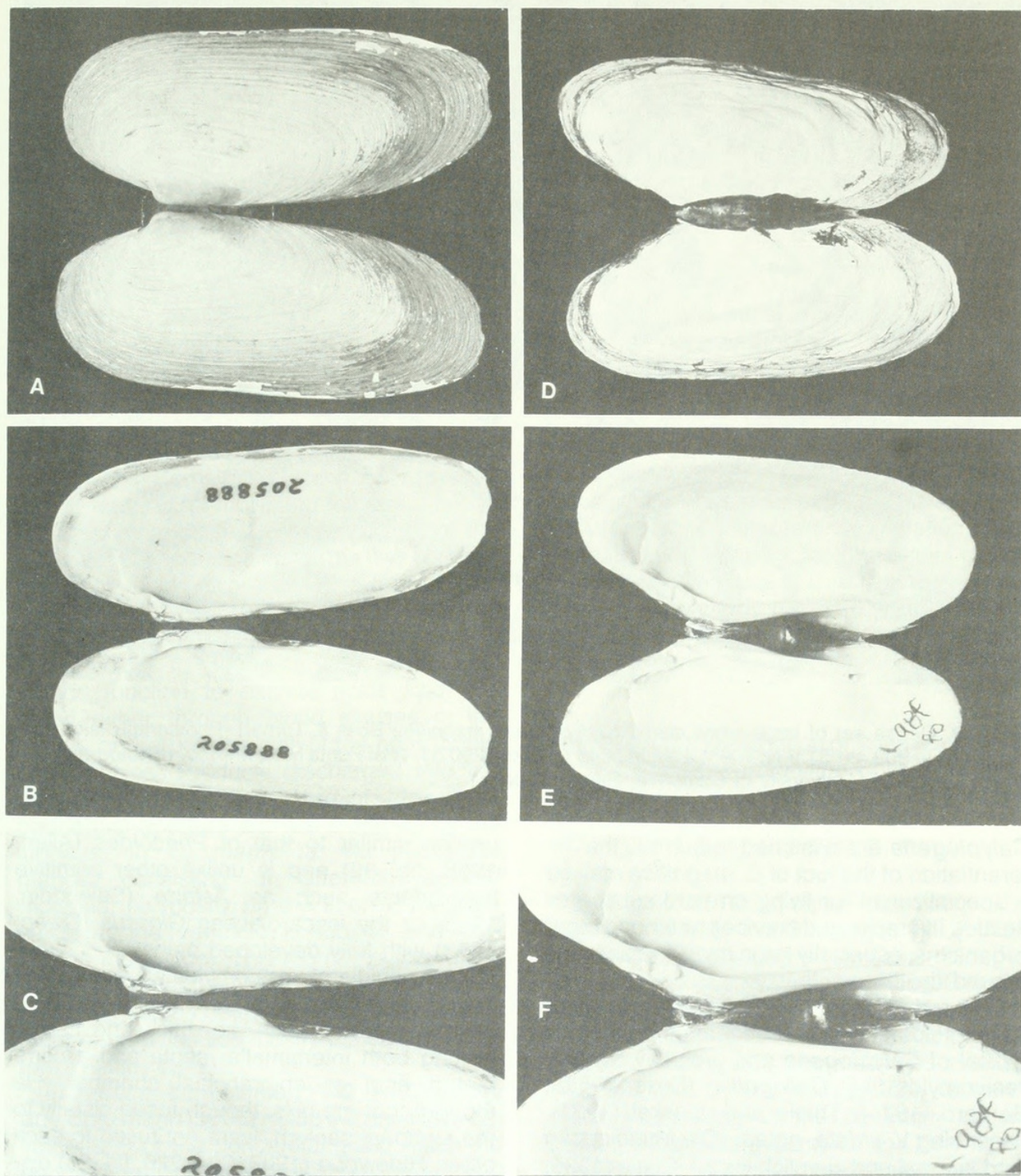


FIG. 12. Comparison of *Calyptogena elongata* Dall and *C. magnifica* Boss & Turner. A–C) *Calyptogena elongata*, paratype USNM 205888 (Albatross sta. 4432, off Point Loma, California, in 275 fathoms, 8 mi. S of Brockway Point, Santa Rosa Id., Channel Ids. (see also footnote 2). A) Outer view of valves to show position of the umbos in the anterior $\frac{1}{4}$ of the valves and retention of the periostracum. B) Inner view of valves to show hinge and position of the relatively weakly impressed muscle scars. C) Close-up of hinge area to show small ligamental area (specimen 38.8 mm long). D–F) *Calyptogena magnifica*, paratype MCZ, ALVIN Dive 984, $0^{\circ}48.24'N$; $86^{\circ}13.47'W$ in 2450 m. Galapagos Rift. A) Outer view of valves showing lack of periostracum except on the edge of the valves, the position of the umbos at the anterior $\frac{1}{3}$ of the valves and the large ligament extending the length of the posterior dorsal margin. B) Inner view of valves showing the large cardinal teeth, the large ligament and the well-impressed muscle scars. C) Close-up of the hinge area to show the large ligament and the shelf bordering it (specimen 34.5 mm long). (Photographs by R. D. Turner and C. B. Calloway.)

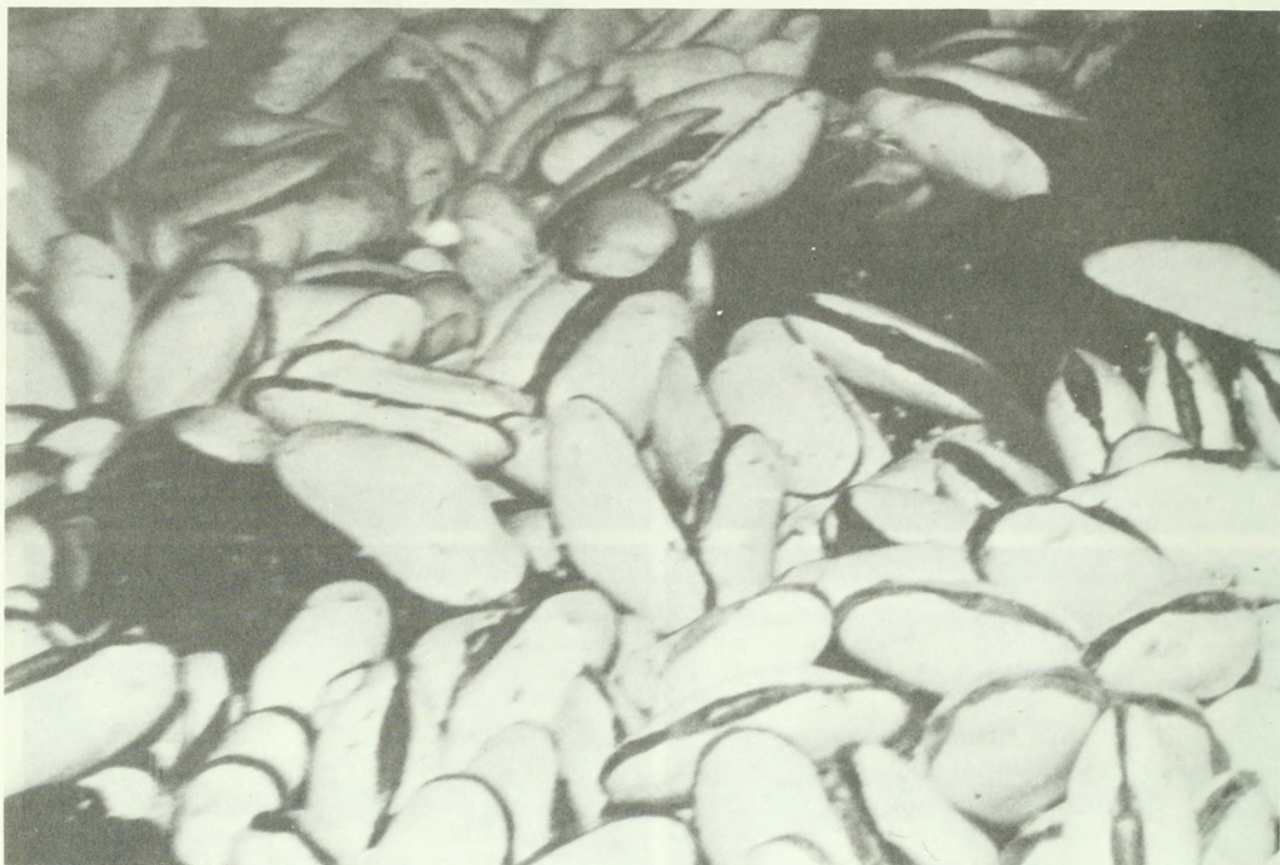


FIG. 13. Dense set of large white clams (*Calyptogena magnifica* Boss & Turner). Photograph taken on ALVIN Dive 909, 20°51.9'N; 109°4.4'W, in 2645 m, about 200 mi. W of Punta Mita, Mexico. (Photograph by Bruce Luyendyk, University of California, Santa Barbara.)

Calyptogena are assumed to burrow, the differentiation of the foot of *C. magnifica* may be a specialization for living on hard substrates nestled in cracks and crevices or among other organisms, especially large mytilids also found around the hot vents.

The reduction of the labial palps to mere lip-like folds above and beneath the mouth is typical of *Calyptogena* and probably of other vesicomysids (e.g. *Callogonia*) (Boss, 1969a; Bernard, 1974). Thiele and Jaekel (1931), describing *V. striata*, noted: "Die Mundlappen sind schmal und ziemlich kurz." Thiele (1935) incorporated that observation in his remarks on the family Kellyellidae (sic) in which he included *Vesicomys*. However, reduction or loss of labial palps, usually correlated with reduced selection of particulate food, is a secondarily derived feature convergent in several distinct lineages of bivalves: lucinids (Thiele, 1886: 247, fig. 23; Purchon, 1939; Allen, 1958), limids (Stuardo, 1968); dimyids (Waller, 1978; Yonge, 1978b), mytilids (Yonge, Goreau & Goreau, 1972) and teredinids (Turner, 1966).

Calyptogena shows a reduced palp config-

uration similar to that of *Phacoides* (Allen, 1958: fig. 39) and is unlike other primitive heterodonts such as *Astarte* (Saleuddin, 1965) or the isocardiacean *Glossus* (Owen, 1953) with fully developed palps.

The ctenidia of vesicomysids were originally described by Dall (1895a: 505; 1895b: 696) as being protobranch-like, thick and fleshy, lacking both interlamellar septa and a completed anal or epibranchial chamber. He thought that the gills, though fused distally to the siphonal septum, were not fused to each other. Ridewood (1903: 224–226, fig. 23) disagreed with Dall and showed that the gills of *V. stearnsi* were eulamellibranch with small outer demibranchs and closely packed filaments. He stated that in *V. stearnsi* the ascending lamellae of the outer demibranchs were not fused to the mantle nor were the gills fused to each other posteriorly but pointed out that the gills were so rigid that they would 'readily come away from adjacent parts even if organically united to them.' Such a configuration is certainly not true of *C. magnifica*. We were able to see the connections before beginning the dissection; however, these quickly

separated, leaving no evidence of connections. The interlamellar septa in *V. stearnsi* are weak, and the ctenidia readily separate into plates. In contrast, the interlamellar septa in *C. magnifica* (Fig. 7B) are strong and hold the lamellae of the demibranchs together. According to Bernard (1974), neither *C. pacifica* nor *C. kilmeri* possess interlamellar septa.

Ridewood (1903) concluded that *Vesicomya* resembled *Lucina* rather than the Protobranchia but it is probable that the similarities are, in part, convergent as both these genera have long geological histories, especially lucinids which date from the Paleozoic. In fact the ctenidia are rather poor distinguishing familial taxobases in lamellibranch bivalves. Ridewood himself (1903: 186) was unable to give diagnoses for the numerous suborders he employed, much less discriminating features of individual families.

The placement and gross structure of the kidney of *C. magnifica* conforms with the type found in eulamellibranch bivalves as described by Odhner (1912) and is similar to that of *Kelliella miliaris* (Clausen, 1958).

According to White (1942), pericardial glands function to excrete acids from the blood either through blood sinuses in the mantle or through the wall of the pericardium and auricles. Products discharged into the pericardial cavity pass through the renopericardial aperture and are extracted by the kidneys. In *C. magnifica* the pericardial glands, consisting of differently colored moieties, lie mostly on the floor of the pericardium; the ventricle is tubular and embraces the rectum. This morphology is unlike that of the Carditidae, with which vesicomysids have sometimes been placed in that the ventricle of carditids lies mostly beneath the rectum (White, 1942).

In *Arctica*, both White (1942 [as *Cyprina*]) and Boltzmann (1906) noted the extensive development of the pericardial gland within the pericardium and anteriorly over the visceral pedal mass in the mantle. However, unlike that of *Calyplogena*, the ventricle in *Arctica* is short and rectangular; the renopericardial apertures are on the posteroventral wall of the pericardium.

In its general anatomy, the nervous system of *Calyplogena magnifica* does not differ significantly from most eulamellibranchs (Lammens, 1969; Bullock & Horridge, 1965). Unlike the statocysts of *Kelliella miliaris*, which are close to or incorporated in the pedal ganglion (Clausen, 1958), the statocysts in

Calyplogena are large, well-developed and located in the foot some distance from the pedal ganglia (Fig. 5).

Specimens available to us were not in proper condition for detailed work on the reproductive system and no previous descriptive work is known; however, sections taken in the visceral mass just anterior to the pericardium and dorsal to the stomach showed the presence of numerous, large, yolky oocytes, measuring 150–195 μm in greatest diameter, in germinal vesicle stage.

On the basis of anatomical evidence, *C. magnifica* can be separated from *C. pacifica* and *C. kilmeri* by the development of strong interlamellar septa between the lamellae of the demibranchs. Lesser features in *C. magnifica* include the glandular structure on the surface of the foot, the more extensive development of the anterior portion of the edge of the mantle and the greater proliferation of the periostracum. Possibly the pericardial glands may differ from those of *C. pacifica* which are prolonged anteriorly (Bernard, 1974), but it is not known whether they enter the visceral mass or mantle tissue.

APPENDIX 1. Description of living specimens of *Calyplogena magnifica* Boss & Turner with notes on their distribution and ecology

Carl J. Berg and Ruth D. Turner

During the 1979 Biological expedition to the thermal vents of the Galapagos Rift (LULU-ALVIN Cruise 102, leg 9 and Cruise 103, leg 5) we made observations on living *Calyplogena magnifica* to supplement the description of the species by Boss & Turner based on preserved specimens. We made observations of specimens in situ from ALVIN, of specimens maintained in the aquarium aboard LULU, while taking samples for histological and electrophoretic studies, while preparing valves for age determinations, and while preserving the soft parts for anatomical studies. Additional data on distribution, orientation and behavior of the large white clams were obtained from discussions with other scientists who had visited the sites in ALVIN as well as from videotapes and photographs taken on the various dives. During these two series of dives 61 living *Calyplogena magnifica* were collected, 15 on Cruise 102 and 46 on Cruise 103. Specimens ranged in size from 34.5 to 241 mm in length, the largest ones (188–

241 mm in length) were taken at the vent named "Mussel Bed" (0°48.5'N; 86°09.0'W in 2480 m and the smaller ones (34.5–151 mm in length) from "Rose Garden" (0°48.3'N; 86°13.8'W in 2450 m). The smaller size of the white clams, the lighter color and smaller size of the mussels combined with the abundance and great size of the vestimentiferans at "Rose Garden" suggest that this may be the younger and more active of these two vent areas. Although large groups of empty clam shells were seen at most of the vents, the living clams were scattered and in small groups, usually of ten or fewer. They were nestled among dead clams, living mussels or in rock crevices, usually oriented in a nearly vertical position, the iridescent pink mantle and the openings of the siphons often showing between the slightly gaping valves. This suggests that larval clams settle in the presence of other clams and/or in response to warm water issuing from the fissures in the lava rock and that, as they grow, they maintain a position with the foot probing for warmth.

The clams were never observed with the valves more than slightly gaping and they would often remain closed for long periods of time, particularly in the aquarium. The mantle of living specimens is an iridescent purple-pink, the papillae on the incurrent siphon yellowish. In situ observations showed that the siphons opened and closed frequently, that they could be extended slightly but that they never extended beyond the valves. They are capable, however, of forcibly ejecting material a distance of at least 30 cm from the siphonal aperture.

A yellowish, transparent, tough and stretchy, plastic-like periostracum extends from the periostracal groove of the mantle margin out over the valve protecting the growing edge of the shell. When removing the soft parts from the valves it was necessary to cut this with scissors so firmly was it attached to the outside of the valve and to the mantle. It appeared as a brown wrinkled border along the margins of the valves, being thin posteriorly and increasing to multiple ruffles at the anterior end.

An isolated specimen, possibly disturbed by ALVIN activity was observed lying on its side at the edge of a cluster of clams. The specimen, approximately 150 mm in length, had extended its foot about half the length of its shell but showed little activity except weak probing movements during the half hour it

was in view (while the pilot was picking up microbiological experiments for return to the surface). The foot was lighter but similar in color to the mantle and appeared smooth. Specimens brought to the surface, however, all appeared to have a strongly rugose foot, a condition which might be due partly to contraction and/or reduction in pressure. The rugosities were blister-like and when punctured released a clear fluid. The foot of a specimen kept for two days in the aquarium, maintained at about 2°C, became less rugose, and the foot of one maintained under pressure became smooth, suggesting the possibility that these clams have some ability to adapt to changes in pressure. The proximal half of the foot, visible only after the shell has been opened and the mantle and gills turned back, is smooth light brown and streaked with dark red blood vessels. Small clams are lighter in color and have a cream-colored foot reminiscent of *Mercenaria*.

The ctenidia in large, newly collected specimens are light brown with pronounced zigzag longitudinal streaks of red and finer, more-or-less vertical mottlings of reddish-brown. These markings are perhaps a reflection of the 'herring-bone' configuration of the gill filaments described by Boss & Turner. The ventral margins of the ctenidia were a purple-pink and there was a grayish line at the junction of the inner demibranch with the visceral mass. The gills of small clams were a uniform cream color. Many clams had notches on the posterior ventral margin of the outer gills, the number varied from one to three and was not necessarily the same on both sides of the animal. We have no explanation for these notches which occurred on clams found at all vents from which material was collected.

The large white clams, unlike the mussels commonly found around the vents, have red blood, which gives a red appearance to the animals when the shell is opened. The red pigment is intracellular, and is a haemoglobin but it has not been fully characterized as yet. The pericardial region has a dark red coloration which extends laterally down to the ctenidia. No pumping of the heart was observed, nor did the blood spurt when the clams were cut or when blood samples were taken. The non-muscular portion of the mantle was thin, nearly transparent and reddish-brown. Small specimens are much lighter in color than the larger ones but the red color of all specimens increased with time as they remained in the aquarium.

The position of the gonads, though typical for bivalves, cannot be determined by general examination of the body surface even in living specimens, probably due to the overall red coloration of the animal. Dissection and histological examination of specimens collected in February 1979 showed ova in all stages of development and yolky eggs 309 μm in diameter. Eggs found lying free in a jar with a preserved clam ranged from 364–482 μm in diameter. These data suggest that *C. magnifica* releases large yolky eggs.

The clams did not react when crabs or shrimp crawled over their shells and touched the mantle but they closed slowly when handled by the submarine's manipulator. Crabs are obviously not predators on the larger clams though they may feed on young specimens. Octopus have been seen at the vents and are suspected predators on the larger clams.

APPENDIX 2. Annotated list of fossil and living species currently referable to *Calyptogena*

Kenneth J. Boss

?*Calyptogena akanudaensis* Tanaka

Calyptogena akanudaensis Tanaka, 1959: 119, pl. 2, figs. 1–8; Hanzawa, Asano & Takai, 1961: 219 (type-locality, cliff along the mountain-side, about 1.5 km E of the Nishikibe Elementary School, Shigamura, Higashi-Chikuma-gun, Nagano Prefecture, Bessho Formation, Miocene; Holotype, no. 510; paratypes, nos. 524–531, Geological Institute, Faculty of Education, Matsumoto Branch, Shinshu University); Okutani, 1966b: 301).

Remarks. Despite considerable efforts, we have not been able to obtain the original reference and follow Okutani (1966b: 301) in considering this species, though initially referred to *Calyptogena*, as a questionable member of the genus.

Range. Fossil in Miocene of Japan.

Calyptogena (Calyptogena) chitanii (Kanehara)

Adulomya chitanii Kanehara, 1937: 19–20, pl. 5, figs. 1, 6, 7, 8, 9 (localities, Ashikaya-Zawa, Sekinami-mura; Takai and Nakosono-seki, Sekimoto-mura; Hatanaka Shizuzaku, Izumi-mura; Nishinakada, Watanabe-mura; geological horizon, Mizunoya Shale, Kamen-

owo Shale, Yunagaya Series; Shirado Series; [Jôban coal field, Fukushima Prefecture, Japan, Miocene; for type-specimens, see Hanzawa, Asano & Takai, 1961: 211); Aoki, 1954: 31–32 as "*Adulomya*," pl. 1, figs. 9, 10, 11 (localities, cliff of small valley, Dônosaku, Kamikatayose, Kabeya and small cliff of path-side in small valley of Kamikatayose, Kabeya. Kabeya Formation [Ishimori district, Jôban coal field, Fukushima Prefecture, Japan; Miocene]); Hanzawa, Asano & Takai, 1961: 211 (type-locality, Ashikaya-zawa, Sekinami-mura, Jôban coal field, Fukushima Prefecture, Mizunoya Shale, Miocene; holotype and paratype, Geological Survey, Japan); Kamada, 1962: 39–41 (localities, Shisawa, Nakoso City. Kamenoo Formation; Fukuda, Sekinami, Kitaibaraki City. Kamenoo Formation; Nagako, Nishikimachi, Nakoso City. Kamenoo Formation; Kanegasawa, Hisanohama-machi. Kamenoo Formation; Tangozawa, Shiroyama, Taira City. Honya Formation; northern cliff of Taira railroad station, Shiroyama, Taira City. Honya Formation. Yagawase cliff, Taira City. Honya Formation; Tsuruga-machi, Iino, Taira City. Misawa Formation [Jôban coal field, Fukushima Prefecture, Japan, Miocene]).

Akebiconcha chitanii (Kanehara). Kanno & Ogawa, 1964: 285–286, pl. 1, figs. 17–18 (upper part of the Takinoue Formation [Hokkaido, Japan]); Kanno, 1967: 401–402, pl. 1, figs. 9–11, 15 (Itsukaichi [machi group] Basin, Tokyo Prefecture; Miocene).

Calyptogena chitanii (Kanehara). Kanno, 1971: 80–82, pl. 7, figs. 5, 6a–b; pl. 17, fig. 12, text-figs. 10, 11, and 12 (Kayak Island [Alaska], Yakataga Formation [upper middle Miocene or upper Miocene]).

Remarks. We include this species in *Calyptogena* following its placement there by Kanno (1971), who figured the hinge, showed the range of its allometric change in shape, documented its extensive occurrence in the fossil record, and contrasted it with both *C. elongata* and *C. pacifica*. Probably referable to *Calyptogena*, s.s., *C. chitanii* is similar to *C. pacifica*, especially in regard to the dentition of its left valve (contrast Kanno, 1971: text-fig. 10, nos. 2, 3 with Fig. 10, Ba, Ca). Representing a Miocene ancestor of *Calyptogena* in the northern Pacific Basin, *C. chitanii* is apparently separable from *C. pacifica* only by its more narrowly elongate and arcuate form; further distinctions might be made in regard to the development of the escutcheon and nature of the dentition of the right valve, if suites of

specimens were available for comparative analysis.

Range. Miocene (upper middle or upper) in Alaskan and Japanese formations [Kamenoo Formation, Itsukaichi-machi group, Honya Formation, Kabeya Formation, Takinoue Formation, and Yakataga Formation] (see Kanno, 1971).

Calyptogena (Ectenagena) elongata Dall

Remarks. See text, p. 164.

Calyptogena (Calyptogena) kawamurai elongata (Ozaki)

Akebiconcha kawamurai elongata Ozaki, 1958: 123, pl. 5, figs. 3, 4, pl. 6, figs. 1–5 (cotype from Ebishima (type-locality, small islet off Inuwaka, Tyôsi, Na-arai Formation (Lower Pliocene) and paratype from roadside cutting in front of Electric Car Station of Zinmuzi, Miura Peninsula, Kanagawa Prefecture; Ikego Formation (Lower Pliocene) *non* Dall, 1916; Hanzawa, Asano & Takai, 1961: 221 (syntype from Ebishima, off Inuwaka, Choshi City, Na-arai Formation (Miocene); Shikama, 1962: 53; Okutani, 1966b: 301 (Pliocene).

Remarks. This is a synonym of *C. kawamurai*, *C. nipponica* and probably *C. soyoae*, and, since it was originally described in *Akebiconcha*, it became, when transferred to *Calyptogena*, a secondary homonym of *C. elongata* Dall; the population named by Ozaki (1958) constitutes only an individual variation (Shikama, 1962).

Calyptogena (?*Calyptogena*) *gibbera* Crickmay

Calyptogena gibbera Crickmay, 1929: 93, 1 fig. (type-locality, lowest bed of the Santa Barbara Formation, on Deadman's Island, near San Pedro, California [Pliocene]; Woodring, 1938: 51 (early Pleistocene silt of Deadman's Island [Arnold's Pliocene; Alex Clark's Timms Point Formation]); Woodring, Bramlette & Kew, 1946: 83.

Remarks. When naming this species, Crickmay (1929) compared it with *C. elongata* and *C. pacifica*, though the hinge was not described and therefore a subgeneric placement is uncertain; however, *C. gibbera* very much resembles *C. pacifica*, especially in its size, proportions and gross outline (52 × 29 × 15 mm) and is probably synonymous with *C.*

pacifica; it differs from *C. elongata* in not being narrowly elongate.

Range. Pleistocene, Deadman's Island, California.

Calyptogena (Calyptogena) kawamurai (Kuroda)

Akebiconcha kawamurai Kuroda, 1943: 17, text figs. 1–3 (type-locality, off Odawara, Sagami Bay, in about 100 fathoms); Habe, 1952: 159, pl. 22, figs. 20–31; Hatai & Nisiyama, 1952: 33 (as synonym of *Calyptogena nipponica*); Habe, 1961: 122, pl. 55, fig. 16 (100–200 m, Sagami Bay); Okutani, 1957: 28; Ozaki, 1958: 124, pl. 3, figs. 1–3, pl. 4, figs. 1–3, pl. 5, figs. 1, 2 (Kashima-Nada); Okutani, 1962: 23 (700–750 m, Sagami Bay); Okutani, 1966b: 301; Shikama, 1962: 53, pl. 3, figs. 6a–d, 7a–c (about 46 miles east to southeast of Chôshi, 200–230 fathoms); Habe, 1968: 179, pl. 55, fig. 16 (100–600 m in Sagami Bay to Kashima-Nada, Honshû); Habe, 1977: 237, pl. 50, figs. 3–4.

Calyptogena kawamurai (Kuroda). Bernard, 1974: 18.

Remarks. The original Japanese description of *C. kawamurai* by Kuroda (1943) has been rendered into English by Ozaki (1958). The nomen is a synonym of *C. nipponica* as indicated by Hatai & Nisiyama (1952: 33). In all probability, *C. nipponica* will come to be recognized as the senior synonym of not only *C. kawamurai*, and *C. elongata* Ozaki, but of *C. soyoae* as well.

Range. Recent from Kashima-Nada and from off Chôshi to Sagami Bay, in 100 to 750 m.

Calyptogena (Calyptogena) kilmeri Bernard

Calyptogena (Archivesica) kilmeri Bernard, 1974: 17–18, text-figs. 1B, 2B, 3B and 4E (type-locality, off west coast of Moresby Island, Queen Charlotte Islands, British Columbia, Canada, in 1170 m).

Remarks. Bernard (1974) provides several additional localities besides the type-locality. Because of the similar nature of its dentition and the absence of any reliable distinguishing anatomical traits from *C. pacifica* (see Bernard, 1974: 18), we place *C. kilmeri* in *Calyptogena*, s.s. although we have not included *Archivesica* in the synonymy of *Calyptogena*. Bernard apparently utilized *Archivesica* for *C.*

kilmeri because of its relatively thin shell, stating "Archivesica . . . thinner shelled . . . modioliform . . . small pallial sinus." *Archivesica*, based on its type-species *Callocardia gigas* Dall, from the Gulf of California, may indeed be thinly shelled but it also can be thick and heavy (e.g. USNM 266874).

Previously, Boss (1967; 1968) related *Archivesica gigas* to such species as *Vesicomya caribbea* Boss from the Caribbean Sea, *V. chuni* Thiele & Jaeckel from off West Africa, *V. winckworthi* Prashad from the East Indies and *V. leeana* Dall from North Carolina to Tobago in the western Atlantic. One might also include: *V. angulata* Dall from Panama Bay, *V. longa* Thiele & Jaeckel from the Gulf of Guinea and *V. suavis* from off Lower California. Thiele & Jaeckel (1931) placed *V. chuni* in *Callogonia*, a procedure subsequently followed by Boss (1969a: 254; 1970: 69), who suggested that *Archivesica* might be considered a synonym of *Callogonia*.

Until we have a better understanding of the supraspecific categories of this group and although *Archivesica* may fall into the synonymy of *Calyptogena*, we presently consider it a synonym of *Callogonia*, and conserve that as a subgenus of *Vesicomya* for *Archivesica gigas* and its relatives as mentioned above. This group, which may have shells of variable thicknesses, usually shows inflation of the valves, a short prominent ligament with a concomitant subtending nymphal callosity; a demarcated escutcheon is lacking and the pallial sinus, or posterior sinuosity of the pallial line is slight but usually noticeable, and sometimes rather pointed or angled above.

Range. Living from British Columbia, Canada, to northern California (53°–40°N), in 549–1464 m.

Calyptogena (Calyptogena) lasia
(Woodring)

Phreagena lasia Woodring, 1938: 50, pl. 5, figs. 3, 4, text-fig. 2a (type-locality, Standard Oil Co., Baldwin No. 73, Montebello field, depth 3340–3358 feet, United States Geological Survey locality 13864, Repetto Formation, Lower Pliocene, Los Angeles Basin; holotype, USNM 496097).

Calyptogena lasia (Woodring). Winterer & Durham, 1962: 295, 302, 307, 308 (Ventura Basin, Los Angeles County); Boss, 1968: 739.

Remarks. Woodring (1938) lists numerous additional localities for *C. lasia* in the Repetto and Pico formations of the Los Angeles Basin

and discusses the relationship of this species with other vesicomyids, especially *C. pacifica* and *C. elongata*. Winterer & Durham (1962) add several other occurrences of *C. lasia* in the Ventura Basin. Woodring (personal communication) concurred in the synonymy of *Phreagena* and *Calyptogena*.

Range. Fossil in Lower Pliocene of Los Angeles and Ventura Basin, California.

?*Calyptogena longissima* (Yokoyama)

Cucullaea longissima Yokoyama, 1925: 20, pl. 3, fig. 1 (type-locality, Shigarami); Makiyama, 1958: pl. 27.

Calyptogena longissima (Yokoyama). Hatai & Nisiyama, 1952: 56 ([Shigarami] Pliocene, Shigarami [a short distance N of Shimosoyama, Shigarami-mura, Kami-Minouchi-gun, N. Nagano, 36°40'N; 138°04'E]; holotype, GT no. ?); Hanzawa, Asano & Takai, 1961: 233 (holotype, Geological Institute, University of Tokyo; Shigarami, Nagano Prefecture, Shigarami Formation, Pliocene); Okutani, 1966b: 301.

Remarks. We have followed several different Japanese authorities (Hatai & Nisiyama, 1952; Hanzawa, Asano & Takai, 1961), in placing this species in *Calyptogena*, s.l., with some doubt as to the propriety of this assignation (Okutani, 1966b: 301). The species is based on an internal cast, measuring 115 × 55 × 35 mm, roughly shaped like a *Calyptogena*. The pallial line is distinctly visible, relatively wide, strongly impressed, and weakly sinuate posteriorly.

Range. Fossil in Japan, Shigarami Formation, which was considered Pliocene by Hatai & Nisiyama (1952: 332) and Hanzawa, Asano & Takai (1961); Okutani (1966b) cited its occurrence as Miocene.

Calyptogena (Ectenagena) modioliforma
(Boss)

Ectenagena modioliforma Boss, 1968: 742–746, figs. 10, 21–24, 26–27 (type-locality, Pillsbury station 394, 9°28.6'N; 76°26.3'W, Golfo del Darien, 66 miles NNE of Punta Caribana, Colombia in 42–641 m; holotype, MCZ 256973).

Remarks. As noted earlier in the text, we no longer consider *Ectenagena* of generic rank and follow Keen (1969) in placing it as a subgenus of *Calyptogena*; *C. modioliforma* is the Caribbean homolog of *C. elongata* and a close living relative of *C. magnifica*.

Range. Known only from the holotype.

Calyptogena moraiensis (Suzuki)

Unio moraiensis Suzuki, 1941: 55, pl. 4, figs. 2–5 (type-locality Morai hard shale formation in Pliocene); Hanzawa, Asano & Takai, 1961: 293 (Holotype and paratype, Oilwell no. 2, Shunbetsu, Ishikari-machi, Atsuta-gun [sic], Hokkaido, Morai hard shale, Pliocene, Geological Institute, University of Tokyo).

Calyptogena moraiensis (Suzuki) Ôtsume, 1942: 437 (Morai, Atuta-mura, Atuta-gun, Ishikari Province, Mio-Pliocene); Okutani, 1962: 23; Okutani, 1966b: 301.

Remarks. This is recognized as a synonym of Japanese fossils of Mio-Pliocene age from Hokkaido referred to *C. pacifica* Dall (Ôtsume, 1942; Okutani, 1962; 1966b).

Range. Mio-Pliocene of Morai shale, Hokkaido, Japan.

Calyptogena (?*Calyptogena*) *nipponica*
Oinomikado & Kanehara

Calyptogena nipponica Oinomikado & Kanehara, 1938: 677–678, pl. 21, figs. 1–5 (type-locality, Ushigakubi Bed, Lower Pliocene, Higashiyama Oil-field, Niigata Prefecture; range: Kubiki Bed, Niigata Prefecture [Mio-Pliocene]; Katsuura Bed, Chiba Prefecture [Pliocene]; Ôtsume, 1942: 197 + 199; Hatai & Nisiyama, 1952: 33 (Ushigakubi Lower Pliocene [Miocene]. On the eastern bank of the Maekawa, about 1.2 km S of the village office at Nakamura, about 200 m W of the shrine at Shigebuko, Nishitani-mura, Koshi-gun, Niigata. Nagaoka, 37°24.30'N; 138°59'E; holotype and paratype destroyed; also Kubiki Miocene. The wall of the water well, 33 m deep from surface at the primary school, Nakanosawa, Higashiyama-mura, Koshi-gun, N; [Kojiya, 37°19'N; 138°52'E] paratype destroyed (is *Akebiconcha* cf. *A. kawamurai* Kuroda); Okutani, 1957: 218; Itoigawa, 1958: 251 (Teradomari Formation Kubiki Group, Upper Miocene, Higashiyama Oil-field, Niigata Prefecture); Hanzawa, Asano & Takai, 1961: 219, holotype and paratype, eastern bank of the river [Mae-kawa], about 1.2 km south of the village office of Nishitani-mura at Nakamura, Nishitani-mura, Koshi-gun, Niigata Prefecture, Ushigakubi Formation, Pliocene; Okutani, 1962: 23 as *Akebiconcha*? *nipponica* (Oinomikado and Kanehara); Okutani, 1966b: 301, Pliocene.

Remarks. Oinomikado & Kanehara (1938) established this species on specimens from

several Japanese localities of Miocene and Pliocene age. It is quite probable that, as indicated by Hatai & Nisiyama (1952), *C. kawamurai* Kuroda, 1943 and *C. k. elongata* Ozaki, 1958 are synonyms of *C. nipponica*. We suggest that even *C. soyoae* may be considered in this lineage and might prove to be synonymous if critical comparable suites were available.

Apparently, there are conflicting opinions concerning the primary type-material of *C. nipponica*. Hatai & Nisiyama (1952) noted that the holotype & paratype were destroyed, while Hanzawa, Asano & Takai (1961) cited both a holotype & paratype!

Range. Fossil species from the Miocene and Pliocene of Japan in Ushigakubi Bed, Kubiki Bed, and Teradomari Formation of the Kubiki Group in Niigata Prefecture and from the Katsuura Bed, Chiba Prefecture.

Calyptogena (*Calyptogena*) *pacifica* Dall

Calyptogena pacifica Dall, 1891: 190 (type-locality, Albatross Station 3077, off Dixon Entrance, Alaska, in 322 fathoms; 1895b: 713, pl. 25, figs. 4, 5 (holotype, USNM 122549); 1903a: 700, 712 (Pliocene and Recent); 1903b: 1435–1436 (Pliocene of Los Angeles, California; Recent, in Clarence Strait, southeastern Alaska); 1916: 408; 1921: 32 (Clarence Strait, Alaska to Santa Barbara Channel, California); Lamy, 1922: 349; Oldroyd, 1924: 116; Crickmay, 1929: 93; Grant & Gale, 1931: 278–279, pl. 13, figs. 13a–b (Pliocene, Los Angeles; blown out of big Amalgamated Gas well, from depth of 2500 feet with *Dendraster interlineatus* Stimpson, Wolfskill Lease, Salt Lake oilfield, near Beverly Hills, Los Angeles County (coll. by J. O. Lewis, 1912); Thiele, 1935: 848; Otuka, 1937: 231 (Wakimoto Bed, Pliocene of Oga Peninsula, Akita-ken, Japan); Oinomikado & Kanehara, 1938: 678; Woodring, 1938: 50–52 (in Clarence Strait, Alaska, in 322 fms.; off Santa Cruz in 506–680 fms.; off Santa Rosa Island in 30–41 fms.); Ôtsume, 1942: 198, pl. 16, figs. 1–12 (Morai Bed of Ishikari Oil-field, Hokkaido, Mio-Pliocene); Okutani, 1957: 28; Okutani, 1962: 23; Okutani, 1966b: 301, pl. 27, figs. 1, 3; Boss, 1968: 739, figs. 16, 17, 19, 20; Keen, 1969: N664, fig. E 138, 11a, b; Boss, 1970: 70; Oberling & Boss, 1970: 82; Kanno, 1971: 81; Habe, 1977: 237.

Calyptogena (*Calyptogena*) *pacifica* Dall. Bernard, 1974: 11, text figs. 1A, 2A, 3A, 4A–D (anatomy; localities off British Columbia, Canada, and northern California).

Remarks. This, the type-species of *Calyp-togena*, is probably the best known, most widely distributed species of the genus. Bernard (1974) studied its anatomy and showed that there are but few minor features to distinguish it from closely related species.

Unio moraiensis Suzuki was a nomen used for populations in the Morai Beds of Japan which have been referred to *C. pacifica* (Ôtatumé, 1942; Okutani, 1962). Certain fossil species in the Americas might well fall into the synonymy of *C. pacifica* or at least constitute a portion of its geological lineage, namely, *C. gibbera* Crickmay and *C. panamensis* Olsson. The species might even be cosmopolitan since *C. valdiviae* Thiele & Jaekel really is hardly distinguishable except for its provenance, off West and South Africa.

Range. According to published reports, this species is known as a fossil from Mio-Pliocene times in the Morai Bed of Ishikari Oil-field, Hokkaido, Japan (Ôtatumé, 1942), in the Pliocene of the Oga Peninsula, Akita Prefecture, Japan, as well as in Los Angeles, California (Grant & Gale, 1931). Living samples are known from Clarence Strait, Alaska to off southern California in 55–1244 m.

Calyp-togena (?*Calyp-togena*) *panamensis*
Olsson

Calyp-togena panamensis Olsson, 1942: 33(185), pl. 2 (15), figs. 2, 3 (type-locality, Punta Burica [sandstone], Costa Rica and Panama; lower Pliocene and uppermost Miocene).

Remarks. From the internal view of the left valve (Olsson, 1942: pl. 2 (15), fig. 2), the dental configuration of *C. panamensis* suggests a relationship to *C. pacifica* and thus to the subgenus *Calyp-togena* rather than *Ectenagena*. The samples of *C. panamensis* appear to be an in situ thanatocenosis and are associated with other sometimes deeper water, offshore forms (e.g. *Solemya*, *Thyasira*).

Range. Fossil in lower Pliocene and uppermost Miocene of Punta Burica, Costa Rica and Panama (Pacific Coast).

Calyp-togena (*Calyp-togena*) *ponderosa*
Boss

Calyp-togena ponderosa Boss, 1968: 737–742, figs. 9, 11–15, 18 (type-locality, M/V Oregon I station 1426, 29°07'N; 87°54'W, about 77 miles south of Mobile Bay, Gulf of Mexico, in 600 fathoms (1,097 m); additional

localities, Pillsbury station 364, 9°28.7'N; 76°34.3'W, Golfo del Darien, 63 miles NNE of Punta Caribana, Colombia, in 933–961 m. Pillsbury station 394, 9°28.6'N; 76°26.3'W, Golfo del Darien, 66 miles NNE of Punta Caribana, Colombia, in 421–641 m. Pillsbury station 391, 10°03.0'N; 76°27.0'W, Golfo del Darien, 69 miles SSW of Cartagena, Colombia in 1417–1767 m) Oberling & Boss, 1970: 81–90, 2 figs. 1 pl.; Boss, 1970: 70.

Remarks. As previously indicated (Boss, 1968), *C. ponderosa*, though similar to *C. pacifica*, has not only a thicker, heavier shell but a strong posterior radial ridge; additionally the dentitions differ.

Range. Living in the Caribbean Sea and Gulf of Mexico, in 421–1767 m.

Calyp-togena (*Calyp-togena*) *soyoe*
Okutani

Calyp-togena soyoe Okutani, 1957: 27, pl. 1, figs. 1, 4, 5a–b (type-locality, 6 miles WSW of Jôgashima [islet], eastern part of Sagami Bay, Honshû, at 750 m muddy bottom, 35°05.1'N; 139°33.3'E); Habe, 1961: 122, pl. 55, fig. 17; Okutani, 1962: 22, pl. 2, figs. 10–11, pl. 4, fig. 14 (in 710–770 m, Sagami Bay); Habe, 1968: 179, pl. 55, fig. 17 (750 m in Sagami Bay and off Bôsô Peninsula, Honshû); Boss, 1970: 70; Bernard, 1974: 18; Habe, 1977: 237 (in 750–1000 m, Sagami Bay).

Akebiconcha soyoe (Okutani). Okutani, 1966a: 11, pl. 1, fig. 7 (in 1005–1020 m, Sagami Bay); Okutani, 1966b: 300, pl. 28, figs. 1–2.

Remarks. Okutani (1957) introduced this name for specimens between 50 and 140 mm in length taken by the R/V Soyo-Marû in Sagami Bay at a depth of 750 m; he remarked on its similarity to *C. pacifica*, *C. elongata*, and *C. nipponica* and also noted a relationship with *Akebiconcha kawamurai* as well but suggested that the mesial constriction of the valves was diagnostic for *C. soyoe*. In 1962, he presented a key to the species, *C. soyoe*, *C. nipponica*, *C. elongata* and *C. pacifica*, wherein one of the diagnostic features was size, now known to be highly variable. He (1966a, b) transferred *C. soyoe* to *Akebiconcha* and placed the genus in the Arctici-dae (as Cyprinidae). However, *Akebiconcha* seems to be indistinguishable from *Calyp-togena* (Boss, 1968) and the genus does not show familial affinities with the Arctici-dae (see *Remarks* in text on the genus *Calyp-togena*).

Were large series of *C. soyoae* and *C. nipponica* available, it is quite possible that *C. soyoae* would prove to be synonymous with *C. nipponica* (and its synonyms, *C. kawamura* and *C. k. elongata* Ozaki, see Hatai & Nisiyama, 1952).

Range. Living in Sagami Bay, Honshû, between 750–1020 m.

Calyptogena (Calyptogena) valdiviae
(Thiele & Jaeckel)

Vesicomys valdiviae Thiele & Jaeckel, 1931: 229 (71), pl. 9 (4), fig. 101 (*Valdivia* stations 33 and 103).

Calyptogena valdiviae (Thiele & Jaeckel). Boss, 1968: 742; Boss, 1970: 69–70, figs. 3, 4, 22, 23 (type-locality designated, *Valdivia* station 33, 24°35.3'N; 17°4.7'W, about 140 miles (23 km) off Morro Garnet, Rio de Oro, West Africa, in 2500 m; additional locality, *Valdivia* Station 103, 35°10.5'S; 23°2'E, about 72 miles (120 km) south of Knysna, Republic of South Africa, just off Agulhas Bank, in 500 m).

Remarks. As noted in Boss (1968: 742; 1970: 70), *C. valdiviae* closely resembles *C. pacifica* and may be separable on such features as minor differences in outline (*C. valdiviae* has a more convex ventral margin) and sculpture (*C. valdiviae* has less weakly expressed growth lines and concentric lirations).

Range. Living (?). From off west Africa to off south Africa in 500–2500 m.

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