A NEW GENUS OF CHTHAMALIDAE (CIRRIPEDIA) FROM THE SOUTHEASTERN PACIFIC ISLAND OF SAN AMBROSIO

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ABSTRACT.—Jehlius gilmorei n. gen., n. sp. is proposed for a chthamalid apparently endemic to Isla San Ambrosio, a volcanic island about 800 km west of Chañaral, Chile. This new barnacle has a grade of shell construction transitional between 6 and 4 plates.

From 15 May through 6 July 1970 the U.S. Antarctic Research Program (USARP) trawler *Hero* cruised the southwest and central coasts of Chile, and visited Isla Robinson Crusoe of the Juan Fernandez group, and Islas San Ambrosio and San Félix of the Desventurados group. The cruise objectives were to obtain data on marine mammals and birds. But at my request barnacles were collected as opportunity permitted. Gilmore (1971: 10)

gave a preliminary report of this cruise.

The Islas de los Desventurados include the oceanic islands of San Ambrosio and San Félix, together with a lesser rock, Gonzalez, at about 26° south and 80° west, or approximately 800 km off the coast of Chañaral, Chile (Fig. 1). These volcanic islands rise some 4000m from the sea floor. The surface waters here have a salinity of about 34.5% and an average surface temperature during February-March of 20°-21° C, and during July-September of 17°-18° C (Meteorological Office, 1956; Murphy, 1936: 104; Wyrtki, 1966: 40). San Ambrosio, type locality for the new chthamalid described herein, is about 4 km long and 1 km wide with an estimated maximum elevation of 480 m (Fig. 2).

PREVIOUS STUDIES ON THE BIOTA

The biota of the Desventurados islands remains poorly known owing to their relative inaccessibility and the lack of good landing sites (Fig. 3; see Douglas, 1970: 345). On the basis of a short visit, Bahamonde N. (1966) presented a popular, broad, and general account of the biota.

Studies on the flora were published by Johnston (1935) and by Skottsberg (1937, 1952), both of whom listed references to earlier studies. The avifauna was treated by Murphy (1936) and by Johnson (1965, 1967), who also cited earlier references. Allen (1899) discussed briefly the hunting and virtual extermination of fur seals (*Arctocephalus*) in rookeries on the two major islands (see also Gilmore, 1971: 10), and Kellogg (1943: 306) presented data on the size of the catch during the early years of American sealing in these waters. Other studies are those by Serafy (1971: 165) who described a new *Clypeaster* from San Félix, and by McLean (1970: 362), who described two new fissurellid gastropods.

The only mention of the crustacean fauna of the island with which I am familiar is by Bahamonde N. (1966: 7) who stated "En la zona supramareal hay una franja muy nítida de Cirripedos. En sus cercanías es posible capturar ejemplares de la 'jaiba corredora' (*Leptograpsus variegatus*), designada por Philippi como *Grapsus obscurus*, por su coloración. Allí es muy abundante. También se halla habitualmente en las pozas profundas ejemplares de *Rhynchocinetes balsii* y en las áreas en que predomina las algas de los géneros *Padina* y *Corallina* se obtuvieron individuos de *Plagusia chabrus*."

CHTHAMALID COLONIZATION OF ISLA SAN AMBROSIO

Under the influence of the west wind drift, South Pacific Temperate Water flows east

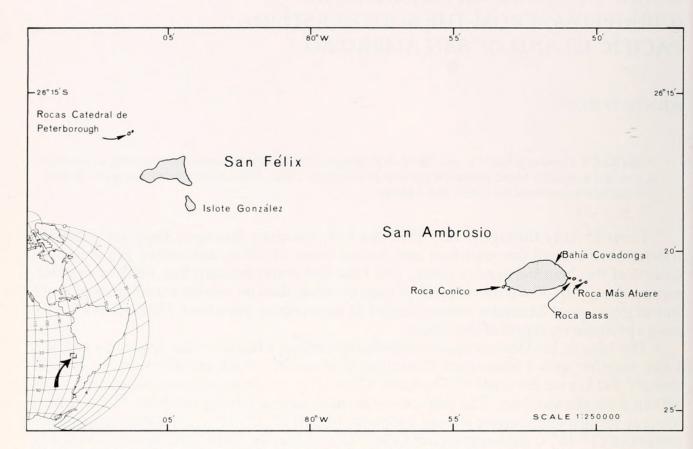


Figure 1. Map showing position of Isla San Ambrosio relative to other islands in the Desventurados group, Chile.

toward South America (Wyrtki, 1968: 131). Near Chile at about 50° S this water mass divides, one branch turning south and eastward around the tip of South America, the other flowing northward along the coast as the Peru Current (= Humboldt Current) or the Peru-Chile Current System. The offshore Desventurados Islands are under the influence of this current system. The Peru Current extends as far north as Ecuador and then swings west just south of the Equator to become part of the South Equatorial Current. The northward flow of the Peru Current, generally at 25° S, is divided into two components, the Peru Coastal Current and the Peru Oceanic Current, between which is a southward moving subsurface current, the Peru Countercurrent, which carries equatorial subsurface water as far as 22° S (Wyrtki, 1966: 59; 1968: 121).

The prevailing north-flowing currents argue for colonization of San Ambrosio from the southeast, much as the biota of the Juan Fernandez Islands, in the main, also appears to have been derived from South America. I have discounted a direct Australia-New Zealand origin of the Desventurados chthamalid largely because of the vast distance separating the two regions, the apparent absence of any living or extinct populations of chthamalids in the region between, and because the temperate Southeast Pacific chthamalids have their greatest affinity with the Tropical American fauna (Zullo, 1966: 142). Elminius and Austrobalanus in the southeastern Pacific, although seemingly good indicators of biogeographical affinities, are two groups that remain poorly known (the type species of Austrobalanus is apparently a six-plated tetraclitid and the remainder true balanids; Elminius until recently contained two species referable to the tetraclitid Epopella and the remaining two or three widely separated species offer no clues as to their origin [Ross, 1970: 9]).

Based on morphological and hydrographic evidence, this new chthamalid probably evolved from or shared a common ancestry with *Chthamalus cirratus* Darwin, 1854, which

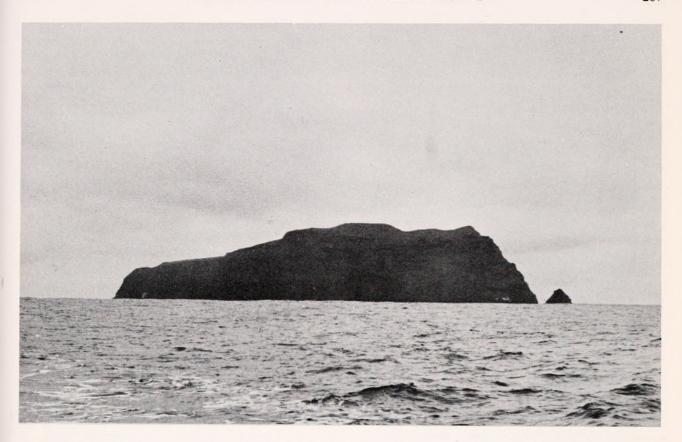


Figure 2. View from the northwest of Isla San Ambrosio. Small prominence to the right of San Ambrosio is Roca Conico. Photo by R. M. Gilmore.

occurs commonly along the west coast of South America from the Chonos Archipelago in Chile (about 45° S) to Guayaquil, Ecuador (2° 13′ S) (Pilsbry, 1916: 321; Nilsson-Cantell, 1957: 11).

Three possible modes of colonization are offered in what I believe to be increasing probability, 1) introduction by or through an agency of man, 2) larval colonization, and 3) adult colonization by natural drift or rafting. I have discounted the first because *Chthamalus* and its derivatives are essentially shore barnacles, although they are known to foul marine structures. Also, the evolutionary state of this new species argues for colonization prior to the origin of man in the new world. I also doubt that the islands were colonized by larvae, because the nauplii of *Chthamalus* and other balanomorphs in general lack the long tomentose flotation setae characteristic of pelagic species, and because the nauplii of intertidal barnacles probably remain in the plankton less than two weeks, which is apparently not long enough to reach San Ambrosio. The efficacy of natural rafting is well documented in the literature, and it appears most probable that colonization of San Ambrosio was effected by rafting.

As Crisp and Southward concluded (1953: 209), even narrow seas pose a barrier to animals that are predominantly intertidal. The relatively small size of the two major islands in the Desventurados Group (San Ambrosio—4 km long, 1 km wide; San Félix—3 km long, 1 km wide), and their great distance from the South American mainland, would tend to preclude repetitive colonization from the mainland. Many workers have remarked that in order to establish a viable population some minimum density is required. However, since there is good evidence that many species of *Chthamalus* are readily capable of self fertilization under certain conditions (Barnes and Barnes, 1958: 550), the initial propagule could have been only a single individual.



Figure 3. View of landing site at Bahía Covadonga, Isla San Ambrosio. The two wooden shacks are used by transient lobster fishermen. Photo by R. M. Gilmore.

SYSTEMATICS

Family Chthamalidae Darwin, 1854

Remarks.—The new taxa described below are assigned to this family, which was diagnosed recently by Newman, Zullo, and Withers (1969: 283) and emended subsequently by Newman and Ross (1971: 139). The assignment of genera to this family differs in several details between that of the above workers and that proposed by Utinomi (1968: 36). Type Genus.—Chthamalus Ranzani, 1817 (for Lepas stellatus Poli, 1791, by original designation, Recent, Bay of Naples, Italy).

KEY TO GENERA OF LIVING CHTHAMALIDAE

1.	Shell composed of 8 parietal plates	2
1.	Shell composed of 6 or 4 parietal plates	5
2.	Shell with 2 or more whorls of basal plates	3
	Shell without whorls of basal plates	
	Shell with 6-8 whorls of basal plates; caudal	
	appendages lacking (1 sp.)	Catomerus
3.	Shell with 2-6 whorls of basal plates; caudal	
	appendages present (2 spp.)	Catophragmus
	Shell in young individuals with eight plates, in older	1 8
	individuals with 6 or 4; mandible quadridentoid;	
	cirrus III more like cirrus II than IV; caudal	
	appendages present (8 spp.)	Pachylasma
	Shell never with fewer than 8 plates, mandible	
	tridentoid; cirrus III more like cirrus IV than II,	
	caudal appendages lacking (3 spp.)	Octomeris
5.	Shell with a single whorl of basal plates (1 sp.)	Chionelasmus
5.	Shell without whorls of basal plates	6
6.	Mandible tridentoid (12 spp.)	Euraphia
6.	Mandible quadridentoid	7
7.	Shell with inflected basal rim (1 spp.)	Tetrachthamalus
7.	Shell without inflected basal rim	8
	Shell of adult with 6 wall plates (13 spp.)	Chthamalus
8.	Shell of adult with 4 wall plates, or transitional	
	between 6 and 4 wall plates	9
9. '	Wall plates coalescing in juvenile stage; scutum with	
;	adductor ridge; anterior cirri armed with grapple-like	
	spines (3 spp.)	Chamaesipho
9.	Wall plates coalescing in adult stage; scutum without	
	adductor ridge; anterior cirri lacking grapple-like	
:	spines (1 sp.)	Jehlius

Jehlius n. gen.

Definition.—Shell of adult in transitional stage between 6 and 4 plates; reduction in number of plates by fusion rather than exclusion; in 4 plated stage wall plates not secondarily coalesced; plates disposed asymmetrically or symmetrically; fusion pattern variable throughout population; compartments lacking radii and inflected basal rim; basis membranous; scutum with well defined depression for adductor muscle, but no adductor ridge; cirrus III structurally and probably functionally more similar to cirri IV-VI than to cirrus II;

cirrus II lacking grapple-like spines; caudal appendages lacking; mandible with four teeth, basal comb, and spine-like inferior angle.

Type species.—Jehlius gilmorei new species.

Remarks.—Jehlius is unique in that the parietal plates are not always symmetrically disposed and that the pattern of fusion of the plates has not become fixed at least within the few specimens available for study (Fig. 4). Also, shell development is obviously transitional between six and four plates, and in the two specimens with only four plates there is no indication whatsoever that these plates will secondarily coalesce.

The shell of *Chamaesipho* is fundamentally composed of six plates, rostrum, carina, and paired rostrolaterals and laterals, but the genus is regarded as tetramerous (see Moore, 1944; Pope, 1965; Newman, Zullo and Withers, 1969). The six sutures separating these plates in *C. columna* are rarely seen in individuals beyond 2 mm in rostro-carinal diameter and occasionally they are obliterated in individuals as small as 0.5 mm in diameter (Moore, 1944: 317). In *C. brunnea*, on the other hand, the sutures delimiting the plates are no longer visible by the time individuals reach 6 mm in diameter (Moore, 1944).

In both species of *Chamaesipho* mentioned above, the rostrolaterals are united with the laterals. In specimen 1 of *Jehlius* (see Fig. 4), the arrangement of the wall plates appears to be the same as in *Chamaesipho columna*. In specimen 3, the right lateral is fused and secondarily coalesced in part with the carina, but the left lateral is fused with the rostrolateral. In specimen 2 the right lateral and rostrolateral are fused with the rostrum, and the left

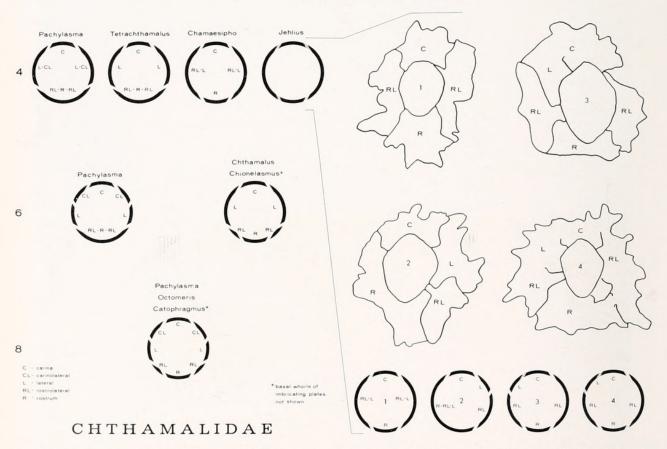


Figure 4. Plan views of wall construction in the Chthamalidae. Numerals at left indicate grades of decreasing complexity. Shell outlines of *Jehlius* on right side are camera lucida drawings of the internal surface showing degree of development of sutures, which are not readily discernible on external surface of shell (right side of shell is on left side in drawing). Number in center of orifice refers to number in plan view below. Specimen No. 3 is holotype, S.D.S.N.H. No. 4003/3.

rostrolateral and lateral remain separate. Specimen 4 is the most unusual of the lot. It has one major suture, between the rostrum and the right rostrolateral, and all of the other plates are partially coalesced (Fig. 5). Aside from the unusual arrangement of the wall plates there is nothing to suggest that the shells are pathologically malformed.

Jehlius also differs from Chamaesipho in the articulation of the opercular plates. The junction between the scutum and tergum on each side, when viewed internally, in Chamaesipho takes the form of the Greek letter omega, but in Jehlius it is simpler and only slightly sinuous. Jehlius also differs in that cirri I-III lack the grapple-like spines and the scutum lacks an adductor ridge but has a well defined deep pit for the insertion of the adductor muscle (Fig. 6).

Jehlius obviously is derived from an Eastern Pacific stock of Chthamalus, whereas Chamaesipho probably was derived from an Indo-Pacific stock. Furthermore, Chamaesipho is restricted to the austral region and the probability of penetrating the East Pacific barrier is remote.

Tetrachthamalus, also a genus with four plates that evolved from Chthamalus, differs from Jehlius in that the rostrolaterals are fused with the rostrum to form a tripartite plate, and during the ontogeny of individuals in this genus the four plates coalesce.

Etymology.—Named for Dr. Joseph R. Jehl, Jr., San Diego Museum of Natural History, longtime friend and colleague, and collector of the specimens reported on herein.

Jehlius gilmorei n. sp.

Diagnosis.—Crest of labrum armed with 50-60 simple conical teeth; cutting edge of maxilla II with 10-13 long spines in medial cluster; intermediate articles of posterior cirri, which have rami of equal length, bear 5 pairs of setae; basal segment of anterior ramus of cirrus I armed with stout spines.

Description.—Shell white or grayish-white, low conic, broadly ovate to subcircular in outline; basal portion of compartments ribbed and periphery of shell irregular or strongly toothed (Fig. 5); upper portion of external surface corroded, exfoliating; aperture relatively large owing to corrosion; radii lacking; sheath less than ¼ height of compartments, basal margin not depending; surface below sheath smooth. Basis membranous.

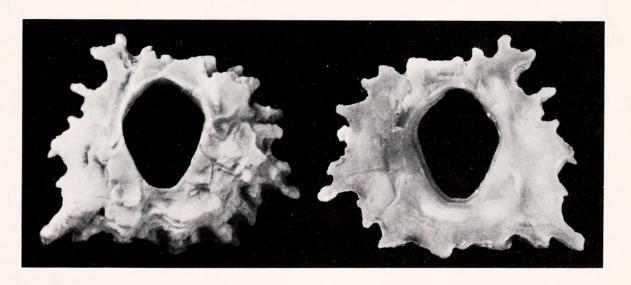


Figure 5. *Jehlius gilmorei* n. gen., n. sp. External and internal views, respectively, of shell. Paratype, S.D.S.N.H. No. 4004/4; actual rostro-carinal diameter, 8.1 mm.

Scutum transversely elongated (Fig. 6); length about ½ greater than height; external surface poorly preserved, exfoliating; only last 3-4 newly formed growth ridges preserved along basal margin of plate; articular ridge poorly differentiated from articular surface; adductor ridge absent; depression for adductor muscle deep, well delimited; depression for lateral depressor muscle deep, well defined, crossed by 3-4 septa; depression for rostral depressor muscle commonly shallow, poorly delimited; apical portion of plate lacking ridges, crests, or pits.

Tergum higher than wide (Fig. 6); external surface poorly preserved, exfoliating; external longitudinal furrow apparently lacking; spur rounded or pointed distally, and not distinctly separated from articular margin; articular ridge low, poorly developed; parallel and immediately adjacent to articular ridge there is a row of shallow, oblong pits; there are 2 prominent and 1-2 lesser crests for the insertion of the lateral depressor muscle; apical

portion of plate either slightly pitted or roughened.

Measurements of the holotype (in mm) are as follows: rostro-carinal diameter 9.7, lateral diameter 9.1, height 5.1, rostro-carinal diameter of orifice 5.2, height of scutum 3.0, width of scutum 3.9, height of tergum 2.8, width of tergum 2.0. The range in rostro-carinal diameter of the four specimens is 8.1-10.1 ($\bar{x} = 9.2$), and the range in height is 2.6-5.1 ($\bar{x} = 3.3$).

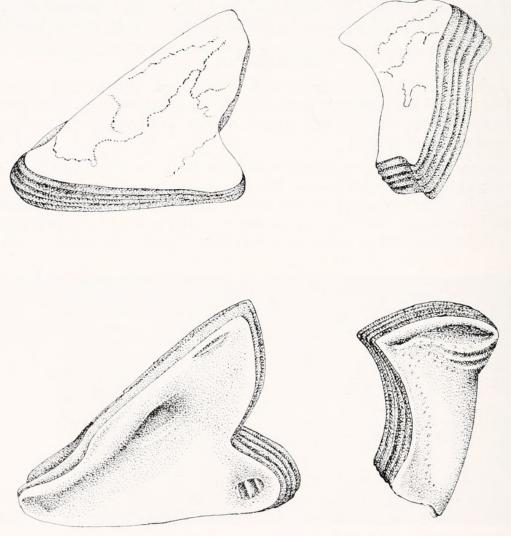


Figure 6. Opercular plates of *Jehlius gilmorei* n. gen., n. sp. External views of scutum and tergum, respectively (top row), and internal views of scutum and tergum, respectively (bottom row). Paratype, S.D.S.N.H. No. 4004/2. Drawings by Anthony D'Attilio.

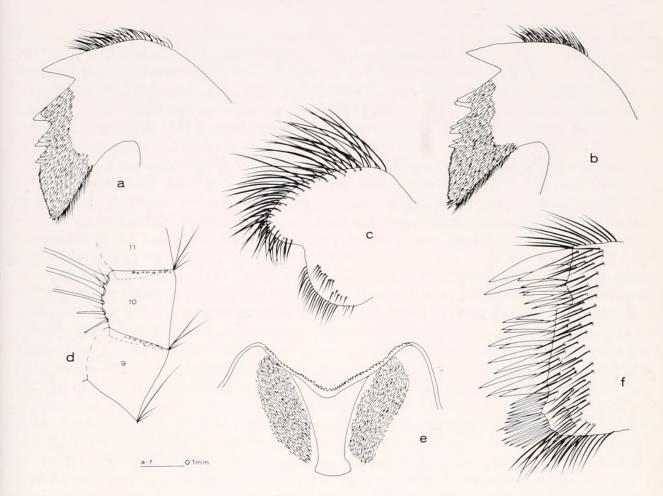


Figure 7. Jehlius gilmorei n. gen., n. sp. a, right mandible; b, left mandible; c, maxilla II; d, intermediate articles of cirrus VI; e, crest of labrum; f, maxilla I. Holotype, S.D.S.N.H. no. 4003/3.

Crest of labrum thin, with broad U-shaped medial notch toothed its whole width; teeth 50-60, close spaced, simple, conical; bristles behind and parallel to teeth along crest short and densely packed (Fig. 7). Palps elongate, rounded distally, the basal margin convex and free of setae; superior margin densely clothed with coarsely bipinnate, long, slender setae; setae on distal extremity longer than on proximal, and finely bipinnate. Cutting edge of mandible armed with 4 teeth, basal comb, and spine-like inferior angle; teeth 2-4 bicuspate; comb between tooth 4 and inferior angle with 50-60 acicular teeth (Fig. 7). Maxilla I with 2 long stout and 1-2 shorter stout spines above subapical notch, 4-5 short slender spines in notch, 10-13 long stout spines medially, 14-20 slender spines in basal cluster (Fig. 7). Cutting edge of maxilla II distinctly bilobate; setae along apical margin long, finely bipinnate, setae progressively shorter toward notch; notch free of setae; setae on basal lobe finely bipinnate (Fig. 7).

Anterior ramus of cirrus I about 1/5 longer than posterior ramus; intermediate articles of both rami about twice as broad as high; proximal segment of anterior ramus armed with 5 or 6 short, stout spines along posterior border (Fig. 8); 1 row of coarse ctenae present on lateral face of segments of each ramus immediately below articulation; ctenae better developed on posterior ramus than on anterior ramus; setae on both rami bipinnate. Rami of cirrus II essentially equal in length and about same length as rami of cirrus I; 1 row of coarse ctenae present on lateral face of segments of both rami immediately below articulation; setae on both rami bipectinate. Cirri III-VI essentially equal in length and with equal rami; 1-2 long slender, and 1-2 shorter slender setae at each articulation along greater cur-

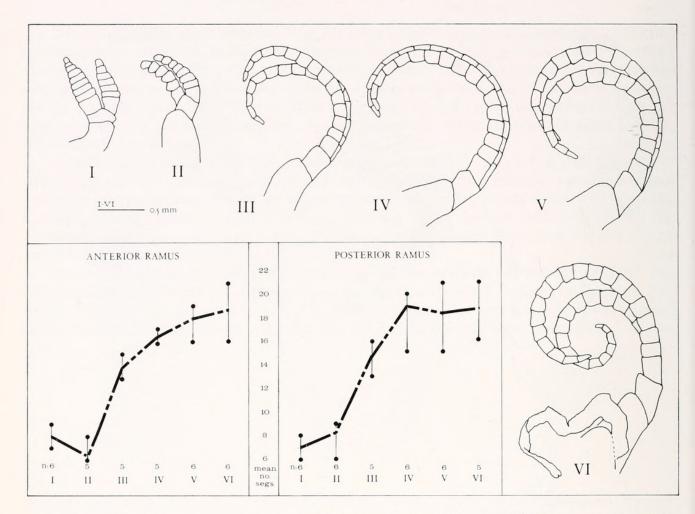


Figure 8. Outline drawings of cirri I-VI (setae omitted; paratype, S.D.S.N.H. No. 4004/2) and summary of data on cirral counts for the holotype and two paratypes.

vature of intermediate articles; 1 row of ctenae on lateral face of intermediate segments below articulation; setation ctenopod, with 5 pairs of setae on each intermediate segment; at base of each pair of setae there are 2-3 short, slender setae. Cirral counts for specimens in the type lot are summarized in Figure 8.

Intromittent organ annulated throughout its length, and sparsely covered with short, slender bristles; distal extremity bilobed and each lobe bearing about 15 or 16 short, slender setae.

Type Locality.—On northeast coast, just west of Bahía Covadonga, Isla San Ambrosio, Islas de los Desventurados, Chile, approximately 26° 20′ 15″ S., 79° 15′ 45″ W., I. M. W. SG 17; intertidal on volcanic rock; J. R. Jehl, Jr. coll., 27 June 1970; USARP cruise 70-3.

Disposition of types.—The holotype and three paratypes are housed in the collections of the San Diego Society of Natural History, Marine Invertebrate catalogue numbers 4003/3 and 4004/1, 4004/2 and 4004/4 respectively.

Etymology.—The specific epithet honors Dr. Raymond M. Gilmore, Research Associate, San Diego Natural History Museum, and chief scientist aboard the trawler *Hero* during USARP cruise 70-3.

INTRAFAMILIAL RELATIONSHIPS

Four families are presently recognized within the suborder Balanomorpha, namely

Chthamalidae, Bathylasmatidae, Tetraclitidae, and Balanidae (see Newman and Ross, 1971: 137). Of these, the Chthamalidae are more generalized structurally and appear in the fossil record before any of the others.

Within the Balanomorpha the evolutionary history has been one of reduction in the number of compartments composing the shell (Pilsbry, 1916: 291; Withers, 1928: 46). In the Chthamalidae this reduction has been accompanied further by structural modification

of the mouth parts and cirri for feeding (Zullo, 1963: 190).

Based on the probable mode of reduction in the number of shell elements, two lineages are evident in the Chthamalidae. In the first, consisting solely of *Pachylasma*, the shell initially contains 8 plates, including rostrum, carina, and paired rostrolaterals, laterals, and carinolaterals. Subsequently, the rostrolaterals coalesce with the rostrum forming a tripartite plate, and the carinolaterals may coalesce with the laterals yielding a shell of

only 4 plates (Fig. 4).

The second lineage (Octomeris-Chthamalus group) includes the remaining genera (Fig. 4; see Newman and Ross, 1971: 141; cf. Utinomi, 1968: 36). Of these, Catophragmus (including the subgenera Catomerus and Pachydiadema) and Octomeris have the same number and arrangement of the plates as does Pachylasma. Early in the evolution of this lineage, the number of shell elements was reduced through elimination or exclusion since Chthamalus has only six wall plates (rostrum, carina, and paired rostrolaterals and laterals), the carino-laterals lacking. The small size of the carina and the presence of alae point to reduction by exclusion. From Chthamalus a further reduction in the number of wall plates, by fusion, is evident in Tetrachthamalus and Chamaesipho. In Tetrachthamalus the rostrolaterals are fused with the rostrum, as shown by the size of the composite plate and by the fact that it has radii, thus forming a tripartite plate essentially similar to that in Pachylasma and the bathylasmatid Tessarelasma. In Chamaesipho columna and C. brunnea the shell initially contains six plates; the rostrolaterals fuse with the laterals (Withers, 1928: 45; Moore, 1944: 324) rather than with the rostrum as in Tetrachthamalus. By the time individuals of C. columna reach a rostrocarinal diameter of 2 mm and individuals of C. brunnea a diameter of 5-6 mm, all the plates coalesce secondarily, and the sutures are obliterated. In adults of Tetrachthamalus oblitteratus, which reach a rostrocarinal diameter probably not much greater than 6 mm, the sutures are commonly distinct; but then coalescence occurs, and remnants of these sutures can be observed in the sheath (Newman, 1967: 427).

In all chthamalids with 6 or 4 plates fusion of shell elements and their subsequent coalescence proceeds in a uniform manner. To judge from the specimens available, this apparently is just the opposite of what takes place in *Jehlius* (Fig. 4). Although two specimens of *Jehlius* have in part attained a grade of construction comparable with that found in 4-plated individuals of *Chamaesipho*, two specimens are effectively intermediate between six and four plates. In the two specimens that have attained a 4-plated grade of construction, there is no secondary coalescence and obliteration of the sutures uniting these wall plates.

In his classification of the chthamalids Zullo (1963:190) stressed the modification in mandibular and cirral structures attending the reduction in number of the wall plates. In Octomeris, Chthamalus, Chamaesipho, Tetrachthamalus and Jehlius the mandible is characteristically quadridentoid, but in Catophragmus, Catomerus, Chionelasmus, Euraphia and Pachylasma it is tridentoid. In the Octomeris-Chthamalus lineage the third cirrus is relatively unmodified; but in the Pachylasma lineage, feeding adaptations involve the modification of cirrus III as a mouth appendage, such as is found in the balanids.

Pachydiadema from the Cretaceous (U. Senon.) of Sweden is the oldest known

chthamalid with eight wall plates and at least two whorls of imbricating basal plates. The number and arrangement of wall plates, simple opercular valves, caudal appendages, and unmodified third cirrus all tend to link *Pachydiadema* with the scalpellid lepadomorphs (Newman, Zullo, and Withers, 1969: R 269).

Pachydiadema is probably ancestral to Catomerus (Withers, 1935: 390; Pope, 1965: 15), which also possesses eight wall plates and several whorls of imbricating plates. Catophragamus also may have been derived from Pachydiadema, or possibly from Catomerus. The presence of caudal appendages in Catophragamus suggests derivation from Pachydiadema rather than from Catomerus which lacks these appendages. Chionelasmus with but six wall plates (carinolaterals lacking) and a single whorl of basal plates, and with caudal appendages, is probably an off-shoot from Catophragmus.

Octomeris lacks the basal whorls of plates and caudal appendages, and hence is probably derived from Catomerus, which also lacks caudal appendages, and the articulation of the opercular plates is simple rather than complex as it is in Catophragmus. From Octomeris it is a single step, through loss of the carinolaterals, to Chthamalus and Euraphia, which probably share a common ancestry. However, Euraphia has retained the lepadomorph or early chthamalid tridentoid mandible whereas Chthamalus has evolved the quadridentoid mandible with a basal comb.

Chamaesipho evolved from Chthamalus (Newman, 1967: 431), and probably rather recently. Although young individuals of Chamaesipho brunnea and C. columna develop rostrolateral plates initially, these soon fuse with the laterals forming a shell with only four plates; later the sutures coalesce, and are obliterated. In Euraphia the plates apparently never coalesce but they do develop an inflected basal rim (see Newman, 1961). Tetrachthamalus is also an offshoot from Chthamalus (Newman, 1967: 431) but apparently of greater antiquity than Chamaesipho. In Tetrachthamalus there is no evidence in the ontogeny of a stage having six plates as in Chamaesipho, but as in Chamaesipho the plates eventually coalesce. The wall plates in Tetrachthamalus, unlike those in Chamaesipho and Jehlius, develop an inflected basal rim. Jehlius is apparently the most recent offshoot from Chthamalus, and is most closely related to C. cirratus.

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