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SYSTEMATICS OF *FISSURELLA* IN THE PERUVIAN AND MAGELLANIC FAUNAL PROVINCES (GASTROPODA: PROSOBRANCHIA)

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Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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SYSTEMATICS OF *FISSURELLA* IN THE PERUVIAN AND MAGELLANIC FAUNAL PROVINCES (GASTROPODA: PROSOBRANCHIA)

James H. McLean[1]

ABSTRACT. Fifty-eight names have been proposed for the large and abundant species of *Fissurella* in the Peruvian and Magellanic faunal provinces. Fieldwork in Peru and Chile and to a lesser extent in Argentina, has produced large collections. Following study of these collections, as well as most of the type specimens, I reduce the number of species to 13, three of which have geographic subspecies.

Peruvian-Magellanic species of *Fissurella* Bruguière, 1789, are members of the nominate subgenus, in which the shell has an inner layer of crossed lamellar aragonite and a thick outer layer of prismatic calcite. In contrast, most tropical species of *Fissurella,* which are in the subgenus *Cremides* H. and A. Adams, 1854, have a shell composed entirely of aragonite. The outer layer of calcite is evidently an adaptation to cold water in the Peruvian-Magellanic species.

Three species groups in *Fissurella* (*sensu stricto*) are recognized. The group of *Fissurella peruviana* Lamarck, 1822, is smaller-shelled and has a thinner calcitic layer than species in the other groups; this group includes the type species *F. nimbosa* Linnaeus, 1758, in the southern Caribbean (the only tropical member of the subgenus) and *F. volcano* Reeve, 1849, in California and Baja California.

The group of *F. maxima* Sowerby, 1833, is characterized by strong primary and secondary ribs (at least in juvenile stages) and also includes *F. latimarginata* Sowerby, 1835, *F. cumingi* Reeve, 1849, and *F. costata* Lesson, 1831, in the Peruvian Province, and *F. picta* (Gmelin, 1791), *F. radiosa* Lesson, 1831, *F. oriens* Sowerby, 1835, and *F. nigra* Lesson, 1831, in the Magellanic Province. The group of *F. limbata* Sowerby, 1835, is characterized by broad primary ribs and lack of secondary ribs; it includes *F. crassa* Lamarck, 1822, *F. bridgesii* Reeve, 1849, and *F. pulchra* Sowerby, 1835, all in the Peruvian Province.

Geographic subspecies are here recognized for three species broadly distributed in the Magellanic Province: *F. picta picta* (Gmelin, 1791) in southern Chile, and *F. picta lata* Sowerby, 1835, in central Chile; *F. radiosa radiosa* Lesson, 1831, in southern Chile, *F. radiosa tixierae* Métivier, 1969, in the vicinity of the Gulf of San Matias in Argentina; *F. oriens oriens* Sowerby, 1835, in southern Chile, and *F. oriens fulvescens* Sowerby, 1835, in central Chile.

Three species, *F. cumingi, F. bridgesii,* and *F. pulchra,* have been poorly understood by previous authors and are newly defined here.

Distributions of the Peruvian and Magellanic species overlap in south-central Chile, where 12 of the 13 species occur.

This account includes observations on shell epibionts and borers, and reviews the sparse literature on the biology of these species.

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RESUMEN. Hasta ahora habían sido propuestos 58 nombres para las grandes y abundantes especies de *Fisssurella* de las provincias biogeográficas Peruana y Magallánica. Trabajos de terreno en Perú y Chile, y en menor intensidad en Argentina, han proporcionado importantes colecciones. Realizado el estudio de estas colecciones y de muchos de los ejemplares tipo, se reduce a 13 el número de especies, tres de las cuales poseen subespecies geográficas.

Las especies de *Fissurella* de las provincias Peruana y Magallánica son integrantes del subgénero *Fissurella* Bruguière, 1789 (*sensu stricto*), en las cuales la concha tiene una capa interna compuesta de aragonita laminar cruzada y una capa más externa de calcita prismática. En cambio, muchas especies de *Fissurella* que pertenecen al subgénero *Cremides* H. y A. Adams, 1854, tienen la concha compuesta íntegramente de aragonita. La capa más externa de calcita es considerada como una adaptación de las especies de las provincias Peruana y Magallánica a aguas frías.

Se reconocen tres grupos de especies. Un primer grupo de *Fissurella peruviana* Lamarck, 1822, de concha más pequeña y cuya capa de calcita es más delgada que en las otras especies de los demás grupos. Este grupo comprende la especies tipo *F. nimbosa* Linnaeus, 1758, del sur del Caribe (único miembro tropical del subgénero) y *F. volcano* Reeve, 1849, de California y Baja California.

Un segundo grupo de *F. maxima* Sowerby, 1833, caracterizado por la presencia de gruesas costillas primarias y secundarias (al menos en los estados juveniles). Comprende también a *F. latimarginata* Sowerby, 1835, *F. cumingi* Reeve, 1849, y *F. costata* Lesson, 1831, de la provincia Peruana y a *F. picta* (Gmelin, 1791), *F. radiosa* Lesson, 1831, *F. oriens* Sowerby, 1835, y *F. nigra* Lesson, 1831, de la provincia Magallánica.

El tercer grupo de *F. limbata* Sowerby, 1835, está caracterizado por la presencia de costillas primarias anchas y ausencia de costillas secundarias. Comprende también a *F. crassa* Lamarck, 1822, *F. bridgesii* Reeve, 1849, y *F. pulchra* Sowerby, 1835, todas de la provincia Peruana.

Se reconocen las siguientes subespecies geográficas para tres especies ampliamente distribuídas en la provincia Magallánica: *F. picta picta* (Gmelin, 1791) del sur de Chile y *F. picta lata* Sowerby, 1835, de la zona central de Chile; *F. radiosa radiosa* Lesson, 1831,

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Figure 1. A *Fissurella* "shell pile," consisting of large specimens of *F. latimarginata, F. cumingi,* and *F. maxima* at Los Molles, Aconcagua Province, Chile, October 15, 1975. The specimens had presumably been taken by shallow diving in the vicinity and the shells discarded. All shells were covered with the algal mat, which completely obscures the color pattern.

del sur de Chile y *F. radiosa tixierae* Métivier, 1969, de las cercanías del golfo de San Matías en Argentina; *F. oriens oriens* Sowerby, 1835, del sur de Chile y *F. oriens fulvescens* Sowerby, 1835, de Chile central.

Las especies *F. cumingi, F. bridgesii* y *F. pulchra,* que han sido escasamente tratadas por autores anteriores, son definidas nuevamente.

Se observa una sobreposición en la distribución de las especies de las provincias Peruana y Magallánica en la zona central-sur de Chile, donde 12 de las 13 especies se encuentran presentes.

En el presente trabajo se incluye, además, observaciones sobre los epibiontes y organismos perforadores de las conchas y se revisa la esparcida literatura que trata sobre la biología de algunas de estas especies.

INTRODUCTION

The *Fissurella* species of the cool waters of Peru, Chile, and southern Argentina are large and abundant, comprising a major element of the mollusk fauna of the west coast of South America. They are extensively used for food and are known locally as "lapas" (Fig. 1). The importance of the fishery is second only to that of *Concholepas,* the "loco," the large limpetlike thaidid gastropod of the region. Despite this importance, the taxonomy of the South American species of *Fissurella* has been poorly understood.

It has been recognized that a large number of highly variable, sympatric species occur in the region. Some 58 names for Recent species have been introduced in the literature. Widely varying estimates of the number of actual species have been given: Pilsbry (1890) recognized about 20 species; Ziegenhorn and Thiem (1925) treated 11 species and three "varieties"; Riveros-Zuñiga (1951) recognized 26 species and three "varieties"; Dell (1971) listed 11 possible species; and finally Ramirez-Boehme (1974) gave a key to 30 species and two "varieties."

The collection of mollusks from Iquique, Chile, reported upon by Marincovich (1973), and deposited in the Natural History Museum of Los Angeles County, included five species of *Fissurella.* Although this material introduced me to the subject, fieldwork of my own in Peru in 1972 and 1974, and in Chile for two months in 1975, and southern Argentina in 1978, enabled me to collect and observe the *Fissurella* species from many different localities. I have therefore been able to observe these mollusks throughout their entire geographic range from north-central Peru to southern Chile and Argentina.

The Magellanic Province of southern Chile and southern Argentina is also the center of distribution of another fissurellid group comprising the species *Fissurellidea megatrema* Orbigny, 1841, *F. patagonica* (Strebel, 1907), *Pupillaea annulus* (Odhner, 1932), and the shell-less *Buchanania onchidioides* Lesson, 1830. A report on these species has been published (McLean, 1984b).

In this work I offer a revised classification of the South American species of *Fissurella,* based on my field observations, study of the large collection now housed at the Los Angeles County Museum of Natural History, and study of type material borrowed from other museums. The classification cannot be exhaustive and does not offer a cladistic hypothesis of relationships. In the absence of anatomical, biochemical (electrophoretic), and other characters, that is beyond the scope of the present work. It is hoped that this paper will provide a basis for future work on the systematics and ecology of these species.

MATERIALS AND METHODS

Fieldwork

The collection upon which this report is chiefly based is now in the Los Angeles County Museum of Natural History. Some material from miscellaneous sources is represented in the collection, but the bulk of it resulted from nine major expeditions as follows:

1. Peru: Isla San Lorenzo, Isla Chinchas, and Bahía Independencia. Allan Hancock Expeditions, January, 1935, and February, 1938, intertidal and dredging stations.
2. Chile: Iquique. Louie Marincovich, June–September, 1964, June–July, 1970, intertidal stations.
3. Argentina: Isla de los Estados (E of Tierra del Fuego). R/V HERO, April, 1971, and October, 1971, intertidal and dredging stations; collections received from the Smithsonian Oceanographic Sorting Center.
4. Peru: Pucasana, Laguna Grande, Isla Chincha Norte, Paracas, Asia. James H. McLean, April, 1972, intertidal and diving stations.
5. Chile: south of Isla de Chiloe. Paul Dayton, on R/V HERO, October–November, 1972, intertidal and diving stations.
6. Chile and Argentina: Strait of Magellan and Isla de los Estados. Paul Dayton, on R/V HERO, May, 1973, intertidal and diving stations.
7. Peru: Isla Guanape, Ancon, and Isla San Lorenzo. James H. McLean, January, 1974, intertidal and diving stations.
8. Chile: Iquique, Antofagasta, Coquimbo, Los Molles, Montemar, Cartagena, Concepción, Mehuin, Pargua, Guabun, Pumalin, Islota Nihuel, Isla Laitec, Puerto Hambre, Punta Arenas. James H. McLean, October–November, 1975, intertidal and diving stations.
9. Argentina: Golfo Nuevo and Golfo San Jose. James H. McLean, on R/V HERO, July 1978, intertidal and dredging stations.

Other Collections Examined

Upon returning from Chile in 1975, I compared the field-collected specimens with as many of the types of species described by nineteenth-century authors as could be located for me in the British Museum (Natural History) and the Paris Museum. I have also studied the collections of *Fissurella* in the U.S. National Museum of Natural History, Washington, D.C., the Academy of Natural Sciences, Philadephia, and the American Museum of Natural History, New York. Other specimens were received on loan from the Museum of Comparative Zoology, Harvard, and the National Museum of New Zealand, Wellington. After conducting my fieldwork in Argentina in 1978, I examined the *Fissurella* material in the Museo Argentino de Ciencias Naturales, Buenos Aires, and the Museo Nacional de Historia Natural, Santiago. Records from these collections enabled further refinements in species distributions.

Preparation of Specimens

Although most of the field-collected specimens were either kept dry or the entire specimen preserved in alcohol, without cleaning the shell, the photographed specimens had to be cleaned of encrusting organisms. Shells were placed in full strength laundry bleach, which softens the algal mat and loosens other encrusting organisms so that the shell can be scraped clean with a knife or wire brush. Color was restored with a light application of mineral oil.

Shells of each species were embedded in plaster and cut with a diamond rock saw for the examination and photography of the shell layers. Scanning electron microscopy (SEM) was used for the examination of shell structure in a fragment of a small specimen of *F. latimarginata.* Radulae of large specimens of each species were air-dried for macrophotography; radulae of small specimens were prepared for both light microscopy and SEM.

Conventions

Figured specimens for each species are arranged by localities from north to south, including type specimens of nominate taxa and synonyms. All shell specimens are illustrated with the anterior at the top; lateral views are those of the left side of the shell. Measurements for the figured specimens are given in the captions, not repeated in the text. Measurements are given in this order: length, width, and height. Unless otherwise indicated, the figured specimens were collected in the intertidal zone. Latitude and longitude for the figured specimens from LACM stations are given in a locality list following the systematic section.

Abbreviations

Abreviations of institutions mentioned in the text are as follows:

AHF	Allan Hancock Foundation Collection (at LACM)
AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History), London
LACM	Los Angeles County Museum of Natural History, Los Angeles
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MNHN	Museo Nacional de Historia Natural, Santiago
MNHNP	Museum National d'Histoire Naturelle, Paris
NMNZ	National Museum of New Zealand, Wellington

USNM United States National Museum of Natural History, Washington, D.C.

HISTORICAL REVIEW

The Strait of Magellan was probably the origin of the earliest collected shells of *Fissurella* to reach Europe. The first species to be known was the common Magellanic *F. picta,* which was well described and figured in the non-binomial work of Davila (1767), who called it "Un Lepas rare de Magellan" (Pilsbry, 1890:114). The name *Fissurella picta* dates from J.F. Gmelin (1791), whose knowledge of it came in part from Davila.

J.B.P.A. de Lamarck (1822) validated *F. crassa* and *F. peruviana* in his "Histoire naturelle des animaux sans vertébrés." Lamarck's types are preserved at the Geneva Museum (Mermod, 1950).

G.B. Sowerby (1825) introduced a synonym for *F. crassa,* but was later to recognize Lamarck's unfigured species.

G.P. Deshayes (1830) named two Chilean species in the "Encyclopédie Méthodique," but one of them was a synonym of *F. peruviana* and the other, *F. rudis,* although prior to *F. costata* Lesson, 1831, is preoccupied. Types are extant at the Paris Museum.

R.P. Lesson (1831), in his report on collections from the South American voyage of the "Coquille," described four species of *Fissurella* without illustrations, all from the southern and southernmost regions of Chile. The names for three of his species are now in use: *F. nigra, F. radiosa* and *F. costata.* One other, *F. obovalis,* remains a *nomen dubium.* Lesson's work has frequently been cited as published in 1830, but the pages that included the *Fissurella* descriptions are correctly dated 1831. Although some of Lesson's types have been recognized at the Paris Museum, P. Bouchet reports (personal communication) that he has been unable to locate any of the *Fissurella* types.

By 1831, six of the currently recognized species had been established. Eleven names had then been proposed, but very few of these taxa had been illustrated.

In 1835, no less than 13 names were introduced by G.B. Sowerby, based on specimens received from the British collector Hugh Cuming, who had lived in Valparaíso, Chile, from 1819 to 1831. Brief descriptions were given in the Proceedings of the Zoological Society of London for 1834. Dating for these species has frequently been cited as 1834, but the publication date for the pages involved is 1835. Illustrations were published simultaneously in the "Conchological Illustrations" (Sowerby, 1835b). Sowerby recognized some of the species described earlier by French authors; seven of his names remain useful: *F. maxima, F. latimarginata, F. limbata, F. oriens, F. pulchra, F. lata* (here *F. picta lata*), and *F. fulvescens* (here *F. oriens fulvescens*). The Sowerby types are preserved at the British Museum (Natural History).

By 1835, 11 of the 13 species I recognize from Chile had been named, and the total number of described taxa had reached 25.

R.A. Philippi (1845, 1845–46) proposed five names, but none of these has any current utility. One of these, *F. alba,* has been used by some authors, but is here regarded as a synonym of *F. oriens.* Unfortunately, the present whereabouts of Philippi's *Fissurella* types is unknown.

A.A. Gould (1846) introduced one name, here regarded as a synonym for *F. peruviana.* The holotype is in the United States National Museum.

Lovell Reeve (1849–50), in his monograph of *Fissurella* in the Conchologica Iconica, added two more of the species recognized here, *F. cumingi* and *F. bridgesii,* both of which have been enigmatic until now. However, he also introduced nine superfluous names, based on further splitting of Cuming's material. Some were described without locality. Reeve gave colored illustrations for all the previously recognized species but did not give any interior views of the shells, thereby not treating the broad margin, one of the most useful characters. Also, he did not always figure the same specimen illustrated by Sowerby, a factor contributing to confusion in some cases. The Reeve types are housed in the British Museum (Natural History).

An attempt at summarizing the recognizable species in Chile was made by L.H. Hupé, 1854, who added Spanish translations of original descriptions of earlier species, and included some of his own commentary, but gave no illustrations. Twenty-one species were recognized. One new taxon was introduced, the renaming of a preoccuppied name of Philippi.

Philippi (1857) proposed another name now having no value. In 1860 Philippi briefly treated eight species of *Fissurella* from Paposa (near Antofagasta) in his "Reise durch die Wueste Atacama . . . ."

G.B. Sowerby II's treatment of *Fissurella* in the "Thesaurus Conchyliorum" (1862) was scarcely an advance over that of Reeve. Specimens illustrated were not always those of Sowerby or Reeve. One additional synonym was named. Little new information was given, nor was opportunity taken to reduce the number of names. The figures were smaller than those given by Reeve, and there were no interior views.

A.T. de Rochebrune and J. Mabille (1885) proposed three taxa from the southernmost region, none of which were compared to established species; the names are now regarded as junior synonyms. Two of the three type specimens are housed in the Paris Museum; the whereabouts of the other is unknown.

H.A. Pilsbry's (1890) treatment of *Fissurella* in the "Manual of Conchology" was an admirable effort at summary and review. For most taxa he provided English translations of text by German and French authors and copied original illustrations for all taxa, whether recognized as valid or placed in synonymy. Synonyms were allocated as far as possible. Approximately 20 were treated as good species. However, the specimens available to Pilsbry were limited, and many questions remained unanswered. Only one unnecessary new species was introduced, the holotype of which is preserved at the Academy of Natural Sciences, Philadelphia.

J.C. Melvill and R. Standen (1898, 1907, 1914) listed and gave notes on mollusks from the Falkland Islands. The *Fissurella* species were briefly treated.

H. Strebel (1907) treated the Magellanic and Patagonian *Fissurella.* For three of the species that I consider to inhabit this southern area, he recognized six, but introduced no synonyms. A year later, Strebel (1908) listed *F. exquisita* from Paulet Island, Antarctic Peninsula, a record that needs further verification. Unfortunately, the Strebel Collection was destroyed in World War II (Dance, 1966:302).

W.H. Dall (1909) listed 18 species of *Fissurella* in his checklist of mollusks from the Peruvian faunal province. Those pertaining to the Magellanic area were omitted. Some of Dall's records are now clearly erroneous: *F. crassa* at the Galapagos Islands and both *F. maxima* and *F. picta* at Manta, Ecuador. The records from Manta had previously been cited by Stearns (1891).

A. Ziegenhorn and H. Thiem (1925) reported upon a collection made in Chile by L.H. Plate. From a collection of only 15 specimens, they discussed and illustrated 11 species. They omitted three species that I recognize and treated two others as "varieties," but their scheme is the best effort available in the literature. Some external features of the animal were mentioned, and good illustrations of the shells were given, but no interior views. Among the subsequent authors, only Odhner (1932) and Dell (1971) cited their work.

I. Perez-Farfante (1943) mentioned only *F. picta* in her account of Atlantic Fissurellidae. She made this species the type of her new subgenus, *Balboaina,* which I here synonymize with *Fissurella, sensu stricto.*

The "Catalogo descriptivo de fisurelidos Chilenos" of F. Riveros-Zuñiga (1951) was compiled almost entirely from the literature. Text from previous authors was translated into Spanish. Illustrations were single exterior views, most of which were copied from other sources. Twenty-six species and three varieties were recognized. Three of the common Peruvian Province species were erroneously cited from Fuerte Bulnes, near Punta Arenas in the Strait of Magellan.

A.R. Carcelles (1950), Carcelles and S.I. Williamson (1951), and Carcelles (1953), produced a series of faunal checklists for the Patagonian, Magellanic, and Antarctic regions, in which *Fissurella* species were listed.

Pérez-Farfante (1952) proposed the subgenus *Carcellesia,* with the new type species *F. doellojuradoi,* which I regard as a synonym of *F. oriens.* The subgeneric name is here regarded as a synonym of *Fissurella, sensu stricto.*

B. Métivier (1969) named *F. tixierae* from the Golfo Nuevo, Argentina, a name here treated as a geographic subspecies of *F. radiosa* Lesson. The type specimen is preserved at the Paris Museum.

G.M. Peña (1970) included six species (five that I recognize) in his list of the intertidal mollusks of Peru, and cited a number of his own collecting localities for each.

R.K. Dell (1971) illustrated many Sowerby and Reeve syntypes from the Cuming Collection in the British Museum in his report on mollusks from the Royal Society Expedition to southern Chile. His collection, however, was not sufficiently complete to enable a full revision, and his list of 11 "possible species" differs considerably from that adopted here.

L. Marincovich (1973) figured the five most abundant species from Iquique in northern Chile but did not discuss their synonymy. The Marincovich collection is preserved at the Los Angeles County Museum of Natural History.

J. Christiaens (1973) did not treat the Chilean species in his review of the tropical *Fissurella* species; however, he proposed the subgenus *Corrina* for *F. alba* Philippi, a species here placed in the synonymy of *F. oriens. Corrina* is here regarded as a synonym of *Fissurella, sensu stricto.*

J. Ramirez-Boehme (1974) gave a key that included 30 different species (plus two varieties) of *Fissurella* from Chile. Some of the taxa recognized in his key have never been illustrated and have been considered indeterminate by other authors. He also introduced four synonymous names in *Fissurella* (along with 21 "new species" names for acmaeid limpets). All were figured in watercolor. Types are preserved at the Museo Nacional de Historia Natural, Santiago.

In July, 1978, I distributed copies of a preliminary draft of this manuscript to a number of Chilean biologists whom I had met in 1975. That version differed from this primarily in recommending the replacement of *F. rudis* Deshayes, 1830, for *F. costata* Lesson, 1831. However, Deshayes' name is preoccupied, so the better known name of Lesson is reinstated here. I am gratified to see that my present classification scheme has been adopted by Chilean biologists, and am grateful for the help they have provided in making this account the more complete.

Recent papers on the biology of *Fissurella* species are those of Acuna (1977), Bretos (1978, 1979, 1980, 1982, 1983), Jara and Moreno (1984), Moreno and Jaramillo (1983), and Moreno et al. (1984).

STRUCTURE

Internal Anatomy

Anatomy in the Fissurellidae has been treated by Boutan (1885), Illingworth (1902), Tobler (1902), Ziegenhorn and Thiem (1925), and Odhner (1932). The latter two accounts included references to Chilean species of *Fissurella.* Fretter and Graham (1962) gave a number of useful drawings of fissurellid anatomy. The reader is referred to these works for details.

Although some incidences of hermaphroditism are known in fissurellids (see Fretter and Graham, 1964), to my knowledge, *Fissurella* species are gonochoristic, having separate sexes. There are no apparent external sexually dimorphic features, although the testis of males is beige-colored and the ovary of females is bright green. The gonads discharge through the right kidney, which therefore has a reproductive as well as an excretory function. The Fissurellidae are unusual among archaeogastropods in having a highly reduced left kidney, which is nearly vestigial. In contrast, the left kidney is a prominent papillary sac in the archaeogastropod families Pleurotomariidae, Haliotidae, and Trochidae. These families also differ in having the spiral caecum appendage to the stomach and a well-developed hypobranchial gland attached to the mantle skirt, structures that are lacking in the Fissurellidae.

Anatomy in the Fissurellidae is so unlike that of the Pleurotomariidae, Haliotidae, and Trochidae, that the affinity is

Figure 2. External anatomy of *Fissurella picta.* Two views of same preserved specimen removed from shell, the mantle skirt cut above the head to the excurrent siphon and folded back to show the paired gills in the mantle cavity. Bahía York, Isla de los Estados, Argentina. LACM 71-177, shell length 75.4 mm. Left, anterior view, showing radular ribbon protruding from mouth. Right, dorsal view.

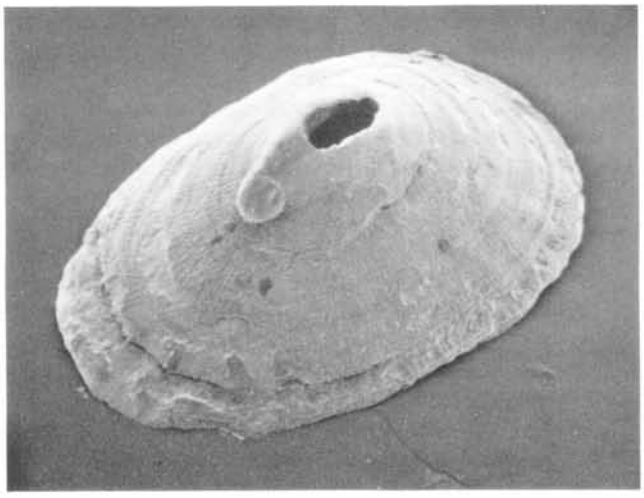


Figure 3. *Fissurella oriens,* SEM view of juvenile shell 1.9 mm in length, showing coiled protoconch and early foramen. Islota Nihuel, Chiloe Province, Chile. LACM 75-42.

distant from these groups. I have argued (McLean, 1984a) in support of the theory that the Fissurellidae were derived from the extinct Paleozoic Bellerophontacea. The bilateral symmetry of the Fissurellidae would therefore not be secondarily derived, as has been assumed by most authors, but primitive.

External Anatomy

Structures of the head are the snout, which terminates in a broad oral disc (Fig. 2), and cephalic tentacles, the eyes at the bases of the tentacles. The cephalic tentacles extend forward when the animal is active.

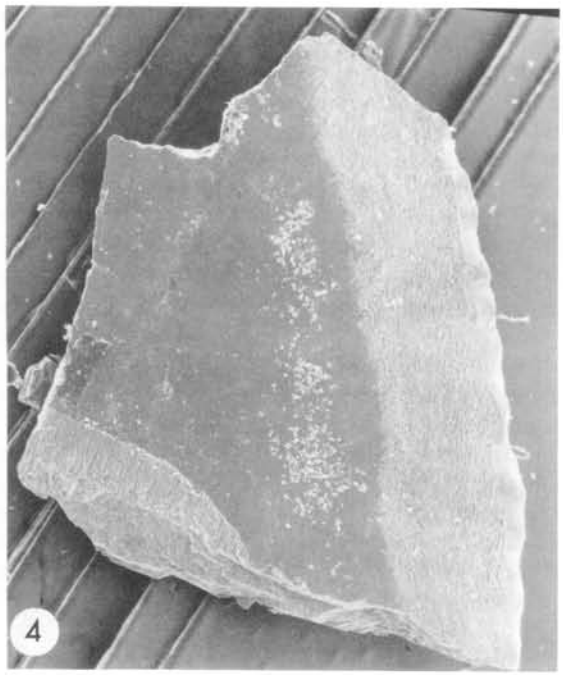
The body is attached to the shell by a horseshoe-shaped shell muscle, which is open anteriorly, corresponding to the mantle cavity above the head. The animal may be detached from the shell by severing the shell muscle. Structures within the mantle cavity (Fig. 2) may then be observed by cutting the thin mantle roof tissue above the head. This exposes a pair of large, bipectinate gills, which fill most of the space in the mantle cavity on either side. The gills are attached by a long ventral (efferent) membrane and a short dorsal (afferent) membrane. The anus opens close to the foramen. Water currents enter above the head, pass the gills, and exit through the foramen of the shell, sweeping the fecal material out at the same time. The currents are propelled by bands of cilia on the gill filaments. Left and right kidney openings are positioned near the anus.

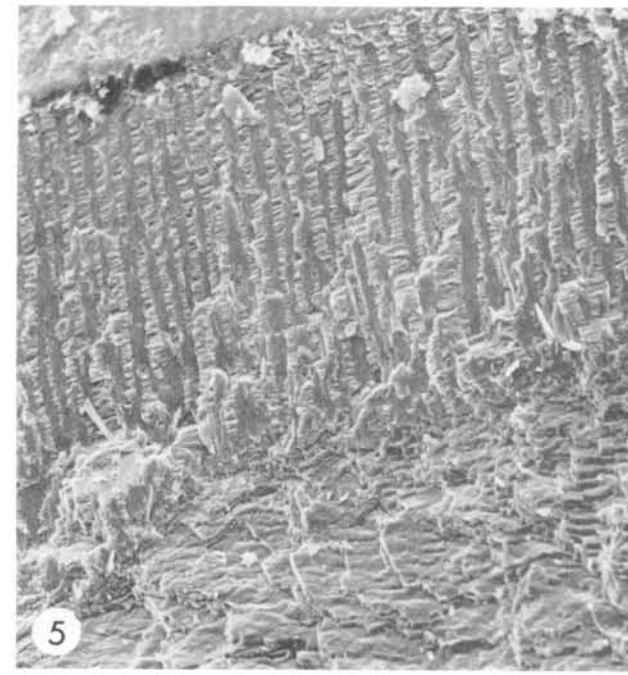
In living *Fissurella,* the shell edge is enveloped by the mantle fold, which secretes and protects the growing edge of the shell and has sensory papillae scattered on its surface. The mantle fold is color-banded to match the rayed pattern of the shell. The mantle fold is capable of expanding to cover the entire shell and foot sides. The foramen is also bordered by mantle folds that have papillae and a pigment pattern similar to that of the mantle at the shell margin. The diameter of the excurrent opening in the mantle skirt varies under differing conditions of exposure to air or water.

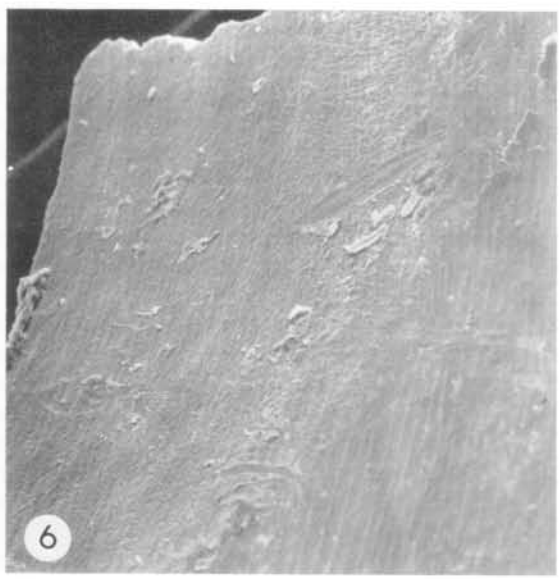
The pigmented side of the foot has a single row of short, stubby epipodial tentacles, extending anteriorly to the head. These tentacles are poorly developed. The elaborate mantle lobes probably have more of a sensory function than do the epipodial tentacles. In other archaeogastropod families, particularly the Haliotidae, the epipodium is well developed, forming several rows of tentacles on a separate fold called the epipodial lobe.

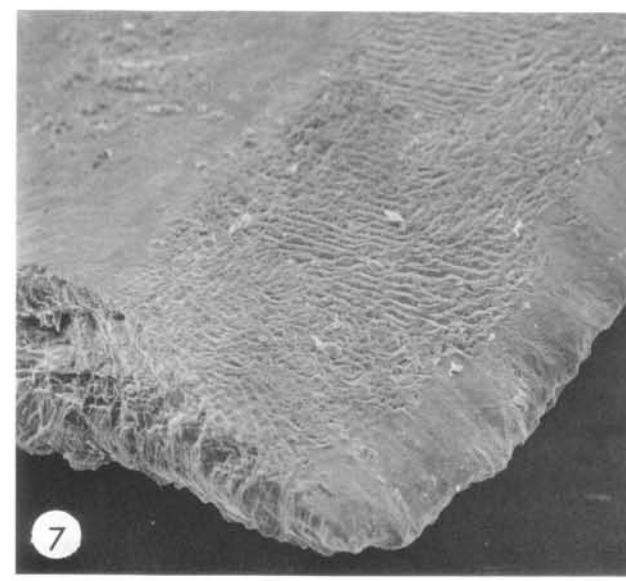
Radula

The radula consists of rows of chitinous teeth on a long ribbon (shown projecting through the mouth in Fig. 2). The entire radular ribbon may be as much as ⅓ the length of the shell. The teeth rows are rhipidoglossate, with a narrow rachidian (central tooth), four pairs of lateral teeth shaped like the rachidian, a pair of large, four-cusped outer lateral teeth, a pair of uncusped lateromarginal plates, and a large number of marginal teeth. The lateromarginal plates separate the large outer laterals from the "books" of marginal teeth. The fissurellid radula is markedly asymmetrical (Hickman, 1981, 1984), with teeth on the left side of the ribbon higher or more anteriorly placed than those on the right, extending forward of the rachidian, which itself is asymmetrical. This pronounced asymmetry enables the large outer laterals to interlock like the teeth of a zipper when the ribbon is folded and retracted at the close of the feeding stroke. The teeth are folded in the same way while developing in the radular sac.









Figures 4 through 7. Shell structure of *Fissurella latimarginata*. SEM views of single fragment from young specimen, courtesy H.A. Lowenstam. LACM 64-16, Iquique, Chile. (**4**) Interior view of shell fragment, the broad, beveled interior margin (calcitic layer of exterior) of shell at right (length at margin 2.14 mm), and the smooth interior aragonitic layer in center and left. Fractured area at lower left exposes the crossed lamellar structure of the aragonitic layer and the platy calcitic layer below. ×30. (**5**) Enlargement of lower left area of shell fragment, showing the smooth interior at top, the fractured surface of crossed lamellar aragonite below, and the transition between the latter and the fractured platy calcitic layer at the lower edge of the frame. ×200. (**6**) Enlargement of upper left corner of shell fragment. Vertical lines are the lamellae of the smooth interior aragonitic layer. Curved lines represent the successive positions of the expanding muscle attachment area. ×120. (7) Enlargement of lower right corner of fragment, showing the smooth growing edge (calcitic layer), the undulations reflecting the external sculpture of radial ribs. The broad, beveled margin has an irregular surface (for mantle contact) between the smooth edge and the smooth aragonitic surface at the left. ×80.

The large outer laterals are the functional teeth; the rachidian and inner laterals are so small that their role is minimal.

Shell Morphology

The apical perforation, or foramen, is the most striking shell feature. It enlarges as the shell grows; shell material is resorbed by the mantle tissue that surrounds the foramen. Young shells have a coiled protoconch, but this is obliterated by the expanding foramen and is generally present only in juvenile specimens of up to two mm in length (Fig. 3). Although the postprotoconch stage of *Diodora* has a selenizone (slitband), this is lacking altogether in developing stages of *Fissurella* (McLean, 1984a).

Prominent features of the shell interior are the horseshoe-shaped muscle scar, open in front, and the apical callus, a broad flat area surrounding the foramen. The two round terminations of the muscle scar are connected by a line that marks the anterior attachment zone of the mantle skirt.

Shell Structure

Most fissurellids have the shell composed entirely of the aragonitic form of calcium carbonate (Bøggild, 1930; MacClintock, 1963, 1967). Bøggild (1930) noted that the Chilean *Fissurella crassa* also has an outer layer composed of the calcitic form of calcium carbonate. Other species treated here were not mentioned by Bøggild, but all have a similar two-layered shell (Figs. 4–7). The shell structure of radial ribs and the pigmentation is confined to the outer layer. This layer has a waxen, translucent appearance. A periostracum is lacking.

In the Peruvian and Magellanic species, it is the outer calcitic layer that comprises the broad, pigmented interior margin of the shell. This layer is secreted by the mantle lobe only at the growing edge. In contrast, the opaque white aragonitic inner layer is deposited throughout the interior and thickens with growth. The interior aragonitic layer is thick only in the apical region, where it has greatly augmented the thin calcitic layer of the early shell. Away from the apical area, the inner layer becomes thinner, its depth only one-third to one-fifth the thickness of the calcitic layer; it is lacking altogether at the shell edge (margin).

The prismatic structure of the calcitic layer is not readily apparent under low magnification; however, the structure of the opaque white aragonitic layer can be seen under the dissecting microscope. It shows a series of lines running parallel to the shell margin, a typical feature of "concentric cross-lamellar" shell structure. The lamellae may be seen throughout the interior of the shell, including the muscle scar and the apical callus (Fig. 6).

Tropical species of *Fissurella* have shells composed entirely of aragonite and lack the distinctively colored inner shell margin. This difference between the tropical species (Fig. 30) and the cooler-water species is here treated as a subgeneric distinction.

In molluscan species with both calcite and aragonite deposited in separate shell layers, the ratio of calcite to aragonite deposition varies with temperature. A greater percentage of calcite deposition takes place at colder latitudes and seasonally, during winter months (Lowenstam, 1954, 1964; Vermeij, 1978). Lowenstam (1954) noted a greater percentage of calcite deposition in species of *Mytilus* and *Littorina* as latitude increased. This is apparent in specimens of *Fissurella picta* from different latitudes. In *F. picta* from the Strait of Magellan at 53°37′ S (Fig. 145) the aragonitic layer is noticeably thinner than in *F. picta* from 42°42′ S (Fig. 144). The greater calcitic deposition in cold water helps to explain why these species are so prolific at high latitudes, where they reach a much larger size than do their tropical counterparts. The calcitic layer of the South American species is evidently an adaptation to cold water.

Calcite is more stable than aragonite, and fossil calcitic shells are generally better preserved. This is evident in the specimen of the Pliocene *F. concolor* Philippi, 1887, from Antofagasta (Fig. 17). Only the calcitic outer layer remains; the aragonitic interior is completely missing. However, specimens in old shell piles indicate that when exposed to subaerial weathering, the calcitic layer fractures and separates, whereas the aragonitic layer tends to remain intact.

BIOLOGY AND ECOLOGY

Habitat

As in other limpet families with large numbers of sympatric species, each of the Peruvian-Magellanic *Fissurella* species has a unique habitat or niche.

All tropical species of *Fissurella* are limited to the intertidal zone, but some of the Peruvian-Magellanic species extend into the subtidal zone. *Fissurella peruviana, F. pulchra,* and *F. oriens* may occur more abundantly in the sublittoral than in the lower intertidal zone. *Fissurella maxima, F. cumingi,* and *F. latimarginata* occur commonly from the lower intertidal zone to a depth of about 5 m. The intertidal occurrence of these species is limited to areas protected from strong wave exposure.

The remaining species are intertidal and do not occur in the sublittoral zone. The highest occurring species is *Fissurella crassa,* which is tightly wedged in crevices when exposed at low tide. *Fissurella limbata* and *F. costata* live exposed to surf in the lower intertidal zone, *F. limbata* on horizontal surfaces, and *F. costata* on vertical surfaces. *Fissurella nigra* occurs on the undersides of large rocks in protected tide pools at mid-tidal to lower intertidal levels.

Fissurella bridgesii has a unique habitat. It occurs on rocks near sandy areas, unlike the others, which avoid proximity to sand.

Fissurella picta has a more ubiquitous occurrence. It is rare at its northern limit, where it is sympatric with other species, but to the south of the southern limit of most of the other species it occurs from the mid-tidal to lower intertidal zone under various conditions of exposure, filling niches that are occupied by other species in the north.

Feeding

Little is known of the feeding habits of Peruvian and Magellanic *Fissurella.* Many genera of fissurellids feed upon

sponges and detritus (Fretter and Graham, 1976), but Ward (1966a) has shown that the tropical species *F. (Cremides) barbadenisis* (Gmelin, 1791) feeds upon algae. Bretos (1978) indicated that *F. crassa* feeds upon such green algae as *Ulva* and *Enteromorpha.*

At Mehuin in southern Chile, *Fissurella picta lata* is a nocturnal herbivore, feeding upon the red alga *Iridaea boryana* and the green alga *Ulva rigida* (Jara and Moreno, 1984; Moreno and Jaramillo, 1983; Moreno et al., 1984).

Information on the diets of the other South American species is needed.

Reproduction and Growth

Bretos (1983) treated reproduction in *F. maxima,* finding that spawning occurred in late November–December (late spring) and again in July–August (winter). The breeding cycle of the tropical *F. barbadensis* was treated by Ward (1966b). That species is known to have a pelagic phase of two to three days duration.

Bretos (1978, 1980) studied the growth rate of *F. crassa,* finding that growth is rapid in early spring and late summer, slower in late spring, autumn, and winter. Harvestable sizes were reached in 2 to 4 years. Two growth rings were formed each year and were considered reliable indicators of growth for the first 6 years, after which growth was slowed and the rings could not be identified. *Fissurella maxima* was also determined to form two growth rings each year (Bretos, 1982). Growth in *F. latimarginata* was studied by Acuna (1977).

The El Nino event of 1982–1983 had a major effect on the *Fissurella* populations in northern Chile. According to J. Tomicic (personal communication), all large *Fissurella* species near shore were killed during the austral summer of 1982–1983. However, in November, 1983, fast growing juveniles were reported as abundant.

Epibiotic Associations

Fissurella shells offer a surface for colonization by many species of algae and invertebrates. Many shells are so encrusted that color patterns are obscured (Fig. 1). Only those species that occur high in the intertidal zone (*F. crassa*), or predominantly on the undersides of large rocks in the lower intertidal (*F. nigra* and *F. pulchra*), have shells that stay relatively free of encrusting organisms.

Species of the shallow sublittoral zone (*F. latimarginata, F. cumingi,* and *F. maxima*) generally have a thick algal mat consisting of dense tufts of finely branched red algae, which reaches a height of 5 mm above the shell (Figs. 1, 8). This algal growth is absent on the rocky substrate because grazing by the black urchin *Tetrapygus niger,* and presumably by the *Fissurella* species, leaves the rock barren except for encrusting coralline algae.

Although the algal mat on the shells of a living *Fissurella* would be a source of food for other individuals of *Fissurella* as well as the urchins, they evidently do not tolerate grazing by their own kind or by the urchins, because the algal mat is usually intact. I observed thick algal mats on most shells seen in the course of diving, those in shell piles on the shore, and those sold in markets. The chiton *Chaetopleura peruviana* is able to graze successfully on the algal mat of shells (Fig. 8).

Balanus psittacus is frequently found on subtidal *Fissurella* shells, and *B. flosculus* occurs on shells in exposed intertidal habitats, particularly on *F. costata* and *F. limbata.*

The mussel *Semimytilus algosus* may form aggregations on specimens of *F. latimarginata* (Fig. 74).

Epibiotic growths on *Fissurella* shells provide a protective advantage, making it more difficult for boring organisms to penetrate the shell. Those specimens of *F. latimarginata* that have lost the algal mat are usually deeply eroded. The advantage of epibionts to chamid bivalves was discussed by Vance (1978).

Epibiotic *Scurria parasitica*

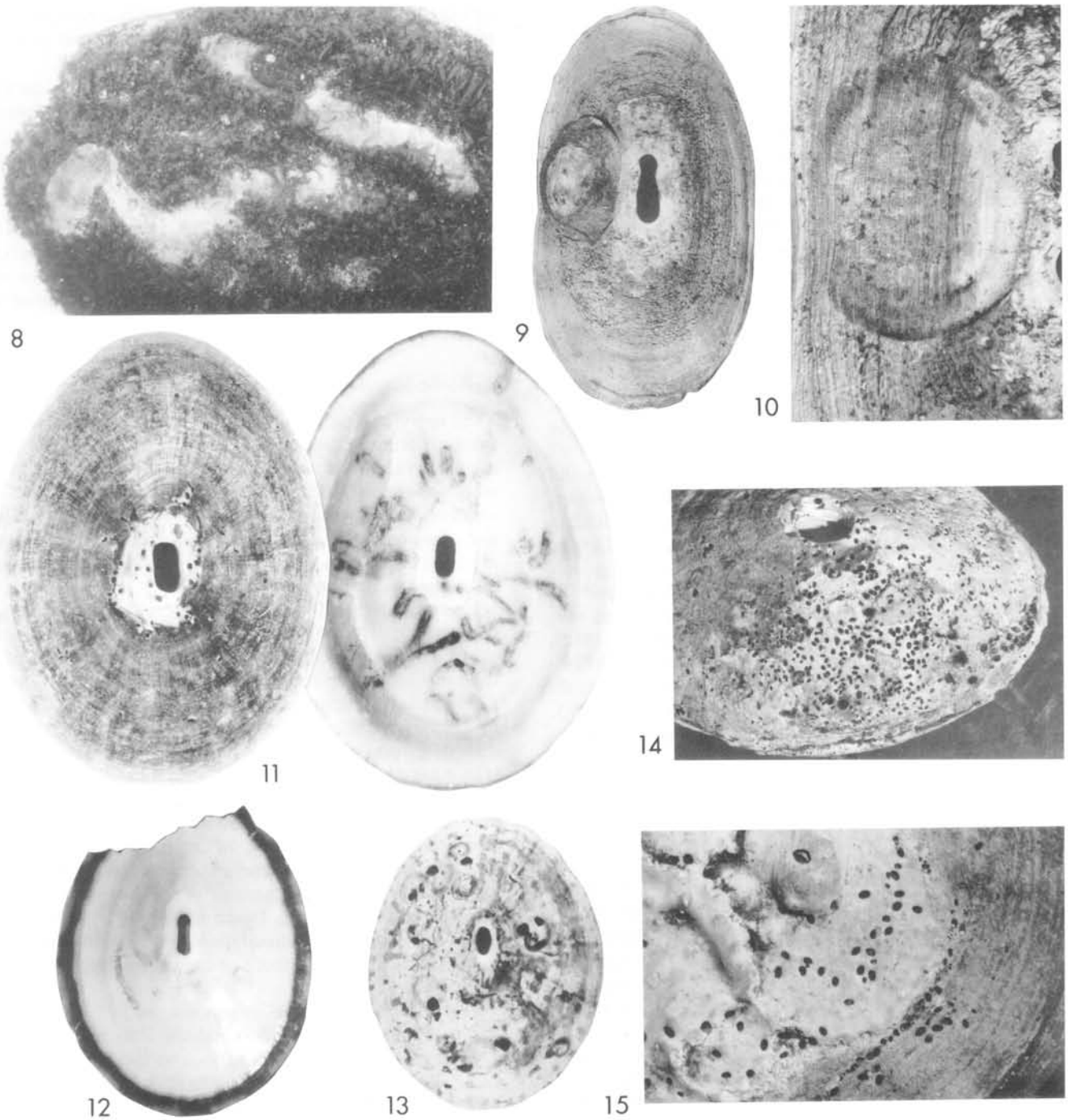
Most individuals of *F. crassa* and *F. limbata,* two species that only occur in the intertidal zone, have a single (or rarely two) *Scurria parasitica,* an acmaeid limpet, attached to "home scars" on the shell (Figs. 9, 10). This limpet occurs also on shells of *Scurria viridula* and the chitons *Enoplochiton niger* and *Acanthopleura echinata* (see Marincovich, 1973) and rarely on other species of intertidal *Fissurella.* I am aware of no studies on its biology.

Lindberg (1976), Dwyer and Lindberg (1981), and Lindberg and Dwyer (1983) described the home-scar depression of the Californian acmaeid *Collisella scabra* on the shells of the mussel *Mytilus californianus* and the acmaeid limpet *Lottia gigantea,* noting the similarity of the scar to that formed by *Scurria parasitica* on chitons. These epibiotic limpets produce deep scars on their host shells (Fig. 10), in which there is an outer depression corresponding to the shell margin, and an inner depression to correspond to the breadth of the foot. The outer depression provides a seal that helps to prevent desiccation and dislodgment. Microscopic examination of the home scars shows the presence of radular scraping marks, which indicates that enlargement of the scar is an activity unassociated with feeding. Lindberg and Dwyer (1983) also found evidence of shell dissolution by acidic mucopolysaccharides secreted by the foot and carbonic anhydrase by the mantle edge.

The feeding range of the limpets studied by Lindberg and Dwyer (1983) was restricted to the shells of the host mollusks. This is probably true for *S. parasitica* on shells of *F. limbata* and *F. crassa.* Scar-bearing *Fissurella* shells do not have other encrusting organisms and are always deeply eroded.

Shell Borers

Cirratulid polychaetes of the genus *Dodecaceria* (identified both by K. Fauchald and J.C. Castilla) commonly burrow into *Fissurella* shells, riddling and weakening them (Fig. 11). The polychaete tubes open at the exterior surface, where they are ordinarily concealed by the algal mat. The inside diameter of the tube reaches 1.3 mm. The burrows are visible on the shell interior, but do not break the surface except in gerontic shells. Gibson (1978) briefly discussed Chilean species of



Figures 8 through 15. Shell epiphytes, shell grazers, shell borers. (**8**) Dense mat of red algae on exterior of *F. latimarginata,* with chiton *Chaetopleura peruviana* and grazing trails made by the chiton. LACM 75-29, Los Molles, Aconcagua Province, Chile, shell length 106 mm. (**9**) Epizoic limpet *Scurria parasitica* on *F. crassa.* LACM 90796, Iquique, Chile, shell length 57.5 mm. (**10**) Scar of *S. parasitica,* showing inner and outer depression of scar. Same specimen, length of scar 13.1 mm. (**11**) Shell of *F. latimarginata* infested with borings by cirratulid polychaete *Dodecaceria* sp., exterior view of cleaned shell showing openings to burrows; interior view showing trace of burrows. LACM 75-29, Los Molles, Aconcagua Province, Chile, shell length 115 mm. (**12**) Shell of *F. cumingi* removed from stomach of clingfish *Sicyases sanguineus,* showing breakage pattern caused by this predator. LACM 75-31, Islota Concon, Valparaíso Province, Chile, shell length 50.8 mm. (**13**) Shell of *F. costata* with excavated depressions made by vermetid gastropod *Dendropoma* sp. LACM 75-27, beach-worn specimen, Bahía El Teniente, Coquimbo Province, Chile, length 50 mm. (**14**) Shell of *F. cumingi* with burrows of barnacle *Cryptophialus minutus.* MACN 9027-11, specimen studied by Tomlinson (1969), locality unknown, shell length 83.7 mm. (**15**) Exterior surface of *F. limbata* showing burrows of *Cryptophialus.* LACM 75-19, Los Colorados, Antofagasta Province, Chile, length of field 21 mm.

Dodecacaeria. However, the systematics of the group remains poorly known.

K. Fauchald (personal communication) has also identified the spionid polychaete *Polydora* sp. as a borer in *F. latimarginata.*

Polychaete burrows in *Fissurella* shells provide shelter for young specimens of the bivalve *Hiatella solida,* which may then bore further into the shell, as has been reported in shells of *F. nigra* by Gallardo and Osorio (1978).

Acrothoracican barnacles (burrowing barnacles) penetrate the shells of Chilean *Fissurella* species (Figs. 14, 15). Tomlinson (1969:88) reported the species *Cryptophialus minutus* Darwin, 1854, in a shell of *Fissurella maxima.* The specimen examined by Tomlinson (actually *F. cumingi*) is illustrated here (Fig. 14). I have found this pattern of burrows in a specimen of *F. limbata* from Antofagasta (Fig. 15) and in *F. latimarginata* from a number of localities.

Burrows of a vermetid gastropod, *Dendropoma* sp., have been noted on specimens of *F. costata* (Fig. 13), forming one-whorled depressions nearly flush with the surface of the host shell, but not penetrating to the interior.

Parasites

Bretos and Jiron (1980) reported that digenetic trematodes of the genus *Proctoeces* Odhner, 1911, family Fellodistomidae, were present in the gonads of eight species of *Fissurella* in northern Chile. Percentages of infected individuals in each species ranged from 14% to 97%. The effect of this parasitism on reproduction in the host species is unknown.

Seastar Predators

The seastar *Heliaster helianthus* is a voracious predator upon many species of mollusks in the lower intertidal zone (Paine and Palmer, 1978; Castilla, 1981). However, *Fissurella* has a highly effective escape response. *Fissurella* respond to initial contact with *Heliaster* by first raising the mantle fold above the edge of the shell, preventing the seastar's tube feet from making contact with the shell; thereupon they move rapidly out of reach. A collector with a seastar in hand may dislodge tightly wedged specimens without using a tool. The raising of the mantle to cover most of the shell surface is similar to the response of the north Pacific fissurellid *Diodora aspera* to various seastar predators (Margolin, 1964).

Fissurella costata is the only species that fails to show an escape response to *Heliaster.* It remains tightly appressed. Its foramen, the smallest among the larger species, is evidently too small for penetration by *Heliaster.*

The overall effect of *Heliaster* on populations of various species of *Fissurella* probably is not significant. Large individuals can move fast enough to escape and the small, less motile ones stay out of reach in crevices, or on the undersides of rocks.

In southern Chile, the asteroid *Meyenaster gelatinosus* is a major predator on many mollusks (Dayton et al., 1977). *Fissurella* and other gastropods escape predation from this seastar in surging water by allowing the water motion to move them away.

Vertebrate Predators

Non-human vertebrate predators that include *Fissurella* species in their diets in central Chile are the Chilean sea otter *Lutra felina,* the seagull *Larus dominicanus,* the oyster catcher *Haematopus ater,* and the clingfish *Sicyases sanguineus* (see Castilla, 1981).

The Chilean sea otter, the "nutria de mar," has a restricted and localized distribution, but where it occurs, the effect of this carnivore is significant. It feeds upon *Sicyases, Concholepas, Fissurella* species, the acmaeid limpets *Scurria* species and at least three species of crabs. Castilla and Bahamonde (1979) gave a more complete account of the ecology of *Lutra felina.*

According to Castilla (1981), *Haematopus ater* feeds upon *Concholepas, Scurria* species and *Fissurella* species; *Larus dominicanus* feeds upon *Concholepas,* crabs, herbivorous snails, *Fissurella* species, chitons, *Scurria* species, and mussels.

Sicyases feeds on a wide variety of invertebrates and algae on vertical walls in the surf-exposed intertidal zone (Paine and Palmer, 1978). Those authors reported small specimens of several species of *Fissurella,* and even one relatively large specimen of *F. cumingi* (Fig. 12), in clingfish stomachs. Most of the *Fissurella* shells were broken at one end, presumably by the strong teeth of this predator. Many shells cast up on beaches are broken in a similar way, suggesting that *Sicyases* is a major predator on *Fissurella.* A study of the breakage pattern in beach-worn shells would be useful to further document the feeding of *Sicyases.*

Fissurella costata is well adapted to habitats where *Sicyases* occurs. It attaches tightly, making it difficult for the clingfish to get hold of the shell. Other species of *Fissurella* have poor defense against *Sicyases* because the shell edge normally is raised and the mantle and foot exposed. *Sicyases* may be such an effective predator that it completely removes other species that stray into its habitat.

Human Predation and Economic Importance

Man is the chief predator upon *Fissurella.* Large individuals of all species are used for food throughout Chile and Peru. I found six species for sale in the municipal market at Iquique: *F. crassa, F. maxima, F. latimarginata, F. cumingi, F. limbata,* and *F. bridgesii.* They are collectively know as "lapas" and are not sorted by species when sold. Although the fishery for the lapa is on a small scale compared to that of the "loco," *Concholepas,* it amounts to a significant predation pressure on the larger-shelled species. Those sold in the market are kept intact in the shell. However, the shorelines in Chile have numerous piles of discarded shells (Fig. 1). According to figures from the Chilean Servicio Nacional de Pesca (SERNAP), 451,000 tons of *Fissurella* species were harvested in 1982 (C.A. Moreno, personal communication).

In populated areas, human predation on *Fissurella* is significant. Moreno et al. (1984) found few specimens of *F.*

picta lata over 4 cm in length in the vicinity of Valdivia. Much larger sizes occurred in areas where human access was restricted. Where the *Fissurella* were experimentally removed from the habitat, there were dramatic increases in the algal cover of *Iridaea boryana,* its chief food source. This alga is also harvested in Chile. Human predation on *Fissurella* therefore helps to ensure a good harvest of the alga.

Fishermen in Chile know each species by a common, descriptive name (Bretos, personal communication). The names in use in northern Chile are mentioned in the species accounts.

SYSTEMATIC CHARACTERS

Useful shell characters include: size; outline in dorsal view; sculpture—the strength and spacing of the radial ribs; color pattern; interior shell margin—the thickness and pigmentation pattern; and foramen—the size, shape, and placement. Other shell characters such as the muscle scar and the internal callus show few significant differences and are therefore not treated unless they have unusual features. The organisms that encrust the surface of shells can provide important ecological information, but shells must be cleaned in order to see the sculpture and color pattern.

Juvenile shells are commonly very different from mature shells and are therefore separately described in this account.

Features of external anatomy such as color of the cephalic tentacles and development of mantle lobe papillae and tubercles on the foot are specific characters that may enable identification of species.

The morphology of the large outer lateral tooth of the radula provides a specific character.

The most useful specific characters are discussed in greater detail as follows.

Size and Shape

The anterior end of the shell is narrower than the posterior. The muscle scar opens anteriorly. All shells are illustrated here with the anterior at the top; the lateral view shows the left side.

The outline in most species is elongate-oval. *Fissurella costata, F. picta lata,* and *F. peruviana* are generally rounder than other species. *Fissurella latimarginata, F. cumingi,* and *F. pulchra* are wedge-shaped, having a relatively narrow front end and tapered sides.

Shells seldom lie flat in one plane. In most species, the sides are slightly elevated relative to the ends. This is particularly true of such highly motile species as *F. maxima,* and enables a better fit on rounded rock surfaces. Species that commonly nestle in crevices or have a habitual site of home attachment may instead have elevated ends for a better fit. Both extremes are possible in *F. nigra* and *F. oriens.* Some specimens of these species have both elevated sides and elevated ends, so that the shell rests on four corners.

Shell height is fairly constant in some species and variable in others. Species with relatively low shells (length 3.2 to 5.9 times height) include *F. crassa, F. bridgesii,* and *F. pulchra.* Those that vary from low to medium in height (length 2.8 to 4.5 times height) include *F. maxima, F. latimarginata, F. costata, F. radiosa,* and *F. oriens. Fissurella peruviana* varies from extremely low to high (length 1.5 to 4.8 times height).

In some species, the shell may be steeply conical in young stages and abruptly become more flattened at later stages. This commonly happens in *F. oriens, F. costata,* and *F. limbata.*

Fissurella nigra may grow by increasing the shell height while contracting the length and width, especially in gerontic specimens. This makes the slopes convex and the shell margin very thick. This growth form has not been observed in other species.

Sculpture

Shell sculpture is relatively consistent within most species. The radial ribs produced in the earliest growth stages are called the primary ribs and those arising between the primary ribs at later growth stages are called the secondary ribs. Secondary ribs attain the size and prominence of the primary ribs in *F. latimarginata, F. cumingi,* and *F. oriens.* Primary ribs are stronger than the secondary ribs at all growth stages in *F. picta, F. radiosa, F. costata, F. maxima,* and *F. peruviana. Fissurella crassa, F. pulchra,* and *F. bridgesii* generally have smooth shells in mature stages, although their young stages have rounded primary ribs, but no secondary ribs.

Color Pattern

Color patterns in all species have definite limits of variation, extensive in some, limited in others. Most species have a pattern of dark-colored rays on a lighter ground color. Least variable in color pattern are *F. maxima, F. limbata,* and *F. pulchra.* Such strongly rayed shells as those of *F. picta, F. radiosa, F. cumingi,* and *F. oriens* have ground colors ranging from light to dark gray or tan and correspondingly darker rays. White shells occur only in *F. oriens.* The most variable species, having both rayed forms and uniformly colored forms, are *F. peruviana, F. latimarginata, F. radiosa,* and *F. oriens.*

In addition to the radial rays, all species may have concentric growth bands of varying color intensity. Changes in the coloration of growth bands have been correlated with changes in diet in such herbivorous archaeogastropods as *Haliotis* (Olsen, 1968a, 1968b). Changes in supply of food or a shift in the algal composition of the diet can probably be correlated with changes in the banding of *Fissurella* shells. Concentric color changes are most pronounced in *F. picta, F. radiosa,* and *F. oriens,* the three species that range to the high southern latitudes where ecological conditions are most extreme. Bretos (1978, 1980) has shown that there are seasonal growth rings in *F. crassa.*

Shells exposed to weathering fade. The dark purple or gray rays change to red, particularly in *F. maxima* and *F. picta lata.*

Interior Margin

The interior margin or border, composed of the calcitic layer of the shell, generally has several bands or zones, visible also

in cut or broken pieces of the shell. Color differences in the margin are useful specific characters. The width of the margin changes with growth. In young, rapidly growing shells, it is relatively broad; in mature shells it is proportionately narrower, and in old shells it may be nearly obliterated by the encroachment and thickening of the inner aragonitic layer. It is consistently narrow in all growth stages of *F. radiosa* and *F. peruviana.* In most species the margin or growing edge is flat, but in *F. maxima* it is convex, and in *F. crassa* the entire edge is rounded.

In some species the margin of the shell is uniformly pigmented across its full width, in others the pigment is concentrated near the surface or deeper within the layer. Only in *F. nigra* is the outermost zone darker than the inner zone. In *F. latimarginata* and *F. pulchra* the outer edge is lighter and in *F. limbata* the outer edge is much lighter and contrasts sharply with the inner zone. Color rays are confined to the outermost layers of the margin in *F. limbata* and *F. maxima,* but extend the full width of the margin in *F. cumingi* and *F. oriens.*

Foramen

The relative size and the configuration of the foramen changes with growth. In young shells it is elongate, broad in the middle and constricted in two places on the sides. The foramen can be described as tripartite, and the side walls as bidentate if the three-lobed aspect is especially conspicuous. In most species the foramen changes from tripartite in young stages to oval in mature stages. In some species its size in mature specimens varies greatly; it may become very large in some old shells of *F. oriens.* In *F. peruviana,* the tripartite aspect of the foramen is lost at a very early stage, and the foramen becomes oval. *Fissurella costata* has a particularly small foramen at all growth stages. *Fissurella limbata* is unusual in retaining an elongate foramen in mature sizes. *Fissurella crassa* also retains an elongate foramen that is constricted in the middle, although the young shells are bidentate like those of other species.

In most species the position of the foramen is slightly posterior to the midpoint of the shell, but in *F. nigra* and *F. radiosa* it is more markedly so.

Juvenile Shell

The earliest juvenile shells of all species are more elevated and conical than later stages. Primary ribs appear at an early stage. In forms with a rayed pattern, the elevated ribs are light-colored and the interspaces are dark-rayed. Juveniles of many species have a pair of broad white rays extending laterally, more prominently than the other light-colored rays. This pattern is especially evident in the juveniles of *F. latimarginata,* in which the light rays persist until the shell is 10 or 20 mm in length. In *F. nigra, F. crassa, F. peruviana, F. cumingi,* and *F. maxima,* the two light rays are seen only in juveniles of less than 5 mm length. Some have characteristic early colorations unlike the adults. Young *F. nigra* are light-colored rather than black; *F. oriens, F. maxima,* and *F. peruviana* are reddish when young; *F. limbata* has a zigzag pattern of lines; *F. maxima* and *F. cumingi* have speckled patterns.

External Anatomy

The relative size of the animal in proportion to its shell is a useful comparison for at least those species at either extreme; the animals of most species are relatively large and just barely containable within the shell. The extremes are *Fissurella crassa* and *F. bridgesii,* which have flat shells that cannot contain the animal, and *Fissurella costata* and *F. peruviana,* which have high conical shells, the animal easily contained within the shell.

In most species, the cephalic tentacles are dark, reddish on the inner side and yellowish at the tips. *Fissurella nigra* is the only species that shows only shades of gray and black on the tentacles as well as on the mantle and foot.

The mantle lobe has three edges, here called the inner, the upper, and the lower. The inner lobe lacks papillae and is in direct contact with the growing margin of the shell. The upper lobe extends up over the edge of the shell, and the lower lobe extends down. The edges of the upper and lower lobes have finely branched papillae. The papillae of the upper lobe are generally more strongly developed than those of the lower edge. The area between, which is greatly expandable, is usually vertically banded to match the pattern of rays on the shell. This area may also show dark pigment in concentric grooves. The edge of the lower lobe of *F. latimarginata* is a striking orange color, the only species so marked, making it readily recognizable.

In all species the side of the foot is rugose or pustular. Coloration is mottled, the tips of the pustules or tubercles lighter in color. Overall coloration of the foot is brown or gray in most species; however, the foot of *F. cumingi* has a distinctive strawberry-red color and that of *F. costata* has a pale pinkish-brown color.

Epipodial tentacles extend along the foot sides. They are short and stubby but are slightly more prominent that the ordinary tubercles on the foot side. They are particularly prominent in *F. oriens.*

Radula

There are few specific differences in the rachidian and inner lateral teeth in *Fissurella,* although those of *F. pulchra* (Figs. 266, 267) are somewhat unusual in having longer overhanging cusps. The larger outer laterals, however, show interspecific differences, as will be noted in comparing the illustrations for the radula of *F. nimbosa* (Figs. 21, 25), *F. picta* (Figs. 138, 142, 143), *F. peruviana* (Figs. 43, 44), *F. oriens* (Figs. 193, 194), and *F. pulchra* (Figs. 266, 267).

NAMES, ALLOCATIONS, AND KEY CHARACTERS

Names and Allocations

Fifty-eight names have been proposed for Recent species of *Fissurella* from the Peruvian Faunal Province, which encompasses central Peru to central Chile, and the Magellanic Fau-

Table 1. Names proposed for Recent species of *Fissurella* from the Peruvian and Magellanic faunal provinces, with allocations as discussed in this paper.

affinis Sowerby, 1835 = *F. peruviana*
alba Philippi, 1845 = *F. oriens oriens*
arenicola Rochebrune and Mabille, 1885 = *F. oriens oriens*
atrata Reeve, 1850 = *F. picta picta*
australis Philippi, 1845 = *F. oriens oriens*
bella Reeve, 1849 = *F. latimarginata*
biradiata Sowerby, 1835 = *F. latimarginata*
bridgesii Reeve, 1849
clypeiformis Sowerby, 1825 = *F. crassa*
clypeus Sowerby, 1835 = *F. peruviana*
cheullina Ramirez-Boehme, 1974 = *F. oriens oriens*
chilensis Sowerby, 1835 = *F. costata*
concinna Philippi, 1845 = *F. maxima*
costata Lesson, 1831
crassa Lamarck, 1822
cumingi Reeve, 1849
darwinii Reeve, 1849 = *F. radiosa radiosa*
depressa Lamarck, 1822 = *F. crassa*
doellojuradoi Pérez-Farfante, 1952 = *F. oriens oriens*
dozei Rochebrune and Mabille, 1885 = *F. radiosa radiosa*
exquisita Reeve, 1850 = *F. radiosa radiosa*
flavida Philippi, 1857 = *F. oriens oriens*
fulvescens Sowerby, 1835 = *F. oriens fulvescens*
galericulum Reeve, 1850 = *F. latimarginata*
grandis Sowerby, 1835 = *F. nigra*
grisea Reeve, 1849 = *F. radiosa*
hedeia Rochebrune and Mabille, 1885 = *F. oriens oriens*
hondurasensis Reeve, 1849 = *F. maxima*
lata Sowerby, 1835 = *F. picta lata*
latimarginata Sowerby, 1835
limbata Sowerby, 1835
maxima Sowerby, 1835
mexicana Sowerby, 1835 = *F. oriens oriens*
multilineata, limbata var., Ziegenhorn and Thiem, 1925 = *F. limbata*
muricata Reeve, 1850 = *F. picta picta*
navidensis Ramirez-Boehme, 1974 = *F. picta lata*
nigra Lesson, 1831
nigra Philippi, 1845, not Lesson, 1831 = *F. radiosa radiosa*
oblonga Ramirez-Boehme, 1974 = *F. oriens oriens*
obovalis Lesson, 1831 = ?
occidens Gould, 1846 = *F. peruviana*
oriens Sowerby, 1835
papudana Ramirez-Boehme, 1974 = *F. peruviana*
peruviana Lamarck, 1822
philippiana Reeve, 1850 = *F. radiosa radiosa*
philippii Hupé, 1854 = *F. radiosa radiosa*
picta Gmelin, 1791
polygona Sowerby II, 1862 = *F. radiosa radiosa*
pulchra Sowerby, 1835
punctatissima Pilsbry, 1890 = *F. latimarginata*
radiosa Lesson, 1831
rubra, costata var., Ziegenhorn and Thiem, 1925 = *F. costata*
rudis Deshayes, 1830, not Roeding, 1798 = *F. costata*
solida Philippi, 1845 = *F. maxima*
stellata Reeve, 1850 = *F. cumingi*
subrotunda Deshayes, 1830 = *F. peruviana*
tixierae Métivier, 1969 = *F. radiosa tixierae*
violacea Rathke, 1833 = *F. nigra*

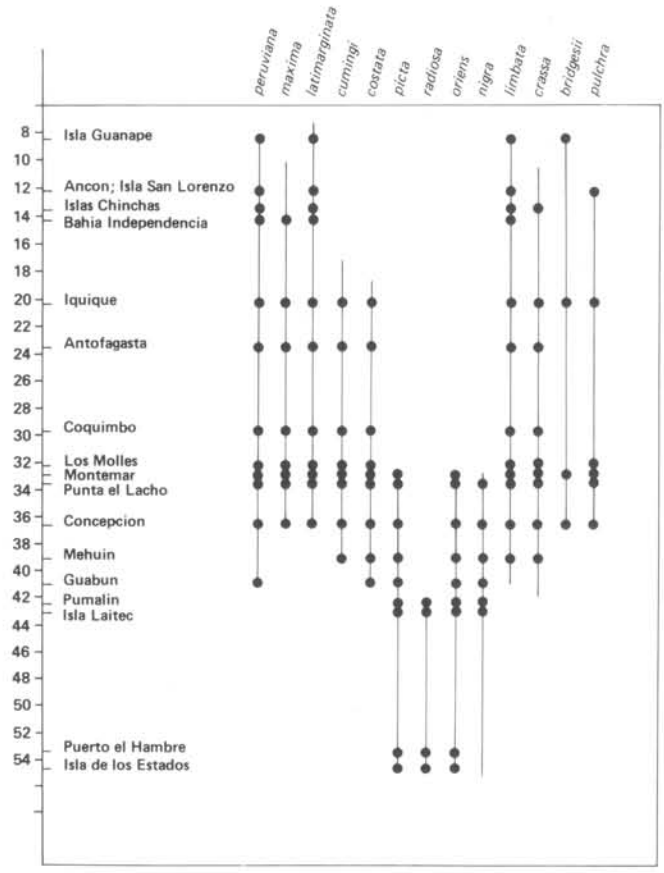


Figure 16. Distribution of *Fissurella* species in Peru, Chile, and southern Argentina by degrees south latitude. The identified place names are major LACM localities, some comprising several stations. The dots indicate that specimens are represented in the LACM collection. Lines without dots indicate distributions taken from other sources (see text).

nal Province, which includes southern Chile and southern Argentina. These names are listed alphabetically in Table 1, followed by my allocation. In the text that follows, I discuss the limits of variation for each species, but do not use variety or form names, even though some may be based upon readily recognizable variants. Geographic subspecies are discernible in three species of the Magellanic Faunal Province: *F. picta, F. radiosa,* and *F. oriens.* Trinomial designations are therefore used for these three species.

Difficulty in determining the taxa of such early authors as Lesson (1831) and Philippi (1845, 1857) has been due to a lack of illlustrations. I have not succeeded in locating the type specimens of these two authors. Nevertheless, using evidence from the original descriptions and type localities, I feel confident of the allocation of all names, except for *F. obovalis* Lesson, which is unassigned.

Chart of Key Characters

Attempts to prepare a dichotomuous key have not been successful because of the extreme variability of some of the

species. Instead, the key characters are summarized in Table 2.

DISTRIBUTION AND ZOOGEOGRAPHY

Distributions of the 13 species of the subgenus *Fissurella* known from Peru, Chile, and Argentina are shown by latitude in Figure 16.

Nine species occur in the warm-temperate Peruvian Province, which extends from central Peru to central Chile: *F. peruviana, F. maxima, F. latimarginata, F. cumingi, F. costata, F. limbata, F. crassa, F. bridgesii,* and *F. pulchra.* Their northern and southern distributional records differ, but all nine are present between Iquique and Concepción, Chile (20° S to 37° S).

Four species are primarily members of the cold-temperate Magellanic Province, which includes southern Chile and southern Argentina: *F. picta, F. radiosa, F. oriens,* and *F. nigra.* Their distributions also differ, but all are present between 43° S and 54° S.

Except for *F. radiosa,* three of the four Magellanic species extend north in Chile to overlap with the distributions of the Peruvian species. The region of overlap is that between Valparaíso and Concepción, from 33° S to 37° S, in which 12 of the 13 species occur. At some point to the south of Concepción, four of the Peruvian Province species (*F. maxima, F. latimarginata, F. pulchra,* and *F. bridgesii*) drop out. I did not find them at Mehuin, Valdivia Province (39° S). Stuardo (1964) noted a transition zone between the two provinces from 38° S to 43° S. The transition zone noted here is therefore considerably to the north of that reported by Stuardo.

The number of *Fissurella* species occurring between Valparaíso and Concepción is significantly greater than the number known either to the north or the south. Distributions of species in other families should be considered to determine whether this transition area has a higher number of species than either of the two provinces treated separately.

The northernmost occurrence of the Peruvian Province species of *Fissurella* is at Isla Guanape, Peru (8°33′ S), where I have found *F. latimarginata, F. limbata, F. bridgesii,* and *F. peruviana.* I found none in January, 1974, in the transitional region between the Peruvian Faunal Province and the tropical Panamic Faunal Province at the Lobos Afueras Islands in northern Peru.

None of the species is known from the offshore islands of central Chile, Isla San Felix or Islas Juan Fernandez, either from literature records or recent expedition material from ANTON BRUUN cruises. A number of common Chilean mollusks are known from these islands. The absence of *Fissurella* correlates with the brief planktonic larval stage and resulting poor colonizing potential of fissurellids and other archaeogastropod larvae.

Fissurella picta, F. radiosa, and *F. oriens* are abundant at the southern limits of their distributions, where they undoubtedly extend to Cape Horn. These three species also occur at the Falkland Islands, which region is included in the Magellanic Faunal Province. They do not, however, occur at South Georgia or any of the subantarctic islands east of the Falklands (Powell, 1951). Strebel (1908:79) reported *F. exquisita* [here = *F. radiosa*] at Paulet Island, Antarctic Peninsula, a record that should not be accepted without further confirmation.

The Magellanic Faunal Province extends north through the Patagonian region of Argentina to the Gulf of San Matias, but only one of the Magellanic species, *F. radiosa,* occurs to the north of Tierra del Fuego in Argentina. It has a subspecies, *F. radiosa tixierae,* in its northernmost extent in Argentina. Absence of the other three species in Chubut and Santa Cruz Provinces of Argentina may be due to the vastly different ecological conditions. In Argentina, the tidal range is extreme, broad tidal flats are exposed, and inshore sediments often consist of fine beach sand. In southern Chile, the tidal range is less extensive, inshore waters are deep and clear, and beaches are few.

FOSSIL RECORD

There is little information in the literature about the fossil record of *Fissurella* in Peru and Chile. Ihering (1907) particularly noted the abundance of *Fissurella* in the Recent and the complete lack of the genus in the lower Tertiary of Chile and Patagonia.

In the most recent report on the mollusks of the Pliocene and Pleistocene formations of Chile (Herm, 1969), none of the *Fissurella* species was given formal systematic treatment. Herm listed five characteristic Pleistocene species: *F. microtrema* Sowerby, 1833 [undoubtedly *F. peruviana,* rather than the tropical *F. microtrema*], *F. costata, F. crassa, F. lata* [*F. picta lata* here], and *F. concinna* [*F. maxima* here]. In his list of Pliocene species he noted only: "*Fissurella,* div. sp."

One species has been described from fossil material: *F. concolor* Philippi, 1887, from Pliocene beds of Mejillones, north of Antofagasta, Chile. I have received specimens identified as this species from E. Martinez, collected from two of the Pliocene localities near Antofagasta detailed by Herm: the Cerro Costino locality south of Antofagasta, and the Hornito locality north of Antofagasta. Specimens (Fig. 17) agree with Philippi's description in having three smaller ribs between each of the larger ribs. The overall shape and profile is similar to that of *F. maxima,* but the primary ribs are stronger than those of *F. maxima.* The interior aragonitic layer is missing entirely from the specimens, in agreement with the principle that calcitic structures are best preserved in fossils.

A fragmentary specimen of another species from the Cerro Costino locality has also been received from E. Martinez. This species (Fig. 18) has some affinity to *F. crassa.* In the absence of additional specimens, I am unable to further treat the fossil record of the group.

Fissurella, sensu stricto, is one of the youngest genera in the Fissurellidae, traced only to the Pliocene (Herm, 1969). Except for the Caribbean type species, it is an eastern Pacific genus, well represented in the Peruvian and Magellanic faunal provinces, and with a single species ranging from California to Baja California, Mexico (Fig. 19). The type species may have become established in the Caribbean during the

Table 2. Chart of key characters.

	Size	Height	Mature sculpture	Outline of base
F. peruviana	small 25–40 mm	low to high	medium ribs, strong primaries	oval to elongate
F. maxima	large 80–135 mm	medium	strong ribs, strong primaries	elongate oval
F. latimarginata	large 70–115 mm	low to medium	fine ribs	tapered oval
F. cumingi	large 80–100 mm	medium	medium ribs	tapered oval
F. costata	medium 50–80 mm	low to medium	strong ribs, strong primaries	oval
F. picta picta	large 65–95 mm	medium	strong ribs, strong primaries	elongate oval
F. picta lata	medium 50–80 mm	medium to high	strong ribs, strong primaries	oval
F. rad. radiosa	small 40–55 mm	low to medium	medium ribs, strong primaries	tapered elongate
F. rad. tixierae	small 25–45 mm	medium	medium ribs, strong primaries	tapered elongate
F. oriens oriens	medium 40–70 mm	low to medium	fine, broad ribs	elongate oval
F. o. fulvescens	medium 45 mm	low	fine, broad ribs	elongate oval
F. nigra	large 70–110 mm	medium	fine, weak ribs	elongate oval
F. limbata	large 60–90 mm	medium	undulations	elongate oval
F. crassa	medium 60–90 mm	low	undulations	elongate oval
F. bridgesii	large 65–90 mm	low	irregular striae	tapered oval
F. pulchra	medium 35–75 mm	low	undulations	tapered oval

period in which the Central American seaway provided free access between the western Atlantic and eastern Pacific during the Miocene and early Pliocene (see Woodring, 1965, 1966).

FORMAT FOR SPECIES ACCOUNTS

Description. Shell descriptions treat the following characters in order: the size range (length in mm) of examples considered to be mature, the relative height, the outline in dorsal view, whether the sides or ends are raised, strength of the radial ribs, the color pattern, the shell layers, the interior margin, and the position and shape of the foramen. Dimensions for shell length, width, and height are given in that order in the captions for the figured specimens, not duplicated in the text. For specimens with uneven basal margins, shell height is the maximum elevation when the shell rests upon a plane surface.

Juvenile Shell. A separate description.

Mantle and Foot. Anatomical characters include the relative size of the body and shell, the relative prominence of papillae on the upper and lower edges of the mantle lobe, coloration of the cephalic tentacles, the color of the foot-side and the relative prominence of the foot-side tubercles.

Habitat. The intertidal or subtidal occurrence, conditions of exposure, and the epibiotic associations.

Distribution. The northernmost and southernmost verified record, the latitude coordinates for these records, and the source of the record. The source is the museum catalog number if the specimen has been examined, or an author and date, if the record is based on a published account considered to be correctly identified. This is followed by commentary about its possible occurrence beyond the verified limits and corrections of previous records now considered to be inaccurate.

Table 2. Continued.

Shell color	Shell margin	Mature foramen	Foot side color
red, gray, white rayed or solid	narrow showing rays	oval	gray-brown mottled
reddish brown rays on white	broad, rays on outer edge	oval	dark brown mottled
solid purple gray	broad, solid reddish brown	elongate oval	black with yellow outer edge of mantle
reddish rays on dark yellow	broad, rays show on full width	elongate oval	reddish brown mottled
gray rays on yellow	broad, rays show on full width	elongate oval, small	pinkish gray mottled
split gray rays on light ground	broad, rays strong on outer edge	elongate	light brown-black mottled
split gray rays on light ground	broad, rays strong on outer edge	elongate	brown-black mottled
gray or reddish rays on white	narrow, showing rays	elongate	gray-brown mottled
gray or reddish rays on white	narrow, showing rays	elongate	gray-brown mottled
red to gray rays on light ground	medium width, showing rays	elongate oval	pinkish brown mottled
reddish rays on dark yellow gr.	medium width, showing rays	elongate oval	not seen
solid gray, rays faint	broad, gray, dark at edge	elongate oval beveled	gray mottled
purple rays on dark yellow	broad, purple, white at edge	elongate	light gray mottled
solid brown, faint rays	brown upturned	very long, constricted	mantle brown banded foot gray mottled
gray brown, rays faint	broad, solid reddish brown	elongate oval	brown-black mottled
rays and speckles on pinkish brown	broad, reddish brown	elongate	light pinkish mottled

Number of Lots Examined. The total number of lots and the number in each of the following museum collections: LACM, AMNH, ANSP, MACN, MNHN, and USNM. These counts also provide an indication of the relative abundance of each species.

Taxonomic History. Indicates whether authors have understood the species with the limits now recognized, or if the present treatment is a departure from past classifications.

Abundance and Use. The fishery use and potential of each species, and the common name, as provided by M. Bretos.

Characteristics and Variability. The first statement under this heading is a brief description meant to convey the most characteristic features of the species, followed by an assessment of the variability, and whether variation may be correlated with geographic distribution.

Affinity and Comparisons. As assessment of the affinity to the most closely related species and the chief means of distinguishing the species from similar forms. Remarks about affinity are inferences. Future work may support or contradict these suggestions.

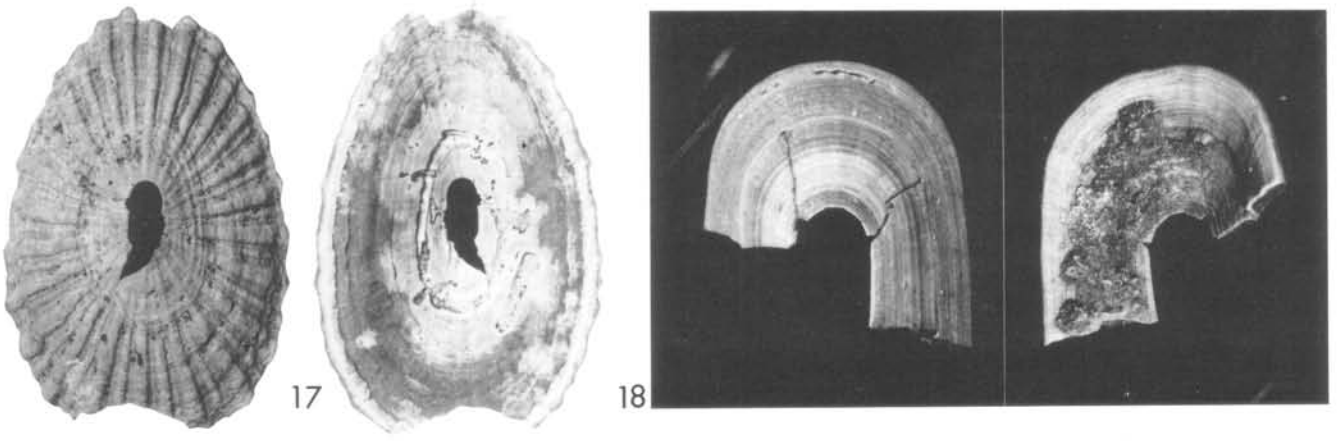
Synonymy and Types. Reasons for the assignment of each taxon; the type locality, measurements, and repository of type specimens. Lectotypes are designated for lots consisting of more than one original specimen.

SYSTEMATICS

Family Fissurellidae Fleming, 1822

I recognize two subfamilies in the Fissurellidae: the Emarginulinae, which I further subdivide into tribes (McLean, 1984b, and other work in progress), and the Fissurellinae.

The Fissurellinae are the youngest members of the family,



Figures 17 and 18. Fossil specimens of *Fissurella* spp. of Pliocene age, Cerro Costino, 12 km S of Antofagasta, Chile (23°45′ S, 70°26′ W), collected by E. Martinez. Specimens have lost the interior aragonitic layer. (**17**) *F. concolor* Philippi, 1887. LACM 90797, 60.6 × 40.8 × 9.5 mm. (**18**) *Fissurella* sp., cf. *F. crassa,* LACM 90798, 25.2 × 24.4 × 8.6 mm (specimen incomplete).

appearing in the Cenozoic; the Emarginulinae arose in the Mesozoic, with a burst of radiation in the Jurassic.

Subfamily Fissurellinae Fleming, 1822

DIAGNOSIS. Apex of mature shell wholly absorbed by the foramen; foramen bordered inside by a ring of callus that is not truncated or excavated posteriorly. Selenizone not present in juvenile stage. Shell muscle and muscle scar lacking inturned hooked processes. Rachidian tooth of radula narrow at the tip, its base broad, no larger than the adjacent laterals; the massive fifth lateral usually with four cusps; marginals numerous.

The subfamily Fissurellinae differs from the subfamily Emarginulinae in radular characters and in the morphology of the shell muscle. In the Emarginulinae the rachidian tooth is rhomboidal in shape (whether broad or narrow) and the enlarged fifth lateral has only two prominent cusps; in the Fissurellinae the rachidian tooth is narrow at the tip and the enlarged fifth lateral has four cusps (except three in *Amblychilepas,* one very small). Also, the muscle scar and corresponding shell muscle of the fissurelline genera lack the hook-shaped process of such emarginuline genera as *Puncturella* and *Diodora.* Early stages of emarginuline genera have a selenizone that may be lost in mature stages, but the selenizone is not present at any stage in the Fissurellinae.

Other genera in the subfamily Fissurellinae are *Amblychilepas* Pilsbry, 1890, and *Macrochisma* Sowerby, 1839, both of which are limited to the Indo-Pacific, and have animals too large to be contained in the shell.

Genus *Fissurella* Bruguière, 1789

DIAGNOSIS. Shell conical, sculpture chiefly radial; foramen nearly central.

Two subgenera of *Fissurella* are here recognized: *Fissurella, sensu stricto,* with a two-layered shell, the outer layer composed of calcite, the inner layer of aragonite, and *Cremides* H. and A. Adams, 1854, in which the shell is composed entirely of aragonite (Fig. 30). This is the first time that the subgenera have been so defined. As discussed above, it has not previously been noted that the shell margin is indicative of a two-layered shell rather than merely a color difference.

Recent authors (e.g., Keen, *in* Knight et al., 1960) have

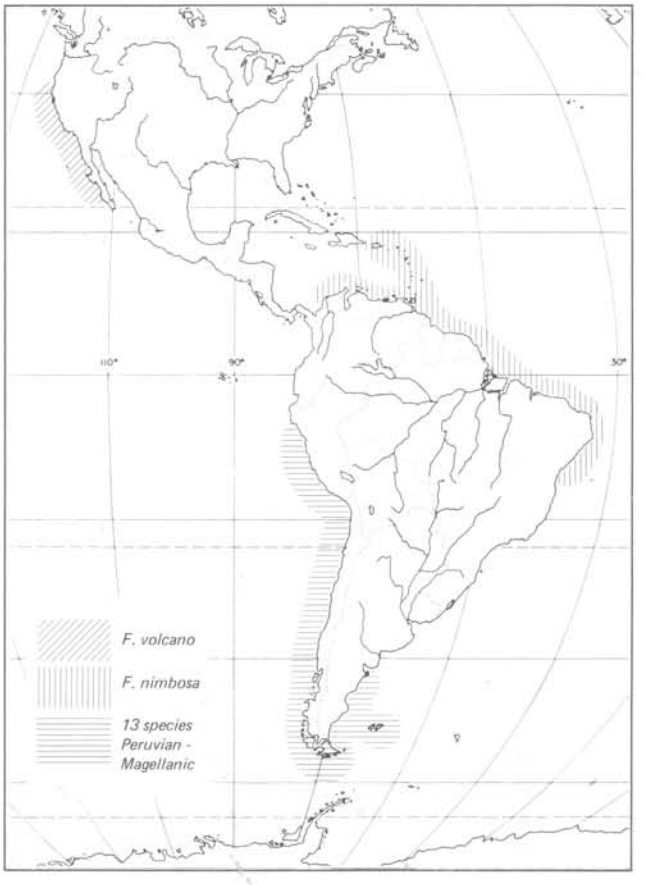


Figure 19. Distribution of *Fissurella, sensu stricto,* in North and South America.

regarded *Fissurella, sensu stricto,* as monotypic, and have placed the tropical species lacking the shell margin in *Cremides* and the South American species having the shell margin in *Balboaina* Pérez-Farfante, 1943. In the present treatment, the scope of the subgenus *Cremides* remains unchanged, but *Balboaina* is synonymized with *Fissurella, sensu stricto.*

Cremides has a fossil record from the Oligocene (Keen, *in* Knight et al., 1960), whereas *Fissurella, sensu stricto,* dates from the Pliocene.

Subgenus *Fissurella* Bruguière, 1789

Fissurella Bruguière, 1789:xiv (genus without named species). Type species, by subsequent monotypy of Lamarck, 1799: *Patella nimbosa* Linnaeus, 1758.

Balboaina Pérez-Farfante, 1943:2. Type species, by original designation, *Fissurella picta* (Gmelin, 1791).

Carcellesia Pérez-Farfante, 1952:31. Type species, by original designation, *Fissurella* (*Carcellesia*) *doellojuradoi* Pérez-Farfante, 1952 [= *F. oriens* Sowerby, 1835].

Corrina Christiaens, 1973:93. Type species, by original designation, *Fissurella* (*Corrina*) *alba* Philippi, 1845 [= *F. oriens* Sowerby, 1835].

DIAGNOSIS. Shell moderately large, composed of pigmented, outer calcitic layer that forms broad margin on inner side; interior aragonitic layer relatively thin except in apical area, extending to shell margin only in some fully mature specimens. Mantle papillae well developed; foot side tubercles well developed, epipodial tentacles short and stubby.

The species of *Fissurella, sensu stricto,* total 15: the 13 species of Peru and Chile treated in detail here, plus the Caribbean type species *F. nimbosa* (Figs. 20–25) and the Californian *F. volcano* Reeve, 1849 (Figs. 26–29). The distribution of *Fissurella, sensu stricto,* is shown in Figure 19.

Generic Synonymy. Bruguière's introduction of the name without reference to species has caused some confusion over the type designation. Although many authors have followed Pilsbry (1890) in the usage of *F. picta* as the type species, more recent authors have followed Wenz (1938) in citing *F. nimbosa,* by subsequent monotypy of Lamarck (1799).

Fissurella nimbosa (Figs. 20–25) is unlike all other tropical species of the genus. Pilsbry (1890) described the interior of *F. nimbosa* as having a "black line around the edge." He also observed that the species "has more the aspect of the Chilean species than that of the West Indian," a comment overlooked by subsequent authors. *Fissurella nimbosa* is the only species with the two-layered shell that has a tropical distribution. It differs from all the Peruvian and Magellanic species in having a green suffusion to the interior, a character shared with the Californian *F. volcano* (Figs. 26–29).

Pérez-Farfante (1943) did not notice that young shells of *F. nimbosa* have a well-defined dark margin. The shell she figured (1943, pl. 1, figs. 1, 2) is mature, with the aragonitic layer obliterating the dark border. She considered *Fissurella* to be a monotypic subgenus consisting only of *F. nimbosa* for reasons not clearly stated, but presumably because *F. nimbosa* is larger and more conical than most of the tropical species. She therefore missed the affinity of *F. nimbosa* with the Peruvian and Chilean species and proposed the subgenus *Balboaina* for those species with the dark border.

In my opinion, *F. nimbosa* is sufficiently similar to other species having the two-layered shell that it can not be separated from them on a subgeneric level. It is premature to offer a final opinion about the subgeneric division of the group, and I am, therefore, following a conservative course in uniting those with the calcitic layer. Further evidence about the affinity of the species with the calcitic outer layer needs to be offered from other lines of investigation, for example, electrophoresis. Until convincing arguments can be advanced to separate the Chilean species from *F. nimbosa* and *F. volcano,* I am treating *Balboaina* as a synonym of *Fissurella, sensu stricto.*

Pérez-Farfante's original diagnosis of *Balboaina* included the following provisions: "Margin of the shell entirely in one plane, simple, not crenulated . . . ." Neither of these traits is true for the majority of the southern species. Those species having radial ribbing are in fact finely crenulate at the margin, and most are raised at the sides.

Two other subgeneric names have been proposed: *Carcellesia* Pérez-Farfante, 1952, and *Corrina* Christiaens, 1973. Both names are based on type species that are here regarded as synonyms of *F. oriens. Carcellesia,* type species *F. doellojuradoi* Pérez-Farfante, 1952, was based upon a single aberrant example of *F. oriens* with prominently raised ends. *Corrina,* type species *F. alba* Philippi, 1845, was intended to apply to thin-shelled forms lacking sculpture. I consider *F. alba* a synonym of *F. oriens,* based upon the scarce white-shelled form of the species. Christiaens also included in *Corrina* the South African species *F. mutabilis* Sowerby, 1835, but that species has no dark margin and is therefore unrelated. *Fissurella oriens* is a readily recognizable species in which the sculpture is weak, but I find no reason to single it out as representing a subgenus. Consequently, both names are relegated to the synonymy of *Fissurella, sensu stricto.*

Species Groups. Pilsbry (1890) placed the species having a "distinct dark marginal border inside" in four groups of species based on shell characters. I recognize a somewhat similar scheme of three groups within the subgenus *Fissurella, sensu stricto,* based on the presence or absence of complex radial sculpture and the relative thickness of the calcitic and aragonitic shell layers. Affinity among the species within each group is inferred, but this should be tested by future workers.

1. Aragonitic layer as thick as calcitic layer . . . . . Group of *F. peruviana*
   Aragonitic layer markedly thinner than calcitic layer 2
2. Sculpture of primary and secondary ribs . . . . . Group of *F. maxima*
   Sculpture of broad primary ribs only . . . . . Group of *F. limbata*

Group of *Fissurella peruviana*

Relatively small-shelled species in which the thickness of the aragonitic layer equals or approximates that of the external

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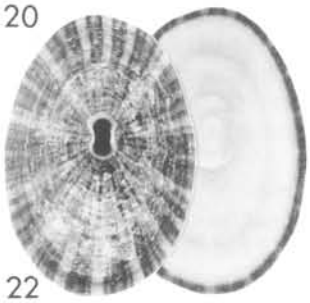

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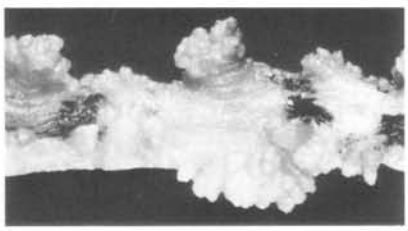

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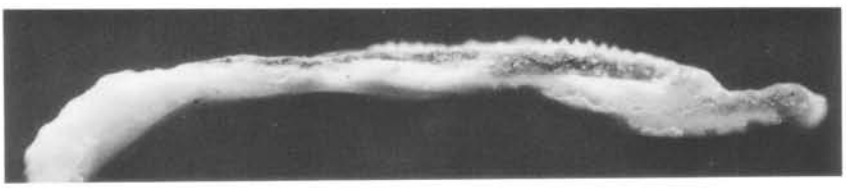

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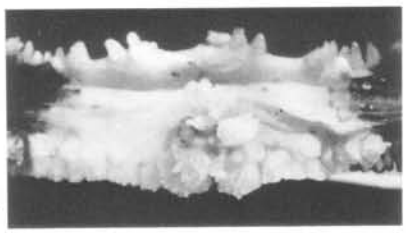

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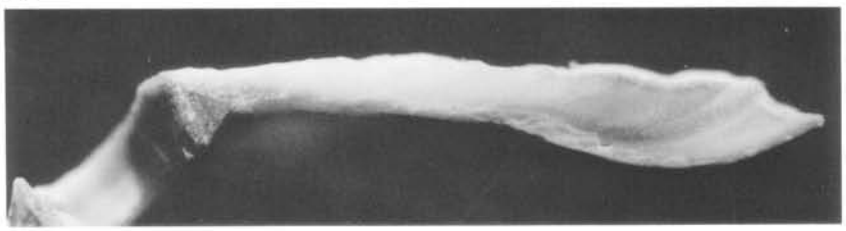

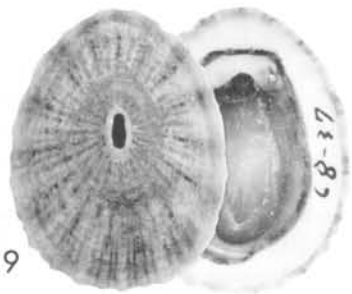

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Figures 20 through 30. Shells, radulae, mantle lobes, and cut shells of *Fissurella nimbosa* (Linnaeus, 1758), *F. volcano* Reeve, 1849, and *F.* (*Cremides*) *virescens* Sowerby, 1835. **Figures 20 through 25.** *F. nimbosa.* (**20**) Cut shell, showing thin, dark calcitic layer. LACM 76-30, Puerte La Cruz, Venezuela, length of cut edge 20.5 mm. (**21**) Radular ribbon. Same locality, width of ribbon, 1.4 mm. (**22**) Shell, Frigate Bay, St. Christopher, U.S. Virgin Islands. LACM 76-25, 27.0 × 24.9 × 8.1 mm. (**23**) Shell, Cabo Blanco, Isla Margarita, Venezuela, showing partial loss of the external calcitic layer and wear obliterating the dark margin in beach-worn shell. LACM 76-28, 37.9 × 26.2 × 14.0 mm. (**24**) Mantle edge, Frigate Bay, St. Christopher, U.S. Virgin Islands. LACM 76-25, length 3.5 mm. (**25**) SEM view of radula. LACM 76-30, Puerte La Cruz, Venezuela, width of field 0.8 mm. **Figures 26 through 29.** *Fissurella volcano.* (**26**) Cut shell, showing thin calcitic layer. LACM 66-1, Santo Tomas, Baja California, Mexico, length of cut edge 20 mm. (**27**) Mantle edge. AHF 1595-47, Río Santo Tomas, Baja California,

calcitic layer; the shell margin (calcitic layer) narrow at all growth stages and in mature specimens often obliterated by encroachment of the aragonitic layer. Radial sculpture of primary and secondary ribs, which remain pronounced at all growth stages.

This group differs from both the group of *F. maxima* and the group of *F. limbata* in its relatively smaller size and in having a thicker aragonitic layer and a relatively thin and narrow calcitic layer.

In addition to *F. peruviana,* this group includes the type species of *Fissurella, F. nimbosa* (Linnaeus, 1757), of the tropical Caribbean faunal province (Figs. 20–25), and *F. volcano* Reeve, 1849, of the warm temperate Californian Faunal Province (Figs. 26–29). None of the species extends into the cold temperate Magellanic Faunal Province.

Although *F. radiosa* has an unusually narrow margin, as do the members of this group, it does not have a sufficiently thick aragonitic layer to suggest that it is related to these species.

In having a relatively thick aragonitic layer, this group of species represents the connecting link between the tropical species lacking the calcitic layer (subgenus *Cremides*), and the South American species with thick calcitic layers (subgenus *Fissurella, sensu stricto*).

Fissurella peruviana Lamarck, 1822

Figures 31–50

Fissurella peruviana Lamarck, 1822, 6(2):15; Orbigny, 1841: 74; Delessert, 1841, pl. 24, fig. 7; Reeve, 1849, pl. 5, figs. 26a–d; Hupé, 1854:241; Philippi, 1860:181; Sowerby II, 1862:185, figs. 38–41; Pilsbry, 1890:155, pl. 33, figs. 41–45, pl. 42, figs. 57–59; Dall, 1909:178, 242; Mermod, 1950: 713, fig. 22; Riveros-Zuñiga, 1951:130, fig. 35; Peña, 1970: 156; Dell, 1971:190; Christiaens, 1973:86; Ramirez-Boehme, 1974:31 [key].

Fissurella subrotunda Deshayes, 1830:135; Deshayes *in* Lamarck, 1836, 7:602; Orbigny, 1841:74 [under *F. peruviana*]; Reeve, 1849, pl. 5 [under *F. peruviana*].

Fissurella affinis "Gray," Sowerby, 1835a:125; Sowerby, 1835b:4, fig. 44; Sowerby II, 1862:185, figs. 46, 179; Christiaens, 1973:83.

Fissurella clypeus Sowerby, 1835a:128; Sowerby, 1835b:4, fig. 44; Reeve, 1850, fig. 76; Sowerby II, 1862:185, fig. 63; Pilsbry, 1890:156, pl. 60, fig. 82, pl. 31, fig. 20; McLean *in* Keen, 1971:901; Christiaens, 1973:83 [under *F. asperella*].

Fissurella occidens Gould, 1846:156; Gould, 1852:364, pl. 31, figs. 473a, b; Pilsbry, 1890:155 [under *F. peruviana*]; Johnson, 1964:118 [holotype, USNM 5863].

Fissurella papudana Ramirez-Boehme, 1974:18, 31 [key], pl. 2, figs. 5a, b, c.

Shell. Relatively small (25–40 mm mature length); variable in height from low to high conical; variable in outline from broadly oval to elongate and uneven; plane of margin also varying and probably conforming to an attachment site. Sculpture of fine, often imbricate, radial ribs, primary ribs remaining strong. Color highly variable, including some that are solid dark red to reddish gray, some that are faintly rayed, and some with rays of brown and white; lateral rays of elongate specimens often curving forward. Margin relatively narrow at all growth stages, reflecting pattern of rays through full thickness of calcitic layer. Cut shells show aragonitic layer slightly thicker than calcitic layer. Foramen elongate and tripartite in earliest stages but quickly becoming oval in juvenile shells and broadly oval in mature shells.

Juvenile Shell. Strongly sculptured, conical; frequently reddish with two lateral white rays. Mature specimens with brown and white rays have a red ring in the calcitic layer surrounding the foramen, a remnant of the juvenile red phase.

Mantle and Foot. Fully retractable in the shell. Mantle banded to match the rays of the shell. Mantle lobe relatively narrow, upper and lower edges with branched papillae. Foot side brown to black, with numerous, projecting, light-tipped tubercles.

Habitat. Lower intertidal zone to 20 m, but most abundant in the sublittoral zone. Scattered individuals occurring at low tide, nestled in crevices on the sides of rocks, the shell outline moulded to fit the site of attachment. Occurring at greater depths than any other of the species in northern Chile. At Mejillones (23°02′ S) it was the only species that I saw at 10–20 m on a sloping rocky bottom dominated by the mussel *Aulacomya ater.*

Distribution. Chiclayo, Peru (6°47′ S) (LACM, collector unknown; also reported at Chiclayo by Peña, 1970), to Guabun, northwestern tip of Isla de Chiloe, Chile (41°50′ S) (LACM 75-40, McLean). I have found specimens at most localities between Isla Guanape, Peru (8°32′ S), and Río Biobio, Concepción Province, Chile (36°48′ S), but did not find it at Mehuin, Valdivia Province.

Number of Lots Examined. 118 (LACM 52, AMNH 11, ANSP 11, MACN 3, MNHN 17, USNM 24).

Taxonomic History. *Fissurella peruviana* has been reasonably well understood by authors, at least with reference to its occurrence in Peru. Its presence in Chile has not been adequately discussed; Riveros-Zuñiga (1951) merely listed previous authors who cited records from Chile. A low form of this species with irregular outline is common in Chile (Figs. 36, 37, 39–42) and was illustrated by Riveros-Zuñiga (1951), misidentified as *F. stellata* Reeve, 1850. This form was twice named by Sowerby in 1835 and again by Ramirez-Boehme in 1974. Christiaens (1973) considered *F. affinis* Sowerby to be a good species, but there is little justification for such a

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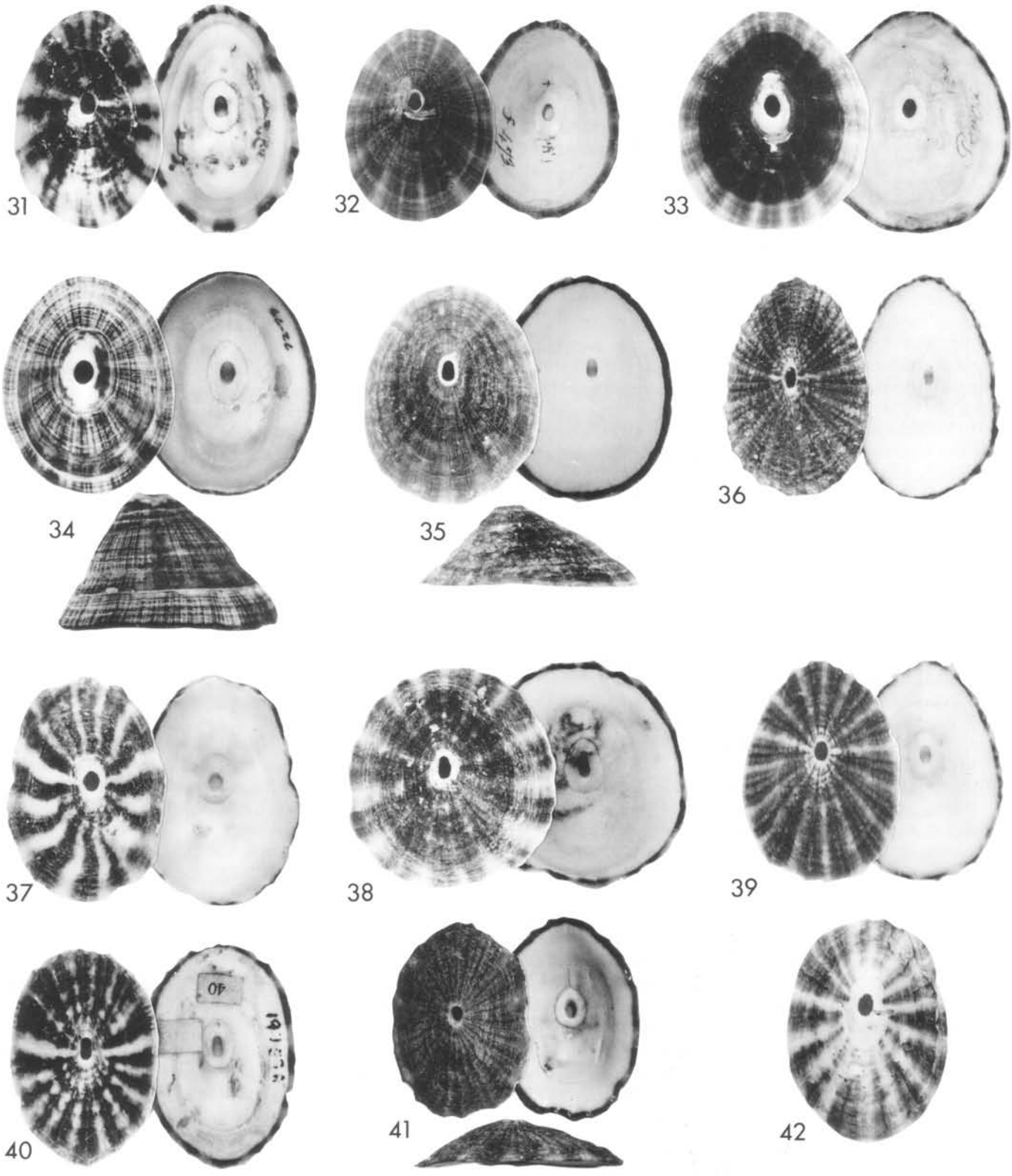
Mexico, length 5 mm. (**28**) Shell, White's Point, Los Angeles County, California. LACM 69-37, 28.7 × 20.0 × 11.7 mm. (**29**) Shell, same locality, 27.2 × 21.0 × 8.3 mm. (**30**) *Fissurella* (*Cremides*) *virescens,* cut shell, calcitic layer lacking, La Cruz de Juanacaxtl, Nayarit, Mexico. LACM 71-33, length of cut edge 23.7 mm.



Figures 31 through 42. *Fissurella peruviana* Lamarck, 1822. Mature shells. **(31)** 3–5 m, Isla Guanape, Peru. LACM 74-3, 45.1 × 23.5 × 12.8 mm. **(32)** Holotype, *F. occidens* Gould. Callao, Peru. USNM 5863, 35 × 27 × 19 mm. **(33)** Lectotype, *F. subrotunda* Deshayes. "Peru." MNHNP, 31.3 × 27.4 × 16.8 mm. **(34)** Paracas, Ica Province, Peru. LACM 72-79, 31.5 × 24.0 × 17.8 (beach shell). **(35)** Laguna Grande, Ica Province, Peru. LACM 72-77, 31.2 × 25.9 × 11.5 mm (beach shell). **(36)** Iquique, Chile. LACM 64-16, 24.0 × 16.7 × 7.6 mm. **(37)**

view, as discussed below. The broad distribution and the extent of intraspecific variation in *F. peruviana* have not previously been understood.

Abundance and Use. Because of its chiefly sublittoral habitat, *F. peruviana* seems to be uncommon, although beach-worn shells are common throughout the range. This is the smallest species of *Fissurella* in Peru and Chile and therefore has little importance as a food resource. According to M. Bretos, the species has no common name in northern Chile, perhaps because it is considered the juvenile form of such species as *F. maxima.*

Characteristics and Variability. *Fissurella peruviana* is characterized by its small size, imbricate radial ribs, oval foramen, narrow margin, and relatively thick aragonitic layer. In lateral profile it varies from low to extremely conical; in outline it varies from broadly oval to elongate and irregular. Its color varies from uniformly dark reddish to gray or rayed with brown and white. It is the most variable species of *Fissurella* in the Peruvian Faunal Province.

Specimens from Peru tend to be more conical and more uniformly colored, whereas those from central Chile tend to be flatter and are more likely to be rayed with brown and white. However, I am not convinced that a geographic distinction can be drawn. I have noticed that the more conical forms occur on rocks adjacent to sandy bottoms, whereas the flattened forms with irregular outlines are found on rocky bottoms away from sand. At Iquique and Antofagasta the flattened irregular forms occur, but I have found some highly conical forms associated with the scallop beds north of Antofagasta at Bahia Morena. Conical specimens have also been seen from the Concepción vicinity. The recognition of geographic subspecies is therefore not justified.

Affinity and Comparisons. *Fissurella peruviana* differs from all other Peruvian and Magellanic species in having a relatively thick aragonitic layer and in having the oval foramen well developed at an early stage. Yet these differences do not seem sufficient to regard it as unrelated to those species with well-defined primary and secondary ribs in the group of *Fissurella maxima.* Of those species, it has the most in common with *F. costata,* with which it shares overall shape and the small, oval foramen. It more closely resembles *F. volcano* from California, which is also relatively small, with a narrow margin and proportionately thick aragonitic layer. *Fissurella peruviana* differs from *F. volcano* in having a more oval foramen and in lacking the green tinge of the interior and pink-bordered callus of *F. volcano. F. volcano* is an intertidally occurring species and *F. peruviana* is characteristically sublittoral.

When compared to young specimens of other Peruvian and Chilean species, *F. peruviana* can be distinguished by its narrow margin and oval foramen. Small specimens may be distinguished from the juveniles of *F. maxima* in having the foramen more oval and the margin not rounded. The primary ribs are not as strongly developed as those in young stages of *F. costata, F. picta lata,* or *F. radiosa.*

Synonymy and Types. *Fissurella peruviana* Lamarck, 1822, is one of the three earliest-named species of the region. Lamarck's specimens were from the "coasts of Peru," and some of the specimens were said by Lamarck to be less conical than others. Unfortunately, the first illustration of Lamarck's species (Delessert, 1841) may be a specimen of some other species, as suggested by Pilsbry (1890), Mermod (1950), and Christiaens (1973). Mermod (1950) discussed two Lamarckian specimens in the Geneva Museum collection considered to be original. "Specimen no. 2" discussed by Mermod fits the present concept of *F. peruviana* and is inscribed by the hand of Lamarck, according to Mermod. I am not able to determine the identity of "specimen no. 1," which is apparently the specimen figured by Delessert. Inasmuch as Lamarck indicated that there were several specimens, I hereby designate "specimen no. 2" as the lectotype, which is in accord with the original intent of the author. The lectotype (see Mermod, 1950, fig. 22-2) represents the high conical form of *F. peruviana* with a nearly circular foramen; length 20, width 25, height 16 mm.

I have examined 8 syntypes and the original mounting board of *F. subrotunda* Deshayes, 1830, received on loan from the Paris Museum. Lengths are 35.6, 31.3, 30.3, 30.0, 25.7, 22.7, and 20.7 mm. The original measurements were 32 mm in length and 28 mm in width; the second largest specimen is here designated the lectotype (Fig. 33); it is 31.3 mm in length and 27.4 mm in width and is probably the measured specimen. Type material, from "Perou," apparently has not previously been illustrated. All specimens are dark reddish rayed, moderately conical, and with an oval basal outline. No comparisons were originally made with *F. peruviana;* Orbigny (1841) relegated the name to the synonymy of *F. peruviana.*

Type material of *F. affinis* Sowerby, 1835, has not been located. Reeve (1849) regarded it as an elongate, flattened form of *F. peruviana.* Sowerby II (1862) doubtfully recognized it as a species "in order to avoid the extreme inconvenience of including opposite characters under the same name . . . ." Christiaens (1973) maintained it as a species, but in my opinion the original figure in the "Conchological Illustrations" represents the extreme flattened form of *F. peruviana,* which occurs throughout the range of the species in Chile. Several localities were mentioned originally: "Insulas Mexillones et Lobos, Iquiqui, and Valparaíso."

The holotype of F. *clypeus* Sowerby, 1835 (Fig. 40), was said to have come from "Sanctam Elenam," presumably the Santa Elena Peninsula, Ecuador. This name has baffled sub-

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Iquique, Chile. LACM 75-12, 23.6 × 16.4 × 7.4 mm (beach shell). (**38**) 2–4 m, El Rincon de Mejillones, Antofagasta Province, Chile. LACM 75-23, 32.0 × 29.8 × 15.0 mm. (**39**) 2–5 m, Antofagasta, Chile. LACM 75-20, 27.0 × 18.8 × 17.6 mm. (**40**) Holotype, *F. clypeus* Sowerby. Locality doubtful. BMNH 197578, 28.0 × 18.9 × 5.8 mm. (**41**) Holotype, *F. papudana* Ramirez-Boehme. Papudo, Aconcagua Province, Chile. MNHN 200374, 36 × 26 × 10 mm. (**42**) Guabun, Chiloe Province, Chile. LACM 75-40, 27.3 × 19.7 × 7.9 mm (beach shell).

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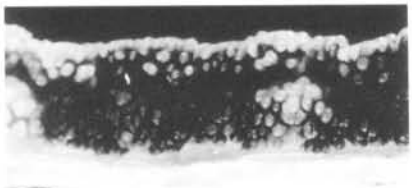

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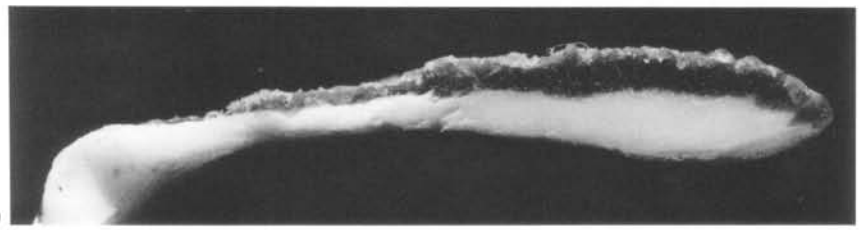

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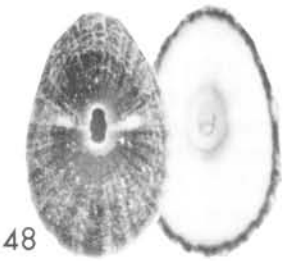

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Figures 43 through 50. *Fissurella peruviana* Lamarck, 1822. Radula, mantle lobe, cut shell, juvenile shells, and intact specimens. (**43**) Radula, light microscope preparation. Montemar, Valparaíso Province, Chile. LACM 75-30, width of ribbon 0.4 mm. (**44**) Radula, SEM. 7–20 m, Mejillones, Chile. LACM 75-21, width of field 1 mm. (**45**) Mantle edge. 1–2 m, Playa Hermosa, Ancon, Peru. LACM 74-21, length 4 mm. (**46**) Cut shell. Los Colorados, Antofagasto, Chile. LACM 75-19, length 21 mm. (**47**) Juvenile shell. Same locality. 4.5 × 2.7 × 1.5 mm. (**48**) Juvenile shell. 3–5 m, Isla Guanape, Peru. LACM 74-3, 9.0 × 5.3 × 2.4 mm. (**49**) Body of preserved specimen. Antofagasta, Chile. LACM 75-15, shell length 25.1 mm. (**50**) Living specimen. Same locality, same specimen.

sequent authors, especially because a view of the internal margin has never been given and the foramen has been figured to be much longer that it actually is. In my opinion it is the flattened form of *F. peruviana,* as was suspected by Sowerby II (1862), and the shell more likely came from Chile. The Ecuadorian locality is well to the north of the northern limit of *F. peruviana,* and the flattened form of the species is particularly common in Chile. The foramen of the specimen is slightly longer than normal. Pilsbry (1890) copied the Reeve figure, but his figure 82, said to be a copy of the Sowerby figure, is not that, which has contributed to the confusion.

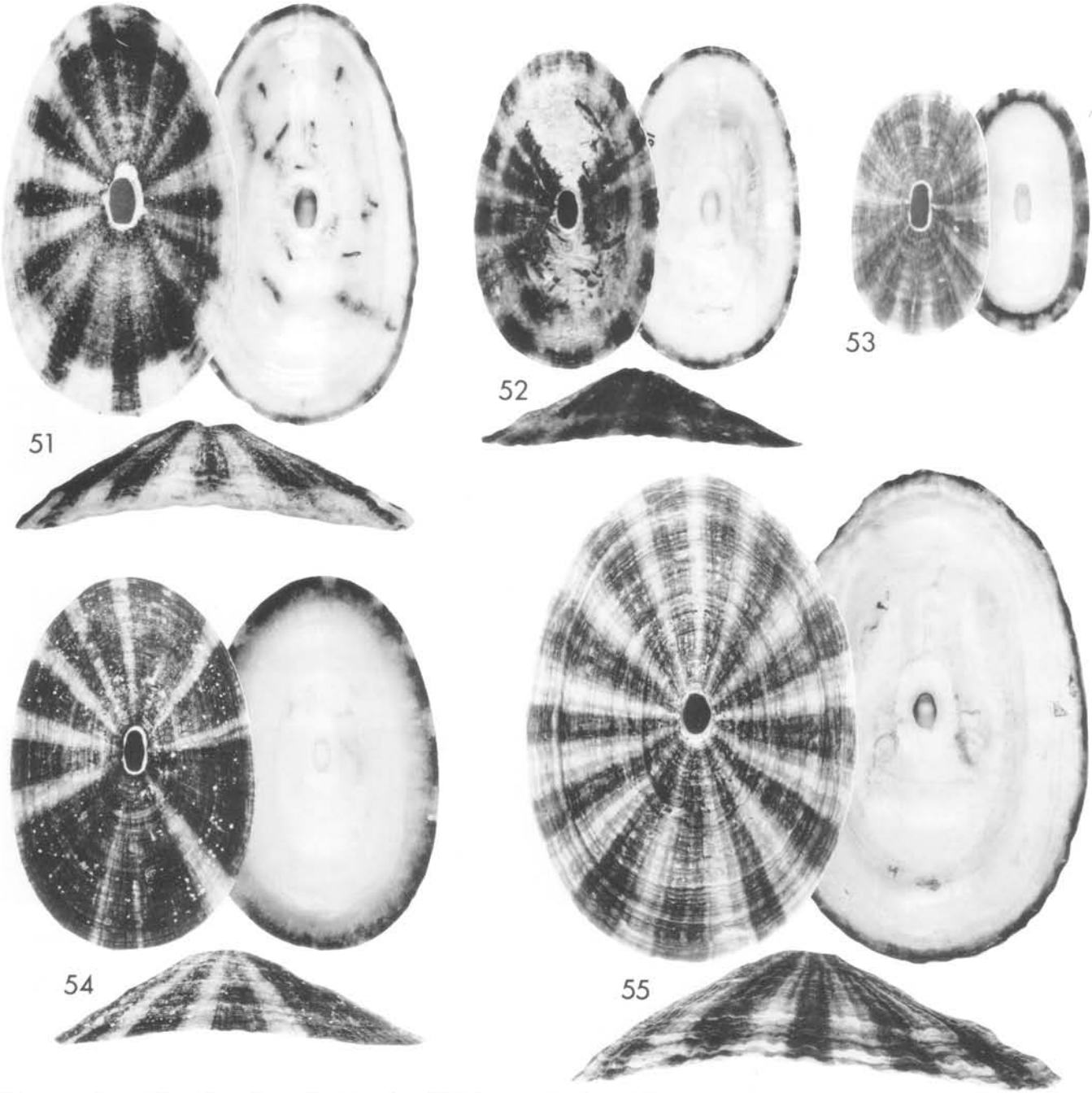
The holotype of *F. occidens* Gould, 1846, is USNM 5863, length 35 mm (Fig. 32). There are two paratypes, MCZ 155766 (Johnson, 1964). The type locality is Callao, Peru. The holotype represents the high-conical, reddish rayed form so abundant in Peru.

Fissurella papudana Ramirez-Boehme, 1974, was described without comparisons to other species. The type locality was Papudo, Aconcagua province, Chile. The holotype (Fig. 41), MNHN 200374, is an example of the flattened form of F. *peruviana,* with a narrow margin, irregular outline, oval foramen, and brown and white rays.

Group of *Fissurella maxima*

Relatively large-shelled species in which the thickness of the exterior calcitic layer of the shell greatly exceeds that of the interior aragonitic layer. All species have strong radial sculpture, at least in the early stages. Sculpture consists of primary ribs and weaker secondary ribs that arise between the primary ribs. Mature shells may retain the distinction between primary and secondary ribs, or all the ribs may attain a similar strength, whether coarse or very fine.

There are eight species in the group of *F. maxima,* four in the Peruvian Provice and four in the Magellanic Province. Most of the species in this group are highly variable and eurytopic, tolerant of a broad range of conditions of intertidal



Figures 51 through 55. *Fissurella maxima* Sowerby, 1835. Mature shells. (**51**) Bahia Independencia, Peru. AHF 380-35, 84.0 × 47.7 × 23.0 mm. (**52**) Lectotype, *F. hondurasensis* Reeve. Locality unknown. BMNH 1976139, 56.6 × 32.5 × 13.5 mm. (**53**) Iquique, Chile. LACM 64-16, 26.0 × 14.4 × 5.8 mm. (**54**) Los Molles, Aconcagua Province, Chile. LACM 75-28, 73.9 × 47.4 × 18.0 mm. (**55**) Holotype, *F. maxima* Sowerby. Valparaíso, Chile. BMNH 197569, 128.8 × 85.4 × 34.7 mm.

exposure. Most species, particularly those with high variability, have been overnamed, the synonyms applying to variant specimens.

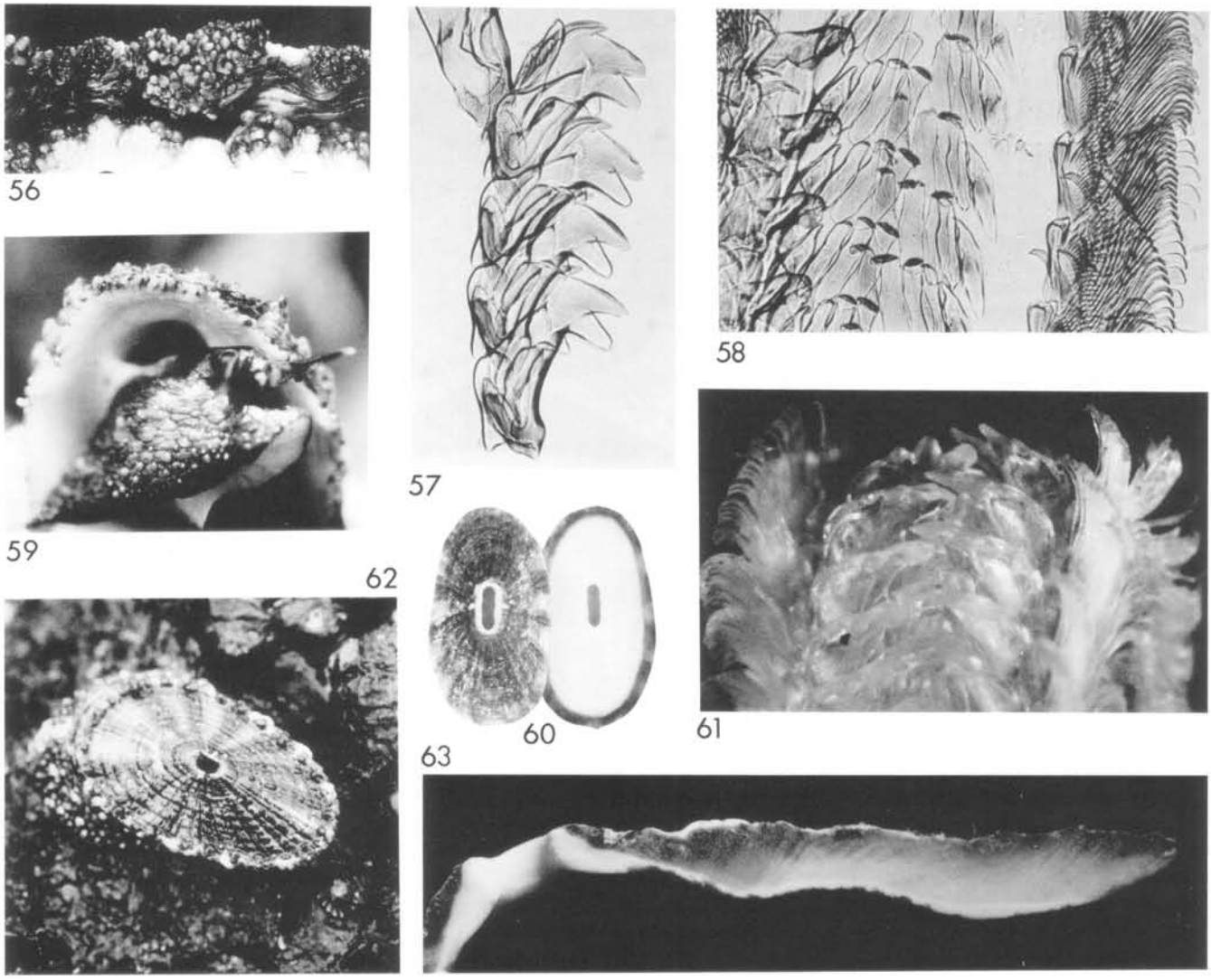
Only one species in this group, *F. nigra*, is stenotopic, with a narrow ecological tolerance, and low variability. It also differs from the other in having primary and secondary ribs pronounced only in juvenile stages.

Three of the four Magellanic species in this group have geographic subspecies.

Fissurella maxima Sowerby, 1835

Figures 51–63

Fissurella maxima Sowerby, 1835a:123; Sowerby, 1835b:3, fig. 18; Orbigny, 1841:475, pl. 64, figs. 4–7; Philippi, 1845:



Figures 56 through 63. *Fissurella maxima* Sowerby, 1835. Radula, mantle lobe, cut shell, juvenile shell, and living specimens. **(56)** Mantle lobe. Iquique, Chile. LACM 75-12, length 9 mm. **(57)** Radular teeth, lateral view of large outer lateral teeth. Iquique, Chile. LACM 70-68, width of ribbon 0.4 mm, shell length 20.5 mm. **(58)** Radular ribbon, same specimen. Width of field 1.0 mm. **(59)** Living specimen, anterior end, showing head with cephalic tentacles and foot side. Iquique, Chile. LACM 75-12. **(60)** Juvenile specimen. Punta El Lacho, Santiago Province, Chile. LACM 75-32, 14.0 × 7.8 × 2.9 mm. **(61)** Radular ribbon, air-dried. Bahía San Juan, Peru. AHF 828-38, width of ribbon 2.5 mm, shell length 58.9 mm. **(62)** Living specimen on rock substrate, anterior at right. Pozo Toyo, Tarapaca Province, Chile. LACM 75-10. **(63)** Cut shell. Montemar, Valparaíso Province, Chile. LACM 75-30, length of cut edge 37 mm.

3, pl. 1, fig. 1; Reeve, 1849, pl. 4, fig. 22; Hupé, 1854:239; Philippi, 1860:180; Sowerby II, 1862:187, figs. 8, 9; Watson, 1886:33; Pilsbry, 1890:145, pl. 30, figs. 8, 9, pl. 33, figs. 46, 47; Dall, 1909:242; Ziegenhorn and Thiem, 1925: 11, pl. 1, figs. 8a, 8b, 9a, 9b; Peña, 1970:156; Riveros-Zuñiga, 1951:102, fig. 18; Dell, 1971:188, pl. 4, figs. 1–3; Marincovich, 1973:18, fig. 31; Ramirez-Boehme, 1974:31 [key].

Fissurella solida Philippi, 1845:142; Carcelles and Williamson, 1951: 256; Dell, 1971:193; Ramirez-Boehme, 1974: 31 [key].

Fissurella concinna Philippi, 1845:143; Philippi, 1846:66, pl. 2, fig. 5; Reeve, 1850, pl. 15, fig. 112; Hupé, 1854:245; Sowerby II, 1862:187, figs. 4, 178, 206; Rochebrune and Mabille, 1889:71; Pilsbry, 1890:146, pl. 32, figs. 32, 33, pl. 45, figs. 7, 8 [as var. of *F. maxima*]; Carcelles and Williamson, 1951:256; Peña, 1970:156; Dell, 1971:183; Ramirez-Boehme, 1974:30 [key].

Fissurella hondurasensis Reeve, 1849, pl. 7, fig. 48; Pilsbry, 1890:146, pl. 35, fig. 6.

Shell. Relatively large (80 to 135 mm mature length), low

to medium in height, outline elongate-oval; sides of shell elevated. Radial ribs prominent, low and rounded, alternating in strength, crenulating margin. Ground color pale yellow; rays dark purple, broad, uninterrupted; primary ribs centered in each light and dark ray. Margin very broad in growing shells, narrow in mature shells, rounded at junction with aragonitic layer; margin zoned; outer zone narrow, showing color rays; inner zone broader, uniformly pale and translucent. Cut shells show pigment of rays concentrated at surface. Foramen nearly central, elongate in young shells, oval in mature shells.

Juvenile Shell. High conical, base elongate, margin rounded; ribs rounded, strong; color reddish, with two lateral white rays and scattered black flecks. After length of 6 mm shell becomes flatter, the primary ribs nodulous and much more prominent than the secondary ribs; the light and dark rayed pattern emerges and the black flecks are lost.

Mantle and Foot. Not fully retractable in shell; cephalic tentacles brown, tipped with yellow. Mantle lobe broad, banded with purplish-brown and light gray to match rays on shell; papillae of upper edge bulbous, finely branched, those of lower edge smaller. Side of foot brown; tubercles strongly developed, tips lighter colored.

Habitat. Partially exposed rocky areas at low tide to 4 m. Some individuals are free of encrusting algae and live on the under sides of large flat rocks at low tide, but most live in the open and are covered with a dense low growth of red algae. When exposed at low tide they are tightly wedged in crevices. Only rarely do specimens have attached *Scurria parasitica* on the shell.

Distribution. Huarmey, Peru (10°06′ S) (LACM 70-97, E del Solar), to Lirquen, Concepción Province, Chile (36°41′ S) (LACM 72-207, Univ. Concepción). The southermost range of *F. maxima* in Chile is not as extensive as that of most of the other common species of the Peruvian Faunal Province. I found no trace of it at Río Bio-bio, Concepción Province, Mehuin, near Valdivia, or Guabun on the northwest tip of Isla de Chiloe. More extreme records in the literature are rejected: Dall's (1909) record from Manta, Ecuador, and Riveros-Zuñiga's (1951) record from Fuerte Bulnes in the Strait of Magellan. Dell's (1971) records from Isla de Chiloe are based upon specimens of *F. picta lata.*

Number of Lots Examined. 128 (LACM 34, AMNH 25, ANSP 7, MACN 14, MNHN 30, USNM 18).

Taxonomic History. *Fissurella maxima* has been recognized by previous authors. Its three synonyms have not been considered important, although *F. concinna* Philippi has sometimes been given status as a narrow "form" of the species.

Abundance and Use. Common throughout its range and particularly abundant in central and northern Chile. It is one of the major species used for food, taken by shore collectors and divers in relatively shallow water. It is called the "lapa de huiros," because it frequently occurs near the brown algae *Lessonia,* known as "huiros."

Characteristics and Variability. Always strongly ribbed and having a consistent color pattern of dark purple rays, the most characteristic feature is the interior border, which is uniquely rounded and has two zones. The margin is always crenulated by the radial ribs, even in the largest specimens. It is not a highly variable species; color pattern and shell height are consistent. Width of the shell is the most variable feature; some specimens may be especially elongate (Fig. 51); oval specimens are rare. Largest specimens come from shell piles in central Chile; those from Peru are small. Elongate specimens are frequently those from Peru. However, I do not consider the geographic differences of sufficient importance to warrant recognition of subspecies.

Affinity and Comparisons. *Fissurella maxima* has features that represent an extreme; its rounded margin is not shared by other species. It most resembles *F. cumingi,* which has a similarly large mantle and foot, and similar size, height, and color pattern. *Fissurella maxima* differs in having a rounded margin, stronger sculpture, and more pronounced primary ribbing. It might also be confused with *F. picta lata,* but it is lower, more elongate, and has broader ribs than that species. Juveniles are reddish like those of *F. peruviana,* but differ in having an upturned margin, a more elongate foramen, and are more elongate.

Synonymy and Types. *Fissurella maxima* was described by Sowerby, 1835, from a specimen collected by Cuming at Valparaíso, Chile. The holotype, BMNH 197569 (Fig. 55), length 128.8 mm, matches the specimen figured by Sowerby (1835b). Reeve (1849) figured a different specimen; these two specimens have also been figured by Dell (1971, pl. 4, fig. 1, holotype; figs. 2, 3, Reeve specimen).

I have not located any type material of *F. solida* Philippi, 1845, from "Chile." It has not been illustrated. Philippi's description mentions what I interpret as the rounded internal border of *F. maxima* and states that he did not know the young of *F. maxima;* other features are in accord with *F. maxima,* so I am confident that the name should be relegated to the synonymy of *F. maxima.*

Type material of *F. concinna* Philippi, 1845, also from "Chile," has not been located. Philippi's figures have suggested to most authors that it is a small, laterally compressed form of *F. maxima.* As with *F. solida,* Philippi noted the rounded margin. Stunted, narrow specimens matching his figure are present in collections; those from central Peru (Fig. 51) may be predominantly narrow, but broader specimens occur at the same localities and it is doubtful that the name has any taxonomic utility. Rochebrune and Mabille (1889) used the name incorrectly for specimens from Tierra del Fuego (no doubt confusing it with *F. radiosa*); this accounts for the Fuegan records of the "variety" *concinna* repeated by subsequent authors.

Fissurella hondurasensis Reeve, 1849, supposedly (in error) from "Honduras," was correctly placed in the synonymy of *F. maxima* by Pilsbry (1890). There are four specimens with the original mounting board now labeled syntypes, BMNH 1976139, lengths 56.6, 36.8, 33.0, and 28.5 mm; the largest is here figured (Fig. 52) and designated the lectotype. All are young specimens, more thin-shelled and with narrower margins than usual, but the dark flecks of the juveniles of *F. maxima* are apparent, and I am confident of their identity

with *F. maxima.* A fifth specimen originally mounted on the same board is a young specimen of *F. pulchra.*

Fissurella latimarginata Sowerby, 1835

Figures 64–79

Fissurella latimarginata Sowerby, 1835a:126; Sowerby, 1835b:3, fig. 69; Gray, 1839:148, pl. 39, fig. 8; Reeve, 1849, pl. 3, fig. 19; Hupé, 1854:242; Philippi, 1860:180; Sowerby II, 1862:185, figs. 6, 7, 12; Pilsbry, 1890:153, pl. 32, figs. 36–38; Dall, 1909:242; Ziegenhorn and Thiem, 1925:17, pl. 2, figs. 22a, 22b; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:125, fig. 33; Peña, 1970:156; Dell, 1971:187, pl. 3, figs. 12–14; Marincovich, 1973:17, fig. 29; Ramirez-Boehme, 1974:31 [key].

Fissurella biradiata Sowerby, 1835a:124; Sowerby, 1835b:3, figs. 23, 52; Orbigny, 1841:477; Reeve, 1849, pl. 3, fig. 20; Philippi, 1860:180; Sowerby II, 1862:185, figs. 1–3; Ziegenhorn and Thiem, 1925:17, pl. 2, fig. 23; Dell, 1971: 182, pl. 3, figs. 10, 11.

Fissurella latimarginata var. *biradiata,* Pilsbry, 1890:154, pl. 35, fig. 3, pl. 46, figs. 12–14; Riveros-Zuñiga, 1951:126, fig. 34; Ramirez-Boehme, 1974:31 [key].

Fissurella bella Reeve, 1849, pl. 3, fig. 21; Sowerby II, 1862: 185, fig. 25; Pilsbry, 1890:150, pl. 33, fig. 48; Riveros-Zuñiga, 1951:119; Dell, 1971:182, pl. 3, figs. 3, 4; Ramirez-Boehme, 1974:32 [key].

Fissurella galericulum Reeve, 1850, pl. 11, fig. 77.

Fissurella latimarginata var. *galericulum,* Ramirez-Boehme, 1974:31 [key].

Fissurella punctatissima Pilsbry, 1890:150, pl. 58, figs. 21–23; Dall, 1909:124; Riveros-Zuñiga, 1951:118, fig. 26; Dell, 1971:192.

Shell. Relatively large (70 to 115 mm mature length); low to moderately high; outline oval, markedly tapered anteriorly; base of shell in one plane or slightly elevated on sides. Sculpture of very fine, sharply raised radial ribs. Color uniformly dark purplish red to gray, except for two lighter rays extending laterally in young shells, fading away in mature shells; occasional specimens faintly rayed throughout. Margin very broad and flat in young shells, solid dark red, outer edge with narrow gray zone. Cut shells showing gray outer zone in calcitic layer; recent growth of outermost zone in some mature shells changing from gray to nearly colorless. Foramen very long and tripartite in young shells, elongate-oval in mature shells.

Juvenile Shell. Elongate and elevated, radial ribs faint, nearly black except for two lateral white rays. After shell length of 5 mm, new growth less conical, fine radial ribs stronger, and shell lighter in color, not yet showing gray outer zone to calcitic layer.

Mantle and Foot. Not fully retractable in shell; mantle lobe usually enveloping and capable of great expansion over edge of shell. Upper edge with finely branched tongue-shaped papillae that alternate with shorter papillae. Lower edge with closely spaced tongue-shaped papillae of lesser size. Mantle lobe and foot side black except for lower mantle edge, on which branched papillae are bright yellow-orange. The bright yellow color of the lower edge makes a very conspicuous ring that encircles the animal, a coloration not present in other species. Determination of living specimens is readily made on this feature alone; in preserved specimens it remains lighter colored that the rest of the mantle lobe.

Habitat. Lowermost intertidal zone in partially protected areas, and in the sublittoral to depths of 5 m, living exposed on the upper surfaces of rocks. At Antofagasta I found that the sublittoral population occurred along with a few specimens of *F. cumingi* and still fewer *F. maxima.* The rocky substratum there looked barren from urchin grazing, but all *Fissurella* shells had a thick algal mat.

Distribution. Chiclayo, Peru (6°47′ S) (Peña, 1950), to Río Bio-bio, Concepción Province, Chile (36°48′ S) (LACM 75-35, McLean). I have found it abundantly as far north as Isla Guanape, Peru (8°32′ S), and at all stations throughout the range. It undoubtedly occurs further south than Concepción, but I did not find it at Mehuin, near Valdivia, or at Guabun at the northwest tip of Isla de Chiloe.

Number of Lots Examined. 82 (LACM 26, AMNH 18, ANSP 8, MACN 7, MNHN 10, USNM 13).

Taxonomic History. The normal color form of *F. latimarginata* has been understood by authors. Its synonyms are based upon color forms with the rayed pattern, except for Pilsbry's *F. punctatissima,* which was based upon a gerontic specimen.

Abundance and Use. *Fissurella latimarginata* is common throughout its range. It occurs widely in Peru, where few of the other species are known. It is one of the most important food species, more so than any other in northern Chile. The largest specimens are taken by divers. Its common name is the "lapa viuda," which means widow, for its black aspect.

Characteristics and Variability. *Fissurella latimarginata* is characterized by its generally uniform gray to reddish-brown color, fine but persistent ribs, and tapered anterior end. The lateral white rays that characterize juvenile shells of so many of the species are likely to persist through later growth stages in this species. The broad, dark internal border

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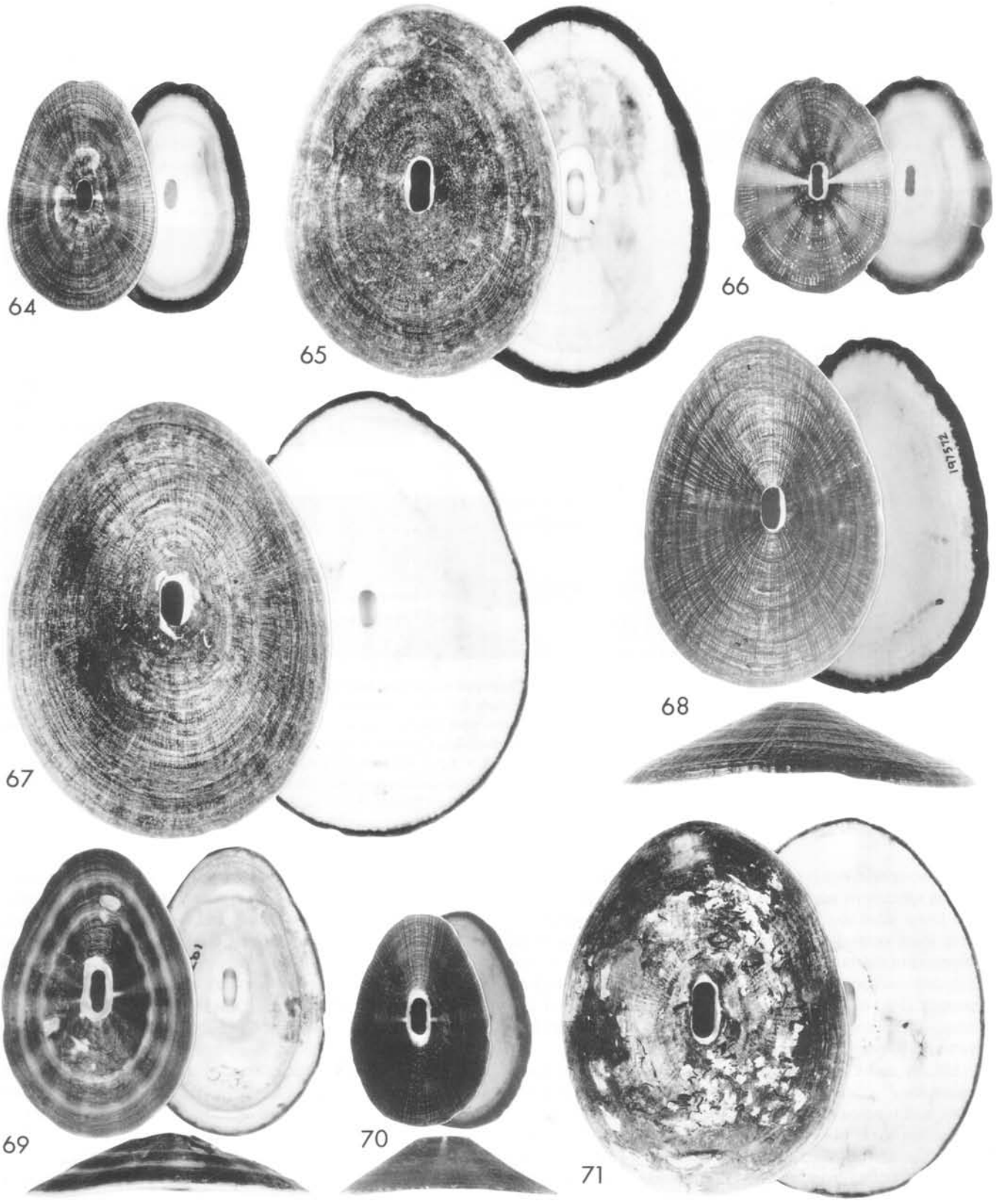
Figures 64 through 71. *Fissurella latimarginata* Sowerby, 1835. Mature shells. **(64)** 3–5 m, Isla Guanape, Peru. LACM 74-3, 41.9 × 27.1 × 11.7 mm. **(65)** Iquique, Chile. LACM 64-16, 87.9 × 64.2 × 20.7 mm. **(66)** Los Molles, Aconcagua Province, Chile. LACM 75-28, 34.8 × 25.5 × 9.0 mm. **(67)** Los Molles, Aconcagua Province, Chile. LACM 75-29, 116.5 × 85.5 × 37.5 mm. **(68)** Lectotype, *F. latimarginata* Sowerby. Valparaíso or Iquique, Chile. BMNH 197572, 80.2 × 55.0 × 18.7 mm. **(69)** Syntype, *F. bella* Reeve. Cape Horn (probable error). BMNH 197567, 56.7 × 37.4 × 12.7 mm. **(70)** Lectotype, *F. galericulum* Reeve. Locality unknown. BMNH 1976138, 33.0 × 21.5 × 9.5 mm. **(71)** Holotype, *F. punctatissima* Pilsbry. Valparaíso, Chile. ANSP 50262, 88 × 66 × 22 mm.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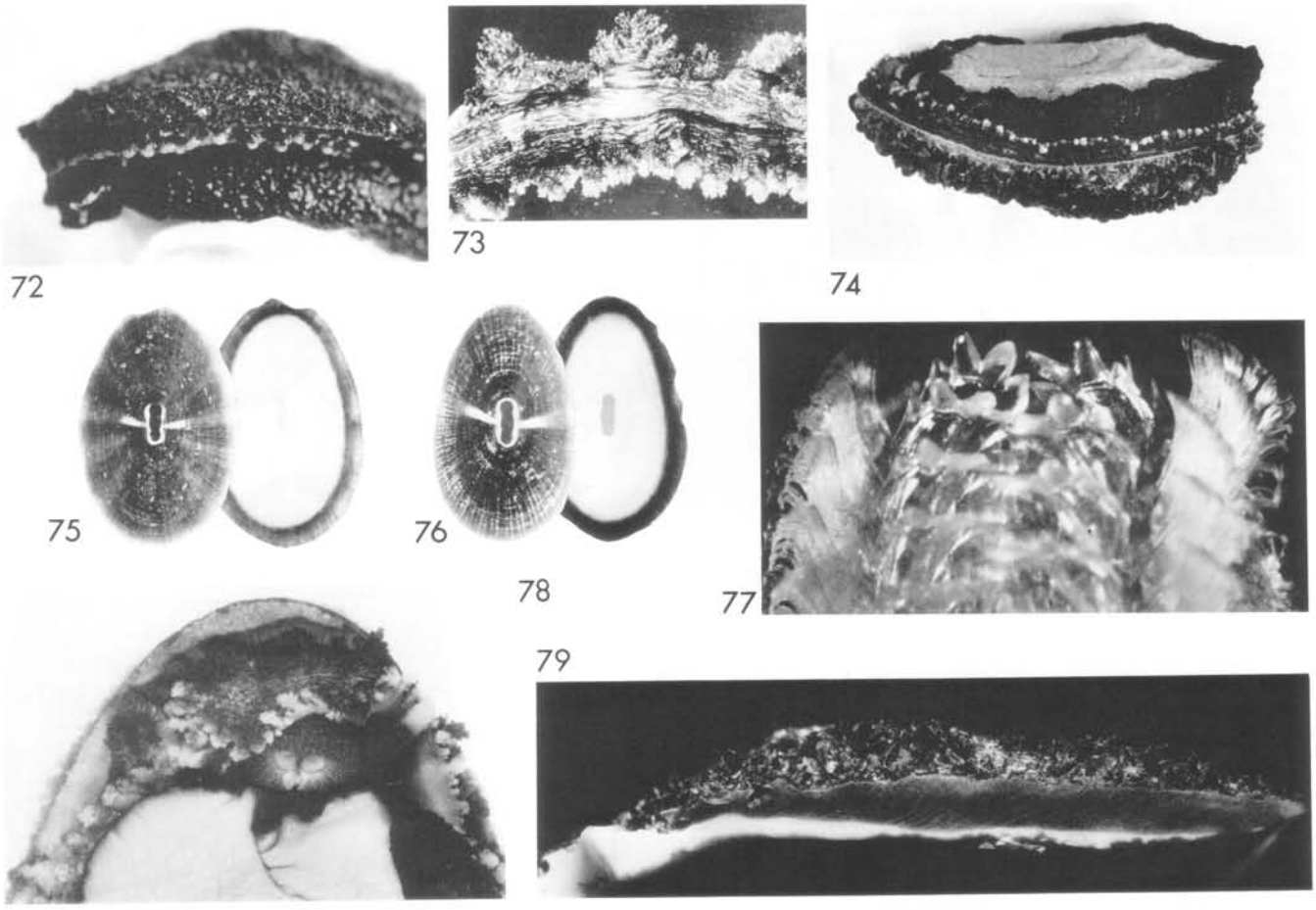


Figures 72 through 79. *Fissurella latimarginata* Sowerby, 1835. Preserved specimens, mantle edge, juvenile shells, radula, and cut shell. **(72)** Living specimen, showing light colored lower mantle edge against dark foot side. Antofagasta, Chile. LACM 75-20. **(73)** Mantle lobe. Isla Guanape, Peru. LACM 74-2, length, 24 mm. **(74)** Preserved specimen with epizoic mytilids *Semimytilus algosus* on shell. 1–4 m, Isla San Lorenzo, Peru. LACM 74-24, 66.2 × 42.5 × 22.0 mm. **(75)** Juvenile shell. Los Colorados, Antofagasta Province, Chile. LACM 75-19, 16.0 × 10.5 × 3.9 mm. **(76)** Juvenile shell. Iquique, Chile. LACM 64-16, 13.8 × 3.5 × 3.6 mm. **(77)** Radula, air-dried. Antofagasta, Chile. LACM 75-20, width of ribbon 3.4 mm, shell length 85.0 mm. **(78)** Head of preserved specimen, showing mantle lobe and mouth. Isla Guanape, Peru. LACM 74-2, shell length 70.0 mm. **(79)** Cut shell, also showing algal mat. Los Molles, Aconcagua Province, Chile. LACM 75-29, length of cut edge 42 mm.

is characteristic, but it is a feature shared with other species. Living specimens are always recognizable by the bright yellow lower edge to the mantle lobe. Largest specimens seen were from central Chile; smaller specimens occur at both extremes of the range. Shell height varies extensively within populations. Specimens with patterns of rays like those of *F. cumingi* (Fig. 61) are uncommon but occur throughout the range. There are no geographic differences of sufficient importance to warrant recognition of subspecies.

Affinity and Comparisons. *Fissurella latimarginata* most resembles *F. cumingi,* having in common the size, proportions, and tapered anterior end. The unusual pattern of rays in variant specimens of *F. latimarginata* is similar to the normal pattern in *F. cumingi.* The sculpture of *F. latimarginata* is finer, sharper, and less beaded than that of *F. cumingi;* the rare color form of *F. latimarginata* may always be distinguished on this difference in sculpture. Shells of *F. latimarginata* may resemble those of *F. nigra* but are more sharply ribbed, have a reddish rather than gray interior border, and lack the inwardly tapered, white bordered foramen of *F. nigra.* A similar elaboration of the tongue-shaped papillae of the mantle lobe is known only in *F. bridgesii.* Both have broad margins and are dark colored with an incipient tendency to produce faintly rayed variants. *Fissurella latimarginata* may always be distinguished by its fine, sharp ribbing, which is lacking in *F. bridgesii.*

Synonymy and Types. There are six syntypes of *F. latimarginata* Sowerby, 1835, described from "Valparaíso and Iquique," Chile, four from one lot, BMNH 197572, lengths 80.2, 73.8, 61.7, and 51.1 mm, and two in BMNH 197573, lengths 56.3 and 27.3 mm. Both original mounting boards are penned with "Valparaíso and Iquique," so it is not known from which of the two localities each shell originated. The shells are clean and uniformly dark red, faintly, or not at all,

showing the lateral white rays. The largest specimen is figured here (Fig. 68) and designated the lectotype; Dell (1971) figured the 73.8 mm specimen.

Type material of *F. biradiata* Sowerby was not received on loan from the British Museum. The type locality is Valparaíso, Chile. Figure 23 of the "Conchological Illustrations" shows a finely ribbed shell 41 mm long (presumed life-size) in which the only color pattern consists of the two lateral white rays. The type figure can therefore be relegated to the normal form of *F. latimarginata* without question. Figure 52 of the "Conchological Illustrations" is stated to be a "var." of *F. biradiata* from Iquique; this specimen is the one figured by Reeve (1849) and Dell (1971). Reeve's coloration shows it to be reddish brown and faintly rayed. Until I can examine the sculpture of that specimen I am unable to decide whether it is *F. cumingi* or the rare, rayed form of *F. latimarginata,* but the question is of minor importance because the type of *F. biradiata* is clearly recognizable as a specimen of *F. latimarginata.*

Fissurella bella Reeve, 1849, supposedly from Cape Horn, is represented by two syntypes, BMNH 197567, lengths 56.7 and 42.5 mm. The smaller specimen was figured by Reeve (here designated the lectotype) and the larger one by Dell (1971) and refigured here (Fig. 69). No author has recognized a species based on this name. Dell suggested an affinity with *F. pulchra,* but the absence of flecking rules that out. The narrowed anterior end and rayed pattern is shared only with the rare color form of *F. latimarginata* and normal *F. cumingi.* The shells appear to be acid-cleaned, the fine radial ribs are like those of *F. latimarginata* rather than *F. cumingi.* The margin in both shells is narrow, suggesting a degree of maturity that can be matched with *F. latimarginata* at extremes of its distribution, but not with similarly sized *F. cumingi.* I therefore identify the syntypes as the rare color form of *F. latimarginata.* The Cape Horn locality is therefore erroneous.

There are three syntypes of *F. galericulum* Reeve, 1850, BMNH 1976138, lengths 33.0, 31.0, and 30.5 mm, described with unknown locality. The largest (here designated the lectotype) is illustrated here (Fig. 70). It is clearly the normal white-rayed young stage of *F. latimarginata* and has been so recognized by previous authors.

Fissurella punctatissima Pilsbry, 1890, from Valparaíso, Chile, was considered by Pilsbry to differ from *F. latimarginata* in being more elevated and having a narrower internal margin. Shell proportions of the holotype (ANSP 50262, Fig. 71) and paratype (ANSP 61923) are within the normal range of variation and the narrow margin is that of mature examples of the species. The interior pitting, which suggested the name, is not unusual in large shells. Dell's records (1971) under this name are based upon specimens of *F. nigra.*

Fissurella cumingi Reeve, 1849

Figures 80–94

Fissurella cumingi Reeve, 1849, pl. 3, fig. 17; Hupé, 1854: 238; Sowerby II, 1862:187, figs. 5, 132; Carcelles and Williamson, 1951:256; Dell, 1971:184, pl. 3, figs. 15, 16; Ramirez-Boehme, 1974:32 [key].

Fissurella latimarginata var. *cumingi,* Pilsbry, 1890:154, pl. 30, fig. 1; Riveros-Zuñiga, 1951:28.

Fissurella stellata Reeve, 1850, pl. 12, fig. 80; Hupé, 1854: 245; Sowerby II, 1862:187, fig. 82; Pilsbry, 1890:148, pl. 32, fig. 32; Dall, 1909:242; Riveros-Zuñiga, 1951:113, fig. 23 [looks like *F. peruviana*]; Dell, 1971:193, pl. 4, figs. 7, 8 [not 5, 6]; Ramirez-Boehme, 1974:30 [key].

Shell. Large (80 to 100 mm mature length); height medium; outline oval, tapered anteriorly; sides slightly raised. Sculpture of fine to medium strength radial ribs, nodulous or beaded in early stages along growth increments; primary ribs only slightly more prominent than secondary ribs. Ground color dark yellowish gray, patterned with dark rays of reddish-purple, anteriormost rays often split. Margin very broad and flat in young shells, showing pattern of rays across the full width. Cut shells not showing zoning of calcitic layer, pigmentation of rays of equal intensity throughout layer. Foramen elongate and tripartite in young shells, elongate-oval in mature shells.

Juvenile Shell. Oval, conical, with straight slopes, earliest area white, reddish rays emerging with edges darkly outlined as if split; lateral white-rayed area prominent. At length of 4 mm scattered brown flecks may be present, forming zigzag pattern in some specimens; by this size ribs have become prominent, secondary ribs nearly the size of primary ribs.

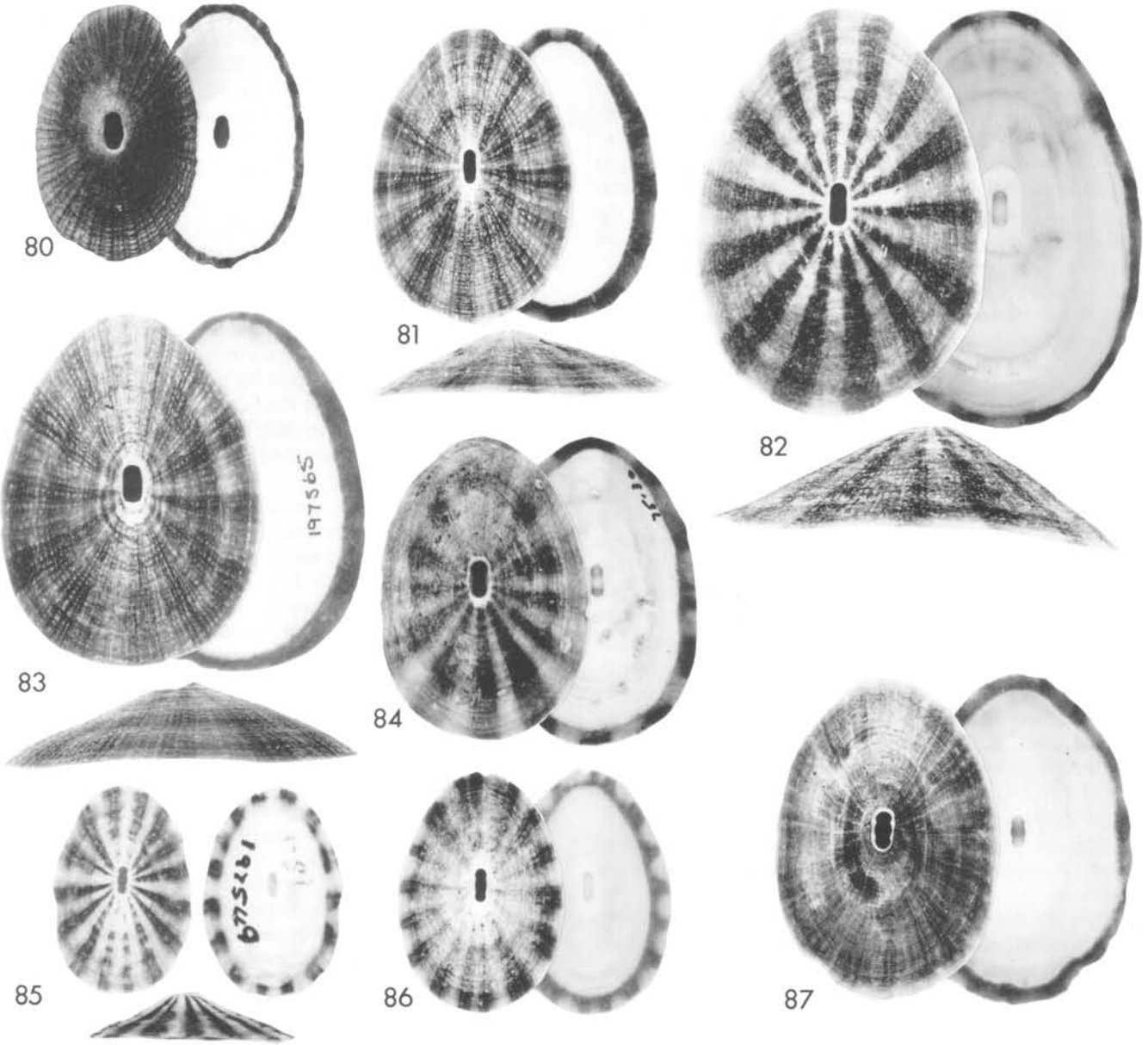
Mantle and Foot. Nearly retractable in shell. Cephalic tentacles yellowish on inner surface. Side of foot with strongly developed tubercles; mantle lobe broad, upper edge with finely branched papillae, lower edge with more prominent papillae, banded in light and dark to correspond to rays on shell. Foot and mantle colored purplish red, lighter or tending toward pink in individuals with lightly pigmented shells. The reddish coloration is characteristic and differs from that of all other species.

Habitat. Lowermost intertidal zone and immediate subtidal zone to 15 m, living on the upper surfaces of rocks. At low tide chiefly in deep tide pools that occur in surf exposed areas. I obtained living specimens from the municipal market at Iquique, evidently taken by divers. Living specimens were collected in lesser numbers along with *F. latimarginata* at 5 m on a rocky bottom at Antofagasta. Large specimens were found in shell piles at Los Molles (32°14′ S). Intertidally occurring specimens were common at Montemar and Mehuin.

Distribution. Matarani, Peru (17°00′ S) (AMNH 150892, B. Marco), to Mehuin, Valdivia Province, Chile (39°23′ S) (LACM 75-36, McLean). The distribution probably extends farther to the north and south. Its distribution is more southern than that of *F. latimarginata* and *F. maxima,* both of which extend much farther to the north in Peru, but seem not to be represented at Mehuin, where *F. cumingi* is common.

Number of Lots Examined. 41 (LACM 16, AMNH 6, ANSP 1, MACN 3, NMHN 10, USNM 5).

Taxonomic History. *Fissurella cumingi* has not hitherto been understood and recognized as a separate species. Previous authors have repeated the early published descriptions

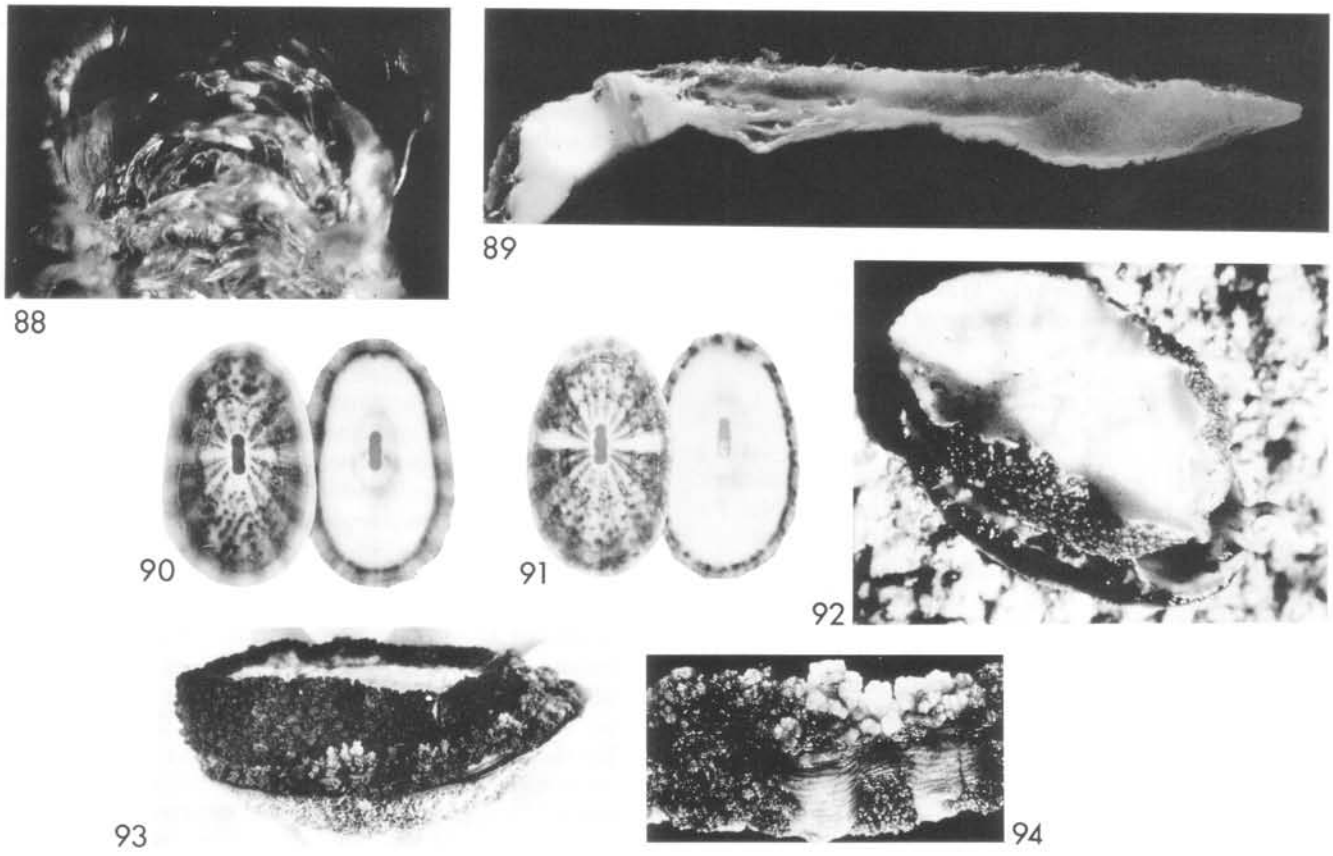


Figures 80 through 87. *Fissurella cumingi* Reeve, 1849. Mature shells. (**80**) 17 m, Huayquique, Tarapaca Province, Chile. LACM 90799, 32.5 × 20.5 × 11.2 mm. (**81**) Los Molles, Aconcagua Province, Chile. LACM 75-28, 50.3 × 34.2 × 10.5 mm. (**82**) Same locality (shell pile). LACM 75-29, 96.3 × 61.1 × 22.8 mm. (**83**) Lectotype, *F. cumingi* Reeve. Valparaíso, Chile. BMNH 197565, 67.2 × 49.1 × 15.2 mm. (**84**) Montemar, Valparaíso Province, Chile. LACM 75-30, 49.9 × 34.4 × 12.8 mm. (**85**) Lectotype, *F. stellata* Reeve, 1850. 11–22 m, Valparaíso, Chile. BMNH 197549, 16.2 × 10.8 × 3.8 mm. (**86**) Montemar, Valparaíso Province, Chile. LACM 75-30, 30.0 × 20.4 × 7.9 mm. (**87**) 75-36, Mehuin, Valdivia Province, Chile. LACM 75-36, 61.2 × 42.2 × 17.7 mm.

and have considered it to be a color form or "variety" of *F. latimarginata.* Confusion over the identity of *F. biradiata* Reeve (a synonym of *F. latimarginata*) and *F. bridgesii* Reeve (a good species) has also contributed to the difficulty. Cleaned specimens found in old collections have usually been misidentified as *F. maxima;* specimens covered with the algal mat are easily mistaken for *F. latimarginata.*

Abundance and Use. *Fissurella cumingi* is not as common as *F. maxima* and *F. latimarginata,* but large specimens can be found by divers, and the species is exploited for food in central and northern Chile. I have seen it in the market at Iquique, and it is a major component in the shell piles in central Chile. The common name is "lapa frutilla," meaning strawberry, which aptly describes the color of the mantle and foot sides.

Characteristics and Variability. The most characteristic features of *F. cumingi* are its tapered front, consistent color pattern of dark ribs on a relatively dark ground, beaded ribs,



Figures 88 through 94. *Fissurella cumingi* Reeve, 1849. Radula, cut shell, juvenile shells, living and preserved bodies, mantle lobe. (**88**) Radular ribbon, air-dried. 2–5 m, Antofagasta, Chile. LACM 75-20, width of ribbon 2.8 mm. (**89**) Cut shell. Los Molles, Aconcagua Province, Chile. LACM 75-29, length of cut edge 38.0 mm. (**90**) Juvenile shell. Los Molles, Aconcagua Province, Chile. LACM 75-28, 12.8 × 7.8 × 3.4 mm. (**91**) Juvenile shell. Same locality. LACM 75-28, 9.4 × 5.5 × 2.5 mm. (**92**) Ventral view of living specimen, head at right. Montemar, Valparaíso Province, Chile. LACM 75-30. (**93**) Preserved specimen. 2–5 m, Antofagasta, Chile. LACM 75-20, shell length 73.9 mm. (**94**) Mantle lobe. Same locality. LACM 75-20, length 14 mm.

and the unique reddish color of the mantle and foot. Variation in the species is minimal. The chief variable feature seems to be the intensity of ground color, which may be pale to dark yellow. The rayed pattern is consistent; none have been seen that lack it. Specimens received from M. Bretos from the subtidal mussel beds at Iquique (Fig. 80) are small, elevated, and have narrow margins. Those from the southernmost locality collected (Mehuin, Chile) appeared stunted, and many had narrow shells. However, there seem to be no geographic differences of sufficient importance to recognize subspecies.

Affinity and Comparisons. *Fissurella cumingi* has certain features in common with both *F. maxima* and *F. latimarginata,* suggesting that it is related to both. Its color pattern combines the rayed pattern of *F. maxima,* with the addition of some of the darker ground color of *F. latimarginata.* Its margin shows the pattern of rays across the full, flat width, unlike the solid margin of *F. latimarginata* and the rounded, crenulate and zoned margin of *F. maxima.* It has the same size and proportions as *F. latimarginata,* but specimens with the algal mat may be recognized by the rayed pattern of the margin. The normal, rayed form of *F. cumingi* may be distinguished from the unusual rayed form of *F. latimarginata* by the strength of the ribs; they are fine and sharp in *F. latimarginata,* coarser and beaded in *F. cumingi.* Its outline is more tapered and its ribbing finer than that of either *F. picta lata* or *F. costata;* it does not have the more distinct primary ribbing of either of these species. Juvenile shells of *F. cumingi* have a characteristic color pattern of split rays; they do not have the rounded margin of *F. maxima* nor the primary rays of *F. costata* or *F. picta lata.* The reddish color of the animal is so different from that of any other species that it may be recognized by this feature.

Synonymy and Types. There are 6 syntypes of *F. cumingi* Reeve, 1849, from Quintero, Chile, BMNH 197565, lengths 77.0, 67.2, 62.5, 57.1, 32.7, and 22.5 mm. Reeve (1849) and Dell (1971) figured the 67.2 mm shell; Dell's interior view is of the 77 mm specimen. The 67.3 mm specimen is here figured and designated the lectotype (Fig. 83).

Fissurella stellata Reeve, 1850, was based on small specimens from "Valparaíso, attached to dead shells at a depth of from six to twelve fathoms." There are four syntypes,

BMNH 197549, lengths 16.9, 16.2, 15.0, and 14.5 mm. The 16.2 mm specimen is illustrated and designated the lectotype (Fig. 85). These specimens are clearly the juveniles of *F. cumingi;* they are red-rayed, the ribbing of medium strength and nodular, the primary and secondary ribs nearly equivalent. The original specified depth is probably accurate; the species is known from the shallow sublittoral. Other authors have guessed incorrectly with respect to this name; Riveros-Zuñiga (1951) figured the brown and white rayed form of *F. peruviana* as *F. stellata.* Dell (1971) mixed the figure numbers on his plate 4: his figure of a syntype of *F. stellata* should be figs. 7, 8, rather than 5, 6.

Fissurella costata Lesson, 1831

Figures 95–108

Fissurella rudis Deshayes, 1830:134; Deshayes *in* Lamarck, 1836:61; Orbigny, 1841:474 [under *F. costata*]. Not *Patella rudis* Roeding, 1798 [= *F. nodosa* Born, 1778].

Fissurella costata Lesson, 1831:41; Sowerby, 1835b:4, fig. 28; Orbigny, 1841:474; Reeve, 1849, pl. 2, fig. 14; Hupé, 1854:243; Philippi, 1860:181; Sowerby II, 1862:187, figs. 15, 205; Pilsbry, 1890:148, pl. 30, fig. 10, pl. 35, fig. 11; Dall, 1909:177, 241; Ziegenhorn and Thiem, 1925:14, pl. 2, fig. 12; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:108, fig. 21; Dell, 1971:183, pl. 4, figs. 7, 8; Marincovich, 1973:16, fig. 28; Ramirez-Boehme, 1974:31 [key].

Fissurella chilensis Sowerby, 1835a:124; Sowerby, 1835b:3, fig. 36; Orbigny, 1841:474 [under *F. costata*].

Fissurella costata var. *rubra* Ziegenhorn and Thiem, 1925: 14, pl. 2, figs. 13a, b.

Shell. Medium sized (50 to 80 mm mature length), low to medium; outline elongate in young shells, broadly oval in mature shells; base of shell resting flat in one plane. Sculpture of distinctly raised narrow ribs that crenulate margin; interspaces narrower than ribs. Primary ribs more prominent in young shells, but in large shells not differing from secondary ribs. Ground color light yellowish gray; rays gray, often becoming faint in later growth stages. Margin broad, flat, showing gray rays across full width but more distinctly at outer edge. Calcitic layer of cut shells not zoned; rays showing through full width. Foramen exceptionally small, elongate and tripartite in young shells, elongate-oval in mature shells.

Juvenile Shell. Conical at earliest stage, becoming flattened and elongate; primary ribs light yellow, strongly elevated, becoming nodular after shell reaches length of 5 mm; earliest rays reddish, changing to black by shell length of 4 mm; black rays fill interpsaces between primary ribs. With growth, secondary ribs appear between primary ribs and black rays become gray or disappear altogether.

Mantle and Foot. Fully retractable in shell; shell margin not raised and mantle not projecting in living specimens. Cephalic tentacles dark on outer side, yellowish on inside and at tips. Mantle lobe very narrow, papillae of both edges small and width little branching. Side of foot light pinkish brown, surface marbled. Projecting tubercles are not readily apparent in living specimens but visible in preserved specimens. Elaboration of the mantle lobes is the least pronounced in this species.

Habitat. In northern Chile at Iquique and Antofagasta *Fissurella costata* occurs on vertical surfaces of surf-exposed rock walls at the low tide line, near the holdfasts of the large brown alga *Lessonia,* where its habitat is not shared by other species of *Fissurella.* In central Chile I found it more abundantly. At Los Molles and Montemar it also occurs on horizontal surfaces in less exposed areas; here it shares the habitat with other species. The shell margin fits the contours of a habitual site of attachment; when exposed at low tide the shell margin is in tight contact with the substrate. Unlike the other species, individuals do not move when touched by *Heliaster;* the small foramen may protect them from access by this seastar. The shell also seems suited to resist removal by the clingfish *Sicyases* because the margin is less raised that that of other species, which are more subject to predation by *Sicyases.* Specimens are rarely seen with attached *Scurria parasitica.*

Distribution. Punta Pichalo, Tarapaca Province (19°36′ S) (AMNH 137232, J. Bird), to Guabun, Isla de Chiloe, Chile (41°50′ S) (LACM 75-40, McLean). Dall's (1909) record from Mollendo, Peru, was based on a specimen of *F. maxima* (USNM 27743). However, the distribution of this species may extend farther to the north into Peru. In my collecting only the northwestern tip of Isla de Chiloe was sampled at Guabun; the southern limit of the species is therefore not certain. It is apparent, however, that this species has a more southern center of distribution than most species of the Peruvian Faunal Province.

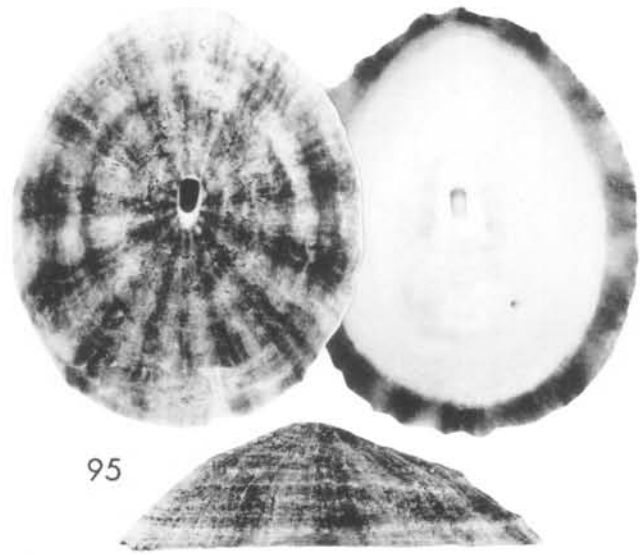
Number of Lots Examined. 70 (LACM 23, AMNH 15, ANSP 3, MACM 9, MNHN 12, USNM 8).

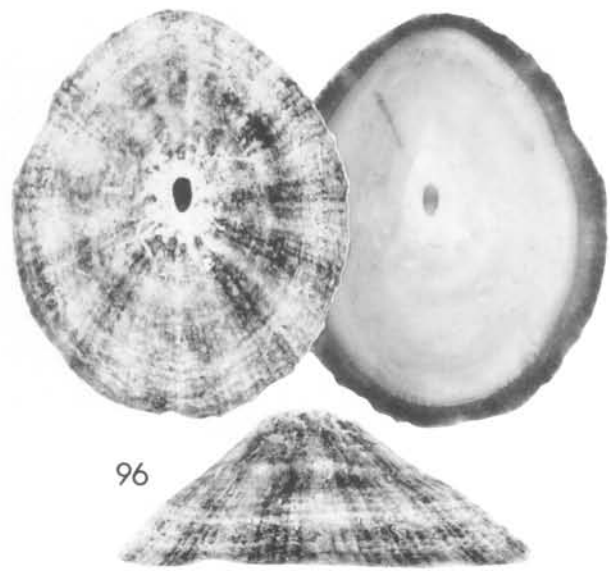
Taxonomic History. *Fissurella costata* has been reasonably well understood by recent authors.

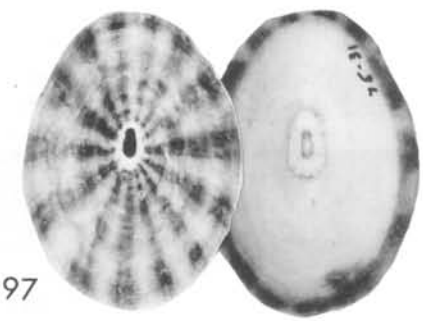
Abundance and Use. *Fissurella costata* is moderately common throughout its range. In northern Chile it is little used for food because its habitat is so exposed to surf that it is usually inaccessible to shore collectors. Beach-worn shells are common along the shore but fresh shells are seldom seen in the shell piles. The common name is "lapa senorita," because of its resemblance to *Scurria viridula,* which is known as the "senorita."

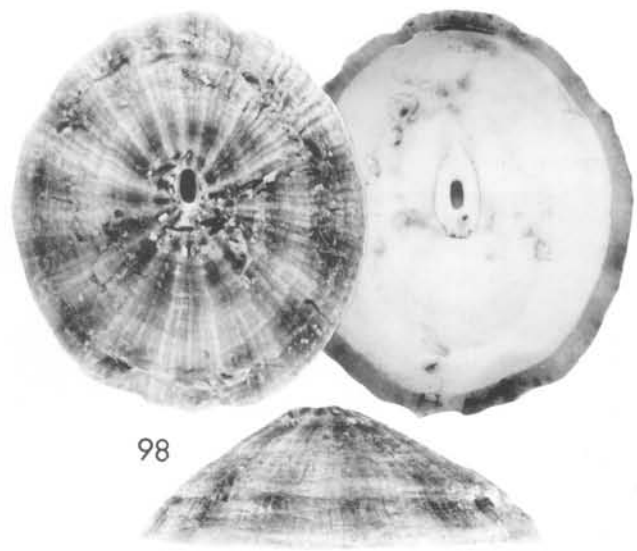
Characteristics and Variability. *Fissurella costata* is characterized by its relatively small foramen, which is broadly oval when mature and narrow in young stages, its relatively low height, and its consistent color pattern of gray rays on a yellow ground. Its mantle lobe is very narrow, and the foot color is light pinkish brown. Variations in height and outline are minor; color variation results from rays that either persist or fade in later stages. There are no geographic differences worthy of note. The low variability of this species is correlated with its rather restricted habitat on surf-exposed rocks in the lower intertidal zone.

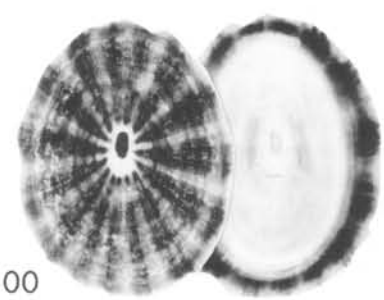
Affinity and Comparisons. *Fissurella costata* seems to be most closely related to, and difficult to distinguish from, *F. picta lata.* Both have similar color patterns, a similar, broadly oval outline, strong ribs, and primary ribs that remain strong. Differences are that mantle and foot colors are lighter in *F.*

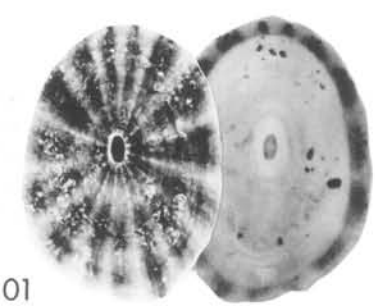




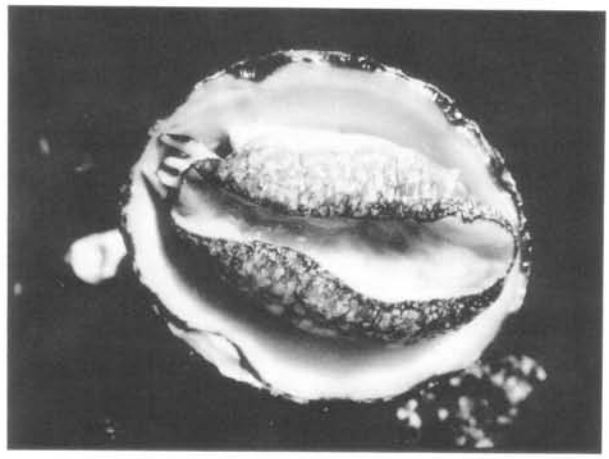


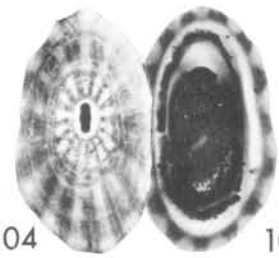


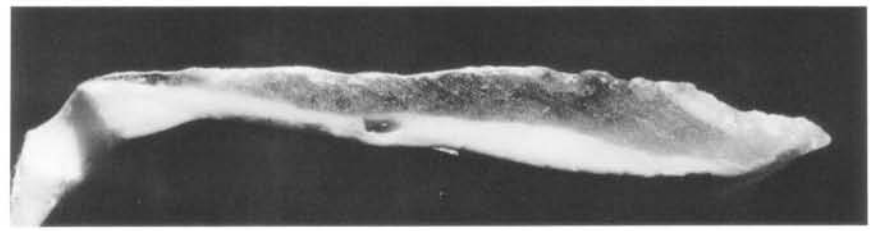




Figures 95 through 101. *Fissurella costata* Lesson, 1831. Mature shells. (**95**) Punta Jara, Antofagasta Province, Chile. LACM 75-18, 72.3 × 59.0 × 20.4 mm. (**96**) Los Molles, Aconcagua Province, Chile. LACM 75-28, 66.8 × 54.5 × 23.3 mm. (**97**) Islota Concon, Valparaíso Province, Chile. LACM 75-31, 43.3 × 31.8 × 9.9 mm. (**98**) Lectotype, *F. rudis* Deshayes. Paita, Peru (probable error). MNHNP, 69.1 × 61.1 × 24.7 mm. (**99**) Río Bio-bio, Concepción Province, Chile. LACM 75-35, 57.7 × 56.4 × 15.3 mm (beach shell). (**100**) Mehuin, Valdivia Province, Chile. LACM 33-2, 33.2 × 25.7 × 9.4 mm. (**101**) Ancud, Chiloe Province, Chile. LACM 62-62, 35.5 × 25.5 × 7.9 mm.



Figures 102 through 108. *Fissurella costata* Lesson, 1931. Living specimens, juvenile shells, radula, and cut shell. (**102**) Ventral view, living specimen. Punta Jara, Antofagasta Province, Chile. LACM 75-18. (**103**) Living specimens in place. Los Molles, Aconcagua Province, Chile. LACM 75-28. (**104**) Juvenile specimen. Same locality. LACM 75-28, 14.2 × 7.9 × 3.1 mm. (**105**) Juvenile specimen (dead shell). Bahía Herradura, Coquimbo Province, Chile. LACM 75-25, 10.9 × 7.3 × 2.4 mm. (**106**) Radula of small specimen. Montemar, Valparaíso Province, Chile. LACM 75-30, width of field 0.8 mm, shell length 24.5 mm. (**107**) Mantle lobe. Punta Jara, Antofagasta Province, Chile. LACM 75-18, length 10 mm. (**108**) Cut shell. Los Molles, Aconcagua Province, Chile. LACM 75-28, length of cut edge 31 mm.

costata; F. costata is somewhat lower than *F. picta lata,* although the extremes of variation seem to overlap; *F. costata* does not have the tendency to reddish rays nor the penciled pattern of the rays of *F. picta lata.* Juveniles of *F. costata* are more elongate, flatter, and have more nodulous primary ribs than those of *F. picta lata.* In northern Chile where *F. picta lata* does not occur, there is no difficulty in recognizing *F. costata* as the species that is the most broadly oval and has the smallest foramen.

Synonymy and Types. Four syntypes of *F. rudis* Deshayes, 1830, have been examined, received on loan from the Paris Museum. The lot is accompanied by a cardboard mount; the shells are 75.8, 69.1, 53.6, and 51.9 mm in length. The largest of these shells is the polished specimen mentioned in the original description. The original dimensions were given as 55 mm length and 43 mm width; one of the specimens is 53.6 mm long and 42.8 mm wide. The 69.1 mm shell is designated the lectotype (Fig. 98). All four specimens are typical and agree with the thorough and accurate original description. The original locality was Paita, Peru: "This shell was first given to us by our friend Lesson, who found it at Paita, Peru; then later we have found it commercially, likewise from Peru." [Translation.] Later, Deshayes *in* Lamarck (1836) changed the locality to "Habite le Chile." The actual occurrence of the species in Peru is uncertain, and Paita is north of the known occurrence of any of the Peruvian species of *Fissurella.* This name is preoccupied by *Patella rudis* Roeding, 1798, a synonym of the Caribbean *F. nodosa* (Born, 1778).

Type material of *Fissurella costata* Lesson, 1831, has never

been illustrated, and specimens are not in the collection of the Paris Museum, where some of Lesson's types are known (Bouchet, personal communication). Lesson's description is insufficient to distinguish the species from *F. picta lata,* which is closely related and also abundant in the vicinity of Talcahuano, Chile, the type locality. Lesson described the animal as blackish and the shell margin as bluish with stains of red, features that would more appropriately apply to *F. picta lata.* However, the species is well known under the name *F. costata* and no purpose would be served in rejecting this name, even though there is doubt as to its identity.

Type material for *F. chilensis* Sowerby, 1835, has not been located. It came from "Valparaíso, found on rocks in exposed situations at low water." The habitat is accurately described; *F. costata* is much more common than *F. picta lata* at Valparaíso, and the original illustration shows a densely ribbed shell with a very small foramen. Its identity is certain, in agreement with treatment by previous authors.

Type material of *Fissurella costata* var. *rubra* Ziegenhorn and Thiem, 1925, has not been located. The specimen came from Coquimbo, Chile, and measured 60 × 48 × 15 mm, distinguished from the typical form in having reddish rays. Judging from the illustration, it could be either *F. costata* or *F. picta lata,* although I have not seen reddish rayed specimens of *F. costata.* Lateral profile of the figure is about right for *F. costata;* for *F. picta lata* it would be at the low extreme of variation; the locality is reasonable for *F. costata;* to my knowledge *F. picta lata* does not occur north of Valparaíso, where it is uncommon. I therefore favor retaining this taxon in the synonymy of *F. costata,* admitting that the other alternative is a possibility.

Fissurella picta (Gmelin, 1791)

Figures 109–146

Fissurella picta is here considered to have two geographic subspecies: *F. picta picta* in the Magellanic region of Chile and *F. picta lata* in south-central Chile.

Synonymy for *F. picta picta:*

Patella picta Gmelin, 1791:3729.

Fissurella picta, Lamarck, 1822:10; Deshayes, 1830:131; Sowerby, 1835b:1, figs. 4, 26; Lamarck, 1836:559; Orbigny, 1841:472; Reeve, 1849, pl. 1, fig. 6; Hupé, 1854:237; Sowerby II, 1862:186, figs. 10, 11, 35; Watson, 1886:33; Rochebrune and Mabille, 1889:70; Pilsbry, 1890:144, pl. 45, figs. 9–11; Melvill and Standen, 1898:102; Strebel, 1907:83, pl. 2, fig. 22; Melvill and Standen, 1907:98; Strebel, 1908:79; Dall, 1909:242; Melvill and Standen, 1914: 115; Ziegenhorn and Thiem, 1925:6, pl. 1, figs. 1–4; Carcelles, 1950:51; Powell, 1951:85; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951:96, fig. 15; Dell, 1971: 191; Ramirez-Boehme, 1974:31 [key].

Fissurella atrata Reeve, 1850, pl. 11, fig. 73; Sowerby II, 1862:186, fig. 71; Pilsbry, 1890:147, pl. 34, fig. 59 [under *F. philippiana*]; Dell, 1971:190, pl. 3, fig. 7 [under *F. philippiana*].

Fissurella muricata Reeve, 1850, pl. 14, fig. 103; Sowerby II, 1862:106, pl. 4, fig. 68; Pilsbry, 1890:156, pl. 39, fig. 5.

Synonymy for *F. picta lata:*

Fissurella lata Sowerby, 1835a:124; Sowerby, 1835b:3, fig. 63; Reeve, 1849, pl. 1, fig. 5; Hupé, 1854:243; Sowerby II, 1862:187, fig. 13; Pilsbry, 1890:147, pl. 31, figs. 18, 19; Dall, 1909:241; Ziegenhorn and Thiem, 1925:13, pl. 1, fig. 11; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:107; Dell, 1971:187, pl. 4, figs. 12–14; Ramirez-Boehme, 1974:31 [key].

Fissurella navidensis Ramirez-Boehme, 1974:17, 31 [key].

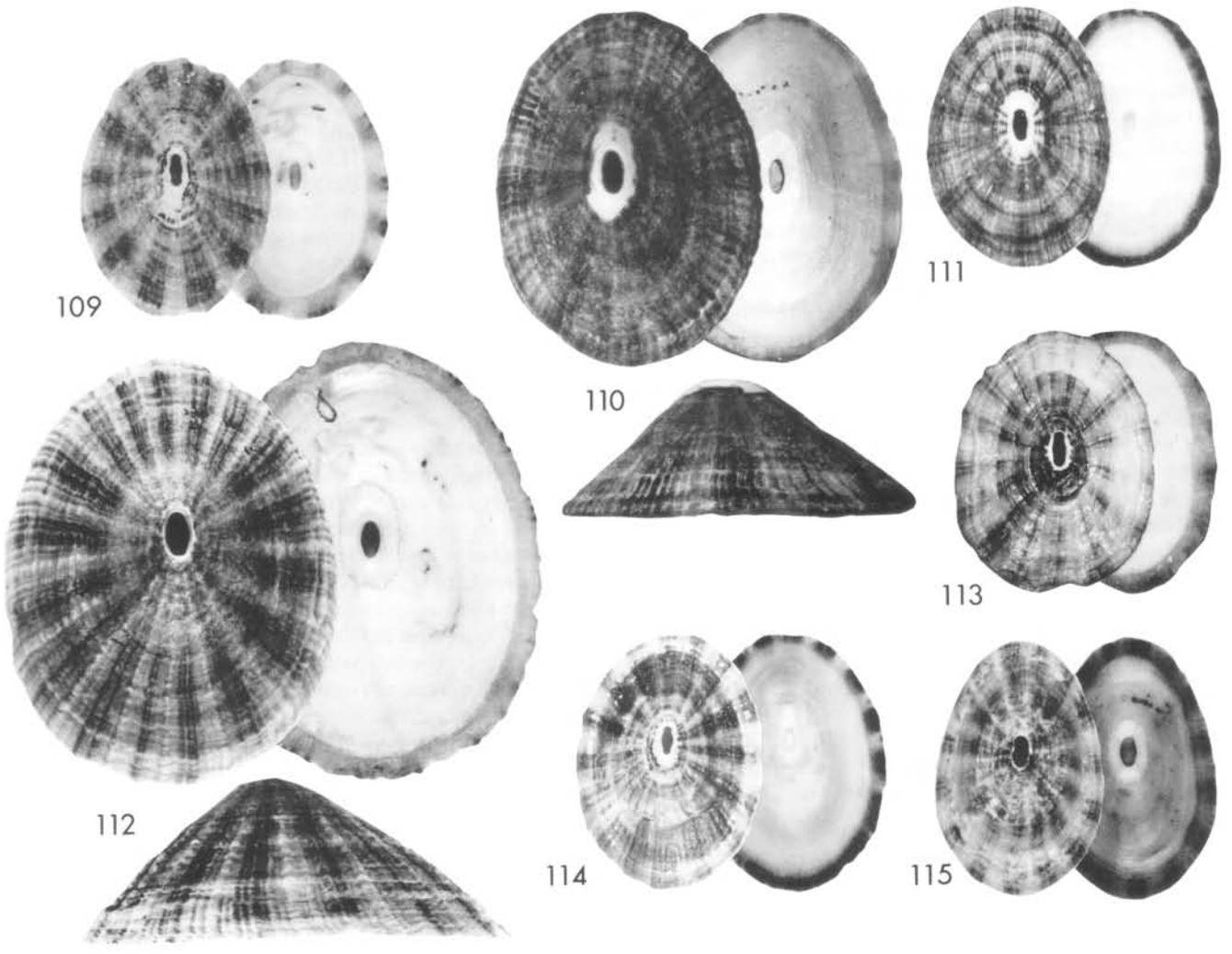
Shell (*F. picta picta*). Medium large (65–95 mm mature length), moderately elevated; outline elongate oval, sides of shell slightly raised. Sculpture of sharp, narrow radial ribs; primary ribs remaining stronger than secondary and tertiary ribs; occasional specimens with weak ribs. Ground color white, sometimes gray, rayed with black and white; strongest ribs centered on both light and dark rays; dark rays usually split into number of fine lines of black, a result of lack of pigment in grooves between fine ribs. Rays faint on light ground in some, or black on gray ground and with rays interrupted to produce concentric patterns of banding. Margin broad and flat, showing penciled pattern of rays. Cut shells show that pigment of rays extends through calcitic layer. Foramen elongate in juvenile shells, elongate to oval in mature shells.

Shell (*F. picta lata*). Medium large (50–80 mm mature length), height moderately to strongly elevated; outline elongate-oval to oval, sides of shell slightly raised. Sculpture of strong radial ribs; primary ribs remaining strong at all growth stages. Ground color yellowish white, rayed with yellowish purple; strongest ribs centered on both light and dark rays; dark rays usually split into number of fine lines coinciding with secondary and tertiary ribs; pigment tending to be absent in grooves between ribs. Color pattern fairly uniform, with dark rays on lighter ground. Margin broad and flat in young shells, sharply defined, gray, showing pattern of rays and penciled pattern. Cut shells showing pigment of rays throughout calcitic layer. Foramen elongate in young shells, oval in mature shells.

Juvenile Shell. Juveniles of both subspecies are oval and high, margin broad; strong primary ribs coincide with light rays, becoming stronger and slightly nodulous in specimens longer than 5 mm. Secondary ribs develop in interspaces between primary ribs; dark rays develop in rib interspaces and show some concentric interruptions in intensity.

Mantle and Foot. Body nearly retractable within shell; cephalic tentacles dark on outer side, reddish on inner side, and yellowish at tips. Mantle lobe relatively narrow, banded to correspond to pattern of rays; papillae of both edges of mantle lobe moderately developed. Side of foot marbled with light and dark, tubercles lighter tipped; southernmost specimens often lighter overall.

Habitat. Mid-tidal to lower intertidal zone on vertical to horizontal surfaces and on the sides of loose boulders; wedged in crevices under more exposed conditions; not extending into the sublittoral zone. At the north end of the range in the



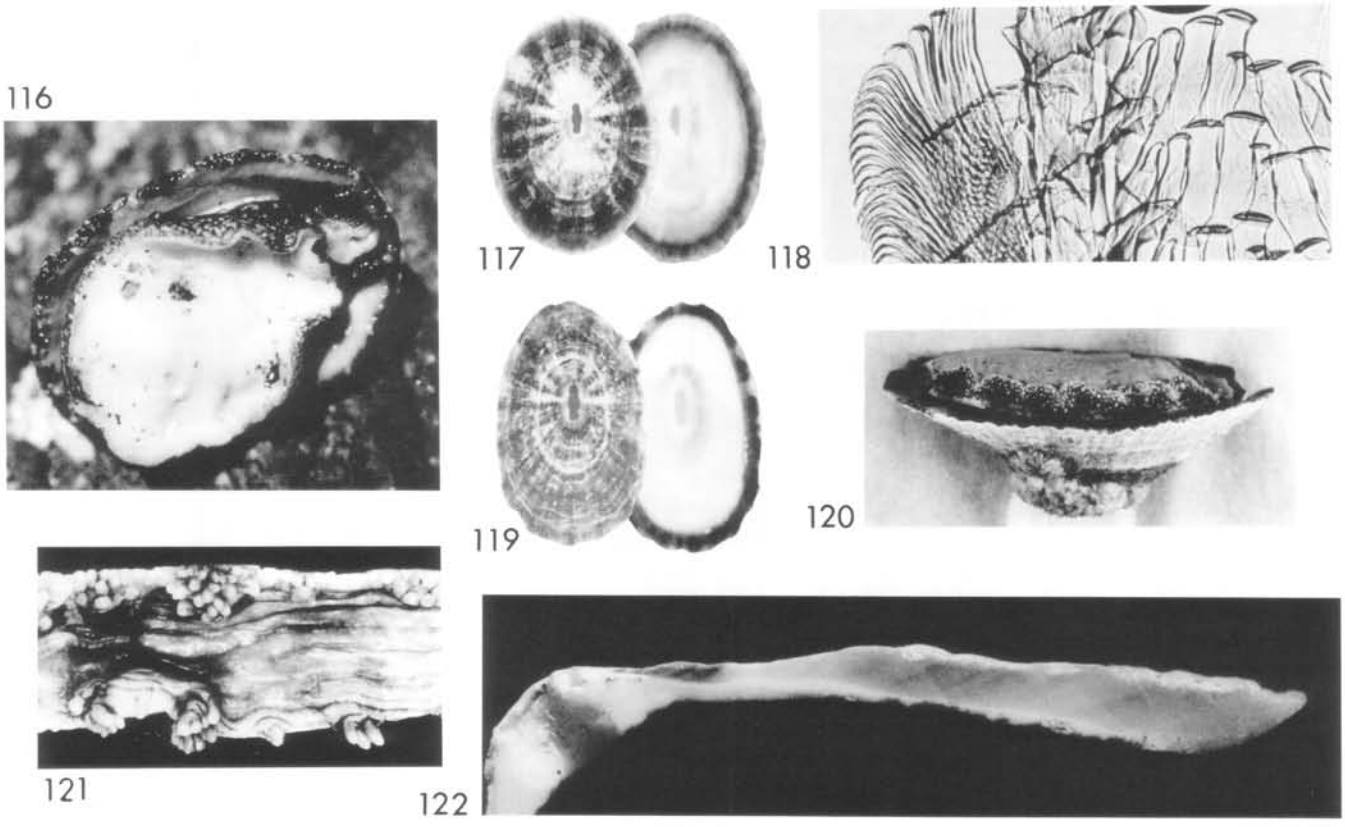
Figures 109 through 115. *Fissurella picta lata* Sowerby, 1835. Mature shells. (**109**) Montemar, Valparaíso Province, Chile. LACM 75-30, 37.9 × 27.8 × 13.4 mm. (**110**) Holotype, *F. navidensis* Ramirez-Boehme. Bahía Navidad, Santiago Province, Chile. MNHN 200376, 66 × 51 × 22 mm. (**111**) Río Bio-bio, Concepción Province, Chile. LACM 75-35, 24.8 × 17.6 × 8.2 mm. (**112**) Lectotype, *F. lata* Sowerby. Isla Santa Maria, Bahía Concepción, Chile. BMNH 197571, 83.4 × 64.3 × 31.6 mm. (**113**) Río Bio-bio, Concepción Province, Chile. LACM 75-35, 37.9 × 28.7 × 8.8 mm. (**114**) Mehuin, Valdivia Province, Chile. LACM 75-36, 40.4 × 29.2 × 11.7 mm. (**115**) Same locality. LACM 75-36, 40.4 × 26.5 × 12.5 mm.

vicinity of Valparaíso, *F. picta lata* is uncommon; the only two living specimens that I found occurred on horizontal surfaces adjacent to *F. limbata*. At Concepción and Mehuin and in the Strait of Magellan where *F. picta picta* occurs, specimens were common under all conditions of exposure. At these localities, such characteristic northern species as *F. latimarginata* and *F. maxima* were scarce or missing, suggesting a correlation between the dominance of *F. picta lata* and absence of competition from the other species.

Distribution. Islote Concon, Valparaíso Province, Chile (32°52′ S) (LACM 75-31, McLean), to Tierra del Fuego and Isla de los Estados, Argentina, probably south to Cape Horn and east to the Falkland Islands. Fossil specimens are known from shoreline terraces at Comodora Rivadavia, Chubut Province, Argentina (45°52′ S) (MCZ 28329), but living specimens are unknown on the mainland Patagonian coast north of Tierra del Fuego. The subspecies *F. picta picta* occurs in the Magellanic region of Chile, extending north to the vicinity of Isla de Chiloe. Populations that occur in the area of overlap, chiefly in the vicinity of Isla de Chiloe, are consistent but may have features that make assignment to either subspecies arbitrary (see further discussion below).

Number of Lots Examined. *F. picta picta:* 95 (LACM 19, AMNH 15, ANSP 5, MACN 33, MNHN 10, USNM 13). *F. picta lata:* 64 (LACM 11, AMNH 7, ANSP 2, MACN 5, MNHN 35, USNM 4).

Taxonomic History. The typical form of *Fissurella picta* from the Strait of Magellan has been well known and understood by all authors. Juvenile specimens have been given the name *F. atrata* Reeve, but it has otherwise not been burdened



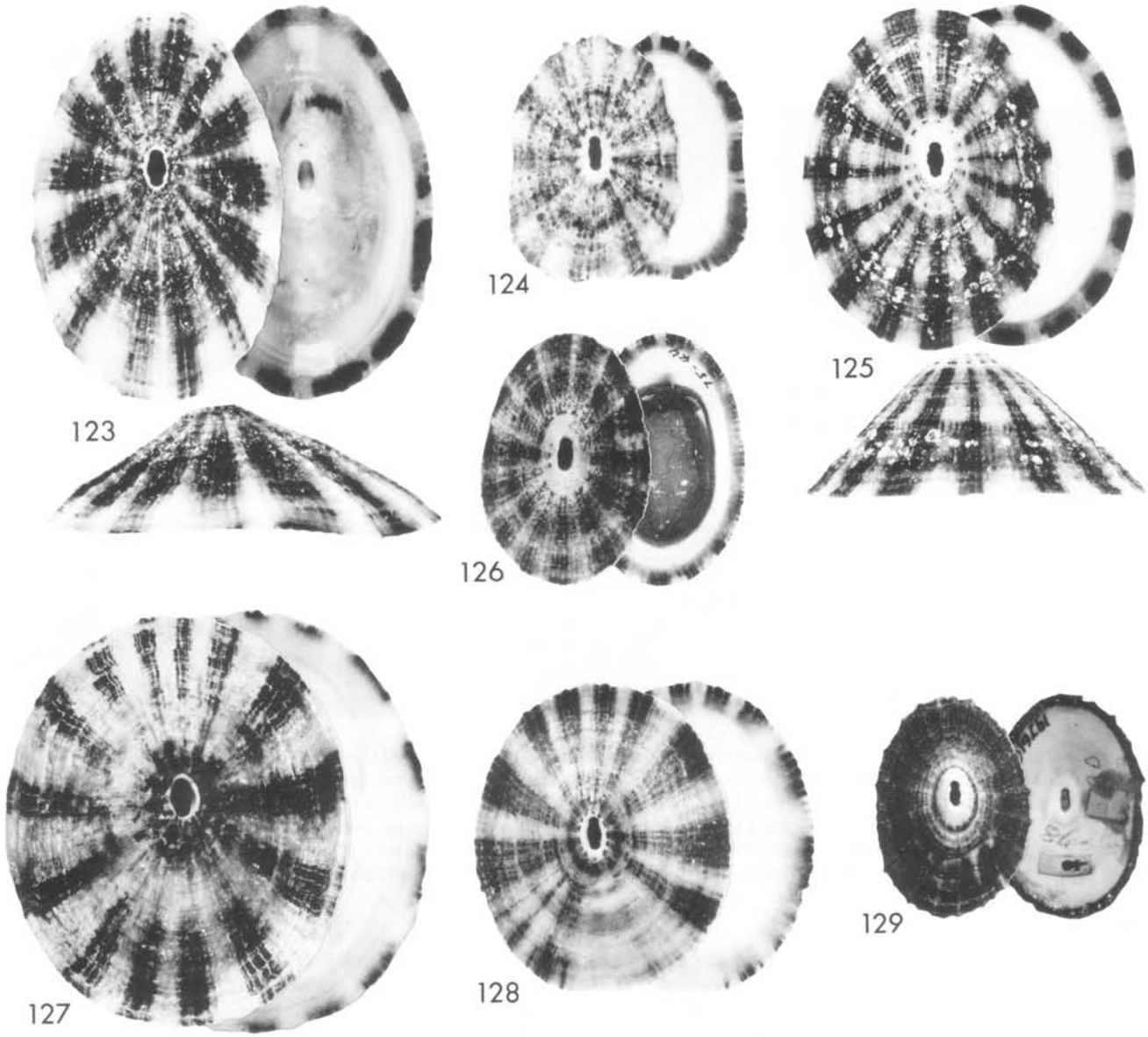
Figures 116 through 122. *Fissurella picta lata* Sowerby, 1835. Bodies of living and preserved specimens, juvenile shells, radula, mantle lobe, and cut shell. (**116**) Living specimen, ventral view, head at right. Río Bio-bio, Concepción Province, Chile. LACM 75-35. (**117**) Juvenile shell. Guabun, Chiloe Province, Chile. LACM 75-40, 12.6 × 8.6 × 3.3 mm. (**118**) Radula of small specimen. Río Bio-bio, Concepción Province, Chile. LACM 75-35, width of field 0.9 mm, shell length 27.3 mm. (**119**) Juvenile shell. Same locality. LACM 75-35, 13.5 × 8.3 × 4.3 mm. (**120**) Preserved specimen. Same locality. LACM 75-35, shell length 59.5 mm. (**121**) Mantle lobe. Island off Mehuin, Valdivia Province, Chile. LACM 75-37, length 8 mm. (**122**) Cut shell. Same locality. LACM 75-37, length of cut edge 32 mm.

with excessive numbers of synonyms, as have the other two common southern species, *F. radiosa* and *F. oriens*. Sowerby's *Fissurella lata* has not previously been a well understood taxon, perhaps because it is rare in the most populated region of central Chile. It is here for the first time regarded as a northern subspecies of the well-known *F. picta*. The original description of *F. lata* included the remark: "This species approaches, in form and colouring, very near to *Fiss. picta,* Lam.," an accurate observation not noticed by subsequent authors. In his discussion of this taxon, Riveros-Zuñiga merely quoted previous authors and figured what is more likely to be a specimen of *F. costata*. However, the Ziegenhorn and Thiem (1925) figure is a good representation of *F. picta lata*.

Abundance and Use. Both subspecies are large enough and common enough, at least at Concepción and to the south, to be important as a food resource. Numerous specimens were seen in shell piles at Mehuin. Moreno et al. (1984) have given an account of the fishery and ecology of this species at Mehuin. I have no information on the utilization of the species at more southern localities.

Characteristics and Variability. The typical *F. picta picta* is large-shelled, with coarse radial ribs and primary ribs that remain strong; the margin is broad; the dark colored rays are split into numerous fine lines by grooves that lack pigment and separate the fine ribs. Variation is extensive, chiefly in strength of ribbing and color pattern. Variations in outline of the base are unusual; some oval shells have been seen (Figs. 127, 128). Sculpture varies from coarse to nearly smooth. Most specimens are colored with gray rays on a white ground; variants with dark ground color are common. There are frequent concentric bands of different color intensity, probably representing seasonal changes in temperature and food availability.

Fissurella picta lata has a broad outline, as the name implies. Like *F. picta picta* it is also characterized as a large-shelled form with coarse ribbing and primary ribs that remain strong; the color rays are also split into thin lines by deep grooves in which the color is lacking. The margin is broad at all growth stages, and the mantle lobe papillae and foot tubercles are developed as in *F. picta picta*. As in the typical subspecies, there is extensive variation in *F. picta lata*. Al-

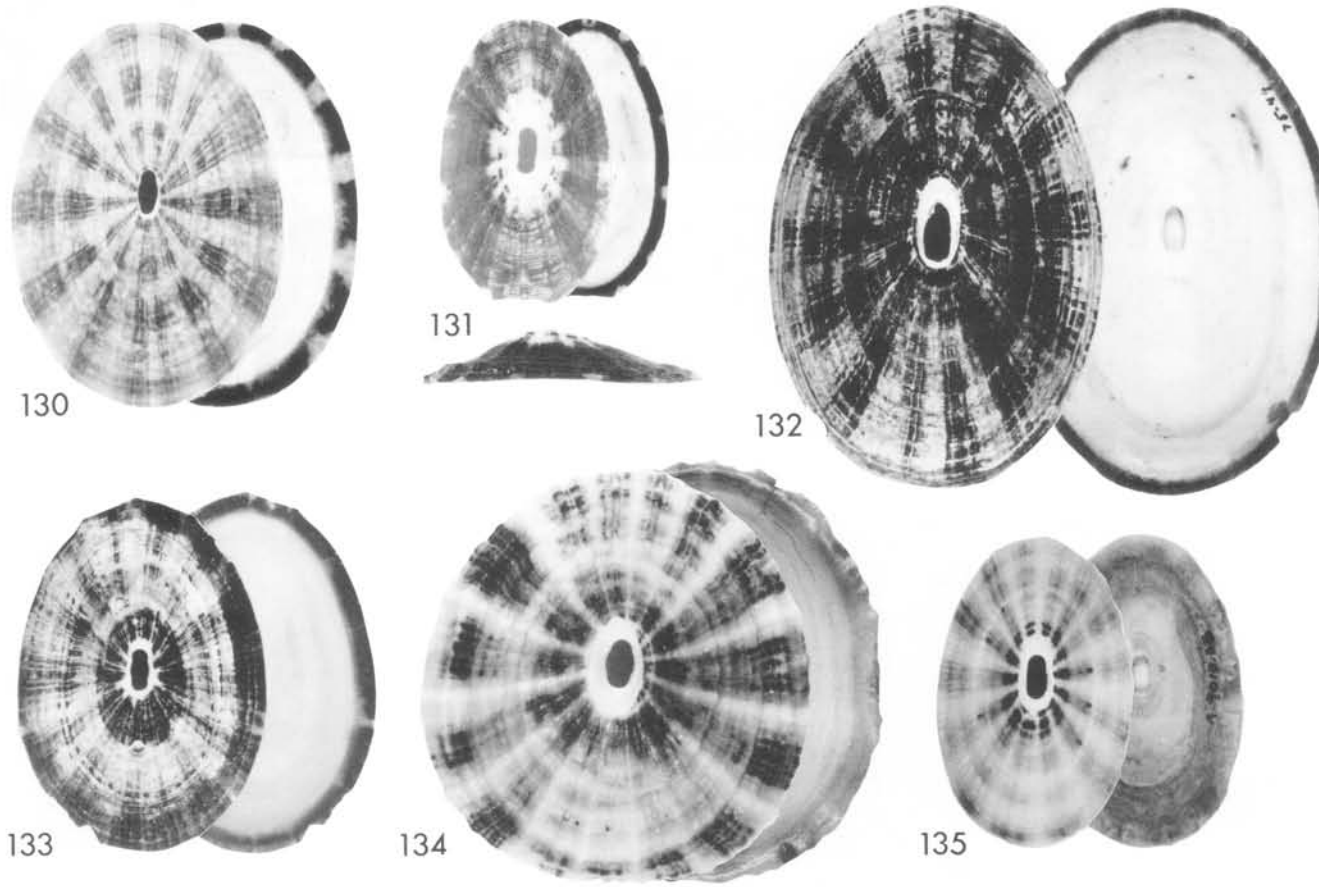


Figures 123 through 129. *Fissurella picta picta* Gmelin, 1791. Mature shells. (**123**) Pargua, Llanquihue Province, Chile. LACM 75-39, 77.2 × 49.3 × 23.1 mm. (**124**) Pumalin, Chiloe Province, Chile. LACM 75-41, 24.5 × 16.9 × 6.5 mm. (**125**) Same locality. LACM 75-41, 59.6 × 43.5 × 24.5 mm. (**126**) Islota Nihuel, Chiloe Province, Chile. LACM 75-44, 39.8 × 26.4 × 16.4 mm. (**127**) Quellón, Chiloe Province, Chile. LACM 75-45, 83.5 × 68.8 × 36.8 mm. (**128**) Pumalin, Chiloe Province, Chile. LACM 75-41, 48.4 × 39.6 × 18.2 mm. (**129**) Holotype, *F. muricata* Reeve. Locality unknown. BMNH 1976144, 25.8 × 18.4 × 13.0 mm.

though most specimens are elevated, the height is variable, and low forms occur in some populations along with more elevated specimens. Ground color ranges from light to dark gray; the rays are usually darker than the ground color but in some cases only slightly darker.

The major difference between the two subspecies is that *F. picta lata* has a more oval outline and usually is more elevated than *F. picta picta*. However, these are variable features within the species as a whole, and specimens occur at either extreme of the distribution having proportions typical of the other extreme. Specimens from the area of overlap, however, are more likely to have the intermediate proportions. Another difference is that of the coloration of the rays: *Fissurella picta picta* has dark purple to gray rays, whereas *F. picta lata* has rays that more clearly show the purple or reddish coloration. In both subspecies, however, the rays change color to reddish if the shells are faded by exposure to the sun. Shells from shell piles along the shore are much redder than those of live-collected or beach-worn specimens.

The extreme differences noted in some populations around Isla de Chiloe seem to be correlated with conditions of exposure to the open coastline on the west, or to a more pro-

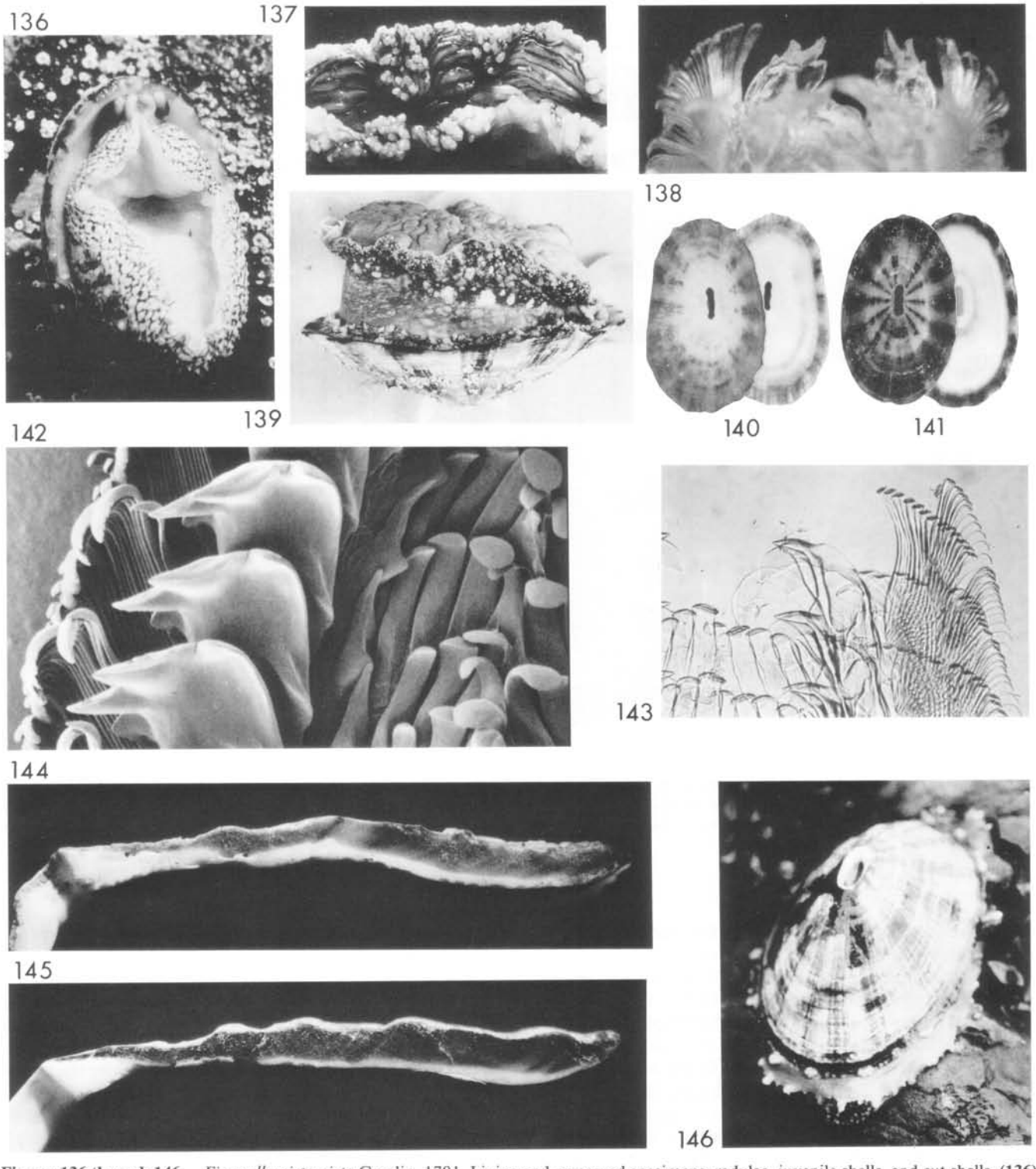


Figures 130 through 135. *Fissurella picta picta* Gmelin, 1791. Mature shells. **(130)** Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, 58.2 × 40.4 × 18.3 mm. **(131)** Holotype, *F. atrata* Reeve. Locality unknown. BMNH 197564, 23.8 × 14.0 × 5.0 mm. **(132)** Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, 86.3 × 58.3 × 28.3 mm. **(133)** Same locality. LACM 75-49, 49.2 × 34.3 × 13.7 mm. **(134)** Laredo Bay, Magallanes Province, Chile. USNM 118235, 68.6 × 61.7 × 30.0 mm. **(135)** Fox Bay, Falkland Islands. LACM 90800, 43.3 × 27.3 × 11.5 mm.

tected habitat along the channels to the east, where tidal extremes are greater than those of the open coast and water movement is produced by tidal currents. At Guabun, on the northwest, exposed side of the island (41°50′ S, 74°02′ W), the typical purple-rayed, oval, elevated form of *F. picta lata* occurs. Not far away at Pargua, on the mainland side of the Canal de Chacao (41°47′ S, 73°28′ W), I found the gray-rayed, low, elongate form typical of *F. picta picta* (Fig. 123). At Pumalin on the mainland opposite the southern tip of Isla de Chiloe (42°42′ S, 72°52′ W), the population was intermediate between the two extremes, more oval than typical for *F. picta picta,* but having no trace of the reddish rays (Fig. 125). At Isla Laitec off the southeast end of Isla de Chiloe (43°12′ S, 73°36′ W), shells were proportionately more elongate, typical of *F. picta picta.* Based on these four populations, I consider that *F. picta lata* occurs south along the outer coast of Isla de Chiloe and *F. picta picta* occurs to the north along the inner side of Chiloe Island. I do not know, however, whether populations from the exposed sides of islands to the south of Chiloe Island would also agree with *F. picta lata.*

Affinity and Comparisons. *Fissurella picta picta* most resembles *F. radiosa,* a smaller-shelled species that is similar in overall proportion, has sculpture of strong ribbing with persistently strong primary ribs, and has a similar color pattern. However, *F. picta picta* reaches nearly twice the size of *F. radiosa,* has a much broader margin at all growth stages, and has a more centrally placed foramen. The penciled effect of the dark rays of *F. picta picta* is not seen in *F. radiosa. Fissurella picta picta* does not occur sympatrically with any of the large species of northern Chile. It differs from all of them sufficiently to require no comparison.

The subspecies *F. picta lata* does occur sympatrically with many of the other species. The latter subspecies is most closely related to, and difficult to distinguish from, *F. costata. Fissurella picta lata* tends to be higher, more darkly rayed, and to have sculpture with stronger primary ribs and a slightly larger foramen than that of *F. costata.* Separation of the two



Figures 136 through 146. *Fissurella picta picta* Gmelin, 1791. Living and preserved specimens, radulae, juvenile shells, and cut shells. (**136**) Ventral view of living specimen. Pumalin, Chiloe Province, Chile. LACM 75-41. (**137**) Mantle lobe. Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, length 12 mm. (**138**) Air-dried radula. Isla Laitec, Chiloe Province, Chile. LACM 75-47, width of ribbon 1.9 mm, shell length 54.3 mm. (**139**) Preserved specimen. Isla de Los Estados, Argentina. LACM 71-284, shell length 71.8 mm. (**140**) Juvenile specimen. Pumalin, Chiloe Province, Chile. LACM 75-41, 10.9 × 6.7 × 3.6 mm. (**141**) Juvenile specimen. Puerto Espanol, Bahía Aguirre, Tierra del Fuego, Argentina. LACM 73-67, 17.4 × 10.6 × 3.6 mm. (**142**) SEM photo of radula. Width of field 1.0 mm. (**143**) Radula of small specimen. Isla Laitec, Chiloe Province, Chile. LACM 75-47, width of field 0.7 mm, shell length 27.9 mm. (**144**) Cut shell. Pumalin, Gulfo Corcovado, Chile. LACM 75-41, length of cut 37 mm. (**145**) Cut shell. Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, length of cut 33.2 mm. (**146**) Living specimen attached to substrate. Same locality. LACM 75-49.

species on shell characters may be difficult and sometimes entirely arbitrary, as the range of variation in the two species seems to overlap. It is easy to distinguish the living animals, however. The foot and mantle lobe of *F. picta lata* are gray, those of *F. costata* a pale pinkish brown.

Synonymy and Types. *Fissurella picta* was known to pre-Linnaean authors. It was probably the first of the Chilean species to reach Europe because it is so common in the Strait of Magellan. Gmelin (1791) is credited with the name; his knowledge of it came from figures in several previous non-binomial works. Lamarck and Deshayes referred to it as the "Fissurelle de Magellan." Deshayes credited the name *picta* to Lamarck, but Sowerby II (1862) and Pilsbry (1890) correctly credited the authorship to Gmelin. Type material is unknown.

The holotype of *Fissurella atrata* Reeve, 1850, is BMNH 197564 (Fig. 131), length 23.8 mm, locality unknown. It is a small, dark-colored specimen of *F. picta,* easily recognized by its relatively broad, dark inner margin.

The holotype of *F. muricata* Reeve is BMNH 1976144, locality unknown (Fig. 129). It is a small dark specimen, the margin sufficiently broad to relate it to *F. picta* rather than *F. radiosa.* Because the interior has not previously been figured, the dark margin has been missed, which explains why no author has related it to any of the Peruvian-Magellanic species.

There are two syntypes of *F. lata* Sowerby, BMNH 197571, from Isla Santa Maria, Bahía Concepción, Chile, dimensions 83.4 mm × 64.3 × 31.6 mm, and 77.0 × 61.3 × 25.5 mm. The larger specimen, figured by Dell (1971), is figured here and designated the lectotype (Fig. 112). Both specimens are reddish rayed and clearly show the strong primary ribs in the light interspaces between the rays.

The holotype of *F. navidensis* Ramirez-Boehme, 1974, from Bahía Navidad, Santiago Province, Chile (33°56′ S, 71°52′ W), MNHN 200376 (Fig. 110), is a worn specimen of *F. picta lata,* with which it was not compared. Its similarity to *F. picta* was noted by its author, however, and the differences described are those that are here used to distinguish the two subspecies of *F. picta.*

Fissurella radiosa Lesson, 1831

Figures 147–175

Fissurella radiosa is here considered to have two geographic subspecies: *F. radiosa radiosa* in the Magellanic region of Chile and Argentina, and *F. radiosa tixierae* in the Golfo San Matias and Peninsula Valdez region of Argentina.

Synonymy for *F. radiosa radiosa:*

Fissurella radiosa Lesson, 1831:411; Orbigny, 1841:473; Pilsbry, 1890:157; Strebel, 1907:85, pl. 1, figs. 4, 5a–d, pl. 9, fig. 6; Melvill and Standen, 1914:115; Carcelles, 1950: 51; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951:111; Dell, 1971:192; Ramirez-Boehme, 1974:32 [key]; Scarabino, 1977:178, pl. 1, fig. 5.

Fissurella picta var. *radiosa,* Ziegenhorn and Thiem, 1925: 8, 11, pl. 1, fig. 6.

Fissurella nigra Philippi, 1845:60; Philippi, 1846, pl. 2, fig. 22; Reeve, 1849, pl. 6, fig. 37. Not *F. nigra* Lesson, 1831.

Fissurella darwinii Reeve, 1849, pl. 1. fig. 7; Hupé, 1854: 247; Rochebrune and Mabille, 1889:74; Pilsbry, 1890:144, pl. 30, fig. 7, pl. 46, figs. 15–17; Melvill and Standen, 1898: 102; Strebel, 1907:93; Carcelles, 1950:51; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951:98, fig. 16; Dell, 1971:185, pl. 4, fig. 4; Ramirez-Boehme, 1974:30 [key].

Fissurella picta var. *darwinii,* Ziegenhorn and Thiem, 1925: 8, 11, pl. 1, fig. 5.

Fissurella grisea Reeve, 1849, pl. 6, fig. 6; Sowerby II, 1862: 184, pl. 239, fig. 85; Pilsbry, 1890:152, pl. 39, fig. 9.

Fissurella exquisita Reeve, 1850, pl. 11, fig. 74; Hupé, 1854: 246; Sowerby II, 1862:186, figs. 32, 128; Rochebrune and Mabille, 1889:74; Strebel, 1908:78, pl. 5, figs. 74a–c; Carcelles and Williamson, 1951:256; Riveros-Zuñiga, 1951: 112, fig. 22; Métivier, 1969:115, fig. 1B [radula]; Dell, 1971:185, pl. 5, figs. 1, 3; Ramirez-Boehme, 1974:30.

Fissurella philippiana Reeve, 1850, errata page; Sowerby II, 1862:186, fig. 30; Pilsbry, 1890:146, pl. 33, fig. 40, pl. 58, figs. 24–26; Dall, 1909:242; Ziegenhorn and Thiem, 1925: 13, pl. 1, figs. 10a, 10b; Carcelles and Williamson, 1951: 253; Riveros-Zuñiga, 1951:106, fig. 19; Dell, 1971:190.

Fissurella philippii Hupé, 1854:245 (new name for *F. nigra* Philippi, not Lesson).

Fissurella polygona Sowerby II, 1862, fig. 177 (not fig. 137); Pilsbry, 1890:148, pl. 60, fig. 84; Melvill and Standen, 1898:102; Melvill and Standen, 1914:115; Carcelles and Williamson, 1951:254; Dell, 1971:192, pl. 4, figs. 9–11.

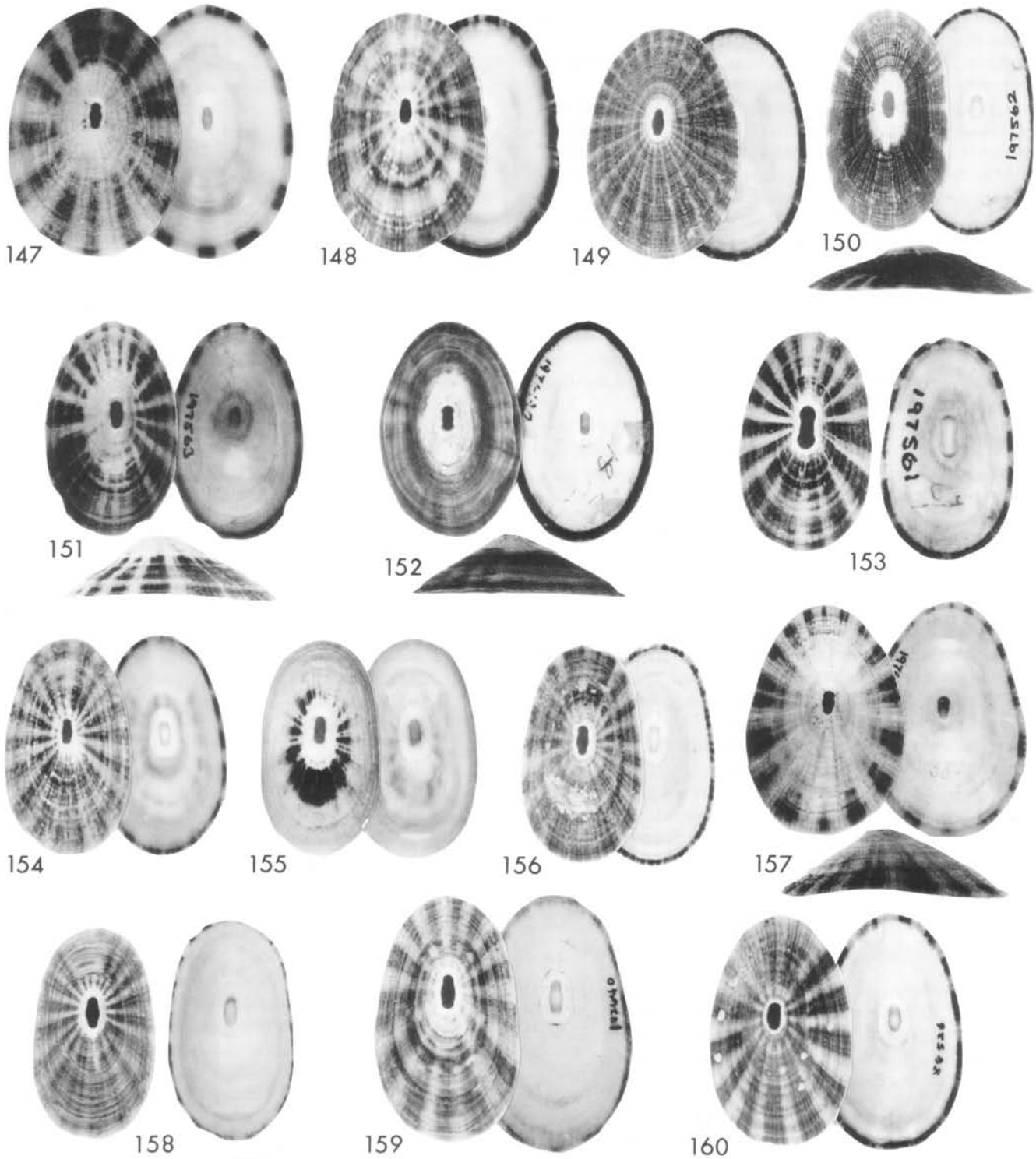
Fissurella dozei Rochebrune and Mabille, 1885:108; Rochebrune and Mabille, 1889:72, pl. 5, fig. 4; Carcelles, 1950: 51; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:101, fig. 17; Dell, 1971:185.

Synonymy for *F. radiosa tixierae:*

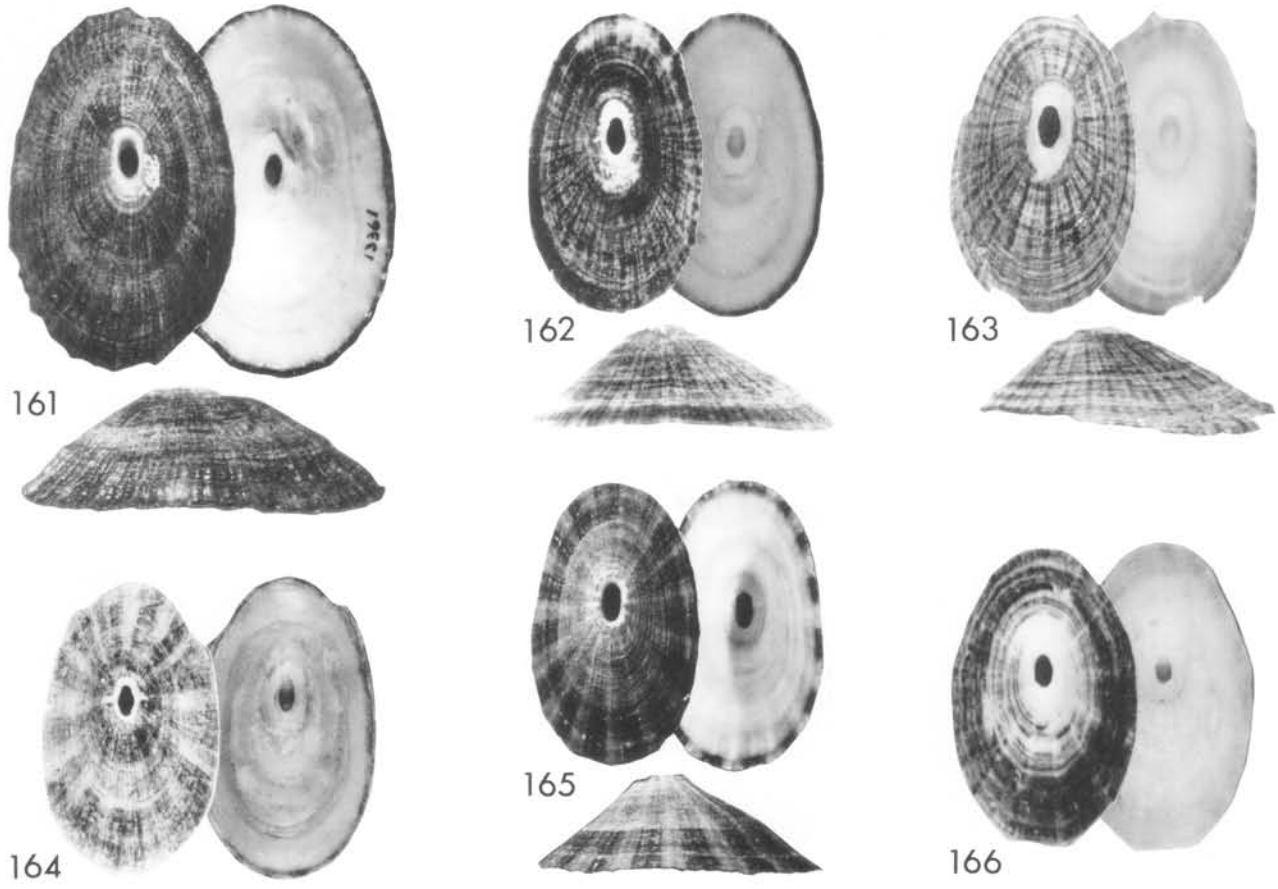
Fissurella tixierae Métivier, 1969:116, fig. 1A [radula], pl. 1, figs. 1–3, 9.

Shell (*F. radiosa radiosa*). Small to medium sized (40 to 55 mm mature length), low to moderately elevated; outline elongate oval, somewhat tapered anteriorly; sides of shell raised. Sculpture of sharply raised, narrow ribs that crenulate margin; primary ribs remaining stronger and more prominent at all growth stages. Ground color varying from white to gray or black with gray or reddish gray rays; the pattern of rays frequently interrupted by concentric changes in color intensity. Primary ribs coinciding with light rays; in uniformly dark shells primary ribs slightly lighter in color. Margin relatively narrow at all growth stages, not zoned; cut shells showing ground color or pattern of rays of uniform intensity throughout calcitic layer. Foramen just anterior of center, elongate and tripartite at all growth stages.

Shell (*F. radiosa tixierae*). Small (20 to 45 mm mature length), moderately to strongly elevated; outline elongate oblong, tapered anteriorly; margin more or less in same plane. Sculpture of narrow ribs that finely crenulate margin. Ground color white to dark gray or black with gray or reddish gray rays, often interrupted by concentric changes in intensity. Primary ribs coinciding with light rays. Margin narrow at all growth stages, showing pattern of rays. Foramen slightly anterior of center, elongate and tripartite at all growth stages.



Figures 147 through 160. *Fissurella radiosa radiosa* Lesson, 1831. Mature shells. (**147**) Pumalin, Chiloe Province, Chile. LACM 75-41, 47.0 × 32.0 × 13.1 mm. (**148**) Same locality. LACM 75-41, 41.9 × 27.4 × 11.8 mm. (**149**) Same locality. LACM 75-41, 43.5 × 28.4 × 13.7 mm. (**150**) "Syntype" [no standing as type] *F. philippiana* Reeve. "Chile." BMNH 197562, 42.0 × 22.8 × 8.6. (**151**) Lectotype, *F. darwinii* Reeve. Strait of Magellan, Chile. BMNH 197563, 36.9 × 22.8 × 11.0 mm. (**152**) Lectotype, *F. grisea* Reeve. Locality unknown. BMNH 1975140, 30.3 × 19.9 × 9.9 mm. (**153**) Lectotype, *F. exquisita* Reeve. Locality uncertain. BMNH 197561, 23.4 × 14.2 × 5.2 mm. (**154**) Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, 40.2 × 23.0 × 10.6 mm. (**155**) Same locality. LACM 75-49, 38.2 × 21.4 × 8.2 mm. (**156**) Falkland Islands. USNM 368377, 46.7 × 20.1 × 9.4 mm. (**157**) Lectotype, *F. polygona* Sowerby II. Falkland Islands. BMNH 1976151,



Figures 161 through 166. *Fissurella radiosa tixierae* Métivier, 1969. Mature shells. (**161**) San Antonio Oeste, Rio Negro Province, Argentina. MACN 13361, 48.3 × 31.3 × 14.3 mm. (**162**) Puerto Lobos, Chubut Province, Argentina. MCZ 288334, 24.6 × 14.3 × 8.3 mm. (**163**) Holotype, *F. tixierae* Métivier. Golfo Nuevo, Chubut Province, Argentina. MNHNP, 22.5 × 13.7 × 8.0 mm (beach shell). (**164**) Puerto Madryn, Golfo Nuevo, Chubut Province Argentina. LACM 34858, 24.9 × 14.9 × 8.5 mm (beach shell). (**165**) Punta Cracker, Golfo Nuevo, Chubut Province, Argentina. LACM 78-90, 27.0 × 18.8 × 8.8 mm. (**166**) Puerto Madryn, Golfo Nuevo, Chubut Province, Argentina. USNM 152895, 25.5 × 15.6 × 10.6 mm (beach shell).

Juvenile Shell. Elongate, margin narrow, ribs fine and sharp, primary ribs lighter in color, secondary and tertiary ribs arising after shell reaches 5 mm in length.

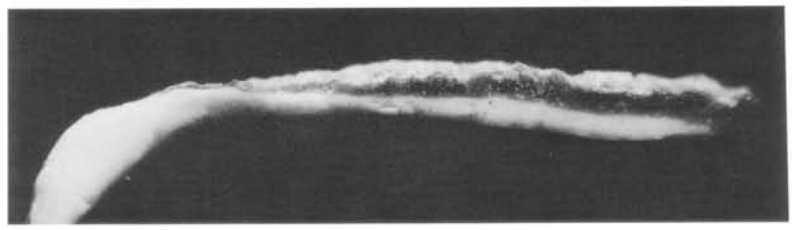
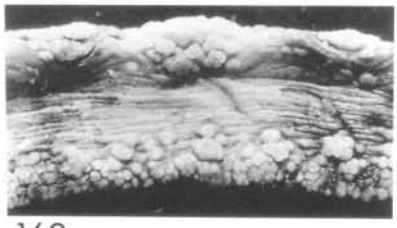
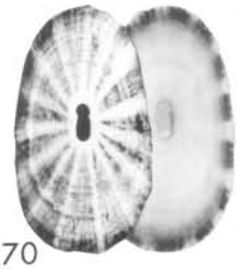
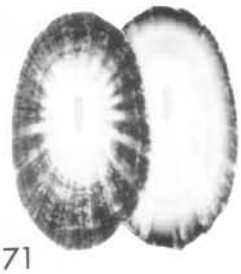
Mantle and Foot. Nearly retractable within shell. Mantle lobe relatively narrow, banded to correspond to pattern of rays; black-shelled individuals also banded. Papillae moderately developed, finely branched; side of foot dark, tubercles with lighter tips.

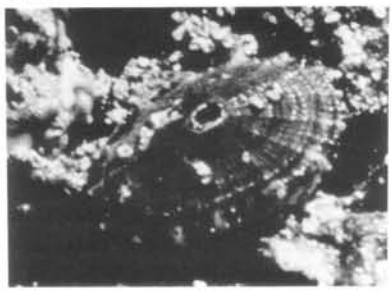
Habitat. Lowermost intertidal zone and offshore to at least 20 m. In 1975 I found it common at Pumalin in the Golfo Corcovado on the undersides of rocks in an area where the exposure is limited chiefly to swiftly moving tidal currents; I also observed it in the sublittoral at Isla Talcon. In the Strait of Magellan it was common at low tide under rocks at Puerto Hambre. Paul Dayton collected it by diving at Isla de los Estados in 1973. In 1978 I found *F. radiosa tixierae* to be common in the Golfo Nuevo and Golfo San Jose, Argentina, on undersides of rocks at low tide and dredged offshore to 20 m.

Distribution. Golfo Corcovado on the east side of Isla Chiloe, Chile (northernmost specimens examined from Pumalin, Chiloe Province, Chile, 42°42′ S, 72°52′ W, LACM 75-41) to Tierra del Fuego, probably south to Cape Horn, east to the Falkland Islands, and north in Argentina to the Golfo San Matias (northernmost specimens from San Antonio Oeste, Rio Negro Province, 40°45′ S, 64°58′ W, MACN 13361, A.

←

42.4 × 28.9 × 12.3 mm. (**158**) Puerto Deseado, Santa Cruz Province, Argentina. LACM 34851, 27.5 × 15.7 × 5.8 mm. (**159**) Puerto San Julian, Santa Cruz Province, Argentina. AMNH 182640, 45.0 × 26.4 × 12.4 mm. (**160**) Santa Cruz River, Santa Cruz Province, Argentina. ANSP 88526, 41.4 × 25.4 × 13.5 mm.



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Figures 167 through 175. *Fissurella radiosa radiosa* Lesson, 1831, and *F. radiosa tixierae* Métivier, 1969. Radula, cut shell, mantle lobe, juvenile shell, living and preserved specimens. **Figures 167 through 172.** *F. radiosa radiosa.* (**167**) Radula. Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, width of field 0.8 mm, shell length 20.8 mm. (**168**) Cut shell. Pumalin, Chiloe Province, Chile. LACM 75-41, length of cut edge 18.5 mm. (**169**) Mantle lobe. Fuerte Bulnes, Magallanes Province, Chile. LACM 75-48, length 11 mm. (**170**) Juvenile shell. Puerto el Hambre, Magallanes Province, Chile. LACM 75-49, 13.8 × 7.8 × 3.3 mm. (**171**) Juvenile shell. Pumalin, Chiloe Province, Chile. LACM 75-41, 10.0 × 6.0 × 2.7 mm. (**172**) Preserved specimen. Fuerte Bulnes, Magallanes Province, Chile. LACM 75-48, shell length 56.5 mm. **Figures 173 through 175.** *Fissurella radiosa tixierae.* (**173**) Living specimen attached to substrate. Punta Cracker, Golfo Nuevo, Chubut Province, Argentina. (**174**) Preserved specimen. Punta Ninfas, Golfo Nuevo, Chubut Province, Argentina. LACM 78-88, shell length 19.3 mm. (**175**) Ventral-lateral view of living specimen. Same locality. LACM 78-88.

Carcelles). The subspecies *F. radiosa tixierae* is characteristic only of the Golfo San Matias and the Golfo Nuevo and Golfo San Jose; specimens from such localities as Puerto Deseado and Puerto San Julian, Santa Cruz Province, Argentina, are consistently larger and lower in profile, identified as *F. radiosa radiosa.* This is the only species of *Fissurella* that ranges throughout the Magellanic Faunal Province in both Chile and Argentina, and the only one that does not extend into the region of overlap with the Peruvian Faunal Province in south-central Chile.

Number of Lots Examined. *F. radiosa radiosa:* 55 (LACM 14, AMNH 5, ANSP 1, MACN 27, MNHN 1, USNM 7); *F. radiosa tixierae:* 28 (LACM 7, AMNH 1, MACN 19, USNM 1).

Taxonomic History. *Fissurella radiosa* Lesson, 1831, was not originally illustrated. Most of the accounts dealing with this species have consisted of copies and translations of original descriptions of its numerous synonyms. Accounts with additional observations are those of Strebel (1907), who was the first to recognize the species, Ziegenhorn and Thiem (1925), and Riveros-Zuñiga (1951), who recognized a specimen under the name of *F. dozei* Rochebrune and Mabille. The species has been misidentified as *Lucapinella henseli* (Martens, 1900), from Puerto Deseado, Santa Cruz Province, Argentina, by Ringuelet et al. (1962).

The Argentinian subspecies *F. radiosa tixierae* was described as a distinct species by Métivier (1969), based on a single specimen. He also identified *F. exquisita* Reeve from the Golfo Nuevo (here considered a synonym of *F. radiosa*), apparently not having sufficient specimens to realize that a single species is represented in the Golfo Nuevo.

Abundance and Use. *Fissurella radiosa* is common throughout its range. It is a rather small form occurring to the south of the populated regions of Chile; I have no information as to whether it has been exploited for food.

Characteristics and Variability. The shell of *Fissurella ra-*

diosa radiosa is relatively small and elongate, with a narrow dark margin, the ribbing fine and sharp, and the primary ribs evident at all growth stages. Shell height varies from low to moderately high. Color variation includes rayed forms and some that are uniformly dark. Changes in color often occur with growth. Some shells are nearly colorless in early stages and later acquire rays; others are strongly rayed at first and then lose the rays entirely. Normally rayed specimens may have growth increments that are uniformly dark. The ribs can be very evident or so weak that one can barely distinguish primary ribs from secondary ribs. In the collections at hand there seem to be more of the weakly sculptured examples from the vicinity of the Strait of Magellan, whereas the strongly sculptured specimens are known from more northern localities in Chile and Santa Cruz Province, Argentina. The uniformly dark specimens have been seen only at Pumalin, in the Golfo Corcovado, where they occur with rayed forms. The largest observed specimen of the typical subspecies is 65 mm in length (LACM 75-42, Isla Talcon, Chile).

The large series of specimens of *F. radiosa tixierae* that I collected in the Golfo Nuevo and Golfo San Jose in 1978 are as variable in color as those of the typical subspecies, including many that are uniformly dark (Figs. 161, 162). There is such a preponderance of elevated specimens that the separation of a geographic subspecies based on this feature is justified. However, some specimens are as low as the typical subspecies. The largest specimen observed measures 48.3 mm in length (Fig. 161).

Affinity and Comparisons. *Fissurella radiosa* most resembles *F. picta. Fissurella radiosa* is smaller, has a narrower margin, a more anterior foramen, and lacks the penciled pattern of the rays. Unlike *F. picta picta,* which has gray rays only, there are some reddish-rayed forms. In shell morphology *F. radiosa* approaches *F. oriens,* which it may resemble in size, shape, and range of color possibilities, but it differs in having a narrower margin, more anterior foramen, and primary ribs that are raised, slightly nodular, and larger than the adjacent ribs, in contrast to the nearly smooth aspect of *F. oriens.* The papillae of the mantle fold are more strongly developed in *F. radiosa* than in *F. oriens. Fissurella radiosa* is more elongate than *F. peruviana* and has an elongate rather than oval foramen.

Synonymy and Types. Type material of *F. radiosa* Lesson, 1831, from the Falkland Islands, has never been illustrated and may not be extant. It is not housed in the Paris Museum where some of Lesson's material is now known (Bouchet, personal communication). Lesson's description stated: "The ribs are separated by profound narrow grooves, and they are arranged with three small ribs between each pair of larger ones, all over." This could also apply to *F. picta,* which was then well known, but the broad margin of *F. picta* was not mentioned; hence, by elimination we are left with *F. radiosa.* Strebel (1907) was the first to use the name *F. radiosa* in the sense adopted here.

Type material of *F. nigra* Philippi, 1845, not Lesson, 1831, has not been located. The locality was given only as "Chile." Philippi's illustration and description indicate that the shell was predominantly black, the young stages with lighter rays, the ribbing strong and unequal, and the margin narrow. Specimens collected at Pumalin, east of Isla de Chiloe, are a good match (Fig. 149), and the synonymy with *F. radiosa* is certain. Both Reeve and Hupé were to offer replacement names for the preoccupied name of Philippi.

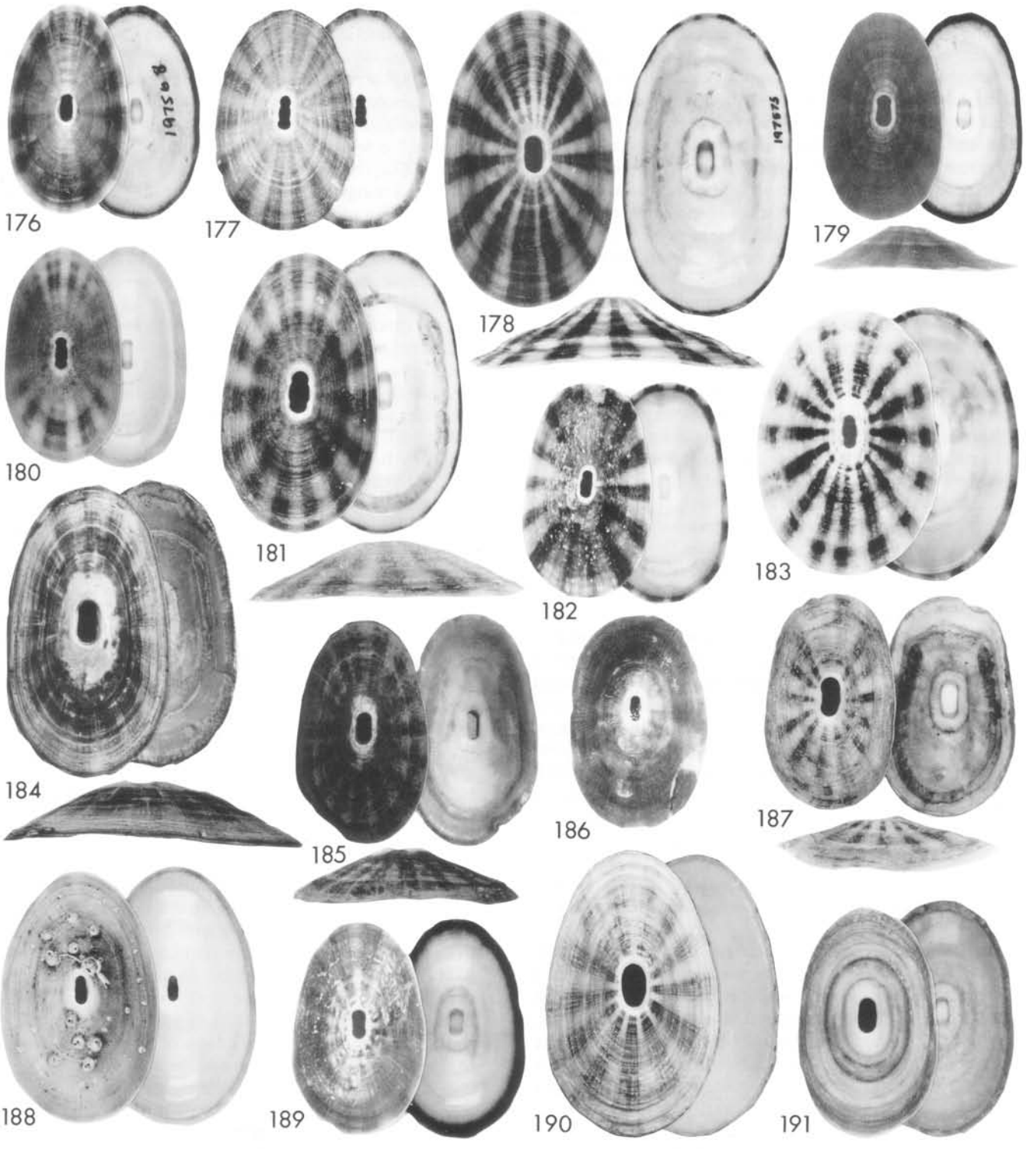
Fissurella darwinii Reeve, 1849, from the "Straits of Magalhaens," is represented by four syntypes, BMNH 197563, lengths, 37.0, 36.9, 33.9, and 21.3 mm. The smallest specimen has a margin broader than any in the three larger ones and is clearly a young *F. picta.* Dell (1971) figured the second largest specimen (36.9 mm in length); this is here figured and designated the lectotype (Fig. 151). The rays are reddish purple. Because the margin, which has not previously been illustrated, is narrow, I identify the type lot as *F. radiosa.* Pilsbry (1890) copied Reeve's illustration but also identified and figured a shell with a broader margin—that figure is here identified as *F. picta.*

Fissurella grisea Reeve, 1849, described without locality, is represented by two syntypes, BMNH 1976140, measuring 30.3 and 21.1 mm in length. The largest (Fig. 152) has been figured by Reeve and Sowerby II (1866) and is here designated the lectotype. Authors have not recognized this taxon. The shell is gray and has faint dark rays. The surface of the shell has evidently been treated with acid and only a trace of radial sculpture remains. I tentatively assign it to the synonymy of *F. radiosa,* suggested particularly by the tripartite foramen.

There are 5 specimens labeled *F. exquisita* Reeve, 1850, BMNH 197561. One small specimen is broken; the other four measure 45.3, 37.8, 34.0, and 23.4 mm in length. The Reeve locality is "Strait of Magalhaens," but the original label reads "Falkland Islands." The smallest intact specimen (Fig. 153) is a good match for the Reeve figure and was figured and designated the lectotype by Dell (1971). The largest specimen was also figured by Dell. All specimens are relatively low, have a narrow margin, are similarly rayed with reddish brown, and clearly show strong primary ribs.

Fissurella philippiana Reeve, 1850, was a name introduced on the errata page of the *Fissurella* monograph: "Sp. 37. For *F. nigra* Philippi, read *F. philippiana* Reeve." Reeve was renaming a homonym, although he did not explicitly state this. The specimens considered syntypes by Dell therefore have no standing as types. There are four specimens, BMNH 197562, the locality "Chile" in ink on the original mounting board, although Reeve gave the locality as "Southern Chile." The specimens measure 42.0, 38.6, 33.6, and 32.3 mm in length. They represent the dark form of *F. radiosa* in which the primary ribs are prominent and the margin narrow. Dell (1971) figured the 38.6 mm specimen; the largest is figured here (Fig. 150). The "syntypes" are very similar to those I found at Pumalin (Fig. 149). Dall (1909) inexplicably gave the locality as "Concepción, Chile," and this has been repeated by subsequent authors. No specimens corresponding to this locality have been found at the USNM. Concepción is well to the north of the known distribution of *F. radiosa.*

Fissurella philippii Hupé, 1854, was proposed as a replacement name for *F. nigra* Philippi, not Lesson. Hupé was unaware of the similar name proposed by Reeve.



Figures 176 through 191. *Fissurella oriens fulvescens* Sowerby, 1835, and *F. oriens oriens* Sowerby, 1835. Mature shells. **Figures 176 and 177.** *F. oriens fulvescens.* (**176**) Lectotype, *F. fulvescens* Sowerby. Valparaíso, Chile. BMNH 197568, 39.7 × 23.0 × 6.8 mm. (**177**) Islota Concon, Valparaíso Province, Chile. LACM 75-31, 23.2 × 14.8 × 4.5 mm (beach shell). **Figures 178 through 191.** *F. oriens oriens.* (**178**) Paralectotype, *F. oriens* Sowerby. Locality uncertain. BMNH 197575, 62.4 × 35.7 × 14.8 mm. (**179**) Lectotype, *F. mexicana* Sowerby. Locality unknown. BMNH 1944593, 38.6 × 22.2 × 8.6 mm. (**180**) Pargua, Llanquihue Province, Chile. LACM 75-39, 45.8 × 19.6 × 6.8 mm. (**181**) Pumalin, Chiloe Province, Chile. LACM 75-41, 58.0 × 32.7 × 12.0 mm. (**182**) 4–13 m, Islota Nihuel, Chiloe Province, Chile. LACM 75-43, 41.5 × 24.3 × 8.5 mm. (**183**) Same locality. LACM 75-42, 49.3 × 33.0 × 18.4 mm. (**184**) Holotype, *F. oblonga* Ramirez-Boehme. Punta

There are two syntypes of *F. polygona* Sowerby II, 1862, BMNH 1976151, from the Falkland Islands. The largest measures 42.4 mm in length and was figured by Dell (1971). It is here designated the lectotype (Fig. 157). The smaller specimen measures 22.2 mm in length and has proportions similar to the larger. Primary ribs are not as pronounced as shown in the original figure (copied by Pilsbry, 1890); the rays are reddish brown. The specimens represent the broad, elevated extreme of *F. radiosa,* which may be the typical form, as it has the same general type locality as that of the senior synonym.

Type material of *Fissurella dozei* Rochebrune and Mabille, 1885, described from Santa Cruz, Patagonia, was not located in the Paris Museum by P. Bouchet, although type material of two other Rochebrune and Mabille taxa is known in the Paris Museum. The drawing given by the authors in 1889 is a fair rendition of *F. radiosa* with well marked ribs, the figure showing that there are primary ribs that are slightly more prominent than the secondary ribs; the width of the margin is not mentioned. Puerto Santa Cruz, Santa Cruz Province, Argentina (50°01′ S) is north of the eastern entrance to the Strait of Magellan. This is a region in which *F. radiosa* is now known to be the only living species of *Fissurella.* The synonymy of *F. dozei* with *F. radiosa* is therefore reasonably certain.

Fissurella tixierae Métivier, 1969, was based on one specimen in poor condition, MNHNP uncataloged, from the intertidal zone in the Golfo Nuevo, Argentina (42°56′ S, 64°24′ W), length 22.5 mm, width 13.7 mm, height 8 mm (Fig. 163).

Fissurella oriens Sowerby, 1835

Figures 176–199

Fissurella oriens is here considered to have two geographic subspecies: *F. oriens oriens* in the Magellanic region of Chile and *F. oriens fulvescens* in south-central Chile.

Synonymy for *F. oriens oriens:*

Fissurella oriens Sowerby, 1835a:124; Sowerby, 1835b:3, figs. 25, 60; Reeve, 1849, pl. 2, fig. 13; Hupé, 1854:237; Sowerby II, 1862:186, figs. 19, 20; Pilsbry, 1890:152, pl. 46, figs. 18, 19, pl. 34, fig. 58; Melvill and Standen, 1907:97; Strebel, 1907:88, pl. 1, figs. 8–14, pl. 2, figs. 15–20; Strebel, 1908:78, pl. 6, figs. 97a, b; Dall, 1909:242; Melvill and Standen, 1914:114; Powell, 1951:85; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951:123, fig. 30; Dell, 1971:185, pl. 5, figs. 3, 4; Ramirez-Boehme, 1974:30 [key].

Fissurella mexicana Sowerby, 1835b:8, fig. 61; Reeve, 1849, pl. 6, fig. 40; Sowerby II, 1862:186, figs. 26–28; Pilsbry, 1890:153, pl. 34, fig. 60; Melvill and Standen, 1898:102; Strebel, 1907:88 [under *F. oriens*].

Fissurella australis Philippi, 1845:61; Philippi, 1845:142; Strebel, 1907:88 [under *F. oriens*].

Fissurella alba Philippi, 1845:61; Philippi, 1845:34, pl. 1, fig. 4; Hupé, 1854:247; Rochebrune and Mabille, 1889:71; Pilsbry, 1890:292, pl. 62, figs. 3–5; Strebel, 1907:94, pl. 1, figs. 1–3, pl. 2, fig. 21; Ziegenhorn and Thiem, 1925:14, pl. 2, figs. 14a, 14b, 15; Carcelles, 1950:51, pl. 1, fig. 11; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951:100; Dell, 1971:181; Ramirez-Boehme, 1974:30 [key].

Fissurella (*Corrina*) *alba* Christiaens, 1973:93, pl. 4, figs. 46, 47.

Fissurella flavida Philippi, 1857:165; Pilsbry, 1890:292; Strebel, 1907:97; Carcelles and Williamson, 1951:254; Riveros-Zuñiga, 1951:121; Dell, 1971:186; Ramirez-Boehme, 1974:30 [key].

Fissurella hedeia Rochebrune and Mabille, 1885:109; Rochebrune and Mabille, 1889:72, pl. 5, fig. 3; Carcelles, 1950:51; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951, fig. 32; Dell, 1971:186; Ramirez-Boehme, 1974:30 [key].

Fissurella arenicola Rochebrune and Mabille, 1885:109; Rochebrune and Mabille, 1889:73, pl. 5, fig. 1; Carcelles, 1950:51; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:124, fig. 31; Dell, 1971: 182; Ramirez-Boehme, 1974:30 [key].

Fissurella (*Carcellesia*) *doellojuradoi* Perez-Farfante, 1952: 32, fig. 1; Christiaens, 1973:92, pl. 4, fig. 45.

Fissurella cheullina Ramirez-Boehme, 1974:17, 30 [key], pl. 1, figs. 2a–c.

Fissurella oblonga Ramirez-Boehme, 1974:18, 30 [key], pl. 2, figs. 4a–c.

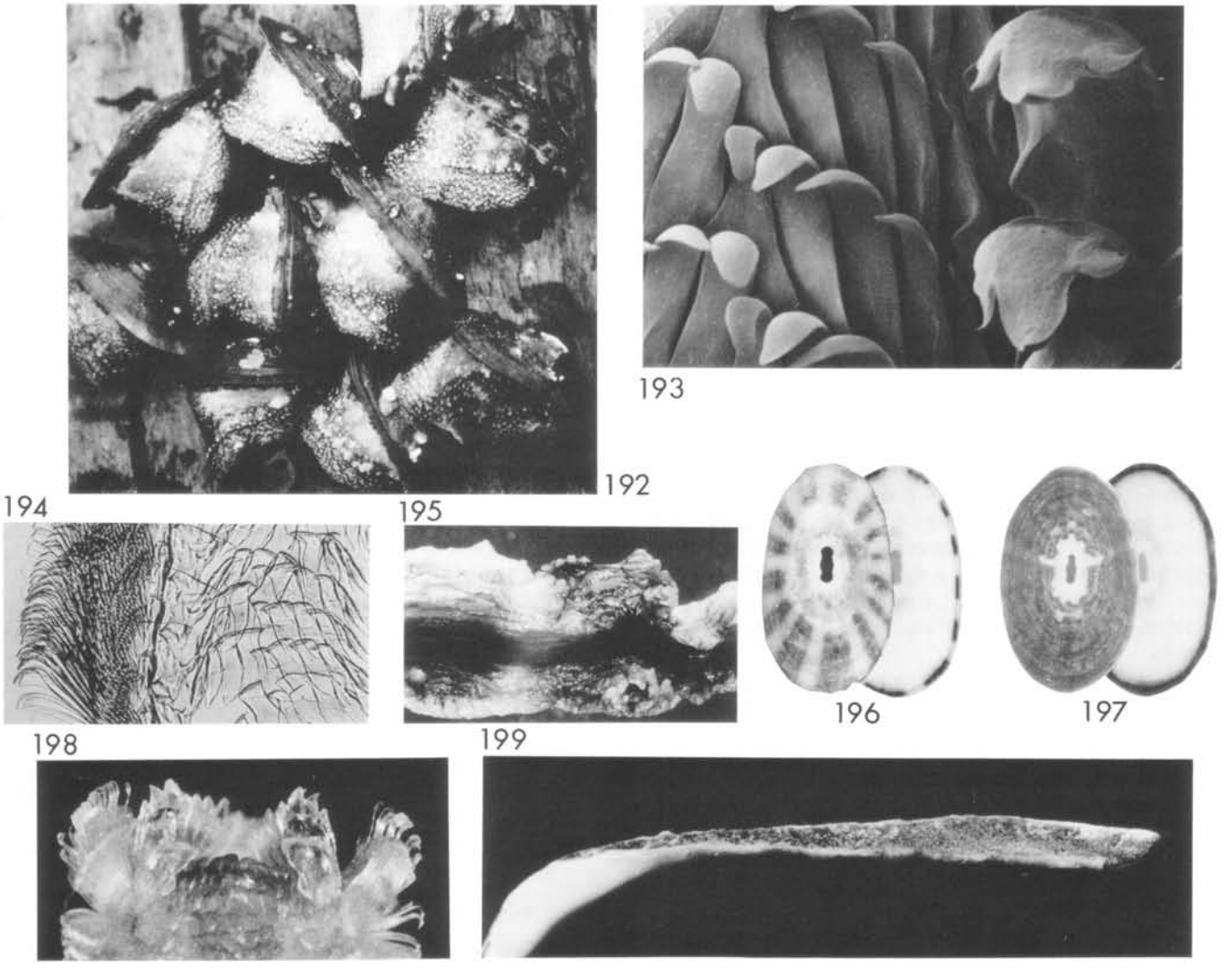
Synonymy for *F. oriens fulvescens:*

Fissurella fulvescens Sowerby, 1835a:127; Sowerby, 1835b: 6, fig. 49; Reeve, 1849, pl. 6, fig. 42; Hupé, 1854:245; Sowerby II, 1862:184, fig. 36; Pilsbry, 1890:152, pl. 33, fig. 49; Dall, 1909:241; Riveros-Zuñiga, 1951:122, fig. 29; Dell, 1971:186, pl. 5, fig. 6; Ramirez-Boehme, 1974:30 [key].

Shell (*F. oriens oriens*). Small to medium sized (mature length 40–70 mm), low to moderately elevated; outline elongate oval to very elongate, lateral profile variable, ranging from flat or with either ends or sides raised. Sculpture of fine radial ribs, ribs very broad and flat at margin, ending in extremely fine crenulations; under magnification fine con-

←

Chulao, Chiloe Province, Chile. MNHN 200375, 55.5 × 31.0 × 12.2 mm. **(185)** Holotype, *F. cheullina* Ramirez-Boehme. Isla Quellin, Llanquihue Province, Chile. MNHN 200327, 43 × 23 × 9 mm. **(186)** Holotype, *F. hedeia* Rochebrune and Mabille. Punta Arenas, Magallanes Province, Chile. MNHNP, 29 × 24 × 7 mm. **(187)** Orange Harbor, Chile. USNM 17328, 37.4 × 22.9 × 8.2 mm. **(188)** 13–29 m, Strait of Magellan, Chile. LACM 90801, 47.3 × 29.7 × 10.6 mm. **(189)** 18–27 m, Falkland Islands. USNM 368309, 23.2 × 14.7 × 5.0 mm. **(190)** Punta Arenas, Magallanes Province, Chile. LACM 75-50, 54.2 × 33.2 × 16.9 mm. **(191)** Holotype, *F. arenicola* Rochebrune and Mabille. Locality uncertain. MNHNP, 42.2 × 26.5 × 14.2 mm.



Figures 192 through 199. *Fissurella oriens oriens* Sowerby, 1835. Living specimens, radula, mantle lobe, juvenile shells, and cut shell. (**192**) Detached living specimens. 4–13 m, Islota Nihuel, Chiloe Province, Chile. LACM 75-43. (**193**) SEM view of radular ribbon. Pargua, Llanqihue Province, Chile. LACM 75-39, width of field 0.7 mm. (**194**) Radula. Pumalin, Chiloe Province, Chile. LACM 75-41, width of field 0.5 mm. (**195**) Mantle lobe. Same locality. LACM 75-41, length 9 mm. (**196**) Juvenile shell. 11–13 m, Isla Carlos III, Magallanes Province, Chile. LACM 73-70, 7.8 × 4.5 × 1.9 mm. (**197**) Juvenile shell. 4–13 m, Islota Nihuel, Chiloe Province, Chile. LACM 75-43, 13.4 × 8.2 × 3.4 mm. (**198**) Air-dried radula. Pumalin, Chiloe Province, Chile. LACM 75-41, width of ribbon 3.0 mm, length of shell 48.8 mm. (**199**) Cut shell. 4–13 m, Islota Nihuel, Chiloe Province, Chile. LACM 75-42, length of cut edge 17 mm.

centric lamellae visible in early growth stages. Ground color variable, from colorless to yellow or dark red; rays mostly reddish or gray, solid or split into two or more broad bands and frequently with concentric interruptions; gray rays often changing to reddish or black to gray. Some specimens completely colorless. Margin relatively narrow, somewhat broader in rapidly growing specimens, not zoned, showing full pigmentation of rays throughout calcitic layer. Foramen elongate and tripartite in young shells, elongate-oval in mature shells.

Shells of the northern subspecies, *F. oriens fulvescens,* smaller (maximum length 45 mm), relatively low, ends usually elevated relative to sides. Color consistent; ground color yellow orange, rays dark red, rays frequently split into two adjacent bands, young shells speckled with red. This coloration and the speckled pattern of young shells is not matched by that in any specimens of the typical subspecies.

Juvenile Shell. Elongate oval, more conical than at later stages, usually reddish overall, with white apical area and color pattern emerging unevenly; rays arising after shell reaches about 4 mm in length.

Mantle and Foot. Animal usually large, not retractable in flattened shell. Cephalic tentacles reddish brown, yellowish at tips. Mantle lobe rather thin in preserved specimens, edges with finely branched papillae, banded to correspond to rayed pattern; side of foot mottled brown to pinkish brown, light

in specimens with colorless shells. Epipodial tentacles especially prominent.

Habitat. Chiefly sublittoral throughout the range, but extending up to the lower intertidal zone in places exposed to currents but not heavy surf. The northern subspecies *F. oriens fulvescens* is probably limited to the sublittoral zone, for I was unable to find living specimens at low tide. I observed the typical subspecies at Mehuin in deep tide pools. I found it at Pumalin in the Golfo Corcovado, occurring at low tide in rocky areas free of sand where tidal currents were strong; at Islote Nihuel in the Golfo Corcovado I found it at a depth of 10 m on rocks near the sand–rock interface. At Puerto Hambre in the Strait of Magellan I found it at low water in sheltered rocky areas. Specimens have been dredged to depths of 30 m by the R/V HERO near Isla de los Estados, Argentina.

Distribution. Islote Concon, Valparaíso Province, Chile (32°52′ S) (LACM 75-31, McLean), south to Tierra del Fuego and probably Cape Horn, east to Isla de los Estados, Argentina, and the Falkland Islands. Not known living from mainland Argentina. Pleistocene specimens are known from Comodoro Rivadavia, Chubut Province, Argentina (MCZ 288329), as is also true for *F. picta.* Scarabino's (1977) record of the species from the Golfo San Matias, Argentina, is probably based upon specimens of *F. radiosa tixierae.* Populations from the northern end of the range in the vicinity of Valparaíso and south at least to Concepción are of the subspecies *F. oriens fulvescens.* Those at Mehuin and to the south are the typical subspecies *F. oriens oriens.*

Number of Lots Examined. *F. oriens oriens:* 97(LACM 34, AMNH 10, ANSP 6, MACN 28, MNHN 6, USNM 13); *F. oriens fulvescens:* 4 (LACM).

Taxonomic History. *Fissurella oriens* Sowerby has been reasonably well understood by most authors, although the extent of its variability and the extreme number of synonyms has not generally been recognized. Most of the synonyms have not come into general use, with one exception, that of *F. alba* Philippi, which was based on white-shelled forms. The northern subspecies, *F. oriens fulvescens* Sowerby, is here recognized for the first time.

Abundance and Use. *Fissurella oriens* is primarily a species of the Magellanic Faunal Province, where it is common at low water and much more abundant in the sublittoral. Although many shells are small, it reaches sizes large enough to be used for food. I have no information on the extent of its use.

Characteristics and Variability. The most characteristic features of *F. oriens* are the relatively small size and lack of strong ribbing, the radial sculpture being better described as consisting of striae or grooves. It is one of the most variable species in proportions, size of the foramen, and color pattern. Local populations tend to be consistent, with many similarly appearing individuals. The ground color of the typical subspecies ranges from colorless to dark red, but most commonly has strong rays that may change with growth from gray to reddish and increase or diminish in intensity. White shelled specimens have been noticed in scattered populations throughout the range of the species. Some populations have shells that are relatively flat, while in others the shells are more elevated. This is one of the few species in which the variation includes specimens with either elevated sides or elevated ends. The margin is usually narrow, though not as narrow as that of *F. radiosa.* However, some specimens that are growing rapidly may have a relatively broad margin. In some gerontic specimens, the foramen may become very large and broadly oval; in others it remains narrow and elongate.

Affinity and Comparisons. *Fissurella oriens* most resembles *F. radiosa,* a species of similar size in which there is similar variation in proportions and color. *Fissurella oriens* differs chiefly in lacking the strong ribbing of *F. radiosa* and in having a more centrally placed foramen. However, some conspicuously ribbed specimens of *F. oriens* may so resemble weakly ribbed specimens of *F. radiosa* that the only reliable character to separate them is the presence of primary ribs larger than the adjacent ribs on *F. radiosa,* and the absence of such primary ribs on *F. oriens.* Strongly rayed specimens of *F. oriens* may have a superficial resemblance to uneroded specimens of *F. limbata,* but *F. oriens* lacks the broad two-zoned margin that is the hallmark of *F. limbata.*

Synonymy and Types. Eleven names seem to be referable to *F. oriens,* the large number of synonyms correlated with the high variability of the species and the tendency for local populations to have uniform features.

There are five syntypes of *F. oriens* Sowerby, 1835, BMNH 197575, lengths 69.3, 62.4, 59.6, 53.7, and 16.7 mm. The largest specimen, that figured by Reeve (1849) and Dell (1971) is designated the lectotype; the second largest specimen, a paralectotype, is figured here (Fig. 178). Although Reeve gave the locality as Valparaíso, Sowerby's original locality is "Insulam Chiloe," with a "variety" mentioned from Valparaíso. The specimens are relatively large, rayed in reddish brown, and represent the normal, elongate, moderately elevated form, similar to what I have observed from the vicinity of Isla de Chiloe. The type locality should therefore be limited to Isla de Chiloe. Sowerby's original figure in the "Conchological Illustrations" was of a smaller specimen, probably the 59.6 mm specimen.

Sowerby did not clearly document the above-mentioned "variety" of *F. oriens* from Valparaíso. However, in the same publication (Sowerby, 1835a) he described *F. fulvescens* from Valparaíso, which may have been intended as the "variety." In 1975 I found beach-worn specimens matching the type lot on cobble beaches in that vicinity of Chile (Fig. 177). The type lot consists of four specimens, BMNH 197568, lengths 39.7, 37.0, 33.0, and 27.9 mm. The largest specimen (Fig. 176) was figured originally by Sowerby (1835b), later by Reeve (1849), and more recently by Dell (1971), who designated it the lectotype. All the specimens are low and elongate, yellow-orange in ground color, the rays reddish, and the margin narrow. The specimens are in good condition and were evidently collected alive; according to Sowerby, they were taken under rocks on the shore.

Fissurella mexicana Sowerby, 1835, was said to come from "Real Llejos, Mexico," obviously in error. There are four specimens in the type lot, BMNH 1966493, lengths 40.6,

40.4, 38.6, and 29.6, the smallest specimen broken and repaired. They are elongate, moderately elevated, and rather thin-shelled, well within the range of variation of *F. oriens*. The 38.6 mm specimen is designated the lectotype (Fig. 179).

Fissurella australis Philippi, 1845, from "Fretum Magellanicum," was never illustrated and I have not been able to locate type material. Philippi described its color and sculpture as similar to that of a young *F. oriens*, but thinner-shelled and with extremities raised, the shell resting on the sides. Inasmuch as specimens of *F. oriens* with raised ends and thin shells are well known, the synonymy is reasonably certain.

Fissurella alba Philippi, also from "Fretum Magellanicum," was illustrated subsequently by Philippi, but again, type material has not been located. A white, finely sculptured shell was figured, and Philippi himself indicated that it could be a variant of *F. oriens*. This note was, surprisingly, overlooked by Pilsbry (1890) and the taxon has been accepted without question by subsequent authors and even made the type species of a subgenus based upon the character of weak ribbing. Nevertheless, it is clearly a white-shelled variant of *F. oriens*. I have seen white shells from numerous stations at which rayed forms also occur (see Fig. 188, from a lot of six specimens, four of which are white and two are rayed).

Fissurella flavida Philippi, 1857, from the "Magellenstrasse," has not been figured and I have not located type material. The description indicates a shell that is solid, elliptical, moderately convex, with obscure sculpture, and a moderately broad margin. The coarse sculpture that characterizes *F. picta* and *F. radiosa* were not mentioned. Inasmuch as only three species occur in the region, this name can be relegated to the synonymy of *F. oriens* by eliminating the other possibilities.

The holotype of *F. hedeia* Rochebrune and Mabille, 1885, from Punta Arenas in the Strait of Magellan, was received on loan from the Paris Museum (Fig. 186). Although not compared by its authors to other species, it is an elongate, finely sculptured specimen of *F. oriens*.

Fissurella arenicola Rochebrune and Mabille, 1885, also was not compared to other species. Two specimens in the Paris Museum labeled "type et paratype," were studied. The locality inked on the mounting board is "Baie Orange"; the published locality is "Punta-Arenas Patagoniae, Baie Orange." The holotype (Fig. 191) is a white-shelled *F. oriens*, 42.2 mm in length, very worn except at the margin, where no traces of primary ribs are evident. The paratype is 38.2 mm in length, also white-shelled, but primary ribs are apparent throughout. I therefore identify the paratype as *F. radiosa*. Based on the holotype, the name *F. arenicola* is placed in the synonymy of *F. oriens*.

Fissurella (*Carcellesia*) *doellojuradoi* Pérez-Farfante, 1952, was based on a single specimen from "Tierra del Fuego." The specimen, 35 mm in length, was borrowed by its author from the Museo Argentino de Ciencias Naturales in Buenos Aires. A new subgenus was based on the single feature of the raised ends of the specimen, but as discussed above, such variants are frequently seen in *F. oriens*, with which it was not originally compared. The synonymy of this taxon therefore seems certain.

Fissurella cheullina Ramirez-Boehme, 1974, was based on eight specimens from Isla Queullin, Llanquihue Province, Chile (41°53′ S, 72°55′ W), holotype MNHN 200377 (Fig. 185). *Fissurella oblonga* Ramirez-Boehme, 1974, was based on a single specimen from Punta Chulao, Chiloe Province, Chile (42°17′ S, 72°50′ W), holotype MNHN 200375 (Fig. 184). Neither taxon was compared by its author to any other species. Both were described as moderately elevated, elongate, weakly sculptured, and with narrow margins. These specimens are well within the range of variation known for *F. oriens*.

Fissurella nigra Lesson, 1831

Figures 200–211

Fissurella nigra Lesson, 1831:412; Orbigny, 1841:473; Philippi, 1846:65, fig. 2; Reeve, 1849, pl. 2, fig. 11; Hupé, 1854:241; Sowerby II, 1862:184, fig. 14; Pilsbry, 1890: 149, pl. 35, figs. 1, 2; Dall, 1909:177, 242; Ziegenhorn and Thiem, 1925:15, pl. 2, figs. 16a, b; Carcelles and Williamson, 1951:255; Riveros-Zuñiga, 1951:116, fig. 25; Dell, 1971:188, pl. 3, figs. 17–19; Ramirez-Boehme, 1974:31 [key].

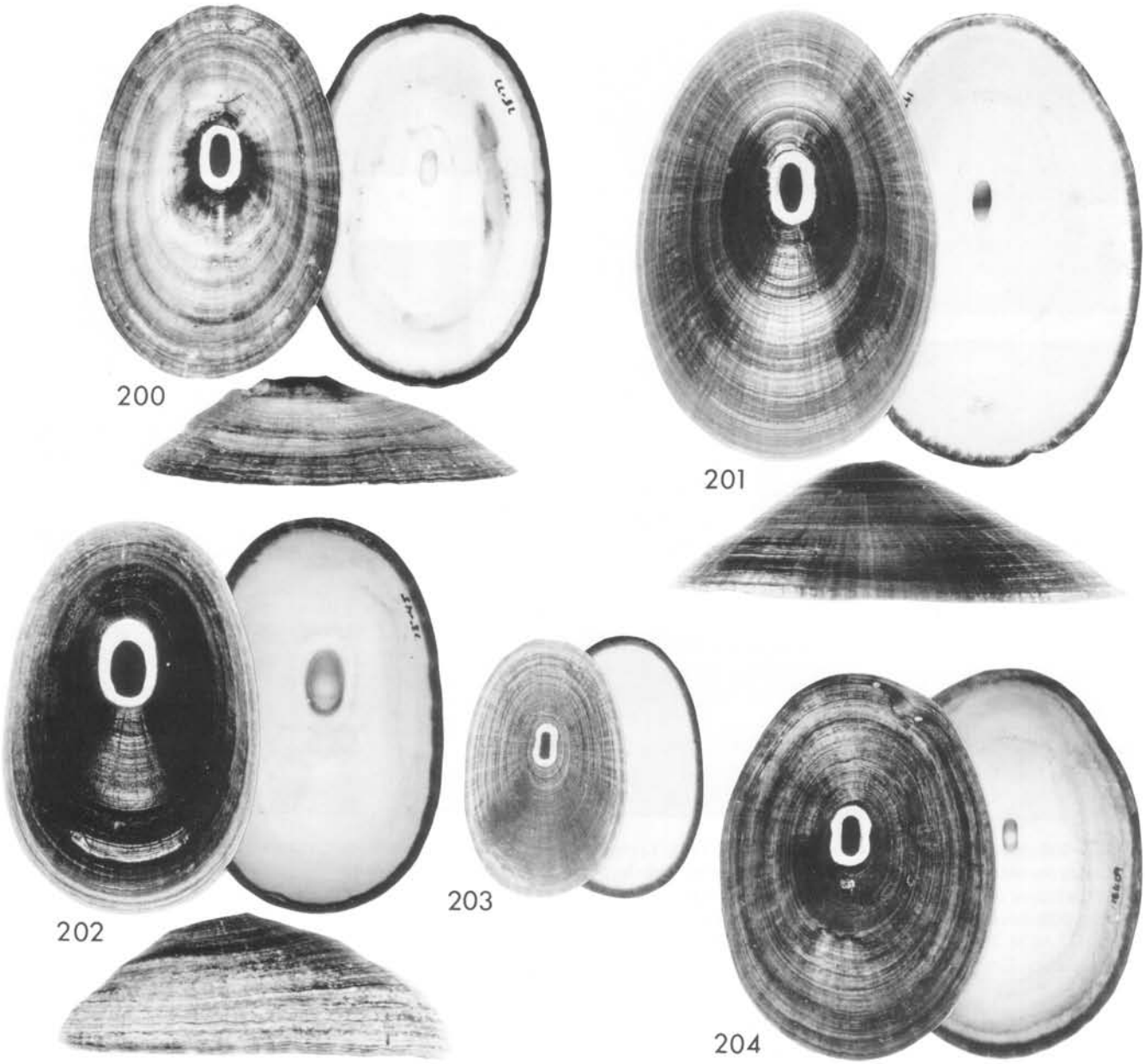
Fissurella violacea Rathke, 1833 [*ex* Eschscholtz manuscript]:21, pl. 23, fig. 6; Orbigny, 1841:473 [under *F. nigra*]; Philippi, 1846:66, pl. 2, fig. 3.

Fissurella grandis Sowerby, 1835a:123; 1835b:3, fig. 48; Orbigny, 1841:473 [under *F. nigra*]; Philippi, 1846:65, pl. 2, fig. 1.

Shell. Relatively large (70 to 110 mm mature length), moderately elevated; outline elongate oval, base resting flat or with ends slightly raised, rarely with raised sides. Overall appearance smooth, sculptured with fine radial ribs that persist to margin. Color black or gray, sometimes pale and showing concentric variation in shading; rays lacking or faint, consisting of narrow lines slightly darker than adjacent ground. Margin broad and flat in growing shells, narrow in mature shells; two-zoned, outer zone black, inner zone translucent gray; cut shells showing that two zones are nearly equal in thickness. Foramen anterior to center, elongate and tripartite in young shells, elongate-oval in mature shells, worn or beveled at apex to reveal aragonitic layer, so that it always appears white-bordered. Old shells that continue to grow by increasing height without expanding at base may contract basal area, forming thick edge and losing distinct zoning of margin.

Juvenile Shell. Radial ribs fine and sharp; primary and secondary ribs appearing early. Whitish in earliest stage, changing abruptly or gradually to black, some showing two lateral white rays that quickly fade.

Mantle and Foot. Nearly containable in shell. Entire animal gray; yellow coloration lacking in cephalic tentacles. Mantle lobe greatly expandable, faintly banded, narrow when preserved; papillae of upper edge moderately developed, finely branched; those of lower edge nearly equal in size. Side of

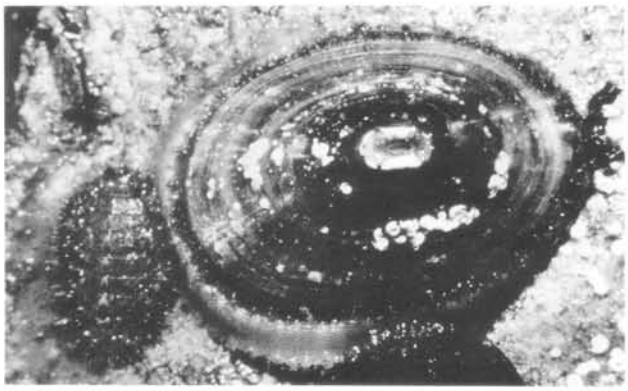


Figures 200 through 204. *Fissurella nigra* Lesson, 1831. Mature shells. (**200**) Island off Mehuin, Valdivia Province, Chile. LACM 75-37, 74.7 × 50.2 × 19.5 mm. (**201**) Lectotype, *F. grandis* Sowerby, 1835. Locality uncertain. BMNH 1976143, 101.0 × 67.9 × 30.9 mm. (**202**) Quellón, Chiloe Province, Chile. LACM 75-45, 79.5 × 51.1 × 30.1 mm. (**203**) Pumalin, Chiloe Province, Chile. LACM 75-41, 43.8 × 27.5 × 12.4 mm. (**204**) Isla Bertrand, off Isla Navarino, Magallanes Province, Chile. NMNZ 18409, 78.9 × 56.5 × 25.4 mm.

foot darker than mantle lobe; tubercles small and widely scattered. This is the only species with a completely gray animal.

Habitat. Intertidal zone only, on the undersides of rocks in the mid-tidal to lower intertidal zone. Several large specimens may occur close together on the undersides of large rocks. Shells are mostly clean, except for scattered incrustations of barnacles, bryozoa, or spirorbid worms. None have been found with attached *Scurria parasitica,* as would be expected if the habitat were more exposed. This is the only species occurring under rocks in the mid-littoral of south central and southern Chile; only juveniles of other species of *Fissurella* occur in this habitat in northern Chile.

Distribution. Valparaíso, Santiago Province, Chile (33°02′ S) (USNM 48218, Bridges), to Puerto Grandi, Isla Bertrand, off south side Isla Navarino, Chile (55°12′ S, 67°02′ W) (Dell,



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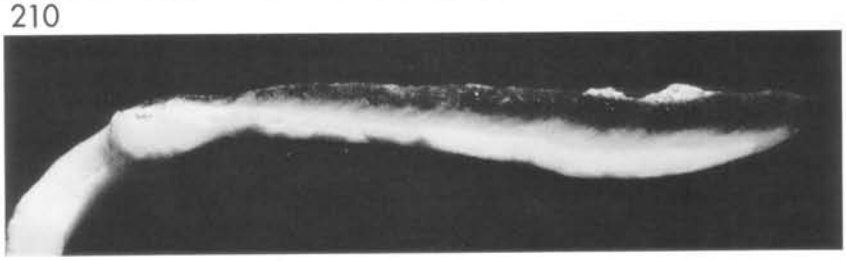

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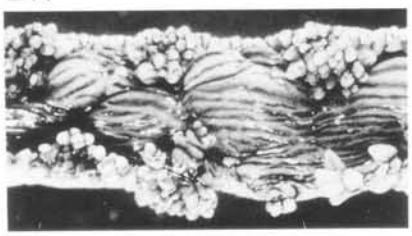


Figures 205 through 211. *Fissurella nigra* Lesson, 1831. Living specimens, radulae, juvenile shell, cut shell, and mantle lobe. **(205)** Living specimen on underside of overturned boulder. Island off Mehuin, Valdivia Province, Chile. LACM 75-37. **(206)** Radula. Same locality. LACM 75-37, width of field 0.8 mm, shell length 26.4 mm. **(207)** Ventral view of living specimen. Río Bio-bio, Concepción Province, Chile. LACM 75-35. **(208)** Juvenile shell. Island off Mehuin, Valdivia Province, Chile. LACM 75-37, 5.5 × 3.5 × 1.5 mm. **(209)** Air-dried radula. Same locality. LACM 75-37, width of ribbon 2.6 mm. **(210)** Cut shell. Same locality. LACM 75-37, length of cut edge 39 mm. **(211)** Mantle lobe. Same locality. LACM 75-37, length 10 mm.

1971). The northernmost specimen personally collected is a single beach-worn juvenile from Punta el Lacho, Santiago Province, Chile (33°30′ S). The species is rare in the vicinity of Valparaíso, if it now occurs there at all. Dall's (1909) record from Callao, Peru, is not represented by USNM specimens and should be discounted. I found this species commonly at Concepción and Mehuin, and at all stations in the vicinity of Isla de Chiloe, both on the exposed outer coast and on the eastern side where water motion is primarily that of tidal currents. It is evidently uncommon and sporadic in the southernmost region, for I found no trace of it at Punta Arenas or Puerto Hambre in the Strait of Magellan. It is unknown from the Falkland Islands. In addition to the above record of Dell (1971), the following southern records are known to me: USNM 170205, Port Otway, Chile (46°49′ S); MACN 12491, Canal Smyth (at western end of Strait of Magellan); AMNH 173403, Beagle Canal (south side Tierra del Fuego).

Number of Lots Examined. 67 (LACM 11, AMNH 8, ANSP 3, MACN 8, MNHN 33, USNM 4).

Taxonomic History. *Fissurella nigra* is an easily recognized species that has been understood by most authors.

Abundance and Use. Common, at least in the northernmost portion of the range. Its intertidal habitat is accessible, and it is exploited for food.

Characteristics and Variability. The most characteristic features of *F. nigra* are the gray to black surface, the rays, if present, being faint and split into lines, and the prominent zoning of the calcitic layer at the margin, the outer zone dark and the inner zone a light translucent gray. Variation is chiefly in color pattern. Some specimens change from black to gray or light brown; such specimens being more likely to show the fine brown radial pattern. There may be changes in color intensity with growth, but never as pronounced as that which occurs in *F. picta, F. radiosa,* or *F. oriens.* The size record

for the species, perhaps for the genus as well, is length 135 mm, width 100 mm, height 62 mm (Isla de Chiloe, collected in 1892, MNHN).

Affinity and Comparisons. *Fissurella nigra* does not closely resemble any other species. Although its overall appearance is smooth, juvenile shells are sharply ribbed, and there are definite primary and secondary ribs. The presence of these ribs in the juvenile dissociates it from the smooth-shelled species in the "group of *F. limbata*" in which early sculpture consists only of broad primary ribs. Its closest affinity is probably with *F. radiosa,* with which it shares similar proportions, an anteriorly positioned foramen, and the three series of ribs, although the total number of ribs is greater in *F. nigra.* The dark outer zone of *F. nigra* is unique. There is only a superficial resemblance of *F. nigra* to dark gray specimens of *F. latimarginata.* Compared to the latter, *F. nigra* has fine radial ribs, a dark rather than lighter outer zone to the margin, and a more anterior and more inwardly beveled foramen.

Synonymy and Types. Type material of *F. nigra* Lesson, 1831, is unknown. It is not represented in the Paris Museum where some of the Lesson collection is now housed. Although there were no original illustrations, the species is easily recognized from the description. It is common in the vicinity of its type locality "Saint-Vincent," now San Vicente (36°43′ S), near Concepción, Chile.

Fissurella violacea Rathke, 1833, was described before the Lesson work was known. The original figure is clear; the type locality is Concepción. Type material may be in Leningrad, where some of the Eschscholtz and Rathke types are extant.

Fissurella grandis Sowerby, 1835, is another early name evidently introduced before Lesson's work was known. There are two specimens in the type lot, BMNH 1976143, lengths, 110.1 and 77.2 mm. The larger specimen was figured by Sowerby (1835b), Reeve (1849), and Dell (1971). It is here designated the lectotype (Fig. 201). The original locality was given as "Valparaíso and Chiloe," so it is not certain whether both specimens are from the same place. The correct locality may be Isla de Chiloe, because the species is rare in the vicinity of Valparaíso.

Group of *Fissurella limbata*

Relatively large-shelled species in which the thickness of the calcitic layer greatly exceeds that of the interior aragonitic layer. Radial sculpture in the early stage is either absent or consists of broad, low primary ribs; there are no secondary ribs. Mature shells may retain the broad primary ribs as low undulations or be entirely smooth.

Although shells of this group have the thick calcitic layer of the *F. maxima* group, they differ from the latter in not having secondary ribs. Whether this difference in sculpture has taxonomic significance should be tested at the biochemical level. It is premature to justify a separation at the subgeneric level.

There are four species in this group: *F. limbata, F. crassa, F. bridgesii,* and *F. pulchra.* The latter three have elongate shells with low profiles, the animals too large to be retracted within the shell. These species tend to be more stenotopic than those of the *F. maxima* group. Variation in each species is less extreme, which is correlated with the relatively few synonyms in the group.

The four species in the group are limited to the Peruvian Faunal Province, unlike the *F. maxima* group, in which there are both Peruvian and Magellanic members.

Fissurella limbata Sowerby, 1835

Figures 212–224

Fissurella limbata Sowerby, 1835a:123; Sowerby, 1835b:3, figs. 42, 66, 74; Orbigny, 1841:474; Reeve, 1849, pl. 2, figs. 10, 12; Hupé, 1854:239; Sowerby II, 1862:184, figs. 23, 24; Pilsbry, 1890:149, pl. 32, figs. 26–39; Dall, 1909: 242; Ziegenhorn and Thiem, 1925; 15, pl. 2, figs. 17–19, 20a, 20b; Riveros-Zuñiga, 1951:114, fig. 24; Peña, 1970: 156; Dell, 1971:188, pl. 5, fig. 5; Marincovich, 1973:18, fig. 30; Ramirez-Boehme, 1974:32 [key].

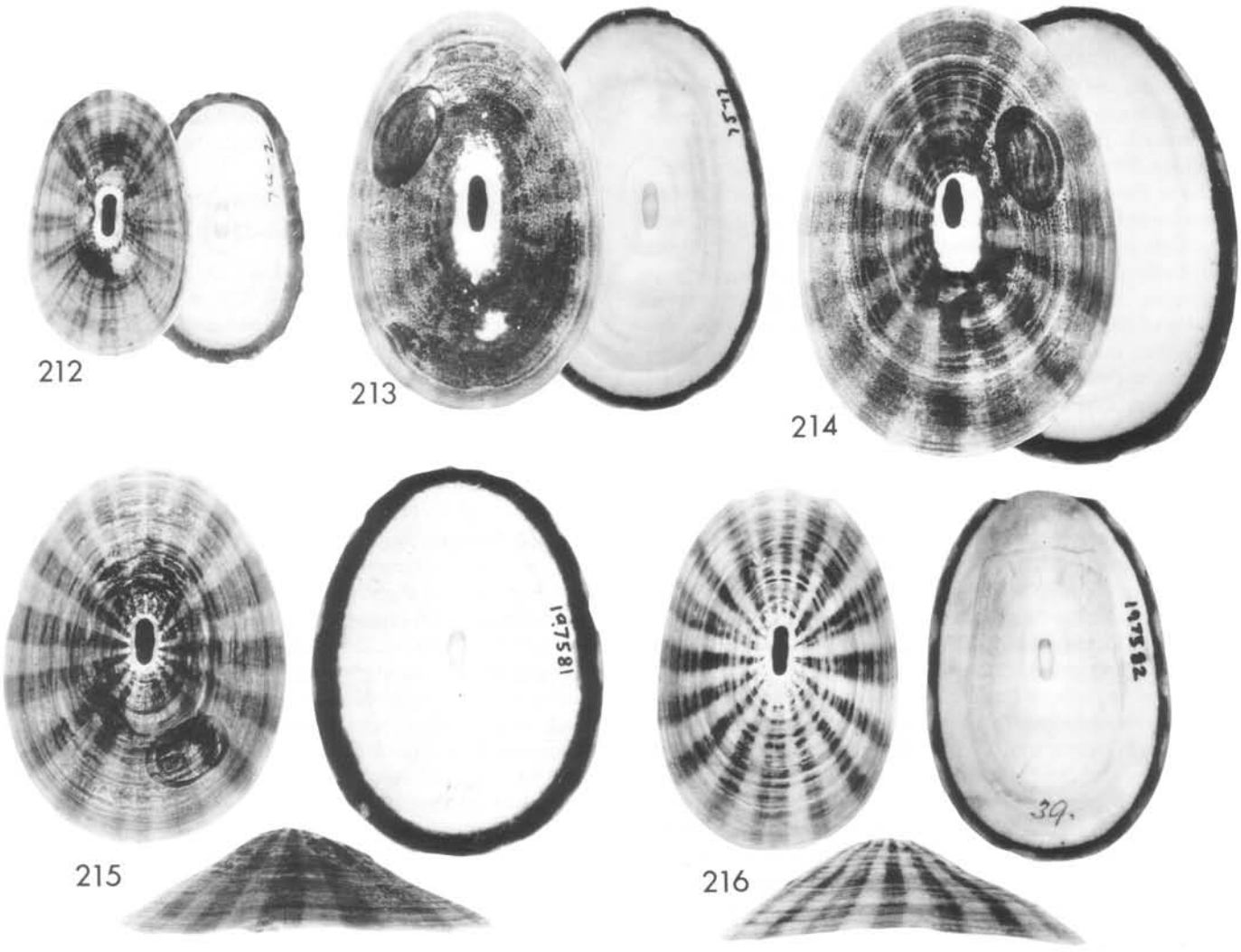
Fissurella limbata var. *multilineata* Ziegenhorn and Thiem, 1925:16, pl. 2, fig. 21.

Shell. Medium large (60–90 mm mature length), moderately elevated; outline elongate oval; base usually resting flat, with ends or sides slightly raised. Sculpture of wavy, irregular radial ribs; overall aspect mostly smooth. Color of uneroded shells (lacking epibiotic *Scurria*) consisting of yellowish ground and purple rays, rays often split. Calcitic layer zoned, consisting of inner layer of solid dark purple and translucent outer layer. Eroded shells (those with *Scurria*) worn to white aragonitic layer near foramen; area farther away from foramen consisting of deep purple portion of calcitic layer, with pattern of rays evident only near margin. Margin broad in growing shells, dark purple next to aragonitic interior, outer edge lighter and revealing pattern of rays. Cut shells showing outer zone about one-fourth thickness of solid purple zone. Foramen elongate at all stages, tripartite in young shells, constricted in middle in mature shells.

Juvenile Shell. Elongate-oval, elevated; primary ribs broad, weak. Color generally white, marked with concentric zigzag purple lines coalescing into purple rays; inner purple zone of calcitic layer apparently lacking in juvenile shells.

Mantle and Foot. Shell edge enveloped by mantle on attached specimens exposed at low tide, body retractable within shell. Mantle lobe light gray, appearing narrow in preserved specimens, marked with concentric lines of black, and only faintly banded to correspond to rays of shell. Papillae at edges very small, finely branched. Side of foot gray; tubercles small, scattered. Preserved specimens retaining broad dark ring with lighter edge where the smooth innermost edge of mantle lobe is in contact with shell. This is the only species in which a dark zone on the inner lobe shows in preserved specimens.

Habitat. Mid-intertidal to low-intertidal zones in surf-exposed areas, primarily on horizontal and sloping surfaces, rather than vertical surfaces. This is the predominant species on flat areas of exposed reefs. I saw no specimens in the sublittoral zone at localities where I dived. Most shells have a single *Scurria parasitica,* which produces a deeply etched attachment scar.



Figures 212 through 216. *Fissurella limbata* Sowerby, 1835. Mature shells. (**212**) Isla Guanape, Peru. LACM 74-2, 37.0 × 22.9 × 12.1 mm. (**213**) Shore opposite Isla Santa Maria, Antofagasta Province, Chile. LACM 75-17, 65.8 × 41.0 × 20.0 mm. (**214**) Los Molles, Aconcagua Province, Chile. LACM 75-28, 82.4 × 57.7 × 25.0 mm. (**215**) Paralectotype, *F. limbata* Sowerby. Valparaíso, Chile. BMNH 197581, 65.0 × 48.5 × 117.8 mm. (**216**) Lectotype, *F. limbata* Sowerby. Valparaíso, Chile. BMNH 197582, 60.5 × 40.0 × 17.4 mm.

Distribution. Isla Guanape, Peru (8°30′ S) (LACM 74-2, McLean), to Isla de Chiloe, Chile (AMNH 155914, O. Ruiz). The exact locality for the southern record is not known, but it was probably the accessible northwestern tip at approximately 41°50′ S. However, I was unable to find specimens in that vicinity at Guabun, Isla de Chiloe. The species does not occur in the sheltered waters of the Golfo Corcovado on the eastern side of Isla de Chiloe. I discount the record of Riveros-Zuñiga (1951) from Fuerte Bulnes in the Magellan Strait.

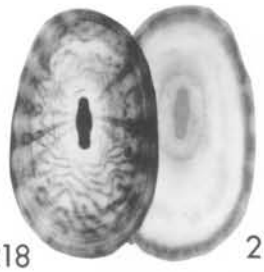
Number of Lots Examined. 100 (LACM 35, AMNH 20, ANSP 8, MACN 8, MNHN 10, USNM 19).

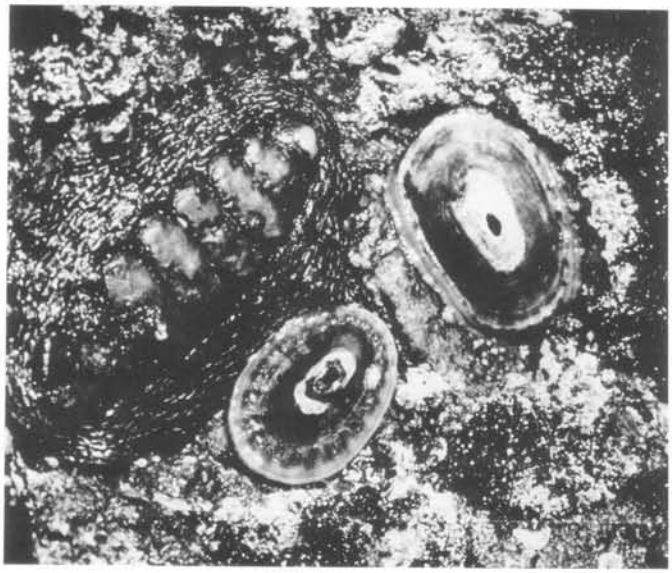
Taxonomic History. *Fissurella limbata* has been correctly interpreted by most authors.

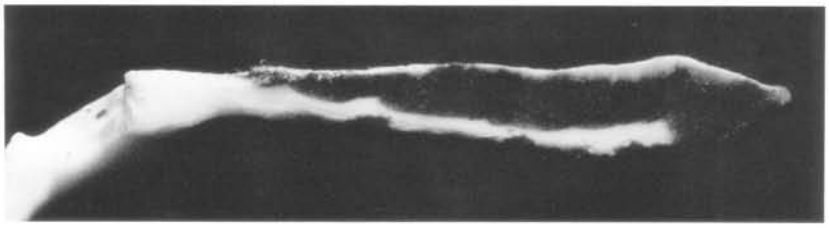
Abundance and Use. This species is common throughout its range and is exploited for food. Large specimens are seldom seen, because of the accessibility of the habitat at low tide. It is called the "lapa gaviota" at Iquique. Gaviota is the name for seagull, a predator on this species.

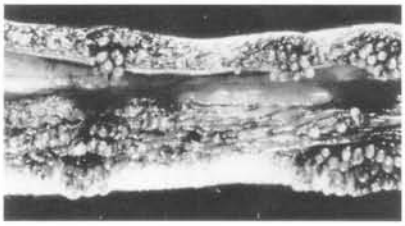
Characteristics and Variability. The most characteristic and unusual feature of *F. limbata* is the zonation of the calcitic layer, in which the pattern of rays is confined to the thin, lighter colored surface layer. The greater thickness of the calcitic layer consists of the dark purple inner zone, which is much darker than the rays. There is little variation; differences in appearance are a result of patterns of wear in which the outermost rayed layer is lost, leaving a uniform purple layer. Further wear results in complete loss of the calcitic layer near the foramen, which exposes the white aragonitic layer. Erosion of the shells is greatly accelerated when *Scurria parasitica* is present.

Affinity and Comparisons. *Fissurella limbata* seems not





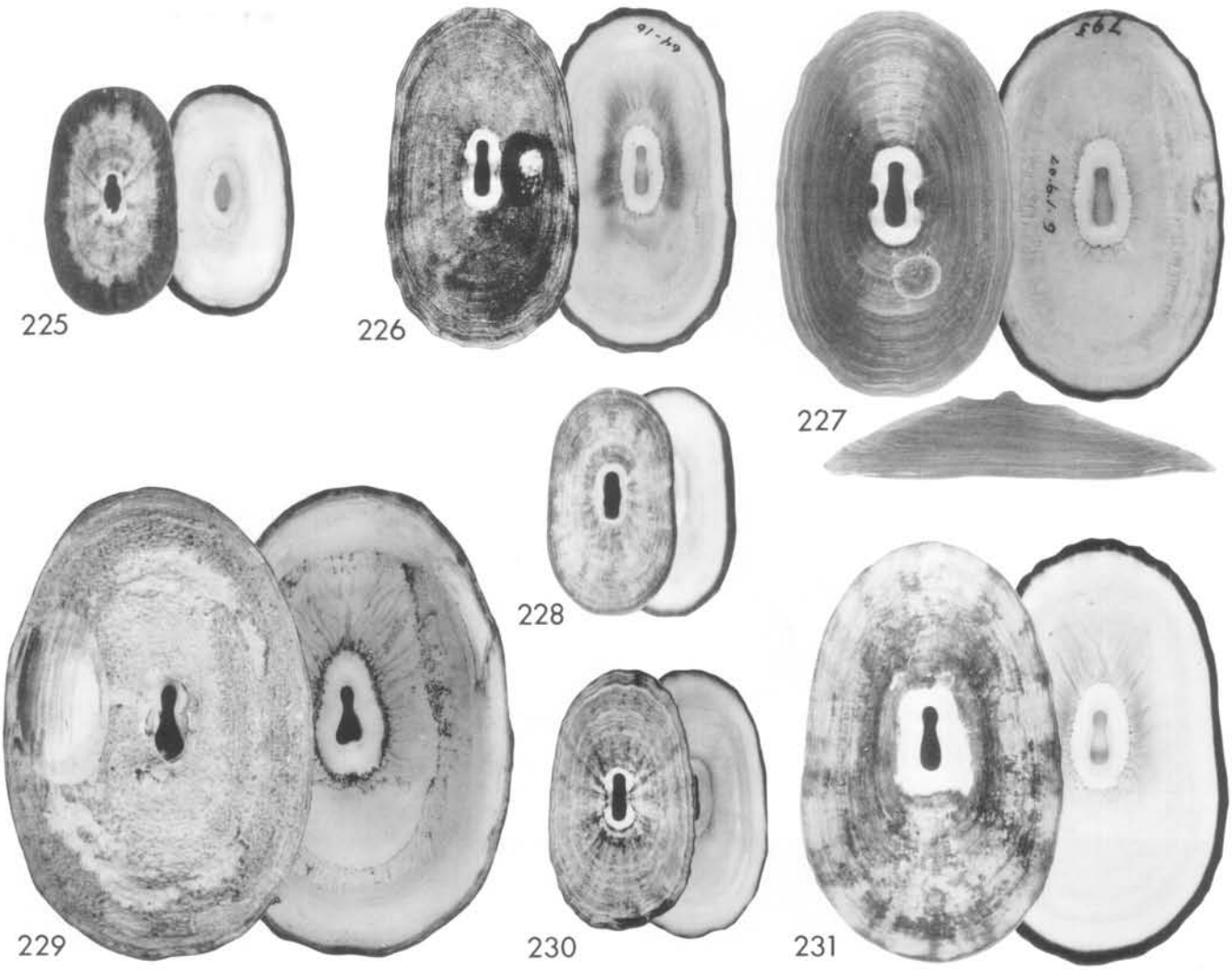




Figures 217 through 224. *Fissurella limbata* Sowerby, 1835. Living specimens, juvenile shells, radula, cut shell, and mantle lobe. (**217**) Ventral view of living specimen. Cumbres Borascosas, Tarapaca Province, Chile. LACM 75-14. (**218**) Juvenile shell. Iquique, Chile. LACM 64-14, 11.8 × 6.8 × 3.0 mm. (**219**) Air-dried radula. Montemar, Valparaíso Province, Chile. LACM 75-30, width of ribbon 2.4 mm. (**220**) Radula of small specimen. Ancon, Lima Province, Peru. LACM 74-21, width of field 0.5 mm, shell length 18.8 mm. (**221**) Juvenile shell. Iquique, Chile. LACM 64-16, 5.4 × 3.3 × 1.6 mm. (**222**) Living specimens with mantle extended next to chiton *Enoplochiton niger*. Iquique, Chile. LACM 75-12. (**223**) Cut shell. Mehuin, Valdivia Province, Chile. LACM 75-36, length 24 mm. (**224**) Mantle lobe, Islota Concon, Valparaíso Province, Chile. LACM 75-31, length 12 mm.

closely related to any other species. It has some features in common with *F. crassa*—sculpture essentially lacking and a very elongate foramen. Both are limited to the intertidal zone, although *F. limbata* is found at lower levels than is *F. crassa*. The margin is broad and flat, unlike the upturned margin of *F. crassa*. Also, *F. limbata* has relatively weak development of mantle papillae and foot tubercles, whereas both of these features are strongly developed in *F. crassa*. It probably has more in common with *F. nigra*, with which it shares a relatively smooth shell, similar weak development of mantle papillae, and foot tubercles. However, the zoning of the calcitic layer is reversed; the darkest layer is at the surface in *F. nigra*. *Fissurella oriens* has a rayed pattern similar to that of *F. limbata*, but has some radial sculpture and an unzoned calcitic layer.

Synonymy and Types. Two lots of *F. limbata* from the Cuming Collection in the British Museum have been examined. For each lot the locality "Valparaíso" is written in ink on the boards. Single specimens from each lot were illustrated by Reeve, 1849, although neither of the two spec-



Figures 225 through 231. *Fissurella crassa* Lamarck, 1822. Mature shells. **(225)** Bahía Independencia, Ica Province, Peru. AHF 375-35, 15.6 × 9.3 × 3.5 mm. **(226)** Iquique, Chile. LACM 64-16, 56.9 × 32.3 × 14.0 mm. **(227)** Holotype, *F. clypeiformis* Sowerby. Locality unknown. BMNH 40.6.1.9, 71.4 × 43.4 × 15.6 mm. **(228)** Cumbres Borascosas, Tarapaca Province, Chile. LACM 75-14, 19.8 × 11.4 × 4.6 mm. **(229)** Los Molles, Aconcagua Province, Chile. LACM 75-28, 92.0 × 61.0 × 27.4 mm. **(230)** Viña del Mar, Valparaíso Province, Chile. LACM 66-46, 45.5 × 19.8 × 7.0 mm. **(231)** Mehuin, Valdivia Province, Chile. LACM 75-36, 80.3 × 49.0 × 22.1 mm.

imens illustrated by Sowerby in the "Conchological Illustrations" are included in these lots. However, there is no mistaking the type figure of Sowerby (1835b, figs. 66, 74, internal and external view) as this species. Of the lots figured by Reeve, BMNH 197582 has six specimens, length, 60.5 (anterior end chipped), 59.2, 49.2, 48.4, 33.6, and 28.2. The largest was figured by Reeve (1849) and Dell (1971) and is here refigured and designated the lectotype (Fig. 216). All specimens in this lot lack *Scurria*-made scars and show the complete normal color pattern of the outer zone of the calcitic layer. BMNH 197581 has four specimens, length 67.3, 65.0, 63.1, and 61.1 mm. The largest was figured by Reeve, although the scar of a *Scurria* was omitted; most of the rayed outer zone of the calcitic layer was removed by the *Scurria*, leaving the shell dark purple except for later growth stages. The 65.0 mm shell is figured here (Fig. 215); it has a *Scurria*-made scar but is less eroded.

Fissurella limbata var. *multilineata* Ziegenhorn and Thiem, 1925, was based on two shells from Coquimbo, Chile, the largest 16.5 mm in length. The figure shows the normal zigzag pattern of purple lines found in all juveniles (Figs. 218, 221); the name, therefore, has no systematic value.

Fissurella crassa Lamarck, 1822

Figures 225–237

Fissurella crassa Lamarck, 1822, 6(2):11; Deshayes, 1830: 134; Sowerby, 1835b:1, figs. 9, 11; Deshayes *in* Lamarck, 1836, 7:592; Gray, 1839:148, pl. 39, fig. 9; Orbigny, 1841: 472; Reeve, 1849, pl. 1, fig. 4; Hupé, 1854:240; Philippi,

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Figures 232 through 237. *Fissurella crassa* Lamarck, 1822. Juvenile shell, radula, preserved and living specimens, cut shell, and mantle lobe. (**232**) Juvenile shell. Miraflores, Lima Province, Peru. LACM 71-187, 6.9 × 3.5 × 11.6 mm. (**233**) Radula of small specimen. Cartagena, Santiago Province, Chile. LACM 75-34, width of field 1.5 mm, shell length 22.1 mm. (**234**) Living animal submerged in tidepool. Iquique, Chile. LACM 75-12. (**235**) Preserved specimen. Mehuin, Valdivia Province, Chile. LACM 75-36, shell length 46.9 mm. (**236**) Cut shell. Bahía Moreno, Antofagasta Province, Chile. LACM 75-16, length 35 mm. (**237**) Mantle edge, Iquique, Chile. LACM 75-12, length 11 mm.

1860:181; Sowerby II, 1862:184, figs. 16, 17; Watson, 1886: 32; Pilsbry, 1890:154, pl. 34, figs. 51–53; Dall, 1909:177, 241, pl. 24, figs. 5, 6 [fig. looks like *F. limbata*]; Ziegenhorn and Thiem, 1925:18, pl. 2, fig. 24; Carcelles and Williamson, 1951:255; Mermod, 1950:702; Riveros-Zuñiga, 1951: 93, fig. 14; Peña, 1970:156; Dell, 1971:184; Marincovich, 1973:17, fig. 27; Ramirez-Boehme, 1974:30 [key].

Fissurella depressa Lamarck, 1822, 6(2):15; Sowerby, 1835b: 1 (under *F. crassa*); Mermod, 1950:713 [type lost].

Fissurella clypeiformis Sowerby, 1825, app., p. vi; Sowerby, 1835b:1 [under *F. crassa*].

Shell. Medium large (60–90 mm mature length), height low to moderately elevated, elongate oval to very elongate, some with elevated sides, others with elevated ends or with both (so that shells rests on four corners). Sculpture smooth except for early primary ribs that become broad and low, forming wide marginal crenulations. Color caramel brown, occasionally with faint rays of darker brown, surface eroded if epibiotic *Scurria* is present, clean and uneroded if not. Margin upwardly rounded at all growth stages. Shell margin showing light inner zone and darker outer zone. Cut shells also showing very thin lighter-colored layer, layer not evident at edge. Foramen elongate and tripartite in young shells, very elongate and constricted in middle in mature shells, posterior portion much wider and longer than anterior; foramen in mature shells beveled inward at ends. Aragonitic layer of interior between callus and muscle scar pinkish gray throughout and radially ridged.

Juvenile Shell. Sculpture of strong light-colored primary ribs that become wide and low, interspaces wide and dark-colored, two lateral white rays prominent. Shell becomes dark overall on reaching length of 7 mm. Upwardly rounded margin begins in earliest stages.

Mantle and Foot. Shell too low to accommodate large animal within it. Cephalic tentacles brown; mantle lobe broad, banded in light and dark, bands not matched by shell rays but no doubt corresponding to rayed pattern of early juveniles. Papillae of upper edge very large, those of lower edge much less developed. Side of foot with large, bulbous,white-tipped tubercles. Papillae project at both ends of foramen.

Habitat. Mid-intertidal zone, in crevices on rocky reefs, in surf-exposed or partially protected areas, occurring at higher levels than the other species, tightly wedged in narrow crevices during low tide. The upturned margin may be an adaptation to the rather cramped position of the animal when

exposed at low tide. Most specimens have a single *Scurria parasitica* on the shell. Bretos (1978, 1980) has studied growth in this species.

Distribution. Huarmey, Peru (10°06′ S) (AMNH 134571), to Punta Pulga, Isla de Chiloe, Chile (42°06′ S) (Dell, 1971). Dall (1909) cited the Galápagos Islands, Ecuador, and USNM 59260 is so labeled, but this record is discounted. The southern limit is uncertain. The species is known from the northwestern tip of Isla de Chiloe but may extend farther south. I did not find it on the eastern side Isla de Chiloe, where there is little exposure to surf. The record of Riveros-Zuñiga (1951) from Fuerte Bulnes in the Magellan Strait is rejected.

Number of Lots Examined. 88 (LACM 31, AMNH 23, ANSP 7, MACN 7, MNHN 10, USNM 10).

Taxonomic History. *Fissurella crassa* has been correctly interpreted by authors. It differs sufficiently from all other species that it can not be confused with any of them.

Abundance and Use. Common throughout its range and widely exploited for food. The upper intertidal habitat is so accessible that large specimens are seldom seen. It is known as the "lapa de sol," because it occurs relatively high, where it is exposed to the sun.

Characteristics and Variability. The most characteristic features of *F. crassa* are the uniformly brown color of the shell, the lack of radial ribs other than the broad undulations, the lavender staining of the interior, the great enlargement of the posterior end of the foramen, and of most importance, the upturned margin. The foot also has the strongest development of tubercles in any of the species. Variation is not extensive and is limited to rather minor differences in height and amount of elevation of the sides or ends.

Affinity and Comparisons. The closest affinity of *F. crassa* seems to be with *F. limbata.* In both species the foramen remains elongate, the sculpture is undulating, and strong ribs are lacking. As in *F. limbata* there is a thin outermost zone to the calcitic layer that is lighter in color. The upturned margin of *F. crassa* is unique. Although the margin of *F. maxima* is also unusual, in that species only the junction between the margin and the internal aragonitic layer is rounded.

Synonymy and Types. The original description of *F. crassa* Lamarck mentioned no locality. Mermod (1950:702), in his report on types of Lamarck in the Geneva collection, gave notes on a specimen 73 mm in length, which he considered to be Lamarck's original.

The locality for the very briefly described *F. depressa* Lamarck, 1822, was given as the "Indian Ocean." Sowerby (1835b:1) stated under *F. crassa:* "Lamarck's *F. depressa* is only a worn fragment of this species, as Mr. Gray informs me." Presumably, Gray had examined the Lamarck collection. Mermod (1950:713) reported that the type specimen now is lost.

The holotype of *F. clypeiformis* Sowerby, 1825, is an unworn specimen of *F. crassa,* BMNH 40.6.1.9, 70.4 mm in length (Fig. 227). It was described without locality and was placed in synonymy shortly after publication by Sowerby (1835b) himself.

Fissurella bridgesii Reeve, 1849

Figures 238–253

Fissurella bridgesii Reeve, 1849, pl. 3, fig. 15; Hupé, 1854: 238; Philippi, 1860:180; Sowerby II, 1862:184, figs. 21, 22, 34; Pilsbry, 1890:151, pl. 30, fig. 3; Dall, 1909:241; Riveros-Zuñiga, 1951:121, fig. 28; Dell, 1971:183, pl. 3, figs. 8, 9; Ramirez-Boehme, 1974:31 [key].

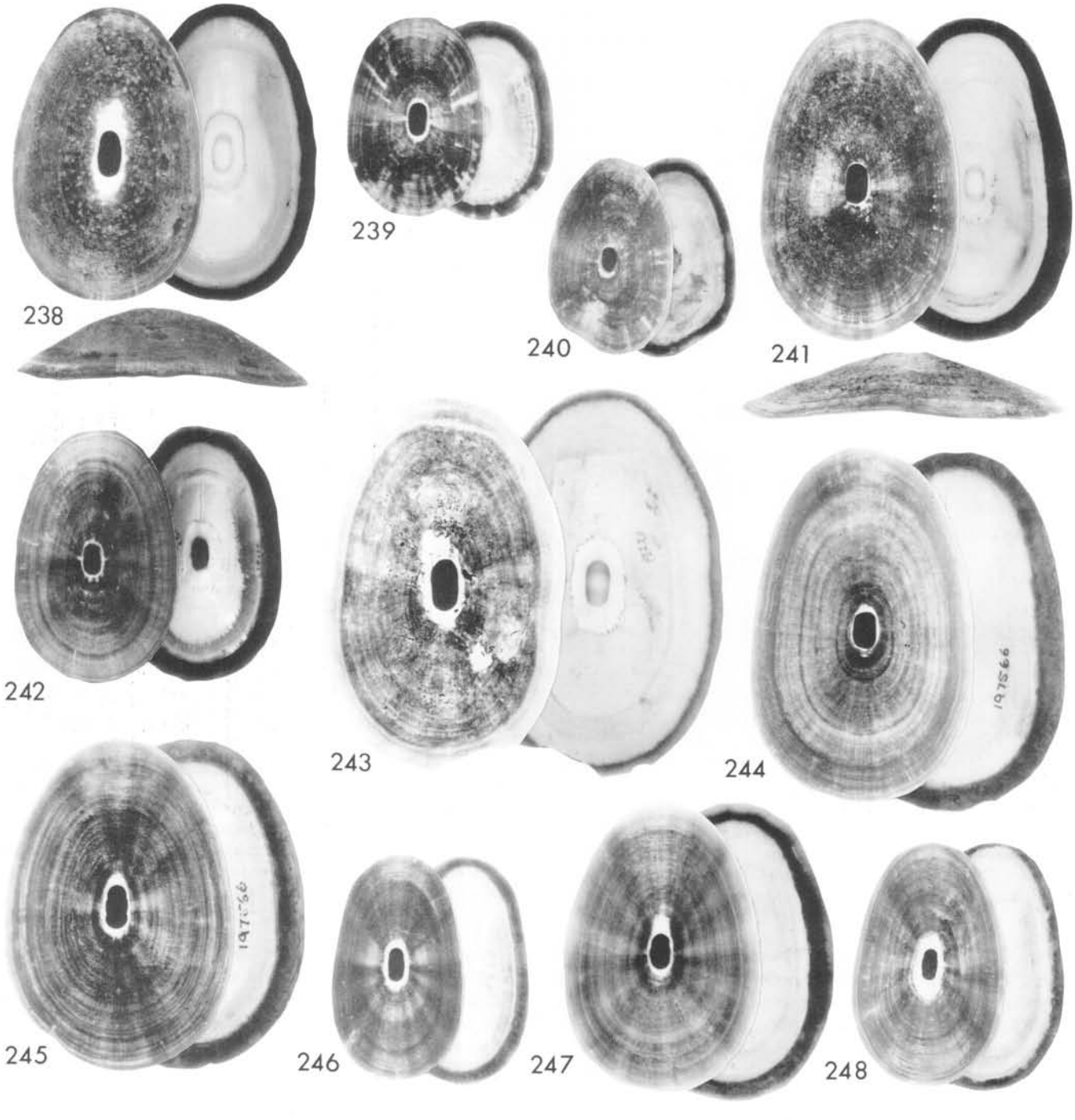
Shell. Medium large (65–90 mm mature length), low; outline elongate-oblong, lateral profile mostly straight, but some specimens with slightly raised sides or ends. Sculpture of fine low ribs in young shells; mature shell nearly smooth, with traces of very broad, irregular radial ribs and irregular radial striae. Color grayish or reddish brown, with faint lighter and darker rays, two lateral rays often more prominent; ground color changing gradually to light gray in large shells. Margin broad in growing shells, flat and often beveled out and up (except at front end) so that its edge is not in contact on a flat surface; margin narrower and rounded in mature shells. Calcitic layer zoned, inner zone dark reddish brown, changing to translucent gray at outer surface, outer zone usually lighter. Foramen unusually large and oval at all growth stages, broadly tripartite in some and showing two projections at sides, others lacking these projections.

Juvenile Shell. None seen under 20 mm in length; primary and secondary ribs weak, nearly equal in size at shell length of 20 mm; foramen large and oval at this shell length. Young shells have two lateral white rays.

Mantle and Foot. Body too large to retract beneath low shell; the mantle lobe broad and thin, enveloping shell edge. Papillae of upper edge tongue-shaped, finely branched, those of lower lobe similarly shaped but smaller and more numerous. Mantle lobe vertically banded with light and dark to correspond to weak pattern of rays on shell. Side of foot marbled; in preserved specimens, dark tubercles are surrounded by lighter areas.

Habitat. *Fissurella bridgesii* occurs on surf exposed rocks surrounded by sandy areas in the intertidal zone and the shallow sublittoral zones, a habitat entirely unlike that of the others. I missed seeing this species because I did not examine this habitat in Chile in 1975. However, the occurrence of *F. bridgesii* has been detailed by Bretos (1979). Shells are usually overgrown with an algal mat. Only rarely do shells have attachment scars of *Scurria,* indicating that they usually live deeper than the mid- to upper intertidal zone preferred by *Scurria.* The Californian acmaeid limpet *Notoacmea fenestrata* (Reeve, 1855) has a comparable habitat on rocks surrounded by sand.

Distribution. Isla Guanape, Peru (8°32′ S) (LACM 74-3, McLean), to Río Bio-bio, Concepción Province, Chile (36°48′ S) (LACM 75-35, McLean). There is but a single record from



Figures 238 through 248. *Fissurella bridgesii* Reeve, 1849. Mature shells. (**238**) 3–5 m, Isla Guanape, Peru. LACM 74-3, 66.0 × 46.0 × 15.0 mm. (**239**) Iquique, Chile. LACM 90802, 22.4 × 15.7 × 5.3 mm. (**240**) Same locality. LACM 90802, 20.0 × 12.8 × 5.9 mm. (**241**) Iquique, Chile. LACM 90803, 65.5 × 41.3 × 14.5 mm. (**242**) Paposo, Antofagasta Province, Chile. LACM 54764, 44.4 × 28.6 × 9.3 mm. (**243**) Quintero, Valparaíso Province, Chile. USNM 48221, 89.3 × 57.0 × 23.5 mm. (**244**) Paralectotype, *F. bridgesii* Reeve. Quintero, Valparaíso Province, Chile. BMNH 197566, 77.6 × 49.1 × 114.3 mm. (**245**) Lectotype, *F. bridgesii* Reeve. Quintero, Valparaíso Province, Chile. BMNH 197566, 68.0 × 47.5 × 13.7 mm. (**246**) Valparaíso, Chile. USNM 56255, 33.0 × 19.5 × 10.2 mm. (**247**) Valparaíso, Chile. AMNH 20055, 52.8 × 36.0 × 10.4 mm. (**248**) Río Bio-bio, Concepción Province, Chile. LACM 75-35, 42.4 × 26.5 × 9.0 mm.

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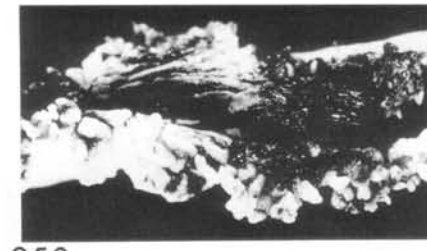

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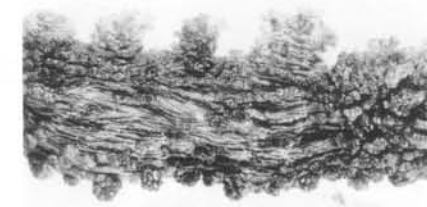

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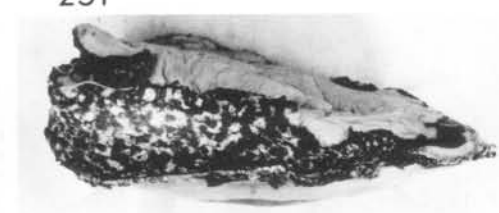

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Figures 249 through 253. *Fissurella bridgesii* Reeve, 1849. Living and preserved specimens, mantle lobe and radula. (**249**) Three living specimens in place. Tocopilla, Antofagasta Province, Chile, photo courtesy A. Viviani. (**250**) Mantle lobe. Iquique, Chile. LACM 90803, length 15 mm. (**251**) Mantle lobe. 3–5 m, Isla Guanape, Peru. LACM 74-3, length 20 mm. (**252**) Preserved specimen. Iquique, Chile. LACM 90803, shell length 65.5 mm. (**253**) Air-dried radula. Iquique, Chile. LACM 90804, width 3.5 mm, shell length 74.4 mm.

Peru, the living specimen I collected in 1974 at Isla Guanape (Fig. 238). I have examined specimens from the following localities in Chile: Iquique, Paposa, Quintero, Valparaíso, and Río Bio-bio, near Concepción.

Number of Lots Examined. 15 (LACM 8, AMNH 1, MACN 1, MNHN 3, USNM 2). This species is uncommon in the collections examined.

Taxonomic History. Accounts of *F. bridgesii* in the literature prior to the report of Bretos (1979) were copies of the original description of Reeve (1849). Dell (1971) considered this taxon a synonym of *F. latimarginata*. The validity of the species was confirmed in 1977, when I compared a preserved specimen sent to me for identification by M. Bretos with the syntypes from the British Museum then on loan at the LACM. Although I was unable to find living examples of this species during my fieldwork in Chile, puzzling beach-worn shells were collected at several localities, and I later discovered that I had purchased live specimens at the market in Iquique. The specimen I had earlier collected in Peru at Isla Guanape was then recognized as *F. bridgesii*. The specialized habitat of this species accounts for its scarcity in collections. It may be, however, that Ramirez-Boehme (1974) had recognized the species, because his key mentions the characteristic upwardly beveled margin ("bordes laterales reflejados hacia arriba"), a feature not discussed elsewhere in the literature.

Abundance and Use. *Fissurella bridgesii* is used for food at Iquique, and it may have more economic importance than suggested by the paucity of specimens in collections. According to M. Bretos, it is known to the fishermen as the

"lapa jerguilla," or the "lapa de arena" (sand). The jerguilla is a fish, *Aplodactylus punctatus,* which has a color pattern resembling that of the body of *F. bridgesii.*

Characteristics and Variability. The most characteristic features of *F. bridgesii* are the lack of regularly defined radial sculpture in mature shells, a relatively large foramen, a faintly rayed pattern on a gray-brown ground, and the broad, flat margin, which is beveled upward in young, growing specimens. Some specimens have an elongate foramen that is bidentate on the sides; others of the same size may have a more oval foramen. Color patterns include faintly rayed specimens and some uniformly gray shells lacking traces of rays. The northernmost specimen from Isla Guanape, Peru, lacks rays (Fig. 238).

Affinity and Comparisons. *Fissurella bridgesii* most resembles *F. latimarginata.* The normal weakly rayed pattern of *F. bridgesii* can be related to the unusual rayed color form of *F. latimarginata.* Both have a broad margin and a lighter outer zone to the calcitic layer, but only *F. bridgesii* has an upwardly beveled margin. Both species have similar elaboration of the tongue-shaped papillae of the mantle edge, more so than do other species. In its light outer shell layer it also resembles *F. limbata,* but may be distinguished from that species in lacking the purple coloration to the shell. *Fissurella bridgesii* also resembles *F. pulchra* in its low profile, weakly contrasting pattern of rays, and the lighter outermost zone to the calcitic layer. It differs in lacking the speckled pattern of *F. pulchra* and in having a larger foramen and a more pronounced upward-beveled margin. Although the size of the foramen varies somewhat in *F. bridgesii,* it is always larger than that of similarly sized specimens of *F. pulchra.* Before I understood *F. bridgesii,* my guess was that young beach-worn specimens, such as the one from Concepción (Fig. 248), were most likely to be variants of *F. pulchra.*

Synonymy and Types. There are four syntype specimens of *F. bridgesii* Reeve, 1849, from Quintero, Valparaíso Province, Chile (32°47′ S), BMNH 197566, lengths 77.7, 68.0, 61.8, and 46.0 mm. The 68.0 mm specimen was figured by Reeve (1849), Sowerby II (1862), and Dell (1971), and is here designated the lectotype (Fig. 245); the larger 77.7 mm specimen has been figured only by Sowerby II (1862). These two large specimens (Figs. 244, 245) illustrate two of the most variable features of the species. They are nearly of the same width, but one is much more elongate. The larger, elongate specimen has an oval foramen; the broader specimen has a bidentate foramen. The two remaining paralectotypes are broad; the 61.8 mm specimen has an oval foramen; the 46.0 mm specimen has an elongate foramen with the bidentate structure nearly imperceptible. Shape of the foramen is therefore not correlated with shell proportions.

Fissurella pulchra Sowerby, 1835

Figures 254–267

Fissurella pulchra Sowerby, 1835a:124; Sowerby, 1835b:3, fig. 24; Reeve, 1849, pl. 2, fig. 9; Hupé, 1854:244; Philippi, 1860:181; Sowerby II, 1862:184, fig. 31; Pilsbry, 1890: 151, pl. 33, fig. 50; Dall, 1909:242; Riveros-Zuñiga, 1951: 120, fig. 27; Dell, 1971:191, pl. 3, fig. 5; Ramirez-Boehme, 1974:30 [key].

Shell. Medium-sized (35–75 mm mature length), consistently low; outline elongate oval, tapered anteriorly, sides slightly raised relative to ends. Radial sculpture in early growth stages consisting of low, rounded primary ribs, becoming obsolete when shell reaches length of 20 mm; mature shell smooth except for faint radial striae. Color grayish lavender to pink, with alternating lighter and darker rays; entire surface with fine reddish speckles or zigzag markings especially pronounced near foramen; concentric interruptions to rays changing color from pink to gray or brown in some. Margin of moderate width, flat, reddish gray, zoned to make edge slightly lighter in color; broken shells showing lighter outer zone of calcitic layer; margin becoming very narrow in large, full grown shells. Foramen elongate and tripartite in young shells, only slightly less elongate in mature shells; interior callus bordered by pink colored ring in attachment region.

Juvenile Shell. Primary ribs rounded, coinciding with lighter rays, speckled pattern conspicuous. Sides of shell raised bordering foramen, indicating that earliest stage is more conical.

Mantle and Foot. Not retractable in flattened shell; mantle lobe normally extending well over shell edge. Cephalic tentacles lavender, yellowish at tips. Mantle lobe pinkish gray or brown, faintly banded to match rayed pattern, lined concentrically with brown. Papillae of upper edge well developed, those of lower edge more numerous and smaller. Side of foot same color, tubercles well developed.

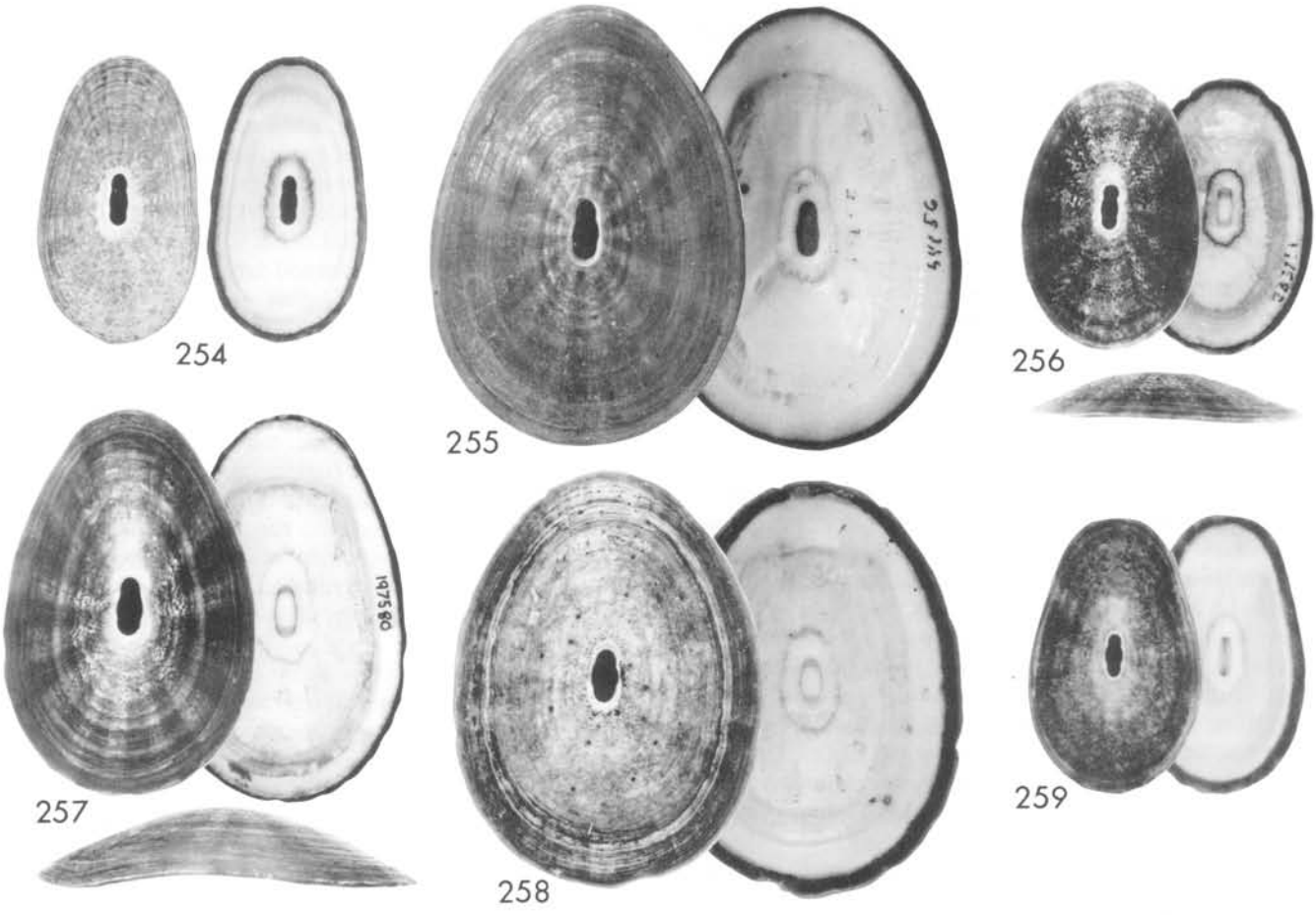
Habitat. Low intertidal and sublittoral zones in crevices or on undersides of large rocks in deep tidepools, protected from direct exposure to surf. Shells are free of algal incrustations; epibiotic organisms on the shell are bryozoans and spirorbid polychaetes.

Distribution. Salaverry, Peru (8°14′ S) (USNM 368490, W. Schmitt), to Río Bio-bio, Concepción Province, Chile (36°48′ S) (LACM 75-35, McLean). Except for *F. bridgesii,* this is the least common species in the Peruvian Faunal Province. I have found small specimens at most localities in central Peru. In northern Chile it was rare at Iquique; at Antofagasta there was no trace of it, even in the beach-worn shell debris. It was more common in central Chile, where I found living specimens on undersides of boulders in tidepools at Los Molles, Aconcagua Province. Beach-worn specimens were found at other localities in central Chile.

Number of Lots Examined. 21 (LACM 13, AMNH 1, ANSP 3, USNM 4, none at MACN or MNHN).

Taxonomic History. Most authors have merely copied the original account of *F. pulchra,* except for Pilsbry (1890), who emphasized the characteristic speckled pattern. The habitat is cryptic, and beach-worn shells are sufficiently scarce that the species has escaped notice in recent years. Riveros-Zuñiga (1951) merely quoted previous authors, and Peña (1970) did not mention it. The collection from Iquique of Marincovich (1973) did not include it. Ramirez-Boehme (1974) included it in his key but did not mention the conspicuous speckles.

Abundance and Use. The species is sufficiently uncommon



Figures 254 through 259. *Fissurella pulchra* Sowerby, 1835. Mature shells. (**254**) Miraflores, Lima Province, Peru. LACM 71-187, 24.2 × 13.5 × 4.1 mm. (**255**) Pupudo, Aconcagua Province, Chile. LACM 54656, 78.5 × 56.0 × 17.0 mm. (**256**) Paralectotype, *F. pulchra* Sowerby. Valparaíso, Chile. BMNH 197580, 39.6 × 25.8 × 6.6 mm. (**257**) Lectotype. *F. pulchra* Sowerby. Valparaíso, Chile. BMNH 197580, 62.2 × 40.2 × 12.8 mm. (**258**) Cartagena, Santiago Province, Chile. LACM 75-34, 68.5 × 50.8 × 14.3 mm. (**259**) Río Bio-bio, Concepción Province, Chile. LACM 75-35, 37.5 × 23.3 × 6.6 mm.

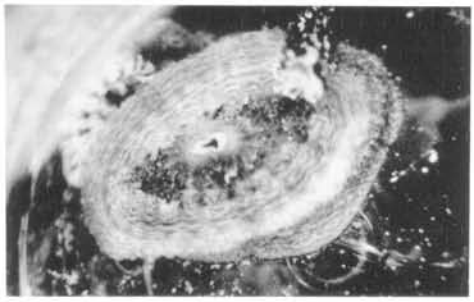
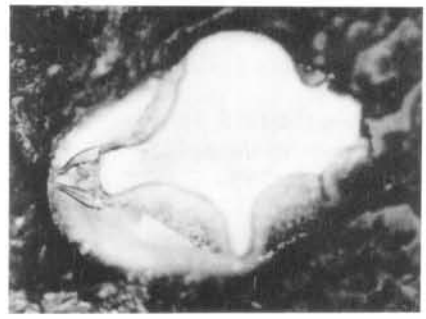
to be negligible as a food resource. Large specimens are particularly uncommon; living specimens that I found were about half the size of shells in the type lot, although I found some beach-worn shells that approached the maximum size. The largest specimen I have examined is 78.5 mm in length, from Papudo, Aconcagua Province, Chile, donated to the LACM by J. Ramirez-Boehme (Fig. 255). The species has no common name in northern Chile, according to M. Bretos.

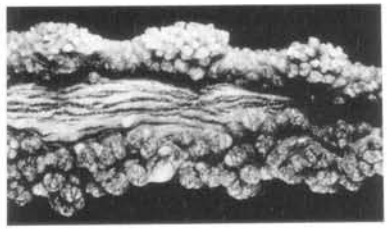
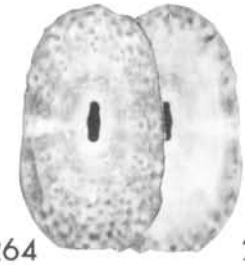
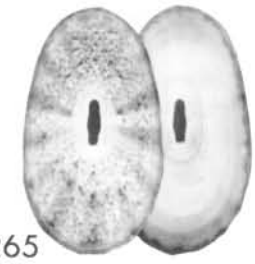
Characteristics and Variability. *Fissurella pulchra* is aptly named. It is rayed in pinkish brown and gray and is the only species in which a speckled pattern persists through all growth stages. It is one of the least variable species; I have noticed no unusual color forms. Shells are consistently low and tapered anteriorly. Most shells are relatively smooth, although the weak primary ribs may be more pronounced in some specimens.

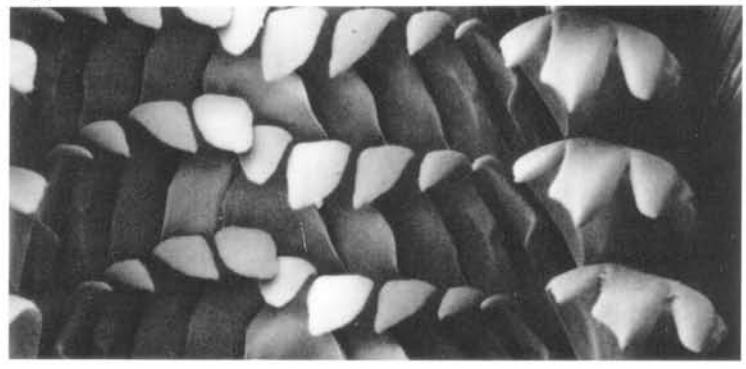
The radula of *F. pulchra* (Figs. 266, 267) is the most distinctive among the Peruvian-Magellanic species. The inner laterals have longer overhanging cusps than the other species, and the enlarged outer lateral is unique in having a concave edge to the second cusp.

Affinity and Comparisons. On shell characters, *F. pulchra* surely fits within the group having broad primary ribs and no secondary ribs. It is closest to *F. bridgesii,* with which it shares similar proportions, general overall coloration, and faint rays. It differs in its speckled pattern, more consistently narrowed foramen, and pink bordered internal callus. The margin is less broad than that of *F. bridgesii;* it is similarly beveled upward but to a lesser extent than in *F. bridgesii.* The tapered anterior end of *F. pulchra* resembles the condition of the otherwise not closely related *F. latimarginata* and *F. cumingi.*

Synonymy and Types. There are 5 syntypes of *F. pulchra* Sowerby, 1835, from Valparaíso, Chile, BMNH 197580, lengths 70.8 (broken in half), 62.2, 48.7, 39.6, and 24.0 mm. The largest of these has not been figured. The 62.2 mm specimen was figured originally by Sowerby (1835b), then by Reeve (1849) and by Dell (1971); it is here designated the



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Figures 260 through 267. *Fissurella pulchra* Sowerby, 1835. Living specimens, mantle lobe, juvenile shells, radulae. (**260**) Living specimen with mantle expanded, in tidepool. Cumbres Borascosas, Tarapaca Province, Chile. LACM 75-14. (**261**) Same specimen, ventral view. (**262**) Living specimen on underside of overturned boulder. Los Molles, Aconcagua Province, Chile. LACM 75-28. (**263**) Mantle lobe. Cumbres Borascosas, Tarapaca Province, Chile. LACM 75-14, 8 mm. (**264**) Juvenile specimen. Los Molles, Tarapaca Province, Chile. LACM 75-28, 5.8 × 3.5 × 1.3 mm. (**265**) Juvenile shell. Pucusana, Lima Province, Peru. LACM 72-76, 11.7 × 6.7 × 2.0 mm. (**266**) Radula of small shell. Same locality. LACM 72-76, 1.5 mm, shell length, 22.1 mm. (**267**) SEM view of radula. Los Molles, Aconcagua Province, Chile. LACM 75-28, width of field 0.6 mm.

lectotype. The lectotype and the 39.6 mm paralectotype are figured here (Figs. 256, 257).

LACM LOCALITIES FOR FIGURED SPECIMENS

[All collections from intertidal zone, unless otherwise indicated.]

AHF 375-35. Bahía Independencia, Ica Province, Peru (14°14′ S, 76°12.7′ W), 13 January 1935.

AHF 380-35. Bahía Independencia, Ica Province, Peru (14°14′ S, 76°08.5′ W), 14 January 1935.

AHF 828-38. Bahía San Juan, Ica Province, Peru (15°20.7′ S, 75°09.3′ W), 8 February 1938.

62-26. Ancud, Chiloe Province, Chile (41°52′ S, 73°05′ W), H.C. McMillin, 24 March 1962.

64-16. Iquique (near Ave. Baquedena), Tarapaca Province, Chile (20°13′ S, 70°10′ W), L. Marincovich, June through August, 1964.

66-46. Renaca, Viña del Mar, Valparaíso Province, Chile (33°06′ S, 71°50′ W), R. Seapy, 24 July 1966.

70-68. Iquique (10 km S), Tarapaca Province, Chile (20°15′ S, 70°09′ W), L. Marincovich, July, 1970.

71-187. Miraflores, Lima Province, Peru (12°08′ S, 77°04.5′ W), T. Bratcher, 24 February 1971.

71-277. Bahía York, Isla de los Estados, Argentina (54°47.11′ S, 64°17.9′ W), 5 May 1971.

71-284. Puerto San Juan del Salvamento, Isla de los Estados, Argentina (54°43.9′ S, 63°52′ W), 13 May 1971.
72-76. 0–5 m, Pucusana, Lima Province, Peru (12°30′ S, 76°49′ W), J.H. McLean, 30 March 1972.
72-77. Laguna Granda, Ica Province, Peru (14°18′ S, 76°15′ W), J.H. McLean, 31 March 1972 (beach-worn shells).
72-79. Paracas, Ica Province, Peru (13°49′ S, 76°14.5′ W). J.H. McLean, 2 April 1972 (beach-worn shells).
74-2. NE side, Isla Guanape, La Libertad Province, Peru (08°32′ S, 78°58′ W), J.H. McLean, 18 January 1974.
74-3. 3–5 m, NE side, Isla Guanape, La Libertad Province, Peru (08°32′ S, 78°58′ W), J.H. McLean, 18 January 1974.
74-21. 1–2 m, Playa Hermosa, Ancon, Lima Province, Peru (11°47′ S, 77°11.5′ W), J.H. McLean, 26 January 1974.
74-24. 1–4 m, Isla San Lorenzo, Lima Province, Peru (12°06.7′ S, 77°13′ W), J.H. McLean, 29 January 1974.
75-10. Pozo Toyo (S of Iquique), Tarapaca Province, Chile (20°25′ S, 70°10.5′ W), J.H. McLean, 29 September and 1 October 1975.
75-12. Iquique (at Marine Laboratory, Universidad del Norte), Tarapaca Province, Chile (20°15.5′ S, 70°08′ W), J.H. McLean, 2 October 1975.
75-14. Cumbres Borascosas, Tarapaca Province, Chile (20°42′S, 70°11.5′ W), J.H. McLean, 3 October 1975.
75-15. Antofagasta (S end of city), Antofagasta Province, Chile (23°42′ S, 70°27′ W), J.H. McLean, 5 and 6 October 1975.
75-16. Bahía Moreno, Antofagasta Province, Chile (23°28′ N, 70°31′ W), J.H. McLean, 7 October 1975 (beach shells).
75-17. [Shore opposite] Isla Santa Maria, Antofagasta Province, Chile (23°25′ S, 70°36′ W).
75-18. Punta Jara, Antofagasta Province, Chile (23°49′ S, 70°29′ W), J. Tomicic, 8 October 1975.
75-19. Los Colorados, Antofagasta Province, Chile (23°29′ N, 70°22′ W), J.H. McLean, 9 October 1975.
75-20. 2–5 m, Antofagasta (S end of city), Antofagasta Province, Chile (23°42′ S, 70°27′ W), J.H. McLean, 10 October 1975.
75-21. 7–20 m, El Rincon de Mejillones, Antofagasta Province, Chile (23°02′ S, 70°31′ W), J.H. McLean, 11 October 1975
75-23. 2–4 m, El Rincon de Mejillones, Antofagasta Province, Chile (23°05′ S, 70°30′ W), J. Tomicic, 12 October 1975.
75-25. Bahia Herradura, Coquimbo Province, Chile (29°59′ S, 71°22′ W), J.H. McLean, 14 October 1975.
75-27. Bahia El Teniente, Coquimbo Province, Chile (30°58′ S, 71°39′ W), J.H. McLean, 15 October 1975.
75-28. Los Molles, Aconcagua Province, Chile (32°14′ S, 71°32′ W), J.H. McLean, 16 through 18 October 1975.
75-29. Los Molles, Aconcagua Province, Chile (32°14′ S, 71°32′ W), J.H. McLean, 16 October 1975 (shell pile).
75-30. Montemar (at Estacion de Biología Marina), Valparaíso Province, Chile (32°57′ S, 71°32′ W), J.H. McLean, 19 and 20 October 1975.
75-31. Islota Concon, N of Vina del Mar, Valparaíso Province, Chile (32°52′ S, 71°33′ W), J.H. McLean, 21 and 22 October 1975.
75-34. Cartagena, Santiago Province, Chile (33°33′ S, 71°38′ W), J.H. McLean, 23 October 1975.
75-35. Río Bio-bio, Concepción Province, Chile (36°48′ S, 73°11′ W), J.H. McLean, 29 October 1975.
75-36. Mehuin, Valdivia Province, Chile (39°23′ S, 73°14′ W), J.H. McLean, 31 October and 2 November 1975.
75-37. [Island off] Mehuin, Valdivia Province, Chile (39°26′ S, 73°16′ W), J.H. McLean, 1 November 1975.
75-39. Pargua, Canal de Chacao, Llanquihue Province, Chile (41°47′ S, 73°28′ W), J.H. McLean, 3 November 1975.
75-40. Guabun, Isla de Chiloe, Chiloe Province, Chile (41°50′ S, 74°02′ W), J.H. McLean, 4 November 1975.
75-41. Pumalin, Golfo Corcovado, Chiloe Province, Chile (42°42′ S, 72°52′ W), J.H. McLean, 4 through 6 November 1975.
75-42. 2–4 m, Punta Estero, Isla Talcon, Golfo Corcovado, Chiloe Province, Chile (42°46′ S, 72°56′ W), J.H. McLean, 6 November 1975.
75-43. 4–13 m, Islota Nihuel, Golfo Corcovado, Chiloe Province, Chile (42°38′ S, 72°57′ W), J.H. McLean, 7 November 1975.
75-44. Islota Nihuel, Golfo Corcovado, Chiloe Province, Chile (42°38′ S, 72°57′ W), J.H. McLean, 7 November 1975.
75-45. Quellón, Isla de Chiloe, Chiloe Province, Chile (43°09′ S, 73°37′ W), J.H. McLean, 8 November 1975.
75-47. Isla Laitec, off SE side Isla de Chiloe, Chiloe Province, Chile (43°14′ S, 73°36′ W), 9 November 1975.
75-48. Fuerte Bulnes, Peninsula Brunswick, Magellan Strait, Magallanes Province, Chile (53°38′ S, 70°54.5′ W), J.H. McLean, 16 November 1975.
75-49. Puerto el Hambre, Peninsula Brunswick, Magellan Strait, Magallanes Province, Chile (53°37′ S, 70°56′ W), J.H. McLean, 16 and 19 November 1975.
78-88. Punta Ninfas, Golfo Nuevo, Chubut Province, Argentina (42°56.5′ S, 64°19.5′ W), J.H. McLean, 18 July 1978.
78-90. Punta Cracker, Golfo Nuevo, Chubut Province, Argentina (42°56.5′ S, 64°30′ W), J.H. McLean, 19 July 1978.

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