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A NEW SPECIES OF THE GENUS *ECHININUS* (MOLLUSCA: LITTORINIDAE: ECHININININAE) WITH A REVIEW OF THE SUBFAMILY

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Abstract.—A new ovoviviparous species, *Echininus viviparus,* inhabiting high intertidal and supratidal areas in the Mariana Islands is described in the littorinid subfamily Echinininae which previously consisted of the polytypic Indo-Pacific species *Echininus cumingi* (Philippi, 1846) and the west Atlantic species *Tectininus nodulosus* (Pfeiffer, 1839). Characteristics of the subfamily are reviewed.

I received for identification from L. G. Eldredge of the University of Guam specimens of an *Echininus* which upon close examination proved to be not only a new species, but one which exhibits ovoviviparity. The species described here I originally thought to be *Echininus cumingi spinulosus* (Philippi, 1847), and the realization that it is not prompted me to take a fresh look at the subfamily Echininae resulting in the following review.

Family Littorinidae Gray, 1840
Subfamily Echinininae Rosewater, 1972

Diagnosis.—The subfamily *Echinininae* is characterized by spinose to bluntly spinose shells; umbilicate or imperforate; opercula multispiral; radulae with moderately to greatly narrowed rachidians. Distribution is tropical west Pacific and west Atlantic.

The subfamily Echinininae was established by Rosewater (1972) to contain the genus *Echininus* which differs in matters of sculpture, radula, animal morphology, and ecology from either Littorininae or Tectariinae. This subfamily concept is strengthened by findings enumerated in the present paper. Members of the subfamily have a unique habitat among Littorinidae, for they inhabit highest shore levels, at times seeming almost to be terrestrial. The radula of *Echininus,* while said to be "not unusual" (Rosewater 1972:507), is distinctive when examined with the SEM (Fig. 1A–D). The radula of *Tectininus* is unique (Fig. 1E–F). The operculum is multispiral, a departure from all other known littorines. Characteristics of both radulae and opercula are here considered adaptations to a high shore habitat, as is the occurrence of ovoviviparity in the new species of *Echininus* described herein. All are indicative of a basic evolutionary trend in Echininae toward a terrestrial habit. Shells of this group are also distinctive, especially that of *E. cumingi cumingi,* which is characterized by rather long, open spines and a deep umbilicus. These latter features, also, may be of significant adaptive value to an animal living on tropical shores enabling easier dissipation of heat.

Tectininus Clench and Abbott, 1942

Tectininus Clench and Abbott, 1942:4; type-species by original designation *Echininus nodulosus* (Pfeiffer, 1839).—Abbott, 1954:458–462.

Diagnosis.—Shells bluntly spinose, succeeding spiral rows of spines non-synchronous; imperforate; opercula multispiral; radula with very reduced rachidian, modified lateral, and marginals with few denticles. Distribution is subtropical to tropical west Atlantic.

As originally proposed by Clench and Abbott (1942) and elaborated by Abbott (1954) the monotypic subgenus, *Tectininus,* was distinguished from *Echininus* s.s. because its type, *E. nodulosus,* possesses a unique radula, although still exhibiting the formula 2-1-1-1-2 and a modified littorinid embayment (Fig. 1E–F). It is unlike any other radula in the family, having massive lateral teeth and a diminutive rachidian which appears almost vestigial. The operculum is multispiral. It possesses a penis bearing a subterminal penial gland surrounded with fleshy papillae, which differs from the condition in the nominate subgenus and combines characteristics noted in the genera *Littorina, Nodilittorina,* and *Tectarius.* Although Rosewater (1972) had not seen the paper and reported that nothing was known of reproduction in Echinininae, it had already been shown that *T. nodulosus* is oviparous and produces a pelagic egg capsule (Borkowski 1971).

Until further evidence for its true relationships comes to light, I am satisfied to permit *Tectininus* to remain in its present position. As stated by Abbott, after careful study of the type-species of *Tectininus,* it appears to be ". . . a specialization of the ancestral stock . . . in the family Littorinidae" (Abbott 1954), whose apparent closest relations are in the Echinininae. Because of its unique radula *Tectininus* should be accorded full generic status.

Echininus Clench and Abbott, 1942

Echininus Clench and Abbott, 1942:3; type-species by original designation *Trochus cumingii* Philippi, 1846.—Rosewater, 1972:525.

Diagnosis.—Shells spinose to bluntly spinose; often with partly open spines; umbilicate to imperforate; opercula multispiral; radulae with moderately narrowed rachidians, laterals and marginals with moderately numerous denticles. Distribution is west Pacific from southern Japan through western Pacific arc to Cook Islands.

The genus *Echininus* was delineated as consisting of 2 subgenera containing a total of 2 living species and 1 subspecies (Rosewater 1972). The nominate subgenus, *Echininus,* inhabits the west Pacific and contains *E. cumingi cumingi* (Philippi, 1846) known from the southern Philippines southward through Melanesia (including New Guinea, Solomon Islands, New Hebrides, New Caledonia) eastward to the Cook Islands, and, *E. cumingi spinulosus* (Philippi, 1847) which occurs in southern Japan, the Ryukyu Islands, Taiwan and northern Philippines. *Echininus adelaidensis* (Cotton, 1947) is a Pliocene fossil from South Australia, which resembles certain trochaceans (Rosewater 1972). New evidence from preserved specimens indicates that the Mariana Islands population, previously believed to be part of *E. cumingi spinulosus,* is different from either of the previously known Pacific subspecies and is a new species.

Echininus cumingi cumingi, type-species, is comparatively large, reaching 20.9 mm (Table 1), with 3 spiral rows of conspicuous projecting, open spines on the body whorl; it has a narrow, deep umbilicus; a multispiral operculum is present; the radula has a moderately narrow rachidian, lateral and inner marginal teeth

each having one large and several smaller cusps, and slender outer marginals having 4–5 cusps. *Echininus cumingi spinulosus* is very close in appearance to *E. c. cumingi,* although it never reaches as large a size (18.3 mm), is less spinose, and has a narrower umbilicus which occasionally is closed. The specimens from the Mariana Islands which were included with the former by Rosewater (1972) are consistently different from either *E. c. cumingi* or *E. c. spinulosus*. Available records indicate they are limited in distribution to the southern Mariana Islands, and, so far have been reported only on the islands of Saipan, Tinian, Rota and Guam. Specimens are smaller in size, the largest measuring 12.3 mm in length; have only 2 major rows of blunt spines on the body whorl. In addition, the shell shape is different; obesity of the Mariana specimens averages 0.76 compared with 0.87 in *cumingi* and 0.78 in *spinulosus*. There are a number of quite absolute anatomical and biological differences also. Females of the Mariana population reproduce ovoviviparously, and the expanded oviduct may contain large numbers of young. The embryos are visible through the transparent dorsal mantle tissue in various stages of development including young snails with shells of 1.25–1.5 whorls. This condition is very similar to that described in *Littorina saxatilis* by Thorson (1946), and Fretter and Graham (1962). The reproductive modes of *E. c. cumingi* and *E. c. spinulosus* are not known, but there is no evidence from examination of preserved specimens to indicate ovoviviparity in them. There are also morphological differences between radulae and penes of the Mariana species and the more western and northern *Echininus*.

Echininus viviparus, new species
Figs. 1–6, Table 1

Description.—Shell: reaching 12.3 mm (about ½ inch) in length, turbinate in shape, with blunt spines; average obesity (width/length) about 0.76 (76 specimens range from 0.65–0.84) relatively thick in structure, usually non-umbilicate or with only a thin slit between columella and parietal callus; suture usually evident although often partially obscured by spiral sculpture; whorls 3–6, moderately shouldered below suture, relatively flat-sided; usually with 2 major rows of blunt spines on body whorl and one on spire whorls; occasionally with one or more additional major rows of spines. External shell color varying from grayish to tannish orange, the darker color characteristic of shells retaining periostracum; periostracum frequently worn away on spines which then appear grayish white. Apertural coloration light to dark orange with occasional light or darker orange lines revolving within. Base moderately flattened, sculptured with weakly nodulose cords. Length of spire greater than half length of shell. Spire convex; spire angle quite variable: from 60–72°. Aperture subquadrate; outer lip thickened, smooth within, only slightly wavy at edge reflecting external sculpture; inner lip with small but distinct toothlike bulge. Suture evident when not partly obscured by sculpture. Primary sculptural feature: 2 spiral rows of irregular blunt spines on body whorl, and one row on spire whorls. Rows of spines not well aligned axially; body whorl spine count 11–16 in posterior row and 12–16 in anterior row; 13–14 on penultimate whorl of spire. Secondary spiral sculpture consists of 3–4 fat, non-spinose cords between each spinose row, which occasionally become nearly as spinose as spinose cords they separate. In addition, an overall micro-

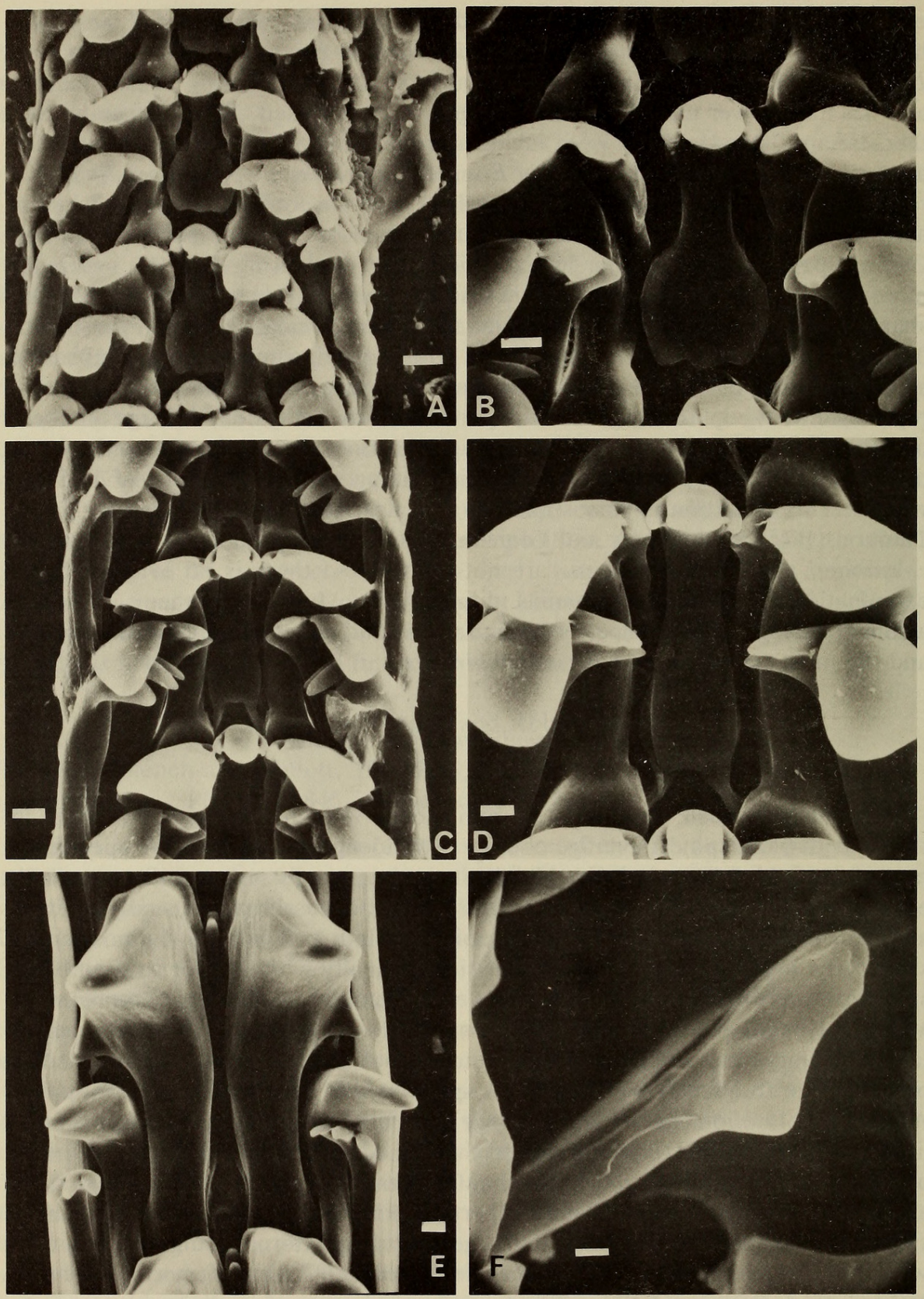

Fig. 1. Radulae: A, B, *Echininus viviparus*, ♀ from northeast coast of Tinian, Mariana Islands (USNM 796244): A, Showing 2 complete transverse rows, Bar = 10 μm, 875×; B, Rachidian tooth, Bar = 5 μm 1800×. C, D, *Echininus cumingi cumingi*, ♀ from Davao, Mindanao, Philippines (USNM 747765): C, Showing 2 complete transverse rows, Bar = 10 μm, 700×; D, Rachidian tooth, Bar = 5 μm, 1400×. E, F, *Tectininus nodulosus*, ♀ from San Salvador, Bahamas (USNM 596683): E, Showing 1 complete transverse row; note small, narrow rachidian tooth and massive laterals, Bar = 10 μm, 510×; F, Oblique view of rachidian tooth, Bar = 2 μm, 3500×.

Table 1.—Measurements (mm). Columns 1–6 correspond with numbered localities in *Material examined*; columns ♂ and ♀ summarize measurements of sexed specimens in 1–6; Summary *E. v.*, *E. c. c.*, and *E. c. s.*, summarize measurements of *Echininus viviparus*, *E. cumingi cumingi*, and *E. c. spinulosus*. Last 2 items in Table: Aperture length and ratio of L. Aperture to L. Shell are based on partial material as noted. ("no. P.-N. whorls" = number of post-nuclear whorls; "no. rows tub. B.W." = number of rows tubercles on body whorl).

Locality, sex or summary	1	2	3	4	5	6	♂	♀	Summary *E. v.*	Summary *E. c. c.*	Summary *E. c. s.*
N	25	16	9	10	9	7	10	27	76	26	58
Range L	4.4–10.3	8.1–12.3	5.9–8.7	5.6–7.3	6.8–10	4.8–8.0	4.8–10.9	5.0–10.9	4.4–12.3	13.4–20.9	5.1–18.3
Range W	3.3–7.7	6.2–8.2	4.4–6.7	4.1–5.6	4.9–7.8	3.7–6.1	3.7–7.6	4.1–7.8	3.3–8.2	11.5–18.4	3.7–14.1
Obesity:											
W/L Range	0.70–0.83	0.65–0.78	0.71–0.84	0.71–0.79	0.70–0.78	0.76–0.82	0.70–0.78	0.70–0.84	0.65–0.84	0.78–1.0	0.73–0.84
Average	0.76	0.74	0.76	0.75	0.74	0.79	0.75	0.77	0.76	0.87	0.78
No. P.-N. whorls:											
Range	3–6	4–6	4–5	3–5	4–5	4–5	4–5	4–6	3–6	5–7	4–6
Average	4.2	5	4.2	4	4.8	4.3	4.2	4.5	4.4	5.9	5.4
No. rows tub. B.W.:											
Range	2–3	2	2	2	2	2	2	2–3	2–3	3	3
Average	2	2	2	2	2	2	2	2	2	3	3
N	—	16	7	6	—	—	—	—	29	26	47
Range											
Aperture L	—	4.2–5.2	3.3–4.7	2.8–3.4	—	—	—	—	2.8–5.2	6.6–10.9	2.3–8.0
L. Aperture											
L. Shell											
Range	—	0.40–0.52	0.51–0.56	0.45–0.50	—	—	—	—	0.40–0.56	0.44–0.56	0.44–0.55
Average	—	0.47	0.54	0.47	—	—	—	—	0.49	0.51	0.50

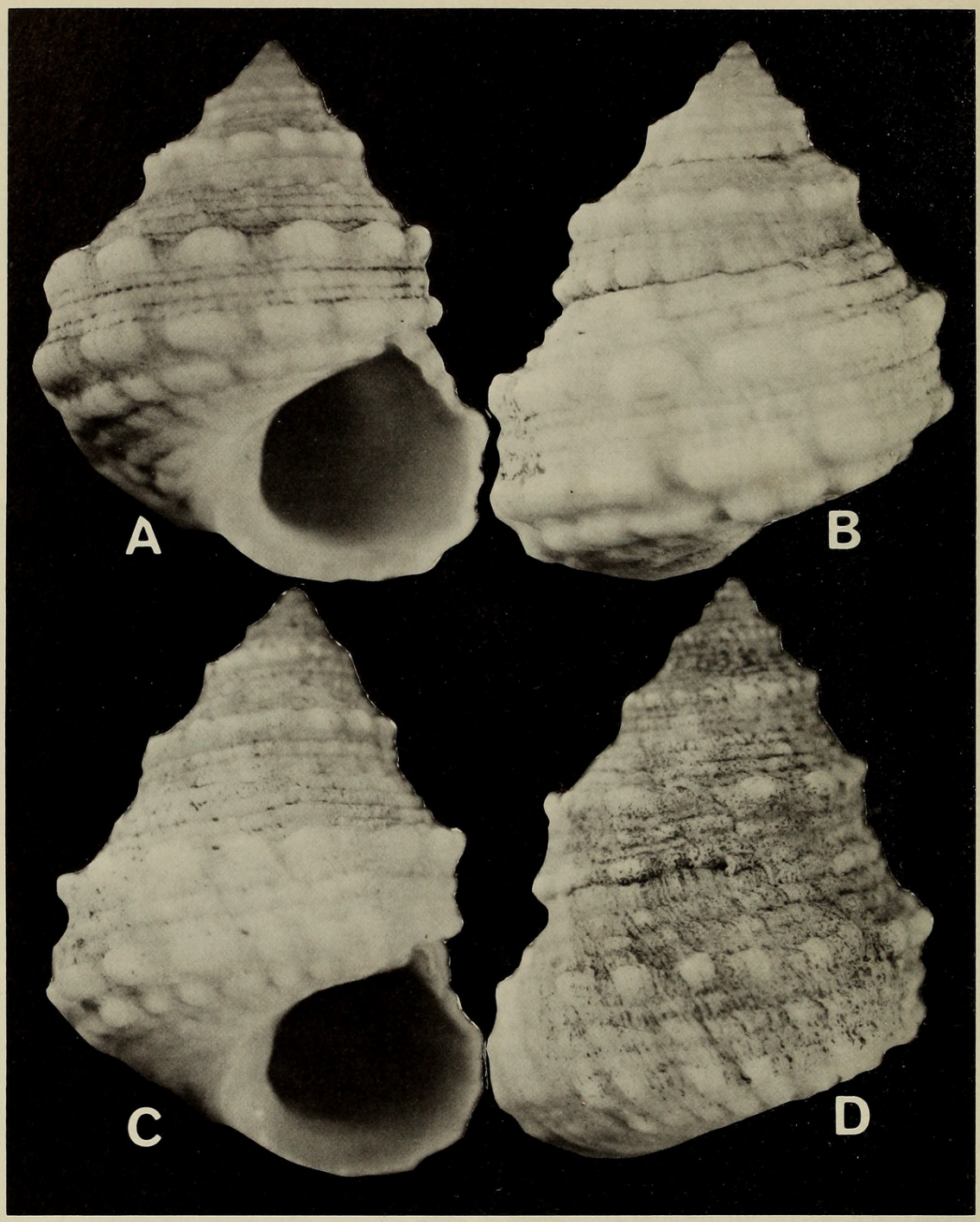

Fig. 2. Shells of *Echininus viviparus*: A, B, Holotype (USNM 792356), 9.7 × 7.4 mm; C, D, Paratype (USNM 803296) 10.7 × 7.6 mm.

scopical sculpture of fine, closely-spaced threads. Axial sculpture consists of irregular lines of growth. Operculum small in size, multispiral (polygyrous spiral type of Fretter and Graham 1962) having 5–6 volutions, chitinous, light brown in color. Nuclear whorls usually present, smooth, light brown to reddish brown; reaching about 1.25–1.50 volutions before developing spiral sculpture.

Animal: Radula littorinoid, 2-1-1-1-2; rachidian narrow, but with bulbous base having 3 basal denticles; lateral tooth with large central cusp and smaller lateral cusps and with distinct littorinoid embayment in which inner marginal tooth ar-

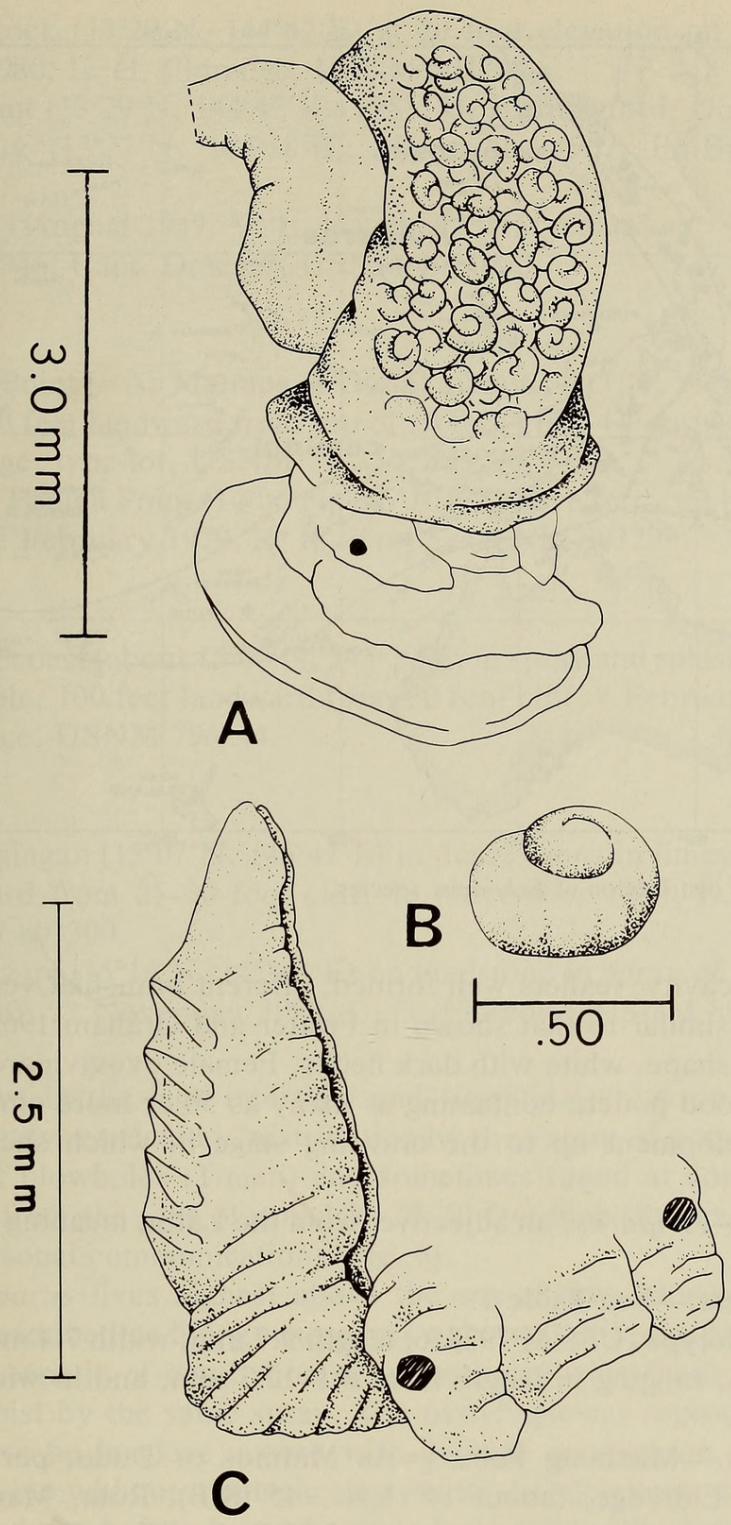

Fig. 3. *Echininus viviparus*: A, ♀ with well developed young in expanded oviduct seen through dorsal mantle; B, Detail from A: shell of young snail of about 1.5 whorls; C, ♂ showing arrangement of penial glands. All from northeast coast Tinian, Mariana Islands (USNM 796244).

ticulates; inner marginal with 4 cusps of which third from medial is largest; outer marginal with 4–5 cusps increasing in size laterally. Animal littorinoid; in the male penis is unbranched; wide and deep sperm groove runs along its posterior surface, the edges of which are brown pigmented; penis with 5–8 penial glands arranged in straight line along outer edge; well developed ctenidium present in

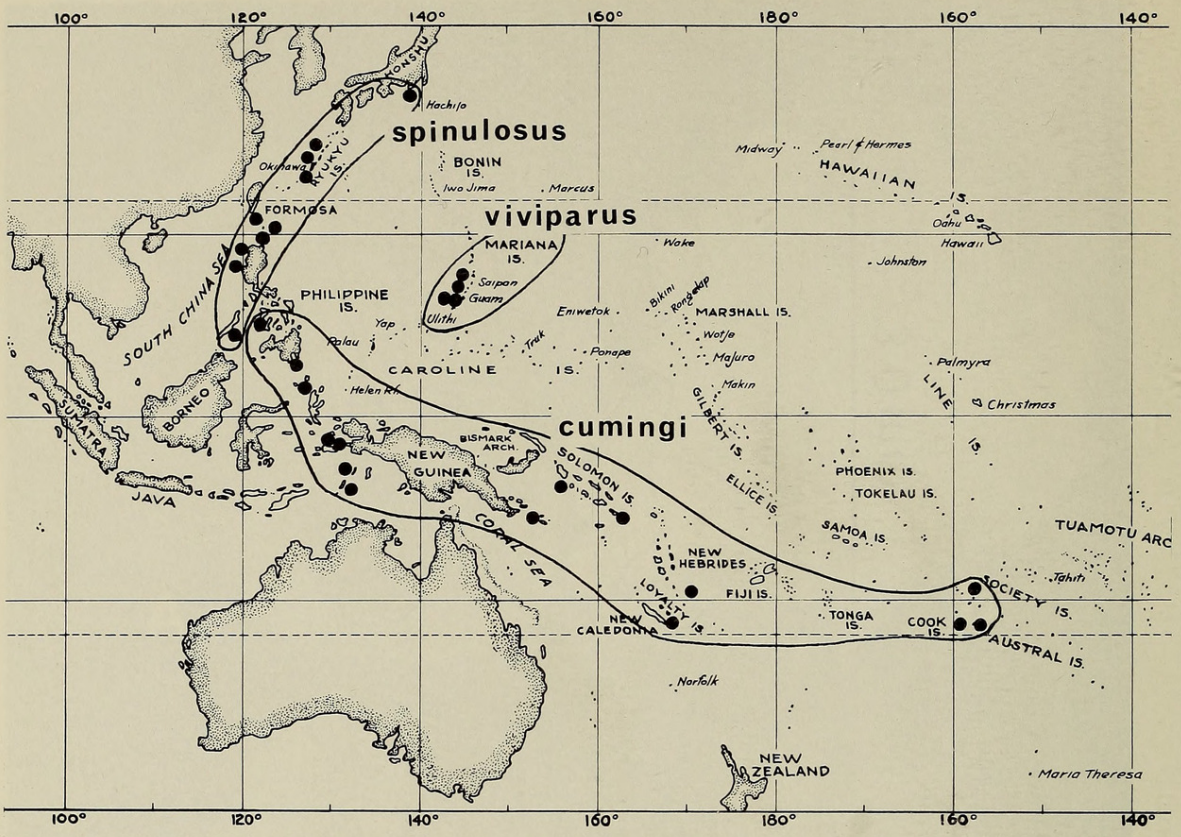

Fig. 4. Known distribution of *Echininus* species.

dorsal mantle cavity; leaflets well formed; efferent branchial vessel and osphradium present (similar to that shown in Fretter and Graham 1962, Fig. 7). Fecal pellets oval in shape, white with dark flecks. Female ovoviviparous with oviduct modified as brood pouch; containing as many as 50 or more embryos in various stages of development up to the crawling stage in which shell has 1.25–1.50 whorls.

Etymology.—*Viviparus,* an adjective, from the Latin, meaning "bearing active, living young."

Measurements.—See Table 1.

Types.—Holotype, USNM 792356; length 9.7 mm, width 7.4 mm; 15 paratypes, USNM 803296, ranging in length from 8.1–12.3 mm, and in width from 6.2–8.2 mm.

Type-locality.—Machong Point [=As Matmos or Dudu, personal communication, L. G. Eldredge] (about 14°11′N, 145°18′E), Rota, Mariana Islands; in spray zone 30 feet landward from top of 50 foot cliff; 4 February 1979; L. G. Eldredge, collector.

Material examined.—Mariana Islands, West Pacific Ocean.

Guam:

[1*] Agfayan Point (13°16′N, 144°44′E) high intertidal on limestone; July 1980, R. H. Randall, USNM 803297.

* Figure "1" refers to column 1 in Measurements Table 1; specimens from Guam are summarized together.

Camel Rock (13°29′N, 144°42′E) at 20 foot elevation on limestone; 13 June 1980, L. G. Eldredge, USNM 803298.
Asan Point (13°29′N, 144°42′E); 1951, D. B. Langford, USNM 613687.
Apra Bay (13°27′N, 144°38′E); November 1907, P. Bartsch, USNM 233323.
Guam, 29 August 1949, V. L. Haack, USNM 620383.
Guam, 1946, Capt. Draeger, USNM 707190.

Rota:

[2] Machong Point [=As Matmos or Dudu] (about 14°11′N, 145°18′E) in spray zone 30 feet landward from top of 50 foot cliff; 4 February 1979, L. G. Eldredge, type-lot, USNM 792356, 803296.
[3] West side Poniya Point (14°06′N, 145°10′E) above terraced bench in spray zone, 2 February 1979, R. K. Kropp, USNM 803299.

Tinian:

[4] Northeast coast (about 15°06′N, 145′39′E) in spray and splash zone of large blowhole, 100 feet landward from 20 foot cliff, 8 February 1979, L. G. Eldredge, USNM 796244.

Saipan:

[5] Puntan Agingan (15°07′N, 145°42′E) in depressions in limestone 6–10 feet landward from 25–30 foot cliff, 19 November 1980, L. G. Eldredge, USNM 803300.
[6] Puntan Magpi (15°16′N, 145°48′E) on limestone in spray of blowhole, 5–8 foot cliff, 21 November 1980, L. G. Eldredge, USNM 803301.

Ecology.—Lives in the high intertidal and supratidal areas on rough, pitted limestone apparently restricted in distribution by the extent of ocean spray; often in the vicinity of blowholes (Tinian) and sometimes found at considerable distances landward from the tops of sea cliffs 20–50 feet high (Rota and Tinian) (L. G. Eldredge, personal communication) (Fig. 6).

Echininus viviparus lives highest above the sea of any littorinid that I have observed. It is described as living where it is only wet by spray from surf or the blowholes characteristic of coral shores, where it probably feeds on vegetation which is kept moist by the same spray. The ovoviviparous reproduction of this species appears to be in close accord with its high position on the shore and permits it to survive without a pelagic stage in its development. Careful studies need to be carried out before it can be stated unequivocally, however, that *E. viviparus* has no need to return to the sea for any part of its life history.

Geographical distribution.—Southern Mariana Islands: Guam, Rota, Tinian, and Saipan.

Comparative remarks.—Morphometrics of *Echininus viviparus* are compared with those of *E. c. cumingi* and *E. c. spinulosus* in Table 1. Note that *E. viviparus* is smaller than the other two species, reaching only 12.3 mm in maximum length versus 20.9 and 18.3 mm respectively. On the average it is less obese, 0.76 versus 0.87 and 0.78, although difficulties of measuring spinose shells may artifically enhance the obesity of *E. c. cumingi*. Numbers of postnuclear whorls and rows

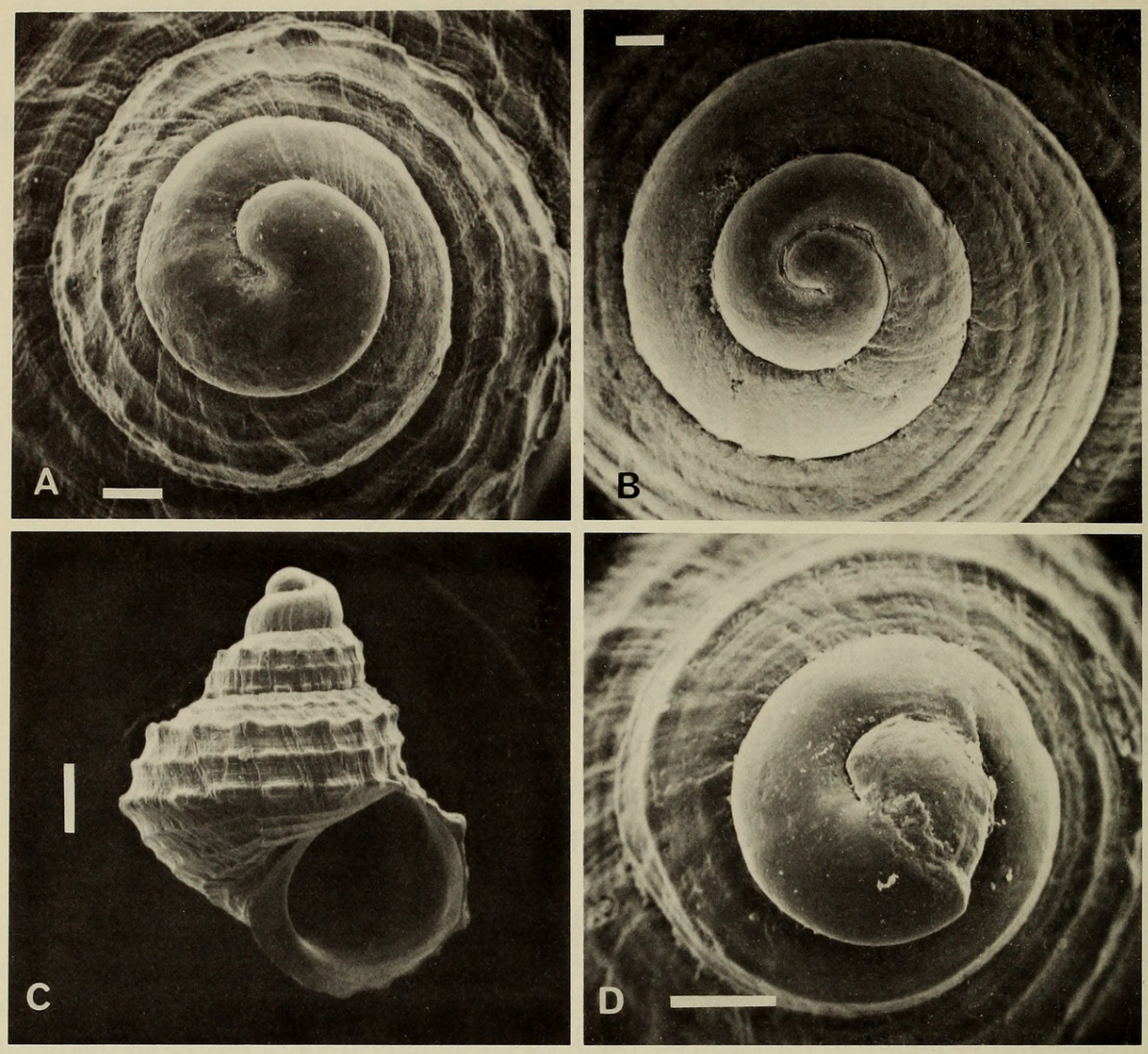

Fig. 5. A, Apex of *Echininus viviparus*, showing smooth protoconch of about 1.25 whorls (compare with Fig. 3B), specimen from northeast coast Tinian (USNM 796244), Bar = 100 μm, 100×; B, Apex of *Littorina saxatilis*, another ovoviviparous littorine, showing smooth protoconch of about 1.5 whorls, specimen from Odiorne Point State Park, Rye, Rockingham County, New Hampshire (USNM 803282), Bar = 100 μm, 80×; C, Apertural view of young *E. viviparus* showing 2 major rows of blunt spines on body whorl separated by moderately strong intermediate row, same data as A, Bar = 250 μm, 40×; D, Apex of *E. cumingi cumingi*, showing decollate tip, specimen from Philippines (USNM 89449), Bar = 100 μm, 185×.

of tubercles are less in *E. viviparus*. The aperture length/shell length index is smaller in *E. viviparus*. These data show the new species is smaller in size and more slender than previously known species. It is also non-umbilicate where the other two usually have an umbilicus. There is a rather weak but persistent tooth-like bulge on the inner lip.

The animal of *E. viviparus* is typically littorinoid, having a blunt snout and tentacles with eyes at the outer bases. It is significant that females of *E. viviparus* produce young ovoviviparously (Fig. 3A) because this has not been noted in other *Echininus* species. The penis of *E. viviparus* differs markedly from other species: in *E. viviparus* there are 5–8 penial glands in a straight line along the outer edge of the unbranched penis (Fig. 3C), while in *E. c. cumingi*, the glands occur only

at the junction of the bulbous base and the penial extremity, laterally and posteriorly (Rosewater 1972: plate 406, fig. B). The arrangement in *E. c. spinulosus* is similar to the latter. Radulae of the three species of the genus *Echininus* are similar, with differences in some details. In all species the teeth are small (see magnifications, Fig. 1) and reminiscent of the "pick type" (Rosewater 1980). Rachidian teeth of all three species of *Echininus* are narrow distally, but in *E. viviparus* the base is bulbous with 3 denticles (Fig. 1B). The tip of the protoconch is frequently present in *E. viviparus,* but is smaller and often decollated in *E. cumingi* and *E. spinulosus* (Fig. 5).

Discussion.—When I initially mapped the distribution of *Echininus* (Rosewater 1972, plate 407), information from museum specimens indicated that the ranges of the two subspecies, *E. c. cumingi* and *E. c. spinulosus,* were divided into northern and southern components by an east-west line drawn just south of Puerto Princessa, Palawan, Philippines (9°N). Some additional records have come to light for *E. c. cumingi*: Guimaras Island, Philippines [verifying the type-locality of *E. cumingi*] (10°35'N) (Kevin Marx, personal communication 1979); Lifou, Loyalty Islands (C. Lamb 1979, USNM) not very far from the Tana, New Hebrides record reported by Rosewater (1972). The discovery of the new species, *Echininus viviparus,* changes the pattern of distribution of the genus *Echininus* in the Indo-Pacific (Fig. 4). Although obviously related generically, the Mariana species is quite distinct from the other *Echininus* taxa in its distribution, in certain aspects of its morphology and, so far as is known, in reproducing ovoviviparously. In my previous evaluation of a few small, worn shells from Guam (Rosewater ibid.) I referred them to *E. c. spinulosus* because no anatomical evidence was available to the contrary. The additional freshly collected specimens provided by L. G. Eldredge have shown without doubt that *E. viviparus* is a separate species distinct from the subspecies group of *E. cumingi.* It is rather difficult to speculate upon the origin of *E. viviparus.* Little fossil evidence exists to trace the evolutionary history of the genus *Echininus* or, in fact, of any members of the family Littorinidae. Some littorinid fossils may have been assigned to such families as Turbinidae and Trochidae which are almost indistinguishable as fossils. The most similar in appearance is the fossil, *Tectarius rehderi* Ladd, 1966, from Lower Miocene, Marshall Islands (Ladd 1966, Rosewater 1972, pl. 404, figs. 5–7). According to Ladd (1960) much of the mollusk fauna now inhabiting west Pacific islands and the East Indies may have migrated in successive waves from east to west during Cretaceous and Tertiary times when an archipelago of islands existed through which species could move with relative ease. Such species as *Tectarius rehderi* may be the precursors of Recent *Echininus* and *Tectarius* species now inhabiting the western Pacific arc. It seems unlikely that the fossil species *Echininus adelaidensis* (Cotton, 1947) from the Pliocene of South Australia belongs in the Littorinidae and probably should be referred to the Trochacea. In the absence of data indicating a more widespread distribution, it appears that *Echininus viviparus* has evolved as an endemic species in the Mariana Islands where its ancestors became established during one of these earlier migrations. Other littorinid inhabitants of the Mariana Islands fail to show any indication of such endemicity (Roth 1976, Rosewater 1970, 1972).

Echininus viviparus joins the small but increasing group of mollusks whose life histories are known to include ovoviviparity, or brooding of young by the parent

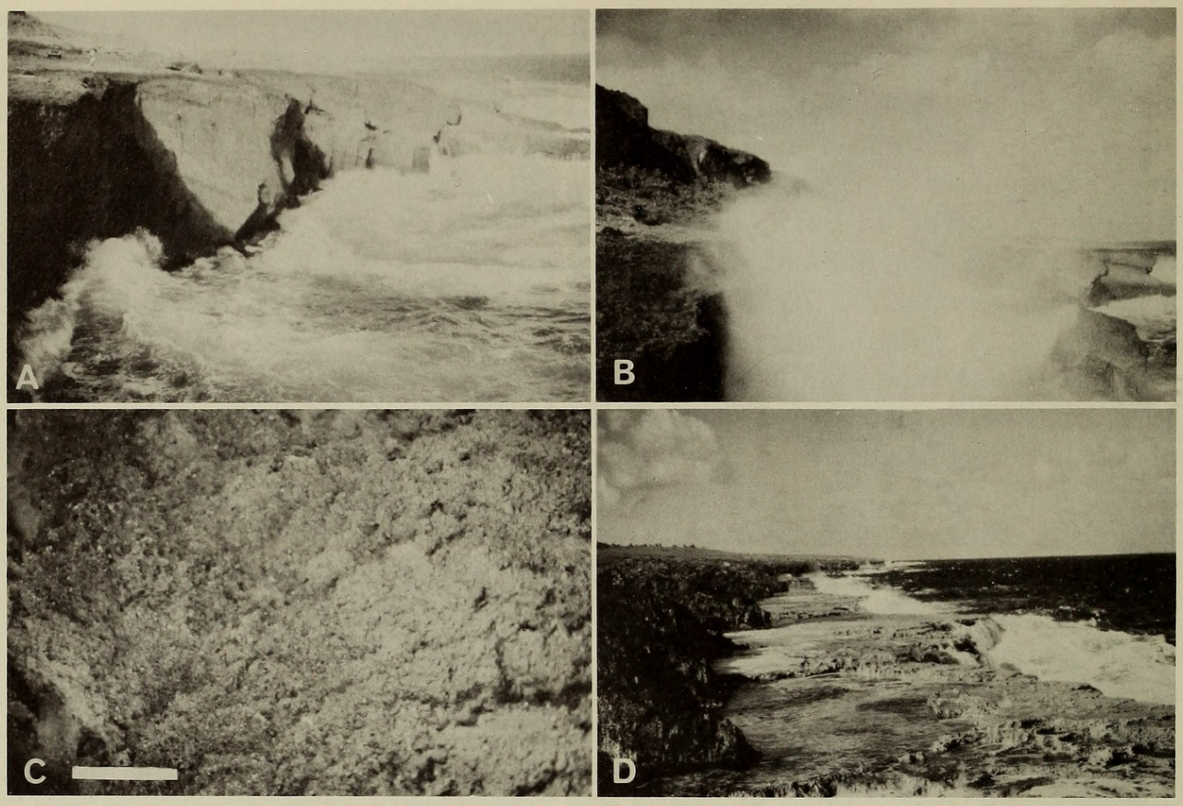

Fig. 6. A, Machong Point, Rota Island, Mariana Islands, habitat of *Echininus viviparus* 30 feet landward from top of 50 foot cliff; B, Same, showing spray reaching habitat; C, Same, showing pitted limestone; white dots are *Echininus*; Bar = 20 cm; D, Northeast coast Tinian, Mariana Islands, where *Echininus* lives 100 feet landward from top of 20 foot cliff. (Photos courtesy of L. G. Eldredge.)

through early stages of development. The occurrence of this form of reproduction in mollusks was reviewed by Van der Schalie (1936) who attributed its development to being of survival value for animals subjected to unfavorable environment. Ovoviviparity now is known to occur in several additional groups to those cited by Van der Schalie (1936). In Littorinidae it is known in at least three species, *L. saxatilis* (=*L. littoralis* of Van der Schalie), and *E. viviparus*. *Littorina scabra scabra* and *L. scabra angulifera* release young in various stages of development, as summarized by Mileikovsky (1975). Other instances of ovoviviparity in gastropods occur in Siliquariidae, Struthiolariidae, Nassariidae, and Turridae (Morton 1958); Coralliophilidae (Wells and Lalli 1972); Janthinidae and Hydrobiidae (Fretter and Graham 1962); Acmaeidae, Hipponicidae, Planaxidae, Vermetidae, Thiaridae, a few opisthobranchs, many Stylommatophora, a number of chitons, and some Aplacorphora (Hyman 1967). Among the Bivalvia there are also scattered cases: Nuculidae (Drew 1901); freshwater bivalves except *Dreissensia* [sic] (Cooke 1895); Arcidae, Ostreidae, Erycinacea (Morton 1958); Carditacea (Jones 1963, Yonge 1969); Veneridae (personal observation in the genus *Gemma*); Teredinidae (Turner 1966).

Ovoviviparity occurs within groups of mollusks often in what appears to be a rather haphazard fashion, although occasionally it will occur in an entire family such as Unionidae or Viviparidae. The development of this special type of parental care, as Van der Schalie (1936) has suggested, appears associated with animals living under special stress for which ovoviviparity contributes survival

value, i.e. larvae of freshwater mussels are distributed on fish; crawl-away young of *Echininus* living on cliffs far above the sea will survive where a pelagic developer could not. There is no way to predict when ovoviviparity will occur in a group. But the frequency with which it does occur lends credence to its value under the proper conditions.

Summary.—As presently defined the littorinid subfamily Echinininae consists of the following units distributed as noted:

Family Littorinidae Gray, 1840
Subfamily Echinininae Rosewater, 1972
Genus *Echininus* Clench and Abbott, 1942, type-species by original designation *Trochus cumingii* Philippi, 1946
Echininus cumingi cumingi (Philippi, 1846)—southern Philippines and along the western Pacific arc to New Hebrides and the Cook Islands
Echininus cumingi spinulosus (Philippi, 1847)—southern Japan through the Ryukyu Islands to northern and western Philippines
Echininus viviparus, new species—southern Mariana Islands
?†*Echininus adelaidensis* (Cotton, 1947)—Pliocene, South Australia
Genus *Tectininus* Clench and Abbott, 1942, type-species by original designation, *Litorina nodulosa* Pfeiffer, 1839
Tectininus nodulosus (Pfeiffer, 1839)—southern Florida, Bermuda, the Bahamas, and the Greater Antilles

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