

A CLARIFICATION OF THE GENUS *PERNA* (MYTILIDAE)

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ABSTRACT

Many morphological features of adult mussels are variable and often of limited value in establishing taxonomic relationships. Synonymies in the Mytilidae are numerous, the genus *Perna* notwithstanding. The historical development and geographical distribution of the three species placed in the genus *Perna* are reviewed.

As a post-metamorphic character, the presence of Lateral hinge teeth which develop after metamorphosis are unique and consistent criteria for distinguishing juvenile mussels of the genus *Perna*. The development and fate of provincular, primary lateral, secondary lateral and dysodont hinge teeth is presented in a series of scanning electron micrographs. Distinguishing features of soft-part anatomy and adult shells are summarized. Several anatomical features are discussed with respect to a possible trend in specialization among the genera *Perna*, *Choromytilus*, *Aulacomya* and *Mytilus*.

The Mytilidae, or true mussels, demonstrate a great deal of variation in morphological features which are taxonomically important in the Bivalvia. Thus the taxonomic status of species within the Mytilidae is often confused. For want of reliable morphological features by which to distinguish species and genera, the inconsistent or "plastic" character of gross adult shell morphology has, in the past, shaped the family's hierarchy. The existence of physiological races and a wide range of eco-morphs in the Mytilidae has complicated the interpretation of experimental evidence and created a taxonomic challenge for the researcher working with mytilids. Only recently have warm water mussels of the genus *Perna* been studied extensively, primarily because of their value as a food resource. Nomenclatural errors have persisted in these studies which have separately treated synonymous species of mussels and reported on eco-physiological differences between two or more races of the same species. In this paper, I describe several larval and adult characteristics of the three living species currently placed in the genus *Perna* (*P. perna*, *P. viridis* and *P. canaliculus*), briefly review the historical development and geographical distribution of the species, and present criteria for distinguishing larvae and adults of the genus *Perna* from those of the genus *Mytilus*.

HISTORICAL REVIEW

In 1932, the rosters of *Index Animalium* reported on the use of approximately 400 different species names in the genus *Mytilus* and another 71 names in the genus *Perna*. Unfortunately, the name *Perna* had been used to describe two genera of mytilids, *Perna* (Retzius, 1788) and *Modiolus* (H. and A. Adams, 1858), and a genus of Pteriacea, *Isognomon* (Bruguiere, 1792). When Retzius (1788) set forth the genus *Perna*, he listed the type specimen as *Perna magellanica* which according to Lamy (1936-1937) is synonymous with Linnaeus' *Mya perna* and whose holotype was presumably collected from the Straits of Magellan. Both are properly referred to as *Perna perna* (L.) (Lamy, 1936-1937). *P. magellanica* as described by Retzius must not be confused with *Mytilus magellanicus* Chemnitz which, as Soot-Ryen (1955) details, probably belongs to the genus *Aulacomya*.

Linnaeus (1758) first described *Mytilus viridis* while Gmelin (1791) is credited for *M. canaliculus* in spite of Martyn's (1784) earlier work which has been de-

termed to possess no status in zoological nomenclature (I.C.Z.N. opinion 456). The several works of Born, Chemnitz, Dillwyn, Gmelin and Lamarck expanded the list of species in the genus *Perna* but Hanley (1843, 1855) temporarily reversed this trend by lumping together several species. One notable point of confusion was Lamarck's use of *M. latus* (a synonym for *Choromytilus chorus*; Soot-Ryen, 1952), a name also employed by Chemnitz for the New Zealand green mussel, now referred to as *Perna canaliculus* (Fleming, 1959). In Hanley's work (1843) the synonymy of *M. viridis* L. and *M. smaragdinus* Chemnitz was discussed as was the synonymy between *M. canaliculus* (Gmelin) and *M. latus* Chemnitz. Morch (1853) set aside the genus *Chloromya* for those species belonging to Retzius' earlier genus, *Perna*. The use of the genus *Chloromya* added to the confusion, persisting beyond Lamy's later work.

Following the turn of the century, von Ihering (1901, 1907) and particularly Jukes-Browne (1905) discussed hinge and ligament structures and muscle scars as bases for establishing the taxonomic hierarchy of the Mytilidae. This work laid the foundation for Lamy's (1936–1937) analysis of museum specimens involving both the genera *Mytilus* and *Perna*. The confused taxonomic interrelationships involving *Mytilus* and *Perna* which developed in the 19th century were simplified by Lamy's comprehensive works followed by those of Soot-Ryen (1952, 1955). Dodge (1952) still regarded *Chloromya* as a subgenus of *Mytilus*. In 1952, Soot-Ryen divided the genus *Perna* (at the time, still referred to as *Chloromya*) into two groups: 1) those having a pitted resilial ridge belonging to the genus *Chloromya*, and 2) those having a compact resilial ridge forming a new genus, *Choromytilus* with the genotype *C. chorus* Molina 1782. Soot-Ryen (1955) showed *Chloromya* to be an invalid synonym for *Perna* and clarified much of the taxonomic nomenclature of the mytilids by retaining *Perna* (Retzius) 1788 for those species of mytilids resembling *Mytilus* s. str. but which have a pitted resilial ridge and discontinuous posterior retractor muscle scars and lack an anterior adductor muscle. Dance (1974) placed *C. chorus* Molina in the genus *Perna* but gave no new evidence supporting this change. The close taxonomic relationships among the genera *Mytilus*, *Perna*, *Choromytilus*, and *Aulacomya* are briefly described by Soot-Ryen (1952). In Beupherthuy's (1967) analysis of the Venezuelan mytilids, including *P. perna*, the genus "*Chloromytilus*" appears most probably as a typographical error referring to Soot-Ryen's valid genus *Choromytilus*.

Table 1 is not a comprehensive survey of the historical development of the genus *Perna*, but it summarizes a great many synonymies involving the three species.

MATERIALS AND METHODS

Larvae and adults of the three species of *Perna* were collected from 21 locations distributed throughout known geographical ranges including type localities. Specimens of *P. perna* were collected in Venezuela, Brazil and South Africa, *P. viridis* from Pakistan, India (both coasts), Singapore and the Philippines (two stations 600 km distant), and *P. canaliculus* from the north island of New Zealand. Observations of soft-part anatomy were made from adult specimens preserved in buffered 5% formalin. Live adults of *P. perna* (Cumaná, Venezuela) and *P. viridis* (Bacoar Bay, Philippines) were imported to Miami and quarantined. Current New Zealand governmental policy does not permit exportation of living specimens of *P. canaliculus*.

Live *P. perna* and *P. viridis* adults were held in running seawater (28–32‰ at 22–26°C) while being conditioned for spawning. Adults and developing larvae were fed a mixed phytoplankton diet of *Chaetoceros calcitrans*, *Dunaliella tertiolecta*, *Isochrysis galbana*, *Monochrysis lutheri*, and *Tetraselmis suecica*. Ripe adults spawned regularly within one half hour of being exposed to 35°C seawater for 10 min. Details of the culture procedures are outlined in Siddall (1979a). Larval cultures were maintained for 24 days while samples of larvae were withdrawn and preserved in Carriker's (1950) solution every 24 h for later examination. The lack of suitable substrates for settlement within the

Table 1. Important works describing *P. perna*, *P. viridis* and *P. canaliculus* and summary of synonymies

<i>Perna perna</i> (Linnaeus) 1758		
1758	<i>Mya perna</i>	Linnaeus, Syst. Nat., Ed. X
1780	<i>Mytilus pictus</i>	Born, Test. Mus. Caes. Vindob.
1785	<i>Mytilus africanus</i>	Chemnitz, Conch. Cab. VIII
1791	<i>Mytilus afer</i>	Gmelin, Syst. Nat., Ed. XIII
1817	<i>Mytilus elongatus</i>	Lamarck (non Chemn.), Anim. s. Vert. VI
1819	<i>Mytilus perna</i> L.	Lamarck, Anim. s. Vert. VI
1843	<i>Mytilus perna</i> L.	Hanley, Cat. Rec. Biv. Sh.
1855	<i>Mya perna</i> L.	Hanley, Ipsa Linn. Conch.
1901	<i>Mytilus perna</i> L.	von Ihering, Proc. Malac. Soc. Lond. IV
1905	<i>Mytilus (Chloromya) perna</i> L.	Jukes-Browne, Proc. Malac. Soc. Lond. VI
1905	<i>Mytilus (Chloromya) pictus</i> Born	Jukes-Browne, Proc. Malac. Soc. Lond. VI
1905	<i>Mytilus (Chloromya) afer</i> Gmelin	Jukes-Browne, Proc. Malac. Soc. Lond. VI
1907	<i>Mytilus perna</i> L.	von Ihering, Anal. Mus. Nac. Buenos Aires XIV
1919	<i>Mytilus (Chloromya) perna</i> L.	Lamy, Bull. Mus. Hist. Nat. XXV
1931	<i>Mytilus (Chloromya) perna</i> L.	Lamy, Bull. Mus. Hist. Nat. III. 2e Ser.
1936	<i>Mytilus (Chloromya) perna</i> L.	Lamy, Rev. Mytilidae J. Conchyl. LXXX
1952	<i>Chloromya perna</i> L.	Dodge, Bull. Amer. Mus. Nat. Hist., 100
1955	<i>Perna perna</i> L.	Soot-Ryen, Allan Hancock Pac. Exped. 20(1)
1964	<i>Perna perna</i> L.	Barnard, Ann. S. Afr. Mus. 47
1965	<i>Mytilus (Chloromya) venezolanus</i>	Andreu, Inst. Invest. Pesq. Barcelona 5
1965	<i>Chloromya perna</i> L.	Padilla, Rev. Inst. Invest. Pesq. Uruguay 1(4)
1967	<i>Perna perna</i> L.	Beauperthuy, Bol. Inst. Oceanogr. Univ. Oriente, VI
1969	<i>Perna perna</i> L.	Nordsieck, Die Europaischen Meeresmuscheln
1969	<i>Perna picta picta</i> Born	Nordsieck, Die Europaischen Meeresmuscheln
1973	<i>Perna perna</i> L.	Lubet, F.A.O. Synopses sur les Peches, Vol. 88
1973	<i>Perna perna</i> L.	Zaoualt, Rapp. Comm. Inst. Mer. Med. 22
1974	<i>Perna perna</i> L.	Day, Guide Mar. Life. S. Afr. Shores
1975	<i>Perna perna</i> L.	Rios, Brazilian Mar. Moll. Iconography
1976	<i>Perna (Perna) picta</i> (Born)	Buccheri and Palisano, Conchiglie 12
<i>Perna viridis</i> (Linnaeus) 1758		
1758	<i>Mytilus viridis</i>	Linnaeus, Syst. Nat., Ed. X
1785	<i>Mytilus smaragdinus</i>	Chemnitz, Conch. Cab. VIII
1791	<i>Mytilus smaragdinus</i> Chemnitz	Gmelin, Syst. Nat., Ed. XIII
1819	<i>Mytilus opalus</i>	Lamarck, Anim. s. Vert. VI
1819	<i>Mytilus smaragdinus</i> Gmelin	Lamarck, Anim. s. Vert. VI
1843	<i>Mytilus smaragdinus</i>	Hanley, Cat. Rec. Biv. Sh.
1843	<i>Mytilus viridis</i> L.	Hanley, Cat. Rec. Biv. Sh.
1855	<i>Mytilus viridis</i> L.	Hanley, Ipsa Linn. Conch.
1857	<i>Mytilus smaragdinus</i> Chemnitz	Reeve, Conch. Icon.
1905	<i>M. (Chloromya) smaragdinus</i> Chemnitz	Jukes-Browne, Proc. Malac. Soc. Lond. VI
1906	<i>Mytilus viridis</i> L.	Dautzenberg and Fischer, J. Conchyl. LIV
1936	<i>Mytilus (Chloromya) viridis</i> L.	Lamy, Rev. Mytilidae, J. Conchyl. LXXX
1937	<i>Mytilus smaragdinus</i> Chemnitz	Serene, Invent. Invert. Mar. Indochine
1937	<i>Mytilus viridis</i> L.	Serene, Invent. Invert. Mar. Indochine
1950	<i>Mytilus smaragdinus</i> Chemnitz	Suvatti, Fauna Thailand
1950	<i>Mytilus viridis</i> L.	Suvatti, Fauna Thailand
1952	<i>Chloromya viridis</i> L.	Dodge, Amer. Mus. Nat. Hist., 100
1968	<i>Mytilus viridis</i> L.	Cheriyian, Symp. Mollusca 3
1974	<i>Perna viridis</i> L.	Ahmed, Bol. Inst. Oceanogr. Univ. Oriente XIII
1974	<i>Perna viridis</i> L.	Dance, Encyc. of Shells

Table 1. Continued

<i>Perna canaliculus</i> (Gmelin) 1791		
1784	<i>Mytilus canaliculus</i>	Martyn, Univ. Conch. II
1785	<i>Mytilus latus</i>	Chemnitz (non Lamarck), Conch. Cab. VII
1791	<i>Mytilus canaliculus</i>	Gmelin, Syst. Nat., Ed. XIII
1843	<i>Mytilus canaliculus</i> Martyn	Hanley, Cat. Rec. Biv. Sh.
1873	<i>Mytilus latus</i> Chemnitz	Hutton (non Lamarck), Cat. Mar. Moll.
1873	<i>Mytilus smaragdinus</i>	Hutton (non Chemnitz), Cat. Mar. Moll.
1913	<i>M. (Chloromya) canaliculus</i> Martyn	Suter, Man. N. Zealand Moll.
1924	<i>Mytilus canaliculus</i> Martyn	Odhner, Vidensk. Medd. fra Dansk. Foren., Bd. 77
1959	<i>Perna canaliculus</i> Martyn	Fleming, Trans. Roy. Soc. N. Zealand 87

cultures forced a delay in completion of metamorphosis. Onset of metamorphosis was determined by presenting a suitable substrate to a subsample of larvae; if more than half of the larvae secreted a byssus, that culture was deemed capable of initiating metamorphosis. This procedure was carried out every 12 h beginning 6 days after fertilization. These metamorphosing pediveligers were cultured separately through completion of metamorphosis (secretion of the dissoconch shell; see Bayne, 1965).

Preserved samples were cleaned of organic matter in a buffered 1–2% sodium hypochlorite solution for 30 sec to 3 min, rinsed, air-dried and then examined with an AMR-900 scanning electron microscope. Structures associated with the hinge line, i.e., provincular and lateral hinge teeth and ligament pit, were examined in detail. Micrographs of periostracum cross sections were made from fractures of juvenile (0.5 cm) and small adult (1–2 cm) shells.

RESULTS

Morphogenesis of the hinge lines in larvae and juveniles of the three species is shown in Figure 1. At 26°C, the prodissoconch I stage ("D" stage larvae) is reached 14–18 h after fertilization by larvae of *P. perna* and *P. viridis*. At the prodissoconch II stage, larval shells of all three species have a variable number of provincular hinge teeth (Fig. 1A–C). Prior to metamorphosis (upper two rows of Fig. 1), the ends of the provinculum (as defined by Rees, 1950) widen as the outer hinge teeth enlarge. Throughout larval growth, the number of provincular hinge teeth increases.

At 26°C, both *P. perna* and *P. viridis* secrete the first byssus 10–20 days after fertilization. This indicates the onset of metamorphosis. In pediveligers preserved at this time, the ligament pit is apparent just below the central area of the provinculum (li, Fig. 1G). Also a series of what will be referred to as primary lateral hinge teeth (l_1 , Fig. 1H) forms on the dorsal margin posterior and adjacent to the provincular teeth of both right and left valves. These primary lateral teeth, like the provincular teeth, interdigitate with those of the opposing valve. Between 10 and 18 primary lateral teeth are present in pediveligers which are allowed to complete metamorphosis (Fig. 1J–L). In contrast, metamorphosed postlarvae of *Mytilus edulis* do not develop primary lateral hinge teeth immediately adjacent to the provincular teeth (Cox, 1969).

However, following completion of metamorphosis, plantigrades of *Perna* (and *Mytilus*; Cox, 1969 and Le Pennec and Masson, 1976) develop two additional series of teeth. A series of hinge teeth (l_2 in Fig. 2) appears on the dorsal shell margin immediately posterior and adjacent to the primary lateral hinge teeth. These hinge teeth, herein referred to as secondary lateral teeth, are distinctly larger than the primary lateral teeth in *Perna*. The differences between primary and secondary lateral teeth are most clearly shown in the upper plate of Figure

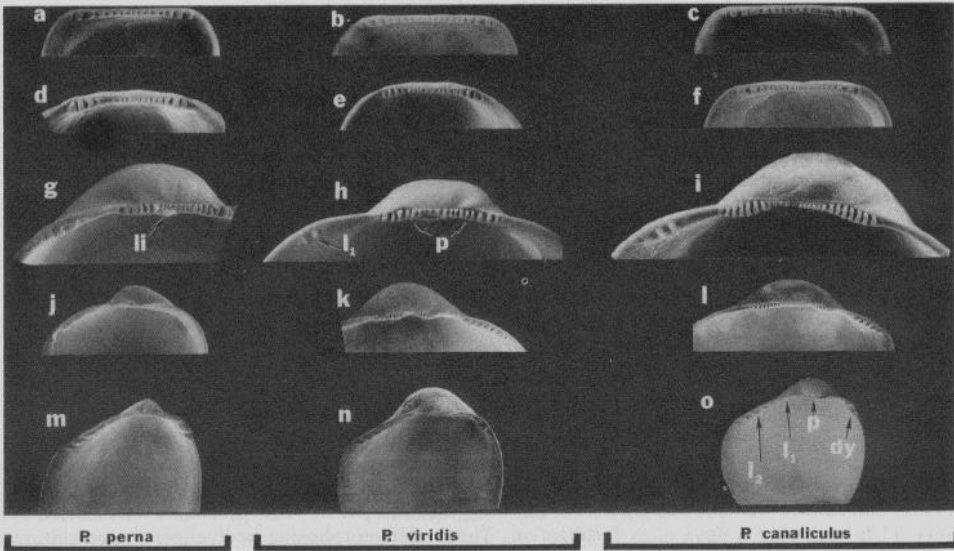


Figure 1. Morphogenesis of hinge lines in three species of *Perna*; all views are of left valves with the exception of lk and ll. a-c, early prodissoconch II shells (1000 \times); shell lengths are: a = 102 μm , b = 105 μm , c = 110 μm . d-f, late prodissoconch II shells, 6 to 8 days old (500 \times); shell lengths are: d = 198 μm , e = 190 μm , f = 180 μm . g-i, metamorphosing pediveligers, 10 to 12 days old (500 \times); shell lengths are: g = 230 μm , h = 215 μm , i = 235 μm . j-l, plantigrades, 18 to 24 days old (250 \times); maximum shell dimensions are: j = 315 μm , k = 310 μm , l = 285 μm . m-o, juvenile mussels, 40 to 45 days old (50 \times); maximum shell dimensions are: m = 500 μm , n = 430 μm , o = 480 μm . dy = dysodont teeth, l₁ = primary lateral hinge teeth, l₂ = secondary lateral hinge teeth, li = ligament pit, and p = provincular hinge teeth.

2. While provincular teeth are oriented perpendicularly to the provinculum, the secondary laterals are oriented longitudinally and more nearly parallel to the adjacent shell margin. In metamorphosed *Mytilus galloprovincialis*, Le Pennec and Masson (1976) described these posterior laterals as having the same longitudinal or fan-shaped orientation. In juvenile *Perna*, the definitive ligament appears along the posterodorsal shell margin and subsequently expands obscuring the primary and secondary lateral hinge teeth.

The second series of teeth develops anterior to the beaks and somewhat distant from the provincular teeth (dy in Fig. 2). These anteroventral teeth are not part of the dorsal hinge structure, are not covered by the ligament and are the only hinge teeth which remain distinctly visible in the adult. As discussed by Cox (1969), these are the typical dysodont of mytilids. Le Pennec and Masson (1976) refer to these dysodont teeth as ventral cardinal teeth in juvenile *Mytilus galloprovincialis*. In *Perna*, dysodont teeth are oriented perpendicularly to the anteroventral shell margin in juveniles, yet oriented longitudinally in adults. In members of the genus *Perna*, dysodont teeth usually number two (Fig. 2, lower plate), interdigitate with one or two teeth present on the opposing valve, and may be formed by the radial ridges of the lunule (Soot-Ryen, 1955). The interspecific differences between *P. perna* and *P. viridis* regarding the position and number of dysodont teeth as mentioned by Dodge (1952) were not consistent in the material examined in this study. As Jukes-Browne (1905), Lamy (1936), Beuperthuy (1967) and others have observed, the number of dysodont teeth (1-2) and position (right or left valve) vary.

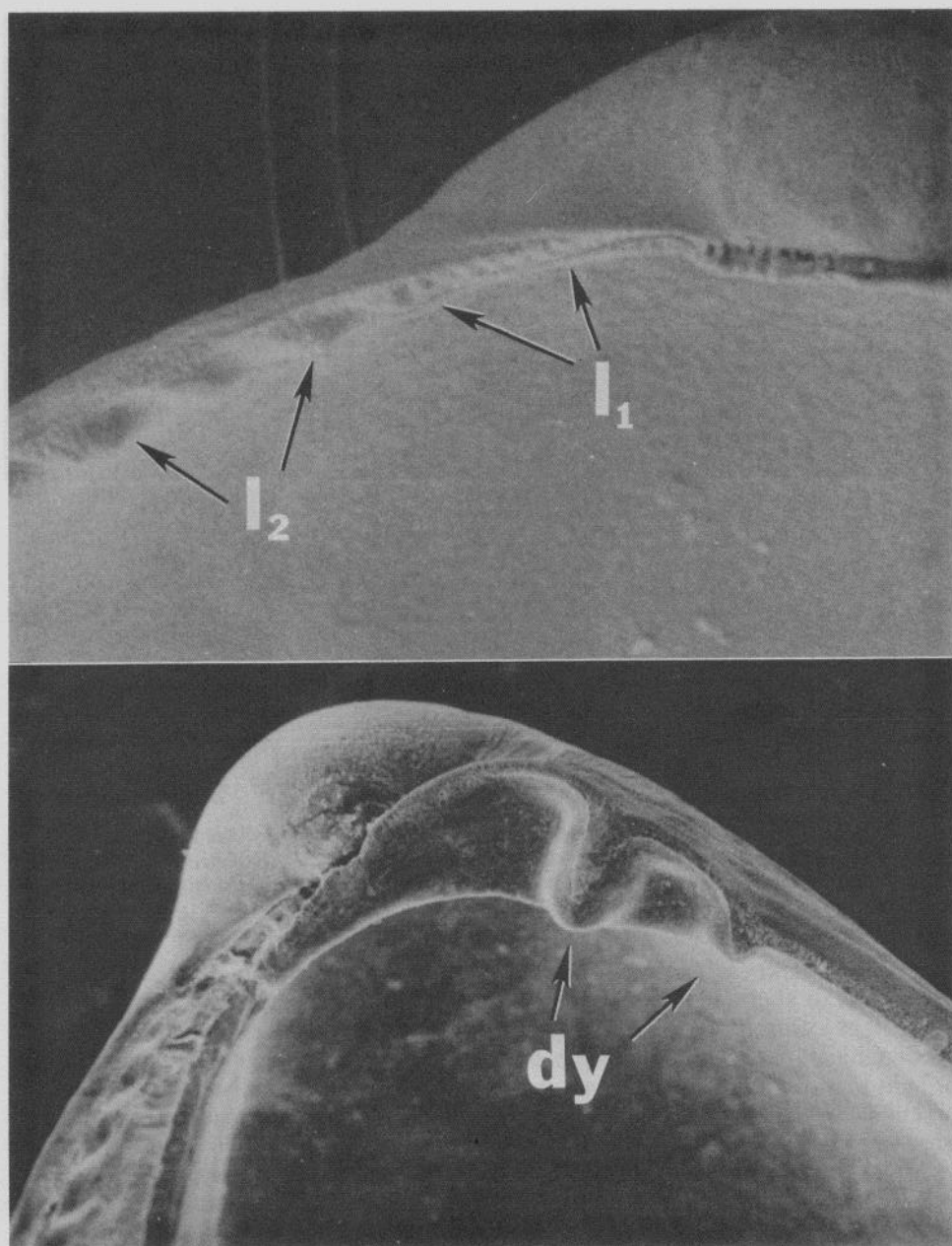


Figure 2. (upper) High magnification detail of primary (l_1) and secondary (l_2) lateral hinge teeth of left valve of a juvenile *P. canaliculus* (maximum shell dimension = 480 μm). (lower) Dysodont hinge teeth (dy) along anteroventral shell margin (left valve) of juvenile *P. perna* (maximum shell dimension = 3 mm).

Though the number and size of the provincial, primary lateral and secondary lateral teeth show considerable variation, there are no significant differences among the three species of *Perna* studied. Examination of preserved larval and adult specimens of all three species confirmed Seed's (1968) contention that shell

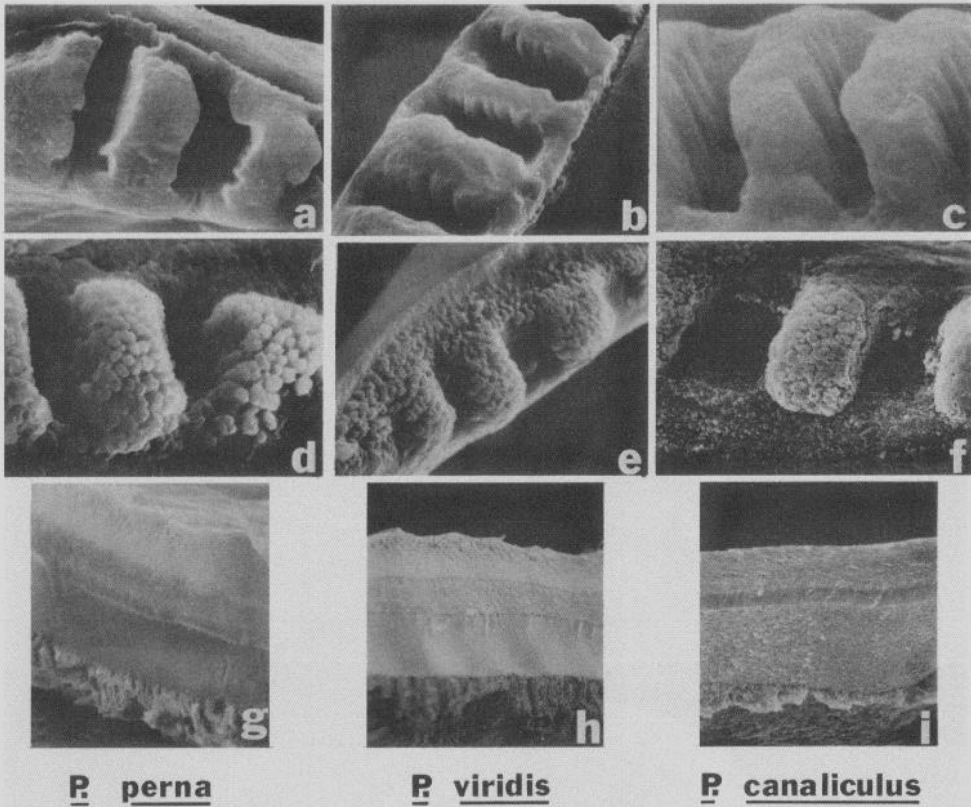


Figure 3. Ultrastructural details of three species of *Perna*: a-c, provincular hinge teeth showing ridges along teeth (5000 \times); d-f, primary lateral hinge teeth of dorsal shell margins demonstrating coarse ultrastructure (2500 \times); g-i, cross sections of three-layered periostracum as seen in juvenile shell fractures (500 \times).

shape and thickness are characters of little taxonomic value in the Mytilidae. Variations in shell coloration and patterns are considerable in all material; however, light colored zigzag markings are most common in young *P. canaliculus* specimens. *P. perna* adults are typically brown to red-maroon with irregular areas of light brown and green. Brilliant green and blue-green predominate in *P. viridis* juveniles while adult shells are less brilliant and have a greater proportion of brown. In older specimens of all species, abrasion of the external anterior surface removes the periostracum exposing the white to pink outer shell surface.

Interspecific variations in soft-part anatomy are inconsistent and difficult to document. Bifurcating papillae or tentacles along the mantle edge are most pronounced in *P. perna*, less so in *P. viridis*. The upper edges of the gill lamellae are more strongly attached to the mantle in all three species of *Perna* than in *Mytilus edulis*. Finally, in *P. perna* and *P. viridis*, two separate gonoducts lead to the mantle cavity; distinct streams of gametes are visible in spawning adults. This is in contrast to *M. edulis* which has a single gonoduct opening (Field, 1922).

Figure 3 presents ultrastructural details of the hinge and periostracum. Figures 3A-C reveal the ridged nature of the provincular hinge teeth. Where right and left valves remained articulated during examination, it was apparent that these ridges consistently interlock with their counterparts on the teeth of the opposing

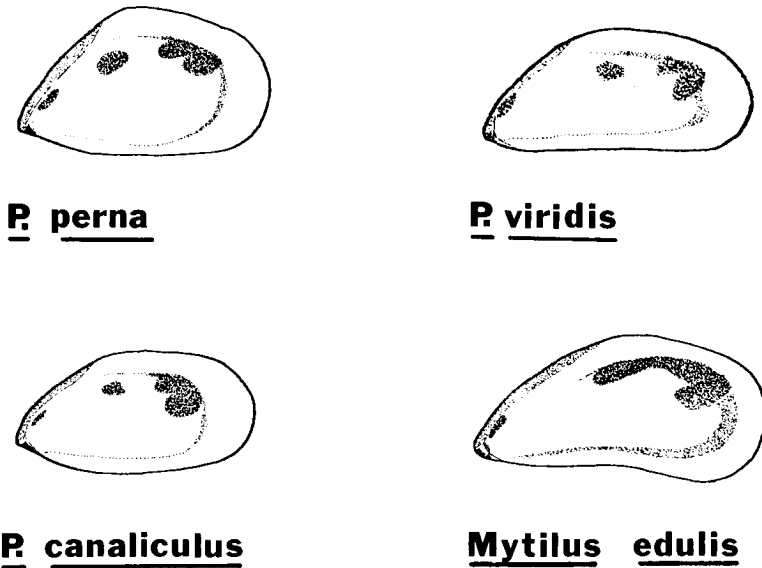


Figure 4. Muscle scar patterns on cleaned right valves of *Perna* and *Mytilus*. Contrast two-part retractor muscle scars of *Perna* with the single scar of *Mytilus*. Anterior adductor muscle of *Mytilus* is only partially visible in the anteroventral angle of the shell. No anterior adductor is present in the genus *Perna*. Drawn $\frac{1}{2}$ life size.

valve. Lutz and Hidu (1979) also observed these ridges in other mytilids. Presumably the function of the ridges is to stabilize motions of larval valves which must gape widely to accommodate the relatively large velum (Stanley, 1978, and Waller's discussion following Stanley's paper). Stanley (1978) refers to these ridges in the Trigoniidae as secondary dentition, a term which should not be confused with secondary lateral teeth defined above. Figures 3D-F depict the ultrastructure of the primary lateral teeth which contrasts with the smooth or amorphous character of the provincial teeth. Because this feature is consistent and restricted to the primary lateral teeth, it is not an artifact resulting from the brief exposure to hypochlorite during sample preparation. Carriker (1979) describes in detail the minor ultrastructural effects of cleaning molluscan shells with sodium hypochlorite. Figures 3g-i show the three layered structure of the juvenile periostracum resembling that described by Dunachie (1963) for *M. edulis*. Analysis of X-ray dispersion during scanning electron microscope examination confirmed the organic nature of the periostracum but also revealed an elevated calcium content in the middle layer 2.5 times greater than that of the surrounding layers of periostracum. Such levels of calcium are probably related to the presence of calcified, spicule-like structures in the periostracum (Carter and Aller, 1975). Though the coloration of the adult mytilid is a feature of the periostracum, the presence or distribution of trace elements within the periostracum did not correlate with adult color patterns.

Variations in the pattern of muscle scars left on juvenile and adult shells are shown in Figure 4. On a macroscopic level, the shell layer associated with sites of muscle attachment, the myostracum, may be seen as muscle scars and the pallial line. The discontinuous nature of the retractor muscle scar is one of the definitive characters of the genus *Perna*. The anterior-most component of the retractor muscle complex is attached to the shell at a point removed from the

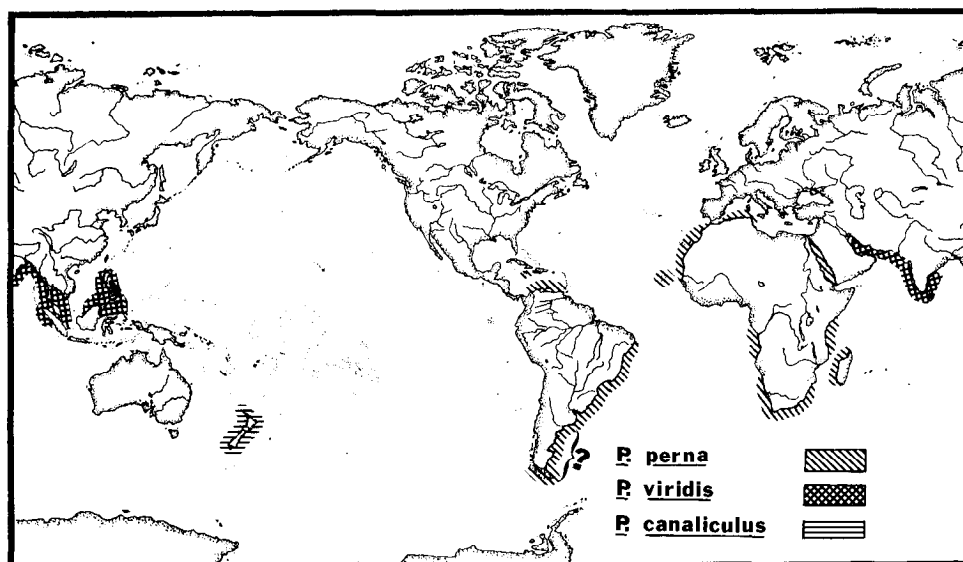


Figure 5. Geographical distribution of the three species of *Perna*.

point of attachment of posterior retractors. This results in a two-part or discontinuous muscle scar. In contrast, the middle and posterior retractor muscles in *Mytilus* are united and leave a continuous band of myostracum along the dorsal margin of the pallial line (see also Fig. 4). In Figure 4, the white resilial ridge, which is distinctly pitted or porous in both *Perna* and *Mytilus*, appears as the stippled band along the dorsoanterior shell margins. None of the three species of *Perna* have an anterior adductor muscle. *Mytilus edulis*, on the other hand, does have an anterior adductor muscle, although relatively small, which attaches along the anteroventral margin (partially seen in Fig. 4). Newell (1969) stated that an anterior adductor is present in *P. perna* juveniles but such was not the case for material examined in this study.

DISCUSSION

Geographic distributions of the species of *Perna* are shown in Figure 5. This figure was compiled primarily from the literature with minor geographical extensions resulting from personal communications with the many researchers and malacologists who assisted in the collection of material for this study. Reports in the literature of *P. perna* in cooler waters south of Rio de la Plata, Argentina, to the Straits of Magellan are open to question (Penchaszadeh, personal communication). Beupersuy (1967, p. 35) discusses the possibility that the type locality of *P. perna*, the Straits of Magellan, was erroneously assigned. Although Lamy (1920, 1936–1937) and Soot-Ryen (1955) do not rule out the presence of a mussel conspecific with *P. perna* in South America (*M. achatinus*, *M. elongatus*?), the preserved material examined in this study indicated a single species, *P. perna*, present in Venezuela, along the coast of Brazil at Recife, in the Straits of Magellan, and along the African continent. Experimental evidence on the limited duration of planktonic stages in *Perna* (Siddall, 1979 and unpublished data) indicates that this distribution could not be a result of long distance transport of *P. perna* across the North or South Atlantic oceans. The possibility for widespread

Table 2. Summary of distinguishing characteristics of four genera in the Mytilidae

<i>Mytilus</i>	<i>Aulacomya</i>	<i>Choromytilus</i>	<i>Perna</i>
Anterior adductor always present	Anterior adductor present in young; absent in adult	No anterior adductor	No anterior adductor
One retractor scar	One retractor scar	One retractor scar, sometimes two	Two retractor scars
No primary lateral teeth	Condition unknown	Condition unknown	10 to 18 primary lateral teeth
One to two dysodont teeth	Ridge, no teeth	One to two dysodont teeth	Usually two dysodont teeth, sometimes one
Pitted resilial ridge	Compact or dense resilial ridge	Compact or dense resilial ridge	Pitted resilial ridge
Smooth shell	Strongly ribbed shell	Faintly ribbed shell	Smooth shell

geographical distribution by step-wise larval dispersal ("island hopping") does exist for *P. viridis* in the Indo-Pacific.

Nordsieck (1969) refers to a near-cosmopolitan distribution for *P. perna* but he also differentiates two other mussels, *P. picta picta* (an eco-morph of *P. perna* from the Mediterranean and North Africa) and *P. picta mauritanica* (= *M. galloprovincialis*; Lamy, 1936). Buccheri and Palisano (1976) also argue for the presence of *P. picta* (Born) as a separate species in the Mediterranean. Beauperthuy's (1967) statement that *P. perna* extends to New Zealand and the tropical Pacific is unsubstantiated and probably reflects the great morphological variation within the genus *Perna*. Because of the degree of variation in characters of taxonomic importance within the genus *Perna*, it is difficult to reliably distinguish the species without knowing from what locality the material was collected. In this respect, it is fortunate that the geographical ranges of the three species are not known to overlap. Aside from the minor differences in coloration already noted, only the presence of enlarged sensory papillae along the mantle margins in *P. perna* aids in species identification.

At the generic level, however, there are a variety of distinguishing characteristics which are summarized in Table 2. In the material examined for this work, the presence or absence of anterior adductor muscles and variations in the number of retractor muscle scars are consistent characters of both juveniles and adults on which to base taxonomic differentiation of *Perna* and *Mytilus*. The order of the genera listed in Table 2 (left to right) is based on a trend involving these two anatomical variations. The anterior adductor is always present in *Mytilus*, absent only in older *Aulacomya* specimens, and completely absent in *Choromytilus* and *Perna*. There is a single retractor muscle scar in *Mytilus* and *Aulacomya*, one and occasionally two in *Choromytilus*, and two in *Perna*. Until the presence or absence of primary lateral teeth in *Aulacomya* and *Choromytilus* can be determined, this criterion neither supports nor refutes any trend suggested by muscle arrangements. However, the order of the trend (*Mytilus-Aulacomya-Choromytilus-Perna*) does break down when we consider dysodont hinge teeth, resilial ridges, and external shell sculpture. At this point, there is no reason to emphasize the taxonomic value of any one set of these characters over another. Certainly more information is required before this trend may be properly evaluated. The

underlying significance of the suggested trend, if there is any, remains unclear but may relate to the degree of evolutionary "specialization" of each genus. From that standpoint, *Perna*, having lost the anterior adductor muscle, divided the retractor muscle complex, and developed primary lateral hinge teeth and branching papillae on the mantle margin may be more specialized, yet the advantages of such morphological alterations are not obvious. Some support for this trend in specialization may be found in Ahmed (1974) and Ahmed and Sparks (1970), who showed that the diploid chromosome number in *M. edulis*, *M. californianus*, and *P. perna* is 28 while in *P. viridis* it is 30. Based on the potential mechanisms for such numerical differences in karyotypes, Ahmed (1974) tentatively concluded that the genus *Perna* is more specialized than *Mytilus* and that *P. viridis* is more specialized than *P. perna*.

In his 1969 review, Cox points out that following metamorphosis, *M. edulis* develops hinge teeth "along the posterodorsal margin some distance beyond the row of crenulations persisting from the prodissoconch, which are obliterated as the ligament extends posteriorly. Similar teeth appear along the margin anterior to the beak, also beyond the row of crenulations, and some of these persist to form the dysodont teeth of the adult mussel." I have termed Cox's posterodorsal series of teeth secondary laterals. Primary lateral teeth immediately adjacent to the provincular teeth are not mentioned by Cox or by Lutz and Hidu (1979) who examined larvae and early post-larvae of *M. edulis* or by Le Pennec and Masson (1976) working with *M. galloprovincialis*. In *Perna*, both the primary lateral teeth and the ligament pit are present in stage 3 pediveligers (Bayne, 1965) which had not yet completed metamorphosis. Secondary lateral and dysodont teeth appear very soon after (less than 24 h) completion of metamorphosis as indicated by secretion of the dissoconch shell. However, because of the 24-h sampling interval used in this study, it is not possible to further resolve the timing of these events in *Perna*. Furthermore, one would expect significant differences in the timing of ontogenetic events between *Mytilus*, a temperate genus, and the subtropical to tropical species of *Perna*. Though larval hinge structure appears to be a relatively conservative taxonomic character (Rees, 1950; Cox, 1969), there are significant variations within the families Ostreidae (Ranson, 1948) and Mytilidae (present study).

The presence of primary lateral hinge teeth allows us to differentiate larvae of *Perna* from those of *Mytilus*. Adults of the genera are most reliably distinguished by patterns of muscle scars. Fewer criteria are available for distinguishing among the three species of *Perna*; geographic origin, coloration and some aspects of soft-part morphology are useful. Recognition of environmental variations which favor the development of ecomorphs of these mussels should minimize the current tendency to confuse the taxonomic status and nomenclature of the three species of *Perna*.

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