NOTES ON THE GENUS PSEUDOMALAXIS FISCHER (MOLLUSCA: GASTROPODA) AND ITS FOSSIL SPECIES IN AUSTRALIA

by M. F. BUONAIUTO

Summary


Two fossil species of Pseudomalaxis Fischer are discussed: P. asculpturatus Maxwell (Late Eocene) and P. praemeridionalis (Chapman) (Early Middle Miocene). The former is a new discovery in Australia and is one of a few forms common to both Australia and New Zealand; the latter is poorly known and is redescribed herein. The taxonomic position of Pseudomalaxis Fischer is reviewed and the genus is restored to the Architectonicidae.

The possible synonymous or subgeneric relationship of Mangonuia Mestayer to Pseudomalaxis Fischer, of Calodisculus Rehder to Awarua Mestayer, and of Claraxis Iredale to Torinista Iredale, are considered.

Introduction

The genus Pseudomalaxis Fischer is represented in Australia only by three known species, two fossil and one living: the Late Eocene P. asculpturatus Maxwell, 1966; the Miocene P. praemeridionalis (Chapman, 1912); and the living P. meridionalis (Hedley, 1903). Only the two fossil species will be discussed and described here. However, it is necessary to discuss (a) the taxonomy of the genus Pseudomalaxis and the related genera Mangonuia and Awarua Mestayer; (b) in which family the genus should be placed.

(a) Fischer (1885, p. 714) found in a living form, then referred to the Neogene Bifrontia zanclae (Philippi), a torinioid operculum and therefore instituted for it Pseudomalaxis as a new subgenus of Torinia Gray. Sacco (1892, p. 75) considered Pseudomalaxis Fischer a subgenus of Discohelix Dunker. Dall (1892, p. 331) recognized the intrageneric relationships between the Recent American Omalaxis nobilis Verrill and P. zanclae (Philippi), but instituted Discosolis for O. nobilis as a section or possible subgenus of Discohelix, because of Verrill’s description of the operculum of O. nobilis as trochoid. Iredale (1911, pp. 253-7) tidied up the confusion existing in the use of the names Discohelix Dunker, Omalaxis Deshayes, Bifrontia Deshayes, and Pseudomalaxis Fischer; he placed Bifrontia in synonymy with Omalaxis, and separated the three remaining genera as distinct taxa. Also, he distinguished one of the two living forms previously referred to P. zanclaeae (Philippi) as a different species, P. macandrewi Iredale, because of the latter’s more evolute coiling, and restricted Pseudomalaxis to this new living form.

Later, Monterosato (1913, pp. 362-3), from a different viewpoint, restored P. zanclaeae as type-species of Pseudomalaxis and described the other living Mediterranean form, P. actoni Monterosato, previously mistaken by authors for P. zanclaeae. Monterosato also instituted for the above evolute form the subgenus Spirolaxis with P. (Spirolaxis) centrifuga Monterosato, 1890 (syn P. macandrewi Iredale, 1911) as type-species (Monterosato 1913, fig. 2). Cossmann (1915, pp. 122, 141) restricted Discohelix Dunker to the Mesozoic forms and Pseudomalaxis to the Cretaceous-Recent, referred both to Euomphalinac, and separated Omalaxis Deshayes in the Omalaxinae, a new subfamily.

Rehder (1935, p. 129) recognized a very close affinity between Discosolis nobilis (Verrill) and Pseudomalaxis actoni Monterosato and therefore placed Discosolis Dall in synonymy with Pseudomalaxis s. str. Rehder (1973, pers. comm.) remarks: “Mangonuia Mestayer, 1930, is probably a junior synonym..."
or at least a subgenus of *Pseudomalaxis* Fischer, 1885". Mestayer (1930, pp. 144–5) refers *P. meridionalis* (Hedley) to *Mangonui*. In fact, the recent *Mangonui hollumi* Mestayer, the type of this genus, displays the general pattern of spiral ornaments, the quadrangular outer and the subcircular inner shape of body whorl characteristic of the Neogene-Recent *Pseudomalaxis* s. str., described below, and the same type of pseudoplanispiral coiling of this group.

Rehder further comments, "Calodiscus" and *Torinista* Iredale, 1935, is very close to *Awarna* Mestayer, 1930, and is probably its synonym". Wenz (1939, p. 667) considers *Awarna* a subgenus of *Mangonui*. However, *Calodiscus* and *Awarna* display the same kind of specialization in spiral ornaments, in particular a marked development of heavily beaded circumumbilical cords.*Awarna amoenia* (Murdoch & Suter) (Suter 1913, p. 318; 1915, PI. 15, fig. 21 a–b) displays also a toroid operculum (Mestayer 1930, p. 146).

*Claraxis* and *Torinista* Iredale are very similar, possibly synonymous, and might be separated as a distinct genus which may be closer to *Helaxis* d'Orbigny*. Wenz (1939, pp. 666, 668) considers the former two as subgenera of *Mangonui* and the latter as a synonym of *Torinista* Gray. In this case, *Claraxis* should fall into synonymy with *Torinista*. However, the restoration of *Pseu* dolaxit to the Architectonicidae to he justified.

"There is support for this statement both on the basis of the turridid conical operculum and the protoconch coiling of *Pseudomalaxis*. Therefore the author, in agreement with Rehder, regards the restoration of *Pseudomalaxis* Fischer to the Architectonicidae to be justified.

**Collections**

The specimens of *P. asculpturatus* Maxwell here studied are kept in the Palaeontological Section of the New Zealand Geological Survey (NZGS), and in the Department of Mines of South Australia (GSSA). The figured specimen of *P. praemeridionalis* (Chapman) is kept in the Palaeontological collection of the South Australian Museum of Natural History (SAM).

Specimens M3298 and M3299 were found by the author and specimens M3300–M3303 were found subsequently by J. M. Lindsay.

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Fig. 1. *Pseudomalaxis* (Pseudomalaxis) asculpturatus Maxwell, McCullough's Bridge, New Zealand, NZGS, 9508-2; a, adapical; b, abapical; c, axial views (all X 17.50).

Fig. 1. *P. (Pseudomalaxis) asculpturatus* Maxwell, McCullough's Bridge, New Zealand, NZGS, 9508-1: a, adapical; b, abapical; c, axial views (all X 17.3).

Fig. 3. *Pseudomalaxis* (Pseudomalaxis) asculpturatus Maxwell, Adelaide Plains Sub-Basin, Adelaide Children's Hospital Bure No. 5; GSSA, M3299; a, adapical (X 16); b, abapical (X 16); c, axial views (X 15).

Fig. 4. *Pseudomalaxis praemeridionalis* Chapman, Clifton Bank, Muddy Creek; SAM. P(8342): a, adapical (X 10.6); b, abapical (X10.6); c, axial views (X 12.3).
Synopsis of the history of the genus *Pseudomalaxis* Fischer on the basis of the major authors.

<table>
<thead>
<tr>
<th>Author</th>
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<th>Subgenus</th>
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This paper

Systematic Descriptions
Phylum MOLLUSCA
Class GASTROPODA
Order MesoGASTROPODA
Superfamily CERITHIACEA
Family ARCHITECTONICIDAE

Genus PSEUDOMALAXIS Fischer, 1885

*Diagnosis*: Shell discoidal, pseudoplanispiral; abapical side concave to subconcave, adapical flattened to subconcave; outer shape of the body-whorl rectangular to quadrangular, inner shape subcircular to similar to the outer; thin margins, two carinae at abaxial-adapical and abaxial-abapical ends. Straight growth lines between the abaxial keels. Aperture rectangular to quadrangular; protoconch heterostrophic-anastrophic; operculum torinioid, thin, multispiral, outside flat or conical (after Wenz 1939, p. 668).
Subgenus *Pseudomalaxis* s. str.

*Diagnosis.* Shell medium-large to very small; margins thin; pseudoplanispiral with tangent whorls; suture flush to subimbricated; two adapical and two abapical keels; the four keels can be smooth or crenulated; growth lines a little irregularly packed; operculum flat (after Wenz 1939).

*Observations:* *Pseudomalaxis* s. str. appears to be represented in the Tertiary by two main forms. The first, predominant in the Eocene-Oligocene, is commonly characterized by growth lines and the four carinae as the only ornaments; a few species bear also spiral ornaments of fine riblets as in the Eocene *P. dixoni* (Vasseur) and the Oligocene *P. italica* (Sacchi), or of beaded cords and keels as in *P. texana* (Aldrich); the outer shape of the body whorl is rectangular to quadrangular, the inner is subcircular or subquadrangular, depending on the thickness of the margins (the latter characteristic could be ontogenetic and related to age).

The second form, predominant in the Neogene-Recent, is characterized by the development of a main spiral rib or cord on the abaxial region of the adapical margin, and often of spiral costellae on the abaxial margin. The four carinae and the adapical rib usually bear beads or short spines. The outer shape of the body whorl is commonly quadrangular to subquadrangular, the inner shape is subcircular.

**Pseudomalaxis (Pseudomalaxis) asculpturatus** Maxwell, 1966

*FIGS 1–3.*


*Material:* 4 specimens very well preserved with the peristome slightly damaged (GSSA, M3298–9; NZGS, 9508–1, 9508–2) and another 4 juvenile or damaged (GSSA, M3300–3).

*Description:* Shell very small and thin, biconvex, nearly planispiral; protoconch heterostrophic-anastrophic; whorls increasing far more in diameter than in height and overlapping entirely in relation to the coiling axis and very scarcely in relation to the normal to it. Suture flush to subimbricated. Body-whorl shape: outer subquadrate-subtrapezoidal; inner subcircular-ovoidal, wider than high. Whorl regions: adapical and abapical subconvex; abaxial flattened or subconcave, nearly vertical. Body-whorl regions connected by prominent smooth abaxial carinae. Abapical side more concave than the adapical one.

*Ornaments:* Growth lines and rugae, prosoconcal in the adapical and abaxial regions, opisthocyrt in the abapical. Four carinae: abaxial-adapical, abaxial-abapical, adaxial-adapical, and adaxial-abapical ends.

**DIMENSIONS** (in mm): (see Fig. 5)

<table>
<thead>
<tr>
<th>Specimen</th>
<th>No. whors</th>
<th>Dw</th>
<th>N</th>
<th>Nis</th>
<th>Hw</th>
<th>Lis</th>
<th>Hge</th>
<th>D eg</th>
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<td>2.55</td>
<td>0.95</td>
<td>0.40</td>
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<td>0.30</td>
<td>0.40</td>
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<td>0.50</td>
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<td>0.35</td>
<td>0.58</td>
<td>0.00</td>
<td>0.58</td>
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**RATIOS:** (see Fig. 5)

<table>
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<th>Specimen</th>
<th>Hw/Dw</th>
<th>K = Lis/Hw</th>
<th>v = Nis/N</th>
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<td>0.0000</td>
<td>0.3889</td>
<td>1.1600</td>
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*Localities:* Adelaide Plains Sub-Basin (St Vincent Basin, S. Aust.); Adelaide Children’s Hospital, North Adelaide; hundred of Yatala, Town Acre 717, Bore 5, at 20.42–20.75 m (M3298) and 21.64–21.95 m (M3299); Bore 2, at 22.25–22.56 m (M3302, M3303); Adelaide Metropolitan Subway, Bore 3, north bank of Torrens Lake, opposite Kintore Avenue, at 20.10 m (M3300) and 24.50 m (M3301). New Zealand: McCullough’s Bridge.

m in Bore 5 is low in Blanche Point Marls (Aldingan, Late Eocene). The Hantkenina primitiva zone occurs in this bore at 19.20–19.51 m, i.e. slightly above P. asculpturatus. In the type section at Maslin Bay, Hantkenina primitiva is present only in a restricted band 0.80–1.15 m above the base of Blanche Point Transitional Marls.

Other specimens from Adelaide Children’s Hospital, Bore 2, are within the Hantkenina primitiva zone. Although H. primitiva has not yet been found in Adelaide Metropolitan Subway Bore 3, the specimens of P. asculpturatus are certainly from near, and probably from slightly above, the H. primitiva zone.

Thus the vertical distribution of all the specimens of P. asculpturatus found in the Adelaide area spans a narrow interval from slightly below to probably slightly above the H. primitiva zone, in Blanche Point Transitional Marls, Late Eocene.” (J. M. Lindsay, Dept. of Mines, pers. comm., 1974.)

New Zealand: Upper Waipao Greensand, Kaiatan, Late Eocene.

**Observations:** The two Australian specimens show an inversion in the coiling, variable in

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**Fig. 5.** The parameters measured in planispiral (a) and in pseudoplanispiral (b) gastropod shell are here defined as follows:

**No:** the total number of the whorls, as the total number of revolutions of the generating curve around the coiling axis.

**Hw:** height of any whorl (in this case the last one) as the projection of the coiling axis of the distance between the adapical point of the generating curve at the initial position and its abapical point at the final position after a $2\pi$ revolution in the given interval $2\pi(n+1) = 2(n+1)\pi$.

**Nis:** the intersulural distance as the projection on the normal to the coiling axis of the distance between the initial and final position of a point placed on the adaxial line of shell after a $2\pi$ revolution, where the adaxial line is the geometrical locus of any point placed at the adaxial end of the generating curve.

**Dw:** the maximum diameter of any whorl as the projection on the normal to the coiling axis of the distance between the initial and final position of a point placed on the adaxial line of the body whorl after a $2\pi$ revolution, where the adaxial line is the geometrical locus of any point placed at the adaxial end of the generating curve.

**Dgc:** diameter of the generating curve as the projection on the normal to the c. axis of the distance between its adaxial and its abaxial point.

The generating curve is here considered the projection on a plane, containing entirely the coiling axis, of the outline of the growing edge of a gastropod shell. The body whorl here represents the part of shell cone generated by the growing edge in a given interval $2\pi(n+1) = 2(n+1)\pi$. $T$ is the translation of the generating curve along the coiling axis per revolution. $K$ and $v$ are respectively the indexes of overlapping of any whorl; $K$, parallel to the coiling axis; $v$, normal to the coiling axis, and are defined by the ratios $K = L_{is}/Hw$ and $v = Nis/Nw$. (After Raup 1966. Observations consistent with this theory will be presented in a subsequent publication.)
amount, from a more helicoideal protoconch to a more planispiral teleoconch. Undescribed in Australia, this form was directly compared with two topotypes of the only coeval species of *Pseudomalaxis* known in Australasia, *P. asculpturatus* Maxwell. These two topotypes, more juvenile than the Australian ones, display a somewhat higher spire, producing a decreasing concavity and consequent flattening of the adapical side, as a result of the same inversion of the coiling; fainter carinac, but the younger of the two has them more marked. Protoconch, growth lines, outer and inner shape of the body whorl are the same. Because the amount of inversion in the coiling of the New Zealand forms appears to differ only slightly from that of the Australian forms, and is also variable in the Australian and New Zealand specimens, it is very difficult to distinguish at the specific level between these two forms. Hence, they are here considered conspecific and representing probably different geographical morphs.

From *P. asculpturatus* Maxwell, the Anglo-Parisian Eocene *P. dixoni* (Vasseur) (Cossmann 1915, pp. 142–31), differs by its higher spire and presence of spiral riblets; the Proto-Adriatic Priabonian *P. beyrichi* (Oppenheim, 1896) by its much higher spire and an abaxial margin abapically more convergent to the axis; the Liguria-Piemonte Middle Oligocene *P. italicus* Sacco, 1892, by its lower spire and by the presence of spiral riblets. The Indian Eocene *P. punjabensis* Eames, 1952, seems on the contrary very close, but the holotype being very juvenile and the original illustration very poor, it is impossible to determine the actual differences and affinities among them.

The American Cretaceous Eocene *P. rotella* (Lea) (Palmer 1937, p. 176) differs by its rectangular aperture, higher spire, and lesser number of whorls; *P. texana* (Aldrich) (Palmer 1937, p. 176) by crenulated abaxial keels and spiral cords on the adapical margin; and *P. plummerae* Palmer (Palmer 1937, p. 178, by subelliptical margins, more imbricated sutures, and the adoral part of the last whorl twisted to the adapical.

Other Eocene species (Cossmann 1915) are the Anglo-Parisian *P. patellatus* (Sowerby), and the Egyptian *P. lybiclus* (Oppenheim).

Maxwell (Nov. 1974, pers. comm.) states: “Two specimens of a *Pseudomalaxis* have recently been obtained from a Mangapapan (Lower Eocene) sample from North Canterbury. The material is not well preserved but the shells closely resemble *P. asculpturatus* except for their much smaller size (the larger specimen is only 1 mm in diameter). I don’t think that the Lower Eocene shells are juveniles of *P. asculpturatus*, however, as they also have much smaller protoconchs”.

He quotes also the occurrence of *P. cf. asculpturatus* Maxwell from Wharckuri, South Canterbury (Dunroamin, Oligocene) (Maxwell 1969, p. 161) but “The sole specimen is broken”, however it “is certainly close to the Eocene species”.

**Pseudomalaxis** *(Pseudomalaxis)*

**praemeridionalis** *(Chapman, 1912)*

FIG. 4

1912 *Homalaxis praemeridionalis* Chapman, p. 186, pl. 12, figs 4–6.

**Material:** 1 specimen very well preserved (SAM, P18342).

**Description:** Shell small, thin, planoconcave, pseudoplanispiral, with the adapical side flattened and the abapical concave; whorls increasing far more in diameter than in height and overlapping entirely in relation to the coiling axis and very scarcely to the normal to it. Heterostrophic-anastrophic protoconch with three smooth whorls; the inversion of the coiling already displayed in the third whorl. Suture grooved. Body-whorl shape: outer subquadrate-trapezoidal; inner subcircular-ovoidal; slightly wider than high. Body whorl regions: adapical convex in the adaxial part, concave in the abaxial; abaxial flattened; abapical convex; aperture with subquadrate peristome. Lip: adapical elliptical with a gutter-shaped reflection in the middle; parietal and abaxial straight; abapical elliptical. Lip and region connections angular, marked by carinae.

**Ornament:** Four spiral beaded carinae, the abaxial ones with very short axially elongated spines: adapical-adapical, adaxial-abapical, abaxial-adapical, abaxial-abapical; a spiral crenulated cord on the abaxial part of the adapical region and a smooth costella on the adapical part of the abaxial region. Growth lines: prosocline in the adapical region; prosocline in the abaxial; orthocyrt in the abapical.
Localities and Stratigraphic Distribution:
Muddy Creek Marls, Clifton Bank, Muddy Creek, 6.4 km west of Hamilton; "blue slates".
Newport Formation, Alum Bay Coal Shale, Vic.

Stratigraphic Range: Balcolean, Early Middle Miocene (Ludbrook 1973).

Observations: P. praenundionalis (Chapman) was referred to Darragh (1970, p. 188) to Magonoidia Westray. The specimen here described represents the second discovery of this species. From P. praenundionalis, the Paleo-Mediterranean Neogene *P. ranclaca* (Philippi) (Wenz 1939, p. 668, fig. 1906) differs by a slimmer body whorl, higher spire, adapical spiral costa closer to the adapical-abaxial carina, absence of spiral riblets on the abaxial margin; from the Paleo-Mediterranean Pliocene *P. uldremondi* (Foresti) (Sacco 1892, p. 75, pl. 2, fig. 65 a–d, 65 bis a–d) by smooth adapical-abaxial carina, absence of spiral abaxial riblets, higher spire, and adapical costa closer to the adapical-abaxial carina; from the Parahethyes Miocene *P. boettgeri* Cossmann (Cossmann 1915, p. 143) by a larger body-whorl, lower spire, lesser number of whorls, lack of spiral ornaments except rarely, beaded abaxial carinae, a semi-circular inner shape of the body whorl; from the Mediterranean Recent *P. actoni* Monterosato (1913, p. 362) by a greater number of whorls, slimmer body-whorl, lower spire, more marked growth lines, more abaxial riblets, and an abaxial margin more parallel to the coiling axis. The Australian Recent *P. meri-
dialalis* (Hedley) (Hedley 1903, p. 351) displays, on the other hand, a very close affinity to *P. praenundionalis* (Chapman), differing from it only by two more abaxial riblets and the abapical-abaxial carina with heavier beads.

The New Zealand Recent *P. boltoni* (Mestayer, 1930, p. 144) differs by more whorls, two beaded abaxial cords, broader abapical-abaxial carina and slightly opisthocline growth lines on the adapical region.

The American Recent *P. nobilis* (Verrill) (Verrill 1885, p. 423, pl. 44, fig. 12) differs by its shorter spire, a greater number of whorls, slimmer body-whorl, adapical cord closer to the abaxial-adapical carina, five spiral ribs on the abaxial margin, and fine spiral ribs on the abapical margin.

Acknowledgments
I am very grateful to Dr P. A. Maxwell of the Geological Survey of New Zealand for his assistance, particularly in lending topotypes of *Pseudomalaxis asculpturatus*; to the Director of Mines, South Australia, for the loan of material; to Dr H. A. Rehder, National Museum of Natural History, Smithsonian Institution, for the information on taxonomy; to Dr H. Silcock, Department of Pure Mathematics, University of Adelaide, for verifying the definitions of the parameters; to Dr N. H. Ludbrook for encouragement and for reading the manuscript. The work was carried out in the Department of Geology and Mineralogy, University of Adelaide, during tenure of a University Research Grant.

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THE CLINGING MECHANISM OF PSEUDOPHRYNE BIBRONI (ANURA: LEPTODACTYLIDAE) TO AN ALGA ON GLASS

BY N. GRADWELL*

Summary


Despite the absence of an oral sucker, tadpoles of all stages from 26 to 40 (of Gosner 1960) were found to be capable of clinging by their jaws to an alga on vertical glass. When the glass was wiped clean of the alga, Phyllobium sp., tadpoles were no longer able to attach themselves. Therefore substratum algae are necessary for the clinging of the tadpoles to glass.

As the nares appear to suffice as inhalent channels, the dental apparatus of tadpoles is adapted to maintain a firm grip on the alga. There is an absence of peripheral papillae adjacent to the most posterior of the tooth rows of the lower lip. Therefore this tooth row can bend farther forward and the security of its grip on the alga is probably increased.

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