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EVOLUTION OF THE ZENATIINAE (MACTRIDAE: LAMELLIBRANCHIATA)

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Abstract

The Zenatiinae are herein defined as comprising three closely related genera confined to Australasia, viz. *Zenatia* (Oligocene to present, New Zealand), *Zenatiopsis* (Oligocene to Pleistocene, Australia), and *Zenatina* gen. nov. (Lower Pliocene to present, Australia). A new species *Zenatiopsis phorca* is described. The zenatiins are elongate, thin-shelled mactrids with gaping valves and anterior hingeplates specialized probably for burrowing.

Introduction

Mactrid lamellibranchs are common in occurrence and cosmopolitan in distribution, but the subfamily Zenatiinae (*Zenatia, Zenatiopsis, Zenatina* gen. nov.) are comparatively rare in collections, and in distribution are limited. This subfamily has been studied evolutionally, and this has shown the need for a new genus to represent the line of molluscs ending with the form living in Australia at present. The study began as a contribution to the elucidation of the Pliocene-Pleistocene boundary. Although the morphological changes in zenatiins with time are not great, they are nevertheless useful for stratigraphic purposes. Thus even a very conservative group of organisms, if studied in detail, can be stratigraphically useful. A similar evolutional study of the genus *Placamen* has been reported in outline (Gill 1962). Fleming's (1962) study of *Bassina* is an excellent example of this approach.

Evolution

The evolution of the subfamily has resulted in the alteration of the typical subtriangular, thick-shelled mactrid stock with its more or less central hingeplate and short pallial sinus associated with a lack of gape between its valves into an elongate-oblate, commonly thin-shelled type of mactrid with an anterior hingeplate, long pallial sinus, and gape of the valves at both ends. This change of skeleton and soft parts is an accommodation to a different mode of life. The typical mactrids are found round the world as shallow burrowers in the sand of open beaches. The living zenatiins are not worldwide but limited to Australasia, and do not belong to the sandy open ocean beaches so much as to the muddy sand of bays and inlets or ocean sites protected by reefs. Ecological information is very limited, but it is understood they live in vertical burrows. The anterior gape of the valve apparently accommodates the strong burrowing foot, while the posterior gape allows space for the large siphons. If this be correct, then it would explain the shift of hinge structures to the anterior end where most leverage is exerted. This part of the shell is further strengthened by the presence of ridge and or callus structures on the valve walls. Also the resilifer has dropped from the plane of the hinge. The development of an internal ridge and similar structures has happened a number of times in lamelli-

branch history. The internal buttress of the Palaeozoic *Nuculites* (family Nuculidae) appears to fulfil this function. Among Cainozoic shells *Leptosolen siliqua* (Solenidae), *Laternula* (Laternulidae), *Capistrocardia* (Saxicavidae), and *Cleidophorus* (Ledidae) may be quoted as examples of genera developing internal ridges.

Distribution in Time

The earliest known zenatiins are from the Duntroonian and Awamoan (Lower and Upper Oligocene respectively) of New Zealand, and from the Janjukian (Upper Oligocene) of N. Tasmania. All the sub-family characters were fully developed by this time, and so must have emerged earlier still. Many indigenous genera first appear in the early Tertiary. The New Zealand genus *Zenatia* has a known range in time of Oligocene to the present, while the Australian genus *Zenatiopsis* lasted from the Oligocene to the Pleistocene, and *Zenatina* gen. nov. from Lower Pliocene to the present. These genera are all very conservative, so that the fossil forms are quite like the living or recently living ones. They exhibit no convergence that might throw light on the origins of the genera, but maintain their distinctive morphologies throughout their known occurrence.

The ages attributed to Tertiary formations in Australia follow Glaessner (1959), except as modified by Wilkins (1963), and the Pliocene-Pleistocene boundary is that defined by Gill (1957a, 1961a).

Geographical Distribution

Iredale (1930, p. 401) and Joyce Allan (1950, p. 350) state that living *Zenatina victoriae* occur in E. Australia from S. Queensland to Victoria. The writers have seen specimens from Noosa R., N. of Brisbane in Queensland, to Port Albert in Victoria. The holotype thus comes from the S. limit of the range. The shells of this genus are comparatively rare as fossils which is not surprising in view of their delicate structure and their facies limitations. At present it has been collected from only two Pliocene localities—Muddy Ck near Hamilton in W. Victoria, and the uppermost shell bed in the Bunga Ck road cuttings on the Princes Highway NE. of Lakes Entrance, Victoria (Wilkins 1963). The species has also been collected from a Quaternary coquina at Seaspray, Gippsland, Victoria.

The only other living zenatiin is *Zenatia acinaces* in New Zealand, of which Suter (1913, p. 972) says, 'Habitat: North and South Islands from below low water mark to about 30 fathoms. In some places like New Brighton it is evidently common in a depth of from 3 to 5 fathoms'.

Zenatiopsis, now extinct, is known from Adelaide, S.A., in the N., to Wynyard, Tasmania, in the S., where it lived in a time of warmer climate (Gill 1961b, c).

Palaeoecology

Zenatiins appear to favour a habitat of muddy or marly sand, and not to favour an environment of turbulent waters. As far as we are aware, no fossil zenatiins have been found in strata which contain pebbles, gravel or other evidences of strongly moving waters. Thus *Zenatiopsis phorca* has not been found by us in the pebble-bearing 'upper shell bed' (Singleton 1941, p. 41-2) at Lakes Entrance, but this species is not uncommon in the same bed in the road cutting on the Princes Highway at Bunga Ck, NE. of Lakes Entrance where this shell bed is not conglomeratic. *Zenatiopsis phorca* and *Zenatina victoriae* occur in the Hamilton district in marly beds. At Minhamite, 25 miles SE. of Hamilton, *Zenatiopsis phorca* is present in a marly sand, but was not found in the underlying pebbly coquina. *Zenatiopsis fragilis* occurs in marly sandstone at Fossil Bluff near Table Cape in

N. Tasmania, but it appears to be absent from the underlying shelly conglomerate. *Zenatiopsis angustata* s.s. comes from the Cadell Marl Lens, Murray R. Cliffs.

Zenatiopsis sp. nov. is present in a marly sand in the Maretimo beds at Portland (but appears to be absent from the overlying oyster bed), and in the sandy coquina of Limestone Ck, a tributary of the Glenelg R. The living *Zenatina victoriae* is found in the muddy sands of the large inlet leading to Port Albert, and is known from other similar habitats up the E. coast of Australia. However, it must be stressed that only the most general information is available concerning the occurrence of this species. Likewise little is known about the conditions of life of the New Zealand *Zenatia acinaces*, but the fossil forms from that country present in a matrix and examined by us were in marly or muddy sands.

Classification

Class LAMELLIBRANCHIATA

Family MACTRIDAE Gray 1853

Equivalve inequilateral mactracean lamellibranchs with a small posterior cardinal tooth (4b) and central bifid cardinal teeth (2a, 2b) in the left valve, with bifid cardinal (3a, 3b) only in the right; subtriangular resilifer.

TIME RANGE: Cretaceous to present.

DISTRIBUTION: Cosmopolitan.

Subfamily ZENATIINAE Dall 1895

Elongate mactrids, gaping both ends, with large deeply excavated resilifer bent out of the plane of the hingeplate and separate from the cardinal socket; internal ridge (*Zenatiopsis, Zenatina*) or imperfect ridge (*Zenatia*) extending across each valve from the hingeplate; umbo one-third to one-fifth length of shell from anterior end.

TIME RANGE: Oligocene to present.

DISTRIBUTION: Australia and New Zealand.

NOTE: As defined here, the subfamily excludes—

1. *Vanganella* (= *Resania*) where the resilifer is fused to an internal ridge, is not separate from the cardinal socket, and lies parallel to the plane of the hingeplate.
2. *Darina*, a South American mactrid with zenatiin-like shell but no internal ridge, or callus ridge as in *Zenatia*.
3. *Lutraria*, which possesses no internal ridge or imperfect ridge, and the resilifer is in the plane of the hingeplate.

The Zenatiinae, as now defined, comprise three Australasian evolutionary lines consisting of shells of very similar structure that point to a common origin.

Genus **Zenatia** Gray 1853

DIAGNOSIS: Zenatiins with callus forming an imperfect internal ridge; hingeplate not supported by this ridge; umbo about one-fifth of length of shell from anterior end.

TYPE SPECIES (monotypy): *Lutraria zelandica* Gray 1837 = *L. acinaces* Quoy and Gaimard 1835. Living and fossil.

TIME RANGE OF GENUS: Oligocene to present.

DISTRIBUTION: New Zealand.

OTHER SPECIES: *Z. flemingi* Marwick, Pliocene. *Zenatia* sp. nov. Oligocene to Miocene.

NOTE: Dr C. A. Fleming kindly lent to us a series of New Zealand fossil and living *Zenatia*. This New Zealand genus has a similar time range to the Australian *Zenatiopsis*, has a similar range of shell thickness (papery to solid), but overall the New Zealand shells are larger. Shells of the living Australian *Zenatina victoriae* approach nearest in size and thickness the large *Zenatia* specimens.

Genus **Zenatiopsis** Tate 1879

DIAGNOSIS: Zenatiins with well-defined internal ridge rising under the cardinal socket but not fusing with its ventral margin; ridge extends more than half way obliquely across the valve; dorsal end of ridge is shaped round the contiguous part of the adductor muscle scar; hingeplate supported by pillar that forms umbonal end of ridge; umbo about one-fifth of length of shell from anterior end.

TYPE SPECIES (original designation): *Zenatiopsis angustata* Tate.

TIME RANGE OF GENUS: Upper Oligocene to Pleistocene.

DISTRIBUTION: Australia.

OTHER SPECIES: *Z. fragilis* Pritchard, Oligocene (Janjukian); *Z. phorca* sp. nov., Upper Miocene-Lower Pliocene (Cheltenhamian-Kalimnan); *Zenatiopsis* sp. nov., Werrikooian (Lower Pleistocene).

Genus **Zenatina** gen. nov.

DIAGNOSIS: Zenatiins with internal ridge rising from the ventral edge of the tooth socket, and extending a small distance approximately normal to the hinge-line, then flattening and widening to become a flat-topped rise on the wall of the valve; ridge extends under hingeplate providing support for it; umbo about one-third of length of shell from anterior end.

TYPE SPECIES: *Zenatia victoriae* Pritchard and Gatliff, living and fossil.

TIME RANGE: Lower Pliocene to present.

DISTRIBUTION: Australia.

Systematic Descriptions

Zenatiopsis angustata Tate 1879

(Pl. XXIX, fig. 1, 3-4; Pl. XXXI, fig. 1-2, 6, 10)

MATERIAL DESCRIBED: Pair of valves, believed to be a topotype (see below), from the Cadell Marl Lens of the Morgan Limestone, 4 miles S. of Morgan on the left bank of the Murray R., South Australia. Age: Batesfordian (Lower Miocene), Cudmore Coll. P22527-8, hypotype (numbers so given are in the palaeontological collection of the National Museum of Victoria).

DESCRIPTION: Shell thin, elongate oval, gaping at both ends, concentrically striated with very fine growth lines. Umbos small, raised orthogyral. Shell anterior to the umbo about one-fifth the length of the shell. Posterior to the umbo, shell attentuates slightly in height. Lunule hardly encroaching on the inner dorsal margin of the valve. Interior of valves porcellanous. Hinge narrow and short. Right valve with two cardinals (3a, 3b) of equal length united above, forming an inverted V; no posterior laterals. Left valve with two large cardinals (2a, 2b) united above,

vertex directed slightly to posterior, a very thin cardinal (4b) between 2b and resilifer, a thin anterior lateral (LAII) parallel to 2a, no posterior laterals. Resilifer subtriangular, anterior side making an angle of about 40° with the dorsal margin. Ligament area raised, situated just above the vertex of the resilium; the dorsal raised edge of the resilifer forms this flat area on fusion with the dorsal side of the valve. Extending from under the hingeplate (under anterior cardinal) to more than half way across the interior surface of each valve is a narrow ridge making an angle of about 80° with the posterior dorsal margin. This ridge also curves round the posterior side of the muscle scar, forming part of the dorsal margin of the scar. Muscle scars subequal, the anterior one being situated close to the dorsal and anterior margins of the valves, while the posterior scar is close to the dorsal side and about one-third of the length of the shell from the posterior end. Pallial sinus deep, extending slightly beyond the middle of the valve.

COMMENT: These valves are not complete, but the shells are so fragile that it has not been possible to obtain a pair of complete valves; as they are incomplete, measurements are not given.

In *Zenatiopsis angustata* the internal ridge is narrower than is normal in *Z. phorca*, and closer to the anterior end, viz. it is under the anterior cardinal tooth. The internal ridge is also usually at a greater angle to the margin of the valve in *Z. angustata* than in *Z. phorca*. The teeth point very slightly posteriorly—not nearly as much as in *Z. phorca*. The shells are usually a little smaller and more slender, but this is not regarded as a character of much taxonomic significance. *Zenatiopsis angustata* s.s. is intermediate in both age and morphology between the Oligocene *Z. fragilis* and the Pliocene *Z. phorca*.

The hypotypes figured are from Cudmore's collection and labelled as being from 'Tate's locality of 4 miles below Morgan, Murray River' and from 'Tate's beds 6-8 (Tate 1885)'. These beds are now called the Cadell Marl Lens and their age is Batesfordian (Ludbrook 1961, p. 53).

In his description of *Z. angustata* as the type species of his new genus *Zenatiopsis*, Tate (1879) wrote 'Locality and horizon. The older Tertiary of Muddy Creek, Hamilton, Victoria, and the contemporaneous "Upper Murravian", near Morgan (North-West Bend), on the River Murray'. Through the kind co-operation of Dr M. F. Glaessner, we have examined Tate's types which are labelled 'Loc. R. Murray—Miocene. Muddy Creek. Gippsland Lakes'. The type specimens are in the Tate Collection in the Department of Geology, University of Adelaide (T1205). There are 8 specimens glued on to a plaque so that the reverse sides cannot be examined. The first specimen on the plaque in the top left hand corner is *Z. angustata* s.s., and is obviously figure 6b of Tate 1879; this is here chosen as the lectoholotype. The specimen beside the foregoing is figure 6a of Tate 1879. Some of the other specimens are *Z. angustata* s.s. while others are *Z. phorca* sp. nov.

At about the same time as he described the new genus *Zenatiopsis*, Tate (1878) listed the strata comprising the Murray R. Cliffs, stating that the 'Upper Marine Series' is about 50 ft thick. Seven years later, Tate (1885) gave a section of the Murray R. Cliffs 4 miles S. from Morgan, but reduced the thickness of the above series (Upper Murravian) from 50 ft to 12 ft (= the 'oyster bank'), while the Middle Murravian was extended from 40-45 ft to 157 ft 4 in. reaching river level. There is thus a change in definition of the Upper Murravian as Singleton (1941, p. 43) has already noticed. Tate lists *Zenatiopsis* (p. 36) among the fossils of the 'older Tertiary deposits', i.e. beds older than Upper Murravian as re-defined. On p. 35 the gasteropod bed is placed in the Middle Murravian. This is the bed with

Zenatiopsis (Tate 1887, p. 31) and is part of the Cadell Marl Lens. In the foregoing reference Tate gives the localities for *Z. angustata* as 'Gasteropod bed of the River Murray cliffs near Morgan, upper and lower beds at Muddy Creek, Table Cape'. He included in his one species the specimens that are now divided into three species.

Thus the gasteropod bed containing *Zenatiopsis* in the Murray R. Cliffs near Morgan was in 1878 included in the Upper Murravian but in 1885 removed to the Middle Murravian. This may account for the erroneous belief that the type of *Z. angustata* came from the Pliocene of Northwest Bend whereas it came from the Miocene of the Cadell Marl Lens. It should be noted that a well preserved delicate translucent shell like the lectoholotype could not be collected from the leached Northwest Bend formation where only phosphatic and calcitic shells are well preserved. In the original description Tate refers to the *Zenatiopsis* shells from the Murray R. Cliffs as being 'thin, fragile, semi-pellucid tests'. Such could not come from the oyster bed which is now called the Northwest Bend formation. The lectoholotype has a similar colour to our hypotypes collected by Cudmore from the Cadell Marl Lens, and the minute grains of matrix still adhering are of a similar orange colour.

On the foregoing evidence our hypotypes are topotypes.

DISTRIBUTION: The description given is of topotype material of the type species of the genus *Zenatiopsis*. This is *Z. angustata* s.s., which is not rare at the type locality, but appears to be rare elsewhere, probably because of lack of beds of suitable facies and age. However, a shell (P22608) referable to this species, although varying a little from the type, was found by Mr R. W. T. Wilkins in the Tambo River Formation at Cunningham's (Old Rosehill Farm), near Bairnsdale in Gippsland, Victoria. The top of the shell bed at Rosehill Farm is by definition the upper limit of the Mitchellian Stage as re-defined by Wilkins (1963). Another specimen (P21903) comes from the nearby locality of Underwood's which belongs to the same stage. This fossil was found in the Dennant Collection in the National Museum of Victoria.

Dr O. P. Singleton kindly allowed us to examine a left valve of *Zenatiopsis* from Balcombe Bay, Victoria, in his possession which appears to be the only specimen from there collected to date; it is referable to *Z. angustata*. Its rarity is accounted for in the notes on the ecology of *Zenatiopsis*. The Balcombe Bay deposit is a silt deposited in deep water. In the Cudmore Collection there is a specimen referable to *Zenatiopsis angustata* s.s. (P21836) from the Abattoirs Bore, Adelaide, South Australia. Cudmore (pers. comm. to E.D.G.) collected his specimens from the spoil heap of the bore and so the depth from which it came is unknown.

Specimens from the Abattoirs Bore, Adelaide, were examined by us in the collections of the Department of Geology, University of Adelaide. The shells possess a thin internal ridge with its dorsal end under cardinal tooth 2a as in *Zenatiopsis angustata*. There is no curving of the ridge round the muscle scar as in *Z. phorca*. While there is some variation from the type, we refer these shells to *Z. angustata*, which is a Miocene species elsewhere.

Zenatiopsis fragilis Pritchard 1896

(Pl. XXVIII, fig. 1-2; Pl. XXXI, fig. 3)

MATERIAL DESCRIBED: Hypotype and topotype P21900-1. Pair of valves from 'Table Cape', i.e. Fossil Bluff at Wynyard, N. Tasmania. From the 'Turritella Bed'

(see Gill 1957 b, Fig. 2), i.e. Fossil Bluff Calcareous Sandstone (Banks 1957, p. 74-76); Oligocene. Coll. F. A. Cudmore.

DESCRIPTION: Shell thin, elongate oblong, gaping at both ends, equivalve, very inequilateral, concentrically striated with growth lines; dorsal and ventral margins slightly curved. Umbos small, pointed and very little raised, orthygyral; umbo to anterior end about one-fifth of shell length. Lunule small and only slightly encroaching on the inner dorsal margin. Interior of valves porcellanous. Hinge narrow and short. Left valve with two cardinals (2a, 2b) united above, vertex directed slightly anteriorly, a very thin cardinal (4b) between 2b and the resilifer, a thin anterior lateral LAII parallel to 2a, no posterior laterals; right valve with two cardinals (3a, 3b) of equal length forming an inverted V, no posterior laterals. Resilifer subtriangular, anterior side making an angle of about 35° with the dorsal margin. Ligament area raised, striated, immediately posterior to the vertex of the cardinals, and continuous with the raised anterior edge of the resilifer. Extending from under the hingeplate to past the midline of the shell in each valve is a ridge making an angle of 70° with the hingeline, forming the posterior side of the muscle scar, and curving anteriorly to form part of the dorsal side of the scar; under the anterior cardinal is a pillar supporting the hingeplate and fusing on its anterior side with the internal ridge (alternately it could be interpreted as part of the ridge). Anterior muscle scar close to dorsal and anterior margins of the valve; posterior scar close to dorsal side and about one-third length of shell beyond the midline.

MEASUREMENTS: Holotype (P3045) height 12 mm, length 33 mm, umbo to anterior end 6 mm. The same measurements respectively for other type specimens are: Paratype (P3044) 17 mm, 46 mm, 7 mm. Hypotype (P21900-1) 17 mm, 50 mm, 8 mm. Hypotype (P21902) 20 mm, 57 mm, 10 mm.

COMMENT: 11 specimens (mostly paired valves) were available for study. Pritchard based the species on three imperfect specimens from Fossil Bluff near Wynyard, Tasmania, whence all the known specimens come. The holotype (P3045) is a young specimen with paired valves. The outer surface of the right valve is all that is exposed, the shell is cracked over much of its surface, and part of the posterior end is missing. Paratype P3044, a larger specimen, consists of a pair of valves filled with matrix; both valves are covered with cracks. Paratype P3046 is a right valve, most of which is missing. It is of the same order of size as the holotype. None of the types has any internal structures visible. Pritchard erected *Z. fragilis* on external features only. Pritchard's specimens are too fragile to be dissected, and so topotype specimens from the Cudmore collection were used. Hypotype P21900-1 has both valves present. The surface of one of these was fully exposed, and then the specimen set in plaster of Paris with the exposed surface in the plaster. The matrix was then carefully removed until the other valve was exposed. Being cracked, like all the valves examined by us, and the carbonate of the shell being rather chalky, the removal of this valve to bring to view the internal structures was a problem. The exposed valve was held together with adhesive tape and then removed, but (as might be expected) the cardinal teeth of the right valve broke off, remaining in the left valve socket. However, this dissection made possible for the first time the study of the internal structures of *Z. fragilis*.

Zenatiopsis phorca sp. nov.

(Pl. XXVIII, fig. 3-4; Pl. XXIX, fig. 2, 5-6; Pl. XXXI, fig. 4, 7-8)

MATERIAL DESCRIBED: Syntypes, a right valve (P21899) and a left valve (P21898), not a pair, from the 'Upper beds, Muddy Creek', i.e. Grange Burn

Coquina (Gill 1957b) at MacDonald's Bank, Muddy Ck, about 4 miles W. of Hamilton, Western Victoria. Age: Kalimnan, Lower Pliocene. Dennant Coll. P21922 is a paratype from MacDonald's Bank, Hamilton, coll. T. S. Hall.

DESCRIPTION: Shell thin, elongate oval, gaping at both ends, very inequilateral, concentrically striated with growth lines. Umbos small, very little raised, orthogyral. Shell anterior to umbo about one-fifth the length of shell; shell posterior to umbo attenuates slightly in height. Lunule encroaching on the inner dorsal margins of the valves. Interior of valves porcellanous. Hinge narrow and short. Right valve with two cardinal teeth (3a, 3b) of equal length, united above, forming an inverted V; no posterior laterals. Left valve with two large cardinals (2a, 2b) united above, vertex directed posteriorly; a very thin cardinal 4b between 2b and the resilifer; a thin lateral LAII parallel to 2a; no posterior laterals. Resilifer subtriangular, anterior side making an angle of about 40° with the dorsal margin. Ligament area raised, striated, just above the vertex of the resilium; the dorsal raised edge of the resilifer forms this flat area on fusion with the dorsal side of the valve. Extending from under the hingeplate to more than half way across the interior surface of each valve is a ridge making an angle of about 70° with a line parallel to the hingeline at the umbo, although occasionally the angle varies up to 90°. This ridge also curves round the posterior side of the muscle scar towards the anterior end, forming part of the dorsal margin of the scar. Muscle scars subequal, the anterior situated close to the dorsal and anterior margins of the valve; posterior scar close to the dorsal side, and about a quarter of length of shell from posterior end. Pallial sinus deep, extending to slightly beyond the middle of the valve. A latex impression (P22573) has been made of steinkern P21904 from 'Cheltenham', (= Beaumaris) from the Dennant collection. It shows from the dorsal aspect the relationship of the articulating structures along the hingeline (Pl. XXIX, fig. 2).

MEASUREMENTS: P21898 height 18 mm, length 54 mm, umbo to anterior end 8 mm. The same measurements respectively for P21899 are 19 mm, 53 mm, and 10 mm; for P21922, 23 mm, 67 mm, and 10 mm.

COMMENT: This species is named after the sea god of Greek mythology. Lower Pliocene localities for *Z. phorca* are the various outcrops of the Grange Burn Coquina on Muddy Ck and Grange Burn, near Hamilton, under tuff on Spring Ck at Minhamite, SE. of Hamilton, Western Victoria, and at Nyerimalang (Cudmore locality), cliff at Kalimna Jetty, Jemmy's Point, Maringa Ck (about one half mile upstream from L. King), and the road cutting on the Princes Highway on the W. side of Bunga Ck, all near Lakes Entrance, Gippsland, Victoria. *Z. phorca* also occurs in the uppermost Miocene (Cheltenhamian) above the nodule bed at Beaumaris (Cudmore coll.) P21906, at Black Rock (Colliver coll.) P21905, and in the lowest shell bed in the road cutting on the Princes Highway just E. of Bunga Ck, (P22539-41) near Lakes Entrance, Victoria. A steinkern which may belong to this species comes from between the Brighton Cemetery and Red Bluff, i.e. Point Ormond, Melbourne (Dennant coll.) P22574. An indeterminable *Zenatiopsis* in ironstone from Shelford (P22605) is in the National Museum collection.

The following differences between *Z. angustata* (type species), *Z. fragilis,* and *Z. phorca* sp. nov. were noted. The time sequence of these species is *fragilis* (Oligocene)—*angustata* (Miocene)—*phorca* (upper Miocene-Lower Pliocene).

1. Teeth. Cardinal vertex directed slightly anteriorly in *fragilis*, but posteriorly in *angustata* and *phorca* (more so in *phorca*). The cardinal teeth diverge about 10° more in *angustata* than in the other two species.

2. Internal ridge. The dorsal end of the ridge is practically in front of the cardinal teeth in *fragilis*, under the anterior cardinal 2a in *angustata*, and between the cardinals or under 2b in *phorca*. With time the ridge has migrated posteriorly.
3. Muscle scars. The posterior scars are relatively closer to the midline in *fragilis* and *angustata* (i.e. about one-third of the shell length from the posterior end) than in *phorca* (about one quarter of the length from the posterior end). There has thus been a posterior migration of the scars.
4. Pallial sinus. The sinus extends further into the valve in *fragilis* and *angustata* than in *phorca*.
5. Shape of shell. *Z. fragilis* generally has slightly curved dorsal and ventral margins, whereas in *angustata* and *phorca* they are relatively straight. There are slight differences in the rounding of the ends of the shells. The *Z. phorca* from the lowest shell bed at Bunga Ck (Cheltenhamian) tend towards the *Z. angustata* found earlier in the Miocene. The latest *Z. angustata* known are in the Mitchellian (which immediately precedes the Cheltenhamian) and these tend towards the *Z. phorca* of the Cheltenhamian-Kalimnan. These facts suggest that *Z. angustata* evolved into *Z. phorca*, and that the latter is not a species from a different evolutionary line that migrated into the area. Where two species approach one another, there may be doubt in determining a single specimen, but where a few can be viewed, the species can be determined by using the key provided.

Zenatiopsis sp. nov.

MATERIAL DESCRIBED: From the Dennant collection a right valve P21841 and a left valve P21840, not a pair, and both incomplete, found at Limestone Ck on the W. bank of the Glenelg R., Western Victoria (see map, Singleton 1941). From the Pritchard collection a left valve P21957, incomplete, from the same locality. During a visit to Limestone Ck in 1962 a search was made for *Zenatiopsis*; only fragments were found, but four were determinable (P21958-9, P22607-8). Large scale slipping is present at this locality and we have not seen the beds yielding these fossils in situ, neither did Singleton (pers. comm.) nor Pritchard (pers. comm.). However, there is no reason to doubt that they are part of the Werrikoo Member of the Whaler's Bluff Formation, now given a Lower Pleistocene age (Gill 1957a, 1961a).

DESCRIPTION: This form is regarded as new, but a new species is not erected because there is not adequate type material.

The following features may be noted:

1. The cardinal teeth are relatively large and project more strongly than noted in other species.
2. The internal ridges are well developed but are somewhat irregular and less distinct, especially at their ventral ends. P21840 has a ridge with an asymmetrical profile, the posterior side tending to merge into the wall of the valve.
3. The hingeplate does not disappear into the dorsal margin of the valve, but swings around it and merges with it on the anterior end (as in *Zenatia*), so that the lunule is more prominent than in other species. This arrangement does occur elsewhere but is rare. A larger series of shells is needed to check this feature in the new species.
4. The shell is more solid than in the other species of *Zenatiopsis*.

COMMENT: Specimens of *Zenatiopsis* from the underlying Maretimo Member at Dutton Way, Portland, have been collected, but they are very poorly preserved

and it has not been possible to determine them. Also specimens have been found in the calcareous sandstones overlying the Werrikoo Member, where they are preserved as casts and moulds. The Parr Collection contains a specimen from the Glenelg crossing at Dartmoor, and one of us (E.D.G.) collected four specimens (P21907-21910) from about 7 ft from the top of the cliff at Devil's Den near Myaring bridge on the Glenelg R. These fossils are not determinable either, but they represent, as far as is known, the end of the *Zenatiopsis* evolutionary line. No specimens of *Zenatiopsis* have been found in later Quaternary beds, and no species is still living.

Zenatina victoriae (Pritchard and Gatliff) 1903

(Pl. XXX, fig. 3-5; Pl. XXXI, fig. 5, 9)

MATERIAL DESCRIBED: Two valves of holotype from Port Albert, Victoria. National Museum of Victoria F440.

DESCRIPTION: Both valves thin, elongate oval, compressed, gaping at both ends but posterior gape greater than anterior, equivalve, very inequilateral, concentrically striated by growth lines. Umbos small, pointed, very little raised, orthogyral. Part of shell anterior to umbo one-third length of shell. Dorsal margin slopes from umbo at about the same declivity anteriorly and posteriorly, but as the posterior part is longer, the dorsal margin reaches a lower point posteriorly than anteriorly. Lunule encroaches on the inner dorsal margin. Interior of valves whitish and porcellanous. Hinge narrow and short. Right valve with two cardinal teeth (3a, 3b) united above, forming an inverted V. One poorly developed posterior lateral (LAI) subparallel to dorsal margin. Left valve with two large cardinals (2a, 2b) united above, vertex directed very slightly to the posterior end, a very thin cardinal (4b) between 2b and the resilifer. A thin anterior lateral (LAII) parallel to 2a. A long thin posterior lateral (LPII) subparallel to dorsal margin. Resilifer subtriangular, anterior side making an angle of about 30° with the dorsal margin. Ligament short, situated in a small furrow behind the umbo and above the posterior lateral. Prominent ridge fused to base of cardinal teeth and extending across valve for about 2·5 mm approximately normal to the hingeline, then continuing as a flat callus about 3 mm wide for another 4 mm. Adductor scars subequal, close to hingeline. Adductor scar separated from the 'umbonal ridge' by the pedal muscle impressions and associated callus. Posterior scar situated one-third of length of shell from posterior end. Pallial sinus deep, extending to the middle of the valve.

MEASUREMENTS: Height (line normal to hingeline to umbo) 31 mm. Length (maximum length normal to line of height) 73 mm. Thickness (maximum distance through both valves) 10 m. Position of umbo (distance of height line from most anterior part of margin) 24 mm. Maximum gape: anterior 4 mm, posterior 6 mm. Angle between hingeline and line formed by junction of resilifer with valve, approx. 30°.

COMMENT: Port Albert, whence the holotype comes, is an inlet with sandy mud and shallow waters. *Zenatina* is usually obtained by dredging and is apparently not common there. However, further N., shells of *Zenatina* can be collected on beaches in numbers (e.g. Boydtown, N.S.W.). The holotype comes from the S. extremity of the range of this species. In the National Museum of Victoria and the Australian Museum, Sydney, specimens of *Zenatina victoriae* have been seen from Snake I., Mallacoota and the Ninety Mile Beach (e.g. Seaspray) in Victoria, from Boydtown, Middle Harbour at Sydney, Fingal Bay near Port Stephens, L. Macquarie, Trial

Bay, Coff's Harbour, Sussex Inlet and Byron Bay in New South Wales, and from Noosa R. in Queensland.

In the fossil record, *Zenatina victoriae* is known from the Lower Pliocene (Kalimnan) of Macdonald's Bank, Muddy Ck, W. of Hamilton (5 specimens P21837-9, 22543-4) and from a bed of about the same age in the cuttings on the Princes Highway at Bunga Ck near Lakes Entrance, Victoria (numerous specimens including P22323-8, 22531-8, 22542). A Quaternary *Zenatina* was collected at Seaspray, Victoria (P22667). There are small differences between the Lower Pliocene shells and the living ones (e.g. in the resilifer) but we think they belong to the same species. *Zenatiopsis phorca* and *Zenatina victoriae* are sympatric at the above two Pliocene localities, the former being the more numerous, e.g. at Bunga Ck we have collected 91 valves of *Zenatiopsis* and 57 of *Zenatina.*

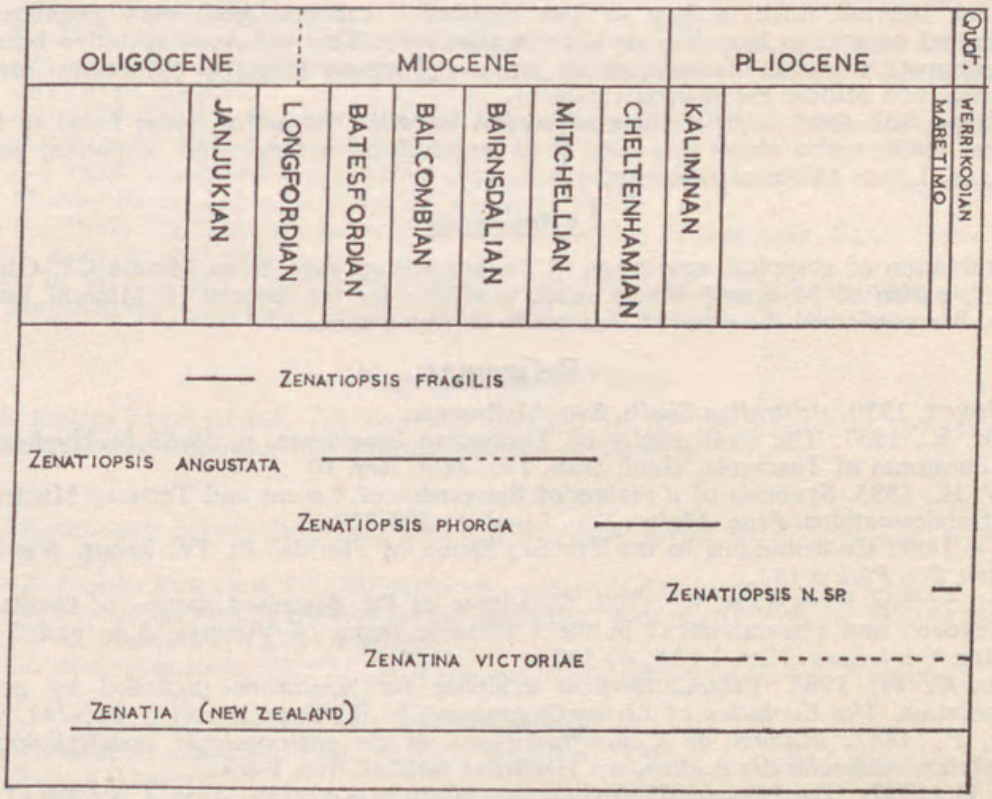

FIG. 1

Stratigraphy

The Zenatiinae are a particularly conservative group, and through the 30 million years of their known history, their morphological changes have been comparatively minute. However, careful study shows that these changes, though small, were sustained, and provide a sound basis for classification. On present knowledge *Zenatiopsis fragilis* is confined to the Upper Oligocene, *Z. angustata* to the Middle Miocene, *Z. phorca* to the uppermost Miocene and Lower Pliocene, and *Zenatiopsis* sp. nov. to the Pleistocene. *Zenatina victoriae* ranges from the Lower Pliocene to the present. The stratigraphical ranges of these evolutionary lines are indicated in Fig. 1.

The Zenatiinae are thus useful for stratigraphy in spite of their conservative nature.

Key to the Zenatiinae (using left valve only)

1. Zenatiinae with callus forming rise on inner shell surface beneath the hinge structure and sometimes forming distinct low ridge; umbo about one-fifth shell length from anterior end. *Zenatia*, New Zealand, Oligocene to present.
2. Zenatiinae with well-defined internal ridge extending more than halfway across valve; umbo about one-fifth shell length from anterior end. *Zenatiopsis*, Australia, Oligocene to Pleistocene (extinct).
   a. Dorsal end of thin ridge practically in front of cardinal teeth; vertex of cardinal teeth directed anteriorly. *Z. fragilis*, Oligocene.
   b. Dorsal end of thin ridge under cardinal tooth 2a; vertex of cardinal teeth directed normal to hingeline or slightly posteriorly. *Z. angustata*, Miocene (except Cheltenhamian).
   c. Dorsal end of thick ridge between cardinal teeth or under 2b; vertex of cardinal teeth directed posteriorly. *Z. phorca*, Uppermost Miocene (Cheltenhamian) and Lower Pliocene.
   d. Thick internal ridge tending to lose regularity; cardinal teeth very prominent and directed normal to hingeline or slightly anteriorly. This definition tentative because of inadequate material. *Zenatiopsis* sp. nov., Uppermost Pliocene (Maretimo member), Lower and Middle Pleistocene (extinct).
3. Zenatiinae with short internal ridge succeeded by wide flat callus; ridge fused to base of cardinal teeth; umbo about one-third shell length from anterior end. *Zenatina*, gen. nov. Australia, Lower Pliocene to present.

Addendum

Examination of complete specimens of *Zenatiopsis* sp. nov. from Minnie Ck, Glenelg R. (Allot. 27, parish of Myaring) kindly made available by the Bureau of Mineral Resources, Canberra, has confirmed the observations made on this species.

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Explanation of Plates

All figures unretouched. All numbers prefixed by 'P' are registered specimens in the palaeontological collection of the National Musum of Victoria.

PLATE XXVIII

Fig. 1—*Zenatiopsis fragilis* Pritchard, P21900, topotype, Fossil Bluff, Wynyard, N. Tasmania, x 2 approx.

Fig. 2—*Z. fragilis* Pritchard, P21902, topotype, same locality as fig. 1, x 2 approx.

Fig. 3—*Z. phorca* sp. nov., P21898, syntype left valve, MacDonald's Bank, Muddy Ck, 4 miles W. of Hamilton, Vict., x 2 approx.

Fig. 4—*Z. phorca* sp. nov., P21922, paratype, same locality as fig. 3, x 1·7 approx.

PLATE XXIX

Fig. 1—*Zenatiopsis angustata* Tate, P22527, topotype, Murray R. cliffs 4 miles S. of Morgan, S.A., x 2 approx.

Fig. 2—*Z. phorca* sp. nov., P22573, a latex cast of P21904, showing dorsal view of articulated teeth plus resilifers, hypotype, Beaumaris, Vict., enlarged.

Fig. 3—*Z. angustata* Tate, P22528, topotype, same locality as fig. 1, x 2 approx.

Fig. 4—*Z. angustata* Tate, internal structures in hinge region of P22528 enlarged.

Fig. 5—*Z. phorca* sp. nov., P21899, syntype right valve from MacDonald's Bank, Muddy Ck, 4 miles W. of Hamilton, Vict., x 2 approx.

Fig. 6—*Z. phorca* sp. nov., P21898, syntype left valve from same locality as fig. 5, x 2·7 approx.

PLATE XXX

Fig. 1—*Zenatia acinaces* (Quoy & Gaimard), enlarged view of structures in hinge region of left valve, New Zealand.

Fig. 2—*Z. acinaces* (Quoy & Gaimard), enlarged view of structures of hinge region of right valve, New Zealand.

Fig. 3—*Zenatina victoriae* (Pritchard & Gatliff), gen. nov. F440, holotype, enlarged view of structures in hinge region of left valve, Port Albert, Vict.

Fig. 4—*Z. victoriae* (Pritchard & Gatliff), gen. nov., ditto, right valve.

Fig. 5—*Z. victoriae* (Pritchard & Gatliff), gen. nov., P21837, hypotype, MacDonald's Bank, Muddy Ck, 4 miles W. of Hamilton, Vict., x 4·5 approx.

PLATE XXXI

Fig. 1—*Zenatiopsis angustata* Tate, lectoholotype, Tate 1879, fig. 6b, Murray R. Cliffs 4 miles S. of Morgan, S.A., x 2 approx.
Fig. 2—Enlargement of hinge region x 4 approx.
Fig. 3—*Zenatiopsis fragilis* Pritchard, P21900, enlargement of hinge region.
Fig. 4—*Z. phorca* sp. nov., P21898, enlargement of hinge region.
Fig. 5—*Zenatina victoriae* (Pritchard & Gatliff), gen. nov., P21839, enlargement of hinge region.
Fig. 6—*Zenatiopsis angustata* Tate, P22527, enlargement of hinge region.
Fig. 7—*Z. phorca* sp. nov., P21899, enlargement of hinge region.
Fig. 8—*Z. phorca* sp. nov., P21922, enlargement of hinge region.
Fig. 9—*Zenatina victoriae* (Pritchard & Gatliff), gen. nov., P21839, hypotype, MacDonald's Bank, Muddy Ck, Vict.
Fig. 10—*Zenatiopsis angustata* Tate, P22527, topotype, Murray R. Cliffs, 4 miles S. of Morgan, S.A.

All illustrations are National Museum of Victoria photographs (by Frank Guy), except Plate XXXI, fig. 1-2 which are Department of Geology, University of Adelaide (photographs by K. J. Pocock).