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The Nodoconchiinae, a new subfamily of Cytheridae (Crustacea, Ostracoda)

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Abstract: The new subfamily Nodoconchiinae of the Cytheridae Baird is erected to accommodate three genera: *Austrocythere* Hartmann, 1989*a*, *Nodoconcha* Hartmann, 1989*a* and *Ectonodoconcha* gen. nov.. *Austrocythere* seems to be known only from the type species *A. reticulotuberculata* Hartmann, from its type locality in the Recent Antarctic and from the Antarctic Oligocene. *Nodoconcha*, however, apart from its original record by Hartmann from the Antarctic as *Nodoconcha minuta*, has also been encountered in the Oligocene of the Antarctic. In the present study, we have identified seven species of *Nodoconcha* from the Maastrichtian and Danian of the Neuquén Basin, together with a new genus from the Danian, *Ectonodoconcha lepidotus* gen. et sp. nov.. The new species of *Nodoconcha* are *N. polytorosa* sp. nov., *N. sanniosis* sp. nov. and *N. upsilon* sp. nov., and *Nodoconcha*? sp. that is the possible ancestor of the entire group. Previously described species now placed in the genus are: *N. paleocenica* (Bertels, 1973), *N. jaguelensis* (Bertels, 1974) and *Nodoconcha* sp. (Bertels, 1974). The *Nodoconcha* species are divided into the Minuta and Upsilon groups.

Keywords: Ostracoda; Cytheridae; Nodoconchiinae; evolution; Maastrichtian–Danian; Neuquén Basin

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Hartmann (1989*a*) described two new genera, *Austrocythere* and *Nodoconcha* from the Oligocene and Recent. These genera were encountered in extremely cold conditions in the Antarctic. Hartmann classified *Austrocythere* as Cytheridae (*Cytheride*? sp. 1987; *Austrocythere reticulotuberculata* Hartmann 1989*a*). He found it in South Georgia, Lavoisier Island and Adelaide Island, at depths between 116 m and 215 m. The type locality of *Austrocythere* is South Georgia.

Although Hartmann (1997) classified *Austrocythere* as family Cytheridae on the basis of both hard and soft parts, he classified *Nodoconcha incertae sedis*. However, the present authors believe that, because of its great similarity to *Austrocythere, Nodoconcha* is a member of the same family and subfamily. This is indeed suggested by Hartmann in his earlier works as listed in synonymy of *Nodoconcha* (see below).We have consulted a number of colleagues who all consider *Nodoconcha* to be Cytheridae.

There have been some subsequent records of *Austrocythere reticulotuberculata* Hartmann from the Recent of Lützow Holm Bay, East Antarctic (Yasuhara *et al.* 2007), Admiralty Bay, King George Island, West Antarctica (Majewski & Olempska 2005) and Oligocene CRP-2/2A and CRP-3 Drill holes, Victoria Land Basin, Antarctic (Dingle & Majoran 2001). On the other hand, *Nodoconcha* has been recorded by various authors as early as the Oligocene (Lower Miocene of New Zealand, Milhau 1993; Victoria Land Basin, Antarctica, Dingle 2000; and King George, Antarctic, Blaszyk 1987).

The genus *Nodoconcha* was classified by Hartmann (1997) *incertae sedis*, although every indication from his early work is that it belongs to the Cytheridae. The type species *Nodoconcha minuta* Hartmann, 1989*a* has been recorded from the Antarctic Peninsula, South Georgia, South Orkneys, Lavoisier Island, Hope Bay and Adelaide Island, between 185–370 m depth (Hartmann 1988, 1989*a*, *b*, 1990) and Ross Island (Briggs 1978).

In the present study the antiquity of the occurrence of *Nodoconcha* is confirmed and extended into the Danian and Maastrichtian. The new occurrence of seven species of *Nodoconcha* in the Neuquén Basin, well known for its rich fossil content, represents a place of species cluster and migration route for many species (Whatley & Ballent 1996; Ballent & Whatley 2006, 2007; Piovesan *et al*. 2012; Ceolin *et al.* 2015).

The three genera *Nodoconcha, Austrocythere* and *Ectonodoconcha* gen. nov. are grouped together as a distinct subfamilial entity within the family Cytheridae Baird. We base our suprageneric assignations on both soft and hard part characteristics in respect of the first two genera by Hartmann (1988, 1989*a*, *b*, 1990) and the obvious close relationship between *Austrocythere* and *Nodoconcha.* Although *Ectonodoconcha* is only known fossil and from closed carapaces, it is included within the new subfamily on grounds of putative carapace similarities with *Nodoconcha* and *Austrocythere.*

The Cytheridae (all other Cytheridae genera) are a somewhat heterogeneous group and do not bear the characteristic carapace components (see diagnosis below) of the Nodoconchiinae. They themselves are currently in need of a serious taxonomic review. However, Dr Mark Warne, probably the ostracod worker with most knowledge of the Cytherinae, considers that *Cythere* O. F. Müller, *Loxocythere* (*Loxocythere*) Warne, *Microcytherura* and *Tetracytherura* Ruggieri (possibly a junior synonym of *Microcytherura*) are certainly members of the Cytherinae, but none of these genera resembles any of the three genera we include in the Nodoconchiinae.

The aim of this paper is to present new species of *Nodoconcha* belonging to our new subfamily Nodoconchiinae, some previously

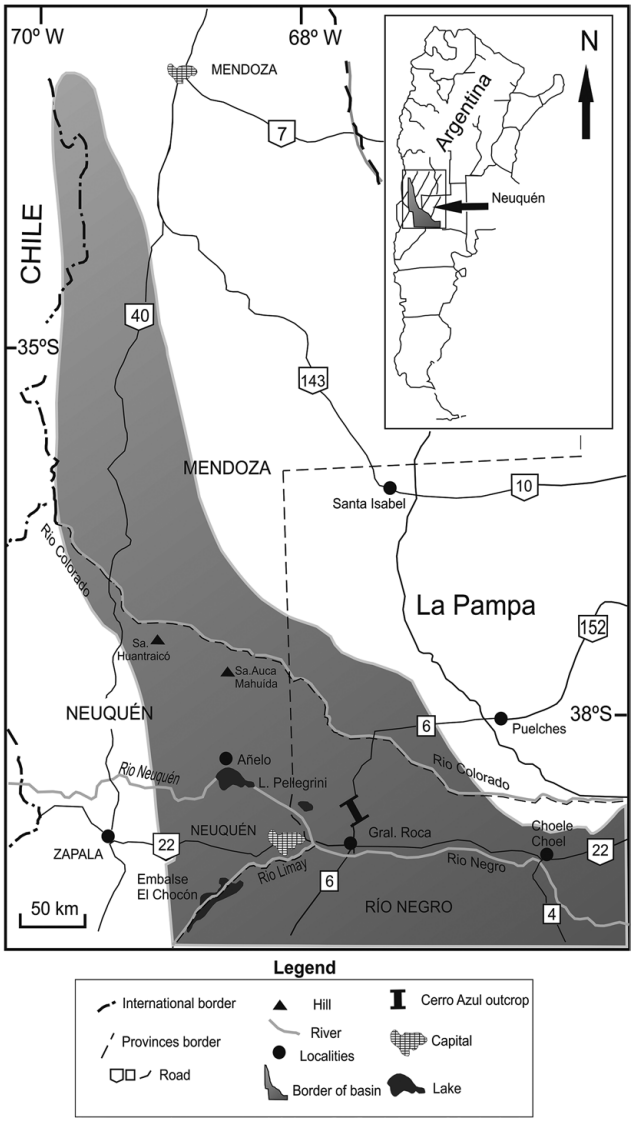


Fig. 1. The Neuquén Basin showing the location of the Cerro Azul section (modified from Del Río *et al.* 2011).

identified as '*Cytherura*?' and '*Wolburgia*' by Bertels (1973, 1974) and to demonstrate possible evolutionary trends and relationships with the Recent species of this genus.

Geological setting

The Neuquén Basin is located in west-central Argentina between latitudes 32° S and 40° S. It is developed in the provinces of Mendoza, Neuquén, Río Negro and La Pampa. In latitude 35° S, the basin extends to form the Neuquén embayment that comprises 600 km of extension in a north–south direction and 300–400 km east–west. It has a maximum thickness of 7000 m of marine and non-marine sedimentary rocks, ranging from the late Jurassic to the Paleocene (Concheyro *et al.* 2002; Howell *et al.* 2007; Aguirre-Urreta *et al.* 2011; Fig. 1 herein).

The marine sediments from the Cerro Azul section (38° 50' 48" S, 67° 52' 20" W), a relatively new site for micropaleontological studies in the eastern sector of Lake Pellegrini, Neuquén Basin, were deposited during the first transgression from the Atlantic Ocean in the Late Maastrichtian–Lower Danian (Jagüel Formation) and Danian (Roca Formation). The samples are composed of calcareous siltstones and claystones and, according to Musso *et al.* (2012), the samples from the Jagüel Formation have a homogeneous lithology of grey calcareous mudstone. An alternation of carbonate rocks and greenish-grey calcareous mudstones characterize the Roca Formation and the base of the Jagüel Formation was defined, according to criteria adopted by Uliana & Dellapé (1981), by the first appearance of organogenic limestone. The age of the samples was determined by calcareous nannofossils (Musso *et al.* 2012; Fig. 2).

Material and methods

Twenty-seven samples were studied, seven from the Maastrichtian and 20 from the Danian, from the Cerro Azul section. Approximately 20 g of dried rock was crushed and soaked in 200 ml of a 35% hydrogen peroxide solution for 24 hours. Residues were then washed and divided into grain fractions 63, 180 and 250 μm and dried at 60° C. All ostracods were hand-picked under a stereo-microscope from each size fraction. Selected specimens were photographed using an EVO MA15 Zeiss scanning electron microscope.

Systematic descriptions

The suprageneric classification adopted is that proposed by Moore & Pitrat (1961) with some modifications. In the systematic descriptions, the following conventions are employed: L, length; H, height; W, width, RV, right valve, LV, left valve, CMS, central muscle scars. All dimensions are in millimetres. Size, based on length, is as follows: very small (<0.400 mm); small (0.410–0.500 mm); medium (0.510–0.700 mm); large (0.710–0.900 mm); very large (>0.900 mm). Type and figured specimens are deposited in the collections of the Facultad de Ciencias Exactas y Naturales, Laboratorio de Micropaleontología, Buenos Aires, Argentina, under their respective catalogue numbers LM-FCEN 3210–3231; 3540–3541.

Subfamily Nodoconchiinae subfam. nov. Ceolin & Whatley

This group forms a distinct entity within the family Cytheridae. In their ornamentation and carapace organization, they are quite different from other Cytheridae.

The Cytherinae – those members of the family not in Nodoconchiinae subfam. nov., such as *Cythere* O. F. Müller and *Loxocythere* Hornibrook – are a group of ovate, subovate, often ventrolaterally tumid genera, which usually do not bear tubercles, nor strong sulcae and there is an essential similarity about them in carapace morphology and ornamentation. It would be very difficult to accommodate the taxa we include in the Nodoconchiinae with the other members of the Cytheridae. We have consulted the World Ostracoda Database (Brandão 2015) but find that in the section on the Cytheridae (as defined above), the database authors include genera that we would include in other well-established families and it is evident that this family in the database is in need of a modern review. Therefore, we feel justified in erecting the new subfamily Nodoconchiinae and including within it the genera *Austrocythere* Hartmann, *Nodoconcha* Hartmann and *Ectonodoconcha* gen. nov..

This new subfamily first appears in the Maastrichtian and ranges through to the Recent in the form of *Austrocythere* and *Nodoconcha*.

Class **Ostracoda** Latreille, 1806
Order **Podocopida**, Müller, 1894
Suborder **Podocopina** Sars, 1866
Family **Cytheridae** Baird, 1850
Subfamily **Nodoconchiinae** new subfamily

Diagnosis. Cytheridae with subovate/subrectangular to subrhomboidal carapaces in lateral view and subelliptical, parallel-sided with constricted but flared end margins in dorsal view. Anterior

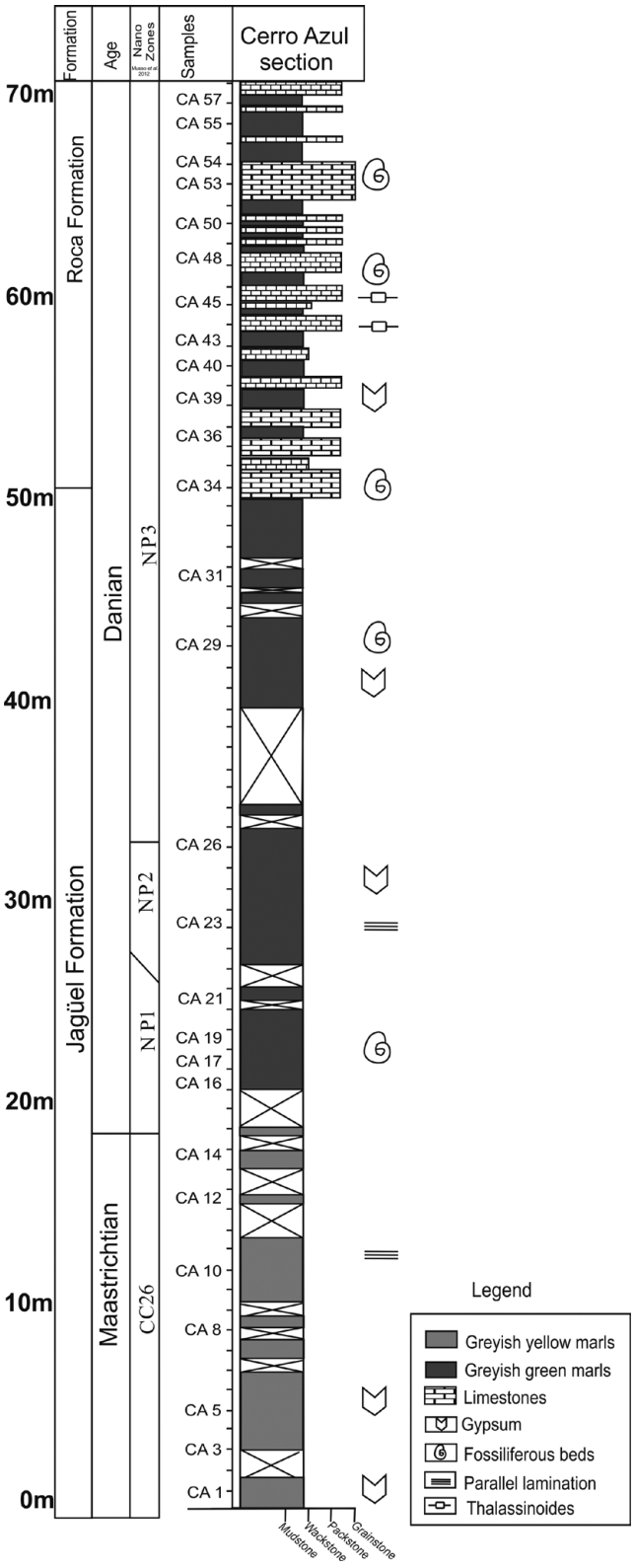


Fig. 2. Cerro Azul profile with sample positions (modified from Musso *et al.* 2012).

margin well rounded; posterior margin bluntly pointed with apex at or near mid-height. Dorsal margin straight; ventral margin biconvex about an oral concavity of variable depth. Marginal rim ranging from poorly to strongly developed. Surface ornament tuberculate, reticulate and costate, these elements interacting to various degrees between species. Most species have two prominent dorsal-dorsolateral tubercles separated by a median sulcus and, ventrolaterally, a concave rib bearing three tubercles. Hinge modified antimerodont with a long straight, crenulated median element and rather small terminal sockets in the LV bearing small locules, CMS four similar adductors in a straight row with a single oval to heart-shaped antennal scar.

Remarks. The Minuta Group comprise all those species that in their overall carapace morphology and particularly their carapace ornament resemble variations on that of *Nodoconcha minuta* Hartmann. This, therefore, comprises most of the species of *Nodoconcha*: *N. minuta, N. polytorosa* sp. nov., *N. sanniosis* sp. nov. and *Nodoconcha.* sp. (Bertels, 1974).

Genus *Nodoconcha* Hartmann, 1989*a*

Type species. *Nodoconcha minuta* Hartmann, 1989*a*

Minuta group

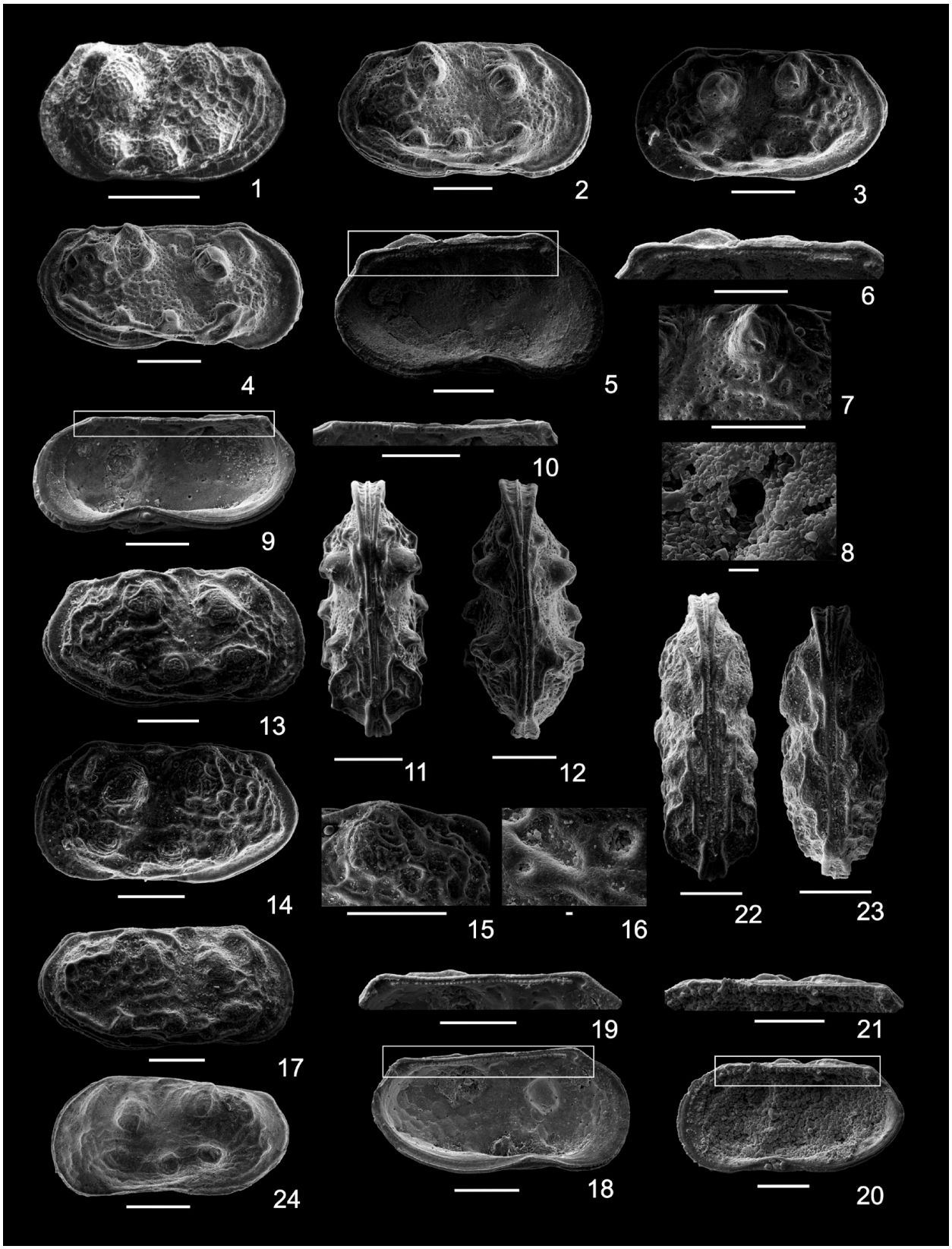
Nodoconcha minuta Hartmann, 1989*a*

(Pl. 1, fig. 1)

1978 '*Roundstonia*' sp. Briggs: 29, figs 2–12.
1988 *Cytheride*? Hartmann: 149, pl. 1, fig. 8.
1989*a* *Nodoconcha minuta* gen. et sp. nov. Hartmann: 218–219, figs 42–49b.
1989*b* *Nodoconcha minuta* Hartmann; Hartmann: 251.
1990 *Nodoconcha minuta* Hartmann; Hartmann: 211–121, figs 70–71; pl. 7, figs 63–65.
2000 *Nodoconcha minuta* Hartmann; Dingle: 489, fig. f.
2001 *Nodoconcha* aff. *N. minuta* Hartmann; Dingle & Majoran: 375.
2007 *Nodoconcha minuta* Hartmann; Yasuhara *et al.*: 486, fig. 9.

Description. A medium to large species of the genus *Nodoconcha* of the Nodoconchiinae, subovate in lateral view. Anterior margin well rounded and extending below ventral margin; posterior margin with apex above mid-height with a long keel-like posteroventral slope. Dorsal margin straight, overhung ocularly, medianly and posteromedianly by valve ornament. Ventral margin biconvex about a distinct oral incurvature, in the centre of which internally is a circular snap-knob. Ornament of tubercles, sulci and reticulation. There is a small eye tubercle, behind which is a large tubercle behind mid-length on the dorsal margin and projecting beyond it is another, smaller tubercle. These two latter tubercles are separated by a distinct, diagonally inclined median sulcus. Between these two tubercles and close to the dorsal margin, there are two small circular tubercles *en echelon*, while a further two small tubercles occur posterior to the posteromedian tubercle. Three tubercles, all of the same size, and approximately the same size as the posteromedian tubercle, occur on a ventrolateral rib in a shallowly concave-upwards curve. The summits of all five major tubercles bear a very fine reticulation within the larger reticulation that covers the entire valve surface, except the extreme end margins, and much of that reticulation is itself secondarily reticulate, but not as finely as on the summit of the tubercles. Hinge modified antimerodont with, in the RV, the anterior terminal element being a dentate bar with three large teeth and one small proximal tooth; while the posterior terminal element bears five teeth; the median element is a finely locellate groove. CMS not seen. Inner lamella vestibulate at each end with a well-developed selvage anteriorly.

Remarks. Dingle & Majoran (2001) recorded *N.* aff. *N. minuta* Hartmann from the Oligocene of the Antarctic, but neither described nor illustrated it. We are, therefore, unable to compare it with *N. minuta* Hartmann nor any of the species of the Minuta group. However, we believe it belongs to *N. minuta*.



Explanation of Plate 1. Scale bars are 100 µm, except those in figures 8 and 16, which are 2 µm. **fig. 1.** *Nodoconcha minuta* Hartmann, 1989*a*, valve, left view (illustration from Hartmann 1990, pl. VII, fig. 63, Hope Bay). **figs 2–12.** *Nodoconcha polytorosa* sp. nov.: **2**, holotype LM-FCEN 3210, carapace, female, right view; **3**,**7–8**, paratype LM-FCEN 3211, **3**, carapace, female, left view; **7**, detail of ornament; **8**, detail of simple pore; **4**, paratype LM-FCEN 3212, carapace, male, right view; **5–6**, paratype LM-FCEN 3213, **5**, female, left valve, internal view; **6**, detail of the hinge; **9–10**, paratype LM-FCEN 3541, **9**, male, right valve, internal view; **10**, detail of the hinge; **11**, paratype LM-FCEN 3214, dorsal view, male; **12**, holotype LM-FCEN 3210, dorsal view, female. **figs 13–23.** *Nodoconcha sanniosis* sp. nov.: **13**, holotype LM-FCEN 3215, carapace, right view, female; **14**, paratype LM-FCEN 3216, female, carapace, left view; **15–16**, paratype LM-FCEN 3218, **15**, detail of mask-like reticulation, **16**, detail of sieve-type pore; **17**, paratype LM-FCEN 3217, carapace, male, right view; **18–19**, paratype LM-FCEN 3218, **18**, left valve, male, internal view; **19**, detail of the hinge; **20–21**, paratype LM-FCEN 33540, right valve, internal view; **21**, detail of the hinge; **22**, paratype LM-FCEN 3217, carapace, male, dorsal view; **23**, paratype LM-FCEN 3219, carapace, female, dorsal view. **fig. 24**. *Nodoconcha* sp. (Bertels, 1974), LM-FCEN 706, carapace, left view.

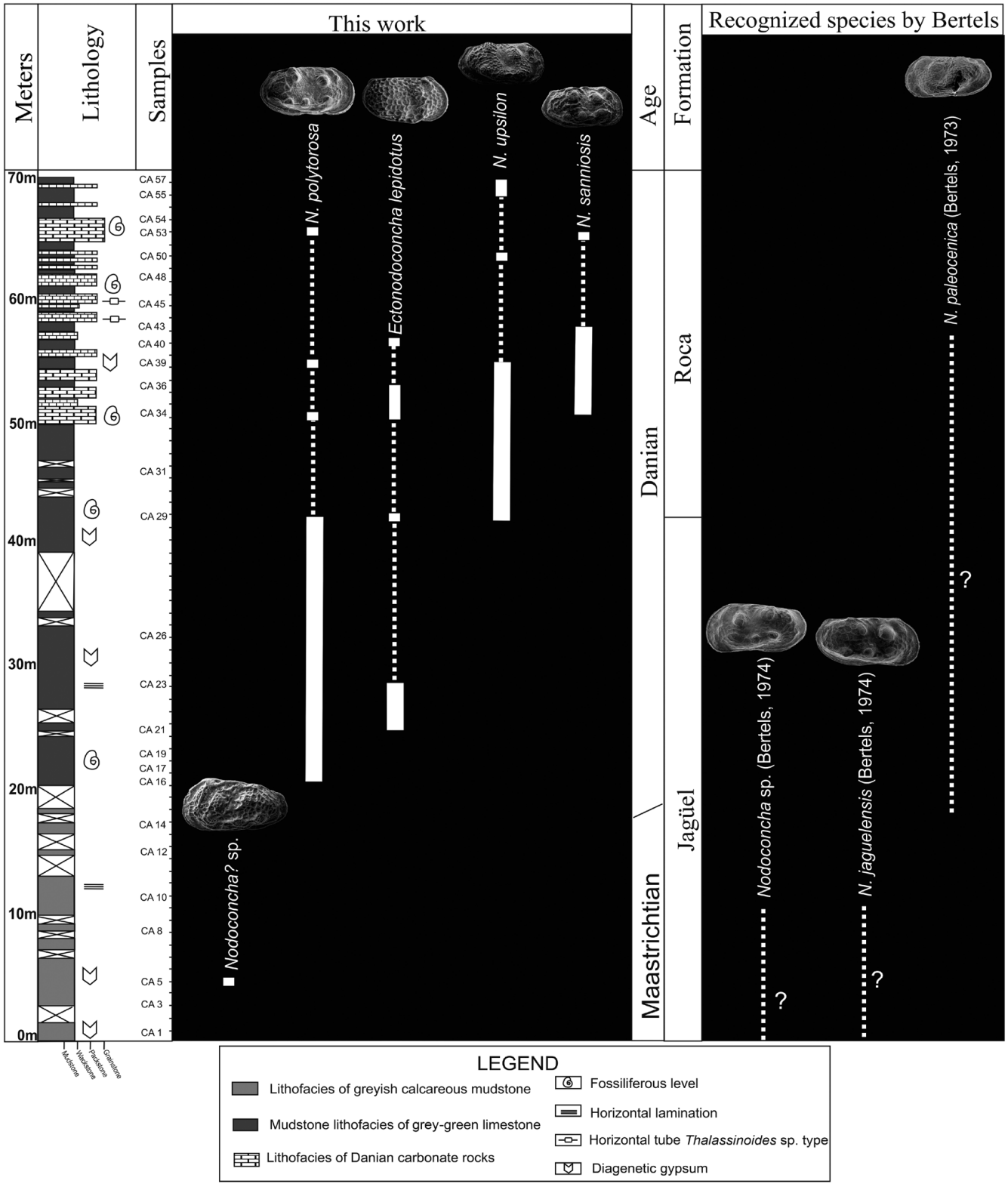


Fig. 3. Stratigraphical distribution of *Nodoconcha* species and *Ectonodoconcha* gen. nov.. Dashed lines in the diagram on the right-hand side represent the distribution reported by Bertels of species not occurring in the Cerro Azul Section. Solid lines represent actual distribution ranges.

Nodoconcha polytorosa sp. nov. Ceolin & Whatley
(Pl. 1, figs 2–12)

Derivation of name. Greek *πολύς*, many, numerous; plus Latin *torus*, elevation, protuberance, 'many tubercles' referring to the numerous rounded tubercles that occur on the carapace of this species.

Diagnosis. A small species of *Nodoconcha* characterized by a ventrolateral rib on which three small tubercles are disposed longitudinally and a double posteromedian rib on the dorsal margin. An anterior marginal ridge extends from the anterior cardinal angle to an anteroventral position. Surface of the carapace strongly punctate and reticulate in part.

Holotype. One complete female carapace, LM-FCEN 3210.

Paratypes. LM-FCEN 3211–3214, 3541.

Material. 47 specimens from samples 16, 17, 19, 21, 23, 26, 29, 34, 39 and 53. Danian.

Description. Subrectangular in lateral view with rounded end margins. In dorsal view, subovate with compressed extremities, mainly anteriorly, which is somewhat flared. Shell of medium thickness. Anterior margin broadly rounded, more narrowly below mid-height. Posterior more narrowly rounded with apex above mid-height. Dorsal margin straight but overhung in posterior part by a tubercle. Ventral margin biconvex about an anterocentral oral concavity and obscured in lateral view by valve tumidity, more prominent in males, in which posteroventral keel is better developed. Dorsal cardinal angles pronounced, especially anteriorly. LV larger than RV with some overlap anteroventrally and from the mid-posterior to posteroventral region of the valve. Greatest length at mid-height; greatest height at both anterior cardinal angles; greatest width in posterior one-third. Ornament reticulopunctate, more pronounced in anterior and posterior areas. A pronounced, mainly smooth marginal rim extends peripherally around the free and dorsal margins. There is a distinct ventrolateral rib, which bears three longitudinally disposed tubercles. This rib divides into two with the lower rib overhanging the ventral surface and terminating anteroventrally. An irregular, sinuous rib extends from the eye tubercle adjacent to the dorsal rim, to a posterodorsal complex. Two tubercles occur anterodorsally and posterodorsally. A distinct subvertical median sulcus extends ventrally to the ventrolateral rib. A smaller, post-ocular sinus separates the eye-tubercle from the anterodorsal tubercle. Apart from some smooth ribs and the marginal rim, the carapace is covered by small puncta, which also occur on the flanks and summits of some tubercles. The reticulation is more or less confined to the anterior and posterior and it is not preferentially oriented. Normal pore canals are simple, most on the elevation of muri or the tubercles. Large, simple pore conuli occur across the valve, especially posteriorly. Hinge modified antimerodont. In the LV, the anterior terminal element is a biloculate socket in which the two locules are disposed obliquely, with the proximal one above the distal. The entire socket is buttressed by an anti-slip structure ventrally. The posterior terminal element is a curved, loculate socket with six smaller loculae. The median element is a long, strongly denticulate bar with numerous relatively long circular denticles. Calcified inner lamella very wide posteroventrally; avestibulate. Radial pore canals not seen and CMS imperfectly seen. The position of the larger tubercles are reflected internally. Sexual dimorphism with males more elongate and less inflated at posterior one-third than females.

Dimensions.

				L	H	W	Sample
Holotype	LM-FCEN 3210	♀	carapace	0.462	0.240	0.213	23
Paratype	LM-FCEN 3211	♀	carapace	0.424	0.227	0.201	17
Paratype	LM-FCEN 3212	♂	carapace	0.585	0.235	0.192	23
Paratype	LM-FCEN 3213	♀	valve	0.490	0.272		17
Paratype	LM-FCEN 3214	♂	carapace	0.434	0.211	0.187	21
Paratype	LM-FCEN 3541	♂	valve	0.443	0.199		21

Stratigraphical range. Danian of Cerro Azul, General Roca.

Remarks. Differs from *Nodoconcha minuta* Hartmann in being slightly smaller, in possessing, as well as a median sulcus, a post-ocular sulcus and in its ornament, which is much more punctate than *N. minuta*. It also has a much better developed marginal rim, particularly anteriorly. A further difference is that in *N. polytorosa* sp. nov. the posteromedian tubercle is a double structure, unlike the single structure of *N. minuta*.

Nodoconcha sanniosis sp. nov. Ceolin & Whatley
(Pl. 1, figs 13–23)

Derivation of name. Latin *sanniosis* 'one who makes faces'. With reference to the rather face-like appearance of the ornamentation on the surface of the lateral tubercles.

Diagnosis. A small species of *Nodoconcha* characterized by a group of five tubercles, three of which are disposed ventrolaterally and whose ornament is mask-like. Surface reticulopunctate.

Holotype. One complete female carapace, LM-FCEN 3215.

Paratypes. LM-FCEN 3216–3219.

Material. 43 specimens from samples 34, 36, 39, 40 and 53. Danian.

Description. Small, subrectangular in lateral view. Subovate in dorsal view. Shell of medium width. Anterior margin broadly rounded with apex at mid-height. Anteroventrally there are small, blunt, rounded, marginal denticles. Posterior margin bluntly pointed with apex at mid-height. Dorsal margin straight but overhung in posterior part by ornament. Ventral margin biconvex about shallow anterocentral oral concavity and not obscured by valve tumidity. LV overlaps the RV, mainly on posterior and ventral margins. Dorsal cardinal angles distinct. Ornamentation reticulotuberculate. The reticulum posteriorly is extremely coarse due to the fact that most of the muri have been enlarged into strong ribs that are chaotically disordered across the ventral surface. Except anterodorsally, there are relatively few interconnecting muri so that over most of the area there are no reticular cells. The muri, especially posteriorly, bear simple pores on small conuli. Anteriorly, the muri are less strong and there is a genuine reticulum where much larger conuli and perforations occur distally. There are five large tubercles on the carapace surface plus an eye tubercle. The two largest tubercles on the dorsolateral surface have flanks that are ornate with a distinct reticulation pattern in a group of three mask-like structures on each tubercle. These are separated from each other by a vertical median sulcus, the anterior-most tubercle is separated by the post-ocular sinus from a strongly buttressed eye tubercle. Three smaller tubercles occur in a line posteroventrally, the largest being anterior. Each tubercle is surrounded dorsally by an inverted 'U'-shaped rib and centrally comprises several short, horizontal striae. From the eye tubercle, a sinuous rib extends closely parallel to the dorsal rib on to a posterodorsal complex above the posterodorsal tubercle and, from this complex, a strong mural rib extends ventrally and eventually joins the ventrolateral rib. A strong, smooth marginal rim surrounds the entire valve margin. Rare sieve-type pores are present mainly in the anterior region. Greatest length near mid-height; greatest height in posterior third. Hinge modified antimerodont, with median element in LV a long, strongly denticulate bar with numerous relatively strong circular denticles. Calcified inner lamella very wide posteroventrally; avestibulate. Radial pore canals not seen. CMS with four adductors in a vertical line and a single oval frontal scar. The positions of the larger tubercles are reflected internally. Sexual dimorphism pronounced with males more elongate and less inflated than females.

Dimensions.

				L	H	W	Sample
Holotype	LM-FCEN 3215	♀	carapace	0.462	0.240	0.212	34
Paratype	LM-FCEN 3216	♀	carapace	0.410	0.210	0.211	34
Paratype	LM-FCEN 3217	♂	carapace	0.502	0.243	0.170	34
Paratype	LM-FCEN 3218	♀	valve	0.441	0.217		26
Paratype	LM-FCEN 3219	♂	carapace	0.452	0.201	0.180	34
Paratype	LM-FCEN 3540	♀	valve	0.470	0.236		29

Stratigraphical range. Danian of Cerro Azul, General Roca.

Remarks. This species differs from *Nodoconcha polytorosa* sp. nov. in the better developed pattern of reticulation and in the absence of a strong ventrolateral rib that joins the three tubercles. It also differs from *N. minuta* in being more elongate and in the pattern of reticulation, in the absence of a strong ventrolateral rib that joins the three tubercles and in being more elongate.

Nodoconcha sp. (Bertels, 1974)
(Pl. 1, fig. 24)

1974 *Cytherura*? sp. Bertels: 392, pl. 2, figs 12 a–b.

Type material. One carapace from Bertels' material, LM-FCEN 706, from Lower Jagüelian Substage (Lower Maastrichtian?), Fortín General Roca. Rio Negro Province. Argentina.

Dimensions. L: 0.429; H: 0.220; W: 0.200.

Diagnosis and remarks. An elongate subrectangular species of Nodoconchiinae typified by reticulotuberculate ornament. Unlike any others species of genus, the chain of the three ventrolateral tubercles extends on to the anterior marginal surface with a further two tubercles. The reticulation is rather irregular and variable. In places there seems to be a micro-ornament between the two tubercles and the reticulation. Marginal rim better developed than in *N. minuta* Hartmann, but much less well developed than in *N. polytorosa* sp. nov.. However, this is clearly a member of Minuta group.

Nodoconcha jaguelensis (Bertels, 1974)
(Pl. 2, figs 1–2)

1974 *Cytherura*? *jaguelensis* Bertels: 392, pl. 2, figs 10a–b, 11.

Type material. Two carapaces and two valves from Bertels' material. Holotype LM-FCEN 703; paratypes LM-FCEN 704 and 705 from lower beds of the upper member of the Jagüel Formation, Fortín General Roca, Rio Negro Province. Argentina. Approximately 67° 32' W; 39° 00' S.

Diagnosis. A very elongate, subrectangular species of *Nodoconcha* with anterior margin obliquely rounded. Surface reticulotuberculate with the third tubercle on the upper ramus of the ventrolateral rib absent or only feebly developed. Posterodorsal tubercle not well defined. Intertubercular area posterocentrally with horizontal or oblique riblets.

Description. A small, elongate carapace, subrectangular in lateral view, subovate in dorsal view with a well-defined median sulci. Anterior margin well rounded with apex at about mid-height and with dorsal part of anterodorsal slope straight to almost concave. Posterior margin narrow, bluntly pointed with apex at mid-height. On the posterodorsal slope, there is a small concavity while the posteroventral slope is convex. Dorsal margin straight and only slightly overhung mid-posteriorly by small, nodose inflation. Anterior and posterior cardinal angles well defined. Ventral margin biconvex about slight oral concavity. Greatest height at anterocardinal angle, greatest length at mid-height, greatest width at posterior third. Ornamentation reticulotuberculate, with an irregular reticulum that covers the entire surface, except anteriorly. It is very chaotic posterodorsally with a tendency for the muri to be preferentially oriented ventrally, while more medianly, they are orientated laterally. A ventrolateral rib joins three small, poorly defined, horizontally aligned tubercles. A median sulcus disposed almost vertically separates the antero and posterodorsal tubercles. The posterior tubercle is poorly defined. A small, post-ocular sulcus is also developed. Eye tubercle small and close to valve margin and with small ocular rib. Marginal rim rather weakly developed. Other features not seen. Sexual dimorphism present with males more elongate and narrower than females.

Dimensions. Paratype LM-FCEN 704, L: 0.382; H: 0.187; W: 0.157.

Remarks. Differs from *Nodoconcha sanniosis* sp. nov. in the absence of an exclusive ornamentation on the tubercles, the absence of reticulation on the anterior margin and less well-defined tubercles, especially the most posterior on the ventrolateral rib. Differs from *Nodoconcha polytorosa* sp. nov. in its more elongate shape, more developed reticulation pattern and larger nodes, mainly antero- and posterodorsally.

Upsilon group

Diagnosis. The distinct 'U'-shaped lobe encircling the median sulcus sets all members of this group apart from the Minuta group. They also lack the characteristic ventral and ventrolateral tubercles of members of the Minuta group.

Remarks. The Upsilon group comprises *Nodoconcha upsilon, N. palaeocenica* (Bertels, 1973), *Nodoconcha*? sp. and *Ectonodoconcha*.

Nodoconcha upsilon sp. nov. Ceolin & Whatley
(Pl. 2, figs 3–9)

Derivation of name. Greek *υπσιλον*, upsilon, with reference to the reclining 'U'-shape of the lobe that surrounds the median sulcus.

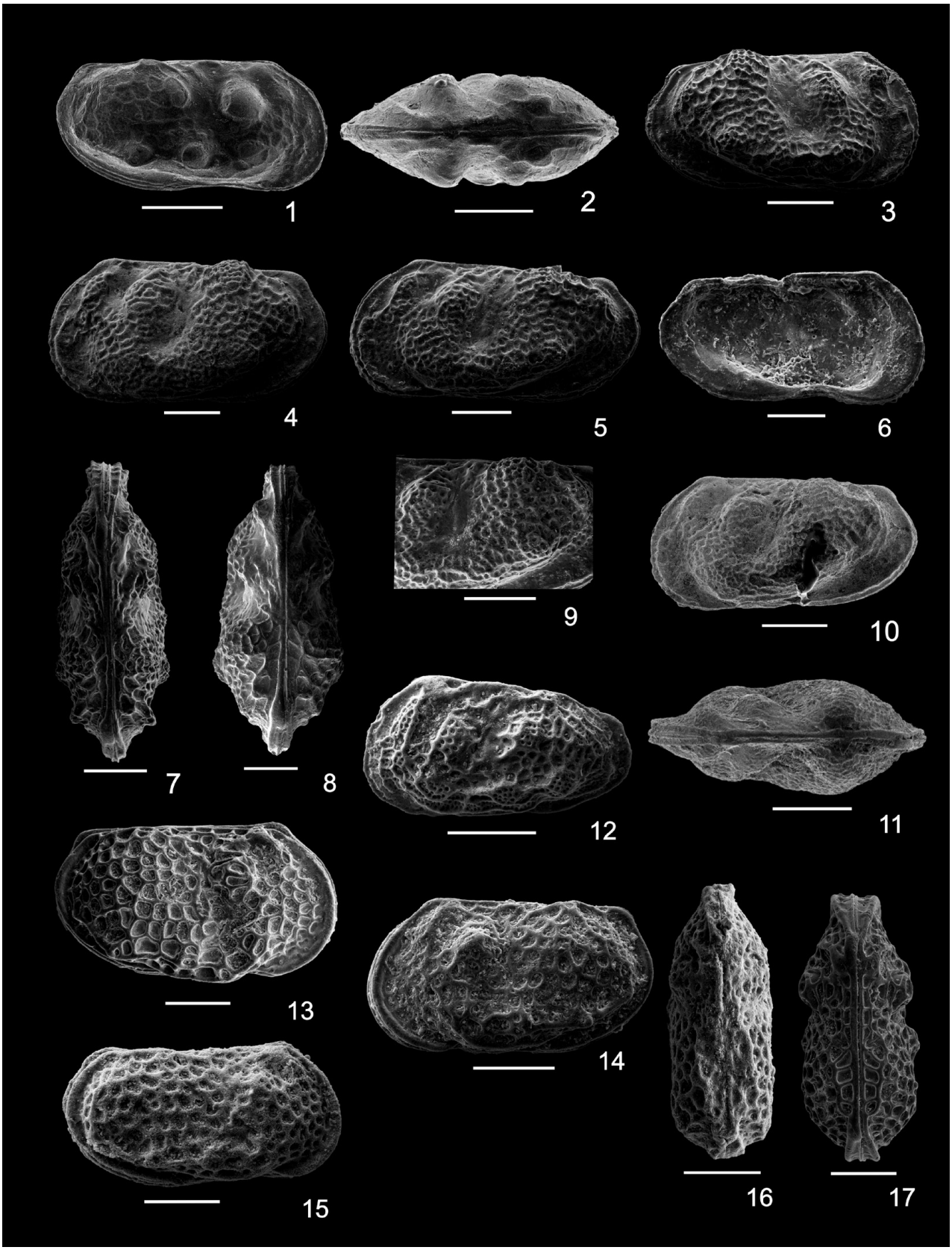
Diagnosis. A medium species of *Nodoconcha* characterized by the reclining 'U'-shaped lobe that surrounds the median sulcus and the fact that the ventrolateral tubercles are not developed. Ornament of irregular reticulation.

Holotype. One complete female carapace, LM-FCEN 3220.

Paratypes. LM-FCEN 3221–3225.

Material. 62 specimens from samples 29, 31, 34, 36, 39, 50, 55 and 57. Danian.

Description. Subrectangular in lateral view with rounded end margins; in dorsal view subovate with compressed extremities, especially anteriorly. Females more inflated in the posterior one-third than males. Moderately thick-shelled. Anterior margin broadly rounded, most narrowly below mid-height. Posterior margin more narrowly rounded with apex above mid-height. Both end margins bear very small marginal denticles on their ventral edges. Dorsal margin straight and overhung only by the posterior dorsal tubercle. Ventral margin biconvex, about an anterocentral oral concavity and not obscured in lateral view. Dorsal cardinal angles



Explanation of Plate 2. Scale bars are 100 µm. **figs 1–2.** *Nodoconcha jaguelensis* (Bertels, 1974): **1**, paratype LM-FCEN 704, carapace, female, right view; **2**, paratype LM-FCEN 705, female, carapace, dorsal view. **figs 3–9.** *Nodoconcha upsilon* sp. nov.: **3**, holotype LM-FCEN 3220, carapace, female, right view; **4**, **9**, paratype LM-FCEN 3221, **4**, female, carapace, left view; **9**, detail of reticulation; **5**, paratype LM-FCEN 3222, male, left view, carapace; **6**, paratype LM-FCEN 3223, valve, female, internal view; **7**, paratype LM-FCEN 3224, male, carapace, dorsal view; **8**, paratype LM-FCEN 3225, female, dorsal view. **figs 10–11.** *Nodoconcha paleocenica* (Bertels, 1973): **10**, paratype LM-FCEN 516, female, carapace, left view; **11**, paratype LM-FCEN 517, female, carapace, dorsal view. **fig. 12**, *Nodoconcha*? sp., LM-FCEN 3226, valve, left view. **figs 13–17**. *Ectonodoconcha lepidotus* gen. et sp. nov.: **13**, holotype LM-FCEN 3227, carapace, female, right view; **14**, paratype, LM-FCEN 3228, carapace, female, left view; **15**, paratype LM-FCEN 3229, carapace, male, right view; **16**, paratype LM-FCEN 3230, male, carapace, dorsal view; **17**, paratype LM-FCEN 3231, female, carapace, dorsal view.

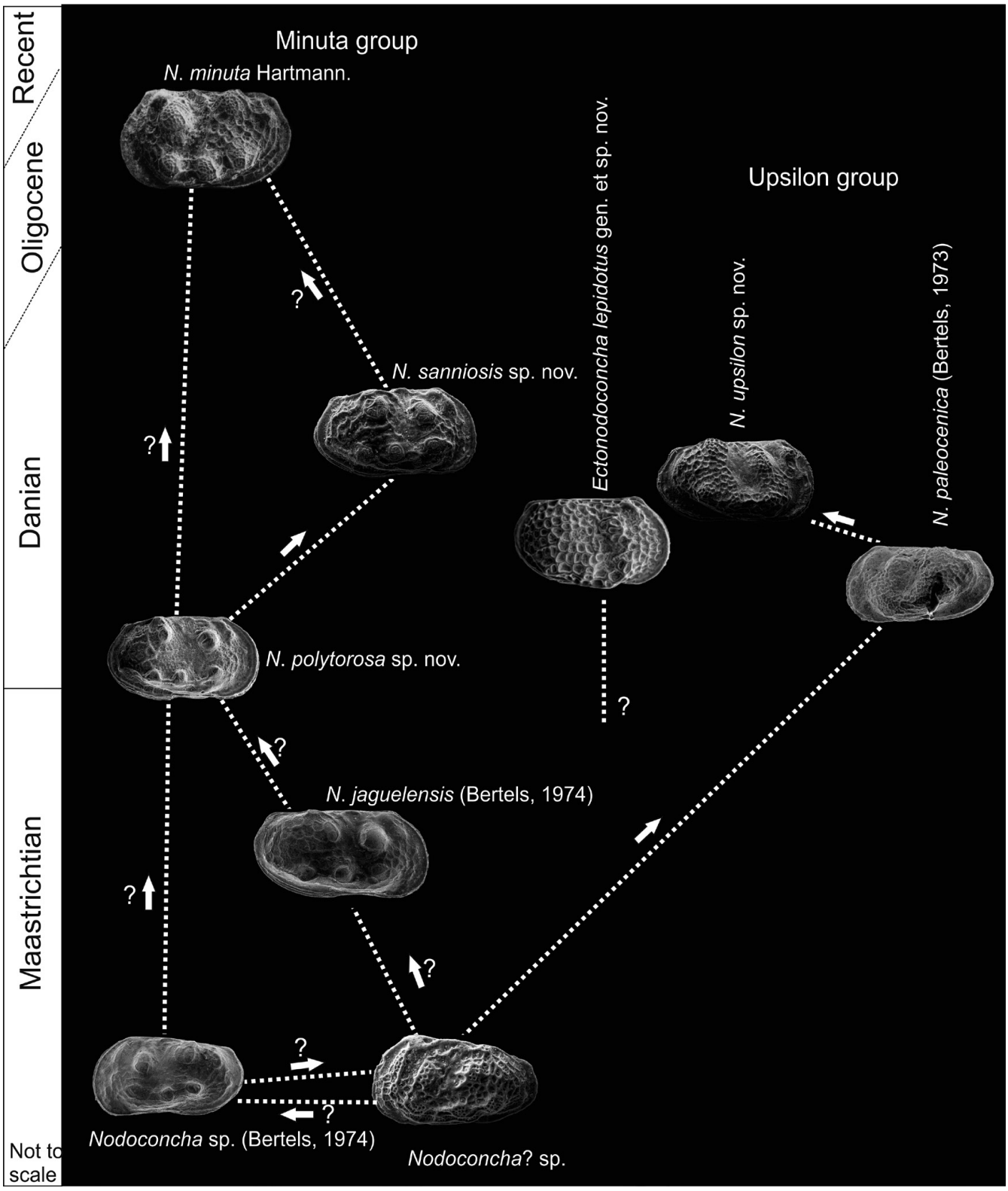


Fig. 4. Evolutionary trends in the new subfamily Nodoconchiinae including Bertels species and based upon external carapace morphology and stratigraphical occurrence.

pronounced, especially posteriorly. LV larger than RV with some overlap posterodorsally and anterodorsally. Greatest length at mid-height; greatest height at anterior cardinal angle and in the position of the posterodorsal tubercle; greatest width in posterior one-third. Ornamentat reticulopunctate. There is a distinct oblique median sulcus, the base of which is largely smooth, which terminates just below mid-height. Another, longer oblique postocular sulcus, also largely smooth extends from just behind the small, but prominent, eye tubercle. Anteroventrally, it is bridged by a small elevated area that is reticulated. A large, reclined 'U'-shaped lobe surrounds the median sulcus. It expands posterodorsally into a long, irregular tubercle that overreaches the dorsal margin. Another elongate tubercular area extends anteroventrally from near the eye tubercle, which in some specimens bears a rib from just above mid-height. Some specimens have small tubercles close to the ocular rib. The reticulation is strongly developed and, in most individuals, the

horizontal muri are strongest, giving rise to small, longitudinal riblets. These are often pronounced on the summits of the larger tubercles. Normal pore canals are of two types: one on the muri that are small, simple and mainly conjunctive, while the other, larger in the solae, are clearly sieve-type. Hinge modified antimerodont. In the LV, the anterior terminal element is a bi-loculate socket in which the two loculae, are disposed obliquely, with the proximal above the distal. The entire socket is buttressed ventrally by an anti-slip structure. The posterior terminal element is a curved, loculate socket with six smaller loculae. The median element is a long, strongly denticulate bar with numerous relatively large circular denticles. In the anterior part of the median element, there are larger denticles than other parts. Calcified inner lamella very wide posteroventrally; anteriorly the inner lamella and line of concrescence are coincident and there is no vestibulum. Radial pore canals not seen. CMS as for family, the anterior scar is ovate. Sexual dimorphism with males more elongate than females.

Dimensions.

				L	H	W	Sample
Holotype	LM-FCEN 3220	♀	carapace	0.528	0.274	0.139	34
Paratype	LM-FCEN 3221	♀	carapace	0.461	0.227	0.137	34
Paratype	LM-FCEN 3222	♂	carapace	0.540	0.258	0.125	34
Paratype	LM-FCEN 3223	♂	valve	0.491	0.251		26
Paratype	LM-FCEN 3224	♂	carapace	0.515	0.152	0.198	34
Paratype	LM-FCEN 3225	♀	carapace	0.589	0.251	0.275	34

Stratigraphical range. Danian of Cerro Azul, General Roca.

Remarks. Bertels' species, *Nodoconcha paleocenica* (ex. *Wolburgia*) (1973) from the Danian, differs in lacking the type of reticulation of the present species and the structures paralleling the anterior margin. In addition, the 'U'-shaped elevation surrounding the median sulcus is incomplete in Bertels' species. The two species differ in dorsal view and in details of ornament.

Nodoconcha paleocenica (Bertels, 1973)
(Pl. 2, figs 10–11)

1973 *Wolburgia*? *paleocenica* Bertels: 332, pl. 5, figs 12a–b, 13.

Type material. Two carapaces and two valves from Bertels' material. Holotype LM-FCEN 515; paratypes LM-FCEN 516–517 from Roca Formation of Fortín General Roca, Río Negro Province, Argentina.

Description. An elongate subovate species of *Nodoconcha* with a distinct marginal rim and two strong, lobe-like structures, somewhat resembling certain species of the Palaeozoic Palaeocopida. These two lobes are distinctively rounded dorsally and joined ventrally to form a large 'U'-shaped structure. Both the two lobes and the remainder of the shell surface are distinctly punctate.

Dimensions. Paratypes LM-FCEN 516–517, L: 0.446; H: 0.226; W: 0.175.

Remarks. This species differs from *N. upsilon* sp. nov., to which group it clearly belongs, by the fact that in *N. upsilon* the ornament is distinctly reticulate while in *N. paleocenica* (Bertels, 1973) it is punctate. Also in *N. upsilon* the dorsal terminations of the lobes are not rounded and the post-ocular sulcus is in two distinct parts separated by a ridge. The lower part of this sulcus is absent in *N. paleocenica*. There are also many other differences in the ornament of the two species, such as the divergence into two of the anteromarginal rim in *N. upsilon*.

Nodoconcha? sp.
(Pl. 2, fig. 12)

Material. Five poorly preserved specimens from sample 5, Maastrichtian.

Dimensions. LM-FCEN 3226, L: 0.347; H: 0.260.

Description. Elongate subtriangular in lateral view; anterior margin rounded with apex below mid-high. Posterior margin subtruncate with apex at about mid-height. Dorsal margin straight and sloping posteriorly; obscured by sinuous ribs dorsally. Ventral margin with large, shallow oral concavity. There are two large sulci, a median and a post-ocular, both extending forward diagonally. Ornament reticulate with muri around free margins parallel to those margins with short intervening ribs giving rise to numerous, largely circular, but some quadrate reticulae. The bases of all sulci are smooth. A sinuous ventrolateral rib bears distinct swellings and another occurs on the dorsal margin posteromedianly. Internal features not seen.

Remarks. While this species lacks, for example, the three ribs in a curved row ventrolaterally, the site of the ribs exists putatively as does the site of the posteromedian rib. We believe this to be an ancestor of *Nodoconcha* and we have used that name questionably. It is our intention in the very near future to seek further examples of the species in the Maastrichtian of the Neuquén Basin.

Genus *Ectonodoconcha* gen. nov. Ceolin & Whatley

Type species. *Ectonodoconcha lepidotus* sp. nov. Ceolin & Whatley

Derivation of name. Greek *εκτο* ecto, without, away; plus *Nodoconcha*. With reference to the fact that, although related, this species belongs to a genus different from *Nodoconcha*.

Diagnosis. A genus of the Upsilon group of the Nodoconchiinae subfamily nov. with a strongly developed ventrolateral keel. Subovate to subrectangular in lateral view with a well-rounded, anterior marginal rim, accentuated both anteriorly and posteriorly by a proximal and parallel depression. Posterior margin rather less pointed than other members of the group. Dorsal margin straight, only slightly overhung by lateral ornament in the female and not at all in the male. In dorsal view the male is very laterally compressed and flat-sided, with the female much less so. The female's outline is modified by the median sulcus and the tubercles that flank it. The lateral surface is strongly reticulate and the reticulae (see Pl. 2, fig. 13) are heavily secondarily reticulate. The median sulcus is rather feebly developed and is delineated anteriorly by two poorly developed tubercles. Other tubercles, also feebly developed, occur in a concave row immediately above the delineation of the ventral and lateral surfaces. Males less high and more elongate than females. Eye tubercle with a simple pore.

Remarks. It differs from species of *Nodoconcha* in lacking large nodes posteroventrally and in its massively strong reticulation. We believe this genus to be an early Danian offshoot of *Nodoconcha*.

Ectonodoconcha lepidotus sp. nov. Ceolin & Whatley
(Pl. 2, figs 13–17)

Derivation of name. Greek *λεπῐδωτός* lepidotus; covered in scales. With reference to the fact that in the posterior half of the valve, the reticulae are rather like fish-scales.

Diagnosis. A species of the genus *Ectonodoconcha* with a smooth, strongly developed ventrolateral keel. Strong ventrolateral rib, becoming almost alate anterior of mid-length. Ornament of extremely strong reticulation with circular, ovate, scale-like and quadrate cells and strong subcentral tubercle, which is also reticulate. Reticulae very like the scales of a carp. Smooth rim around free margins. Eye partially ornamented.

Type material. One complete female carapace, LM-FCEN 3227.

Paratypes. LM-FCEN 3228–3231.

Material. 20 complete carapaces from samples 21, 23, 29, 34, 36 and 40. Danian.

Description. Small, elongate and subrhomboidal in lateral view. In dorsal view, both end margins are splayed due to the angle of the peripheral rims. The alar process is not prominent in this view, although the tubercle immediately below and behind the eye is very prominent. Anterior margin widely and evenly rounded about mid-height. Posterior margin more narrowly rounded, asymmetrical with apex above mid-height and very long, gently curved ventral slope. Dorsal margin straight, slightly obscured posteriorly by valve surface. Ventral margin irregularly biconvex with marked oral incurvature, largely obscured by alar process. LV larger than RV with overlap around the entire margin, especially at the dorsal cardinal angles and posteroventrally. Greatest length above mid-height; greatest height medianly; greatest width at one-third posteriorly. Eye tubercle large and over-reaching the dorsal margin. A strong, smooth marginal rim with a small denticle anteriorly, occurs peripherally at both end margins. Ornament of extremely strong reticulae, embracing cells ranging in shape from circular through oval to quadrate and polygonal; and giving an aspect of the scales of such fish as carp, bass or mullet. Small simple pores, mostly conjunctive, occur on the muri and there are small pore conuli elsewhere. Some pore conuli in the solae are apparently sieve-type. The ornament extends on to the alar process and covers an elevated area immediately posteroventral to the eye tubercle. Internal features not seen.

Dimensions.

				L	H	W	Sample
Holotype	LM-FCEN 3227	♀	carapace	0.453	0.253	0.175	23
Paratype	LM-FCEN 3228	♀	carapace	0.369	0.200	0.125	29
Paratype	LM-FCEN 3229	♂	carapace	0.404	0.206	0.153	36
Paratype	LM-FCEN 3230	♂	carapace	0.384	0.200	0.151	36
Paratype	LM-FCEN 3231	♀	carapace	0.440	0.225	0.225	26

Stratigraphical range. Danian of Cerro Azul, General Roca.

Remarks. Differs from *Nodoconcha polytorosa* sp. nov. in the absence of ventrolateral and posterodorsal tubercles and in the pattern of the fish-scale like reticulation.

Evolutionary history of the Nodoconchiinae

The new evidence presented in this paper allows us to demonstrate that this subfamily has a long and varied phylogenetic history dating from the Lower Maastrichtian to the present day.

Austrocythere

Austrocythere seems to exist only as a single species. *A. reticulotuberculata* Hartmann, 1989*a* is from the Oligocene to Recent. All records are from the Antarctic and from cold water (Blaszyk 1987; Dingle & Majoran 2001).

Nodoconcha

By contrast with *Austrocythere*, the genus *Nodoconcha* is represented by a number (7) of species as well as the type species *N. minuta* Hartmann (see Fig. 3). The Minuta group which comprises, in stratigraphical order, *Nodoconcha* sp. (Bertels, 1974), *N. polytorosa* sp. nov., *N. sanniosis* sp. nov. and *N. minuta* Hartmann, represents what seems to be a straight line of evolution within four species (Fig. 4).

Nodoconcha sp. (Bertels, 1974), which overall is somewhat similar to *N. minuta*, ranges from Lower to Upper Maastrichtian within the Jagüel Formation of Neuquén. This seems to give rise to *N. polytorosa* sp. nov., which first appears early in the Danian and extends well into the late Danian, Roca Formation. This, in turn, is thought to be ancestral to *N. sanniosis* sp. nov., which first appears in the Danian, Roca Fm. but does not survive this formation. With respect to *N. minuta*, which first appears in the Oligocene, it is difficult to determine whether it evolved from *N. sanniosis* or *N. polytorosa*. In terms of morphology, either one could be the ancestor. *Nodoconcha* sp. aff. *N. minuta* is reported from the Miocene Ross Sea by Dingle (2000). However, since it is neither described nor illustrated, we are unable to comment on its possible status.

Nodoconcha jaguelensis (Bertels, 1974), which has approximately the same Maastrichtian biochron as *Nodoconcha* sp. (Bertels, 1974), can either be seen as a potential ancestor of the Minuta group, or as a short lived descendant from either that group or a common ancestor. The same can be said of *Nodoconcha*? sp., in that it could be either the ancestor of *Nodoconcha* sp. (Bertels, 1974) or a derivative form from a common ancestor. While it lacks many of the biocharacters of the Minuta group, it shares enough, notably the two major sulci and the posterodorsal tubercle, to denote a close relationship.

Two closely related species are *N. paleocenica* (Bertels, 1973) from the early Danian, Jagüel Formation to the late Danian, Roca Formation and *N. upsilon* sp. nov., with a more restricted biochron within in the middle and upper Danian. The two species are noted for a 'U'-shaped structure in their ornament and constitute the Upsilon group. It is thought that *N. paleocenica* (Bertels, 1973) may have evolved from *Nodoconcha*? sp. and *N. upsilon* sp. nov. from *N. paleocenica* (Bertels, 1973).

Lastly, a species that we have placed in the subfamily differs sufficiently from *Nodoconcha* to demand separate generic status. This is *Ectonodoconcha lepidotus* gen. et sp. nov., a genus that appears early in the Danian and just survives to the upper part of the Danian. Although it evidently derives from *Nodoconcha*, we are unable to state with any degree of certainty from which of the two groups mentioned above it has evolved.

Conclusions

The Nodoconchiinae subfam. nov. are a close-knit group of three genera *Austrocythere* Hartmann, *Nodoconcha* Hartmann and *Ectonodoconcha* gen. nov.. They arose in the Maastrichtian where they rapidly diversified, survived the Cretaceous–Tertiary boundary event and continued to proliferate in the Danian. They seem to have declined somewhat in the later Paleocene and are represented today by only two species, *Austrocythere reticulotuberculata* Hartmann and *Nodoconcha minuta* Hartmann.

One of the areas of our future work in the Upper Cretaceous–Tertiary strata of Neuquén Basin will be to seek more evidence on

the early origins of this group, which we presently believe to reside in either of the two species *Nodoconcha*? sp. or *N. jaguelensis* (Bertels, 1974).

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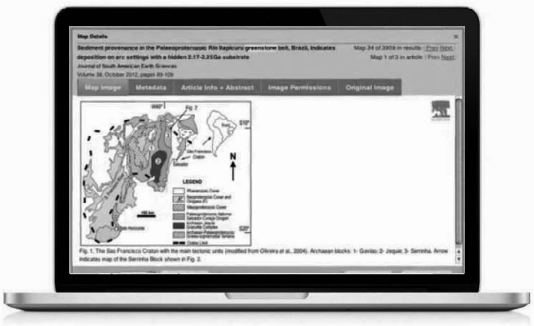

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