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Carboniferous atomodesmids (Mollusca: Bivalvia) from central Patagonia, Argentina

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with 6 text-figures and 2 tables

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A group of bivalves from the Carboniferous rocks of central Patagonia shows some resemblances with the Permian family Atomodesmidae. These specimens are known from fragmentary material; some may be in the early stages of the atomodesmids and kolymiids, and are provisionally assigned to that taxon. Four distinct forms are revised; these are *Atomodesma? amleri* n. sp., *Aphanaia*? sp. indet., *Aphanaia precursa* n. sp., and *Kolymia*? sp. indet.

Eine Gruppe von Bivalven aus karbonischen Gesteinen von Zentral-Patagonien zeigt Ähnlichkeiten zu permischen Atomodemidae. Die vorliegenden Exemplare sind nur fragmentarisch erhalten und stellen vermutlich die frühen Vertreter der Familie. Es handelt sich um *Atomodesma? amleri* n. sp., *Aphanaia*? sp. indet., *Aphanaia precursa* n. sp., and *Kolymia*? sp. indet. und werden unter Vorbehalt zu diesem Taxon gestellt.

Keywords: marine bivalves, Atomodesmidae, Upper Pennsylvanian, Argentina
Schlüsselwörter: marine Bivalvia, Atomodesmidae, Oberes Pennsylvanium, Argentinien

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Introduction

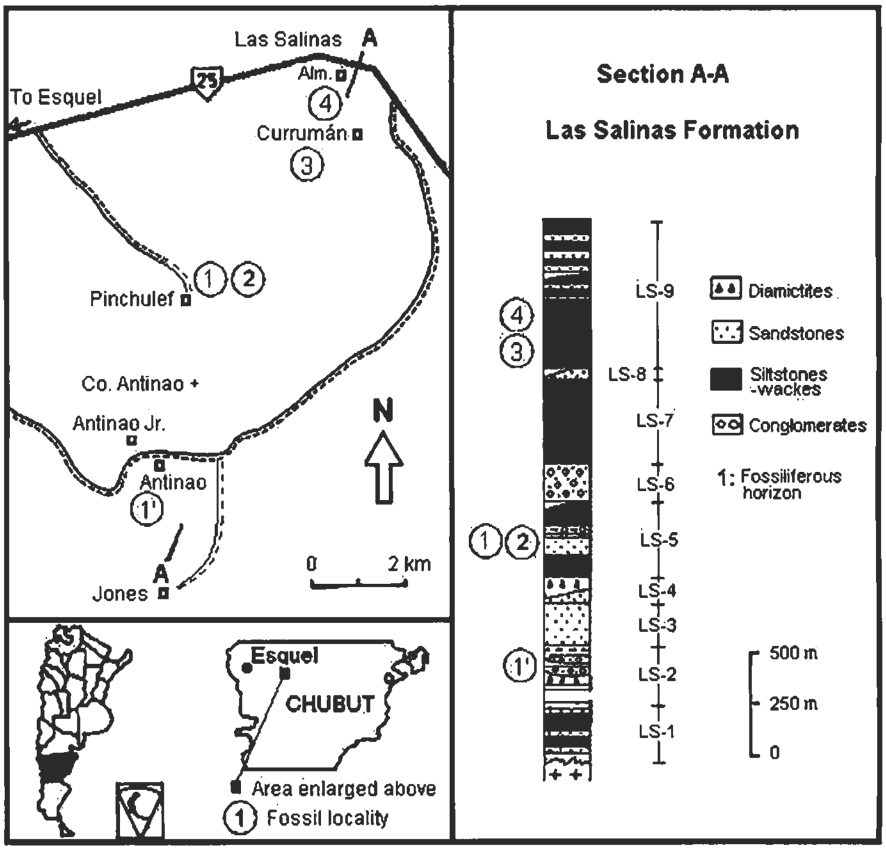
Carboniferous glacial deposits of central Patagonia furnish abundant fragmentary remains of bivalve shell and moulds that can be assigned to endemic Gondwana fauna. Some could be ancestors of Permian genera; others are new forms that may be short-lived experiments that vanished after the first glacial stages. The material revised in this paper consists of few incomplete specimens that are referred with reservations to atomodesmids, mainly because their external characteristics suggest close alliance with genera of this family. Some specimens are known only from their exterior, and some show well preserved morphologic characteristics of the interior. All the specimens probably belong to new taxa, but the available material is insufficient for a full assignation.

Atomodesmids are widespread in cool and temperate sea-waters during the late early to middle Permian in Australia, New Zealand and Siberia.

The specimens described here come from the mid-Carboniferous Las Salinas Formation of central Patagonia (Text-fig. 1), where fragments of shells and incomplete moulds are especially abundant. They probably occur also in the Carboniferous deposits of western Argentina (GONZÁLEZ 2002) and New Zealand (WATERHOUSE 2001). The present paper is a part of a wider study of these bivalves.

Palaeobiogeography

Forms like those herein described are not known to occur in Carboniferous deposits of other regions of Gondwana, perhaps because of poor or non-preservation. When the Gondwana-wide Ice Age ended at the latest Asselian or Tastubian (DICKINS 1985, SHI & WATERHOUSE 2010), atomodesmids became infrequent components of Australian faunas and Himalayan faunas and common to very abundant in New Zealand and Timor, and from these regions migrated to Siberia. HARRINGTON (1955) described *Aphanaia orbirugata* HARRINGTON as component of the relict *Eurydesma* fauna from Lower Permian deposits of



Text-fig. 1: Sketch map and simplified section of the Las Salinas Formation to show fossiliferous locality and stratigraphic occurrence of fossils. 1-1': *Aphanaia?* sp. indet.; 2: *Atomodesma? amleri* n. sp.; 3: *Kolymia?* sp. indet.; 4: *Aphanaia precursa* n. sp.

eastern Argentina, but they are lacking in the Lower Permian deposits of central Patagonia and western Argentina, perhaps because the post-glacial warming began earlier in these regions (GONZÁLEZ 2006). Following WATERHOUSE (1967) and USTRITSKY (1974), ASTAFIEVA (1991) pointed out the bipolar distribution of Permian faunas and according their different ages in these regions, she concluded that the "*Inoceramus*-like" bivalves of the Southern Circumpolar region appeared a little earlier than those in the Northern Circumpolar region, and that they migrated in that sense across the Tropical (Equatorial) region. During the Permian Period, atomodesmids diversified and adapted to warmer sea waters, being able to reach the North American seas (KAUFFMAN & RUNNEGAR 1975). ASTAFIEVA's (1991) theory of unidirectional migration of "*Inoceramus*-like" bivalves from southern to northern circumpolar regions agrees with their appearance in central Patagonia during the Carboniferous, and their subsequent dispersion during the Late Pennsylvanian or earliest Permian.

Evolution

Upper Palaeozoic Atomodesmidae reached maximum diversification and palaeogeographic distribution during the Permian, and probably have roots in the Carboniferous. The forms described here appeared associated with the oldest glacial sediments at the onset of the Late Palaeozoic Ice Age; they are abundant in the *Levipustula levis* Zone of central Patagonia. Richly fossiliferous Carboniferous deposits within the *Levipustula* Zone of similar facies also occur in eastern Australia, but no certain occurrences of atomodesmids are known in this region, although an incomplete specimen from New South Wales, described as *Posidonia* sp. by CAMPBELL (1961) may be an atomodesmid. The record of unquestionable Atomodesmidae begins at the Sakmarian of Australia; there is a large gap in the record during the latest Pennsylvanian–earliest Permian.

DICKINS (1963, 1989), KAUFFMAN & RUNNEGAR (1975), and GONZÁLEZ (2002) suggested that *Atomodesma* may have an ancestor in *Posidoniella*. *Posidoniella malimanensis* GONZÁLEZ, 1994 (upper Tournaisian, western Argentina) has a channel-form ligament area, the canalivincular type of WATERHOUSE (2001), and prismatic shell, but lacks an umbonal plate or deck. GONZÁLEZ (1994) considered that *Posidoniella* and *Atomodesma* arose from the same phylogenetic stock, and that the Atomodesminae may have differentiated from forms like *Posidoniella malimanensis* during the middle Carboniferous by the development of an umbonal septum. WATERHOUSE (2001) pointed out that *malimanensis* lacks the right anterior auricle that is characteristic of *Posidoniella* (DICKINS 1983), and *Posidoniella malimanensis* became the type species of *Malimanina* WATERHOUSE. This author placed *Malimanina* in the Atomodesmidae (Malimanininae WATERHOUSE, 2001) with questions because lacks an umbonal deck or plate. He argued that the channel-like ligament area of *Atomodesma* and *Malimanina* is higher than in *Posidoniella,* suggesting that *Malimanina* is the oldest known member of the Atomodesmidae at a phase before the development of the umbonal deck. One of us (CRG) was able to assemble a new collection of well preserved *Malimanina malimanensis* from the type locality; after examination of this material can be confirmed that a true auricle is not present in the right valve. However, the specimens have a small fold in the anterior margin of the right valve that slightly overlaps the left valve margin, which may have evolved in an incipient or relict auricle.

WATERHOUSE & CHEN (2006) assumed that *Atomodesma* evolved from single folded species like *Atomodesma uniplicatum* WATERHOUSE, 1979, to species that developed more and more radial grooves. WATERHOUSE (2001) suggest that a possible ancestor of *Atomodesma uniplicatum* was *Maitaia* MARWICK, 1934. WATERHOUSE (1979) considers that *Atomodesma uniplicatum* (Artinskian, western Australia) is the oldest species of the genus, but *Atomodesma? amleri* n. sp., described below, from the lower *Levipustula levis* Zone of central Patagonia (Serpukhovian or early Bashkirian) shows radial plication. However, there is a long time involved between the occurrences of *Atomodesma? amleri* n. sp. and *Atomodesma uniplicatum.* If *Atomodesma? amleri* n. sp. should be proved a true *Atomodesma*, it may be directly linked with *Atomodesma uniplicatum*, and the suggestion that *uniplicatum* evolved from *Maitaia* must be set aside.

Kolymia differs significantly with *Atomodesma* especially in the lack of umbonal septum or strong radial sulci and folds. It has a well developed posterior ear and anterior lobe on each valve and a prominent byssal gape. Considering the muscle insertion areas, *Malimanina malimanensis* bear more morphologic resemblance to *Kolymia* than to *Atomodesma*; both *Kolymia* and *Atomodesma* may have originated from an ancestral form like *Malimanina.* The specimen described below as Kolymiidae nov gen. et nov. sp. shows a pattern of muscle insertions somewhat resembling that of *Malimanina.*

The morphologic diversity shown by the bivalves in the Carboniferous deposits of central Patagonia, suggest that they attempted different evolutive trends, and reveal the complex history and great genetic potential early in the existence of this group. Other genera, such as *Pyramus, Myonia, Megadesmus, Myofossa, Merismopteria*, and probably *Vacunella*, also occur early in the course of the Carboniferous glacial period (GONZÁLEZ 2002), showing that most of the endemic Gondwana bivalve fauna appeared during this epoch.

Repository: The specimens described here are lodged in the collections of Instituto de Paleontología, Miguel Lillo Foundation (collection prefix IPI), and Instituto Miguel Lillo, Universidad Nacional de Tucumán (collection prefix PIL), San Miguel de Tucumán. All the material was collected before 2000.

Systematic Palaeontology

Class BIVALVIA LINNAEUS, 1758
Order PTERIIDA NEWELL, 1965
Suborder PTERIIDINA Newell, 1965
Superfamily INOCERAMOIDEA GIEBEL, 1852

Observations: AMLER (1999) referred Inoceramidae to Ambonychioidea MILLER, but Inoceramidae GIEBEL, 1852 was proposed well before Ambonychiidae MILLER, 1877. In the usage promulgated by MCCORMICK & MOORE (1969) in the Treatise, Inoceramidae were referred to Pterioidea. NEVESSKAYA et al. (1971) recognised both groups as separate superfamilies, and this is followed herein. Some doubt remains over the relationship between the two: they are close in many respects, but Inoceramoidea also shows some attributes of Pteriidina, notably in ligament, which is opisthodetic and often multivincular, and in the shell structure, which is largely prismatic. The ligament is platyvincular or with multiple ligament pits, and teeth are as a rule lacking.

Family ATOMODESMIDAE WATERHOUSE, 1976

Diagnosis: Medium to large shells, inequivalve to equivalve, inequilateral, umbones anteriorly placed, byssal notch or gape may be present in both valves but generally absent, ligament platyvincular external to semi-internal, posterior adductor scar large, no clear anterior adductor scar, pallial line discontinuous, pitted, shell prismatic, hexagonal.

Discussion: Neither the source nor descendents of Atomodesmidae are clearly established. NEVESSKAYA et al. (1971) and STAROBOGATOV (1992: 21) recognized superfamilies Inoceramoidea, Ambonychioidea and Pterioidea in infra-order Pterioinei BEURLEN, 1944. Kolymiidae KUZNETSOV, 1973 is close in size, shape and prismatic shell to Atomodesmidae, but a small anterior wing is developed in each valve and a prominent byssal gape may be enclosed by the anterior wings of the two valves, whereas in atomodesmids, the two valves are often adpressed along the anterior commissure. The ligament is developed above the inner shell layer in Kolymiidae, whereas that of atomodesmids is placed above the prismatic layer. That suggests Kolymiidae are like Retroceramidae PERGAMENT in KOSCHELKINA, which is shown to be close in the development of its ligament to the pterioid Isognomonidae (CRAMPTON 1988), whereas atomodesmids are closer to the arrangement in the Inoceramidae. There are further differences between members of the two families. *Kolymia* displays a very large pedal scar close to the hinge, with a row of pits extending anteriorly to the inner umbo, unlike musculature seen in atomodesmids. It has been speculated that the anterior adductor possibly lay within the umbonal septum of atomodesmids, but this is uncertain. Recent studies on classification that were summarized in AMLER (1999: 239) ignored both Kolymiidae and Atomodesmidae, possibly because KAUFFMAN & RUNNEGAR (1975) had argued that *Atomodesma* and *Kolymia* were Late Palaeozoic representatives of Inoceramidae. They preferred an economy of classification, and their approach has been overtaken by the diversification of biota recognized in current studies, both at family and higher level and at generic level amongst atomodesmids and kolymiids, and MUROMSEVA (1984), ASTAFIEVA (1993) and BIAKOV (eg. 1992, 2007) have dismissed the views of KAUFFMAN & RUNNEGAR by recognizing a number of genera, separated from a large diverse group of Late Mesozoic genera placed in Inoceramidae. Given the fossil record, it is still uncertain that atomodesmids gave rise directly to Inoceramidae, and if cryptic descendents did survive through the Triassic Period, their morphological affinities remain unknown. ASTAFIEVA (1993) allocated Kolymiidae to Pterineoidea, *Atomodesma* and allies to Atomodesmidae, and *Permoceramus* WATERHOUSE to Inoceramidae: WATERHOUSE (2001: 107) considered atomodesmids and kolymiids could be allied and so tentatively grouped the two as Pterineoidea, but offered an alternative evolutionary path.

The source of the atomodesmids remains open. Ambonychiids provide the most commonly preferred root. CARTER (1990) noted the similarity of atomodesmids to ambonychiid genera *Cleionychia* ULRICH and *Amphicoelia* HALL of Ordovician and Silurian age respectively. As shown below, Atomodesmidae are represented in Serpukhovian and probably Bashkirian fauna of Argentina, but add limited information about the nature of early Carboniferous or Devonian root-stock.

It was underlined by DICKINS (1983: fig. 1A) that the early Carboniferous genus *Posidoniella* DE KONINCK, 1885 showed a right anterior auricle and byssal notch, like that of specimens ascribed to *Atomodesma mytiloides* BEYRICH by DICKINS (1963: pl. 10 fig. 5) from the younger Early Permian Wandagee and Norton Formations of the Carnarvon Basin and Nooncanbah Formation in the Fitzroy Basin in Western Australia. No information was provided about the nature of the ear – and in particular, whether the ligament lay within the ear, or stopped under the umbo behind the ear. As well, DICKINS implied that the left valve lacked an anterior ear. The arrangement is thus close to that of Buchiidae, but we consider that much closer study is need to clarify the hinge of *Posidoniella* behind any firm placement can by suggested, and indeed the left valve of *P. vetusta* DE KONINCK (1885: pl. 31 fig. 8) shows an anterior wing. The *Posidoniella* ear is not the same as the anterior lobe characteristic of Kolymiidae. As a rule atomodesmids do not have an ear on either valve, and normally, do not show any byssal gape (see for instance KAUFFMAN & RUNNEGAR 1975: pl. 3 fig. 1; MUROMSEVA 1984: pl. 7 fig. 9b, pl. 11 fig. 5b; WATERHOUSE & CHEN 2006: text-fig. 9D), unlike *Kolymia* and allies, in which the anterior lobe terminate with large byssal gape (see MUROMSEVA 1984: pl. 18 fig. 3b; ASTAFIEVA 1993: pl. 13 fig. 5). The left valve of *Posidoniella* was shown by DE KONINCK (1885) as having an anterior ear or auricle. Unfortunately *Posidoniella* is so poorly known internally that any purported relationship between *Posidoniella* and atomodesmids provides little firm information on the development of the group, and the need for caution remains, because the presence externally of a byssal notch and anterior right valve ear does not closely accord with aspects of *Atomodesma*. CARTER (1990: 197) regarded *Posidoniella* as ambonychiid, whereas RUNNEGAR (1979) regarded it as cyrtodontid. *Posidoniella* has calcitic regular prismatic and nacreous structure in the right valve, but the left valve shell structure is not known.

A more meaningful alliance has been established through *Malimanina* WATERHOUSE (2001: 112), named for *Posidoniella malimanensis* GONZÁLEZ, 1994, from middle lower Carboniferous of San Juan province, Argentina. The shell is characterized by strong concentric rugae and channel-form ligament, with no umbonal deck or anterior ears. Small rounded pits extend along the pallial line. The shell is predominantly of calcite prisms. In all known attributes, the species accords with atomodesmids, except for the absence of an umbonal deck. WATERHOUSE (2001) therefore proposed a new genus, placed in a new family, which was regarded as an early atomodesmid. The age of *Malimanina* was given as Tournaisian by GONZÁLEZ (1994), which would rule out derivation of *Atomodesma* and allies from either the mid Carboniferous (Serpukhovian–Bashkirian) *Amosius* GONZÁLEZ & WATERHOUSE, 2004 by loss of the teeth and development of an umbonal septum, or from Kolymiidae, by movement of the anterior lobe and septum back under the umbones, as proposed by WATERHOUSE (2001: 107) in suggesting a pterioid origin for Atomodesmidae. The origin of *Malimanina* remains obscure, and options remain open for derivation from an ambonychiid or pteriid source. *Kolymia* is pterioid in shell shape, wings and musculature, and the appearance of numerous ligament pits in both atomodesmid and kolymiid stock and persistence in inoceramid stock is consonant with pteriidin relationships.

Subfamily ATOMODESMINAE WATERHOUSE, 1976

Diagnosis: Umbonal deck developed below under platyvincular ligament.

Discussion: Members of Atomodesminae are most prominent in Permian temperate palaeolatitudes, particularly in Siberia and New Zealand, and extend widely over Gondwana and into North America. The genera in Australia, Himalaya, and New Zealand are based on external appearance of ornament and shape, and on internal features. More emphasis has been placed on external appearance in Russian studies, following the analysis of Inoceramiidae, for which taxa are well established, and particularly well justified for such distinctive forms as *Cigarella* ASTAFIEVA. Genera and species are most abundant in Siberia and New Zealand, with a much longer time range in New Zealand (possibly Late Carboniferous), whereas Siberian forms are Late Permian. Occurrences are more scattered in the Himalaya and Australia, and are moderately diverse in the middle-late Carboniferous of Argentina.

Atomodesma? amleri n. sp.

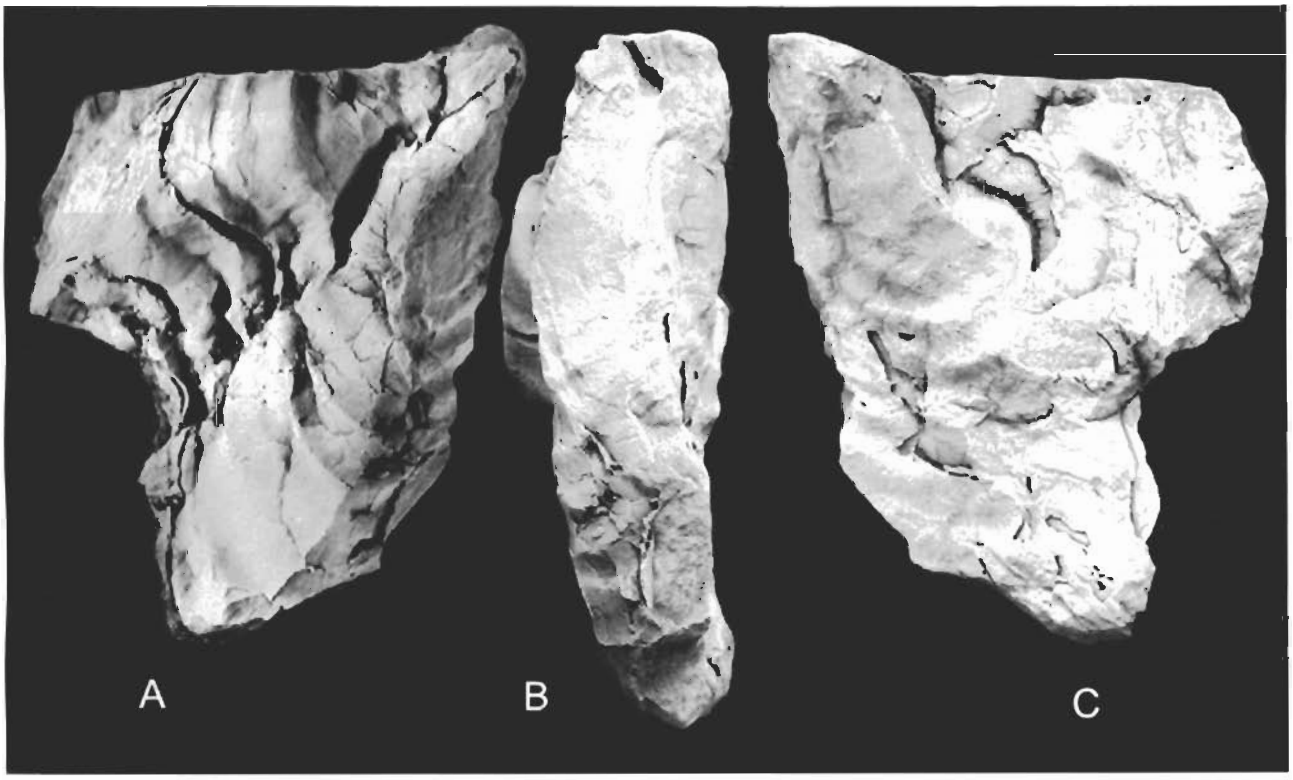
Text-figs. 2A-C, 5A

v 1983 *?Atomodesma* sp. B. González, Especies de Atomodesminae:156, pl. 1 figs. 4-6.

Derivation of name: Honour to Prof. Dr. Michael R.W. Amler, University of Marburg, Germany.
Holotype: PIL.12310, a steinkern lacking fragment of dorsal margin (Text-figs. 2A-C).
Paratype: PIL.12855, internal mould of left valve lacking fragment of anterior margin (Text-fig. 5A).
Type locality: 4500 m south of Route N° 25, 300 m NE of casa Pinchulef, Languiñeo Hills, Las Salinas, Chubut (Text-fig. 1: 2).
Type stratum: Member LS-5, Las Salinas Formation, *Levipustula levis* Zone, Serpukhovian Bashkirian.
Occurrence: Found only at the above mentioned locality.

Measurements: See Tab. 1.

Discussion: Radial folds are characteristic of the Permian *Atomodesma* (Waterhouse & Chen 2006), but the interior of *Atomodesma? amleri* n. sp. is unknown. Pteriiform shells that were adapted to pleurothetic life were regarded by Newell & Boyd (1970) as dextral or sinistral, depending if they rest on right or left valve respectively on the sea-floor. The holotype of *Atomodesma? amleri* n. sp. is a steinkern that shows that the radial sulcus and fold of the right valve interlock with the fold and sulcus of the left valve. In this specimen the left valve is much less convex than the right, but this may be caused by deformation although it can not be decided to what extent, so that a pleurothetic habit can not be established. In this regard, the paratype is a single not deformed left valve that show well developed convexity. Waterhouse & Chen (2006) postulated that many species of *Atomodesma* rested on a flat anterior face which was adapted as a platform below the umbones. Although the anterior margin of the steinkern is broken along the commissure, it seems to have been not straight and lacking a flat face or "platform" below the umbones (Text-fig. 2 B). A species exteriorly similar to *Atomodesma? amleri* n. sp. is *Atomodesma uniplicatum* Waterhouse, 1979 (late Early Permian, Western Australia), which also has a single groove and its interior is unknown. The Australian species, however, is more quadrate, the umbones are not projected from the shell body and the anterior face of each valve is flatter than in *Atomodesma amleri* n. sp.



Text-fig. 2: *Atomodesma amleri* n. sp.; middle Carboniferous (Serpukhovian–Bashkirian). Specimens A-C from 4,500 m S of Route 25, (member LS-5, Las Salinas Formation), Languiñeo Hills, Chubut. All specimens natural size.
A: Steinkern, view of right valve, **Holotype**, PIL.12310; **B**: Idem anterior, tilted view of anterior to show commissure (broken) and different convexity of valves, **Holotype**, PIL.12310; **C**: Idem anterior, view of left valve, **Holotype**, PIL.12310.

Diagnosis: Shell sub-trapezoidal. Umbones slightly projected above dorsal margin. Broad radial sulcus.

Morphology: Shell sub-trapezoidal to sub-triangular of moderate size. Umbones prosogyrous anterior, slightly projecting above dorsal margin. Anterior margin straight. Radial sulcus from umbonal region to posterior margin, forming angle of 50° with anterior margin. Greater convexity of shell at radial fold above groove. Radial sulcus and fold of one valve interlock with those of opposite valve. Ventral margin sinuate at end of radial groove. Small irregular muscle scars at umbonal cavity. Exterior with comarginal rugae, somewhat diffuse at umbonal region, and thin growth lines near ventral margin. Shell thin, prismatic. Other characteristics unknown.

Specimen	Material	Length	Height	Illustration
PIL.12310 H	S, f.	70 e	70	Text-fig. 2A, B, C
PIL.12855 P	L, f.	38 e	39 e	Text-fig. 3A

Tab. 1: *Atomodesma amleri* n. sp. Dimensions (in mm). Abbreviations: H = holotype; L = left valve; P = paratype; R = right valve; S = steinkern; e = estimated; f = fragmentary; i = internal mould.

Aphanaia DE KONINCK, 1877

Type species: *Inoceramus mitchelli* M'COY, 1847 (: 299), SD DICKINS (1956: 23).

Diagnosis: Shells without radial grooves and plicae, characterized by left valve being much more inflated than right valve, growth steps usually prominent, no anterior auricle, posterior wings variably developed or absent.

Discussion: The ligament of type *Aphanaia* is narrower and less well formed than in *Maitaia* MARWICK (1934, 1935). Its growth habit often involves one to three major growth steps, especially in the right (smaller) valve (DICKINS 1956: pl. 4 fig. 1), but specimens from one station in the Hunter Valley, New South Wales, vary considerably in the strength and spacing of comarginal ornament. *Atomodesma* BEYRICH, 1864, differs in being sub-equivalve to equivalve, with lateral grooves and ridges, and a strong tendency for the anterior face of each valve to form a platform (WATERHOUSE & CHEN 2006: fig. 9D): it was anteroposited on the sea-floor.

Aphanaia precursa n. sp.

Text-figs. 3A-B, 4

1983 ?*Atomodesma* sp. A. – GONZÁLEZ, Especies de Atomodesminae:156, pl. 1 figs. 1-3.

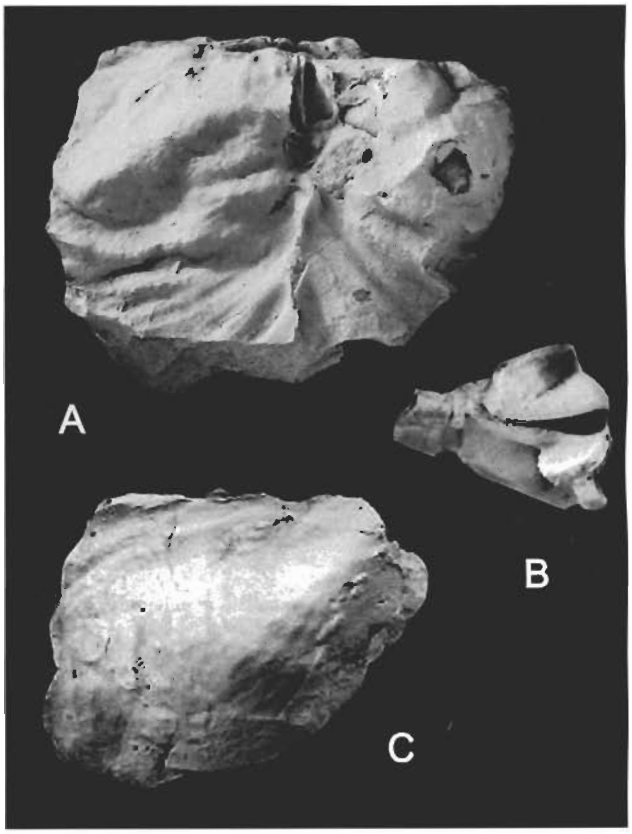
Derivation of name: Latin, praecursa = that precede.
Holotype: A fragmentary steinkern deformed by compression. The specimen lacks fragments of the ventral margins, PIL.12854 (GONZÁLEZ 1983: pl. 1 fig. 1) (Text-figs. 3A-B, 4).
Type locality: Nearly 800 m SW of Route 25, Languiñeo Hills, Las Salinas, Chubut (Text-fig. 1: 4).
Type stratum: Member LS-9 of the Las Salinas Formation, Upper *Levipustula levis* Zone, Serpukhovian-Bashkirian.
Occurrence: Known only from the above mentioned locality.

Diagnosis: Small sub-equivalve elongate shells with coarse sub-equal rugae on each valve. No right valve growth stops, umbonal septum narrow, concave, with concave anterior.

Morphology: Mytiloid shell of medium to large size. Umbones terminal, prosogyrous. Short, channel-shape ligament area with thin longitudinal striae. Spoon shaped subumbonal deck or septum below anterior end of ligament area. Anterior segment of pallial line discontinuous, a row of irregular pits. Exterior with rough, irregular concentric folds.
Other characteristics unknown.

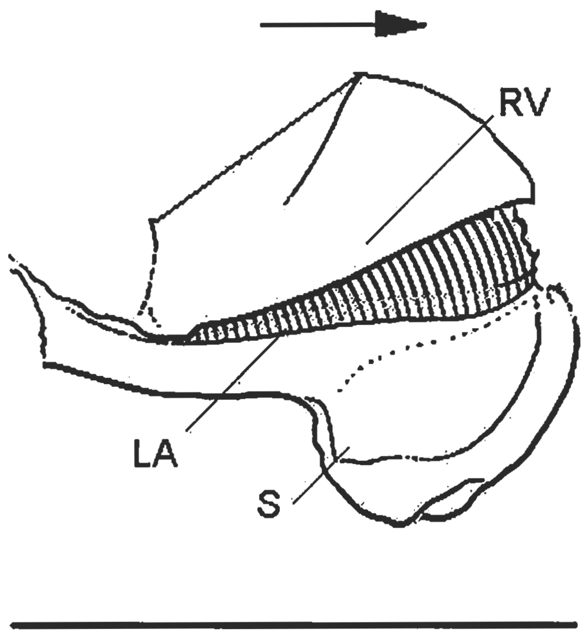
Measurements: Dimensions of Holotype PIL.12854 (a deformed steinkern) (Text-fig. 3A): estimated length more than 40 mm, estimated height more than 35 mm.

Observations: Unfortunately it is not possible to ascertain the relative inflation of the two valves, but they are likely to have been of comparable width, because the ornament of coarse comarginal rugae is similar on each valve. The species is distinguished from other species ascribed to *Aphanaia* by the relatively elongate shape and coarse rugae, that suggest a degree of impersistence (see GONZÁLEZ 1983: pl. 1 fig. 1). The umbonal deck has a curved anterior margin, which is common in some species, and is narrow, somewhat like that of type *Aphanaia*. Further material may well demonstrate that the species is generically separate from *Aphanaia*, but on present knowledge, it is the closest of genera. *Atomodesma* has lateral furrows and folds. *Evenia* KUZNETSOV has well defined posterior wings and the left anterior bulges strongly into the right commissure. *Mytilidesmatella* WATERHOUSE, 1979 has a very large and elongate umbonal septum with smooth exterior; *Maitaia* MARWICK, 1934 has smooth or closely wrinkled exterior and triangular umbonal septum, and *Trabeculatia* WATERHOUSE, 1979 has well defined posterior wings, close-set and subdued wrinkles, and small umbonal septum



Text-fig. 3: *Aphanaia precursa* n. sp. and *Kolymia*? sp. indet.: middle Carboniferous (Serpukhovian Bashkirian). Specimens A-B from nearly 800 m SW of Route 25, member LS-9, Las Salinas Formation; specimen C from 3000 m south of Route 25, member LS-9; Las Salinas Formation, Languiñeo Hills, Chubut.
A-B: *Aphanaia precursa* n. sp.; **A**: fragmentary steinkern deformed by compression, dorsal view, PIL.12854, slightly larger than natural size; **B**: idem anterior, polyvinylsiloxane cast of the cardinal area showing short channel-like ligament area and spoon-shaped subumbonal deck or septum of left valve, PIL.12854 (see Text-fig. 4), x2.
C: *Kolymia*? sp. indet. Internal mould of fragmentary right valve, PIL.11444 (see Text-fig. 6), natural size.

with thickened hinge. *Cigarella* ASTAFIEVA, 1988 is a very high shell with long and extended umbones. *Undosusia* WATERHOUSE, 2008 has strong regular comarginal rugae. Genera *Costatoaphanaia* BIAKOV, 2008 and *Okhotodesma* BIAKOV, 2008 are recognized for genera with distinctive commarginal ornament, as discussed by BIAKOV (2008).



Text-fig. 4: *Aphanaia precursa* n. sp. Camera lucida drawing of polyvinylsiloxane cast of PIL12854. Tilted view of cardinal structure of left valve to show ligament area (LA) and spoon-shaped subumbonal septum (S) below anterior end of ligament area, RV: upper margin of right valve. – Scale bar = 1 cm.

Aphanaia? sp. indet.

Text-figs. 5B-D

Material: IPI.4080 (S, f, lacking dorsal) (Text-fig. 5B), IPI.4081 (R, i, f, lacking posterior and dorsal margins) (Text-fig. 5C), PI.4086 (R, i, f, lacking anterior) (Text-fig. 5D), and seven fragments, mainly external moulds IPI 4082/5 and IPI.4087/9. See abbreviations in Tab. 1.
Locality: 4500 m south of Route Nº 25, 300 m NE of casa Pinchulef, Languiñeo Hills, Las Salinas, Chubut (Text-fig. 1: 1).
Stratigraphy: Members LS-5 and LS-2 of the Las Salinas Formation, *Levipustula levis* Zone, Serpukhovian–Bashkirian.
Occurrence: 7500m south of Route Nº 25, near casa Antinao (Text-fig. 1: 1')

Morphology: Triangular shell of moderate size. Umbo not prominent. Anterior and dorsal margins nearly straight. Posterior margin rounded. Exterior with comarginal rugae.

Measurements:

Specimen	Material	Length	Height	Illustration
IPI.4080	S, f.	80 e	65 e	Text-fig. 3B
IPI.4081	R, i, f.	73 e	65 e	Text-fig. 3C
IPI.4086	R, i, f.	70 e	60 e	Text-fig. 3D

Tab. 2: *Aphanaia?* sp. indet. – Dimensions (in mm).

Observations: These specimens lack any sign of lateral furrow, and do not have a separate posterior wing. The ornament of comarginal rugae is stronger than that generally observed for species of *Aphanaia*, and is not step-like, unlike the rugae in *Intomodesma* POPOV. Without the left valve, the specimens are difficult to identify, but of all genera so far named, they come closest in shape and ornament and lack of posterior wing to *Aphanaia*, but it should be noted that right valves of type and other *Aphanaia* usually show one to three growth-stops, and none can be observed on present material.

Family KOLYMIIDAE KUZNETSOV, 1973

Diagnosis: Pteriiform shells with short anterior wings that gape, anysomyarian musculature, platyvincular ligament and prismatic shell.

Discussion: Although *Kolymia* has been associated closely with *Atomodesma* by KAUFFMAN & RUNNEGAR (1975), the two belong at the very least to two different families, given the differences in anterior auriculation and gape, musculature, and attachment mode of the ligament. Even superfamilial relationships remain uncertain. The two suites are associated geographically in the Late Permian of Siberia, and we demonstrate, in the middle Carboniferous of Argentina. Elsewhere, atomodesmids are widespread, and kolymiids virtually unknown. In both atomodesmids and kolymiids the hinge rarely became duplivincular, *Aphanaia* giving rise to *Permoceramus* WATERHOUSE, and *Kolymia* to *Varvaria* MUROMSEVA, so there is a degree of commonality, and whether this is due to convergence or to close kinship is difficult to determine. But the nature of the hinge and the shell structure might at least to indicating common ancestry amongst Pteriida.

A single internal mould from the upper (LS-9) member of the Las Salinas Formation that was previously assigned to *Naiadites?* sp. (GONZÁLEZ 1977), is reassigned with reservations to *Kolymia*. The specimen although fragmentary, clearly shows the muscle insertion areas, which apart from some minor differences, is very close with the pattern of Permian atomodesmids figured by KAUFFMAN & RUNNEGAR (1975). It has anterior lobe and no trace of umbonal septum, just as in the Upper Permian Kolymiidae.

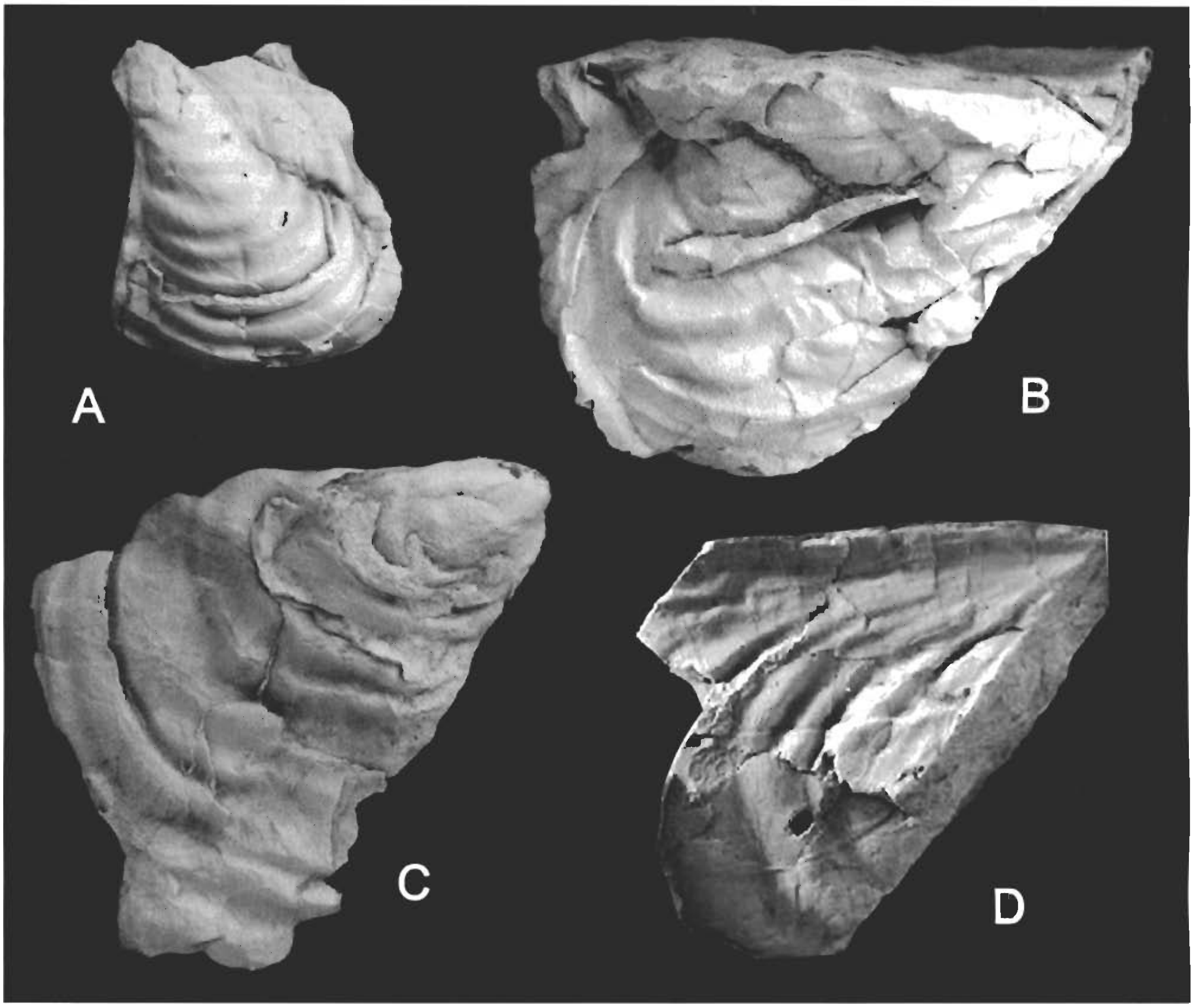
Kolymia? sp. indet.

Text-figs. 3C, 6

v 1977 *Naiadites?* sp. - GONZÁLEZ, Bivalvos del Carbónico Superior: 117.

Material: A fragmentary internal mould of right valve lacking cardinal margin and part of the anterior and posterior, PIL.11444 (Text-figs. 3C, 6).
Locality: 3000 m south of Route 25, Las Salinas, Languiñeo Hills (Text-fig. 1: 3), Chubut.
Stratigraphy: Member LS-9 of the Las Salinas Formation, *Levipustula levis* Zone, Serpukhovian–Bashkirian.
Occurrence: Found only at the above mentioned locality.

Morphology: Pterioid shell. Umbo slightly prosogyrous, slightly incurved, slightly projected above dorsal margin. Anterior lobe present. Posterior umbonal ridge extends from umbo to posteroventral margin. Posterior adductor muscle insertion area nearly 1/7 shell length, kidney-shaped or tear-shaped, with lower margin circular, sited at the posterior central part of the valve. A large oval muscle impression



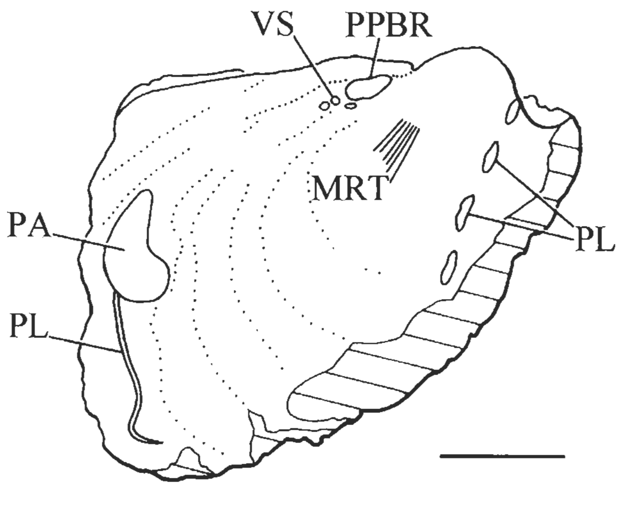
Text-fig. 5: *Atomodesma amleri* n. sp. and *Aphanaia?* sp. indet.; middle Carboniferous (Serpukhovian Bashkirian). Specimens A-D from 4,500 m S of Route 25, (member LS-5, Las Salinas Formation), Languiñeo Hills, Chubut. All specimens natural size.
A: *Atomodesma amleri* n. sp., internal mould of left valve, paratype PIL.12855.
B-D: *Aphanaia?* sp. indet.; **B**: fragmentary steinkern, view of right valve, IPI.4080; **C**: fragmentary internal mould of right valve, IPI.4081; **D**: fragmentary external mould of right valve IPI.4086.

at postumbonal slope, probably represents pedal-byssal retractor muscle insertion area. Three small scars lie behind and below posterior pedal-byssal (Text-fig. 6: VS).

Posterior part of pallial line continuous extending straight from lower margin of posterior adductor to the posterior ventral margin. This segment of the pallial scar shows a gentle inflection at its lower edge before turning anteriorly (Text-figs. 3C, 6). Median (ventral) segment of pallial line not seen. Anterior part of pallial line a row of deeply impressed elongate scars that probably continue with smaller scars at apex of umbonal cavity.

Measurements: Dimensions of PIL.11444 (incomplete internal mould of right valve) (Text-fig. 3C): length 50 mm (estimated), height 37 mm (estimated).

Discussion: *Kolymia*? sp. indet. shows a pterioid shape as in Permian genus *Kolymia* KUZNETSOV. The anterior part of the mould is partially destroyed, but is clearly seen part of the surface of an anterior lobe, and there are no traces of an umbonal septum. The muscle insertions are exceptionally preserved in the specimen (Text-figs. 3C, 6). The specimen lacks the dorsal margin, although fragments of a thin groove probably belonging to the ligament area is preserved. There are inconspicuous radial striations at a small area below the umbo (Text-fig. 6: MRT), a character that KAUFFMAN & RUNNEGAR (1975: fig. 7B) ascribed to a track of the mantle retractor muscle leading to the pallial line. The three small scars located behind and below the posterior pedal-byssal retractor at the posterior umbonal slope (Text-fig. 6: VS), may be related to the visceral suspensor scars that were described and figured by KAUFFMAN & RUNNEGAR (1975: fig. 6A: VS?). The posterior segment of the pallial scar is deeply impressed and extends straight down from the lower margin of the posterior adductor, showing a gentle sinuation near the ventral margin. This characteristic is unknown in the Atomodesmidae. Although there is a long time without record until the appearance of the Kolymiidae in east Siberia, perhaps their ancestor was a form like this.



Text-fig. 6: *Kolymia?* sp. indet. Camera lucida drawing of PIL.11444 (Text-fig. 3C) showing position of the muscle insertion areas. PA: posterior adductor, PL: anterior and posterior pallial line, PPBR: posterior pedal-byssal retractor, VS: visceral suspensors, MRT: track of mantle retractor. – Scale bar = 1 cm.

Conclusions

Carboniferous deposits of central Patagonia furnished abundant remains of invertebrate fossils, which are regarded the oldest known within the endemic (Gondwana) fauna that developed in the course of the Late Paleozoic Ice Age. During the middle Carboniferous (Serpukhovian–Bashkirian) glacial period in the cold seas of this region appeared new forms of bivalves, some of which are probably antecessors of Permian genera; other were not successful and are regarded short-lived experiments that disappeared soon after the first glacial phases.

The Atomodesmidae and Kolymiidae lived in the Early Permian cold and temperate sea waters of Australia, New Zealand and Siberia. Middle Carboniferous specimens from central Patagonia revised in this paper are assigned to these families because of their close morphologic relationships. Two new species are described: *Atomodesma? amleri* n. sp. and *Aphanaia precursa* n. sp. Other incomplete specimens probably belong to new taxa, but because insufficient material are designated with reservation; they are assigned after their external and internal morphologic characteristics to *Aphanaia?* sp indet. and *Kolymia?* sp. indet. The importance of these forms is because they are probably in the earliest known stages of the evolution of the Atomodesmidae and Kolymiidae. All the specimens come from the Las Salinas Formation, where shell fragments and moulds are found disseminated in fine-grained sediments. These bivalves are also present, although rarely, in the middle Carboniferous deposits of western Argentina (GONZÁLEZ 2002) and possibly New Zealand (WATERHOUSE 2001).

Resumen

Los depósitos del Carbonífero medio (Serpukhoviano–Bashkiriano) de la Patagonia central han proporcionado abundantes fragmentos de conchillas y moldes de bivalvos que son considerados los miembros más antiguos de la fauna endémica que se desarrolló en Gondwana en el transcurso de la Edad de Hielo del Paleozoico Superior. Durante el período glacial del Carbonífero medio, aparecieron en la Patagonia central nuevas formas de bivalvos, algunas de las cuales serían antecesores de géneros Pérmicos; otras no tuvieron éxito y fueron experimentos de corta existencia que se extinguieron luego de las primeras fases glaciales.

Los representantes de las familias Atomodesmidae y Kolymiidae estuvieron ampliamente distribuidos en los mares de aguas frías y templadas del Pérmico Temprano a Medio de Australia, Nueva Zelandia y Siberia. Los especímenes revisados en este trabajo muestran estrecha relación morfológica con géneros conocidos de esas dos familias. Se describen dos nuevas especies: *Atomodesma amleri* n. sp. y *Aphanaia precursa* n. sp. Otros especímenes incompletos probablemente pertenecen a nuevos taxones, pero debido a que el material disponible es insuficiente son identificados con reservas; ellos son asignados según sus características morfológicas externas o internas a *Aphanaia*? sp. indet. y *Kolymia?* sp. indet. La importancia de estas formas reside en que ellas se encuentran probablemente en la etapa más antigua de la evolución de los Atomodesmidae y Kolymiidae. El material descripto procede de la Formación Las Salinas, donde sus restos fragmentarios se encuentran diseminados en sedimentos finos. Estos bivalvos también se hallan, aunque raramente, en los depósitos del Carbonifero medio del centro oeste de Argentina (GONZÁLEZ 2002) y de Nueva Zelandia (WATERHOUSE 2001).

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