

To Dr. Zakharov,
with author's compliments
S. Damborenea

SONDER-ABDRUCK

aus

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BEITRÄGE ZUR NATURGESCHICHTE DER VORZEIT

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EARLY JURASSIC BIVALVIA OF ARGENTINA PART 2: SUPERFAMILIES PTERIACEA, BUCHIACEA AND PART OF PECTINACEA



BIVALVEN AUS DEM UNTEREN JURA VON ARGENTINIEN
TEIL 2: DIE ÜBERFAMILIEN PTERIACEA, BUCHIACEA UND z. T. PECTINACEA

BIVALVOS DEL JURASICO INFERIOR DE ARGENTINA
PARTE 2: SUPERFAMILIAS PTERIACEA, BUCHIACEA Y PARTE DE PECTINACEA

BY

SUSANA E. DAMBORENEA

With 14 plates, 31 figures and 2 tables in the text



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Zusammenfassung

In dieser Arbeit wird eine ausführliche systematische Untersuchung von 22 unterjurassischen Bivalven-Arten vorgenommen. Diese betreffen 17 Gattungen und Untergattungen aus 11 Familien, die den folgenden Überfamilien angehören: Pteriacea, Buchiacea und einem Teil der Pectinacea. Von diesen wurden zwei Untergattungen: *Gervilleioerna* (*Gervilletia*) und *Weyla* (*Lywea*) sowie sechs Arten neu aufgestellt: *Aguilerella neuquensis*, *Bakevellia* (*Neobakevellia* ?) *pintadae*, *Gervillella araucana*, *Pulvinites* (*Hypotrema*) *liasicus*, *Otapiria neuquensis* und *Otapiria* ? *frenguelli*. Diese Untersuchung wurde hauptsächlich aufgrund eigener Aufsammlungen durchgeführt, und zwar unter strikter stratigraphischer Kontrolle. Das Material stammt aus etwa 50 fossilreichen Vorkommen in den argentinischen Provinzen San Juan, Mendoza und Neuquén.

Einige Gattungen bzw. Untergattungen wurden im unteren Jura Argentiniens erstmals erkannt und abgebildet. Ferner werden in dieser Arbeit die bis jetzt ältesten bekannten Pulviniten der Welt beschrieben. Die meisten der Arten besitzen in den südlichen Anden eine beschränkte geographische Verbreitung, obgleich die Bivalven im allgemeinen große Affinitäten zu den typischen Tethys-Faunen aufweisen. Darüber hinaus sind einige der Arten mit europäischen Arten nahe verwandt oder identisch.

Die Kenntnis mancher Gattungen, wie z. B. *Aguilerella* CHAVAN und *Weyla* BÖHM, wird wesentlich erweitert. Ferner werden die phylogenetischen Beziehungen behandelt. Eine Übersicht der paläoautökologischen Merkmale der einzelnen beschriebenen Arten wird beigefügt. Die Kenntnis der stratigraphischen Verbreitung mehrerer dieser Arten wurde bedeutend verbessert. In einigen Fällen (wie z. B. *Weyla*-Arten und *Posidonotis cancellata* (LEANZA)) konnte eine biostratigraphische Verwendungsfähigkeit festgestellt werden. Die Analyse der paläogeographischen Verbreitung von *Weyla*, *Posidonotis* LOSACCO und *Eopecten* DOUVILLÉ beweist erneut die Möglichkeit eines faunistischen Austausches zwischen den Bivalven des östlichen Pazifik und der westlichen Tethys während des frühen Jura.

Schlüsselwörter: Bivalvia - Unterjura - Argentinien - Pteriomorpha.

Abstract

A detailed systematic study has been made of 22 species of Early Jurassic bivalves belonging to 17 genera and subgenera and to 11 families of the superfamilies Pteriacea, Buchiacea and Pectinacea. Of these, two subgenera: *Gervilleioerna* (*Gervilletia*) and *Weyla* (*Lywea*) and six species: *Aguilerella neuquensis*, *Bakevellia* (*Neobakevellia* ?) *pintadae*, *Gervillella araucana*, *Pulvinites* (*Hypotrema*) *liasicus*, *Otapiria*

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neuquensis and *Otapiria ? frenguelli*, are new. The research was based mainly upon the author's own material collected stratigraphically from about 50 fossiliferous localities in the provinces of San Juan, Mendoza and Neuquén (Argentina).

Some of the genus-group taxa are recognized and illustrated for the first time in the Early Jurassic of Argentina, and this study has also revealed the oldest pulvinitids so far worldwide. Although the bivalves studied reveal, as a whole, strong affinities with typically Tethyan ones at the generic level, most of the species have a restricted geographical distribution within the South American Andes. Some of the species are nonetheless indistinguishable or very closely related to European forms.

The understanding of some of the genera, such as *Aguilerella* CHAVAN and *Weyla* BÖHM, has been substantially improved, whilst the phylogenetic relationships of some of them are also discussed. An outline of the palaeoautecology of each species is provided, too. Knowledge about the stratigraphical range of many species has been significantly improved and some of them (as in *Weyla* and *Posidonotis* LOSACCO) are shown to be stratigraphically useful. Palaeobiogeographical data analysis of genera such as *Weyla*, *Posidonotis* and *Eopecten* DOUVILLÉ strengthens the available evidence favouring a faunal exchange between the east-central Pacific and the western Tethys during Early Jurassic times.

Key words: Bivalvia – Lower Jurassic – Argentina – Pteriomorpha.

Resumen

Se ha realizado un estudio sistemático de 22 especies de bivalvos del Jurásico inferior pertenecientes a 17 géneros y subgéneros y a 11 familias de las superfamilias Pteriacea, Buchiacea y Pectinacea. De ellos, dos subgéneros: *Gervilleioperna* (*Gervilletia*) y *Weyla* (*Lywea*) y seis especies: *Aguilerella neuquensis*, *Bakevellia* (*Neobakevellia* ?) *pintadae*, *Gervillella araucana*, *Pulvinites* (*Hypotrema*) *liasicus*, *Otapiria neuquensis* y *Otapiria ? frenguelli*, son nuevos. El estudio se basó mayormente sobre colecciones propias de material coleccionado con estricto control estratigráfico en alrededor de 50 localidades fosilíferas de las provincias de San Juan, Mendoza y Neuquén (Argentina).

Algunos de los taxa del grupo del género han sido reconocidos e ilustrados por primera vez para el Jurásico inferior de Argentina, y este estudio ha revelado los más antiguos pulvinitidos hasta ahora conocidos. A pesar de que los bivalvos estudiados presentan, en conjunto, grandes afinidades con faunas típicamente tethyanas a nivel genérico, la mayoría de las especies posee una distribución geográfica restringida dentro de los Andes meridionales. Sin embargo algunas de las especies se hallan estrechamente relacionadas o son referibles a formas europeas.

Se ha mejorado sustancialmente el conocimiento sobre algunos de los géneros, como *Aguilerella* CHAVAN y *Weyla* BÖHM, y se han discutido las relaciones filogenéticas de algunos géneros. También se da una breve reseña de las características paleoautecológicas de cada una de las especies descriptas. Se ha ampliado considerablemente el conocimiento sobre la distribución estratigráfica de varias especies, evidenciándose en ciertos casos (como en especies de *Weyla* y *Posidonotis* LOSACCO) la utilidad bioestratigráfica de las mismas. El análisis de los datos de distribución paleogeográfica de géneros como *Weyla*, *Posidonotis* y *Eopecten* DOUVILLÉ corrobora una vez más la evidencia de la existencia de una vía de intercambio faunístico accesible a los bivalvos entre el Pacífico oriental y el Tethys occidental durante el Jurásico temprano.

Palabras claves: Bivalvia – Jurásico inferior – Argentina – Pteriomorpha.

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Introduction

The early Jurassic faunas of Argentina are rich and diverse. The bivalves, which dominate the fossil assemblages, have not previously been treated in a monographic way. This work is an attempt to revise the systematics, geographical and stratigraphical distribution of this group. Accordingly, extensive collections were made at several localities in San Juan, Mendoza and Neuquén provinces. Where possible, the type localities for species described by previous authors were examined. The field work was carried out between 1973 and 1984. The greater part of the collecting was done in several trips during 1973, 1974 and 1979 with A. C. RICCARDI and M. MANCERNIDO. A second visit to the area of Cordón del Espinacito (San Juan province) was made in 1975 with M. MANCERNIDO and W. VOLKHEIMER. Some additional localities in Neuquén province were examined with M.

MANCEÑIDO and S. BALLENT in 1980. A. RICCARDI and M. MANCEÑIDO provided data and fossil material collected during their field trip to the Valle Hermoso region (Mendoza province) in 1982. Some stratigraphical sections in southern Mendoza were measured with M. MANCEÑIDO in 1983; and the central Neuquén region was visited with M. MANCEÑIDO and M. GRIFFIN in 1984. The study also included the examination of type specimens and other material from collections deposited in several museums (especially at the La Plata Natural Sciences Museum).

The first part of this monograph dealt with the superfamilies Nuculanacea, Arcacea, Mytilacea and Pinnacea (DAMBORENEA 1987). This second part deals with the Pteriacea, Buchiacea and part of the Pectinacea. Further parts of this monograph will deal with the remaining Pectinacea and the subclasses Palaeoheterodonta, Heterodonta and Anomalodesmata.

Previous Work

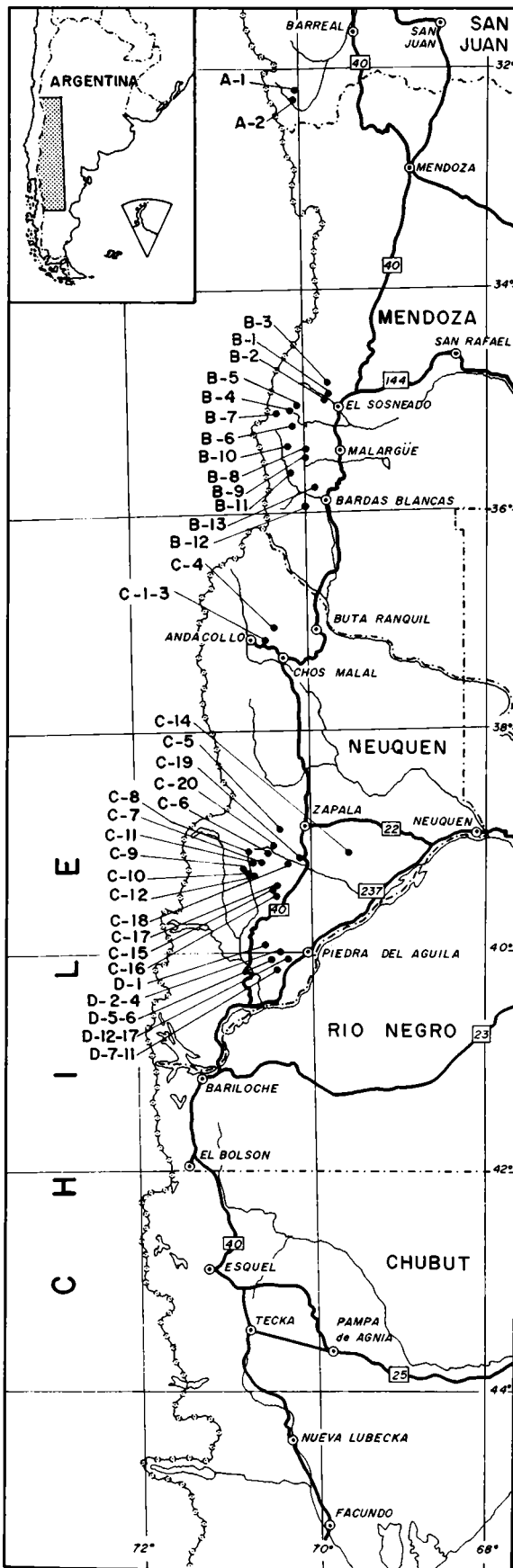
A brief summary of the previous literature on early Jurassic bivalves from Argentina was provided in DAMBORENEA (1987).

Terminology and Measurements

The biostratigraphical terminology used is according to RICCARDI (1983, 1984), who summarized the Argentinian ammonite assemblages and their equivalence to European Standard Zones and Subzones (see table I).

STAGES & SUBSTAGES		EUROPE	ARGENTINA	
TOARCIAN	UPPER	<i>Dumortieria levesquei</i>	<i>Dumortieria</i> faunule <i>Phlyseogrammoceras tenuicostatum</i> Z.	
		<i>Grammoceras thouarsense</i>	<i>Phymatoceras</i> faunule	
		<i>Haugia variabilis</i>		
	LOWER	<i>Hildoceras bifrons</i>	<i>Collina chilensis</i> Zone <i>Peronoceras pacificum</i> Zone <i>Peronoceras largaense</i> Zone	
		<i>Harpoceras falcifer</i>	<i>Dactylioceras hoelderi</i> Zone	
		<i>Dactylioceras tenuicostatum</i>	<i>D. tenuicostatum chilense</i> Zone <i>Dactylioceras simplex</i> Zone	
		UPPER = DOMERIAN	<i>Pleuroceras spinatum</i>	<i>Fanninoceras</i> Zone
			<i>Amaltheus margaritatus</i>	
LOWER = CARIXIAN	<i>Prodactylioceras davoei</i>	<i>Uptonia</i> faunule		
	<i>Tragophylloceras ibex</i>			
	<i>Uptonia jamesoni</i>			
SINEMURIAN	UPPER	<i>Echioceras raricostatum</i>	<i>Miltoceras</i> faunule	
		<i>Oxynoticeras oxynotum</i>	<i>Oxynoticeras</i> faunule	
		<i>Asteroceras obtusum</i>	<i>Epophioceras</i> faunule	
	LOWER	<i>Caenisites turneri</i>		
		<i>Arnioceras semicostatum</i>		
		<i>Arietites bucklandi</i>		
HETTANGIAN		<i>Schlotheimia angulata</i>		
		<i>Alsatites liasicus</i>		
		<i>Psiloceras planorbis</i>		

Table 1. Early Jurassic ammonoid assemblages from Argentina compared to standard European chronozones (simplified from RICCARDI 1984).



LOCATION MAP

0 50 100 km

FOSSILIFEROUS LOCALITIES

- A-1 : Quebrada Honda
- A-2 : Arroyo La Laguna
- B-1 : Puesto Araya
- B-2 : Cerro La Brea
- B-3 : Arroyo La Manga
- B-4 : Portezuelo Ancho
- B-5 : Arroyo del Portezuelo Ancho
- B-6 : Rio Salado
- B-7 : Arroyo Santa Elena
- B-8 : Arroyo Serrucho
- B-9 : Cerro Puchenque
- B-10 : El Infiernillo
- B-11 : Cerro Tricolor
- B-12 : Arroyo Poti Malal
- B-13 : Arroyo Chacayco
- C-1 : Cordillera del Viento
- C-2 : Arroyo Lista Blanca
- C-3 : Arroyo Chacay Melehue
- C-4 : Arroyo Ñiraico
- C-5 : Arroyos del Gringo - Los Toldos
- C-6 : Arroyo Pichi Picún Leufú
- C-7 : Vuta Picún Leufú
- C-8 : Arroyo Puruvé Pehuén
- C-9 : Arroyo Lonqueo
- C-10 : Espinazo del Zorro
- C-11 : Arroyo Ltao Ltao
- C-12 : Mallín de la Piedra
- C-13 : Rahue - Aluminé
- C-14 : Cerro Granito
- C-15 : Arroyo Lapa
- C-16 : Estancia Charahuilla
- C-17 : Cerro Keli-Mahuida
- C-18 : Los Molles
- C-19 : Puente Picún Leufú
- C-20 : Arroyo Ñireco
- D-1 : South of Estancia Santa Isabel
- D-2 : Carrán Curá
- D-3 : Salitral Grande
- D-4 : Between Ayo. Los Chilenos -
and Ayo. Los Pantanos
- D-5 : North of Sañicó
- D-6 : NW of Puesto Manqueú
- D-7 : Subida a Sañicó
- D-8 : Cerro Grande
- D-9 : SW of School N° 27
- D-10 : Cerro Corona
- D-11 : Cerro Mesa
- D-12 : Cerro del Vasco
- D-13 : Cañadón La Pintada
- D-14 : Between Co. del Vasco - Co. Roth
- D-15 : South of Cerro Roth
- D-16 : Cerro Roth
- D-17 : Cañadón Los Chilenos

Text-fig. 1.
Index map of the
region investigated
in western Argentina.

A summary of some of the sections measured during field work for this monograph was given in DAMBORENEA (1987), as well as the exact location of each fossiliferous bed within the stratigraphical sections and their precise geographical location (DAMBORENEA 1987, text-fig. 2 to 5). A generalized locality map is provided here (text-fig. 1). Each fossiliferous locality is given a letter-number symbol that is used throughout the text.

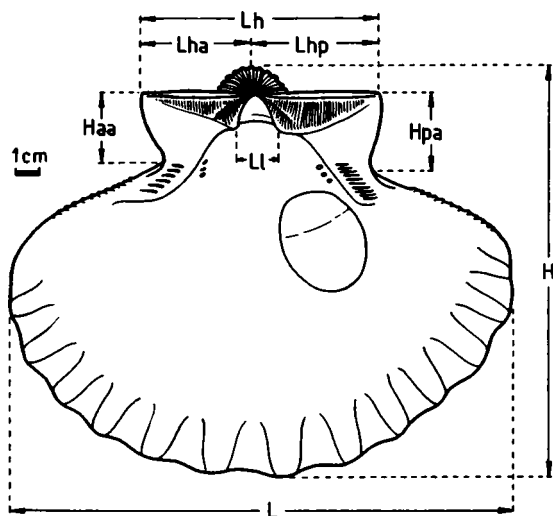
The morphological terms used in this work are those listed and defined by COX et al. (1969) and by WALLER (1984) for pectinaceans. Measurements (see text-fig. 2) were made using either a pair of vernier calipers (accurate to 0.1 mm) or, on small specimens, an eye-piece micrometer (accurate to 0.01 mm). In order to facilitate comparisons, this procedure is indicated in the tables, as well as the mode of preservation of each measured specimen (S = shell present; IM = internal, EM = external, or CM = composite moulds) and the nature of the material (LV = left, RV = right, or BV = both valves). Measurements are recorded in mm. In addition to the numerical data, scatter diagrams have been plotted for certain species.

Other abbreviations used throughout the text are as follows: L = length; H = height; W = width or inflation of single valves; 2W = width or inflation of both valves together; Lh = length of the hinge-line; Lha = length of the anterior portion of hinge-line; Lhp = length of posterior portion of hinge-line; Ll = length of ligamental area; Al = anterior length; Lb = length of the byssal gape; DL = length of the dorsal margin of the shell; Ud = distance between the umbones of both valves; Hu = height of the shell along a line that passes through the umbones; Wl = width of the hinge-platform just below the umbones; AA = anterior adductor muscle scar; PA = posterior adductor muscle scar.

Angular measurements are accurate to the nearest degree ($^{\circ}$): α = angle between the dorsal and anterior margins of the shell; β = angle between the dorsal and posterior margins; γ = angle between the hinge-line and a line from the umbones to the postero-ventral corner of the shell; ϵ = umbonal angle in pectinaceans. Other angular measurements used in special cases are explained in the text.

Shell size is said to be small, medium or large as compared with other members of the same genus or family.

The synonymy lists were prepared according to the indications given by MATTHEWS (1973) to indicate the degree of confidence in allocation of each entry.



Text-fig. 2. Schematic inner view of a right valve of *Weyla alata angustecostata* (Philippi), DNGM 12463 (= MLP 19076), Sierra de Agnia, Chubut province, BARRENECHE's collection, Toarcian (?), showing the measurements used throughout this paper. For abbreviations see text (Introduction).

Repositories

The specimens studied are deposited in the following collections under the catalogue numbers listed in the text and figure captions:

BMNH = British Museum (Natural History), Cromwell Road, London SW7 5BD, Great Britain.

DNGM = Servicio Geológico Nacional de Argentina, Avenida Santa Fe 1548, 1060 Buenos Aires, Argentina.

FCENBA = Facultad de Ciencias Exactas y Naturales (Departamento de Geología), Universidad de Buenos Aires, Ciudad Universitaria, Pabellón 2, 1428 Buenos Aires, Argentina.

MLP = Museo de Ciencias Naturales de La Plata (División Paleozoología Invertebrados), Paseo del Bosque, 1900 La Plata, Argentina.

- NHMB — Naturhistorisches Museum Basel, CH-4051 Basel, Augustinergasse 2, Switzerland.
SGO-PI — Museo Nacional de Historia Natural, Santiago de Chile, Chile.
SMNHL — Staatliches Museum für Naturkunde, Zweigstelle, Arsenalplatz 3, Ludwigsburg, Germany.
USNM — United States National Museum of Natural History, Washington, D. C. 20560, United States.

The numbers in brackets that are given after catalogue numbers represent field sample numbers. Their location in the stratigraphical sections is given in text-fig. 2 to 5 of the first part of this monograph (DAMBORENEA 1987).

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Dr. A. C. RICCARDI, La Plata Natural Sciences Museum, introduced the author to the study of Mesozoic bivalves and ever since contributed with his knowledge and experience on Jurassic mollusks and stratigraphy. He also gave advice and critical comments on the manuscript. Dr. D. V. AGER, University College of Swansea, helped in many ways with bibliography, reference material, field excursions, research facilities and friendly hospitality during an overseas stay in Wales (1975–1978), and more recently contributed with valuable suggestions and idiomatic improvement of the text. Dr. M. O. MANCEÑIDO, La Plata Natural Sciences Museum, provided invaluable help in all stages of the research and preparation of the manuscript. They are all warmly acknowledged.

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Systematic Descriptions

Order Pterioida NEWELL 1965

Suborder Pteriina NEWELL 1965

Superfamily Pteriacea GRAY 1847 (1820)

The early Jurassic Argentine pteriaceans are diverse, but nevertheless they have never received much attention from former authors. Eleven species are described here, belonging to five different families. From the palaeogeographic point of view the presence of *Pteroperna*, *Aguilerella*, *Bakevella*, *Gervillia* (*Cultriopsis*), *Gervillella*, *Parainoceramus* and *Gervilleioperna*, some of them only mentioned in general reports before (DAMBORENEA et al. 1975; CAMACHO & RICCARDI 1978), is quite important. The material here referred to *Pulvinites* is certainly of special interest, since it considerably extends the stratigraphical range of the Pulvinitidae, up to now only known since the Bathonian.

Pteriacea gen. et sp. indet.

Plate 1, fig. 11

v. 1982 Pteriacea gen. et sp. indet. — DAMBORENEA, p. 148–149; lám. 59, fig. 1.

Material: An internal mould of a left valve from the Toarcian of Cerro Tricolor (B.11), Mendoza province, author's collection: MLP 16369 (M 806) and one left valve and an internal mould of a left valve from early Toarcian beds of Arroyo Ñiraico (C.4), northern Neuquén province: MLP 15547, GULISANO's collection.

Description: Small pteriform shell, left valve inflated, right valve unknown. The shell is thin. The dorsal margin is long and straight, the posterior margin is concave and the ventral margin is evenly convex. The anterior

margin is straight to slightly concave. The shell has a well developed anterior auricle and a long and pointed posterior wing that merges into the body of the shell without any interruption. The maximum shell length does not correspond to the dorsal margin, because the postero-ventral corner of the shell extends backwards beyond the end of the posterior wing. The umbo is wide and prosogyrous and is very anteriorly placed. A low carina extends from the beak to the postero-ventral corner of the shell, which is thicker along it.

The commissure plane seems to be slightly twisted, with an anticlockwise torsion of a few degrees in posterior view. There is shell thickening just in front of the umbones. The internal margin of the shell is smooth. The outer surface of the shell is smooth, only irregularly spaced growth lines can be seen on it. Hinge, ligamental area and muscle scars are unknown.

Measurements:

Specimen	Material	L (mm)	H (mm)	W (mm)	DI (mm)
MLP 15547-a	LV	21.95	16.40	5.25	19.80
MLP 15547-b	LV	29.45	20.05	5.10	-

Affinities: The inflated twisted shell of these specimens differentiate them from *Pteroperna* sp. described below, from the Pliensbachian of Argentina.

These specimens differ from *Gervillaria* ? *pallas* (LEANZA) from the Pliensbachian to (?) early Toarcian of Argentina by the lack of a double-ridged umbonal carina.

ESCOBAR (1980: 43–46) described a couple of species from the Hettangian and Sinemurian of Curepto, Chile and referred them to *Gervillia* sp. A and *G.* sp. B. Both of them are similar to the material described here in general shell outline, though the Chilean specimens are smaller and have a well-developed anterior auricle.

Remarks: The systematic position of these specimens is uncertain since the hinge and the ligamental area are unknown. They can even be young specimens of one of the bakevellid species described, such as *Gervillaria* ? *pallas* (LEANZA), but the right valve, which is necessary to assure the relationships, is unknown.

Family Pteriidae GRAY 1847 (1820)

Genus *Pteroperna* MORRIS & LYCETT 1853

(ex LYCETT 1850, nom. nud.)

Type species: *Gervillia costatula* J. A. EUDES-DESLONGCHAMPS, 1824, from the Bathonian of Europe, northern Africa, Israel and Malagasy, by original designation (MORRIS & LYCETT 1853: 17).

Pteroperna is a widely spread genus that ranges from late Triassic to late Jurassic times and which shows its greatest diversity during the Middle Jurassic. COX (1940) made a detailed discussion of the diagnostic characters of the genus and correctly observed that the ligament is external and not internal as originally described by MORRIS & LYCETT (1853).

Pteroperna sp.

Plate 2, fig. 9

Material: This species was found in (early ?) Pliensbachian beds of Arroyo Serrucho (B.8), Mendoza province, where the author collected two right valves, three internal moulds of right valves and five left valves: MLP 19637, 19651, 19660 and 19661 (M 1313, 1321 and 1324).

Description: Medium-sized pteriiform shell, very inequilateral and oblique oval. Subequivalve, left valve slightly more inflated than the right one. The shell is thin. The dorsal margin is long and straight, the posterior margin is concave and the ventral margin is evenly convex. The anterior margin is straight to slightly concave. The shell has a well-developed, acute, anterior auricle and a long and pointed posterior wing that merges into the body of the shell. The maximum shell length does not correspond to the dorsal margin since the postero-ventral corner of the shell extends backwards beyond the end of the posterior wing. The umbones are wide and low and anteriorly placed. There is no umbonal carina. There is a narrow byssal gape below the anterior auricle.

The outer surface of the shell is covered with commarginal accentuations of the growth-stages, about 15 per cm and regularly spaced near the umbones but more irregularly arranged and distant to each other in the posterior portion of the shell.

The right valve hinge is made up of an anterior vertically crenulated portion and two parallel ridges that extend along the posterior wing. The left valve hinge is unknown. The ligament is external. The posterior adductor muscle scar is only very faint and appears to be oval in outline. There is also a small rounded muscle scar just in front of the umbones that may correspond to a much-reduced anterior adductor.

Measurements:

Specimen	Material	L (mm)	H (mm)	W (mm)	DI (mm)	L/H
MLP 19637-a	RV IM	33.70	32.15	2.70	32.75	1.04
MLP 19637-b	LV EM	(26.30)	(28.65)	2.50	-	-
MLP 19637-c	RV EM	(28.00)	21.10	2.55	-	-
MLP 19637-k	RV IM	(26.00)	19.05	2.00	26.00	-
MLP 19637-h	LV IM	40.95	34.05	-	35.60	1.20
MLP 19651, pl. 2, fig. 9	RV IM	38.30	25.35	2.25	34.60	1.51

Affinities: The shell outline of *Pteroperma* sp. is similar to that of *P. emarginata* MORRIS & LYCETT (1853: 19-20, pl. 2, fig. 10; COX & ARKELL 1948: 8), from the British Bathonian, but this species has a more oblique shell and bears stronger longitudinal ridges on the posterior wing. *P. polyodon* (BUVIGNIER) from the Oxfordian of England and France has a larger shell and an acute postero-ventral angle, but is otherwise comparable to *P. sp.* (see ARKELL 1933: 201-202, pl. 25, fig. 6-10). The specimens from the middle Jurassic of China described by ZHANG et al. (1979: 293, pl. 86, fig. 3, 4, 9, pl. 92, fig. 7) as *P. decorata* REED have a similar outline, but the anterior auricle is smaller and the external posterior ridges on the posterior wing are more conspicuous.

The type species, *P. costatula* (J. A. EUDES-DESLONGCHAMPS), from the Bathonian of Europe, northern Africa, Israel and Malagasy (MORRIS & LYCETT 1853: 18, pl. 2, fig. 8, 11, 13; de LORIOI 1883: 64-65, pl. 11, fig. 1; NEWTON 1889: 335; 1895: 81-82, pl. 3, fig. 1; COSSMANN 1900: 176-177; COX & ARKELL 1948: 8; FRENEIX 1965: 8-9, pl. 1, fig. 6-8; FISCHER 1969: 86, pl. 9, fig. 13; PARNES 1981: 30-31, pl. 3, fig. 43) differs from the Argentine species by its longer posterior wing and by the presence of radial ribs on the left valves of young specimens.

P. plana MORRIS & LYCETT (1853: 128, pl. 14, fig. 4; COSSMANN 1924: 34, pl. 4, fig. 17; CASTELL 1962, pl. 14, fig. 2) from the Bajocian of Europe, *P. cf. plana* from the Tithonian of Bavaria (YAMANI 1975: 51, Taf. 2, fig. 8, Abb. 12) and *P. sp. indet.* (Cox 1940: 88-89, pl. 6, fig. 1) from the Oxfordian of Cutch, all have a very long and pointed posterior wing which is delimited by a straight umbonal carina and bears four parallel strong ridges, thus differing from *P. sp.* described here.

The lack of radial ornamentation differentiates the Argentine species from *P. asinusoides* FISCHER (1969: 86-87, pl. 9, fig. 15-16) from the Bathonian of France and *P. reticularis* PARNES (1980: 108-111, pl. 1, fig. 18-23) from the earliest Jurassic of Israel. On the other hand, *P. pygmaea* (DUNKER) from the Oxfordian to Callovian of Europe (DUFF 1978: 46-48, pl. 3, fig. 1-5, text-fig. 13, 14) and *P. bajociensis* GREPPIN (1899: 108-109, pl. 9, fig. 7), from the Middle Jurassic of continental Europe, are smaller and more oblique than the species here described.

The early Jurassic species of *Pteroperma* are few and imperfectly known and they all differ from *P. sp.* *P. deshayesi* (TERQUEM) from the Hettangian and Sinemurian of France and Italy (TERQUEM 1855: 315, pl. 21, fig. 13; SIMONELLI 1884: 124-125, tav. 19, fig. 22; ALLASINAZ 1962: 341, tav. 25, fig. 1-2; GAETANI 1970: 397-398, tav. 33, fig. 2; LENTINI 1974: 20, tav. 13, fig. 7) is a smaller shell with a more pointed and longer posterior wing. *P. ? camoensi* BÖHM (1901: 230, Taf. 9, fig. 2) from the early Jurassic of Portugal is only known by incomplete specimens, which show a hinge with oblique anterior teeth stronger and different to those of the Argentine material.

“*Avicula*” *longiaxis* BUCKMAN (1845: 97, pl. 10, fig. 2) from the early Jurassic of Cheltenham, has a longer and narrower posterior wing and a very small anterior auricle. *Pteria carixensis* Cox (1928: 241-242, pl. 18, fig. 6) from the lower Pliensbachian of England shows a similar ornamentation pattern but is less oblique, its anterior auricle and internal characters remain unknown. Some Triassic species referred to *Pteria*, such as *Pteria sturi* (BITTNER) and *Pteria cortinensis* (BITTNER) as described by ALLASINAZ (1966: 651-653, tav. 42, fig. 4-9) could belong to *Pteroperma* instead. They can be distinguished from the Argentine material by their more oblique shell with a longer and more pointed posterior wing.

Autecology: This species is homoeomorphic with some species of *Pteria* and was a byssate (probably epibyssate) bivalve. *Pteria hirundo* (LIN.) lives on mud, sandy mud or coarser sediments up to a considerable depth in the northeastern Atlantic and Mediterranean (TEBBLE 1966), whilst other species, such as *P. colymbus* (RÖDING) attach to alcyonarians (STANLEY 1970: 136). A similar mode of life was assumed by DUFF (1978) for *Pteroperna*, although he did not observe byssal gape on his specimens. The Argentine material show a clear byssal gape and the specimens were all found in clusters with a high concentration of individuals, some of them preserved with both valves, thus suggesting a pendent epifaunal life-habit.

Family Bakevellidae KING 1850 (see COX 1954)

The diversification of Argentine early Jurassic bakevellids is similar to other Jurassic faunas, especially European ones. Some of the Argentine taxa could be of some interest in the analysis of the phylogeny of this family, since they have intermediate characters between genera otherwise well delimited from each other. They were here referred to genus-group taxa using an open nomenclature, as a detailed discussion of their phylogenetic affinities is beyond the scope of this monograph. This situation seems to be similar in other circumpacific localities, as hinted by HAYAMI (1957a and 1957b). The phylogeny of the Bakevellidae was analyzed several times (see HAYAMI 1957b, FRENEIX 1965) and some aspects will be considered here in each generic discussion.

Genus *Aguilerella* CHAVAN 1951

Type species: *Perna kobyi* DE LORIO 1901, from the Oxfordian of Switzerland, original designation.

Synonyms: *Isognomon* (*Dentoperna*) OKUNEVA 1960 (type species: *Perna khudyaevi* KRIMHOLTZ 1938)

? *Plagia* R. PHILIPPI 1899 (type species: *Plagia andina* R. PHILIPPI 1899) non MEIGEN 1838, Diptera.

The generic name *Aguilerella* was proposed by CHAVAN (1951: 211) for a group of pteriaceans characterized by a special kind of hinge (see other characters on table 2). This name was later used with two different meanings by Russian (ZAKHAROV 1965; POLUBOTKO 1968b) and other European writers (especially COX in COX et al. 1969).

ZAKHAROV (1965) included in the synonymy of this genus *Cuneigervillia* COX 1954; *Isognomon* (*Dentoperna*) OKUNEVA 1960 and *Lenella* KOSHELKINA 1963, using *Aguilerella* in a wide sense, comprising about 14 species and ranging from the late Triassic (?) and early Jurassic to Neocomian. Some of these species had been considered by COX (1954) as belonging to a different genus, which he called *Cuneigervillia* (see its characters, in COX's original sense, on table 2). In 1954 COX included the genus *Edentula* WAAGEN 1907 non NITZCH 1820 in the synonymy of *Cuneigervillia*, but later (in COX et al. 1969) considered it to be an isognomonid (*Waagenoperna* TOKUYAMA 1959).

As there are some characters differentiating these three genera (see table 2) the arrangement proposed by COX (in COX et al. 1969) is followed here. *Aguilerella* is then restricted to the Hettangian (?), Pliensbachian to Oxfordian and is represented by the following species: *A. kedonensis* POLUBOTKO, late Pliensbachian of USSR (POLUBOTKO 1968b); *A. neuquensis* n. sp., Pliensbachian of Argentina; *A. khudyaevi* (KRIMHOLTZ), *A. zabaicalica* (OKUNEVA) and *A. kulindensis* (OKUNEVA) from the Toarcian-Aalenian (?) of USSR (ZAKHAROV 1965), *A. kobyi* (de LORIO 1901) from the Oxfordian of France (de LORIO 1901) and *A. sp.* from the Hettangian of Hunan, China (see CHEN & LIU 1981).

Some other small mytiliform bakevellids may also belong here, but their hinge characters are unknown. This would considerably widen the known geographical range of this genus (see under discussion of the species below). For instance HAYAMI (1975: 46-47) included *Cuneigervillia quadrata* NAKAZAWA and MURATA, from the Japanese Neocomian, in *Aguilerella*.

Aguilerella neuquensis n. sp.

Plate 2, fig. 6-8; text-fig. 3

v. 1975 *Aguilerella* - DAMBORENEA et al., cuadro 1, 10.

! v. 1982 *Aguilerella neuquensis* n. sp. - DAMBORENEA, p. 151-155; lám. 41, fig. 1-4; lám. 59, fig. 2-5 (unavailable name).

Derivation of name: From the province of Neuquén, Argentina, where all the material studied here was found.

Material: This species was only found in late Pliensbachian beds of southern Neuquén province (hill south of Cerro Roth, locality D-15). The material consists of four bivalved specimens preserved as internal moulds, five internal moulds of left valves and one of right valve, all from author's collection. **Holotype:** MLP 16372-a, an internal mould of a left valve, figured in pl. 2, fig. 6. **Paratypes:** MLP 16370 to 16374 (M 94 and 95).

Table 2. Characters of *Aguilerella*, *Cuneigervillia* and *Lenella* in the sense used in this paper

Character	<i>Aguilerella</i> CHAVAN	<i>Cuneigervillia</i> COX	<i>Lenella</i> KOSHELKINA
Outline	Rhomboidal, mytiliform	Rhomboidal or trapezoidal, oblique, elongate	Mytiliform
Valves	Subequivalve	Subequivalve	Equivalve
Shell inflation	low	low	
Umbones	Subterminal, not prominent	Terminal to subterminal, acute	
Anterior teeth	One or more, short, oblique	Young stages with two anterior teeth and long posterior teeth, that become obsolete in adult specimens	
Posterior teeth	Narrow, long and oblique, one on LV, one or two on RV		
Posterior wing	Absent, posterior margin straight to convex	Not always clearly delimited from shell, obtuse, posterior margin concave	Obtuse, flat
Anterior auricle	Absent or small	Absent or small	Well-defined, acute, with byssal sinus below it
Length/Height ratio	H > L	L > H	
Ligament	Multivincular, few separated and well-defined pits	Multivincular	Multivincular, few, separated and well-defined pits
Shell thickness			Moderately thick
External surface	Smooth		Concentric folds and a postero-ventral sinus
Anterior adductor	Unknown		Small, present only in young specimens
Pallial line	Discontinuous		Discontinuous
Type species	<i>Perna kobyi</i> DE LORIOI	<i>Gervillia hagenowi</i> DUM.	<i>Lenella tiungensis</i> KOSHELKINA
Stratigraphical range	Hettangian ?, Pliensbachian to Oxfordian	Earliest Jurassic to Cretaceous	Early Jurassic
Geographical range	Europe, Asia, north Africa ?, South America	Europe, North Africa	Eastern Siberia

Diagnosis: Compressed shell, subequivalve, mytiliform in outline, with a strong and sharp umbonal carina and without well-defined auricles. Hinge with oblique anterior teeth, one on the left valve and one (or two) on the right valve and long and oblique posterior teeth, one on each valve. Multivincular ligament with few pits. Posterior adductor muscle scar tear-shaped, dorsoventrally elongated. Pallial line discontinuous, formed by a row of pits.

Description: Shell of medium size, subequivalve, thin and laterally compressed, mytiliform-rhomboidal in outline, length almost equal to height. Length/height ratio varies between 0.90 and 1.07. The dorsal margin is straight to slightly convex. It meets the anterior margin at an acute angle and the posterior margin at a slightly obtuse angle. The posterior margin is straight to slightly convex and merges into an evenly convex ventral margin. The anterior margin is sigmoidal, concave dorsally, then straight and then ventrally convex. The concave portion probably corresponds to the place where the byssus emerged from the shell. The umbones appearance and position are unknown, as all the available material is preserved as internal moulds, nevertheless it could be observed that the beaks were terminal or almost terminal.

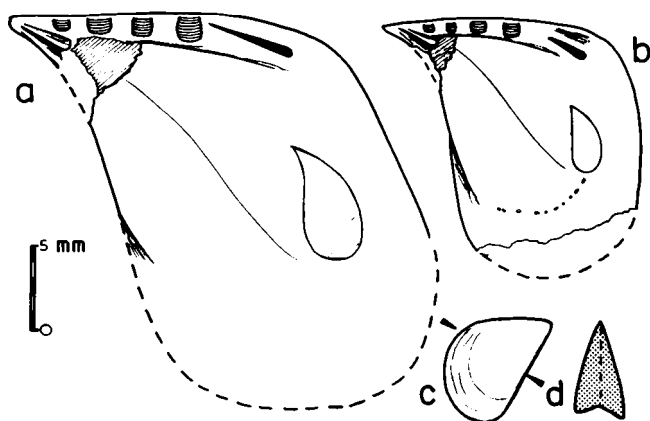
The shell surface is divided into two areas by a sharp and straight umbonal carina that runs from the umbones to the antero-ventral corner of the shell. In internal moulds the area anterior to this carina has a concave surface,

whilst the posterior portion of the shell is slightly convex. The shell has a triangular profile in anterior view (see text-fig. 3d).

The ligament is multivincular, in the best preserved specimens four ligamental pits were observed, separated by spaces of equal width. The left valve has a short tooth, oblique to the dorsal margin, that extends from almost the anterior end to below the first ligamental pit (see text-fig. 3a). The tooth is bordered by a couple of elongated sockets, the upper one deeper. Below the lower socket there is a weak ridge that could not be regarded as a second tooth. The same left valve also has a strong and oblique posterior tooth that extends behind the last ligamental pit and which does not reach the posterior margin.

In the few right valves the anterior region of the shell is not preserved and therefore that part of the hinge is unknown. The two sockets on the left valve suggest that the right valve had two oblique anterior teeth, of which the upper one was stronger. The right valve has one strong posterior tooth and a socket above it to receive the left posterior tooth.

The muscle scars are quite clear on all internal moulds. The posterior adductor muscle scar is tear-shaped and dorso-ventrally elongated. It stands on a low platform that extends from the beaks. The pallial line is discontinuous and formed by a series of small pits parallel to the ventral margin, as in some extant pteriids. No specimen shows traces of an anterior adductor muscle scar and this was probably a monomyarian (or at least highly heteromyarian) shell. The inner margin of the shell is smooth and the external characters are unknown, though some small fragments of external moulds indicate a smooth surface.



Text-fig. 3. *Aguilierella neuquensis* n. sp. Hill south of Cerro Roth, Pliensbachian. a-b: internal moulds of left valves with broken umbonal regions. a: MLP 16372-a, holotype; b: MLP 16372-b, paratype; c-d: exterior view and section of right valve, MLP 16370-ab, paratype. Scale refers to figs. a-b only.

Measurements:

Specimen	Material	L (mm)	H (mm)	W (mm)	L/H	DI (mm)	L PA (mm)	H PA (mm)
MLP 16370, paratype	LV IM	25.30	26.85	4.65	0.94	18.50	5.50	8.65
MLP 16371-d, paratype	RV IM	20.90	23.00	4.85	0.90	15.10	4.15	7.50
MLP 16371-f, paratype	LV IM	23.25	24.80	4.25	0.93	17.60	-	-
MLP 16372-a, holotype	LV IM	22.50	21.60	-	1.04	17.95	5.20	7.80
MLP 16372-b, paratype	LV IM	13.35	13.00	2.40	1.02	12.50	2.25	4.30
MLP 16374, paratype	RV IM	22.45	21.35	6.00	1.05	18.50	4.80	7.80

Affinities: The type species of *Aguilierella*, *A. kobyi* (DE LORIO) is known from the middle Oxfordian of France (DE LORIO 1897 as *Perna mytiloides*; DE LORIO 1901: 99-100, pl. 7, fig. 5-6) and has a general outline very similar to that of *A. neuquensis*, but it is larger, has two posterior teeth on the right valve and a larger number of ligamental pits.

A. kedonensis POLUBOTKO (1968 b: 59, tabl. 23, fig. 1-4), from the late Pliensbachian of the USSR, is also similar but of larger size. *A. sp.* from the Hettangian of Hunan, China (CHEN & LIU 1981) has an elongated posterior auricle and is more ortocline than *A. neuquensis*.

The material described by DESIO et al. (1960: 92-93) from the Bathonian of Lybia, identified as *Isognomon jefrensis* DESIO et al. and *I. sp.*, probably belongs to *Aguilierella* if the structures that can be seen on the figures (pl. 11, fig. 1-5) are teeth, despite the author's mention of the lack of teeth. Anyway the African specimens can be

compared with the species under consideration, but they differ in a blunter anterior end, a smaller shell and a lower umbonal carina. *I. jefrensis* DESIO et al. was nevertheless included into *Inoceramus (Mytiloperna)* by FRENEIX (1965: 20).

The specimen figured by R. PHILIPPI (1899, lám. 22, fig. 4) and named *Plagia andina* has a certain resemblance to *A. neuquensis* in general shape, but it is more elongated and according to PHILIPPI (1899: 42) lacks anterior teeth. COX (in COX et al. 1969) considered *Plagia* PHILIPPI 1899 (non MEIGEN 1838) as a potential synonym of *Bakevella* KING, but the possibility of an identity with *Aguilerella* cannot be dismissed.

The species nowadays included in *Cuneigervillia* COX generally have a more elongated shell and a well-defined posterior auricle, with a concave posterior margin.

Remarks: The hinge morphology of this new species is, together with that of the type species, one of the best known for this genus. The extremely well-preserved internal moulds provide additional new data on the muscular characters of these bakevellids.

Autecology: STANLEY (1972) considered *Aguilerella* as one of the few epibyssate bakevellids. The following morphological characters strongly uphold this idea: triangular shape, mytiliform shell, flat ventral region, lack of anterior lobe and terminal umbones. Nevertheless, FÜRŠICH (1980: 296; 1981, p. 213) found the Portuguese Portlandian species *Isognomon (Mytiloperna) lusitanicum* (SHARPE) in vertical position with the umbones directed downwards. Despite this species has the same general characters already mentioned, he suggested a semi-infaunal mode of life. FÜRŠICH also warned about the dangers of employing functional morphology alone to interpret the mode of life of extinct species. His observations of *I. lusitanicum* in vertical position are not definite, however, since they all correspond to crowded populations and, therefore, the position could be a response to close packing instead of a semi-infaunal habit (see STANLEY 1970, pl. 8, fig. 3 and 6; and also compare with *Mytilus* and *Brachydontes* crowded populations on sandy or rocky substrates). FÜRŠICH's hypothesis needs confirmation from observation of isolated specimens in the same "life" position.

The Piedra Pintada specimens are mostly isolated valves, but some bivalved specimens have their valves open, only joined at the hinge line. The fact that this species was up to now found at only one locality and in one particular bed suggests that it probably lived in clusters. DE LORIOI (1901: 100) also noted the difficulty of obtaining complete specimens of *A. kobyi* due to the brittleness of the shell.

Genus *Bakevella* KING 1848

Type species: *Avicula antiqua* MÜNSTER in GOLDFUSS 1836 (non DEFRANCE 1816) (= *Avicula binneyi* BROWN 1841), from the late Permian of Great Britain, original designation.

Bakevella was defined by KING and later emended by COX (1940). It includes pteriaceans with multivincular ligament, pteriform outline and a hinge with anterior and posterior teeth. An interesting discussion on the affinities between this genus and other pteriaceans was provided by COX (1940: 105–108). This author considered that *Bakevella* extended from the late Palaeozoic to the Cretaceous. During the Triassic and Jurassic the Bakevellidae exhibit a great variability of hinge characters; this fact has complicated the taxonomy of this group, with the naming of a lot of generic or subgeneric taxa not always clearly defined.

There is a group of bakevellid species, to which the taxon here described belongs, whose correct systematic position requires a careful revision of the type species of several nominal genera. This group can be characterized by a medium to large pteriform shell, subequivalve, very anisomyarian or monomyarian, with a multivincular ligament made up of three to nine irregular ligamental pits separated by spaces wider than the pits and a hinge with a few anterior teeth and one or two posterior teeth, with the spaces between these two series of teeth either smooth or with transversal crenulations over all the interspace or only on the anterior portion.

Although this group of bakevellid species, that ranges from the Triassic to the Cretaceous, was included in *Bakevella* by COX (1940) and HAYAMI (1957a), as early as 1891 FRECH (1902) set apart a subgenus that he called *Gervilleia (Odontoperna)*, with *Perna bouei* HAUER as type species. *P. bouei* could be included in the group here discussed if it is considered, following COX (in COX et al. 1969), that posterior teeth are present besides the anterior ones originally described by FRECH. In 1922 GILLET separated *Gervilleia (Pseudogervilleia)* as a new subgenus, typified by the Cretaceous species *P. episcopalis* GILLET, with two subvertical cardinal and two long posterior teeth (see GILLET 1922). She also included the Triassic species *G. costata* (SCHLOTH.) in this subgenus. COX (1940) also recognized this group of species but preferred to include them in *Bakevella* at the generic level.

TOKUYAMA (1959, see HAYAMI 1975) regarded the species with anterior pseudotoxodont teeth that diverge from the umbones as a separate genus, which he called *Bakevelloides*, with the Triassic *Gervilleia hekiensis* KOBAYASHI and

ICHIKAWA as the type species. The same year NAKAZAWA, working on Permian and Triassic faunas, segregated the Mesozoic "*Bakevellia*", characterized by a reduction or even absence of the anterior adductor muscle and distinguished two subgenera (see ALLASINAZ 1964 and HAYAMI 1975): *Neobakevellia* (type species *Mytulites costatus* SCHL.) and *Maizuria* (type species *B. (M.) kambei* NAKAZAWA), restricting the scope of the nominotypic subgenus to dimyarian Palaeozoic species. This criterion was agreed by LOGAN (1967) and both Triassic subgenera were used by BYCHKOV et al. (1976), among others.

ALLASINAZ (1964) figured well-preserved hinges of some species from the Italian Triassic that show transverse crenulations on the central portion of the hinge and referred them to *B. (Neobakevellia)*. This author also discussed the systematic relationships of already proposed taxa and considered that *Bakevellia* should include the following re-defined subgenera: *Bakevellia* s. s. only known from Permian strata, *Neobakevellia* and *Maizuria*, with Triassic species, and *Pseudogervilleia*, from the Jurassic and Cretaceous. He also regarded *Odontoperna* as a synonym of *Bakevellia* (without indicating under which subgenus), yet two years later (ALLASINAZ, 1966) he included the type species of *Odontoperna* within *Bakevellia (Neobakevellia)*, but failed to realize that in such case FRECH's name becomes the senior synonym. SKWARKO (1967) included Triassic species with numerous divergent teeth in *B. (Maizuria)*.

The situation was complicated further with publication of the Treatise on Invertebrate Paleontology (COX et al. 1969), where *Odontoperna*, *Pseudogervilleia* and *Maizuria* are treated as synonyms of *Bakevellia* s. s., whilst *Bakevelloides* is considered a subgenus of *Bakevellia* with *Neobakevellia* as a synonym. HAYAMI (1975) points out that this systematization is quite inconsistent, especially concerning *Neobakevellia* and *Maizuria*. He accepted that *Bakevellia* could include the following subgenera: *Neobakevellia* (with *Maizuria* as a synonym), *Bakevelloides* and *Yoshimopsis* OHTA. The inconsistency in the Treatise treatment is also shown by the fact that CREDNER's (1851) fig. 3 of a specimen referred to *G. costata* (SCHLOTH.), type species of *Neobakevellia*, is reproduced there (COX et al. 1969, p. N306, fig. C40, 1e) to illustrate the inner view of *Bakevellia* s. s.

FARSAN (1972) described several species from the Triassic of Afghanistan, but he preferred to subdivide the group in several subgenera: *Bakevellia (Neobakevellia)*, *B. (Costibakevellia)* FARSAN, *B. (Maizuria)* and *B. (Integribaldiella)* FARSAN, which are differentiated by minor differences in size, ligamental area and ornamentation. The sympatric group of species described by FARSAN (1972) can be referred to a single subgenus of *Bakevellia* without difficulty.

Most contemporaneous authors (ALLASINAZ 1964; FARSAN 1972; HAYAMI 1975) faced the impossibility of clarifying the affinities between *Neobakevellia*, *Odontoperna* and *Pseudogervilleia* and thus preferred to use the subgeneric name *Neobakevellia* to include species that are similar to the taxon here described. This criterion is also followed here and an open nomenclature is used in the tentative subgeneric status of the species to be described next.

? Subgenus *Neobakevellia* NAKAZAWA 1959

Type species: *Mytulites costatus* SCHLOTHEIM 1820, from the Triassic of Europe, by original designation.

Synonyms: ? *Odontoperna* FRECH 1891 (type species: *Perna Bouéi* HAUER 1857).

? *Pseudogervilleia* GILLET 1922 (type species: *Gervilleia (Pseudo-Gervilleia) episcopalis* GILLET 1922).

? *Maizuria* NAKAZAWA 1959 (type species: *Bakevellia (Maizuria) kambei* NAKAZAWA 1959).

Note: In case *Perna bouei* is proved to have the same sort of hinge-pattern as *M. costatus*, the subgenus should be called *Odontoperna* on priority grounds.

Bakevellia (Neobakevellia ?) pintadae n. sp.

Plate 1, fig. 1-5; text-fig. 4

v . p 1975 *Pteroperna* - DAMBORENEA et al., cuadro 1, 09 (sample 125 only).

! . v 1982 *Bakevellia (Neobakevellia ?) pintadae* n. sp. - DAMBORENEA, p. 158-164, lám. 41, fig. 5-9; lám. 59, fig. 6-13 (unavailable name).

Derivation of name: The specific name in genitive case refers to Cañadón La Pintada, a classic Lower Jurassic locality in southern Neuquén, where all the specimens described were collected.

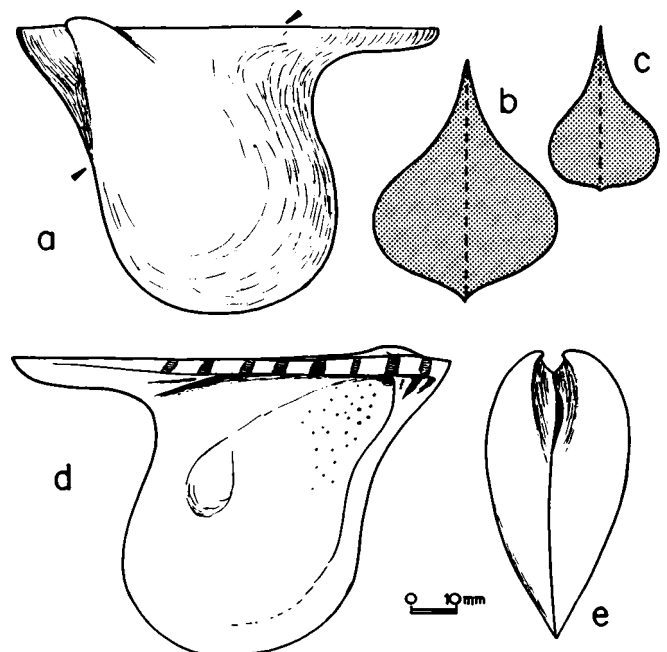
Material: All the material assigned to this species was collected by the author in the Late Pliensbachian beds of the Piedra Pintada region, southern Neuquén province, at the following localities: Cerro Roth (D.16), hill south of Cerro Roth (D.15) and Cerro Del Vasco (D.

12). The holotype is an almost complete shell with both valves mostly preserved as internal mould, from the hill south of C ero R oth, figured in pl. 1, fig. 1, MLP 16377. Paratypes: MLP 16243, 16375, 16376, 16378 to 16385 (M 100, 103, 104 and 125), four complete shells, eight left valves and two right valves, some of them preserved as internal moulds.

Diagnosis: Pteriform shells, relatively thin, almost equivalve, left valve slightly more inflated than the right. Dorsal margin almost straight corresponding to the maximum shell length. Auricles not clearly delimited from the rest of the shell surface, the anterior triangular and the posterior very long. Prosogyrate low umbones. Multivincular ligament with irregular shallow pits. Shell surface smooth, without radial ridges. Posterior adductor muscle scar only slightly impressed, subcircular in outline. Inner surface with several pits irregularly arranged in the central portion of the shell.

Description: Shell relatively thin, medium to large-sized, pteriform and with a well-developed posterior wing, almost equivalve, the left valve is slightly more convex than the right one. The dorsal margin is almost straight and corresponds to the maximum shell length; the posterior margin is strongly concave, the ventral one evenly convex, and the anterior margin is convex dorsally and ventrally, but somewhat concave in the middle section. Both auricles are very well developed, but they are not clearly separated from the main body of the shell. The anterior auricle has a triangular shape and an evenly convex surface. The anterodorsal end of the shell is pointed and below it, the anterior commissure shows a slight concavity on the left valve (see pl. 1, fig. 1 b; text-fig. 4 e) that corresponds to a narrow byssal gape. The long and thin pointed end of the posterior wing is only preserved on a few specimens and is usually indicated by the trace of the growth lines. In dorsal view the shell has a rhomboidal outline. In anterior view and in a section perpendicular to the anterior margin just below the anterior auricle, the shell is tear-shaped, ventrally expanded. The angle between the dorsal margin and the oblique length (γ) is always acute and near 50° , but varies considerably from one specimen to the other.

The umbones are small and prosogyrous, nearly level with the dorsal margin and anteriorly placed. The right umbo is less prominent than the left one. The ligamental area is flat and triangular, relatively wide in big specimens, but long and thin in young specimens. It dips about 30° outwards from the commissural plane. The ligament is multivincular and the pits are very irregular and shallow, narrower than the spaces between them. They extend through almost all the dorsal margin, at least up to the maximum concavity of the posterior margin. Some specimens show a posterior toothlike structure that is short, low and oblique to the dorsal margin. The few specimens that have the posterior wing preserved show a long internal ridge parallel to the dorsal margin on the free distal part of the wing that corresponds to an extension of the hinge margin. Just in front of the umbones and



Text-fig. 4. *Bakevellia* (*Neobakevellia* ?) *pintadae* n. sp. from Piedra Pintada region. a: reconstruction of the external view of the left valve based on MLP 16376, paratype; b: section of the same specimen; c: section of MLP 16378, paratype; d: inner view of a left valve, reconstructed from several specimens; e: MLP 16378, anterior view showing slightly inequivalve shell and slit-like byssal gape.

almost touching the dorsal margin there is a shell thickening bearing a pair of short low anterior teeth (see text-fig. 4 d). A deep commarginal groove extends from this thickening to the ventral portion of the shell. On the central portion of the shell there are numerous internal pits irregularly arranged. The posterior adductor muscle scar is only slightly impressed in the shell surface; it has a subcircular outline and is placed somewhat back of the main body of the shell. No other muscle scar is preserved.

The shell surface is smooth, except for the presence of faint growth lines irregularly spaced.

Measurements: Only the specimen marked (*) has a complete posterior wing. For all the others only the preserved length is given.

Specimen	Material	L (mm)	H (mm)	W (mm)	L/H	DI (mm)	γ
MLP 16376, paratype	LV S	62.10	66.70	19.15	0.93	—	54°
MLP 16377-ab, holotype	BV IM	52.00	48.80	25.40	1.06	—	—
MLP 16378-cd, paratype	BV S	53.85	42.90	24.95	1.25	—	—
MLP 16379-e, paratype	LV S	64.90	60.40	20.70	1.07	—	—
MLP 16379-f, paratype	LV S	32.85	32.00	6.35	1.02	—	—
MLP 16380-gh, paratype	BV IM	40.45	40.60	16.55	0.99	—	—
MLP 16379-i, paratype	LV IM	22.35	24.60	8.55	0.90	—	—
MLP 16382-a, paratype (*)	LV IM	49.75	41.55	4.15	1.19	49.75	—
MLP 16384-e, paratype	RV IM	40.35	35.10	10.55	1.14	—	—

Affinities: This species shows its greatest affinities with *Bakevellia waltoni* (LYCETT), with a group of Japanese early Jurassic species described by HAYAMI (1957a) and with some Triassic species, as is discussed below.

Bakevellia waltoni (LYCETT), from the Bathonian of Great Britain, France and Cutch, India (LYCETT 1863: 110–111, pl. 32, fig. 4; PARIS 1911a: 251, pl. 29, fig. 2a–c; ARKELL 1931a: 579, pl. 49, fig. 1–3; COX 1940: 108–111, pl. 7, fig. 1–7; COX & ARKELL 1948: 8; and FISCHER 1964: 16) has a shell outline and inflation similar to *B. pintadae* but can be distinguished by its smaller size, its wider posterior wing and its subterminal umbones.

From the Japanese Lower Jurassic, HAYAMI (1957a) described several species that he first referred to *Bakevellia* and then (HAYAMI 1975) to *B. (Neobakevellia)*. Some of them are similar to *B. pintadae*. *B. otariensis* HAYAMI (1957a: 53, pl. 3, fig. 2–5), from the Pliensbachian, is smaller, has a larger anterior auricle and a wider ligamental area. *B. cassianelloides* KOBAYASHI & HAYAMI (in HAYAMI 1957a: 57, pl. 3, fig. 7–9), also a Pliensbachian species, although having similar outline, has radial ribs and is more inflated than *B. pintadae*. *B. magnissima* HAYAMI (1957a: 57, pl. 2, fig. 6–10, pl. 3, fig. 1) from the Pliensbachian-Toarcian, has similar hinge characters but a subtriangular shape, the posterior wing is not long and the anterior auricle is almost absent. The ligamental area of the Japanese species is wider and the shell thicker than those of the Argentine species. *B. trigona* YOKOYAMA, from the Hettangian of Japan (HAYAMI 1957a, p. 51–52, pl. 2, fig. 3) has a rounded anterior end, is more inequivalve and has a subtriangular outline, with a small anterior auricle.

B. rhombica (COSSMANN 1904: 507–509, pl. 6, fig. 19–21), from the Hettangian of France, has a similar hinge but can be distinguished from *B. pintadae* by its blunter posterior wing.

From the late Triassic of Perú COX (1949: 21–22, pl. 1, fig. 6–7) described *B. douglasi*, which has smaller auricles and a similar hinge, though the anterior teeth are more forwardly placed in *B. pintadae*. Some specimens belonging to this Peruvian species had been previously compared with the type species of *Odontoperna*.

The type species of *Neobakevellia*, *B. (N.) costata* (SCHLOTHEIM), from the Triassic of Germany (CREDNER 1851, Taf. 6, Fig. 3a–b) has a smaller size and major differences in the hinge characters.

FARSAN (1972) described several *Bakevellia* species from two localities in the Middle Triassic of Afghanistan, to which *B. pintadae* can be compared. These species, though, have a more triangular outline, fewer ligamental pits and better developed posterior teeth. The anterior teeth of FARSAN's specimens dip in the opposite way to those of *B. pintadae*. FARSAN (1972) included his material in several species and in three different subgenera, in spite of the fact that the great intraspecific variability within this group of bivalves has been known since long ago and in some instances it concerns not only the general shape of the shell but also some hinge characters (see for example COX 1940: 106).

The general shell shape of *B. pintadae* is similar to that of *G. bouei* HAUER (type species of *Odontoperna*), from the Middle Triassic of Europe (FRECH 1902, fig. p. 617; TOULA 1910, fig. 3–4, p. 390–392; ALLASINAZ 1966: 653–654, tav. 42, fig. 10–11) and the anterior teeth dip in the same direction. Nevertheless the posterior teeth of this species were never illustrated, and the shell is thicker than in *B. pintadae*.

The Argentine species can be also compared to some Lower Jurassic species from Sicily referred to *Pteria* s. l. by LENTINI (1974), though the hinge and ligamental characters of these taxa are unknown. *B. pintadae* can be distinguished from *P. ? dunkeri* (TERQUEM) (LENTINI 1974: 42–43, tav. 13, fig. 8) by its more developed posterior wing, and from *P. ?* sp. (LENTINI 1974: 43, tav. 13, fig. 6) by its better defined anterior auricle.

Some Jurassic species referred to *Cuneigervillia* have superficial similarities to *B. pintadae*, but they all lack teeth in adult specimens. *C. hagenowi* (DUNKER), the type species, is known from the Hettangian of Europe and differs from *B. pintadae* by its obtuse postero-dorsal angle, by its lack of an anterior auricle and by its smaller size (see TERQUEM 1855: 316–317; QUENSTEDT 1867, Taf. 52, Fig. 29; TATE 1876; E. PHILIPPI 1897: 436, Taf. 16, Fig. 3; COSSMANN 1904: 509–510, pl. 16, fig. 25–27; TROEDSSON 1951: 205–206, pl. 4, fig. 15–16; COX 1954, fig. 1). From the Lower Jurassic of France *C. amperci* (DUMORTIER & FONTANNES 1876: 14, pl. 2, fig. 3) is larger, but is more oblique and its posterior margin is not so excavated as in *B. pintadae*. *B. coimbrica* (CHOFFAT) from the early Lower Jurassic of Europe (BÖHM 1901: 231, Taf. 9, Fig. 3, 12; NAGY 1970: 89) has a similar outline but the posterior wing is shorter and the shell is smaller. *C. polita* (SHARPE) from the Oxfordian-Kimmeridgian of Portugal (SHARPE 1850: 190, pl. 24, fig. 1–2) lacks an anterior auricle and the angle between the umbonal ridge and the dorsal margin is larger than in *B. pintadae*. *C. quoixi* FRENEIX (1965: 18–19, pl. 2, fig. 7–8) from the late Bathonian of Tunisia, has a more inflated shell and a flat right valve.

The bivalve described here as “*Pteriacea* gen. et sp. indet.” from the early Toarcian of Cordillera del Viento, Neuquén province, can be distinguished from *B. pintadae* by a shorter posterior wing, wider umbones and less developed anterior auricles.

Remarks: This species is tentatively included in the subgenus *Neobakevellia*. This name is provisionally adopted here in HAYAMI’s sense (1975), pending the question of probable subjective synonymy with *Odontoperna* to be adequately solved. HALLAM mentioned *Bakevellia* s. l. from the South American Sinemurian (1977a: 71) and from the Pliensbachian of the southern Andes (1983: 184) but he did not give any indication as to which record this mention referred.

Autecology: The shell shape, thickness and size of *B. pintadae* are very similar to extant *Pteria* species, which are epibyssate. This resemblance could indicate a similar mode of life for the two groups. LOGAN (1967: 10) suggested an equivalent habitat for the Permian *Bakevellia*, but STANLEY (1972: 186) and SEILACHER (1984) consider that most Mesozoic bakevellids were endobyssate, living with the commissure plane vertical. STANLEY (1972: 191) also analyzed the function of the pteriform posterior wing and his conclusions can be applied to *B. pintadae*. He suggested that this wing could be used in agitated waters to separate effectively the inhalant from the exhalant currents. *B. pintadae* has a slightly inequivalve shell, perhaps indicating an incipient pleurothetic habit.

Genus *Gervillia* DEFRANCE 1820

Type species: *Gervillia solenoidea* DEFRANCE 1824, from the late Cretaceous of Germany, subsequent monotypy.

The first serious attempt at the systematization of this group of bivalves was made by FRECH (1902) who, based mainly on Triassic species and on their hinge characters, recognized four groups, that he called: “of *Gervilleia aviculoides*”, “of *Gervilleia angusta*”, “of *Gervilleia Hartmanni*” and “of *Gervilleia solenoides*”. This basic arrangement was later followed by other authors and new names at generic or subgeneric level were proposed for them. These are *Gervillella* WAAGEN 1907, *Cultriopsis* COSSMANN 1904, *Gervillaria* COX 1954 and *Gervillia* s. s., respectively.

The classification of this group among others was discussed by WAAGEN (1907), DIETRICH (1910), GILLET (1924c), GILLET & POPOVIĆ (1924), COX (1946), HAYAMI (1957b) and FRENEIX (1965) and will not be considered here in detail. COX (1946) proposed to limit the genus *Gervillia* to the narrow, ensiform species and to divide it in subgenera according to the hinge characters.

Gervillia was repeatedly mentioned from the South American Lower Jurassic and the present status of these records after this revision will be briefly discussed.

From the Lower Jurassic of Argentina the following species were known: *G. pallas* LEANZA 1942, *G. ? turgida* LEANZA 1942, and *G. sp.* WAHNISH 1942. None of these are referable to *Gervillia*, the first and last mentioned records are here included into *Gervillaria* ? and the second one into *Gervilleioperna*.

MÖRICKE (1894) cited a *Gervillia* sp. from the Chilean Lower Jurassic, but he neither provided descriptive data

nor discussed the affinities of his material and no further comments can be made here. R. PHILIPPI (1899) illustrated two new species from Chile, *G. chilensis* and *G. mytiloides*, without giving any data of their stratigraphic position. *G. chilensis* PHILIPPI (1899: 43, lám. 22, fig. 7), probably found in the Tinguiririca valley, has radial ribs and, if a bakevellid, it would have affinities with the species referred to *Cuneigervillia* COX & ARKELL. On the other hand *G. mytiloides* PHILIPPI (1899: 42–43, lám. 22, fig. 6), found at Caracoles, is only an internal mould without diagnostic characters and its determination is even difficult at a family level. From the four species described and illustrated by ESCOBAR (1980) from the Hettangian and Sinemurian of Chile, only one could be doubtfully referred to *Gervillia*. This is the "*G. cf. angusta* von MÜNSTER" (ESCOBAR 1980: 41–42, lám. 2, fig. 1d) which, although different from *G. angusta* (MÜNSTER), is similar to *G. olifex* QUENSTEDT. The other three species, "*G. cf. aviculoides* (SOW.)" (ESCOBAR 1980: 42–43, lám. 2, fig. 1b–c), "*G. sp. A*" (p. 43–44, lám. 2, fig. 2) and "*G. sp. B*" (p. 44–46, lám. 2, fig. 1a and 9) have a well developed anterior auricle (i. e. their umbones are not terminal), have a pteriform outline and their hinge characters are unknown. None can be included into *Gervillia* and they could belong to other bakevellid genus or even to other pteriaceans. The Chilean author did not mention R. PHILIPPI's species in his discussion.

From the early Jurassic of Chunumayo, Perú, JAWORSKI (1915: 416; 1925b: 43) described *G. cf. lamellosa* LEPSIUS. LEPSIUS' species is probably a bakevellid "with an *Avicula* aspect" and thus is not referable to *Gervillia* (TAUSCH 1890).

Subgenus *Cultriopsis* COSSMANN 1904

Type species: *Gervillia (Cultriopsis) falciformis* COSSMANN 1904, from the Lower Jurassic of France, original designation (see below).

Synonyms: "Gruppe der *Gervilleia angusta*" FRECH 1902: 613.

Angustella WAAGEN, 1907 (type species: *Gervillia angusta* MÜNSTER 1836).

? *Gervillella (Ensigeruilleia)* DIETRICH 1901 (type species: *G. (E.) silicea* var. *husii* DIETRICH 1910).

In his preliminary arrangement of *Gervillia* species, FRECH (1902) segregated those forms with posterior lateral teeth and sometimes also with anterior teeth and a length between 8 and 12 times the height. He exemplified this group by *G. angusta* MÜNSTER, from the Upper Triassic of the Alps. Only two years later COSSMANN (1904: 510) proposed the name *Cultriopsis* as a new "section" within the genus "*Gervilleia*". He named "*G. cultellus* COSSM." as the type species (p. 510), but this seems to be a nomen nudum. On the following page he said: "This new section, whose type is the infralassic species here described, corresponds to the group of *G. angusta* MÜNST. from the Triassic, i. e. to FRECH's group 'Aa2' ...". Since *G. (C.) falciformis* is the only new species described by COSSMANN in that paper which meets all the requirements of the ICZN, the type species is then established by original designation (COSSMANN 1904: 511).

In 1907 WAAGEN (p. 170) overlooked COSSMANN's paper, gave to the same group the name *Angustella* and provided a detailed diagnosis of the taxon, with *G. angusta* MÜNSTER as the type species by later designation by DIENER (1923: 97). He also described specimens that he referred to "*Angustella angulata* (MÜNSTER)". *Angustella* is clearly a subjective junior synonym of *Cultriopsis*, since both were based on the same concept, as was already discussed by COX (1940). Nevertheless some authors, notably ICHIKAWA (1954), HAYAMI (1957b: 96) and FRENEIX (1965: 13) consider that they can be distinguished at a subgeneric level due to hinge details (presence of only one posterior lateral tooth in *Angustella* and two or three in *Cultriopsis*) and stratigraphical range (*Angustella* would be only known from the Triassic, whilst *Cultriopsis* ranges from the Rhaetian to the early lower Jurassic according to ICHIKAWA 1954: 55).

COX (1940: 105) suggested that the hinge of *Gervillia* s. s., with numerous cardinal and lateral teeth, could have derived from the dentition of *Cultriopsis*, which only has lateral teeth. An intermediate group could be *Ensigeruilleia* DIETRICH 1910, which has numerous posterior lateral teeth and lacks cardinal teeth, as was already depicted by FRENEIX (1965: 63). COX (1940; 1946; in COX et al. 1969) preferred to consider the species of *Ensigeruilleia* as the first representatives of *Gervillia* s. s., but with similar arguments they could be regarded as the last *Cultriopsis*, or even as a separate group.

The type of hinge arrangement and general outline of *Gervillia* s. s. were reached as early as the late Triassic, in a couple of species from Papua New Guinea that SKWARKO (1981: 63) described as belonging to a new subgenus of *Bakevellia*, *B. (Spia)*.

G. (Cultriopsis), known from the Permian(?) and late Triassic, exhibits its greatest variability and widest geographical range during the early Jurassic and extends in Europe up to the middle (or even late) Jurassic. Although only a few specimens from each locality are generally known, there are about 20 available species names within this subgenus.

Gervillia (Cultriopsis) sp.

Plate 3, fig.4-6; text-fig. 5

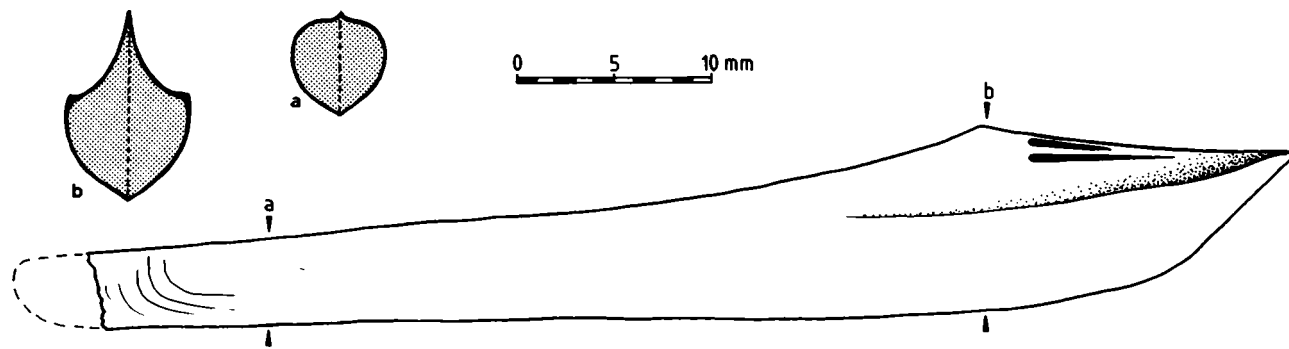
- v . p 1975 *Gervillia* - DAMBORENEA et al., cuadro 1, 11 (sample 104 only).
- v ? 1978 *Gervillia (Cultriopsis) sp.* - DAMBORENEA in VOLKHEIMER et al., tab. 2.
- v . 1982 *Gervillia (Cultriopsis) sp.* - DAMBORENEA, p. 167-170; lám. 42, fig. 1-2; lám. 64, fig. 1-3.

Material: Most of the material was found by the author in the upper Pliensbachian beds of southern Neuquén province (hill South of Cerro Roth, D. 15 and 8 km south of Estancia Santa Isabel, D. 1): MLP 16386 to 16391, 16393 (M 104, 1051 and 1053), four left valves and four right valves, preserved mostly as internal moulds and none of them complete. Also MLP 16503, collected by RICCARDI at Cañadón Chapingo, 3 km SE of Cerro Carnerero, Chubut province, Toarcian, an incomplete left valve.

Doubtfully included in this species are some fragments from the Toarcian of Arroyo La Laguna (A. 2), San Juan province: MLP 16392 (M 437).

Description: Medium to large shell, very long, ensiform, arched, subequivalve, with terminal umbones and a posterior auricle clearly separated from the main body of the shell. The hinge margin is straight and meets the posterior margin at an angle of 145° to 155°. The posterior margin is gently concave and parallel to the ventral margin for almost all its length. The anterior is almost straight to slightly convex and surrounds a wide byssal gape that affects equally both valves and extends from the umbones to the antero-ventral region. The anterior margin meets the ventral one without angulation. The posterior wing is limited by a ridge and a posterior sulcus. The shell height remains constant along all the length, which is more than ten times the height measured at the end of the posterior wing.

The transverse section of the shell back to the posterior wing has an ovate outline, with the height slightly exceeding the width of the two valves (see text-fig. 5a). The transverse section that contains the posterior wing is rhombic, with well-marked ridges and the surface of the wings concave (see text-fig. 5b).



Text-fig. 5. *Gervillia (Cultriopsis) sp.* Hill south of Cerro Roth, Pliensbachian, reconstruction of the internal mould of the right valve based on specimens MLP 16389 and 16391. a-b: two transverse sections.

The umbones are terminal, pointed and do not extend beyond the dorsal margin. The shell lacks anterior auricles. The left valve has two very long, posterior lateral teeth that are subparallel to the dorsal margin. The ligamental area and muscle scars are unknown.

The shell surface is smooth, with only commarginal growth lines that in some places, especially in the anterior region of the shell, coalesce to produce a lamellose pattern. The greatest thickness of the shell coincides with the postumbonal ridge, which is more prominent in complete specimens than in internal moulds.

Paratypes: MLP 16239, 16394 to 16399, 16401 to 16404, 16562, 19632 and 19636 (M 100, 105, 106, 109, 125, 141, 143, 1040, 1310, 1312) from the Pliensbachian of southern Neuquén province (Cerro Roth, D.16; hill south of Cerro Roth, D.15; Cerro Del Vasco, D.12 and Salitral Grande, D.3) and Mendoza province (Arroyo Serrucho, B.8), author's collection. They are ten left valves, four right valves and one internal mould of a right valve.

Doubtfully included in this species: MLP 16405 and 19640 (M 351 and 1314), some fragments from the Pliensbachian of southern Mendoza province (Rio Atuel, B.1 and Arroyo Serrucho, B.8).

Diagnosis: Medium-sized shell, thick, of spatulate outline, twisted. Inequivalve, the left valve is more globose than the right one and with a posterior carina ventrally limited by a sulcus. The anterior auricle is separated from the main body of the shell by a deep sulcus on the left valve. No byssal gape. Shell length twice the height, with the dorsal margin equal to half the total length.

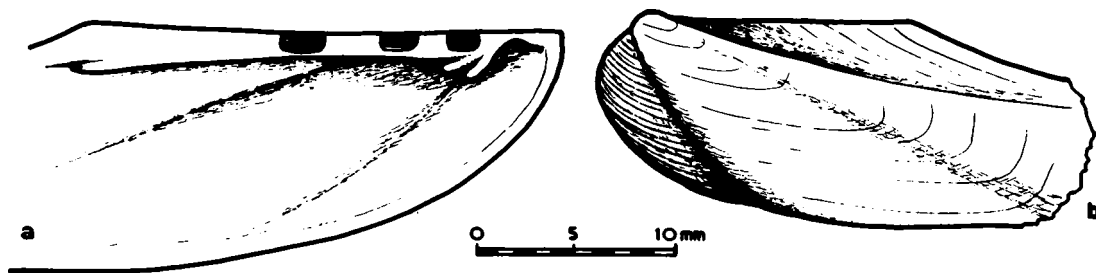
Description: Small to medium-sized shell, thick, spatulate in outline, arched and elongated, inflated, inequivalve, twisted, with anti-clockwise torsion in posterior view and posterior and anterior auricles developed. The dorsal margin is straight and occupies about half the total length. The posterior margin is sigmoidal, concave at the posterior wing and convex near the posterior end. The postero-dorsal corner is obtuse. The ventral and anterior margins are evenly convex. The left valve is more inflated than the right one. The length of the shell equals twice its height.

The umbones are prosogyrous, pointed and low, the left one a little more prominent and anteriorly placed though not terminal. A well-developed carina extends from the umbones to the postero-ventral corner of the shell on the left valve. This carina does not coincide with the greatest inflation of the shell but is dorsal to it and between them there is a shallow but clear sulcus.

The anterior auricle has a lobate shape and extends along all the anterior portion of the shell; on the left valve it is limited by a posterior sulcus. Apparently there was no byssal gape. The ligament is multivincular, with few ligamental pits separated by equally wide interspaces. The hinge has at least one posterior elongated tooth subparallel to the dorsal margin and two short cardinal teeth below the umbones projecting into the internal part of the shell on the left valve (see text-fig. 6 a).

The posterior adductor muscle scar is large and occupies the central portion of the shell below the posterior wing. The anterior adductor muscle scar is small and is placed on a platform on the dorsal part of the anterior lobe.

The shell outer surface is smooth except for growth lines which become scaly and imbricated on the anterior lobe. On the largest available specimens the torsion is about 50°, but this seems to be a very variable character.



Text-fig. 6. *Gervillella araucana* n. sp. Arroyo Sañicó near Carrán Curá, Pliensbachian. a: latex cast from paratype, MLP 16404, left valve; b: external view of left valve, paratype MLP 16403-a.

Measurements: The width is only an approximate value, due to the difficulty of measuring it on twisted shells.

Specimen	Material	L (mm)	H (mm)	W (mm)	L/H	Dl (mm)
MLP 16395, paratype	RV S	45.55	20.80	3.00	2.28	21.25
MLP 16396, paratype	LV S	33.85	16.90	3.70	2.00	18.45
MLP 16397, paratype	LV S	28.00	15.05	4.20	1.86	15.40
MLP 16400, holotype	LV S	46.30	21.25	7.05	2.17	—
MLP 16401, paratype	LV CM	50.15	27.30	5.35	1.83	19.85

Affinities: As already mentioned, *G. araucana* belongs to a group of species very well characterized by several morphological features. It will be compared here only with members of this group, since the size, shape and torsion allow the distinction of this taxon from the species of the other group, to which the type species of the genus belongs.

From all the species that will be discussed here, *G. araucana* differs in having a post-umbonal carina that bounds the posterior wing.

G. acuta (J. DE C. SOWERBY) a very common species in Europe from the Aalenian to the Oxfordian (J. DE C. SOWERBY 1826: 15, pl. 510, fig. 5; MORRIS & LYCETT 1853: 20, pl. 3, fig. 12; p. 21, pl. 3, fig. 13 as *G. subcylindrica*; TERQUEM & JOURDY 1869: 124; GREPPIN 1899: 110–111; PARIS 1911a: 249; COX & ARKELL 1948: 9; KSIĄZKIEWICZ 1956: 172 & 336, tabl. 18, fig. 1–2; CASTELL 1962, pl. 15, fig. 1), this and comparable material from Israel in PARNES (1981: 31, pl. 4, fig. 6) can be distinguished from the Argentine species by its pointed anterior end and more straight shell. The same differences can be found with *G. scarburgensis* PARIS (1911b: 255–256).

G. siliqua (EUDES-DESLONGCHAMPS), known from the Upper Jurassic, especially Oxfordian of Europe, India, East Africa, Sinai and northwest China (DOUVILLÉ 1916, pl. 9, fig. 11; COX 1940: 112, pl. 7, fig. 12–14; COX 1965: 44, pl. 4, fig. 10; VÖRÖS 1971: 176–177, pl. 1, fig. 4; ZHANG et al. 1979: 294–295, pl. 85, fig. 10, 11, 13, 15, 17, 18, 21; CHEN 1982a: 235–236, pl. 3, fig. 11, 14) also has a pointed anterior end. This species has a very thick shell and the general outline is more rhombic.

G. semitorta COX & ARKELL, from the Aalenian of Great Britain and France (LYCETT 1863: 37, pl. 40, fig. 25 as *G. tortuosa* SOW. var.; COX & ARKELL 1948: 10; FRENEIX et al. 1956: 4, pl. 1, fig. 4) has a more developed torsion that mostly affects its anterior region and a concave right valve. Another species that is also different from *G. araucana* by being more inequivalve is *G. monotis* (EUDES-DESLONGCHAMPS), from the Bathonian of Europe (MORRIS & LYCETT 1853: 22, pl. 2, fig. 14; PARIS 1911a: 248, pl. 29, fig. 3; COSSMANN 1923: 7, pl. 5, fig. 14–15; pl. 6, fig. 13; COX & ARKELL 1948: 9; ZHANG et al. 1979: 294, pl. 85, fig. 5). This species has a rounded anterior end, just like *G. araucana* and can also have two umbonal ridges.

G. araucana is very similar to *G. sulcata* (ETALLON), from the Oxfordian of Great Britain and France, sharing the blunt anterior end and the general shape, but the European species is shorter and not so twisted (DE LORIOI 1892: 298, pl. 32, fig. 6–8; GREPPIN 1893: 71, pl. 4, fig. 10; ARKELL 1933: 205, pl. 26, fig. 6).

G. qinghaiensis (in ZHANG et al. 1979: 294, pl. 85, fig. 3, 6–9, 12, 14, 16, 19, 20, 23, 24), from the Middle Jurassic of northeastern China, differs by having a pointed posterior wing and a smaller size.

G. consobrina (D'ORBIGNY), according to DIETRICH's figure (1910: 238, fig. 4), from the Middle Jurassic of Europe, has a double sulcus on the anterior auricle and very narrow umbones. A species that shows affinities to *G. consobrina* is *G. spatulata* (TERQUEM & JOURDY), from the Bathonian of France, and it can be distinguished from *G. araucana* by its acute anterior end and more triangular shape, with a flat posterior area (TERQUEM & JOURDY 1869: 123, pl. 13, fig. 13).

Autecology: Species highly twisted and with more inflated left valves are usually represented in the strata by their left valves, a fact observed for *G. araucana* and previously reported by MORRIS & LYCETT (1853: 23) for *G. monotis* from the Great Oolite Series of Great Britain.

? Genus *Gervillaria* COX 1954

Type species: *Modiola* ? *alaeformis* J. SOWERBY 1819, from the early Cretaceous of Europe, by original designation.

Gervillaria ? *pallas* (A. LEANZA 1942)

Plate 2, fig. 1–5; text-fig. 7

!* v. 1942b *Gervillia pallas* LEANZA; p. 155–156, lám. 4, fig. 1.

v. 1942 *Gervillia* sp. – WAHNSH, p. 31.

v. 1975 *Gervillaria* – DAMBORENEA et al., cuadro 1, 12.

v. 1978 *Gervillaria pallas* (LEANZA) – CAMACHO & RICCARDI, cuadro 1.

! v. 1982 *Gervillaria* ? *pallas* (A. LEANZA) – DAMBORENEA, p. 175–180; lám. 43, fig. 1–5; lám. 61, fig. 1–7.

Type material: A. LEANZA only had a left valve, MLP 6133, which is thus the holotype of the species, from the Pliensbachian of Cerro Roth (D.16), southern Neuquén province. Figured by A. LEANZA (1942b, lám. 4, fig. 1) and here in pl. 2, fig. 3a-b.

Additional material: Seven left valves, some of them as internal moulds, nine almost complete shells with both valves and several fragments collected by the author from Pliensbachian beds of southern Neuquén province (Cerro Roth, D.16; hill south of Cerro Roth, D. 15; Salitral Grande, D.3; and 8 km south of Estancia Santa Isabel, D.1): MLP 16406 to 16414, 16416 (M 99, 101, 103, 141, 1051) and Mendoza province (Rio Atuel, B.1): MLP 16415 (M 349) and also from the early Toarcian of Mendoza (Arroyo Serrucho, B.8): MLP 19679 (M 1343).

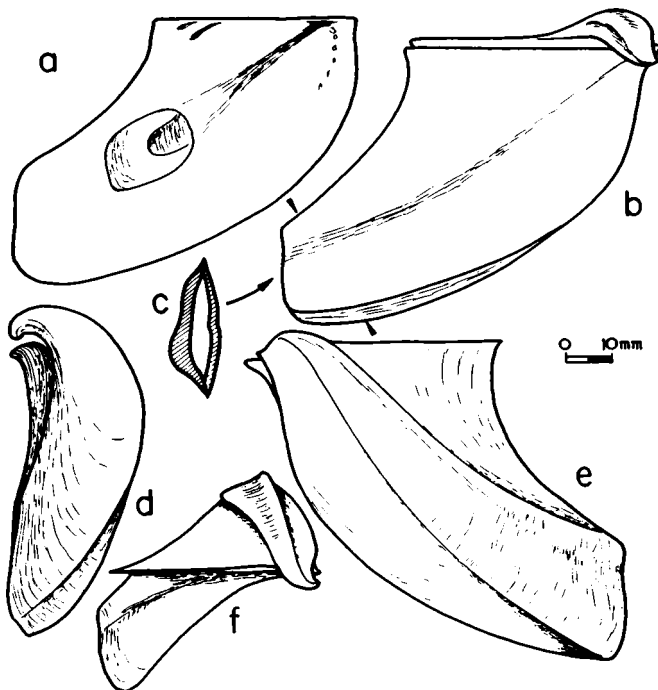
Also DNGM 8646 (= MLP 19079), an almost complete shell, collected by KEIDEL and described by WAHNISH (1942) from Nueva Lubecka, Chubut province, early Jurassic (Toarcian ?, Pliensbachian ?) is included in this species.

Description: Shell of medium size, trapezoidal in outline, longitudinally elongated, almost as long as high. Very inequilateral and very inequivalve, some specimens are twisted in an anti-clockwise direction in posterior view, with a torsion angle (in MCGHEE's sense, 1978) up to about 20°. The left valve is highly convex and bears a conspicuous carina. The right valve has a gently concave surface.

The dorsal margin is long and straight, but is shorter than the shell total length. The posterior margin meets the dorsal one at a slightly acute angle, but then dips backwards, being first concave, then straight to slightly convex and meeting the ventral margin at an acute angle. The ventral and anterior margins are sigmoidal in lateral and frontal view. In some specimens the portion near the anterior margin is clearly more concave than the ventral one.

The shell lacks an anterior auricle, but the posterior wing is well developed and is clearly separated from the main body of the shell. The umbones are terminal and prosogyrous on both valves. On the left valve the beak is narrow but prominent and arched, exceeding the hinge line towards the right valve. In some specimens it overhangs the right beak. The right umbo is pointed and arched outwards from the hinge line.

The left valve shows two carinae that extend from the umbones to the postero-ventral region of the shell. These develop as shell thickenings, so that the internal mould only reflects them weakly. The anterior carina is more prominent and corresponds to the greatest inflation of the shell surface. The posterior carina is lower and limits the posterior wing. The triangular area that is limited within both carinae has a somewhat concave surface and in some specimens a weak sulcus is present near the posterior carina. Both carinae are bounded exteriorly by two deep sulci, one in front of the anterior carina and the other behind the posterior carina; they are deeper on the posterior portion of the shell. The right valve has a shallow sulcus that extends from the umbones to the postero-



Text-fig. 7. *Gervillaria* ? *pallas* (A. LEANZA). Reconstruction based on several specimens, Cerro Roth, Pliensbachian. a: internal mould of right valve; b: right lateral view; c: posterior section; d: anterior view; e: left lateral view; f: dorsal view.

ventral region, fitting the sulcus on the left valve. The right valve also has a strong anterior ridge running parallel to the anterior margin, which delimits the area where there is only growth in shell thickness but not in shell length.

The ligamental pits are only present in some specimens, the maximum observed number is four (pl. 2, fig. 5a-b). They are wide, irregular in shape and narrower than the spaces between them. The material does not show the presence of true teeth, but on one specimen there are two longitudinal thickenings on the posterior portion of the right valve (pl. 2, fig. 2).

On the internal moulds of the right valve the adductor muscle scar is deeply impressed, it is crescent-shaped in outline and subcentrally placed, somewhat posteriorly shifted. An anterior scar, surrounded by the other one, oval in shape and less deeply impressed (see text-fig. 7-a) probably belongs to the posterior pedal retractor. On the anterior umbonal region there are four to five pit-like muscle scars, aligned parallel to the anterior margin, similar to those described by SKWARKO (1967) in *Gervillancea coxiella* SKWARKO.

The outer surface of the shell only bears commarginal growth lines that become asymptotic on the anterior portion of the valves.

Although there is no evidence of a byssal gape, the byssus probably emerged between both valves at the most concave portion of the anterior margin.

Measurements: The width was taken with both valves together because the twisted shell makes it impossible to consider the valves separately. The right valve is not globose but nevertheless it is not flat, as it closely fits the torsion of the other valve.

Specimen	Material	L (mm)	H (mm)	W (mm)	L/H	DI (mm)
MLP 6133, holotype	LV S	56.30	61.50	-	0.91	47.75
MLP 16407, pl. 2, fig. 4	BV S	78.25	70.00	25.35	1.11	-
MLP 16408-ef	BV S	100.20	99.30	27.25	1.00	-
MLP 16410, pl. 2, fig. 1	BV S	77.90	66.70	27.45	1.16	52.40
MLP 16411, pl. 2, fig. 2	BV S	94.40	72.00	25.00	1.25	52.50
MLP 16414	LV IM	40.20	41.30	13.05	0.97	30.90
MLP 19079, pl. 2, fig. 5	BV S	61.70	55.30	26.10	1.11	61.70

Affinities: Pteriacean species exteriorly similar to *G. ? pallas* are known from the Upper Triassic to the Upper Cretaceous. The Upper Triassic forms were grouped in the genus *Lilangina* DIENER (placed in the Cassianellidae in COX et al. 1969 on account of internal characters). The Argentine species has a shell shape and inflation of the valves similar to those of *L. nobilis* DIENER, from the Upper Triassic of Kashmir and China (see DIENER 1908 and WEN et al. 1976: 42, pl. 15, fig. 13 a-c), but *G. ? pallas* has two well-developed carinae on the left valve and a less prominent left umbo.

In his paper on bivalve torsion MCGHEE (1978: 327) mentions the presence of twisted bivalves in the middle Sinemurian to Pliensbachian of Cerritos Bayos, Chile. SEILACHER (1984, text-fig. 7) figures them as “cf. *Hoernesia* sp.”. This is certainly the most closely related taxon to *G. ? pallas* and it could even be conspecific, differing from the Argentine material only by its divaricate adhesion ribs on the left valve and the non-pointed posterior wing.

Gervillaria alaeformis (J. SOWERBY), from the early Cretaceous of Europe and Asia, which is the type species of the genus, has a similar general shape, but it is not twisted and the right valve is more convex (see WOODS 1905: 79-83, pl. 11, fig. 9-11, text-fig. 9-14; DOUVILLÉ 1916, pl. 20, fig. 10-11; GILLET 1924c, fig. 16; PIRYATINSKI et al. 1962, tabl. 41, fig. 1). The European species lacks the pair of carinae on the left valve that are so typical of the Argentine species. From the early Cretaceous of Mexico and South America two species have been described, *Gervillaria alator* (IMLAY) (see WEAVER 1931: 201-203, pl. 15, fig. 61-63 as *G. alaeformis*; IMLAY 1940: 150-151, pl. 10, fig. 1-2; pl. 11, fig. 1-6; DAMBORENEA et al. 1979: 27-28, lám. 5, fig. 6-7), that also differs from the species here described in the presence of radial ribs on the left valve and the similar inflation of both valves; and *G. militaris* (BURCKHARDT) (see BURCKHARDT 1903: 70, Taf. 15, fig. 3-5; WEAVER 1931: 211-212, pl. 15, fig. 65) that has a more square shape than *G. ? pallas* and a radial ornamentation.

Gervillia ? montanaensis (MEEK), from the Bajocian of western USA (IMLAY 1967a: 77, pl. 1, fig. 1, 7-10; USNM 7795 = MLP 19116; USNM 13272 = MLP 19115) has an outline similar to *G. ? pallas*, but it is not twisted, the right valve is feebly convex and both valves have radial ribs.

G. leufuensis (WEAVER) described from the Callovian of Neuquén province (WEAVER 1931: 199, pl. 15, fig. 60) differs from *G. ? pallas* by having both valves convex and by lacking the double carinae on the left valve.

Gervillia costata LYCETT, from the Bathonian of Great Britain (LYCETT 1863, pl. 50, fig. 21) has two umbonal carinae, but is smaller and has a well developed anterior auricle and is thus referred to *Gervillella monotis* (EUEDES-DESLONGCHAMPS) by COX & ARKELL (1948: 9).

The torsion of the Argentine species makes it similar to *Gervillia tortuosa* (SOWERBY) from the early and middle Jurassic of Europe (QUENSTEDT 1856, Taf. 48, Fig. 19–20) and *Gervillia subtortuosa* OPPEL (non MEEK & HAYDEN) from the European Aalenian (BENECKE 1905: 132, Taf. 6, Fig. 2–3; Taf. 7, Fig. 1; Taf. 12, Fig. 1). Both species have, unlike *G. ? pallas*, a well-developed anterior auricle. *G. subtortuosa* MEEK & HAYDEN (non OPPEL) (MEEK 1876: 65, pl. 16, fig. 7), from the Cretaceous of Missouri, USA, is twisted but it is larger and lacks the pointed auricles and the carinae that are present in *G. ? pallas*.

The left valve of *Bakevellia trigona* (YOKOYAMA), from the early Jurassic of Japan (HAYAMI 1957a: 51–52, pl. 2, fig. 1–5) has a similar outline and umbones, but lacks the umbonal carinae. The right valve of the Japanese species seems to be more convex than that of *G. ? pallas* and the hinge is typically bakevelloid.

The internal mould described by R. PHILIPPI (1899: 42–43, lám. 27, fig. 6) as *Gervillia mytiloides* PHIL., from an undetermined bed at Caracoles, Chile, may have an overall resemblance to *G. ? pallas*, but the Chilean specimens are almost equivalve. *Gervillaria hartmanni* (GOLDFUSS), from the Aalenian of Alsace (GOLDFUSS 1835, Taf. 115, Fig. 7; FRECH 1902: 614, text-fig.) is also almost equivalve. *Gervillaria* sp. from the middle Oxfordian of Cuba (PUGACZEWSKA 1978: 169, pl. 9, fig. 5) has a smooth left valve.

Remarks: This species was originally assigned by A. LEANZA (1942b) to *Gervillia*. Even though more material has been added since then, the generic identification can only be doubtfully accepted; it can surely not be regarded as a *Gervillia*. It was here referred to *Gervillaria*, though the lack of anterior auricle and the great torsion of the valves remind one of the Triassic genus *Lilangina*, described by DIENER (1906, 1908) and grouped together with *Hoernesia* and *Cassianella* in a different family, called Paraviculidae by GUGENBERGER (1935) and later in the Cassianellidae by ICHIKAWA (1958). The members of this family differ from the Bakevellidae in the presence of an internal septum in the umbonal region that limits the anterior auricle and they seem to be restricted to the Permian and Triassic.

On the Argentine material neither the oblique hinge crenulations of the adult *Gervillaria*, nor the internal septum of the Cassianellidae, were observed.

From the Upper Triassic of New Guinea SKWARKO (1967: 54) described the new genus *Gervillancea* that is characterized by the high torsion of the valves, that even affects the cardinal margin, as happens in the species here described. Although the species of this genus could be related to *G. ? pallas*, they have a very long anterior wing that distinguishes them. The affinities concerning the hinge and muscle characters on the other hand are quite strong.

Autecology: The suggestion of MCGHEE (1978) that the torsion within the bakevellids was used in conjunction with the increase on shell weight at the umbonal region to solve the problem of stability on soft substrates, seems to be perfectly applicable to *Gervillaria ? pallas*. This species has the umbonal region, especially that of the left valve, thickened, and the surface of the right valve is smoother than that of the left valve. These could have been supplemented by a weak byssus. To the strategy described by MCGHEE (1978) for some bakevellids, this species probably added the one described by SAVAZZI (1981) for certain arcaceans. *G. ? pallas* was probably a pleurothetic endobysate bivalve, always living with the posterior end of the shell above the sediment-water interface. Nevertheless no specimen in life position was found and the Argentine material does not show the divaricate adhesion ribs on the left valve figured by SEILACHER (1984, text-fig. 7) for this or a very closely related species from Chile.

Genus *Gervilleioerna* KRUMBECK 1923

Type species: *Gervilleioerna timoriensis* KRUMBECK 1923, from the early Jurassic of Timor, by monotypy.

The genus *Gervilleioerna* was originally described by KRUMBECK (1923: 76) to include one species from the Lower Jurassic of Timor, that showed intermediate characters between species of "*Gervilleia*" (= *Gervillia*) and "*Perna*" (= *Isognomon*). KRUMBECK compared his species with *Gervillia buchi* DE ZIGNO, from the Lower Jurassic of the Alps. DUBAR (1948: 152) later included this and two other new species from the Lower Jurassic of Morocco in *Gervilleioerna*. That author also suggested that these species could have derived from forms similar to *Gervillia gemellaroi* TOMM. from the Rhaetian of the Alps.

Gervilleioperna is then restricted to the Lower Jurassic, when it was widely, though sporadically, distributed (see text-fig. 8).

The genus *Gervilleioperna* is characterized by its large size, left valve highly inflated with vertically extended cuneiform body, prominent and narrow umbones and a broad and very long posterior wing. The beak is strongly prosogyrous, the shell has a deep "lunule" below it and a narrow byssal gape. The ligamental pits are few and narrow, with wider intervals. The right valve is only imperfectly known (Cox in Cox et al. 1969).

The species *Gervillia* ? *turgida* A. LEANZA, from the Lower Jurassic of Neuquén province, was referred to *Gervilleioperna* in a previous paper (DAMBORENEA et al. 1975) and a subgeneric name is proposed here to include this species.

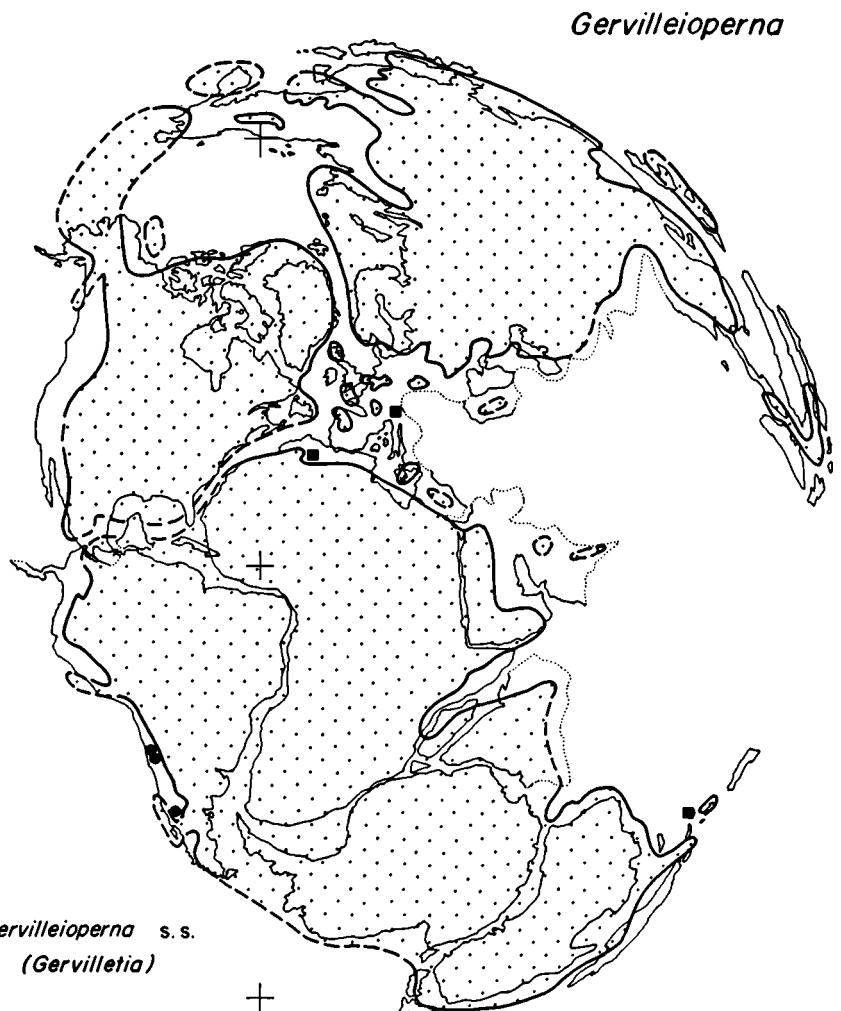
Cox (in Cox et al. 1969) included *Gervilleioperna* in the Isognomonidae, though this genus and the newly described subgenus have bakevellid characters such as the pteriform outline and the presence of radial carinae. This genus is thus regarded here as a bakevellid, noting in this way its relationships with other early Jurassic bakevellid taxa from Argentina.

Subgenus *Gervilletia* nov.

Type species: *Gervillia* ? *turgida* A. LEANZA 1942b, from the Lower Jurassic of Neuquén, Argentina.

Derivation of name: From *Gervilleioperna* and *Mulletia*, two bivalve generic taxa that share characters with this new subgenus.

Diagnosis: Thick shell, very inequivalve, inequilateral, pteriform and subtrapezoidal in outline, very large. Left valve highly convex with a prosogyrous beak, narrow and prominent and an oblique double carina from the



Text-fig. 8. Palaeogeographic distribution of the genus *Gervilleioperna*. Palaeocontinental reconstruction from SMITH & BRIDEN (1977) for the early Jurassic, hypothetic coast-lines compiled from various sources.

umbones to the postero-ventral corner; right valve slightly concave. Long posterior wing well differentiated from the body of the shell and posterior margin strongly concave. Anterior margin also concave, with a pointed antero-ventral corner. Shell highly twisted. Ligament multivincular, hinge edentulous in adults. No byssal gape.

Discussion: Like *Gervilleioperna* s. s., this new subgenus has a highly inequivalve, thick shell, with a concave anterior margin and a long and straight dorsal margin. It differs from the species referred to *Gervilleioperna* in its high torsion, the absence of a "lunule", by the very prominent umbonal carina and the alate posterior end with a concave posterior margin. These last mentioned characters remind one of the genus *Mulletia* FISCHER, from the Lower Cretaceous. This genus has a subequivalve shell and two divergent ribs, see for instance *Mulletia mulletii* (DESHAYES) (D'ORBIGNY 1847, pl. 400, pl. 401, fig. 1-3) and *Mulletia quintucoensis* (WEAVER 1931: 210-211, pl. 17, fig. 76 and 79; pl. 19, fig. 92).

HILLEBRANDT & SCHMIDT-EFFING (1981) repeatedly mentioned the presence of "Isognomonidae nov. gen. nov. sp. (cf. *Gervilleioperna*)" in the early Aalenian of several Chilean localities. Unfortunately this taxon is yet undescribed and cannot be compared with this new subgenus.

Range: Only the type species is here referred to this new subgenus, from the Pliensbachian of southern Neuquén province, Argentina, and Chile.

Gervilleioperna (*Gervilletia*) *turgida* (A. LEANZA 1942)

Plate 3, fig. 1-3; text-fig. 9

- ! * v. 1942b *Gervillia* (?) *turgida* n. sp. A. LEANZA, p. 156-157; lám. 3, fig. 1-3.
v. 1975 *Gervilleioperna* - DAMBORENEA et al., cuadro 1, 15.
p v 1975 *Pteroperna* - DAMBORENEA et al., cuadro 1, 09 (sample 96 only).
v. 1978 *Gervillia* ? *turgida* Leanza - CAMACHO & RICCARDI, cuadro 1.
? 1981 *Gervilleioperna turgida* Leanza - HILLEBRANDT & SCHMIDT-EFFING, p. 12, 22.
! v. 1982 *Gervilleioperna* (*Gervilletia*) *turgida* (A. LEANZA) - DAMBORENEA, p. 182-187; lám. 43, fig. 6-9; lám 62, fig. 1-6; lám. 63, fig. 1-5 (unavailable subgeneric name).

Type material: Lectotype (here designated): MLP 6059, an incomplete shell with both valves (the right one mostly covered by matrix) from Cerro Roth (D.16), Neuquén province, Pliensbachian, FRENGUELLI's collection, figured by A. LEANZA (1942b, lám. 3, fig. 2) and here in pl. 3, fig. 2a-b. Paralectotype: MLP 6260, an incomplete shell with the left valve preserved and the right valve as internal mould, same locality.

Additional material: Six left valves, one specimen with both valves preserved together and one with the right valve preserved as internal mould: MLP 16417 to 16419, 16676 and 17905 (M 96, 105 and 125) collected by the author in late Pliensbachian deposits at hill south of Cerro Roth (D.15) and Cerro del Vasco (D.12), southern Neuquén province.

HILLEBRANDT & SCHMIDT-EFFING (1981) mentioned this species from the early Pliensbachian and late early Pliensbachian (*davoei* Zone) from El Peñón and Majada del Carrizo (rio Jorquera), Chile.

Description: Very large, thick shells, very inequivalve and inequilateral. The shells are twisted in an anti-clockwise direction (in posterior view) with an angle of torsion (in MCGHEE's sense, 1978) between 40° and 45°. The left valve is highly convex, whilst the right valve is slightly concave.

The general outline of the shell is trapezoidal with a well-developed posterior wing. The left valve has two subparallel carinae that extend from the umbones to the postero-ventral corner of the shell. These carinae enclose an elevated area that is slightly convex and is divided in two portions by a weak sulcus parallel to the carinae. These carinae meet the dorsal margin at an angle between 40° and 50°. The upper carina limits the posterior wing, which is flatter than the remaining shell. The right valve bears only one low ridge from the umbo to the postero-ventral end. A shallow sulcus extends parallel and dorsal to this ridge and limits the posterior wing.

The dorsal margin is long and straight in lateral view, but arched in dorsal view due to shell torsion. The postero-dorsal end is narrow and pointed. The posterior margin is strongly concave at the posterior wing, then it is asymptotic to the dorsal carina and it ends straight, only slightly sinuous between the two carinae. The ventral margin is gently convex and meets both the anterior and posterior margins at nearly right angles. The anterior margin is evenly concave. The maximum shell length is ventrally placed and the maximum height is coincident with the posterior end of the shell. The maximum width is variably located within the anterior half of the shell.

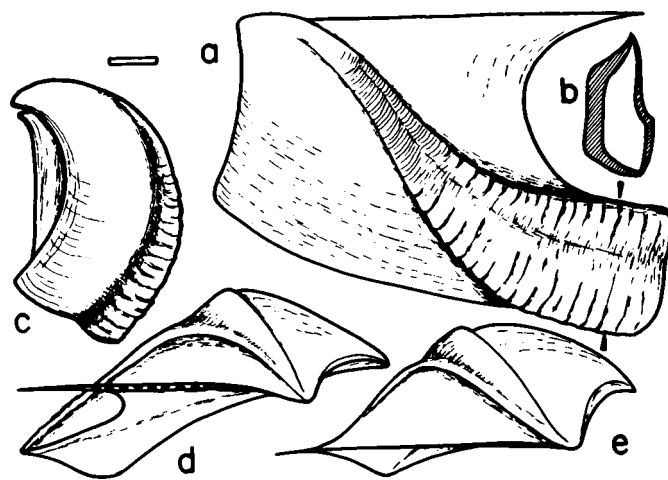
The beaks are prosogyrous and terminal. The left one is narrow and very prominent, whilst the right one only slightly extends beyond the main shell.

The adult shell seems to be edentulous. The ligament is multivincular and the ligamental pits are regularly spaced along all the dorsal margin; they are narrower than the intervals between them, which are flat. The ligamental pits are narrower and closer to each other towards the anterior end. The shell is monomyarian and the adductor muscle scar is large and oval, placed slightly behind the middle part of the shell, at the base of the posterior wing. On the right valve near the umbo there are a couple of small muscle scars.

The outer shell surface of the right valve is smooth with only growth lines. The surface of the left valve is also smooth on the area anterior to the lower carina and on the posterior wing. The raised region between the two carinae has, besides the already mentioned sulcus, a transverse ornamentation that changes during ontogeny. On the first half of this region or on small specimens, only thin transverse crenulations are present, very regularly spaced and separated by slightly broader intervals. On the last half of this region (only in fully-grown specimens) there are transverse, broad and irregular rugae that in some instances become true nodes on the upper and lower carinae. This change or ornamentation is sudden and coincides with a deepening of the central sulcus and a widening of the area between the two carinae.

Due to torsion and the concave right valve, the more prominent points of the shell are the beak, the postero-ventral corner and the antero-ventral angle, all of them on the left valve. There is no proper byssal gape, though between the anterior margin of the left and the right valves a narrow elongated space could correspond to the emergence of the byssus, as the right valve is slightly shorter than the left one.

The shell thickness is greater at the umbonal region of both valves and in the intercarinal area on the left valve. The thinnest part of the shell is the posterior wing.



Text-fig. 9. *Gervilleioperna* (*Gervilletia*) *turgida* (A. LEANZA). Reconstructions based on several specimens. Cerro Roth, Pliensbachian. a: left lateral view; b: posterior section; c: anterior view; d-e: two dorsal views with different orientation of the twisted shell. Bar equals 1 cm.

Measurements:

Specimen	Material	L (mm)	H (mm)	W (mm)	L/H	DI (mm)	γ
MLP 6059, lectotype	LV S	118.85	94.80	47.70	1.25	-	43°
MLP 6260, paralectotype	LV S	86.20	78.50	41.40	1.09	-	50°
MLP 16417, pl. 3, fig. 1	LV S	95.00	71.10	39.00	1.33	92.40	45°
MLP 16418, pl. 3, fig. 3	LV S	75.00	68.00	28.00	1.10	-	50°

Affinities: *G. timoriensis* KRUMBECK, from the middle Lower Jurassic of Timor (KRUMBECK 1923: 76-78, Taf. 4, Fig. 2-3) has a different outline, with a convex posterior margin and lacks strong carinae, there is only a change of shell convexity that limits the posterior wing and that meets the dorsal margin at about 60°. The shell torsion seems to be smaller than in *G. turgida*, which in turn lacks the "lunule" observed in *G. timoriensis*. The right valve of KRUMBECK's species was not figured.

G. atlantis DUBAR (1948: 152-153, pl. 12, fig. 11-13; pl. 13, fig. 1-2), from the Domerian of Morocco, has a triangular outline and a rounded posterior margin, with the right valve feebly convex. It also has a typical radial ornamentation. *G. ? buchi* DE ZIGNO (TAUSCH 1890, p. 14, Taf. 7, Fig. 10-14; DUBAR 1948: 154, text-fig. 50) from the

Lower Jurassic of the Alps and the Pliensbachian, Carixian or early Domerian of Morocco (Middle Atlas) lacks well-defined carinae and the right valve is slightly convex. The smaller specimens seem to have a poorly-developed anterior auricle.

Also from the Lower Jurassic of Morocco DUBAR (1948: 155–157, pl. 30, fig. 11–12, pl. 17, fig. 7) described *G. ? termieri*, that has a radial ornamentation similar to the species of *Cuneigervillia* COX & ARKELL, to which it could possibly be related. Also the hinge characters resemble that genus, though the adult specimens, as observed by DUBAR, are edentulous.

A comparison of *G. turgida* with *Gervillaria ? pallas* (LEANZA), that occurs at the same localities (though not at the same levels), shows that the shell outline is quite different, since *G. turgida* has a pointed antero-ventral angle and a very long posterior wing, being also much more inflated. The external ornament is also different on the two species.

Remarks: A. LEANZA's original description (1942b: 156–157) is incomplete and erroneous in some important morphological features. Leanza only described the left valve and assumed that this was an equivalve shell, despite the fact that on both his specimens the right valve was present, as an internal mould in one case and covered by matrix in the other. This made him imagine the presence of anterior and posterior gapes. Both specimens have the posterior wing broken and so the posterior margin was described by A. LEANZA as "oblique backwards and downwards, forming an obtuse angle with the hinge line". The real outline of the shell can be directly observed on the more complete specimens collected for this study, but nevertheless, it can be also easily reconstructed from a careful observation of the growth lines on the original material.

A great morphologic variability is observed among the few available specimens, especially with respect to the L/H ratio, from almost square specimens (MLP 6260) to longitudinally-elongated trapezoidal specimens (MLP 6059).

Autecology: MCGHEE (1978: 327) suggested that the twisted bivalves were semi-infaunal, living with the left valve downwards. The bivalves that he analyzed lacked the antero-ventral pointed projection of *G. turgida*, that could represent a point of support on hard substrate. Even if this species was epibyssate, the torsion would serve as a way of rising the postero-dorsal portion of the shell (i. e. the pointed posterior wing) above the substrate, if the shell rested on these three points: the left umbo, the antero-ventral end and the postero-ventral angle. Nevertheless, an endobyssate semi-infaunal way of life seems more possible, as the left valve is considerably heavier than the right one, agreeing with SEILACHER'S (1984, text-fig. 5) interpretation of *Gervilleoperma* as a cup-shaped recliner on soft substrates.

Family Inoceramidae GIEBEL 1852

The family Inoceramidae is poorly represented in early Jurassic deposits, as the great diversification of the group happened later during the Middle Jurassic. Nevertheless there are late Triassic inoceramids, and these together with most early Jurassic species, are grouped into the genus *Parainoceramus*. Only very few mentions of Argentine Lower Jurassic inoceramids are found in the literature: BEHRENDSEN (1891, 1922), JAWORSKI (1925a, 1926) and LEANZA (1942b), the last one the only with figured material. In the author's collections only a few specimens were found, all of them are referred here to one species.

Genus *Parainoceramus* COX 1954 (ex VORONETZ 1936)

Type species: *Parainoceramus bulkuriensis* VORONETZ 1936, from the Late Triassic (Carnian) of northern Siberia, USSR, designation by COX 1954: 47.

VORONETZ (1936: 23, 34) included in his new genus *Parainoceramus* four species from the Late Triassic of northern Siberia, all of them represented by poorly preserved material. This author did not name a type species and thus he did not fulfill the requirements of the ICZN (Art. 13b, 50). Some years later COX (1954: 47) designated one of VORONETZ' species, *P. bulkuriensis*, as type. This author also included in this genus two well-known European species. He provided a more complete description of the characters of this genus, adding to the original one the presence of an anterior auricle and anterior teeth at least in some species. COX's concept of the genus is wider than VORONETZ', who only included edentulous forms with "lunule".

Several authors followed COX in considering *Parainoceramus* in its wide sense, such as HAYAMI (1960), who not

only described some early and middle Jurassic Japanese species, but also included within this genus other early Jurassic species from the Alps, Carpathians, Anatolia, Caucasus, Siberia, New Caledonia and Argentina (the species here considered) and extended even more the genus concept to include species with posterior teeth. SPEDEN (1970) described a new species from the early Jurassic of New Zealand and also pointed out the difference between VORONETZ' original meaning and the wider concept of later authors. DUFF (1978: 49) also provided a diagnosis of this genus, accepting species with anterior and posterior teeth. Some of the species included by COX and HAYAMI in *Parainoceramus* were later referred to *Pseudomytiloides* KOSCHELKINA (in HAYAMI 1975, for instance), a genus characterized by inflated shells, without anterior auricle, with short dorsal margin and regular concentric folds (see for example COX in COX et al. 1969: N320; POLUBOTKO 1968b: 60). There is no recent revision of this group and the differences between these two genera vary according to the authors. NUTSUBIDZE (1966) refers some of these doubtful species to *Mytiloides* BRONGNIART.

The presence of anterior and posterior teeth could imply a direct relation to the Bakevellidae, as such teeth are absent from all other inoceramids. HAYAMI (1960) considered that the middle Jurassic and younger inoceramids could have derived, at least partially, from the early Jurassic *Parainoceramus*, taking into account that the small size and the hinge are primitive characters within this family.

The species here described could not be included in *Parainoceramus* if it were considered in its restricted original sense, because it has posterior teeth and a well-developed anterior auricle. *Parainoceramus* in its wide sense, as is used here, has a restricted geographical range during the late Triassic (only known from Siberia), but is almost cosmopolitan during the early Jurassic, including all the Circum-Pacific and also China (see CHEN 1982b) and is only known from the middle and late Jurassic of boreal and probably also austral (see CRAME 1984) regions.

Parainoceramus apollo (A. LEANZA 1942)

Plate 4, fig. 1-6; text-fig. 10, 11

- ? 1891 *Inoceramus* cf. *substriatus* MSTR. - BEHRENDSEN, p. 387.
- ? 1922 *Inoceramus* cf. *substriatus* MSTR. - BEHRENDSEN, p. 172.
- ? 1925 *Inoceramus* cf. *substriatus* MUEST. - GERTH, p. 18.
- *!v. 1942b *Inoceramus apollo* n. sp. - A. LEANZA, p. 157-158, lám. 2, fig. 1.
- v. 1975 *Parainoceramus* ? sp. - DAMBORENEA et al., cuadro 1, 13.
- v. 1978 *Inoceramus apollo* Leanza - CAMACHO & RICCARDI, cuadro 1.
- !v. 1982 *Parainoceramus apollo* (A. LEANZA) - DAMBORENEA, p. 188-193, lám. 44, fig. 1-2; lám. 64, fig. 4-9.

Type material: From the five specimens mentioned by A. LEANZA in his original description (1942b) only two were found in the MLP collections. LEANZA's figured specimen is selected here as lectotype: MLP 6252, a left valve, figured in A. LEANZA (1942b, lám. 2, fig. 1) and here in pl. 4, fig. 1. Although LEANZA indicated that his figure is X 1.5, the specimen was represented in its natural size on his figure. The right valve MLP 6254 is the only extant paralectotype. The type material was collected by FRENGUELLI at Subida a Sañicó (D.7), southern Neuquén province, Pliensbachian.

Additional material: From author's collection: 16 composite moulds of right valves, 15 of left valves and several fragments, MLP 16420 to 16431, 19715 (M 107, 113, 118, 119, 133, 136, 140) and one specimen collected by GULISANO (MLP 15882), all of them from the Piedra Pintada region, southern Neuquén province (Cerro Roth, D.16; SW of School N° 27, D.9; Cerro Del Vasco, D.12; cañadón La Pintada between Cerro Del Vasco and Cerro Roth, D.13; Subida a Sañicó, D.7), Pliensbachian.

Probably also from Espinazo del Zorro region, central Neuquén province, uncatalogued samples at the FCENBA.

Description: Small thin shell, equivalve and inequilateral. Modioliform to sub-trapezoidal in outline, length greater than height and shell moderately inflated in the umbonal region.

The dorsal margin is straight to feebly convex and meets the posterior margin at an obtuse angle. The posterior margin is straight to slightly convex and the ventral margin is evenly convex. The angle between the hinge-line and the maximum oblique length (γ) varies between 55° and 73°.

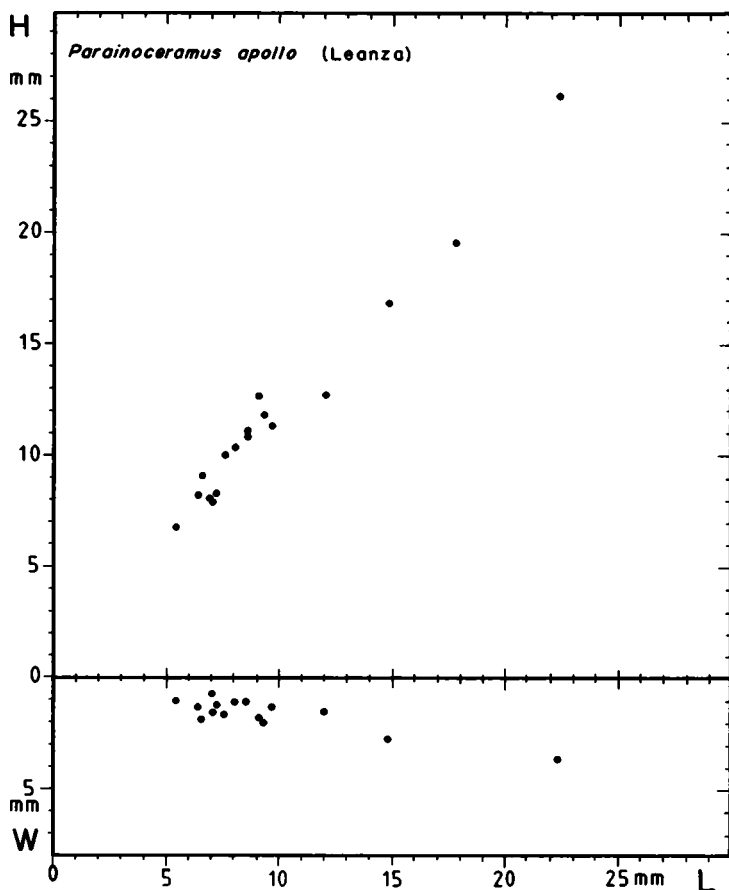
The umbones are prosogyrous and low, slightly exceeding the dorsal margin and are placed very anteriorly. In front of the umbones there is a variably developed anterior lobe, that is not clearly limited from the remaining of the shell. A shallow sulcus extends from the umbones to the middle of the anterior margin, probably corresponding to the emergence of the byssus. The presence of anterior teeth was not observed, though this region is not well preserved in any specimen. A weak posterior tooth, subparallel to the dorsal margin, is present. The

ligamental area is only present on a few specimens, it is narrow and bears numerous multivincular ligamental pits with equally wide interspaces. The muscle scars and pallial line are unknown.

The shell surface has commarginal growth-lines irregularly spaced, sometimes grouped in faint commarginal folds.

Measurements: See also scatter diagram on Text-Fig. 10.

Specimen	Material	L (mm)	H (mm)	W (mm)	DI (mm)	L/H	γ
MLP 6252, lectotype	LV CM	22.25	26.15	3.85	13.70	0.85	58°
MLP 6254, paralectotype	RV CM	7.20	8.25	1.25	4.80	0.87	76°
MLP 16420-a, pl. 4, fig. 5	RV CM	7.65	10.10	1.70	6.00	0.75	65°
MLP 16422-f, pl. 4, fig. 2	LV CM	8.00	10.35	1.15	5.70	0.77	55°
MLP 16424-b, text-fig. 11a	LV CM	12.05	12.65	1.60	8.90	0.95	53°
MLP 16427, pl. 4, fig. 4	RV CM	9.65	11.30	1.30	7.35	0.85	70°
MLP 16429, pl. 4, fig. 3	LV CM	6.95	8.00	0.70	5.75	0.86	67°

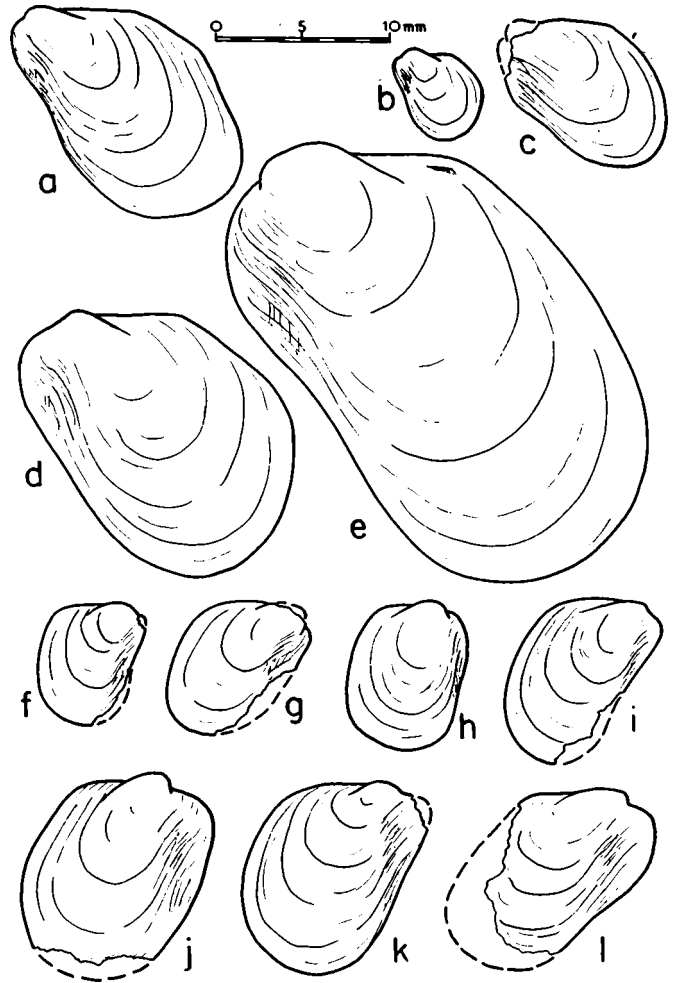


Text-fig. 10. Scatter diagram showing the length/height (L/H) and length/width (L/W) ratios of *Parainoceramus apollo* (A. LEANZA).

Affinities: Within the most similar species is *P. matsumotoi* HAYAMI (1960: 297, pl. 15, fig. 2-8) from the Toarcian of Japan. The only differences are a better-developed anterior auricle and more prominent umbones in *P. apollo*. *P. lunaris* HAYAMI (1960: 295-296, pl. 15, fig. 1) has a more square outline and terminal umbones, but this species is considered as a synonym of *P. matsumotoi* by SPEDEN (1970: 836). CHEN & LIU (1981) mentioned the presence of *P. matsumotoi* in the Lower Jurassic of southern China. On the other hand HAYAMI (1975) referred both species to *Pseudomytiloides*.

The type species of the genus, *P. bulkuriensis* VORONETZ (1936, tabl. 1, fig. 2, 8, 10), from the Carnian of Siberia, is also similar, but it has a more oblique shell and a smaller anterior lobe. The other Siberian Triassic species can be

Text-fig. 11. *Parainoceramus apollo* (A. LEANZA), Pliensbachian. a-e: left valves, a: MLP 16424-b, Cerro Del Vasco; b: MLP 16422-g, Cerro Roth; c: MLP 16422-f, Cerro Roth; d: lectotype, MLP 6252, Subida a Sañicó. f-l: right valves, f: MLP 16425-a, south of School N° 27, Piedra Pintada; g: MLP 16426-a, Subida a Sañicó; h: paralectotype, MLP 6254, Subida a Sañicó; i: MLP 16420-a, Cerro Roth; j: MLP 16431-g, Subida a Sañicó; k: MLP 16427, Subida a Sañicó; l: MLP 16428, Subida a Sañicó.



easily distinguished from *P. apollo*: *P. nicolaievi* VORONETZ (1936, tabl. 1, fig. 4, 6, 12, 13) has an alate posterior region; *P. lenaensis* VORONETZ (1936, tabl. 1, fig. 5, 7, 9) and *P. ? gervillia* VORONETZ (1936, tabl. 1, fig. 11) have more elongated shells.

In the early Jurassic of Europe there are several *Parainoceramus* species with a wide geographical range. A systematic revision of them would probably demonstrate that several of them are synonyms. HAYAMI (1960) provided a list of nominal species and their geographic and stratigraphic range. One of the most cited species is *P. substriatus* (MÜNSTER), to which even Argentine material has been referred (see BEHRENDSEN 1891), from the Pliensbachian of Germany, Italy and Great Britain (GOLDFUSS 1835: 108, Taf. 109, Fig. 2; Taf. 115, Fig. 1; TATE 1876: 375; FUCINI 1920; de GREGORIO 1930: 27, tav. 5, fig. 4; COX 1954: 47; Cox in Cox et al. 1969, fig. C48-4). This species has a very inflated shell, terminal umbones, concave anterior margin and an anterior lobe smaller than in *P. apollo*.

Another Pliensbachian species is *P. ventricosus* (J. DE C. SOWERBY) from Great Britain and France (DUMORTIER 1869; 134, pl. 21, fig. 5-6; TATE 1876: 375; COX 1928: 241; COX 1936: 467) that has a larger shell and an expanded posterior wing. *P. gryphoides* (SCHLOTHEIM, 1813, non *I. gryphaeoides* J. DE C. SOWERBY 1828) (GOLDFUSS 1835: 109, Taf. 115, Fig. 2; QUENSTEDT 1856: 260, Taf. 37, Fig. 11-12) and *P. pernoides* GOLDFUSS (1835: 109, Taf. 109, Fig. 3) from the Pliensbachian - Toarcian of Europe, lack an anterior lobe and are more inflated than *P. apollo*.

P. depressus (MÜNSTER in GOLDFUSS 1835: 109, Taf. 109, Fig. 3), from the Hettangian-Sinemurian of Germany, has a smaller anterior lobe but the shell is more quadrate and the obliquity angle nearer 90° than in the Argentine species.

A Pliensbachian – Toarcian species is also known from New Zealand, *P. martini* SPE DEN (1970: 831, fig. 2–10), which has a very variable shape but has a distinctive sulcus between the umbo and the antero-ventral margin; it lacks lateral teeth.

The species *Inoceramus dubius* (J. DE C. SOWERBY), referred by some authors, such as HAYAMI (1960) to *Parainoceramus* and by others, such as COX in COX et al. (1969) to *Pseudomytiloides* or even to *Mytiloides* (NUTSUBIDZE 1966), is known from the Toarcian – Aalenian of Europe and other places. This species has terminal umbones, regular concentric folds and is inequivalve. It can thus be distinguished from *P. apollo* (see J. DE C. SOWERBY 1828: 162, pl. 584, fig. 3; DUMORTIER 1874: 186, pl. 42, fig. 5–6; TATE 1876: 375; NEUMAYR 1879: 16; QUENSTEDT 1856: 260; DUBAR 1925; COX in COX et al. 1969, fig. C49–2, for instance). Material from the early Jurassic of Malagasy was compared to this species (THEVENIN 1908: 24, pl. 3, fig. 10) and also from the early Jurassic of Iran (FANTINI-SESTINI 1966: 811, tav. 57, fig. 2a–b) and from the Toarcian of the Rocky Mountains of Canada (FREBOLD 1957a: 11). JAWORSKI (1925a: 158–159) referred to this species a specimen from the “late Liassic” of cerro Puchén (= Puchenque), Mendoza province, but the description provided by this author is not sufficiently detailed for comparison with the shells here described, which are, nevertheless, smaller.

HAYAMI (1960: 295, 321) referred to *Parainoceramus* an undetermined specimen figured by AVIAS (1953: 151, pl. 23, fig. 5) from the lowest Jurassic (Hettangian ?) of New Caledonia. This specimen has a similar outline to *P. apollo* but has concentric folds. Also HAYAMI (1964: 167, pl. 7, fig. 8) mentions *Parainoceramus* sp. from the early Jurassic of Vietnam, on the basis of a poorly preserved specimen that lacks an anterior lobe.

There are some inoceramid species in the late early Jurassic of Iran that were studied by FANTINI-SESTINI (1966), who referred them to several species, two of them new. At least part of his material could belong to *Parainoceramus*, the presence of posterior lateral teeth is mentioned for some specimens. *P. apollo* can be compared to *Inoceramus elburzensis* FANTINI-SESTINI (1966: 812, tav. 57, fig. 5–7), but this has a more inflated shell and a less developed anterior lobe.

P. subtilis (LAHUSEN), from the Callovian of Great Britain and USSR (DUFF 1978: 49–51, pl. 3, fig. 12, 17, 18, 21, 22; pl. 4, fig. 1, 2, 12; text-fig. 15–16) lacks an anterior lobe, has anterior teeth and a postero-dorsal angle more acute than in *P. apollo*.

Inoceramus sp. described by ESCOBAR (1980: 46–48, lám. 3, fig. 9), from the Chilean Hettangian, can be distinguished from *P. apollo* by its strong concentric folds and a different shell shape, with length greater than height.

Remarks: BEHRENDSEN (1891: 387; 1922: 172) and GERTH (1925: 18) mentioned specimens from Rio Salado, Mendoza province, probably belonging to *Parainoceramus*, as is suggested by the original identification as *Inoceramus* cf. *substriatus* MÜNSTER. Nevertheless they cannot be unquestionably referred there because BEHRENDSEN’s description is uninformative.

Material compared by TILMANN (1917: 674–675) to *P. amygdaloides* (GOLDFUSS), *P. dubius* (SOWERBY) and *P. substriatus* (MÜNSTER) was mentioned from the Sinemurian of Yerba Buena and Pomacocha, Peru. Unfortunately this author did not provide a good description that would at least help to decide whether it is referable to *Parainoceramus* or to *Pseudomytiloides*.

Autecology: According to STANLEY (1972) species of this genus are typically modioliform and he considered them as endobyssate, semi-infaunal or infaunal forms. For the species *P. martini*, SPE DEN (1970) proposed an epibyssate habit, similar to that of *Pseudauccella*, the great morphological variability observed being due to the crowded mode of life. DUFF (1978: 16) also suggested an epibyssate habit for *P. subtilis* and compared it to other inoceramid species that commonly appear in clusters within beds rich in wood fragments.

The Argentine material does not provide additional information, as they are all single valves. Nevertheless the relation of *P. apollo* to certain sedimentary facies is quite remarkable, as it only appears in dark shales (see DAMBORENEA et al. 1975).

Family Isognomonidae WOODRING 1925

Genus *Isognomon* SOLANDER in LIGHTFOOT 1786

Type species: *Ostrea perna* LINNÉ 1767, by monotypy.

Synonyms: *Pedalion* HUDDLESFORD in LISTER 1770 (vernacular name).

Isognoma SOLANDER in LIGHTFOOT 1786 (objective synonym).

Isognomum (ex KLEIN) MÖRCH 1853 (error pro *Isognomon*).

Subgenus *Isognomon* s. s.

- Synonyms: *Melina* PHILIPSSON [RETZIUS], 1788 (type species: *Ostrea ephippium* LINNÉ 1758).
Perna BRUGUIÈRE 1789 (non PHILIPSSON [RETZIUS], 1788, see VOKES 1967: 156, Bivalvia, Mytilidae; nec OKEN 1815, Bivalvia, Mytilidae, inv. ICZN Opinion 417; nec ADAMS & ADAMS 1858, Bivalvia, Mytilidae; nec WALKER 1855, Insecta).
Perna LAMARCK, 1799.
Pernigenus RENIER, 1807 (nom. van., inv. by ICZN Opinion 427).
Sutura MEGERLY VON MÜHLFELD 1811 (type species: *Ostrea ephippium* LINNÉ 1758).
Pernaria RAFINESQUE 1815 (unjustified emend. pro *Perna* BRUGUIÈRE).
Pernaridea PAETEL 1875 (error pro *Pernaria* RAFINESQUE).
? *Mytiloperna* IHERING 1903 (type species: *Perna americana* FORBES in DARWIN 1846) (non ROLLIER 1914).
? *Pernomytilus* ROLLIER 1914 (type species: *Mytilus pernoides* ROEMER 1836).
Aviculoperna SCHELINTSEV 1931 (non COSSMANN 1887, Bivalvia, Pteriidae).
Casteria TUCKER & WILSON 1933 (type species: *Pedalion (Casteria) kecia* TUCKER & WILSON 1933).
Parviperna IREDALE 1939 (type species: *Parviperna perexigua* IREDALE 1939).
Anisoperna IREDALE 1939 (type species: *Perna australis* REEVE, 1858).

A detailed discussion of the correct use of the generic name *Isognomon* was provided by IREDALE 1915 (fide ARKELL 1933: 207). Some misunderstandings seem to remain about the authorship of the generic name, originally proposed in an anonymous catalogue. COX (1954: 47) and COX & ARKELL (1948: 10) attributed it to HUMPHREY 1786; COX (in COX et al. 1969) to LIGHTFOOT 1786; ARKELL (1933: 207) and YONGE (1968) to SOLANDER, 1786; and VOKES (1967, 1980) to SOLANDER in LIGHTFOOT, 1786.

This genus includes bivalves with subequivalve, compressed shells, of very variable shape, with anterior prosogyrous and low umbones, edentulous. The ligamental area is wide and flat and has numerous ligamental grooves regularly arranged. The shell has a byssal sinus on the right valve, lacks an anterior auricle and the posterior wing is generally not well differentiated. The adductor muscle scar is large and subcentral.

Specimens of this genus are the more frequent pteriaceans in the early Jurassic of Argentina and were found at almost every visited locality. Nevertheless, knowledge about them is very incomplete. All the material is here referred to only one polytypic species.

Isognomon (Isognomon) jupiter (A. LEANZA 1942)

Plate 4, fig. 8-10; pl. 5, fig. 1-5; text-fig. 12, 13

- 1915 *Perna isognomonoides* STAHL - JAWORSKI, p. 415.
1925b *Perna isognomonoides* STAHL - JAWORSKI, p. 41-42.
1925 *Perna isognomonoides* STAHL - GROEBER, p. 459.
non 1931 *Perna isognomonoides* STAHL - WEAVER, p. 204-205; pl. 13, fig. 55.
*!v. 1942b *Perna jupiter* n. sp., A. LEANZA, p. 154-155; lám. 2, fig. 2-4.
. 1953 *Mytiloperna jupiter* LEANZA - GROEBER et al., p. 156.
v. 1975 *Isognomon* - DAMBORENEA et al., cuadro 1, 14.
non 1978 *Isognomon isognomonoides* (STAHL) - CAMACHO & RICCARDI, cuadro 1.
v. 1978 *Isognomon jupiter* (LEANZA) - CAMACHO & RICCARDI, cuadro 1.
v. 1978 *Isognomon* sp. - DAMBORENEA in VOLKHEIMER et al., Tab. 2.
v. 1982 *Isognomon (Isognomon) jupiter* (A. LEANZA) - DAMBORENEA, p. 195-201; lám. 45, fig. 1-7; lám. 65, fig. 1-4; lám. 66, fig. 1-4; lám. 67, fig. 1-2.

Type material: A. LEANZA (1942b) did not designate types, and figured several fragmentary valves. The most complete figured specimen (LEANZA 1942b, lám. 2, fig. 2) could not be located in the MLP collections and is considered lost. Consequently, another specimen figured by LEANZA (1942b, lám. 2, fig. 4) is here selected as the lectotype, MLP 6259-a, a right valve fragment, collected by FRENGUELLI at Cerro Roth (D.16), southern Neuquén province, Pliensbachian. Paralectotypes: MLP 6057, 6058, 6201 and 6259-b, same locality and collector.

Additional material: Most of the material referred to this species was collected in the Piedra Pintada area, southern Neuquén, though it has a very wide geographical distribution and it is also present in Lower Jurassic localities of San Juan and Mendoza provinces, ranging from the early Pliensbachian to the Toarcian in age, although its vertical range could be even wider.

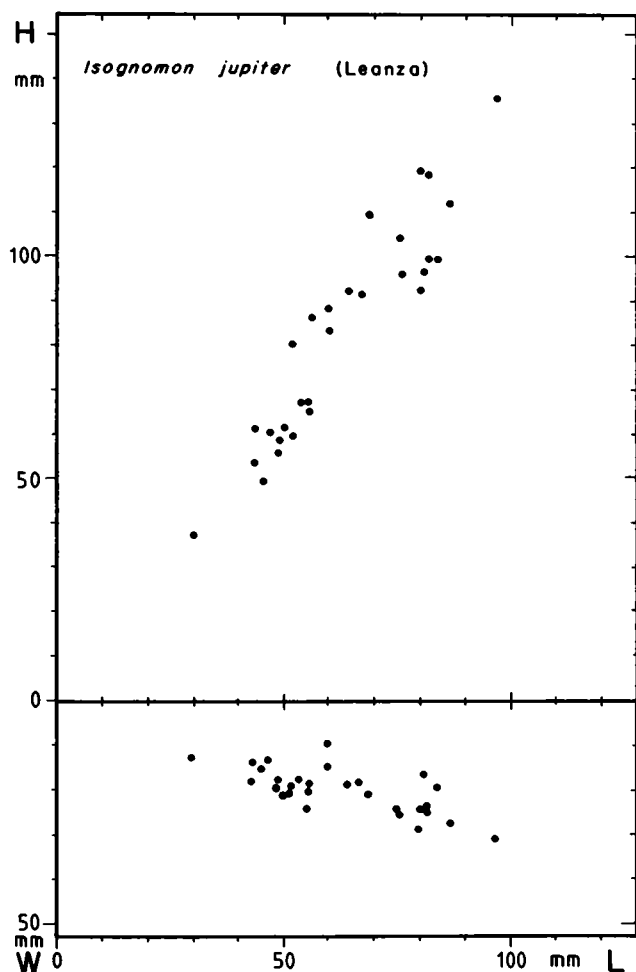
I. jupiter was collected by FRENGUELLI at Cañadón La Pintada and north of Sañicó (D.5) and by the author and colleagues at Cerro Roth (D.16), hill south of Cerro Roth (D.15), Cerro Del Vasco (D.12), Salitral Grande (D.3), 8 km south of Estancia Santa Isabel (D.1), southern Cordillera del Viento (C.1), Cerro Puchenque (B.9), Arroyo Serrucho (B.8), Arroyo Santa Elena (B.7), Arroyo del Portezuelo Ancho (B.5) and Arroyo La Laguna (A.2). The examined material consists of 55 shells with both valves together, 16 of them almost complete, more than 28

fragments of right valves and 23 of left valves, most of them with a recrystallized shell, only a few as internal moulds: MLP 4123, 5614, 16243, 16247, 16312, 16432 to 16470, 19654, 19667, 19672 and 19722 (M 94, 97, 99, 100, 101, 104, 105, 108, 121, 124, 125, 142, 143, 144, 320, 321, 322, 331, 431, 1040, 1041, 1052, 1221, 1298, 1321, 1332, 1334, 1383).

Some specimens are housed at the DNGM (DNGM 8833) and were collected by WAHNISH at Nueva Lubecka, Chubut province. Also from Chubut there is one specimen collected by PIATNITZKY at Mulanguíneo (MLP 18126).

Description: Shell of medium to large size, subequivalve and very inequilateral, outline quite variable, mytiliform to oval. Height greater than length. The dorsal margin is feebly convex and always shorter than the maximum shell length. The anterior margin meets the dorsal one at an acute angle, it is concave in its dorsal portion and then it is straight to slightly convex. The ventral margin is evenly convex. The posterior margin is convex and meets the dorsal one at a variable obtuse angle. The auricles are not differentiated, though in some specimens the posterior region is flatter than the rest of the shell.

The umbones are terminal, prosogyrous and not prominent; the left one is always larger than the right one, but none of them protrudes over the dorsal margin. The shell outline is very variable, there are some mytiliform subtriangular inflated shells (see pl. 5, fig. 3) and some almost flat oval shells (pl. 5, fig. 1, 2) with a whole range of intermediate forms. Also the thickness of the shell is quite variable. In the concave anterior margin the shell has a lamellose appearance and this lamellose region has a variable width that increases considerably with the shell size. Besides this low and lamellose region, the right valve also has an elongated concavity that forms an anterior slit or narrow gape for the emergence of the byssus. The relative convexity of both valves is also variable, either the right or the left valve can be more inflated than the other. An anterior low ridge that limits the concave anterior region of the shell is present on both valves, though this is more prominent on the right valve.



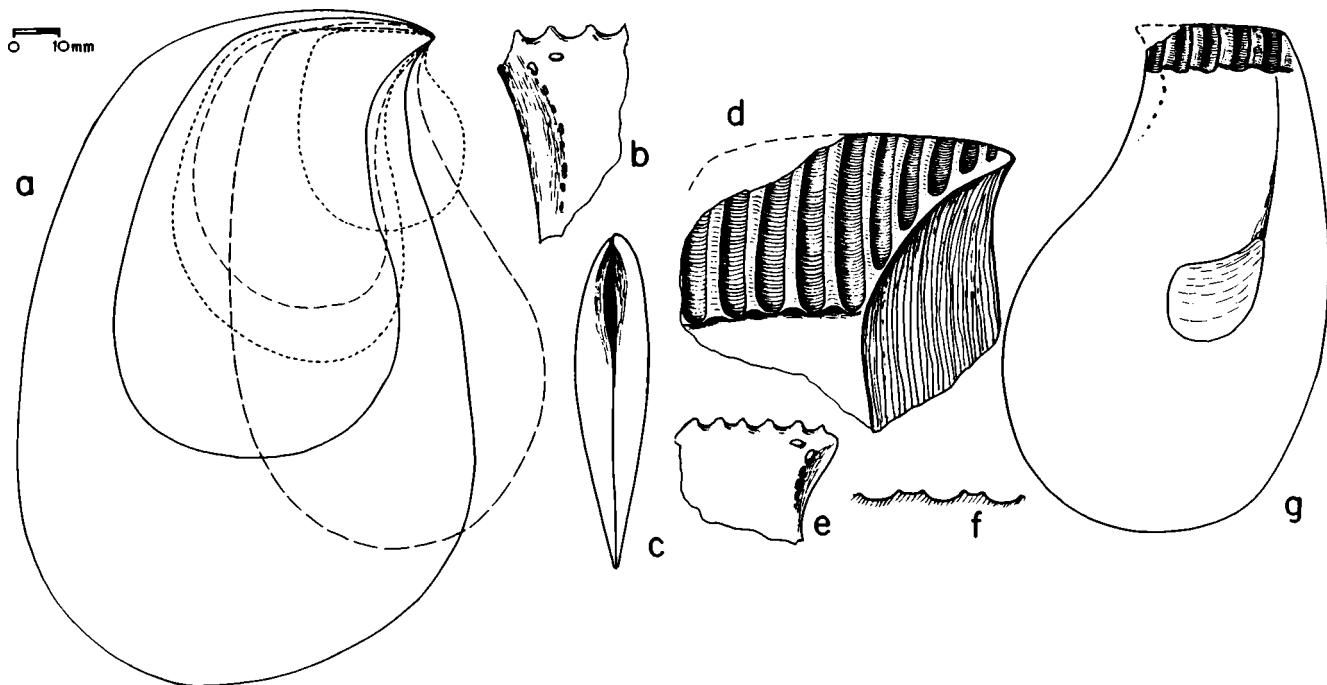
Text-fig. 12. Scatter diagram showing the length/height (L/H) and length/width (L/W) ratios of *Isognomon jupiter* (A. LEANZA).

The hinge is edentulous. The ligament is multivincular, with regular ligamental grooves. The number of ligamental grooves is also variable, but on the inner margin of the ligamental area there are always between seven and five grooves, which were the functional ones. Several other grooves (up to six) are left in the anterior region without function (see pl. 5, fig. 4). The intervals between the grooves are flat with somewhat elevated margins (see text-fig. 13-f). The width of the intervals is almost equal to the grooves in young specimens, but becomes narrower in the functional part of the ligament in fully-grown shells.

The ligamental area is almost flat and forms a very acute angle with the commissural plane between the valves. The space between the valves has a spindle shape in dorsal view, with its maximum width at about mid-length (see pl. 4, fig. 9 b). In some big specimens the grooves are arched and anteriorly concave, i. e., the growth was faster at the posterior region of the ligamental area. This was possibly related to a change in shell outline, as in young specimens the shell is prosocline and in fully grown specimens it is ortocline to even opistocline (see text-fig. 13 a). This relation is evident with the measurement of the angle between the dorsal margin and a tangent to the most protruded point of the anterior margin that passes through the umbones (similar to the angle considered by ARKELL 1933: 208, called here δ): this is nearly 90° , slightly less in young specimens and slightly more in adult shells.

The adductor muscle scar is tear-shaped, higher at the posterior end. The byssal muscles or anterior pedal retractors leave deep scars near the umbones and along the dorsal portion of the anterior margin. There are two larger scars near the umbo and a row of pit-like impressions (see text-fig. 13 b, e). The inner margin of the shell is smooth.

The shell surface is smooth with commarginal growth lines, and in some specimens also commarginal folds more or less regularly arranged are present.



Text-fig. 13. *Isognomon jupiter* (A. LEANZA), all specimens from Piedra Pintada region, Pliensbachian. a: outline of some right valves, showing great variability of shape; b: MLP 16449-b, internal mould of a left valve, umbonal region; c: anterior view; d: MLP 6085-f, paralectotype, ligamental area of left valve; e: MLP 16450-d, internal mould of right valve, umbonal region; f: section of the ligamental area, showing its relief; g: MLP 16450, internal mould of left valve.

Measurements: See also scatter diagram on text-fig. 12.

Specimen	Material	L (mm)	H (mm)	2W (mm)	Dl (mm)	L/H	δ
MLP 6058-ab, paralectotype	BV S	51.85	70.05	20.75	36.60	0.74	82°
MLP 16433	BV S	66.85	91.10	18.45	53.60	0.73	87°
MLP 16438, pl. 5, fig. 2	BV S	59.90	78.10	15.00	36.05	0.76	-

MLP 16452, pl. 4, fig. 9	BV	S	96.90	135.00	30.40	56.90	0.71	95°
MLP 16453, pl. 4, fig. 10	BV	S	63.70	92.50	19.05	43.85	0.68	82°
MLP 16455	BV	S	47.15	60.20	13.10	37.00	0.78	99°

Affinities: Due to the wide range of morphological variation displayed by *I. jupiter*, it is very difficult to establish proper comparisons with species that are known through only a few specimens or illustrations. The comparison was then established on the basis of apparently more stable features, such as the number, form and pattern of the ligamental grooves, instead of variable characters such as the shell outline. ARKELL (1933) used, for the Corallian British species, the angle δ , which allowed him to recognize several taxa. Nevertheless it must be pointed out that the variation in this value observed within *I. jupiter* equals the range observed by ARKELL in all the species studied by him.

I. isognomonoides (STAHL), to which some early Jurassic Argentine material was referred, is a widely distributed species in the Middle Jurassic of Europe. According to the available figures of this species (GOLDFUSS 1836, LYCETT 1863 as *P. mytiloides* LAMARCK; PHILLIPS 1871 also as *P. mytiloides*; GREPPIN 1899–1900; FISCHER 1969; COX et al. 1969) this species has a better delimited posterior auricle, more numerous ligamental grooves, a narrower ligamental area and a more acute umbonal angle, but the general outline is similar, especially in specimens of *I. jupiter* having a δ angle less than 90°.

The Argentine species is also similar to *I. subplanus* (ETALLON), from the Oxfordian of Great Britain. A complete description of this species was provided by ARKELL (1933: 212–214, pl. 27, fig. 1–4; text-fig. 49, 53). The variability in outline, shell thickness and other features in *I. jupiter* is wider than the admitted range for the European species. Some big specimens of *I. jupiter* also resemble *I. flambarti* (DOLLFUSS), as was already described by ARKELL (1933: 214–216, text-fig. 54), though the posterior auricle is better delimited and the posterior margin is sinuous in *I. flambarti*.

Some Argentine specimens are also similar to *I. lugdunensis* (DUMORTIER, 1869: 297–298, pl. 36, fig. 1–2; FUCINI 1897, tav. 24, fig. 12–14) from the Domerian of France and Italy, but the shell shape of this species, with the height greater than the length, is not common in *I. jupiter*, which also has fewer ligamental grooves and a comparatively wide ligamental area.

I. perplanus (WHITFIELD), from the Middle Jurassic of the United States (IMLAY 1964b: 24–25, pl. 1, fig. 32–34; 1967a: 78–79) differs from *I. jupiter* by the irregular ligamental grooves.

I. oolithicus (ROLLIER) (1914: 431; MORRIS & LYCETT 1855: 25, pl. 3, fig. 1 as *P. rugosa* GOLDFUSS; COX & ARKELL 1948: 10) has an outline that resembles some specimens of *I. jupiter* with posterior wing and thin shell, but the general shape is more quadrangular in the Bathonian European species.

There are several *Isognomon* (or “*Perna*”) species that have been described for the South American Mesozoic. A comparison with each of them follows. “*Perna*” *americana* FORBES (in DARWIN 1846: 266, pl. 5, fig. 4–5; R. PHILIPPI 1899: 45, lám. 22, fig. 8; IHERING 1903: 123–125, fig. 1) from the early Jurassic of Chile, apparently lacks the byssal gape. This is, nevertheless, a very poorly known species, for which IHERING proposed the new genus *Mytiloperna* IHERING 1903 (non ROLLIER 1914). On the other hand “*P.*” aff. *americana* FORBES (HAUPT 1907: 207–208, Taf. 10, Fig. 2a–c) and “*P.*” cf. *americana* FORBES (WEAVER 1931: 209) from the Neocomian of Cerro Lotena, Neuquén province, do not belong to FORBES’ species and have a very arched beak, a clear byssal sinus on the right valve and a very thick shell.

“*P.*” *ricordeana* D’ORBIGNY (WEAVER 1931: 208–209, pl. 16, fig. 66–70) also from the Neocomian of Cerro Lotena, has a very thick shell and a clearly delimited posterior wing. From the same locality and similar stratigraphic position comes “*P.*” *lotenoensis* WEAVER (1931: 206–207, pl. 17, fig. 73–75, 77–78), which has a mytiliform shape with a very small δ angle and an almost straight anterior margin.

“*P.*” cf. *bayani* DE LORIO (HAUPT 1907: 207) from the early Tithonian of Cerro Lotena, was not figured by HAUPT, but DE LORIO’s species (DE LORIO & PELLAT 1874–1875, pl. 20, fig. 8–9) has a very high shell, with numerous ligamental grooves and narrow ligamental platform.

“*P.*” *nana* BEHRENSSEN (1892: 11, Taf. 1, Fig. 6; 1922: 20, lám. 3, fig. 6; MANCENIDO & DAMBORENEA 1984, lám. 2, fig. 19–23), from the early Cretaceous of Neuquén and Rio Negro provinces, and the material referred as “*P.*” *isognomonoides* STAHL by WEAVER (1931: 204–205, pl. 13, fig. 55) has a smaller shell and an acute postero-dorsal angle, with a sinuous posterior margin and a pear-shaped outline.

From this comparison the following species must be excluded: “*P.*” *militaris* BURCKHARDT (1903: 70, pl. 15, fig.

3-5; WEAVER 1931: 211-212, pl. 15, fig. 65) which is a *Gervillaria*, as already said; and "*P.*" *quintucoensis* WEAVER (1931: 210-211, pl. 17, fig. 76-79, pl. 19, fig. 92), which is a *Mulletia*.

From the Chilean material described by R. PHILIPPI (1899) without stratigraphical data, "*P.*" *stolpi* PHILIPPI (1899: 45, lám. 23, fig. 5) resembles *I. jupiter* in outline, but the internal characters of the Chilean species are unknown. "*P.*" *subaurita* PHILIPPI (1899: 44-45, lám. 21, fig. 4) has a well-developed wing. "*Avicula*" ? *colchaguensis* PHILIPPI (1899: 40, lám. 21, fig. 2), a doubtful *Isognomon*, differs from *I. jupiter* in being antero-posteriorly elongated. *Avicula euryptera* PHILIPPI (1899: 39-40, lám. 21, fig. 1) and its probable synonym *A. alberti* PHILIPPI (1899: 40, lám. 21, fig. 3) could belong to or be closely related to *Isognomon (Rostroperna)*, a subgenus from the Cretaceous of the Near East (see COX 1964).

Remarks: Material from the type locality of this species had been described by JAWORSKI (1915: 415; 1925b: 41-42) and referred to the Middle Jurassic European species *I. isognomonoides* (STAHL). JAWORSKI erroneously thought that the beds that yielded this species were of Bajocian - Bathonian age (see GROEBER in JAWORSKI 1925b, footnote p. 42).

Some remarks must be added about the material described and figured by WEAVER (1931: 204-205, pl. 13, fig. 55) as *Perna isognomonoides* STAHL and referred to Lower Jurassic strata by this author. WEAVER's fossil locality 1034 was described (WEAVER 1931) as "about 17 km north of the town of Sañicó in Neuquén". However, in a survey of the area no Lower Jurassic strata were observed. This material may be referred to *I. nanus* (BEHRENSSEN, 1892: 11, Taf. 1, Fig. 6; 1922: 206, lám. 3, fig. 6; MANCENIDO & DAMBORENEA 1984, lám. 2, fig. 19-23), originally found by BODENBENDER in the Quintuco beds that crop out on the left bank of the Catán Lil river somewhat to the north of Catán Lil and erroneously referred by BEHRENSSEN (op. cit.) to the early Middle Jurassic (see also GROEBER in JAWORSKI 1925b, footnote on p. 68 and ROLLERI et al. 1984).

A. LEANZA (1942b) only had fragmentary shells of *I. jupiter* and thus his original description did not include the general outline and other related characters. The arched ligamental grooves, to which LEANZA assigned special importance as a distinctive character, are quite common among *Isognomon* species, especially in fully-grown specimens.

In spite of the observed morphological variation, not enough specimens are available to attempt a statistical analysis. The intermediate forms and the fact that several morphotypes are commonly found in the same bed point to a very variable species rather than a group of species.

Autecology: Extant species of *Isognomon* live in tropical seas (YONGE 1968; STANLEY 1970) in shallow waters. YONGE (1968: 363) analyzed the species *I. ephippium* (LINN.) and observed that it lives attached by a strong byssus to intertidal rocky bottoms, lying on its right valve. Other extant species, such as *I. alatum* (GMELIN) attach to mangroove roots or to coral colonies, as does *I. radiata* (ANTON), as was reported by STANLEY (1970: 135-136). In all cases the shell shape is very variable due to the gregarious habits resulting in spatial restriction.

I. jupiter had a strong byssus and probably lay on its right valve. There is no evidence to interpret which was the preferred substratum for this species.

Family Pulvinitidae STEPHENSON 1941

The family Pulvinitidae includes bivalves with multivincular ligament, byssal foramen on the right valve and laterally compressed and lamellose shells. It is represented by at least ten nominal species that range from the Jurassic to the Recent in very discontinuous records. The present one is the first record of this family in continental South America and one of the oldest in the world (i. e. Pliensbachian).

Only three genus-group taxa are included in this family: *Hypotrema* D'ORBIGNY, with Late Jurassic representatives in Europe and to which the Early Jurassic Argentine material is referred; *Pulvinites* DEFRANCE, with one mid-Jurassic and several Late Cretaceous to Palaeocene species from East Asia, Europe, North America and Antarctica; and *Foramolina* HEDLEY, that includes the only living species of the family. The lack of records in the long intervening time intervals was commented upon by previous authors. COX (in COX et al. 1969) thought that those stratigraphical gaps are due to imperfection of the fossil record, an opinion admitted by ZINSMEISTER (1978), but this last mentioned author also considered it a possibly polyphyletic family and suggested that *Foramolina* could be an "aberrant" *Isognomonidae* and the poorly known *Hypotrema* a doubtfully related taxon. Nevertheless the morphological similarity of all these three taxa is very strong, as they share important characters already mentioned

by other authors and also an opistogyrous subcentral umbo, a very rare feature among the Isognomonidae. Recently PALMER (1984) revised every species of the Pulvinitidae known to him and concluded that all of them should be accommodated in only one genus, i. e. *Pulvinites*. Though his opinion seems soundly based and is accepted here, it still seems useful to recognize *Hypotrema* as a separate subgenus, since some of the characters listed by COX (in COX et al. 1969) in his revised diagnosis of *Hypotrema* allow the separation of both groups (cf. DAMBORENEA 1982: 203).

The best known subgenus is *Pulvinites* s. s., especially the species *P. argenteus* CONRAD from the Late Cretaceous of the United States, very well illustrated by WADE (1926: 52, pl. 13, fig. 5, 6, 8, 9). To the classical records of this genus from the Late Cretaceous of France and the United States, some recent records from the Late Cretaceous of Antarctica and Palaeocene of California were added by ZINSMEISTER (1978). On the other hand *Hypotrema*, traditionally known from the French Late Jurassic, was also reported for the English middle Bathonian by HALLAM (1977a: 71) and PALMER (1979: 196 and 219), but those specimens are presumably the same that have been just described as *Pulvinites mackerrowi* PALMER (1984).

The need for a further unnamed subgenus has been claimed by YAMANI (1975: 54) for a couple of unusual specimens from the lower Tithonian of Bavaria.

Genus *Pulvinites* DEFRANCE in BLAINVILLE 1824

Type species: *Pulvinites adansonii* DEFRANCE in BLAINVILLE 1824, from the Upper Cretaceous of France, by monotypy.

Synonyms: *Puvinites* D'ORBIGNY 1847: 522 (error pro *Pulvinites*).

Pulvinitis D'ORBIGNY, 1847: 522 (error pro *Pulvinites*).

Subgenus *Hypotrema* D'ORBIGNY 1853

Type species: *Pulvinites rupellensis* D'ORBIGNY 1850, from the Upper Jurassic of France, subsequent designation by COX 1969 (in COX et al. 1969: N326) (= ? *Pulvinitis oblonga* D'ORBIGNY 1847: 522, nomen nudum, see VOKES 1941).

Although only left valves are known, the material here described is referred to *Pulvinites* (*Hypotrema*) on the grounds of the muscle scar pattern and the characters of the umbo and arched ligamental area.

Pulvinites is characterized by an elongated and pointed postero-ventral corner of the shell, resembling the branchitellum in some oysters, whilst in *Hypotrema* this character is less developed or absent and the shell is more rectangular in outline. It is interesting to note that in other bivalve groups the presence/absence of "branchitellum" is used as a distinctive character at a generic level, for instance between *Acutostrea* VYALOV and *Crassostrea* SACCO, between *Praeexogyra* CHARLES & MAUBEGE and *Liostrea* DOUVILLÉ, between *Eligmus* EUDES-DESLONGCHAMPS and *Chalmasia* STOLICZKA.

Pulvinites (*Hypotrema*) *liasicus* n. sp.

Plate 6, fig. 13-14

!v.1982 *Hypotrema liasica* n. sp. - DAMBORENEA, p. 203-205; lám. 64, fig. 10 (unavailable name).

Derivation of name: The specific name refers to the stratigraphical occurrence of this species.

Material: Only three composite moulds of left valves are available: holotype: MLP 16471 (M 320), figured here in pl. 6, fig. 13; paratypes: MLP 13901 (M 1051) and 19023 (M 1285), collected by the author from the late Pliensbachian (*Fanninoceras* Zone) of Cerro Puchenque (B.9) and Paso del Portezuelo Ancho (B.4), southern Mendoza province and Estancia Santa Isabel (D.1), Neuquén Province.

Doubtfully included in this species: a left valve, MLP 16472 (M 322), from the late Pliensbachian of Cerro Puchenque (B.9), Mendoza (pl. 6, fig. 15).

Diagnosis: Shell of elliptical irregular outline, height greater than length, flattened, of lamellose appearance. Low opistogyrous umbones, placed at the posterior half of the shell. Arched multivincular ligamental area with five to ten regular ligamental grooves, with intervals of equal width. Right valve unknown.

Description: Medium-sized shell, of elliptical irregular outline, sometimes subtriangular, slightly elongated posteriorly, flattened. The dorsal margin is short and convex, the anterior margin is regularly convex. The posterior margin is almost straight and the ventral one evenly convex. There are no auricles. The shell has a lamellose appearance, similar to some oyster shells, with irregularly spaced commarginal growth lines and lacks any trace of radial ornamentation.

The umbones are low and opistogyrous and they are almost centrally placed, slightly shifted posteriorly. The hinge is edentulous. The ligamental area has an even width but is slightly arched, parallel to the dorsal margin. It bears five to ten tall and narrow ligamental grooves that are separated by intervals of equal width. The ligamental grooves are feebly concave backwards.

On the composite mould of the holotype a pair of very tenuous muscle scars can be seen, one of them near the umbo, that probably corresponds to the byssal muscle, and the other, which is ventral to the first one, is larger and corresponds to the adductor muscle. Both are very close to each other, but it cannot be determined if they are actually in contact. Other internal characters are unknown.

Measurements:

Specimen	Material	L (mm)	H (mm)	W (mm)	L/H	Ll (mm)	Wl (mm)	pit n°	Ll/n°	L/Ll
MLP 16471, holotype	LV CM	32.55	38.90	3.40	0.83	11.35	2.60	10	1.13	2.86
MLP 19023, paratype	LV CM	36.15	37.70	1.90	0.95	5.40	2.75	5	1.08	6.69

Affinities: *P. (Hypotrema) rupellensis* D'ORBIGNY, the type species of this subgenus from the "Corallian" (probably Kimmeridgian) of France (D'ORBIGNY 1853: 437, pl. 10, fig. 1–12; COTTREAU 1929, pl. 20, fig. 17–19; COX in COX et al. 1969, fig. C53–1; PALMER 1984: 820, pl. 72, fig. 2) has a similar outline but is higher, more rectangular and more inflated than *P. (H.) liasicus*. On the other hand the ligamental area and the form and number of the ligamental pits are about the same in both species.

It is also possible to establish comparisons with species of *Pulvinites* s. s., though all of them differ from *P. (H.) liasicus* because their ligamental area has a straighter ventral edge. The shell outline of the Argentine species reminds one of that of *P. argenteus* CONRAD, from the late Cretaceous of Tennessee, U.S.A. (WADE 1926: 52, pl. 13, fig. 5, 6, 8, 9; STEPHENSON 1941: 151, pl. 24, fig. 15–16; COX et al. 1969, fig. C53–2; PALMER 1984, pl. 72, fig. 3–4), though *P. (H.) liasicus* is higher and has fewer (five to ten instead of ten to fifteen) ligamental grooves. *P. mackerrowi* PALMER (1984: 822, pl. 72, fig. 5, text-fig. 2), from the Bathonian of Oxfordshire, is more inflated and has a more orbicular outline than the Argentine species.

P. adansonii DEFRANCE, from the upper Cretaceous of Normandy, Lebanon and Antarctica (VOKES 1941: 8, fig. 14–15, under the name *P. auriculus*; ZINSMEISTER 1978: 567, pl. 1, fig. 1–4 under the name *P. antarctica*; PALMER 1984: 819, pl. 72, fig. 1) has a trigonal shape and a larger size than *P. (H.) liasicus*. *P. californicus* ZINSMEISTER and *P. pacificus* ZINSMEISTER, from the early Tertiary of California (ZINSMEISTER 1978: 568–569) have fewer ligamental grooves (four to five), besides, as references to illustrations in text and plate-legends are conflictive it is nearly impossible to know which is which. It is also worth pointing out that both the foramen and the suture may naturally increase their distance from the hinge during ontogeny.

Hypotrema (subgen. indet.) n. sp. from the Lower Tithonian of southern Germany (YAMANI 1975: 54, Taf. 2, Fig. 12–13) is conspicuously distinctive since it has a strongly inflated left valve, more incurved rather mesogyrous left beaks, 12–13 ligamental pits confined behind the umbo.

It is interesting to note that from the Hettangian of France COSSMANN (1904: 501, pl. 16, fig. 6) described one specimen as "sp. indet.?" that could be included into *Hypotrema* according to its ligamental characters and opistogyrous umbo. This specimen is smaller than the Argentine ones and has only five ligamental grooves. If this is a true pulvinitid, the range of the family might be extended back to the earliest Jurassic.

Autecology: There is very little knowledge about the mode of life of the extant members of this family. Some of the fossil pulvinitid species appear in life position on coral fronds or brachiopod shells (D'ORBIGNY 1853; PALMER 1984), or are associated with corals (YAMANI 1975), and some specimens show xenomorphic sculpture (PALMER 1984). However, PALMER (1979: 219) observed that in the White Limestone Formation *Hypotrema* sp. seems to be restricted to (or at least shows a marked preference for) the micritic facies. The Argentine specimens also appear in fine-grained calcarenites.

Order Ostreoida FÉRUSAC 1822
Suborder Pectinina WALLER 1978

Superfamily Buchiacea COX 1952

WALLER (1978) proposed the superfamily Buchiacea to include the Buchiidae, Oxytomidae, Pseudomonotidae and Monotidae and also some genera referred by COX et al. (1969) to the Aviculopectinidae. All these taxa share, according to WALLER, a peculiar shell structure and they lack a true ctenolium. They are a group of edentulous bivalves with a disjunct pallial line and an ostreid-type resilifer, usually inequivalve and with a right anterior auricle limited by a deep subauricular notch.

Family Monotidae P. FISCHER 1887

Most recent authors agree in regarding *Otapiria* as a Monotidae. Nevertheless, while *Monotis* has been revised on a global scale (ICHIKAWA 1958; WESTERMANN 1973a, GRANT-MACKIE 1976, 1978a, 1978b, 1978c, 1978d, 1979) and its geographical and stratigraphical range is known in detail after articles by WESTERMANN (1970, 1973a, 1973b) and GRANT-MACKIE (op. cit.) *Otapiria* only received occasional attention. This difference is due to several factors: *Monotis* is more abundant and varied and there was a need to study organisms that could provide a detailed biostratigraphical zonation for the late Triassic in areas with poorly preserved ammonites.

Genus *Otapiria* MARWICK 1935

Type species: *Pseudomonotis marshalli* TRECHMANN 1923, from the early Jurassic (Aratauran) of New Zealand, by original designation.
Synonym: *Pleuromysidia* ICHIKAWA 1954 (type species: *Pleuromysidia dubia*. ICHIKAWA 1954, from the late Triassic of Japan, by original designation).

The systematic position of this genus, originally described from the early Jurassic of New Zealand, has been the object of several discussions. *Otapiria* was referred to the Pteriidae by MARWICK (1935: 302; 1953: 53, 94) and COX & ARKELL (1948: 7); to the Aviculopectinidae by COX et al. (1969: N374) and to the Monotidae by ZAKHAROV (1962: 23–25), KIPARISOVA et al. (1966: 109), IMLAY (1967b: 3), CECIONI & WESTERMANN (1968), GRANT-MACKIE & ZAPFE (1973), ZAPFE (1973), OKUNEVA (1976), KOCHANOVÁ (1977), COVACEVICH & ESCOBAR (1979) and DAMBORENEA (1980) among others; and more recently to the Buchiidae by ZAKHAROV (1981).

MARWICK included the hinge characters in his original diagnosis of the genus and he provided a set of drawings based on specimens of the type species. These features are rarely preserved and the fact that they were not adequately illustrated by photographs produced a long controversy about *Otapiria*'s family status. Besides the original diagnosis, MARWICK later published a new definition (1953: 95) and some years later IMLAY (1967b: 1) provided a summary and a discussion of its characters.

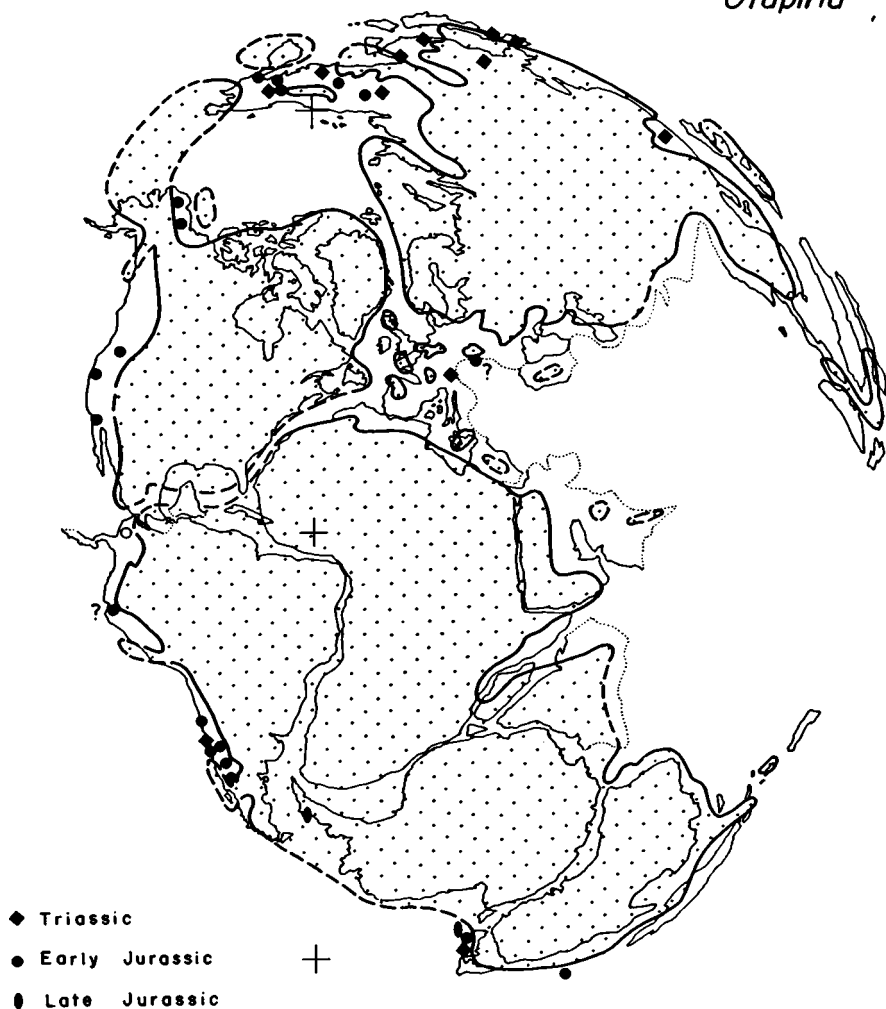
COX (in COX et al. 1969) included *Otapiria* in the Aviculopectinidae because "... the presence (according to MARWICK) of a triangular ligamental pit precludes reference to ... Monotidae". Nevertheless, these hinge characters were not included in a subsequent definition of the genus by MARWICK himself (1953). SPEDEN (pers. comm., 1975) considered that the ligamental area of the type species differs from MARWICK's original description in two main aspects: the depression in front of the ligament in the left valve probably received the byssal auricle of the right valve and the grooved margin at its back is probably the result of the arrangement of the shell layers and is not part of the ligamental area.

According to IMLAY (1967b: 2) *Otapiria* differs from *Monotis* in having a deep ligamental pit, less differentiated posterior wings, a different ornamentation with thinner and less regular radial ribs that may be wavy and more and stronger concentric folds.

MARWICK (1935: 302) considered *Otapiria* to be related to *Entomonotis* MARWICK, a taxon that is nowadays regarded as a subgenus of *Monotis* BRONN (ICHIKAWA 1958; COX et al. 1969: 374, GRANT-MACKIE 1978a) or even as a synonym of it (MÜLLER 1938; MARWICK 1953: 57; TOZER 1961; WESTERMANN 1962: 756; 1973b: 253).

KIPARISOVA et al. (1966: 109–110) also discussed the relationships between *Otapiria* and *Monotis* and gave examples in which the reference to one genus or the other was quite difficult. More recently OKUNEVA (1976) illustrated the ligamental characters in a couple of specimens from the Triassic of Siberia.

Text-fig. 14. Palaeogeographic distribution of the genus *Otapiria* during the Triassic and Jurassic. Palaeocontinental reconstruction from SMITH & BRIDEN (1977) for the early Jurassic, hypothetical coastlines compiled from various sources.



Another taxon that is related to *Otapiria* is *Lupherella* IMLAY (1967b: 2) but this last one has a smaller and less oblique shell, longer dorsal margin and posterior wing, more and thinner concentric folds and a small anterior auricle on the left valve (IMLAY 1967b: 2). These same features, together with a less prominent radial ornamentation, allow the distinction between *Lupherella* and *Monotis* (see also GRANT-MACKIE 1978a: 100).

There is a strong relation then among the genera *Monotis*, *Otapiria* and *Lupherella* and all of them can be grouped in the same bivalve family.

A supraspecific arrangement of *Otapiria* species is attempted here, in order to understand the morphological variability of these bivalves, as well as their geographic and stratigraphic distribution (shown on text-fig. 14). These groups of species could either be named as subgenera or be maintained as such. Their main features and composition are as follows:

a) *O. marshalli* (TRECHMANN), *O. marshalli alpina* ZAPFE, *O. tailleuri* IMLAY, *O. omolonica* POLUBOTKO, *O. neuquensis* n. sp. and perhaps also *O. versicostata* (BYCHKOV) and *O. sp.* in KOCHANOVÁ (1977). These species, grouped around the type species of *Otapiria*, are characterized by the elongated shells, the left valve more inflated than the right one and radial ornamentation prevailing over the concentric and equally developed on both valves. This group extends from the late Triassic to the Sinemurian of New Zealand, New Caledonia, Alaska, northern Siberia, South America, Carpathians and Austria. *O. neuquensis* n. sp. is intermediate between this group and group (c).

b) *O. limaeformis* (ZAKHAROV), *O. limaeformis affecta* POLUBOTKO, *O. ussuriensis* (VORONETZ), *O. ussuriensis chankaika* (VORONETZ), *O. dissimilis* (COX), *O. pacifica* COVACEVICH & ESCOBAR and perhaps also *O. masoni*

MARWICK. Elongated shells, with the left valve more inflated than the right one, strong and dense radial ornamentation on the left valve and weaker ornamentation on the right valve. Norian to Kimmeridgian of northeast Siberia, Chile and New Zealand. *O. masoni* MARWICK, from the Kimmeridgian of New Zealand, is intermediate between this group and the next two.

c) *O. pseudooriginalis* (ZAKHAROV), *O. originalis* (KIPARISOVA) and *O. ? frenguelli* n. sp. Subcircular shells with umbones slightly anteriorly placed, compressed shells with very faint radial ornamentation on both valves. Hettangian to Sinemurian of northeast Siberia and Pliensbachian (?) of South America. If *O. inaequicostata* GEYER is an *Otapiria*, it could be included in this group.

d) *O. dubia* (ICHIKAWA), *O. annulata* POLUBOTKO, *O. korkodonensis* POLUBOTKO and *O. kanmerai* (TAMURA). Small and very inflated shells without (or with very faint) radial ornamentation and with strong concentric folds. The name *Pleuromysidia* ICHIKAWA is available for this group if it is distinguished as a subgenus. It is known from the Carnian ? – Norian of northeast Siberia and Japan.

Lupherella boechiformis (HYATT) from the Pliensbachian of the United States, probably represents an extreme in the variability of these bivalves. It is related to the group of *O. pseudooriginalis*, from which it can be distinguished by a central umbo and a characteristic cancellate ornament. It is interesting to note that GRANT-MACKIE (1978a: 100) tentatively placed both *O. originalis* and *O. pseudooriginalis* in the genus *Lupherella*. This study revealed that the young specimens of some species of *Otapiria*, such as *O. originalis* and *O. neuquensis*, show a strong resemblance to the adult shells of *L. boechiformis*. An analogous relation is apparent between the young specimens of group (b) with the adults of group (d). On that basis *Lupherella* could be considered as a subgenus of *Otapiria*, perhaps originated by pedomorphosis of organisms from the groups (a) or (c), in the same way as *Pleuromysidia* could be a pedomorphic subgenus in respect to the group (b) of *Otapiria*.

These morphologic groups within *Otapiria* are analogous to the groups recognized within *Monotis* (WESTERMANN 1973a, 1973b, GRANT-MACKIE 1978a). This resemblance could be explained as a result to the adaptation to similar environments and way of life. An interesting hypothesis for *Monotis* subgenera was offered by GRANT-MACKIE (1979).

Otapiria neuquensis n. sp.

Plate 6, fig. 1-5

v. 1975 *Otapiria* – DAMBORENEA et al., cuadro 1, 16.

! v. 1982 *Otapiria neuquensis* n. sp., DAMBORENEA, p. 228-232; lám. 48, fig. 3-7; lám. 67, fig. 3-7 (unavailable name).

Derivation of name: The name *neuquensis* derives from Neuquén, the Argentine province where this species occurs.

Material: All the available material was found at one locality of the Piedra Pintada area: Cañadón La Pintada between Cerro del Vasco and Cerro Roth (D.13), in the lowest sediments that crop out in this region, that could be of latest Sinemurian to early Pliensbachian age. MLP 16480 to 16490, 19715 to 19718 (M 118), 16 right valves, 16 left valves and several fragments from author's collections. The holotype is the composite mould of a left valve MLP 16480-a, figured here on pl. 6, fig. 1.

Diagnosis: Oblique oval shell, length slightly exceeding the height, laterally compressed, with the left valve somewhat more convex than the right and the straight dorsal margin longer than half the total length. The umbo is placed in the anterior half of the shell. The posterior auricle is not well differentiated. The surface is ornamented by thin, irregular, radial ribs, that increase by intercalation and bifurcation, similar on both valves, between 40 and 90 ribs on each valve. There are also irregular concentric folds, of equal strength on both valves.

Description: Medium to small shell, ovate, oblique, inequilateral and slightly inequivalve. Laterally compressed, the maximum width is near the umbones. The left valve is slightly more inflated than the right. The dorsal margin is long and straight and somewhat longer than half the total shell length. The anterior, ventral and posterior margins are evenly convex. The shell length is always larger than the height, the length/height ratio varies between 1.08 and 1.28.

The umbones are prosogyrous and are placed at 1/4 of the total length from the anterior end of the left valve. On the right valve the umbo is slightly more posteriorly placed, but it is never central. The left umbo is prominent and protrudes above the hinge margin, whilst the right one is low and does not exceed the hinge margin.

The posterior wing is long but is not delimited from the main body of the shell. The anterior auricle on the right valve is small. The hinge, ligament and other internal characters are unknown.

The shell surface is ornamented by thin radial ribs which are closely spaced and irregularly increase in number towards the ventral margin by intercalation and bifurcation. There are also irregular concentric folds that are stronger on young specimens and near the umbones. The radial ribs are equally developed on both valves, though their number and distribution are variable (between 40 and 90 on left valves, and 40 and 70 on right valves). These ribs are weaker and even disappear on the posterior wing towards the dorsal margin, but there is not a sharp difference of ornamentation. The radial ribs appear sometimes wavy, especially when they cross the concentric folds.

Measurements:

Specimen	Material	L (mm)	H (mm)	L/H	W (mm)	L/W	W/H	Al (mm)	Lhp (mm)	N° ribs
MLP 16480-a, holotype	LV CM	15.17	13.50	1.12	2.10	7.22	0.15	4.17	5.67	75
MLP 16481, paratype	LV CM	10.33	8.33	1.17	1.60	6.46	0.19	2.67	4.00	55
MLP 16482, paratype	LV IM	13.33	12.33	1.08	1.90	7.01	0.15	3.83	4.67	58
MLP 16485-g, paratype	LV EM	15.67	13.33	1.17	1.10	14.24	0.08	4.33	6.33	90
MLP 16485-h, paratype	LV IM	7.33	6.17	1.19	1.00	7.33	0.16	1.83	3.83	42
MLP 16484, paratype	RV IM	13.95	11.35	1.22	1.40	9.96	0.12	5.75	6.20	70
MLP 16489-d, paratype	RV IM	13.10	11.75	1.11	1.35	9.70	0.11	5.40	6.05	61

Affinities: This Argentine species is similar to the group of *O. marshalli* and it also shows some affinities to forms included in the group of *O. pseudooriginalis* (ZAKHAROV).

O. neuquensis can be compared with *O. tailleuri* IMLAY (1967b: 3-6, pl. 1, fig. 1-23; pl. 2, fig. 32), from the early Jurassic of Alaska. Although this author originally indicated the stratigraphic position of this species as Toarcian to Bajocian, in a later personal communication (1974, 1975) he added that it was found near beds with Sinemurian ammonites. The Argentine species is of smaller size and has both valves almost equally convex and a longer posterior wing. Although the radial ribs are closer to each other in *O. neuquensis*, the ornamentation pattern is very similar on both species. *O. omolonica* POLUBOTKO (1968b: 37, tabl. 4, fig. 8-10), from the early Sinemurian of northeast Siberia, is closely related to *O. tailleuri*, but differs from *O. neuquensis* in its more elongated shell and narrower umbones.

The type species, *O. marshalli* (TRECHMANN), is known from the Hettangian - Sinemurian of New Zealand and New Caledonia (TRECHMANN 1923: 270, pl. 15, fig. 6-9; MARWICK 1935: 305, fig. 10, 12, 28-32, 34, 35; ROUTHIER 1950: 30; AVIAS 1951: 172; 1953: 149-150, pl. 20, fig. 1-4; MARWICK 1953: 95, pl. 11, fig. 7-8; SPEDEN & MCKELLAR 1958: 649; SPEDEN 1971: 15, 46, 48). This species has a larger shell than *O. neuquensis*, much more numerous radial ribs, a shorter posterior wing and an extended postero-ventral region. The subspecies *O. marshalli* ZAPFE, from the late Norian of Austria (GRANT-MACKIE & ZAPFE 1973: 48 as *O. aff. marshalli*; ZAPFE 1973: 152-156, pl. 1) has a size equal to *O. neuquensis* but the umbones are more prominent and it has more numerous radial ribs.

From the species of the group of *O. limaeformis*, *O. neuquensis* differs by having a similar ornamentation on both valves, with prevalent radial ribs. *O. pacifica* COVACEVICH & ESCOBAR, from the Sinemurian of Chile, is closely related to *O. limaeformis* (ZAKH.). Both show, besides the above mentioned differences, a more elongated and more inequivalve shell, with a sinuous posterior margin (see COVACEVICH & ESCOBAR 1979: 177-182, lám. 1, fig. 1-13, text-fig. 3a-d; HILLEBRANDT 1980, lám. 1, fig. 4-5).

O. neuquensis could also be compared to some species of group (c), from which it differs by a well-developed radial ornamentation. *O. pseudooriginalis* (ZAKH.), widely distributed in the early Jurassic of northeastern Siberia (ZAKHAROV 1962: 29-30, tabl. 1, fig. 17-21; POLUBOTKO 1968b: 34, tabl. 3, fig. 4-8) is very similar to *O. neuquensis* but it is smaller and the posterior wing is clearly limited. *O. originalis* (KIPARISOVA), from the Hettangian and Sinemurian of northeast Siberia (KIPARISOVA 1960: 27-28, pl. 5, fig. 5-7; POLUBOTKO 1968b: 33-34, tabl. 3, fig. 1-3) has a subcentral umbo on both valves, more densely packed radial ribs and an almost flat right valve.

O. ? frenguelli n. sp., here described, has a larger shell, is more equilateral and the radial ornamentation, only visible near the valve margins, is different.

Remarks: *O. neuquensis* has all the diagnostic characters of the genus (MARWICK 1935, 1953). The ligamental area and the anterior auricle of the right valve are not well preserved in the available material. This species was

referred to as *Otapiria* sp. in DAMBORENEA et al. (1975). Casts of some specimens were sent to Dr. COVACEVICH in Chile for him to compare them with *O. pacifica* COVACEVICH & ESCOBAR (1979). This authors (1979) doubt the generic assignment of the Argentine material and relate it to *Lupherella*. The species *O. neuquensis* has, as is shown here, its strongest relations with the group of *Otapiria* s. s. as here understood. Only some young specimens superficially resemble *Lupherella*, a taxon that probably is, anyway, a subgenus of *Otapiria*.

Autecology: The palaeoecology of *Monotis* was previously discussed by ICHIKAWA (1958), WESTERMANN (1962, 1973a, 1973b) and HALLAM (1967). WESTERMANN (1973b) recognized an ecological substitution in time as follows: *Daonella* – *Halobia* – *Monotis*, based on the similar shell shape and distribution. For the subequivalve *Monotis* species several authors (ICHIKAWA 1958; WESTERMANN 1962, 1973a) accept a pseudoplanktonic to epizoic mode of life, neritic to epipelagic, while for the typically inequivalve species WESTERMANN (1973a) suggests a benthonic, mainly sublittoral, habit.

JEFFERIES & MINTON (1965) analyzed the mode of life of "*Posidonia*", which they thought nectonic, and extended their conclusions to *Monotis*.

On the other hand GRANT-MACKIE (1979) accepted the epizoic habit of *Monotis*, and suggested that the different morphotypes were attached to different parts of the algal thallus. Periodically *Monotis* could have been carried as a pseudoplanktonic organism when the thallus was freed (see also HILLEBRANDT 1980: 126). *Maorimonotis* is considered by GRANT-MACKIE as a benthonic endobysate bivalve.

Otapiria ? *frenguelli* n. sp.

Plate 6, fig. 7–8

!v. 1982 *Otapiria frenguelli* n. sp., DAMBORENEA, p. 233–234, lám. 48, fig. 1–2, lám. 67, fig. 8–9 (unavailable name).

Derivation of name: After the late Dr. J. FRENGUELLI, who made extensive collections in the Argentine Jurassic and who was Director of the La Plata Museum.

Material: Three right valves and one left valve, preserved as internal moulds with fragments of shell, collected by FRENGUELLI, MLP 10418. Holotype: an almost complete right valve, figured here in pl. 6, fig. 7 (MLP 10418-a). The label on the specimens only reads "Chacaico, Neuquén, Liásico". There are no precise data about the exact stratigraphical occurrence of this material. The same sample contains some very poorly preserved ammonites that did not add any significant information.

Diagnosis: Subcircular flattened shell, with the left valve slightly more inflated than the right valve, length equal to height. Low central umbones on the right valve and slightly anterior on the left valve. The posterior wing is not clearly defined. Anterior auricle of the right valve small, smooth, with deep byssal notch. Surface of the valves covered by thin radial ribs, that are stronger towards the shell margins. The radial ribs are more numerous on the left valve. The right valve also bears stronger concentric folds.

Description: Shell of medium size, almost circular in outline, inequivalve and slightly inequilateral. Both valves are feebly convex, the left valve is more inflated than the right valve.

The left valve has a straight and long dorsal margin and the anterior, ventral and posterior margins are evenly convex. The umbo is prosogyrous and low; it is placed at about 1/3 of the total length with respect to the anterior margin. The right valve has subcentral umbo and a shorter dorsal margin. The length/height ratio is near one.

On the left valve a poorly-defined posterior wing can be distinguished as a flatter portion of the valve. The right valve has a small anterior auricle limited by a deep notch that almost reaches the umbo. This auricle is directed outwards from the sagittal plane of the valve and the free end is broken in the available specimen. The internal characters of the shell are unknown.

The surface of the shell shows thin radial ribs, stronger near the shell margins. These ribs are more numerous and are closer to each other on the left valve. There are also concentric, irregularly spaced folds. The concentric ornamentation is weaker on the left valve. The posterior wing bears the same kind of ornamentation that the disc. The anterior auricle of the right valve is smooth and only bears feeble growth lines.

Measurements:

Specimen	Material	L (mm)	H (mm)	L/H	W (mm)	L/W	Al (mm)	Lhp (mm)	Nº ribs
MLP 10418-a, holotype	RV S	21.30	18.80	1.13	2.00	10.65	10.20	–	52
MLP 10418-b, paratype	LV S	21.55	21.20	1.02	2.55	8.45	7.65	9.25	123

Affinities: From the other members of the group of *O. pseudooriginalis* within which *O. ? frenguelli* could be placed, it can be distinguished by a larger shell and by weaker radial ribs.

O. versicostata (BYCHKOV), from the Norian of northeastern Siberia (KIPARISOVA et al. 1966: 106–109, tabl. 6, fig. 3–18; BYCHKOV et al. 1976: 39, tabl. 55, fig. 6–8) has more anteriorly placed umbones, stronger radial ribs and a more inflated left valve.

This species differs from the taxa here grouped in (a) and (b) by having a subcircular shell and from group (b) by having radial ornamentation and flatter shells.

Remarks: FRENGUELLI determined his material as *Pectinula* ? sp. The resemblance to *P. cancellata* (LEANZA) is very superficial, the auricles are quite different and allow the allocation to another bivalve group.

The generic determination is left open because the available material is very scarce and most internal characters are unknown.

Otapiria ? sp.

Plate 6, fig. 6

v.1982 *Otapiria* ? sp., DAMBORENEA, p. 235, lám. 67, fig. 10.

Material: One left valve, MLP 16491 (M 361), collected by the author from the Pliensbachian of the left bank of the Rio Atuel near Puesto Araya (B.1), southern Mendoza province.

Description: Medium-sized shell, almost circular in outline, oblique, inequilateral. Although the specimen is not complete, the dorsal margin seems to be long and straight and the other margins are evenly convex. The shell length is slightly greater than the height. The umbo is prosogyrous and prominent and is placed at $\frac{1}{3}$ of the total shell length from the anterior margin. The auricles are not preserved.

The outer surface of the valve has thin radial ribs that are stronger near the margins of the shell and concentric irregular folds. Other characters unknown.

Measurements: L = 19.50 mm; H = 15.05 mm; L/H = 1.21; W = 2.15 mm; L/W = 9.07; Du = 6.50; Lp = 9.10; number of radial ribs on the outer margin = 73.

Affinities: This specimen is very similar to *O. inaequicostata* GEYER (1973: 45, Taf. 5, Fig. 1–3) from the Sinemurian of Colombia. The only differences are a denser and less regular radial ornamentation in the Argentine specimen.

It can also be compared to *O. originalis* (KIPARISOVA), from the Lower Jurassic of Siberia (KIPARISOVA 1960: 27–28, tabl. 5, fig. 5–7; POLUBOTKO 1968 b: 33–34, tabl. 5, fig. 1–2) though this species is smaller and has a denser ornamentation and flatter valves.

From *O. ? frenguelli* n. sp. it can be distinguished by a wider and more prominent umbo and a more inflated shell.

Family Oxytomidae ICHIKAWA 1958

The genera *Oxytoma* MEEK, *Meleagrinnella* WHITFIELD and *Maccoyella* ETHERIDGE were grouped by ICHIKAWA (1958) in a new subfamily Oxytominae within the Aviculopectinidae. In 1961 COX proposed to raise it to the family level on the grounds of the special features in shell structure (calcitic instead of aragonitic ostracum) and shell morphology. He also suggested that this family originated in the Aviculopectinidae and that the similarities with the Pteriidae could have been produced by convergence.

Genus *Oxytoma* MEEK 1864

Subgenus *Oxytoma* s. s.

Type species: *Avicula münsteri* BRONN (figured by GOLDFUSS 1835, Taf. 118, Fig. 2 a–h), from the middle to late Bajocian of Germany, original designation.

The variability displayed by species of this group has successfully resisted several attempts to systematize them adequately (such as the revisions by WAAGEN 1902; ROLLIER 1914; GILLET 1924b; DECHASEAUX 1938). Thus, as

ARKELL (1933: 191) stated, the group of *O. inequivalvis* (SOWERBY) produced more differences of opinion than any other group of Jurassic bivalves.

Whilst WAAGEN (1902) included all the available names in the synonymy of *O. inequivalvis*, only using some of them as "varieties" (followed by GILLET 1924b) other authors preferred to maintain a large number of specific names for the Jurassic material (BORISSJAK 1909; ROLLIER 1914; DECHASEAUX 1938). Details concerning these differences were extensively commented upon by ARKELL (1933), COX (1940), TROEDSSON (1951) and DUFF (1978). The point of view of the last author, who analyzed syntypes and a large number of specimens, is accepted here.

According to COX et al. (1969) this genus comprises three subgenera: *Oxytoma*, *Hypoxytoma* and *Palmoxytoma*. While the first two are cosmopolitan and have a wide stratigraphical range, *Palmoxytoma* seems to be restricted to the Lower Jurassic of boreal regions, both European and circumpacific. *Palmoxytoma* is known from northern Europe (COX 1961; TROEDSSON 1951), Siberia (POLUBOTKO 1968a), Canada (FREBOLD 1957a, 1964, 1966) and they probably derive from forms like *O. mojsisovicsi* TELLER from the late Triassic of Siberia and Japan (KIPARISOVA et al. 1966; KOBAYASHI & ICHIKAWA 1950 under several specific names; see also HAYAMI 1975: 62).

Oxytoma (*Oxytoma*) *inequivalvis* (J. SOWERBY 1819)

Plate 6, fig. 9-12; text-fig. 15

- *! 1819 *Avicula inequivalvis* sp. nov. J. SOWERBY, p. 78, pl. 244, fig. 2 (3?)
- 1876 *Monotis inaequivalvis*, SOWERBY - TATE, p. 371.
- 1878 *Pseudomonotis Münsteri* BRONN - GOTTSCHKE, p. 22; Taf. 6, Fig. 15.
- p 1902 *Avicula (Oxytoma) inaequivalvis* SOWERBY - WAAGEN, p. 1-23, Taf. 1.
- 1903 *Oxytoma inaequivalve* SOWERBY sp. - BURCKHARDT, p. 9.
- 1914 *Pteria phillipsi* nom. nov. ROLLIER, p. 400.
- 1917 *Avicula (Oxytoma) inaequivalvis* SOW. - TILMANN, p. 671.
- 1925 *Pseudomonotis Münsteri* BRONN - GOTTSCHKE, p. 254, lám. 6, fig. 15.
- 1925 *Oxytoma inaequivalva* SOW. - GERTH, p. 14.
- 1931 *Oxytoma inaequivalve* (SOWERBY) - WEAVER, p. 213-214; pl. 19, fig. 87.
- ! 1933 *Oxytoma inaequivalvis* (SOWERBY) - ARKELL, p. 194; pl. 24, fig. 9.
- ? 1938 *Pseudomonotis* sp. - FUENZALIDA, p. 78, lám. 3, fig. 2.
- 1940 *Oxytoma inequivalve* (J. SOWERBY) - COX, p. 98-101, pl. 6, fig. 9-12 (with synonymy).
- v. 1942a *Pteria inaequivalvis* SOW. - A. LEANZA, p. 17.
- v. 1942b *Pteria (Oxytoma) inaequivalvis* SOW. - A. LEANZA, p. 158; lám. 4, fig. 2; lám. 5, fig. 1.
- ? 1967 *Oxitoma* (sic) cf. *inequivalva* (sic) SOW. - THIELE-CARTAGENA, p. 32-33, lám. 6, fig. 23a-b.
- ? 1968 *Oxytoma* cf. *O. inaequivalvis* (SOW.) - CECIONI & WESTERMANN, p. 72, lám. 4, fig. 2.
- v. 1975 *Oxytoma* - DAMBORENEA et al., cuadro 1, 17.
- 1978 *Oxytoma (Oxytoma) inaequivalvis* (SOWERBY) - CAMACHO & RICCARDI, cuadro 1.
- ! 1978 *Oxytoma (Oxytoma) inequivalve* (J. SOWERBY) - DUFF, p. 54-57, pl. 4, fig. 7, 9, 11, 13, 15-19, 21-23, text-fig. 17 (with synonymy).
- 1980 *Oxytoma münsteri* (BRONN) - ESCOBAR, p. 53-55, lám. 3, fig. 1.
- v. 1982 *Oxytoma (Oxytoma) inequivalvis* (J. SOWERBY) - DAMBORENEA, p. 213-218, lám. 46, fig. 4-6; lám. 68, fig. 1-5.

Material: In Argentina this species occurs in the Pliensbachian of Neuquén province at the following localities: Cerro Granito (C.14), Arroyo Lapa (C.15), 8 km south of Estancia Santa Isabel (D.1), Arroyo Sañicó near Carrán Curá (D.2), 4 km north of Sañicó (D.5), Subida a Sañicó (D.7), SW of School N° 27, Piedra Pintada (D.9), eastern slope of Cerro Corona (D.10), Cañadón La Pintada (D.13). It was also found in the Pliensbachian of several localities of Mendoza province: Rio Atuel near Puesto Araya (B.1), Arroyo del Portezuelo Ancho (B.5), Arroyo Serrucho (B.8) and Cerro Puchenque (B.9). This species probably extends into the Toarcian.

The material analyzed here consists of 21 left valves and three right valves, most of them preserved as moulds: MLP 5615, 5984, 6088, 6098, 6212, 6256, 15831, 15832, 16473 to 16478, 19072 and 19677 (M 118, 129, 136, 167, 336, 365, 1031, 1055, 1305 and 1340).

Besides the specimens here described, this species is known from South America, possibly in the Upper Triassic of Chile (FUENZALIDA 1938; THIELE-CARTAGENA 1967; CECIONI & WESTERMANN 1968) and with certainty from the Lower Jurassic of Chile (ESCOBAR 1980) and Perú (TILMANN 1917). It also extends to the middle Jurassic of Argentina (GOTTSCHKE 1878, 1925), in the Bajocian of Paso del Espinacito, San Juan province (MLP 4091).

This species also has a wide stratigraphical range in other places in the world, for instance it is known in Europe from the Rhaetian to the Lower Cretaceous (WAAGEN 1902; GILLET 1924b; COX 1940) and in Japan from the Sinemurian to the Bajocian (HAYAMI 1975: 63).

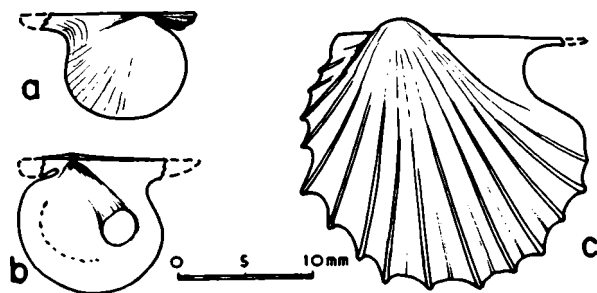
Description: Shell of medium-size, pteriform, with a long and straight dorsal margin and a pointed posterior wing. Very inequivalve shell, the left valve is convex and has strong radial ornamentation, the right valve is smaller than the left one, less convex and with only faint radial ornamentation.

The left valve has a dorsal margin which is shorter than the total shell length. The posterior margin is sinuous, strongly concave below the posterior wing and the ventral and anterior margins are evenly convex. The prominent umbo is anteriorly placed, protruding above the hinge line, and the valve is prosocline.

In the right valve, on the other hand, the dorsal margin corresponds to the maximum shell length, the posterior wing largely exceeds the posterior part of the disc. The shell is discoidal, with very low umbones. The posterior wing is long and flat and the sinus that separates it from the remaining part of the shell is equal to that of the left valve. The right valve has a large anterior auricle which is limited by a deep byssal notch without a ctenolium. The auricle is subtriangular with radial ribs.

The ligamental pit has a triangular shape and it is located immediately behind the umbones. The posterior adductor muscle scar is large and subcircular, and is subcentrally placed nearer the posterior end of the shell (text-fig. 15 b). Just below the umbones there is a pit-like scar that DUFF (1978) interpreted as the anterior adductor muscle scar. The pallial line is discontinuous, made up of a row of pit-like impressions. There is a shell thickening at the anterior end of the left valve interior, into which fits the anterior auricle of the right valve.

The ornamentation is quite different on both valves. The left valve has thin and straight radial ribs, separated by broad intervals, which may have a second order ribbing and that always have very thin radial riblets. The primary ribs are 12 to 15 and are also reflected on the shell inner surface. Both second and third order ribs are not marked on the inner surface. The surface of the posterior auricle may also have thin radial ribs, slightly stronger than the third order riblets of the shell, but it is smooth in some specimens. The growth-lines are faint and concave outwards in the intervals between two primary ribs.



Text-fig. 15. *Oxytoma (Oxytoma) inequivalvis* (SOWERBY). a: composite mould of right valve, MLP 16475, Subida a Sañicó, Pliensbachian; b: interior view of a right valve, MLP 16478, Estancia Santa Isabel, late Pliensbachian (?); c: internal mould of a left valve, MLP 5984, Chacaico, Neuquén, early Jurassic.

The right valve also has radial riblets, though these are very weak and are not evident on the inner surface, which is smooth. The radial lines do not reach the umbones and thus young specimens are completely smooth. On larger specimens there are radial sulci that also do not reach the umbones and that correspond to the primary ribs of the left valve.

The ventral margin of the left valve is scalloped, each primary rib is outwardly extended.

Measurements:

Specimen	Material	L (mm)	H (mm)	W (mm)	L/H	DI (mm)	Nº ribs
MLP 5615	LV IM	32.85	29.80	3.15	1.10	-	-
MLP 5984, pl. 6, fig. 11	LV IM	19.10	18.20	3.80	1.05	15.00	14
MLP 6088	RV S	22.90	16.80	0.90	1.36	22.90	-
MLP 6089	RV S	19.25	17.70	1.60	1.09	-	13
MLP 6256	LV S	31.80	21.75	4.65	1.46	19.00	14
MLP 16473, pl. 6, fig. 9	RV IM	11.65	8.35	0.80	1.39	11.65	-
MLP 16475, pl. 6, fig. 12	RV IM	10.90	7.50	0.70	1.45	10.90	-

Affinities: The Argentine specimens fall within the range of morphological variability of *O. (O.) inequivalvis* (SOWERBY), which was the subject of several studies (WAAGEN 1902; GILLET 1924b; ARKELL 1933; DECHASEAUX 1938; COX 1940; TROEDSSON 1951 and DUFF 1978). This species has a cosmopolitan distribution and a long stratigraphical

range. It was illustrated many times (GOLDFUSS 1835; MORRIS & LYCETT 1853 as *O. muensteri*; LYCETT 1863 as *Monotis subcostata* ROEM.; RICHARDSON 1904; BORISSJAK 1909; JEKELIUS 1915; GILLET 1924b, 1924c; COHEN 1931; COX 1940; TROEDSSON 1951; HAYAMI 1959a, 1959b; COX 1965; COX et al. 1969; DUFF 1978; URLICHS et al. 1979; KOCHANOVÁ 1979).

ARKELL (1933: 194) selected as lectotype the specimen figured by SOWERBY (1819) in his pl. 244, fig. 2 left, from the Pliensbachian of Dursley, Great Britain. This specimen was re-illustrated by ARKELL (1933, pl. 24, fig. 9) and by DUFF (1978, pl. 4, fig. 16) and is an incomplete internal mould of a left valve that only shows the primary ribs. The internal moulds of the material here described closely match this specimen. Although the scope of the species varies considerably according to different authors, the Argentine specimens can be referred to it even in its strictest sense. Also *O. trechmanni* QUILTY (1983: 400, fig. 9–10) from the middle-late Bajocian of Antarctica, is within the variability range of *O. inequivalvis* and is thus similar to the Argentine specimens, but it is more globose and has sharp-crested primary ribs.

O. sinemuriensis (D'ORBIGNY) was a name proposed for a Sinemurian European species (including *O. inequivalvis* figures in GOLDFUSS 1835) and is considered by some authors (WAAGEN 1902; COX 1940) as a synonym of *O. inequivalvis*, by others as a variety of this species (GILLET 1924b), or as a different species (ROLLIER 1914; DECHASEAUX 1938; TROEDSSON 1951; KOCHANOVÁ 1961, among others). In the last case, the criteria used to differentiate it vary considerably and are even contradictory. ROLLIER (1914: 398) and DECHASEAUX (1938: 146) say that the posterior wing of *O. sinemuriensis* is smooth; but TROEDSSON (1951: 196–198) insists on the presence of radial ribs and growth striae parallel to the posterior margin (see figures in POLUBOTKO 1968b, tabl. 5, fig. 7–9; TROEDSSON 1951, pl. 9, Fig. 1–11; pl. 10, Fig. 1–10).

The type species of the genus, *O. muensteri* (BRONN) is also considered as a synonym of *O. inequivalvis* by COX (1940 and in COX et al. 1969). Other authors believe that it can be distinguished by the more numerous radial ribs and because it seems to be more equivalve (fide DUFF 1978: 54). This question is not yet completely settled. This species was first figured by GOLDFUSS (1835, Taf. 118, Fig. 2a–h) with specimens from the Braunjura δ of Franconia, Germany. Subsequently, material from other regions was referred to this species (QUENSTEDT 1856, Taf. 60, Fig. 6–9; DUMORTIER 1874, pl. 40, fig. 10–11; GREPPIN 1899, pl. 9, fig. 10, pl. 12, fig. 4; COSSMANN 1906, pl. 3, fig. 23–26). The material from the Bajocian of Paso del Espinacito referred to *O. muensteri* and described by GOTTSCHKE (1878: 22, Taf. 6, Fig. 15; 1925: 254, lám. 6, fig. 15) is here included in the synonymy list of *O. inequivalvis* on the basis of material from that locality (MLP 4091), though the right valve is unknown. On the other hand the right valve figured by ESCOBAR (1980, lám. 3, fig. 1) from the Chilean Sinemurian and referred to "*Oxytoma münsteri*" is certainly an *O. inequivalvis* (compare ESCOBAR's figure with pl. 6, fig. 12 here).

Oxytoma costata (TOWNSEND) (= *O. laubei* ROLLIER 1914), from the middle Jurassic (SOWERBY 1819; MORRIS & LYCETT 1853; COX & ARKELL 1948; FISCHER 1969) differs from *O. inequivalvis* in its fewer primary ribs (six to nine) and by its smooth intervals. This species was also mentioned for the Middle Jurassic of Paso del Espinacito, San Juan (GOTTSCHKE 1878: 23, Taf. 6, Fig. 16–17; 1925: 254) and material from Arroyo Blanco, Rio Atuel, Mendoza province, was compared with it (JAWORSKI 1915: 435–436; 1925b: 38), but in both instances they are only internal moulds and the identification is uncertain.

In the Australian Bajocian the species *O. decemcostata* WHITEHOUSE (SKWARKO 1974: 22–23, pl. 24, fig. 1–8) is known. This species has fewer primary ribs (nine to eleven) and a longer posterior wing.

O. startense POLUBOTKO (1968b: 47, tabl. 39, fig. 6–9), from the Toarcian of Siberia, has an outline similar to *O. inequivalvis* but it has more numerous primary ribs. Another clearly distinguishable taxon is *O. jacksoni* (POMPECKJ 1900, pl. 1, fig. 13–16), from the Aalenian – Bajocian, apparently restricted to boreal regions (NEWTON & TEAL 1898; FREBOLD 1957b, 1964; POLUBOTKO 1968b). This species has a very large shell with very numerous radial ribs on both valves.

O. mclearnii WARREN (1932, pl. 1, fig. 26–27; FREBOLD 1964, pl. 17, fig. 5) from the Bajocian of Burns Mine, Canada, is similar to the Argentine material in outline and shell obliquity, but it also has more radial ribs.

Autecology: All species of *Oxytoma* were epibyssate. KAUFFMAN (in COX et al. 1969) considered that the mode of life of this genus can be compared with that of *Pteria*. DUFF (1978: 16) suggested an epizoic habit arguing that the fine-grained sediments where these organisms are normally found would prevent a direct attachment to the substrate. GILLET (1924b: 453) tried to establish a direct correlation of the shells having a deep posterior sinus to rocky bottoms and those having a shallow sinus to soft substrates. But the high variability shown by large populations is against that type of speculation.

Superfamily uncertain

Family Posidoniidae FRECH 1909

The family Posidoniidae includes bivalves that generally appear in black, sometimes bituminous, shales, together with ammonites, aptychi, rhyncholites, plant remains and almost no other organism. This facies was widely represented during the Jurassic all over the world (see JEFFERIES & MINTON 1965).

The Jurassic specimens are traditionally referred to a few cosmopolitan species that have a great intraspecific variability. The generic affinities of these species are not easy to establish, since well-preserved specimens are few and some features, such as the type of ligament, are only known in exceptional circumstances.

South American Mesozoic material referable to this family has been repeatedly described and figured from Perú, Chile and Argentina (GOTTSCHKE 1878, 1925; STEINMANN 1881; BEHRENDSEN 1892, 1922; R. PHILIPPI 1899; BURCKHARDT 1900, 1903; TILMANN 1917; GROEBER 1918; STEHN 1923; JAWORSKI 1925a, 1926; WEAVER 1931; HILLEBRANDT 1980). Most of them refer to Middle Jurassic material, the only Lower Jurassic references are those by TILMANN (1917: 671–672) of *Posidonia* cf. *bronnii* VOLTZ from Perú and by PIATNITZKY (1936: 91, 101, 102) of *P. alpina* from Chubut, Argentina.

Genus *Bositra* DE GREGORIO 1886

Type species: *Posidonia ornati* QUENSTEDT 1851 (= *Posidonomya alpina* GRAS 1852) from the Braunjura ζ from Germany, posterior designation by COX 1964: 47, who referred to QUENSTEDT's figure (1857, Taf. 67, Fig. 27) instead of to the original description of this species (QUENSTEDT 1851).

The genus *Posidonia* BRONN (= *Posidonomya* BRONN) includes bivalves that are known from the early Carboniferous and to which the Jurassic species were traditionally referred. Nevertheless, due to ligamental differences, DE GREGORIO (1886) separated the group of *P. buchii* RÖMER (restricted to the Jurassic) in a subgeneric taxon that he called *Bositra*. See COX (1964: 47) for the type species designation and JEFFERIES & MINTON (1965) for the description of this species.

On the basis of very well preserved specimens STEINMANN (1881) erected the genus *Aulacomya* (later replaced, due to homonymy, by *Steinmannia* FISCHER), with the Toarcian species *Posidonia brononii* VOLTZ as type. This genus, despite the superficial resemblance to the Posidoniidae, is regarded as an inoceramid by COX et al. (1969) due to the hinge type, which was observed on only one specimen.

GUILLAUME (1928) made a critical revision of the Jurassic species of Posidoniidae and he recognized three groups: a) *Posidonomya* (? *Daonella*) *radiata* GOLDFUSS (Middle Toarcian), b) *Steinmannia brononii* (VOLTZ) (early and middle Toarcian) and c) *Posidonomya alpina* GRAS (Aalenian – late Jurassic). GUILLAUME considered *Steinmannia* as a section of the genus *Posidonia* and he overlooked DE GREGORIO's proposal of a new name for the group (c). Therefore, he continued using *P. alpina* and not *P. buchii* or *P. ornati*, although the last mentioned names have priority. On the other hand HALLAM (1976) grouped all Jurassic species into the genus *Bositra*.

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Bositra ornati (QUENSTEDT 1851)

Plate 4, fig. 7; text-fig. 16

- *! 1851 *Posidonia ornati* sp. nov., QUENSTEDT, p. 517; Taf. 42, Fig. 16.
- 1852 *Posidonomya alpina* sp. nov. GRAS, p. 11, pl. 1, fig. 1.
- 1856 *Posidonia opalina* QUENSTEDT, p. 324, Taf. 45, Fig. 11.
- 1857 *Posidonia ornati* QUENSTEDT, p. 501, 551, Taf. 67, Fig. 27, Taf. 72, Fig. 29.
- 1867 *Posidonia ornati* QUENSTEDT, p. 615, Taf. 53, Fig. 16.
- 1876 *Posidonomya ornati* QUENSTEDT - TRIBOLET, p. 254-255.
- 1881 *Posidonomya* cf. *ornati* QU. - STEINMANN, p. 257-259, Taf. 10, Fig. 3-4 (only).
- 1899 *Posidonomya Bronni* GOLD. (sic) - R. PHILIPPI, p. 41, lám. 22, fig. 3 (only).
- 1899 *Posidonomya ornati* QUENST. - R. PHILIPPI, p. 41, lám. 22, fig. 9 (copy from STEINMANN, 1881).
- 1900 *Posidonia opalina* QUST. - BURCKHARDT, p. 29, pl. 20, fig. 8.
- 1903 *Posidonomya alpina* GRASS - BURCKHARDT, p. 20, Taf. 2, Fig. 11.
- 1918 *Posidonomya alpina* GRASS - GROEBER, p. 17, 67.
- ? 1923 *Posidonomya ornata* QUENSTEDT - STEHN, p. 141.
- ? 1923 *Posidonomya Buchii* ROEM. - STEHN, p. 143.
- 1925 *Posidonomya alpina* GRASS - GERTH, p. 25.
- 1925 *Posidonomya ornati* QUENST. - GERTH, p. 23.
- 1925a *Posidonomya* ex grupo *alpinae* GRASS - JAWORSKI, p. 155-157.
- 1926 *Posidonomya* ex grupo *alpinae* GRASS - JAWORSKI, p. 388-390.
- 1928 *Posidonomya alpina* - GUILLAUME, p. 222, text-fig. 4-5, pl. 10, fig. 4-13.
- 1931 *Posidonomya* from the group of *P. alpina* GRASS - WEAVER, p. 216-218, pl. 18, fig. 80.
- ? 1936 *Posidonomya alpina* A. GRASS - PIATNITZKY, p. 91, 101-102.
- 1940 *Posidonia ornati* QUENSTEDT - COX, p. 103-105, pl. 7, fig. 10-11 (with synonymy).
- ? 1942 *Posidonomya alpina* - SUERO, p. 40.
- v. 1943 *Posidonomya* sp. del group *P. alpina* GRASS - GARCÍA-VIZCARRA, p. 29, 43.
- v. 1943 *Posidonomya* cf. *alpina* GRASS - FERNÁNDEZ, p. 22, 27, 43, 58, 61.
- 1953 *Posidonomya alpina* GRASS - GROEBER et al., p. 160, 162, 164.
- p. 1978 *Bositra ornati* (QUENSTEDT) - CAMACHO & RICCARDI, cuadro 2 (only WEAVER's reference)
- 1980 *Bositra buchi* (ROMER) - HILLEBRANDT, lám. 1, fig. 6.
- v. 1982 *Bositra ornati* (QUENSTEDT) - DAMBORENEA, p. 207-212, lám. 46, fig. 1-3; lám. 64, fig. 11.

Note: Only South American references or especially important ones are included in this synonymy list. To complete see Cox (1940, 1965).

Material: Several tens of specimens, that cover the bedding surfaces. Most of them are disarticulated valves, there are some that have both valves wide open: MLP 15764 to 15766, 15838, 15841, 15866, 17149, most of them from GULISANO's collection.

The material occurs in middle to upper Toarcian beds, associated with *Peronoceras* cf. *bolitoense* HILLEBRANDT & SCHMIDT-EFFING, *Harpoceras exaratum* (YOUNG & BIRD), *Phymatoceras* cf. *erbaense* (HAUER) and *Hildoceras* (*Hildaites*) sp. at Arroyo Lapa (C.15) and with *Phymatoceras* sp. and *P. cf. lilli* (HAN.) at Arroyo La Jardinera, both localities from central Neuquén province.

This cosmopolitan species has a long stratigraphical range from the Toarcian to the Callovian. In South America it was also found in the Toarcian - Aalenian of Chubut province (PIATNITZKY 1936), late Toarcian - Bajocian of Arroyo Picún Leufú (GROEBER et al. 1953); Aalenian of Portezuelo Ancho, Cerro Tricolor, rio del Cobre, Arroyo Infernillo and Santa Elena, Mendoza province (BURCKHARDT 1900; JAWORSKI 1925a, 1926; GERTH 1925; also material at the MLP and author's collections), Cerro Lotena, Picún Leufú and Los Molles, Neuquén province (WEAVER 1931, also MLP and author's collections); in the Bajocian-Bathonian of Chile (HILLEBRANDT 1980) and in the Callovian of Chacay-Melehue, Neuquén and Caracoles, Chile (STEINMANN 1881; STEHN 1923; GERTH 1925; also MLP collections).

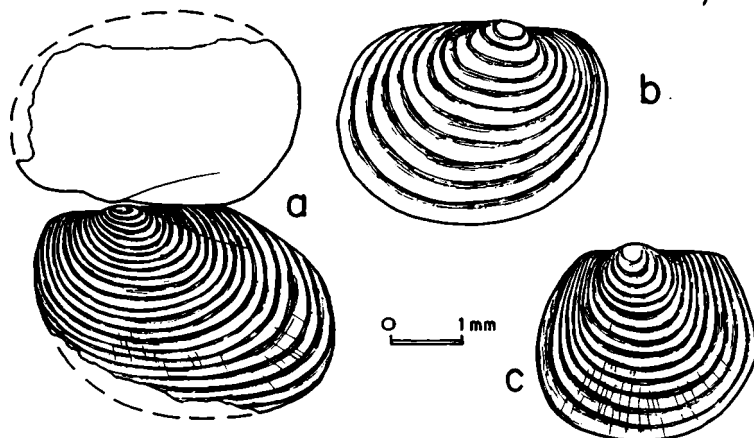
Description: Shell small, oval in outline, equivalve and inequilateral, without auricles, length exceeding height. The dorsal margin is long and straight and meets the posterior one at an obtuse angle. The other shell margins are evenly convex. The umbo is prosogyrous and is placed within the anterior half of the shell, though its position in relation to the anterior margin is variable.

The shell is very thin and has regular concentric folds that become less prominent towards the ventral margin in the largest specimens. On some specimens also very faint radial lines can be seen, which can be restricted to some parts of the shell surface. The lines can either be primary or have a diagenetic origin. On a few specimens a posterior, shallow sulcus can be seen.

Ligament, hinge and other internal characters unknown.

Affinities: Although several authors (GUILLAUME 1928; JEFFERIES & MINTON 1965; COX et al. 1969; DUFF 1978; KOCHANOVÁ 1979) have recently considered that *P. ornati* QU. is a synonym of *P. buchii* ROEMER, this cannot

Text-fig. 16. *Bositra ornati* (QUENSTEDT), external views. a: specimen with both valves, MLP 15841, Rahue-Aluminé, Toarcian; b: right valve, MLP 15866, Pozo YPF Barda Colorada Este, Neuquén, Toarcian (?); c: left valve, MLP 15841, Rahue-Aluminé, Toarcian.



be confirmed without examination of the original material, because QUENSTEDT's and ROEMER's figures show considerable differences. DUFF (1978: 52) indicates that ROEMER's material is lost, which adds another uncertainty.

On the other hand, the identity of *P. ornati* QUENSTEDT and *P. alpina* (GRAS) is more probable and almost nobody objects to it. QUENSTEDT's name has priority, as was shown by TRIBOLET (1876) and COX (1940: 103–105).

The morphological features of the Argentine specimens are well within the variation that the species exhibits all over the world (QUENSTEDT 1856, 1857; BÖCKH 1874; JIMÉNEZ DE CISNEROS 1923; RENZ 1925; GUILLAUME 1928; DARESTE DE LA CHAVANNE 1930; COX 1940; IMLAY 1945; COX & ARKELL 1948; IMLAY 1955; KSIAZKIEWICZ 1956; HAYAMI 1961; IMLAY 1963; 1964a; COX 1965; BADALUTA et al. 1969; DUFF 1978; HILLEBRANDT 1980).

P. ? orbicularis MÜNSTER (DUMORTIER 1874: 305, pl. 62, fig. 2), from the Aalenian of France can be distinguished by its more orbicular outline with subcentral umbones and a larger size. *P. albertimagni* SCHNITTMANN (1966: 83, Taf. 2, Fig. 10), from the Toarcian of Franconia (Germany) is possibly a synonym of *B. ornati*.

In the European Sinemurian there is a species that can be distinguished from the Argentine material by its very short hinge-line, straight posterior margin and larger size. This species was named *P. mosellana* by GUILLAUME (1942) for French material, while similar specimens from northeast Siberia were referred to *P. ex gr. brononii* VOLTZ by POLUBOTKO (1968b: 76, tabl. 8, fig. 1–4).

Bositra somaliensis (COX), from the Kimmeridgian of Somalia and Tanzania (COX 1935a: 166, pl. 15, fig. 7–8; 1965: 50, pl. 6, fig. 2) has subcentral umbones and more widely spaced concentric folds. A similar outline, but with smaller size is found in another Kimmeridgian species from France described by DE LORIOI (in DE LORIOI & PELLAT 1874–1875, pl. 21, fig. 3–5) as *P. bononiensis*.

P. muelleri GREPPIN (1899: 11, pl. 13, fig. 8), from the Bajocian of central Europe, has a shell outline that resembles *B. ornati*, but the ornamentation is different, as the concentric folds are widely spaced near the umbo and closer together on the remaining shell.

Steinmannia brononii (VOLTZ), from the European Toarcian, has almost equilateral valves, which are almost orbicular and with subcentral umbones (GOLDFUSS 1838; QUENSTEDT 1858; DUMORTIER 1874; TRAUTH 1909; DUBAR 1925; RENZ 1925; URLICHS et al. 1979).

The Middle Jurassic specimens from Chile and Argentina referred to "*P.*" *steinmanni* BEHRENDSEN (GOTTSCHKE 1878; 1925; STEINMANN 1881; BEHRENDSEN 1892; 1922; WINDHAUSEN 1931) also have equilateral valves with subcentral umbones. Comparable material is also known from the late Bajocian of Quebrada de Pucayacu, Perú, mentioned by WESTERMANN et al. (1980: 26) as *Bositra* sp.

Small posidoniids similar to the Argentine material are also present in the Lower Jurassic of Malagasy and were identified as "*Posidonomya* sp." by THEVENIN (1908: 25, pl. 4, fig. 6).

Remarks: Almost all mentions of "*Posidonia*" from the Lower and Middle Jurassic of South America are included in the synonymy list, as it is not possible to separate groups with discontinuous morphological differences, from the figures and material analyzed from Argentina and Chile. Though a statistical study has not been performed yet, a possible general comment concerns the smaller size of the Lower Jurassic specimens in comparison with Middle Jurassic ones, a feature which might be significant, bearing in mind RENZ' (1925) observations in the late Lias – Dogger sequence of western Greece.

Although the climax of this species in South America seems to have come in the Aalenian (about *opalinum* Zone), the species was already present as early as middle Toarcian, as proved by the specimens here described. GROEBER (in GROEBER et al. 1953) had reported that this species was known in central Neuquén from the latest Toarcian. PIATNITZKY (1936) had also recorded *P. alpina* in the late Toarcian – Aalenian of Chubut province. COX (1965: 50) said that the oldest record for this species corresponds to the Toarcian of Argentina and HILLEBRANDT (1981) also mentioned *Bositra* in the latest Toarcian of South America.

In those stratigraphical sections in which there are Toarcian black shales, *Bositra ornati* was found thus far as early as in mid- and late Toarcian beds, replacing *Posidonotis cancellata* (LEANZA), which appears up to the lowermost Toarcian, as will be discussed later. The first appearance of *B. ornati* cannot then be used, as was repeatedly done by South American geologists, to indicate Aalenian times. On the other hand the début of this species in the several sections examined seems to be related to the beginning of the deposition of black shales.

Only the Middle Jurassic material from Argentina and Chile referable to *P. steinmanni* BEHRENDSEN was excluded from the synonymy list (GOTTSCHÉ 1878: 44, Taf. 8, Fig. 8; 1925, lám. 8, fig. 8 as *P. bronni*; STEINMANN 1881, Taf. 10, Fig. 5 only, as *P. cf. ornati*; BEHRENDSEN 1892, Taf. 1, Fig. 7a–b; 1922, lám. 3, fig. 7; WINDHAUSEN 1931, lám. 26, fig. 8 as *P. alpina* GRAS, copy of GOTTSCHÉ's figure). On the available information, it is not possible to decide whether these records can be referred to *Steinmannia* or represent an extreme morphological variety of *B. ornati* instead.

Likewise, there are not enough elements to decide if TILMANN's (1917: 671–672) mention of *P. cf. bronni* VOLTZ from the "Lias" of Perú is referable to *Steinmannia* or *Bositra*.

Autecology: The subject of the mode of life of *Bositra* and other Posidoniidae has been extensively discussed. All the opinions can be grouped in two: those that consider that the Posidoniidae were pseudoplanktonic organisms (see for instance STANLEY 1972; DUFF 1978) and those that argue that at least some species of *Bositra* were nektonic (see synthesis in JEFFERIES & MINTON 1965, also in WESTERMANN 1975: 35). Serious doubts about this last possibility were put forward by others (such as TEBBLE, YONGE and ALLEN: in AGER & NICHOLS 1963, or STANLEY 1972) and are also shared here.

Superfamily Pectinacea RAFINESQUE 1815

The Pectinacea are characterized by a monomyarian condition and reorganization of the body around the central adductor, with assumption of a pleurothetic habit which also involves a functional asymmetry (YONGE 1981). This implies a laterally flattened and almost circular shell and a reduction or loss of the foot. The wide separation of the valves is made possible by a very elastic inner ligament layer concentrated in a small pad. Highly organized pallial eyes are present on the middle fold of the mantle margins (DAKIN 1928) in both the free and attached pectinids and spondylids, but absent in extant species of the now abyssal Propeamussiidae (YONGE 1981). The Pectinacea are a very successful group of bivalves which exhibits a wide range of adaptations, recently summarized by YONGE (1981). Most of these adaptations were already present in early Jurassic forms, as will be discussed later.

Family Neitheidae SOBETZKY, 1960

The Cretaceous species included in the genus *Neithea* DROUET were regarded by SOBETZKY (1960) as a new subfamily Neitheinae, which is now considered as a family by some authors (WALLER 1984: 214). DHONDT (1973) revised the European Cretaceous Neitheinae and discussed the origin of the genus *Neithea*, commenting upon its possible relations to *Weyla*. On the basis of a silicified specimen housed in the BMNH she concluded that "*Weyla* is not in the direct ancestry of *Neithea*", as that specimen shows "no trace of isodont teeth or vertical striae on the cardinal line" (DHONDT 1973: 9).

The Argentine material revised here shows the vertically striated hinge in several internal moulds of both valves (see pl. 10, fig. 3) and also in complete and well-preserved isolated valves such as DNGM 12463 (pl. 7, fig. 2). The vertical striation of the hinge was already noticed and figured by JAWORSKI (1914a, fig. 7), CRICKMAY (1933a, pl. 25, fig. 3) and is also recognizable in imperfectly silicified valves housed in the BMNH such as the left valve of the specimen figured here in text-fig. 18–4.

Moreover, specimen DNGM 12463, a complete isolated right valve, shows to each side of the resilifer a triangular, smooth thickening of the shell and a triangular, striated depression (see pl. 7, fig. 2). Both the thickening

and the depression are more strongly developed in the anterior portion of the shell. These features are quite similar in position, orientation and appearance to the well-developed hinge-teeth and sockets known in some *Neithea* species and, together with the apparent lack of a ctenolium, certainly allow the allocation of *Weyla* (as here understood) within the same family as *Neithea*, which undoubtedly is the most closely related genus among the Pectinacea. This statement does not necessarily imply a direct ancestor-descendant relation between the two genera, but re-opens the old and yet unsolved question of the origin of the various pectinacean families. The similarity between *Weyla* and *Neithea* is thus not only based on the external morphology of both genera. *Neithea* has a full development of isodont teeth, which are only incipiently formed in *Weyla*, but on the other hand it lacks the auricular crura and the marginal "chomata", which are well developed in *Weyla* (see text-fig. 21).

The last mentioned structure is likewise present in some species of *Spondylus*, a genus which also has a well-developed isodont hinge in adults and a "taxodont" hinge in early stages of growth. The possible relationships between the early members of the Neitheidae and the Spondylidae must be re-assessed on the basis of the new features here described, but it is beyond the scope of this monograph and will be treated elsewhere.

It is interesting to note that the hinge characters in these pectinaceans, such as in *Spondylus*, are easily lost when the inner layer of the shell is weathered and thus they are not seen in poorly preserved specimens which may even appear edentulous (cf. pl. 9, fig.1). Many Cretaceous species are referred to *Neithea* only on the basis of the external morphology and on the assumption of a similar hinge-type. This happens with early Jurassic species referred to *Weyla* as well and thus the variation of the hinge-characters within each genus is not yet sufficiently known.

Genus *Weyla* J. BÖHM 1922

Type species: *Pecten alatus* VON BUCH 1838, from the South American Jurassic, by original designation.

Synonyms: "Janiren des Lias" E. PHILIPPI 1899.

"Lias-Volen" JAWORSKI 1914a.

Weyla EBERZIN (ed.) 1960 (error pro *Weyla* ?, emend. pro *Weyla* ?).

Emended diagnosis: Pectiniform shell, right valve very convex, left valve flat, concave or convex (but less than the right one). External ornamentation consisting of strong radial ribs, which may be simple or branched. Subequal auricles with or without non-ctenolate byssal notch. Hinge with cardinal lamellae vertically striated, presence of "chomata" on the anterior and posterior inner margins of the valves.

Remarks: Since VON BUCH (1838, 1839) and D'ORBIGNY (1843) described fossil material from South America as *Pecten alatus* v. BUCH and *P. dufrenoyi* D'ORBIGNY, this group of large inequivalve pectinaceans has been the subject of many discussions. From the beginning the age of the sediments where these species were found was a matter of disagreement, since VON BUCH, D'ORBIGNY in part and even DARWIN (1846) referred them to the Cretaceous. One of their arguments was the alleged relation of these bivalves with pectinaceans from the early Cretaceous, today known as *Neithea* DROUET. When the correct stratigraphic origin of these and other related species was established as early Jurassic according to the associated fauna (BAYLE & COQUAND 1851) the question of the biological affinities of the group emerged.

It was originally thought that *Weyla* was restricted to South America and was known towards the end of the last century as the "group of *Pecten alatus*". The superficial resemblances between these species and the Cretaceous *Neithea* on one hand and Tertiary and Recent *Pecten* s. s. on the other, were immediately evident to most authors.

E. PHILIPPI (1900) considered the names *Janira* SCHUMACHER 1817, *Vola* KLEIN 1753 and *Neithea* DROUET 1825, as synonyms and named the group "Form *Janira*" under the genus *Pecten*. There he included *P. alatus*, *P. dufrenoyi*, *P. bodenbenderi* BEHRENDSEN and also the Spanish species *P. pradoanus* VERNEUIL & COLLOMB. PHILIPPI maintained nevertheless that the "Liassic *Janiras*" were not directly related to either the Cretaceous or the Cainozoic stocks.

JAWORSKI (1914a) referred these species, which he analyzed in detail, to the genus *Vola* KLEIN, including as synonyms *Janira*, *Neithea* and *Pecten*. On the basis of ornamentation differences he recognized two subgroups and also discussed within them some extra-American species, such as *P. pradoanus* and *P. ambongoensis* THEVENIN. He further thought that both groups could be phylogenetically traced in the Cretaceous and even in the Tertiary. This last idea was rejected by BÖHM (1922), who maintained that the Tertiary and Recent species, which he referred to

Pecten MÜLLER, are directly related neither to the Cretaceous ones, which he grouped in *Neithea*, nor to the early Jurassic forms, for which he proposed the generic name *Weyla*. His conclusions did not have immediate consensus, in part because JAWORSKI persisted in grouping the Cretaceous and early Jurassic species together in the same genus, which he called by the pre-Linnean name *Vola* (1925a, 1926) or else *Neithea* (1929). His ideas were the leading opinions followed in the most important papers on early Jurassic fossils from South America (such as WEAVER 1931; LEANZA 1942b).

Only GILLET (1924a, 1924c) adopted the name *Weyla*, as she considered that *Weyla*, *Neithea* and *Pecten* were convergent and iterative groups.

Species of this group were also known from North America (MEEK 1864), but they were not compared with the South American ones, not even by CRICKMAY (1930, 1933a), who proposed the new genus *Parapecten* for an early Jurassic species from western Canada, which he thought to be Bajocian. This name is regarded here as a synonym of *Weyla* s. s., on the basis of both external features and hinge characters.

The name *Weyla* only reappeared much later in the literature in connection with species of this group (see for instance COX 1965; QUINTERO and DE LA REVILLA, 1966, etc.).

COX et al. (1969) provided a diagnosis of the genus and considered *Parapecten* as its synonym, but also included the Triassic taxon *Tosapecten* KOBAYASHI & ICHIKAWA as a subgenus of *Weyla*. *Tosapecten* and *Weyla* are regarded here as different genera, as they were by HAYAMI (1975: 161), who even rejected all possible phylogenetic relations between them. This last statement is not yet supported by a detailed knowledge of the taxa. Similarly, *Pseudovola* LISSAJOUS is here considered as a different genus (as did also JAWORSKI 1925a, 1926) and not as a subgenus of *Weyla* as in COX et al. (1969).

The reasons for considering *Weyla* as a Neitheidae are stated above.

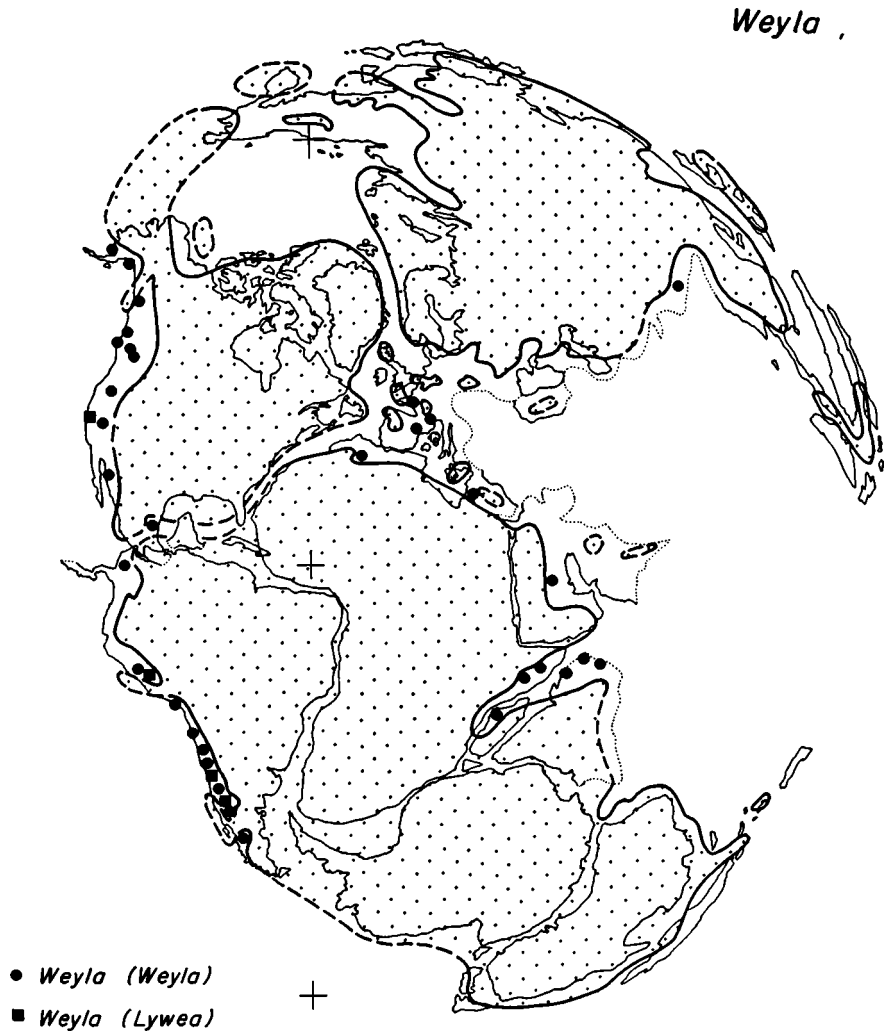
A revision of the Argentine species of *Weyla* is attempted here and two subgeneric groups are recognized: *Weyla* s. s. and *W.* (*Lywea*) a new subgenus, both restricted to the early Jurassic. The first one is known from several places around the world, as will be shown, and the latter is known from the western American margins (North America, Perú, Chile, Argentina).

The features of the new subgenus also allow a reassessment of the relations between *Weyla* and other bivalve genera. Thus both *Antijanira* BITTNER and *Amphijanira* BITTNER could perhaps be included in the Neitheidae, as they seem to be related to the new subgenus *Lywea*.

The palaeogeographic distribution of this genus was dealt with in several recent papers (HALLAM 1969, 1971, 1973; GEYER 1973; AGER 1975; HALLAM 1975, 1977b; DAMBORENEA & MANCENIDO 1979; HALLAM 1983) and was used favouring different early Jurassic migration routes between the eastern Pacific coast and the central and eastern Tethys. HALLAM (1973, 1977a, 1977b), overlooking the European and Moroccan records of Pliensbachian *Weyla*, proposed that the disjunct distribution during the Toarcian could be explained by the existence of a narrow epi-continental passway connecting southern Argentina, Antarctica and South Africa. On the other hand DAMBORENEA & MANCENIDO (1979) reviewed the global distribution of the genus and concluded that the Hettangian occurrences seem to be restricted to Canada, whilst by Sinemurian times *Weyla* has spread along the Pacific coasts of the Americas from Canada to Patagonia, where it persisted through to Toarcian times. Furthermore, Pliensbachian occurrences were noticed for France, Spain and Morocco, although no certain Toarcian records were recognized from Europe. Whilst persisting in northern Africa, by this time it spread also to Turkey, Saudi Arabia, Pakistan, Kenya and Malagasy. These occurrences support the idea of a shallow marine Mid-Atlantic connection between the western Tethys and the eastern Pacific as early as Pliensbachian times, now known as the Hispanic corridor or the "proto-Atlantic" (HALLAM 1983; WESTERMANN & RICCARDI 1985). This hypothesis is reinforced by the presence of *Weyla* in intermediate areas, such as southeastern Mexico (SCHMIDT-EFFING 1976, 1980) and Portugal (MOUTERDE et al. 1983), and was recently accepted by HALLAM (1983). *Weyla ambongoensis* (THEVENIN) has also been mentioned for the early Jurassic of southern China (WEN et al. 1976: 101), which is the easternmost Tethyan record of the genus (see text-fig. 17).

A list of the nominal species referred to *Weyla* was provided by DAMBORENEA & MANCENIDO (1979, appendix). The taxonomy of the genus was complicated by the proliferation of names, based only on incomplete or deformed internal moulds, proposed by R. PHILIPPI (1899), who also ignored BEHRENDSEN'S (1891) paper. After a careful revision of several species of this genus, it is concluded here that the internal moulds are, in most cases, indeterminate at a specific level and thus some of R. PHILIPPI'S names are dubious. A revision of the Chilean represen-

Text-fig. 17. Palaeogeographic distribution of *Weyla* (*Weyla*) and *Weyla* (*Lywea*) during the early Jurassic. Palaeocontinental reconstruction from SMITH & BRIDEN (1977) for the early Jurassic, hypothetical coastlines compiled from various sources.



tatives of *Weyla* is under way (PÉREZ & REYES, pers. comm., 1983). Meanwhile, a tentative attempt to clarify PHILIPPI's nomenclature is proposed in the synonymy of the species here described. This task was made easier by the observation of plastotypes of some of PHILIPPI's specimens sent by PÉREZ D'ANGELO.

In this revision the material preserved as internal moulds was only identified at the generic level when hinge and/or auricles provided enough evidence.

The present revision provides important additional data on the internal characters of *Weyla*, excellently preserved in a specimen collected in Chubut by BARRENECHE (DNGM 12463, pl. 7, fig. 2 here).

The position and proportions of the striated (vitreous or quick) and smooth (nacreous or catch) muscle fibers in the adductor muscle are more similar to the Spondylidae and Ostreidae than to extant *Pecten* species. The larger smooth portion of the adductor muscle is probably related to a sedentary mode of life and it could also be needed to maintain closure in the event of subaerial exposure of this shallow water bivalve (see THAYER 1972). The presence of strong muscle scars on the right valve in the position of pedal retractors would suggest at first sight an active foot in *Weyla* and an important byssal attachment period, but it is also possible that those scars belong to other muscles, homologous to the pedal ones, which could have performed a different function.

Other interesting feature is the presence of the here called "chomata", small tubercles on the periphery of the inner surface of the anterior and posterior margins of the valves. These structures may not be completely homologous to the true chomata described in ostreid bivalves (STENZEL 1971) as they are a row of small tubercles on both valves. The name was nevertheless used because it is illustrative of the general aspect of this peculiar structure, which is also found in some Spondylidae species (see for instance GOLDFUSS 1835, Taf. 106, Fig. 3d). The

“chomata” as here understood are variously developed but always present in all the Argentine species of *Weyla* (see text-fig. 21).

The growth tracks of the “chomata” can be seen on the outer surface of the shell as oblique parallel ridges on the anterior and posterior portions of both valves. These tracks were already noticed but unexplained by VON BUCH (1838: 55) and JAWORSKI (1914a, fig. 1a and 4a) and are also present in some Spondylidae (see for instance *Spondylus hystrix* GOLDFUSS, figured by d'ORBIGNY 1847, pl. 454 and *Spondylus truncatus* GOLDFUSS 1835, Taf. 106, Fig. 4; d'ORBIGNY 1847, pl. 459). They also resemble the “fine striae” present in some species of *Merklinia* as described by DHONDT (1975: 4, pl. 2, fig. 2B), though in this last case, their relation to internal structures is unknown.

Subgenus *Weyla* s. s.

Synonym: *Parapecten* CRICKMAY 1930 (type species: *P. nilakapamuxanus* CRICKMAY 1930).

Diagnosis: Right valve very convex, left valve flat or concave, but may be slightly convex in the early stages of growth. Auricles separated by deep furrows from the disc of the shell. With shallow byssal notch below the right valve anterior auricle and subauricular crura. Incipient development of subtriangular divergent isodont teeth. External surface of valves with strong radial ribs of equal magnitude that may be simple or split.

Weyla (Weyla) alata alata (VON BUCH 1838)

Plate 9, fig. 1; pl. 10, fig. 1-5; text-fig. 18, 19-1, 22a and 24

- * 1838 *Pecten alatus* m., v. BUCH, p. 55-56.
- ! 1839 *Pecten alatus* v. BUCH, p. 3-4, pl. 1, fig. 1-3.
- 1843 *Pecten Dufrenoyi* d'ORBIGNY, p. 106, pl. 22, fig. 5-9.
- v. 1846 *Pecten Dufrenoyi* (sic) d'ORB. - DARWIN, p. 486, 488, 493, 494, 495, 498, 500.
- 1851 *Pecten alatus* DE BUCH - BAYLE & COQUAND, p. 3, 5, 6, 14-15, 38, 45, pl. 5, fig. 1-2.
- 1854 *Pecten Dufrenoyi* - HUPÉ, p. 291-292.
- 1855 *Pecten ? alatus* (VON BUCH) - CONRAD, p. 283, pl. 41, fig. 2.
- 1861 *Pecten alatus* v. BUCH - BURMEISTER & GIEBEL, p. 22-23.
- 1867 *Janira alata* d'ORB. (sic) - RÉMOND de CORBINEAU, p. 116.
- ? 1870 *Pecten alatus* v. BUCH - STROBEL, p. 300.
- ? 1875 *Pecten alatus* v. BUCH - STROBEL, p. 61.
- ? 1876 *Pecten alatus* v. BUCH - BURMEISTER, p. 261, 314.
- ? 1877 *Neithea alata* v. BUCH - GABB, p. 294-295.
- 1878 *Pecten alatus* v. BUCH - GOTTSCHKE, p. 20.
- 1881 *Pecten (Janira) alatus* v. BUCH - STEINMANN, p. 243, 255, 293.
- ? 1891 *Pecten alatus* BUCH - BEHRENDSEN, p. 371, 390.
- ? 1891 *Pecten Dufrenoyi* d'ORB. - BEHRENDSEN, p. 390-391.
- ? 1892 *Pecten alatus* - BEHRENDSEN, p. 2.
- ? 1892 *Pecten alatus* v. BUCH - BODENBENDER, p. 13, 15, 32.
- 1894 *Vola alata* v. BUCH - MÖRICKE, p. 39-41.
- ! . 1899 *Pecten alatus* v. BUCH - R. PHILIPPI, p. 24, lám. 13, fig. 1 and 2 (right) (reproduction from v. BUCH, 1839, fig. 1-3).
- ? 1899 *Pecten excavatus* PH., R. PHILIPPI, p. 31, lám. 18, fig. 1a-b.
- ? 1899 *Pecten curvicosta* PH., R. PHILIPPI, p. 31-32, lám. 18, fig. 3.
- 1899 *Pecten Stolpi* PH., R. PHILIPPI, p. 34, lám. 19, fig. 5 (Text-Fig. 19-1 here).
- 1899 *Pecten subcarinatus* PH., R. PHILIPPI, p. 34, lám. 19, fig. 4a-b.
- . 1899 *Pecten commutatus* PH., R. PHILIPPI, p. 38, lám. 41, fig. 1-2 (from BAYLE & COQUAND, 1851).
- ? 1899 *Pecten compressus* PH., R. PHILIPPI, p. 38, lám. 41, fig. 3-4.
- ? 1903 *Pecten alatus* BUCH - IHERING, p. 121.
- ? 1904 *Pecten alatus* v. BUCH - STEINMANN, p. 17.
- . 1914a *Vola alata* var. *aspera* JAWORSKI, p. 275-276.
- . 1914a *Vola alata* (v. BUCH) BAYLE & COQUAND - JAWORSKI, p. 276-283, fig. 1-7, 8b.
- 1914b *Vola alata* v. BUCH - JAWORSKI, p. 287, 289, 297, 299, 300, 302.
- 1915 *Vola alata* (v. BUCH) BAYLE et COQU. - JAWORSKI, p. 439.
- ? 1916 *Vola alata* v. BUCH - GERTH, p. 142.
- 1917 *Vola alata* (v. BUCH) BAYLE et COQU. - TILMANN, p. 636, 644, 645, 681, 712.
- 1917 *Pecten alatus* v. BUCH - LISSON, p. 26-28, 31-83.

- ? 1921 *Vola alata* v. BUCH - DOUGLAS, p. 264-265.
 ? 1922 *Pecten alatus* v. BUCH - BEHRENDSEN, p. 174.
 ? 1922 *Pecten Duffrenoyi* d'ORB. - BEHRENDSEN, p. 174-175.
 1922 *Pecten alatus* (v. BUCH) - BÖHM, p. 138.
 1923 *Vola alata* v. BUCH - JAWORSKI, p. 87-88.
 ? 1923 *Janira alata* v. BUCH - STEINMANN in STEHN, p. 56.
 1925a *Vola alata* (v. BUCH) BAYLE et COQU. - JAWORSKI, p. 162-163.
 ? 1925 *Vola alata* (v. BUCH) - GERTH, p. 14, 16, 18.
 ? 1925 *Pecten Duffrenoyi* (sic) d'ORB. - GERTH, p. 18.
 1925b *Vola alata* (v. BUCH) BAYLE et COQUAND - JAWORSKI, p. 53.
 1926 *Vola alata* (v. BUCH) BAYLE u. COQU. - JAWORSKI, p. 390-391, 419.
 . 1929 *Vola alata* v. BUCH - STEINMANN, p. 71, fig. 77a-c.
 p 1931 *Vola alata* (v. BUCH) BAYLE et COQUAND - WEAVER, p. 281-283, pl. 31, fig. 179; pl. 32, fig. 181.
 . 1964 *Vola alata* (v. BUCH) - HÖLDER, p. 546, Taf. 155, Fig. 1 (reproduction from JAWORSKI, 1914a).
 ? 1973 *Weyla duffrenoyi* (d'ORB.) - IMLAY & DETTERMANN, p. 23.
 1973 *Weyla alata* (BUCH) - GEYER, p. 44, fig. 15a-b.
 ? 1973 *Weyla* cf. *bodenbenderi* (BEHRENDSEN) - GEYER, p. 44, fig. 15-c.
 ? 1977 *Weyla alata* (VON BUCH) - PÉREZ & REYES, p. 35, 40, 42, 43.
 . 1978 *Weyla alata* (v. BUCH) - RANGEL, p. 28-29, lám. 3, foto 7, p. 32-33, lám. 5, fotos 4 and 5, lám. 6, foto 1.
 ? 1978 *Weyla* cf. *W. alata* (v. BUCH) - RANGEL, p. 32.
 p 1978 *Weyla (Weyla) alata* (v. BUCH) - CAMACHO & RICCARDI, cuadro 1.
 . 1980 *Weyla alata* (v. BUCH) - HILLEBRANDT, lám. 1, fig. 1a-c.
 . 1982 *Weyla alata* (VON BUCH) - PÉREZ, lám. 19, fig. 3, 7, 9.
 v. 1982 *Weyla (Weyla) alata* (VON BUCH) - DAMBORENEA, p. 247-255, lám. 70, fig. 1-4.

Material: The material available for this revision consists of 23 shells with both valves, most of them preserved as internal moulds with only fragments of the shell, 21 right valves, nine left valves and several shell fragments. The subspecies *W. alata alata* was found in lower Pliensbachian beds of southern Mendoza province. Some specimens from old collections have vague indications of locality, but they seem to come from the Rio Atuel region, such as the material MLP 3905 and 8957, said to have been found at "Mina Tránsito", MLP 8033 labelled as coming from "afluencia del Rio Atuel" and BMNH 48690 which label only reads "Sosneado". The author's collections at the left bank of the Rio Atuel near Puesto Araya (B.1) contain several specimens: MLP 16526 to 16529 (M 349, 352 and 370) and one specimen was collected by UGARTE at Cerro La Brea (B.2): MLP 6676. This subspecies was collected by the author from the area of Arroyo del Portezuelo Ancho (B.5): MLP 19031 to 19035, 19039, 19040, 19044, 19045, 19047 to 19055, 19057, 19063, 19064 (M 1287 to 1292, 1294 and 1298) and from the Paso del Portezuelo Ancho (B.4) by BETTINI: MLP 16530. This taxon is also abundant at Arroyo Serrucho (B.8): MLP 19640, 19645, 19649, 19652 and 19656 (M 1314, 1317, 1320 to 1323, author's collection) and at Cerro Puchenque (B.9): MLP 16519 to 16525 (M 299, 307, 309, 312, 313 and 320).

Range and distribution: *W. alata* has a wide geographical range in the South American Andes, material that surely belongs to this species is known from Colombia to the North (GEYER 1973) to the upper Catán Lil river to the South (WEAVER 1931). Peruvian and Chilean specimens were observed at the BMNH and NHMB. The supposed records of *W. alata* in more southern localities, such as the outcrops of the Piedra Pintada region, are doubtful, since all the material from those localities (collections made by ROTH, GROEBER, FRENGUELLI, A. LEANZA, DAMBORENEA and colleagues, etc.) seen by the author belong to other species, especially *W. bodenbenderi*. Therefore WEAVER's (1931) record of *W. alata* for Piedra Pintada remains doubtful. Some of the records from Chubut can also be disregarded, or at least they cannot be confirmed now, since the specimen figured by FERUGLIO (1934: 45-46, tav. 5, fig. 1) can be referred to *W. bodenbenderi* and from the examination of WAHNISH' (1942: 33-35) material it is concluded that one of her specimens (DNGM 8844) is incomplete and only identifiable at the generic level, whilst the other (DNGM 8856) is close to *W. bodenbenderi* according to the ribbing pattern. Other material from Chubut (PIATNITZKY and BARRENECHE collections) belong to the subspecies *W. alata angustecostata* (see below), which is also present to the south of Espinazo del Zorro in Neuquén. In summary, the subspecies *W. alata alata* was only found in Argentina in lower Pliensbachian beds of Mendoza province.

IMLAY & DETTERMANN (1973: 23) mentioned the presence of *W. duffrenoyi* (d'ORBIGNY) in the Toarcian of southwest Alaska, but they did not provide any illustration. *W. aff. alata* was also cited by TIPPER & RICHARDS (1976: 11-18, 62) for the Canadian Sinemurian and *W. alata* for several localities of the United States by MÜLLER & FERGUSON (1939: 1611-1613), SILBERLING (1959: 2729), HALLAM (1965: 1491).

At least part of the references to this species for different South American localities may in fact belong to other *Weyla* species and were therefore listed in the synonymy with a question mark.

Description: Large shell, inequivalve and subequilateral, pectiniform. Right valve very convex, with a very prominent umbo that extends beyond the hinge-line; left valve slightly concave, flat to weakly convex in the young stage.

The anterior and posterior triangular auricles are big and clearly limited in both valves, the posterior auricles are slightly larger than the anterior ones. The dorsal margin is straight, the right valve hinge margin bends and covers the left one near the umbones. The free margins of each auricle meet the dorsal margin at an angle slightly

smaller than 90° and are subequal to each other. The surface of the right valve auricles is convex, whilst the left one is concave. All the auricles are clearly limited from the disc of the shell by a deep groove, the right anterior auricle has a shallow byssal notch without a ctenolium. The anterior margin of the shell below the auricles is almost straight and meets the convex ventral margin without any interruption. The posterior margin is slightly convex. The ventral margin is scalloped, having the ribs of the right valve and the furrows of the left valve as the most prominent points.

The right valve umbo is very prominent and mesogyrous and greatly extends a long way beyond the hinge margin. The left umbo is not prominent and is generally covered by a fold of the right valve dorsal margin. The apical angle of the left valve varies between 100° and 115°.

The resilifer is triangular and relatively large in both valves, and is centrally placed, just below the umbones in a surface that dips towards the interior of the right valve. There are two subtriangular areas vertically striated along all the dorsal margin and both sides of the resilifer. The crenulations are as long as the resilifer near it, but they decrease in length towards the auricular external ends on the right valve. On the left valve the striated portion of the hinge is narrow. In the ventral portion of each auricle there is a variable number of auricular crura that are subparallel to the hinge-line. Only the last 2 or 3 of these appear to be functional in the adult, though on some right valves a greater number can be seen (from 8 to 10) over almost all the internal margin of the auricles. The remaining part of the inner surface of the auricles is smooth, without teeth or horizontal hinge crura.

The adductor muscle scar is big and subcircular in shape and it is posteriorly placed just below the base of the posterior auricle, not reaching the central line of symmetry of the valves.

The shell surface is ornamented with 12 to 14 strong radial ribs, that are different on each valve. In complete specimens there is always one more rib on the right valve than on the left one. On the right valve the ribs are straight and strong, never bifurcate, and are separated by deep furrows that are equal or wider than the ribs. In transverse section these ribs have an almost flat top and nearly vertical sides, although the angle of dipping varies according to the region of the shell. Near the ventral margin the flanks dip outwards and the ribs are lower. The intervals have a slightly concave smooth bottom. Both the ribs and the furrows are crossed by growth-lines that are convex towards the ventral margin on the interspaces and concave to straight on the ribs. The two most external ribs on each side are lower than the others and their top surface is narrower, in transverse section they have a more triangular profile. The inner surface of the right valve shows the ribs and furrows through almost all their length, though weaker than on the outer surface. Only the umbonal region is smooth or nearly so, in a variable extension. On the internal moulds the furrows are flat and the ribs are convex, flanked on each side by a shallow but well-defined sulcus. Near the ventral margin the inner surface has a quite different aspect, because it is strongly crenulated, the ribs become taller and the furrows deeper and these last ones taper suddenly towards the margin of the shell in a short triangle.

On the left valve the ribs are also straight but they are narrower and triangular in section and are flanked by a pair of minor ridges along all their length. The interspaces are always wider than the ribs and have a slightly concave bottom. The growth-lines are convex towards the ventral margin in the interspaces and straight on the ribs. Again on this valve the most external ribs are lower with less steep flanks. On the inner surface of the shell the ribs of the left valve are seen from the umbo as flat-bottomed furrows, having a small rib at each side. The interspaces are flat. The inner margin of the left valve is similar to that of the right valve.

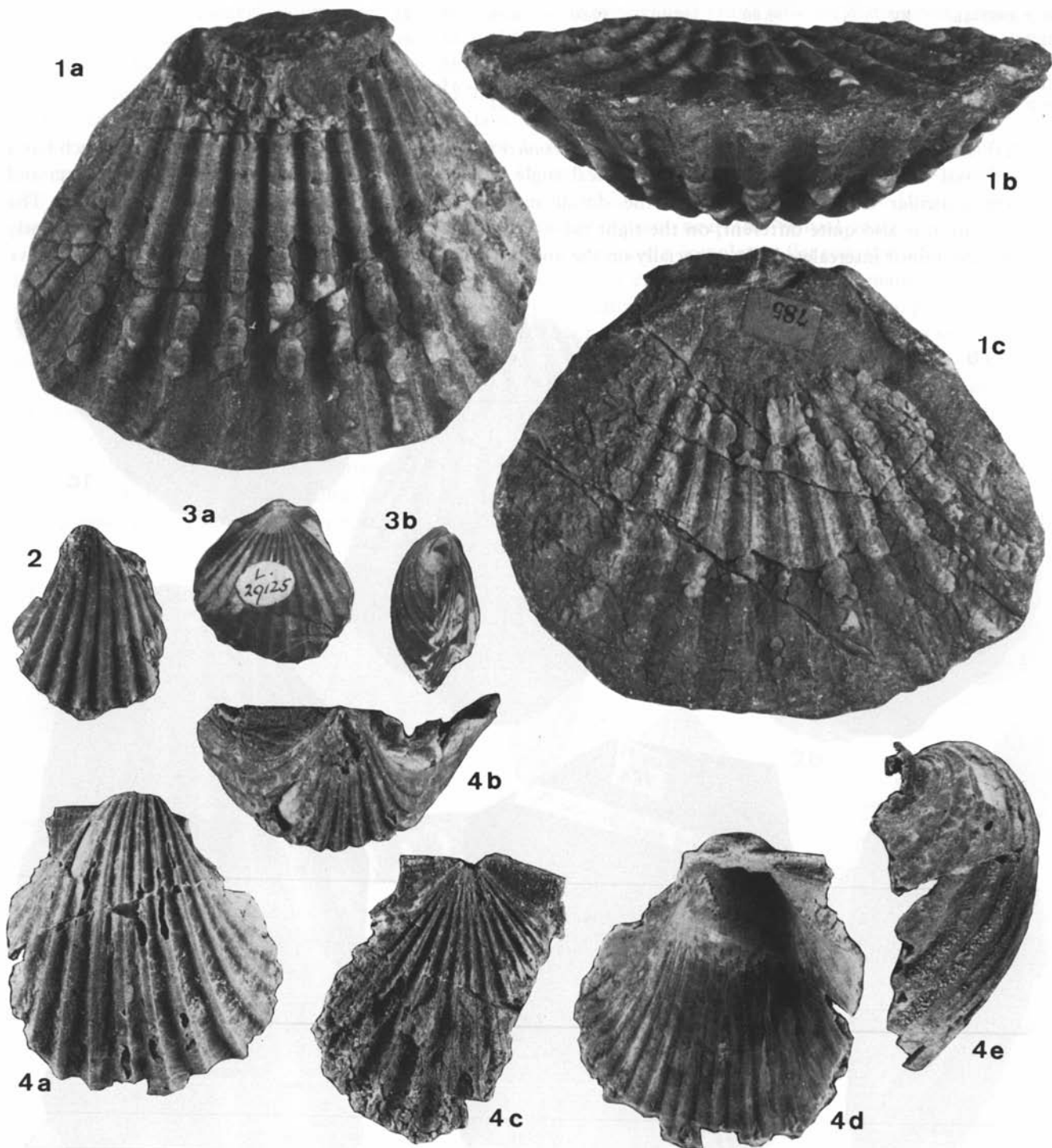
On the inner anterior and posterior margins just below the auricles a row of small tubercles or "chomata" are present on both valves. These structures sometimes correspond to oblique parallel ridges on the outer surface of the valve, which appear as a result of the growth and migration of the "chomata".

The auricles of the left valve have on their outer surface, besides the growth lines, a pair of radial ribs near the dorsal margin and sometimes also weak radial lines below them. The right valve auricles have only growth-lines.

The surface of the left valve auricles is concave and they are limited by a clear suture from the disc of the shell, which is deeper on the posterior side.

Measurements: See also scatter diagram on text-fig. 24.

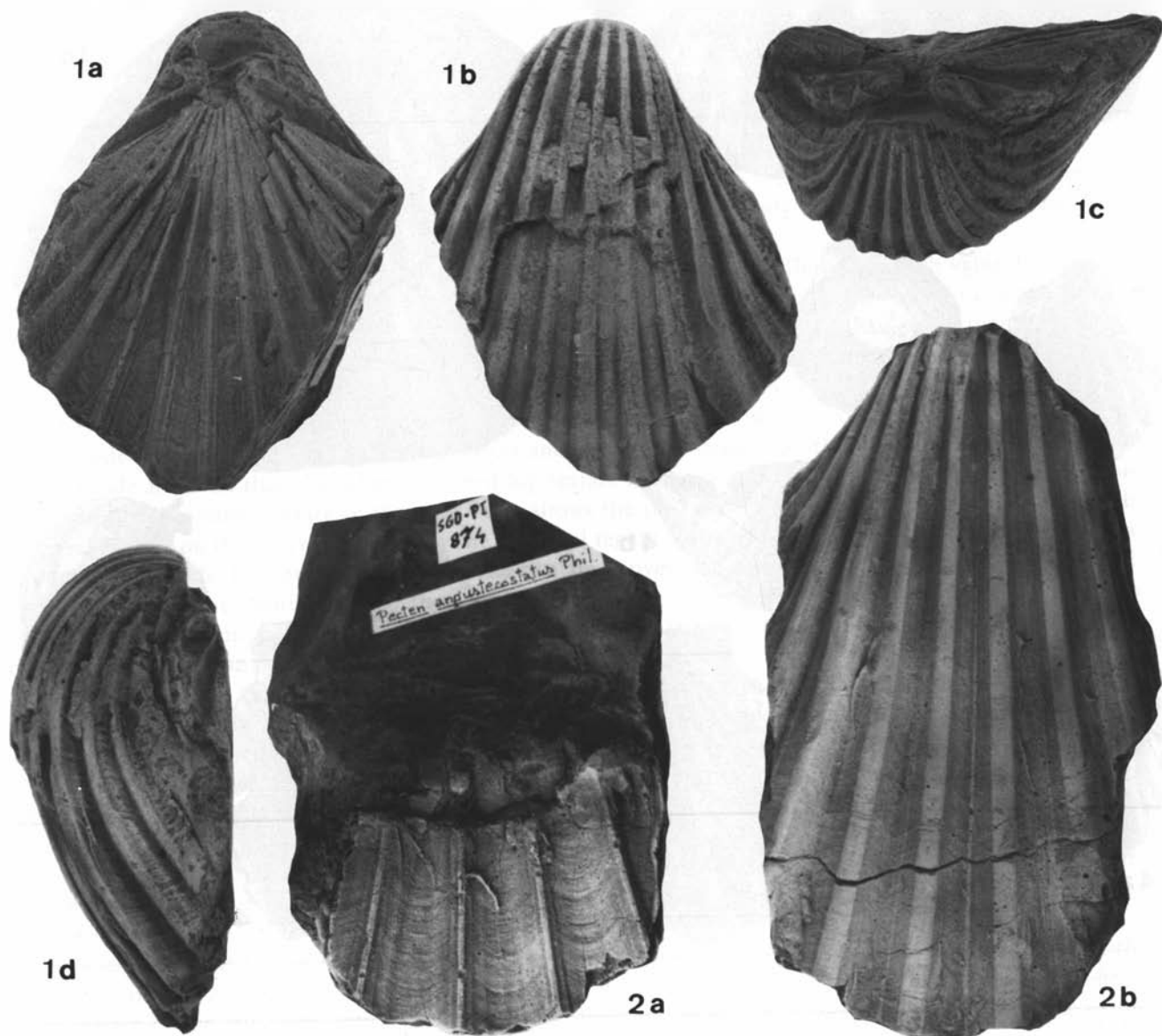
Specimen	Material		L (mm)	H (mm)	W (mm)	L/H	n° ribs		e
							RV	LV	
MLP 3905-ab	BV	IM	77.90	108.20	36.10	0.72	13	12	100°
MLP 6676-ab	BV	IM	92.80	108.10	36.00	0.86	13	12	108°



Text-fig. 18. *Weyla alata alata* (von Buch). 1: specimen with both valves collected by DARWIN in Chile, BMNH Darwin 785, 1a: right valve; 1b: ventral view; 1c: left valve. 2: incomplete right valve collected by DARWIN in Chile, BMNH Darwin 978. 3: almost complete young specimen collected by REYNOLDS at Peñón near Pedernales, Chile, BMNH L.29125, 3a: left lateral view; 3b: anterior view. 4: silicified specimen with both valves collected by PETIT in Perú, BMNH (unnumbered), 4a: exterior of right valve; 4b: dorsal view of right valve; 4c: exterior of left valve; 4d: interior of right valve; 4e: posterior view of right valve. All figures natural size.

MLP 8957-ab	BV	S	95.00	110.40	30.60	0.86	12	11	100°
MLP 16525-b	RV	IM	41.45	37.40	14.00	1.11	13	-	-
MLP 16526	BV	S	87.40	95.60	33.00	0.91	13	12	102°
MLP 16528	BV	S	112.00	106.40	30.30	1.05	14	13	115°
MLP 16529-cd	BV	IM	83.60	103.30	25.40	0.81	13	12	110°

Affinities: The most similar species is *W. bodenbenderi* (BEHR.), which is also described here and which has a deeper byssal sinus and subequal auricles. The apical angle is larger in *W. bodenbenderi*, which also has fewer and different auricular crura, not parallel to the dorsal margin but to the inner margin of the auricles. The ornamentation is also quite different; on the right valve the ribs are less prominent, wider and they are frequently split or have minor intercalated ribs, especially on the anterior and posterior portions of the shell. On the left valve



Text-fig. 19. 1: Holotype of *Pecten stolpi* R. PHILIPPI, SGO-PI 897 (= MLP 18323), Valle de Tinguiririca, Chile, figured by R. PHILIPPI (1899, lám. 19, fig. 5). Photographs from plaster cast. 1a: left valve; 1b: right valve; 1c: dorsal view; 1d: anterior view. 2: One of the syntypes of *Pecten angustecostatus* R. PHILIPPI, SGO-PI 874 (= MLP 18320), Amolanas, Chile, figured by R. PHILIPPI (1899, lám. 14, fig. 2). Photographs from plaster cast. 2a: left valve; 2b: right valve. All figures natural size.

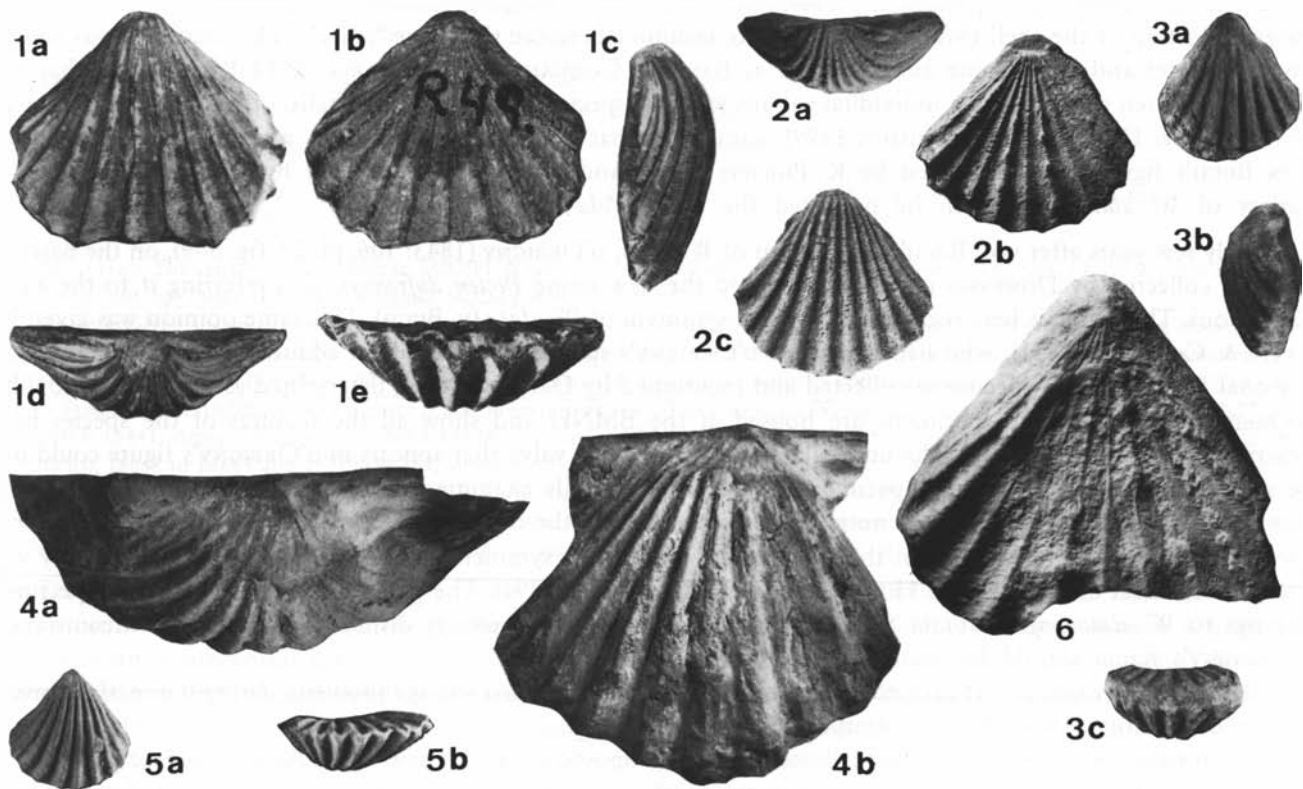
the difference in ornamentation is even greater; in *W. bodenbenderi* the radial ribs are flat-topped, convex in transverse section, and at least as wide as the interval between them. They can also be subdivided or have minor intercalated ribs, especially on the flanks (see BEHRENDSEN 1891, Taf. 22, Fig. 3; 1922, lám. 1, fig. 10; BURCKHARDT 1902, pl. 4, fig. 1-2; JAWORSKI 1914a, fig. 9-10; 1925b, lám. 1, fig. 1; 1926, text-fig. 2 as *Vola simplex*; WEAVER 1931, pl. 33, fig. 184; LEANZA 1942b, lám. 7, fig. 6; lám. 8, fig. 1-2; and here on pl. 10, 11 and 12).

Weyla titan (MÖRICKE), which may be considered as a subspecies of *W. alata*, is known from some Chilean localities (MÖRICKE 1894: 41; R. PHILIPPI 1899: 29, lám. 15) and it was also mentioned from Perú (BRAVO 1906: 106-108) and Argentina (JAWORSKI 1914a: 283-284; 1915: 439; 1925b: 53). This shell is much larger, posteriorly elongated and the ribs become flat and wider than the interspaces near the ventral margin.

Weyla alata angustecostata (PHILIPPI) has narrower ribs which have a completely flat top, the intervals between the ribs are wider and the inner surface of the shell is smooth except near the ventral margin (text-fig. 23).

The species *W. rollieri* (COSSMANN), from the early Pliensbachian of France (COSSMANN 1916, pl. 5, fig. 13-15; DUBAR 1925, fig. 41-42, pl. 5, fig. 10-12) differs in having fewer radial ribs (8 to 10), a different cross section of the right valve ribs and larger and more pointed auricles.

W. alata shares with *W. mexicana* (JAWORSKI), from the early Jurassic of Mexico and Argentina (JAWORSKI 1929: 2-5, Taf. 1, Fig. 1a-c, 2, 3; BURCKHARDT 1930: 23; KING 1939: 1654) the form and relative convexity of both valves. It has the same number of radial ribs and a pair of radial ribs on the left valve auricles, but *W. mexicana* has subequal ribs and intervals that are triangular in transverse section on both valves. This species also has a peculiar concentric ornamentation of strong V-shaped growth lamellae, particularly developed on the interspaces. *W. ambongoensis* (THEVENIN), known from the Toarcian of Malagasy (THEVENIN 1908: 24, pl. 4, fig. 2-3; DUBAR 1948:



Text-fig. 20. *Weyla ambongoensis* (THEVENIN). 1: specimen with both valves from west of Kuzdar, Baluchistan, Pakistan, BMNH (unnumbered), X 1. 1a: right valve, 1b: left valve, 1c: posterior view, 1d: dorsal view, 1e: ventral view. 2: specimen with both valves, Didimtu, Kenya, MLP 19092, X 2. 2a: dorsal view, 2b: left valve, 2c: right valve. 3: specimen with both valves, Didimtu, Kenya, THOMPSON'S collection, BMNH (unnumbered), X 1. 3a: right valve; 3b: anterior view; 3c: ventral view. 4: right valve, Turkey, AGER'S collection, University College of Swansea, X 2. 4a: dorsal view; 4b: lateral view. 5: specimen with both valves, Didimtu, Kenya, THOMPSON'S collection, BMNH (unnumbered), X 1. 5a: right valve; 5b: ventral view. 6: specimen with both valves, Didimtu, Kenya, AGER'S collection, University College of Swansea, X 2.

220; ARKELL 1956: 342; BESAIRES & COLLIGNON 1956: 58), Morocco (DUBAR 1948: 220, pl. 29, fig. 7–9), Pakistan (HOLLAND 1909: 27–28; ARKELL 1956: 398), Kenya (ARKELL 1956: 318; COX 1965: 59, pl. 7, fig. 9; see also text-fig. 20 here), Saudi Arabia (ARKELL et al. 1952; ARKELL 1956: 300) and China (WEN et al. 1976: 101, pl. 24, fig. 6–9) also has subtriangular ribs, but differs from all other *Weyla* species because its shell, originally concave-convex, becomes biconvex in adults and never exceeds 5 cm in length. The radial ribs of *W. ambongoensis*, up to 12 in number, may bear tubercles or spine bases on both valves (see text-fig. 20). Other species that also have V-shaped ribs on both valves are the European *W. pradoana* (DE VERNEUIL & COLLOMB 1853) and *W. lacazei* (HAIME 1855, see also CALZADA 1983, fig. 3: 1a–c and MOUTERDE et al. 1983, pl. 13, fig. 6).

A pair of very closely related (or even possibly synonymous) species were described from Morocco and Spain: *W. ayarti* (DUBAR 1948: 217, pl. 28, fig. 26; ARSICAULT 1965: 41) and *W. almela* (QUINTERO & DE LA REVILLA 1966: 41, lám. 5, fig. 1a–b), but these shells are smaller than *W. alata* and only have up to six radial ribs on each valve. The left valve of these species is unknown.

Other species, here grouped in the new subgenus *Lywea*, can be easily distinguished from *W. alata* by having both valves convex and V-shaped ribs and interspaces.

“*Parapecten*” *nllakapamuxanus* CRICKMAY (1930, pl. 5, fig. f–g), from the Early Jurassic of British Columbia, Canada, and “*Pecten*” *argentarius* GABB (1877: 293–294, pl. 41, fig. 12), from the Pliensbachian (?) of Perú, are both imperfectly known species, with which it is difficult to establish comparisons.

Remarks: *W. alata alata* was described by VON BUCH (1838: 55–56) and first figured one year later by the same author (1839: 3–4, 20, pl. 1, fig. 1–4) on the basis of material collected by HUMBOLDT in Perú, originally referred to the early Cretaceous. VON BUCH’s figure represents a somewhat inequilateral specimen, a common feature in distorted *Weyla* specimens. Nevertheless this author assigned special importance to the fact that the anterior portion of the shell extends in a wing-like fashion (therefore the name “*alata*”). This character was widely discussed later and while some authors (such as BAYLE & COQUAND 1851; JAWORSKI 1914a) considered that the figured specimen was simply an individual variant within a species with equilateral shells, others (such as GIEBEL in BURMEISTER & GIEBEL 1861; R. PHILIPPI 1899) maintained that it is valid as a character and typical of the species. VON BUCH’s figure was reproduced by R. PHILIPPI (1899) and incorrectly interpreted by JAWORSKI (1914a) as a variety of *W. alata*, for which he proposed the name *Vola alata* var. *aspera*.

Only few years after VON BUCH’s description of *W. alata*, D’ORBIGNY (1843: 106, pl. 22, fig. 5–9), on the basis of material collected by DOMEYKO in Chile, proposed the new name *Pecten dufrenoyi*, also referring it to the early Cretaceous. This name is here regarded as a junior synonym of *W. alata* (v. BUCH). This same opinion was given by BAYLE & COQUAND (1851), who had examined D’ORBIGNY’s specimens and is here additionally supported by the personal observation of specimens collected and mentioned by DARWIN (1846), determined as *Pecten Dufrenoyi* by D’ORBIGNY himself. These specimens are housed at the BMNH and show all the features of the species here described (see text-fig. 18, 1–2). The unusual ribbing of the right valve that appears in D’ORBIGNY’s figure could not be seen on any of the numerous specimens of *Weyla* from Chile examined in different museum collections. As BURMEISTER & GIEBEL (1861) already noticed, it is probable that the drawing was a reconstruction from incomplete specimens based on the assumption that the ribbing was strictly symmetrical on both valves. This synonymy was accepted by most authors, except HUPÉ (1854) and BEHRENDSEN (1891). The possibility that D’ORBIGNY’s specimen belongs to *W. alata angustecostata* (PHILIPPI) instead, cannot be completely dismissed and in that circumstance, D’ORBIGNY’s name should be used for this subspecies of *W. alata*.

BAYLE & COQUAND (1851) excellently illustrated *W. alata* and settled the age problem, dating it as early Jurassic. All other authors followed their interpretation of the taxon.

R. PHILIPPI (1899) reproduced their illustration and proposed for it the new name *Pecten commutatus*, which is not only unnecessary but also a junior homonym of *P. commutatus* MONTEROSATO 1875, and thus invalid.

The first early Jurassic fossil mentioned for Argentina was also referred to *Pecten alatus*, mentioned by STROBEL (1870, 1875) from the Portezuelo Ancho region. Unfortunately there are not enough data to establish if this record corresponds to *W. alata* or to the species from the same place later described by BEHRENDSEN (1891) as *W. bodenbenderi*, since both species occur near that locality.

W. alata was very soon regarded as a characteristic Andean early Jurassic species and as early as 1878 GOTTSCHÉ provided a summary of its geographical distribution.

Some of the numerous species described by R. PHILIPPI (1899) are here tentatively included as synonyms of *W. alata*, pending a revision of the Chilean material.

This species was frequently mentioned for several South American localities and was figured by JAWORSKI (1914a, figures reproduced in HÖLDER 1964 and in COX et al. 1969), STEINMANN (1929, figures reproduced in COX et al. 1969), WEAVER (1931), GEYER (1973), RANGEL (1978), HILLEBRANDT (1980) and PÉREZ (1982).

SCHLAGINTWEIT (1912) doubted of the early Jurassic age of at least part of VON BUCH's material, especially that collected between Guambos and Montán, where according to SCHLAGINTWEIT there are no outcrops of early Jurassic age. On the other hand early Cretaceous beds do crop out there and could bear bivalves referable to *Neithea*. This raises the question of the real identity of the species, because it is probable that the rest of the specimens that VON BUCH examined (i. e. from Huancavélica) are in fact of early Jurassic age. The designation of a lectotype to stabilize the concept of *Pecten alatus* VON BUCH (and consequently the genus that it typifies) is thus of fundamental importance, but cannot be done without the observation of VON BUCH's specimens, if they are still available.

Autecology: As already said (DAMBORENEA & MANCENIDO 1979: 85) this pectinid is superbly adapted to a semi-infaunal reclining mode of life, like extant species of *Pecten*. BAIRD (1958), TEBBLE (1966: 57) and STANLEY (1970: 140) provide a description of the way in which living specimens of *Pecten maximus* (LIN.) and *P. ziczac* (LIN.) respectively attain their life position after being removed. Both species live partially buried in the sandy substrate and they clap their valves together at brief intervals to scour the sand from around the margins of the shell, forming a horseshoe-shaped depression into which they sink. Some of the sand thrown into suspension settles on the surface of the concave upper valve, completing the "camouflage". Extant *Pecten* species prefer clean sandy bottoms, or even sandy gravel, below the low-tide line down to about 100 m depth. GILLET (1924a) accepted this mode of life for the *Neithea* species. The relation between the striated and smooth portions of the adductor muscle scar also support the interpretation of a sedentary habit for this bivalve species (see THAYER 1972).

Weyla (Weyla) alata angustecostata (R. PHILIPPI 1899)

Plate 6, fig. 17b; pl. 7, fig. 1-2; pl. 8, fig. 1-3; pl. 9, fig. 2-3; text-fig. 2, 19-2, 21

- * ! v. 1899 *Pecten angustecostatus* PH., R. PHILIPPI, p. 27, lám. 16, fig. 1; lám. 14, fig. 2.
- p v 1930 *Pecten prodoanus* (sic) VERN. y COLL. - RIGAL, p. 6, lám. 1, fig. 2 (only).
- p v 1942 *Vola alata* - SUERO, p. 21.
- p v 1951 *Pecten alatus* v. BUCH - SUERO, p. 11, 14.
- v. 1982 *Weyla (Weyla) alata angustecostata* (R. PHILIPPI) - DAMBORENEA, p. 256-258, lám. 34, fig. 4; lám. 71, fig. 3; lám. 72, fig. 1-3.

Material: The syntypes are housed in SGO-PI. A cast of one of R. PHILIPPI's figured specimens (1899, lám. 14, fig. 2) from Amolanas, Chile, was sent by PÉREZ D'ANGELO (original SGO-PI 874, cast at MLP 18320).

Three bivalved specimens, a complete right valve, seven incomplete right valves, six left valves and several fragments, from different collections, but always from Toarcian beds, is the material here described. In Chubut province it was found in the Sierra de Agnia region by BARRENECHE: DNGM 12463 (= MLP 19076), Lomas Occidentales de Estancia Ferraroti, Nueva Lubecka by PIATNITZKY: MLP 15347, and near Arroyo Pescado: MLP 18208. This subspecies is also known from central and northern Neuquén province in southern Cordillera del Viento (C.1): MLP 15441; Arroyo Ñiraico (C.4): MLP 15534, both collected by GULISANO; Cerro Granito (C.14): MLP 2653, 4848, 4872 (old MLP collections), 16662 to 16664 and 19710 (M 167, author's collections); and Arroyo Tin-Tin (C.17): MLP 14284. The author also collected it in Cerro Tricolor (B.1), Mendoza province: MLP 16531; and there is one specimen from old MLP collections (MLP 9423) said to come from "south of Mendoza". The specimen from Quebrada Honda, southern San Juan province originally referred by RIGAL (1930, lám. 1, fig. 2) to *Pecten prodoanus* is an incomplete right valve and its internal mould: DNGM 9428 = MLP 19078.

Description: Large shell, right valve very convex, left valve flat (slightly concave near the umbo), pectiniform, with the umbonal angle of the right valve less than 90°, thick shell. The dorsal margin is long and straight, with a subcentral umbo and subequal auricles. The anterior margin meets the dorsal one at an angle slightly less than 90°, then it bends backwards as the shell has a deep byssal notch. Below the auricle the anterior margin is almost straight. The dorsal part of the posterior margin is unknown, but below the auricles it is also nearly straight. The ventral margin is scalloped and evenly convex. The auricles of the right valve, which are feebly convex, are limited from the disc of the shell by a deep suture.

The hinge comprises a deep furrow, parallel to the dorsal line, probably occupied by the outer ligament layer, with below it two very big, subtriangular areas, vertically striated, one on each side of the resilifer. The striae are narrow, very close together and in places may have a sinuous pattern. The striated posterior area is higher than the anterior one. They each have a radiating subtriangular depression and a triangular thickening in the region adjacent to the resilifer, here interpreted as incipient isodont teeth and sockets, which are better developed on the anterior half. The triangular resilifer is wide and deep and appears to have been occupied by the ligament up to a little more

than $\frac{3}{4}$ of its total height. At the base of the auricles there are auricular crura placed on top of an elevated portion of the inner shell surface. These crura, which are subparallel to the dorsal margin, are ten in number on the posterior and at least six on the anterior auricle of the right valve. The anterior crura are placed slightly more dorsally than the posterior ones.

The inner anterior and posterior margins below the auricles have a row of small "chomata" that can be traced on the outer surface of the shell as straight or sinuous parallel ridges that indicate their growth migration. These growth tracks appear between the margin of the shell and the first rib, on both valves, and are oblique to the growth-lines, which they intersect sometimes producing a zig-zag pattern (text-fig. 21 b).

The adductor muscle scar is posteriorly placed. It is big and subcircular in outline, being more impressed postero-dorsally. It is divided in two areas by an oblique line. The antero-dorsal portion, which is interpreted as belonging to the striated muscle, is smaller than the postero-ventral one, which probably belongs to the smooth muscle. A group of three spot-like scars appears near the inner margin of each auricle, aligned roughly parallel to it. The anterior group is more dorsally placed than the posterior one. According to their position, these scars may belong to the pedal retractor muscles.

The shell is ornamented with 15 strong radial ribs, which differ from one valve to the other. On the right valve the ribs are narrower than the intervals between them, their tops are almost flat and their flanks also flat and dipping outwards. The bottoms of the interspaces are also flat. On the flanks and bottoms of the intervals the growth lines are clearly seen, but the tops of the ribs are almost smooth. One very thin intercalated rib may appear on the flanks of the primary ribs near the bottom. The right valve auricles only bear growth-lines, which are more prominent than those on the disc. The inner surface of the right valve is almost smooth, only near the ventral margin is there some relief, where the shell thickness decreases and the ribs and intervals are then well marked. On both sides of each interval there is an inner rib and the outer ribs reflect on the inner surface as depressions with evenly concave bottoms.

On the left valve the ribs are simple, very thin, V-shaped and are separated by very wide, flat-bottomed intervals. On both sides of each primary rib and very close to it, there is a step-like ridge all along. The intervals are covered by thin growth-lines that are convex towards the ventral margin. The ribs reflect only weakly on the inner surface of the valve.

Measurements: Measurements of the specimen DNGM 12463 (a right valve): L = 181.5 mm, H = 159.5 mm, W = 53.6 mm, L/H = 1.14, L of resilifer = 14.55 mm, W of resilifer = 13.05 mm, H of adductor = 44.4 mm, W of adductor = 38.5 mm, H base of anterior auricle = 30 mm, W base of anterior auricle = 35 mm.

Affinities: This taxon is here considered as a subspecies of *W. alata* (v. BUCH) due not only to external but also to internal characters. Nevertheless, *W. alata angustecostata* has a thicker shell, the inner surface of the right valve being almost smooth and has thinner ribs on both valves, with wider and flat-bottomed intervals.

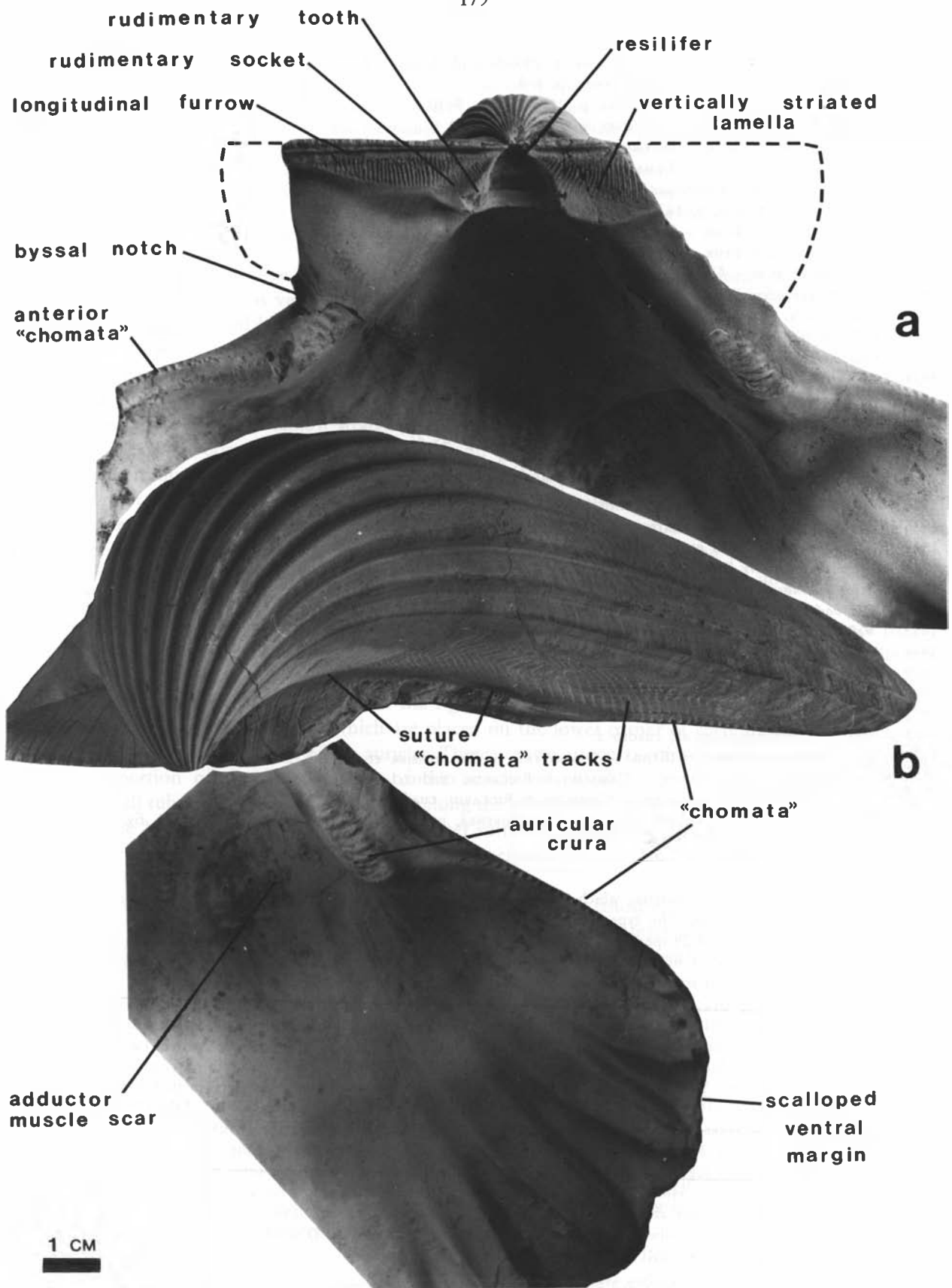
Concerning the differences from other *Weyla* species, the comparison already established with the nominotypic subspecies are also valid for this one (see also text-fig. 23).

Remarks: The Argentine material here referred to this subspecies is identical to R. PHILIPPI's original specimens in every detail (see also text-fig. 19-2), as seen on R. PHILIPPI's figures (1899) and on the plaster cast of one of his specimens (SGO-PI 874). This taxon, which had not been mentioned again since the original description, is present in Argentina from southern San Juan to Chubut provinces. R. PHILIPPI (1899) only indicated "Amolanas" as the locality where his specimens were found and unfortunately the taxon has not been recorded by JENSEN & VICENTE (1977) in a recent survey of that area. Although it seems to be restricted to Toarcian levels in Argentina, the possible stratigraphical use of this subspecies is still tentative due to the scarcity of material.

Weyla (Weyla) bodenbenderi (BEHRENDSEN 1891)

Plate 7, fig. 3; pl. 10, fig. 6; pl. 11, fig. 1-2; pl. 12, fig. 1-3; text-fig. 22b-c, 24

- * ! . 1891 *Pecten Bodenbenderi* BEHRENDSEN, p. 391, Taf. 22, Fig. 3.
- ?? 1899 *Pecten dilatatus* PH., R. PHILIPPI, p. 30, lám. 17, fig. 4.
- v . 1899 *Vola alata* v. BUCH - ROTH, p. 155.
- ? 1900 *Pecten (Vola) alatus* v. BUCH - BURCKHARDT, p. 24-25, 57, 69, 72, pl. 19, fig. 12.



Text-fig. 21. *Weyla (Weyla) alata angustecostata* (R. PHILIPPI). DNGM 12463 (= MLP 19076), right valve showing hinge details. Natural size. a: inner view of dorsal region; b: oblique dorso-posterior view; c: inner view of posterior region.

- v . 1902 *Vola* aff. *alata* von BUCH - BURCKHARDT, p. 244-245, pl. 4, fig. 1-2.
p ? 1903 *Vola alata* von BUCH sp. - BURCKHARDT, p. 8-9.
. 1914a *Vola Bodenbenderi* (BEHR.) - JAWORSKI, p. 285-288, fig. 9-10.
1914b *Vola Bodenbenderi* (BEHR.) - JAWORSKI, p. 298, 300.
1915 *Vola Bodenbenderi* BEHR. - JAWORSKI, p. 439-440.
1917 *Vola Bodenbenderi* BEHR. - TILMANN, p. 682, 645.
! . 1922 *Pecten bodenbenderi* BEHRENSSEN, p. 175, lám. 1, fig. 10.
1925a *Vola simplex* JAWORSKI, p. 163-164, lám. 1, fig. 1.
1925b *Vola Bodenbenderi* BEHR. - JAWORSKI, p. 54.
1925 *Vola Bodenbenderi* BEHR. - GERTH, p. 18.
1925 *Vola simplex* JAW. - GERTH, p. 18.
v . 1925 *Vola Bodenbenderi* BEHR. - GROEBER, p. 460, 461, 462.
? 1925 *Vola alata* v. BUCH - GROEBER, p. 463.
. 1926 *Vola simplex* - JAWORSKI, p. 391-392, text-fig. 2.
. 1931 *Vola bodenbenderi* BEHRENSSEN - WEAVER, p. 283-284, pl. 33, fig. 184.
! . 1931 *Pecten Bodenbenderi* BEHR. - WINDHAUSEN, lám. 22, fig. 6 (copy from BEHRENSSEN, 1891).
. 1931 *Vola simplex* JAW. - WINDHAUSEN, lám. 22, fig. 3 (copy from JAWORSKI, 1925a).
v . 1931 *Vola alata* v. BUCH - WINDHAUSEN, lám. 22, fig. 2 (copy from BURCKHARDT, 1902).
. 1934 *Vola alata* (v. BUCH) BAYLE et COQUAND - FERUGLIO, p. 45-46, tav. 5, fig. 1.
? 1934 *Vola* aff. *simplex* JAW. - FERUGLIO, p. 38-39, tav. 4, fig. 8.
1936 *Vola alata* (v. BUCH) BAYLE et COQUAND - PIATNITZKY, p. 88, 90.
? 1936 *Vola* aff. *simplex* JAW. (sic.) - PIATNITZKY, p. 88.
1936 *Vola bodenbenderi* BEH. - PIATNITZKY, p. 89, 100.
p v . 1942 *Vola alata* (von BUCH) et COQUAND - WAHNSH, p. 33-35.
v . 1942b *Pecten bodenbenderi* BEHRENSSEN - A. LEANZA, p. 168-169, lám. 7, fig. 6; lám. 8, fig. 1-2.
v . 1945 *Pecten bodenbenderi* BEHRENSSEN - A. LEANZA, p. 86, fig. 8a-b.
v . 1953 *Vola bodenbenderi* BEHR. - GROEBER et al., p. 155, 156, 214, 220.
1953 "*Vola alata*" v. BUCH - GROEBER et al., p. 152, 155.
v . 1958 *Pecten bodenbenderi* BEHRENSSEN - A. LEANZA, p. 240-241, fig. 3.
cf. 1969 *Weyla* sp. indet. - FREBOLD & TIPPER, p. 13, pl. 1, fig. 1.
1969 *Weyla* sp. indet. aff. *W. bodenbenderi* (BEHRENSSEN) - FREBOLD & TIPPER, p. 69-73, p. 1, fig. 2-4.
p v . 1972 *Weyla alata* - SZEKELY & GROSE, p. 424.
v . 1975 *Weyla* - DAMBORENEA et al., cuadro 1.
v . 1978 *Weyla (Weyla) bodenbenderi* (BEHR.) - DAMBORENEA in VOLKHEIMER et al., Tab. 2.
p v . 1978 *Weyla (Weyla) alata* (v. BUCH) - CAMACHO & RICCARDI, cuadro 1.
v . 1978 *Weyla bodenbenderi* (BEHRENSSEN) - CAMACHO & RICCARDI, cuadro 1.
v . 1982 *Weyla (Weyla) bodenbenderi* (BEHRENSSEN) - DAMBORENEA, p. 259-266, lám. 73, fig. 1-3; lám. 74, fig. 1-2; lám. 75, fig. 1-3; lám. 76, fig. 1-2; lám. 77, fig. 1-2.

Material: BEHRENSSEN's original material, which should be housed at Göttingen, Germany, could not be examined and thus no lectotype designation is proposed here. The type locality is Paso del Portezuelo Ancho, Mendoza province (B.4).

The examined material consists of 29 specimens with both valves, 53 left valves and 52 right valves, most of them with at least part of the shell, and several fragments. Most of the material was collected by the author and colleagues. *W. bodenbenderi* comes from the Pliensbachian to early Toarcian beds in San Juan, Mendoza, Neuquén and Chubut provinces.

From north to south, this species was found in the following localities: Arroyo La Laguna (A.2): MLP 16567 to 16573 (M 428, 429, 430, 433); Río Atuel near Puesto Araya (B.1): MLP 16566 (M 368); Paso del Portezuelo Ancho (B.4): MLP 16584, 19012, 19016, 19022, 19028 (M 1283 to 1286); Arroyo del Portezuelo Ancho (B.5): MLP 19058 to 19060 (M 1294, 1296, 1297); Arroyo La Bajada (B.6): MLP 16580 to 16583; Arroyo Serrucho (B.8); Cerro Puchenque (B.9): MLP 16563 to 16565 (M 315, 328); South of Cordillera del Viento (C.1): MLP 15419 (GULISANO's collection); Vuta Picún Leufú (C.7): MLP 16578, 16579 (M 1080); Arroyo Tin-Tin (C.17): MLP 14283, 14285; Estancia Santa Isabel (D.1): MLP 16574 to 16577 (M 1050 to 1053); Salitral Grande (D.3): MLP 16552 to 16562 (M 141 to 145, 1038, 1040); north of Sañicó (D.5): MLP 5608 (FERNÁNDEZ' collection); Cerro Mesa de La Pintada (D.11): MLP 6104, 6105 (FRENGUELLI's collection); Cerro Del Vasco (D.12): MLP 16550, 16551 (M 122, 125); hill south of Cerro Roth (D.15): MLP 16536 to 16549 (M 99, 100, 101, 105); Cerro Roth (D.16): MLP 6035, 6037, 6038, 6463 (FRENGUELLI's collection). In the old MLP collections there is some material labelled as coming from "Piedra Pintada": MLP 5479, 5480, 5485, 5487, 5807, 8705, 8789, 10404. The material collected by ROTH and described by BURCKHARDT (1902, pl. 4, fig. 1-2) from Piedra Pintada was also examined: NHMB G 16637 and G 16638 (casts MLP 18157 and 18158).

The material from Chubut was described by WAHNSH (1942) from Nueva Lubecka: DNGM 8856; and there is also some material collected by PIATNITZKY in Mulanguineo (MLP 18116).

Range and distribution: *W. bodenbenderi* has a wider geographic range in Argentina than *W. alata* (v. BUCH). Other Argentine localities (apart from the already mentioned) are: Chacaico, Neuquén (GARCÍA VIZCARRA 1943), Cerro La Brea, Mendoza (UGARTE 1955), Río Genoa and other places in Chubut province (FERUGLIO 1934; WAHNSH 1942; GROEBER et al. 1953).

Specimens referable to *W. bodenbenderi* were also figured from the Sinemurian (?) of Canada (FREBOLD & TIPPER 1969). It was mentioned for the lower Jurassic of Perú (JAWORSKI 1914a, 1915; TILMANN 1917; at least part of SZEKELY & GROSE's 1972 material mentioned as *W. alata* was seen at the BMNH). *W. cf. bodenbenderi* is listed by MULLER & FERGUSON (1939: 1611) from the lower Jurassic of Nevada, USA, and from the lower Jurassic of Mexico was mentioned by BURCKHARDT (1930: 12, 13, 18).

Surprisingly there is no mention of this species from Chile, though one of the names proposed by R. PHILIPPI (1899) is probably synonym of *W. bodenbenderi*, as recorded here in the synonymy. MPODOZIS et al. (1973) mentioned "*W. sp. (W. bodenbenderi)*" from the Toarcian of the Alta Cordillera de Ovale, Coquimbo. The presence of this species in Chile is more than probable and perhaps it is disguised in the literature under other names. On the other hand all the material from Chile studied at the BMNH and MLP certainly belongs to *W. alata*, indicating that this is probably the most abundant species in Chile.

Description: Shell very large, very inequivalve and almost equilateral, pectiniform. Whilst the left valve is feebly concave, the right valve is very globose and its umbonal region extends dorsally over the hinge line. The auricles are big and are limited by deep furrows from the disc. The shell is concave-convex in lateral profile and also in anterior view.

The dorsal line is straight and the umbones are centrally placed. Thus the dorsal margins of each auricle are of subequal length. The dorsal margin of the right valve has a central fold towards the left valve. The posterior margin of the posterior auricle forms an almost straight angle with the dorsal margin, whilst the anterior margin of the anterior auricle meets the dorsal one at an acute angle and then bends backwards, limiting a relatively deep byssal notch that is present not only on the right valve but also, as a shallow sinus, on the left one (see pl. 11, fig. 1a). The surface of the right valve auricles is strongly convex, whilst the left valve auricles have a feebly concave top. The parts of the anterior and posterior margins below the auricles are straight and slightly convex and the ventral margin is evenly convex (subcircular) and scalloped, outwardly projecting at the ribs of the right valve.

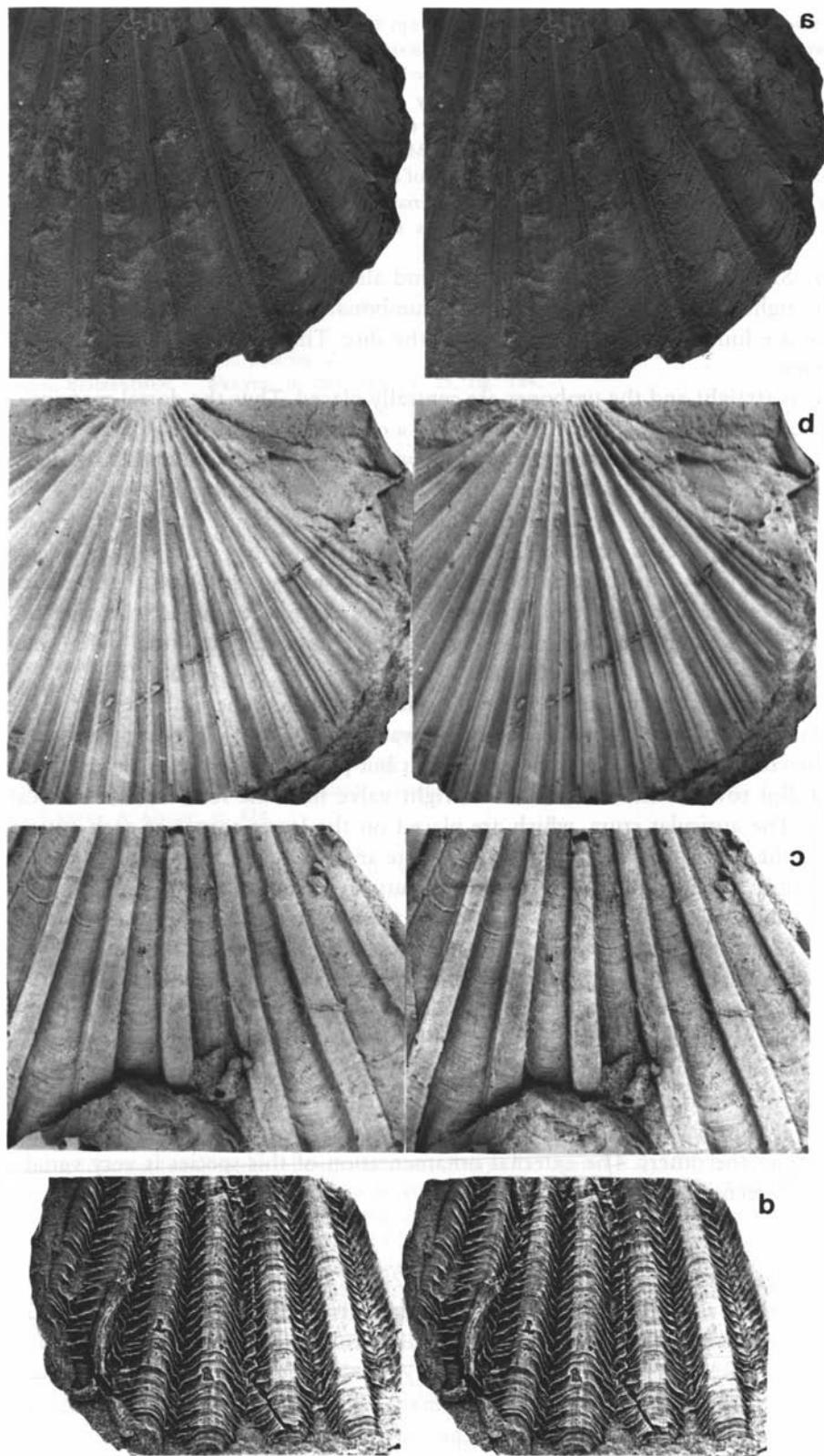
The left umbo is low and does not project above the hinge-line, but the right umbo is very wide and prominent. The umbonal angle of the left valve varies between 110° and 135°.

The resilifer is triangular and big and is centrally placed just below the umbones, but its axis is not parallel to the commissural plane between the valves and it dips towards the interior of the right valve. The vertically striated dorsal areas are subrectangular and their surface is not flat but parallel to the commissural plane at the anterior and posterior ends and dips towards the interior of the right valve near the resilifer. The vertical crenulations are as high as the resilifer. The auricular crura, which are placed on the lower corner of each auricle, are strong and dip outwards, parallel to the inner margin of the auricles. There are two auricular crura on each auricle of the left valve. The remaining portion of the inner surface of the auricle is smooth.

A row of small tubercles or "chomata" extends along the anterior and posterior margins of the internal surface of the shell. These "chomata" can be traced on the outer surface of the shell as a group of ridges perpendicular to the margin, these are crossed by the growth-lines which are especially evident on the lateral ribless portions of the left valve (pl. 11, fig. 1a-c).

Both valves are ornamented by strong radial ribs. The primary ribs (those that extend from the umbones) vary from 12 to 15 on each valve, but this number may considerably increase by intercalation or splitting of the primary ribs, as will be discussed below. The ribs are convex in transverse section, with somewhat flattened tops and between them there are intervals with concave or flat bottoms. The two or three most external ribs on each side of the shell are lower than the others. The external ornamentation of this species is very variable and the following types of ribs can be recognized:

- I. Simple ribs: straight, not split (for instance, pl. 12, fig. 3; text-fig. 22c).
- II. Intercalated ribs: these are secondary ribs on the intervals between two primaries and are, at least at their origin, smaller than the primary ribs. They can appear at variable distances from the umbones (for instance, pl. 10, fig. 6; pl. 11, fig. 2). These ribs may or may not be evident on the inner surface of the valves.
- III. Dichotomous ribs: formed by splitting of one primary rib into two smaller but subequal ribs (for instance, pl. 11, fig. 1b). This is commonly evident on the internal moulds.
- IV. Fasciculated ribs: small bundles of ribs originated by the branching of one primary rib. The secondary ribs decrease in strength away from the primary one and they can originate either (a) only towards the distal face of the rib (for instance pl. 12, fig. 1b on the posterior half), or (b) only towards the internal surface of the primary ribs (for instance pl. 11, fig. 1a; text-fig. 22 b).



Text-fig. 22. Stereoscopic pairs of the ornamentation of the left valve of *Weyla* species. a: *Weyla alata* (von BUCH), MLP 19047, Arroyo del Portezuelo Ancho, Pliensbachian. b: *Weyla bodenbenderi* (BEHRENDSEN), MLP 16566, Rio Atuel near Puesto Araya, Pliensbachian. c: *Weyla bodenbenderi* (BEHRENDSEN), MLP 6104-c, Cerro Mesa, Pliensbachian. d: *Weyla mexicana* (JAWORSKI)?, MLP 16533, Vuta Picùn Leufú, Pliensbachian.

- V. Adventitious ribs: a pair of smaller ribs are present on both sides of each primary rib, appearing at a variable distance from the umbo (see pl. 12, fig. 1b on the anterior half).
- VI. Multiple ribs: the primary rib is made up of several subequal riblets. These may also appear on the intervals between ribs (see pl. 12, fig. 1b, near the ventral margin).

Two or more of these ribbing-types are generally combined on a single valve (see for instance pl. 7, fig. 3; pl. 12, fig. 1b). Only young specimens may show a single kind of ribbing, generally the simple ribs. These ribbing types appear both on the left and the right valve. On the left valve the ribs are normally lower and flatter than on the right one. Near the margin the intervals are wider than the ribs themselves, whilst on the right valve the ribs tend to be wider than the intervals.

The central part of the valves generally shows simple (I), intercalated (II) or adventitious (V) ribs, whilst the most external three or four ribs may be dichotomous (III) or fasciculated (IV). Only on the left valve the central ribs may be also dichotomous (III). The multiple ribs (VI) only appear on a peripheral strip on some very large right valves. The left valves have a stronger tendency to develop intercalated and fasciculated ribs than the right valve. The types of ribs are not necessarily equivalent on both valves of the same specimen. The fasciculated ribs of (a) type are almost exclusively found on right valves, whilst the (b) type appears more frequently on left valves and often a specimen has right valve with IVa ribs and left valve with IVb ribs.

The primary ribs are seen on the inner surface of the valves up to near the umbones, but the intervals are relatively wider and the ribs lower than on the outer surface. On the internal mould of left valves each primary rib is flanked by a pair of sulci that are deeper than the interval between the ribs. Towards the ventral margin the inner surface of the valve is scalloped, with the ribs and intervals much more clearly impressed. These end at the margin in a triangular shape, in such a way that the intervals of the left valve house the ribs of the right valve and vice-versa, achieving a tight closure.

The right valve auricles bear only commarginal growth-lines, but the left valve auricles also have strong ribs subparallel and close to the dorsal margin.

The adductor muscle scar is big, of subcircular outline and is placed posteriorly in such a way that its anterior end only nearly reaches the middle line. A pair of deep spot-like scars appear near the internal margins of each auricle, the anterior one placed slightly more dorsally than the other. These two scars may correspond to the pedal retractor muscle according to their position.

Measurements: See also scatter diagram on text-fig. 24.

Specimen	Material		L (mm)	H (mm)	W (mm)	L/H	ant. DL (mm)	post. DL (mm)	n° ribs		ε
									RV	LV	
MLP 5608-a	LV	IM	79	73	-	1.08	23	22	-	12	120°
MLP 6038-ab	BV	S	128	140	65	0.91	-	48	15	-	125°
MLP 16540	BV	S	138	149	68	0.92	-	40	15	13	130°
MLP 16542	BV	S	141	144	72	0.98	35	-	14	14	129°
MLP 16544	BV	S	144	142	64	1.01	-	42	15	-	135°

Affinities: *W. bodenbenderi* shows strong affinities with *W. alata* (v. BUCH). Their relations have already been discussed. These two species were never found together and *W. bodenbenderi* appears always after *W. alata* has disappeared in those localities where both of them occur.

The peculiar ribbing of this species, especially on the left valve, distinguishes it from all other *Weyla* species, which generally have a more regular and simpler ribbing. The flat-topped ribs on the left valve of *W. bodenbenderi* are not found in any other known species of *Weyla*.

According to GROEBER (in GROEBER et al. 1953: 233) the specimens that R. PHILIPPI (1899) referred to *Pecten dufrenoyi* D'ORBIGNY are very similar to *W. bodenbenderi*. On the other hand JAWORSKI (1914a, 1915) suggested that that material may be referred to *W. domeykoi* (PHIL.). In fact, the two specimens figured by R. PHILIPPI seem to be internal moulds or weathered shells and thus their specific relations are not evident. The illustration of the left valves of these specimens is surely needed to settle the matter. The specimens from "Neuquén" referred by JAWORSKI (1914a, 1915) to *P. domeykoi* were not figured. Nevertheless, and according to R. PHILIPPI's (1899) figures, *P. domeykoi* differs from *W. bodenbenderi* by its simple ribs that have neither split nor have intercalated costae and by the more wavy cross-section of the ribbing.

TAXON CHARACTER	<i>Weyla (W.) alata alata</i> (v. Buch)	<i>Weyla (W.) alata angustecostata</i> (Phil.)	<i>Weyla (W.) bodenbenderi</i> (Behr.)	<i>Weyla mexicana</i> (Jaw.) ?	<i>Weyla (Lywea) unca</i> (Phil.)
Relative convexity of valves					
Right valve ornamentation					
Left valve ornamentation					
Right valve hinge				?	
Left umbonal angle	100°–115°	~ 110°	110°–135°	100°–115°	115°–125°

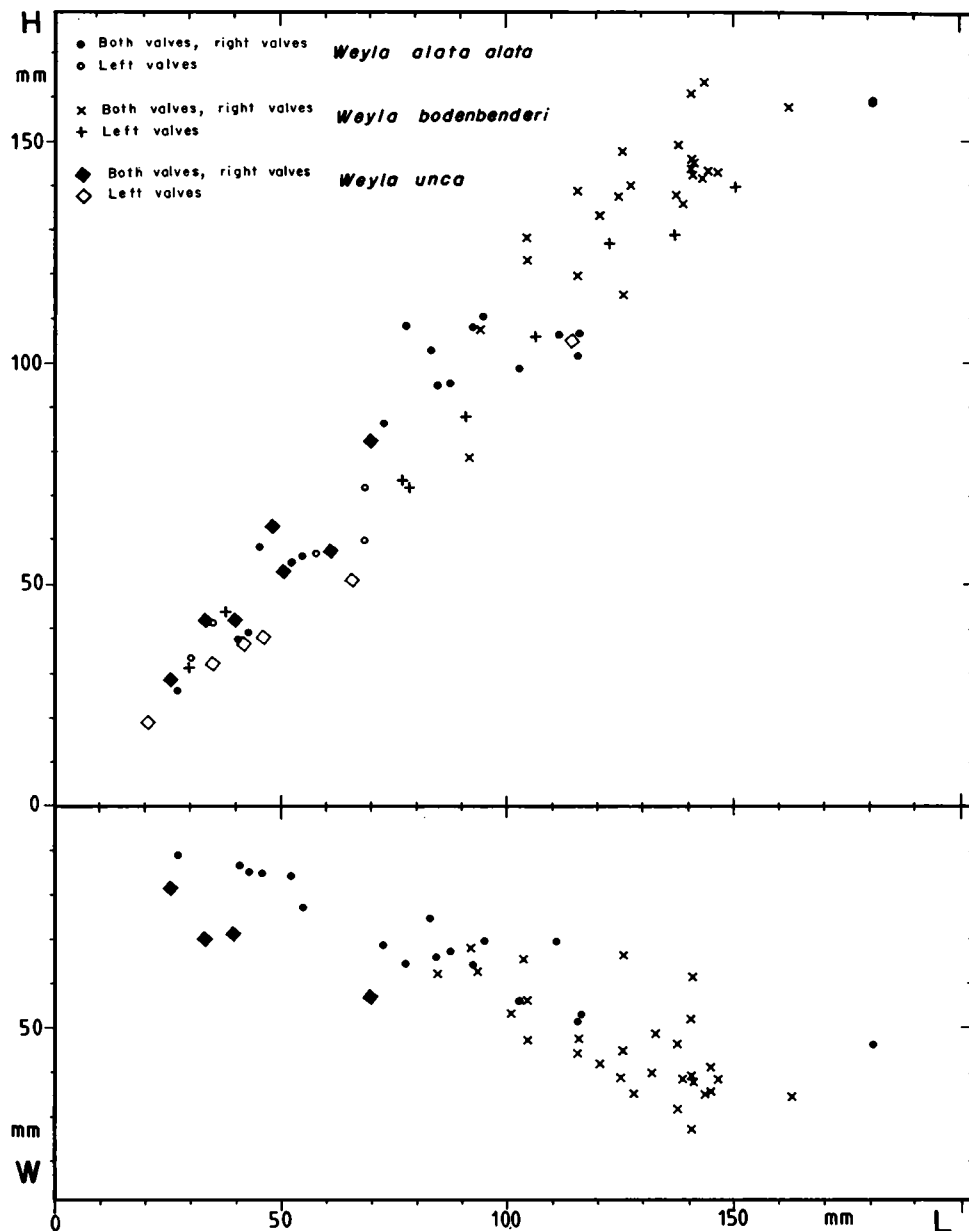
Text-fig. 23. Table displaying some of the morphological features of the *Weyla* species from Argentina. The figures are not to scale.

Remarks: This species, widely distributed in the early Jurassic beds of Argentina, was originally described by BEHRENDSEN (1891, 1922) based mainly on right valves collected by BODENBENDER at Paso del Portezuelo Ancho, Mendoza province. He only figured one right valve with intercalated ribs. Although LEANZA (1942b: 168) argued that BEHRENDSEN's drawing does not depict the secondary ribs in their actual position, such a pattern is indeed present in several specimens from various localities, such as Piedra Pintada, Rio de Los Patos, Paso del Portezuelo Ancho and Rio Salado (compare BEHRENDSEN's Taf. 22, Fig. 3, with pl. 11, fig. 2 here).

When the marine lower Jurassic beds of Piedra Pintada were discovered, the *Weyla* specimens collected there were preliminary determined as "*Vola alata*" (ROTH 1899: 155; BURCKHARDT 1902: 244–245, pl. 4, fig. 1–2, reproduced by WINDHAUSEN 1931, lám. 22, fig. 2; GROEBER 1925: 463; GROEBER et al. 1953: 152, 155). In his revision of the South American species of the genus, JAWORSKI (1914a: 285–288, fig. 9–10) provided a detailed description of *W. bodenbenderi* mainly on the basis of material from that locality. He illustrated one specimen with a very complex ornamentation on the left valve (compare his fig. 10 with pl. 7, fig. 3 here). Nevertheless, his description was based on only four specimens and thus JAWORSKI could not recognize the range of morphological variation of this species. Probably this fact prompted him to consider a left valve from Portezuelo Ancho, characterized by intercalated ribs, as a new species, which he called "*Vola simplex*" (JAWORSKI 1925a: 163–164, lám. 1, fig. 1; 1926: 391–392, text-fig. 2, reproduced by WINDHAUSEN 1931). This name is here regarded as a junior synonym of *W. bodenbenderi*, not only bearing in mind the analysis of the morphological variation of this species, but also upon consideration of a specimen found near Portezuelo Ancho, which has a right valve that is identical to BEHRENDSEN's original figure of *W. bodenbenderi*, and a left valve that agrees with JAWORSKI's (op. cit.) illustration of *W. simplex* (see pl. 10, fig. 6). It must be noticed as well that BEHRENDSEN did not provide data on the left valve of his species and JAWORSKI did not include any right valve when describing *W. simplex*. Also both sets of specimens were found at the same locality. The presence of intercalated ribs is a common feature of this species, as the only type of ribbing, or combined with other ribbing patterns.

The details of the internal morphology of *W. bodenbenderi* are first described in this paper and an attempt to analyse the complex variability of ribbing pattern is also made here. Although some of the observed morphotypes seem to be more abundant at certain localities and/or levels, the available material is not enough to attempt a statistical analysis. In the samples with a large number of specimens, such as M 101, from the hill south of Cerro Roth, where they are found in life position, almost all the possible combinations of the ribbing patterns are present and thus the mere record of one or other morphotype lacks any stratigraphical, palaeobiogeographical or palaeoecological significance.

Text-fig. 24. Scatter diagram showing the length/height (L/H) and length/width (L/W) ratios of *Weyla alata* (von BUCH), *Weyla bodenbenderi* (BEHRENDSEN) and *Weyla (Lywea) unca* (R. PHILIPPI).



Autecology: The way of life of this species was probably very similar to that already described for *W. alata*. Specimens in life position were observed in several localities: Rio Salado, Arroyo del Portezuelo Ancho and Piedra Pintada. In these cases *W. bodenbenderi* was the most abundant bivalve in those beds and the concentration of specimens was generally high.

Subgenus *Lywea* n. subgen.

Type species: *Pecten uncus* R. PHILIPPI 1899, from the Lower Jurassic of South America.

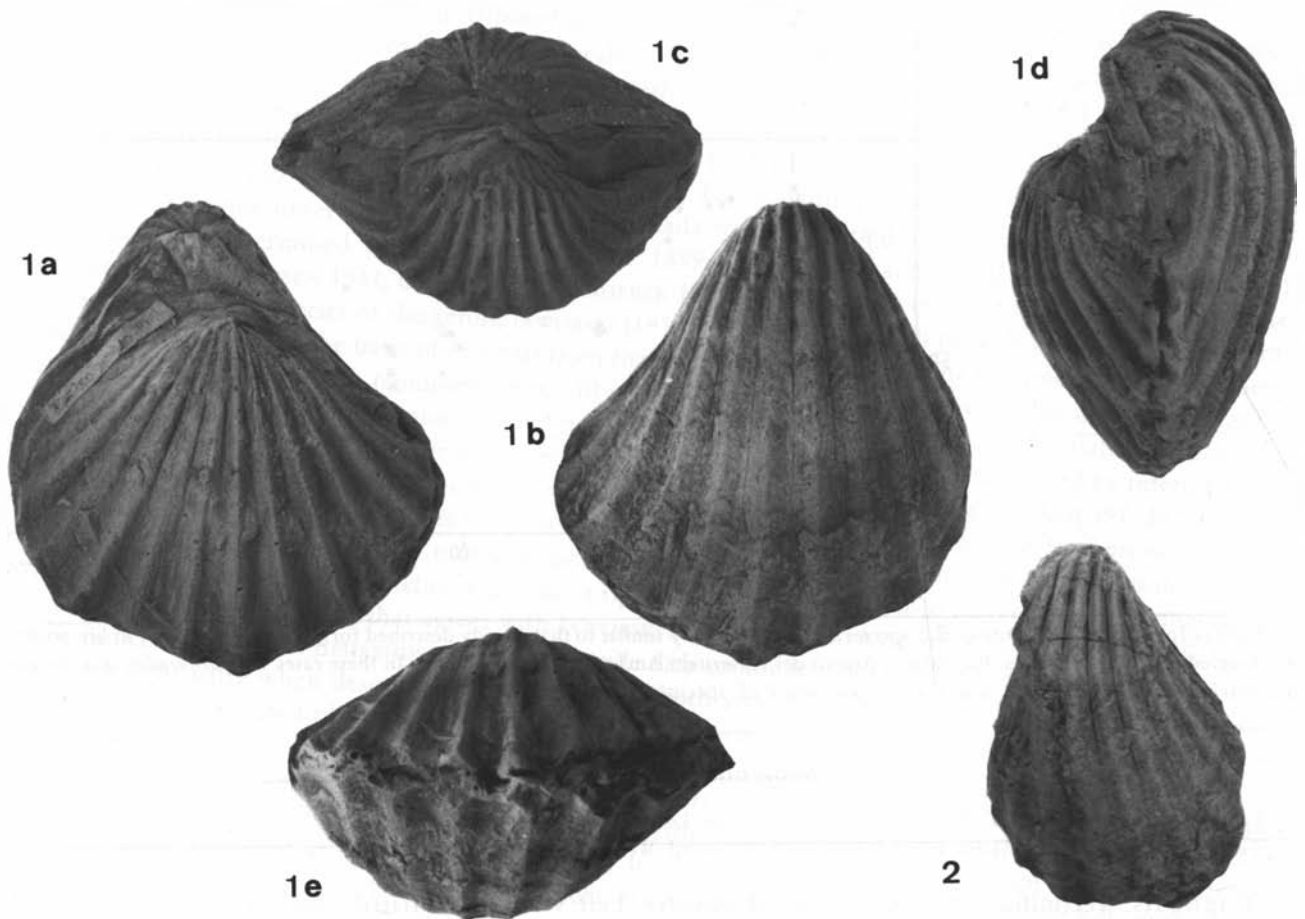
Derivation of name: *Lywea* is an anagram of the word *Weyla*.

Diagnosis: Pectiniform biconvex shell, inequivalve. Left valve less inflated than the right one. The right valve umbo is very prominent and extends well above the hinge-line. The shell is very thick. The auricles are subequal in size and not separated by a sulcus from the disc of the shell. Without byssal notch. The external ornamentation consists of simple radial ribs, V-shaped in cross-section, some of which may be more prominent than the others.

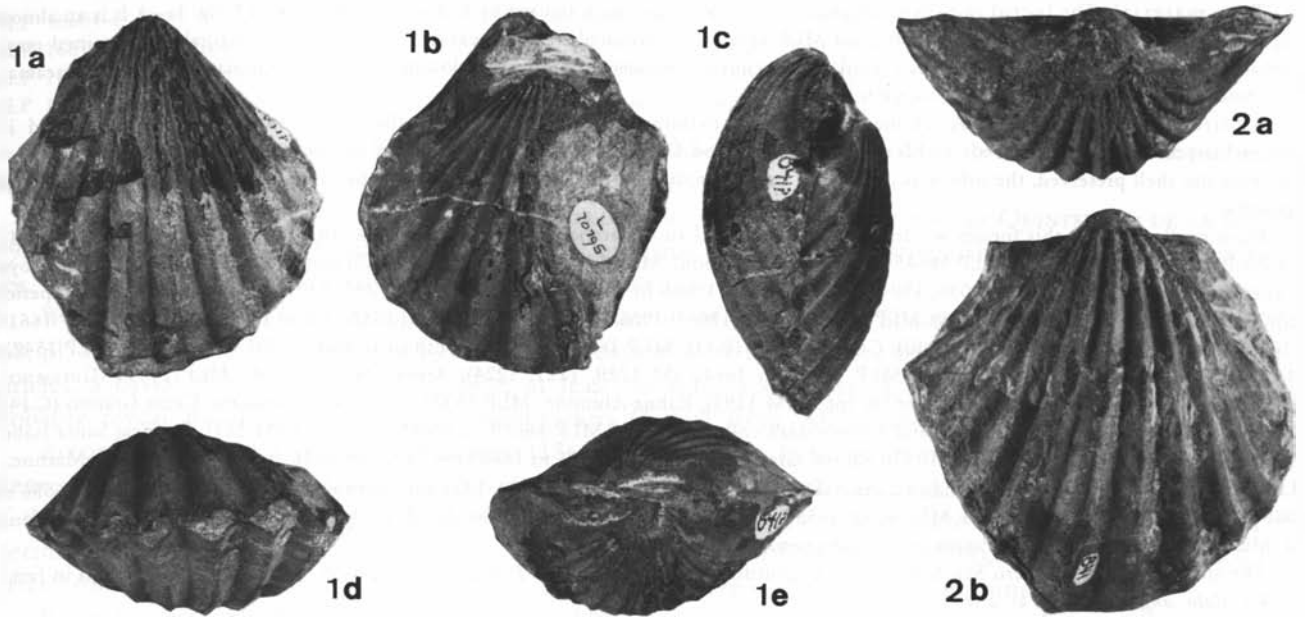
Remarks: This new taxon is considered here as a subgenus of *Weyla*, since the observed hinge characters indicate their close affinities. Nevertheless it has some important differences with *Weyla* s. s. concerning the relative convexity of both valves, the shell-thickness and the absence of a byssal notch. All these characters suggest a slightly different mode of life. The great convexity of both valves and the brachiopod-like appearance of the shell also distinguish this subgenus from all known pectinids. In this respect, it reminds one of the Spondylidae by the high convexity of the shell (see for instance ZAVAREI 1973, pl. 13, fig. 4 and compare with pl. 13, fig. 7a here), the lack of a byssal notch, the dorsally withdrawn auricles and the presence of “chomata” on the anterior and posterior margins of the shell. It differs from the Spondylidae, though, by the recurved right valve umbo and hinge details.

Included species: Besides the type species, the nominal species *Pecten lycorrhynchus* R. PHILIPPI 1899, from the lower Jurassic of Chile, also belongs to this subgenus and may even be a synonym of *P. uncus* (see text-fig. 25).

This subgenus is also present in western North America, as shown by a couple of specimens from Gabb's Valley Range, Nevada (USA), collected and determined by S. W. MULLER and housed in the BMNH (L 70795 and L 70796). These specimens certainly belong to this subgenus but probably to a different species (see text-fig. 26). They are labelled as “*Pecten acutiplicatus* MEEK”. If this identification is correct and both specimens belong in fact to MEEK's poorly known species, then *W. acutiplicata* (MEEK 1864) belongs to *Weyla* (*Lywya*). If this is in fact different from *W. (L.) unca*, it needs a new name, since it is pre-occupied by *Pecten acutiplicatus* ALTH 1850. The name *Weyla meeki* nov. name is here proposed to replace *Pecten acutiplicatus* MEEK 1864 non *Pecten acutiplicatus* ALTH 1850.



Text-fig. 25. 1: Lectotype of *Pecten uncus* R. PHILIPPI, SGO-PI 909 (cast MLP 18322). 1a: right valve; 1b: left valve; 1c: dorsal view; 1d: posterior view; 1e: ventral view. Figured by R. PHILIPPI (1899, lám. 17, fig. 3a-c). 2: Holotype of *Pecten lycorrhynchus* R. PHILIPPI, SGO-PI 887 (cast MLP 18321), figured by R. PHILIPPI (1899, lám. 17, fig. 1). Photographs from plaster casts. All figures natural size.



Text-fig. 26. *Weyla (Lywea) meeki* nov. nom. All figures natural size. 1: specimen with both valves, BMNH L.70795, collected by MULLER at Gabb's Valley Range, Nevada, USA, early Jurassic. 1a: right lateral view; 1b: left lateral view; 1c: anterior view; 1d: ventral view; 1e: dorsal view; 2: Right valve, BMNH L.70796, same locality, 2a: dorsal view; 2b: lateral view.

Geographical and stratigraphical range: In South America this subgenus ranges from the late Sinemurian to the early Toarcian and is known from Perú, Chile and Argentina.

W. meeki nov. name, which is doubtfully included in this subgenus, is known from the Lower Jurassic of California and Nevada (HYATT 1892).

Weyla (Lywea) unca (R. PHILIPPI 1899)

Plate 12, fig. 4; pl. 13, fig. 1-11; text-fig. 24, 25

- p ? 1891 *Pecten Pradoanus* VERN. et COLL. - BEHRENSSEN, p. 391-392, Taf. 22, fig. 1a-d.
- * ! v 1899 *Pecten uncus* PH., R. PHILIPPI, p. 30, lám. 17, fig. 3a-c.
- ? v 1899 *Pecten lycorrhynchus* PH., R. PHILIPPI, p. 29, lám. 18, fig. 1.
- ? 1914a *Pecten Pradoanus* VERNEUIL et COLL. - JAWORSKI, p. 289-290, fig.
- v . 1915 *Pecten Pradoanus* VERN. et COLL. - JAWORSKI, p. 437-438.
- p ? 1922 *Pecten Pradoanus* VERN. et COLL. - BEHRENSSEN, p. 175-176, lám. 1, fig. 1a-d.
- v . 1925b *Pecten Pradoanus* VERN. et COLL. - JAWORSKI, p. 52.
- ? 1925 *Pecten pradoanus* (sic) VERN. et COLL. - GERTH, p. 14, 18.
- ? 1929 *Pecten Pradoanus* VERN. et COLL. - STEINMANN, p. 71, fig. 78 A-C (p. 72).
- p 1930 *Pecten pradoanus* (sic) VERN. y COLL. - RIGAL, lám. 1, fig. 3 (only).
- ? 1931 *Pecten* sp. cf. *P. pradoanus* VERN. et COLL. - WEAVER, p. 272.
- p v . 1942 *Vola alata* - SUERO, p. 21.
- v . 1942b *Pecten* cf. *uncus* PHIL. - A. LEANZA, p. 170-171, lám. 9, fig. 1-3, 6.
- p v 1951 *Pecten alatus* v. BUCH - SUERO, p. 11, 14.
- ? 1953 *Pecten pradoanus* VERN. et COLL. - GROEBER et al., p. 214.
- 1977 *Weyla unca* (PHIL.) - PÉREZ & REYES, p. 42.
- 1978 *Weyla* sp. - RANGEL, lám. 3, fig. 5 (mentioned in the text as Pectinidae indet, p. 28).
- v . 1978 *Weyla* sp. - CAMACHO & RICCARDI, cuadro 1.
- 1980 *Weyla* cf. *unca* (Philippi) - ESCOBAR, p. 57, lám. 2, fig. 7-8.
- v . 1981 *Pecten* cf. *uncus* PHILIPPI - CUERDA et al., p. 9.
- v . 1982 *Pecten* cf. *uncus* PHILIPPI - CUERDA et al., p. 331.
- v . 1982 *Weyla (Lywea) inaequicostata* n. sp., DAMBORENEA, p. 269-273; lám. 77, fig. 1-14; lám. 78, fig. 1-4; lám. 79, fig. 1-4 (unavailable name).

Type material: The lectotype (here designated) is the only specimen figured by R. PHILIPPI (1899, lám. 17, fig. 3a-c). It is an almost complete shell, without auricles, SGO-PI 909 (cast MLP 18322), re-illustrated here on text-fig. 25-1. PHILIPPI's original set contained more material, as he said that he figured "the best available specimen". PHILIPPI's indication of locality is merely "Amolanas, prov. de Atacama", Chile, and there is no stratigraphical location.

Additional material: The Argentine material here examined, mostly collected by the author and colleagues, was found in Pliensbachian to lower Toarcian beds of Mendoza, Neuquén and Chubut provinces. It consists of 16 specimens with both valves, five of them with the shell preserved, the others as internal or external moulds. There are also about 89 right valves and 48 left valves and several fragments.

From north to south, this species was found in the Rio Atuel area (material described by JAWORSKI 1915, 1925b, housed in the DNGM); Paso del Portezuelo Ancho (B.4): MLP 16645 (GULISANO's collection), MLP 19009, 19013, 19017, 19020 and 19026 (M 1282 to 1286); Arroyo del Portezuelo Ancho (B.5): MLP 19036, 19041, 19046, 19061, 19066 to 19068 (M 1288 to 1290, 1297, 1301 to 1303); Rio Salado Superior (B.6): MLP 16644; Arroyo Serrucho (B.8): MLP 19647, 19657, 19664, 19669 (M 1318, 1323, 1329, 1332); Cerro Puchenque (B.9): MLP 16610 to 16621 (M 299, 301, 309, 314 to 317, 330); Cerro Tricolor (B.11): MLP 16643 (M 805); south of Cordillera del Viento (C.1): MLP 15423, 15432, 15447 (GULISANO's collection) and MLP 16640 to 16642 (M 1220, 1221, 1224); Arroyo Ñiraico (C.4): MLP 15534 (GULISANO's collection); Arroyo Lonqueo (C.9): MLP 16638, 16639 (M 1193); Rahue-Aluminé: MLP 15323 (CUERDA's collection); Cerro Granito (C.14): MLP 4860, 4861, 13005, 13006 (SUERO's and FRENGUELLI's collections) and MLP 16659 to 16661 and 19711 (M 167); Estancia Santa Isabel (D.1): MLP 16622 to 16637 (M 1049 to 1053); Salitral Grande (D.3): MLP 16601 to 16609 (M 143, 144, 1036 and 1040); Cañadón Martínez: MLP 5476 (FERNÁNDEZ collection); Subida a Sañicó (D.7): MLP 16589 to 16600 (M 134, 135); hill south of Cerro Roth (D.15): MLP 16586 to 16588 (M 99, 101); Cerro Roth (D.16): MLP 6132, 16587 and 19723 (M 1383); Piedra Pintada: MLP 4207, 6046, 13007 (old MLP collections) and Mulanguíño: MLP 18123 (PIATNITZKY's collection).

The specimen from southern San Juan province identified by RIGAL (1930) as *P. pradoanus* (DNGM 9428, cast MLP 19078) is in fact a *W. (W.) alata angustecostata*, as already said.

W. unca is known from Chile (R. PHILIPPI 1899; PÉREZ & REYES 1977; ESCOBAR 1980) and probably also from Perú (RANGEL 1978 as *Weyla* sp.)

Description: Shell of medium size, pectiniform, biconvex, thick-shelled. The left valve is less convex than the right one. The right valve has the height greater than the length, the opposite happens in the left valve. The dorsal margin is straight, the anterior and posterior margins meet it at an obtuse angle. The auricles are subequal and are not limited from the disc of the shell by a sulcus. The surface of the left valve auricles is slightly concave, whilst the right ones are feebly convex. The ventral margin is evenly convex. The umbones are wide and prominent, mesogyrous and although both project beyond the hinge-line, the right one is higher and incurved, giving the shell a characteristic brachiopod-like profile in lateral view.

The hinge is *Weyla*-like, with a subrectangular, vertically-striated region near the dorsal margin. The resilifer is subtriangular and centrally placed just below the umbones, on a plane almost perpendicular to the commissural plane, directed towards the inside of the right valve. Other internal characters unknown.

The shell is ornamented by 11 to 13 simple radial ribs on each valve, which are V-shaped in transverse section and are separated by similarly shaped grooves. At the bottom of each groove a narrow furrow flanked by two small riblets may be present. The ribs become lower towards the ventral margin. The ribs are similar on both valves, but on the left valve the second, fourth, seventh and tenth (and sometimes also the eleventh) counted from the anterior end, are higher than the others. This peculiar feature is not so evident on weathered shells, such as the lectotype. The commarginal growth lines have a zig-zag appearance and are stronger on the bottom of the grooves and near the ventral margin of the shell where the ribs become flatter. The apices of the zig-zag point towards the umbones on the ribs and towards the margin on the intervals. Before the first rib and after the last one there is a sub-triangular area which is covered by faint growth lines and sometimes also by thin, subparallel ridges which run oblique to the margin. They represent the external growth tracks of the "chomata" that are present on the anterior and posterior margins of the shell, on the auricles and below them.

The inner surface of the right valve is almost smooth, except near the ventral margin, where it is scalloped as the shell-thickness decreases. The ribs are more clearly evident on the inner surface of the left valve, they are not V-shaped but rounded shallow furrows.

Measurements: See also scatter diagram on text-fig. 24.

Specimen	Material		L (mm)	H (mm)	W (mm)	L/H	n° ribs	
							RV	LV
MLP 5476, pl. 12, fig. 10	BV	EM	70.00	82.70	44.00	0.85	13	12
MLP 6046-c, pl. 12, fig. 11	RV	S	61.00	73.60	26.80	0.83	13	-
MLP 16593-a, pl. 12, fig. 4	LV	EM	34.75	32.60	8.70	1.06	-	12

MLP 16604-c	LV	IM	115.00	106.10	33.00	1.08	-	12
MLP 16618, pl. 12, fig. 2	LV	EM	20.90	19.80	6.50	1.05	-	12
MLP 16631-ab, pl. 12, fig. 7	BV	S	40.00	42.00	29.00	0.95	12	-
MLP 16632-c, pl. 12, fig. 6	RV	S	48.00	64.60	24.80	0.74	12	-

Affinities: This species differs from all *Weyla* s. s. species by its globose left valve, the auricles not separated from the disc by a furrow and the absence of a byssal sinus.

The ornamentation of the right valve is similar to that observed in *Weyla almelae* QUINTERO & DE LA REVILLA (1966: 41, lám. 5, fig. 1a-b), from the Lower Jurassic of Spain, which can be distinguished by having only six radial ribs. The left valve of the Spanish species is unknown.

Weyla pradoana (VERN. & COLL.), from the lower Jurassic of Guadalajara, Spain (DE VERNEUIL & COLLOMB 1853: 163, pl. 3, fig.4), to which some South American specimens were referred (see below), is smaller, has more pointed auricles, a byssal sinus and a flat left valve, at least on some specimens. A detailed study of this species will probably reveal its affinities to *Weyla ambongoensis* (THEV.) from Africa and Asia.

According to MEEK's original description (1864: 46, pl. 8, fig. 3) *W. meeki* new name (= *Pecten acutiplicatus* MEEK, 1864 non *P. acuteplicatus* ALTH 1850) shares the V-shaped ribs with *W. unca*, but has two radial ribs on one of the auricles and between 14 and 15 radial ribs on the disc. These features are not shown, however, in the specimens referred to *W. acutiplicata* and housed at the BMNH (L 70795 and L 70798), see text-fig. 26, which only differ from *W. unca* in the ribbing pattern of the left valve, lacking more prominent ribs.

Pecten lycorrhynchus R. PHILIPPI (1899) is probably a synonym of *W. unca*, but even in that case the name *unca* is preferred because it was introduced for better preserved material and was later used by several authors.

Remarks: Since the end of the last century the presence of "*Pecten pradoanus*" has been repeatedly mentioned for the lower Jurassic of Argentina. Several of these records were here considered as belonging to *W. unca*, on the basis of the observation of material from the same localities. Thus, at least part of the material described as "*Pecten pradoanus*" by BEHRENDSEN (1891, 1922, Taf. 22, fig. 1d) may belong to this species. WEAVER (1931) suggested that it was a young shell of *W. alata* and in fact, the specimen in BEHRENDSEN's figure 1a-b may be a juvenile of other *Weyla* species, as it can be distinguished from *W. unca* by the presence of radial ribs on the internal mould of the right valve.

The specimens referred to *W. pradoana* by JAWORSKI (1914a), GERTH (1925) STEINMANN (1929) and WEAVER (1931), certainly belong to the new subgenus, but their specific determination is not easy as they apparently lack the differently prominent left valve ribs. On the other hand the material figured by RANGEL (1978) from the lower Jurassic of Perú, shows the typical unequally strong ribs on the left valve and almost certainly belongs to *W. unca*.

W. pradoana is therefore thought to be absent from South America. This is a very poorly known species and its affinities with either *Weyla* s. s. or *Weyla* (*Lywea*) cannot be established yet.

It must be pointed out, nevertheless, that the unequally strong radial ribs of the left valve, though a typical character for this species, are not always evident, especially on poorly preserved or weathered specimens, and are not evident on the inner moulds, which are almost smooth.

Autecology: The morphological differences between this taxon and the other *Weyla* species here described may be functionally important and thus a close parallel to them cannot be established. The main differences are the absence of a byssal sinus in adult shells and the biconvex and very thick shell. This species could also have had a semi-infaunal habit, but the life position was probably with the commissural plane oblique to the sediment-water interface.

It is also noted that, unlike what happens on *W. alata* and *W. bodenbenderi*, the specimens preserved with both valves together are few and, even in those cases, the valves are generally slightly disarticulated and shifted. The right valves are nearly double in number than the left ones in the samples here examined. A ligament-hinge system less efficient to maintain the valves together after the death of the animal is possibly the cause of these differences.

Weyla mexicana (JAWORSKI 1929)?

Plate 11, fig. 3; text-fig. 22d

- ? 1914a *Pecten cardioides* PHIL. - JAWORSKI, p. 290, 308, 309.
- ? 1915 *Pecten cardioides* PHIL. - JAWORSKI, p. 438.
- ? 1925b *Pecten cardioides* PHIL. - JAWORSKI, p. 52.
- * ! v ? 1929 *Neithea mexicana* nov. spec., JAWORSKI, p. 2-5; pl. 1, fig. 1a-c, 2, 3.
- v . 1982 *Weyla* (*Weyla*) *mexicana* (JAWORSKI) ? - DAMBORENEA, p. 266-268, lám. 77, fig. 3-4.

Material: There are only few specimens that can be doubtfully referred to this species, preserved as external moulds: MLP 16532 to 16535, 19653 and 19665 (M 145, 1048, 1085, 1321 and 1331, author's collections). These fragmentary valves were found in Pliensbachian beds from Neuquén (Salitral Grande, north of Sañicó and Vuta Picún Leufú) and Mendoza province (Arroyo Serrucho).

The material originally referred to this species by JAWORSKI (1929) and previously identified by him as *P. cardioides* PHIL. comes from Milla Michicó, southern Cordillera del Viento, Neuquén province.

The Mexican specimens figured by JAWORSKI (1929) are housed in the NHMB (A 18/35) with the following collection numbers: holotype: 52², illustrated paratypes 52¹ (fig. 2) and 51^{b1} (fig. 3). These were found at two localities: mina Santa Rosa and Cajón de Las Amarillas, both in the Altar District, Sonora, Mexico.

Description: Medium to large shell, very inequivalve but equilateral, pectiniform. The left valve is slightly convex near the umbo and then it becomes flat, the right valve is highly convex.

The auricles are flat and subequal. The available material does not show the base of the auricles and thus the presence or absence of byssal sinus and the type of auricular crura are unknown.

The shell is ornamented by 12 to 13 strong radial ribs, which are different on each valve. On the right valve the ribs seem to be V-shaped with intervals of the same section. On the right valve the ribs are also simple and V-shaped, though the rib-tops become flatter towards the shell margin. The intervals are always deep and V-shaped and have very strong growth-lines, lamellose and regularly spaced, which sometimes also cross the rib-tops (see pl. 11, fig. 3).

The inner surface of the shell is not known in detail, but apparently the ribs are not evident on it.

The auricles bear growth-lines and the lateral areas of the valves show weak lines subparallel to the dorsal margin that may correspond to "chomata" on the inner anterior and posterior margins of the shell.

Affinities: This taxon differs from all other *Weyla* species in the peculiar arrangement of the growth lamellae on the left valve. *W. mexicana* belongs to the planoconvex group of species with V-shaped ribs on both valves, such as *W. lacazei* (HAIME), *W. ambongoensis* (THEVENIN) and *W. ayarti* (DUBAR), from which it differs in its greater number of radial ribs and the unusual ornamentation of the left valve. JAWORSKI (1929) already provided a very detailed comparison with these and other species.

W. alata angustecostata (PHIL.) has flat rib tops on the right valve and the growth-lines are not so strong.

Remarks: Although the available material only consists of fragments, the auricular crura seem to be *Weyla*-like. The details of the ornamentation figured by JAWORSKI (1929, fig. 1b) agree better with the aspect of the external moulds of left valves than with the ornamentation of the right valves, as stated by him. The identification of this species is quite difficult in the absence of left valves. Although it seems to be related to the *Weyla* s. s. group of species, its affinities with the new subgenus *Weyla* (*Lywea*) cannot be completely disregarded, taking into consideration the shape of the radial ribs and their ornamentation and the fact that the shell is biconvex in the early growth stages.

Family Entoliidae VON TEPPNER 1922

There are several species of *Entolium* in the early Jurassic of Argentina. Most of them will be dealt with in another part of this monograph. Only one pectinacean species, previously known and now included in this family, will be analyzed here.

Genus *Posidonotis* LOSACCO 1942

Type species: *Posidonotis dainellii* LOSACCO 1942, from the late early Jurassic of Sabina, Italy, by monotypy.

Synonym: *Pectinula* A. LEANZA 1943 (type species: *Pectinula cancellata* A. LEANZA 1943, original designation).

Emended diagnosis: Bivalves with discoidal flat shells, thin-shelled, with pectinid auricles in both valves. The dorsal margin of the auricles project above the hinge margin. The posterior auricle has a triangular shape with the posterior margin dipping backwards. The anterior auricle is similar to the posterior one in shape and size in adult specimens, but in young shells has a shallow byssal sinus without a ctenolium in the right valve and is larger than the posterior auricle. The main body of the shell is ornamented with regular concentric folds and radial irregular ribs, that increase in number by intercalation. Both types of folds form a reticulate pattern on the shell

surface. This ornamentation does not affect the shell thickness and is thus evident in internal moulds. The auricles are only covered by growth lines. The apical angle is larger than 90°.

Included species: This genus, as here understood, includes the following nominal species: *Monotis semiplicata* HYATT 1894 (non *Pecten semiplicatus* ALTH 1850); *Monotis symmetrica* HYATT 1894; *Entolium balteatum* CRICKMAY 1928; *Posidonotis dainellii* LOSACCO 1942 and *Pectinula cancellata* LEANZA 1943.

Remarks: The genus *Pectinula*, originally thought to be represented by a unique species, *P. cancellata*, from the late Pliensbachian – early Toarcian, was described by A. LEANZA in 1943. He broadly discussed its relations to *Diotis*, *Posidonia*, *Halobia* and other genera and preferred to include it into the Pectinidae.

One year before, LOSACCO (1942) had described a new genus that he referred to the Aviculidae, which he called *Posidonotis*, with only one species from the late early Jurassic of Sabina, Italy. These two generic names are here considered as synonyms. The poor preservation of the specimens prevented up to now the provision of a detailed description of both species, especially the Italian one, which shows only one auricle preserved, the posterior one according to LOSACCO. This auricle is identical to the posterior auricle of *P. cancellata*, although in this species the anterior auricle is also preserved in a few specimens. This difference, which is probably due to incomplete preservation in *P. dainellii*, is the only important one, and thus both are thought to be congeneric. The generic name that must be used according to the rules of priority is *Posidonotis* LOSACCO 1942.

Both A. LEANZA (1943) and LOSACCO (1942) compared their new taxa with *Diotis* SIMONELLI (1884: 125, non SCHMARDA 1859, Vermes). This genus, which is known from the early Jurassic of Italy and Spain (HÖRNES 1855; ZITTEL 1869: 117, 119; DE STEFANI 1876; CANAVARI 1880; PARONA 1883; FUCINI 1897; JIMÉNEZ DE CISNEROS 1923: 19) can be distinguished from *Posidonotis* because its auricles are not clearly limited from the main body of the shell and because the ends of the dorsal margin are not raised, but lowered, with respect to the hinge-line. This differences could also be due to imperfect preservation, but it is a constant character that appears in all the figured specimens. Furthermore, the ornamentation of *Diotis* seems to be more irregular and variable than in *Posidonotis*.

This genus differs from *Entolium* MEEK by the presence of a byssal sinus in young specimens and by the cancellate ornamentation; from *Syncyclonema* MEEK by lacking a byssal sinus in adult shells and by the presence of radial and concentric folds on both valves; from *Posidonia* BRONN by having two well-defined auricles and radial folds and from *Amonotis* KITTL, *Aulacomyella* FURLANI and *Halobia* BRONN by having well-defined auricles.

The systematic position of this genus within the Pectinacea is difficult to establish and was already discussed by LOSACCO (1942) and A. LEANZA (1943). The study of the shell structure would be of fundamental importance. In COX et al.'s (1969) systematic arrangement this genus was included in the Posidoniidae by reason of the peculiar kind of ornamentation, shell-thickness and type of preservation. However, the presence of two auricles on both valves allows its distinction from that family.

The presence of a byssal notch in young specimens and the cancellate ornamentation prevent their reference to the Amusiidae, with which they share the shape of the adult auricles. These, as well as the byssal notch in young specimens and the general shell outline, resemble the so-called *Lentipecten* group within the Pectinidae, from which *Posidonotis* differs by its peculiar ornamentation.

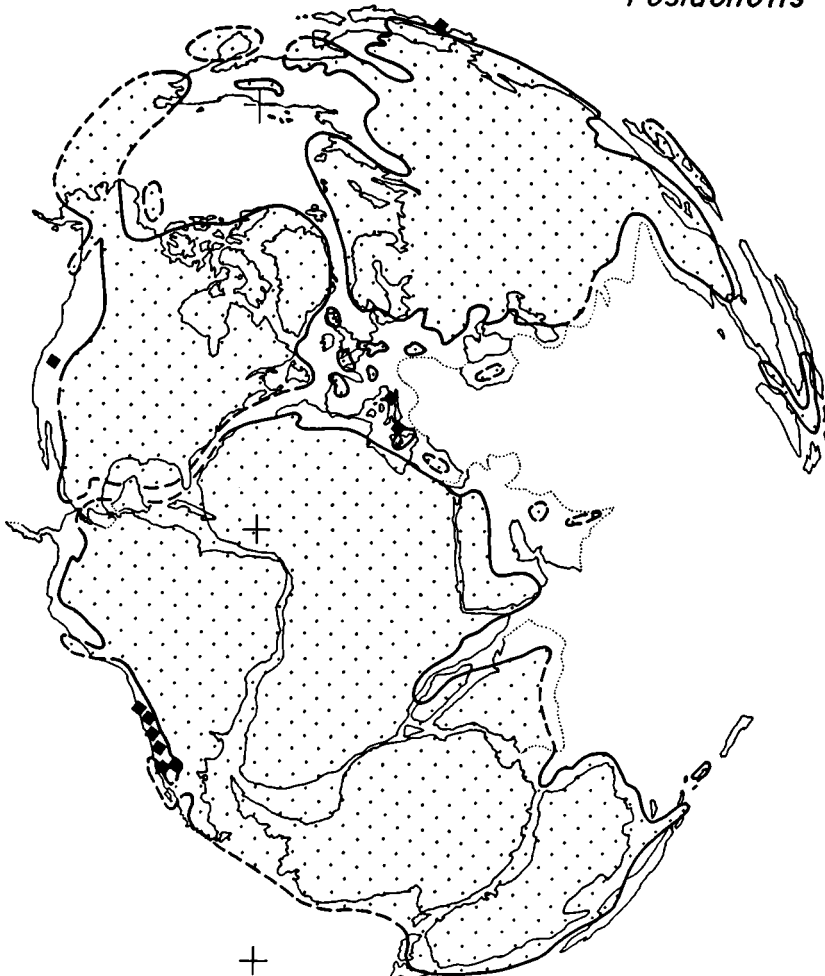
This genus shares with the Entoliidae the discoidal flattened shell, the auricles that protrude above the hinge-line, the presence of a non-ctenolate byssal notch restricted to young stages, the smooth auricles and the presence of auricular crura. They differ in their ornamentation pattern. It is interesting to note that a group of bivalves, doubtfully considered to belong to the Entoliidae by COX et al. (1969) and to the Pectinidae by SPEDEN (1967) was separated by WALLER (1978: 353, 354) as a new family, the Syncyclonemidae, characterized by a special kind of shell structure (lacking the prismatic calcitic layer, with thin or absent foliated calcitic layer and dominated by the crossed-lamellar aragonitic layer). Except for the lack of byssal notch in the adults and by the peculiar ornamentation pattern, *Posidonotis* has strong affinities with *Syncyclonema*. Both genera have the same kind of auricles, they lack a true ctenolium, the dorsal margin of the auricles protrudes above the hinge-line, the auricles have anterior crura and the shell is very thin. According to DHONDT (1971) the species *Syncyclonema hagenowi* DHONDT has concentric macroscopical ornamentation and *S. ? semiplicata* (ALTH) has a peculiar radial ornamentation of low folds that do not reach the margin of the shell. WALLER (1984) described the pseudoctenolium present in the type species of *Pectinella* and further reduced the Syncyclonemidae to a subfamily within the Entoliidae.

This genus is therefore included in the Entoliidae, but the assignment to the Syncycloneminae, if accepted as a separate subfamily from the Entoliinae, is left open. At any rate *Pectinula* LEANZA should be removed from the “*Antijanira* group” as envisaged by HERTLEIN (in COX et al. 1969, N355), which now seems artificial.

Range and occurrence: The palaeogeographic distribution of *Posidonotis* is shown on text-fig. 27. In North America, *Posidonotis* is represented by the *P. semiplicata* – *P. balteata* plexus, known since long ago from the Sailor Canyon Formation in American Canyon, California (HYATT 1894; CRICKMAY 1933b; IMLAY 1968) and the Harbledown Formation in Parson Bay, near Vancouver Island, British Columbia (CRICKMAY 1928, 1933b). In those formations the closest ammonites recorded are *Crucilobicerias* (in California) and *Melanhippites* (in Vancouver Island). Thus, a late Sinemurian age (about *raricostatum* Zone) is currently accepted for both occurrences (cf. IMLAY 1968: C7, fig. 7; CRICKMAY 1928: 57, 59; FREBOLD & TIPPER 1970: 4, table 1). Nevertheless, *Melanhippites* is a taxon of controversial affinities, which is probably best regarded as a nomen dubium (GETTY 1973: 27) and, bearing in mind that *Crucilobicerias* does range into the Carixian (*ibex* Zone) in Canada (FREBOLD 1970: 444, table 1), the possible persistence of *Posidonotis* into the Pliensbachian times in western North America should be considered. HALLAM alternatively referred these records to the Pliensbachian (1977a) or to the Sinemurian (1983: 185).

Posidonotis is known from Europe by its type species, which was referred by LOSACCO (1942) to the “upper Lias (Aalenian)” only on the basis of indirect evidence, since his specimens were not found directly associated with *Fimbrilytoceras lineatum* SCHL. and could be somewhat older. Additional specimens had been collected earlier in the upper Labnitz gorge, on the north slope of the Chionistra massif (Greece) by RENZ (1927: 487, 504), who recorded them as “längsgestreiften Bivalven vom Habitus der *Pseudomonotis substriata* MÜNSTER”. Examination of his

Posidonotis



Text-fig. 27. Palaeogeographic distribution of the genus *Posidonotis*. Palaeocontinental reconstruction from SMITH & BRIDEN (1977) from the early Jurassic, hypothetical coast-lines compiled from various sources.

original material housed in Basel (NHMB G 16802, text-fig. 30 here) has revealed the presence of *Posidonotis* in western Greece during early Toarcian times (certainly pre-*jurense* Zone).

The stratigraphical range of this genus in South America seems to be restricted to the late Pliensbachian – early Toarcian in all the numerous localities from Argentina and Chile where it is associated with ammonites (see range and occurrence of the species described below).

The Japanese record corresponds to material identified by HAYAMI (1961, pl. 4, fig. 7) as *Amonotis* n. sp., from the late Pliensbachian of the Toyora area, southwest Honshu (see also HALLAM 1977a: 64, 71). HILLEBRANDT (1981) indicated on his map a locality in the Philippines, but this might be a mistake for Japan.

Posidonotis cancellata (A. LEANZA 1943)

Plate 14, fig. 1–12; text-fig. 28, 29

- * ! v. 1943 *Pectinula cancellata* n. sp. A. LEANZA, p. 244–249, lám. 1, fig. 1–6.
- v. 1973 *Pectinula cancellata* GROEBER (sic) – HILLEBRANDT, p. 354.
- v. 1978 *Pectinula cancellata* LEANZA – CAMACHO & RICCARDI, cuadro 1.
- p v. 1978 Pectinidae indet. – DAMBORENEA in VOLKHEIMER et al., Tab. 2.
- . 1980 *Pectinula cancellata* LEANZA – HILLEBRANDT, p. 126, lám. 1, fig. 2.
- . 1981 *Pectinula cancellata* LEANZA – HILLEBRANDT & SCHMIDT-EFFING, p. 10, 12, 14, 18, 19, 27.
- . 1982 *Pectinula cancellata* LEANZA – PÉREZ, lám. 20, fig. 2–3.
- ! v. 1982 *Posidonotis cancellata* (A. LEANZA) – DAMBORENEA, p. 221–225, lám. 47, fig. 1–8; lám. 69, fig. 1–8.

Type material: A. LEANZA (1943) did not choose a type specimen and the almost complete internal mould of a right valve MLP 10003–a is here selected as lectotype. This specimen was collected by FERNÁNDEZ and figured by A. LEANZA (1943, lám. 1, fig. 1), COX et al. (1969, fig. C77–3a) and here in pl. 14, fig. 1. LEANZA described the type locality as “southern extremity of the Sierra de Chacaico and, more precisely, on the eastern slope of the Cerro Charahuilla, near Estancia Charahuilla”, central Neuquén province. The material was probably collected in lower Toarcian beds (or upper Pliensbachian). Paralectotypes: some specimens collected by FERNÁNDEZ at the same locality MLP 10001 to 10004, and one sample collected by GROEBER at Los Molles, Picún Leufú, central Neuquén: MLP 10000.

Additional material: About two hundred specimens were available, most of them incomplete, generally preserved as internal or external moulds.

This species ranges in Argentina from southern San Juan province to central Neuquén. From north to south, it occurs at the following localities: Arroyo La Laguna (A.2): MLP 16498 and 19075 (M 431 and 435); Cerro Tricolor (B.11): MLP 16499 (M 805); Arroyo Ñiraico (C.4): MLP 15554 (GULISANO’s collection); Cerro Granito (C.14): MLP 1810 (FRENGUELLI’s collection); eastern slope of Cerro Keli-Mahuida (C.17): MLP 4595 (FRENGUELLI’s collection); Arroyo Lapa (C.15): MLP 15761 and 15789 (GULISANO’s collection) and MLP 16492 to 16497 (M 192; and Mallín de La Piedra (C.12): MLP 19725 to 19729, 19732 to 19755 (M 1375 to 1381). The material mentioned by HILLEBRANDT (1973a: 354) was seen at the NHMB.

This species is also known from several Chilean localities between 26° and 37° S lat. (HILLEBRANDT & SCHMIDT-EFFING 1981; PÉREZ 1982; CORNEJO et al. 1982; MARTICORENA & TAPIA 1982), always in dark shales and marls, rich in organic content and frequently also with aptychi. HILLEBRANDT & SCHMIDT-EFFING (1981) called these beds “Pectinulaschiefer” by analogy to the Toarcian “Posidonienschiefer” of Germany.

The stratigraphical range of this species merits a detailed discussion. A. LEANZA (1943) originally indicated that his material was found in levels “younger than Lotharingian (*oxynotum* Zone) but older than Toarcian (*jurense* Zone), and thus are probably of middle early Jurassic age”. In fact his specimens are associated to early Toarcian ammonites, determined as *Dactylioceras* (? *Orthodactylites*) sp. (cf. *belianthoides* YOKOYAMA).

At Río de Los Patos Sur, San Juan province, this species was found together with ? *Whithyceras* sp. and ? *Maconiceras* sp. and above *Protogrammoceras* sp. (see VOLKHEIMER et al. 1978, table 2). The material from Arroyo Lapa was also found with an early Toarcian ammonite fauna (*tenuicostatum-falcifer* Zone) with *Harpoceras* cf. *falcifer* (SOWERBY), *Tauromeniceras* sp., *Lytoceras* ? sp. and *Harpoceras* sp., whilst at Arroyo Ñiraico the associated ammonites are *Bouleiceras* sp. and *Dactylioceras* (? *Orthodactylites*) sp. HILLEBRANDT (1973) assigned the beds with *Posidonotis* from Chacaico to the earliest Toarcian on the grounds of a similar ammonite fauna. This author also mentioned this species from several localities in Chile where, according to the stratigraphical sections, it is always near the Pliensbachian-Toarcian boundary (HILLEBRANDT 1980: 126; 1981: 577; HILLEBRANDT & SCHMIDT-EFFING 1981: 10, 12, 14, 18, 19, 27). The oldest records correspond to beds immediately above the last horizon with *Fanninoceras*.

This is then a species with a short stratigraphical range, between the latest Pliensbachian and the early Toarcian.

Description: Small to medium-sized shell, very thin and flat, equi-valve and almost equilateral, of subcircular outline, with anterior and posterior auricles on both valves.

The dorsal line is not straight, as the dorsal margins of both auricles protrude above the hinge-line, forming between them an angle of 155° to 170° (ζ). The posterior auricle always has a sigmoidal posterior margin, whilst the anterior auricle has a convex anterior margin with a shallow byssal sinus in young specimens and becomes very similar to the posterior auricle in adult shells. In some specimens the orientation of the shell is very difficult due to the similarity of both auricles. In well-preserved specimens they can be distinguished because the anterior auricle only bears very faint growth lines (which may show the ontogenetic change from a byssate shell) and the posterior auricle has regularly spaced and stronger growth lines. The anterior auricle is limited by a deeper suture than the posterior one. The surface of the auricles is not flat, but feebly convex, leaving two elongated slits at the commissural plane at both ends. The dorsal margin of the anterior auricle is slightly longer than the posterior one in young specimens, but this relation is the opposite in adult shells.

The disc of the shell has continuous circular margins. In some specimens the anterior margin has a slightly angular portion after an almost straight disc flank below the auricle, but this is not a constant character. The shell is commonly slightly higher than long and the apical angle (ϵ) is always more than 110° (it varies between 112° and 128° in the measured specimens). The surface is evenly convex and the inflation is equally low on both valves. They have two triangular sections in the anterior and the posterior regions, which are flatter than the middle portion.

The umbones are small and do not protrude above the hinge margin. There are no hinge teeth. In some specimens a horizontal shell-thickening at the base of the auricles is present, similar to the auricular crus in *Entolium*. The ligamental pit could not be observed due to poor preservation. The muscle scars are also unknown.

The ornamentation is very peculiar. The surface has a cancellate appearance as a result of the intersection of concentric and radial folds that are both evident on the inner surface of the shell. The concentric folds are regularly spaced with intervals of equal width. They are stronger than the radial folds near the umbones, but become weaker after about 10 mm and then even completely disappear in very large shells. They vary between 11 and 15 in the first 10 mm near the umbones. The radial folds are weaker than the concentric ones and more irregular. They may increase in number by intercalation. The primary folds are slightly more elevated than the intercalated ones. On different specimens between nine and 23 radial folds were counted, the number depending on shell-size. They do not cover the whole shell surface but only the middle portion, leaving two lateral areas covered only by concentric ornamentation. The distribution of the radial folds is very uneven, they may concentrate on some portions of the valves. The radial folds are very weak near the umbones and they also disappear in very large shells at about 25 mm height. The largest shells have the peripheral surface smooth, with only growth lines. The concentric and radial folds intersect each other without changing their direction, occasionally forming small nodes at the intersection points.

Measurements: See also scatter diagram on text-fig. 29.

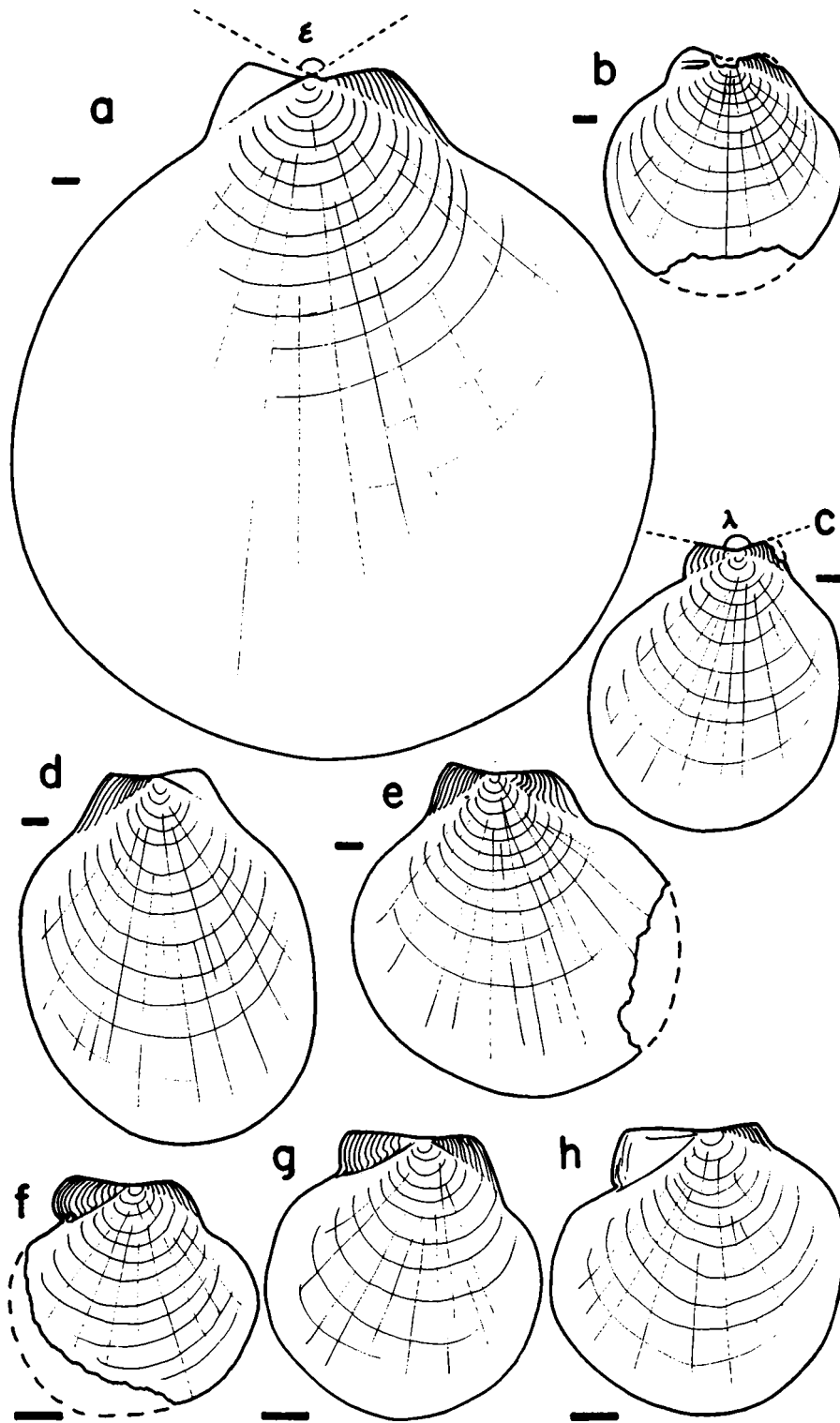
Specimen	Material		L (mm)	H (mm)	W (mm)	L/H	Lha (mm)	Lhp (mm)	a	b	ϵ	ζ
MLP 10000	RV	IM	13.40	15.15	0.40	0.88	1.80	1.80	18	11	115°	169°
MLP 10001	RV	IM	17.25	21.90	1.25	0.78	2.30	3.90	20	12	112°	-
MLP 10003-a	RV	IM	13.10	17.60	0.95	0.74	1.30	1.50	14	12	113°	172°
MLP 10004-a	RV	IM	14.00	14.20	0.95	0.98	2.05	1.90	14	13	118°	167°
MLP 10004-e	RV	IM	7.10	7.10	0.60	1.00	1.30	0.90	10	11	128°	170°
MLP 16498	LV	IM	28.15	31.20	1.90	0.90	2.85	3.30	12	12	121°	156°

a = total number of radial folds.

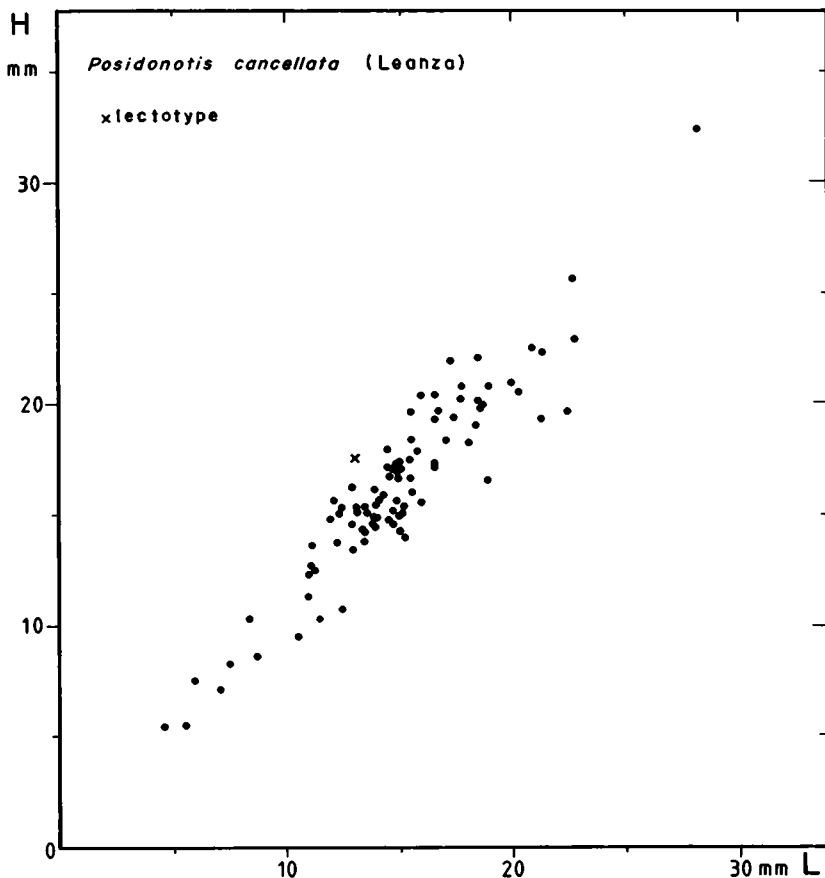
b = number of concentric folds in the 10 mm near the umbo.

Affinities: *P. dainellii* LOSACCO, from the late early Jurassic of Italy (LOSACCO 1942) is similar to the South American species in size and ornamentation pattern, but has a wider apical angle and more numerous radial folds (up to 36). The anterior auricle of the European species is unknown. The same differences are shown by the Greek material here tentatively assigned to *P. dainellii* (see text-fig. 30 here). Part of the material from the upper Lias of Monte San Giuliano, Sicily, named by DE GREGORIO (1930, tav. 5, fig. 12-13 only) as *Daonella elegantissima* could also belong to the Italian species of *Posidonotis*, though his illustrations and description are insufficient for a definite opinion.

The North American material was referred to three nominal species that are probably synonyms, their "differences" seem to be the result of post-depositional distortion, as already noticed by CRICKMAY (1933b: 52): *P.*



Text-fig. 28. Camera lucida drawings of some specimens of *Posidonotis cancellata* (A. LEANZA). The bar represents 1 mm. a: MLP 16498, left valve, Arroyo La Laguna, early Toarcian; b: MLP 15761, right valve external mould, Arroyo Lapa, early Toarcian; c: paralectotype, MLP 10004-m, left valve (?) internal mould, Charahuilla, early Toarcian; d: lectotype, MLP 10003-a, right valve internal mould, Charahuilla, early Toarcian; e: paralectotype, MLP 10004-a, right valve internal mould, Charahuilla, early Toarcian; f: MLP 15789, right valve interior, Arroyo Lapa early Toarcian; g: MLP 15789, right valve interior, Arroyo Lapa, early Toarcian; h: paralectotype, MLP 10004-e, right valve interior, Charahuilla, early Toarcian.



Text-fig. 29. Scatter diagram showing the length/height (L/H) ratio of *Posidonotis cancellata* (A. LEANZA).

semiplicata (HYATT 1894: 414; CRICKMAY 1933b: 52, pl. 14, fig. 4-7), *P. symmetrica* (HYATT 1894: 414; CRICKMAY 1933b: 52, pl. 14, fig. 1-3) and *P. balteata* (CRICKMAY 1928: 62, pl. 4, fig. e-g). Their shells are all smaller than those of *P. cancellata*, their auricles are relatively larger and their radial ribs seem to be stronger. Nevertheless, there is an overlap in the ranges of morphological variability of both the North and South American material and it is even difficult to decide whether they should be considered as separate species or not. On account of the subtle differences mentioned above *P. cancellata* is provisionally maintained as a different taxon for the time being.

HAYAMI (1961, pl. 14, fig. 7) illustrated material from the late Pliensbachian of Japan that he identified as *Amonotis* n. sp. These specimens are referable to *Posidonotis*, though the auricles are not known. They are smaller than *P. cancellata* shells and resemble *P. dainellii* in shape and number of radial folds.

Autecology: HILLEBRANDT (1980: 126; 1981: 577) suggested a pseudoplanktonic mode of life for this species, which is more abundant in the ammonite facies than in the bivalve-brachiopod facies.

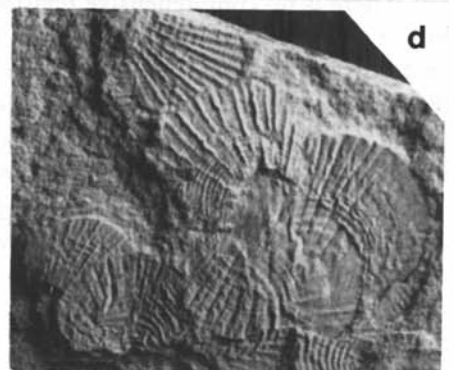
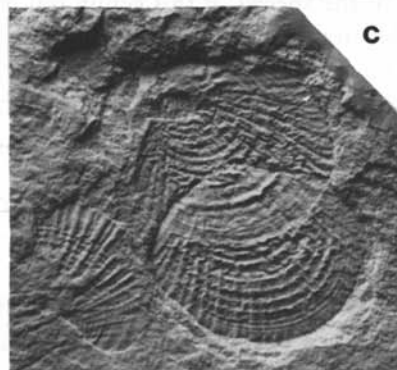
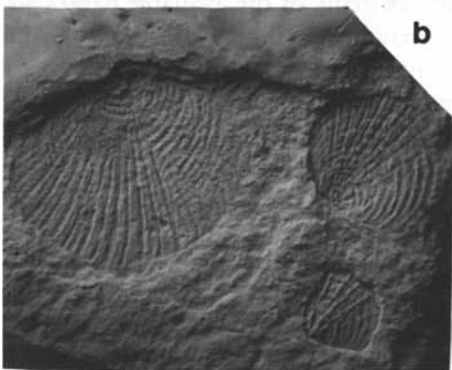
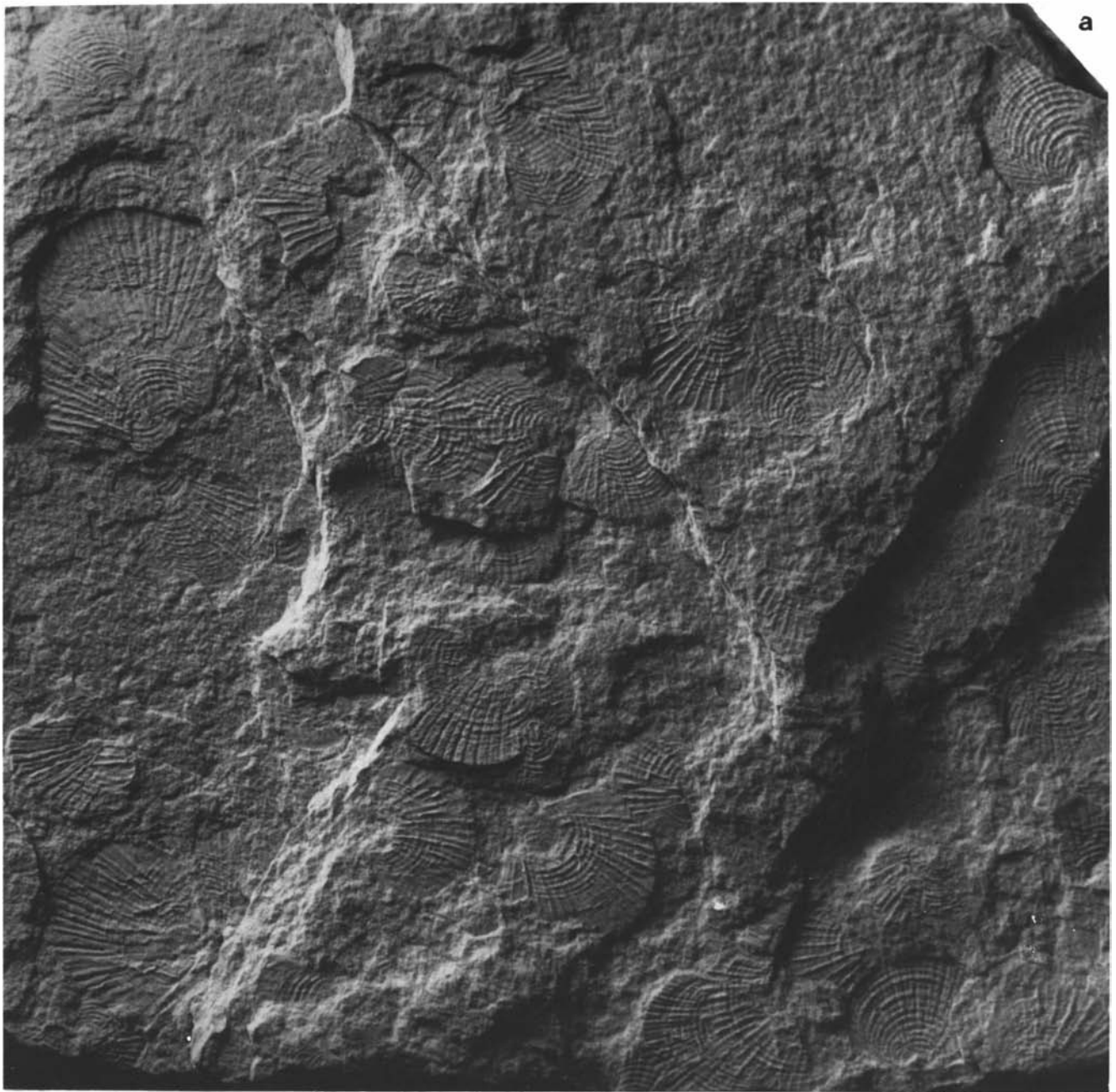
HALLAM (1977a) considered that *Pectinula* was a taxon from relatively deep waters, typically found in platform deposits, covering the bedding planes in large numbers, with a very poor associated fauna, mainly ammonites. All these features suggest an opportunistic life-strategy.

In Argentina this species is also abundant in that kind of facies, but isolated specimens were found in other rock-types, such as fine-grained calcarenites and fine-grained shelly sandstones. It must be noticed that in those facies the specimens attain a larger size than in dark shales.

Family Pectinidae RAFINESQUE 1815

The family Pectinidae was recently restricted by WALLER (1984) to the pectinaceans with a ctenolium present at least in early ontogeny. The adaptive radiation within the family was summarized by YONGE (1981).

Only one species of Pectinidae will be described here, the remaining species from the lower Jurassic of Argentina will be treated in another part of this monograph.



Text-fig. 30. *Posidonotis dainellii* LOSACCO? from the upper Labnitza gorge, north slope of Chionistra massif, Greece, early Toarcian, collected by RENZ, NHMB G 16802. a-d: slab with many specimens. X 2.

Genus *Eopecten* DOUVILLÉ 1897

Type species: *Hinnites tuberculatus* GOLDFUSS 1835 (error pro *Spondylus tuberculatus* GOLDFUSS 1835), from the middle Jurassic of Germany, by original designation.

Synonyms: *Velata* QUENSTEDT 1856 (non GRIFFITH & PIDGEON 1834, Gastropoda) (type species: *Spondylus tuberculatus* GOLDFUSS 1835, according to COX 1928: 244).

Velopecten E. PHILIPPI 1899 (pro *Velata* QUENSTEDT, non *Velates* MONTFORT 1810).

Prospondylus sensu ROLLIER 1915 (type species: *Spondylus comptus* GOLDFUSS) non ZIMMERMANN 1886 (type species: *Prospondylus liebeanus* ZIMMERMANN).

p. *Hinnites* auct. (non *Hinnites* DEFRANCE 1821).

? *Ventalium* DE GREGORIO 1930 (type species: *Ventalium insigne* DE GREGORIO 1930, by monotypy).

Eopecten DOUVILLÉ (1897: 203) is an objective synonym of *Velata* QUENSTEDT non GRIFFITH and PIDGEON. Although the name *Velata* was proposed by QUENSTEDT in 1856, during almost all the second half of the last century (and even to the present day) some of the species belonging to this taxon were commonly referred to *Hinnites* DEFRANCE. One of the possible causes for the misunderstanding about *Velata* (= *Eopecten*) and *Hinnites* is the fact that GOLDFUSS (1835, Taf. 105, Fig. 2b) reconstructed the right valve of the type species of *Eopecten* from an incomplete specimen that did not show the byssal sinus, as was already pointed out by ARKELL (1929: 124). E. PHILIPPI (1899, 1900) clearly distinguished both concepts and he stated that whilst in *Eopecten* the left valve is the more inflated one, in *Hinnites* the right valve is more globose, certainly reflecting the close relationships between this last genus and the Pectinidae s. s. E. PHILIPPI thought that *Velata* QUENSTEDT was preoccupied by *Velates* MONTFORT and thus proposed the name *Velopecten* as a replacement name, although he already knew about the erection of the name *Eopecten* by DOUVILLÉ (1897). He erroneously considered that *Velopecten* would maintain the priority of the concept from QUENSTEDT (1856).

On the other hand ROLLIER (1915: 450) also recognized this group, which he called "thin-shelled *Hinnites*" and used for them the subgeneric name *Prospondylus* ZIMMERMANN. This name was in fact originally introduced for a group of late Palaeozoic species that according to most authors should be included in the Pseudomonotidae (see NEWELL & BOYD 1970: 253).

COX (1942) illustrated and described for the first time the interior of the right valve of two species of *Eopecten* and discussed the possible affinities of this genus. He thought that *Eopecten* could have derived from a pseudomonotid bivalve by a process that involved a considerable change in the hinge characters and at the same time only a slight modification of the external shell characters. Certainly, although the shell morphology is comparable to that of *Pseudomonotis*, a fact already recognized by ROLLIER (1915), the ligament area of *Eopecten* as was described by COX (1942) is very similar to the true pectinids in the triangular subinternal resilifer, although *Eopecten* still preserves the subtriangular cardinal area. The type of ornamentation exhibited by *Eopecten* is common among the Aviculopectinidae and Oxytomidae, but very rare within the Pectinidae. Yet the deep byssal notch with a well-developed ctenolium is regarded as diagnostic for the Pectinidae sensu stricto as understood by WALLER (1984).

Only in 1950 did COX & ARKELL realize that QUENSTEDT's name is a junior homonym of *Velata* GRIFFITH & PIDGEON 1834, and must thus be replaced by the next oldest synonym, in this case *Eopecten* DOUVILLÉ 1897.

There is no comprehensive revision of the species of this genus and probably many of the available names are in fact synonyms and the species have therefore a wider stratigraphical and geographical range than the superficial analysis of all the proposed names and their ranges suggests. Differences in interpretation can be exemplified by the different author's attitudes towards the European material: whilst ROLLIER (1915) admitted 39 species, HALLAM (1976) only recognized two. DECHASEAUX (1936) drafted an arrangement of the known species of the Paris basin into groups, but she considered that those groups did not have any stratigraphical value (p. 100).

Unfortunately HERTLEIN (in COX et al. 1969, fig. C94, 4a) reproduced GOLDFUSS' figure (1835, Taf. 105, Fig. 2b), a restoration of an incomplete right valve, as a left valve. On the other hand HERTLEIN's diagnosis is the most complete so far.

The name *Ventalium* DE GREGORIO (1930: 23) is doubtfully included here in the synonymy of *Eopecten*. This genus from the early Jurassic of Sicily was based on incomplete specimens that are in all aspects comparable with fragments of *Eopecten*, especially in ornamentation pattern.

Eopecten was left aside within a "Group uncertain" of the Pectinidae by COX et al. (1969). In fact, its distinct

shell features and presumed peculiar life habits remind one of representatives of the genera *Pleuronectites* VON SCHLOTHEIM from the Triassic and early Jurassic of Europe, ? *Radulonectites* HAYAMI from the Triassic (?) to early Jurassic of Japan and *Hemipeecten* ADAMS & REEVE from the Indopacific Tertiary and Recent seas. Therefore, these four taxa, which share an acline shell of subcircular irregular outline, a flattish right valve closely adpressed to the substrate by a strong byssus, a deeply indented ctenolate byssal notch, an obsolescent posterior auricle and a convex left valve, may either represent an early side branch or highly specialized stock, or be the result of iterative evolution within the Pectinidae.

Eopecten hartzii (ROSENKRANTZ 1957) ?

Plate 6, fig. 16-19; text-fig. 31

- 1891 *Hinnites* conf. *velatus* GOLDF. - BEHRENDSEN, p. 393.
 1922 *Hinnites* conf. *velatus* GOLDF. - BEHRENDSEN, p. 176.
 1925 *Hinnites* cf. *velatus* GOLDF. - GERTH, p. 18.
 ? 1936 *Velopeecten velatus* GOLDFUSS - PIATNITZKY, p. 102.
 ? 1957 *Velata hartzii* n. sp. ROSENKRANTZ, p. 79-84, pl. 1-7.
 v. 1982 *Eopecten hartzii* (ROSENKRANTZ) ? - DAMBORENEA, p. 238-242, lám. 46, fig. 7-11; lám. 68, fig. 6-10.

Material: Ten left valves, four right valves and two specimens with both valves together, from Pliensbachian to lower Toarcian of southern Mendoza and Neuquén provinces. This species occurs at Paso del Portezuelo Ancho (B.4): MLP 19008 and 19015 (M 1282 and 1284); Arroyo del Portezuelo Ancho (B.5): MLP 19063 (M 1297); Arroyo Serrucho (B.8): MLP 19651, 19658, 19661 (M 1321, 1323 and 1324); Cerro Puchenque (B.9): MLP 16500 to 16502 (M 313 and 316); Arroyo Ñiraico (C.4): MLP 15534 (GULISANO's collection); southern Cordillera del Viento (C.1): MLP 15440 (GULISANO's collection); Rahue-Aluminé (C.13): MLP 15323 (CUERDA's collection) and doubtfully at Cerro Granito (C.14): MLP 4873 (SUERO's collection).

BEHRENDSEN's (1891, 1922) and GERTH's (1925) records correspond to material from Portezuelo Ancho, Mendoza province, whilst PIATNITZKY's mention (1936) refers to the Toarcian of Pampa de Agnia, Chubut province.

Description: Medium-sized valves, thin-shelled, inequilateral and very inequivalve, of subcircular irregular outline, with the height normally exceeding length. Left valve convex, right valve flat or slightly concave, conforming the surface to which it is adpressed. Low umbones placed slightly posteriorly to the mid-length. Left valve with large, triangular auricle not clearly delimited from the disc and small posterior auricle with posterior margin forming a right angle with the dorsal margin. The anterior margin of the left valve is straight and meets the dorsal one at about 110°. The right valve has a large anterior auricle, limited by a deep and pointed byssal notch with a well-developed ctenolium on its ventral margin and a wide byssal fasciole.

The hinge and ligamental characters of the left valve are not seen. The right valve has a central triangular resilifer, partly internal and a triangular external cardinal area. There is a tubercle or auricular crus at the base of the anterior auricle on the right valve. On the inner surface of the right valve there is also a posterior radial ridge, which is low and does not reach the ventral margin.

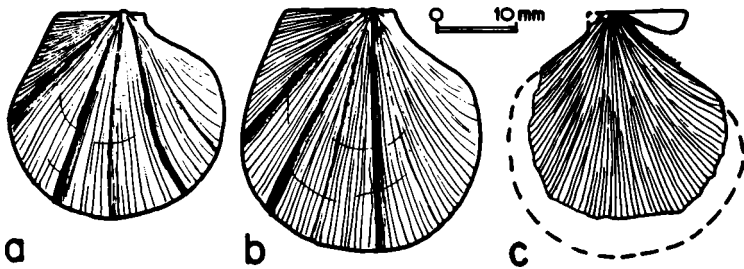
The external ornamentation consists of irregular radial ribs, with rounded and sometimes nodose tops, that can be classified in several orders. The primary ribs are between 5 to 8 on the left valve, but three of them are much more prominent than the others. From these three, one is slightly posterior of the middle line of the shell and the other two are anterior. Between the primary ribs there are irregular ribs of second and third orders, that maintain their different strength up to the ventral margin. The total number of radial ribs is about 90 on the left valve, from which about 30 belong to the anterior auricle, and nearly 75 on the right valve. The right valve has a different kind of ornamentation, with equally strong radial ribs. The posterior auricle apparently lacks radial ribs, while the anterior auricle of the left valve has radial ribs that are spaced more equally than on the disc. The shell also shows concentric folds that are stronger on the left valve.

Measurements:

Specimen	Material		L (mm)	H (mm)	W (mm)	L/H	Lha (mm)	Lhp (mm)	Al (mm)	Nº ribs
MLP 15323	LV	S	22.80	26.00	3.20	-	-	-	9.00	-
MLP 15440	LV	S	57.55	65.45	15.00	0.88	-	-	27.60	80
MLP 16500-a	LV	IM	36.30	37.70	6.20	0.96	13.60	3.40	20.55	90
MLP 16500-b	RV	IM	30.40	32.00	0.80	0.95	11.80	-	-	75
MLP 16501-c	LV	IM	32.65	31.35	3.75	1.04	10.30	3.25	17.40	-
MLP 16502	LV	IM	26.00	28.40	3.60	0.91	10.40	-	13.60	-

Affinities: The Argentine material here described was doubtfully assigned to *E. hartzi* (ROSENKRANTZ 1957), originally described from the early Pliensbachian of Greenland. The only apparent difference is the larger size of the Greenland specimens. All other characters, especially the ornamentation of the shell, are so similar that specimens of equal size are almost identical (compare for instance pl. 6, fig. 18 here and ROSENKRANTZ 1957, pl. 7).

There are other species that also have some primary ribs stronger than the others, such as *E. abjectus* (PHILLIPS), from the Aalenian – Bajocian of Great Britain and France (ARKELL 1931b: 434; DECHASEAUX 1936: 68; COX 1942, pl. 4, fig. 2–3) and *E. tegulatus* (MORRIS & LYCETT) as figured by KOCHANOVÁ (1979, tabl. 2, fig. 1) from the Bathonian of Czechoslovakia. A similar sculpture pattern, with three ribs more prominent than the others, is present in *E. gradus* (LYCETT), a Bathonian – early Callovian species from Europe (LYCETT 1863, pl. 33, fig. 10; FISCHER 1969, pl. 9, fig. 18a–b), but this species has a smaller anterior left auricle, a more anterior left umbo, more prominent primary ribs and less radial ribs than the Argentine material.



Text-fig. 31. *Eopecten hartzi* (ROSENKRANTZ)? a: MLP 16501, left valve, Cerro Puchenque, early Pliensbachian; b–c: MLP 16500, specimen with both valves, Cerro Puchenque, early Pliensbachian, b: left valve; c: right valve.

The type species, *E. tuberculosus* (GOLDFUSS) from the European Middle Jurassic (GOLDFUSS 1835, Taf. 105, fig. 2; ROLLIER 1915: 454; DUBAR 1925: 285; DECHASEAUX 1936: 68, pl. 9, fig. 2; CHARLES 1948: 133; NUTSUBIDZE 1966: 32, tabl. 3, fig. 11) has a similar ornamentation, though all primary ribs are equally prominent. Outside Europe there are records of this species from Malagasy (THEVENIN 1908: 127), from the Aalenian of Mendoza, Argentina (JAWORSKI 1925a: 167–168) and several localities in Chile (HILLEBRANDT & SCHMIDT-EFFING 1981: 20, 25, 27, 29). As these specimens have not been figured, comparisons are not possible.

From the Middle Jurassic of Chile HUPÉ (1854: 292–293, lám. C5, fig. 3–3a; R. PHILIPPI 1899: 37–38, lám. 20, fig. 12) described a “*Pecten abnormis*”, a probable *Eopecten* of the group of *E. tuberculosus*, to which perhaps the South American records mentioned in the previous paragraph might be referred to.

E. velatus (GOLDFUSS 1833) (= *Pecten tumidus* HARTMANN in ZIETEN 1833, non TURTON 1822), from the early Jurassic of Europe, has a nomenclatorial problem, since GOLDFUSS described two German species referable to *Eopecten* with the specific name *velatus*: *Pecten velatus* GOLDFUSS (1833: 45, Taf. 90, Fig. 2) from the early Jurassic, and *Spondylus velatus* GOLDFUSS (1835: 94, Taf. 105, Fig. 4), from the late Jurassic. Although both secondary homonyms were described in the same work, the first one has two years of priority as most authors realized. Thus E. PHILIPPI (1899: 598) used *E. velatus* (GOLDFUSS 1833) for the early Jurassic species and *E. albus* (QUENSTEDT 1856, proposed as a variety) for the late Jurassic one (COX 1928, 1931; ARKELL 1931b). On the other hand ROLLIER (1915: 463) and STAESCHE (1931: 84–87) preferred to preserve the name *velatus* GOLDFUSS 1835, for the late Jurassic species, a choice followed by others (for instance BLANCHET 1924: 76; WEAVER 1931: 285; CHARLES 1948: 134). *E. velatus* (GOLDFUSS 1833) has a shape and size similar to the species here described but has more numerous primary ribs, more regular ornamentation and subequal auricles (GOLDFUSS 1833: 45, Taf. 90, Fig. 2; QUENSTEDT 1856, taf. 18, fig. 26; DUMORTIER 1874: 308, pl. 62, fig. 3–4; COHEN 1931: 72, pl. 2, fig. 22; COX 1935b: 4, pl. 1, fig. 2–3; JOLY 1936: 106, pl. 2, fig. 2–4; BEHME & GEYER 1966: 28, Taf. 5, Fig. 3; SACCHI-VIALLI & CANTALUPPI 1967: 114, tav. 16, fig. 10–11). Material from the Aalenian – Bajocian of Cañada Colorada, Mendoza (WEAVER 1931: 284–285, pl. 28, fig. 172–173) was referred to *E. velatus* GOLDFUSS, 1835 (i. e. *Spondylus velatus* non *Pecten velatus* GOLDFUSS, see discussion above). Although there is some confusion in WEAVER’s description about the orientation of the shell, it is evident that his specimen has a larger posterior auricle than the material here described and it has more numerous primary ribs. The records of *E. velatus* (GOLDFUSS 1833) from the lower Jurassic of Portezuelo Ancho, Mendoza (BEHRENSSEN 1891, 1922; GERH 1925) are included in the synonymy on the basis of material from that area.

PIATNITZKY's record (1936: 102) from Chubut province (Toarcian of Pampa de Agnia), is doubtfully included in the species here described.

E. davoei (DUMORTIER 1869) from the late Pliensbachian of Europe, was considered by CHARLES (1948: 133) as a synonym of *E. velatus*. This species can be distinguished from *E. hartzi* ? by its almost straight radial ribs (DUMORTIER 1869: 141, pl. 21, fig. 9–10; ROLLIER 1915: 452; DUBAR 1925: 276; DECHASEAUX 1936: 67). MÖRICKÉ (1894: 38) compared with *E. davoei* material from the lower Jurassic of Chile and he also mentioned the straight ribs. The ornamentation of *E. hettangiensis* (DECHASEAUX) from the Hettangian of Belgium and Czechoslovakia (DECHASEAUX 1936: 71–72, pl. 9, fig. 1; KOCHANOVÁ 1961: 107) is also different.

The species *E. aubryi* (DOUVILLÉ), from the Bathonian – Oxfordian of north and east Africa, India and eastern Europe (COX 1942; 1965; FRENEIX 1965; VÖRÖS 1971: 184, pl. 3, fig. 2) has regularly spaced primary ribs more prominent than the others. It also lacks the internal ridge on the inner surface of the right valve.

The two species from the “Corallian” (upper Oxfordian) of Great Britain *E. anglicus* (ARKELL 1929: 120, pl. 9, fig. 1–2) and *E. wiltonensis* (ARKELL 1929: 123, pl. 9, fig. 3) have more numerous radial ribs, which although divisible into different orders are similarly prominent.

Remarks: In addition to the South American records already mentioned, GOTTSCHÉ (1878: 21; 1925: 252) cited *Hinnites* sp. in the Middle Jurassic of Paso del Espinacito, but he did not provide enough data. On the other hand, both *Velopecten covuncoensis* WEAVER (1931: 285–286, pl. 28, fig. 171) and *Hinnites leymerii* DESHAYES in WEAVER (1931: 286–287, pl. 29, fig. 175; pl. 30, fig. 177; pl. 31, fig. 178), from the lower Cretaceous of Neuquén province, probably belong to *Prohinnites* GILLET according to their morphological features.

Autecology: COX (1942: 120) dealt with the life habits of species of *Eopecten*, concluding that they were epibyssate. This author also discussed the presence of xenomorphic sculpture in some specimens, such as *E. ammoniticus* (ROLLIER 1915: 461, pl. 30, fig. 5), that would indicate, at least for those examples, that the lower valve was cemented to the substratum. This also would explain the more frequent findings of left valves. The Argentine material does not show any trace of cementation areas on the right valves, which are almost flat in their young portions. The more complete specimens were found on the inside of large *Weyla* shells (see pl. 6, fig. 17), and their right valve perfectly conforms to the inner surface of the *Weyla* shells. This, together with the well-developed ctenolium, suggests that they lived attached by a strong byssus in sheltered and dimly lit places. Such a mode of life is present nowadays in a closely comparable pectinid genus, *Hemipecten* ADAMS & REEVE, recently described in detail by YONGE (1981).

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Explanation of plates

(All specimens are coated with ammonium chloride. Figures natural size except where otherwise indicated. Specimens from author’s collection except where otherwise indicated).

Plate 1

- Figs. 1–5. *Bakevellia* (*Neobakevellia* ?) *pintadae* n. sp.
1. Holotype, MLP 16377, steinkern with shell remains attached. Hill south of Cerro Roth, Pliensbachian. 1a: right valve; 1b: anterior view; 1c: left valve; 1d: dorsal view.
 2. Paratype, MLP 16382, composite mould of left valve. Cerro Del Vasco, Pliensbachian.
 3. Paratype, MLP 16380, right valve of steinkern. Hill South of Cerro Roth, Pliensbachian.
 4. Paratype, MLP 16376, left valve. Cerro Roth, Pliensbachian.
 5. Paratype, MLP 16375, left valve. Hill south of Cerro Roth, Pliensbachian.
- Figs. 6–10. *Gervillella araucana* n. sp.
6. Paratype, MLP 16398, internal mould of right valve, X 2. Hill south of Cerro Roth, Pliensbachian.
 7. Paratype, MLP 16404–a, internal mould of left valve, X 2. Salitral Grande, Pliensbachian. 7a: dorsal view; 7b: lateral left view; 7c: latex cast, interior view.

8. Holotype, MLP 16400, left valve, X 2. Cerro Roth, Pliensbachian. 8a: lateral view; 8b: latero-ventral view.
 9. Paratype, MLP 16403-a, left valve of young specimen. Salitral Grande, Pliensbachian. 9a: anterior view; 9b: lateral view; 9c: latero-dorsal view.
 10. Paratype, MLP 16395-a, right valve interior. Hill South of Cerro Roth, Pliensbachian.
- Fig. 11. Pteriacea gen. et sp. indet. MLP 15547, left valve. Arroyo Ñiraico, early Toarcian, GULISANO's collection.

Plate 2

- Figs. 1-5. *Gervillaria ? pallas* (A. LEANZA).
1. MLP 16410, specimen with both valves. Hill South of Cerro Roth, Pliensbachian. 1a: right valve; 1b: left valve; 1c: anterior view.
 2. MLP 16411, internal mould of right valve. Hill south of Cerro Roth, Pliensbachian.
 3. Holotype, MLP 6133, left valve. Cerro Roth, Pliensbachian. Figured by A. LEANZA (1942, lám. 4, fig. 1). 3a: left valve; 3b: antero-ventral view.
 4. MLP 16407, right valve of specimen with both valves. Hill south of Cerro Roth, Pliensbachian.
 5. DNGM 8646 (= MLP 19079), specimen with both valves. Nueva Lubecka, Chubut, KEIDEL's collection. 5a: dorsal view; 5b: right valve; 5c: left valve.
- Figs. 6-8. *Aguilerella neuquensis* n. sp. Hill south of Cerro Roth, Pliensbachian.
6. Holotype, MLP 16372-a, internal mould of left valve.
 7. Paratype, MLP 16370, internal mould of shell with gaping valves. 7a: left valve; 7b: antero-ventral view.
 8. Paratype, MLP 16374, internal mould of right valve.
- Fig. 9. *Pteroperna* sp., MLP 19651, internal mould of right valve. Arroyo Serrucho, Pliensbachian.

Plate 3

- Figs. 1-3. *Gervilleioperna (Gervilletia) turgida* (A. LEANZA).
1. MLP 16417, left valve. Hill south of Cerro Roth, Pliensbachian. 1a: lateral view; 1b: anterior view.
 2. Lectotype, MLP 6059, left valve. Cerro Roth, Pliensbachian. FRENGUELLI's collection. Figured by A. LEANZA (1942b, lám. 3, fig. 2). 2a: lateral view; 2b: dorsal view.
 3. MLP 16418, specimen with both valves. Hill south of Cerro Roth, Pliensbachian. 3a: anterior view; 3b: right valve; 3c: left valve; 3d: dorsal view.
- Figs. 4-6. *Gervillia (Cultriopsis)* sp.
4. MLP 16387, left valve. Hill south of Cerro Roth, Pliensbachian.
 5. MLP 16386, internal mould of right valve, X 2. Hill south of Cerro Roth, Pliensbachian.
 6. MLP 16503, left valve. Cañadón Chapingo, 3 km SE of Cerro Carnerero, Chubut, early Toarcian, RICCARDI's collection.

Plate 4

- Figs. 1-6. *Parainoceramus apollo* (A. LEANZA).
1. Lectotype, MLP 6252, composite mould of left valve, X 2. Subida a Sañicó, Pliensbachian, FRENGUELLI's collection. Figured by A. LEANZA (1942b), lám. 2, fig. 1).
 2. MLP 16422-f, composite mould of left valve, X 4. Cerro Roth, Pliensbachian.
 3. MLP 16429, composite mould of left valve, X 4. Subida a Sañicó, Pliensbachian.
 4. MLP 16427, composite mould of right valve, X 4. Subida a Sañicó, Pliensbachian.
 5. MLP 16420-a, composite mould of right valve, X 4. Cerro Roth, Pliensbachian.
 6. Paralectotype, MLP 6254, composite mould of right valve, X 2. Subida a Sañicó, Pliensbachian. FRENGUELLI's collection.
- Fig. 7. *Bositra ornati* (QUENSTEDT), MLP 15766, X 4. Arroyo Lapa, Toarcian. GULISANO's collection.
- Figs. 8-10. *Isognomon jupiter* (A. LEANZA).
8. MLP 16451, left valve hinge. Hill south of Cerro Roth, Pliensbachian.
 9. MLP 16452, specimen with both valves. Cerro Roth, Pliensbachian. 9a: right valve; 9b: dorsal view.
 10. MLP 16453, left valve of specimen with both valves. Cerro Roth, Pliensbachian.

Plate 5

- Figs. 1-5. *Isognomon jupiter* (A. LEANZA). Hill south of Cerro Roth, Pliensbachian, except where otherwise indicated.
1. MLP 16450, steinkern with right valve attached. 1a: right valve exterior; 1b: internal mould of left valve.
 2. MLP 16438, right valve of bivalved specimen.
 3. MLP 16460, right valve of bivalved specimen. Salitral Grande, Pliensbachian.
 4. MLP 16440, right valve hinge.
 5. MLP 16439, left valve of specimen with both valves.

Plate 6

- Figs. 1-5. *Otapiria neuquensis* n. sp. All X 2, Cañadón La Pintada between Cerro Del Vasco and Cerro Roth.
1. Holotype, MLP 16480-a, left valve.
 2. Paratype, MLP 16486, left valve.
 3. Paratype, MLP 16484, left valve.
 4. Paratype, MLP 16482, left valve.
 5. Paratype, MLP 16483, right valve.
- Fig. 6 *Otapiria* ? sp. MLP 16491, left valve, X 2. Rio Atuel near Puesto Araya, Pliensbachian.
- Figs. 7-8. *Otapiria* ? *frenguelli* n. sp., X 2. Chacaico, Neuquén, early Jurassic, FRENGUELLI's collection.
7. Holotype, MLP 10418-a, right valve.
 8. Paratype, MLP 10418-b, left valve.
- Figs. 9-12. *Oxytoma* (*Oxytoma*) *inequivalvis* (SOWERBY), all X 2.
9. MLP 16437, right valve. Cañadón La Pintada between Cerro Del Vasco and Cerro Roth, Pliensbachian ?. 9a: internal mould; 9b: matching external mould.
 10. MLP 16477, left valve. Arroyo Sañicó near Carrán Curá, Pliensbachian.
 11. MLP 5984, internal mould of left valve. Chacaico, Neuquén, early Jurassic, FERNÁNDEZ' collection.
 12. MLP 16475, composite mould of right valve. Subida a Sañicó, Pliensbachian.
- Figs. 13-14. *Pulvinites* (*Hypotrema*) *liasicus* n. sp.
13. Holotype, MLP 16471, composite mould of left valve. Cerro Puchenque, Pliensbachian.
 14. Paratype, MLP 19023, composite mould of left valve. Paso del Portezuelo Ancho, Pliensbachian.
- Fig. 15. *Pulvinites* (*Hypotrema*) *liasicus* ?, MLP 16472, exterior of left valve, Cerro Puchenque, Pliensbachian.
- Figs. 16-19. *Eopecten hartzii* (ROSENKRANTZ) ?
16. MLP 16500, bivalved specimen. Cerro Puchenque, Pliensbachian. 16a: external mould of right valve; 16b: composite mould of left valve.
 17. MLP 15534, right valve preserved inside a right valve of *Weyla* (*Weyla*) *alata angustecostata* (PHILIPPI). Arroyo Ñiraico, early Toarcian, GULISANO's collection. 17a: latex cast; 17b: internal mould.
 18. MLP 16502, composite mould of left valve. Cerro Puchenque, Pliensbachian.
 19. MLP 19008, right valve. Paso del Portezuelo Ancho, Pliensbachian.

Plate 7

- Figs. 1-2 *Weyla* (*Weyla*) *alata angustecostata* (R. PHILIPPI).
1. DNGM 9428 (= MLP 19078), incomplete right valve. Quebrada Honda, early Toarcian ?, RIGAL's collection. 1a: posterior view; 1b: external view.
 2. DNGM 12463 (= MLP 19076), isolated right valve. Cajón de Ginebra, Sierra de Agnia, Chubut; early Toarcian ?, BARRENECHE's collection. Internal view (see also pl. 8, fig. 2 and pl. 9, fig. 2).
- Fig. 3. *Weyla* (*Weyla*) *bodenbenderi* (BEHRENDSEN), MLP 5608-c, latex cast of left valve, showing ornamentation details. North of Sanicó, Pliensbachian. FERNÁNDEZ' collection.

Plate 8

- Figs. 1-3. *Weyla* (*Weyla*) *alata angustecostata* (R. PHILIPPI).
1. MLP 15534, latex cast from external mould of left valve. Arroyo Ñiraico, early Toarcian. GULISANO's collection.
 2. DNGM 12463 (= MLP 19076), same specimen as pl. 7, fig. 2. 2a: external view; 2b: dorsal view.
 3. MLP 19077, a fragment of the hinge region of a left valve showing rudimentary teeth, a-b: same specimen with different light.

Plate 9

- Fig. 1. *Weyla* (*Weyla*) *alata alata* (VON BUCH), MLP 19051, internal view of left valve, Arroyo del Portezuelo Ancho, early Pliensbachian.
- Figs. 2-3. *Weyla* (*Weyla*) *alata angustecostata* (R. PHILIPPI).
2. DNGM 12463 (= MLP 19076), same specimen as pl. 8, fig. 2. 2a: posterior view; 2b: oblique internal view showing muscle scars.
 3. MLP 15534, latex cast from external mould of left valve. Arroyo Ñiraico, early Toarcian. GULISANO's collection.

Plate 10

- Figs. 1-5. *Weyla* (*Weyla*) *alata alata* (V. BUCH).
1. MLP 16528, specimen with both valves. Rio Atuel near Puesto Araya, Pliensbachian. 1a: left valve; 1b: dorsal view.
 2. MLP 16519, latex cast from an external mould of left valve. Cerro Puchenque, early Pliensbachian.

3. MLP 16523, steinkern, left lateral view. Cerro Puchenque, Pliensbachian.
4. MLP 19031, specimen with both valves, Arroyo del Portezuelo Ancho, Pliensbachian. 4a: posterior view; 4b: right lateral view; 4c: left lateral view.
5. MLP 19063, specimen with both valves. Arroyo del Portezuelo Ancho, Pliensbachian. Anterior view.
- Fig. 6. *Weyla (Weyla) bodenbenderi* (BEHRENDSEN), MLP 16580, left lateral view of bivalved specimen, same as pl. 11, fig. 2. Headwaters of the Rio Salado, Pliensbachian ?

Plate 11

- Figs. 1-2. *Weyla (Weyla) bodenbenderi* (BEHRENDSEN).
1. MLP 16543, specimen with both valves. Hill south of Cerro Roth, Pliensbachian. 1a: left lateral view; 1b: anterior view; 1c: dorsal view.
 2. MLP 16580, right lateral view of specimen with both valves, same as pl. 10, fig. 6.
- Fig. 3. *Weyla mexicana* (JAWORSKI) ?. MLP 16533, external mould of left valve, detail. Vuta Picún Leufú, Pliensbachian. Same specimen as text-fig. 22-d.

Plate 12

- Figs. 1-3. *Weyla (Weyla) bodenbenderi* (BEHRENDSEN).
1. MLP 16545, specimen with both valves. Hill south of Cerro Roth, Pliensbachian. 1a: dorsal view; 1b: right lateral view.
 2. MLP 5608-a, latex cast from internal mould of left valve. Hill south of Cerro Roth, Pliensbachian, FERNÁNDEZ' collection.
 3. MLP 16561, latex cast from external mould of left valve. Salitral Grande, Carrán Curá, Pliensbachian. With serpulid epizoan.
- Fig. 4. *Weyla (Lywea) unca* (R. PHILIPPI), MLP 15323, latex cast from external mould of right valve. Rahue-Aluminé, Pliensbachian ?, CUERDA's collection.

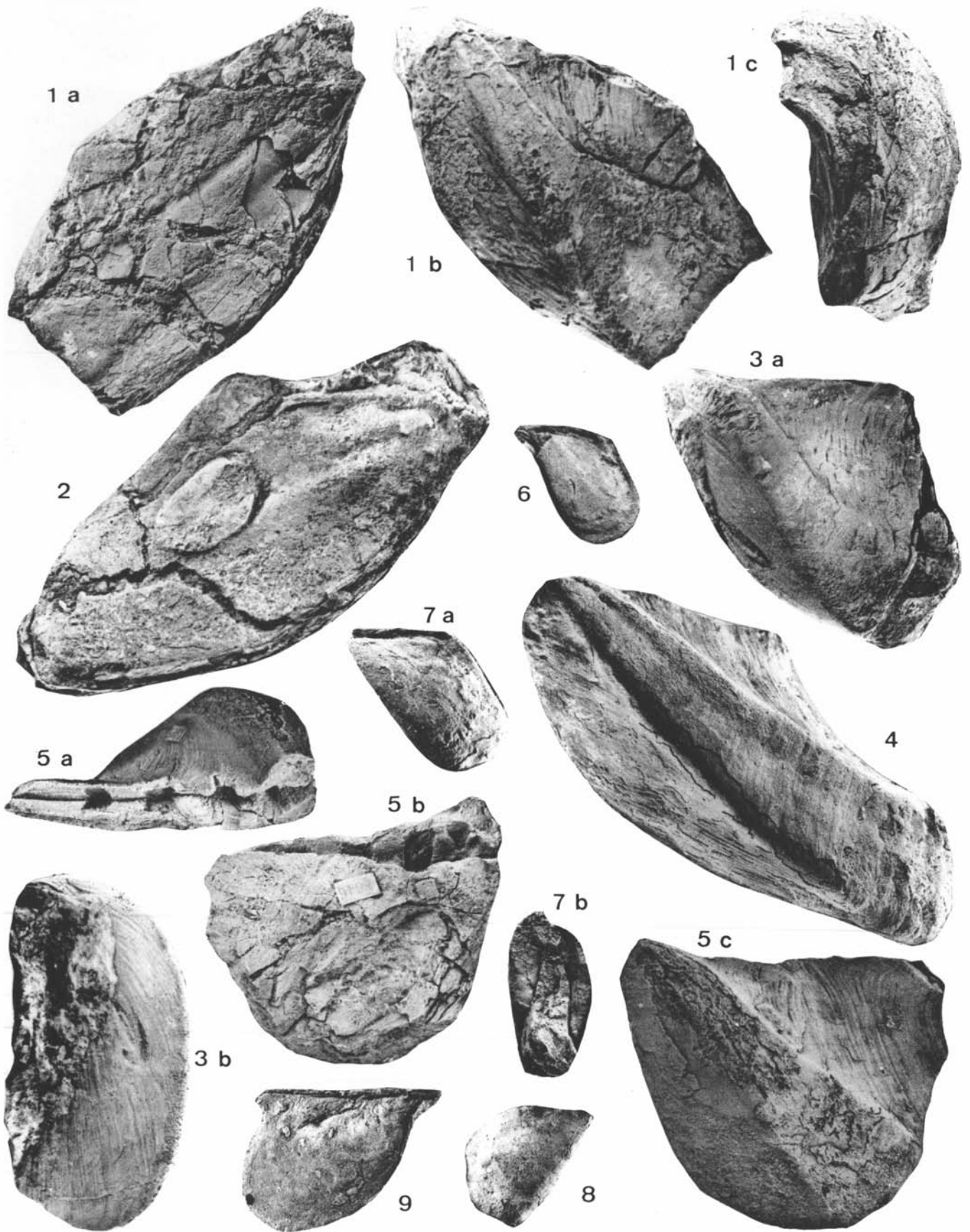
Plate 13

- Figs. 1-11. *Weyla (Lywea) unca* (R. PHILIPPI).
1. MLP 16636, latex cast from external mould of left valve. Estancia Santa Isabel, late Pliensbachian ?
 2. MLP 16618, latex cast from external mould of left valve. Cerro Puchenque, Pliensbachian.
 3. MLP 16585, left valve. Hill south of Cerro Roth, Pliensbachian.
 4. MLP 16593, latex cast from external mould of left valve. Subida a Sañicó, Pliensbachian.
 5. MLP 16633, right valve, X 2. Estancia Santa Isabel, late Pliensbachian ? 5a: dorsal view; 5b: lateral view.
 6. MLP 6132, left valve. Cerro Roth, Pliensbachian. Figured by A. LEANZA (1942b, lám. 9, fig. 6). 6a: dorsal view; 6b: lateral view.
 7. MLP 16631, specimen with both valves. Estancia Santa Isabel, late Pliensbachian ?. 7a: posterior view; 7b: right lateral view; 7c: dorsal view.
 8. MLP 16613, internal mould of left valve. SW of School N° 27. Piedra Pintada, Pliensbachian.
 9. MLP 16659, specimen with both valves. Cerro Granito, early Toarcian. 9a: anterior view; 9b: ventral view; 9c: right valve exterior; 9d: left valve exterior.
 10. MLP 5476, latex cast from external mould of bivalved specimen. Cañadón Martínez, Neuquén. FRENGUELLI's collection. 10a: left lateral view; 10b: right lateral view; 10c: stereoscopic pair of dorsal view.
 11. MLP 6046-c, right valve. Piedra Pintada, Pliensbachian. FRENGUELLI's collection. 11a: right lateral view; 11b: dorsal view.

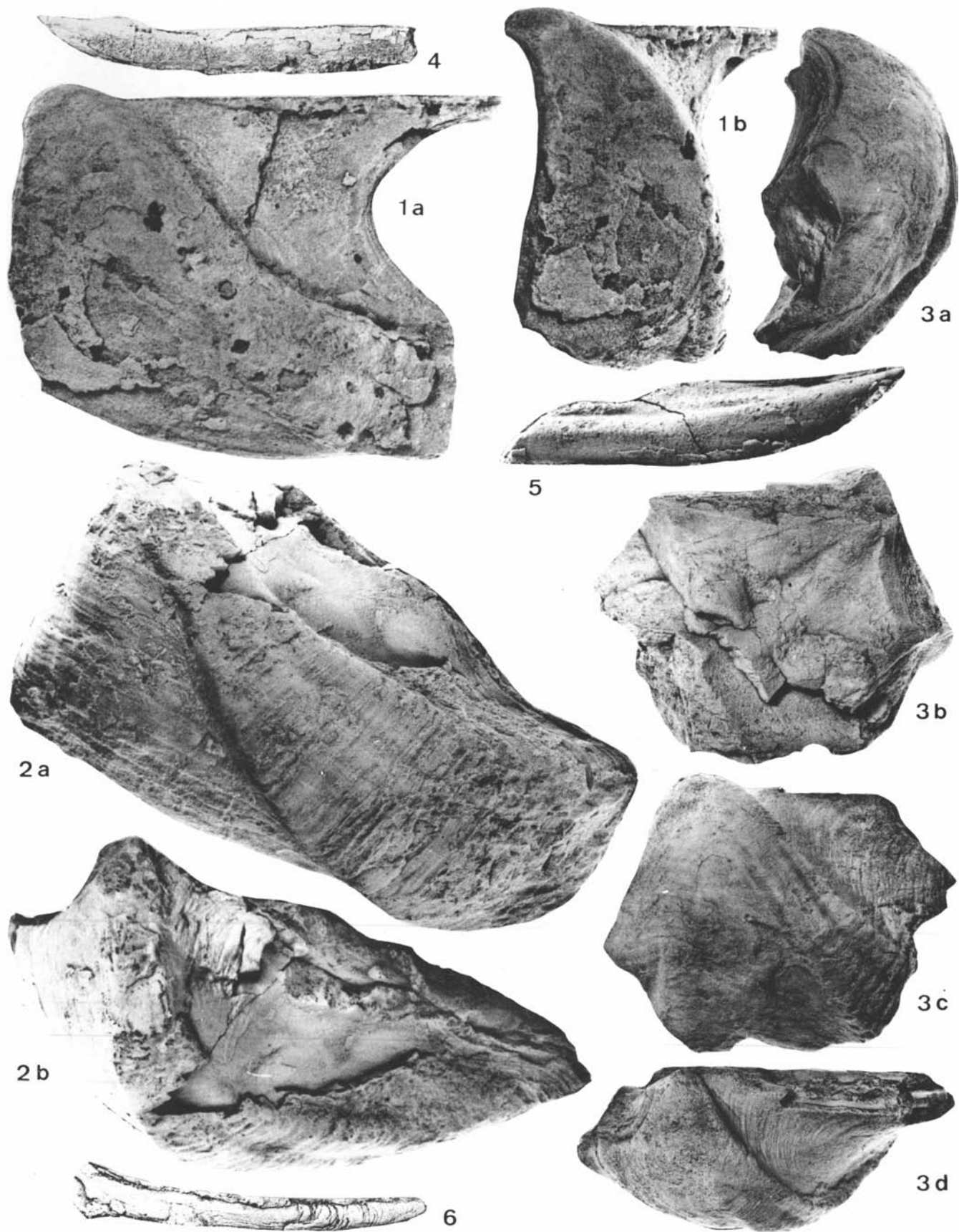
Plate 14

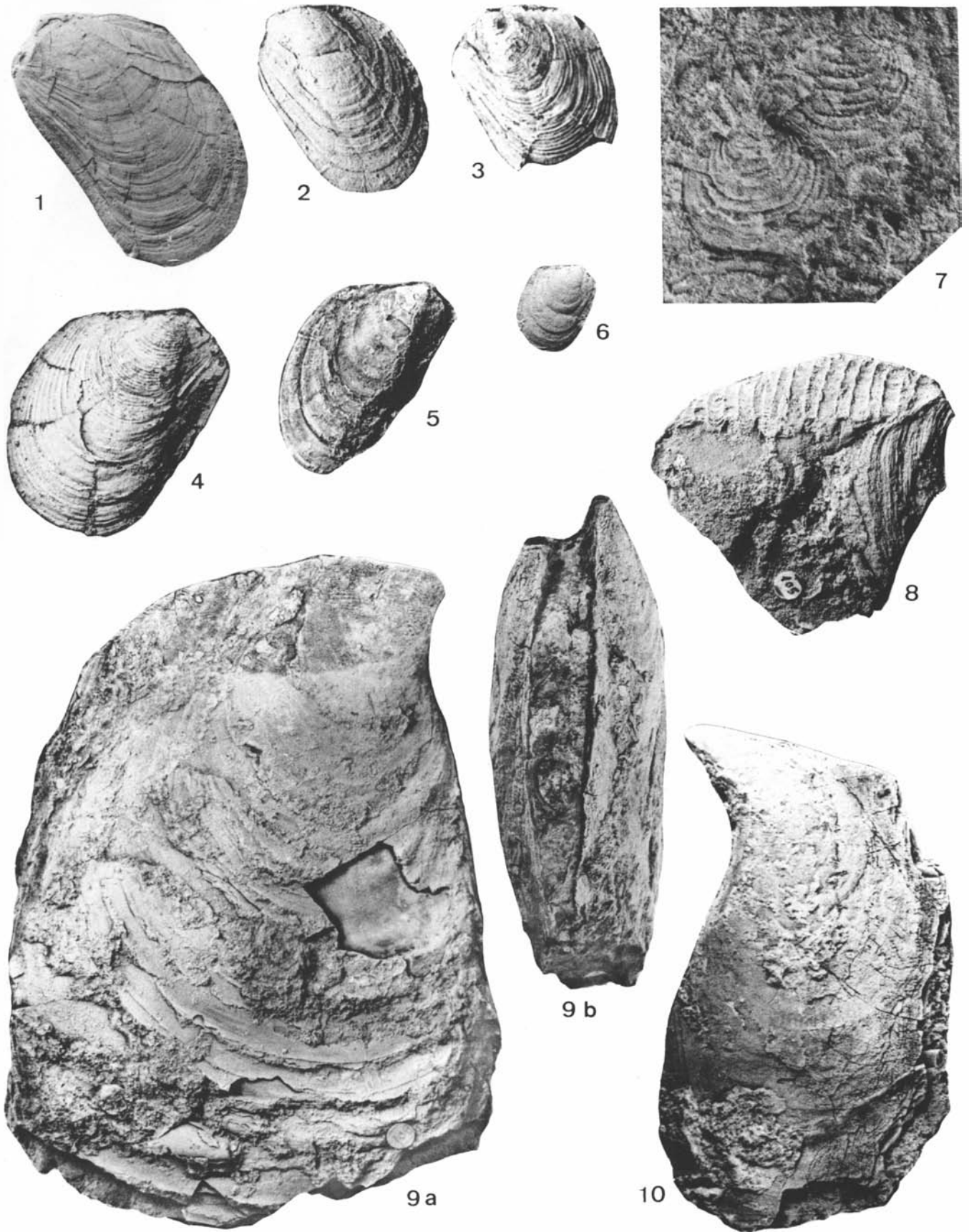
- Figs. 1-12. *Posidonotis cancellata* (A. LEANZA). All X 2, except where otherwise indicated.
1. Lectotype, MLP 10003-a, right valve. Charahuilla, Neuquén, early Toarcian. FERNÁNDEZ' collection.
 2. Paralectotype, MLP 10001, right valve. Charahuilla, Neuquén, early Toarcian. FERNÁNDEZ' collection.
 3. MLP 19746, Mallín de Ibáñez, early Toarcian. 3a: internal view; 3b: internal mould.
 4. MLP 16498, left valve. Arroyo La Laguna, early Toarcian.
 5. MLP 15761-a, Arroyo Lapa, early Toarcian, GULISANO's collection.
 6. MLP 19748-a, external mould. Mallín de Ibáñez, early Toarcian.
 7. MLP 1810, incomplete specimen. Cerro Granito, early Toarcian, FRENGUELLI's collection.
 8. MLP 19748-b, incomplete young specimen. Mallín de Ibáñez, early Toarcian.
 9. MLP 15789, interior of a young right valve, X 4. Arroyo Lapa, early Toarcian. GULISANO's collection.
 10. MLP 4595, one adult and two young specimens. East of Cerro Keli-Mahuida, early Toarcian. FRENGUELLI's collection.
 11. Paralectotype, MLP 10000, right valve. Los Molles, early Toarcian, GROEBER's collection.
 12. MLP 15761, slab with several specimens. Arroyo Lapa, early Toarcian. GULISANO's collection.

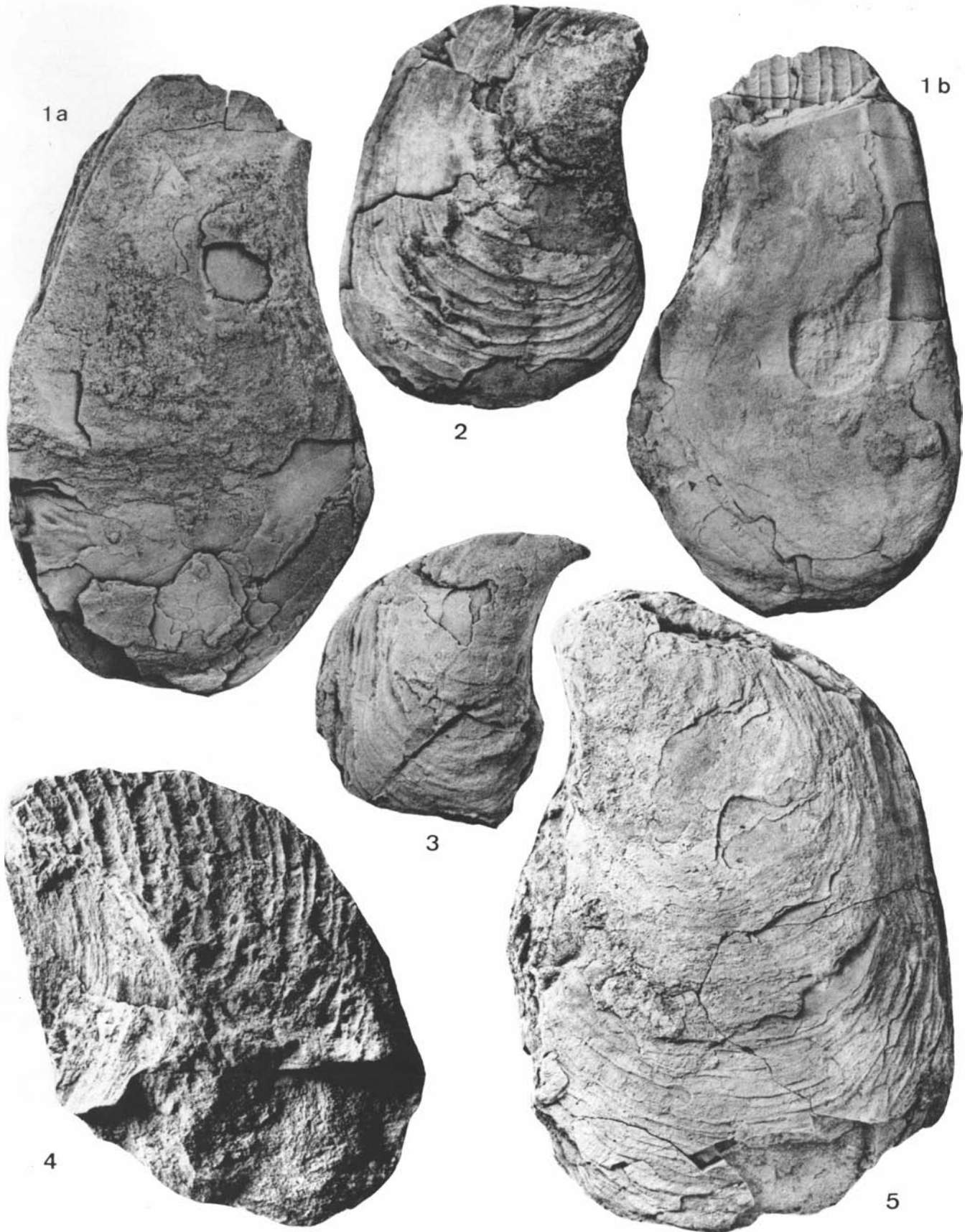


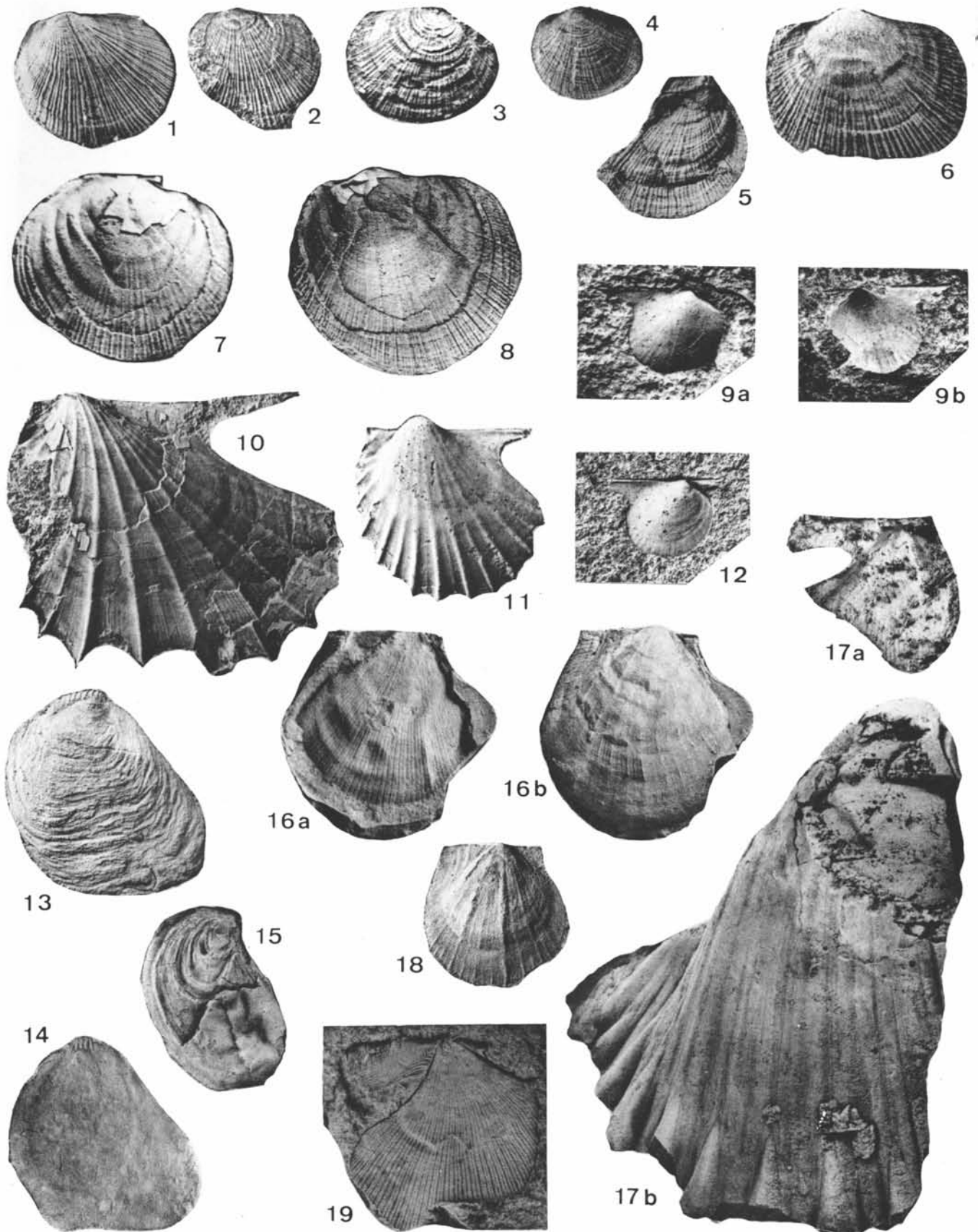


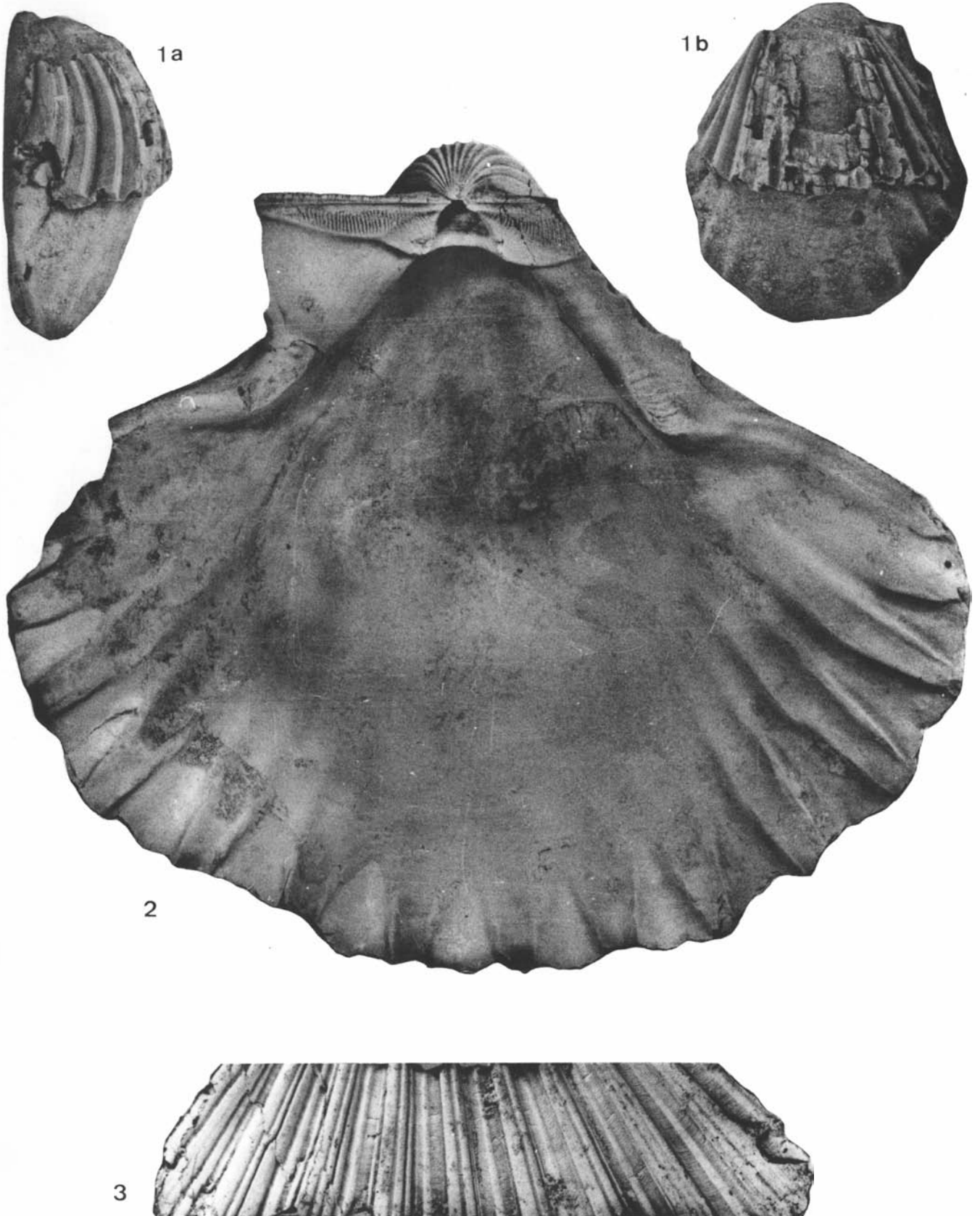
S. Damborenea: Early Jurassic Bivalvia of Argentina, Part 2.







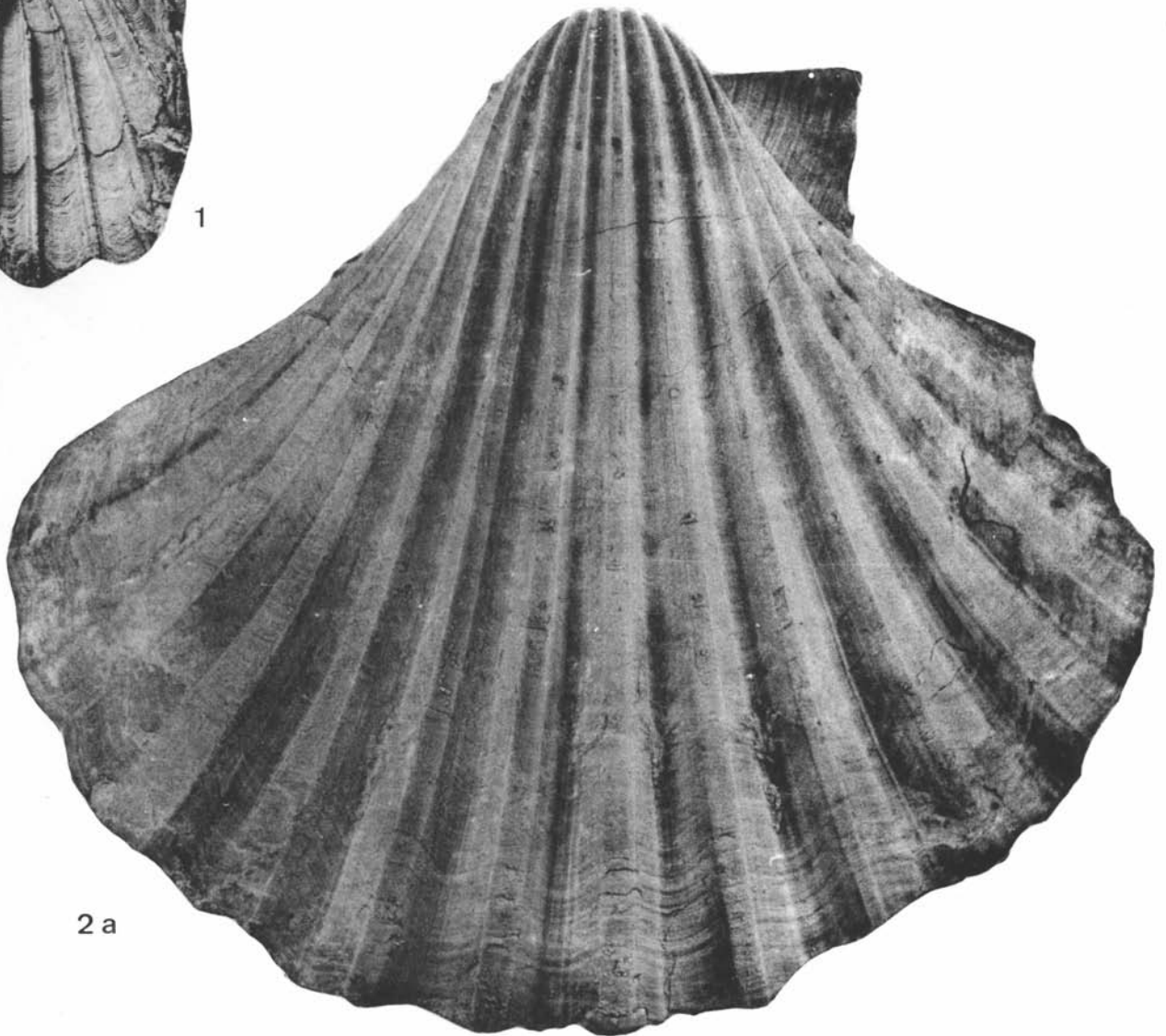




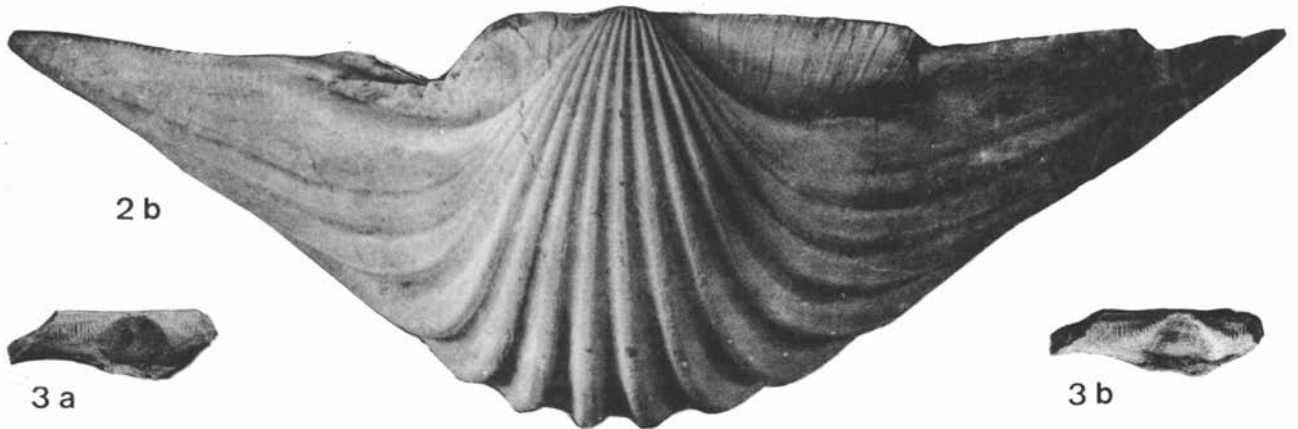
S. Damborenea: Early Jurassic Bivalvia of Argentina, Part 2.



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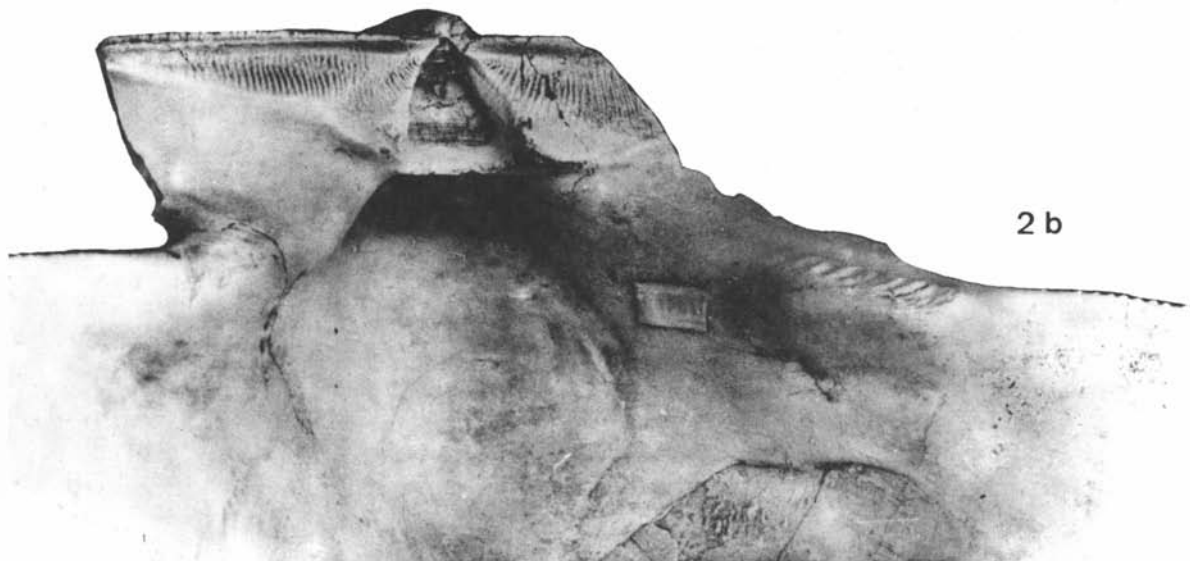
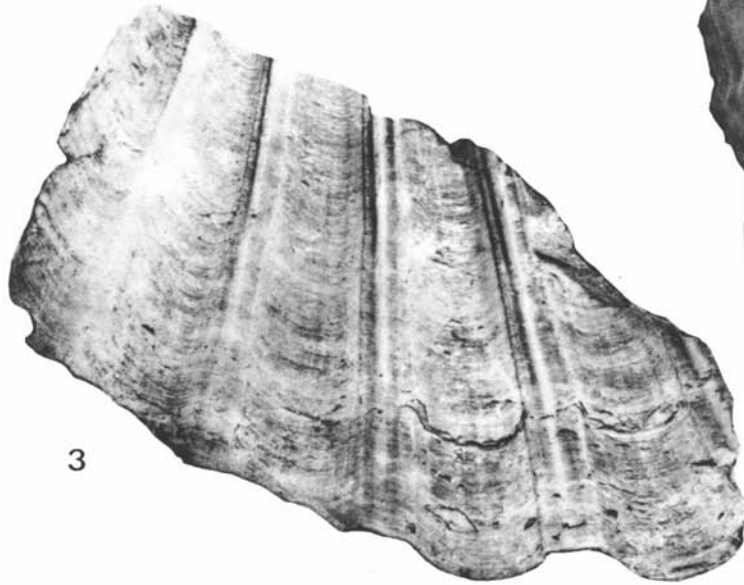
2 b

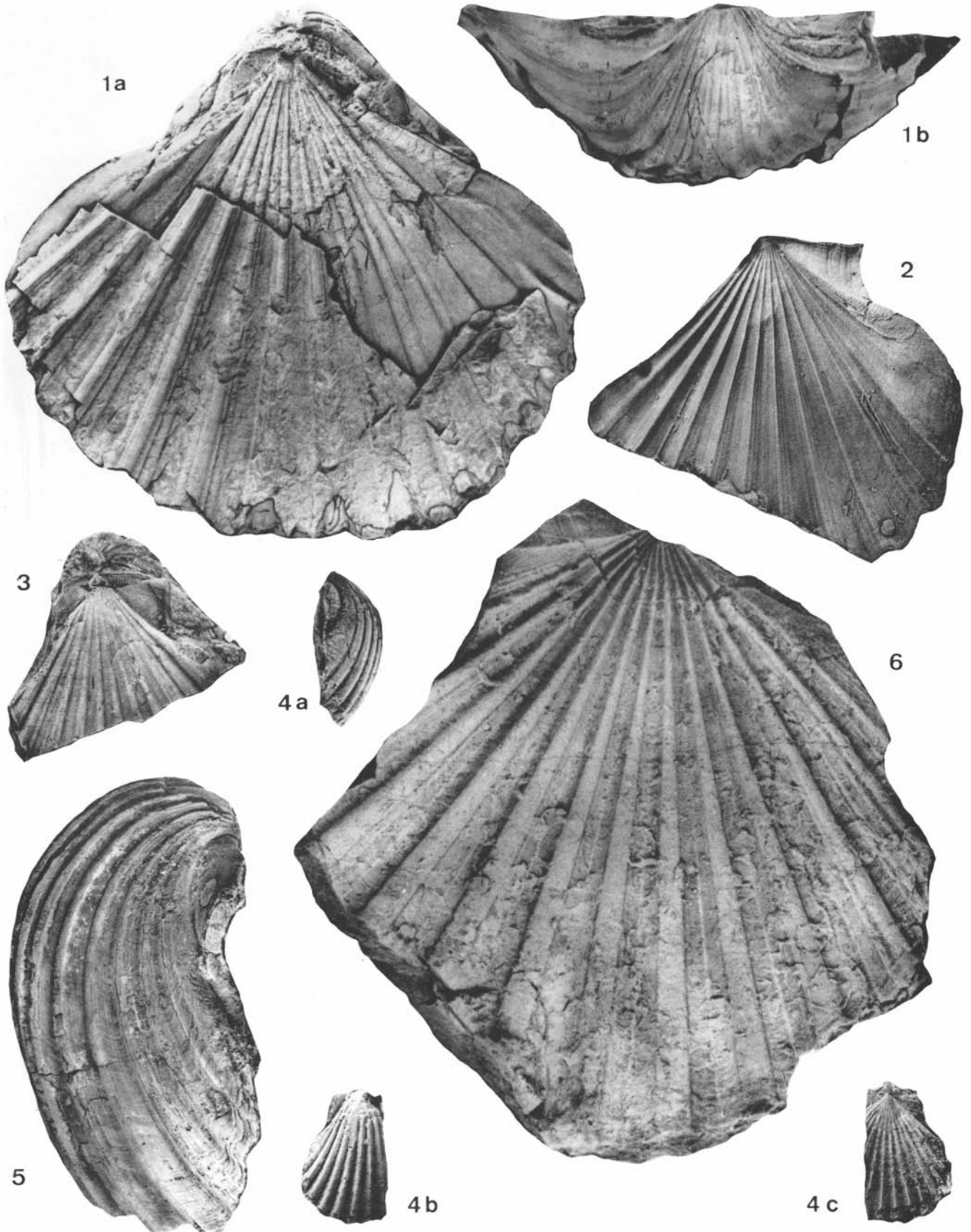


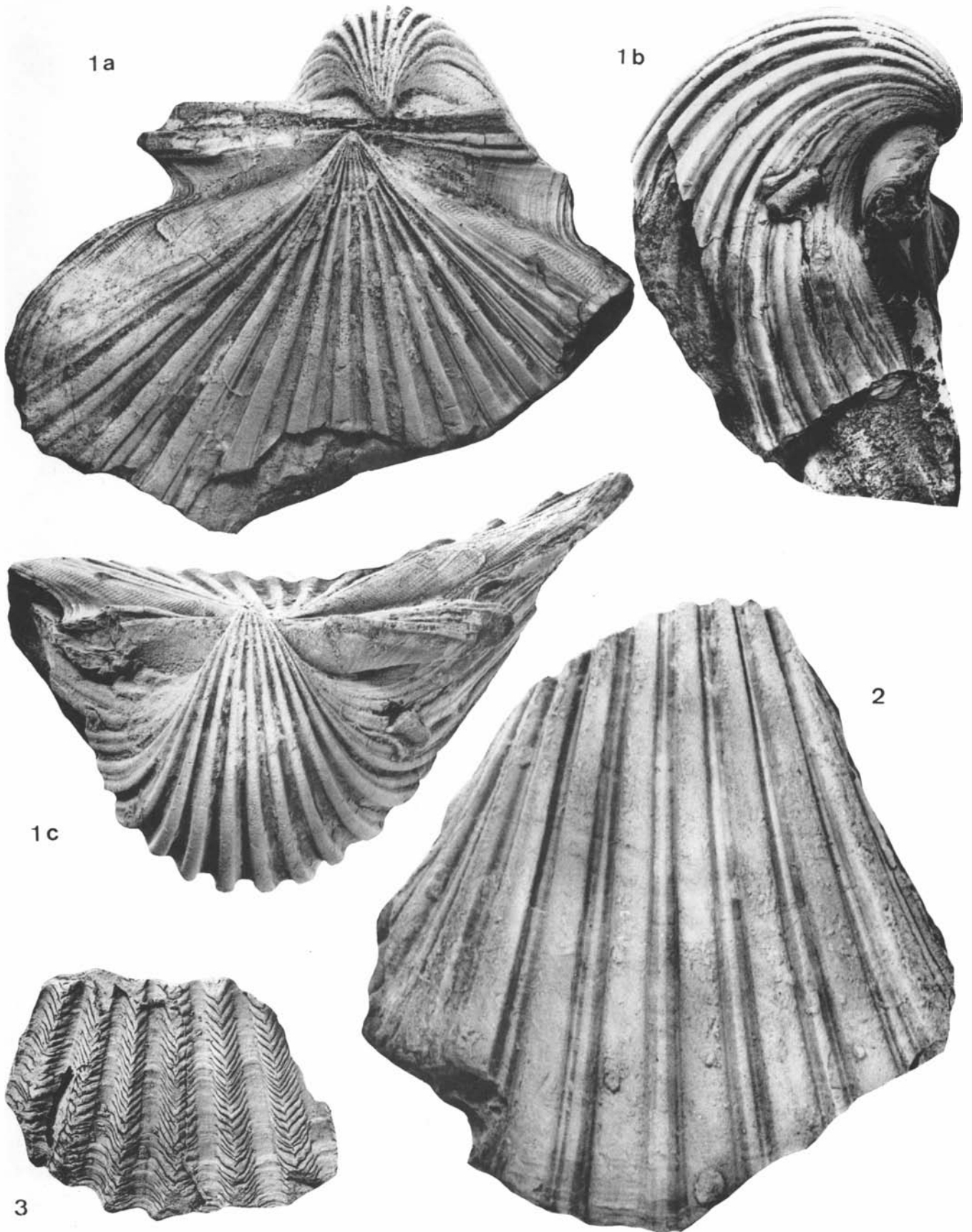
3 a



3 b







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