

# The Beudanticeratinae and Cleoniceratinae (Ammonitida) from the Lower Albian of Patagonia

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## Abstract

Albian Beudanticeratinae and Cleoniceratinae of the Patagonian Andes are revised taxonomically and chronologically, based on the re-examination of all available specimens and of most Albian localities of Santa Cruz Province, Argentina. Types and figured specimens of previously described species are reillustrated, but a few appear to be lost. Cleoniceratinae are represented by *Cleoniceras* PARONA & BONARELLI and *Aioloceras* WHITEHOUSE, and Beudanticeratinae by *Beudanticeras* HITZEL (?) and *Uhligella* JACOB. They include *Cleoniceras?* cf. *santacrucense* LEANZA, C. sp., *Aioloceras argentinum* (BONARELLI), *A. rollerii* and *A. aff. rollerii* (LEANZA), A. sp., *Beudanticeras revoili* (PERVINQUIERE), B. cf. *laevigatum* (J. de C. SOWERBY), B. sp., ?*Uhligella* sp. a and ?*U.* sp. b. Affinities with Beudanticeratinae and Cleoniceratinae from other areas of the globe are discussed. Because the type species of *Aioloceras* was based on two incomplete, juvenile, macroconch phragmocones, all previous diagnoses and systematics of *Aioloceras* based on these are inadequate. *Paracleoniceras* COLLIGNON is synonymous with *Aioloceras* and differences from *Pseudosaynella* SPATH and *Grycia* IMLAY are stressed. Inclusion of *Aioloceras* in Cleoniceratinae is based on ribbing, whorl section and the relatively simple septal suture with wide asymmetric L. Reports of *Aioloceras* from other continents are doubtful. Patagonian Beudanticeratinae and Cleoniceratinae are present in several sections between San Martin and Cardiel lakes, where they characterize stratigraphic levels. They are associated with other ammonoids, such as *Douvilleiceras* sp., *Puzosia recteradiata* COLLIGNON, *Puzosia* sp., *Rossalites imlayi* (LEANZA) and *Pictetia ovalis* COLLIGNON. This fauna belongs to the *Aioloceras argentinum* and to the *A. rollerii* (new) Assemblage Zones, coeval to the upper Lower Albian Mammillatum Superzone.

## Key words

Ammonoidea, Beudanticeratinae, Cleoniceratinae, Albian, Patagonia.

## Résumé

**Les Beudanticeratinae et les Cleoniceratinae (Ammonitida) de l'Albien inférieur de Patagonie.**- Les Beudanticeratinae et Cleoniceratinae de l'Albien des Andes Patagoniques font l'objet d'une révision taxonomique et chronologique, basée sur le re-examen des spécimens et des gisements albiens de la province de Santa Cruz (Argentine). Les exemplaires, types et figures des espèces décrites antérieurement, sont ici refigurés, bien que certains soient perdus. Les Cleoniceratinae sont représentés par *Cleoniceras* PARONA & BONARELLI et *Aioloceras* WHITEHOUSE, et les Beudanticeratinae par *Beudanticeras* HITZEL (?) et *Uhligella* JACOB. Ces genres comprennent *Cleoniceras?* cf. *santacrucense* LEANZA, C. sp., *Aioloceras argentinum* (BONARELLI), *A. rollerii* et *A. aff. rollerii* (LEANZA), A. sp., *Beudanticeras revoili* (PERVINQUIERE), B. cf. *laevigatum* (J. de C. SOWERBY), B. sp., ?*Uhligella* sp. a et ?*U.* sp. b. Les affinités des Beudanticeratinae et Cleoniceratinae avec d'autres régions sont aussi discutées. En raison de l'espèce-type du genre *Aioloceras*, basée sur deux phragmocones juvéniles incomplets de macroconques, toutes les diagnoses et la systématique antérieure du genre *Aioloceras* sont inadéquates. *Paracleoniceras* COLLIGNON est considéré comme synonyme de *Aioloceras* et les différences avec *Pseudosaynella* SPATH et *Grycia* IMLAY sont discutées. L'attribution de *Aioloceras* à la sous-famille des Cleoniceratinae est fondée sur la costulation, la section des tours et la ligne cloisonnaire qui est relativement simple avec un lobe (L) ample et asymétrique. La présence de *Aioloceras* dans d'autres continents est douteuse. Les Beudanticeratinae et Cleoniceratinae de la Patagonie sont connus dans quelques gisements situés entre les lacs San Martin et Cardiel. Ils sont associés avec d'autres ammonites, telles que *Douvilleiceras* sp., *Puzosia recteradiata* COLLIGNON, *Puzosia* sp., *Rossalites imlayi* (LEANZA) et *Pictetia ovalis* COLLIGNON. Cette faune fait partie de l'"Assemblage Zone" (partie supérieure de l'Albien inférieur) à *Aioloceras argentinum* et à *A. rollerii* (neuf), de la Superzone à Mammillatum de l'Albien Inférieur supérieur.

## Mots-clés

Ammonoidea, Beudanticeratinae, Cleoniceratinae, Albien, Patagonia.

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## INTRODUCTION

Beudanticeratinae and Cleoniceratinae have been described or recorded, mainly from Albian strata, from many parts of the globe (see Fig. 2). However, most species and genera are based on European material and known secondarily from North America, usually from isolated and/or fragmentary specimens. Intraspecific morphological variation, sexual dimorphism, and taxonomic significance of most shell features are therefore poorly known.

This situation existed in Patagonia, from where only few specimens have been figured to date (see BONARELLI & NÁGERA, 1921; PIATNITZKY, 1938; LEANZA, 1970; RICCARDI, 1988). That was in spite of the fact that Albian marine strata are exposed in a large area of the Austral Basin between the lakes San Martin, Cardiel and Argentino, where some localities have abundant and well preserved material.

This situation had prompted our study of a quite large collection of about 200 specimens, 20 of Beudanticeratinae and 180 of Cleoniceratinae, assembled by the authors. This study includes re-examination of type specimens, type localities, and of collections deposited in Museums, Institutes and Companies (cf. Acknowledgements), as well as our own collection from 8 localities in southern Patagonia. Field work was carried out throughout the last 35 years. RICCARDI visited the Lago San Martin area in 1966-1967, 1971, the Lago Cardiel area, together with H. VALICENTI, in 1973 and with M.P. IGLESIAS LLANOS and R. LANZA in 1999. He also visited both areas with E. ROLLERI and M.B. AGUIRRE URRETA in 1985. MEDINA collected in the Lago Cardiel area in 1981-2.

The associated fauna has partly been described (see description of the stratigraphic sections) or will be described in the future under separate or joint authorship.

This paper includes a stratigraphic summary of the area with a detailed description of the sections from which the fauna was collected, and a systematic part. One appendix supplements this work, where we list (as interpreted by us) all figured material that has been referred thus far to Albian Beudanticeratinae and Cleoniceratinae.

## STRATIGRAPHY

The Magallanes or Austral Basin is located on the eastern border of the Patagonian Cordillera, south of 45° S. The older units recognized in this area include Paleozoic sedimentary and metamorphic rocks and Jurassic volcanics. The basin was filled with chiefly marine Upper Jurassic to Tertiary sediments (see RICCARDI & ROLLERI, 1980).

The Cretaceous of the studied area (see RICCARDI, 1988) overlies the Jurassic volcanics of El Quemado Complex, and consists of Berriasian-early Valanginian continental to marine sandstones, the Springhill Formation, the late Valanginian - late Albian marine black shales of the Rio Mayer Formation, and the Albian - Cenomanian shallow marine to continental sandstones and conglomerates of the Kachaike and Piedra Clavada formations. Late Cretaceous sequences consist of continental sedimentites and pyroclastic rocks. Marine Upper Cretaceous is mostly restricted to the area south of 49° 30' S.

## FOSSIL LOCALITIES

### Lago San Martin

1. *Estancia La Federica*: East of Estancia La Federica, at the headwaters of Arroyo Calafate (see Fig. 1). The general stratigraphy and lower Cretaceous fossils of the area have been studied previously by STOLLEY (1912), BONARELLI & NÁGERA (1921); PIATNITZKY, 1938; LEANZA (1970); WATERHOUSE & RICCARDI (1970); RICCARDI (1971, 1976, 1977, 1988); RICCARDI *et al.* (1987); AGUIRRE URRETA & RICCARDI (1988).

### Kachaike Formation

c. 200-250 m White-greenish sandstones, conglomerates and tuffs with middle-late Albian ammonites and other invertebrates and plants.

### Río Mayer Formation

c. 700 m Dark-grey shales, with intercalated limestones in lower part, changing to marls with calcareous concretions in upper part.

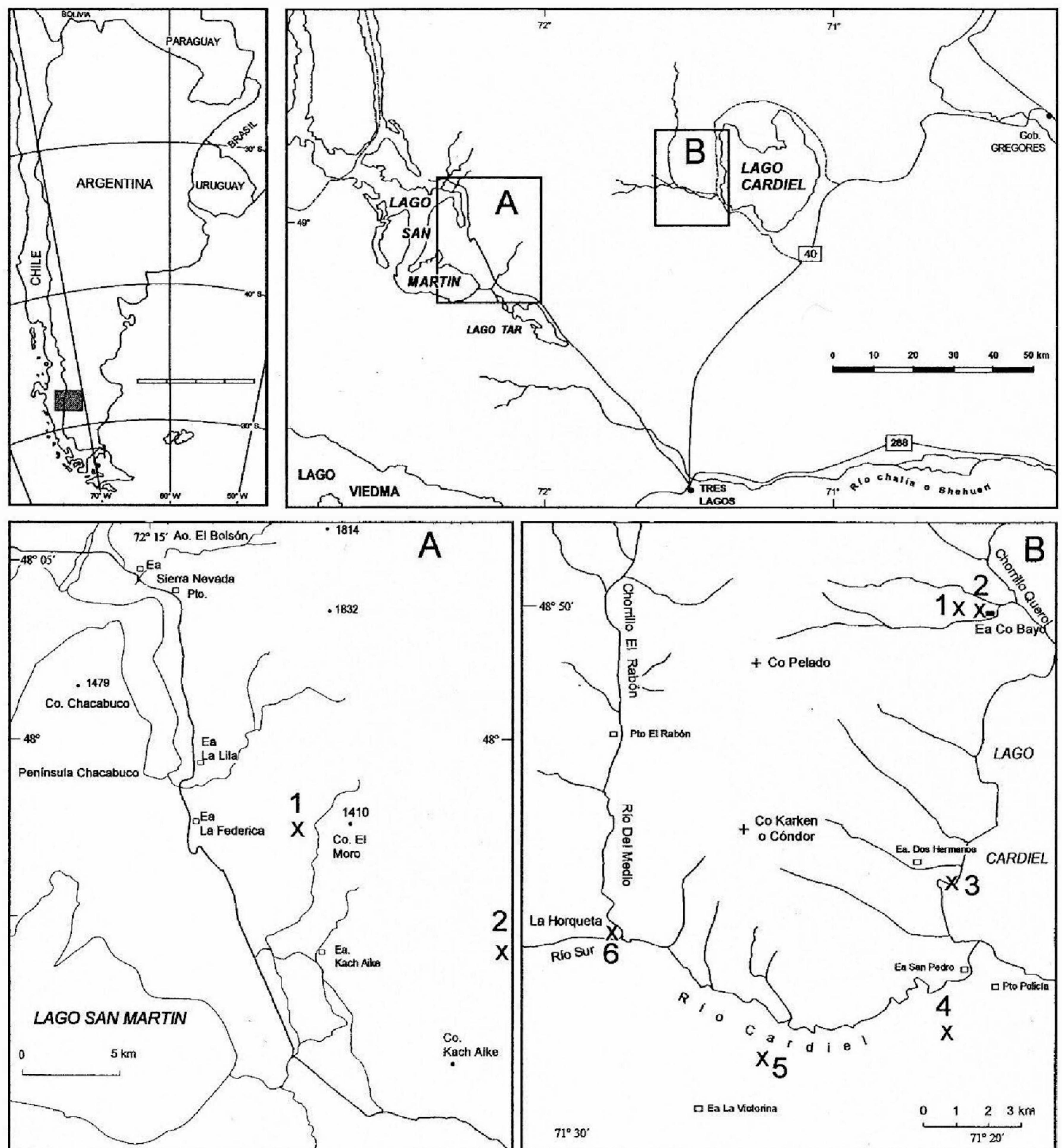
c. 680 m above base, concretions with *Aioloceras rollerii* (LEANZA) (Loc. A XXII 26; 19; 71-1, 5, 6, 20, 28; AC 1; M5; My, loose), and a single specimen of *Aioloceras argentinum* (Loc. 71-28, MLP 29074).

c. 650 m above base, concretions with *Aioloceras rollerii* (LEANZA). Loc. A XXII 22; 71-8, 22, 23; AC2; M4.

c. 635 m above base, concretions with *Aioloceras argentinum* (BONARELLI) and *A. rollerii*. Loc. 71-9; M3.

c. 580-635 m above base, concretions with *Aioloceras argentinum* (BONARELLI), *Rossalites imlayi* (LEANZA), *Puzosia recteradiata* COLLIGNON, *Maccoyella bonarellii* (LEANZA), [loose from same level: *Douvilleiceras* sp., *Protanisoceras* sp. and *Phylloceras* sp.]. Loc. A XXII 21; 71-13; AC4; M1, Mx.

Fig. 1: Index and locality maps of investigated region in Patagonia. A, Lago San Martin area; B, Lago Cardiel area. Locality numbers as in descriptions of stratigraphic sections.



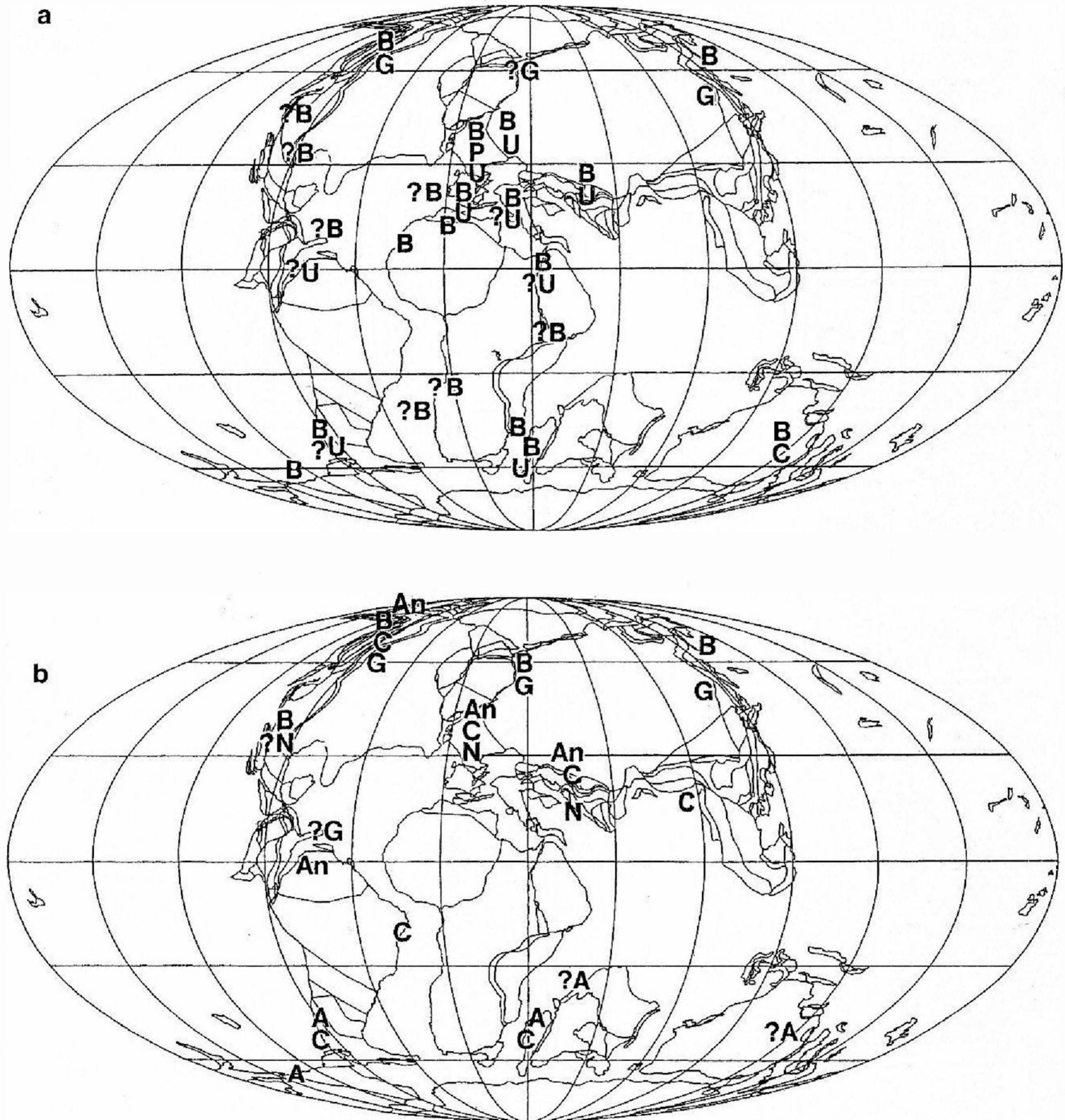
470-500 m above base, concretions with *Peltocrioceras deeckeii* (FAVRE), *Tetragonites heterosulcatus* Anthula, *Sanmartinoceras waslhense* (ETHERIDGE), *Sinzovia piatnitzkyi* and *S. leanzai* RICCARDI et al., *Ptychoceras* sp.  
410-460 m above base, abundant but crushed

*Helicancylus bonarellii* (LEANZA) and *Sanmartinoceras* sp.

Concretions with ?*Tropaeum* sp.

300-330 m above base, concretions with poorly preserved *Hatchericeras* sp.

Fig. 2: Geographic distribution of (a) Beudanticeratinae (B, *Beudanticeras* s.s.; C, *Cophinoceras*; G, *Grantziceras*; P, *Pseudorbulites*; U, *Uhligella*) and (b) Cleoniceratinae (A, *Aioloceras*; An, *Anadesmoceras*; B, *Brewericeras*; C, *Cleoniceras*; G, *Grycia*; N, *Neosaynella*) on the Albian globe. Distribution of continents after HAY et al. (1999).



135-150 m above base, essexite sill  
 90-135 m above base, crushed *Favrella wilckensi* (FAVRE), *Belemnopsis* sp.  
 55-90 m above base, very abundant but crushed *Favrella americana* (FAVRE), *Belemnopsis patagoniensis* (FAVRE).  
 11-55 m above base, *Belemnopsis* cf. *gladiatoris* WILLEY and *Belemnopsis* sp.

#### Springhill Formation

c. 100 m Brown-yellowish sandstones with intercalated tuffs and carbonaceous shales. In upper part with *Jabronella* aff. *michaelis* (UHLIG), *Neocosmoceras* sp., *Delphinella* sp., *Belemnopsis* spp., and bivalves.

#### El Quemado Complex Volcanic rocks.

2. *Estancia Kachaike*: About 6-8 km east of Estancia Kachaike (see Fig. 1). Locality described and figured by PIATNITZKY (1938, p. 52, fig. 2).

#### Kachaike Formation

Cliff of white-greenish sandstones, conglomerates and tuffs.

#### Río Mayer Formation

c. 80 m Dark-gray shales and marls. Base covered by Quarternary sediments.

60-65 m above base, level about 1 m thick of fine grained gray sandstone with *Aioloceras* aff. *rollerii* (LEANZA). Loc. KA1

c. 45 m above base, loose material of *Aioloceras* aff. *rollerii* (LEANZA). Loc. KA2

At base of section, loose material of *Aioloceras* aff. *rollerii* (LEANZA). Loc. KA 3

#### Lago Cardiel

Lago Cardiel is located in west-central Santa Cruz Province (Fig. 1). The first geological and paleontological investigations of this area were made by PIATNITZKY (1938) and a summary was given by FERUGLIO (1949).

The next major geologic synthesis was by RAMOS (1982). Ammonites were described by LEANZA (1970), AGUIRRE URRETA (1985) and RICCARDI *et al.* (1987).

1-2. *Estancia Cerro Bayo*: 1. About 1 km west of Estancia Cerro Bayo. The exposed section belongs to the upper part of the Piedra Clavada Formation.

The section is about 50 m thick and consists of light, fine- to coarse-grained grey-green-yellowish sandstones, in part cross-bedded and with some interbedded conglomerates and tuffs.

At the base are 3 m of very fine-grained grey-green sandstones with dark brown concretions, yielding *Puzosia recteradiata* COLLIGNON and *Beudanticeras* sp.

2. Immediately to the north of Estancia Cerro Bayo. The section is about 50 m thick, is lithologically similar to that described above and belongs to the upper part of the Piedra Clavada Formation, but is more fossiliferous.

At the base are 3 m very fine-grained, grey-green sandstones with dark brown concretions, yielding *Puzosia recteradiata* COLLIGNON, *Beudanticeras* sp. and *Aioloceras argentinum* (BONARELLI).

3. *Bahía Estancia Dos Hermanos*: About 1.2 km southeast of Estancia Dos Hermanos. The exposed section corresponds to the upper part of the Piedra Clavada Formation. It consists of c. 10 m fine- to medium- grained, greenish-grey sandstone, at base yielding *Cleoniceras* sp.

4. *Puesto Policía*: About 1.8 km southwest of Puesto Policía. In this section the upper part of the Piedra Clavada Formation is unconformably overlain by the continental rocks of the Cardiel Formation.

The Piedra Clavada Formation consists of 75 m of fine- to coarse-grained, light greenish to yellowish brown sandstones.

At about 45 m are intercalated calcaeous concretions and limestones with *Beudanticeras revoili* (PERVINQUIERE), ?*Uhligella* sp. a, *Cleoniceras* cf. *santacrucense* LEANZA and *Pictetia ovalis* COLLIGNON.

5. *Estancia La Victorina*: The section exposed at this locality is 5 m thick and a lateral equivalent of the fossiliferous beds of loc. 4.

It consists of medium-grained, yellowish sandstones with concretions bearing *Beudanticeras revoili* (PERVINQUIERE), ?*Uhligella* sp. b.

6. *La Horqueta*: Upstream of Río Cardiel, about 0.4 km west of the confluence with Río del Medio.

#### Piedra Clavada Formation

c. 125 m At base are c. 30 m fine- to coarse-grained, light grey and grey-green sandstones, partly cross-bedded, interbedded with grey shales with coal.

At about 107 m above base are medium-grained, yellow-grey sandstones with *Beudanticeras* cf. *laevigatum* (J. de C. SOWERBY).

#### Río Mayer Formation

c. 242 m Dark grey shales with some interbedded sandstones.

Top 30 m are fine-grained, green grey

- sandstone with *Parasilesistes turici* (LEANZA).
- c. 210 m above base: level with *Phyllopachyceras* sp., *Lithancylus guanacoense* LEANZA, *Helicancylus patagonicus* (STOLLEY), *Toxoceratoides nagerai* (BONARELLI), *Peltocrioceras* sp.
- c. 170 m above base: fine-grained, grey sandstone with *Phyllopachyceras* sp., *Lithancylus guanacoense* LEANZA, *Helicancylus patagonicus* (STOLLEY), *Toxoceratoides nagerai* (BONARELLI), *Parasilesistes turici* (LEANZA).
- 150 m above base: level with *Hypacanthoplites* sp. and *Acanthoplites* sp.

Below are beds with *Tropaeum* spp., *Sanmartinoceras walshense* (ETHERIDGE) and *Sanmartinoceras* sp. cf. b

## BIOSTRATIGRAPHY AND AGE

The Albian of southern Patagonia has been divided into four assemblage zones on the basis of its ammonoids (see RICCARDI, 1984a, 1984b, 1988): the index species are *Aioloceras argentinum* (Lower Albian), *Sanmartinoceras patagonicum* (Middle Albian) and *Puzosia vegaensis* and *Mariella patagonica* (Upper Albian). Only the first two zones are present in the area and sections studied here.

The *argentinum* Assemblage Zone was characterized (RICCARDI, 1984a, b, 1988; RICCARDI *et al.*, 1987 by "Aioloceras argentinum" (BONARELLI), *Rossalites imlayi* (LEANZA), *Beudanticeras* sp. and *Sinzovia leanzai* RICCARDI *et al.*"; the *patagonicum* Assemblage Zone by "Sanmartinoceras patagonicum", *Feruglioceras piatnitzkyi*, *Beudanticeras rollerii*, *Cleoniceras santacrucense*" (RICCARDI, 1984a, b, 1988; RICCARDI *et al.*, 1987).

The present study has shown that in the La Federica section, Lago San Martin, 1) all material previously included in "Beudanticeras sp." and "Beudanticeras rollerii" belongs to *Aioloceras rollerii*, and 2) that the levels with *Aioloceras rollerii* are intermediate to those with *Aioloceras argentinum* and *Sanmartinoceras patagonicum*. It is therefore possible to refine the regional biostratigraphic scheme by proposing a new biozone, i.e. *Aioloceras rollerii* Assemblage Zone, between the *argentinum* and *patagonicum* Assemblage Zones (Fig. 3).

Levels from Estancia Kachaike and lago Cardiel (North of Cerro Bayo) bearing *Aioloceras rollerii* (from Ugarte's collection), are correlated with those from La Federica yielding that species. The horizon that in Lago Cardiel (Puesto Policia and la Victorina) contained *Beudanticeras revoili*, *Cleoniceras* cf. *santacrucense*, *Pictetia ovalis* and ?*Uhligella* spp. is also characterized

by *Anopaea* sp., a bivalve that north of Cerro Bayo occurs 10 m above the level with *Aioloceras argentinum*. The stratigraphic position of *Beudanticeras cf. laevigatum* at La Horqueta suggests that this horizon is older than the *Aioloceras argentinum* level at the north of Cerro Bayo.

As a result the *argentinum* Zone is characterised by: *Aioloceras argentinum*, ?*Aioloceras* sp., *Puzosia recteradiata* COLLIGNON, *Rossalites imlayi* (LEANZA), *Phylloceras* sp. and, perhaps, *B. cf. laevigatum* (J. de C. SOWERBY), *Douvilleiceras* sp. and *Protanisoceras* sp. Whilst the *rollerii* Assemblage Zone is characterised by the nominal species and perhaps by *Cleoniceras* sp., *Cleoniceras santacrucense* (LEANZA), *Beudanticeras revoili* (PERVINQUIERE), *Beudanticeras* sp., ?*Uhligella* sp. a, ?*Uhligella* sp. b and *Pictetia ovalis*.

In the Lower Albian of Europe, *Beudanticeras* and *Cleoniceras* are mainly present in the Chalensis and Auritiformis (= Perinflata to Steinmanni) Zones (Subzones) of the Mammillatum Superzone.(Zone) (see OWEN 1988a). *Uhligella* is known to range from the Upper Aptian to the Middle Albian. *Beudanticeras laevigatum* (J. de C. SOWERBY) is a species recorded (see CASEY, 1961b; OWEN, 1988a) from levels coeval to the Auritiformis Zone of the Mammillatum Superzone. *Cleoniceras morgani*, a species closely related to *C. santacrucense*, has been recorded (see OWEN, 1988a) from the Chalensis Zone. Absence of hoplitid representatives, however, hinder a close correlation with the European zonal scheme. Although some faunal links can be established through similarities with Madagascar, the only region in the Southern Hemisphere with abundant figured Albian faunas (including Tethyan representatives; see BESAIRIE & COLLIGNON, 1971).

Of the Lower Albian biozones recognised in Madagascar (see COLLIGNON, 1963, 1976), the lowest, i.e. the "Pseudosonneratia sakalava" Zone, has been correlated (OWEN, 1988b) with the Leymeriella acuticostata Standard Subzone, Tardefurcata Standard Zone of Europe. The "Cleoniceras besairiei" (recte *Aioloceras besairiei*) Zone, where *Aioloceras* is more abundant and *Beudanticeras revoili* occurs, is regarded as coeval with the Chalensis (or Perinflata to Floridum) Zone(s). *Rossalites* and *Uhligella* spp. as well as *Puzosia recteradiata* COLLIGNON, however, characterize the "Lemuroceras spathi" and *Brancoceras besairiei* Zone, which has been tentatively correlated (OWEN, 1988b) with the Steinmanni Zone at the top of the Mammillatum Superzone of Europe, although it contains taxa suggesting an earlier Mammillatum age (see OWEN, 1988a). Thus, in Europe *Rossalites* is present in the upper part of the Chalensis Zone (see DESTOMBES, 1979) and lower part of the Auritiformis Zone (see OWEN, 1988a).

*Pictetia ovalis* COLLIGNON is present in the

Fig. 3: Assemblage Zones of Albian ammonite of southern Patagonia and Madagascar compared with the European Chronozones.

STAGE		EUROPE		MADAGASCAR	PATAGONIA
ALBIAN	Upper	S.(S.) <i>dispar</i>		<i>N. madagascariense</i> <i>P. inflata</i>	<i>Mariella patagonica</i>
		<i>M. inflatum</i>		<i>H. binum</i> <i>D. cristatum</i>	<i>Puzosia vegaensis</i>
	Middle	<i>E. laetus</i>		<i>"O. acutocarinatum &amp; M. jacobi"</i>	<i>Sanmartinoceras patagonicum</i>
		<i>E. loricatus</i>			
		<i>H. dentatus</i>	<i>H. spathi</i> <i>L. lyelli</i>		
	Lower	<i>D. mammillatum</i>	<i>O. auritiformis</i> <i>S. chalensis</i>	( <i>L. spathi</i> & <i>B. besairiei</i> ) <i>Douvilleiceras inaequinoctium</i> "Aioloceras besairiei"	<i>Aioloceras rollerii</i>
		<i>L. tardefurcata</i>	<i>L. regularis</i> <i>L. acuticostata</i> <i>L. schrammeni</i>	"Pseudosonneratia" <i>sakalava</i>	<i>Aioloceras argentinum</i>

"*Lyelliceras lyelli*" Zone of Madagascar (COLLIGNON, 1963), a zone that in Europe is at the base of the Middle Albian.

*Protanisoceras* in Madagascar occurs above the Zone of *A. besairiei*, i.e. in the Zones of "*Douvilleiceras inaequinoctium*" and "*Lyelliceras spathi*" and "*Brancoceras besairiei*".

A fauna coeval to that of the Patagonian *argentinum* and *rollerii* Zones is probably present in the "Albian III" of South Africa (see KENNEDY & KLINGER, 1975, p. 276), although thus far it has not been described.

Another area in the Southern Hemisphere from which where similar faunas have been recorded, is in the Great Artesian Basin of Australia. There, *Beudanticeras* occurs in levels dated as late Early Albian (see DAY, 1969, p. 160), although the presence of *Aioloceras* is doubtful because the material figured by DAY (1974) comes from Aptian levels and that of GREGORY & SMITH (1902) is of uncertain provenance (see DAY, 1974, p. 16).

Elements of this fauna are also present in Antarctica. Thus, *Beudanticeras* aff. *revoili* (PERVINQUIERE) has been recorded (THOMSON, 1984a, b) from a concretion in conglomerates of James Ross Island. *Aioloceras argentinum* is also present in this island, found *in situ* at the type section of the Kotick Point Formation and in a derived concretion at Whisky Bay (MEDINA *et al.*, in press).

According to the occurrences mentioned above, the *argentinum* and *rollerii* Zones are coeval to the Mammillatum Standard Superzone, most probably to the upper Chalensis and lower Auritiformis Standard Zones. But there is evidence for younger levels, up to the base of the Middle Albian.

## SYSTEMATICS

**Terminology:** Phr., phragmocone; b.ch., body chamber. Conventional dimensions (D, H, W, U) of specimens in

mm. Ribs: number of P, primaries, and S, secondaries, per half-whorl.

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**Order Ammonitida ZITTEL, 1884**  
**Suborder Ammonitina HYATT, 1889**  
**Family Desmoceratidae ZITTEL, 1895**  
**Subfamily Beudanticeratinae BREISTROFFER, 1953**

**Comments:** When introducing the Subfamily Beudanticeratinae, BREISTROFFER (in BREISTROFFER & VILLOUTREYS, 1953, p. 74) only mentioned its type genus, *Beudanticeras*, and introduced the subgenus *Pseudorbulites* (type species *Uhligella convergens* JACOB, 1908, pl. 2, fig. 25). WRIGHT (in ARKELL *et al.*, 1957, p. 368-369, and in WRIGHT *et al.*, 1996, p. 78-82) included in this Subfamily *Zuercherella* CASEY (Barremian-Aptian), *Uhligella* JACOB (U. Aptian - M. Albian), and *Cophinoceras* WHITEHOUSE (incl. *Beudantiella* BREISTROFFER, 1947). *Boliteceras* WHITEHOUSE was first (in ARKELL *et al.*, 1957) considered as a probable synonym of *Beudanticeras*, but later (in WRIGHT *et al.*, 1996) tentatively recognized as a valid genus of this Subfamily, whilst *Grantziceras* IMLAY (1961) was placed as a subgenus in *Beudanticeras*. Other genera first placed in the Subfamily, such as *Pseudosaynella* SPATH and *Brewericeras* CASEY, were later (in WRIGHT *et al.*, 1996) transferred respectively to the *Pseudosaynellinae* and *Cleoniceratinae*.

The Albian genera “*Boliteceras*” and *Cophinoceras* appear to be restricted to Australia. Material referred to “*Boliteceras*” WHITEHOUSE, 1928, i.e. *B. daintreei* (ETHERIDGE, 1872, pl. 24, fig. 1, apert. view; refigured in ETHERIDGE, 1892, p. 495, pl. 29, fig. 1; WHITEHOUSE, 1928, p. 203, pl. 26, fig. 2; HILL *et al.*, 1968, p. K18, pl. K8, fig. 4), including “*B. perlatum*” WHITEHOUSE (1928, p. 204, pl. 26, fig. 3; same specimen as in ETHERIDGE, 1872, pl. 24, fig. 1, lateral view and ETHERIDGE, 1892, p. 495, pl. 29, fig. 2; refigured in WRIGHT *et al.*, 1996, fig. 61.4), is quite close to that included in *Beudanticeras mitchelli* (ETHERIDGE, 1872, p. 345, pl. 23, fig. 1, including “*B. flindersi*” WHITEHOUSE, 1928, pl. 25, fig. 3). The supposed distinction of “*Boliteceras*” from *Beudanticeras* on the basis of slight differences in ornament (see WHITEHOUSE, 1928, p. 203) or a more rounded venter (WRIGHT, *in* WRIGHT *et al.*, 1996, p. 81) are hardly acceptable, and it could be considered a synonym of the later.

An Australian genus probably related to *Beudanticeras* is *Cophinoceras* WHITEHOUSE, 1928 (= *Beudantiella* BREISTROFFER, 1947), type species *C. ogilviei* (WHITEHOUSE, 1928, p. 205, pl. 26, fig. 4). The sparse and nearly straight ribs present on the flanks of this species are reminiscent of the ridges present in *B. beudanti*, but the latter has short intercalatories on the upper flanks. Species and genus are insufficiently known to assess the taxonomic significance of these features.

Thus, the Albian Beudanticeratinae appear to consist mainly of *Beudanticeras* and *Uhligella*. *Beudanticeras* is almost pandemic being present throughout Europe, northern Africa, Mozambique, Madagascar, USA, Australia, Antarctica and Patagonia, although records outside the Mediterranean are rather sparse and in some cases doubtful.

However, most North American representatives of *Beudanticeras* belong to the subgenus *Grantziceras*. *Grantziceras* IMLAY (1961, p. 56), type species “*G. multiconstrictum*” IMLAY (1961, pl. 14, fig. 1; pl. 15, figs. 1-12; 1960, p. 105, pl. 14, figs. 1-2), was distinguished as a subgenus of *Beudanticeras* by its numerous, regularly spaced, falcoid constrictions in the juvenile. Similar features are shown by the only other species from North America included in this subgenus, i.e. *B. (G.) affine* (WHITEAVES, 1892, p. 113, pl. 8, pl. 11, figs. 1-1a; WARREN, 1947, p. 121, pl. 30, figs. 3-4), which was considered as a senior synonym of *G. multiconstrictum* by JONES (*in* JONES & GRANTZ, 1967, p. 31). Both species were compared by IMLAY (1961, p. 57) with “*B. ligatum* (NEWTON & JUKES-BROWN)” (*recte B. newtoni*, see below) as figured in SPATH (1923, pl. 3, figs. 3a-d), and said to differ in the stouter whorls, and the stronger and regular presence of constrictions.

The diagnosis of *Grantziceras* was revised by JONES (*in* JONES & GRANTZ, 1967, p. 30-31) who considered the subgenus to include specimens with and without constrictions. In his opinion the diagnostic feature between *Grantziceras* and *Beudanticeras* s.s. is the nature of the umbilicus, which is narrow and funnel shaped in *Grantziceras*. JONES (*in* JONES & GRANTZ, 1967) recognized two species within this subgenus, i.e. *G. affine* and *G. glabrum*, distinguished by the less complex septal suture, higher whorl compression, more angular umbilical shoulder and less pronounced constrictions in *B. glabrum*. Thus *G. glabrum* is in fact closer to *Beudanticeras* s.s.

*B. glabrum* (WHITEAVES, 1889, p. 172, pl. 24, fig. 1; WARREN, 1947, p. 121, pl. 30, figs. 1-2, ?5; IMLAY, 1960, p. 105, pl. 16, fig. 19) appears to be a species of *Beudanticeras* that is characterized by the narrow umbilicus, the relatively rounded whorl section with maximum width at mid-flank, and by the almost smooth flanks bearing striae and riblets and barely visible constrictions, which begin in intermediate growth stages. The presence of this species in Spitzbergen (NAGY, 1970, text-fig. 7a) can not be confirmed on the basis of a figured septal suture.

This species was included in *Grantziceras* by JONES (*in* JONES & GRANTZ, 1967, p. 31) and JELETZKY & STELCK (1981, p. 2), but, even with the redefinition of that subgenus as proposed by JONES (*in* JONES & GRANTZ, 1967), the species *glabrum* appears to be intermediate between both subgenera and could therefore be considered as an extreme variant of either subgenus.

The classification of *Grantziceras* as a subgenus of *Beudanticeras* is accepted here.

In *Grantziceras* was also included (see CASEY, 1961a; WRIGHT, *in* WRIGHT *et al.*, 1996) material from France described under “*Desmoceras (Uhligella) convergens*” by JACOB (1908, p. 29, pl. 2, figs. 24-26) that was transferred to *Pseudorbulites* by BREISTROFFER (*in* BREISTROFFER & VILLOUTREYS, 1953, p. 74; *nomen nudum* subsequently validated by CASEY, 1961b, p. 145). Although the material figured by JACOB (1908, pl. 2, figs. 24-26; refigured in KENNEDY *et al.*, 2000, fig. 43a-h) does not clearly show regular constrictions, these are visible from specimens illustrated by CASEY (1961b, text-fig. 46d-g) and KENNEDY *et al.* (2000, fig. 42w-y). Similarity between *Grantziceras* and *Pseudorbulites* is further enhanced by the stout section and funnel-shaped umbilicus that both have in common. *Pseudorbulites* was therefore considered as a synonym of *Grantziceras* by WRIGHT (*in* WRIGHT *et al.*, 1996), although KENNEDY *et al.* (2000, p. 165) placed it as a synonym of *Beudanticeras* s.s. On account of its stout section, funnel-shaped umbilicus, and stratigraphy it is probable that *Pseudorbulites* is a junior synonym of *Grantziceras*.

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Material from the Albian of Canada described as "*Proplacenticeras*" *sutherlandbrowni* McLEARN (1972, p. 56, pl. 8, fig. 3A, B) appears to have been correctly compared with *Beudanticeras*. The species was later designated as the type of "*Rapidoplacenticeras*" ALABUSHEV (1988, p. 110), but the North American material is hardly separable from *Beudanticeras* on account of its compressed, involute whorls with narrowly rounded venter and smooth flanks. Even if it is doubtful the inclusion in this species of the specimens figured by ALABUSHEV (1988, p. 111, fig. 1) because of their Cenomanian age, the Canadian material appears to be a true *Beudanticeras*. *Rapidoplacenticeras* is therefore a junior subjective synonym of *Beudanticeras*, as suggested by WRIGHT (in WRIGHT *et al.*, 1996, p. 81).

### Genus *Beudanticeras* HITZEL, 1905

(= *Boliteceras* WHITEHOUSE, 1928;  
*Rapidoplacenticeras* ALABUSHEV, 1988)

**Type species:** *Ammonites beudanti* BRONGNIART (1822, p. 610, pl. 7, fig. 2) from the Upper Albian of Rochers des Fiz, Haute-Savoie, France; original designation.

**Diagnosis:** Involute and compressed, flanks convex to flat; venter narrowly arched; smooth or with weak periodic ridges; usually with shallow to deep, falcate or biconcave constrictions; septal suture rather complex (modified from WRIGHT, in WRIGHT *et al.*, 1996, p. 80).

**History:** The genus *Beudanticeras* was introduced by HITZEL (1905, p. 875) in a footnote (year of publication of HITZEL's article is recorded on p. 865 of the Bulletin de la Société Géologique de France, Serie 4, Tome 2). In his opinion *Ammonites cleon* and *A. beudanti* were interrelated, but the name *Cleoniceras* PARONA & BONARELLI (1897, p. 83) was a poor proposal as there were doubts about the type material of the type species *A. cleon*. In passing he mentioned that *A. beudanti* would have been a better type ("main") species for the group, that should have been named *Beudanticeras*. Nevertheless, in the text and tables he used the name "*Cleoniceras Beudanti* BRONGN. sp.". JACOB (1907, p. 347-8) regarded HITZEL's name *Beudanticeras* as a "formal proposal", but then rejected it. Instead, he accepted the inclusion of "*A. beudanti*" in *Desmoceras* ZITTEL, 1884. Even if the type species of *Desmoceras* was *Ammonites latidorsatum* MICHELIN, as remarked by LEMOINE (1911, p. 181), *A. beudanti* headed the species list included in *Desmoceras* by different authors (see SARASIN, 1897; CHOFFAT, 1903; JACOB, 1907, 1908; PERVINQUIERE, 1907) and was still included in that genus by H. DOUVILLE (1916). Only ROMAN (1938, p. 401-403) clearly

defined *Ammonites beudanti* as "genotype" of *Desmoceras*. He (p. 403) stressed that there were different opinions about the type species of *Desmoceras*, and sided with LEMOINE (1911) and JACOB (1907) in accepting the original species group of ZITTEL (1884), headed by *A. beudanti*, as defining the type.

The name *Beudanticeras* was, however, adopted by KILIAN in 1915 (see ROMAN, 1938, p. 402) and subsequently used by BONARELLI & NÁGERA (1921), SPATH (1923), WHITEHOUSE (1928), COLLIGNON (1929), PASSENDORFER (1930), SEITZ (1932) and BREISTROFFER (in BESAIRIE, 1936), and is accepted as a valid genus.

**Comments:** The type species of *Beudanticeras*, *B. beudanti*, was reviewed by SPATH (1923, p. 49; see also KENNEDY, 1993). The lectotype, designated by SPATH (1923, p. 50; cf. KENNEDY, 1993, p. 235), was illustrated by BRONGNIART (1822, pl. 7, fig. 2), SPATH (1923, text-fig. 2) and KENNEDY (1993, figs. 1-2). Other specimens correctly referred to *B. beudanti* were figured by QUENSTEDT (1849, p. 222, pl. 17, fig. 10; refigured in SEITZ, 1932, pl. 17, fig. 3a-d) and DELAMETTE *et al.* (1997, pl. 14, fig. 8, pl. 18, fig. 3, pl. 38, fig. 4), from France; SPATH (1923, p. 49, pl. 2, fig. 4a-d; fig. 4a-b refigured in CASEY, 1961b, text-fig. 46a-c) from the Upper Albian of England; MARCINOWSKY & WIEDMANN (1990, p. 59, pl. 7, fig. 1) from the Middle-Upper Albian of Poland; SEYDEMAMI & IMMEL (1995, p. 388, fig. 30a-b; 1996, p. 11, pl. 1, figs. 4-7, pl. 2, fig. 4, pl. 6, figs. 5-6) from the Middle-Upper Albian of Iran; and by GEYER *et al.* (1997, p. 224, figs. 2e, 3e) from the Middle-Upper Albian of Egypt.

Doubtful records are those of PASSENDORFER (1921, p. 239, pl. 8, fig. 3; 1930, p. 645, fig. 14) from Poland; HAAS (1942, p. 165, pl. 42, fig. 2) from Angola; COLLIGNON (1966, p. 15, pl. 3, fig. 1) from Tarfaya, Morocco; SCHOLZ (1979, p. 68, pl. 13, fig. 1, 6) from Hungary; and of FÖLLMI (1989, p. 140, pl. 10, fig. 3) from Austria.

*B. beudanti* is characterized by the involute, compressed whorls with ogival venter and almost vertical umbilical wall; the smooth flanks with fine and slightly falcoid striae and periodic stronger and nearly straight ridges mainly on the upper flanks; and by the complex septal suture with wide and deep, asymmetric lateral lobe L. The only specimen of "*Beudanticeras sphaerotum* (Seeley)", figured by SPATH (1923, pl. 3, fig. 1a-c), is almost identical with *B. beudanti* and come from a similar level. The only difference was said to be in the more rounded venter, although transitional forms were mentioned. "*B. sphaerotum*" is here included in the synonym of *B. beudanti* as proposed by SCHOLZ (1979).

The only other Upper Albian "species" of *Beudanticeras* described and figured is "*B. subparadieri*" SPATH (1923, p. 62, pl. 4, fig. 2a-e; ?DIMITROVA, 1967, p. 147, pl. 74, fig. 1; ?FÖLLMI, 1989, p. 139, pl. 10, fig. 1). On account of its ribbing, which is more prominent than in any other *Beudanticeras*, this form probably belongs to *Uhligella walleranti* JACOB, 1908, as proposed by SCHOLZ (1979).

*Beudanticeras* appears to be more abundant in the Lower than in the Upper Albian. The first Lower Albian species of this genus described is *B. laevigatum* (J. de C. SOWERBY, 1827, p. 93, pl. 549, fig. 1; refigured by SPATH, 1923, text-fig. 13 and CASEY, 1961b, text-fig. 49) from England (see also SPATH, 1923, p. 55, pl. 3, fig. 2a-c; CASEY, 1961b, pl. 28, fig. 6a-b). The species is also known from the Lower Albian of St. Croix, Switzerland (PICTET & CAMPICHE, 1858-60, p. 227, pl. 40, fig. 1), (?)Russia (TRAUTSCHOLD, 1861, pl. 12, fig. 2), Austria (FÖLLMI, 1989, p. 139, pl. 9, fig. 14), and France (DELAMETTE *et al.*, 1997, pl. 22, fig. 7). A specimen from Pech de Foix, France, placed in this species by KENNEDY *et al.* (1997, p. 465, pl. 10, fig. 7) seems to belong in *B. newtoni* on account of its constrictions (cf. CASEY 1961b, pl. 29, fig. 2).

*B. laevigatum* is similar to *B. beudanti* but differs in the simpler septal sutures, slightly larger umbilicus, less acute venter and in the absence of periodic ridges on the flanks.

Associated with *B. laevigatum* are specimens included in *B. sanctaecrucis* (BONARELLI, in BONARELLI & NÁGERA, 1921), which are characterized by constrictions on the intermediate and outer whorls (see PICTET & CAMPICHE, 1858-1860, pl. 40, figs. 3-4). These constrictions are deeper and wider than in *B. dupinianum* (see below). CASEY (1961b, p. 160) noted a morphological transition between *B. sanctaecrucis* and *B. laevigatum*. However, the specimens referred to *B. laevigatum* usually consist of phragmocones with diameters at which constrictions are not yet present in *B. sanctaecrucis*. On these grounds the last could be a junior synonym of *B. laevigatum*.

A species closely related to *B. laevigatum* is *B. newtoni* CASEY (1961a, p. 591; 1961b, p. 147, pl. 26, fig. 12; pl. 27, figs. 2-5; pl. 28, figs. 7-8; pl. 29, fig. 2, text-fig. 47a-c, e-f), including "*B. ligatum* (NEWTON & JUKES-BROWN)" in SPATH (1923, p. 58, pl. 3, fig. 3a-b, e; see also SEITZ, 1932, pl. 17, fig. 4)), from the Mammillatum Zone of England, Austria (FÖLLMI, 1989, p. 139, pl. 10, fig. 2), France (?KENNEDY *et al.*, 1997, p. 464, pl. 1, figs. 9-10, pl. 4, figs. 1-4, pl. 5, figs. 10-11, pl. 8, figs. 3-5, 8-9; also including pl. 10, figs. 7-8, described as "*B. laevigatum*"), Kazakhstan (SAVE-LIEV, 1992, pl. 36, fig. 2), and Iran (SEYED-EMAMI & IMMEL, 1996, p. 12, pl. 1, fig. 3, pl. 2, figs. 1-2). Tentatively referred to this species was also poorly preserved material from two boreholes in the Atlantic,

one in the North Atlantic, 90 km west from the Iberian Peninsula (RENZ, 1979, p. 364, pl. 2, fig. 2a-b), and the other in the South Atlantic close to the Angolan coast (WIEDMANN & NEUGENBAUER, 1978, p. 711, pl. 2, fig. 2). The material from Austria (KENNEDY & KOLLMANN, 1979, p. 7, pl. 3, figs. 1-4, 6-7, 10) compared with this species, however, probably belongs to another genus, and was included by KENNEDY *et al.* (2000, p. 665) in "*Beudanticeras convergens* (JACOB)", type species of *Pseudorbulites* CASEY (see above).

*B. newtoni* has more compressed whorls with more rounded umbilical margins and a more acute venter than *B. laevigatum*, as well as a more complex septal suture and regular constrictions on intermediate growth stages. *B. newtoni* differs from *B. beudanti* in the less acute venter, simpler suture, well developed constrictions, absence of periodic ridges on the flanks and in the slightly larger umbilical diameter.

Specimens with slightly thicker whorls occurring together with *B. newtoni*, were included, in *B. dupinianum* (D'ORBIGNY) (lectotype in D'ORBIGNY, 1841, p. 276, pl. 81, figs. 6, 8; refigured in SPATH, 1923, p. 61, text-fig. 14 and CASEY, 1961b, p. 154, text-fig. 48a-g; for other specimens see SPATH, 1923, pl. 4, fig. 1a-d; CASEY, 1961b, pl. 26, fig. 11, pl. 27, figs. 6-8, pl. 28, fig. 5a-b, FÖLLMI, 1989, p. 138, pl. 9, fig. 13; AVRAM *et al.*, 1993, p. 292, fig. 13d; ?SEYED-EMAMI & IMMEL, 1996, p. 13, pl. 4, figs. 2-4; KENNEDY *et al.*, 1997, p. 465, pl. 1, fig. 1-4). This species is also slightly more evolute and has a slightly more complex suture and more prominent ornament. According to SPATH (1923, p. 60) there are transitions between both "species". This covariation in whorl thickness, coiling and ornament (also suture) probably is an example of the common intraspecific "Buckman Law of Covariation" (WESTERMANN, 1966). Therefore *B. newtoni* appears to be a junior subjective synonym of *B. dupinianum* (D'ORBIGNY).

Included in the range of *B. dupinianum*, as an extreme variant, could also be the specimen figured by CASEY (1961b, p. 155, pl. 27, fig. 8a-b) as "*Beudanticeras dupinianum* (D'ORBIGNY) var. *evolutum*", and that from Tunisia figured by PERVINQUIERE (1907, p. 133, pl. 5, figs. 16-17; and ascribed to "*Beudanticeras dupinianum* var. *africanum*" (see FALLOT, 1920, p. 35; CASEY, 1961b, p. 155; as "*B. africana*" and dated Late Aptian in KENNEDY *et al.*, 2000, p. 667). The specimen from the Albian of Spain referred to this last variety by ALMELA & DE LA REVILLA (1957, p. 25, pl. 6, fig. 2) is too small for sure identification. Material from Italy (BACCELLE & GARAVELLO, 1967, p. 93, pl. 1, fig. 2) compared with *B. dupinianum* differs in the regular ribbing from the type and other material now included in this species (see above).

The specimens from Madagascar placed by COLLIGNON (1963, p. 71, pl. 267, fig. 1163) in

"*Beudanticeras dupini* D'ORB. var. *percostata*", as well as the specimen considered as closely affiliated (COLLIGNON, 1950, p. 39, pl. 6, fig. 4), do not belong in this species and genus on account of differences in ribbing and umbilicus.

The specimen from the Albian of France figured by DESTOMBES *et al.* (1973, p. 62, pl. 3, fig. 8) and considered close to *B. dupinianum* is clearly different in ornament, whorl section and ribbing.

The morphologic range here ascribed to *B. dupinianum* matches that for *B. laevigatum*. The slight stratigraphic difference recorded in Europe for both species (see OWEN, 1988a) suggests examination of possible morphological criteria supporting an age difference. Alternatively the stratigraphic span of *B. laevigatum* could be enlarged to include all material discussed above.

*B. dupinianum* should also include the specimens from the Mammillatum Zone of France and England, and probably Madagascar, Austria and Iran, placed in "*Beudanticeras arduennense* BREISTROFFER" (1947, p. 79, for "*Ammonites dupinianus*" of DOUVILLÉ, 1911, pl. 218, fig. M; refigured in CASEY, 1961b, p. 154, text-fig. 48h; see also CASEY 1961b, p. 156, pl. 27, fig. 1; pl. 28, figs. 9-11; COLLIGNON, 1963, p. 74, fig. 1166; FÖLLMI, 1989, p. 138, pl. 9, fig. 12; SEYED-EMAMI & IMMEL, 1996, p. 12, pl. 2, fig. 3, pl. 4, fig. 1).

Closely related to *B. dupinianum* in coiling, whorl section and ornament is the specimen from the Mammillatum Zone of France figured by DESTOMBES (1979, p. 65, pl. 4-19, fig. 1a-b) under *B. perchoisense* DESTOMBES. It differs only in the stronger ventral projection of the constrictions and could possibly be a variety of *B. dupinianum* as understood in this paper.

A probably valid species comes from the Auritiformis and Dentatus Zones, slightly above *B. dupinianum*, i.e. *B. albense* BREISTROFFER (1947, p. 79, see PICTET in PICTET & ROUX, 1847, pl. 2, fig. 4, ?refigured in DELAMETTE *et al.*, 1997, pl. 38, fig. 3; PICTET & CAMPICHE, 1858-60, pl. 39, figs. 3-7; DESTOMBES *et al.*, 1973, p. 62, fig. 4a-b). This species may be present also in Madagascar (COLLIGNON, 1949, p. 58, pl. 11, fig. 2). *B. albense* differs from *B. dupinianum* by its more numerous and stronger constrictions throughout the ontogeny and the more convergent flanks.

In Europe, only two additional species of *Beudanticeras* have been recognized, *B. revoili* (PERVINQUIERE) and *B. bulbosum* CASEY. The figured material included in *B. bulbosum* CASEY (1961b, p. 156, pl. 28, figs. 3-4) consists of an incomplete phragmocone characterized by lateral ridges, and otherwise considered close to *B. dupinianum*. The inclusion of this species in *Beudanticeras* is doubtful; it could belong in *Uhligella*, as suggested by SEYED-EMAMI & IMMEL (1996, p. 14). *B. revoili* was originally described from the Lower

Albian of Tunisia (PERVINQUIERE, 1907, p. 131, pl. 5, figs. 13-15, text-fig. 48) and later identified from Poland (PASSENDORFER, 1930, p. 644, pl. 4, fig. 62a-b; refigured in MARCINOWSKI & WIEDMANN, 1990, fig. 25e, f), Spain (ALMELA & DE LA REVILLA, 1957, p. 25, pl. 6, fig. 1; MARTÍNEZ, 1979, pl. 1, fig. 4a-c; MARTÍNEZ, 1982, p. 79, pl. 6, fig. 6), Madagascar (COLLIGNON, 1950, p. 40, pl. 7, fig. 1; 1963, p. 71, 74, figs. 1164, 1167); Somalia (TAVANI, 1948, p. 36, pl. 8, fig. 4), and Egypt (MAHMOUD, 1955, p. 98, pl. 5, figs. 19-20). A specimen close to this species was also mentioned from the Albian of Ross Island, Antarctica (THOMSON, 1984a, b).

*B. revoili* is characterized by compressed whorls with almost flat and convergent flanks, angular umbilical margin and vertical wall, rounded venter and smooth flanks with barely visible constrictions, and complex septal suture.

Part of the material from Madagascar ascribed to *Beudanticeras* by COLLIGNON (1963 and in BESAIRIE, 1936) seems to belong in other genera. *B. besairiei* BREISTROFFER (in BESAIRIE, 1936, p. 156, pl. 15, figs. 17-18), *B. dupiniforme* (COLLIGNON, 1963, p. 78, pl. 270, fig. 1171) and *B. ampanihense* COLLIGNON (1963, p. 78, pl. 270, fig. 1170) have fairly strong ribbing, never observed in the figured European representatives of the genus. *B. caseyi* (COLLIGNON, 1963, p. 72, pl. 267, fig. 1165) has ribs less prominent but extending onto the outer flanks. Similar ornament is visible in specimens referred to *B. komihevitraense* COLLIGNON (1950, p. 41, pl. 6, fig. 3; 1963, p. 80, pl. 271, fig. 1172).

True *Beudanticeras* are the specimens from Madagascar and Mozambique described under *B. hourcqi* COLLIGNON (1949, p. 59, pl. 10, figs. 5-6; pl. 11, figs. 1a-b; 1963, p. 76, fig. 1169) and "*B. hirtzi*" COLLIGNON (1950, p. 42, pl. 8, fig. 1; FÖRSTER, 1975, p. 213, pl. 10, figs. 3-5). The latter is a junior subjective synonym of the former. *B. hourcqi* is closely related to, if not identical with (same type of constrictions), *B. laevigatum* (D'ORBIGNY). Also belonging in *Beudanticeras* are "*B. ambanjabense*" COLLIGNON (1963, p. 82, pl. 272, fig. 1174) and "*B. subrotundum*" COLLIGNON (1963, p. 82, pl. 272, fig. 1175). Both are closely interrelated and could also be placed in *B. hourcqi*, if not in *B. laevigatum*. Other true *Beudanticeras* is *B. rectisulcatum* COLLIGNON (in BESAIRIE, 1936, p. 192, pl. 21, figs. 10-11, text-fig. 10j). COLLIGNON compared it with *B. beudanti* and *B. laevigatum*, but the figured material is insufficient to identify its true affinities.

Material from Australia referred to *Beudanticeras* (see ETHERIDGE, 1872, 1892, 1901, 1902; WHITEHOUSE, 1928; HILL *et al.*, 1968) consisted on a few specimens which were refigured repeatedly and in part were subsequently placed in "*Boliteceras*" WHITEHOUSE, 1928, a junior subjective synonym of

*Beudanticeras* (see above under Beudanticeratinae). Commonly placed in *Beudanticeras* are *B. mitchelli* (ETHERIDGE, 1872, p. 345, pl. 23, fig. 1; refigured in ETHERIDGE, 1892, pl. 30, fig. 1 and WHITEHOUSE, 1928, p. 201, pl. 25, fig. 2), "*B. flindersi*" (MCCOY) (see WHITEHOUSE 1928, pl. 25, fig. 3) and *B. sutherlandi* (ETHERIDGE, 1872, p. 345, pl. 21, fig. 4; refigured in ETHERIDGE, 1892, p. 496, pl. 29, fig. 4; WHITEHOUSE, 1928, p. 202, pl. 25, fig. 4; HILL *et al.*, 1968, p. K20, pl. K9, fig. 2). The first two "species", closely interrelated and probably synonymous, are characterized by almost smooth flanks with periodic, almost straight ridges, reminiscent of the ornament found in *B. beudanti*. The only specimen referred to *B. sutherlandi* is characterized by smooth flanks with constrictions that become wider and deeper towards the aperture. This features indicated affinity to *Anadesmoceras*. Other material from Australia placed in *Beudanticeras* was included in "*B.* *ingente*" WHITEHOUSE (1928, p. 202, pl. 25, fig. 1), a species illustrated only in a lateral view. Original description and figure rather suggest the genus *Desmoceras*. Features closer to *Desmoceras* than *Beudanticeras* are also shown by "*Beudanticeras* sp." HENDERSON (1990, p. 112, fig. 2L-S).

*Beudanticeras* has also been recorded from Japan, i.e. "*Beudanticeras shikokuense* YABE and SHIMIZU" of SHIMIZU (1931, p. 26, pl. 4, figs. 5-6). This material was correctly transferred to *Desmoceras (Pseudouhligella)* (see OBATA & MATSUMOTO, 1977; HIRANO *et al.*, 1977).

In North America, *Beudanticeras* was recorded repeatedly (see ANDERSON, 1938, p. 189-191), but almost all material was later transferred to other genera, e.g. *Brewericeras* CASEY, 1954; "*Leconteites*" CASEY, 1954; *Grantziceras* IMLAY, 1961. WHITEAVES (1884, p. 205, pl. 26, fig. 1) had even described the type species, *B. beudanti*, on material that was later placed in *Desmoceras (Pseudouhligella) dawsoni* (WHITEAVES) (see MATSUMOTO, 1959, p. 59; McLEARN, 1972, p. 45). A species included in *Brewericeras* by CASEY (1954, p. 112), *A. haydeni* GABB (1864, p. 62, pl. 10, fig. 8, 8a; ANDERSON, 1958, p. 212, pl. 8, fig. 1, 1a; MURPHY & RODDA, 1960, p. 851, pl. 104, fig. 4; pl. 105, figs. 1-2), was tentatively transferred to *Beudanticeras* by ANDERSON (1958, p. 212) and by MURPHY & RODDA (1960, p. 851; 1996, p. 245), a conclusion upheld by JONES *et al.* (1965, p. F15). Although the scarce material makes it impossible to arrive at a definite conclusion, we support for now the transfer of *A. haydeni* to *Beudanticeras*. SCOTT (1940) stated that the holotype of *Beudanticeras hatchetense* SCOTT (1940, p. 1000, pl. 56, figs. 3-5) from New Mexico, USA, has features close to those of "*B. ligatum*" (= *B. newtoni*). Material from Mexico referred to this species by YOUNG (1993, p. 167, figs. 2: 4-6,

14-15, 3: 5, 7) appears to differ by the presence of umbilical nodes.

Now excluded from *Beudanticeras* are "*B. robustum*" WARREN (1947, p. 122, pl. 30, figs. 7-8) and "*B. diablocense*" ANDERSON (1958, p. 214, pl. 10, fig. 4; GABB, 1869, pl. 22, fig. 13) because of the thick whorls. *B. victoris* STOYANOW (1949, p. 127, pl. 18, figs. 18-21) is a doubtful *Beudanticeras*. Its inner whorls have sigmoidal ridges of varying prominence suggesting affinity with *Uhligella walleranti* (see STOYANOW, 1949, p. 127). "*B. argonauticum*" and "*B. alamoensis*" ANDERSON (1958, p. 213, pl. 9, figs. 1-2 and pl. 5, fig. 2, 2a) were correctly included in *Desmoceras (Pseudouhligella)* by MATSUMOTO (1959, p. 59).

*Beudanticeras* has also been reported from the Caribbean (WIEDMANN, 1978, p. 362, fig. 2A-B), although the material is too poor to confirm its presence in that area.

In India, a few specimens were placed in "*A. beudanti*" by STOLICZKA (1865, p. 142, pl. 71, figs. 1-4; pl. 72, figs. 1-2) and later referred to "*Puzosia stoliczkai*" by KOSSMAT (1895, p. 119, pl. 18, fig. 6) or *Desmoceras* by JACOB (1905, p. 404). BONARELLI (*in* BONARELLI & NÁGERA, 1921, p. 23) placed "*P. soliczkai*" in *Beudanticeras*, but it was subsequently transferred to *Bhimaites* MATSUMOTO, with additional records from the Lower Cenomanian of Madagascar (COLLIGNON, 1961, 1964), the Upper Albian of South Africa (CRICK, 1907; VENZO, 1936), Sardinia (WIEDMANN & DIENI, 1968), Spain (WIEDMANN & BOESS, 1984), Venezuela (RENZ, 1972, 1982) and Iran (DOUVILLE, 1904). No other record of *Beudanticeras* is known from India.

***Beudanticeras cf. laevigatum* (J. de C. SOWERBY, 1827)**

**Pl. I, fig. 4; Fig. 4a**

**Material:** 2 incomplete phragmocones, poorly preserved and partly embedded in matrix (MLP 29032, 29033) from La Horqueta, Lago Cardiel, col. F. MEDINA.

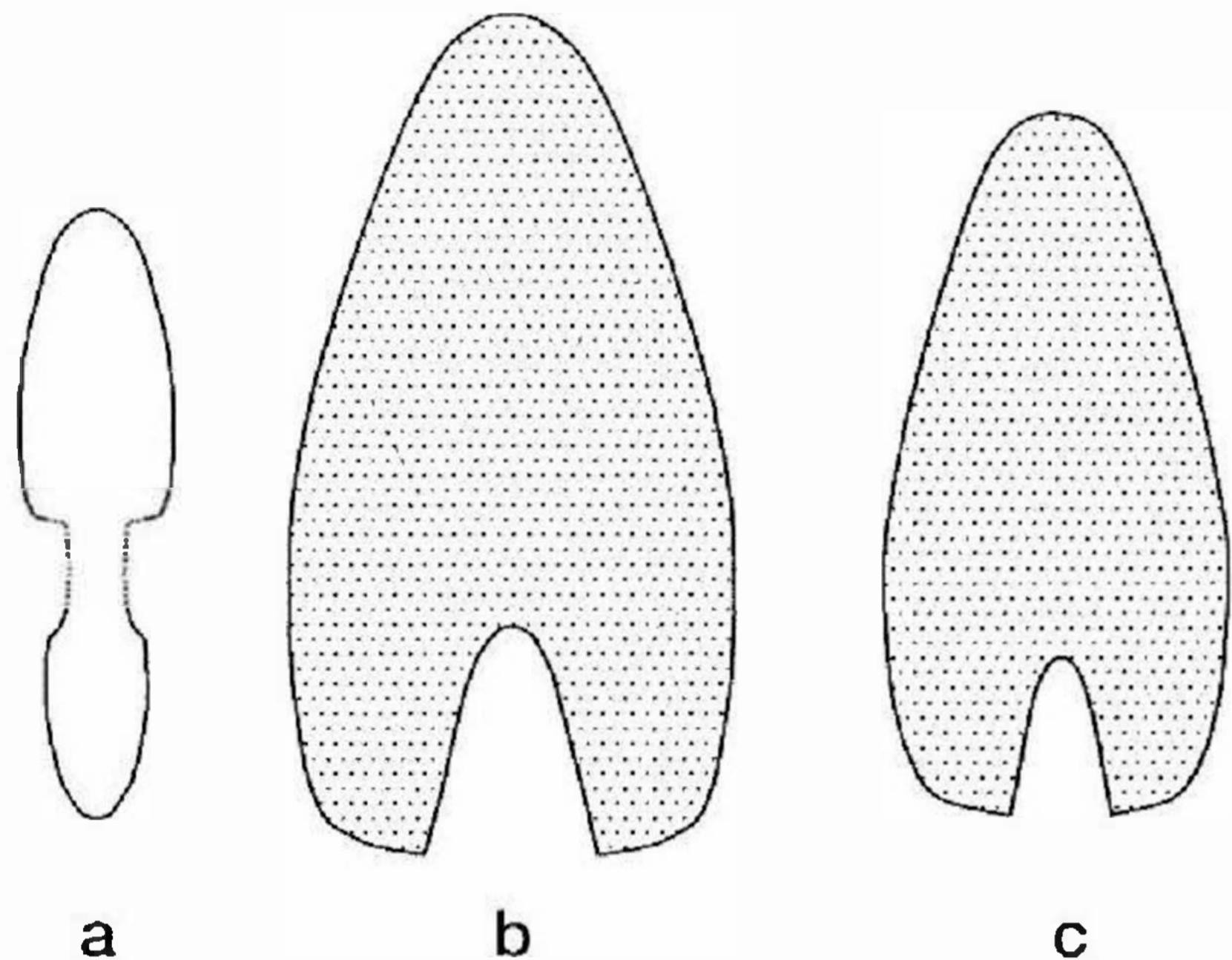
**Description:** Involute ( $U/D = 0.18$ ), with vertical umbilical wall and rounded margin, ovate compressed section ( $H/W = 2.16$ ) with slightly convex flanks, maximum width below mid-flank and converging to broadly rounded venter. Surface almost smooth with barely visible striae on the upper flank. Suture not available.

**Measurements (in mm):**

	D	H	W	U	H/W
MLP 29032, phr.	61	30.3(0.49)	14(0.23)	11.2(0.18)	2.16
MLP 29033, phr.	c.27.3	—	—	—	—

**Remarks:** The largest specimen available resembles *B. laevigatum* (J. de C. SOWERBY, 1827, p. 93, pl. 549, fig. 1; refigured in SPATH, 1923, text-fig. 13 and

Fig. 4: a, *Beudanticeras* cf. *laevigatum* (J. de C. SOWERBY), cross section (X1) of MLP 29032 (see Pl. I, fig. 4). b-c, *Beudanticeras* sp., cross sections (X1) of MLP 29034 (see Pl. II, fig. 2a-b).



CASEY, 1961b, text-fig. 49a-b; PICTET & CAMPICHE, 1858-60, pl. 40, fig. 1; SPATH, 1923, pl. 3, fig. 2a-c; CASEY, 1961b, pl. 28, fig. 6a-b and DELAMETTE *et al.*, 1997, pl. 22, fig. 7) in coiling, cross section and absence of ribbing, but is slightly more compressed.

*Beudanticeras revoili* (PERVINQUIERE, 1907)  
Pl. I, figs. 1-3; Pl. II, fig. 1; Pl. III, figs. 1-2; Figs. 5a-g

- 1907. *Desmoceras Revoili* PERVINQUIERE, p. 131, pl. 5, figs. 13-15, text-fig. 48.
- ?1913. *Uhligella Kiliani* PETKOVICH, p. 71, pl. 4, fig. 1, 1a, non 2, 2a.
- 1930. *Desmoceras Revoili* PERVINQUIERE.-PASSENDORFER, p. 644, pl. 4, figs. 62a-b, text-fig. 13.
- 1938. *Beudanticeras* cfr. *stoliczkai* KOSSM.-PIATNITZKY, p. 79, pl. 8, fig. 38.
- ?1948. *Desmoceras Revoili*; TAVANI, p. 36, pl. 8, figs. 4, B.
- 1950. *Beudanticeras Revoili* PERV.-COLLIGNON, p. 40, pl. VII(V), fig. 1a-b.
- 1955. *Beudanticeras Revoili* PERV. sp. var. *elegans* nov. var.- MAHMOUD, p. 98, pl. 5, figs. 19-20.
- 1957. *Beudanticeras revoili* PERVINQ.- ALMELA & DE LA REVILLA, p. 25, pl. 6, fig. 1, 1a, 1b.
- 1963. *Beudanticeras* sp. aff. *revoili* PERV.-COLLIGNON, p. 71, pl. 267, fig. 1164.
- 1963. *Beudanticeras revoili* PERV.-COLLIGNON, p. 74, pl. 268, fig. 1167.
- 1970. *Cleoniceras (Neosaynella) cardielense* LEANZA, p. 228, fig. 25.1-2.
- 1970. *Anadesmoceras constrictum* LEANZA, p. 253

- (for "B. cfr. *stoliczkai*" in PIATNITZKY, 1938, pl. 8, fig. 38).
- ?1979. *Beudanticeras ("Uhligella") rebouli* (JACOB).-MARTÍNEZ, p. 345, pl. 1, fig. 4a-c.
- ?1982. *Beudanticeras ("Uhligella") rebouli* (JACOB).-MARTÍNEZ, p. 79, pl. 6, fig. 6a-c, text-fig. 14 (same specimen as MARTÍNEZ, 1979).
- 1990. *Beudanticeras revoili* (PERVINQUIERE).-MARCINOWSKI & WIEDMANN, p. 59, fig. 25e, f (same specimen as PASSENDORFER, 1930).

**Lectotype:** Here designated, the specimen of PERVINQUIERE, 1907, pl. 5, fig. 15a-b, from the Lower Albian of Dj. Hamaina, Tunisia. FALLOT (1920, p. 35) mentioned the "type de PERVINQUIERE" in giving the proportions of one specimen. But these proportions are not in close agreement with any of those given by PERVINQUIERE (1907, p. 131). Only two of them agree with specimen I of PERVINQUIERE, but that specimen is the only one that, according to PERVINQUIERE, was not figured.

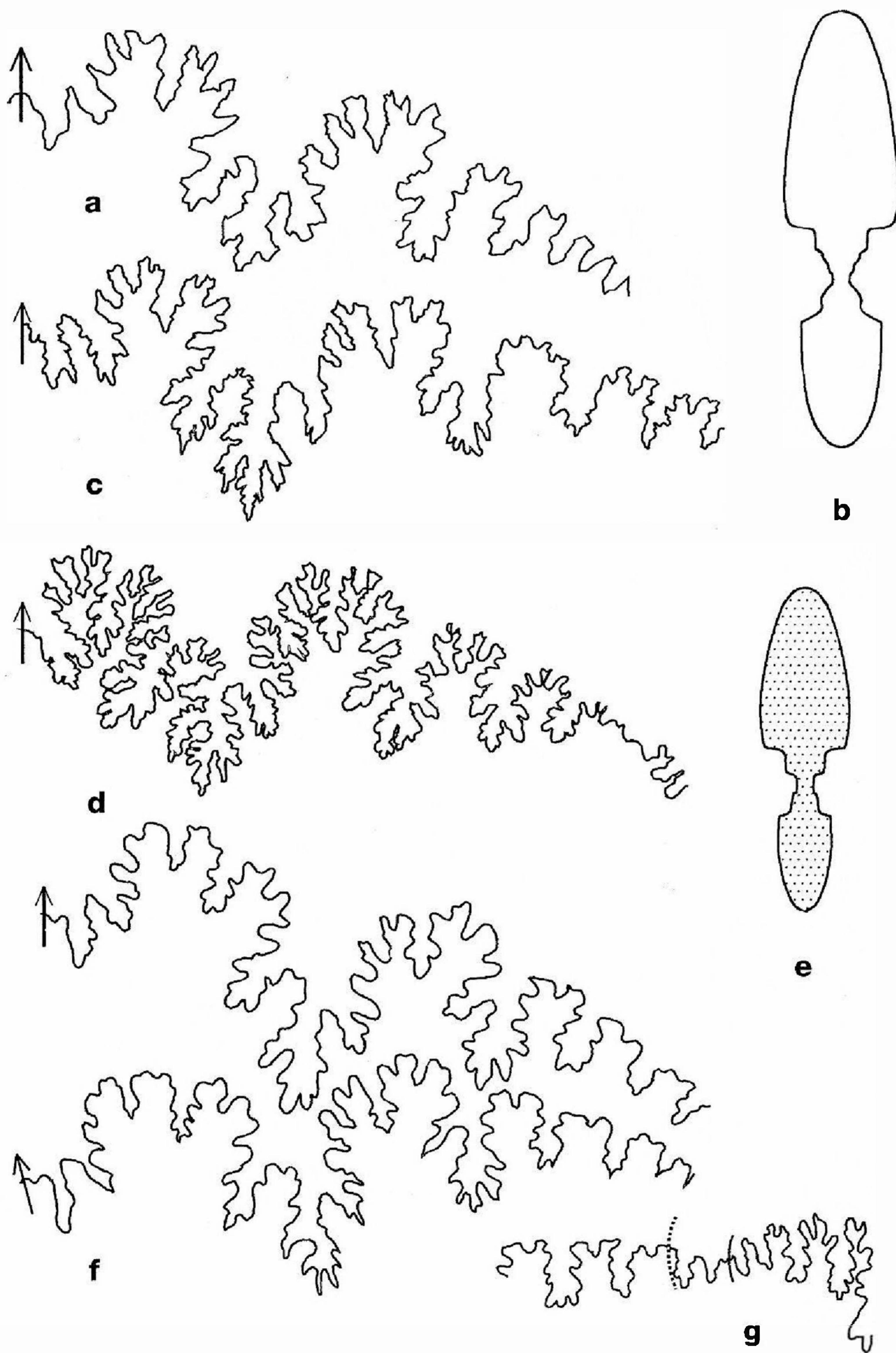
**Material:** The holotype of "*Cleoniceras (Neosaynella) cardielense*" LEANZA (1970), incomplete phragmocone (CPUNC 4316) from Lago Cardiel (?col. MARTÍNEZ CAL), here Pl. I, figs. 3a-c; 2 incomplete phragmocones (MLP 29026, 29027); 1 adult phragmocone with beginning of body-chamber (MLP 29029) and 1 complete adult with body-chamber (MLP 29031) from Puesto Policía, and 2 incomplete phragmocones (MLP 29025, 29028), 1 adult phragmocone with almost complete body-chamber (MLP 29030) from Estancia La Victorina, all Lower Albian Piedra Clavada Formation of Lago Cardiel (col. F. MEDINA); 1 incomplete phragmocone (MLP 16804), from Arroyo Estancia La Elena, H. ARBE col.

**Diagnosis.** Large *Beudanticeras*, umbilical wall vertical and with angular margin, inner flanks flat and subparallel, outer flanks gradually converging towards well narrowly rounded venter. Barely visible ribbing on inner whorls, later only striae and finally becoming smooth; weak constrictions. Suture complex with asymmetrically trifid L and 4-5 umbilical lobes.

**Description.** Inner whorls ( $D = 17.2$  mm) are moderately involute ( $U/D = 0.20$ ) with almost vertical umbilical wall and angular shoulder. Whorls are compressed ( $H/W = 1.39$ ) with maximum width near umbilicus; flanks converge gradually into narrowly rounded venter. Surface covered by barely visible falcoid ribbing with primaries restricted to inner flanks. Two secondaries are usually borne from each primary at mid-flank; they project and cross the venter forming an apicad arc. There are two very weak constrictions per whorl.

At larger diameter ( $D = 52-57$  mm), phragmocone coiling remains the same ( $U/D = 0.16 - 0.23$ ), but

Fig. 5: *Beudanticeras revoili* (PERVINQUIÈRE). **a-b**, suture at  $H = 36$  mm and cross section (X1) of holotype of "*Cleoniceras cardielense*" LEANZA, 1970 (see Pl. I, fig. 3a-c). **c**, suture at  $H = 59.7$  mm of MLP 29030 (see Pl. III, fig. 1a-b); **d-e**, suture at  $H = 61.4$  mm and cross section (X0.30) of MLP 29025 (see Pl. I, fig. 2); **f-g**, sutures at  $H = 12$  and  $20.7$  mm of MLP 29027 (see Pl. I, fig. 1a-e).



whorls become more compressed ( $H/W = 1.85 - 1.86$ ) by negative allometry of width ( $W/D = 0.27 - 0.28$ ), although shape is unchanged. Very blunt ornament is mainly restricted to a few riblets at mid-flank; surface is covered by fine, subdued striae; 1-2 poorly defined constrictions are also present on each whorl.

At diameters between 108 and 280 mm, whorls become still more compressed ( $H/W = 1.9 - 2.3$ ) by negative allometry of width ( $W/D = 0.22 - 0.25$ ). Surface has only fine striae and 2-3 constrictions per whorl. Striae form apertural concave arc on the umbilical wall and are prorsiradiate on flanks. Adult phragmocone reaches 154 - 281.8 mm in D.

Suture is highly indented with asymmetrically trifid L, twice as deep as E, and 4-5 umbilical lobes of decreasing size. Saddles are narrow and strongly indented.

Body-chamber is 1/2 - 2/3 whorl long and egresses gradually (final  $U/D = 0.25 - 0.26$ ). Whorls become more compressed ( $H/W = 1.9 - 2.4$ ) by negative allometry of width ( $W/D = 0.20 - 0.22$ ). Surface is covered by 2-3 projected constrictions with greater ventral projection, which vary from clear to barely visible, with well marked anterior margin when relatively well developed.

#### Measurements (in mm):

	D	H	W	U	H/W
<b>Holotype of "Cleoniceras cardielense LEANZA"</b>					
CPUNC 4316, phr.	83.3	42.1(0.50)	22.6(0.27)	16.5(0.20)	1.86
	59	29(0.49)	16.6(0.28)	13.4(0.23)	1.74
MLP 29029, adult					
b.ch.	348	139.5(0.40)	75(0.21)	91(0.26)	1.86
end phr.	281.8	126.5(0.45)	63.6(0.22)	58.8(0.21)	1.99
phr.	205.9	102.3(0.49)	45(0.22)	34.6(0.17)	2.27
MLP 29030, ?adult					
b.ch.	251.8	110(0.43)	50(0.20)	63.4(0.25)	2.2
end phr.	154	74.3(0.48)	37(0.24)	33.7(0.22)	2.0
phr.	93	47.4(0.51)	21.2(0.23)	20.5(0.22)	2.2
MLP 29025,					
phr.	180	89(0.49)	c.46(0.25)	32(0.18)	1.9
phr.	154.5	79.5(0.51)	—	27(0.17)	—
MLP 29027					
phr.	57	29.7(0.52)	c.16(0.28)	10(0.17)	1.85
	39.4	20 (0.50)	11.5(0.29)	7.3(0.18)	1.74
	22.1	13.4(0.60)	8.5(0.38)	5.1(0.23)	1.57
	17.2	8.8(0.51)	6.3(0.36)	3.5(0.20)	1.39
MLP 29028					
phr.	?108	53 (0.49)	27.6(0.25)	20.8(0.19)	1.9

**Comparisons:** Material of this species from Patagonia was first described by PIATNITZKY (1938, pl. 8, fig. 38) and LEANZA (1970), respectively under "*Beudanticeras cfr. stoliczkai*" and "*Cleoniceras (Neosaynella) cardielense*". LEANZA's specimen here refigured (Pl. I, fig. 3a-c) agrees in all features with other material from the same area available to us. As mentioned by LEANZA (1970, p. 229) there is no evidence of the tabulate venter present in *Neosaynella* CASEY (1954). Furthermore, *Neosaynella* is more involute, more compressed with more acute venter and with obscure crescents on outer flanks. *Neosaynella* is known only from Europe to central Asia. Poorly preserved material from North America, described by IMLAY (1961) as *N.*

*whittingtoni*, was transferred by NAGY (1970) to *Grycia*.

PIATNITZKY's specimen appears to be lost, but its provenance, figure, description and measurements agree quite well with the other material we here include in *B. revoili*. The figured specimen is not at natural size as indicated by PIATNITZKY (1938, p. 85), but reduced to about half. Constrictions appear deeper and wider in uncoated specimens, due to preservation, as shown in one body-chamber fragment available to us (MLP 29031).

PIATNITZKY's specimen, type of "*Anadesmoceras constrictum*" LEANZA (1970, p. 253) differs from *Anadesmoceras* in several features. For example, it has no ornament in the inner whorls; constrictions are shallower, narrower and restricted to the final stages of relatively large specimens; and the body-chamber is relatively narrow. In *Anadesmoceras* the inner whorls usually have striae or bundled riblets; constrictions tend to be deep and restricted or more prominent on the outer flank; and adult whorls change from narrowly arched to subrectangular with a broadly rounded venter (see JACOB, 1908, pl. 7, fig. 25; SPATH, 1923, pl. 4, fig. 6a-b; 1942, text-fig. 247; CASEY, 1954, fig. 2; 1966, pl. 90, fig. 5, pl. 95, fig. 1, pl. 96, figs. 1-5, pl. 97, figs. 6-7; SAVELIEV, 1973, pl. 8, fig. 1, pl. 13, fig. 3, pl. 14, figs. 1-3, pl. 15, figs. 2-3, pl. 17, figs. 3-4, pl. 19, fig. 2, pl. 20, fig. 1; ETAYO SERNA, 1979, pl. 10, figs. 1, 5, pl. 11, fig. 9).

The Patagonian material is indistinguishable from the *B. revoili* figured from Tunisia, Egypt, Spain, Poland and Madagascar (see PERVINQUIERE, 1907; PASSENDORFER, 1930; COLLIGNON, 1950, 1963; MAHMOUD, 1955; ALMELA & DE LA REVILLA, 1957; MARTÍNEZ, 1979, 1982; MARCINOWSKI & WIEDMANN, 1990).

Two specimens from Serbia, described as "*Uhligella Kiliani*" by PETKOVICH (1913, p. 71, pl. 4, fig. 1, 1a), and transferred to this species by BREISTROFFER (in BESAIRIE, 1936, p. 155) agree in whorl section and coiling, but appear to differ in ribbing.

This species is very distinctive. It differs from the similarly smooth *B. newtoni* by its flat flanks, angular umbilical margin, very feeble and less falcoid constrictions and the more slender sutural saddles (CASEY, 1961b, p. 151).

A "var. *elegans*" of *B. revoili* was distinguished by MAHMOUD (1955) on account of its more flexuous ribbing, but this is not evident from the figured material. *B. revoili* has also been recorded from Antarctica by THOMSON (1984a-b), but the material has not yet been described and/or figured.

#### *Beudanticeras* sp. Pl. II, figs. 2a-b; Fig. 4b-c

**Material:** One end of phragmocone and almost com-

plete body-chamber (MLP 29034) from west of Estancia Cerro Bayo, lago Cardiel, Santa Cruz; 1 incomplete phragmocone and (?)1 incomplete body-chamber and phragmocone (MLP 15911) from Rio Cardiel, H. ARBE col.

**Description:** Outer whorls are involute ( $U/D = 0.15 - 0.18$ ) with subvertical umbilical wall and rounded margin. Whorls are compressed ( $H/W = 2.75 - 2.41$ ) with arched flanks and maximum width below mid-flank. The upper flanks are almost flat and pass into a narrowly arched venter. Surface is smooth on internal mould and on some shell remnants. There are three shallow constrictions on the last third of the body-chamber. They are slightly flexuous, prorsiradiate on lower flank and with oral concave arch at mid-flank. Aperture is simple. Septal suture is poorly preserved but probably complex.

#### Measurements (in mm):

	D	U	H	W	H/W
MLP 29034, b. ch.	209 c.134	39(0.18) —	96.3(0.46) 65(0.48)	c.40 (0.19) 31.5(0.23)	2.41 2.06
MLP 15911, phr.	134	20(0.15)	71.4(0.53)	26(0.19)	2.75

**Remarks:** Lack of preserved inner whorls prevent us to assess the specific affinities of these specimens. In involution, compression and the smooth surface that is crossed only by faint constrictions, these specimens resemble material figured under *B. sanctae crucis* BONARELLI (see PICTET & CAMPICHE, 1858-60, pl. 40, figs. 3-4) and *B. newtoni* CASEY (1961b, pl. 27, figs. 2-4), but the constrictions of these two species differ by being deeper, in the first, and in shape, in the second. Furthermore, both species have different whorl sections, with maximum width in the lower third of the flanks. A similar whorl section as in the Patagonian material is present in *B. komihevitraense* COLLIGNON (1963, p. 80, pl. 271, fig. 1172), although the Madagascan species differs by its ribbing.

### Genus *Uhligella* JACOB, 1907

**Type species:** *Desmoceras clansayense* JACOB, 1905, p. 403, from the Upper Aptian of France, by subsequent designation of KILIAN (1907, p. 63) (see HOWARTH, 1974, p. 728).

**Diagnosis:** Whorls rather involute and high with broadly or narrowly rounded venter, flanks slightly convex to flat, and maximum width typically near umbilical edge; constrictions irregular and shallow; ribs more or less broad and blunt, sinuous, sometimes raised into umbilical bullae, with several intercalated ribs (modified from WRIGHT, in WRIGHT et al., 1996, p. 80).

**History and comments:** The genus *Uhligella* was introduced by JACOB (1907, p. 350) for several species in order of increased ornamentation, i.e. "*Uhl. seguenzae* COQ., *Uhl. zürcheri* JACOB et *Uhl. clansayense* JACOB". The type species, *U. clansayensis* (JACOB), from the Upper Aptian of France, was described by JACOB

(1905, p. 403, pl. 12, fig. 2a-b -holotype-, 3a-b) and repeatedly refigured (CASEY, 1961b, p. 162, text-fig. 50a-b, c-d; ARKELL et al., 1957, p. L369, fig. 482, 1a-b; ORLOV, 1958, pl. 50, fig. 4; WRIGHT, in WRIGHT et al., 1996, fig. 61, 3a-c). It is characterized by involute whorls with elliptical section, primary ribs with umbilical bullae and by constrictions. Specimens similar to *U. clansayensis* have also been described from the Aptian-Albian of the Baleares (FALLOT, 1920, p. 38, pl. 2, figs. 2-5; FALLOT & TERMIER, 1923, p. 27, 30, pl. 3, figs. 3-6). "*U.*" *seguenzae* and "*U.*" *zuercheri* are not congeneric with *Uhligella* and were included in *Zuercherella* CASEY (1954, p. 112; 1961b, p. 161). The genus *Uhligella* has been reviewed by CASEY (1949). He noted the variation in prominence and persistence of the ornamented juvenile stage. The most ornamented variants were referred (CASEY, 1949, p. 334) to *U. balmensis* JACOB (1908, p. 33, pl. 4, figs. 6-9), a species recorded from the Albian of France (see also KENNEDY et al., 1997, p. 465, pl. 6, figs. 4-5, 25-27; pl. 7, fig. 5; pl. 9, figs. 4-5; DELAMETTE et al., 1997, pl. 21, fig. 8), Poland (PASSENDORFER, 1930, p. 647, pl. 4, fig. 63; refigured in MARCINOWSKI & WIEDMANN, 1990, p. 61, pl. 6, fig. 8), Madagascar (COLLIGNON, 1950, p. 43, pl. 5, figs. 3-4; 1963, p. 71, pl. 267, fig. 1162; p. 74, pl. 268, fig. 1168) and Spain (ALMELA & DE LA REVILLA, 1957, p. 24, pl. 5, fig. 5). Specimens from France with relatively subdued costae were included in *U. rebouli* JACOB (1908, p. 32, pl. 4, figs. 1-5; see also DELAMETTE et al., 1997, pl. 38, fig. 2), as were specimens from the Baleares (FALLOT, 1910, p. 4, pl. 2, figs. 1-2), Poland (PASSENDORFER, 1930, p. 647, pl. 3, figs. 56a, 60a-b; refigured in MARCINOWSKI & WIEDMANN, 1990, p. 61, pl. 6, fig. 6a-c and fig. 7a-c), Spain (ALMELA & DE LA REVILLA, 1957, p. 24, pl. 5, fig. 4; MARTÍNEZ, 1982, p. 79, pl. 6, fig. 6), Italy (WIEDMANN & DIENI, 1968, p. 129, pl. 10, fig. 6) and Iran (SEYED EMAMI & IMMEL, 1995, p. 388, figs. 31, 32, 37). Material from Venezuela referred to this species (RENZ, 1982, p. 35, pl. 4, figs. 14-15) probably does not belong in this genus because of different ribbing. Material of this species from England was placed in "*Uhligella subornata*" CASEY (1949, p. 337, pl. 19, fig. 1; 1961b, p. 163, pl. 28, figs. 1-2).

Transitional morphs between *U. balmensis* and *U. rebouli* have been mentioned (CASEY, 1949), and there are "species" that could be placed within this transition, e.g. *U. derancei* CASEY (1949, p. 340, pl. 19, figs. 2-3; KENNEDY et al., 1997, p. 465, pl. 3, figs. 3-4); *U. sohensis* SEYED-EMAMI & IMMEL (1996, p. 14, pl. 3, figs. 1-3).

Specimens even smoother than those listed above, and with features similar to those of *Beudanticeras* were included in *U. walleranti* (JACOB, 1908, p. 31, pl. 3, figs. 1-4). The specimen figured by JACOB does not show umbilical tubercles, but they may have worne

away (see pl. 3, fig. 1). Similar material was figured by DOUVILLE (1916, p. 107, pl. 12, fig. 8, see BREISTROFFER *in BESAIRIE*, 1936, WIEDMANN & DIENI, 1968, p. 128) under "*Desmoceras beudanti*". Other material previously referred to this species either belongs elsewhere or is not good enough for identification. For example, the specimen from the Balearics (FALLOT, 1910, p. 77, pl. 3, fig. 5) seems to have a keel; those from Madagascar (COLLIGNON, 1929, p. 20-21, pl. 2, figs. 2-3; 1932, p. 10, pl. 1, fig. 7) are too small; others from Madagascar as well as Poland (BREISTROFFER, *in BESAIRIE*, 1936, p. 154, pl. 23, fig. 1; PASSENDORFER, 1930, p. 648-649, pl. 3, fig. 55a-b, refigured *in MARCINOWSKI & WIEDMANN*, 1990, p. 60, pl. 6, figs. 4-5) and Venezuela (RENZ, 1982, p. 35, pl. 4, figs. 12-13) show rather uncharacteristically strong ribbing on the flanks. It is, therefore, not clear if "*U.*" *walleranti* is an ornamented variant of *Beudanticeras* as proposed by CASEY (1949, 1961a) or a (relatively) smooth variant of *Uhligella*, as shown by material from Iran figured by SEYED-EMAMI & IMMEL (1996, p. 13, pl. 1, figs. 1-2, pl. 4, fig. 5).

Other smooth specimens have been included in *Uhligella*, such as those from the Barremian of Tunisia (PERVINQUIERE, 1907, p. 135, pl. 5, figs. 21-24) and the Aptian of Majorca (FALLOT, 1920, p. 36, pl. 2, fig. 1) figured under "*Uhligella monicae* COQ.". But their almost smooth flanks indicate that they do not belong in *Uhligella*.

Material from the Balearics referred to "*Uhligella bretoni*" FALLOT (1920, p. 41, pl. 2, fig. 6) does not belong in the genus, according to the presence of tubercles on the upper flanks, and the relatively strong ventral projection of the constrictions.

A doubtful *Uhligella* is *U. dubia* COLLIGNON (1949, p. 61, pl. 17, fig. 10) based in a specimen from Madagascar apparently without umbilical tubercles or bullae. *Uhligella* has also been recorded from North and South America. The record from the southern USA (SCOTT, 1940, p. 998, pl. 57, fig. 1) was, however, tentative because the figured specimen is poor. From the Aptian of Mexico, several specimens were figured under "*Uhligella aguilerae*" BURCKHARDT (1925, p. 10, pl. 2, figs. 4-6) and "*Uhligella jacobi*" BURCKHARDT (1925, p. 11, pl. 2, figs. 7-10; see also HUMPHREY, 1949, p. 154, pl. 18, figs. 5, 6, 9). Not only do they seem to belong in a single species, but most probably to *Zuercherella* CASEY. Other Mexican material included in *Uhligella* by BURCKHARDT as "*U. mexicana*" (1925, p. 10, pl. 3, figs. 1-3), does not belong to the genus, because of its ribbing and absence of umbilical bullae or tubercles, and could be a large form of "*U.*" *agUILerae*. The same species probably includes specimens figured under "*U. reesidei*" HUMPHREY (1949, p. 152, pl. 18, figs. 3-4) and "*U. riedeli*" HUMPHREY (1949, p. 153, pl. 18, figs. 1-2). "*U. mullerriedi*"

HUMPHREY (1949, p. 153, pl. 18, figs. 10, 13) is probably another *Zuercherella*, although umbilical bullae may be present.

Material from Venezuela compared with "*U. mullerriedi*" by RENZ (1982, p. 23, pl. 2, fig. 21a-b) has similar thickening of the ribs, although these appear to be less conspicuous and the inner whorls are smooth. Although this specimen resembles *Uhligella*, its generic placement remains doubtful. Material from Colombia referred to *Uhligella*, i.e. *U. latecostata* RIEDEL (1938, p. 21, pl. 5, figs. 1-3), is better placed in *Zuercherella*.

Material from Patagonia placed in *Uhligella* by BONARELLI (*in BONARELLI & NÁGERA*, 1921) is discussed below under *Aioloceras*.

*Uhligella* is mainly present in Europe, Madagascar, ?USA and ?Venezuela.

### ?*Uhligella* sp. a

Pl. III, figs. 3a-b; Fig. 6a

**Material:** One incomplete phragmocone (MLP 29036) and two phragmocone fragments (MLP 29035a-b) from Puesto Policía, Lago Cardiel; col. F. MEDINA.

**Description:** Whorls relatively involute (U/D = 0.23) with compressed ovate section (H/W = 1.54), marked umbilical margin and vertical wall, weakly convex flanks with maximum width near umbilicus and converging into narrowly arched venter. Flanks are smooth except near venter where ribs (c. 18/ 1/2 whorl) are blunt, prorsiradiate and with varying prominence and spacing. Constrictions are also present (c. 3/last 1/2 whorl) that deepen on venter. Septal suture is not available.

**Measurements (in mm):**

	D	H	W	U	H/W
MLP 29036 phr.	66.4	29.2(0.44)	19(0.28)	c.15.5(0.23)	1.54

**Remarks:** The Patagonian material is too poor for generic and specific identification. Coiling, whorl compression and ribbing on upper flanks are as in some specimens figured under *Uhligella rebouli* JACOB (see JACOB, 1908, pl. 4, figs. 1-2; MARCINOWSKI & WIEDMANN, 1990, pl. 6, fig. 7), but our material is more evolute and has more compressed whorl section. Specimens of *U. rebouli* with more compressed whorls (see WIEDMANN & DIENI, 1968, pl. 10, fig. 6a-b) have ribs on the inner flank also.

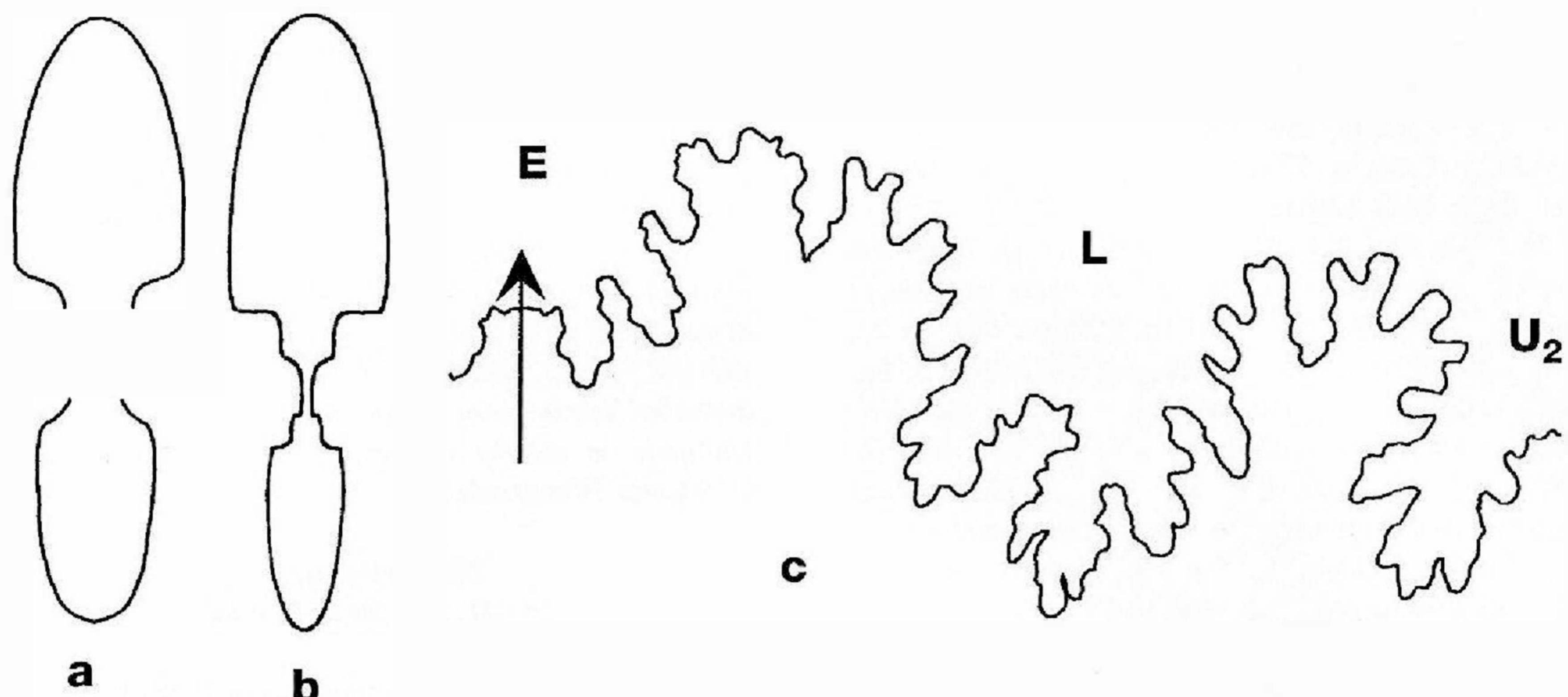
### ?*Uhligella* sp. b

Pl. II, figs. 3-4; Fig. 6b-c

**Material:** Two incomplete phragmocones (MLP 29037 a, b) from Estancia La Victorina, Lago Cardiel; col. F. MEDINA.

**Description:** Inner whorls (MLP 29037b) are quite involute (U/D = 0.16) with ovate section (H/W = 1.67), vertical umbilical wall and rounded margin, weakly convex flanks passing into a rounded venter. Barely

Fig. 6: a, ?*Uhligella* sp. a, cross section (X1) of MLP 29036 (see Pl. III, fig. 3a-b). b-c, ?*Uhligella* sp.b, cross section (X1) and suture at H = 18.1 mm of MLP 29037b (see Pl. II, fig. 3a-b).



visible primaries, prorsiradiate, some being slightly more prominent and forming a shallow apicad arc below mid-flank. Secondaries arising at different heights by twos and threes, weakly prorsiradiate on outer flank and subdued on venter. Outer septate whorls (MLP 29037a) are slightly more evolute ( $U/D = 0.20$ ), compressed ( $H/W = 2.09$ ), with less convex flanks and more narrowly rounded venter. There are only obscure striae on inner third of the flanks, except at  $D = c. 40$  mm where a few blunt prorsiradiate ribs are present. Striae on inner flank become denser and ribs more prominent on outer flank, where they are wider and form a shallow orad arc before crossing the venter. Shell surface becomes progressively smoother on the last third of the whorl.

#### Measurements (in mm):

	D	H	W	U	H/W	S
MLP 29037a, phr.	65.6	33(0.50)	15.8(0.24)	13.1(0.20)	2.09	-
	46.6	22(0.47)	c.11 (0.24)	9.3(0.20)	2.0	25
MLP 29037b, phr.	21.9	12(0.55)	7.2(0.33)	3.6(0.16)	1.67	28

**Remarks:** The sample is too small to assess the variability and taxonomic significance of the described features. The largest specimen resembles relatively highly ornamented variants of *U. walleranti* JACOB (see BREISTROFFER, in BESAIRIE, 1936, pl. 23, fig. 1; RENZ, 1982, pl. 4, figs. 12-13), but other similar specimens placed in that species appear to be smoother (see JACOB, 1908, pl. 3, fig. 1a-c; DOUVILLE, 1916, pl. 12, fig. 8).

duced by WHITEHOUSE (1926, p. 206) and included *Pseudosaynella* SPATH, *Aioloceras* WHITEHOUSE, *Cleoniceras* PARONA & BONARELLI, and *Sonneratia* BAYLE.

The Family has been reviewed by WRIGHT (in ARKELL *et al.*, 1957), CASEY (1966), SAVELIEV (1973) and OWEN (1988a), who placed it within the Hoplitaceae or Hoplitidae at the Family or Subfamily level respectively. Whilst JELETZKY & STELCK (1981) and WRIGHT (in WRIGHT *et al.*, 1996) placed it in the Desmocerataceae or Desmoceratidae. While it is beyond the scope of this paper to discuss this matter, we follow the last authors on account of its general morphology. Nevertheless, it is important to remark that, as pointed out by SCHINDEWOLF (1966, p. 623-624, 654) and JELETZKY & STELCK (1981, p. 2) sutural morphogeny indicates close relationship between Cleoniceratiniae and Beudanticeratiniae, and support their placement under the same Superfamily Hoplitaceae (see KULLMANN & WIEDMANN, 1970).

Number of genera and morphological diversity suggest Family rank, following OWEN (1988a) and WRIGHT (in WRIGHT *et al.*, 1996). It also seems advisable to adopt some type of Subfamily division such as that proposed by OWEN (1988a). The Cleoniceratiniae s. str. include discoidal to compressed and moderately involute shells with narrowly arched to acute venters; ornament consists of sigmoid to falcoid ribs originating in umbilical bullae.

*Aioloceras* WHITEHOUSE, 1926, certainly belongs here, as was first suggested by WHITEHOUSE (1926), followed by WRIGHT (in ARKELL *et al.*, 1957), JELETZKY & STELCK (1981, p. 4) and OWEN

**Family Cleoniceratidae WHITEHOUSE, 1926**  
**Subfamily Cleoniceratiniae WHITEHOUSE, 1926**

**Comments:** The Family Cleoniceratidae was intro-

(1988a, p. 215). As discussed below, *Aioloceras* clearly differs from *Pseudosaynella* (see under *Aioloceras*) and we reject its inclusion in the Pseudosaynellinae as proposed by CASEY (1966, p. 169) and WRIGHT (in WRIGHT et al., 1996, p. 71).

Other genera/subgenera (and synonyms) included here or closely related are: *Neosaynella* CASEY, *Anadesmoceras* CASEY, *Grycia* IMLAY, *Brewericeras* CASEY (incl. "Leconteites" CASEY), "Eocleoniceras" SAVELIEV, "Anacleoniceras" MIRZOYEV and "Cleonella" DESTOMBES are synonyms of *Cleoniceras*, and "Paracleoniceras" COLLIGNON is synonymous with *Aioloceras*.

SAVELIEV (1992) introduced the genus "Eocleoniceras" with "*E.*" *remotum* as type species (1992, p. 84, pl. 1, fig. 1, text-fig. 14), and included *C. leightonense* SPATH. These species, however, have all the diagnostic features of *Cleoniceras*. Therefore, following WRIGHT (in WRIGHT et al., 1996, p. 96), "Eocleoniceras" is considered to be a synonym of *Cleoniceras*.

"Anacleoniceras" MIRZOYEV, with "*A.*" *caseyi* as type species (MIRZOYEV, 1969, p. 32, pl. 4, figs. 1-2), was said to differ from *Cleoniceras* by its growth trend and whorl section, i.e. in "Anacleoniceras" the venter widens and becomes more rounded with increasing size, whereas it becomes narrow and sharp in *Cleoniceras*. These differences presumably represent sexual dimorphism, *C. caseyi* being a microconch (WRIGHT, in WRIGHT et al., 1996, p. 96) and "Anacleoniceras" becomes a synonym of *Cleoniceras*.

In "Cleonella" DESTOMBES (1970, p. 2063), with *Cleoniceras dimorphum* CASEY (1966, pl. 92, fig. 10a-b) as type species, DESTOMBES (1979, p. 91-96) included *C. floridum* CASEY, *C. cantianum* CASEY, *C. ornatum* DESTOMBES, *C. lanceolatum* DESTOMBES and *C. mocqueryi* DESTOMBES.

The type species *C. dimorphum* CASEY (1966, p. 568, pl. 92, figs. 10-11; DESTOMBES, 1979, p. 95, pl. 4-15, fig. 2a-b), a complete microconch, is intermediate between *Cleoniceras* and *Neosaynella*, on account of its weaker ribbing (OWEN, 1988a, p. 216). *C. cantianum* CASEY (1966, p. 574, pl. 95, figs. 4-5), including the specimens figured by DESTOMBES (1979, p. 96, pl. 4-15, fig. 1), is clearly a *Neosaynella*, as indicated by CASEY (1966, p. 574) and OWEN (1988a, p. 216). *C. floridum* CASEY (1961a, p. 599, pl. 84, figs. 6-7; CASEY, 1966, p. 566, pl. 92, figs. 1, 5, 7; DESTOMBES, 1979, p. 92, pl. 4-15, figs. 3-5), another microconch, has stronger ribbing than the previous species. "*C. lanceolatum*" DESTOMBES (1979, p. 94, pl. 4-16, figs. 1-2) closely resembles *C. floridum* and *C. dimorphum*. OWEN (1988a, p. 216) places it in *C. floridum*. "*C. mocqueryi*" DESTOMBES (1979, p. 96, pl. 4-17, fig. 3; pl. 4-18, figs. 1-2), also a microconch, and "*C. ornatum*" DESTOMBES (1979, p. 94, pl. 4-16, figs. 4-6), are synonyms of *C. jannelli* (PARENT)

(OWEN, 1988a, p. 216). "Cleonella" is therefore a synonym of "Anacleoniceras" and, hence, of *Cleoniceras*, as already indicated by WRIGHT (in WRIGHT et al., 1996, p. 96).

*Brewericeras* was introduced by CASEY (1954) for material differing from *Beudanticeras* by very flat, subparallel flanks, scarce constrictions and with falcoid ribs on the outer flanks. These features are well developed in the type species, *B. breweri* (GABB, 1864, p. 62, pl. 10, fig. 7; JONES et al., 1965, pl. 8, figs. 3, 5) and the closely related, if not synonymous, *B. hulenense* (ANDERSON, 1938, p. 190, pl. 44, figs. 3-4; see also WHITEAVES, 1876, p. 21, pl. 1, fig. 2, 2a; IMLAY, 1960, p. 106, pl. 17, figs. 11, 14, 16; MURPHY & RODDA, 1960, pl. 105, fig. 3; JONES et al., 1965, p. F16, pl. 8, figs. 1, 2, 4; pl. 9, 10; pl. 11, figs. 1-3, 13-14; JONES in JONES & GRANTZ, 1967, p. 29, pl. 6, figs. 10, 11, 15-19), a species also figured from the Russian Far East (ZONOVA et al., 1986, p. 141, pl. 1, fig. 1; pl. 2, fig. 3).

"Leconteites" CASEY (1954) is characterized by small to medium size, the moderately narrow umbilicus and ornament consisting of flexed primary ribs that arise, singly, paired or bundled from umbilical bullae (JONES et al., 1965, p. F9). As indicated by JONES et al. (1965, F15), this genus is closely related if not synonymous with *Brewericeras* CASEY. The type species *Leconteites lecontei* (ANDERSON, 1938, p. 192, pl. 38, fig. 4; pl. 47, figs. 3-5; IMLAY, 1960, p. 109, pl. 19, figs. 1-3; JONES et al., 1965, p. F9, pl. 1, figs. 1-3, 6-11, 13-22; pl. 2, figs. 1-8, 10-14, 17, 21; pl. 3-5; pl. 11, figs. 4-6) includes "*L. modestum*" (ANDERSON, 1938, p. 193, pl. 50, figs. 2-4) and is closely related to *B. hulenense* (see JONES et al., 1965, p. F17), differing only in minor details of ribbing. The remaining "differences" are mainly stratigraphical and both genera could be considered synonymous (JONES et al., 1965, p. F15).

### Cleoniceras PARONA & BONARELLI, 1897

(= *Anacleoniceras* MIRZOYEV, 1969; *Cleonella* DESTOMBES, 1970; *Eocleoniceras* SAVELIEV, 1992)

**Type species:** *Ammonites cleon* D'ORBIGNY (1850, p. 124), for *A. bicurvatus* D'ORBIGNY non MICHELIN (in D'ORBIGNY, 1841, p. 286, pl. 84, figs. 1-3), Lower Albian, Mammillatum Zone, France, by original designation.

**Diagnosis:** Rather involute and compressed; venter arched to acute, rarely tabulate; typically with strong, sigmoid to falcoid ribs at some growth stage, single or arising in pairs from distinct umbilical bullae, commonly branching again or intercalated at midflank, tending to disappear on outer whorls of macroconchs, and commonly weak on venter (WRIGHT, in WRIGHT et al., 1996, p. 96).

**Remarks:** The genus *Cleoniceras* was introduced by PARONA & BONARELLI (1897, p. 83) with *Ammonites cleon* D'ORBIGNY as type species, although material figured by them (PARONA & BONARELLI, 1897, pl. 11, fig. 5) belongs to *Beudanticeras* HITZEL (see CASEY, 1966, p. 553, 557).

The type species is poorly known. Material ascribed to it by SEUNES (1887, p. 558, pl. 11 and pl. 12, fig. 1a-b; see CASEY, 1966, text-fig. 214) was selected as type of "*Cleoniceras seunesi*" BONARELLI (*in* BONARELLI & NÁGERA, 1921, p. 24). It differs from *C. cleon* in the coarser ribbing and thicker whorls (see CASEY, 1966, p. 562, pl. 92, figs. 3, 4, 8). Specimens placed here by SINZOW (1909, p. 32, pl. 2, figs. 1-6) are now included in *Neosaynella* (see CASEY, 1954, p. 106; 1966, p. 572). A fragment illustrated by SPATH (1925, pl. 5, fig. 8) was discounted by CASEY (1966, p. 555). Specimens figured by CASEY (1966, pl. 91, fig. 5a-b, pl. 92, fig. 9, pl. 93, fig. 1), are fragmentary and poorly preserved. A specimen quite similar to the lectotype of *C. cleon* (see CASEY, 1966, fig. 211d-e) has been figured by DESTOMBES (1979, pl. 4-14, fig. 1a-b), whilst his other specimens (pl. 4-14, figs. 2-5) differ in the stronger and sparser ribbing as clearly visible in the largest specimen (fig. 5) that lacks umbilical bullae. These differences are also evident in the specimen of THOMEL (1980, p. 137, fig. 271).

*Cleoniceras quercifolium* (D'ORBIGNY, 1841, p. 284, pl. 83, figs. 4-6) differs from *C. cleon* in the coarser ribbing and thicker whorls (see also PICTET & CAMPICHE, 1858-1860, pl. 36, fig. 1; JACOB, 1908, pl. 9, figs. 3-5). "*C. janneli*" (PARENT, 1893, p. 266, pl. 6, fig. 2a-b) differs from *C. quercifolium* by fewer bullae, more ribs per fascicule and a wider venter. DESTOMBES (1979, p. 91), however, suggested that *C. janneli* is synonymous with *C. quercifolium*. In fact, *C. seunesi*, *C. quercifolium* and *C. janneli* are all closely interrelated if not synonymous. *C. seunesi* and *C. janneli* have similar whorl sections and prominence of bullae, whilst *C. quercifolium* has smaller bullae and a more acute venter.

*C. sublaeve* CASEY (1966, p. 559, pl. 91, figs. 8, 9a-b; 1980, p. 660, pl. 109, fig. 7a-b) is a rather smooth variant of *Cleoniceras*, with more obtuse ribs than in *C. cleon*, that are mostly restricted to the outer flank and end in weak bullae on the umbilical margin. *C. antiquum* CASEY (1966, p. 563, pl. 91, fig. 6, pl. 94, figs. 1, 2) resembles *C. cleon*, but is said to differ in the younger stages, where it has straighter ribbing and less pronounced tubercles. *C. morgani* SPATH (1927, pl. 17, fig. 7; pl. 18, fig. 5; SPATH 1942, text-fig. 248; CASEY, 1966, p. 564, pl. 93, figs. 3-5; pl. 94, figs. 3-6) and *C. leightonense* SPATH (1942, p. 701, text-fig. 247) are also similar to *C. cleon*, but appear to differ in the coarser ribbing and the less acute venter, best developed in *C. morgani*. *C. strigosum* CASEY (1966, p.

566, pl. 93, fig. 6a-b) is also close to *C. cleon*, but differs in the absence of umbilical bullae.

*C. floridum* CASEY (1961b, p. 599, pl. 84, figs. 6-7; 1966, p. 566, pl. 92, figs. 1, 5, 7) is a coarsely ribbed species and resembles *C. quercifolium*, *C. seunesi* and *C. janneli*. According to CASEY (1966, p. 567) *C. floridum* is characterized by uncoiling of the body chamber, accompanied by coarsening of ribbing and, finally, change of whorl section. These features are, however, typical of adult microconchs. Nevertheless, CASEY (1966, p. 568) claims that it differs from *C. quercifolium*, because the latter species lacks the zone of incipient smoothness at mid-flank that is already present in young *C. floridum*. The ribbing becomes finer, not coarser, with growth, and the venter increasingly acute, not more broadly rounded, as in *C. floridum*. *C. dimorphum* CASEY (1966, p. 568, pl. 92, figs. 10-11) is morphologically intermediate between *C. floridum* and *Neosaynella cantiana*, with ribbing mostly restricted to the outer flank (see also DESTOMBES, 1979, p. 95, pl. 4-15, fig. 2a-b). "*C. imitator*" CASEY (1966, p. 570, pl. 91, fig. 7, pl. 92, fig. 6) is similar to *C. floridum*, but said to be smaller and more planulate. The record from Mangyschlak by SAVELIEV (1992, pl. 2, fig. 1a-c) is based on a larger specimen with smoother outer whorls, but identity of the inner whorls cannot be established.

Representatives of *Cleoniceras* described from Kazakhstan and Tajikistan include "*C. mangyschlakense*" LUPPOV (*in* LUPPOV *et al.*, 1949; see SINZOW 1909, p. 32, pl. 2, figs. 1-5; LUPPOV *et al.*, 1949, pl. 24, figs. 7-8; LUPPOV, 1961, p. 191, pl. 3, fig. 1; pl. 4, fig. 2; SAVELIEV, 1992, p. 91, pl. 1, fig. 2, pl. 3, fig. 2, pl. 5, figs. 1-2, pl. 6, fig. 1, pl. 7, fig. 1), a junior subjective synonym of *Neosaynella platidorsata* SINZOW (see CASEY, 1966, p. 574). *C. kugitangense*, also described by LUPPOV (1961, p. 993, pl. 3, fig. 2) from Tajikistan and by SAVELIEV (1992, pl. 40, fig. 1) from Kazakhstan, appears to be a true *Cleoniceras*, with coarse ribbing on the inner whorls becoming blunt on the outer, distant umbilical bullae (c. 7 per whorl) and a sagitate whorl section. *C. discors* SAVELIEV (1973, p. 113, pl. 8, fig. 1, pl. 17, figs. 3-4) was also described from Kazakhstan, and MIRZOYEV (1967) introduced three new names for material from the Gissar Range, Tajikistan. *C. renatae* MIRZOYEV (1967, p. 39, pl. 3, fig. 1) and *C. tenuis* MIRZOYEV (1967, p. 44, pl. 4, fig. 1) are coarsely ornamented and closer to the *C. seunesi*-*quercifolium* plexus, whilst *C. planum* MIRZOYEV (1967, p. 40, pl. 3, fig. 2; pl. 4, fig. 2) is probably a *Neosaynella*. ILJIN (1961) assigned two other species from Uzbekistan to *Cleoniceras*. *C. baisunense* ILJIN (1961, p. 51, pl. 3, fig. 1; pl. 4, fig. 1) belongs to *Neosaynella* as indicated by CASEY (1966, p. 574), whilst *C. rudiki* ILJIN (1961, p. 53, pl. 3, fig. 2; pl. 4, figs. 2-3; pl. 7, fig. 3) appears to be a true *Cleoniceras* close or identical with *C. tenuis* MIRZOYEV (1967).

A specimen from the Lungma region, Himalayas, described as "*Cleoniceras xizangense*" CHAO (1976, p. 538, pl. 17, figs. 15-19) resembles *Anadesmoceras bayleyi* (JACOB).

Material from the Samana Range, West Pakistan, included in *Cleoniceras* by SPATH (1930, p. 53-54, pl. 8, figs. 7, 8, 11, 17), does not appear to belong in here, but rather to *Uhligella* according to ribbing and whorl section. Material from India included in *C. ramachandrii* RAO (1953, p. 109, fig. 5) is too poorly known for confirmation of affinities. The lateral view (only figure published) shows a very involute and smooth specimen, but the description is "keeled and ornamented by many radial ribs...".

Material from Bornholm Island, Denmark, referred to *Cleoniceras* by KENNEDY *et al.* (1981, p. 235-6, pl. 6, fig. 5; pl. 8, figs. 5-7; pl. 15, figs. 1-4) is poorly preserved, so that its generic assignation is questionable. All large specimens (KENNEDY *et al.*, 1981, pl. 8, fig. 7; pl. 15, fig. 1) have subrectangular whorls that are unknown from the genus. Only some of the small specimens (KENNEDY *et al.* 1981, pl. 15, figs. 3-4) with more compressed whorls and vestigial bullae have some resemblance to *Cleoniceras*.

Material from Madagascar included in *Cleoniceras* has been figured under *C. madagascariensis* COLLIGNON (1949, p. 84, pl. 17, figs. 11-12; 1963, p. 85, figs. 1181-1183) and *C. quercifolium* (D'ORB.) (COLLIGNON, 1963, p. 86, fig. 1184). The specimens are coarsely ribbed and somewhat resemble *C. quercifolium* (but see CASEY, 1966, p. 558). The specimen figured in BESAIRIE (1936, p. 157, fig. 10g) under "*Cleoniceras* sp. aff. *baylei* JACOB" (in text p. 157 as "*Cleoniceras* sp. nov.") and considered by COLLIGNON (1949, p. 85) as a *Cleoniceras*, appears to be an *Aioloceras*, as indicated by its involute whorls and style of ribbing, with almost smooth inner flanks.

Most records of *Cleoniceras* in Arctic and western North America has been either questioned or denied (see CASEY, 1966, p. 553, 554; NAGY, 1970, p. 36; OWEN, 1971, p. 138). *C.? schlaudti* STOYANOW (1949, p. 130, pl. 24, figs. 4-5) is based on poorly preserved material from SE Arizona that cannot even be identified generically. The specimens from northern California described by MURPHY & RODDA (1959, p. 104, pl. 20, figs. 1, 3, 4) under "*C. susukii*" MURPHY & RODDA differ from any known species of *Cleoniceras* in being more involute and lacking ribbing on the lower flanks. Its affinities lie more probably with *Grycia* IMLAY or *Pseudopulchellia* IMLAY. The specimen from Oregon described by JONES (1960, p. 157, pl. 29, figs. 5, 13, 14) under "*C.? dilleri*" JONES is too involute for the genus and lacks ribbing on the inner whorls. JONES (1960, p. 157) already noted its probable relationship to *Neosaynella*. *C. overbecki* IMLAY (1960, p. 108, pl. 19, figs. 36-39) from southern Alaska

appears to be a true *Cleoniceras* whilst *C. tailleuri* IMLAY (1961, p. 63, pl. 20, figs. 1-5; JELETZKY, 1964, pl. 26, figs. 14A-B) is a doubtful *Cleoniceras*. Most of the figured specimens (IMLAY, 1961, pl. 20, figs. 1-3) are too involute and with almost straight ribs; only a few figured specimens (IMLAY, 1961, pl. 20, fig. 5 and JELETZKY, 1964, pl. 26, fig. 14) resemble *Cleoniceras*. But ribs are less flexuous than in other specimens. OWEN (1988b, p. 484) nevertheless upheld IMLAY's identification. *C. canadense* JELETZKY (1980, p. 2, pl. 1, figs. 5, 6; pl. 2, figs. 1, 2, 4, 5) changes from ribbed and feebly bullate inner whorls to almost smooth outer whorls, with the ribbing as in *C. morgani* (see JELETZKY, 1980, p. 23). But *C. canadense* is more involute and, significantly, lacks the umbilical bullae of *Cleoniceras* (develops best in ribbed species, e.g. *C. morgani*). Inclusion of the species in *Cleoniceras* was accepted by OWEN (1988b, p. 484). Specimens from northeastern Russia, figured by MICHAILOVA & TERECHOVA (1975, p. 62, figs. 5-10) under "*C.* dubium", are almost completely smooth and do not belong to *Cleoniceras* s.s. ALABUSHEV (1987) pointed out the differences between this species and European *Cleoniceras*, and ALABUSHEV & ALABUSHEVA (1988, p. 21) place "*C.* dubium" in *Grycia*. *C. discors* SAVELIEV (1973, p. 113, pl. 8, fig. 1; pl. 17, figs. 3-4; text-figs. 19-20) is characterized by ribbed inner whorls and almost smooth outer whorls of relatively large size ( $D = c. 100-110$  mm). OWEN (1988b, p. 484) includes there the specimen from Arctic Canada figured by JELETZKY (1964, pl. 23, fig. 3A-B) under "*Cleoniceras* (*Anadesmoceras*?) aff. *subbaylei* SPATH". JELETZKY's apparently complete specimen, however, is smaller ( $D = 34$  mm) and clearly ribbed, especially on the outer flanks.

*Cleoniceras* has also recently been reported from Sergipe, Brasil, and referred to *C. aff. tenuis* MIRZOYEV and *C. (C.) cf. quercifolium* (D'ORBIGNY) (see SOUZA LIMA & BENGTSON, 1999, fig. 1a-b).

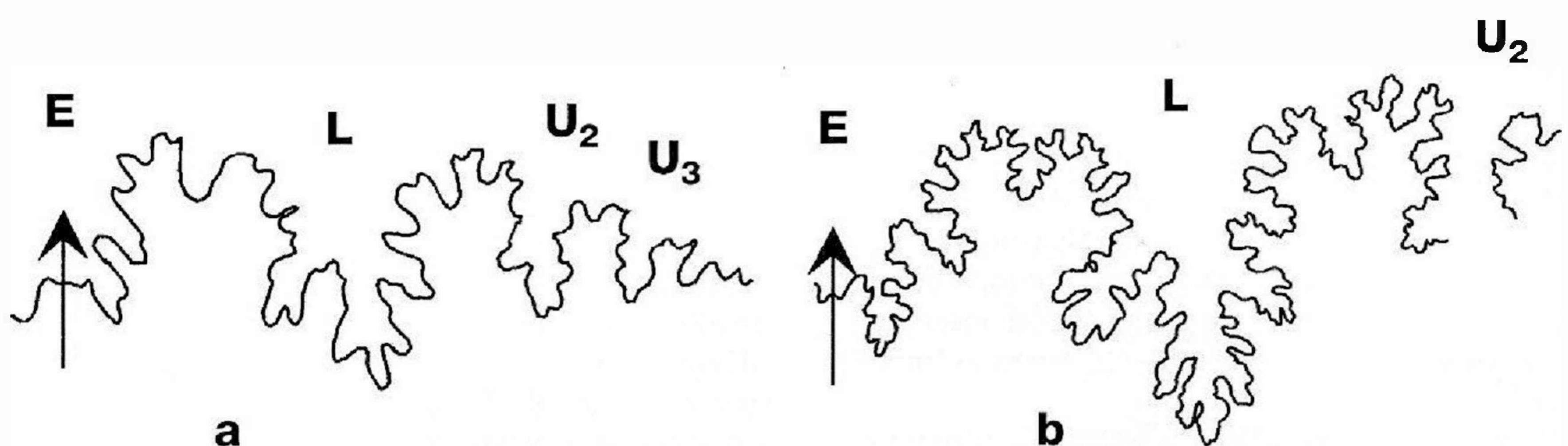
#### *Cleoniceras? cf. santacrucense* LEANZA, 1970 Pl. III, figs. 5-7; Fig. 7a

cf. 1970. *Cleoniceras santacrucense* LEANZA, p. 226, fig. 24, 1-2.

**Material:** two almost complete specimens (MLP 29038, MLP 29040) from Estancia La Federica, Lago San Martin, col. F. MEDINA and A.C. RICCARDI, respectively; 1 incomplete juvenile (MLP 29039) from Puesto Policia, Lago Cardiel, col. F. MEDINA.

**Description:** Septate whorls up to 20 mm diameter are moderately involute ( $U/D = 0.21 - 0.22$ ) with somewhat compressed ( $H/W = 1.20$ ) section, rather steep umbilical wall with rounded margin, maximum width below mid-flank, gently converging flanks and a broadly rounded

Fig. 7: a, *Cleoniceras?* cf. *santacruense* LEANZA, MLP 29039, suture at H = 9 mm (see Pl. III, fig. 5a-b). b, *Cleoniceras* sp., MLP 29041, suture at H = 9.7 mm (see Pl. III, fig. 4).



venter. Primary ribs ( $P = 6$ ) are barely visible on the umbilical wall, but become relatively prominent on the umbilical margin where they form bullae-like thickenings; they are gently prorsiradiate on the inner flank, become retroverse at mid-flank and are again slightly inclined forward before crossing the venter with a shallow arc. Secondary ribs (c. 16-18 /half-whorl) originate near mid-flank by intercalation or obscure division of primaries.

Body-chamber egresses slightly and is about a half whorl in length. Umbilicus widens ( $U/D = 0.24$ ) and whorl section becomes more compressed ( $H/W = 1.57$ ). Ribs become more rounded and wider ( $P = 11$ ,  $S = 18-21$ ), are more projected on the outer flank and division below mid-flank becomes more obvious.

#### Measurements (in mm):

	D	H	W	U	H/W	P	S
MLP 29039, phr.	22	10.7(0.48)	8.9(0.40)	5(0.23)	1.20	6	16-18
MLP 29038, b.ch.	22.9	10.8(0.47)	8 (0.35)	5(0.22)	1.35	8	21
MLP 29040, b.ch.	30	14.6(0.48)	9.3(0.31)	7.3(0.24)	1.57	11	18

**Remarks:** *Cleoniceras santacruense* was based on one almost complete phragmocone with about 1/4 whorls of body-chamber. The species was correctly compared with *C. morgani* SPATH, which is similar in whorl height and width and the density of primaries and secondaries, but differs in the smaller umbilicus ( $U/D = 0.17$  vs. 0.25). Furthermore, *C. santacruense* differs in the more acute venter and the maximum whorl width in the outer third of the whorls, and in the primaries that arise from bullae close to the umbilical margin. It appears also to be smaller, because all figured specimens of *C. morgani* are phragmocones with larger diameter.

The material here described consists of specimens smaller than the holotype of *C. santacruense*, and therefore not directly comparable. Our specimens are similar in coiling, whorl section and spacing of primaries and secondaries. The holotype is lost so that it is

not possible to compare the inner whorls, although from LEANZA's (1970, fig. 24, 1-2) figure it suggests that the umbilical bullae are larger.

#### *Cleoniceras* sp. Pl. III, fig. 4; Fig. 7b

**Material:** One partially weathered complete phragmocone (MLP 29041), from Bahía Estancia Dos Hermanos, Lago Cardiel; col. F. MEDINA.

**Description:** Rather involute ( $U/D = 0.27$ ), compressed whorls ( $H/W = 2.08$ ) with gently curved flanks passing into a slightly inclined umbilical wall and a narrowly acute venter. Primaries, ( $P = c. 11$ ) are radial on the umbilical wall and form bullae-like thickenings on the umbilical margin. They divide into 2-3 fine rounded secondaries ( $S = c. 23$ ), which begin prorsiradiate and become retroverse forming an apicad concave arc below mid-flank. On the upper half of the flank, secondaries become projected forming an arc, and become obsolete on the venter.

#### Measurements (in mm):

	D	H	W	U	H/W	P	S
MLP 29041	33.4	16(0.48)	7.7(0.23)	9(0.27)	2.08	11	23

**Remarks:** This specimen appears to be a fine-ribbed *Cleoniceras*, similar to *C. strigosum* CASEY (1966, p. 566, pl. 93, fig. 6a-b), although comparison is difficult due to scarcity of material and differences in growth stages (figured *C. strigosum* is a large and incomplete phragmocone lacking umbilical bullae). The Patagonian material, otherwise, is close to that species except for the more evolute ( $U/D = 0.23$  vs. 0.18) and compressed ( $H/W = 2.08$  vs. 1.61) whorls, the more acute venter, smaller umbilical bullae, and interrupted ribs on venter.

#### Genus *Aioloceras* WHITEHOUSE, 1926 (=*Paracleoniceras* COLLIGNON, 1963)

**Type species:** *Cleoniceras argentinum* BONARELLI

(*in* BONARELLI & NÁGERA, 1921, p. 24, pl. 4, fig. 3, 6), from Lower Albian of Lago San Martin, Santa Cruz, Argentina, by original designation of WHITEHOUSE (1926, p. 206).

**Diagnosis:** Whorls involute, umbilicus shallow with rounded margin, flanks converging into narrowly rounded venter, becoming more rounded with broad venter; ornament formed by blunt, flexuous ribs on inner whorls, becoming sparser and thicker on body-chamber, fading on inner third of flank and missing on venter; constrictions usually shallow, restricted to intermediate whorls; septal suture rather simple with wide, asymmetric L and up to four umbilical lobes.

**History:** The genus *Aioloceras* was introduced by WHITEHOUSE (1926, p. 206) for material from Patagonia, described (*in* BONARELLI & NÁGERA, 1921) as *Aioloceras argentinum*, "*Beudanticeras cf. stoliczkai*" and "*Uhligella quercifolia*", and from Australia ("*Desmoceras jonesi*" of GREGORY & SMITH, 1902). Most were originally included in *Beudanticeras*, *Cleoniceras* and *Uhligella*. *Aioloceras* was said to differ from *Cleoniceras* "in the sharper ribs and absence of umbilical tubercles" (WHITEHOUSE, 1926).

*Aioloceras* has remained a poorly known genus. An additional specimen was figured from Patagonia under "*Cleoniceras argentinum*" by PIATNITZKY (1938). On that basis, the genus was included in the Cleoniceratinae by WRIGHT (*in* ARKELL *et al.*, 1957, p. L394). CASEY (1961b, p. 169) erected the subfamily Pseudosaynellinae within the Desmoceratidae for *Pseudosaynella* SPATH and *Aioloceras* BONARELLI. Inclusion of the Pseudosaynellinae in Desmocerataceae, rather than Hoplitaceae was based chiefly on the invariable presence of constrictions and absence of tubercles. The new subfamily was mainly based on material included in *Pseudosaynella*, but *Aioloceras* was not discussed.

LEANZA (1970) and DAY (1974) described new material, respectively from Patagonia and Australia, but did not clarify the status of *Aioloceras*. Furthermore, LEANZA (1970, p. 220), by transferring material described by BONARELLI (*in* BONARELLI & NÁGERA, 1921) under "*Beudanticeras cfr. stoliczkai*" to *Pseudosaynella*, gave indirect support to the generic affinities proposed by CASEY (1961b).

Outside Patagonia and Australia, *Aioloceras* was mentioned from Madagascar, i.e. "*Cleoniceras (Aioloceras) besairiei*" (COLLIGNON, 1949, p. 86, pl. 18, figs. 1-3; pl. 21, fig. 7) and placed as a subgenus in *Cleoniceras*. Later he placed this species in "*Paracleoniceras*" COLLIGNON (1963). *Aioloceras* has also been recorded from West Pakistan (FATMI, 1972, p. 324).

Inclusion of *Aioloceras* in Cleoniceratinae was tentatively upheld by OWEN (1988a, p. 215), whilst WRIGHT (*in* WRIGHT *et al.*, 1996, p. 71) maintained *Aioloceras*, together with *Pseudosaynella*, in Pseudosaynellinae.

**Comments:** *Pseudosaynella* was introduced by SPATH (1923, p. 66) for the "*Sonn. bicurvata* (Michelin)" from the Aptian of France figured by SARASIN (1893, p. 161, pl. 4, 5, figs. 1-3, text-fig. 8; partially refigured in CASEY, 1961b, text-fig. 53a-c). Other species included are *P. fimbriata* IMLAY (1945, p. 278, pl. 42, fig. 1; pl. 43, figs. 1-5; CASEY, 1961b, p. 172, pl. 29, fig. 3a-d) from the Lower Aptian of England, *P. undulata* (SARASIN, 1893, p. 162-163, pl. 4-5, figs. 8a-b; CASEY, 1961b, p. 173, pl. 29, fig. 4a-c) from the Upper Aptian of France, and *P. raresulcata* (LEYMERIE, *in* D'ORBIGNY, 1841, p. 288, pl. 85, figs. 5-7; SARASIN, 1893, p. 161, pl. 4-5, figs. 4-6; refigured in CASEY, 1961b, text-fig. 53) and *P. heimi* (SARASIN, 1893, p. 162, pl. 4, 5, fig. 7) from the Lower Aptian of France. On that basis the genus includes strongly compressed, discoidal and involute shells; whorls are sagittate with flat sides and sharp venter, and low subvertical umbilical wall with distinct rim. Ribbing differs from that of *Cleoniceras* by blunt, sigmoidal or falcoid ribs, smooth venter and absence of umbilical tubercles. Ribbing fades with growth until the shell is smooth or nearly smooth.

Material from the Aptian of Texas figured by SCOTT (1940, p. 995, pl. 56, fig. 1-2) under "*Pseudosaynella walcotti* (HILL)" is poorly preserved, but does not appear to belong in *Pseudosaynella* on account of its large umbilicus and apparently rounded venter and the presence of constrictions at large sizes.

*Pseudosaynella* appears to be present in the Upper Aptian of Colombia, where at least three specimens were described under *P. ralphimlayi* ETAYO SERNA (1979, p. 29, pl. 3, fig. 1, text-fig. 4N, 4O). Presence of this genus in Patagonia (see LEANZA, 1970, p. 220) is discounted here; the material figured and mentioned by LEANZA (1970, p. 220, fig. 17, 1-2) belongs in *Aioloceras*.

*Pseudosaynella* clearly differs from *Aioloceras* by more involute coiling, vertical umbilical wall, sagittate whorl section with flat flanks and acute venter, and falcoid ribbing usually restricted to the inner whorls and with tendency to fade on outer whorls.

In introducing "*Paracleoniceras*", as subgenus of *Cleoniceras*, COLLIGNON (1963, p. 85) noted as diagnostic the absence of ornament on the umbilical margin and inner flank, the rounded venter and the large size ( $\geq 200$  mm). Affinities to *Aioloceras* were not discussed, although the type species, "*P.* besairiei", had previously been referred to that genus (*in* COLLIGNON, 1949, p. 85) based on the absence of umbilical tubercles.

"*P.* besairiei" was based in three specimens, including the complete type (COLLIGNON, 1949, pl. 18, figs. 2, 2a, 2b) and two incomplete phragmocones, one small and the other large (COLLIGNON, 1949, pl. 18, figs. 1a, 1b, 3, 3a) from the Albian of Madagascar. Four additional specimens were added by COLLIGNON

(1963, pl. 275, figs. 1186, 1187; pl. 276, fig. 1188, 1189). All them, with the possible exception of that illustrated last are incomplete phragmocones. Thus, the species can be characterized by being quite involute; flanks converging into a rounded venter; almost smooth on inner third of flanks and with blunt, widely spaced and slightly flexuous ribs on outer two-thirds, which become stronger on body chamber and obsolete on the venter.

Other closely related material from Madagascar was included by COLLIGNON (1963) under seven specific names. "*P. inaequale*" COLLIGNON (1963, p. 86, pl. 274, fig. 1185) is based on an incomplete phragmocone, which according to COLLIGNON (1963, p. 86) has close affinities in ornament with *Cleoniceras madagascariensis*, even if lacking incipient tubercles. "*P. cleoniforme*" (COLLIGNON, 1963, p. 89, pl. 276, figs. 1190-1191), based on one incomplete and one juvenile specimen, barely differs from "*P.* *besairiei*" in spite of the apparent subdued ribbing (COLLIGNON, 1963, p. 89). The single specimen referred to "*P. morganiforme*" COLLIGNON (1963, p. 89, pl. 276, fig. 1192) is also quite close to "*P.* *besairiei*". "*P. tenuicostulatum*" COLLIGNON (1963, p. 92, pl. 277, figs. 1193, 1194), based on two complete adults, was compared with "*P.* *besairiei*" by COLLIGNON (1963) and considered distinct by its finer and denser ribbing. "*P. crassefalcatum*" COLLIGNON (1963, p. 94, pl. 278, fig. 1195), based in one incomplete specimen, was considered distinct by its large umbilicus and strong ribbing. "*P. ambiguum*" COLLIGNON (1963, p. 94, pl. 278, fig. 1196), another incomplete phragmocone, is quite close to the previous "species" but with deep constrictions. Finally, "*P. ptychitiforme*" (COLLIGNON, 1949, p. 88, pl. 18, fig. 4, 4a; pl. 21, fig. 6), based in one incomplete phragmocone, differs in being more involute and almost smooth. Excepting the last specimen, which resembles a *Beudanticeras* in coiling and lack of ornament, all others probably belong in a single species, i.e. "*P.* *besairiei*". "*Paracleoniceras*" was first considered as a subgenus of *Cleoniceras* by MIRZOYEV (1967, p. 39) and later as a probable junior synonym of *Grycia* IMLAY by WRIGHT (in WRIGHT *et al.*, 1996, p. 96). *Grycia* was introduced by IMLAY (1961, p. 64) as a subgenus of *Cleoniceras*, with *Cleoniceras (G.) sablei* IMLAY (1961, p. 64, pl. 20, figs. 13-20) as type species. It was characterized by the whorls becoming more rounded and ribbing more prominent during growth, by lacking distinct umbilical tubercles, developing indistinct bifurcation on the outer whorls, and a tendency of the body-chamber to become scaphitoid in coiling. The type species is known only from seven poorly preserved specimens from the (?middle) Albian of Alaska.

*Grycia* was given full generic status by NAGY (1970, p. 36) based on material from Spitzbergen. Besides *G. sablei*, type species, NAGY (1970) included material

which previously was tentatively placed in *Neosaynella*, i.e. *N. whittingtoni* IMLAY (1961, p. 64, pl. 20, figs. 6-9). The few specimens figured by NAGY (1970, pl. 1, figs. 8-10, pl. 2, figs. 1-4) are rather small and poorly preserved, yet exhibit all features characteristic of the Alaskan material.

*Grycia* also tentatively included material from the Albian of Queen Charlotte Islands, Canada (MCLEARN, 1972, p. 59), originally described under "*Ammonites perezianus*" WHITEAVES (1876, p. 19, pl. 2, fig. 1a-b). MCLEARN (1972, p. 61) objected to the inclusion of this material in *Aioloceras* because "it appears to be necessary to include within the species the variants with broadened venters and other adult features". As stressed by MCLEARN (1972, p. 61), however, both *Grycia* and *Aioloceras* were poorly known. If *perezianus* indeed belongs to *Grycia*, it would belong to the best preserved material of that genus (see MCLEARN, 1972, p. 59, pl. 23, fig. 2; pl. 38, figs. 1-3; pl. 39, fig. 1; pl. 42, figs. 1, 2), along with material from the middle Albian of Arctic Canada figured by JELETZKY (1980, p. 3, pl. 1, figs. 1-4; pl. 2, fig. 3; pl. 3, fig. 4; pl. 9, fig. 2) under *Cleoniceras (Grycia) densicostata* JELETZKY. This appears to be a species of *Grycia* with rather dense, fine and evenly spaced ribbing. As pointed out by JELETZKY (1980, p. 3) it may be morphologically intermediate between *Grycia sablei/whittingtoni* and *Pseudopulchellia flexicostata* (IMLAY, 1961, p. 63, pl. 18, figs. 10-20; JELETZKY, 1980, p. 19, pl. 1, figs. 13-16; pl. 5, figs. 1, 3-5; pl. 7, fig. 4).

Material from northeastern Russia described by MICHAILOVA & TERECHOVA (1975, p. 62, figs. 5-10) under "*Cleoniceras* *dubium*" should be transferred to *Grycia* (see ALABUSHEV & ALABUSHEVA, 1988, p. 21).

*Grycia* has also been recorded from the Caribbean (see WIEDMANN, 1978, p. 362, fig. 2C), although the material is too poor for confirmation.

When comparing the material referred to *Grycia* with that included in "*Paracleoniceras*", several differences are evident. *Grycia* is usually smaller in size, has more involute and rounded whorls, with less convergent flanks and broader venter. Ribbing is less flexuous, more marked, especially on the inner whorls, the costae slightly widening towards the venter and usually beginning at the umbilical margin, where they may have bullae-like thickenings. On that basis "*Paracleoniceras*" should be excluded from the synonymy of *Grycia*, in contrast to WRIGHT (1996, p. 96). "*Paracleoniceras*" is here treated as a junior synonym of *Aioloceras*, because the Patagonian and Madagascan species are similar in coiling, whorl section and ornament type (compare H/D and W/D for *Aioloceras argentinum* and *A. rollerii* and all "species" of "*Paracleoniceras*"). The only difference is in umbilical width, all Patagonian species being more evolute.

*Aioloceras* is here included in the Cleoniceratidae on the basis of presence and style of ribbing, as well as whorl section and disposition of constrictions. Furthermore, the rather simple suture with wide and asymmetrical L match that of other Cleoniceratidae and splitting of U<sub>1</sub> and "suturallobenbildung" in U<sub>4</sub> is as figured for *Cleoniceras* (see SCHINDEWOLF, 1963, p. 395, fig. 239; 1966, p. 655, fig. 401).

*Pseudosaynella* SPATH should provisionally be left in the Pseudosaynellinae although the status of this subfamily and its position in the Desmoceratidae (see CASEY, 1966; WRIGHT, *in* WRIGHT *et al.*, 1996) should be revised (see SCHINDEWOLF, 1966, p. 624).

*Aioloceras argentinum* (BONARELLI, 1921) ♀/M &  
♂/m

Pl. IV, figs. 1-7; Pl. V, figs. 1-6; Pl. VI, figs. 1-4; Figs.  
8a-n, 9a-i, 10, 11.

- 1921. *Cleoniceras argentinum* BONARELLI *in* BONARELLI & NÁGERA, p. 24, pl. 4, figs. 3, 6.
- 1921. *Cleoniceras argentinum* var. *meseticum* BONARELLI *in* BONARELLI & NÁGERA, p. 24, pl. 4, fig. 7.
- 1921. *Beudanticeras* cfr. *Stoliczkai* (KOSSM.).- BONARELLI *in* BONARELLI & NÁGERA, p. 23, only pl. 3, figs. 2, and 4 (refigured *in* LEANZA, 1970, as *Pseudosaynella bonarellii* LEANZA)
- 1921. *Beudanticeras Daintreei* (ETH.).- BONARELLI *in* BONARELLI & NÁGERA, p. 23, pl. 3, fig. 5.
- 1921. *Uhligella quercifolia* D'ORBIGNY.- BONARELLI *in* BONARELLI & NÁGERA, p. 25, pl. 3, fig. 6.
- 1921. *Cleoniceras* f.f. (D'ORBIGNY).- BONARELLI *in* BONARELLI & NÁGERA, p. 24 (part).
- 1931. *Cleoniceras argentinum* BON.- WINDHAUSEN, pl. 39, fig. 1 (reproduction of BONARELLI & NÁGERA, pl. 4, fig. 6).
- 1931. *Beudanticeras Stoliczkai* (KOSSM.).- WINDHAUSEN, pl. 39, fig. 2 (reproduction of BONARELLI & NÁGERA, pl. 3, fig. 4).
- 1938. *Cleoniceras argentinum* BON.- PIATNITZKY, p. 79, pl. 3, fig. 13a-b.
- 1957. *Aioloceras argentinum* (BONARELLI).- WRIGHT *in* ARKELL *et al.*, p. L394, fig. 513.3a-b (reproduction of BONARELLI & NÁGERA, 1921, pl. 4, figs. 3 and 6.).
- 1970. *Pseudosaynella bonarellii* LEANZA, p. 220, fig. 17 1-2 (same specimen as *in* BONARELLI & NÁGERA, 1921, pl. 3, fig. 4).
- 1988. *Aioloceras argentinum* (BONARELLI).- RICCARDI, p. 99, pl. 13, figs. 2-3.
- 1996. *Aioloceras argentinum* (BONARELLI).- WRIGHT *in* WRIGHT *et al.*, p. 71, fig. 51, 2a-b (reproduction of BONARELLI & NÁGERA, 1921, pl. 4, figs. 3 and 6).

**Holotype.** The incomplete phragmocone of a macroconch figured by BONARELLI, *in* BONARELLI & NÁGERA, 1921, pl. 4, figs. 3, 6 (SEGEMAR 9293). Here refiugured on pl. IV, fig. 1. Rio Mayer Formation, cerro Meseta, lago San Martin.

**Type material:** holotype of *A. argentinum*; holotype of *A. argentinum meseticum*, incomplete phragmocone (SEGEMAR 9301) of macroconch (*in* BONARELLI & NÁGERA, 1921, pl. 4, fig. 7); one ?juvenile macroconch with body-chamber (SEGEMAR 9290) figured by BONARELLI (*in* BONARELLI & NÁGERA, 1921, pl. 3, fig. 6) as "*Uhligella quercifolia*"; holotype of "*Pseudosaynella bonarellii*" LEANZA, complete adult microconch (SEGEMAR 9309a) figured by BONARELLI (*in* BONARELLI & NÁGERA, 1921, pl. 3, fig. 4) and refiugured by Windhausen (1931, pl. 39, fig. 2) and LEANZA (1970, fig. 17, 1-2); one adult septate ?macroconch with body-chamber (SEGEMAR 14914), recorded by BONARELLI (*in* BONARELLI & NÁGERA, 1921, p. 24); one incomplete adult with part of phragmocone and body-chamber (SEGEMAR 9309b), figured by BONARELLI (*in* BONARELLI & NÁGERA, 1921, pl. 3, fig. 2) as "*Beudanticeras* cfr. *Stoliczkai*"; one incomplete body chamber of ?microconch (SEGEMAR 9292) figured by BONARELLI (*in* BONARELLI & NÁGERA, 1921, pl. 3, fig. 5) as "*Beudanticeras Daintreei*"; one incomplete adult topotype with parts of phragmocone and body-chamber (SEGEMAR 14912).

**Other material:** Lago San Martin (loc. A XXII 21; AC4; 71-9, 13, 28; M1, 3, Mx; col. A. RICCARDI): 13 almost complete microconchs (MLP 29042, 29043, 29047, 29049, 29053, 17368, 29060, 29061, 29066, 29071, 29099, 29118, 29158) and 13 incomplete adult phragmocones, some with part of body-chamber (MLP 29055, 29058, 29064, 29067, 29068, 29100-29105, 29116, 29176); 10 juvenile phragmocones with part of body-chamber (MLP 29044, 29052, 29056, 29059, 29063, 29069, 29074, 29106, 29177), 2 adult phragmocones of macroconch (MLP 29050, 29117) and 4 incomplete juvenile phragmocones of macroconchs (MLP 29045, 29046, 29051, 29062); 55 fragmentary specimens (SEGEMAR s/n., col. BONARELLI and NÁGERA; MLP 29077, 29078, 29084-29087, 29107-29113, 29130, 29138, 29142, 29146, 29149, 29151-29153, 29174, 29175, 29178); 5 almost complete body-chambers of microconchs (MLP 16009), and 2 incomplete septate juveniles (MLP 16014), H. ARBE col. North of Estancia Cerro Bayo, Lago Cardiel: 1 incomplete phragmocone (MLP 29436), col. F. MEDINA.

**Diagnosis:** Rather involute, compressed phragmocone, venter narrowly arched becoming broader at end of body-chamber; inner whorls with sharp, falcoid ribs, tending to withdraw to upper flanks and to disappear on body-chamber; sometimes 1 to 3 shallow constrictions on body-chamber.

Fig. 8: Cross sections (X1) of *Aioloceras argentinum* (BONARELLI) ♀/M & ♂/m. **a**, holotype, macroconch SEGEMAR 9293 (see Pl. IV, figs. 1a-c); **b**, holotype of "Cleoniceras argentinum var. *meseticum*" BONARELLI, macroconch SEGEMAR 9301 (see Pl. IV, figs. 3a-b); **c**, holotype of "Pseudosaynella bonarellii" LEANZA, microconch SEGEMAR 9309a (see Pl. IV, figs. 2a-b); **d**, macroconch MLP 29045 (see Pl. VI, fig. 2a-b); **e**, macroconch MLP 29046; **f**, ?microconch SEGEMAR 14912 (see Pl. V, figs. 5a-b); **g**, juvenile MLP 29052; **h**, microconch MLP 29042; **i**, microconch MLP 29043 (see Pl. V, figs. 2a-b); **j**, juvenile MLP 29044 (see Pl. V, figs. 3a-b); **k**, microconch SEGEMAR 9309b (see Pl. V, fig. 4a-b); **l**, macroconch SEGEMAR 9290 (see Pl. VI, figs. 4a-b); **m**, macroconch MLP 29051 (see Pl. IV, figs. 7a-c); **n**, macroconch MLP 29050.

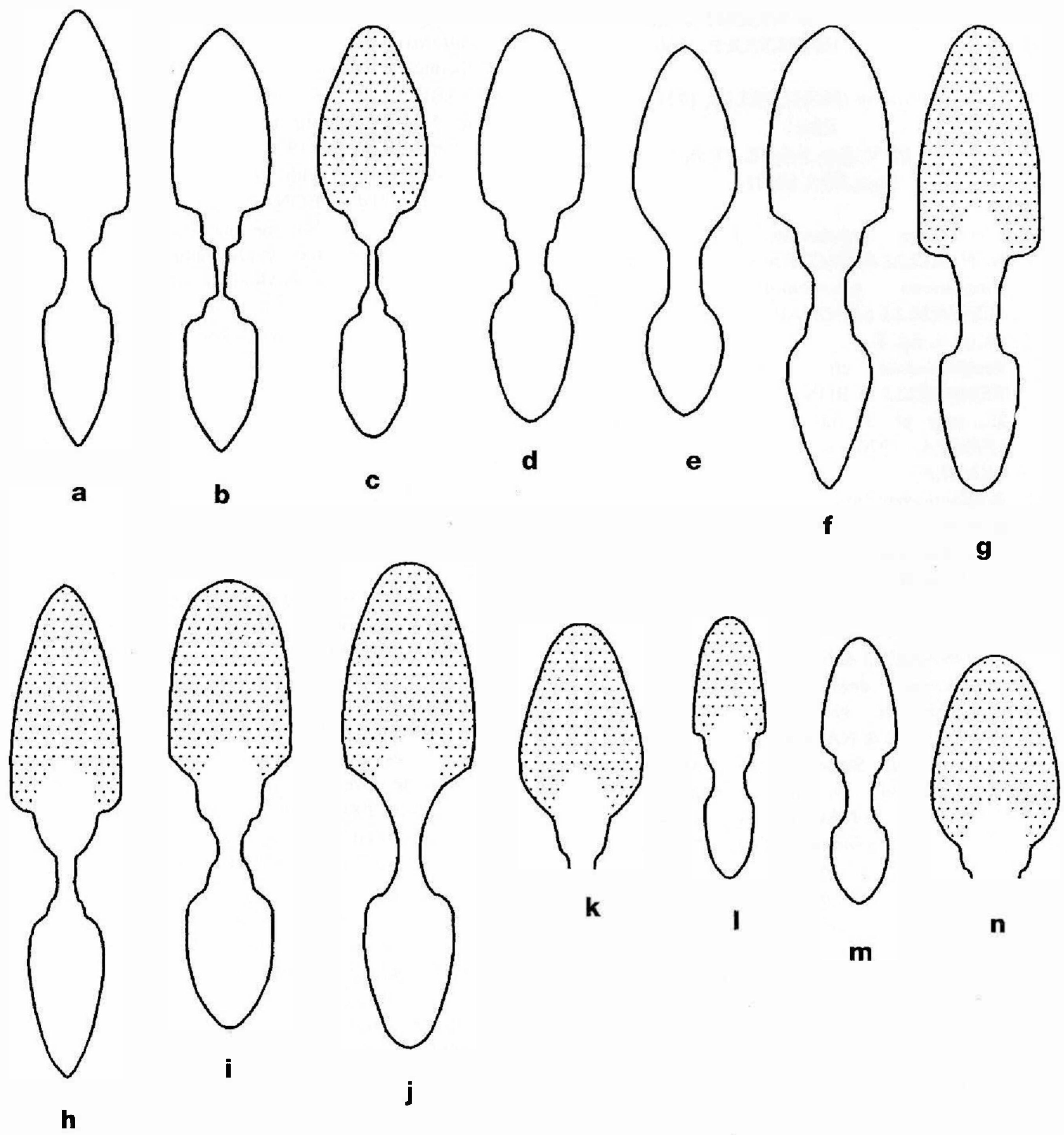
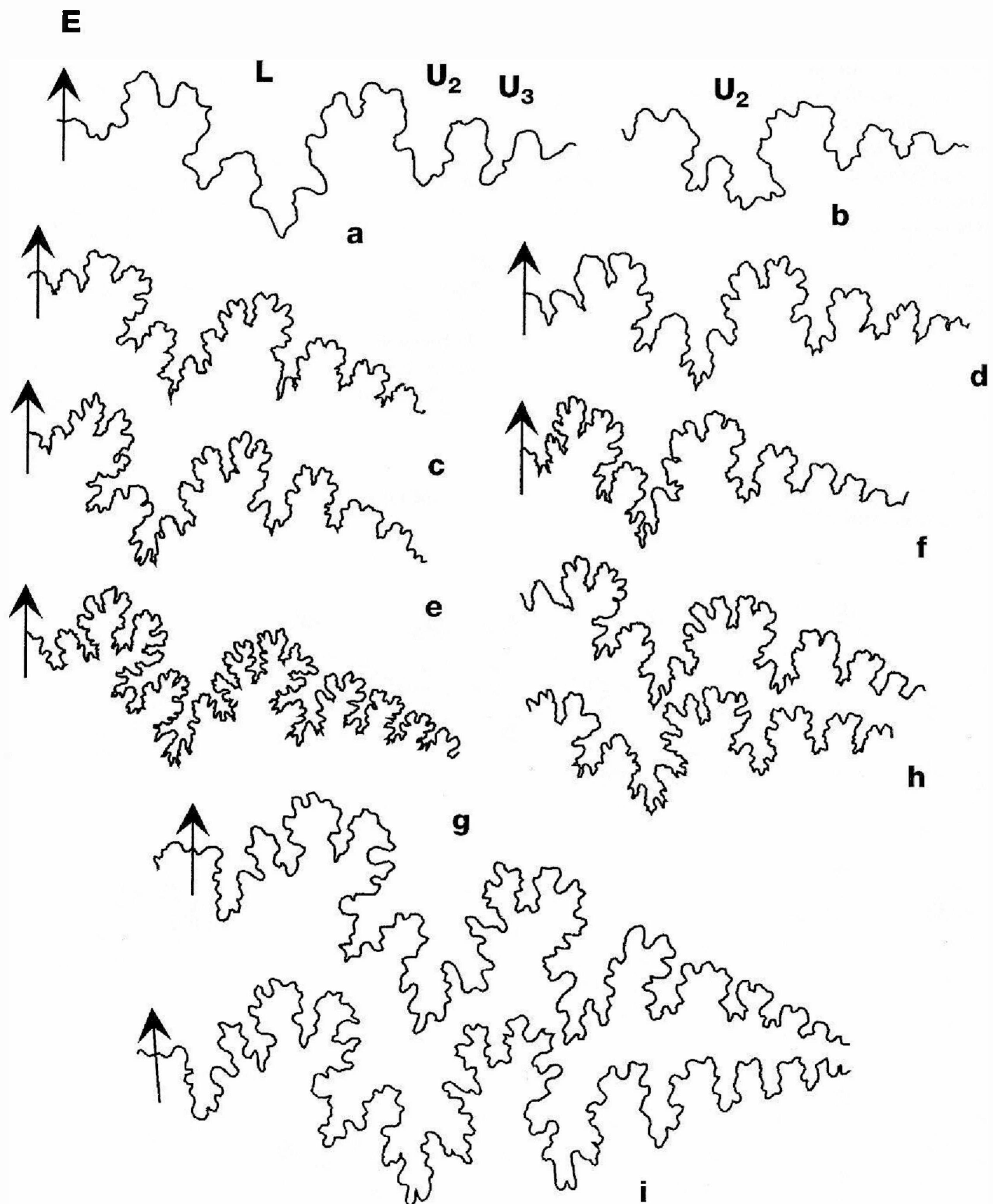


Fig. 9: Sutures of *Aioloceras argentinum* (BONARELLI) ♀/M & ♂ m. **a**, holotype, macroconch SEGEMAR 9293 at H = 27 mm (see Pl. IV, figs. 1a-c); **b**, microconch SEGEMAR 9309b at H = 25.7 mm (see Pl. V, figs. 4a-b); **c**, microconch MLP 29042 at H = 26.5 mm; **d**, microconch MLP 29047 at H = 25 mm; **e**, macroconch MLP 29050 at H = 31.6 mm; **f**, macroconch MLP 29046 at H = 22 mm; **g**, macroconch MLP 29045 at h = 29 mm (see Pl. VI, figs. 2a-b); **h**, juvenile MLP 29044 at H = 25 mm (see Pl. V, figs. 3a-b); **i**, juvenile MLP 29436 at H = 23 mm (see Pl. IV, figs. 5a-b).



**Description:** Juvenile septate whorls ( $D = c. 30-40$  mm) are relatively evolute ( $U/D = 0.20-0.25$ ), with rounded umbilical margin and vertical wall, and slightly convex flanks. Flanks converge into narrowly rounded venter. Whorls are compressed ( $H/W = c. 1.79 - 2.00$ ) with maximum width at  $1/3$  whorl-height. At 20-25 mm diameter, ornament consists of short primaries, well marked to obsolete, that begin on umbilical margin, are slightly proradiate and almost immediately divide into two secondaries, which on outer flank form weak orad arches, weakly project on shoulders, before becoming obsolete on venter. Between 30-40 mm diameter, primaries are longer and divide below mid-flank; ribs are rounded and interspaces broad.

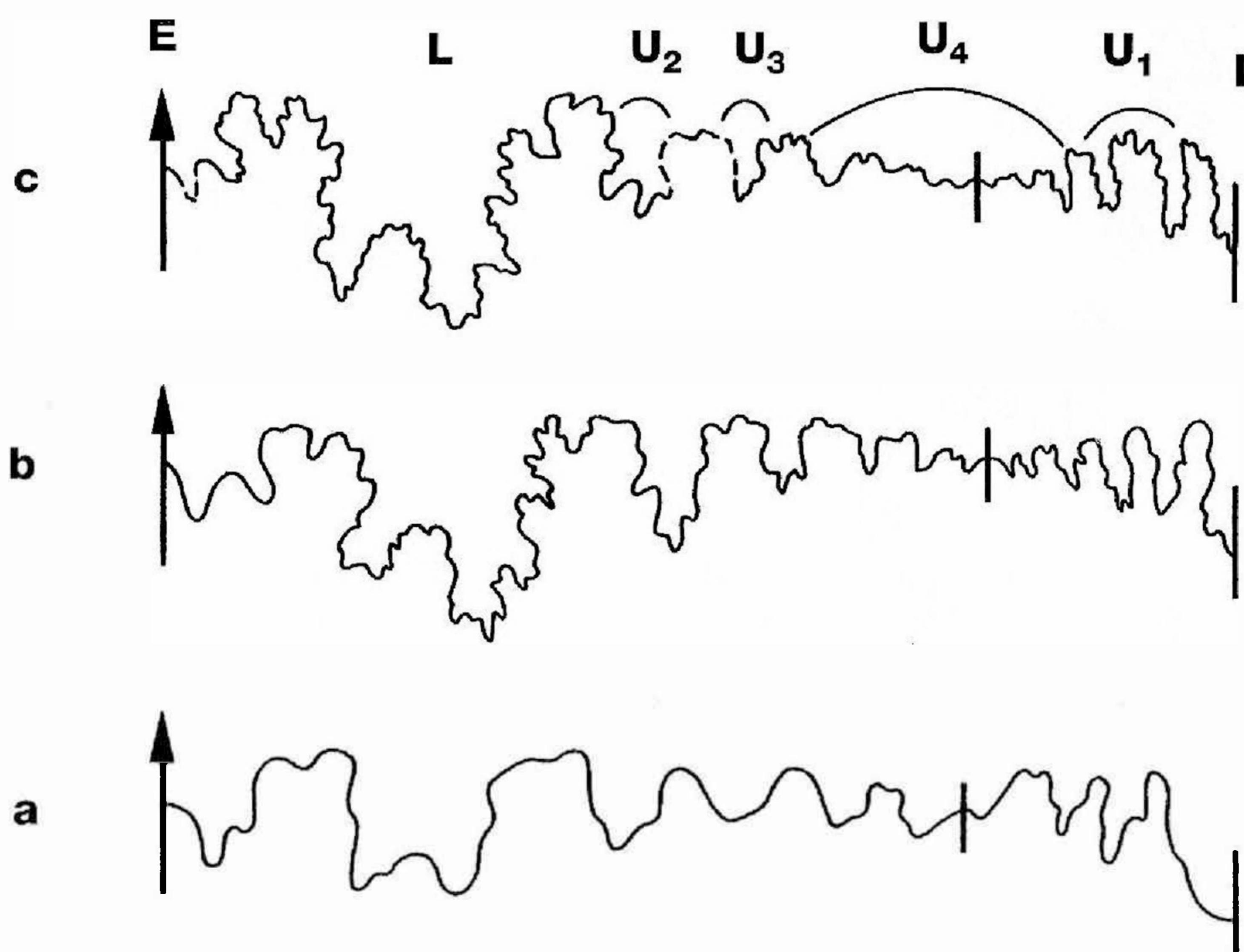
**Macroconch** (♀/M): Diameter of adult phragmocone generally are 58 to 74 mm. Up to phragmocone end the umbilicus has a rounded edge and an almost vertical wall. Whorls become less compressed ( $H/W = c. 1.60 - 1.77$ ) by negative allometry of height ( $H/D = 0.46 \rightarrow 0.40$ ) and the venter narrowly rounded. Ornament becomes subdued, especially on inner flanks, where striae and primaries are barely visible. Secondaries ( $S=20-22$ ) gradually withdraw to outer flanks, become more projected but are interrupted on smooth venter.

Septal suture (Fig. 9) is rather simple and has subradial saddle envelope. Lobe L is wide, asymmetrically trifid and about three times deeper than lobe E.  $U_2$  is similar to L and as deep as E. Saddles are moderately divided and wide. E/L and L/ $U_2$  are similarly indented by two main lobules.

Complete body-chamber reaches at least 80-110 mm diameter. Coiling remains narrow ( $U/D = 0.17 - 0.25$ ) with subvertical wall and rounded edges; whorls are ogival with maximum width at lower third of height and flanks converge into narrowly rounded venter. Ornament becomes subdued, with striae present on smooth lower third of flanks and weak ribbing on outer flanks. Striae begin projected, then bend backwards close to mid-flanks where they accompany subdued, projected ribs ( $S=22-26$ ) which form shallow arcs before disappearing close to venter. Usually there are 2-3 shallow constrictions which are barely visible where ribbing is present. The aperture, preserved only in a few remnants (MLP 29055, 29058, 29067), appears to be simple and parallel to the ornament.

**Microconch** (♀/m): Adult phragmocone is c. 35-55 mm in diameter, and complete (c.  $180^\circ$ ) body-chamber, is c. 55-73 mm. Coiling widens with last whorl ( $U/D =$

Fig. 10: Sutural ontogeny of *Aioloceras argentinum* (BONARELLI) ♂/m, from Estancia La Federica. At H: a, 5.3 mm; b, 19.5 mm; c, 26.8 mm (MLP 29042).



0.20 - 0.22) and umbilical wall remains subvertical with rounded margin. Whorl section is ogival at end of phragmocone, becoming less compressed ( $H/W = 1.60$ ) with body-chamber by negative allometry of height. Maximum width is within lower third of height. Flanks converge towards venter which is narrowly rounded and smooth but broadens towards aperture. Ornament becomes subdued at end of phragmocone and on body-chamber, with ribbing withdrawing progressively to outer flanks. On inner half of flanks striae project, then bend backwards at mid-flank. On outer flanks, ribs ( $S=22-26$ ) form shallow apicad arcs, and disappear on venter. There are one or two barely visible constrictions on last half of body-chamber. Aperture appears to be "simple" and follows the ornament (MLP 29043, 29066), with greatest projection near mid-flank (in the macroconchs the aperture appears to form a shallow concave arc). Septal suture (Fig. 9) is rather simple; L is wide, asymmetrically trifid and deeper than E;  $U_2$  is similar but narrower and smaller, and there is "suturallobenbildung" in  $U_4$  (Fig. 10). Saddles are wide and asymmetrically divided; E/L is smaller than L/U.

#### Measurements:

	D	H	W	U	H/W
<b>BONARELLI &amp; NÁGERA col.</b>					
SEGEMAR 9293					
Holotype, phr.	73.6 c.46	37.5(0.51) 23.9(0.51)	20.2(0.27) 12.5(0.27)	13.2(0.18) 8.8(0.19)	1.85 1.91
SEGEMAR 9301					
Holotype of					
<i>A.argentinum "meseticum"</i> ,					
phr.	65.3 45	29.7(0.45) 20.1(0.44)	16(0.24) 11.2(0.24)	16.2(0.24) 11 (0.24)	1.85 1.79
SEGEMAR 9290					
(BONARELLI & NÁGERA, 1921, as " <i>Uhligella quercifolia</i> ")					
b. ch.	41.8	20.9(0.50)	12.4(0.29)	9.8(0.23)	1.68
SEGEMAR 9309a					
Holotype of					
<i>"Pseudosaynella bonarellii"</i> LEANZA,					
b. ch.	67	32.3(0.48)	18.7(0.28)	16(0.23)	1.72
SEGEMAR 14914					
phr.	44.6	22.6(0.50)	11.6(0.26)	8.7(0.19)	1.94
SEGEMAR 9309b. (BONARELLI & NÁGERA, 1921, pl. 3, fig. 2, as " <i>B. cfr. Stoliczka</i> ")					
b. ch.	c.75.3	33.1(0.44)	21.1(0.28)	16.9(0.22)	1.56
SEGEMAR 9292					
(BONARELLI & NÁGERA, 1921, as " <i>B. Daintreei</i> ")					
b. ch.	61.5	25.6(0.41)	15.7(0.25)	16.2(0.26)	1.66
SEGEMAR 14912					
b. ch.	74	32(0.43)	19.8(0.27)	20.7(0.28)	1.61
<b>Microconchs</b>					
MLP 29043					
b.ch.	72	31.7(0.44)	19.7(0.27)	19(0.26)	1.60
phr.	50	23 (0.46)	13 (0.26)	11.7(0.23)	1.76
MLP 17368					
b.ch.	64.5	30.4(0.47)	16.7(0.26)	14.5(0.22)	1.82
MLP 29060					
b.ch.	55.7	26.2(0.47)	14.6(0.26)	12.2(0.21)	1.79
<b>Macroconchs</b>					
MLP 29055					
b.ch.	92.8	46.1(0.49)	28.5(0.31)	16(0.17)	1.62
MLP 29058					
b.ch.	86	40.5(0.47)	21.9(0.25)	—	1.85
b.ch.	81.4	38.1(0.46)	21.4(0.26)	19.2(0.23)	1.78
b.ch.	67.2	32 (0.47)	18 (0.26)	16.2(0.24)	1.77

MLP 29044	b.ch.	77.8	37.6(0.48)	21.4(0.27)	19 (0.24)	1.85
MLP 29045	phr.	63.1	30 (0.47)	16.9(0.26)	14.4 (0.23)	1.77
MLP 29051	phr.	42.6	19.6(0.46)	12.7(0.29)	11.8(0.27)	1.54
MLP 29436	phr.	103.6	52.6(0.51)	24.6(0.24)	18.2(0.17)	2.14

**Comparisons:** *Aioloceras argentinum* resembles some of the specimens figured from Madagascar under "*Paracleoniceras*" *besairiei* COLLIGNON. There is a particularly striking similarity between the holotype of that species (cf. COLLIGNON, 1949, pl. 18, fig. 2) and the microconchs of *A. argentinum*. As discussed above, all material described by COLLIGNON (1963) under several specific names, but one, apparently belongs to a single species, i.e. "*P.*" *besairiei*. That species also appears to include both macro and microconch, according to the growth stages and diameters of the specimens figured by COLLIGNON (1963). Most of them are incomplete phragmocones ranging to 177 mm in diameter, whilst the holotype is fully adult at only 68 mm. The holotype presumably is a microconch and incomplete larger phragmocones are macroconch.

"*P.*" *besairiei*, type species, belongs without doubt in *Aioloceras*, so that "*Paracleoniceras*" is a junior synonym of that genus. The Madagascan *A. besairiei* agrees with the Patagonian species of *Aioloceras* in coiling ( $U/D = 0.17 - 0.22$  vs. 0.17 - 0.28), whorl dimension ( $H/D = 0.47 - 0.51$  vs. 0.41 - 0.52 and  $W/D = 0.25 - 0.32$  vs. 0.24 - 0.31). *A. argentinum* and *A. besairiei* differ, however, in a number of features. Thus *A. besairiei* has flatter and more convergent flanks, and a broader more rounded venter, and its ornament is generally coarser throughout. *A. besairiei* also appears to be larger, at least for the macroconchs.

Outside Patagonia and Madagascar, *Aioloceras* has been recorded from Australia, where a specimen of unknown age was described by GREGORY & SMITH (1902, p. 142, pl. 22, figs. 1-2) under "*Desmoceras jonesi* n. sp." and transferred to *Aioloceras* by WHITEHOUSE (1926, p. 207). This macroconch, which at 250 mm diameter is still septate, was figured only in lateral view but said to have a "narrow bluntly rounded" venter. No other material of this species has been figured, although 3 fragments from the Aptian of Queensland were tentatively compared by DAY (1974, p. 16, pl. 8, figs. 1-3, text-fig. 4). This material seems to be broader in the larger whorls, whilst the inner whorls (DAY, 1974, pl. 8, fig. 3b) have a rounded venter, differing from that present in *Aioloceras* known from Patagonia and Madagascar.

Albian material of western Pakistan described by SPATH (1930, p. 53, pl. 8, fig. 17a-c) under *Cleoniceras daviesi* SPATH, was compared by him with the Patagonian material of BONARELLI & NÁGERA (1921). The poorly preserved specimen has compressed whorls with rounded venter and flexiradiate ribbing and constrictions on the inner whorls, whilst the outer

whorls appear to be smooth. These features indicate that this species belongs to neither *Cleoniceras* nor *Beudanticeras*. It could be included in *Uhligella* if the smaller specimens figured by SPATH (1930, pl. 8, figs. 7-8, 11) as “*Cleoniceras* sp. juv. ind.” and “*Cleoniceras* sp. nov.? ind.” are the inner whorls. There is a resemblance to *Aioloceras*, but the venter appears to be more rounded. The material is too poor to settle its status. A doubtful *Aioloceras* has also been recorded from the Aptian of the same area by FATMI (1972, p. 324), but the material has not been figured.

*Aioloceras rollerii* (LEANZA, 1970) ♀/M & ♂/m  
Pl. VI, figs. 5a-c; Pl. VII, figs. 1-4; Pl. VIII, figs. 1-3;  
Pl. IX, figs. 1-3; Pl. X, figs. 1-2; Figs. 11, 12a-e.

- 1921. *Beudanticeras* cfr. *Stoliczkai* (KOSSM.).- BONARELLI *in* BONARELLI & NÁGERA, p. 23, pl. 3, figs. 1 and 3.
- 1921. *Beudanticeras Beudanti* (BRONGN.).- BONARELLI *in* BONARELLI & NÁGERA, p. 22, pl. 2, fig. 11; pl. 4, fig. 1.
- 1921. *Beudanticeras* cfr. *Mitchelli* (ETH.).- BONARELLI *in* BONARELLI & NÁGERA, p. 2, pl. 4, fig. 5.
- 1921. *Cleoniceras seunesi* n.f.- BONARELLI *in* BONARELLI & NÁGERA, p. 24 (part).
- 1970. *Beudanticeras rollerii* LEANZA, p. 221, fig. 18.1-2.
- ?1981. *Beudanticeras* sp..- NULLO *et al.*, pl. 2, fig. 3.

**Holotype.** The incomplete phragmocone with part of body-chamber (CPUNC 4366) figured by LEANZA (1970, fig. 18.1-2). Here refigured on pl. VII, fig. 1, from “Arroyo Calafate, 1. Lago Tarn” (*recte* Arroyo Calafate, Lago San Martin, Rio Mayer Formation).

**Material:** Lago San Martin: the holotype; 2 incomplete adult microconch phragmocones with body-chamber (SEGEMAR 9307, 9309c.), “*Beudanticeras* cfr. *Stoliczkai* (KOSSM.)” of BONARELLI (*in* BONARELLI & NÁGERA, 1921, pl. 3, figs. 1 and 3); 7 almost complete adult microconchs (MLP 29070, 29072, 29075, 29057, 29065, 29119, 29156), 5 incomplete microconch body-chambers (MLP 29083, 29090, 29091, 29079) and 1 complete microconch (MLP 29092) [the last five ?adults], and 17 microconch fragments (MLP 29114, 29115, 29120, 29131, 29148, 29162, 29163); one incomplete body-chamber of a ?macroconch (SEGEMAR 9300), “*Beudanticeras* cfr. *Mitchelli* (ETH.)” of BONARELLI (*in* BONARELLI & NÁGERA, 1921, pl. 4, fig. 5); one adult macroconch phragmocone with beginning of body-chamber (SEGEMAR 9299) from BONARELLI & NÁGERA’s original col., “*Beudanticeras Beudanti*” of BONARELLI (*in* BONARELLI & NÁGERA, 1921, p. 22, pl. 2, fig. 11); one adult macroconch phragmocone (SEGEMAR

14904) of same collection, “*Cleoniceras seunesi* n.f.” of BONARELLI (*in* BONARELLI & NÁGERA, 1921, p. 24); 3 almost complete adult macroconchs (MLP 29121, 29122, 29199), 5 incomplete phragmocones, three adults (MLP 29048, 29073, 29096) and two juveniles (MLP 29054, 29088), 4 incomplete macroconch phragmocones with beginning of body-chamber (MLP 29082, 29136, 29144, 29150, 29160), 3 adult macroconch phragmocones with incomplete body chambers (MLP 29089, 29094, 29097), 1 almost complete adult macroconch (MLP 29095), ?1 large macroconch (29093), 11 (+ ?3) incomplete macroconch phragmocones (MLP 29127-29129, 29132, 29134, 29135, 29137, 29145, 29147, 29161, 29155, 29918) and 12 fragmentary macroconchs (MLP 29076, 29080, 29081, 29123-29126, 29140, 29157, 29164), all from Estancia La Federica (loc. A XXII - 21, 22, 26; 19; 71-1, 2, 5, 6, 9, 13, 20, 22, 23, 28; AC4, M1, 3, 4, 5, Mx, My), col. A.C. RICCARDI and F.A. MEDINA (MLP 29918). Lago Cardiel: Two incomplete microconch phragmocones (MLP 6877, 6899), col. UGARTE.

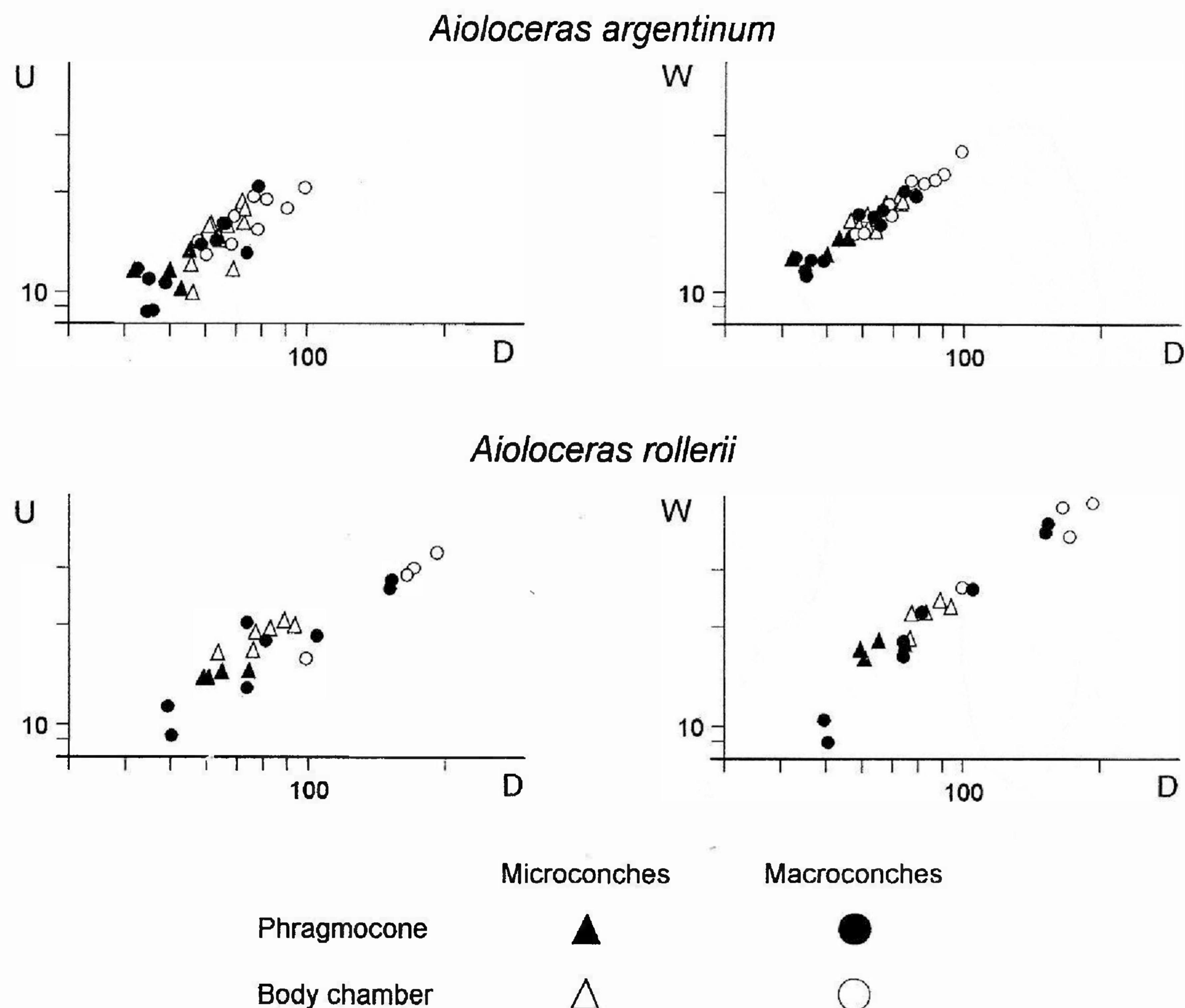
**Diagnosis.** Rather involute and compressed whorls, venter narrowly arched in phragmocone, becoming broader and thicker in the body chamber; inner whorls with falcoid ribbing, usually restricted to upper flank; body-chamber without ornament but bearing 4-6 broad and deep, falcoid constrictions which widen from umbilical margin towards venter.

**Description:** At about 50 mm diameter, the phragmocone is rather evolute ( $U/D = 0.21 - 0.22$ ) with subvertical umbilical wall and rounded margin. Whorls are compressed ( $H/W = 1.8$ ) and ogival with slightly convex flanks and acutely rounded venter. Ornament consists of orad projected primaries ( $P = c.16$ ) on inner third of flank, long secondaries and some intercalatories. Secondaries ( $S = c.30$ ) form a shallow orad arc and are interrupted on venter. At larger sizes, ribbing disappears progressively, beginning on the lower flank. Septal suture is relatively complex, with wide asymmetrically trifid L, two to three times as deep as E. Three to four umbilical lobes are present towards the umbilical seam.

**Macroconch (♀/M):** At about 70 mm diameter, the shell/internal mould is almost smooth, except for 2-4 constrictions, which occur at c. 1/4 whorl intervals up to 105 mm diameter. Phragmocone reaches c. 150-240 mm diameter and is quite evolute ( $U/D = 0.17 - 0.18$ ) and compressed ( $H/W = 1.88 - 2.23$ ). Umbilical wall is steep to vertical with rounded margin. Whorls are ogival with flanks converging into narrowly acute venter. Ribbing is absent or obsolete on upper flanks, formed by blunt, well spaced ribs ( $S = 22$ ) forming an orad concave arc, between which there are faint constrictions. Venter is smooth.

Body-chamber reaches 192 - 320 mm diameter. Coiling is as involute as in phragmocone. Specimens of average diameter are more compressed ( $H/W = 1.97 - 2.5$ ) than

Fig. 11: Plots of umbilical width (U) and whorl width (W) against diameter (D) for *Aioloceras argentinum* (BONARELLI) ♀/M & ♂/m, and *A. rollerii* (LEANZA) ♀/M & ♂/m.



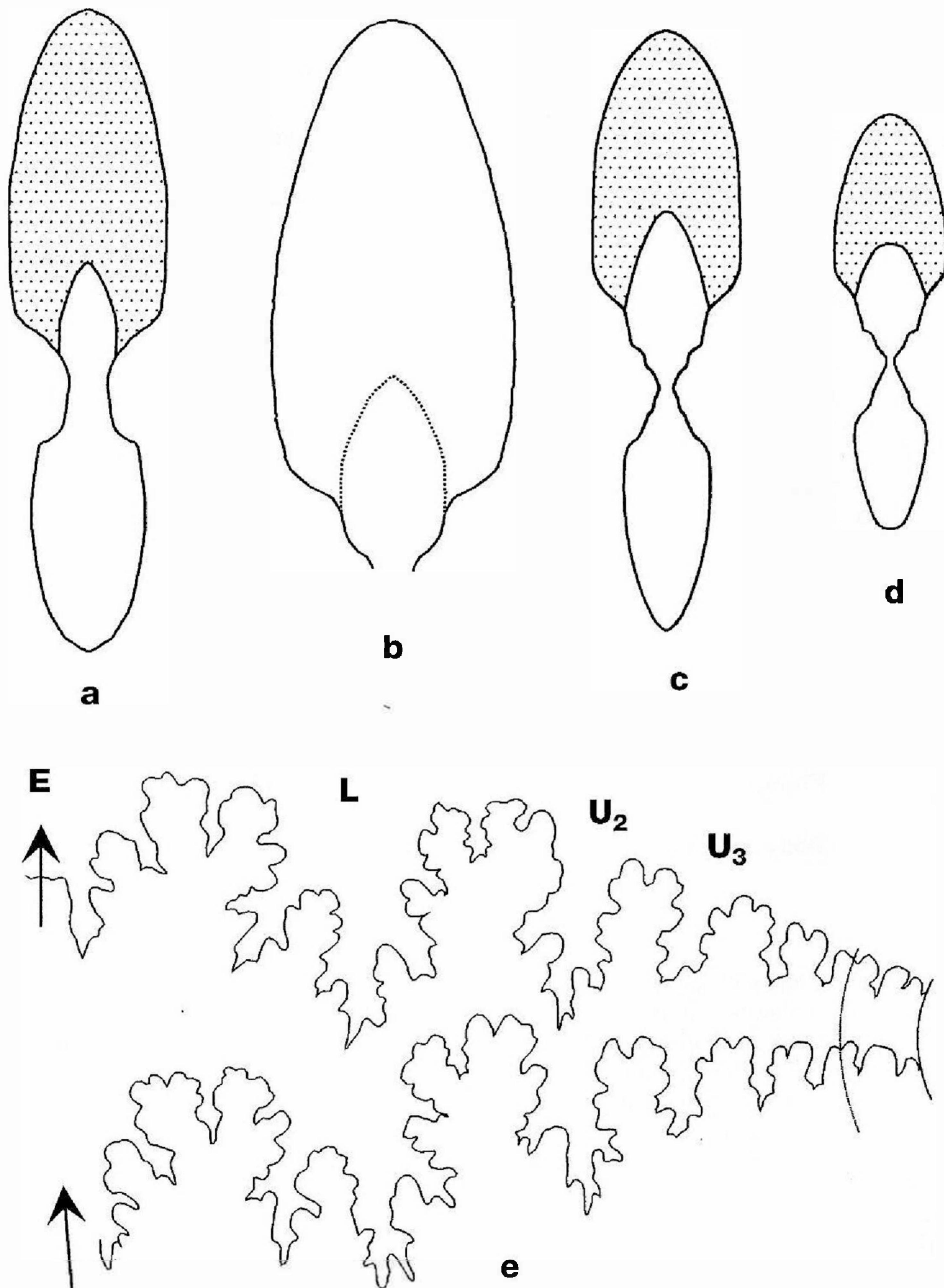
the largest ones ( $H/W = 1.76$ ), with ogival section that becomes broader and more rounded towards the aperture. Surface is smooth except for fine striae and 1-2 very shallow constrictions close to the aperture.

**Microconch (♂/m):** Phragmocone, known only close to its end, attains a maximum diameter of c. 60-75 mm. Between 40-75 mm, it is rather evolute ( $U/D = 0.21 - 0.24$ ) with subvertical umbilical wall and rounded margin. Section is compressed ogival with maximum width in inner third ( $H/W = 1.6 - 1.84$ ). Flanks are slightly convex and converge into narrowly rounded venter. Ornament consists of obsolete ribs on inner third of flanks. Where better developed, they are single and projected, bend backwards and divide in twos before forming a

shallow arc orad concave, before becoming obsolete on venter ( $S = 22$ ).

Body chamber reaches c. 70 - 109 mm. Umbilicus remains rather evolute ( $U/D = 0.21 - 0.24$ ) with subvertical wall and rounded margin. Whorls are compressed ( $H/W = 1.63 - 1.90$ ) with slightly convex flanks and a thicker and more broadly rounded venter than on phragmocone. Ribbing becomes restricted to outer flank or disappears altogether at beginning of body-chamber. The internal mould is crossed by 4-6 deep and wide constrictions. They begin on the umbilical wall and are projected to mid-flank where they form a shallow, apicad concave arc. On outer flank they bend forward forming a shallow orad arc before crossing the venter.

Fig. 12: *Aioloceras rollerii* (LEANZA) ♀/M & ♂/m. **a-d**, cross sections (X1) of: **a**, macroconch SEGEMAR 9299 (see Pl. X, figs. 2a-b); **b**, macroconch SEGEMAR 14904 (see Pl. X, figs. 1a-b); **c**, microconch MLP 29070 (see Pl. VII, figs. 3a-b); **d**, microconch MLP 29072 (see Pl. VII, figs. 2a-b). **e**, sutures of macroconch MLP 29918 at H = 16.3 mm.



At beginning of body-chamber they are parallel to ribbing, but towards the aperture become more projected. Constriction width increases from umbilicus towards venter. Surface is smooth between constrictions or has obsolete growth lines.

#### Measurements (in mm):

	D	H	W	U	H/W
<b>Microconchs</b>					
Holotype, CPUNC 4366					
b.ch.	c.69.5	34(0.49)	+15.7(0.22)	17.6(0.25)	2.16
SEGEMAR 9309c (BONARELLI & NÁGERA, pl. 3, fig. 3, as "B. cfr. stoliczkai")					
b. ch.	76.3	36.9(0.48)	18.7(0.24)	17(0.22)	1.97
phr.	51.8	23.9(0.46)	12.7(0.24)	—	1.88
SEGEMAR 9307 (BONARELLI & NÁGERA, pl. 3, fig. 1, as "B. cfr. stoliczkai")					
b. ch.	76	34.7(0.45)	20.2(0.26)	c. 20(0.26)	1.71
MLP 29065					
b.ch.	89	40(0.45)	24.4(0.27)	20.8(0.23)	1.64
MLP 29070					
b.ch.	94	44.5(0.47)	23.3(0.25)	20.2(0.21)	1.90
MLP 29072					
b.ch.	77.1	36.5(0.47)	22.3(0.29)	19.2(0.24)	1.63
<b>Macroconchs</b>					
SEGEMAR 9299 (BONARELLI & NÁGERA, pl. 2, fig. 11, as "B. beudanti")					
b. ch.	99.4	52.5(0.52)	26.6(0.26)	16(0.16)	1.97
phr.	74	36.8(0.49)	18.3(0.25)	13(0.17)	2.01
SEGEMAR 9300 (BONARELLI & NÁGERA, 1921, pl. 4, fig. 5, as "B. cfr. Mitchellii")					
b. ch.	?94	44.3(0.47)	23.5(0.25)	—	1.88
SEGEMAR 14904 (BONARELLI & NÁGERA, as "C. seunesi")					
phr.	c.151.5	78.5(0.52)	39(0.25)	26(0.17)	2.01
phr.	50.6	21.4(0.42)	9(0.17)	9.3(0.18)	2.37
MLP 29054					
phr.	81.2	41.5(0.51)	22.4(0.27)	18.1(0.22)	1.85
MLP 29121					
b.ch.	280	—	—	—	—
phr.	205	100(0.49)	52(0.25)	—	1.92
MLP 29122					
b.ch.	245	110(0.45)	55(0.22)	57.7(0.23)	2
phr.	190	86.8(0.46)	47.1(0.25)	—	1.84

**Comparison:** *A. rollerii* differs from *A. argentinum* in whorl section and ornament of the body-chamber. In *A. rollerii* the whorls become thicker with more broaden rounded venter and the ornament consists almost exclusively of 4 to 6 wide and deep constrictions with intervening smooth spaces. *A. rollerii* is close to Madagascan representatives of *Aioloceras*. The range, in U/D, W/D and H/D of the entire Madagascan material is almost identical to that present in *A. rollerii* of Patagonia. Especially large Madagascan macroconchs match *A. rollerii* ♀/M. The microconchs are also identical, as are the constrictions. The only difference is the stronger ribbing of some Madagascan specimens. Before considering the Patagonian and Madagascan material as conspecific it is therefore necessary to revise the systematics of the various African "species".

#### *Aioloceras aff. rollerii* (LEANZA) Pl. VII, fig. 5

**Material:** 5 almost complete body-chambers with part of phragmocones (MLP 29165-29169), 2 incomplete body-chambers (MLP 29170, 29171), 1 incomplete phragmocone and body-chamber (MLP 29172), from KA1-3, Estancia Kachaike, col. A.C. RICCARDI.

**Description:** Shell diameter ranges from 60 to 75 mm, with phragmocone range of 33 - 51 mm D. Body-chamber is slightly longer than 1/2 whorl. No inner septate whorls are available.

Shell is quite involute ( $U/D = 0.18 - 0.21$ ), with subvertical to vertical umbilical wall and rounded umbilical margin. Whorl section is subogival compressed ( $H/W = 2.2 - 2.4$ ) with slightly convex to subparallel flanks converging into narrowly arched venter, which broadens towards the aperture. Ornament consists of fine ribbing or striae mostly on outer flank, prorsiradiate on inner third of flank forming shallow, apicad concave arc below mid-flank, and slightly projected before crossing venter. The last 1/4 whorl has 2-3 shallow constrictions following the rib pattern. Septal suture is not available.

#### Measurements (in mm):

	D	H	W	U	H/W
MLP 29165					
b. ch.	57	29.7(0.52)	13.5(0.24)	10.8(0.19)	2.2
phr.	35.7	—	—	—	—
MLP 29166					
b.ch.	75	33.4(0.44)	—	15.9(0.21)	—
phr.	51	—	—	—	—
MLP 29167					
b.ch.	73.7	36.2(0.49)	—	14 (0.19)	—
phr.	51	—	—	—	—
MLP 29171					
b.ch.	40	22.2(0.55)	9.3(0.23)	8.4(0.21)	2.4
MLP 29168					
b.ch.	62	32.5(0.52)	—	11 (0.18)	—
phr.	37.3	—	—	—	—
MLP 29169					
b.ch.	50.5	25(0.49)	—	9.2(0.18)	—
phr.	33	—	—	—	—

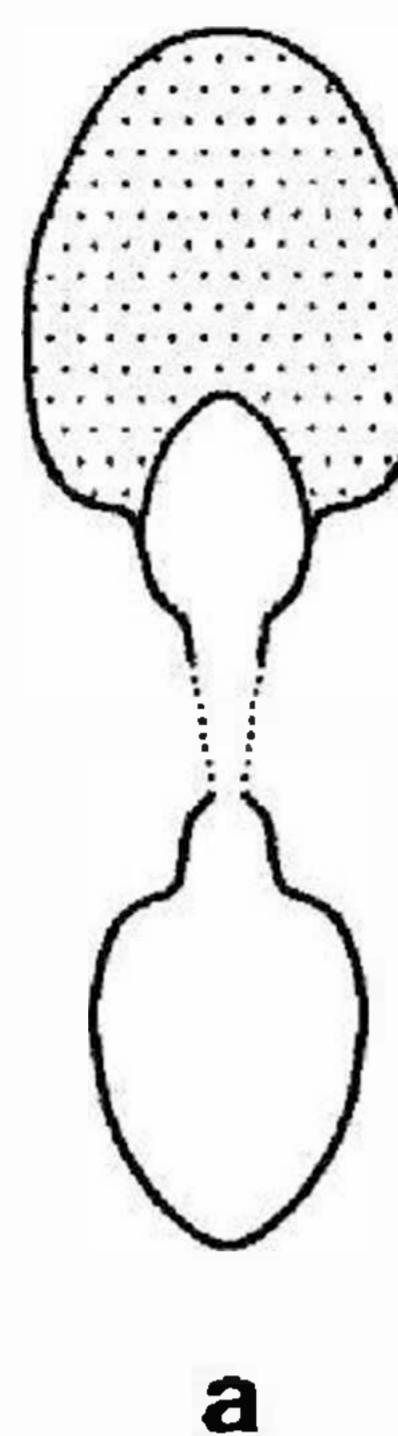
**Remarks:** This material differs from *A. rollerii* in being smaller ( $D = 60 - 75$  vs.  $70 - 109$ ), more involute ( $U/D = 0.18 - 0.21$  vs.  $0.21 - 0.24$ ), more compressed ( $H/W = 2.2 - 2.4$  vs.  $1.63 - 1.90$ ), and in the more acute venter, finer ribbing and less conspicuous constrictions.

#### ?*Aioloceras* sp. Pl. X, fig. 3; Fig. 13

**Material:** One partially preserved phragmocone with part of body-chamber (MLP 29159), from Estancia La Federica, lago San Martin (loc. Mx), col. A.C. RICCARDI.

**Description:** Relatively small to medium size ( $D = 71.3$ ), quite evolute ( $U/D = 0.31$ ), with subvertical umbilical wall and rounded margin. Ovate section has maximum width in lower third of flank, which are arched and converge into broadly rounded venter. Phragmocone ornament has blunt ribs ( $P = 12$ ) which on umbilical slope are fine and prorsiradiate, and become

Fig. 13: ?*Aioloceras* sp., cross section (X1) of MLP 29159 (see Pl. X, figs. 3a-b).



more prominent on flank where they project and some partly divide below mid-flank; secondaries ( $S = c.$  16) form a shallow (adorad concave) arc on upper flank and become obsolete on crossing venter. On body-chamber ribbing becomes obsolete on inner flank. Last whorl has about six shallow and barely visible constrictions.

#### Measurements (in mm):

	D	H	W	U	H/W	P	S
MLP 29159							
b.ch.	71.3	30.8(0.43)	21.4(0.30)	22.2(0.31)	1.44	12	16

**Remarks:** This species differs from other *Aioloceras* in the relatively wide umbilicus, rounder whorl section ( $H/W = 1.44$ ) and the coarser, sparser ribbing. In coiling and ribbing, it somewhat resembles *Uhligella walleranti* figured by JACOB (1908, pl. 3, fig. 2), although this species (and genus) is usually more compressed and involute, and with bullae or tubercles on the umbilical margin.

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#### Appendix 1

**List of species and figured material referred to Albian Beudanticeratinae and Cleoniceratinae**  
(Names in quotation marks are considered by us as generically and/or specifically incorrect. In some cases their correct placement is indicated).

**Beudanticeratinae BREISTROFFER, 1953**  
**Genus *Beudanticeras* HITZEL, 1905**  
(= *Boliteceras* WHITEHOUSE, 1928; *Rapidoplacenticeras* ALABUSHEV, 1988)

**Type species:** *Ammonites beudanti* BRONGNIART in

CUVIER & BRONGNIART, 1822, by original designation.

***Beudanticeras beudanti* (BRONGNIART)**, 1822, p. 610, pl. 7, fig. 2 (refigured in SPATH, 1923, text-fig. 12a-b and KENNEDY, 1993, figs. 1-2); D'ORBIGNY, 1840, p. 278, pl. 33, figs. 1-3 (figs. 2-3 as "var. *exhornata*" in BONARELLI & NÁGERA, 1921, p. 22), pl. 34, figs. 1-3, France; QUENSTEDT, 1849, p. 222, pl. 17, fig. 10 (as "var. *exhornata*" in BONARELLI & NÁGERA, 1921, p. 23, refiugured in SEITZ, 1932, pl. 17, fig. 3a-d), Germany; SPATH, 1923, p. 49, pl. 2, fig. 4a-d (refiugured in CASEY, 1961b, text-fig. 46a-c), and p. 53, pl. 3, fig. 1a-c [as "*Beudanticeras sphaerotum* (SEELEY)"], England; ?PASSENDORFER, 1930, p. 645, fig. 14, Poland; ?HAAS, 1942, p. 165, pl. 42, fig. 2, Angola; ?COLLIGNON, 1966, p. 15, pl. 3, fig. 1, Tarfaya, Morocco; ?SCHOLZ, 1979, p. 68, pl. 13, fig. 1, 6, Hungary; FÖLLMI, 1989, p. 140, pl. 10, fig. 3, Austria; MARCINOWSKI & WIEDMANN, 1990, p. 59, pl. 7, fig. 1, Poland; SEYDEMAMI & IMMEL, 1995, p. 388, fig. 30a-b; 1996, p. 11, pl. 1, figs. 4-7, pl. 2, fig. 4, pl. 6, fig. 5-6, Iran; GEYER *et al.*, 1997, p. 224, figs. 2e, 3e, Sinai, Egypt; DELAMETTE *et al.*, 1997, pl. 14, fig. 8, pl. 18, fig. 3, pl. 38, fig. 4, Alps, France.

*non*: PICTET & ROUX, 1847, pl. 2, fig. 3 (see PARONA & BONARELLI, 1897, p. 85); PICTET & CAMPICHE, 1858, p. 277, pl. 40, figs. 1-2 (= *Beudanticeras laevigatum*), 3-4 (= *Beudanticeras sanctae crucis*), Switzerland; TRAUTSCHOLD, 1861, pl. 12, fig. 2, Russia (=? *Beudanticeras laevigatum*); STOLICZKA, 1865, p. 142, pl. 71, figs. 1-4; pl. 72, India [= "Puzosia soliczkai" (KOSSMAT), = *Bhimaites*]; WHITEAVES 1884: 205, pl. 26, fig. 1, W. Canada [= *Desmoceras (Pseudouhligella) dawsoni* (WHITEAVES), in MATSUMOTO, 1959, p. 59]; LAPPARENT & FRITEL, 1888, pl. 14, figs. 13-14, France (= *B. laevigatum*); PARONA & BONARELLI, 1897, p. 86, pl. 2, fig. 6, France (as "var. *exhornata*" in BONARELLI & NÁGERA, 1921, p. 23, =? *B. laevigatum*); CHOUFFAT 1903, p. 22, pl. 6, fig. 2, Mozambique (as "var. *petersi*"); DOUVILLÉ, 1916, p. 107, pl. 12, fig. 8, Sinai, Egypt (=? *Uhligella walleranti*, see MAHMOUD, 1955, p. 13 and WIEDMANN & DIENI, 1968, p. 128); BONARELLI & NÁGERA 1921: 22, pl. 2, fig. 11, pl. 4, fig. 1, Patagonia (= *Aioloceras rollerii*); COLLIGNON, 1929, p. 19, pl. 2, fig. 1, Madagascar; PAINVIN, 1939, pl. 22, France (=? *Beudanticeras newtoni* CASEY); WIEDMANN & DIENI, 1968, p. 128, pl. 11, fig. 10, Sardinia; THOMEL, 1980, p. 124, fig. 247, France.

"*Beudanticeras alamoense*" ANDERSON, 1958, p. 213, pl. 5, fig. 2-2a, northern California, USA [= *Desmoceras (Pseudouhligella) dawsoni*, see MATSUMOTO, 1959, p. 59].

***Beudanticeras albense* BREISTROFFER**, 1947, p. 79; PICTET in PICTET & ROUX, 1847, pl. 2, fig. 4 (? refiugured in DELAMETTE *et al.*, 1997, pl. 38, fig. 3); PICTET & CAMPICHE, 1861, p. 280, pl. 39, figs. 3-7, Switzerland (as "Ammonites parandieri"); ?DESTOMBES *et al.*, 1973, p. 62, text-fig. 4a-b, France; COLLIGNON, 1949, p. 58, pl. 11, fig. 2, Madagascar.

"*Beudanticeras ambanjabense*" COLLIGNON, 1963, Madagascar (= *Beudanticeras hourcqi*).

"*Beudanticeras ampanihense*" COLLIGNON, 1963, p. 78, pl. 270, fig. 1170, Madagascar.

"*Beudanticeras arduennense* BREISTROFFER" 1947, France (= *Beudanticeras dupinianum*).

"*Beudanticeras argonauticum*" ANDERSON, 1958, p. 213, pl. 9, figs. 1-2, northern California, USA [= *Desmoceras (Pseudouhligella) dawsoni*, see MATSUMOTO, 1959, p. 59)].

"*Beudanticeras (?) besairiei*" BREISTROFFER, in BESAIRIE, 1936, p. 156, pl. 15, figs. 17-18, Madagascar (= *Uhligella cf. balmensis*).

"*Beudanticeras*" *bulbosum* CASEY, 1961b, p. 156, pl. 28, figs. 3-4, England (=? *Uhligella*).

"*Beudanticeras burchanense*" EGOYAN, 1969, p. 175, pl. 25, figs. 1-5, N. Caucasus, Russia (=? *Zuercherella*).

"*Beudanticeras caseyi*" COLLIGNON, 1963, p. 72, pl. 267, fig. 1165, Madagascar.

***Beudanticeras daintreei* (ETHERIDGE)**, 1872, pl. 24, fig. 1, apert. view, 3 (type species of "Boliteceras", refiugured in ETHERIDGE, 1892, p. 495, pl. 29, figs. 1, 3, WHITEHOUSE, 1928, p. 203, pl. 26, fig. 2, HILL *et al.*, 1968, p. K18, pl. K8, fig. 4); ?ETHERIDGE, 1901, p. 30, pl. 1, fig. 3, pl. 2, fig. 6; ?ETHERIDGE, 1902, p. 44, pl. 7, fig. 1; including "Boliteceras perlatum" WHITEHOUSE, 1928, p. 204, pl. 26, fig. 3 (same specimen as in ETHERIDGE, 1872, pl. 24, fig. 1, lateral view, and ETHERIDGE, 1892, p. 495, pl. 29, fig. 2; refiugured in WRIGHT, 1996, fig. 61.4); all Queensland, Australia.

*non* BONARELLI & NÁGERA, 1921, p. 23, pl. 3, fig. 5, Patagonia (= *Aioloceras argentinum*).

"*Beudanticeras diabloense*" ANDERSON, 1958, p. 214, pl. 10, fig. 4; GABB, 1869, pl. 22, fig. 13 (as "Ammonites jugalis"), California (=? *Desmoceras*).

***Beudanticeras dupinianum* (D'ORBIGNY)**, 1841, p. 276, pl. 81, figs. 6, 8 (refiugured in DOUVILLÉ, 1911, pl. 218 –*non* fig. M-, SPATH, 1923, text-fig. 14 and CASEY, 1961b, text-fig. 48a-g), France; PICTET & ROUX, 1847, pl. 2, fig. 3, Switzerland; PERVINQUIERE, 1907, p. 133, pl.

5, figs. 16-17, Tunisia (as var. *africanum*, ?non KENNEDY *et al.*, 2000, p. 667, fig. 40y); DOUVILLÉ, 1911, pl. 218, fig. M, France (type of "*Beudanticeras ligatum* var. *arduennensis*" BREISTROFFER, 1947, p. 79; refigured in CASEY, 1961b, p. 154, text.-fig. 48h); SPATH 1923, p. 60, pl. 4, fig. 1a-d; ?PASSENDORFER, 1930, p. 643, pl. 3, figs. 52a-b, Poland; SEITZ, 1932, pl. 17, fig. 4, Germany; COLLIGNON, 1950, p. 39, pl. 6, fig. 4. Madagascar; ?ALMELA & DE LA REVILLA, 1957, p. 25, pl. 6, fig. 2, Spain; CASEY, 1961b, p. 152, pl. 26, fig. 11, pl. 27, figs. 6-8 (fig. 8a-b as var. *evolutum*); pl. 28, fig. 5, p. 155, pl. 27, fig. 8, England; FÖLLMI, 1989, p. 138, pl. 9, fig. 13, Austria; AVRAM *et al.*, 1993, p. 292, fig. 13d, Rumania; SEYED-EMAMI & IMMEL, 1996, p. 13, pl. 4, figs. 2-4, Iran; KENNEDY *et al.*, 1997, p. 465, pl. 1, figs. 1-4, France; includes "*Beudanticeras arduennense*" BREISTROFFER (in SPATH, 1923, p. 58, pl. 3, fig. 3c-d; CASEY, 1961b, p. 156, pl. 27, fig. 1, pl. 28, figs. 9-11, England; ?COLLIGNON, 1963, p. 74, pl. 268, fig. 1166, Madagascar; ?FÖLLMI, 1989, p. 138, pl. 9, fig. 12, Austria; SEYED-EMAMI & IMMEL, 1996, p. 12, pl. 2, fig. 3, pl. 4, fig. 1, Iran; and ?"*Beudanticeras perchoisense*" DESTOMBES, 1979, p. 65, pl. 4-19, figs. 1a-b, France).

*non*: PICTET, *in* PICTET & ROUX, 1847, p. 291, pl. 2, fig. 4, Switzerland; KARSTEN, 1858, p. 112, pl. 5, fig. 5, Colombia; COLLIGNON, 1950, p. 39, pl. 6, fig. 4; COLLIGNON, 1963, p. 71, pl. 267, fig. 1163, Madagascar (as "*Beudanticeras dupini* var. *percostata*"); BACCELLE & GARAVELLO, 1967, p. 93, pl. 1, figs. 2a-c, Italy; ?DESTOMBES *et al.*, 1973, p. 62, pl. 3, fig. 8a-b; France.

**"*Beudanticeras dupiniforme*" COLLIGNON**, 1963, p. 78, pl. 270, fig. 1171, Madagascar.

**"*Beudanticeras flindersi*" WHITEHOUSE**, 1928, Queensland, Australia (= *Beudanticeras mitchelli*).

**"*Beudanticeras hatchetense*" SCOTT**, 1940, p. 1000, pl. 56, figs. 3-5 (= ? *B. dupinianum* D'ORBIGNY), New Mexico, USA; *non* YOUNG, 1993, p. 167, figs. 2: 4-6, 14-15, 3: 5, 7, Mexico.

***Beudanticeras haydeni* (GABB)** 1864, p. 62, pl. 10, fig. 8, 8a; MURPHY, 1956, p. 2119, fig. 6; ANDERSON, 1958, p. 212, pl. 8, fig. 1, 1a; ?MURPHY & RODDA, 1960, p. 851, pl. 104, fig. 4, pl. 105, figs. 1-2; 1996, fig. 5A, northern California, USA.

*non*: ANDERSON, 1938, pl. 48, figs. 2-3, California (= *Brewericeras breweri*).

**"*Beudanticeras hirtzi*" COLLIGNON**, 1950, Madagascar (= *Beudanticeras hourcqii*).

***Beudanticeras hourcqii* COLLIGNON**, 1949, p. 59, pl. 10, figs. 5-6, pl. 11, figs. 1, 1a-b; 1963, p. 76, pl. 269, fig. 1169, Madagascar; including "*Beudanticeras hirtzi*" COLLIGNON, 1950, p. 42, pl. 8, fig. 1, Madagascar; FÖRSTER, 1975, p. 213, pl. 10, figs. 3-5, Mozambique; "*Beudanticeras ambanjabense*" COLLIGNON, 1963, p. 82, pl. 272, fig. 1174 and "*Beudanticeras subrotundum*" COLLIGNON, 1963, p. 82, pl. 272, fig. 1175, Madagascar.

**"*Beudanticeras ingente*" WHITEHOUSE**, 1928, p. 202, pl. 25, fig. 1, Queensland, Australia (= ? *Desmoceras*).

**"*Beudanticeras komihevitraense*" COLLIGNON**, 1950, p. 41, pl. 6, fig. 3; 1963, p. 80, pl. 271, fig. 1172, Madagascar.

***Beudanticeras laevigatum* (J. DE C. SOWERBY)**, 1827, p. 93, pl. 549, fig. 1, England (refigured in SPATH, 1923, text-fig. 13 and CASEY, 1961b, text-fig. 49a-b); PICTET & CAMPICHE 1858-1860, p. 277, pl. 40, figs. 1, Switzerland (as "*Ammonites beudanti*"); ?TRAUTSCHOLD, 1861, p. 442, pl. 12, fig. 2, Russia (as

### Plate I All figures in natural size

Figs. 1-3: *Beudanticeras revoli* (PERVINQUIERE), Lower Albian, Lago Cardiel.

1a-e: Incomplete phragmocone, MLP 29027, a, lateral view, b-d, lateral, ventral and apertural views of inner whorls, e, lateral view of intermediate whorls. Puesto Policia.

2: Incomplete ?adult phragmocone, MLP 29025, lateral view. Estancia La Victorina.

3a-c: Holotype of "*Cleoniceras cardielense*" Leanza, incomplete phragmocone. CPUNC 4316, lateral, ventral and apertural views.

Fig. 4: *Beudanticeras cf. laevigatum* (J. DE C. SOWERBY), incomplete phragmocone, MLP 29032, lateral view. Lower Albian, La Horqueta, Lago Cardiel.



"*Ammonites beudanti*"); LAPPARENT & FRITTEL, 1888, pl. 14, figs. 13-14, France (as "*A. beudanti*"); PARONA & BONARELLI, 1897, p. 86, pl. 11, fig. 6, France (as "*Cleoniceras beudanti*"); SPATH, 1923, p. 55, pl. 3, fig. 2a-c, CASEY, 1961b, p. 157, pl. 28, fig. 6a-b, England; FÖLLMI, 1989, p. 139, pl. 9, fig. 14, Austria; KELLER *et al.*, 1989, p. 277, pl. 2, fig. 1a-b, Germany; DELAMETTE *et al.*, 1997, pl. 22, fig. 7, France; including: ?"*Beudanticeras sanctae crucis*" BONARELLI, in BONARELLI & NÁGERA, 1921; PICTET & CAMPICHE 1858-1860, p. 277, pl. 40, figs. 3-4, France.  
*non*: J. DE C. SOWERBY, 1827, p. 135, pl. 570, fig. 3, England; DESTOMBES *et al.*, 1973, p. 61, pl. 3, fig. 7a-b, France.

***Beudanticeras mitchelli* (ETHERIDGE) 1872**, p. 345, pl. 23, fig. 1 (refigured in ETHERIDGE, 1892, pl. 30, fig. 1 and WHITEHOUSE, 1928, p. 201, pl. 25, fig. 2); including "*Beudanticeras flindersi*" WHITEHOUSE, 1928, pl. 25, fig. 3; both Queensland, Australia.

*non*: BONARELLI in BONARELLI & NÁGERA, 1921, p. 24, pl. 4, fig. 5, Patagonia (= *Aioloceras rollerii*).

***Beudanticeras newtoni* CASEY**, 1961b, p. 147, pl. 26, fig. 12, pl. 27, figs. 2-5, pl. 28, figs. 7-8, pl. 29, fig. 2, text-fig. 47 a-c, e-f, England; FÖLLMI, 1989, p. 139, pl. 10, fig. 2, Austria; including "*Beudanticeras ligatum* (NEWTON & JUKES-BROWNE)", SPATH, 1923, p. 58, pl. 3, fig. 3a-b, e, England; SEITZ, 1932, pl. 17, fig. 4, Germany; ?PAINVIN, 1939, pl. 22, France (as "*Desmoceras Beudanti*"); ?WIEDMANN & NEUGENBAUER, 1978, p. 711, pl. 2, fig. 2, DSDS 363, Walvis Ridge, South Atlantic; ?RENZ, 1979, p. 364, pl. 2, fig. 2a-b, DSDS 398D, south of Vigo Seamount, North Atlantic; SAVELIEV, 1992, pl. 36, fig. 2, Kazakhstan; SEYED-EMAMI & IMMEL, 1996, p. 12, pl. 1,

fig. 3, pl. 2, fig. 1-2, Iran; KENNEDY *et al.*, 1997, p. 464, pl. 1, figs. 9-10, pl. 4, figs. 1-4, pl. 5, figs. 10-11, pl. 8, figs. 3-5, 8-9 and pl. 10, fig. 7, France (as "*Beudanticeras laevigatum*").  
*non*: ORLOV, 1958, pl. 51, fig. 10, Kazakhstan (as "*Beudanticeras ligatum*"); KENNEDY & KOLLMANN, 1979, p. 7, pl. 3, figs. 1-4, 6-7, 10, Austria.

**"*Beudanticeras perchoisense*" DESTOMBES**, 1979, France (=? *Beudanticeras dupinianum*), France.

**"*Beudanticeras ? planulatum*" EGOYAN**, 1969, pl. 14, fig. 6, N. Caucasus, Russia (=? *Zuercherella*).

**"*Beudanticeras rectisulcatum*" COLLIGNON** in BESAIRIE, 1936, p. 192, pl. 21, figs. 10-11, text-fig. 10j, Madagascar.

***Beudanticeras revoili* (PERVINQUIERE)**, 1907, p. 131, pl. 5, figs. 13-15, C, text-fig. 48, Tunisia; ?PETKOVICH, 1913, p. 71, pl. 4, fig. 1, 1a, 2, 2a, Serbia (as "*Uhligella kiliani*"); PASSENDORFER, 1930, p. 644, pl. 4, fig. 62, Poland (refigured in MARCINOWSKI & WIEDMANN, 1990, p. 59, fig. 25e-f); PIATNITZKY, 1938, p. 79, pl. 8, fig. 38, Patagonia (as "*Beudanticeras cfr. stoliczkai*" = "*Anadesmoceras constrictum*" LEANZA, 1970); ?TAVANI, 1948, p. 36, pl. 8, fig. 4, Somalia; COLLIGNON, 1950, p. 40, pl. 7, fig. 1, Madagascar; ?MAHMOUD, 1955, p. 98, pl. 5, figs. 19-20, Sinai, Egypt (as "var. *elegans*"); ALMELA & DE LA REVILLA, 1957, p. 25, pl. 6, fig. 1, Spain; COLLIGNON, 1963, p. 71, pl. 267, fig. 1164, pl. 268, fig. 1167, Madagascar; LEANZA, 1970, p. 228, figs. 25, 1.2, Patagonia (as "*Cleoniceras (Neosaynella) cardielense*"); ?MARTÍNEZ, 1979, p. 345, pl. 1, fig. 4a-c, Spain [as "*Beudanticeras ("Uhligella") rebouli*"; refigured in MARTÍNEZ, 1982, p. 79, pl. 6, fig. 6a-c].

**"*Beudanticeras? robustum*" WARREN**, 1947, p. 122, pl. 30, figs. 7-8, NW Canada.

**"*Beudanticeras rollerii*" LEANZA**, 1970, Patagonia (= *Aioloceras rollerii*).

## Plate II

All figures in natural size unless stated otherwise

- Figs. 1a-b: *Beudanticeras revoili* (PERVINQUIERE), Lower Albian, Puesto Policía, Lago Cardiel, incomplete adult phragmocone with beginning of body chamber, MLP 29029, ventral and lateral views, X 0.5.
- Figs. 2a-b: *Beudanticeras* sp., Lower Albian, west of Estancia Cerro Bayo, Lago Cardiel, adult phragmocone with incomplete body chamber, MLP 29034, ventral and lateral views, X0.5
- Figs. 3-4: ?*Uhligella* sp. b, Lower Albian, Estancia La Victorina, Lago Cardiel.  
 3a-b: Incomplete phragmocone, MLP 29037b, lateral and ventral views.  
 4a-b: Incomplete phragmocone, MLP 29037a, lateral and apertural views.



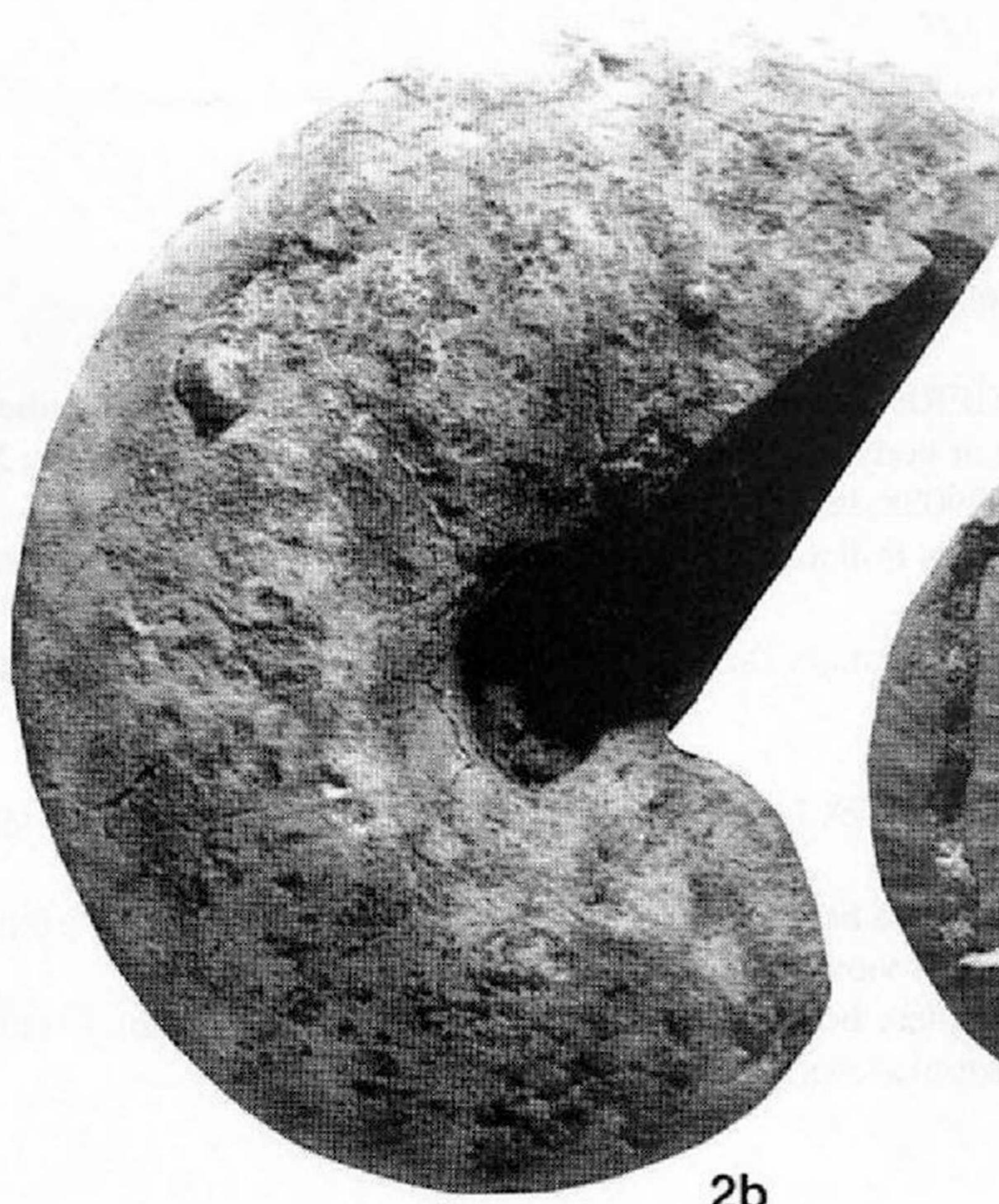
1a



1b



2a



2b



4a



4b



3a



3b

*"Beudanticeras sanctaecrucis"* BONARELLI in BONARELLI & NÁGERA, 1921, France (=? *Beudanticeras laevigatum*).

*"Beudanticeras shikokuense"* YABE & SHIMIZU, SHIMIZU, 1931, p. 26, pl. 4, figs. 5-6, Japan [= *Desmoceras (Pseudouhligella)*, see OBATA & MATSUMOTO, 1977].

*"Beudanticeras sphaerotum (SEELEY)"*, SPATH, 1923, pl. 3, fig. 1a-c, England (= *Beudanticeras beudanti*).

*"Beudanticeras stoliczkai"* (KOSSMAT) 1895, p. 119, pl. 18, fig. 6 (see BONARELLI & NÁGERA, 1921, p. 23); STOLICZKA, 1865, pl. 142, pl. 71, figs. 2-4, pl. 72, figs. 1-2, India (as "Ammonites Beudanti"; = *Bhimaites*).

*non*: BONARELLI & NÁGERA, 1921, p. 23, pl. 3, figs. 1, 3 (= *Aioloceras rollerii*), 2, 4 (= "Pseudosaynella bonarellii LEANZA", = *Aioloceras argentinum*); PIATNITZKY, 1938, p. 79, pl. 8, fig. 38 (= "Anadesmoceras constrictum" LEANZA, 1970; = *Beudanticeras revoili*); all Patagonia.

*"Beudanticeras subparandieri"* SPATH, 1923, England (=? *Uhligella walleranti* JACOB).

*"Beudanticeras subrotundum"* COLLIGNON, 1963, Madagascar (= *Beudanticeras hourcqi*).

*Beudanticeras sutherlandbrowni* (MCLEARN) 1972, p. 56, pl. 8, fig. 3A-B, Canada (type species of "Rapidoplacenticeras" ALABUSHEV, 1988).  
*non*: ALABUSHEV, 1988, p. 111, fig. 1, NE Russia.

*Beudanticeras(?) sutherlandi* (ETHERIDGE) 1872, p. 345, pl. 21, fig. 4, Queensland, Australia (refigured in ETHERIDGE, 1892, p. 496, pl. 29, fig. 4,

WHITEHOUSE, 1928, p. 202, pl. 25, fig. 4 and HILL *et al.*, 1968, p. K20, pl. K9, fig. 2), Queensland.

*non*: PIATNITZKY, 1938, pl. 7, fig. 35a-b, ?Lago Cardiel, Patagonia (= ? *Puzosia* sp.).

*"Beudanticeras victoris"* STOYANOW, 1949, p. 127, pl. 18, figs. 18-21, Arizona, USA.

*"Beudanticeras sp."* WIEDMANN, 1978, p. 362, fig. 2A, DSDP 363, Walvis Ridge, S. Atlantic.

*"Beudanticeras sp."* RENZ, 1979, p. 364, pl. 2, fig. 3, DSDP 398D, south of Vigo Seamount, N. Atlantic.

*"Beudanticeras sp."* NULLO *et al.*, 1981, pl. 2, fig. 3, Patagonia (= ? *Aioloceras rollerii*).

*"Beudanticeras sp."*, HENDERSON, 1990, p. 112, fig. 2L-S, New Zealand (= ? *Desmoceras* sp.).

*"Beudanticeras sp. indet."*, MAHMOUD, 1955, p. 99, pl. 5, fig. 21, Sinai, Egypt.

*"Beudanticeras sp. juv."*, KENNEDY & KOLL-MANN, 1979, p. 7, pl. 3, figs. 1-4, 6-7, 10, Austria (= *Pseudorbulites convergens*).

*"Beudanticeras (?) f."*, BONARELLI in BONARELLI & NÁGERA, 1921, p. 23, Colombia (for *Desmoceras* sp. of GERHARDT, 1898, p. 163, pl. 4, fig. 2).

### Subgenus *Grantziceras* IMLAY, 1961

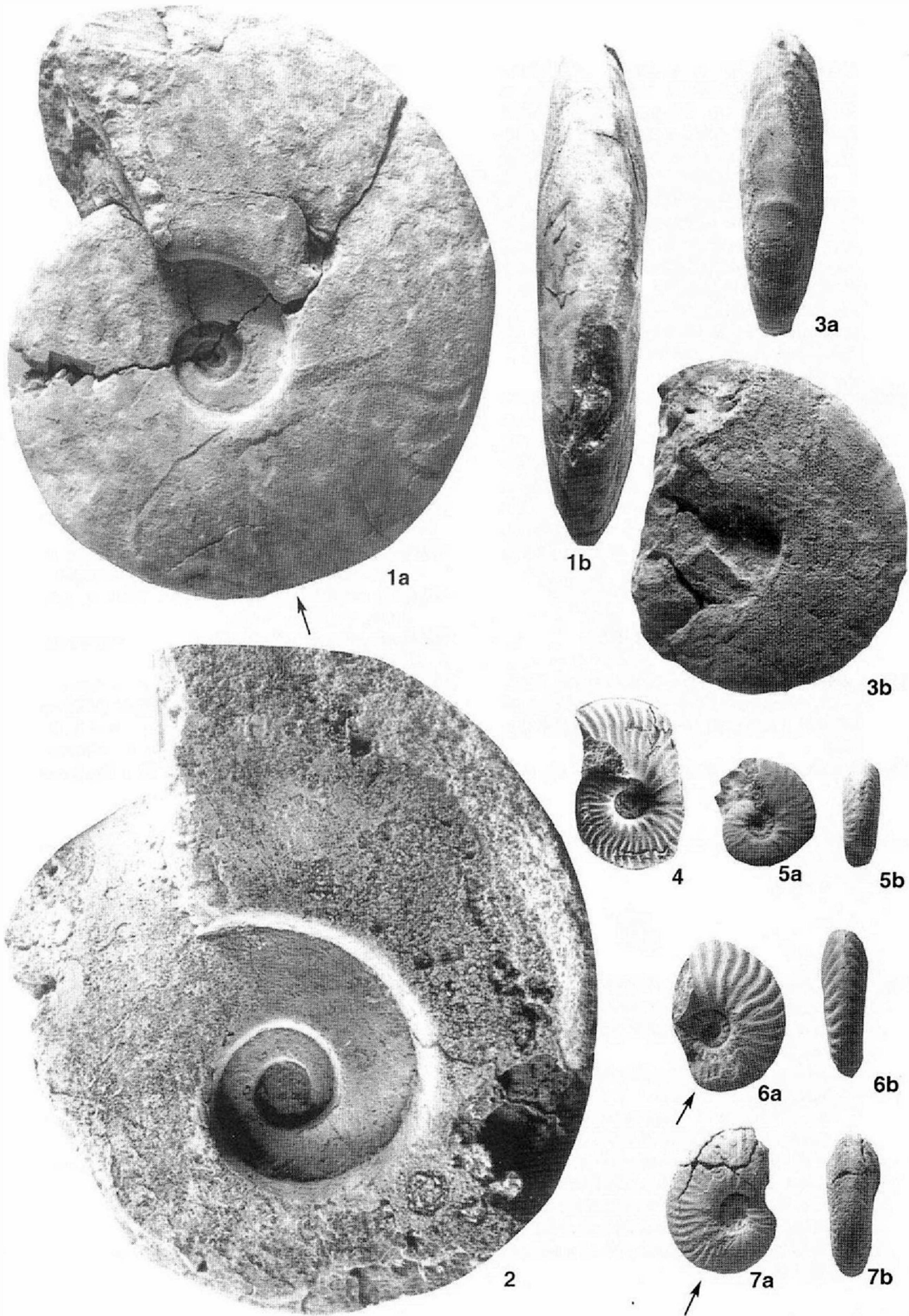
Type species: *Beudanticeras (Grantziceras) multiconstrictum* IMLAY, 1961 [= *B. (Grantziceras) affine*], by original designation.

*Beudanticeras (Grantziceras) affine* (WHITEAVES) 1892, p. 113, 115, pl. 8, pl. 9, pl. 11, figs. 1-1a;

### Plate III

All figures in natural size unless stated otherwise

- Figs. 1-2: *Beudanticeras revoili* (PERVINQUIERE), Lower Albian, Estancia La Victorina, Lago Cardiel.  
1a-b: Adult phragmocone with part of body chamber, MLP 29030, lateral and ventral views, X0.5.  
2: Incomplete phragmocone, MLP 29028, lateral view.
- Figs. 3a-b: ?*Uhligella* sp. a, Lower Albian, Puesto Policía, incomplete phragmocone, MLP 29036, ventral and lateral views.
- Fig. 4: *Cleoniceras* sp., Lower Albian, Bahía Estancia Dos Hermanos, Lago Cardiel, juvenile phragmocone, MLP 29041, lateral view.
- Figs. 5-7: *Cleoniceras?* cf. *santacrucense* LEANZA.  
5a-b: Incomplete phragmocone, MLP 29039, Lower Albian, Puesto Policía, Lago Cardiel, lateral and ventral views.  
6a-b: Phragmocone with almost complete body chamber, MLP 29040, Lower Albian, Estancia La Federica, Lago San Martín, lateral and ventral views.  
7a-b: Phragmocone with almost complete body chamber, MLP 29038, Lower Albian, Estancia La Federica, Lago San Martín, lateral and ventral views.



MCLEAR, 1945, pl. 4, figs. 1, 2-3, Alberta (refigured in JELETZKY, 1964, pl. 24, fig. 3); WARREN, 1947, p. 121, pl. 30, figs. 3-4, NW Canada; IMLAY, 1960, p. 105, pl. 16, figs. 14-18, 20-21; 1961, p. 57, pl. 13, fig. 24, pl. 14, fig. 2, Alaska; JELETZKY, 1964, pl. 24, fig. 4, Alberta (refigured in DOUGLAS, 1976, pl. 25, fig. 13); JONES in JONES & GRANTZ, 1967, p. 31, pl. 5, figs. 1-15, pl. 6, figs. 4-6, S. Alaska; ALABUSHEV & ALABUSHEVA, 1988, p. 6, pl. 1, fig. 2, NE Russia; including "*B. (G.) multi-constrictum*" IMLAY, 1961, p. 56, pl. 14, fig. 1, pl. 15, figs. 1-12, N. Alaska; 1960, p. 105, pl. 14, figs. 1-2, S. Alaska; ?NAGY, 1970, p. 33, pl. 1, fig. 2, Spitzbergen.

*Beudanticeras* (? *Grantziceras*) *glabrum* (WHITEAVES) 1889, p. 172, pl. 24, fig. 1; WARREN, 1947, p. 121, pl. 30, figs. 1-2, 5, W. Canada; IMLAY, 1960, p. 105, pl. 16, figs. 19, S. Alaska; JELETZKY, 1964, pl. 24, figs. 5-6, Alberta; JONES in JONES & GRANTZ, 1967, p. 33, pl. 6, figs. 1-3, 7-9, S. Alaska; ?NAGY, 1970, p. 33, text-fig. 7a, Spitzbergen; ALABUSHEV & ALABUSHEVA, 1988, pl. 1, fig. 3, NE Russia.

#### Genus *Uhligella* JACOB, 1907

Type species: *Desmoceras clansayense* JACOB, 1905, p. 403, Aptian, by subsequent designation of KILIAN, 1907, p. 63 (see HOWARTH, 1974, p. 728).

*Uhligella balmensis* JACOB, 1908, p. 33, pl. 3, figs. 6-9,

France; PASSENDORFER, 1930, p. 647, pl. 4, fig. 63, Poland (refigured in MARCINOWSKI & WIEDMANN, 1990, p. 61, pl. 6, fig. 8); ?BREISTROFFER in BESAIRIE, 1936, p. 156, pl. 15, figs. 17-18, Madagascar (as "*Beudanticeras?* *besairiei*"); ALMELA & DE LA REVILLA, 1957, p. 24, pl. 5, fig. 5, Spain; COLLIGNON, 1950, p. 43, pl. 5, figs. 3-4, 1963, p. 71, pl. 267, fig. 1162 and ?p. 74, pl. 268, fig. 1168 (as *U. balmensis* var. *pinguis*) Madagascar; KENNEDY et al., 1997, p. 465, pl. 6, figs. 4-5, 25-27, pl. 7, fig. 5, pl. 9, figs. 4-5; DELAMETTE et al., 1997, pl. 21, fig. 8, all France.

"*Uhligella convergens*" JACOB, 1908 (type species of *Pseudorbulites* CASEY).

*Uhligella derancei* CASEY, 1949, p. 340, pl. 19, figs. 2-3 (fig. 3 as "var. *erugata*"), England; KENNEDY et al., 1997, p. 465, pl. 3, figs. 3-4, France.

"*Uhligella dubia*" COLLIGNON, 1949, p. 61, pl. 17, fig. 10, Madagascar.

"*Uhligella kiliani*" PETKOVICH, 1913, p. 71, pl. 4, figs. 1-2, Serbia. (fig. 1 = *Beudanticeras revoili*).

"*Uhligella milleti*" PERVINQUIERE, 1907, p. 136, pl. 5, fig. 25a-b, Tunisia.

"*Uhligella pinguis*" COLLIGNON, 1963, Madagascar (=? *U. balmensis*).

*Uhligella rebouli* JACOB, 1908, p. 32, pl. 4, figs. 1-5 (fig. 3 as var. *renculerensis* BREISTROFFER in BESAIRIE, 1936, p. 156), France; ?FALLOT, 1910, p. 78, pl. 2, figs. 1-2, Balearis; PASSENDORFER, 1930, p. 647, pl. 3, fig. 56a-b

#### Plate IV All figures in natural size

Figs. 1-7: *Aioloceras argentinum* (BONARELLI) ♀/M & ♂/m, Lower Albian, 1-4 and 6-7 from Estancia La Federica, Lago San Martín, 5 from north of Estancia Cerro Bayo, Lago Cardiel.

1a-c: Holotype, incomplete phragmocone of macroconch, SEGEMAR 9293, lateral, apertural and ventral views.

2a-b: Holotype of "*Pseudosaynella bonarellii*" LEANZA, 1970, complete microconch, SEGEMAR 9309a, lateral and ventral views.

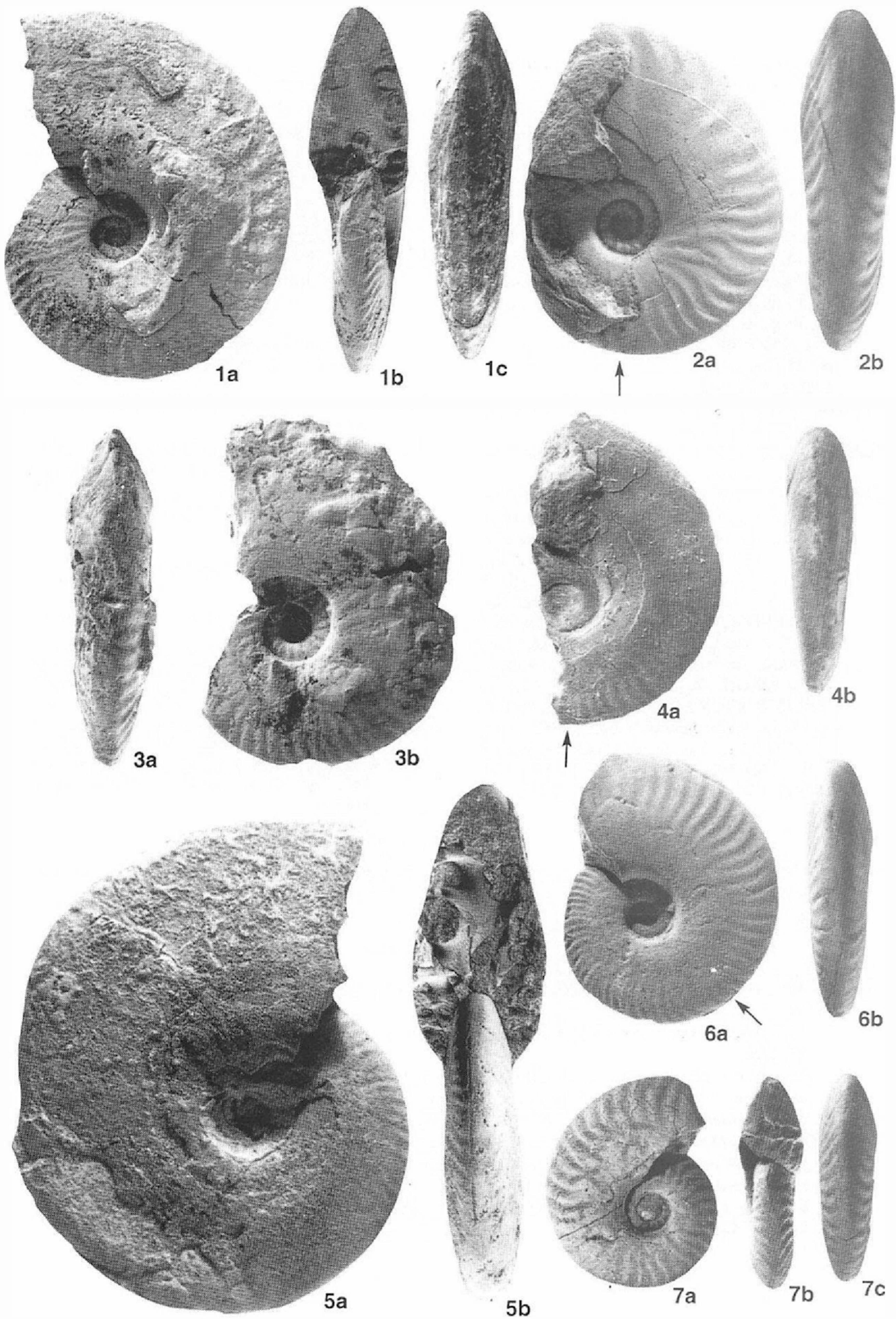
3a-b: Holotype of "*Cleoniceras argentinum* var. *meseticum*" BONARELLI, incomplete phragmocone of ?macroconch, SEGEMAR 9301, ventral and lateral views.

4a-b: "*Beudanticeras Daintreei*" of BONARELLI in BONARELLI & NÁGERA, 1921, microconch(?) with incomplete body chamber, SEGEMAR 9292, lateral and ventral views.

5a-b: Incomplete phragmocone, MLP 29436, lateral and apertural views.

6a-b: Almost complete microconch, MLP 29060, lateral and ventral views, loc. AC4.

7a-c: Incomplete phragmocone of a macroconch, MLP 29051, lateral, apertural and ventral views, loc. A XXII 21.



(refigured in MARCINOWSKI & WIEDMANN, 1990, p. 61, pl. 6, figs. 6), 60a-b, Poland; ALMELA & DE LA REVILLA, 1957, p. 24, pl. 5, fig. 4, Spain; WIEDMANN & DIENI, 1968, p. 129, pl. 10, fig. 6, Sardinia; MARTÍNEZ, 1979, p. 345, pl. 1, fig. 4 (refigured 1982, p. 79, pl. 6, fig. 6), Spain; MARCINOWSKI & WIEDMANN, 1990, p. 61, pl. 6, fig. 7, Poland; SEYED-EMAMI & IMMEL, 1995, p. 388, figs. 31, 32, 37, Iran; DELAMETTE *et al.*, 1997, pl. 38, fig. 2, France; including "*Uhligella subornata*" CASEY, 1949, p. 337, pl. 19, fig. 1; 1961b, p. 163, pl. 28, figs. 1-2, England.  
*non*: EGOYAN, 1969, p. 177, pl. 15, figs. 6-7, pl. 25, fig. 63, N. Caucasus, Russia; ?RENZ, 1982, p. 35, pl. 4, figs. 14-15, Venezuela.

*Uhligella sohensis* SEYED-EMAMI & IMMEL, 1996, p. 14, pl. 3, figs. 1-3, Iran.

"*Uhligella subornata*" CASEY, 1949, England (= *Uhligella rebouli*).

*Uhligella walleranti* JACOB, 1908, p. 31, text-fig 17-18, pl. 3, figs. 1-4, France; ?DOUVILLÉ, 1916, p. 107, pl. 12, fig. 8, Sinai (as "*Desmoceras beudanti*"); ?COLLIGNON, 1929, p. 20, pl. 2, fig. 2 (as *U. walleranti* var. *jacobi*), p. 21, pl. 2, fig. 3 (as *U. walleranti* var. *waterloti*), Madagascar; ?PASSENDORFER, 1930, p. 648, pl. 3, fig. 55a-b (as "var. *rotunda*"), p. 649, text-fig 16, pl. 3, fig. 50a-b (as "var. *lateumbilicata*"), Poland; ?COLLIGNON, 1932, p. 10, pl. 1, fig. 7; ?BREISTROFFER in BESAIRIE, 1936, p. 154, pl. 23, fig. 1, Madagascar; ?RENZ, 1982, p. 35, pl. 4, figs. 12-13, Venezuela; ?MARCINOWSKI & WIEDMANN, 1990, p. 60, pl. 6, figs. 4-5, text-fig. 26, Poland; SEYED-EMAMI &

IMMEL, 1996, p. 13, pl. 1, figs. 1-2, pl. 4, fig. 5, Iran; probably includes "*Beudanticeras subparandieri*" SPATH, 1923, p. 62, pl. 4, fig. 2a-e, England; ?BACCELLE & GARAVELLO, 1967, p. 94, pl. 1, fig. 4a-b, Italy; FÖLLMI, 1989, p. 139, pl. 10, fig. 1, Austria.  
*non*: ?FALLOT, 1910, p. 77, pl. 3, fig. 5, Baleares; ?DIMITROVA, 1967, p. 147, pl. 74, fig. 1, Bulgaria.

*Uhligella* sp., SEYED-EMAMI & IMMEL, 1996, p. 14, pl. 3, figs. 4-5, Iran.

(?)Genus *Cophinoceras* WHITEHOUSE, 1928  
 (= *Beudantiella* BREISTROFFER, 1947)

Type species: *C. ogilviei* WHITEHOUSE, 1928, by original designation.

*Cophinoceras ogilviei* WHITEHOUSE, 1928, p. 205, pl. 26, fig. 4a-b, Queensland, Australia (refigured in HILL *et al.*, 1968, pl. KVIII, fig. 5; WRIGHT in WRIGHT *et al.*, 1996, fig. 61, 1a-b).

Genus *Pseudorbulites* CASEY, 1961

Type species: *Uhligella convergens* JACOB, 1908, by original designation.

*Pseudorbulites convergens* (JACOB), 1908, p. 29, pl. 2, figs. 24-26, France (refigured in CASEY, 1961b, p. 146, text-fig. 46d-g, KENNEDY *et al.*, 2000, fig. 43a-h); FÖLLMI, 1989, p. 138, pl. 9, figs. 10-11, Austria; DELAMETTE *et al.*, 1997, pl. 12, fig. 5; KENNEDY *et al.*, 2000, p. 665, figs. 37j, 41j-o, 42w-h', 47p-q, 48a, all France.

Plate V  
 All figures in natural size

Figs. 1-6: *Aioloceras argentinum* (BONARELLI) ♀/M & ♂/m, Lower Albian, Estancia La Federica, Lago San Martín.

1a-b: Adult phragmocone with almost complete body chamber, MLP 29055, lateral and ventral view, loc. A XXII 21.

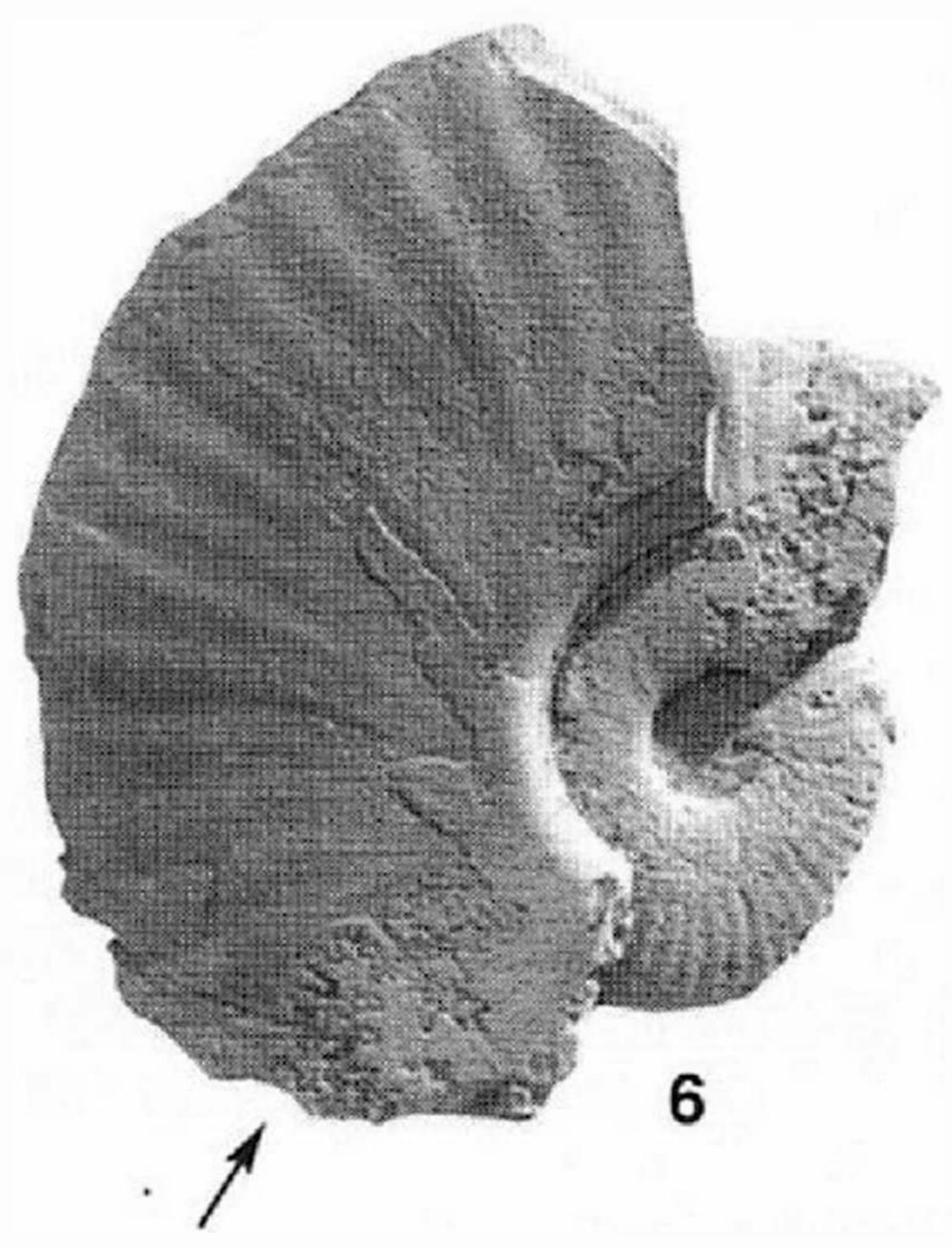
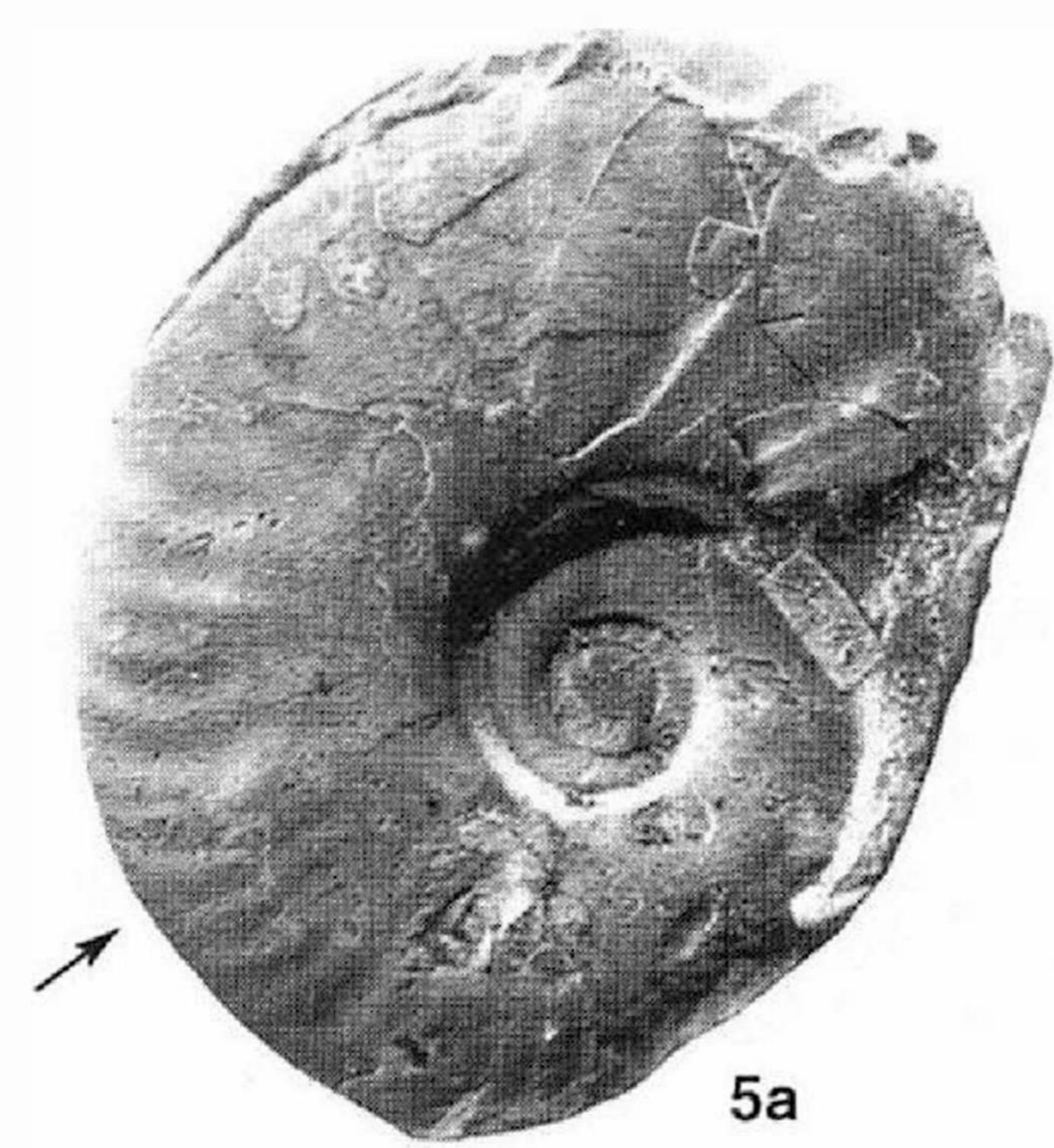
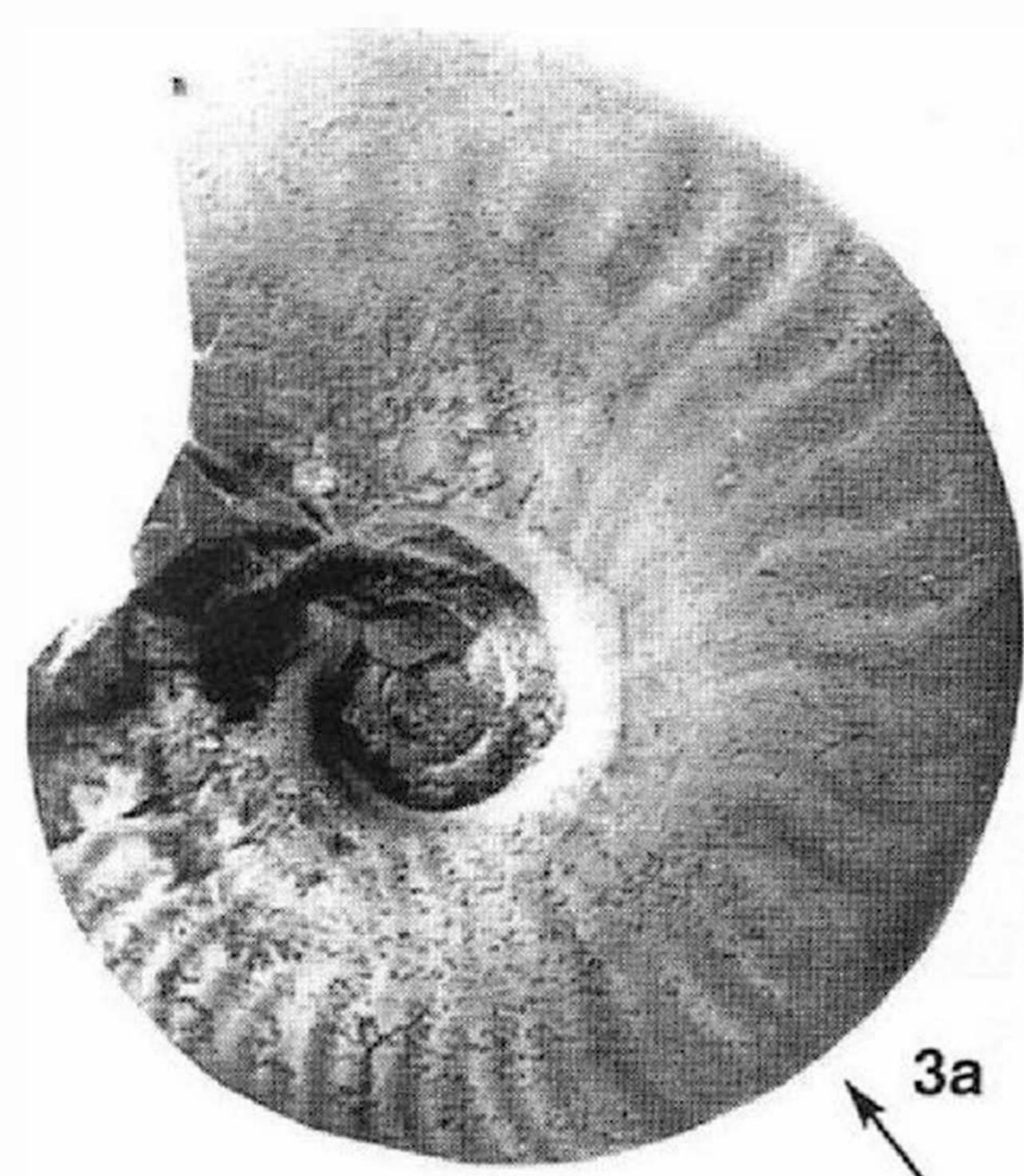
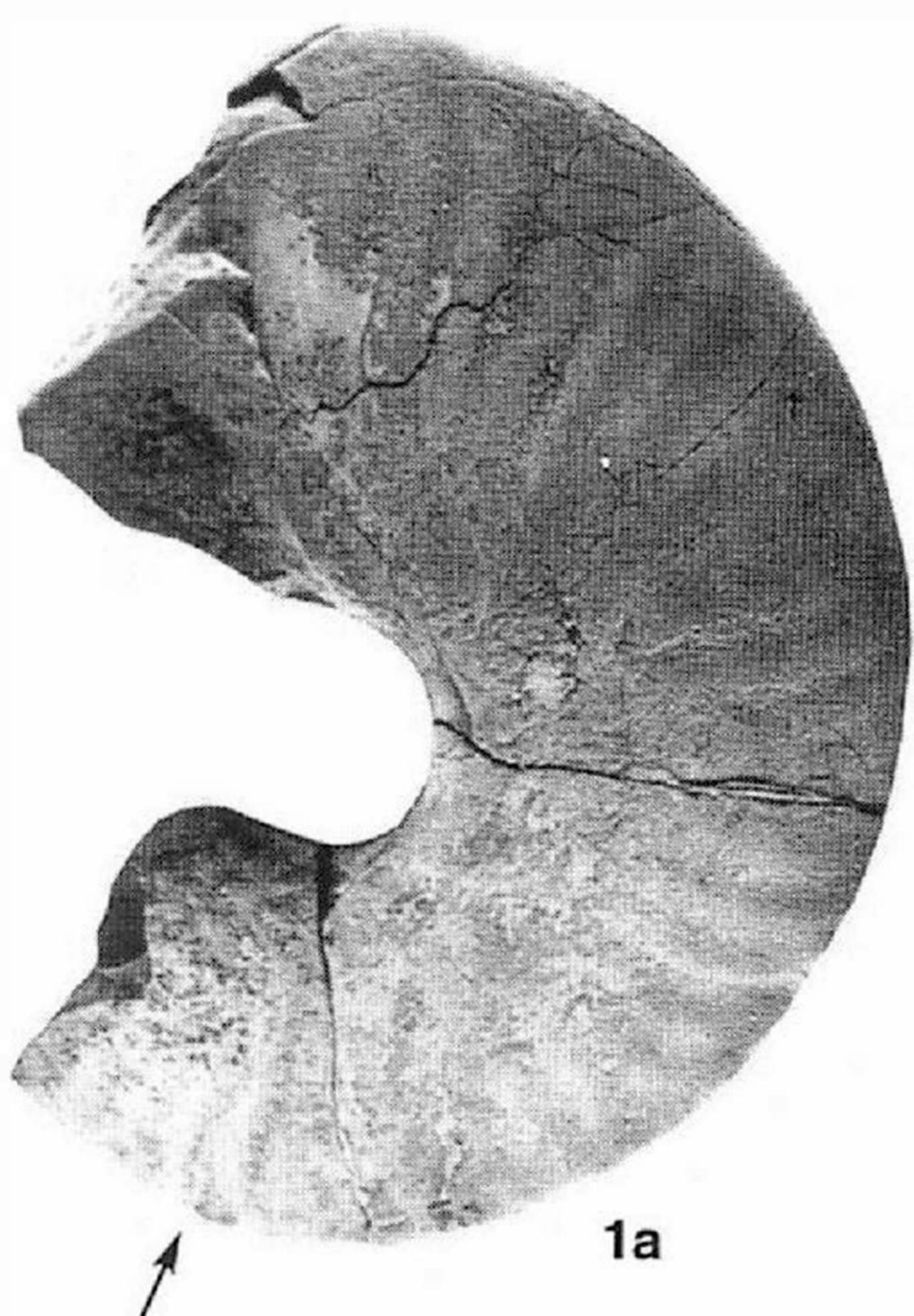
2a-b: Almost complete microconch, MLP 29043, lateral and ventral views, loc. A XXII 21.

3a-b: Juvenile phragmocone with part of body chamber, MLP 29044, lateral and ventral views, A XXII 21.

4a-b: "*Beudanticeras* cfr. *Stolickzkai*" of BONARELLI in BONARELLI & NÁGERA (1921, pl. 3, fig. 2), almost complete microconch, SEGEMAR 9309b, lateral and ventral views.

5a-b: Adult microconch with incomplete phragmocone and body chamber, SEGEMAR 14912, lateral and ventral views, BONARELLI & NÁGERA col.

6: Incomplete macroconch, with adult phragmocone and body chamber, SEGEMAR 14914, lateral view, BONARELLI & NÁGERA col.



*non*: PETKOVICH, 1913, p. 69, pl. 3, fig. 7, 7a, Serbia.

### Cleoniceratinae WHITEHOUSE, 1926

Genus *Cleoniceras* PARONA & BONARELLI, 1897  
 (= *Anacleoniceras* MIRZOYEV, 1969; *Cleonella* DESTOMBES, 1970; *Eocleoniceras* SAVELIEV, 1992)

Type species: *Ammonites cleon* D'ORBIGNY, 1850, p. 124, by original designation.

*Cleoniceras cleon* D'ORBIGNY, 1850; D'ORBIGNY, 1841, p. 286, pl. 84, figs. 1-3, France (as "*Ammonites bicurvatus*") (refigured in PICTET & ROUX, 1848, p. 32, pl. 2, fig. 2; SPATH, 1925, text-fig. 19; WRIGHT, 1957, fig. 513, 2a-b; CASEY, 1966, fig. 211a-e); SPATH, 1925, p. 91, pl. 5, fig. 8, England; IMLAY, 1961, pl. 20, figs. 10-12, England; CASEY, 1966, p. 554, pl. 91, fig. 5, pl. 92, fig. 9, pl. 93, fig. 1, text-fig. 211f-h, England; DESTOMBES, 1979, p. 89, pl. 4-14, fig. 1a-b, ? pl. 4-14, figs. 2-3, 5, France.  
*non*: SEUNES, 1887, p. 558, pl. 11, pl. 12, fig. 1a-b (= "C. seunesi", = ? *C. quercifolium*); PARONA & BONARELLI, 1897, p. 85, pl. 11, fig. 5 (= *Beudanticeras*); JACOB, 1908, p. 60, pl. 9, fig. 6a-c, all France; SINZOW, 1909, p. 32, pl. 2, figs. 1-6, Kazakhstan (= *Neosaynella platidorsata*); SPATH, 1925, p. 91, pl. 5, fig. 8, England (= *C. dimorphum*); ?THOMEL, 1980, p. 137, fig. 271, France.

*Cleoniceras antiquum* CASEY, 1966, p. 563, pl. 91, fig. 6, pl. 94, figs. 1, 2, England.

"*Cleoniceras argentinum*" BONARELLI in BONARELLI & NÁGERA, 1921, Patagonia (type species of *Aioloceras*).

"*Cleoniceras baisunense*" ILJIN, Uzbekistan (= *Neosaynella*, see CASEY, 1966, p. 574).

"*Anacleoniceras bicostatum*" MIRZOYEV", SAVELIEV, 1992, pl. 7, fig. 2, pl. 8, fig. 2, Kazakhstan.

*Cleoniceras canadense* JELETZKY, 1980, p. 2, pl. 1, figs. 5, 6, pl. 2, figs. 1, 2, 4, 5, Arctic Canada.

*Cleoniceras caseyi* (MIRZOYEV) 1969, p. 32, pl. 4, figs. 1-2, Tajikistan (type species of "Anacleoniceras").

"*Cleoniceras daviesi*" SPATH, 1930, p. 53, pl. 8, fig. 17a-c, Pakistan (= ? *Uhligella*).

*Cleoniceras? devisense* SPATH, 1925, p. 94, pl. 4, fig. 7, England.

*Cleoniceras? dilleri* JONES, 1960, p. 157, pl. 29, figs. 5, 13, 14, Oregon (= ? *Neosaynella*).

*Cleoniceras dimorphum* CASEY, 1966, p. 568, pl. 92, figs. 10, 11a-b, England (type species of "*Cleonella*"); SPATH, 1925, p. 91, pl. 5, fig. 8, England; DESTOMBES, 1979, p. 95-96, pl. 4-15, figs. 1a-b, 2a-b (fig. 1a-b as "*Cleoniceras aff. cantianum*"), France.

*Cleoniceras discors* SAVELIEV, 1973, p. 113, pl. 8, fig. 1, pl. 17, figs. 3-4, text-figs. 19-20, Kazakhstan.

"*Cleoniceras dubium*" MICHAILOVA & TERECHOVA, 1975, p. 62, figs. 5-10, NE Russia (= ? *Grycia*).

*Cleoniceras floridum* CASEY, 1961a, p. 599, pl. 84, figs. 6-7, England (refigured in CASEY, 1966, pl. 92, figs. 5, 1b); 1966, p. 566, pl. 92, figs. 1a, 7, England; DESTOMBES, 1979, p. 92, pl. 4-15, figs. 3-5, France; includes "*Cleoniceras imitator*" CASEY, 1966, p. 570, pl. 91, fig. 7, pl. 92, fig. 6, England; ?SAVELIEV, 1992, pl. 2, fig. 1a-c, Kazakhstan; ?"*Cleoniceras lanceolatum*" DESTOMBES, 1979, p. 94, pl. 4-16, figs. 1-2, France.

### Plate VI All figures in natural size

Figs. 1-4: *Aioloceras argentinum* (BONARELLI) ♀/M & ♂/m, Lower Albian, Estancia La Federica, Lago San Martín.

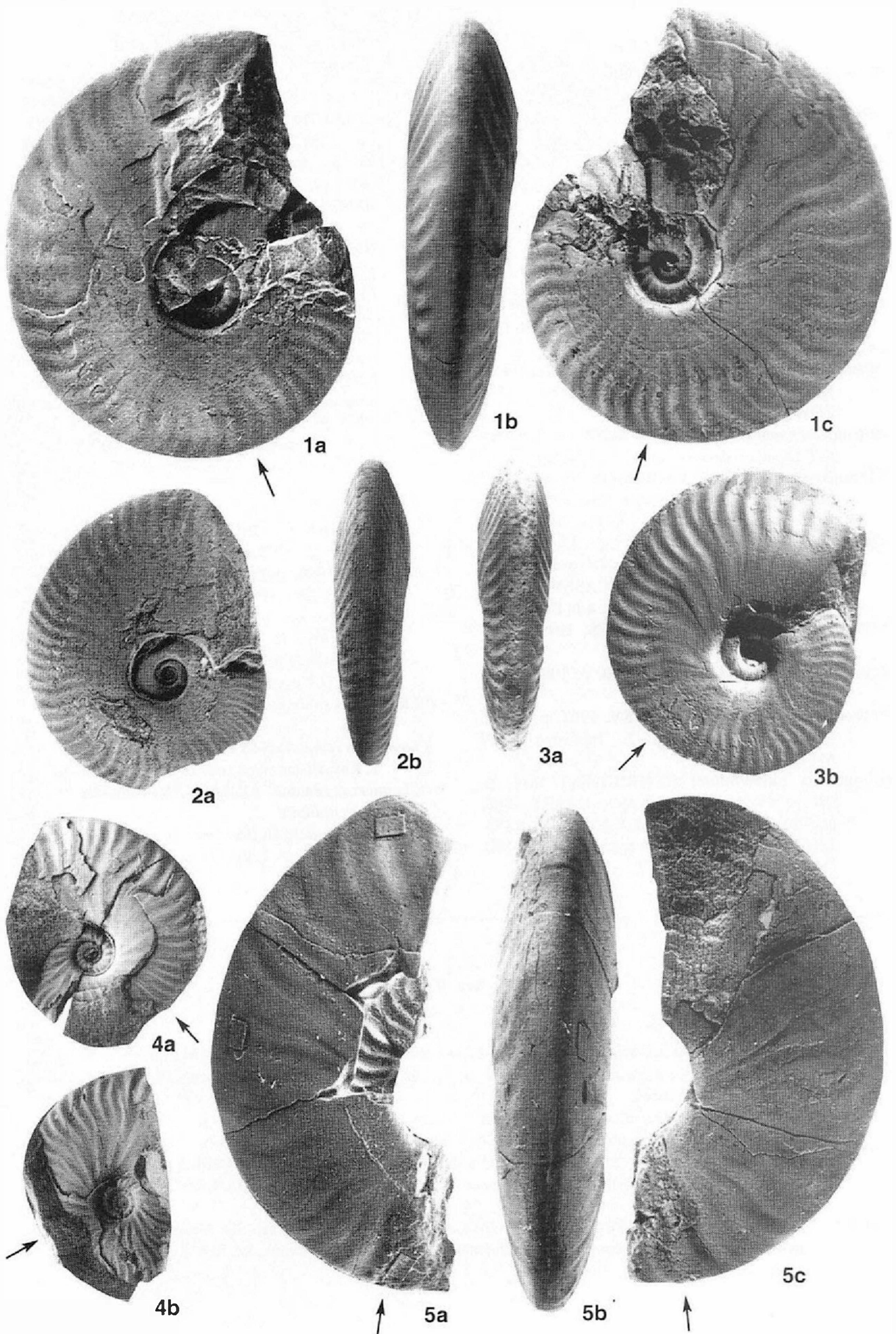
1a-c: Adult phragmocone with incomplete body chamber, MLP 29058, lateral, ventral and lateral views, loc. AC4.

2a-b: Incomplete juvenile phragmocone of a macroconch, MLP 29045, lateral and ventral views, loc. A XXII 21.

3a-b: Complete microconch, MLP 17368, ventral and lateral views, loc. A XXII 21.

4a-b: "*Uhligella quercifolia*" of BONARELLI in BONARELLI & NÁGERA, 1921, juvenile(?) macroconch with incomplete body chamber, SEGEMAR 9290, lateral views.

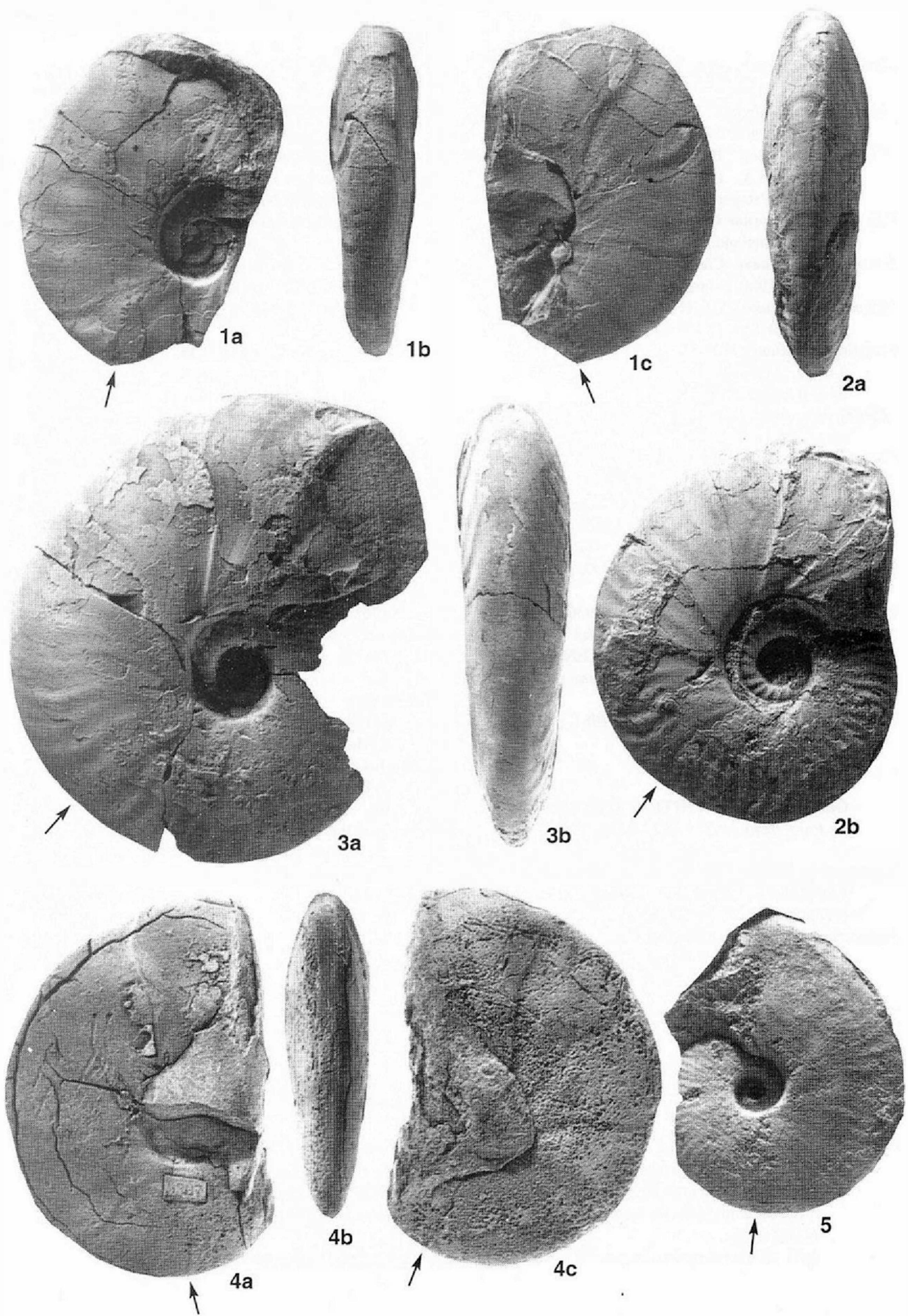
Figs. 5a-c: *Aioloceras rollerii* (LEANZA) ♀/M, Lower Albian, Lago San Martín. Incomplete body chamber of a ?macroconch, SEGEMAR 9300, lateral, ventral and lateral views. BONARELLI & NÁGERA col.



- “*Cleoniceras imitator*” CASEY, 1966, England (= *C. floridum*).  
 “*Cleoniceras janneli*” PARENT, 1893, France (= ? *Cleoniceras quercifolium*).  
*Cleoniceras kugitangense* LUPPOV, 1961, p. 193, pl. 3, fig. 2, Tajikistan; SAVELIEV, 1992, pl. 40, fig. 1, Kazakhstan.  
 “*Cleoniceras lanceolatum*” DESTOMBES, 1979, France (= ? *Cleoniceras floridum*).  
*Cleoniceras leightonense* SPATH, 1942, p. 701, text-fig. 247, England.  
*Cleoniceras madagascariense* COLLIGNON, 1949, p. 85, pl. 17, figs. 11-12; 1963, p. 85, pl. 274, figs. 1181-1183, Madagascar.  
 “*Cleoniceras mangyschlakense*” LUPPOV, Tajikistan, Kazakhstan (= *Neosaynella platidorsata* SIN-ZOW).  
 “*Cleoniceras mocqueryi*” DESTOMBES, 1979, France (= ? *Cleoniceras quercifolium*).  
 “*Cleoniceras modestum*” ANDERSON, 1938, p. 193, pl. 50, figs. 2, 3-4, California (figs. 3-4 = *Leconteites lecontei*).  
*Cleoniceras morgani* SPATH, 1927, pl. 17, fig. 7, pl. 18, fig. 5; 1942, text-fig. 248 (refigured in CASEY, 1966, pl. 94, fig. 3); CASEY, 1966, p. 564, pl. 93, figs. 3-5, pl. 94, figs. 4-6; England.  
 “*Cleoniceras ornatum*” DESTOMBES, 1979 (= ? *C. quercifolium*).  
*Cleoniceras overbecki* IMLAY, 1960, p. 108, pl. 19, figs. 36-39, S. Alaska.  
 “*Cleoniceras planum*” MIRZOYEV, 1967, p. 40, pl. 3, fig. 2, pl. 4, fig. 2, Tajikistan (= ? *Neosaynella*).  
*Cleoniceras quercifolium* (D'ORBIGNY) 1841, p. 284, pl. 83, figs. 4-6 (refigured in CASEY, 1966, text-fig. 212a-c); PICTET & CAMPICHE, 1858-1860, p. 274, pl. 36, fig. 1a-b; DOUVILLÉ 1890, p. 289, fig. 14; SARASIN, 1897, p. 790, fig. 17; JACOB, 1908, p. 59, pl. 9, figs. 3-5; all France; COLLIGNON, 1963, p. 86, fig. 1184, Madagascar; CASEY, 1966, p. 557, pl. 93, figs. 2a-b, pl. 95, fig. 6a-b, England; DELAMETTE *et al.*, 1997, pl. 31, fig. 1, France; SOUZA LIMA & BENGSTON, 1999, fig. 1b, Brasil; ?includes “*C. seunesi*” BONARELLI *in* BONARELLI & NÁGERA, 1921, p. 24, SEUNES, 1887, p. 558, pl. 11, pl. 12, fig. 1a-b, France (as “*Sonneratia cleon*”; refi gured in CASEY, 1966, text-fig. 214); CASEY, 1966, p. 562, pl. 92, figs. 3, 4, 8, England; DESTOMBES, 1979, p. 90, pl. 4-17, fig. 2a-c, France; “*Cleoniceras janneli*” PARENT, 1893, p. 266, pl. 6, fig. 2a-b, France (refi gured in CASEY, 1966, text-fig. 213); CASEY, 1966, p. 560, pl. 92, fig. 2, pl. 95, fig. 7, England; “*Cleoniceras renatae*” MIRZOYEV, 1967, p. 39, pl. 3, fig. 1, Tajikistan; SAVELIEV, 1992, pl. 44, fig. 3, Kazakhstan; “*Cleoniceras tenuis*” MIRZOYEV, 1967, p. 44, pl. 4, fig. 1, Tajikistan; SOUZA LIMA & BENGSTON, 1999, fig. 1a, Brasil; “*Cleoniceras ornatum*” DESTOMBES, 1979, p. 94, pl. 4-16, figs. 4-6, France, ? SAVELIEV, 1992, pl. 19, fig. 1, Kazakhstan; “*Cleoniceras mocqueryi*” DESTOMBES, 1979, p. 96, pl. 4-17, fig. 3, pl. 4-18, figs. 1-2, France. non: BONARELLI & NÁGERA, 1921, p. 25, pl. 3, fig. 6, Patagonia (= *Aioloceras argentinum*).  
 “*Cleoniceras ramachandrii*” RAO, 1953, p. 109, fig. 5, India.  
*Cleoniceras remotum* SAVELIEV, 1992, p. 84, pl. 1, fig. 1, Kazakhstan (type species of “*Eocleoniceras*”).  
 “*Cleoniceras renatae*” MIRZOYEV, Tajikistan (= ? *C. quercifolium*).  
*Cleoniceras rudicki* ILJIN, 1961, p. 53, pl. 3, fig. 2, pl. 4, figs. 2-3, pl. 7, fig. 3, Turkmenistan.

#### Plate VII All figures in natural size

- Figs. 1-4: *Aioloceras rollerii* (LEANZA) ♂/m, Lower Albian, Estancia La Federica, Lago San Martín.  
 1a-c: Holotype, incomplete microconch with part of phragmocone and body chamber, CPUNC 4366, lateral, ventral and lateral views.  
 2a-b: Almost complete microconch, MLP 29072, ventral and lateral views, loc. 71-1.  
 3a-b: Almost complete microconch, MLP 29070, lateral and ventral views, loc. 71-8.  
 4a-c: “*Beudanticeras* cfr. *Stolickzkai*” of BONARELLI *in* BONARELLI & NÁGERA (1921, pl. 3, fig. 1), incomplete microconch with part of phragmocone and body chamber, SEGEMAR 9307, lateral, ventral and lateral views.  
 Fig. 5: *Aioloceras* aff. *rollerii* (LEANZA), Lower Albian, Estancia Kachaike, Lago San Martín, incomplete specimen with part of phragmocone and body chamber, MLP 29165, lateral view, loc. KA-1.



- Cleoniceras santacrucense* LEANZA, 1970, p. 226, fig. 24, 1-2, Patagonia.
- “*Cleoniceras? schlaudti*” STOYANOW, 1949, p. 130, pl. 24, figs. 4-5, Arizona, USA.
- “*Cleoniceras seunesi*” BONARELLI in BONARELLI & NÁGERA, 1921, France (= ? *C. quer-cifolium*), Patagonia (= *Aioloceras rollerii*).
- Cleoniceras strigosum* CASEY, 1966, p. 566, pl. 93, fig. 6a-b, England.
- Cleoniceras sublaeve* CASEY, 1966, p. 559, pl. 91, figs. 8-9; 1980, p. 660, pl. 109, fig. 7, England.
- “*Cleoniceras susukii*” MURPHY & RODDA, 1959, p. 104, pl. 20, figs. 1, 3, 4, California.
- Cleoniceras tailleuri*, IMLAY, 1961, p. 63, pl. 20, figs. 1-5, N. Alaska; JELETZKY, 1964, p. 26, figs. 14A-B, Alberta.
- “*Cleoniceras tenuis*” MIRZOYEV, Tajikistan (= ? *C. quer-cifolium*)
- Cleoniceras (?) xizangense* CHAO, 1976, p. 538, p. 17, figs. 15-19, China.
- “*Cleoniceras* nov. sp.” or “*Cleoniceras* sp. aff. *baylei*”, BREISTROFFER in BESAIRIE, 1936, p. 157, fig. 10g. Madagascar (= ? *Aioloceras*).
- “*Cleoniceras* sp. juv. ind.” SPATH, 1930, p. 54, pl. 8, figs. 7-8, Pakistan (= ? *Uhligella*).
- “*Cleoniceras* sp. nov.? ind.”, SPATH, 1930, p. 54, pl. 8, fig. 11a-b, Pakistan (= ? *Uhligella*).
- “*Cleoniceras* species undetermined”, KENNEDY et al., 1981, p. 235, pl. 15, figs. 3-4, non pl. 8, figs. 5-7, pl. 15, figs. 1-2, Denmark.
- “*Cleoniceras* sp.??”, KENNEDY et al., 1981, p. 236, pl. 6, fig. 5, Denmark.

**Genus *Aioloceras* WHITEHOUSE, 1926**  
(= *Paracleoniceras* COLLIGNON, 1963)

**Type species:** *Cleoniceras argentinum* BONARELLI in BONARELLI & NÁGERA, 1921, by original designation.

*Aioloceras argentinum* (BONARELLI), BONARELLI

& NÁGERA, 1921, p. 24, pl. 4, figs. 3, 6, 7 (fig. 7 as var. *mesetica*; fig. 6 refigured in WINDHAUSEN, 1931, pl. 39, fig. 1, ARKELL et al., 1957, fig. 513. 3a-b and WRIGHT in WRIGHT et al., 1996, fig. 51, 2a-b), pl. 3, figs. 2, 4 (as “*Beudanticeras* cfr. *stoliczkai*”, refigured in WINDHAUSEN, 1931, pl. 39, fig. 3, = “*Pseudosaynella bonarellii*” LEANZA, 1970, p. 220, fig. 17, 1-2), fig. 5 (as “*Beudanticeras daintreei*”), fig. 6 (as “*Uhligella quer-cifolia*”); PIATNITZKY, 1938, p. 79, pl. 3, fig. 13a-b; RICCARDI, 1988, p. 99, pl. 13, figs. 2-3; all Patagonia.

*Aioloceras besairiei* COLLIGNON, 1949, p. 86, pl. 18, figs. 1-3, pl. 21, fig. 7 (type species of “*Paracleoniceras*”); 1963, p. 88, pl. 275, figs. 1186, 1187, pl. 276, fig. 1188, 1189; ?including “*P.*” *inaequale*” COLLIGNON, 1963, p. 86, pl. 274, fig. 1185; “*P.*” *cleoniforme*” COLLIGNON, 1963, p. 89, pl. 276, figs. 1190-1191; “*P.*” *morganiforme*” COLLIGNON, 1963, p. 89, pl. 276, fig. 1192; “*P.*” *tenuicostulatum*” COLLIGNON, 1963, p. 92, pl. 277, figs. 1193-1194; “*P.*” *crassefalcatum*” COLLIGNON, 1963, p. 94, pl. 278, fig. 1195; “*P.*” *ambiguum*” COLLIGNON, 1963, p. 94, pl. 278, fig. 1196; all Madagascar.

*Aioloceras?* *jonesi* (GREGORY & SMITH), 1902, p. 142, pl. 22, figs. 1-2; non DAY, 1974, p. 16, pl. 8, figs. 1-3, Australia.

“*Cleoniceras* (*Aioloceras*) *ptychitiforme*” COLLIGNON, 1949, p. 88, pl. 18, fig. 4, pl. 21, fig. 6, Madagascar (= ? *Beudanticeras*).

*Aioloceras rollerii* (LEANZA) 1970, p. 221, fig. 18, 1-2; BONARELLI & NÁGERA, 1921, p. 22, pl. 2, fig. 11, pl. 4, fig. 1 (as “*Beudanticeras beudanti*”), p. 23, pl. 3, figs. 1, 3 (as “*Beudanticeras* cfr. *stoliczkai*”), p. 25, pl. 4, fig. 5 (as “*Beudanticeras* cfr. *mitchelli*”); ?NULLO et al., 1981, pl. 2, fig. 3 (as “*Beudanticeras* sp.”); all Patagonia.

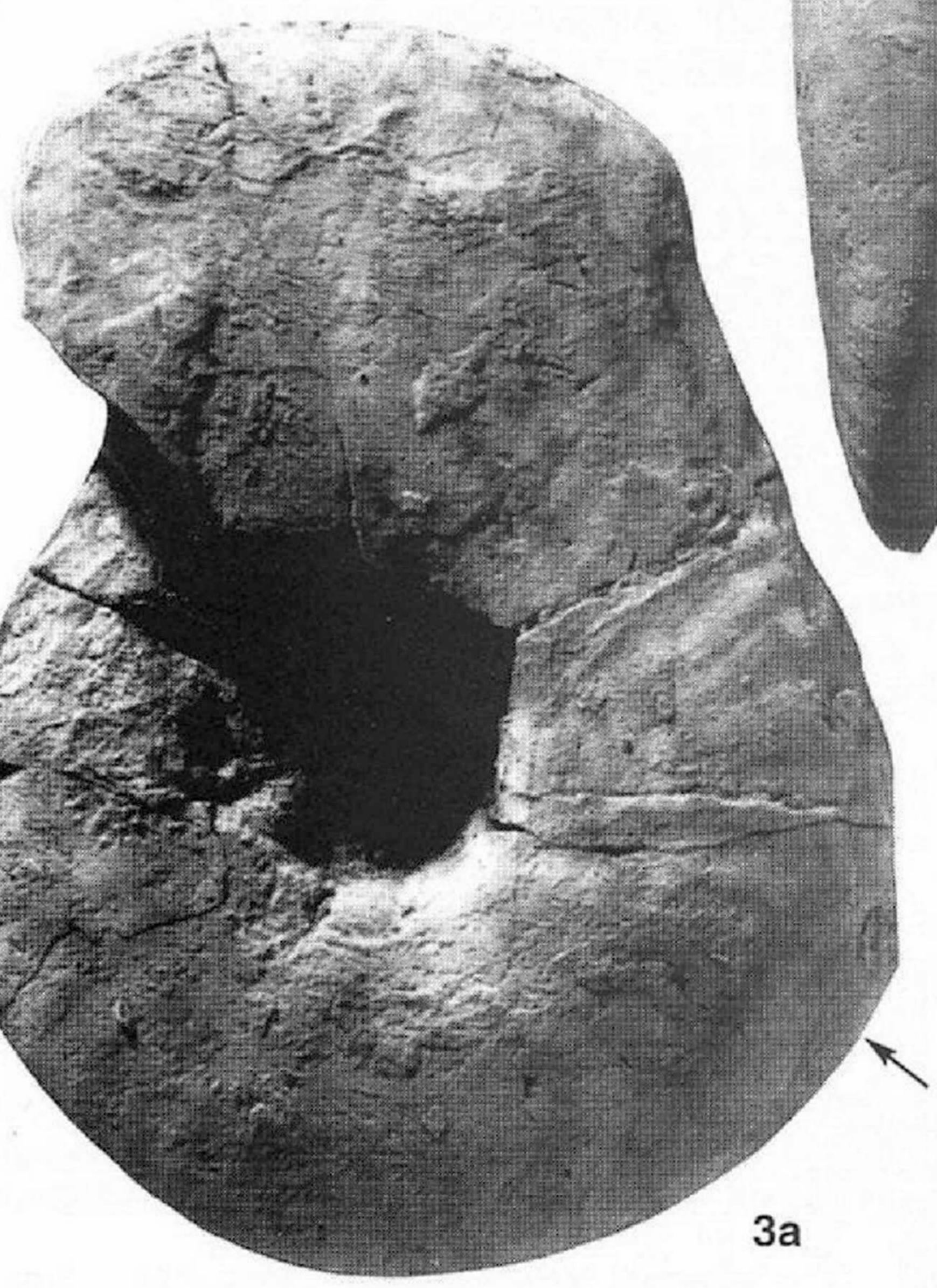
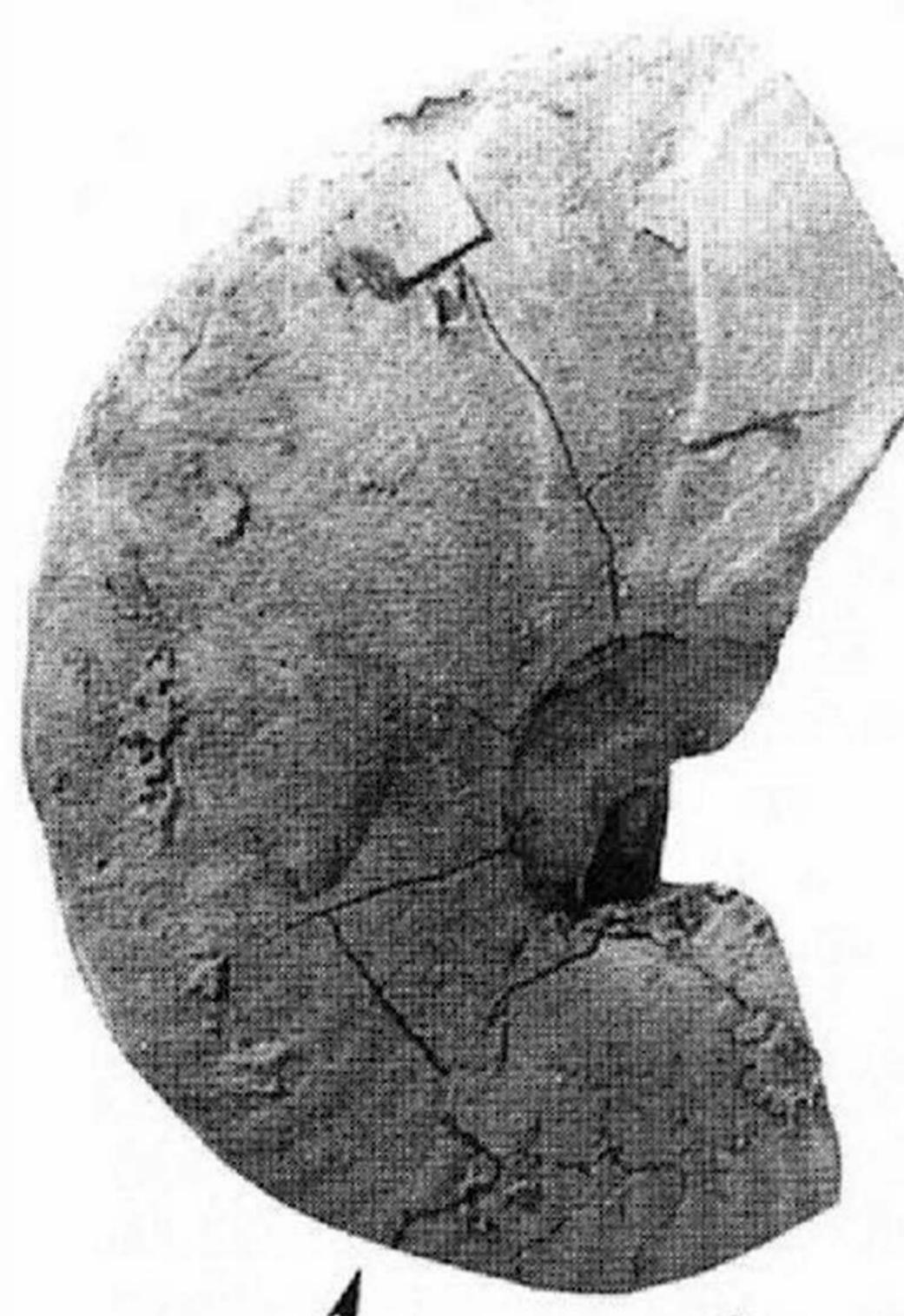
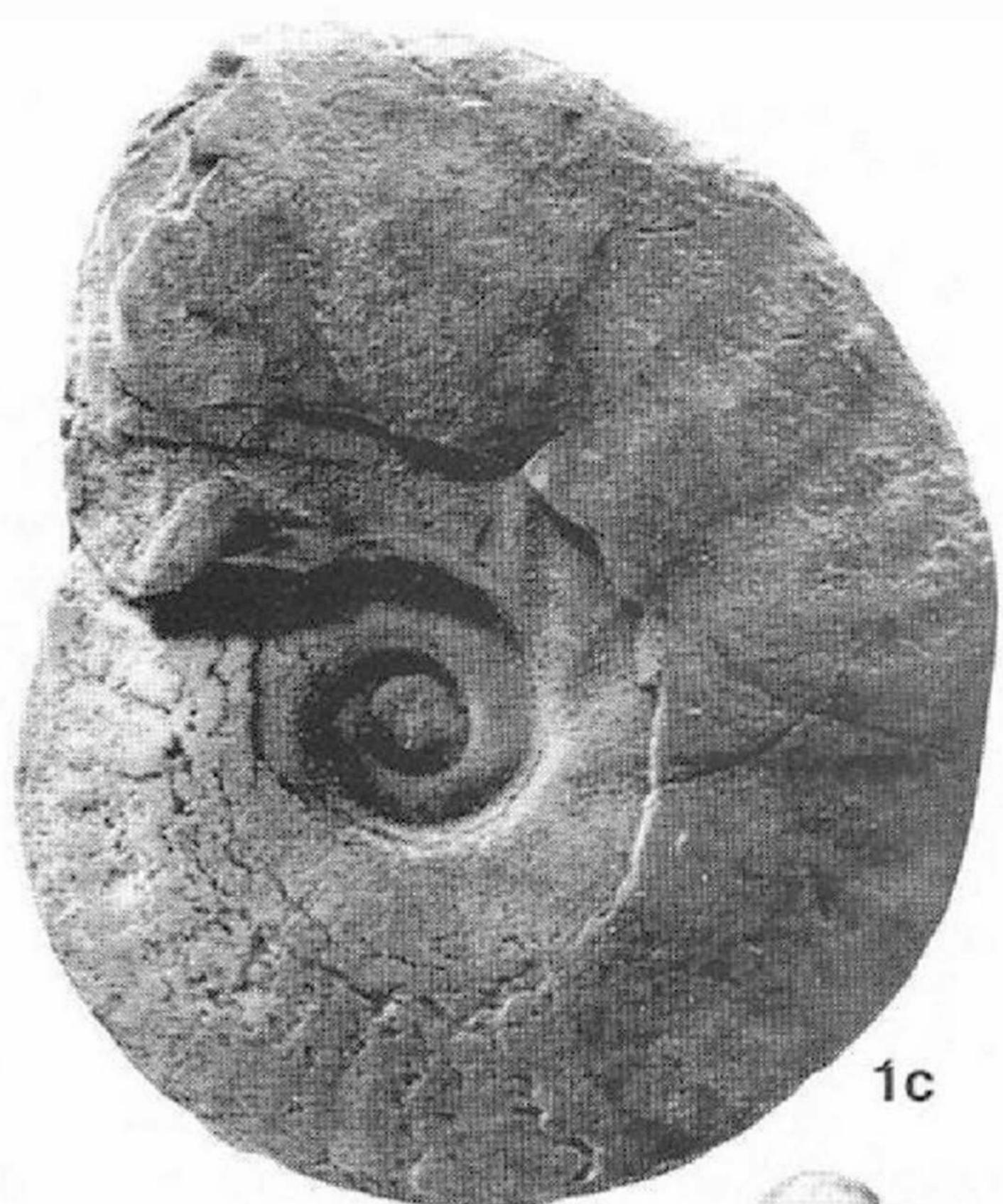
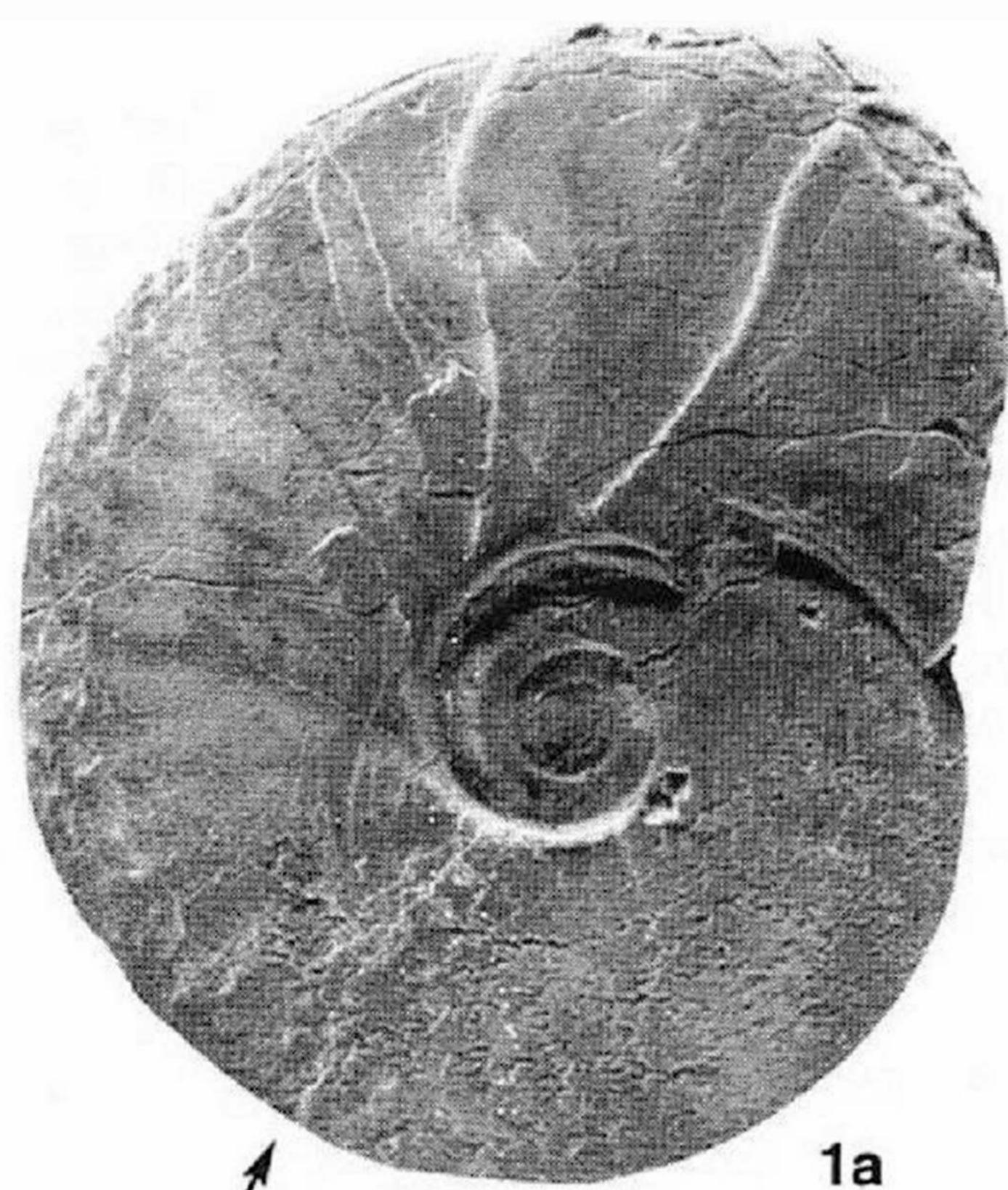
**Plate VIII**  
All figures in natural size unless stated otherwise

Figs. 1-3: *Aioloceras rollerii* (LEANZA) ♀/M & ♂/m, Lower Albian, Estancia La Federica, Lago San Martín.

1a-c: Almost complete adult microconch, MLP 29065, lateral, ventral and lateral views, loc. 71-2.

2a-c: “*Beudanticeras* cfr. *Stoliczkai*” of BONARELLI in BONARELLI & NÁGERA (1921, pl. 3, fig. 3), incomplete microconch with part of phragmocone and body chamber, SEGEMAR 9309c, lateral, ventral and lateral views.

3a-b: Almost complete macroconch, MLP 29122, lateral and ventral views, X0.50, loc. M4.



**Genus *Anadesmoceras* CASEY, 1954**(=*Carloscaceresiceras* ETAYO SERNA, 1979)

**Type species:** *Anadesmoceras strangulatum* CASEY, 1954, by original designation.

*Anadesmoceras strangulatum* CASEY, 1954, p. 107, fig. 2a-b, England (refigured in ARKELL *et al.*, 1957, fig. 513, 4; CASEY, 1966, pl. 96, fig. 3; WRIGHT *et al.*, 1996, fig. 74, 3a); 1966, p. 576, pl. 96, fig. 4, pl. 97, figs. 2, 4, 5, England; ?KENNEDY *et al.*, 1981, p. 237, pl. 7, fig. 4a-b, Denmark.

*Anadesmoceras acutum* SAVELIEV, 1973, p. 135, pl. 14, figs. 1-2, Kazakhstan.

*Anadesmoceras baylei* (JACOB) 1908, p. 59, pl. 7, fig. 25a-b, France (refigured in SPATH, 1925, text-fig. 20; CASEY, 1966, text-fig. 219); SPATH, 1925, p. 93, pl. 4, fig. 6a-b; CASEY, 1966, p. 582, pl. 95, fig. 1a-b, England; KEMPER, 1975, p. 100, pl. 3, fig. 9, Germany; ?including *A. costatum* CASEY, 1966, p. 578, pl. 96, figs. 1-2, England; KENNEDY *et al.*, 1981, p. 236, pl. 7, fig. 3, pl. 8, fig. 1, Denmark.

*Anadesmoceras caceresi* (ETAYO SERNA), 1979, p. 26, pl. 10, fig. 1, text-fig. 4A-B, 10, Colombia (type species of "*Carloscaceresiceras*").

"*Carloscaceresiceras*" *chimuense* (BENAVIDEZ CACERES)", ETAYO SERNA, 1979, p. 27, pl. 11, fig. 9, text-fig. 4J-K, Colombia (= ? *Desmoceras*).

"*Anadesmoceras constrictum*" LEANZA, 1970, p. 253, Patagonia (= *Beudanticeras revoili*).

"*Anadesmoceras costatum*" CASEY, 1966, England (= ? *A. baylei*).

*Anadesmoceras gravis* SAVELIEV, 1973, p. 137, pl. 19, fig. 2, pl. 20, fig. 1, text-fig. 27 Kazakhstan.

*Anadesmoceras matutinum* SAVELIEV, 1973, p. 141, pl. 14, fig. 3, pl. 15, figs. 2-3, Kazakhstan.

"*Carloscaceresiceras*" *monteroi* ETAYO SERNA, 1979, p. 26, pl. 10, fig. 5, Colombia.

"*Anadesmoceras nudum*" CASEY, 1966, England (= ? *Anadesmoceras tenue*).

*Anadesmoceras subbaylei* (SPATH) 1942, p. 700, text-

fig. 246, England (refigured in CASEY, 1966, p. 577, pl. 97, fig. 6); ?JELETZKY, 1964, pl. 23, figs. 3, 4, 6, Arctic Canada (= non *Cleoniceras discors* SAVELIEV, in OWEN 1988b, p. 484); ?KENNEDY *et al.*, 1981, p. 237, pl. 8, fig. 2a-b, Denmark.

*Anadesmoceras tenue* CASEY, 1966, p. 579, pl. 96, fig. 5a-b, England, ?including "A. nudum" CASEY, 1966, p. 581, pl. 97, fig. 7, England.

?*Anadesmoceras sp.*, SKEAT & MADSEN, 1898, p. 196, pl. 8, fig. 2, Denmark (as "*Hoplites splendens* var. *Fittoni*").

*Anadesmoceras sp.*, SAVELIEV, 1973, p. 140, pl. 13, fig. 3, Kazakhstan.

**Genus *Brewericeras* CASEY, 1954**(=? *Leconteites* CASEY, 1954)

**Type species:** *Ammonites breweri* GABB, 1864, p. 62, by original designation.

*Brewericeras breweri* (GABB) 1864, p. 62, pl. 10, fig. 7, California; CRICKMAY, 1927, p. 509, figs. 1-3; ANDERSON, 1938, p. 189, pl. 43, fig. 3, pl. 44, figs. 1-2, California; IMLAY, 1960, p. 105, pl. 17, figs. 5-10, 12, 13; JONES *et al.*, 1965, pl. 8, figs. 3, 5, S. Alaska; ?including *Brewericeras hulenense* (ANDERSON), 1938, p. 190, pl. 44, figs. 3-4; and pl. 48, figs. 2-3 (as "*Beudanticeras haydeni*", but see MURPHY & RODDA, 1960, p. 851), all California; WHITEAVES, 1876, p. 21, pl. 1, fig. 2, 2a, W. Canada; ANDERSON, 1938, p. 190, pl. 44, figs. 3-4, California; IMLAY, 1960, p. 106, pl. 17, figs. 11, 14-16, S. Alaska; MURPHY & RODDA, 1960, pl. 105, fig. 3, California; JONES *et al.*, 1965, p. F16, pl. 8, figs. 1, 2, 4, pl. 9, 10, pl. 11, figs. 1-3, 13-14; JONES in JONES & GRANTZ 1967, p. 29, pl. 6, figs. 10, 11, 15-19, all S. Alaska; ?NAGY, 1970, p. 34, pl. 1, fig. 3, Spitzbergen; McLEARN, 1972, p. 42, pl. 17, figs. 2-4, pl. 20, figs. 1-3, pl. 21, fig. 2, pl. 29, fig. 2, pl. 40, fig. 1, pl. 44, fig. 1, W. Canada; ZONOVA *et al.*, 1986,

## Plate IX

Figs. 1-3: *Aioloceras rollerii* (LEANZA) ♀/M, Lower Albian, Estancia La Federica, Lago San Martín.

1a-b: Complete macroconch, MLP 29199, lateral and ventral views, X0.30, loc. A XXII 22.

2a-b: Incomplete juvenile phragmocone of a macroconch, MLP 29054, lateral and ventral views, x1, loc. A XXII 21.

3a-b: Almost complete macroconch, MLP 29121, ventral and lateral views, X0.50, loc. M4.



1a



2a



1b



3a



3b



2b

p. 141, pl. 1, fig. 1, pl. 2, fig. 3, Russian Far East.

*Brewericeras deansi* (WHITEAVES), 1893, p. 442-444, pl. 7, fig. 1-1a, W. Canada; IMLAY, 1960, p. 109, pl. 19, figs. 7-27, JONES *et al.*, 1965, pl. 6, figs. 10, 11, 15, 16, all S. Alaska; ALABUSHEV & ALABUSHEVA, 1988, p. 19, pl. 2, fig. 1, NE Russia.

*Brewericeras hulenense* (ANDERSON), 1938 (= ? *Brewericeras breweri*).

*Brewericeras lecontei* (ANDERSON) 1902, p. 95, pl. 3, figs. 94, 95, pl. 10, fig. 190; 1938, p. 192, pl. 38, fig. 4, pl. 47, figs. 3-5, California (type species of "Leconteites"); IMLAY 1960, p. 109, pl. 19, figs. 1-3, S. Alaska; JONES *et al.*, 1965, p. F9, pl. 1, figs. 1-3, 6-11, 13-22, pl. 2, figs. 1-8, 10-14, 17, 21, pl. 3-5, pl. 11, figs. 4-6; pl. 6, figs. 1-9, 12-14; pl. 7, figs. 1-3 (as "subsp. *whiteavesi*"), Oregon, N. California, W. Canada, S. Alaska ; including "Leconteites modestus" ANDERSON, 1938, p. 193, pl. 50, figs. 3-4, California; IMLAY, 1960, p. 109, pl. 19, figs. 4-6, S. Alaska.

#### Genus *Neosaynella* CASEY, 1954

Type species: *Cleoniceras (Neosaynella) inornatum* CASEY, 1954, by original designation.

*Neosaynella inornata* CASEY, 1954, p. 106, figs. 3a-b (refigured in ARKELL *et al.*, 1957, figs. 513, 1a-b; 1996, fig. 75, 1a-b; CASEY, 1966, pl. 95, fig. 2); 1966, p. 571, pl. 91, fig. 10, pl. 95, fig. 3, all England.

*Neosaynella baisunense* (ILJIN) 1961, p. 51, pl. 3, fig. 1, 3, pl. 4, fig. 1, Uzbekistan.

*Neosaynella cantiana* (CASEY) 1966, p. 574, pl. 95, figs. 4-5, England; DESTOMBES, 1979, p. 96, pl. 4-15, fig. 1a-b, France.

"*Cleoniceras (Neosaynella) cardielense*" LEANZA, Patagonia (= *Beudanticeras revoili*)

*Neosaynella? dilleri* (JONES), 1960, p. 157, pl. 29, figs. 5, 13, 14, Oregon.

*Neosaynella glabra* SAVELIEV, 1992, p. 96, pl. 13, figs. 1-2, Kazakhstan.

*Neosaynella lupovi* CASEY, 1966, p. 574, text-fig. 217a-b, Kazakhstan.

*Neosaynella mirabilis* SAVELIEV, 1992, p. 94, pl. 6, fig. 2, pl. 8, fig. 1, pl. 9, figs. 2-3, Kazakhstan (= ? *N. platidorsata*)

*Neosaynella platidorsata* (SINZOW), 1909, pl. 2, fig. 6, Kazakhstan (as "*Desmoceras cleon* var. *platidorsata*"), refiugured in CASEY, 1966, p. 572, text-fig. 216c); CASEY, 1966, p. 573, text-fig. 217c-d, Kazakhstan; DESTOMBES, 1979, p. 91, pl. 4-17, fig. 1a-b, France; SAVELIEV, 1992, p. 86, pl. 3, fig. 1, pl. 4, figs. 1-3, Kazakhstan; including "*Cleoniceras mangyschlakense*" LUPPOV in LUPPOV *et al.*, 1949, p. 246, pl. 24, figs. 7-8, SINZOW, 1909, p. 32, pl. 2, figs. 1-5, Kazakhstan (as "*Desmoceras cleon*", figs. 1-2 refiugured in ORLOV, 1958, pl. 54, fig. 4, CASEY, 1966, p. 572, text-fig. 216a-b); LUPPOV, 1961, p. 191, pl. 3, fig. 1, pl. 4, fig. 2, Tajikistan; SAVELIEV, 1992, p. 91, pl. 1, fig. 2, pl. 3, fig. 2, pl. 5, figs. 1-2, pl. 6, fig. 1, pl. 7, fig. 1, Kazakhstan.

*Neosaynella rostrica* SAVELIEV, 1992, p. 98, pl. 9, fig. 1, pl. 10, fig. 1, pl. 11, fig. 1, pl. 12, fig. 1, Kazakhstan.

"*Cleoniceras (Neosaynella)? whittingtoni*" IMLAY, 1961, N. Alaska (= *Grycia*).

"*Cleoniceras (Neosaynella?) sp. 1 & 2*", ZONOVA *et al.*, 1986, p. 142-143, pl. 2, figs. 1-2, Russian Far East.

#### Genus *Grycia* IMLAY, 1961

Type species: *Cleoniceras (Grycia) sablei* IMLAY, 1961, by original designation.

*Grycia sablei* IMLAY, 1961, p. 64, pl. 20, figs. 13-20,

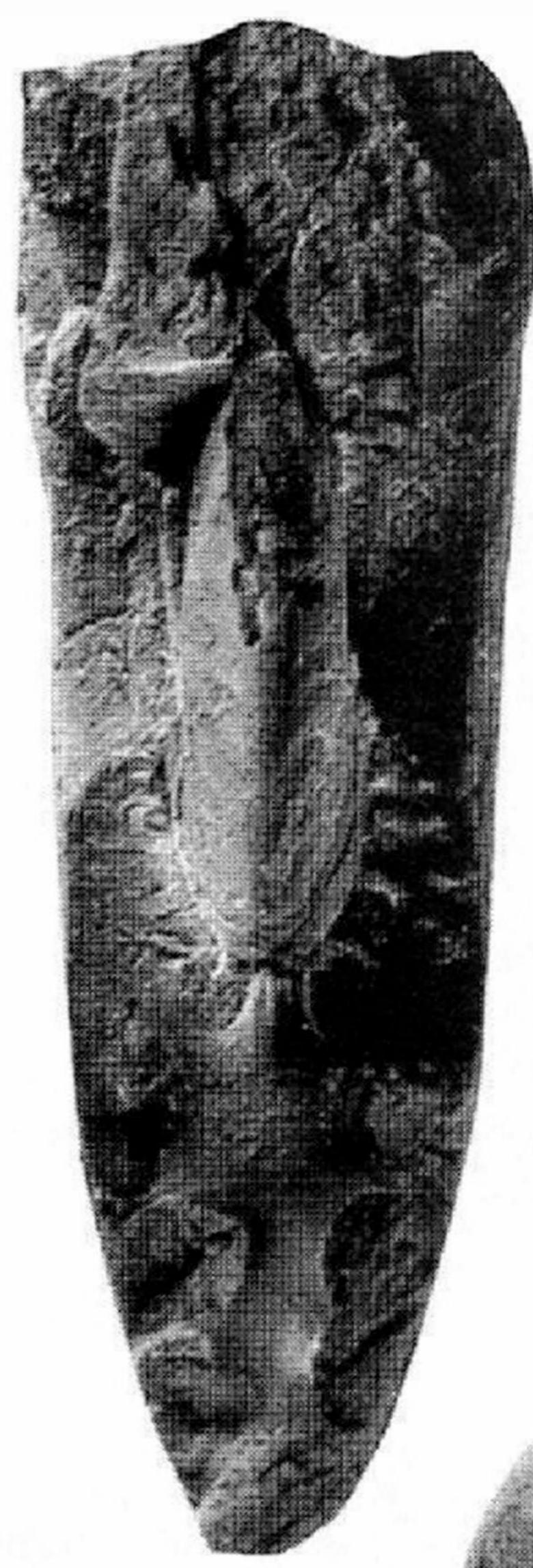
#### Plate X

All figures in natural size

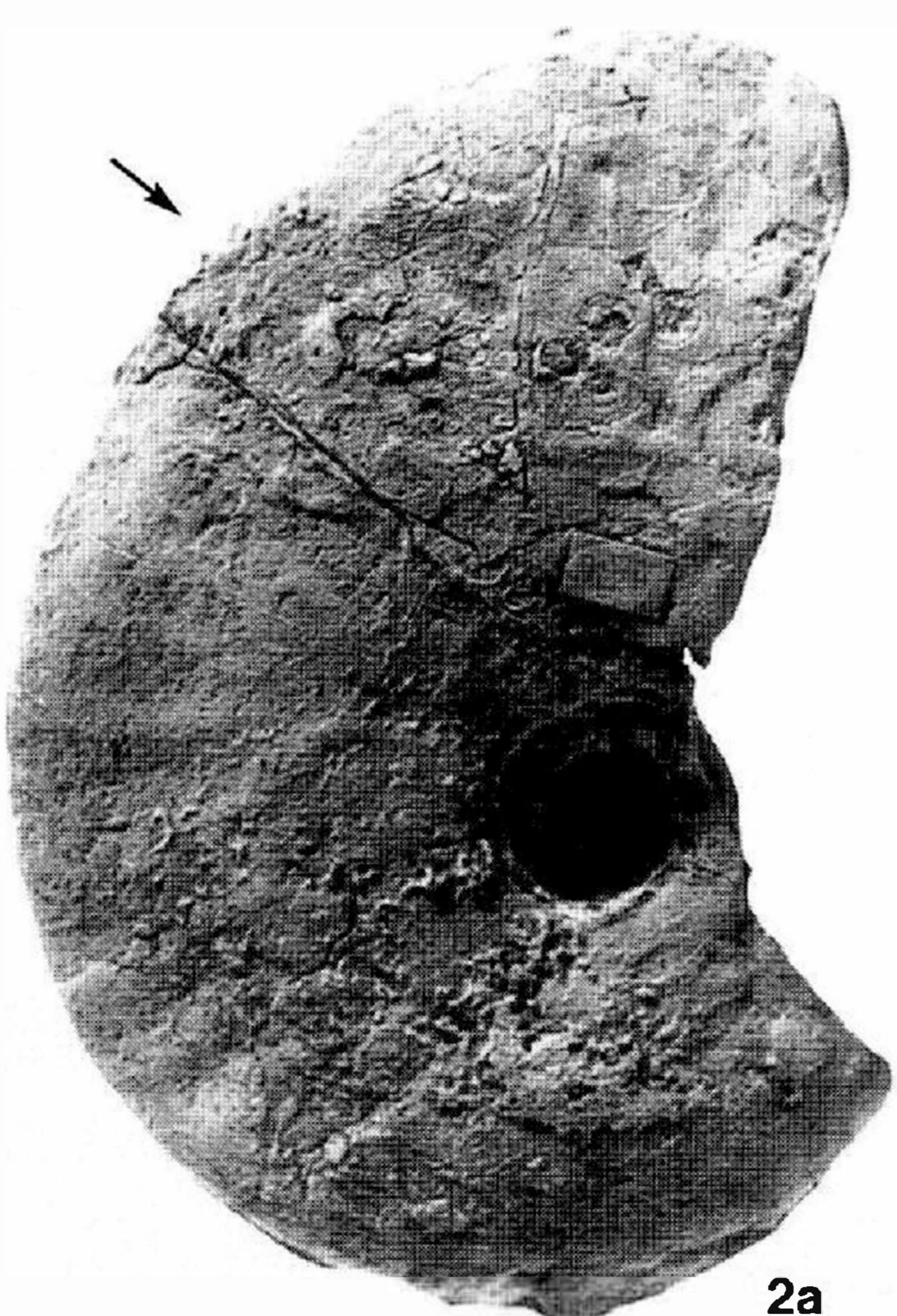
- Figs. 1-2: *Aioloceras rollerii* (LEANZA) ♀/M, Lower Albian, Estancia La Federica, Lago San Martín.  
 1a-b: "*Cleoniceras Seunesi*" of BONARELLI in BONARELLI & NÁGERA, 1921 (part), incomplete phragmocone of a macroconch, SEGEMAR 14904, lateral and apertural views.  
 2a-b: "*Beudanticeras Beudanti*" of BONARELLI in BONARELLI & NÁGERA (1921, pl. 2, fig. 11), incomplete macroconch with begining of body chamber, SEGEMAR 9299, lateral and ventral views.
- Figs. 3a-b: ?*Aioloceras* sp., Lower Albian, Estancia La Federica, Lago San Martín, incomplete specimen with part of body chamber, MLP 29159, lateral and apertural views, loc. Mx.



1a



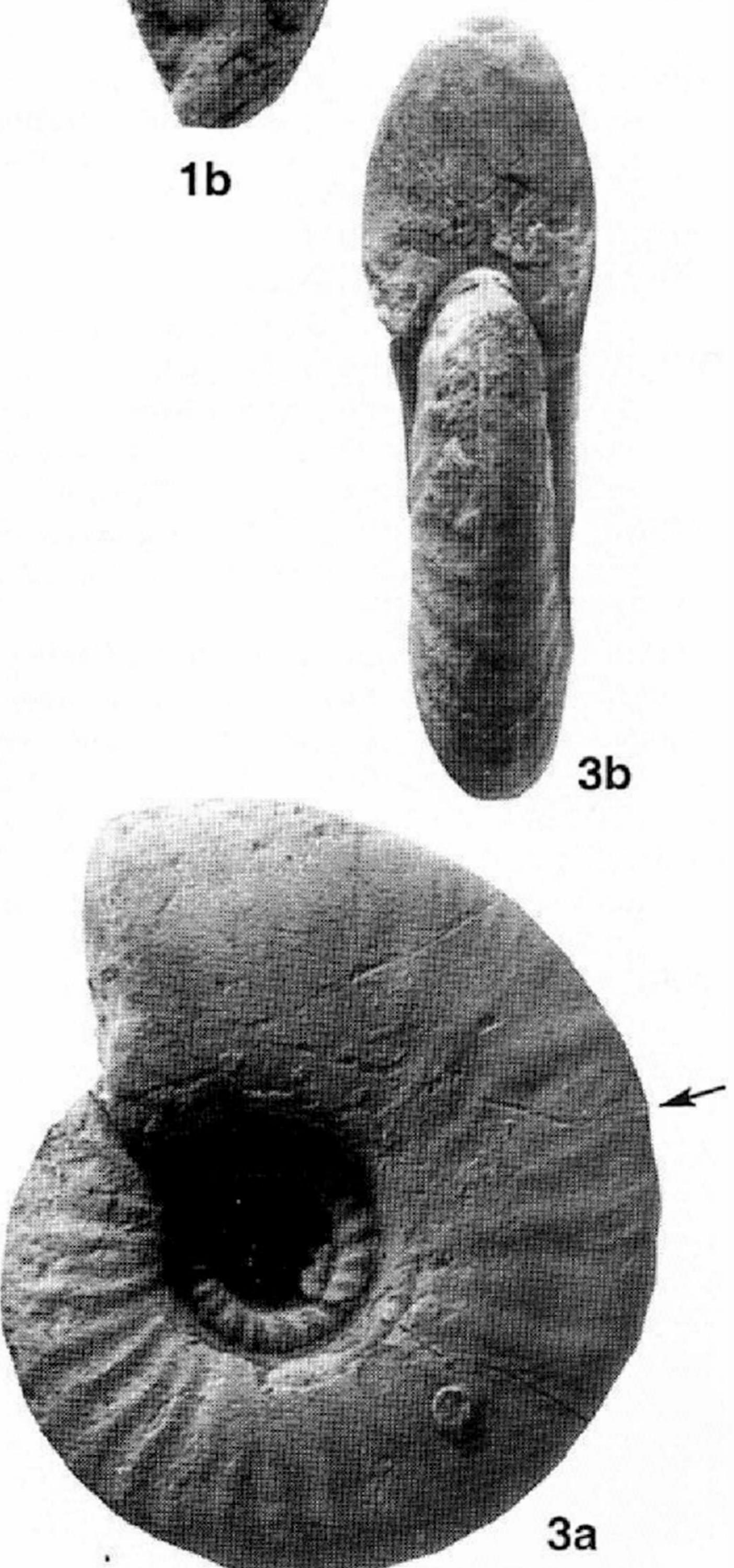
1b



2a



2b



3a



3b

- N. Alaska; NAGY, 1970, p. 37, pl. 1, figs. 8-10, pl. 2, fig. 1, Spitzbergen.
- Grycia densicostata* JELETZKY, 1980, p. 3, pl. 1, figs. 1-4, pl. 2, fig. 3, pl. 3, fig. 4, pl. 9, fig. 2, Arctic Canada.
- Grycia(?) dubia* (MICHAILOVA & TERECHOVA) 1975, p. 62, figs. 5-10, ALABUSHEV & ALABUSHEVA, 1988, p. 22, pl. 2, figs. 2-3, NE Russia.
- Grycia pereziana* (WHITEAVES), 1876, p. 19, pl. 2, fig. 1a-b; McLEARN, 1972, p. 59, pl. 23, fig. 2 (refigured in DOUGLAS, 1976, pl. 25, fig. 2), pl. 38, figs. 1-3, pl. 39, fig. 1, pl. 42, figs. 1-2, W. Canada; ALABUSHEV & ALABUSHEVA, 1988, p. 22, pl. 2, fig. 4, NE Russia.
- Grycia whittingtoni* (IMLAY) 1961, p. 64, pl. 20, figs. 6-9, N. Alaska; NAGY, 1970, pl. 2, figs. 2-4, Spitzbergen.
- Grycia* sp., NAGY, 1970, p. 39, pl. 1, fig. 11, Spitzbergen.
- "*Cleoniceras* (*Grycia*) sp.", WIEDMANN, 1978, p. 362, fig. 2c, e, Curaçao.

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