

THE LOWER CRETACEOUS AMMONITINA OLCOSTEPHANUS, LEOPOLDIA, AND FAVRELLA FROM WEST-CENTRAL ARGENTINA

DIE UNTERKRETAZISCHEN AMMONITINEN OLCOSTEPHANUS, LEOPOLDIA
UND FAVRELLA AUS DEM WESTLICHEN MITTEL-ARGENTINIEN

BY

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With Plates 11—14 and 19 Text-figures

Abstract

Based on new material from the quasi-type locality of BEHRENSSEN (1892) near Chos-Malal, Neuquén province, the *Olcostephanus-Leopoldia* assemblage is taxonomically revised and the type specimens are redescribed. The *Olcostephanus* is assigned to the almost cosmopolitan *O. atherstoni* (SHARPE) and demonstrated to be dimorphic; "*Amaltheus* (?) *attenuatus*" BEHRENSSEN is also dimorphic and placed in *Leopoldia*; *Favrella angulatiformis* (BEHRENSSEN) is present at a higher stratigraphic level. Seven to ten species names are placed in synonymy. This *Olcostephanus-Leopoldia* assemblage is dated as uppermost Valanginian/basal Hauterivian and *F. angulatiformis* as Lower Hauterivian. The other South American occurrences are discussed and the distribution of the genera is reviewed on a global scale.

Key words: Ammonitina — Lower Cretaceous — South America.

Zusammenfassung

Auf Grund von neuen Aufsammlungen im unmittelbaren Bereich der Typlokalität von BEHRENSSEN (1892) bei Chos-Malal, Provinz Neuquén, wird die *Olcostephanus-Leopoldia*-Fauna taxonomisch revidiert und die Typen neu beschrieben. *Olcostephanus* gehört der fast globalen dimorphen Art *O. atherstoni* (SHARPE) an; „*Amaltheus* (?) *attenuatus*“ BEHRENSSEN ist ebenfalls dimorph und wird zu *Leopoldia* gestellt; *Favrella angulatiformis* (BEHRENSSEN) liegt stratigraphisch höher. Insgesamt werden sieben bis zehn Art-namen synonymisiert. Die *Olcostephanus-Leopoldia*-Fauna wird an die Grenze Valanginium/Hauterivium und *F. angulatiformis* in das Untere Hauterivium gestellt. Die anderen südamerikanischen Vorkommen werden diskutiert, und die Verbreitung der Gattung auf anderen Kontinenten wird besprochen.

Schlüsselworte: Ammonitina — Untere Kreide — Südamerika.

Resumen

Sobre la base de nuevo material proveniente de la localidad tipo de BEHRENSSEN (1892), sudeste de Chos-Malal, Provincia de Neuquén, se revisa taxonómicamente la asociación de *Olcostephanus-Leopoldia*, y se redescrive el material tipo. Se prueba la naturaleza dimórfica de *Olcostephanus* que es asignado a la especie, casi cosmopolita, *O. atherstoni* (SHARPE). "*Amaltheus* (?) *attenuatus*" BEHRENSSEN es también dimórfico y referido a *Leopoldia*. *Favrella angulatiformis* (BEHRENSSEN) se halla representada en una posición estratigráfica superior. Entre 7 y 10 nombres específicos son colocados en sinonimia. La asociación de *Olcostephanus-Leopoldia* es considerada valanginiana superior-Hauteriviana inferior y *F. angulatiformis* hauteriviana inferior. Se discuten otras menciones de estos géneros en Sud América y se revisa su distribución mundial.

Palabras de referencia: Ammonitina — Cretácico inferior — Sud América.

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Introduction

Previous Work

Almost a century ago, G. BODENBENDER made a small collection of fossils from the "Arroyo Triuguico [recte Truquicó], 10 km before its junction with the Neuquen River" in the immediate vicinity of the locality here described (fig. 1). The molluscan fossils were sent to Göttingen, Germany, and described by BEHRENDSEN (1892) who assigned the ammonoids to *Olcostephanus* sp., *Hoplites angulatifformis* n. sp., *H. neumayri* n. sp. [= "*H. leopoldinus* NEUMAYR & UHLIG, non D'ORBIGNY"], *H. desori* PICTET & CAMPICHE, *H. cf. dispar* D'ORBIGNY, and *Amaltheus* (?) *attenuatus* n. sp. In 1909 DOUVILLÉ (p. 166) referred *H. angulatifformis* to *Favrella* n. gen. and in 1911 UHLIG (p. 425) placed *H. desori*, *H. neumayri* and *A. (?) attenuatus* in *Hatchericeras* STANTON (cf. GERTH, 1925 a, p. 46), an assignment soon doubted by WINDHAUSEN (1918, p. 114) mainly because of poor preservation.

The entire collection of BODENBENDER studied by BEHRENDSEN was sent to us on loan by Dr. S. RITZKOWSKI of the Geologisch-Palaeontologisches Institut der Georg-August Universität, in Göttingen (GPIG) and has been reexamined. All new species names had been based on single or a few fragments only, many of which are crushed or partly distorted. The revised listing is as follows, the number of specimens placed in parentheses:

- | | |
|---|--|
| <i>Olcostephanus</i> spec. (1) | = <i>Olcostephanus atherstoni</i> (SHARPE) ♀ |
| <i>Amaltheus</i> (?) <i>attenuatus</i> nov. spec. (1) | = <i>Leopoldia attenuata</i> (BEHRENDSEN) ♀ |
| <i>Hoplites</i> <i>Neumayri</i> nov. spec. (4) | = <i>Leopoldia</i> sp. [<i>L. neumayri</i> (BEHRENDSEN) nom. dub.] ♂ (+♀) |
| <i>Hoplites</i> conf. <i>dispar</i> D'ORB. (1) | = <i>Leopoldia</i> ? ♀ |
| <i>Hoplites angulatifformis</i> nov. spec. (7) | = <i>Favrella angulatifformis</i> (BEHRENDSEN) (♀ + ♂?) |
| <i>Hoplites Desori</i> PICT. et CAMP. (1) | = Neocomitinae indet. (? <i>Sarasinella</i> sp.) |

The briefly described (BEHRENDSEN, 1892, p. 18) but not illustrated fragment of "*Olcostephanus* sp." (GPIG 498—30) stems from a partly crushed large phragmocone with whorl height approximating 50 mm and whorl width approximating 70 mm. Strong blunt complete secondaries are borne in threes and fours from prominent periumbilical tubercles. The specimen falls within the morphological range here attributed to *O. atherstoni*.

The fragmentary immature septate holotype (monotypy) of "*A. (?) attenuatus*" (GPIG 498—29), described below under *Leopoldia attenuata*, is closely matched by a larger number of new quasi-topotypes from Cerro Pitrén. The name can therefore now be usefully employed for the most common species in west-central Argentina.

"*Hoplites neumayri*" BEHRENDSEN (1892, p. 17, pl. IV, fig. 1 a—b), was based on four whorl fragments of which one (GPIG 498—26) was figured in lateral view and another (GPIG 498—27) was diagrammatically represented in the cross-section. The figured incomplete small body chamber (here re-figured, pl. 12, fig. 2 a—b)

is designated as the lectotype if the name does not remain a nomen dubium due to incomplete knowledge of the species. The lectotype is an adult microconch (♂), the body chamber bearing flexuous faint ribs, without clear ventral interruption and periumbilical tubercles; it is thus distinct from *L. attenuata* ♂ and any other known species. BEHRENDSEN's cross-section (GPIG 498—27) was drawn from a body chamber fragment probably of a small macroconch (♀) (D ≈ 60 mm, H = 31.7 mm, W = 18.1 mm). This fragment bears periumbilical tubercles and is distinguished from *L. attenuata* by the presence of prominent not markedly interrupted ribs on the outer flanks and the more strongly inflated whorl section which appears to place it in the species group of *L. leopoldina*. The other two fragments (GPIG 498—229/230) although poorly preserved, closely resemble the *L. attenuata* sample from Cerro Pitrén.

The large body chamber fragment identified with "*Hoplites* conf. *dispar* D'ORB." (BEHRENDSEN, 1892, p. 17, no fig.) may also belong to *Leopoldia* according to whorl section and ornament. It is however, distinguished from all other material of this region by the presence of broad blunt plications on the inner flanks.

Two of the seven fragments of "*Hoplites angulatiformis* nov. spec." were figured (BEHRENDSEN, 1892, pl. IV, figs. 2 a—c). The larger specimen (figs. 2 b—c, GPIG 498—24) was designated as the lectotype by SPATH (1939, p. 147, footnote 3); both are newly illustrated (pl. 14, figs. 1—2), and the sample is discussed under *Favrella angulatiformis*.

The crushed fragment referred to "*Hoplites Desori* PICT. et CAMP." by BEHRENDSEN (1892, p. 15, pl. IV, fig. 4; here pl. 14, figs. 6 a—b), a species placed in *Sarasinella* UHLIG by KILIAN (1910, p. 223), has no match in our collection. The specimen shows some resemblance to *Neocomites crassicostatus* GERTH (1925 b, p. 108, pl. IV, fig. 3) which is probably also a *Sarasinella*.

From the proximity of Chacay Melehue, 35 km northwest of Arroyo Truquicó and Cerro Pitrén, GERTH (1925 a, p. 46) recorded *Olcostephanus* aff. *atherstoni* (SHARPE) together with *Favrella* sp., and LEANZA & GIOVINE (1949, p. 255) reported *Olcostephanus* and *Leopoldia*.

From the Cordillera del Durazno, northern Neuquén province, LEANZA (1957) reported a single bed bearing *Favrella* cf. *angulatiformis* (BEHRENDSEN) and *Hatchericeras* cf. *tardense* STANTON, and several levels with *Olcostephanus* sp.

Present Work

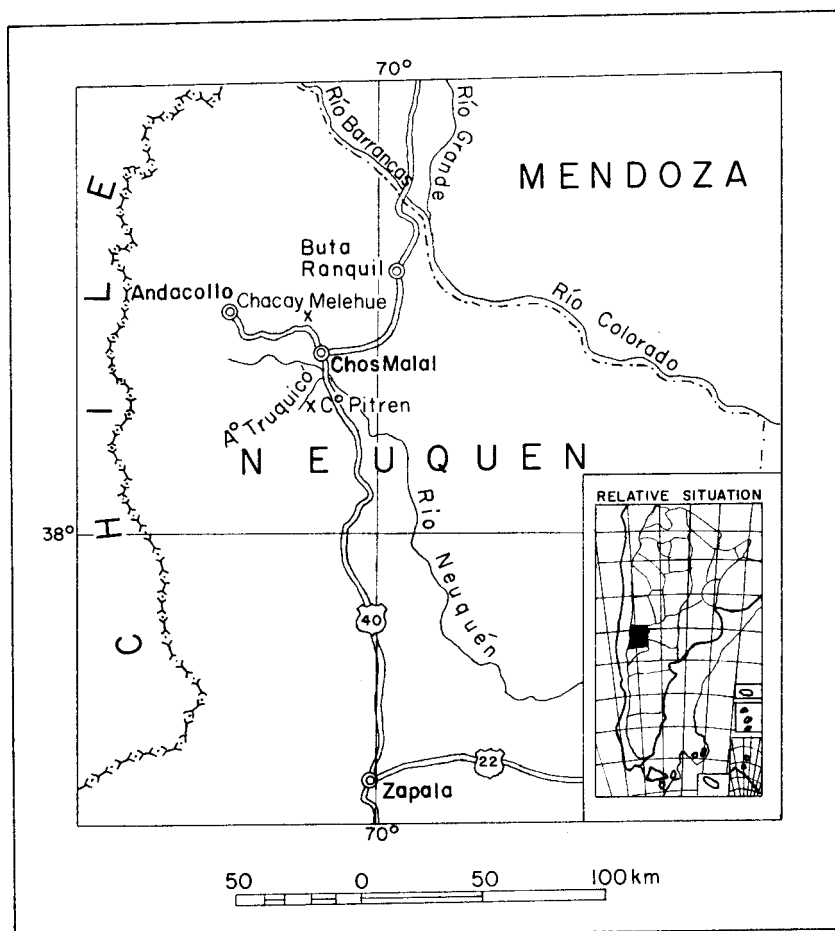
Two of the authors (A. C. R. and G. E. G. W.) briefly revisited the immediate vicinity of BODENBENDER's locality (BEHRENDSEN, 1892) in 1965, and again in 1970, while this paper was in press. At Cerro Pitrén, 15 km southwest of Chos-Malal, Neuquén province (fig. 1), the *Olcostephanus-Leopoldia* assemblage occurs in a series of shales with several intermittent oyster beds, dipping 25° South (but 70—85° in an adjacent fault block). The collection described herein comes from a 6 m shale interval well exposed at the collapsed tunnel entrance of an abandoned coal mine; its base is 12 m above a yellowish-brown weathering sandstone bed. Approximately 120 m above the *Olcostephanus-Leopoldia* assemblage is a bed bearing fragmentary *Favrella angulatiformis* (BEHRENDSEN) and *Holcoptychites* sp. Midway between these two assemblages lies the striking trigoniid *Yaadia transitoria* (STEINMANN).

In 1970, the same authors also briefly inspected the Lower Cretaceous section of Chacay Melehue (Cerro de la Parva) (fig. 1) and noted the close similarity to Cerro Pitrén in lithofacies and faunal succession.

The lower assemblage of Cerro Pitrén is comprised almost entirely of *Olcostephanus* and *Leopoldia*, both with macroconchs (♀) and microconchs (♂). The ammonite shells are well preserved as internal calcareous moulds with some recrystallized test remains. While the large macroconchs usually lack the body chambers, these are more or less completely preserved but commonly crushed in the smaller specimens. Significantly, in *Olcostephanus* crushing has affected the immature macroconchs much more than the adult microconchs of similar diameter, probably owing to thickened test of the adult body chamber.

Age

The assemblage with *Olcostephanus atherstoni* (SHARPE), and *Leopoldia elauta* LEANZA, is present over much of west-central Argentina and apparently in the same biostratigraphic position; it is said to be overlain by the Lower Hauterivian assemblage with *Acanthodiscus* cf. *radiatus* (BRUGIERE) and *Lyticoceras pseudo-*



Text-fig. 1. Index map of northwestern Neuquén province, Argentina, showing fossil locations of Cerro Pitrén, Arroyo Truquico and Chacay Mehue.

regale (BURCKHARDT) and to be underlain by the (Lower) Valanginian assemblage with *Neocomites wichmanni* LEANZA and *Thurmanniceras pertransiens* (SAYN) (WINDHAUSEN, 1918; GERTH, 1925 b; WEAVER, 1931; LEANZA, 1945, 1957; GIOVINE, 1950). Consequently, this assemblage has consistently been placed in the Upper Valanginian (cf. also IMLAY, 1960; CAMACHO, 1966; WIEDMANN, 1968).

However, no detailed stratigraphic work of the beds containing this assemblage has been carried out in west-central Argentina so that the ranges of its constituents remain unknown. Of particular interest in this regard is the genus *Leopoldia* which some specialists (V. V. DRUŽCZIC, personal communication) believe to be restricted to the Hauterivian; this agrees with its occurrence in Mexico, where *Olcostephanus* ranges from the Upper Valanginian well into the Lower Hauterivian while *Leopoldia* is essentially restricted to the Lower Hauterivian (IMLAY 1940, 1960). On the other hand, there is good agreement between the west-central Argentinian *Olcostephanus atherstoni* assemblage and the "Astieria-Schicht" of the Hauterivian in the Swiss Jura Mountains (see DEBELMAS & THIEULOY, 1965, p. 87). The "Astieria-Schicht" contains *Olcostephanus* ("Rogersites") *atherstoni*, *O. scissus* (SAYN) and *Leopoldia* ("Karakaschiceras") *biassalensis* (KARAKASCH), a close affiliate of *L. attenuata* while the main occurrence of *Olcostephanus* and *Leopoldia* is in the superjacent *Acanthodiscus radiatus* Zone of the Hauterivian. The "Astieria-Schicht" was placed at the Valanginian-Hauterivian boundary by DEBELMAS & THIEULOY (1965, p. 90) who inserted the new *Lyticoceras* sp. Zone in the Hauterivian below the *A. radiatus* Zone.

The Argentinian *Olcostephanus atherstoni* assemblage is therefore tentatively dated as late Valanginian to earliest Hauterivian, pending detailed biostratigraphic revision on a world-wide scale.

Favrella angulatiformis (BEHRENDSEN) occurs at Cerro Pitrén and Chacay Melehue (Cerro de la Parva) 100—150 m above the *Olcostephanus-Leopoldia* assemblage, contrary to the respective statements by BEHRENDSEN (1892) and GERTH (1925 a). At both localities, *F. angulatiformis* is associated with *Holcoptychites* sp., a genus usually placed in the Lower Hauterivian (WEAVER, 1931; LEANZA, 1957; ARKELL et al., 1957) although possibly ranging somewhat higher upwards into the middle Hauterivian (GERTH, 1925 b; GIOVINE, 1950; CAMACHO, 1966).

The record of a *F. angulatiformis* from the Upper Valanginian by WEAVER (1931, p. 56) is probably based on misidentification. *Favrella angulatiformis* is therefore dated as Lower Hauterivian, pending detailed biostratigraphic revision of the Lower Cretaceous in west-central Argentina.

Geographic Distribution

The three genera here described vary greatly in distributional patterns, from almost worldwide for *Olcostephanus* to essentially South American for *Favrella* (Text-fig. 2).

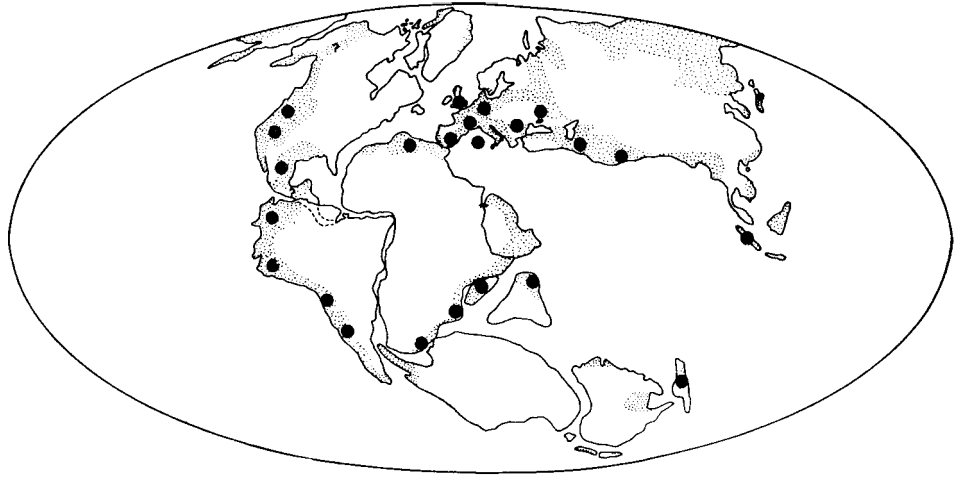
In the Central Andes of Argentina and Chile, *Olcostephanus* seems to be more abundant as pointed out by CORVALAN (in HOFFSTETTER et al., 1957, p. 24) than is apparent from the scarcity of literature. At least in Neuquén province it is usually associated with *Leopoldia* and below *Favrella* (for *Favrella* in Santiago province, see MARTÍNEZ & ERNST, 1965, p. 10). Yet, to the South, *Olcostephanus* and *Leopoldia* are missing in southern Patagonia while *Favrella* continues to be present quite abundantly. To the North, *Olcostephanus* has been reported from Atacama province, Chile (HOFFSTETTER et al., 1957, p. 13) and all three genera seem to be present in west-central Peru (LISSON, 1907; DOUVILLÉ, 1909; RIVERA, 1951; ROSENZWEIG, 1953; FERNANDEZ CONCHA, 1958). Although too poorly known for specific comparison, the Peruvian representatives link the Chile-Argentinian occurrences with the slightly better records from Colombia and Venezuela (RIEDEL, 1938; SPATH, 1939; ROYO y GOMEZ, 1945; KEHRER, 1956; BÜRGL, 1957, 1960; HAAS, 1960, 1966; ETAYO SERNA, 1968) where *Olcostephanus* in particular seems to be well represented by forms closely resembling those of Argentina on the one hand and Mexico on the other (SPATH, 1929, 1939).

Olcostephanus, *Leopoldia* and possibly also a few *Favrella* occur again in Mexico (CASTILLO & AGUILERA, 1895; BÖSE, 1923; IMLAY, 1937, 1938, 1940; PEÑA MUÑOZ, 1964). *Olcostephanus* includes forms closely affiliated to *O. atherstoni* (SHARPE) (BURCKHARDT, 1906; BÖSE, 1923; SPATH, 1939) and to species from Salt Range, Pakistan (SPATH, 1939, p. 149). The record of *Favrella* (IMLAY, 1937) is based on a single fragment and, although doubted by SPATH (1939), is here confirmed (specimen examined).

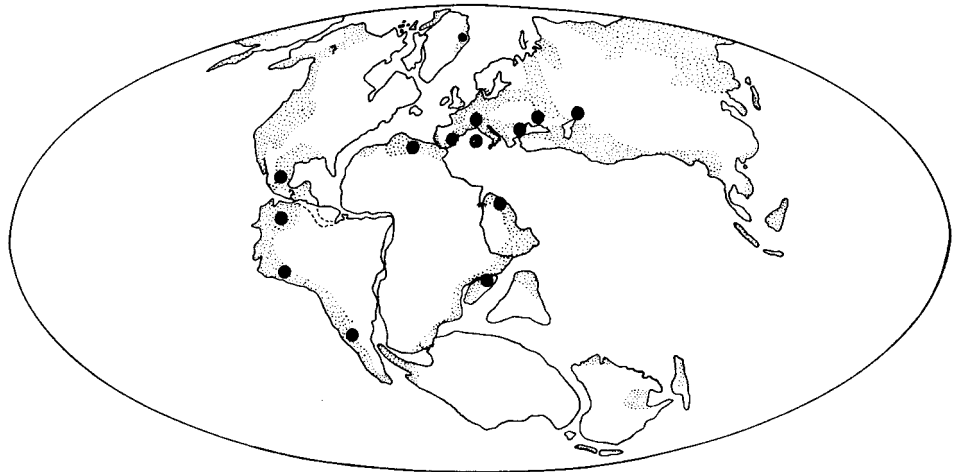
In the western United States, *Leopoldia* and *Favrella* are absent, while *Olcostephanus* is represented in Oregon and Washington states by species affiliated with *O. jeannoti* (D'ORB.) (type species of the subgenus *Jean-noticerias* THIEULOY, 1964, p. 212) and probably in California ("*O. atherstoni*" in PAVLOW, 1892, p. 497; but not mentioned in ANDERSON, 1938, and IMLAY, 1960). All three genera are unknown from Canada and Alaska; forms described under *Olcostephanus* by WHITEAVES (1882, 1884, 1893) are now assigned to *Seymourites* and *Dichotomites* (MCLEARN, 1929; JELETZKY, 1965). However, DONOVAN (1955, p. 21, 1957, p. 207) listed *Leopoldia* from Greenland.

The only and very doubtful record of *Favrella* outside of America is by DOUVILLÉ (1909). He included in the genus *Favrella*, *Neocomites volgensis* UHLIG, 1905 ["*Hoplites amblygonius*" PAVLOW, 1886, non NEUMAYR & UHLIG, 1881] supposedly from the Upper Jurassic of the Volga River, U.S.S.R.

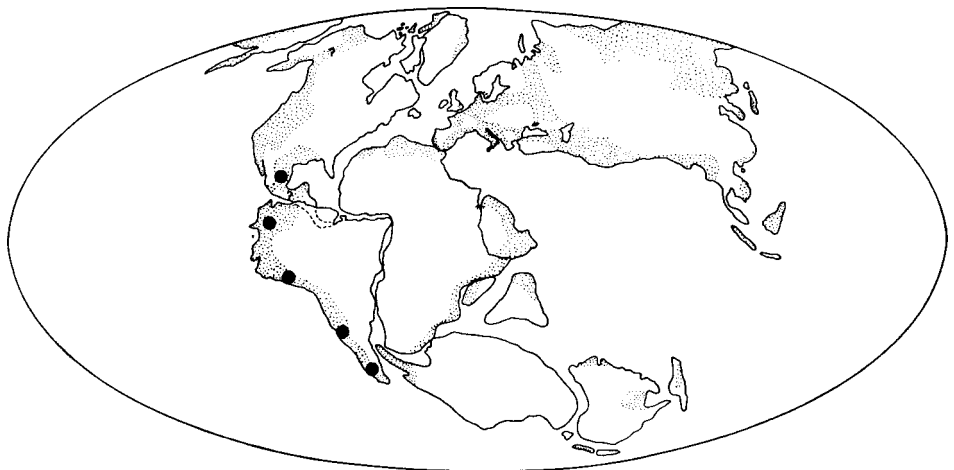
The European occurrences of *Olcostephanus* and *Leopoldia* include northeastern Spain (MALLADA, 1878; NICKLÈS, 1890), Sardinia (WIEDMANN & DIENI, 1968), and particularly the Alps (D'ORBIGNY, 1840—42; KILIAN & LEENHARDT, 1895; SARASIN & SCHÖNDELMAYER, 1901; KILIAN, 1902, 1910; BAUMBERGER, 1903—1910; WEGNER, 1909; KILIAN & REBOUL, 1915; RODIGHIERO, 1919; ROMAN, 1933; BREISTROFFER, 1936; BARBIER & THIEULOY, 1965; DEBELMAS & THIEULOY, 1965; BUSNARDO et al., 1966) where the presence of *O. atherstoni* and *L. bias-salensis* indicates faunistic affinities to the southern hemisphere. Similar forms occur also in Bulgaria (TZANKOV, 1943; NIKOLOV, 1962 a, b, 1965, 1969), in the Carpathian Mountains of U.S.S.R. (SLAVIN, in LIKHAREV 1958) and in the Crimea (KARAKASCH, 1889, 1902, 1907; DRUŻCZIC, 1960). But in northern Europe, *Leopoldia* and *Olcostephanus* are seldom represented in northern Germany (NEUMAYR & UHLIG, 1881; v. KOENEN, 1902) and at Speeton, England (SPATH, 1924).



Olcostephanus



Leopoldia



Favrella

Text-fig. 2. Geographic distribution of *Olcostephanus*, *Leopoldia* and *Favrella* on the early Cretaceous globe. Maximal marine transgression dotted; small plots indicating questionable occurrence. (Distribution of continents modified after WILSON, 1963, and SMITH & HALLAM, 1970).

In Asia, *Leopoldia* has been reported from the Emba River, south of the Ural Mountains in U.S.S.R. (KOLTYPIN, in LIKHAREV, 1958), and from Israel (BENTOR et al., 1960; RAAB, 1962), while only *Olcostephanus* is known from Iran, Tibet, Pakistan, northwest India (OPPEL, 1863; SPATH, 1939; AHMAD, 1961), and possibly Japan (SATO, 1958).

Olcostephanus of the *O. atherstoni* group is also known from Sumatra (BAUMBERGER, 1925), western New Guinea (WESTERMANN & GETTY, 1970) and New Caledonia (KILIAN & PIROUTET, 1905).

On the African continent, *Olcostephanus* and *Leopoldia* are present in Morocco, Algeria and Tunisia (ROCH, 1930; MEMMI, 1965; FURON, 1966). Only *Olcostephanus* is known from continental eastern Africa where species not closely related to *O. atherstoni* occur in Tanzania (KRENKEL, 1910; ZWIERYZYCKI, 1914) and Mozambique (SPATH, 1929) and *O. atherstoni* is well represented in South Africa (SHARPE, 1856; KITCHIN, 1908; SPATH, 1929). Both *Olcostephanus* and *Leopoldia* were described from Madagascar (LEMOINE, 1906; BESAIRIE, 1930, 1936; COLLIGNON, 1962).

The fact that this fauna is unknown from the eastern parts of the American subcontinents, most of western Africa, from Australia and Antarctica is a consequence of the absence of early Neocomian marine deposits.

Global faunistic comparisons at the species level are, as usual, of dubious significance with regard to dissimilarity (negative evidence), which may be due to either limited geographic distribution, biofacies and/or to erroneous time-correlation. This was quite evident to SPATH (1929, 1939) when attempting to explain the close affinities of *Olcostephanus* species between South Africa and Colombia or between Salt Range and Mexico, and the specific dissimilarities between South Africa and eastern Africa. If consideration is given to infraspecific variation based on single samples, positive evidence for geographic distributions indicates to us that *Olcostephanus atherstoni*, i. e. the "*atherstoni-schenki* group" of SPATH, was globally distributed in the lower latitudes, and that *Leopoldia* species were only slightly more restricted. In the boreal realm the Olcostephaninae seem to have been largely replaced by the Polypitichitinae, also of the family Olcostephanidae, and *Leopoldia* by related Neocomitidae, as indicated by IMLAY (1960) in a comparison of Mexican with northwestern United States faunas. *Olcostephanus* and *Leopoldia* appear to be absent in southern Patagonia, where the occurrence of *Favrella* indicates the presence of marine strata only slightly younger in age.

Abbreviations

Fossil Storage:	GPIG	— Geologisch-Paläontologisches Institut, Georg-August Universität, Göttingen, Germany.
	FCEN	— Facultad de Ciencias Exactas y Naturales (Departamento de Ciencias Geológicas, Catedra de Paleontología), Universidad Nacional de Buenos Aires, Argentina.
	McM.	— McMaster University (Department of Geology), Hamilton, Canada.
	MLP	— Museo de Ciencias Naturales (División Paleozoología de Invertebrados), Universidad Nacional de La Plata, Argentina.
Tables:	ad.	— Adult
	b. ch.	— Body chamber
	D	— Diameter
	H	— Whorl height
	juv.	— Juvenile
	M	— Macroconch (♀)
	m	— Microconch (♂)
	phr.	— Phragmocone
	U	— Umbilical width
W	— Whorl width	

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Systematic Descriptions

Superfamily Perisphinctaceae STEINMANN, 1890
Family Olcostephanidae HAUG, 1910
Subfamily Olcostephaninae HAUG, 1910

Genus *Olcostephanus* NEUMAYR, 1875

[*Holcostephanus* G. SAYN, 1889, rejected as an unjustified emendation of *Olcostephanus* NEUMAYR, 1875 — Opinion 575 I.C.Z.N.; *Astieria*, PAVLOW, 1892; *Rogersites* SPATH, 1924; *Taraisites* CANTU CHAPA, 1966].

Type species by original designation — *Ammonites astierianus* D'ORBIGNY, 1840.

Discussion:

The genus *Olcostephanus* has been described or recorded from many parts of the globe (Text-fig. 2). The descriptions and illustrations suggest that several species were almost cosmopolitan or at least that distant assemblages bore close resemblances as already pointed out by PAVLOW (1892, p. 492). In spite of their extensive description and illustration, many of the numerous named "species" and the three subgenera can be discriminated only with the utmost difficulty, if at all, and there is the additional problem of dimorphism. Obviously, much "splitting" is to be rectified by thorough new taxonomic work based on sufficiently large samples. Thus, in spite of the statement of UHLIG (1903, p. 84) that "if one is dependent solely on the literature, and is not in a position to make a complete monograph on the group, one is treading on rather unsafe ground", some of the "existing" genera and species are here reviewed in an attempt to clarify the status of the Argentine material.

Sexual dimorphism was already suggested for the type species *O. astierianus* by D'ORBIGNY (1840, p. 115) and UHLIG (1903, p. 86) who distinguished small forms with lappets and large ones without lappets; on the other hand, IMLAY (1960, p. 203) found the presence of dimorphism improbable because of numerical mismatch. The new evidence is, again, in favour of dimorphism. Thus, besides the abundant macroconch (females) "species", microconchs (males) with lappets have been named *O. psilostomus* (NEUMAYR and UHLIG), *O. wilmanae* (KITCHIN), *O. auriculatus* (ZWIER.), *O. otoitoides* (SPATH), *O. salinarius* SPATH, *O. wynnei* SPATH, *O. midas* (LEANZA), *O. auritus* (LEANZA), and *O. popenoei* IMLAY.

Our entire material of *Olcostephanus* belongs to the "*atherstoni-schenki* group" of SPATH (1939, p. 142) which he usually placed tentatively in *Rogersites* SPATH, 1924, type species *O. modderensis* (KITCHIN). SPATH attempted only once (1939) to formulate a diagnosis for *Rogersites* (now mostly lowered to the subgenus level) after he had included several South African species (1929): forms like *O. modderensis*, *O. baini* (SHARPE) and *O. kitchini* (SPATH) "with few and very coarse primary and secondary ribs and prominent umbilical edge" were regarded as typical *Rogersites* (1939, p. 11) displaying, the "typical *Rogersites* characters . . . coronate cadicone and vertical umbilical wall, at larger diameter, while retaining coarse ribbing" (1939, p. 31). A similar diagnosis is given in the Treatise (ARKELL et al., 1957, p. L 347) where *Rogersites* is retained as a subgenus of *Olcostephanus*: "Generally large and inflated; ribs on outer whorls coarser and less dense and umbilical edge more angular than in *O. (Olcostephanus)*."

However, these alleged diagnostic characters are not clearly present in several species referred by SPATH (1939) to *Rogersites*, according to his own description, and he also noted that several species are intermediate to *Olcostephanus* (s. str.). Quoting from SPATH (1939, p. 32): "The adult *O. (R.) schenki* differs from *O. (R.) atherstoni* (SHARPE) merely in being slightly more coarsely ribbed; and both these species are transitional between *Olcostephanus* and typical *Rogersites*" or (p. 19) "I previously referred *O. uitenhagensis* to *Rogersites* but like *R. atherstoni*, *R. sphaeroidalis* and the many passage forms between these species, *O. uitenhagensis* is one of the transitions from *Rogersites* to *Olcostephanus*". In the same monograph, SPATH inconsistently referred to *Rogersites* as either a genus (p. 16) or subgenus (p. 30—32) and the same species may be placed in it with or without query on different pages. SPATH (1939) excluded many cadicone species from *Rogersites* and apparently used coarse ribbing as the principle (sub-)generic character. But inconsistency is again seen in his (p. 138) inclusion of the "finely ribbed" "*O. (R.)* sp. nov. indet." from Madagascar.

The close affinity between *O. modderensis* KITCHIN and the common "*atherstoni-schenki* group" is also evident from the fact that the holotype of *O. modderensis* had been referred to *O. schenki* by PAVLOW (1892, p. 493).

“*Rogersites*” *modderensis* has not been reexamined nor has new material become available, except for a single specimen briefly described but not figured by SPATH (1929, p. 148). Although the holotype (KITCHIN, 1908, p. 202, pl. X, figs. 3, 3a) clearly has more globose involute whorls than the “*atherstoni-schencki* group”, *O. sublaevis* SPATH and *O. globosus* SPATH are similarly globose. On the other hand, rib prominence and spacing seems to be independent of globosity, since *O. baini* and *O. rogersi* (KITCHIN) are coarsely ribbed but less globose than “*R.*” *modderensis*.

Subsequent discrimination of “*Rogersites*” from *Olcostephanus* was mainly based on the coarser ribbing of the former. Thus SPATH (1939, p. 149) accepted the classification of *Rogersites paucicostatus* IMLAY and *R. tenuicostatus* IMLAY from Mexico, and IMLAY (1960) later excluded from “*Rogersites*” the globose and densely ribbed *O. filifer* (IMLAY). However, the infraspecific variation of the better known *O. salinarius* SPATH (1939) ranges from 62 secondaries per halfwhorl on the holotype (pl. I, fig. 1a) to 43 in “var. *crassa*” (pl. I, fig. 3a), so that the generic or subgeneric discrimination of “*R.*” *modderensis*, based on a single specimen, appears highly dubious.

If we add to these considerations of *Rogersites* the taxonomic complications ensuing from apparent sexual dimorphism usually with cadicone finely ribbed macroconchs and more planulate coarsely ribbed microconchs, it becomes clear that this taxon does not serve any useful function. *Rogersites* is therefore regarded as a junior subjective synonymy of *Olcostephanus*, in agreement with WIEDMANN & DIENI (1968, p. 95).

The genus *Taraisites* CANTU CHAPA (1966, p. 16) was based on the type species *T. bosei* CANTU CHAPA [“*Astieria* aff. *Baini* SHARPE” in BÖSE, 1923, p. 76, pl. II, figs. 3—5; non SHARPE] and discriminated from *Olcostephanus* and “*Rogersites*” on the distant secondary ribs said to be borne in twos and threes from the periumbilical tubercles. Thus the small and more distantly ribbed paratypes of “*Rogersites*” *paucicostatus* and “*R.*” *prorsiradiatus*, IMLAY spp. (1937), were separated from the larger and more densely ribbed holotypes and transferred to the new genus under the new species names *T. carrillense* and *T. neoleonense*. No proper consideration was given to growth stage and morphologic variation which were presumably known to IMLAY; CANTU CHAPA omitted the critical evidence that the small paratypes differ from the inner whorls of the large holotypes. Even if the supposed differences in rib density should exist, distinction at the species level might have sufficed.

The number of secondaries per tubercle in *O. modderensis* (KITCHIN), type species of *Rogersites* SPATH, is usually three and rarely four, while it is usually three and less commonly two in most specimens and “species” assigned to “*Taraisites*”. This difference seems insignificant, since infraspecific variation in *Olcostephanus* is commonly greater, as shown above. *Taraisites* is therefore identical with *Rogersites* (junior subjective synonym at the subgeneric level) and both are regarded as synonymous with *Olcostephanus*.

Olcostephanus atherstoni (SHARPE, 1856)

(Pl. 12, figs. 3—4; Pl. 13, figs. 1—5; Text-figs. 3—10)

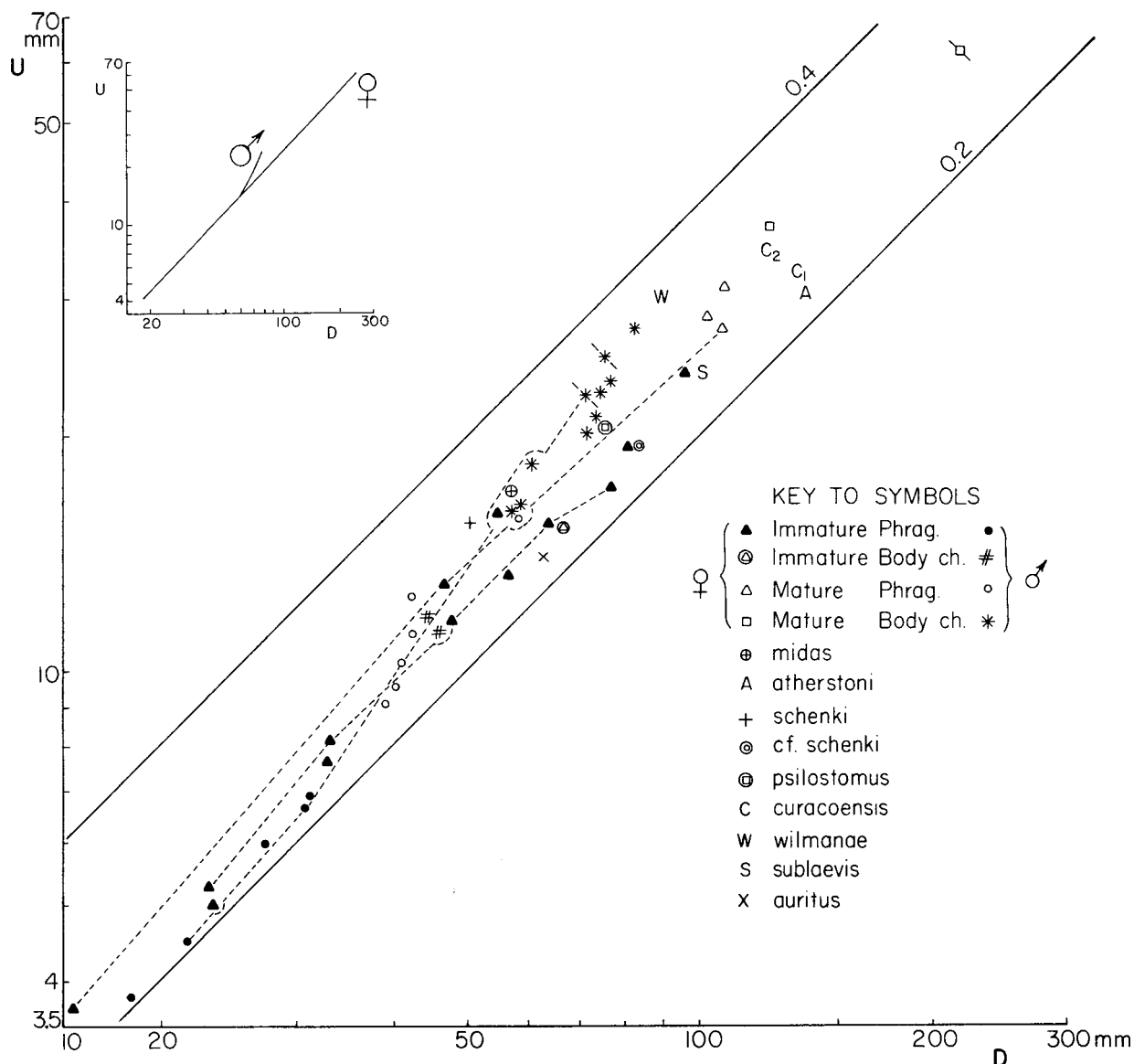
O. atherstoni ♀

- 1856 *Ammonites Atherstoni* SHARPE, p. 196, pl. XXIII, figs. 1a—b.
- 1863 *Ammonites Schenki* — OPPEL, p. 286, pl. 81, figs. 4a—c.
- 1892 *Olcostephanus* sp. BEHRENDSEN, p. 18.
- 1903 *Holcostephanus (Astieria) schenki* — UHLIG, p. 130, pl. XVIII, figs. 2a—c [holotype refigured].
- ?1931 *Astieria curacoensis* WEAVER, p. 427, pl. 49, figs. 326, 327, pl. 50, fig. 328.
- 1931 *Astieria sudandina* (sp. ined.), WINDHAUSEN, pl. 33, fig. 1 [nom. nud.].
- ?1939 *Olcostephanus sublaevis* SPATH, p. 21, pl. III, figs. 1—3; pl. XIX, fig. 2.

O. atherstoni ♂

- 1881 *Olcostephanus psilostomus* n. f., NEUMAYR & UHLIG, p. 149, pl. XXXII, fig. 2.
- 1908 *Holcostephanus wilmanae* KITCHIN, p. 195, pl. IX, figs. 1, 1a.
- 1944 *Holcostephanus midas* LEANZA, p. 16, pl. I, figs. 1a—c.

Diagnosis: A cadicone species of *Olcostephanus*; phragmocone whorls strongly depressed oval to semi-circular with rounded umbilical margin and narrow umbilicus ($U \sim 26\%$); about 20 periumbilical bullae-like tubercles per whorl each dividing into 3 to 4 secondaries. Body chamber of microconch medium-sized, highly ornate, with lappets; large macroconch with prominent periumbilical tubercles or spines and dense secondaries on the last two whorls.



Text-fig. 3. Plot of umbilical width (U) against shell diameter (D) for *Olcostephanus atherstoni* (SHARPE) with synonymous "species" (type specimens). Several growth lines dotted. Inset with visually drawn median-lines.

Material: Chacay Melehue: 1 microconch [*O. midas*, holotype]; Cerro Pitrén: 13 macroconchs including 1 adult with complete body chamber, 11 (? + 4) microconchs with incomplete or complete body chamber, 2 juveniles with body chamber.

Description:

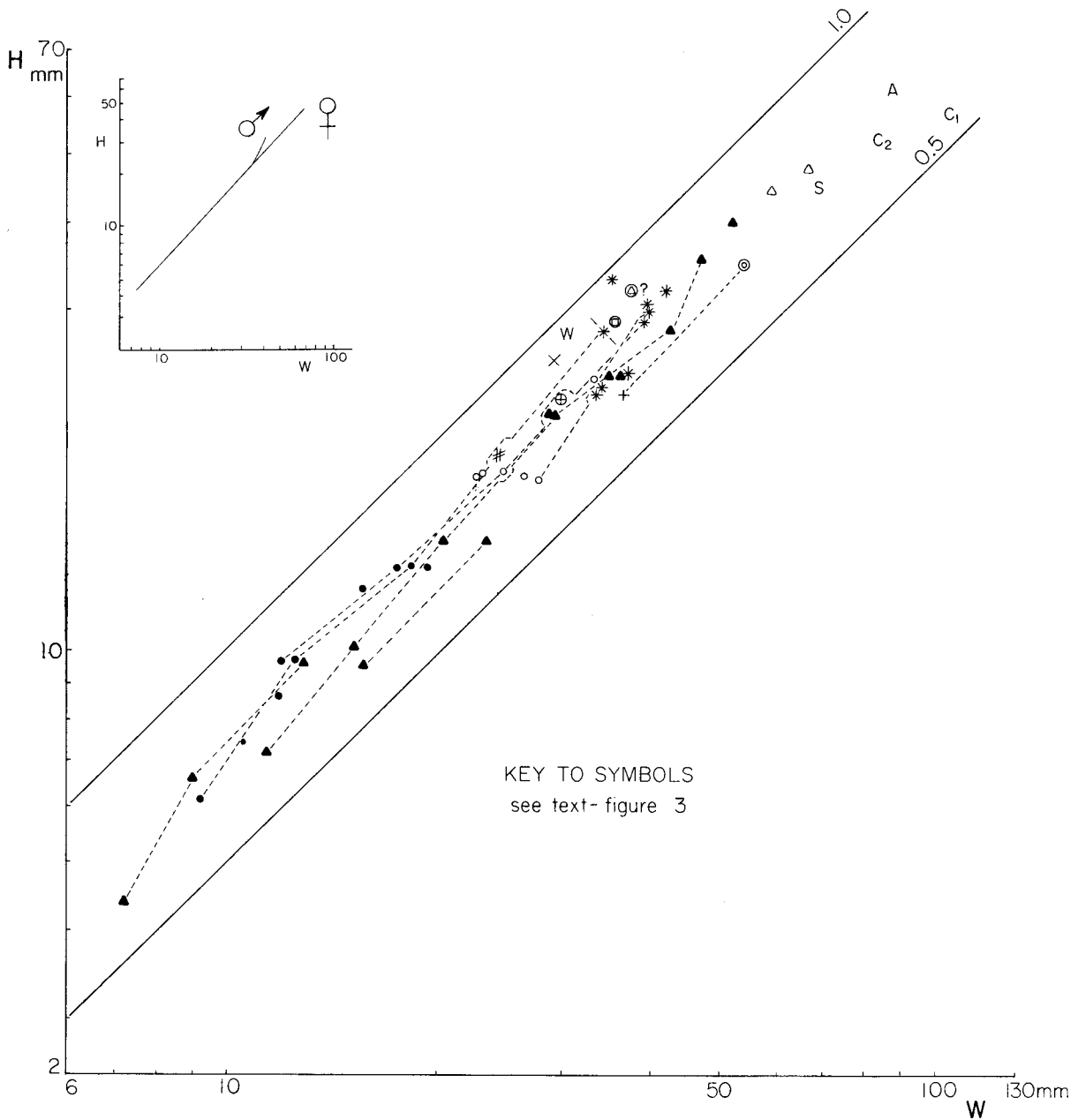
Protoconch — The small protoconch is barrel-shaped with a diameter of 0.25 mm and a width of 0.38.

Phragmocone — The shell is cadicone with depressed subovate to semicircular whorls bearing a rounded umbilical margin and a deep moderately narrow umbilicus.

The whorls are at first strongly depressed ($H/W \sim 0.7$ at 10 mm D) and involute ($U/D \sim 0.21$ at 20 mm D), but usually become later somewhat higher and more evolute ($H/W \sim 0.8$, $U/D \sim 0.24$) (Text-figs. 3—4). However, the changes in growth rates controlling the whorl section are barely perceptible to the eye and infraspecific variation within any size group is larger than morphogenetic development which consists of a somewhat higher negative allometry for width than for height ($H/D \sim 0.45 \rightarrow 0.41$; $W/D \sim 0.65 \rightarrow 0.55$) (Text-figs. 5—6). Weakly positive allometry for umbilical width is consistently present up to about 35 mm diameter, coinciding with the adult size of the microconch phragmocone, but seemingly disappears in the larger phragmocone of the macroconch.

The umbilical wall is high and steep, not quite vertical, rounding slightly into the umbilical margin. The whorl overlap approximates two-thirds of the preceding whorl and tends to increase on the outer whorls of the macroconch phragmocone. Again, there is much individual variation. The dorsal impression of the whorls is about one-third of the whorl height.

The inner whorls up to 6 mm diameter are entirely smooth. Costae and tubercles become prominent at about 13 mm diameter. The ribs are borne near the umbilical seam, progressively become prominent and rursi-radiate on the umbilical wall, and usually form bullae-like tubercles on the upper part of the umbilical margin. From these arise bundles of slightly prosoradiate secondaries which, together with some irregular intercalatories, cross the venter in full strength. The inner whorls up to 30—40 mm diameter of both macroconch and microconch have about 8 primaries and 30—35 secondaries per halfwhorl (Text-fig. 7). Subsequently, the number of secondaries in the macroconch increases up to the end of the phragmocone, reaching 35—50 per halfwhorl; in



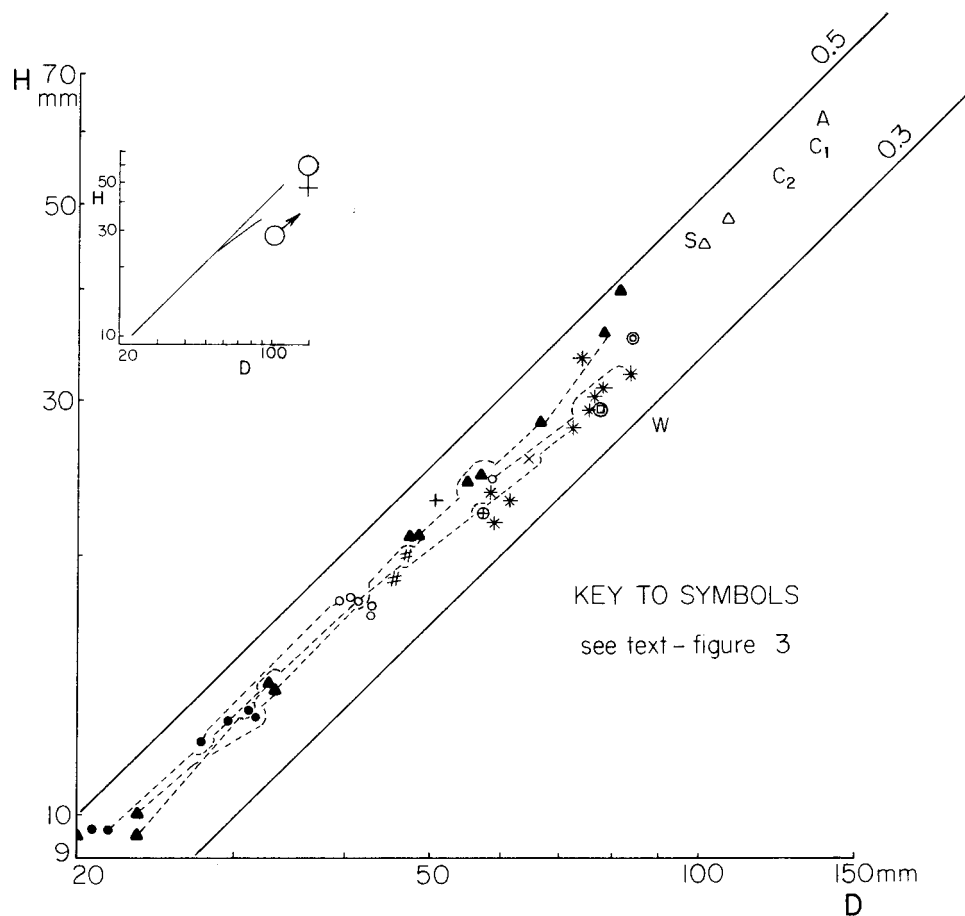
Text-fig. 4. Plot of whorl height (H) against whorl width (W) for *Olcostephanus atherstoni* (SHARPE) with synonymous "species" (type specimens). Growth lines dotted.

the microconch, their number remains more or less constant or decreases slightly. The number of primaries per whorl remains approximately constant in both macroconch and microconch. Not all primaries form tubercles on the umbilical margin, particularly if they are relatively dense, e. g. 20—21 tubercles (per whorl) are developed on a specimen with 23 primaries.

The number of secondaries borne from each tubercle varies greatly, from two to five, with three to four found most commonly. They intergrade into intercalatories by poorer connection with the tubercles. As usual, the number of ribs is inversely related to their strength. The ribs are prominent and usually sharp except for the last whorls of the macroconch phragmocone where they become blunt.

Constrictions are irregularly developed, generally about one per whorl on the adult phragmocone. However, up to three may be present on the inner whorls with even spacing. The width of the constrictions approximates the intercostal spaces.

Septum and Suture — The septum is typically eubullate, i. e. with several continuous lobe and saddle axes directed towards the protoconch. The morphogeny of the suture is figured in a complete series from the macroconch and commencing at 2 mm diameter from the microconch (Text-figs. 9—10). One of the first true sutures (0.8 mm D) has two umbilical lobes, U_1 and U_2 , with the seam centred on the saddle between them (U_1/U_2). Subsequently, at 1.0 mm diameter, a new indentation appears on the dorsal flank of this saddle, internally adjacent to the umbilical seam. This mode of development closely resembles the examples of olcostephanids given by SCHINDEWOLF (1966, p. 387) who interpreted it as asymmetric subdivision of the U_1 lobe, rather than of the U_1/U_2 saddle, and consequently included the new indentation as a ventral branch in a divided (split) U_1 . Although the distinction of lobe from saddle division is not clear in this case and the terminology therefore somewhat arbitrary, this mode is nevertheless distinct. Two new umbilical elements are added respectively at about 2 and

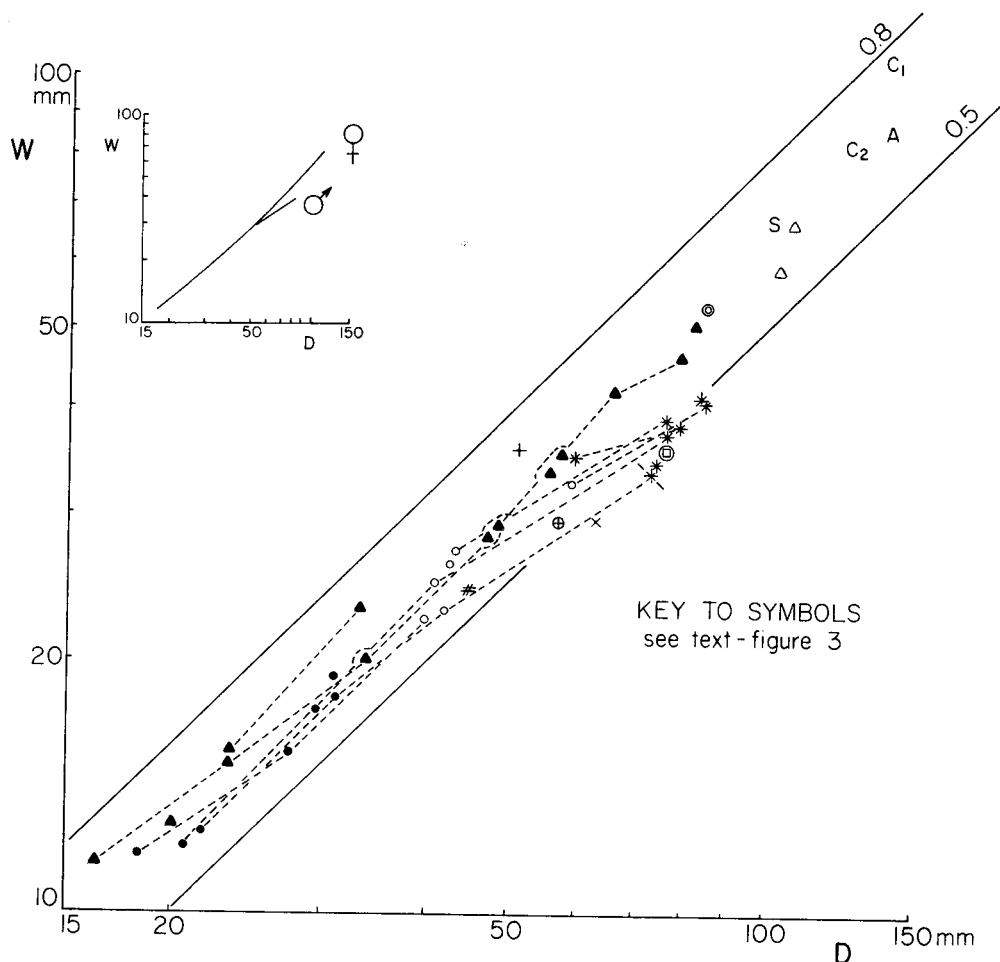


Text-fig. 5. Plot of whorl height (H) against shell diameter (D) for *Olcostephanus atherstoni* (SHARPE) with synonymous "species" (type specimens). Several growth lines dotted.

5—8 mm diameter. The internal part of the maturing suture has two identical saddles separated by the “internal lateral lobe” (all or part of) U_1 (not U_n as in the abullate septum); this pattern is repeated in the external suture by the two identical saddles E/L and L/U separated by L . All mature lobes and saddles are long, narrow and moderately complex and at least the smaller external umbilical lobes are slightly oblique. The microconch suture closely resembles that of the macroconch. The strong obliquity of the small umbilical lobe of the largest microconch suture (Text-fig. 10e), however, is only apparent owing to strong asymmetry, i. e. hypertrophy of the ventral indentation.

Body Chamber — Macroconch (♀): The body chamber is approximately one full whorl in length and closely resembles the adult phragmocone, except for the weak uncoiling of the umbilical seam and the slightly more shallow umbilical wall (pl. 13, fig. 1). The number of secondaries increases further to about 130 per whorl and the tubercles become much stronger. The terminal diameter is approximately 220 mm. The aperture is marked by a strong oblique constriction preceded by an incompletely preserved flange, and the peristome seems to have been flared. The exact whorl section is unknown because of crushing.

Microconch (♂): The body chamber is almost one full whorl in length. The whorl overlap decreases to about one-half of the preceding whorl as the umbilical seam egresses markedly. The whorl section becomes somewhat more rounded by negative allometry of width growth. The ornamentation increases in strength, particularly the long secondaries as their number per whorl remains about constant or decreases with much variation (25—40 secondaries per halfwhorl). Immediately preceding the peristome is a strong flange, projecting ventrally, followed by a constricted (internal mould only?) collar and short lateral lappets which converge slightly.



Text-fig. 6. Plot of whorl width (W) against shell diameter (D) for *Olcostephanus atherstoni* (SHARPE) with synonymous “species” (type specimens). Several growth lines dotted.

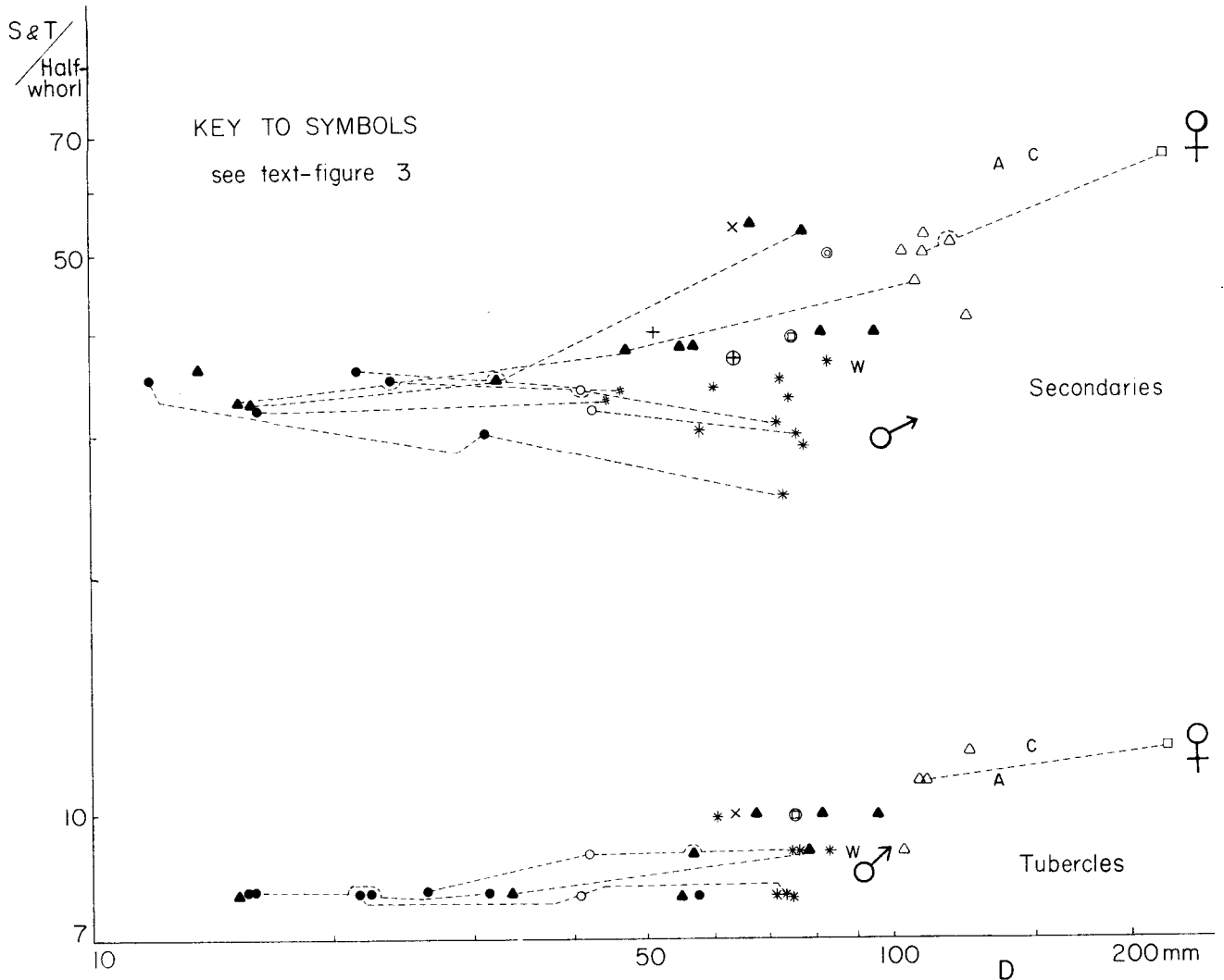
Sexual Dimorphism:

As has been shown, the microconch phragmocone and the inner macroconch whorls are identical in whorl section and coiling, while identity of ornamentation is restricted to the nucleus under 20 mm diameter. Significantly, difference in immature density of ribbing (from 15 mm diameter) is known to occur between dimorphs of *Pectinatites* (COPE, 1967, p. 17). In the microconch *O. atherstoni*, the ribs strengthen up to the end of the adult body chamber; in the macroconch, the secondaries continue to weaken or remain similar relative to size without becoming obsolete. Although not a case of “varicostation”, this contrasting development is nevertheless characteristic for dimorphic differentiation (CALLOMON, 1963, p. 28). The number of periumbilical tubercles per whorl remains almost constant in both dimorphs, and their development is thus much stronger in the adult large macroconch.

Distinctive features of adult body chambers are the egression of the umbilical seam, the concurrent decrease of whorl overlap, and the rounding of the whorls by lateral contraction. All are clearly developed in the microconch and possibly also in the poorly preserved macroconch.

There is also close similarity between the dimorphs in the septal suture. The slight difference in position of the elements on the umbilical slope are not regarded as significant.

Both dimorphs were found together in approximately equal numbers at Cerro Pitrén (54% microconchs), and probably Chacay Melehue. They are associated at both localities with *Leopoldia attenuata* ♀ and ♂.



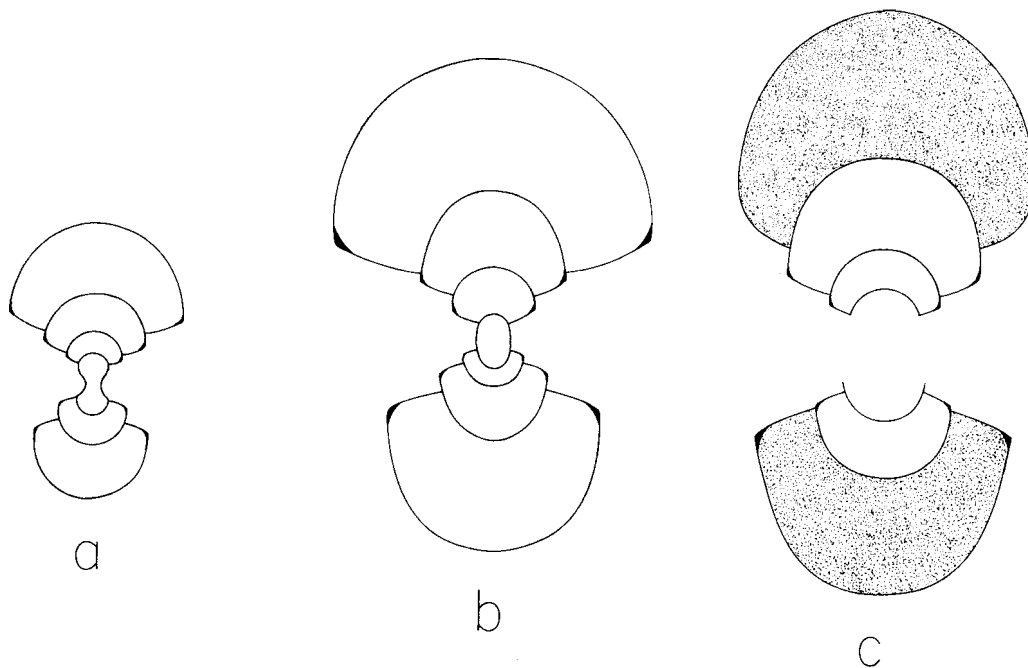
Text-fig. 7. Plot of the number of secondary ribs (S) and tubercles (T) per half-whorl against shell diameter (D) for *Olcostephanus atherstoni* (SHARPE) with synonymous “species” (type specimens). Several growth lines dotted.

The *Olcostephanus* macroconchs and microconchs are therefore regarded as complementary sexual dimorphs and classified as *O. atherstoni* (SHARPE) ♀ and ♂.

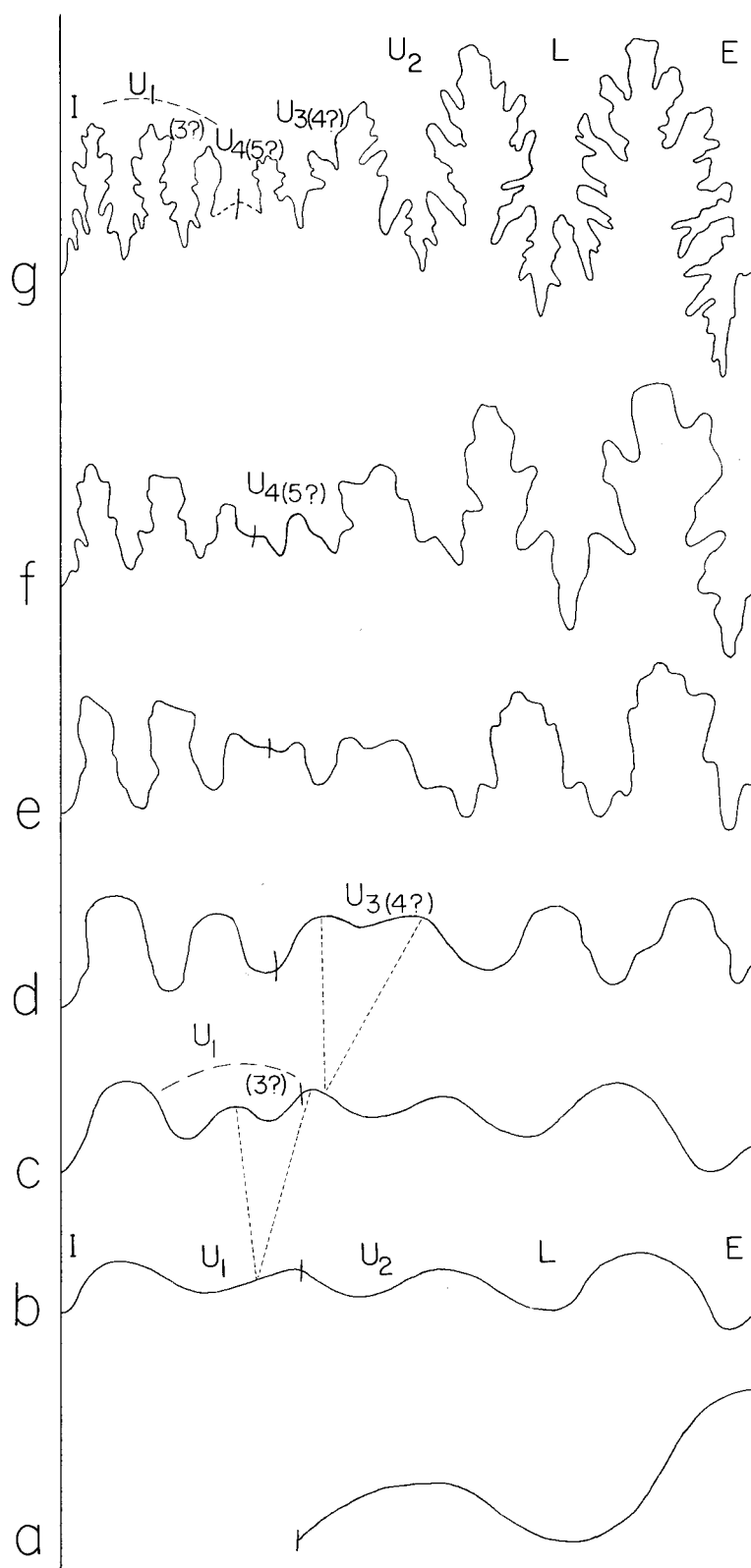
Comparison and Discussion:

“*Holcostephanus midas*” LEANZA 1944 and “*H. auritus*” LEANZA 1944, both based on single microconchs with lappets from Chacay Melehue, were said to differ from one another in the degree of involution and the density of secondaries. According to the original description, the last whorl of *Olcostephanus midas* has 20 primaries with 3 to 4 secondaries each, and *O. auritus* 21 to 22 primaries with 3 to 6 secondaries each; the photographic illustrations show 36 secondaries on the last halfwhorl of *O. midas* and 54 on *O. auritus*. The single *O. auritus* value of 54 lies well outside the Cerro Pitrén sample of *O. atherstoni* ♂ with a range of 25—37 (11 specimens). There is, nevertheless, close resemblance with the macroconch of *O. atherstoni* except for the reduced size, but the inner whorls of *O. auritus* are unknown. The holotype of *O. midas* (by monotypy) on the other hand, according to the illustration, resembles “average” *O. atherstoni* in the major morphologic features (Text-figs. 3—7); the measurements recorded by LEANZA (1944, p. 17, 19) are largely erroneous. *O. midas* perfectly resembles *O. schenki* (OPPEL, 1863; holotype from Spiti Shales Tibet, refigured by UHLIG, 1903, pl. XVIII, fig. 2) here regarded synonymous with *O. atherstoni*. The differences alleged by LEANZA (1944, p. 18) were due to neglect of the growth stages, i. e. the body chamber of *O. midas* ♂ was compared with the phragmocone of *O. schenki* ♀(?), and faulty measurements (our corrected measurements of the holotype of *O. midas* are: H = 21.5 mm, W = 28.0 mm; H/W = 0.76). The difference in whorl section (H/W = 0.76 in *O. midas* vs. 0.64 in *O. schenki*, fide UHLIG, 1903, p. 131) matches the adult modification in the Cerro Pitrén sample.

The completely septate holotype of *O. schenki* (OPPEL) which with 58 mm diameter is probably the nucleus of a macroconch, and the larger “quasi-topotype” [*H. (Astieria) cf. Schenki*] in UHLIG, 1903, pl. XLII, fig. 1], an incomplete macroconch, agree with the Argentine specimens in all measured features (Text-figs. 3—7). The holotype is a perfect match to the macroconch phragmocone figured here on plate 13, figures 5 a—c. The comparative dimensions of the holotype (according to UHLIG’s measurements, said to be imperfect due to distortion) and our specimen at 51 mm diameter are U = 15.5 vs. 14.8 mm, H = 23 vs. 22 mm, and W = 36 vs. 34.3 mm. The rib counts from UHLIG’s figures agree with the Argentine macroconchs (Text-fig. 7). There is little doubt in our minds that “*H. (Astieria) cf. Schenki*” of UHLIG is conspecific with the holotype; SPATH (1939, p. 17) appears to place it in *O. sublaevis* SPATH here regarded as probably another synonym (see below).



Text-fig. 8. Cross section through the phragmocone and body chamber (grey) of *Olcostephanus atherstoni* (SHARPE), from Cerro Pitrén, x 1 a, c microconchs (♂) (McM. K 930 and K 926); b, macroconch (♀) (McM. K 928).



Text-fig. 9. Sutural ontogeny of *Olcostephanus atherstoni* (SHARPE) ♀ from Cerro Pitrén. At shell diameters: a, 0.6 mm; b, 0.8 mm; c, 1.0 mm; d, 2.3 mm; e 4.8 mm; f, 10 mm; g, 36 mm. (a—e, g, McM. K 940; f, McM. K 924).

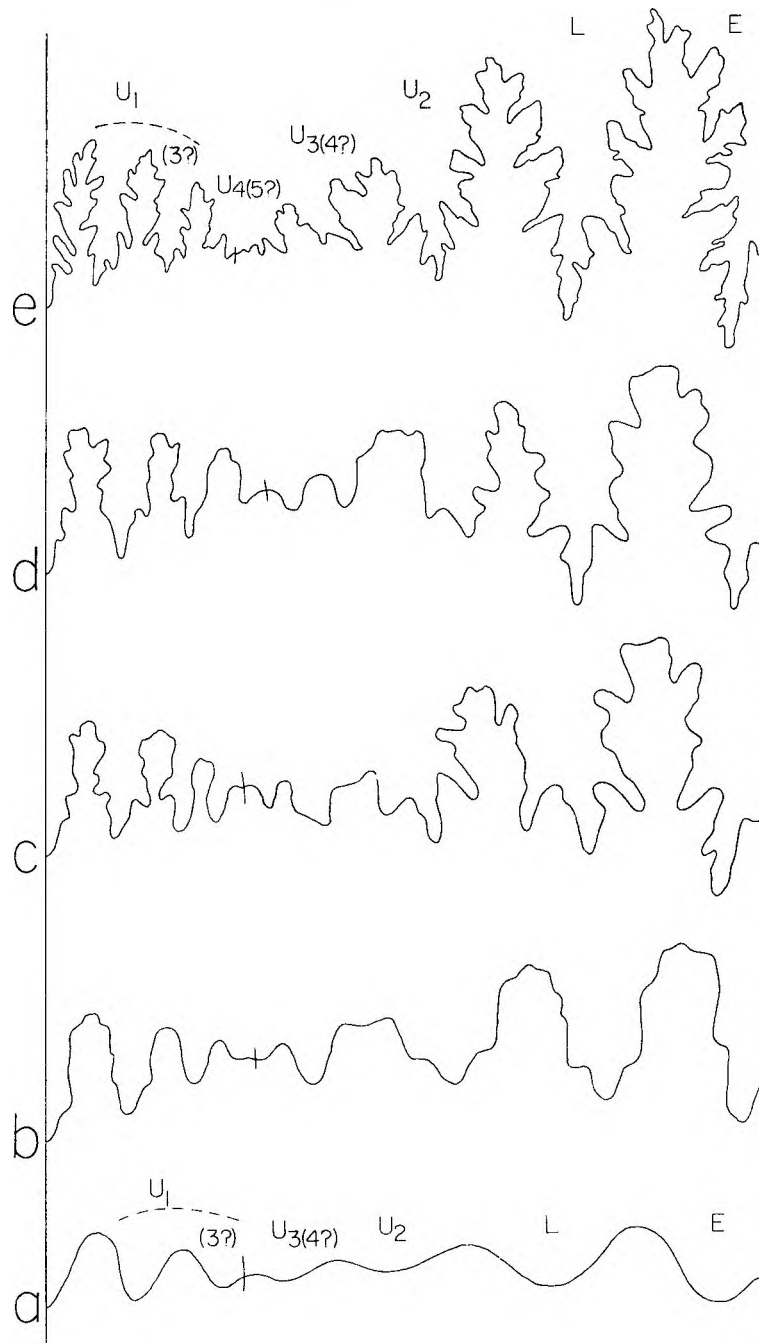
As already pointed out by PAVLOW (1892, p. 492), *Olcostephanus* "populations" in many parts of the world form a closely knit morphological group. In fact their classification comprising many species and "varieties", is largely an artefact made by disbelievers of wide species distributions. This group of doubtfully distinct species includes microconchs and macroconchs, e. g. *O. psilostomus* NEUMAYR and UHLIG, *O. atherstoni* (SHARPE), *O. schenki* (OPPEL), *O. rigidus*, *O. leptoplanus* and *O. imbricatus*, BAUMBERGER spp., *O. wilmanae* (KITCHIN), *O. salinarius*, *O. sublaevis* and *O. glaucus*, SPATH spp.; *O. atherstoni* (SHARPE) is the oldest name.

O. psilostomus, *O. wilmanae* and *O. salinarius* were based on indubitable microconchs. *O. psilostomus* appears to be highly variable, according to the large number of named "varieties", e. g. "var. *koeneni*" and "var. *picteti*" WEGNER (1909, p. 85—86), "var. *crassa*" and "var. *lateumbilicata*" ROCH (1930, p. 314—315, pl. XVI, figs. 3 a—b), "var. *quadricostata*" TZANKOV (1943, p. 190, pl. V, fig. 1—2—3), and "*psilostoma (tipo veneto)*" RODIGHIERO (1919, p. 88). However, their status and relationships remain conjectural because the infraspecific variation of *O. psilostomus* is unknown owing to a lack of large samples and poorly studied morphogeny. Furthermore, these "varieties" seem to include macroconchs as well as microconchs, such as "var. *koeneni*" (in v. KOENEN 1902, p. 151, Taf. LIV, figs. 2 a—b), which are not directly comparable. *O. wilmanae* KITCHIN (1908, p. 195) based on a microconch, was already assigned to *O. psilostomus* as a "variety" by WEGNER (1909, p. 86) and KILIAN (1910, p. 214). The difference of *O. wilmanae* in diameter, whorl height, umbilical width, and ribbing (21 vs. 19—20 primaries and 40 vs. 37 secondaries on the last halfwhorl) is indeed small when compared with the variability within "species" such as *O. salinarius* SPATH; SPATH (1929, p. 146) retained *O. wilmanae* "only because the holotype is partly crushed and its inner whorls are as yet unknown". *O. salinarius* SPATH was regarded as closely affiliated with *O. psilostomus* "in spite of its rather distinctive aspect" (SPATH, 1939, p. 14). Even accounting for the possibility that some of the specimens and "varieties" of SPATH are macroconchs ("var. *involuta*", pl. 1, fig. 2; pl. 2, fig. 4; "var. *subfilosa*", pl. 1, fig. 6), according to the holotype (pl. 1, figs. 1 a—b), there is obviously much variation particularly in the number of ribs, e. g. "var. *crassa*" has about the same number of secondaries at 69 mm diameter as *O. psilostomus* has at 75 mm. The coiling is similar, and the slight differences in whorl section between *O. salinarius* and *O. psilostomus* are probably not significant since comparative differences exist between "var. *obesa*" and "var. *crassa*" of *O. salinarius*.

"Species" based on single microconchs, such as *O. otoitoides* (SPATH) and *O. wynnei* SPATH, also seem to be close to *O. psilostomus* notwithstanding their coarser ribbing. However, more precise statements cannot be made at this time on the small amount of material available. *O. auriculatus* (ZWIERZ.) differs markedly from the above mentioned forms in the larger number of ribs (25—27 primaries per whorl) and the smaller diameter of the microconch which bears lappets at 20 mm diameter (ZWIERZYCKI, 1914, pl. IV, fig. 17). Significantly, ZWIERZYCKI (1914) noted the marked morphogenetic changes and variation in whorl section in his African material. Increased whorl compression is commonly found in the microconch. *O. midas* LEANZA was also compared (LEANZA, 1944) with *O. psilostomus*, but considered distinct because of the more depressed whorl section, the straighter ribs, the more mid-lateral position of the lappets, and the presence of an apertural constriction with collar. However, the supposed differences in whorl shape and ribbing are within the range of variation of the microconch sample described here; the apertural features are almost the same as in *O. psilostomus*.

The close affinity of some of the aforementioned microconchs with the macroconchs of the "*atherstoni-schenki* group" was already pointed out by PAVLOW (1892) who regarded *O. psilostomus* and *O. atherstoni* as mere varieties of a single species (cf. also KARAKASCH, 1902). UHLIG's (1903, footnote, p. 132) and KITCHIN's (1908) opinions to the contrary were based on the comparison of different growth stages, i. e. phragmocone vs. body chamber. It seems therefore that *O. atherstoni* (SHARPE) and *O. psilostomus* (NEUMAYR & UHLIG) are macroconch and microconch, respectively, of a single species, i. e. *O. atherstoni*. The study of their geographic distribution needs special attention, since the first "species" was originally described from South Africa and the second from Europe.

O. atherstoni was based on a few South African outer phragmocone whorls of a "gigantic form" still septate at 140 mm diameter (SPATH, 1929, 1939; KITCHIN, 1908) with uncoiling of the last whorl (cf. KITCHIN, 1908, p. 188). Later descriptions of South African material by KITCHIN (1908) and SPATH (1929) gave no illustrations. A single specimen was figured from Madagascar (COLLIGNON, 1962, p. 38, fig. 860) while most other specimens attributed to this species came from Europe. It seems that KITCHIN's (1908, p. 190) statement: "much remains to be known about the true *H. atherstoni* . . . the limits of individual variation, the characters of shape



Text-fig. 10. Sutural ontogeny of *Olcostephanus atherstoni* (SHARPE) ♂, from Cerro Pitrén. At shell diameters: a, 2.0 mm; b, 3.0 mm; c, 6.5 mm; d, 12 mm; e, 30.5 mm. (a, e, McM. K 929; d, McM. K 936).

and sculpture in successive growth-stages . . .” explains why, then and subsequently, many specimens were described under new names in spite of close resemblance. Thus a topotype (Sunday River) of KITCHIN (1908, p. 193), “*H. cf. atherstoni*”, was named *O. sphaeroidalis* by SPATH (1929, p. 144) because of its more globose shape and depressed whorl section, in spite of the recognition of resemblance with *O. atherstoni*, morphologic variation and presence of intermediate forms.

There is also the possibility that some small septate type specimens are the nuclei of larger forms placed under other specific names. Thus KILIAN (1902, p. 866) suggested that *O. bairni* (SHARPE) was based on a juvenile *O. atherstoni*. This was later rejected by KITCHIN (1908, p. 199) on the grounds that *O. atherstoni* “at a compar-

able growth stage is much more finely ribbed, to mention only one point of distinction". Our studies have shown that in the macroconchs the number of ribs per whorl, i. e. the relative rib density, increases with size and that *O. atherstoni*, therefore, appears to be an overgrown *O. schenki*. SPATH (1939, p. 32—33), on the other hand, used this ribbing feature discriminately between the two species although he had observed similar marked ontogenetic changes in the holotype of *O. atherstoni* which "shows fine peripheral ribbing at one stage (after the coarsely ribbed early stage to about 40 mm diameter) to become coarse once more at about 80 mm". The slight difference in ribbing shown in his illustrations of *O. schenki* (SPATH, 1939, pl. XVIII, fig. 10) and of *O. aff. atherstoni* (pl. XX, fig. 3) are here not considered taxonomically significant. UHLIG (1903) tentatively assigned to *O. schenki* a specimen of intermediate diameter which is also intermediate in the type of ribbing.

SPATH (1929, p. 149), however, suggested that *O. schenki* is a juvenile of *O. kitchini* (SPATH). *O. baini* closely resembles *O. schenki*, as already pointed out by KILIAN (1910, footnote p. 214), although the first has 40 and the second 55 secondaries per whorl at similar size. Yet BESAIRIE (1936) created "*O. baini* var. *ambiky*" characterized by intermediate rib density (holotype refigured by COLLIGNON, 1962, and assigned to "*Rogersites dowvillei* BES.", a nomen nudum).

Two "typical" specimens of *O. schenki* figured by SPATH (1939, p. XVIII, fig. 9; pl. II, fig. 6) closely resemble "var. *ambiky*" in the secondary ribbing; their secondaries are somewhat coarser than in the holotype of *O. schenki* at similar whorl height (9 vs. 10 secondaries per 21.5 mm periphery), while "*O. aff. schenki*" of SPATH (1939, pl. II, fig. 8) is somewhat more densely ribbed (11 secondaries per 21.5 mm periphery). The minimum range of infraspecific variation of *O. schenki* auct. is therefore at least as large as the apparent interspecific variation between this "species" and *O. baini* auct., with 7 secondaries for the same peripheral distance (measured on fragments). *O. rogersi* (KITCHIN) is intermediate in ribbing between *O. schenki* and *O. baini* and SPATH (1929, p. 148) pointed out that many immature specimens are indistinguishable from *O. schenki*; another immature specimen was said (op. cit., p. 148) to be intermediate between *O. rogersi* and *O. baini*.

Great variability in rib density was illustrated in a series of *O. salinarius* SPATH (1939, p. 13) in which he distinguished a number of "varieties". Nevertheless, *O. crassicosatus* (SPATH) (1929, p. 147), based on "*H. cf. baini*" of KITCHIN (1908, pl. IX, fig. 2; pl. X, fig. 1), was discriminated from *O. baini* merely because of the more coarsely ribbed inner whorls. We conclude that most of these "species" are of dubious taxonomic status.

In the description of his new species *O. sublaevis*, SPATH (1939, p. 21) referred to the "great resemblance to UHLIG's *O. cf. schenki*, which if not identical with the present form, must be a very close ally" and stated that "the true *O. (Rogersites?) schenki* (OPPEL) is more coarsely ribbed and has a more prominent umbilical edge". SPATH regarded the development of the umbilical edge as a taxonomically significant feature but at the same time stated that although "these differences may not be of any importance, they are at least as conspicuous as differences among the many other species of *Olcostephanus*". Significantly, BESAIRIE (1930, p. 629) disregarded such minute differences when assigning to *O. schenki* a specimen from Madagascar (refigured by COLLIGNON, 1962, pl. CLXXXVII, fig. 859) with a more rounded umbilical margin (the compared specimen from Mozambique in the London Museum is probably the *O. schenki* confirmed by SPATH, 1929, p. 133). The whorl section of the Madagascar specimen is slightly higher than in "*O. cf. schenki*" of UHLIG (1903, p. 132, pl. XLII, figs. 1 a—c) and seems to have more periumbilical tubercles (?24) at a corresponding diameter; the umbilical margin seems even more rounded than in *O. sublaevis* (cf. BESAIRIE, 1930, pl. LXIV, fig. 1 a, with SPATH 1939, pl. III, fig. 3 b).

The comparison of the type specimens of *O. schenki* and *O. sublaevis* shows close resemblance in the umbilical margin (SPATH, 1939, pl. III, fig. 3 b; UHLIG, 1903, pl. XVIII, fig. 2 c) while the differing numbers of secondaries and primaries would all fall within the range of variation of the *O. atherstoni* sample from Cerro Pitren. *O. sublaevis* is therefore tentatively regarded as a junior subjective synonym of *O. atherstoni*. When comparing *O. sublaevis* with the Argentine *O. curacoensis* WEAVER (1931), SPATH (1939, p. 22), however, attached more significance to geographical distance than to the shape of the umbilical margin and wall, stating that "it seems inadvisable to attach the Indian form to an Argentine species and thus suggest a possible wrong relationship".

The presence of *Olcostephanus* in Argentina was first reported by BEHRENDSEN (1892) who recorded an undetermined species from Arroyo Truquicó, Neuquén. Several new species described under *Olcostephanus* by STEUER (1897) and FAVRE (1908) were transferred to *Spiticeras* and *Himalayites* by UHLIG (1903) and GERTH (1925 a). "*Astieria*" *laticosta* GERTH (1925 b) was based on material from the Arroyo Blanco near its mouth at

Measurements (in mm):

LOCALITY		COLL. NO.	ONTOGEN. STAGE	M/m	D	U	H	W	
Chacay Melehue	Cerro Pitrén	MLP 10.400	ad. b. ch.	m	57	17.5	21.5	28.0	
		K 922	ad. b. ch.	m	83.4	27.5	32	41.6	
			phr.		~ 58.8	15.8	24	33	
		K 923	juv. phr.	M	55	16	24	34.7	
		K 924	juv. b. ch.	M	—	—	—	—	
			phr.			20	—	9.6	12.8
						13.8	—	6.6	9
					9	—	4.4	7.2	
		K 925	juv. phr.	M	~ 57	13.3	24.7	36	
		K 926	ad. b. ch.	m	77.8	23.3	30.8	39	
						58.3	16.2	24.7	36.2
				phr.		42.2	11.3	17.4	26.2
		K 927	ad. b. ch.	m	60.6	18.6	23	33	
		K 928	juv. phr.	M	78.4	17.3	35.8	46.4	
						65.4	15.6	28.4	42.1
						48	11.6	21.4	29
						33.1	8.2	14.3	20.2
						23.2	5.3	10.2	15.1
						16.1	~ 3.4	7.2	~ 11.5
			K 929	ad. b. ch.	m	~ 73.8	21.4	33.2	34.6
			juv. phr.		31.4	6.9	13	19.2	
		K 930	ad. b. ch.	m	~ 76	25.4	30	39	
				phr.		42.5	12.5	17.3	27.1
		K 931	ad. phr.	M	~ 104	28.2	44.4	59	
		K 932	ad. b. ch.	m	57.8	16.2	23.7	33.2	
		K 933	ad. b. ch.	m	~ 72	~ 22.5	28	34	
				phr.		41.7	10.3	17.7	23
						31	~ 6.7	13.2	18.2
					21.7	4.5	~ 9.7	12.5	
					14.5	—	6.1	9.2	
		K 934	juv. phr.	M	~ 82	19.5	~ 40	51	
		K 935	juv. b. ch.	M	67.6	15.2	32	~ 37	
		K 936	juv. b. ch.	m	45	11.8	18.8	24.6	
		K 937	juv. b. ch.	m?	33.6	7.2	15.4	16.7	
		K 938	juv. b. ch.	m	46.8	11.3	20	—	
		K 939	juv. ? b. ch.	?	52.6	13.5	23.2	—	
		K 940	ad. phr.	M	~ 107.4	27.8	47.2	~ 66	
						47	13	21.1	28.5
						15.5	3.7	—	—
		K 941	ad. phr.	M	?110	30.7	—	—	
		K 942	ad. b. ch.	M	125	37	—	—	
		K 943	ad. b. ch.	M	?220	62	—	—	
				phr.		?110	—	—	—
		K 944	juv. b. ch.	M	—	—	—	—	
		K 945	juv. phr.	M	~ 96	24	—	—	
						33	7.7	14.2	23.1
						23.3	5	9.5	15.7
		K 946	ad. b. ch.	m	75	22.8	29	38.5	
				phr.		40.4	9.7	17.8	24.8
						29.5	—	13	17.4
					20.6	—	9.7	12	
		K 947	ad. b. ch.	m	72	20.4	—	—	
				phr.		39.6	9.2	17.6	22.5
						27.1	6	12.1	15.7
					18.2	3.8	8.6	11.9	
		K 948	juv. ? b. ch.	m?	53.5	14.8	23	29.2	
		K 949	juv. ? b. ch.	m?	49	14.5	19.3	30.5	
		K 950	juv. b. ch.	m?	~ 64	18	—	—	
		K 951	juv. b. ch.	?	23.7	5.5	10.7	14.2	

Río Diamante, Mendoza. According to the description and supplementary material from Cerro Salado at Río Salado, Neuquén (WEAVER, 1931), this species differs from *O. atherstoni* in the more depressed whorls, fewer tubercles and broader ribs.

"*Astieria*" *curacoensis* WEAVER (1931) was based on two specimens from Lago Auquinco, Neuquén. The inner whorls seem to be unknown and the large holotype is an almost complete phragmocone. The whorls are broad and involute, but probably not outside the range of the Cerro Pitrén form. The supposed verticality of the umbilical wall is not borne out by the side view of the holotype (WEAVER, 1931, cf. figs. 327 and 328) and the examination of the plastotype shows that it is due to deformation and the presence of a matrix fragment attached to the umbilical margin. The correct slope of the umbilical wall is apparent in the side view (op. cit., fig. 327) and the slope is even less steep than in the paratype. Although the ornamentation of the holotype seems to be somewhat worn, the plastotype shows that there are fewer periumbilical tubercles than reported by WEAVER (20 vs. 24 per whorl) coinciding with the paratype. Also the secondaries seem to be slightly less numerous than originally reported, resembling specimens of comparable size here described under *O. atherstoni*. "*O. curacoensis*" was also recorded from Mallin Redondo in the Sierra Azul, Mendoza (LEANZA, 1945, p. 83).

WINDHAUSEN (1931, pl. 33, fig. 1) illustrated an "*Astieria sudandina* WINDH. (sp. ined.)" in a single lateral view, without description; locality and scale are unknown. This is therefore a nomen nudum (invalid) according to the International Code of Zoological Nomenclature. Judging from the illustration, the almost complete specimen resembles *O. atherstoni* ♀ from Neuquén except for the apparently much smaller size (?illustration reduced). However, decision is impossible without knowledge of the whorl section and the type specimen seems to be lost (LEANZA, 1944, p. 20 and new search for it). The much smaller "*Astieria* sp." figured in the side view on the same plate (fig. 2) was tentatively assigned to *O. midas* by LEANZA (1944, p. 18), a species name here considered synonymous with *O. atherstoni*. *O. leanzai* GIOVINE (1950) was based on "varios ejemplares" from Cerro Mesa, Neuquén. While the supposed differences from *O. midas* [= *O. atherstoni*] in whorl width and coiling fall within the range of variation demonstrated for the Cerro Pitrén sample, the larger number of primaries (27 per whorl) is probably significant.

Family Berriasellidae SPATH, 1922

Subfamily Neocomitinae SPATH, 1924

Genus *Leopoldia* MAYER-EYMAR, 1887

[*Hoplitides* von KOENEN, 1902; *Solgeria* UHLIG, 1905].

Type species by subsequent designation of BAUMBERGER, 1905. — *Ammonites Leopoldinus* D'ORBIGNY, 1840.

Discussion:

MAYER-EYMAR (1887, p. 77) listed under the new generic name of *Leopoldia* the two species "*Leopoldia Leopoldi* ORB." [recte *L. leopoldina* (D'ORBIGNY)] and *L. radiata* (BRUGIÈRE) (designated type species of *Acanthodiscus* UHLIG, 1905). The type species designation is contained in BAUMBERGER's (1905, p. 26) statement about the "Leopoldireihe": "So enthalten die Sammlungen verschiedener Museen eine stattliche Zahl von Ammoniten, die wohl der Reihe des *Ammonites Leopoldi* angehören, aber vom Typus abweichen". Therefore the Treatise (ARKELL et al. 1957, p. L 361) is incorrect in stating that ROMAN (1938) designated the type species. *A. leopoldinus* may be regarded as the type species of *Leopoldia* also by the rule of tautonymy although the strict requirement of absolute tautonymy is lacking (Int. Code Zool. Nomencl., Art. 68, inc. d).

The specimen figured by D'ORBIGNY, 1840, plate 23, was designated by BAUMBERGER (1905, p. 28) as the lectotype of *Leopoldia leopoldina* notwithstanding the possibility that the illustrations are synthetograms. D'ORBIGNY's other syntype on plate 22 was at the same time designated the holotype of *L. buxtorfi* BAUMBERGER (1905, p. 33). Confusion of the plate references to D'ORBIGNY's Atlas by BAUMBERGER (loc. cit.) and ROMAN (1938, p. 341, pl. XXXIII, fig. 321) stems from the original error of D'ORBIGNY (1840, p. 105—106) who clearly exchanged plates 22 and 23. Subsequently, BAUMBERGER & ROMAN referred to the plate numbers in the text rather than to the plate numbers in the Atlas; the large syntype (200 mm diameter according to D'ORBIGNY's table = *L. buxtorfi*) on plate 22, is reduced by $\frac{1}{3}$; and is not $\frac{1}{3}$ natural size. Since D'ORBIGNY's table of mea-

surements included only this latter macroconch (female shell), BAUMBERGER's lectotype designation of the other specimen was unwise but, nevertheless, within the Code. The lectotype, also refigured in the Treatise (ARKELL et al., 1957, fig. 472—6), appears to be a fully grown microconch (male shell). Significantly, WIEDMANN & DIENI (1968, p. 101) have recently placed *L. buxtorfi* in synonymy with *L. leopoldina*.

Hoplitides VON KOENEN 1902, and *Solgeria* UHLIG 1905, were also based on *A. leopoldinus* and are therefore junior objective synonymys of *Leopoldia*.

Lyticoceras HYATT 1900, with the type species *A. cryptoceras* D'ORBIGNY, was regarded as a junior subjective synonym of *Leopoldia* by THIERMANN (1963, p. 349) and WIEDMANN & DIENI (1968, p. 100), while BUSNARDO et al. (1966, p. 234) have retained both genera. The subgenus *Karakaschiceras* was used by BARBIER & THIEULOY (1965, p. 82) and by DEBELMAS & THIEULOY (1965, p. 87) in connection with *Leopoldia biassalensis* KARAKASCH, which therefore should be its type species (Int. Code Zool. Nomencl., Art. 68 inc. c), but no statement has been given about the characters differentiating the new taxon. Dimorphism or apertural lappets have apparently not previously been reported from *Leopoldia*. The only record of lappets is from "*Hoplites Leopoldinus* D'ORB. var. *Peruana*" LISSON (1907, p. 45) which LISSON & BOIT (1924) later designated as the type species of the dubious genus *Limaites* (recognized in the Treatise, p. L 358, but not by RIVERA, 1951).

Leopoldia attenuata (BEHRENDSEN, 1892)

(Pl. 11, figs. 1—6; Pl. 12, fig. 1; Text-figs. 11—19)

L. attenuata ♀

1892 *Amaltheus* (?) *attenuatus* BEHRENDSEN, p. 17, pl. II, fig. 6, pl. IV, figs. 5 a—b.

1949 *Leopoldia elauta* LEANZA & GIOVINE, p. 257; pl. I, figs. 2, 4; non pl. III, figs. 3, 4.

L. attenuata ♂

1949 *Leopoldia elauta tumida* LEANZA & GIOVINE, p. 258, pl. 1, fig. 1.

1949 *Leopoldia elauta* LEANZA & GIOVINE, pl. III, figs. 3, 4; non pl. I, figs. 2, 4.

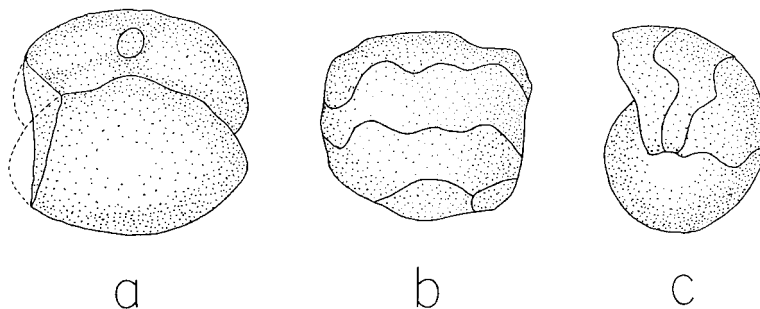
Diagnosis: A species of *Leopoldia* with strongly involute whorls (phragmocone) and weak ornamentation bearing distant umbilical tubercles.

Material: Chacay Melehue: 1 (+ 1?) macroconch [*L. elauta* s. s.] and 2 microconchs [*L. elauta* var. *tumida*] (type specimens); Cerro Pitrén: 20 (+ 1?) macroconchs, 7 (+ 1?) microconchs and 1 juv.; Arroyo Truquicó: the holotype.

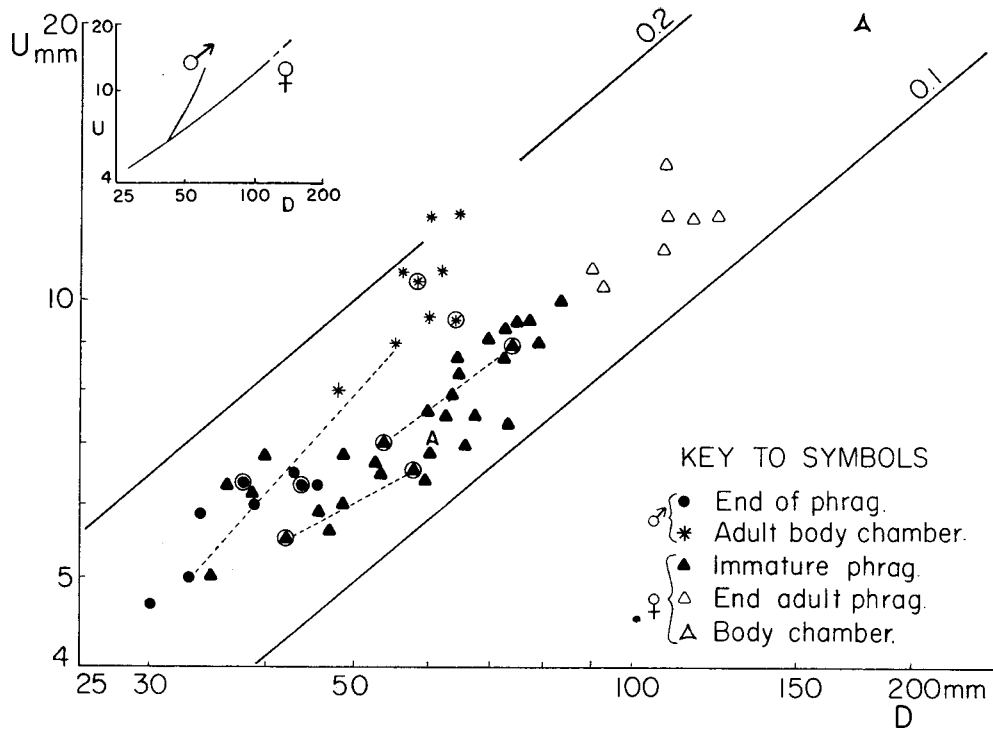
Description:

Protoconch — The specimen developed from an incompletely preserved macroconch (MLP 11068) is perfectly smooth and barrel-shaped with a width of 0.58 mm and a diameter of 0.43 mm (Text-fig. 11).

Phragmocone — The first whorl is depressed; subsequent whorls grow less depressed by negative allometry of whorl width, becoming subquadratic at about 5—6 mm diameter and finally compressed. Increased whorl compression is accompanied by flattening and converging of the flanks and slight tabulation of the venter. The venter becomes arched at about 45 mm diameter in both macroconch and microconch; i. e. on the intermediate whorls of the macroconch phragmocone and toward the end of the microconch phragmocone (Text-fig. 14).



Text-fig. 11. Protoconch and three first chambers of *Leopoldia attenuata* (BEHRENDSEN), from Cerro Pitrén; apertural, ventral and lateral views (MLP 11068).



Text-fig. 12. Plot of umbilical width (U) against shell diameter (D) for *Leopoldia attenuata* (BEHRENDSEN), from Cerro Pitrén and Chacay Melehue (encircled symbols); A, holotype (GPIG 498—29). Inset with visually drawn median lines.

The umbilical wall becomes progressively steeper reaching the rounded umbilical margin vertically towards the end of the phragmocone. The maximum width of mature whorls lies within the lower third of the whorls. Owing to the increasing overlap of the whorls, the coiling becomes progressively more involute (negative allometry for umbilical width). The end of the adult phragmocone is at about 30—45 mm diameter in the microconch and at 90—100 mm in the macroconch (Text-figs. 12—13).

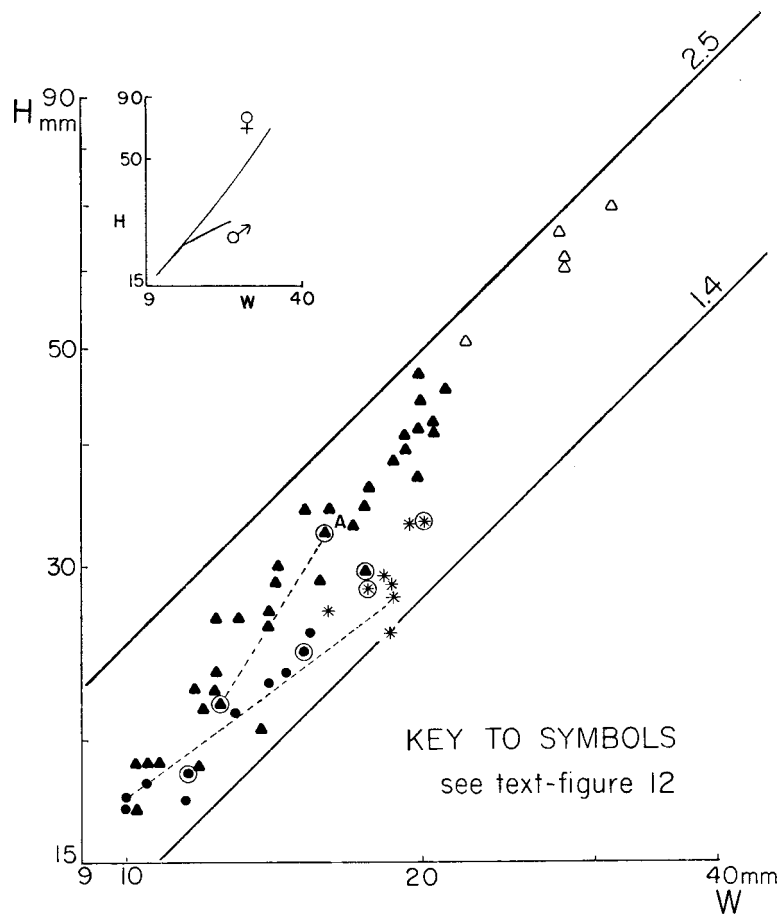
The innermost whorls up to about 4 mm diameter are smooth. Subsequent whorls bear sharp, slightly prosoradiate primaries, about 18—20 per whorl. These are somewhat swollen near the umbilicus and divide at midflank into 40—50 secondaries ending in small ventro-lateral nodes on the shoulder. The venter is smooth.

On the intermediate whorls, commencing at 17—20 mm diameter, the ribs weaken on the middle of the flank and develop into slightly flexed prosoradiate striae which are borne in bundles from distant umbilical tubercles (10—13 per whorl). The bundles remain raised even when the individual striae become obsolete resulting in weak surface undulation. Umbilical and ventro-lateral tubercles are retained up to the end of the phragmocone on the microconch; they become obsolete on the macroconch, the umbilical tubercles at approximately 70 mm and the ventro-lateral tubercles at 45 mm diameter.

The morphogeny of the septal suture is illustrated from one macroconch and two microconchs (Text-figs. 15—16). Prosuture and primary suture are known only from the macroconch. U_3 is early added to U_1 and U_2 both being present in the primary suture, and subsequently develops by somewhat asymmetric lobe division into a sutural lobe. The macroconch resembles the microconch, also in the unusually high infraspecific variation of the width of the lateral lobe L (Text-figs. 15—19).

Sutural approximation at the end of the phragmocone is common indicating that these shells are adult.

Body Chamber — Macroconch (♀): From the few preserved incomplete body chambers of which only one (MLP 11074) is adult, it appears that there is no marked change of growth rate after the last phragmocone whorl. The whorl section is compressed oval with a vertical umbilical wall, rounded umbilical margin, and acutely rounded venter. Ornamentation is absent except for striae. The adult body chamber shows slight uncoiling of the umbilicus. The aperture is unknown.

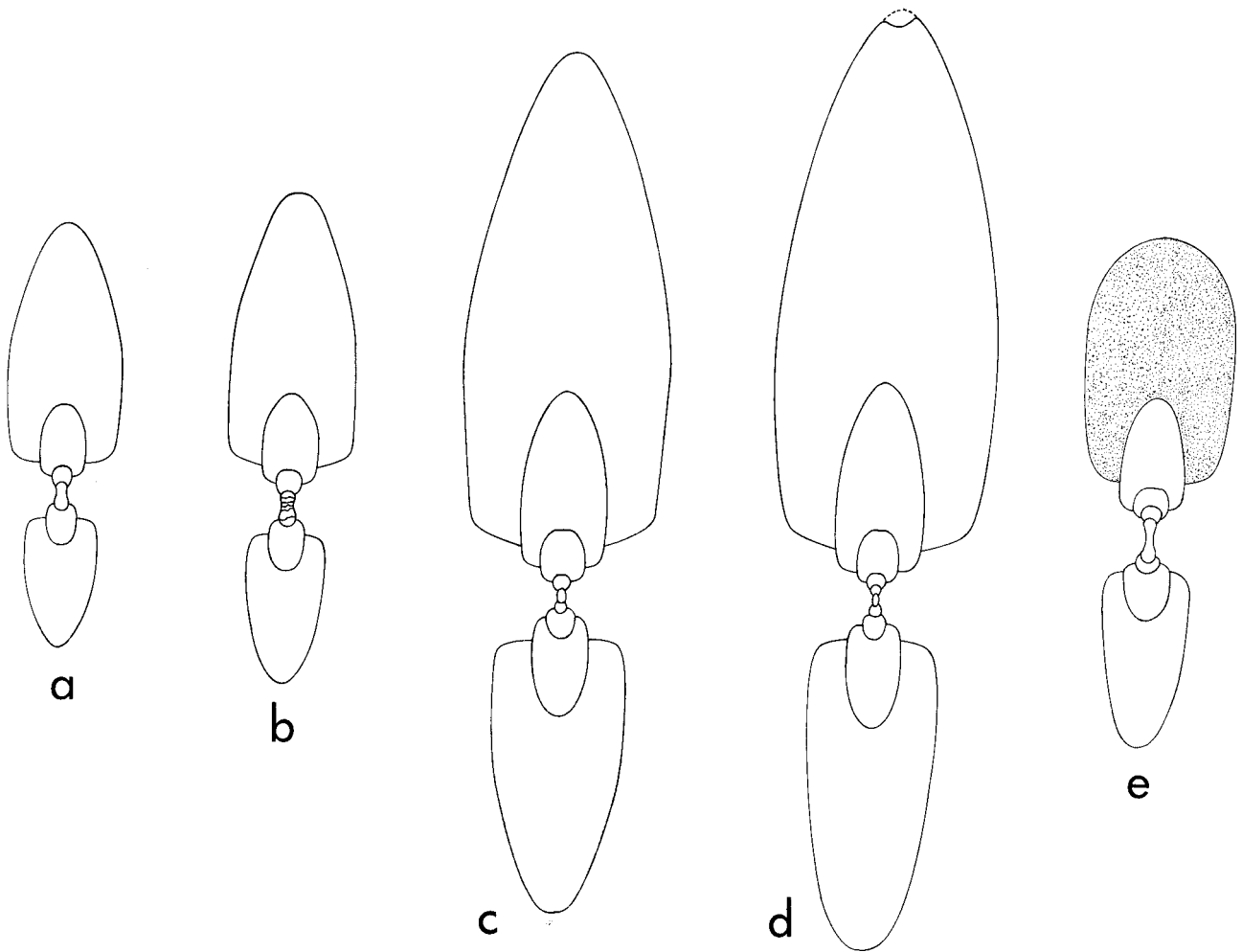


Text-fig. 13. Plot of whorl width (W) against whorl height (H) for *Leopoldia attenuata* (BEHRENDSEN), from Cerro Pitrén and Chacay Melehue (encircled symbols); A, holotype (GPIG 498—29). Inset with visually drawn median lines.

Microconch (♂): The well preserved body chambers are about three-quarter whorls in length. The whorl section becomes clearly modified by inflation, more acute rounding of the venter and egression of the umbilical seam. The ornamentation consists of widely spaced periumbilical tubercles (12—13 per whorl) retained from the phragmocone. The aperture is marked by a feeble constriction and the peristome, preserved only on a single specimen (pl. 11, fig. 6), bears small simple mid-lateral lappets.

Sexual Dimorphism:

We have shown that the large “typical” *Leopoldia attenuata* [*“L. elauta s. s.”*] and the small *“L. elauta var. tumida”* have identical immature stages (at least beyond 5 mm D) with regard to shape and ornamentation. Up to the diameter of the adult small phragmocone (30—45 mm), they have the same compressed and slightly tabulate whorls, the same number of primaries with periumbilical blunt tubercles or swellings, and the same number of secondaries with ventro-lateral nodes. Subsequently, the ribs become obsolete in both forms; the periumbilical bullae disappear on the large form at a diameter not reached by the small form. The small adult body chamber becomes inflated with rounded venter, uncoils and bears lappets; the outer whorls of the much larger shells remain involute and compressed at least to the beginning of the body chamber (their aperture is unknown). Besides size, the most marked difference between the small and the large forms is therefore in the whorl section. The ranges in adult diameters of the two forms are clearly segregated. According to LEANZA & GIOVINE (1949), the sample from Chacay Melehue came from a single bed; the specimens from Cerro Pitrén were also found together. The molluscan assemblage is the same in both localities. The small form [*“L. elauta var. tumida”*] is therefore identified as the microconch or male shell and the large form as the macroconch or female shell of *L. attenuata*.

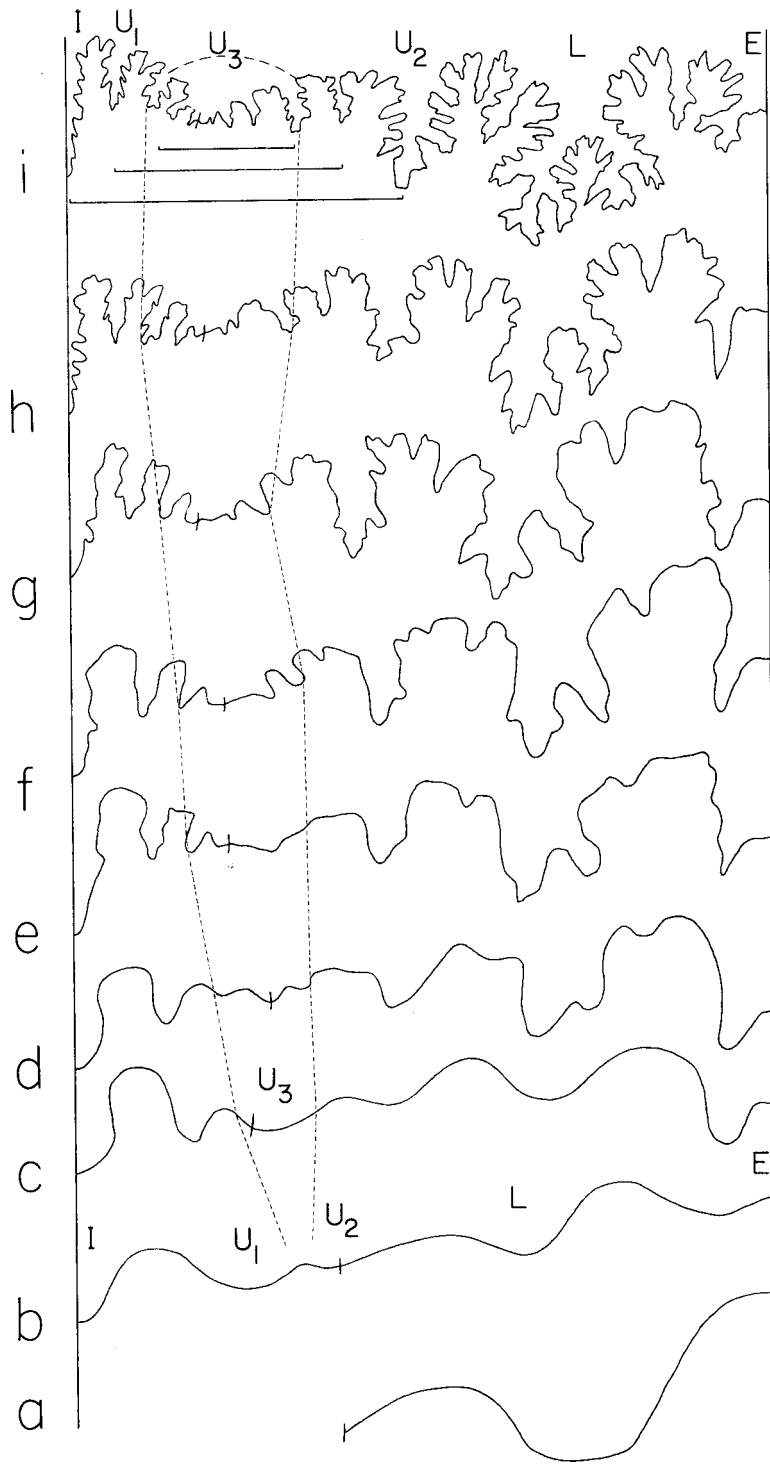


Text-fig. 14. Cross section through the phragmocone and body chamber (grey) of *Leopoldia attenuata* (BEHRENDSEN), from Cerro Pitrén; x 1; a—d, macroconchs (♀) (MLP 11061, 11060, 11072, 11073); e, microconch (♂) (MLP 11059).

The numerical ratio of macro- to microconchs is about 3:1 (~27% microconchs). This apparent mismatch is not at all exceptional for dimorphic pairs; for example, PALFRAMAN (1966) recorded a dimorphic ratio of 2:1 in oppeliids and GUEX (1968) listed microconch percentages of 17, 30 and 35 for other Jurassic ammonites. Although the (secondary) sex ratio in living cephalopods appears to be always approximately 1:1 (WESTERMANN, 1969, p. 19), sex segregation during migration and oviposition is common (op. cit.) and there are many natural processes and collecting bias which may influence the ratio of microconchs to macroconchs. Consequently, numerical mismatches are by themselves no evidence against the presence of dimorphism (MAKOWSKI, 1962, p. 14; WESTERMANN, 1964, p. 36).

The problems of classification and nomenclature of dimorphs have been discussed in most papers on dimorphic ammonoids, particularly in a recent symposium edited by WESTERMANN (1969). Although no general consensus has been reached, most authors now agree to treat well established cases of dimorphism as such under the International Code of Zoological Nomenclature. Complementary dimorphs are therefore placed in a single species and distinguished by the respective sex symbols or, alternately (descriptively) by the micro- and macroconch symbols, i. e. *L. attenuata* ♀ and *L. attenuata* ♂.

Holotype: The holotype, by monotypy, of *Amaltheus* (?) *attenuatus* (GPIG 498—29) is illustrated again (pl. 1, figs. 1 a—c; text-fig. 19 a) because BEHRENDSEN's figure (pl. IV, fig. 5 a) of the lateral view is incorrect and misleading with regard to the whorl section. The completely septate fragmentary specimen is worn and partly crushed, particularly the nucleus, so that the umbilical margin and slope have been distorted, the ornament obliterated on the inner flank, and the septal suture (inverted) simplified. The



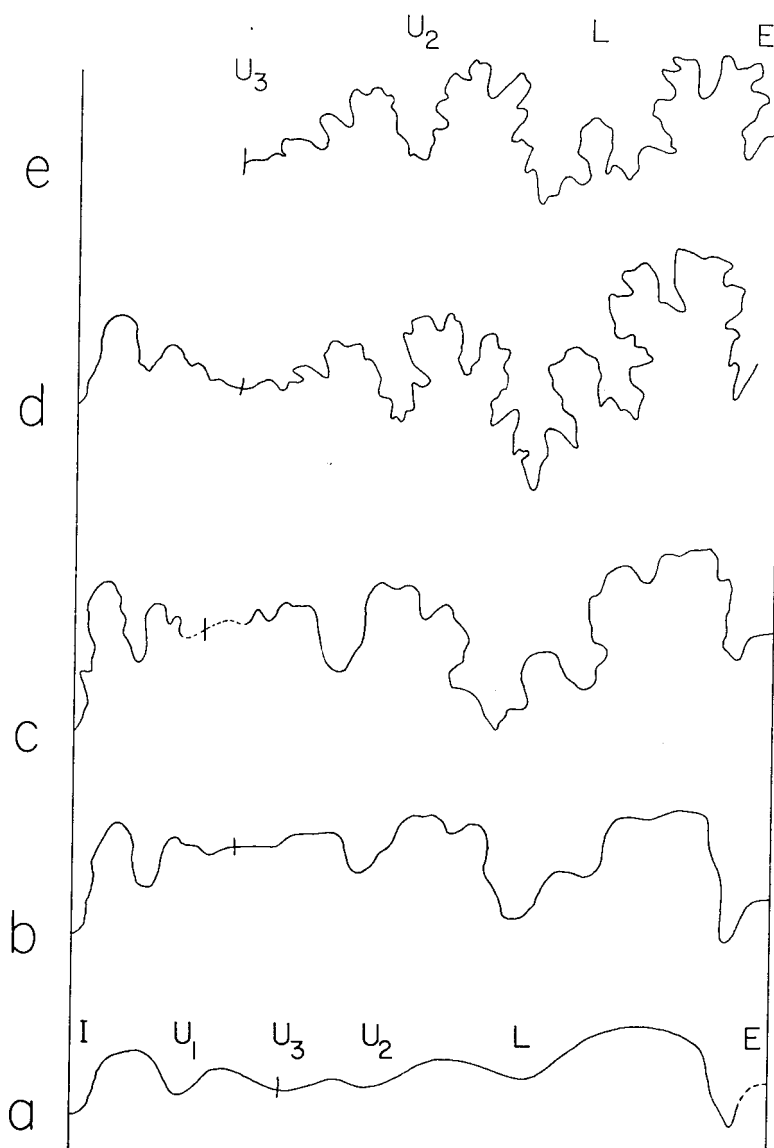
Text-fig. 15. Sutural ontogeny of *Leopoldia attenuata* (BEHRENSSEN) ♀, from Cerro Pitrén. At shell diameters: a, 0.49 mm; b, 0.51 mm; c, 2.5 mm; d, 4.7 mm; e, 9.0 mm; f, 13.7 mm; g, 24 mm; h, 35 mm; i, 66.7 mm. (MLP 11068).

umbilical slope was steep and separated from the flank by a narrowly rounded margin, similarly as in BEHRENDSEN's figure (pl. IV, fig. 5 b) of the cross-section which is, however, more compressed than drawn. There can be no serious doubt that this specimen is a *Leopoldia*, and not a *Hatchericeras*, and that the new *Leopoldia* material from approximately the same locality is conspecific.

Comparison:

Besides "*Leopoldia elauta*" [= *L. attenuata*], LEANZA & GIOVINE (1949) assigned three more new species to this genus based on four specimens from the same Chacay Melehue outcrop: *L. trivialis* (2 specimens) resembles *L. attenuata* ♀ in whorl shape but is more strongly ornate while *L. incondita* (1 specimen) is also more evolute and less compressed; *L. lycoris* (1 specimen) differs from *L. attenuata* ♂ only in the larger diameter, since it appears to be an incomplete microconch. More material is necessary to judge the status of these "species".

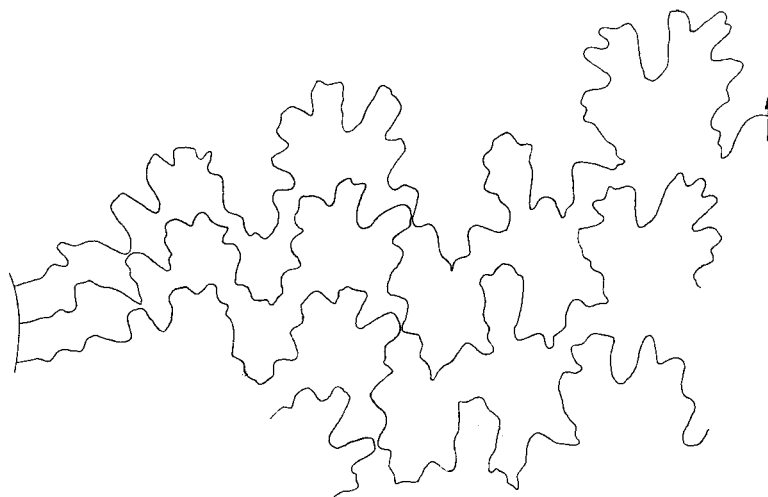
Leopoldia attenuata closely resembles *L. biassalensis* (KARAKASCH) and some related forms described by BAUMBERGER (1905) under different specific names. *L. biassalensis* as illustrated from the Crimea by KARAKASCH (1889, 1907), BAUMBERGER (1905) and DRUŻCZIC (1960), and from Madagascar by COLLIGNON (1962) apparently



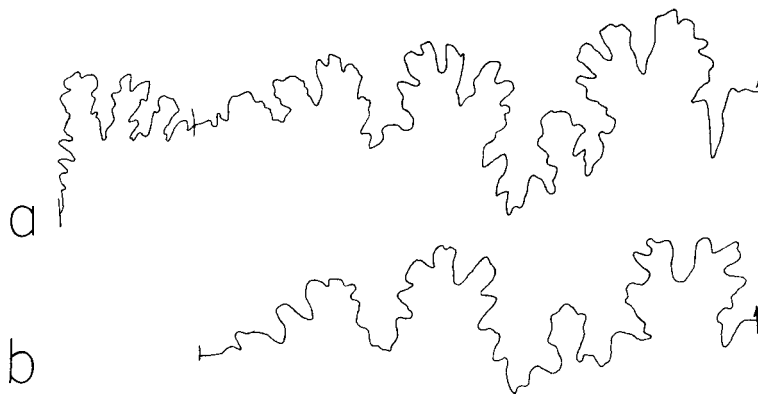
Text-fig. 16. Sutural ontogeny of *Leopoldia attenuata* (BEHRENDSEN) ♂, from Cerro Pitrén (a—d) and Chacay Melehue (e). At shell diameters: a, 2.5 mm; b, 7.5 mm; c, 17.5 mm; d, 27.5 mm; e, 35 mm. (a—d, MLP 11059; e, FCEN 4073).

differs only in the more evolute whorls and possibly in the larger number of periumbilical tubercles (BAUMBERGER, 1905, p. 48; DRUŻCZIC, 1960, pl. XXVIII, fig. 4a). BAUMBERGER's specific discrimination mainly on minor sutural differences, i. e. symmetry, width and height of lobes and saddles of otherwise similar patterns, is highly conjectural as already pointed out by KARAKASCH (1907, p. 83). KARAKASCH noted close sutural resemblances also between *L. biassalensis*, *L. kiliani* (v. KOENEN) and *L. brandesi* (v. KOENEN) which was regarded as synonymous with *L. biassalensis* by BAUMBERGER (1905, p. 48). New studies on larger samples and of the ontogenetic stages are required. *L. buxtorfi* BAUMBERGER [*A. Leopoldinus* D'ORBIGNY, 1840, pl. 22] differs from *L. attenuata* in the larger number of periumbilical tubercles (20 vs. 13) and probably in the coiling. Another related form is *L. neocomiensis* BAUMBERGER which seems to differ from *L. attenuata* in whorl shape. *L. hoplitoides* BAUMBERGER is slightly more inflated and may also differ in the ribbing, but the growth stages corresponding to the changes of ornament are unknown.

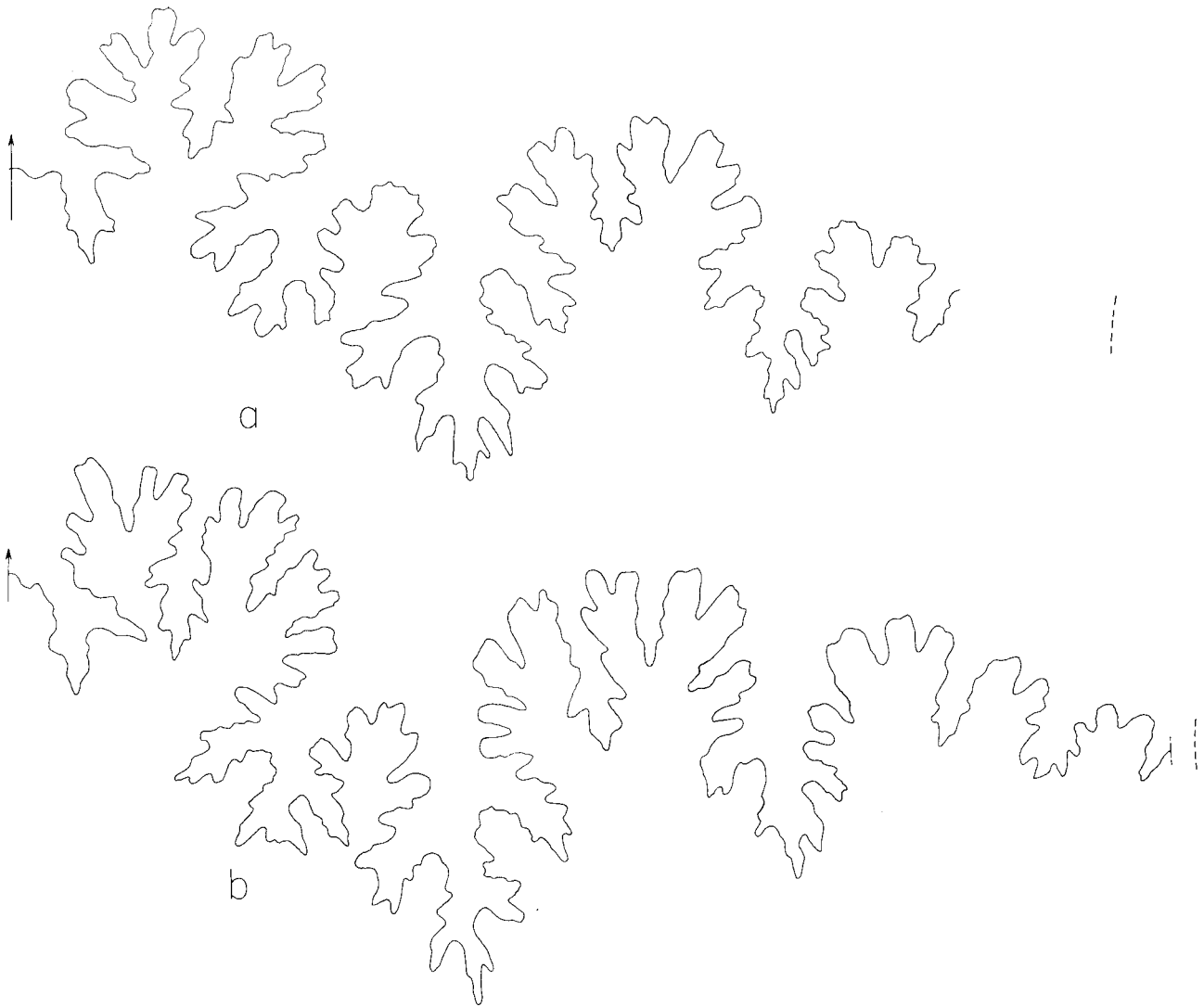
Leopoldia attenuata seems to be clearly different from a number of species described from France (SAYN, 1907; KILIAN & REBOUL, 1915; ROMAN, 1933; BREISTROFFER, 1936), Mexico (IMLAY, 1938, 1940), Madagascar (COLLIGNON, 1962), Israel (RAAB, 1962) and from a dubious species from Peru (LISSON, 1907; RIVERA, 1951).



Text-fig. 17. Terminal approximation of the septal suture in an adult *Leopoldia attenuata* (BEHRENSSEN) ♂, from Chacay Melehue, at ca. 35 mm diameter. (FCEN 4073).



Text-fig. 18. Septal suture of *Leopoldia attenuata* (BEHRENSSEN), at ca. 35 mm diameter; a, macroconch (♀) from Cerro Pitrén (MLP 11068); b, microconch (♂) from Chacay Melehue (FCEN 4073).



Text-fig. 19. Septal suture of *Leopoldia attenuata* (BEHRENDSEN) ♀, at ca. 34 mm whorl height; a, holotype (GPIG 498—29); b, specimen from Cerro Pitrén (MLP 11068).

Measurements (in mm):

LOCALITY	COLL. NO.	ONTOGEN.					
		STAGE	M/m	D	U	H	W
Arroyo Truquicó (holotype)	GPIG 498—29	juv.	M	~ 60	7	33.5	16.5
	Chacay Melehue	FCEN 4069*	juv.	M	74	9	40
FCEN 4070		juv.		54	7	29.4	17.5
	ad.	m	64.6	9.5	33.2	20.2	
FCEN 4071	juv.	M	44	6.3	24.5	15.2	
			58	6.5	32.5	16	
FCEN 4073	ad.	m	42	5.5	23.5	12.4	
			58.7	10.5	28.5	17.6	
Cerro Pitrén	MLP 11051	ad.	m	38	~ 6.3	18.7	11.6
				56.3	10.7	25.5	18.5
MLP 11052*	ad.	m	34	5.9	17.3	11.5	
			—	—	—	—	
MLP 11053	ad.	m	60.9	12.3	28	18.7	
			39	6	17.5	9.5	

* Ontogenetic stage and/or sex determination uncertain because of poor preservation; stage tentatively inferred from coiling and diameter.

Continuated page 111

LOCALITY	COLL. NO.	ONTOGEN.		D	U	H	W
		STAGE	M/m				
	MLP 11054	juv.	M	62.6 48.5 ? 35	7.5 6.8 5	34.7 26.4 19	15.3 14 10.7
	MLP 11055	juv.	M	59.2	6.4	34.5	—
	MLP 11056	juv.	?	—	—	—	—
	MLP 11057	juv.	M	60 48.4	6.8 6	34.7 26.5	16 13
	MLP 11058	juv.	M	63.4 52.8 46	8 6.7 5.9	36 29 25.3	— 14.3 14
	MLP 11059	ad.	m	~ 64.6 45.8	~ 12.3 6.3	33 25.4	19.5 15.5
	MLP 11060	juv.	M	64.5 36.2	8.3 6.3	36 18.8	17.5 11.8
	MLP 11061	juv.	M	67.4 47 30.5	7.5 5.6 —	38.5 26.3 17	18.7 12.3 10
	MLP 11062	juv.	M	65.5 53.7	7 6.5	38 30	— 14.4
	MLP 11063	juv.	M	—	—	—	—
	MLP 11064	juv.	M	72.1 59.7 —	8.7 7.6 —	39 33.7 21.5	19.1 15.4 12
	MLP 11065	juv.	M	—	—	—	—
	MLP 11066	juv.	M	78.4 54 —	9 7 —	45 29 19	21.2 15.6 11.7
	MLP 11067	juv.	M	69.6 64.4 —	9.2 8.7 —	37 34.4 22.4	19.6 17.5 12.3
	MLP 11068	ad.	M	90 ~ 38.5	10.7 6.2	50.5 20.4	— 13.8
	MLP 11069	ad.	M	92.4	10.4	50.8	22.4
	MLP 11070	ad.	M	107 73.7	11.4 7.3	60 42	28 20.5
	MLP 11071	ad.	M	109 72.5	12.4 9.2	62 40.3	28 19.3
	MLP 11072	ad.	M	115 78.4 64.6 40	12.3 9.4 8.7 6.8	65.5 44.3 33 22.5	27.5 20 17 11.7
	MLP 11073*	ad.	M	123.6 83	12.3 10	69.7 47	31.3 19.8
	MLP 11074	ad.	M	175 108	20 14	98.4 61	— 27.4
	MLP 11075	juv.	M	74.3	9.5	41.5	20.4
	K 917	juv.?	M	77	9.5	41	20
	K 918	ad.	m	60 —	9.6 —	29 21.3	18.5 12.7
	K 919	ad.	m	55 33	9 5	27 18	16 10.5
	K 920	ad.	m	62 43	10.8 6.5	29 22.5	18.5 14
	K 921	ad.	m	48 30	8 4.7	23.5 17	14.5 10

* Ontogenetic stage and/or sex determination uncertain because of poor preservation; stage tentatively inferred from coiling and diameter.

Genus *Favrella* R. DOUVILLÉ, 1909

[*Patagoniceras* WETZEL, 1960, non LEANZA 1963]

Type species by original designation — *Neocomites americanus* FAVRE, 1908.

Discussion:

Taxonomy — The original genus diagnosis by R. DOUVILLÉ (1909, p. 165) was: “Formes à large ombilic, ornées de côtes simples, bi ou trifurquées passant sans s’interrompre sur la région siphonale dès un diamètre de 7 à 8 centimètres et y formant un sinus aigu dirigé vers l’avant.” The diagnosis used in the Treatise (ARKELL et al., 1957, p. L 358) reads: “Evolute. Sides at first are flat and parallel on inner half, then converge to flat and grooved venter; whorl section later rounded; regular strong ribs, at first simple or biplicate high on whorl sides later becoming all simple, projected on shoulders and venter.”

The original diagnosis would include most of the species placed in *Favrella* by different authors. The Treatise diagnosis was more detailed restricting the distribution to Patagonia and designated the lectotype of the type species *F. americana* (FAVRE, 1908, pl. XXXIII, figs. 1—2, refigured p. L 357, fig. 470—3 a; fig. 470—3 b, however, is of a different specimen). The subsequent designation by WETZEL (1960, p. 248; FAVRE, 1908, pl. XXXII, figs. 11—14) is invalid. The alleged restriction to Patagonia agrees with earlier statements by SPATH (1939, p. 147) that *Favrella* is a typically Patagonian genus and that “it is very doubtful whether it spread as far as Chile or the Argentine Andes”; many of the Salt Range specimens which FOLGNER (in SPATH, 1939, p. 49, 147) had included in *Favrella* were referred to *Subthurmannia* by SPATH (1939). Similarly, LEANZA (1963, 1967) and HALLAM (1967) accepted the same restricted distribution even after the genus had been reported from Colombia (HAAS, 1960), mainly by taxonomic exclusion of several extra-Patagonian species.

A similar, related contradiction and confusion exists regarding the vertical range of *Favrella* (HAAS, 1966, p. 1078), given as questionably Lower Hauterivian in the Treatise (ARKELL et al. 1957, p. L 358), inferred as Aptian by LEANZA (1963), and assumed to be Valanginian to Barremian by most authors. Since the problem of vertical and horizontal distribution is partly of a taxonomic nature, the included and affiliated excluded species are discussed.

F. americana, type species, and *F. wilckensi* (FAVRE), also from Patagonia, vary greatly in ornamentation, both morphogenetically and infraspecifically according to their original description. *F. americana* was said to include large specimens with or without ventral interruption of ribs and ventro-lateral tubercles, suggesting two species if it were not for the presence of intermediate forms. Nevertheless, WETZEL (1960) advocated the splitting of *F. americana* into two species. This apparent variation of the type species suggests that the broad interpretation of the genus as given in DOUVILLÉ’s original diagnosis was correct. Any reassessment of *F. americana* has to be based on new material and only then will any serious reconsideration of the status and affinity of other species be possible. In the meantime, the following reviews and comments are made regarding several important species and their records:

Hoplites protractus BEHRENDSEN (1891, p. 401, pl. XXV, figs. 1 a—b) was tentatively placed in *Favrella* by DOUVILLÉ (1909, p. 166). From the description and figures, this species seems to differ from *F. americana* and *F. wilckensi* in the whorl section, the less projected ribs and the irregular ornamentation. “*Favrella* n. sp.” of DOUVILLÉ (1909) from Lima, Peru, has not been described or figured.

Neocomites volgensis UHLIG, 1905 [“*Hoplites amblygonius*” PAVLOW, 1886, non NEUMAYR and UHLIG, 1881], was included in *Favrella* by R. DOUVILLÉ (1909, p. 166). However, according to PAVLOW’s description, this species is from the Upper Jurassic of Gorodistche of the Volga River, U.S.S.R., and is distinguished from the Patagonian *Favrella* by the more strongly compressed shell and the different division of the ribs. THIERMANN (1963, p. 372) confirmed the exclusion of this form from *Endemoceras amblygonium* (NEUMAYR & UHLIG).

Neocomites steinmanni FAVRE (1908, p. 620, pl. XXXII, figs. 6—7) was correctly transferred to *Favrella* by FERUGLIO (1936, p. 61) on the basis of material from Lago Argentino. WETZEL (1960, p. 249) designated this species as the type of *Patagoniceras* WETZEL which was characterized by the absence of divided ribs and the presence of the interruption of the ventral costae on the immature whorls. According to WETZEL, these features militate against DOUVILLÉ’s diagnosis of *Favrella*. However, WETZEL misread the original diagnosis quoted above which includes simple, bifurcate and trifurcate ribs and ventral costae interruption under 70—80 mm diameter; these features are also clearly displayed by the type species as originally figured (FAVRE, 1908, pl. XXXIII, figs.

1—2). The alleged difference of *Patagoniceras* from *Favrella* was enhanced by his erroneous 'Wahltypus' designation for the type species *F. americana* (see above). The four figures referred to by WETZEL are obviously based on two specimens; both are small and therefore not strictly comparable with the lectotype. *Patagoniceras* is therefore regarded as a junior subjective synonym of *Favrella*.

Hoplites lorensis LISSON, 1907 (lectotype subsequently designated by SPATH, 1939, p. 56: fig. 4 a), from Peru was placed in *Favrella* by LISSON and BOIT (1942). This seems correct according to DOUVILLÉ's original definition. *H. lorensis* had earlier been referred to *Kossmatia* UHLIG (BURCKHARDT, 1912, p. 132) and *Subthurmannia* SPATH (1939, p. 147). SPATH (op. cit.), after pointing out that this species was incompletely known, compared fragments from Salt Range mainly with "the adult whorl portion attached by LISSON to his species" (p. 56) but, at the same time (p. 50), exemplified the difference between the genera with the inner whorls and septal suture which are unknown from *H. lorensis*. DOUVILLÉ (1909) omitted *H. lorensis* from the species listing under *Favrella*.

"*Hoplites* aff. *australis* BURCK." of LISSON (1907, p. 45, pl. VI, figs. 1 a—b), also from Peru, is too poorly preserved for even a good guess as to its affinity.

"*Favrella* sp." reported by IMLAY (1937, p. 565, pl. 80, figs. 1—2) from north-central Mexico, was based on a small whorl fragment. Although considered as a "very doubtful *Favrella*" by SPATH (1939, p. 149), the generic assignment is here confirmed after reexamination of the specimen kindly sent to us which is quite similar to the small paralectotype of *F. angulatiformis*. "*Favrella costulosa*" FUENZALIDA (in HOFSTETTER, FUENZALIDA & CECIONI, 1957, p. 87) from Chile is a *nomen nudum* since it was neither described nor figured.

Favrella colombiana HAAS 1960 (p. 29, figs. 69—74, 76—79) from Colombia, appears to be correctly assigned to this genus. *Leopoldia belgranensis*, *L. hauthali* and *L. baumbergeri*, FAVRE 1908 spp., from Lake Belgrano, Santa Cruz province, Argentina, were placed in *Favrella* by FUENZALIDA (1964, p. 13). However, the last two species are involute and the ornamentation differs strongly from that on *Favrella*; they probably belong to the Hoplitidae as pointed out by LEANZA (1967).

Age — The age of *Favrella* depends on which species are included or excluded by the individual paleontologist. There is also much conjecture even regarding the occurrence of the Patagonian species.

LEANZA (1963, 1967) stated recently that the Mesozoic marine sequence of Santa Cruz province, Argentina, and southern Chile commences in the Aptian, and that this is the age of the Patagonian *Favrella*. His arguments were: (1) The beds with *Favrella* are allegedly subjacent to a bed bearing "*Crioceras*" *deekei* FAVRE which he placed in the Aptian genus *Tropaeum* SOWERBY; (2) his assignment to *Tropaeum* of a "*Crioceras* without tubercles and intercalatory ribs" (from HOFFSTETTER et al., 1957, p. 126) which CECIONI (1955, p. 244) recorded in association with *Favrella* from a drilling core of Tierra del Fuego; (3) the "*Streblites* (aff. *patagoniensis* FAVRE)" of CECIONI (loc. cit.) recorded from the same assemblage was placed in *Protaconeceras* CASEY following the classification of *Oppelia patagoniensis* by CASEY (1954); in 1963, LEANZA stressed the Aptian-Albian age of the Aconeceratinae which include *Protaconeceras*, but in 1967 (p. 169) alleged that CASEY (1954) dated *Protaconeceras* as Hauterivian because of its association with *Favrella*; (4) FERUGLIO's (1936—37) early Cretaceous fauna from Lago Argentino was assigned to Kimmeridgian-Berriasian and Aptian-Albian genera (1967); finally (5) records of *Favrella* outside southern Patagonia were ignored (1963) or discredited (1967) without explanation.

The following counter-arguments are offered: (1) *Crioceras deekei* FAVRE is the type and only known species of *Peltocrioceras* SPATH (1924). *Peltocrioceras* was placed in tentative synonymy with *Paracrioceras* SPATH in the Treatise (ARKELL et al., 1957, p. L 208), but affinities appear indeed closer to *Tropaeum*. HOWEVER, FERUGLIO (1949, p. 173) reported a stratigraphic interval of 450 m between the beds bearing *Favrella* and *C. deekei*. The evidence for the Treatise (loc. cit.) record of *Tropaeum* from Patagonia is unknown to us. (2) The assignment to *Tropaeum* of the undescribed *Crioceras* without tubercles and intercalatory ribs is pure conjecture, particularly since the author who reported this form (CECIONI, 1955, p. 245) had compared the specimen with the Hauterivian *Crioceratites duvali* (LEV.). (3) *Protaconeceras* CASEY was dated as Hauterivian (CASEY, 1954) based on the type species "*Oppelia*" *patagoniensis* FAVRE which was "dated as Lower Hauterivian by its association with *Leopoldia*, *Argentiniceras* and *Lyticoceras*" (p. 269), and on a new species from the Upper Hauterivian C₄ beds of Speeton. (4) The Lago Argentino fauna is poorly preserved so that the relevant specimens cannot be identified and dated with any degree of certainty. There is consequently no faunistic evidence for a stratigraphic gap. (5) It would seem necessary to demonstrate that the species described from outside southern

Patagonia do not belong to *Favrella*, particularly since LEANZA (1957, p. 9) had earlier recorded *Favrella* cf. *angulatiformis* (BEHR.) from the Hauterivian of Neuquén in association with *Hatchericeras* cf. *tardense* STANTON. The tentative assignment of "*Leopoldia*" *belgranensis*, "*L.*" *hautthali* and "*L.*" *baumbergeri*, FAVRE spp. (1908), to the Gastroplitinae seems to be irrelevant to the age of *Favrella*, since the stratigraphic levels are unknown, nor is the superposition of beds with *Hatchericeras stantoniense* FAVRE and *H.* cf. *pueyrriydonensis* STANTON in Lake Belgrano of much use for the exact dating of *Favrella*; the same is true for the doubtful assignment of *Belemnopsis patagoniensis* (FAVRE), associated with *Favrella americana* (FAVRE) in San Martin Lake, to *Mesohibolites* STOLLEY (LEANZA, 1967, p. 170) since this genus is of Neocomian age (STEVENS, 1965, p. 175; but Barremian-Aptian according to KRYMHOLTS, 1958, p. 160); the close resemblance of *B. patagoniensis* to certain Upper Jurassic to Lower Cretaceous species of Madagascar was already pointed out by STEVENS (1965, p. 160).

Most recently, LEANZA (1970) has stated that at San Martin Lake, *Favrella americana* (FAVRE) occurs at the same stratigraphic level as *Tropaeum deeckei* (FAVRE). However, this alleged association was not mentioned previously and has not been observed by one of us (A. C. R.) while mapping the area in question. Such association, therefore, remains doubtful, particularly also in consideration of the confusion in LEANZA's paper of the supposed occurrences of *F. americana* (cf. RICCARDI, 1970).

Consequently, LEANZA's conclusion of Aptian age for *Favrella* as well as for the marine transgression over all of southern Patagonia cannot be accepted. *Favrella* has been mentioned also from the Valanginian of Santiago Province by BÍRO (in MARTÍNEZ & ERNST, 1965). Its supposed mention by BIESE (1942) from Copiapó, quoted by MARTÍNEZ & ERNST (1965) is inexact. The necessary revision of *Favrella* has to be based on new stratigraphic and palaeontologic studies of different exposures in southern Patagonia including the type locality at Lago Belgrano.

Affinities — Affinities of *Favrella* to certain European forms recently united under *Endemoceras* THIERMANN (1963), e. g. *E. noricum* (F. A. ROEMER) and *E. amblygonium* (NEUMAYR and UHLIG), had earlier explicitly or implicitly been inferred by BEHRENDSEN (1892), FAVRE (1908) and WETZEL (1960). According to the original descriptions of *F. americana* FAVRE and *F. wilckensi* FAVRE and the original diagnosis of *Endemoceras*, *Favrella* is distinguished by the more regular, laterally more straight but ventrally more strongly projected ribs, the often absent periumbilical tubercles, and the more simple septal suture. *Endemoceras* appears to be morphologically quite distinct and restricted to northwestern Europe, while *Favrella* is unknown from Europe with the possible exception of the dubious *F. volgensis* (UHLIG, 1905). We agree with the classification of *Favrella* in the Berriasellidae of the Perisphinctaceae by ARKELL et al. (1957: Treatise) while urging morphogenetic studies.

Favrella angulatiformis (BEHRENDSEN, 1892)

(Pl. 14, figs. 1—5)

1892 *Hoplites angulatiformis* BEHRENDSEN, p. 16, pl. 4, figs. 2 a—c [Transl. into Spanish and syntypes refigured: Act. Acad. Cienc. Cordoba, 1921, 7, p. 210, pl. IV, figs. 10 a—c].

1925 *Favrella* cf. *angulatiformis* — GERTH, p. 111.

?1931 *Favrella angulatiformis* — WEAVER, p. 460, pl. 57, fig. 366.

Lectotype designated by SPATH, 1939, p. 147, footnote 3 — *Hoplites angulatiformis* BEHRENDSEN, pl. 4, figs. 2 b—c.

Material: Cerro Pitrén: 1 impression of inner whorls with mould of incomplete body chamber and 9 whorl fragments mostly of body chambers (McM. K 973—6); Arroyo Truquicó: the holotype (GPIG 498—24) and 6 other whorl fragments (GPIG 498—25/253—257).

Description:

The shell is planulate with wide umbilicus ($U \sim 40\%$ of D) and moderately compressed ovate whorls ($H/W = 1.2$ to 1.3); the inner whorls are almost as broad as high ($H/W \sim 1.1$). The umbilical slope is steep to vertical rounding into the decreasingly convex flanks. The venter appears tabulate on the inner whorls owing to the ventro-lateral tubercles but becomes narrowly rounded on the body chamber where the flanks converge more strongly. The maximum diameter is about 80—100 mm.

The ornament consists of irregularly prominent ribs which are borne gradually on the umbilical slope where they are strongly rursiradiate. The ribs are most prominent on the umbilical shoulder, somewhat prosoradiate on the flanks with slight mid-lateral flexure on the inner whorls, and distally projected with increasing strength as

growth proceeds. The most strongly ornate specimen bears small tubercles on the umbilical shoulder and just above mid-flank where bifurcation may occur from time to time particularly on the inner whorls. Secondaries are usually borne by intercalation in singles and sometimes in pairs, irregularly near the centre of the flank, moving onto the outer flank on the body chamber. Intercalatories and secondaries are usually weaker than the simple primaries. On the inner whorls, the smaller body chamber fragments, and the large fragment of the highly ornate variant, most ribs end in prominently ventro-lateral tubercles, leaving a smooth venter. On most large body chamber fragments, however, these tubercles become obsolescent and the ribs continue strongly projected to the venter where finally some or all of them form chevrons.

Although there is much variation within the sample, the individual variation in prominence of the ribs is even more outstanding. The presence of intermediate forms and sizes strongly suggests that all belong to a single species.

Lectotype — The lectotype (GPIG 498—24) designated by SPATH (1939, p. 147 footnote 3) and here again illustrated (pl. 14, figs. 1 a—b) is a 75 mm long body chamber fragment with moderately compressed section ($W = 25.3$, $H = 30.4$ mm). The simple ribs are gently curved, strongly projected and complete forming chevrons on the venter. One or two intercalatories are borne at mid-flank.

Discussion:

Some of our specimens closely resemble the lectotype and other type specimens of "*Hoplites*" *angulatiformis* BEHRENDSEN (1892) which came from the same restricted area. The assignment of this species to *Favrella* by DOUVILLÉ (1909) was supported by GERTH (1925) and WEAVER (1931) who briefly described single incomplete specimens from Mendoza and Neuquén, respectively. The good resemblance of WEAVER's specimen apparent from the text (p. 460), however, is not matched by his illustration (pl. 57, fig. 366), particularly with regard to the ribs said to be "very strongly forwardly directed as they approach the venter".

F. angulatiformis remains poorly known owing to inadequate material. Comparisons with related species, therefore, are restricted and conclusions tentative.

F. colombiana HAAS (1960) from supposed Lower Hauterivian of Colombia closely resembles *F. angulatiformis*. *F. americana* and *F. angulatiformis* were said (op. cit., p. 30) to be distinguished "in their more uniform and less sigmoidal costation"; however, similar ribs may be present in small (inner?) whorls of *F. angulatiformis*. *F. wilckensi* (FAVRE) from Patagonia is distinguished from *F. angulatiformis* mainly by the more uniform ribbing and thus appears intermediate between the Argentinian-Colombian forms and the simple-ribbed *F. americana*, type species of *Favrella*. The variability of the Patagonian forms described by FAVRE (1908) strongly favours the assignment of the *angulatiformis* group to the same genus because of morphological contiguity, although the fact that his illustrations of only part of his material do not show such variability may cast doubt on the generic identity of all of the species.

On the other hand, there is also resemblance to the Peruvian "*Hoplites* juv. *Raimondii*" LISSON (1907; non GABB, 1877), type "species" of *Raimondiceras* SPATH 1924. This poorly known Peruvian species has even more strongly differentiated ribbing than the central Argentinian and Colombian forms and seems to differ mainly in the presence of sharp lateral tubercles, the more strongly acute ventral chevron and the smaller umbilicus.

R. (?) salinarium SPATH (1939, p. 62, pl. XIV, figs. 4—5) from the Salt Range, Pakistan, appears to be intermediate to the *F. angulatiformis* group, while the "*Raimondiceras* sp. nov." (op. cit., pl. XV, figs. 3—4) shows little resemblance to either. *F. angulatiformis* thus appears morphologically intermediate between "typical" *Favrella* and *Raimondiceras*. Again, new evidence is needed. The more distant resemblances of *Favrella* with *Endemoceras* and *Lyticoceras* were discussed above. The intimate interrelationship of the mentioned early Cretaceous genera and their correspondingly poor taxonomic delimitation is quite apparent.

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Explanation of Plates

Plate 11

All figures natural size

- Figs. 1—4. *Leopoldia attenuata* (BEHRENDSEN) ♀, from Neuquén.
1 a—c. Holotype, juvenile (incomplete) phragmocone, lateral and ventral views (GPIG 498—29). Arroyo Truquicó.
2 a—b. Juvenile specimen with part of crushed body chamber, ventral and lateral views (MLP 11058). Cerro Pitrén.
3 a—b. Juvenile phragmocone, lateral and ventral views (MLP 11066). Cerro Pitrén.
4 a—b. Syntype of "*Leopoldia elauta*" LEANZA & GIOVINE (1949), ? juvenile phragmocone, ventral and lateral views (FCEN 4069). Chacay Melehue.
- Figs. 5—6. *Leopoldia attenuata* (BEHRENDSEN) ♂, from Neuquén.
5 a—c. Almost complete adult specimen, lateral, ventral and apertural views (FCEN 4073). Chacay Melehue.
6 a—b. Complete adult specimen with small lappets, apertural and lateral views (MLP 11051). Cerro Pitrén.

Plate 12

All figures natural size

- Figs. 1 a—b. *Leopoldia attenuata* (BEHRENDSEN) ♀, adult phragmocone, lateral and apertural views (MLP 11071). Cerro Pitrén.
Figs. 2 a—b. *Leopoldia* sp. ("*Hoplites neumayri*" BEHRENDSEN, syntype, nom. dub.), almost complete adult body chamber (GPIG 498—26). Arroyo Truquicó.
Figs. 3 a—b. *Olcostephanus atherstoni* (SHARPE) ♀, immature phragmocone, lateral and ventral views (McM. K 928). Cerro Pitrén.
Figs. 4 a—b. *Olcostephanus atherstoni* (SHARPE) ♂, juvenile (incomplete) phragmocone, lateral and ventral views (McM. K 930). Cerro Pitrén.

Plate 13

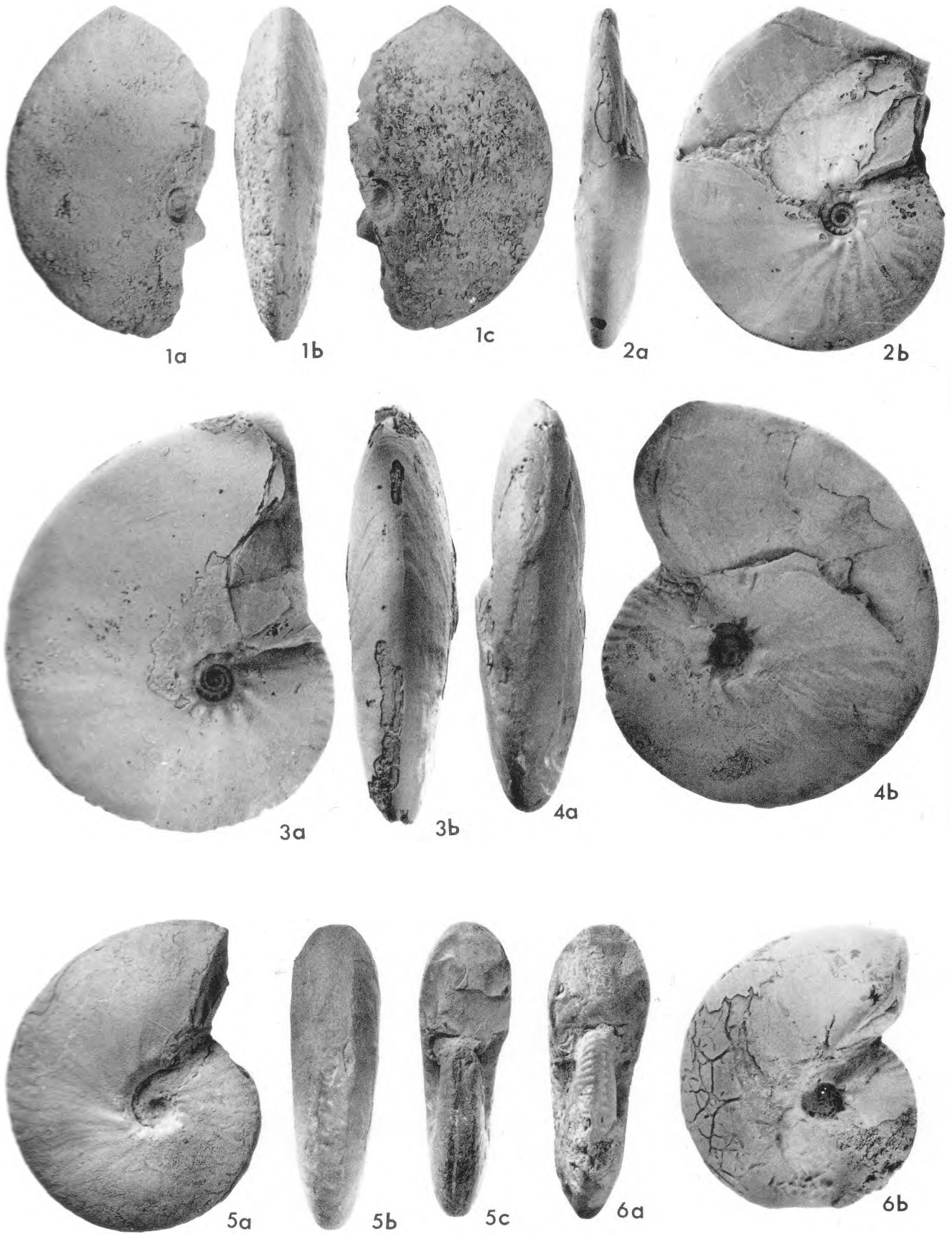
All figures natural size unless stated otherwise.

- Figs. 1—5. *Olcostephanus atherstoni* (SHARPE) ♀ & ♂, from Cerro Pitrén.
1. Macroconch (♀), X 1/2, adult specimen with complete aperture, lateral view (McM. K 943).
2. Microconch (♂), complete adult specimen with lappets, lateral view (McM. K 930).
3 a—b. Microconch (♂), almost complete adult specimen, ventral and lateral views (McM. K 922).
4 a—b. Macroconch (♀), fragment of juvenile phragmocone, lateral and ventral views (McM. K 940).
5 a—c. Macroconch (♀), juvenile (incomplete) phragmocone, lateral, apertural and ventral views (McM. K 923).

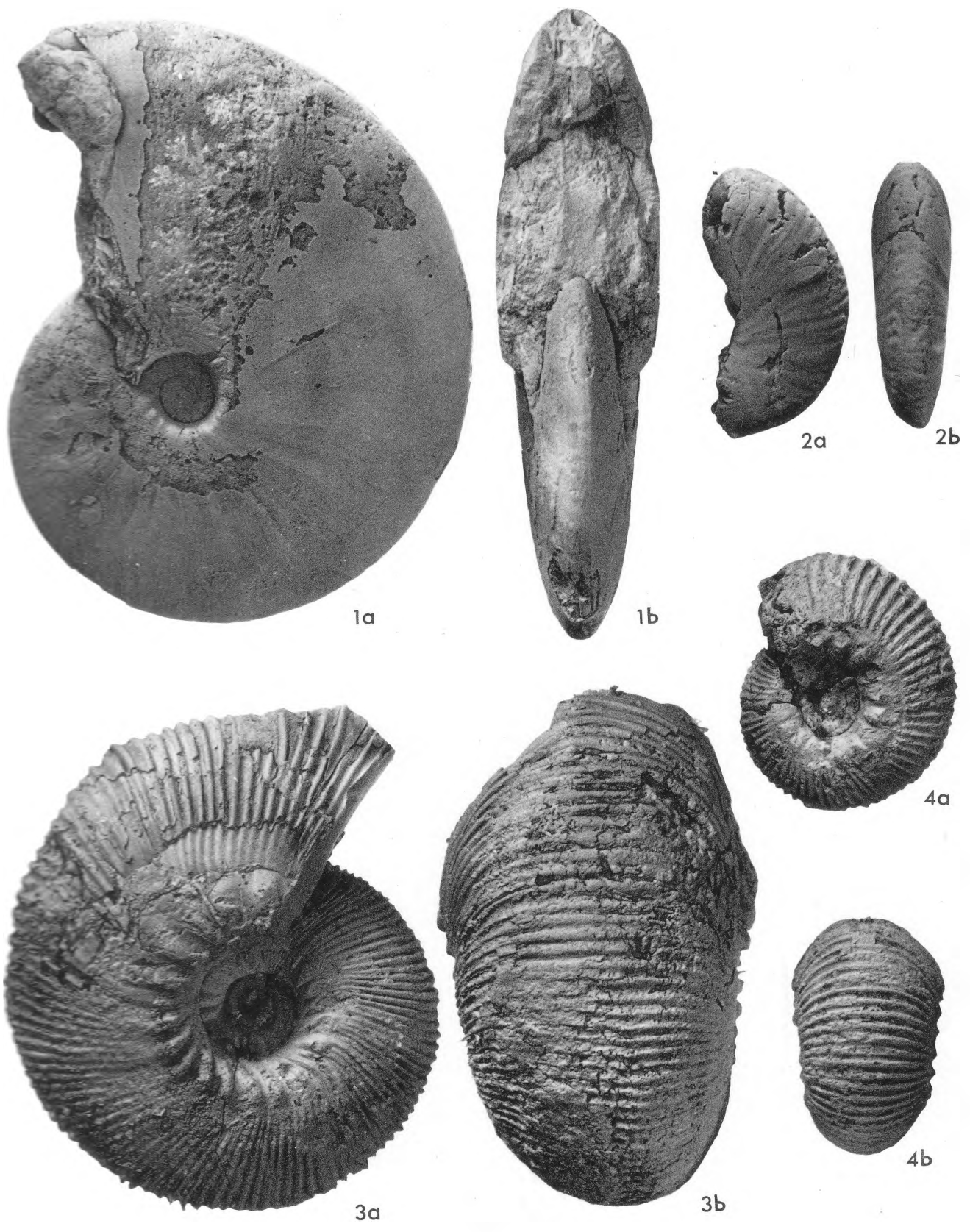
Plate 14

All figures natural size

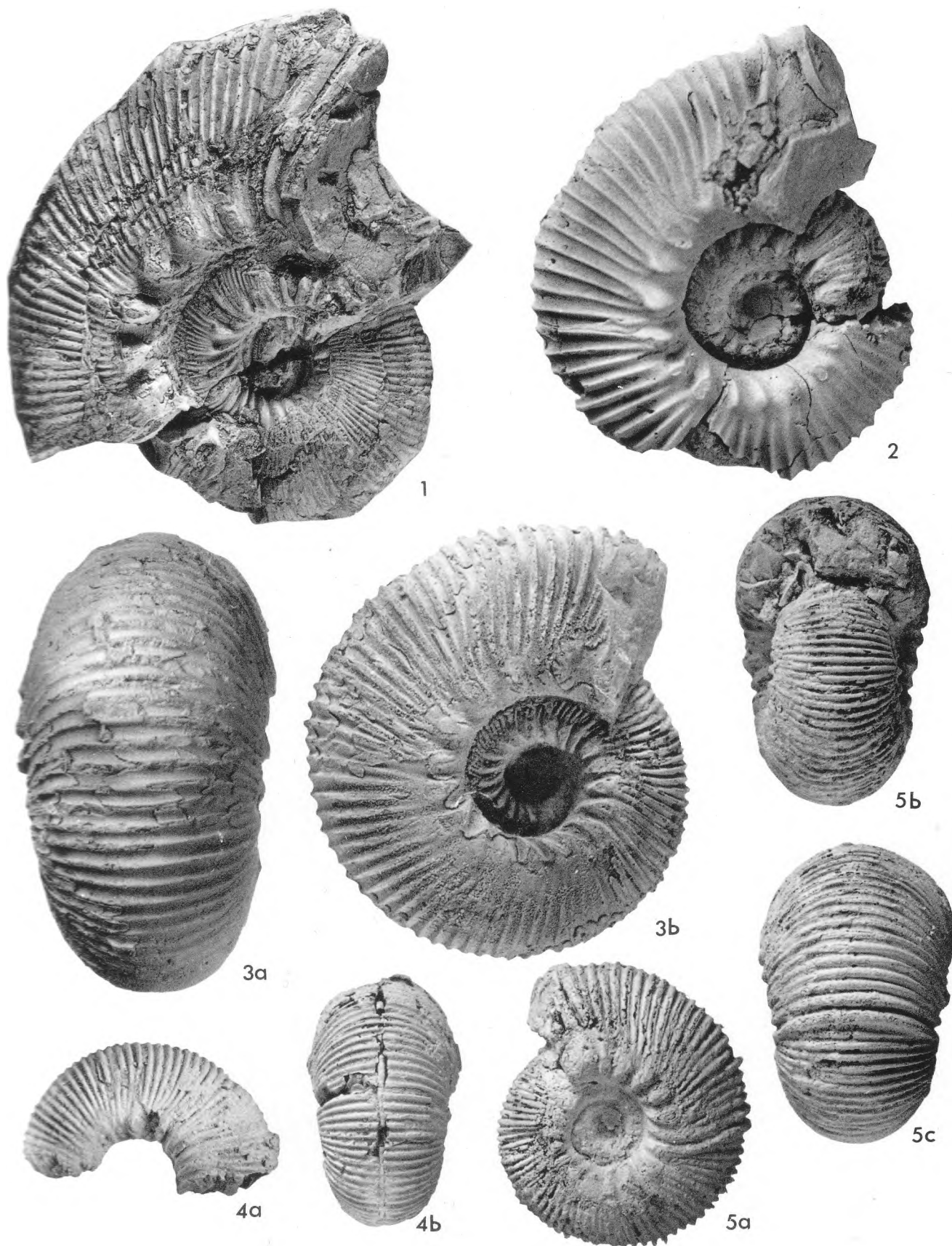
- Figs. 1—5. *Favrella angulatiformis* (BEHRENDSEN), from Neuquén.
1 a—b. Lectotype, fragment of body chamber, lateral and ventral views (GPIG 498—24). Arroyo Truquicó.
2 a—b. Paralectotype, fragment of body chamber, lateral and ventral views (GPIG 498—25). Arroyo Truquicó.
3. Fragment of body chamber with impression of phragmocone, lateral view (McM. K 973). Cerro Pitrén.
4 a—b. Fragment of body chamber, lateral and ventral views (McM. K 975). Cerro Pitrén.
5 a—b. Fragment of body chamber, lateral and ventral views (McM. K 974). Cerro Pitrén.
- Figs. 6 a—b. *Sarasinella* (?) aff. *S. crassicotata* (GERTH) ("*Hoplites Desori* PICT. et CAMP." of BEHRENDSEN, 1892), incomplete crushed body chamber, lateral and ventral views (GPIG 498—23). Arroyo Truquicó.



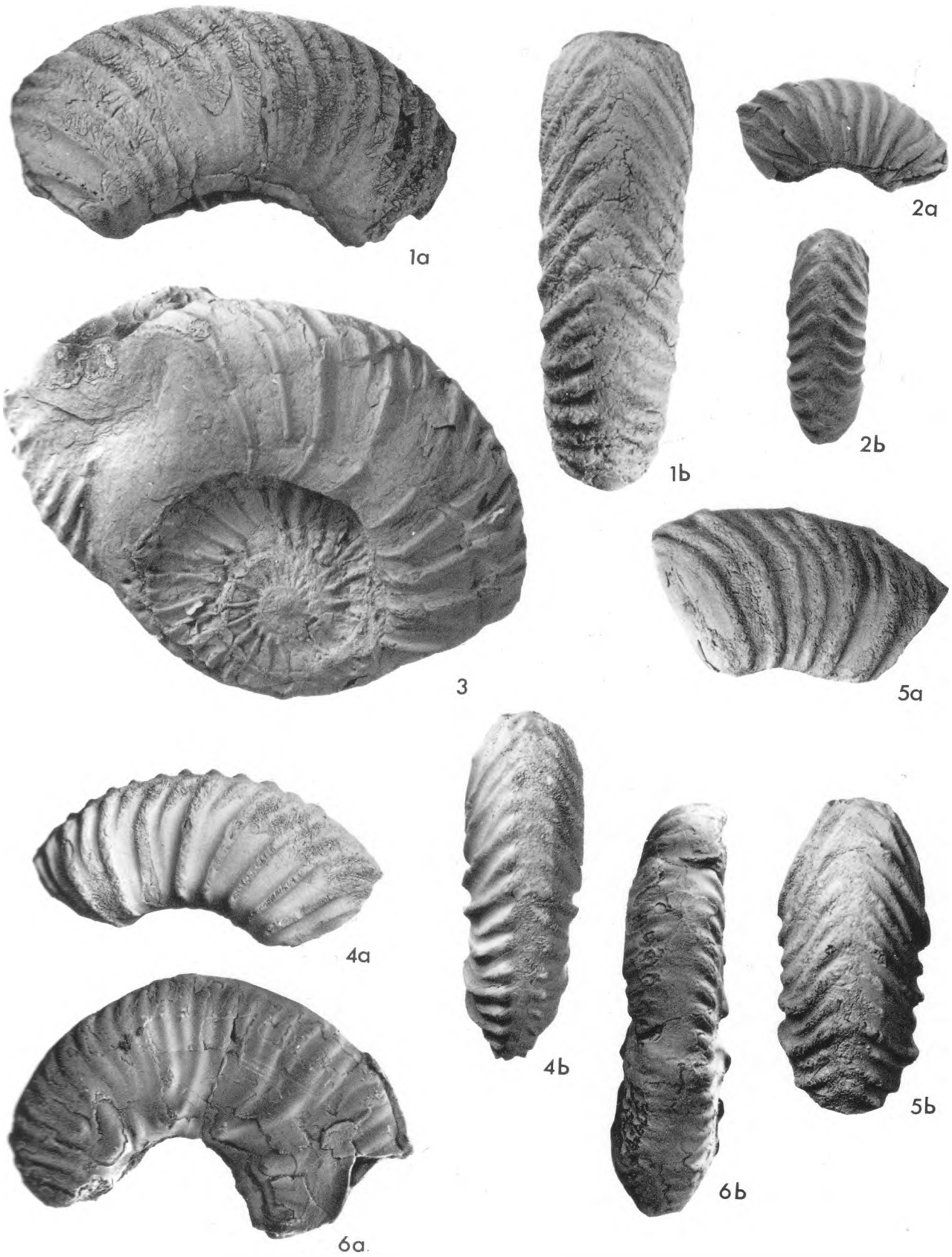
A. C. Riccardi, G. E. G. Westermann & R. Levy: Cretaceous Ammonitina *Olcostephanus*, *Leopoldia* and *Favrella*.



C. Riccardi, G. E. G. Westermann & R. Levy: Cretaceous Ammonitina *Olcostephanus*, *Leopoldia* and *Favrella*.



A. C. Riccardi, G. E. G. Westermann & R. Levy: Cretaceous Ammonitina *Olcostephanus*, *Leopoldia* and *Favrella*.



A. C. Riccardi, G. E. G. Westermann & R. Levy: Cretaceous Ammonitina *Olcostephanus*, *Leopoldia* and *Favrella*.