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(With 19 figures)

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ABSTRACT

Representatives of the subfamily Helicancylinae are locally common in deposits of Aptian age in the northern central Austral Basin, Patagonia. A stratigraphical synthesis of the Lower Cretaceous deposits in the area studied is outlined. Schematic sequences of the measured sections at the principal localities, which also exhibit the various levels containing ammonites, are shown. The section on systematic palaeontology comprises a discussion of the subfamily Helicancylinae, and generic and specific descriptions of all taxa represented in the Austral Basin. In addition to the study of the Patagonian material, bibliographical research reveals the necessity of redefining the genera *Helicancylus* and *Hamiticeras* in order to clarify the systematics of the subfamily. The following species are identified: *Helicancylus patagonicus, Helicancylus bonarellii, Toxoceratoides nagerai, Toxoceratoides* cf. *biplex, Toxoceratoides? haughtoni, Toxoceratoides?* sp., and *Tonohamites aequicingulatus*. The fauna shows some affinities with that of Zululand and western Europe.

CONTENTS

INTRODUCTION

The subfamily Helicancylinae comprises a group of small ancyloceratids that have a nearly worldwide distribution. In the Austral or Magellanes Basin, Patagonia, Argentina, they are locally common in rocks of Aptian age. Although small heteromorphs, now referred to this subfamily, were described from this

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basin by various authors, those works dealt with general faunal descriptions; taxonomic and stratigraphic problems concerning this group were still unresolved. A description of the representatives of the subfamily Helicancylinae is necessary in order to advance our knowledge of the Aptian palaeontology and biostratigraphy of the Austral Basin.

Generic comparisons allow a nearly cosmopolitan correlation. At specific level, most of the taxa seem to be geographically restricted; some species,

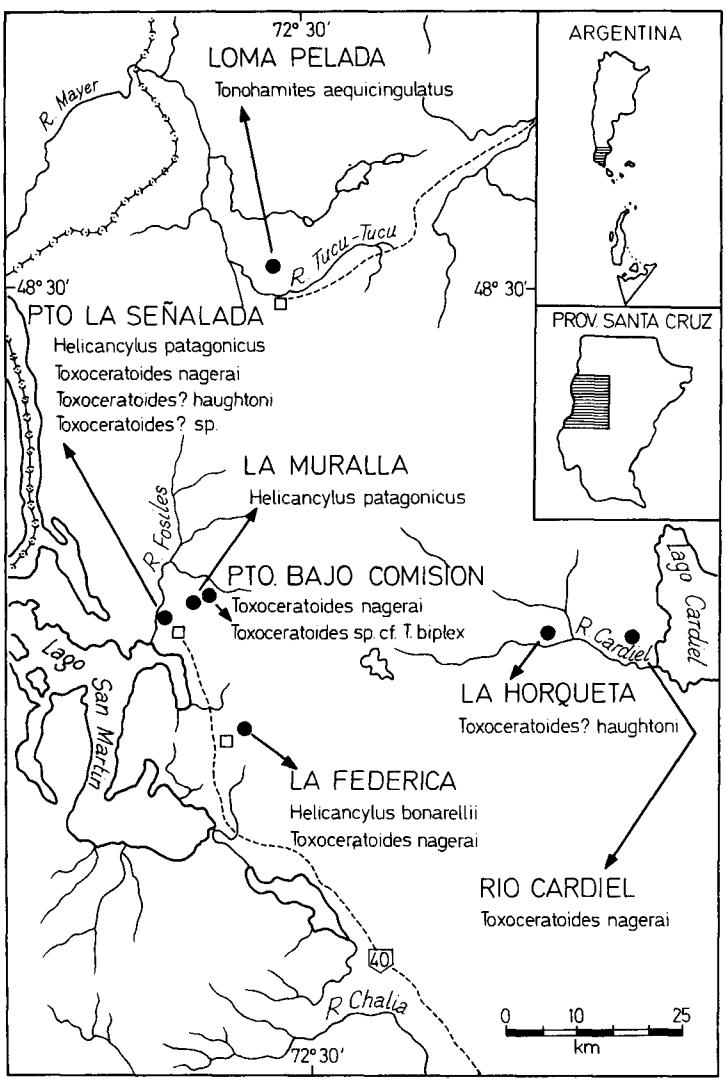

Fig. 1. Index map of the western region of the Province of Santa Cruz, showing location of the collecting sites.

however, show affinities with species described from Zululand and western Europe.

The localities studied are situated in the north-western province of Santa Cruz, in the northern central part of the Austral Basin (Fig. 1).

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the source of the material:

CPBA Cátedra de Paleontología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires.

MLP División Paleozoología de Invertebrados, Museo de Ciencias Naturales de La Plata.

CORD-Pz Cátedra de Paleontología, Universidad Nacional de Córdoba.

DNGM División Paleontología, Servicio Geológico Nacional, Argentina.

Casts of some of the figured specimens are deposited at the Department of Invertebrate Palaeontology of the South African Museum.

Most of the specimens were collected by the author. If not, the name of the collector is given in the systematic descriptions.

DIMENSIONS

No standard set of abbreviations is in common use for heteromorph ammonoids. The abbreviations used here are as follows:

L	=	total length
H_M	=	maximum whorl height
H_O	=	whorl height opposite to aperture
H_m	=	minimum whorl height
Wh/Wb	=	relation between whorl height and whorl breadth.

Dimensions of specimens are given in millimetres.

STRATIGRAPHIC SYNTHESIS

All ammonites studied are (with one exception) from the upper part of the Río Mayer Formation. This unit was defined by Hatcher (1897) as 'a series of black, very hard, but much fractured slates, with ammonites fairly abundant, but not sufficiently well-preserved to admit of identification' on the upper reaches of the Mayer River. The Río Mayer Formation outcrops over an extensive belt parallel to the present main cordillera. The exposures in the area studied, extending to the north and south of the type locality, have a complex distribution, controlled by a complicated series of faults and folds (Ramos 1981). Complete exposures of the Río Mayer Formation are rare and it is difficult to correlate partial sections. The selected sections, although not always complete, show at least definite relations with the under- or overlying formations.

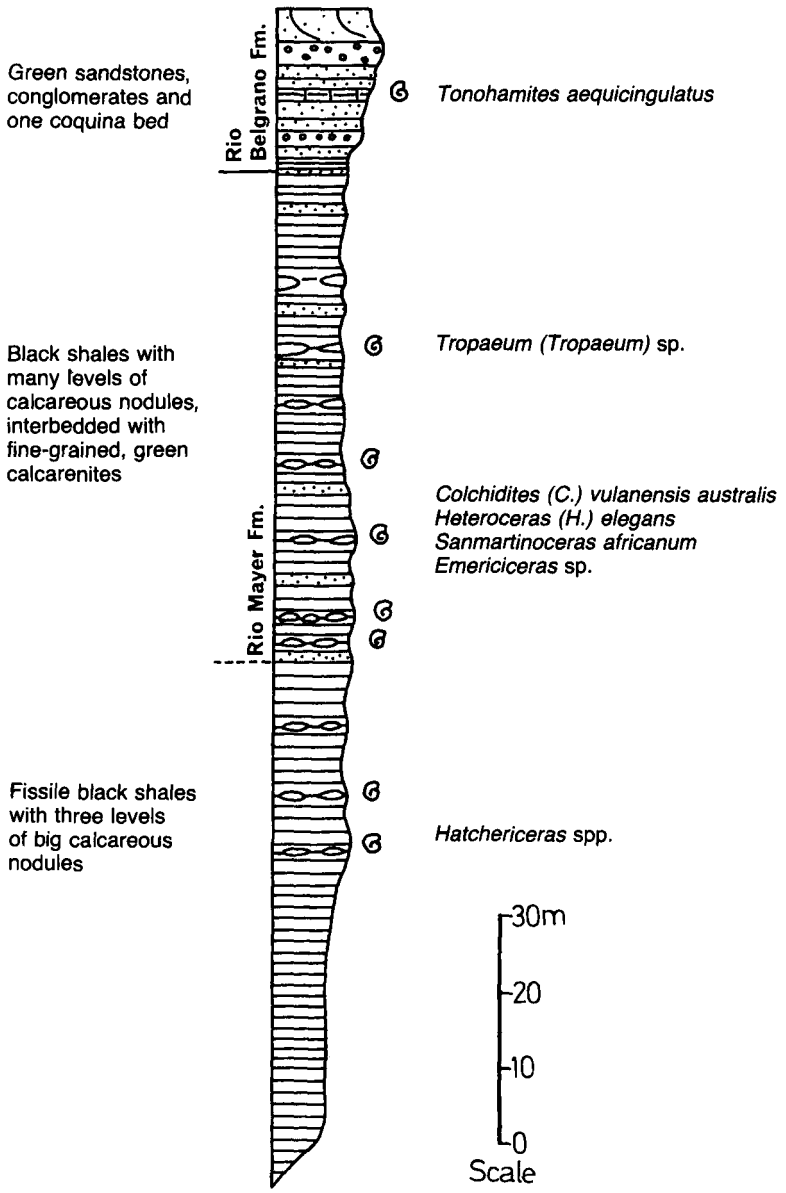

Fig. 2. Stratigraphical section at Loma Pelada, Tucu-Tucu.

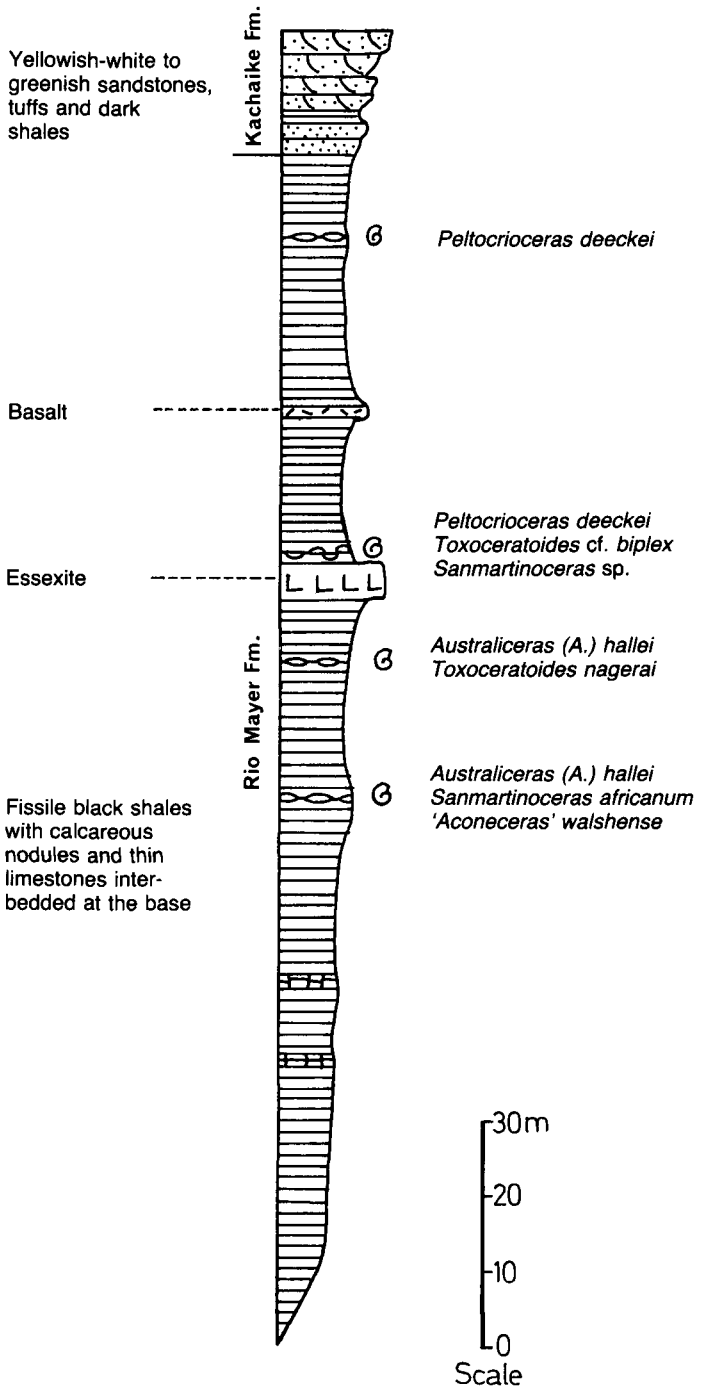

Fig. 3. Stratigraphical section at Puesto Bajo Comisión, Lake San Martín.

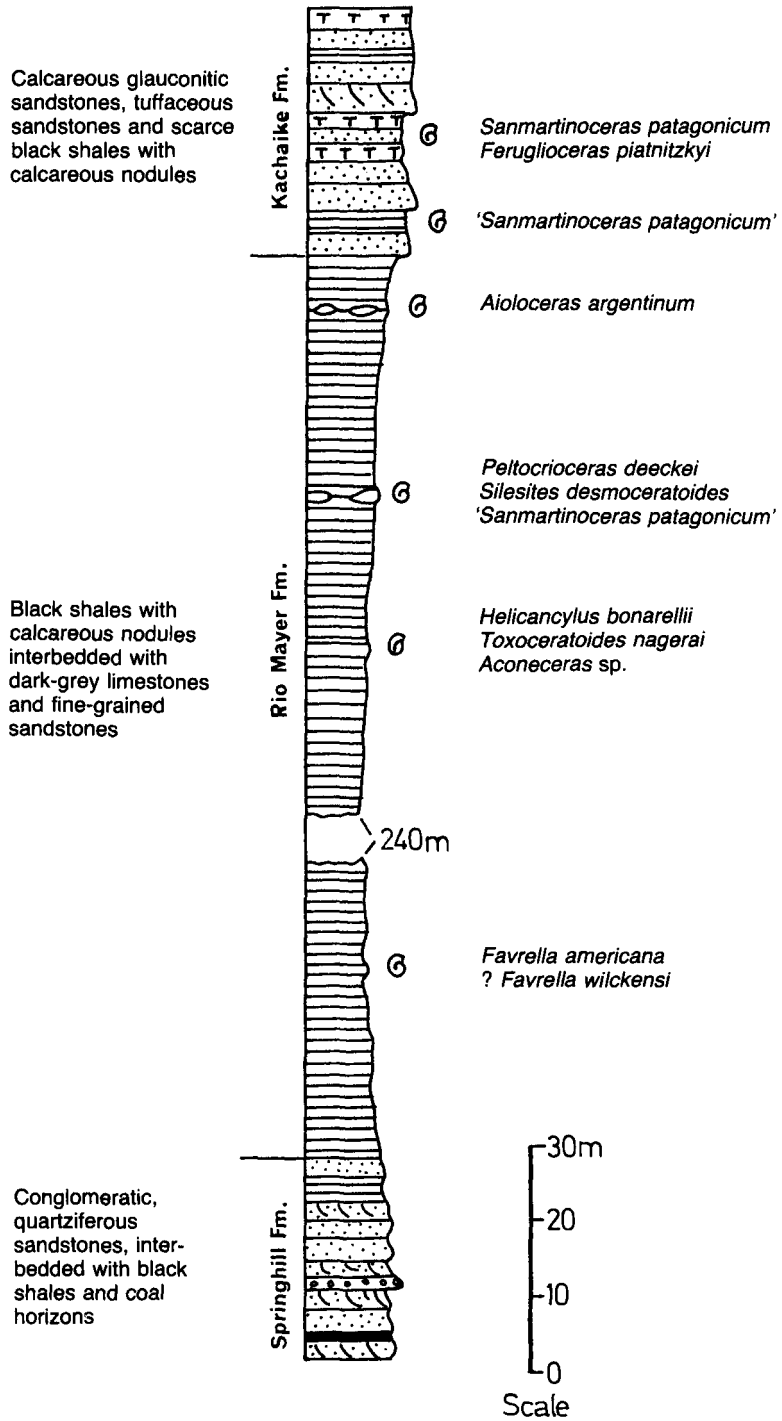

Fig. 4. Stratigraphical section at La Federica, Lake San Martín.

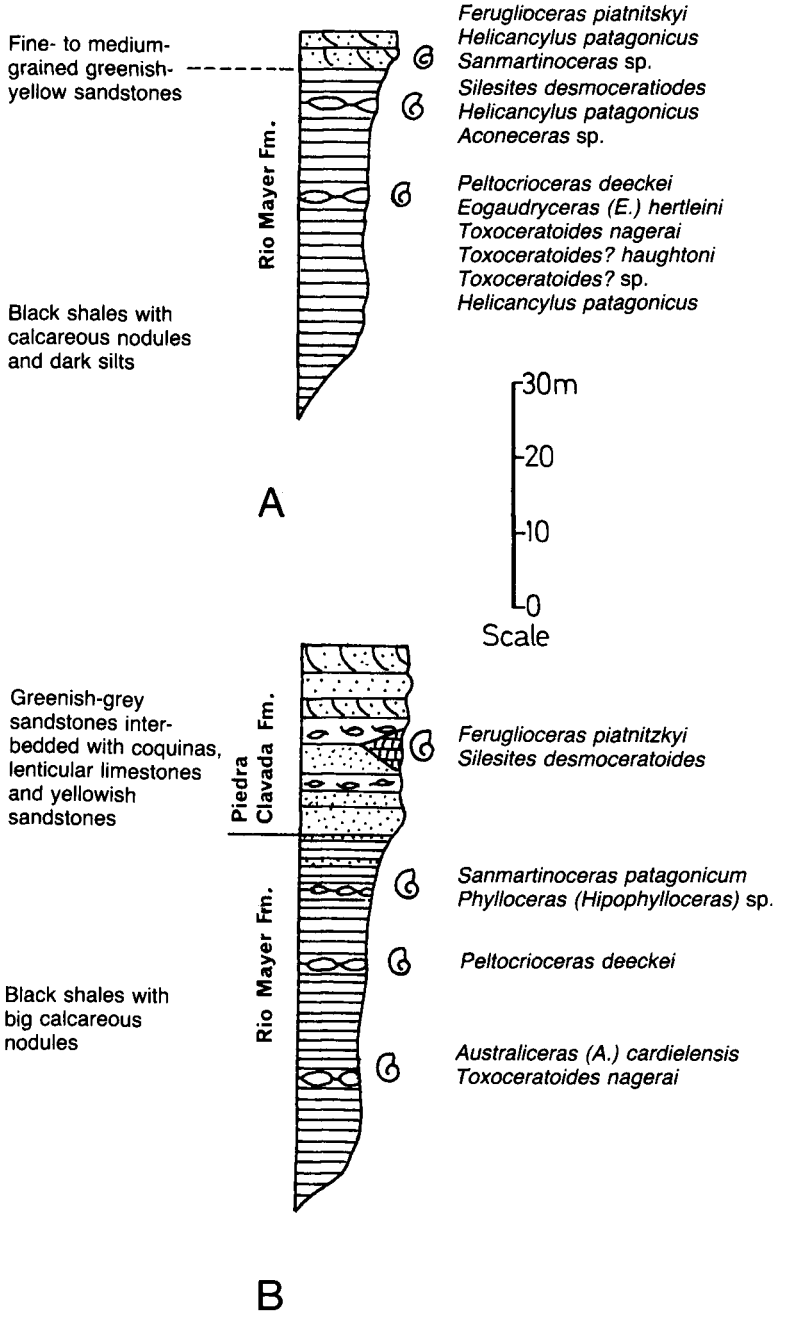

Fig. 5. Stratigraphical sections. A. Puesto La Señalada, Lake San Martín. B. La Horqueta, Lake Cardiel.

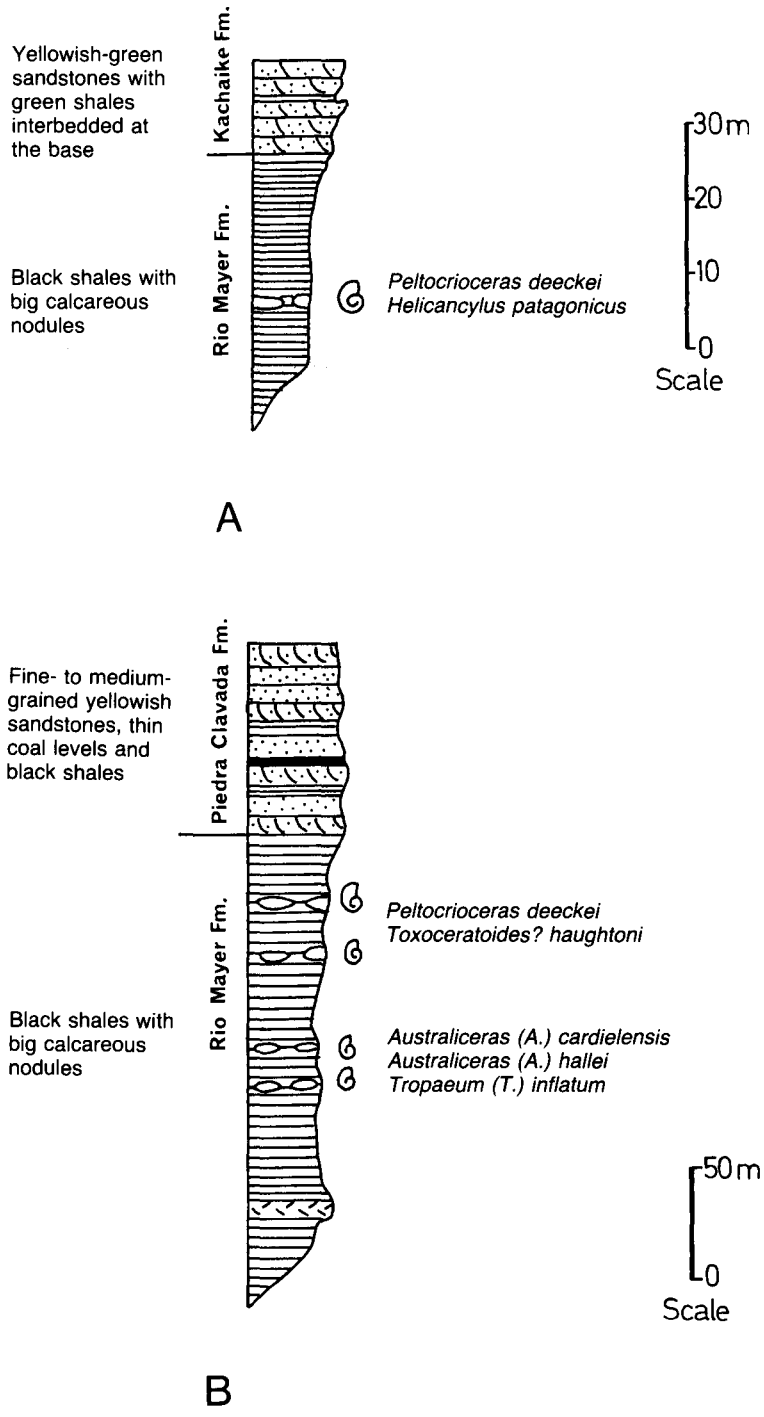

Fig. 6. Stratigraphical sections. A. La Muralla, Lake San Martín. B. Río Cardiel, Lake Cardiel.

The Río Mayer Formation consists of a monotonous succession of black shales, poorly to strongly indurated, sometimes yellowish due to alteration, with many levels of calcareous nodules. The size of the nodules ranges from a few centimetres up to more than a metre in diameter. All the fossils are preserved in these nodules. Different, small-scale facies may be present locally. They are indicated in Figures 2 to 6, in which the various fossiliferous horizons are also shown.

The Río Mayer Formation usually rests conformably on marine and continental sandstones of the Springhill Formation. In some sections, however, the unit directly overlies the Jurassic Complejo El Quemado volcanics.

In the northern area the Río Mayer Formation is conformably overlain by the sandstones of the Río Belgrano Formation (Ramos 1979), whilst to the south, in the Andean region, it is succeeded by the Kachaike Formation. This last unit is characterized by marine to continental interbedded sandstones and tuffs (Riccardi 1971). In the extra-Andean region the Piedra Clavada Formation, a mainly shallow marine sequence composed of sandstones, shales and tuffs, rests upon the Río Mayer Formation (Ramos 1982).

HISTORY OF PALAEONTOLOGICAL RESEARCH

In 1912 Stolley described two specimens of *'Ancyloceras' patagonicum* amongst other cephalopods. The material on which Stolley based his study was collected by Halle (1913), who also studied the palaeoflora and stratigraphy of the Cretaceous deposits near Bahía de La Lancha, Lake San Martín.

A few years later, Bonarelli & Nágera (1921) published the results of their geological and palaeontological expedition to Lake San Martín. Amongst other invertebrate fossils they described and figured two specimens, *Leptoceras* gr. *silesiacum* Uhlig and *Leptoceras* sp. indet., that were typical of the 'Level with *Leptoceras*' or 'Level c' in their biostratigraphic subdivision of the Lower Cretaceous.

A complete regional study dealing with the geology of the western part of the Province of Santa Cruz was carried out by Piatnitzky (1938). This author also gave short descriptions and illustrations of the most relevant faunas, including one specimen of *Leptoceras* sp. from Arroyo de la Mina and another of *Ancyloceras patagonicum* from Río Cardiel.

After Piatnitzky there were no major palaeontological contributions until 1968 when Riccardi, in an unpublished thesis, described and figured the Lower Cretaceous invertebrate faunas of Bahía de La Lancha, with a detailed study of the stratigraphy of this area. Riccardi (1968) described a series of crushed specimens of *'Ancyloceras' patagonicum*. He also gave an exhaustive account of the representatives of this group, not only in the Austral Basin, but also in other regions of the world.

Finally Leanza (1970), in a monograph dealing with the Cretaceous ammonite faunas of the Austral Andes, described and figured one specimen of

Helicancylus cf. *patagonicus* (Stolley) and also referred Bonarelli & Nágera's *Leptoceras* to the genus *Acrioceras*, proposing two new species: *A. nagerai* and *A. bonarellii*.

SYSTEMATIC PALAEONTOLOGY

Class CEPHALOPODA Zittel, 1884

Order AMMONOIDEA Zittel, 1884

Suborder ANCYLOCERATINA Wiedmann, 1966

Superfamily ANCYLOCERATACEAE Gill, 1871

Family **Ancyloceratidae** Gill, 1871

Subfamily Helicancylinae Hyatt, 1894

Discussion

Casey (1961: 76) grouped in the subfamily Helicancylinae a series of small ancyloceratids in which the sculpture is simplified on the terminal hook. He included three Aptian genera, *Helicancylus* Gabb, *Toxoceratoides* Spath, and *Tonohamites* Spath, while three Barremian genera, *Acrioceras* Hyatt, *Lytocrioceras* Spath, and *Leptoceras* Uhlig, were provisionally assigned to the subfamily.

Casey (1961: 77) also extensively discussed the nomenclatorial problems that involved the type-genus *Helicancylus* Gabb, 1869. Gabb (1869) included in *H. aequicostatus* a series of fragmentary specimens from which he believed a complete specimen could be reconstructed. These consisted of an initial helix, a shaft, and a body chamber; this last fragment was previously referred to *Ptychoceras aequicostatus* Gabb, 1864 (pl. 13 (fig. 20)). Anderson (1938: 215) indicated that the material referred to *H. aequicostatus* by Gabb (1869) included at least three species. He restricted the name *Helicancylus* to the helical part, redescribing it as *H. gabbi* (Anderson 1938: 222, pl. 79 (figs 4–5)). He proposed the new generic name *Hamiticeras* for the original *Ptychoceras aequicostatus* Gabb, 1864 specimen, and for the specimen figured later by Gabb (1869, pl. 25 (figs c–f)). The latter was assigned to *Hamiticeras pilsbryi* and proposed as the type-species of the genus. Casey (1961) pointed out that *Ptychoceras aequicostatus* is the type-species of *Helicancylus* and that it is congeneric with *Hamiticeras pilsbryi*. Thus the latter genus became a synonym of *Helicancylus*.

The present author disagrees with Casey and partially agrees with Anderson, in that the original *Helicancylus* comprises three different genera. The helical fragment shows no relation to any of the other specimens and is here excluded from the subfamily. The helical coiling of the specimen recalls *Helicancyloceras* Klinger & Kennedy, 1977, and even more *Kutatissites* Kakabadze, 1970 (= *Simionescites* Avram, 1976*b*), being similar in particular to *Kutatissites princeps* (Avram, 1976*b*, pl. 3 (fig. 1a–c)) and *K. rachathasensis* Kakabadze, 1981 (pl. 11 (fig. 3a–c)). Although Casey (1961) considered the helical fragment as 'irrelevant to the interpretation of *Helicancylus*', it can be seen from recent

literature that this is not so. Its inclusion in the genus and even in the subfamily only leads to misconceptions. This was the case with Thieuloy (1976), who referred *Kutatissites* to the subfamily Helicancylinae when comparing it with 'the helical part of *Helicancylus*'. The large ancyloceratid *Kutatissites* can hardly be placed in a subfamily that groups 'those diminutive ancyloceratids in which the sculpture is simplified on the terminal hook' (Casey 1961: 76).

With reference to the shaft and body-chamber fragments assigned to *Helicancylus* by Gabb (1869) and to *Hamiticeras* by Anderson (1938), it is here believed that *Hamiticeras pilsbryi*, type-species of *Hamiticeras*, is not congeneric with *Ptychoceras aequicostatus*, type-species of *Helicancylus*. It is proposed to consider both as valid genera. *Helicancylus* will be discussed later; *Hamiticeras* can be diagnosed as follows: 'Small size. Shaft straight and final hook long, almost parallel to the shaft. Ornament of the phragmocone consists of strong trituberculate and thin intermediate ribs. Final hook with sharp, high, non-tuberculate ribbing.' To *Hamiticeras* can be referred *H. pilsbryi* from the Upper Aptian (*Argonauta* zone) of California (Anderson 1938) and from the Caucasus (Drushchits & Kudryavtsev 1960: 295, pl. 11 (figs 6a–b, 7a–b)), and *Hamiticeras* sp. (Avram 1976*a*, pl. 2 (fig. 1 only)) from the Upper Aptian of the Carpathian mountains (Romania).

After Casey's (1961) monograph, some authors adopted his classification (Day 1974; Thomson 1974; Klinger & Kennedy 1977; Martínez 1982), while others (Murphy 1975; Förster 1975; Etayo Serna 1979; Kakabadze 1981) assigned the different genera to the family Ancyloceratidae, without any reference to the subfamilies.

More complicated is the history of the assignation of the Barremian genera *Acrioceras, Leptoceras* and *Lytocrioceras*. Sarkar (1955) described and illustrated a series of species of *Acrioceras* and *Leptoceras*, and reviewed the original material of *Lytocrioceras*. He expanded the original conception of *Acrioceras* Hyatt, proposing four new subgenera. They were mainly based on the coiling and on the ornament:

Acrioceras (Acrioceras) s.s.: coiling acrioceratid; ornament with tuberculate ribs.
Acrioceras (Paraspinoceras) (Breistroffer): coiling acrioceratid; non-tuberculate ribs.
Acrioceras (Aspinoceras) (Anderson): coiling aspinoceratid; non-tuberculate ribs.
Acrioceras (Protacrioceras) Sarkar: coiling aspinoceratid; tuberculate ribs.

(See Figure 7 for the different types of coiling.)

Unfortunately Sarkar (1955) based his revision on material of D'Orbigny and from other collections of the nineteenth century, which lack precise stratigraphic data. According to Sarkar (1955: 26) *Acrioceras* ranges from the Hauterivian to the Lower Aptian. He described one species of *Leptoceras* and redescribed the type of *Lytocrioceras jauberti* (Astier, 1851: 25, pl. 9 (fig. 17)) but no photographic illustration was given.

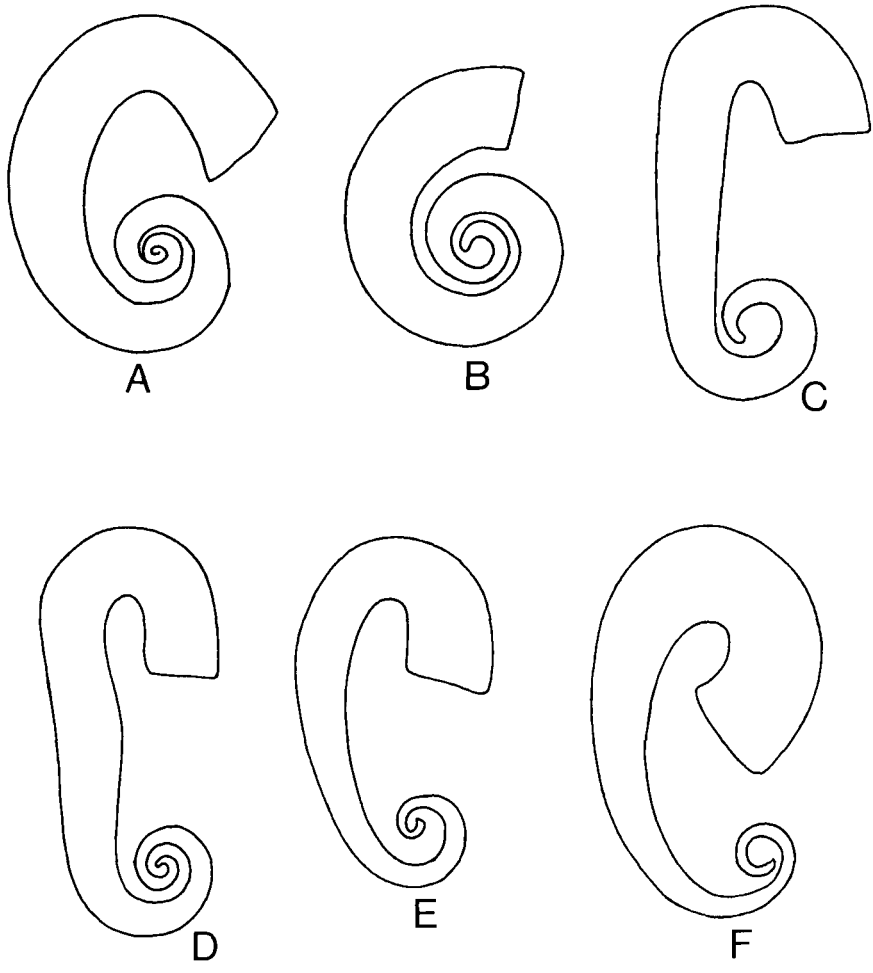

Fig. 7. Different types of coiling referred to in the text. A. Aspinoceratid. B. Crioceratitid. C. Acrioceratid. D. Ancyloceratid. E. Toxoceratid. F. Labeceratid.

Wright (1957: L211) maintained *Aspinoceras* as a valid genus and included *Paraspinoceras* as a doubtful synonym of *Lytocrioceras*. He interpreted *Helicancylus* in the sense of Anderson (1938) and regarded *Tonohamites* and *Toxoceratoides* (the latter with doubt) as synonyms of *Hamiticeras*. While Thomel (1964) accepted Sarkar's (1955) revision of *Acrioceras*, Wiedmann (1962) dissented and regarded all four subgenera as synonyms of *Acrioceras* s.l. Manolov (1962: 531) proposed the new subfamily Leptoceratinae for a group of small Barremian forms that he considered to be early representatives of the family Ancyloceratidae. He also pointed out the close relationship between all these forms. His subfamily comprised *Leptoceras* Uhlig, *Karsteniceras* Royo y Gómez, *Veleziceras* Wright,

and *Eoleptoceras* Manolov. Manolov (1962) furthermore questioned the occurrence of *Leptoceras* in the Berriasian (Nikolov 1960), as that genus is unknown from the Valanginian and Hauterivian. Thieuloy (1966), however, maintained that the true *Leptoceras* occurs in the Berriasian and erected the new genus *Leptoceratoides* for the homeomorphic Barremian forms. Dimitrova (1970) proposed a completely new arrangement of the Cretaceous heteromorphs, spreading the different genera united in the Helicancylinae by Casey (1961) into a number of families and subfamilies. Although she based her study on suture lines, she did not accept Wiedmann's (1966) suborder Ancyloceratina, which included all Cretaceous ammonoids with quadrilobate primary suture. Dimitrova's (1970) proposal was generally avoided by later authors, except for Avram (1976*a*), who followed her classification.

As interpreted here, the subfamily Helicancylinae comprises the Aptian genera *Helicancylus* Gabb, *Hamiticeras* Anderson, *Tonohamites* Spath, and *Toxoceratoides* Spath, and the Barremian *Acrioceras* Hyatt and *?Lytocrioceras* Spath. The last genus is very enigmatic and as far as can be established it is only known from the single specimen of the type-species. The Barremian genus '*Leptoceras*' (= *Leptoceratoides*) has been referred to a different stock (Manolov 1962; Wiedmann 1973).

In Patagonia, the subfamily Helicancylinae is represented by *Helicancylus, Toxoceratoides*, and *Tonohamites*.

Genus *Helicancylus* Gabb, 1869

Type-species. Ptychoceras aequicostatus Gabb, 1864, from the Aptian of California, by original designation (Gabb 1869).

Diagnosis

Coiling variable, usually with a straight or curved shaft and a final hook. Ornament on the shaft consists of ribs of equal size, each one bearing one to three rows of tubercles. Final hook with single, non-tuberculate ribs. Suture line with bifid saddles and asymmetrical, trifid lobes.

Discussion

As interpreted here, *Helicancylus* differs from *Toxoceratoides* by the total lack of intercalatory ribbing and the presence of tubercles on every rib of the shaft as well as the simple ribbing on the final hook. *Toxoceratoides* shows strong trituberculate and fine intercalatory ribs on the shaft and sharp ribs springing in bundles from umbilical tubercles on the final hook (Casey 1961; Klinger & Kennedy 1977).

Tonohamites is easily distinguished from *Helicancylus* by the rounded, non-tuberculate ribs on the shaft and the strong, rounded or flat ribbing on the final

hook. *Hamiticeras* Anderson has similar ornament on the final hook but shows strong trituberculate ribs separated by thin intermediaries on the shaft.

According to Casey (1961: 93) the only European record of *Helicancylus* was the Upper Aptian *'Hamites'* sp. figured by Jacob & Tobler (1906, pl. 2 (figs 10–11)). Besides this material, which most probably belongs to the genus, several species can be assigned to it, although some are included tentatively. They are as follows:

Ancyloceras elatum von Koenen (1902: 375, pl. 38 (fig. 8a–c), pl. 40 (fig. 2a–b), pl. 45 (fig. 9), pl. 53 (figs 6–7)).
Toxoceratoides? elatum (von Koenen) (Kemper 1976, pl. 33 (fig. 1)).
Ancyloceras fustiforme von Koenen (1902: 384, pl. 49 (figs 4–5, 7, 9), pl. 53 (figs 8–9)).
Toxoceratoides cf. *fustiformis* (von Koenen) (Casey 1961: 83, pl. 17 (fig. 4)).
Hamiticeras aequicostatum (Gabb) (Anderson 1938: 216, pl. 37 (figs 2–2a, 3), pl. 79 (fig. 6)).
Hamiticeras philadelphium Anderson (1938: 216, pl. 79 (figs 2–3)).
Ancyloceras patagonicum Stolley (1912: 11, pl. 1 (figs 3–3a, ?2–2a)).
Acrioceras bonarellii Leanza (1970: 207, fig. 6 (1)).
Genus uncertain. Group of *'Ancyloceras' patagonicum* Thomson (1974: 19, pl. 3 (figs c, g–h)).

'Ancyloceras' elatum von Koenen was doubtfully referred to *Toxoceratoides* by Kemper (1976), who also figured one fragmentary specimen. This species as well as *'Ancyloceras' fustiforme* von Koenen, assigned to *Toxoceratoides* by Casey (1961) are here both included in *Helicancylus* (see p. 290).

The group of *'Ancyloceras' patagonicum* referred to an indeterminate genus by Thomson (1974) can also be placed in *Helicancylus*. Thomson compared the suture line of *'Hamiticeras' aequicostatum* (illustrated by Anderson 1938, pl. 79 (fig. 6)) with that of the lectotype of *'Ancyloceras' patagonicum*. He noted that 'The suture of "*Hamiticeras*" is more complex and has a narrow external saddle, a broad trifid first lateral lobe and a slightly smaller second lateral lobe' (Thomson 1974: 20). He concluded that the *'A.' patagonicum*-group most probably represented a new genus.

The suture line of the lectotype of *'A.' patagonicum*, as illustrated by Thomson (1974, text-fig. 4b) appears very similar to that of the Patagonian material studied here and referred to *Helicancylus patagonicus*. Both are figured (Fig. 9D–G) for comparison. Recently Thomson (1982) included the Patagonian material in *Helicancylus*, but in open nomenclature.

Occurrence

Helicancylus occurs in the Aptian of Antarctica (Thomson 1974), California (Gabb 1869; Anderson 1938), England (Casey 1961), Germany (Von Koenen 1902; Kemper 1976), Patagonia (Stolley 1912; Riccardi 1968; Leanza 1970), and Switzerland (Jacob & Tobler 1906) (Fig. 8).

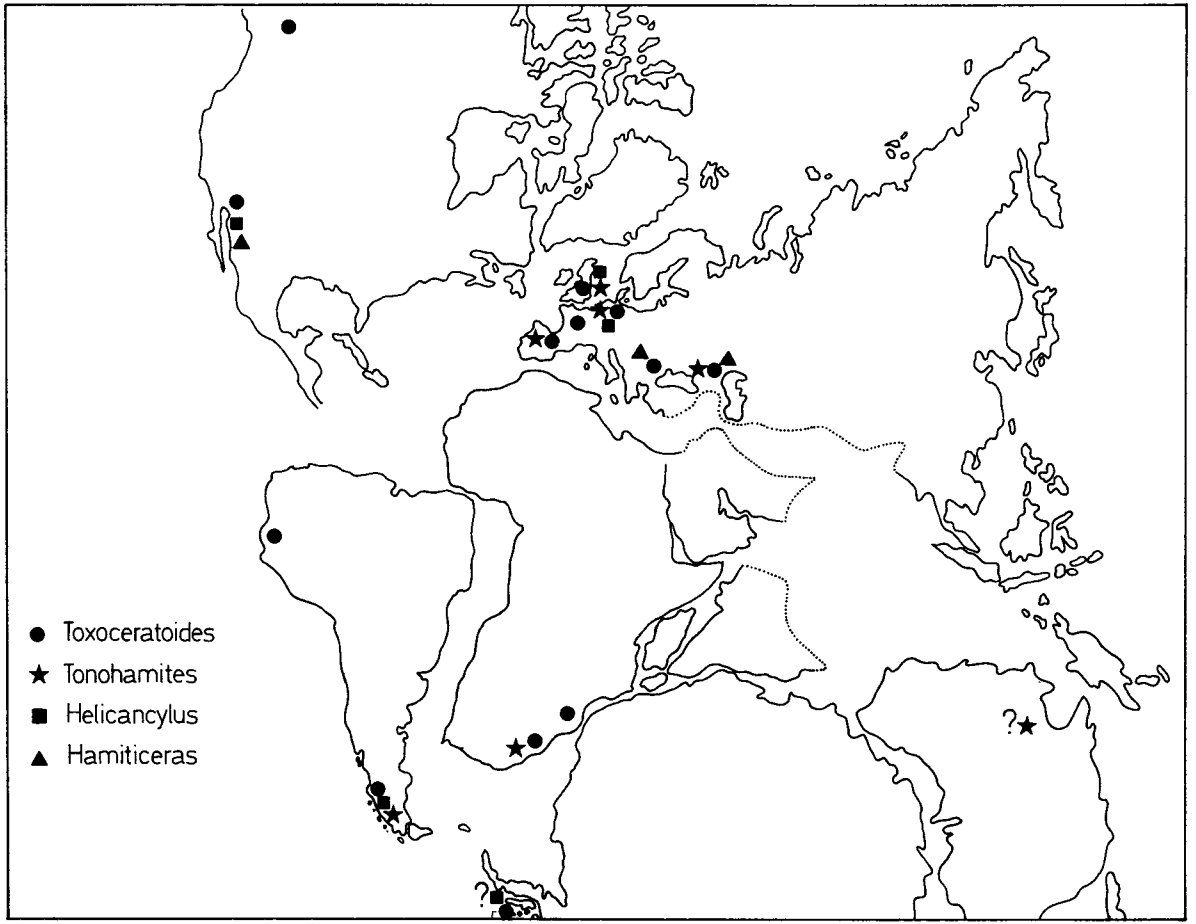

Fig. 8. Palaeobiogeographical distribution of the four Aptian genera of Helicancylinae.

The report of *Helicancylus furcata* Kakabadze from the Aptian of the Soviet Union (Kakabadze 1981) is not accepted here. Kakabadze interpreted the genus in the sense of Anderson (1938), referring to the initial helix only.

Helicancylus patagonicus (Stolley, 1912)

Figs 9A–G, 10, 11A–C, 12A–F, 19A–B

Ancyloceras patagonicum Stolley, 1912: 11, pl. 1 (figs 3–3a, ?2–2a).
non *Ancyloceras patagonicum* Stolley: Howarth, 1958: 4, pl. 1 (fig. 4).
non *'Ancyloceras' patagonicum* Stolley: Riccardi, 1968 *(pars)*, pl. 21 (fig. 1).
non *Helicancylus* cf. *patagonicus* Leanza, 1970: 205, fig. 4 (1).
non *'Ancyloceras' patagonicum* Stolley: Thomson, 1974: 19, pl. 3 (figs c, g–h).

Lectotype

The specimen figured by Stolley (1912, pl. 1 (fig. 3–3a)). Original at Riksmuseum N Mo. 117877, Stockholm, by subsequent designation Thomson (1974: 19).

Material

CPBA 11062 from La Muralla, Lake San Martín; CPBA 10898, 10848, 10844 and ?10887 from Puesto La Señalada, Lake San Martín. Río Mayer Formation. Upper Aptian.

Description

The most complete specimen, CPBA 11062 (Fig. 11A–C), shows ancyloceratid coiling, with a nearly straight shaft and a recurved crozier. The early stage of growth is unknown.

The whorl section is initially compressed (Wh/Wb = 1,13–1,20), subovoid, with rounded dorsum and venter and flat to gently inflated flanks. With increasing diameter, the whorl section becomes more rounded and on the final hook it is nearly circular (Fig. 9A–C).

Ornament on the shaft consists of prominent, narrow, obliquely prorsiradiate, tuberculate ribs. They are separated by interspaces wider than themselves. They pass with a slight forward curvature over the dorsum, sometimes showing duplications, and are distinctly interrupted over the venter. All the ribs bear at least two rows of tubercles, one siphonal and the other ventrolateral. In some specimens there is also a third row of small dorsolateral tubercles.

Towards the end of the shaft the tuberculation gradually disappears and on the final hook the ornament consists of radial, simple, sharp ribs. They cross the venter without interruption. On the dorsum they are reduced to striae with a forward curvature.

The suture line is quite simple, with trifid lateral, umbilical and internal lobes; the first is broad and slightly asymmetrical (Fig. 9E–G).

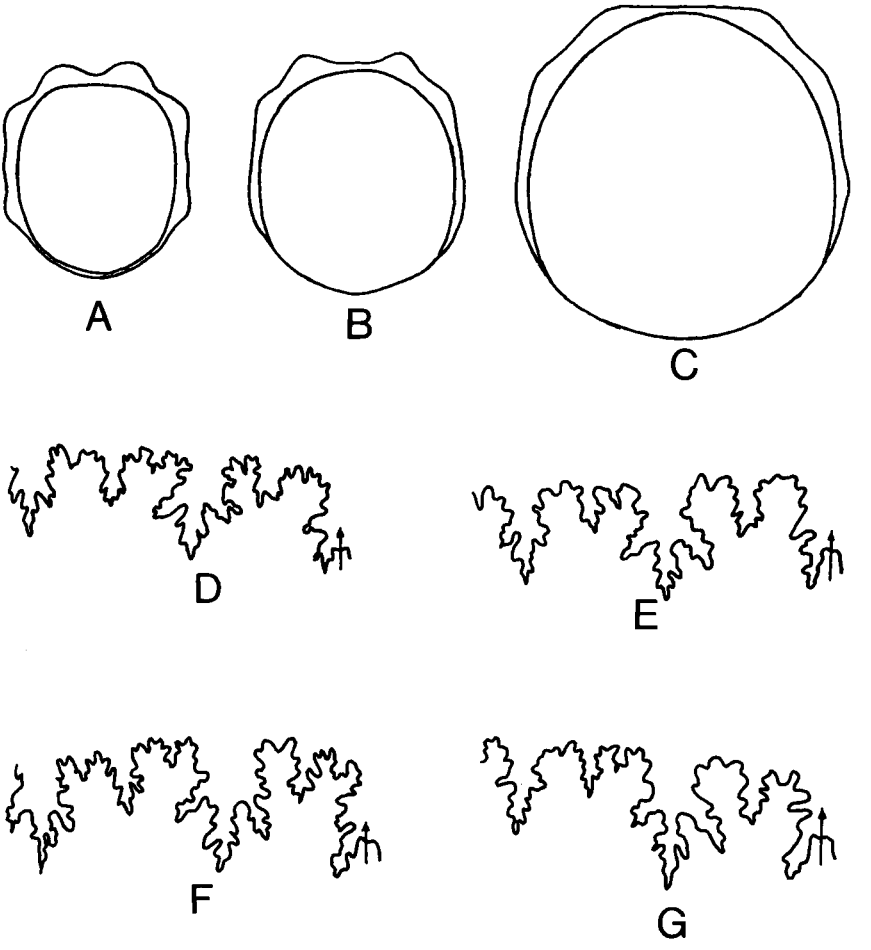

Fig. 9. *Helicancylus patagonicus* (Stolley). A–C. Whorl section of CPBA 11062. × 2,5. D. Suture line of lectotype (after Thomson 1974). E–F. Suture line of CPBA 11062. × 4. G. Suture line of CPBA 11087. × 4.

Dimensions

Specimen	H_M	H_O	H_m
Lectotype*	20,0	14,0	13,0
CPBA 11062	16,0	11,0	9,0
CPBA 10848	14,0	—	11,0
CPBA 10844	20,0	—	16,0
CPBA 10887	10,0	—	4,0

* Deposited at the Riksmuseum N Mo. 117877 (Stockholm). Measurements taken from Stolley's (1912, pl. 1 (fig. 3–3a)) original photograph.

Discussion

When Stolley (1912) proposed this species, he described two fragmentary specimens. He was in doubt whether to refer both to the same species, but pointed out that the difference in ornament was no greater than that in other species of *'Ancyloceras'* known from the Lower Cretaceous of northern Germany. As far as can be seen from the original illustrations, the main difference between Stolley's two specimens is the degree of curvature of the shaft, rather than the ornament. The small specimen figured by Stolley (1912, pl. 1 (fig. 2–2a)) is here doubtfully referred to the species. According to Thomson (1974) both may belong to different genera.

Helicancylus patagonicus (Stolley) differs from *H. bonarellii* (Leanza) in the coiling and in the ornament. In the former, the coiling is ancyloceratid, with a straight shaft and a recurved crozier, and a slow increase in the whorl section. In the latter, the coiling is open crioceratitid or toxoceratid, with a rapid increase in the whorl section, especially on the final hook. Besides, in *H. bonarellii* the ribs are rounded, closely spaced, and with feeble tubercles, while in *H. patagonicus*

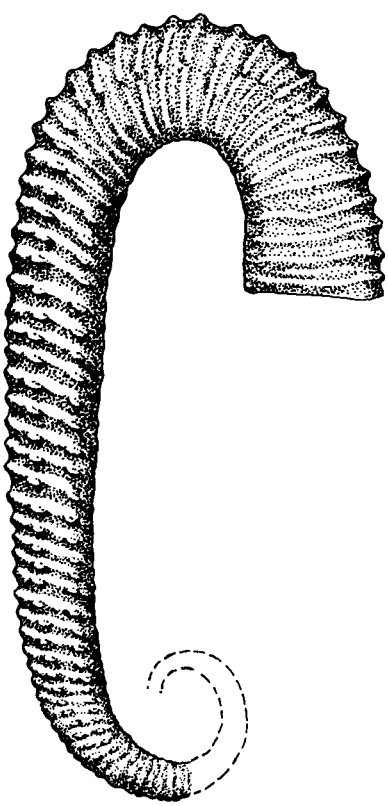

Fig. 10. Reconstruction of *Helicancylus patagonicus* (Stolley).

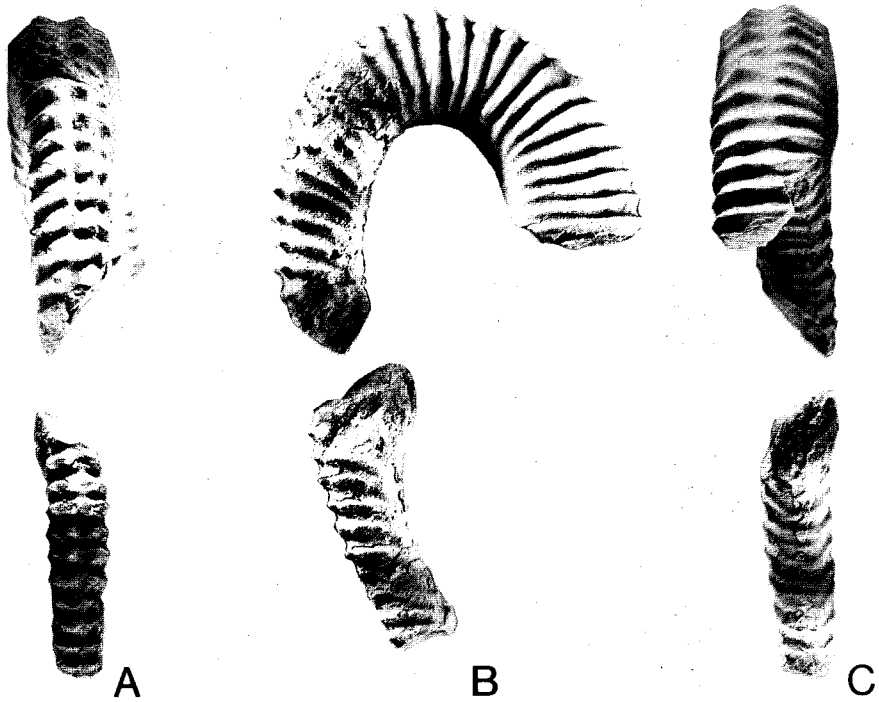

Fig. 11. *Helicancylus patagonicus* (Stolley). CPBA 11062 from La Muralla. × 1.

they are high and sharp, with well-developed tuberculation, and they are separated by wider interspaces.

The Antarctic material figured by Howarth (1958, pl. 1 (fig. 4)) as *'Ancyloceras' patagonicum* or by Thomson (1974, pl. 3 (figs c, g–h)) as group of *'A.' patagonicum* seems to be more related to *H. bonarellii*.

Helicancylus aequicostatus Gabb differs from *H. patagonicus* in the whorl section, ornament, and suture line. The former species has a subtrapezoid whorl section with flat dorsum, shaft ornamented with dense rounded ribs that cross the venter without interruption and bear faint siphonal tubercles only. The suture line in *H. aequicostatus* is more incised than in the Patagonian species, with a narrow ventral saddle (Anderson 1938: 217, pl. 37 (figs 2–3), pl. 79 (fig. 6)).

Helicancylus philadelphium (Anderson) is very closely related to *H. aequicostatus*. Although Anderson (1938) did not compare them, it seems that a row of faint ventrolateral tubercles in the former species is the only different feature.

The European species *H. fustiformis* and *H. elatum* described by Von Koenen (1902) are known from fragmentary specimens only. Although Von Koenen's descriptions are precise, he described each fragment in detail and it is difficult to interpret each species as a whole.

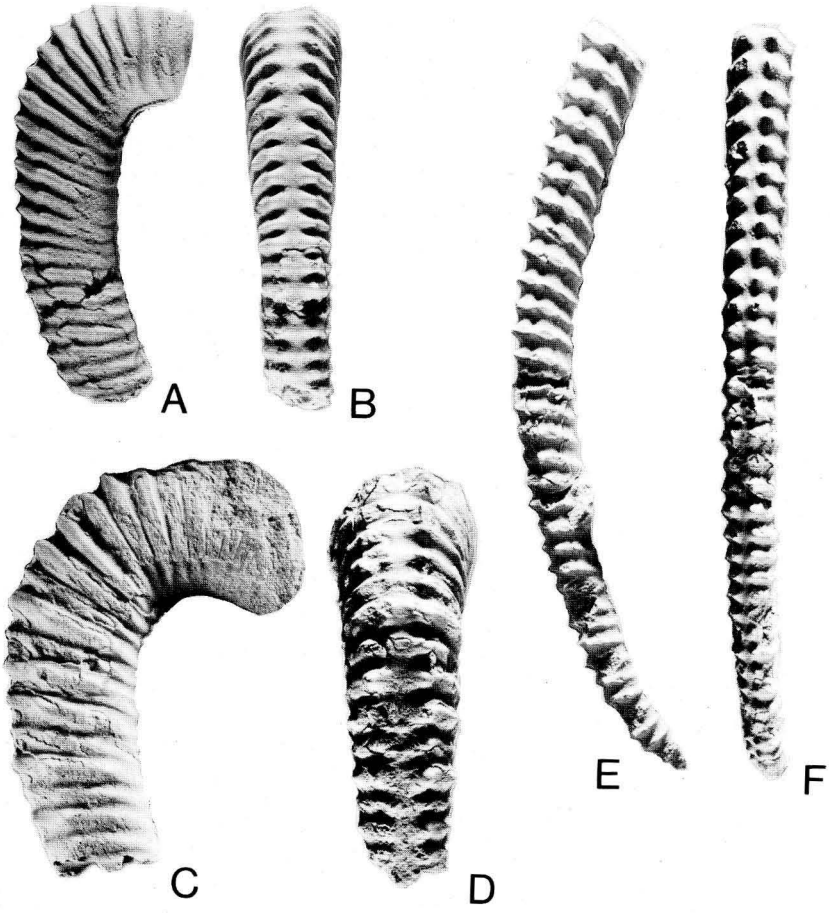

Fig. 12. *Helicancylus patagonicus* (Stolley). A–B. CPBA 10844. C–D. CPBA 10848. E–F. CPBA 10887. All from Puesto La Señalada. All × 1.

Helicancylus elatum (von Koenen) (1902: 375, pl. 38 (fig. 8a–c), pl. 40 (fig. 2a–b), pl. 45 (fig. 9), pl. 53 (figs 6–7)) has a rapid increase in the whorl section, and fine dense ribs that are trituberculate on the shaft and bend of the crozier. *Helicancylus fustiformis* (von Koenen) (1902: 384, pl. 41 (figs 4–5, 7a–c, 9a–b), pl. 53 (figs 8a–b, 9a–b)) is mostly known by small shaft fragments with subcircular whorl section and trituberculate ribs. Casey (1961: 83, pl. 17 (fig. 4)) described a fragmentary specimen as *Toxoceratoides* cf. *fustiformis*, pointing out that this species is very similar to *T. royerianus* but with tubercles in every rib.

In Patagonia, Piatnitzky (1938, pl. 6 (figs 31–32)) figured a fragment of a shaft of *'Ancyloceras' patagonicum*. It may belong to this species because of its well-marked tubercles, although the ribbing is quite dense.

The small specimen referred to *Helicancylus* cf. *patagonicus* by Leanza

(1970) has bi- or trifurcate ribs arising from an umbilical tubercle on the bend of the crozier. It is here referred to *Toxoceratoides nagerai*.

It is interesting to discuss the range of this species. Halle (1913) collected one specimen, illustrated by Stolley (1912, pl. 1), in sandstones referred to his division 6, in Calafate Stream (fig. 2–2a), and another from the summit of a high ridge on the south side of a stream (today known as Bajo Comisión Stream) also in his division 6. This informal lithologic unit is at present known as Kachaike Formation, of Upper Aptian to Albian age.

When describing Halle's material, Stolley (1912) compared it with European species of Upper Neocomian to Lower Aptian age, but concluded that *'Ancyloceras' patagonicum* might be of Upper Aptian age. This idea was ratified in his description of *?Oppelia (Adolphia)* sp. in the same publication. Thomson's (1974: 20) reference to an Upper Neocomian or Lower Aptian age of this species seems to be a misreading of Stolley's work.

All the material described here was collected in the uppermost section of the Río Mayer Formation, in a level characterized by the abundance of giant specimens of *Peltocrioceras deeckei* (Favre). This fact partially corroborates Riccardi's (1968) opinion that *'A.' patagonicum* was not present in Halle's division 6, but only in his division 5 (at present the Río Mayer Formation). Unfortunately, this statement was based on a negative fact: that after Halle, no one has collected specimens of this species in the Kachaike beds, but always in the Río Mayer Formation. Another problem is that Riccardi (1968) described as *'A.' patagonicum* what is here referred to *Helicancylus bonarellii* and *H. patagonicus*. The former species is actually restricted to the upper section of the Río Mayer Formation in a level *below* that of *Peltocrioceras deeckei*, while *H. patagonicus* occurs *with* it.

Further problems arise with the statement by Halle (1913) that *'A.' patagonicum* occurs above a level with a well-preserved taphoflora in Bajo Comisión Stream. According to Baldoni & Ramos (1981) this apparent position is just topographic. They pointed out that this species occurs in the middle section of the Río Mayer Formation at that locality. The present author had the opportunity to study the specimen of *'A.' patagonicum* of Baldoni & Ramos (1981). It does not belong to *Helicancylus patagonicus* but to *Toxoceratoides nagerai* (see Fig. 17A–B), which actually occurs in the middle section of the Río Mayer Formation at the Puesto Bajo Comisión locality, well below the level with the flora.

At the locality La Muralla, which seems to be very close to the place where Halle collected his second specimen of *'A.' patagonicum*, this species is associated with *Peltocrioceras deeckei*. They were found in the uppermost section of the Río Mayer Formation. Although the latter species does not provide a precise age, its association with *Eogaudryceras (Eogaudryceras) hertleinei* (Wiedmann) at Puesto La Señalada and with *Acantohoplites (Nolaniceras) uhligi* (Anthula) at Vega Montes de Oca, together with stratigraphical evidence, points to an Upper Aptian age for the horizon of *Peltocrioceras deeckei* (Aguirre Urreta 1985).

The author also had the opportunity to study one beautifully preserved specimen of *Helicancylus patagonicus* collected by Piatnitzky. The latter stated (1936) that the specimen was found loose in the Cerro Pelado, in the Río Cardiel area. At that locality only the lower member of the Piedra Clavada Formation (Ramos 1982, fig. 2) is exposed. The lithology of the nodule in which the specimen is preserved confirms its origin. The Piedra Clavada Formation overlies the Río Mayer Formation comformably and has its chronological equivalent in the Kachaike Formation.

All this indicates that *Helicancylus patagonicus* is associated with *Peltocrioceras deeckei* and that it appears at some higher horizons. It means that we cannot rule out its possible presence in the Kachaike Formation, as was already stated by Halle (1913).

Helicancylus bonarellii (Leanza, 1970)

Fig. 13A–F

Leptoceras gr. *silesiacum* Uhlig: Bonarelli & Nágera, 1921: 18, fig. 3.
Leptoceras sp. Piatnitzky, 1938: 79, pl. 4 (fig. 20).
?*Ancyloceras patagonicum* Stolley: Howarth, 1958: 4, pl. 1 (fig. 4).
'*Ancyloceras*' *patagonicum* Stolley: Riccardi, 1968 *(pars)*, pl. 21 (fig. 1).
Acrioceras bonarellii Leanza, 1970: 209, fig. 6 (1).
Paraleptoceras singulare Leanza, 1970: 209, fig. 8 (5).
?'*Ancyloceras*' *patagonicum* Stolley: Thomson, 1974: 19, pl. 3 (figs c, g–h).

Holotype

The specimen figured by Bonarelli & Nágera (1921, fig. 3). Geological Survey Collection DNGM 9308 from locality Bahía de La Lancha (here referred to as La Federica), Lake San Martín, Río Mayer Formation. ?Upper Aptian.

Material

Apart from the holotype, MLP 17094–96 (collected by A. Riccardi), CORD–Pz 4360 (collected by M. Flores), MLP 16018a–b (collected by H. Arbe), CBPA 11065–6 from the same level and locality as the holotype. Río Mayer Formation. ?Upper Aptian.

Description

All the available specimens are crushed or preserved as impressions. Coiling is variable. On most of the specimens it is toxoceratid, but in some it is open crioceratitid with the whorls not touching. The most complete specimen (Fig. 13A) shows a small open spire followed by a gently curved shaft and a final recurved crozier. Nothing can be said about the whorl section as the specimens are extremely crushed.

Ornament consists of fine, simple, rounded ribs, separated by interspaces narrower than the ribs. On the initial spire rib density is about four per whorl height, on the shaft or at mid-growth stage (in specimens with crioceratitid coiling) it is about five, and at the final stage nine ribs are present per whorl

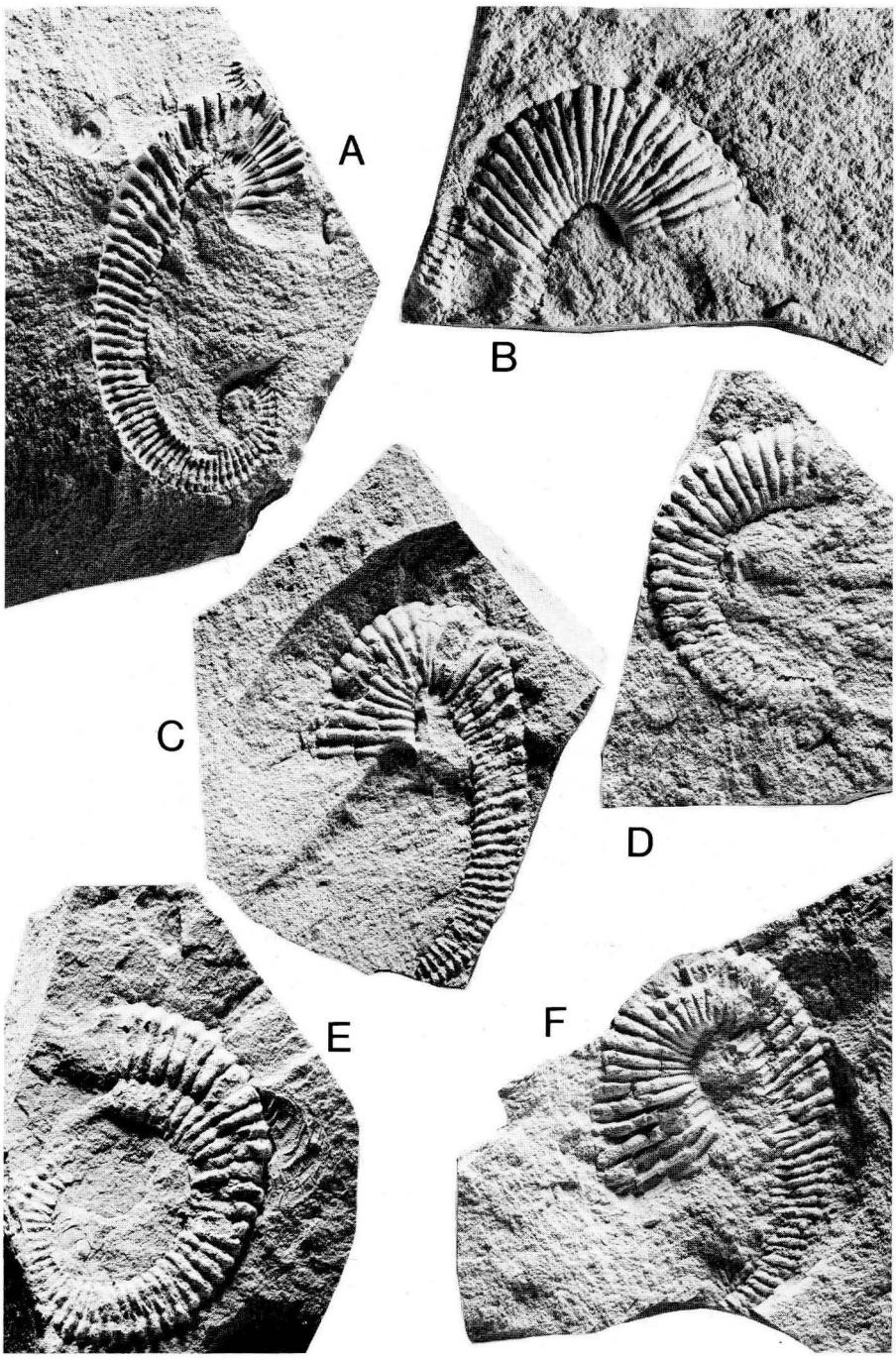

Fig. 13. *Helicancylus bonarellii* (Leanza). A. MLP 17094. B. CPBA 11065. C. MLP 16018a. D. MLP 16018b. E. MLP 17095. F. MLP 17096. All from La Federica. All × 1.

height. The ribs bear tubercles, but not only their number but also their appearance and disappearance are extremely variable. When present at the early stage, the tubercles are only ventral. As size increases, the ribs also show small ventrolateral and even smaller umbilical tubercles.

On the final hook the tuberculation gradually disappears and the ornament consists of simple, rounded radial ribs, which cross the venter apparently without interruption.

The suture line is unknown.

Dimensions

Specimen	L	H_M	H_O	H_m
MLP 17094	56,0	10,0	9,5	1,0
MLP 17096	50,0	17,0	9,0	4,0
MLP 16018*a*	53,0	13,0	8,5	4,0
MLP 17095*	47,0	16,5	—	5,5
MLP 16018*b*	38,0	7,0	—	3,0
DNGM 9308	—	20,0	13,0	6,0

* Specimens with crioceratitid coiling.

Discussion

Leanza (1970), when proposing this species, indicated that it belonged to the *'Leptoceras' silesiacum* group. He also pointed out that according to Anderson (1938) the species had to be referred to the genus *Acrioceras* Hyatt. Riccardi (1968) had already stated that Uhlig (1883) never included *'Crioceras' silesiacum* in his subgenus *Leptoceras*. It is irrelevant to discuss here the generic affinities of Uhlig's species, but it differs from the Patagonian material in the coiling and in the ornament of the shaft and final hook (Uhlig 1883: 142, pl. 28 (fig. 4)).

Helicancylus bonarellii differs from *H. patagonicus* in its smaller size and in its crioceratitid or toxoceratid instead of the latter's ancyloceratid coiling. The ornament of the former species consists of rounded, dense ribs with weak tubercles.

As stated before, the specimens illustrated by Thomson (1974, pl. 3 (figs c, g–h)) and referred to an indeterminate genus of the group *'Ancyloceras' patagonicum*, as well as the material figured by Howarth (1958, pl. 1 (fig. 4)) as *'A.' patagonicum*, show more similarities with *H. bonarellii* than with *H. patagonicus*. It is interesting to point out the close morphological resemblance between some specimens of *Antarcticoceras antarcticum* Thomson (1974: 20, pl. 3 (figs i–k, m–n)) and those of *H. bonarellii* with crioceratitid coiling.

Antarcticoceras antarcticum was first referred to an unknown genus of the subfamily Helicancylinae (Thomson 1971: 158) and afterwards to an uncertain family (Thomson 1974). Thomson was in doubt whether to assign this taxon to the Crioceratitidae or to the Ancyloceratidae. He stated that in the morphology of the shell the genus seems to be allied to the Crioceratitidae, but it also has some

non-crioceratitid features such as ribbing of similar size, a rather simple suture line and a high dorsolateral tubercle.

Further research on the possible relationships between the Antarctic specimens of *'Ancyloceras' patagonicum*, *Antarcticoceras antarcticum*, and the Patagonian *Helicancylus bonarellii* might be worthwhile.

Genus *Toxoceratoides* Spath, 1924

Type-species. Toxoceras royerianum d'Orbigny, 1842, from the Lower Aptian of France, by original designation (Spath 1924: 78).

Diagnosis

Coiling ancyloceratid or toxoceratid. Ornament of initial spire and shaft consists of trituberculate and intermediate ribs. On the final hook the ornament is simpler, with single ribs intercalated with others that bi- or trifurcate from an umbilical tubercle. Suture line with bifid saddles and trifid lobes.

Discussion

Spath (1924: 78) erected this genus without giving any diagnosis. Wright (1957: L212) doubtfully regarded *Toxoceratoides* as a synonym of *Hamiticeras*, taking into account that the type-species of the former genus was only known by fragments that do not allow a proper description.

Drushchits & Eristavi's (1958) first diagnosis of *Toxoceratoides* referred only to the coiling, suture line, and ornament of the shaft. Casey (1961: 77) accepted the validity of the genus and characterized it as: 'Coiling ancyloceratid or leptoceratid; may commence with a very small helix. Phragmocone ornamented as in *Ancyloceras*, with periodic trituberculate ribs. Final hook with close, narrow, sharp ribbing which bifurcates or trifurcates irregularly from an umbilical tubercle. Suture line as in *Ancyloceras*.'

Although Casey stated the presence of leptoceratid coiling in his diagnosis none of the species he refers to this genus actually shows it. The term 'leptoceratid coiling' is difficult to interpret as *Leptoceras* includes species with crioceratitid as well as open coiling. Thus it is preferable to use the term toxoceratid instead of leptoceratid coiling (Fig. 7E).

None of the species referred to *Toxoceratoides* shows any trace of an initial helix, except for a doubtful record of Day (1974: 13). Day identified three fragments as *Toxoceratoides?* sp. The present author had the opportunity to see plaster casts of two of them. The ornament as well as the coiling do not fit in *Toxoceratoides* and they may be inner whorls of a big ancyloceratid (e.g. *Peltocrioceras*). The third fragment, as seen in the illustration (Day 1974, pl. 1 (fig. 2)), shows a partially preserved initial helix followed by a shaft ornamented with narrow, close, non-tuberculate, sharp ribs—a feature not common in *Toxoceratoides*. Therefore the presence of an initial helix is ruled out in the present diagnosis of *Toxoceratoides*. If this feature proves to be present, it would be necessary to analyse the taxonomic position of this genus again, as the

presence of an initial helix is a typical feature of the nearly contemporaneous Heteroceratinae (Klinger 1976).

Klinger & Kennedy (1977: 307) partially accepted Casey's diagnosis; they pointed out the close relationship between *Toxoceratoides* and *Tonohamites*, and stated that species like *Tonohamites decurrens*, with strong trituberculation on the shaft, link both genera.

Later, Etayo Serna (1979: 20) proposed the subgenus *Colomboceratoides*, type-species *Toxoceratoides (Colomboceratoides) renzoni*, with the following diagnosis: 'Coiling as in *Toxoceratoides* but differs from the latter genus by the development of sculpture characterized by a retarded development of the subdue lateral trituberculation: early ribs without tubercles, followed by the appearance on both sides of venter of slender spines, subsequently lateral tubercles appear and much later the nipple-like peridorsal tubercles show up. The suture line is much simplified, it has massive subrectangular saddles and subtrifid L.'

According to Kakabadze (1981: 129) this subgenus is superfluous as its main characteristics are the same as those present in *Toxoceratoides*. The only apparent difference is the delayed appearance of the trituberculation, but this is a very variable character and it does not seem to have any specific value.

Toxoceratoides differs from *Tonohamites* mainly in the ornament of the final hook. In the latter genus tuberculation on the shaft is usually reduced but, as stated by Klinger & Kennedy (1977), species like *Tonohamites decurrens*, with a strong trituberculate phragmocone, show the close relationships between these two genera.

Hamiticeras has a *Toxoceratoides*-like shaft, but the final hook is long, parallel to the shaft, and the ribs are sharp, strong, single, and wide-spaced. These features are sufficient to distinguish the genera.

It is very difficult to find complete specimens of *Toxoceratoides*, perhaps due to their small size and open coiling. This has led to the erection of a large number of species in this genus. Some of these are monotypic or based on fragments, while others were erected in the nineteenth century and never restudied. There is no complete agreement between different authors as to which features are of specific value. The only distinct characteristics for specific separation are the coiling, whorl section, and the ornament of the body chamber. To a lesser degree, the ornament of the shaft can be used; little can be said about the initial spire as it is virtually unknown.

Species referred to or possibly belonging to *Toxoceratoides* are:

T. biplex (von Koenen) (1902: 381, pl. 41 (figs 3, 10a–b, 11a–b)).
T. biplicatum (von Koenen) (1902: 379, pl. 41 (figs 2a–b, 8a–b)).
T. caucasicus (Kasansky) (1914: pl. 1 (fig. 8a–c)).
T. corae Murphy (1975: 33, pl. 5 (figs 1, 5)).
T. emericianum (d'Orbigny) (1842: 487, pl. 120 (figs 5–9)).
T.? greeni Murphy (1975: 33, pl. 5 (figs 2–3, 6)).
T.? haughtoni Klinger & Kennedy (1977: 310, figs 59A–D, 60A–I, 61A–C, 62A–D, 63, 64A–C, 65A–B, 66B, 79A–B).

T. krenkeli Förster (1975: 160, pl. 4 (figs 1–2), text-fig. 33a–b).
T. nagerai (Leanza) (1970: 206, fig. 5 (1)).
T. obliquatus (Young & Bird) (1828: 278, pl. 18 (fig. 11)).
T. proteus (Spath) (1930: 461, pl. 16 (fig. 7)).
T. (Colomboceratoides) renzoni Etayo Serna (1979: 20, pl. 6 (fig. 19), text-fig. 3O–P).
T. rochi Casey (= *Ancyloceras royerianum* Roch, 1927: 30, pl. 1 (fig. 4)).
T. rotundus (Phillips) (1875: 264, pl. 1 (fig. 24)).
T. royerianus (d'Orbigny) (1842: 481, pl. 118 (figs 7–11)).
T. saulae Murphy (1975: 31, pl. 4 (figs 4, 6)).
T. seminodosus (Roemer) (1841: 93).
T. sheperdi (Spath) (1924: 173, figs 5–6).
T. starrkingi (Anderson) (1938: 207, pl. 59 (fig. 4–4A), pl. 45 (fig. 4A)).
T. subproteus Casey (1980: 651, pl. 103 (fig. 3)).
Toxoceratoides sp. 1 Murphy (1975: 35, pl. 6 (figs 1–2, 11)).
Toxoceratoides? sp. 2 Murphy (1975: 35, pl. 3 (fig. 6), pl. 6 (figs 5–6)).
Toxoceratoides sp. nov. Thomson (1974: 16, pl. 3 (figs a, d)).
Ancyloceras (Acrioceras) aff. *starrkingi* Anderson (Jeletzky 1964: 66, pl. 19 (fig. 2A–C)).
Toxoceratoides sp. 1 Martínez (1982: 140, pl. 24 (fig. 3a–c), text-fig. 21).
Toxoceratoides sp. 2 Martínez (1982: 141, pl. 24 (fig. 4a–d), text-fig. 22).
Toxoceratoides sp. 3 Martínez (1982: 142, pl. 24 (fig. 5a–d)).

Toxoceratoides biplicatum (von Koenen), referred to *Toxoceratoides* by Klinger & Kennedy (1977: 307), with bifurcate and ventrally tuberculate ribs on the shaft, is doubtfully included in this genus. According to Murphy (1975) *Ancyloceras (Acrioceras)* aff. *starrkingi* described by Jeletzky (1964) does not belong to Anderson's species and may be new.

Occurrence

Toxoceratoides occurs in Germany (Von Koenen 1902), Antarctica (Thomson 1974), Canada (Jeletzky 1964), Colombia (Etayo Serna 1979), Spain (Martínez 1982), California (Anderson 1938; Murphy 1975), France (D'Orbigny 1842; Roch 1927), England (Spath 1924, 1930; Casey 1961, 1980; Howarth 1962), Mozambique (Krenkel 1910; Haughton & Boshoff 1956; Wachendorf 1967; Förster 1975), Romania (Avram 1967*a*), south-western USSR (Kakabadze 1981), Zululand (Klinger & Kennedy 1977) and Patagonia (Leanza 1970; present paper).

Reports of *Toxoceratoides* from Australia are not accepted here. *'Ancyloceras' taylori* Etheridge, referred to *Toxoceratoides* by Whitehouse (1926), is believed to be a *Tonohamites* species, as discussed later in this paper. The fragments described by Day (1974) as *Toxoceratoides?* sp. seem to belong to more than one genus, but not to *Toxoceratoides*.

According to Casey (1961) *Toxoceratoides* ranges from the Upper Barremian to the Lower Aptian (*deshayesi* zone), and it appears to be replaced by

Tonohamites at the top of the Lower Aptian (*bowerbanki* zone). However, more recent publications (Klinger & Kennedy 1977; Etayo Serna 1979) show that *Toxoceratoides* ranges up to the Upper Aptian. In Patagonia this genus is present in deposits of Lower and Upper Aptian age.

Toxoceratoides nagerai (Leanza, 1970)

Figs 14, 15A–C, 16A–D, 17A–D

Leptoceras sp. indet. Bonarelli & Nágera, 1921: 19, fig. 4.
Helicancylus cf. *patagonicus* (Stolley): Leanza, 1970: 205, fig. 4 (1).
Acrioceras nagerai Leanza, 1970: 206, fig. 5 (1).

Holotype

An external mould found in a loose calcareous nodule in the bed of Fósiles River, Lake San Martín (Bonarelli & Nágera 1921: 19). It seems that the holotype is lost, but plaster casts are available (Geological Survey Collection DNGM 9297).

Material

Apart from a plaster cast of the holotype, CPBA 10880–81 from Río Cardiel; CPBA 10843 from Puesto La Señalada; CPBA 10830, 11061 from Puesto Bajo Comisión; and CORD–Pz 4368 from La Federica, Lake San Martín (collection Dr M. Flores). Río Mayer Formation. Lower–Upper Aptian.

Description

The very early stage of growth is unknown. The coiling is toxoceratid with an open initial spire followed by a slightly arcuate shaft and a recurved terminal hook (Fig. 14).

The whorl section is initially subquadrate or suboctagonal if measured over the trituberculate ribs (Fig. 15A–B). It is equidimensional or slightly compressed (Wh/Wb = 1,00–1,07) with a nearly flat dorsum and moderately curved flanks converging to a rounded venter. With increasing diameter, the whorl section becomes more rounded. On the body chamber it is nearly circular with inflated flanks converging to a broad rounded venter (Fig. 15C).

At the smallest diameter (3 mm) ornament consists of single, rounded ribs, bearing a small ventral tubercle and separated by wider interspaces. At a slightly larger diameter (6 mm), the ribs become differentiated and the ornament consists of alternating tuberculate ribs and non-tuberculate intermediaries, both of equal strength. With increasing diameter the tuberculate ribs become stronger and ventrolateral tubercles appear. One to five intermediate non-tuberculate ribs are present at this stage. At a larger diameter (10 mm) the ornament comprises fine intermediaries and strong trituberculate ribs, with small umbilical tubercles. The ribs pass straight, or bend forward in a gentle arc, over the dorsum and run prorsiradiate over the flanks; while the thin intermediaries cross the venter without interruption, the strong trituberculate ribs end on the ventral tubercle. Some ribs are duplicated over the dorsum and unite at the umbilical tubercle,

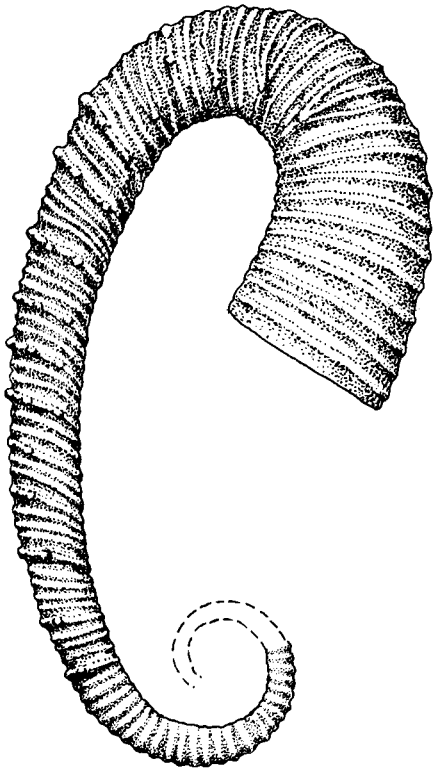

Fig. 14. Reconstruction of *Toxoceratoides nagerai* (Leanza).

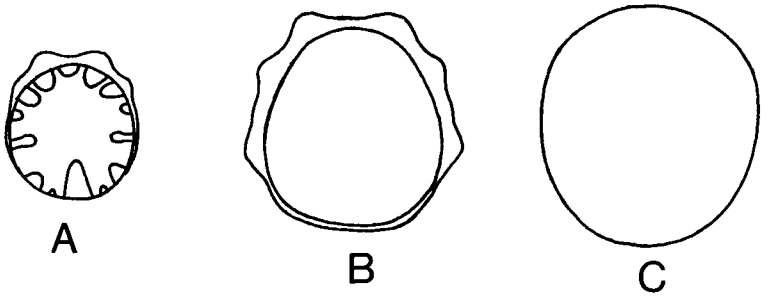

Fig. 15. Whorl section of *Toxoceratoides nagerai* (Leanza). A. CPBA 10881. B. CPBA 10843. C. CPBA 10880. All × 2.

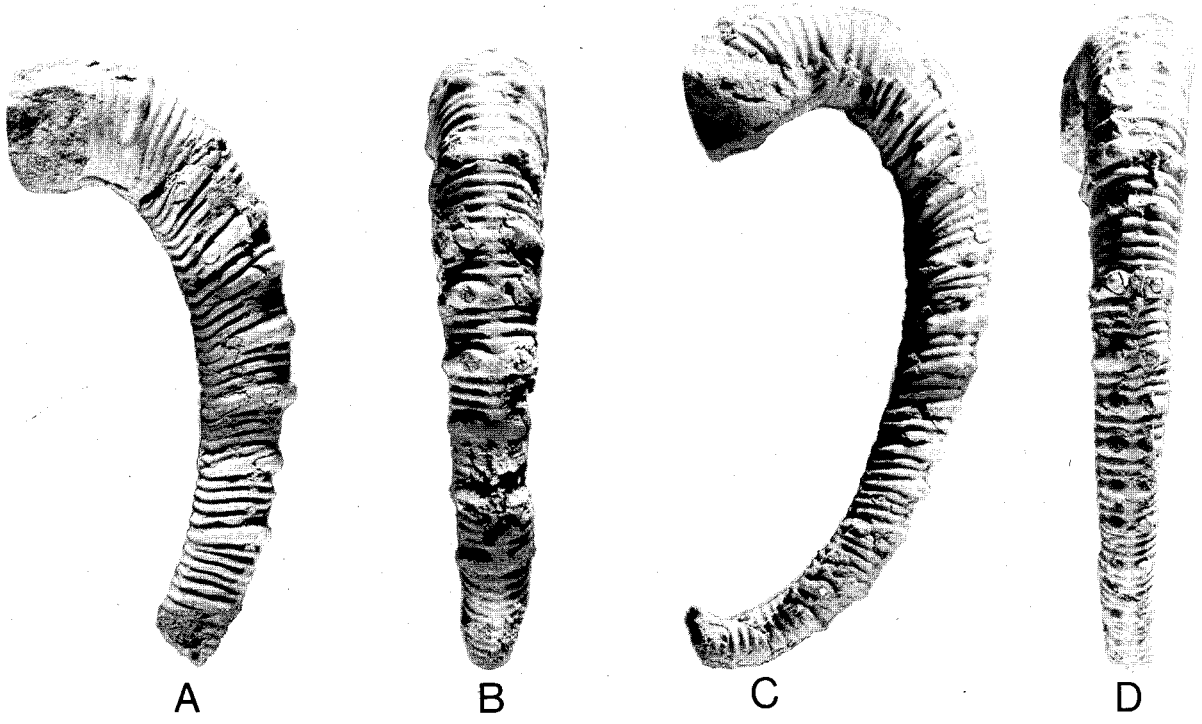

Fig. 16. *Toxoceratoides nagerai* (Leanza). A–B. CPBA 10880. C–D. CPBA 10881. Both specimens were found in the same calcareous nodule at Río Cardiel. All × 1.

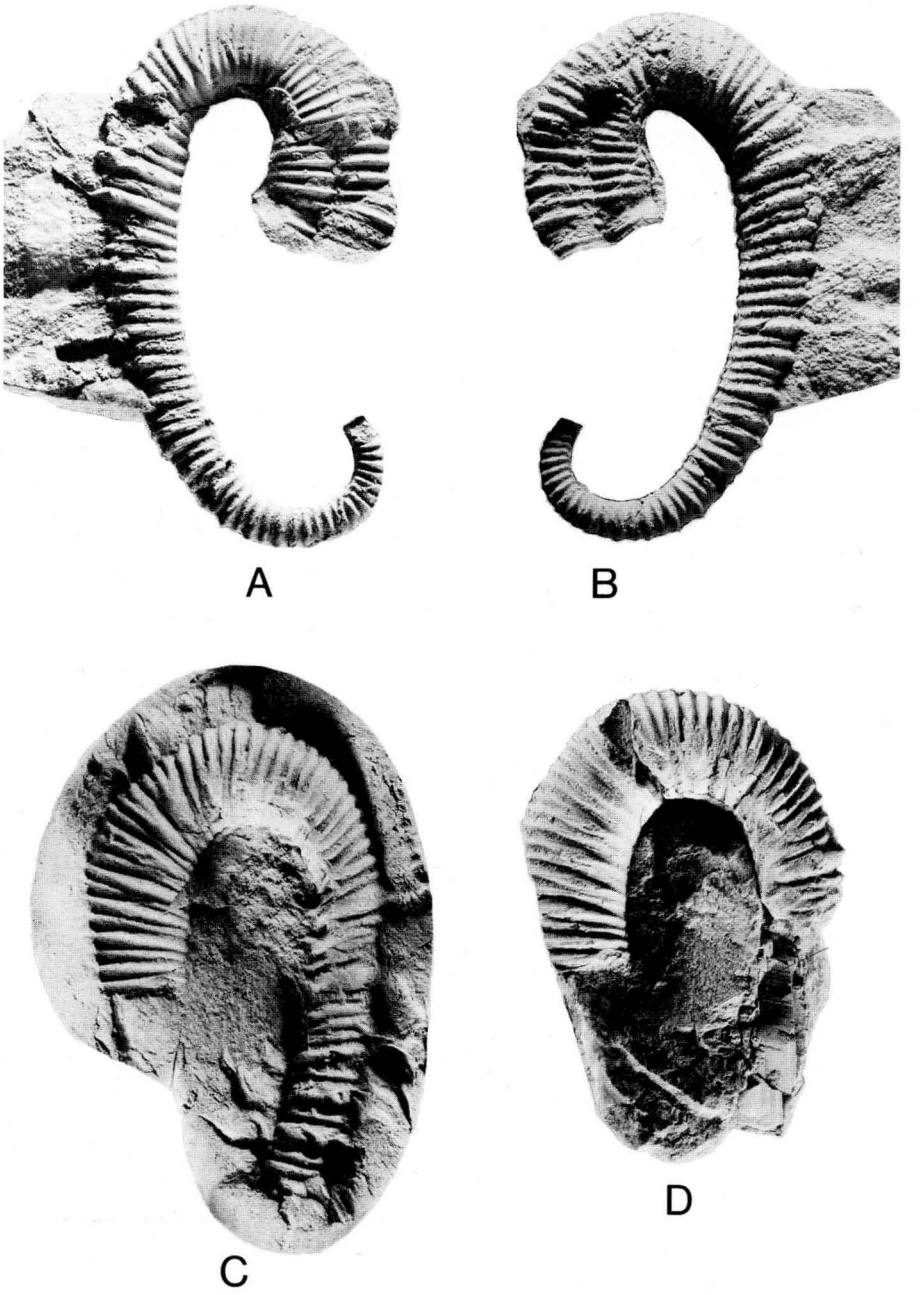

Fig. 17. *Toxoceratoides nagerai* (Leanza). A–B. CPBA 10830 from Puesto Bajo Comisión. C. Resin cast of CPBA 10843 from Puesto La Señalada after removing the calcite infilling the phragmocone. D. CPBA 10843. All × 1.

while others bifurcate on the umbilical wall and cross the flank as two fine intermediaries.

At the end of the shaft and beginning of the hook, the lateral and ventral tubercles disappear and the ornament changes to narrow, simple, sharp ribs that pass radially around the whorl and to ribs arising in groups of two or three from an umbilical tubercle. On the final hook these tubercles also disappear and the ribbing is simple.

The suture line is quite simple with trifid internal, umbilical, and lateral lobes.

Dimensions

Specimen	*L*	H_M	H_O	H_m
DNGM 9297	*c.* 80,0	22,0	9,0	5,5
CPBA 10880	*c.* 90,0	16,0	—	8,0
CPBA 10881	*c.* 88,0	14,0	—	5,5
CPBA 10830	69,0	*c.* 18,0	9,0	3,0

Discussion

Leanza (1970: 206) referred this species to the genus *Acrioceras*, pointing out that it belongs to the '*Ancyloceras*' *tabarelli* group (Uhlig 1883: 114, pl. 28 (fig. 2)). He also stated that the curved shaft resembles that of '*Ancyloceras*' *silesiacum* illustrated by Uhlig (1883: 142, pl. 28 (fig. 4)). Uhlig (1883), however, did not refer the latter species to '*Ancyloceras*' but to '*Crioceras*'. In any case, although *Acrioceras tabarelli* shows superficial similarities with *Toxoceratoides nagerai*, the coiling and ornament of the latter species plead for its attribution to *Toxoceratoides*.

Toxoceratoides royerianus has a depressed whorl section, with a flat dorsum and a shaft ornamented with alternate strong trituberculate ribs and fine intermediaries (Casey 1961: 80, pl. 6 (fig. 2a–b), pl. 17 (fig. 3a–b), text-fig. 30a–h), while *T. nagerai* has a compressed to equidimensional whorl section and more intermediate ribs on the shaft. Besides, the suture line of the first species is very incised, while in the latter it is quite simple.

Toxoceratoides rochi Casey is very close to *T. royerianus*, but differs from that species and from *T. nagerai* by the presence of very strong ribs on the final hook with very weak umbilical tubercles (Roch 1927: 30, pl. 1 (fig. 4)).

Toxoceratoides saulae Murphy, 1975, differs from *T. nagerai* mainly in having an ovoid, depressed whorl section and coarser trituberculate ribs on the end of the shaft.

Toxoceratoides krenkeli Förster (1975, pl. 4 (figs 1–2)) has a more depressed whorl section, mainly trituberculate ribs on the shaft with few intermediaries and coarse ribbing on the final hook.

Toxoceratoides proteus (Spath) shows lateral tubercles on the final hook from which the bifurcate ribs arise (Casey 1961: 82, pl. 10 (fig. 2a–c)). This feature allows an easy separation from all the other known species of the genus.

The shaft of *T. starrkingi* (Anderson) bears some resemblance to that of *T. nagerai*, but the final hook has not only umbilical but also lateral and ventral tubercles (Anderson 1938: 207, pl. 59 (fig. 4–4A), pl. 65 (fig. 4A)).

Tonohamites decurrens has a *Toxoceratoides*-like shaft, which resembles that of *Toxoceratoides nagerai*, especially in the number of fine intermediate ribs. However, both species are easily distinguished by the ornament of the final hook. In the former, there are radial, broad and rounded single ribs (Casey 1961: 80, pl. 5 (fig. 3a–b), pl. 21 (fig. 2)), while in *T. nagerai* the ribbing on the final hook is sharp, narrow and with some umbilical tubercles.

Leanza (1970, fig. 4 (1)) described a fragmentary specimen of *Helicancylus* cf. *patagonicus*. He stated the close similarities with Stolley's (1912, fig. 3–3a) *'Ancyloceras' patagonicum*. Although Leanza's specimen is poorly preserved, it shows umbilical tubercles on the bend of the hook, as well as bi- and trifurcate ribs. These features are not present in *Helicancylus patagonicus* and Leanza's specimen is therefore referred to *Toxoceratoides nagerai*.

Toxoceratoides cf. *biplex* (von Koenen, 1902)

Figs 18C–D, 19C

Compare:

Ancyloceras? biplex von Koenen, 1902: 381, pl. 49 (figs 10a–b, 11a–b).
Toxoceratoides cf. *biplex* (von Koenen): Casey, 1961: 83, pl. 20 (fig. 6).

Material

CPBA 10910 from Puesto Bajo Comisión, Lake San Martín. Río Mayer Formation. Upper Aptian.

Description

One specimen is available, consisting of the end of the shaft and final hook, and preserved as an internal cast partially covered with the original shell.

The whorl section on the earliest preserved part, which coincides with the end of the phragmocone, is depressed (Wh/Wb = 0,83), ovoid, with a flat dorsum, a broadly rounded umbilical edge, strongly inflated flanks, and a broadly rounded venter. The maximum width is at the dorsal third of the flanks. On the final hook the whorl section is more rounded, slightly depressed (Wh/Wb = 0,93) with a narrower dorsum, moderately inflated flanks converging to a rounded venter (Fig. 18C–D).

Ornament consists of fine, sharp, dense ribs. They run prorsiradiate over the flanks. On the bend of the crozier there are frequent low-angle bifurcations near the umbilical margin. On some ribs, slight tubercle-like elevations are present at the umbilical edge. Over the dorsum the ribs are reduced to striae with a forward flexure. The upper half of the flanks as well as the venter are heavily abraded, but it seems that the ribs cross the venter without interruption, and at the distal end they are simple, dense and radial.

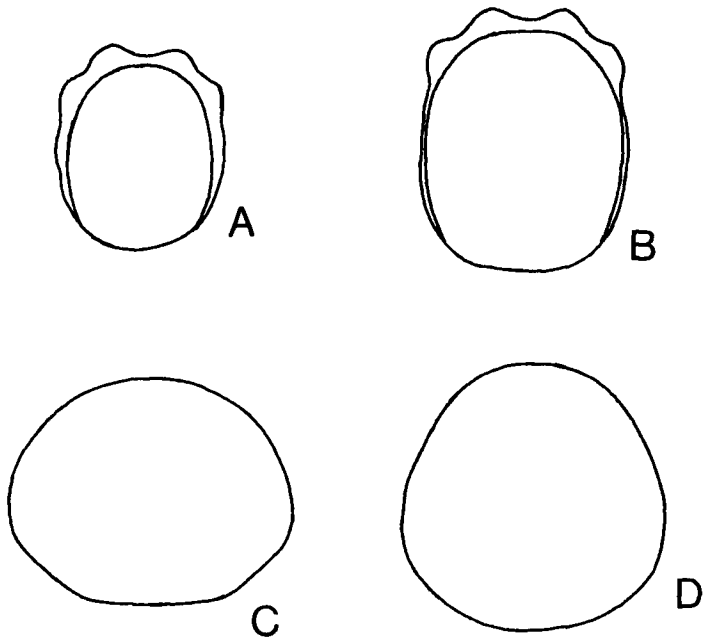

Fig. 18. A. Whorl section of *Toxoceratoides? haughtoni* Klinger & Kennedy, CPBA 10901. × 2. B. Whorl section of *Toxoceratoides?* sp., CPBA 11049. × 2,5. C–D. Whorl sections of *Toxoceratoides* cf. *biplex*, CPBA 10910. × 2,5.

Discussion

The single specimen compares well with that of Von Koenen (1902, pl. 49 (figs 10b–11b)) in ornament and whorl section, although the latter is more depressed and with the maximum width on the dorsal half of the flank. Von Koenen (1902: 381) indicated the presence of lateral tubercles, but did not illustrate these. In the Patagonian specimen faint elevations can be seen occasionally on some ribs where the original shell is still preserved.

Drushchits & Kudryavtsev (1960: 295, pl. 39 (fig. 3a–c)) described and figured two fragmentary specimens of *Leptoceras biplex* von Koenen. The presence of strong bituberculate ribs on the shaft and bifurcate ribs on the bend of the crozier casts doubt on the specific assignation of these specimens. According to Förster (1975: 162) the Russian material may belong to *Toxoceratoides fustiformis*. As the latter species does not have umbilical tubercles on the bend of the crozier and the shaft is ornamented with trituberculate ribs, it is doubtful that the Russian material can be assigned to *T. fustiformis* or to *T. biplex*.

Casey (1961: 83, pl. 20 (fig. 6)) referred a small fragmentary specimen to *T.* cf. *biplex*, which resembles the one here described. According to him, the most characteristic feature of this species is the presence of 'fine, sharp, wiry ribbing'.

Toxoceratoides? haughtoni Klinger & Kennedy, 1977

Figs 18A, 19H–J

Toxoceratoides? haughtoni Klinger & Kennedy, 1977: 310, figs 59A–D, 60A–I, 61A–C, 62A–C, 64A–C, 66B, 79A–B.

?*Toxoceratoides (Colomboceratoides) renzoni* Etayo Serna, 1979: 20, pl. 6 (fig. 19), text-fig. 3O.

Holotype

SAS 64/T_1 from locality 168, Mfongozi Creek, northern Zululand, Aptian III–IV (Upper Aptian). South African Geological Survey Collection, Pretoria. Collected by H. Klinger, 1970.

Material

CPBA 10901 from La Horqueta, Cardiel River (collection Lic. G. Marín), and CPBA 10849 from Puesto La Señalada, Lake San Martín. Río Mayer Formation. Upper Aptian.

Description

Both specimens are fragments of curved shafts. The whorl section is initially subcircular, slightly compressed (Wh/Wb = 1,07) with a feeble convex dorsum and rounded flanks converging to a flattened venter. As size increases the whorl section becomes more laterally compressed (Wh/Wb = 1,25) (Fig. 18A).

At the smallest diameter (Wh = 7,5 mm) ornament consists of single rounded ribs, slightly prorsiradiate and with rounded ventral tubercles, which are marginal to a siphonal depression. At this stage small ventrolateral tubercles can also be seen. At a diameter of 10 mm there are two kinds of ribs; some are fine, non-tuberculate, and the others are strong, high with ventrolateral and ventral tubercles. Both types alternate regularly. While the first type crosses the venter without interruption, the second one ends on both sides of a siphonal depression. Both cross the dorsum straight or slightly curved and run prorsiradiate over the flanks.

Some of the strong ribs duplicate from the ventrolateral tubercle and on the lower flank and dorsum they form two fine ribs, while between the ventrolateral and ventral tubercle there is only a single flat and broad rib. At large diameters, the intercalatory ribs disappear.

The suture line cannot be traced on the present material.

Discussion

The shaft fragments correspond well with those of Klinger & Kennedy (1977). These authors assigned this species to *Toxoceratoides* with doubt because of the peculiar ornament of the early whorls as well as the absence of simple ribbing on the recurved crozier. According to Klinger & Kennedy (1977) those atypical features serve to distinguish *T.? haughtoni* from other species assigned to

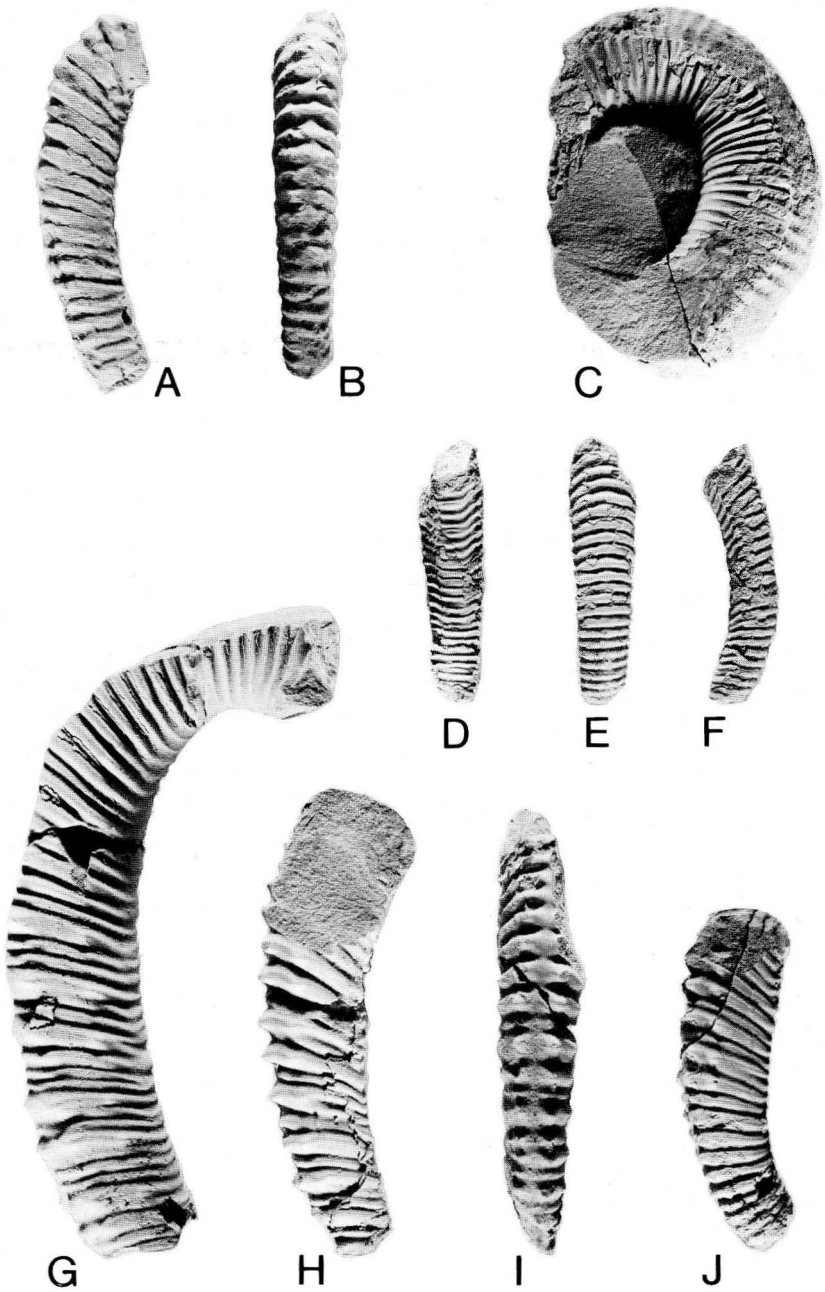

Fig. 19. A–B. *Helicancylus patagonicus* (Stolley), CPBA 10898 from Puesto La Señalada. C. *Toxoceratoides* cf. *biplex*, CPBA 10910 from Puesto Bajo Comisión. D–F. *Tonohamites aequicingulatus* (von Koenen), CPBA 11897 from Loma Pelada. G. *Toxoceratoides?* sp., CPBA 11049 from Puesto La Señalada. H–J. *Toxoceratoides? haughtoni* Klinger & Kennedy. H–I. CPBA 10849 from Puesto La Señalada. J. CPBA 10901 from La Horqueta. All × 1.

this genus. Unfortunately neither the early whorls nor the final hook are preserved in the Patagonian material.

Toxoceratoides krenkeli is to some extent a comparable species, as the ornament on the shaft is similar to that of *T.? haughtoni*. However, the former species has a depressed whorl section and the tuberculation appears at a very small diameter (Förster 1975; Klinger & Kennedy 1977).

Etayo Serna (1979) proposed a new subgenus and new species of *Toxoceratoides: T. (Colomboceratoides) renzoni*. The ornament and whorl section of the single fragment of this species shows close similarities to *T.? haughtoni*, so that *T. renzoni* may be a junior synonym.

Occurrence

Toxoceratoides? haughtoni occurs in the Upper Aptian of Zululand and Patagonia.

Toxoceratoides? sp.
Figs 18B, 19G

Material

CPBA 11049 from Puesto La Señalada, Lake San Martín. Río Mayer Formation. Upper Aptian.

Description

The single fragment is 80 mm long and comprises the upper part of the shaft (55 mm) and the beginning of the final hook. The ventral region is heavily abraded.

At the smallest diameter (Wh = 14 mm) the whorl section is ovoid, laterally compressed (Wh/Wb = 1,27) with a feeble convex dorsum, slightly curved flanks and rounded venter. The whorl section, measured over a tuberculate rib, is subhexagonal (Fig. 18B). As size increases, the whorl section becomes more rounded.

The shaft is ornamented with strong tuberculate ribs and thin non-tuberculate intermediaries, which are arranged in an irregular pattern. Both types cross the dorsum with a forward curvature, are prorsiradiate over the flank and straight over the venter, where the strong ribs are interrupted. The ribs show two rows of tubercles: one ventral and the other ventrolateral. On the upper part of the shaft some bear a third row of small tubercles near the umbilical edge.

As in *Toxoceratoides? haughtoni*, some of the strong ribs are duplicated at the ventrolateral tubercle and cross the dorsum as two fine single ribs; between the tubercles they are broad and flat. Only the dorsolateral part of the end of the shaft and the beginning of the crozier is preserved. The ornament consists of single, fine, narrow, dense, non-tuberculate ribs. There is no indication of umbilical tuberculation.

The suture line, partially exposed, shows relatively high elements and it is quite incised, with trifid lateral, umbilical, and internal lobes.

Discussion

Generic allocation of the specimen is difficult as it shares characteristics of *Toxoceratoides* and *Tonohamites*.

The absence of umbilical tubercles on the bend of the crozier and the ornament of single ribs are features of *Tonohamites* rather than of *Toxoceratoides*. However, in the former genus the ribs are usually broad and rounded, not thin and sharp as in the Patagonian specimen. The shaft ornament is more *Toxoceratoides*-like, but not typical if compared with species like *Toxoceratoides royerianus* (Casey 1961: 78, pl. 6 (fig. 2)) or *T. krenkeli* (Förster 1975: 160, pl. 4 (figs 1–2)). Besides, *Tonohamites decurrens* has the shaft ornamented as in *Toxoceratoides*, which shows the close relationship between both genera, as stated by Klinger & Kennedy (1977: 319).

The only feature that allows a comparison with another species is the longitudinal duplication of the strong ribs. This character is also present in *Toxoceratoides? haughtoni*. Both species differ markedly in the ornament of the bend of the crozier.

Finally, *Tonohamites* and *Toxoceratoides* show a typical ancyloceratid pattern in the suture line, with bifid saddles and trifid lobes, but the former usually has low, simple elements while in the latter the suture line may be more incised with relatively higher elements.

Based on the suture line and to a lesser extent on the ornament of the shaft, the present fragment is referred with doubt to *Toxoceratoides*, aware that the ornament of the final hook is atypical.

Genus *Tonohamites* Spath, 1924

Type-species. Tonohamites decurrens Spath, 1924, from the Lower Aptian of Germany, by original designation.

Diagnosis

Coiling toxoceratid or labeceratid. Ribbing usually rounded, tuberculation may be present, but the tubercles are weak and mostly confined to the venter. On the body chamber the ribs are simple, strong, rounded or flat and non-tuberculate. Suture line simple, with bifid saddles and trifid lobes.

Discussion

The type-species of this genus is difficult to interpret, and nomenclatural problems are involved. Casey (1961: 84) extensively discussed this point. Wright (1957: L212) regarded *Tonohamites* as a synonym of *Hamiticeras*, while Casey (1961: 84) maintained the genus and gave the first diagnosis.

The type-species of *Tonohamites* does not show the main features present in other species assigned to this genus. In fact, the ornament of the shaft, with strong trituberculate ribs, closely resembles that of *Toxoceratoides* and isolated fragments can hardly be distinguished. However, the ornament of the body

chamber of *Tonohamites*, with broad, rounded, or flat ribs, allows an easy separation from *Toxoceratoides*, which shows fine, sharp, single ribs intercalated with bi- or trifurcate ones arising from umbilical tubercles on the final hook.

Hamiticeras Anderson, as interpreted here, differs from *Tonohamites* in its coarse trituberculate and intermediate ribs on the shaft and its long, parallel final hook with radial, sharp, high ribbing.

Helicancylus Gabb, redefined here, is easily distinguished from *Tonohamites* by the complete lack of minor ribbing, and the presence of tubercles on every rib on the shaft and on the recurved crozier.

According to Klinger & Kennedy (1977), Casey (1961) referred the following species to *Tonohamites*:

Tonohamites decurrens Spath (1924: 85). (Lectotype is the specimen illustrated by Von Koenen 1902, pl. 33 (fig. 2, and the lower part of fig. 3a).)
Tonohamites aequicingulatus (von Koenen) (1902: 394, pl. 37 (figs 5a–c, 6a–e)).
Tonohamites? hunstantoniensis Casey (1961: 90, pl. 21 (fig. 1a–d)).
Tonohamites koeneni Casey (1961: 89). (Holotype is the specimen illustrated by Von Koenen 1902, pl. 33 (fig. 3a, upper part only).)
Tonohamites limbatus Casey (1961: 89, pl. 21 (fig. 3a–b), pl. 22 (figs 3a–c, 4)).
Tonohamites? eichwaldi (Jasykow) (*in* Sinzow 1872: 36, pl. 6 (figs 7–9)).
Tonohamites? undosus (von Koenen) (1902: 393, pl. 35 (fig. 13a–f)).

It is interesting to mention that Casey (1961) noted similarities between some fragments of *Tonohamites aequicingulatus* and *Hamites? undosus* von Koenen. He also indicated that the latter species is only known by a small fragment of the shaft and that it is really difficult to decide whether it is a separate species. Finally, Casey decided to join all the fragments as belonging to a single, variable species and placed *T.? undosus* as a possible synonym of *T. aequicingulatus*.

To the list given above must be added *Tonohamites? caseyi* Klinger & Kennedy (1977: 324, figs 46, 49) and perhaps *Tonohamites? taylori* (Etheridge). Etheridge (*in* Jack & Etheridge 1892: 498, pl. 42 (fig. 13)) described and figured one specimen of *'Ancyloceras' taylori* showing a tightly coiled initial spire followed by a straight shaft, both ornamented with simple annular ribs. Later the same author (Etheridge 1909: 162, pl. 49 (figs 3–6)) included that fragment with other specimens and described them all as *'Crioceras' taylori*.

The type specimen of *'Ancyloceras' taylori* was placed in *Toxoceratoides* by Whitehouse (1926), who figured a small additional fragment, while the specimens of *'Crioceras' taylori* were included in the Albian genus *Labeceras* Spath.

Finally Day (1974: 14) noted that *'Ancyloceras' taylori* might be placed more suitably in *Tonohamites* than in *Toxoceratoides*. This view is supported by the *Tonohamites*-like ornament of the small fragment illustrated by Whitehouse (1926: pl. 36 (fig. 5)).

Kakabadze (1981) recorded *Tonohamites picteti* (Ooster) from the Lower Aptian of southern USSR. As he did not describe nor figure the specimens, it is not possible to decide if they belong to this genus or not. Ooster's (1857, pl. 50 (figs 1–6)) type specimen of *'Ancyloceras' picteti* does not resemble *Tonohamites*.

Specific differentiation within the genus *Tonohamites* is rather difficult, especially when dealing with fragments. It is based mainly on the coiling, ornament, and whorl section.

Occurrence

Tonohamites occurs in the Lower Aptian of Germany (Von Koenen 1902), Spain (Martínez 1982), England (Casey 1961), and ?southern USSR (Kakabadze 1981). It also occurs in the Upper Aptian of Madagascar (Collignon 1962) and Zululand (Klinger & Kennedy 1977). This is the first record from Patagonia (see Fig. 8).

Tonohamites aequicingulatus (von Koenen, 1902)

Fig. 19D–F

Hamites aequicingulatus von Koenen, 1902: 394, pl. 37 (figs 5a–c, 6a–e).
Tonohamites aequicingulatus (von Koenen): Casey, 1961: 87, pl. 9 (figs 2a–b, 3a–b, 4), text-fig. 32. Klinger & Kennedy, 1977: 322, figs 38C, 68A–E, 88D.
Tonohamites sp. aff. *aequicingulatus* (von Koenen): Collignon, 1962: 14, pl. 221 (fig. 960).

Lectotype

The original of Von Koenen (1902, pl. 37 (fig. 5a–c)) from the Lower Aptian of northern Germany, by subsequent designation of Casey (1961: 87).

Material

CPBA 11897 from Loma Pelada, Tucu-Tucu. Río Belgrano Formation. Lower Aptian.

Description

The small part of a shaft, 35 mm long and preserved as an internal cast, is partially covered with the original shell.

The whorl section is ovoid, depressed (Wh/Wb = 0,75–0,77), with flat dorsum, slightly convex flanks, and broadly rounded venter. Ornament consists of annular, rounded ribs. They are nearly radial on the dorsum and prorsiradiate on the flanks. There are four ribs within a distance equal to the whorl diameter. In the early stage some ribs bear siphonal, lateral and umbilical tubercles; these are very small and rounded and disappear with increase in size.

The partially exposed suture line is simple with asymmetrical lateral lobe.

Discussion

As Casey (1961: 88) noted, this species is only known from fragments. The Patagonian specimen resembles both the European (Von Koenen 1902; Casey 1961) and Zululand (Klinger & Kennedy 1977) material. The only apparent difference between those specimens and the present fragment is that in the latter some early ribs bear three rows of tubercles, whilst the figured specimens show none or a ventral row only (Von Koenen 1902, pl. 37 (fig. 5); Casey 1961, pl. 9 (fig. 2b), text-fig. 32b).

The Madagascan specimen figured by Collignon (1962, pl. 221 (fig. 960)) shows a more rounded whorl section and the ribs are stronger. It has tentatively been referred to this species.

Tonohamites decurrens Spath has strong trituberculate ribs separated by intermediaries on the shaft (Casey 1961: 86, pl. 21 (fig. 2), pl. 5 (fig. 3a)). *Tonohamites limbatus* Casey has a slightly compressed subrectangular whorl section and strongly prorsiradiate, narrow ribs (Casey 1961: 89, pl. 20 (figs 3a–c, 4)).

According to Klinger & Kennedy (1977: 322) the body chamber of *T. koeneni* Casey resembles that of *T. aequicingulatus*, but the latter species shows ventral tubercles on the shaft.

Martínez's (1982: 142, pl. 24 (fig. 6a–b), text-fig. 23) small shaft fragment referred to *Tonohamites* sp. has comparable ornamentation and whorl section. It differs, however, in its more simple suture line at the same diameter.

Occurrence

Tonohamites aequicingulatus is known from the Aptian of Germany (Von Koenen 1902) and Lower Aptian (*bowerbanki* zone) in England (Casey 1961). The Madagascan and Zululand specimens are from the Upper Aptian (Collignon's (1962) *Aconeceras nisus* and *Melchiorites melchioris* zone, and Kennedy & Klinger's 1975 Aptian III–IV—see Klinger & Kennedy (1977)).

CONCLUDING REMARKS

The most important results of this study are:

— The redefinitions of *Helicancylus* (type-genus of the subfamily Helicancylinae) and of *Hamiticeras* clarify the systematics of the subfamily Helicancylinae.

— *Helicancylus*, as here interpreted, accommodates some species (one of which is *Helicancylus patagonicus*) of hitherto uncertain affinities.

— The systematic study allows the recognition of three genera of this subfamily in the Austral Basin: *Helicancylus*, *Toxoceratoides* and *Tonohamites*. They are recorded for the first time in this basin. Seven species have been identified.

— The representatives of this subfamily are locally common in several horizons of the Río Mayer Formation and in one level of the Río Belgrano; all are of Aptian age. Their recognition means an important increase in our knowledge of the Aptian biostratigraphy of the northern part of the Austral Basin.

— The identified fauna facilitates the correlation with previously known assemblages, especially from western Europe and south-eastern Africa.

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