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Tithonian–Berriasian ammonites from the Baños del Flaco Formation, central Chile

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The Baños del Flaco Formation in central Chile contains abundant and well-preserved Tithonian (Late Jurassic) and scarce Berriasian (Early Cretaceous) ammonites. At Rio Maitenes in Curicó Province an assemblage referred to 10 genera and 12 species is here described. *Windhauseniceras internispinosum*, *Corongoceras alternans* and *Substeueroceras koeneni* were mentioned previously, but not described and discussed. *Aulacosphinctes proximus*, *Micracanthoceras spinulosum* and *Corongoceras evolutum* are new records for the Baños del Flaco Formation. *Pseudolissoceras* cf. *zitteli*, *Lithacoceras malarguense*, *Choicensisphinctes windhauseni*, *Catutosphinctes* cf. *americanensis*, *Virgatosphinctes scythicus* and *Micracanthoceras microcanthum* are documented in Chile for the first time. *Micracanthoceras spinulosum* shows strong ontogenetic changes. *Virgatosphinctes scythicus* is a morphologically variable species and is synonymous with the South American species *Virgatosphinctes andesensis*, *V. mendozanus*, *V. mexicanus* and *V. leñaensis*. *Windhauseniceras internispinosum* is relatively abundant at Rio Maitenes but rare elsewhere; its morphology varies considerably during ontogeny. *Virgatosphinctes* aff. *pseudolictor* and *V.* cf. *raja*, both recorded from Argentina, and *V. guadalupensis*, are synonymous with *L. malarguense*; *V. tenuilineatus* is synonymous with *C. windhauseni* and *Aulacosphinctes chilensis* with *A. proximus*. *Micracanthoceras lamberti* and *M. tapiai* are junior synonymies of *M. microcanthum. Windhauseniceras internispinosum* and *Corongoceras alternans* are Tithonian index fossils for Chile and Argentina, whereas *Virgatosphinctes scythicus* and *Micracanthoceras microcanthum* are Tithonian index fossils for the Russian platform and Tethys, respectively. Their co-occurrence at Río Maitenes confirms that most of the Baños del Flaco Formation is Tithonian (Upper Jurassic). However, the presence of *Substeueroceras koeneni* demonstrates that the uppermost strata of the Baños del Flaco Formation should be referred to the Lower Cretaceous (Berriasian).

Keywords: Andes; Jurassic; Cretaceous; ammonites; biostratigraphy; palaeobiogeography

Introduction

In central Chile, Upper Jurassic rocks are exposed in a north–south belt in the High Andes, extending from Santiago in the north, to Curicó in the south (Fig. 1). The Tithonian sedimentary rocks are known as the San José, Lo Valdés and Baños del Flaco formations (e.g. Corvalán 1956; Klohn 1960; González 1963; Biro 1964; Covacevich *et al.* 1976). The Baños del Flaco Formation is well developed in the Baños del Flaco area, which is located in the valley of the Río Tinguiririca, Colchagua Province, and along the Río Maitenes, tributary of the Río Teno, Curicó Province (Fig. 1). These sections are named Rio Maitenes and Baños del Flaco (respectively RM and BF in Fig. 1). Fossils are rare at Baños del Flaco, but more abundant at Rio Maitenes. It is from this latter section that the ammonites described and discussed here were collected. The Río Maitenes section is an open pit, called 'Minera el Fierro' that belongs to the 'Cementos Bio Bio' company. This section was described in detail and the fossils were collected bed-by-bed in 1964 by Mr Lajos Biro whose field notebook was available to us and who allowed the section to be reconstructed. Except for the echinoderms (Larrain & Biro 1985), the fossil material is undescribed and/or unpublished.

Previous work

The Baños del Flaco Formation was defined by Klohn (1960). It is composed of marine fossil-bearing grey limestone, sandy limestone, calcareous sandstone, and minor conglomerate, glauconitic sandstone and siltstone. Klohn (1960) and Covacevich *et al.* (1976) focused on the lithofacies within the lower part of the formation and recorded the fossil content. Additional lithological aspects were treated in unpublished reports by Chilean cement mining

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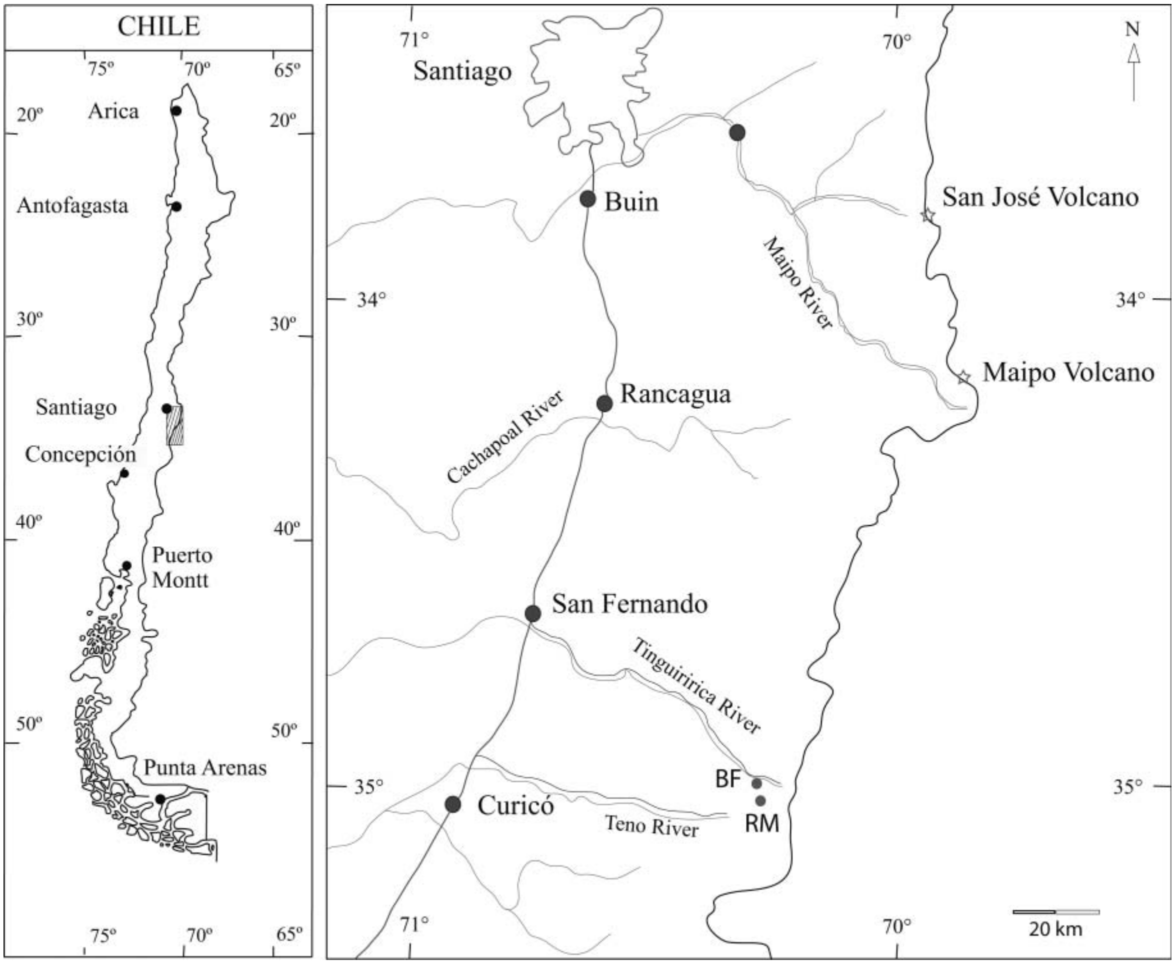

Figure 1. Map of Chile showing the location of outcrops of the Baños del Flaco Formation. Abbreviations: BF, Baños del Flaco type locality; RM, Rio Maitenes section.

companies and in university theses (e.g. Arcos 1987; Zapata 1995).

Fossils from the area were first published by Domeyko (1862), who considered the sediments as Lower Jurassic. Philippi (1899) described several fossil taxa from the Tinguiririca area in the high Andes, interpreting the fossil-bearing unit to range from Lower Jurassic to Lower Cretaceous. Klohn (1960) collected fossils along the south side of the Tinguiririca River and at Rio Maitenes (RM). The assemblage he collected was described by Corvalán (1956) who referred the Baños del Flaco Formation to the Tithonian–Hauterivian (i.e. from the uppermost Jurassic to the Lower Cretaceous). Based on ammonite assemblages, Covacevich *et al*. (1976) restricted the lower part of the formation to the Tithonian, while Hallam *et al.* (1986) considered the Rio Maitenes section to extend from the lower middle Tithonian into the Berriasian.

These articles do not include detailed taxonomic descriptions or illustrations of the fossils. So far, only Larrain & Biro (1985) figured some echinoderms, including the species *Pygurus (P.) andinus*. Moreno & Pino (2002) and Moreno & Benton (2005) reported on the occurrence of sauropods from the south side of the Tinguiririca River.

The aim of this paper is to describe systematically the ammonites collected from the area and to correlate the fauna to other regions.

Geological setting and localities

Upper Jurassic sediments are widespread in the Tinguiririca River and along the Maitenes River. The oldest unit known from the area is the Nacientes del Teno Formation (?Bajocian, Bathonian to Oxfordian; Klohn 1960), which consists of conglomerate, sandstone, siltstone, limestone, marl, gypsum and pyroclastic rocks. The Nacientes del Rio Teno Formation is overlain conformably by the Rio Damas Formation (Kimmeridgian), which is a unit composed of continental, siliciclastic sediments and andesite (Klohn 1960). The Baños del Flaco Formation conformably overlies the Rio Damas Formation and represents an open marine phase in the Tithonian, possibly extending across the Jurassic–Cretaceous boundary.

The contact between Baños del Flaco Formation and the overlying lithological unit is disconformable and lithologically variable. In some localities it is marked by a lenticular unit of white tuff, while in other areas by a brown to red siliciclastic unit. Klohn (1960) interpreted this unit as the lower continental member of the Coya Machalí Formation. Upsection, Upper Cretaceous volcanic rocks and intercalated limestone were also assigned to the Coya Machalí Formation (Klohn 1960; Zapatta 1995).

At Rio Maitenes (Fig. 1), strata of the Baños del Flaco Formation strike 12° NE and dip 45–50°W, conformably overlying Kimmeridgian siliciclastic sediments and volcanic rocks of the Rio Damas Formation. The Baños del Flaco Formation is 536 m thick and is here subdivided into two informal members, lower and upper, based on lithological characteristics.

The lower member is 325 m thick (Fig. 2). The lowermost 50 m is a basal conglomerate, composed of subrounded volcanic rock fragments and quartz. Upsection, a 53-m-thick interval of layered calcareous sandstone and sandy limestone is present and contains ammonoids, oysters, trigoniids and other bivalves, rare gastropods and corals. Overlying this unit, a 21-m-thick grainstone contains scarce oysters, inoceramids, trigoniids, other bivalves and gastropods. This is followed by a 91-m-thick unit of sandstone and intercalated calcareous sandstone, with ammonoids, oysters, inoceramids, trigoniids and other bivalves, gastropods and rare algae. The sandstone unit underlies 60 m of calcareous sandstone and intercalated limestone, with scarce ammonoids, oysters, inoceramids, trigoniids, other bivalves, gastropods and the echinoid *Pygurus (P.) andinus.* The lower member is capped by a sandy limestone, 50 m thick, in which ammonoids, oysters and other bivalves occur but are rare.

The upper member is 192 m thick (Fig. 2). A 22-m-thick unit of siltstone with rare fragments of ammonoids and bivalves is overlain by a 57-m-thick calcareous sandstone containing ammonoids. Upsection, a 107-m-thick unit consists of intercalated sandy limestone, limestone and sandstone with scarce ammonoids, inoceramids and other bivalves. The top of the upper member is 25 m thick and consists of calcareous sandstone with rare fragments of oysters and other bivalves (Fig. 2).

Material and methods

The description of the Rio Maitenes section is based on the notes from the fieldnote book of Lajos Biro. The Rio Maitenes ammonite assemblage described here is based on 243 well-preserved specimens. They are all internal moulds and most preserve the ornamentation. Preservation is in three dimensions and deformation is minor. Suture lines are not observable. The material described and discussed here consists of specimens collected in the 1960s by the late Lajos Biro from the Baños del Flaco Formation at Rio Maitenes (RM in Fig. 1).

Figured ammonites were coated with magnesium oxide prior to photography, except where otherwise indicated. They were analysed at the Institut für Geowissenschaften, Universität Heidelberg, Germany, with the authorization of the Chilean *Monumentos Nacionales* council, and are currently deposited at the Departamento Ciencias de la Tierra, Universidad de Concepción, Chile.

Systematic nomenclature follows the *Treatise on Invertebrate Palaeontology* (Arkell *et al.* 1957; Wright *et al.* 1996) to the genus level, and *Fossilium catalogus I: Animalia, Lower Cretaceous Ammonites I* (Klein 2005). For *Lithacoceras* and *Choicensisphinctes*, the interpretations of Parent (2011a) are followed; for *Catutosphinctes* the recommendations given by Leanza & Zeiss (1992) are followed.

All dimensions are given in millimetres. Uncertain values due to deformation of specimens and ratios resulting from uncertain measurements are in brackets.

Morphological abbreviations

D: diameter; **W**: whorl width; **H**: whorl height; **U**: umbilical.

Repository abbreviations

CPUC: Colección Paleontológica, Universidad de Concepción (followed by the code of the section from which the fossils were collected (RM: Rio Maitenes) and the registered number, e.g. CPUC/RM/65–45) (Concepción, Chile); **UWBM**: University of Washington Burke Museum (Seattle, Washington State, USA); **SGN**: Servicio Geológico Nacional República Argentina (Buenos Aires, Aregntina); ГГМ.экз: Новости из Геологического музея им. В. И. Вернздского (Vernandsky State Geological Museum), Moscow, Russia; **GZG**: Geowissenschaftliches Zentrum, Göttingen, Germany; **STIPB**: Steinmann–Institut für Geologie, Mineralogie und Paläontologie, Bonn, Germany; **SNGM**: Servicio Nacional de Geología y Mineria de Chile (Santiago, Chile); **NHMUK**: Natural History Museum, London, UK.

Systematic palaeontology

Order **Ammonoidea** Zittel, 1884
Suborder **Ammonitina** Hyatt, 1889
Superfamily **Haploceratoidea** Zittel, 1884
Family **Haploceratidae** Zittel, 1884
Genus ***Pseudolissoceras*** Spath, 1925

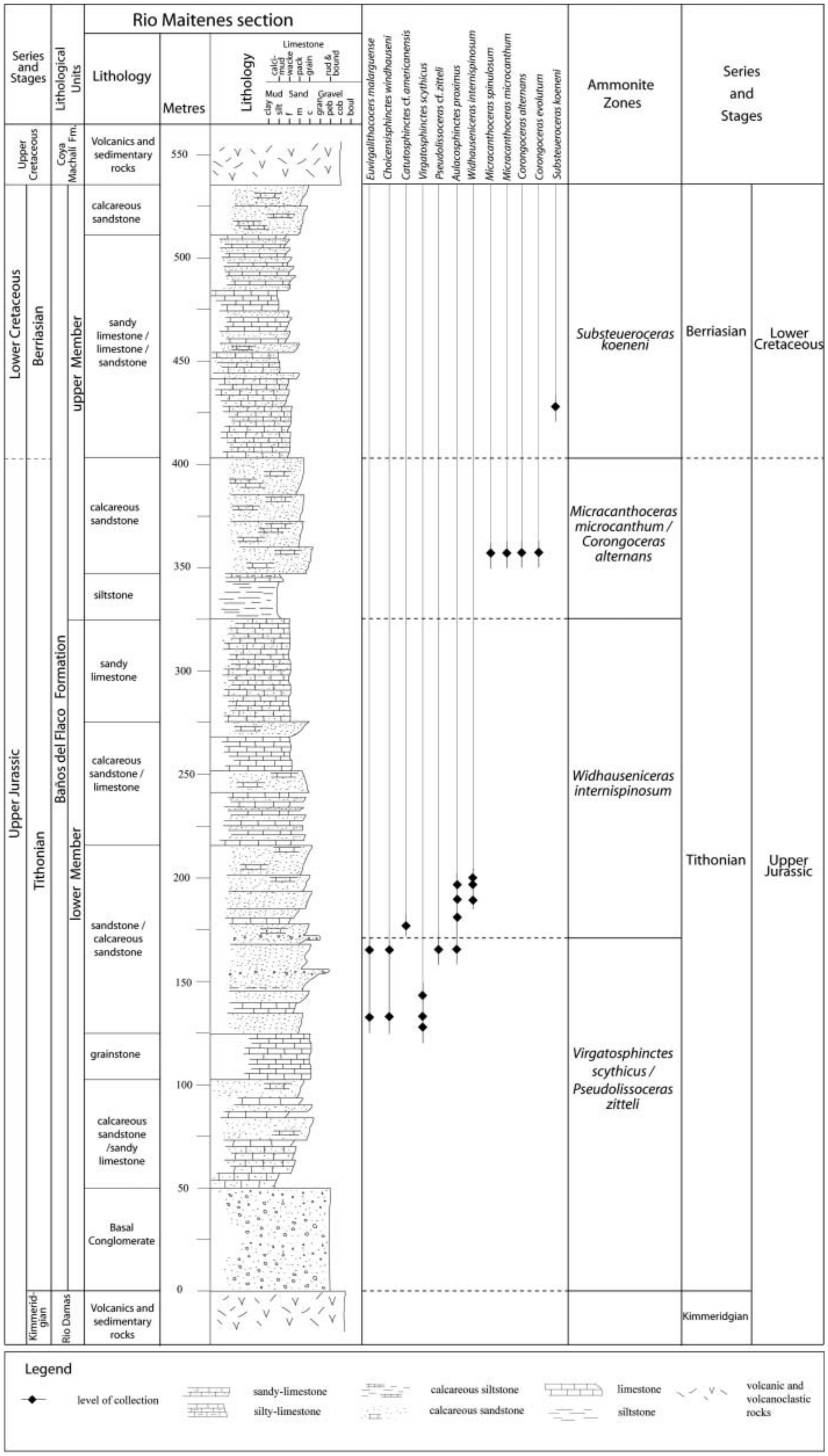

Figure 2. Stratigraphical log and ranges of ammonites in the Baños del Flaco Formation at Rio Maitenes. The description of sections and the levels of collection of fossils are based on L. Biro's field book and new personal observations in the field.

Type species. *Neumayria zitteli* Burckhardt, 1903, p. 55, pl. 10, figs 1, 2; by subsequent designation of Roman (1938, p. 176).

Pseudolissoceras* cf. *zitteli (Burckhardt, 1903)
(Fig. 7A)

cf. 1903 *Neumayria zitteli* Burckhardt: 55, pl. 10, figs 1, 2.
cf. 1926 *Haploceras* (*Pseudolissoceras*) *zitteli* (Burckhardt); Krantz: 436, pl. 17, figs 4, 5.
cf. 1928 *Haploceras* (*Pseudolissoceras*) *zitteli* (Burckhardt); Krantz: 18, pl. 1, fig. 6.
cf. 1931 *Pseudolissoceras zitteli* (Burckhardt); Weaver: 401, pl. 43, fig. 291.
cf. 2001 *Pseudolissoceras zitteli* (Burckhardt); Parent: 23 (*cum syn*.), figs 2, 3a, b, 4a, b, 5a–e, 6, 7a–g, table 1.
cf. 2009 *Pseudolissoceras zitteli* (Burckhardt); Aguirre-Urreta & Vennari: 35, fig. 5a–h.
cf. 2011a *Pseudolissoceras zitteli* (Burckhardt); Parent *et al.*: 45, fig. 34A–C.
cf. 2011b *Pseudolissoceras zitteli* (Burckhardt); Parent *et al:* 79, fig. 39B.

Lectotype. Designated by Parent (2001) from the originals illustrated by Burckhardt (1903, pls 6, 7) from Mendoza (Argentina), middle Tithonian (Upper Jurassic).

Material. One specimen, CPUC/RM/47-11 (Supplementary Table 1), an incomplete and poorly preserved phragmocone.

Description. Involute and whorls depressed. The whorl section is discoidal, umbilical border rounded, flanks are first parallel and then slightly convex; the venter is rounded. Ornamentation is not preserved.

Remarks. The specimen is tentatively referred to this species due to its poor preservation. The coiling and whorl section are characters of *Pseudolissoceras zitteli*, but the specimen is a piece of the phragmocone without preserved ornamentation, precluding ceratin species determination. Parent (2001) gave a full description and discussion of *Pseudolissoceras zitteli*.

Occurrence. Our poorly preserved specimen was collected at Rio Maitenes in the lower member of the Baños del Flaco Formation, in the unit of sandstone/calcareous sandstone 166 m from the base of the section (Fig. 2).

Pseudolissoceras zitteli is known from the middle Tithonian of Argentina (Burckhardt 1903; H. A. Leanza 1980; Parent 2001; Parent *et al.* 2011a), middle Tithonian of Mexico (Cantu-Chapa 1967), lower Tithonian of Cuba (Myczynski 1990), and middle Tithonian of East Russia (Sey & Kalacheva 1996), amongst other regions (see Parent 2001).

Superfamily **Perisphinctoidea** Steinmann, 1890
Family **Perisphinctidae** Steinmann, 1890
Subfamily **Virgatosphinctinae** Spath, 1925
Genus ***Virgatosphinctes*** Uhlig, 1910

Type species. *Virgatosphinctes broilii* Uhlig, 1910, p. 336, pl. 91, fig. 1a–d; by subsequent designation of Douvillé (1910b, p. 737).

Remarks. This genus is moderately evolute, with whorls rounded to slightly compressed. The ribs are biplicate, gradually becoming triplicate, virgatotome, then fasciculate; they gradually become more prominent and more distant. At all stages ribs are less pronounced than in *Pseudovirgatites* (Uhlig 1910; see also Arkell *et al.* 1957). Ribs in the inner whorls are fine and dense; in the outer whorls they are stronger and spaced, grouped in branches that divide into three or more secondaries around the middle part of the flank.

Virgathosphinctes is closely related to *Choicensisphinctes.* The type species of both genera have only a few isolated virgatotome ribs, which are intercalated with simple and irregularly arranged bi- or trifurcate ribs (Enay & Cariou 1997; Yin & Enay 2004). *Virgathosphinctes* and *Choicensisphinctes* are similar in the ornamentation of their inner whorls (Parent *et al.* 2011a). However, ribs in *Choicensisphinctes* are finer in the inner and outer whorls than *Virgathosphinctes*, and the latter genus is moderately evolute. Ribs of the outer whorls are distanced, stronger, and grouped in branches that are divided into three or more secondaries above or below the middle part of the flank.

Virgatosphinctes scythicus (Vischniakoff, 1882)
(Figs 4–6)

1882 *Ammonites scythicus* Vischniakoff: pl. 3, figs 1, 2.
1890 *Perisphinctes scythicus* Vischniakoff; Michalski: 121, 425, pl. 5, figs 6, 7, pl. 7, figs 1–7, pl. 8, fig. 1, pl. 13, fig. 10.
1900a *Perisphinctes* aff. *lothari* Oppel; Burckhardt: 41, pl. 25, figs 6–8.
1903 *Virgatites scythicus* (Vischniakoff); Burckhardt: 45, pl. 7, figs 1–8.
1906 *Virgatites mexicanus* Burckhardt: 115, pl. 31, figs 5–9.
1910a *Virgatites andesensis* Douvillé: 7, pl. 1, figs 3a, b, 4a–f.
1910a *Virgatites mexicanus* Douvillé: 8, pl. 1, figs 1, 2.
1923 *Provirgatites scythicus* (Vischniakoff); Lewinski: 101, pl. 9, figs 3, 4.
1931 *Virgatosphinctes andesensis* (Douvillé); Weaver: 422, pl. 47, figs 313, 314, pl. 48, figs 318–321.
?1943 *Subplanites* aff. *reisi* (Scheid); Imlay: 533, pl. 91, fig. 1.

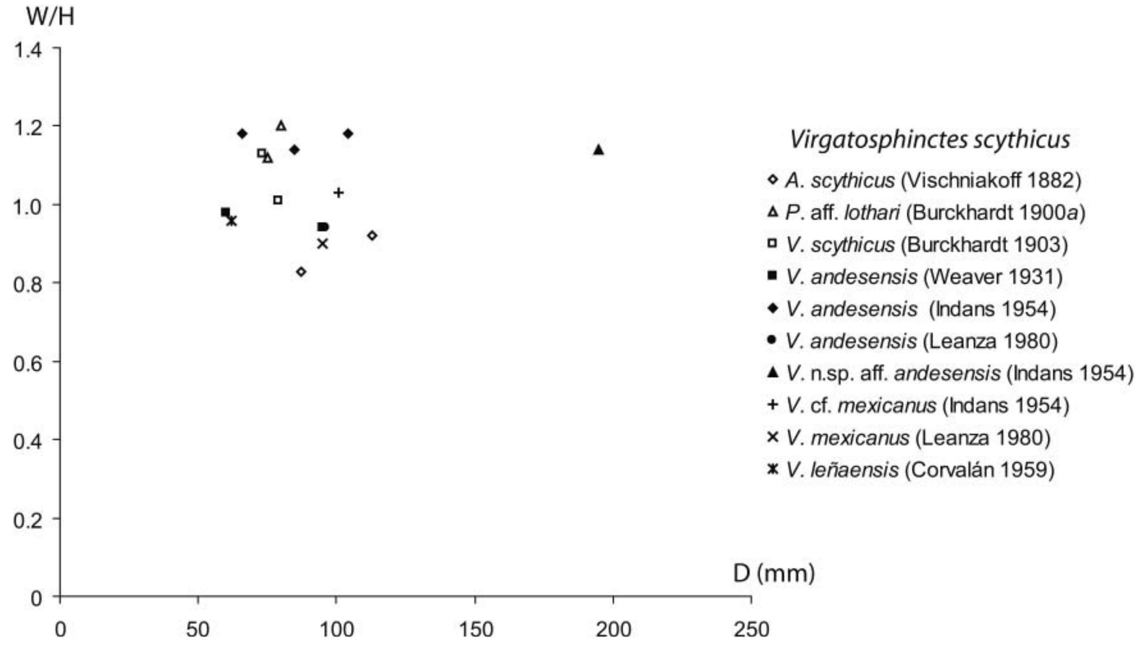

Figure 3. Relationship between W/H and D in *Virgatosphinctes scythicus* (Vischniakoff, 1882), showing the wide range of morphological variation.

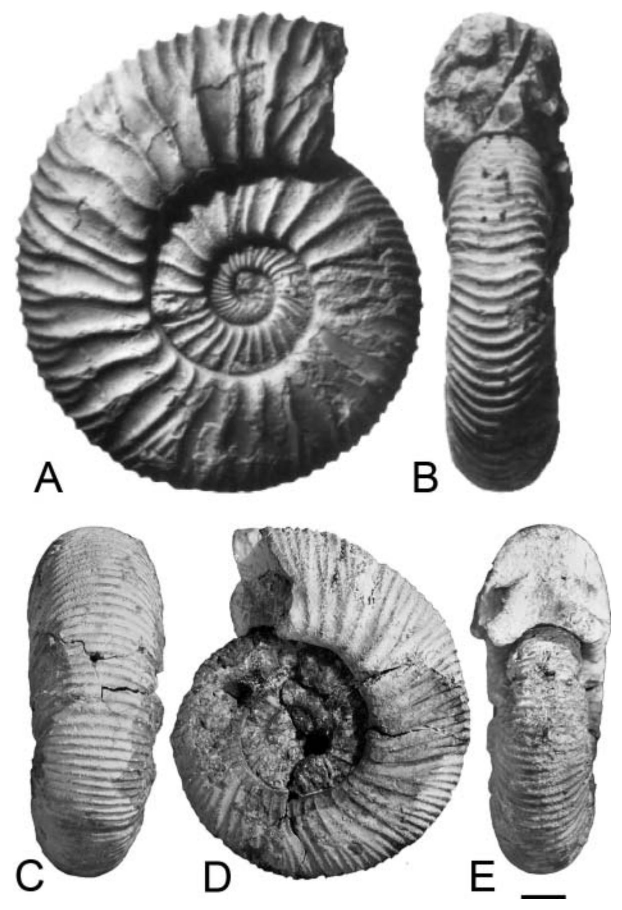

Figure 4. *Virgathosphinctes scythicus* (Vischniakoff, 1882). **A, B,** lectotype (ГГМ.экз N° VI-64/35) of *Ammonites scythicus* Vischniakoff. **C–E,** STIPB-16a, specimen originally described by Indans (1954) as *Virgatosphinctes andesensis* (Douvillé 1910a). Scale bar = 10 mm.

1954 *Virgatosphinctes andesensis* (Douvillé); Indans: 111, pl. 13, fig. 9, pl. 16, figs 1–5.

1954 *Virgatosphinctes*n. sp. aff. *andesensis* (Douvillé); Indans: 112, pl. 17, figs 1–3.

1954 *Virgatosphinctes* cf. *mexicanus* (Burckhardt); Indans: 113, pl. 18, fig. 1.

1958 *Virgatosphinctes andesensis* (Douvillé); Corvalán & Pérez: 43, pl. 8, fig. 18a, b.

1959 *Virgatosphinctes andesensis* (Douvillé); Corvalán: 23, pl. 4, fig. 18, pl. 5, fig. 19.

1959 *Virgatosphinctes leñaensis* Corvalán: 22, pls 14, 15.

1970 *Virgatosphinctes andesensis* (Douvillé); Tavera: 181, pl. 2, fig. 3.

1973 *Zaraiskites scythicus* (Vischniakoff); Dembowska: 65, pl. 5, figs 2, 4, 5.

1974 *Zaraiskites scythicus* (Vischniakoff); Kutek & Zeiss: 531, pl. 27, figs 2–5, pl. 28, figs 1–4, pl. 29, figs 1–3, pl. 30, figs 1, 2, pl. 31, figs 1–4, pl. 32, figs 3–5.

1979 *Virgatosphinctes* sp. nov. aff. *andesensis* (Douvillé); Thomson: 18, pl. 4e–g.

1979 *Virgatosphinctes* aff. *mexicanus* (Burckhardt); Thomson: 20, pl. 4h.

1980 *Virgatosphinctes mexicanus* (Burckhardt); H. A. Leanza: 28, pl. 2, fig. 1a, b, text-fig. 7c.

1980 *Virgatosphinctes andesensis* (Douvillé); H. A. Leanza: 29, pl. 2, fig. 5a, b, text-figs 7d, 9.

1980 *Virgathosphinctes evolutus* H. A. Leanza: 31, pl. 5, fig. 4a–c, text-fig. 7g.

1980 *Virgatosphinctes mexicanus* (Burckhardt); H. A. Leanza: pl. 1, figs 5, 6.

1989 *Virgatosphinctes* cf. *mexicanus* (Burckhardt); Howlett: 16, pl. 1, fig. 4, pl. 2, fig. 3.

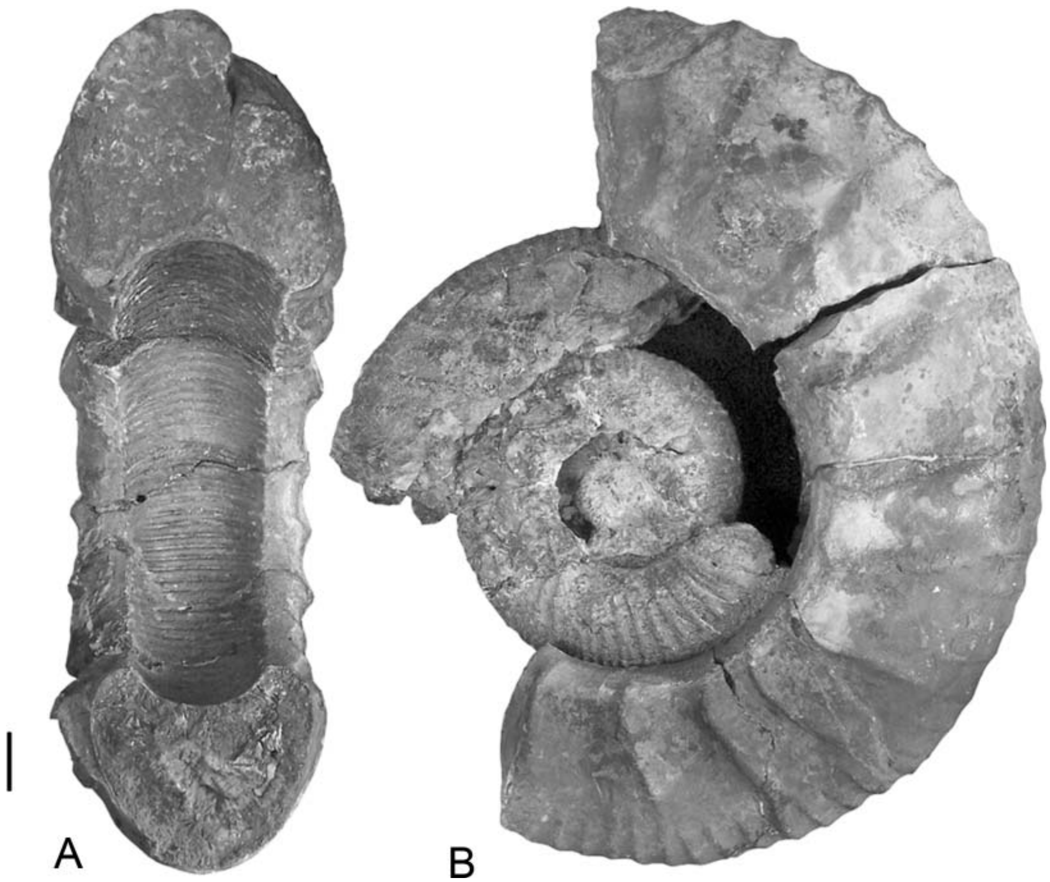

Figure 5. **A, B,** *Virgathosphinctes scythicus* (Vischniakoff, 1882), ГГМ.экз, specimen originally described by Indans (1954) as *Virgatosphinctes* n. sp. aff. *Andesensis.* Scale bar = 7.5 mm.

1989 *Virgatosphinctes* cf. *andesensis* (Douvillé); Howlett: 17, text-fig. 2C.
1992 *Virgatosphinctes* cf. *mexicanus* (Burckhardt); Sey *et al*.: pl. 90, fig. 16.
1997 *Virgatosphinctes* cf. *andesensis* (Douvillé); Riley *et al*.: 438, fig. 3j.
1999 *Zaraiskites scythicus* (Vischniakoff); Mitta *et al.*: 36, pl. 2, fig. 6, pl. 3, figs 1, 2, pl. 8, fig. 1.
2006 '*Torquatisphinctes*' cf. *mendozanus* (Burckhardt); Parent *et al.*: 259, fig. 4c, d.
2011a *Choicensisphinctes* cf. *mendozanus* (Burckhardt); Parent *et al.*: 77, fig. 24.

Type. The lectotype is ГГМ.экз N° VI-64/35, originally figured by Vischniakoff (1882, p. 41, pl. 25, figs 6−8), designated by Mitta *et al*. (1999). The specimen is from the Russian Platform.

Material. Nine internal moulds of fragmentary phragmocones (Supplementary Table 2). CPUC/RM/10-5, CPUC/RM/33-12 and CPUC/RM/Rd-45 are well preserved. CPUC/RM/10-4, CPUC/RM/14-1, CPUC/RM/20-12, CPUC/RM/20-13 and CPUC/RM/33-20 are small and poorly preserved fragments. CPUC/RM/10-8 is an imprint of a fragmentary phragmocone.

Description. Evolute and discoidal. Whorl section suboval, higher than wide. The umbilical border is rounded, flanks are convex and the venter is rounded. Maximum width is reached dorsolaterally. Ornament consists of prominent primary ribs that initiate near the umbilical shoulder; the latter is crossed in rursiradiate direction. From the umbilical border to the middle part of the flank ribs are more prominent and prorsiradiate. At the middle part of the flank they exhibit a slight inflection backwards and are divided into secondary ribs at different heights on the middle part of the flank (virgatotomic pattern). These virgatotomic secundaries are grouped as branches of two to four. Intercalated single ribs are also present but disappear dorsolaterally. All ribs cross the venter without interruption. Fragmentary phragmocone CPUC/RM/Rd-4 also shows a constriction.

Remarks. Specimens described by Indans (1954) as *Virgatosphinctes andesensis* and *V. mexicanus* are regarded as synonymous (see below) and included in this species. Specimen STIPB-17 is an adult (D = 195 mm); its last whorl has a suboval whorl section which is higher than wide. The umbilical border is rounded, flanks are convex and the venter rounded. Maximum width is reached

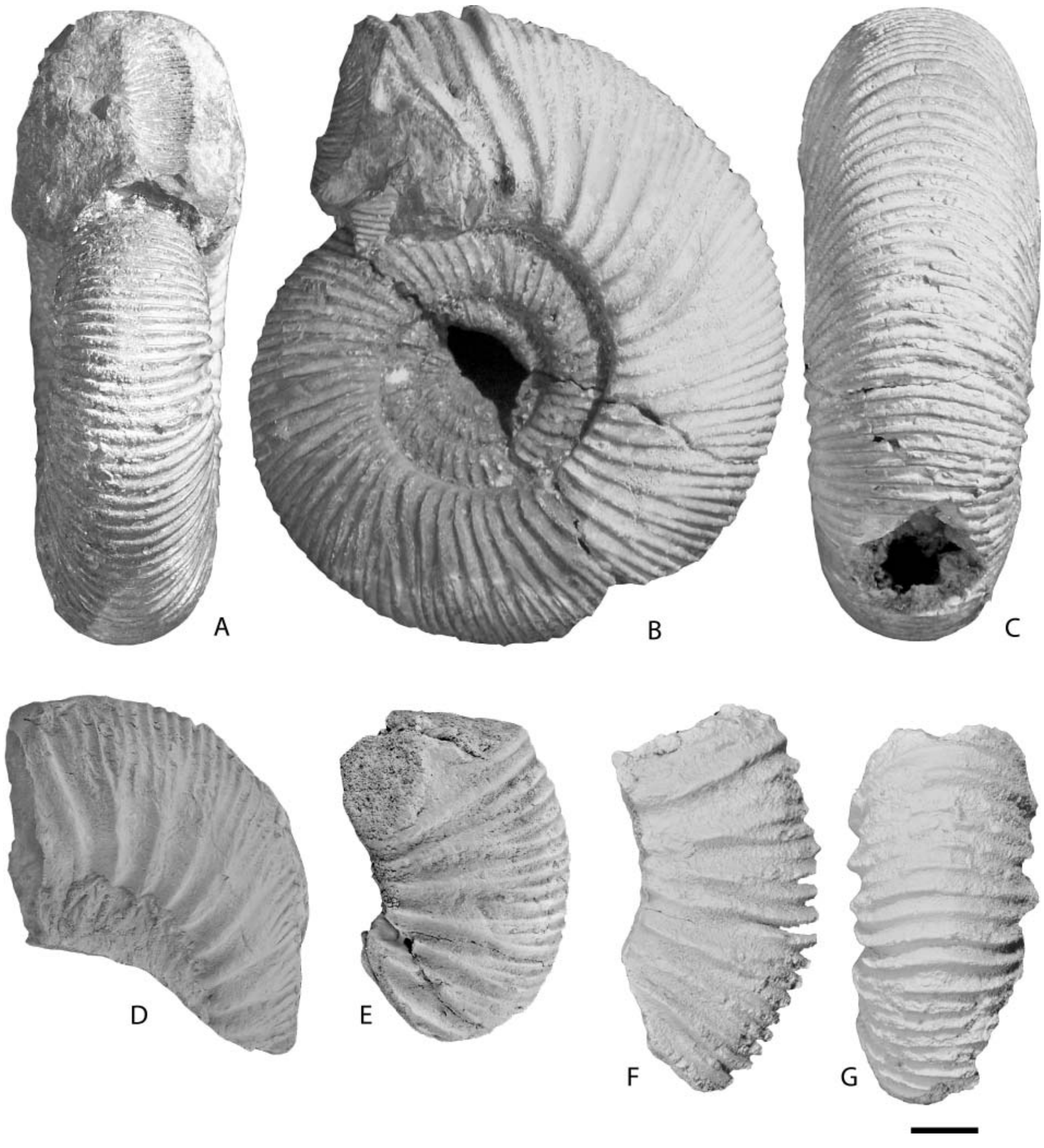

Figure 6. *Virgathosphinctes scythicus* (Vischniakoff, 1882). **A−C,** STIPB-13 (= *Virgatosphinctes* cf. *mexicanus* of Indans 1954). **D−G,** *Virgathosphinctes scythicus* from the Baños del Flaco Formation; **D,** CPUC/RM/10-05; **E,** CPUC/RM/33-12; **F, G,** CPUC/RM/Rd-45. Scale bar = 10 mm.

dorsolaterally. Ornament consists of primary ribs that are bi- to trifurcated and intercalate with one to two single ribs on the ventrolateral area and the venter. Ribs are more distanced than in the inner whorls. The specimen shown in Figure 6A−C is a well-preserved complete adult microconch with lappets.

With regard to generic assignment, '*Ammonites*' *scythicus* was assigned to the genus *Zaraiskites* by Semenov (1898), based on the ornamentation, which is similar to that of *Z. zarajskensis* (Oertli 1965). Both taxa have inner whorls bifid to triplicate and outer whorls with strong virgatotome ribs (Semenov 1898; Arkell *et al*. 1957). On the other hand, *Virgatosphinctes*, based on *V. broili* (Uhlig, 1910) is "moderately evolute, whorls are rounded to slightly compressed, ribs biplicate, gradually triplicate, virgatotome and gradually becoming more distant" (Uhlig

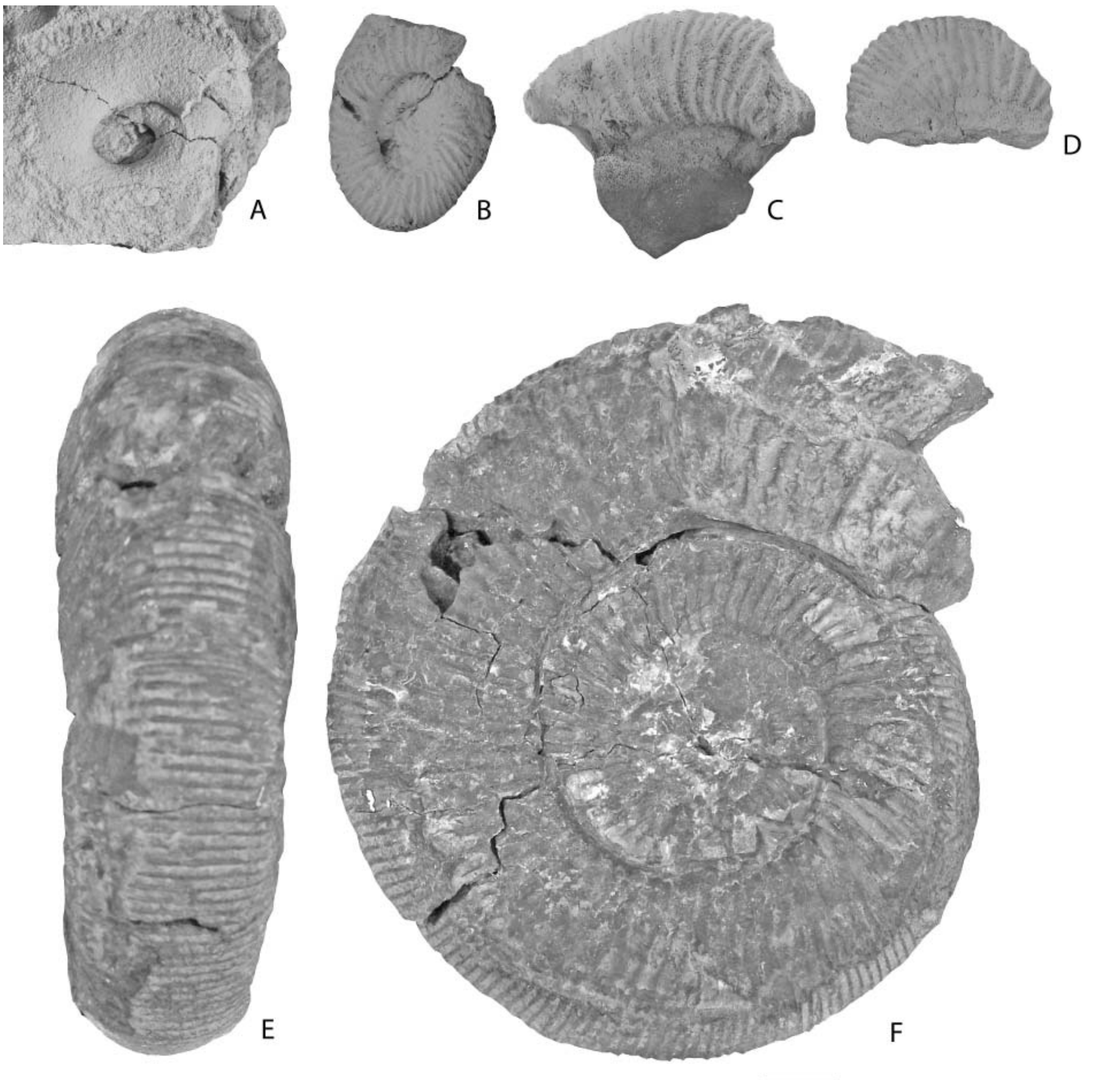

Figure 7. A, *Pseudolissoceras* cf. *zitteli* (Burckhardt, 1903), CPUC/RM/47-11. **B–F,** *Lithacoceras malarguense* (Spath, 1931); **B,** CPUC/RM/47-3; **C,** CPUC/RM/47-13; **D,** CPUC/RM/47-4; **E, F,** STIPB-24 (= *Virgatosphinctes* (*S.*) aff. *pseudolictor* of Indans 1954). Scale bar = 10 mm.

1910, p. 328; Arkell *et al*. 1957). Considering the diagnosis of *Zaraiskites* and *Virgatosphinctes*, the morphological characteristics of '*Ammonites*' *scythicus* Vischniakoff (1882) and the Andean individuals agree with *Virgatosphinctes*.

Parent *et al*. (2011a) designated the lectotype of '*Virgatites*' *mendozanus* and assigned this taxon to *Choicensisphinctes*. The type specimen shows only a few isolated virgatotome ribs intercalated with conspicuous polyschizotomic, simple, bi- or trifurcate ribs which are irregularly arranged. This kind of ornamentation is unknown from *Virgatosphinctes* (e.g. Yin & Enay 2004). *Virgatosphinctes scythicus* figured here (Fig. 4A, B) from the type material of Vischniakoff (1882) from the Baños del Flaco Formation, however, shows ribs which are grouped in branches of 2–4. This morphological feature is also observed in other Andean–Antarctic specimens of this species (e.g. Burckhardt 1903; Weaver 1931; Indians 1954; Corvalán 1959; Thomson 1979; H. A. Leanza 1980; Howlett 1989), even though some exhibit isolated ribs, or ribs unconnected to branches, but this may be the result of preservational bias.

Major confusion exists regarding the possible presence of *Virgatosphinctes scythicus* (Vischniakoff, 1882) in

South America. Weaver (1931) indicated that this taxon, originally described from the Tithonian of Russia, is closely allied with *V. andesensis* (Douville, 1910a) and *V. mexicanus* described by Burckhardt (1906) from Mexico. The three species are here considered to be conspecific. The originals of '*Ammonites*' *scythicus* Vischniakoff, 1882 were redescribed and refigured by Mitta *et al.* (1999). In the inner whorls (Mitta *et al.* 1999, pl. 2, fig. 6, pl. 3, fig. 2) the ribs are dense and grouped in branches of 2−4, coiling is evolute, and the whorl section suboval, higher than wide. In the outer whorls (Mitta *et al.* 1999, pl. 3, fig. 1, pl. 8, fig. 1) ribs are gradually more spaced and occasionally preceded by a constriction; the whorl increases in height. The Andean specimens described as '*V. andesensis*' (and its synonyms) show a wide morphological range and are indistinguishable from the Russian '*Ammonites*' *scythicus* (Fig. 3) (e.g. Burckhardt 1900a, 1903; Weaver 1931; Indians 1954; H. A. Leanza 1980).

Douville (1910a) suggested that '*Virgatites*' *scythicus* differs from *V. andesensis* by having more distanced ribs, a slightly higher whorl section, and finer ribs. However, the Russian type is an adult specimen (D = 113 mm) and morphological differences with '*Virgatites*' *andesensis* are here interpreted to be the result of ontogenetic variation through comparison between juvenile and adult stages (Fig. 3). Ribs on the last whorl of the type specimen of '*Ammonites*' *scythicus* Vischniakoff, 1882 are more distant than in the internal whorls. According to Uhlig (1910) these changes are diagnostic of the genus *Virgathosphinctes.* Juvenile specimens figured by Vischniakoff (1882) show evolute coiling, a discoidal shell, suboval−rounded whorl section, and prominent primary ribs that are tri−tetrafurcated.

Virgatosphinctes mexicanus from Mexico was distinguished based on the presence of constrictions on the last whorl (Burckhardt 1906; Douvillé 1910a; Indans 1954; H. A. Leanza 1980). Occasional constrictions are also reported for *V. andesensis* (e.g. Douvillé 1910a; Weaver 1931; Indans 1954; H. A. Leanza 1980). In *V. mexicanus* constrictions are bordered by a stronger rib, and in *V. andesensis* by a fine prominent rib (Douvillé 1910a; Indans 1954; H. A. Leanza 1980). These differences are here attributed to preservational bias. In addition, Thomson (1979) indicated that *V. andesensis* changes ornamentation during ontogeny. Here we consider *V. mexicanus* and *V. andesensis* to be conspecific.

Virgatosphinctes lenaensis Corvalán, 1959 corresponds to a fragment of an inner whorl, in which ribs may be denser than in adults; its morphological dimensions are within the range of *V. andesensis* (Fig. 3) and the species can be considered as conspecific.

Virgatosphinctes evolutus H. A. Leanza, 1980 was considered to be slightly more inflated than *V. andesensis*, but all other morphological characteristics are identical (Parent *et al*. 2011a). Based on the high variability of *V. andesensis* as suggested here, *V. evolutus* is a junior synonym.

Virgatosphinctes mexicanus and *V. andesensis* closely resemble *V. mendozanus* (e.g. Burckhardt 1903; Douvillé 1910a; Weaver 1931; Indians 1954; Thomson 1979; H. A. Leanza 1980; Howlett 1989), but the nomenclatural history of *V. mendozanus* is complex. According to H. A. Leanza (1980, p. 13), Burckhardt (1900a) figured the taxon as *Perisphinctes* aff. *lothari*, but later (Burckhardt 1903) referred it to *Virgatites scythicus* (Vischniakoff). Douvillé (1910a) proposed *Virgatites andesensis* and considered the *Virgatites scythicus* of Burckhardt (1903) to a synonym. Burckhardt (1911) partly accepted Douville's opinion and proposed that *V. scythicus* could be a synonym of *V. andesensis*. Burckhardt (1911) proposed a new name, *Virgatites mendozanus*, for the same specimens, retaining *V. andesensis* only for the specimens figured by Douville (1910a).

'*Ammonites*' *scythicus* Vischniakoff, 1882 (see descriptions by Lewinski 1923; Dembowska 1973; Kutek & Zeiss 1974) may thus be inseparable from *V. mexicanus*, *V. andesensis* and *V. mendozanus* (e.g. Burckhardt 1903; Douvillé 1910a; Weaver 1931; Indians 1954; Thomson 1979; H. A. Leanza 1980; Howlett 1989), suggesting the existence of an oceanic connection between South America and Russia during latest Jurassic times.

Occurrence. At Rio Maitenes, this taxon is present in the lower member of the Baños del Flaco Formation, in the unit of sandstone/calcareous sandstone (Fig. 2). *Virgatosphinctes mexicanus* was described from the Tithonian of Mexico (Burckhardt 1906), the lower Tithonian of Far East Russia (Sey *et al.* 1992), the lower Tithonian of Mendoza in Argentina (Indians 1954), and the uppermost lower Tithonian of the Vaca Muerta Formation at Cerro Lotena in Argentina (H. A. Leanza 1980). *Virgatosphinctes andesensis* was reported from the lower Tithonian of Mendoza and Neuquen in Argentina (Weaver 1931; Indians 1954; H. A. Leanza 1980), and from the lower Tithonian of Central Chile (Corvalán & Pérez 1958; Corvalán 1959; Biro 1980; Hallam *et al.* 1986). *Virgatosphinctes mendozanus* is considered a lower Tithonian biozone index in the Neuquen Basin in Argentina (H. A. Leanza 1980). In Antarctica, *V. andesensis* and *V. mexicanus* were recorded from Alexander Island in rocks assigned to the lowermost Tithonian (Thomson 1979; Howlett 1989). In Poland, *V. scythicus* was assigned to the lower to middle Volgian by Kutek & Zeiss (1994), or to the middle Volgian by Rogov (2004). In Russia the taxon has been documented from the lowermost middle Volgian (Rogov 2010).

Family **Ataxioceratidae** Buckman, 1921
Subfamily **Lithacoceratinae** Zeiss, 1968
Genus ***Lithacoceras*** Hyatt, 1900

Type species. *Ammonites ulmensis* Oppel, 1858, by original designation.

Lithacoceras malarguense (Spath, 1931)
(Figs 7B–F, 8A, B, 9A–C)

1900a *Perisphinctes lictor* Fontannes; Burckhardt: 43, pl. 24, fig. 4.
1900a *Perisphinctes tiziani* Oppel; Burckhardt: 43, pl. 24, fig. 3.
1900a *Perisphinctes pouzinensis* Toucas; Burckhardt: 45, pl. 24, fig. 8.
1903 *Perisphinctes* aff. *pseudolictor* Choffat; Burckhardt: 36, pl. 4, figs 1–4.
?1906 *Virgatites* sp. Burckhardt: 119, pl. 30, fig. 4.
?1906 *Perisphinctes* sp. Burckhardt: 113, pl. 30, fig. 8.
non 1906 *Virgatites mexicanus*; Burckhardt: 115, pl. 31, figs 5–9.
1906 *Perisphinctes* cf. *danubiensis* Schlosser; Burckhardt: 112, pl. 32, fig. 1.
?1906 *Virgatites* sp. Burckhardt: 118, pl. 32, fig. 2.
1931 *Subplanites malarguensis* nom. nov. Spath: 468.
?1943 *Virgatosphinctes guadalupensis* Imlay: 533, pl. 90, figs 1–6.
1954 *Virgatosphinctes* (*Subplanites*?) aff. *pseudolictor* Choffat; Indans: 119, pl. 19, figs 3, 4.
1954 *Virgatosphinctes* cf. *raja* Uhlig; Indans: 110, pl. 14, figs 1–3.
1954 *Virgatosphinctes communis* Spath; Indans: 108, pl. 15, fig. 6.
?1964 *Perisphinctes* (*Dichotomosphinctes*) *bangei* Burckhardt; Muñoz: 9, pl. 2, fig. 3.
?1964 *Substeueroceras durangoensis* Muñoz: 21, pl. 8, figs 1, 2.
?1980 *Lithacoceras* (*Virgalithacoceras*) *acricostatum* Ohmert & Zeiss: 19, pl. 3, fig. 1, pl. 5, figs 1, 2.
?1988 *Discosphinctoides* (?) aff. *D. neohispanicus* (Burckhardt); Poulton *et al*.: 106, pl. 5.3, figs 1, 2, 4–9.
1997 *Subplanites* sp. Kraemer & Riccardi: 339, fig. 4.3.
non 1999 *Lithacoceras* (*Virgalithacoceras*) cf. *acricostatum* Ohmert & Zeiss; Parent & Capello: 349 (= *Lithacoceras picunleufuense*).
non 2001 *Euvirgalithacoceras malarguense* (Spath); Gründel & Parent: 147, figs 6A, D, 7B, E.
non 2003a *Euvirgalithacoceras malarguense* (Spath); Parent: 147, figs 1, 4, 5A, 6A–D, 7A–E (= *Choicensisphinctes platyconus*).
non 2006 ‘*Lithacoceras*’ n. sp. aff. *malarguense* (Spath); Parent *et al*.: 257, figs 2, 3A, B.

Type. Holotype is the specimen of *Perisphinctes lictor* Fontannes *sensu* Burckhardt, 1900a.

Material. Nine moderate- to well-preserved specimens (Supplementary Table 3). CPUC/RM/47-3 is complete and only slightly deformed. CPUC/RM/17-19, CPUC/RM/47-2, CPUC/RM/47-4, CPUC/RM/47-5, CPUC/RM/47-6, CPUC/RM/47-8, CPUC/RM/47-13 and CPUC/RM/Rod-43 are fragmentary phragmocones with moderate to good preservation. Specimens STIPB-12, STIPB-15 and STIPB-24 are originals from the Indans (1954) collection. Specimen STIPB-15 preserves the body chamber (Fig. 8A).

Description. Evolute and compressed. The section of the inner whorls (D < 40 mm) is oval to subrectangular. Umbilical border rounded, flanks slightly convex and venter rounded. Ornament consisting of fine prorsiradiate ribs. Primaries slightly flexuous, bifurcating on the middle part of the flank; rare virgatotome ribs are intercalated. Constrictions are present in some specimens. In the outer whorls (D > 40 mm) whorl section is wider than high. The umbilical border is rounded, flanks are slightly convex and converge towards the rounded–arched venter. Primary ribs branch into 4–6 secondaries. On the umbilical border the primary ribs are thickened forming elongated tubercles. Three to 4 constrictions are present on the last whorl.

Remarks. Parent (2003a) presented a full description and discussion of this species. *Perisphinctes lictor* Fontannes *sensu* Burckhardt, 1900a was the only specimen available to Burckhardt. The specimen was collected at Casa Pincheira, Argentina, and is housed in the collection of the Museo de La Plata, Argentina. It was illustrated by Burckhardt (1900a, pl. 24, fig. 4; refigured 1903, pl. 4, fig. 1), and referred to as *Subplanites malarguense* nom. nov. by Spath (1931, pp. 468, 501) but in fact is a new species here assigned to *Lithacoceras*.

Virgatosphinctes guadalupensis described by Imlay (1943) closely resembles *L. malarguense* in morphology and ornamentation and may be conspecific. *Virgatosphinctes* (*Subplanites*?) aff. *pseudolictor* described by Indans (1954) clearly matches with *L. malarguense*. *Virgatosphinctes* cf. *raja* described by Indans (1954) is an adult specimen of *L. malarguense*.

Lithacoceras cf. *acricostatum* Parent & Campello (1999), subsequently described as *L. malarguense* by Gründel & Parent (2001), Parent (2003a) and Parent *et al*. (2006), corresponds to *L. picunleufuense*, according with Parent *et al.* (2011b).

Parent (2003a) included ?*Virgatites mexicanus* (Burckhardt, 1906) in his synonymy of *L. malarguense*. However, based on the morphological elements described by Burckhardt (1906), we prefer to assign this taxon to *Virgathosphinctes*.

Occurrence. At Rio Maitenes, *Lithacoceras malarguense* is present in the lower member of the Baños del Flaco Formation, in the unit of sandstone/calcareous sandstone (Fig. 2). Elsewhere, the species has been recorded from the lower Tithonian in Mexico (Burckhardt 1906; Imlay 1943; Muñoz 1964), western Canada (Poulton *et al.* 1988), probably south Germany (Ohmert & Zeiss 1980),

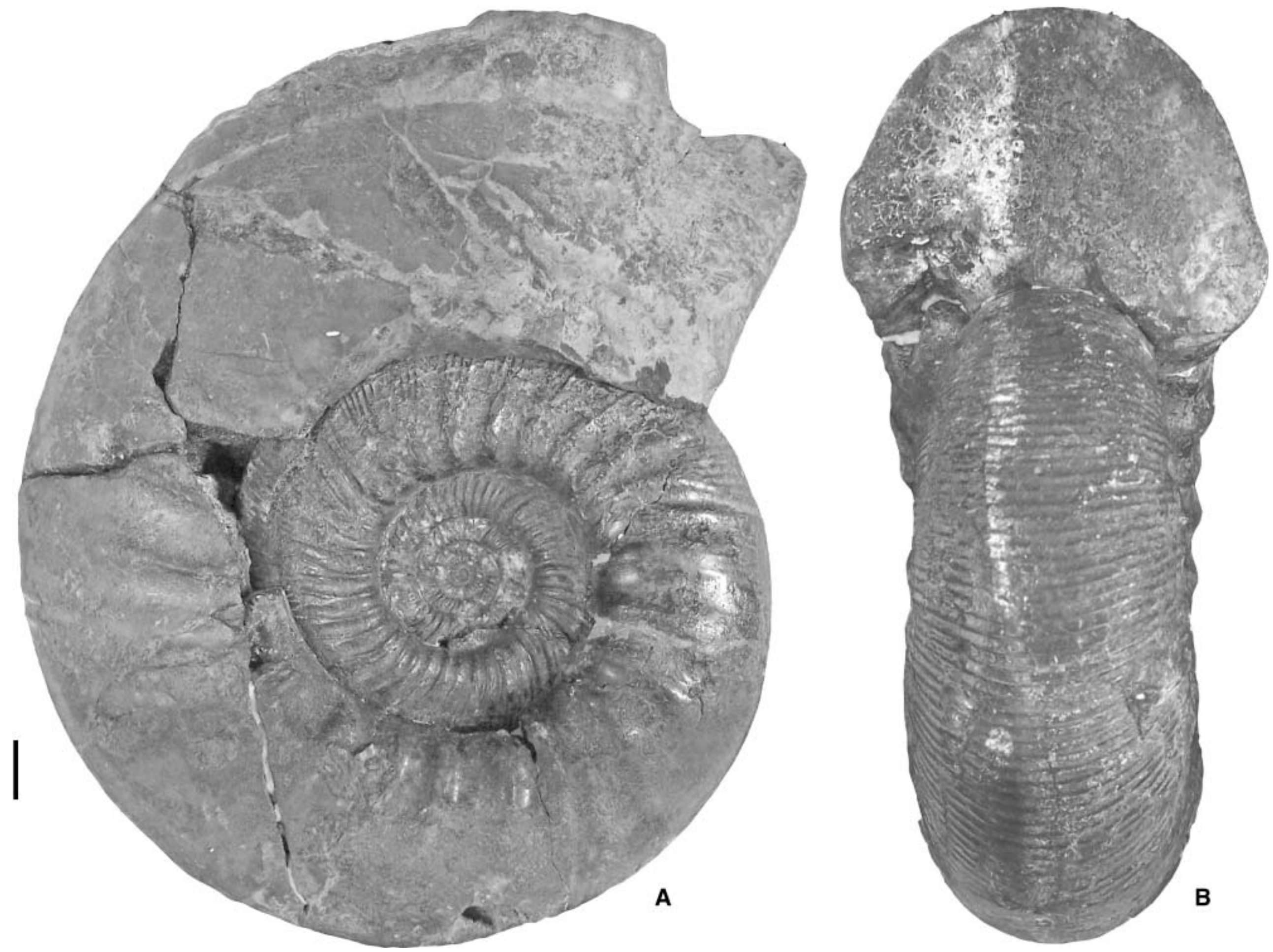

Figure 8. **A, B,** *Lithacoceras malarguense* (Spath, 1931), STIPB−15 (= *Virgatosphinctes* cf. *raja* of Indans 1954). Scale bar = 7.5 mm.

India (Spath 1931), Patagonia (Kraemer & Riccardi 1997) and Central Argentina (Burckhardt 1900; Indans 1954; Parent 2003a). Parent (2003a) gave a full discussion about the age and distribution of *L. malarguense*.

Genus ***Choicensisphinctes*** Leanza, 1980

Type species. *Perisphinctes choicensis* Burckhardt, 1903, p. 50, pl. 6, figs 10−12, pl. 8, fig. 6; by original designation.

Remarks. Parent *et al.* (2011a) gave a full discussion of this genus, including the following diagnosis: "Macroconchs moderately stout, serpenticonic to platyconic or compressed platyconic to suboxyconic, moderately involute, with a deep umbilicus formed by a relatively high, vertical umbilical wall. Inner (most) whorls covered by a simple sculpture of prosocline primaries bifurcated on the upper half or third of the flanks. Ribbing of outer whorls of phragmocone is rather fine and dense, slightly prosocline to flexuous, arising from the umbilical seam (but from the umbilical shoulder in the adult body chamber). Primary ribs bifurcate or polygyrate at about mid-flank. During ontogeny isolated virgatotomes are developed and intercalated with trifurcates or bifurcates with intercalars; some profusely divided polygyrates and/or polyschizotomics occur, especially behind constrictions. The adult body chamber may be strongly variocostate to completely smooth; commonly primary ribs are strong and inflated, raising on the umbilical shoulder and profusely divided in sheaves of three up to thirteen or more secondaries, all of them crossing the venter or vanishing completely towards the peristome. In the microconchs the phragmocone is identical with that of the macroconchs at comparable diameters; the adult body chamber is platyconic to inflate serpenticonic, more rarely suboxyconic, with a peristome possessing a pair of rather short and wide, subtriangular lappets." (Parent *et al.* 2011a, p. 63).

The following species were placed in *Choicensisphinctes* by Parent *et al.* (2011a): *Perisphinctes densistriatus* Steuer, 1897, *Virgatites australis* Burckhardt, 1903, *P. involutus* (Burckhardt, 1900a), *Virgatites buckhardti* Douvillé, 1910a, *Holcodiscus wilfridi* Douvillé, 1910a, *Virgatosphinctes andesensis* Douvillé, 1910a, *Virgatosphinctes mexicanus* Burckhardt, 1906, *Virgatites mendozanus* Burckhardt, 1911, *Pseudoinvolunticeras decipiens* Spath, 1925, *Pseudoinvolunticeras douville* Spath, 1925, *Virgatosphinctes windhauseni* Weaver, 1931, *Virgatosphinctes lotenoensis* Weaver, 1931 and *Virgatosphinctes evolutus* Leanza, 1980.

Virgatosphinctes evolutus Leanza, 1980 coincides with *Choicensisphinctes* regarding the inner whorls, but significant differences exist in the ornamentation of the outer whorls, where ribs are grouped in prominent branches. These are always divided into three or more secondaries without intercalated isolated ribs in the dorsolateral part of the flank. Ribs are spaced and strong, and coiling is evolute and compressed. These characteristics exclude an assignation to *Choicensisphinctes* and the three taxa are here included in *Virgathosphinctes* as was previously suggested by other authors.

Choicensisphinctes windhauseni (Weaver, 1931) (Fig. 9D–F)

1900a *Perisphinctes involutus* Quenstedt; Burckhardt: 40, pl. 25, figs 3–5, pl. 29, fig. 9.
1903 *Virgatites australis* Burckhardt: pl. 6, figs 5–7.
1910a *Virgatites australis* Burckhardt; Douvillé: 10, pl. 1, fig. 5a, b.
1931 *Virgatosphinctes windhauseni* Weaver: 425, pl. 48, figs 324, 325.
1954 *Virgatosphinctes* (*Lithacoceras*) *tenuilineatus* Indans: 103, pl. 13, figs 1, 2.
1980 *Pseudinvolunticeras windhauseni* (Weaver); H. A. Leanza: 26, pl. 3, figs 2, 4a, b, text-fig. 7b.
non 2006 *Choicensisphinctes* cf. *windhauseni* (Weaver); Parent *et al.*: 259, fig. 5a, b (= *Choisisphinctes platyconus*).
2011a *Choicensisphinctes windhauseni* (Weaver); Parent *et al.*: 64, fig. 13a, b.

Type. The lectotype is specimen UWBM No. 346 (Weaver 1931), designated by Parent *et al.* (2011a, p. 20), from the Tithonian of Central Argentina.

Material. Six fragments (Supplementary Table 4). CPUC/RM/18-1 is an incomplete, well-preserved phragmocone. CPUC/RM/47-1 is a fragmentary phragmocone with moderate preservation. CPUC/RM/14-2, CPUC/RM/18-2, CPUC/RM/20-14 and CPUC/RM/Rd-17 are poorly preserved fragments. We also include specimen STIPB-1 of Indans (1954).

Description. Involute and whorl section oval, higher than wide. The umbilical border is almost vertical, flanks are flat to slightly convex and the venter is arched. Ornament consists of fine, equally spaced ribs, which initiate on the umbilical wall with rursiradiate direction and gradually turn towards the aperture dorsolaterally. In the lower flank primary ribs bifurcate and sometimes trifurcate, and cross the venter without interruption. Shallow constrictions are present; they are convex and prorsiradiate and interrupt the ribs.

Remarks. '*Virgatosphinctes*' (*Lithacoceras*) *tenuilineatus*Indans, 1954 is here included in *Choicensisphinctes* and considered conspecific with *C. windhauseni*. *Perisphinctes involutus* described by Burckhardt (1900a) differs only from *C. windhauseni* in the occasional presence of simple ribs intercalated between the regular bi- and trifurcated ribs. These two taxa are also considered to be conspecific.

Choicensisphinctes windhauseni is a close relative of *Virgatites australis* described by Burckhardt (1903) and Indans (1954). Coiling, ornamentation and whorl section are identical, but ribs are more distant in *V. australis*. It is also closely related to *Virgatosphinctes denseplicatus* (Waagen, 1875), but the whorl section in the latter species is wider than high. *Virgatosphinctes denseplicatus* changes morphology during ontogeny and is generally a variable species (Waagen 1875; Uhlig 1910; Spath 1931; Indans 1954; H. A. Leanza 1980).

Occurrence. At Rio Maitenes, this taxon is recorded from the lower member of the Baños del Flaco Formation, in the unit of sandstone/calcareous sandstone (Fig. 2). In Argentina, *Virgatosphinctes* (*Lithacoceras*) *tenuilineatus*, here regarded as synonymous with *C. windhauseni*, was described from the lower Tithonian of Mendoza (Indans 1954). The species also occurs in the middle Tithonian of Central Argentina (Weaver 1931), the uppermost lower Tithonian of Neuquén (H. A. Leanza 1980), and the lowermost Tithonian of the Neuquén–Mendoza basin (Parent *et al.* 2006).

Subfamily **Torquatisphinctinae** Tavera, 1985
Genus ***Catutosphinctes*** Leanza & Zeiss, 1992

Type species. *Catutosphinctes rafaeli* Leanza & Zeiss, 1992; by original designation. Parent *et al.* (2011b) give a description and discussion of this genus.

Catutosphinctes* cf. *americanensis (Leanza, 1980) (Fig. 10)

cf. 1980 *Pachysphinctes americanensis* Leanza: 41, pl. 7, fig. 1a–d, text-fig. 7k.

Type. The holotype is specimen SGN 8952/1, designated by H. A. Leanza (1980, pl. 7, fig. 1a–d), from the middle Tithonian Vaca Muerta Formation, Argentina.

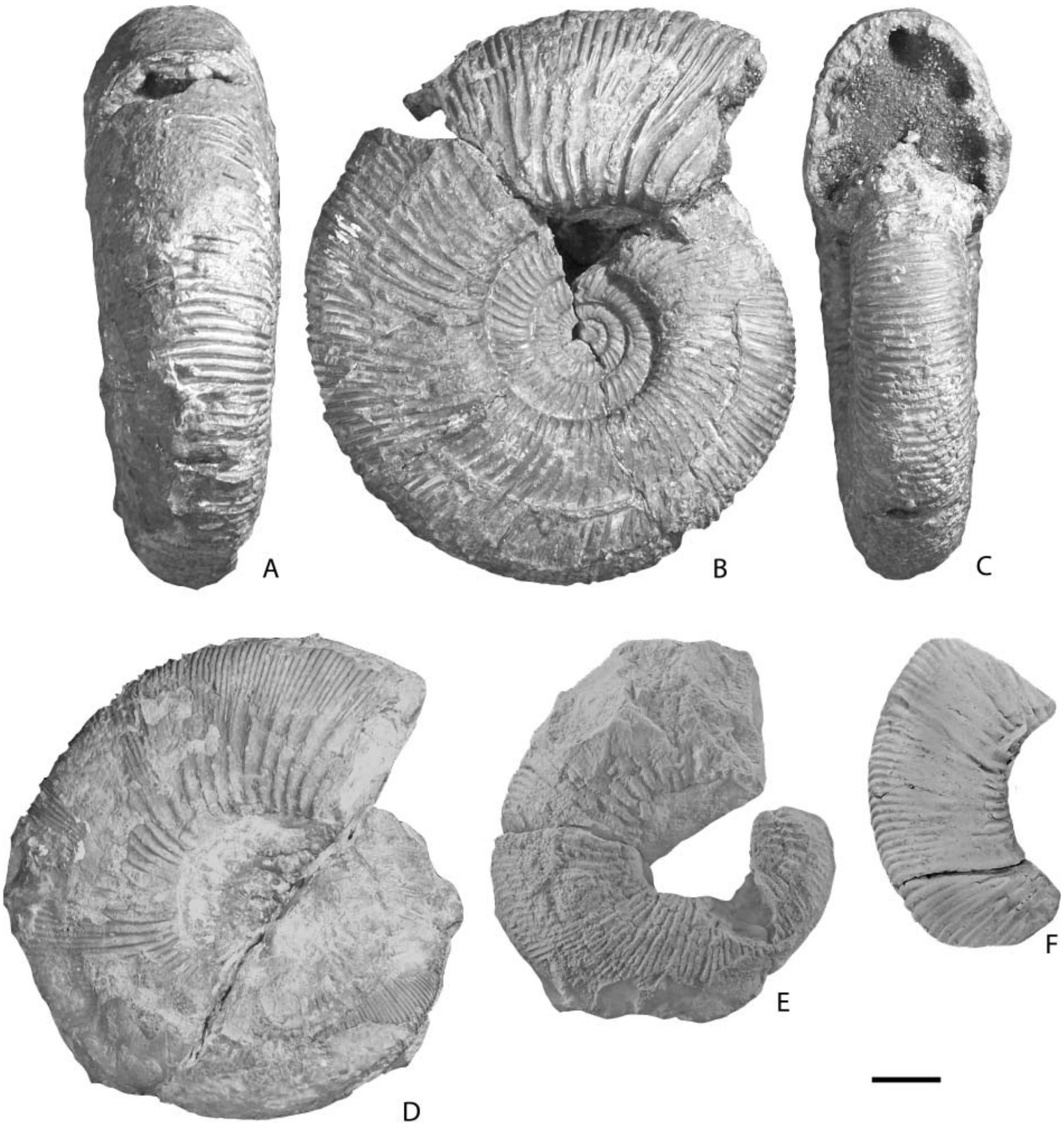

Figure 9. **A−C,** *Lithacoceras malarguense* (Spath 1931), STIPB-12 (= *Virgatosphinctes communis* of Indans 1954). **D−F,** *Choicensisphinctes windhauseni* (Weaver, 1931); **D,** STIPB-1 (= *Virgatosphinctes* (*L.*) *tenuilineatus* of Indans 1954); **E,** CPUC/RM/18-1; **F,** CPUC/RM/47-1. Scale bar = 10 mm.

Material. A single internal mould, CPUC/RM/55-1 (Supplementary Table 5), of an incomplete and poorly preserved phragmocone.

Description. Evolute, with a wide umbilicus. Whorl section deformed but apparently discoidal. The umbilical border is rounded, flanks are convex and the venter is rounded. Maximum width is reached on the lower flank. Ornamentation on the last whorl consists of distant and wide ribs with elongated tubercles on the umbilical border. Two ribs initiate at each tubercle. Inner whorls are ornamented by slightly prorsiradiate single ribs that bifurcate on the middle part of the flank.

Remarks. The specimen is poorly preserved and is therefore tentatively referred to this species. H. A. Leanza (1980) gave a full description and discussion of this species.

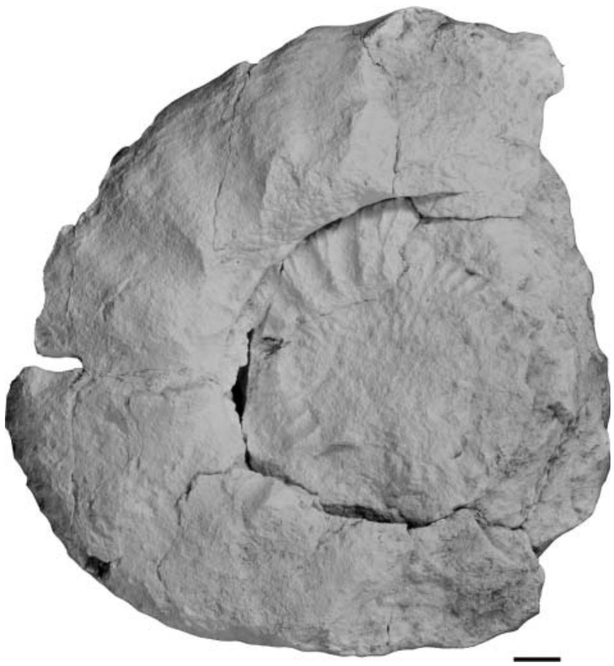

Figure 10. *Catutosphinctes* cf. *americanensis* (Leanza, 1980), CPUC/RM/55-01. Scale bar = 10 mm.

Occurrence. At Rio Maitenes, this taxon is present in the lower member of the Baños del Flaco Formation, in the upper part of the sandstone/calcareous sandstone unit (Fig. 2). In Argentina *Catutosphinctes americanensis* is recorded from the uppermost middle Tithonian of the Vaca Muerta Formation (H. A. Leanza 1980).

Family **Himalayitidae** Spath, 1925
Genus ***Windhauseniceras*** Leanza, 1945

Type species. *Perisphinctes internispinosus* Krantz, 1926, p. 453, pl. 14, figs 1, 2.

Windhauseniceras internispinosum (Krantz, 1928)
(Fig. 12)

1897 *Reineckeia* cf. *stephanoides* Oppel; Steuer: 157, pl. 28, figs 11, 12.
1926 *Perisphinctes internispinosus* Krantz: 453, pl. 14, figs 1, 2.
1928 *Perisphinctes internispinosus* Krantz: 39, pl. 2, figs 3, 4.
1928 *Aulacosphinctes hebecostatus* Krantz: 42, pl. 3, fig. 8.
1931 *Perisphinctes internispinosus* Krantz; Weaver: 419, pl. 47. fig. 312.
1945 *Windhauseniceras* cf. *internispinosum* (Krantz); A. F. Leanza: 23, pl. 21, fig. 6.
1957 *Windhauseniceras internispinosum* (Krantz); Arkell *et al.*: L356, fig. 468.7a–d.
1958 *Windhauseniceras internispinosum* (Krantz); Corvalán & Pérez: 44, pl. 10, fig. 23a–c.
1959 *Windhauseniceras internispinosum* (Krantz); Corvalán: 16, pl. 4, figs 16, 17.
1960 *Windhauseniceras* aff. *internispinosum* (Krantz); Bürgl: 197, pl. 1, fig. 5.
1980 *Windhauseniceras internispinosum* (Krantz); H. A. Leanza: 43, pl. 8, fig. 4a, b, pl. 9, fig. 1a, b, text-fig. 10d.
1980 *Hemispiticeras* aff. *steinmanni* (Steuer); H. A. Leanza: 43, pl. 9, fig. 2.
1981a *Windhauseniceras internispinosum* (Krantz); H. A. Leanza: pl. 2, figs 7, 8.
1990 *Windhauseniceras* sp. cf. *internispinosum* (Krantz); Aguirre-Urreta & Charrier: 265, pl. 1, fig. 9.
2003b *Windhauseniceras internispinosum* (Krantz); Parent: 354, fig. 1a–d.
2007 *Windhauseniceras internispinosum* (Krantz); Parent *et al.*: 20, figs 9, 10.

Type. The lectotype, designated by Parent (2003b, p. 354) is specimen STIPB 25a, the original of Krantz (1926, p. 453, pl. 14, figs 1, 2), from the Tithonian of Mendoza, Argentina.

Material. Seventy-one internal moulds (Supplementary Table 6). CPUC/RM/60-45, CPUC/RM/60-49, CPUC/RM/60-52, CPUC/RM/60-55, CPUC/RM/60-75b, CPUC/RM/Rd-21, CPUC/RM/Rd-22, CPUC/RM/Rd-24 are complete phragmocones, moderately to well preserved. CPUC/RM/59-18, CPUC/RM/59-55, CPUC/RM/59-63, CPUC/RM/60-22, CPUC/RM/60-28, CPUC/RM/60-50, CPUC/RM/60-70, CPUC/RM/60-74, CPUC/RM/60-75a, CPUC/RM/Rd-18, CPUC/RM/Rd-23 are well preserved, fragmentary phragmocones. CPUC/RM/59-14, CPUC/RM/59-22, CPUC/RM/59-27, CPUC/RM/59-36, CPUC/RM/59-37, CPUC/RM/59-39, CPUC/RM/59-40, CPUC/RM/59-49, CPUC/RM/59-50, CPUC/RM/59-51, CPUC/RM/59-59, CPUC/RM/59-64, CPUC/RM/60-20, CPUC/RM/60-21, CPUC/RM/60-25, CPUC/RM/60-26, CPUC/RM/60-31, CPUC/RM/60-32, CPUC/RM/60-33, CPUC/RM/60-34, CPUC/RM/60-35, CPUC/RM/60-36, CPUC/RM/60-37, CPUC/RM/60-52, CPUC/RM/60-55, CPUC/RM/60-58, CPUC/RM/60-59, CPUC/RM/60-60, CPUC/RM/60-61, CPUC/RM/60-62, CPUC/RM/60-63, CPUC/RM/60-64, CPUC/RM/60-68, CPUC/RM/60-69, CPUC/RM/60-72, CPUC/RM/60-75, CPUC/RM/60-79, CPUC/RM/60-80, CPUC/RM/62-07, CPUC/RM/Rd-09, CPUC/RM/Rd-14, CPUC/RM/Rd-25, CPUC/RM/Rd-15, CPUC/RM/Rd-20, CPUC/RM/Rd-37, CPUC/RM/Rd-41, CPUC/RM/Rd-42 are moderately to poorly preserved fragmentary phragmocones. CPUC/RM/59-29, CPUC/RM/59-45, CPUC/RM/60-43, CPUC/RM/60-54, CPUC/RM/60-57, CPUC/RM/Rd-1, CPUC/RM/Rd-5 are small fragments.

Description. Coiling evolute and umbilicus wide. Sections of inner whorls ($D < 50$ mm) are wider than high.

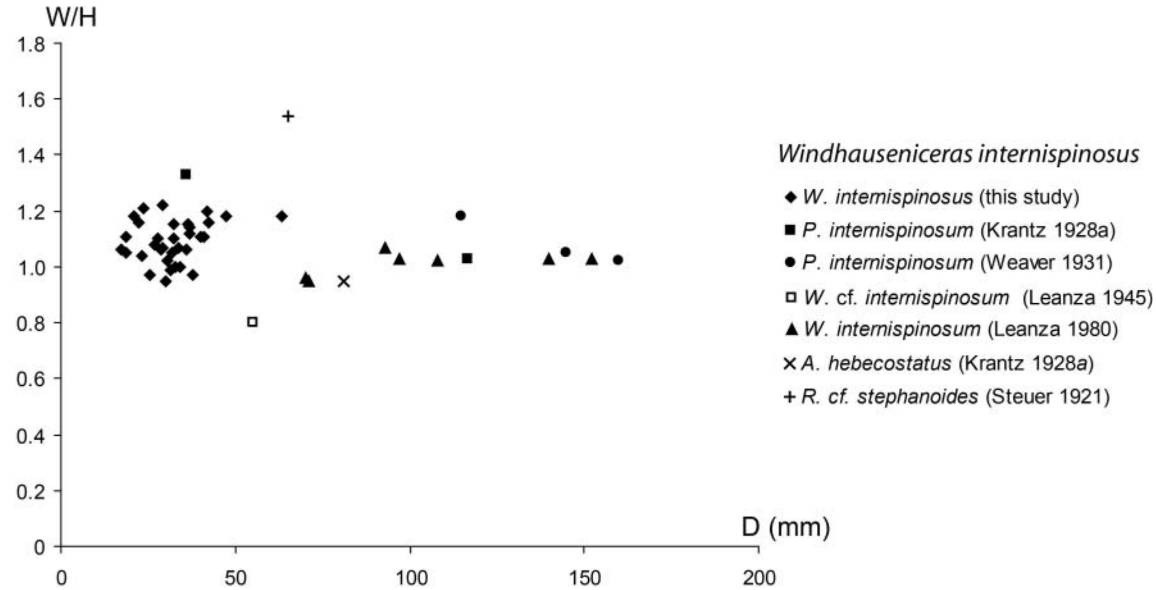

Figure 11. *Windhauseniceras internispinosum* (Krantz, 1926). Relationship between W/H and D. Note that the whorl section changes gradually between juvenile and adult stages.

The umbilical border is rounded, flanks are convex and converge towards the narrowly rounded venter. Maximum width is reached on the lower part of the flank. Ornamentation consists of strong primary ribs, which are slightly prorsiradiate. Ribs bi- to trifurcate on the middle part of the flank. Elongate tubercles were not observed, but their absence may result from preservation of the material as internal moulds. One to 2 constrictions are present on the last whorl and are parallel to primary ribs. Whorl section changes gradually towards higher than wide in adult stages (D > 50 mm) (Fig. 11). The umbilical border is rounded, flanks are convex and converge towards the rounded venter. Maximum width is reached on the lower part of the flank. Ornament consists of primary ribs which are slightly prorsiradiate and bifurcate on the middle part of the flank. On the last whorl 1–2 constrictions are parallel to the primary ribs.

Remarks. Parent (2003b) and Parent *et al.* (2007) gave a full description and discussion of this species and its important intraspecific variation.

Occurrence. At Rio Maitenes, this taxon is present in the lower member of the Baños del Flaco Formation, in the upper part of the unit of sandstone/calcareous sandstone (Fig. 2). In Argentina, *W. internispinosum* is recorded from the upper part of the middle Tithonian in Mendoza and Neuquén provinces (Steuer 1897–1921; Krantz 1926–8; Weaver 1931; A. F. Leanza 1945; H. A. Leanza 1980; Leanza & Zeiss 1990–2). In Colombia it has been recorded from the upper Tithonian (Bürgl 1960), and in central Chile from the middle–upper Tithonian boundary at Nacientes del Maipo (Aguirre-Urreta & Charrier 1990) and the upper Tithonian of Rio Leñas (Corvalán 1959).

Genus ***Aulacosphinctes*** Uhlig, 1910

Type species. *Ammonites mörikeanus* Oppel, 1863, p. 281, fig. 2a, b; by subsequent designation of Spath (1924, p. 16).

Remarks. Evolute and compressed. Ribs are strong, distant, widely biplicate, some simple. Tubercles are absent, ventral groove deep and persistent; rather long lappets (Oppel 1863; Uhlig 1910; Arkell *et al.* 1957). The style of ribbing is closely related to Himalayitinae (Arkell *et al.* 1957), but these morphological characteristics are also present in Berriasellinae, the density and spacing of the ribs being the main difference.

Aulacosphinctes proximus (Steuer, 1897)
(Fig. 13)

1897 *Reineckeia proxima* Steuer: 160, pl. 8, figs 7–9.
1900a *Reineckeia* aff. *cimbrica* Neumayr; Burckhardt: 40, pl. 24, fig. 2.
1900a *Perisphinctes colubrinus* Reinecke; Burckhardt: 44, pl. 24, figs 5, 6.
1900a *Perisphinctes contiguus* Catullo; Burckhardt: 45, pl. 24, fig. 1.
1900a *Perisphinctes colubrinus* Reinecke; Burckhardt: 46, pl. 26, fig. 4.
1921 *Reineckeia proxima* Steuer: 61, pl. 8, figs 7–9.

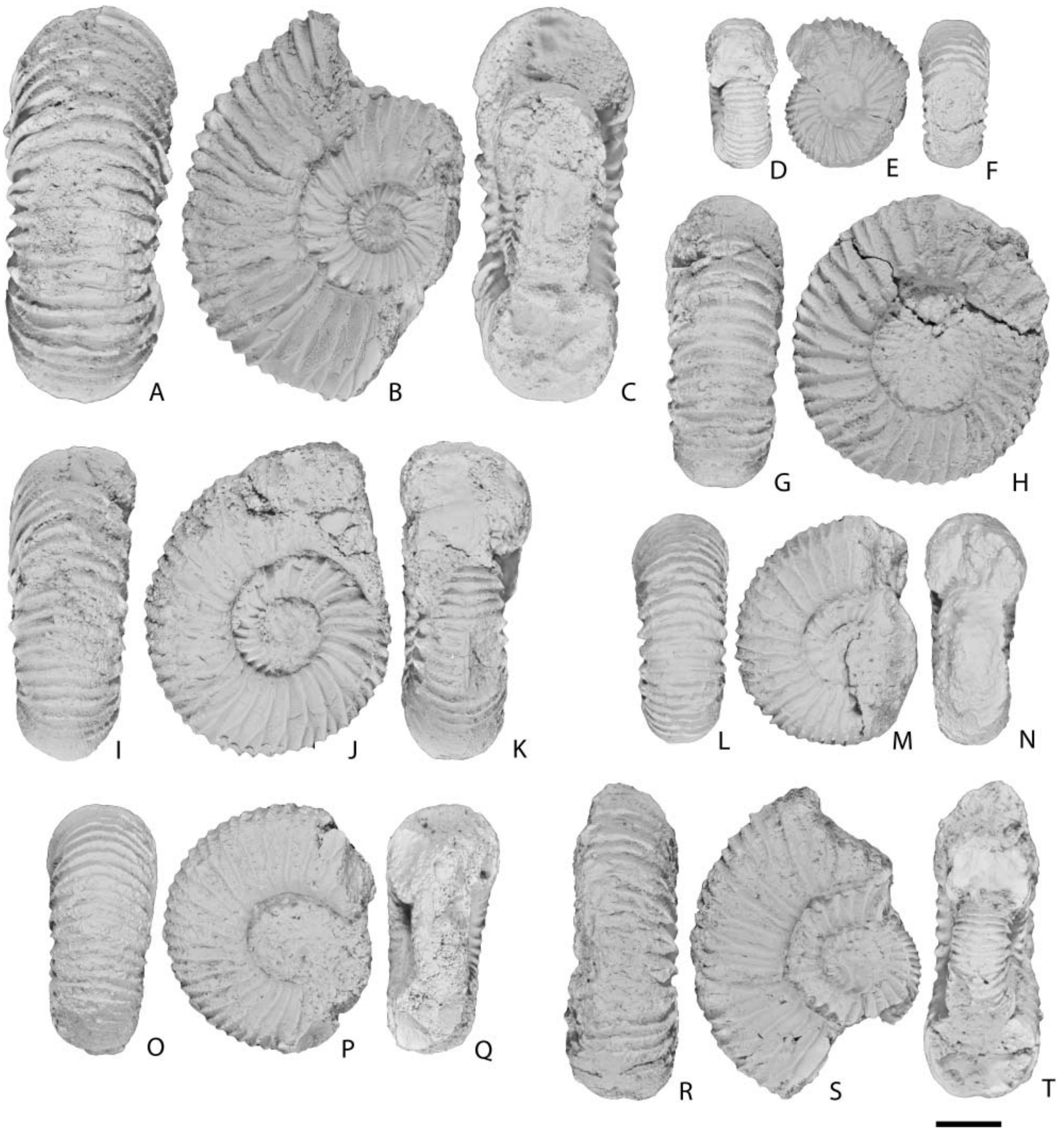

Figure 12. *Windhauseniceras internispinosum* (Krantz, 1926), Baños del Flaco Formation, **A−C,** CPUC/RM/Rd-18; **D−F,** CPUC/RM60-49; **G, H,** CPUC/RM/60-45; **I−K,** CPUC/RM/Rd-24; **L−N,** CPUC/RM/60-13; **O−Q,** CPUC/RM/Rd-21; **R−T,** CPUC/RM/60-70. Scale bar = 10 mm.

1931 *Aulacosphinctes proximus* (Steuer); Weaver: 411, pl. 44, figs 298, 299.

1931 *Aulacosphinctes colubrinus* (Reinecke); Weaver: 413, pl. 44, figs 301−303.

1959 *Aulacosphinctes* sp. aff. *A. colubrinus* (Reinecke); Corvalán: 12, pl. 5, fig. 22.

1959 *Aulacosphinctes proximus* (Steuer); Corvalán: 13, pl. 6, fig. 23.

1959 *Aulacosphinctes chilensis* Corvalán: 15, pl. 6, fig. 24.

1980 *Aulacosphinctes proximus* (Steuer); H. A. Leanza: 44, pl. 6, figs 2, 4, 5.

1980a *Aulacosphinctes proximus* (Steuer); Biro: 143.

1981a *Aulacosphinctes proximus* (Steuer); H. A. Leanza: pl. 2, figs 9, 10.
2003a *Troquatisphinctes proximus* (Steuer); Parent: 159, figs 1, 9i–l, 12a, b, 13a–c.
2004 *Aulacosphinctes* cf. *proximus* (Steuer); Yin & Enay: 673, pl. 3, fig. 4a, b.
?2009 *Aulacosphinctes proximus* (Steuer); Aguirre-Urreta & Vennari: 39, fig. 5r–t.
2011a *Catutosphinctes proximus* (Steuer). Parent *et al.*: fig. 25B.
2011b *Catutosphinctes proximus* (Steuer); Parent *et al.*: 45, figs 8C–E, 18A–F, 19A–C, app. 1.

Type. The lectotype is specimen GZG 499-30, the original of Steuer (1897, p. 160, pl. 8, figs 7–9) from the Tithonian of Mendoza, Argentina, designated by Parent (2003a, p. 159, fig. 9i,j).

Material. Fifty-one specimens (Supplementary Table 7). CPUC/RM/47-14, CPUC/RM/59-2, CPUC/RM/59-4, CPUC/RM/59-24, CPUC/RM/59-71 and CPUC/RM/Rd-30 are complete phragmocones moderately to well preserved. CPUC/RM/59-3, CPUC/RM/59-6, CPUC/RM/59-21, CPUC/RM/59-20, CPUC/RM/59-26, CPUC/RM/59-32, CPUC/RM/Rd-7 and CPUC/RM/Rd-33 are fragmentary, well-preserved phragmocones. CPUC/RM/58-64, CPUC/RM/59-1, CPUC/RM/59-5, CPUC/RM/59-7, CPUC/RM/59-15, CPUC/RM/59-19, CPUC/RM/59-30, CPUC/RM/59-34, CPUC/RM/59-42, CPUC/RM/59-48, CPUC/RM/60-27, CPUC/RM/60-83, CPUC/RM/61-1, CPUC/RM/62-6 and CPUC/RM/Rd-40 are fragmentary phragmocones with moderate to poor preservation. CPUC/RM/59-44, CPUC/RM/59-8, CPUC/RM/59-9, CPUC/RM/59-10, CPUC/RM/59-11, CPUC/RM/59-13, CPUC/RM/59-16, CPUC/RM/59-17, CPUC/RM/59-28, CPUC/RM/59-31, CPUC/RM/59-33, CPUC/RM/59-35,

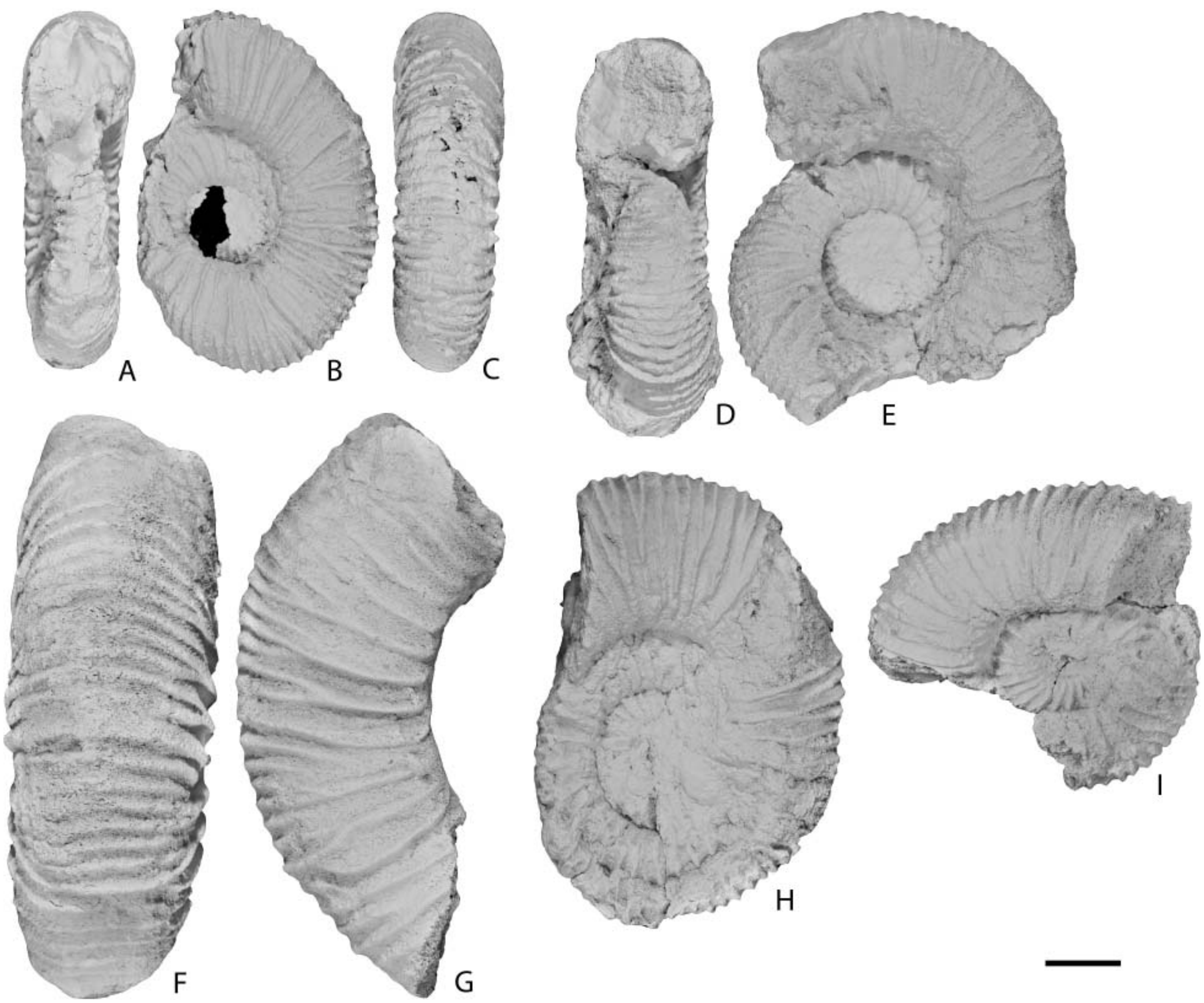

Figure 13. *Aulacosphinctes proximus* (Steuer, 1897), Baños del Flaco Formation. **A–C,** CPUC/RM/59-24; **D–E,** CPUC/RM/59-02; **F, G,** CPUC/RM/59-06; **H,** CPUC/RM/59-20; **I,** CPUC/RM/59-21. Scale bar = 10 mm.

CPUC/RM/59-46, CPUC/RM/59-47, CPUC/RM/59-60, CPUC/RM/59-66, CPUC/RM/59-67, CPUC/RM/59-69, CPUC/RM/59-70, CPUC/RM/60-42, CPUC/RM/60-44 and CPUC/RM/Rd-34 are small fragments.

Description. Evolute, umbilicus wide and shell discoidal. Whorl section is subquadrate, slightly higher than wide. The umbilical border is rounded, flanks are convex and slightly converge towards the venter. Maximum width is reached in the middle part of the flank. Ornament consists of primary ribs that are slightly flexuous, rursiradiate to prorsiradiate, slightly convex on the lower flank and on the middle part of the flank. On the upper flank ribs bend forwards and are prorsiradiate. Ribs bifurcate in the middle part of the flank and some trifurcate. With increasing diameter, trifurcate ribs are gradually more common. Shallow constrictions are seen in larger specimens.

Remarks. Parent (2003a) gave a full description and discussion of this species, assigning the taxon to *Torquatisphinctes*. However, this genus is characterized by denser ribs, a more inflated whorl section and occasional virgatitid-like triplicates at constrictions throughout its ontogeny. These morphological characteristics are absent in *Aulacosphinctes proximus*. Parent *et al.* (2011b) assigned the taxon to *Catutosphinctes*, but this genus differs by having an outer flank with bifurcated ribs alternating with trifurcated or intercalatory ribs. Constrictions are followed by distant primaries and secondaries which show bifurcation, polygyration or irregular splitting (Leanza & Zeiss 1992).

In the diagnosis of *Catutosphinctes*, Parent *et al.* (2011b) indicated that lamellar tubercles may be present at the points of rib furcation. These are also present in the paralectotype of *A. proximus* figured by Steuer (1897–1921), a small phragmocone with himalayitid characteristics, and on the inner whorls of *Aulacosphinctes proximus* (Verma & Westermann 1973). Based on this character, Parent *et al.* (2011b) suggested that *A. proximus* forms part of *Catutosphinctes*. However, all other morphological characters coincide with those for himalayitid ammonites. We therefore do not consider the presence of tubercles to be an argument strong enough to differentiate *Aulacosphinctes* from *Catutosphinctes* and we follow Oppel (1863), Uhlig (1910) and Spath (1924) in assigning the taxon *proximus* to *Aulacosphinctes*.

Aulacosphinctes chilensis Corvalán (1959) differs only by having constrictions on the last whorl of a large specimen with a diameter of 95 mm. The area with constrictions may correspond to the living chamber of the individual, and not the phragmocone; the species is here synonymized with *A. proximus*.

Aulacosphinctes colubrinus, described by Burckhardt (1900a), Weaver (1931) and Corvalán (1959), exhibits a morphology corresponding to the variability seen in *A. proximus* and is here considered to be a junior synonym.

Specimens described by Aguirre-Urreta & Vennari (2009) as *A. proximus* are more evolute and the ribs are more spaced. They may thus belong to *Corongoceras mendozanum.*

Occurrence. At Rio Maitenes, this species is present in the lower member of the Baños del Flaco Formation, in the upper part of the unit of sandstone/calcareous sandstone (Fig. 2). Elsewhere in Chile *A. proximus* has been recorded from the middle Tithonian of the Rio Leñas Formation (Corvalán 1959), which today is considered as the Baños del Flaco Formation (Charrier 1982), and from the middle to uppermost Tithonian of the Lo Valdés Formation (Biro 1964, 1980; Hallam *et al.* 1986). In Argentina, *A. proximus* was recorded from the middle Tithonian of Neuquén and Mendoza (Steuer 1897–1921; Burckhardt 1900a; Haupt 1907; Krantz 1926–8; Weaver 1931; H. A. Leanza 1980; Parent 2003a; Aguirre-Urreta & Vennari 2009). *A.* cf. *proximus* is also recorded for the upper part of the lower Tithonian in Tibet (Yin & Enay 2004).

Genus *Micracanthoceras* Spath, 1925

Type species. *Ammonites microcanthus* Oppel in Zittel (1868).

Micracanthoceras microcanthum (Oppel, 1865) (Fig. 15)

1868 *Ammonites microcanthus* Oppel in Zittel: 93, pl. 17, figs 3a, b, 4, 5a–c, *non* pl. 17, figs 1a, 2 (= *Himalayites* sp.), ?pl. 17, fig. 1b, *non* pl. 17, fig. 4.

1897 *Reineckeia microcantha* (Oppel); Steuer: 156, pl. 21, figs 3–5.

1921 *Hoplites* aff. *microcanthus* (Oppel); Burckhardt: pl. 18, figs 5–9.

1921 *Reineckeia microcantha* (Oppel); Steuer: 56, pl. 7, figs 3–5.

1945 *Micracanthoceras tapiai* A. F. Leanza: 43, pl. 6, figs 5, 6.

1945 *Himalayites concurrens* A. F. Leanza: 46, pl. 3, figs 5, 6.

1945 *Micracanthoceras lamberti* A. F. Leanza: 44, pl. 3, figs 9, 10.

1981b *Micracanthoceras lamberti* A. F. Leanza; H. A. Leanza: 570, pl. 3, figs 5, 6.

1981b *Himalayites concurrens* A. F. Leanza; H. A. Leanza: pl. 3, figs 9, 10.

1981b *Micracanthoceras tapiai* A. F. Leanza; H. A. Leanza: 570, pl. 3, figs 14, 15.

1985 *Micracanthoceras* (*Micracanthoceras*) *microcanthum* (Oppel); Tavera: 169, pl. 21, figs 1–4, pl. 22, figs 1–6.

2009 *Micracanthoceras* cf. *microcanthum* (Oppel); Shome & Bardhan: 6, pl. 4, figs a–g.

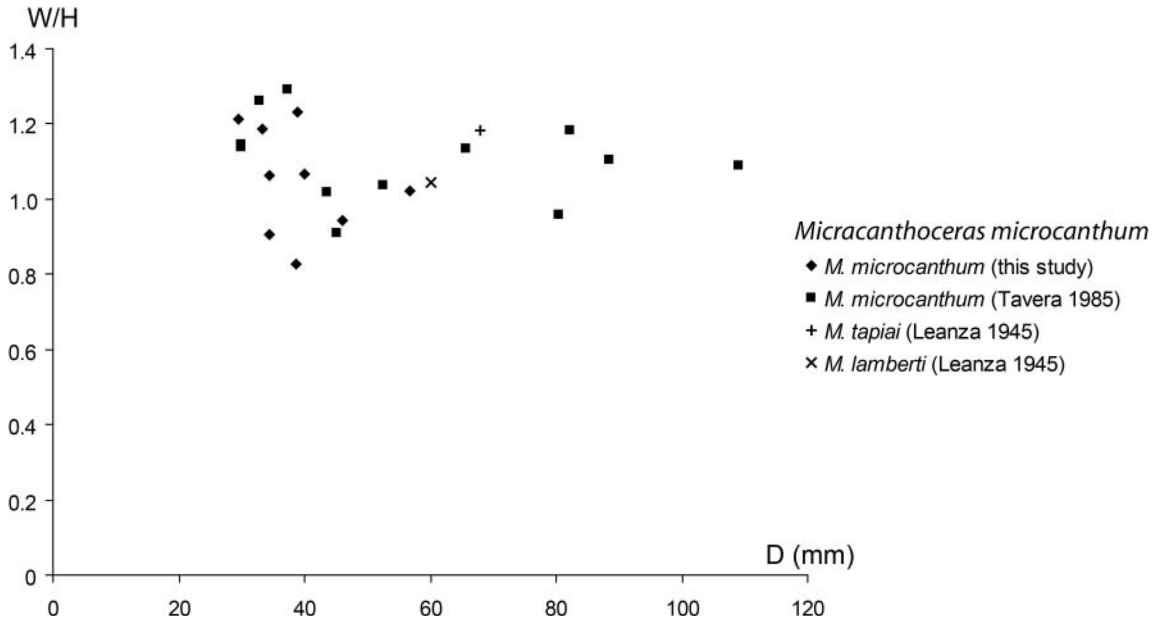

Figure 14. Relationship between W/H and D in *Micracanthoceras microcanthum* (Oppel, 1865). During juvenile stages (D <50 mm), the whorl section is considerably more variable than in adults (D >50 mm).

?2011b *Micracanthoceras* sp. A Parent *et al.*: 75, fig. 29E.

Type. The lectotype of *Ammonites microcanthus* is the specimen figured by Zittel (1868, pl. 17, fig. 3) designated by Spath (1925, footnote p. 144).

Material. Thirty-five specimens (Supplementary Table 8). CPUC/RM/99-43, CPUC/RM/99-72, CPUC/RM/99-75 are complete phragmocones, moderately to well preserved. CPUC/RM/99-08, CPUC/RM/99-70, CPUC/RM/99-71, CPUC/RM/99-83, CPUC/RM/Rd-31, CPUC/RM/Rd-32, CPUC/RM/Rd-35 are well-preserved fragmentary phragmocones. CPUC/RM/99-03, CPUC/RM/99-23, CPUC/RM/99-36, CPUC/RM/99-37, CPUC/RM/99-38, CPUC/RM/99-51, CPUC/RM/99-73, CPUC/RM/99-82, CPUC/RM/99-84, CPUC/RM/Rd-04, CPUC/RM/Rd-19 and CPUC/RM/Rd-44 are moderately to poorly preserved fragmentary phragmocones. CPUC/RM/99-05, CPUC/RM/99-06, CPUC/RM/99-12, CPUC/RM/99-20, CPUC/RM/99-21, CPUC/RM/99-22, CPUC/RM/99-27, CPUC/RM/99-29, CPUC/RM/99-30, CPUC/RM/99-34, CPUC/RM/Rd-38, CPUC/RM/99-42 and CPUC/RM/Rd-02 are small fragments.

Description. Evolute and umbilicus wide. Whorl section is rounded and wider than high. Maximum width on the middle part of the flank. Umbilical border is rounded, flanks are convex and the venter is widely rounded with a smooth furrow. Ornament is composed of fine rectiradiate ribs. Simple and bifurcated ribs alternate irregularly. Many bi- and trifurcated ribs show fine tubercles at point of division. All ribs end in fine tubercles on the venter where a smooth furrow is present. Some specimens show constrictions parallel to the ribs. Inner whorls (D < 50 mm) are rather variable in ornamentation, but outer whorls are more homogenous (Fig. 14).

Remarks. *Micracanthoceras microcanthum* is well known for its wide range of morphological variation (Tavera 1985). *Micracanthoceras lamberti* described by A. F. Leanza (1945) was separated based on the point of rib bifurcation being situated more externally than in *M. microcanthum*. The same author distinguished *M. tapiai* based on a more irregular ornamentation and lateral tubercles. These morphological differences are, however, within the variability of *M. microcanthum*, and *M. lamberti* and *M. tapiai* are here considered to be synonymous.

The morphological elements of *Micracanthoceras concurrens* described by A. F. Leanza (1945) are within the variability of *M. microcanthum* as described by Tavera (1985). *M. concurrens* is therefore considered a junior synonym of *M. microcanthum.*

Micracanthoceras spinulosum is closely related but distinguished by a more rounded whorl section, denser and ventrolaterally more prorsiradiate ribs.

Occurrence. At Rio Maitenes, *Micracanthoceras microcanthum* is recorded from the upper member of the Baños del Flaco Formation, from the unit of calcareous sandstone (Fig. 2). It has been also recorded from the Tithonian of Mexico (Burckhardt 1919) and from the Tithonian of Mendoza in Argentina (Steuer 1897−1921). *Micracanthoceras lamberti*, which is here regarded conspecific with *M. microcanthum*, is recorded from the upper Tithonian of Mendoza, Argentina (A. F. Leanza 1945). In the Tethys region, *M. microcanthum* is recorded at

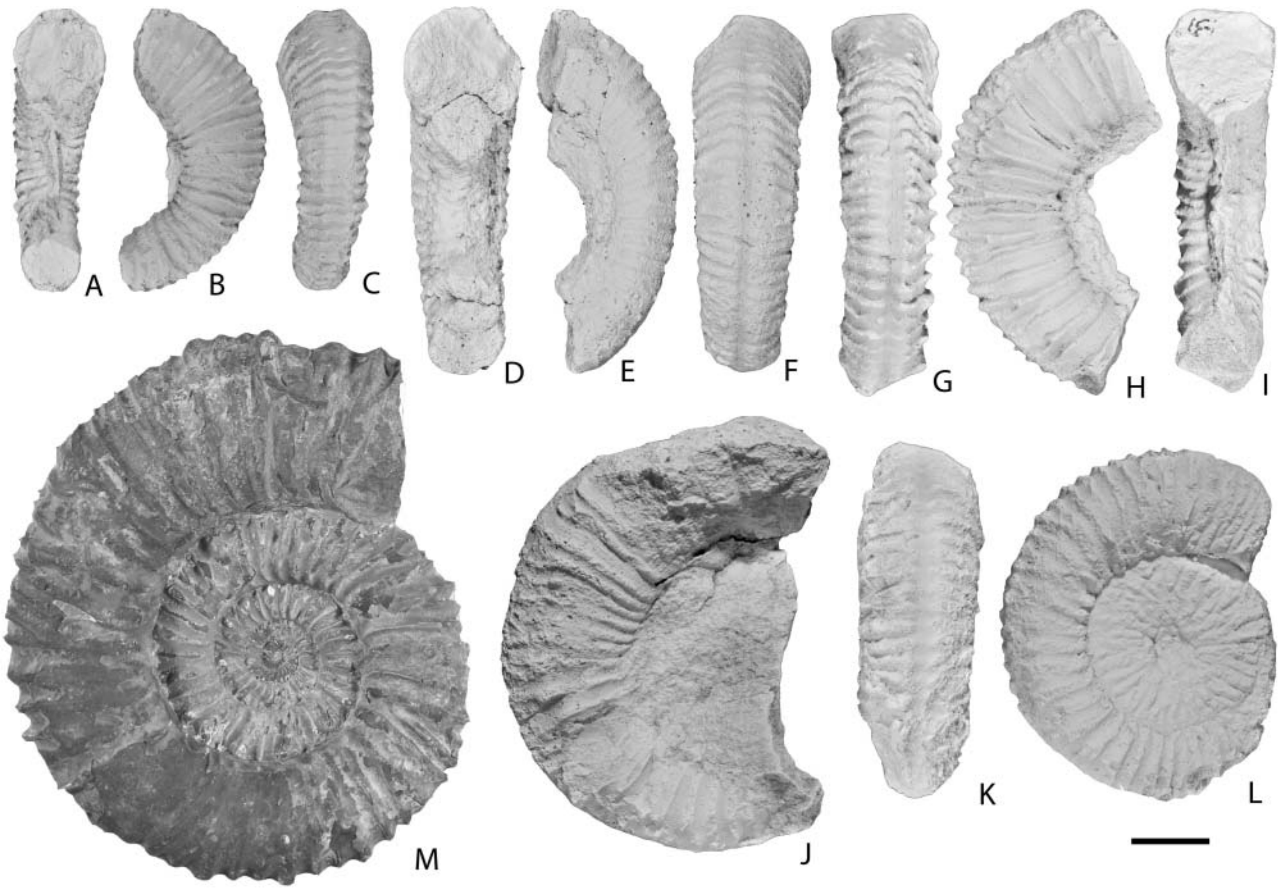

Figure 15. *Micracanthoceras microcanthum* (Oppel, 1865), Baños del Flaco Formation. **A–C,** CPUC/RM/99-71; **D–F,** CPUC/RM/Rd-32; **G–I,** CPUC/RM/Rd-31; **J,** CPUC/RM/99-83; **K, L,** CPUC/RM/99-43; **M,** GZG 499-21 (= *Reineckeia microcantha* in Steuer 1897). Scale bar = 10 mm.

Stromberg, Germany, and from the Italian Alps (Zittel 1868), south-east France (Mazenot 1939), south Spain (Tavera 1985), Bulgaria (Sapunov 1979), Hungary (Főzy 1990), Sicily, Italy (Főzy 1995), Pakistan (Fatmi & Zeiss 1999) and Western India (Shome & Bardhan 2009). This taxon is considered to be an index fossil of the lowermost upper Tithonian *M. microcanthum* Zone (Enay & Geyssant 1975; Tavera 1985; Ogg 2004).

Micracanthoceras spinulosum (Gerth, 1925)
(Fig. 17)

1921 *Berriasella spinulosa* Gerth: 147 (*nomen nudum*).
1921 *Berriasella inaequicostata* Gerth: 147 (*nomen nudum*).
1925 *Berriasella spinulosa* Gerth: 91, pl. 6, figs 1, 2, 2a.
1925 *Berriasella inaequicostata* Gerth: 90, pl. 6, figs 4, 4a, 4b.
1928 *Berriasella spinulosa* Gerth; Gerth: 475, pl. 19, fig. 11.
1937 *Berriasella spinulosa* Gerth; Feruglio: 65, pl. 8, figs 7–13.
1945 *Berriasella inaequicostata* Gerth; A. F. Leanza: 34, pl. 4, fig. 2.
1960 *Berriasella* aff. *spinulosa* Gerth; Bürgl: 194, pl. 5, fig. 13.
1964 *Berriasella inaequicostata* Gerth; Biro: 101, pl. 2, figs 1, 2.
1983 *Berriasella* (*Malbosiceras*?) *inaequicostata* (Gerth); Geyer: 341, text-fig. 3i.
2011b *Steueria alternans* (Gerth); Parent *et al.*: 66, fig. 29A–D.

Type. The lectotype is STIPB 949 (Gerth 1925, p. 91, pl. 6, fig. 1), from the Tithonian of Mendoza, Argentina, designated by Parent *et al.* (2011b, pp. 65–69, fig. 29A).

Material. Twenty-seven specimens (Supplementary Table 9). CPUC/RM/99-25, CPUC/RM/99-26, CPUC/RM/99-28, CPUC/RM/99-52, CPUC/RM/99-60, CPUC/RM/99-70, CPUC/RM/99-88, CPUC/RM/99-11 and CPUC/RM/99-89 are moderately to well-preserved complete phragmocones. CPUC/RM/99-44, CPUC/RM/99-50, CPUC/RM/99-63, CPUC/RM/99-68 and CPUC/RM/99-98 are well-preserved fragmentary phragmocones.

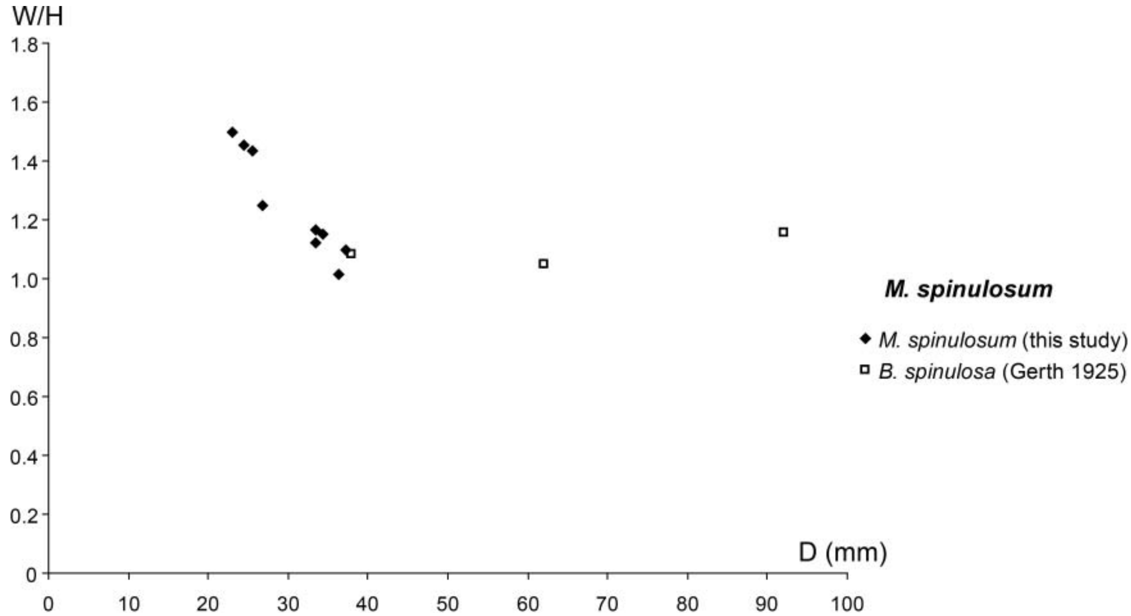

Figure 16. Relationship between W/H and D in *Micracanthoceras spinulosum* (Gerth, 1925). Whorl section is wider than high in juveniles (D < 30 mm) and gradually changes to wider than high in adults (D > 30 mm).

CPUC/RM/99-01, CPUC/RM/99-13, CPUC/RM/99-18, CPUC/RM/99-19, CPUC/RM/99-24, CPUC/RM/99-45 and CPUC/RM/99-97 are moderately to poorly preserved fragmentary phragmocones. CPUC/RM/99-02, CPUC/RM/99-27, CPUC/RM/99-35, CPUC/RM/99-51, CPUC/RM/99-52, CPUC/RM/99-56 and CPUC/RM/99-99 are small fragments.

Description. Evolute and umbilicus wide. Whorl section is rounded and gradually changes during ontogeny, from wider than high in inner whorls (D < 30 mm) to slightly higher than wide in outer whorls (D > 30 mm) (Fig. 16). Umbilical border is rounded, flanks are convex and the venter rounded with a smooth furrow. Maximum width is reached in the middle part of the flank. Ornamentation consists of rectiradiate ribs, bending to slightly prorsiradiate on the ventrolateral area. Most ribs bifurcate on the middle part of the flank, but others are unbranched and a few show trifurcation. At their point of bifurcation, small tubercles are commonly present; their absence in some cases may be the result of preservation as internal moulds. All ribs end in small ventral tubercles at both sides of the smooth furrow.

Remarks. *Micracanthoceras* is characterized by an evolute shell, rounded whorls, small tubercles at bifurcation points of ribs, and small ventral tubercles on each side of the smooth furrow (Arkell *et al.* 1957). *Berriasella* aff. *spinulosa* described by Bürgl (1960) differs only by the absence of unbranched ribs. '*Berriasella*' *inaequicostata* described by Gerth (1921–5) is based mainly on the morphology of the outer whorls, which is similar to *Micracanthoceras spinulosum* as originally described by the same author. After revision of the lectotype (STIPB 949), and taking into consideration the description of *M. spinulosum* given here, we consider '*B.*' *inaequicostata* to be a junior synonym of *M. spinulosum*.

Parent *et al.* (2011b, p. 66, fig. 29A–D) placed '*B.*' *inaequicostata* and *M. spinulosum* in synonymy with *Corongoceras alternans*, but the latter taxon is more evolute and has a whorl section that progressively changes from wider than high in inner whorls, to higher than wide in outer whorls (Fig. 19). Ribs are strong and distanced; both simple and bifurcate ribs occur (see description and remarks for C. *alternans* below).

Micracanthoceras vetustum (Steuer, 1897), *Corongoceras duraznense* (Krantz, 1928) and *Riasanites rjasanensoides* Krantz, 1928 are closely related, but ribs in these species are more spaced.

Occurrence. At Rio Maitenes, *Micracanthoceras spinulosum* is present in the upper member of the Baños del Flaco Formation, in the unit of calcareous sandstone (Fig. 2). In Central Argentina, the species has been recorded to co-occur with *Kilianella burckhardti* by Gerth (1925, p. 128); according to A. F. Leanza (1945), this horizon corresponds to the level of *Corongoceras alternans* in the upper Tithonian. In Colombia *M. spinulosum* was described from the upper Berriasian (Bürgl 1960), and in Chile Biro (1964, p. 56) recorded the species from the *Corongoceras alternans* zone of the upper Tithonian.

Genus ***Corongoceras*** Spath, 1925

Type species. *Corongoceras lotenoense*, pro *Hoplites köllikeri* (Oppel, 1863), Haupt (1907, pl. 9, fig. 7a, b),

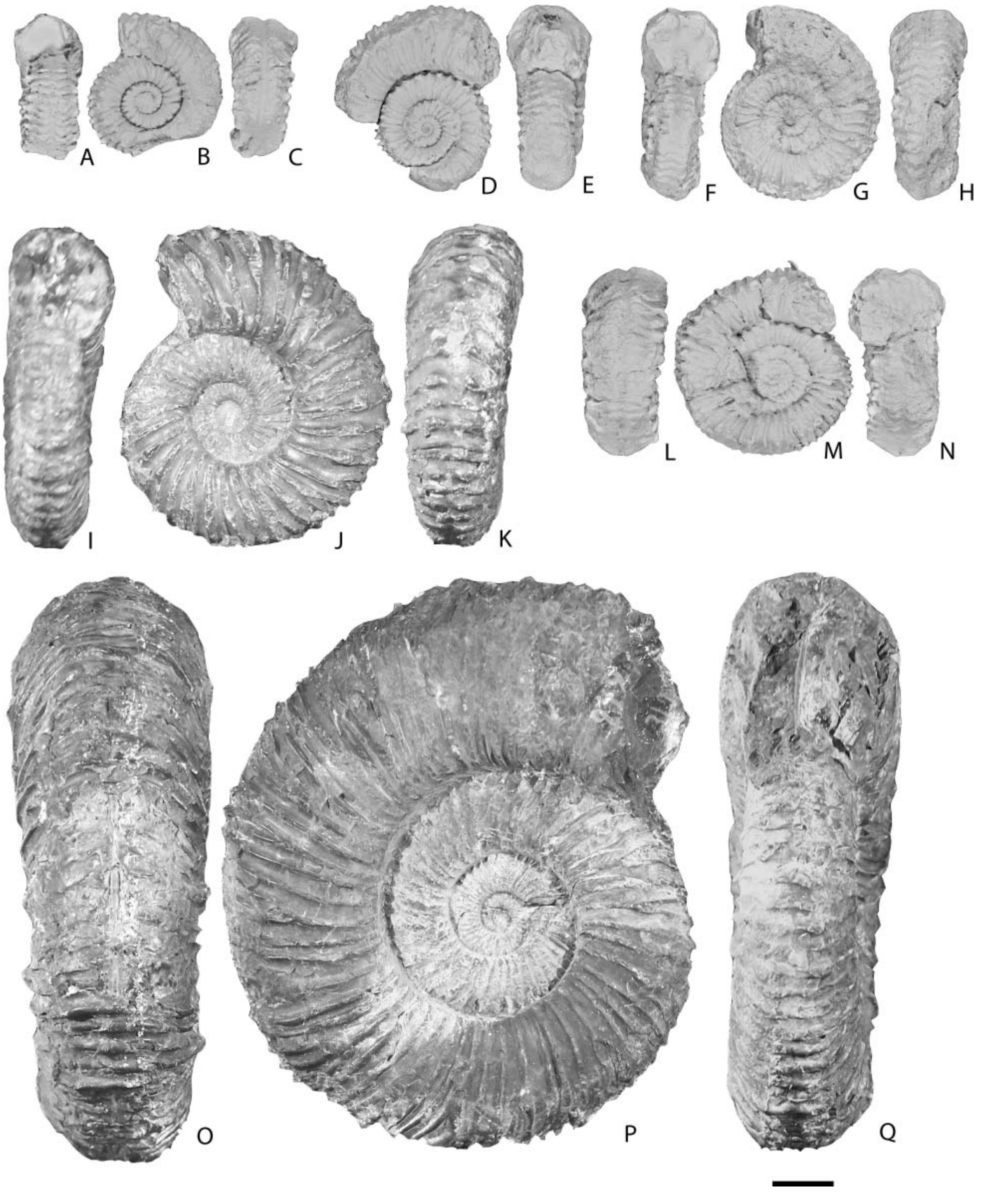

Figure 17. A–H, L–N, *Micracanthoceras spinulosum* (Gerth, 1925), Baños del Flaco Formation; **A–C,** CPUC/RM/99-26; **D, E,** CPUC/RM/99-44; **F–H,** CPUC/RM/99-52; **L–N**, CPUC/RM/99-60. **I–K, O–Q,** *Berriasella spinulosa*, from Gerth (1925); **I–K,** STIPB-947; **O–Q,** STIPB-949 (lectotype). Scale bar = 10 mm.

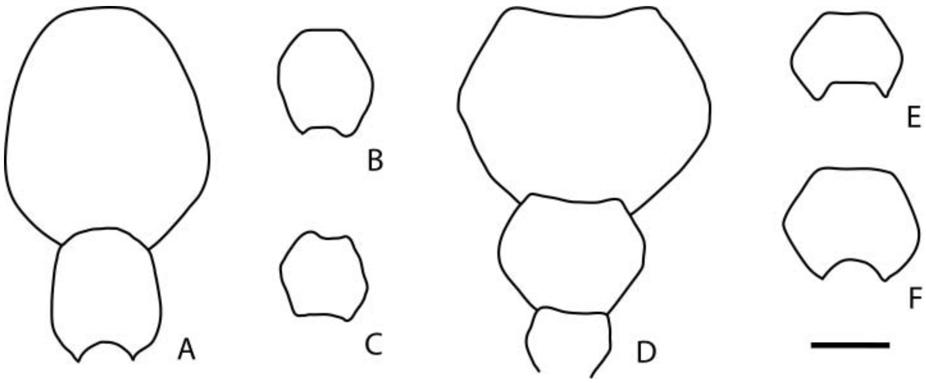

Figure 18. Whorl sections in *Corongoceras*. **A–C,** *Corongoceras alternans* (Gerth, 1925); **A,** holotype, STIPB-939; **B,** CPUC/RM/99-95; **C,** CPUC/RM/99-96. **D, E,** *Corongoceras evolutum* Corvalán, 1959; **D,** holotype, SNGM 7001 (= IIG 133); **E,** CPUC/RM/99-80. **F,** *Corongoceras lotenoense* Spath, 1925, holotype (= *Hoplites köllikeri* Haupt, 1907), STIPB-201. Scale bar = 10 mm.

STIPB 201, by subsequent designation of Spath (1925, p. 144).

Remarks. Parent (2001) fully discussed this genus. The venter in juvenile inner whorls is rounded to flat and gradually changes to slightly flat in adults.

Corongoceras alternans (Gerth, 1925)
(Figs 19, 20)

1900b *Reineckeia koellikeri* (Oppel); Burckhardt: 16, pl. 20, figs 14, 15, pl. 21, fig. 1.

1900b *Reineckeia microcantha* (Oppel); Burckhardt: 16, pl. 20, figs 16, 17 (cf. *Corongoceras alternans*).

1921 *Berriasella alternans* Gerth: 89, pl. 6, fig. 3, 3a (*nomen nudum*).

1928 *Berriasella alternans* Gerth; Gerth: 474, pl. 19, fig. 10, 10a.

1931 *Berriasella alternans* Gerth; Windhausen: pl. 30, Fig. 6.

non 1937 *Berriasella spinulosa* Gerth; Feruglio: 65, figs 7–13 (= *Micracanthoceras spinulosum*).

non 1937 *Berriasella alternans* (n var.?) Gerth; Feruglio: 70, pl. 8, fig. 6 (= *Lytohoplites burckhardti*).

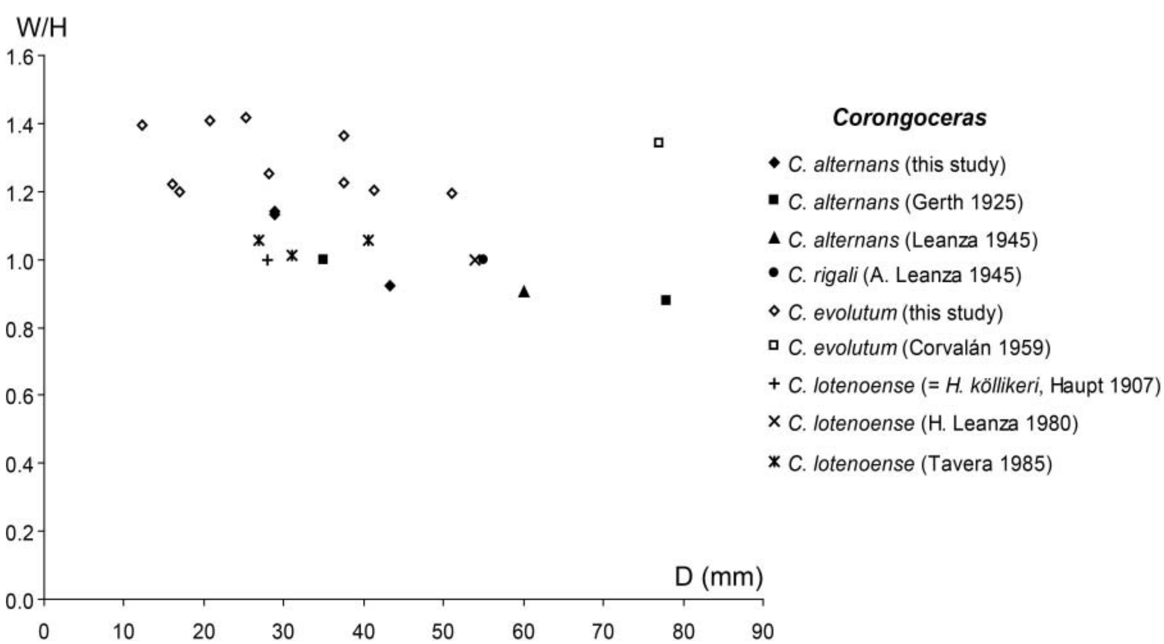

Figure 19. Relationship between W/H and D in *Corongoceras alternans* (Gerth, 1925), *Corongoceras evolutum* Corvalán, 1959 and *Corongoceras lotenoense* Spath, 1925. These three species of *Corongoceras* are closely related, but *C. evolutum* is clearly distinguished from the other two.

1945 *Berriasella pastorei* A. F. Leanza: 33, pl. 3, figs 12, 13.
non 1945 *Berriasella inaequicostata* Gerth; A. F. Leanza: 34, pl. 4, fig. 2 (= *Micracanthoceras spinulosum*).
non 1945 *Berriasella groeberi* A. F. Leanza: 37, pl. 4 (= *Corongoceras mendozanum*).
non 1945 *Berriasella* (?) *delhaesi* A. F. Leanza: 39, pl. 6, figs 1, 2 (= *Corongoceras mendozanum*).
non 1945 *Himalayites concurrens* A. F. Leanza: 46, pl. 3, figs 5, 6 (= *Micracanthoceras microcanthum*).
1945 *Corongoceras alternans* (Gerth); A. F. Leanza: 47, pl. 1, figs 2, 3.
1945 *Corongoceras rigali* A. F. Leanza: 48, pl. 6, figs 3, 4.
1959 *Corongoceras alternans* (Gerth); Corvalán & Pérez: 46, pl. 13, fig. 32a, b.
non 1960 *Berriasella* aff. *spinulosa* Gerth; Bürgl: 194, pl. 5, fig. 13 (= *Micracanthoceras spinulosum*).
1964 *Corongoceras alternans* (Gerth); Biro: 103, pl. 24, figs 1a, b, 2a, b, 3a, b, pl. 25, figs 1a, b, 2a, b.
1966 *Berriasella* cf. *alternans* Gerth; Fuenzalida: 135, figs 24–26.
non 1967 *Berriasella spinulosa* Gerth; A. F. Leanza: 145 (= *Micracanthoceras spinulosum*).
non 1972 *Micracanthoceras spinulosa* (Gerth); Enay: 375 (= *Micracanthoceras spinulosum*).
1973 *Blanfordiceras* aff. *pastorei* (Leanza); A. F. Leanza: 83, fig. 29.
1981 *Berriasella pastorei* Leanza; H. A. Leanza: pl. 3, figs 13, 14.
non 1981 *Himalayites concurrens* Leanza; H. A. Leanza: pl. 3, figs 9, 10 (= *Micracanthoceras microcanthum*).
2001 *Corongoceras* cf. *alternans* (Gerth); Parent: 32, figs 5F, 8K, L.
2001 *Corongoceras alternans* (Gerth); Parent: fig. 9D, E.
non 2005 *Micracanthoceras concurrens* (Leanza); Klein: 18 (= *Micracanthoceras microcanthum*).
non 2005 *Micracanthoceras*? *spinulosum* (Gerth); Klein: 20 (= *Micracanthoceras spinulosum*).
non 2005 *Berriasella* (*Berriasella*)? *delhaesi* Leanza; Klein: 169 (= *Corongoceras mendozanum*).
non 2005 *Berriasella* (*Berriasella*) *groeberi* Leanza; Klein: 170 (= *Corongoceras mendozanum*).
2005 *Blanfordiceras* (*Blanfordiceras*) *pastorei* (Leanza); Klein: 202.
non 2005 *Malbosiceras*? *inaequicostatum* (Gerth); Klein: 209 (= *Micracanthoceras spinulosum*).
non 2011b *Steueria alternans* (Gerth); Parent *et al.*: 66, fig. 29A–D (= *Micracanthoceras spinulosum*).
non 2011b *Steueria alternans* (Gerth); Parent *et al.*: 66, figs 30–31 (= ?*Micracanthoceras spinulosum*).

Type. The holotype is specimen STIPB 939, the original of Gerth (1925, p. 89, pl. 6, fig. 3, 3a) from the Tithonian of Mendoza, Argentina. It was refigured and discussed by Parent (2001, p. 32, fig. 9D, E).

Material. Six internal moulds (Supplementary Table 10). CPUC/RM/99-07, CPUC/RM/99-69, CPUC/RM/99-95, CPUC/RM/99-96 and CPUC/RM/99-97 are well-preserved fragmentary phragmocones. CPUC/RM/99-46 is a regular to poorly preserved fragmentary phragmocone. CPUC/RM/99-14 is a small fragment.

Description. Evolute and umbilicus wide. Whorl section is rounded and wider than high in inner whorls (D < 30 mm), and progressively higher than wide in outer whorls (D > 30 mm), when the whorl section becomes oval and flanks are rounded. The venter is rounded with a smooth furrow (Fig. 18). Ornamentation consists of prominent and widely spaced primary ribs which are slightly prorsiradiate and convex. They initiate on the umbilical border and either remain single or bifurcate on the middle or upper part of the flank. These secondary ribs are as strong as primaries. Points of rib bifurcation are characterized by tubercles. On the venter, ribs end in tubercles on both sides of the smooth furrow.

Remarks. *Corongoceras* is characterized by spaced ribs on the outer whorl and less distant ribs on inner whorls; these ribs are bifurcated with tubercles at the division point and spinous tubercles on the ventral ends of the ribs. Parent *et al.* (2011b) included *Corongoceras alternans* in the new genus *Steueria*. This genus was differentiated by having a well-rounded venter, and finer and denser ribs. According to the original description of Spath (1925) and Arkell *et al.* (1957), and the description of *Corongoceras* given here, a rounded venter is present in inner whorls of *Corongoceras* and during ontogeny grades into the flat venter seen in outer whorls. These characteristics are observed in the specimens described here, which are therefore assigned to *Corongoceras*.

Corongoceras alternans is characterized by an evolute shell and a whorl section that progressively changes from wider than high in inner whorls, to higher than wide in outer whorls (Fig. 19). Ribs are strong and distanced; both simple and bifurcate ribs occur. Specimens described as *Steueria alternans* by Parent *et al.* (2011b, p. 66, figs 30, 31) are characterized by denser ribs throughout ontogeny; the whorl section is wider and tubercles are finer than those in the lectotype of *Corongoceras alternans*. The Parent *et al.* (2011b) specimens are here assigned to *Micracanthoceras spinulosum*.

Both *Micracanthoceras spinulosum* and '*Berriasella*' *inaequicostatum* were considered synonyms of *Corongoceras alternans* by Parent *et al.* (2011b, p. 66, fig. 29A–D). The morphological characteristics that define *C. alternans* do not agree with *M. spinulosum* as described by Gerth (1925) and here. *M. spinulosum* shows a rounded whorl section that changes gradually from wider than high in the inner whorls to slightly higher than wide in outer whorls (see Fig. 16); rectiradiate ribs are slightly prorsiradiate on the upper flank, most ribs bifurcate on the middle part of the flank; at the point of bifurcation, small tubercles are commonly present; all ribs end in small ventral tubercles at both sides of the smooth furrow.

Corongoceras rigali Leanza (1945) was distinguished from *C. alternans* based on fine and dense ribs on inner whorls but these differences are minor and are here considered part of a common intraspecific variation. The related *C. evolutum* differs by closer-standing ribs, wider umbilicus, wider than high whorl section and venter that is wider and presents a well-marked furrow (Fig. 19). *Corongoceras lotenoense* differs by having a subhexagonal whorl section, a flat venter, a slightly wider coiling and denser ribs in young stages.

Occurrence. At Rio Maitenes, this taxon is present in the upper member of the Baños del Flaco Formation, in the unit of calcareous sandstone (Fig. 2). *Corongoceras alternans* was recorded from the lower part of the upper Tithonian in Mendoza, Argentina (Gerth 1925; Leanza 1945; Parent 2001; Parent *et al.* 2011b). In Chile, the taxon has been recorded from the upper Tithonian of Alto Palena (Fuenzalida 1966) and from the middle part of the upper Tithonian at Lo Valdés (Biro 1964).

Corongoceras evolutum Corvalán, 1958
(Fig. 21A–Q)

1958 *Corongoceras evolutum* Corvalán in Corvalán & Pérez: 43, pl. 10, fig. 21a, b (*nomen nudum*).
1959 *Corongoceras evolutum* Corvalán: 18, pl. 7, figs 25, 26.
1964 *Corongoceras evolutum* Corvalán; Biro: 104, pl. 26, fig. 1a–d.

Type. The holotype is SNGM 7001 (= IIG 133), the original of Corvalán (1959, p. 18, pl. 7, figs 25, 26), by monotypy. The specimen is from the upper Tithonian of Rio Leñas, Chile.

Material. Twenty-six specimens (Supplementary Table 11). CPUC/RM/99-80, CPUC/RM/99-90, CPUC/RM/99-91, CPUC/RM/99-92, CPUC/RM/99-94 and CPUC/RM/99-100 are complete phragmocones and are moderately to well preserved. CPUC/RM/99-64, CPUC/RM/99-93, CPUC/RM/99-97 are well-preserved fragmentary phragmocones. CPUC/RM/99-09, CPUC/RM/99-15, CPUC/RM/99-32, CPUC/RM/99-40, CPUC/RM/99-41, CPUC/RM/99-44, CPUC/RM/99-47, CPUC/RM/99-48, CPUC/RM/99-04, CPUC/RM/99-55, CPUC/RM/99-62, CPUC/RM/99-73, CPUC/RM/99-75, CPUC/RM/Rd-16 are moderately to poorly preserved fragmentary phragmocones. CPUC/RM/99-16, CPUC/RM/99-33, CPUC/RM/99-65 are small fragments.

Description. Very evolute and umbilicus wide (U/D = 0.42–0.58). Whorl section is subhexagonal, wider than high. The umbilical border is straight and steep, flanks are strongly convex, and the venter is wide with a well-marked wide and smooth furrow (Fig. 18). The maximum width is on the middle part of the flank. Ornamentation consists of strong primary ribs which are rectiradiate to slightly prorsiradiate. They initiate on the umbilical border. On the middle part of the flank, most primaries bifurcate into secondary ribs, as strong as the primary ribs. Acute tubercles are preserved in some specimens on the point of bifurcation. On the ventral shoulder, all ribs terminate in acute tubercles on both sides of the smooth ventral furrow.

Remarks. *Corongoceras evolutum* was briefly described in Corvalán & Pérez (1958 p. 43, pl. 10, fig. 21a, b) from the upper Tithonian of Río Leñas, Chile but remained a *nomen nudum* until Corvalán (1959, p. 18, pl. 7, figs 25, 26) designated a holotype (SNGM 7001 = IIG 133). *C. evolutum* is characterized by a wide umbilicus, strong ribs, and a wide venter with a well-marked wide and smooth furrow (Corvalán 1959).

Corongoceras mendozanus and *C. involutum* are closely related, but *C. evolutum* clearly differs by the wide umbilicus and the wide venter with a well-marked furrow. The closely related *C. lotenoense* is more involute, ribs are more distanced, and the whorl section is higher (Fig. 18). *Corongoceras alternans* is also closely related but the whorl section is higher than wide, the coiling more involute and the ribs are more separated (Fig. 18). The whorl section of *C. evolutum* is wider than high and clearly differs from *C. alternans* and *C. lotenoense* (Figs 18, 19).

Occurrence. At Rio Maitenes, this species occurs in the upper member of the Baños del Flaco Formation, in the unit of calcareous sandstone (Fig. 2). *Corongoceras evolutum* is endemic to central Chile, recorded by Corvalán (1959) from the upper Tithonian of Rio Leñas, and by Biro (1964) from the middle part of the upper Tithonian of Lo Valdés (Lo Valdés Formation).

Family **Neocomitidae** Salfeld, 1921
Subfamily **Berriasellinae** Spath, 1922
Genus ***Substeueroceras*** Spath, 1923

Type species. *Odontoceras koeneni* Steuer, 1897, p. 171, pl. 17, figs 1–3; by subsequent designation of Spath (1923, p. 305).

Substeueroceras koeneni (Steuer, 1897)
(Fig. 21R)

1897 *Odontoceras koeneni* Steuer: 171, pl. 31, figs 1–5.
1906 *Perisphinctes* cfr. *Koeneni* (Steuer); Burckhardt: 137, pl. 39, fig. 1.

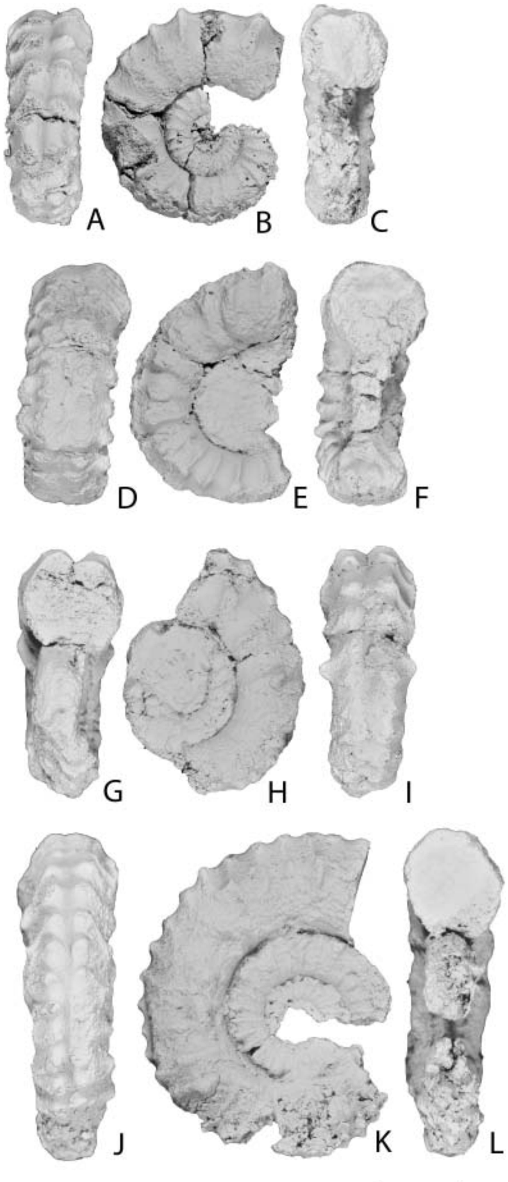

Figure 20. *Corongoceras alternans* (Gerth, 1925), Baños del Flaco Formation. **A–C,** CPUC/RM/99-69; **D–F,** CPUC/RM/99-07; **G–I,** CPUC/RM/99-96; **J–L,** CPUC/RM/99-95. Scale bar = 10 mm.

1921 *Odontoceras Koeneni* n. sp. Steuer: 73, pl. 17, figs 1–5.
1925 *Steueroceras Koeneni* (Steuer); Gerth: 83, pl. 6, fig. 6.
1945 *Substeueroceras koeneni* (Steuer); A. F. Leanza: 28, pl. 5, figs 7, 8, pl. 7, fig. 4.
1959 *Substeueroceras koeneni* (Steuer); Corvalán: 20, pl. 7, fig. 27.
1990 *Substeueroceras koeneni* (Steuer); Aguirre-Urreta & Charrier: 266, pl. 1, fig. 3.

Type. As for the genus.

Material. A single imprint of half a phragmocone (CPUC/RM/115–4), which is regular to well preserved.

Description. Involute coiling and ornament consists of fine and dense ribs. On the umbilical border the ribs are slightly rursiradiate. On the flank they bend forward to a prorsiradiate direction and they are concave on the ventrolateral area. Ribs are divided on the dorsolateral area and again on the middle part of the flank, where bifurcation is irregular. Some ribs are undivided.

Remarks. The single specimen here described is an imprint of a fragmentary phragmocone, but preserves the typical ornamentation elements of *S. koeneni*.

Occurrence. At Rio Maitenes, this taxon is registered in the upper member of the Baños del Flaco Formation, in the unit of sandy limestone (Fig. 2). In Argentina and Chile *S. koeneni* has been considered an index for the upper Tithonian (Steuer 1897; Gerth 1925; Corvalán 1959) and even the uppermost part of the upper Tithonian (Biro 1964; H. A. Leanza 1981b; Parent & Capello 1999; Parent 2001). In their review on ammonites of the Baños del Flaco Formation Hallam *et al.* (1986) indicate that the occurrence of *Substeueroceras koeneni* may correspond to the basal Berriasian, if Zeiss's (1983) correlation is accepted.

In the upper Tithonian *S. koeneni* has been recorded from Perú (Rivera 1951), Mexico (Burckhardt 1906), Pakistan (Fatmi & Zeiss 1999), and in the Berriasian from Colombia (Haas 1960), Mexico (Burckhardt 1906) and eastern Russia (Sey & Kalacheva 1999, 2001). In Yemen *S. koeneni* occurs in the *Durangites* zone of the upper Tithonian, and the *Occitanica* Zone of the Berriasian (Howarth 1998). In Mexico the species has been recorded from calpionellid zone C of the Berriasian (Adatte *et al.* 1994).

Biostratigraphy

Ammonites presented here from the Baños del Flaco Formation at Rio Maitenes were collected *in situ* and bed-by-bed. The most abundant species are *Windhauseniceras internispinosum*, *Aulacosphinctes proximus*, *Micracanthoceras microcanthum*, *M. spinulosum* and *Corongoceras evolutum*. The distribution of the species is summarized in Figure 2, and the boundaries of the biozones using lithological control and are tentative. Hallam *et al.* (1986) distinguished three biozones based on ammonites collected at Rio Maitenes. Here, we refine this zonation (Fig. 2) and propose (from bottom to top) the following zonation:

***Virgatosphinctes scythicus–Pseudolissoceras zitteli* Zone.** This zone is characterized by the presence of *V. scythicus* and *P. zitteli* and also contains *Lithacoceras*

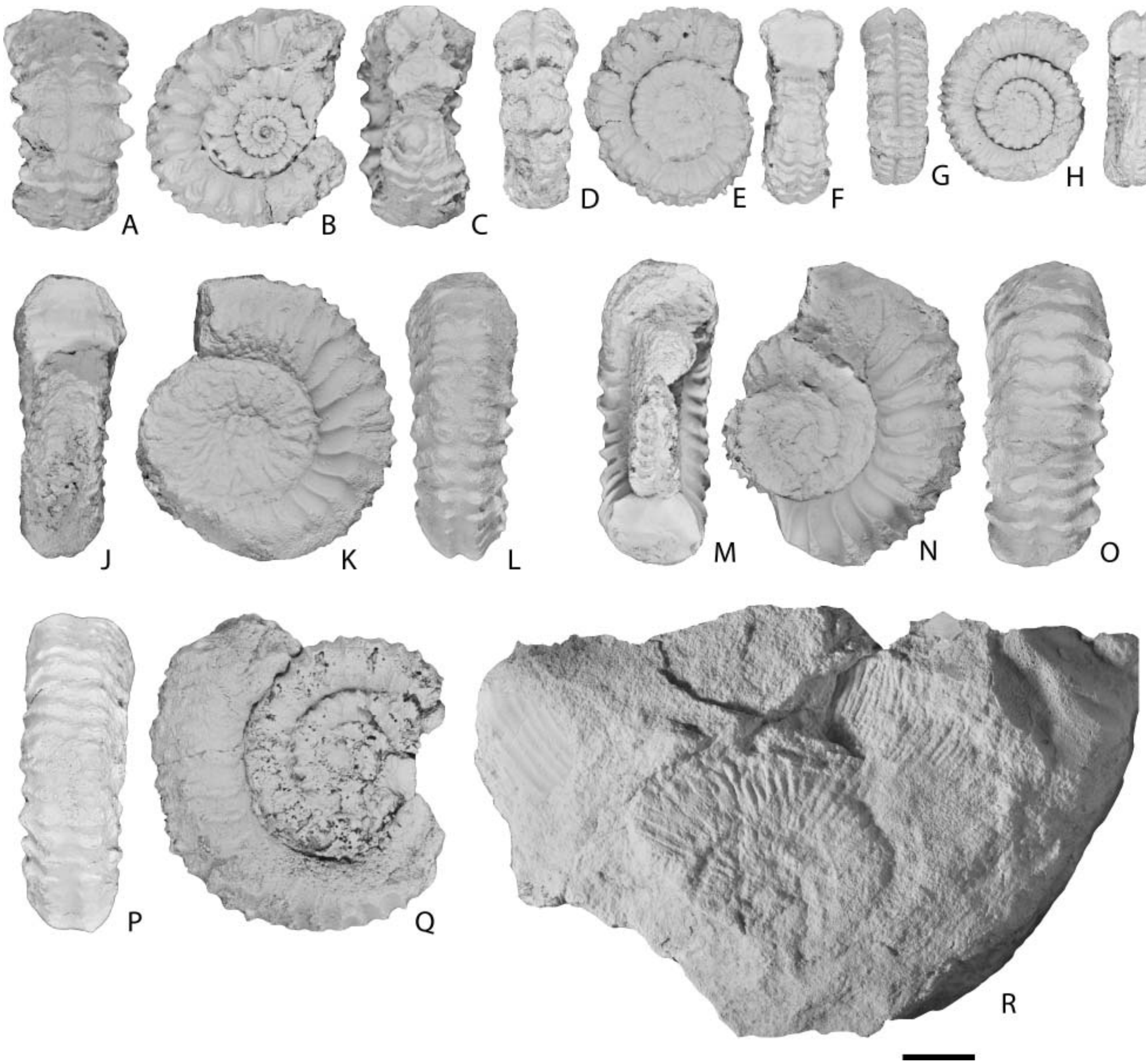

Figure 21. **A–Q,** *Corongoceras evolutum* Corvalán, 1959, Baños del Flaco Formation; **A–C,** CPUC/RM/99-100; **D–F,** CPUC/RM/99-94; **G–I,** CPUC/RM/99-90; **J–L,** CPUC/RM/99-80; **M–O,** CPUC/RM/99-64; **P, Q,** CPUC/RM/99-97. **R,** *Substeueroceras koeneni* (Steuer, 1897), Baños del Flaco Formation, CPUC/RM/115-04. Scale bar = 10 mm.

malarguense and *Choicensisphinctes windhauseni*. It is present in the lower part of the lower member of the Baños del Flaco Formation (Fig. 2).

Windhauseniceras internispinosum **Zone.** This zone is defined by the occurrence of *W. internispinosum*. *Catutosphinctes* cf. *americanensis* and *Aulacosphinctes proximus* are also present (Fig. 2). The zone is recorded in the upper part of the lower member of the Baños del Flaco Formation.

Micracanthoceras microcanthum–Corongoceras alternans **Zone.** *M. microcanthum* and *C. alternans* are index fossils for this unit, which occurs in the lower part of the upper member of the Baños del Flaco Formation. *Micracanthoceras spinulosum* and *Corongoceras evolutum* are also present.

Substeueroceras koeneni **Zone.** *S. koeneni*, the index fossil for this zone, is rare in the zone, which is present in the upper part of the upper Member of the Baños del Flaco Formation (Fig. 2).

Correlation

The presence of *Windhauseniceras internispinosum* and *Corongoceras alternans* indicates that the Baños del Flaco Formation is Tithonian in age. These taxa are widespread in South America (e.g. Zeiss & Leanza 2010; Parent *et al.*

2011b). In addition, Tethyan index fossils of the Tithonian are here recorded for the first time in South America.

Virgatosphinctes scythicus is an index fossil in Russia for the lower part of the middle Volgian (e.g. Rogov 2010), whereas *Micracanthoceras microcanthum* is an index fossil for the upper Tithonian in the European Tethys and Mexico (e.g. Enay & Geyssant 1975; Tavera 1985; Ogg 2004; Ogg & Hinnov 2012). The expected occurrence in South America of these species has not been recorded.

The range of *Substeueroceras koeneni* in the Chilean sections is controversial. In Argentina, the taxon has long been considered an index of the uppermost Tithonian (e.g. A. F. Leanza 1945; H. A. Leanza 1980). Zeiss (1983) thus began a dispute when he proposed that this species extended into the basal Berriasian. This latter interpretation received support when Adatte *et al*. (1994) recorded *S. koeneni* from the early Berriasian of Mexico, consistent with the calpionellid record. In Argentina, the taxon has also recently been considered as an index for the basal Berriasian (e.g. Zeiss & Leanza 2010; Parent 2011b).

Based on the biozonation presented above, we assign the Baños del Flaco Formation to middle Tithonian–early Berriasian (Fig. 2). The *Virgatosphinctes scythicus–Pseudolissoceras zitteli* Zone corresponds to the lower part of the middle Tithonian based on the presence of *V. scythicus*, which is the index fossil for the lower middle Volgian (= middle Tithonian). The *Windhauseniceras internispinosum* Zone is referred to the upper middle Tithonian. The *Micracanthoceras microcanthum–Corongoceras alternans* Zone corresponds to the upper Tithonian Stage, based on the fact that *M. microcanthum* is the zonal index fossil of the upper Tithonian in the Tethys. The *Substeueroceras koeneni* Zone is referred to the lower Berriasian Stage (Lower Cretaceous).

Palaeobiogeographical significance of the Baños del Flaco ammonites

The Baños del Flaco assemblage contains several taxa currently known only from central Chile and central Argentina. These taxa, endemic to the region, are *Choicensisphinctes windhauseni*, *Catutosphinctes americanensis*, *Windhauseniceras internispinosum*, *Micracanthoceras spinulosum*, *Corongoceras alternans* and *C. evolutum* (Fig. 22). Other taxa (e.g. *Virgatosphinctes scythicus*, *Pseudolissoceras zitteli* and *Lithacoceras malarguense*) are known elsewhere from southern high latitude and Pacific regions, such as Antarctica, and also from East Russia and Mexico (Fig. 22). Indo-African species such as *Aulacosphinctes proximus* and *Substeueroceras koeneni* (which is also reported from Mexico) are less abundant;

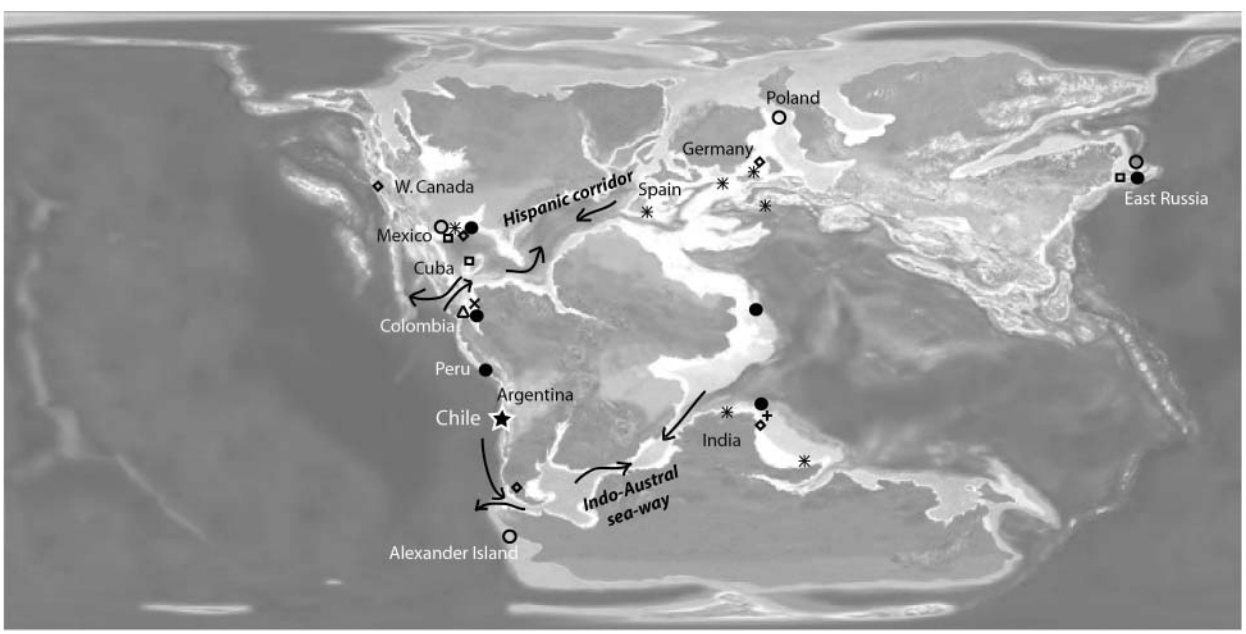

Figure 22. Palaeobiogeographical map (Blakey 2002) for the Late Jurassic (Tithonian), showing localities from which taxa of the Baños del Flaco ammonite assemblage have been recorded. Note that two alternative migration routes likely existed for the exchange of marine fauna, the Hispanic corridor and the Indo–Austral seaway. Species endemic to Chile or Argentina are: *Choicensisphinctes windhauseni*, *Catutosphinctes americanensis*, *Corongoceras alternans*, *Corongoceras evolutum* (Chile). Symbols are: △ *Windhauseniceras internispinosum*; × *Micracanthoceras spinulosum*; ○ *Virgatosphinctes scythicus*; ▭ *Pseudolissoceras zitteli*; ◇ *Lithacoceras malarguense*; + *Aulacosphinctes proximus*; • *Substeueroceras koeneni*; * *Micracanthoceras microcanthum*, ★ammonites from Rio Maitenes section, Baños del Flaco Formation, that contain the ammonites species listed.

the single cosmopolitan species is *Micracanthoceras microcanthum* (Fig. 22).

The new findings at Rio Maitenes indicate that some Late Jurassic ammonites known from South America may be taxonomically close, or even conspecific, with Tethyan forms and even with taxa from the Northern Boreal realm. The possible occurrence of these taxa was earlier suggested by, for example, H. A. Leanza (1981a, b) and Cecca (1999). Migration between these faunal realms could have occurred via two possible corridors:

1. A northern route through the Mexican basin and the Caribbean region ('Hispanic corridor') has frequently been proposed based on brachiopod, ammonite, plesiosaurid and crocodilian affinities (e.g. Riccardi 1991; Gasparini & Fernandez 1997; Fig. 22). However, this idea has recently been challenged by the discovery of endemic Late Jurassic marine reptile assemblages in Mexico (Frey *et al*. 2002; Buchy 2007), with the exception of *Ophtalmosaurus icenicus* (Buchy 2007). Direct and long-term faunal exchange and transatlantic correlation was not achieved in this region until the middle Berriasian, as indicated by the appearance in eastern Mexico of abundant calpionellid assemblages and typically Mediterranean ammonites (Adatte *et al*. 1994, 1996).
2. A southern route, called the Indo-Madagascar seaway, has been proposed by Cecca (1999). This marine corridor opened near the Jurassic–Cretaceous boundary and thus prior to South Atlantic breakup through interconnected grabens that developed south of Africa and connected Patagonia and the Tethys via a system of grabens through Mozambique, Somalia, Madagascar, eastern India and eastern Antarctica (Fig. 22). The existence of this Indo-Austral seaway is indicated by the presence of the ammonite *Chigaroceras* in both the Andes and Iraq (H. A. Leanza 1996), and by marine reptiles common in both regions (e.g. Gasparini & Fernandez 1997). The occurrence of Tethyan ammonites in central Chile further supports the existence of a southern seaway that connected the Pacific with the Tethys around the southern end of South America.

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Supplementary material

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