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RESEARCH PAPER

Zapaliinae, a new subfamily of Tithonian–Berriasian ataxioceratid ammonites

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Abstract The recent recognition of the earliest Andean Tithonian ammonite fauna (Picunleufuense Zone) has allowed a balanced classification of the ataxioceratid ammonites, reflecting their phylogenetic relationships. The Picunleufuense Zone fauna, first recognized in the Neuquén Basin at the base of the Vaca Muerta Formation, is represented by numerous records of sparse ammonite faunas from Antarctica, the Austral Basin and the Tarapacá Basin (N. Chile and S. Peru). These Southeastern Pacific faunas include the Tithonian genera *Indansites*, *Choicensisphinctes*, *Zapalia*, *Krantziceras* (Tithonian–lower Berriasian) and *Platydiscus*. These five genera are grouped in a new subfamily established in this paper: Zapaliinae subfam. nov. (type genus: *Zapalia*). The origin of *Indansites* and *Choicensisphinctes* (possibly via *Indanistes*) from *Lithacoceras* is discussed. *Zapalia* must have been originated from *Indanistes* in the upper Proximus Zone. *Platydiscus* could have been originated from *Krantziceras*. The Tithonian Southeastern Pacific ataxioceratids (Zapaliinae subfam. nov.) form a group well separated from the Tithonian Indo-Madagascan Virgatosphinctinae.

Keywords Southeastern Pacific · Ammonoidea · *Choicensisphinctes* · *Indansites* · *Zapalia* · *Krantziceras* · *Platydiscus*

Kurzfassung Die kürzlich entdeckte älteste andine Tithonium-Ammonitenfauna (Picunleufuense-Zone) ermöglichte eine ausgewogene Klassifikation der ataxioceratiden Ammoniten unter Berücksichtigung ihrer stammesgeschichtlichen Verwandtschaftsverhältnisse. Die Fauna der Picunleufuense-Zone, die als erstes an der Basis der Vaca Muerta-Formation des Neuquén-Beckens entdeckt wurde, setzt sich aus vielen seltenen Ammoniten aus der Antarktis, dem Australischen Becken sowie dem Tarapacá-Becken (Nord-Chile und Süd-Peru) zusammen. Diese südostpazifischen Faunen beinhalten die tithonischen Gattungen *Indansites*, *Choicensisphinctes*, *Zapalia*, *Krantziceras* (Tithonium–unteres Berriasium) und *Platydiscus*. Diese fünf Gattungen werden in einer hier neu eingeführten Unterfamilie zusammengefasst: Zapaliinae subfam. nov. (Typusgattung: *Zapalia*). Der Ursprung von *Indansites* und *Choicensisphinctes* (möglicherweise via *Indansites*) in der Gattung *Lithacoceras* wird diskutiert. *Zapalia* muss sich in der oberen Proximus-Zone aus *Indansites* entwickelt haben. *Platydiscus* könnte von *Krantziceras* abstammen. Die tithonischen südostpazifischen Ataxioceratiden (Zapaliinae subfam. nov.) bilden eine von den tithonischen indo-

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madegassischen Virgatosphinctinae gut abgegrenzte Gruppe.

Schlüsselwörter Südöstlicher Pazifik · Ammonoidea · *Choicensisphinctes* · *Indansites* · *Zapalia* · *Krantziceras* · *Platydiscus*

Introduction

The earliest Andean Tithonian ammonite fauna, recorded from the base of the Vaca Muerta Formation of the Neuquén Basin (Fig. 1A), has been recognized and differentiated only in the last years (Parent et al. 2006, 2011a, b). The recognition of this fauna has allowed important advances:

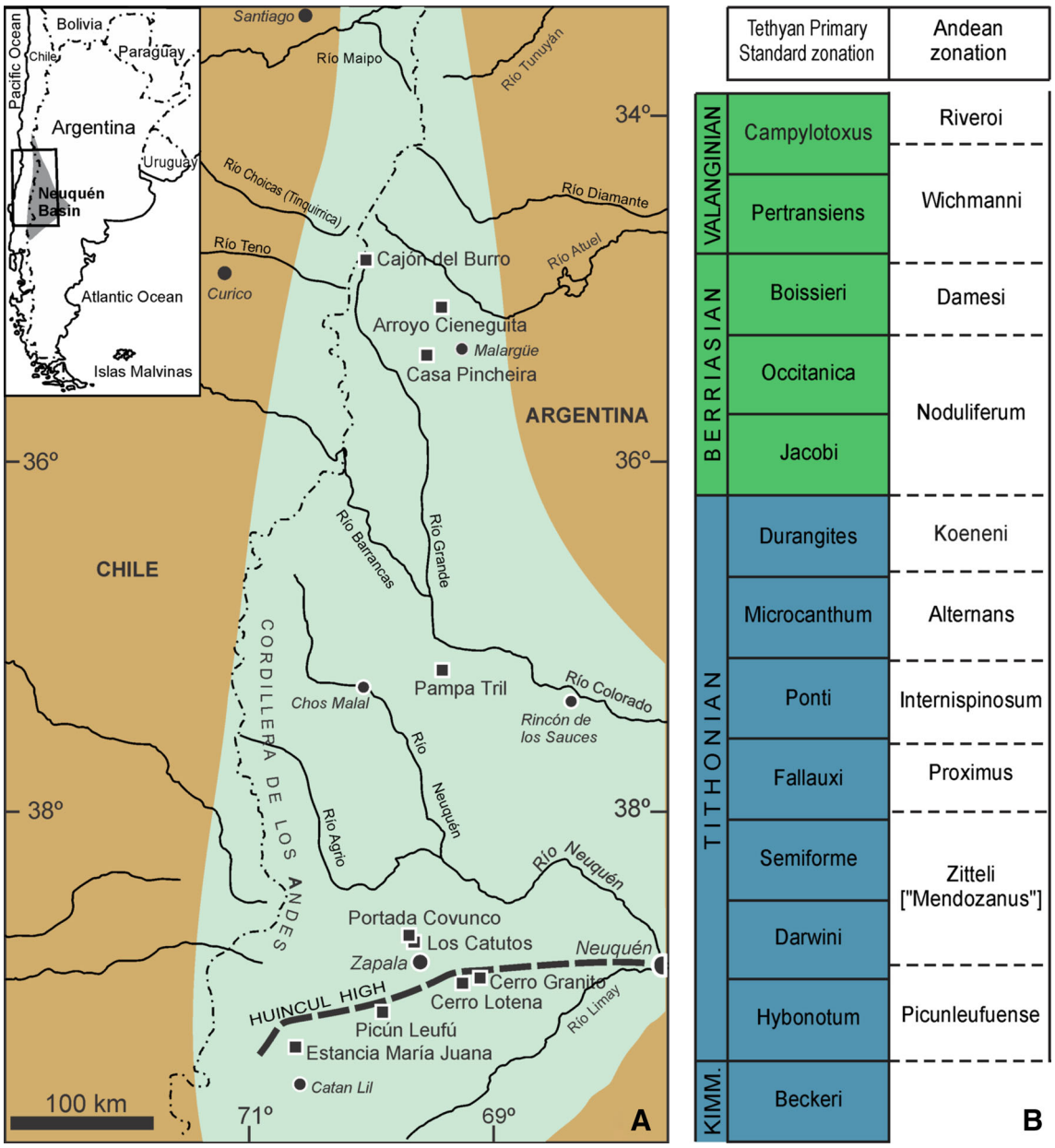


Fig. 1 **A** Approximate emplacement of the Neuquén (or Neuquén–Mendoza) Basin (*light green*) in a recent geography with indication of the localities cited in text. Adapted from Parent et al. (2011a). **B** Reference Andean chronostratigraphic ammonite zonation (based on Leanza 1945, 1981; Aguirre-Urreta and Rawson 1999; Parent et al. 2015), correlated with the Tethyan Primary Standard Scale (Geyssant in Cariou and Hantzpergue 1997; Reboulet et al. 2014). *Dotted lines* indicate approximate correlation with the standard scale

1. The introduction of the Picunleufuense (Standard Chronostratigraphic) Zone (Fig. 1B) as the base of the Andean Tithonian ("Andean Tithonian" is used to denote that its base probably does not correspond exactly to that of the Tethyan standard);
2. The possibility of a balanced classification of the ataxioceratid ammonites through the Tithonian of the Neuquén Basin which reflects the phylogenetic relationships of local lineages;
3. A reasonable classification of many records of sparse ammonite faunas from Antarctica and the Austral Basin, as well as from Chile (cf. Salazar and Stinnesbeck 2015), the Tarapacá Basin, N. Chile and Peru (Fig. 1A) which allow the study of their palaeobiogeography and ages.

The fauna of the Picunleufuense Zone consists mainly of ataxioceratids, among which occur abundantly the index species *Indansites picunleufuense* (Parent, Garrido, Scherzinger and Schweigert, 2011a), formerly included in *Lithacoceras* Hyatt, 1900 (Fig. 2A–C). The strong resemblance of this species to Early Tithonian (two-fold division) *Lithacoceras*, e.g. *L. eigeltingense* (Ohmert and Zeiss, 1980), is probably due to the phyletic origin of *Indansites* in such forms of *Lithacoceras*. In the last years, as the species was recorded through different horizons within the Picunleufuense Zone in virtually all parts of the basin, some differences from *Lithacoceras* have appeared, especially in the evolutionary trends shown by representatives of *Indansites* in the Zitteli ["Mendozanus"] and Proximus zones (Parent et al. 2011b, 2015). Vennari (2016) introduced the genus *Indansites* including its type species *Subplanites malarguensis* Spath, 1931 (Fig. 2D) and *Lithacoceras picunleufuense* (Fig. 2A–C). *Indansites malarguensis* has a well-established stratigraphic position as part of the ammonite assemblage of the *malarguensis* Hz. (Parent et al. 2011a: 95) in the lower (or lowermost) part of the Zitteli ["Mendozanus"] Zone. Vennari (2016) considered *I. picunleufuense* as a synonym of *I. malarguensis*. However, this comparison was based on poor material, so that the significant morphological differences between these two species, which occur at different horizons, were not noted.

The Proximus Zone representatives of *Indansites* (Fig. 2E, F), recorded from Arroyo Cieneguita and Cerro Lotena (Parent et al. 2011b), are thought to be the ancestors of *Zapalia* Leanza and Zeiss, 1990 (Fig. 2G), which seems to be confined to the Internispinosum Zone (Leanza and Zeiss 1990; Zeiss and Leanza 2010).

Based on the records of these lineages which have been constructed from abundant material found at several localities (Parent 2001, 2003; Parent et al. 2006, 2011a, b, 2013a, b, 2015; Vennari et al. 2012; Vennari 2016), a rather homogeneous group of Southeastern Pacific ataxioceratids is evidenced. These lineages must be classified in a suprageneric ranking denoting especially their distinction from the Lithacoceratinae and their palaeobiogeographic setting in the marine basins of the Southeastern Pacific region.

The purpose of this note is to establish a new subfamily, grouping together these and other closely related ataxioceratids.

Systematic Palaeontology

Suborder **Ammonitina** Fischer, 1882
Superfamily **Perisphinctoidea** Steinmann, 1890
Family **Ataxioceratidae** Buckman, 1921

Remarks. The composition of the family adopted herein follows Donovan et al. (1981) updated: Ataxioceratinae Buckman, 1921 (Late Oxfordian–Late Kimmeridgian), Lithacoceratinae Zeiss, 1968 (Late Kimmeridgian–Late Tithonian), Virgatosphinctinae Spath, 1923 (late Early–early Late Tithonian), Torquatisphinctinae Tavera, 1985 (Early Kimmeridgian–Late Tithonian) and the new subfamily introduced below.

Subfamily **Zapaliinae** nov.

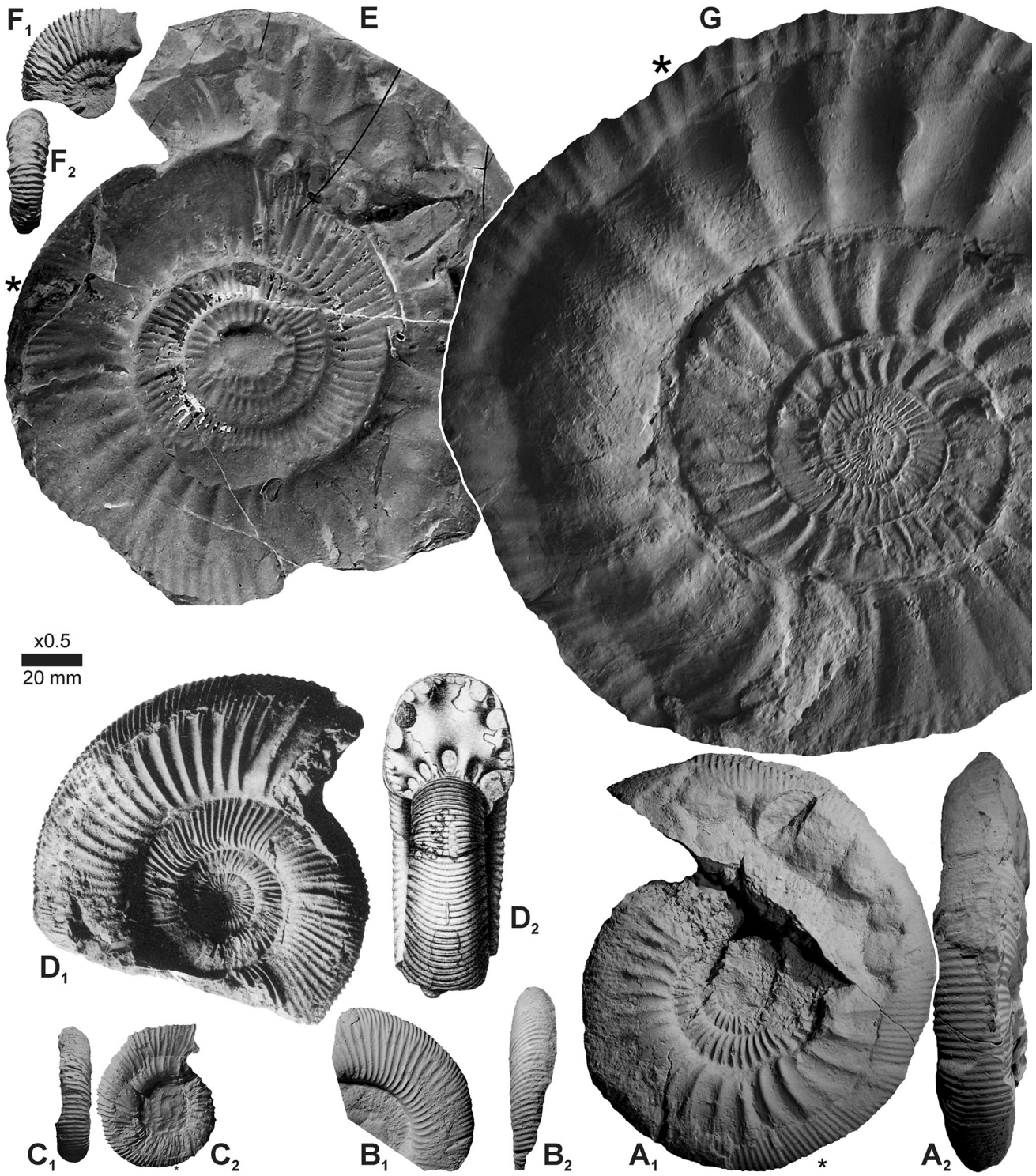
Type genus. *Zapalia* Leanza and Zeiss, 1990; Tithonian.

Diagnosis. Southeastern Pacific homoeomorphs of the Lithacoceratinae; evolute platycones to more or less involute and inflated suboxycones; ribbing with frequent more or less short virgatotome stages, polyschizotome ribs, or branching as fascipartite secondaries.

Genera included. *Indansites* Vennari, 2016 (Lower Tithonian); *Zapalia* (upper Lower Tithonian); *Choicensisphinctes* Leanza, 1980 (Lower–Upper Tithonian); *Krantziceras* Parent, Scherzinger and Schweigert, 2011 (Lower Tithonian–Lower Berriasian); *Platydiscus* Parent, Scherzinger and Schweigert, 2011 (Lower–Upper Tithonian).

Remarks. This new subfamily includes a group of Southeastern Pacific ataxioceratid lineages, mostly described from the Neuquén Basin, regarded here as homoeomorphs of the Tithonian Lithacoceratinae (sensu Zeiss et al. 1996).

The adult size of the macroconchs is broadly variable, ranging from some 150 to more than 1000 mm in diameter. The morphotypes range from inflate, more or less involute suboxycones to platycones (*Choicensisphinctes*, see Fig. 3), to more or less compressed, evolute platycones (*Indansites*, Fig. 2A–F; *Zapalia*, Fig. 2G; *Krantziceras*, Fig. 4A–C; *Platydiscus*, Fig. 4D, E). Primary ribs may be unchanged or may strengthen through the ontogeny,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◀**Fig. 2** Typical representatives of *Indansites* and *Zapalia* in the Tithonian of the Neuquén Basin (Vaca Muerta Fm). *A–C*: *Indansites picunleufuense* (Parent, Garrido, Schweigert and Scherzinger, 2011), Picunleufuense Zone. *A*: Holotype, [M] of transient alfa, complete view of the right face, Picún Leufú, *picunleufuense* alfa Hz. (modified from Parent et al. 2011a). *B*: [M] of transient beta, Estancia María Juana, *picunleufuense* beta Hz.; inner whorls (MOZ-PI-2410/2) showing the style of furcation with the anterior secondary tending to twist backwards. *C*: Paratype 2, complete adult [m], Picún Leufú, *picunleufuense* alfa Hz. (modified from Parent et al. 2011a). *D*: *Indansites malarguensis* (Spath, 1931), holotype, complete? adult phragmocone (D_1: modified from Burckhardt 1900: pl. 24: 4; D_2: modified from Burckhardt 1903: pl. 4: 2), Casa Pincheira, lower Zitteli ["Mendozanus"] Zone, *malarguensis* Hz. *E–F*: *Indansites* sp. nov. aff. *picunleufuense*. *E*: complete adult [M] (refigured from Parent et al. 2011b), Arroyo Cieneguita, Proximus Zone, *falculatum* Hz. *F*: adult [m], Cerro Lotena, upper Proximus Zone. *G*: *Zapalia fascipartita* Leanza and Zeiss, 1990, almost complete adult [M] (MOZ-PI-1763) from Los Catutos, Internispinosum Zone. All ×0.5. *Asterisk* marks last septum

bifurcating on inner whorls passing to polyfurcate in fasciculate or virgatotome style; polyschizotome ribs may occur at subadult or adult stages.

The microconchs are lappeted; one-tenth to one-third of the size of the corresponding macroconch; serpenticonic to suboxyconic, moderately evolute to involute; ribbing as in juvenile macroconchs, with bifurcating to polyfurcating primary ribs in the adult body chamber.

In terms of sculpture ontogeny, the new subfamily includes two main groups: (1) *Choicensisphinctes*, *Indansites* and *Zapalia* are more or less strongly variocostate with relatively fine ribs in the phragmocone, becoming stronger, sometimes bold and blade-like in the adult body chamber; (2) *Krantziceras* and *Platydiscus* with isocostate ribbing, composed of wiry ribs simply bifurcating from the inner whorls up to the adult body chamber, with undivided primaries frequently intercalated.

Choicensisphinctes and *Indansites* bear almost identical aptychi of the Praestriaptychus type (Fig. 3B, Parent et al. 2013b: Fig. 4C, Vennari 2016: pl. 2: 3).

Leanza and Zeiss (1992) and later Zeiss and Leanza (2010) have proposed a subfamily "Windhauseniceratinae" (name invalid: see Klein 2005; Parent et al. 2013a) in which they included both the himalayitid *Windhauseniceras* and the ataxioceratid *Zapalia*.

Origin and evolution. In Fig. 5 we present a summary of the composition and phyletic relationships of the main lineages of Zapaliinae subfam. nov. This diagram is a summary of hypotheses already proposed, based on the studies of the representatives of each genus as discussed in detail in Parent et al. (2011a, b, 2013a, 2015).

The genus *Indansites* most likely originated from *Lithacoceras* Hyatt, 1900. The palaeobiogeographic arguments are that (1) we can exclude an autochthonous origin in the area, because the Andean basins were unfavourable for ammonites before the Picunleufuense Zone, during the Kimmeridgian, and (2) there are no similar forms in the Indo-Madagascan domain, which was mainly inhabited by torquatisphinctids. Boreal areas were inhabited by Aulacostephaninae. There are no lithacoceratid-like forms in New Zealand, Indonesia or Nepal as well. The only similar forms in the present-day "Circum-Pacific" area are in Japan (Fig. 6), but Japan consists of numerous microplates with poorly known geographic position in the Jurassic. So the only similar forms are Submediterranean and Mediterranean Lithacoceratinae. The forms from Southern Germany must have originated in the Tethys as well, because there are no ancestors in the older parts of the Beckeri Zone.

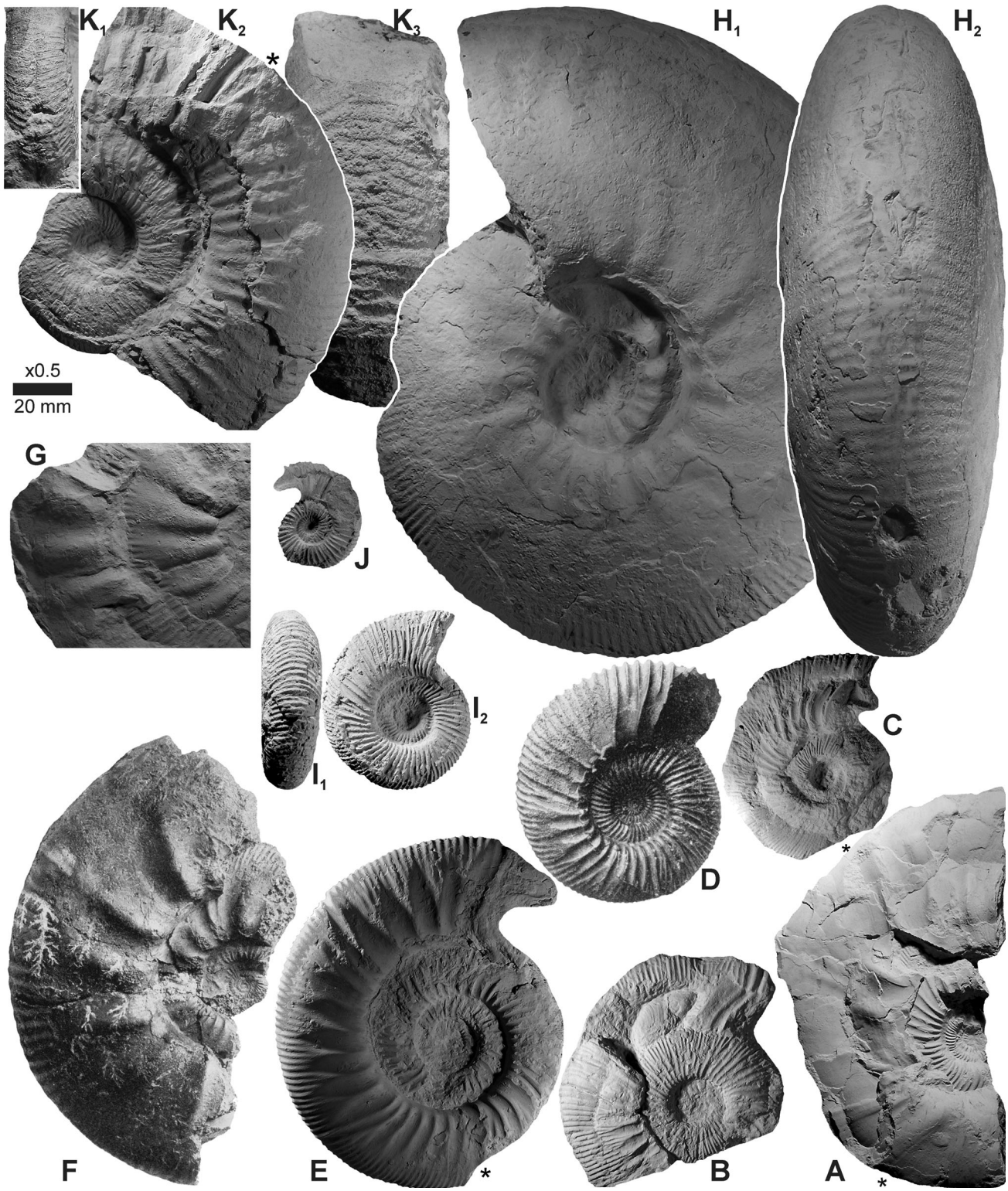
The best arguments for the origin of the *Indansites* lineage from *Lithacoceras* are the strong morphological and sculptural similarity, and that their microconchs look like *Silicisphinctes* Schweigert and Zeiss, 1999 (type species: *Subplanitoides hoelderi* Sapunov, 1979), the microconch of *Lithacoceras*; furthermore, the size ratio between these microconchs and the corresponding macroconchs is the same (Fig. 2A, C). What still remains unknown is the exact ancestor and exact time.

Even in Southern Germany within *Lithacoceras*, homoeomorphic (but phyletically related) forms occur, which have produced many problems in the past regarding the correlation between Swabia and Franconia (discussion in Scherzinger et al. 2015); For example, lithacoceratids from the Ulmense Subzone and lithacoceratids from the Moernsheimensis Subzone are rather similar. Therefore, we must of course take into account iterative immigrations from a Tethyan pool, and some migrants reached the Andean basins by the opening Caribbean seaway (Fig. 6). There is evidence of related ammonites in Mexico described by Burckhardt (1906) and Olóriz et al. (1993), discussed by Callomon (1992), Parent (2003) and Parent et al. (2006, 2011a).

The origin of *Choicensisphinctes* and *Indansites* from *Lithacoceras* (or *Choicensisphinctes* via *Indansites* in Parent et al. 2011a) is further supported by their praestriaptychi, which are indistinguishable from that of *Lithacoceras* (Fig. 3B; see Parent et al. 2013b).

Zapalia is thought to have originated from *Indansites* in the upper Proximus or lower Internispinosum Zone via *Indansites* sp. nov. aff. *picunleufuense* (Fig. 2E, F). Under this hypothesis, *Indansites* and *Zapalia* conform to a conservative lineage still retaining great similarity with *Lithacoceras*.

Platydiscus could have been originated from *Krantziceras* considering their general resemblance, but the records of these genera are still too scarce for a closer examination.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◀**Fig. 3** Typical representatives of *Choicensisphinctes* in the Tithonian of the Neuquén Basin (Vaca Muerta Fm). *A–C*: *Choicensisphinctes platyconus* Parent, Garrido, Schweigert and Scherzinger, 2011, Picunleufuense Zone, *picunleufuense* alfa Hz., Picún Leufú. *A:* holotype, adult [M], Picún Leufú. *B*: juvenile [M] with in situ *Praestriaptychus* in body chamber (specimen from Los Catutos figured in Parent et al. 2013a: Fig. 5B, showing herein the opposite face with additional preparation to uncover the aptychus). *C*: paratype 2, complete adult [m], Picún Leufú. *D–H*: *Choicensisphinctes erinoides* (Burckhardt, 1903), Zitteli ["Mendozanus"] Zone. *D*: adult [m], lectotype of *Virgatites mendozanus* Burckhardt, 1911 (modified from Burckhardt 1900: pl. 25: 7), Cajón del Burro–Río Choicas. *E*: complete adult [m] of early transient from Cerro Granito (MOZ-PI-8420). *F*: holotype of *Perisphinctes erinoides* Burckhardt, 1903 (modified from Burckhardt 1900: pl. 25: 1), adult? [M] phragmocone, Cajón del Burro–Río Choicas. *G*: portion of adult [M] with body chamber of the morph limits, showing the characteristic fascipartite branching (palm-like bundles of secondary ribs branching from a wide primary; compare with *C*, *D*, *E* and *G*), modified from Parent et al. (2011b), Arroyo Cieneguita. *H*: adult [M] phragmocone of the morph limits (modified from Parent et al. 2015), Pampa Tril. *I-J*: *Choicensisphinctes* sp. A (in Parent et al. 2011b), Pampa Tril. *I*: [M] phragmocone from the Internispinosum Zone, *internispinosum* alfa Hz., Pampa Tril (modified from Parent et al. 2015). *J*: complete adult [m] from Arroyo Cieneguita, Proximus Zone, *falculatum* Hz. *K*: *Choicensisphinctes striolatus* (Steuer, 1897), adult macroconch with incomplete body chamber, Pampa Tril, Alternans Zone, *azulense* Hz.; K_1: ventral view of the last whorl of phragmocone; modified from Parent et al. (2015). All ×0.5. *Asterisk* marks last septum

Palaeobiogeographic distribution (Fig. 6). Representatives of Zapaliinae subfam. nov. are known through the western margin of South America, from Antarctica up to Peru. The records from Antarctica consist of *Indansites* and *Choicensisphinctes* (Howlett 1989; Thomson 1979, see Parent et al. 2015). In the Austral Basin (southern Patagonia, Argentina), *Indansites* and *Choicensisphinctes* occur (Blasco et al. 1979; Kraemer and Riccardi 1997, see Parent 2003). The best record is known from the Neuquén Basin, where the five genera included in the new subfamily are well represented (Fig. 5). In the Tarapacá Basin (N. Chile and Peru), the records, although poor, indicate the probable occurrence of *Indansites* (data from Rüegg 1957; Cecioni 1961) and *Choicensisphinctes* as well (data from Welter 1913 and Knetchel et al. 1947, discussed in Parent et al. 2015).

To our knowledge, there are only two ammonite records from outside the Southeastern Pacific region which have been assigned to genera included in Zapaliinae subfam. nov.: (1) a possible record (unfigured) of *Choicensisphinctes* cf. *choicensis* (Burckhardt, 1903) from southwestern Turkey (Enay et al. 1971: 408); (2) poorly preserved specimens from the uppermost Tithonian–Lower

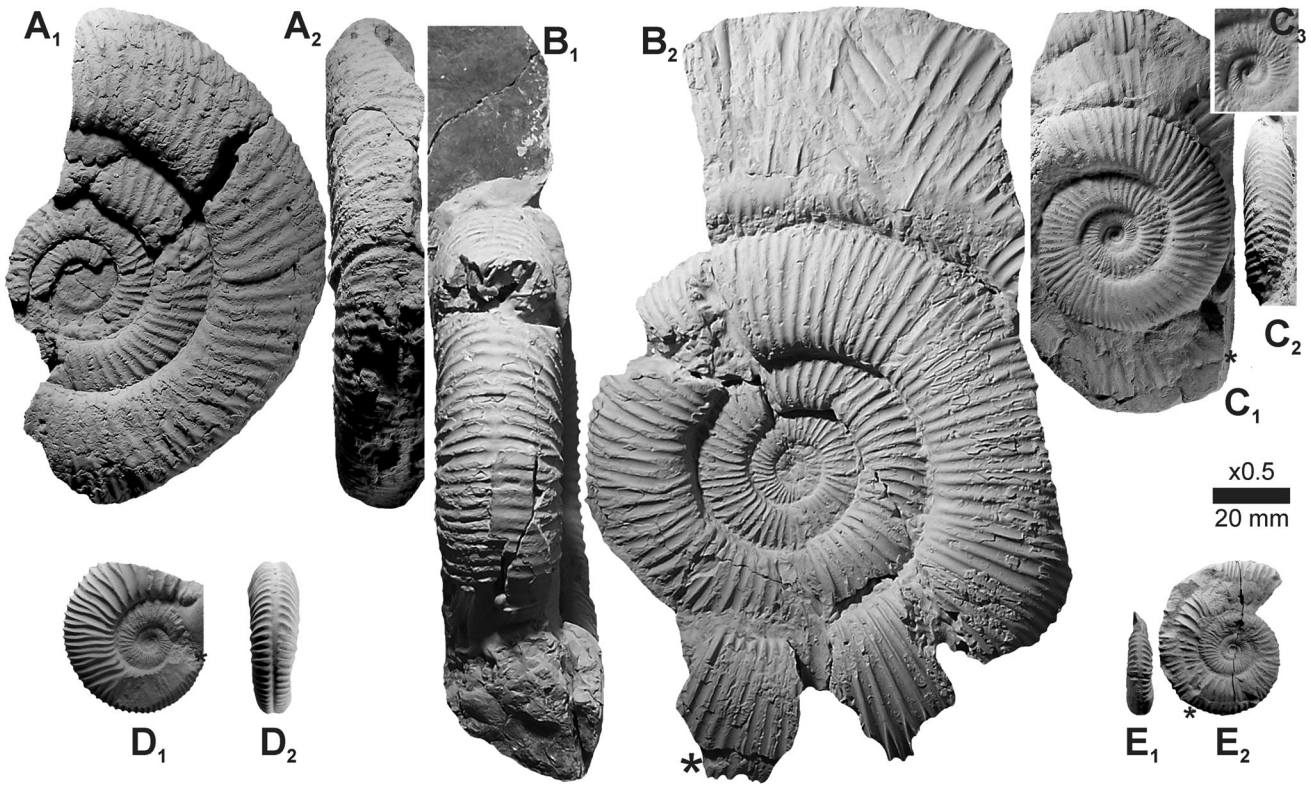

Fig. 4 Typical representatives of *Krantziceras* (Tithonian–Berriasian) and *Platydiscus* (Tithonian) in the Neuquén Basin (Vaca Muerta Fm). All modified from Parent et al. (2011b, 2015). *A*: *Krantziceras*? sp. nov. A, adult? [M?] phragmocone from Pampa Tril, Picunleufuense Zone, *picunleufuense* alfa Hz. *B*: *Krantziceras azulense* (Leanza, 1945), adult [M] with part of body chamber, from Pampa Tril, Alternans Zone, *azulense* Hz. *C*: *Krantziceras compressum* Parent, Scherzinger and Schweigert, 2011 from Arroyo Cieneguita, Noduliferum Zone, *compressum* Hz. *D–E*: *Platydiscus beresii* Parent, Scherzinger and Schweigert, 2011 from Arroyo Cieneguita, Proximus Zone, *falculatum* Hz. *D*: holotype, almost complete adult [M]. *E*: paratype 4, complete adult [m]. All ×0.5. *Asterisk* marks last septum

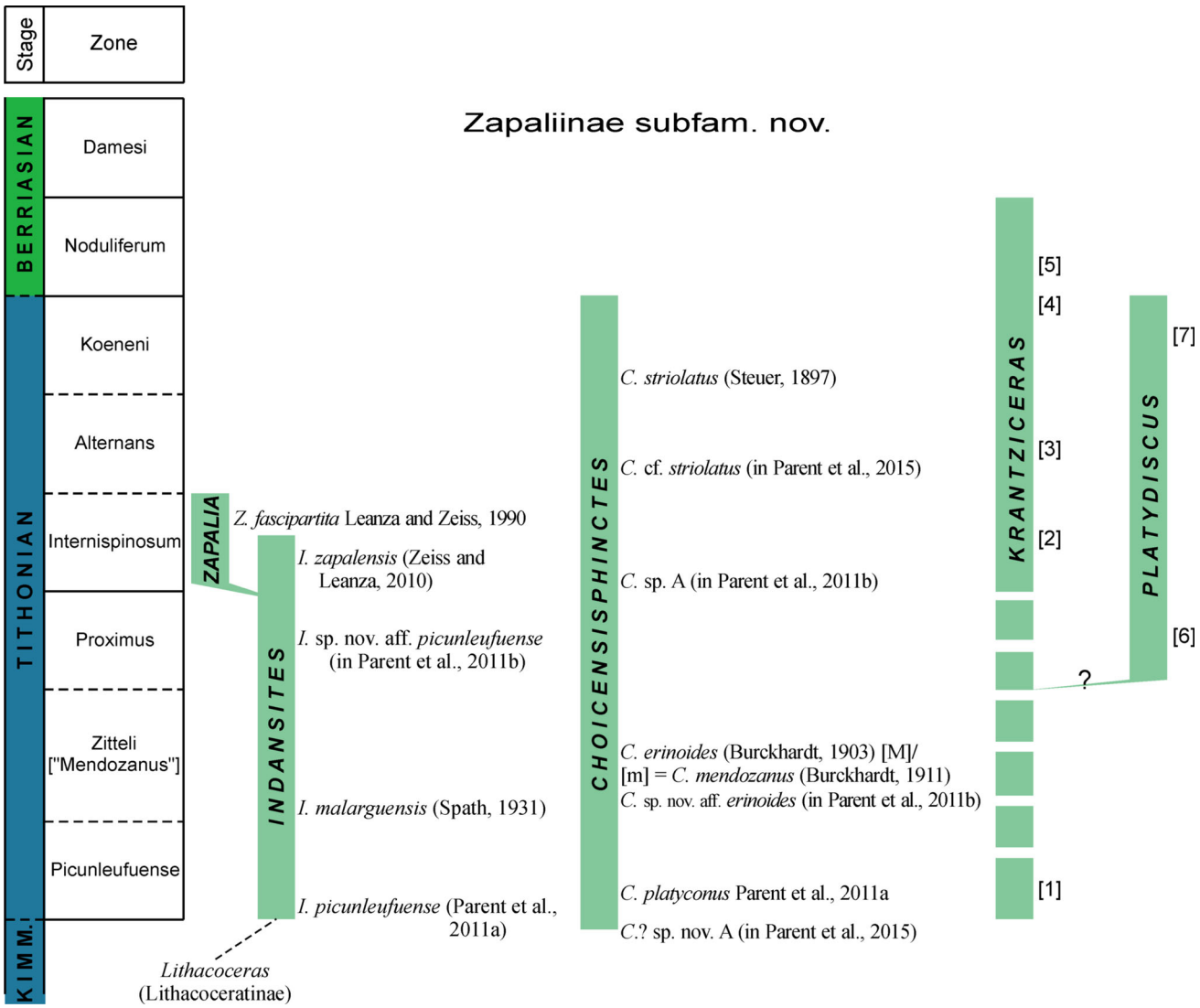

Fig. 5 Composition of Zapaliinae subfam. nov. showing the stratigraphic range currently known of the lineages and their main evolutionary steps indicated by representative species (see Figs. 2, 3, 4). Most of the data come from the Neuquén Basin as explained in text. [*1*] *Krantziceras*? sp. nov. A (see Fig. 4A herein). [*2*] *Krantziceras* cf. *disputabile* (Leanza, 1945) in Parent et al. (2015: Figs. 3, 4B). [*3*] *Krantziceras azulense* (see Fig. 4B herein). [*4*] *Krantziceras planulatum* (Vennari et al. 2012). [*5*] *Krantziceras compressum* (see Fig. 4C herein). [*6*] *Platydiscus beresii* (see Fig. 4D, E herein). [*7*] *Platydiscus* sp. nov. aff. *beresii* [as *Aulacosphinctes mangaensis* (Steuer, 1897) in Leanza 1945: pl. 3: 1-2]. *Solid lines* at the base of the zones standardized

Berriasian of southern Yemen described by Howarth (1998) as *Choicensisphinctes limits* (Burckhardt, 1930). These specimens have a stratigraphic position higher than any other species of the genus, thus they could represent late excursion or geographic expansion of the genus.

Zapaliinae subfam. nov. and Virgatosphinctinae Spath, 1923 (as reviewed by Enay 2009) have their own palaeobiogeographic distributions (Fig. 6). The Indo-Madagascan Virgatosphinctinae (upper Lower–Upper Tithonian, two-fold division) seem to derive from *Choicensisphinctes* as suspected already by Enay and Cariou (1997), and in the last years, evidence in support of this hypothesis has emerged (Parent et al. 2013a, 2015). The Trans-Gondwanan Seaway (Fig. 6) should have allowed faunal exchanges during the Tithonian (cf. Cecca 1999), as well as from the Oxfordian (see Enay and Cariou 1997; Parent 2006).

Conclusions

Lineages of ammonites evolving independently but sharing significant combinations of morpho-ornamental features which indicate a common origin within a palaeobiogeographic domain are conveniently grouped in a subfamily.

Fig. 6 Tithonian geographic distribution (*shaded*) of Zapaliinae subfam. nov. (Southeastern Pacific: Antarctica, Austral Basin, Neuquén Basin and Tarapacá Basin) and the Virgatosphinctinae (Indo-Madagascan region). Palaeogeography (Mollweide oval globe projection) based on Blakey (2008), Pszczółkowski (1987), Macdonald et al. (2003), Parent (2006), Gasparini and Iturralde-Vinent (2006) and Golonka (2007). *RVB:* Rocas Verdes Basin, *AB*: Austral Basin, *NB*: Neuquén Basin, *TB*: Tarapacá Basin

The Southeastern Pacific genera *Indansites*, *Zapalia*, *Choicensisphinctes*, *Krantziceras* and *Platydiscus* are grouped in the new subfamily Zapaliinae. These genera represent lineages mainly developed in the Tithonian, with *Krantziceras* ranging up to the Andean Berriasian Noduliferum Zone. These genera are best recorded in the Andean successions, especially in the Neuquén Basin.

The ammonites grouped in Zapaliinae subfam. nov. (Andean Lower Tithonian–Lower Berriasian) show unique phylogenetic trends which, on the one hand, give coherence to the subfamily and, on the other, indicate a clear differentiation from those of the Virgatosphinctinae (upper Lower–Upper Tithonian), which are characteristic and mostly restricted to the Indo-Madagascan domain.

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References

Aguirre-Urreta, M.B., and P.F. Rawson. 1999. Stratigraphic position of *Valanginites, Lissonia* and *Acantholissonia* in the lower Valanginian (lower Cretaceous) sequence of the Neuquén basin, Argentina. In *Advancing research on living and fossil Cephalopods*, eds. F. Olóriz, and F.J. Rodríguez-Tovar, 521–529. New York: Kluwer Academic/Plenum Publishers.

Blakey, R.C. 2008. Gondwana paleogeography from assembly to breakup—A 500 m.y. odyssey. In *Resolving the Late Paleozoic Ice Age in Time and Space*, eds. C.R. Fielding, T.D. Frank and J.L. Isbell. *Geological Society of America Special Paper* 441: 521–529.

Blasco, G., F. Nullo, and C. Proserpio. 1979. *Aspidoceras* en Cuenca Austral, Lago Argentino, Prov. de Santa Cruz. *Revista de la Asociación Geológica Argentina* 34: 282–293.

Burckhardt, C. 1900. Profils Géologiques transversaux de la Cordillera Argentino-Chilienne. Stratigraphie et tectonique. *Anales del Museo de La Plata, Sección Geológica y mineralógica* 2: 1–136.

Burckhardt, C. 1903. Beiträge zur Kenntnis der Jura- und Kreideformation der Cordillere. *Palaeontographica* 50: 1–144.

Burckhardt, C. 1906. Le faune Jurassique de Mazapil avec un appendice sur les fossiles du Cretaciqué inferieur. *Boletín del Instituto Geológico de México* 23: 1–216.

Burckhardt, C. 1911. Bemerkungen über die russischborealen Typen im Oberjura und Kreide in Mexico. *Centralblatt für Mineralogie, Geologie und Paläontologie* 15: 477–483.

Burckhardt, C. 1930. Etude synthétique sur le Mesozoïque Mexicain. *Mémoire de la Société Paléontologique Suisse* 49: 1–280.

Callomon, J.H., 1992. Upper Jurassic, especially of Mexico. Part 4: Biochronology. 12. Ammonite Zones of the Circum-Pacific Region. Hillebrandt A. von, Smith P., Westermann G.E.G. and Callomon J.H. In *The Jurassic of the Circum-Pacific*, ed. Westermann G.E.G., 247–272. Cambridge: Cambridge University Press.

Cariou, E., and P. Hantzpergue. 1997. Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonations paralléles et distribution des invertébres et microfossiles. *Bulletin du Centre de Recherche Elf-Exploration et Production* 17: 79–86.

Cecca, F. 1999. Palaeobiogeography of Tethyan ammonites during the Tithonian (latest Jurassic). *Palaeogeography, Palaeoclimatology, Palaeoecology* 147: 1–37.

Cecioni, G. 1961. El Tithoniano inferior marino en la Provincia de Tarapacá y consideraciones sobre el arqueamiento central de los Andes. *Comunicaciones de la Escuela de Geología* 1: 1–18.

Donovan, D.T., J.H. Callomon and M.K. Howarth. 1981. Classification of the Jurassic Ammonitina. In *The Ammonoidea*, eds. M.R. House and J.R. Senior. *Systematics Association, Special Volume* 18: 101–155

Enay, R. 2009. Les faunes d'ammonites de l'Oxfordien au Tithonien et la biostratigraphie des Spiti-Shales (Callovien supérieur-Tithonien) de Thakkhola, Népal Central. *Documents des Laboratoires de Géologie Lyon* 166: 1–246.

Enay, R., C. Martin, O. Monod, and J.-P. Thieuloy. 1971. Jurassique Supérieur à ammonites (Kimmeridgien-Tithonique) dans l'autochtone du Taurus de Berysehir (Turquie Méridionale). *Annales Instituti Geologici Publici Hungarici* 54: 397–422.

Enay, R., and E. Cariou. 1997. Ammonite faunas and palaeobiogeography of the Himalayan belt during the Jurassic: initiation of a Late Jurassic austral ammonite fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* 134: 1–38.

Fischer, P.H. 1882. *Manuel de conchyliologie et de paléontologie conchyliologique*, 1–1369. Paris: Librairie F. Savy.

Gasparini, Z., and M. Iturralde-Vinent. 2006. The Cuban Oxfordian herpetofauna in the Caribbean Seaway. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 240: 343–371.

Golonka, J. 2007. Phanerozoic paleoenvironment and paleolithofacies maps. Mesozoic. *Geologia* 33: 211–264.

Howarth, M.K. 1998. Ammonites and nautiloids from the Jurassic and Lower Cretaceous of Wadi Hajar, southern Yemen. *Bulletin of the Natural History Museum London (Geology)* 54: 33–107.

Howlett, P.J. 1989. Late Jurassic-Early Cretaceous cephalopods of eastern Alexander Island, Antarctica. *Special Papers in Palaeontology* 41: 1–72.

Hyatt, A. 1900. Cephalopoda. In *Eastman's Zittel textbook of Paleontology*, First edition, 502–604. New York.

Knetchel, M.M., E.F. Richards, and M.V. Rathbun. 1947. Mesozoic fossils of the Peruvian Andes. *The John Hopkins University Studies in Geology* 15: 1–150.

Klein, J. 2005. Lower Cretaceous Ammonites I. Perisphinctaceae 1 (Himalayitidae, Olcostephanidae, Holcodiscidae, Neocomitidae, Oosterellidae. In Fossilium Catalogus I: Animalia, ed. W. Riegraf, 1–484. Leiden: Backhuys.

Kraemer, P.E., and A.C. Riccardi. 1997. Estratigrafía de la región comprendida entre los lagos Argentino y Viedma (49°40′–50°10′ lat. S), Provincia de Santa Cruz. *Revista de la Asociación Geológica Argentina* 52: 333–360.

Leanza, A.F. 1945. Ammonites del Jurasico Superior y del Cretáceo Inferior de la Sierra Azul, en la Parte Meridional de la Provincia de Mendoza. *Anales del Museo de la Plata, nueva serie* 1: 1–99.

Leanza, H.A. 1980. The Lower and Middle Tithonian Ammonite fauna from Cerro Lotena, Province of Neuquén, Argentina. *Zitteliana* 5: 3–49.

Leanza, H.A. 1981. The Jurassic-Cretaceous boundary beds in West Central Argentina and their ammonite zones. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 161: 62–92.

Leanza, H.A., and A. Zeiss. 1990. Upper Jurassic Lithographic limestone from Argentina (Neuquén Basin): stratigraphy and fossils. *Facies* 22: 169–186.

Leanza, H.A. and A. Zeiss. 1992. On the ammonite fauna of the lithographic limestones from the Zapala region (Neuquén province, Argentina), with the description of a new genus. *Zentralblatt für Geologie und Paläontologie, Teil I* 1991(6): 1841–1850.

Macdonald, D., I. Gomez-Perez, J. Franzese, L.A. Spalletti, L. Lawver, L. Gahagan, I. Dalziel, C. Thomas, N. Trewin, M. Hole, and D. Paton. 2003. Mesozoic break-up of SW Gondwana: implications for regional hydrocarbon potential of the southern South Atlantic. *Marine and Petroleum Geology* 20: 287–308.

Ohmert, W., and A. Zeiss. 1980. Ammoniten aus den Hangenden Bankkalken (Unter-Tithon) der Schwäbischen Alb (Südwestdeutschland). *Abhandlungen des Geologischen Landesamtes Baden-Würtemberg* 9: 5–50.

Olóriz, F., L. Lara, A. De La Mora, A.B. Villaseñor, and C. Gonzáles-Arreola. 1993. The Kimmeridgian-Tithonian boundary in the Barranquito del Alacrán section at Cuencame (Durango, Mexico): its biostratigraphy and ecostratigraphic interpretation. *Acta Geologica Polonica* 43: 273–288.

Parent, H. 2001. The Middle Tithonian (Upper Jurassic) ammonoid fauna of Cañadón de los Alazanes, Southern Neuquén-Mendoza Basin, Argentina. *Boletín del Instituto de Fisiografía y Geología* 71: 19–38.

Parent, H. 2003. The Ataxioceratid ammonite fauna of the Tithonian (Upper Jurassic) of Casa Pincheira, Mendoza (Argentina). In *Jurassic of South America*, eds. H. Parent, F. Olóriz and G. Meléndez. *Journal of South American Earth Sciences* 16: 143–165

Parent, H. 2006. Oxfordian and late Callovian ammonite faunas and biostratigraphy of the Neuquén-Mendoza and Tarapacá basins (Jurassic, Ammonoidea, Western South America). *Boletín del Instituto de Fisiografía y Geología* 76: 1–70.

Parent, H., A. Scherzinger, and G. Schweigert. 2006. The earliest ammonite faunas from the Andean Tithonian of the Neuquén-Mendoza Basin, Argentina. Chile. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 241: 253–267.

Parent, H., A.C. Garrido, G. Schweigert, and A. Scherzinger. 2011a. The Tithonian ammonite fauna and stratigraphy of Picún Leufú, southern Neuquén Basin, Argentina. *Revue de Paléobiologie* 30: 45–104.

Parent, H., A. Scherzinger, and G. Schweigert. 2011b. The Tithonian-Berriasian ammonite fauna and stratigraphy of Arroyo

Cieneguita, Neuquén-Mendoza Basin, Argentina. *Boletín del Instituto de Fisiografía y Geología* 79–81: 21–94.

Parent, H., A.C. Garrido, G. Schweigert, and A. Scherzinger. 2013a. The Tithonian stratigraphy and ammonite fauna of the transect Portada Covunco-Cerrito Caracoles (Neuqúen Basin, Argentina). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 269: 1–50.

Parent, H., A.C. Garrido, G. Schweigert, and A. Scherzinger. 2013b. Andean Lower Tithonian (Picunleufuense Zone) ammonites and aptychus from Estancia María Juana, Southern Neuquén Bain, Argentina. *Boletín del Instituto de Fisiografía y Geología* 83: 27–34.

Parent, H., A.C. Garrido, A. Scherzinger, G. Schweigert, and I. Fözy. 2015. The Tithonian-Lower Valanginian stratigraphy and ammonite fauna of the Vaca Muerta Formation in Pampa Tril, Neuquén Basin, Argentina. *Boletín del Instituto de Fisiografía y Geología* 86: 1–96.

Reboulet, S., et al. 2014. Report on the 5th International Meeting of the IUGS Lower Cretaceous Ammonite Working Group, the Kilian Group (Ankara, Turkey, 31st August 2013). *Cretaceous Research* 50: 126–137.

Rüegg, W. 1957. Geologie zwischen Cañete-San Juan 13°00′-15°24′ Südperu. *Geologische Rundschau* 45: 775–858.

Salazar, C., and W. Stinnesbeck. 2015. Tithonian-Berriasian ammonites from the Baños del Flaco Formation, central Chile. *Journal of Systematic Palaeontology* 14: 149–182.

Sapunov, I.G. 1979. Jurassique supérieur, Ammonoidea. In *Les fossiles de Bulgarie. III.3*, ed. V. Cankov, 1–263. Sofia: Academie Bulgare des Sciences.

Scherzinger, A., H. Parent, and G. Schweigert. 2015. A new species of the ammonite genus *Neochetoceras* Spath (Oppeliidae) from the Hybonotum Zone (Lower Tithonian) of Southern Germany, with comments on the phylogeny of the genus. *Boletín del Instituto de Fisiografía y Geología* 85: 1–12.

Schweigert, G., and A. Zeiss. 1999. *Lithacoceras ulmense* (Oppel) (Ammonitina)—eine wichtige Leitart des Ober-Kimmeridgiums. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 211: 49–73.

Spath, L.F. 1923. On Ammonites from New Zealand. *Quarterly Journal of the Geological Society* 79: 286–312.

Steinmann, G. 1890. Cephalopoda. In *Elemente der Paläontologie*, eds. G. Steinmann and L. Döderlein, 344–475. Leipzig: Engelmann.

Steuer, A. 1897. Argentinische Jura-Ablagerungen. Ein Beitrag zur Kenntnis der Geologie und Paläontologie der argentinischen Anden. *Palaeontologische Abhandlungen (N.F. 3)* 7: 129–222.

Tavera, J.M. 1985. Los ammonites del Tithónico superior-Berriasense de la Zona Subbética (Cordilleras Béticas). *Tésis doctorales Universidad de Granada* 587: 1–381.

Thomson, M.R.A. 1979. Upper Jurassic and lower Cretaceous ammonite faunas of the Ablation Point area, Alexander Island. *British Antarctic Survey Scientific Reports* 97: 1–37.

Vennari, V.V. 2016. Tithonian ammonoids (Cephalopoda, Ammonoidea) from the Vaca Muerta Formation, Neuquén Basin, West-Central Argentina. *Palaeontographica* A306: 85–165.

Vennari, V.V., P.P. Álvarez, and M.B. Aguirre-Urreta. 2012. A new species of *Andiceras* Krantz (Cephalopoda: Ammonoidea) from the Late Jurassic-Early Cretaceous of the Neuquén Basin, Mendoza, Argentina. Systematics and biostratigraphy. *Andean Geology* 39: 92–105.

Welter, O.A. 1913. Beiträge zur Geologie und Palaeontologie von Südamerika. XIX. Eine Tithonfauna von Nord-Perú. *Neues Jahrbuch für Mineralogie etc.* 1913: 29–42.

Zeiss, A. 1968. Untersuchungen zur Paläontologie der Cephalopoden des Unter-Tithon der Südlichen Frankenalb. *Abhandlungen der Bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse, Neue Folge* 132: 1–190.

Zeiss, A., G. Schweigert, and A. Scherzinger. 1996. *Hegovisphinctes* n. gen. eine neue Ammonitengattung aus dem Unter-Tithonium des nördlichen Hegau und einige Bemerkungen zur Taxonomie der Lithacoceratinae. *Geologische Blätter für Nordost-Bayern* 46: 127–144.

Zeiss, A., and H.A. Leanza. 2010. Upper Jurassic (Tithonian) ammonites from the lithographic limestones of the Zapala region, Neuquén Basin, Argentina. *Beringeria* 41: 25–75.