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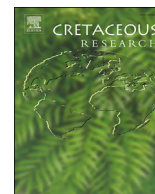
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Ammonite biostratigraphy and bioevents in the Jurassic – Cretaceous boundary of central Chile

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ABSTRACT

Ammonites are abundant and well preserved in the Tithonian-Valanginian (Upper Jurassic – Lower Cretaceous) sedimentary successions of the central Chilean Andes, known as the Lo Valdés and Baños del Flaco Formations. A total of 1429 ammonites were collected from these stratigraphic units and the following index zones based on ammonites are here proposed, from base to top: *Virgatosphinctes mexicanus*/*Pseudolissoceras* cf. *zitteli*, *Windhausenicerias internispinosum*, *Micracanthoceras microcanthum*/*Corongoceras altermans*, *Substeueroceras koeneni* (*Berriasella fraudans* and *Groebericeras rocardi* sub-zones) and *Thurmannicerias thurmanni*/*Argentincerias fasciculatum*.

Our analyses indicate that “Ammonite Richness” is high in the middle and upper Tithonian and into the lower Berriasian part of the succession, but decreases towards the lower Valanginian. Highest similarity values are established for the upper Tithonian, coincident with a high diversity; similarity declines in the lower Berriasian. The main faunal turnover occurred between the early and late Berriasian followed by a secondary bioevent between the late Berriasian and early Valanginian.

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1. Introduction

Even though the position of the Jurassic/Cretaceous (J/K) boundary has been discussed for more than a century, no internationally valid position and Global Stratigraphic Section and Point (GSSP) has yet been agreed upon (e.g. [Remane, 1991](#); [Reboulet et al., 2014](#)). It is thus the only system boundary of the Phanerozoic to date that does not have an accepted global definition ([Ogg and Hirnov 2012](#)). The Tithonian/Berriasian boundary was recommended as a potential candidate for the J/K boundary by the Lyon/Neuchâtel colloquium of 1973 ([Remane, 1991](#)), but placement to this chronostratigraphic level has not been majorly accepted by subsequent authors, resulting from a complex tectonostratigraphic situation at the end of the Jurassic leading to extreme faunal provincialism, the absence of a significant faunal turnover, and the absence of well-established intercontinental correlation. As an alternative to the Tithonian/Berriasian boundary, some authors (e.g. [Rawson, 1990](#); [Remane, 1991](#); in [Zakharov et al., 1996](#)) “have favoured placement of the J/K boundary above the Berriasian, at the

base of the Valanginian”. The option of the base of Valanginian as the J/K boundary deserves consideration as it coincides with a biological crisis and is easy to correlate over long distances ([Granier, 2019](#)).

During the Cretaceous Symposium held in Vienna, in August 2017, the Berriasian Working Group decided to resume the issue and suggested that a future GSSP of the Jurassic/Cretaceous boundary should be defined in the Tethys ([Wimbledon, 2017](#)). The Working Group further discussed that prior to a potential placement of the boundary by ammonites, a systematic revision of taxa was needed from established sections and that new ammonite-bearing sections should be considered ([Reboulet et al., 2018](#)).

Here we present detailed ammonite biostratigraphic data from five expanded and sedimentologically monotonous J/K boundary sections in central Chile ranging from the Tithonian (Upper Jurassic) to Hauterivian (lower Cretaceous) ([Fig. 1](#)); these are among the fossil-richest sections for this interval known to date from the southern hemisphere. We focus on the biostratigraphy and on bioevents in the Baños del Flaco and Lo Valdés formations ([Fig. 1](#)); these lithostratigraphic units were originally analysed by [Biro \(1964\)](#) and [Hallam et al. \(1986\)](#) and recently revised by [Salazar \(2012\)](#) and [Salazar and Stinnesbeck \(2016\)](#). The present analysis is

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based on a total of 1429 ammonites grouped into 45 species (Salazar, 2012; Salazar and Stinnesbeck, 2016).

All studied specimens are registered and housed in the “Colección Paleontológica de la Universidad de Concepción, Chile”, with the acronym CPUC followed by the code of the section from which the fossils were collected (RM: Río Maitenes; CP: Cruz de Piedra; CM: Cajón del Morado; LV: Lo Valdés) and the number of registration (e.g. CPUC/LV/5–23).

2. Jurassic/Cretaceous (J/K) boundary and zonation in South America: a historical view

In South America, ammonites across the J/K boundary (Tithonian-Hauterivian) are well registered in Colombia, Peru, Argentina and Chile (e.g. Leanza 1981a). The best studied sections and faunal assemblages are known from the Neuquén basin in Argentina (e.g. Steuer, 1897, 1921, Gerth, 1921, 1925, Leanza 1945, Leanza 1980, Parent et al., 2011a and 2011b, Reboulet et al., 2014, Aguirre – Urreta et al., 2019). For this region, Harrington (1962, *vide* Leanza 1981a) suggested that the J/K boundary should best be placed between the Kimmeridgian and the Tithonian stages. Leanza (1981a)

considered the Berriasian to be the last stage of the Jurassic, in contrast to the historical classification of the basal Cretaceous as discussed above. The author argued that ammonites of the Berriasian show a phylogenetic continuity with respect to the Tithonian assemblages and that the major faunal turnover occurs near the Berriasian-Valanginian boundary. Wiedmann (1967, 1968, 1973, 1975, see Leanza 1981a) also proposed the Berriasian to be the highest stage of the Jurassic. This interpretation was followed by Volkheimer (1973, 1978, in Leanza 1981a) and Leanza (1981b).

A South American standard ammonite biozonation across the J/K boundary was proposed by A. Leanza (1945) and later modified by H. Leanza (1980); subsequent adjustments and supplements were added for Argentina by Zeiss and Leanza (2010), Parent et al. (2011b), and the last biozonation by Vennari et al. (2017), Aguirre–Urreta et al. (2019), combined with the Mediterranean (Reboul et al., 2014; Wimbledon, 2017) and the Chilean biozonation (Biro, 1964, 1980; Hallam et al., 1986; Mourgues, 2007) and this study (Fig. 2). According to these surveys, *Substeueroceras* is the only Argentinian ammonite genus also registered outside South America (e.g. in Mexico and India). An intercontinental correlation of Argentinian ammonite assemblages with those of the

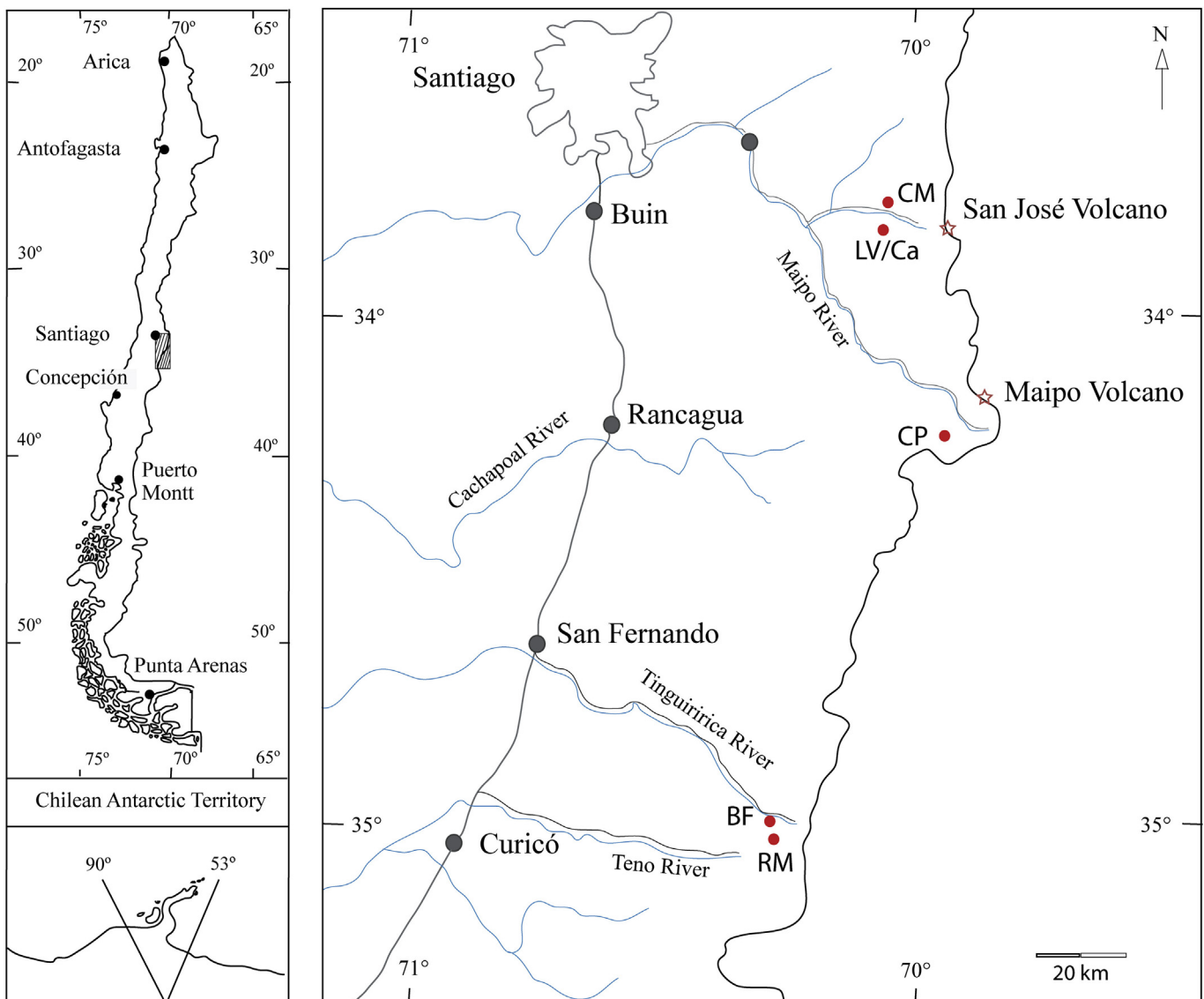


Fig. 1. Map of Chile showing the location of outcrops of the Baños del Flaco and Lo Valdés Formations. CM: Cajón del Morado; LV: Lo Valdés; CP: Cruz de Piedra; Baños del Flaco and RM: Río Maitenes.

European Tethys is therefore hampered by an explicitly discontinuous distribution (vicariance) of taxa in the two faunal realms. This marked vicariance is also seen in calpionellids, a group of calcareous microfossils of explicit Tethyan distribution. While calpionellids are abundant in the western-most Tethys, for instance in Mexico (e.g. Adatte et al., 1994, 1996; Zell et al., 2015), they are almost absent in southern high latitude locations such as Argentinian sections and Chile (Lo Valdés and Baños del Flaco formations).

In Chile, the first biozonation across the J/K boundary was proposed by Biro (1964, 1980), which was subsequently modified

by Hallam et al. (1986). It only included ammonite species endemic to central Argentina and Chile (Fig. 2). Based only on “genera” in common, Zeiss and Leanza (2010), on the other hand, proposed a correlation of Argentinean-Chilean ammonite assemblages with other regions, including Antarctica, Pakistan, the Himalayas, Mexico, South Africa, and Northern Europe. No valid correlation exists to date at “species” level between central Argentina and Chile and other regions.

Part of the extreme faunal provincialism, between South American ammonite assemblages on one side, and those of Tethyan

| System | Stage | Substage | Mediterranean | Central Argentina | | North Chile | Central Chile | | | | |
|------------------|----------------|------------------------------------|--------------------------------------|--------------------------------------|--|---|---|---|---|--|---|
| | | | Reboul et al. 2014 / Wimbledon 2017 | Aguirre-Urreta et al. 2007 | Aguirre-Urreta et al. 2019 | Mourgues 2007 | Biro 1980 & 1964 | Hallam et al. 1986 | This study | | |
| Lower Cretaceous | Valanginian | upper | <i>Criosarasinella furcillata</i> | <i>Pseudofavrella angulatiformis</i> | | | <i>Favrella</i> cf. <i>angulatiformis</i> | <i>Favrella</i> cf. <i>angulatiformis</i> | | | |
| | | | <i>Neocomites peregrinus</i> | | | <i>Olcostephanus</i> (V.) <i>permolestus</i> | | | | | |
| | | | <i>Saynoceras verrucosum</i> | | | <i>Olcostephanus</i> (O.) <i>atherstoni</i> | | | | | |
| | | lower | <i>Karakaschiceras inostranzewi</i> | <i>Lissonia riveroi</i> | | <i>Lissonia</i> n. sp. | | | | | |
| | | | <i>Neocomites necomiensiformis</i> | <i>Neocomites wichmanni</i> | | | | | | | |
| | | | <i>“Thurmanniceras” pertransiens</i> | | | <i>Parandiceras</i> | | | | | |
| | Berriasian | upper | <i>Subthurmannia boissieri</i> | <i>Spiticeras damesi</i> | <i>Argentiniceras noduliferum</i> | | <i>Cuyaniceras transgrediis</i> | <i>Cuyaniceras transgrediis</i> | <i>Argentiniceras bituberculatum / Thurmannites discoidalis</i> | <i>Substeuerocheras koeneni</i> | <i>Groebericeras roccardi</i> |
| | | | <i>Subthurmannia occitanica</i> | | | | | | | | |
| | | lower | <i>Berriassella jacobi</i> | <i>Substeuerocheras koeneni</i> | | <i>Argentiniceras bituberculatum / Thurmannites discoidalis</i> | <i>Substeuerocheras koeneni</i> | <i>Berriassella jacobi</i> | | | |
| | Upper Jurassic | Tithonian | upper | <i>“Durangites”</i> | <i>Corongoceras alternans</i> | <i>Windhauseniceras internispinosum</i> | <i>Substeuerocheras koeneni</i> | <i>Corongoceras alternans</i> | <i>Windhauseniceras internispinosum</i> | <i>Microcantoceras microcanthum / Corongoceras alternans</i> | <i>Windhauseniceras internispinosum</i> |
| | | | | <i>Microcanthum</i> | | | | | | | |
| | | | lower | <i>Ponti</i> | | | | | | | |
| <i>Fallauxi</i> | | <i>Pseudolissoceras zitteli</i> | | | | | | | | | |
| <i>Semiforme</i> | | <i>Virgatosphinctes andesensis</i> | | | | | | | | | |
| <i>Darwini</i> | | | | | | | | | | | |
| <i>Hybonotum</i> | | | | | <i>Virgatosphinctes mexicanus / Pseudolissoceras zitteli</i> | | | | | | |

Fig. 2. Biozonation of Tithonian-Valanginian ammonites in the Mediterranean Realm and South America. Mediterranean ammonite distribution according to Reboul et al. (2014) and Wimbledon (2017), and central Argentinian distribution according to Aguirre-Urreta et al. (2007, 2019). Central Chilean ammonite biozonation is based on Biro (1964, 1980) and Hallam et al. (1986) for central Chile and Mourgues (2007) for northern Chile.

and Boreal Realms on the other (Reboulet et al., 2018), may nevertheless be artificial and caused by the historical splitting of taxa in each geographical realm. Interestingly, European paleontologists working on South American faunal assemblages in the first half of the 20th century (e.g. Steuer, 1897, 1921, Gerth, 1921, 1925) identified important similarities between European and South American taxa. Only subsequent workers, especially in the 1940s (e.g. Leanza 1945), emphasized minor morphological differences by subdividing species and introducing new taxa. This approach of “splitting” of taxa has now led to ammonite assemblages with only restricted value and mostly endemic distribution. Biozonations based on these taxa do no longer allow for intercontinental correlation.

In the past 20 years, however, new concepts were introduced to the Systematic Paleontology of ammonites, such as sexual dimorphism and major intraspecific variability of shell morphology. These concepts now allow for a detailed re-evaluation of ammonite species present in the Chilean part of the Andes. Our review of the faunal assemblages still indicates that endemism is an important factor in the region, but that Tethyan, Boreal, Antarctic and Indian taxa are also present. The biogeographical similarities between South America and other regions worldwide thus appear to be significantly higher than previously considered. Consequently, Chilean ammonite assemblages may now again allow for intercontinental faunal correlation with other regions, including the Tethys (Salazar and Stinnesbeck, 2016).

In addition, biozones presented to date for the J/K boundary transition in South America and other regions, only consider the “presence and absence” of taxa; no statistical analyses have yet been performed including species richness and abundance, or “statistical turnover”. We strongly advocate the idea that statistical tests are key to interpret the problem of bioevents and to discuss biostratigraphical changes across the Jurassic-Cretaceous boundary.

3. The J/K boundary in central Chile

3.1. Ammonite biozones in the Baños del Flaco Formation

In central Chile, sediments of the J/K boundary transition are well represented by the Baños del Flaco and Lo Valdés formations (e.g. Biro, 1964; Covacevich et al., 1976; Biro, 1980; Hallam et al., 1986). Covacevich et al. (1976) assigned the Baños del Flaco Formation to the lower–upper Tithonian and proposed the following biozones, from base to top: *Virgatospinectes andesensis*, *Pseudolissoceras zitteli* and *Corongoceras alternans*. This subdivision was revised by Hallam et al. (1986). The authors suggested the following biostratigraphical units, from bottom to top: *Windhausenicerias internispinosum*, *Corongoceras alternans* and *Substeueroceras koeneni* biozones (Fig. 2), but without specifying other ammonite species or indicating first and last appearances in the stratigraphical column. The authors also assigned a lower–middle Tithonian to lower Berriasian stratigraphic range for the Baños del Flaco Formation.

Ammonites from Rio Maitenes section revised here were originally collected in 1965 by the late Lajos Biro. Collection was *in situ* and layer-by-layer, as indicated by the code used in the original field book of Biro, which was available to us. The faunal assemblage was described and discussed by Salazar and Stinnesbeck (2016).

The stratigraphical distribution of ammonites in the section is summarized in Fig. 3, also including the assignment of lithological units within the Baños del Flaco Formation described by Salazar and Stinnesbeck (2016) and their relative abundance, range and distribution; the important index ammonites of the Rio Maitenes

Formation are illustrated in Fig. 4, and a summary of the abundance of every species assigned is presented in Fig. 5.

Even though we are aware that the occurrence of ammonites is discontinuous in the Rio Maitenes section, we tentatively propose the following four biozones, from bottom to top (Fig. 3):

***Virgatospinectes mexicanus*/*Pseudolissoceras zitteli* biozone:** This biozone is identified in sandstone/calcareous sandstone of the lower member of the Baños del Flaco Formation (Fig. 3). The index ammonites *Virgatospinectes mexicanus* and *Pseudolissoceras zitteli* (Fig. 4a–b) are associated with *Euvirgalithacoceras malarguense*, *Choisispinectes windhausenii* and a single specimen of *Aulacospinectes proximus*. No ammonites were registered in the lowermost lower member of the Baños del Flaco Formation (e.g. basal conglomerate, grainstone units; see Salazar and Stinnesbeck, 2016).

***Windhausenicerias internispinosum* biozone:** This biozone is based on the presence of *Windhausenicerias internispinosum* (Fig. 4c) in the upper part of the lower sandstone/calcareous sandstone unit of the Baños del Flaco Formation (Fig. 3). The sandy limestone up-section from this unit has not yielded ammonites. Ammonites associated with *Windhausenicerias internispinosum* are *Catospinectes cf. americanensis* and *Aulacospinectes proximus*.

***Micracanthoceras microcanthum*/*Corongoceras alternans* biozone:** This biozone is characterized by the occurrence of *Micracanthoceras microcanthum* and *Corongoceras alternans* (Fig. 4d–g) in the lower part of the upper member of the Baños del Flaco Formation, specifically in the calcareous sandstone unit (Fig. 3). Other ammonites in this biozone are *Micracanthoceras spinulosum* and *Corongoceras evolutum*.

***Substeueroceras koeneni* biozone:** This biozone is identified by the presence of a single specimen of *Substeueroceras koeneni* in the upper part of the upper member of the Baños del Flaco Formation, in the sandy limestone/limestone/sandstone unit (Fig. 3).

3.2. Biozones of the Lo Valdés formation

The most detailed biozonation of the Lo Valdés Formation was presented by Biro (1964) and subsequently used in other publications on the Lo Valdés Formation (e.g. by Biro, 1980 and Hallam et al., 1986, Fig. 2). Eight ammonite biozones were proposed, but the authors did not indicate first and last appearances of taxa in the stratigraphic column.

Ammonites of the Lo Valdés Formation revised here were collected by us in sections at Lo Valdés, Cajón del Maipo and at Cruz de Piedra (Fig. 1) and are described and discussed in Salazar (2012). Most fossils were collected *in situ*, but a small number of fossils were picked up from debris adjacent to the sections. The approximate position of these latter specimens was estimated within the stratigraphic column, based on the fossil assemblage associated with the ammonites and lithological characteristics of the bed rock.

Important index ammonites of the Lo Valdés Formation are illustrated in Fig. 6, their relative abundance, ranges and distribution at Cruz de Piedra (CP), Cajón del Maipo (CM) and Lo Valdés (LV) in Figs. 7 to 9. We here describe three biozones, using index taxa with a wide geographical distribution and high abundance, where the number of specimens is exposed in Fig. 10. Definition of lithological units within the Lo Valdés Formation follows Salazar and Stinnesbeck (2015):

***Micracanthoceras microcanthum*/*Corongoceras alternans* biozone:** This biozone is characterized by the range of *Micracanthoceras microcanthum* and *Corongoceras alternans* (Fig. 6a–d), in the Escalador Member of the Lo Valdés and Cajón del Morado sections (Figs. 8 and 9), and in the lower part of the Placa Roja Member at Cruz de Piedra (Fig. 7). This zone also contains *Aspidoceras rogoznicensis*, *Micracanthoceras spinulosum*, *Corongoceras evolutum*, *Corongoceras involutum*, *Corongoceras lotenoense*,

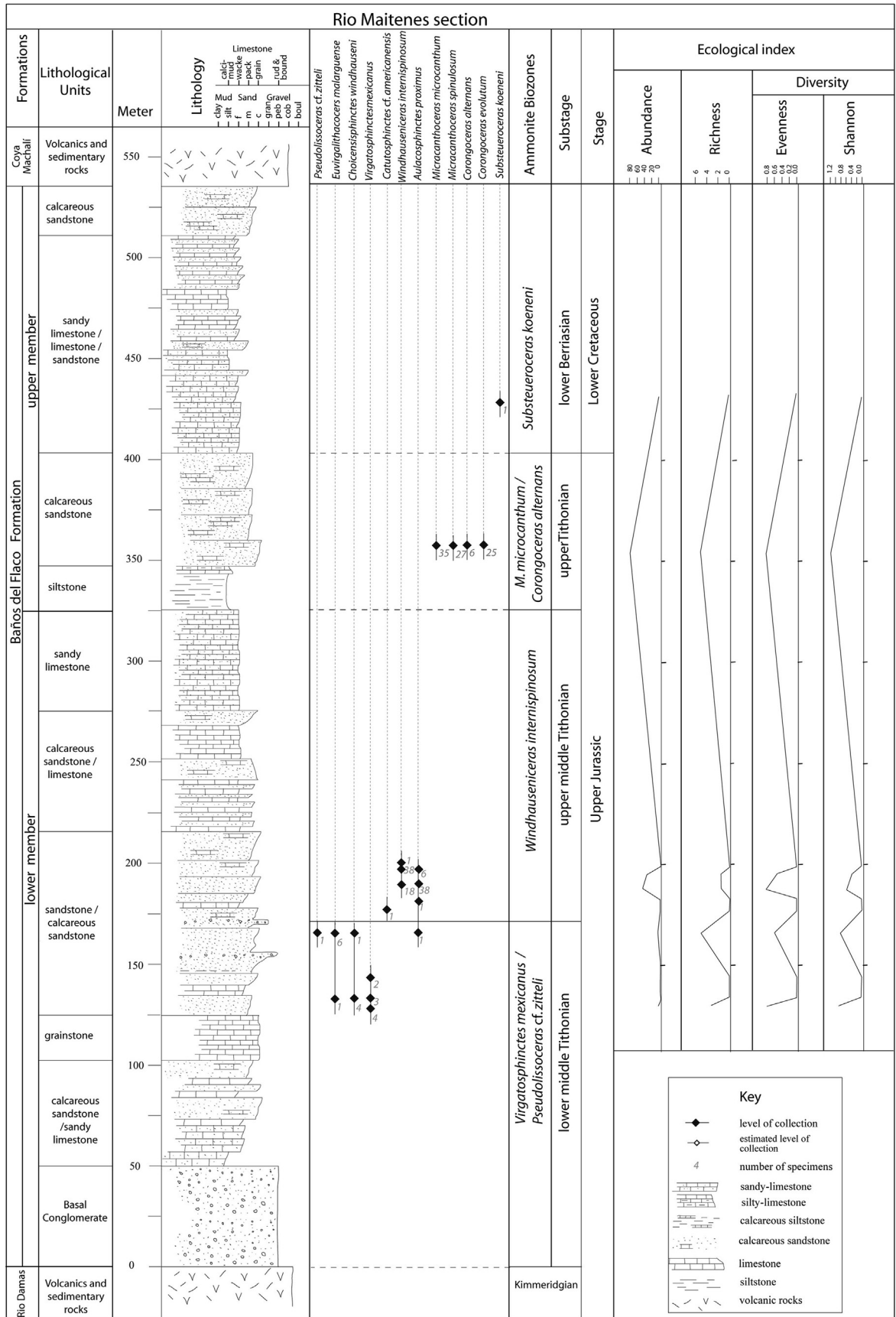


Fig. 3. Baños del Flaco Formation at Rio Maitenes, including ages, lithological units, amonite zones, ranges of amonite species and abundance of amonites, as well as the ecological index (abundance, richness and diversity).

Corongoceras mendozanum, *Substeueroceras calistoide*, *Lytohoplites paredesi*, *Lytohoplites zambranoi*, *Lytohoplites varelae*, *Lytohoplites rauoi* and *Bochianites* sp., and a single specimen of *Chigaroceras bardensis* (Figs. 7, 8, and 9).

***Substeueroceras koeneni* biozone:** This biozone is identified by the presence of *Substeueroceras koeneni* (Fig. 6e). Within this biozone, two sub-biozones are identified:

- ***Berriasella jacobi* sub-biozone:** This sub-biozone is identified in the lower part of the Placa Roja Member at Lo Valdés and Cajón del Morado (Figs. 6f, 8 and 9), and the middle part of the Placa Roja Member at Cruz de Piedra (Fig. 7); the sub-biozone is characterized by the presence of *Berriasella jacobi*, and *Pterolytoceras exoticum*, *Aspidoceras rogoznicensis*, *Aulacosphinctes proximus*, *Micracanthoceras spinulosum*, *Micracanthoceras vetustum*, *Corongoceras koellikeri*, *Corongoceras mendozanum*, *Spiticeras acutum*, *Spiticeras tripartitum*, *Substeueroceras calistoide*, *Substeueroceras striolatissimum*, *Tirnovella kayseri*,

Cuyanicerias transgrediens, *Malbosciceras malbosi* and *Chigaroceras bardensis* (Figs. 7, 8 and 9).

- ***Groebericeras rocardi* sub-biozone:** This sub-biozone is identified in the upper part of the Placa Roja Member in all sampled sections and is characterized by the presence of *Groebericeras rocardi* (Fig. 6g). *Spiticeras spitiense*, *Spiticeras tripartitum*, *Spiticeras acutum*, *Cuyanicerias transgrediens*, *Substeueroceras striolatissimum*, *Neocosmoceras sayni* and *Freguelliceras magister* are also present (Fig. 7, 8 and 9).

***Thurmanniceras thurmanni*/*Argentiniceras fasciculatum* biozone:** This biozone was identified in the uppermost 12 m of the Placa Roja Member and lower part of the Cantera Member at Lo Valdés (Fig. 9), and in the upper part of the Placa Roja Member at Cajón del Morado (Fig. 8). In addition to the index taxon *Thurmanniceras thurmanni* (Fig. 6h), *Spiticeras pricei*, *Spiticeras spitiense*, *Spiticeras tripartitum*, *Freguelliceras magister* and *Pseudofavrella angulatiformis* are also present.

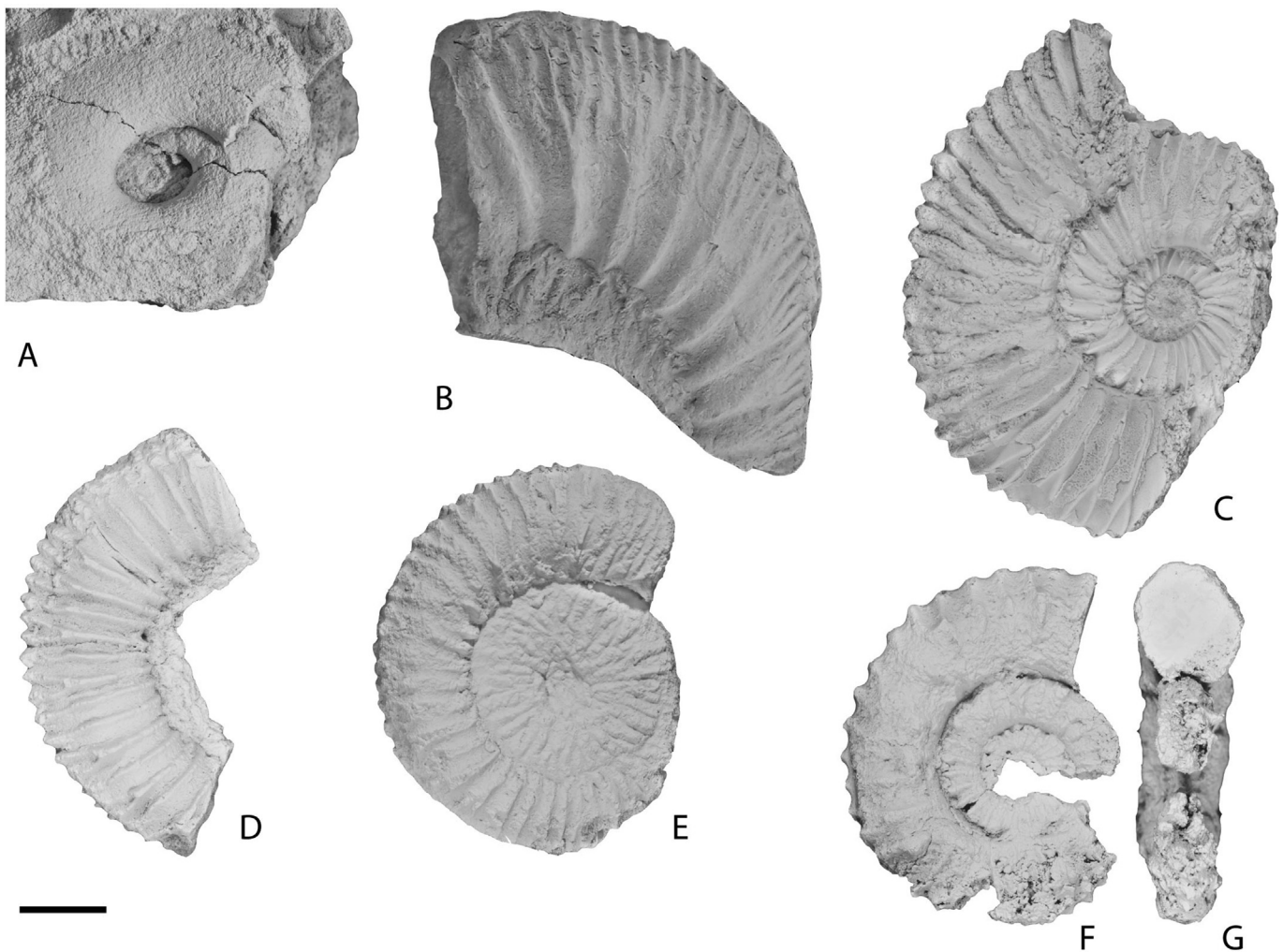


Fig. 4. Ammonites from the Baños del Flaco Formation used as biozone markers. **A** - *Pseudolissoceras* cf. *zitteli*, CPUC/RM/47–11 (= Fig. 7A in Salazar and Stinnesbeck, 2016); **B** - *Virgathosphinctes mexicanus*, CPUC/RM/10–05 (= Fig. 6D in Salazar and Stinnesbeck, 2016); **C** - *Windhauseniceras internispinosum*, CPUC/RM/Rd–18 (= Fig. 12B in Salazar and Stinnesbeck, 2016); **D-E** *Micracanthoceras microcanthum*, **D**, CPUC/RM/Rd-31; **E**, CPUC/RM/99–43 (= Fig. 15H and L in Salazar and Stinnesbeck, 2016); **F-G** *Corongoceras alternans*, CPUC/RM/99–95 (= Fig. 20K–L in Salazar and Stinnesbeck, 2016). Scale bar = 10 mm.

3.3. Remarks on the chronostratigraphic distribution of biozonal index taxa

3.3.1. *Virgatosphinctes mexicanus*/*Pseudolissoceras zitteli* biozone

The paleobiogeographic importance of *Virgatosphinctes mexicanus* was discussed by Salazar and Stinnesbeck (2016). It was then presented by the authors as *Virgatosphinctes scythicus* but is now assigned to *V. mexicanus*, a taxon also present in Argentina, Antarctica and Mexico (e.g., Burckhardt, 1906; Thomson, 1979; Howlett, 1989; Sey et al., 1992; Parent et al., 2011a; Aguirre–Urreta, 2019).

Pseudolissoceras zitteli is well known from the middle Tithonian of Argentina (Burckhardt, 1903; Leanza, 1980; Parent, 2001; Parent et al., 2011a), the middle Tithonian of Mexico (Cantú-Chapa, 1967), the lower Tithonian of Cuba (Myczynski, 1990), and the middle Tithonian of East Russia (Sey and Kalacheva, 1997). *Pseudolissoceras zitteli* is here considered to be geographically widespread and therefore well suited as an index for the middle Tithonian. The *Virgatosphinctes mexicanus*/*Pseudolissoceras zitteli* zone is thus assigned here to the middle Tithonian (Figs. 2 and 11).

3.3.2. *Windhausenicerias internispinosum* biozone

Windhausenicerias internispinosum was previously registered in South America from Argentina, Chile and Colombia. In Argentina, records are from the upper part of the middle Tithonian (e.g. Leanza, 1945; Leanza, 1980; Aguirre–Urreta et al., 2019), and in central Chile from the middle–upper Tithonian (Corvalán, 1959; Aguirre–Urreta and Charrier, 1990). In Colombia, the species was tentatively recorded from the upper Tithonian (Bürgl, 1960). In the Baños del Flaco Formation, the presence of *W. internispinosum* is indicative of the upper part of the middle Tithonian (Figs. 2 and 11).

3.3.3. *Micracanthoceras microcanthum*/*Corongoceras alternans* biozone

Micracanthoceras microcanthum was previously recorded in the central and western Tethys, e.g. in México. In this region, it is

considered an index fossil of the lowermost upper Tithonian *M. microcanthum* biozone (e.g. Wimbledon, 2017).

Corongoceras alternans was recorded from the upper Tithonian of Argentina (e.g. Leanza, 1945; Parent, 2001); in Chile, the taxon is present in the upper Tithonian of Alto Palena (Fuenzalida, 1966) and the middle part of the upper Tithonian at Lo Valdés (Biro, 1964).

The *Micracanthoceras microcanthum*/*Corongoceras alternans* biozone is here assigned to the upper Tithonian (Figs. 2 and 11).

3.3.4. *Substeuerocheras koeneni* biozone

S. koeneni was recorded from Argentina and Chile, but also from Perú, Mexico, Yemen and East Russia (e.g. Fatmi and Zeiss, 1999), but considerable discussion exists regarding the range of this taxon. In Argentina and Chile, the species was regarded an index for the upper Tithonian (e.g. Leanza, 1945; Corvalán, 1959; Biro, 1964; Parent, 2001), an interpretation followed by Rivera (1951) for Peru, by Imlay (1939) and Verma and Westermann (1973) for Mexico, by Vašíček et al. (2018) for Europe, and by Fatmi and Zeiss (1999) for Pakistan. A upper Tithonian (*Durangites* biozone) to Berriasian (*Occitanica* biozones) range was suggested by Howarth (1998) for Yemen.

On the other hand, Zeiss (1983) and Hallam et al. (1986) proposed *Substeuerocheras koeneni* to be basal Berriasian in age, as also suggested by Sey and Kalacheva (1999, 2001) for Far East Russia. We here follow the interpretation that the *S. koeneni* biozone is assigned to the lower Berriasian (Figs. 2 and 11) based on data presented by Adatte et al. (1994, 1996) from Mexico. The authors documented abundant and diverse calpionellids representing the Berriasian alpina and elliptica biozones, associated with *Substeuerocheras koeneni*.

The *Substeuerocheras koeneni* biozone is divided into two sub-biozones:

- **Berriassella jacobi sub-biozone:** In the Tethys Realm, *B. jacobi* is considered an index fossil for the lowermost Berriasian (e.g. Reboult et al., 2014). The presence of *B. jacobi* in South America is discussed in Salazar (2012) and the taxon is here assigned to

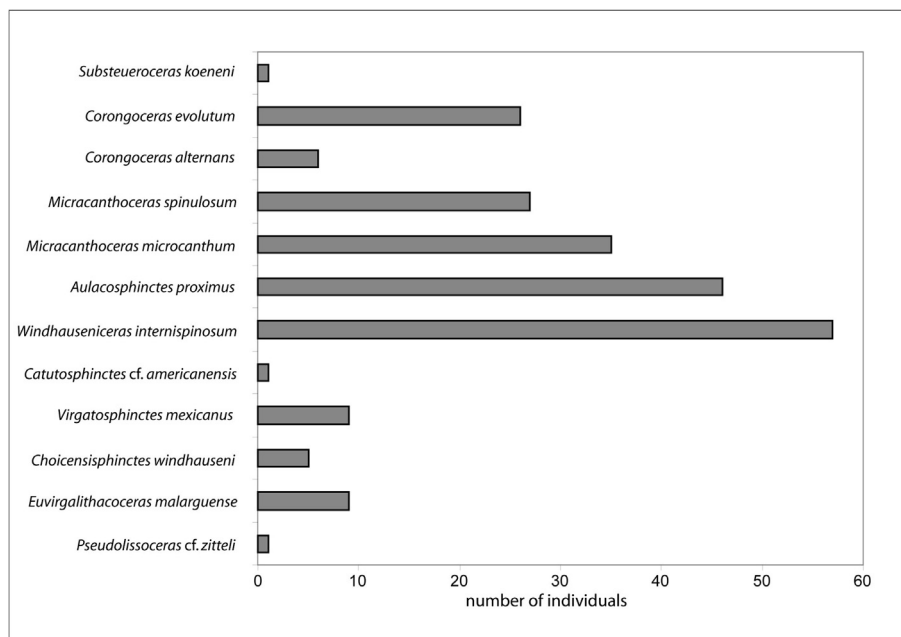


Fig. 5. Abundance of the ammonites in the Baños del Flaco Formation at Rio Maitenes.

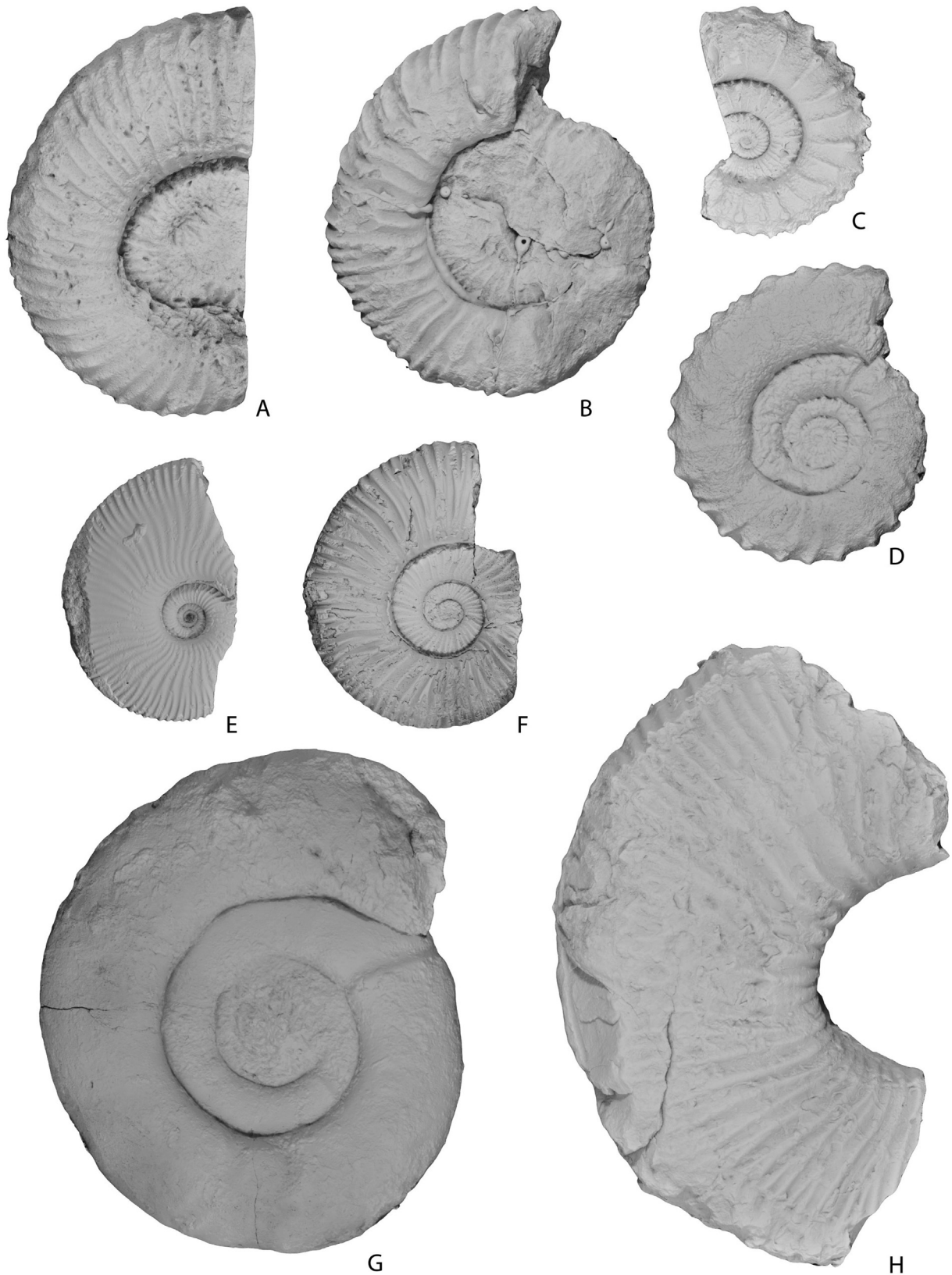


Fig. 6. Ammonites from the Lo Valdés Formation used as biozone markers. **A–B** *Micracanthoceras microcanthum*, **A**, CPUC/CM/16–110; **B**, CPUC/LV/3–356 (= Fig. 4.27a y 4.27 g in Salazar, 2012). **C–D** *Corongoceras alternans*, **C**, CPUC/LV/3–379; **D**, CPUC/LV/3–194 (= Fig. 4.33 g y 4.33e in Salazar, 2012). **E**, *Substeueroeras koeneni*, CPUC/LV/3–341 (= Fig. 4.61i in Salazar, 2012). **F**, *Berriasella jacobii*, CPUC/CP/50–20 (= Fig. 4.52b in Salazar, 2012). **G**, *Groebericeras rocardi*, CPUC/CM/18–56 (= Fig. 4.49b in Salazar, 2012). **H**, *Thurmanniceras thurmanni*, CPUC/LV/8–86 (= Fig. 4.85 g in Salazar, 2012). Scale bar = 10 mm.

the lower Berriasian (Figs. 2 and 11), based on its well-established Tethyan range.

- **Groebericeras rocardi sub-biozone:** The taxon is well recorded for the upper Berriasian of Algeria (Pomel, 1889), south-east Spain (Hoedemaeker, 1982), Nepal, western Canada and Iraq (Howarth, 1992). *G. bifrons* from Argentina is here considered to be a junior synonym; this taxon was registered for the lower Berriasian (Leanza, 1945; Aguirre-Urreta and Alvarez, 1999). The *Groebericeras rocardi* Sub-biozone is here assigned to the upper Berriasian (Figs. 2 and 11).

3.3.5. *Thurmanniceras thurmanni*/*Argentiniceras fasciculatum* biozone

In Argentina, "*T. duraznensis*" is a junior synonym of *Thurmanniceras thurmanni* and was registered for the upper Berriasian (Leanza, 1945). Elsewhere, *T. thurmanni* was recorded for the lower Valanginian of Perú (Lisson, 1907), Mexico (Burckhardt, 1906; González-Arreola et al., 1995), south France (Pictet and Campiche, 1860; Roman, 1938), south Spain (Hoedemaeker, 1982) and Bulgaria (Nikolov, 1960). In south Spain (Company, 1987) and south-west Morocco (Wippich, 2001, 2003) *Thurmanniceras thurmanni*

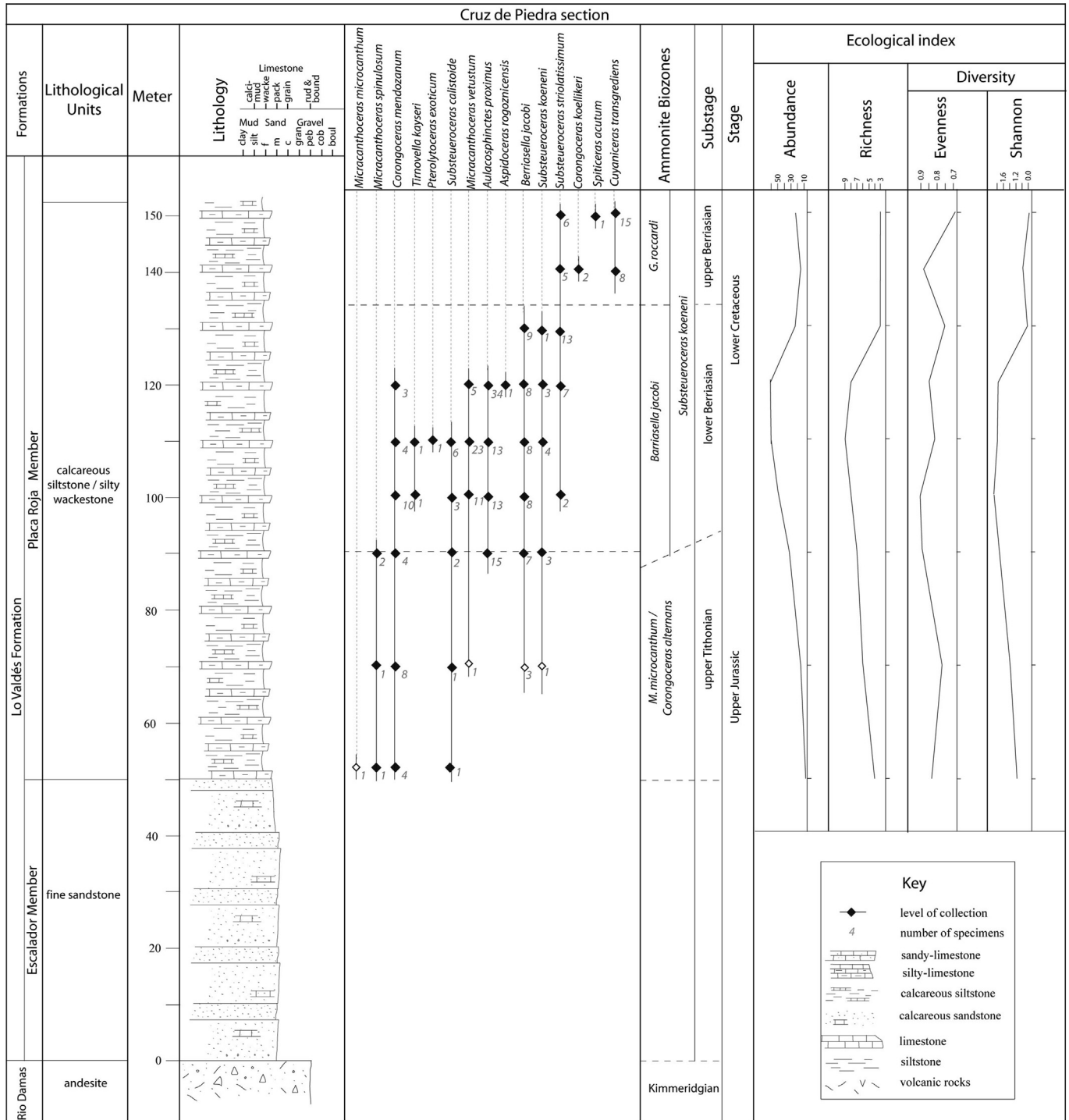
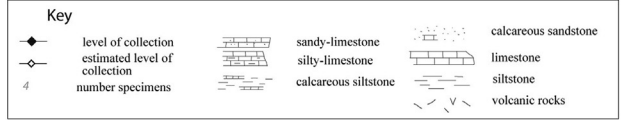
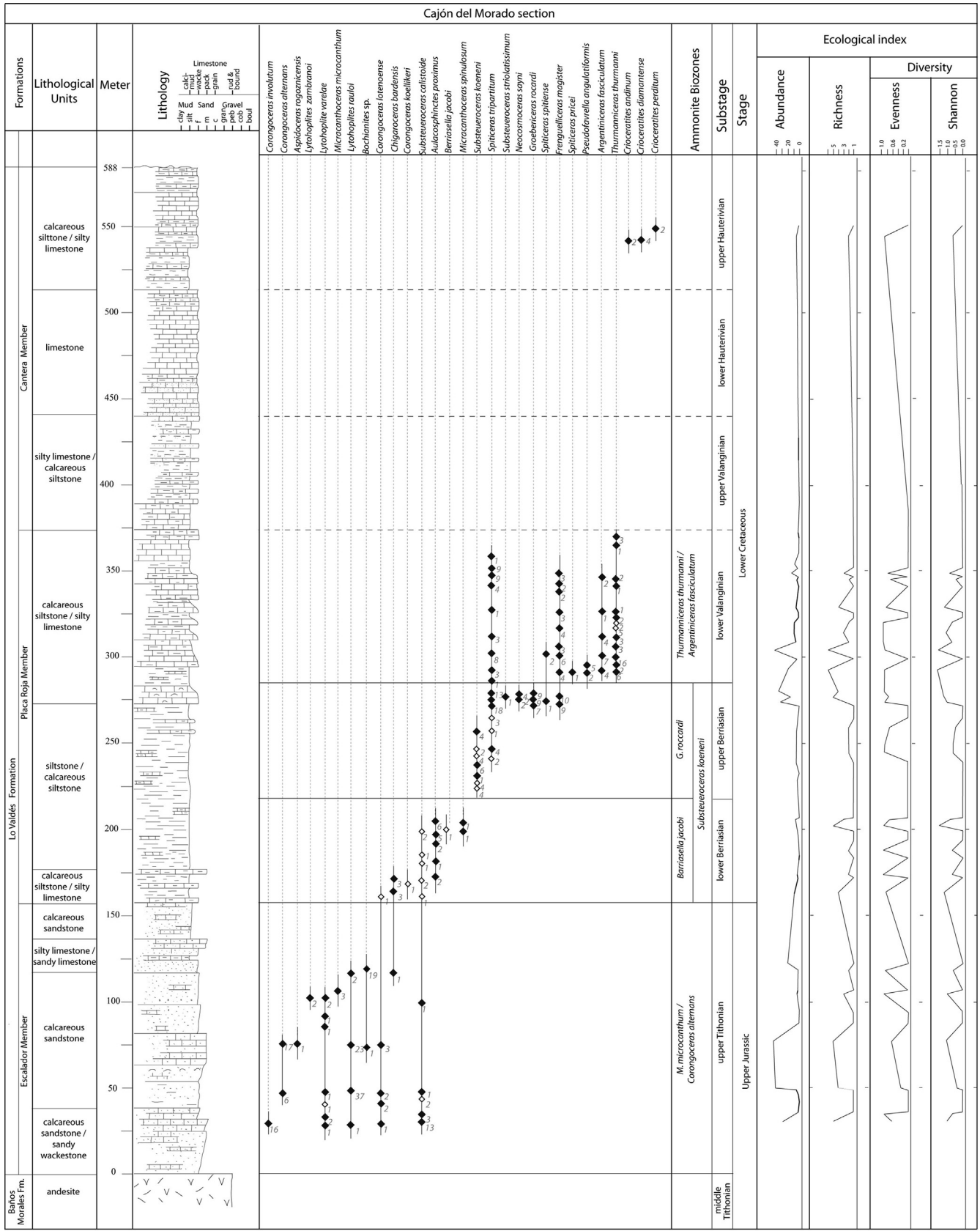


Fig. 7. Lo Valdés Formation at Cruz de Piedra section, including ages, lithological units, ammonite zones, ranges of ammonite species and abundance of ammonites, as well as the ecological index (abundance, richness and diversity).



is recorded from the *T. pertransiens* biozone of the lower Valanginian.

Argentiniceras fasciculatum was recorded from Argentina (Steuer, 1897, 1921) for the upper Tithonian, Valanginian (Gerth, 1925; Weaver, 1931), and for the lower Berriasian (Leanza, 1945). Elsewhere the taxon was recorded from the Berriasian of Antarctica (Tavera, 1970), Colombia (Royo y Gómez, 1945) and Canada (Jeletzky, 1984).

The *Thurmanniceras thurmanni*/*Argentiniceras fasciculatum* biozone is assigned here to the lower Valanginian (Figs. 2 and 11).

Up-section, the upper Valanginian to upper Hauterivian section is continuous, but was not included here because of collection bias due to bad outcrop conditions (Figs. 8 and 9).

4. Bioevents and paleoecology

Statistical analyses are discussed for each section of the Baños del Flaco and Lo Valdés Formations and include the “relative abundance” (accounted as relative number of specimens), “relative richness” (accounted as relative number of species) and as well as the “Evenness” and “Shannon” diversity indices. The data are integrated in a faunal turn-over analysis.

Species turn-over was quantified as the similarity between neighboring (overlying/underlying) layers using the Jaccard index (related to the richness) and Bray-Curtis index (related to the abundance) which varies between 100% (identity in the species composition) and 0% (no common species between compared layers). Increasing values in these indices thus represent decreasing, or increasing, species turn-over (Koleff et al., 2003). The calculations were performed using the Diversity Calc software (Möseler et al., 2009).

4.1. Baños del Flaco Formation

A total of 223 specimens were collected in the Baños del Flaco Formation at Rio Maitenes, and referred to 12 different species. *Windhauseniceras internispinosum* is the most abundant taxon (57 specimens), followed by *Aulacosphinctes proximus* (46 specimens), *Micracanthoceras microcanthum* (35 specimens), *Micracanthoceras spinulosum* (27 specimens) and *Corongoceras evolutum* (26 specimens) (Fig. 5).

“Relative abundance” is highest in the sandstone/calcareous sandstone unit of the lower member, with a total of 128 specimens (Fig. 3). 94 specimens were sampled in the lower part of the calcareous sandstone unit of the upper member. The highest “relative abundance” is reached in the lower part of the calcareous sandstone unit of the upper member (at meter 354 of the stratigraphical column), with 94 specimens, followed by the unit between 188 and 195 m of the stratigraphic column, with 56 specimens registered at 188 m and 44 specimens at 195 m (Fig. 3).

The “relative richness” is highest at 354 and at 166 m, with 4 species registered in each level (Fig. 3).

The “Evenness diversity index” shows two points of highest diversity, at 354 m in the calcareous sandstone unit of the upper member, and at 188 m in the sandstone/calcareous sandstone unit (Fig. 3). The “Shannon diversity index” also indicates highest diversity at 354 m, followed by the 166 m-level in the sandstone/calcareous sandstone unit (Fig. 3).

Ammonoids at Rio Maitenes (Baños del Flaco Formation) are thus discontinuously distributed. They are most abundant and distributed continuously in the sandstone/calcareous sandstone

unit, with 128 specimens referred to 7 species; this interval was dated to the middle Tithonian (Fig. 3). No ammonites are present in the units overlying this interval and up to the 354 m-level, in the calcareous sandstone unit, where 94 specimens referred to 4 species were identified and assigned to the upper Tithonian. The uppermost record of ammonites is at 428 m of the section in the sandy limestone/limestone/sandstone unit, but only a single specimen (assigned to *Substeuerocheras koeneni*) was discovered and assigned to the lower Berriasian (Fig. 3). The three data points do not share any species in common.

The ecological indices (“relative abundance”, “relative richness”, diversity indices of “Evenness” and “Shannon”) show that abundance, richness and diversity increase in the Baños del Flaco Formation (RM) from the middle Tithonian to upper Tithonian, but decrease, abruptly from the upper Tithonian to lower Berriasian. The highest abundance, richness and diversity is at meter 354 (upper member, calcareous sandstone unit) in the upper Tithonian (Fig. 3).

4.2. Lo Valdés Formation

1206 ammonite specimens were collected in the Lo Valdés Formation (sections LV, CM and CP) and referred to 39 species. The most abundant taxa are *Spiticeras tripartitum* (148 specimens), *Substeuerocheras koeneni* (104 specimens), *Aulacosphinctes proximus* (100 specimens), *Corongoceras alternans* (72 specimens), *Lytohoplites rauloi* (72 specimens) and *Thurmanniceras thurmanni* (66 specimens) (Fig. 10).

At Cruz de Piedra, the “relative abundance” is highest at meters 110 and 120, with 60 and 61 specimens collected, and 48 specimens at 100 m of the section. The “relative richness” is high at meters 100, 110 and 120, with 7, 8 and 7 species, respectively (Fig. 7).

According to the “Evenness diversity index”, diversity is highest at meter 100, followed by the meter 90 m level. The “Shannon diversity index” suggests that diversity is highest at 100 m of the section, followed by 90 and 120 m (Fig. 7).

The stratigraphical record at Cruz de Piedra section is continuous, without a visible interruption. Highest diversity is reached near the base of the lower Berriasian (100 m level), whereas richness and abundance are highest between 110 and 120 m of the section, also in the lower Berriasian. A major bio-event was detected in the transition between the uppermost Tithonian (*Micracanthoceras microcanthum* biozone) and lower Berriasian (*Substeuerocheras koeneni* biozone). *Micracanthoceras microcanthum* and *M. spinulosum* are registered only in the uppermost Tithonian while *Corongoceras mendozanum* is equally present in both the *M. microcanthum* and *S. koeneni* biozones. *S. callistoide* is also recorded in both biozones, but is more abundant in the *S. koeneni* biozone. From 120 to 140 m, diversity declines gradually (Fig. 7).

The transition between the upper Tithonian and lower Berriasian is thus characterized by a gradual change in the ammonite assemblage, with highest rates for abundance, richness and diversity in the lower Berriasian, and a subsequent decline of the ecological index in the upper Berriasian (Fig. 7).

At Cajón del Morado “relative abundance” and “relative richness” show abundance peaks between 50 and 77 m in the *M. microcanthum*/*C. alternans* biozone (upper Tithonian, Fig. 8), and between 277 and 309 m, in the lower part of the *Thurmanniceras thurmanni*/*Argentiniceras fasciculatum* biozone (lower Valanginian). Other significant peaks of the “relative richness” are identified around the 200 m-level of the section in the *Berriasella jacobii*

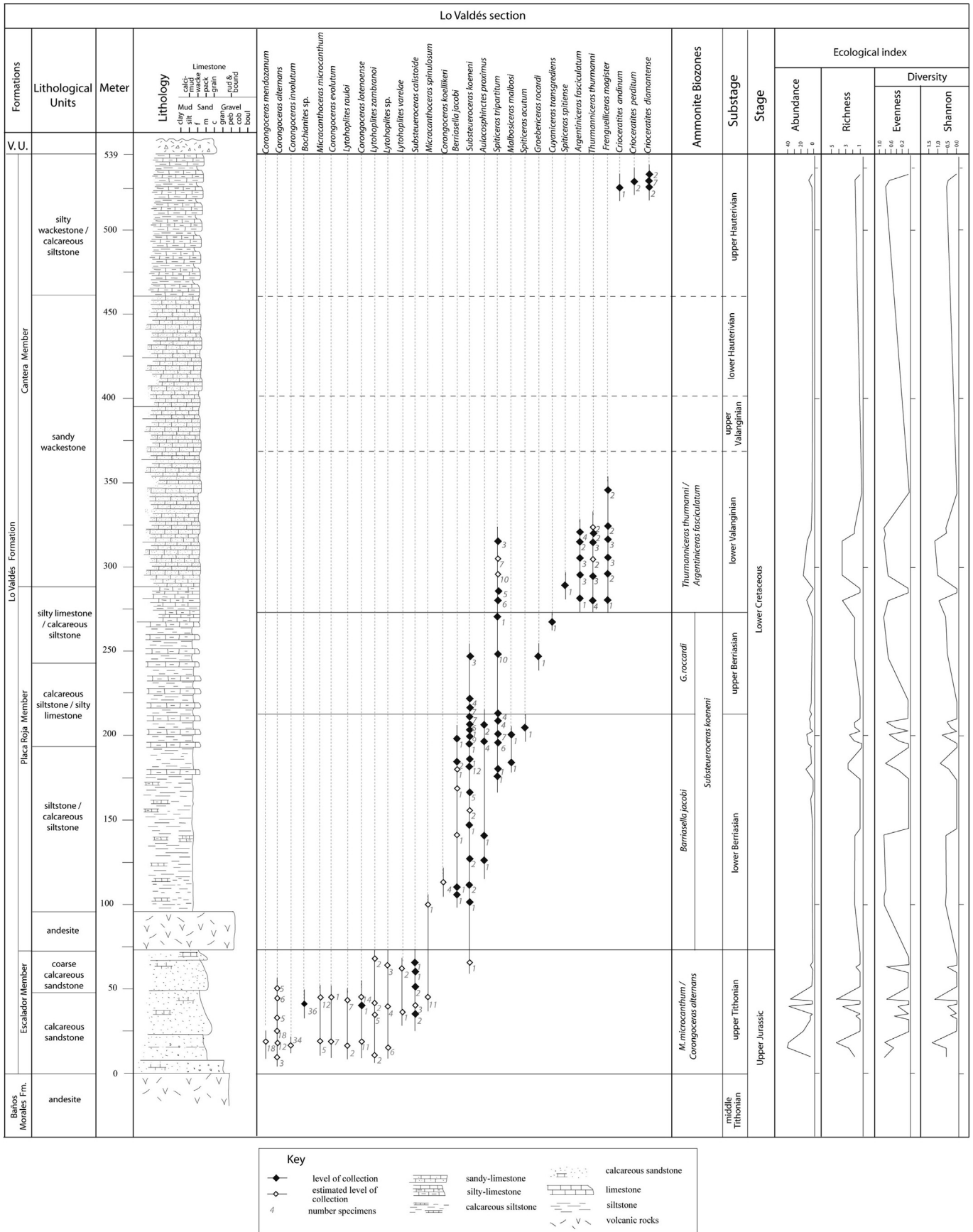


Fig. 9. Lo Valdés Formation at Lo Valdés (type section), including ages, lithological units, ammonite zones, ranges of ammonite species and abundance of ammonites, as well as the ecological index (abundance, richness and diversity).

biozone (lower Berriasian). Four levels with high diversity are identified using the “Evenness diversity index”, at 30 m, between 100 and 120 m, 160–210 m, and between 240 and 320 m. Two levels with high diversity are recognized using the “Shannon diversity index”, between 160 and 210 m and between 290 and 310 m (Fig. 8). Ammonites are therefore continuously present at Cajón del Morado between the *M. microcanthum*/*C. alternans* biozone of the upper Tithonian to the *T. thurmanni*/*A. fasciculatum* biozone of the lower Valanginian, Fig. 8).

“Relative abundance”, “relative richness” and diversity are high in the lower part of the upper Tithonian and in the lowest part of the upper Tithonian (Fig. 8). The transition between the upper Tithonian and the lower Berriasian is marked by an abrupt change; only two of the eleven species recorded in the upper Tithonian are also present in the lower Berriasian, and the ecological index is low in the lower Berriasian. In the upper Berriasian, the “relative abundance”, “relative richness”, and diversity, increase gradually and reach peak values for the lower Valanginian (Fig. 8).

Two peaks of the “relative abundance” and “relative richness” are identified at Lo Valdés section, between 15 and 18 m and between 40 and 44 m, in the *M. microcanthum*/*C. alternans* biozone of the upper Tithonian (Fig. 9). Five peak abundance levels are recognized using the “Evenness diversity index”, between 15–18 m and 40–44 m in the *M. microcanthum*/*C. alternans* biozone of the upper Tithonian, between 100 and 150 m in the *Berriasella jacobi* biozone of the lower Berriasian, at 275 m and between 300 and 325 m in the *T. thurmanni*/*A. fasciculatum* biozone of the lower Valanginian. Four levels of high diversity are present using the “Shannon diversity index”, between 15–18 m and 40–44 m in the *M. microcanthum*/*C. alternans* biozone of the upper Tithonian, and at 280 m and between 290 and 325 m in the *T. thurmanni*/*A. fasciculatum* biozone of the lower Valanginian. At Lo Valdés, the distribution

of ammonites is therefore continuous from the *M. microcanthum*/*C. alternans* biozone (upper Tithonian) to the *T. thurmanni*/*A. fasciculatum* biozone (lower Valanginian, Fig. 9).

The ecological index shows highest values in the upper Tithonian but marks a significant drop in the transition between the upper Tithonian and the lower Berriasian; only a single specimen of a possible Tithonian ammonite was registered in the lower Berriasian, and only a single specimen of a “typically Berriasian” ammonite was identified from uppermost Tithonian strata. The ecological index is low in the lower part of lower Berriasian, but increases gradually within the upper part of the lower Berriasian. In the upper Berriasian the ecological index is low, but increases in the lower Valanginian (Fig. 9).

Combining the relative abundance (number of specimen) of every species recorded in the three sections study here, show clearly the index fossils used, are between the most abundant (Fig. 10).

Fig. 11 integrates ecological data of “relative abundance”, “relative richness” and “Evenness, as well as the Shannon diversity index”, of the Baños del Flaco and Lo Valdés formations (Rio Maitenes, Cruz de Piedra, Cajón del Morado and Lo Valdés sections). The data set was grouped in stratigraphic intervals which correspond to the 5 biozones identified. The “relative abundance” increases gradually from the lower part of the middle Tithonian to the upper Tithonian, with highest values reached in the upper Tithonian. From the upper Tithonian to the upper Valanginian the “relative abundance” decreases gradually (Fig. 11).

Values for the “relative richness” are high in the middle and upper Tithonian and into the lower Berriasian (Fig. 11). From there numbers decrease to the lower Valanginian. No ammonites were identified for the upper Valanginian and lower Hauterivian interval. “Relative richness” is low for the upper Hauterivian (Fig. 11).

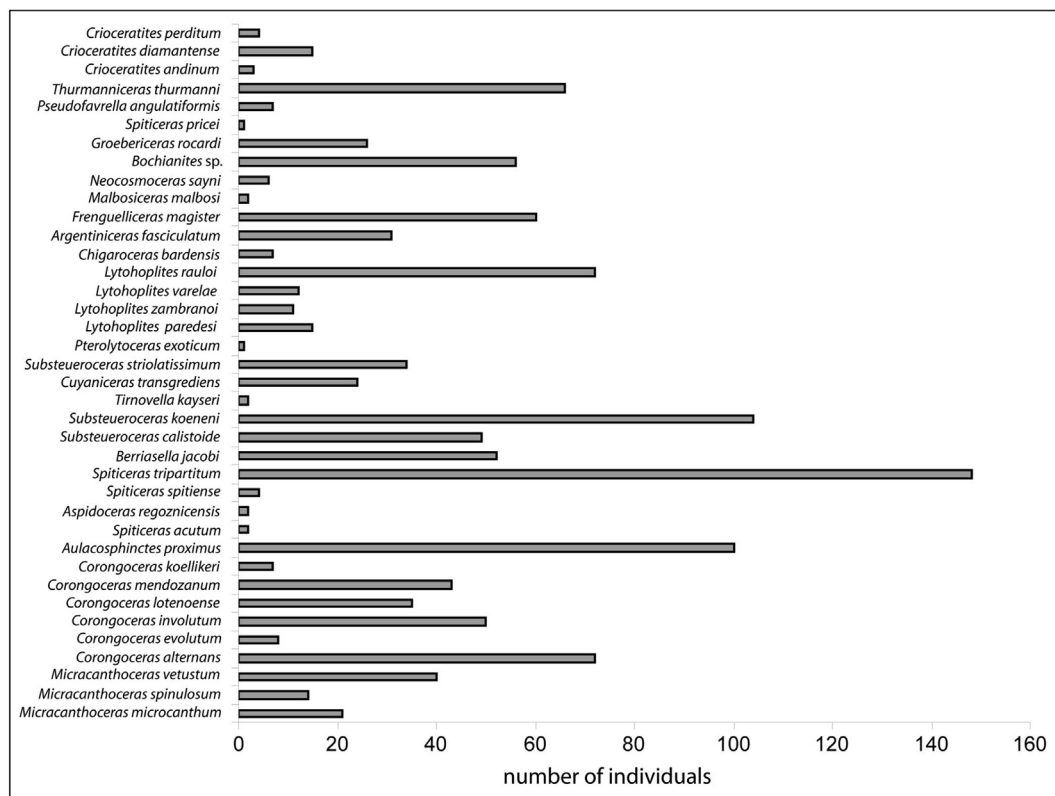


Fig. 10. Abundance of the ammonites identified in the Lo Valdés Formation.

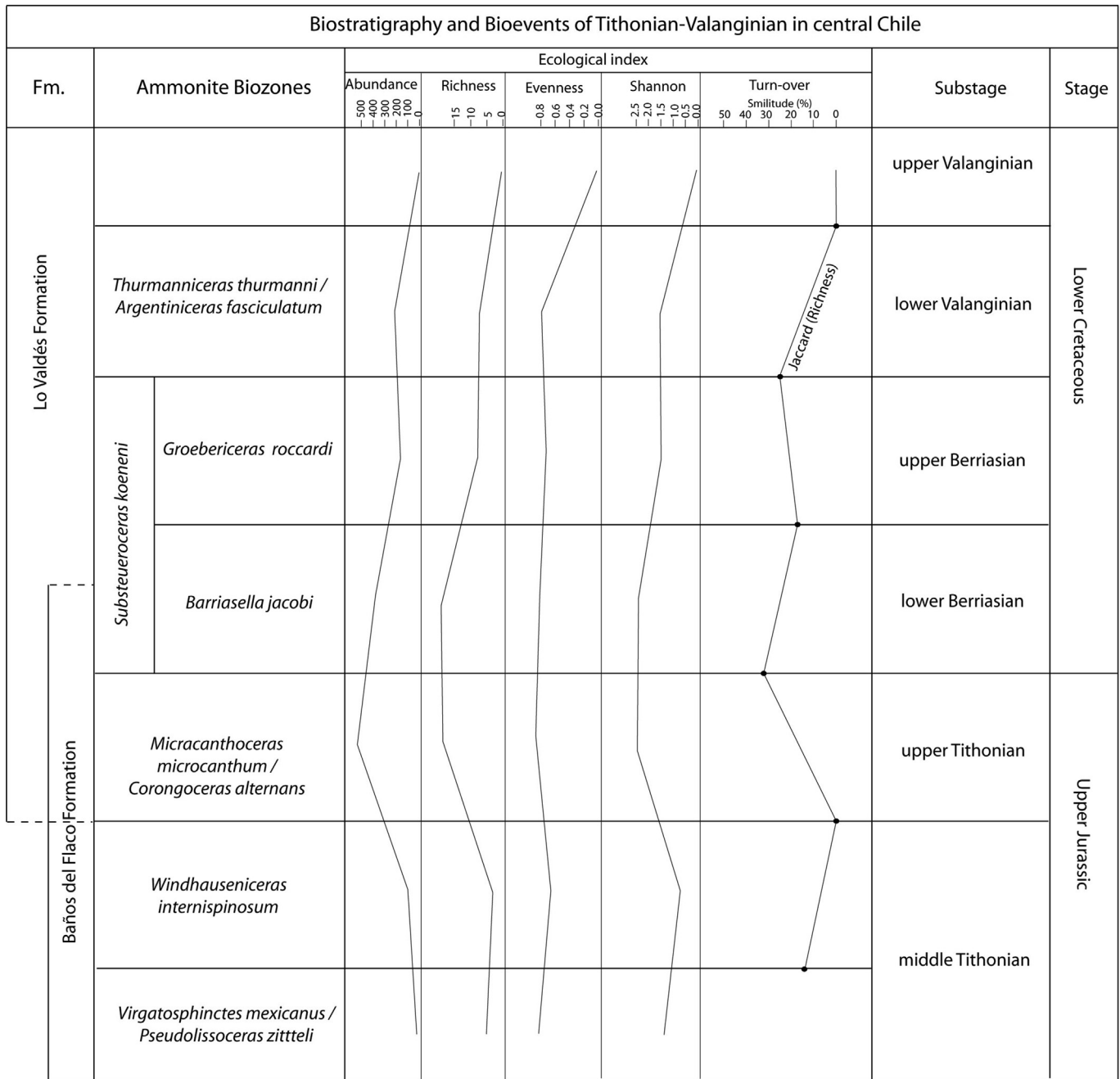


Fig. 11. “Relative abundance”, “relative richness”, and “Evenness and Shannon diversity indices” of the Baños del Flaco and Lo Valdés formations (Rio Maitenes, Cruz de Piedra, Cajón del Morado and Lo Valdés sections). Data from these sections are grouped in intervals which correspond to the biozones identified, and the age.

The “Evenness factor” is interpreted to be a proxy for the relative faunal diversity and shows high values from the lower part of the middle Tithonian to the lower Valanginian, with peak values in the upper Tithonian. The “Shannon factor” is also a proxy for the relative abundance and suggests that diversity increased from the lower part of middle Tithonian to the upper Tithonian, with highest diversity values in the upper Tithonian. From this peak, diversity declines gradually towards the lower Valanginian (Fig. 11).

Our species turn-over analysis of ammonites across the Jurassic-Cretaceous boundary in central Chile quantifies the similarity between neighboring (overlying/underlying) biozones. We used the Jaccard index, which varies between 100% (identity in the species composition) and 0% (no common species between compared

levels). Increasing values in the Jaccard index thus represent decreasing values of species turn-over, and vice versa (Koleff et al., 2003). Calculations were performed using the Diversity Calc software (Möselers et al., 2009). “Zero” similarity is indicated between the lower and the middle Tithonian. Jaccard values indicate highest similarity values in the upper Tithonian, coincident with a high diversity; similarity declines (to 20%) between the lower and the upper Berriasian; this boundary is here interpreted to represent an important bioevent (Fig. 11).

Ammonite distribution is thus continuous in the middle–upper Tithonian, with a sharp drop in the lower Berriasian. Only *Substeuerocheras callistoide* is registered in both the upper Tithonian and lower Berriasian. Diversity changes are continuous and show

gradually increasing values from the lower Berriasian to the lower Valanginian. In this interval the species richness decreases, but according to both turn-over analyses without “abrupt” changes (Fig. 11). No ammonites were recovered for the upper Valanginian and lower Hauterivian, and only three taxa were identified from the upper Hauterivian.

Ecological indices indicate that the highest relative abundance and diversity were reached in the middle to upper Tithonian, while lowest values are seen at the lower to upper Berriasian boundary. The ecological index is still high for the lower Berriasian, with the highest values for richness, but an almost complete taxonomical change is seen at the lower/upper stage boundary, except for *Substeueroceras callistoide*, and the Jaccard index is low. Our paleoecological analysis therefore indicates that a main turnover in ammonite assemblages occurred between the early and late Berriasian (Fig. 11).

5. Conclusions

The presence of internationally useful biozonal index ammonites in the Baños del Flaco and Lo Valdés formations of central Chile (e.g. *Micracanthoceras microcanthum*, *Berriasella jacobi*), indicates that marine connections and faunal exchange must have existed in the Jurassic/Cretaceous boundary transition between the southwestern margin of Gondwana and other paleobiogeographical realms, notably the western Tethys. Our paleoecological analysis indicates that a main turnover in Chilean ammonite assemblages occurred between the early and late Berriasian, followed by a secondary bioevent between the late Berriasian and the early Valanginian.

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