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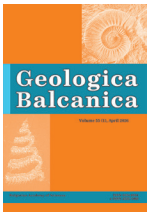

The calpionellid crisis – the defining marker for the Jurassic/Cretaceous boundary in all continents

William A.P. Wimbledon[1,], Daniela Reháková[2], Silviya Petrova[3], Camille Frau[4], Diego A. Kietzmann[5,6], Rafael López-Martínez[7]*

[1] *School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, United Kingdom; e-mail: mishenka1@yahoo.co.uk*
[2] *Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, 84215 Bratislava, Slovakia; e-mail: daniela.rehakova@uniba.sk*
[3] *Geological Institute, Bulgarian Academy of Sciences, Acad. G. Bonchev Str., Bl. 24, 1113 Sofia, Bulgaria; e-mail:* silviya_p@geology.bas.bg
[4] *Groupement d'Intérêt Paléontologique, Science et Exposition, 60 bd Georges Richard, 83000 Toulon, France; e-mail: camille_frau@hotmail.fr*
[5] *Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Departamento de Ciencias Geológicas, Ciudad Universitaria, Pabellón II, Intendente Güiraldes 2160, C1428EHA Ciudad Autónoma de Buenos Aires, Argentina; e-mail: diegokietzmann@gl.fcen.uba.ar*
[6] *CONICET-Universidad de Buenos Aires, Instituto de Geociencias Básicas, Ambientales y Aplicadas de Buenos Aires (IGeBA), Ciudad Universitaria, Pabellón II, Intendente Güiraldes 2160, C1428EHA Ciudad Autónoma de Buenos Aires, Argentina; e-mail: diegokietzmann@gl.fcen.uba.ar*
[7] *Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Delegación Coyoacán, C.P. 04510, México D.F., Mexico; e-mail: rafaelopez83@hotmail.com*
**Corresponding author*

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Abstract. In latest Tithonian times, in the *Crassicollaria colomi* Subzone, dominant *Crassicollaria* species suffered a decline. Next, the ultimate calpionellid crisis occurred in the *Calpionella alpina* Subzone, where practically nothing, but the taxon *C. alpina*, survived. The same succession of calpionellid associations and the same crisis has been demonstrated in all continents in a large body of literature, as we illustrate it herein. The event, and the base of the Alpina Subzone that it marks, is the outstanding level for definition of the Tithonian/Berriasian (J/K) boundary.

This level is also close to the original top of the "Portlandian", d'Orbigny's topmost Jurassic stage. And, in Tethys, close above the ammonite level (Jacobi Subzone) that was previously used to define the boundary. In the Jacobi Subzone, the appearance of the ammonite genus *Delphinella* acts as a proxy for the base of the calpionellid Alpina Subzone. In the Caribbean and Mexico, the Alpina Subzone is also proved. In the Andes, the Alpina subzone's base lies close to the base of the ammonite *Substeueroceras koeneni* Zone, and it is marked by the last appearance of *Calpionella elliptalpina*, as it is at sites in Tethys. No other boundary level that has been suggested in the J/K interval has such a strong primary marker, and no other has so many proxies to support it.

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INTRODUCTION

At the 1973 colloquium on the Jurassic/Cretaceous boundary, the base of the ammonite *Berriasella jacobi* Zone was the most favoured marker for the boundary. However, ammonites, which dominated correlations up to the Tithonian, in the Tithonian–Berriasian (T–B) interval suffered from provinciality, and they were frequently discontinuous in their distribution, sparse or absent (*e.g.*, Lehmann *et al.*, 2015). Provinciality meant that even if ammonite correlations within Tethys in the T–B interval had been perfect, Tethyan ammonites had only rarely been identified in other parts of the globe: and spot finds do not make for secure correlations.

There followed a move towards calpionellids as the better J/K boundary markers, *e.g.*, Jeletzsky (1984), Ogg and Lowrie (1986), Channell and Grandesso (1987) and Özkan (1993). The boundary, more and more, was taken to be the boundary between the calpionellid zones A and B (Crassicollaria–Calpionella zones), then tied to the base of the ammonite Jacobi Zone (Remane *et al.*, 1986; Zakharov *et al.*, 1996). Though, Tavera *et al.* (1994), correctly, questioned the direct equivalence between the ammonite and calpionellid zones. With more documentation, when ammonites occurred and could be tied to magnetostratigraphy, the base of Jacobi Zone was placed at or close to the base of M19n.2n. A significant turnover in ammonites, Himalayatidae to Neocomitidae, occurs at the base of the *Berriasella jacobi* (=Jacobi) Subzone/Zone of authors, but though the Jacobi Zone base was repeatedly cited as the boundary in the literature, the problems with recognition of the index species remained, and, even in western Tethys, the zone could not always be recognised (Wimbledon *et al.*, 2013; Bulot *et al.*, 2014; Frau *et al.*, 2015; Wimbledon *et al.*, 2020a). The correlative superiority of calpionellids over other fossil groups became clear: in section after section, calpionellids were found to occur in most, if not all, beds and they showed the same consistent zonal succession.

It is now almost four decades since calpionellids were generally promoted, and the *usefulness of the base of the Calpionella Zone as the best J/K boundary marker was affirmed at the Sümeg conference (*Remane *et al.*, 1986*)*. From being used as a support for ammonites in western Tethys (Le Hégarat and Remane, 1968), numerous studies have proved their independent reliability for correlation in ever-wider regions, from their extensive occurrences all around Tethys (Wimbledon *et al.*, 2011; Michalík and Reháková, 2011), via the Atlantic to the Caribbean and Mexico, and via Panthallassa to the Andes (López-Martínez *et al.*, 2013a, b, 2015a, b; Kietzmann, 2017; Kietzmann *et al.*, 2021a), and south to the Antarctic Peninsula (López-Martínez *et al.*, 2024). So, in essence, that encompasses the entirety of the world's larger J/K marine water bodies and certainly the majority of its well-studied profiles.

In the last twenty years, bed-by-bed sampling and ever improving resolution has fixed the base of the Alpina Subzone in mid M19n.2n (lower than Ogg and Lowrie (1986) had it). No other fossil group has such a widespread distribution or allows such correlative precision, and calpionellids alone are efficacious in calibrating magnetozone boundaries. The J/K boundary (base of the Berriasian Stage) defined at the base of the *Calpionella alpina* Subzone had been the usage for several decades, and in 2016, after examination of numerous sections, this was endorsed by a formal vote the Berriasian Working Group (ISCS). The 70-strong Berriasian WG voted that the Alpina Subzone base should be used as the primary marker for the base of the Berriasian (Wimbledon *et al.*, 2020a).

This overwhelming majority in the voting was a reflection of the group's prolonged work of documentation and of the voluminous literature on the boundary calpionellids (Lakova, 1993, 1994; Pop, 1994, 1998; Houša *et al.*, 1996, 1999, 2004, 2007; Blau and Grün, 1997; Grün and Blau, 1997; Lakova *et al.*, 1999, 2017; Andreini *et al.*, 2007; Wimbledon, 2008; Boughdiri *et al.*, 2009; Michalík *et al.*, 2009, 2012, 2016, 2019, 2021, 2022; Grabowski *et al.*, 2010a, b, 2013, 2019; Lukeneder *et al.*, 2010; Pruner *et al.*, 2010; Dragastan, 2011; Michalík and Reháková, 2011; Reháková *et al.*, 2011; Sallouhi *et al.*, 2011; Wimbledon *et al.*, 2011, 2013, 2017, 2020a, b, c, 2022, 2024; Benzaggagh *et al.*, 2012; Guzhikov *et al.*, 2012; Petrova *et al.*, 2012, 2017, 2019, 2023, 2025; Lakova and Petrova, 2013; López-Martínez *et al.*, 2013a, b, 2015a, b, 2017, 2024; Hoedemaeker *et al.*, 2016; Svobodová and Košťák, 2016; Vašíček *et al.*, 2017; Wohlwend *et al.*, 2017; Atasoy *et al.*, 2018, 2022; Bakhmutov *et al.*, 2018; Elbra *et al.*, 2018a, b, 2024; Košťák *et al.*, 2018, 2023; Fekete *et al.*, 2019; Kowal-Kasprzyk and Reháková, 2019; Reháková and Rožič, 2019; Svobodová *et al.*, 2019; Vaňková *et al.*, 2019; Benzaggagh, 2020; Casson *et al.*, 2021; Kietzmann *et al.*, 2021a; Cherif *et al.*, 2022; Lodowski *et al.*, 2022, 2024, 2025; Bryers *et al.*, 2024; Bubík *et al.*, 2024; Rožič and Reháková, 2024; Skupien *et al.*, 2024; Touansa *et al.*, 2024; Kietzmann and Encinas, 2025). The Alpina Subzone's base, situated in the middle part of magnetosubzone M19n.2n (Wimble-

don *et al*., 2020a, b), has been dated at about 143.3 Ma (Ogg in Gradstein *et al*., 2020).

With the Alpina event identified in north and south America, the Carribbean, middle Atlantic and across Tethys, that left only Antarctica with no record. However, López-Martínez *et al*. (2024) have reported calpionellids in the Antarctic Peninsula. There *Saccocoma* facies gives way to calpionellids (including *Crassicollaria brevis*, *Tintinopsella carpathica*, *Calpionella alpina* and *Tintinopsella remanei*). This most southern report of calpionellids validates the hypothesis of their widespread distribution and their value in transdomain correlations.

Of course, other options were considered in lengthy discussions in the former BWG about selecting a primary marker for the base of the Berriasian. Several were considered, tested and disgarded. Our first decision was that we should seek a marker that had a distribution as close as possible to global. Our first guiding principle was that we should consider the best marker in an interval close to the traditional level *(circa* base of Jacobi Zone – lower to middle M19n.2n), keeping to the decision of the 1973 J/K colloquium. So consideration would therefore focus, approximately, on M19r and M19n. Otherwise, a chosen marker outside this interval would be a danger, threatening to disrupt international nomenclature and to invalidate hundreds of publications (and maps) which recognised the normal delimitation of Upper Tithonian and Berriasian. Our second guiding principle was that any suggested non-biotic marker (magnetostratigraphic, geochemical, cyclostratigrahic, *i.e*.) could only be considered if it was conclusively tied to biostratigraphy, with fossil indicators that had the widest possible distribution.

First considered was Ogg's suggestion of the base of M18r (Ogg and Lowrie, 1986; Ogg *et al*., 1991), but eventually this was found to coincide with no biotic event (calpionellid, ammonite, nannofossil). Similarly the base of M19n coincides approximately with the top of the Andreaei Zone, but this marker fossil has a limited geographical extent (*see* ammonite events below). At Bosso, as an example, M19r is entirely within the Intermedia Subzone (Houša *et al.* 2004). But this calpionellid subzone is highly variable relative to magnetozones: at Brodno the Intermedia Subzone covers most of M19r and more than half of M20n.2n, whereas at Strapkova only the lower half of M19r is recorded within the Intermedia Subzone (Michalík *et al.* 2021). The Intermedia Subzone has been highlighted as a problematic interval when it comes to stable correlatable markers. In well-documented western Tethyan sites, redeposition is frequently encountered in it, and cryptoturbidites appear in some profiles. In the overlying Colomi Subzone, such features subside, although they do not completely disappear. Neither subzone was considered to be the primary marker for the base of the Berriasian for the reasons stated. Of calcareous nannofossils that occur at sites with magnetostratigraphy, there are several species with apparent FADs within M19r, but not at its top or bottom. This takes us to 1 My before the base of the Alpina Subzone, well into the traditional Upper Tithonian.

Above the Alpina Subzone, the ammonite Subalpina Subzone (Occitanica Zone) base was suggested previously as a putative boundary marker. Its subzonal base has been documented at several levels in M17r (notably the longest reversal in the J–K interval). It does not coincide with the base of the calpionellid Elliptica Subzone. Quite apart from the difficulties in definition of the zonal index, an exclusively Tethyan taxon, this was a time interval where ammonites suffered a crisis and became scarce (see below). Further it sits about 1.3 my above the base of the Alpina Subzone: unreasonably close to the base of the Valanginian to be considered as a new base for the Berriasian.

CALPIONELLID STRATIGRAPHY

Towards the end of the Tithonian (M20n into M19r), *Saccocoma* microfacies were substituted by calpionellid facies, carbonate 'rain' increased, with markedly enhanced sedimentation rates (Michalík *et al*., 2021). This has been tied to the "Nannofossil Calcification Event" (Bornemann *et al*., 2003), based on DSDP cores from the middle Atlantic. In latest Tithonian times (into M19n.2n) *Crassicollaria* species dominated calpionellid assemblages.

A grouping of about eight species typifies this interval (*Crassicollaria intermedia*, *Cr. brevis*, *Cr. massutiniana*, and *Cr. parvula* plus *Tintinnopsella carpathica*, *Calpionella grandalpina*, *C. elliptalpina*, and *C. alpina*). But from a peak in the middle of the Crassicollaria Zone (Intermedia Subzone) there was a decline in the Colomi Subzone. Next followed an even sharper change, with the collapse of the population (Remane, 1983, 1986; Ascoli *et al*., 1984; Borza, 1984; Remane *et al*., 1986; Pop, 1986, 1994), and its substitution by dominant, small orbicular *Calpionella alpina* (the so-called *C. alpina* 'bloom'), occurring together with rare *Cr. parvula* and *T. carpathica* (see Fig. 1).

Also closely associated with the Colomi/Alpina boundary is a negative shift in $\delta^{13}C$, that has been proved in numerous profiles (summarized in Košťák *et al*., 2023).

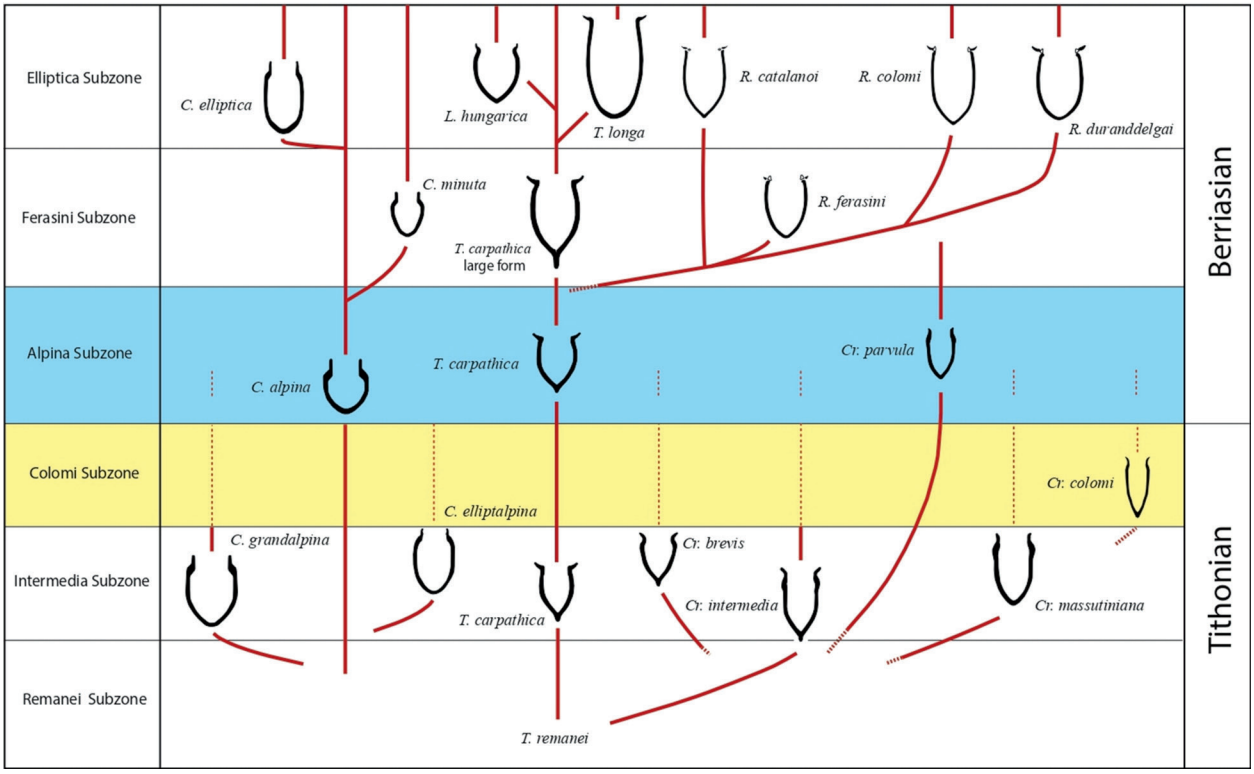

Fig. 1. Calpionellid evolution across the Tithonian–Berriasian boundary.

The traditional Tithonian–Berriasian (J/K) boundary lies in the interval covered by M19n.2n – in the Jacobi ammonite Zone/Subzone, that is, in line with the 1973 colloquium decision and all subsequent considerations. Attempts at fixing a J/K boundary since the colloquium have tried to keep to the traditional level for that boundary, rather than moving down or up and thus requiring 'deletion' of a substantial piece of either the Tithonian or the Berriasian. With the limited geographic extent of *Strambergella jacobi* (and problems of its taxonomic definition), and other alternative ammonite taxa being limited to western Tethys (Frau *et al*., 2016a, 2021), in the traditional interval the much more widespread and consistent *Calpionella alpina* event (sensu Kowal-Kasprzyk and Reháková, 2019) has been found to be the best contender for the boundary marker.

THE SUPRA NOTRE DAME AND FIUME BOSSO SUCCESSIONS – EXEMPLARS OF THE COLOMI–ALPINA SUBZONAL INTERVAL

Here we use two exemplar sites to demonstrate calpionellid distibutions in the Colomi and Alpina subzones: one in France and a second in Italy. The first is Supra Notre Dame (La Faurie), a hill-track section 1800 m NE of the Le Hégarat profile at La Faurie (Le Hégarat, 1973) (45°35′00″ N, 5°45′06″ E), and the second is the well-known section in the valley of Fiume Bosso (Houša *et al*., 2004; revising the magnetostratigraphy of Lowrie and Channell, 1984) (43°35′00″ N, 12°34′22″ E), which we have re-examined and re-collected (a fuller description of calpionellids, calcareous dinoflagellates and nannofossils, plus C and O isotopes is in progress). A comparison of the Colomi–Alpina interval at Supra Notre Dame (SND) and Bosso is shown in Fig. 2.

The lowest part of the Maiolica Formation (Fm) in the Bosso valley was well described in the account of Houša *et al*. (2004) – our representation shows minor variations, mostly due to lateral variations in chert development. Houša *et al*. (2004) followed the metre scale used by Micarelli *et al*. (1977). The profile with the base of the Maiolica Fm, crops out around 900 m NNE of the village of Pianello, Umbria-Marche (Italy). The section comprises 28 m of Maiolica Fm above 11 m of the Calcari a *Saccocoma* ed Aptici Fm. The Maiolica Fm, which is our focus, is mostly well and sometimes massively bedded, comprising biomicrites and slightly laminated biomicrites, with a few silty units. Contorted beds,

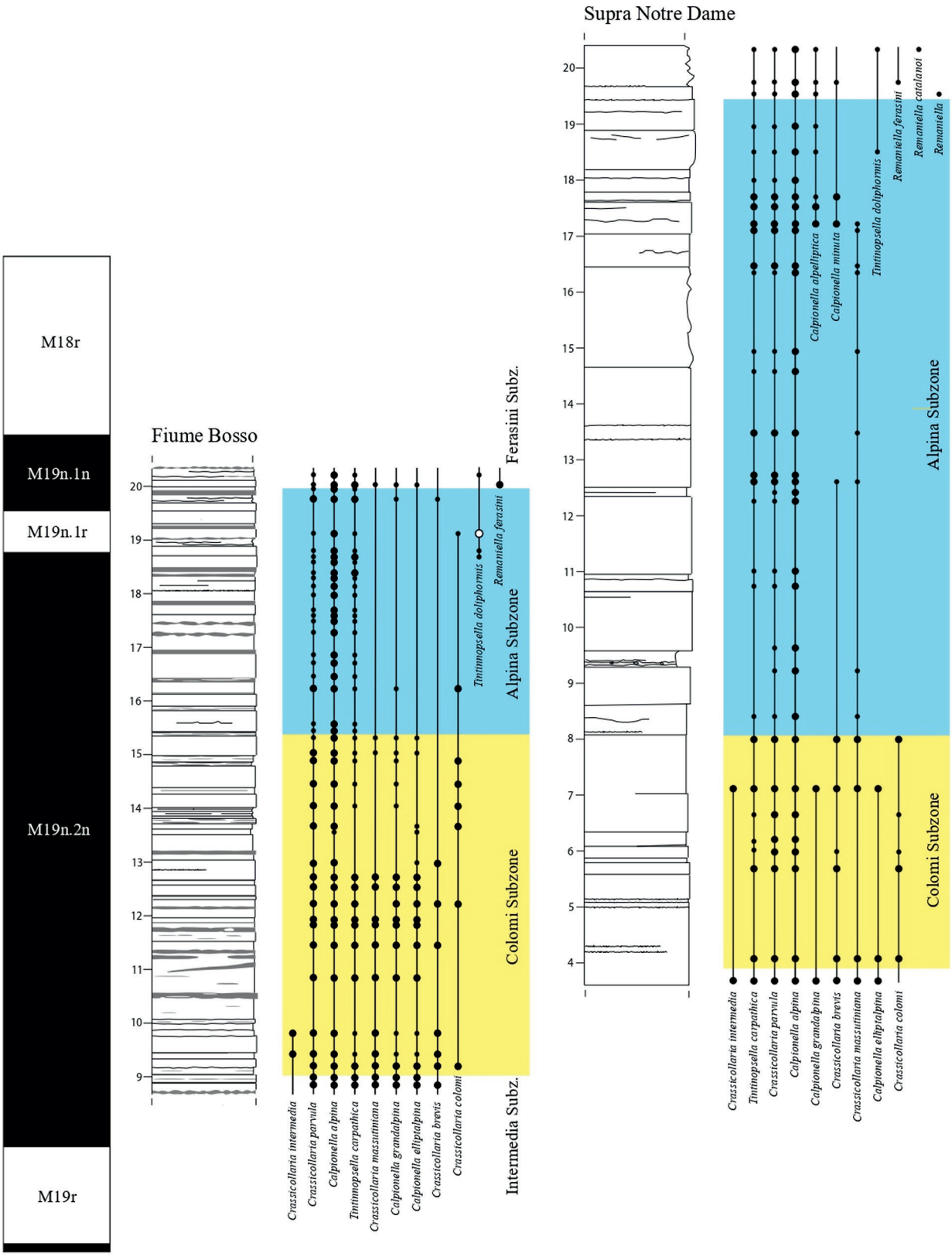

Fig. 2. Comparison of calpionellid ranges in the Colomi and Alpina subzones in profiles at Fiume Bosso (Italy) and Supra Notre Dame (France). Magnetozones for Bosso after Houša *et al*. (2004).

the result of slumping, are present in the section at about 11 m (Colomi Subzone) and 24 m (Ferasini Subzone). Macrofossils are rare, but calpionellids, calcareous dinocysts, nannofossils, and radiolarians are common.

The SND locality is situated to the north and uphill from the Monastery of the Dormition above the village of La Faurie, in Hautes-Alpes (France). The locality is equidistant to, and may be compared, to other described local Tithonian–Berriasian sections at St Bertrand (N), Tré Maroua (S) and Le Chouet (W) (Wimbledon *et al*., 2013, 2020a, b). The profile is located on an unpaved hill road, the Chemin de Sueil, and situated below a second parallel section in a degraded cutting on an older course of the road. Here we describe part of the lower section: the profile is 27 m in thickness, it starts in the Remanei Subzone (Crassicollaria Zone) and ends in the Elliptica Subzone (Calpionella Zone). The beds are typical of the Calcaires Blancs Fm of the Vocontian Basin, well-bedded and massive-bedded micritic limestones, mostly biomicrites, sometimes slightly bioturbated. The marl-limestone alternations typical at higher levels, as seen at St Bertrand, La Faurie etc., are not exposed at SND. Macrofossils are infrequent, a handful of horizons yield ammonites, but the micrites consistently yield calpionellids and calcareous dinoflagellate cysts.

Both profiles demonstrate typical assemblages of calpionellids through the Colomi and Alpina subzones, and at the boundary between.

PROXIES FOR THE BASE OF THE CALPIONELLA ALPINA SUBZONE

Onset of the "Nannoconus world"

The almost monospecific calpionellid assemblage of the lower Alpina Subzone has been linked to a nannofossil turnover, to an upsurge in nannoconids that followed (superimposed) declines of the genera *Conusphaera* and *Polycostella: Nannoconus* showing a marked percentage rise, "under warmer and possibly more nutrient-depleted surface waters" (*fide* Tremolada *et al*., 2006). This rise was placed in mid-M19n.2n, where these authors positioned the base of the Berriasian (DSDP hole 534A) – tied (inaccurately) to the base of the Jacobi Zone. This Middle Atlantic study has often been cited. However, some variations have been noted in other regions that lead to questions about the synchroneity of the change, and we can cite some examples. At Puerto Escaño, the closest Tethyan relevant site to DSDP 534A, *Polycostella* is insignificant in M19n, *Conusphaera* is dominant and *Nannoconus* does not exceed 20% until M18r (Svobodová and Košťák, 2016). Results from Theodosia follow the 534A pattern (Wimbledon *et al*., 2022), whereas at Lokút and at Hárskút *Conusphaera* is dominant through M19n (Lodowski *et al*., 2024), and at Kurovice only small percentages of the three genera were recorded (Svobodová *et al*., 2019).

Calcareous nannofossil proxies

Calcareous nannofossils in the J/K interval promised in the 1980s to be so useful, but subsequently they have exhibited a lack of correlative consistency and precision. Pioneering studies of nannofossils offered the prospect of their first occurrences being a precise tool for calibration with magnetozones (*e.g*., Ogg and Lowrie, 1986; Bralower *et al*., 1989) and calpionellids. However, as more results have been published, and numerous sites documented, a vertical scatter of FADs/FOs has materialised. For some species this diachronous scatter covers several million years, and putative nannofossil zonal boundaries have become more vague (Wimbledon *et al*., 2022, Fig. 3). It is the reason that the bases of the NC0a and NC0b calcareous nannofossil zones are imprecisely positioned in M19n.2n.

Nannoconus wintereri and *Cruciellipsis cuvillieri* are examples: they have reported FADs that are not in a limited interval, not closely synchronous, but which have been recorded over a time-span of about 2 million-years, between M19r and M18n (sites and references in Wimbledon *et al*., 2022). Even with these unavoidable facts, the first species has still been noted as a "highly reliable" marker (Casellato and Erba, 2021). A recently redescribed section is indicative, that at Torre de' Busi (Petrova *et al*., 2025): there, several nannofossil species exhibit consistently late first appearances: *e.g*., *Nannoconus steinmannii minor* (in M19n.1n), *N. kamptneri minor* (in M18r), *N. wintereri* and *Cruciellipsis cuvillieri* (in mid M19n.2n). This lack of regularity/consistency means that nannofossil species will have limited stratigraphic use, unless or until their FAD positions stabilise.

There are better cases, however. Combining results from several profiles, clusters of FADs of some species can be discerned in a limited interval. Two such cases are the FAD clusters of *N. steinmannii minor* and *N. kamptneri minor* (Wimbledon *et al*., 2020a). These two species have conspicuous groupings at and around the base of the Alpina Subzone, *i.e*. in mid M19n.2n. Only one published account

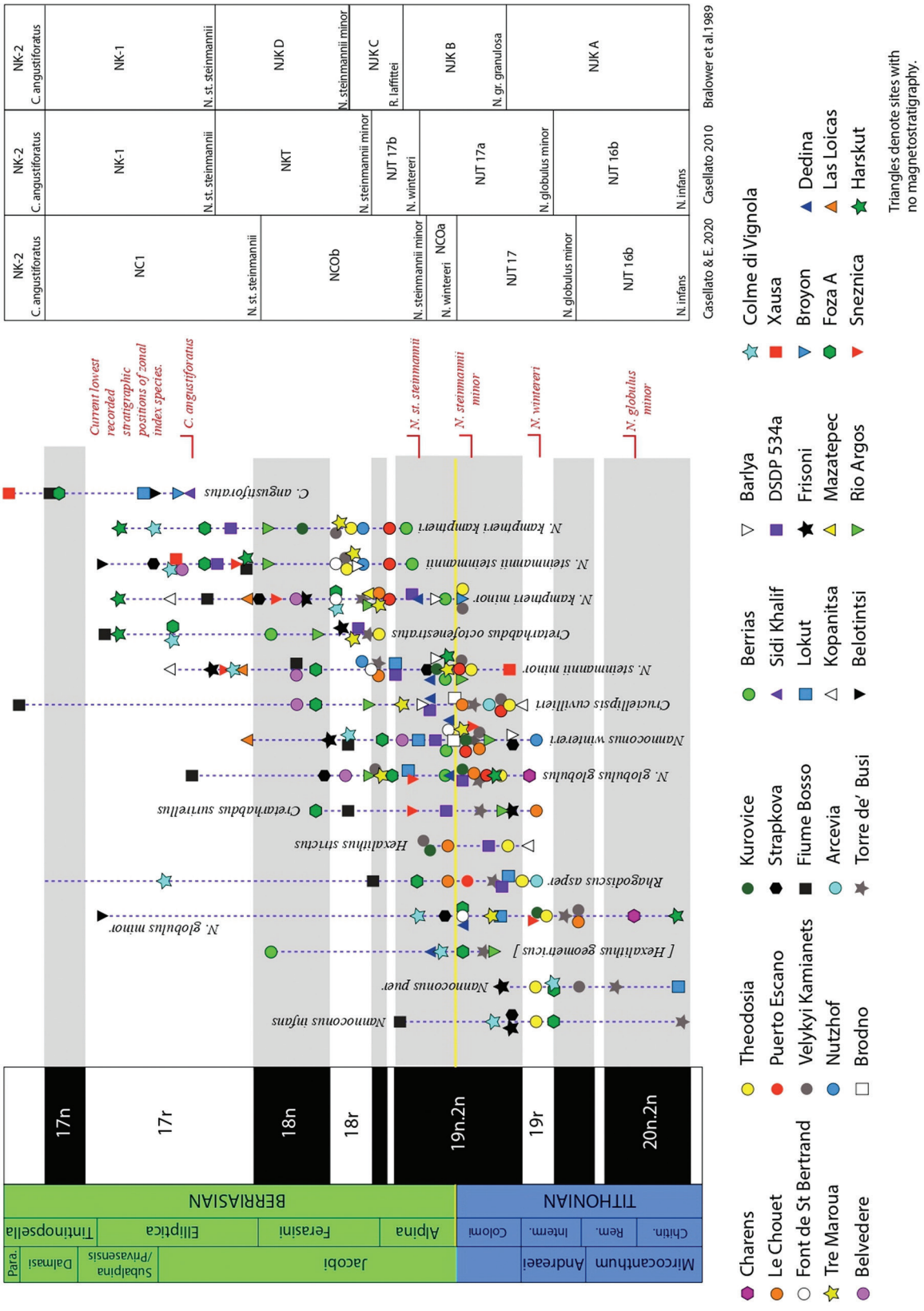

Fig. 3. "FOs/FADs" of selected calcareous nannofossil species from published accounts. [NB: These are not total ranges for the cited taxa, but the reported positions of first appearances.] After Wimbledon *et al.* (2022; Fig. 7), plus data from Bubík *et al.* (2024; for Dedina) and Vennari *et al.* (2014; for Las Loicas).

puts *N. steinmannii minor* lower in M19n.2n, and that is an older record, from Xausa (Channell and Grandesso, 1987).

Data on nannofossils from the Andes, thus far, are few, and somewhat inconsistent with results from Tethys. Published ranges for nannofossils (for Las Loicas; Vennari *et al*., 2014) showed aberrant FADs, notably with *N. kamptneri minor* occurring high in the Koeneni Zone, and *N. steinmannii minor* 2 m below the Noduliferum Zone: levels that in other sections in the Neuquén Basin yield the calpionellid assemblage of the Elliptica Subzone. Finds of *N. kamptneri minor* and *N. steinmannii steinmannii* together at Cara Cura (Vennari *et al*., 2017) in the ?lower Koeneni Zone need verification (see below).

Magnetic markers

The mid-M19n.2n base of the Alpina Subzone has been assigned an age of 143.3 Ma (Ogg in Gradstein *et al*., 2020). Where magnetostratigraphy has been applied, even when marine marker fossils are lacking, the short reversal M19n.1r (base 142.7 Ma) is an independent datum close above the J/K boundary. It has been recorded in many profiles since it was identified as one of several "fingerprint" magnetic markers in the J/K interval (Ogg and Lowrie, 1986). The lowest occurrences of the calcareous nannofossil *N. steinmannii steinmannii* are at Puerto Escaño and Berrias, respectively, in M19n.1r and in topmost M19n.2n.

The disappearance of *Calpionella elliptalpina* immediately prior to the *C. alpina* event

The top of the Colomi Subzone is marked at numerous localities by the disappearance of *Calpionella elliptalpina.* That is, its extinction occurred immediately before the *C. alpina* event. In effect, this LO is the most accurate marker for the top of the Tithonian.

At some well-documented localities, the species does not quite reach the top of the Colomi Subzone, *e.g*., Le Chouet (Wimbledon *et al*., 2013), Río Argos (Hoedemaeker *et al*., 2016), Belvedere (Wimbledon *et al*., 2020c), Snežnica, Strapkova (Michalík *et al*., 2021), Dedina (Bubík *et al*., 2024) and La Faurie (this work). At others, the species has not so far been identified, *e.g*., Pośrodnie (Grabowski and Pszczółkowski, 2006), Nutzhof (Lukeneder *et al*., 2010), Tré Maroua (Wimbledon *et al*., 2020a), Lokút and Hárskút (Lodowski *et al*., 2022).

The following localities show the disappearance of *C. elliptalpina* at the top of the Colomi Subzone: Sviniţa (Pop, 1998), section "Y" (Benzaggagh *et al*., 2010), Puerto Escaño (Pruner *et al*., 2010), Bosso (this work), Yavorets (Petrova *et al*., 2019), Barlya, Gintsi I and II (Lakova and Petrova, 2013), Gorno Belotintsi 1 (Lakova *et al*., 1999; Petrova *et al*., 2023), Kara köpek cutting (near Kel, Turkey – unpublished), Arroyo Loncoche, Cuesta del Chihuido, Puerta Curaco, El Trapial and Narambuena (Kietzmann *et al*., 2021a), Ravin Bleu I (Cherif *et al*., 2022), Jebel Azreg and Jebel Toumbaït (Touansa *et al*., 2024), Ropice (Skupien *et al*., 2024), Río Volcán (Kietzmann and Encinas, 2025), and Torre de' Busi (Petrova *et al*., 2025). In Mexico this event has been recognized in the Apulco profile (Lopez-Martínez *et al*., 2013a).

Radiolarian markers

Radiolarians have been little studied in the many well-documented J/K profiles listed above, largely because radiolarians, where present, are often calcified in these sections. The radiolarian zonal boundaries in the J/K interval (Baumgartner *et al*., 1995), based on "unitary associations", depend for their positioning on calibration with the calpionellid zonation. Fiume Bosso and Snežnica (Goričan in Michalík *et al*., 2022) are the only well-known Tethyan sites where this radiolarian stratigraphic scheme has been applied. The recent study at Bosso by Matsuoka *et al*. (2020) did not amplify the results in Baumgartner *et al*. (1995): though it was said to describe the "J/K transition", it was restricted to a short interval entirely within the Colomi Subzone.

In low-latitude regions where radiolarian-rich facies occur, the scheme of Baumgartner *et al*. (1995) has been applied, but boreal and austral radiolarian biostratigraphies do not coincide with this Tethyan zonal scheme. Its zones are rather extended, and their limits a little imprecise. Nevertheless, they still afford a proxy for the J/K boundary in radiolarian-rich terrains. The base of radiolarian "unitary zone" 13 is stated to coincide with the base of the Crassicollaria Zone, and the base of zone 14, the next above (Baumgartner *et al*., 1995), "just above" the A/B calpionellid boundary in M19n. Thus, this closely, if not exactly, coincides with the base of the Alpina Subzone.

One possible parallel to the calpionellid crisis has been documented. Mitta and Vishnevskaya (2006) documented synchronous episodes of significant decrease in taxonomic diversity of radiolarians (and ammonites) in the late Jurassic in boreal Russia. Those authors described changes in the morphotypes (lilliput size) radiolarian skeletons as

a "late Volgian" crisis. This was accompanied by the extinction of some of radiolarians at the presumed end of the Jurassic, as a consequence of marine regression and cooling. Synchronisation here is the problem, as the isolated boreal of Russia cannot be correlated with any accuracy with Tethys (or the rest of the globe), but the situation is still reminiscent of the calpionellid crisis in those other regions.

Ammonite proxies

The appearance of *Delphinella* provides an ammonite proxy for the base of the Berriasian in Tethys, as it can be calibrated with the base of the calpionellid Alpina Subzone. The ammonite discussion below gives more detail of this within the context of ammonite evolution related to calpionellid zones across the J/K boundary, at least in western Tethys.

A footnote may be added on the ammonite genus *Chigaroceras*, which occurs quite close below the J/K boundary. The taxon has not been recorded in western Tethys (between Iberia and Crimea), but it occurs in northern Iraq, and, in other domains, it is known only in Argentina. In the latter, it has been positioned in the upper Alternans to lower Koeneni zones at Mallin Redonso (Leanza, 1945), Bardas Blancas (Leanza, 1996) and at Cerrito Caracolas (Parent *et al*., 2013). At Banik in Kurdistan (Howarth, 1992) *Chigaroceras* is abundant high in the Crassicollaria Zone (Wimbledon *et al*., 2016).

Negative shift in the $\delta^{13}C$ curve at the Colomi/Alpina boundary

Older accounts of $\delta^{13}C$ in western Tethyan sites showed a long-term decline across the J/K boundary (*e.g*., Weissert and Channell, 1989). Later accounts, with more precise biostratigraphy, enable the recognition of a negative shift in the curve at the boundary level. Examples are: Bosso (Kudielka *et al*., 2000, and unpublished), Brodno (Michalík *et al*., 2009), Puerto Escaño (Žák *et al*., 2011), Lokút (Price *et al*., 2016), Snežnica (Michalík *et al*., 2019), Tré Maroua (Wimbledon *et al*., 2020c), Kurovice (Košťák *et al*., 2023), and Rettenbacher (Elbra *et al*., 2024). Outside Tethys the same negative shift has been noted in Mexico (Apulco, Iturbide and Puerto Pinones in Barragán *et al*., 2020).

In the Apulco section Barragán *et al*. (2020) described a marked negative shift in $\delta^{13}C$ at the boundary between the Crassicollaria and the Calpionella zones. In the uppermost Tithonian, there was a microfacies change from a radiolarian-rich facies to a more *Globochaete*-dominated one, and then, abruptly, a change to a monospecific calpionellid assemblage with *Calpionella alpina*. After this negative event, a positive trend is registered through the Berriasian up to the Oblonga Subzone (Calpionellopsis Zone).

A negative excursion in $\delta^{13}C$ has also been documented in Argentina, at Puerta Curaco (Rodríguez Blanco *et al*., 2022; Weger *et al*., 2023). Although these authors did not present an independent biostratigraphic framework, correlation of thicknesses with depositional sequences, together with the isotope data from the Chacay Melehue section (Capelli *et al*., 2021), reveals general trends and a negative excursion comparable to those recorded in Tethys.

AMMONITE CORRELATION IN THE JURASSIC–CRETACEOUS INTERVAL

Simplistic correlation charts with zonal boundaries matched (ammonite, calpionellid, nannofossil, etc.) often are suggested in publications on the J/K interval, but a more detailed and precise examination of ammonite assemblages related to calpionellids is possible and more productive. A compilation of bed-level ammonite occurrences from key basinal settings in southeastern France serves as a standard for western Tethys. It is based on published sections in Drôme (Le Chouet, Charens, and Saint Bertrand; Bulot *et al*., 2014; Wimbledon *et al*., 2013; Frau *et al*., 2015, 2016a, b) and the Hautes-Alpes (Tré Maroua; Wimbledon *et al*., 2020a, b), and is plotted against calpionellid and magnetic polarity zones (Fig. 4). This framework enables the calibration of first appearance datums and total stratigraphic ranges for biostratigraphically diagnostic Perisphinctoidea ammonites. Five successive phases of faunal change (FC.1 to FC.5) and two well-defined pinpoint events (PE.1 to PE.2) can be distinguished. These results can be compared with long-standing ammonite biozonation schemes and recently published data (*e.g*., Szives *et al*., 2024) for the same time interval.

FC.1 – The first phase of faunal turnover, documented at Charens (Frau *et al*., 2016a), is characterized by the initial appearance and coeval epibole of the Himalayitinae *Micracanthoceras*, which may have derived from pre-himalayitid forms such as "*Burckhardticeras*". This phase is located within the upper part of the Chitinoidella Zone, at the base of the M20n.2n. Additionally, various Ataxioceratidae, notably *Paraulacosphinctes*, occur within this interval: together, these define the *Micracan-*

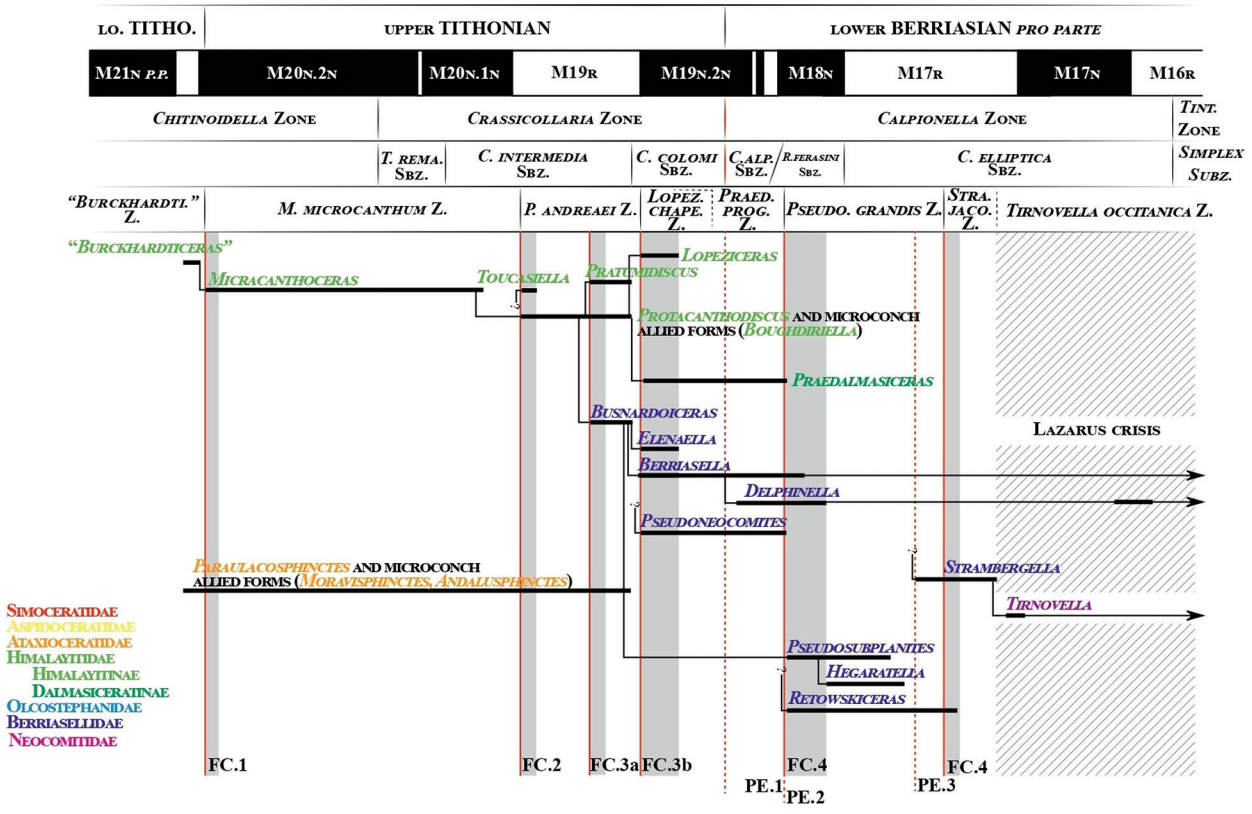

Fig. 4. Ammonite events across the Tithonian–Berriasian boundary.

thoceras microcanthum ammonite Zone of Frau *et al*. (2016a).

FC.2 – The second phase of faunal change defines the base of the *Protacanthodiscus andreaei* Zone of Wimbledon *et al*. (2013) as first established at Le Chouet, is characterized by significant taxonomic turnovers. This includes the appearance of the himalayitine *Protacanthodiscus*, derived from *Micracanthoceras*, alongside the emergence of the closely related genus *Toucasiella*. FC.2 occurs within the upper Intermedia Subzone (middle Crassicollaria Zone) and is positioned at or near the base of the M19r magnetozone.

FC.3 – The third phase of faunal change can be subdivided into two successive steps (FC.3a and FC.3b).

FC.3a is marked by a pronounced radiation within the Himalayitinae, denoted by abundant *Protacanthodiscus* and the first appearance of *Ardesciella* and the endemic *Pratumidiscus*. This phase also records the emergence and epibole of the basal Berriasellidae *Busnardoiceras*, which may have evolved from gracile morphotypes of *Protacanthodiscus* near the top of the Andreaei Zone. FC.3a occurs within the lower Colomi Subzone (upper Crassicollaria Zone) corresponding to the M19r magnetozone.

FC.3b is characterized by an extinction event affecting the Ataxioceratidae, marked by the last occurrence of the *Paraulacosphinctes–Moravisphinctes* dimorphic plexus: whereas the Himalayitidae persist, with the appearance of the late himalayitine *Lopeziceras* and *Praedalmasiceras*, the earliest dalmasiceratine. Best documented at Le Chouet, there occurs here a radiation among the Berriasellidae, with the first occurrences of *Elenaella*, *Berriasella*, and *Pseudoneocomites*. FC.3b thus represents a complex turnover affecting subfamilies, genera, and species, and it marks the base of the *Berriasella jacobi* ammonite Zone auctorum (see Tavera *et al*., 1994)(= *Lopeziceras chaperi* Zone, "Standard Mediterranean Ammonite Zonation", Szives *et al*., 2022, 2024). It correlates with the middle Colomi Subzone and occurs near the base of the M19n.2n.

FC.4 – The fourth phase of faunal change represents another complex turnover, correlating with the lower part of the calpionellid Ferasini Subzone and situated within the lower M18n magnetozone.

It is marked by the local extinction of the Dalmasiceratinae (*Praedalmasiceras*) and of certain Berriasellidae, including *Pseudoneocomites*. These losses are accompanied by the appearance of closely allied genera such as *Pseudosubplanites*, *Hegaratella*, and *Retowskiceras*, defining the *Pseudosubplanites grandis* ammonite Zone of Le Hégarat (1973). This phase also records the decline of the genus *Delphinella*.

FC.5 – Above the last beds containing *Pseudosubplanites*, we observe the inception and subsequent diversification of the Berriasellidae *Strambergella*, to which the species *Berriasella jacobi* has been transferred (Frau *et al*., 2016b; Szives *et al*., 2024). Its first occurrence is recorded in the uppermost part of the Ferasini Subzone, in lower M17r. Higher up, the first representatives of *Tirnovella* sensu lato (earliest Neocomitidae) appear, likely having evolved peramorphically from *Strambergella*, and marking the base of the subsequent *Tirnovella occitanica* ammonite Zone in the sense of Le Hégarat (1973). In the lower part of this zone, ammonite diversity and abundance decline sharply, manifested by the near-total disappearance of almost all Perisphinctoidea families during the middle part of the Elliptica Subzone – best exemplified at Saint Bertrand and Tré Maroua. Within this barren interval, only isolated occurrences of a late *Delphinella* species and sporadic *Tirnovella* specimens have been documented. This loss of ammonite faunas spans Le Hégarat's (1973) entire *Tirnovella subalpina* ammonite Subzone, according to his database, and it can be traced throughout most, if not all, Vocontian settings. Ammonite assemblages recover only partially above this interval, with the reappearance of two berriasellid genera (*Berriasella* and *Delphinella*) and two subfamilies (Dalmasiceratinae and Spiticeratinae) in the upper part of the *Tirnovella occitanica* Zone. The factors driving this Lazarus-type ammonite crisis, however, remain unresolved and warrant further investigation.

Beyond the main phases of faunal change, three pinpoint events of particular importance for regional correlations can be recognized within the Calpionella Zone:

PE.1 – Occurring between FC.3 and FC.4, this event is marked by the first appearance of the Berriasellidae *Delphinella*. PE.1 approximates the base of the Alpina Subzone (Calpionella Zone) and falls within the upper part of the magnetosubzone M19n.2n.

PE.2 – This event is marked by the first appearance of the Berriasellidae *Pseudosubplanites*. PE.2 falls within the lower part of the Ferasini Subzone, corresponding with the base of M18n.

PE.3 – This event corresponds to the inception and subsequent diversification of the Berriasellidae *Strambergella*. Its first occurrence is recorded in the uppermost part of the Ferasini Subzone and occurs in lower M17r.

Comparable biostratigraphic patterns can be recognized, in part or in full, in several recently published ammonite-bearing successions across the western Tethys, including northwest Iran (Cecca *et al*., 2012), the Prerif of Morocco (Benzaggagh *et al*., 2010), central Tunisia (Maalaoui and Zargouni, 2016), the Spanish Prebetic (Hoedemaeker *et al*., 2016), south-west Bulgaria (Stoykova *et al*., 2018), the Western Carpathians of the Czech Republic (Vašíček *et al*., 2018), eastern Serbia (Vašíček *et al*., 2023), and Crimea (Arkadiev *et al*., 2012). In these successions, the ammonite assemblages are broadly comparable to those of south-eastern France, with only a few exceptional neoendemic ammonite occurrences. However, these datasets still require thorough taxonomic revision, as they are often complicated by oversplitting and conflicting systematic interpretations.

Nevertheless, it should be noted that the first occurrence of *Delphinella* (our PE.1) and *Pseudosubplanites* (our PE.2) are both widely recorded in the areas cited above, with the exception of Morocco, to the best of our knowledge. The third event (PE.3) has been confirmed in southern Spain, Italy, Bulgaria, central Tunisia, and Crimea, in addition to southeastern France, and possibly in Georgia. However, none of these regions allow for more precise dating of these three biostratigraphic pinpoints than southeastern France, where calpionellid and magnetostratigraphic frameworks are best integrated. In some few areas, calpionellids are not useful (*e.g*., due to persistent redeposition, Theodosia – Bakhmutov *et al*., 2018; Clue de Taulanne – Lodowski *et al*., 2025), or dating relies on nannofossils with their associated uncertainties, or Berriasian ammonite material is derived in resedimented blocks.

CALPIONELLID NORMS AND EXCEPTIONS

Deformed loricae – horizons and significance

In many of the studied profiles, in the Colomi Subzone there is the temporally irregular presence of deformed (aberrant) calpionellid loricae (Nowak, 1971; Reháková, 2000; Lakova and Petrova, 2013; López-Martínez *et al*., 2013a, b, 2015a; Hoedemaeker *et al*., 2016; Reháková *et al*., 2017; Svobodová *et al*., 2019; Vaňková *et al*., 2019, Grabowski

et al., 2019; Michalík *et al*., 2021; Bubík *et al*., 2024; Rožič and Reháková, 2024). Deformed loricae are usually concentrated in thin laminae, or at levels with indications of bioturbation. Loricae that lie parallel to bedding are elongated and narrow, while vertical examples are shortened and widened. In the Bosso section (here described) bioclast-enriched laminae, containing deformed calpionellid loricae derived from underlying deposits, and thus older calpionellid subzones, have been continuously documented through the studied sequence from the higher part of the Intermedia Subzone to the Ferasini Subzone. On the other hand, in the La Faurie section, loricae deformations were observed predominantly in the Intermedia Subzone, as is the case in the Torre de' Busi section (Petrova *et al*., 2025). Kowal-Kasprzyk in Lodowski *et al*. (2025) observed deformed crassicollarians at the base and in the middle part of the Alpina Subzone.

Nowak (1971) associated deformed crassicollarians with periods of adaptative radiation, followed by degeneration and total regression. Sholle (1978) correlated deformation of thin-walled organisms in a chalk facies with intense, bedding-parallel compaction and crushing, with extremely rapid loading by overburden (thick basalt flows overlie the chalk). Thinning and deformation of loricae could have been associated with distant volcanic effusions producing metallic contaminants and salinity variation (Reháková *et al*., 2017). This could be correlated with deformed calpionellids that appear in the Colomi Subzone in the Tamazunchale section (Mexico), associated with an intense volcanic input to the basin (López-Martínez *et al*., 2015b). Local earthquakes could have triggered sediment liquefaction, which might, in turn, have contributed to deformation of loricae.

Crassicollaria parvula 'acme' event/s

A sudden increase in the abundance of *Crassicollaria parvula* species occurs in the lower part of the Alpina Subzone in some profiles: a thin horizon that interrupts the monotonous association dominated by the small spherical form of *C. alpina* (Remane *et al*., 1986; Olóriz *et al*., 1995). This event has been described as the *Crassicollaria parvula* "acme zone" (Houša *et al*., 1996, 1999; 2004; Pruner *et al*., 2010; Grabowski *et al*., 2010a; Michalík and Reháková, 2011; Lakova and Petrova, 2013; Lakova *et al*., 2017; Kietzmann *et al*., 2021a; Petrova *et al*., 2023). It even served to define a Alpina/Parvula Subzone (Benzaggagh, 2020). A level with an abundance of *Cr. parvula* is rather the result of the repeated reworking of pre-existing sediments and their mixing and redeposition during the Calpionella Zone. Such inputs are visible mainly in sediments of more distal environments where *Cr. parvula*, still abundant in the Colomi Subzone, could be a part of subtle winnowing of calcareous sediment and thus, contribute to the increase in the abundance of calpionellid associations in a given sediment layer. Further, the local and quite sporadic presence of some crassicollarians, as well as large and elongated *Calpionella* species (typical for the Intermedia Subzone to Ferasini Subzone) can be explained rather as a consequence of environmental dynamics, erosion and re-sedimentation of underlying, frequently bioturbated and partially unconsolidated, sediments (Ölveczká and Reháková, 2022; Petrova *et al*., 2025).

Common *Crassicollaria colomi* associated with a *Cr. parvula* 'acme' in Bulgaria

Lakova (1993) studied two sections, Barlya and Komshtitsa (Western Balkan Mts) and found in the lower half of the Alpina Subzone, about 2 m, above the J/K boundary, a level where amounts of *Cr. parvula* and *Cr. colomi* increased sharply. This level is characterised by the presence of abundant (>100 specimens per sample) representatives of *C. alpina* (mainly the small spherical form), frequent (11–40 specimens per sample) to common (41–100 specimens per sample) *Cr. parvula*, frequent *Cr. colomi* and rare (4–10 specimens per sample) *T. carpathica*. These data have subsequently been confirmed in other sections: at Gorno Belotintsi (Lakova *et al*., 1999; Petrova *et al*., 2023) and Gintsi 1 and Gintsi 2 (Lakova and Petrova, 2013). An exception to this pattern is the Yavorets section, located in the eastern part of the Western Balkan Mts, where, although *Cr. parvula* and *Cr. colomi* are present, they do not reach such quantities. What distinguishes these Bulgarian sections from the others elsewhere is the increased quantity not only of *Cr. parvula*, but also of *Cr. colomi*. In contrast to them, in the other sections where the 'acme' of *Cr. parvula* is recorded, *Cr. colomi* is rare (*e.g*., Houša *et al*., 1999) or absent (*e.g*., Houša *et al*., 2004; Pruner *et al*., 2010). In the Bulgarian sections mentioned above, occurrences of *Cr. colomi* in the lower samples are singletons or they are rare, and there are no clear signs of erosion, redeposition, or significant bioturbation. The degree of preservation of the calpionellids is very good. Thus, the most likely reason for the increase in the number of representatives of the genus *Crassicollaria* is favourable environmental conditions where some locally surviving population of *Cr. colomi* existed.

Cr. colomi, is represented by a handful of specimens at levels in the Colomi Subzone, but in the 'acme' of *Cr. parvula* as dozens of specimens (usually 30–50 per slide), alongside a hundred or more representatives of *Cr. parvula*. It is hard to visualize how calpionellid refugia could have existed in oceanic deep waters, but in isolated regions some few crassicollarians (apart from *Cr. parvula*) apparently persisted above the base of the Alpina Subzone, as is evidenced in some Bulgarian profiles already mentioned by very small/tiny numbers of some species and common *Cr. colomi*. These limited appearances are still not understood.

All this being said, in no way does the global pattern for the J/K boundary differ in any of the sections discussed in this work. Everywhere it is fixed on the basis of the same criteria: 1) the disappearance of *C. elliptalpina* and 2) the immediate preeminence of the small spherical form of *C. alpina* (*e.g.* Fig. 2). Here at the base of the Berriasian and up to the middle of the Alpina Subzone, the small form of *C. alpina* is absolutely dominant in the association, with significantly small quantities of *T. carpathica* and *Cr. parvula*.

THE CRASSICOLLARIA/CALPIONELLIA BOUNDARY IN THE ANDES

The Jurassic and Cretaceous successions of the Argentine–Chilean Andes (Fig. 5) comprise hundreds to thousands of metres of sedimentary and

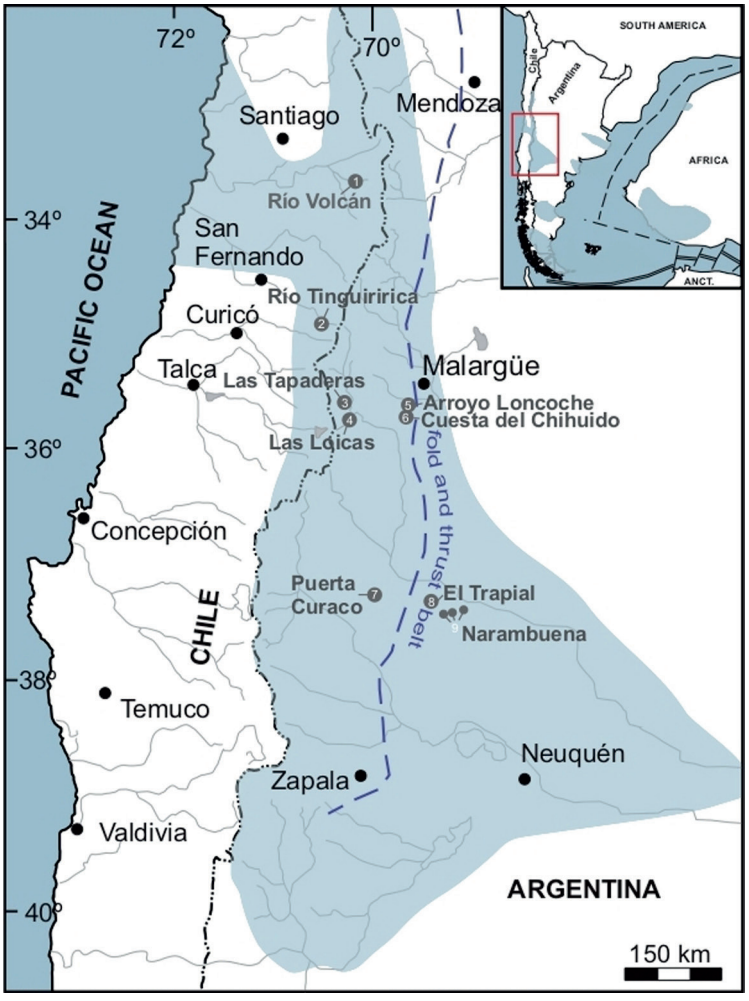

Fig. 5. Palaeogeography and main marine basins for the Jurassic/Cretaceous interval in southern Gondwana (modified from Ramos *et al*., 2020), and location of localities with calpionellid biostratigraphy: *1*) Río Volcán (Kietzmann and Encinas, 2025); *2*) Río Tinguiririca (Kietzmann *et al*., 2022); *3*) Las Tapaderas (Kietzmann *et al*., 2021b); *4*) Las Loicas (López Martinez *et al*., 2017); *5*) Arroyo Loncoche (Kietzmann, 2017; Kietzmann *et al*., 2021a); *6*) Cuesta del Chihuido, *7*) Puerta Curaco, *8*) El Trapial, and *9*) Narambuena (6–9 all from Kietzmann *et al*., 2021a).

volcanic, marine and continental, deposits, which contain abundant ammonites and microfossils (Leanza, 1980; Riccardi, 2008, 2015; Riccardi *et al*., 2011). These features underscore the important role of the Andean successions in global chronostratigraphy. The Andean ammonite species show marked provincialism and display characteristics of the Pacific Province, with only a few Tethyan genera represented (*e.g*., Riccardi, 1991), thereby complicating correlations between the Andean and Tethyan regions. This situation, however, has been reversed in recent years, by combining magnetostratigraphy and detailed biostratigraphic analyses of calpionellids (Iglesia Llanos *et al*., 2017; Iglesia Llanos and Kietzmann, 2020; Kietzmann *et al*., 2021a).

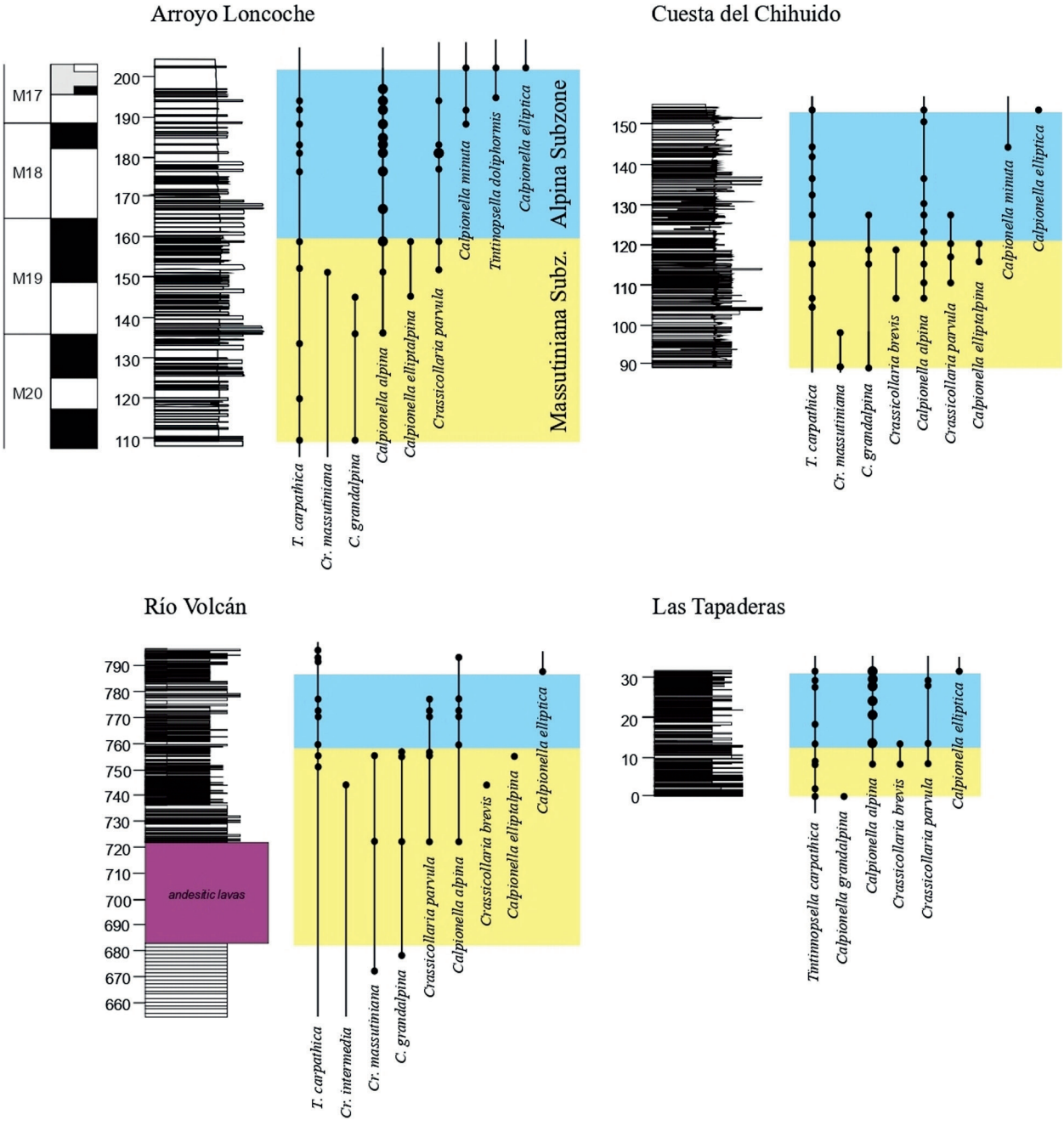

Fig. **6**. Selected stratigraphic sections illustrating the transition between the Massutiniana and Alpina subzones (Jurassic/Cretaceous boundary) in the Neuquén Basin (see corresponding references in Fig. 5). Larger and smaller dots indicate relative common or limited occurrences.

Calpionellids in the Neuquén Basin were first reported in outline by Fernández Carmona *et al*. (1996) and Fernández Carmona and Riccardi (1999), who documented *Calpionella alpina*, *Crassicollaria* sp., and *Tintinnopsella carpathica* associated with upper Tithonian to upper Berriasian ammonites. Later, Kietzmann (2017) described chitinoidellids and calpionellids from the Tithonian (Chitinoidella and Crassicollaria zones), and López-Martínez *et al*. (2017) reported assemblages assigned to the Colomi and Alpina subzones. Some of these assignments were subsequently revised by Kietzmann *et al*. (2021a), who provided the first regional synthesis based on multiple localities and a substantial number of samples, later extended to the Upper Jurassic–Lower Cretaceous units of Chile (Kietzmann *et al*., 2022; Kietzmann and Encinas, 2025). At present, calpionellid biostratigraphy in the Neuquén Basin is defined by the Chitinoidella, Crassicollaria, Calpionella, Calpionellopsis, Calpionellites and Tintinnopsella zones, which are further subdivided into the Slovenica, Boneti, Remanei, Massutiniana, Alpina, Elliptica, Simplex, Oblonga, and Darderi subzones (Figs 6 and 7).

The upper Tithonian Crassicollaria Standard Zone in the Neuquén Basin can be subdivided into the Remanei (sensu Remane *et al*., 1986) and Massutiniana (sensu Lakova, 1993) subzones (Kietzmann *et al*., 2021a). The Remanei Subzone contains the species *Tintinnopsella remanei*, *T. carpathica*, *Chitinoidella boneti*, *Crassicollaria intermedia*, and *Cr. massutiniana*. The Massutiniana Subzone yields *Calpionella grandalpina*, *T. carpathica*, *C. alpina*, *C. elliptalpina*, *Cr. massutiniana*, *Cr. intermedia*, *Cr. brevis*, *Cr. parvula*, and rarely *Cr. colomi*.

The lower Berriasian Calpionella Zone can currently be divided only into the Alpina and Elliptica subzones (sensu Pop, 1974), as specimens of *Remaniella* have not yet been recorded in the basin (Kietzmann *et al*., 2021a; Kietzmann and Encinas,

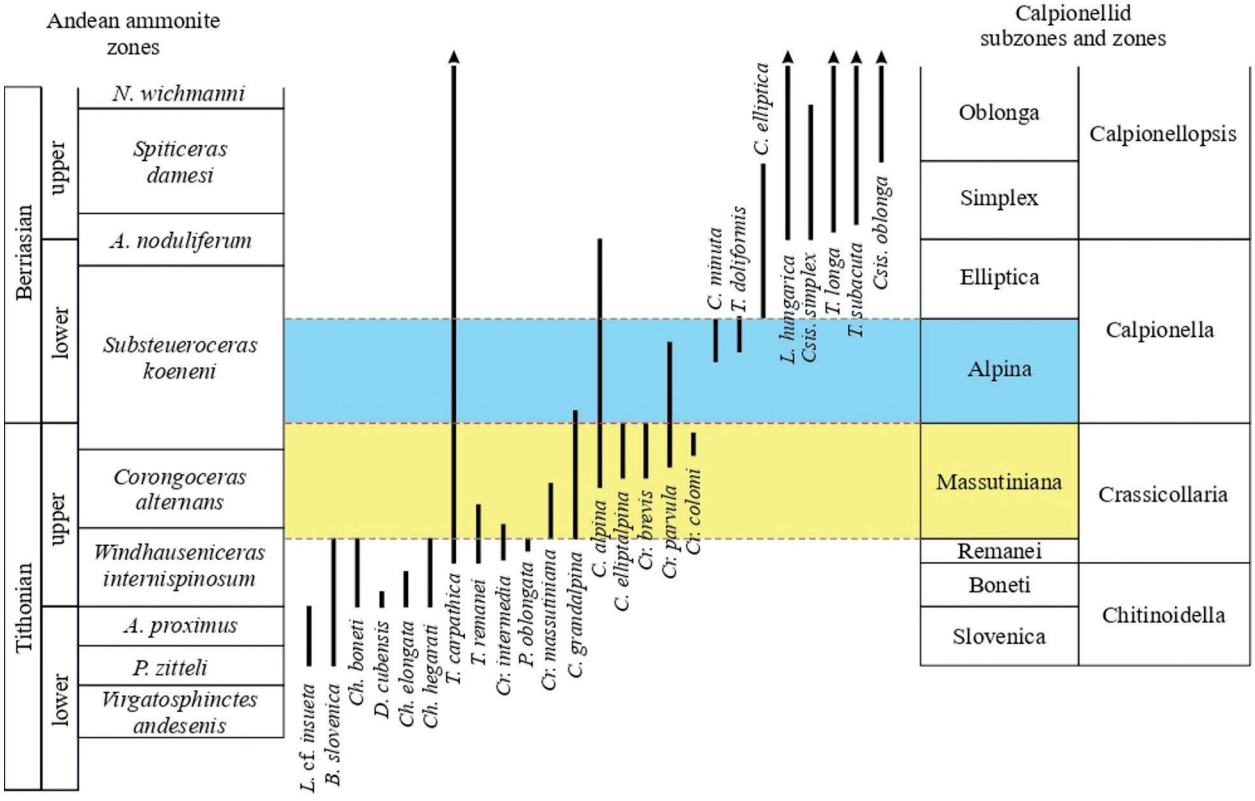

Fig. 7. Synthesis of the distribution of calpionellid species from the Vaca Muerta, Lo Valdés, and Baños del Flaco formations in the Neuquén Basin of Argentina and Chile. Note that the transition from the Massutiniana Subzone to the Alpina Subzone shows the same distribution patterns observed in the Tethys (*i.e*., an increase in the spherical variety of *Calpionella alpina*, accompanied by the disappearance of *Calpionella grandalpina*, *Calpionella elliptalpina*, *Crassicollaria massutiniana*, and *Crassicollaria brevis*), making it an excellent tool for global correlation.

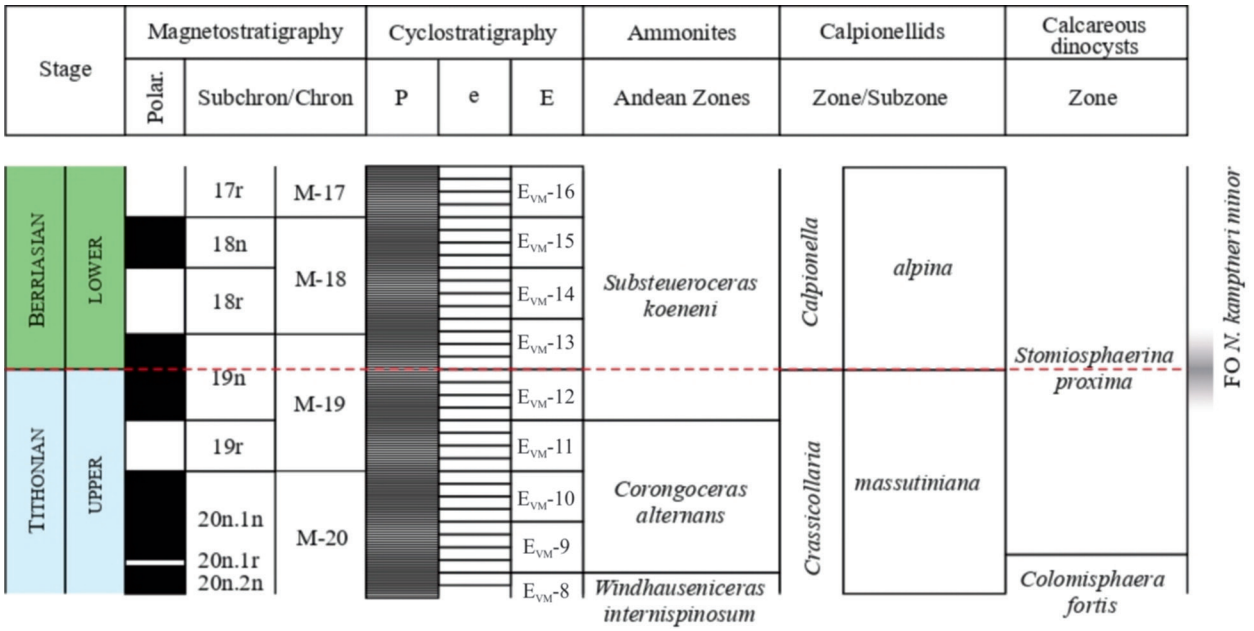

Fig. 8. Tithonian–Berriasian stratigraphy in the Neuquén Basin: magnetostratigraphy (Iglesia Llanos *et al*., 2017), cyclostratigraphy (Kietzmann *et al*., 2018), ammonites (Riccardi, pers. comm. in Kietzmann *et al*., 2018), calpionellids (Kietzmann *et al*., 2021a), calcareous dinocysts (Kietzmann *et al*., 2023), and nannofossils (Vennari *et al*., 2017).

2025). The Alpina Subzone is dominated by *C. alpina* and *Cr. parvula* plus *T. carpathica*, which are accompanied later by *C. minuta*, and *T. doliphormis*. The Elliptica Subzone contains *C. elliptica*, *C. alpina* and *T. carpathica*.

The acme of the spherical variety of *C. alpina*, which defines the base of the Calpionella Zone in the Tethys, is not straightforward to recognize in the Neuquén Basin. The overall abundance of calpionellids is low, and the increase in the globular form of *C. alpina* extends over several tens of metres (both the Vaca Muerta Fm in Argentina and the Lo Valdés Fm in Chile can reach more than 1000 m in thickness). However, the turnover observed in Tethys is also observed here: increase in the spherical variety of *C. alpina* is accompanied by the disappearance of *C. grandalpina* and *C. elliptalpina*, together with *Cr. massutiniana* and *Cr. brevis* (Figs 6 and 7). This turnover provides the most reliable biostratigraphic marker for establishing the Jurassic/Cretaceous boundary in the basin, which also occurs within the middle part of a normal polarity zone consistent with magnetosubzone M19.2n (Iglesia Llanos *et al*., 2017; Iglesia Llanos and Kietzmann, 2020; Kietzmann *et al*., 2021a).

Other markers used as proxies for this system boundary include nannoconids, such as *N. kamptneri minor* (*e.g.*, Wimbledon *et al*., 2020a). Its first occurrence was recognized by Vennari *et al*. (2017) in the lower to middle part of the *S. koeneni* ammonite Zone (Fig. 8). However, this taxon occurs there together with *N. steinmannii steinmannii*, which in the Tethys (*e.g.*, Berrias and Puerto Escaño) appears significantly higher in the succession. Consequently, the boundary would lie somewhat lower within the *S. koeneni* Zone, as indicated by the magnetostratigraphic data in conjunction with the calpionellids. Nannofossil bioevents have not been demonstrated regionally in the basin, and in one section, at Las Loicas, the two species were described in a much higher stratigraphic position (*i.e.*, uppermost *S. koeneni* ammonite Zone).

DISCUSSION

Generally, a uniform/standard trend in the development of calpionellids can be observed through J/K boundary sequences. Such a calpionellid succession (and zonation) has been documented in numerous profiles, for instance at: Brodno, Strapkova, Snežnica, Kóta 720 (Slovakia), Puerto Escaño, Río Argos (Spain), St Bertrand, Belvedere, Tré Maroua, (France), Fiume Bosso, Frisoni, Diesi II, (It-

aly), Gintsi sections (Bulgaria), Lókút and Hárskút (Hungary), Dedina (Serbia), Paramythia (Greece), Sviniţa (Romania), Pośrednie III (Poland), Oman, Banik (Iraq), Jebel Amar (Tunisia), Ain Hammouch, Igourar (Morocco), Jebel Azreg, Jebal Toumbait (Algeria), Kel (Turkey), Rancho San Vicente (Cuba), Apulco, Tamazunchale and Iturbide (Mexico). Figure 6, above, shows more recent finds in the Andes which demonstrate the same calpionellid pattern across the J/K boundary.

Herein we illustrate the standard calpionellid succession with new records from two geographically widely separated profiles: Fiume Bosso and Supra Notre Dame (Fig. 2). Both demonstrate the typical events of the Colomi and Alpina subzones.

The first hyaline species in the Remanei Subzone gave way to a rich and diversified assemblage of species in the Intermedia Subzone. Higher up, in the Colomi Subzone, there is a transition to an impoverished association. Typically small forms of *C. alpina* and *Cr. parvula* occur therein (in a ratio of about 3:1). Finally, the onset of the Alpina Subzone is marked by the incoming of small forms of *C. alpina*, which dominate over rare *Cr. parvula* and *T. carpathica*. Locally, even the last-mentioned species may be absent (*e.g.*, Apulco section, Mexico – López-Martinez *et al*. (2013a), and the Goleszow section, unpublished data). This is related to the influence of local environmental conditions.

Regardless of whether *Cr. colomi* is cited as the subzonal index or not (Massutiniana, Intermedia or Brevis may be substituted, *see* Benzaggagh, 2020; Lodowski *et al*., 2025; Petrova *et al*., 2025), in profiles that show a well-preserved topmost Crassicollaria Zone, the change from calpionellid association established in the Intermedia Subzone is distinct: in addition to small *C. alpina*, there are numerous *Cr. parvula* accompanied by rare *Cr. colomi*. In the published accounts already mentioned, mixed calpionellid associations influenced by constant recycling of underlying deposits persisted through the Colomi Subzone. In such profiles, poor, but definable, associations make an appearance only just below the boundary with the Alpina Subzone.

In the Mazatapec section, there is much organic matter in Upper Tithonian deposits, and thus calpionellids are rare (as compared to pure carbonate sequences) – due to the predominant disoxic conditions that are suggested by framboidal pyrite (López-Martínez *et al*., 2013a). With the onset of pure carbonates at the beginning of the Berriasian, a distinct monoassociation of small forms of *C. alpina* appears (López-Martínez *et al*., 2013a), coincident with a negative shift in $\delta^{13}C$. Similar preservation is also shown by calpionellids in less oxic environments where there is sedimentation of dark shales, such as in the Néuquen Basin (Kietzmann, 2017).

Some areas were periodically supplied with nutrients (*e.g.*, Torre de' Busi) and this stimulated the development of microplankton with siliceous shells (and also sponges). Where more siliceous microplankton is found, there are less calcareous taxa, and vice versa (Reháková and Michalík, 1994).

Thus, small spherical *C. alpina* remained as a survivor in the earliest Berriasian, a residual species of the calpionellid association from the Colomi Subzone; the calpionellid association had fallen below the critical limit under stressful conditions (Wignall and Benton, 1999). Calpionellid quantification has been well documented (Lakova, 1994; Michalík *et al*., 2021; Petrova *et al*., 2025). From some profiles it is possible, in a thin section, to count a few hundred specimens of *C. alpina*, in others only a few dozen, or even just a handful of loricae. Also, slight dolomitization of limestones, with partially preserved calpionellid loricae, just above the onset of the Alpina Subzone has been observed (Reháková and Rožič, 2019; un-published data from La Faurie, France). Thus the quantity and composition of that residual assemblage was influenced and shaped by the variability of the primary environment and a number of external and internal factors, which ultimately determined how much of the original sediment was preserved in the record. Therefore, the quantity of calpionellids is of secondary importance: events labelled as the "acme" or "explosion" of *C. alpina* or *Cr. parvula* species (Remane, 1985, Houša *et al*., 1996, 2004; Pruner *et al*., 2010) represent a taphocenosis with recycled, allochthonous calpionellid species from underlying deposits that have quantitatively enriched the in-situ association.

In terms of sequence stratigraphy, an impoverished calpionellid association in the Alpina Subzone reflects the maximum lowering of sea level (Reháková, 2000; Haq, 2014). This sea-level fall has been documented in the Tamazunchale section (López-Martínez *et al*., 2015b), with a total collapse of the carbonate platform and the formation of a thick breccia layer.

Most sporadic reappearances of crassicollarian species during the early Berriasian (after, sometimes, metres of section where they are absent; *see* Bosso and SND above, Fig. 2) can only be the result of the repeated reworking of pre-existing sediments and their mixing and redeposition into Calpionella Zone sediments.

With the onset of the Alpina Subzone, the environment stabilized for a certain time. From the

biological point of view, the only significant survivors in the lower Alpina Subzone were *C. alpina* and *T. carpathica*, and they were the progenitors for later calpionellid revivals (Lazarus effect; Wignall and Benton, 1999) during the Berriasian – with the appeareance of new homeomorphs of *C. alpina* (*C. minuta*) and *T. carpathica* (*T. doliphormis*) and new calpionellid taxa, starting with remaniellids. No new crassicollarian species has been documented during the Early Cretaceous. Therefore, in the light of this, the earlier presented views (Ascoli *et al*., 1984; Reháková, 2000; López-Martínez *et al*., 2013a) that most crassicollarians became extinct during the latest Tithonian are still relevant.

CONCLUSION

Early studies by Remane (1963, 1971), Allemann *et al*. (1971) and Borza (1984), in Tethys, and Trejo (1980), in Mexico, led to the establishment of a standard calpionellid zonation. Allemann's Alpina Subzone became the practical marker for the base of the Berriasian, and a better alternative to less widespread and less consistent ammonites, as recognised by the 1990s (*e.g*., Zakharov *et al*., 1996). The Alpina Subzone's base with its impoverished survivor assemblage was identified as easy to identify, and thus it has been effectively applied as the base of the Berriasian by multiple stratigraphers. It is not marked simply by the appearance of one taxon: the Alpina crisis event is marked by a cluster of indicators, it is clearly synchronous and it has been recognized in key sites around the globe – from the Andes to Mexico and through Tethys.

When one considers the remarkable geographic extent and definition of the Alpina event, it is interesting to note that some Cretaceous stages (with already ratified GSSPs) have bases defined, no doubt constrained by limited evidence, by a single ammonite species. The Hauterivian (Mutterlose *et al*., 2020) and Barremian (Company *et al*., 2024) are examples: the former has a marker (*Acanthodiscus radiatus*) that has an extent only between the Mediterranean and the Caucasus, and the latter (marker *Taveraidiscus hugii*), again, has a Mediterranean–Caucasian distribution, plus (probably non-coeval) spot occurrences in the UK and Germany. When compared to the Alpina Subzone, these markers seem to have decidedly limited geographical extents.

At the 2013 Warsaw meeting of the BWG there was consensus that the calpionellid Alpina Zone should be confirmed as the primary marker for the base of the Berriasian Stage: there were no dissenting voices (Wimbledon, 2014).

In June 2016, the then 70-plus BWG held a formal vote to select the primary marker for the Tithonian/Berriasian boundary. With a (remarkable) 76% majority, the base of the *C. alpina* (Alpina) Subzone was chosen, Thus the proposed boundary level adopted by the BWG conformed to the usage of recent generations, respected historical precedent, and was still situated within the Jacobi Zone, between the two ammonite zonal levels (Grandis and Jacobi) put forward during the 1963 and 1973 J/K colloquia. This decision was announced by the working group (WG) at the Vienna Cretaceous Symposium (Wimbledon *et al*., 2017). No voice was raised in opposition to this decision, and therefore the base of the Alpina Subzone, with its prominent calpionellid turnover, was applied by the WG when it moved to consideration of candidate GSSPs.

Hitherto, the onset of the Alpina Subzone and the dominance of a small form of *C. alpina* has sometimes been described as an "explosion" or "bloom". We propose that such misleading terms should be abandoned. It should be defined as a manifestation of the first calpionellid crisis, characterized by a globally recorded decrease in calpionellid abundance and associations that have minimal species variability. The crisis was influenced by a global fall in sea level, which excluded possibilities for the development of specialized niches and new species.

The primary J/K marker discussed in this work has been verified in numerous profiles in mid M19n.2n, as summarized in the preamble of this article. New localities repeatedly show the same pattern. Herein we record two new sites that, again, demonstrate the evidence of a calpionellid crisis at the Colomi–Alpina subzonal boundary: most crassicollarian species disappeared, *C. elliptalpina* became extinct, and the survivors in the early Alpina Subzone comprised dwindled numbers of *T. carpathica* and *Cr. parvula* together with relatively more common, small *C. alpina*.

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