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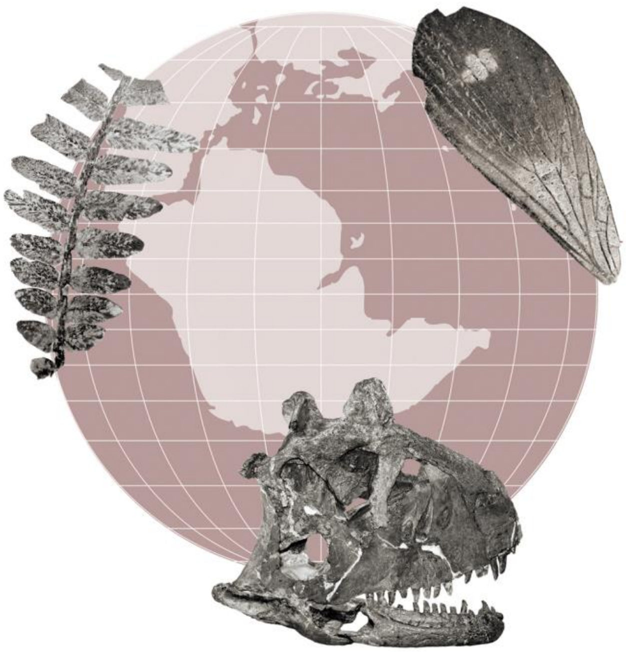

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CALCAREOUS NANNOFOSSILS ASSOCIATED TO THE CHACAICO SUR MARINE REPTILES IN THE LOS MOLLES FORMATION, NEUQUÉN BASIN: AGE AND PALEOENVIRONMENTAL INSIGHTS

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Running Header: CHAUMEIL RODRÍGUEZ *ET AL.*: CALCAREOUS NANNOFOSSILS FROM CHACAICO SUR

Short Description: First calcareous nannofossil report from Chacaico Sur (Neuquén) adds up to the biostratigraphic framework of locality's marine reptile record.

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Abstract. World's record of ichthyosaurs and plesiosaurs from the Aalenian-Bathonian interval (Middle Jurassic) is very scarce, and their presence in the Neuquén Basin is particularly significant for understanding the evolutionary history of these marine reptiles during the Jurassic. At Chacaico Sur (southwestern Neuquén), the Los Molles Formation yields a unique record of these animals, accounting for the presence of *Maresaurus coccai*, *Chacaicosaurus cayi*, and *Mollesaurus periallus*. The age assigned to this unit in the mentioned area is lower Bajocian, based on microfossils and macroinvertebrates. We studied the calcareous nannofossils to contribute to the age constraint and paleoenvironmental reconstruction. The recovered assemblage is composed of *Carinolithus magharensis*, *Carinolithus superbus*, *Cyclagelosphaera margerelii*, *Discorhabdus striatus*, *Retecapsa incompta*, *Watznaueria britannica*, *Watznaueria contracta*, *Watznaueria manivitiae*, *Watznaueria* sp. indet., and *Schizosphaerella punctulata*. This assemblage presents typical Bajocian features in the Neuquén Basin: low abundance and diversity and dominance of *W. britannica*. Overall, this assemblage would indicate an early Bajocian age, Subzone NJT10a, based on the co-occurrence of *C. superbus* and *W. manivitiae*. The low diversity and abundance might indicate shallow marine conditions related to the onset of a regressive phase in the basin. These results provide new temporal and paleoenvironmental context for understanding the evolutionary history and ecology of Mesozoic marine reptiles.
Keywords. Calcareous Nannofossils. Marine Reptiles. Middle Jurassic. Biostratigraphy. Los Molles Formation. Chacaico Sur. Neuquén Basin.
Resumen. NANOFÓSILES CALCÁREOS ASOCIADOS A LOS REPTILES MARINOS DE CHACAICO SUR EN LA FORMACIÓN LOS MOLLES: EDAD Y PERSPECTIVAS PALEOAMBIENTALES. El registro mundial de ictiosaurios y plesiosaurios del intervalo Aaleniano-Bathoniano (Jurásico Medio) es muy escaso, y su

presencia en la Cuenca Neuquina es particularmente significativa para comprender la historia evolutiva de estos reptiles marinos durante el Jurásico. En Chacaico Sur (sudoeste de Neuquén), la Formación Los Molles alberga un registro único de estos animales, dando cuenta de la presencia de *Maresaurus coccai*, *Chacaicosaurus cayi*, y *Mollesaurus periallus*. La edad asignada a esta unidad en el área de Chacaico Sur es Bajociano temprano, basada en micro y macroinvertebrados. Presentamos aquí datos bioestratigráficos de nanofósiles calcáreos. El ensamble recuperado está compuesto por *Carinolithus magharensis*, *Carinolithus superbus*, *Cyclagelosphaera margerelii*, *Discorhabdus striatus*, *Retecapsa incompta*, *Watznaueria britannica*, *Watznaueria contracta*, *Watznaueria manivitiae*, *Watznaueria* sp. indet., y *Schizosphaerella punctulata*. Este ensamble presenta características típicas del Bajociano de Cuenca Neuquina: baja abundancia y diversidad, y dominancia de *W. britannica*. En conjunto, el ensamble indicaría una edad Bajociano temprano, Subzona NJT10a, en base a la co-ocurrencia de *C. superbus* y *W. manivitiae*. La baja diversidad y abundancia indicarían condiciones de un mar somero que corresponderían con el establecimiento de una fase regresiva en la cuenca. Estos resultados proporcionan nueva información sobre el contexto temporal y paleoambiental para comprender la historia evolutiva y la ecología de los reptiles marinos del Mesozoico.

Palabras clave. Nanofósiles calcáreos. Reptiles marinos. Jurásico Medio. Bioestratigrafía. Formación Los Molles. Chacaico Sur. Cuenca Neuquina.

MARINE REPTILE COMMUNITIES underwent turnover during the Early-Middle Jurassic, leaving behind a very poor and discontinuous fossil record, especially in the Middle Jurassic, a key interval when diversification and demise of different groups occurred (Benson *et al.*, 2012; Fischer *et al.*, 2021; Reolid *et al.*, 2024) (Fig. 1.1). Ichthyosaurs and plesiosaurs diversified at the beginning of the Jurassic and thrived until the Toarcian (Thorne *et al.*, 2011; Benson *et al.*, 2012; Druckenmiller & Maxwell*et al.*, 2014). From then on, both groups' record is discontinuous and relatively scarce for the Aalenian-Bajocian interval (Fernández, 1994; Gasparini, 1997; Motani, 2005; Gasparini *et al.*, 2007; Maisch, 2010; Talevi & Fernández, 2015a; Tutin & Butler, 2017; Sachs *et al.*, 2019; Campos, 2022).

The Neuquén Basin has a unique record of marine reptiles (Gasparini & Fernández, 2005, 2006; Gasparini *et al.*, 2015, 2022), including ichthyosaurs (Cabrera, 1939; Fernández, 1994, 1999; Talevi *et al.*, 2012, 2021; Talevi & Fernández, 2012; Fernández & Talevi, 2014; Lazo *et al.*, 2018; Fernández *et al.*, 2019, 2021; Campos *et al.*, 2020; Campos, 2022), mosasaurs (Fernández *et al.*, 2008; Fernández & Talevi, 2015), plesiosaurs (O'Gorman *et al.*, 2015, 2023; Talevi & Fernández, 2015b; Talevi *et al.*, 2021), pliosaurs (Gasparini, 1988, 1997; Gasparini & O'Gorman, 2014; Matelo Mirco *et al.*, 2024), crocodiles (Gasparini & Dellapé, 1976; Gasparini *et al.*, 2005; Herrera *et al.*, 2013; Herrera, 2015), and turtles (Fernández & de la Fuente, 1988, 1993; De Lapparent de Broin *et al.*, 2007; González Ruíz *et al.*, 2020). In this regard, the classic Middle Jurassic locality of Chacaico Sur stands out. There, the upper portion of the Los Molles Formation (Weaver, 1931) outcrops and, at that site, it is assigned to the early Bajocian (Spalletti *et al.*, 1994). More than a decade dedicated to fieldwork in the area resulted in the description of the ichthyosaurs *Chacaicosaurus cayi* Fernández, 1994 and *Mollesaurus periallus* Fernández, 1999, the only evidence to date of the co-occurrence of ophthalmosaurids and non-ophthalmosaurid ichthyosaurs (Miedema *et al.*, 2024), and the only Aalenian-Bathonian diagnostic specimens of the group besides German and Swiss taxa (Maxwell *et al.*, 2012; Miedema *et al.*, 2024). This locality also registered the presence of *Maresaurus coccai* (Gasparini, 1997), the first early Bajocian rhomaleosaurid plesiosaur in the Eastern Pacific, and the oldest from the Argentine Patagonia (Fig. 1.2). Thus, the presence of marine reptiles in the basin is particularly significant for understanding the evolutionary history of the group during the Jurassic (Gasparini & Fernández, 2005).

The age assigned to these specimens is mainly based on biostratigraphic studies carried out on macroinvertebrates, which include ammonites, bivalves and brachiopods (Spalletti & Gasparini, 1993; Riccardi *et al.*, 1994; Zavala, 1996). On the other hand, microfossils were little studied at this site (Ballent, 1985; Martínez & Olivera, 2016). Nevertheless, micropaleontology can make a significant contribution to the study of marine organisms, as a key tool in paleoenvironmental and paleogeographic reconstructions and biostratigraphic analyses (*e.g.*, Saraswati & Srinivasan, 2016; O'Gorman *et al.*, 2023; Larkin *et al.*, 2024; Bolton & Stoll, 2025). Indeed, calcareous nannofossils have excellent stratigraphic resolution (Mutterlose *et al.*, 2005; Gradstein *et al.*, 2020) and, due to their small size, only a very small sediment sample is required for their study. In this contribution, we add the information provided by calcareous nannofossils recovered from the level where the reptiles of Chacaico Sur were collected, completing the age constraint and paleoenvironmental context, given by other fossil invertebrates.

GEOLOGICAL SETTING

The first wide-extended marine transgression recorded in the Neuquén Basin occurred in the Early Jurassic, being represented by the Los Molles Formation. In the Chacaico

Sur area (Fig. 2) the upper part of this unit outcrops and is composed of dark shales and marls with intercalated sandstones (Gasparini, 1997), interpreted as offshore deposits dominated by pelagic sedimentation. Sandstone layers are interpreted as storm-induced deposits by orbital and gravitational flows (Spalletti *et al.* 1994; Zavala, 1996; Franzese *et al.*, 2007). In the mentioned area, the formation has been previously assigned to the lower Bajocian (Spalletti *et al.*, 1994), according to its invertebrate fauna (Westermann & Riccardi, 1979; Leanza *et al.*, 1987; Ballent, 1985; Riccardi *et al.*, 1994).

MATERIAL AND METHODS

The studied material comes from the locality of Chacaico Sur (39° 15’ S; 70° 18’ W), 70 km southwest of the city of Zapala, Neuquén province (Fig. 2). Sediment was extracted from the upper part of the Los Molles Formation, at the level where the reptiles were collected. Sample processing for calcareous nannofossil analysis involved a simplification of the gravity settling technique (Pérez Panera *et al.*, 2023).

The qualitative analysis of nannofossils was carried out with a Leica DMP750 petrographic microscope, under x1000 magnification. Photographs were taken with a Leica MC170 HD camera.

Calcareous nannofossils samples are deposited in the Museo Provincial de Ciencias Naturales “Prof. Dr. Juan A. Olsacher” (Zapala, Neuquén, Argentina) under the acronym MOZ-Pm, numbers 61-64.

RESULTS AND DISCUSSION

The recovered calcareous nannofossil assemblage shows very low abundance, low species-richness, and poor preservation (Tab. 1). However, among few undeterminable coccoliths, the identification of *Carinolithus magharensis, Carinolithus superbus, Cyclagelosphaera margerelii*, *Discorhabdus striatus*, *Retecapsa incompta*, *Watznaueria britannica*, *Watznaueria contracta*, *Watznaueria manivitiae*, *Watznaueria* sp. indet., and

Schizosphaerella punctulata (Fig. 3), indicates an early Bajocian age, NJT10a Subzone for the assemblage (Mattioli & Erba, 1999; Ferreira *et al.*, 2019; Hesselbo *et al.*, 2020) (Fig. 4). This age is constrained by the co-occurrence of *C. superbus,* and small-sized specimens of *W. manivitiae.* comparable to those recorded by Ferreira *et al.* (2019) in Peniche, Portugal. The first occurrence of *W. manivitiae* is at the base of the NJT10 Zone (Mattioli & Erba, 1999; Ferreira *et al.*, 2019; Hesselbo *et al.*, 2020) and is correlable to the base of the *Sonninia propinquans* Tethyan Ammonite Zone (TAZ) (Figure 4). *Carinolithus superbus* has its last occurrence within the NJT10 Zone (Ferreira *et al.*, 2019) indicating the top of the NJT10a Subzone, which correlates to the top of the *S. humphriesianum* TAZ (Mattioli & Erba, 1999; Hesselbo *et al.,* 2020). The other recovered species, like *C. magharensis, C. margerelii, D. striatus, W. britannica, W. contracta, S. punctulata,* are typical components of the Bajocian – Bathonian worldwide. Even though Bajocian calcareous nannofossil associations have been already documented for the Los Molles Formation (Gutiérrez Pleimling *et al.*, 2021), this is the first time that NJT10a Subzone is identified in the Neuquén Basin.

Marine reptiles from Chacaico Sur were found in association with ammonites, which provided biostratigraphic age control. Fernández (1994) documented ammonites in the same stratigraphic level as *Chacaicosaurus cayi,* which were previously identified in that site by Spalletti & Gasparini (1993) and assigned to the *Emileia giebeli* Argentina Ammonite Zone (AAZ), equivalent to the *Sonninia propinquans* TAZ (Figure 4). More precisely, Spalletti & Gasparini (1993) correlate it to the *E. multiformis* Subzone, early Bajocian (Riccardi, 2008). Similarly, the remains of *Maresaurus coccai* were recovered from a level within this same subzone (Gasparini, 1997). Later, Fernández (1999) reported *Mollesaurus periallus* associated with *Sonninia (Papilliceras) espinazitensis,* also referable to the *Emileia giebeli* AAZ.

Additional fossil evidence for the early Bajocian age of the Los Molles Formation at Chacaico Sur, includes bivalves attributed to the *Propeamussium andium* association Zone, brachiopods from the *Cymatorhynchia-Monsardithyris* association Zone, and foraminifera belonging to the *Lenticulina varians suturaliscostata* association Zone (Riccardi *et al.*, 1994).

In general, the microfossils from Chacaico Sur area are barely represented in the literature by palynomorphs and foraminifera (Volkheimer, 1973, 1974; García *et al.*, 1994, 2006; Riccardi *et al.*, 1994; Martínez *et al.*, 2005; Martínez & Olivera, 2016; Olivera *et al.*, 2020). In these contributions, Los Molles Formation is inferred as a marine, partially restricted environment, with oxic-dysoxic conditions of Middle Jurassic age (García *et al.*, 2006). There are no previous calcareous nannofossil studies for the Los Molles Formation in this area.

The nannofossil assemblage studied here show similar features to others documented in different sectors of the Neuquén Basin (both outcrop and subsurface) in the Bajocian: low diversity, low abundance, poor preservation and a dominance of *Watznaueria britannica* (Ballent *et al.*, 2000; Gutiérrez Pleimling *et al.*, 2021). The relatively high abundance of *Watznaueria britannica* is related to mesotrophic conditions, due to an increment of the nutrient supply (Pittet & Mattioli, 2002; Olivier *et al.*, 2004; Giraud *et al.*, 2006). Furthermore, the high relative abundance of *W. britannica* observed herein would corresponds to the turnover experienced by calcareous nannoplankton in the late Aalenian, after which the diversification of the genus *Watznaueria* began (Cobianchi *et al.*, 1992; Mattioli & Erba, 1999; Cobianchi & Picotti, 2001; Tiraboschi & Erba, 2010; Sucherás-Marx *et al.*, 2015; Giraud *et al.*, 2016; Wiggan *et al.*, 2018; Visentin *et al.*, 2023), mastering the assemblages worldwide and becoming the most successful Mesozoic nannofossil until the Tithonian (Bown *et al.*, 1988; Bown & Cooper, 1998).

Moreover, the *Watznaueria* radiation, accompanied by a dominance of specimens without structures or a bridge in the central area, matches a major turnover of many microinvertebrate organisms which are at the base of the food-web chain (Giraud *et al.*, 2016). Such microplankton radiation might have triggered the evolution of other marine organisms higher in the food-web chain, such as marine reptiles. These suite of events is also related to major climatic and palaeoceanographic changes in the early Bajocian, as an expression of the Mid-Mesozoic marine revolution (Sucherás-Marx *et al.*, 2012; 2015; Aguado *et al.*, 2017; Fantasia *et al.*, 2022). In the other hand, the species *Carinolithus magharensis* and *C. superbus* are associated with open marine shelf environments, with clear and warm waters (Ballent *et al.*, 2000). The overall low diversity and abundance of the assemblage would indicate a shallowing event related to a regressive hemicycle in the basin (Gutiérrez Pleimling *et al.*, 2021).

This study provides a new age constraint and paleoenvironmental information for the marine reptiles of Chacaico Sur, highlighting calcareous nannofossils as a valuable proxy to enhance this kind of studies, and contributing to better understanding the Mesozoic marine reptile evolutionary history and ecology.

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Figure and table captions

Table 1. Distribution chart of the recorded calcareous nannofossil species in the studied samples. All the samples display a poor preservation state (P) with significant overgrowth (Roth, 1984). Relative abundance values are as follow: **R,** rare = up to 5 specimens; **F,** few = 6-10 specimens; **C,** common = 11-20 specimens; **A,** abundant = more than 20 specimens.

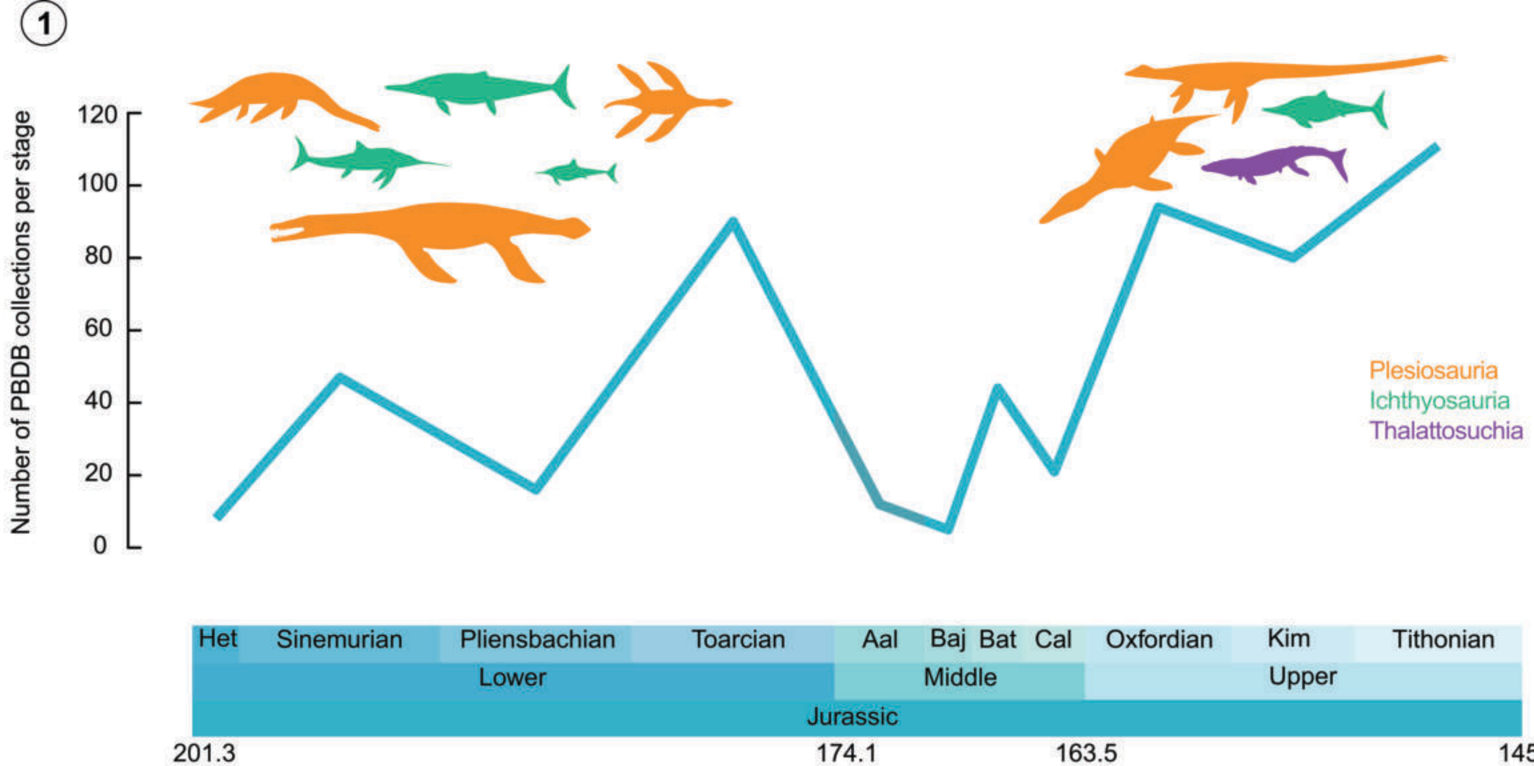
Figure 1. 1, Jurassic marine reptile worldwide records (modified from Fischer *et al.*, 2021); **2,** Ichthyosauria and Plesiosauria records for the Aalenian-Bajocian interval: Argentina (Cabrera, 1939; Fernández, 1994, 1999, 2003; Gasparini, 1997), China (Zhang, 1985; Gao *et al.*, 2004; Zhang *et al.*, 2020), France (Godefroit, 1994; Vincent *et al.*, 2007, 2013), Germany (Maxwell *et al.*, 2012), Luxembourg (Fischer *et al.*, 2021), Switzerland (Miedema *et al.*, 2024), and U.S.A. (Druckenmiller & Maxwell, 2014). The Neuquén Basin, Argentina, is the only location in the South Hemisphere where both groups are recorded.

Figure 2. 1, Geographic location of the studied area (modified after Coria *et al.*, 2025); **2,** Geological map of the studied area (modified after Gasparini & Spalletti, 1993).

Figure 3. Calcareous nannofossils recovered from Chacaico Sur sediments. **1-3, *Carinolithus magharensis*** (Moshkovitz & Ehrlich, 1976) Bown, 1987; **4, *Retecapsa***

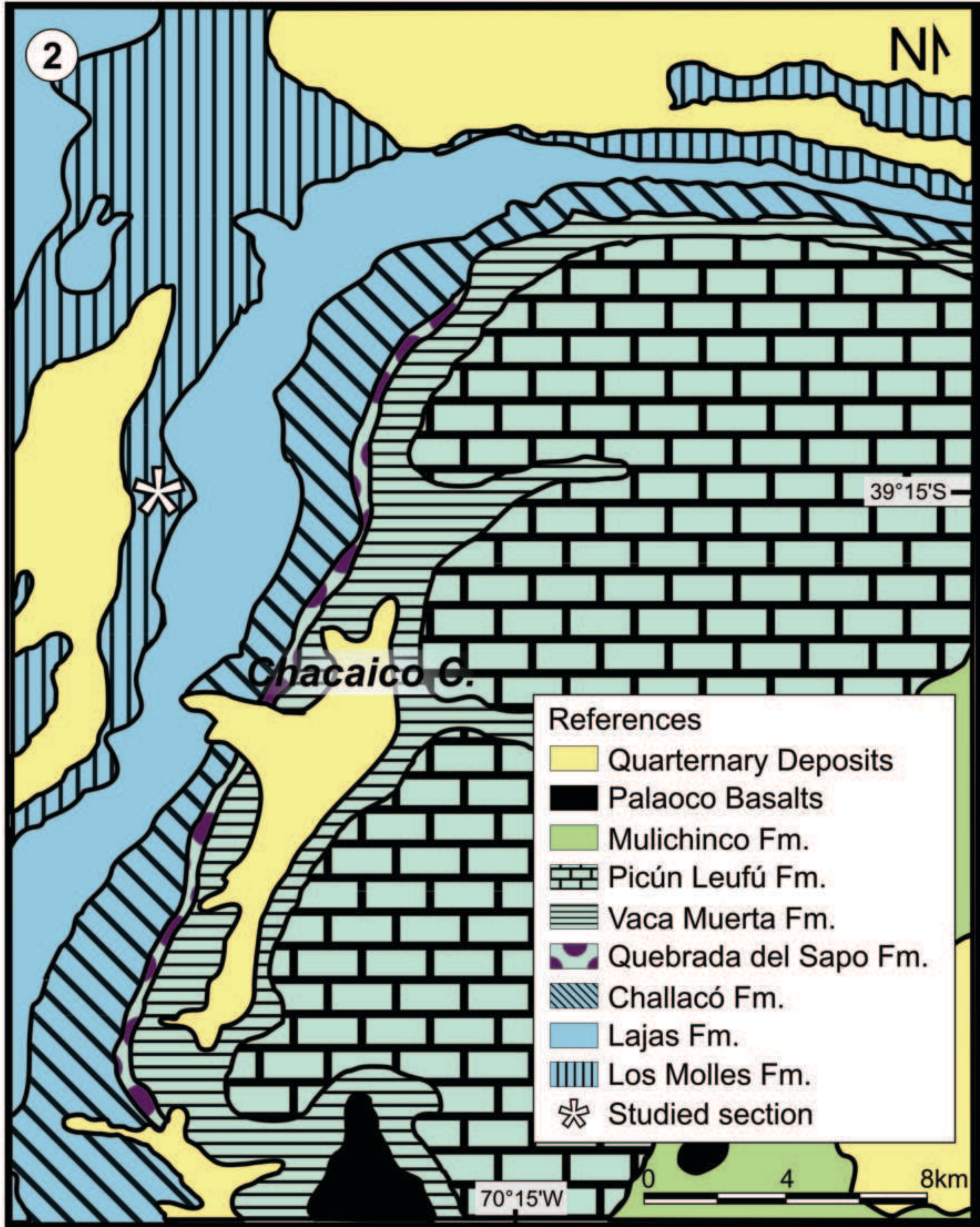
incompta Bown & Cooper, 1989; **5-6, *Discorhabdus striatus*** Moshkovitz & Ehrlich 1976; **7-8, *Carinolithus superbus*** (Deflandre in Deflandre & Fert, 1954) Prins in Grün *et al.*, 1974; **9-10, *Watznaueria contracta*** (Bown & Cooper, 1989) Cobianchi *et al.* 1992; **11-12, *Watznaueria britannica*** (Stradner, 1963) Reinhardt, 1964; **13-14, *Watznauria manivitiae*** Bukry, 1973; **15, *Schizosphaerella punctulata*** Deflandre & Dangeard, 1938; and **16, *Schizosphaerella punctulata*** fragment Deflandre & Dangeard, 1938. All pictures from sample MOZ-Pm-61. Scale bar = 5 µm.

Figure 4. Aalenian – Callovian calcareous nannofossil and ammonite zonation schemes (Age and Zone correlation according to Riccardi, 2008 and Hesselbo *et al.*, 2020. Figure prepared with and modified after TSCreator v 8.1 - 02April2023).


1
Number of PBDB collections per stage
0
20
40
60
80
100
120
Plesiosauria
Ichthyosauria
Thalattosuchia
Het
Sinemurian
Pliensbachian
Toarcian
Aal
Baj
Bat
Cal
Oxfordian
Kim
Tithonian
Lower
Middle
Upper
Jurassic
201.3
174.1
163.5
145


2
Aalenian-Bajocian Records
Plesiosauria
Ichthyosauria


1
Atlantic Ocean
Pacific Ocean
Argentina
Neuquén


2
N
39°15'S
Chacaico C.
70°15'W
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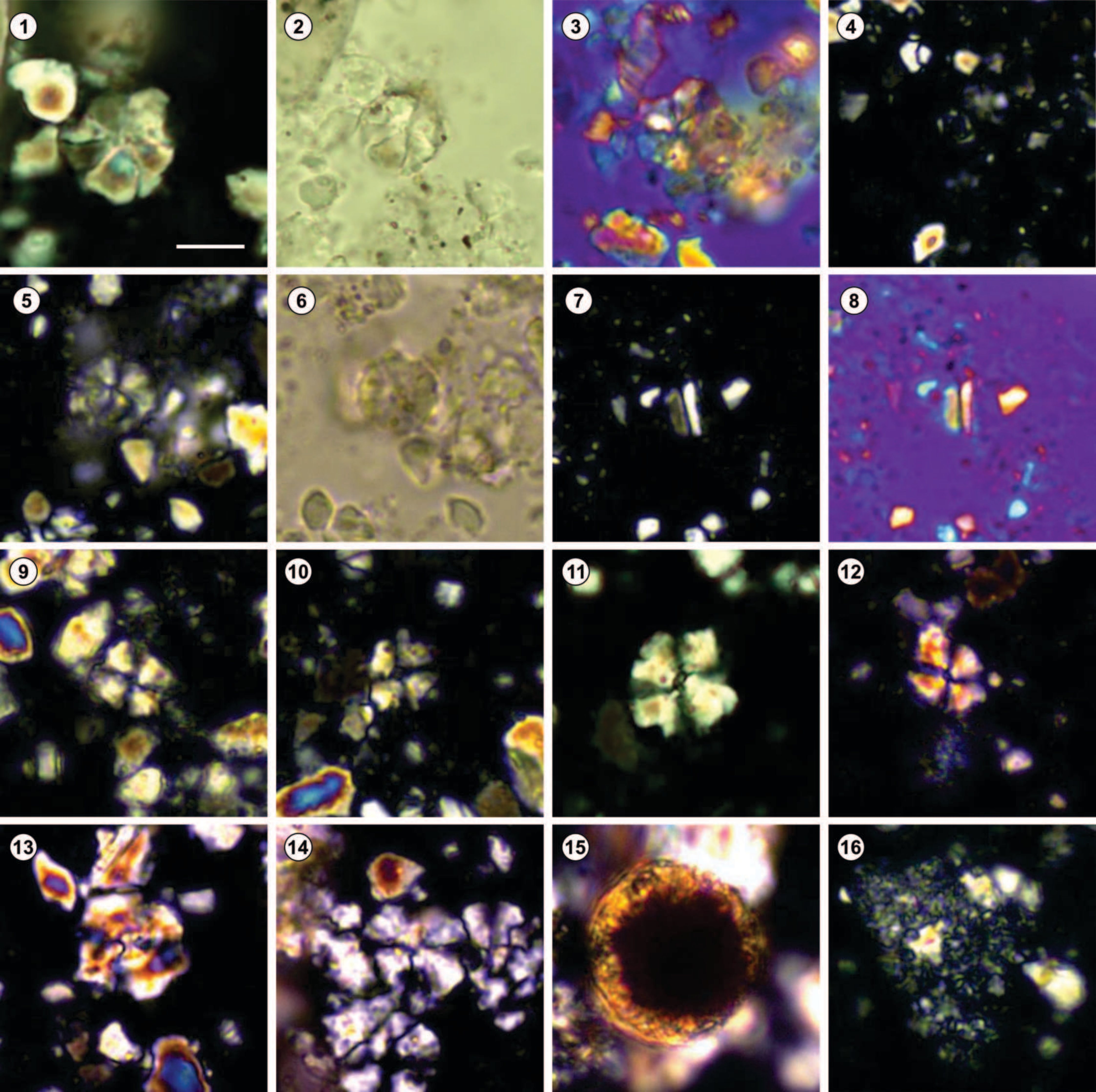
4
8km
References
Quarternary Deposits
Palaoco Basalts
Mulichinco Fm.
Picún Leufú Fm.
Vaca Muerta Fm.
Quebrada del Sapo Fm.
Challacó Fm.
Lajas Fm.
Los Molles Fm.
Studied section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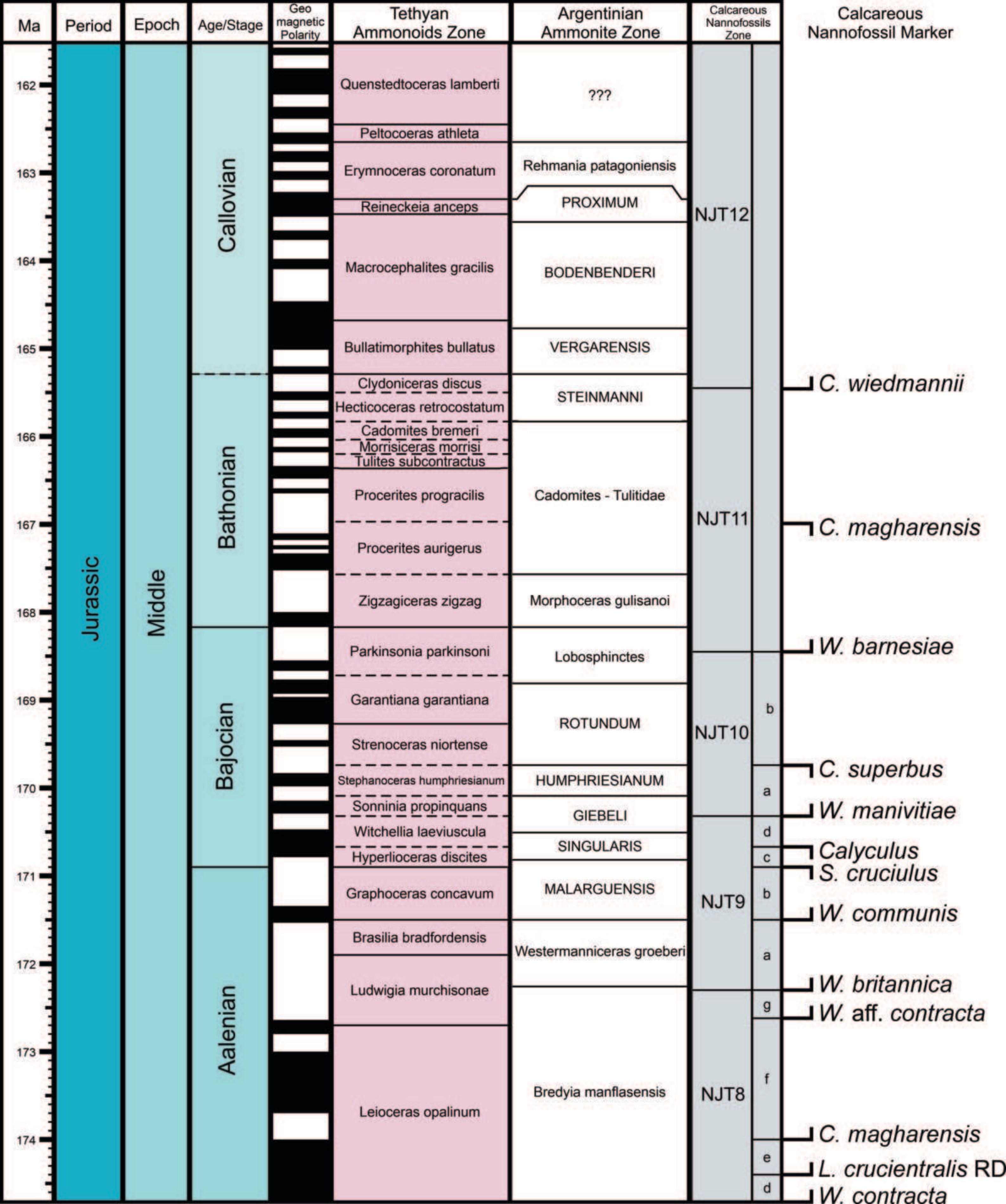
Ma
Period
Epoch
Age/Stage
Geo magnetic Polarity
Tethyan Ammonoids Zone
Argentinian Ammonite Zone
Calcareous Nannofossils Zone
Calcareous Nannofossil Marker
162
163
164
165
166
167
168
169
170
171
172
173
174
Jurassic
Middle
Callovian
Bathonian
Bajocian
Aalenian
Quenstedtoceras lamberti
Peltocoeras athleta
Erymnoceras coronatum
Reineckeia anceps
Macrocephalites gracilis
Bullatimorphites bullatus
Clydoniceras discus
Hecticoceras retrocostatum
Cadomites bremeri
Morrisiceras morrisi
Tulites subcontractus
Procerites progracilis
Procerites aurigerus
Zigzagiceras zigzag
Parkinsonia parkinsoni
Garantiana garantiana
Strenoceras niortense
Stephanoceras humphriesianum
Sonninia propinquans
Witchellia laeviuscula
Hyperlioceras discites
Graphoceras concavum
Brasilia bradfordensis
Ludwigia murchisonae
Leioceras opalinum
???
Rehmania patagoniensis
PROXIMUM
BODENBENDERI
VERGARENSIS
STEINMANNI
Cadomites - Tulitidae
Morphoceras gulisanoi
Lobosphinctes
ROTUNDUM
HUMPHRIESIANUM
GIEBELI
SINGULARIS
MALARGUENSIS
Westermanniceras groeberi
Bredyia manflasensis
NJT12
NJT11
NJT10
NJT9
NJT8
b
a
d
c
b
a
g
f
e
d
C. wiedmannii
C. magharensis
W. barnesiae
C. superbus
W. manivitiae
Calyculus
S. cruciulus
W. communis
W. britannica
W. aff. contracta
C. magharensis
L. crucientralis RD
W. contracta

TABLE 1. Calcareous nannofossils distribution chart

Sample*	Fields of View	Preservation	***Carinolithus magharensis***	***Carinolithus superbus***	***Cyclagelosphaera margerelii***	***Discorhabdus striatus***	***Retecapsa incompta***	***Watznaueria britannica***	***Watznaueria contracta***	***Watznaueria manivitiae*** small-sized	***Watznaueria*** sp. indet.	***Schizosphaerella punctulata***	Thoracosphaerales indet.	Unidentified heterococcolith	Abundance per field of view	Richness
MOZ-Pm 61	1200	P	R	R	R	R	R	A	R	F	F	F	R	R	0.06	12
MOZ-Pm 62	600	P	R		R			C	R	R	R	F		R	0.05	8
MOZ-Pm 63	600	P			R			C	R	R	R	R		R	0.05	7
MOZ-Pm 64	600	P		R	R			C		R	R	R		R	0.04	7

*Replicates. All belong to the same rock sample.