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Abstract: The outstanding discovery of two heteromorph ammonites in Late Callovian and Early Oxfordian deposits, where such ammonites were deemed absent, substantially reduce the interval without heteromorph ammonite known into the Jurassic. A new species is described for the Early Oxfordian: *Acuariceras acucostis* sp. nov., which expands our knowledge of the latest Parapatoceratinae and complete their stratigraphic distribution. The evolution of ornamentation between *A. acuaricus* / *Paracuariceras incisum* and *A. acucostis* sp. nov., from which it is derived, tends toward a net reinforcement at least on the body chamber. Without the preservation of the suture lines however, it is difficult to know the relationships maintained between the new species and the genera *Acuariceras* and *Paracuariceras*. It is not excluded that these two genera, which are distinguished only on the basis of relatively discrete suturing criteria, could be synonymous.

# First record of Late Callovian to Early Oxfordian heteromorph ammonites

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## Abstract

The outstanding discovery of two heteromorph ammonites in Late Callovian and Early Oxfordian deposits, where such ammonites were deemed absent, substantially reduce the interval without heteromorph ammonite known into the Jurassic. A new species is described for the Early Oxfordian: *Acuariceras acucostis* sp. nov., which expands our knowledge of the latest Parapatoceratinae and complete their stratigraphic distribution. The evolution of ornamentation between *A. acuaricus* / *Paracuariceras incisum* and *A. acucostis* sp. nov., from which it is derived, tends toward a net reinforcement at least on the body chamber. Without the preservation of the suture lines however, it is difficult to know the relationships maintained between the new species and the genera *Acuariceras* and *Paracuariceras*. It is not excluded that these two genera, which are distinguished only on the basis of relatively discrete suturing criteria, could be synonymous.

## Résumé

La découverte exceptionnelle de deux ammonites hétéromorphe dans des dépôts du Callovien supérieur et de l'Oxfordien inférieur, où ce type d'ammonites sont réputées absentes, réduit sensiblement l'intervalle sans ammonite hétéromorphe connu dans le Jurassique. Une nouvelle espèce est décrite pour l'Oxfordien : *Acuariceras acucostis* sp. nov., qui élargit notre connaissance des derniers Parapatoceratinae et complete leur distribution stratigraphique. L'évolution de l'ornementation entre *A. acuarius* / *Paracuvariceras incisum* et *A. acucostis* sp. nov., à partir desquels il est dérivé, tend vers un net renforcement au moins sur la chambre d'habitation. Cependant, sans la préservation des lignes de suture, il est difficile de connaître les relations entretenues entre la nouvelles espèces et les genres *Acuariceras* et *Paracuvariceras*. Il est pas exclu que ces deux genres, qui se distinguent uniquement sur la base de critères suturaux relativement discrets, soient synonymes.

**Key-words:** Jurassic heteromorph ammonites; Callovian; Oxfordian; France; *Acuariceras*.

**Mot-clés:** Ammonites hétéromorphes jurassiques; Callovien; Oxfordien; France; *Acuariceras*.

## 1. Introduction: Mesozoic occurrences of heteromorph ammonites

### 1.1. The Mesozoic heteromorph groups

During the Mesozoic Era, heteromorph ammonites are usually known in the Cretaceous with the vast diversification of the Ancyloceratina Wiedmann, 1966 (since late Valanginian-early Hauterivian), the Turilitina Beznov & Michailova, 1983 (since late Hauterivian), and also the Protancyloceratina Vermeulen, 2005. However, older occurrences of uncoiled ammonites exist, in the Late Triassic, Middle Jurassic and Late Jurassic.

The earliest occurrence of Mesozoic uncoiled ammonites is the Triassic Choristocerataceae Hyatt, 1900 (with Choristoceratidae Hyatt, 1900, Cochloceratidae Hyatt, 1900 and Rhabdoceratidae Tozer, 1979). They range over an interval between the Norian and Rhaetian (Fig. 1), and then they go out with no known descendants.

The older heteromorph Cretaceous ammonites belong to the Protancyloceratina and derive from late Jurassic forms of the genus *Protancyloceras* Spath, 1924 (Fig. 1). According to Cecca (1997), the *Protancyloceras* appeared with *P. guembeli* (Oppel, 1865) in the northern Carpathians early Tithonian (late Hybonotum Zone). However, an older specimen has been collected in the lower part of the same zone by Sarti (1999) in the Southern Alps (Trento Plateau, Italy), where it is extremely rare (one specimen over several thousand ammonites). Its ancestor is unknown with certainty, but Cecca suggested that it could derive from *Hybonotoceras* Breistroffer, 1947 (Aspidoceratidae Zittel, 1895, Hybonoticeratinae Breistroffer, 1947) because of a similar ventral groove and raised strong ribs. Nevertheless, as the earliest *Protancyloceras* have no ventral groove (Sarti, 1999), the best challenger is probably the one proposed by Schweigert & Zeiss (1998): the genus *Berkhemeria* Schweigert & Zeiss, 1998, which the type-species *B. scherzingeri* Schweigert & Zeiss, 1998 appears at the earliest part of the Hybonotum Zone, the Eigeltingense Horizon. If this link was confirmed, the *Protancyloceras* would come from the Perisphinctidae Steinmann, 1890 (Perisphinctaceae Steinmann, 1890), and more specifically from the Passendorferiinae Meléndez, 1989.

Except the Tithonian diversification of the subfamily Protancyloceratinae, the lone other Jurassic known occurrence of heteromorph ammonites is in the Middle Jurassic with two iteratively groups (Fig. 1), distinguished within the Parkinsoniidae Buckman, 1920; they have been fully reviewed by Dietl (1978). The oldest group corresponds to the *Spiroceras*

Quenstedt, 1858 diversification (subfamily Spiroceratinae Hyatt, 1900), appearing in the Niortense Zone (Baculata Subzone, late Bajocian), just after the rising of the genus *Strenoceras* Hyatt, 1900 from which they may derive. The Spiroceratinae disappear without known descendants in the Parkinsoni Zone (Acris Subzone – Pavia, 1971).

The second subfamily (Parapatoceratinae Buckman, 1926) ranges from the late Bathonian (Retrocostatum Zone, Fig. 1 – Fernandez-Lopez, 2001) to the early Middle Callovian (Anceps Zone). Following Dietl (1978), it appears that the Parapatoceratinae are probably not directly related to the *Spiroceras* phyletically, but may derive from *Epistrenoceras* Bentz, 1928. The genus *Parapatoceras* Spath, 1924 has the most extensive stratigraphic range, from the late Bathonian to the Middle Callovian. The genus *Paracuariceras* Schindewolf, 1963 is only known in the Callovian. It appears in the Bullatus Zone and disappears before the end of the Anceps Zone. The genus *Acuariceras* is the earliest but it has a shorter stratigraphic range, only occurring in the Anceps Zone.

No more now than by the time of Dietl's work (1978), there are reliable data on possible heteromorph ammonites from the early to middle Bathonian. Thus, there is no phylogenetic relationship between these different Mesozoic occurrences, and the concerned groups were each time turned off with no known descendants, except for the Protancyloceratina, which continue and diversify mainly in the Early Cretaceous.

So, during the Mesozoic, there are three wide time-ranges considered as *lacking heteromorph ammonites* (zones I, II and III in Fig. 1), two of them extending through the Jurassic. Particularly, this is acute during the whole Lias (Early Jurassic), and between late Middle Callovian to Late Kimmeridgian (late Middle to Topmost Jurassic).

### 1.2. The discussed occurrence of Early and Late Jurassic heteromorphs

However, some authors referred to the presence of heteromorphs during these periods; these records are:

- (1) *Acuariceras marthae* Potonié, 1929 was described first by Quenstedt (1887, pl. 70, fig. 45), and based on a Liassic fossil from Württemberg, identified as 'Hamite'. Potonié formally described this ammonite in 1929 (p. 226); Arkell (1950; 1957) attributed it a great phylogenetic importance, regarding it as the ancestor of the Dogger heteromorph ammonites. More recently, Donovan & Hölder (1958) studied this material with details, and they demonstrated it belongs to ... remains of crinoids!

- (2) *Ancyloceras mosellense* Terquem, 1857 was described as a late Liassic form from the Metz area (Moselle, France); but Maubeuge (1947) clearly assumed that this fossil was not an ammonite, and may be of vegetal nature...

- (3) *Helicoceras alpinum* Thalmann, 1923 is from the Aalenian of the Schildhorn Formation (Pletschbach, Müssen area, Switzerland). This highly altered fossil was rather considered as a possible *Tmetoceras* Buckman, 1892 by Westermann (1956).

- (4) The best-known citations of Oxfordian heteromorph ammonites are *Ancyloceras ischeri* Favre, 1876 and *Ancyloceras* sp. by Favre (1876, p.60, pl. 6, fig. 4-6). These specimens came from the 'Ammonites bimammatus beds' of the Fribourg Alps (Switzerland). Actually, it is now clear that they may belong to the classic *Epipeltoceras* Spath, 1924 and to a tectonically-deformed Perisphinctidae; therefore, according to Dietl studies (1978, p. 50), that these ammonites were specifically restored to make them an heteromorph-like shape; then, such character was highly idealized on Favre's figurations...

- (5) Some heteromorphs described in the 19th century have been placed originally into the "lower Oxfordian field", but are now included in the top of the Dogger, for example *Parapatoceras distans* (Baugier & Sauzé, 1843) and *Parapatoceras tuberculatum* (Baugier &

Sauzé, 1843). Such confusion, combined to the wrong data of Favre's data (see above point 4) subsequently very likely induced some researchers in error about the assumed presence of heteromorph ammonites in the Oxfordian (Ochoterna, 1966, fig. 5; Arkell, 1957, p. 207).

## 2. The new – and true – heteromorph ammonites from Late Callovian / Early Oxfordian

### 2.1. Material / stratigraphical occurrence

Based on accessible and checkable literature data, it is obvious that there are no known Jurassic heteromorph ammonites from the late Middle Callovian (disappearance of the ultimate Parapatoceratinae) to the early Tithonian (with the onset of Protancyloceratina).

Actually, it seems that all records result by systematic misinterpretations. Two exceptions must be quoted, with two distinct unpublished fossils collected *in situ* at the very end of the 80's:

- One specimen from the Crotenay section (Central Jura, France), mentioned as an “heteromorph” by Courville et al. (2000, p. 388, end of second paragraph); it was collected in Unit 134, in which characteristic pyritized *Cardioceratidae* may indicate the *Costicardia* Subzone (Cordatum Zone, Early Oxfordian). This discovery has not been subsequently quoted, and the specimen was never figured. Quick morphological observations show that although very fragmented, it is unquestionably an heteromorph ammonite, which right shell is morphologically close to the genera *Acuariceras* / *Paracuariceras*. Its originalities led us to propose a new name for it (*A. acucostis* sp. nov.).

- Another small and very fragmentary specimen was conserved, from one of the studied and published cross-section around Etrochey (north of Châtillon-sur-Seine, Côte-d'Or, North-East France; Courville & Bonnot, 1998). It was collected from Unit 5, level 41 (*ibidem*,

p.318); it was not mentioned in the text, but was preserved in the PC collection, University of Rennes 1. It is of youngest Athleta Zone age (Collotiformis Subzone, Late Callovian of the Submediterranean stratigraphic chart; [Cariou & Hantzpergue, 1997](#)). Despite its small size and quite poor preservation, this unquestionable heteromorph specimen may be compared to *Parapatoceras* cf. *tuberculatum* Baugier & Sauzé, 1843.

## 2.2. Systematics

Order **Ammonoidea** Zittel, 1884

Superfamily **Stephanocerataceae** Neumayr, 1875

Family **Parkinsoniidae** Buckman, 1920

Subfamily **Parapatoceratinae** Buckman, 1926

Genus *Acuariceras* Spath, 1933

**Type-species.** *Baculites acuarius* Quenstedt, 1887

*Acuariceras acucostis* sp. nov.

([Fig. 2](#))

**Derivation of the name.** From the latin *acus* (needle, in relation to the general shell shape of the *Acuariceras*) and *costis* (rib).

**Holotype.** The specimen No. GR PC 1773 quoted by Courville et al. ([2000](#), p. 388), stored in the PC's collection (University of Rennes 1).

**Type locality.** The cross-section of Crotenay (Central Jura, France) studied by Courville et al. ([2000](#)).

**Type Level.** Unit 134 of the type locality (Courville et al., [2000](#), p. 387-388).

**Material.** Only one specimen is actually known (the Holotype). No other specimen was collected, despite several field-trips in the type locality between 1997 and 2013.

**Geographical/stratigraphic occurrence.** The species is currently only known in its type locality. Age: Early Oxfordian, more precisely the species is recorded from the Costicardia Subzone, Cordatum Zone.

**Diagnosis/Description.** Cross section subcircular. Ornamentation consisting by strong but not sharp main ribs, increasingly blunt approaching the siphonal area. Ribs layout very proverse, drawing an inflexion on the venter. Visible wide and deep constriction on the preserved fragment, following the same path as the main ribs. Post-constriction visible pair of highly attenuated secondary ribs in the inter-main rib interval, expressed on the top of the shell and on the venter.

This is a 20 mm long fragment (13 mm in whorl height) of a right shell turned into pyrite. No suture line is visible, so this specimen is here regarded as of a body chamber fragment.

**Generic assigning.** Without observation of the suture line, it is difficult to decide on the membership of the new species to the genus *Acuariceras* rather than *Paracuariceras*. Indeed, the both taxa have an identical ornamentation and are separated only by the sutural character alone, the former genus having a less cut suture than the later, particularly with the absence of the secondary umbilical lobe ( $U_2$ ). However, no study of the variability of this parameter is available (Dietl, 1978, p. 50), and it may therefore be possible that the two genera *Acuariceras* and *Paracuariceras* can be grouped one day. Should this be the case, the genus *Acuariceras* would have seniority.

**Remarks.** *Acuariceras acucostis* sp. nov. differs from *Acuariceras acuarius* (Quenstedt, 1887), *Paracuariceras incisum* Schindewolf, 1963 or *P. acuforme* Dietl, 1981, by its highly defined ornamentation with many unattenuated main ribs (predominant in the ornamental pattern). These species have a common blunt appearance and proverse path of the ribs, the

presence of stronger main ribs and secondary ribs highly attenuated, and the presence of constrictions. *A. acucostis* sp. nov. looks close to *P. giganteum* Dietl, 1981, but the ribs are stronger. These very typical characters, and the absence of siphonal attenuation of the ornamentation, depart clearly these forms from the genus *Parapatoceras*. All these heteromorph ammonites are older in age (Early Callovian, ‘Macrocephalus’ Zone).

Genus *Parapatoceras* Spath, 1924

Type-species: *Parapatoceras distans* Baugier & Sauzé, 1843

*Parapatoceras* cf. *tuberculatum* Baugier & Sauzé, 1843

(Fig. 3)

**Material.** The lone collected specimen (No. GR PC 1774, PC’s collection, University of Rennes 1) is a very small fragment (9 mm long for a whorl height of 6 mm), which indisputably belongs to an heteromorph ammonite.

**Geographical/stratigraphical occurrence.** Collected in 1996 during field prospection around Etrochey (NE Burgundy, France). Etrochey section, Unit 5, lev.41 (in Courville & Bonnot, 1998, p.318). Late Callovian: Collotiformis Subzone, Athleta Zone (=upper part of Spinosum Zone, subboreal chart – see Cariou & Hantzpergues, 1997).

**Description/remarks.** However, the specimen is quite worn. Ornamentation only visible on one flank as 5 single ribs, which does not impart a precise specific assignment to this specimen. It is not possible to say whether the ribs were tuberculate or not. The shape of the ribs departs this specimen from the genera *Acuariceras* / *Paracuariceras*, and it is left in open nomenclature in the vicinity of *P. tuberculatum*. The two main reasons for this choice are: (1) the slightly inclined path of the ribs reminiscent of the Baugier & Sauzé’s genus (well illustrated in Dietl, 1975, pl. 1, fig. 7); and (2) this species was previously known to be the

latest *Parapatoceras*, since its stratigraphic distribution spreads into the Anceps Zone (Middle Callovian). An extension of this distribution to the middle of the Athleta Zone therefore, seemed less shocking than the other older species of the genus.

### 3. Discussion/conclusions

The exceptional and new discovery of two heteromorph ammonites in Late Callovian and Early Oxfordian substages deposits, from which such ammonites were deemed absent, can extend our knowledge of the latest Parapatoceratinae and complete their stratigraphic distribution. Particularly, the evolution of the ornamentation between the group of *Acuariceras acuarius* / *Paracuariceras incisum* (including *P. giganteum* and *P. acustis* – see [Dietl, 1981](#)) and *A. acucostis* sp. nov., from which it may be derived, tends toward a net reinforcement at least on the body chamber. Of course, more material with the preservation of suture lines is needed in order to know the relationships between the new species *acucostis* sp. nov. and the genera *Acuariceras* and *Paracuariceras*. It is not excluded that these two genera, distinguished only based on a relatively discrete suture criterion, could be synonyms: Dietl also recognized that this criterion is variable within the uncoiled ammonites of the Dogger ([1978](#), pp. 54, 63).

If this discovery reduces significantly the interval without heteromorph ammonite known into the Jurassic (orange arrow at the bottom of the zone III in [Fig. 1](#)), these ammonites are rare and represent only a very marginal percentage of the ammonite fauna. Thus, this fact must not challenge the recognized nonexistence of a phylogenetic link between the Parapatoceratinae and the Protancyloceratina.

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### Caption of the figures

**Figure 1.** Range chart of the occurrences of heteromorphic ammonite groups in the Mesozoic. The three orange bands, zones I, II and III, shows the ranges without heteromorphs according to the literature data. The new specimens here described are in red. The orange arrow shows the reduced intervalle without heteromorph ammonites at the Dogger/Malm boundary.

**Figure 2.** Lateral and 3/4 view of *Acuariceras acucostis* sp. nov. (Holotype). Specimen No. GR PC 1773 (PC's collection, University of Rennes 1), from the Unit 134 of Crotenay (Central Jura, France): Costicardia Subzone, Cordatum Zone (Early Oxfordian). The scale bar is 1 cm.

**Figure 3.** Lateral view of *Parapatoceras* cf. *tuberculatum* Baugier & Sauzé, 1843. Specimen No. GR PC 1774 (PC's collection, University of Rennes 1), from the Unit 5, lev.41 of Etrochey (NE Burgundy, France): Collotiformis Subzone, Athleta Zone (Late Callovian). The scale bar is 1 cm.

Figure 1  
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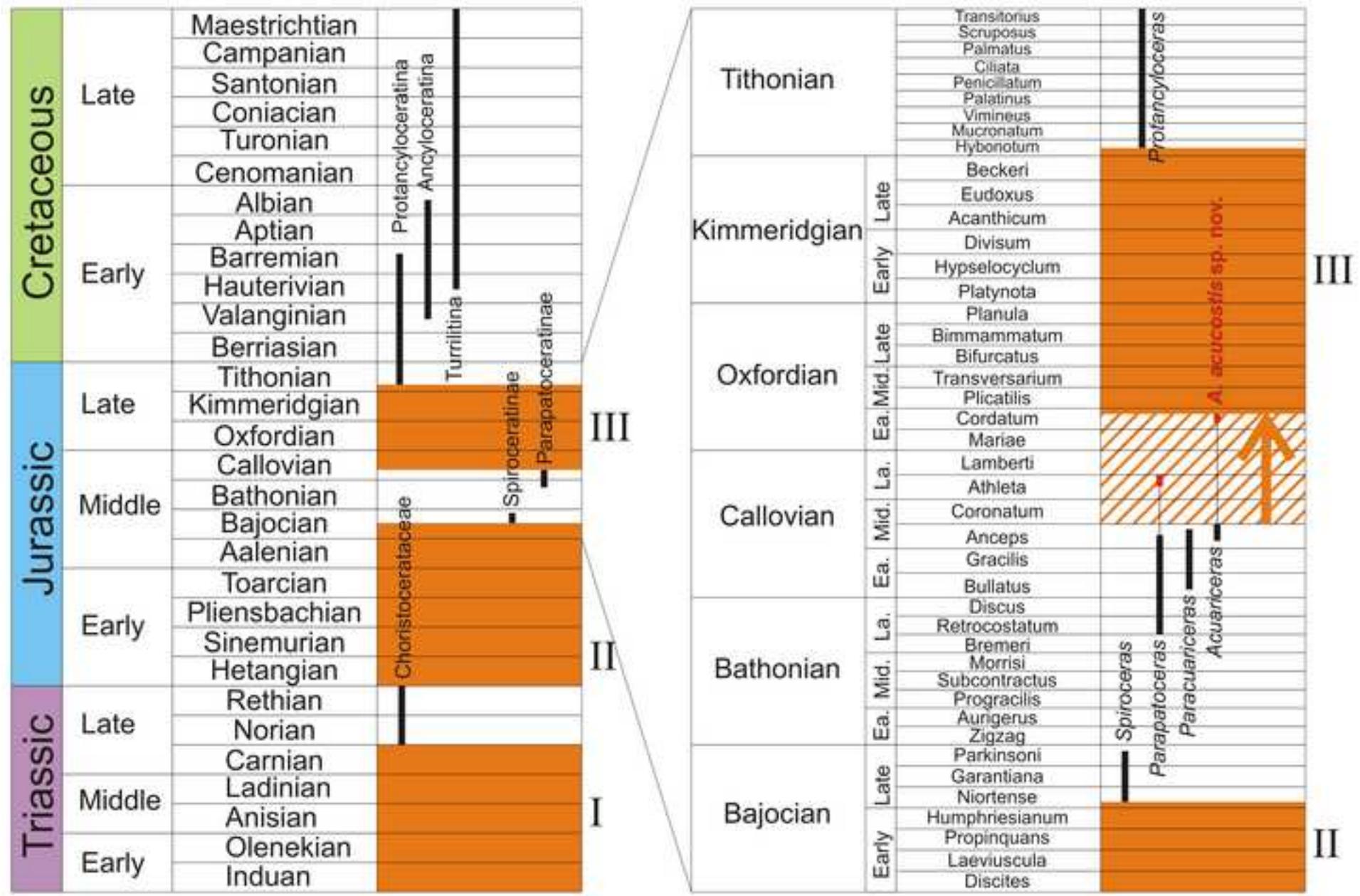


Figure 2  
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Figure 3  
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1 cm