“Papers in Press” includes peer-reviewed, accepted manuscripts of research articles, reviews, and short notes to be published in Paleontological Research. They have not yet been copy edited and/or formatted in the publication style of Paleontological Research. As soon as they are printed, they will be removed from this website. Please note they can be cited using the year of online publication and the DOI, as follows:

doi:10.2517/2019PR015

Paleobiogeographic distribution of the Early Cretaceous radiolarian

*Turbocapsula costata* and its correlation potential

XIN LI¹ and ATSUSHI MATSUOKA²

¹ State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of
Geology and Palaeontology and Center for Excellence in Life and Palaeoenvironment,
Chinese Academy of Sciences, Nanjing 210008, China (e-mail: lixivindida@163.com)

²Faculty of Science, Niigata University, Niigata 950-2181, Japan

Abstract. *Turbocapsula*, three (or four) segments with characteristic oval shape and a
hemi-closed segmental end, is a radiolarian genus with a high stratigraphic value due
to its phyletic evolution in the mid-Cretaceous period. An overview of lithology,
depositional setting, associated fossil records, and paleomagnetic data from each
locality of *Turbocapsula costata* (Wu) is summarized. All these data lead to the
conclusion that locations of known *T. costata*-bearing strata are restricted to the low-
to mid-latitude Mediterranean and eastern Tethys of the Tethyan realm. The results
emphasize that the phyletic evolution of the genus *Turbocapsula* is significant in the
correlations within the Tethys. The zonation established by the phyletic evolution of
the genus *Turbocapsula* cannot be utilized for Early Cretaceous zonal correlations
beyond the *T. costata* territory.
Key words: Atlantic, Mediterranean, Pacific, paleogeography, Tethys, Turbocapsula

Introduction

The genus Turbocapsula, the paleogeographic distribution of which is presented in this paper, was originally established by O'Dogherty (1994) by using specimens from the Northern Apennines (Italy) and the Betic Cordillera (Spain). The holotype (Figure 1.17) and paratype (Figure 1.18) of its type species, Turbocapsula costata (Wu), were obtained from the chert of the Congdu Formation, Xiagaze, southern Tibet. The range of this genus and the phyletic evolution at species level were well documented from the uppermost Barremian to Aptian pelagic sequence (section BB1) near Babazhadong, southern Tibet (Li et al., 2017). This comprehensive study concludes that Turbocapsula comprises with four species and two subspecies: Turbocapsula tetras Li and Matsuoka, T. fugitiva O'Dogherty, T. giennensis O'Dogherty, T. costata multicostata Li and Matsuoka, and T. costata costata (Wu) (Figure 1). As discussed later, these species and subspecies were reported in marine sediments in the Indian Ocean (Renz, 1974; Sanfilippo and Riedel, 1985), Australia (Ellis, 1993), Spain (Aguado et al., 1991, 1993, 2014; Riedel and Sanfilippo, 1974), Tunisia (Elkhazri et al., 2015), Italy (Li et al., 2019; O'Dogherty, 1994), Slovakia (Báč, 1999; Ozvoldová, 1990), Poland (Górka and Geroch, 1989), Montenegro (Goričan, 1994), Slovenia (Goričan and Šmuc, 2004; Rožič et al., 2014; Šmuc et al. 2010), southern Tibet (Matsuoka et al., 2002; Wu, 1986; Ziabrev et al., 2003, 2004; Li et al., 2017, 2019), Ladakh (Kojima et al., 2001; Zyabrev et al., 2008), and the southwestern Japan (Ishida
et al., 2008) (Figure 2). One *Turbocapsula* species was reported from the Middle Jurassic Akgöl Formation, northern Turkey as *Turbocapsula jurassica* Bragin and Tekin in Bragin et al. (2002), but later this was synonymized with the Jurassic *Unuma gordus* Hull by Suzuki and Gawlick (2003). Consequently, the phylogenetic and stratigraphic continuity indicates that *Turbocapsula* is a mid-Cretaceous genus so as to define the *Turbocapsula* Zone of O’Dogherty (1994). Based on the phyletic evolution of *Aurisaturnalis* and *Turbocapsula*, two radiolarian zones have been defined: the *Aurisaturnalis carinatus* Zone and the *Turbocapsula costata* Zone (Li et al., 2017) (Figure 3). The first appearance biohorizon (FAB) of *T. costata* was detected above the oceanic anoxic event (OAE) 1a interval, while the first representative of the genus *Turbocapsula* preceded the onset of the OAE 1a (Aguado et al., 2014).

Studies of Pessagno and Blome (1986), Pessagno et al., (1987, 1993), Baumgartner et al., (1992), Kiessling (1999), and Carter and Haggart (2006) indicated the existence of radiolarian biogeographic provinces in the Late Jurassic to Early Cretaceous. The Mesozoic radiolarian provinces are differentiated by latitude and include the Austral, Tethyan, and Boreal realms (Carter and Haggart, 2006; Kiessling, 1999; Pessagno and Blome, 1986; Pessagno and Hull, 2002). The bioprovinces are characterized by distinct changes in species abundance and the presence or absence of certain species.

This paper extends topic on the paleogeographic distribution of the genus *Turbocapsula*, because the occurrence of this genus seems to be geographically limited by preliminary examinations. This paper mainly focuses on occurrence
locations of *Turbocapsula costata* in publications in order to constrain the scope of application of the *Turbocapsula costata* Zone of Li *et al.* (2017) and the *Turbocapsula* Zone of O’Dogherty (1994) (Figure 3). Other *Turbocapsula* species like *T. tetras* and *T. fugitiva*, were in fear of overlooking in some previous literatures, because these species were first described as late as 2017 (Li *et al.*, 2017). These two species are referred, but are not discussed in detail here. The occurrence of *Turbocapsula* is reviewed with stratigraphic positions, depositional age, and radiolarian assemblages from publications. In reconstructing the paleo-location on a paleomap, the determination of original location is important. Paleomagnetic data for *T. costata*-bearing strata or associated volcanic rocks are provided where available. The relationship between the *T. costata* territory and the Mesozoic radiolarian provincialism is proposed. The adaptability of the zonation established by the bio-horizons of the genus *Turbocapsula* is discussed.

**Occurrence of *Turbocapsula costata* (Wu)**

Localities where *Turbocapsula costata* (Wu) has been reported are briefly summarized below (Figure 2). They are categorized into three regions: Mediterranean realm, the Indus–Yarlung–Tsangpo Suture Zone, and Rotti Indonesia. Information on lithology, depositional setting, associated fossil records, and paleomagnetic data, is also included where available. Locations of known Barremian–Aptian radiolarite deposits on an Early Cretaceous paleogeographic map are illustrated in Figure 4. The paleogeographic map is according to ODSN Plate
Tectonic Reconstruction Service (http://www.odsn.de). The map is made from the
datafiles used for Hay et al. (1999) and uses paleomagnetic reference frame for North

The Mediterranean realm

Betic Cordillera.—The Betic Cordillera (location 1 in Figure 2) of southern Spain
is divided into three major zones: a central part, the Middle Subbetic, and two
marginal areas (the Internal and the External Subbetic). Turbocapsula costata was
found from the Internal Subbetic Zone (Aguado et al., 1991; O'Dogherty, 1994; Riedel
and Sanfilippo, 1974) and the transition between the External Subbetic and the
Middle Subbetic zones (Aguado et al., 1993; Aguado et al., 2014).

Riedel and Sanfilippo (1974) illustrated Turbocapsula costata as “Theocorys
antiqua Squinabol” (p. 781, pl. 10, fig. 9 in Riedel and Sanfilippo, 1974) from east of
Velez Blanco, southeast Spain (location 1 in Figure 2). The depositional age is
assigned as late Barremian by calcareous nannofossils listed in Riedel and Sanfilippo
Brönnimann, N. elongatus Brönnimann, Watznaueria barnesae (Black), Rhagodiscus
asper (Stradner), Parhabdolithus embergeri (Noel), Micrantholithus hoschulzi
(Reinhardt), Lithraphidites carniolensis Deflandre, Braarudosphaera bigelowi (Gran
and Braarud), Biscutum supracretaceum (Reinhardt), Manivitella pemmatoides
(Deflandre), and Parhabdolithus splendidens (Deflandre).

Aguado et al. (1991) reported the occurrence of Turbocapsula costata as
“Cyrtophormis? costata Squinabol” (text-fig. 7.15 in Aguado et al., 1991) from the
Fardes Formation in the north of Velez Blanco (Internal Subbetic) (location 1 in Figure 2). The Fardes Formation is pelagic facies and in many places has intercalations of carbonate turbidite deposits, oolitic turbidites, and breccias. The illustrated specimen was obtained from the upper Aptian. The radiolarian assemblage is in low diversity and includes *Hexapyramis pantanellii* Squinabol and *Zifondium* sp.

Aguado *et al.* (1993) reported *Turbocapsula costata* as “*Tricolocapsa* sp.” (pl. 3, fig. 7 in Aguado *et al.*, 1993) from “Membro II” of the Carbonero Formation in the transition between the External Subbetic and the Middle Subbetic (location 1 in Figure 2). The “Membro II” is correlated with the lower member of the Fardes Formation. Co-existing species include: *Dibolachras tytthopora* Foreman, *Archaeodictyomitra lacrimula* (Foreman), *Pantanellium lanceola* (Parona), and *Williriedellum gilkeyi* Dumitrica. The radiolarian association is characteristically of Early Aptian.

Aguado *et al.* (2014) integrated the biostratigraphies of calcareous nannofossils, planktonic foraminifera, and radiolarians for the uppermost Barremian–lower Aptian succession in the La Frontera area which is located in the Subbetic Zone of the Betic Cordillera (location 1 in Figure 2). The stratigraphy is characterized by the pelagic rhythmite succession of the Carretero Formation (Barremian) and the dark marls, radiolaritic claystones, and green marls of the Carbonero Formation (lower Aptian). The first appearance biohorizon (FAB) of *Turbocapsula costata* (text-fig. 10.5 in Aguado *et al.*, 2014) was detected above the OAE 1a interval. As *T. costata* phyletically evolved from *T. fugitiva*, and *T. fugitiva* came from *T. tetras* according to
Li et al. (2017), the *Turbocapsula* lineage apparently crossed the onset of the OAE 1a.

**Northern Apennines.**—O’Dogherty (1994) carried out mid-Cretaceous radiolarian biostratigraphic analyses of the Pantano section in the Betic Cordillera in Spain (location 1 in Figure 2) and the Gorgo a Cerbara section, the Monte Casalini section in the Northern Apennines in Italy (location 2 in Figure 2). A new genus *Turbocapsula* was defined from the Carretero Formation and Fardes Formation in the External Subbetic and the Scisti a Fucoidi Formation in the Umbria-Marche in the Northern Apennines. The Carretero Formation consists of limestones and marls rhythmites. The Fardes Formation is characterized by predominant marly constituents. The Scisti a Fucoidi Formation consists of thinly interbedded red and green marlstone and calcareous mudstones, marly claystone, and marly limestone. Two species, *T. fugitiva* and *T. giennensis*, were described under the genus *Turbocapsula*.

A paleolatitude of 20–25°N has been inferred for the Aptian position of sections in the subbetic Basin (southern Spain) (Masse et al., 1993). The 125–150 Ma high-resolution Apparent Polar Wander Path for Adria from magnetostratigraphic sections in the Umbria–Marche (Northern Apennines, Italy) indicates a paleolatitude of 20–25°N in the Early Cretaceous (Satolli et al., 2007) (Figure 4).

**Budva Zone.**—Goričan (1994) reported Jurassic and Cretaceous radiolarite sedimentation in the Budva Zone in the Dinarides, Montenegro (location 3 in Figure 2). *Turbocapsula costata* (p. 93, pl. 10, figs. 3, 4 in Goričan, 1994) was recovered from the upper part of the Bijela Radiolarite, corresponding to the Aptian.
**Slovenian Basin.**—The Slovenian Basin is a Mesozoic deep-water paleogeographic unit located between the south-lying Dinaric Carbonate Platform and the north-lying Julian Carbonate Platform (Buser, 1996) (location 4 in Figure 2). Two samples from Cretaceous cherts and siliceous mudstones of the lower flyschoid formation contain *Turbocapsula costata* (pl. 4, figs. 7–10 in Rožič et al., 2014). Based on the co-occurrence with *Xitus clava* (Parona) and *Pantanellium* sp., one sample is restricted to the Costata Subzone of O’Dogherty (1994), indicating an age of late Aptian. Based on the occurrence of *Archeodictyomitra montisserei* (Squinabol), the other sample is correlated with the Romanus Subzone of O’Dogherty (1994), indicating an age of middle Albian. As Rožič et al. (2014) pointed out, *Turbocapsula costata* (Wu) extending above the Costata Subzone may correspond to the missing early Albian interval in O’Dogherty (1994). Specimens of Goričan and Šmuc (2004, pl. 2, fig. 3) and Šmuc (2010, text-fig. 19.14) were reported as *Turbocapsula costata* (Wu). However, these specimens should be *T. giennensis* O’Dogherty because of their discontinuous costae.

**Carpathian Klippen Belt.**—Ozvoldová (1990) showed two specimens of *Turbocapsula costata* as “Protunuma sp.” (p. 143, pl. 2, figs. 4, 5 in Ozvoldová, 1990) from the green to gray limestones in the 1498–1499 m depths in the drillhole Smolinske 17, in the Slovakian part of the Vienna Basin (location 5 in Figure 2). The composition of the pyritized radiolarians includes: *Acanthocircus amissus* (Squinabol), *Amphipyndax stocki* (Campbell and Clark), *Archeodictyomitra pugae* Schaaf, *Cryptamphorella dumiiricae* Schaaf, *C. macropora* Dumitrica, *Cyrtocapsa grutterinki*

*Turbocapsula costata* (p. 191, pl. 2, fig. 3 in Górka and Geroch, 1994) was reported from the Outer Carpathians, Poland. Although we could not give the precise location according to the limited information in their reports. It should be located in the Mediterranean realm.

**North Africa.**—Elkhazri et al. (2015) showed one specimen of *Turbocapsula costata* (text-fig. 12.31 in Elkhazri et al., 2015) from the northeastern Tunisia (location 6 in Figure 2). The co-occurrence of *Turbocapsula costata* and planktonic foraminifera with radially elongated chambers belonging to the “*Leupoldina*” genus indicates an age of Early Aptian. The studied section belongs to the south-Tethyan margin (Bodin et al., 2010).

**The Indus–Yarlung–Tsangpo Suture Zone**

The Indus–Yarlung–Tsangpo Suture Zone (IYTSZ), which is traced from Pakistan in the west to Tibet in the east, marks where the previously vast Tethys eventually closed with the India-Asia collision. Ophiolitic massifs and mélanges, which form an ophiolitic belt, are distributed along the IYTSZ (e.g Ding et al., 2005; Guilmette et al., 2009).

**Indus Suture Zone.**—The Nidar ophiolite is a large fragment of oceanic
lithosphere preserved along the western continuance of the suture, the Indus Suture Zone, in the Ladakh Himalaya, northern India (Kojima et al., 2001; Sachan, 2001). The occurrence of *Turbocapsula costata* (text-fig. 5.35, 5.36 in Zyabrev et al., 2008) was reported from the marine sedimentary sections of the Nidar ophiolite in the Indus Suture Zone (location 7 in Figure 2). Based on radiolarian biostratigraphic correlation, the marine sedimentary succession is upper Barremian to upper Aptian. Kojima et al. (2001) illustrated *T. costata* (pl. 5, fig. 11 in Kojima et al., 2001) as *Turbocapsula* sp. from the sedimentary-volcanic member of the Nidar ophiolite.

**Yarlung–Tsangpo Suture Zone.**—*Turbocapsula costata* was repeatedly reported from the ophiolite belt along the Yarlung–Tsangpo Suture Zone (YTZS), southern Tibet. The Xigaze ophiolite, which is the best known ophiolite in southern Tibet, stretches for ~150 km between Dazhuqu to the east and Sangsang to the west (location 8 in Figure 2). Wu (1986) mentioned the occurrence of *Turbocapsula costata* (p. 359, pl. 3, figs. 6, 16 in Wu, 1986) as *Tricapsula costata* Wu from the red chert just above the boundary between chert and pillow basalt in the Xigaze ophiolite. A specimen of *Turbocapsula costata* (p. 359, pl. 3, fig. 17 in Wu, 1986) was reported as *Tricapsula costata* Wu from the siliceous mudstone 30 m above the boundary between chert and pillow basalt. Ziabrev et al. (2003) reported *Turbocapsula costata* (text-fig. 5.50 in Ziabrev et al., 2003) from siliceous mudstone in mid-Cretaceous cover sediments on the Xigaze ophiolite. The siliceous mudstone yielded *Acaeniotyle diaphorogona* Foreman, *A. umbilicata* (Rüst), *Becus gemmatus* Wu, *Crolanium puga* (Schaaf), *Crucella euganea* (Squinabol), *Dictyomitra communis*
(Squinabol), *Pseudodictyomitra hornatissima* (Squinabol), *Pseudoeucyrtis hannii* (Tan Sin Hok), *Thanarla brouweri* (Tan Sin Hok), and *Xitus clava* (Parona).

The existence of a northward dipping equatorial intra-oceanic subduction zone and island arc system within the Neo-Tethys is supported by seismic tomographic images of subducted lithosphere below the Indian plate, where high-velocity mantle anomalies appear to exist at equatorial latitudes (e.g. anomaly III of Van der Voo et al. (1999), see also Van Hinsbergen et al. (2012)). The Xigaze ophiolite was viewed as a geological archive of near-equatorial subduction within the Neo-Tethys. New paleomagnetic data, after correction of the inclination shallow bias of the sedimentary rocks, yielded a robust paleolatitude of the Xigaze ophiolite at ∼16.5°N.

Available Early Cretaceous paleomagnetic results obtained from volcanic rocks provide paleolatitudes of 14.7±5.5°N and 18.6±2.1°N for the Lhasa terrane (Chen et al., 2012; Ma et al., 2014; Yang et al., 2015). These data indicate that the distribution of the cover sediment of the Xigaze ophiolite occurred in the Gangdese forearc, and formed the basement of the Xigaze forearc strata (Huang et al., 2015) (location 8 in Figure 4). Both the Nidar and Xigaze ophiolites contain similar arc volcanism and equivalent upper Barremian to upper Aptian sedimentary successions. The Nidar and Xigaze ophiolites were interpreted as distant chronological equivalents (Zyabrev et al., 2008).

Ziabrev et al. (2004) reported *Turbocapsula costata* (text-fig. 3.51 in Ziabrev et al., 2004) from a siliceous mudstone, which indicates the hemipelagic part of Jurassic—Early Cretaceous siliceous sequence in the Bainang terrane (location 9 in
Figure 2). Matsuoka et al. (2002) reported the occurrence of *T. costata* (text-fig. 7.12 in Matsuoka et al., 2002) from siliceous mudstone and mudstone samples in the Xialu-E section. The *Turbocapsula costata* Zone, which can be assigned to the Aptian, was introduced.

Radiolarites from the Bainang sections yield low paleomagnetic inclinations that would suggest a sub-equatorial paleolatitude, but the distribution of the paleomagnetic directions in these rocks strongly suggests a low inclination bias by compaction (Huang et al., 2015). The Xialu fauna of the *Pseudodictyomitra carpatica* Zone (KR 1) of Tithonian–early Valanginian age contains many taxa common to the Torinosu fauna that inhabited northern hemisphere middle-latitude (temperate) locations and is less similar to low-latitude (tropical) assemblages represented by the coeval Mariana fauna (Matsuoka et al., 2005). The middle-latitude (temperate) fauna from the Xialu chert suggests that Xialu radiolarians were deposited in middle latitudes of the Southern Hemisphere. Aptian *Turbocapsula*-bearing hemipelagic siliceous mudstone above the Xialu chert must be accumulated in locations north to the Tithonian–early Valanginian (KR 1) chert. The existence of terrigenous components in the siliceous mudstone indicates the sediments were accumulated close to a subduction zone (location 9 in Figure 4).

Li et al. (2017) reported specimens of *Turbocapsula costata* (text-figs. 4.14–4.30, 5.13–5.22 in Li et al., 2017) and discussed its phyletic relationship with other species of the genus *Turbocapsula* based on radiolarian biostratigraphic analyses on passive margin sediments off the Indian continent near Babazhadong
Paleomagnetic investigation was conducted on the Xiare and Weimei formations (Jurassic) and Chuangde formation (Cretaceous) in the Chuangde area of southern Tibet. The paleomagnetic results were interpreted to represent remanence of a normal polarity based on geological constraints and thus indicate that Tethyan Himalaya was located at 33.1±5.6°S in Late Cretaceous (80.1±6.2 Ma) (Zhang et al., 2017). The paleolatitude of Tethyan Himalaya is similar to the coeval paleolatitude of India (reference site: 28.0°N, 88.5°E), suggesting that Tethyan Himalaya and India were not separated by oceans, but likely formed a single crustal block in the Campanian. Section studied by Li et al. (2017), which is located 600 km west to the Chuangde area, belongs to the Tethyan Himalaya. Therefore, the T. costata-bearing strata near Babazhadong should be close to the north margin of the Indian continent during the Early Cretaceous.

**Rotti Island, Indonesia**

Rotti Island is situated east off Timor Island. Timor Island and adjacent small islands belong to the Outer Banda arc, part of Australian continental margin (Audley-Charles, 2011). From the chalks on the Indonesian island of Rotti (location 11 in Figure 2), a specimen of *Turbocapsula costata* (p. 623, fig. 14.6d in Sanfilippo and Riedel, 1985) was reported as *Theocorys antiqua* Squinabol.

**Regions without Turbocapsula costata (Wu)**

Although Barremian to Aptian radiolarian assemblages were discovered from the Pacific, the North Atlantic, and the northwestern Australia, no *Turbocapsula*
costata has been reported from these regions (Figures 2, 4).

The Pacific

Site 463 of Deep Sea Drilling Project (DSDP) Leg 62 was drilled at the Mid-Pacific Mountains (location 12 in Figure 2). Remarkable amounts of well-preserved radiolarians were recovered in the late Early Cretaceous sediments (Schaaf, 1981). Radiolarian faunas of the Dibolachras tythopora Zone, the Crolanium pythiae Zone, the Archicapsa similis Zone, the Acaeniotyle umbilicata Zone, and the Obesacapsula somphedia Zone range from the late Barremian to the Cenomanian. Turbocapsula fugitiva (Schaaf, 1981, p. 440, pl. 24, fig. 10a, b) was reported as Theocorys antiqua Squinabol. However, no T. costata has been reported. Four segmented closed nassellaria Theocorys renzae Schaaf (Schaaf, 1981, p. 440, pl. 27, fig. 1a, b) was reported from Lower Cretaceous strata. It differs from T. tetras in having pores aligned horizontally and diagonally instead of longitudinally. These specimens are not included in the genus Turbocapsula because of the lack of longitudinal costae.

The Jurassic and Cretaceous materials recovered from DSDP Leg 17 in the Pacific are commonly neither well preserved nor abundant. The Early Cretaceous radiolarians were found only from Site 167 on the Magellan Rise (location 13 in Figure 2). Material of Early Aptian was not found. Radiolarian association of Zone RK3, which ranges from Hauterivian to Early Albian, contains no Turbocapsula costata (Moore, 1973).

Age equivalent Early Cretaceous radiolarian assemblages have also been reported from Southwest Japan (location 14 in Figure 2). Acaeniotyle umbilicata
assemblage, *Holocryptocanium barbui* assemblage (Kumon *et al.*, 1986), and *Thanarla conica*–*Ultranapora* sp. assemblage (Matsuyama *et al.*, 1982) were reported from the Hidakagawa Group in the Shimanto Belt, Kii Peninsula. Early Cretaceous *Acaeniotyle umbilicata*–*Ultranapora praespinifera* assemblage and *Holocryptocanium barbui*–*H. geyserensis* assemblage were reported from the Shimanto Belt, Southwest Japan (Nakaseko and Nishimura, 1981; Nakaseko *et al.*, 1979). Okamura (1992) also reported Cretaceous radiolarians from the Shimanto belt in Shikoku, southwest Japan. No *Turbocapsula costata* has been reported from the Barremian–Aptian radiolarian assemblages in southwest Japan, which were deposited in the Proto-Pacific. Early Cretaceous radiolarian assemblage was found in mudstone samples from the Gumizaki Formation in the northwestern part of Kagoshima Prefecture, Japan (location 15 in Figure 2). *Turbocapsula fugitiva* (p. 533, fig. 2.32 in Ishida *et al.*, 2008) was reported together with *Dictyomitra communis* (Squinabol), *Thanarla conica* (Aliev) sensu Taketani (1982), *T. brouweri* (Tan Sin Hok), *T. lacrimula* (Foreman), *Pseudodictyomitra carpatica* (Lozyniak), *P. hornatissima* (Squinabol), *P. lodogaensis* Pessagno, *Crolanium puga* (Schaff), *Stichomitra simplex* (Smirnova and Aliev), *Pseudoeucyrtis hanni* (Tan Sin Hok), *Gangylothorax verbeeki* (Tan Sin Hok), *Hiscocapsa grutterinki* (Tan Sin Hok), and *Godia decora* (Li and Wu). The assemblage indicates the late Early to middle Aptian in age.

The East Sakhalin accretionary wedge is a part of the Cretaceous–Paleogene accretionary system, which developed in eastern Asia first as an island arc and then as a continental margin structure in response to subduction of the oceanic plates of
the Northwest Pacific (Parfenov, 1984). The accretionary wedge represents a scaly–thrust structure composed of intensely deformed volcanogenic–siliceous, terrigenous, and metamorphic rocks with ophiolitic massifs. The Berriasian–Valanginian, Barremian, and Aptian radiolarians were reported from the East Sakhalin Mountains (Kurilov and Vishnevskaya, 2011; Zyabrev, 2011) (location 16 in Figure 2). Specimens (pl. 3, fig. 10, pl. 4, figs. 2, 3 in Kurilov and Vishnevskaya, 2011) morphologically similar to *Turbocapsula costata* were reported as *T. costata* in the Aptian–Albian radiolarian assemblage from tuffaceous cherty rocks of the Khoe Formation, which are exposed in the Pravyi Nabil River basin. One specimen (pl. 6, fig. 10 in Kurilov and Vishnevskaya, 2011) morphologically similar to *Turbocapsula costata* was reported as *Turbocapsula aff. costata*. Similar specimen was reported as *T. costata* (pl. 3, fig. 34 in Zyabrev, 2011) from the Lower Aptian to Middle Albian hemipelagic siliceous mudstones in the Nabil zone of the East Sakhalin accretionary wedge. Similar specimen was reported as *Protunuma* sp. (pl. 6, fig. 19 in Tumanda, 1989) from one black chert from the Poronupuri Formation in the Nakanogawa Section, Hokkaido, Japan (location 17 in Figure 2). The sample yielded abundant radiolarian species belonging to the *Staurosphaera septemporata*–*Parvicingula usotanensis* assemblage Zone. However, according to the phyletic evolution of *Turbocapsula*, specimens with fewer than 5 obvious costae (*T. costata costata*) in lateral view bear an inflated spherical abdomen (Li *et al.*, 2017). *Turbocapsula aff. costata*, *T. costata*, and *Protunuma* sp. reported by Kurilov and Vishnevskaya (2011), Tumanda (1989), and Zyabrev (2011), which bear a slender abdomen and are
probably four segmented, are not *T. costata* with three segments.

Paleolatitudes of 18± 5°N and 28± 5°N are estimated for the Kiselevka-Manoma Terrane and West Sakhalin basin using the data sets of Abrajevitch *et al.* (2012) and Didenko *et al.* (2014), respectively. The Zhuravlevka-Amur Terrane, the Kiselevka-Manoma Terrane, and the East Sakhalin accretionary wedge were extended in east–west direction during Early Cretaceous, while their declinations were directed toward north. Based on the schematic reconstructions of these three terranes in the Late Jurassic to Early Cretaceous, the East Sakhalin accretionary wedge was located in low latitudes of the northern hemisphere (Ichihashi *et al.*, 2015).

**The North Atlantic**

Cretaceous radiolarians in the North Atlantic deep-sea sequences are not well documented. Radiolarian associations at ODP Sites 638 and 641 in the North Atlantic (Thurow, 1988) (location 18 in Figure 2), which are assigned to the *Crolanium pythiae* Zone, the *Stichocapsa euganea* Zone, and the *Acaeniotyle umbilicata* Zone, indicate an age range of Barremian to Aptian. However, no *Turbocapsula costata* has been reported from the Cretaceous sediments.

**Western Australia**

Mid- to high-latitude austral faunas were reported from the Windalia Radiolarite in the Carnarvon Basin of Western Australia (location 19 in Figure 2). The Windalia Radiolarite is late (latest) Aptian to Albian in age indicated by ammonites and belemnites. *Turbocapsula fugitiva* (p. 974, pl. 4, figs. 17, 22 in Ellis, 1993) is present in the austral faunas. However, no *Turbocapsula costata* (Wu) has been
Abundant and well-preserved Barremian to Albian radiolarian faunas were also reported from ODP Site 765, Leg 123 (location 20 in Figure 2) and DSDP Site 261, Leg 27 (location 21 in Figure 2), off northwestern Australia. Radiolarians from ODP Site 765 are characterized by the dominance of a small number of non-Tethyan forms and by the scarcity of Tethyan taxa. No species of *Turbocapsula* was reported from Site 765 (Baumgartner, 1992, 1993). *Turbocapsula tetras* (p. 623, fig. 14.6c in Sanfilippo and Riedel, 1985) and *T. fugitiva* (p. 798, pl. 6, figs. 4–7 and pl. 11, fig. 4 in Renz, 1974; p. 623, figs. 14.6a, b in Sanfilippo and Riedel, 1985) were present at Site 261. However, no *T. costata* (Wu) was reported off the northwestern Australia.

**Discussion**

The distribution of the *Turbocapsula costata* territory

*Turbocapsula costata* (Wu) has been discovered at many localities in the world (Figure 2). The localities are distributed in the present northern hemisphere except one scattered record from the southern hemisphere locality in the Indonesian island of Rotti. Possible depositional sites of *T. costata*-bearing rocks during the Early Cretaceous are shown in Figure 4. The occurrences of *T. costata* show a latitudinal spread of 30°N to 40°S. They are concentrated in low latitudes of the Mediterranean and the eastern Tethys. The occurrences of *T. costata* are also located in the middle latitude of the southern margin of the eastern Tethys (north of Indian and Australian continents). No *T. costata* has been reported from mid- to high-latitudes off
northwestern Australia. On the basis of the occurrences of *T. costata*, we propose the term, *Turbocapsula costata* territory, is proposed for the water mass where *T. costata* inhabited. The northern and southern limits of the *Turbocapsula costata* territory are drawn based on the land masses around the Mediterranean and eastern Tethys. However, the latitude, width, location, and depth of sills in the Tethys seaway vary in different paleogeographic reconstructions (Hay, 2009).

Study on living radiolarians shows a close relationship between some radiolarian taxa and worldwide water masses and circulation patterns (Boltovskoy *et al.*, 2010; Gordon, 1973; Ishitani *et al.*, 2008; Welling *et al.*, 1996). Early Cretaceous radiolarian assemblages can be recovered both in the Mediterranean and the eastern Tethys. The Mediterranean and the North Atlantic were connected through a strait. The strait was narrowed since the Aptian, and circulation in the North Atlantic has decreased, causing the North Atlantic to become a restricted basin (Thurow, 1988).

The paleobathymetry of the Atlantic and Tethys would make it likely that each basin might have its own source for deep water, its own nutrient supply, and its own recycling system. It is unlikely that there were many unobstructed passages from Tethys of dense water formation into the Pacific basin. The absence of *Turbocapsula costata* in the North Atlantic and Pacific may be explained by that this species inhabited a particular water mass within the Mediterranean and the Tethys. Radiolarian assemblage of the latest Barremian to the Aptian interval in the North Atlantic was only reported by Thurow (1988). Poor preservation and incomplete faunal description are also likely to explain the lack of *T. costata* in the North Atlantic.
More research is needed to testify whether *T. costata* is an endemic species restricted to the Tethys.

A great number of specimens of *Turbocapsula costata* were reported from the Betic Cordilella (southern Spain), the Umbria–Marche (Northern Apennines, Italy), the eastern Tethys (Ladakh Himalaya and southern Tibet), and Rotti Island. The presence of *T. costata* at the localities mentioned above indicates that this species has different tolerance on environmental parameters, including the latitudinal relative position and the water depth. The Betic Cordilella and the Umbria–Marche Basin were located in restricted marginal seas and at a water depth shallower than the calcium carbonate compensation depth (CCD). Radiolarites in the Bainang terrane were deposited in a hemipelagic setting and at a water depth deeper than the CCD. *Turbocapsula costata*-bearing siliceous sequence occupied the latitudes between 30°N to 40°S. Although meridional and ocean-continent temperature gradients during the Cretaceous were lower than today, there was clearly a meridional climatic zonation, reflected in the modern use of the terms “Boreal” and “Tethyan”, based on the biogeographic distribution of ammonites and other marine molluscus (Hay, 1995; Hay, 2008; Neumayr, 1883; Uhlig, 1911). However, their “Boreal realm” was in northern Europe, Greenland, and Alaska. On modern plate tectonic reconstructions the boundary between the Tethyan and Boreal realms plots at a latitude of about 40°N (Mutterlose *et al*., 2003; Voigt *et al*., 1999; Wagreich, 1992). The Mesozoic radiolarian provinces are differentiated by latitude and include the Austral, Tethyan, and Boreal realms (Carter and Haggart, 2006; Kiessling, 1999;
Pessagno and Blome, 1986; Pessagno and Hull, 2002). Temperature is presumably a latitudinal component (Petrushevskaya, 1971). The fact that no *T. costata* was reported from mid- to high-latitudes off northwestern Australia indicates that *T. costata* could not survive in a cold water environment.

The *Turbocapsula costata* territory and correlation of radiolarian zonation

*Turbocapsula costata* (Wu) occurred in low and middle latitudes of the Mediterranean and eastern Tethys. No *T. costata* has been reported from the Atlantic and the Pacific so far. Pessagno and Hull (2002) placed the boundary between the Tethyan and Boreal realms at 30°N and the boundary between the Tethyan and Austral realms at 30°S. *Turbocapsula costata* (Wu) is concentrated in the Mediterranean and eastern Tethys of the Tethyan realm. The results indicate that the zonation provides useful correlations within the Tethys because of the rapid and easily recognizable phyletic evolution of the genus *Turbocapsula*. O'Dogherty (1994) reported mid-Cretaceous radiolarian biostratigraphic results in the Betic Cordillera (southern Spain) and the Apennines (Italy). *Asseni* Zone and *Turbocapsula* Zone (*Verbeeki* Subzone and *Costata* Subzone) were defined for the Barremian to Aptian (Figure 3). The first appearance bio-horizon (FAB) of the genus *Turbocapsula* was used to define the base of the *Turbocapsula* Zone. The total range of this genus defines the *Turbocapsula* Zone. The FAB of *T. costata* was used to define the base of the *Costata* Subzone. The rare occurrence and small size of *Turbocapsula* specimens during the primitive stage make it difficult to recognize the base of his *Turbocapsula*
Zone. Matsuoka (1995), in a zonal scheme for the Middle Jurassic to Lower Cretaceous in Japan and the western Pacific, introduced the *Acanthocircus carinatus* Zone for the interval above the *Cecrops septemporatus* Zone. Dumitrica (1997) revised this zone as *Aurisaturnalnis carinatus* Zone and divided it into the *Aurisaturnalnis carinatus carinatus* Subzone and the *Aurisaturnalnis carinatus perforatus* Subzone. The base of the *Aurisaturnalnis carinatus* Zone is marked by the evolutionary first appearance bio-horizon (EFAB) of *Aurisaturnalnis carinatus carinatus* (Foreman). The *Aurisaturnalnis carinatus perforatus* Subzone was defined as the interval between the EFAB of *A. carinatus perforatus* Dumitrica and Dumitrica-Jud and the last appearance of this subspecies. Based on the phyletic evolution of *Aurisaturnalnis* and *Turbocapsula*, two radiolarian zones have been defined: the *Aurisaturnalnis carinatus* Zone and the *Turbocapsula costata* Zone (Li *et al*., 2017). The top of the *Aurisaturnalnis carinatus* Zone of (Dumitrica, 1997) was revised as the evolutionary first appearance bio-horizon (EFAB) of *Turbocapsula costata multicostata* (Li and Matsuoka). *Costata* Subzone of O'Dogherty (1994) is correlative to the *Turbocapsula costata* Zone of Li *et al*. (2017). The EFAB of *T. costata costata*, which marks the evolution of *T. costata*, is used for subdividing the *Turbocapsula costata* Zone into two subzones: the *Turbocapsula costata multicostata* Subzone and the *Turbocapsula costata costata* Subzone (Li *et al*., 2017). Radiolarian zonations established by O'Dogherty (1994) and Li *et al*. (2017) are important zonal scheme for the Barremian to Aptian interval (Figure 3). The EFAB of *T. costata costata* are key horizon for these zonations. However, both of these zonations established based on
the genus *Turbocapsula* cannot be utilized for Early Cretaceous zonal correlations beyond the *T. costata* territory. More detailed radiolarian biostratigraphic research is needed to establish an inter-regional correlation of zonal schemes.

**Conclusion**

The phyletic evolution of the genus *Turbocapsula* has a high stratigraphic value. Lithology, depositional setting, associated fossil records, and paleomagnetic data of *Turbocapsula costata*-bearing strata are overviewed. *Turbocapsula costata* (Wu) occurred in low and middle latitudes of the Mediterranean and eastern Tethys in Early Cretaceous time. No *T. costata* was reported from the Atlantic and the Pacific. This indicates *Turbocapsula costata* (Wu) is a paleobiogeographic indicator restricted to the Mediterranean and eastern Tethys of the Tethyan realm. The results emphasize that the phyletic evolution of the genus *Turbocapsula* is significant in the correlations within the Tethys. The zonation established by the phyletic evolution of the genus *Turbocapsula* cannot be utilized for Early Cretaceous zonal correlations beyond the *T. costata* territory.

**Acknowledgements**

We thank Dr. Toshiyuki Kurihara of Associate Editor, Dr. Yojiro Taketani, and Dr. Hisashi Suzuki for carefully and critically reviewing our paper. We thank Dr. Noritoshi Suzuki for helpful comments on our paper. This research was financially supported by the Strategic Priority Research Program of Chinese Academy of Sciences.
(XDB26000000); the Second Tibetan Plateau Scientific Expedition and Research (2019QZKK0706); the Chinese Academy of Sciences (CAS) Pioneer Hundred Talents Program; National Natural Science Foundation of China (grant number 41802013, 41572188 and 41772020); the Japan Society for the Promotion of Science KAKENHI (grant numbers 15K05329 and 15H02142); the Project of China Geological Survey (grant number 1212011086037 and 1212011121229); and the National Natural Science Foundation of China (grant number 41572188 and 41772020).

References


Górka, H. and Geroch, S., 1989: Radiolarians from a Lower Cretaceous section at...


Huang, W., Van Hinsbergen, D. J., Maffione, M., Orme, D. A., Dupont-Nivet, G.,


northern India. *News of Osaka Micropaleontologists (NOM), Special Volume*, no. 12, p. 257–270.


O'Dogherty, L., 1994: Biochronology and paleontology of mid-Cretaceous radiolarians from northern Apennines (Italy) and Betic Cordillera (Spain). *Mémoires de Géologie (Lausanne)*, no. 21, p. 1–415.


Renz, G. W., 1974: Radiolaria from Leg 27 of the Deep Sea Drilling Project. In,

Riedel, W. R. and Sanfilippo, A., 1974: Radiolaria from the Southern Indian Ocean,
DSDP Leg 26. In, Davies, T. A., Luyendyk, B. P. et al. eds., Initial Reports of the Deep
Washington, D. C.

Rožič, B., Goričan, Š., Švara, A. and Šmuc, A., 2014: The Middle Jurassic to Lower
Cretaceous succession of the Ponikve Klippe: the southernmost outcrops of the
Slovenian basin in western Slovenia. Rivista Italiana di Paleontologia e Stratigrafia,
vol. 120, no. 1, p. 83–102.

Sachan, H. K., 2001: Supra-subduction origin of the Nidar Ophiolitic sequence, Indus
Suture Zone, Ladakh, India: evidence from mineral chemistry of upper mantle


Satolli, S., Besse, J., Speranza, F. and Calamita, F., 2007: The 125–150 Ma
high-resolution Apparent Polar Wander Path for Adria from magnetostratigraphic
sections in Umbria–Marche (Northern Apennines, Italy): Timing and duration of
the global Jurassic–Cretaceous hairpin turn. Earth and Planetary Science Letters,


Thurow, J., 1988: Cretaceous radiolarians of the North Atlantic Ocean: ODP Leg 103 (Sites 638, 640 and 641) and DSDP Legs 93 (Site 603) and 47B (Site 398). In, Boillot, G., Winterer, E. L. et al. eds., Proceedings of the Ocean Drilling Program, Scientific Results, vol. 103, p. 379–418. College Station, TX (Ocean Drilling Program).


Wu, H. R., 1986: Some new genera and species of Cenomanian Radiolaria from


**Caption**

**Figure 1.** Scanning electron microscopic images and light microscopic images of the genus *Turbocapsula*. 1–3, *Turbocapsula tetrast* Li and Matsuoka; 1,= text-fig. 5.1b in Li *et al.*, 2017, holotype; 2,= text-fig. 5.3 in Li *et al.*, 2017, paratype; 3,= text-fig. 4.1a in Li *et al.*, 2017; 4–6, *Turbocapsula fugitiva* O'Dogherty; 4,= pl. 37, fig. 14 in O'Dogherty, 1994, holotype; 5,= pl. 37, fig. 12 in O'Dogherty, 1994; 6,= text-fig. 5.10 in Li *et al.*, 2017; 7–9, *Turbocapsula giennensis* O'Dogherty; 7,= pl. 37, fig. 23 in O'Dogherty, 1994, holotype; 8,= pl. 37, fig. 22 in O'Dogherty, 1994; 9,= pl. 37, fig. 21 in O'Dogherty, 1994; 10–18, *Turbocapsula costata* (Wu); 10–13, *Turbocapsula costata* (Wu) *multicostata* Li and Matsuoka; 10,= text-fig. 4.21 in Li *et al.*, 2017, holotype; 11,= text-fig. 4.18a in Li *et al.*, 2017, paratype; 12,= text-fig. 4.14b in Li *et al.*, 2017; 13,= pl. 37, fig. 27 in O'Dogherty, 1994; 14–18, *Turbocapsula costata* (Wu) *costata*; 14,= text-fig. 4.28a in Li *et al.*, 2017; 15,= text-fig. 4.29 in Li *et al.*, 2017; 16,= pl. 3, fig. 6 in Wu, 1986; 17,= pl. 3, fig. 16 in Wu, 1986, holotype; 18,= pl. 3, fig. 17 in Wu, 1986, paratype.

**Figure 2.** World map showing localities of the Barremian–Aptian radiolarian-bearing deposits. *Turbocapsula costata*-present localities are indicated by closed circles. *Turbocapsula costata*-absent localities are indicated by crosses (Genus *Turbocapsula*-absent localities) and open circles (Locations without *Turbocapsula costata* but with other species of *Turbocapsula*). 1, Betic Cordillera (Aguado *et al.*, 1991, 1993, 2014; O'Dogherty, 1994; Reidel and Sanfilippo, 1974); 2, Northern Apennines (O'Dogherty, 1994; Li *et al.*, 2019); 3, Budva Zone Montenegro (Goričan, 1994); 4, Slovenian Basin (Rožič *et al.*, 2014); 5, Vienna Basin (Ozvoldová, 1990); 6,
Northeastern Tunisia (Elkhazri et al., 2015); 7, Mid-Cretaceous cover sediments on the ophiolite in Ladakh (Kojima et al., 2001; Zyabrev et al., 2008); 8, Mid-Cretaceous cover sediments on the ophiolite in southern Tibet (Wu, 1986; Ziabrev et al., 2003); 9, Hemipelagic part of Jurassic–Early Cretaceous chert represented by the Xialu Chert and the Bainang terrane in southern Tibet (Matsuoka et al., 2002; Ziabrev et al., 2004); 10, Passive margin sediments off the Indian continent (Li et al., 2017, 2019); 11, Rotti Island (Sanfilippo and Riedel, 1985); 12, DSDP Site 463 at Mid-Pacific Mountains (Schaaf, 1981); 13, DSDP Site 167 at Magellan Rise (Moore, 1973); 14, Shimanto Belt, Southwest Japan (Kumon et al., 1986; Matsuyama et al., 1982; Nakaseko et al., 1979; Nakaseko and Nishimura, 1981; Okamura, 1992); 15, Kagoshima Prefecture, Japan (Ishida et al., 2008); 16, East Sakhalin (Kurilov and Vishnevskaya, 2011; Zyabrev, 2011); 17, Northern Hokkaido, Japan (Tumanda, 1989); 18, ODP Site 638 and 641 in the North Atlantic (Thurow, 1988); 19, Western Australia (Ellis, 1993); 20, ODP Site 765, Leg 123 off northwestern Australia (Baumgartner, 1992, 1993); 21, DSDP site 261, Leg 27 off northwestern Australia (Renz, 1974; Sanfilippo and Riedel, 1985).


Figure 4. Locations of known Barremian–Aptian radiolarite deposits on Early Cretaceous paleogeographic map (ODSN Plate Tectonic Reconstruction Service http://www.odsn.de/odsn/services/paleomap/paleomap.html). Arrows indicate
ocean currents modified from Hay (2009). Gray area indicates the *Turbocapsula costata* territory. *Turbocapsula costata*-present localities are indicated by closed circles. *Turbocapsula costata*-absent localities are indicated by crosses (Genus *Turbocapsula*-absent localities) and open circles (Locations without *Turbocapsula costata* but with other species of *Turbocapsula*). 1, Betic Cordillera (Aguado et al., 1991, 1993, 2014; O’Dogherty, 1994; Reidel and Sanfilippo, 1974); 2, Northern Apennines (O’Dogherty, 1994; Li et al., 2019); 3, Budva Zone Montenegro (Goričan, 1994); 4, Slovenian Basin (Rožič et al., 2014); 5, Vienna Basin (Ozvoldová, 1990); 6, Northeastern Tunisia (Elkhazri et al., 2015); 7, Mid-Cretaceous cover sediments on the ophiolite in Ladakh (Kojima et al., 2001; Zyabrev et al., 2008); 8, Mid-Cretaceous cover sediments on the ophiolite in southern Tibet (Wu, 1986; Ziabrev et al., 2003); 9, Hemipelagic part of Jurassic–Early Cretaceous chert represented by the Xialu Chert and the Bainang terrane in southern Tibet (Matsuoka et al., 2002; Ziabrev et al., 2004); 10, Passive margin sediments off the Indian continent (Li et al., 2017, 2019); 11, Rotti Island (Sanfilippo and Riedel, 1985); 12, DSDP Site 463 at Mid-Pacific Mountains (Schaaf, 1981); 13, DSDP Site 167 at Magellan Rise (Moore, 1973); 14, Shimanto Belt, Southwest Japan (Kumon et al., 1986; Matsuyama et al., 1982; Nakaseko et al., 1979; Nakaseko and Nishimura, 1981; Okamura, 1992); 15, Kagoshima Prefecture, Japan (Ishida et al., 2008); 16, East Sakhalin (Kurilov and Vishnevskaya, 2011; Zyabrev, 2011); 17, Northern Hokkaido, Japan (Tumanda, 1989); 18, ODP Site 638 and 641 in the North Atlantic (Thurow, 1988); 19, Western Australia (Ellis, 1993); 20, ODP Site 765, Leg 123 off northwestern Australia (Baumgartner,
1992, 1993); 21, DSDP site 261, Leg 27 off northwestern Australia (Renz, 1974; Sanfilippo and Riedel, 1985).
<table>
<thead>
<tr>
<th>Ma</th>
<th>Jud 1994</th>
<th>O’Dogherty 1994</th>
<th>Matsuoka, 1995</th>
<th>Matsuoka et al., 2002</th>
<th>Dumitrica et al., 1997</th>
<th>Li et al., 2017</th>
</tr>
</thead>
<tbody>
<tr>
<td>113</td>
<td>Aphan</td>
<td>Turbochitina</td>
<td>Turbocapsula</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Costata</td>
<td>costata</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>126</td>
<td>Asseni</td>
<td>G2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>131</td>
<td>Hett</td>
<td>G1</td>
<td>Asseni</td>
<td>Acanthocircus carinatus</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>134</td>
<td>Volgianian</td>
<td>F2</td>
<td>KR3</td>
<td>Acanthocircus carinatus</td>
<td>Aurisaturnais</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>corinatus perforatus</td>
<td></td>
</tr>
<tr>
<td>139</td>
<td>Berriasian</td>
<td>F1</td>
<td>KR2</td>
<td>Aurelia tenuis</td>
<td>Aurisaturnais</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>carinatus carinatus</td>
<td>corinatus perforatus</td>
<td></td>
</tr>
<tr>
<td>145</td>
<td></td>
<td>E1a</td>
<td>KR1</td>
<td>Pseudodictyonitria</td>
<td>Aurisaturnais</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>carpica</td>
<td>corinatus carinatus</td>
<td></td>
</tr>
</tbody>
</table>

**Keys**

- ▲ Last occurrence
- ◆ Evolutionary first appearance